ECOLOGICAL INTERACTIONS OF THREE LITTORINA (GASTROPODA, PROSOBRANCHIA) ALONG THE WEST COAST OF NORTH AMERICA

by

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GENERAL INTRODUCTION

Littorines, or periwinkles, can be found on barnacles, rocks and seaweed throughout the rocky intertidal regions of the world (Stephenson and Stephenson, 1949). Since they are ubiquitous and easy to collect, they have been the object of many studies.

As early as 1911 Haseman attempted to describe the physical factors responsible for the oscillatory movements of *Littorina littorea* which corresponded to tidal cycles. In 1916 Kanda looked at the negative geotropic response of littorines to a combination of factors such as light, angle of inclination, submergence and emergence, texture and moisture of substratum. He noted that animals were sensitive to desiccation in that they moved down if the substratum was dry.

Hertling and Ankel (1927) describe the mode of development of various Atlantic *Lacuna* and *Littorina* species. *Littorina littorea* and *L. neritoides* both have planktonic egg capsules and veliger larvae. *Littorina littoralis* fasten their gelatinous egg masses to the fonds of fucoids. The veliger stage is passed inside the egg and the young snails hatch as miniature adults. *Littorina saxatilis*, on the other hand, is viviparous. Struhsaker and Costlow (1968) reared the Hawaiian *Littorina picta* from egg capsules to miniature adults by feeding the veligers on phytoplankton. Just before metamorphosis the veligers were observed to prefer substrata with algal cover to substrata without algae.

Much attention has been devoted to the study of Atlantic and Hawaiian littorines but no long term studies have been carried out on the three eastern Pacific species, *Littorina scutulata*, *Littorina sitkana* and *L. planaxis*. *Littorina scutulata* (Gould 1849) has the widest distribution being found on both exposed and sheltered beaches from Alaska to Baja California (Oldroy, 1926 and Keen, 1937). This species is rare or absent in habitats that are relatively isolated from the open sea, such as high tide pools and lagoons. *Littorina sitkana* (Philippi, 1845) is present from the Bering Sea to southern Oregon and is characteristic of wave and sun-sheltered locations such as mud flats, tide pools, lagoons and rocky shores containing numerous crevices (Behrens, 1971). *Littorina planaxis* (Philippi, 1847) occurs from southern Oregon to Baja California and lives in the splash zone, above the high water mark. Both *Littorina scutulata* and *L. planaxis* develop by means of planktonic larvae, whereas *L. sitkana* lays benthic egg masses from which juvenile snails hatch directly (Behrens, 1971). By transplanting animals beyond their range, I have attempted in this study to define the factors limiting the southern distribution of *L. sitkana* and the northern distribution of *L. planaxis*.

The *Littorina scutulata*-*L. sitkana* species pair co-exists at the same tidal level on most beaches near the city of Vancouver, British Columbia and in Puget Sound. Co-existence, however, is not the rule with the *L. scutulata*-*L. planaxis* species pair. *Littorina scutulata* is found in the high intertidal zone and *L. planaxis* lives in the spray zone above the high water mark (Bock and Johnson, 1968).

The competitive exclusion principle, or Gause's principle states that two ecologically similar species using the same resource, be it food or shelter, cannot co-exist indefinitely for one species would be more efficient at utilizing that resource and thus would increase in numbers and displace the other species (Hardin, 1960). This was the case with Paramecium caudatum and P. aurelia grown in culture vials (Gause, 1934). In single species cultures both species survived indefinitely but when grown together, the smaller species P. caudatum, with a greater rate of increase, could acquire food more efficiently than P. aurelia and thus P. caudatum increased in numbers and displaced P. aurelia. The more complex the laboratory environment becomes and the more genetic variability there exists within the competing species, the greater will be the chances of their co-existence. Ayala (1972) summarizes a number of such studies. Since in nature, environmental conditions are more variable in time and space than in laboratory cultures, co-existing species utilizing the same resource are not uncommon (Harger, 1972).

Usually two competing species are adapted to different extremes of an environmental gradient with only one species living at either end. Littorina scutulata does not live in high splash pools or lagoons, presumably because its planktonic larvae cannot settle there. L. sitkana cannot live on exposed coasts without shelter from waves and sun, as adults tend to get dislodged by wave action and juveniles tend to die from desiccation (Behrens, 1972). In intermediate habitats usually both species can co-exist. This co-existence does not necessarily imply a lack of competition between the species, for in the case of *L. sitkana* and *L. scutulata* caged for one year at various densities and species compositions in an intermediate habitat, evidence for competition was found (Behrens, 1971). This study attempts to explain the great degree of overlap in the distribution of *L. sitkana* and *L. scutulata* and the lack of overlap between *L. scutulata* and *L. planaxis*.

The array of environmental gradients within which a species can persist has been described as an "n-dimensional hypervolume" or "niche" of that species (Hutchinson, 1957). Since each environmental gradient is measured in different units, it is very difficult to quantify the niche size of a species. In the present study niche-size and overlap for the three species of littorines has been rated on a relative scale based on spatial distribution. An attempt is made to relate niche size to the degree of specialization of a species.

CHAPTER 1

GEOGRAPHIC RANGE LIMITATION OF LITTORINA SITKANA AND LITTORINA PLANAXIS

Among marine intertidal organisms, tolerance to such physical factors as temperature or salinity probably would not directly dictate geographic boundaries, for intertidal organisms experience great variations in these factors within their latitudinal range. With species having a planktonic dispersal stage, currents could play a large role in determining distribution. Likewise, wide expanses of unsuitable habitats such as sandy beaches could hinder the dispersal of a species lacking planktonic larvae. Eastern Pacific littorines are suitable species for looking at such problems, since *Littorina scutulata* and *L. planaxis* possess planktonic larvae whereas *L. sitkana* develops directly from eggs attached to intertidal rocks.

Littorina scutulata has the widest distribution, occurring from Alaska to Baja California, (58°N to 19°N latitude). Oldroy, 1929, and Keen, 1937, state that *L. sitkana* is present from the Bering Sea to Puget Sound and that *L. planaxis* occurs from Puget Sound to Baja California. I find, however, that the meeting place of the latter two species is in Charleston, Oregon and not Puget Sound (Fig. 1-1).

All references of *Littorina planaxis* occurring in Puget Sound date

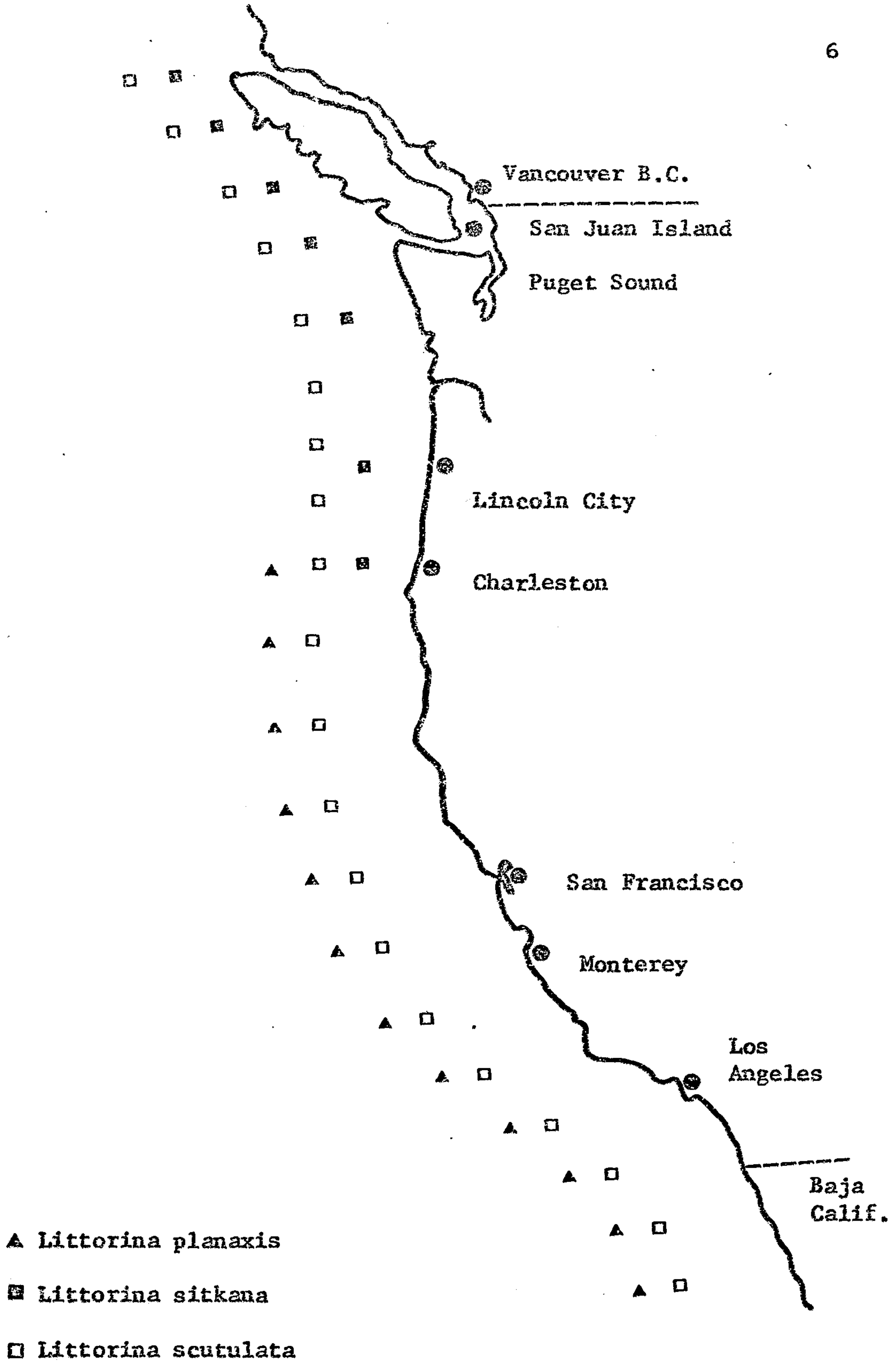


Fig. 1-1 Distribution of Littorines

back to Dall, 1921. Dr. J. Rosewater of the Smithsonian Institute kindly made available Dall's type specimens #3928. These specimens are of _L. planaxis_, however, the collection site was not Puget Sound but San Francisco. The specimens labelled _L. planaxis_ in the Friday Harbor collection are actually misidentified _L. sitkana_ with their grooves eroded away. It is therefore very unlikely that _L. planaxis_ extends as far north as Puget Sound.

Thomas (1966) found _Littorina sitkana_ in bays just north and south of Lincoln City, Oregon. Isolated populations of small individuals can also be found associated with the alga, _Prasiola_, and barnacle cover at Cape Arago near Charleston. This species has direct development and is found only in favorable habitats in which both adults and juveniles can survive. Since adults are susceptible to being dislodged by waves, and egg masses and juveniles are susceptible to desiccation, this species is most abundant in sun- and wave-protected sites such as crevices and tide pools (Behrens, 1972). When such habitats are scarce, or isolated as are the rocky outcroppings along the sandy southern Washington and northern Oregon coasts, _L. sitkana_ is absent.

To determine the factors limiting the geographic distribution of a species, one has to transplant a population of that species beyond its range. If the transplanted population persists, i.e. if individuals survive, grow and reproduce, then some factor or factors must prevent that species from dispersing into such favorable habitats. If individuals survive, but fail to grow and reproduce, it may indicate that the new environment only allows them enough energy for maintenance. Low food abundance and/or high energy expenditures necessary for resisting the effects of a harsh physical environment may be active factors resulting in low growth and reproduction. If predators are excluding a species from a physically benign environment, one would expect that species to thrive in predator free refuges.

A program involving transplantation of Littorina populations was undertaken in an attempt to define factors responsible for determination of the southern limit in L. sitkana and northern limit in L. planaxis on the west coast of North America.

In conjunction with the field experiments, interactions between shore crabs and littorines were also investigated in the laboratory.

Materials and Methods

For the transplantation experiments, littorines were collected from a given locality and the lips of their shells painted so that growth could be detected. Animals were either transported by car in plastic bags or mailed in cardboard boxes containing damp paper towels. Animals were mailed at the beginning of the week and received three days later. Jim Rote and Dale Straughn report that all the Littorina sitkana shipped in this fashion survived. Likewise, Littorina planaxis transported in plastic bags survived the two day car trip. Before animals were released on the shore, they were immersed in salt water so that they could open their operculum and attach to the substratum. Sites were searched periodically for the presence of transplanted animals.

Locations in which animals were collected and released, and their survival in the new habitats are listed in Table 1-1.

To investigate crab predation on littorines, two plastic dishpans were filled with 5 cm of sea water and cooled by setting them in a water table with circulating tap water. A male and female pair of *Hemigrapsus nudis* was introduced into one pan and a pair of *H. oregonensis* into the other. A rock was placed into the center of each pan to provide shelter for the crabs. Six *Littorina planaxis*, six *L. scutulata* and six *L. sitkana* were then introduced into the bottom of each pan. The number of crushed dead snails were noted and dead animals were replaced with living ones in an attempt to keep the number of each prey species constant.

Results

Both *Littorina planaxis* transplants to more northern habitats were quite successful. At least 17 individuals survived at Friday Harbor, San Juan Island, for two years. Not only did some adults survive the unusually cold winter of 1972/73, but they also grew and produced egg capsules. In the laboratory these eggs gave rise to actively swimming veliger larvae in 1½ days.

The *Littorina sitkana* transplants were relatively unsuccessful. Only one out of five persisted for any length of time. From a cohort of 50 *L. sitkana* released into a very high splash pool at Monterey, six survived and grew from December 31, 1970 to May 27, 1971. These animals died as their pool dried up by June 14, 1971. The presence of empty cracked shells in May suggests that the beach crab *Pachygrapsus crassipes* may have been responsible for some of their deaths.

In a laboratory situation in which the beach crabs *Hemigrapsus nudis* and *H. oregonesis* were offered a choice among *L. sitkana*, *L. scutulata* and *L. planaxis*, they only attacked and ate *L. sitkana*. *Littorina planaxis* and *L. scutulata* seem to escape crab predation by crawling out of the water and by having thicker shells than *L. sitkana*.

Discussion

Since at least some *Littorina planaxis* grew, reproduced, and survived the cold winter at Friday Harbor temperature or other physical factors do not appear to prohibit this species from living further north. I postulate that either south flowing currents during planktonic development or decreased larval survival might limit the northern distribution of *L. planaxis*.

Thorson (1950) showed that a greater proportion of northern prosobranch species pass the veliger stage inside egg capsules than do their southern counterparts. This trend holds for the littorines in that *Littorina sitkana*, the most northern of the three species has benthic egg masses, whereas the southern species *L. scutulata* and *L. planaxis* have planktonic larvae. Thorson suggests that direct development might be an adaptation to the unpredictability of phytoplankton food sources for veligers in northern waters.

Whipple, 1966, estimated that 99% of the mortality of Hawaiian littorines, *L. pintado* and *L. picta*, occurs during planktonic larval life. Any factor such as a decrease in temperature or food supply that would prolong planktonic larval development would also increase the exposure time to such hazards as predation and seaward flowing currents. To compensate for possible increase in larval mortality at higher latitudes, L. planaxis would have to be more fecund than at lower latitudes to maintain a breeding population.

Drift bottle studies indicate that coastal surface currents along Washington and Oregon tend to follow the seasonal changes in prevailing winds that result in a southerly flow in the summer and a northerly flow in the winter (Barnes, Duxbury and Morse, 1972). A south flowing current during summer, when L. planaxis larvae are in the plankton would prevent the northward spreading of this species and the self-perpetuation of transplanted northern L. planaxis populations.

Ricketts and Calvin (1968) state that the shore crab Pachygrapsus crassipes is abundant from the Gulf of California to Charleston, Oregon. This distribution pattern suggests, that the presence of Pachygrapsus may contribute to limitation of the southern distribution of L. sitkana around Charleston, Oregon. These shore crabs move higher up the shore at low tide than do the smaller Hemigrapsus crabs which overlap geographically with L. sitkana. At low tide, Pachygrapsus can be found in damp rocky cracks and crevices and in pools. Since L. sitkana is also dependent on crevices and pools, it is conceivable that, in their search for these damp and wave protected sites, they fall prey to Pachygrapsus.

I predicted that the site just below the seawater system over-flow pipe at Hopkins Marine Station would be an ideal refuge from desiccation, wave action and predation for L. sitkana. This site is constantly sprayed with seawater, and is about six feet above the high water mark. Unfortunately the seawater system was turned off for four days right after the animals were released in June 1973 (Table 1-1). Upon closer observation, this site was also found to harbor about 20 Pachygrapsus under boulders and in rock crevices. I was unable to find a suitable site for L. sitkana in the Monterey area.

CHAPTER 2

THE EFFECT OF SHELTER IN THE INTERACTION OF *LITTORINA SITKANA* AND *LITTORINA SCUTULATA*

Two species of intertidal snails, *Littorina scutulata* and *Littorina sitkana*, co-exist at the same tidal level on most beaches near the city of Vancouver, British Columbia and in Puget Sound. The relative abundance of these two species, however, varies along a wave exposure gradient with only one species living at either extreme (Table 2-1). *Littorina scutulata* does not live in high splash pools or lagoons, presumably because its planktonic larvae do not settle there. *Littorina sitkana* does not live on sun or wave exposed shores without shelter since adults tend to get dislodged by waves and eggs and juveniles tend to get desiccated (Behrens, 1972).

It appears that *Littorina sitkana* compensates for its greater susceptibility to adverse physical effects of waves and desiccation by keying in on sheltered micro-habitats. The following evidence was found in a previous study (Behrens, 1971):

1. In a field experiment, 93% of *L. sitkana* egg masses were deposited in wave and sun sheltered places (Table 2-2).
2. As the tide recedes on a dry day, proportionately more *L. sitkana* than *L. scutulata* tend to be found in crevices (Table 2-3).

3. When placed on clean and barnacle covered oyster shells, both species tended to leave the smooth, cleaner shells, but tended to remain on the rougher barnacle covered shells (Table 2-4). When animals were put into a seawater aquarium with rocks of different roughness, significantly more L. sitkana were found on the extremely jagged rocks than L. scutulata (Fig. 2-1). This may suggest that L. sitkana is better able to find shelter than L. scutulata.

Given habitats with tide pools, horizontal shelves or crevices that mitigate the effects of wave action and desiccation, both species of littorines co-exist over a wide range of wave exposures. This co-existence between L. scutulata and L. sitkana does not necessarily imply a lack of competition between them. A field experiment in which species composition and density were varied indicated that at high densities both species survived better in single than in mixed species treatments (Behrens, 1971, Fig. 2-2, 2-3). At low and at medium density no such species interaction effects were detected. At high density, L. sitkana and L. scutulata probably did not compete for food since food abundance and growth rates were always the same in single and mixed species cages. Shelter may have been an important factor in the species interaction at high densities. An indication that shelter may have been limiting in high density treatments comes from a survey of animals found in exposed sites inside experimental cages (Fig. 2-4). Proportionately more animals of both species were found in exposed places as the density increased.

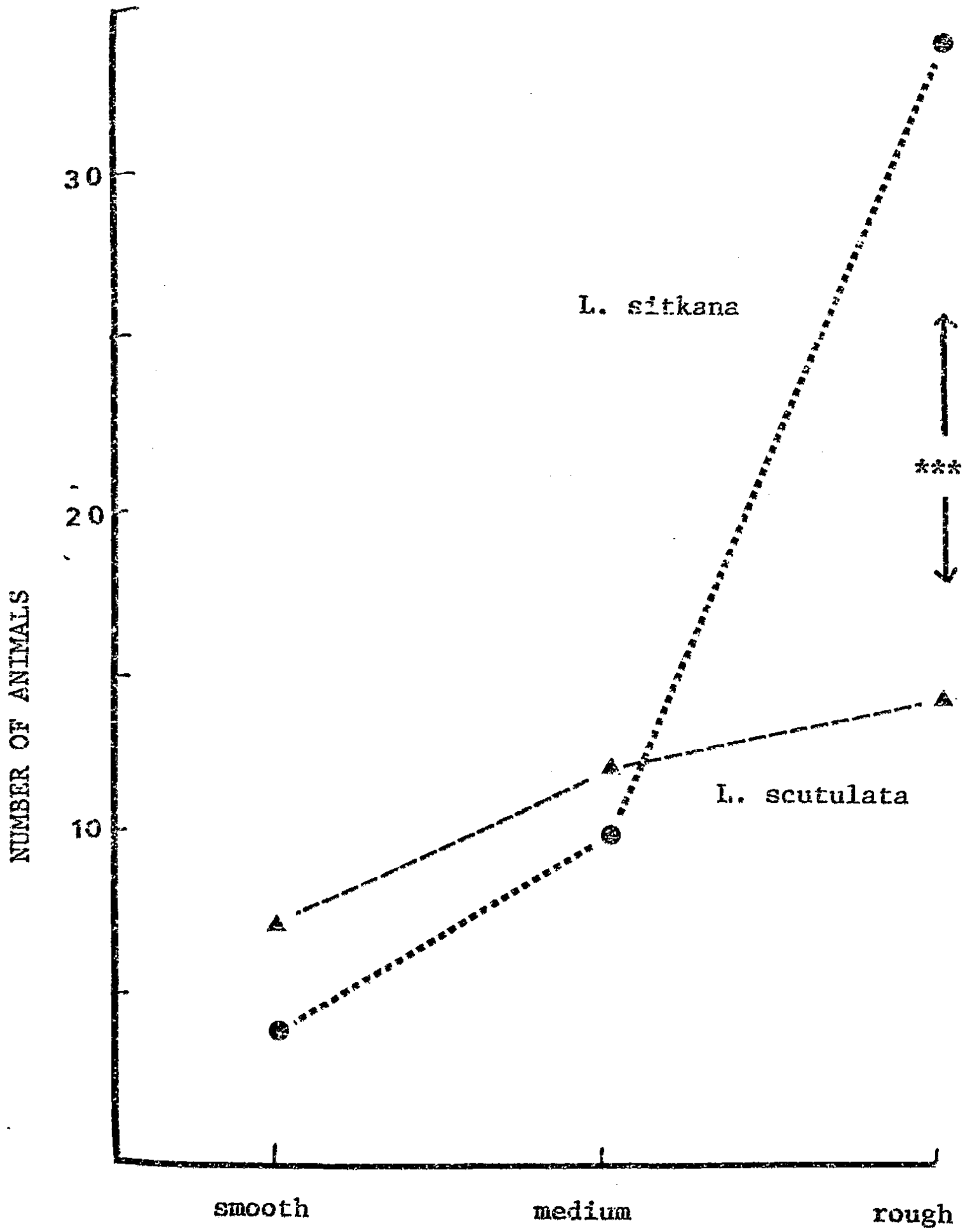


Fig. 2-1 Number of animals found on rocks of different roughness. Note that significantly more *L. sitkana* were found on rough rocks than *L. scutulata*.

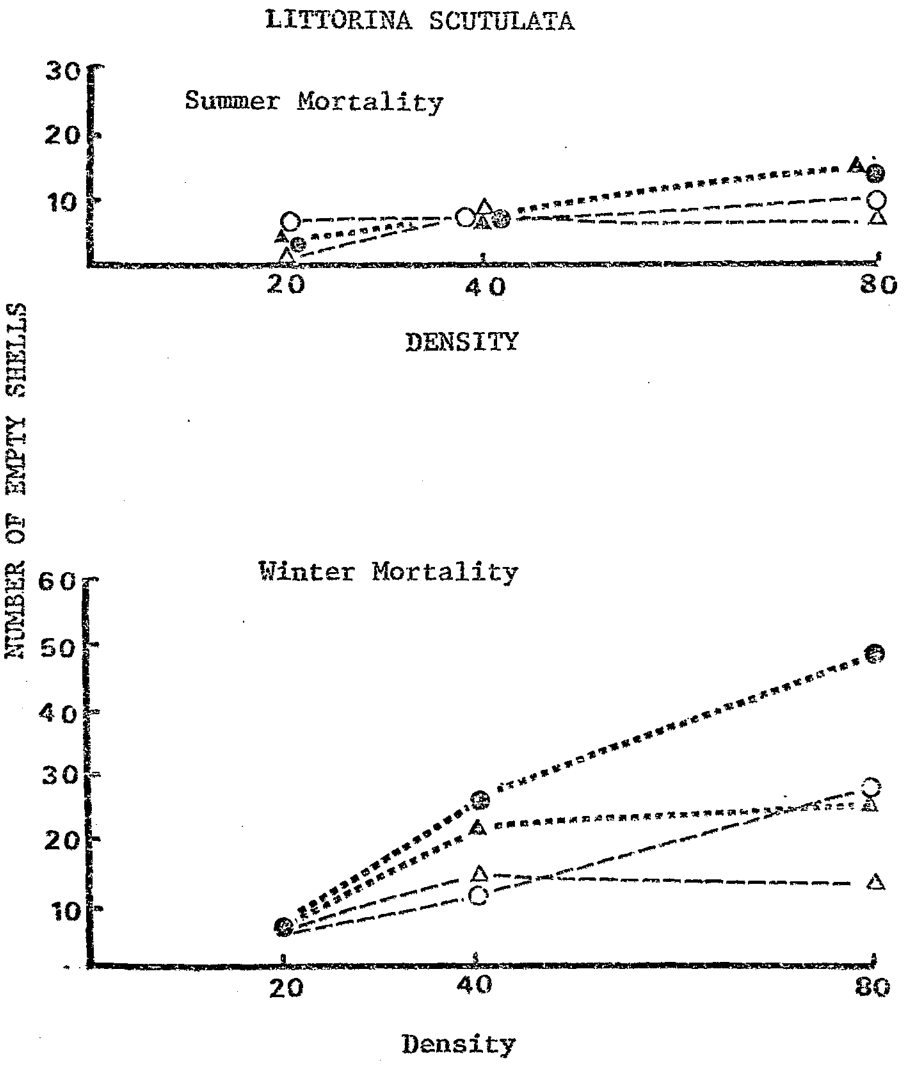


Fig. 2-2 Number of dead L. scutulata found in the summer and in the winter. Note that in the winter animals in more sheltered cages survived better than those in more exposed cages (X^2= 15.22***). In the winter animals in single species cages survived better than animals in mixed species cages (X^2= 21.63***).

wave exposed cages	sheltered cages
▲ ···· single species	△——single species
● ···· mixed species	○——mixed species

Fig. 2-3 Number of Dead L. sitkana found in the Summer and in the Winter. During the winter at high density animals in single species cages survived better than animals in mixed species cages (X^2= 21.63***). Animals in sheltered cages survived better than animals in exposed cages (X^2= 15.22***).

wave exposed cages	sheltered cages
▲ single species	△ single species
● mixed species	○ mixed species

LITTORINA SITKANA

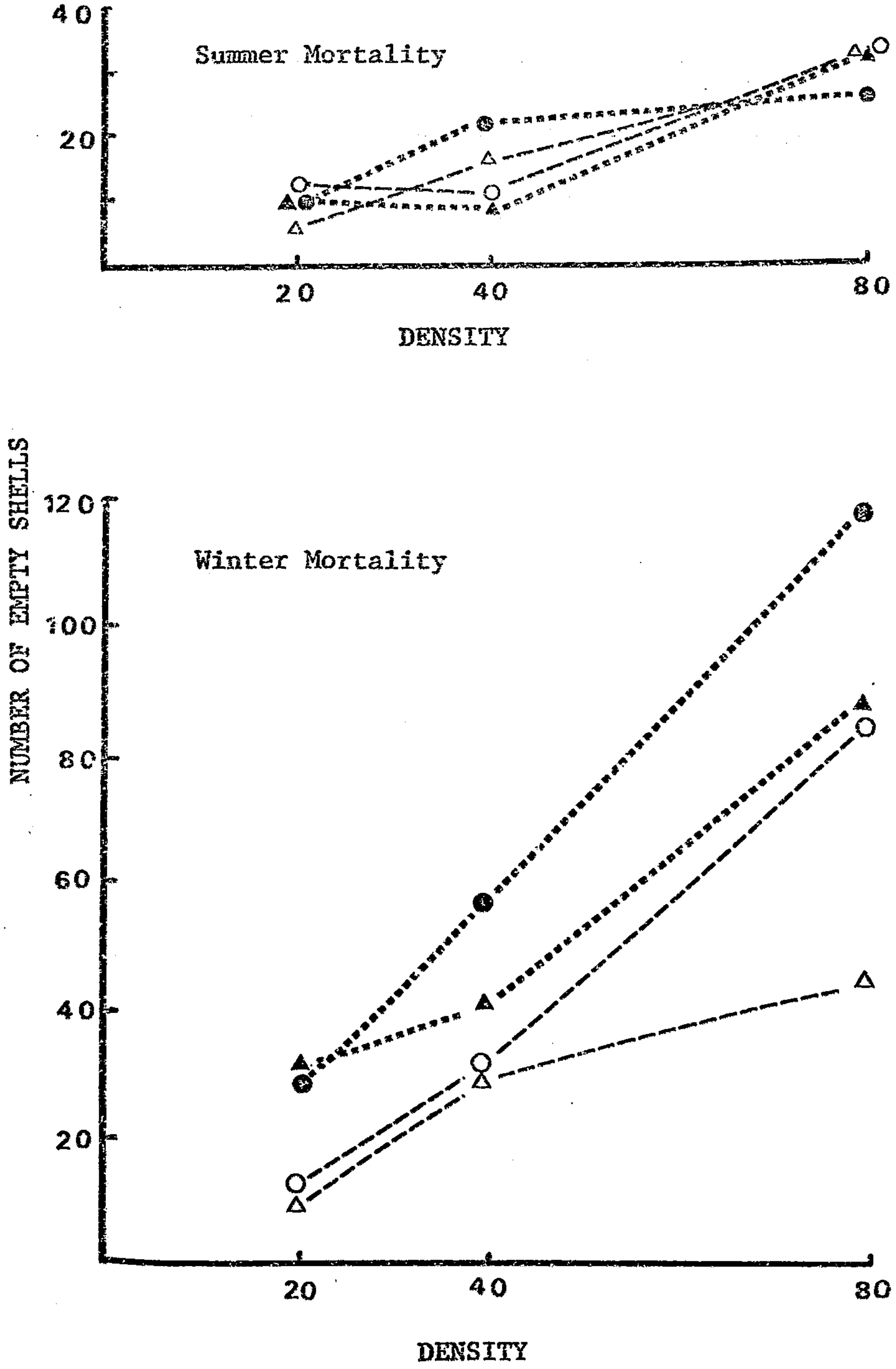
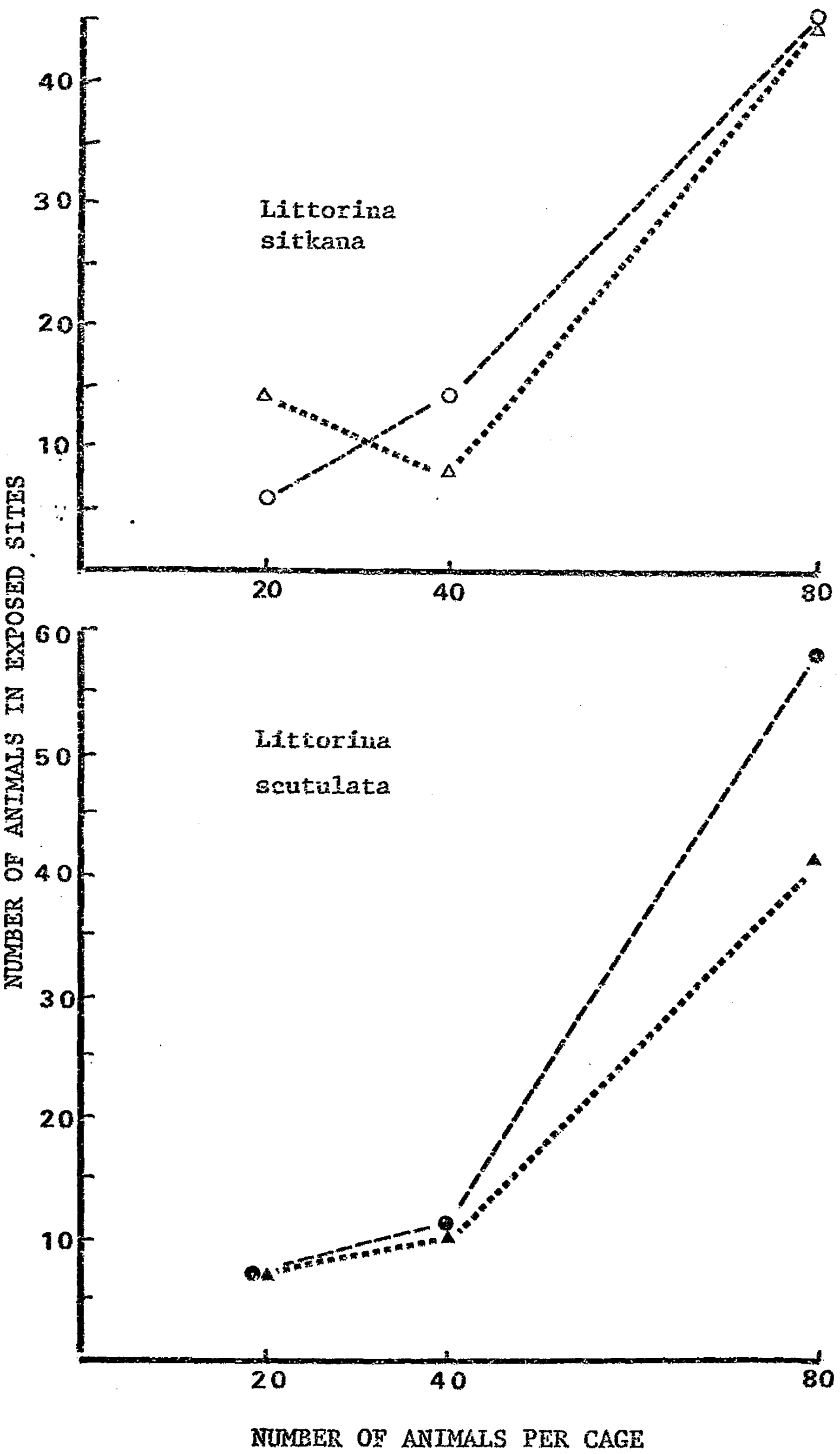


Fig. 2-4 Total Number of Animals found in Exposed Sites in Experimental Cages on two Occasions (March 3 and March 6 1970) as a Function of Density. Proportionately more animals were found in exposed sites as the density increased (X^2 pooled species treatments, d.f.=2, *L. sitkana*= 9.93** *L. scutulata*= 15.76***).


Littorina
sitkana
Littorina
scutulata
40
30
20
10
60
50
40
30
20
10
20
40
80
20
40
80
NUMBER OF ANIMALS IN EXPOSED SITES
NUMBER OF ANIMALS PER CAGE

Littorines would especially need shelter during storms and in wave exposed sites. While diving in rough water on the west coast of Vancouver Island, I noticed that all littorines were wedged into crevices, whereas in quiet waters they tend to be outside of shelters. The greatest mortality in littorines occurs during the winter (Figs. 2-2, 2-3) when food is most abundant. During this time significantly more animals of both species died in the more wave-exposed block of cages than in the more sheltered block (Figs. 2-2, 2-3). No such difference in mortality rates between the two blocks of cages occurred during the summer. This evidence may indicate a greater need for shelter during the winter storm season than during the summer.

In order to elucidate the mechanism of the suspected competition for shelter, species interaction experiments were set up in three habitats, wave exposed, wave sheltered and intermediate. Shelters were added to half of the experimental cages at each site. Other experiments were set up in the hope of detecting species ratio effects.

Materials and Methods

a) For a long term species interaction experiment 72 cages consisting of stainless steel mesh baskets (13 by 13 by 3 cm) were constructed by braiding the corners of a square piece of hardware cloth (3.2 meshes/cm). Two such cages were inverted and screwed to a cement slab (4 by 19.5 by 39 cm) using plastic washers, plastic screw anchors and stainless steel screws (Fig. 2-5). The surface of the cement slab under one of the two cages was perforated with "crevices," 12 holes 1 cm deep and 1 cm wide. Twelve such slabs were taken to each of the three experi-

Fig. 2-5 Stainless Steel Mesh Cages

mental sites varying in wave exposure. At False Bay and Cantilever Pier, the sheltered and intermediate habitat, the slabs were placed on the gravel substratum (Fig. 2-6) but at McGinities, the most exposed habitat, they were cemented to the basaltic rock substratum.

Animals were collected from a site of intermediate wave exposure next to Cantilever Pier and the lips were marked with a cellulose base paint. Twenty animals, either all *L. sitkana*, all *L. scutulata* or 10 of each species were put into each cage. Twice as many replicates were run for mixed than for single species treatments in order to keep the number of animals the same in both treatments. The experiments were set up around December 8, 1971 and monitored on February 21 and April 4, 1972.

In the summer, when the storms subside, animals in wave exposed and intermediate sites would not be expected to benefit from crevices as much as in the winter. Crevices, however, would provide damp microhabitats during mid-day low tides in the summer. Since the most wave protected habitat is also the most sun-exposed, one might expect differences in survivorship and growth rates in crevice and smooth treatments. A similar experiment, varying the density of snails was set up in the three sites on April 18, and monitored July 20, 1972. Ten, 20, or 40 *L. scutulata* or *L. sitkana* were put into each cage. Unfortunately, there were not enough cages to run mixed species treatments.

b) Experiments to test for species ratio effects were set up at the intermediate habitat from Oct. 3, 1971 to December 5, 1971 and from February 2, 1973 to March 26, 1973. In the first experiment the treatments consisted of:

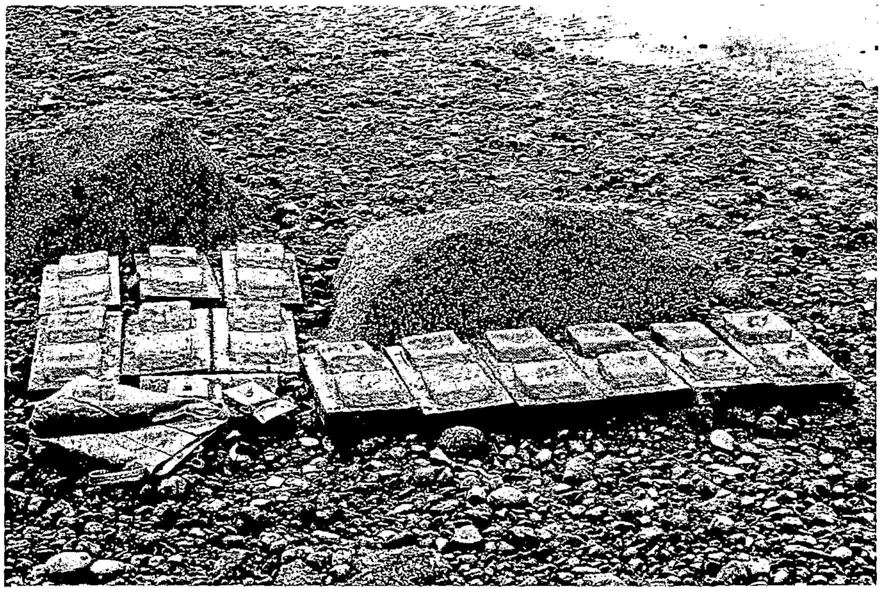


Fig. 2-6 Experimental Cages at False Bay

40 L. sitkana per cage with crevices

30 L. sitkana and 10 L. scutulata per cage with crevices

20 L. sitkana and 20 L. scutulata per cage with crevices

10 L. sitkana and 30 L. scutulata per cage with crevices

40 L. scutulata per cage with crevices

Since no significant growth occurred during this time, the proportion of animals inside and out of crevices was noted.

The treatments for the second species ratio experiment consisted of:

24 L. sitkana

18 L. sitkana and 6 L. scutulata

12 L. sitkana and 12 L. scutulata

24 L. scutulata

12 L. sitkana

12 L. scutulata

Half of the cages allotted for each treatment had "crevices" and half of them did not. The positions of each animal was noted February 22 and March 25, 1973. Growth rates were measured April 26, 1973.

c) To test for recognition between species, individual Littorina scutulata and L. sitkana were placed into depressions of a blood sample tray so that each animal had the same chance of encountering individuals of both species (Fig. 2-7). Animals were wetted and allowed to move on the tray. After animals had attached to one another, the lower and upper member of each aggregation was noted.

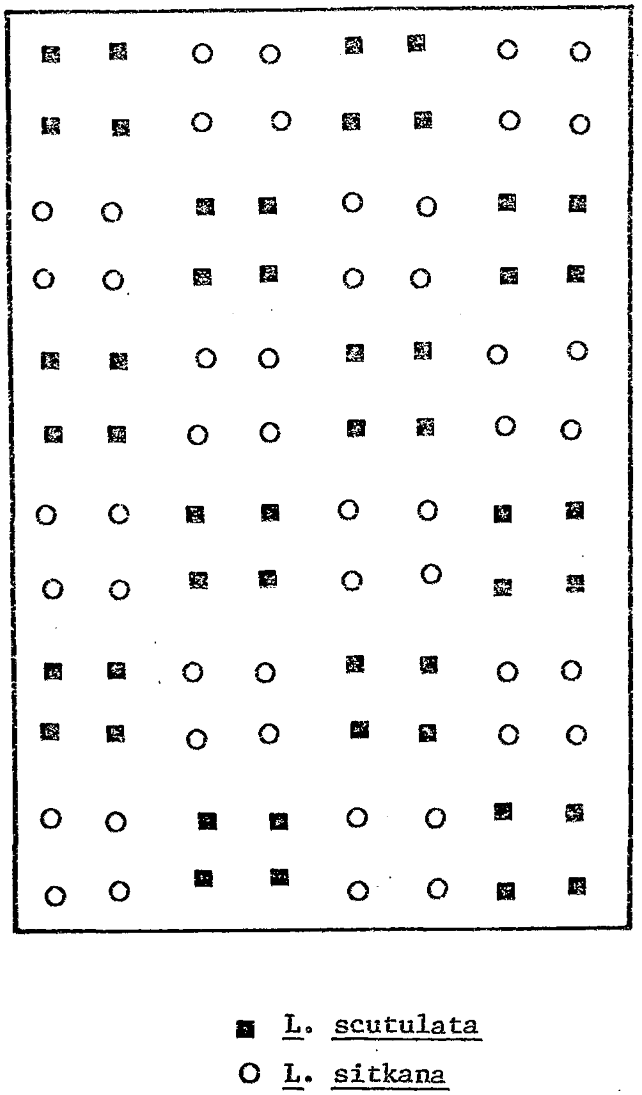


Fig. 2-7 Blood Sample Tray used in Aggregation Experiment showing Dispersion of Littorines.

d) An attempt was made to relate weather conditions to the proportion of Littorina sitkana and L. scutulata found in sheltered sites. Position data from the previous experiments were used.

e) In order to gain some information on the recruitment pattern of littorines, the number of animals less than 4 mm in shell height inside experimental cages was noted. Comparisons were made among sites and between smooth and crevice cages.

Results

a) In the most sheltered habitat animals in all the species and substratum treatments grew at the same rate (Table 2-5). As the habitat became more exposed, animals in "crevice" cages tended to grow better than animals in smooth cages. This was especially true for mixed species Littorina sitkana.

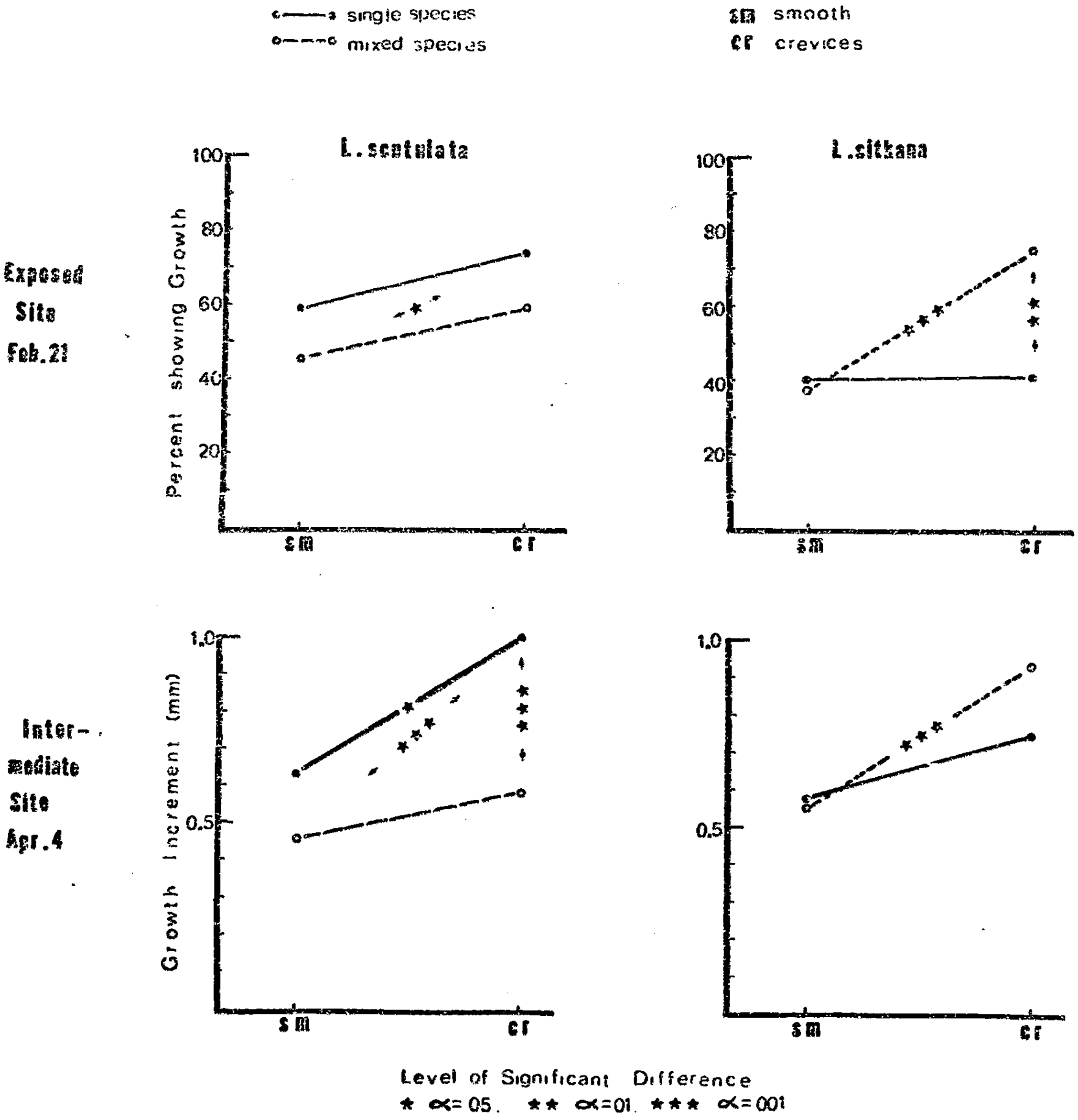
No species interaction effects were ever detected within smooth substratum cages (Fig. 2-8). The exposed site on February 21 and the intermediate site on April 4 showed similar trends. When crevices were provided, L. sitkana tended to grow more and L. scutulata tended to grow less in mixed species than in single species cages. This may indicate that in mixed species cages L. sitkana benefits from crevices at the expense of L. scutulata.

The summer density experiment did not yield the desired information. Too many cages were damaged and too many animals escaped to make valid growth rate comparisons between smooth and crevice treatments.

Food in the intermediate and exposed habitats was relatively

Fig. 2-8

Growth of Littorines under various Treatments



abundant and both species grew and survived as well in all the treatments (Tables 2-6, 2-7). Food in the sheltered habitat, however, was scarce (Tables 2-6, 2-7). Since no obvious pattern in survivorship and growth rate was observed between smooth and crevice cages, they were lumped.

In the sheltered habitat L. scutulata survived better as densities increased. The proportion of animals showing growth, however, decreased with density (Fig. 2-9). The mortality of L. sitkana increased with density. The few remaining survivors all grew at the same rate (Fig. 2-9).

b) The species ratio of littorines had no effect on the percent of animals in crevices on December 5, 1973 (Table 2-8). Since all animals survived, but did not grow no other comparisons could be made.

The relative proportion of Littorina sitkana and L. scutulata had no effect on growth rates for the period February 2 to April 26, 1973 (Fig. 2-10). Animals of both species grew significantly more at low than at higher density (Fig. 2-11). Littorina sitkana at low density and in the 18 L. sitkana and 6 L. scutulata treatment benefited significantly from crevices (Figs. 2-10, 2-11).

c) Littorines do not discriminate between individuals of the two species in that they showed no preference with which species they formed aggregations (Table 2-9).

d) Since readings of the proportion of animals in crevices were taken at different times of the day, it is difficult to make valid comparisons

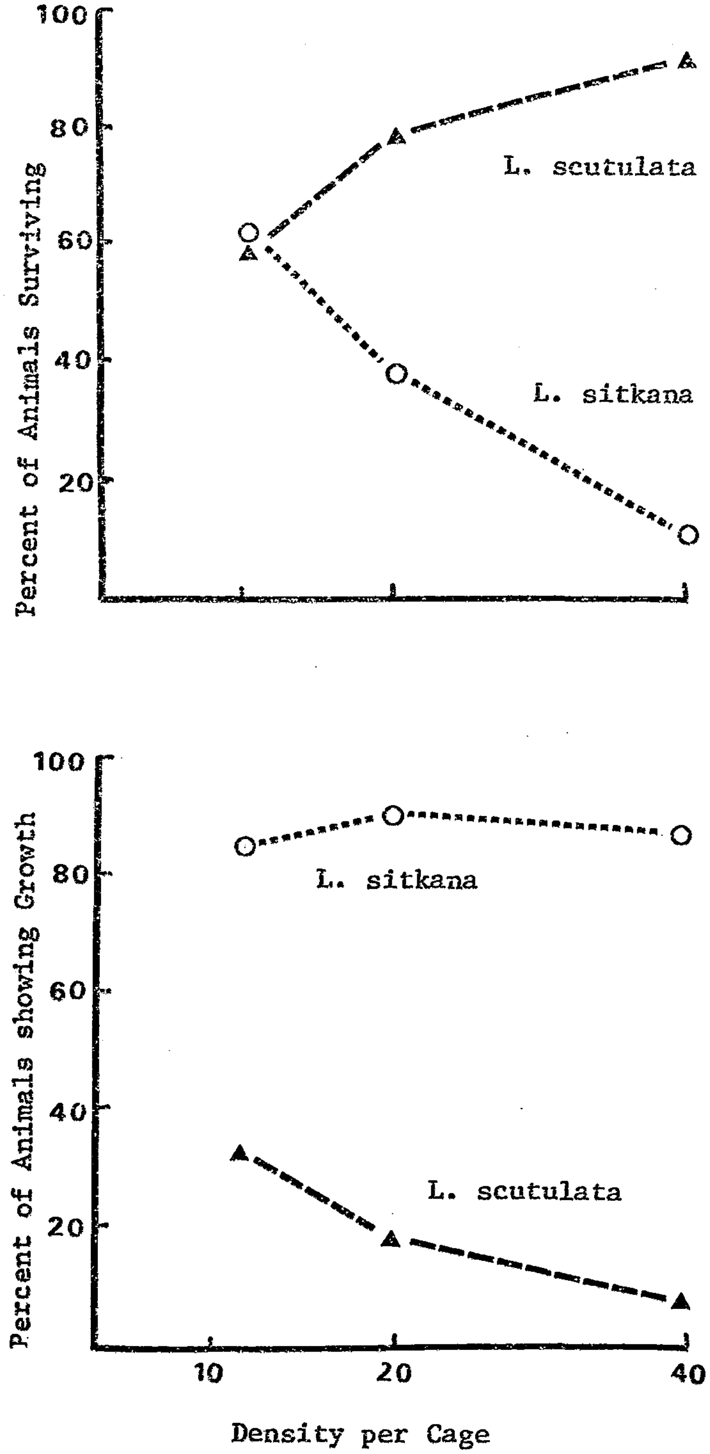


Fig.2-9Survivorship and Growth Index as a
Function of Density of Animals caged
at False Bay from April 16-July 20 '72

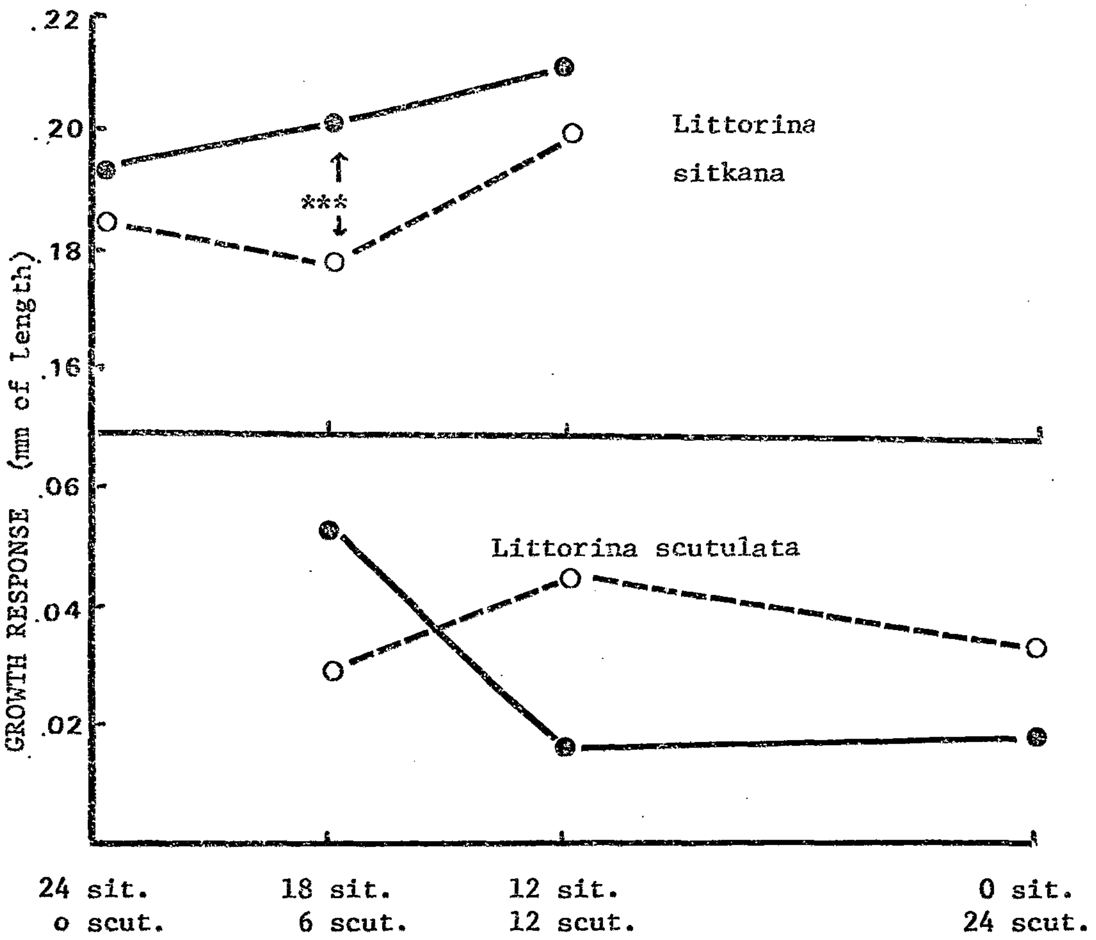


Fig.2-10 Growth Response of Littorines caged at various Species Ratios from Feb. 2 to April 26, 1973. Note that in the 18 L. sitkana/6 L. scutulata Treatment L. sitkana grew significantly more in crevice than in smooth cages.

○ crevice cages ● smooth cages

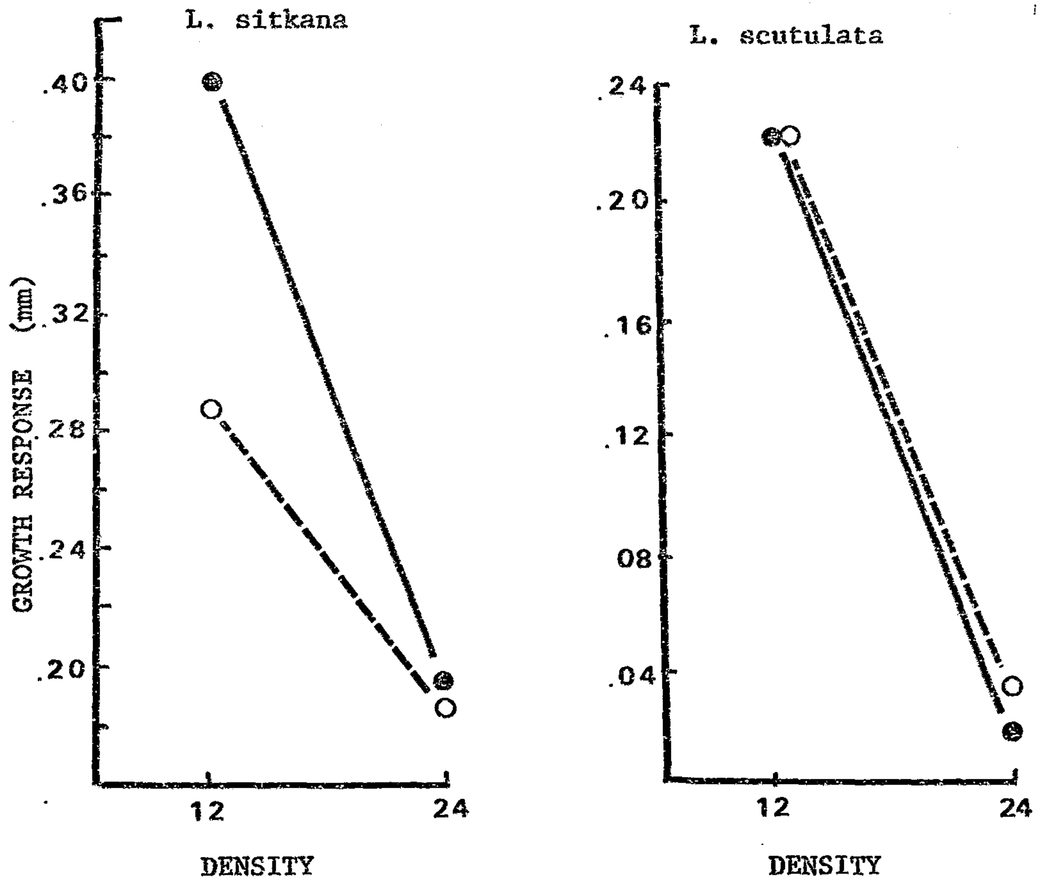


Fig.2-11 The Effect of Density on Growth Response of Littorines caged at Cantilever Pier from Feb. 2 to April 26, 1973.
○ smooth substratum ● crevice substratum

Animals in all the treatments grew significantly more at low than at high density (F values d.f.= 1/∞ L. sitkana smooth =10.44**, crevice =62.92***, L. scutulata smooth =42.70***, crevice =63.97***).
In the low density cages L. sitkana grew significantly more in the crevice than in the smooth treatment (F value d.f.= 1/∞ was 13.19***).

under different weather conditions. Under bad weather conditions of desiccation or during storms significantly more L. sitkana than L. scutulata evidently are generally found in crevices. On sunny and calm days with relatively high humidity L. sitkana appear more commonly to be outside of crevices than L. scutulata (Table 2-10).

e) Significantly greater recruitment of littorines occurred at the sheltered sites than at the intermediate and exposed sites (Table 2-11). In every case recruitment was greater inside crevice cages than inside smooth cages. In these situations L. sitkana had a greater recruitment rate than L. scutulata.

Discussion

Two resources, food and shelter, can become important factors in limiting the distribution and abundance of littorines. In the summer, when algal growth is inhibited due to desiccation, littorines at high densities can die from starvation. During the winter, storms would sweep away any littorine not found in shelters. Growth responses by experimental animals substantiate the importance of food in the summer and shelter in the winter.

Littorina sitkana appears more sensitive to food levels than L. scutulata in that growth and survivorship appears to be inversely related to density (Behrens, 1971). Littorina scutulata grow less, but survive better as the densities increase. Since for animals of a given size, L. scutulata have finer radular teeth than L. sitkana, they may be able to utilize a lower standing crop of food. Littorina scutulata often decreased in size (e.g. erosion is greater than growth of shell), whereas *L. sitkana* either maintained their size or else died. Higher growth rates together with a greater locomotor activity would indicate that *L. sitkana* may have a higher metabolic rate and may require more food per individual than *L. scutulata*.

The greatest recruitment of littorines occurred in the most sheltered habit and inside crevice cages. Both species thus seem to benefit from shelter during their juvenile stages. Adult *L. sitkana* seem more sensitive to shelter than *L. scutulata*, but also are better able to locate shelter than *L. scutulata*. *Littorina sitkana*'s greater need for shelter is borne out by experiments in that *L. sitkana* tended to grow better in crevice cages during the winter and spring than in smooth cages. This effect was not as consistently observed for *L. scutulata*.

Species interaction between *Littorina scutulata* and *L. sitkana* appears to be very subtle. It cannot be detected over a short period, nor under relatively benign conditions. Since littorines do not discriminate against individuals of the opposite species, no antagonistic behavior seems to be involved in the interaction.

Littorina sitkana appear to be more sensitive to environmental changes than *L. scutulata*. They tend to be the first ones to seek out shelter when desiccation sets in or storms strike, but also the first ones to come out of shelters and forage when conditions are favorable. It is probable that the greater utilization of crevices by *L. sitkana* under stormy conditions is responsible for the observed species interaction effects. Under bad weather conditions *L. sitkana* appear to be better competitors for crevices than *L. scutulata*. One would expect the 10 *L. sitkana* in mixed species cages to benefit more from the 12 crevices than the 20 *L. sitkana* in the single species cages. Likewise, single species *L. scutulata* would benefit more from crevices than *L. scutulata*. caged with *L. sitkana*.

Littorina scutulata's advantage in its resistance to being dislodged by waves appears to be counterbalanced by *L. sitkana*'s superior ability to seek out crevices. The greater survival rate of *L. scutulata* is counterbalanced by *L. sitkana*'s greater recruitment rate. *Littorina scutulata* can survive on very little food, but *L. sitkana* is better able to locate food. The balancing effects of these differential advantages may be part of the mechanism allowing these two species to co-exist over such a wide range of habitats.

CHAPTER 3

INTERTIDAL ZONATION OF LITTORINA SCUTULATA AND LITTORINA PLANAXIS

Two common periwinkles of the genus Littorina inhabit the upper intertidal and spray zones of the California coast. Littorina scutulata (Gould, 1849) has the widest geographic distribution; occurring from Alaska to Baja California whereas L. planaxis (Philippi, 1847) occurs from southern Oregon to Baja California. Locally, L. scutulata is found on wave exposed as well as on sheltered shores. It lives throughout the intertidal range, but its greatest abundance is in the barnacle zone. Littorina planaxis predominates in wave exposed places and seldom is found in harbors. It occurs below the high water mark in sheltered habitats, but in exposed habitats it is found only in the splash and spray zones; above the high water mark.

Subtidal marine animals live in a physically benign environment. The higher an intertidal organism lives on the shore, the longer it is exposed to air and the harsher the physical environment becomes. Connell (1961) suggests that as a rule, harsh physical factors such as desiccation and temperature extremes set the upper limit to the distribution of intertidal organisms and biological interaction such as predation and competition set the lower limits of distribution.

In the absence of heavy wave wash and spray, L. planaxis and L. scutulata have similar upper limits to their vertical distribution. In exposed habitats the two species, however, occupy discrete zones with very little overlap (Fig. 3-1). I decided to determine the factors responsible for this discrete zonation pattern with L. planaxis living in the spray zone and L. scutulata below the high water mark.

Possible Factors Limiting the Upper Distribution of Littorina scutulata

Desiccation

Mattox (1949) found that the higher an intertidal species is found on the shore, the more resistant it is to desiccation. Littorines are very well adapted for shore life, for under drying conditions they will close their horny operculum and glue themselves to the substratum by means of mucus. Whipple (1966) claims that Littorina pintado survive at least two years without being submerged in water or being fed. Littorina planaxis can be kept out of water for at least 64 days without being submerged in sea water (Hewatt, 1937). Unpublished accounts set the record time for L. planaxis at 148 days desiccation without lethal effects.

For equal sized animals, Littorina scutulata has a faster rate of water loss than L. planaxis (Bowlus, 1966). Unfortunately, no studies have been done on relative survival of the two littorine species exposed to desiccation. I kept 30 animals of each species out of water next to a water table for one month with no lethal effects. Just on the basis

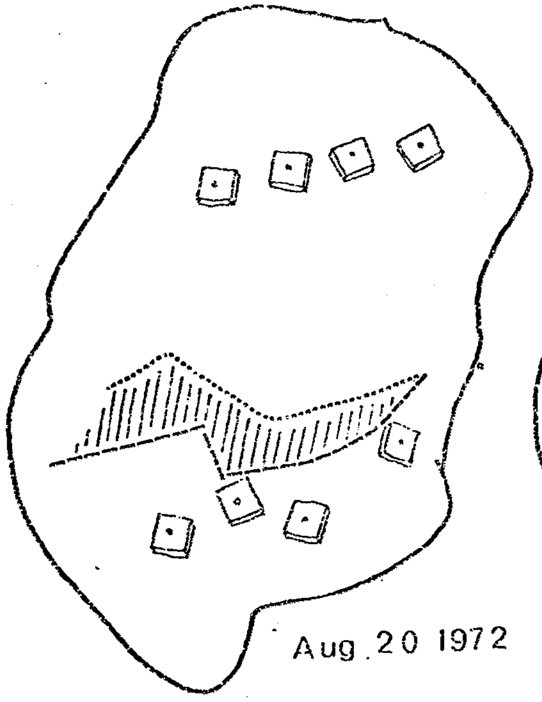
Fig. 3-1 Zonation of *Littorina* at Hopkins Marine Station.

------ Upper limit of *L. planaxis*

▬▬▬▬ Lower limit of *L. planaxis*

•••••••• Upper limit of *L. scutulata*

\\\\\\\ Region of overlap



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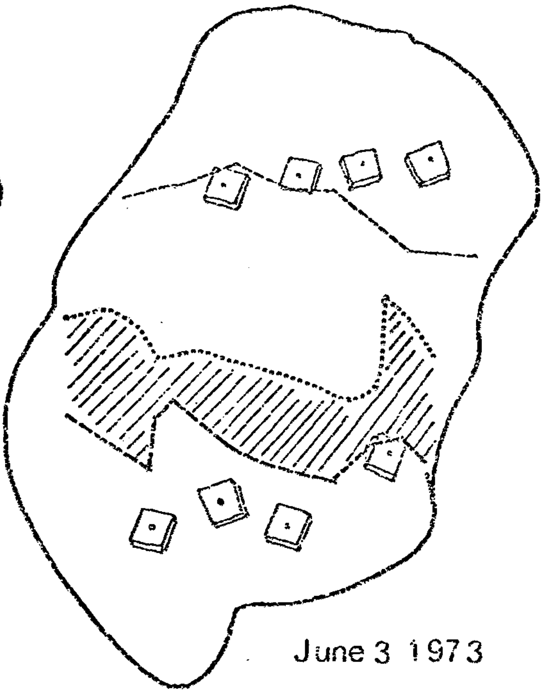

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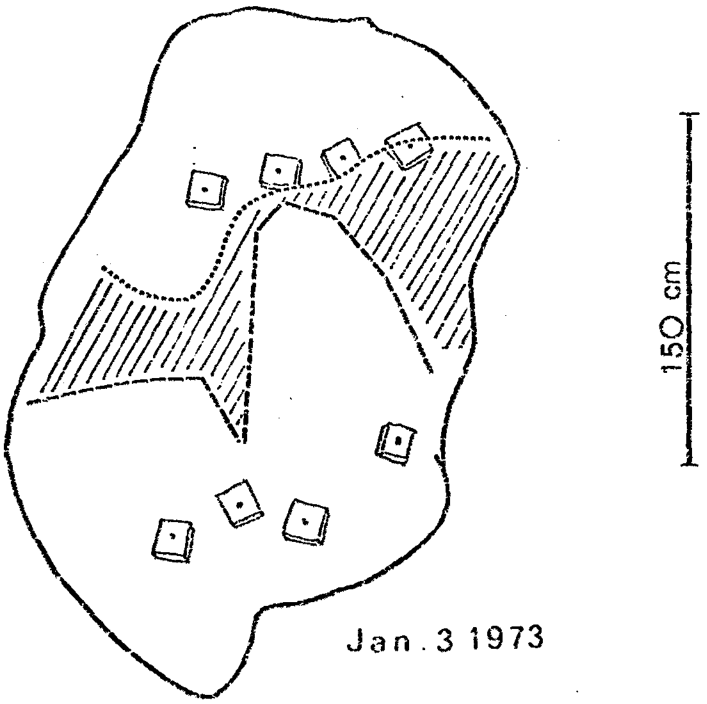

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of size, since *L. scutulata* tend to be smaller than *L. planaxis*, one would not expect them to resist desiccation as well as *L. planaxis*.

Starvation

Bock and Johnson (1968) propose that the inability of *L. scutulata* to eat microscopic algae and lichens may explain the absence of this species in the spray zone. At Friday Harbor, Washington, *L. scutulata* ate almost exclusively microscopic algae (Behrens, 1971). Remnants of black lichens were found in the feces of *L. scutulata* collected from the lower spray zone at Hopkins Marine Station. *Littorina scutulata* definitely does not require macroscopic algae, but it is possible that food in the spray zone is too scarce for maintenance of *L. scutulata*.

Competition with *Littorina planaxis*

It is also possible that *Littorina planaxis* may keep *L. scutulata* from penetrating the spray zone. On the southern Oregon coast where *L. planaxis* is extremely scarce, large *L. scutulata* live in the spray zone above the high water mark and small *L. scutulata* live in the intertidal zone below the high water mark. It is postulated that in the absence of *L. planaxis*, *L. scutulata* is capable of exploiting the spray zone.

Possible Factors Limiting the Lower Distribution of *Littorina planaxis*

Drowning

Ricketts and Calvin (1968) erroneously claim that littorines drown when continually submerged. An obvious refutation of this theory is the existence of tide pool littorines of both species. The littorines in some large pools appear to be permanently submerged residents. Ralph Dykes (personal communication), caged *L. planaxis* in a submarine canyon for 3 months with no detrimental effect.

Starvation

Bock and Johnson (1968) suggest that *L. planaxis* are unable to eat macroscopic algae and thus are not found low on the shore. If this hypothesis were true, *L. planaxis* should have reduced survival and growth rates low on the shore in comparison to the spray zone.

Wave Force

Bigler (1964) found that wave shock was capable of removing a sizable number of *L. planaxis* from the shore. Differences in susceptibility to being dislodged by wave action may account for some aspects of the final disposition of both species.

Competition with *Littorina scutulata*

Littorina scutulata may be more efficient than *L. planaxis* in utilizing resources such as food supplies within the intertidal zone and thus may keep *L. planaxis* out of this zone. Species interaction experiments carried out in the field would test for this hypothesis.

Predation

Bigler (1964) tested various intertidal predators as well as ground squirrels and birds with respect to their ability to eat L. planaxis. The only predators that would take L. planaxis were crabs (Cancer antennarius), starfish (Patiria miniata and Leptasterias pusilla), and the snail Acanthina spirata. The crab and starfish are low intertidal species and would present a threat to dislodged snails; but Acanthina spirata penetrates the lower limits of L. planaxis distribution. Bigler observed frequent Acanthina attacks on L. planaxis in the field and describes how this predator catches and consumes its prey. One can get an estimate of the proportion of deaths due to Acanthina predation, since Acanthina leaves a characteristic drill mark on the prey's shell next to the columella. By looking at empty shells obtained from hermit crabs, Bigler found a drilling frequency of 20% and concluded, that Acanthina must be an important predator on L. planaxis. Differential behavioral responses of the two littorine species to Acanthina may help explain the observed zonation of the littorines.

Feeding Experiments

Materials and Methods

To determine whether Littorina scutulata and L. planaxis specialize on different diets, five animals of each species were collected from different levels on the shore. Animals were isolated and put into individual petri dishes with a thin layer of sea water. After a day the dishes were examined for the presence of fecal pellets.

Littorines of three species were observed feeding on a patch of the green macroscopic algae Enteromorpha sp. in the laboratory. Each animal was isolated and put into an individual petri dish with a thin layer of sea water. After 4 hours these dishes were examined for the presence of fecal pellets.

Results

Both *Littorina scutulata* and *L. planaxis* collected from higher shore levels contained remnants of black lichens in their feces (Table 3-1). Both species collected from the barnacle zone produced from light to dark brown fecal pellets of unidentifiable digested matter.

All the animals observed grazing on *Enteromorpha* produced fecal pellets. Some of the fecal pellets were of the same shade of green as *Enteromorpha* and some of them were brown. Adding 1% HCL, to stimulate the digestive process, to the green pellets turned them brown.

The fact that *Littorina scutulata* and *L. planaxis* produced identical looking fecal pellets in the two experiments would indicate that these two species are capable of handling the macroscopic algae *Enteromorpha* and black lichens equally well.

Wave Force Experiment

Material and Methods

One hundred littorines of each species were collected at Hopkins Marine Station, matched for size and marked with cellulose base paint. These animals were allowed to attach to a sloping rocky intertidal protuberance which was facing the ocean. A gully formed the base of this protuberance. After one high tide the snails remaining attached to the rocky protuberance were counted and all the animals found in the gully were assumed to have been dislodged by waves.

Results

For equal size animals, Littorina planaxis are better able to remain attached to the substrate than L. scutulata (Table 3-2). This information appears contradictory, since L. scutulata in the intertidal zone are exposed more to the direct impact of the waves than L. planaxis in the spray zone. The size frequency distribution of littorines from the experimental site, however, reveals that Littorina scutulata are considerably smaller than L. planaxis (Fig. 3-2). The smaller L. scutulata can persist in the intertidal exposed to heavy surf by seeking shelter in barnacle or rock crevices. Animals too large to fit into these crevices would have to migrate out of the wave zone or be dislodged.

Competition Experiment

Materials and Method

In order to test the hypotheses:

a) Littorina planaxis prevents L. scutulata from exploiting the splash zone;

b) L. scutulata prevents L. planaxis from exploiting the intertidal zone

I attached 24 cages to the rocky shore at Hopkins Marine Station on December 28, 1970. The cages, inverted wire mesh baskets (13 by 13 by

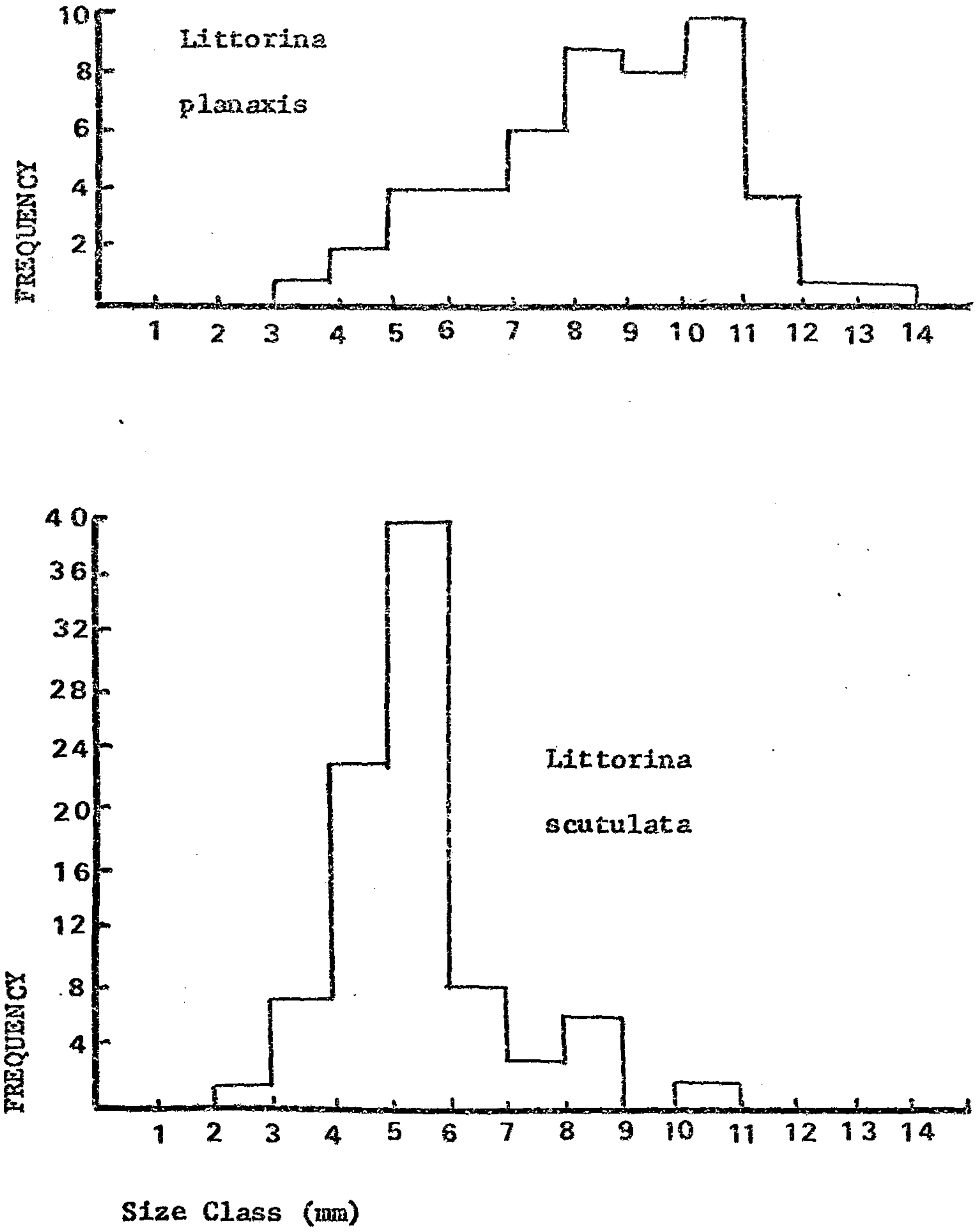


Fig. 3-2 Size Frequency Distribution of L. planaxis and L. scutulata at Hopkins Marine Station.
Area sampled consisted of eight 20 by 20 cm quadrats taken in the high intertidal and in the spray zone.

3 cm), were made from square pieces of stainless steel hardware cloth with 3.2 meshes to the cm (Figs. 2-5, 3-3). Twelve .636 cm wide holes, 2½ cm deep were drilled in the slash zone and 12 in the high interdial using a Skil rotohammer. Plastic screw anchors were inserted into holes and cages were attached using plastic washers and stainless steel screws. "Marine-Tex" (epoxy putty, Travaco Laboratories, Chelsea, Mass.) or "Life Calk" (Boat Life Division, Flo-Paint Inc., 545 49th Ave., Long Island City, New York 11101) was run along the edges of cages so that littorines could not escape through the rock-cage interface.

Littorines of both species were collected from surrounding areas and matched for size. The lips of snails were marked using cellulose base paint (techpen paint 161 Coolide Ave., Mark-Tex Corp., Engelwood, N.J.) so that growth could be measured as lip increments. Twenty marked animals were introduced into each cage. Two of the cages at each level contained 20 _L. planaxis_, two contained 20 _L. scutulata_ and four contained 10 animals of each species. The initial experiments were designed to test the hypothesis that species interaction results in sharp zonation. Later experiments were modified to determine whether increasing snail density would magnify any competition effects. Cages were monitored in spring, late summer and winter; new experiments were set up in spring and winter. Survivorship data were analyzed using X^2 tests and growth data using analysis of covariance.

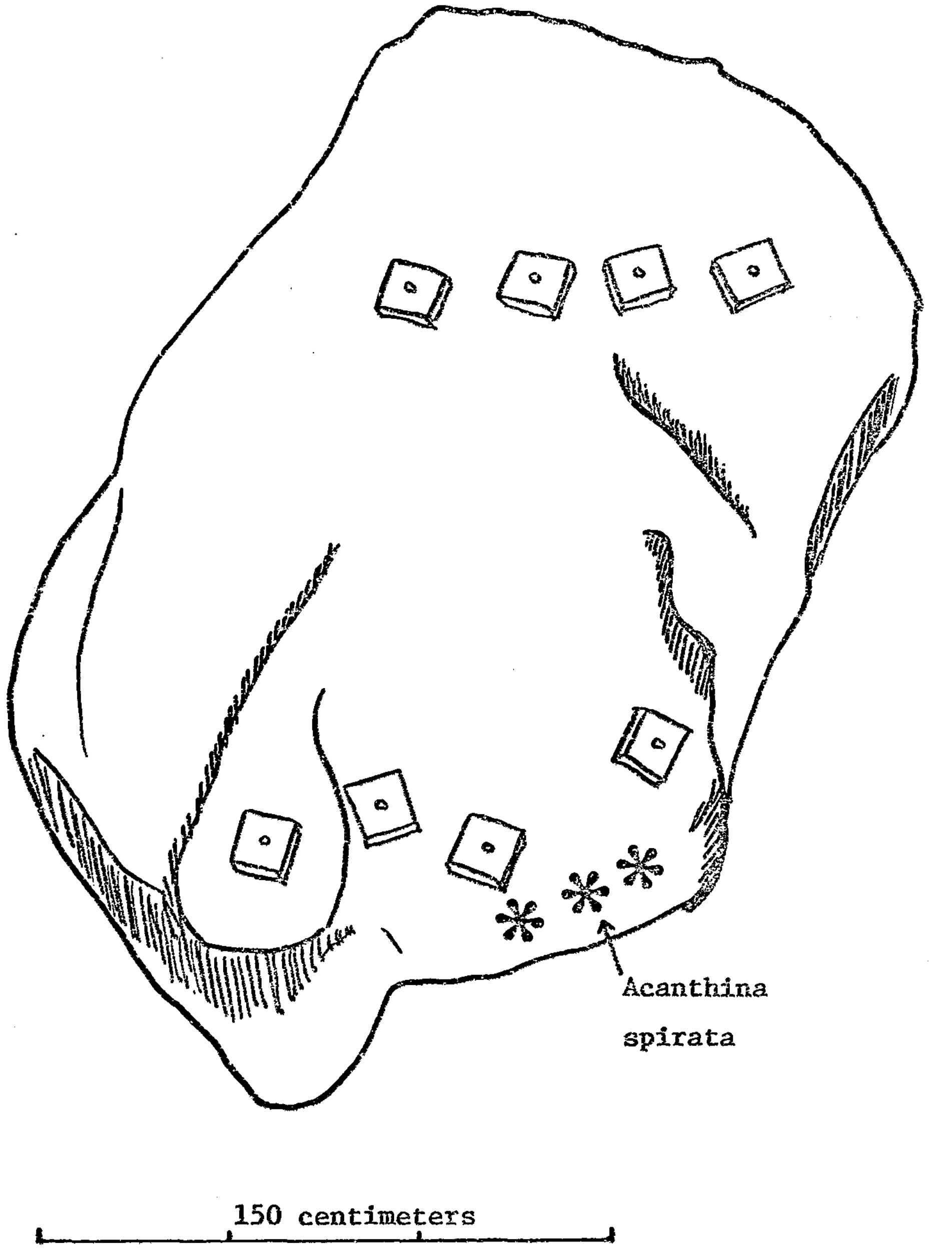


Fig. 3-3 Upper Distribution of <u>Acanthina</u> <u>spirata</u> in Relation to Experimental Cages.

Results

Tidal Level Effects

Desiccation does not appear to prevent *Littorina scutulata* from living in the splash zone. At no time did this species survive more poorly in the splash than it did in the intertidal zone. The cages may have offered some shelter from desiccation, for in the summer all the *L. scutulata* tended to aggregate in the bottom corner of the upper cages (Table 3-3). Miyamoto (1964) found that aggregation behavior in *L. planaxis* increased with an increase in temperature and also with a decrease in moisture, and suggests that it may be an adaptive mechanism to minimize desiccation. Cage walls and corners would have the same sheltering quality that long vertical rock crevices have in allowing littorines to extend further up the shore than they are found on adjacent sun exposed sites.

In two out of three years, *Littorina planaxis* survived just as well in the intertidal as they did in the spray zone. In August 1971 animals of both species in the lower cages appeared sick and by December 1972 only 36% of the *B. planaxis* at the low level survived as opposed to 88% at the high level. For *L. scutulata* the differential mortality at the two tidal levels was not as pronounced in that 10% survived at the low level as opposed to 18% at the high level (Tables 3-4, 3-5).

An unusual high number of Pelagic Cormorants were roosting on the experimental site in the winter of 1972. The upper rock was totally covered with bird droppings except inside the cages in which the grazing action of the snails cleaned the surfaces. Comparing survivorship data of single species cages for 1971 with 1972 indicates that the upper cages showed the same survival rates for the two years, whereas the lower *L. planaxis* cages showed a decrease in survival in 1972 (Table 3-6).

I suspect that death due to parasitism might have been responsible for the decrease in survival at the low tide level in 1972. The incidence of parasitism in snails appears to be directly related to the density of bird colonies. Since there were so many birds in my study area, the snails' chances of being inoculated with parasites, mainly fluke larvae, would have been quite great. Oyster culturists use a simple trick to rid oysters of their parasites before taking them to market. They simply expose them to the desiccating and heating effect of the sun. This treatment kills the parasites but not the oysters. Similarly, the littorines caged at the upper level may have been avoiding parasitism in this way. Surviving littorines were examined for signs of parasitism in December 1972 with negative results. This is to be expected, if selection for parasite susceptibility had already taken place.

Species Interaction Effects

At the low tidal level, both species survived equally well in mixed and single species treatments at all times (Table 3-7). This would indicate that *Littorina scutulata* does not prevent *L. planaxis* from living lower on the shore.

It would appear, however, that Littorina planaxis did inhibit the survival of L. scutulata in mixed species cages at the high tidal level in two out of three experiments. This inhibitory effect of L. planaxis on L. scutulata at this level is probably linked to resource competition, for in the winter of 1972 the effect was increased with snail density (Table 3-7). No consistent effect of L. scutulata on L. planaxis was observed.

Another way of looking at species interaction is to compare single species low density cages with mixed species high density cages. In this case we are looking at the effect of adding 20 individuals of species B to a constant number of 20 individuals of species A. Table 3-8 shows that the addition of L. scutulata increases the survival of L. planaxis. However, the addition of L. planaxis decreased the survival of L. scutulata. Littorina planaxis have finer toothed radulae than L. scutulata (Table 3-9), and may be grazing the algae to such a low standing crop that L. scutulata cannot maintain themselves. Likewise the grazing action of L. scutulata with their coarser radulae may not affect the potential food for L. planaxis.

Density Effects

The survivorship data indicate that Littorina planaxis are relatively insensitive to increased density. Littorina scutulata, however, survived better at low density than at high density in three out of four cases (Table 3-10).

Data for the period winter to spring 1972 indicate that doubling the density had no effect on *L. planaxis* growth response and that quadrupling the density decreased growth rate by only 20% (Table 3-11). This relative insensitivity of *L. planaxis* to density may be a reflection of this species' ability to utilize lower food abundance levels than *L. scutulata*.

Predation Experiments

Materials and Method

Hermit crabs inhabiting *Littorina* shells were collected from various sites to determine the percentage of littorine mortality due to *Acanthina spirata* predation. Each hermit crab shell was measured to the nearest 1/20 of a mm and examined for drill holes.

In order to determine behavioral responses of littorines to *Acanthina*, the empty cages of the competition experiments were used. One *Acanthina* was introduced into 6 of the 12 lower cages on June 2, 1973. The next day 10 *L. scutulata* and 10 *L. planaxis* were added to each of the 12 lower cages. After each high tide the proportion of littorines in the lower one eighth of the cages was noted. Similar experiments were run in September using 4 adjacent stainless steel enclosures 20 by 40 cm (Fig. 5-1). Six *Acanthina* were placed at the bottom of two of the fenced off areas. Six hours later 25 *L. planaxis* and 25 *L. scutulata* were added to each enclosure. Three hours later, just after a high tide, the positions of the snails for each treatment were noted.

Results

Significantly more *L. planaxis* shells obtained from hermit crabs around Hopkins Marine Station showed drill marks than *L. scutulata* shells (Table 3-12). Menge (unpublished manuscript) found that *Acanthina punctulata* from southern California prefers *L. planaxis* over *L. scutulata*. From an energetic standpoint, it would pay for *Acanthina* to choose *L. planaxis* over *L. scutulata* since for animals of a given biomass *L. scutulata* takes longer to drill and eat than *L. planaxis* (Fig. 3-4).

Size frequency data reveal, that larger *Littorina scutulata* may be preferred over smaller ones since a significantly higher proportion of *L. scutulata* were drilled above 8 mm in length than below 8 mm (Fig. 3-5, Table 3-13). This preference would also be adaptive from an energetic standpoint since the energy expenditure in drilling a larger *L. scutulata* would not be much greater than drilling a smaller one, but the energy return from a larger snail would be so much greater. No size preference could be detected for the *L. planaxis* shells drilled by *Acanthina* in that most of the animals were larger than 6.5 mm in length (equivalent in biomass to a 8 mm *L. scutulata* [Figs. 3-6, 3-7]).

When no *Acanthina* were present, *L. planaxis* were evenly distributed in the cages, e.g. 1/8 (24/190) of them were found in the bottom 1/8 of the cages (Table 3-14). *Littorina scutulata* had a greater tendency to aggregate in the bottom of the cage. Adding *Acanthina* to the cages had the effect of causing animals to spend more time in the upper parts of the cages. The percent *L. scutulata* remaining in the bottom parts of

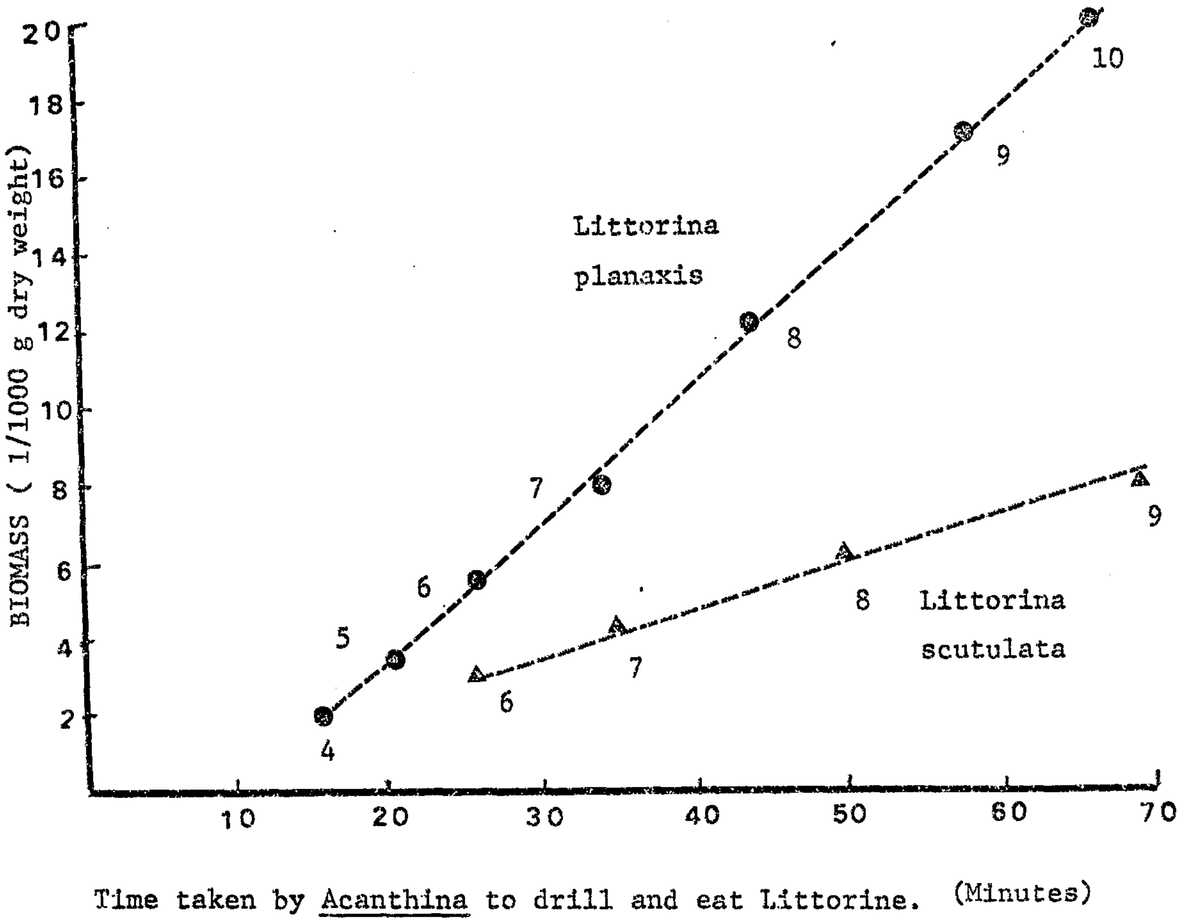


Fig. 3-4Time taken by Acanthina to extract a given biomass of L. planaxis and L. scutulata. Numbers indicate corresponding shell height of littorines in mm. Data adapted from Menge, 1973.

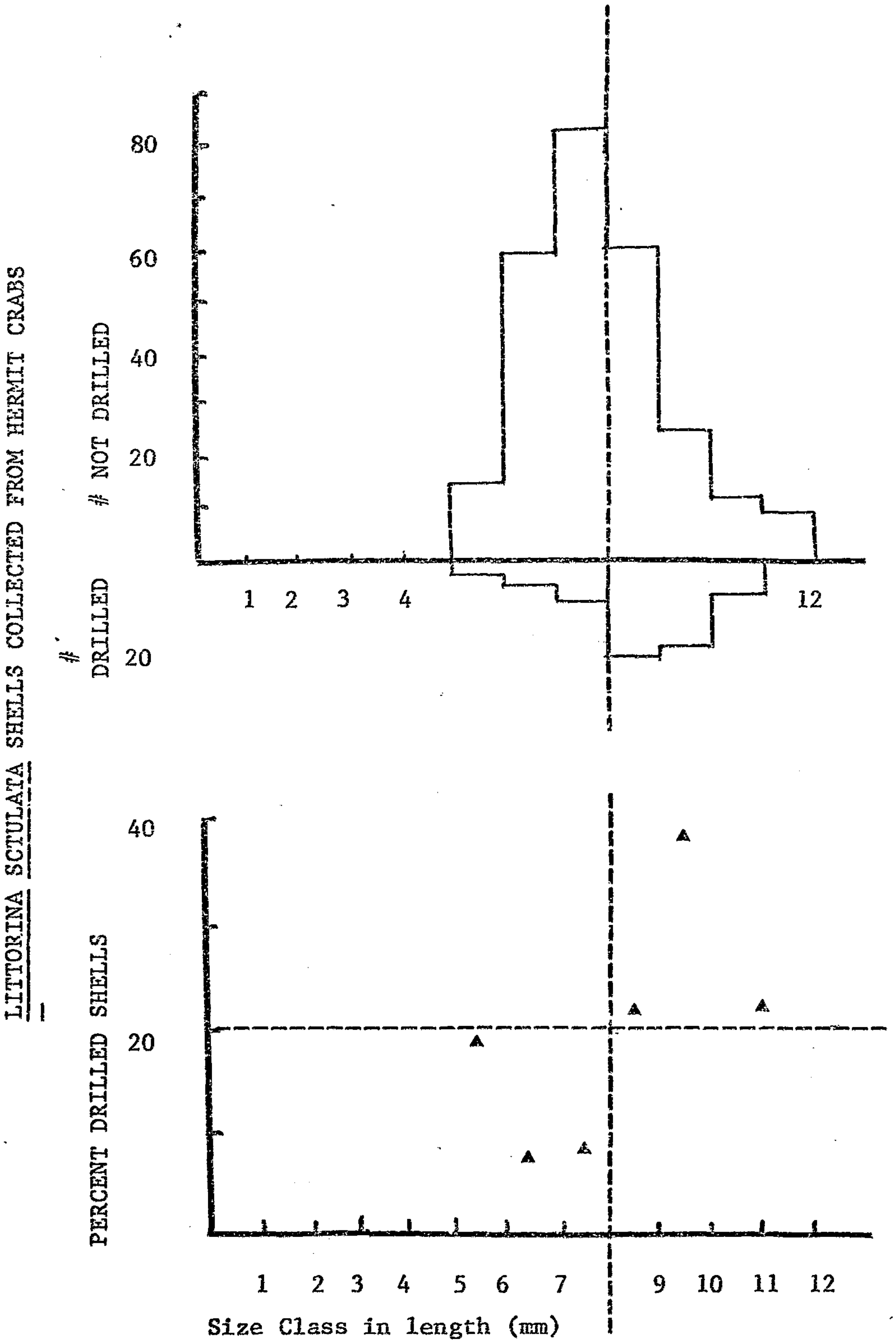


Fig. Number and Percent of Littorina scutulata shells drilled by Acanthina as a function of size class.

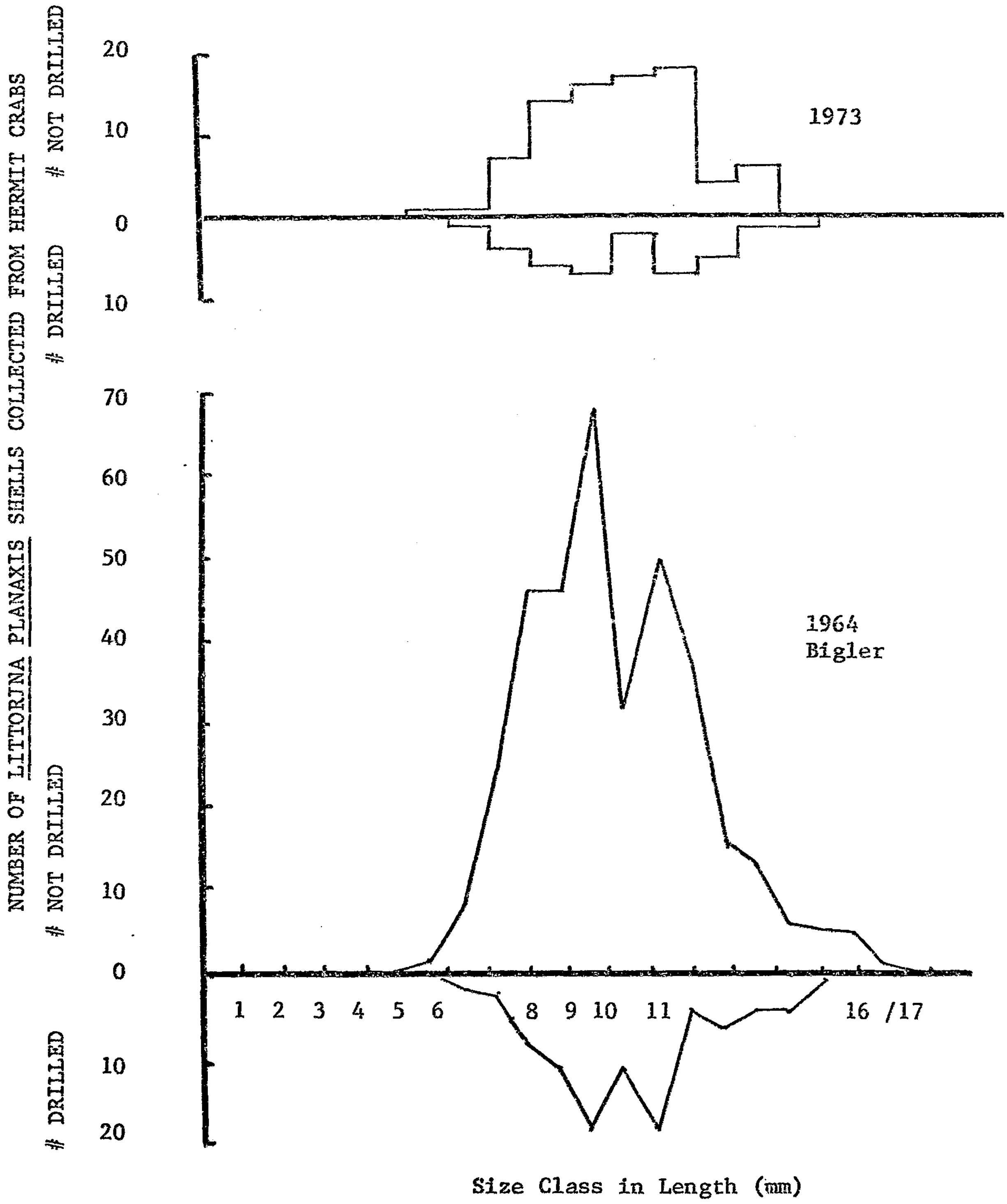


Fig. 3-6 Number of Littorina planaxis shells drilled by Acanthina as a function of size class.

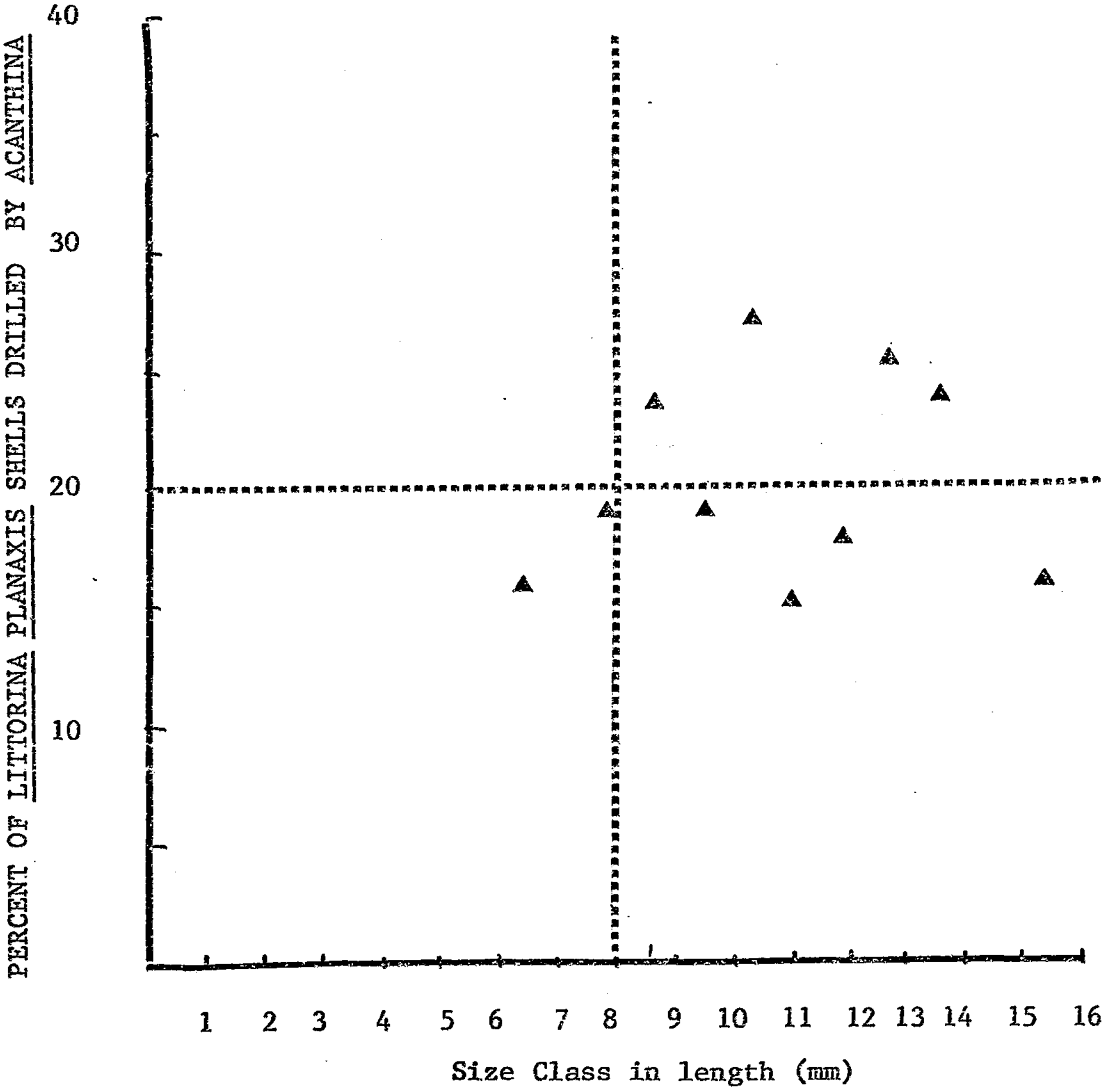


Fig. 3-7 Percent of Littorina planaxis shells drilled by Acanthina as a function of size class. (Pooled 1964 and 1973 data)

the cages was reduced by one half from 33% to 17%. The relative reduction for L. planaxis was much greater, from 12.6% to .08%.

Discussion

Both species of littorine have to escape the hazards of wave action and intertidal predation. Littorina planaxis is adapted to the harsh spray zone habitat above the high water mark and thus escapes both these factors. Littorina scutulata's solution to avoiding these factors is in being small and hiding inside crevices. The predatory snail Acanthina spirata appears to be size selective in that it takes a higher proportion of snails above 8 mm in length than below 8 mm. Snails inside crevices are less likely to be dislodged by waves than on smooth surfaces. In wave sheltered and predator free sites, L. planaxis will live lower on the shore and L. scutulata will be larger.

Inside the cages L. scutulata survive in the splash zone just as well as in the intertidal. The presence of L. planaxis tended to decrease the survival of L. scutulata in the higher cages. Littorina planaxis are probably better competitors for limited amounts of food than L. scutulata. Conversely, the presence of L. scutulata had no effect on the survival of L. planaxis at the lower level. Competition with L. scutulata thus is not preventing L. planaxis from living lower on the shore.

In one year out of three, Littorina planaxis in the intertidal had a higher mortality rate than in the spray zone. It is believed that parasitism may have been responsible for this effect, since during this year an unusual high number of pelagic cormorants roosted on the experimental rocks thus greatly increasing the snails' chances of ingesting fluke eggs from the bird feces. Animals living in the dry cages in the splash zone may have been immune to parasitism.

Wave spray as well as the physical presence of the predatory snails *Acanthina spirata* induces *L. planaxis* to migrate up the shore. This behavioral trait is an adaptation to being dislodged by the wave of the incoming tide and to being preyed upon.

CHAPTER 4

THE ROLE OF TIDE LEVEL CONDITIONING AND PREDATORS ON THE UPWARD MOVEMENT OF *LITTORINA PLANAXIS*

Littorines are most active during the rise and fall of the tides. Under continuously dry conditions littorines are quiescent, withdrawing into the shell and closing their operculum. As the moisture content of air and substratum increases from the incoming tide, littorines open their operculum and initiate feeding excursions. On vertical surfaces these excursions are in an upward direction. As the tide recedes and desiccation sets in, littorines reverse the direction of their migration and seek out shelter in damp crevices. *Littorina planaxis* in wave exposed habitats limit their vertical migrations to the spray zone. Individuals transplanted from the spray zone to a level below the high water mark will migrate back into the spray zone. Bock and Johnson (1968) suggest that this negative geotaxis is an important factor limiting the lower distribution of *L. planaxis*. Any such behavior, however, must have an evolutionary reason. This study seeks to investigate the effect of tide level conditioning as well as the presence of predators on the negative geotactic behavior of *L. planaxis*.

Materials and Methods

Four adjacent enclosures (20 by 40 cm) attached to a vertical rock face in the splash zone at Hopkins Marine Station were used for the upward migration experiment (Fig. 4-1). These enclosures consist of stainless steel mesh fences 3 cm high glued to the substrate with Marine Tex (Travaco Laboratories, Chelsea, Mass.).

At low tide six individuals of the predatory snail *Acanthina spirata* were placed on the lower wall of two enclosures and six individuals of the herbivorous snail *Tegula funebralis* into the other two enclosures. Two hours later 50 *Littorina planaxis* were added to the lower section of each enclosure. Half of the littorines in each enclosure had been previously caged for four months in the splash zone above the high water mark and half below the high water mark. Initially both batches of littorines were collected from the same location. Animals conditioned to the lower level were painted orange and those conditioned to the splash zone blue.

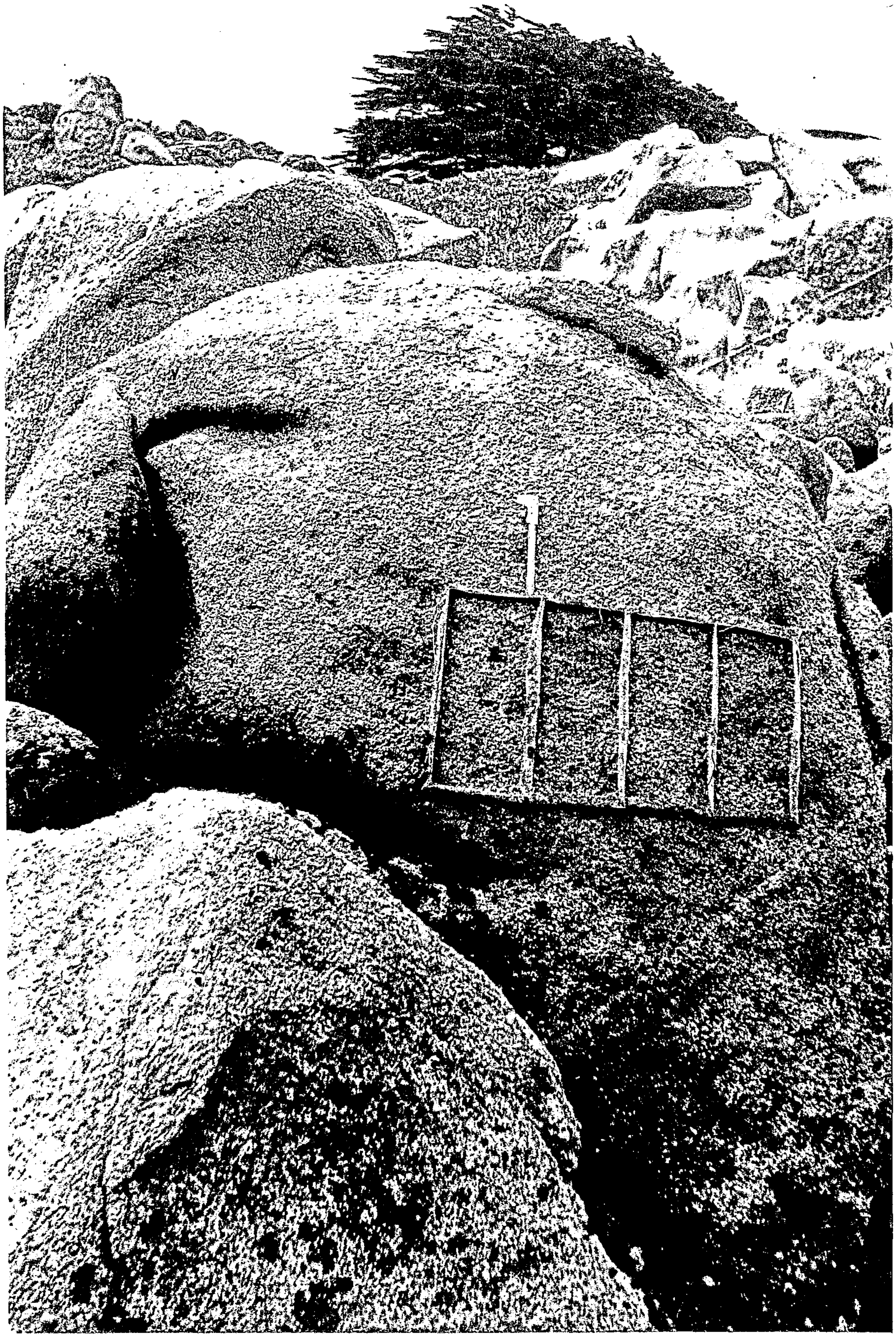
The position of animals was noted periodically as they moved up the rock with the incoming tide. For each 5 cm an animal moved up the enclosure, it received a score of one point. In order to discount dislodged animals, the score for each treatment was divided by the number of animals remaining.

Results

The rate of upward migration of *Littorina planaxis* increased with the amount of spray and wave wash (Fig. 4-2).

Animals conditioned to the spray zone showed a greater tendency to move up the shore than animals conditioned to the high intertidal

Fig. 4-1 Experimental Enclosures at Hopkins Marine Station



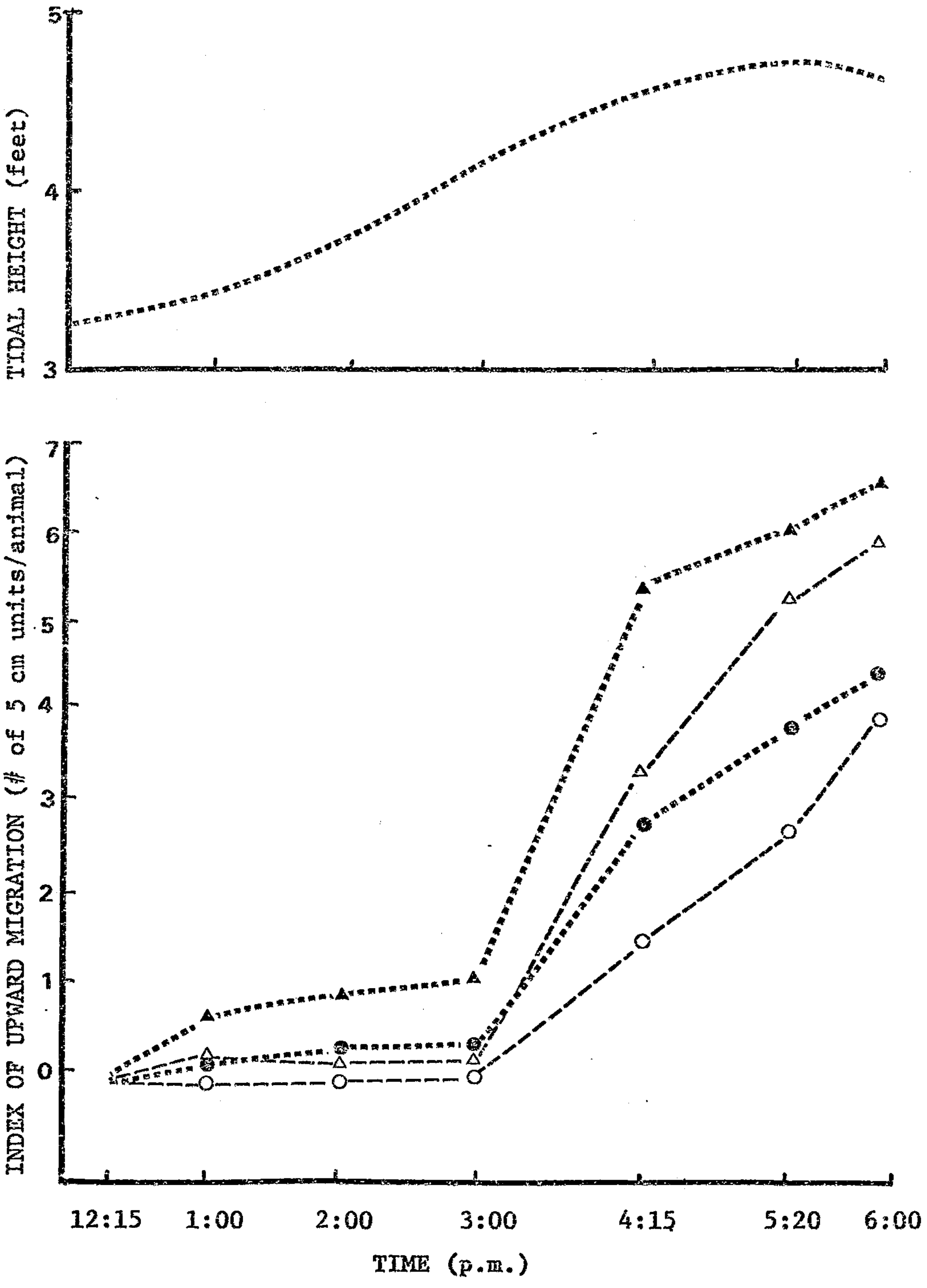


Fig. 4-2 Upward Migration of L. planaxis under various Treatments.

Splash Zone Conditioned	Lower Level Conditioned
▲ with Acanthina	● with Acanthina
△ without Acanthina	○ without Acanthina

(Table 4-1). The presence of the predator *Acanthina* also increased the rate of upward migration (Table 4-1).

After two consecutive high tides, significantly more spray zone conditioned *Littorina planaxis* were found on the rock above the enclosures than their low level conditioned counterparts (Table 4-2).

A significantly greater number of low conditioned animals were dislodged by waves than were high conditioned animals (Table 4-3).

Discussion

Littorines only feed when the substrate is moist. High shore littorines thus have less time available for feeding than those living low on the shore. Newell, et al. (1971) finds that high shore *Littorina littorea* compensate for the reduced feeding time by increasing their radular activity when immersed. A similar compensation mechanism for reduced feeding time may be operating in splash zone conditioned *L. planaxis*. Radular activity was not measured, but splash zone conditioned animals became active at a lower moisture level than their low zone conditioned counterparts. An increased sensitivity to moisture levels would assure splash zone conditioned *L. planaxis* the longest possible time for feeding.

The increased upward migration of splash zone conditioned *Littorina planaxis* may be an adaptation to escaping the dislodging effects of waves and splash. After two consecutive high tides, more spray zone *L. planaxis* were found on the rock above the enclosures than low level *L. planaxis*. Since the number of animals remaining in the enclosure was the same, a significantly greater number of low level *L. planaxis* must have been dislodged by waves.

The presence of the predatory snail *Acanthina spirata* resulted in a magnification of the upward migration of *Littorina planaxis*. Tittle (1964) found that this escape response was elicited by a protein-like chemical produced in the foot and deposited in the mucus trail of such predatory snails as *Acanthina* and *Thais*. Herbivorous snails such as *Tegula* do not produce such a chemical and thus do not elicit an escape response in *Littorina*. There would be strong survival value in being able to detect the presence of a predator and moving out of its range.

It appears that strong selection must be operating for the tendency of *L. planaxis* to move into the spray zone. This habitat may be very harsh, but it is free from the hazards of waves and predators.

CHAPTER 5

NICHE RELATIONSHIPS IN LITTORINES

The three species, *Littorina sitkana*, *L. scutulata* and *L. planaxis* exhibit different physiological tolerances, behavioral trait life history phenomena and environmental ranges. For any one of these characteristics, *Littorina sitkana* and *L. planaxis* always occupy opposite extremes of the scale and *L. scutulata* the middle (Table 1).

Littorina sitkana is able to add as much as 82% new body weight in two months. Under the same conditions, *L. scutulata* only added 7% (Behrens, 1971). Growth, measured at Hopkins Marine Station, was always much lower for *L. planaxis* than for *L. scutulata*.

Faster growth rates in *L. sitkana* are related to higher mortality and recruitment rates. Only 9% of 560 experimental *L. sitkana* survived one year compared to 49% of the *L. scutulata*. Three years after the experiment was discontinued five original *L. scutulata* were recovered on the shore. This observation together with growth data leads me to suspect that *L. sitkana* live from 1 to 2 years and *L. scutulata* for about 7 years. I suspect that *L. planaxis*' life span would be even longer than 7 years, since at Hopkins Marine Station they grew less but were much larger than *L. scutulata*. More juveniles were recruited from *L. sitkana*'s lecithotrophic eggs than from *L. scutulata*'s planktotrophic eggs (Table 2-12). Recruitment of *L. planaxis* at Hopkins Marine Station was always much poorer than that of *L. scutulata*.

According to Murdoch (1970), long-lived species such as elephants, generally are more independent of environmental changes and thus tend to be numerically constant over time. Short lived species such as bacteria react faster to fluctuations in environmental favorability by increasing or decreasing their number. These generalizations also seem to apply to *Littorina sitkana* and *L. planaxis*. *Littorina planaxis* are long lived, very tolerant of adverse physical conditions but unresponsive to environmental favorability. The reverse is true for *L. sitkana*. In good years juvenile *L. sitkana* are found at extremely high densities in the splash pools on the west coast of Vancouver Island. In other years, the same pools may dry up completely or fill with rain water and support a fresh water fauna. Great variations in density were also recorded for *L. sitkana* on Galiano Island mud flat but not for *L. scutulata* (Fig. 5-1). Since *L. planaxis* and *L. scutulata*, unlike *L. sitkana*, have planktonic larvae, any recruitment response to environmental favorability would not be detected in the same environment.

Field experiments indicate that *L. sitkana* is very responsive to intraspecific crowding. The growth response in *L. sitkana* is directly related to grazing area per individual. Decreasing the observed grazing area per *L. scutulata* by one half caused a significant decrease in growth rate; however doubling the grazing area had no effect. Similar results were obtained for *L. planaxis* but at much lower grazing areas per individual (Table 5-2). When food gets scarce, *L. sitkana* exhibit density dependent mortality. This response was not exhibited by

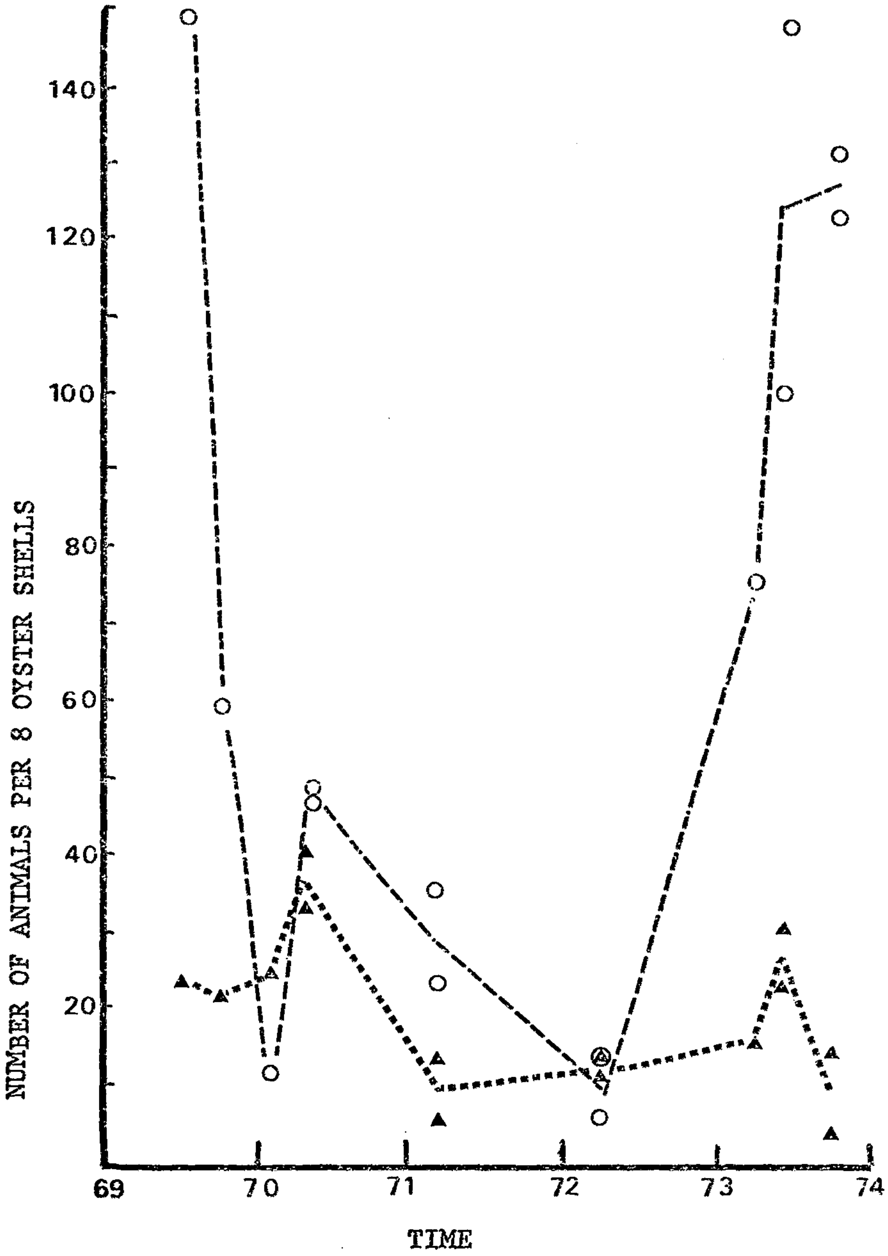


Fig. 5-1 Changes in Number of Littorines on Galiano Mud Flat from 1969 to 1973.

○ L. sitkana ▲ L. scutulata

L. scutulata under the same conditions (Fig. 2-9), nor for *L. planaxis* caged at four times normal density.

The observed differences in growth and mortality responses may in part be related to the anatomy of the food extracting structures, or radulae, of littorines. The spacing, size shape and hardness of the teeth would determine the type of food that can be scraped. For equal size animals, *L. sitkana* has the coarsest and *L. planaxis* the finest radular teeth (Table 3-9). *Littorina sitkana* feed mostly on diatoms, but also key in on drift algae, especially the kelp, *Nereocystis*. *Littorina planaxis* feed mostly on black lichens. Fine radular teeth would probably not penetrate the surface layer of macroscopic algae and coarse teeth would not be able to pick up encrusting lichens. *Littorina scutulata*'s radular teeth are intermediate in coarseness. This species feeds mostly on diatoms, but can also utilize macroscopic algae as well as black lichens.

Looking at geographic, vertical and local distribution patterns, *L. scutulata* occupies the widest and *L. planaxis* the narrowest range. *Littorina scutulata* occurs from Alaska to Baja California, *L. sitkana* from the Bering Sea to southern Oregon, and *L. planaxis* from southern Oregon to Baja California. *Littorina scutulata* can be found from the low tide mark to the spray zone. As a rule, *L. scutulata* is found lower as well as higher on the shore than *L. sitkana*. In California, the vertical range of *L. planaxis* seems to be directly related to the width of the spray zone. The width of this zone varies with wave exposure, but on the average, *L. scutulata* would have a wider vertical range than *L. planaxis*. *Littorina scutulata* appears to have the widest distribution along a wave exposure gradient. *Littorina sitkana* becomes relatively more abundant towards the sheltered extreme and *L. planaxis* toward the exposed extreme.

Hutchinson, 1957, views the array of environmental gradients such as temperature, wave exposure, food abundance, within which a species can persist as an "n-dimensional hypervolume," or the "niche" of the species. From the above ranges we could say that *Littorina scutulata* must have the widest and *L. planaxis* the narrowest niche of the three species. Hutchinson finds it useful to distinguish between the "fundamental niche" and the "realized niche." The fundamental niche is set by a species' tolerance to physical factors whereas the realized niche is that part of the fundamental niche from which a species is not excluded by biotic factors. *Littorina sitkana* could possibly live south of Charleston if *Pachygrapsus* were removed, *L. planaxis* might live lower on the shore if *Acanthina* did not exist and *L. scutulata* in California might infiltrate the spray zone in the absence of *L. planaxis*. A previous study indicates that two species of starfish and a predatory snail tend to prevent *L. sitkana* and *L. scutulata* from occupying lower shore levels (Behrens, 1971).

Colwell and Futuyma (1973) define niche width as the reciprocal of specialization. *Littorina scutulata*, with the widest niche, does appear to be the "jack of all trades," *L. planaxis* the specialist on the spray zone and *L. sitkana* the specialist on sheltered sites. Each specialist is more efficient at exploiting a critical limited resource. *Littorina* sitkana appears to be a better competitor for crevices during storms and desiccation than L. scutulata and L. planaxis appears to be better able to utilize a low standing crop of food than L. scutulata.

McNaughton and Wolf (1970) quote two examples whereby a physiologically more tolerant species is forced to occupy a marginal habitat by a competitively superior and physiologically less tolerant species. Their generalization, that physiological generalists become ecological specialists and physiological specialists ecological generalists does not apply to L. scutulata and L. planaxis. Littorina planaxis, the more tolerant species prefers to live in the marginal habitat of the spray zone. This zone may present a refuge from predators, wave action and possibly parasites, but not from competitors. Littorina scutulata in no way prevent L. planaxis from living lower on the shore, but the grazing activities of L. planaxis tends to prevent L. scutulata from utilizing the spray zone. An important requirement for specialists must be a refuge in which they are competitively superior to the generalists.

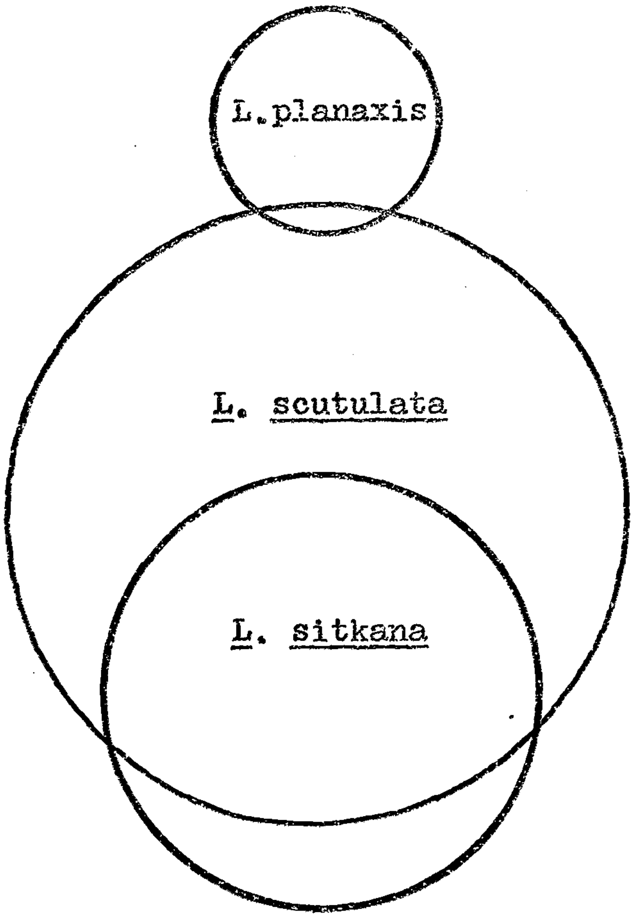


Figure 5-2 Relative Niche Widths and Overlap for the Three Species of Littorines.

APPENDIX

TABLES 1-1 TO 5-2

Significant Difference between Comparisons

* $\alpha = .05$

** $\alpha = .01$

*** $\alpha = .001$

TABLE 1-1

Littorina planaxis Transplants

Date of Release	Number	Location	Comment	Date Checked	Comment
March 28, 1969	7	Brockton Point, Vancouver, B.C.	sea wall	June 2, 1969	4 animals were recovered all had grown
Dec. 16, 1971	10 10	False Bay, caged MacGinities beach, caged	San Juan Is.	Feb. 21, 1972	all caged animals died, but caged local *L. sitkana* and *L. scutulata* survived
Dec. 16, 1971	500	Univ. of Washington Friday Harbor Laboratories San Juan Is.	old pier by Lab. #5	Feb. 21, 1972	survivors were found
				July 20, 1972	animals were copulating in field, released egg masses in lab. development from egg to actively swimming veliger took 1½ days at room temperature.
				Dec. 5, 1972	survivors were found
				Mar. 2, 1973	survivors were found one individual 10 mm long had grown 1.5mm since July 1972.
				Nov. 4, 1973	17 animals were recovered, some had grown.

TABLE 1-1 cont.

Littorina sitkana Transplants

Date of Release	Number	Location	Comment	Date Checked	Comment
Dec. 31, 1970	500	Hopkins Marine Station Monterey	3 wave sheltered pools	May 27, 1971 Pool	1-high splash pool 5 live *L. sitkana* all had grown 3 cracked shells
				Pool	2 small high intertidal none recovered
				Pool	3 Larger high intertidal none recovered
				June 14, 1971 Pool	1 dried up all remaining animals died
				Pool	2-salty 1 dead *L. sitkana*
				Pool	3 1 marked *L. sitkana* alive and grew
Feb. 18, 1973 Jim Rote	200	Point Pinos Monterey	wave exposed site A-Pool full of *Pachygrapsus* site B rocky mid-intertidal	May 4, 1973	No animals recovered
May 4, 1973 Dale Straughn Bob Cimbers	500	Horse Pastures Los Angeles	isolated rocks surrounded by sand	Oct. 14, 1973	No animals recovered

TABLE 1-1 cont.

Littorina sitkana Transplants

Date of Release	Number	Location	Comment	Date Checked	Comment
June 18 1973 Jim Rote	500	Hopkins Marine Station Monterey	6 ft. above high tide mark, below drain of sea water system, wet, no waves, Pachygrapsus	Sept. 2, 1973	Sea water system was turned off June 21 for 4 days. No L. sitkana were found, but resident L. planaxis and L. scutulata survived dry period.
Sept. 4 1973	200	Hopkins Marine Station Monterey	below drain of sea water system		

TABLE 1-2

Total Prey Organisms Eaten by Shore Crabs in 23 Days.

	PREDATOR one male and one female	
	Hemigrapsus nudis	*Hemigrapsus oregonensis*
PREY		
L. sitkana	10/12	8/12
L. scutulata	0/12	0/12
L. planaxis	0/12	0/12

TABLE 2-1

Density and Species Ratio of Littorines found in Three Sites Varying in Wave Exposure on April 4, 1972. Density measurements were taken by pooling the results from four 50 cm by 50 cm quadrats.

Site	Density per m^2		Ratio #sit./#scut.
	L. sitkana	L. scutulata	
Mc Ginities wave exposed	124	211	0.6
Cantilever Pier intermediate	79	69	1.1
False Bay wave sheltered	450	140	3.2

TABLE 2-2

Position of L. sitkana egg masses found in sixteen cages at Cantilever Pier beach.

Position	Surface Area (cm^2)	Number of Egg Masses on Oct.22/'69
Sheltered Sites		
1. sheltered side of slab	76	29
2 bottom of slab	760	26
3. right or left side of slab	320	19
4. in crevice of cage seam	small	47
Exposed Sites		
5. exposed side of slab	76	0
6. top of slab	760	1
7. on side or bottom of cage	large	8

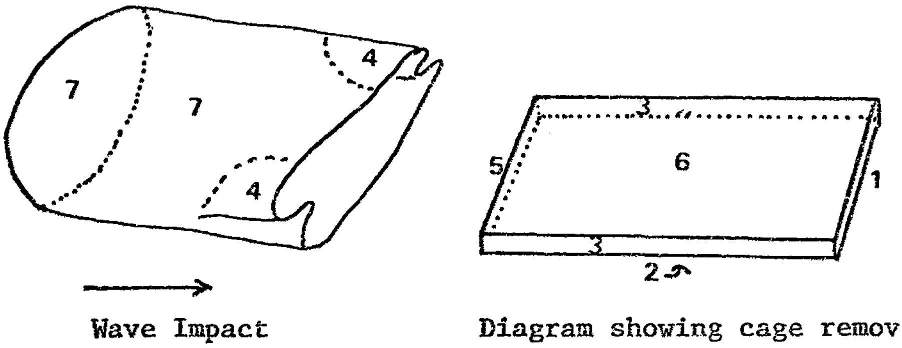


Diagram showing cage removed from cement slab with positions marked.

TABLE 2-3

Number of animals of both species found on the surface and in crevices of quadrats (50 cm by 50 cm) taken at two sites on San Juan Island. Animals in surface sample were brushed off and animals in crevice sample were picked out with forceps.

Marvista Resort

small animals

	L. sitkana		*L. scutulata*	
	Obs.	Exp.	Obs.	Exp.
crevice	59	48.3	118	128.7
surface	12	22.7	71	60.3

$X^2 = 10.$**

large animals

	L. sitkana		*L. scutulata*	
	Obs.	Exp.	Obs.	Exp.
crevice	15	4.3	12	22.8
surface	10	20.8	122	111.3

$X^2 = 39$ ***

False Bay

	L. sitkana		*L. scutulata*	
	Obs.	Exp.	Obs.	Exp.
crevice	271	251.9	30	49.1
surface	201	220.1	62	42.9

$X^2 = 19$ ***

TABLE 2-4

Behavioral Response of Littorines to Crevices. Five *L. sitkana* and five *L. scutulata* were allowed to attach to oyster shells with barnacles (crevice substratum) and to oyster shells without barnacles (smooth substratum). After 10 minute intervals the number of littorines on each type of shell was noted.

	Smooth Shells		Shells with Barnacles	
L. sitkana	1	1	7	7
	0	0	5	8
	3	3	5	4
	1	0	4	7
Total	9		47	

X^2, 1d.f. = 27.6***

	Smooth Shells		Shells with Barnacles	
L. scutulata	0	2	3	11
	4	2	7	6
	0	1	4	7
	1	0	6	7
Total	10		51	

X^2, 1d.f. = 25.8***

TABLE 2-5

Growth Responses of Animals Caged at Three Sites, Two Substrate Textures and Two Species Combinations.

	FALSE BAY		CANTILEVER		McGINITIES		
Dec. 8 to Feb. 21, 1972	Percent of Animals showing Growth						
	N	%	N	%	N	%	
L. sitkana							
smooth, single species	Not counted	0	58	26	20	40	
smooth, mixed species		0	41	34	40	37	
crevice, single species		0	49	45	24	41	
crevice, mixed species		0	43	44	51	75	
L. scutulata							
smooth, single species		0	12	92	17	59	
smooth, mixed species		0	42	83	33	45	
crevice, single species		0	11	82	19	74	
crevice, mixed species		0	42	86	59	58	
Dec. 8 to April 4, 1972	Growth Increment (mm)						
	N		N		N		
L. sitkana							
smooth, single species	27	.18	39	.57	14	.94	
smooth, mixed species	42	.23	35	.56	17	1.11	
crevice, single species	39	.29	43	.74			sample size too small
crevice, mixed species	40	.26	27	.93	3	1.08	
L. scutulata							
smooth, single species	41	.07	7	.63			
smooth, mixed species	35	.06	34	.46	13	.59	
crevice, single species	19	.04	11	1.01	9	.41	sample size too small
crevice, mixed species	33	.04	39	.58	23	.63	

TABLE 2-6

Growth and Survivorship Responses of *L. scutulata* caged at various Densities from April 16 to July 20, 1972.

Relative Food Abundance		
	0	clean surface
	+	Faint brown film of diatoms
	++	brown film of diatoms
	+++	thin mat of diatoms
	++++	medium thick mat of diatoms
	+++++	thick mat of algae, mostly diatoms

Original Density	Number Alive	Prop. showing Growth	Number Dead	Number Missing	Relative Food Abundance	Number Alive	Prop. showing Growth	Number Dead	Number Missing	Relative Food Abundance
EXPOSED SITE										
10	9	3/4	0	1	+++	10	3/3	0	0	++++
						7	6/6	0	3	+++
40	21	10/10	0	19	+++	38	33/33	0	2	+++
INTERMEDIATE SITE										
10	9	7/7	1	0	+++++	4	3/3	0	6	+++
20	20	20/20	0	0	++++	20	18/18	0	0	++++
20	20	12/12	0	0	++	20	10/10	0	0	++
40	38	24/25	0	2	+	35	21/22	0	5	+
						13	3/4	0	27	++
SHELTERED SITE										
10	6	2/4	0	4	+	5	3/5	5	0	+
10	4	0/4	6	0	+					
20	5	0/5	0	15	+	13	3/11	5	2	+
40	1	0/1	0	39	+	35	2/28	4	1	+

TABLE 2-7

Growth and Survivorship Responses of <u>L. sitkana</u> caged at various Densities from April 16 to July 20, 1972.

Original Density	Number Alive	Prop. showing Growth	Number Dead	Number Missing	Relative Food Abundance	Number Alive	Prop. showing Growth	Number Dead	Number Missing	Relative Food Abundance
EXPOSED SITE										
10	6	5/5	1	3	++	9	9/9	0	1	+
40						3	3/3	0	37	++
INTERMEDIATE SITE										
10	8	8/8	0	2	+++	4	3/3	1	5	+++
						9	9/9	0	1	+++
20	19	18/18	1	0	++	2	2/2	0	18	+++
	20	18/18	0	0	++	14	13/13	0	6	++
40	28	28/28	0	12	++	9	8/8	0	31	++
	37	32/32	0	3	+	35	28/29	0	5	+
SHELTERED SITE										
10	5	4/5	5	0	+					
	6	5/5	1	3	+	3	2/3	3	4	+
20	11	9/9	7	2	+	3	3/3	7	10	+
	6	4/6	8	6	+	2	2/2	14	6	+
40	5	3/4	28	7	+	3	3/3	9	28	+
						0		35	5	+

TABLE 2-8

Percent of Animals found in Crevices at Cantilever Pier on December 5, 1972.

TREATMENT	TOTAL NUMBER		PERCENT IN CREVICES	
Ratio L.sit/L.scut	L.sit	L.scut	L.sit	L.scut
40 : 0	158		46	
30 : 10	109	36	42	52
20 : 20	75	72	37	47
10 : 30	41	109	51	60
0 : 40		115		47

TABLE 2-9

Laboratory Aggregation Experiment. The species of lower and upper member of each aggregation of littorines was noted.

		LOWER ANIMAL		
		L. sitkana	*L. scutulata*	X^2
UPPER ANIMAL	L. sit.	2	4	
	L. scut.	4	9	Non-significant
UPPER ANIMAL	L. sit.	11	16	
	L. scut.	13	24	Non-significant
UPPER ANIMAL	L. sit.	5	19	
	L. scut.	6	13	Non-significant

TABLE 2-10

Percent of Animals in Crevices under various Weather Conditions

Date	Location	Number		Percent	Weather
		sit.	scut	sit. scut	
Aug.23 1972	sheltered	144	113	54 > 5***	very dry
	interm.	131	108	42 > 22*	very dry
Dec.11 1971	exposed	120	80	90 = 93	windy
Sep.8 1972	Sheltered	140	121	49 > 24**	windy
	Interm.	132	106	35 > 22*	windy
Dec.5 1972	interm.	230	184	58 = 54	very cold -5°C
Mar.25 1973	interm.	93	110	52 = 52	overcast 9°C
Dec.15 1971	interm.	120	120	65 < 88***	calm
Oct.3 1972	sheltered	119	108	32 < 53**	sunny
	interm.	125	91	19 = 28	sunny
Feb.22 1973	interm.	90	112	31 < 53**	sunny

* values are significantly different

at $\alpha = .05$ *
$\alpha = .01$ **
$\alpha = .001$ ***

TABLE 2-11

Number of Juvenile Animals (less than 4 mm long) found inside Experimental Cages.

	FALSE BAY		CANTILEVER		McGINITIES	
	cr.	sm.	cr.	sm.	cr.	sm.
Number of L. sitkana						
Feb. 19 1972	177	34	5	2	4	0
Apr. 5 1972	221	98	12	6	15	0
July 18 1974	134	33	45	22	16	6
TOTAL	532	165	62	30	35	0
Number of L. scutulata						
Feb. 19 1972	28	10	1	0	5	0
Apr. 5 1972	130	36	1	2	10	0
July 18 1974	27	12	17	10	26	8
TOTAL	185	58	19	12	41	8

cr.= crevice substratum
sm.= smooth substratum

TABLE 3-1

Fecal Pellets produced by littorines collected from various levels at Hopkins Marine Station.

ZONE	*Littorina planaxis*	*L. scutulata*
Next to black lichen zone (grazed clean)	black to dark brown *	
Under ledge in black lichen zone, damp	black to dark brown *	black to dark brown *
brown sand stone shelf	black to dark brown * _Calothrix_ sp.?	black to dark brown * unidentified digested matter
vertical wall	mostly unidentified digested matter *	*
Barnacle zone	unidentified digested matter	*
	light brown	light brown
	light brown	light brown
	dark brown	light and dark brown
	light and dark brown	light and dark brown
	no fecal pellets	light brown

* denoted positive identification of black lichen remains

TABLE 3-2

Number of Animals Remaining Attached to Substratum after one High Tide.

	L. planaxis	*L. scutulata*
Number Remaining Attached	77	36
Number Washed Into Gully	9	35
Number Missing	14	29

Disregarding the number of animals missing, a significantly greater proportion of *L. planaxis* remained attached to substratum than *L. scutulata*.

X2 = 27.18 ***

TABLE 3-3

Proportion of Animals Aggregated in Lower Portion of Cages During August 1972. (sum of two runs).

HIGH SHORE LEVEL

	L.scut.	*L.plan.*	X^2
	Low Density		
lower portion of cage	46	6	
upper portion of cage	14	54	51.62 ***
	High Density		
lower portion of cage	140	34	
upper portion of cage	20	126	138.87***

LOW SHORE LEVEL

	Low Density		
lower portion of cage	45	9	
upper portion of cage	35	71	34.24 ***
	High Density		
lower portion of cage	77	12	
upper portion of cage	83	148	63.75 ***

TABLE 3-4

Comparisons of L. scutulata Survival Rates at High and Low Shore Levels from Spring to Winter 1972.

			Low Level	High Level	X^2
SINGLE SPECIES					
	Low Density	alive	5	12	
		dead	25	27	N.S.
	High Density	alive	4	16	
		dead	74	64	7.89**
Mixed species					
	Low Density	alive	7	3	
		dead	14	17	N.S.
	High Density	alive	1	1	
		dead	37	38	N.S.

Total Survival at Low Level = 17/167 = 10%

Total Survival at High Level = 32/178 = 18%

X^2 value = 4.30 *

TABLE 3-5

Comparisons of L. planaxis Survival Rates at High and Low Shore levels from Spring to Winter 1972.

			Low Level	High level	X^2
SINGLE SPECIES					
	Low Density	alive	17	28	
		dead	23	9	7.4**
	High Density	alive	24	63	
		dead	47	10	39.31***
MIXED SPECIES					
	Low Density	alive	6	19	
		dead	12	1	13.38**
	High Density	alive	15	38	
		dead	29	0	35.92***

Total Survival at Low Level = 62/173 = 36%

Total Survival at High Level = 148/168 = 88%

X^2 = 98.38***

TABLE 3-6

Proportion and Percent of Animals Surviving in Low Density, Single species Cages in 1971 and 1972.

	1971		1972		X^2
	prop.	%	prop.	%	
L. scutulata					
High Level	12/57	21	12/33	31	N.S.
Low Level	16/46	35	5/30	17	N.S.
L. planaxis					
High Level	45/57	79	28/37	76	N.S.
Low Level	37/54	68	17/40	43	6.41*

TABLE 3-7

Comparisons of Survival Rates in Single and Mixed Species Cages.

	Winter to Spring 71		Spring to Winter 71		Spring to Winter 72			Spring to Fall 73	
	s	m	s	m	s	m		s	m
L. scutulata									
High Level									
20 animals per cage	61*	36	21	8	31	15	**		
40 animals per cage					20*	3			
Low Level									
20 animals per cage	48	38	35	19	17	33			
40 animals per cage					5	3			
L. planaxis									
High Level									
20 animals per cage	100	96	79*	57	76	95	**	100	96
40 animals per cage					86	100		100	100
Low Level									
20 animals per cage	100	83	69	71	43	33		100	100
40 animals per cage					34	34		99	98

s = single species m= mixed species

TABLE 3-8

The Effect of Adding 20 Animals of Species B to 20 Animals of Species A from May'72 to January 1973.

HIGH SHORE LEVEL

	# alive	# dead	X^2
	L. scutulata		
low density single species	12	27	
high density mixed species	1	38	9.23 **
	L. planaxis		
low density single species	28	9	
high density mixed species	38	0	8.33 **

LOW SHORE LEVEL

	# alive	# dead	X^2
	L. scutulata		
low density single species	5	25	
high density mixed species	1	37	N.S.
	L. planaxis		
low density single species	17	23	
high density mixed species	15	29	N.S.

TABLE 3-9

Number of Rows of Radular Teeth per Microscopic Field (1 mm) for Littorines of Equal Size.

Species	Number of Measurements	Number of Animals	Mean	Range	Standard Error
L. sitkana	15	3	22.3	21-24	
L. scutulata	15	4	26.6	25-29	.70
L. planaxis	26	5	31.6	28-37	1.16

The mean number of rows of radular teeth for _L. scutulata_ and _L. planaxis_ were significantly different.

t = 3.8*

TABLE 3-10

Comparisons of Survival Rates (Percent) in Low and High Density Cages.

	Winter to Spring 1972			Spring to Winter 1972			Spring to Fall 1973	
Number of Animals per Cages	10	20	40	20	40		20	40
L. scutulata								
High shore level								
Single sp.				31	20			
Mixed sp.				15	3		70*	33
Low shore level								
Single sp.	animals escaped			17	5	**		
Mixed sp.				33*	3		55*	17
L. planaxis								
High shore level								
Single sp.	100	100	90	76	86		100	100
Mixed sp.				95	100		96	100
Low shore level								
Single sp.				43	34		100	99
Mixed sp.				33	34		100	98

* indicates significant difference of X^2 comparisons.

* $\alpha = .05$

** $\alpha = .01$

TABLE 3-11

Growth Response of L. planaxis caged at various Densities in the Splah Zone above the High Water Mark from January to May 1972.

Number of Animals per Cage	10	20	40
Mean Growth Increment (mm)	.29	.29	.23

Comparing the Growth Responses

20 versus 40 Animals per Cage F, d.f. = 1/∞ =21.22***

TABLE 3-12

Survey of Hermit Crab Shells for _Acanthina_ drill marks.

		L. planaxis shells		_L. scutulata_ shells		
		N	% drilled	N	% drilled	
Hopkins Marine Station	June 2, 1973	10	40	19	15.8	
	June 3, 1973	21	24	63	4.7	
	June 6, 1973	14	43	34	9.8	
	Total	45	33.3	116	7.7	***
Hopkins Marine Station	Sept. 3, 1973	19	42	59	13.5	*
Monterey Boat Works	Sept./73	10	20	33	22	
Bird Rock Sept./73 12/16 of _Acanthina_ were feeding on littorines		19	32	13	31	
Fan Shell Beach Sept./73		30	16.7	130	25	
Lover's Point Sept./73 no _Acanthina_ present		11	0	35	0	
Bodega Bay Marine Station no hermit crabs were found						

* Indicates that X^2 values of comparison between species were significantly different

* at $\alpha = .05$ *** at $\alpha = .001$

TABLE 3-13

Number of L. scutulata drilled more and less than 8 mm in length.

	Drilled	Not Drilled
< 8 mm	16	157
> 8mm	43	106

$X^2 = 19.28^{***}$

TABLE 3-14

The Effect of Adding *Acanthina* on the Distribution of Littorines. in Experimental Cages.

June 1973 (total of 4 runs)

	with *Acanthina*	without *Acanthina*	χ^2
	L. planaxis		
# in lower 1/8 of cage	2	24	
# in upper 7/8 of cage	238	166	135.55 ***
	L. scutulata		
# in lower 1/8 of cage	41	63	
# in upper 7/8 of cage	199	127	112.69 ***

September 1973

	with *Acanthina*	without *Acanthina*	χ^2
	L. planaxis		
# in lower 1/8 of cage	6	36	
# in upper 7/8 of cage	44	15	33.31 ***
	L. scutulata		
# in lower 1/8 of cage	29	47	
# in upper 7/8 of cage	15	3	10.18 ***

TABLE 4-1

Position in the enclosure of *Littorina planaxis* conditioned to the splash zone and to a lower level. at 4:15 pm.

No *Acanthina*

Position in Enclosure	*L. planaxis* conditioned to splash zone	*L. planaxis* conditioned to a lower level
Upper 20 cm	36	11
Lower 20 cm	42	63

With *Acanthina*

Upper 20 cm	79	32
Lower 20 cm	21	57

		X^2
Effect of *Acanthina*	High Conditioned	19.26***
	Low Conditioned	8.20**
Effect of Conditioning		
	No *Acanthina*	16.44***
	With *Acanthina*	34.24***

Table 4-2

Number of low and high conditioned Littorina planaxis found in the enlosures and on rock face above the enlosures after two consecutive high tides.

	Low conditioned	High conditioned
Above Enclosure	17	50
in Enclosure	84	82

Chi-Square = 11.37 **

TABLE 4-3

Number of low and high conditioned *Littorina planaxis* remaining on substratum.

	Low Conditioned	High Conditioned
Remaining on substratum	101	132
Dislodged	99	68

X^2 = 26.97***

TABLE 5-1

Comparisons of the Three Species of Littorines.

	sitkana	*scutulata*	*planaxis*
Development	direct	planktotrophic	
Life span (Years)	1-2	7	7+
Growth rate	rapid		slow
Mortality rate	high		low
Recruitment	high		low
Variation in Recruitment	great	little	?
Intraspecific Crowding Effects	great	little	negligible
Diet	diatoms macroscopic algae	diatoms black lichen	black lichen
Radular Teeth	coarse		fine
Tolerance to Desiccation	least		most
Ability to Remain attached	least		most
Need for Shelter	greatest		least
Relative Range			
Latitudinal	2	1	3
Vertical	2	1	3
Along Wave Exposure Gradient	2	1	3

TABLE 5-2

Growth Responses to Varying Grazer Densities.

<u>Littorina</u> <u>sitkana</u>					
grazing area per animal (cm^2)	37		18.5		9
July 15-Aug.11/69 new length (mm)	2.11	***	1.28	***	0.88
April 17-June 22/70	3.01	**	2.54	***	2.04
<u>Littorina</u> <u>scutulata</u>					
July 15-Aug.11/69	0.21		0.24	***	0.00
April 17-June 22/70	1.12		1.31	**	0.76
<u>Littorina</u> <u>planaxis</u>					
grazing area per animal (cm^2)	16		8		4
Dec. 29/71-May 23/72	0.29		0.29	***	0.23

* values are signigicantly different

at $\alpha = .05$ *
$\alpha = .01$ **
$\alpha = .001$ ***

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