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THE ROLE OF SPATIAL AND SIZE REFUGES IN THE INTERACTION BETWEEN JUVENILE BARNACLES AND GRAZING LIMPETS

By

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ABSTRACT

The effect of grazing by limpets (*Collisella digitalis*) on the distribution and abundance of three species of juvenile barnacles (*Balanus glandula*, *Balanus crenatus*, and *Semibalanus cariosus*) was assessed using slate settling plates with different types of refuges, as well as the use of fenced areas on natural rock. The two possible effects of limpets on juvenile barnacles, namely ingestion and bulldozing, in relation to types of refuges utilized, were further studied in the laboratory. The field studies showed that while shallow depressions offered only minimal refuge against being grazed, proximity to adult barnacles was a more effective refuge. The minimal degree of protection offered by depressions is explained by the unexpected ability of the limpets to graze and ingest juvenile barnacles from most depressions.

When *Balanus glandula* and *Balanus crenatus* reached a basal area of 5-6.7mm^2, the barnacles had obtained a refuge in size from mortality caused by the activity of *Collisella digitalis*. *Semibalanus cariosus* reached a refuge-size at a smaller basal area and, thus, at a younger age, due to its overall stronger attachment to the substrate.

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INTRODUCTION

Predation and disturbance can be major determinants of distribution of organisms on rocky shores (Crowder and Cooper 1982; Dethier 1980; Menge 1976, 1978; Paine 1976; Werner *et al.* 1983; Woodin 1978). Organisms inhabiting areas exposed to these factors experience lower survival rates than those in protected areas. Thus, the presence of disturbance and/or predation can lead to a greater percentage of organisms living in areas protected from these factors. Such protected areas are termed refuges (Connell 1961a, 1970; Menge 1976; Woodin 1978).

The concept of refuges can be explained in terms of a decreased risk of mortality by a disturbance process (physical or biological). However, one refuge may not provide lowered risk from all sources of mortality. For example, many organisms can obtain refuge from predation by living high in the intertidal zone (Connell 1961a,b; Dethier 1980; Paine 1976), but in this zone they can suffer increased risk of mortality due to desiccation. In addition, living higher intertidally reduces the submergence time during which most intertidal organisms feed. Thus, this high intertidal habitat may be suboptimal for some organisms. Therefore, in order for a refuge to benefit a species, the risk of mortality from a given source when out of a refuge must be greater than possible suboptimal conditions and/or risk of mortality from other sources when in the refuge.

Many organisms may not actually "choose" to be in a refuge; the refuge areas may merely be the only places they survive. Thus the mortality-risk and possible sacrifices are "decided" for them in favour of the refuge. Keough and Downes (1982), however, found that some larvae prefer to settle in refuge areas. They showed that the bryozoans *Celleporaria brunnea* and *Scrupocellaria berthoietti* both settled preferentially on pitted surfaces where fish predation was minimal. Other studies have shown that barnacles, which also preferentially settle in depressions, are protected from wave action and strong currents (Rice *et al.* 1935).

Furthermore, protection from wave action and currents has been documented for limpets that preferentially settle amongst barnacles (Lewis and Bowman 1975).

Despite the possible suboptimal conditions present in refuges, the habitation of refuges enables organisms to survive in areas where they might otherwise be excluded by providing protection from predation, desiccation, competition, and other causes of mortality. This tends to stabilize community structure by insuring that some individuals of a species will survive long enough to reproduce and perpetuate that species (Crowder and Cooper 1982; Hughes 1980; Paine 1976). In the case of prey refuges, a predator's choice of food may be influenced by the increased difficulty in obtaining certain refuge-inhabiting species. In addition, an abundance of different kinds of refuges (i.e. habitat heterogeneity) may better allow competitors to coexist (Ayal and Safriel 1982; Werner *et* al. 1983). All of these factors may lead to increased diversity in a community containing refuges (Brock 1979; Dayton 1971; Menge 1976).

There are certain criteria that must be met to determine if a refuge is present. Firstly, mortality from predation or a disturbance process upon the individuals in a potential refuge must be less than that for individuals out of the refuge. In addition, a greater percentage of individuals must use the refuge in the presence of a predator or disturbance process than when the predator or disturbance process is absent. Both of these criteria are used to establish that a certain mortality source is a major cause of the refuge use. It should be emphasized that the individuals of a species cannot all be in a refuge at all times. There must be some individuals not using the refuge, otherwise one could not establish that mortality from a given source is greater in a non-refuge. Finally, organisms inhabiting a refuge need not survive better than those found outside of the refuge from all mortality sources, but some individuals must survive.

Most studies that involve testing for refuges focus on the adult stages of an organism (Berstein *et al.* 1981; Werner *et al.* 1983; Woodin 1978; and others). In addition, many of these studies equate settlement with recruitment. These terms may not be synonymous.

Settlement refers to the total number of individuals that settle, no matter how long they survive; recruitment refers to the number of individuals found after a given period of time or reaching a given stage (i.e. the surviving individuals; Keough and Downes 1982). For the purpose of this study, recruitment will be defined as those individuals (barnacles) reaching 5-7 weeks of age after metamorphosis.

Thus, the distribution of recruited individuals can be affected by the settlement pattern of the larvae and their subsequent mortality. When either settlement or mortality is selective with regard to the location in which it occurs, a non-random distribution may result. Therefore, in order to use recruitment to make inferences about the causes of the distribution of the adults or patterns of community structure, one must separate settlement due to active larval choices from the differences in early mortality of organisms in different locations within a habitat (Keough and Downes 1982). Without distinguishing between larval choice and early mortality, an accurate description of the causes of community structure cannot be made.

The use of refuges by adult barnacles has been studied extensively. Connell (1961a) found that *Balanus* living high in the intertidal zone suffered less mortality due to predation by *Thais* and *Pisaster* than those living lower. As a result, *Chthamalus* was freed from competition with *Balanus* by living low intertidally because the density of *Balanus* was reduced by predation. In addition, Dayton (1971) found that as *Balanus* grew larger, they occupied a size refuge safe from *Thais* predation. These studies and others all stressed mortality and use of refuges by adult barnacles, but gave little indication as to the factors affecting the distribution of juvenile barnacles. Connell (1961a) suggested that the time of settlement, weather, crowding, grazing by limpets, and desiccation may all cause mortality of juvenile barnacles, but the importance of these factors in determining the distribution of juvenile barnacles was not assessed.

Knowledge of factors governing distribution of juvenile barnacles is needed to fully understand what influences the distribution of adults. For example, many studies have used cages to enclose barnacles, with and without predators, and have used analyses of monthly samples to assess differences in barnacle distribution (Connell 1961a, 1970; Dayton 1971; Menge 1976). However, since these studies did not follow the settlement or early mortality of the barnacles, it was not determined how the juveniles were affected by the presence of the predator (eg. if the barnacles preferentially settled where the predator was absent). Disregarding the factors governing distribution of juvenile barnacles might lead to an overestimation of the importance of predators of adult barnacles in determining the distribution of barnacles as a whole.

One cause of mortality to juvenile barnacles suggested in many studies is the grazing activity of limpets and snails (Bertness *et al.* 1983; Branch 1975a; Choat 1977; Connell 1961a; Dayton 1971; Denley and Underwood 1979; Lewis 1954; Menge 1976; Petraitis 1983). By scraping the surface with their radulae and shells, limpets and snails effectively "bulldoze" the substrate, removing algae and small invertebrates in their path. Included with these small invertebrates are newly settled barnacles (Branch 1975a; Choat 1977; Connell 1961a; Dayton 1971; Denley and Underwood 1979; Lewis 1954; Menge 1976). Dayton (1971) found that some limpet species can actually ingest newly settled barnacles. As the barnacles grow, however, their shells become thicker and more resistant to the effects of limpet grazing and, upon their reaching about 2-4mm in diameter, limpet grazing no longer causes mortality to juvenile barnacles (Denley and Underwood 1979).

Limpets can also exert positive effects on barnacles by grazing algae and leaving bare patches upon which cyprids can settle (Bertness *et al.* 1983; Petraitis 1983). Although most limpets graze primarily on microalgae, their feeding activity can also remove the sporelings of macroalgae, thus inhibiting both micro and macroalgal recruitment (Choat and Black 1977; Dayton 1971). Therefore, limpets can cause a temporary release from competition for space between algae and barnacles by opening up new space and allowing more barnacle settlement to occur (Dayton 1971; Petraitis 1983).

If the pattern of grazing by limpets on a smooth substrate approached randomness, every barnacle would have an equal probability of being encountered by a grazing limpet.

This would be a function of the density of limpets feeding. If the rock contained areas that the limpets could not graze, juvenile barnacles inhabiting these areas would have a lowered probability of mortality due to limpet grazing and would thus be in a refuge. If grazing pressure were high enough, barnacles might even be restricted to the refuge areas. An example of this may be found with small depressions on a rock surface where the limpet's shell may be too large to scrape. A juvenile barnacle inhabiting such a depression might escape contact with the limpet and survive in areas where it would otherwise be eliminated.

Another type of refuge for juvenile barnacles may be found within aggregations of adult barnacles (Bertness *et al.* 1983; Choat 1977; Connell 1961a; Denley and Underwood 1979; Lewis 1954). Limpets may not be able to graze the areas right next to the adults due to the encumberance of their shells. Thus limpets would be restricted to the large spaces between barnacles and juvenile barnacles living next to the adult barnacles would be in a refuge from the limpets.

The purpose of this study is to test if grazing by the limpet *Collisella digitalis* causes sufficient mortality to juvenile *Balanus glandula* to limit the barnacles to refuges. The possible refuges tested include depressions, proximity to adult barnacles, and large size.

HYPOTHESES

The experiments in this study were designed to test three hypotheses. Firstly, it was hypothesized that juvenile barnacles utilize spatial refuges to withstand mortality caused by limpets. This hypothesis was tested with slate plates in the field, where the use by juvenile barnacles of depressions and proximity to adult barnacles as possible spatial refuges was examined; with intertidal rocks, where depressions were tested as possible refuges; and with laboratory plates, where depressions of various sizes were tested for effectiveness as refuges.

Secondly, it was hypothesized that limpets can ingest and bulldoze juvenile barnacles and further, that the way in which the barnacles are removed depends upon the substrate they are on. The following observations were made: 1) barnacles on small rocks—limpets were allowed to graze on rocks from the field on which barnacles had settled, after which the presence of barnacles in and out of limpet feces was assessed; 2) barnacles in grooves on corrugated pvc pipes—limpets were allowed to graze on pipes with lengthwise grooves (barnacles were settled in these grooves), after which the presence of barnacles in and out of the limpet feces was assessed; and 3) the mechanisms of removal of barnacles by limpets—limpets were observed in the acts of bulldozing and ingesting barnacles.

Lastly, it was hypothesized that there is a maximum size of barnacle a limpet can remove, and upon reaching this size, a barnacle is in a size refuge against mortality caused by limpets. Furthermore, it was hypothesized that this critical size can vary between species of barnacles. Testing this hypothesis involved the use of field plates, where the maximum size of barnacle removed by limpets was obtained from photographically assessed survival data using slate plates, and from laboratory rocks, where limpets were allowed to graze on rocks with barnacles varying in size from 0.6-10.0mm^2 (basal area) collected from the field. Maximum size of the barnacles killed was assessed by measuring the barnacles that had been removed by limpets from the rocks. Rocks with various species of barnacles were tested.

STUDY SITE DESCRIPTION

The field study sites were located on the West Coast of Vancouver Island at a longitude of 125^{0} 10'N and a latitude of $48^{0}50$'W (Figure 1). The West Coast of Vancouver Island is typical of a temperate climate with coastal upwelling. Summer water temperatures range between 15-18^{0} C and salinity ranges between 28-$32^{0}/_{00}$. Experiments were conducted on intertidal rocks at a moderately wave-exposed site at Ross Islets and a moderately wave-protected site at Dixon Island. In both of these locations there was an abundance of *Balanus glandula*, *Chthamalus dalli*, *Collisella digitalis*, *Littorina* spp., and *Fucus* spp.. In addition, Ross Islets contained *Semibalanus cariosus*, *Mytilus* spp, and *Thais* spp. Field experiments using slate plates were located in a protected area at the mouth of Bamfield Inlet. The plates were hung off a pier in front of the Bamfield Marine Station at levels corresponding to abundant *Balanus glandula* (high-level plates) and to *Balanus crenatus* and *Semibalanus cariosus* (low-level plates).

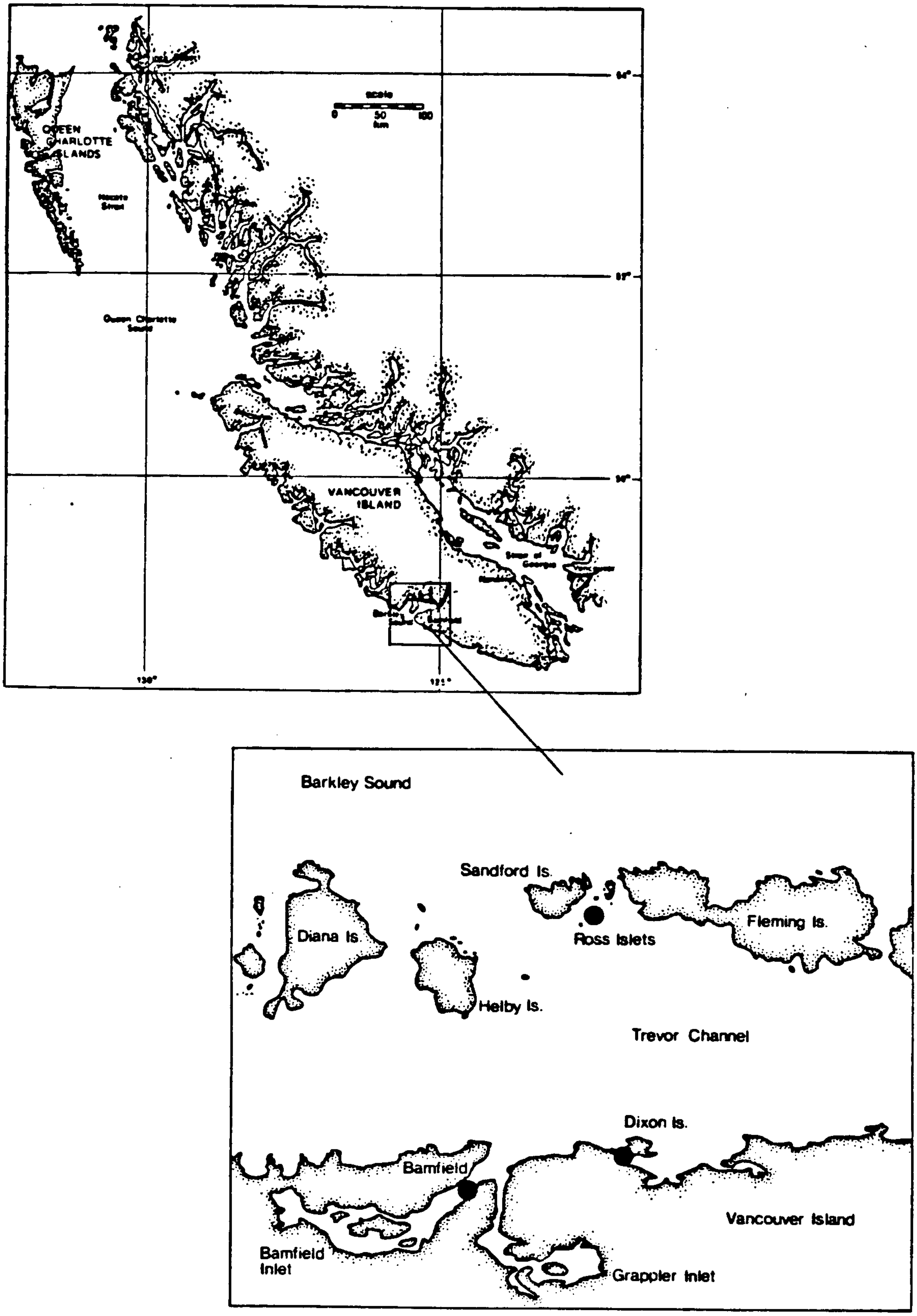


Figure 1. Map of B.C. Coast showing location of study sites. Field sites include Ross Islets, Dixon Island, and Bamfield Inlet.

FIELD PLATES

MATERIALS AND METHODS

Thirty slate plates with dimensions 20 x 20 x 1.9cm thick were bolted to pieces of plywood with two stainless steel screws (0.6cm dia) inserted at opposite corners of the plates. The plates were divided between four boards such that each board contained seven or eight plates. These boards were hung off a pier at the Bamfield Marine Station in Bamfield Inlet at two tidal levels as described below. Each plate was divided into four sections with vexar fencing (0.3cm mesh size) sewn onto stainless steel metal dividers. The 3cm high vexar fencing both divided and surrounded each plate to prevent limpets from moving between sections (details to follow).

The surface of each plate was modified to provide one of two types of possible refuge. The first type of plate contained 30 depressions (approximately 2.5mm deep and 6.0mm dia) in each quadrat of the plate, placed randomly and drilled out with a bit. This resulted in 43% of the surface area of the plate being allocated to depressions, with the remaining 57% being smooth surface. These are later referred to as "depression plates". The second type of plate contained 30 randomly placed adult *Balanus glandula* shells from which the animals were removed and the shells filled with silicon for extra support. These were cemented with epoxy resin onto each of the four plate sections (later referred to as "adult barnacle plates" or "AB PLATES"). Of the 30 plates, 20 were of the "depression" type and 10 were of the "adult barnacle" type.

The plates were divided between the boards such that a pair of boards contained 10 depression plates and 5 adult barnacle plates. Each pair of boards was hung at a different tidal height, 0.7m above chart datum and 2.0m above chart datum. The low-level plates (0.7m) were hung at a level corresponding to maximum abundances of *Semibalanus cariosus* and *Balanus crenatus* in the field, whereas the high-level plates (2.0m) were hung in a zone of corresponded to the species of barnacle most common at the level in which the plates were hung.

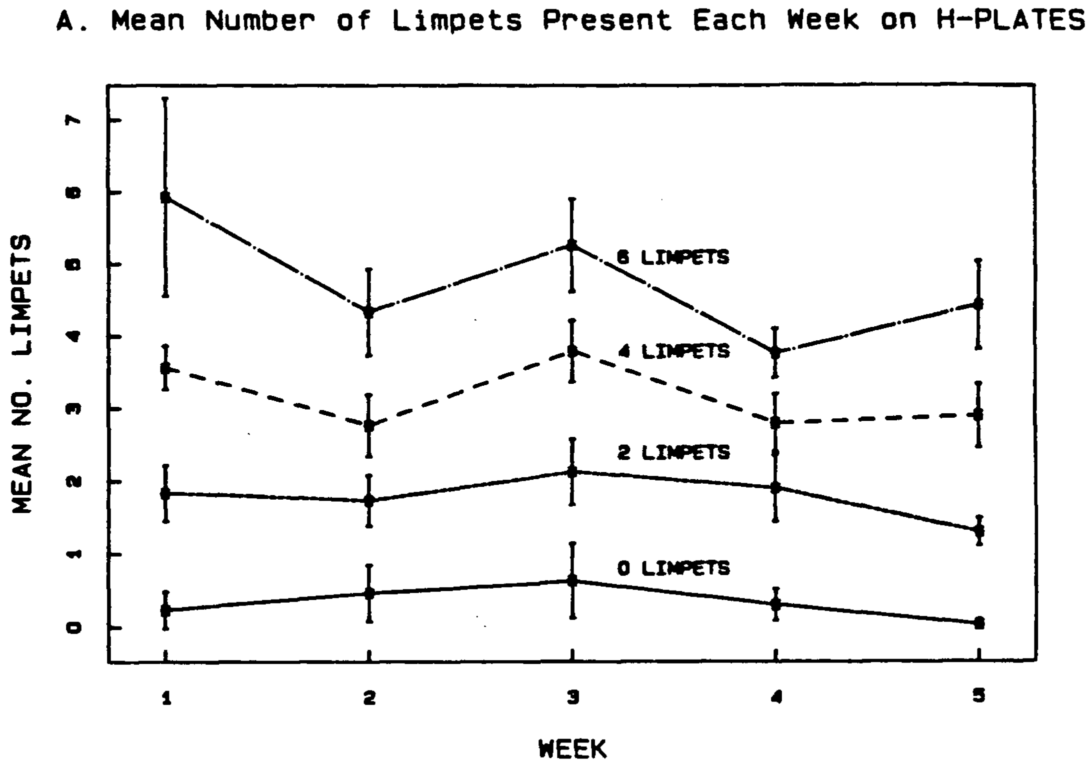
The plates were hung off the pier for 2 months prior to the first barnacle settlement (in April). This "conditioning" of the plates allowed possible contaminants (eg. from the epoxy glue) to leach out and provided time for the build-up of diatoms on the surface of the plates, thus increasing the attractiveness of the plates to settling cyprids.

After some cyprids had settled, each of the four plate sections received a different density of adult *Collisella digitalis* (0, 2, 4, and 6). These densities were not unusual for *C. digitalis* in the field as they are an unevenly dispersed, aggregating species of limpet (Willoughby 1973). Most of the barnacles had settled by the second week after the experiment had begun, although a low rate of settlement continued throughout the 5-7 weeks of sampling.

The plates were removed from the field and photographed once weekly. During this time, they were kept in the laboratory for approximately 2 hours, after which they were returned to the field. Sampling lasted for 5 weeks for the high intertidal-level plates (designated "high-level plates" or "H-Plates") and 7 weeks for the low intertidal-level plates (designated "low-level plates" or "L-Plates").

During weekly sampling, the number of limpets in each plate section was checked and limpets were replaced or removed according to the treatment. Figure 2 shows the mean number of limpets present each week in each treatment. Although some limpets escaped, the relative proportion of limpets present in each limpet treatment was fairly constant.

Photographs were used to assess differences in survival of barnacles with and without limpets, and at different densities of limpets. In addition, differential mortality of young barnacles due to location in and out of refuges was examined as well as growth rates and maximum sizes of barnacles affected by the limpets.



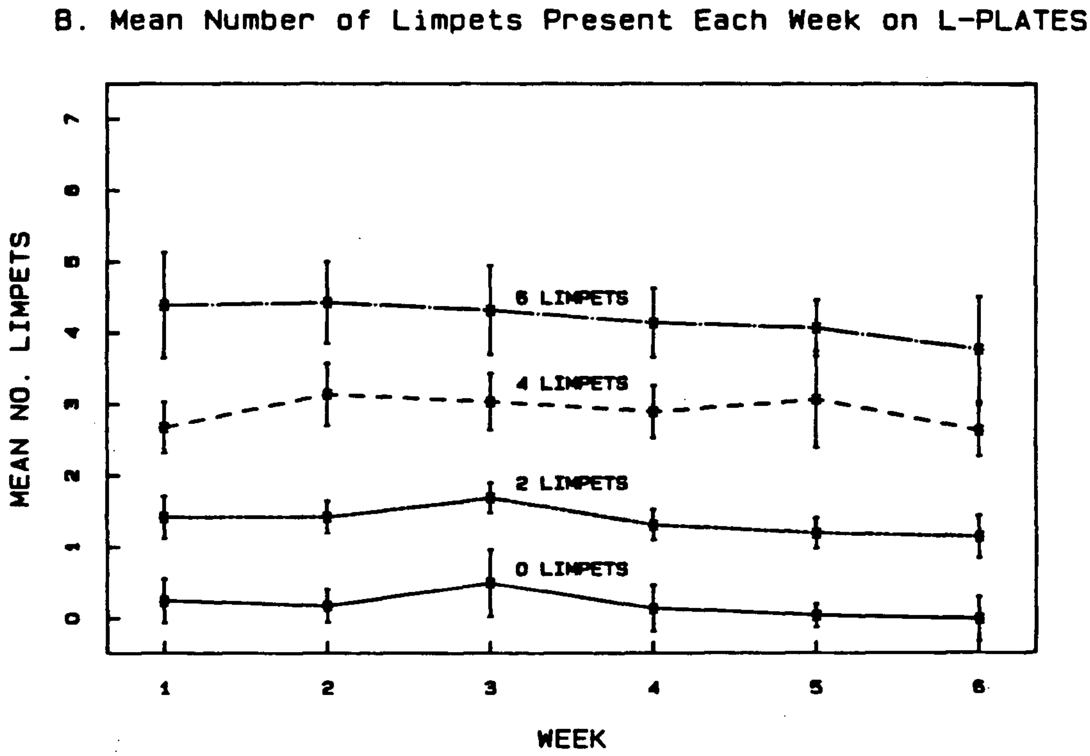


FIGURE 2. Mean number of limpets present each week on high-level (H-PLATE) and low-level (L-PLATE) plates (GRAPHS A and B respectively; N = 15). Data were combined for both depression and adult barnacle plates. Variances are presented as $\pm$ 2SE. The number of limpets present in a given week was calculated as the mean of the number present at the beginning of the week plus the number remaining at the end of the week.

On the adult barnacle plates, locations of newly settled barnacle spat were categorized as follows:

(1) less than 2mm from an adult barnacle shell

(2) 2-4mm from an adult barnacle shell

(3) 4-6mm from an adult barnacle shell

(4) further than 6mm from an adult barnacle shell

Barnacle size, expressed as basal area, was estimated using the formula for an ellipse, pi/4 x length x width (Bourget and Crisp 1975). Length was measured from the base of the rostrum to the base of the carina while width was measured from the maximum distance between the lateral plates at the base. Basal area was used to measure size since it estimated the actual area of contact between the base of the barnacle and the substrate. This was considered a better measurement for the purposes of this study than was length, which is most often used in other studies, since the force to remove a barnacle is proportional to the area of attachment (Miller, MS in prep.).

Survival rates for barnacles were obtained by projecting photographic slides of the weekly samples and marking the position of each barnacle on acetate sheets. For a given treatment, the barnacles present in each sample date were marked in a different colour on the same acetate sheet. From these acetates, the date of settlement and the date each barnacle was last sampled was obtained. The age of each barnacle was calculated by subtracting the date of settlement from the date last sampled. For example, the death of a three-week-old barnacle did not necessarily occur on the third sample date, instead, the barnacle may have settled during the second week and died during the fifth week. Barnacles that were still present in the last sample, which were considered "surviving barnacles", were similarly assessed for age.

Data obtained from the acetates were converted to percentage survival/mortality of barnacles with regard to the following factors:

(1) location in and out of possible spatial refuges

(2) density

(3) number of limpets present

(4) age

For the first three factors, survival was estimated as the number of barnacles present in the final sample over the total number that settled. Although settlement occurred throughout the experiment, the majority of the barnacles settled by the second week. Thus the barnacles in the final sample were mostly 4-5 weeks old on the high-level plates (last sampled in the fifth week) and 6-7 weeks old on the low-level plates (last sampled the seventh week). These barnacles were termed "first cohort barnacles". The survival rate obtained was therefore an estimate of the survival of the first cohort of barnacles.

By estimating survival in this manner, it was assumed that all of the barnacles that had settled had an equal chance of being recorded, regardless of how many limpets were present. However, if limpets reduced the survival of newly metamorphosed barnacles before the barnacles were sampled, the number of barnacles that were perceived to have settled would be expected to be inversely proportional to the number of limpets present. Thus, the survival rates calculated are only reliable in estimating the survival of barnacles that had previously reached one week of age or more.

By taking the density of barnacles in the last sample for each treatment with limpets, and dividing by the density of barnacles in the treatment without limpets (control) on the same plate, a survival rate (termed "percentage end density") was estimated which might account for any differences in perceived and actual settlement. This estimate assumes that the settlement of barnacles was equal in all areas of a single plate, but not between plates. In addition, it is only an estimate of the survival of barnacles from mortality caused by limpets, since the survival of barnacles in the treatment without limpets was factored out in dividing by that treatment.

For the final factor age, survival was estimated somewhat differently. Because barnacles continued to settle out on the plates throughout the study period, any given sample would include barnacles of a variety of ages (from 1-7 weeks). To estimate survival of barnacles of a given age (termed "age-specific survival"), the number of barnacles living past that age was divided by the same number of barnacles plus those known to have died in the interval between samplings. As earlier stated, the age of a barnacle was not equivalent to the date of the sample; rather the age of each individual barnacle in each sample date was calculated from the date of settlement for each barnacle. For example, survival of three-week-old barnacles was calculated as:

$$\text{Age-Specific Survival at 3 Weeks of Age} = \text{No. Alive at 3 Weeks of Age} \Big/ \text{No. Alive at 2 Weeks of Age}$$

These rates were tested for significance using an Analysis of Variance (ANOVA). Since an ANOVA assumes that variances are homogeneous, and since the variances of percentage data, expressed in proportions out of 100 (i.e. 95% expressed as .95), tend to decrease as the proportion nears unity or zero, an arc-sin transformation was performed on the data. By transforming the data in this manner, the variances were almost all homogeneous, as shown by Bartlett's Chi-Squared Test. In addition, for a more detailed description of the relationship between mortality and each variable tested (presented above), Duncan's Multiple Range Test was performed on the data. When significant trends in the effects of certain variables are discussed for the tables and figures, significance is based on the results of Duncan's test. Where p-values are presented, these indicate probabilities obtained from ANOVA. For presentation, survival rates were converted to percentage mortality by subtracting them from unity and multiplying by 100.

The data presented in the tables and figures for the high-level plates represent the mortality of *Balanus glandula*, and, for the low-level plates, a combined mortality of *Balanus* *crenatus* and *Semibalanus cariosus*. Since *B. crenatus* and *Semibalanus cariosus* were difficult to distinguish until they reached four weeks of age, separate mortality rates for these species were not obtained.

RESULTS

I. THE EFFECT OF DEPRESSION REFUGES ON SURVIVAL OF BARNACLES

Results of ANOVA on data for the depression plates are presented in Table I. Mortality of the first cohort, percentage end density, and age-specific mortality are all shown. Percentage end density represents the difference in the density of barnacles from treatments with limpets and treatment without limpets (control) at the final week of sampling (week 5 for high-level plates and week 7 for low-level plates). This was converted, as were the survival rates, to percentage mortality of barnacles by subtracting the proportion obtained from unity and multiplying by 100.

A. FIRST COHORT MORTALITY AND PERCENTAGE END DENSITY

High-Level Plates

Limpets had a significant effect on mortality of the first cohort of barnacles (i.e. the barnacles that settled before the second week) on the high-level plates (Table I; $p=.05$). However, percentage end density showed no significant differences with and without limpets ($p=.17$). This is further illustrated in Table II, which shows a comparison of mortality of the first cohort and percentage end density of barnacles in each limpet treatment. On the high-level plates, mortality increased from 19-64% as the number of limpets increased from

Table I. Analysis of Variance Tests (ANOVA) Performed on First Cohort Mortality, Age-Specific Mortality and Percentage End Density of Barnacles on High-Level (H-Plate) and Low-Level (L-Plate) Depression Plates (N=10).

ANOVA	TYPE	VARIABLES TESTED	H-PLATE RESULTS	F	P	L-PLATE RESULTS	F	P
FIRST COHORT MORTALITY	2-way	Limp-Dens	Limp	3.20	.05	No Sig Effect	—	—
%END DENSITY	1-way	Limp	No Sig Effect	—	—	Limp	9.71	.00
AGE-SPECIFIC MORTALITY	4-way	Limp-Loc-Dens-Age	Limp	12.85	.00	Loc	16.62	.00
			Loc	12.95	.00	Age	3.09	.01
			Age	4.27	.00	Dens	17.71	.00
						Loc-Dens	3.87	.02
						Loc-Age-Dens	3.07	.00
FIRST COHORT MORTALITY FOR LOC	3-way	Limp-Loc-Dens	Limp	8.80	.00	No Sig Effect	—	—
			Loc	5.11	.03			

NOTES:

a) Bartlett's X^2 test shows the variances are equal over 90% of the time.
b) Data were transformed with arcsin transformation (Sokal and Rohlf 1969).
c) H-Plate refers to the plates placed at the higher tidal level (2.0m above chart datum); L-Plate refers to the plates placed at the lower tidal level (0.7m above chart datum).
d) Symbols: loc=location, limp=limpets, dens=density, sig=significant.
e) Barnacles settling on the low-level plates were a mixture of *Balanus crenatus* and *Semibalanus cariosus* while those on the high-level plates were all *Balanus glandula*.
f) Results indicate only statistically significant variables.
g) "First Cohort Mortality" was calculated from survival rates such that:
   Mortality = 1 - (#barnacles in last sample/total #barnacles settled)
h) "Percentage End Density" was calculated by taking the number of barnacles present in the last sample recorded for each limpet treatment and dividing by the number present in the 0-limpet treatment for each plate. By subtracting this number from unity, the value was converted to a mortality estimate.
i) "Age-Specific Mortality" was calculated by the formula:

$$\text{Age-Specific Mortality at 3 Weeks of Age} = \text{No. Dying in Period Between 2-3 Weeks} \Big/ \text{No. Alive at Beginning of Week 2}$$

TABLE II. A Comparison of First Cohort Mortality and Percentage End Density of Barnacles on High-Level and Low-Level Depression Plates (N=10).

	FIRST COHORT MORTALITY ± 2SE		%END DENSITY ± 2SE	
# OF LIMPETS	HIGH PLATE	LOW PLATE	HIGH PLATE	LOW PLATE
0	19 ± 2	13 ± 1	0	0
2	41 ± 2	13 ± 1	10 ± 20	26 ± 8
4	52 ± 2	22 ± 1	29 ± 19	40 ± 8
6	64 ± 2	23 ± 1	28 ± 19	52 ± 8

NOTES:

a) Calculation of First Cohort Mortality and %End Density as in Table I. There is no value for %End Density in the treatment with zero limpets since %End Density is only an estimation of the mortality caused by the limpets.

zero to six. The percentage end density expression of mortality increased more slowly from 0-28% and had a variance almost as great as the mean. Thus, although limpets decreased the survival of barnacles on the high-level plates, they did not significantly affect the density of the barnacles. Possibly, there were differences in settlement of barnacles after space was made available as barnacles were removed by limpets.

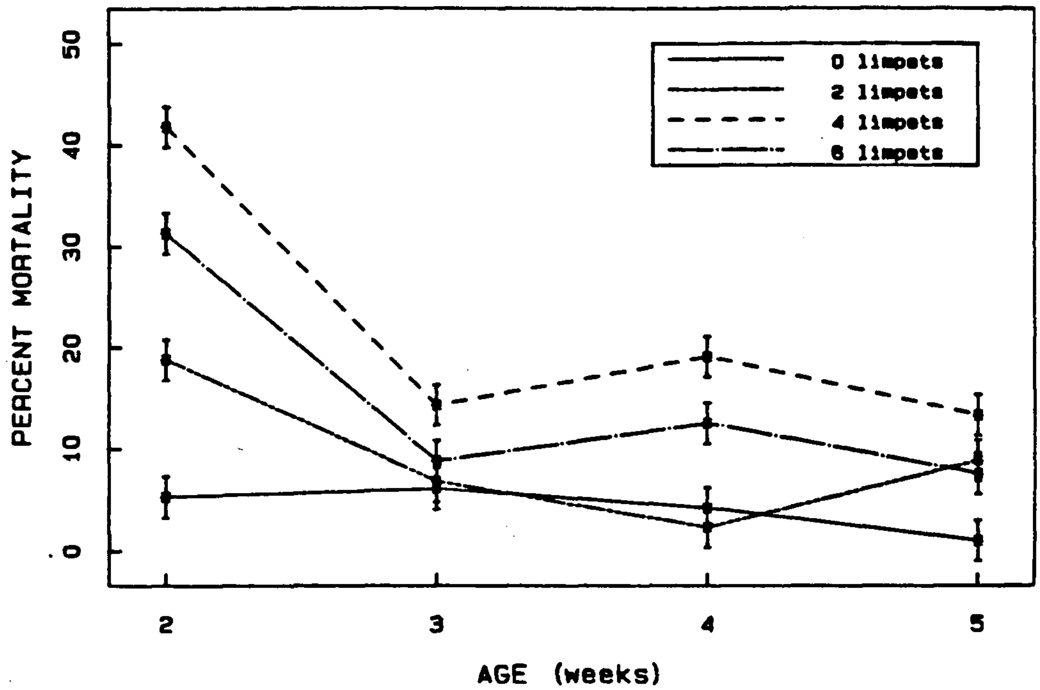
Low-Level Plates

From examination of Table II, a gradual increase (of up to 10%) in mortality of barnacles on the low-level plates is apparent as the number of limpets increased, athough this is not a significant result judging from the ANOVA on Table I ($p=.36$). Percentage end density shows a more dramatic, highly significant ($p<<0.001$) increase in mortality in the presence of limpets; limpets were responsible for over 50% mortality in the 6-limpet treatment on the low-level plates. Therefore, the presence of limpets either decreased the settlement of barnacles or caused high mortality to barnacles less than one week of age. Limpets did not, however, increase the mortality of barnacles that were sampled and, thus the proportion of barnacles in each limpet treatment remained constant.

B. AGE-SPECIFIC MORTALITY: AGE AND LOCATION

Age-specific mortality of barnacles generally decreased with age on both the high- and low-level plates (Figs. 3 and 4, respectively). In addition, barnacles located in depressions experienced a lower mortality than those on the open surface for all ages and in both high and low intertidal positions ($p<<0.001$ for barnacles on both high- and low-level plates).

A. Mortality of Barnacles on H-Plate Surface



B. Mortality of Barnacles in H-PLATE Depressions

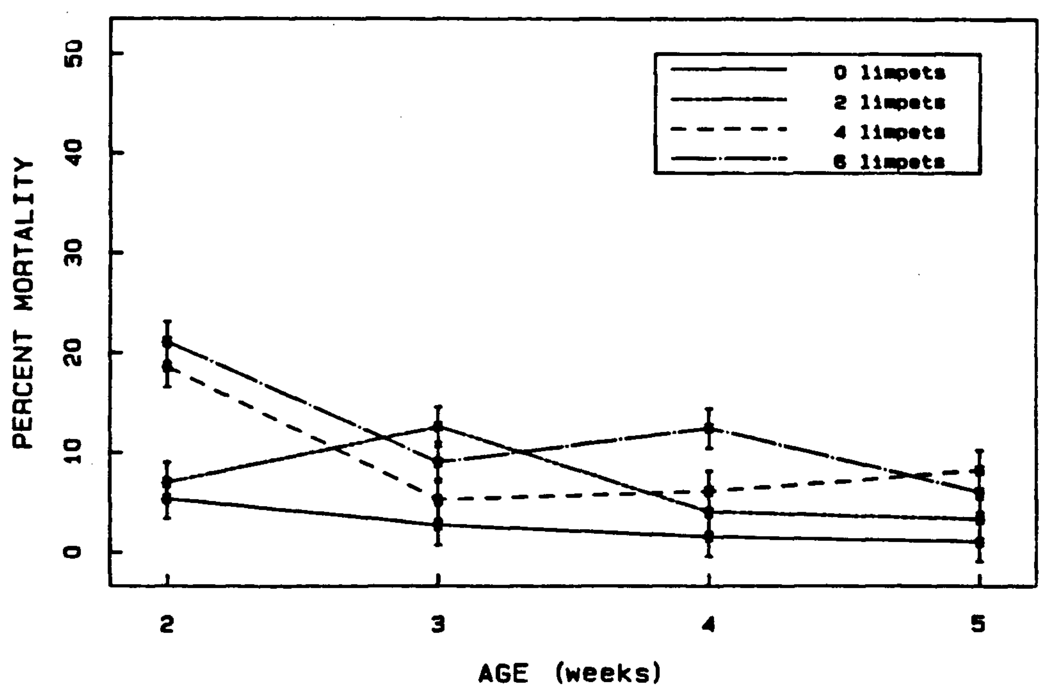


FIGURE 3. Mean mortality for different age-groups of barnacles on the open surface (GRAPH A) and in depressions (GRAPH B) of high-level depression plates (N=10). Variances are presented as ± 2SE calculated from ANOVA.

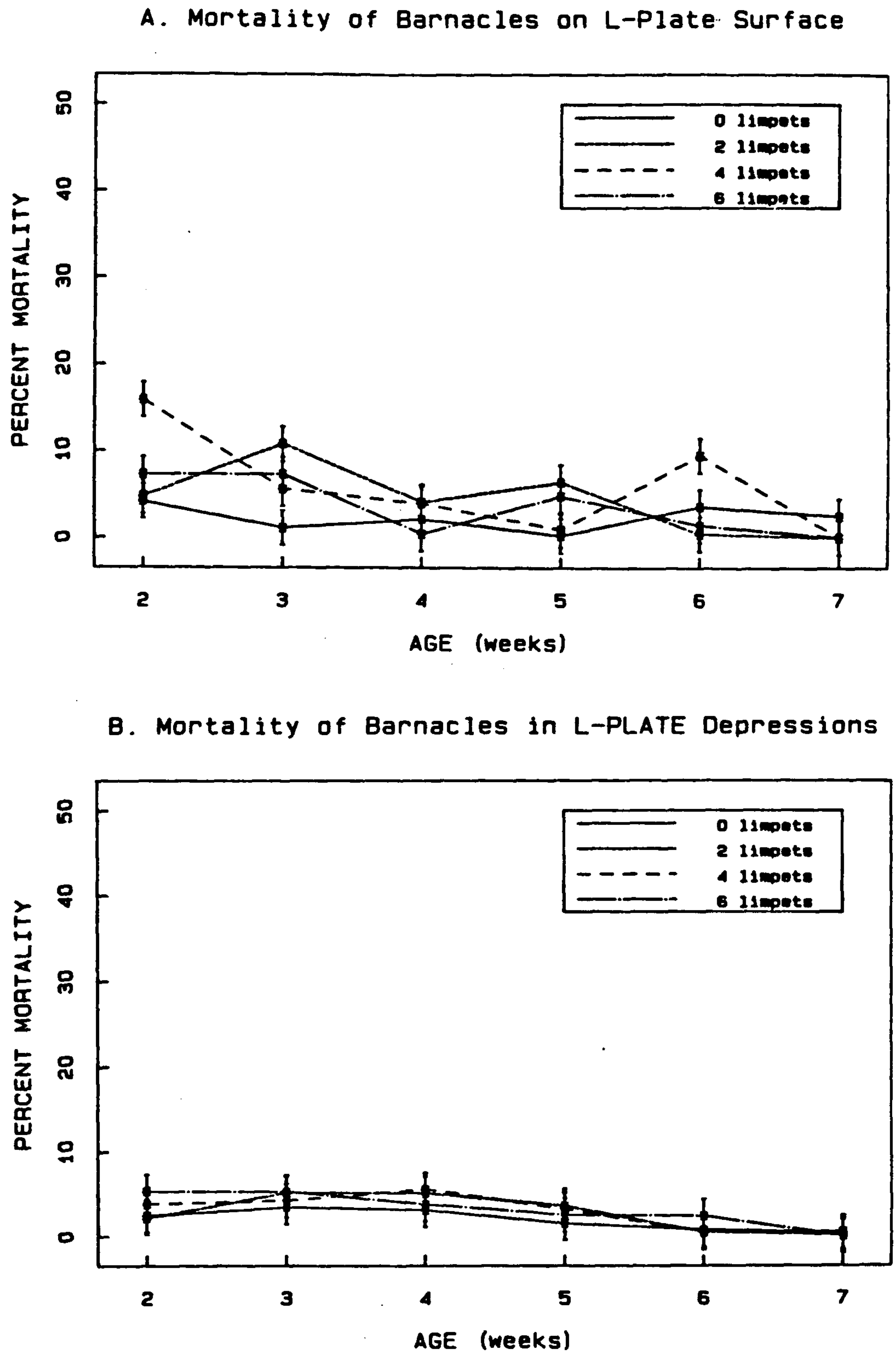


FIGURE 4. Mean mortality for different age-groups of barnacles on the open surface (GRAPH A) and in depressions (GRAPH B) on low-level (L-PLATE) depression plates (N=10). Variances are expressed as $\pm$ 2SE calculated from ANOVA.

High-Level Plates

On the high-level plates (Fig. 3), when no limpets were present, mortality remained below 8% regardless of the age or location of the barnacles. In treatments with four to six limpets, however, mortality was higher than 8% for all ages of barnacles occupying the open surface of the plates (Fig. 3A). The mortality rates of barnacles in the treatment with two limpets were similar to the treatment without limpets for all but two-week-old barnacles, which experienced 20% mortality on the open surface of the plates. Mortality on the high-level plates in treatments with four and six limpets was highest for two-week-old barnacles on the open surface of the plates, where barnacles suffered as much as 43% mortality (4-limpet treatment). In comparison, two-week-old barnacles in depressions experienced a maximum of 22% mortality (6-limpet treatment; Fig. 3B). Mortality of three-week-old barnacles dropped by two-fold both on the open surface and in depressions. In fact, three- to five-week-old juvenile barnacles died at a rate of less than 20% per week on the surface and less than 15% in depressions. Sampling on the high plates was terminated at the fifth week due to a chemical spill that occurred between the fifth and sixth week. This spill only affected the barnacles on the high-level plates since, at the time, these plates were only slightly below the surface of the water. Thus, estimates for mortality of six- and seven-week-old barnacles were not possible.

There was no significant interaction between the number of limpets and location of the barnacles for barnacles on the high-level plates, as shown in the ANOVA presented in Table I. However, each of these factors alone was significant. On the high-level plates, the combined effect of the low survival of barnacles on the open surface of the plates and the high mortality of barnacles in treatments with limpets was an increase in the mortality of juvenile barnacles experiencing both of these situations (Fig. 4). This is more clearly illustrated in the overall mortalities of barnacles in and out of depressions (Table III). Mortality of barnacles in treatments without limpets was under 22% for barnacles on the open surface or in depressions. In addition, mortality increased with increasing density of limpets more rapidly

TABLE III. First Cohort Mortality of Barnacles in Depressions and on the open Surface of High-Level and Low-Level Depression Plates (N=10).

# OF LIMPETS	LOCATION	H-PLATE MORTALITY	L-PLATE MORTALITY
0	surface	17 ± 2	14 ± 4
	depression	21 ± 2	14 ± 4
2	surface	51 ± 4	13 ± 2
	depression	32 ± 2	13 ± 2
4	surface	72 ± 2	15 ± 2
	depression	45 ± 2	16 ± 2
6	surface	75 ± 4	36 ± 2
	depression	57 ± 2	21 ± 2
	OVERALL MEAN =	46	18

NOTES:

a) First Cohort Mortality calculated as in Table I.
b) H-Plate refers to plates placed in high intertidal area (2.0m above chart datum) and L-Plate refers to plates placed in the lower intertidal area (0.7m above chart datum). Species of barnacles on high- and low-level plates are described in Table I.
c) Variances are presented as ± 2SE calculated from ANOVA.

on the open surface than in depressions. For example, in the treatment containing four limpets on the high-level plates, 72% of the barnacles on the surface were killed versus 45% in depressions. Alternatively, in the 0-limpet treatment, 17% of the barnacles on the open surface were killed versus 21% in depressions.

Low-Level Plates

Although the effect of limpets on barnacles on the low-level plates was not significant ($p=.36$), and there were no significant differences in overall mortality of barnacles in each location ($p=.27$; Tables I and III), there were still significant differences in (age-specific) mortality of barnacles of different ages ($p=.01$) and of barnacles in and out of depressions ($p<<0.001$; Fig. 4). Mortality of barnacles in depressions was consistently below 8% for all ages of barnacles, regardless of the number of limpets present. On the open surface of the plates (Fig. 4A), however, mortality was significantly higher for all ages of barnacles as compared with mortality in depressions (Fig. 4B). Furthermore, for barnacles in depressions or on the open surface of the plates, when all treatments were combined, there was a significant decrease in mortality as the age of the barnacles increased (Duncan's test).

C. AGE-SPECIFIC MORTALITY: DENSITY OF BARNACLES

Low-Level Plates

Density of barnacles was tested as a variable in two of the four ANOVA's (Table I), and it was significant in only one of the ANOVA's, namely "age-specific mortality", and then only on the low-level plates. The effect of density on the low-level plates was complicated further by its interaction with location and age. Firstly, on the low-level plates, mortality was lowest when there were less than 20 barnacles present, and increased as the number of barnacles increased. In addition, this increase in mortality was most apparent for barnacles on the open surface of the plates. At the same time, mortality decreased with the age of the barnacles (Fig. 4). Further, differences in mortality for each density of barnacles located in depressions were only significant in the older barnacles. However, differences in mortality for each density of barnacles located on the open surface of the plates were significant for all ages of barnacles (Duncan's test).

D. DISTRIBUTION OF BARNACLES

The distribution of barnacles on the high- and low-level plates, calculated as percentages of barnacles in depressions and on the open surface at settlement and in the final sample, is shown in Table IV. Since settlement occurred throughout the experiment, the location of all barnacles that settled, regardless of the week, was used in calculating these percentages.

High-Level Plates

The distribution of barnacles in and out of depressions was similar for all limpet treatments at settlement on the high-level plates (29-36% on the surface and 64-71% in depressions; Table IV). On these plates, depressions, which made up 43% of the total area available, were the preferred settling sites (mean=68% of all barnacles settling). After five weeks, the distribution of barnacles in the treatment with zero limpets remained essentially unchanged from that at settlement (1% difference in distribution); but, where limpets were present, a slightly smaller proportion of barnacles resided on the surface (5-10% decreases). Thus, by killing more barnacles on the open surface on the high-level plates, and fewer in depressions, the limpets caused a substantial change in the distribution of the barnacles.

TABLE IV. Percentage (± 2SE) of Barnacles Present in Depressions and on the open Surface of High-Level and Low-Level Depression Plates at Settlement and After 5-7 Weeks of Exposure to Different Densities of Limpets (0, 2, 4, or 6) (N=10).

	AT SETTLEMENT		AFTER 5-7 WEEKS	
	ON THE SURFACE	IN DEPRESSIONS	ON THE SURFACE	IN DEPRESSIONS
	HIGH PLATES (5 weeks exposure to limpets)			
# OF LIMPETS				
0	29 ± 12	71 ± 12	28 ± 8	72 ± 8
2	33 ± 18	67 ± 18	28 ± 8	72 ± 16
4	36 ± 10	64 ± 10	26 ± 12	74 ± 12
6	31 ± 14	69 ± 14	23 ± 12	77 ± 12
OVERALL MEAN =	32	68	26	74
	LOW PLATES (7 weeks exposure to limpets)			
0	39 ± 12	61 ± 12	39 ± 10	61 ± 10
2	41 ± 10	59 ± 10	41 ± 8	59 ± 8
4	31 ± 12	69 ± 12	32 ± 12	68 ± 12
6	25 ± 10	75 ± 10	22 ± 14	78 ± 14
OVERALL MEAN =	34	66	34	66

Low-Level Plates

Alternatively, there was no apparent change in distribution of barnacles on the low-level plates from settlement to seven weeks post settlement (Table IV). However, the distribution of barnacles differed between treatments at settlement. In the treatments with four and six limpets, 69% and 75%, of the barnacles were located in depressions at settlement. In comparison, only 61% and 59% of the barnacles were located in depressions in the treatments with zero and two limpets. Further, the distribution of the barnacles after seven weeks was similar to the distribution at settlement for all treatments of limpets. The discrepancy between the treatments at settlement may be caused by disproportionately more newly metamorphosed barnacles being killed before sampling where limpets were present (i.e. the limpets may have already removed a high proportion of the barnacles on the open surface of the plates).

II. THE SURVIVAL OF JUVENILE BARNACLES WHERE ADULT-BARNACLE REFUGES WERE PRESENT

Table V shows the results of ANOVA's performed on the mortality data for barnacles on the adult barnacle plates. The presence of limpets significantly increased the mortality of barnacles on the high-level plates ($p<.005$ for all high-level plate ANOVA's) and had a somewhat lesser effect on the mortality of barnacles on the low-level plates (p varies from $<.005$ to $>.05$ depending on the ANOVA).

Table V. Analysis of Variance Tests (ANOVA) Performed on First Cohort Mortality, Age-Specific Mortality and Percentage End Density of Barnacles on High-Level (H-Plate) and Low-Level (L-Plate) Adult Barnacle Plates (N=5).

ANOVA	TYPE	VARIABLES TESTED	H-PLATE RESULTS	F	P	L-PLATE RESULTS	F	P
FIRST COHORT MORTALITY	2-way	Limp-Dens	Limp	7.90	.00	No Sig Effect	—	—
%END DENSITY	1-way	Limp	Limp	17.56	.00	No Sig Effect	—	—
AGE-SPECIFIC MORTALITY	3-way	Limp-Age-Loc	Limp	25.28	.00	Limp	5.29	.00
			Loc	14.97	.00	Loc	3.27	.02
			Age	8.45	.00	Age	7.80	.00
						Limp-Age	1.93	.03
						Loc-Dens	2.18	.05
FIRST COHORT MORTALITY FOR LOC	3-way	Limp-Dens-Loc	Limp	30.58	.00	Limp	7.84	.00
			Loc	17.66	.00	Loc	4.34	.01

NOTES:

a) Bartlett's X^2 tests shows variances are equal over 90% of the time.
b) Data were transformed with arcsin transformation (Sokal and Rohlf 1969).
c) Symbols and calculations as in Table I.

A. FIRST COHORT MORTALITLY AND PERCENTAGE END DENSITY

High-Level Plates

On the high-level plates the effect of limpets on mortality of juvenile barnacles was significant for first cohort mortality and for percentage end density ($p<.005$ in both cases; Table V). Table VI shows a comparison of first cohort mortality and percentage end density. On the high-level plates, mortality of barnacles increased from 17-72% with an increasing density of limpets. Percentage end density similarily increased from 0-71% with an increasing number of limpets.

Low-Level Plates

As on the depression plates, there was no significant effect of the limpets on mortality of the first cohort of barnacles on the low-level plates (Table V; $p=.66$), but in this instance, there was also no significant effect on the percentage end density of the barnacles ($p=.10$). From Table VI, first cohort mortality on the low-level plates varied from 10-20% with increasing limpet density. When mortality was estimated by percentage end density, however, mortality varied from 0-34% with different densities of limpets. Neither of these differences were significant in the ANOVA's (Table V). Thus, there was no apparent difference between limpet treatments in the settlement or survival of barnacles less than one-week-old on the adult barnacle plates (as there was on the depression plates).

B. AGE-SPECIFIC MORTALITY: AGE AND LOCATION

Figures 5 and 6 show the effect of age and location of the barnacles on mortality with different densities of limpets. There were significant effects of limpets, location, and age on age-specific mortality of juvenile barnacles on both the high- and low-level plates (Table V). At

TABLE VI. A Comparison of First Cohort Mortality and Percentage End Density of Barnacles on High-Level and Low-Level Adult Barnacle Plates (N=5).

# OF LIMPETS	FIRST COHORT MORTALITY ± 2SE		%END DENSITY ± 2SE	
	HIGH PLATE	LOW PLATE	HIGH PLATE	LOW PLATE
0	17 ± 1	10 ± 1	0	0
2	53 ± 2	19 ± 1	66 ± 9	34 ± 9
4	60 ± 2	17 ± 1	63 ± 9	9 ± 9
6	72 ± 1	21 ± 1	71 ± 8	19 ± 9

NOTES:

a) Calculations as described in Table I.

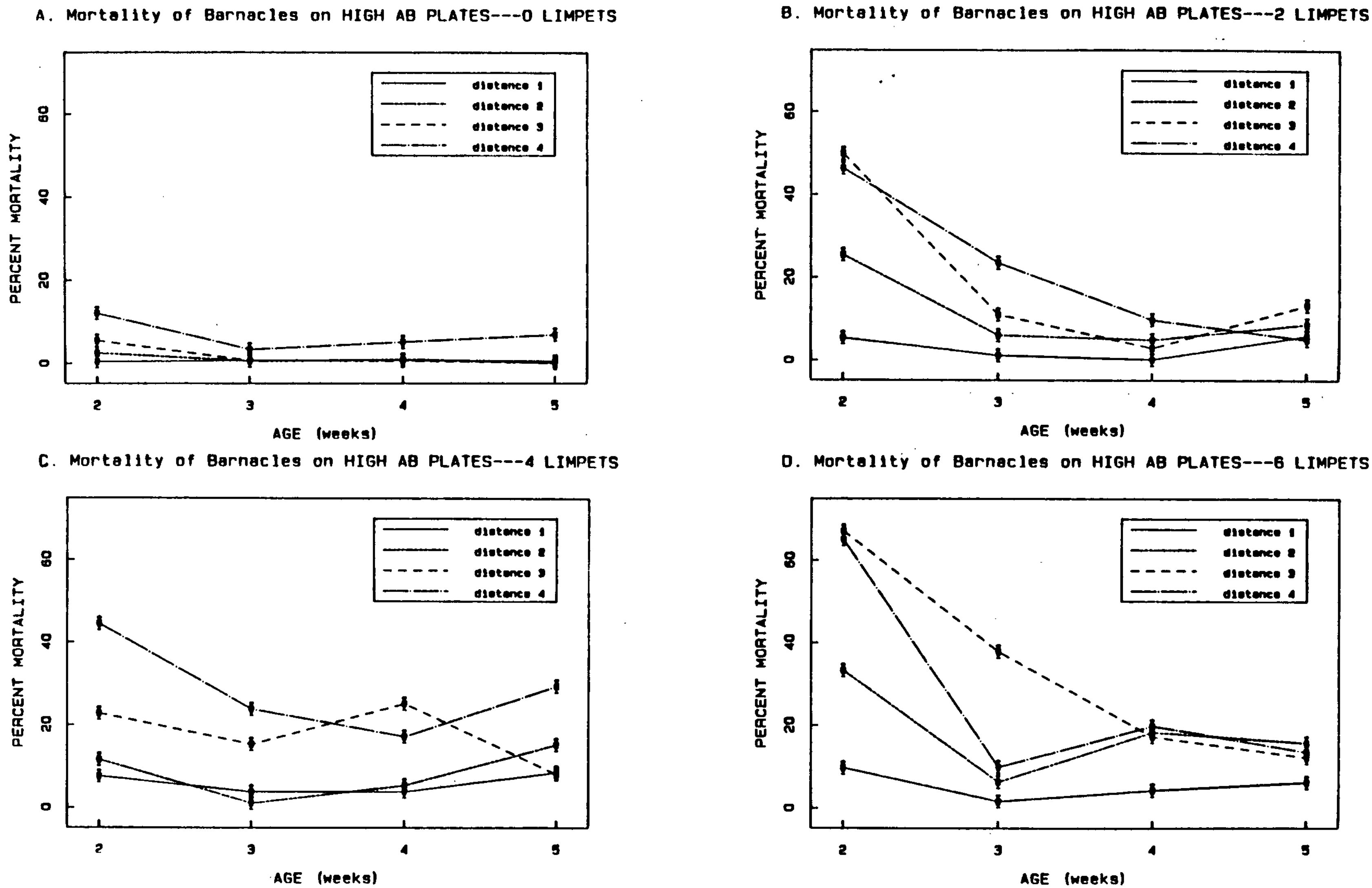


FIGURE 5. Mean mortality for different age-groups of barnacles at varying distances from adult barnacle shells and at varying densities of limpets on high-level adult barnacle (AB) plates (N=5). Variances are expressed as $\pm$ 2SE calculated from ANOVA. Distances as defined on pg. 12 of text.

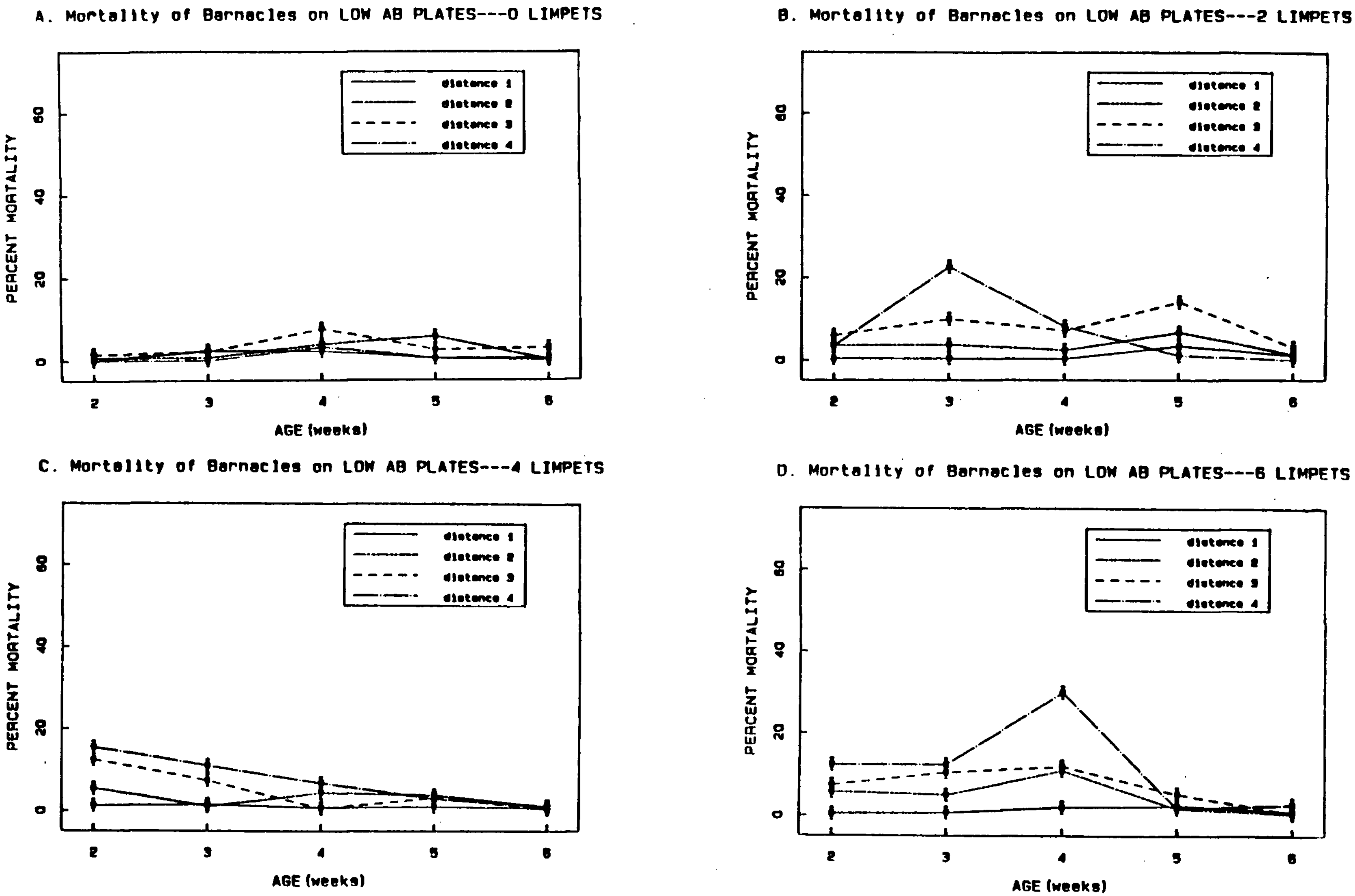


FIGURE 6. Mean mortality for different age-groups of barnacles at varying distances from adult barnacle shells and at varying densities of limpets on low-level adult barnacle (AB) plates (N=5). Variances are presented as $\pm$ 2SE calculated from ANOVA. Distances as defined on pg. 12 of text.

high and low intertidal levels there was a general trend of decreasing mortality with increasing age of barnacles for all but the treatments with zero limpets (Figs. 5 and 6). In the 0-limpet treatment, mortality was usually below 10%. Furthermore, on both high- and low-level plates there was an increase in the mortality of barnacles with increasing distance from adult barnacle shells ($p<.01$ on L-Plates and $p<.005$ on H-Plates, Table V). As expected, this did not occur in the treatment with zero limpets. Barnacles living less than 2mm from adult barnacle shells (distance 1) suffered less than 10% mortality regardless of age of the barnacles or the number of limpets present.

High-Level Plates

On the high-level plates (Fig. 5), in treatments with limpets, two-week-old barnacles that were located more than 2mm from adult barnacle shells (distances 2, 3 and 4) experienced mortality rates of up to 64% (6-limpet treatment). As the age of the barnacles increased, mortality decreased at all locations, but was never as low as for those barnacles less than 2mm from adult barnacle shells or for those in treatments without limpets. Thus, on the high-level plates, the highest mortalities were suffered by young, two- or three-week-old barnacles located more than 2mm from adult barnacle shells.

Low-Level Plates

Age-specific mortality of barnacles on low-level plates in the treatment with zero limpets was below 7% for all ages and locations of barnacles (Fig. 6). There was generally higher mortality of barnacles less than five weeks of age in the treatments with limpets. This higher mortality was enhanced as the distance from adult barnacle shells increased. Barnacles living at least 4mm from adult barnacle shells (distances 3 and 4) experienced mortality rates of up to 28% in weeks 2-4 while those living closer to adult barnacle shells (distances 1 and 2) showed no significant difference in mortality with limpet density or age

(Duncan's test). When the barnacles reached 5-6 weeks of age, all effects on mortality of age, location, and limpet density were diminished. By the time barnacles were six weeks of age, mortality was less than 8% for barnacles in all locations and limpet treatments.

C. FIRST COHORT MORTALITY: LOCATION

The mortality of the first cohort of barnacles at each distance from adult barnacle shells is shown in Table VII.

High-Level Plates

Mortality of barnacles on the high-level plates showed general trends of increase as the number of limpets increased and as the distance from adult barnacle shells increased (Table VII). However, even the mortality of barnacles less than 2mm from adult barnacle shells (distance 1) was affected by the increasing number of limpets. In addition, there was high mortality of barnacles greater than 6mm away from adult barnacle shells (distance 4) in the treatment with zero limpets (29%). Mortality reached a maximum of 95% in the treatment with six limpets at distance 3.

Low-Level Plates

On the low-level plates, no significant differences in mortality were apparent between limpet treatments for juvenile barnacles less than 2mm from adult barnacle shells (distance 1). In addition, no significant differences in mortality in the 0-limpet treatment was shown for barnacles living any distance away from adult barnacle shells (Duncan's test). Mortality on the low-level plates did generally increase, however, as the density of limpets increased.

TABLE VII. First Cohort Mortality of Juvenile Barnacles Located at Varying Distances From Adult Barnacle Shells on High-Level (H-Plate) and Low-Level (L-Plate) Adult Barnacle Plates (N=5).

# OF LIMPETS	DISTANCE	H-PLATE MORTALITY	L-PLATE MORTALITY
0	1	3 ± 2	5 ± 2
	2	5 ± 2	9 ± 2
	3	9 ± 2	17 ± 2
	4	29 ± 2	3 ± 2
2	1	12 ± 4	5 ± 2
	2	51 ± 4	16 ± 2
	3	67 ± 4	34 ± 2
	4	68 ± 4	10 ± 2
4	1	26 ± 4	7 ± 2
	2	48 ± 4	16 ± 2
	3	65 ± 4	26 ± 2
	4	84 ± 4	41 ± 2
6	1	36 ± 2	8 ± 2
	2	78 ± 2	8 ± 2
	3	95 ± 2	34 ± 2
	4	86 ± 2	53 ± 2

NOTES:

a) Distances defined as:
Distance 1 = <2mm from adult barnacle shell
Distance 2 = 2-4mm from adult barnacle shell
Distance 3 = 4-6mm from adult barnacle shell
Distance 4 = >6mm from adult barncle shell

b) Variances are presented as ± 2SE calculated from ANOVA.

c) Symbols and calculations as in Table I.

Where limpets were present, mortality also increased as the distance from adult barnacle shells increased (an exception was the 2-limpet treatment where a decrease in mortality for barnacles greater than 6mm from adult barnacle shells was shown). Mortality reached a maximum of 53% for barnacles living greater than 6mm from adult barnacle shells (distance 4) in the 6-limpet treatment.

D. DISTRIBUTION OF BARNACLES

The distribution, calculated in percentages, of barnacles at settlement and in the final sample in relation to the fixed adult barnacle shells is shown in Table VIII. In addition, Figure 7 shows a graphical representation of the change in numbers of barnacles at each location from adult barnacle shells.

High-Level Plates

Barnacles on the high-level plates preferentially settled next to adult barnacle shells (40-51% less than 2mm from adult barnacle shells; Table VIII). At settlement, there was a decreasing gradient of settled barnacles as the distance from adult barnacle shells increased. Up to 51% of the juvenile barnacles settled less than 2mm from adult barnacle shells, while only 15% settled more than 6mm from the adult barnacle shells. The change in distribution over time with limpets is shown in Figure 7. After 5 weeks in the 6-limpet treatment, up to 9% more of the barnacles occupied the area less than 2mm from adult barnacle shells as opposed to distances greater than 2mm. In contrast, only 2% more barnacles occupied these areas in the 0-limpet treatment. The differences between treatments are due to a higher mortality of barnacles living further from adult barnacle shells where limpets were present.

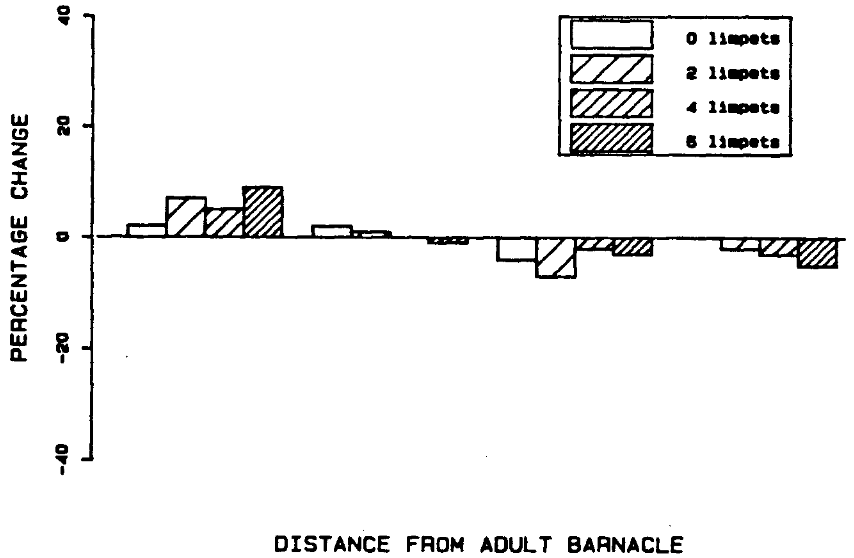
TABLE VIII. Percentage (± 2SE) of Juvenile Barnacles at Varying Distances From Adult Barnacle Shells at Settlement and After 5-7 Weeks of exposure to limpets on High-Level and Low-Level Adult Barnacle Plates (N=5).

	AT SETTLEMENT				AFTER 5-7 WEEKS			
	DISTANCE FROM ADULT BARNACLE SHELL							
# OF LIMPETS	1	2	3	4	1	2	3	4
	HIGH PLATES (6 weeks exposure to limpets)							
0	40 ± 14	27 ± 4	26 ± 18	8 ± 6	42 ± 14	29 ± 6	22 ± 12	8 ± 6
2	44 ± 6	26 ± 4	23 ± 14	8 ± 6	51 ± 6	27 ± 2	16 ± 6	6 ± 4
4	45 ± 12	24 ± 2	16 ± 4	15 ± 10	50 ± 12	24 ± 4	14 ± 4	12 ± 10
6	51 ± 8	24 ± 4	13 ± 4	12 ± 2	60 ± 8	23 ± 4	10 ± 2	7 ± 4
	LOW PLATES (7 weeks exposure to limpets)							
0	28 ± 6	15 ± 6	12 ± 6	45 ± 18	33 ± 8	17 ± 6	12 ± 6	38 ± 16
2	22 ± 10	12 ± 6	18 ± 12	48 ± 16	42 ± 20	12 ± 6	13 ± 28	33 ± 26
4	31 ± 14	11 ± 6	15 ± 4	43 ± 16	56 ± 12	13 ± 6	13 ± 6	18 ± 8
6	28 ± 14	9 ± 4	13 ± 2	50 ± 18	62 ± 18	6 ± 6	5 ± 4	27 ± 14

NOTES:

a) Distances as defined in Table VII.

A. Change in Percentage of Barnacles on H-Plates



B. Change in Percentage of Barnacles on L-Plates

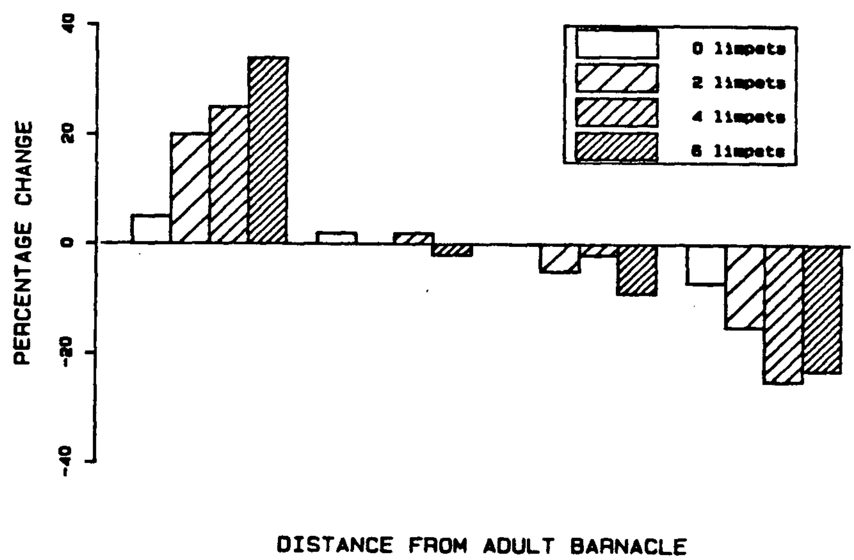


FIGURE 7. Change in percentage of barnacles at varying distances from adult barnacle shells on high-level (GRAPH A) and low-level (GRAPH B) adult barnacle plates. "Change in Percentage" is calculated by subtracting the percentage of barnacles in each location in the final sample from the percentage at settlement (obtained from TABLE VIII). Distances as defined in Table VII.

Low-Level Plates

On the low-level plates, up to 50% of the barnacles settled at a distance of 6mm or more from the adult barnacle shells (distance 4), while only 30% settled less than 2mm from adult barnacle shells (distance 1). After 6 weeks of exposure to limpets, as many as 60% of the barnacles were located less than 2mm from adult barnacle shells, whereas less than 30% of the surviving barnacles were at distances greater than 6mm from the adult barnacles. This represents a 30% shift (Figure 7). The percentage of barnacles that had settled 2-6mm from adult barnacle shells (distances 2-3) remained unchanged. In addition, there was generally no change in distribution in treatments without limpets.

III. GROWTH RATES OF BARNACLES ON HIGH- AND LOW-LEVEL PLATES

Growth rate, measured as change in basal area, increased as the size of the barnacles increased for all three species settling on the plates (Table IX), but did not occur at the same rate for all species. On the high-level plates, for example, *Balanus glandula* was the sole species of barnacle that settled. The mean basal area of one-week-old *Balanus glandula* was $0.66mm^2$. By week four, the mean size was $2.71mm^2$ basal area. At this size, the barnacles had not yet reached a refuge in size from mortality caused by limpets as the limpets still appeared to be removing barnacles between four and five weeks of age.

Barnacles that settled on the low-level plates included *Balanus crenatus*, the most abundant species, and *Semibalanus cariosus*, somewhat more variable in abundance. The mean basal area of *B. crenatus* at one week of age was $0.93mm^2$ (Table IX), and by four weeks of age it was $5.01mm^2$. At this size, *B. crenatus* on the low-level plates were just beyond the maximum size a limpet could remove (judging from the similar mortality rates of barnacles between four and five weeks of age in all of the limpet treatments). Thus, at

TABLE IX. Mean Basal Area (AREA) and Growth Rate (GR) of High-Level (H-Plate) and Low-Level (L-Plate) Plate Barnacle Species (N=20).

	H-PLATE		L-PLATE		L-PLATE	
WEEK	Area of *Balanus glandula*	GR	Area of *Balanus crenatus*	GR	Area of *Semibalanus cariosus*	GR
1	0.66 ± .16	--	0.93 ± .36	--	0.63 ± .22	--
2	0.83 ± .14	.05	1.27 ± .52	.08	0.86 ± .16	.04
3	1.29 ± .18	.07	2.16 ± .60	.14	1.45 ± .26	.06
4	2.71 ± .34	.23	5.01 ± 1.14	.43	3.08 ± .54	.23
5	5.23 ± .62	.35	9.64 ± 1.82	.77	6.57 ± 1.26	.58
6	-- --	--	22.55 ± 2.28	1.29	18.37 ± 2.36	1.18

NOTES:

a) Mean Basal Area = pi/4 x length x width
b) GR: "Growth Rate" expressed as mm^2 increase in basal area per day.
c) Variances are ± 2SE.
d) No value for the size of 6-week-old Balanus glandula is presented since a chemical spill killed many of the barnacles and any growth measurements would have been unreliable.

5.01mm^2, *B. crenatus* were in a refuge in size from mortality caused by limpets.

Conversely, *Semibalanus cariosus* on the low-level plates had a mean basal area of 0.63mm^2 in their first week, and by four weeks of age, they had reached 3.08mm^2. *Semibalanus cariosus* may have been in a refuge at this size, however, due to their inconsistent presence on the low-level plates, the absolute refuge-size could not be determined.

The growth rates of *Balanus crenatus* and *Semibalanus cariosus* on the low-level plates were similar for similarly sized barnacles. These rates were slightly less for most sizes of *Balanus glandula* on the high-level plates.

In summary, the plate experiment has shown that the presence of limpets decreases the survival of juvenile barnacles, and that depressions and proximity to adult barnacle shells provide spatial refuges for barnacles. In addition, mortality decreases as barnacles approach a refuge size. *Balanus crenatus* reached a size refuge at 5.0mm^2 in basal area.

FIELD ROCKS

MATERIALS AND METHODS

Experiments similar to those done on the slate plates were conducted on natural rock surfaces to insure that the same general trends, as found for the plates, would occur in a natural situation. Data obtained from these experiments were used to assess the effects of grazing activity by limpets on the density and distribution of juvenile barnacles in the field.

Vexar fencing (0.3mm mesh), 3cm high, was cemented around 100cm^2 areas of natural rock with Zespar$_{Tm}$ marine cement. Prior to fencing, these areas were scraped clean of encrusting organisms with a putty knife and a wire brush. Each area was provided with a density of 0, 2, 4, or 6 limpets, as in the plate experiment.

The fences were set up on vertical rock faces at two locations, Ross Islets and Dixon Island (see Fig. 1). In both locations, fences were positioned in the upper-middle section of the *Balanus glandula* zone where *Collisella digitalis* was abundant. Four replicates of each limpet treatment were placed in each of the two sites.

One unavoidable factor that may have contributed to differences between treatments was tidal height. The fences, which could not all be placed at exactly the same tidal level due to the limited space on the rock, were placed as much as 0.12m apart vertically at Dixon Island and 0.05m apart vertically at Ross Islets. This factor was incorporated into the analysis of the results (see below).

At two-week intervals, the density of limpets in each fenced area was checked, and the absence or overabundance of limpets for each treatment density was noted. Missing limpets were replaced and extra ones removed. In general, escapement was highest in the lower areas, where the limpets tended to move upward. Even so, escapement from the fenced areas was not a large problem since the mean number of limpets present in each area at the end of a two-week sampling period remained in constant proportion to the number that were originally placed there.

Barnacles began to settle in the fenced areas on 10 April 1984, and continued settling for 10-20 days thereafter. Beginning on 17 April, photographs of each area were taken every two weeks for a total of eight weeks. To insure that the photographs were in precisely the same orientation from sample to sample, wire markers were cemented inside each fenced area. The camera used for sampling was placed in the plexiglass base of a wire frame. From the plexiglass base projected a 56cm long wire support that held a 8 x 10cm wire rectangle at the end. This kept the distance from the camera to the sampling area constant. The $80cm^2$ area photographed inside the wire frame was a subsample of the entire area inside the fence ($100cm^2$). This was done to eliminate any possible edge effects of the fence.

At the end of the experiment the photographs were projected and the end density of barnacles in a $53cm^2$ area (a subsample of the total area photographed) was established for each limpet treatment. At Dixon Island, these end densities included both *Balanus glandula* and *Chthamalus dalli* (the two species settling there) whereas at Ross Islets, *Balanus glandula* was the only barnacle present, and thus the only barnacle included in the end densities. End densities of barnacles were taken from the last sample on 18 June, seven weeks after the majority of the barnacles had settled. At this time, based on the results of other experiments, the mean size of the barnacles was considered to be beyond that which the limpets could bulldoze or graze (greater than $7.0mm^2$).

An ANOVA was performed on the mean end densities of barnacles in each treatment. The treatment areas at Ross Islets and Dixon Island were tested separately. Due to the greater settlement of barnacles at lower tidal heights, tidal height was separated into high- and low-level categories such that at Dixon, low-level areas were 1.8-2.4m above chart datum (ACD) and high-level areas were 2.5-3.1m ACD and at Ross Islets, the low-level areas were 1.7-1.9m ACD and the high-level areas were 2.0-2.2m ACD.

The depressions present on the surface of the rocks were relatively small, both in width and depth, compared to those present on the plates. If limpets were not capable of removing barnacles from these depressions then the distribution of the barnacles should have become more restricted to depressions as grazing pressure increased. Since barnacles settle preferentially in depressions, which would result in a clumped distribution, the change in distribution of barnacles occuring in the presence of limpets should lead to an increase in aggregation.

To test the above hypothesis, the x and y coordinates of each barnacle at Ross Islets within a $53cm^2$ area were recorded on a digitizing pad. These were used to assess the distribution of barnacles at settlement and in the last sample. From the differences in distribution between barnacles at settlement and those in the final sample, the use of depressions by the barnacles were analysed for areas with a varying densities of limpets.

The distribution of barnacles in each fenced area was established using Clark and Evans' (1954) Nearest Neighbor method. This method of estimating distribution tests for significant deviations from a random distribution and gives a relative value of the extent of deviation, toward an aggregated or toward a regularly dispersed distribution. This analysis was performed only on the data for *Balanus glandula* at Ross Islets since data were incomplete at Dixon Island. The nearest distance between each barnacle and its neighboring barnacles was calculated from the x and y coordinates obtained from the acetates. Nearest distances were calculated separately for barnacles at settlement, which included all of the barnacles sampled throughout the experiment regardless of the date of settlement, and for barnacles remaining in the last sample, seven weeks after the experiment had begun. From these values, Clark and Evans' test was used to estimate the mean nearest neighbor distance (R-obs), the expected mean nearest neighbor distance if the population were randomly distributed (R-exp), the absolute density of animals per cm^2 (P), the standard error expected in a random population (SE), a relative measure of the spatial distribution (R), and a test of the statistical significance of R (i.e. if R significantly deviates from a random distribution) (Z). The value of

R is 1 for a random distribution, approaches zero for a clumped distribution, and approaches 2.15 for a uniform distribution. If Z is greater than 1.96, the null hypothesis of a random distribution is rejected (at $p=.05$ level).

RESULTS

I. END DENSITIES

Table X shows the results of the ANOVA's and a graphical representation of these results is presented in Figure 8. Limpets were shown to decrease significantly the density of barnacles at Dixon Island ($p=.001$; Table X). The strongest effect of limpets was in the low intertidal areas where there was an almost 5-fold decrease in the density of barnacles from the 0-limpet treatment to the 6-limpet treatment (Fig. 8A). In the high intertidal areas, although there was a decrease in density in the 2- and 4-limpet treatments, in the 6-limpet treatment, the density of barnacles equalled that in the 0-limpet treatment.

Limpets did not have a significant effect on the end density of barnacles at Ross Islets (Table X and Fig. 8B). Although a general decrease in end density with increasing numbers of limpets is apparent in Figure 8B, the ANOVA showed this difference was not significant ($p=.10$).

II. DISTRIBUTION

The results of Clark and Evans' test on the distribution of barnacles at settlement and in the final sample are presented in Table XI. The values in Table XI represent a single set of treatments (0, 2, and 4 limpets) that had similar densities of barnacles at settlement. No values for 6-limpet treatments are shown since the density of barnacles at settlement was much lower than that in the other limpet treatments. The data presented in

TABLE X. Analysis of Variance tests (ANOVA) performed on End Densities at Dixon Island and Ross Islets (N=5).

ANOVA	TYPE	VARIABLES TESTED	RESULTS	F	P
DIXON ISLAND END DENSITY	2-way	Limp-Tidal Level	Limp Tide	8.91 6.57	.00 .00
ROSS ISLETS END DENSITY	2-way	Limp-Tidal Level	No Sig Effects	—	—

NOTES:

b) Bartlett's X^2 shows that variances are equal over 90% of the time.
c) Data were transformed with log transformation (Sokal and Rolf 1969).
d) Results indicate only the variables that were statistically significant.
e) "End Density" is the density of barnacles present in the final sample, eight weeks after most settlement occurred.
f) The Tidal level factor was divided into two groups: low-level and high-level. The low-level, expressed in meters above chart datum, was 1.8-2.4m and the high-level was 2.5-3.1m.

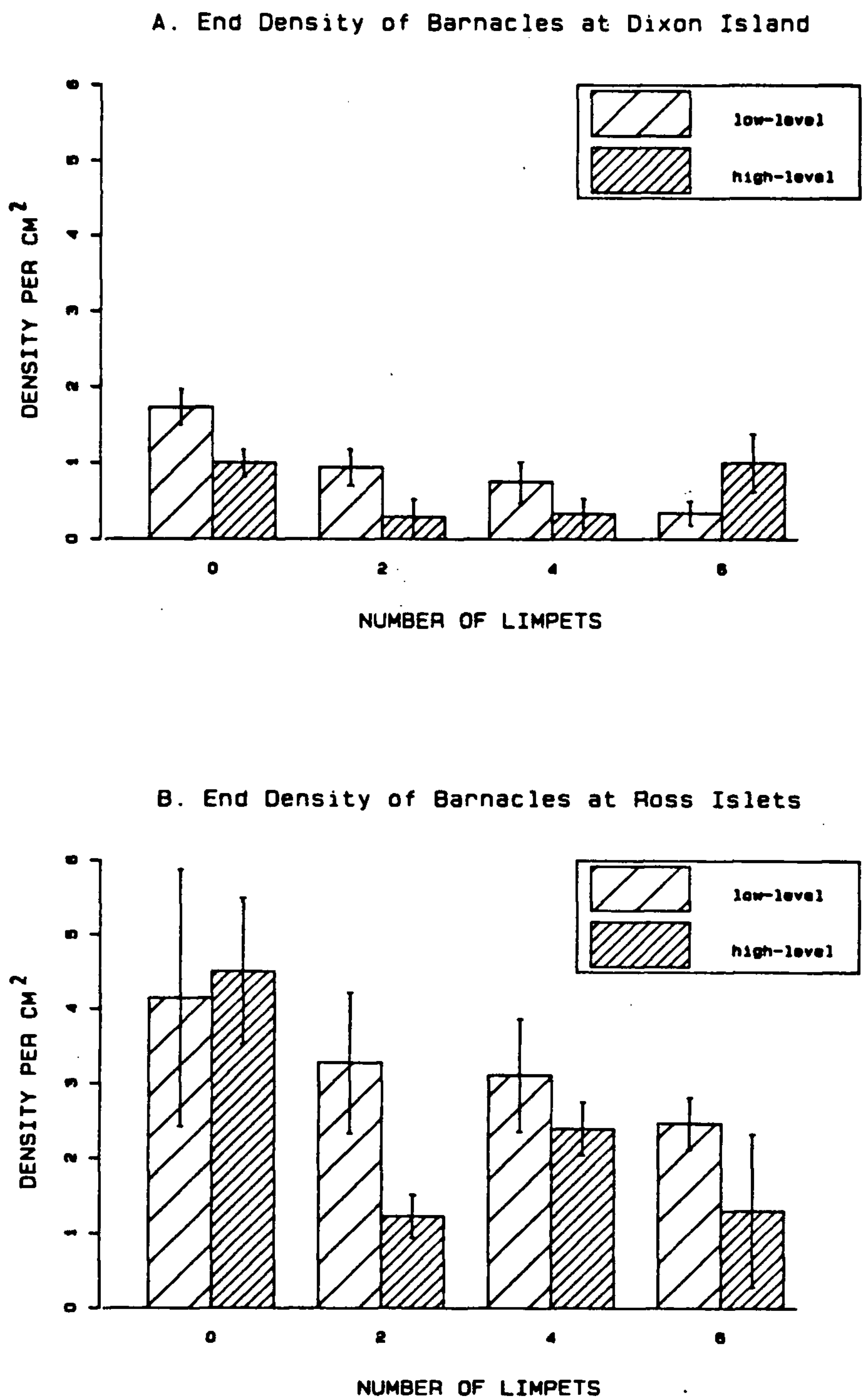


FIGURE 8. Mean end densities of barnacles per cm^2 at Dixon Island (GRAPH A) and at Ross Islets (GRAPH B). Barnacles were exposed to different densities of limpets at low and high intertidal-level sites (N=2 for each level). Variances are presented as $\pm$ 2SE calculated from ANOVA. The Tidal height range, expressed in meters above chart datum, was 2.20-2.50m for the low-level and 2.51-2.80m for the high-level. Dixon Island barnacle species included both *Balanus glandula* and *Chthamalus dalli*.

TABLE XI. Distribution of Balanus Glandula at Ross Islets Calculated From Clark and Evans' (1954) Nearest Neighbor Test of Distribution.

# OF LIMPETS	P	R-obs	R-exp	SE	R	Z	PATTERN
AT SETTLEMENT							
0	.847	.032	.207	.008	.080	*	clumped
2	.879	.035	.203	.008	.091	*	clumped
4	.847	.032	.207	.008	.082	*	clumped
AFTER 8 WEEKS							
0	.605	.037	.245	.012	.078	*	clumped
2	.674	.040	.233	.010	.091	*	clumped
4	.626	.035	.241	.011	.076	*	clumped

NOTES:

a) Meaning of symbols for Clark and Evans' (1954) Nearest Neighbor Distribution Test as follows:

P = absolute density per cm^2
R-obs = observed mean distance to nearest neighbor (cm)
R-exp = predicted mean distance to nearest neighbor (cm)
SE = standard error expected in a random population
R = observed over expected mean distance to nearest neighbor
if R equals 1 = random distribution
if R approaches 0 = clumped distribution
if R approaches 2.15 = uniform distribution
Z = statistical test of R, designated * if R significantly deviates from a random distribution

b) Data presented represent the distribution in a single fenced area for each density of limpets. Areas chosen contained a similar density of barnacles at settlement.

Table XI are, however, representative of the results obtained in all treatments.

The distribution of barnacles was significantly clumped in all limpet treatments at Ross Islets (R approaches zero; $Z > 1.96$; Table XI). In addition, the degree of aggregation was similar in all limpet treatments. For the treatments shown in Table XI, there was a mean density of 0.858 barnacles per cm^2 at settlement and a mean nearest distance of 0.033cm. The mean nearest distance observed in these treatments was over six times closer than would be expected had their distribution been random. The density of barnacles decreased after seven weeks to 0.635 barnacles per cm^2 in all three limpet treatments. The decrease in density resulted in a slight increase in mean nearest distance of .004cm. But, the mean nearest distance between barnacles in the last sample remained six times closer than would be expected had it been random.

In summary, the field rock experiment showed that limpets can decrease the density of barnacles on intertidal rocks in the field, but they do not necessarily change the distribution of the barnacles.

BARNACLES ON SMOOTH SURFACES

MATERIALS AND METHODS

To evaluate the method of removal of barnacles by limpets on smooth rock surfaces, limpets were allowed to graze on small, smooth rocks from the field. These rocks were approximately 10cm in diameter and contained various sizes of newly settled barnacles ranging from 0.6-10.0mm^2 in basal area. The rocks were suspended in an aquarium with string and kept under continual submersion in quiet water conditions for 5-7 day intervals. Plastic pans were positioned under the rocks so that limpet feces and falling fragments of barnacles could be collected. These collections were used to determine: (1) the percentage of barnacles ingested versus bulldozed, (2) the maximum size of barnacle removed by limpets, and (3) the condition of the barnacles that were removed by limpets (i.e. whole, crushed, or in fragments).

At the same time, rocks containing *Balanus glandula*, *Balanus crenatus*, *Semibalanus cariosus*, or *Chthamalus dalli* were collected from the field and sampled to determine the maximum size of each species of barnacle a limpet can remove. The condition after death of each barnacle was assessed as: (1) whole, (2) crushed (shell compressed, but still in one piece), and (3) fragmented (shell plates separated). Whole or crushed barnacles which had fallen from the rocks were measured for maximum length (rostro-carina axis) and, where possible, width. These measurements were converted to basal area using the formula of an ellipse, as described earlier. In most instances, each rock contained only one species of barnacle, making the identification of the species easy. Other species, when present, were identified from their shell fragments.

The percentage of barnacles ingested versus bulldozed was calculated by noting their presence in and out of the limpet feces. Where the shells of barnacles were broken into small fragments, estimates of the number of barnacles comprising a pile of barnacle fragments were made. When the fragments were in the feces, each feces pellet with fragments was counted as one barnacle (a preliminary study showed this to be the case).

RESULTS

I. METHOD OF REMOVAL

During the course of the experiment, 435 barnacles were removed from rocks by limpets. Of these, 18% were found in the feces (ingested) and 82% were separate from the feces (bulldozed).

The percentages of each species found whole, crushed, or fragmented are presented in Table XII. It is curious that in the two species of barnacles with calcareous bases, *Balanus glandula* and *Balanus crenatus*, a high percentage of the shells were fragmented (57% and 66%, respectively), indicating that they had weak plate junctions. The opposite was true for the two species with membranous bases, *Semibalanus cariosus* and *Chthamalus dalli*, both of which were removed whole or crushed a higher percentage of the time (23% and 49% fragmented, respectively).

II. MAXIMUM SIZE REMOVED

The maximum size of barnacle removed varied from 3.51mm^2 for *Semibalanus cariosus* to 6.69mm^2 for *Chthamalus dalli*. In comparison, maximum size removed of *Balanus crenatus* was 6.07mm^2, and of *Balanus glandula* was 6.67mm^2.

In summary, limpets most often bulldoze barnacles on smooth surfaces, although they do have the ability to ingest the barnacles. When *B. glandula, B. crenatus,* or *C. dalli* reached 6.7mm^2 in basal area, limpets were no longer able to remove the barnacles. The maximum size of *S. cariosus* removed by limpets was 3.5mm^2 in basal area.

TABLE XII. Condition of Shells of Barnacles (Whole, Crushed, or Fragmented) Expressed as Percentages of the Total Removed by Limpets for Populations of Barnacles on Laboratory Rocks.

SPECIES	WHOLE	CRUSHED	FRAGMENTED	N
Balanus glandula	24%	19%	57%	168
Balanus crenatus	13%	21%	66%	79
Semibalanus cariosus	39%	38%	23%	13
Chthamalus dalli	29%	22%	49%	63
OVERALL MEAN	26%	25%	49%	

NOTES:

a) "Conditions" defined as:
Whole = barnacle shell intact
Crushed = barnacle shell compressed (usually laterally), but in one piece
Fragmented = barnacle shell plates separated, plates may be in pieces

BARNACLES IN DEPRESSIONS ON PIPES

MATERIALS AND METHODS

French pipes, which are corregated pvc tubes with parallel grooves running their length (used in mariculture operations as an artificial substrate for the collection of oyster spat), were found to be excellent substrates for the settlement of barnacle larvae. It was assumed that because barnacles settling onto French pipes were confined to fairly deep, closely packed grooves, the artificial substrate on French pipes might be similar to that in crevices or deep grooves in natural rock.

A large set of two- to three-week-old *Balanus glandula* spat (0.96-1.67mm^2 basal area; 65 per linear cm of 2cm dia pipe) was found on French pipes in Pipestem Inlet near Bamfield, B.C. in January 1985. Two 200cm-long pipes were brought into the laboratory where they were cut into 15cm pieces. Corks were placed at the ends of the hollow pipes, which allowed them to float on the surface of the water. Ten limpets per pipe were then added and the pipes were placed in a seawater-filled plastic pan. The movement of limpets around a pipe caused the pipe to rotate on the surface of the water, which subjected both limpets and barnacles to partial exposure and submersion. Limpet feces and shell particles dropping from the pipes were retained on the bottom of the pan. These were removed once weekly and assessed for the presence of barnacles. Bulldozing versus ingestion by limpets and the condition of the barnacles after removal was assessed as in the laboratory-rock experiment.

RESULTS

I. METHOD OF REMOVAL

Fifty-eight percent of the barnacles removed from the pipes were found in the feces of limpets. Most of these barnacles were fragmented (67%) or crushed (26%), and relatively few were found whole (7%). The remaining barnacles which were not in the feces (42% of the total), were in slightly better condition. Of these, 45% were fragmented, 27% were crushed, and 28% were whole.

Of the barnacles that were crushed, both in and out of the feces, over 70% were laterally compressed. Most of the remaining 30% were compressed on the ends.

In summary, the French pipe experiment showed that limpets can remove barnacles from depressions, even though their ability to do this may be somewhat hindered. Most barnacles in depressions that were removed were ingested, indicating that they were probably removed by the mouths or radulae of the limpets. Removal of barnacles by the shells of the limpets may have been hindered in the depressions.

BARNACLES IN DEPRESSIONS ON PLATES

MATERIAL AND METHODS

Balanus glandula were reared in the laboratory for use in experiments when larvae were not available in the field. Ripe eggs were collected from gravid barnacles in the field and hatched in 12-liter jars filled with 10 liters of 1-micron filtered sea water. Within a day of hatching, the larvae were placed in new 12-liter jars at a density of approximately one larva per ml sea water, and incubated at 15 ^{0} C. The water in these jars was aerated so that the larvae mostly stayed in the water column. The water was changed once every two days and filtered to 1 micron with GAF bags. The larvae were fed a mixture of *Skeletonema costatum* and *Chaetocerus didymes*. In approximately 10 days the nauplii began changing to cyprids. These cyprids were kept in the incubators for approximately one week and then put into settling trays.

The cyprids were allowed to settle onto 10 x 10cm slate plates (described below) in a highly aerated and magnetically stirred 22 x 30cm plastic pan of sea water. The plates were propped up against the sides of the pan so that the cyprids could settle onto a vertical surface. Once the cyprids settled the plates were hung in an aquarium with flow-through seawater.

The purpose of this experiment was to determine the maximum depth and the minimum width of depression from which a limpet could remove a barnacle. To determine this, depressions of varying width and depth were drilled into each plate as follows: (1) 5 x 3mm, (2) 5 x 2mm, (3) 3 x .75mm, (4) 3.5 x 2.5mm, (5) 2 x 2mm, (6) 2 x .50mm, (7) 1.5 x 1.5mm. Each plate contained 35 (five of each size) randomly located depressions.

Initially, the distribution of barnacles on the plates was mapped on acetates and photographs of each barnacle were taken. These photographs were later used to determine the size and position (edge or middle of depression) of the barnacles. Ten limpets were then placed on each plate and allowed to graze for three one-week intervals. The plates were checked and re-photographed weekly to determine the growth and survival of the barnacles. When less than three barnacles remained on a plate, the plate was discontinued. Since the availability of food for the barnacles in the laboratory was minimal and the growth of the barnacles was slow, differences in size from week to week were not as great as in the field experiments.

RESULTS

I. DEPRESSION REFUGE

Twenty-five barnacles settled onto the plates in all. The number of barnacles inhabiting each type of depression is shown in Table XIII. At least one barnacle settled into every type of depression . However, the wider depressions were more often utilized (eg. 56% settled in the 5mm-wide depressions).

Limpets were able to remove barnacles from most of the depressions tested. The width and/or depth of the depressions did not seem to hinder the ability of the limpets to remove the barnacles. The two depression types in which barnacles were not removed were both narrow and deep (3 x .8mm and 3.5 x 2.5mm), but too few barnacles settled in these depressions to make any judgement on the absolute limits of the limpets' ability to remove the barnacles. The limpets were shown to be capable of removing barnacles from even very small depressions (eg. 1.5 x 1.5mm; Table XIII).

In summary, the laboratory plate experiment showed that limpets can remove barnacles from even very deep or narrow depressions.

TABLE XIII. The Number of Juvenile *Balanus Glandula* removed by *Collisella Digitalis* From Various Sizes of Depressions (barnacles present: N=25; barnacles removed: N=11).

NUMBER OF BARNACLES	SIZE OF DEPRESSION (MM) LENGTH X DEPTH						
	5 X 3	5 X 2	3 X .8	3.5 X 2.5	2 X 2	2 X .5	1.5 X 1.5
SETTTLED INITIALLY	9	5	1	3	2	4	1
REMOVED BY LIMPETS	4	3	0	0	1	2	1

OBSERVATIONS OF LIMPETS REMOVING BARNACLES

Balanus glandula that had settled on the transparent new growth of oyster shells were collected from Pipestem Inlet in February of 1985. Pieces of shell with barnacles were mounted onto 5 x 7.5cm glass slides with quick drying clear epoxy glue. A single limpet was then placed on the slide and observed under a dissecting microscope. When a barnacle was removed it was noted whether or not the limpet was grazing. In addition, the method of removal (i.e. the part of the limpet's body or shell removing the barnacle), or whether the limpet ingested the barnacle were noted.

A total of ten barnacles were removed in a variety of ways by limpets under observation. Of these, five were removed by bulldozing with the shell, two were removed by bulldozing with the foot, and two were pushed off with the mouth of the limpet, but not ingested. In addition, one $0.95mm^2$ (in basal area) barnacle was pushed off by the tentacle of the limpet. None of the barnacles observed were ingested.

DISCUSSION

It is known that the presence of barnacles enhances the settlement of juvenile limpets (Lewis and Bowman 1975; Choat 1977; Tsuchiya 1984). The limpets that settle amongst barnacles can obtain protection from desiccation (Lewis and Bowman 1975; Choat 1977; Branch 1975a,b; Creese 1982), storms (Creese 1982; Underwood and McFadyen 1983), and possibly predation (Choat 1977). All of this is available to a small, juvenile limpet that can move freely amongst the barnacles. However, as a limpet grows, the areas that were once large enough for it to graze in become too confined, and the heterogeneity of the surface caused by the barnacles begins to restrict the grazing activities of the growing limpets (Lewis and Bowman 1975; Choat 1977; Creese 1982; Hawkins and Hartnoll 1982; Branch 1976; Workman 1983). In addition, the barnacles may even reduce the available food for the limpets by restricting settlement of algal spores through their filter-feeding activities (Branch 1976; Ballantine 1961). Thus, the barnacles become competitors for space with the larger limpets.

There are three documented ways that larger limpets respond to competition for space with barnacles. Firstly, some limpet species move upwards as they grow and, upon reaching a certain size, live in a high intertidal habitat free from barnacles and their influence (Branch 1975b). Secondly, some limpet species grow more slowly and may remain small when they are in areas with high densities of barnacles (Lewis and Bowman 1975; Choat 1977). This may result from a decrease in availability of easily grazed surfaces where adult barnacles predominate, but at least the limpets are allowed to be cohabitants in these areas. Finally, certain limpet species can bulldoze the rock surface, sweeping away the young barnacles in their path (Choat 1977; Hatton 1938; Dayton 1971; Creese 1982; Menge 1976). This may help keep the density of barnacles low, thus reducing further competition.

Bulldozing of the substrate by limpets occurs in two ways. Some limpet species, for example *Patella vulgata* and *Lottia gigantia*, respond to competition for space by grazing only in a defined territory and bulldozing off all sessile organisms that settle in that territory (Branch

1975a,b; Choat 1977). Other limpet species, such as *Collisella pelta* and *C. digitalis*, graze over a larger less defined area in a more or less random manner, and temporarily clear space by removing attached organisms (Connell 1961a, 1970; Branch 1981; Hatton 1938; Denley and Underwood 1971; Creese 1982).

In the present study I examined the way in which *Collisella digitalis*, a non-territorial limpet (Choat and Black 1977; Haven 1970), removes barnacles from the surface of a rock. As *Collisella* moves across a rock surface its shell is carried above the substrate. If a small barnacle on the surface of the rock is in the way of the limpet, *Collisella* may inadvertently dislodge it with its foot or shell. Alternatively, if *Collisella* is grazing, the barnacle may be dislodged by the mouth or radula, or even tentacle, and then ingested. Furthermore, even barnacles dislodged by the foot or shell may be ingested if the limpet's mouth comes into contact with the dislodged barnacle.

Barnacles can escape being removed by limpets in two ways. Firstly, barnacles can be too strongly attached for a limpet to dislodge. This can occur when the barnacle reaches a certain size, at which time attachment is too strong and too rigid to be affected by a limpet. At this time barnacles obtain a refuge in size. Barnacles in the present study obtained refuges in size when they were 5-6.7mm^2 in basal diameter. Secondly, barnacles can escape being bulldozed by limpets by living in an area of the rock on which the motility of the limpet is hindered. Barnacles inhabiting these areas have obtained a refuge in space. Two such spatial refuges were found in this study: depressions and proximity to adult barnacles.

In order for refugia to exist at all for juvenile barnacles, limpets must cause substantial mortality to the barnacles such that living in non-refuge areas or being less than refuge-size is a risk. In the present study, the extent of mortality caused by *Collisella digitalis* was determined on slate plates in the field and on intertidal rocks. On the plates, *C. digitalis* caused an increase in the mortality of juvenile barnacles located on the open surface, as opposed to being located in depressions, of up to 58% (high-level depression plates). In addition, on the intertidal rocks at Dixon Island, limpets caused a decrease in the density of juvenile barnacles of up to 33%.

In both examples, barnacles suffered considerable mortality from limpets. However, mortality from limpets was not as severe for the barnacles on the low-level plates. On the low-level depression plates the presence of limpets did not significantly affect survival rates (age-specific and first cohort) of barnacles, but it did significantly affect the percentage end density (decrease of up to 52%; Table II). Furthermore, limpets on the low-level adult barnacle plates significantly decreased age-specific survival of barnacles, but did not significantly decrease percentage end density or first cohort survival. Thus, on the low-level plates the limpets had a variable and somewhat weaker effect on barnacles than on the high-level plates. However, *C. digitalis* is normally a high intertidal limpet, and the low-level plates were placed below the level at which this limpet would normally occur. Therefore the physiological constraints imposed on the limpets at the lower level may have limited their activity on these plates. In addition, *C. digitalis* was noted to move upward when placed in intertidal areas lower than their normal occurrence. The relatively higher escapements of limpets on the low-level plates, as compared to the ones on the high-level plates, may have been examples of such upward migratory movements.

As they approached a refuge size, barnacles were able to escape the detrimental effects of limpets. On the low-level plates, *Balanus crenatus* reached a refuge-size at 5.0mm^2 basal area (at four weeks of age). At the end of four weeks, *Balanus glandula* on the high-level plates were still not sufficiently large to avoid limpet displacement; they had reached a basal area of only 2.7mm^2. *Balanus glandula* did not reach 5.0mm^2 in basal area until their fifth week of age.

In laboratory experiments the maximum size of each of three species of barnacle (*Balanus glandula*, *B. crenatus*, and *Chthamalus dalli*) which *C. digitalis* could remove was slightly greater than that shown on the slate plates in the field experiments (6-6.7mm^2 in basal area as opposed to 5.0mm^2). In addition, both the laboratory and field experiments indicated a smaller refuge size between 3-3.5mm^2 for *Semibalanus cariosus*, but this may not have been a reliable estimate due to the small sample sizes of this barnacle (inconsistently distributed on the field plates; N=12 for *S. cariosus* in the laboratory as compared with N=63-168 for the other three species). Therefore, although barnacles on the field plates that were 5.0mm^2 in basal area appeared to be safe from mortality caused by *C. digitalis*, they were not entirely so (i.e. their refuge was not complete) until they reached almost 7mm^2 in basal area. The maximum size range of 5-6.7mm^2 basal area, estimated in the present study to be the minimum size-refuge dimension, corresponds to a length of approximately 2.7-3.5mm. This is similar to lengths of 2-4mm estimated by Dayton (1971) to be a minimum size refuge for *Balanus* spp. from mortality caused by *Acmaea* (*Collisella*) spp., and lengths of 3-4mm estimated by Denley and Underwood (1979) to be minimum for *Tesseropora rosea* to occupy a size refuge from mortality caused by *Cellana tramoserica*.

The ability of barnacles to withstand removal by limpets was related to the sizes and species of barnacles present (see Figures 3-6 and Table IX). Are these differences with size and species reflections of differing strengths of attachment of the barnacles? Do the maximum sizes of barnacles removed by limpets relate to maximum forces that limpets can exert? I have conducted further experiments in this regard to assess the actual force required to remove *Balanus glandula*, *Balanus crenatus*, *Semibalanus cariosus*, and *Chthamalus dalli* from rocks (Miller, MS in prep). The results of this latter study showed that the force required to remove the two *Balanus* species increased with size (measured in basal area) at a slower rate than it did for *Semibalanus cariosus* and *Chthamalus dalli*. For example, the removal of *Balanus glandula* or *B. crenatus* of 5-7mm^2 in basal area required 1.1-1.5 Newtons (112-150g) of laterally directed force, while the removal of similarly sized *Semibalanus cariosus* or *Chthamalus dalli* required 1.4-2.1 Newtons (137-200g) of force. Thus, the strength of attachment of the barnacles may explain differences in the removal of various sizes of barnacles. In addition, differing strengths of attachment may explain why the refuge size of *S. cariosus* was smaller than that of the two *Balanus* species. However, since the refuge size of *C. dalli* obtained in the laboratory was similar to that for the *Balanus* species, even though *C. dalli* is more strongly attached to the substrate, force of removal may not be the only determining factor in the refuge sizes of barnacles.

It must be emphasized that a limpet does not dislodge every barnacle it contacts. Even some of the small barnacles observed in this study were capable of withstanding removal as the limpets moved over them. Dislodgment of barnacles was only observed when the limpets applied a force to the sides of the barnacles. Thus, the shell plates and the connections between them may have been stronger than the attachment of the barnacles to the substrate.

A number of studies have shown that size refuges are commonly used by sessile organisms to escape being eaten by predators. For example, size refugia have been noted for *Mytilus edulis* in response to predation by *Pisaster* spp. and *Thais* spp. (Paine 1976; Palmer 1983), and for *Balanus* spp. and *Semibalanus* spp. in response to predation by *Thais* spp. and certain fish (Palmer 1983; Menge and Lubchenco 1981). Menge and Lubchenco (1981), in their study comparing the occupation of refuges in temperate and tropical intertidal areas, found that in tropical Panama, there were many predators and grazers but relatively few sessile species (mostly *Chthamalus* spp. and oysters), and that *Balanus* spp. were absent. They proposed that the reason *Chthamalus* was successful in the tropics, as opposed to *Balanus*, was due to the flat, massive shells of the former. They theorized that *Chthamalus* obtains a refuge in size from fish grazers and from gastropod and crab predation where the taller thinner-shelled *Balanus* spp. possibly would not. Indirect support for this theory was provided in Dayton's (1971) study of intertidal populations in a temperate region, where he found that limpets did not affect the mortality of *Chthamalus* to nearly the extent that they affected the mortality of *Balanus*. Thus, in temperate areas where slow moving grazers are abundant, *Chthamalus* is provided with a competitive edge over *Balanus* by reaching a size refuge, not so much in large size, but in strength and low profile, faster than does *Balanus*. This theory is supported in my study on force required to remove barnacles where *Chthamalus* required a force that was .5 Newtons (50g) greater than that required to remove *Balanus*

(Miller, MS in prep). The refuge in size reached by *Chthamalus* may not be important to its survival in areas where grazers and predators do not predominate because the normally superior competitor, *Balanus,* can still overgrow it (Connell 1961b; Dayton 1971). However, in areas where predators and grazers do not affect *Chthamalus* because of its size refuge, but do reduce the population of *Balanus*, *Chthamalus* is able to survive.

The presence of any factor which increases growth rate should favour the survival of the prey species exposed to that factor by decreasing the time when its young stages are susceptible to certain predators (Paine 1976; Sebens 1982). In the present study, barnacles on the low-level plates grew faster than those on the high-level plates and, as a result, reached a refuge size of 5mm^2 basal area one week earlier than did ones on the high-level plates. If the barnacles on the high-level plates had reached a refuge-size one week earlier they might have escaped as much as 25% mortality that occured between 4-5 weeks of age.

Thus, although barnacles can obtain a refuge in size from mortality caused by limpets, the attainment of this refuge takes time. How then, do barnacles survive their weak, vulnerable stages of early growth? For barnacles at this stage refuges in space may be available. Spatial refuges, as opposed to size refuges, do not operate on a time scale. Instead, they make the prey inaccessible to predators and are thus termed "non-coexistent refuges" by Menge and Lubchenco (1981). Spatial refuges, along with size refuges, act to stabilize predator-prey interactions by allowing some prey to survive (Menge and Sutherland 1976). In the present study, barnacles obtained a spatial refuge from removal by limpets by occupying depressions (also noted by Menge and Lubchenco 1981; Connell 1961a; Denley and Underwood 1979; and Lewis 1954).

A common hypothesis regarding the effectiveness of depression refuges states that limpets cannot graze the surface of a depression and therefore algae and small barnacles in these depressions are "safe" from removal by the radulae of limpets (Menge and Lubchenco 1981; Connell 1961a; Lewis 1954). In the present study, in the experiment where French pipes were used as substrates (containing only depressions and no smooth surfaces), limpets consumed many barnacles, thus showing that, in fact, barnacles in depressions are not entirely safe from limpets during grazing. Nevertheless, although depressions do not provide complete protection to juvenile barnacles, those living in depressions may still have a better chance of survival due to the fewer ways in which limpets can remove them. Menge and Lubchenco (1981) noted that as a limpet moves over a depression a barnacle inhabiting the depression may escape being removed by the shell of the limpet if the shell is wider than the depression and the test of the barnacle is completely contained within the depth of the depression. Although this idea was not directly tested in the present study, the lower mortality of barnacles in depressions on slate plates in the field, as opposed to that on the open surface of the plates, indicates that limpets encounter more difficulty in removing barnacles from depressions. As an example, barnacles on the open surface of the high-level plates suffered a 21% higher mortality compared to barnacles occupying depressions (mean of all treatments with limpets combined).

As a result of increased mortality of barnacles inhabiting open space rather than depressions, a higher percentage of the barnacles on the high-level plates were located in depressions when limpets were present. For example, in the 4-limpet treatment there was a shift from settlement to 5 weeks post settlement of 64-74% of barnacles occupying depressions (of the total number present). Alternatively, there was only a 1% shift in the 0-limpet treatment. Therefore, limpets limited the barnacles on the high-level plates to refuges located in depressions.

Degree of aggregation can be used to assess the extent of depression use by barnacles. Thus, if depressions provide refuges for juvenile barnacles, then the apparent degree of aggregation of the barnacles should increase with time when limpets are present. When this theory was tested at the Ross Islets site the distribution of barnacles was highly aggregated in the limpet treatments and the relative degree of aggregation was similar regardless of the number of limpets present. For example, for all limpet treatments where barnacles were at a density of 0.86 per cm^2, the mean nearest-neighbour distance at settlement was six times closer than that which would be expected if the distribution were random. The distribution of barnacles after 8 weeks of exposure to different densities of limpets was similarly six times closer than expected. Therefore, the occupation of depressions was high at settlment and did not change as the limpets removed barnacles. However, since mortality of barnacles at Ross Islets was not higher in the presence of limpets, conclusions about the effectiveness of depressions on natural rock could not be made.

In summary, the results of the intertidal-plate experiments supported the hypothesis that barnacles located in depressions are in a spatial refuge from mortality caused by limpets. However, since the distribution of barnacles on the natural rock substrates did not change in the presence of limpets and since limpets were shown to be highy capable of removing barnacles from even very deep or narrow depressions in the laboratory, not all depressions occupied by barnacles act as effective refuges.

Limpets are not the only factors that may cause increased use of depressions by juvenile barnacles. Connell (1970) found that small predatory whelks (*Thais* spp.) have difficulty in preying on barnacles in depressions. Menge and Lubchenco (1981) also found that fish did not prey as heavily on barnacles in depressions as opposed to those on the open surface. Further, Rice *et al.* (1935) speculated that physical factors in the environment, such as desiccation and log-battering, may operate less intensely in depressions than on the open rock surface. Of all of these factors, however, limpets and possibly whelks should be the most limiting causes of mortality to juvenile barnacles due to their consistently greater presence, at least in the sites examined in the present study. Other factors, such as fish predation, desiccation, and log-battering, which may at times cause devastatingly high mortality to barnacle populations, have highly localized effects both in time and space and thus would probably not consistently limit the distribution of the barnacles. Nevertheless, when all factors are present they cause disproportionately higher mortality to juvenile barnacles which are located on the open surface and thus tend to limit their distribution to depression refuges.

The other spatial refuge tested in this study was proximity to adult barnacles. A number of studies have been conducted that tested whether or not algae and/or juvenile limpets were in a refuge from mortality caused by adult limpets when they were located in the small spaces between adult barnacles, usually termed "crevices" (Lewis and Bowman 1975; Hawkins 1981; Lubchenco 1983; Jernakoff 1985, 1983; Choat 1977; Branch 1975a,b; Creese 1982; Hawkins and Hartnoll 1982; Underwood 1979; Underwood and Mcfadyen 1983; Denley and Underwood 1979). All but Jernakoff's study showed that survival of young limpets and/or algal spores was enhanced in such "crevices". This increase in survival is thought to be caused by the inability of the larger limpets to graze in the confined areas between barnacles (Connell 1961a; Hawkins 1981; Lewis and Bowman 1975; Branch 1976). Branch (1975b), for example, found that the grazing pressure by adult limpets was so high in areas where barnacles were scarce that juvenile limpets were restricted to the shells of the adult limpets; otherwise, the young limpets were crushed by the adults.

Juvenile barnacles inhabiting the areas next to and between adult barnacles would be in a spatial refuge if limpets were restricted in their movements by the presence of adult barnacles. In the present study, I hypothesized that limpets could not graze close to adult barnacles due to the bulk of their shell and, therefore, barnacles inhabiting areas in direct proximity to adult barnacles would suffer lower mortality than those in more open areas. This hypothesis is supported by the results of my study. For example, proximity to adult barnacles was an effective spatial refuge for juvenile barnacles on both high and low intertidal plates, judging from the lower mortality rates of young barnacles less than 4mm in distance from adult barnacle shells. Juvenile barnacles located further than 4mm from adult barnacles suffered as much as 95% mortality on the high-level plates where limpets were present. This was twice that suffered next to adult barnacles and three times that encountered when no limpets were present. As a result of this differential mortality the pattern of distribution of the young barnacles became more aggregated around the adult barnacle shells. The refuge was not 100% complete, however, since even the mortality of juvenile barnacles next to adult barnacle shells showed an increase of up to 33% on the high-level plates as the number of limpets increased. Thus, the reduction in mortality resulting from living close to an adult barnacle seemed to be caused by a decrease in the ability of the limpets to graze and move about in these areas, but not by a total inability.

The end result of limpet activity on juvenile barnacles in the presence of adult barnacles and sometimes depressions, is one of increasing an already high degree of aggregation present at settlement. As the barnacles in an aggregation grow, their shell plates often fuse, adding support and increasing the strength of their hold on the substrate (Gubbay 1983). This increased strength may limit the effect of predators and other environmental factors in removing these barnacles, but may not affect those predators such as *Pisaster* spp. that can consume barnacles without removing them. In addition, barnacles in aggregations are able to retain moisture longer than solitary individuals and thus during periods of desiccation do not experience as much mortality (Rice *et al.* 1935; Lewis and Bowman 1975; Branch 1975a,b; Choat 1977). Therefore, there are a variety of mortality sources, both biological and physical, that act as selective pressures in the evolution of gregariousness in barnacles. By limiting barnacles to aggregations early on, limpets increase the chances of survival of the remaining barnacles. Moreover, by causing mortality to barnacles on open surfaces limpets increase the chances of their own survival by increasing the space between barnacles to allow more area for grazing, and thus reduce competition between themselves and barnacles.

In summary, when making conclusions about the distribution of adults in a population it is important to consider carefully all factors causing mortality to juvenile stages, especially those that alter the distribution of the young organisms by limiting them to refuges. For example, mortality of juvenile barnacles may be caused by removal by limpets, predation by fish and predatory whelks, and by environmental factors such as storms, desiccation, and log-battering. These factors are the first to act upon the barnacles after settlement and they play an important role in limiting the distribution of the adults. Without knowledge of how such factors work and whether or not they induce differential mortality to juvenile barnacles, our knowledge about the causes of the distribution of adult barnacles is not complete.

SUMMARY

The use by juvenile barnacles of size and spatial refuges from mortality caused by the limpet, *Collisella digitalis*, was assessed by the use of slate plates in the field and intertidal rocks. Mortality caused by the activity of limpets decreased as barnacles grew in size and upon reaching 5-6.7mm^2 in basal area *Balanus glandula* and *Balanus crenatus* reached a refuge in size. This refuge size was slightly less for *Semibalanus cariosus* possibly due to its stronger hold on the substrate.

Depressions offered some degree of protection for barnacles from mortality caused by limpets since the surfaces of depressions were not easily scraped by the shells of limpets. This refuge was not 100% complete, however, since limpets were still able to remove barnacles from depressions with their mouths and radulae. The degree of protection provided by depressions was dependent upon the size of the depressions.

Juvenile barnacles located in close proximity (less than 2mm) to adult barnacles were in an spatial refuge from mortality caused by limpets. As the distance from adult barnacles increased, the effectiveness of this refuge diminished, and barnacles located more than 4mm from adult barnacle shells suffered high mortality (up to 95% per week).

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