THE MAINTENANCE OF SHORE-LEVEL SIZE GRADIENTS

IN

AN INTERTIDAL SNAIL (*LITTORINA SITKANA*)

by

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ABSTRACT

The population size structure of many intertidal animals varies with tidal height so that the mean animal size is increasing or decreasing 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 on basaltic shelves. Size selective predation by fish together with snail movement maintains size gradients on pebble beaches.

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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 intertidal gradient should affect the age/size structure of populations by causing the dynamics of populations to vary within their vertical range. In fact, body size varies with tidal height in many intertidal animals (Vermeij 1972).

Vermeij (1972) synthesized the literature on size gradients in intertidal gastropods. He noted that in animals found in the upper intertidal, body size increased with tidal height. In animals found in the lower intertidal, body size decreased with tidal height. He proposed that the size gradients were a response to gradients in the intensity of juvenile mortality.

Juvenile mortality is not the only factor that may vary with tidal height to produce size gradients. For sessile animals, only differences in growth or juvenile and/or adult mortality can maintain size gradients. But, motile animals can also move to their preferred tidal heights. Growth could affect size gradients if animals grow fastest where they are the largest. Growth rates are known to vary with tidal height for many reasons (Vermeij 1978). For example, food quality and quantity, feeding time, and metabolic rate may vary with tidal height. Mortality could contribute to size gradients if it is greatest where individuals are the smallest or if there are size selective mortality agents present where those size classes are absent. Mortality could vary with tidal height because of differences in exposure (wave action, desiccation) or predation and competition (Connell 1972, Dayton 1971). Movement could produce size gradients if large animals choose to live at different tidal levels from small animals. Food and shelter are two of many habitat features that may influence where an animal decides to live. Studying how and why size gradients are maintained should lead to a greater understanding of how the environment affects the dynamics of intertidal populations.

What is the evidence for size gradients being maintained by growth, survival, or movement? Although many studies have compared growth rates of animals from different tidal levels, few have related growth to the maintenance of size gradients. Sutherland (1970), however, observed that the limpet Collisella (=Acmaea) digitalis grew faster and reached larger sizes at high tidal levels than at low levels. The faster growth rates were due to reduced densities at high tidal levels. In contrast, other studies on barnacles and mussels have shown growth rates to be fastest at low tidal levels, where the animals were the smallest (Connell 1970, Kitching et al. 1959). Therefore, growth could not be contributing to these size gradients.

Connell (1970) and Kitching et al. (1959) showed that differences in predation rates produced the observed size gradients in barnacles and mussels. Predation rates were greatest at low tidal levels. High tidal levels were a refuge from predation where the animals could live longer and so grow larger. Another mortality factor that has been widely studied is exposure to desiccation. Small individuals of animals found in the upper intertidal could have poor survival at high tidal levels because they are more susceptible to desiccation. This has been proposed by researchers who, finding that small individuals were scarce at high tidal levels, did laboratory studies which showed that small individuals were more susceptible to desiccation than large ones (Boyle 1970, Davies 1969, Coombs 1973, Edwards 1969). Wolcott (1973) demonstrated in the field that desiccation mortality occurred and affected small limpets more than large ones. Mortality due to wave action has also been difficult to measure directly in the field. Emson and Faller-Fritsch (1976) and Raffaelli and Hughes (1978) showed that in wave exposed areas the size distribution and abundance of littorines was affected by the size distribution and abundance of crevices. However, it was not known if the crevices were providing shelter from wave action or predation. More field work needs to be done on identifying and quantifying mortality gradients.

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. Body size increases with tidal height in many limpets of the high intertidal zone because the young settle out and survive at low tidal heights and move up as they get larger (Branch 1975, Breen 1972, Frank

1965). The proposed advantages of these migrations are to widen the species' ranges and move into areas with better growth and survival conditions. Breen (1972) showed that migrants grew faster than non-migrants. Bertness (1977) and Butler (1979) suggest that species of Thais maintain size gradients in response to gradients in food, shelter, and differential desiccation tolerances. These hypotheses need further testing. Smith and Newell (1956) showed that movement contributed to size gradients in littorines; Gendron (1977) also found size gradients in littorines and showed that experimentally displaced animals could regain their former position on the shore.

Many of the above studies on movement suggested, with little data, that the animals were moving in response to growth and survival conditions. Before we can propose a robust theory for why size gradients are maintained, we need to know how they are maintained. All three factors may contribute to size gradients, and if they do we need to assess their relative contributions.

I studied how size gradients were maintained in populations of Littorina sitkana near Bamfield, B.C. I compared populations in two distinct habitats, pebble beaches and basaltic shelves, to see what were the common and perhaps most important mechanisms affecting the size distribution patterns.

To determine how the snail size gradients were maintained on pebble beaches and basaltic headlands, I asked the following questions:

1) Does the size gradient pattern vary seasonally?

2) Does snail growth, survival, or movement vary with tidal height?

3) If any or all of the above factors vary with tidal height, are the observed differences sufficient to produce the size gradients?

I found Littorina scutulata with L.sitkana in these upper intertidal habitats, but decided to concentrate on L.sitkana because its grooved shell made it easier to mark and all life history stages are present on the shore. L.scutulata has planktonic larvae, but L.sitkana lays benthic egg masses that hatch directly into young snails. Therefore, I examined the above three questions for L.sitkana, but only sampled L.scutulata in the two habitats and quantified its survival with tidal height on pebble beaches. The results for L.scutulata are reported in a separate section. Chow (1975) found no conclusive evidence for how size gradients were maintained in Californian populations of L.scutulata; body size increased with tidal height as Vermeij (1972) predicted for high intertidal animals. The only ecological studies done on L.sitkana did not investigate size gradients (Behrens 1971, 1972).

STUDY AREAS

All fieldwork was done in Barkley Sound,B.C.,near the Bamfield Marine Station (Figure 1). Pebble beaches containing *L.sitkana* are found in sheltered inlets. The vertical distribution of the snail extends from about 1.3- 3.0m 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- 3.8m 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 flood the higher horizontal shelves more gently except during severe winter storms. These shelves are dotted with tidepools containing many littorines. Basaltic shelves are more heterogeneous snail habitat than pebble beaches because the tidepools are not always connected by streams. Dry areas that have no snails often separate the tidepools. Also, the direction in which the shelves were first flooded depended upon sea surge, tidal height, and wind direction. The tidepools on most of the high horizontal shelves are irregularly flooded by the summer tides. The tides may not flood them for up to two weeks. If this coincides with warm, dry weather many tidepools dry up and the snails form large aggregations on the shelf. In contrast, most of the snail habitat on pebble beaches is flooded daily by summer tides. In addition, the undersurfaces of pebbles provide a moist microhabitat for the snails. The tides on this part of the

Figure 1. Maps showing location of Bamfield and study sites in the Bamfield area.

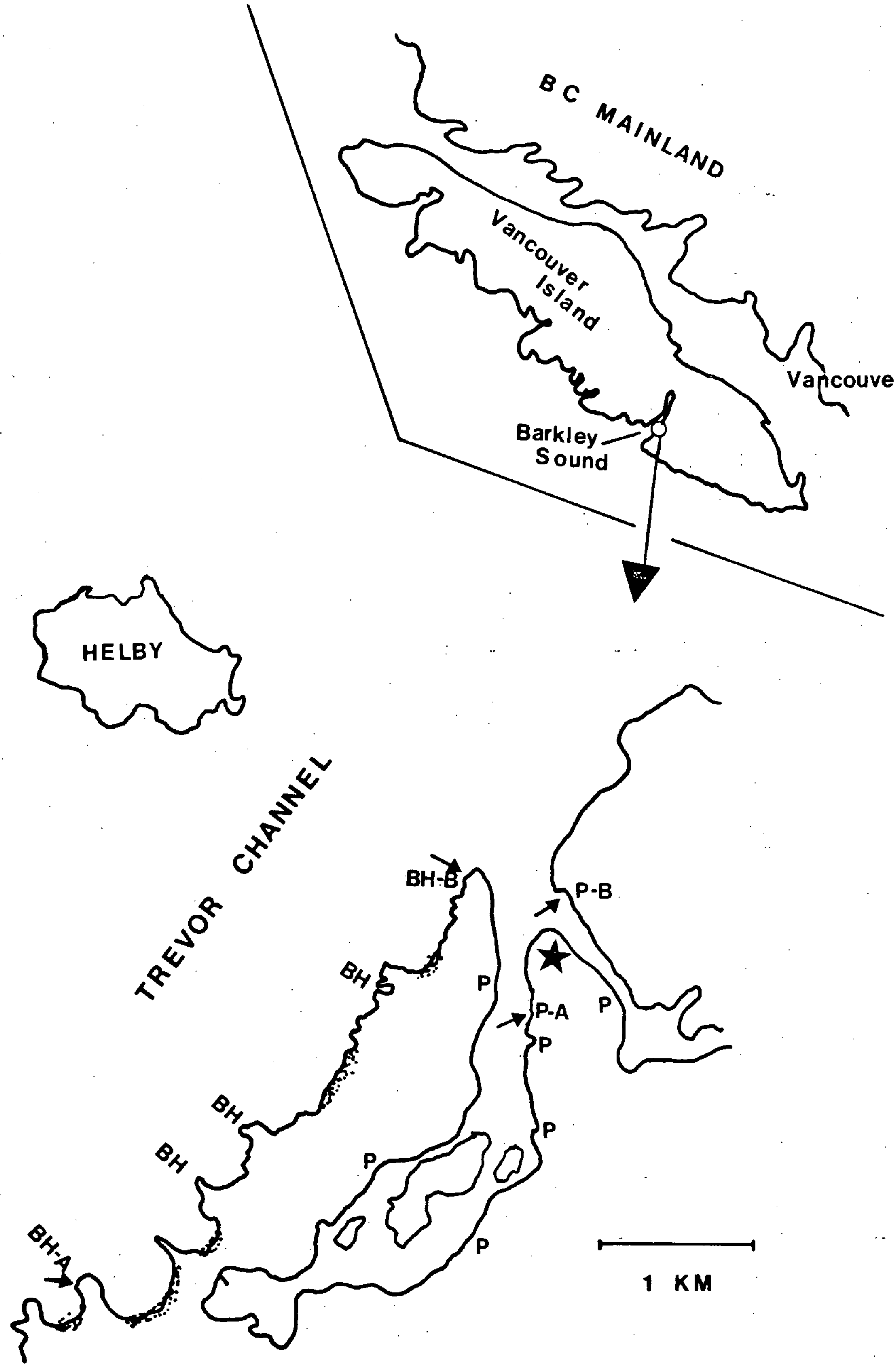
Legend: → study sites

P pebble beaches

BH basaltic headlands

BMS Bamfield Marine Station

(stippled) sandy beaches

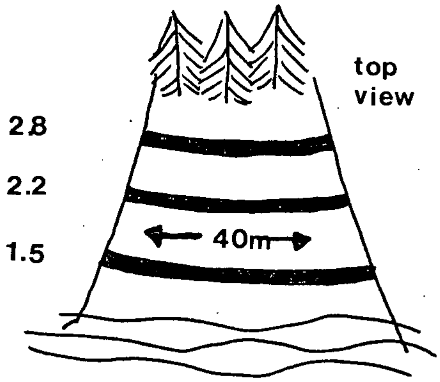

BC MAINLAND
Vancouver Island
Vancouver
Barkley Sound
HELBY
TREVOR CHANNEL
BH-B
BH
BH
BH
BH-A
P-B
P
P-A
P
P
P
P
P
1 KM

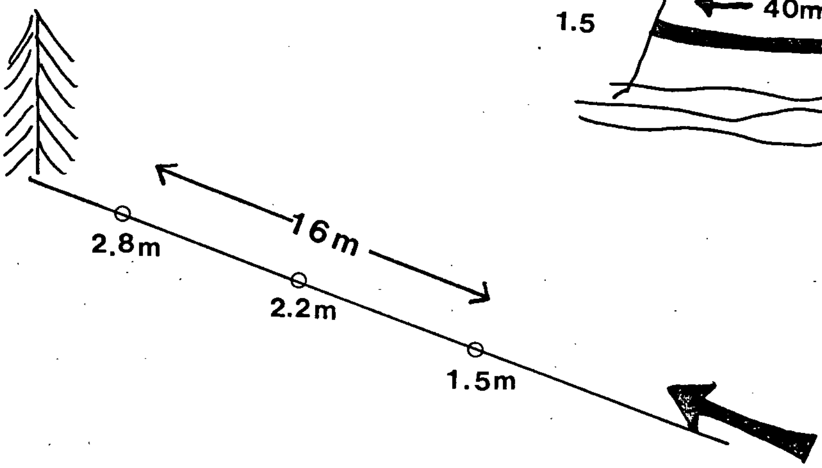
Pacific coast are mixed, mainly semi-diurnal (Canadian Hydrographic Service). In spring and summer the lower low tide occurs during the day and the higher high tide occurs at night. In fall and winter this pattern is reversed. The winter high tides are also higher than the summer high tides. Therefore, basaltic shelves are flooded quite regularly in the winter. In both habitats most snails graze microalgae off the rock surface.

Most experiments on growth, survival, and movement were done on pebble beach A in Bamfield Inlet and basaltic shelf A near Second Beach (Figure 1). However, I did some experiments and sampling on basaltic shelf B at Aguilar Point and pebble beach B in Grappler Inlet. Experiments were conducted at three tidal heights on pebble beaches, and at two tidal heights on basaltic shelves (Figure 2). These stations spanned the vertical distribution of L.sitkana in these two habitats. Unless otherwise stated, 'snails' or 'littorines', always refers to L.sitkana.

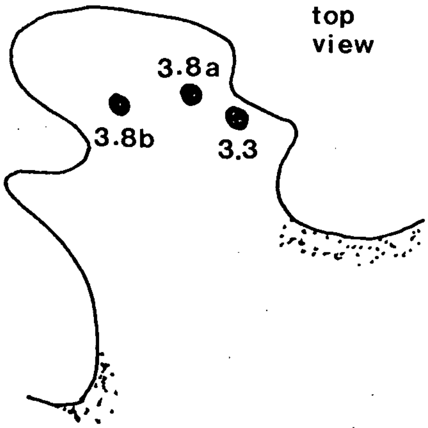
Figure 2. Diagram of the main study sites showing tidal heights and horizontal distances between sampling stations(○). The darkened areas of the top views show approximate areas sampled at each station. Sea access is indicated by the big arrows.

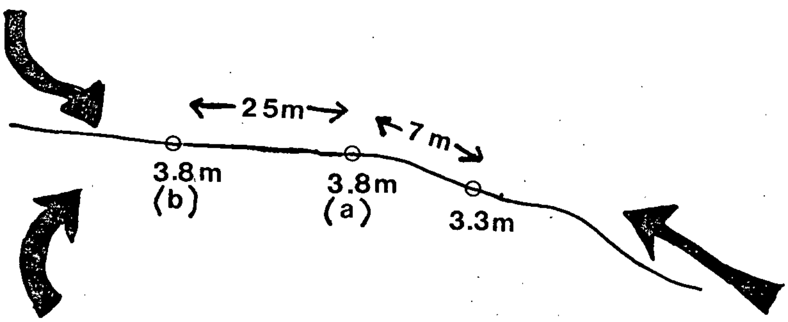
Pebble Beach A





Basaltic Shelf A





METHODS

Table I summarizes how growth, survival, and movement must vary if they produce or contribute to an upshore increase in snail size. I used mark-recapture techniques and controlled transplants to measure the three factors on pebble beaches and basaltic shelves. If any of the factors varied with tidal height, I calculated if the observed differences were sufficient to produce a size gradient. In some cases, I used simulation models to explore the range of differences that were sufficient to affect the size distribution of the population.

Size Distribution

To see if snail size distribution varied with tidal height and season, I sampled the four study sites (Figure 1) every three months. Ten cm^2 quadrats were randomly chosen at each tidal height. The number sampled depended upon the snail density and size distribution at each tidal height. On pebble beach A and basaltic shelf A, as many quadrats were taken as needed to get a representative sample. The replicate habitats, pebble beach B and basaltic shelf B, were not sampled so thoroughly. My measure of snail size was the longest axis of the snail shell. This was measured with vernier calipers.

To see if egg mass distribution varied with tidal height, I also recorded egg mass distribution and abundance on pebble beach A and basaltic shelf A.

Table I. Predictions and tests for the three factors that could cause or contribute to littorine size gradients.

Factors	Predictions if FACTOR contributes to gradients:	TEST: Pebble Beaches	TEST: Basaltic Shelves
1. Growth	rates should be fastest at high tidal levels	measure growth rates of snails enclosed at 3 tidal levels	measure growth rates of snails from high and low tidal levels
2. Survival	rates should be lowest at low tidal levels	transplant large snails to low levels and monitor survival	compare survival of: a)snails marked for growth
		record survival of snails in growth bags	b)large and medium snails transplanted to low levels
3. Movement	large snails should move to high tidal levels	record movements of large snails transplanted to low tidal levels	record movements of transplanted and local snails at low levels.

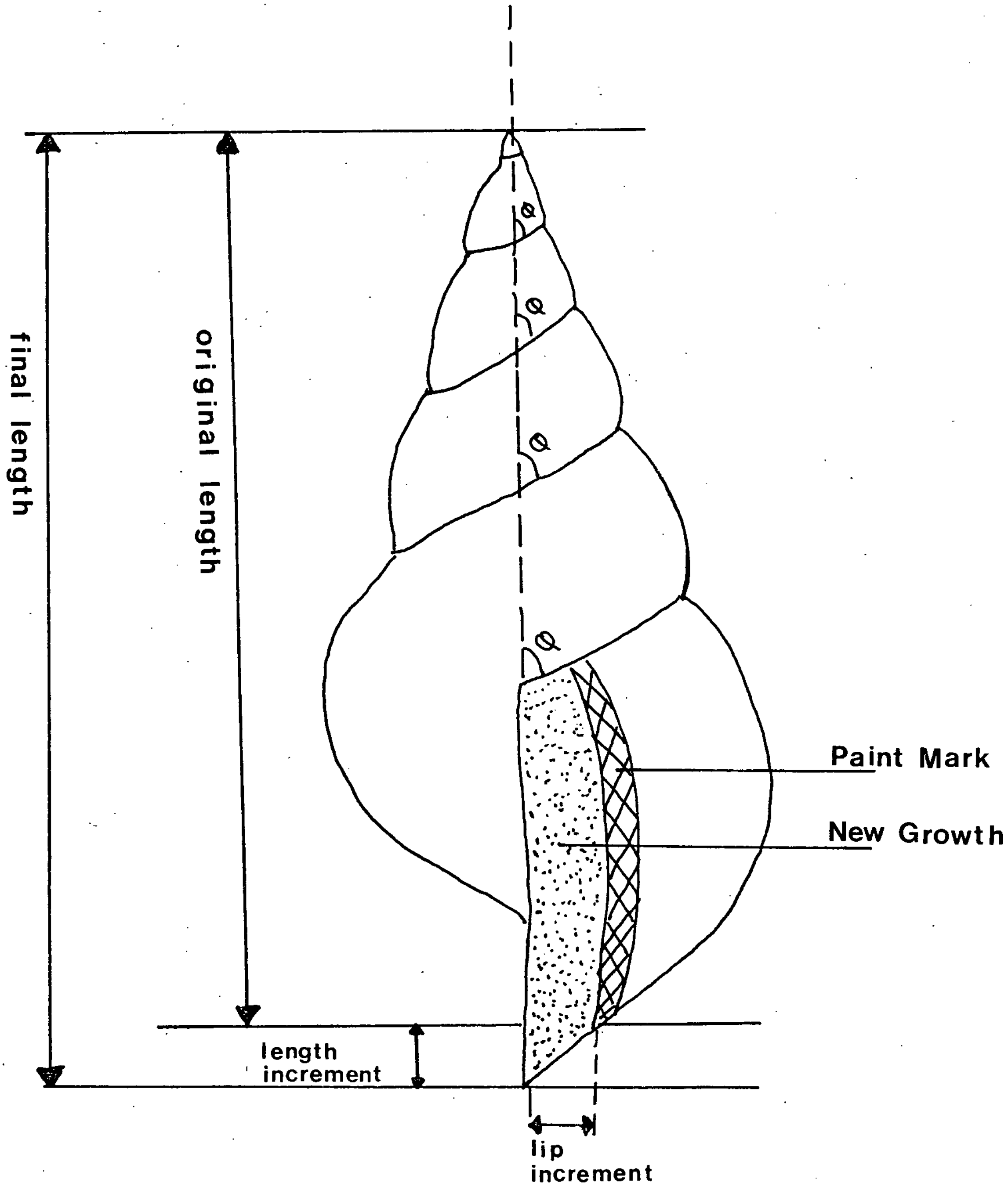
Growth

To measure the variation in growth rates with tidal height, I marked three size classes of snails at the tidal heights on pebble beach A and basaltic shelf A shown in Figure 2. I defined three size classes for all experiments: small (3-4mm), medium (6-7mm), and large (8-11mm). 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 was measured with vernier calipers at weekly to monthly time intervals from May- October 1980. I used lip increment as an index of growth rate. The relationship between lip increment and length increment was calculated by measuring initial shell length, final shell length, and lip increment (Figure 3). This method was used by Behrens (1971).

For all snail sizes and areas, the mean lip increment was calculated for a two month period on pebble beaches (June 15- August 15) and on basaltic shelves (May 15- July 15). Means were tested for differences with paired t-tests for equal but unknown population variances.

On basaltic shelf A , snails were collected, painted, and returned to their original tidepools within 24 hours. The surrounding area was mapped and systematically searched at each visit. On May 13, 80 small and 50 medium snails were painted and returned to a low level tidepool at 3.3m above datum. Fifty small, 50 medium and 50 large were also returned to two high level tidepools (3.8m(a), 3.8m(b)). On May 27, another batch

Figure 3. Diagram of a generalized littorine showing relationship between lip increment (growth index) and shell length increment.


final length
original length
Ø
Ø
Ø
Ø
Paint Mark
New Growth
length increment
lip increment

was collected from the same three tidepools. Fifty medium snails were painted at the low pool, and 50 large and 50 medium snails were painted and returned to the two high pools.

On pebble beaches, small snails were absent at high levels and so were transplanted up from low levels. Large snails were also transplanted down to low levels. 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 (Link Hardware Ltd., Vancouver). Two bags were set up at each of the three tidal heights (1.5, 2.2, 2.8m) on June 11 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. Therefore, bags at low tidal levels contained high densities of snails and high level bags had low densities of snails. I thought my recovery rates of marked small snails might still be poor in the big bags. Therefore, I also set up two small bags (45 by 35 cm) on June 11 at the three tidal heights. The small bags contained only 15 painted small snails each and natural densities of unmarked snails and rocks.

Growth rates were also measured on pebble beach B in Grappler Inlet. Ten medium snails were put in the small bags at the three tidal heights. Three small bags containing ten marked snails, rocks, and unmarked snails were put out at each tidal height on June 17.

Survival

The survival rates of *L.sitkana* could vary with tidal height because of changes in predation or exposure (wave action, desiccation). I measured the survival rates of two groups of marked snails. The first group were snails that were painted and returned to their original tidal level so that their growth rates could be measured. The second group were snails that were transplanted to tidal levels where their size class was rare. If I found differences in survival rates, I then tried to quantify how mortality from predation or exposure varied with tidal height on pebble beaches and basaltic shelves.

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. To stop the snails from dispersing widely, the transplants were put into a 0.8 m^2 aluminum 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 fences 37 m apart at each tidal height. Experiments were carried on from June to August 1980. The design is detailed in the results.

Survivorship of snails in growth bags was also measured.

These measurements gave estimates of survival of all size classes at all tidal levels in the absence of predation.

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.

To find out why the pile perch were regularly visiting this area, I examined the stomach contents of two fish caught in the study area. I also offered the pile perch other potential prey that were common at low tidal levels to see how interested the fish were in pursuing them. I dropped the prey into the water from an anchored boat at high tide and observed the fishes' responses through a viewing box. To see if the pile perch were only attracted to painted snails, I offered the fish both painted and unpainted snails. I recorded the number of live snails and all shell fragments found after one high tide. I used a test for comparing binomial proportions (Walpole and Myers 1972) to see if there was any difference in the proportion found alive in painted and unpainted groups. This test is used in all cases where I am comparing proportions.

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 disappearance rates increased with snail size at the low tidal level, I transplanted large, medium, and small-sized snails from the high shelves to the low pool. On June 26, I transplanted 25 large and 25 small (4-5mm) snails. On August 8, I transplanted an additional 50 large and 50 medium-sized snails to the low pool. The survival rates were recorded at weekly intervals from May to August.

To sort out the effects, if any, of wave action and predation on the disppearance rates of marked snails, I attached large snails to leashes at two low level areas. The leashes should protect the snails from wave action mortality without protecting them from predation. Holes were drilled through the lip of the shell and the snails were attatched to wire bars with one kilogram test nylon monofilament. The bars were cemented to the rock in August 1980 with 'Burke Plug Quick Setting Hydraulic Cement' (Burke Concrete Acces. Inc., 863 Mitten Road, Burlingame, California 94010). 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. If transplanted snails move toward their original tidal levels (homeward), it suggests that the snails are capable of maintaining their preferred position on the shore. To test the hypothesis that snail movement produces size gradients, one would have to follow the movements of small snails and see if they moved to higher tidal levels as they get larger. Transplant experiments are logistically easier and are a good preliminary test because negative results would rule out the possibility that snails can actively select certain tidal heights.

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 4m (a change in tidal height of 0.7m). Small snails were transplanted up the beach 6m (a change in tidal height of 0.8m). Large snails could not be transplanted lower because of heavy loss to predators. To control for the effect of displacement, snails were transplanted laterally (1-5m) 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 hours and 2 high tides later. The area searched was within a 1m 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 the marked snails in the low level tidepool were recorded on four occasions. These marked snails were the large and medium sized snails transplanted there to measure survival and the local snails that were painted to measure growth. A minimum area of 21 m^2 was searched about this low level tidepool. Any snails that had moved 1-2 m down the barnacle slope below the tidepool (a 0.1-0.2 m change in tideheight) 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 tideheight 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 the population varied with tidal height so mean snail size was increasing with tidal height (Figure 4). Sample sizes were small at the high station of pebble beaches, despite sampling twice the area sampled at lower stations. Small snails were always scarce at high tidal levels of 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.

Table II shows that the distribution and abundance of egg masses is correlated with the density of reproductive (>6mm) snails (Spearman's rank correlation =.75, $p<.05$). Egg masses were laid at all levels of basaltic shelf A in the spring. But in October, fall reproduction had only started at 3.8m(b). On pebble beach A, two extra tideheights were sampled to ensure finding the area where most egg masses were laid. Egg masses were never observed at the highest station despite the continual presence of large snails. Nor were they found at the two lowest stations where large snails were very scarce.

Figure 4. Size frequency distributions of L.sitkana sampled in 1980 on main study sites. Sample size is given on each size frequency histogram. Note that larger size classes are absent from low tidal levels of both habitats. Table XIV in Appendix III shows similar trends for populations on Pebble Beach B and Basaltic Shelf B; mean snail size increased with tidal height.

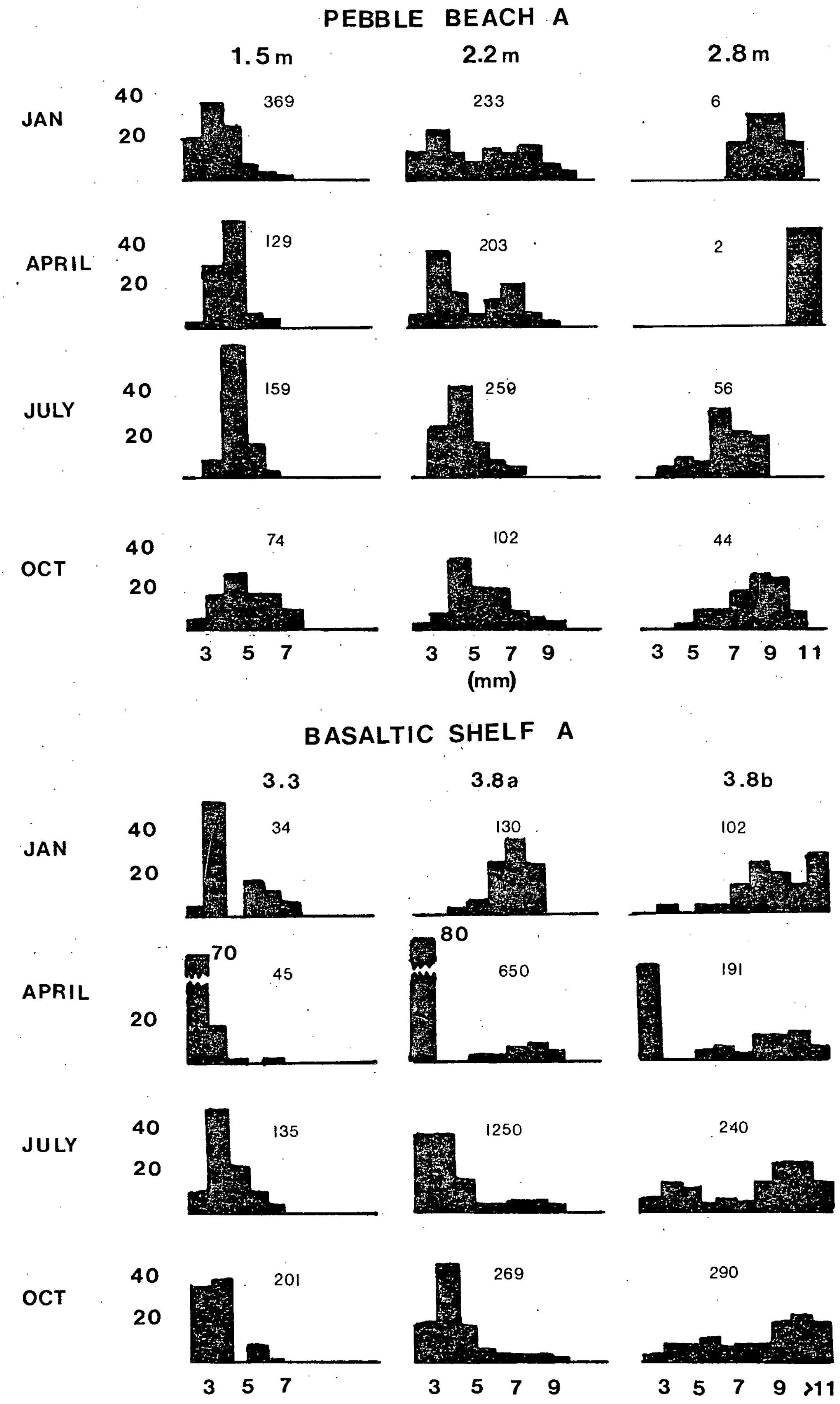

PEBBLE BEACH A
1.5 m
2.2 m
2.8 m
JAN
APRIL
JULY
OCT
40
20
369
233
6
129
203
2
159
259
56
74
102
44
3 5 7
3 5 7 9
3 5 7 9 11
(mm)
BASALTIC SHELF A
3.3
3.8a
3.8b
34
130
102
70
80
45
650
191
135
1250
240
201
269
290
3 5 7
3 5 7 9
3 5 7 9 >11

Table II. Egg mass abundance of *L.sitkana* at different tidal levels. Densities of snails and egg masses are for a 10 cm squared area.

PEBBLE BEACH A

sampling time (1980)	tidal height (m) 1.5	1.7	2.2	2.5	2.8
	Egg Mass density				
Feb.	0	0	4	1	0
April	0	0	1	0	0
July	0	0	0	0	0
Oct.	0	0	0	0	0
April density of snails> 6mm mean (s.d.) in mm.	.1(.5)	2.1(1.6)	9.7(9.5)	3(2.2)	.7(1.2)

BASALTIC SHELF A

sampling time (1980)	tidal height (m) 3.3	3.8a	3.8b
	Egg Mass density		
Feb.	0.5	7.5	4.4
April	0	7.6	5.3
July	0	0	0
Oct.	0	0	2.0
April density of snails> 6mm mean (s.d.) in mm.	.1(.36)	8.2(7.6)	6.2(5.9)

Growth

I measured growth rates of *L.sitkana* at different tidal levels on pebble beaches and basaltic shelves. If variation in growth rates contributes to size gradients, growth rates should be highest at high tidal levels where the snails are largest. Figure 5 summarizes how growth rates vary with tidal height on pebble beaches and basaltic shelves. The plot of lip versus length increment in Appendix II shows how this growth rate index corresponds to changes in shell length.

On pebble beaches, all size classes grew fastest at the low tidal heights. Means from low tidal levels were significantly greater than means from high levels (t-test, $p<.005$). Therefore, variation in growth rates cannot explain why large snails are absent from low levels.

On basaltic shelf A, the littorines at the low station (3.3m) grew slightly faster than the snails at 3.8m(a), but the difference was not significant ($p=.07$). This suggests that variation in growth rates cannot explain why large snails are absent from 3.3m but present at 3.8m(a). Only the growth rates of medium snails are shown in Figure 5 for basaltic shelf A, because large snails were not transplanted to low levels in May to measure growth. Also, my recovery rates of marked small snails were poor at all tidal levels. Snails from some high levels of basaltic shelves grew very fast. For example, the snails at 3.8b grew faster than the snails at 3.8a ($p<.001$).

I conclude that variation in growth rates cannot account for the size gradients found on pebble beaches and basaltic

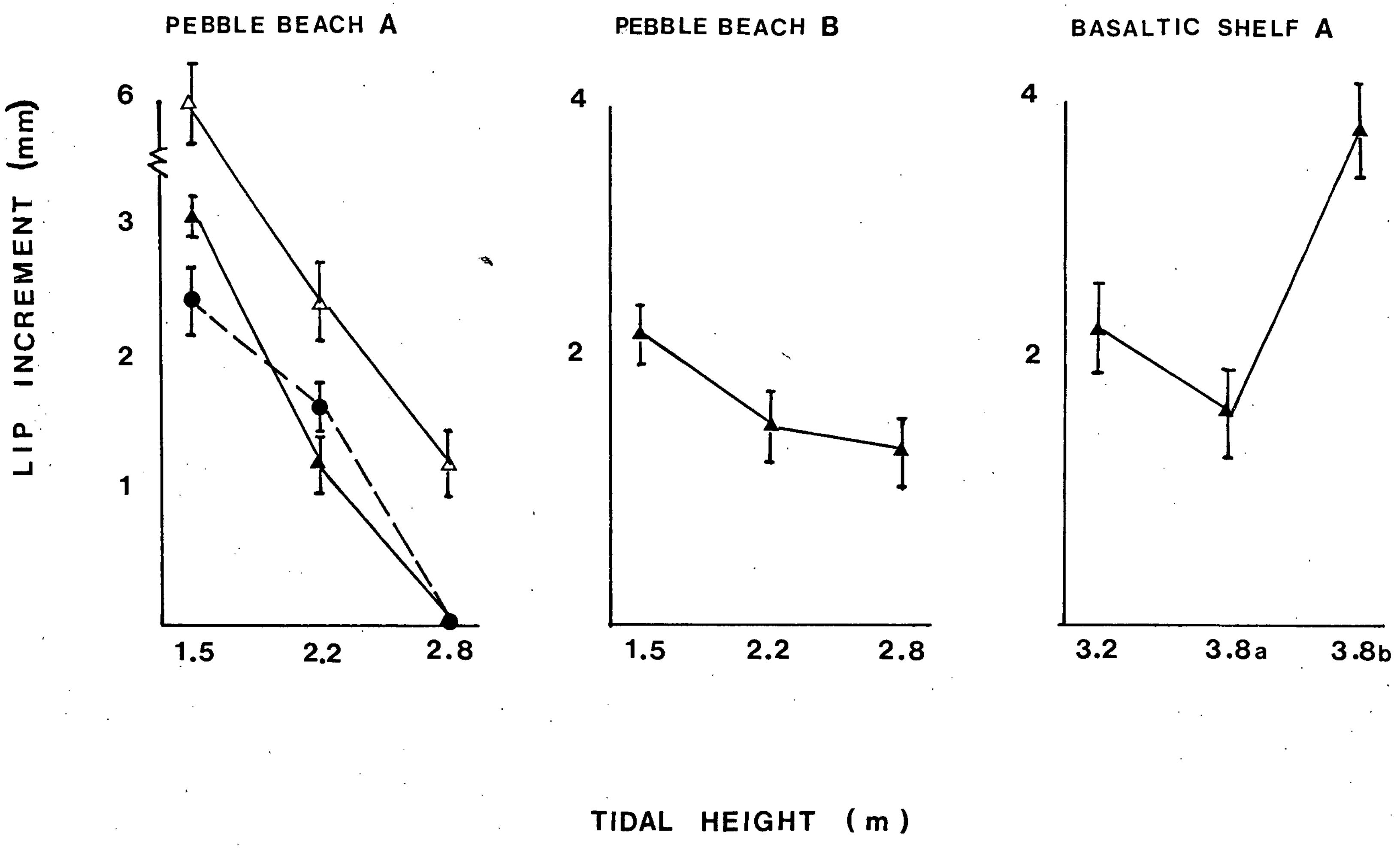
Figure 5. Growth rates of L.sitkana at different tidal levels of Pebble Beach A,B and Basaltic Shelf A. The mean lip increments for two month periods and their standard errors are plotted.

Legend: snail size

△ small

▲ medium

● large


PEBBLE BEACH A
PEBBLE BEACH B
BASALTIC SHELF A
LIP INCREMENT (mm)
6
3
2
1
4
2
4
2
1.5
2.2
2.8
1.5
2.2
2.8
3.2
3.8a
3.8b
TIDAL HEIGHT (m)

shelves. In both habitats snails at low levels (where only small snails are found) grow as fast or faster than snails at high levels (where the largest snails are found).

Survival

Survival on Pebble Beaches

On pebble beaches, large snails were absent from low tidal levels and small snails were absent from high levels. I tested the hypothesis that size selective mortality was causing this gradient by: (1) putting out painted large and medium-sized snails in fences at three tidal heights and recording their survival; (2) enclosing small, medium, and large snails in permascreen bags at three tidal levels and measuring their growth and survival.

1. Predation Experiments

To quantify survival rates of different sized snails, 20 large and 20 medium-sized snails were put inside the snail fences at the three tidal heights on pebble beach A on 6 occasions. At the high station, 414 out of 430 snails were found alive and no snail shell fragments were ever found. Table III 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

Table III. Mean survival of 20 large and 20 medium-size snails after one high tide. The snails were placed in enclosures at 3 tidal heights on 6 occasions. See text for results of high tidal level (2.8m) enclosures.

	tidal height (m)			
	low (1.5)		middle (2.2)	
	snail size		snail size	
	Large	Medium	Large	Medium
mean # alive	9.2	15.2	18.9	19
S.E.	1.1	0.6	0.3	0.3
Total # fragments found	105	31	8	0

=-.90, p<.05).

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<.001). Therefore, survival rate is significantly lower for large snails at the low tidal heights.

To see if, in the absence of large snails, more medium-sized (=M) snails would be eaten, I put out 40 M snails inside the middle and low fences on three occasions. In fact, 89% of the medium-sized snails survived this treatment whereas only 76% survived in the fences containing 20 M and 20 large snails. These proportions were significantly different (test for binomial proportions, p<.001).

These two experiments show that predators preferred large snails and suggest that medium-sized snails were only eaten when the predators were attracted into an area by the presence of large snails.

In all experiments, the high correlation between the number of snails missing and shell fragments found strongly suggests that predation was responsible for the missing snails. I conclude from these experiments that the predation rate is highest on large snails found at low levels of pebble beaches.

Because pile perch were consistently found in pebble beach A at high tide and were observed eating the snails, I believe they were the major predator. Another possible predator is the red rock crab, <u>Cancer productus</u>. It is normally found at lower tidal levels than the littorines. <u>C.productus</u> feeds on other larger gastropods such as <u>Thais</u> spp. (Bertness 1977, Zipser and

Vermeij 1978) that are more abundant below the littorines' distribution.

To see if the predators were eating such a high proportion of the transplanted large littorines only because they were painted, I put out groups of painted and unpainted littorines at low tidal levels on two occasions. Table IV below shows that groups of 25 large unpainted snails disappeared as fast as groups of 25 large painted snails did. There was no difference in the proportions found alive (test for binomial proportions, p=.36). Large numbers of fragments were found in all three low tidal level areas.

Table IV. Numbers of live snails found after one high tide.

	painted	unpainted	unpainted
July 29	4	10	10
July 31	15	5	10

Fish Diet and Feeding Experiments

I examined the diet of the pile perch to see what else they ate on pebble beaches. The stomach contents of two pile perch caught at a low station are shown in Table V. Barnacles and small crabs (mostly *Hemigrapsus* spp.) formed a major part of these fishes' diets. These prey items were commonly found on the pebble beaches between the tidal heights of 1.5 and 2.2 m. Mussels varied in abundance on the pebble beaches studied, but also occurred between the above tidal heights. The fish were

Table V. % Wet weights of stomach contents of two pile perch caught on Pebble Beach A.

	Fish A		Fish B	
	%wet weight	rank	%wet weight	rank
PREY				
mussels	42	1	15	4
crabs	35	2	23	2
barnacles and small bivalves	18	3	44	1
littorines	5	4	18	3
total wet weight (g)	13.5		8.5	
fish length (cm)	20		30	

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.

To see what other potential prey occurred in this zone, I offered the pile perch gastropods whose upper limits begin in this zone. I also offered the fish small crabs and littorines during the same experiment to compare the pile perches' responses. The results are shown in Table VI. While littorines were readily eaten, other larger gastropods were ejected whole almost immediately or were too large to even enter some fishes' mouths. The small crabs dropped into the water attracted the pile perches' attention, but the fish were less successful at catching them (Table VI).

I put out large littorines at low tidal levels of pebble beach B to see if pile perch predation occurred on other pebble beaches. After one high tide, several shell fragments were found. The area was watched for one half hour of the next high tide and pile perch were observed in the area, but none were observed to eat littorines.

Fish Predation Model

Size selective predation by pile perch may be the reason that large littorines are not found at low tidal levels on pebble beaches in Barkley Sound. I made a simulation model to see if the observed predation rates could be sufficient to exclude large snails from low tidal levels. The model allowed

Table VI. Responses of pile perch present on Pebble Beach A to offered live prey.

PREY	offered	RESPONSES ignored	hovered over	ate	ejected whole	fish disappeared
a) gastropods size(mm)*						
sm tegula (9-10)	11			1?	5	5
lg tegula (14-19)	3	1			2	
sm thais (15-19)	6				5	1
lg thais (20-27)	2	1			1	
Searlesia dira (18-20)	6				4	2
littorines (8-11)	15			15		
b) crabs						
lg *H. nudus* (30,30)	3		3			
sm *H. nudus* (15,15)	3		1	2		
sm *H. oregonensis* (15,15)	3		2	1		
Petrolisthes eriomerus (10,10)	1			1		

* for gastropods, size measured was longest axis
for crabs, it was dimensions of carapace
tegula= *Tegula funebralis*
thais= *Thais lamellosa*

me to examine the effects of a few simple assumptions on the survival of large snails. The model was written in Applesoft BASIC and run on an Apple microcomputer. The dynamics of the large size class of the snail population were simulated for a 40m by 4m area. This area is equivalent to the area on pebble beach A where the fish were most active. The model makes the following assumptions:

(1) no littorine movement up to high levels;

(2) the density of large and small snails is similar to that observed at 2.2m above datum on pebble beach A;

(3) the number of young present is directly related to the number of adults. Every year, the number of young is set equal to the number of adults alive;

(4) the fish show a type two functional response to snail density (Holling 1959).

Growth, natural mortality and predation rates were determined from field data and then varied for a range of initial littorine densities.

An outline of the model and results of several simulations are given in Appendix III. Fish predation was sufficient, under a wide range of initial densities and littorine recruitment rates, to eliminate the large snails. Figure 6 plots the results of four simulations which each show the effect of initial littorine density and growth rates on the extinction rates. The rate that small snails grew into large snails had a great effect on when and if extinction occured. The large snail population increased when snail density and growth rates were

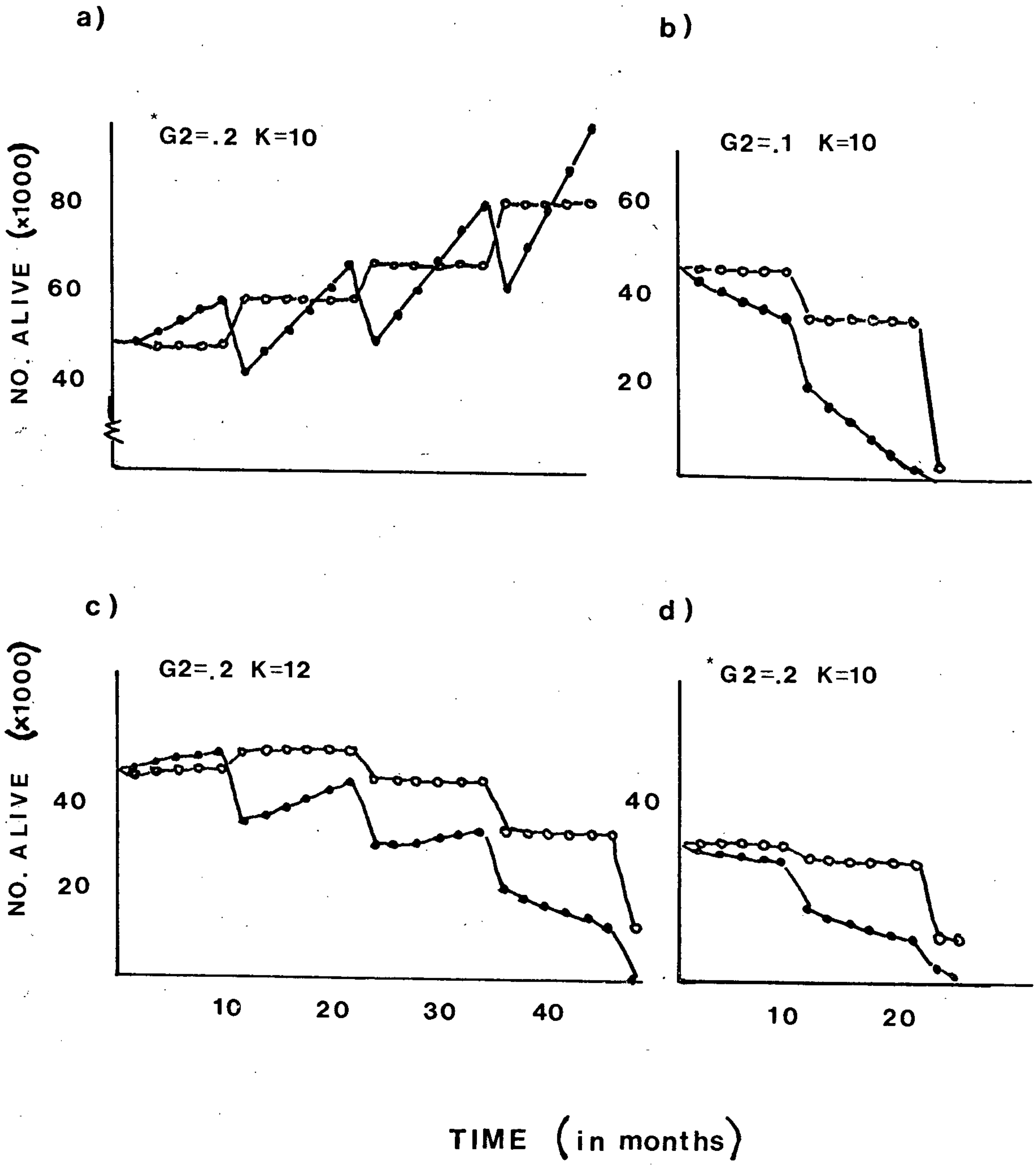
Figure 6. Simulations from fish predation model (outlined in Appendix III) that show effect of snail recruitment and fish predation rates on the survival of large snails. In these examples the initial density of small (D2) and large (D3) snails were 3.0, except in 6d where they were both only 2.0. Fish predation had a much stronger effect on the population at D2=D3=2.0.

Legend: o small (5-7mm) snails

● large (7-11mm) snails

G2=proportion of small snails that grow into large snails

K=maximum number of snails eaten/fish/visit


a)
*G2=.2 K=10
NO. ALIVE (x1000)
80
60
40
b)
G2=.1 K=10
60
40
20
c)
G2=.2 K=12
NO. ALIVE (x1000)
40
20
10
20
30
40
d)
*G2=.2 K=10
40
10
20
TIME (in months)

high and the fish still ate only 10 snails each per visit (Figure 6a). Growth rates in L.sitkana decrease with density (Behrens 1971, author's unpublished data). Therefore, the growth rate-density scenario in Figure 6a is unlikely. Also, my feeding experiments suggest that ten littorines/fish/visit is a conservative estimate in the presence of many large littorines. When the maximum number of snails eaten/fish/visit was increased to 12, the large snail population decreased (Figure 6c). These results strongly suggest that pile perch predation is sufficient to eliminate large snails from low tidal levels of pebble beaches.

2. Survival in Growth Bags

Can poor survival of small snails at high levels, owing to desiccation, be responsible for their absence there? My data do not show decreased survival of young at high tidal levels. For the five month period that I measured growth and survival in the bags, the cumulative percentage of snails found dead at high levels was 6% for small snails and 20% for large and medium-sized snails. However, I think the mortality rates for small snails were underestimated because dead small snail shells were very hard to find. They quickly became covered by the organic and mud matrix. The cumulative percentages of dead large and medium-sized snails were lowest at the low tidal levels (Table VII). This suggests that in the absence of predation, the physical and biotic conditions for growth and survival are best at low tidal levels.

Table VII. Mortality of snails in growth bags put out on Pebble Beach A. The number of dead snails (and total number found) is shown; note the trends in the cumulative percentage of dead snails at different tidal levels.

small snails

	Big Bags tidal height			Small Bags tidal height		
	high	middle	low	high	middle	low
June 26	1(17)	1(39)	0(28)	0(30)	1(25)	3(21)
July 16	2(30)*	0(35)	0(50)*	3(26)	1(28)	1(18)
Aug 12	1(15)	0(30)	0(20)	3(22)	0(23)	2(20)
Oct 27	0(5)	0(15)	0(5)	0(10)	1(20)	2(17)
Cum. freq.	4(64)	1(119)	0(98)	6(88)	3(96)	8(77)
Cum. %	6	0.8	0.0	7	3	10

Big Bags

	medium snails			large snails		
	high	middle	low	high	middle	low
June 26	0(30)	1(54)	0(28)	0(13)	0(28)	0(30)
July 16	10(33)*	0(47)	0(57)*	5(21)	0(28)	0(43)
Aug 12	2(19)	4(44)	1(43)	4(12)	1(27)	0(28)
Oct 27	8(12)	2(30)	2(20)	1(5)	0(21)	2(46)
Cum. freq.	20(94)	7(175)	3(158)	10(51)	1(104)	2(146)
Cum. %	21	4	2	20	1	2

* the total number found increased because only one replicate had been searched on June 26.

Survival on Basaltic Shelves

Are large snails absent from low tidal levels of basaltic shelves because of increased mortality rates at low levels? Figure 7 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. This occurred for the groups of snails released on May 13 (batch A) and on May 27 (batch B). For both batches, the survival curves at the low tidepool are significantly different from the other two (Kolmogorov-Smirnov test, $p<.005$). When large and smaller-sized snails were transplanted to the low station, there was no difference ($p=.5$) in their survival rates (Figure 8). 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 my failure to find the snails. All tidepools were systematically searched and I see no reason for the probability of my finding marked snails to be lower at the low tidepool.

To quantify and compare the survival rates of the snails from the three tidepools of basaltic shelf A, I fitted a negative exponential function to all the survival curves in Figure 7. This function assumes that there is a constant survival rate which is independent of the population size. The proportion surviving is $\exp(-r*t)$, where t is time and r is the mortality parameter. I used a chi-square goodness of fit test to see if this model was a good fit to these data. For the high tidepools, all the survival curves were good fits ($p>.5$) except

Figure 7. Survival rates of batch A and batch B medium-sized snails at the three stations of Basaltic Shelf A. Note that in both cases the survival rate is lowest at the low station.

Legend:

batch A

☆ date released

● 3.3m 31.5*(exp(-.029*t))

○ 3.8a

▲ 3.8b 46.5*(exp(-.016*t))

batch B

☆ date released

● 3.3m 25.7*(exp(-.0137*t))

○ 3.8a 47.0*(exp(-.009*t))

▲ 3.8b 49.0*(exp(-.01*t))

The fitted negative exponential equations are given for the lower station (see Table VIII) and for the other stations where they were a good fit to the data ($p>.5$).

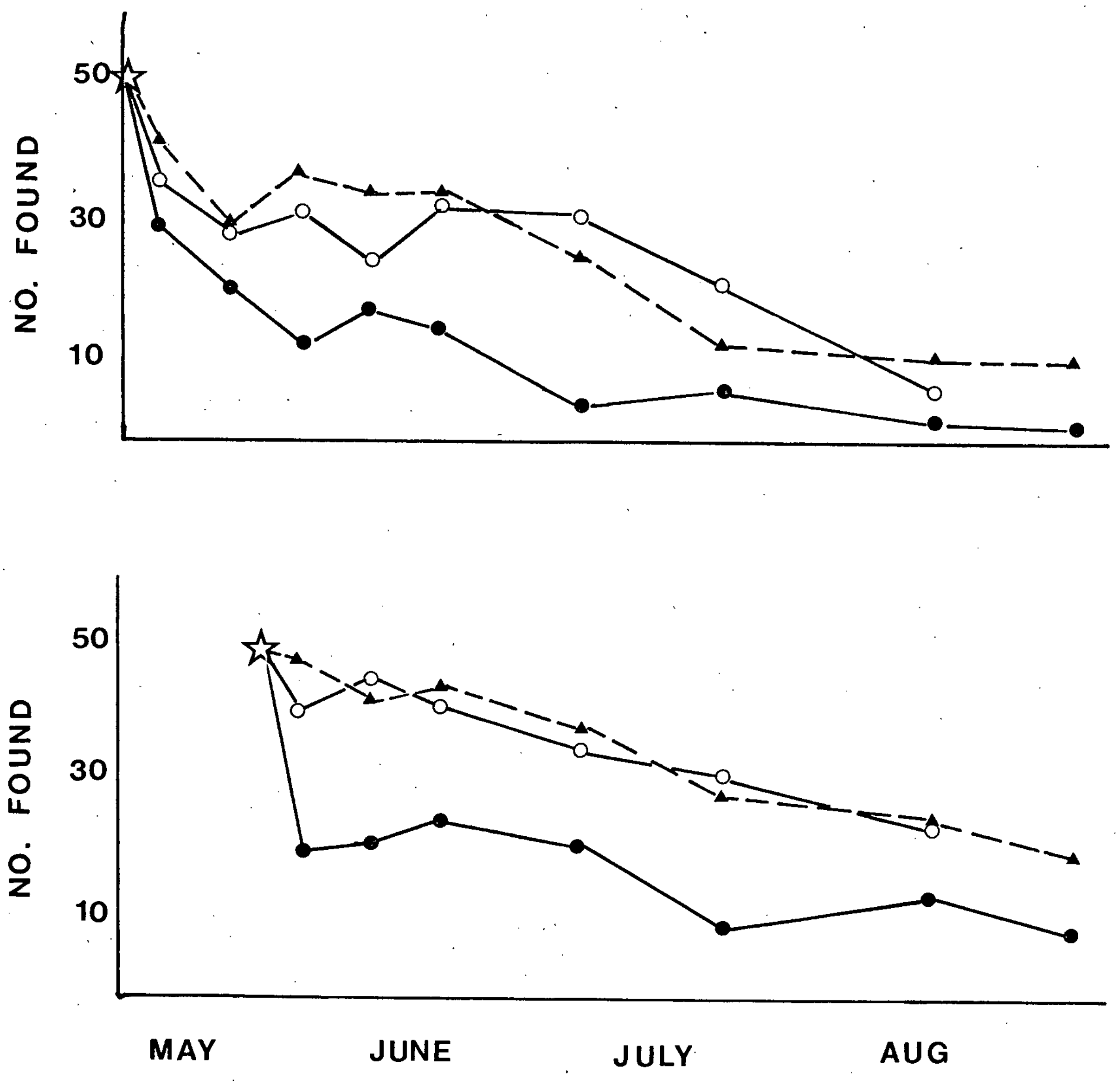

NO. FOUND
50
30
10
NO. FOUND
50
30
10
MAY
JUNE
JULY
AUG

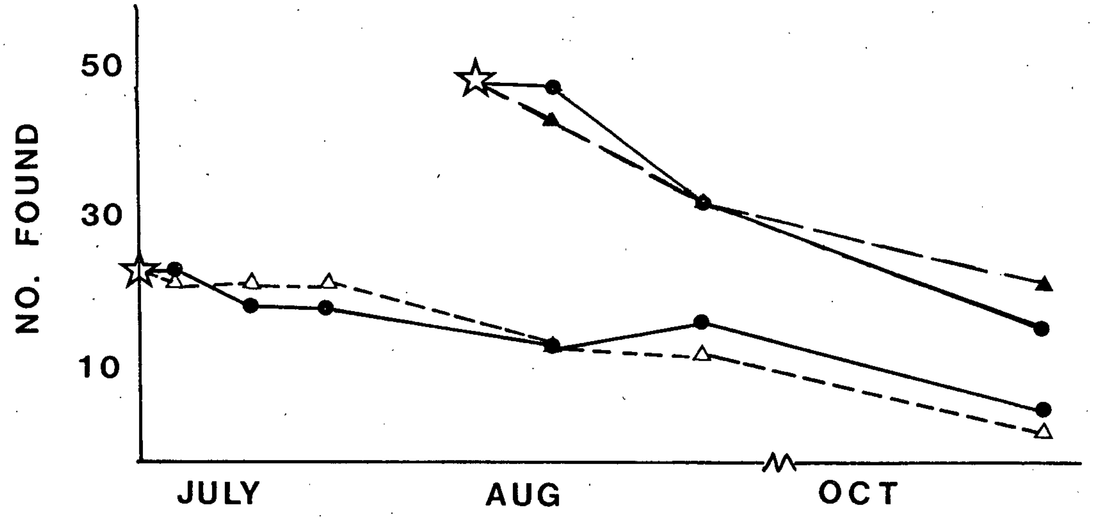
Figure 8. Survival rates of large, medium, and small-sized snails transplanted to the low station (3.3m) of Basaltic Shelf A. Note that the survival rates were unaffected by snail size.

Legend: ☆ date released

● large (9-11mm)

▲ medium (6-7mm)

△ small (4-5mm) -in all other experiments, small= 3-4mm


50
30
10
NO. FOUND
JULY
AUG
OCT

for the batch A 3.8m(a) curve ($p<.05$). In both replicates from the low tidepool, the curves were not a good fit because the predicted initial value underestimated the actual value (Table VIII). This discrepancy occurred because the survival rate was poorest at the low tidepool for the first sampling period. This suggests that the snails at the low tidepool were more affected by being painted and displaced than were snails from the high tidepools. The disturbance may have made the snails from low areas more vulnerable to wave action. This effect would be strongest during the first high tides after they had been returned to their home tidepool.

The r values of the equations shown in Figure 7 predict that for the batch A snails, the percentage of snails recaptured 60 days after tagging would be 17% at the low area and 38% at the high areas. For the batch B snails, 43% would survive at the low area and 58% would survive at the high area. Is this difference in survival rates sufficient to explain why there are no large snails found at low levels of basaltic shelves? To answer this question, I did another simulation model which is outlined in Appendix III. The dynamics of a large size class (6-8mm) was simulated for a $6m^2$ area. Every two months, a certain proportion of the small size class (4-6mm) grew into the large size class. This rate was calculated from the observed proportions of these size classes in the population and their observed growth rates. Also, a proportion $(1-\exp(-r*t))$ was lost every two months. The results of several simulations are given in Appendix III, and Figure 9 shows the

Table VIII. Observed numbers of snails recovered at low tidal levels of Basaltic Shelf A and numbers of snails predicted from fitted equations.

<u>Batch A snails</u>

31.5*exp(-.029*t)

Time	obs	exp	(obs-exp)/exp
0	50	31.5	10.9
4	30	28	.14
10	21	23.5	.26
17	13	19.2	2.0
24	18	15.6	.37
31	15	12.7	.42
45	4	8.5	2.3
63	7	5	.8
86	3	2.5	.1
99	1	1	0

<u>Batch B snails</u>

25.7*exp(-.0137*t)

Time	obs	exp	(obs-exp)/exp
0	50	25.7	22.9
3	20	24.6	.86
10	22	22.4	.01
17	25	20.4	1.04
30	22	17	1.47
49	9	13.1	1.28
73	14	9.5	2.2
87	9	7.8	1.8

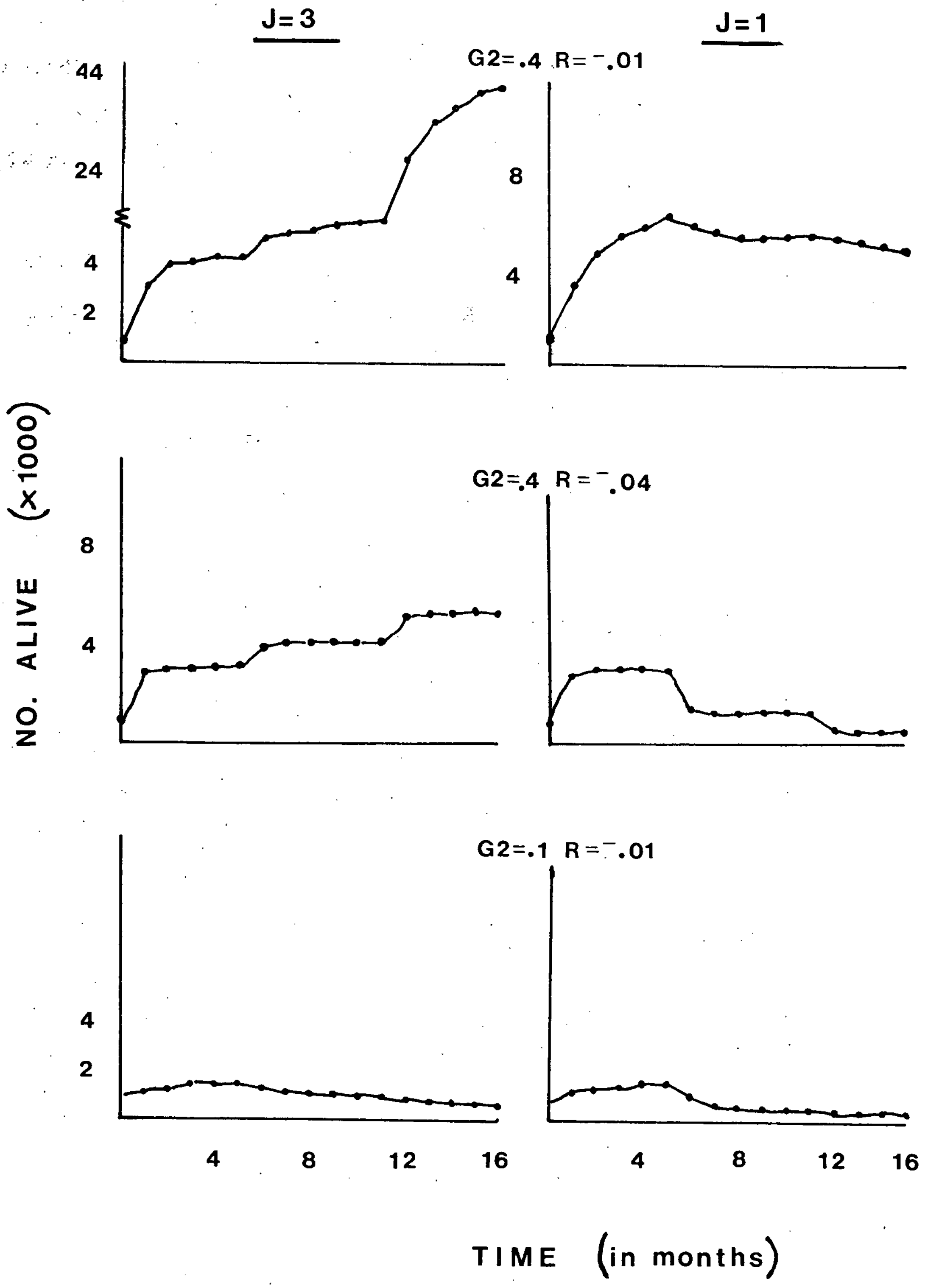
Note that except for the initial values, the equations provide good predictions of the numbers of snails found at all other sampling periods.
Ignoring the initial values, for batch A, $p>.5$
for batch B, $p>.1$

Figure 9. Simulations from basaltic shelf model that show effect of survival rate and recruitment rate of large snails on their survival at low tidal levels. Note the effect of birth rate (J=1,3) on the survival of large snails. In these simulations, D2=2, D3=.25. The model is outlined in Appendix III.

Legend: G2= proportion of small snails that grow into large snails

R = r value in exponential equation

J; every year, #small= J*(#large)



J=3
J=1
G2=.4 R=⁻.01
G2=.4 R=⁻.04
G2=.1 R=⁻.01
NO. ALIVE (×1000)
44
24
4
2
8
4
8
4
4
2
4
8
12
16
4
8
12
16
TIME (in months)

effects of snail growth and survival rates on the large sized snail population. Large snails survived under all conditions, but at much lower densities when snail growth and survival rates were low (Table XVIII). However, it seems that the lower survival rates observed in the field at the low station are not sufficient, under the conditions of the model, to account for the absence of large littorines.

To separate wave action mortality from predation, I put out 60 large snails on leashes that were attached to cemented bars. The results are summarized in Table IX. Seven of the 12 bars disappeared in two months. This shows 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 snails that were completely wrapped around the bar may have been victims of wave action. Snails missing could have been eaten or could have escaped from their leashes. After two weeks, there were 11/50 (equal to an instantaneous mortality rate of -.018) possible victims of wave action and only 5/50 (r=-.007) snails were missing. This experiment suggests that 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 wave action is responsible for poor survival of snails at low levels of basaltic shelves. I do not expect mortality from wave action to be constant. It

Table IX. Fates of 60 leashed snails put out at low tidal levels of Basaltic Shelf A on August 2,1980.

	date checked	
	August 18	October 27
FATES	Number of snails	Numbers of snails
still on leash	34	2
wrapped around bar		
-alive	8	5
-dead	3	6
snails missing	5	9
snails attached to missing bars	10	20
	60	42

should vary with tidal height, sea surge, and season. Survival rates should be lower in the winter when there are more storms. This could explain why my observed summer survival rates of marked snails were not sufficient to explain the absence of large snails from low levels of basaltic shelves.

I conclude that survival is higher at high tidal levels than at low levels on basaltic shelves. Therefore, survival is an important mechanism affecting the snail size gradients on both basaltic shelves and pebble beaches. Reduced survival at low levels is probably due to predation on pebble beaches, and wave action on basaltic shelves.

Movement

Pebble Beach Experiments

The movement experiments on pebble beach A tested if transplanted snails could move homeward. Large snails transplanted downwards showed significant movement up. The snails that were transplanted laterally to serve as controls showed no preferred direction of movement. The results are summarized in Table X and sample data sets are shown in Figure 10.

Small snails transplanted upwards showed strong directional movement down. However, the behaviour of the controls was not clearcut. The positions of the snails in 3 of 6 controls were randomly distributed. The remaining three controls showed significant movement up, but showed more

Table X. Results of Rayleigh test on positions of snails 24 hours after release from origin on Pebble Beach A. The null hypothesis for the Rayleigh test is that the distributions of positions are uniform or random. The alternate hypothesis is that there is a preferred direction of movement (in this example, up or down).

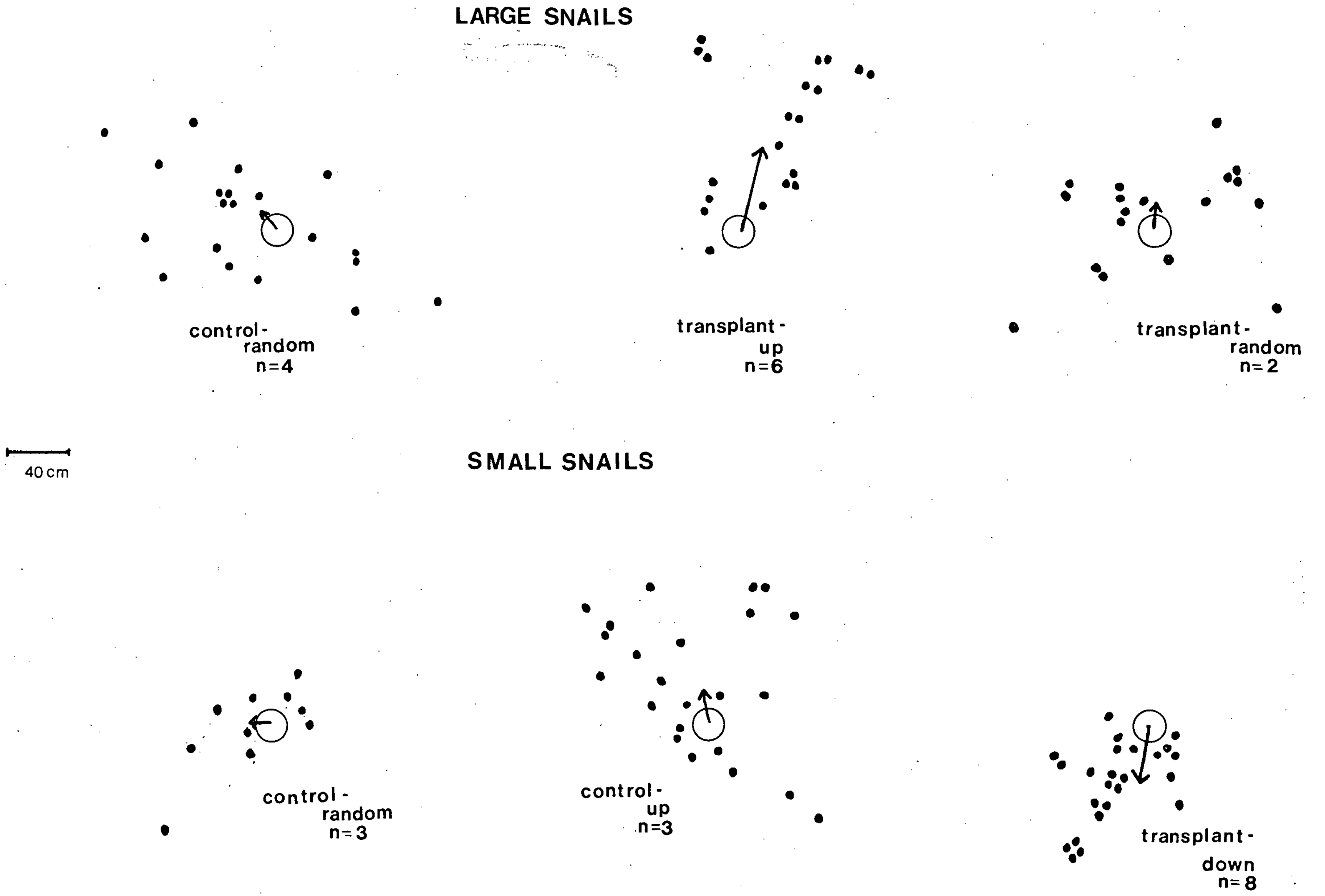
	Large Snails		Small snails	
	controls	transplants	controls	transplants
# of replicates	4	8	6	9
direction moved				
-random	4	2	3	1
-up	0	6	3	0
-down	0	0	0	8
mean vertical distance moved(cm)	-1	43.5	20.5	-22.6
s.e.	9.7	3.5	5.1	3.7

Table X b. Mean angular deviations of the mean direction vectors expressed in degrees; the number of vectors is in parentheses. Angular deviation is the circular analog of standard deviation (Batschelet 1965).

	Large snails	Small snails
controls		
-random	68 (4)	66 (3)
-up	(0)	54 (3)
transplants		
-random	66 (2)	67 (1)
-up	37*(6)	(0)
-down	(0)	37*(8)

* Note that the values are smallest for the vectors of transplanted snails that moved homeward.

Figure 10. Representative scatter diagrams and mean vectors of positions of large and small snails 24 hours after release on Pebble Beach A.


LARGE SNAILS
control-
random
n=4
transplant-
up
n=6
transplant-
random
n=2
40 cm
SMALL SNAILS
control-
random
n=3
control-
up
n=3
transplant-
down
n=8

scatter about the mean direction than the transplants did (Table Xb and Figure 10). Therefore, the transplants showed stronger directional movement than the controls.

The results demonstrate that transplanted snails show strong directional movement homeward. Movement could be contributing to the size gradient pattern on pebble beaches.

Movement on Basaltic Shelves

As littorines become larger, do they move up from low levels of basaltic shelves? This scenario is not supported by the movements of the snails marked at the low tidepool of basaltic shelf A to measure survival and growth (Table XI). There was limited movement both up and down from the low tidepool. The snails painted in May to measure growth, showed a tendency to move down. For example, 22 of the 81 recaptured medium snails moved down, but only 2 moved up. The transplanted snails did not show any marked differences. For example, 9 of the 117 large transplants moved up, but 8 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.

Littorina sitkana populations, studied on basaltic shelves and pebble beaches, showed similar within-habitat variation in survival and growth. However, only on pebble beaches did transplanted snails show strong directional movement homeward.

Table XI. Positions of marked snails released at the low tidepool of Basaltic Shelf A.

Growth Snails

released:	May 13 (batch A) 80small, 50 medium				May 27 (batch B) 50 medium			
date checked	size	#found	#up	#down	size	#found	#up	#down
May 23	s	34	1	3				
	m	21	1	4				
May 30	s	14	0	2				
	m	13	1	4	m	20	0	1
Aug 8	s	1	0	1				
	m	3	0	0	m	14	0	9
Aug 20	s	1	0	1				
	m	1	0	0	m	9	0	4
Totals	s	50	1	7				
	m	38	2	8	m	43	0	14

Transplant Snails

released:	June 26: 25 large, 25 medium				August 2: 50 large, 50 medium			
date checked	size	#found	#up	#down	size	#found	#up	#down
Aug 8	m	16	0	0	m	45	1	1
	l	15	1	0	l	49	2	3
Aug 20	m	14	3	0	m	34	2	2
	l	19	4	0	l	34	2	5
Totals	m	30	3	0	m	79	3	3
	l	34	5	0	l	83	4	8

Littorina scutulata

Littorina scutulata was found with *L.sitkana* on pebble beaches and basaltic shelves in Barkley Sound. I concentrated my field efforts on *L.sitkana* because it is easier to mark and all life history stages are present on the shore. *L.scutulata* showed similar size gradient patterns to *L.sitkana*. In both habitats, snail size increased with tidal height and the largest snails were found at high levels of basaltic shelves (Figure 11). Both species were collected together in the quadrats sampled. Since I was primarily interested in *L.sitkana*, I did not increase sample size where the density of *L.sitkana* was high but the density of *L.scutulata* was low.

To see if *L.scutulata* was also vulnerable to pile perch predation at low tidal levels of pebble beaches, I put out 20 large *L.scutulata* and 20 large *L.sitkana* in the fences on pebble beach A. Table XII shows that both snail species had low survival rates at low tidal levels. A two way ANOVA showed no species preference ($p>.75$) but again showed significant differences between tidal heights ($p<.001$).

Both species may have no large individuals on low levels of pebble beaches because of fish predation.

Figure 11. Size frequency distributions of L.scutulata sampled in 1980 on main study sites. Sample size is given on each size frequency histogram. Note that in both habitats, the largest size classes are present only at high tidal levels. Table XIV in Appendix III shows similar trends for Pebble Beach B and Basaltic Shelf B; mean snail size incresed with tidal height.

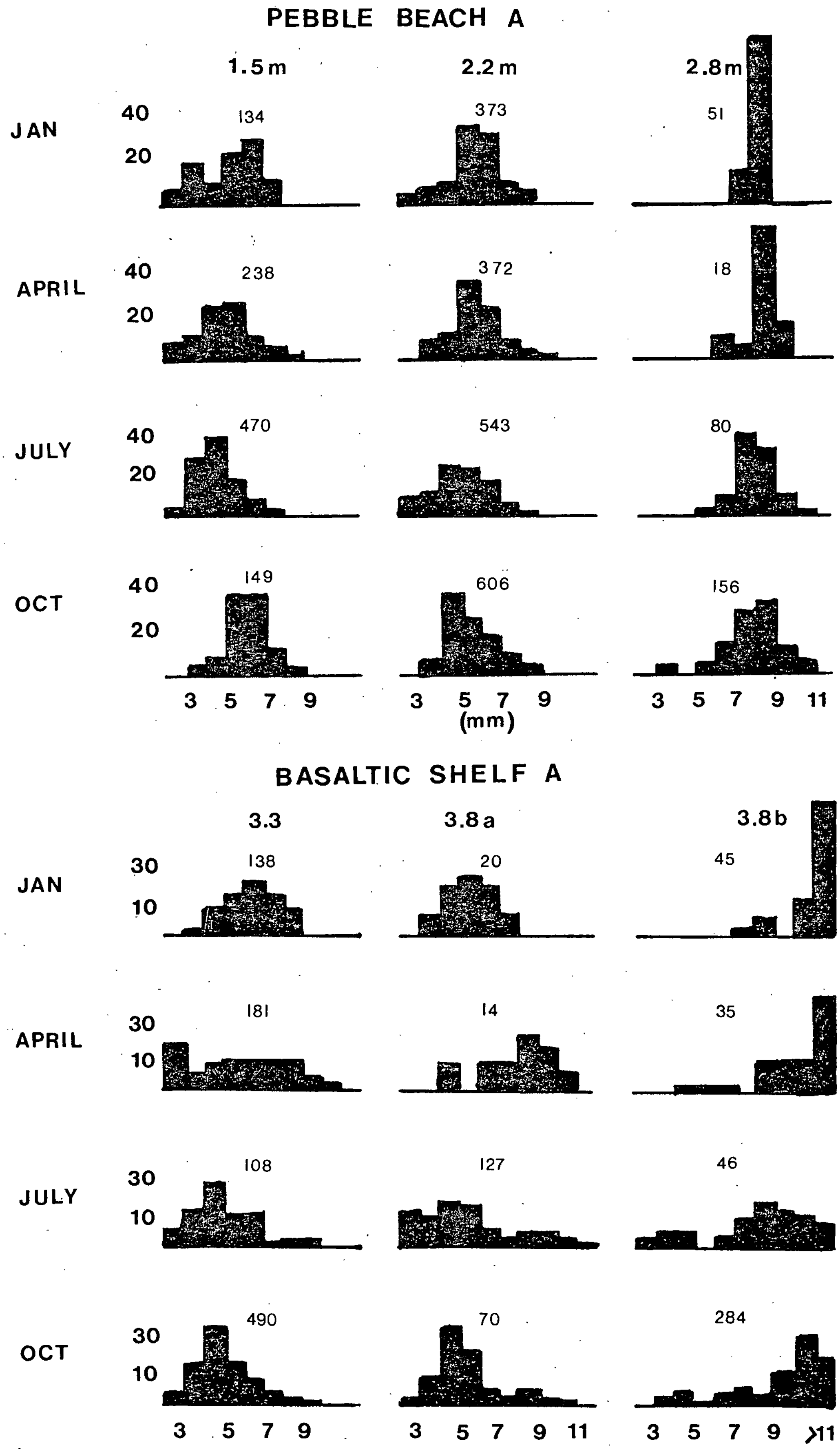

PEBBLE BEACH A
1.5m
2.2m
2.8m
JAN
APRIL
JULY
OCT
40
20
134
373
51
238
372
18
470
543
80
149
606
156
3 5 7 9
3 5 7 9
(mm)
3 5 7 9 11
BASALTIC SHELF A
3.3
3.8a
3.8b
30
10
138
20
45
181
14
35
108
127
46
490
70
284
3 5 7 9
3 5 7 9 11
3 5 7 9 >11

Table XII. Mean survival of 20 large *L.sitkana* and 20 large *L.scutulata* after one high tide. The snails were placed in enclosures at two tidal levels on four occasions.

	tidal height (m)			
	low (1.5)		middle (2.2)	
	snail species		snail species	
	L.sitkana	*L.scutulata*	*L.sitkana*	*L.scutulata*
mean # alive	11.3	12.4	19.0	19.4
s.e.	1.6	0.9	0.3	0.2
total # fragments found	44	35	2	1

DISCUSSION

Table XIII summarizes the size gradient patterns observed in L.sitkana, and the way that growth, survival and movement varied with tidal height. It is clear that size gradients cannot be maintained by variation in 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 helps to maintain size gradients on pebble beaches, but not on basaltic shelves. I will discuss how size gradients are maintained in each habitat and then compare the littorines in the two habitats with each other and with studies on size gradients in other intertidal animals.

Pebble Beaches

On pebble beaches, large snails are absent from low tidal levels and small snails are absent from high tidal levels. My predation and movement experiments strongly suggest that large snails are absent from low levels because of size selective predation and snail movement. The fish predation model showed that predation alone is sufficient to account for the absence of large snails from low tidal levels (Figure 6, Appendix III).

Pile perch ate both large L.sitkana and L.scutulata that were transplanted to low levels. The fish showed no species preference (Table XII). Although the model of fish predation included only L.sitkana, the high density simulations could have described predation on both littorine species. In addition, work by Behrens (1971) suggests that L.scutulata

Table XIII. Summary of size gradient patterns and results of experiments.

PEBBLE BEACHES

tidal height	size classes present	results of experiments*	
		Growth	Predation
high	large	poor	very low
middle	all	good	low
low	small	very good	high

* movement- transplanted snails moved homeward

BASALTIC SHELVES

tidal height	size classes present	results of experiments*		
		Growth	Survival	Wave Action
high	all	very good	high	low
low	small	very good	low	high

* movement- transplanted and local snails showed little upward movement

grows slower and lives longer than L.sitkana. Using growth and recruitment rates for L.sitkana would overestimate the resilience of the L.scutulata population to predation. Therefore, I believe that pile perch predation at low tidal levels can explain the low abundance of large individuals of both littorine species for the following reasons:

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.

This situation is similar to the predator-prey system studied by Connell (1970). At low tidal levels, every barnacle was eaten within two years of settling in the study area. The predators (six species of Thais) preferred large barnacles and had many alternate prey. They did not eat many barnacles at high levels because the submergence period was too short for them to attack and eat a barnacle. The size gradients observed in these barnacle populations were also maintained by size selective predation at low tidal levels. Pile perch may not feed at high tidal levels because the water levels are too shallow for them to enter and there are fewer alternative prey available.

Small snails 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 not high (Table VII). Most egg masses were observed at middle tidal levels of pebble beaches (Table II). They were concentrated in damp areas. Perhaps conditions at high tidal levels are not suitable for egg mass survival. This hypothesis could easily be tested experimentally since egg masses are found on the undersurface of rocks. The rocks could be transplanted to high and low levels and egg mass survival recorded. Small snails may avoid moving up to high areas because growth conditions are poor. Slow growth rates could lower the reproductive output of snails if fecundity is directly related to snail size, as in Littorina planaxis (Schmitt, 1974).

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 (Figure 6). Also, survival of large and medium-sized snails was lowest in the high tidal level growth bags (Table VII). These results seem to negate any possible ameliorative effects 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 (Figure 5) and survival (Tables III,VII). The bulk of egg masses were laid at this level. Yet there were many small snails found at low tidal levels. This suggests that egg mass and juvenile survival is highest at low tidal levels and/or juveniles migrate down to low tidal levels. I found no marked differences in juvenile survival at low and middle tidal heights (Table VII). Because few egg masses were found at low tidal heights, I suspect the high density of juveniles at low tidal levels is caused by juveniles migrating down to low tidal levels.

The movement experiments show that snails can move homeward when dislodged. However, they 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. To differentiate between these alternatives, large and small snails from middle heights could be dislodged both up and down the beach. If the snails are just habituated to a certain tidal height, I would expect no difference in the strength of response between snails transplanted down and up from the release point. If, on the basis of their size, snails are selecting tidal heights I predict:

1. Large snails transplanted down should show stronger homeward movement than large snails transplanted up to high levels;

2. Small snails transplanted up should show stronger homeward movement than small snails transplanted down to low levels.

Despite the alternate explanation for my transplanted snails moving homeward, I think the littorines are selecting a tidal height on the basis of their size. All snail sizes and egg masses are only found together at middle tidal levels. Small snails are found at middle and low levels, but are absent from high levels. They may avoid high levels because of poor growth conditions. Large snails are found at middle and high tidal levels and may avoid low levels because of predation. 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.

Fish predation was an unexpected structuring agent on the pebble beaches that I studied. The role of fish in structuring temperate intertidal communities should be more thoroughly investigated. For example, in watching the low tidal level station of pebble beach A throughout submergence, I noted that most *Hemigrapsus oregonensis* and *H. nudus* were active when the water levels were too shallow for the fish to enter, that is, when the tide was just flooding and receding. Fish predation may be one factor influencing the activity patterns of these crabs. Also, Reimchen (1979) found that the blenny, *Blennius pholis*, selectively altered color morph frequencies in British populations of *Littorina mariae*.

Basaltic Shelves

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 (Figure 5) and movement (Table XI) cannot explain this pattern. Survival varied with tidal level in the predicted direction (Figure 7). Reduced survival at low levels could be due to predation or wave action.

Possible predators include starfish, fish, and shorebirds. The starfish, Pisaster ochraceus, is common on the mussel zone of basaltic headlands. The mussel zone is below the shoreward extension of the littorines. Menge (1972) found that littorines were a small component of the diet of this starfish. I never observed any P.ochraceus feeding in the study area. Large pile perch may feed in these exposed areas on the mussel beds. It is doubtful that they would venture up higher to the wave break zone to visit a less abundant food source. Also, if they did visit this area, I would expect the loss rate of large leashed snails to be much higher (Table IX). 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. Smith (1952) sampled these shorebirds in areas where L.scutulata was present and found this littorine in birds' diets. Feeding studies of related British shorebirds have shown that they may eat small (<5mm) littorines (Pettitt 1975). Shorebirds may have a seasonal and local impact on low level snail populations. But bird predation alone cannot explain the large scale absence (personal observation) of large snails from low levels of all basaltic shelves.

However, waves do affect the low tidal levels of all basaltic shelves. The high levels are spared most of the wave force except during severe winter storms. Many 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 this effect 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).

In this study, large and smaller-sized snails disappeared at similar rates (Figure 8). Either wave action was not size selective or the smallest snails transplanted (4-5 mm) were above the safe size threshold. The mark-recapture and leash experiments suggest that movement and predation were not responsible for the reduced survival rates at low tidal levels of basaltic shelf A. However, repetition of all the above experiments under a variety of weather conditions is needed to draw firmer conclusions.

On high tidal levels 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.

General Discussion

The size distribution of L.sitkana at low tidal levels 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. The hypothesis proposed by Vermeij (1972) that juvenile mortality drives size gradients is not supported by this study. The common feature of littorine size gradients in the two habitats studied is the selective distribution of adults. On basaltic shelves, egg masses and young were found at all tidal levels (Table II, Figure 4). But on pebble beaches, egg masses and young were absent from high tidal levels. Certainly, juvenile survival may contribute to these size gradients and remains a likely hypothesis for why both young L.sitkana and L.scutulata were absent from high levels of pebble beaches (Figures 3,12). Vermeij's synthesis of the literature and hypothesis have stimulated research on how and why size gradients are maintained. Recent studies have not found juvenile survival to be important in maintaining size gradients (Bertness 1977, Butler 1979, Raffaelli and Hughes 1978, Markowitz 1980). Paine (1969) and Markowitz (1980) have looked at why size gradients occur in Tegula funebralis. But the mechanism of how they are maintained is still not clear. Butler (1979) proposed a model for how size gradients are maintained in several species of Thais, but it has yet to be tested. He found that he could not repeat the results of Bertness (1977). Before we can propose a robust theory for why size gradients exist, we must know how they are maintained.

Several studies cited previously (Connell 1970, James 1968, Heller 1976, Kitching et al. 1959, Struhsaker 1968) and the present study suggest that the major factor maintaining size gradients in upper shore animals is poor survival at low tidal heights. Furthermore, they suggest that the the major mortality factor is predation in sheltered habitats and wave action in exposed habitats. Many other studies have shown that the effect of intertidal predators on their prey is much less on wave exposed areas than on sheltered habitats (e.g. Connell 1972, Hughes and Elner 1979, Menge 1978a,b). More work needs to be done on how size gradients are maintained in lower shore gastropods. It would be interesting to compare the factors that maintain size gradients in herbivorous and predatory gastropods.

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APPENDIX

Appendix I. Summary of mean snail sizes of *L.sitkana* and *L.scutulata* sampled in replicate pebble beach and basaltic shelf habitats is shown in Table XIV.

Appendix II. Relationship between lip and length increment in *L.sitkana* is shown in Figure 12.

Table XIV. Summary of mean snail sizes in replicate habitats. Means are in mm and sample sizes are in parentheses.

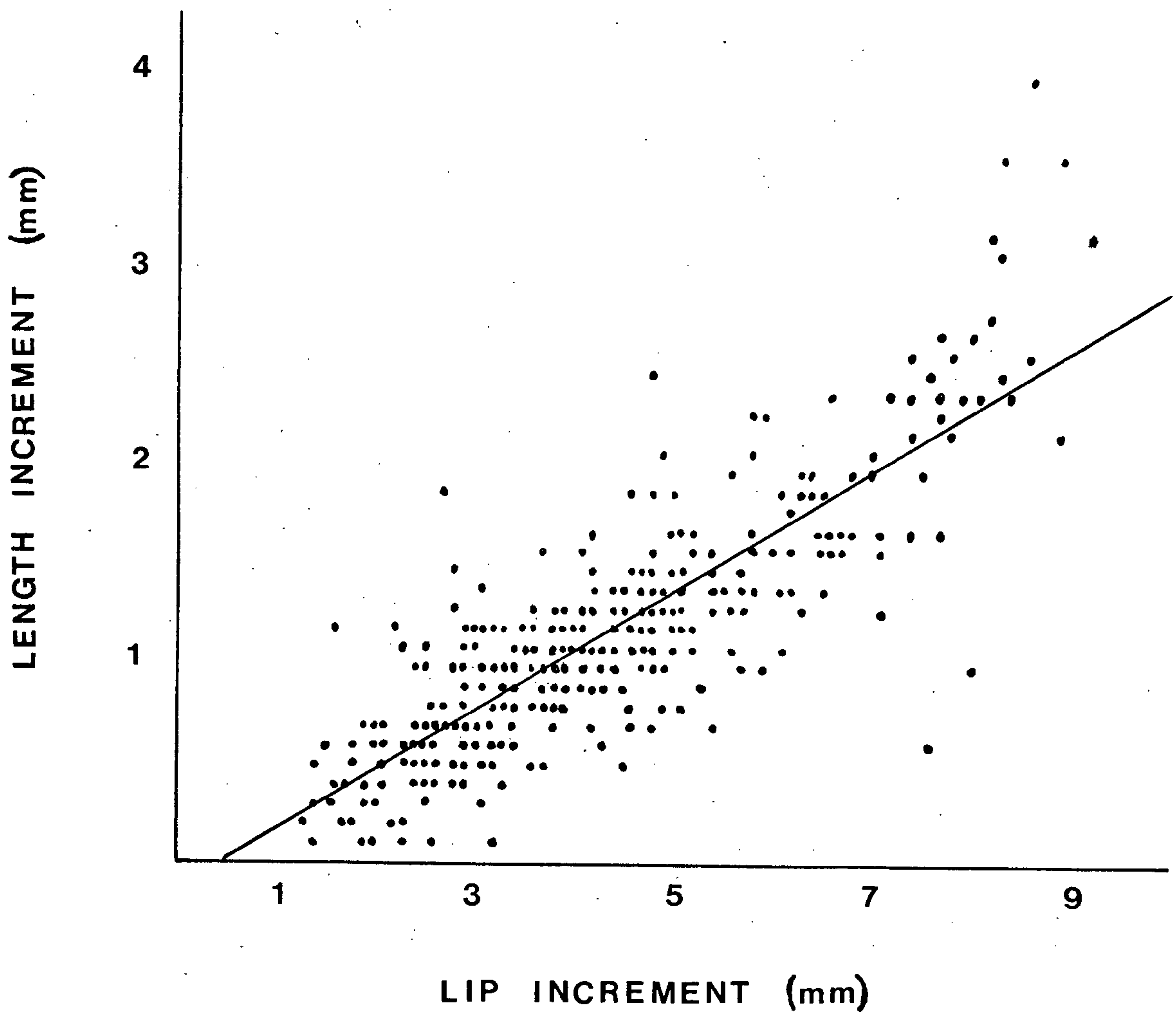
PEBBLE BEACH B

	L. sitkana tidal height (m)			*L. scutulata* tidal height (m)		
	1.5	2.2	2.8	1.5	2.2	2.8
Jan.	4.5 (185)	7.4 (22)	- (0)	5.1 (205)	6.2 (89)	10.0 (2)
April	4.0 (220)	5.5 (28)	11.0 (2)	5.2 (164)	6.0 (181)	10.0 (3)
July	4.5 (148)	6.0 (31)	8.0 (2)	5.1 (221)	5.5 (240)	8.3 (17)

BASALTIC SHELF B

	L. sitkana tidal height (m)		*L. scutulata* tidal height (m)	
	3.3	3.8	3.3	3.8
April	3.5 (35)	6.2 (259)	5.3 (268)	8.2 (143)
July	4.2 (18)	6.7 (330)	5.4 (167)	8.2 (101)

Figure 12. Relationship between lip increment and length increment. All snail size classes were plotted together because regressions done separately were all highly significant ($p<.001$) and all had similar slopes ($p<.01$).


4
3
2
1
LENGTH INCREMENT (mm)
1
3
5
7
9
LIP INCREMENT (mm)

Appendix III. Simulation Models

Predation rates were highest at the low tidal levels of pebble beach A. Survival rates were lowest at the low tidal levels of basaltic shelf A. To see if the observed differences were sufficient to account for the low abundance of large snails at low tidal levels of these habitats, I made two simulation models. The first explores the effect of fish predation at low tidal levels of pebble beaches. The second model explores the effect of reduced survival rates at low tidal levels of basaltic shelves.

Fish Predation Model

The dynamics of the large size class were simulated for a 40 by 4 m area which is equivalent to the area on pebble beach A that the fish were most active. The model makes the following assumptions:

1. No littorine movement up to high levels;
2. The density of large and small snails is similar to that observed at 2.2m above datum on pebble beach A;
3. The number of young present is directly related to the number of adults. Every year, the number of young is set equal to the number of adults alive;
4. The fish show a type two functional response to snail density (Holling 1959).

Growth, natural mortality, and predation rates were determined from field data and then varied for a range of initial snail densities. Table XV outlines the model. Each iteration is equal to two months. Every 12 months (n=6), a proportion of the large size class dies due to old age. Also, the number of young is set equal to the number of adults to provide some feedback between the number of young produced and the number of adults present on the shore. This assumption may artificially lower the resilience of the large snail population to predation because the young may actually have increased survival at low densities of adults and so may provide more recruits into the large size class.

Variable Range

D2 and D3 both had values of 2.5 in the July sample. I varied them both from 2-3.

G2 was varied from .05 to .2

k was varied from 2 to 12

s was varied from 500 to 10000

S2 and S3 were both varied subject to the constraint that they both add to 0.6

m2 was varied from 0-0.5

m3 was varied from 0-0.8

Table XVI gives the results of varying several of the parameters. If the population declined, the iteration at which it went extinct is given. The lower limits of the number of fish and their maximum feeding rate high tide needed to eliminate the large snails (by MO=36) are also given for all

Table XV. Model of the effect of fish predation on survival of large snails at low tidal levels of pebble beaches.

```
10  d2=density of (5-7mm) snails in a 10cm quadrat
20  d3=density of (7-11mm) snails in a 10cm quadrat
30  g2=proportion of (5-7mm) snails growing into
       (7-11mm) snails/iteration
35  k= maximum # of snails eaten/fish/visit
40  s= snail density at which fish eat K/2 snails/visit
50  f2=#of fish in area
60  s2=proportion of (7-11mm) snails that are 1 year old
70  s3=proportion of (7-11mm) snails that are 1.5 years old
80  m2=probability of dying when 1 year old
90  m3=probability of dying when 1.5 years old
100 t= # of high tides per iteration
110 print D2,D3,G2,F2,S2,S3,m2,m3,s,T
120 sm=d2*16000=number of (5-7mm) snails in a 40 by 4m area
130 la=d3*16000=number of (7-11mm) snails in a 40 by 4m area
135 f1=k*la/(s+la)
140 for mo= 1 to 20
150 n=n+1
160 if n=6 go to 400
170 la=la+(g2*sm)-(f1*f2*t)
180 print mo,sm,la
190 go to 500
400 n=0
410 sm=la
420 la=la+(g2*sm)-(f1*f2*t)-(la*s2*m2)-(la*s3*m3)
430 print mo,sm,la
440 if la<0 go to 510
500 next mo
510 stop
```

Table XVI. Results of fish predation model simultions. The itertion (MO) at which the large snail population population (LA) went extinct is given for a variety of fish predation and snail recruitment rates. Variables are defined in Table XIV.

<u>Variables</u>
unless otherwise specified:
s2=.4, s3=.2, m2=.5, m3=.8

	k	f2	s	LA extinct at MO= g2= .05	.10	.15	.20
at d2=d3=2.0	10	6	500	6	7	9	13
	10	6	10000	7	9	13	
m2=m3=0	10	6	500	6	8	11	15
at d2=d3=2.5	10	6	500	7	9	13	25
	10	6	10000	8	12	19	inc
m2=m3=0	10	6	500	8	11	18	inc
at d2=d3=3.0	10	6	500	8	12	18	inc
	10	6	10000	10	14	29	inc
m2=m3=0	10	6	500	9	14	inc	inc

Lower limits of k,f2 required for LA to go extinct by MO=36 (s=500)

	g2= .05	.10	.15	.20	LA extinct at MO= .05	.10	.15	.20
at d2=d3=2.0								
at f2=6, k>	1.5	4	6	8	32	24	24	25
at k=10, f2>	1	2	4	5	30	31	18	21
at d2=d3=2.5								
at f2=6, k>	2	4	7	10	32	34	29	25
at k=10, f2>	1	3	4	6	36	23	34	25
at d2=d3=3.0								
at f2=6, k>	2	5	8	12	36	31	34	25
at k=10, f2>	2	3	5	7	23	31	30	36

initial density and snail growth rates. This model shows that fish predation has a strong effect on the large size class. Under most conditions (which were extrapolated from field observations) the large snail population went extinct.

Basaltic Shelf Model

This model explores the effect of reduced recovery rates at low tidal levels of basaltic shelves. It is outlined in Table XVII. The dynamics of a large size class (6-8mm) was simulated for a $6m^2$ area. Every 2 months, a proportion of large snails disappears, but a proportion of small snails grows into large snails. Every 12 months, the number of small snails is adjusted to the number of large snails present on the shore.

Variable Range

D2 and D3 were calculated from observed values obtained in July, October sampling at 3.3m.

D2-observed 0.5,4.5; varied 2-4

D3-observed 0.2,0.2; varied 0.25-0.5

G2- the mean lip increment observed was 2.2mm which corresponds to 0.6mm increase in shell height (Figure 17). Therefore, G2=proportion of (4-6mm) that were >5.5mm; observed .125 in July and .36 in October:varied .1-.4

R-from equations shown in Figure 9;observed -.01,-.03,varied -.01,-.04

Table XVII. Model of the effect of survival rate on the abundance of large snails at low tidal levels of basaltic shelves.

```
10  d2=density of (4-6mm) snails per 10cm quadrat
20  d3=density of (6-8mm) snails per 10 cm quadrat
30  g2=proportion of (4-6mm) snails growing into
        (6-8mm) snails/iteration
40  r=r value for negative exponential
50  t= # of days per iteration
60  j=every 6th iteration, sm=j*la
70  print d2,d3,g2,r,j,t
80  sm=d2*3600=number of (4-6mm) snails in a 6m by 6m area
90  la=d3*3600=number of (6-8mm) snails in a 6m by 6m area
105 for mo=1 to 20
110 n=n+1
120 if n=6 go to 400
130 rr=la*exp(r*t)
140 la=rr+(sm*g2)
150 print la,rr,sm,mo
160 next mo
400 n=0
410 sm=j*la
420 rr=la*exp(r*t)
430 la=rr+(sm*g2)
440 print la,rr,sm,mo
450 if la<0 go to 510
460 next mo
510 stop
```

T= number of days per iteration=60

J= 1 or 3

Table XVIII shows the numbers of large and small snails present at the 21st iteration of the model. I used another initial density mixture (D2=2,D3=.5) which I did not include because it gave very similar results to D2=2,D3=.25. Under most conditions, the large snail population decreased. But only with high R and low G2 values did it become very low. Therefore, the observed disappearance rates of snails from low tidal levels of basaltic shelf A are not sufficient, under the assumptions of this model, to explain the absence of large snails from low tidal levels of basaltic shelves.

Table XVIII. Results of simulations of basaltic shelf model showing numbers of large (la) and small (sm) snails present at MO=21. Variables are defined in Table XVI.*

		A: J=1, d2=2,d3=.25		B: J=1, d2=4,d3=.25		C: J=3, d2=2,d3=.2	
		la	sm	la	sm	la	sm
g2=.4	r=-.01	4154	4378	8277	8724	174000	29883
	r=-.02	552	788	1105	1576	30892	6173
	r=-.04	132	269	265	540	9395	2183
g2=.2	r=-.01	259	346	515	688	7866	2054
	r=-.02	26	52	52	103	1179	392
	r=-.04	5	17	10	34	314	136
g2=.1	r=-.01	21	32	41	64	433	153
	r=-.02	1.4	3.5	2.8	7	51	25
	r=-.04	0.2	1	0.4	2	11	8

* the initial values for la,sm were la=900 at d3 sm=7200 at d2=2, sm=14400 at d2=4.
Note that the B values are = 2*A; therefore d2 just effects the magnitude and not the form of the response to variation in survival and growth rates. When the fecundity of the large snails is increased (J=3), the large snail population actually increases under most conditions.