



Experimental Evaluation of Ecological Dominance in a Rocky Intertidal Algal Community

Paul K. Dayton

Ecological Monographs, Vol. 45, No. 2. (Spring, 1975), pp. 137-159.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9615%28197521%2945%3A2%3C137%3AEEOEDI%3E2.0.CO%3B2-Y>

Ecological Monographs is currently published by The Ecological Society of America.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

EXPERIMENTAL EVALUATION OF ECOLOGICAL DOMINANCE IN A ROCKY INTERTIDAL ALGAL COMMUNITY¹

PAUL K. DAYTON

Scripps Institution of Oceanography, P. O. Box 1529, La Jolla, California 92037 USA

Abstract. The mechanisms by which various species exert influence disproportionate to their abundance or mass on the structure of a lower intertidal algal community were evaluated experimentally. These functional roles were evaluated by various controlled manipulations at seven stations along the Washington coastline ranked according to an exposure/desiccation gradient. The algae were divided into three categories: canopy species, which grow above the other species and apparently succeed in competitively dominating the light resources as demonstrated by algal blooms following their removal; obligate understory species, which die after the canopy species are removed; and fugitive species, which are quick to colonize new space.

Ecological dominance was exerted in areas of moderate wave exposure by *Hedophyllum sessile*, which competitively displaces a large number of fugitive algal species and which furnishes a protected habitat for many obligate understory algae that die or defoliate after the removal of *Hedophyllum*. *Hedophyllum* loses this dominance in the most exposed areas, although such sites apparently represent its physiologically optimal habitat, because in these areas it is out-competed by *Laminaria setchellii* and *Lessoniopsis littoralis*. In these wave exposed habitats *Lessoniopsis* was demonstrated to exert a strong competitive dominance over all the other species in the association.

The molluscan herbivores were not observed to express any measurable effects on the recruitment or survival of the algae. However, the echinoid *Strongylocentrotus purpuratus* often overexploits its prey and has a pronounced influence on most of the algal species. In this respect *S. purpuratus* enjoys an important community role singular among the many herbivores. Similarly, *Pycnopodia helianthoides* and *Anthopleura xanthogrammica* are disproportionately important carnivores, because their predation on *Strongylocentrotus*, clearing large areas of urchins, results in patches in which algal succession follows.

The rate of algal succession following removal of the dominant algal species or of *Strongylocentrotus* is proportional to the degree of wave exposure. The *Hedophyllum* canopy recovery at the Eagle Point area of San Juan Island, a site exposed to relatively little wave action and thus high levels of desiccation, was relatively slow, with only 10%-26% cover reestablished after 3 yr. In contrast, *Hedophyllum* canopy developed up to 66% cover in only 1 yr in the exposed area of Waadah Island; it then quickly lost its dominance to *Laminaria* and *Lessoniopsis*. Algal succession in deeper Portage Head tidepools was found to be relatively slow with no clear dominance expressed after 5 yr.

Key words: Actinians; algae; asteroid; community organization; competition; dominance; echinoid; grazing; intertidal; obligate relationships; predation; succession.

INTRODUCTION

There are two basically different approaches to the definition of the importance of particular species in the maintenance of the structure of a community. One approach emphasizes a descriptive, usually numerical, definition of importance based on sampling studies designed to measure the relative abundances, biomass, or productivity of the species in a community (Whittaker 1965, McNaughton 1968); such studies yield various measures of diversity with the quantitatively important species referred to as "dominant." A second approach to the study of community organization emphasizes a functional definition of disproportionately important species based on the relative impact these species can exert

on other species in the community (Paine 1969a, Dayton 1971). The latter approach is similar to that of Clements (1916, 1920, 1936) and Weaver and Clements (1938), who considered dominant those plant species exerting an important, competitive control on the abundance and distribution of other species in the community.

The former descriptive concept of dominance emphasizing such measures as diversity, rank order of abundance, or biomass often defines very different suites of important species than do the latter functional concepts (Dayton 1972, Paine 1974). This paper is restricted to a mechanistic approach to community analysis and has the general objective of evaluating the mechanisms by which functional importance is expressed in a simple marine community.

Rocky intertidal shores in temperate latitudes

¹ Manuscript received 2 June 1973; accepted 19 April 1974.

characteristically have an upper barnacle-mussel zone and a lower algal zone (Stephenson and Stephenson 1972, Connell 1972). The absolute levels of these zones vary within and between sites because of the factors influencing desiccation. The amount of splash, the degree of inclination, and the alignment of the substratum to local wave action, as well as such factors as local wind patterns and north-south aspect of the substratum, are obviously important to the general facies of the local zonation, which will vary accordingly at a given location. Many of the mechanisms structuring the barnacle-mussel zone (Dayton 1971, 1973a,b) are elaborated further here; some of the mechanisms by which functionally important species exert their influences in the lower intertidal algal association are described. Specifically, I describe and demonstrate experimentally (1) the positive and negative contributions of the competitively important algal species to other populations, (2) the effects of the disproportionately important herbivore, (3) the roles of the key carnivores in regulating the distribution and abundance of the herbivore populations, and (4) the changing character of the ecological dominance expressed by these species in areas representing a gradient in wave exposure, a factor known to be a critically important determinant of the intertidal community composition within a given zone (Lewis 1968). As in my previous papers (Dayton 1971, Dayton et al. 1974), my method of dissecting a community so as to study its functional components is to make a realistic perturbation and manipulate the subsequent successional events. Since populations evolve within the context of their entire community, insights into such functional relationships should result in a better understanding of important evolutionary processes.

METHODS AND STUDY AREAS

The study areas, detailed previously (Dayton 1971), represent a gradient of wave exposures from the very exposed Tatoosh and Waadah Islands to very protected shores on San Juan Island. Tatoosh Island (48° 24' N, 124° 44' W), off the northeast tip of the Olympic Peninsula, is completely exposed to the oceanic swells and wave action of the eastern Pacific Ocean. The study site was on the northeast point of the island where the upper levels of the intertidal zone are covered with an extremely dense bed of the mussel, *Mytilus californianus* and the palm alga, *Postelsia palmaeformis* (Dayton 1973a). The lower algal zone is dominated by *Lessoniopsis littoralis*. In progressively less exposed areas of Tatoosh Island there are also heavy growths of *Alaria marginata*, *Laminaria setchellii*, and *Hedophyllum sessile*.

Waadah Island (48° 23' N, 124° 36' W) is slightly less exposed to wave shock than is Tatoosh Island. Experiments were done on exposed northern fingers

of the island ("Postelsia Point" of Rigg and Miller 1949), which offer small exposure gradients and substrata angles of incidence ranging from flat to slight overhangs. Three study areas were chosen at Waadah Island in decreasing order of exposure to wave shock: (1) Waadah Island Flat area, (2) Waadah Island Ledge, and (3) Waadah Island 65° Slope area. The algal association was described by Rigg and Miller (1949). Tatoosh and Waadah Islands are particularly valuable research areas because the U. S. Coast Guard protects them from human disturbance. Both represent the typical exposed outer coast communities described by Ricketts et al. (1968).

Shallow offshore water and reefs offer varying degrees of protection from the power of the oceanic swells for three other coastal sites typical of the protected outer coast habitats of Ricketts et al. (1968). Shi Shi reef (48° 16' N, 124° 41' W), Mukkaw Bay (48° 17' N, 124° 40' W), and Portage Head (48° 17' N, 124° 41' W) were chosen as study sites representing decreasing exposure to wave shock and being relatively inaccessible to destructive human interference. A nearby campground and its popularity as a grammar school study site rendered much of my experimental work impossible at Mukkaw Bay.

The algal association of the protected outer coast sites is characterized by very patchy distributions of *Hedophyllum sessile*, various species of red algae, particularly species of *Gigartina*, *Iridaea*, *Microcladia*, *Porphyra*, *Prionitis*, *Polysiphonia*, *Rhodomenia*, and *Ptilota*, and such species of green algae as *Ulva*, *Enteromorpha*, *Codium*, *Spongomorpha*, and *Cladophora*. The offshore or more exposed areas frequently have large populations of *Laminaria setchellii*, and the slightly more protected surge channels and tidepools have scattered individuals of *Egregia menziesii*. The most protected outer coast areas are characterized by heavy covers of the angiosperms, *Phyllospadix scouleri* and *P. torreyi*.

Three study sites on San Juan Island, Washington, were also selected to provide a gradient of exposures to wave shock. Although the San Juan Archipelago is protected from the oceanic swells of the open seas, the Eagle Point site (48° 27' N, 123° 2' W) faces the prevailing winds and is often exposed to severe wave action. Three Eagle Point study sites were chosen which subjectively offered slight differences in wave exposure: (1) Eagle Point main area appeared to be the most exposed, (2) Eagle Point log area appeared to have the median amount of wave exposure, and (3) the Eagle Channel area was slightly more protected than the other areas. The log damage measured and discussed previously (Dayton 1971) was generally confined to the upper level of the intertidal zone, and its effects so dramatically important to the barnacle-mussel were not readily

apparent to the lower level algal association at Eagle Point. This association is composed of patches of *Hedophyllum*, *Rhodomela larix*, *Fucus distichus*, and *Phyllospadix scouleri*.

Turn Rock (48° 32' N, 122° 58' W) is in a channel protected from wave action, but is exposed to strong tidal currents. The algal association is clearly dominated by *Hedophyllum sessile* with occasional patches of *Polysiphonia hendryi*.

The site most protected from wave action was Colin's Cove (48° 33' N, 123° 0' W), approximately 200 m north of the Cantilever Pier of the Friday Harbor Laboratories. Winter storms from the northeast occasionally result in wave action at this site, but normally the heaviest waves come from passing ferry boats and pleasure craft. The algal association at Colin's Cove is rather sparse, with few brown or red algae, most of the cover being ephemeral ulvoids.

The outer coast and San Juan Island sites differ from each other in two important aspects in addition to wave exposure. First, the San Juan Island sites are subjected to more climatological stress, as they have more wind, many more sunny days in the summer, and usually more extreme cold in the winter than do the outer coast sites, which are buffered by the wet maritime weather resulting from offshore upwellings. The detrimental effect of these climatological differences on marine intertidal organisms is exaggerated on San Juan Island because the summer spring low tides usually occur around the middle of the day, subjecting these 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 extremes of winter conditions. In contrast, the spring low tides on the outer coast tend to be very early in the morning during the summer and late in the afternoon in the winter. Thus the outer coast intertidal association is relatively well protected from desiccation and temperature extremes both by the moist weather and by the time of day of the spring tides. The second important difference between the two areas is the nature of the substratum. The outer coast sites are conglomerate siltstone/sandstone, while the San Juan sites are a very hard graywacke. The rough, moist surface of the sandstone is a much more protected habitat for algal spores and sporelings than is the hard, smooth, fast-drying graywacke of San Juan Island.

Most of the study sites were visited at least twice monthly, during each low-tide period, between 1965 and 1970 (dates available in Dayton 1970). My clearing experiments involved the selective removal of particular populations by dislodging individual plants with an axe and cleaning the substratum with a knife. I searched for indication of hapteral regrowth, a potential artifact, but none was seen; the

TABLE 1. Canopy species and areas of occurrence. Study sites arranged in decreasing exposure gradient: TI, Tatoosh Island (exposed northwest point area only); WI, Waadah Island; SS, Shi Shi; MB, Mukkaw Bay; PH, Portage Head; EP, Eagle Point; TR, Turn Rock; and CC, Colin's Cove

Canopy species	TI	WI	SS	MB	PH	EP	TR	CC
<i>Hedophyllum sessile</i>	X	X	X	X	X	X	X	
<i>Costaria costata</i>		X	X	X	X	X	X	
<i>Alaria nana</i>		X	X	X	X			
<i>A. marginata</i>		X	X	X	X	X	X	
<i>Egregia menziesii</i>			X	X	X	X		
<i>Nereocystis luetkeana</i>	X	X	X	X	X	X	X	X
<i>Pleurophycus gardneri</i>			X	X	X	X		
<i>Lessoniopsis littoralis</i>	X	X						
<i>Laminaria setchellii</i>	X	X	X	X	X			

normally long temporal delay in recolonization suggests that the clearing process was successful.

RESULTS

Ecological categories of algae

The patterns and interactions resulting in the occurrence of certain dominant species were examined through a series of experimental manipulations. These studies show that most of the species of intertidal algae fall into the following three ecological categories: (1) canopy species, (2) obligate understory species, and (3) fugitive species.

The canopy species identified are defined as those growing above the other species and apparently succeeding in dominating the light resource, as demonstrated by the presence of an algal bloom following their removal; these species are listed in Table 1. With the exceptions of Colin's Cove, which has no canopy species in the lower intertidal zone, and the localized distribution of *Lessoniopsis*, the areas appear to be characterized by quite similar arrays of dominant plants, especially *Hedophyllum sessile*.

Those plants that either die completely or die back to the holdfast when the canopy is removed I have called obligate understory species. They die either from desiccation, exposure to excessive light (probably ultraviolet) intensity, or physical battering, from which they were protected by the canopy. Many of these species have been demonstrated to be killed by high light intensities (Bieble 1957, Hellebust 1970). The obligate understory category can be further subdivided into two subcategories (Table 2). The first includes species that are primarily subtidal, such as *Hymenena flabellulata*, *Dilsea californica*, *Callophyllis* spp., and *Botryoglossum farlowianum*. These occur intertidally only when they are protected either by a canopy or by the presence of some other form of physical shelter. The large subtidal populations of these species suggests that the fate of the intertidal individuals does not seriously affect the main populations.

TABLE 2. Obligate understory species and areas of occurrence. Circles (○) indicate that there is no experimental proof of obligate nature. No canopy provided refuge for any obligate understory species at Colin's Cove

Obligate understory	Sites						
	TI	WI	SS	MB	PH	EP	TR
Subtidal extension							
<i>Hymenena flabelligera</i>	○	X	X	X	X	X	X
<i>Callophyllis flabellulata</i>	○	X	X	X	X	X	X
<i>C. firma</i>	○	X	X	X	X		X
<i>Plocamium coccineum</i>	○	X	X	X	X	X	
<i>Laurencia spectabilis</i>		X	X	X	X	X	
<i>Schizymenia pacifica</i>	○	X	X		X		
<i>Botryoglossum farlowianum</i>	○	X	X		X		
<i>Delesseria decipiens</i>	○	X	X		X		
<i>Dilsea californica</i>	○	X	X	X			
<i>Cryptopleura violacea</i>		X	X		X		
<i>Rhodymenia pacificum</i>		X	X		X		
<i>Erythrophyllum delesserioides</i>	○	X	X				
<i>Polynura latissima</i>		X			X		
<i>Fauchea fryeana</i>		X				X	
<i>Rhodymenia californica</i>		X			X		
Intertidal species							
<i>Corallina officinalis</i>	○	X	X	X	X	X	X
<i>C. vancouveriensis</i>	○	X	X	X	X	X	X
<i>Bossiella</i> sp.	○	X	X	X	X	X	X
<i>Calliarthron regenerans</i>	○	X	X	X	X	X	X
<i>Serraticardia macmillani</i>	○	X	X	X	X	X	X

The other subcategory of the obligate understory includes species confined basically to the intertidal region in this area. Extensive diving suggests these species do not have large subtidal populations in this geographic region; their reproductive individuals are restricted to intertidal sites under the canopy or areas in which they are permanently wet. This group is composed primarily of articulated coralline algae, species of *Corallina*, *Calliarthron*, *Serraticardia*, and *Bossiella*. The individuals often do not die completely when exposed, as they have encrusting hold-fast systems that may remain alive under moderate conditions of desiccation, but their branches die and fall off; because their conceptacles are on the branches, though alive, these plants must be considered reproductively dormant. In tidepools and other permanently wet areas, these coralline species retain their branches and appear to thrive; however, in the areas studied, most of their populations appear to live as obligate understory species beneath canopies. Additional support of the sensitivity to desiccation of some intertidal algal species, especially among the corallines, has been documented on an uplifted bench at Amchitka Island, Alaska (Lebednik 1973).

The fugitive species (Hutchinson 1951) are the "weeds" of the system. These species are quick to respond to any disturbance, such as the complete denuding of the substratum or the removal of the canopy species. In the common pattern of succession

TABLE 3. Fugitive species and areas of occurrence. Circles (○) indicate no experimental proof of fugitive nature. Asterisk (*) indicates that a species is a subtidal component of the obligate understory appearing in conjunction with the protective cover of the fugitive species

Species	Sites								
	TI	WI	SS	MB	PH	EP	TR	CC	
<i>Spongomorpha coalita</i>	○	X	X	X	X	X	X	X	
<i>Polysiphonia hendryii</i>	○	X	X	X	X	X	X	X	
<i>Porphyra perforata</i>	○	X	X	X	X	X	X	X	
<i>Microcladia borealis</i>	○	X	X	X	X	X	X		
<i>Gigartina papillata</i>	○	X	X	X	X	X	X		
<i>Odonthalia floccosa</i>	○	X	X	X	X	X	X		
<i>Iridaea cordata</i>	○	X	X	X	X	X			
<i>Iridaea heterocarpum</i>	○	X	X	X	X	X			
<i>Callithamnion pikeanum</i>	○		X	X	X		X		
<i>Scytosiphon lomentaria</i>		X	X		X	X	X	X	
<i>Endocladia muricata</i>	○	X	X	X	X	X			
<i>Ulva rigida</i>	○	X	X	X	X				
<i>Schizymenia pacifica*</i>	○	X	X	X	X				
<i>Antithamnion pacificum</i>			X		X	X	X	X	
<i>Halosaccion glandiforme</i>	○	X	X	X	X				
<i>Heterochordaria abietina</i>	○	X	X	X	X				
<i>Rhodomela larix</i>	○		X		X	X	X		
<i>Monostroma fuscum</i>			X		X	X	X		
<i>Enteromorpha intestinalis</i>					X	X	X	X	
<i>Iridaea lineare</i>	○	X	X		X				
<i>Cladophora trichotoma</i>			X	X	X				
<i>Ulva fenestrata</i>					X		X	X	
<i>Desmarestia ligulata</i>					X		X	X	
<i>Erythrophyllum delesserioides*</i>	○	X	X						
<i>Odonthalia washingtoniensis</i>			X		X		X		
<i>Botryoglossum rubrechtiana</i>		X	X		X				
<i>Dilisia californica*</i>		X	X		X				
<i>Cumagloia andersonii</i>			X		X				
<i>Pterochondria woodii</i>			X		X				
<i>Prionitis lyallii</i>			X		X				
<i>Ptilota filicina</i>			X		X				
<i>Ptilota hypnoides</i>			X		X				
<i>Enteromorpha linza</i>							X	X	

in colonization by these fugitive species (cf. Lee 1965, Castenholz 1967, Dayton 1971), the ulvoids and *Porphyra* are usually the first macroscopic species to appear, often completely covering the clearing. The individuals of these species are ephemeral, usually dying within a few months (Lee 1965), but the species continue to be represented in low numbers in the disturbed areas. Following the appearance of the diatoms, ulvoids, and *Porphyra*, the rest of the fugitive species (Table 3), primarily red algae, appear and persist for many years. Individuals of these red algal species such as *Halosaccion*, *Iridaea*, *Gigartina*, *Odonthalia*, and *Microcladia* appear to be rather long lived.

Resources potentially limiting algal populations

Generally, light is one of the most important limiting resources in macro-algal associations (e.g., Kain 1966, 1969, 1971, North and Hubbs 1968). The macroscopic plants of the intertidal zone are

TABLE 4. Mean percent cover of canopy, holdfast, obligate understory, fugitive species, and free space at various tidal levels (in feet) at each site. Data are from 10 to 30 quadrats of 0.25 m² taken randomly along horizontal transects. Variance is presented as 95% confidence interval calculated from untransformed data. Blank spaces represent an absence of respective space occupant. *Hedophyllum sessile* was the canopy species at all sites except the Waadah Island ledge transect and Tatoosh Island, where the canopy species was *Lessoniopsis littoralis*.

Site	Level	% Canopy	% Canopy holdfast	% Obligate understory	% Fugitive species	% Free space	Shaded free space
Colin's Cove	-2-0				34.7 ± 25.6	65.5 ± 25.8	
	0-2				12.2 ± 5.7	75.0 ± 8.6	
Turn Rock	-2 - -1	83.5 ± 25.5	8.1 ± 0.3	5.7 ± 5.9	9.2 ± 19.3	0.5 ± 0.9	71.1 ± 20.6
	-1-0	43.0 ± 22.9	0.8 ± 1.1	9.5 ± 7.9	46.5 ± 22.5		5.9 ± 4.9
	0-+1	46.5 ± 24.2	0.9 ± 1.3	19.5 ± 17.4	47.0 ± 24.2		5.5 ± 2.4
Eagle Point	-2-0	38.4 ± 13.6	0.7 ± 0.2	17.5 ± 6.3	12.4 ± 6.4	49.0 ± 10.9	85.0 ± 45.0
	0-+1	42.0 ± 14.4	0.7 ± 0.5	28.2 ± 8.7	20.8 ± 7.4	26.5 ± 9.5	12.5 ± 18.2
Portage Head	-2-0	85.7 ± 6.2	11.3 ± 1.8	63.5 ± 4.2	13.0 ± 19.3	1.2 ± 3.2	19.2 ± 12.5
	0-2	79.5 ± 10.9	9.5 ± 2.0	51.8 ± 7.3	6.8 ± 7.5	2.0 ± 2.6	24.3 ± 10.7
Shi Shi	-2-0	10.0 ±		3.6 ± 1.5			55.1 ± 5.4
	0-2	10.0 ±	17.9 ± 0.7	10.0 ± 23.0	3.0 ± 3.0		68.1 ± 6.6
Waadah Island	65° slope						
	-2-0	72.0 ± 13.2	8.1 ± 2.5	31.4 ± 7.8	12.9 ± 10.0		49.3 ± 21.0
	0-2	63.5 ± 10.6	5.7 ± 1.6	34.6 ± 13.6	13.6 ± 3.9		32.2 ± 11.5
	2-4	54.5 ± 20.2	7.3 ± 2.4	32.6 ± 16.9	38.7 ± 13.4		7.8 ± 3.4
	4-5	57.3 ± 13.7	7.2 ± 2.7	41.3 ± 10.5	15.0 ± 9.1		25.3 ± 13.4
	Ledge area						
	0-2	73.5 ± 11.7			7.0 ± 3.0		68.5 ± 4.1
Tatoosh Island	-2-0	62.3 ± 8.9		15.5 ± 14.3		5.8 ± 11.1	
	0-2	22.3 ± 6.4					
	2-4	30.6 ± 9.5		3.7 ± 0.7			

bathed by continuously moving, relatively rich sea water, and they probably rarely deplete the supply of dissolved nutrients. Thus light conditions and primary space (e.g., Dahl 1973) seem to be the proximate resources potentially limiting intertidal algal populations. Primary space can limit the nonencrusting algal species only with regard to the development of their holdfast systems. Table 4 lists the percent substratum dominated by those holdfasts; none of the areas has more than 18% holdfast cover, and all areas have considerable amounts of available primary space. For these reasons I assume that primary space is not a particularly important limiting resource. Light, inducing a stratification in the plant community, seems to be a much more important potentially limiting resource than primary space. The encrusting algae, such as *Ralfsia*, *Hildenbrandia*, and various species of *Lithothamnion* and *Lithophyllum*, often cover large areas of primary substratum, but have provided substrate for all the other attached intertidal algae, and I will not discuss the primary space used by them. This assumption is not strictly accurate, for the actual degree of interference via cellular sloughing or allelopathic agents which these encrusting algae have on the recruitment of spores or larvae is unknown, and is an interesting area for future research. I have seen some indication that *Ralfsia* and *Hildenbrandia* inhibit the settlement of other organisms (cf. Conover and Sieburth 1966), and the same could be true of other encrusting algae.

As an indication of successful light utilization, I measured the percent of the primary space covered

(i.e., shaded) by the canopy species. These measurements were usually made photographically; the prints were analyzed with a planimeter or with random dots as discussed earlier (Dayton 1971). When the canopy was not removed the percent cover of the obligate understory was estimated visually with the aid of a 0.25-m² quadrat subdivided into 25 squares. This is a conservative measure of the area of influence, because these plants are lashed about by water motion when they are submerged, and thus they abrade each other and the substratum and effectively cover a much larger area.

Experimental removal of dominant canopy species

The experimental removal of an hypothesized dominant is one of the most direct means of evaluating competition. In order to demonstrate interspecific competition for light, the canopy species in each of the areas was experimentally removed from small plots and the changes in the other algal and invertebrate populations were monitored. For each experimental removal, an adjacent unaltered plot was similarly monitored as a control to the experiment. Because I did not want limitations to spore dispersal (Dayton 1973a) to be a factor, these plots were usually rather small (2-8 m²). But in those areas populated by large plants such as *Lessoniopsis littoralis* or *Alaria marginata* that may have rather far reaching whiplash effects I wished to avoid, I cleared larger plots up to 20 m². In these cases I saw no indication of limitations to spore dispersal.

Hedophyllum.—*Hedophyllum sessile* forms the

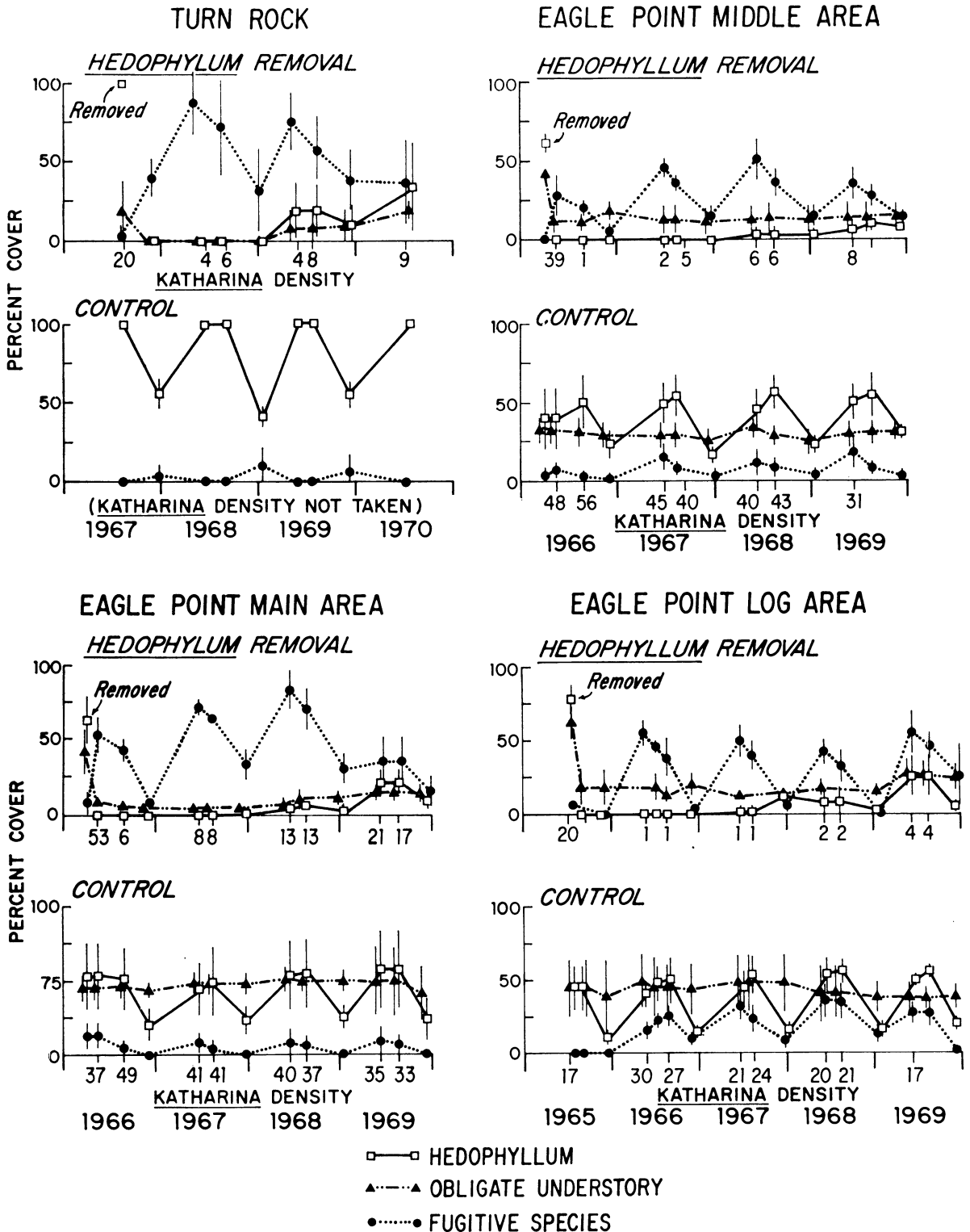


FIG. 1. Mean percent covers of *Hedophyllum sessile* canopy, obligate understory, and fugitive species in *Hedophyllum* removal and control areas at Turn Rock and Eagle Point, San Juan Island, Washington. The *Hedophyllum* removal area was 9 m² at Turn Rock and 4 m² at the Eagle Point sites. The variance is presented as SD of 10 one-fourth-m² samples of the Turn Rock *Hedophyllum* removal area, 6 one-fourth-m² samples of the Turn Rock control area, and 4 one-fourth-m² samples of all the Eagle Point areas. The mean densities per m² of *Katharina tunicata* in each area are recorded below the respective graphs for the summer visit.

PORTAGE HEAD

SHI SHI

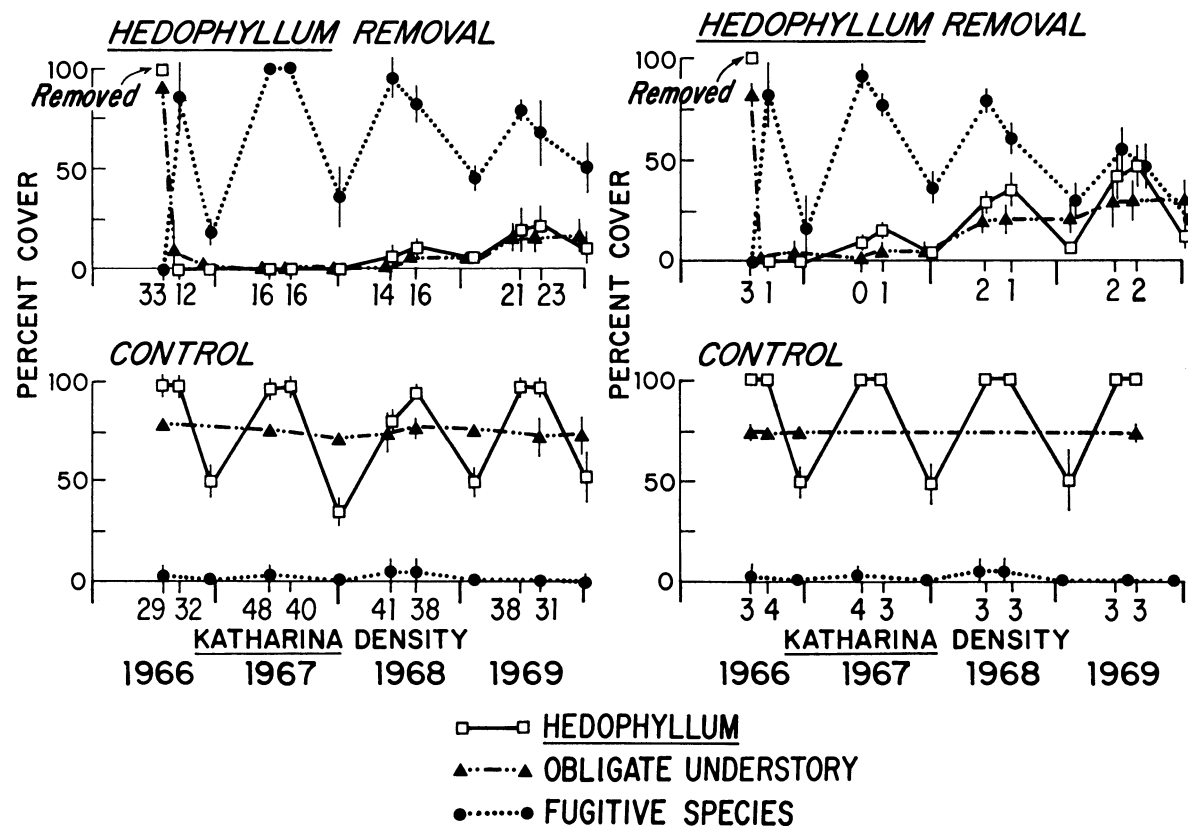


FIG. 2. Mean percent covers of *Hedophyllum sessile* canopy, obligate understory, and fugitive species in *Hedophyllum* removal and control areas at Portage Head and Shi Shi reef on the outer coast of the Olympic Peninsula, Washington. The *Hedophyllum* removal and control areas were 4 m² at each site. The variance is presented as SD of 4 one-fourth-m² samples at each site. The mean density per m² of *Katharina tunicata* are recorded below the respective graphs for the summer visits.

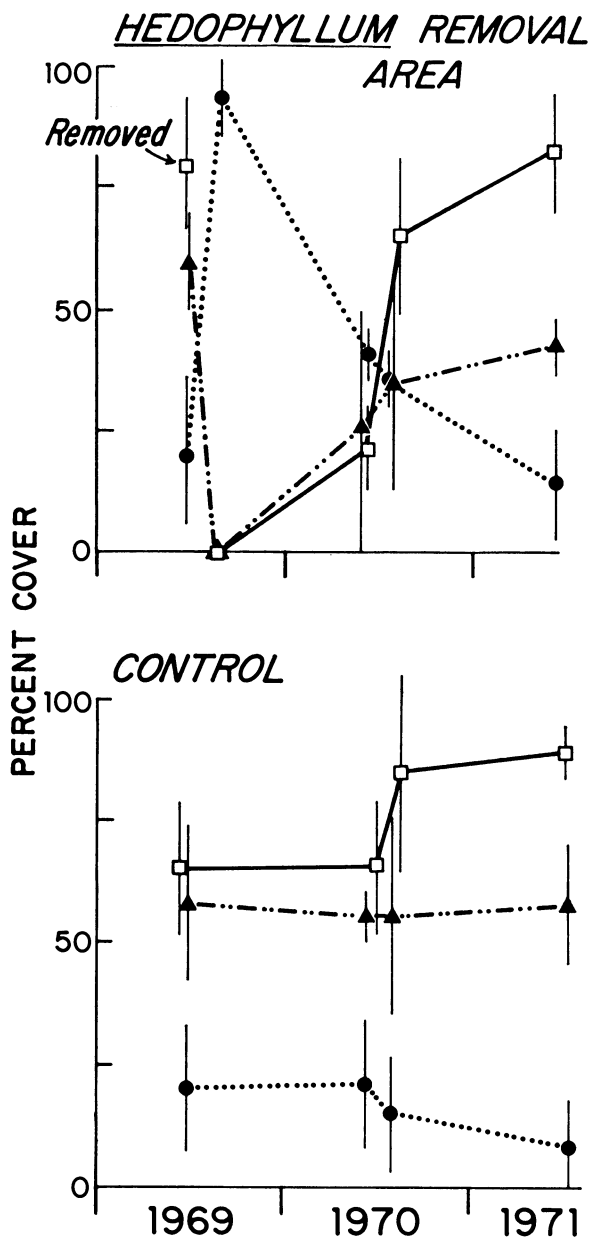
canopy at all the study sites except Colin's Cove and the exposed parts of Tatoosh and Waadah Islands. The successional pattern following the manual removal of the *Hedophyllum* canopy (Fig. 1 and 2) is remarkably consistent. In each of the study sites there was an immediate precipitous drop in the percent cover of populations composing the obligate understory, and a dramatic bloom of the fugitive species. Neither drop nor bloom occurred in any of the control plots. Thus the manipulation provides strong evidence that the major alterations of the obligate understory and fugitive species populations result from the removal of the canopy. As the experiments proceeded, the oscillations in the percent cover of the fugitive species on the experimental sites and in the *Hedophyllum* cover in the controls resulted from occasional deaths of ephemeral algae or, more commonly, from the winter defoliation of the perennials, most of which perennate, that is, overwinter as a small piece of holdfast (Dixon 1965).

Hedophyllum spores are released in the early

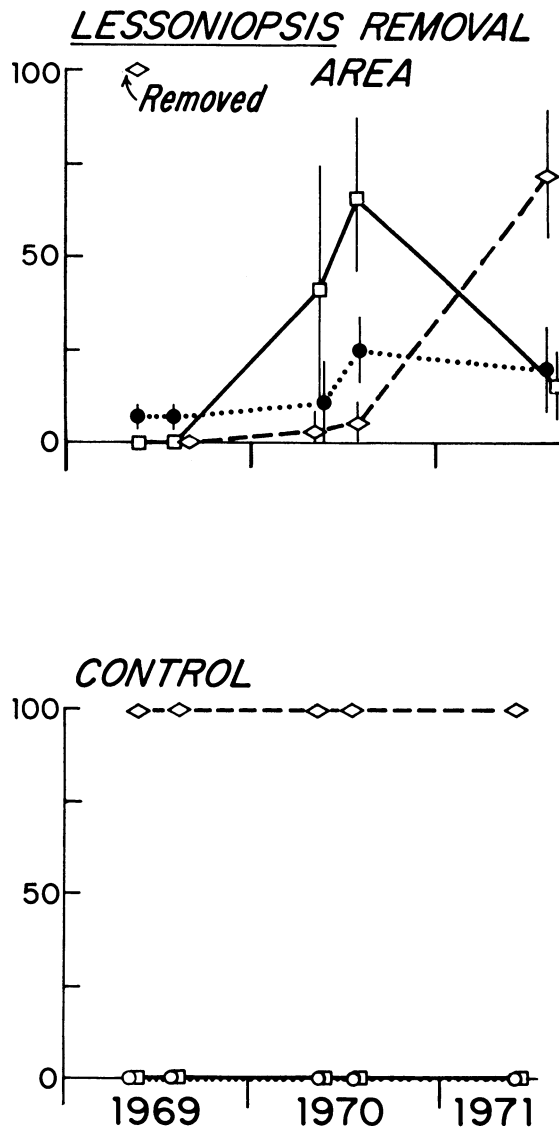
winter (Widdowson 1965) and the new sporophytes first appeared in the experimental plots in the spring. In the *Hedophyllum* removal plots the recovery of the obligate understory populations is closely associated with the recovery of the *Hedophyllum* canopy (Fig. 1 and 2). In each case a decline in the cover of the fugitive species is also associated with the recovery of the *Hedophyllum* canopy.

A shorter term experiment with a much faster recovery was done on the *Hedophyllum*-dominated 65° slope portion of Postelsia Point on Waadah Island. Here the decline of obligate understory and the bloom of fugitive species following removal of an 80% cover of *Hedophyllum* was typical. In contrast to the slower *Hedophyllum* recovery at the other sites, the *Hedophyllum* canopy here recovered to comprise 65% of the canopy cover within 1 yr and 82% by the end of the 2nd yr (Fig. 3). The 60% obligate understory fell to 0% shortly after the *Hedophyllum* removal, but by the 2nd yr had recovered to 41% cover.

WAADAH ISLAND 65° SLOPE AREA



WAADAH ISLAND FLAT AREA



- HEDOPHYLLUM
 ▲---▲ OBLIGATE UNDERSTORY
 ●.....● FUGITIVE SPECIES
 ◇---◇ LESSONIOPSIS
 ○---○ LAMINARIA

FIG. 3. Mean percent covers of *Hedophyllum sessile* and *Lessoniopsis littoralis* canopies, obligate understory, and fugitive species in two areas at Waadah Island, Washington. *Hedophyllum* was removed from the 65° slope area, and *Lessoniopsis* was removed from the flat area at the 1-ft level. In each experimental case, the canopy was removed from a 4-m² area, and the variance is presented as SD of 6 one-fourth-m² samples. Three *Katharina tunicata* remained in the 65° slope experimental area for the duration of the experiment; there were no *Katharina* in the other plots.

In order to test the null hypothesis that adult sporophytes could not survive at Colin's Cove, the most protected site investigated in this study, three rocks with a total of 11 adult *Hedophyllum* sporophytes were transferred from nearby Turn Rock to Colin's Cove in March 1969; the *Hedophyllum* grew and seemed to prosper all summer. The small rocks were eventually lost in a November storm, but since the 11 plants had lived for 9 mo and almost tripled their biomass, the null hypothesis appears to have been negated, and we can conclude that *Hedophyllum* sporophytes can survive at Colin's Cove. Their absence there is due to factors possibly related to the relatively great amount of siltation on the gametophyte.

The exposed areas of Tatoosh and Waadah Islands are dominated by *Lessoniopsis*, *Laminaria*, or *Alaria*; however, the more protected areas on these islands are characterized by extremely heavy covers of *Hedophyllum*. This is particularly true of many of the shallow channels cutting through Tatoosh Island. Therefore the absence of *Hedophyllum* in Table 4 from these sites is a sampling artifact and refers only to the most exposed points on these islands.

The only herbivore population that might have influenced the results of the *Hedophyllum* removal experiments was the large chiton, *Katharina tunicata*. Because the *Katharina* population also responded to the removal of the canopy, its density in both the experimental and control plots was monitored throughout the experiment and the data are recorded in Fig. 1 and 2. The possible effect of the *Katharina* population on the results of the experiments is discussed later.

Laminaria and Lessoniopsis removal.—*Laminaria setchellii* forms a thin canopy on the lower levels of the most exposed rocks in all of the outer coast sites, but the heavy surf prevents effective canopy removal experiments on these rocks. The Postelsia Point area on Waadah Island has heavy surge and wave action; the canopy consists mainly of *Lessoniopsis littoralis*, a large kelp with an extremely massive woody stipe and large holdfast system. *Hedophyllum* is uncommon in this association, although light and primary space available appears adequate (Table 5). In areas where the angle of incidence is large, that is, a nearly vertical wall, the *Lessoniopsis* canopy is not complete and the canopy also contains *Laminaria setchellii*. On vertical walls, *Lessoniopsis* appears to remove many of the other organisms by a whiplash effect. The relative percent cover and primary space utilization by holdfasts on vertical walls is summarized in Tables 4 and 5. Although *Lessoniopsis* dominates the cover, free unshaded space is still 20%. On relatively less steep substrata (angle of incidence $<45^\circ$) the *Lessoniopsis* dominates essentially 100%

TABLE 5. Algal canopy cover at Waadah Island in the *Lessoniopsis* association on a vertical ledge at the 0–2-ft level. The mean cover of fugitive species was 7.0% (SD $\pm$ 4.2), mean uncovered free space was 20.5% (SD $\pm$ 14.2), and the mean total free space was 68.5% (SD $\pm$ 5.8). Data were taken from a strip about 5 m long, 10 sample quadrats of 0.25 m². Variance is presented as SD

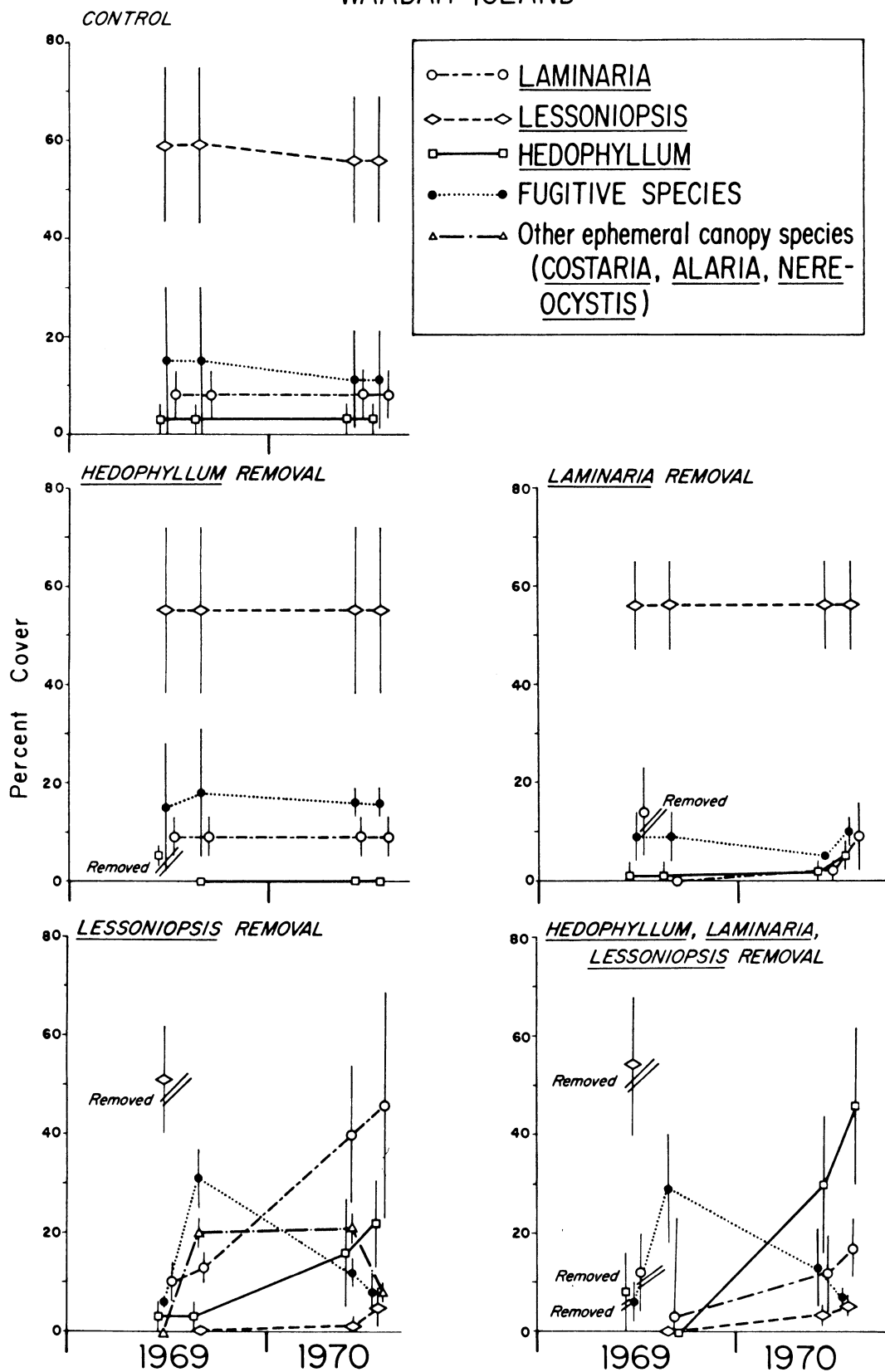
	<i>Lessoniopsis littoralis</i>	<i>Laminaria setchellii</i>	<i>Hedophyllum sessile</i>
% canopy cover	56.0 $\pm$ 11.2	12.0 $\pm$ 5.9	5.5 $\pm$ 7.2
% holdfast cover	10.0 $\pm$ 5.2	8.5 $\pm$ 7.4	2.3 $\pm$ 2.2
No. plants	5.1 $\pm$ 2.3	13.9 $\pm$ 4.0	3.6 $\pm$ 3.0

of the cover of the highly exposed sites and appears to exclude completely the other canopy species.

The three perennial canopy species potentially occupying low intertidal areas characterized by heavy surge have very different growth forms. *Lessoniopsis* has a massive stipe system hanging directly downward from its attachment on a vertical wall or draping heavily over flat substrate. The *Laminaria* frond is supported 30–40 cm above the substratum by a resilient stipe. It thus has little whiplash effect on the understory. *Hedophyllum* has no distinct stipe and grows close to the substratum. *Lessoniopsis* sweeps back and forth in the waves, batters *Hedophyllum*, and presumably brushes it off the wall; but the stipe and blade of *Laminaria* grow outward beyond the hanging *Lessoniopsis* and are flexible enough to bend with the surge and wave action and with the *Lessoniopsis* battering. *Laminaria* frequently settles and grows on a stipe of *Lessoniopsis*, as well as on the wall close to a *Lessoniopsis* holdfast. By thus avoiding some of the potential battering, *Laminaria* coexists with *Lessoniopsis* more successfully than does *Hedophyllum*. I have followed marked *Laminaria* through 3 yr and verified that the growth rings in the stipe are annual rings, and the average age of the *Laminaria* found coexisting with *Lessoniopsis* was 4.5 yr (SD = 2.5 yr, $N = 155$); the oldest was 13 yr. In one case an 8-yr-old *Laminaria* was found growing on a medium-sized *Lessoniopsis* stipe 18 cm from the holdfast. As the *Lessoniopsis* are often much larger than that particular individual, it is apparent that they are long lived and that the *Lessoniopsis*-*Laminaria* association must be relatively stable in time.

To test the hypothesis that each of these three canopy species exerts a strong effect on the other two and/or on the other populations in the community, I cleared each canopy species from separate 3–5 $\times$ 1 m strips along a vertical wall at Postelsia Point on Waadah Island which was quantitatively dominated by *Lessoniopsis* and *Laminaria*. Other clearings were made on flat exposed areas quantita-

WAADAH ISLAND



tively dominated by *Lessoniopsis*. On the vertical wall where the three canopy species were removed their individual influences can be evaluated by comparing the strips from which each was removed with unaltered control areas, with strips from which the other canopy species were individually removed, and with a strip from which all three canopy species were removed (Fig. 4).

Independently removing *Hedophyllum* or *Laminaria* had minor effects on the other populations in the plots. *Hedophyllum* originally occupied only 5% of the canopy cover, and its removal resulted in no changes. The only change following the removal of *Laminaria*, which originally occupied 15% of the canopy, was a slight increase in the *Hedophyllum* cover.

The removal of *Lessoniopsis* had a dramatic effect on all the other algal populations. There was an immediate and significant increase in the percent cover of the fugitive species, particularly species of *Iridaea*, and of the ephemeral brown algal canopy species such as *Nereocystis luetkeana* and *Costaria costata*. All these changes occurred in the presence of the natural 3% and 10% covers of *Hedophyllum* and *Laminaria*, respectively. Of the species colonizing quickly, *Nereocystis* tends to be killed by desiccation and wave battering before maturing, while *Costaria* appears to be an annual that dies late in the fall. Most of the other species are perennial, and in these experiments their exclusion or disappearance is a result of competitive or whiplash effects. In 2 yr after the *Lessoniopsis* was removed, the *Laminaria* cover had increased from 10% to over 50% of the canopy; the cover of fugitive species and ephemeral brown algae had been reduced from a combined peak of more than 50% to less than 5% cover. Some of the increase in *Laminaria* cover resulted from more luxuriant growth of old fronds, but most resulted from the appearance of new plants. Almost all of the 3%–21% *Hedophyllum* increase was the result of recruitment of new plants.

The total canopy removal experiment in which *Lessoniopsis*, *Laminaria*, and *Hedophyllum* were removed produced results similar to the removal of *Lessoniopsis* alone. The only species originally coexisting with these three canopy species in the removal plots were two to three species of coralline algae and the encrusting hydrocoral, *Allopora por-*

phyra. The areas cleared of the canopy species were quickly colonized by fugitive species and ephemeral canopy species, especially *Nereocystis*, *Costaria*, and *Alaria marginata*. *Alaria* appears in January and February, and, in contrast to the annual *Nereocystis* and *Costaria*, appears to live for a number of years. The major differences between the *Lessoniopsis*-only removal and the total-canopy removal experiments involved the different recruitment patterns of *Laminaria* and *Hedophyllum* after 1 yr. In the *Lessoniopsis*-only removal experiment, *Laminaria* increased its cover from 10% to 45%, while *Hedophyllum* increased from 3% to 21%; in contrast, in the total-canopy removal experiment *Laminaria* recovered to only 17% cover while *Hedophyllum* recovered to 48% cover. The differing rates of *Laminaria* and *Hedophyllum* recovery in the two experiments probably resulted from the different times of sporulation of *Laminaria* and *Hedophyllum*. Because *Laminaria* releases its spores in the summer, the *Laminaria* plants in the *Lessoniopsis*-only removal experiment probably released spores over the area during the first summer (1969); the adult and 1st-yr *Laminaria* plants would then have a competitive damping effect on *Hedophyllum*, which sporulates in the winter and thus had no new recruitment until the second summer, at which time the *Laminaria* were well established. The hypothesized spore dispersal limitations of *Alaria esculenta* (Sundene 1962), *Macrocystis pyrifera* (Anderson and North 1966), and *Postelsia palmaeformis* (Dayton 1973a) may also be true of *Laminaria* and may be responsible for reduced *Laminaria* recruitment and concurrent bloom of *Hedophyllum*, released from the hypothesized competition with *Laminaria*, in the total-canopy removal experiment. In both the *Lessoniopsis* removal and total-canopy removal experiments, the *Hedophyllum* cover fell precipitously by the end of the 2nd yr.

A summary of the experiments on the vertical slope shows that *Lessoniopsis* had a pronounced dominance in the areas where the three original canopy species were individually removed. That the removal of *Laminaria* or *Hedophyllum* did not affect the associations in which *Lessoniopsis* persisted suggests *Lessoniopsis* alone prevents other species from colonizing in the absence of *Laminaria* or *Hedophyllum*. The removal of *Lessoniopsis*, resulting in a response similar to that in the total-canopy removal

←

FIG. 4. Mean percent covers of various canopy and fugitive species in control and experimental areas where each of the three conspicuous perennial canopy species were removed individually and simultaneously from a vertical ledge on the exposed Postelsia Point at Waadah Island. The *Hedophyllum* and *Laminaria* were removed from 8-m² patches, the *Lessoniopsis* from a 10-m² patch, and the removal of all three species was from a 20-m² area. The variance is presented as SD of 4 one-fourth-m² samples in each case except the area from which the three canopy species were removed, which had 6 one-fourth-m² samples. *Katharina* were rare (1.3/0.25 m²; SD 1.2, N = 14) at this level (0 to +2 ft) and none was observed to move more than a few cm; therefore individual counts were not maintained.

TABLE 6. Comparison between percent covers of protected and exposed sides of the same surge channel at Shi Shi. Data are means of 10 randomly sampled quadrates along each horizontal level. Variance is presented as 95% confidence interval calculated from untransformed data. The canopy species was *Hedophyllum sessile*

Level (ft)	Exposed slope				
	-2-0	0-2	2-4	4-6	>6
Canopy cover	100.0 ± 0.0	100.0 ± 0.0			
Canopy holdfast		17.9 ± 0.7			
Obligatory understory	3.6 ± 1.5	10.0 ± 23.0			
Fugitive species		3.0 ± 3.0	15.3 ± 7.7		10.3 ± 5.6
<i>Fucus disticus</i>					32.5 ± 19.7
<i>Chthamalus dalli</i>			7.5 ± 2.3		
<i>Balanus glandula</i>			33.9 ± 16.1	82.1 ± 16.7	
<i>B. cariosus</i>					
<i>Mytilus californianus</i>			11.8 ± 9.6	19.0 ± 16.1	74.0 ± 39.4
<i>Anthopleura elegantissima</i>			4.0 ± 3.6	4.4 ± 5.1	
Uncovered free space					
Shaded free space	55.1 ± 5.4	68.1 ± 6.6			15.1 ± 7.3
Total free space			25.9 ± 16.2		

Level (ft)	Protected slope				
	-2-0	0-2	2-4	4-6	>6
Canopy cover					
Canopy holdfast					
Obligatory understory	12.3 ± 3.6	0.4 ± 0.5	0.9 ± 1.1		
Fugitive species	86.7 ± 3.1	2.1 ± 3.9	5.9 ± 4.9	14.9 ± 10.7	
<i>Fucus disticus</i>					7.9 ± 8.2
<i>Chthamalus dalli</i>				2.1 ± 1.5	
<i>Balanus glandula</i>				35.2 ±	5.7 ±
<i>B. cariosus</i>					9.8 ± 8.8
<i>Mytilus californianus</i>				8.0 ± 8.3	80.3 ± 44.2
<i>Anthopleura elegantissima</i>		81.7 ± 24.0	78.7 ± 27.0	7.4 ± 4.7	
Uncovered free space					
Shaded free space					
Total free space		15.6 ± 20.0	14.9 ± 10.9	29.6 ± 12.8	5.1 ± 3.0

experiment, suggests again that it is the competitively dominant species in this association. Similarly, in the absence of *Lessoniopsis* the presence of *Laminaria* has a strong negative effect on *Hedophyllum*, which appears to have no important negative effect on the other canopy species.

The *Lessoniopsis* dominance is even more dramatic on a flat area (Fig. 3). Here the *Lessoniopsis* effectively shades the substratum and comprises 100% of the canopy cover, the scattered *Laminaria* individuals all growing on the *Lessoniopsis* stipes. Essentially no *Hedophyllum* nor understory alga occurs. Removal of the *Lessoniopsis* on the flat area resulted in a rapid luxuriant growth of fugitive species, again primarily species of *Iridaea*. *Hedophyllum* was much more successful in early recolonization of the flat area than it was on a vertical wall; by the middle of the next summer, 66% of the cover was *Hedophyllum*. *Lessoniopsis* began to recolonize within the 1st yr, as in the other *Lessoniopsis* removal areas, and formed 5%–10% of the canopy after the 1st yr. Late in the second summer *Lessoniopsis* regained its dominance (72% cover) and *Hedophyllum* fell from 66% to 16% cover.

Importance of wave exposure to competitive dominance

The numerous physical differences associated with different degrees of wave exposure are well known to dictate the species composition and patterns of abundance of algal associations in different intertidal communities (Lewis 1964, 1968, Morton and Miller 1967, Ricketts et al. 1968, and Stephenson and Stephenson 1972). Often the patterns of distribution and abundance of many species change abruptly, especially of large brown algae, with slight changes in the degree of exposure to wave shock. This fact is dramatically apparent in Table 6, which contrasts two sides of the same surge channel at Shi Shi reef. The exposed side of the channel had a heavy algal cover, but there were almost no algae on the protected side, which was largely covered with the anemone, *Anthopleura elegantissima*.

Hedophyllum removal experiments done in sites along a gradient of wave exposure allow the evaluation of its effect on the *Hedophyllum* recovery rate. The study sites were ranked from most protected to most exposed: Turn Rock, Eagle Point Channel area, Eagle Point log area, Eagle Point main area,

Portage Head, Shi Shi reef, Waadah Island 65° site, Waadah Island ledge, and the Waadah Island flat area. The relative exposure ranks were correlated with the rank percent covers of *Hedophyllum*, which except for those of the Waadah Island sites were from data collected 3 yr after the removal of the *Hedophyllum* canopy. At Waadah Island the counts were made after only 1 yr; if the experiments had been monitored over the two succeeding years and the *Laminaria* and *Lessoniopsis* canopies removed, the percent *Hedophyllum* canopy cover would undoubtedly have continued to increase and would not have altered the rank order. There was a significant Spearman Rank Correlation Coefficient ($.05 \geq P \geq .01$) between wave exposure and the *Hedophyllum* recovery rate.

Assuming that the rate of *Hedophyllum* recruitment is a fair indication of the degree of physiological appropriateness of a given site, the significant rank correlation between the relative degree of wave shock and the rate of *Hedophyllum* recruitment (Fig. 1-3) suggests that the physiologically optimal conditions are those in which the plant is subjected to the highest degree of wave shock. In moderately exposed areas *Hedophyllum* clearly is the competitive dominant; but in the most exposed areas, where its physiological condition improves dramatically as indicated by the relative rapidity of its recovery, *Hedophyllum* loses completely its competitive dominance and is forced to persist in a fugitive role. Thus *Hedophyllum* appears to express its optimal ecological impact in physiologically suboptimal areas.

The influence of herbivores on the algal association

None of the herbivores on the substratum were loosened or removed in the canopy removal experiments; the observed algal canopy, obligate understory, and fugitive species grew and persisted in spite of the grazing pressure of the molluscan herbivores present at each spot. The growth of the algae swamps the ability of these herbivores to eat the young plants, and the plants quickly reach a refuge in size beyond which they no longer suffer mortality at the normal herbivore densities. Such an escape in growth from *Littorina* has been described for diatoms by Castenholz (1961) and for many macro-algae by Dahl (1964). The molluscan herbivores present in the association studied here are *Katharina tunicata*, *Tonicella lineata*, *Mopalia muscosa*, *M. lignosa*, *M. ciliata*, *Margarites* sp., *Calliostoma* sp., *Tegula funebris*, *Lacuna* sp., *Mitrella* sp., *Acmaea mitra*, *A. pelta*, and *A. scutum*. With the exceptions of *Katharina*, which browses extensively on large *Hedophyllum* sporophytes, and *A. mitra* and *Tonicella*, which seem to restrict their diet to encrusting coralline algae, the molluscan herbivores appear to be rather indiscriminate

TABLE 7. Annual peak cover of fugitive species and *Hedophyllum* regrowth in plots with and without *Katharina*, indicating that the presence of *Katharina* in natural densities has little or no effect on these peaks

Year	Plot*	<i>Katharina</i> density no./m ²	Peak % cover of fugitive species	Peak % cover of <i>Hedophyllum</i>
Shi Shi				
1966	HR	3	82 ± 16	0
	SPR	0	100 ± 0	0
1967	HR	1	91 ± 6	15 ± 4
	SPR	0	100 ± 0	1 ± 7
1968	HR	2	79 ± 5	35 ± 8
	SPR	0	81 ± 5	26 ± 10
1969	HR	2	55 ± 10	46 ± 10
	SPR	0	61 ± 11	35 ± 7
Portage Head				
1966	HR	12	86 ± 7	0
	SPR	0	68 ± 13	0
1967	HR	16	100 ± 0	0
	SPR	0	100 ± 0	0
1968	HR	14	95 ± 10	10 ± 4
	SPR	0	90 ± 11	13 ± 9
1969	HR	21	79 ± 5	21 ± 10
	SPR	0	79 ± 8	20 ± 13

* HR = *Hedophyllum* removal plot; SPR = *Strongylocentrotus purpuratus* removal plot.

inate grazers most likely to affect the settling algal spores, sporelings, and gametophytes.

The interpretation of the *Hedophyllum* removal experiments can be questioned because of the simultaneous departure of *Katharina*. Unfortunately, limited time in these low intertidal levels prevented effective *Katharina* removal experiments, which could have evaluated the *Katharina* effect in addition to that of *Hedophyllum*. The decline of the obligate understory cannot be logically explained by the departure of herbivores, but the increase in the fugitive species might result from this departure. The fact that the fugitive species never appeared in the controls to the *Hedophyllum* removal experiments despite highly variable *Katharina* densities (in some areas much lower than in some experimental areas) strongly suggests that the fugitive species bloom is independent of *Katharina* density, an observation also supported by the Waadah Island experiments, where there were very low *Katharina* densities. Finally, the Shi Shi and Portage Head *Strongylocentrotus purpuratus* removal experiments to be discussed allow a comparison with the *Hedophyllum* removal experiments indicating *Katharina* has no significant effect on the rate of *Hedophyllum* regrowth or on the decline in the magnitude of the annual peak in fugitive species cover after the initial bloom. The *S. purpuratus* removal strips were very close to and subject to nearly identical wave exposure as the respective *Hedophyllum* removal sites, but no *Katharina* were initially present in the *S. purpuratus* strips, nor did any immigrate in during the experiment. In contrast, original *Katharina* densities of

33/m² at Portage Head and 3/m² at Shi Shi declined after *Hedophyllum* removal experiments. Table 7 shows little or no difference over the course of the experiments in annual peak cover of fugitive species or of *Hedophyllum* regrowth in plots with and without *Katharina*.

In the lower algal zone, the densities of most molluscan herbivores seem to be maintained at a level far below the presumed carrying capacity of the environment. Although experimental proof is lacking, this is probably a result at least partially of predation by *Pisaster ochraceus*, *Pycnopodia helianthoides*, *Leptasterias hexactis*, and *Searlesia dira*. Paine (1969b and 1971b) has suggested that *Pisaster* kills approximately 25% of the lower level *Tegula* population each year. In addition, Paine (*pers. comm.*) has found in a *Hedophyllum* area at Mukkaw Bay that, numerically, 22% of the diet of *Pisaster* is composed of various molluscan herbivores. The *Pisaster* occur in sufficient density in my outer coast study sites (0.5–1.6/m², Dayton 1971) to prevent these herbivores from increasing their populations enough to have more effect on the algal association. Menge (1972a,b) demonstrated that the combined predation of *Leptasterias* and *Pisaster* is strong enough to eliminate most of the gastropod herbivores each year in the lower algal zone of the intertidal area in the San Juan Islands. *Katharina tunicata* and, to a lesser extent, *Acmaea scutum*, have a refuge in growth, and for *A. scutum*, a behavioral escape response, from *Leptasterias*. But both of these herbivores are often killed by *Searlesia dira* and *Pisaster*. Thus there is no refuge from predation for these lower tidal level molluscan herbivores, and the predators presumably prevent the herbivore populations from increasing sufficiently to affect their algal resources.

In contrast to the molluscs, the purple urchin *Strongylocentrotus purpuratus* has a pronounced influence on all phases of the lower intertidal association. Important effects of intertidal and subtidal grazing by sea urchins have been experimentally documented by Kitching and Ebling (1961), and Jones and Kain (1967) in Europe, North and associates in California (North 1971, for summary) and Vadas (1968) and Paine and Vadas (1969) in Washington. Areas with dense populations of urchins are characteristically barren or have a few species of coralline algae only. In my study sites large patches of space were occupied by dense (up to 300/m²) aggregations of *S. purpuratus* and were devoid of nonencrusting macro-algae. Because *S. purpuratus* feeds extensively on drift algal material carried in the surf (Ebert 1968), it is able to persist in these intertidal areas after having eliminated all the attached algae. Paine and Vadas (1969) found an increase in the species diversity of algae after

TABLE 8. Rate of displacement of *Strongylocentrotus purpuratus* from tidepools by *Pycnopodia helianthoides*

Pool	Original density of <i>S. purpuratus</i> (no./m ²)	Duration of <i>Pycnopodia</i> presence (days)	Rate of <i>S. purpuratus</i> displacement (no./day)	Total area cleared by <i>Pycnopodia</i> (m ²)
PH7A	263	90	7.4	2.4
PH7B	203	60	9.8	2.2
PH17S	244	33	7.4	1.0
PHS	233	30	7.5	1.0
PHR	190	14	12.2	0.9
PHX	240	27	7.4	1.0
PHT	160	15	7.9	0.7

removing *S. purpuratus* from shallow tidepools. I found that similar algal blooms followed the removal of *S. purpuratus* from two strips, each 1 m wide, at Portage Head and Shi Shi (Fig. 5). The algal response to the release from this herbivore is essentially identical to that of the release from competition for light found in the canopy-removal experiments (Fig. 1–3). Furthermore, the urchins exert a much stronger controlling effect on the algae than do the molluscan herbivores.

The indirect influence of carnivores on the algal association

Pycnopodia helianthoides is a major predator of adult *S. purpuratus* in this region (Mauzey et al. 1968) and so indirectly has a potentially important effect on the algal association. Unfortunately it is extremely difficult to experiment with this large asteroid; attempts to move it gently into a tidepool have been ineffective, because the animal usually leaves immediately and moves into the subtidal region; it always behaves somewhat abnormally after having been handled. Thus, controlled experimentation was impossible. I did, however, quantify the results of the presence of *Pycnopodia* that moved naturally into some of the many tidepools in the Portage Head site. The urchin displacement data in Table 8 were collected by observing *Pycnopodia* entering a tidepool and photographing the pool as often as possible (1–3 times a week) until it left the pool. *Pycnopodia* remains in a pool for only a few weeks, regardless of the fact that most pools appear to contain enough sea urchins to feed the *Pycnopodia* for at least a year. For unknown reasons there does not appear to be a numerical response (Solomon 1949) of *Pycnopodia* to high densities of their urchin prey (Mauzey et al. 1968).

Pycnopodia appears to need approximately 24–48 h to digest one urchin. Thus its actual consumption of urchins does not have an overwhelming effect on their density in a tidepool. However, when a *Pycnopodia* moves into a pool, the urchins within 5–10 cm clearly respond to its presence by moving their spines

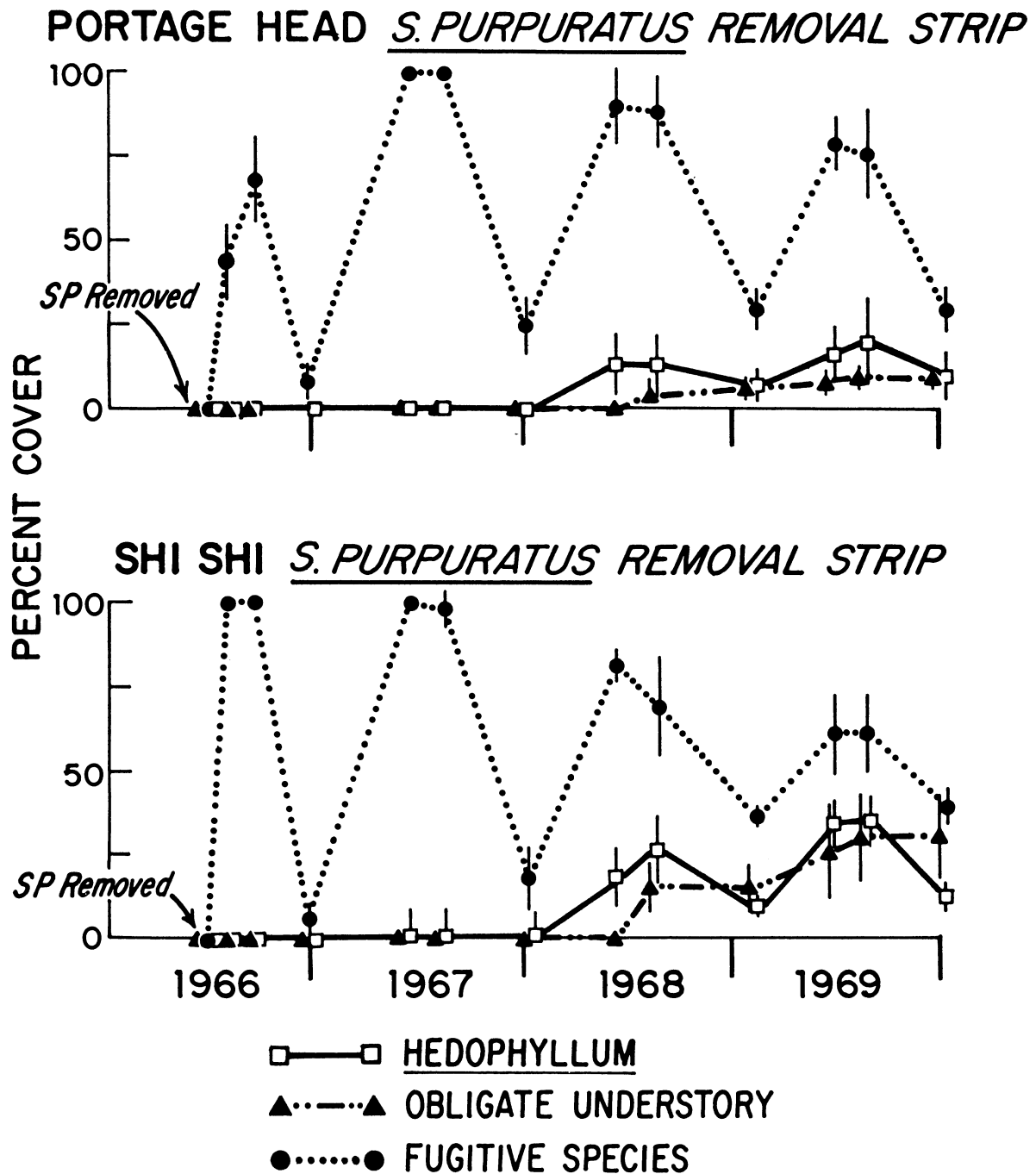


FIG. 5. Mean percent covers of *Hedophyllum* canopy, obligate understory species, and fugitive species following removal of *Strongylocentrotus purpuratus* from two 4-m² outer-coast sites. Variance is presented as SD of 4 one-fourth-m² samples. No *Katharina tunicata* were seen in either area.

and pedicellariae and eventually moving away. In the Portage Head and Shi Shi pools, the extremely high densities of sea urchins usually forced the fleeing urchins to climb onto other urchins. When a *S. purpuratus* is on the rock substratum and particularly when it is in a depression in the substratum, it is

extremely well attached and difficult to dislodge; however, when it is on another urchin it has a tenuous grip; in addition, the individual below appears to attempt to dislodge it with its spines and pedicellariae. Therefore, the fleeing urchin is likely to be dislodged by wave agitation, and most of the *S. purpuratus* that

retreat from the presence of *Pycnopodia* are removed from the pool by wave action with the incoming tide. Thus, by effectively stampeding the sea urchins, *Pycnopodia* is responsible for displacing 7.4–12.2 urchins per day and over a period of a few weeks for clearing 1.0–2.4 m² patches in the middle of dense covers of *S. purpuratus* (Table 8).

A major portion of the diet of the conspicuous green anemone, *Anthopleura xanthogrammica*, is provided indirectly by the foraging of *Pycnopodia* and *Pisaster ochraceus* (Dayton 1973b). The fact that *Anthopleura* consumes the urchins displaced by *Pycnopodia* is important to the organization of this community because many of the displaced urchins would otherwise simply be moved to other patches cleared earlier by *Pycnopodia* or some other disturbance. That is, without *A. xanthogrammica*, the net effect of *Pycnopodia* would be to chase the urchins from one spot to another without maintaining the cleared patches necessary for algal succession. Thus *Anthopleura*, along with *Pycnopodia*, is ultimately partly responsible for the procurement of distinct patches of free space resulting in the characteristic patchy algal cover of the lower intertidal along the outer coast. By acting on the functionally dominant herbivore, *Pycnopodia helianthoides* and *Anthopleura xanthogrammica* have community roles much more important than other carnivores in the association, such as various sponge- Cnidaria, Ectoproct- and gastropod-eating nudibranchs (*Archidoris montereyensis*, *Diaulula sandiegensis*, *Aeolidia papillosa*, *Triopha carpenneri*, *Dirona albolineata*), the generalized carnivorous gastropods such as *Thais lamellosa*, *Ceratosoma foliata*, *Ocenebra* spp., and *Searlesia dira*, which eat barnacles, boring bivalves, chitons, limpets, etc., or the actinians *Tealia crassicornis* or *T. coriacea*, which presumably scavenge and eat planktonic organisms.

Intertidal populations of *S. purpuratus* appear adapted to stay in one spot and wait for drift algae; I know of no observation of their moving into a clearing made by *Pycnopodia*, despite predictable increases in the algal standing crop in these cleared patches. In addition, *S. purpuratus* recruitment is rare. It appears that the only larval recruitment of *S. purpuratus* between 1959 and 1969 was in 1963, when Ebert (1968) and Paine (*pers. comm.*) observed large numbers of young urchins in Oregon and Washington, respectively. From his age studies of *S. purpuratus*, Ebert (1968) concluded that there was no appreciable urchin settlement between 1959 and 1963 in Oregon; between 1964 and 1969 there was no settlement along the Washington coast. In 1969 I observed only four young urchins, but in 1970 Paine (*pers. comm.*) and I found some settlement of juvenile urchins under adults at Mukkaw Bay and Waadah Island. Because the intertidal *S.*

TABLE 9. Anemone-urchin competition. Three tidepools with large urchin-anemone populations at Portage Head were filled with the urchin *Strongylocentrotus purpuratus* in July 1966. The urchins were counted 1 day after the additions were firmly attached to the substratum. Subsequently the anemones, *Anthopleura xanthogrammica*, were observed eating urchins. After 6 wk the urchins were counted; the totals were approximately equal the original urchin densities

Approximate pool size (m ²)	Total no. of anemones	Original no. of urchins	Total no. of urchins 1 day after addition	Total no. of urchins 1.5 mo later
0.40	15	89	241	95
0.75	27	102	285	111
1.20	41	153	490	165

purpuratus are not motile grazers and have an unpredictable and rare larval recruitment, those patches in this region cleared of urchins by *Pycnopodia* remain available for algal colonization for several years.

Competition for space between anemones and sea urchins

While the algae and urchins are major space consumers in this intertidal zone, the anemone *A. xanthogrammica* may use as much as 80% of the space in tidepools and surge channels. In many pools and channels large urchin and anemone populations together utilize most of the substratum space, a condition suggesting the hypothesis of competition for space between these sedentary species. The best test of this hypothesis is to reduce the density of one of the populations and observe an increase in the other; this, however, was not possible because of the uncertain, extremely low recruitment of both the urchins and the anemones. The only means of evaluating the possibility of competition was to test the hypothesis that space was a limiting resource. This was done by doubling or tripling the urchin densities in three tidepools at Portage Head; if space was limiting in these situations, one or both of the populations should have declined. The limiting resource hypothesis was verified because the density of urchins in the tidepool quickly returned to approximately the preaddition density (Table 9). The decrease was not a result of competition alone, however, as the anemones responded to the interspecific crowding by consuming the urchins within reach of their tentacles. Thus, although the urchins and anemones share a potentially limiting resource, the allocation of the spatial resource between the two species is determined by predation.

Patterns of algal succession in tidepools

The pattern of succession following the natural removal of urchins by *Pycnopodia* and *Anthopleura*

was observed for up to 5 yr in 14 Portage Head tidepools (Dayton 1970). The tidepool (mean depth = 60 cm) pattern differs in several respects from that of the exposed intertidal situation. The canopy is composed of more species (*Nereocystis luetkeana*, *Costaria costata*, *Pleurophycus gardneri*, *Cymathere triplacata*, *Laminaria setchellii*, *Egregia menziesii*, and various species of *Desmarestia*), while the understory is composed of fewer species, mostly those identified as subtidal extensions in the obligate understory category. *Hedophyllum sessile* rarely extends more than 20 cm below the water line in a tidepool, and the strictly intertidal component of the obligate understory, the articulated coralline algae, is usually absent, as are most of the other intertidal species in the fugitive category.

In addition to differences in the species composition, the patterns of succession are strikingly different. There is a slow change in the composition of the canopy species as early canopy colonizers such as *Nereocystis* and *Desmarestia* spp. are slowly joined by *Costaria* and sometimes *Cymathere* and *Pleurophycus*; eventually *Laminaria* and *Egregia* appear. In contrast to the clear displacement patterns in the exposed intertidal areas (cf. Fig. 1-4), *Nereocystis* is the only canopy species in the deeper pools that disappears after the first year or two in these urchin-cleared patches. Vadas (1968) found that *Nereocystis* has a very light-dependent life history; its displacement possibly is a result of its being out-competed for light by both the understory and the canopy. Most of the other species in these pools persisted for the period of observation, but the frequencies shifted, with *Egregia* and *Laminaria* becoming relatively more abundant. In addition, again in contrast to the exposed situation in which the fugitive species are displaced by the canopy species, the fleshy algae composing the understory in the tidepools increased their cover over time and persisted throughout the period of observation. Finally, the understory species abundance increased during the same period.

These slow and inconclusive patterns of tidepool succession observed at Portage Head contrast with that in the shallow tidal depressions at Muckaw Bay discussed by Paine and Vadas (1969) in which *Hedophyllum* recovered to complete cover in 20 mo. These depressions cannot be compared with the deeper pools in which *Hedophyllum* does not occur, but Paine (*pers. comm.*) subsequently cleared a deeper pool at Muckaw Bay that became dominated by *Laminaria* within 2 yr. I hypothesize that the succession I observed in the deep but protected Portage Head pools progresses relatively slowly because the canopy species are in suboptimal habitats and do not have a clear dominance. For example, *Desmarestia ligulata*, *Costaria costata*, *Nereocystis*

luetkeana, *Pleurophycus gardneri*, and *Cymathere triplacata* are kelp species which in this area are found in shallow water in protected areas such as the San Juan Islands. When individuals of these species do occur in the more exposed habitats, they are usually ragged and tattered from the wave action. I suggest that the conditions at Portage Head are sufficiently exposed so that these species are unable to exert competitive dominance, but are not sufficiently exposed to give the more durable *Egregia menziesii* and *Laminaria setchellii* a clear competitive dominance. These conclusions are supported by observations at Tatoosh Island, where the exposed points are dominated by *Lessoniopsis littoralis*, *Laminaria setchellii* and *Alaria marginata*. Their very durable stipes probably give them an advantage in exposed areas but become a disadvantage in more protected areas, where other species (such as *Cymathere*, *Costaria*, *Pleurophycus*, *Laminaria groenlandica*, *Nereocystis*, and *Egregia*) with broader and sometimes floating fronds are able to grow above them. Thus, apparently opposing factors influence the succession: wave exposure selects for plants with durable stipe systems, whereas competition for light selects for broad bladed plants or those plants that float on the surface. It seems likely that the Portage Head tidepool site represents a transition area in exposure in which there is no clear dominant.

DISCUSSION

The relative strength of ecological dominance in this community is manifested by those environmental parameters determining the rate of recovery of the populations of canopy-forming species following a perturbation. The following five environmental variables are probably the most important such parameters in this community: (1) physical or physiological stress, (2) grazing, (3) competition with the fugitive species, (4) weak dominance resulting from adaptations to different habitats, and (5) the effects of temporal and spatial heterogeneity.

The effect of water motion and physiological stress is important to *Hedophyllum sessile* as demonstrated by the significant correlation between the degree of wave exposure and its rate of recovery. However, this relationship is neither linear nor clear cut, as the rate of *Hedophyllum* recovery is not directly proportional to my subjective evaluation of increasing wave exposure from Turn Rock to Shi Shi reef. For example, the Turn Rock experimental *Hedophyllum* removal area returned to 34% cover in 3 yr (Fig. 1), whereas at the Eagle Point area, which is exposed to both log battering and relatively high levels of desiccation, the average summer canopy was 51.2% in the control areas and the recolonization was relatively slow, with 10.0%-26.3% canopy cover reestablished after 3 yr (Fig. 1). The recovery at

the Portage Head site, at both the *Hedophyllum* removal and *Strongylocentrotus* removal plots at Shi Shi, and at the various sites at Waadah Island are not proportional to that suggested by the increase in wave exposure and decrease in desiccation stress. This suggests that other ecological factors also strongly influence the rate of algal succession.

Grazing has been considered, and I concluded that the molluscan herbivores have little, if any, delaying effect on the algal succession, but that the echinoderm *Strongylocentrotus purpuratus* commonly over-exploits the algae to the extent that only encrusting coralline algae persist in the presence of concentrations of these urchins. For this reason the algal succession experiments were done in the absence of *S. purpuratus*, and no grazing-induced delays were observed in the rate of algal succession.

I tested the hypothesis that the fugitive species inhibit the growth of the articulated coralline algae and the recruitment of *Hedophyllum*. I thinned the fugitive species cover at Portage Head by non-selectively pulling out handfuls of the fugitive species in two 0.25-m² patches until the cover appeared to be about one-half that in the adjacent control. Within a month the experimental corallines had noticeably more branches than did those in the control, but severe winter weather conditions prevented the collection of quantitative data. By the following spring the experimentally thinned areas had a total of five *Hedophyllum* plants (60% canopy cover) compared to one (10% canopy cover) in the control area. In the San Juan Island sites there is no indication that the recovery of the *Hedophyllum* canopy is delayed by competition with other algae, as the fugitive cover is often sparse. Clearly this experiment is incomplete, but it does suggest the potential competitive influence of the fugitive species.

The reduced successional rate resulting from weak dominance has been discussed with respect to the slow succession observed in the tidepools at Portage Head, which exhibited rates of succession toward monocultures much slower than those found at other sites. I hypothesized that the succession progressed slowly because the canopy species do not have a clear dominance in those particular tidepools. The compromises observed here between the conflicting strategies—toughness in withstanding battering by waves and effectiveness in competing for light—may affect the expression of dominance in many natural situations with more than one dominant species. This does not apply, obviously, to the situation in those areas where *Hedophyllum* was the only canopy species and not able to share its dominance.

Many aspects of algal succession obviously depend upon the season in which appropriate space becomes available, and clearly the availability of disseminules at opportune times is, therefore, a major factor in

algal succession. However, within-season temporal factors in this community may have a rather modest influence, succession occurring in summer and winter patterns that are internally rather consistent. For example, the clearing experiments, with intensive subsequent surveys, of Northcraft (1948), Lee (1965), Castenholz (1967), Vadas (1968), Dayton (1971), and this paper, showing that many algal species in this community recruit over most of the summer, suggest that the spores are released over the entire period. These disseminules, by being available over a relatively long seasonal period, are able to colonize the spatially and temporally somewhat unpredictable patches of primary substratum that become available during the summer. *Hedophyllum*, by releasing its spores and settling in the winter, on the other hand, has apparently adapted very successfully to the predictable availability of space produced by winter storms and the annual winter die-off or defoliation of most algae. Much the same pattern has been described for *Laminaria sinclairii* (Markham 1968, 1973), and there may be such a winter sporulating strategy for a number of other species.

An additional factor that may act to reduce temporal heterogeneity in algal succession is that the actual appearance of an alga is in part a function of the available zoospore population with its seasonal component and in part a function of the essentially unknown microscopic gametophyte life-history phase. A lengthy sporeling or gametophyte phase certainly can make the successful growth of the plant uncertain. On the other hand, the longevity of at least some gametophytes (Sundene 1962, Kain 1964, 1969) makes possible a dormancy strategy by which the appearance of the sporophyte can be delayed until more favorable seasonal or ecological conditions appear. Thus the effects of temporal heterogeneity in habitat availability could influence the successful recruitment of most intertidal species; there is evidence of adaptations to seasonal availability of space, but many algal species appear to have adaptations reducing the importance of temporal uncertainties.

Patches of habitat space are made available under natural conditions by storms and drift logs disrupting the algal cover and by *Pycnopodia* stampeding sea urchins; some fugitive species quickly colonize these patches, but other algal species do so much less predictably. The general importance of the spatial heterogeneity represented by these cleared patches is difficult to resolve, because very little is known about dispersal patterns in algae. I have no evidence of the efficiency of *Hedophyllum* dispersal into isolated cleared patches, but I have demonstrated (Dayton 1973a) that the effective range of spore dispersal of *Postelsia palmaeformis* seems limited to a narrow radius, approximately 3 m. *Hedophyllum* dispersal may operate under constraints similar to those on

Postelsia, which means that spatial heterogeneity would have considerable importance to the strength of *Hedophyllum* dominance.

The physiological well being of the dominant species is, in this case, only one of a number of important variables determining the strength of expression of ecological dominance. The complete loss of dominance of *Hedophyllum* in its physiologically optimal area to a competitively superior species and the strong indication that competition with fugitive species retards the recovery of the dominant species offer convincing support of this conclusion. The common assumption of linearity between physical and ecological variables (discussion in Colwell and Futuyma 1971) is not valid in this community.

Two intertidal associations: one community?

A number of striking parallels occur between this lower intertidal algal community and the higher barnacle/mussel community discussed previously (Dayton 1971): clear competitive superiority vested in a few species, an escape in growth from molluscan consumers, and the continued importance of disturbance by echinoderm predators. In the protected outer coast sites *Mytilus californianus*, like *Hedophyllum*, enjoys a clear dominance in the competition for space and potentially can exclude most of the sessile species. And, while experimental proof is lacking, *Mytilus* appears to be similar to *Hedophyllum* in offering a protected habitat among its byssal threads to an association of species of crabs (two species of *Petrolisthes*), nereid polychaetes, holothurians (particularly species of *Cucumaria* and *Eupentacta*), an isopod, *Cirolana harfordi*, nemerteans, especially *Paranemertes peregrina* and *Emplectonema gracilis*, and various species of flatworms. However, the byssal association of *Mytilus* lacks the obligatory nature of some of the *Hedophyllum* understory because individuals of the *Mytilus*-associated species can be found in numerous other intertidal habitats that offer protection from desiccation. Another difference relating to the establishment of the respective competitive dominants is that molluscs (species of *Acmaea* and *Thais*) are much more effective filters in delaying the establishment of *Mytilus* than are the molluscan herbivores in delaying algal recruitment. Both dominant species have echinoderm consumers (*Pisaster* on *Mytilus* and *Strongylocentrotus* on *Hedophyllum*) capable of removing them from large areas of the intertidal. But *Pisaster* selectively searches out *Mytilus* (Paine 1969), whereas because *S. purpuratus* usually remains stationary and is not a motile adventitious grazer, it thus depends on a numerical rather than functional response to control prey populations. Finally, the lower algal association has an additional

important level of echinoderm predation as *Pycnopodia* consumes and displaces *S. purpuratus*.

In each case these patterns, though analogous, involve different populations and appear to be distinct from one another. Then one asks whether these associations are functionally and evolutionarily distinct or whether they are influenced by common species.

In the San Juan Islands there was little indication of any biological interaction between *Balanus cariosus* and *Hedophyllum sessile*, the competitive dominants of the upper and lower zones, respectively. *Hedophyllum* holdfasts occasionally grow over and kill *B. cariosus*, as well as the very much larger, generally subtidal, *B. nubilus*. However, the *Hedophyllum* holdfasts were never observed to dominate more than 8% of the primary substratum, and the canopy cover is usually not over 60%. Therefore, compared to the regular and heavy predation effects of *Pisaster*, *Lep-tasterias*, and *Thais* defined previously (Dayton 1971, Menge 1972a,b) the effects of space competition with *Hedophyllum* are probably very minor determinants to the establishment of the lower limit of the barnacle/mussel association. Very likely, as in the higher zone (Connell 1972), physical stress, particularly desiccation, sets the upper limit to the distribution of *Hedophyllum* and the other algal species of the lower intertidal.

Paine (1974) has shown in an experiment begun in 1963 that the lower limit of *Mytilus californianus* at Mukkaw Bay can be extended about 1.5 m by the exclusion of *Pisaster ochraceus*. Presumably the only reason that the *Mytilus* distribution did not move even lower was that Paine was unable to exclude *Pisaster* from the low intertidal zone. Thus this experiment did not resolve the question of whether or not the *Mytilus* could have extended through the algal association.

I have seen *Hedophyllum*, *Lessoniopsis*, *Laminaria*, *Postelsia*, and *Alaria* holdfasts grow over and smother and thereby out-compete *Balanus glandula*, *B. crenatus*, *B. cariosus*, and the subtidal *B. nubilus* for primary space; but can they out-compete *Mytilus californianus*? That is, given an appropriate environment, is the lower limit of the *Mytilus* distribution determined by intrinsic settling preferences, by predator pressure, or by competition with the dominant algae? Two natural situations help to answer this question. At the exposed northeast corner of Tatoosh Island a partial escape from *Pisaster* predation allowed the lower limit of the *Mytilus* distribution to move down to approximately the 0 to -1' level by 1970. I have demonstrated that *Lessoniopsis* is competitively the most successful algal dominant in this area. However, at Tatoosh Island, the *Lessoniopsis* were apparently being out-competed by *Mytilus*, which had settled in an aggregation 23–28-cm thick

around the stipe and holdfast systems of *Lessoniopsis*. The aggregation of *Mytilus* had not killed the observed *Lessoniopsis*, but the *Lessoniopsis* population was much less dense than it was below the *Mytilus*. Most important, the individual *Lessoniopsis* growing out through the *Mytilus* appeared relatively old and were all attached to primary substratum, a condition suggesting that *Lessoniopsis* cannot recruit among the *Mytilus*. This negative effect of *Mytilus* on the recruitment of algae was demonstrated experimentally for *Postelsia palmaeformis* at the same site (Dayton 1973a). Since there were many layers of *Mytilus* in the aggregation, it was obvious that the *Mytilus* larvae were successfully recruited among the byssal threads of the adults. Without recruitment the portion of the *Lessoniopsis* distribution observed in the *Mytilus* mat would disappear with the deaths of those few older *Lessoniopsis* individuals. This indicates that *Pisaster* predation is the only important biological influence preventing the downward extension of the *Mytilus*. In fact, *Pisaster* appeared to have raised the lower extension of the *Mytilus* in July 1971, and Paine (*pers. comm.* 1973) now estimates the lower limit of *Mytilus* at +2 ft. Because *Pisaster* cannot be removed here, this particular site will not allow a test of the hypothesis that *Mytilus* eventually dominates competition with *Lessoniopsis* following the experimental removal of *Pisaster*.

Additional evidence that the *Mytilus californianus* population can extend below the intertidal in this geographic region is found at Duncan Rock, a small and mostly submerged reef about 2 km northwest of Tatoosh Island. Here subtidal extension of *Mytilus* to a depth of at least 20 m supports the hypothesis that the lower limit of the vertical distribution of *Mytilus* in the intertidal zone is set not by competition or physical factors, but by the continuous pressures exerted by a number of predators, among which *Pisaster* is one of the most important. Because they eat mussels, sea otters (*Enhydra lutris*) must also have contributed to this predation pressure over evolutionary time.

In contrast to the mussels, the algal populations are restricted to a narrow band in the lower intertidal by such physical factors as desiccation from above and limiting light requirements from below. Because *Mytilus* appears capable of displacing *Lessoniopsis littoralis*, the competitive dominant among the algal association, it is reasonable to hypothesize that the algal niche on the outer coast is currently maintained by *Pisaster* predation on *Mytilus*. Certainly it seems that a few foundation species or disturbances (Dayton 1972) such as *Mytilus*, *Pisaster*, and damage from drift logs in the upper association and *Lessoniopsis*, *Hedophyllum*, *Strongylocentrotus*, and *Pycnopodia* in the lower zone dictate the patterns of distribution and abundance and probably the

evolution of many of the other species in the intertidal zone. Furthermore, *Pisaster* very likely has a keystone role in structuring the entire outer coast assemblage.

CONCLUSION

Ecologically dominant species have a disproportionately important evolutionary role in relation to their abundance or biomass. The relative evolutionary influence of a given population on other populations can be estimated by evaluating its influence on their distribution, growth, and regulation. Many recent experimental studies (e.g., Connell 1961a,b, Paine 1966, 1971a, Dodson 1970, Hall et al. 1970, Dayton 1971, Dayton et al. 1974) have demonstrated an old notion (e.g., Clements 1916) that particular species have disproportionately important roles in their communities. This concept is familiar to most naturalists (Elton's 1966 discussion of "girder species" and Paine's 1969a discussion of "keystone species") but has not found its way into popular ecological theory. I have considered this group of critical species that defines much of the structure of a community as "foundation species" (Dayton 1972) and have experimentally defined the roles of such species in this algal community. Specifically, I have defined the positive and negative roles of the competitive dominant and of the key herbivore and carnivore species.

Negative and positive roles parallel to those of *Hedophyllum* are common in many other communities. Boreal forests, for example, offer a familiar analogy; they are dominated by a few canopy species, but most of the species abundance is composed of the many understory fugitive species growing in the absence of the canopy (Loucks 1970). Parallels of the obligate understory have not been specifically experimentally demonstrated in boreal forests, but they are probably widespread, as species of ferns, mosses, fungi, liverworts, etc., which depend upon overstory protection from desiccation, are legitimate examples. Certainly, numerous obligatory relationships involve animals in boreal forests, since foliage structure furnishes critical habitats for insect, lizard, and bird populations. Furthermore, the different disturbance roles of the relatively inefficient molluscs and very important sea urchin, *S. purpuratus* discussed here, are paralleled in a boreal community by rabbits and deer, respectively (Ross et al. 1970). Finally, the important keystone disturbance role of *S. purpuratus* is paralleled by fire in many, if not most, terrestrial plant communities (Loucks 1970, Vogl 1969, 1973, Mutch 1970, Hanes 1971, Houston 1973, Swan 1970). The broad ecological consequences of this keystone effect of fire and the general nature of its occurrence has been thoroughly documented in many experimental studies published in

the Proceedings Annual Tall Timbers Fire Ecology Conference, Tallahassee, Florida.

The roles of competitively superior species and of the disturbances and natural enemies preventing their competitive monopolization of resources and allowing the proliferation of fugitive niches have been demonstrated or argued in most natural communities—for example, tropical forests (Janzen 1970, Elton 1973, Connell 1971), coral reefs (Branham et al. 1971, Dana et al. 1972, Connell 1974), lakes (Brooks and Dodson 1965, Dodson 1970, Hall et al. 1970), an Antarctic benthic community (Dayton et al. 1974), Phytotelmata (Maguire 1971), fouling communities (Sutherland 1974), and the deep sea (Dayton and Hessler 1972). Similarly, coevolution resulting in obligatory relationships is widespread, including such obvious examples as symbiosis, commensalism, and flowering plants with their pollinating and dispersal vectors. Another important example of an obligatory dependence of many species upon the habitat modification of an important foundation species is the reliance of a large number of benthic deposit feeders upon reworking of the sediment by a few species (e.g., *Molpadia*) described by Rhoads and Young (1970, 1971). This example is particularly interesting because of the possibility that similar obligatory relationships contribute to deep-sea diversity. Thus the existence of foundation species is probably very general in nature, and the fixation of much modern ecological theory on such community parameters as species diversity, rank order of abundance, biomass, etc., is independent of and probably not related to true knowledge of evolutionary relationships.

The expression of the importance of these foundation and keystone species has no relation to their rank order of abundance or biomass, because many such species are rare and/or small. We (Dayton et al. 1974) found this in an Antarctic benthic community potentially dominated competitively by a relatively rare sponge and small carnivores, and it is especially true of biological control situations (e.g., De Bach 1964, Huffaker 1971, and Connell 1971). The definition of the functional importance of these species demonstrates the greater value of the explanatory level of understanding, which is based on a mechanistic appreciation of community organization usually derived from experimentation, than of the simple predictive level of understanding, which usually rests on correlatory description.

ACKNOWLEDGMENTS

This paper is based on a dissertation submitted in partial fulfillment of the requirements for the Ph.D. in the Department of Zoology, University of Washington, Seattle. I thank my major advisor, Robert T. Paine, for his friendship and support. The constructive criticism of my thesis committee, R. T. Paine, A. J. Kohn, and R. L. Fernald were helpful throughout this research program.

Discussions with them and with J. Connell, L. Druehl, P. Illg, J. Kain, M. Neushul, B. Menge, G. Orians, D. Rivera, D. Simberloff, T. Spight, J. Stewart, R. Vadas, and R. Vance have been particularly helpful.

Many people have helped with the field work; in particular I thank A. DeVries, J. Drescher, S. Fullilove, S. Heller, S. Jordan, N. Lelleid, S. Louda, M. McKey, J. Mauck, and B. Rabbit. M. Harlin, P. Lebednik, and R. Norris kindly helped me with algal taxonomy. The cheerful and competent secretarial help of V. Currie is greatly appreciated. Finally, I am grateful to my wife, Linnea for her enthusiastic field work and editorial assistance.

I wish to further acknowledge the help of R. L. Fernald, who provided laboratory space and facilities at Friday Harbor Laboratories as well as personal support and friendship. Research support was provided by an NSF Marine Science Training Grant to Friday Harbor Laboratories, an NSF Ecology Training Grant to the Department of Zoology, and two NSF grants to R. T. Paine. While preparing this manuscript I received support from Sea Grant GH-112 awarded to University of California, San Diego, NSF Grants GA-30877 and GV-32511, and the Marine Life Research Group at Scripps Institution of Oceanography.

LITERATURE CITED

- Anderson, E. K., and W. J. North. 1966. *In situ* studies of spore production and dispersal in the giant kelp *Macrocystis*. Proc. Vth Int. Seaweed Symp.: 73–86. Pergamon.
- Bieble, R. 1957. La resistance des algues marines à la lumière. In *Ecologie des Algues Marines*. Colloq. Int. Cent. Natl. Rech. Sci. 81:191–203.
- Branham, J. M., S. Reed, J. H. Bailey, and J. Caperon. 1971. Coral-eating sea stars *Acanthaster planci* in Hawaii. *Science* 172:1155–1157.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150:28–35.
- Castenholz, R. W. 1961. The effects of grazing on marine littoral diatom populations. *Ecology* 42:783–794.
- . 1967. Stability and stresses in intertidal populations, p. 15–28. In T. A. Olson and F. J. Burgess [ed.] *Pollution and marine ecology*. Interscience, New York.
- Clements, F. E. 1916. *Plant succession*. Carnegie Inst. Wash. Publ. 242. 512 p.
- . 1920. *Plant indicators. The relation of plant communities to process and practice*. Carnegie Inst. Wash. Publ. 290. 388 p.
- . 1936. *Nature and structure of the climax*. J. Ecol. 24:252–284.
- Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. *Ecology* 52:567–576.
- Connell, J. H. 1961a. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710–723.
- . 1961b. Effect of competition, predation by *Thais lappillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.* 31:61–104.
- . 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Proc. Adv. Study Inst. Dynamics Numbers Popul., p. 298–312. In P. J. den Boer and G. R. Gradwell [ed.] *Dynamics of populations*. Oosterbeek 1970.

- . 1972. Community interactions on marine rocky intertidal shores. *Annu. Rev. Ecol. Syst.* **3**:169–192.
- . 1974. Population ecology of reef-building corals. Academic Press, London. (*In press.*)
- Conover, J. T., and J. M. Sieburth. 1966. Effects of tannins excreted from Phaeophyta on planktonic animal survival in tide pools. *Proc. Vth Int. Seaweed Sym. Pergamon*. 424 p.
- Dahl, A. L. 1964. Macroscopic algal foods of *Littorina scutulata* Gould. *Veliger* **7**:139–143.
- . 1973. Surface area in ecological analysis: quantification of benthic coral-reef algae. *Mar. Biol.* **23**:239–249.
- Dana, T. F., W. A. Newman, and E. W. Fager. 1972. *Acanthaster* aggregations: Interpreted as primarily responses to natural phenomena. *Pac. Sci.* **26**:355–372.
- Dayton, P. K. 1970. Competition, predation and community structure: The allocation and subsequent utilization of space in a rocky intertidal community. Ph.D. Thesis. Univ. Washington. 174 p.
- . 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* **41**:351–389.
- . 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. B. C. Parker [ed.] *Proc. Colloq. Conserv. Probl. Antarctic*. Allen Press, Lawrence, Kansas. 1972.
- . 1973a. Dispersion, dispersal, and persistence of the annual intertidal alga, *Postelsia palmaeformis* Ruprecht. *Ecology* **54**:433–438.
- . 1973b. Two cases of resource partitioning in an intertidal community: Making the right prediction for the wrong reason. *Am. Nat.* **107**:662–670.
- Dayton, P. K., and R. R. Hessler. 1972. Role of biological disturbance in maintaining diversity in the deep sea. *Deep-sea Res.* **19**:199–208.
- Dayton, P. K., G. A. Robilliard, R. T. Paine, and L. B. Dayton. 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. *Ecol. Monogr.* **44** (*in press*).
- De Bach, P. 1964. Biological control of insect pests and weeds. Reinhold, New York. 844 p.
- Dixon, P. S. 1965. Perennation, vegetative propagation and algal life histories, with special reference to *Asparagopsis* and other Rhodophyta. *Bot. Gotheburg. III. Proc. Vth Mar. Biol. Symp. Goteborg*. p. 67–74.
- Dodson, S. I. 1970. Complementary feeding niches sustained by size selective predation. *Limnol. Oceanogr.* **15**:131–137.
- Ebert, T. A. 1968. Growth rates of the sea urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. *Ecology* **49**:1075–1091.
- Elton, C. S. 1966. The patterns of animal communities. Methuen & Co., London. 432 p.
- . 1973. The structure of invertebrate populations inside neotropical rain forests. *J. Anim. Ecol.* **42**:55–104.
- Hall, D. J., W. E. Cooper, and E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.* **15**:839–928.
- Hanes, T. L. 1971. Succession after fire in the chaparral of southern California. *Ecol. Monogr.* **41**:27–52.
- Hellebust, J. A. 1970. Light-plants, p. 125–128. In O. Kinne [ed.] *Marine ecology Vol. 1, Part 1*. John Wiley, New York.
- Houston, D. B. 1973. Wildfires in northern Yellowstone National Park. *Ecology* **54**:1111–1117.
- Huffaker, C. B. 1971. Biological control. *Proc. AAAS Symp. Plenum Press, New York*. 1511 p.
- Hutchinson, G. E. 1951. Copepodology for the ornithologist. *Ecology* **32**:571–577.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**:501–528.
- Jones, N. S., and J. M. Kain. 1967. Subtidal algal colonization following the removal of *Echinus*. *Helgolander wiss. Meeresunters* **15**:460–466.
- Kain, J. M. 1964. Aspects of the biology of *Laminaria hyperborea*. 3. Survival and growth of gametophytes. *J. Mar. Biol. Assoc. U. K.* **44**:415–433.
- . 1966. The role of light in the ecology of *Laminaria hyperborea*, p. 319–334. In R. Bainbridge, G. C. Evans, and O. Rackham [ed.] *Light as an ecological factor*. Oxford, England.
- . 1969. Aspects of the biology of *Laminaria hyperborea*. 5. Comparison with early stages of competitors. *J. Mar. Biol. Assoc. U. K.* **49**:455–473.
- . 1971. Continuous recordings of underwater light in relation to *Laminaria* distribution, p. 335–346. In D. J. Crisp [ed.] *Fourth Europ. Mar. Biol. Symp.* Cambridge Univ. Press.
- Kitching, J. A., and F. J. Ebling. 1961. The ecology of Lough Ine XI. The control of algae by *Paracentrotus lividus* (Echinoidea). *J. Anim. Ecol.* **30**:373–383.
- Lebednik, P. A. 1973. Ecological effects of intertidal uplifting from nuclear testing. *Mar. Biol.* **20**:197–207.
- Lee, R. K. S. 1965. Development of marine benthic algal communities on Vancouver Island, British Columbia. In R. L. Taylor and R. A. Ludwig [ed.] *The evolution of Canada's flora*. Univ. Toronto Press. p. 100–120.
- Lewis, J. R. 1964. The ecology of rocky shores. *Engl. Univ. Press, London*. 323 p.
- . 1968. Water movements and their role in rocky shore ecology. 2nd Symp. *Mar. Biol. Sarsia* **34**:13–36.
- Loucks, O. L. 1970. Evolution of diversity, efficiency, and community stability. *Am. Zool.* **10**:17–25.
- Maguire, B. 1971. Phytolelomata: Biota and community structure determination in plant-held waters. *Annu. Rev. Ecol. Syst.* **2**:439–464.
- Markham, J. W. 1968. Studies on the haptera of *Laminaria sinclairii* (Harvey) Farlow, Anderson et Eaton. *Syesis* **1**:125–131.
- . 1973. Observations on the ecology of *Laminaria sinclairii* on three northern Oregon beaches. *J. Phycol.* **9**:336–341.
- Mauzey, K., C. Birkeland, and P. K. Dayton. 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. *Ecology* **49**:603–619.
- McNaughton, S. J. 1968. Structure and function in California grasslands. *Ecology* **49**:962–972.
- Menge, B. A. 1972a. Foraging strategy of a starfish in relation to actual prey availability and environmental predictability. *Ecol. Monogr.* **42**:25–50.
- . 1972b. Competition for food between two intertidal starfish and its effect on body size and feeding. *Ecology* **53**:635–644.
- Morton, J. M., and M. M. Miller. 1967. The New Zealand seashore. Collins, London. 635 p.
- Mutch, R. W. 1970. Wildland fires and ecosystems—a hypothesis. *Ecology* **51**:1046–1051.
- North, W. J. 1971. The biology of giant kelp beds

- (*Macrocystis*) in California. Nova Hedwigia Z. Kryptogamenkd Suppl. 32. 600 p.
- North, W. J., and C. L. Hubbs. 1968. Utilization of kelp-bed resources in southern California. Calif. Fish Game. Fish Bull. 139. 264 p.
- Northcraft, R. D. 1948. Marine algal colonization on the Monterey peninsula, California. Am. J. Bot. 35: 396-404.
- Paine, R. T. 1966. Food web complexity and species diversity. Am. Nat. 100:65-75.
- . 1969a. A note on trophic complexity and community stability. Am. Nat. 103:91-93.
- . 1969b. The *Pisaster-Tegula* interaction: Prey patches, predator food preference, and intertidal community structure. Ecology 50:950-961.
- . 1971a. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. Ecology 52:1096-1106.
- . 1971b. Energy flow in a natural population of the herbivorous gastropod *Tegula funebris*. Limnol. Oceanog. 15:86-98.
- . 1974. Intertidal community structure: Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia (in press).
- Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnol. Oceanog. 14:710-719.
- Rhoads, D. C., and D. K. Young. 1970. The influence of deposit-feeding benthos on bottom stability and community trophic structure. J. Mar. Res. 28:150-178.
- Rhoads, D. C., and D. K. Young. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts II. Reworking by *Molpadia oolitica* (Holothuroidea). Mar. Biol. 11:225-261.
- Ricketts, E. F., J. Calvin, and J. W. Hedgpeth. 1968. Between Pacific tides. 4th ed. Stanford Univ. Press, Stanford, Calif. 614 p.
- Rigg, G. B., and R. C. Miller. 1949. Intertidal plant and animal zonation in the vicinity of Neah Bay, Washington. Proc. Calif. Acad. Sci. 26:323-351.
- Ross, B. A., J. R. Bray, and W. H. Marshall. 1970. Effects of long-term deer exclusion on a *Pinus resinosa* forest in north-central Minnesota. Ecology 51:1088-1093.
- Solomon, M. E. 1949. The natural control of animal populations. J. Anim. Ecol. 18:1-35.
- Stephenson, T. A., and A. Stephenson. 1972. Life between tidemarks on rocky shores. W. H. Freeman, San Francisco. 425 p.
- Sundene, O. 1962. The implications of transplant and cultural experiments on the growth and distribution of *Alaria esculenta*. NYTT Mag. Bot. 9:155-180.
- Sutherland, J. P. 1974. Multiple stable points in natural communities. Am. Nat. (in press).
- Swan, F. R. 1970. Post-fire response of four plant communities in south-central New York State. Ecology 51:1074-1082.
- Vadas, R. L. 1968. The ecology of *Agarum* and the kelp bed. Ph.D. Thesis. Univ. Washington, Seattle. 282 p.
- Vogl, R. J. 1969. One-hundred and thirty years of plant succession in a southeastern Wisconsin lowland. Ecology 50:248-255.
- . 1973. Smokey's mid-career crisis. Sat. Rev. Sci. 1:23-29.
- Vogl, R. J., and P. K. Schorr. 1972. Fire and manzanita chaparral in the San Jacinto Mountains, California. Ecology 53:1179-1188.
- Weaver, J. E., and F. E. Clements. 1938. Plant ecology. McGraw Hill, New York. 601 p.
- Whittaker, R. H. 1965. Dominance and diversity in land plant communities. Science 147:250-260.
- Widdowson, T. 1965. A taxonomic study of the genus *Hedophyllum setchell*. Can. J. Bot. 43:1409-1420.