Oecologia (Berl) (1982) 54:177–183

*Oecologia*


# The Maintenance of Shore-Level Size Gradients in an Intertidal Snail (*Littorina sitkana*)

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**Summary.** The size of many intertidal animals varies with tidal height. These size gradients could be produced by growth or survival varying with tidal height, or by animals moving to a preferred tidal level. The body size of the snail, *Littorina sitkana,* increases steadily with tidal height in rocky high intertidal habitats of British Columbia. To determine how size gradients were maintained in *L. sitkana,* I quantified how growth, survival, and snail movement varied with tidal height. I studied populations of *L. sitkana* found on sheltered pebble beach and exposed basaltic shelf habitats. Mark-recapture studies and experimental transplants showed that growth could not have produced the size gradients because snail growth rates in both habitats were as fast or faster at low tidal levels (where the snails were the smallest) than at high tidal levels. However, survival rates were lowest at low tidal levels. On pebble beaches, this was due to size selective predation on large snails by the pile perch, *Rhacochilus vacca.* On basaltic shelves, heavy wave action at low tidal levels may have caused the poor survival rates. Transplanted snails moved homeward on pebble beaches, but not on basaltic shelves. Reduced survival rates at low tidal levels cause size gradients in both habitats, and snail movement helps to maintain size gradients on pebble beaches.

## Introduction

The intertidal zone is a steep environmental gradient bridging the gap between fully marine and fully terrestrial conditions. Therefore, several physical and biotic conditions may change within an intertidal species' vertical distribution. This gradient will affect the age and size structure of populations by altering the dynamics of populations within their vertical range. For example, body size varies with tidal height in many intertidal gastropods (Vermeij 1972).

Vermeij (1972) proposed that size gradients were a response to gradients in the intensity of juvenile mortality. However, juvenile mortality is not the only factor that may vary with tidal height. Growth could affect size gradients if animals grow fastest where they are the largest. Sutherland (1970) found that size gradients in the limpet, *Collisella (=Acmaea) digitalis*, were maintained only by growth. Mortality will contribute to size gradients if it is greatest where individuals are the smallest or if there are size selective mortality agents. Mortality may vary with tidal height because of differences in exposure (wave action, desiccation) or predation and competition (Connell 1972; Dayton 1971). Connell (1970) and Kitching et al. (1959) showed that high predation rates at low tidal levels produced size gradients in barnacles and mussels.

For sessile animals, only differences in growth or mortality can maintain size gradients, but motile animals can also move to their preferred tidal heights. Although there is good evidence that size gradients can be maintained by movement, not much is known about how and why animals select certain tidal heights (Branch 1975; Bertness 1977; Butler 1979; Gendron 1977).

I studied the maintenance of size gradients in populations of *Littorina sitkana* near Bamfield, British Columbia, Canada. I compared populations in two distinct habitats, pebble beaches and basaltic shelves, to see which mechanism(s) (growth, survival, or movement) affected the size distributions.

## Study Areas

All fieldwork was done in Barkley Sound, B.C., near the Bamfield Marine Station (Fig. 1). Pebble beaches containing *L. sitkana* are found in sheltered inlets. The vertical distribution of the snail extends from about 1.3–3.0 m above chart datum. Datum is a plane below which tides seldom fall. Pebble beaches are gently flooded by the tides.

Basaltic headlands jut out between sandy beaches found on more exposed coasts. *L. sitkana* extended from 3.3–3.8 m above datum on the headlands studied. The lower end of the snails' vertical distribution on basaltic headlands is subject to heavy wave action. Incoming waves break and then flood the higher horizontal shelves more gently except during severe winter storms. These shelves are dotted with tidepools containing many littorines.

Most experiments on growth, survival, and movement were done on pebble beach A in Bamfield Inlet and basaltic shelf. A near Second Beach (Fig. 1). Experiments were conducted at three tidal heights on pebble beaches (1.5, 2.2, 2.8 m) and at two tidal heights on basaltic shelves (3.3, 3.8 m). These stations spanned the vertical distribution of *L. sitkana* in these two habitats.

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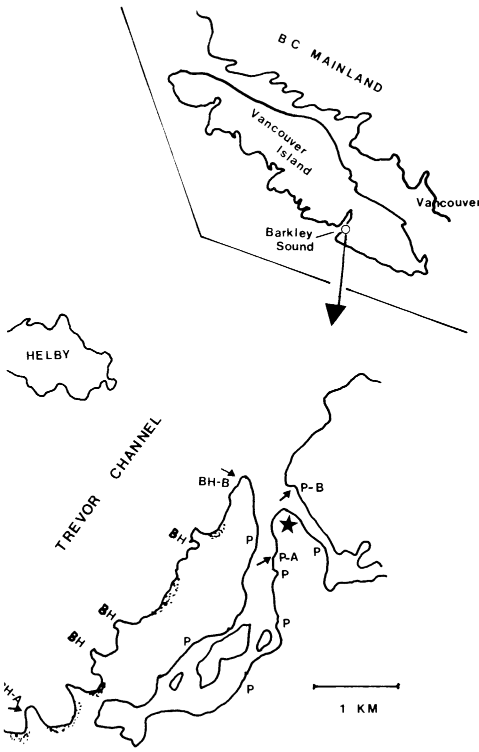


**Fig. 1.** Maps showing location of Bamfield and study sites in the Bamfield area: → study sites; *P* pebble beaches; *BH* basaltic headlands; sandy beaches; star = Bamfield Marine Station

## Methods

### *Size Distribution*

To see if snail size distribution varied with tidal height and season, I sampled the four study sites (Fig. 1) every three months. Quadrats, 10 cm$^2$, were randomly chosen at each tidal height. The number sampled depended upon the snail density and size distribution at each tidal height. Snail size was taken to be the longest axis of the snail shell which was measured with vernier calipers. To see if the egg mass distribution of *L. sitkana* varied with tidal height, I also recorded egg mass distribution and abundance on pebble beach A and basaltic shelf A.

### *Growth*

Snails were marked to measure growth at three tidal heights on pebble beach A and at two tidal heights of basaltic shelf A. Three size classes of snails were marked: small (3–4 mm), medium (6–7 mm), and large (8–11 mm). The snails were sieved with soil sieves for size matching and the size groups were painted differently with 'Humbrol' enamel base model paint. The lip of the shell was painted and lip increment, the growth rate index, was measured with vernier calipers at weekly to monthly time intervals from May–October 1980. On pebble beaches, it was difficult to find marked snails at large in the pebble matrix and so snails were enclosed in 1 m$^2$ bags of 'permascreen', a plastic meshing used for window screening. Two bags were set up at each of the three tidal heights on pebble beach A. The bags contained 30 small, 30 medium, and 15 large marked snails. They also contained natural densities of unmarked snails, rocks, and a shell/mud matrix from the surrounding area. On basaltic shelf A, snails from one low level and two high level tidepools were marked. Fifty small, 100 medium, and 100 large snails were marked in each tidepool. The surrounding area was mapped and systematically searched at each visit.

### *Survival*

*Survival on Pebble Beaches.* To measure how survival rates varied with tidal height and snail size, I put out known size compositions of marked snails at the three tidal heights on pebble beach A. I checked the areas after one high tide. Dispersal was prevented by putting the transplants into a 0.8 m$^2$ aluminium enclosure which was 5 cm high with an attached 10 cm high permascreen fence. The enclosure reduced the snails' movements without hindering any possible predators. I put out two enclosures 37 m apart at each tidal height. Experiments were carried on from June to August 1980. Twenty large and 20 medium-sized snails were put inside each enclosure at low tide on 6 occasions. The number of live snails and shell fragments recovered after one high tide was recorded. To see if, in the absence of large snails, more medium-sized snails would be eaten, I put out 40 medium-sized snails inside the middle and low enclosures before three separate high tides. Two groups of 25 unpainted and one group of painted snails were put out in 3 low level areas on 3 occasions to see if the predators were preferentially eating painted snails.

Survivorship of snails in growth bags was also measured. These measurements estimated survival of all size classes at all tidal levels in the absence of predation.

*Survival on Basaltic Shelves.* Survivorship at different tidal levels of basaltic shelf A was measured by the survival rates of the same snails marked and put out at the three tidepools to measure growth rates. The resulting distributions were compared with a Kolmogorov-Smirnov two-sample test (Siegel 1956). To see if survival rates were size dependent, I also transplanted 75 large and 75 medium-sized snails from the high shelves to the low pool. The survival rates were recorded at weekly intervals from May through August.

To sort out the effects, if any, of wave action and predation on the disappearance rates of marked snails, I attached large snails to leashes at two low level areas. The leashes ideally protected the snails from wave action mortality without protecting them from predation. Holes were drilled through the lip of the shell and the snails were attached to wire bars with 1 kg test nylon monofilament. Five snails were attached to each bar. Twelve bars were cemented to the rock in August 1980 with 'Burke Plug Quick Setting Hydraulic Cement.' The leashed snails were checked two weeks and two months later.

### *Movement*

*Movement on Pebble Beaches.* To test the hypothesis that snail movement maintains size gradients, I did transplant experiments from July 21 to August 7, 1980 on pebble beach A. Large snails were transplanted down from their original tidal levels and small snails were transplanted up. The up/down axis was perpendicular to the shoreline. 0° was defined as straight up the beach; 180° was straight down.

Large snails were transplanted down the beach 4 m (a change in tidal height of 0.7 m). Small snails were transplanted up the beach 6 m (a change in tidal height of 0.8 m). Large snails could not be transplanted lower because of heavy loss to predators. To control for the effect of displacement, snails were transplanted laterally (1–5 m) within their original tidal height.

Each treatment placed 30 large or 40 small marked snails within a 20 cm diameter circle. Positions of the snails (distance and direction from the point of release) were recorded 24 h and 2 high tides later. The area searched was a circle of 1 m radius centered about the release point.

The distributions of the positions of the snails were analyzed with a modified Rayleigh test (Moore 1980). This test weights distance and direction and looks for significant deviations from a random or uniform distribution. A mean vector was calculated for each treatment.

*Movement on Basaltic Shelves.* To measure any movement up from the low level of basaltic shelf A, the positions of marked snails in the low level tidepool were recorded on four occasions. A minimum area of 21 $m^2$ was searched about this low level tidepool. Any snails that had moved 1–2 m down the slope below the tidepool (a 0.1–0.2 m change in tidal height) were recorded as moving down. Snails recorded as moving up, had moved into tidepools that were 2–3 m above the original tidepool (a change in tidal height of 0.1–0.2 m). All other positions recorded were at the same tidal level as the original tidepool.

## Results

### Snail Size Distributions

Within both habitats, the size structure of *L. sitkana* populations varied with tidal height so that mean snail size increased with tidal height (Fig. 2). Sample sizes were small high (2.8 m) on pebble beaches, despite sampling twice the area sampled at lower stations. Small snails were always scarce high on pebble beaches, but were seasonally abundant on basaltic shelves. Small size classes were abundant and larger size classes were rare at low tidal levels of both habitats.

On pebble beach A, egg masses were only found at the middle station (2.2 m) in February and April. No egg masses were observed at other tidal heights and seasons. On basaltic shelf A, egg masses were more abundant at the high stations than at the low station. The egg masses were present from October to April.

### Growth

If size gradients are the result of differential growth rates, snails at high tidal levels should grow the fastest. However, Fig. 3 shows that all size classes grew as fast or faster at low tidal levels than at high levels. On pebble beaches, means from low tidal levels were significantly greater than means from high levels ($P<0.005$). Growth rates were always compared within each size class to control for the effect of snail size on growth rate. On basaltic shelf A, the snails at the low station grew slightly faster than the snails at station 3.8 (a), but the difference was not significant ($P=0.07$). Therefore, variation in growth rates cannot account for the size gradients found on pebble beaches and basaltic shelves.

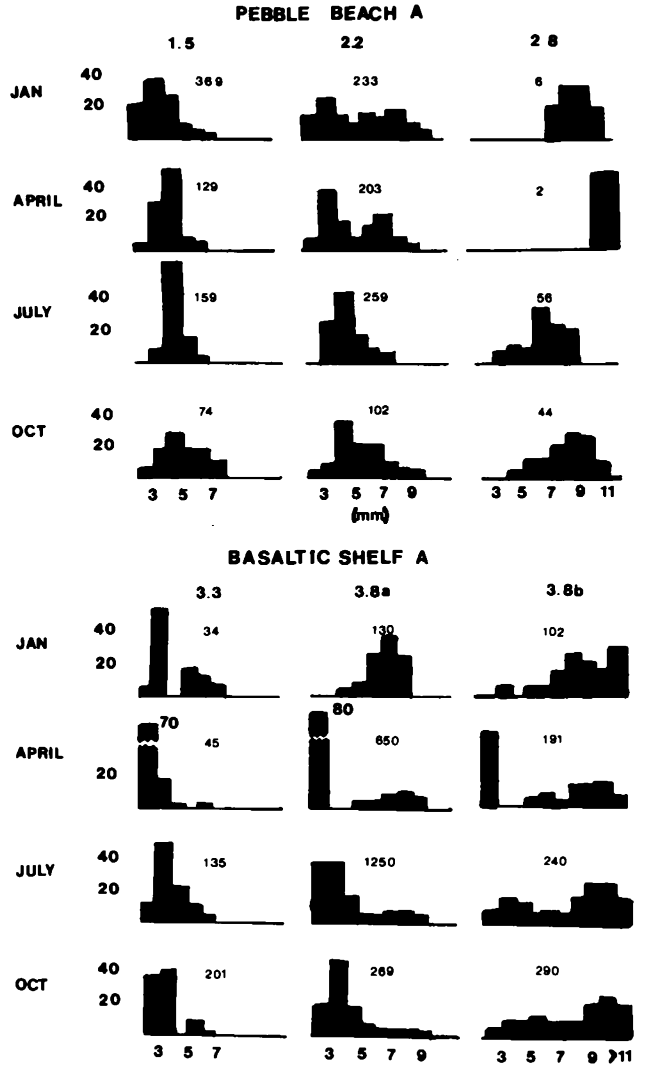


**Fig. 2.** Size frequency distributions of *L. sitkana* sampled in 1980 at three stations on the main study sites. Tidal height (*m*) is shown for each station and sample size is given on each histogram

### Survival

Survival on Pebble Beaches

*1. Predation Experiments.* In preliminary transplants of painted large snails to low levels of pebble beach A, I found many painted shell fragments after only one high tide. To discover what was eating the snails, I closely watched the enclosures at low tidal levels throughout their entire period of submersion. Four pile perch, *Rhacochilus vacca*, were observed entering the area at high tide. They sucked the littorines into their mouths and spat out the fragments moments later. Table 1 shows that the survival rate was much lower at the low stations than at the middle stations. There is a negative correlation between the number of fragments found and the mean number of large snails found alive (Spearman's rank correlation $= -0.90$, $n=36$, $P<0.05$). At the high station, 414 out of 430 snails were found alive and no snail shell fragments were ever found.

A two way ANOVA was done on the number of snails found alive with snail size and tidal height as factors. Both factors were significant ($P<0.001$). Therefore, survival rate

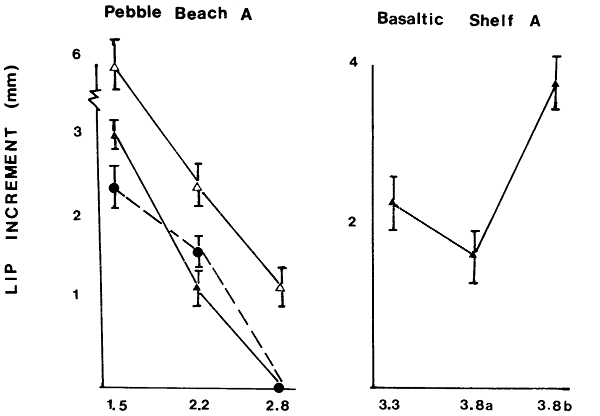


**Fig. 3.** Growth rates of *L. sitkana* at different tidal levels of Pebble Beach A and Basaltic Shelf A. The mean lip increments for two month periods and their standard errors are plotted. snail size: △ small; ▲ medium; ● large

**Table 1.** Mean survival of (n = 12) 20 large and 20 mediumsized *L. sitkana* after one high tide

| | Tidal height (m) | | | |
|---|---|---|---|---|
| | low (1.5) snail size | | middle (2.2) snail size | |
| | Large | Medium | Large | Medium |
| Mean no. alive | 9.2 | 15.2 | 18.9 | 19 |
| S.E. | 1.1 | 0.6 | 0.3 | 0.3 |
| Total no. fragments found | 105 | 31 | 8 | 0 |

is significantly lower for large snails at the low tidal heights. Survival rates for medium-sized snails were higher in enclosures containing 40 medium-sized snails: 89% of the medium-sized snails survived this treatment whereas only 76% survived in the fences containing 20 medium-sized and 20 large snails. These proportions were significantly different (test for binomial proportions, $P < 0.001$).

These two experiments show that predators preferred large snails and suggest that predation on medium-sized snails occurs primarily when the predators are attracted into an area by the presence of large snails.

The predators did not preferentially eat painted snails. Groups of 25 large unpainted snails disappeared as fast as groups of 25 large painted snails did; large numbers of shell fragments were found in all transplant areas. There was no difference in the proportions of unpainted snails (0.35) and painted snails (0.38) found alive (test for binomial proportions, $P = 0.36$).

Pile perch were consistently found in pebble beach A at high tide and were observed eating the snails. I examined the diet of the pile perch to see what else they ate on pebble beaches. The fish were caught while they were observed eating the littorines and marked shell fragments were found in their stomachs. Barnacles, small crabs (mostly *Hemigrapsus* spp.), and mussels (*Mytilus* spp.) were the most abundant prey items. These prey items were commonly found

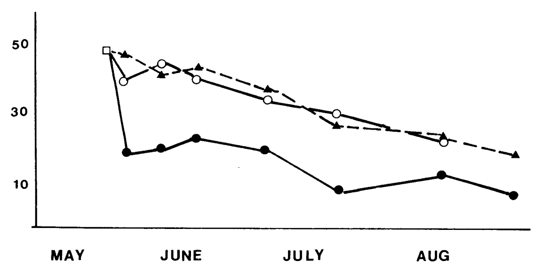


**Fig. 4.** Survival rates (no. found alive) of medium-sized snails at the three stations of Basaltic Shelf A. □ date released; ● 3.3 m; ○ 3.8a; ▲ 3.8b

on the pebble beaches between the tidal heights of 1.5 and 2.2 m. The fish were observed eating barnacles between visits to the snail enclosures. Therefore, it is likely that the fish regularly visit low levels of pebble beaches because their major prey items are abundant there.

*2. Survival in Growth Bags.* For the five month period that I measured growth and survival in the bags, the cumulative percentage of small snails found dead was 6% at high tidal levels, 3% at middle levels, and 6% at low levels. These data do not support the hypothesis that small snails are absent from high levels of pebble beaches because of increased mortality. The cumulative percentages of dead large and medium-sized snails were only 2% at the low and middle tidal levels but were 20% at high tidal levels. This suggests that in the absence of predation, the physical and biotic conditions for survival and growth (Fig. 3) are best at low tidal levels.

### Survival on Basaltic Shelves

Figure 4 shows that there was a lower survival rate of marked snails at the low tidepool of basaltic shelf A than at the two high tidepools. Additional snails were marked and released two weeks before those shown in Fig. 1. For both experiments, the survival curves at the low tidepool are significantly different from the other two (Kolmogorov-Smirnov test, $P < 0.005$). When large and smaller-sized snails were transplanted to the low station, there was no difference ($P = 0.5$) in their survival rates. Therefore, there is no evidence for size-dependent survival rates at the low tidepool.

Disappearance of marked snails from basaltic shelves could be due to predation, wave action, movement, or failure to find the snails. All tidepools were systematically searched and there is no reason for the probability of finding marked snails to be lower at the low tidepool.

To separate wave action mortality from predation, I put out 60 large snails on leashes that were attached to cemented bars. Seven of the 12 bars disappeared in two months confirming that wave action is strong at low tidal levels of basaltic shelves. However, wave force acting on a cemented bar is not equivalent to that acting on a snail. The leashes of some snails were completely wrapped around the bar. These snails were potential victims of wave action. Snails missing could have been eaten or could have escaped from their leashes. After two weeks, there were 11/50 possible victims of wave action and only 5/50 snails were missing. After two months, 11/22 snails were wrapped around the bars and 9/22 were missing. This experiment suggests that

**Table 2.** Results of Rayleigh test on positions of snails 24 h after release from origin on Pebble Beach A

| | Large snails | | Small snails | |
|---|---|---|---|---|
| | controls | transplants | controls | transplants |
| No. of replicates | 4 | 8 | 6 | 9 |
| Direction moved | | | | |
| -random | 4 | 2 | 3 | 1 |
| -up | 0 | 6 | 3 | 0 |
| -down | 0 | 0 | 0 | 8 |
| Mean vertical distance moved (cm) | −1 | 43.5 | 20.5 | −22.6 |
| s.e. | 9.7 | 3.5 | 5.1 | 3.7 |

wave action mortality occurs and that predation rates are much lower than on pebble beaches. I put out 12 leashed snails on pebble beach A and most were missing after one high tide; also shell fragments remained attached to some leashes.

From the above data, I suspect that wave action mortality is responsible for poor survival of snails at low levels of basaltic shelves. I do not expect mortality from wave action to be constant as it should vary with tidal height, sea surge, and season. Repetition of the above experiments under a variety of weather conditions is needed to draw firmer conclusions.

*Movement*

*Movement on Pebble Beaches.* The movement experiments on pebble beach A tested if transplanted snails could move homeward. Large snails transplanted downwards showed significant movement up (Table 2). The snails that were transplanted laterally to serve as controls showed no preferred direction of movement. Small snails transplanted upwards showed strong directional movement down. Three of 6 controls showed a tendency to move up. These results (Table 2) strongly suggest that the snails can select their preferred tidal level and so movement could be contributing to the size gradient pattern on pebble beaches.

*Movement on Basaltic Shelves.* The marked snails at the low tidepool of basaltic shelf A did not show any strong directional movement up. The snails painted in May to measure growth, showed a tendency to move down. For example, by August, 22 of the 81 recaptured medium snails had moved down, but only 2 had moved up. The transplanted snails did not show any marked differences. Nine of the 117 large transplants had moved up, but 8 had moved down.

There may be limited movement upwards from low areas of basaltic shelves, but the observed rates are not sufficient to explain the absence of large snails from low tidal levels.

## Discussion

The common feature of the size gradients in both habitats studied was that, regardless of season, large snails were always absent from low tidal levels. It is clear that the observed size gradients in *L. sitkana* cannot be maintained by differential growth rates. My data support the hypothesis that poor survival at low tidal levels maintains the size gradients in both habitats. In addition, snail movement may help to maintain size gradients on pebble beaches, but not on basaltic shelves.

On pebble beaches, large snails are absent from low tidal levels and small snails are absent from high tidal levels. Because pile perch were consistently found at pebble beach A at high tide and were observed eating the snails, I believe they were the major predator on large snails at low tidal levels. Another possible predator is the red rock crab, *Cancer productus*. It is normally found at lower tidal heights than the littorines. *C. productus* feeds on other larger gastropods such as *Thais* spp. (Bertness 1977; Zipser and Vermeij 1978) that are more abundant below the littorines' distribution.Pile perch predation can probably maintain the low abundance of large individuals because:

1. The fish have enough alternate prey to keep them visiting the low tidal level areas;
2. The fish prefer large snails and are able to find and eat large snails at low density.

Pile perch may not feed at high tidal levels because the water is too shallow for them to enter and there are fewer alternative prey available. This situation is similar to the predator-prey system studied by Connell (1970). The geographic distribution of pile perch overlaps that of *L. sitkana* (Hart 1973). However, further studies of other littorine populations are needed to determine if pile perch predation is a general factor affecting littorine size gradients.

Small individuals of *L. sitkana* could be scarce at high tidal levels of pebble beaches because: (1) large snails do not lay egg masses at high tidal levels; (2) small snails do not move up and remain at high tidal levels; (3) small snails that move up into high tidal levels die quickly. My results suggest that only the first two mechanisms are operating. The third is unlikely because the mortality rates of small snails in growth bags at high tidal levels were low. Small snails may avoid moving up to high areas because growth conditions are poor. Slow growth could lower the reproductive output of snails if fecundity is directly related to snail size, as in *Littorina planaxis* (Schmitt 1974). Egg masses were observed only at middle tidal levels of pebble beaches. They were concentrated in damp areas. Conditions at high tidal levels may not be suitable for egg mass survival. Yet there were many small snails found at low tidal levels. This suggests that juveniles migrate down to low tidal levels.

Why do large snails move up to high areas? Absence of fish predation and reduced densities may be positive features of this area. However, growth rates were poor at high tidal levels for all snail sizes even at the low densities (Fig. 3). Also, survival of large and medium-sized snails was lowest in the high tidal level growth bags. These results seem to negate any benefits of reduced density. It would be interesting to know if these snails move down to lower tidal levels to lay their egg masses. The middle tidal heights of the pebble beaches studied could be the most favourable snail habitat representing a good tradeoff between growth (Fig. 3) and survival (Table 1).

The movement experiments show that *L. sitkana* can move homeward when dislodged. However, the experiments do not differentiate between a snail returning to a tidal level that it is habituated to and a snail selecting a tidal level on the basis of its size. Since all snail sizes and egg masses are only found together at middle tidal levels, some snails must move into upper and lower level habitats. Individuals that avoid high tidal levels when they are small and low tidal levels when they are large should have higher survival and reproductive rates than those that do not avoid these areas.

On basaltic shelves, all snail sizes are found on the high horizontal shelves, but only small snails are found at the low tidal levels. Growth (Fig. 3) and movement cannot explain this pattern. Survival varied with tidal level in the predicted direction (Fig. 4). In this study, transplanted large and small snails disappeared at similar rates suggesting that the mortality agents were not size selective. Reduced survival at low levels could be due to predation or wave action. Possible predators include starfish (Menge 1972), fish (Reimchen 1979), and shorebirds (Pettitt 1975; Smith 1952). Starfish were never observed feeding in the study area. Pile perch may feed in these exposed areas on the mussel beds, but it is doubtful that they would venture up higher to the wave break zone to visit a less abundant food source. The leash experiments suggest that predation occurs at much lower rates on basaltic shelves than on pebble beaches. In the fall and spring, shorebirds pass through Barkley Sound. I observed several flocks of black turnstones (*Arenaria melanocephala*) and surfbirds (*Aphrisa virgata*) at low tidal levels of a few basaltic shelves. Shorebirds may have a seasonal and local impact on low level littorine populations.

Birds only visit a small proportion of the basaltic shelves; but waves affect the low levels of all basaltic shelves. The high levels are spared most of the wave force except during severe winter storms. Several other littorine studies have shown a negative correlation between exposure and shell size (James 1968; Heller 1976; Struhsaker 1968). No one has clearly demonstrated that this correlation is due to size selective mortality by wave action. Struhsaker (1968) and North (1954) both showed that larger snails were lost in flow tube experiments at significantly higher rates than small ones. However, others argue that a large foot size makes large snails better able to withstand wave action (Hylleberg and Christensen 1978).

Perhaps the effect of wave action is overridden by the behavioural mechanism of hiding in crevices. Small snails appear to have access to more crevices (and therefore protection from wave action) than large snails. On exposed coasts, the size distribution and abundance of crevices has been experimentally demonstrated to affect the size distribution and abundance of British littorines (Emson and Faller-Fritsch 1976; Raffaelli and Hughes 1978; Hughes and Roberts 1981). Further work is needed to quantify mortality rates and to identify mortality agents in these exposed habitats.

On high tidal level of basaltic shelves, both growth and survival conditions are good. The largest individuals of *L. sitkana* that I found were in this habitat. These large snails were once thought to be a separate species from the smaller sized *L. sitkana* populations found in other habitats (Urban 1962).

I observed little upward movement of marked snails at low tidal levels of basaltic shelf A. Basaltic shelves are more heterogeneous snail habitat than pebble beaches because the tidepools are not always interconnected by streams. Also, the direction in which basaltic shelf A was first flooded varied with sea surge and the wind direction. Therefore, I suggest that the snails may not have consistent orienting cues available to enable them to move homeward when displaced.

In conclusion, the size distribution of *L. sitkana* at low tidal heights is affected by predation on pebble beaches, and wave action on basaltic shelves. Size gradients occur because there are spatial refuges from these mortality agents at high tidal levels of both habitats. Vermeij's (1972) hypothesis that juvenile mortality drives size gradients is not supported by this study. Other recent studies have also not found juvenile survival to be important in maintaining size gradients (Bertness 1977; Butler 1979; Raffaelli and Hughes 1978; Markowitz 1980).

*Acknowledgements.* Dr. J.N.M. Smith provided many helpful comments on the manuscript as well as logistic and moral support for this study. Many thanks to J. Lynskey for field assistance, P. Morrison for manuscript comments, and the staff of Bamfield Marine Station for research facilities. I was funded by a National Research Council of Canada Scholarship and a U.B.C. Grant to J. Smith.

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Received March 10, 1982