



Mortality, behavior and the effects of predators on the intertidal distribution of littorinid gastropods

Rémy Rochette^{a,b,*}, Lawrence M. Dill^a

^a*Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada V5A 1S6*

^b*Bamfield Marine Station, Bamfield, BC, Canada V0R 1B0*

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Abstract

Predators can affect the vertical distribution of mobile intertidal invertebrates in two ways: they can (1) cause greater mortality of prey at certain intertidal levels, and (2) induce prey to seek safer intertidal areas. In this study, we investigate whether low-intertidal and subtidal predators affect the intertidal distribution of two congeneric species of small herbivorous gastropods of northeastern Pacific shores, *Littorina sitkana* Philippi 1846, and *L. scutulata* Gould 1849. In particular, we tested the hypothesis that predators affect the distribution of these snails by inducing them to seek higher and safer intertidal areas. On a wave-sheltered shore in Barkley Sound, British Columbia, *L. sitkana* and *L. scutulata* were both killed by predatory crabs (e.g., *Cancer productus*) more frequently when tethered near the lower limit of their intertidal distribution (≈ 1 m) than when tethered where they were most common (≈ 2.5 m), suggesting that high mortality rates are partly responsible for the lower-limit of these snails' intertidal distribution. However, two field mark-recapture experiments indicated that the snails' behavioral response to predation risk also influences their distribution. In the first experiment, snails from the 2.5-m level (low risk) transplanted to the 1.0-m level (high risk) displayed a strong and consistent tendency to move shoreward, especially *L. sitkana*, some traveling 10–15 m in 2–3 days to regain their original level. These shoreward movements were especially precise in the northern part of the study area, where predation rates on tethered snails were greatest. Furthermore, larger more vulnerable snails were more strongly oriented shoreward than smaller individuals, indicating that antipredator behavior might also contribute to intertidal size gradients in these species. In the second mark-recapture experiment, we manipulated predation risk using small cages and found that snails exposed to the odors of *C. productus* crabs foraging on conspecific and heterospecific snails displayed more precise (*L. sitkana* and *L. scutulata*) and longer (*L. sitkana*) shoreward movements than snails held in control conditions. These results provide the first experimental evidence that

*Corresponding author. Bamfield Marine Station, Bamfield, BC, Canada V0R 1B0. Tel.: +1-250-728-3301, ext. 251; fax: +1-250-728-3452.

E-mail address: rochette@bms.bc.ca (R. Rochette).

antipredator behavior may contribute to the intertidal distribution patterns of littorinids. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Predation is an important evolutionary and ecological factor, affecting the composition and structure of communities, the demographic characteristics of populations as well as the activity and life style of individual prey (Kerfoot and Sih, 1987; Lima and Dill, 1990). In marine coastal systems, predation is generally thought to increase towards lower-intertidal levels, where physical conditions are less variable and more moderate. This may be especially true in wave-sheltered habitats, where foraging by predatory seastars, gastropods, crabs, and octopuses can limit the lower distribution of sessile invertebrates such as mussels and barnacles (see reviews by Connell, 1972; Menge, 1978), as well as that of mobile herbivorous gastropods (Fawcett, 1984). In the case of mobile prey, however, a relationship between spatial variation in predation risk and prey distribution does not necessarily imply that low densities of prey are a direct result of high mortality rates. The intertidal distribution of mobile invertebrates can also be influenced by their behavior (Underwood, 1979), and such animals may be absent from high-risk areas because they avoid them (Garrity and Levings, 1981, Schmitt, 1982; Fawcett, 1984). Although predation has undoubtedly been a major evolutionary force shaping the lifestyle of intertidal invertebrates (e.g., Bertness et al., 1981), it is less well appreciated how the behavior of these animals is adjusted over ecological time scales to varying conditions of predation risk.

Littorinids are small herbivorous gastropods commonly found in intertidal habitats around the world (Reid, 1996). Whereas early studies of littorinid intertidal distribution patterns (e.g., Gowanloch and Hayes, 1926; Bock and Johnson, 1967; Chow, 1975; Gendron, 1977) mainly focused on physical factors (e.g., thermal stress, desiccation, osmotic stress, wave shock), more recent work has demonstrated the ecological significance of predation. In a recent study, Behrens Yamada and Boulding (1996) compared mortality rates of *Littorina sitkana* tethered at two different heights in the intertidal zone on four wave-protected beaches in the San Juan Islands, northeastern Pacific. At three of these sites, they observed that predator-induced mortality was much greater below, than above, the snails' natural distribution. The majority of snail mortality was apparently caused by low-intertidal and subtidal crabs, *Cancer productus*, which make shoreward excursions when the tide is high to forage on intertidal animals, including mussels, barnacles and snails (Robles et al., 1989). In an earlier study done in a similar wave-protected habitat in Barkley Sound, northeastern Pacific, McCormack (1982) found evidence that size-dependent predation was responsible for the increasing size of *L. sitkana* with increasing height in the intertidal zone. She suggested that most predation in her study was caused by pile perch, *Rhacochilus vacca*, and not by *C.*

productus, although this conclusion has been questioned (Boulding et al., 1999). Whoever the culprit, these studies suggest that predators influence the intertidal distribution of *L. sitkana* by causing size-dependent and habitat-specific mortality patterns. The possibility that antipredator behavior might also contribute to the intertidal distribution of *L. sitkana* has not been investigated, although some observations are suggestive (McCormack, 1982).

The same factors that affect the intertidal distribution of *L. sitkana* are also likely to affect its congener, *L. scutulata*, where they co-occur. The ecology of these snails is similar in many regards: they exploit similar microhabitats (e.g., tide pools, fronds of macroalgae, sediment and pebble substrates) between the mid-littoral and the littoral fringe of both wave-exposed and protected shores (Reid, 1996); they are both opportunistic omnivores, feeding on microalgae, diatom films and, to a lesser extent, on macroalgae and lichens (Voltolina and Sacchi, 1990; Reid, 1996); and they share common predators, such as crabs, fishes, asteroids and shorebirds. These species have different reproductive strategies, however. Whereas *L. sitkana* lays benthic egg masses in moist areas of the intertidal zone from which free-crawling juveniles emerge, *L. scutulata* releases free-floating capsules containing embryos which develop into pelagic larvae (Buckland-Nicks et al., 1973).

The main objective of our study was to examine the relationships between intertidal height, predation risk, and littorinid behavior on a beach where crabs, *C. productus*, are known to be abundant. In particular, we investigated the hypothesis that *L. sitkana* and *L. scutulata* avoid low-intertidal areas because of the inherent high risk of predation there, thus providing an additional explanation (aside from low survival) for their scarcity in such areas. To test this hypothesis, we first documented the intertidal distribution of *L. sitkana* and *L. scutulata* on a wave-protected shore in Barkley Sound, British Columbia (Canada). Second, we did a tethering experiment to compare predation risk near the lower and upper limits of the snails' distribution. Third, we compared movement patterns of high-intertidal individuals of both species transplanted in different regions of the intertidal zone to determine if snail behavior was related to spatial variation in predation risk (as estimated during the tethering experiment). In these latter two experiments, we used snails of two size classes to test whether more vulnerable snails display stronger antipredator behaviors. Finally, we used small enclosures to manipulate the apparent risk of predation in different low-intertidal areas, and examined whether snails exposed to high-risk conditions would display stronger antipredator behaviors than snails exposed to low-risk conditions. In this second mark-recapture experiment, we used small snails of both species from low and high-intertidal levels to investigate intraspecific variability in snail behavior.

2. Materials and methods

We did our study between July 1997 and November 1998 in wave-protected Bamfield Inlet, Barkley Sound (Canada), northeastern Pacific. The main study site extended from ≈ 0 to 3 m above 0 datum (Canadian Hydrographic Service), with ≈ 14 –18 m of intertidal land separating these extremities, and was 50 m long. The substrate varied 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 were present at different levels; the subtidal eelgrass *Zostera marina* extended up to the 0-m mark, the filamentous green algae *Enteromorpha intestinalis* was abundant between 0 and 1 m, and the brown algae *Fucus distichus* was common on boulders and bedrock between the 2- and 3-m intertidal marks.

2.1. Species identification

Littorina sitkana and *L. scutulata* are easily distinguished, the latter having a much higher spire than the former. However, both species often co-occur with closely resembling congeners. *L. sitkana* can be distinguished from *L. subrotundata* based on pigmentation of the head, foot, and tentacles, and *L. scutulata* can be distinguished from *L. plena* based on morphology of the male's penis and the female's egg capsule (Reid, 1996). Prior to our study, we examined 80 snails >6 mm shell length (40 per 'spire morph'), collected within patches of *Fucus* in our study site. All snails of the *scutulata/plena* morph were kept in petri dishes for 24–48 h, and we examined the egg capsules that were shed. A second sample of 80 snails, composed of 20 small (4–6 mm) and 20 large (>6 mm) individuals per morph, was similarly examined in April 1998. More than 90% of the snails examined were positively identified as *L. sitkana* or *L. scutulata*, and the identification of the remaining snails was inconclusive (no snail was positively identified as *L. subrotundata* or *L. plena*). Thus, the vast majority of the snails used in our study were either *L. sitkana* or *L. scutulata*.

2.2. Snail distribution and density

Between 14 and 28 July 1997, we determined the density and intertidal distribution of snails at our study site by sampling 70 quadrats (20 × 20 cm) between 0 and 3 m above 0 datum. At every 0.5-m increment in intertidal height, we sampled 10 quadrats each separated by 5 m. Data obtained from the Canadian Hydrographic Service indicated a +0.12 m tidal anomaly the day our study site was established. For simplicity, however, we present non-corrected (e.g., 2.5 m instead of 2.62 m) tidal amplitudes throughout the paper. All snails found within the quadrats were brought to the laboratory and measured (length and maximum width of the shell) to the nearest 0.01 mm using a dissecting microscope and graduated ocular. We also dissected 16 individuals of each species, spanning the range of sizes observed, to establish the relationship between shell length and dry (10 h at 100°C) body mass (*L. sitkana*: body mass = $0.014 \times \text{shell length}^{3.09}$, $r^2 = 0.96$, $F_{1,14} = 299.9$, $P < 0.0001$; *L. scutulata*: body mass = $0.016 \times \text{shell length}^{2.68}$, $r^2 = 0.92$, $F_{1,14} = 169.0$, $P < 0.0001$). To investigate temporal variability in snail distribution and abundance, we repeated the quadrat sampling between 6 and 11 April 1998, but only near the lower limit of the snails' distribution (i.e., 1 m) and where they were most common (i.e., 2.5 m).

We used Mann–Whitney *U*-tests to compare the density of conspecific snails at the 1- and 2.5-m levels, and Wilcoxon matched-pairs signed-ranks tests to compare the density of the two species at each level. We used non-parametric tests for these analyses because

of normality and/or homoscedasticity assumption violations, which could not be remedied through data transformation.

2.3. Tethering experiment

The main objective of the tethering experiment was to determine if predation risk faced by snails at our study site was greater in the low than in the high intertidal. To investigate this hypothesis, we compared, between 22 February and 15 April 1998, mortality rates of snails tethered at the 1.0-m level, near the lower end of their distribution, and at the 2.5-m level, where both species were most abundant. The 1.0- and 2.5-m levels will henceforth be referred to as the low- and high-intertidal levels, respectively. For each species, we tethered snails of two non-overlapping size categories: 1–2 mg in dry body mass (shell length, 4.0–5.0 mm for *L. sitkana* and 4.7–6.1 mm for *L. scutulata*) and 4–7 mg (shell length, 6.2–7.5 mm for *L. sitkana* and 7.8–9.6 mm for *L. scutulata*), henceforth referred to as small and large snails, respectively. We used *L. sitkana* and *L. scutulata* snails of similar body mass, rather than shell length, so that interspecific differences in mortality would not be caused by differences in gross benefits snails represent for predators; a *L. sitkana* of 8 mm shell length at our study site has a dry body mass of ≈ 8.6 mg, while a similar-size *L. scutulata* weighs only ≈ 4.3 mg.

Tethering procedures can inflate mortality rates (e.g., Zimmer-Faust et al., 1994), particularly in prey that normally rely on outrunning or outmaneuvering their predator (e.g., Barbeau and Scheibling, 1994). However, such experiments can still be used to compare mortality rates among groups of animals or in different habitats, as long as the tether bias is constant, or additive, among groups to be compared. In a review of marine ecological studies, Peterson and Black (1994) found that the assumption of additive tether biases, inherent to such experiments, was rarely made explicit and had never been tested. Since this review was published, at least two studies have tested this assumption (Aronson and Heck, 1995; Pile et al., 1996). One method to investigate the additivity of a (putative) tether bias is to vary the ‘intensity’ of the tethering procedure, and compare mortality rates of ‘strongly’ and ‘weakly’ constrained animals across treatments (Peterson and Black, 1994). Thus, to evaluate the additivity of tether biases during our experiment, we attached snails using both short (≈ 3 cm) and long (≈ 30 cm) tethers. If our tethering procedure introduced a non-additive bias on snail mortality rates, then we expected to find a statistical interaction between tether length and one or more of the other independent variables (i.e., intertidal height, snail species, snail size).

For each replicate, we collected snails within ≈ 10 – 100 m of the study site, and formed groups of 40 small and 40 large snails per species such that body mass was similar between species (*t*-tests, $P > 0.60$ for all comparisons). We then thoroughly air-dried the snails’ shells, attached a piece of 2.25-kg test monofilament (diameter = $130 \mu\text{m}$) to the apex of each shell using epoxy glue (half the snails in each group received a short tether and the other half received a long tether), and put the tethered snails in running seawater overnight. The following morning, we attached eight snails, one of each factor combination (2 species \times 2 sizes \times 2 tether lengths), on 5-m long transects made of 25-kg test monofilament (diameter = $730 \mu\text{m}$); we randomly determined the order of each snail on a given transect, and left a minimum of 60 cm

between snails so they could not interact with one another. For each trial, we placed a total of 20 such transects parallel to the shoreline, 10 high and 10 low, and examined the fate of tethered snails after 3 days. We did five trials involving a total of 800 snails.

Another potential limitation of tethering experiments is the loss or mortality of tethered animals from causes other than predation. If such a bias is constant across treatments, then the experiment can still be used to compare relative mortality rates across habitats or groups of animals. This assumption can be tested experimentally by deploying tethered animals in a predator-proof cage (e.g., Barbeau et al., 1994; Arsenault and Himmelman, 1996). Simply removing missing animals from data sets (e.g., Behrens Yamada and Boulding, 1996; Boulding et al., 1999), while generating conservative mortality estimates, does not protect against the possibility that these biases are not constant across habitats (e.g., if snails are more likely to break from their tethers on wave exposed shores) or among animals (e.g., if smaller snails are more likely to lose their tethers). With this objective in mind, during each trial we tethered 20 snails (five per species and size class; short tethers) at the low-intertidal level under a plastic mesh (1.5 cm) cage that excluded large predators. Because all 100 control snails were recovered alive and still attached to their tethers at the end of the 3-day experimental periods, snails that were not recovered alive on the ‘experimental’ transects were considered to have been killed by predators. Missing snails were unlikely to have been washed away because our study site is extremely sheltered from wave action; only during winter months do strong winds generate small waves up Bamfield Inlet.

We analyzed mean mortality rates (number of snails not recovered alive/number of snails tethered) using a randomized-block factorial ANOVA, in which the five temporal replicates were treated as levels of a random-effect variable, or blocks, and tether length, intertidal height, snail species, and snail size were the fixed-effect factors. All analyses were done with the statistical software JMP® version 3.0.2 (SAS Institute), using a significance level of 0.05 for the main effects and 0.10 for higher-order effects (i.e., interaction terms). We used a less conservative significance level for the interpretation of interaction terms, mainly to reduce the probability of wrongly concluding that tether biases were similar across treatments (i.e., committing Type II errors). We interpreted significant interaction terms with simple main effect tests; we used the Dunn–Bonferroni procedure to adjust the significance level of these tests so that the family was considered the conceptual unit for error rate (Kirk, 1982). In this and all following parametric analyses, we used visual inspection of residual plots and Cochran’s test to determine whether normality and homoscedasticity assumptions were satisfactorily upheld.

Upon recovering the transects, it became apparent that mortality rates were not constant across the low-intertidal level. To investigate horizontal variability in snail mortality, we divided the data set into the five most northerly, and the five most southerly, transects within each intertidal level. We then dropped the non-significant tether length factor (i.e., short and long tethers were pooled), such that there were still 10 snails per category, and used a second randomized-block factorial ANOVA to investigate the effect of horizontal location on snail mortality rates.

2.4. Mark-recapture experiments

We did two mark-recapture experiments to determine whether (1) mortality patterns

of free-roaming snails are consistent with those of tethered snails, (2) snails move towards intertidal heights where they are less vulnerable, (3) snail movement patterns are influenced by local conditions of predation risk, and (4) there exists inter- and intra-specific variability in snail behavior.

2.4.1. Mark-recapture experiment 1

We investigated, between 8 May and 15 May 1998, the mortality and movement patterns of small and large high-intertidal snails that were released at both low (1.0 m) and high (2.5 m) levels on the shore. Within each intertidal level, we released snails in the most northerly and most southerly 15 m of the study area because of differences in predation rates there (see Section 3.2).

For each of four replicates, we collected snails from a high-intertidal *Fucus* patch in the middle of our study area (i.e., between the northern and southern extremities), and formed groups of 40 small and 40 large snails per species such that body mass was similar between species (*t*-tests, $P > 0.60$ for all comparisons). We then air dried the snails, placed them aperture down on double-sided carpet tape, and painted their shells with enamel spray paint to facilitate later recovery; painting snails apparently has little effect on susceptibility to natural predators (McCormack, 1982; Rochette, unpubl. data). The snails remained within their shell while being painted, and resumed normal crawling behavior when subsequently placed in water. No snail died during any of the laboratory manipulations. We used four different color codes (green, red, orange, yellow), one for each snail species/size group, and used a different match between color code and snail category for each replicate (i.e., all snail groups received each color once). After the paint had dried for 1 h, we placed 10 snails of each group in four plastic containers (10 × 10 × 9 cm with 1-mm mesh screens), one for each release site, and submerged the containers in running sea water for 3–4 h before the beginning of the experiment.

We released snails during evening low tides (19:00–21:00 h) within 5 cm of four release points (high south, high north, low south, low north), using different release points for each replicate. At the high-intertidal level, we released snails on bedrock colonized by *Fucus*, where the majority of snails were found. We further selected the 2.5-m level release sites such that the slope within a ≈ 50 -cm radius was relatively uniform and perpendicular to the shore, and we avoided areas where snails could find refuge in deep inaccessible crevices. We then used snorkeling to release snails at the 1.0-m level in alignment with the 2.5-m release sites (slope and substrate characteristics were somewhat more uniform at the 1.0-m level). To ensure that snails would not be washed away by waves or tidal currents, however weak these are at our study site, we waited for snails to resume an on-foot position and replaced those that did not do so within 3–4 min of release (only three snails were replaced during the experiment). To be consistent with earlier studies (Chapman, 1986), and to better keep in mind the various disturbances associated with our different treatments, we refer to snails moved to a foreign, but similar, patch of habitat (e.g., high-origin snails moved laterally in the high intertidal) as having been ‘translocated’, and we refer to snails moved to a different type of habitat (e.g., high-origin snails released in the low intertidal) as having been ‘transplanted’.

The following morning at low tide (06:00–09:00 h), we thoroughly searched for painted snails and shell fragments within a 3-m radius of each release point, and noted

their position (orientation and distance) relative to the release point using a protractor (90° = shoreward) and measuring tape. Snails were thus in the field for ≈ 12 h (preliminary trials in which snails were allowed to move during an entire daily tidal cycle had revealed unexpectedly high net movement rates (up to 7.5 m), and relatively low recovery rates). To avoid counting shell fragments from a single snail more than once, we recorded a predation event only when we recovered the broken apex of a shell. No empty, but otherwise intact, shells were recovered during this experiment. We calculated mortality rates by dividing the number of broken shell apices by the total number of individuals recovered (i.e., apices plus snails alive). We used the number of snails recovered as our denominator, instead of the number of snails released, because we had no means of assessing the probability that non-recovered snails were alive versus dead.

We used a randomized-block factorial ANOVA to analyze mortality rates of free-roaming snails, treating the four temporal replicates as blocks, and snail species, snail size and horizontal position (i.e., release site) as fixed-effect factors. Mortality estimates for the different replicates and treatment combinations at the high-intertidal level were almost always '0' (only three shell apices were recovered). In contrast, mortality rates at low-intertidal level were greater and much more variable, causing heteroscedasticity in the dataset that was not satisfyingly improved by transforming the data. Therefore, this analysis was only done on free-roaming snails released at the low-intertidal level.

All analyses of snail movement were based on the position of snails that were recovered alive and that had moved outside the 5-cm radius release circle. To determine if snails preferentially moved shoreward, we first used a heterogeneity χ^2 (Zar, 1984) to test whether the four replicates for a given experimental group yielded comparable results. When the four replicates were homogeneous, we pooled them and used a χ^2 -test to compare the total number of snails moving shoreward to that expected if snails had moved randomly (i.e., 50% shoreward and 50% seaward).

To investigate the factors influencing the precision and magnitude of shoreward movements, we computed two movement indices for each individual snail released at low-intertidal level. (Similar indices were not calculated for snails released at the high-intertidal level because they did not move shoreward.) First, we calculated the shoreward-orientation index, which reflected the orientation of snails relative to an imaginary line parallel to the shore. For this purpose, the position of each snail at the end of the experiment was expressed between -90° (directly seaward) and 90° (directly shoreward), irrespective of whether the snail moved to the left or the right, and the shoreward-orientation index was obtained by dividing this value by 90° . Thus, a snail that moved directly shoreward had an shoreward-orientation index of 1 ($90^\circ/90^\circ = 1$), one that moved parallel to the shore had an index of 0 ($0^\circ/90^\circ = 0$), and one that moved directly seaward had an index of -1 ($-90^\circ/90^\circ = -1$). We did not use the circular statistic u to quantify the degree to which animals moved close to the 90° shoreward angle because the distribution of this statistic is influenced by sample size, especially when animals are highly clustered around the predicted orientation (Batschelet, 1981), and we recovered a variable number of snails over the course of our experiments. Second, we calculated snail net-shoreward movement, which was taken as the vertical distance (i.e., perpendicular to the shore) separating a snail from its release point. Then,

for both measures, we computed mean values for snails of a given group and replicate (because these snails were not independent), and used a randomized-block factorial ANOVA to investigate how mean indices were affected by snail species, snail size, and predation risk (i.e., north versus south). The analysis of shoreward-orientation indices was done on the raw data, whereas net-shoreward movement was log-transformed to satisfy the assumption of homogeneous variances.

2.4.2. Mark-recapture experiment 2

To investigate the hypothesis that snails would respond to heightened conditions of predation risk by displaying stronger shoreward movement patterns, we did a second mark-recapture experiment, between 7 September and 9 November 1998. We did this experiment on a beach approximately 700 m north of the main study site, because it had more uniform substrate at the low-intertidal level. For this experiment, we collected small snails from both the high- and low-intertidal areas, and released them at the low-intertidal level only.

For each of four replicates, we formed similar-size groups (see above) of 20 small snails of each species and from both intertidal levels, air dried the snails, placed them aperture down on double-sided carpet tape, and painted their shells green or orange depending on their origin (low or high). The match between snail origin and color was alternated between replicates. We then placed 10 snails of each group (2 species \times 2 intertidal levels) in one of two plastic cages (30 \times 20 \times 10 cm with 1-mm mesh screen sides), that were to serve as control and predation treatment cages, and immediately placed the cages 20–30 m apart at the low-intertidal level. The snails were then left to acclimate for \approx 24 h, and experimental treatments were started at low tide the following evening.

For the treatments, snails in each cage were first placed in two small plastic vials (length, 6.5 cm; diameter, 4 cm) with 1-cm mesh screen on their sides, and the vials attached to the bottom of the cages. We then added 75 large snails of each species to both the control and predator cages, and two *C. productus* crabs (60–80 mm carapace width) to the predator cage. Thus, whereas snails in the control and experimental cages were all exposed to conspecific and heterospecific snails, individuals in the predator cage were also exposed to predation stimuli, including cues emitted by the crabs themselves and those resulting from their foraging on the snails (which did occur). The treatments were continued for \approx 24 h, and the experimental snails were released during an evening low tide (19:00–23:00 h) within a 5-cm circle \approx 25 cm shoreward from the cages. (All snails resumed an on-foot position within 3–4 min of release.) At the same time, the predator and control cages were replaced by two cages containing 150 new snails each (75 per species) and two new crabs (experimental cage only) so the snails would still potentially be exposed to control and predator cues while free to move. As in the previous experiment, we recovered the snails the following morning at low tide and noted their position relative to the release point (orientation and distance). Predator and control treatments were replicated on four different occasions, each time using new snails, different predators, different cages (randomly selected from a total of 10 cages), and different release sites. In an attempt to control for the effect of substrate

homogeneity on snail movement, the same four release sites were used for the control and predator cages over the course of the experiment.

We computed the shoreward-orientation index and net-shoreward movement (see above) of each individual snail that was recovered alive (all of which had moved outside the 5-cm radius release circle), calculated mean values for snails of a given group and replicate, and then used a randomized-block factorial ANOVA to investigate how mean indices were affected by snail species, snail origin, and predation risk.

3. Results

3.1. Snail distribution and density

The field surveys revealed similarities as well as differences in the intertidal distributions and size structures of *Littorina sitkana* and *L. scutulata*. Both species were absent below the 1.0-m level, reached a maximum density at the 2.5-m level, and then showed a sharp decline in abundance at the 3-m level (Fig. 1). The difference in density

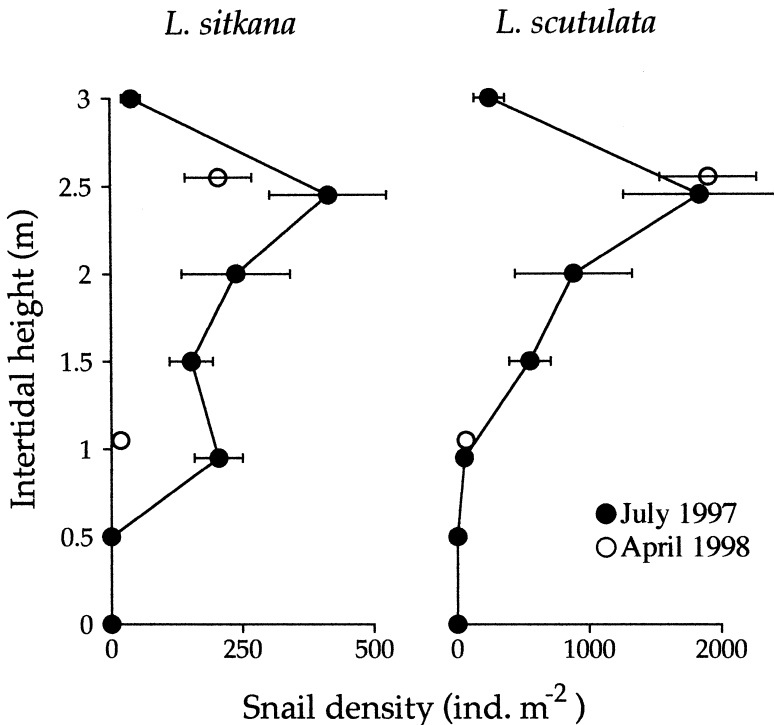


Fig. 1. Mean density (\pm S.E.) of *Littorina sitkana* and *L. scutulata* snails collected in July 1997 and April 1998 at different intertidal heights within the main study site.

between the 1- and 2.5-m levels was significant in July 1997 ($P = 0.001$) and April 1998 ($P = 0.0008$) for *L. scutulata*, but only in April 1998 ($P = 0.009$) for *L. sitkana*.

L. scutulata was more abundant than *L. sitkana* at our study site (Fig. 1). In July 1997, the density of *L. scutulata* was significantly greater than that of *L. sitkana* at the 1.5-, 2.5- and 3-m levels ($P < 0.05$ for all comparisons), and showed the same trend at the 2-m level ($P = 0.11$). However, *L. sitkana* was more abundant than *L. scutulata* at the 1.0-m level ($P = 0.004$). In April 1998, *L. scutulata* was still more abundant than *L. sitkana* at the 2.5-m level ($P = 0.004$), and both species were similarly uncommon at the 1-m level ($P = 0.4$).

3.2. Tethering experiment

Mean mortality rates during the tethering experiment varied between 2 and 40%. Most of this variability was related to a highly significant intertidal-height effect; snails tethered in the low intertidal suffered a three to 10-fold increase in mortality compared to snails tethered in the high intertidal (Fig. 2a and Table 1). A significant, although much smaller, portion of the total variability in snail mortality was explained by snail species and snail size; *L. sitkana* was preyed upon more frequently than *L. scutulata*, and large snails more frequently than small snails (Fig. 2a and Table 1). All interaction terms involving these three main effects were non-significant.

We found no evidence of non-additive effects of tether length on snail mortality rates (Fig. 2 and Table 1). More precisely, all statistical interaction terms involving tether length and one or more of the factors of interest (intertidal height, snail species and snail size) were non-significant ($P > 0.35$). This result suggests that the tethering procedure did not impact differentially the mortality rate of (1) *L. sitkana* versus *L. scutulata*, (2) small snails versus large snails, or (3) snails tethered in the low intertidal versus snails tethered high. The tether-length factor itself was also non-significant ($P = 0.27$), indicating that once snails were constrained to a given intertidal level, their probability of mortality was not affected by whether their movements were limited to ≈ 3 or ≈ 30 cm. The significant block effect indicates that snail mortality rates varied among trials.

In addition to this vertical variation in predation risk, many more snails were killed in the northern than the southern part of the study area (Fig. 2b and Table 2). However, there was a significant interaction between the horizontal (north versus south) and vertical (low versus high) components of predation risk, the horizontal factor having a significant effect on snail mortality at low ($P < 0.05$), but not at high ($P > 0.05$), intertidal level. This second analysis of the tethering data again indicated greater mortality rates for *L. sitkana* than for *L. scutulata*, and for large snails than for small snails. However, there was a significant interaction between snail size and horizontal position, as large snails were more vulnerable than small snails in the northern part of study area ($P < 0.05$), where predation rates were high, but not in the southern part of the study area ($P > 0.05$), where predation rates were low.

A third analysis of the tethering experiment with the data categorized according to all five factors (five snails per category) indicated no higher-order effects (all P values > 0.2) involving the tether-length factor. This result again indicates that if the tethering procedure inflated snail mortality rates during our experiment, the tether bias was more

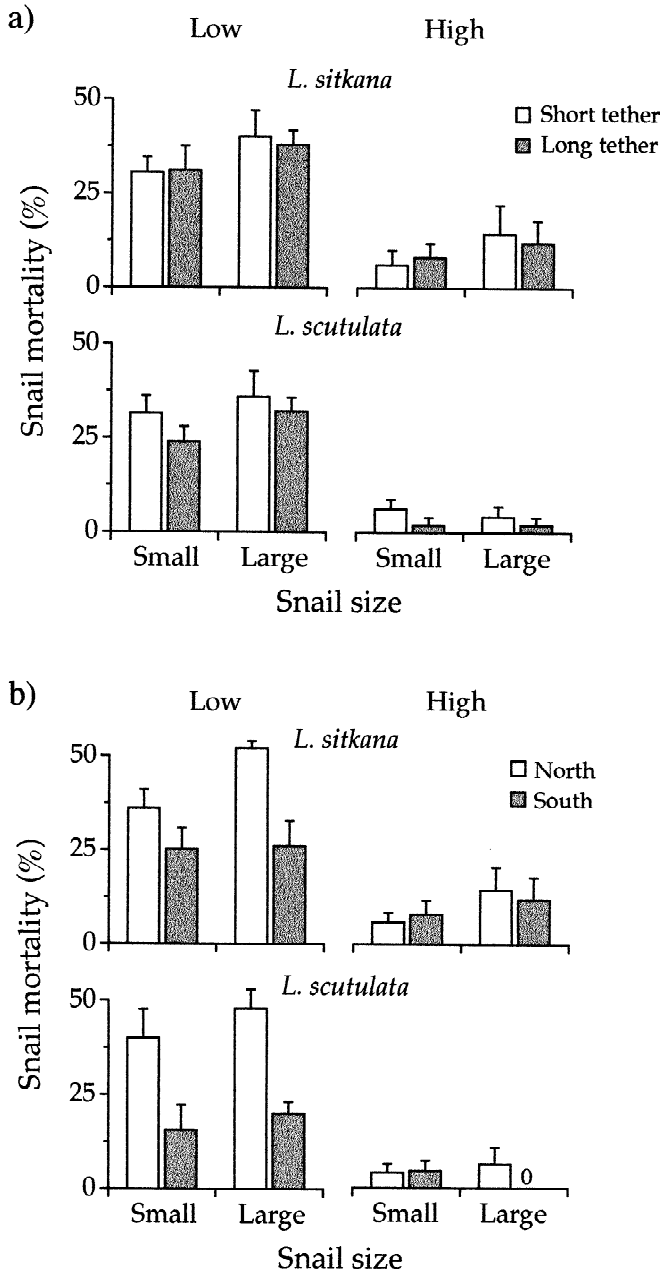


Fig. 2. Tethering experiment. (a) Mean (+ S.E.) percentage of small and large *Littorina sitkana* and *L. scutulata* snails that were killed by predators (see Section 2) after spending ≈ 3 days attached to transects placed at low- and high-intertidal levels. Snails were attached to the transects using short or long monofilament tethers. (b) Results of the same experiment with the data divided into the five most northerly, and five most southerly, transects at each intertidal level to investigate horizontal variability in predation risk (short and long tethers are pooled).

Table 1
Tethering experiment^a

Source of variation	MS ($\times 10^{-2}$)	Df	F	P
Blocks	3.971	4	4.130	0.0051
Snail size (Si)	4.860	1	5.054	0.0283
Snail species (Sp)	5.539	1	5.760	0.0195
Intertidal height (I)	135.358	1	140.763	< 0.0001
Tether length (T)	1.210	1	1.258	0.2665
Error	0.962	60		

^a Randomized block factorial ANOVA on snail percentage mortality. Small and large *Littorina sitkana* and *L. scutulata* were attached, using short or long tethers, to transects placed at low- and high-intertidal levels within the main study site, and their fate recorded after ≈ 3 days. All interaction terms were non-significant ($P > 0.10$) and are not shown.

Table 2
Tethering experiment^a

Source of variation	MS ($\times 10^{-2}$)	Df	F	P
Blocks	3.905	4	3.991	0.0062
Horizontal location (H)	28.501	1	29.125	< 0.0001
Snail size (Si)	4.876	1	4.983	0.0293
Snail species (Sp)	5.279	1	5.394	0.0236
Intertidal height (I)	134.551	1	137.498	< 0.0001
H \times Si	2.831	1	2.893	0.0941
H \times I	21.476	1	21.947	< 0.0001
Error	0.979	60		

^a Randomized block factorial ANOVA on snail percentage mortality testing for differences in predation risk according to horizontal position (north versus south) within the main study site (short and long tethers pooled). Non-significant ($P > 0.10$) interaction terms are not shown.

or less constant across treatments, including between high-risk (north) and low-risk (south) areas ($P = 0.55$).

The condition in which ‘presumptive’ dead snails were recovered suggested potential causes of mortality (Table 3). Slightly more than half the snails that were not recovered alive at the end of the experiment showed patterns of shell damage consistent with the

Table 3
Tethering experiment^a

Diagnostic features	<i>L. sitkana</i> (%)		<i>L. scutulata</i> (%)	
	Small ($n = 37$)	Large ($n = 52$)	Small ($n = 32$)	Large ($n = 37$)
Shell crushed outright	21.6	34.6	25	24.3
Shell ‘peeled’ by crab	10.8	36.5	12.5	37.8
Shell empty but undamaged	21.6	9.6	9.4	2.7 ^b
Snail missing from the tether	46	19.2	53.1	35.1

^a Diagnostic features of snails presumed to have been killed during the tethering experiment (numbers not recovered alive at the end of the experiment in parentheses).

^b The shell of this large *L. scutulata* snail was occupied by the hermit crab *Pagurus hirsutiusculus*.

action of shell crushing predators such as crabs and fishes. Many snails had apparently been crushed outright (26.4%), with only a broken shell apex or small shell fragments found still glued to the tether, while others had seemingly been ‘peeled’ (24.4%). Peeling occurs when a crab is too small to crush a gastropod’s shell, but can still access its prey by gradually chipping back at the shell aperture, leaving as evidence of its activity a shell with an intact columella and chiseled whorl (Zipser and Vermeij, 1978). The remaining presumptive victims of predation were either recovered as empty but otherwise intact shells (10.8%), or were missing from the tethers (38.4%). That these snails were also killed by predators is supported by the spatial relationship observed between the occurrence of missing snails and levels of predation risk. Thus, missing snails were more frequent at low than at high-intertidal level ($P < 0.0001$), and were more frequent in the northern than in the southern part of the study site ($P = 0.005$). Missing snails were probably pulled off their tether by crabs (or fishes), whereas empty snails were perhaps eaten by small seastars (e.g., we found one *Pycnopodia helianthoides* with its stomach protruded next to an empty shell of a small tethered *L. sitkana*) or hermit crabs which could have subsequently abandoned their ‘restraining’ new domicile (we found one *Pagurus hirsutiusculus* in the shell of a tethered *L. scutulata*).

3.3. Mark-recapture experiment 1

We recovered 91% of the snails we released during the first mark-recapture experiment; the lowest recovery rate for any snail group was 85%, and the highest was 100%. Of those snails we recovered, 93% were alive. Almost all broken shell apices (92%) were recovered at the low-intertidal level, so only mortality patterns at that level could be analyzed further (see Section 2). Within the low intertidal, mortality rates were (1) much greater in the northern than in the southern part of the study area, (2) greater for large than for small snails (although the size factor was not quite significant at the 0.05 level), and (3) similar for *L. sitkana* and *L. scutulata* (Table 4). These mortality patterns were consistent with those reported for the tethered snails, with the exception that the species factor was not significant during the mark-recapture experiment ($P = 0.60$). This difference between the two experiments is probably because only low-intertidal snails could be analyzed in the mark-recapture experiment; an analysis of the

Table 4
Mark-recapture experiment 1^a

Source of variation	MS ($\times 10^{-2}$)	Df	F	P
Blocks	1.062	3	0.700	0.5626
Snail size (Si)	6.139	1	4.046	0.0573
Snail species (Sp)	0.429	1	0.283	0.6004
Horizontal location (H)	24.375	1	16.063	0.0006
Error	1.518	21		

^a Randomized block factorial ANOVA on the percent mortality of small and large *Littorina sitkana* and *L. scutulata* snails that were released at the low-intertidal level within the northern and southern parts of the study site (horizontal-location factor). All interaction terms were non-significant ($P > 0.10$) and are not shown.

tethering experiment based solely on low-intertidal data also indicated no difference in mortality rate between *L. sitkana* and *L. scutulata* ($F_{1, 28} = 1.37$; $P = 0.25$).

Snails that were returned to the high-intertidal level generally moved at random relative to the shoreward–seaward axis. For seven of the eight groups of snails released in the high intertidal, the proportion of individuals moving shoreward varied between 44 and 64%, and either showed significant variation among replicates (two groups), or was constant among replicates but not different from 50% (five groups) (Table 5). In only one case did we find significant evidence of shoreward movement; 76% of large *L. sitkana* snails released at the northern end of the study area moved shoreward. In contrast, snails that were released at low-intertidal level showed a strong and consistent tendency to move shoreward, whether they were released in the northern or the southern part of the study area (Table 5). Thus, for both species and size classes of snails, replicate experiments always yielded very similar results ($P > 0.75$ in all cases), and the overall proportion (four replicates pooled) of individuals moving shoreward was always significantly greater than 50%, varying between 88 and 100% (Table 5).

Although snails that were released in the low intertidal all displayed a strong tendency to move shoreward, the indices of snail movement indicated that the intensity or precision of these movements was influenced by release site, snail size and snail species. Thus, the shoreward-orientation index indicated that snails released in the northern part of the study area moved more directly shoreward than individuals released in the southern part (Fig. 3a and Table 6). Furthermore, the shoreward-orientation index was greater for large snails than for small snails, and it tended to be greater for *L. sitkana* than for *L. scutulata*, although the species factor was not significant ($P = 0.09$). We found no higher-order treatment effects (i.e., significant interaction terms) on snail orientation.

The analysis of the magnitude of shoreward movements generally supported the previous results pertaining only to snail orientation. Thus, net-shoreward movement was greater for *L. sitkana* than for *L. scutulata*, and also greater for large snails than for small ones (Fig. 3b and Table 6). In contrast with the orientation data, however,

Table 5
Mark-recapture experiment 1^a

Snail size and species	Snails released low		Snails released high	
	South	North	South	North
Small <i>L. sitkana</i>	94.1 (34)**	92.9 (28)**	58.6 (29)‡	63.9 (36)†
Large <i>L. sitkana</i>	97.1 (35)**	100 (25)**	54.5 (33)‡	75.8 (33)*
Small <i>L. scutulata</i>	88.2 (34)**	96.7 (30)**	43.8 (32)‡	45.7 (35)†
Large <i>L. scutulata</i>	100 (33)**	95.8 (24)**	47.4 (38)‡	58.3 (36)‡

^a Percentage of high-intertidal snails that were recovered shoreward relative to their release point after being transplanted and translocated to low- and high-intertidal levels, respectively, in both the northern and southern parts of the study area. We used a χ^2 -test to compare the percentage of snails moving shoreward to the numbers expected if snails moved at random relative to the shoreward–seaward axis (the analysis was not done in two cases where the heterogeneity χ^2 -test indicated differences among replicates). Numbers in parenthesis indicate the number of snails recovered alive and outside the 5-cm radius release circle.

‡Non-significant; * $P < 0.05$; ** $P < 0.001$; †significant heterogeneity, χ^2 -test.

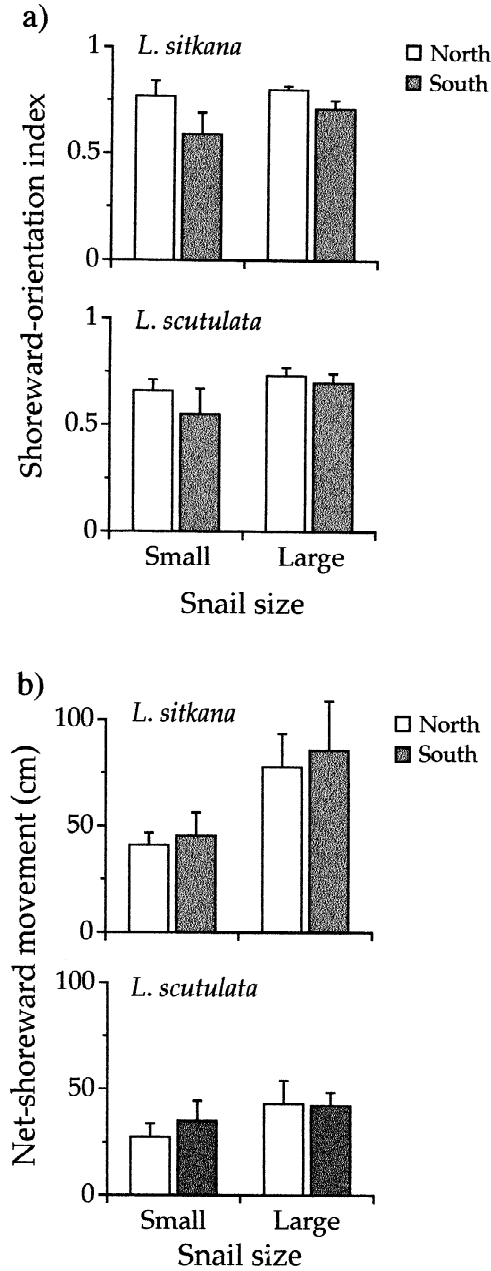


Fig. 3. Mark-recapture experiment 1. Mean (+ S.E.) shoreward-orientation index (a) and net-shoreward movement (b) of high-intertidal snails transplanted to the low-intertidal level. Small and large *Littorina sitkana* and *L. scutulata* were released both in the northern part of the study area, where the tethering experiment revealed high predation rates, and in the southern part of the study area, where predation risk was lower.

Table 6
Mark-recapture experiment 1^a

Source of variation	MS ($\times 10^{-2}$)	Df	F	P
Blocks	8.973/21.976	3/3	10.915/10.914	0.0002/0.0002
Horizontal location (H)	8.000/0.896	1/1	9.732/0.445	0.0052/0.5119
Snail species (Sp)	2.645/37.992	1/1	3.218/18.870	0.0873/0.0003
Snail size (Si)	7.031/36.194	1/1	8.554/17.977	0.0081/0.0004
Error	0.822/2.013	21/21		

^a Results of the randomized block factorial ANOVAs done on the shoreward-orientation index and net-shoreward movement (log-transformed) of high-intertidal snails transplanted in the low-intertidal level (shoreward-orientation index/net-shoreward movement). Small and large *Littorina sitkana* and *L. scutulata* snails were released both in the northern part of the study area, where the tethering experiment revealed high predation rates, and in the southern part of the study area, where predation risk was lower (horizontal-location factor). All interaction terms were non-significant ($P > 0.10$) and are not shown.

net-shoreward movement did not differ between snails released in the northern and the southern parts of the study area. All statistical interaction terms were non-significant. However, because this analysis was done on log-transformed data, interaction terms do not test for additive, but rather for multiplicative, differences between treatment effects. Examination of Fig. 3b suggests that the effect of snail size may have been more pronounced for *L. sitkana* than for *L. scutulata*, although simple main effect tests indicated that this factor significantly influenced the movement of both species ($P < 0.05$).

3.4. Mark-recapture experiment 2

We recovered 88% of the snails released during the second mark-recapture experiment, the lowest recovery rate for any group being 73% (small *L. scutulata* in control treatment) and the highest being 95%. Of those snails we recovered, only four were dead (1%), preventing any analysis of mortality patterns.

The movement pattern of snails was influenced by their origin, their species and the predator treatment (Fig. 4a,b and Table 7). Whereas the majority of high-origin snails were recovered shoreward from their release point (87% of *L. sitkana* and *L. scutulata*), similar to what was observed during the first mark-recapture experiment, less than half of the low-origin snails moved shoreward (42% of *L. sitkana* and 30% of *L. scutulata*). Accordingly, the shoreward-orientation index was significantly greater for high-origin, than for low-origin snails (Fig. 4a and Table 7). Irrespective of their origin, however, snails exposed to the predation cues showed an increased tendency to move shoreward compared to control snails (Fig. 4a and Table 7). All statistical interaction terms were non-significant.

The analysis of the magnitude of shoreward movements generally supported the previous results pertaining to snail orientation (Fig. 4b and Table 7). In particular, high-origin snails were recovered at a greater distance shoreward than low-origin snails. The predator treatment was not significant as a main effect, but it interacted with snail species ($P = 0.076$). Simple main effect tests indicated that *L. sitkana* moved for greater distances shoreward when exposed to predation cues than when held under control

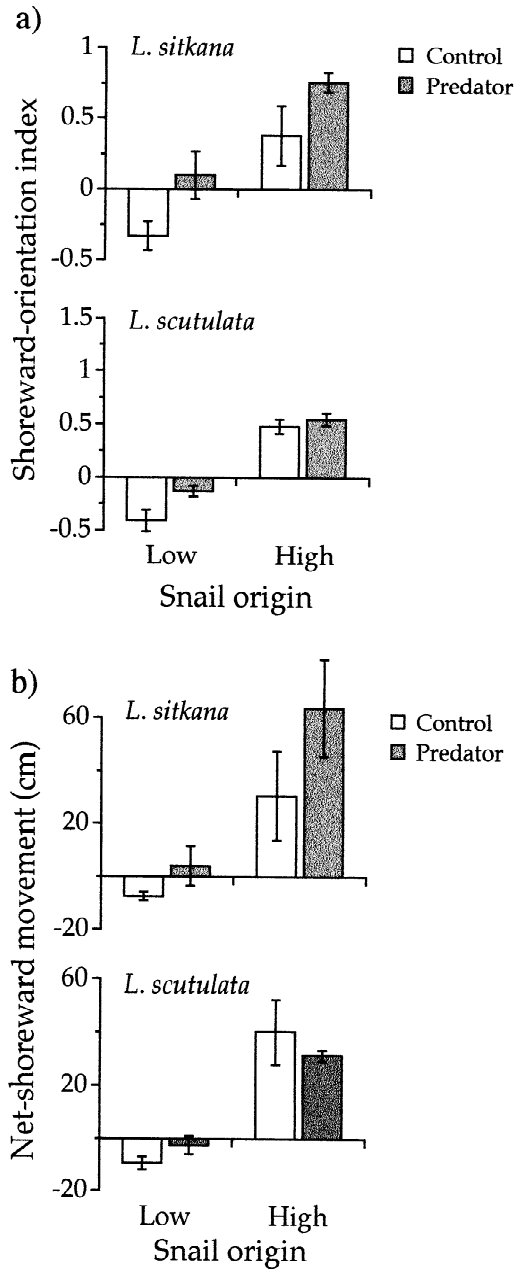


Fig. 4. Mark-recapture experiment 2. Mean (\pm S.E.) shoreward-orientation index (a) and net-shoreward movement (b) of snails. Small *Littorina sitkana* and *L. scutulata* from the high- and low-intertidal levels were released in the low intertidal after being exposed to predation cues or control conditions (see Section 2) for \approx 24 h.

Table 7
Mark-recapture experiment 2^a

Source of variation	MS/MS ($\times 10^2$)	Df	F	P
Blocks	0.146/11.306	3/3	3.569/3.557	0.031/0.032
Snail species (Sp)	0.088/4.857	1/1	2.159/1.528	0.157/0.230
Snail origin (So)	4.366/164.868	1/1	106.859/51.867	< 0.0001/ < 0.0001
Predator treatment (P)	0.684/9.034	1/1	16.752/2.842	< 0.001/0.107
P \times Sp	–/11.057	–/1	–/3.479	NS/0.076
Error	0.041/3.179	21/21		

^a Results of the randomized block factorial ANOVAs done on the shoreward-orientation index and net-shoreward movement of snails (shoreward-orientation index/net-shoreward movement). Small *Littorina sitkana* and *L. scutulata* from the high- and low-intertidal levels were released at the low-intertidal level after being exposed to predation cues or control conditions (see Section 2) for ≈ 24 h. Non-significant ($P > 0.10$) interaction terms are not shown.

conditions ($P < 0.05$), but *L. scutulata* snails were recovered at similar distances from their release point whether tested in the predator or the control treatment ($P > 0.05$).

4. Discussion

Our field study strongly supports the hypothesis that *Littorina sitkana* and *L. scutulata* display shoreward movements in response to the risk of predation from low-intertidal and subtidal predators. In particular, our two mark-recapture experiments indicate that the precision and/or magnitude of such movements are adjusted to local conditions of predation risk. To our knowledge, these results provide the first experimental evidence that antipredator behavior may contribute to the intertidal distribution of littorinids. However, another ubiquitous snail of the western coast of north America, *Tegula funebris*, also responds to the risk of predation by seeking higher and safer intertidal areas (Fawcett, 1984), and salt-marsh snails, *Littorina irrorata*, migrate up cordgrass stems during tidal inundation to avoid predation by the crab *Callinectes sapidus* (Warren, 1985; Vaughn and Fisher, 1988). Similarly, several species of Pacific limpets respond to predatory gastropods and seastars by fleeing shoreward or clamping tightly to their home scars (Phillips, 1976; Iwasaki, 1993).

4.1. Spatial variation in predation risk

On wave-sheltered shores of the northeastern Pacific, *L. sitkana* and *L. scutulata* are uncommon at low-intertidal levels, despite the fact that food abundance and physical conditions contribute to growth conditions being better in such areas (e.g., McCormack, 1982; McQuaid, 1982, 1983; Behrens Yamada and Mansour, 1987). Recent studies indicate that predation by large crabs, and perhaps fishes, prevents *L. sitkana* from exploiting lower, and more-profitable, intertidal levels (McCormack, 1982; Behrens Yamada and Boulding, 1996). Our study supports this conclusion, and further demonstrates that *L. scutulata* is also more susceptible to predators at low-intertidal than at high-intertidal levels. In the northern part of our study area, where snail mortality was

highest during both the tethering experiment and the first mark-recapture experiment, there were numerous boulders below the 1-m level, which served as refuges to many *Cancer productus*, *Lophopanopeus bellus*, and *Hemigrapsus oregonensis*. These three species of crabs prey on snails, although *H. oregonensis* mainly feeds on algae and is somewhat ill-equipped to break the shell of adult snails (Behrens Yamada and Boulding, 1998, and references therein). *C. productus* and *L. bellus* both could have crushed, peeled and pulled snails off their tethers, but we believe the former was responsible for most mortality during our study (see also Behrens Yamada and Boulding, 1998). *C. productus* (up to ≈ 20 cm in carapace width) are known to migrate into higher intertidal areas when the tide is flooding (Robles et al., 1989), and are perhaps more likely than the much smaller *L. bellus* (maximum carapace width of ≈ 2 cm) to have traveled the > 5 m separating the shelters from the tethered snails. We often see *C. productus* crabs foraging at our study site when the tide is high, and twice saw a crab eating a tethered snail.

Intertidal habitats are diverse and variable, so it should not be expected that littorinids and other small herbivorous gastropods will always be at greater risk of predation at lower intertidal levels. For instance, seasonal foraging by shorebirds may occasionally cause predation risk to be greater at high, rather than low, intertidal levels (e.g., Gibb, 1956). Also, crabs may be able to establish residence in unusually high intertidal areas where large rocks and fresh-water seepage offer adequate protection against desiccation (Behrens Yamada and Boulding, 1996). Finally, studies that have shown high snail mortality in low-intertidal areas were all done on wave-protected shores (McCormack, 1982; Behrens Yamada and Boulding, 1996; this study), where crabs and fishes can forage when the tide covers the low intertidal. In areas that are exposed to the action of waves and surge, these same animals will be less capable of intertidal foraging (e.g., Menge, 1978; Boulding et al., 1999), and wave action may be what limits the lower distribution of snails (McCormack, 1982).

4.2. Littorinid shoreward movements: ultimate factors

In wave-sheltered areas of the northeastern Pacific, the lower distribution of littorinids correlates with levels of predation risk on different shores (Behrens Yamada and Boulding, 1996; Rochette, unpubl. data). Although this correlation is likely caused in part by varying mortality rates on different shores, our study indicates it may also result from the snails' behavioral response to predation risk.

L. sitkana and *L. scutulata* snails from the high intertidal (low predation risk) that were transplanted lower on the shore (high predation risk) displayed a strong and consistent tendency to move shoreward, some traveling 10–15 m in 2–3 days to regain their original level. Other studies have similarly found that littorinids tend to move back homeward when transplanted above or below their normal intertidal position (e.g., *L. littorea*: Gowanloch and Hayes, 1926; Gendron, 1977; *L. planaxis* and *L. scutulata*: Bock and Johnson, 1967; *L. sitkana*: McCormack, 1982), and predation risk might be responsible for some of these movements (e.g., McCormack, 1982).

The hypothesis that shoreward movements displayed by *L. sitkana* and *L. scutulata* were antipredator in nature is supported by the fact that snails moved more frequently

and directly shoreward in high-risk parts of the study area (mark-recapture experiment 1), and when exposed to the odors of predators feeding on conspecific and heterospecific snails (mark-recapture experiment 2). In the first mark-recapture experiment, better orientation did not translate into greater net-shoreward movement, probably in part because of substrate heterogeneity; snails released where predation risk was high (i.e., north) had to negotiate cobbles 2–10 times their size, whereas snails released where predation risk was low (i.e., south) were confronted with finer substrate and only a few small cobbles. In the second mark-recapture experiment, where an attempt was made to control for substrate heterogeneity, net-shoreward movement also increased with predation risk in *L. sitkana* (but not in *L. scutulata*).

Another result that supports the interpretation that shoreward movements were antipredator in nature is that larger, more vulnerable snails released at low levels during the first mark-recapture experiment displayed more precise shoreward movements than smaller less vulnerable individuals. Alternatively, one may argue that small snails are less likely to migrate shoreward because they have poorer locomotory capacities than large individuals, or since they are more susceptible to desiccation (aperture area per unit body mass decreases with size; e.g., McQuaid, 1982). However, even small snails showed an overwhelming tendency to move back shoreward (*L. sitkana*, 94%; *L. scutulata*, 92%), and all small and large snails used during the first mark-recapture experiment had been collected from the same high-intertidal areas (2.5 m). We therefore believe that a somewhat weaker response to predation risk by small snails accounts for their less-precise shoreward orientation compared to larger, more vulnerable individuals.

The greater vulnerability of larger snails may seem surprising, because decapods generally prefer small-size molluscan prey (Juanes, 1992). Several laboratory studies indicate that crabs selectively feed on small littorinids when simultaneously offered different-sized snails (Elner and Raffaelli, 1980; Behrens Yamada and Boulding, 1998), whereas others show the reverse pattern (Behrens Yamada et al., 1998). This discrepancy between studies is likely partly due to differences in the size and/or species of predators and prey used. Field studies, on the other hand, have consistently found larger littorinids to be at greater risk of predation than smaller individuals (McCormack, 1982; Behrens Yamada and Boulding, 1996; Boulding et al., 1999; this study).

4.3. Littorinid shoreward movements: proximate factors

At the proximate level, the tendency of *L. sitkana* and *L. scutulata* to move shoreward upon transplantation to low-intertidal areas could have been caused by differences in habitat characteristics between the collection and release sites, such as immersion time, slope, light, and the presence of other animals or plants (see Petraitis, 1982, and references therein). Furthermore, the movement of snails could have been influenced by trails left by other snails (e.g., Gendron, 1977; Chapman, 1986). However, our results indicate that predation cues also influenced snail behavior; snails moved more directly shoreward when transplanted to portions of the study site where predatory crabs were more abundant, and when exposed to crabs feeding on other snails. Whereas results of the first mark-recapture experiment could theoretically have been caused by differences in physical properties between the northern and southern portions of the study site, it

seems more likely that differences in snail behavior were caused by differences in the relative abundance or activity of predatory crabs in these areas. At any rate, the second mark-recapture experiment demonstrated unequivocally that snails respond to cues that are indicative of predation risk by displaying better oriented and longer shoreward movements. This experiment was not designed to determine the cues involved, however, and snails might have responded to predator odors and/or to chemicals leaching from injured snails. There are numerous examples of marine gastropods which chemically detect predators and/or injured conspecifics (see Ansell, 1969; Feder, 1972; Hadlock, 1980; Kats and Dill, 1998 and references therein). In a recent laboratory study, Behrens Yamada et al. (1998) concluded that odors of conspecific snails being killed and consumed by crabs elicited a strong response in *L. sitkana*, inducing snails to crawl to the top of the cages or to hide in crevices, but that snails did not respond to crab odors alone. However, some studies have reported that littorinids can chemically detect their predators (asteroids: Feder, 1963; decapods: Duval et al., 1994).

Several studies have warned against the potential effect of ‘disturbance’ (e.g., collecting, manipulating, and marking) on the movement patterns of snails (see Petraitis, 1982; Chapman, 1986, 1999). Because all our snails were removed from their habitat and marked in the laboratory, we cannot assess the extent to which this disturbance affected their behavior. However, disturbance is unlikely to have contributed to our study’s main conclusions, namely that snails respond to predation risk by displaying oriented movements towards higher and safer intertidal areas. First, high-intertidal snails that were translocated to the high intertidal (disturbed + moved laterally) almost always moved randomly, whereas high-intertidal snails released in the low intertidal (disturbed + moved laterally + transplanted) invariably moved shoreward. (Note that the random movements of snails translocated to the high intertidal did not result from a lack of opportunity to move further upward, as snails of both species did occur above the high-intertidal release points.) Therefore, transplantation to the lower-intertidal level, and not disturbance, is likely responsible for the directionality of snail movement. Similarly, snails exposed to ‘high predation risk’ conditions moved more directly shoreward than snails exposed to ‘low predation risk’ conditions, even though ‘experimental’ and ‘control’ snails had been subjected to the same disturbances.

4.4. Behavioral differences between low- and high-intertidal littorinids

Biotic (e.g., food, predators) and abiotic (e.g., heat stress and desiccation) conditions in coastal marine environments vary markedly with intertidal height, causing conspicuous zonation patterns of plants and animals. Despite this steep gradient in environmental conditions, littorinids often display relatively broad vertical distributions; at our study site, *L. sitkana* and *L. scutulata* were both found from the 1.0-m tidal mark to the supralittoral fringe (≈ 3.5 m). We do not know to what extent *L. sitkana* and *L. scutulata* move between low- and high-intertidal areas over their lifetime. In the North Atlantic, along the western coast of Spain, two ecotypes of the ovoviviparous snail *L. saxatilis* appear to have evolved in response to the varying selective pressures which occur at different heights in the intertidal zone. These low- and high-shore ecotypes show extensive variation in phenotype, including shell and radula morphology, growth rates,

physiological resistance to osmotic stress, and mating behavior, and much of this variation is under genetic control (Johannesson et al., 1993; Johannesson et al., 1995; Rolán-Alvarez et al., 1996; Johannesson et al., 1997). The maintenance of these differences appears due to microhabitat preferences, assortative mating and reduced viability of hybrids outside the contact zone (Johannesson et al., 1995; Rolán-Alvarez et al., 1997). We are currently doing long-term field experiments and surveys to evaluate the natural movement patterns (horizontal and vertical) of *L. sitkana* and *L. scutulata*, and the contribution of environmental and genetic factors to phenotypic differences between high- and low-intertidal snails.

4.5. Interspecific variation in snail vulnerability, distribution and behavior

The demographic and behavioral patterns of *L. sitkana* and *L. scutulata* showed many similarities, as emphasized throughout most of our discussion, but also a few interesting differences. For instance, the thinner-shelled *L. sitkana* was more frequently killed by shell-crushing predators than *L. scutulata* during our tethering experiment, more obviously so at the high (species factor, $P = 0.022$) than the low (species factor, $P = 0.30$) intertidal level (Fig. 2a,b; low mortality rates in the high intertidal might explain why the interaction between snail species and intertidal height was not significant). In a recent study, Boulding et al. (1999) similarly recorded greater mortality rates of *L. sitkana* compared to similar size (i.e., shell width) *L. scutulata* when they tethered snails above *Fucus* in the high intertidal. One potential explanation for this interaction between intertidal height and snail species is that the thicker-shelled *L. scutulata* may better resist attacks from small high-intertidal crabs (e.g., *H. oregonensis* and *H. nudus*) than *L. sitkana*, but may be preyed upon as easily as its congener by bigger crabs living in lower-intertidal areas (e.g., juvenile and adult *C. productus*). This hypothesis warrants further investigation, as it suggests that *L. scutulata* may incur a greater increase in survivorship than *L. sitkana* by exploiting higher-intertidal areas. Interestingly, the distribution of *L. scutulata* appeared more strongly skewed towards the high intertidal than that of *L. sitkana* (see Fig. 1). In particular, *L. scutulata* was less abundant than *L. sitkana* in the low intertidal (i.e., 1.0-m level), even though it was 3.5 times more abundant overall than its congener at our study site.

We also found behavioral differences between *L. sitkana* and *L. scutulata*. During the first mark-recapture experiment, high-origin *L. sitkana* released in the low intertidal moved greater distances shoreward than *L. scutulata*, both in the northern and in the southern parts of the study area. It is unlikely that these differences were simply the result of interspecific differences in locomotory capacities (e.g., foot size), because *L. scutulata* also tended to be less well oriented than *L. sitkana* ($P = 0.087$), and because large *L. scutulata* did not move any further than small heterospecific snails ($P = 0.94$). Furthermore, during the second mark-recapture experiment, high-origin *L. sitkana* moved more directly shoreward when previously exposed to foraging crabs than when held in control conditions, but high-origin *L. scutulata* were seemingly unaffected by the predator treatment.

At first, one might be tempted to attribute the stronger shoreward movements and antipredator responses of high-intertidal *L. sitkana* (versus *L. scutulata*) to its greater

vulnerability. However, that would be ignoring the fact that interspecific differences in snail mortality were only evident at the high-intertidal level (see above), and those results suggest that the adaptive value of crawling shoreward, in terms of reduced probability of mortality, would actually be greater for *L. scutulata* than for *L. sitkana*. An alternative hypothesis for this interspecific difference in behavior is that *L. sitkana* is better adapted to the high-risk conditions of our study site than *L. scutulata*. Whereas *L. sitkana* recruits are born in the same habitat where their progenitors lived, *L. scutulata* embryos and larvae spend more than 20 days (Buckland-Nicks et al., 1973) in the plankton and are thus likely to settle at great distances from the adults. Consequently, *L. scutulata* should experience higher levels of gene flow between populations than *L. sitkana*, and should therefore display less genetic differentiation over small geographic distances (e.g., Behrens Yamada, 1989). This pattern has been reported for several ecologically similar species of prosobranch gastropods in which early-life stages differ in dispersal potential (see references in De Wolf et al., 1998). Note, however, that greater genetic differentiation among populations will not necessarily translate into greater phenotypic variation, because species with higher dispersal potential (e.g., those possessing a pelagic larvae) may have evolved more labile phenotypes which can be adjusted to local conditions prevailing during the individual's development (e.g., Parsons, 1997, 1998). We are currently investigating the extent and mechanisms (i.e., genetic adaptation versus phenotypic plasticity) of phenotypic differentiation among populations of *L. sitkana* and *L. scutulata*.

5. Summary and future research

The role of antipredation-related behaviors in mediating the intertidal distribution of mobile invertebrates has received little attention. Our study provides empirical evidence suggesting that littorinids inhabiting wave-protected shores in the northeastern Pacific respond to predation risk by seeking higher and safer intertidal areas. Future work should address the relative contribution of (predator-induced) mortality and behavior to spatial and temporal variation in littorinid intertidal distribution patterns.

The demographic and behavioral characteristics of *L. sitkana* and *L. scutulata* showed many similarities, but also some intriguing differences. For example, although both species were more frequently killed in low-intertidal areas, the distribution of *L. sitkana* was less strongly skewed towards the high intertidal than that of *L. scutulata*. Also, although high-origin snails of both species displayed a strong tendency to move shoreward upon being transplanted to low-intertidal areas, *L. sitkana* moved at a greater rate, and responded more strongly to predation cues than *L. scutulata*. Because *L. sitkana* undergoes benthic development, and *L. scutulata* undergoes pelagic development, this system offers an opportunity to study the effects of life history and dispersal on geographic variation in demographic characteristics and phenotypic traits.

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