State-dependent habitat selection by an intertidal snail: the costs of selecting a physically stressful microhabitat

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Abstract

Animals often modify their behavior in response to changing environmental conditions. As physical conditions become more severe animals in stressful habitats pay higher costs and should expend additional resources to search for less stressful habitats. We tested whether conditions resulting in more severe thermal and desiccation stress increased selection of more protective microhabitats by the intertidal gastropod Littorina sitkana, Philippi. We found that complex microhabitats such as barnacles and macroalgae were better on warm days because they provided cooler temperatures than less complex microhabitats such as crevices and bare rock surfaces. On warm days on the shore, snails foraged for shorter periods before selecting a microhabitat and large snails chose more complex microhabitats such as barnacles and algae more often than on cool days. We then used artificial substrates made entirely of clay in a laboratory experiment to show that this microhabitat selection by the snails was based on a preference for high topographic complexity. In this experiment snails that selected microhabitats early in the observation period chose topographically complex microhabitats significantly more often than snails that selected microhabitats late; and this became even more marked at higher temperatures. These results demonstrated state-dependent microhabitat selection by L. sitkana. The short-term cost of selecting stressful microhabitats on the shore was increased dehydration during low tide. The long-term costs of remaining in less complex areas without barnacles were lower rates of growth and survivorship. We conclude that topographically complex microhabitats allow the persistence of L. sitkana in the high intertidal zone. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Desiccation; Growth rates; Littorina sitkana; Northeastern Pacific; Survivorship; Topographic complexity

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1. Introduction

Habitat selection has been shown to affect the growth, survival, and fecundity of many animal species (Cowie, 1985; Marchetti and Geller, 1987; Morris, 1992; Ray and Stoner, 1995; Dyer and Landis, 1996; Hunt, 1996). Animals can change their habitat selection behavior in response to changes in the biological environment. Examples of such state-dependent behaviors (Krebs and Kacelnik, 1991) include animals choosing to forage in lower energy but safer patches when predators are present rather than the high energy patches they would choose when predators were absent (Milinski and Heller, 1978; Werner et al., 1983; Dill, 1987; Jordan et al., 1996). Examples of changes in habitat selection with variations in the physical environment are less common and most documented cases involve long-term seasonal changes in the microhabitat selected (Williams and Morritt, 1995; Green, 1996; Hartman, 1996; Hunt, 1996) rather than short-term changes (Leviten and Kohn, 1980; Holbrook and Schmitt, 1984; Moran, 1985; Chapman and Underwood, 1994; Bevelhimer, 1996). Yet short-term changes in habitat selection with changes in environmental conditions (state-dependent habitat selection) may be essential in allowing persistence of an animal population in a particular habitat.

Habitat selection can be defined as selection of one habitat from a variety of potential habitats encountered (Rosenzweig, 1981; Krebs and Davies, 1991; Manly et al., 1993). Habitat selection can occur at a variety of spatial scales. We define habitat as the place where an animal lives that can often be characterized by dominant plant forms or physical features. One spatial scale below habitat, each microhabitat differs in environmental factors that influence the allocation of time and energy by an individual within particular portions of its habitat (Morris, 1987). An animal encounters several microhabitats during one activity cycle. Our investigation deals specifically with how microhabitat selection changes with increasing physical stress. We used an intertidal gastropod, *Littorina sitkana*, as our study animal because the small size and limited mobility of these snails makes it possible for a single observer to follow multiple individuals simultaneously.

Intertidal animals experience extreme physiological stress during the low tide period and those species inhabiting the upper intertidal zone are often more tolerant of thermal and desiccation stress than those found lower down (Connell, 1961; Wolcott, 1973; McMahon and Russell-Hunter, 1977; Newell, 1979; McMahon, 1992). However, temperatures can reach lethal limits for intertidal organisms during summer low tides (e.g., Newell, 1979; Garrity and Levings, 1984) and under desiccating conditions water loss can be even more serious than thermoregulation (Behrens, 1972; Wolcott, 1973). Even if physical conditions are non-lethal there might be a long-term cost to experiencing extreme metabolic stress from water loss. For this reason many intertidal species have behavioral adaptations including the selection of particular microhabitats that alleviate thermal and desiccation stresses (Garrity, 1984; Garrity and Levings, 1984; Cowie, 1985; Gallien, 1985; Marchetti and Geller, 1987; Britton, 1992; Williams and Morritt, 1995) and allow persistence in the intertidal zone. However, it has not been shown whether these behaviors increase on days when the physical stresses are more severe. We tested whether these snails showed stronger preferences for more protective microhabitats on days when thermal and desiccation stresses were higher.
Intertidal gastropods have limited foraging time because they may spend up to 50% of their activity cycles in refuges (Burrows and Hughes, 1991a). They can remain in these protective microhabitats when immersed during high tide to avoid the risk of dislodgment by waves (Leviten and Kohn, 1980; Behrens Yamada, 1992; Hughes, 1995) and/or when emersed during low tide to avoid predation pressure (Bertness et al., 1981; Garrity and Levings, 1984) and thermal stress (Garrity, 1984; Garrity and Levings, 1984; Moran, 1985; Fairweather, 1988). This means there is a trade-off between time spent foraging and time spent in microhabitat refuges (Burrows and Hughes, 1991b). In predator–prey systems such trade-offs often result in state-dependent behavior so that the prey spends more time foraging and less time hiding when the risk of predation is low (Krebs and Kacelnik, 1991). Similar trade-offs might result in gastropods foraging longer before seeking refuges during emersion on days when thermal and desiccation stress are less severe. This premise is supported by the fact that conid gastropods forage actively during night low tides but not during day low tides and occupy any convenient refuge after foraging (Leviten and Kohn, 1980). Our study investigates trade-offs in time spent foraging and selecting a less stressful microhabitat during emersion on days with low temperatures and desiccation stress compared to days with high temperatures and desiccation stress.

An additional cost of foraging longer might be that the snail has less time to search for a high quality microhabitat than if it had begun searching when its body temperature was lower and body water content higher. Some snails may begin their foraging excursions with a lower body water content than other snails and may have to choose a refuge earlier. Small snails might be particularly vulnerable to desiccation stress because they have greater aperture surface area to body volume ratios (Marchetti and Geller, 1987; Monteith and Unsworth, 1990) and may not be able to forage as long. Therefore, additional objectives of our study were to investigate differences between small and large *Littorina sitkana* in the amount of desiccation through evaporative water loss in different microhabitats, and to test whether this affected the amount of time they could forage before being forced to select a microhabitat.

Microhabitat selection by an individual can be altered by the presence of other individuals using the same resources. Competition within and among species forces the use of a wide variety of habitats besides the preferred ones and, as densities increase, the better quality habitats are chosen first (Fretwell and Lucas, 1970; Rosenzweig and Abramsky, 1985; Rosenzweig, 1991). Theories of habitat selection, such as the Ideal Free Distribution (Fretwell and Lucas, 1970), predict that fitness declines as density increases, hence higher quality microhabitats lose their advantage as more individuals settle there. Later arriving individuals often select lower quality microhabitats because they are less crowded; and, therefore, individuals there will have equal fitness with those in more crowded high quality habitats (Fretwell and Lucas, 1970). Intertidal snails are a good system in which to test the Ideal Free Distribution as their density is easily manipulated and the behavior of individuals is easily followed over time.

We investigated how complex microtopography may allow persistence of *Littorina sitkana* in the high intertidal zone. We used field and laboratory experiments to test six hypotheses about how microhabitat selection changes with increasing physical stress and to determine the short- and long-term consequences of choosing a more protective microhabitat. The hypotheses were: (1) more complex microhabitats such as barnacles
and algae would offer more protection from dehydration during emersion at low tide than less complex microhabitats such as crevices and bare rock; (2) snails would decrease their foraging time and increase their degree of habitat selectivity as their physical environment became more stressful; (3) small snails would increase their degree of selectivity with increasing physical stress more than large snails because of their greater surface area/volume ratio; (4) snails that selected microhabitats early during an observation period would acquire a greater proportion of less stressful microhabitats than snails that selected microhabitats late; (5) as snail density increased a lower proportion of snails would be found in the less stressful microhabitats as these become filled; and (6) snails in more complex field enclosures that contained barnacles would experience higher growth and survivorship than snails in less complex field enclosures that contained bare rock. Hypothesis 1 was tested using a short-term field experiment. Hypotheses 2 and 3 were tested in the field on natural substrates and in the laboratory on artificial substrates made entirely of clay. The laboratory habitat selection experiment with artificial substrates was important as it allowed us to separate the effect of the material the microhabitats were composed of from the effect of topographic complexity. This experiment also allowed us to test hypotheses 4 and 5. Hypothesis 6 was tested with a long-term field experiment.

2. Materials and methods

2.1. Study animal

*Littorina sitkana* is an herbivorous gastropod commonly found in sun and wave sheltered locations in the high intertidal zone, and is present from Alaska to southern Oregon (Behrens Yamada, 1992). In comparison to *Littorina scutulata sensu late* of the northeastern Pacific, *L. sitkana* tends to be the first littorinid species to seek out shelter when desiccation stress increases or storms occur, but also tends to be the first species to come out of shelters and forage when conditions are favorable (McCormack, 1982; Behrens Yamada, 1992).

2.2. Study site and snail collection

Field experiments were carried out within the *Fucus* zone at Nudibranch Point (48°48′08″N, 125°10′05″W) near Bamfield Marine Station, Vancouver Island, British Columbia (48°50′00″N, 125°08′00″W). The rocky shores of Nudibranch Point have several types of microhabitats: barnacles (mostly *Semibalanus cariosus*, *Balanus glandula*, and *Chthamalus dalli*), macroalgae (predominantly *Fucus* spp. and *Cladophora* spp.), crevices in the basaltic rock, and bare rock surfaces. Snails used in microhabitat selection experiments at Nudibranch Point were collected from areas near the primary study area.

*Littorina sitkana* used in laboratory experiments were collected from a large tide pool on Seppings Island (48°50′05″N, 125°12′04″W) where they were present in high densities. There were no differences in microhabitat selection behavior between snails

collected from Seppings Island and snails observed at Nudibranch Point (K.M. Jones, unpublished data). Snails were maintained in aerated aquaria with a continuous supply of fresh sea water for 2 weeks prior to use. Individual snails were only used once for habitat selection experiments to prevent familiarity with microhabitats. Snails were sorted into three size classes by dry-sieving (using U.S. standard brass sieves). We defined small snails as those with shell widths of $1.98 \leq x \leq 3.00$ mm, medium snails had shell widths of $3.35 \leq x \leq 4.00$ mm, and large snails had shell widths of $4.75 \leq x \leq 7.00$ mm.

2.3. Protection from dehydration in the field

Our first hypothesis was that topographically complex microhabitats would offer more protection from dehydration, because more complex habitats would protect the snails from the sun and wind thus reducing water loss in the field from convection. To test this we collected snails from different microhabitats (barnacles, algae, crevices, and bare rock surfaces) at low tide; assuming that snails collected from the same tidal height would have been emersed for a similar time. On 25 August 1995 (mean air temperature, $20.1 \pm 0.1^\circ$C (s.e.; $n = 10$); mean relative humidity, $69.7 \pm 0.3\%$ (s.e.; $n = 10$)), directly following the peak of a midday low tide, we randomly collected 20 large snails from each of the four microhabitat types. Low tides typically last for 6 to 8 h and snails were collected after 3 h of immersion, which is long enough for significant water loss to occur. Small snails were collected using the same methods on the following day (mean air temperature, $19.8 \pm 0.2^\circ$C (s.e.; $n = 10$); mean relative humidity, $71.5 \pm 0.3\%$ (s.e.; $n = 10$)). Air temperatures were measured within 5 cm of the substrate with a thermocouple thermometer and relative humidity was measured with a thermohygrometer.

We assumed that the amount of water gained by the snails upon immersion in the laboratory was indicative of the amount of water lost during low tide. To estimate this snails were placed in separate vials and transported to the laboratory within 2 h after collection; and upon arrival they were immediately weighed and their shell lengths measured. They were then immersed in flowing sea water, and reweighed at 30, 60, 120, 240, 480, 720 and 960 min after immersion to determine when rehydration was complete and a constant weight was approached. Before each weighing, except for the first weighing after collection, each snail was gently blotted with an absorbent tissue to remove much of the extravisceral water. The blotting minimized the amount of water contained within the snail shell and improved the accuracy of mass determinations of visceral water content (Palmer, 1982; Etter, 1989). Weight changes were expressed as a percentage of the initial tissue weight (set at 100%). After 960 min of immersion in sea water, snails were sacrificed by heating in a 100°C oven for 30 min, and the tissue removed from the shell. The empty shells were then weighed and shell weight was subtracted from the initial total weight to get the initial body weight at the time of collection. The initial body weight will include tissue weight and also extravisceral water in the shell and mantle cavity and we are assuming that snails that gain less weight were less dehydrated when collected.

To determine if prevention of dehydration was independent of the microhabitats from
which the snails were collected we performed an ANCOVA with microhabitat type as the main factor, snail size (= width) as the covariate, and percentage weight gain 960 min after immersion as the dependent variable. The small and large size classes of snails were analyzed separately because they were collected on separate days and therefore any differences among them may not be solely a result of differences in size. The data were angular transformed to improve normality prior to analysis. We viewed studentized residual plots to check for homogeneity of variances (Kuehl, 1995). We tested the homogeneity of slopes for the ANCOVA by testing for significance of the interaction between the main factor and the covariate. The interaction was not significant for either small snails (P = 0.127) or large snails (P = 0.976) so the covariate was removed from the analyses. We chose weight gain after 960 min as the dependent variable because the snail weights oscillated for 720 min after immersion before constant weight was approached (Jones, 1996). We then used a Tukey post hoc multiple comparison test to determine which microhabitats were significantly different from one another.

2.4. Effect of heat and desiccation stress on microhabitat selection in natural conditions

We tested our second hypothesis, that snails would decrease their foraging time and increase their degree of habitat selectivity as their physical environment became increasingly stressful, in a field ‘arena’ experiment using natural microhabitats. It was expected that small snails would be more affected by increased thermal and desiccation stresses than large snails. During summer 1995, we chose five hot and dry (= ‘warm’) days (air temperature, 22.3±0.8°C (s.e.; n = 5); relative humidity, 60.6±2.6% (s.e.; n = 5)), and five cool and moist (= ‘cool’) days (air temperature, 17.7±0.4°C (s.e.; n = 5); relative humidity, 79.7±1.4% (s.e.; n = 5)), and performed microhabitat selection experiments with snails on natural substrates at Nudibranch Point. Experiments were done at approximately the same time each day and as close as possible to the same point in the tidal cycle. On each day we choose four (20×20 cm) arenas at random that had approximately 25% area coverage of the four microhabitat types. Each arena was fenced with a 5 cm strip of 1 mm aluminium mesh supported with cardboard. We used a total of 40 arenas over the 10 experimental days.

At the beginning of each experiment all resident snails were removed from the arenas. Each arena was rinsed with sea water to simulate the period of aerial exposure directly following low tide and to reduce the amount of snail mucus in the microhabitats. The removal of snail mucus was desirable because snails are known to follow mucus trails from other snails (Chase and Boulanger, 1978; Chelazzi et al., 1987; Della Santina, 1994). To simulate dislodgment by waves, the newly collected small and large snails were shaken in sea water. This induced the snails to emerge from their shells and attach to the substrate. One hundred small snails were placed in each of two arenas, and 100 large snails placed in each of two other arenas.

Preliminary studies showed that initial position had no effect on the final microhabitat selected in Littorina sitkana. To start each experiment, 25 snails were placed haphazardly in each of the microhabitat types. Every 15 min, over a 2 h period, the number of snails in each of the microhabitats was recorded. Throughout the 2 h period, the snails
moved around extensively, sampling different parts of the arena until eventually selecting a microhabitat in which they remained for the duration of the experiment. Microhabitat selection by snails was defined as the process of (1) cessation of movement, (2) retraction of tentacles, and (3) closure of their opercula.

We tested the statistical hypothesis that microhabitat selection was independent of snail size and desiccation stress using ANOVA. The main effects were snail size (small or large) and desiccation stress (warm or cool days) and the response variable was the proportion of snails found in the two microhabitats that were more protective from dehydration (algae + barnacles). Data were not transformed prior to analysis because they were normally distributed (Kolmogorov–Smirnov distribution 0.095; \( P = 0.200 \)) and exhibited homogeneity of variances (Bartlett’s test, \( P = 0.175 \) (as in Zar, 1996)). ANOVA was used rather than contingency table analysis because it allowed us to explicitly test for the effect of different days nested within the levels of desiccation stress. A post hoc Tukey multiple comparison test was used to determine which interaction means (Desiccation stress \( \times \) Size of snail) were different from one another. In addition, we tested whether snails found in each of the four microhabitat types had foraged for different amounts of time before stopping by performing a Kruskal–Wallis test on the ranks of stopping times.

To test our prediction that microhabitats that are more topographically complex (barnacles and macroalgae) provide cooler temperatures on warm days, the temperatures of four randomly chosen spots of the same microhabitat in each of the four arenas were measured (therefore, for each warm or cool day, \( n = 16 \) temperature measurements per microhabitat type). Temperatures were measured by placing the thermocouple directly on the microhabitat surface. ANOVAs were done separately for warm days and cool days because ranks of temperatures of the four microhabitats were reversed. We used a nested and crossed factorial ANOVA (Kuehl, 1995) to incorporate the effects of replicate temperature measurements within each arena, and the effects of four replicate arenas used per day (40 arenas total). Microhabitat temperature was the dependent variable. Normality plots and studentized residual plots revealed minimal deviations from normality and homogeneity of variances, so no transformations were applied prior to analysis. To test which microhabitats had significantly different temperatures, we used Fisher’s LSD multiple comparison tests to compare the means of the main effect of microhabitat.

2.5. Artificial microhabitat selection in controlled conditions

To test predictions from hypotheses 2, 3, 4, and 5 while controlling for factors that fluctuate in the field (e.g., temperature, relative humidity, sun, wind, and snail density) we conducted an experiment using plates made from an artificial substrate with barnacle-shaped, algae-shaped, crevice, and flat microhabitats (Fig. 1). Hypothesis 2 predicts that increased thermal stress would result in increased preferences for more protective microhabitats. Hypothesis 3 predicts that small snails would show an even stronger preference for more protective microhabitats than large snails under increased thermal stress because of their greater surface area/volume ratio. Hypothesis 4 predicts that snails that stopped foraging relatively early in the observation period would be more
likely to obtain a less stressful microhabitat than those that stopped foraging late. Finally, hypothesis 5 predicts that increasing snail density would result in a lower proportion of snails in the less stressful microhabitats as these become crowded.

Artificial microhabitat plates were made from kiln-fired clay, and the resulting smooth surface enhanced the growth of benthic algae which was grazed by the snails. By creating the four types of microhabitats out of a uniform material, we eliminated variability in food quality, water absorption, and chemical stimuli among microhabitats. Thus we were able to test the effect of microtopography alone on habitat selection without those confounding factors. The microhabitats were randomly positioned on the
20×20 cm clay tile in a grid of 16 cells (5×5 cm) (Fig. 1). A 5 cm strip of 1 mm² aluminum mesh was affixed to the edges of the microhabitat plate for fencing.

The effect of temperature, size of snails, and density of snails on microhabitat partitioning was examined in an experiment using a double split plot factorial design (Kuehl, 1995). Temperature had two levels: low (19.5±1.5°C) and high (25.0±1.5°C); size class had three levels: small, medium, and large; and density had three levels: 60, 100, and 300 snails per plate (Fig. 2). Six artificial microhabitat plates were used at one time and different combinations of temperature and snail density were run in a random order and replicated three times. All replicates were run in a temperature-controlled chamber. In each combination two artificial microhabitat plates were used as replicates of the size classes. For example, the first set of experimental conditions was low temperature, low density of snails (60), and two microhabitat plates each with small, medium or large snails. The plates were freshly rinsed with sea water to simulate the receding tidal conditions and to remove snail mucus. The snails were placed randomly on the microhabitats, with snails apportioned equally in each of the microhabitat types (Fig. 1).

The number of snails found in each of the four microhabitats was recorded every 15 min. As before, a microhabitat was considered to have been chosen when the snails stopped moving, retracted their tentacles, and closed their operculum. The snails did not come out of their shell again until they were removed from the habitat plates and

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**Fig. 2.** Flow chart of the double split plot design for the artificial microhabitat selection experiment in the laboratory.
re-immersed in sea water. Paint marks were applied to the apex of the shells of the first 50% of snails that became stationary and these were classified as snails that selected habitats ‘early’. At the end of the 2 h experiment, we then separated ‘early’ and ‘late’ microhabitat selection by counting the number of painted snails (early) and unpainted and unmoving snails (late) in each habitat.

The complete double split plot factorial design (Fig. 2) was analyzed with the ‘mixed’ procedure of the SAS statistical software package. The split plot effects of blocking were found to be non-significant, and were subsequently removed from the analysis. The effect of temperature and density nested within each experimental ‘block’ (since six plates were run at a time with the same temperature and density levels) was not significant (Appendix A). Likewise, the effect of nesting size classes within each experimental ‘block’ was also not significant (Appendix A).

The effect of density was not consistent across treatment combinations (Appendix A), so we pooled densities in the three-way factorial ANOVA presented here (Table 4). We tested for significant effects of the three fixed factors: size class of snails, temperature, and stopping time (Stoptime) of microhabitat selection (whether a snail selected a microhabitat early or late in the observation period) on the proportion of snails found in the barnacle or algal microhabitats. These two microhabitats were chosen because they were the most topographically complex and this experiment allowed us to test whether habitat selection was based solely on topographic complexity. Prior to analysis, the proportions of snails were angular transformed to improve normality. We also examined studentized residual plots to ensure our assumption of homogeneity of variance was justified.

2.6. Long-term benefits of selecting more protective habitats

Hypothesis 6 predicts that the close proximity of protective microhabitats among barnacles over 6 weeks of low tide periods would increase snail growth and survivorship. This effect would be expected to be greater when snail density was low than when high, because at low density there would be less competition for the barnacle microhabitats. Low snail densities (100 snails), or high snail densities (500 snails) were placed in enclosures with or without barnacles (75–100% coverage of *Balanus glandula*) (n = 3 replicates of each treatment combination). The enclosures (20×20 cm) were constructed at Nudibranch Point by drilling concrete anchors into the rock at each of the four corners of the enclosures. Aluminum mesh screening (1 mm openings) was sewn together to form a fence around the concrete anchors and a lid was cut from mesh and sealed with velcro. To estimate the growth of individuals, we marked snails at the lip of their aperture by placing the snails’ aperture down on double-sided carpet tape and spray-painting them with non-toxic blue spray paint. After the paint dried the snails were removed from the carpet tape and immersed in cold sea water to ensure they had survived the marking process prior to placing them in randomly assigned enclosures.

To eliminate any variation in growth rate due to reproductive maturity, we used only juvenile snails of shell length 2.0–4.0 mm. Sexual maturation of *Littorina sitkana* has been estimated to occur at a shell length of 5.5–7.0 mm for females, and 6.0 mm for males (Boulding and Van Alstyne, 1993). After 6 weeks, snails were removed from the
cages and immersed in sea water for 2 h to determine the proportion of snails that survived in each enclosure. The snails were then sacrificed by heating in an oven to prevent any further shell growth. Growth over the 6 week period was estimated by measuring the old shell length (apex to the former base of the columella determined by the extent of the paint) and subtracting it from the new shell length (apex to the present base of the columella) (see Fig. 2 in Behrens Yamada, 1989). We measured the amount of growth in a random sample of 100 snails from each of the high density enclosures and all of the remaining snails from the low density enclosures. Survivorship data were angular transformed and an ANOVA was run with habitat and density as the main effects. Growth rate data were analyzed using ANOVA, with density and substrate as main effects, and enclosures nested within substrate and density treatments. Normality plots and studentized residual plots were examined for deviations from normality and homogeneity of variances. No transformations were applied to the growth data because non-significant deviations from normality were found. Tukey post hoc pairwise comparisons were used to determine which cell means were significantly different from one another.

3. Results

3.1. Protection from dehydration in the field

Natural microhabitats varied in the degree of protection from dehydration for *Littorina sitkana*. Our prediction that more topographically complex habitats would significantly reduce the amount of water loss by the snails was largely supported (Table 1).

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<th>P</th>
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<sup>a</sup> Tukey tests compare the effects of microhabitats from which the snails were collected on % weight gain. Those microhabitats separated by an inequality sign were significantly different (*P* < 0.05) with the sign of the inequality indicating the direction. Microhabitats separated by a comma were not significantly different. The letter represents the type of microhabitat: A, algae; B, barnacles; C, crevice; R, bare rock.
snails showed significant differences in the estimated amount of water lost in each of the four microhabitats (the inverse of the amount gained after re-immersion), with barnacles < algae or crevices, and algae < bare rock surface (Fig. 3a). For the large snails, the estimated amount of water loss by snails collected from barnacle microhabitats did not differ from those collected from algae but both lost significantly less than snails collected from rock or crevice microhabitats (Table 1, Fig. 3b). The amount of dehydration estimated was impressive: small snails lost 45.7 ± 6.6% (s.e.; n = 20) of their wet tissue weight in the bare rock, whereas the large snails lost 27.8 ± 1.7% (s.e.; n = 20).

Fig. 3. Percentage weight loss by (a) small snails and (b) large snails in the high intertidal that were collected from four different microhabitats after aerial exposure from one low tide on a warm day. Percentage weight loss was calculated from the amount of water gained after 16 h of re-immersion. Means have been corrected for the pre-weighing blotting technique. Vertical bars represent one standard error of the mean (N = 20 snails from each microhabitat).
3.2. Effect of heat and desiccation stress on habitat selection in natural conditions

Large snails in our field arena experiments showed stronger preferences for more complex microhabitats on warm days but small snails did not. The interaction of desiccation stress and size of snail was highly significant ($P < 0.001$; Table 2), indicating that desiccation stress had different effects on the microhabitat selection behavior of small snails than on that of large snails. The effect of running the experiment on different days with the same classification of desiccation stress was not significant ($P = 0.08$; Table 2).

On warm days the small snails selected the less complex microhabitats, crevices and bare rock surfaces, instead of barnacles and algae (Fig. 4a). Small snails stopped foraging very quickly on warm days ($21.0 \pm 2.4$ min (s.e.); $n = 10$ arenas). On cool days, small snails foraged for a significantly longer period of time ($54.0 \pm 2.4$ min (s.e.); $n = 10$ arenas; Mann–Whitney, $P < 0.001$), and they showed a significant preference for the more complex microhabitats as we had predicted (Fig. 4b).

Large snails showed a clear rank order preference of microhabitats on warm days. Ranked by number selecting each microhabitat, the order was barnacles > algae > crevice > bare rock (Fig. 4c). On cool days large snails reversed this preference, choosing bare rock surfaces and crevices more frequently than algae and barnacles (Fig. 4d). Large snails foraged significantly longer on cool days ($66.0 \pm 2.4$ min (s.e.); $n = 10$ arenas) than on warm days ($28.5 \pm 1.5$ min (s.e.); $n = 10$ arenas; Mann–Whitney, $P < 0.001$).

There was no difference in stopping time among the four different microhabitats when all days and sizes were combined (Kruskal–Wallis test (K–W): $H = 0.28$, $P = 0.96$). Similarly, for every treatment combination of snail size and level of desiccation stress we found no significant differences in stopping time (K–W results: small snails, high

Table 2
Analysis of variance of the number of snails that stopped moving, sealed their opercula, and withdrew into their shells in algal and barnacle microhabitats after the 2 h field arena experiment. Desiccation stress had levels of warm, dry days, or cool, moist days. Sizes of snails were small or large. Days were nested within the level of desiccation stress ($N = 40$ arenas). Multiple comparisons state the results of a Tukey post hoc test and the differences between the interaction means.

<table>
<thead>
<tr>
<th>ANOVA source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>Multiple comparisons$^a$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Desiccation stress</td>
<td>1</td>
<td>1703.025</td>
<td>76.565</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Size of snail</td>
<td>1</td>
<td>55.225</td>
<td>2.483</td>
<td>0.126</td>
<td></td>
</tr>
<tr>
<td>Desiccation stress × Size of snail</td>
<td>1</td>
<td>8497.225</td>
<td>382.020</td>
<td>&lt;0.001</td>
<td>LA-LO&lt;SM-HI&lt;SM-LO&lt;LA-HI</td>
</tr>
<tr>
<td>Day (Desiccation stress)</td>
<td>8</td>
<td>45.063</td>
<td>2.026</td>
<td>0.080</td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td>28</td>
<td>22.243</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a$ Those conditions separated by an inequality sign were significantly different ($P < 0.001$) with the sign indicating the direction. The first set of letters represents the size of snail (LA, large; SM, small), and the second set of letters represents the desiccation stress (LO, low; HI, high).
desiccation stress: $H = 2.24, P = 0.54$; small snails, low desiccation stress: $H = 3.07, P = 0.38$; large snails, high desiccation stress: $H = 0.67, P = 0.88$; large snails, low desiccation stress: $H = 2.14, P = 0.31$).

The classification of days as low or high physical stress was justified. All low stress days had significantly lower air temperatures ($t$-test, $P < 0.001$) and significantly higher humidities than all high stress days ($t$-test, $P < 0.05$). In addition, low stress days also had lower microhabitat measurements than high stress days (Table 3). The interaction between Microhabitat and Day (Table 3) occurs because the ranks of the microhabitat temperatures were not entirely consistent across days. On warm days, algal microhabitats provided the coolest temperatures on four out of the five experimental days, whereas on cool days, rock microhabitats provided the coolest temperature on average on all five experimental days. Similarly, the interaction between Microhabitat and Arena (Day) occurs because the ranks of the microhabitats may differ from the average ranks in particular arenas on particular days.

### 3.3. Artificial microhabitat selection in controlled conditions

Our prediction that increased thermal stress would cause the snails in our artificial plate experiments to show stronger preferences for more topographically complex microhabitats (barnacle-shaped and algae-shaped microhabitats) was upheld only for the
Table 3
Microhabitat protectiveness as measured by mean natural substrate temperatures in the field (n = 4 measurements of each microhabitat/arena/day). Presented here are the results of a mixed model ANOVA, and Fisher’s LSD tests of multiple comparisons for significant differences among microhabitat temperatures. Relative humidity was 79.7 ± 1.4% (s.e.) on days of low desiccation stress and 60.6 ± 2.6% (s.e.) on days of high desiccation stress (n = 5 days).

<table>
<thead>
<tr>
<th>Temp. (±1 s.e. °C)</th>
<th>ANOVA</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>Multiple comparisons$^a$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cool days</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ambient air</td>
<td>17.7±0.4</td>
<td>Microhabitat</td>
<td>3</td>
<td>21.39</td>
<td>156.80</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Algae</td>
<td>18.4±0.2</td>
<td>Day</td>
<td>4</td>
<td>287.03</td>
<td>369.25</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Barnacles</td>
<td>18.5±0.2</td>
<td>Microhabitat × Day</td>
<td>12</td>
<td>1.75</td>
<td>12.79</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Crevic</td>
<td>18.0±0.2</td>
<td>Arena (Day)</td>
<td>15</td>
<td>0.78</td>
<td>5.70</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bare rock</td>
<td>17.4±0.2</td>
<td>Microhabitat × Arena (Day)</td>
<td>45</td>
<td>1.44</td>
<td>10.55</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Error</td>
<td>240</td>
<td>0.14</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Warm days</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ambient air</td>
<td>22.3±0.8</td>
<td>Microhabitat</td>
<td>3</td>
<td>157.08</td>
<td>235.90</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Algae</td>
<td>20.1±0.2</td>
<td>Day</td>
<td>4</td>
<td>282.61</td>
<td>67.91</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Barnacles</td>
<td>20.6±0.2</td>
<td>Microhabitat × Day</td>
<td>12</td>
<td>4.36</td>
<td>6.55</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Crevic</td>
<td>22.0±0.3</td>
<td>Arena (Day)</td>
<td>15</td>
<td>4.16</td>
<td>6.25</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Bare rock</td>
<td>23.2±0.3</td>
<td>Microhabitat × Arena (Day)</td>
<td>45</td>
<td>1.79</td>
<td>2.69</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Error</td>
<td>240</td>
<td>0.67</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a$ Fisher’s LSD tests for differences in temperatures among the four microhabitats. Those conditions separated by an inequality sign were significantly different (P < 0.05) with the sign indicating the direction. Conditions separated by a comma were not different. The letter represents the type of habitat: B, barnacles; A, algae; C, crevice; R, bare rock.

snails that selected microhabitats early in the observation period (Fig. 5). This occurred for all size classes of snails. The difference between the early and the late groups was even greater in the high temperature treatment (Fig. 5). We observed highly significant effects of size, temperature, stoptime, and size × stoptime (Table 4). Our prediction that small snails should be more selective than large snails turned out to be false; instead we found that small snails were less selective. Part of the differences between the large and small snails may arise because large snails can afford to spend more time searching for a microhabitat.

In preliminary studies, we found a strong positive relationship between the size of the snail and the amount of time spent foraging on an artificial substrate ($r^2 = 0.600$, n = 30 snails, $P < 0.001$) (Jones, 1996). This longer foraging time translated into a longer mean distance traveled by large snails compared to small snails (n = 20 snails per size class, t-test, $P < 0.001$). In addition, the distance traveled by large snails does not appear to be as severely reduced by increasing thermal stress as that of small snails (n = 36 snails, $\chi^2$, $P < 0.01$).

3.4. Long-term benefits of selecting high quality habitats

Our prediction that the availability of less stressful microhabitats among barnacles and reduced competition for such refuges would result in higher rates of growth and
Fig. 5. Cell means from the ANOVA without density for the artificial microhabitat plate experiments (see Table 4 for ANOVA table). The vertical bars represent 95% comparison intervals (calculated using the T-method from Sokal and Rohlf, 1981). If the intervals do not overlap, these treatment combinations are significantly different.

Table 4
ANOVA of the artificial microhabitat plate experiments. The dependent variable is the proportion of snails that selected algal and barnacle microhabitats. The main effects are Size of snail (small, medium, or large), Stoptime of microhabitat selection (early or late), Temperature (low or high temperature), and the interaction between these main effects. See Fig. 4 for plot of means, and Appendix A for the mixed model ANOVA with density included in the model (N = 18 replicates per treatment combination as density levels were combined for this analysis)

<table>
<thead>
<tr>
<th>ANOVA source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size</td>
<td>2</td>
<td>0.179</td>
<td>41.12</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Temperature</td>
<td>1</td>
<td>0.0563</td>
<td>12.95</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Stoptime</td>
<td>1</td>
<td>0.521</td>
<td>119.78</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Size×Temperature</td>
<td>2</td>
<td>0.00273</td>
<td>0.63</td>
<td>0.534</td>
</tr>
<tr>
<td>Size×Stoptime</td>
<td>2</td>
<td>0.0740</td>
<td>17.00</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Temperature×Stoptime</td>
<td>1</td>
<td>0.0288</td>
<td>6.62</td>
<td>0.011</td>
</tr>
<tr>
<td>Size×Temperature×Stoptime</td>
<td>2</td>
<td>0.00175</td>
<td>0.40</td>
<td>0.669</td>
</tr>
<tr>
<td>Error</td>
<td>204</td>
<td>0.00435</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 5
Analysis of variance for survivorship data from the long-term field experiment. There were three enclosures per treatment. The dependent variable was the angular transformation of the percentage of snails that survived each treatment.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Microhabitat</td>
<td>1</td>
<td>1.617</td>
<td>54.650</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Density</td>
<td>1</td>
<td>0.163</td>
<td>5.517</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>Microhabitat×Density</td>
<td>3</td>
<td>0.003</td>
<td>0.101</td>
<td>0.759</td>
</tr>
<tr>
<td>Error</td>
<td>8</td>
<td>0.030</td>
<td>0.030</td>
<td></td>
</tr>
</tbody>
</table>

Survivorship was supported. Both substrate (barnacles or bare rock) and snail density had significant effects on snail survivorship (Table 5). Snails survived better in enclosures where there was 75–100% barnacle coverage than in enclosures with bare rock surfaces (Fig. 6 and Table 5). Snail survivorship was higher at lower snail densities (Fig. 6). Snails in bare rock enclosures with high densities (500 snails) had the lowest...

Fig. 6. Survivorship of snails in the long-term field experiment in each of four treatments. Vertical bars represent one standard error of the mean (N = 3 replicates per treatment). See Table 5 for statistical analysis of angular transformed data.
Table 6
ANOVA for growth rate data from the long-term field experiment. There were three enclosures per treatment and 100 snails (or the total number of snails left in the enclosure if <100) were measured for initial and final shell length. The dependent variable was the new growth of shell measured by the width of the unpainted lip increment. Total number of snails measured: 1094. See Fig. 7 for plot of means.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
<th>Tukey HSD results Multiple comparisons*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Microhabitat</td>
<td>1</td>
<td>120.320</td>
<td>269.172</td>
<td>&lt;0.001</td>
<td>R-H&lt;B-H&lt;R-L&lt;B-L</td>
</tr>
<tr>
<td>Density</td>
<td>1</td>
<td>201.226</td>
<td>450.169</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Microhabitat × Density</td>
<td>1</td>
<td>8.455</td>
<td>18.915</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Enclosure (Density × Microhabitat)</td>
<td>8</td>
<td>11.084</td>
<td>24.796</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>1083</td>
<td>0.447</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Those conditions separated by an inequality sign were significantly different (P < 0.05), with the sign indicating the direction. The first letter represents the microhabitat (R, rock; B, barnacle), and the second letter represents the density (L, low (100 snails); H, high (500 snails)).

survivorship rates, whereas snails in barnacle enclosures and low densities (100 snails) had the highest survivorship rates.

Growth rates were affected by substrate and density of snails and the interaction between substrate and density was significant (Table 6). The significant Enclosure (Density × Microhabitat) interaction implies that, within a treatment, growth rates differed significantly among replicate enclosures. This is likely because some locations on the shore were more favourable than others. Density appears to have a greater effect on growth rates of snails in the barnacle enclosures than bare rock enclosures (Fig. 7). Snails in bare rock enclosures on average grew less than snails in barnacle enclosures (Fig. 7). Snails in high density enclosures grew less than snails in low density enclosures.

4. Discussion

The present study provides evidence that microhabitat selection in Littorina sitkana can be a state-dependent behavior that is affected by the degree of physical stress in the environment. In the field arena experiment, large snails showed increased selection of the barnacle and algae microhabitats on warm days than on cool days as predicted. In a warm environment, snails on artificial habitat plates that chose microhabitats early were more likely to choose barnacle-shaped and algae-shaped microhabitats than snails in a cooler environment. This flexible habitat selection behavior allows snails to prolong their foraging time when the environmental conditions are less severe.

The artificial habitat plate experiment showed that the snails use topographic complexity as an important cue when selecting protective microhabitats and are not necessarily responding to the properties of the biological materials of which barnacles and algae are composed. This experiment also showed that the degree of selectivity of more complex microhabitats did not decrease with increasing densities of snails.

Our study also identifies some short- and long-term costs of selecting a more
protective microhabitat that are likely responsible for the evolution of such sophisticated habitat-selection behavior. Snail dehydration was less in microhabitats, such as barnacles, that had relatively cooler temperatures on warm days. Over the long term, growth rate and survivorship were significantly reduced when barnacles were not available to the snails over an extended time, especially when snail densities were high.

Below we discuss biophysical reasons why topographically complex habitats might be more protective to intertidal snails. We also discuss the trade-offs snails face during emersion when foraging longer before selecting a microhabitat instead of selecting a more protective microhabitat early.

4.1. Biophysics of microhabitat protectiveness from physical stress

Snails in more topographically complex microhabitats (barnacles or algae) lost less water than those in less complex microhabitats. This has also been observed for the black turban snail, *Tegula funebralis* (Marchetti and Geller, 1987). Black turban snails
in high desiccation microhabitats (such as shallow crevices or bare rock surfaces) lose more water than those in low desiccation microhabitats. Water loss from a wet organism increases with wind speed (Campbell, 1977). Spatially complex microhabitats may reduce this water loss from forced convection because they increase the thickness of the boundary layer (Monteith and Unsworth, 1990; Helmuth, 1998) thereby sheltering snails from the wind.

Snails in more topographically complex microhabitats probably also experienced less thermal stress because the barnacle and algal microhabitats were significantly cooler. Additionally, barnacles and algae may be more moist than crevices and bare rock surfaces because they retain more water (especially algae as it secretes mucus to prevent dehydration during low tide). Snails in the present study were small, making it likely that the temperature differences among the four microhabitats would be reflected in the body temperatures of the snails that chose them. It has been shown that body temperatures of littorinid snails very quickly approach rock temperature when placed aperture down in contact with rock substrate (Boulding, 1990).

Selection of a less stressful microhabitat has previously been reported as a behavioral adaptation used by temperate intertidal snails to control their internal temperature (e.g., Colisella digitalis, Gallien, 1985; and Morula marginalba, Moran, 1985). The high shore tropical limpet species Cellana grata also takes refuge in habitats that reduce the effects of thermal and desiccation stress (Williams and Morritt, 1995). Measurements of individuals and their physical environment showed that temperatures varied both spatially and temporally (Williams and Morritt, 1995). In contrast, Marchetti and Geller (1987) found that microhabitat differences had no effect on the body temperature of the black turban snail, but that aggregated snails were significantly cooler. Whether or not microhabitat selection can ameliorate physical conditions likely depends on the size of the snail relative to the microtopography. The adult size of the black turban snail far exceeds that of L. sitkana, although their surrounding microtopography is similar.

Intertidal snails are believed to have several strategies, other than microhabitat selection, to combat thermal and desiccation stress during emersion. One is used by eulittoral species which thermoregulate through evaporative cooling and lose water from their mantle cavity while continuing to forage. Two other strategies are used by eulittoral fringe species who by definition live too high to be rehydrated by daily tidal inundation. These species reduce evaporative water loss by withdrawing into their shell and closing their operculum and they also reduce the heat conduction from the rock substratum by suspending the shell by a mucus thread (McMahon, 1990). On wave-exposed shores, L. sitkana would be considered to be a eulittoral fringe species and seems to use a mixture of the above strategies. We observed that Littorina sitkana forage for a period of time when first emersed to acquire food and during this period thermal stress may be reduced because of evaporative cooling. The snails switched strategies from evaporative cooling while foraging, to withdrawing into their shells and sealing up their opercula as the substrate began to dry and heat up from solar radiation.

Desiccation stress is probably more severe than thermal stress at the site of our field experiments. Rock temperature recorded in the field with a data logger reached a maximum of 26°C (K.M. Jones, unpublished data) and remained at this temperature for less than 6 h. This temperature would not seem extreme as Littorina sitkana can
withstand 38°C with a relative humidity of 16.2% for 9 h with 0% mortality (Boulding, 1990). However, we did observe effects of desiccation stress, as the snails collected from the four microhabitats in the field were greatly dehydrated and had lost up to 45% of their initial body weight. Similarly, Britton (1992) has reported that tropical species of littorinid snails lose up to 47% of their total body water content after 12 days emersion and 38% after 30 days of emersion without any mortality and have heat coma temperatures of over 42°C.

4.2. Trade-offs between foraging and microhabitat selection with size

Large snails selected more complex habitats on warm days but small snails did not. Small snails stopped earlier and remained in the less complex microhabitats (crevices and bare rock) even though their water loss rates are predicted to be higher in these exposed areas. These small snails may have failed to select a complex microhabitat on warm days because they stopped moving very early, hence covering only a small area; they were subsequently unable to find a protective microhabitat. Under natural conditions small snails remain in their protective refuges on warm days and are rarely seen on bare rocks (E.G. Boulding, personal observation). Furthermore, Burrows and Hughes (1991b) have modeled optimal foraging by the intertidal carnivorous snail *Nucella lapillus* as being a decision about whether to remain in a safe but foodless refuge or to venture out to forage in the open where there is a risk of death from physical stress. They find that the snails with high energy reserves are less likely to risk physical stress and that small snails are more likely to maintain high energy reserves.

Our arena experiments suggested that small snails have less time to choose a protective microhabitat than large snails particularly on warm days. There is also a strong positive relationship between the size of the snail and the amount of time spent foraging on the artificial habitat plates (Jones, 1996). In addition, the distance traveled by large snails does not appear to be as severely reduced by increasing thermal stress as that of small snails (Jones, 1996).

Small *L. sitkana* might not forage as far as large *L. sitkana* during emersion because small individuals have a disproportionately smaller reservoir of visceral and extravisceral water that they can lose before reaching the maximum percent water loss they can tolerate. Boulding et al. (1999) consistently observed higher mortality of small *L. sitkana* from heat and desiccation stress compared with larger individuals. Helmuth (1998) calculated that large mussels can maintain lower body temperatures than small mussels because they have greater amounts of tissue per unit body length and therefore can tolerate greater rates of evaporative water loss. Finally, Marchetti and Geller (1987) found that small individuals of the black turban snail dehydrated significantly faster than large individuals.

4.3. Acquiring less stressful microhabitats early versus late

A greater proportion of snails selected more topographically complex habitats early than late in the emersion cycle. This probably occurs because some snails start out the low tide period with a lower body water content than others. These snails likely have to
stop sooner and choose less stressful habitats to prevent fatal desiccation. Other snails start out with a higher body water content and are able to spend more time foraging. Finally, when most of the water on the substrates of the habitats has dried up, the snails that are still foraging must quickly settle for any nearby microhabitat instead of searching longer for better quality microhabitats. Although these findings are from experiments with artificial microhabitats they are likely to also apply in the field. Snail behavior did not greatly differ on artificial substrates in the laboratory conditions than on natural microhabitats in the field (Jones, 1996).

4.4. Decrease in microhabitat selectivity with increased density of individuals

There was no consistent effect of snail density on microhabitat selection (Appendix A). We did not always see a lower proportion of snails in less stressful microhabitats as density increased. Instead, in some treatment combinations with high density we saw a higher proportion of snails in the more complex microhabitats as the density of snails was increased (Jones, 1996); therefore, L. sitkana does not behave as predicted by the Ideal Free Distribution Theory (Fretwell and Lucas, 1970). There are two explanations for sometimes seeing more snails in complex microhabitats at higher densities. Firstly, snails often follow mucus trails of other snails, perhaps attracted by pheromones and hormones (Della Santina, 1994), to the microhabitats chosen by earlier arriving snails. Secondly, the microhabitats containing snails may have increased the topographic complexity (due to the presence of the snails) which may attract more snails. Even at the highest snail density the complex microhabitats were never totally filled which allowed for later arriving snails to join earlier arriving snails. We know that aggregations of L. sitkana also occur in the field in summer but only in areas protected from wave splash where the snails will not be washed off the rocks. Other intertidal snails also exhibit aggregation behavior which is known to reduce temperature and evaporative water loss (Chase and Boulanger, 1978; Garrity and Levings, 1984; Chelazzi et al., 1987; Marchetti and Geller, 1987; Chapman, 1995). Aggregation also has important effects on the microclimate experienced by intertidal bivalves. Aggregated mussels could experience temperatures that were 4–5°C cooler than those of solitary mussels (Helmuth, 1998).

4.5. Long-term benefits of selecting more protective microhabitats

Growth rate and survivorship were significantly reduced when barnacles were not available to the snails over a 6 week period in field enclosures, especially when densities were increased. It is not clear whether the presence of the barnacles causes food availability to be increased, physical stress to be reduced, or both, but the effect was large.

Density had a smaller but significant effect on growth rate and survivorship. Other researchers have shown that if snail densities are increased, then survivorship, growth rates and standing crop of food resources are depressed (Underwood, 1978, 1984a,b; Creese and Underwood, 1982; Quinn and Ryan, 1989; Petraitis, 1992). If growth rate and survivorship are depressed at high densities then snails that select less protective habitats where densities are lower might be expected to have a higher fitness. However,
no consistent effect of density on habitat selection was seen in the artificial microhabitat plate experiment and more work is needed to understand why.

Other experiments with intertidal gastropods have investigated the combined effect of density and microhabitat availability on gastropod abundance (Behrens, 1974; Kohn and Leviten, 1976; Underwood and Chapman, 1989). Dependence on microhabitats for protection from thermal and desiccation stress is likely the reason for the often observed correlation between the density of littorinid snails and the abundance of less stressful microhabitats (e.g., Emson and Faller-Fritsch, 1976; Raffaelli and Hughes, 1978; Boulding and Harper, 1998). The present study is one of the few studies that has investigated the mechanisms by which the association between microhabitat availability and organism abundance occurs. Kohn and Leviten (1976) artificially increased habitat complexity and found it permanently increased the carrying capacity (of a local area) for Conus spp. They could not conclude whether the observed concentrations of gastropods in refuges was due to: (1) their actively selecting refuges; (2) strong water movements dislodging them from smooth areas and washing them passively into areas with refuges; or (3) higher mortality in smooth areas without refuges. Our study extends this previous work by showing that Littorina sitkana is an active habitat selector and that they show higher mortality in enclosures with smooth rock surface.

The results of our study are likely applicable to any animal species that uses refuges for protection from recurring physical stresses but leaves the refuges to forage. As environmental conditions became increasingly stressful, these snails reduced their foraging time and large snails selected more complex microhabitats. Snails that selected more complex microhabitats experienced lower temperatures on warm days and were less dehydrated than snails in microhabitats that had higher temperatures. It was also observed that snails selecting microhabitats early were more likely to locate less stressful microhabitats than snails selecting microhabitats late in the emersion period. The long-term field experiment demonstrated that availability of less stressful microhabitats over several low tide periods had positive effects on snail growth and survivorship. The results provide insight into the mechanisms by which the availability of topographically complex microhabitats allows the persistence of L. sitkana in the high intertidal zone.

In conclusion, the presence of topographically complex microhabitats is important in allowing the long-term persistence of L. sitkana in the high intertidal because these microhabitats function as essential refuges when desiccation and thermal stresses are high.

Acknowledgements

We would like to thank J. Fryxell, T.K. Hay, D. Noakes, B.D. Roitberg, P. Wright, and others for reviewing previous versions of the manuscript and the Director and staff at Bamfield Marine Station for field support. We would especially like to thank A.R. Palmer and T. Rawlings for lending equipment, T.K. Hay who designed computer databases, W. Matthes Sears of the Ashton Statistical Laboratory who helped with statistical analyses, and I.J. McGaw for photographs of the artificial microhabitat plates. Funding for this project was provided by NSERC Research Grants to E.G. Boulding.
Appendix A. Supplemental analysis to the artificial microhabitat plate experiment

To simultaneously analyze the effects of temperature, density, and size of snail, while incorporating the double split plot design, we initially used the ‘mixed’ procedure in SAS. This program iteratively estimates linear models using a Restricted Maximum Likelihood (REML) procedure. The dependent variable was the weighted value of snails in the different microhabitats. We used linear orthogonal contrasts to weight the data with different coefficients for each of the microhabitats: barnacles, algae, crevices, and bare rock (3, 1, −1, −3, respectively). To normalize the data, the numbers of snails in each microhabitat were transformed (square root \(\sqrt{x + 0.5}\)). In this analysis, snails that stopped moving early were analyzed separately from snails that stopped moving late.

Table 7
General Linear Model with random effects for snails that stopped moving early. Performed on SAS-PC. The covariance parameter estimates are estimates of the effect of randomization on the results of the GLM

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>(F)</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>1</td>
<td>75.96</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Density</td>
<td>2</td>
<td>57.61</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Size</td>
<td>2</td>
<td>224.19</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Temperature × Density</td>
<td>2</td>
<td>22.73</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Temperature × Size</td>
<td>2</td>
<td>10.94</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Density × Size</td>
<td>4</td>
<td>8.20</td>
<td>&lt;0.000</td>
</tr>
</tbody>
</table>

Covariance parameter estimates

<table>
<thead>
<tr>
<th>Estimate (± s.e.)</th>
<th>(Z)</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block (Temperature × Density)</td>
<td>0.224 (0.590)</td>
<td>0.38</td>
</tr>
<tr>
<td>Block × Size (Temperature × Density)</td>
<td>0.442 (1.022)</td>
<td>0.43</td>
</tr>
</tbody>
</table>

Table 8
General Linear Model with random effects for snails that stopped moving late. Performed on SAS-PC. The covariance parameter estimates are estimates of the effect of randomization on the results of the GLM

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>(F)</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
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<td>6.59</td>
<td>0.025</td>
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<tr>
<td>Density</td>
<td>2</td>
<td>4.64</td>
<td>0.032</td>
</tr>
<tr>
<td>Size</td>
<td>2</td>
<td>8.23</td>
<td>0.002</td>
</tr>
<tr>
<td>Temperature × Density</td>
<td>2</td>
<td>2.23</td>
<td>0.150</td>
</tr>
<tr>
<td>Temperature × Size</td>
<td>2</td>
<td>6.49</td>
<td>0.056</td>
</tr>
<tr>
<td>Density × Size</td>
<td>4</td>
<td>12.58</td>
<td>&lt;0.000</td>
</tr>
<tr>
<td>Temperature × Density × Size</td>
<td>4</td>
<td>12.09</td>
<td>&lt;0.000</td>
</tr>
</tbody>
</table>

Covariance parameter estimates

<table>
<thead>
<tr>
<th>Estimate (± s.e.)</th>
<th>(Z)</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Block (Temperature × Density)</td>
<td>4.423 (1.120)</td>
<td>3.18</td>
</tr>
<tr>
<td>Block × Size (Temperature × Density)</td>
<td>1.331 (1.178)</td>
<td>5.20</td>
</tr>
</tbody>
</table>
The most significant result from this analysis (Tables 7 and 8, Figs. 8 and 9) is that habitat selectivity does not decrease with increased density. Instead, in some treatment combinations, there was increased habitat selectivity. Given this inconsistent effect of density, we have only incorporated the GLM that pooled densities in the main section of this paper (Table 4, Fig. 5).

Fig. 8. Results from the Restricted Maximum Likelihood (REML) procedure of snails that stopped moving early on artificial microhabitats in laboratory conditions. Vertical bars are one standard error of the mean.
Fig. 9. Results from the REML procedure of snails that stopped moving late on artificial microhabitats in laboratory conditions. Vertical bars represent one standard error of the mean.

The code for the SAS mixed model used to analyze these data was:

```sas
REML procedure;
    proc mixed;
    class temperature density block size;
```
model snailearly = temperature density size temperature*density temperature*size density*size temperature*density size*block (temperature density) lsmeans size*temperature*density/pdiff;

References


\(^{1}\)The response variable, ‘snailearly’, refers to the snails that selected habitats early during the experiment; and a second analysis was run with ‘snaillate’, which refers to snails that stopped moving late.


