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COMPETITION, DISTURBANCE, AND COMMUNITY ORGANIZATION: THE PROVISION AND SUBSEQUENT UTILIZATION OF SPACE IN A ROCKY INTERTIDAL COMMUNITY[1]

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TABLE OF CONTENTS

ABSTRACT

An understanding of community structure should be based on evidence that the growth and regulation of the component populations in the community are affected in a predictable manner by natural physical disturbances and by interactions with other species in the community. This study presents an experimental evaluation of the effects of such disturbances and competitive interactions on populations of sessile organisms in the rocky intertidal community, for which space can be demonstrated to be the most important limiting resource. This research was carried out at eight stations on the Washington coastline which have been ranked according to an exposure/desiccation gradient and subjected to comparable manipulation and observation.

Physical variables such as wave exposure, battering by drift logs, and desiccation have important effects on the distribution and abundance of many of the sessile species in the community. In particular, wave exposure and desiccation have a major influence on the distribution patterns of all the algae and of the anemone *Anthopleura elegantissima*. The probability of damage from drift logs is very high in areas where logs have accumulated along the intertidal. Log damage and wave exposure have complementary effects in the provision of free space in a mussel bed, as wave shock enlarges a patch created by log damage by wrenching the mussels from the substratum at the periphery of the bare patch.

Competition for primary space results in clear dominance hierarchies, in which barnacles are dominant over algae. Among the barnacles, *Balanus cariosus* is dominant over both *B. glandula* and *Chthamalus dalli*; *B. glandula* is dominant over *C. dalli*. The mussel *Mytilus californianus* requires secondary space (certain algae, barnacles, or byssal threads) for larval settlement, but is capable of growing over all other sessile species and potentially is the competitive dominant of space in the community.

Three general levels of biological disturbance result from a limpet guild, a carnivorous gastropod guild composed mainly of species of *Thais*, and the asteroid *Pisaster ochraceus*. Limpets have a negative effect on the recruitment of algae and barnacles. By the end of the summer, however, the limpet disturbance in the absence of *Thais* increases the survival of *Chthamalus* by reducing the survival of the competitively superior *Balanus* spp.; in the presence of *Thais*, all barnacle species are negatively affected by limpets. The effect of *Thais* in the absence of limpets is to increase *Chthamalus* survival by selectively eating the *Balanus* spp.; *Thais*, in the presence of limpets, have a negative effect on all the barnacle species. The competitive dominants, *Mytilus californianus* and *B. cariosus*, have an escape in growth from the gastropod predators and could eventually monopolize all the space. The combined effects of the predation of *Pisaster* and the log damage prevent this from happening.

In natural areas disturbances are sufficient to prevent the monopolization of space by any of the sessile organisms. In contrast to many communities which are thought to be structured around competitive interactions, this intertidal community is characterized by continuous physical and biological disturbances, an abundance of free space, and a large number of species which utilize this same potentially limiting resource.

INTRODUCTION

Many theories of community organization have grown from a descriptive basis heavily dependent upon sampling approaches which stress the structural aspects of the community. Very few biological communities can be manipulated so that there are comparable altered (experimental) and unaltered (control) situations. For this reason little emphasis has been placed on experimentally elucidating the functional roles of the major community components.

The concept of community organization suggests more than a description of the assemblage of populations. Such an organization, incorporating dynamic interactions, trophic structure, and patterns of distribution and abundance, should react predictably to physical and biological disturbances; the most convincing demonstration of community structure would be proof that the growth and regulation of the component populations are affected in a predictable manner by natural physical disturbances and by changes in abundances of other species in the community. Thus a dynamic theory of community structure should be built around an understanding both of the effects of the major community disturbances and of the interactions among the component populations. If such disturbances and interactions do contribute to a community structure, they can be evaluated by studying the factors influencing community succession. Such an examination is useful (1) for identifying the ecological conditions necessary for the establishment of a population and (2) for evaluating the competitive interactions among populations which share a potentially limiting resource. Once the patterns and rates of succession are determined, the effects of physical disturbances can be evaluated and the effects of the predator populations on the competitive patterns can be assessed by selectively removing the predators. The information gained by doing this should suggest the important parameters controlling the community structure and should ex-

plain and predict the observed distribution patterns and abundances of most of the species in the community.

The rocky intertidal community of the northeast Pacific offers many opportunities to assess the importance to its organization of various physical disturbances and biological interactions. It has the logistic advantage of being readily accessible, and it has geographic continuity, in that most of the species have widely overlapping geographic ranges—from Kodiak, Alaska, to Point Conception, California (reviewed by Glynn 1965, Paine 1969). Furthermore, most of the species are limited to the intertidal region and are confined to rocky substrata. The sluggish behavior of most of the invertebrate predators and the sessile habitus of most of the prey species make the community amenable to experimental manipulation. Most important, almost all of the prey species share an essentially two-dimensional space as their single potentially limiting resource. The successful utilization of this resource is easy to evaluate and quantify. Competition theory predicts that in the absence of disturbance a single or very restricted number of species should effectively occupy this simple resource. The fact that space is very rarely fully utilized by those species which are the competitive dominants, i.e., those that successfully outcompete others for space, in this community suggests that much of the community organization is a function of factors interfering with the recruitment and survival of these sessile species.

The main processes involved with the provision, procurement, and subsequent utilization of space are (1) physical stress, (2) natural death, especially of annual algal species, and the defoliation of the perennial algal species, (3) competition for a limiting resource, and (4) biological disturbances or predation-caused mortality.

The basic goal of this research has been to test the hypothesis that the growth and regulation of most

of the populations of sessile species are predictably affected by physical disturbance and by the dominant competitive and predatory populations in the community. Since the competitive dominance is exerted via the common resource of space, one main theme has been the identification of patterns of provision and allocation of free primary space, here taken to mean unoccupied substratum available for colonization of sessile organisms. In situations where there is an algal cover over, but not attached to, available substratum, this substratum is considered "shaded free space." The total available primary substratum or "total free space" is the sum of the shaded free space and the "uncovered free space." In areas where there is no canopy, the total available primary substratum may be referred to as "free space."

Intertidal research has classically involved elaborate descriptions of distribution and abundance patterns of various algal and animal populations. These distribution patterns along the Pacific coast of the United States are described by Ricketts, Calvin, and Hedgpeth (1968). The suggested role of various physical stresses in determining the distribution patterns in the marine intertidal has been summarized by Lewis (1964). This emphasis was on the role of physical stresses and suggested that the populations were indeed random aggregations of species sharing similar physical tolerances. However, a number of other factors appear to influence the distribution patterns and spatial relations of many of the important species in the intertidal community.

Abrupt discontinuous distribution patterns of sessile populations are frequently considered to be the result of competitive interactions (Daubenmire 1966). Such patterns have been so explained for intertidal populations (Endean, Kenny, and Stephenson 1956), and Connell (1961a) has experimentally proven that competitive pressures limit the lower distribution of the barnacle Chthamalus stellatus at Millport, Scotland.

Important and often dramatic effects of predation on distribution patterns of marine organisms have been experimentally demonstrated by Stephenson and Searles (1960), Randall (1961, 1963), and Bakus (1964) on benthic communities in tropical waters and by Blegvad (1928) in the Baltic Sea. Connell (1961b) demonstrated the important effects of the predation of the gastropod Thais lapillus at Millport, and Paine (1966) has experimentally demonstrated that the asteroid Pisaster ochraceus, by selectively preying on the dominant competitor for space, can be responsible for maintaining much of the species richness in the middle intertidal community at Mukkaw Bay, Washington. An intensive study by Connell (1970) has shown that many facets of the distribution pattern of the barnacle Balanus glandula

on San Juan Island, Washington, are a result of predation by three species of Thais.

As the marine environment merges into the terrestrial environment above it, the intertidal organisms are subject to increasingly severe physiological stresses. Because all the intertidal species have different tolerances to these stresses, the different upper limits of their distribution patterns result in conspicuous zones. It is well known that temperate intertidal shores are divided into a lower algal zone and an upper barnacle-mussel zone (see Stephenson and Stephenson 1961, Lewis 1964, and Ricketts, Calvin, and Hedgpeth 1968, for reviews). This paper will be restricted to the discussion of biological interactions in the barnacle-mussel zone with emphasis on the functionally more important species.

STUDY AREAS

Study areas that represented a gradient of physical exposures were chosen because one of the objectives of the work was to describe effects of physical conditions on the intertidal community (Fig. 1). Tatoosh Island (48°24'N, 124°44'W) is completely exposed to the oceanic swells and wave action of the eastern Pacific Ocean. The upper barnacle-mussel association here is dominated by an extremely dense bed of the mussel Mytilus californianus, which occupies from 65–97% of the total space. The barnacles Balanus cariosus and Pollicipes polymerus occur in scattered patches, and the upper level is dominated by Balanus glandula. Postelsia palmaeformis, the palm alga, is a conspicuous alga in the upper intertidal. No experimental work was done at Tatoosh Island because logistic difficulties inherent in getting to the island prohibited regular visits.

Waadah Island (48°23'N, 124°36'W) is slightly less exposed to wave shock than is Tatoosh Island. At this site the predation of Pisaster ochraceus on Mytilus californianus seems to be much more effective than at Tatoosh Island, and the Mytilus are found only in small patches, usually above the Pisaster foraging zone. There are scattered patches of Balanus cariosus, Balanus glandula, Chthmalus dalli, and Pollicipes. Experiments were done on Waadah Island at Postelsia Point (Rigg and Miller 1949) as well as on the protected side of the breakwater. Waadah Island is a particularly useful experimental area, both because of the many available habitats and because the U.S. Coast Guard protects it from human disturbance. Both Tatoosh and Waadah Islands represent the typical exposed outer coast communities described by Ricketts et al. (1968).

Shallow offshore water offers sufficient protection to Shi Shi reef (48°16'N, 124°41'W) to break much
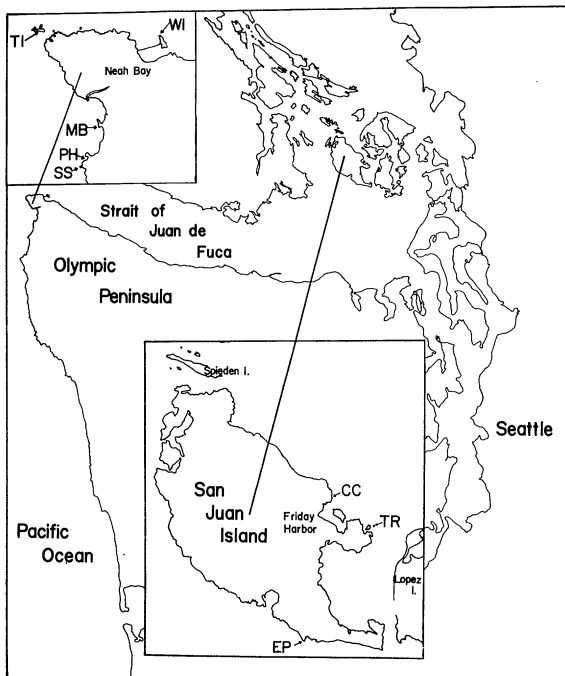
FIG. 1. Map of Olympic Peninsula region of Washington State showing locations of study sites. SS, Shi Shi; PH, Portage Head; MB, Mukkaw Bay; TI, Tatoosh Island; WI, Waadah Island; EP, Eagle Point; TR, Turn Rock; CC, Colin's Cove.

of the power of the deep sea swells so conspicuous at Tatoosh and Waadah Islands. Offshore reefs shelter Mukkaw Bay (48°19′N, 124°40′W), and shallow water and a complex series of offshore reefs considerably protect the Portage Head site (48°17′N, 124°41′W). The topography of the intertidal zone of these three sites is broken by large boulders, surge channels, and deep tidepools. None of these sites has *Postelsia*; all three sites would be classified as protected outer coast environments by Ricketts et al. (1968). Large *Balanus cariosus*, frequently under the *Mytilus*, are also found above the effective level of *Pisaster* predation. *Pollicipes polymerus*, a well-known component of this community (Ricketts et al. 1968), is rare on the rather flat study sites in the protected outer coast areas and on San Juan Island. Its local distribution pattern represents a specialized situation (Barnes and Reese 1960), and it will not be considered further. Large aggregations of the anemones *Anthopleura elegantissima* and *A. xanthogrammica* as well as occasional heavy sets of *Balanus glandula* and *Chthamalus dalli* occupy much of the intermediate levels between the algal association and the *Mytilus* refuge at all three protected outer coast areas.

The Shi Shi and Portage Head experimental sites were chosen because they offer protected outer coast environments and because of their relative inacces-

sibility to marauding human activity. Mukkaw Bay is subject to an increasingly intense human disturbance, and only a few experiments survived the 4 years there. The substratum at all of the outer coast sites is a soft siltstone.

Although the San Juan Islands lack the deep swells of the open seas, the Eagle Point site (48°27′N, 123°2′W) faces the prevailing winds and is frequently exposed to severe wave action. Two areas were studied at Eagle Point: (1) Eagle Point main area, where almost all the experimental work was done, and (2) Eagle Point log area, a spot where drift logs accumulate and are moved around during high tides and storms. The barnacle-mussel association at Eagle Point includes patchy but conspicuous aggregations of the anemone *Anthopleura elegantissima*, many large *Balanus cariosus*, a few large *Mytilus californianus*, a few small patches of *M. edulis*, and frequently heavy sets of *Balanus glandula* and *Chthamalus dalli*.

Turn Rock (48°32′N, 122°58′W) is in a protected channel and has very little wave action, but is exposed to strong tidal currents (3 knots). The barnacle-mussel association above the level of *Pisaster* predation is dominated by a complete cover of very large *Balanus cariosus* and *B. glandula*. Very few mussels were present during the course of this study. Large patches of the alga *Fucus distichus* have settled on the barnacles.

Colin's Cove (48°33′N, 123°0′W), approximately 200 m north of the Cantilever Pier of the Friday Harbor Laboratories, is the most protected study area. Occasional winter storms with winds from the northeast produce heavy wave action at this site, but usually the heaviest waves at Colin's Cove come from passing ferry boats and pleasure craft. The barnacle-mussel association here is essentially nonexistent; the upper levels are mostly bare rock with isolated individuals of *Balanus cariosus, B. glandula,* and *Chthamalus dalli*. The intertidal substratum of San Juan Island is a very hard metamorphosed chert (McLellan 1927).

Mean monthly temperatures and salinities have been described by Connell (1970) for the San Juan Islands and are similar on the outer coast. Although it is easy to measure and has received much attention, temperature per se probably does not limit the distribution of the various organisms among these study areas. As indirect evidence for this, the ranges of most of these organisms extend well into Alaska to the north, where temperatures are much lower, and to southern California and Mexico to the south, where the temperature extremes are much higher than those generally encountered in these study areas.

Desiccation (Kensler 1967) is probably the most important physical factor limiting the local dis-

tribution of most of these organisms within the sites studied. The San Juan sites are subjected to a much greater degree of desiccation than are the outer coast sites. The latter are buffered by the wet maritime weather brought on by offshore upwellings. In contrast, the San Juan Islands have more wind, about twice as many sunny days in the summer, and probably more extreme cold in the winter. The effect of the different climatic conditions on the marine intertidal organisms is exaggerated in the San Juan Islands because the summer spring low tides usually occur around the middle of the day, subjecting the exposed marine organisms to the extreme conditions of summer desiccation, and the winter spring low tides are in the middle of the night, subjecting them to the most extreme climatic conditions of that season. The spring low tides on the outer coast tend to be late in the afternoon in the winter and very early in the morning during the summer. Thus the outer coast intertidal is relatively well protected from desiccation and climatic extremes both by the moist weather and by the time of day of the tides.

Within each area there are obvious biological differences among habitats with differing degrees of exposure. Since one of the objectives was to evaluate the effects of wave action on communities in exposed environments, the study has been restricted to the exposed rocky intertidal localities in each of the study areas.

The height of a level along the shore is given as feet above or below the mean lower low water. The levels at each site were obtained by observing the low point of the low tide. This measure varied considerably from the predicted low of the tide tables because of wind, surf activity, and barometric pressure, but the reference point at each site is believed to be accurate to within ±5 cm. All the other levels at each site were measured in relation to the reference point with surveying equipment. Because of the limited number of visits, comparable data are not available for Tatoosh Island.

The relative utilization of substratum space by the competitively dominant space consumers in the barnacle-mussel association is presented in Table 1 in terms of percentage cover. The occupation of primary space was usually evaluated photographically by placing a piece of acetate with 100 randomly placed points over it or by the use of a planimeter. The former method is similar to the technique described by Connell (1970) and yields a measure of percentage cover which can be converted into square centimeters of cover. The planimeter yields a proportion cover which can be converted into either percentage cover or actual square centimeters of cover. Repeated measurements of large organisms on the same photograph with the planimeter vary

less than measurements with the random dot technique (1–2% as opposed to 1–4%), but with small scattered organisms, such as barnacles, it is essentially impossible to use the planimeter. The planimeter and the random dot method are interchangeable and repeatable with less than 5% difference.

In some situations primary substratum alone is not the most important limiting resource. The distribution patterns of the algae in particular are also critically influenced by light intensity and protection from desiccation. Clear evidence of this are the differences in vertical distribution of algal zones on north- and south-facing exposures. In the areas studied the south exposure is subjected to more desiccation; this probably is why the algal zones occur at lower depths on the south side than do the corresponding zones on the north side of the same rocks. The distribution patterns of the algae are described in Table 1 in terms of general categories such as percentage cover of any algal canopy and percentage cover of an obligate understory category, which includes algal species which either disappear when the canopy cover is removed or are found only in permanently damp spots. The fugitive species (Hutchinson 1951) in Table 1 are those algal species which appear when the canopy or barnacle-mussel cover is disturbed.

The encrusting coralline algae, such as various species of *Lithothamnion* and *Lithophyllum*, often cover large areas of primary substratum. Since these algae have proven to be satisfactory substrata for most of the other attached intertidal algae, the primary space utilized by them will not be discussed. The actual degree of interference via cellular sloughing or allelopathic agents of these encrusting algae with the recruitment of algal spores or animal larvae is unknown. No interference with other algae has been observed, and certainly barnacle cyprids readily settle on the encrusting corallines.

PHYSICAL EFFECTS

The most important physical factors correlated with differences in the relative distributions and abundances of the important sessile species in the intertidal are (1) wave exposure, (2) battering by drift logs, and (3) physiological stresses such as desiccation and heat.

Wave exposure

The importance of wave exposure or wave shock to the distribution and abundances of intertidal populations is well known (Ricketts et al. 1968). Bascom (1964) discusses the degrees of wave activity and the many factors complicating its measurement; Harger (1970) describes a simple device which estimates the force of wave impact directed vertically

TABLE 1. Mean percentage cover of major sessile organisms in upper intertidal zones. Data are from ten to thirty 0.25-m² quadrates taken randomly along horizontal transects. Variance is presented as 95% confidence limits. "Fugitive species" and "obligate understory" categories refer to algae and are described in the text. (* = *Postelsia palmaeformis*; ** = *Fucus distichus*; + = *Pelvetiopsis limitata*; ° = *Hedophyllum sessile*.) Blanks mean species were not seen in samples

Site	Level (ft)	Chthamalus dalli	Balanus glandula	Balanus cariosus	Mytilus californianus	Anthopleura elegantissima	Fugitive species
Tatoosh Island	2–4				94.4± 8.6		1.3± 0.9
	4–6			0.7± 0.1	82.1±27.3		7.5±14.3
	6–8			2.2± 0.1	53.7±20.7		20.6±13.9
	8–10			2.6 ±2.1	54.7±35.7		30.1±25.5
	>10				61.1±26.8		8.6± 6.7
Waadah Island	5–7				20.7±29.8		7.5± 5.6
	7–9			1.1± 1.8	76.3±15.5		1.6± 1.5
Shi Shi	2–4	7.5± 2.3	33.9±16.1		11.8± 9.6	4.0±3.6	7.0± 4.6
	4–6		72.1±16.7		19.0± 6.4	4.4±5.1	
	>6				74.0±24.5		10.3±22.2
Portage Head	2–4	5.7± 2.0	1.5± 1.0			4.1±2.6	72.9±13.1
	4–5	10.1± 3.5	16.5± 9.1			13.6±8.5	5.7± 6.7
	5–6	2.1± 3.1	10.5± 8.5	21.8±10.5	46.9±15.2		1.0± 4.2
	6–7						20.0± 9.5
	7–9	25.0± 6.7	16.0± 6.1				
Eagle Point	1–2	0.6± 0.6		4.3± 3.0			1.0± 4.3
	2–4			30.3± 7.0	3.3± 1.8	6.8± 3.7	8.2± 7.9
	4–6	5.9± 1.8	4.0± 5.8	63.2± 4.6			
	>6	3.0± 2.0	0.8± 0.8	39.7±12.4			
Turn Rock	1–2			2.4± 2.1			20.0±15.8
	2–3			100.0			9.2± 9.1
	3–4			98.3± 4.5			
	4–6		61.3± 5.8	38.9± 9.3			
Colin's Cove	2–4	0.1± 0.7					19.3± 5.8
	4–6	2.0± 3.0	1.7± 1.6	0.8± 1.1			7.5± 9.3
	>6	0.5± 0.9	2.0± 1.8				0.9± 0.7

| Site	Level (ft)	Obligate understory	Canopy cover	Holdfast cover	Uncovered free space	Shaded free space
Tatoosh Island	2–4	3.7± 0.7				
	4–6	10.0±15.1				
	6–8	6.5± 4.6	*6.9± 8.1	4.7±2.5	9.0± 4.2	3.8± 3.6
	8–10	6.2± 5.6			8.4± 7.9	
	>10	23.3±16.8	*4.0± 6.4	3.1±0.9	3.6± 2.7	
Waadah Island	5–7	24.1±12.8	*76.8±24.1	31.8±5.8		17.9±11.3
	7–9				20.9±13.4	
Shi Shi	2–4				35.9±16.2	
	4–6				5.1± 3.7	
	>6				15.1± 5.5	
Portage Head	2–4		**4.5± 6.1		10.8± 5.7	4.5± 1.9
	4–5		**7.0± 7.9		51.1±11.8	3.7± 1.2
	5–6		**9.0± 4.2		19.3± 9.2	
	6–7	3.0± 5.4	**66.7± 22.0		14.0± 5.7	64.4± 8.9
	7–9		+25.0± 5.7		42.1±15.9	15.4± 6.7
Eagle Point	1–2	1.1± 1.3	°5.5± 6.4		92.2±11.7	
	2–4	0.9± 2.1	°1.0± 0.7		50.8± 8.1	
	4–6				26.5± 2.9	
	>6				57.1±11.2	
Turn Rock	1–2	7.8±7.2	**4.8± 5.0		67.0±18.0	4.8± 7.5
	2–3		**37.5±18.5			
	3–4		**83.7±11.4			1.6± 2.4
	4–6					
Colin's Cove	2–4		**53.5±10.7		27.2± 9.0	53.5±11.4
	4–6		**34.5±20.4		54.0±11.4	34.5±22.5
	>6		**6.5± 5.7		97.3± 2.4	
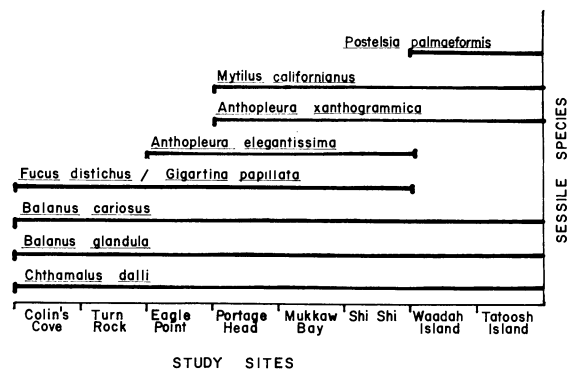
FIG. 2. Distributions between sites of conspicuous sessile organisms. Colin's Cove represents the most sheltered area; Tatoosh Island is the site of greatest wave exposure.

toward the substratum. The complications attendant to an adequate description of wave exposure along broken, heavily exposed shorelines were prohibitive for this study. Study sites were chosen which represent varying degrees of exposure to wave action and were subjectively ranked in decreasing order of the magnitude of wave shock. Tatoosh Island is most exposed, with Waadah Island, Shi Shi, Mukkaw Bay, Portage Head, Eagle Point, Turn Rock, and Colin's Cove following in decreasing order of exposure.

The distribution of the conspicuous sessile organisms in environments representing different degrees of wave-shock conditions is plotted in Fig. 2. Most of these species are found in a number of sites and apparently have wide tolerances to wave exposure.

Drift logs

Many areas along the shores of the San Juan Islands and the outer coasts of Washington and Vancouver Island have large accumulations of drift logs. The battering by these logs destroys the intertidal organisms and is an important factor in the provision of space. On San Juan Island 50% of the logs stranded on shore have been cut and appear to be there as a result of human activity; 15% of the logs still have their root systems intact and are therefore known to be natural drift, probably from erosion along the large coastal river systems or from the coastal shores. The remaining 35% of the San Juan Island drift logs are old and worn, and their source is obscure. The outer coast beaches frequently are covered with great piles of logs; in some cases, particularly where salvage is impossible, the log jam which stretches in a strip along the upper level of the beach is between 30 and 75 m wide. At these coastal sites fewer than 1% of the drift logs show signs of being cut by man, while 85% of them still have their root systems intact, indicating a natural source. The remaining 14–15% are too battered for

a positive evaluation, but also appear to represent natural drift. I have frequently observed natural erosion at the Shi Shi and Portage Head study sites causing large trees to slide onto the intertidal zone. Similar observations were made before logging became a major environmental problem in the Pacific Northwest (Swan 1857). Erosion along the shores of the sea and along the many river systems of the Pacific Northwest has probably always been a source of drift logs. Since these logs persist for many years, their impact on the intertidal community may have been even more profound before commercial interests made their salvage profitable. Certainly the disturbance from this battering is a natural and important ecological phenomenon in this community.

The probability of log disturbance at each study site was measured by embedding cohorts of nails haphazardly into the substratum at three different intertidal levels. The nails were embedded with a construction stud gun using .32 caliber blanks; each nail stood approximately 2 cm high. Survival curves of these nail cohorts show that within most of the study areas there is a 5–30% probability of any given spot being struck by a log within 3 years (Fig. 3). There was no consistent level effect on the "mortality" of the nails.

The exposed organisms are killed regularly in areas such as the Eagle Point log area, where drift logs concentrated by local current action make the site particularly susceptible to log battering. Here the only sessile organisms are found in deep crevices; all the exposed shore is devoid of long-lived sessile organisms. There are many such areas in the San Juan Islands and on the outer coast; however, I confined my experimental studies to sites which, unlike the Eagle Point log area, are struck only by logs carried by the currents, rather than by the shifting of an accumulated drift at high tide.

Turn Rock is an unusual site in the San Juan Islands, because a rapid current pattern carries the drift around the small island and protects it from being struck by this material. Postelsia Point on Waadah Island is apparently similarly protected by an offshore rip current.

Figure 3 also compares the percentage cover at the 4- to 5-ft level of three areas in the San Juan Islands which are similar in most physical parameters, but which have different probabilities of being struck by logs. The 4- to 5-ft level was chosen because the dominant occupant of space, the long-lived *Balanus cariosus*, is not subjected to *Pisaster* predation at this level. Thus the relative amount of available substratum is very likely a result of log damage.

No nails were placed at Tatoosh Island, but four sites were found on the island in 1968 and three in 1970, in an area of about 208 m², which had been
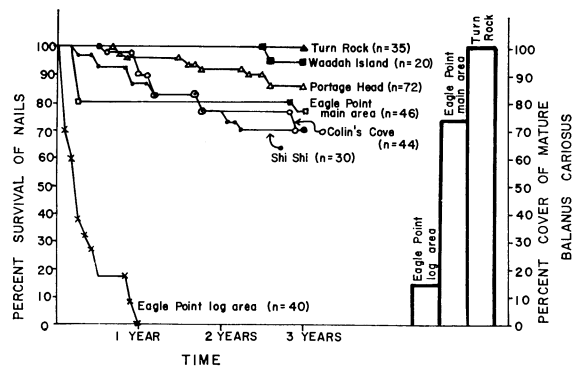
FIG. 3. Survival curves of nails placed at each study site. The percentage cover of mature *Balanus cariosus* at the 4- to 5-ft level at three San Juan Island sites is shown at right.

struck recently by logs, as evidenced by wood chips in crevices in the rocks.

In areas where *Mytilus californianus* dominates, the effects of log battering and wave shock complement each other. *Mytilus* larvae preferentially settle in filamentous algae and among the byssal threads of adult *Mytilus* (Bayne 1964, 1965; also personal observation). In areas where wave action is sufficient to provide the lower individuals with aerated water and adequate food, a mat of mussels up to 25 cm thick can develop. Usually the mat is anchored to the substratum by the byssal threads of relatively few individuals; the majority of individuals are anchored to each other's valves and byssal threads. A thick mussel bed such as this is partially dependent upon its spatial continuity to keep the mussels from working loose in the surf, because such a mat of mussels, developing on an exposed ridge or rocky promontory, can be ripped off by wave action. When log damage or *Pisaster* causes a clearing, the mussels around the edge of the clearing are susceptible to violent twisting by wave action and are often torn off the substratum. Even a small cleared area can be considerably enlarged. In this way wave shock can be responsible for the provision of substratum free from the *Mytilus*.

Much patchiness in the upper intertidal in exposed areas results from log damage creating an initial clearing in the *Mytilus* bed in which the space is then considerably enlarged by wave shock ripping the newly vulnerable mussels from the substratum. The original and utlimate sizes of such clear patches caused by log damage at the Shi Shi and Portage Head sites are shown in Table 2. The mean increases in available primary space, expressed as a percentage of the original clearing, are 3,897% and 24%, respectively. The original clearing was known to be made by a log because either the log was seen or bark and wood were jammed into crevices in the

rock. Seven patches originally created by log damage were observed at Tatoosh Island (Table 2). The percentage increase in these clearings was estimated by assuming that the original clearing was 0.09 m² (the size of the largest Shi Shi original clearing) and using the observed size of each clearing as an estimate of the ultimate size, even though in most cases the clearings were still being enlarged. The resultant conservative estimate of the percentage increase of a cleared patch at Tatoosh is 4,884%. Differences in percentage increase of patch size at the three sites are an indication of relative differences in wave exposure.

Predation by *Pisaster* along the lower edge of the *Mytilus* aggregation creates small clearings which are enlarged by wave action. Thus, clear patches at the lower level of the *Mytilus* bed can result either from *Pisaster* predation or log damage, and it is impossible a posteriori to differentiate between them. In 1970 the 208-m² area on the exposed point of Tatoosh Island had three such cleared patches in the lower intertidal totaling 10.0 m². Twenty-two patches in the upper intertidal, which were sufficiently high so that they were almost certainly originated by logs, totaled 63.8 m². Since the recovery of the *Mytilus* bed is much faster at the lower levels, the relative rates of the provision of space in these two levels cannot be compared. But 35% of the total area in this *Mytilus* bed is composed of free primary space. The physical force of log battering and of wave shock is largely responsible for the clearing of this space.

Physiological stress

The algae seem to be particularly sensitive indicators of physical conditions (Lewis 1964, Druehl 1967). The luxuriant intertidal algal growths of the outer coast seem to be prevented from being established in the San Juan Islands by the higher degree of desiccation there. Most of the outer coast species are found very occasionally in the San Juan Islands, but only in places extremely well protected from desiccation. In comparison to the algal species, the major space-consuming animal species have much wider distribution patterns across the desiccation gradient represented geographically by the study sites and locally by vertical and topographical exposure differences. This suggests that the distribution patterns of sessile animals are less likely to be determined by physiological stress than are those of the algal species. The major exception is *Anthopleura elegantissima*, a spatially important organism at certain study sites (Table 1), whose distribution seems to be limited partially by desiccatory stresses. It is not found at the two exposed outer coast sites, nor at the two most protected San Juan Island sites. However, large areas (50–100 m²), protected from extreme

TABLE 2. Increase of patch size cleared in *Mytilus californianus* beds by log damage and wave shock at three outer coast sites

Site	Date	First observed size (m²)	Ultimate observed size (m²)	Average percentage increase in size of patch due to wave shock
Tatoosh Island	1968 (June)	—ᵃ	0.5ᵇ	
		—	4.3ᵇ	
		—	6.2ᵇ	
		—	16.0	4,884%
	1970 (June)	—	3.1ᵇ	
		—	0.6ᵇ	
		—	0.7ᵇ	
Shi Shi	1967 (May)	0.062	0.950	
		0.050	0.500	
	1968 (June)	0.090	2.790	3,897%
		0.070	8.100	
	1969 (May)	0.050	1.390	
Portage Head	1967 (May)	0.035	0.085	
		0.030	0.030	
		0.045	0.045	24%
	1968 (May)	0.050	0.050	
		0.035	0.035	
	1969 (June)	0.040	0.040	

ᵃFor calculations, original size of the clearing was assumed to be 0.09 m².
ᵇPatch still being enlarged at time of observation.

TABLE 3. Percentage cover of *Anthopleura elegantissima* on protected and exposed sides of the same surge channel at Shi Shi (means of 10 randomly sampled quadrates at each level; variance is presented at 95% confidence limit)

Height (ft)	Exposed slope	Protected slope
0–2	0	81.7 ± 24.0
2–4	4.0 ± 3.6	78.7 ± 27.0
4–6	4.4 ± 5.1	7.4 ± 4.7

surf pounding, at Tatoosh and Waadah Islands have up to 100% cover of this anemone. This correlation of *A. elegantissima* with protected outer coast sites is well demonstrated in a surge channel at Shi Shi, where the side exposed to wave shock always had less than 10% *A. elegantissima* cover, and the protected side had over 80% *A. elegantissima* cover at the 0–2-ft level (Table 3). The restriction of *A. elegantissima* to protected outer coast sites seems to be the result of both competition and physiological stress. Competition appears to reduce its abundance and distribution at the more exposed outer coast sites (see below), whereas physiological stress restricts its abundance and distribution at many of the more protected sites.

The distribution of *Anthopleura elegantissima* seems directly affected by desiccation. On San Juan Island the anemone distribution is essentially confined to isolated areas along the west side of the island which are exposed to sufficient splash to reduce the effects of desiccation. The only natural population of *A. elegantissima* on the calmer east side of the island was found at Colin's Cove in a small crack between two rocks where it is permanently shaded and well protected from exposure to the wind. The survival of *A. elegantissima* seems to be affected more by desiccation than by temperature. To test this, a calibrated thermometer was placed inside the coelenterons of isolated anemones. The area where the anemones were located was marked with paint or with a screw, and the survival of the anemones was followed on successive tides. With no air movement, the dark green anemones absorb the radiant heat and can reach temperatures considerably above the ambient air temperature (Table 4). The highest *A. elegantissima* temperature recorded was 33.6°C, and the greatest temperature differential between the ambient air temperature and the anemone was 13.3°C. When there was no air movement, the anemones were healthy and suffered no mortality. The *A. elegantissima* seem to be protected against desiccation by a volume of sea water maintained in the coelenteron. Wind produces an evaporative effect which often lowers the anemone temperature below that of the surrounding air; however, this evaporation depletes the water in the coelenteron, and eventually the anemone is killed by desiccation. Although the relative humidity of the air is somewhat increased with the wind, this does not seem to help anemone survival.

TABLE 4. Temperature and percentage mortality of *Anthopleura elegantissima* (n = 50) under various conditions of ambient air temperature, relative humidity, and wind—June–July 1966

Air temperature (°C)	Relative humidity (%)	Wind (mph)	Temperature of *A. elegantissima* (°C)	Total percentage mortality
13.0	84	0	28.2±1.1[a]	None
21.5	75	0	31.1±2.4	None
17.6	95	0	27.6±1.9	None
19.5	98	5–15	19.0±1.7	35%
16.5	95	10–20	13.2±1.0	55%
13.0	90	15–20	9.0±1.8	45%

[a]Mean of 20 samples ± standard deviation.

To test whether Turn Rock and the study area at Colin's Cove will support *Anthopleura elegantissima*, patches of anemones were transferred to each of these sites during the autumn night tides of 1966. Two aggregates, each composed of between 100 and 150 anemones, became successfully established at each site. All the anemones that became attached survived the winter, but in March the tides moved into daylight hours, and the anemones began to turn brown and die from desiccation. All had died by the end of April.

BIOLOGICAL INTERACTIONS

Three different types of biological interactions affecting the distribution of the sessile barnacle-mussel association were considered: (1) a sweeping or barrier effect of *Fucus distichus* on barnacles; (2) interspecific competition; and (3) disturbance, especially the effects of predation.

Biological disturbances in the upper intertidal result from the activities of limpets, carnivorous gastropods, and asteroids. Limpets graze on settling algal spores and sporelings (Moore 1938, Southward 1953), and numerous workers have shown that the removal of limpets results in a heavy growth of algae (Jones 1948, Lodge 1948). The large *Patella* in Europe consumes and dislodges settling barnacle cyprids (Hatton 1938, Lewis 1954, Southward 1956, Connell 1961b); and Stimson (1970) has found that the large owl limpet, *Lottia gigantea*, dislodges small *Balanus glandula*. Limpet disturbance is, therefore, an important factor in reducing the settlement and establishment of both the algae and the barnacles.

The importance of carnivorous gastropods as a cause of barnacle mortality in Scotland and on San Juan Island has been experimentally demonstrated by Connell (1961b, 1970), who showed that with the exclusion of all predators, particularly *Thais* species, barnacle mortality is very much reduced.

Paine (1966) demonstrated that in 1963 the exclusion of *Pisaster ochraceus*, an asteroid which preferentially preys on *Mytilus californianus*, was sufficient for *M. californianus* to outcompete all the

other upper intertidal species and monopolize the substratum in the outer coast community at Mukkaw Bay.

Each of these biological disturbances can have a different effect on the populations of sessile organisms. In the analysis of these effects, the limpets and *Thais* are considered as "guilds" such as defined by Root (1967). The limpet guild basically is composed of four species (Table 5); the *Thais* guild is less well defined, as it includes in various areas three species of *Thais*, *Ceratostoma foliatum*, and *Searlesia dira* (Tables 6 and 7).

Methods and field experiments

Experiments designed to measure the effects of competition and predation in the barnacle-mussel association are closely related, and their designs are discussed together. The precise comparisons and tests are discussed in the following sections; the general experimental scheme is diagrammed in Fig. 4. Barriers designed to restrict limpet movement were made by cutting the bottoms out of flexible plastic cereal bowls or dog dishes (Fig. 5). These have the advantages of being inexpensive and sufficiently pliable so that they can be bent over the natural contours of the rock substratum and attached with eye screws. Limpets can be excluded or included with few invasions or escapes; monitoring the dishes every 10–14 days was sufficient to maintain the desired limpet concentration. A dog dish with normal limpet density rather than a "control" area without a barrier around it was used to compare with the exclusion dish in order to keep constant any unknown side effects of the dishes. The limpet concentration to be included in each dish was determined by placing the barrier on the substratum haphazardly 10 times to determine the average densities of the limpet species at that site and level. The dish was then attached to the substratum and the average limpet density was maintained in the dish. Diving observations showed that *Thais* species crawl over these barriers as readily as over the many rock projections and discontinuities of their natural environment. The plastic dishes were

TABLE 5. Density of four species of limpets (*Acmaea*) at various levels at each study site. Data have been converted to number/m^2 and are derived from transects of 10–25 quadrates. Quadrate sizes ranged from 0.01 to 0.250 m^2. Blanks mean data unavailable

Site	Limpet	Level (ft)								
		−2–0	0–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8
Waadah Island	A. scutum	0		0	0	2	96	485	48	0
	A. pelta	0		0	0	15	35	250	96	0
	A. digitalis	0		0	0	2	10	170	540	1150
	A. paradigitalis	0		0	0	0	80	310	110	25
Shi Shi	A. scutum		0	12	32	11	3	0		
	A. pelta		0	0	29	33	44	29		
	A. digitalis		0	0	105	110	183	272		
	A. paradigitalis		0	0	571	600	576	251		
Mukkaw Bay	A. scutum							0	0	
	A. pelta							15	0	
	A. digitalis							544	680	
	A. paradigitalis							240	208	
Portage Head	A. scutum			16		10				
	A. pelta			32		26	38	26		
	A. digitalis			0		101	215	355		
	A. paradigitalis			12		381	360	180		
Eagle Point	A. scutum	2	5	176	54	59	64	73	67	
	A. pelta	2	54	131	310	167	115	22	0	
	A. digitalis	0	0	0	565	592	675	503	378	
	A. paradigitalis	0	0	64	544	528	625	314	144	
Turn Rock	A. scutum	131	112	122	48	46	29	32		
	A. pelta	120	40	60	90	150	0	5		
	A. digitalis	0	0	20	90	83	80	153		
	A. paradigitalis	100	98	110	143	204	0	97		
Colin's Cove	A. scutum	120	132	122	94	29	36	0	0	
	A. pelta	160	9	9	75	16	119	128	110	
	A. digitalis	0	0	0	68	85	76	81	101	
	A. paradigitalis	180	0	0	110	170	310	280	20	

placed either in spots not accessible to *Pisaster ochraceus* or in the middle of *Pisaster* removal areas. *Pisaster* removal areas were maintained at Shi Shi, Portage Head, Eagle Point, and Turn Rock by manually removing *Pisaster*. The areas were policed regularly, but since *Pisaster* is a very motile predator, there is a large edge effect to an experiment of this type; therefore, the *Pisaster* removal areas were usually larger than 1,000 m^2.

Stainless steel mesh cages identical in design and materials to those described by Connell (1961*b*) were used to totally exclude or regulate the densities of both *Thais* and limpets (Fig. 6). These cages, covering approximately 100 cm^2, were attached to the substratum with stainless steel screws, which were inserted into plastic wall anchors embedded in holes drilled in the substratum. The objective of these cages was to exclude *Thais* while maintaining limpet density at zero or at the normal density for that site and level. The limpet density to be included in the normal density cage was sampled in the same manner as for the dog dish. Stainless steel mesh "roofs" of 100 cm^2 supported about 2 cm above the

substratum by plastic washers were also placed beside the cages. The stainless steel cage and roof enclosures were placed in both *Pisaster* removal and normal *Pisaster* areas. In the *Pisaster* removal areas, these roofs served as controls approximating the physical conditions under the cages while allowing free entry of limpets and *Thais*. The effects of *Pisaster* predation were evaluated by comparing roofs in normal *Pisaster* areas with adjacent control plots which allowed access to *Pisaster*, limpets, and *Thais*.

If the comparisons undertaken in the experimental design are legitimate, there should be no consistent differences between the results under the roofs and in the limpet inclusion dog dishes; nor should there be a consistent difference between those areas under the roofs and in the adjacent control plots in *Pisaster* removal areas. Wilcoxon matched-pair signed rank tests (Siegel 1956) on these pairs at Shi Shi and Eagle Point, chosen as areas representative of the outer coast and San Juan Island environments, respectively, showed no significant differences.

One potential artifact or indirect effect of the design was considered. The limpet exclusion dishes and

TABLE 6. Densities at various tidal levels of carnivorous gastropods at three outer coast sites. *Thais lamellosa* is rare at all these sites, as is *T. canaliculata* at Shi Shi and Portage Head. Tagging studies show that *T. emarginata* at Waadah Island do forage as low as the −1 ft level; therefore their mean density is calculated from their entire foraging range despite the fact that they were not found in the lower levels in this sample

Site	Species	Level (ft)	Date	Sample size (m²)	Sample mean	N	SD	Mean density (number/m²)	Mean density in total foraging area (number/m²)
	Thais canaliculata	−1 to +3	5/3/68	0.250	2.6	15	2.3	10.4	
		−1 to +3	6/2/69	0.250	0.9	10	1.3	3.6	
		+3 to +6	5/3/68	0.062	0.1	15	1.2	1.6	5.1
		+3 to +6	6/2/69	0.062	0.3	10	1.4	4.8	
Waadah Island	*Ceratostoma foliatum*	−1 to +3	5/3/68	0.250	2.7	15	3.8	10.8	
		−1 to +3	6/2/69	0.250	1.2	10	0.6	4.8	
		+3 to +6	5/3/68	0.062	0	15		0	6.8
		+3 to +6	6/2/69	0.062	0.1	10	1.4	1.6	
	Thais emarginata	+3 to +6	5/3/68	0.062	3.9	15	2.6	62.4	28.0
		+3 to +6	6/2/69	0.062	3.1	10	8.0	49.6	
Shi Shi	*Thais emarginata*	0 to +1	6/23/68	0.250	9.3	10	8.5	37.2	
		+1 to +3	6/23/68	0.250	14.9	20	12.0	59.6	
		+3 to +4	6/23/68	0.250	56.2	20	26.7	224.8	245.7
		+4 to +5	6/23/68	0.062	25.1	21	8.3	401.6	
		+4 to +5	6/23/68	0.062	26.6	21	7.8	425.6	
		+4 to +5	6/23/68	0.250	81.3	10	31.4	325.2	
Portage Head	*Thais emarginata*	+1 to +2.5	5/2/68	0.062	1.0	10	1.3	16.0	
		+2.5 to +3.5	5/2/68	0.062	1.7	10	2.1	27.2	
		+3.5 to +4.5	6/23/68	0.062	16.0	12	9.6	256.0	198.5
		+3.5 to +4.5	5/2/68	0.062	17.7	10	10.0	283.2	
		+3.5 to +4.5	6/24/68	0.250	70.1	10	32.3	280.4	
		+4.5 to +5.5	6/24/68	0.250	82.0	10	27.2	328.0	

cages, if left unattended, usually developed a heavy cover of *Porphyra* and ulvoids. This protection from desiccation sometimes enabled large populations of the nemertean *Emplectonema gracile* to congregate and eat the barnacles. Thinning this algal growth on the semimonthly visits to the experimental areas was sufficient to eliminate the *Emplectonema* predation.

Fucus *barrier and whiplash effects*

Hatton (1938) and Southward (1956) described a barrier effect in which three species of Fucaceae interfere with the recruitment of *Balanus balanoides* by preventing access of the cyprids to the substratum. Furthermore, a whiplash effect of fucoid fronds may dislodge cyprids and young barnacles (Lewis 1964). This interference effect was tested at Portage Head and Colin's Cove in areas where there were 100% canopies of *Fucus*. At each site two areas ranging from 0.5 m² to 1.5 m² were cleared of only *Fucus distichus*. The numbers of metamorphosed barnacles in these areas where there was no possible *Fucus* effect were compared with the number in control strips. The potential interference of limpets and predators was not controlled, but their densities were monitored, and they did not respond to the altered canopy and thus probably did not differentially affect the barnacle recruitment. Table 8 shows that there was no differ-

ence in barnacle density at Portage Head between the experimental and control strips, but that at Colin's Cove, an area of high desiccation, there was significantly higher barnacle recruitment and survival under the *Fucus*. The positive effect at Colin's Cove is probably due to protection from desiccation. Probably *Fucus* interference such as that found in Europe was not seen in this study because *Fucus distichus* is a smaller plant and does not form as thick or heavy a canopy as is formed by the European fucoids.

Density of limpets and predators

The density data for acmaeid limpets presented in Table 5 are oversimplifications of the natural situation. They were estimated from 0.062-m² or 0.25-m² quadrates placed randomly along a 30-m rope laid horizontally across the intertidal. The data are means of 10–40 such samples at each level. The reliability of these estimates is reduced by environmental heterogeneity, which makes proper sampling difficult (Frank 1965). Furthermore, the limpet larvae have a tendency to settle in the lower levels of the intertidal and move upward (Castenholz 1961, Frank 1965, and personal observation). Thus at times one can find enormous numbers (over 1,000/m²) of tiny (less than 4 mm in length) limpets, unidentifiable as to species, in the lower levels. These limpets as well as many of the adults are consumed

TABLE 7. Densities at various tidal levels of carnivorous gastropods at the San Juan Island sites. The foraging area is calculated from the observed mobility of marked animals

Site	Species	Level (ft)	Date	Sample size (m²)	Sample mean	N	SD	Mean density (number/m²)	Mean density in total foraging area (number/m²)
		−2 to 0	6/20/67	0.062	0.3	10	1.2	4.8	
		0 to +2	6/20/67	0.062	4.3	10	3.9	68.8	
	Thais	+2 to 3	6/20/67	0.062	6.1	10	4.7	97.6	41.3
	canaliculata	3 to 4	6/20/67	0.062	4.0	10	3.0	64.0	
		4 to 5	6/20/67	0.062	0.4	10	0.6	6.4	
		5 to 6	6/20/67	0.062	0.4	10	1.3	6.4	
		0 to 2	6/20/67	0.062	0.4	10	0.7	6.4	
Eagle	Thais	2 to 3	6/20/67	0.062	0.2	10	0.5	3.2	
Point	emarginata	3 to 4	6/20/67	0.062	8.0	10	2.9	128.0	56.3
		4 to 5	6/20/67	0.062	2.6	10	3.4	41.6	
		5 to 6	6/20/67	0.062	9.9	10	5.1	158.4	
	Searlesia	−2 to 0	6/20/67	0.062	0.3	10	0.1	4.8	4.0
	dira	0 to +2	6/20/67	0.062	0.2	10	0.3	3.2	
		0 to 1	5/17/67	0.250	0.6	10	1.2	2.4	
		1 to 2	5/17/67	0.250	0.1	10	0.5	0.4	
	Thais	2 to 3	7/10/68	0.062	1.2	20	1.1	19.2	8.7
	lamellosa	3 to 4	5/17/67	0.250	2.5	10	4.0	10.0	
		3 to 4	7/10/68	0.062	1.1	20	1.4	17.1	
		4 to 5	5/17/67	0.250	0.7	10	1.2	2.8	
		0 to 1	5/17/67	0.250	0.4	10	0.9	1.6	
		1 to 2	5/17/67	0.250	2.2	10	3.5	8.8	
Turn	Thais	2 to 3	7/10/68	0.062	5.6	20	4.0	89.2	42.8
Rock	canaliculata	3 to 4	5/17/67	0.250	25.5	10	22.8	102.0	
		3 to 4	7/10/68	0.062	3.0	20	3.7	48.0	
		4 to 5	5/17/67	0.250	1.8	10	2.5	7.2	
		0 to 1	5/17/67	0.250	0.4	10	1.2	1.6	
		1 to 2	5/17/67	0.250	0.2	10	1.0	0.8	
	Thais	2 to 3	7/10/68	0.062	1.2	20	7.0	19.2	22.1
	emarginata	3 to 4	5/17/67	0.250	13.4	10	12.3	53.6	
		3 to 4	7/10/68	0.062	3.0	20	3.4	48.0	
		4 to 5	5/17/67	0.250	2.3	10	2.7	9.2	
		0 to 1	6/30/68	0.250	21.8	10	15.7	87.2	
	Thais	1 to 2	6/30/68	0.250	14.7	10	13.7	58.8	41.2
	lamellosa	2 to 3	6/30/68	0.250	3.9	10	6.2	15.6	
		3 to 4	6/30/68	0.250	0.8	10	0.7	3.2	
		0 to 1	6/30/68	0.250	0.3	10	1.1	1.2	
Colin's	Thais	1 to 2	6/30/68	0.250	2.0	10	2.4	8.0	
Cove	emarginata	2 to 3	6/30/68	0.250	3.6	10	3.1	14.4	7.9
		3 to 4	6/30/68	0.250	0.3	10	1.2	1.2	
		4 to 5	6/30/68	0.250	3.4	10	3.3	13.6	
	Searlesia	−1 to 0	6/30/68	0.250	0.8	10	1.0	3.2	
	dira	+1 to 2	6/30/68	0.250	2.1	10	2.8	8.4	7.2
		2 to 3	6/30/68	0.250	2.5	10	2.4	10.0	

by *Leptasterias hexactis* (Menge 1970), *Pisaster* (Paine, *personal communication*, and personal observation), and *Searlesia* (Louda, *personal communication*, and personal observation) as well as by the nemertean *Emplectonema gracile* and various polyclad worms (Frank 1965, and personal observation). The result of this predation is that much of the acmaeid population turns over each year, and their observed densities and size frequencies are strongly influenced by the time of year and the level at which they are sampled. The data in Table 5 represent limpets at least 4 mm long sampled in the spring and

early summer, when their activity is most likely to affect the recruitment and survival of the algae and barnacles.

It is equally difficult to estimate the population densities of the species of *Thais* at each site because of bias from at least one of the following sources: (1) *Thais* have a marked tendency to retire into crevices, under algae, and among anemones or mussel byssal threads during low tide; (2) this tendency may be exaggerated during spring tides; (3) during the summer months, when these data were collected, an unknown proportion of the populations of *T.*
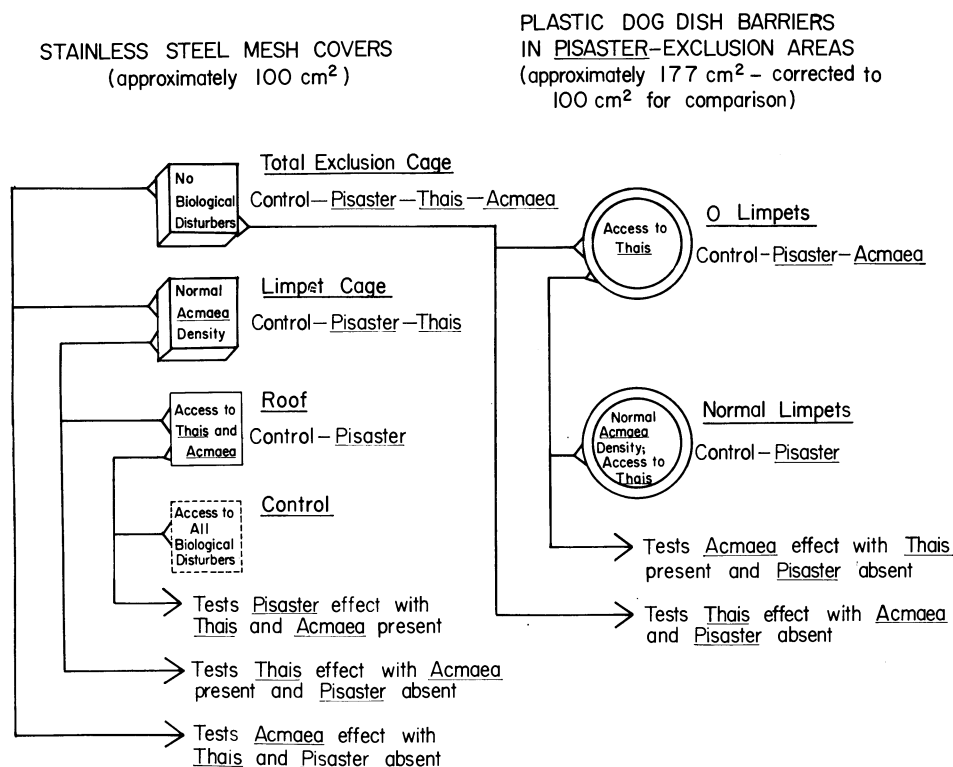
FIG. 4. A diagram of the experimental design used to test the effects of competition and biological disturbance in the barnacle-mussel association. Listed within each enclosure are those biological disturbers enclosed in or having access to the area within. Beside each drawing is the name (underlined) given to that particular type of enclosure and the situation that it represents relative to the control area (— means minus). Comparisons between cages and the effects that they are designed to test are indicated by arrows.

emarginata and *T. canaliculata* retreat into crevices and other protected spots to copulate and to lay eggs; and (4) individuals are highly motile and seem to be able to locate patches of food successfully, thus forming concentrated clumps of individuals. The *Thais* and *Ceratostoma* densities estimated in Table 6 were derived from transects like those for estimating limpet density. Means from these transects at different heights were pooled in a given area at the outer coast sites, where observations of tagged *Thais* have shown that even though the *Thais* are found concentrated at higher levels where there is more food, they definitely also forage in the lower levels.

The same procedure was followed in the San Juan Islands, but was complicated because there were two and occasionally three species of *Thais* involved, as well as another carnivorous gastropod, *Searlesia dira* (Table 7). In the San Juan Islands there is a tendency for *T. emarginata* to occur above *T. lamellosa* and *T. canaliculata* in the intertidal, but at any given site some *T. emarginata* can usually be found feeding and reproducing at the lower levels as well. Furthermore, in situ marking with fast-drying paint has shown that *T. emarginata* will also forage horizon-

tally as far as 15 m within 2 weeks. *Thais canaliculata* and *T. lamellosa* tend to be more sedentary in their foraging behavior and seem to be restricted to lower levels, although on occasion they may forage almost as high as does *T. emarginata*. Therefore, although there is an apparent vertical separation between *T. emarginata* and the other two *Thais* species, after a heavy barnacle set *T. emarginata* readily moves down to forage; *Thais canaliculata* and *T. lamellosa* are less able to exploit prey higher in the intertidal. At the sites where *Searlesia dira* is found, it occurs mainly in the lower levels. Thus lower levels are subjected to a much higher degree of snail predation than are the higher levels, and it is very difficult to predict accurately that a certain area of the shore will be exploited by any given density of predators. For these reasons population estimates from transects or from studying an isolated locality can be very misleading.

During the data analysis it became apparent that the 1969 and 1970 *Thais* densities were much below those of 1967 and 1968. This reduction is probably a result of an unusually cold period in December 1968 and January 1969 which coincided with very

TABLE 8. The mean number of *Balanus glandula* per 0.062 m² to settle and metamorphose in areas where 100% canopy cover of *Fucus distichus* had been removed, contrasted to control areas with 100% canopy cover. The experiment was begun in May 1967 and concluded in August 1967. The variance (based on 8 samples in areas of 0.5 m² and 10 samples in all other areas) is given as the 95% confidence limit. The data for Colin's Cove show significant differences between the *Fucus* removal and control areas

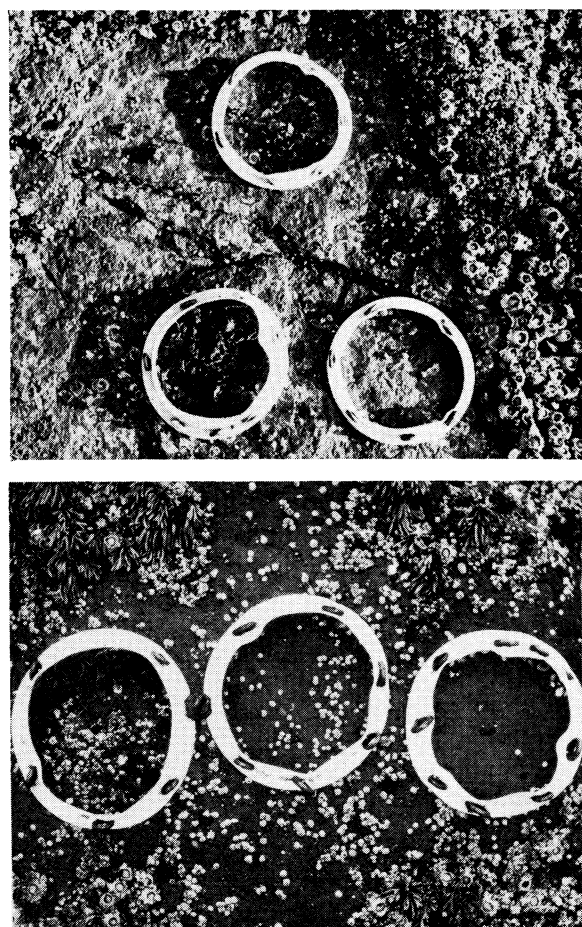|	*Fucus* removal area		Control (100% *Fucus* cover)	
Site	Area (m²)	*Balanus glandula*	Area (m²)	*Balanus glandula*
Portage Head	0.5	191.1±47.2	0.5	239.0±62.3
	1.5	267.4±38.4	1.5	217.1±44.4
	1.5	139.2±27.2	1.5	175.2±56.3
Colin's Cove	0.5	5.0± 6.2	0.5	39.5±10.5
	0.75	19.4± 5.7	0.5	41.3± 7.9
	0.6	32.1±10.1	0.5	65.9±10.5

FIG. 5. Photograph of two sets of dog dishes at Mukkaw Bay. The top plate was taken 3 weeks after the experiment was begun and shows algal settlement in the absence of limpet grazing in the lower left dish. The upper dish had normal limpet density while the lower right dish had twice the normal density. The bottom plate shows the effects of limpet disturbance on barnacle recruitment in an experiment 7 weeks old. The left dish excluded limpets completely, the middle dish had normal limpet density, and the right dish had twice the normal limpet density.

low night tides. Since the effect of the cold on *Thais* populations was not evident at the time, no accurate assessment of the *Thais* populations was made, and unfortunately, direct censuses of *Thais* density in 1969 were limited. Control areas at Portage Head were extensively photographed during all the years of the study. The Portage Head *Thais* densities in Table 9 were obtained from the photographs of one such control area taken during the first day of a minus tide series and are realistic estimates of the *Thais* densities. The data for the San Juan Islands were obtained under less controlled conditions, but still suggest a significant decline in the *Thais* density.

The foraging behavior of *Pisaster ochraceus* involves a vertical movement in which it forages upward during high tide, captures its prey, and then returns back down into a tidepool or surge channel to digest the prey (Mauzey 1966, and personal observation). This retreat to areas protected from desiccation is more apparent during spring tides, which are associated with dry conditions. The *Pisaster* densities reported in Table 10 were derived by counting all the *Pisaster* in a particular locality and estimating the area over which they forage. At Shi Shi, Portage Head, and Waadah Island, this is relatively simple, as one can count all the *Pisaster* in a surge channel, and the upper limits of their foraging excursions are conspicuously marked by browse lines along the *Mytilus* and *Balanus* populations. Repeated counts in these areas show high consistency. The estimate of *Pisaster* density on the exposed point at Tatoosh Island is less reliable. Here the lower limit to the *Mytilus* bed was at the 0–1-ft level. I counted 16 *Pisaster* along a 3–4-m strip below the *Mytilus* on June 7, 1970. Due to a heavy cover of the kelp *Lessoniopsis littoralis*, this count is almost certainly an underestimate. The estimates of *Pisaster* densities in the San Juan Islands were obtained by diving and are in excellent agreement with those of Mauzey (1967) and Menge (1970).

FIG. 6. Photograph of a stainless steel cage experiment at Shi Shi. The center cage is a total exclusion cage, the left is a limpet cage excluding *Thais* and *Pisaster*. On the right is the "roof" which excludes only *Pisaster*. To the right of the roof is the control area. Both cages and the roof have been moved so that the experimental areas can be seen below them in the photo. A light set of *Chthamalus dalli* is not noticeably affected by the limpet cage or the roof, but a heavy settlement of *Balanus glandula* in the total exclusion cage occupies 100% of the space. The scale marker is 15 cm long.

TABLE 9. Densities of *Thais emarginata* at Portage Head determined from photographs taken along the same transect before and after the cold period in December 1968–January 1969; densities of *Thais canaliculata* at Eagle Point were taken from random quadrates along a 10-m line in 1967, 1968, and 1970 and from haphazardly tossed quadrates during high tide in 1969

Site	Date	Sample size (m²)	N	Sample mean	SD	Number/m²
Portage Head	June 8, 1968	0.250	10	70.1	21.4	280
(*T. emarginata*)	June 27, 1969	0.250	10	17.3	28.2	109
	June 8, 1967	0.250	10	30.2	25.3	121
Eagle Point	June 6, 1968	0.062	15	7.2	3.8	115
(*T. canaliculata*)	July 2, 1969	0.062	21	2.1	5.3	34
	July 2, 1970	0.062	20	2.4	6.9	38

Recruitment in the upper intertidal

The most consistent occupants of space in the barnacle-mussel association are the three barnacle species *Chthamalus dalli*, *Balanus glandula*, and *B. cariosus*, the mussel *Mytilus californianus*, and the anemone *Anthopleura elegantissima*. Due to settlement uneven in time and space, the recruitment patterns of these species are difficult to quantify in an experimental manner. However, inferences about the barnacle recruitment patterns can be drawn from the experimental data. The *Mytilus* and *Anthopleura* patterns discussed at the end of this section are based only on general observations from 1965 to 1970.

The percentage cover and numbers of individuals per 100 cm² for each barnacle species under each experimental condition are shown for selected years in Fig. 7–12. In order to present representative patterns for one year, the first year for which there were complete data at each site was used. Inferences about the potential recruitment (i.e., the availability of cyprids ready to settle) at a given level and time can be made by considering the number of barnacles present in each experimental situation in the following manner. Early in the season the number of metamorphosed and identifiable individuals of each species at each level could be observed directly in the "total exclusion cage," where there were no distur-

TABLE 10. Density of *Pisaster* in its total foraging area at each of the study sites. Samples collected on a particular date represent a single search of a given area. The means (given with N and standard deviation) are from a number of searches in a given area

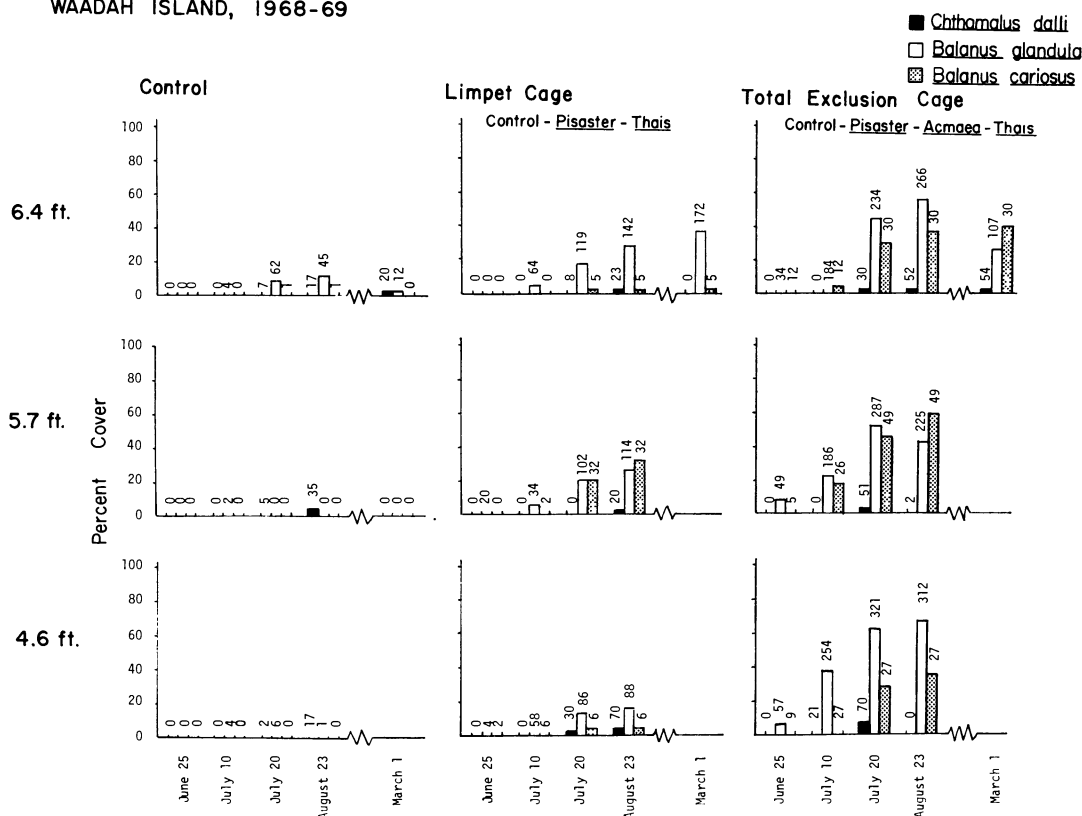| Site	Level (ft)	Date	Foraging area (m²)	Mean	N	SD	Density (number/m²)
Tatoosh Island	? to +1	7/6/70	102	16			0.16
Waadah Island	−2 to +7	1967–69	75	28	7	0.9	0.46
Shi Shi Reef	−2 to +6	1967–69	52	81	14	6.2	1.56
	0 to +5	2/2/67	158	137			0.87
Portage Head	0 to +6	1966–69	442	310	22	7.9	0.70
Eagle Point	−3 to +4	6/22/67	193	17			0.09
Turn Rock	−2 to +3	1/6/67	1,258	78			0.06
Colin's Cove	−3 to +7	6/22/67	487	19			0.04

FIG. 7. Percentage cover (bars) and density/100 cm² (above bars) of barnacles under varying experimental conditions at Waadah Island from June 1968 through March 1969. A conservative estimate of the recruitment is shown by an increase in the density. A decrease in density in predator-free situations (limpet cage and total exclusion cage) indicates barnacles killed as a result of competition for space.

bances to prevent their settling or to kill or remove them. Substratum quickly became limiting in this cage at most levels, however, and after about 50% of the total space was occupied, competition for space became an important factor (see below), and the observed changes in barnacle numbers were no longer a good index of potential recruitment. After the early part of the season, changes in numbers of barnacles in the "0 limpet" and "limpet cage" experiments (Fig. 7–9, 12) were sometimes a better indication

of recruitment. In such experiments where competition or biological disturbances occur, an increase in barnacle number is definite evidence of recruitment. Such demonstrated increases are often underestimates of the recruitment which has occurred, since they are net increases beyond the settlement lost to competition and disturbance; these increases underestimate the potential recruitment even more than they do the the actual recruitment. A decrease in barnacle number cannot be interpreted as a lack of recruitment,
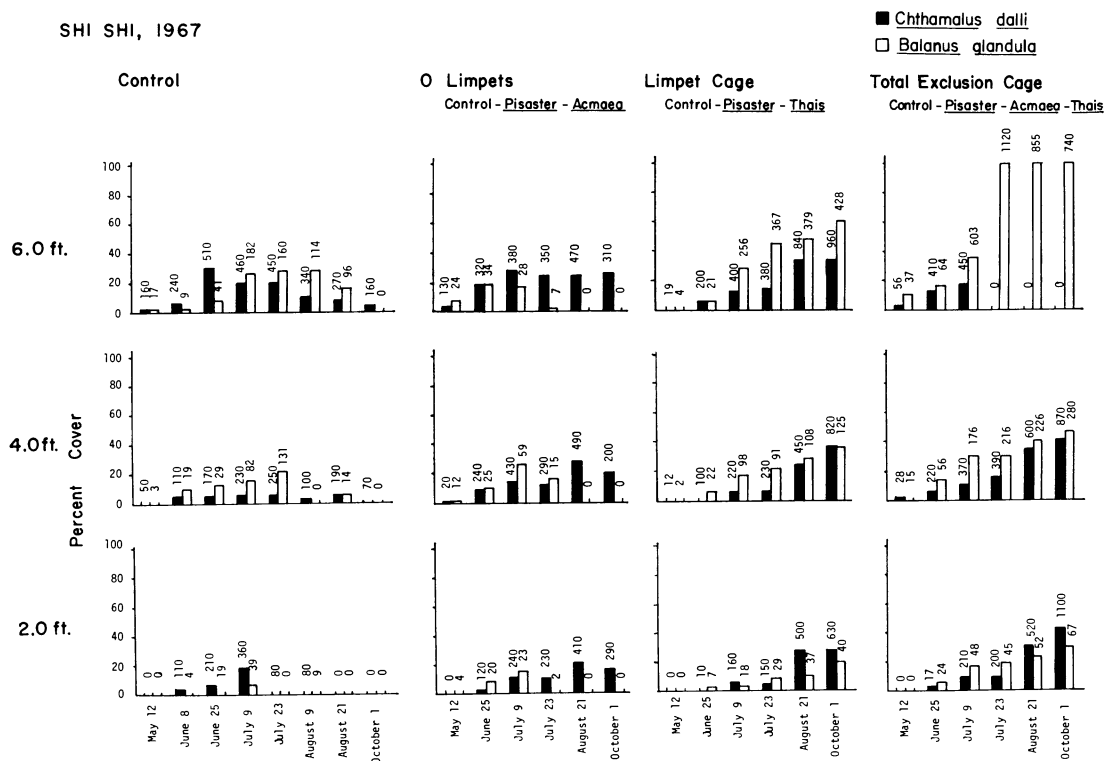
FIG. 8. Percentage cover (bars) and density/100 cm² (above bars) of barnacles under varying experimental conditions at Shi Shi in the summer of 1967. A conservative estimate of the recruitment is shown by an increase in the density. A decrease in density in predator-free situations (limpet cage and total exclusion cage) indicates barnacles killed as a result of competition for space.

as it is possible that new barnacles have settled and these, along with some previously established individuals, have been eliminated. Another complication relevant to all estimates of potential recruitment is that there is a 5- to 20-day lag between the time a cyprid settles and the time that it is identifiable at the next low tide series. Despite these complications, the following results are apparent from considerations of the experimental cages and dishes.

Chthamalus dalli recruitment was seen at all sites and was essentially the same at each level within each site (Fig. 7-10, 12), except at Turn Rock where there was a sporadic recruitment (Fig. 11). On the outer coast the settlement usually began in May (Fig. 8 and 9) and continued throughout the summer (Fig. 7-9, total exclusion and limpet cages). The single outstanding exception was an extremely heavy *Chthamalus* set in August 1968 at Portage Head. In the San Juan Islands *Chthamalus* has a lighter set which begins later in the summer (Fig. 10-12). *Chthamalus dalli*, like its European congener, *C. stellatus* (Connell 1961a), is a very small barnacle, usually less than 4 mm in basal diameter.

Balanus glandula was the most nearly ubiquitous barnacle species in the study sites; its settlement had

begun by late April and was usually heavy from late May through July (Fig. 7-12), continuing at a somewhat reduced rate until September. On the protected outer coast sites there is a strong tendency for *B. glandula* to settle relatively high in the intertidal (Fig. 8 and 9). The growth rates of *B. glandula* are discussed by Connell (1970), who found that they attain diameters of 4-5 mm by October and 9-15 mm by the end of 5 years.

Large *Balanus cariosus* occur in all of the study sites, but the species has a peculiar settlement pattern which is very patchy in time and space. During the years 1965 to 1969, small areas of shoreline, particularly along the west side of San Juan Island, received heavy but very localized recruitment. These areas of recruitment involved perhaps 50 m of shoreline and received 40-60% cover, while the shore 200-300 m away received almost no settlement. Of the study areas, Eagle Point received the most regular *B. cariosus* recruitment; Turn Rock and Colin's Cove generally received light settlements. Although they occur as large adults at Shi Shi, Portage Head, and Mukkaw Bay, I did not observe *B. cariosus* to settle in these areas during this study. Light settlements were observed at Waadah Island, while cleared patches in the exposed areas of Tatoosh
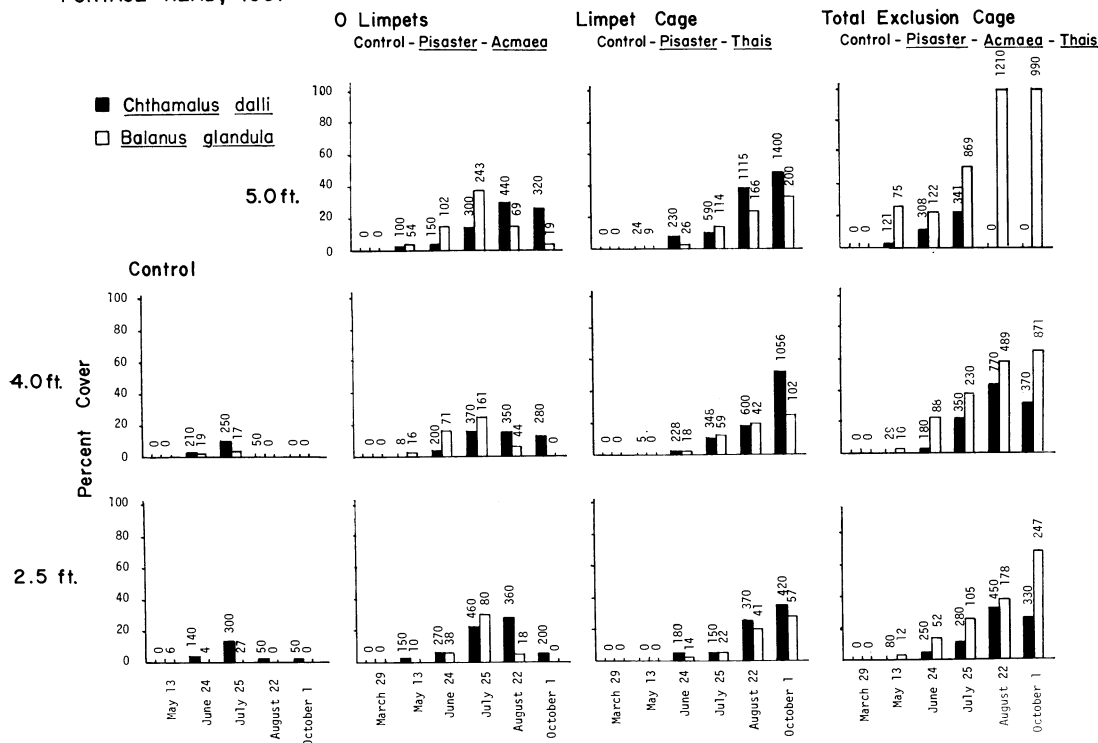
PORTAGE ·HEAD, 1967

FIG. 9. Percentage cover (bars) and density/100 cm² (above bars) of barnacles under varying experimental conditions at Portage Head in the summer of 1967. See Fig. 8 for explanation.

Island (summer 1968 and 1970) received very heavy (approaching 100% cover) settlements. *Balanus cariosus* tends to occur at lower middle levels in the intertidal (Fig. 7, 10–12) and never is found as high as the upper limits of *B. glandula* or *Chthamalus dalli*. *Balanus cariosus* is the largest of the three species, attaining a basal diameter of at least 42 mm at one site; it also has the fastest growth rate of the local barnacles. Since accurate measurements of growth could not be obtained in the experiments because intraspecific competition led to hummocking and distortion of basal diameters, no detailed growth study was done. However, the presence of a few solitary *B. cariosus* in the controls allowed some observation of growth (Fig. 13). Although the growth rates shown are based on inadequate sample sizes, they do indicate that *B. cariosus* has a potentially fast growth rate and grows considerably larger than *B. glandula* and *Chthamalus dalli*.

Interspecific competition in the upper intertidal

With the exception of some evidence of algal competition for light, most of the interspecific interactions between the sessile organisms in this intertidal zone involve competition for primary space (bare, unoccupied rock substratum) as the potentially limiting resource. In the experimental situations when primary space is not abundant, most of the sessile species will utilize secondary space (another organism used as substratum) by settling on barnacles and mussels, thus becoming entirely dependent upon the well-being of their "hosts." Rare instances were observed in which barnacles are overgrown by the secondary settlement of other barnacles and algae and apparently eventually starved; the whole hummock then disappears, thereby freeing primary space. As primary space is rarely in limiting supply in natural situations in the upper intertidal (Table 1), the phenomenon of secondary space has been considered relatively unimportant and has not been studied.

As primary substratum becomes limiting, the various species of algae always lose in the upper intertidal to any of the three species of barnacles. The mechanisms are straightforward: as the barnacle grows in diameter, its plates dislodge or weaken the holdfasts of the nonencrusting algae, and the plants are carried away by wave action; the encrusting algae are simply overgrown by the barnacles. This interaction was observed frequently in upper intertidal situations where algae and barnacles occupied primary substratum immediately adjacent to each other. When the barnacles occupy all the primary space, many algae, particularly *Fucus, Endocladia*, and *Gigartina*, will settle and grow on the barnacles. The
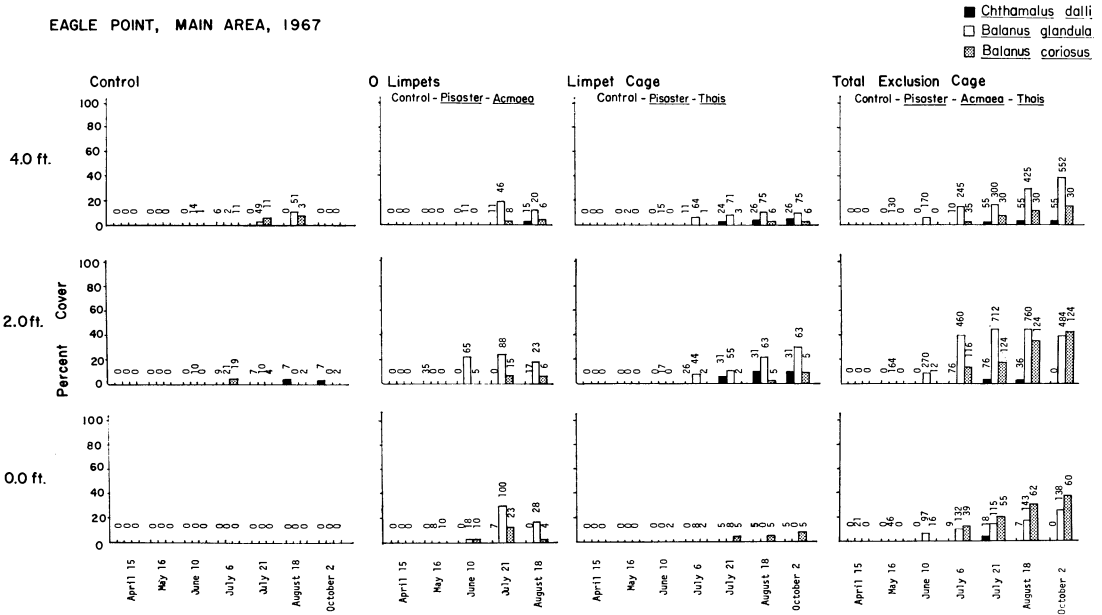
FIG. 10. Percentage cover (bars) and density/100 cm² (above bars) of barnacles under varying experimental conditions at Eagle Point in the summer of 1967. See Fig. 8 for explanation.
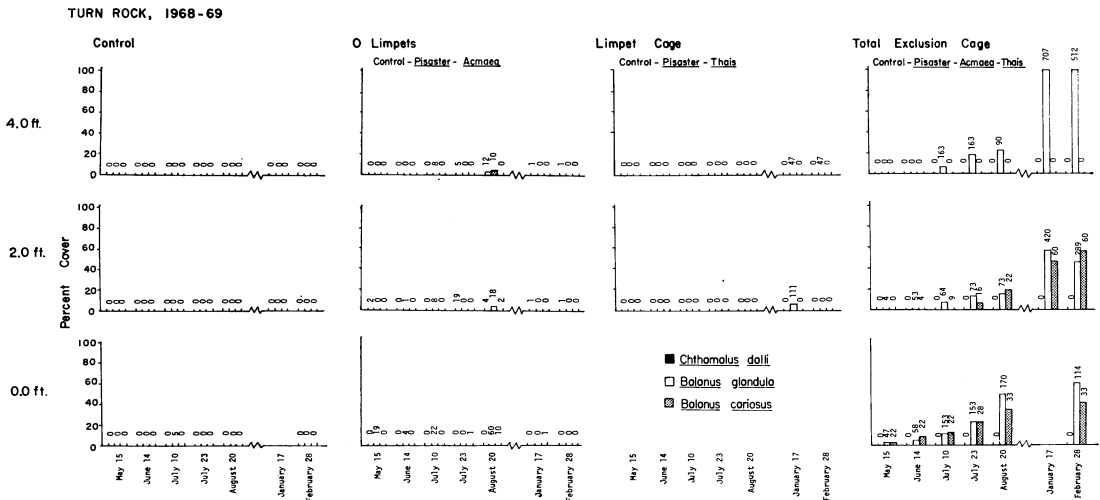

FIG. 11. Percentage cover (bars) and density/100 cm² (above bars) of barnacles under varying experimental conditions at Turn Rock from May 1968 through February 1969. See Fig. 8 for explanation.

articulated coralline algae have large encrusting holdfast systems which appear to offer barnacles an unstable substratum and might be an exception to the generalization that in the upper intertidal the barnacles outcompete the algae. No instance of competitive interaction between barnacles and articulated coralline algae was observed.

The different growth rates of the three barnacle species suggest differences in their ability to competitively dominate the primary space. Such trends were observed in most total exclusion cages with *B. cariosus* dominating in space competition with *B.*

glandula and *Chthamalus*, while *B. glandula* successfully dominates in the competition with *Chthamalus*. The competitive abilities are very clear; the mechanisms in this competition are identical to those described by Connell (1961a): the dominant individual completely grows over or squeezes the other individual.

The competitive trends under the experimental conditions at each site are presented in Fig. 7–12, in which the ordinates are given as percentage cover, an indication of the successful domination of primary space, the resource for which the barnacles
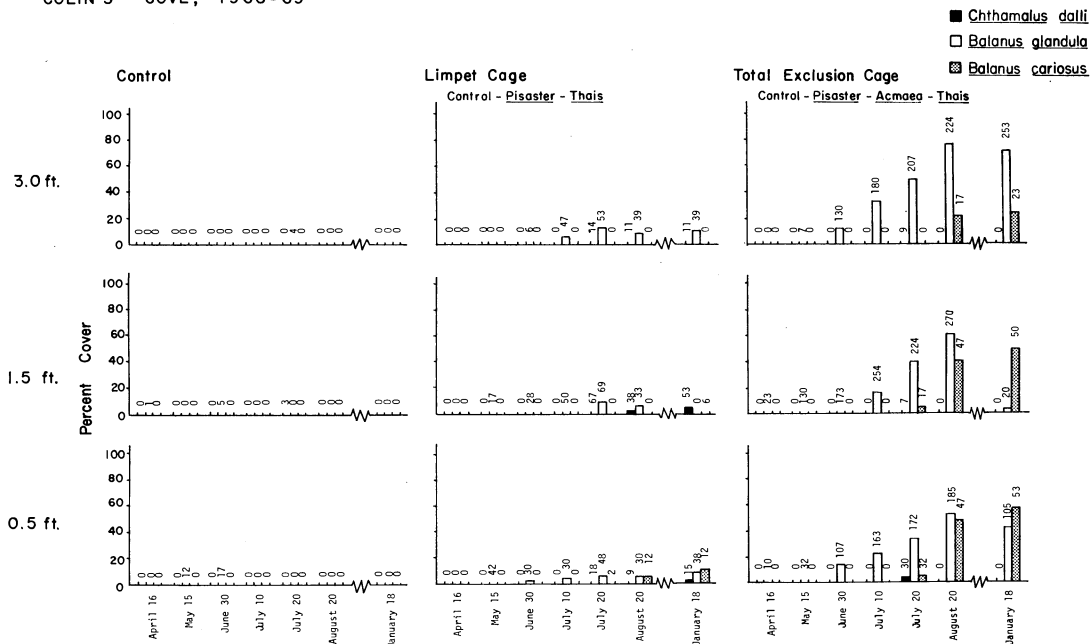
FIG. 12. Percentage cover (bars) and density/100 cm² (above bars) of barnacles under varying experimental conditions at Colin's Cove from May 1968 through February 1969. A conservative estimate of the recruitment is shown by an increase in the density. The loss of *Balanus glandula* in the middle level limpet cage and total exclusion cage is a result of a winter invasion of *Onchidoris* into the cages; in all other cases a decrease in density in those predator-free situations indicates barnacles killed as a result of competition for space.
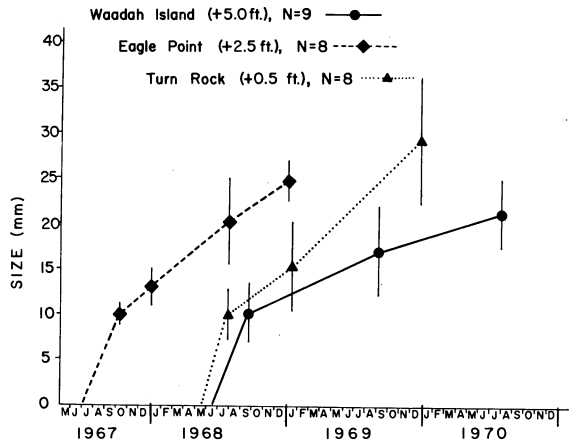
FIG. 13. Growth rates of uncrowded *Balanus cariosus* at three sites. Each point represents the mean basal diameter; N and standard deviation are shown.

compete. In every predator-free situation (total exclusion cage and limpet cage) in Fig. 7–12 in which either the number or the percentage cover of a species is reduced, the reduction resulted directly from barnacles being competitively overgrown or squeezed. The result of this competition for substratum in which *B. glandula* reduces or eliminates *Chthamalus dalli* can be seen in most of the total exclusion cages at Shi Shi and Portage Head (Fig. 8 and 9), while situations in which *B. cariosus* is dominant over both *B. glan-*

dula and *Chthamalus* can be seen in most total exclusion cages at Waadah Island, Eagle Point, Turn Rock, and Colin's Cove (Fig. 7, 10, 11, and 12). As is predictable from the recruitment data, *B. glandula* is strongest in the higher levels (Fig. 8–12), while *B. cariosus* is usually more common in the middle-lower levels (Fig. 7, 10–12).

Another spatially important organism is *Mytilus californianus*, whose larvae settle among filamentous algae and barnacles as well as among byssal threads of their own species (Glynn 1965, and personal observation). After initial settlement, the pediveligers and young mussels are capable of extensive crawling (Bayne 1965, Harger 1968), and frequently the *Mytilus* attach and grow on top of barnacles. Figures 14 and 15 show secondary space utilization during 3 years' competition in the total exclusion cages, which were maintained because many of the competitive situations were incomplete at the end of 1 year and because *Mytilus* rarely were observed in the first year. It was not determined whether the *Mytilus* in these total exclusion cages actually settled on the *Balanus* or settled elsewhere and crawled onto them. Twelve long-term total exclusion cages at Shi Shi and Portage Head showed that in the absence of any disturbance, *Balanus glandula* initially dominates the primary space, but by the end of the second summer, *Mytilus* completely

covers the *Balanus*. Although during the time of this research the *Balanus* were generally not killed by this cover, Paine (1966) has shown that in the absence of starfish predation the *Mytilus* eventually completely dominate the space.

In the San Juan Islands where adult *Mytilus californianus* are rare, long-term total exclusion cages showed that *Balanus cariosus* completely dominates the primary space (Fig. 16). Most of the long-term cages in the San Juan Islands also developed a heavy cover of *Fucus*, which utilized *Balanus cariosus* as secondary space. In those cages from which *Fucus* was not removed, large numbers (50-150) of *Mytilus californianus* and *M. edulis* appeared. How-

ever, because the *Fucus* cover made photoanalysis impossible, the *Mytilus* cover in these cages is not precisely known and does not appear in Fig. 16. It is reasonable to suppose that with protection against desiccation and predation, the San Juan Islands could develop a situation analogous to that of the outer coast.

To test whether the abundance patterns of *Anthopleura elegantissima* described in Table 3 were affected by competition, five separate 0.062-m² patches were cleared of the anemones from the middle of a very large aggregation (50 m²) at Shi Shi in May 1966. In each case the cleared patch was quickly covered with diatoms and *Enteromorpha linza* and *E. intestinalis*. During the first summer there was limited anemone immigration into the clearings. By July 1966 there was a 25–35% cover of *Balanus glandula*. By August, *Thais emarginata* were killing the barnacles, and all the barnacles were dead by

FIG. 14. Percentage cover of barnacles and *Mytilus californianus* in total exclusion cages in 3-year competition experiments at two levels at Shi Shi. The *Mytilus* are occupying secondary space.
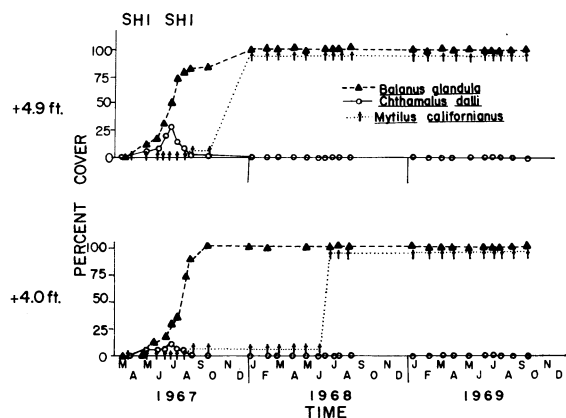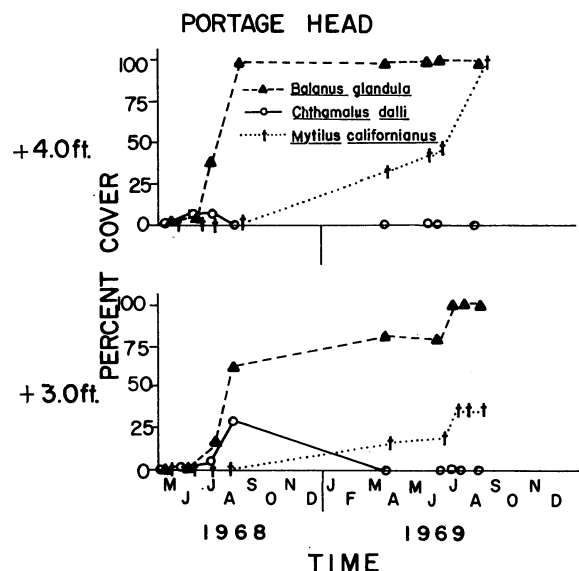

FIG. 15. Percentage cover of barnacles and *Mytilus californianus* in total exclusion cages in 2-year competition experiments at two levels at Portage Head. The *Mytilus* are occupying secondary space.
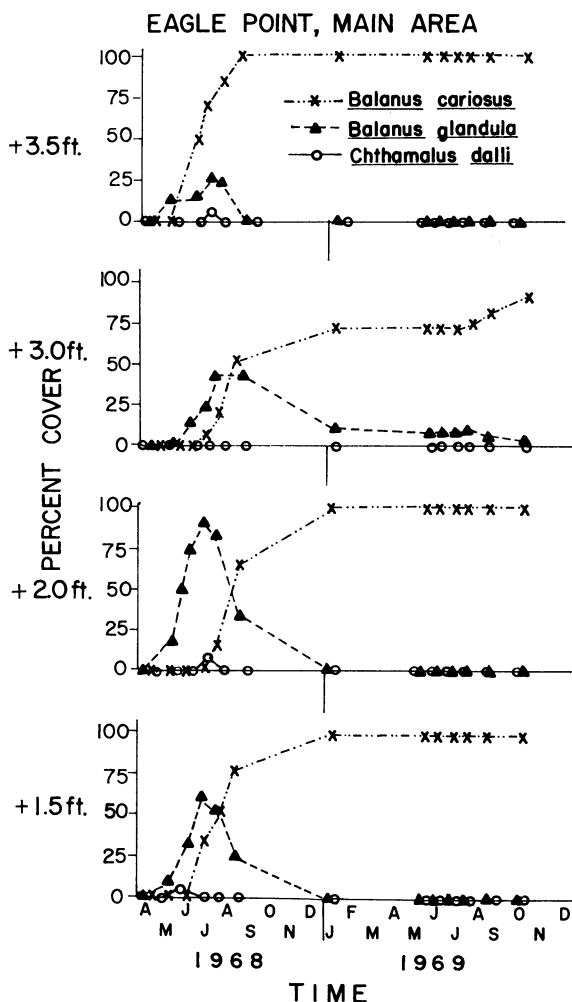

FIG. 16. Percentage cover of barnacles in total exclusion cages in 2-year competition experiments at four levels at Eagle Point.

October. Similar events occurred in 1967 and 1968. By 1969 a few anemones had moved into the cleared patches, but the patches remained distinct and again the barnacles were killed by *Thais*. The anemones offer *Thais* protection from desiccation and thereby increase their predatory efficiency by allowing them to remain close to their major prey patch. But the anemones do not effectively crowd or cover the barnacles, and thus are not efficient space competitors until they completely cover the substratum, at which point the anemones probably could successfully control the space by preventing larval recruitment of potentially competing species. However, such growth of an *Anthopleura elegantissima* population may take many years and was never seen during the period of this study.

Space competition with *Mytilus californianus* and *Balanus cariosus* may prevent the anemones from moving into more exposed conditions. Paine (1966) has shown that when *Pisaster* is removed, *M. californianus* grows over and kills *Anthopleura elegantissima*. However, the reciprocal experiment in 1966 of clearing *Balanus glandula* and *Mytilus californianus* from the exposed side of the surge channel at Shi Shi to see if *Anthopleura* utilized the space was not successful, as neither larval recruitment nor adult immigration into the clearings had occurred by August 1970.

Aggregations of *Anthopleura elegantissima* on the west side of San Juan Island are frequently found among clumps of large *Balanus cariosus*. To test possible effects of competition between these two sessile species, *A. elegantissima* was removed from three 0.062-m² areas in 1966. In contrast to the results on the outer coast, these Eagle Point cleared areas were completely reclaimed by immigrant anemones within 3 months. It is not clear why the San Juan Island *A. elegantissima* are so much more motile than those of the outer coast.

The reciprocal experiment of removing all the *Balanus cariosus* was performed, using two 1.0-m² areas. Figure 17, shows the results of the experimental removal of 45% and 55% covers of large *Balanus cariosus* in these two patches at Eagle Point. The anemone population immediately responded to the release in space competition with a sharp increase in their population as the result of both immigration and asexual fission. These populations were then severely reduced by desiccation during the summer months. Figure 17 also shows that the anemones in the controls, often clumped around the base of large *B. cariosus* and thus protected from the wind and hence from desiccation, suffered relatively little mortality. Thus the *A. elegantissima* populations in the controls appeared more stable in the presence of their space competitors than those experimental anemones with-
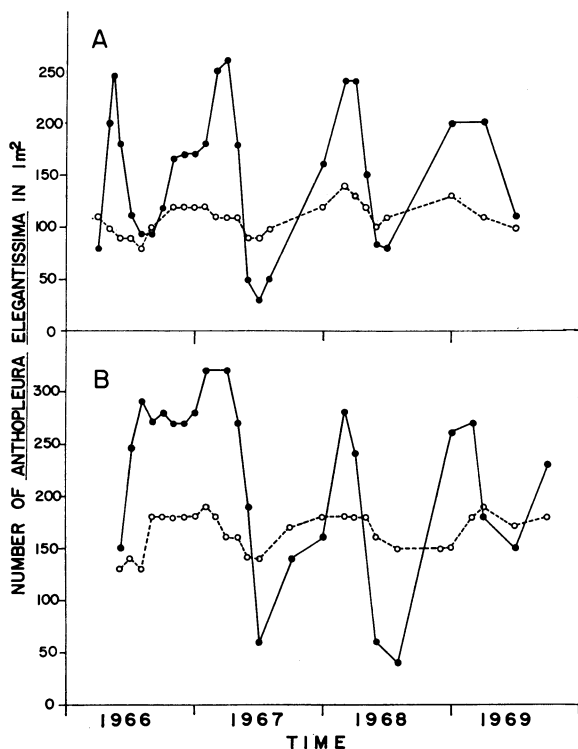

FIG. 17. Eagle Point *Anthopleura elegantissima* density in two 1-m² patches following removal of 55% (A) and 45% (B) covers of *Balanus cariosus*. The adjacent controls had 48% (A) and 55% (B) covers of *B. cariosus*. Solid circles represent *Balanus cariosus* cover removed, open circles the control.

out *B. cariosus*. By 1969 the *A. elegantissima* in the cleared patches were beginning to form aggregations which offer some protection from wind desiccation and, possibly as a result, their population fluctuations seemed to be damping. It appears that the San Juan Island *A. elegantissima* populations are in a more marginal environment than are those on the outer coast; the result is that the San Juan Island populations are maintained in a continuous state of flux, as a result of both desiccation and competitive pressures. The only hypothesis which is forthcoming is that *A. elegantissima* behaviorally respond to desiccation by increasing their movement until they encounter a locality such as an *A. elegantissima* aggregation, a crevice, or a barnacle clump, any of which offer some protection.

Effects of limpets on algal recruitment and survival

Experimental results of limpet exclusions are given as means of all levels and over three summers (Table 11). The dishes were cleared at the end of each season. In all cases where limpets were excluded there was a heavy growth of algae which covered 100% of the surface. In each instance, the initial algal growth was composed of various species of diatoms;

however, it was not possible to exclude the adventitious grazing of littorine gastropods from the cages or dishes. As Castenholz (1961) has shown, this grazing is sufficient to reduce or eliminate most of the diatom growth. The diatom growth quickly gave way to *Porphyra* and various species of *Enteromorpha* and *Ulva*. This is probably a result of both littorine grazing and natural succession, with the larger *Porphyra* and ulvoids outcompeting the diatoms. In the dog dishes, where *Thais* predation prevented the barnacles from outcompeting the algae, there was usually a modest tendency toward succession during the first summer from the diatom-*Porphyra*-ulvoid-group to *Gigartina papillata*, *Iridaea heterocarpa*, *Halosaccion glandiforme*, and *Microcladia borealis*.

Different dishes at Shi Shi, Portage Head, and Mukkaw Bay were left uncleared for 3 years to assess algal succession in the absence of limpets. The limpet exclusion dishes developed up to 100% canopy cover and averaged 21.2 *Fucus distichus* (Portage Head and Shi Shi; $N = 6$; SD = 5.2), 37.4 *Pelvetiopsis limitata* (Mukkaw Bay; $N = 3$; SD = 10.1), 17.8 *Gigartina papillata* (mean of three sites; $N = 9$; SD = 3.0), and 34.0 *Endocladia muricata* (mean of three sites; $N = 9$; SD = 5.5). This can be compared with the control means of 0.8 *Fucus* (Portage Head and Shi Shi; $N = 6$; SD = 0.6), 3 *Pelvetiopsis* (Mukkaw Bay; $N = 3$; SD = 1.4), and means of 3 *Gigartina* and 1 *Endocladia* ($N = 9$; SD = 0.2 and 0.5) for the three sites. This supports the conclusion of European workers that the normal limpet grazing retards the algal succession (see Lewis 1964 for review).

Effects of limpets on barnacle populations

Effects on recruitment.—The effects of limpets on the initial recruitment of barnacles were dramatic. The mechanisms by which limpets interfere with barnacle recruitment involve eating, pushing, and dislodging the cyprid or newly metamorphosed barnacle from the substratum. The quantitative effect of these procedures on barnacle recruitment was evaluated by using pairs of cages. Each pair consisted of a cage from which all *Pisaster*, *Acmaea*, and *Thais* had been excluded and an adjacent cage from which *Pisaster* and *Thais* had been excluded, but in which limpets occurred at approximately the same density as they did naturally outside the cages (Fig. 4). Periodic surveys were done by removing the cages, counting or photographing the organisms underneath, and then replacing the cages.

The dates for statistical comparison of barnacle recruitment in the pairs of cages were selected to allow sufficient settlement to have occurred to show whether limpets had an effect on recruitment and to

avoid any effects of competition that might occur in the cages as available space became limiting. The pairs of cages were compared at the last survey before 50% or more of the primary space in the total exclusion cage was occupied. For example, if a pair was surveyed on April 15, May 16, June 10, and July 6, with 50% cover observed on June 10, the numbers of barnacles occurring in the cages on May 16 were used for the comparison. If 50% cover had not been reached by the final survey of a given year, the final survey date was used for the comparison. A cover of 50% was chosen because space competition should not yet have had an undue influence on the number of barnacles observed.

The pairs of cages were compared by using the randomization test for matched pairs (Siegel 1956) and computing the probability that, if limpets did not affect the barnacles, recruitment (the cyprids which settled, metamorphosed, and grew large enough to identify), the statistic obtained would be as large as or larger than that observed. The results are shown in Table 12. In almost every pair there was less recruitment of *Balanus* spp. in the dish with the natural density of limpets. The limpets generally had less effect on the recruitment of *Chthamalus*. This is probably because the metamorphosed *Chthamalus* is very much smaller than *Balanus* species, and once a small *Chthamalus* settles in a crack, it is much less likely to be bulldozed off than either of the other two barnacle species.

The influence of limpets on barnacle recruitment at each study area for a single year is shown in the limpet cage experiments (Fig. 8–11). In general the limpet interference is much more effective in the San Juan Island sites than in the outer coast sites. There are a number of reasons why this is true. First, the San Juan Island substratum is much smoother than the coastal siltstone. Therefore, the barnacle cyprids and recently metamorphosed barnacles are more likely to be dislodged by the bulldozing effect of the limpets than are the coastal ones, which are somewhat protected by the uneven substratum. Second, the populations of *Acmaea pelta* and *A. scutum* in the San Juan Islands are much denser than they are on the coast, and individuals of these two species, particularly *A. scutum*, are both larger and much more active than are those of *A. digitalis* and *A. paradigitalis*. Therefore there is proportionately more limpet movement in the San Juan sites. This factor is particularly important at Turn Rock and Colin's Cove. And third, at Eagle Point there is a much higher absolute density of all limpet species than at any other site.

Effects on survival.—To evaluate the significance of the net effects of limpet grazing on the populations of barnacles at each of three levels over 3 years, two sets

TABLE 11. Mean number of individuals of each algal species per 177-cm^2 dog dish observed before the end of one summer. Data are averaged for three summers, 1967–1969, and for all levels. Blank areas mean that algae were not seen

Species	Shi Shi (6)[a] O[b]	N[b]	Mukkaw Bay (5) O	N	Portage Head (6) O	N	Eagle Point (5) O	N	Turn Rock (4) O	N
Porphyra perforata	5.3	0.7	7.4	0.4	6.3	1.1	2.0		2.4	
Ulvoids	13.7	2.6	13.4	1.9	15.0	P[c]	3.2	0.6	3.9	
Spongomorpha coalita	P		5.6		2.4		P		P	
Gigartina papillata	7.4	1.0	9.0		1.3		2.0		1.2	
Polysiphonia hendryii	P		P		P		4.1		5.8	
Ceramium pacificum					P					
Heterochordaria abietina	1.4		2.2		P					
Colpomenia sinuosa	4.9	1.6	4.0		4.3	1.1	2.2		0.9	
Halosaccion glandiforme	6.0	1.2	2.1		1.8					
Microcladia borealis	1.4	P	1.3		0.8				P	
Cladophora trichotoma	P		P		P		P		P	
Iridaea spp.	2.3		P		P		P		P	
Ptilota spp.	P				P					
Ralfsia spp.	P		6.4		1.7		2.1		1.3	
Hildenbrandia rosea	P				P					
Membranoptera spp.	P									
Gelidium sp.	P				P					
Rhodomela larix	1.3				P		5.7		3.2	
Prionitis lyallii	P				P					
Fucus distichus	1.4				2.1		3.8		6.8	
Pelvetiopsis limitata			5.3		1.0					
Endocladia muricata	4.2		4.9		3.4		1.4		1.4	
Odonthalia floccosa							3.2		2.9	
Bangia fuscopurpurea							P		P	
Gloiopeltis furcata							2.4		3.0	

[a]Number of experiments in parentheses.
[b]The densities of limpets are represented as normal (N) or excluded (O) (see Table 7).
[c]Where mean was less than 0.5 or where numbers were not available, a species is represented as present (P).

of experiments were conducted at most sites between March and late August, 1967–69. In both sets *Pisaster*, due to its patchy but usually devastating foraging habits, was excluded from the experimental area. To evaluate the effects of limpets in the absence of *Thais*, the numbers of barnacles in total exclusion cages were compared to the numbers in the cages containing the normal density of *Acmaea* for each area and height. To find the effects of limpets in the presence of *Thais*, the numbers of barnacles in the plastic dog dishes with the normal densities of limpets were compared with those in which there were no limpets. The areas under the cages were approximately 100 cm^2; densities of barnacles have been corrected to this dimension for analysis. The area surrounded by the plastic barriers or dog dishes was about 177 cm^2; densities of barnacles were again corrected to 100 cm^2 for comparison. The densities were surveyed during the last August low tide series each year.

When possible, the means were compared with a 3-way analysis of variance considering treatment, height, and year effects, in order to identify significant interactions. Treatment and height effects were considered to be fixed, while year effects were considered to be random. The data were transformed using the log $(x + 1)$ transformation (Snedecor 1966) to provide for additivity, because height, year,

and the grazing habit of the limpets would logically be expected to have a proportional rather than strictly additive effect on the number of barnacles surviving. If no significant difference between treatments was discovered with the 3-way analysis, and interaction effects had been found at a level significant enough to prevent pooling of sums of squares (i.e., "H: no interaction effects" could not be accepted at the 25% significance level) and thus to limit severely degrees of freedom in testing for treatment effects, the untransformed data were subjected to one of two nonparametric tests for matched pairs. The randomization test for matched pairs (Siegel 1956) was used whenever the number of pairs showing some barnacle survival was eight or less, in order to use the most information possible. When $N \geqslant 9$, the Wilcoxon signed-rank matched-pairs test (recommended by Siegel 1956) was used, due to the unwieldiness of the randomization test with a large N.

Effects in the absence of Thais.—Limpet activity in the absence of *Thais* caused significant reductions in the number of both *Balanus glandula* and *B. cariosus* (Table 13). The one exception was at Colin's Cove, where all of the total exclusion cages had more *B. cariosus* than did the limpet cages, but because there were only three pairs

TABLE 12. Effects of *Acmaea* spp. on recruitment of barnacle species. Pairs of cages with and without limpets were compared (Fig. 4), before they had 50% cover of primary space, with the randomization test for matched pairs (Siegel 1956). The *P* values given are for one-tailed tests

Species	Area	Level (ft)	Years	Number of pairs started	Number with settlement	Number in which limpets reduced recruitment	Significance level
Balanus glandula	Waadah Island	−1 to +5	1968–1969	8	7	7	$P = 0.008$
	Shi Shi Reef	2.7 to 5.4	1967–1969	9	9	8	$P = 0.004$
						1: 58% cover by June 28, 1969	
	Portage Head	2.5 to 5.0	1967–1969	9	9	9	$P = 0.002$
	Eagle Point	0 to +1	1967–1969	6	6	5	$P = 0.031$
						1: 52% cover by May 29, 1969	
		1.5 to 2	1967–1969	9	9	7	$P = 0.008$
						2: 100% cover by May 29, 1969	
		2 to 3.5	1967–1969	11	11	10	$P = 0.001$
						1: 100% cover by May 29, 1969	
	Turn Rock	−1 to +5	1968–1969	8	8	7	$P = 0.008$
						1: 72% cover by May 30, 1969	
	Colin's Cove	0.5 to 3	1968–1969	4	4	4	$P = 0.062$
Balanus cariosus	Waadah Island	−1 to +5	1968–1969	8	4	4	$P = 0.062$
	Eagle Point	0 to 1	1967–1969	6	6	5	$P = 0.125$
						1: 52% cover by May 29, 1969	4
		1.5 to 2	1967–1969	9	8	6	$P = 0.016$
						2: 100% cover by May 29, 1969	
		2 to 3.5	1967–1969	11	6	5	$P = 0.031$
						1: 100% cover by May 29, 1969	
	Turn Rock	−1 to +5	1968–1969	8	6	5	$P = 0.031$
						1: 72% cover by May 30, 1969	
	Colin's Cove	0.5 to 3	1968–1969	4	4	4	$P = 0.062$
Chthamalus dalli	Waadah Island	−1 to +5	1968–1969	8	5	5	$P = 0.031$
	Shi Shi Reef	2.7 to 5.4	1967–1969	9	9	8	$P = 0.008$
						1: 50% cover by June 28, 1969	7
	Portage Head	2.5 to 5	1967–1969	9	9	5	$P > 0.05$
	Eagle Point	0.0 to 2	1967–1969	15	9	6	$0.047 \geq P \geq 0.031$
						3: 52% or 100% cover by May 29, 1969	5
		2 to 3.5	1967–1969	11	7	6	$P = 0.172$
						1: 100% cover by May 29, 1969	3
	Turn Rock	−1 to +5	1968–1969	8	4	3	$P = 0.88$
						1: 72% cover by May 30, 1969	1
	Colin's Cove	0.5 to 3	1968–1969	4	3	2	$P = 0.375$

TABLE 13. The effect of *Acmaea* disturbance on barnacle density by the end of each summer in the absence of *Pisaster* and *Thais*. Significance levels are for one-tailed tests. In addition to the comparison of the means, interactions between treatment, year, and intertidal height were evaluated. Anova = analysis of variance

Barnacle species	Site	Tide height (feet)	Year	Mean number of barnacles/100cm² Limpets present (limpet cage)	Mean number of barnacles/100cm² Limpets absent (total excl. cage)	Type of analysis	Significance level	Significant interactions
Balanus glandula	Shi Shi	+2.7 − +5.4	1967–1969	88	257	3–Way Anova	0.05 > P > 0.025	None
	Portage Head	+2.5 − +5.0	1967–1969	76	419	3–Way Anova	0.025 > P > 0.01	*Treatment −Year
	Waadah Island	+4.6 − +7.7	1968–1969	55	222	3–Way Anova	P < 0.001	None
	Eagle Point	0.0 − +3.5	1967–1968	61	459	3–Way Anova	P < 0.001	None
	Colin's Cove	+0.5 − +3.0	1968	39	223	2–Way Anova	0.05 > P > 0.025	—
	Turn Rock	−1.0 − +4.2	1968	1.9	124	2–Way Anova	0.005 > P > 0.001	—
Balanus cariosus	Waadah Island	+4.6 − +7.7	1968–1969	3.0	10	3–Way Anova	0.05 > P > 0.025	None
	Eagle Point	0.0 − +3.5	1967–1968	19	84	Wilcoxon Signed rank	0.01 > P > 0.005	None
	Colin's Cove	+0.5 − +3.0	1968	1.3	34	2–Way Anova	0.10 > P > 0.05	—
	Turn Rock	−1.0 − +4.2	1968	0.7	14	2–Way Anova	0.05 > P > 0.025	—
Chthamalus dalli	Shi Shi	+2.7 − +5.4	1967–1969	529	61	3–Way Anova	P < 0.001	***Height −Treatment
	Portage Head	+2.5 − +5.0	1967–1969	795	73	3–Way Anova	P < 0.001	***Height −Treatment
	Waadah Island	+4.6 − +7.7	1968–1969	57	5.5	Randomization	P = 0.28	*Height −Treatment
	Eagle Point	0.0 − +3.5	1967–1968	25	9.3	Wilcoxon Signed rank	P > 0.05	None
	Colin's Cove	+0.5 − +3.0	1968	21	0	2–Way Anova	0.025 > P > 0.01	None
	Turn Rock	−1.0 − +4.2	1968	0	0	All Zero	—	—

(*0.05 ≤ p > 0.01; ***p ≤ 0.001).

of cages (i.e., few degrees of freedom), P was between 0.10 and 0.05. Although there was a significant treatment-year interaction for *B. glandula* at Portage Head, the average number of *B. glandula* in the total exclusion cages was significantly higher than in the limpet cages.

In contrast to the two *Balanus* species, the survival of *Chthamalus* was significantly increased at all sites in the presence of limpet disturbance, because the limpets had a disproportionately strong negative effect on the populations of the competitively superior *Balanus glandula* and *B. cariosus*. This is true despite the fact that limpet activity reduces the success of initial *Chthamalus* recruitment (Table 12).

Thus, *Balanus* species very quickly dominated most of the available substratum in the absence of limpet and *Thais* disturbance, but the limpet disturbance alone maintained sufficient substratum for the settlement and survival of the very much smaller *Chthamalus*.

The highly significant height-treatment interactions for *Chthamalus* at Shi Shi and Portage Head result from the limpets reducing *Chthamalus* recruitment (see also Table 12) in the lower intertidal and having a positive influence at the higher levels by alleviating competition. Indeed, the upper level positive effect is sufficiently strong that the overall site effect is positive (Table 13), even though at both

TABLE 14. The effect of *Acmaea* disturbance on barnacle density by the end of each summer with *Thais* present at their normal densities for each level and area (Tables 6 and 7) but with *Pisaster* absent. Significance levels are for one-tailed tests. In addition to the comparison of the means, interactions between treatment, year, and intertidal height were evaluated. Anova = analysis of variance

Barnacle species	Site	Tide height (feet)	Year	Mean number of barnacles/100cm² Limpets present (normal limpet)	Mean number of barnacles/100cm² Limpets absent (0 limpet)	Type of analysis	Significance level	Significant interactions
Balanus glandula	Shi Shi	+2.7−+5.4	1967–1968	0.8	0	Randomization	$P=0.25$	None
	Mukkaw Bay	+6.0−+7.6	1968–1969	68	286	Randomization	$P=0.062$	None
	Portage Head	+2.5−+5.0	1967–1969	3.2	9.2	3–Way Anova	$0.005>P>0.001$	*Height–year
	Eagle Point	+0.5−+4.5	1967–1968	0.8	16	Randomization	$P=0.016$	None
	Turn Rock	0.0−+4.0	1967–1968	0	6.8	Randomization	$P=0.031$	None
Balanus cariosus	Eagle Point	+0.5−+4.5	1967–1968	0.3	4.0	3–Way Anova	$0.005>P>0.001$	None
	Turn Rock	0.0−+4.0	1967–1968	0	2.0	3–Way Anova	$0.025>P>0.01$	None
Chthamalus dalli	Shi Shi	+2.7−+5.4	1967–1968	200	386	3–Way Anova	$0.025>P>0.01$	None
	Mukkaw Bay	+6.0−+7.6	1968–1969	158	129	3–Way Anova	$P>0.25$	None
	Portage Head	+2.5−+5.0	1967–1968	235	323	3–Way Anova	$P<0.001$	None
	Eagle Point	+0.5−+4.5	1967–1968	2.4	3.7	Randomization	$P=0.094$	None
	Turn Rock	0.0−+4.0	1967–1968	0	4.0	3–Way Anova	$0.005>P>0.001$	None

(*$0.05 \geq p > 0.01$).

Shi Shi and Portage Head in each of the years tested there were two pairs of cages at the lower levels and only one pair at the higher level. An explanation is that *Balanus glandula* has a strong tendency to settle higher in the intertidal (see above), whereas *Chthamalus* settles much more uniformly throughout (see above). At Waadah Island, all cages were at the higher levels, the highest being above the optimum settling height for *Balanus glandula*. Thus, the Waadah Island height-treatment interaction resulted from *Chthamalus* being positively affected by limpets at 4.6 ft and 5.7 ft, where *Balanus glandula* competition was a factor, and negatively affected at 7.7 ft, where few *B. glandula* settled. The net result, as indicated by the height-treatment interactions, at all these areas is that the disturbance activities of the *Acmaea*, by countering the strong competition effects, are important in providing adequate space for *Chthamalus*.

Effects in the presence of Thais.—In most cases limpet activity significantly reduces the net barnacle survival in the presence of normal *Thais* predation (Table 14). Thus, despite selective predation by *Thais* on the *Balanus* species (see below), the combined influence of *Acmaea* and *Thais* is to increase mortality for all barnacle species (Table 14). This situation contrasts with events in the absence of *Thais* (Table 13), when a significant increase in *Chthamalus* occurs in the presence of limpets.

The significant year-height interaction at Portage Head is the result of relatively small survival of *B. glandula* in the dog dishes in 1968, particularly at the higher levels, where *B. glandula* was relatively more numerous in other years.

Effects of Thais *predation on barnacle populations*

Two independent approaches were used to evaluate the effect of *Thais* predation on the barnacle populations. The first involved the removal of *Thais* from an area and the second was the more refined experimental design outlined in Fig. 4.

At representative outer coast (Portage Head) and San Juan Island (Eagle Point) sites in *Pisaster* removal areas, *Thais* were manually removed from areas of approximately 20 and 25 m² respectively. Clearly this procedure is not as effective as the cage technique, but by carefully removing the *Thais* every 2 weeks for 2 years and by comparing immigration rates and densities with the controls, effective *Thais* predation was reduced by 60–80%. Table 15 shows the degree to which *Thais* eats *Balanus* before eating *Chthamalus*. It can be seen that *Thais* selectively kill most of the *Balanus* by the end of the summer, at which time the *Chthamalus* density is actually greater than in the control, presumably as a result of the release from space competition with *Balanus*. These crude experiments show that *Thais* predation, in addition to other disturbance, can have an important effect on barnacle populations.

Continuing interference caused by the normal activity of limpets reduces all barnacle recruitment;

TABLE 15. *Thais* removal experiment at Portage Head and Eagle Point in 1967. Mean number $\pm$ standard deviation of living and dead barnacles from 25 randomly sampled quadrates of 16 cm² at Portage Head and 100 cm² at Eagle Point

Site	Dates		Chthamalus dalli		Balanus glandula		Balanus cariosus	
			Experimental	Control	Experimental	Control	Experimental	Control
Portage Head	May 14	Alive	9.2±7.0	8.5±6.2	9.7±5.2	10.5±2.6		
		Dead	0.4±1.2	0.4±1.0	3.2±2.5	3.4±0.8		
	June 9	Alive	15.9±12.2	14.6±13.5	13.1±12.3	10.9±8.6		
		Dead	0.9±1.7	2.1±3.0	4.0±4.1	12.2±7.3		
	July 10	Alive	12.5±2.5	17.4±14.1	15.3±8.3	4.1±4.4		
		Dead	1.0±2.2	1.7±2.7	3.0±3.3	15.0±9.8		
	August 21	Alive	19.8±12.8	34.6±17.2	19.6±7.5	2.0±2.6		
		Dead	1.7±2.7	1.9±3.0	4.1±5.0	23.0±8.9		
Eagle Point	June 11	Alive	4.0±5.3	3.7±3.7	6.5±8.2	6.7±12.8	6.0±4.3	5.1±8.0
		Dead	0.8±0.5	0	3.1±4.7	4.0±5.2	1.2±2.1	0.4±3.9
	July 21	Alive	4.3±3.8	4.7±5.0	7.2±6.5	2.1±2.9	7.7±3.2	2.2±3.4
		Dead	0.5±2.1	0.2±1.2	4.5±5.9	9.5±4.1	0.8±1.4	4.4±2.9
	August 18	Alive	3.9±4.7	5.0±4.2	8.0±6.5	0.2±2.1	8.4±3.8	1.9±4.4
		Dead	1.0±1.7	0.5±1.3	5.0±3.6	10.3±3.3	1.1±1.0	5.8±2.6
	October 2	Alive	4.4±4.6	5.4±3.7	7.1±8.9	0	9.2±4.0	0.2±3.7
		Dead	0.8±1.2	0.8±1.4	6.2±5.5	10.0±6.2	1.4±2.2	8.1±1.8

however, some barnacles do metamorphose and escape the limpet disturbance. Within 10–20 days after metamorphosis, the barnacles are sufficiently large that they are not killed by limpets. The escape in growth from limpet disturbance means that the net effect of the limpets is only to introduce a time lag into the eventual barnacle domination of all the available space resource in the upper intertidal. This time lag, due to a necessary interval for *Thais* to find and consume the barnacles, is longer at higher than at lower levels, since *Thais* tend to seek lower level refuge from desiccation during spring tides and must move up to forage during neap tides. During such time lags the continuous limpet pressure on the barnacle recruitment maintains a generally significant negative effect on each of the barnacle populations.

To measure the effect of *Thais* predation in the presence of limpets, comparisons were made of 100-cm² areas under cages containing normal limpet densities but excluding *Thais* and 100-cm² areas under "roofs" which allowed access to both *Thais* and limpets at their normal densities. The effect in the absence of limpets was evaluated by comparing the number of barnacles surviving in the limpet exclusion plastic dishes, corrected to 100 cm², to the number surviving in the total exclusion cages (Fig. 4). Statistical analyses were performed as for the limpet experiments.

In almost every case predation by *Thais* in the absence of other disturbance had a pronounced effect on the survival of all three barnacle species (Table 16). Again there was a trend for *Chthamalus* to have a much higher survival with disturbance because *Thais* selectively eats the competitively dom-

inant *Balanus* species (Table 15). The increased *Chthamalus* survival due to the presence of *Thais* is not as dramatic as was the increase due to limpets. This is because limpets reduce the *Balanus glandula* and *B. cariosus* settlements before they have a chance to outcompete *Chthamalus*, whereas in the absence of limpets, the *Balanus* species often have already grown over many *Chthamalus* by the time *Thais* find and eat the *Balanus*. The significant height-treatment interactions for *Chthamalus* at Portage Head and Shi Shi indirectly result from the strong tendency of *Balanus glandula* to settle above the +4-ft level. *Thais* removes essentially all the *Balanus* in the dog dishes at all the heights. *Chthamalus*, then, survives relatively much better at the higher levels in the presence of *Thais*, because of significant reduction in the intensity of interspecific competition.

Table 17 shows significant reduction of survival of all three barnacle species due to *Thais* predation. As the reduction is not significant at Turn Rock, this site presents an exception to this generalization for each barnacle species, as does Colin's Cove for *Balanus cariosus*. The reason is the extremely effective limpet interference at both sites; limpet activity both in the *Thais* exclusion cage and under the roof is sufficient to prevent the settlement of enough barnacles to allow a proper analysis of *Thais* predation.

Relative influence of limpets and Thais

When the relative influences of limpets and *Thais* on barnacle recruitment and survival over 1 year are examined (Fig. 7–12), the following patterns emerge: (1) the control areas at each level have low recruitment and essentially no survival in the outer coast sites and neither recruitment nor survival in the San Juan Island sites; (2) in the absence of limpets there tends to be a strong recruitment of all barnacle

TABLE 16. The effect of *Thais* predation on barnacle density by the end of each summer with *Acmaea* and *Pisaster* absent. Significance levels are for one-tailed tests. In addition to the comparison of the means, interactions between treatment, year, and intertidal height were evaluated

Barnacle species	Site	Tide height (feet)	Year	Mean number of barnacles/100cm² *Thais* present (0 limpet)	Mean number of barnacles/100cm² *Thais* absent (total excl. cage)	Type of analysis	Significance level	Significant interactions
Balanus glandula	Shi Shi	+2.7 − +5.4	1967–1968	0	253	3-Way Anova	$P < 0.001$	*Height −Treatment
	Portage Head	+2.5 − +5.0	1967–1969	0	431	3-Way Anova	$0.05 > P > 0.025$	None
	Eagle Point	0.0 − +4.5	1967–1968	24	504	3-Way Anova	$0.005 > P > 0.001$	None
	Turn Rock	0.0 − +4.0	1968	25	128	2-Way Anova	$0.10 > P > 0.05$	—
Balanus cariosus	Eagle Point	0.0 − +4.5	1967–1968	4.0	49	3-Way Anova	$P < 0.001$	None
	Turn Rock	0.0 − +4.0	1968	2.2	17	2-Way Anova	$0.025 > P > 0.01$	—
Chthamalus dalli	Shi Shi	+2.7 − +5.4	1967–1968	386	60	Randomization	$P = 0.28$	**Height −Treatment
	Portage Head	+2.5 − +5.0	1967–1969	313	73	3-Way Anova	$P < 0.001$	***Height −Treatment
	Eagle Point	0.0 − +4.5	1967–1968	3.7	11.2	Randomization	$P = 0.047$	None
	Turn Rock	0.0 − +4.0	1968	3.0	0	2-Way Anova	$0.25 > P > 0.10$	—

(*$0.05 \geq p > 0.01$; **$0.01 \geq p > 0.001$; ***$p \leq 0.001$).

species, but *Thais* predation strongly reduces or eliminates these barnacle populations; (3) in the presence of limpets but in the absence of *Thais*, the initial recruitment is reduced, but eventually barnacles do escape the limpet disturbance and these barnacles persist in the absence of predation; and (4) strong interspecific competition is usually seen in the total exclusion cages within the first season in the absence of both limpet and *Thais* disturbance.

Escape by growth of Balanus cariosus and Mytilus californianus from Thais predation

Two cages at Eagle Point and one cage at Turn Rock came loose and were removed in June 1968. These cages had been in place since the summer of 1967 and had mixed size classes of *Balanus glandula* and *Balanus cariosus* under them. The fate of these barnacles was followed throughout the remainder of the period of this study. *Thais canaliculata* and *T. emarginata* killed all 320 of the *Balanus glandula* within 10 days of the removal of the cages, and by the end of July 1968 had killed all 47 of the *Balanus cariosus* with basal diameters less than 10 mm. However, a total of 27 *B. cariosus* at Eagle Point and 10 at Turn Rock with basal diameters between 13 and 19 mm survived. In January 1969 ten were accidentally killed at Turn Rock. The Eagle Point barnacles were still alive when the site was last observed in August 1970. Further evidence of *Balanus cariosus* reaching a refuge in size was observed at the Eagle Point *Thais* removal area. A patch of *Balanus cariosus*

settled in June 1967 and grew in hummocks at the 1- to 3-ft tide levels, with their basal diameters ranging from 7 to 14 mm by October 1967. At this time *Thais* removal was terminated in the area. Very few of the *Balanus cariosus* in this patch had been killed by *Thais* by August 1970; their most severe mortality seems to come from exfoliation of the hummocks. When a *B. cariosus* attains a basal diameter of 13–15 mm it seems quite safe from *Thais* predation. The optimal growth rates found at the lower levels (Fig. 13) suggest that a *B. cariosus* which settles in May or June may have reached this refuge in size by the end of the calendar year. Certainly most *B. cariosus* that escape predation attain this size refuge by the end of their second year.

The escape in growth of *Balanus cariosus* involves the time, energy, and risk parameters affecting *Thais* (Emlen 1966, Connell 1970). Unsuccessful attacks by each of the three species of *Thais* on large *B. cariosus* have been observed, and misplaced or incomplete drill marks are commonly seen on large *B. cariosus*. The actual size at which an individual *B. cariosus* becomes a poor risk for a *Thais* to attack depends on its level in the intertidal and the time of year of its settlement, that is, (1) the ability of *Thais* to drill and consume a barnacle is obviously related to submergence time, and (2) *Thais emarginata* and *T. canaliculata* tend to be relatively inactive during the winter months, and at this time *T. lamellosa* ceases feeding and forms breeding aggregations. Thus, if the *B. cariosus* settle in the fall (see Fig.

TABLE 17. The effect of *Thais* predation on barnacle density by the end of each summer with *Acmaea* present at normal densities (Table 5) but with *Pisaster* absent. Significance levels are for one-tailed tests. In addition to the comparison of the means, interactions between treatment, year, and intertidal height were evaluated, but none was found to be statistically significant (all $p > 0.05$)

Barnacle species	Site	Tide height (feet)	Year	Mean number of barnacles/100cm² *Thais* present (roof)	Mean number of barnacles/100cm² *Thais* absent (limpet cage)	Type of analysis	Significance level
Balanus glandula	Shi Shi	+2.7−+5.4	1967–1969	7.9	102	Wilcoxon Signed rank	$P<0.005$
	Portage Head	+2.5−+5.0	1967–1969	4.3	76	3–Way Anova	$P<0.001$
	Waadah Island	+4.6−+7.7	1968–1969	0.8	54	3–Way Anova	$P<0.001$
	Eagle Point	0.0−+3.5	1967–1968	4.2	61	3–Way Anova	$P<0.001$
	Colin's Cove	+0.5−+3.0	1968	0	43	2–Way Anova	$0.005>P>0.001$
	Turn Rock	−1.0−+4.5	1968	0.5	1.9	2–Way Anova	$P>0.25$
Balanus cariosus	Waadah Island	+4.6−+7.7	1968–1969	0.1	3.0	3–Way Anova	$0.005>P>0.001$
	Eagle Point	0.0−+3.5	1967–1968	2.1	19	3–Way Anova	$P<0.001$
	Colin's Cove	+0.5−+3.0	1968	0	0.8	2–Way Anova	$P>0.25$
	Turn Rock	−1.0−+4.2	1968	0.8	0.7	2–Way Anova	$P>0.25$
Chthamalus dalli	Shi Shi	+2.7−+5.4	1967–1969	312	529	3–Way Anova	$0.05>P>0.025$
	Portage Head	+2.5−+5.0	1967–1969	467	795	Wilcoxon Signed rank	$P<0.005$
	Waadah Isalnd	+4.6−+7.7	1968–1969	29	57	3–Way Anova	$0.25>P>0.10$
	Eagle Point	0.0−+3.5	1967–1968	4.9	25	3–Way Anova	$0.01>P>0.005$
	Colin's Cove	+0.5−+3.0	1968	0	21	2–Way Anova	$0.025>P>0.01$
	Turn Rock	−1.0−+4.2	1968	0.9	1.0	2–Way Anova	$0.25>P>0.10$

11—total exclusion and Fig. 12—total exclusion and limpet cage), they are subjected to reduced *Thais* pressure and have a good chance of attaining a refuge in size by the end of the following summer.

Mytilus californianus has a similar refuge in growth from *Thais*. The actual safe size depends on many factors, particularly the level in the intertidal and the size of the local *Thais*. No detailed study of this was made, but when two protective cages at about the 4-ft level in the *Pisaster* removal areas at Shi Shi were removed late in the second summer after their placement, the newly exposed *Mytilus* were subjected to severe *Thais* predation. No *Mytilus* under 3 cm in length survived, and the *Thais* did kill a number which were over 3 cm. In the San Juan Islands the larger *Thais* appear to be able to kill much larger *Mytilus*. A rock in a *Pisaster* removal area at Turn Rock, heavily covered with both *Mytilus californianus* and *M. edulis*, including individuals at least as large as 8 cm, was denuded in 1967. Many large valves (≧8 cm) were found with drill holes. Thus the size refuge from *Thais* is quite variable, and when *Mytilus* do escape *Thais*, they do so initially by numerically swamping the local *Thais* populations.

Effect of Pisaster *predation on barnacles and mussels*

The importance of *Pisaster ochraceus* to the outer coast community has been stressed by Paine (1966, 1969); yet it is apparent from Tables 15, 16, and 17 that even by late August the *Thais* had killed many of the barnacles at each site. It is of interest, then, to test the effect of *Pisaster* beyond that of limpets and *Thais*. The experimental design allowed the effect of *Pisaster* to be assessed by comparing the number of barnacles remaining in a 100-cm² area under a "roof," which protects the barnacles from *Pisaster*, with the number of barnacles remaining on an adjacent 100-cm² control plot (Table 18). The analyses for Table 18 are similar to those for limpet and *Thais* effects.

On the outer coast the *Pisaster* effect is variable ($P \leq 0.001$ to $P = 0.35$). To a certain extent this is artifactual, because the terminal data each year were collected in late August, while all the predators remain active until at least November. But the most important explanation is related to the foraging behavior of *Pisaster*. Paine (1969) has observed that *Pisaster* tends to bypass *Balanus glandula* in search of the preferred *Mytilus californianus*. It is only late

PAUL K. DAYTON

TABLE 18. The effect of *Pisaster* predation on barnacle densities by the end of each summer in addition to *Acmaea* disturbance and *Thais* predation. Significance levels are for one-tailed tests. In addition to the comparison of the means, interactions between treatment, year, and intertidal height were evaluated, but none was found to be statistically significant (all $p > 0.05$)

Barnacle species	Site	Tide height (feet)	Year	Mean number of barnacles/100cm^2 *Pisaster* present (control)	Mean number of barnacles/100cm^2 *Pisaster* absent (roof)	Type of analysis	Significance level
Balanus glandula	Shi Shi	$+4.2 - +5.4$	1967–1969	3.1	10.1	Randomization	$P = 0.22$
	Portage Head	$+3.0 - +4.0$	1967–1969	0	14	3–Way Anova	$P < 0.001$
	Waadah Island	$+4.6 - +7.7$	1968–1969	4.2	0.8	3–Way Anova	$0.10 > P > 0.05$
	Colin's Cove	$0.0 - +3.7$	1968–1969	0	0	3–Way Anova	$P > 0.25$
Balanus cariosus	Waadah Island	$+4.6 - +7.7$	1968–1969	1.2	0.1	3–Way Anova	$0.25 > P > 0.10$
	Colin's Cove	$0.0 - +3.7$	1968–1969	0	0	All zero	—
Chthamalus dalli	Shi Shi	$+4.2 - +5.4$	1967–1969	141	245	Randomization	$P > 0.50$
	Portage Head	$+3.0 - +4.0$	1967–1969	5.1	546	Randomization	$P = 0.016$
	Waadah Island	$+4.6 - +7.7$	1968–1969	34	29	Randomization	$0.36 > P > 0.34$
	Colin's Cove	$0.0 - +3.7$	1968–1969	0	0.6	3–Way Anova	$P > 0.25$

in the summer or in the absence of the preferred prey that *Pisaster* will begin to consume appreciable quantities of *Balanus glandula*. Therefore, if a *Pisaster* had foraged over a control area in late August, before the last census, the area would be devoid of suitable *Pisaster* prey, but if it had not, a number of barnacles might be surviving.

With the exception of one insignificant difference in *Chthamalus* populations at Colin's Cove, no analysis of *Pisaster* effect was possible in the San Juan Islands, because 100% of all species of barnacles in the experimental areas were killed by the normal limpet and *Thais* activity before the late August census. The fact that there were no interaction effects (Table 18) suggests that the *Pisaster* pressure measured was essentially the same at all levels in all years.

Paine (1969) has discussed the implications of the fact that by consuming *Mytilus californianus*, *Pisaster* procures space for *Endocladia muricata*, the most important settling resource of the *Mytilus* larvae. In the absence of *Pisaster, Endocladia* is overgrown and eliminated from the community by *Mytilus*. A substantial proportion of the diet of *Pisaster* includes limpets (Menge 1970, Paine, *personal communication*). Therefore the theme of the indirect effect of *Pisaster* can be elaborated somewhat by the demonstration that limpets can severely reduce the recruitment of *Endocladia* (see Table 11). Thus, besides procuring space for *Endocladia* by eating *Mytilus*, *Pisaster* increases the chance of *Endocladia* recruitment by preying on limpets and reducing their grazing pressure. The implications are that by using limpets as a secondarily preferred prey, *Pisaster* in-

directly has a positive effect on the recruitment of its major prey.

Effect in absence of Thais.—Paine (1966) has claimed that even though Mukkaw Bay *Thais* may actually kill more barnacles than do *Pisaster*, the *Thais* effect is less important than that of *Pisaster*. We have not seen, however, an important *Pisaster* effect in addition to that of *Thais* and limpets in the experiments of this study. This appropriate controlled experiment, of measuring the *Pisaster* effect completely independently of the *Thais* effect, has not been done, as it would necessitate the removal of *Thais* while maintaining the natural *Pisaster* predation, and this would involve a prohibitive amount of time. To a limited extent, however, this experiment was done naturally by an unusually cold period in December 1968 and January 1969 coinciding with very low night tides, which resulted in the death of many *Thais* (Table 9).

An immediate result of this population crash of *Thais* on the outer coast was an increased survival of the 1969 spring *Balanus glandula* set, many of which became fertile by September 1969, and apparently succeeded in releasing into the plankton an unusually large number of cyprids in the fall of 1969. The late autumn plankton conditions are certainly very different from the conditions prevailing in the spring and summer, and normally the winter *Balanus glandula* settlement and metamorphosis is very rarely seen in my experimental areas. However, the survival of the 1969 winter set seemed to be extremely high, and in March 1970 neither *Thais* nor *Pisaster* had eaten much of the heavy set. By late July 1970 *Pisaster* was consuming large numbers of

Balanus, but by this time many of the barnacles had reproduced, and it appeared possible that there would be another successful set in the fall of 1970. In this case, however, most of the barnacles settling within the Pisaster levels will be consumed before reproduction. The general space allocation pattern, though immediately influenced by the cold kill of Thais will have no long-term effect, due to the activities of Pisaster, which is capable of consuming all sizes of barnacles within its foraging range.

Additional ramifications in the upper intertidal above the level of Pisaster predation could be predicted to result from the Thais cold kill. Here the predicted heavy set of Balanus glandula in the fall of 1970 should have survived and dominated much of the primary space. Thus, by the spring, 1971, there should have been a reduction in the number of Chthamalus and algae utilizing primary space. By February 1971 these predictions were verified at Mukkaw Bay (R. T. Paine, personal communication). In addition to the Chthamalus and algae which suffered in the space competition with B. glandula, Paine reports that the B. glandula have forced even the limpets off the primary space and that intraspecific competition among the B. glandula has resulted in severe hummocking and exfoliation of the barnacles.

The implications to patterns of space utilization of this cold kill are both more delayed and more important in the San Juan Islands. Here the immediate response of Balanus glandula is somewhat buffered, as there are additional predators, especially Leptasterias (Menge 1970, and personal observation), Onchidoris bilamellata (personal observation) and to a certain extent, Searlesia dira (Louda 1968, and personal observation), which may respond to an increase in B. glandula by increasing their predation on it. On the other hand, B. cariosus, the largest, most rapidly growing and hence competitively effective intertidal barnacle, is significantly influenced. The usual strategy of B. cariosus is to swamp Thais with a patchy summer settlement. Some B. cariosus also appear to release a late summer brood of cyprids which results in a light autumn set. Under normal conditions (here 1966–68) the autumn settlement is insignificant and the abundant Thais populations are capable of eliminating most of the B. cariosus which escape the limpets. With the Thais populations drastically reduced in the summer of 1969 (Table 9) many of the individuals of the spring and fall set survived in 1969 and released a very large number of cyprids in early 1970; the spring 1970 B. cariosus set was extremely large. In July 1970 B. cariosus covered 80–100% (mean: 87%; SD $= 5.1\%$; $N = 20$) of all the available surface between +1-ft and +3-ft levels at Eagle Point. The density of Thais canaliculata was still low (Table 9). It is clear that many of the B. cariosus will escape Thais predation during the summer of 1970; further, since many of the lower intertidal B. cariosus, which usually do not survive the summer, had well developed gonads in late July 1970 (S. A. Woodin, personal communication), there should have been a successful autumn set in 1970. The result of the cold kill will be a prolonged, in terms of years, occupancy of space, an event predictable from knowledge of the escape in size of B. cariosus from molluscan carnivores, its superior competitive ability, and the relatively low density of Pisaster.

Effects of other predators

The cages which have been analyzed as representing Thais exclusion effects actually also represent the exclusion of Leptasterias hexactis, a small carnivorous asteroid characterized by a generalized diet. Menge (1970) has found that Leptasterias derives most of its energy from various molluscan herbivores, but that when Balanus glandula is available, it consumes many of these small barnacles. However, Menge has also demonstrated that Leptasterias is very susceptible to desiccation, which limits its foraging effectiveness to low areas in the intertidal. Nevertheless, there is an overlap between the Leptasterias foraging range and the cage experiments at Eagle Point and Colin's Cove. At these sites it is possible that Leptasterias may have contributed to the barnacle mortality in the dog dishes and control plots, and thus may have been mistakenly interpreted as part of the Thais effect. But the relatively low densities of Leptasterias at these sites (Menge 1970) are probably not sufficient to alter appreciably the conclusions.

Onchidoris bilamellata, a dorid nudibranch, is another potentially important barnacle predator in this community. It is present in the winter months, from October to March. The cages were not entirely effective in excluding Onchidoris, but those that entered were quickly removed. Cages containing Onchidoris egg masses in association with dead barnacles were removed from the evaluation. Onchidoris is usually found in protected bays, on pilings, and on floats, where it has a better supply of Balanus glandula and B. crenatus. Onchidoris were never seen in controls or dog dishes and only very rarely along the rocky intertidal.

Colonization in the high intertidal

The most common means of experimentally denuding an intertidal substratum are scraping, burning, and saturating with formalin. None of these methods is absolutely certain to kill all of the organisms, and all of them leave various organic residues

which may differentially affect bacterial growth and diatom recruitment and growth. To evaluate the effects of leaving organic and sometimes living residues, each month for a year virgin rock surfaces were exposed by blasting with dynamite, and the trends compared with those characterizing burned areas, at Portage Head.

A certain amount of leaching or weathering is necessary before any substantial colonization occurs (see also Moore 1938). All the rocks in the middle intertidal area blasted between August 1967 and March 1968 stayed completely bare of sessile organisms until August 1968, when a heavy *Chthamalus dalli* settlement almost covered them. Many *Littorina* had come onto the rocks soon after blasting and may have been responsible for the fact that a heavy diatom film never developed (see also Castenholz 1961). No limpets or *Thais* were seen on the blasted rocks during the first summer. One rock blasted in July, 1967, split along a crack where seawater had already penetrated (as evidenced by the presence in the crack of serpulid worm tubes). This rock was very quickly covered with *Balanus glandula* and *Chthamalus dalli* by August 1967.

Those rocks blasted between April and August 1968 remained bare of sessile organisms until April 1969, when *Balanus glandula* began to appear. In all cases, between 6 months and a year elapsed before there was appreciable colonization on any of the rocks. During and after colonization small pieces of rock flaked off, creating clear patches in the heavy barnacle cover and allowing further colonization to be observed. Approximately 12–18 months after the blast, the algae *Porphyra* spp. and *Gigartina papillata* as well as new *Chthamalus* and *Balanus glandula* appeared. By September 1969 *Gigartina* covered 45–60% of the blasted surfaces, and *Acmaea paradigitalis*, *A. pelta*, *A. digitalis*, and *Thais emarginata* had appeared and had begun to influence the barnacle population.

Of the more common means of denuding an intertidal surface, burning is probably the most satisfactory, as it is much more likely to kill the algal sporelings and gametophytes than is scraping, and it leaves less residue than does soaking in formalin. The surfaces of three large rocks were burned in the upper intertidal at Portage Head in November and December 1966 following a soaking with a mixture of white gas and diesel oil. A careful study of the basal systems of the coralline algae *Gigartina papillata* and *Ralfsia* spp. showed that it was not until after the third burn that all of the plants had been killed. Despite the fact that this was done in the winter and *Littorina* moved in, a very heavy diatom film developed over these rocks after each burning. This strongly contrasts with the situation on the blasted

rocks, which also had *Littorina*, but which had no growth of any sort for many months after blasting. By February 1967 the burned rocks had a very heavy cover of *Porphyra*, which lasted until late March, when the tides moved into daylight hours; at this time most of the *Porphyra* was killed by desiccation. *Balanus glandula* and *Chthamalus dalli* settled on the burned rocks during the summer of 1967, again in contrast to the blasted rocks, which had no barnacle settlement the first summer. As *Porphyra* died out, scattered individuals of *Ulva* spp., *Enteromorpha* spp., *Odonthalia floccosa*, *Halosaccion glandiforme*, and *Polysiphonia hendryii* appeared in 1967. In 1968 most of the same red algae individuals were recognized by their position. In addition, there were numerous cases of *Gigartina papillata* fronds growing up from what appeared to be an extensive rhizoidal growth of the holdfast. By 1969, *Gigartina* had taken over 65% of the surface area and 85% of the canopy, and all of the other algal species were gone. It was not until August 1969 that a few isolated individuals of *Fucus distichus* and *Endocladia muricata* appeared. By early 1970, *Fucus* seemed to be growing through the *Gigartina* canopy. It will certainly be at least 4 years after the burning before *Fucus* regains its original dominance (70%) of the canopy cover.

Patchiness and interactions among the dominant high intertidal species on the outer coast

Much of the flat upper intertidal community at Shi Shi and Portage Head is dominated by either *Mytilus californianus* clumps or *Fucus distichus* or *Gigartina papillata* canopy; there is often very little apparent overlap between these patches (Table 19). In order to test whether there were competitive interactions involved in these apparently nonoverlapping distribution patterns, patches of each species were cleared at Portage Head and Shi Shi in the spring of 1967. The five 0.5- to 1.5-m² *Mytilus*-removed patches all developed essentially as the burning experiment, except that the *Gigartina* appeared during the same summer that the *Mytilus* were removed. By July 1968 these five patches were almost completely dominated by *Gigartina*, which has persisted through 1969. By March 1970 a few *Fucus* individuals had appeared. The failure of *Mytilus* to reoccupy the area is best explained by their failure to recruit in sufficient numbers to swamp the predation of the resident *Thais emarginata*.

Fucus individuals were manually removed in the spring of 1967 from seven patches varying from 0.5 to 2.5 m². The encrusting holdfast system of *Gigartina* was observed to cover much of the substratum under the heavy *Fucus* canopy. The individual *Gigartina* plants had few fronds, but removal of the *Fucus* canopy initiated a large increase in the number of

TABLE 19. Summary of samples of conspicuous organisms in distinct patches of *Mytilus californianus*, *Gigartina papillata*, and *Fucus distichus* in the flat upper (+6 ft to 8 ft) intertidal at Portage Head. Variance is presented as 95% confidence limits. The total percentage cover sums to over 100%, as *Fucus* frequently covers *Mytilus* and *Gigartina*

Species	*Mytilus* patches (N = 17)		*Gigartina* patches (N = 10)		*Fucus* patches (N = 5)	
	Mean % cover	Density[a]	Mean % cover	Density[a]	Mean % cover	Density[a]
Mytilus californianus	100	Not taken	0	0	0	0
Fucus distichus	5.0±7.1	0.1±0.3	12.2±9.3	1.7±0.7	100	6.0±2.6
Gigartina papillata	0	0	100	11.8±0.9	15.2±7.0	2.4±2.0

[a]Number /0.062 m².

fronds. A few of the *Fucus* grew back by October 1967; these individuals were probably from holdfasts which had not been properly removed at the initial clearing. By the end of 1969, *Fucus* had regained about 50% of the canopy in each of the clearings. Experimental removals of *Gigartina* were not effective.

The following pattern of succession for flat upper intertidal surfaces emerges from the blasting experiments, the burning experiments, and the selective removal experiments. *Gigartina* is the first persistent perennial to appear, and it seems to dominate the canopy for at least one summer. In the second season *Fucus* appears but does not completely dominate the canopy for at least 2 years, and probably much longer. Even when *Fucus* does overgrow *Gigartina* and dominate the canopy, the *Gigartina* persists below the *Fucus* as an encrusting rhizoidal system which tends to respond to a break in the *Fucus* canopy with a rapid growth of fronds. At this tidal level (+6 ft to +8 ft) in the protected outer coast habitats, it probably takes many years for a *Mytilus californianus* population to become established. Once *Mytilus* does become established and reaches a refuge in size from *Thais* predation, the patch has a refuge in space from *Pisaster* predation and may survive for a great many years, until the individuals are killed by such physical phenomena as log damage or unusual cold.

DISCUSSION

Sessile marine organisms have in common two resource pools: (1) the primary space, the substratum on which they attach, and (2) the aquatic milieu around them, which is the source of their physical and organic nutrients. There are two corresponding levels of interaction among these organisms in the competition for a potentially limiting resource; they can compete for the primary space and (or) they can grow above and then over their competitors and compete for the physical resources and organic nutrients. Adaptations to both of these levels of competition can be seen in intertidal organisms. Algae and barnacles compete for primary space. *Mytilus* recruitment, on the other hand,

usually requires a secondary space in the form of filamentous algae or barnacles for the initial larval settlement; then its byssal threads become attached to the primary substratum. Thus the *Mytilus* essentially concede the initial competition for primary space, in fact, needing the secondary space for their larval recruitment, and then dominate the competition in the space above the primary substratum. Eventually the *Mytilus* dominate the primary substratum also, as the underlying barnacles either starve or are smothered by sedimentation.

In each study area the barnacle-mussel association is characterized by one potential dominant capable of monopolizing the resource and completely excluding the other species; the identification and evaluation of the effects of the disturbance factors preventing this monopolization are crucial to any functional understanding of the organization of the community.

Three levels of biological disturbance which predictably affect the monopolization of space by the dominant sessile species include (1) grazing by limpets; (2) predation by carnivorous gastropods, particularly species of *Thais*; and (3) predation by the asteroid *Pisaster ochraceus*. At their normal densities, various species of limpets severely restrict the recruitment and survival of almost all the sessile species in the community. However, individuals in all the barnacle species and most of the algae may eventually attain a size at which they are immune to the bulldozing effect and the grazing of the limpets. Nevertheless, after 4 years, in none of the areas cleared of algae but which had normal limpet densities has the algal community returned to its natural state. In contrast to this slow natural succession rate, there was an algal bloom in the areas where limpets had been removed. This usually resulted in a cover of "climax" algal species which within 2 years equaled and usually far surpassed the cover in the undisturbed control areas. A similar algal response to the release from limpet pressure has been observed in Europe (Jones 1948, Southward 1956).

The grazing activity of the limpets significantly reduced the recruitment of all the barnacles in the

presence of *Thais*, but the direct detrimental effects of the limpet grazing were much reduced on the smaller, competitively inferior *Chthamalus dalli*. By the end of the summer season, the *Chthamalus* population in the absence of *Thais* was indirectly but significantly increased through the limpet interference with the competitively superior *Balanus glandula* and *B. cariosus*.

The effects of predators on their prey are detrimental to the prey populations, but the question that concerns us here is how the various predators affect the community through the medium of the common space resource. Paine (1966) has argued that by killing large numbers of barnacles and small *Mytilus* at one time, the Mukkaw Bay *Pisaster* are more important providers of primary space than are *Thais*, which must kill these prey separately; he further points out that the *Pisaster* dislodge the dead barnacles, thereby immediately freeing the space, while the plates of the barnacles killed by *Thais* may occupy space for a number of weeks. However, this work has shown that in 1967–69 the continued limpet disturbance and the predation of *Thais* were usually sufficient to eliminate all the *Balanus glandula* and *B. cariosus* from the experimental areas. There was rarely a significant effect of *Pisaster* in this regard beyond the observed *Thais* effect. What contributions to community structure, then, are made by these two levels of predation?

Part of the answer is found in the growth refuge phenomenon of the prey. In both the outer coast system and the San Juan Islands, those species capable of monopolizing the space, *Mytilus californianus* and *B. cariosus*, respectively, have an escape in growth from *Thais* predation. For example, there were two 3- by 4-m patches in the Shi Shi *Pisaster* removal area where the *Mytilus* recruitment was sufficiently heavy to swamp the ability of *Thais* to kill them, and many of the *Mytilus* reached the length of approximately 3 cm necessary to escape this source of mortality. Likewise in the San Juan Islands, although it did not happen in my experimental areas, the extremely patchy settlement pattern of *Balanus cariosus* sometimes overwhelms the ability of the local *Thais* to kill them, and a few escape (personal observation). Thus, given enough time, one would expect all the space in each of the areas to be monopolized by one of these two long-lived, competitively superior species with the other species being eliminated or forced to subsist on secondary space. The reason that such monopolies fail to develop on the outer coast is that there is very rarely an escape in growth from *Pisaster*. In the study areas of the San Juan Islands, however, the *Pisaster* densities are very much lower, and desiccation apparently prevents *Pisaster* from foraging very high in the intertidal. In the lower areas

(below +2 ft) *Pisaster* eventually kills the *Balanus cariosus* that have escaped the limpet and *Thais* disturbance. Frequently a sharp line of large *B. cariosus* demarcates the upper limit of *Pisaster* predation, and in areas where there are few *Pisaster*, this line may be much lower (Mauzey 1967, Menge 1970, and personal observation).

In the San Juan Islands in the intertidal area immediately above the *Pisaster* foraging levels, *Balanus cariosus* occasionally escapes the limpets and *Thais* and would be expected eventually to occupy 100% of the space. The probability of log damage (Fig. 3) suggests the hypothesis that the frequency of logs striking an area is as high as or higher than the rate of the escape of *B. cariosus*. A test of this hypothesis would be to examine areas where logs do little or no damage; in such areas one would expect to find a heavy cover of escaped *B. cariosus*. This is indeed seen to be the case in cracks which are not accessible to logs. The best test of the hypothesis is Turn Rock, which was never struck by a log during the course of this study and, as expected, has 100% cover of *B. cariosus* above the level of *Pisaster* predation.

Competition, disturbance, and community organization

Proof that the co-occurring populations do form a community is prerequisite to any study of community structure. This community is open ended since much of the primary productivity and decomposition occur elsewhere; however, all communities are open ended in an energetic sense. Many of the species have planktonic larvae, but the relative abundances of most of the reproducing populations are most critically influenced by interactions among the component intertidal species rather than by plankton phenomena. Most of the changes in populations in this community, therefore, occur as predictable responses to other populations in the intertidal community.

This community permits experimental evaluation of the relative importance of competition and predation to the community structure. Much of community theory is classically based on competitive processes (Elton 1946, Elton and Miller 1954, Whittaker 1965, 1969, McNaughton and Wolf 1970). The identification and appraisal of the relative degrees of dominance has been a continuing descriptive problem (Whittaker 1965); some of the measures of a species' importance summarized by McNaughton and Wolf (1970) are (1) cover (2) biomass, and (3) relative abundance; Whittaker (1965) also suggests (4) productivity. With the exception of cover, none of these criteria directly measures competitive dominance of a potentially limiting

resource. Most of the above criteria of "important species" have been considered and found to be of limited or conflicting application by Fager (1968) for a simple benthic marine community. McNaughton and Wolf (1970) proposed the following generalizations from the communities they summarized: (1) dominance was characteristic of the most abundant species; (2) dominant species had broader niches than subordinate species; (3) species are added to the system by compression of niches or expansion of "K," or both; and (4) community dominance is minimum on the most equitable sites.

In this intertidal community on the outer coast and in the San Juan Islands, where *Mytilus californianus* and *Balanus cariosus*, respectively, are the competitive dominants in the community, none of McNaughton and Wolf's generalizations seem to apply. For example, considering (1), the competitive dominants are numerically much less abundant than any number of fugitive species in this intertidal community. Furthermore, the number and distribution of the competitive dominants may be suppressed by disturbance to the point that at times they are even absent. In regard to (2), and considering "the breadth of niche" in the more general sense of Levins (1968), referring here to broadness of physical tolerances as indicated by vertical distribution in the intertidal, we find the competitively inferior *Balanus glandula* and *Chthamalus dalli* having a broader tolerance range, as they survive higher in the intertidal zone than do the dominant *Mytilus* and *Balanus cariosus*. Generalization (3) of McNaughton and Wolf can be evaluated only by examining the relative success of invasions of sessile species into rocky intertidal communities. The best documented invasion was by *Elminius modestus* into the European intertidal; *Elminius modestus* is an "r" species (Crisp 1964). In considering the exposed point of Tatoosh Island as most equitable (referring to the least amount of physiological stress), generalization (4) is contradicted because Tatoosh Island has the maximum dominance, as *Mytilus californianus* monopolizes most of the space.

What are the general implications of the fact that the experimentally derived conclusions of this study conflict with the carefully drawn conclusions of McNaughton and Wolf? The intertidal community may represent a special case, but since controlled experiments have been done in few other communities, it is too early to evaluate this possibility. Another explanation is that the descriptive criteria used to evaluate dominance in the studies discussed by McNaughton and Wolf are not sufficient to characterize functional or competitive dominance. In all of the communities considered by McNaughton and Wolf, the data were collected and analyzed with the assumption that the respective communities were structured solely around competitive niche differentiation and dominance. Another explanation for the differences between this study and the conclusions of McNaugton and Wolf might be that all the earlier community studies which they summarized were analyses of one trophic level, and it is risky to draw generalizations about community organization from one trophic level.

While competition seems to play a rather minor role in structuring this intertidal community, it is of interest to consider the circumstances in which competition does seem to have a significant role in influencing patterns of distribution and survival. The only species considered which is regularly exposed to strong space competition is *Chthamalus dalli*. When two of the three levels of disturbance (*Pisaster* and either *Thais* or the limpets) are removed, the *Chthamalus* population is significantly enhanced by the activities of either of the remaining disturbances (*Thais* or limpets), which exert a stronger negative effect against *Balanus*. However, this situation is artificial, as the community is naturally exposed to both the limpet and the *Thais* levels of disturbance and is usually exposed to *Pisaster* and logs. Thus, the only time that competition is naturally very important is when the dominants have attained a size refuge from limpets and *Thais* and have not been killed by *Pisaster* or logs. This has been seen to occur naturally above the level of *Pisaster* predation in areas not struck by logs, such as Turn Rock, and after the cold-induced *Thais* die-off in the winter of 1968.

The major conclusion of the present study is that although there are clear competitive dominants, this intertidal community is characterized by continuous physical and biological disturbance including the effects of carnivores and herbivores, an abundance of the potentially limiting spatial resource, and a large number of species which utilize this same resource.

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ERRATUM

The following references were omitted from the end of the article "Succession after fire in the chaparral of southern California" by Ted L. Hanes, appearing in Ecological Monographs 41:27–52, Winter 1971:

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