

AN ABSTRACT OF THE THESIS OF

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Succession and organization of rocky intertidal zone surfgrass beds (Phyllospadix scouleri Hook) were examined experimentally at two sites on the Oregon coast. The interaction of three attributes of the plant -- high persistence, high preemption, and slow recovery -- strongly influences the organization of surfgrass beds. Permanent plots indicate that surfgrass is persistent. Comparisons of experimental surfgrass removal and control plots demonstrate its preemptive ability, because removal plots are invaded by many algal species, but these algae are preempted from control plots. The slow growth of surfgrass rhizomes and the slower recruitment of surfgrass seeds indicate its recovery ability is low. The interaction of these phenomena produces a mosaic of surfgrass and algae in different successional stages.

The successional sequence following a disturbance is more complex than predicted by any simple model because of temporal and spatial variation as well as differences in the species replacement mechanism. In some plots the early colonists, the perennial brown algal blade Phaeostrophion irregulare and the annual green algal blade Ulva sp., dominated for three years; in others they were replaced by a suite of

middle successional species including the branched red algae Cryptosiphonia woodii. In other plots the slowest growing middle successional species, the branched red alga Rhodomela larix replaced other species. Part of this variability appears to be caused by large waves in the fall and winter, which remove large areas of algal cover, allowing dominant species to be replaced by either earlier or later successional species. Part of the variability appears to be caused by local differences in the surfgrass understory before disturbance. Rhodomela larix is usually not completely removed by disturbance and regrows from its holdfast more readily than it recruits from spores. The mechanisms by which later species replace earlier ones differ depending on the successional stage. Established Phaeostrophion inhibits Ulva and filamentous diatoms. In contrast, certain middle successional species are necessary for seeds of the late successional surfgrass to recruit. The barbed seeds become attached to algal species with a central axis approximately 1 mm in diameter but not to algae with other forms.

Community Organization and Succession
in Rocky Intertidal Surfgrass Beds

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COMMUNITY ORGANIZATION AND SUCCESSION IN
ROCKY INTERTIDAL SURFGRASS BEDS

Chapter I.

GENERAL INTRODUCTION

The concepts of communities and succession are fundamental to ecology (Godwin 1977, Golley 1977, McIntosh 1981). Nineteenth century biologists studied the physiology of individual species but did not consider groups of species and their interactions. Thus, the concept of communities of species opened a new field of scientific inquiry. Simberloff (1980) believes that the typological philosophical viewpoint, the belief in ideal types originating with Plato, strongly influenced the original concepts of communities and succession advanced by Clements (1916). Clements portrayed communities as discrete entities, as recurring species groups. Areas could be classified into communities in much the same way as individual organisms could be classified into species. He defined succession as the changes from one community to another in an entirely new area or after a disturbance. According to Clements, these changes are analogous to the development of an individual organism. They proceed in an orderly, predictable sequence, each community preparing the way for the next. Succession ends in a mature, self-replacing climax community. Because succession and communities are concepts formulated together, they can be studied in an integrated way (Lubchenco and Menge 1978).

The extent to which Clements' (1916) idea dominated ecology is now controversial. Some authors claim his work was virtually unchallenged (Connell and Slatyer 1977, Egler 1981). Others point out that many older papers were remarkably modern in their outlook (Jackson 1981, McIntosh 1981). Certainly, Clements' (1916) concepts were questioned early. Gleason (1917, 1926), for example, maintained that species are not predictably associated with each other in communities but that their distributions reflect their differing genetic, physiological, and life history characteristics.

Although some modern workers still agree with the traditional ideas (Odum 1969), most are very critical (e.g., Drury and Nisbet 1973, Sutherland and Karlson 1977, Connell and Slatyer 1977). Modern ecologists have stressed the importance of predation both within communities (e.g., Paine 1966, Connell 1975, Menge and Sutherland 1976, Caswell 1978, Huston 1979) and in the species replacement process during succession (e.g., Connell and Slatyer 1977, Lubchenco and Menge 1978, Sousa 1979). Connell and Slatyer's work has stimulated many investigations, because they formulated a testable alternate hypothesis to that of Clements (1916). Their hypothesis states that early space occupiers, rather than enhancing the establishment of later species, actually inhibited later species, and that the deaths of earlier colonizers, by natural enemies or by abiotic conditions, accelerated species replacement.

This dissertation describes an integrated investigation of community organization and succession designed to illuminate portions of the long standing controversies. I studied communities dominated by the

surfgrass Phyllospadix scouleri in the low zone of the rocky intertidal Oregon coast, because the biology of this species allowed me to address many different problems in an integrated manner. The spatial and temporal scales of interactions in this community are amenable to experimental manipulation. Natural disturbances, such as removal of plants by wave action, could be mimicked experimentally. Thus, I studied secondary succession, which occurs after a disturbance, not primary succession, which occurs on new substrata. The two dimensional rock surface eliminates the possibility of underground interactions, such as those that occur in terrestrial plant communities (Harper 1977). The macroscopic seeds allowed me to quantify recruitment. The natural history of most of the organisms in this community is well known.

The dissertation has five chapters. These include (1) the general introduction, (2) organization of the mature community, (3) the early and middle successional stages, (4) the initiation of the last successional stage, and (5) the general conclusions.

Egler (1981) offered \$10,000 to anyone who could demonstrate that succession occurs as it has been traditionally described. He modeled his offer on an offer made by Harry Houdini for evidence of a genuine spiritual medium. The careful reader of this thesis will note that I could not claim Egler's money, because although some species do prepare the way for surfgrass, succession in this community is by no means an orderly, predictable process. But neither could I claim to have demonstrated the alternate hypothesis proposed by Connell and Slatyer (1977) and Sousa (1979). My work suggests that neither simple model

describes succession. This complexity should challenge ecologists. Comparisons among communities could lead to our goal, a general theory explaining why different processes occur in different communities.

CHAPTER II.

PERSISTENCE, PREEMPTION, AND RECOVERY:
ROCKY INTERTIDAL SURFGRASS BEDS

ABSTRACT

Surfgrass beds, composed primarily of Phyllospadix scouleri Hook, are a prominent feature of low zone horizontal benches in rocky intertidal areas on the Oregon coast. Their organization is strongly influenced by the interaction of three attributes of surfgrass--high persistence ability, high preemptive ability, and slow recovery ability. These attributes were investigated by: (1) quantifying community structure and persistence, (2) experimentally removing surfgrass, and (3) measuring rates of recovery from disturbance. The investigation extended over 3 yrs at two sites. The two sites differed dramatically in surfgrass cover. The differences corresponded to differences in their substrata, which were reflected in their disturbance rates. At Squaw Island, the area with a more stable sandstone substratum and less disturbance, permanent quadrats indicated that surfgrass dominates the canopy space (70-80% cover) and that this dominance continued over 3 yrs with little seasonal or year to year variation. At Boiler Bay, the area with a less stable mudstone substratum and greater disturbance, surfgrass occupies much less canopy space (14-29% cover) and is co-dominant with other species.

Experimental removals of surfgrass (0.25 m² plots) resulted in significant increases in algal cover and in upright plant diversity,

suggesting surfgrass preempts space. After clearance, a variety of algal species invaded (including Rhodomela larix, Cryptosiphonia woodii, and Phaeostrophion irregulare). The algae dominated the experimental plots for the remaining 34 mo of the study. During this time only nine surfgrass seeds recruited into 28 plots and occupied less than 1% cover. Mapped seedlings in a 28 m² area experienced a 93%/yr mortality rate. Rhizomes of surrounding surfgrass plants grew into experimental plots at a maximum rate of 6 cm in rhizome length/yr. The estimated time required for full recovery is >6 yr. The slow recovery rate makes even small rates of disturbance important. The persistence, the preemptive ability, and the slow recovery of surfgrass seem to be caused by its ability to capture space by vegetative growth, its large size, and its escape from herbivores.

INTRODUCTION

In many natural communities sessile species provide three dimensional structure and create habitats for other species (Woodin 1978, Suchanek 1979). Prominent examples include temperate forests (Sprugel and Borman 1980), salt marshes (Blum 1968), chaparral (Hanes 1971), kelp forests (Vadas 1968), and mussel beds (Paine and Levin 1981). Because space (or for plants, space in the light) is often a limiting resource in these communities, their organization is strongly influenced by competition for space, by predation and disturbance, which open space, and by the life history characteristics of the organisms that allow them to invade space. Although much progress has been made

in our understanding of such community organization (e.g., Connell 1975, Menge and Sutherland 1976, Caswell 1978, Huston 1979, Grime 1979, Paine and Levin 1981), our knowledge remains incomplete. One way to increase our knowledge is to investigate in an integrated manner the different phenomena organizing communities (Lubchenco and Menge 1978). In this paper, I report on a community in which I could simultaneously study three phenomena -- persistence, preemption, and recovery, all attributes of a dominant organism -- and I suggest that the interaction of these three attributes strongly influence the organization of this community.

The importance of these three features and their role in community organization have been recognized and investigated previously. Persistence ability, for example, is known to differ greatly among species and among populations of a species in different habitats. A dominant species with high persistence will greatly influence the community, and species with a "regeneration niche" (Grubb 1977) will be rare. Persistence ability can be quantified and understood only by long term investigations, but it can be fundamental to community organization (Menge 1976, Lubchenco and Menge 1978, Lewis 1980).

Preemptive ability has also been shown to influence community organization. By preemptive ability I refer to the ability of an established organism to prevent invasion. Many communities of adult organisms are barraged by propagules but are able to resist invasion. Experimental manipulations -- adding space -- can show the existence of these propagules. Sutherland (1981), for example, demonstrated that the tunicate Styela preempts space, preventing invasion by the larvae of other fouling organisms. Clearly, preemptive ability is an adaptive

characteristic, and most species will have some preemptive ability, but the mechanisms of preemption will vary with the biology of the organism.

Characteristics of recovery from disturbance also influence community organization. The rate of recovery influences communities, because slow recovery by a competitive dominant means a longer period of increased diversity following a disturbance (Huston 1979). The type of recovery, whether by adults or by juveniles, could also influence the community. Vegetative growth by adults surrounding disturbed areas could allow for faster recovery. Interactions between adults growing vegetatively might differ substantially from interactions between juveniles (e.g., Buss and Jackson 1979).

I investigated the interaction of these three features, persistence ability, preemptive ability, and recovery ability, in communities dominated by the surfgrass Phyllospadix scouleri Hook in the low zone of rocky intertidal habitats on the Oregon coast. Observations and experiments were designed to answer three questions:

- (1) Does surfgrass dominate space and how persistent is it?
- (2) Can any or all of the following hypotheses explain the dominance of surfgrass: (a) physical conditions and disturbances (e.g., sand scour) prevent other species from colonizing surfgrass habitats; (b) consumers remove all species but surfgrass, or (c) surfgrass preempts space from other species?

- (3) What are the rates of recovery by invasion by adults (i.e., vegetative growth of rhizomes) and invasion by juveniles (i.e., settlement of seeds)?

NATURAL HISTORY OF SURFGRASS
AND DESCRIPTION OF STUDY SITES

Unlike most marine plants, P. scouleri is a seagrass, an angiosperm as opposed to an alga. Although only sixty species exist, seagrasses dominate many marine communities throughout the world (McRoy and Helffferich 1977, Phillips and McRoy 1980). Members of the genus Phyllospadix are the only seagrasses living on rock; they range from Alaska to Baja California (den Hartog 1970). Phyllospadix torreyi lives in the extreme low intertidal zone and in the shallow subtidal zone, and P. scouleri lives in the low intertidal zone. Because I investigated only P. scouleri, in this paper the term surfgrass refers only to this species.

Phyllospadix scouleri is a perennial plant, which has densely-packed, grass-like leaves, 2-4 mm wide and approximately 0.5 m long, borne on a branched rhizome. Adventitious roots from the rhizome secure the plant to the rock. Growth of these rhizomes can produce large beds. Because the rhizomes often break, I could not distinguish genetic individuals; thus, throughout this paper I use the terms surfgrass beds and surfgrass plants synonymously. This study was restricted to emergent horizontal benches where large surfgrass beds

most commonly grow. Mature surfgrass beds often have many associated plants and animals (Stewart and Myers 1980).

Sexual reproduction in seagrasses illustrates how well they are adapted to marine habitats (e.g., Dudley 1893, Pettitt et al. 1981). Pollination occurs underwater. The filamentous pollen is dispersed by water movement, until it adheres to protruded stigmas. P. scouleri plants are dioecious, producing flowers in May. Surfgrass fruits develop over the summer then are released in September. Perhaps the most unusual feature of surfgrass is its barbed seeds, which must attach to algae to recruit (Gibbs 1902, Chapter 3). These barbed seeds are probably barbed as an adaptation to wave-swept rocky habitats, because most other seagrasses, growing on soft substrata in calm areas, lack barbed seeds. Presumably these other species recruit as their seeds fall to the soft substratum. Surfgrass seeds become attached to algae from September through March. They are 6 mm wide and readily detected by a careful visual search of the plant-covered substratum. Soon after attachment the seeds germinate, produce blades and then roots, which eventually anchor the plant to the rock. The plant continues to invade space by vegetative growth. More detailed description of this plant can be found in Dudley (1893, 1894), Chrysler (1907), den Hartog (1970), Tomlinson (1974, 1980), Drysdale and Barbour (1975), Barbour and Radosevich (1979), and Phillips (1979).

This investigation was conducted at two main sites and one secondary site. Squaw Island (43°19'N, 124°23'W, Fig. 1A), a sandstone bench along a spit connecting the island to the mainland, is 4 km south of Charleston on the southern Oregon coast (Fig. 2, Doty 1947a). Boiler

Bay (44°50'N, 124°03'W, Fig. 1B), a mudstone bench, is 1 km north of Depoe Bay on the central coast of Oregon (Fig. 2). Both sites are protected outer coast, and both are scoured by sand. I have observed patches of sand occasionally up to 2 cm deep in my permanent quadrats at both sites; other areas at these sites have even deeper sand. These sites appear to be typical in comparison to other areas of the Oregon coast (Doty 1947a, b, Phillips 1979). A third site 0.5 km south of the Squaw Island site was used to conduct a clipping experiment. It resembles the Squaw Island site both physically and biologically.

The two sites appear to differ most strongly in the rates of disturbance they experience. At Boiler Bay the soft mudstone, riddled with boring animals, breaks apart readily. By contrast, the sandstone substratum at Squaw Island is much more stable. To quantify the differences in disturbance rates between the two sites, I estimated the area of broken rock within a 30 m x 20 m area at each site in May 1982. Newly exfoliated areas are visible for 1 yr. At Squaw Island 0.04% of the area had exfoliated in 1 yr, at Boiler Bay 0.13%. These rates are consistent with unquantified observations over 3 yr.

METHODS

To quantify patterns of community structure, I chose methods comparable to other studies of community organization (Menge 1976, Lubchenco and Menge 1978). To assess surfgrass persistence, I placed ten 0.25 m² quadrats randomly along a 30 m line parallel to the shore at a tide level of approximately +0.3 m at each study site. To allow

repeated sampling of these quadrats, I marked these quadrats at the corners with nails and Sea Goin' Poxxy Putty®. Within these quadrats I estimated the percent cover of sessile invertebrates and plants using a flexible vinyl quadrat with 100 randomly placed dots on it. Cover estimates were obtained by counting the number of dots above each species. Repeated sampling of the same quadrat using this method shows that the error in estimates of percent cover obtained in this way is about $\pm 5\%$ (Menge 1976). Species present but not under a dot were recorded arbitrarily as 0.5% cover; the densities of mobile animals were also recorded. Because several abundant animals were small or buried in sand and surfgrass roots, I could not determine their densities; these include amphipods, isopods, and the gastropod Lacuna marmorata.

I recorded four categories of space utilization. Primary space occupants were those species attached directly to the rock. They included barnacles, anemones, encrusting algae, surfgrass roots and rhizomes, and the holdfasts of erect algae. Understory or secondary space was occupied by the thalli of erect shrubby plants up to 10 cm tall. Canopy space was defined as three dimensional space occupied by the blades of large algae and surfgrass plants over 10 cm tall. Many algal species occupy both canopy and understory space during their lives. Epiphytic algae were recorded separately. Occasional overlap within a layer caused some quadrats to have greater than 100% cover. In other words, if one small plant lay on top of another, each species was counted as having 1% cover. In this respect the method differs from that of Menge (1976) and resembles that of Littler and Littler (1980).

Parametric statistics were computed from percent cover data treated with an angular transformation (Sokal and Rohlf 1969).

To distinguish between the three alternative hypotheses that could account for the dominance of surfgrass (see introduction), I removed surfgrass from experimental plots. The rationale for the experiment runs thus: the physical environment and consumers have not been manipulated; therefore, if different species settle in experimental plots, they can live in this environment and can withstand the consumers, but surfgrass normally preempts the space. I removed surfgrass with a wrecking bar and putty knife from four replicate 0.25 m² areas with a canopy cover >90% surfgrass. Four similar unmanipulated areas served as controls. Similar disturbances occur naturally in these communities (pers. obs). This method does not remove all encrusting algae, but such plants are rare (<10% cover) under the thick surfgrass canopy and often die from desiccation when the surfgrass is removed. Also, when wave action removes surfgrass, encrusting algae remain. The patterns of space utilization and densities of herbivores were recorded before the manipulation and four times/yr for 3 yr thereafter. This experiment was repeated at each site with four replicates in each season.

To determine the relative importance of blades and rhizomes in the preemptive ability of surfgrass, I performed an experiment altering the morphology of plants within a surfgrass bed using four treatments with four replicates each: (1) removal of all surfgrass plants from 0.25 m² experimental quadrats and a 0.5 m wide buffer zone around each replicate to prevent shading (cumulative blade and rhizome effect), (2) monthly

clipping of all surfgrass blades to a uniform 5 cm length in the experimental quadrats and the buffer zone (blade effect), (3) removal of all surfgrass plants from 20 cm x 20 cm quadrats shaded by surrounding surfgrass (rhizome effect), and (4) unmanipulated control plots of 100% surfgrass. The experiments were conducted from September to December 1980. Ulva, an early successional species, was the only species to invade any treatment. The number of newly settled Ulva plants per 0.25 m² was compared to determine the effectiveness of each treatment in preventing invasion.

To determine the rate of recovery, I measured the growth rate of both damaged and undamaged surfgrass rhizomes as well as the recruitment and survivorship of seeds. The rate of rhizome encroachment into experimental removals measures recovery by damaged plants. Changes in the outlines traced on plastic sheets of 16 small, isolated, marked plants measure growth by undamaged plants. To determine the effect of surrounding plants on rhizome growth rate, I removed the surrounding algae (mostly Rhodomela larix) from eight of these traced plants. To determine the rate of juvenile invasion, I monitored seedlings not only in the experimental removals but also on a horizontal bench devoid of large surfgrass plants at Boiler Bay. On this bench survivorship and growth rate of surfgrass seedlings were estimated by mapping all the seeds and seedlings within 1 m along either side of a permanently marked 14 m long transect line (= 28m²). I systematically searched the area using a grid. I mapped seedlings using a meter stick and a compass to determine the bearing and distance of each plant from fixed points marked with a nail every 0.5 m along the transect line.

RESULTS

Community structure and persistence

Surfgrass occupied more space than any other single species at each study site, and it persisted over three years with little seasonal or annual variation (Fig. 1, 3, 4, Table 1). The differences between the two sites seem related to their disturbance patterns. Surfgrass is clearly the dominant space occupant at Squaw Island, the area with the more stable substratum; it occupied 70-80% of the canopy cover. Though P. scouleri occupied more space than any other single species (14-29% canopy cover) at Boiler Bay, the area with the less stable substratum, its congener P. torreyi and the alga Rhodomela larix also occupied up to 20% of the canopy or understory space and are co-dominants. Patterns of primary space occupancy were similar to those in the canopy: surfgrass roots and rhizomes occupied 29-52% cover at Squaw Island and 4-14% cover at Boiler Bay (Fig. 4). At both sites surfgrass covers more primary space than any other single species. Much of the variation in primary cover resulted from changes in sand cover. Within this surfgrass "forest" a variety of rarer small plant species and animals was found (Table 1, Appendix 1). Many of the algal species occasionally grew attached to the surfgrass rhizome. With a few exceptions, the species composition was similar at the two sites. Differences between sites include the complete absence of surfgrass epiphytes (all three years) and the much lower densities of herbivores (Collisella spp. and Tegula funebris) at Boiler Bay.

The pattern of space occupation in these communities is patchy (Fig. 1, note the large variances in Table 1). Vegetative growth of rhizomes or crustose holdfasts contributed to the formation of these patches for many plants, such as P. scouleri, P. torreyi, R. larix, Bossiella plumosa, and Corallina vancouveriensis. Similarly, asexual reproduction results in patches of sea anemones (Sebens 1982). As suggested by Underwood and Jernakoff (1981) plant patchiness may have caused herbivore patchiness, because limpets appeared forced into patches lacking a thick cover of large plants (pers. obs.).

A few seasonal changes occurred along the permanent transect every year (e.g., Table 1, similar changes were observed in other years). For example, although surfgrass cover stayed high throughout the year, in the spring and summer the top layer of leaves became desiccated and lost its color. Underneath this top layer the other leaves were protected and stayed green. Surfgrass epiphytes, Monostroma zostericola and Smithora naiadum, were observed only during this time. Another seasonal plant Phaeostrophion irregulare has a perennial holdfast, but blades grew from this holdfast most profusely in the fall and winter. Most other algae (especially Ulva spp.) had their highest cover in the summer (Table 1, Chapter 2).

In summary, surfgrass not only occupied more space than any other species in both the primary and canopy layers at both sites but also persisted through all seasons for three years. The sites differ dramatically in the abundance of P. scouleri in a way that seems related to their disturbance patterns. This surfgrass dominates space at Squaw Island, but it is a co-dominant at Boiler Bay.

Preemption of space

The surfgrass removal experiments suggest surfgrass preempts space (or space in the light; these resources can not be distinguished) from all algal species. Initially all the treatments had a similarly low algal cover, 0-35% (Table 2, $p > 0.05$, Kruskal-Wallis test, Squaw Island. Boiler Bay data were accidentally destroyed but seemed similar). After surfgrass removal at both sites, algal cover increased significantly over algal cover in control plots (Table 2, $p < 0.05$, Kruskal-Wallis test). An exception to the general trend, a replicate at Boiler Bay initiated in Winter 1979, had only 3% cover and spring 1981. My field observations suggest that this was due to locally extreme sand scour.

Plant diversity changed similarly. At the start, all treatments had a similar low diversity of upright plant cover, because only a few small plants normally live under a 100% cover of surfgrass (Table 3, $p > 0.05$, Kruskal-Wallis test, at Squaw Island. Boiler Bay data were accidentally destroyed but seemed similar). By spring 1981, the Squaw Island experimental plots had a significantly higher diversity than controls ($p < 0.05$, Kruskal-Wallis test), and the Boiler Bay experimental plots also had a higher diversity though not significantly higher ($p > 0.05$, Kruskal-Wallis test) largely owing to one anomalous replicate. Diversity and cover increased regardless of the season in which the experiments were initiated.

Detailed consideration of changes in species composition, variability, and seasonality in succession following surfgrass removal

will be presented elsewhere (Chapter 3) and are only broadly summarized here. At both sites the brown, blade-like alga Phaeostrophion irregulare initially colonized experiments begun in summer, fall, and winter, and the green algae Ulva spp. initially colonized experiments begun in spring. These early successional species colonized within 3 mo of the beginning of the experiment. Algal cover in removal plots increased above that in the control plots within 3 mo. At 3 mo diversity of removal plots was low, because one early colonist dominated (Fig. 5). Then diversity increased dramatically compared to controls within a year and remained above control levels for 15 mo. Diversity peaked in the summer in both control and experimental plots, because many species are summer annuals.

A wide variety of species normally rare or absent from surfgrass beds colonized the surfgrass removals during the three years of this study (Table 4). Only erect coralline algae (B. plumosa and C. vancouveriensis) had greater cover in control quadrats relative to experimental quadrats. Coralline algae appear especially susceptible to desiccation; they may require canopy shade (Dayton 1975a, Taylor and Littler 1982). Many of the invading species became reproductive, including the blade-like red algae Iridaea flaccida, Iridaea heterocarpa, Porphyra sp. and the brown alga Fucus distichus. Therefore, holes or patches in surfgrass beds eventually increase the reproductive populations of several algal species. Nevertheless, no alga appeared to specialize on bare patches in surfgrass beds in the way that the sea palm Postelsia palmaeformis specializes on bare patches in mussel beds (Paine 1979). All the species that colonized the surfgrass

removals normally occur in other intertidal habitats; they appear to opportunistically exploit bare patches in surfgrass beds. For instance, Gigartina papillata, F. distichus, R. larix, and Odonthalia lyalli grow abundantly above the surfgrass zone. Odonthalia floccosa grows more abundantly in tide pools than in surfgrass beds; I. flaccida grows on vertical surfaces (Foster 1982), and Laurencia spectabilis grows below the surfgrass zone. Other algae, P. irregulare, Ulva spp., and Cryptosiphonia woodii, appear to specialize by quickly colonizing disturbed areas throughout the intertidal region (e.g., Littler and Littler 1980, pers. obs.). R. larix appears to benefit most from surfgrass removal (Table 4). It forms large beds and is only slowly overgrown by surfgrass.

One could object to the conclusion that surfgrass preempts other species on the grounds that surfgrass removal might indirectly affect herbivore foraging; i.e., algal cover may have increased after surfgrass removal simply because the herbivores avoided areas without a surfgrass canopy. However, although the herbivores have patchy distributions, no evidence suggests they avoided the 0.25 m² openings in the surfgrass bed (Table 5). In fact, all differences were in the opposite direction.

To determine what morphological characteristics of surfgrass are responsible for preemption, I initiated an experiment designed to separate the effects of blades from the effects of roots and rhizomes. The experiment, involving all possible combinations of canopy and primary surfgrass cover, was initiated in September 1980 and terminated in December 1980. Since only Ulva settled during this time, density of newly settled Ulva is presented to demonstrate the effect of each

treatment on invasion (Table 6). There is no reason to believe other species of algae would respond differently to the various treatments. Because surfgrass blades grew rapidly, the appropriate treatments were clipped twice more after the experiment was initiated. Treatment effects were significant ($p < 0.05$, ANOVA). However, a Student-Newman-Keuls test revealed that only the total removal differed significantly from the other treatments, suggesting that both the blades and the rhizomes of surfgrass played an important role in preemption.

In summary, surfgrass removal leads to invasion by many species, increasing both algal cover and erect plant diversity. These results indicate that propagules of species physiologically able to live in surfgrass beds and able to withstand the consumers are present throughout the year. I therefore conclude that surfgrass preempts space. Preemption appears to involve both surfgrass roots and rhizomes and surfgrass blades.

Recovery from disturbance

Recovery of surfgrass after experimental disturbance was slow and variable and occurred by either of two methods: (1) vegetative growth of rhizomes surrounding the disturbed area, or (2) seed recruitment. In experimental surfgrass removals almost all recovery was by rhizome growth. Only nine seeds recruited into the 28 replicates, and they occupied less than 1% cover in any replicate. The growth rate of rhizomes was faster, but still slow and variable (Table 7). Some rhizomes grew as fast as 12 cm in length in 2 yr, and others did not

grow at all (only increase in length was measured). The reasons for this variability are unknown.

To test the hypothesis that slow rhizome growth rates exhibited in experimental removals resulted from my damaging the rhizome, I followed small, isolated, undamaged plants for 11 mo by tracing their outlines on plastic sheets. Blades were moved aside to trace the rhizomes. None of these plants grew more than 2.5 cm in rhizome length during the observation period (Table 8); and some plants had their rhizomes broken off or did not survive. (Broken rhizomes produced negative values in Table 8.) Further, surrounding plants did not appear to strongly inhibit the growth of surfgrass rhizomes ($p > 0.05$, Mann-Whitney U test). In fact, within 2 weeks after I removed the surrounding plants (mostly R. larix), the experimental surfgrass plants appeared desiccated and more of these unshaded plants died than did control surfgrass plants. These results support the conclusion that rhizome growth is always slow. Further, they suggest that survival of small, isolated plants (= relatively recent recruits) is enhanced by association with algae such as R. larix. (See Chapter 4 for further evidence.) This R. larix removal experiment simulated thallus loss that often occurs naturally (C. D'Antonio pers. comm.).

To further quantify recovery by seed recruitment, I mapped 131 seeds in a 28 m² area at Boiler Bay in February 1981. All of these seedlings recruited during fall or early winter 1980. By February 1982, only nine seedlings remained, a 93% loss rate (Chapter 4). The largest seedling had a rhizome only 2 cm in length. These data on seedling density, mortality rate, and growth rate suggest recovery by seeds is also slow.

To summarize, although both surfgrass rhizomes and seeds can invade space occupied by other species, they invade space very slowly. Rhizome growth appears more important if surfgrass plants surround the disturbed area. I conclude that large ($\geq 0.25 \text{ m}^2$) disturbances drastically alter the community. Such disturbances develop into large patches of algae, which can persist for several (>3) yr before surfgrass eventually regains its dominance over the algal patch. Even assuming maximum rhizome growth, I estimate that 0.25 m^2 hole in a surfgrass bed will require at least 6 yr to recover.

DISCUSSION

Characteristics of surfgrass beds

The interaction of three characteristics of surfgrass -- its persistence ability, its preemptive ability, and its recovery ability -- strongly influence the organization of these communities. In many low zone rocky intertidal communities, surfgrass dominates space and persists in all seasons without serious damage by potential disturbances, such as storm waves. Experimental results suggest surfgrass preempts space, preventing other species from invading. Because the three hypotheses explaining surfgrass dominance (physical conditions, consumers, and preemption) are not mutually exclusive, physical conditions and consumers may also limit the species composition, but the experiments demonstrate the removal of surfgrass alone greatly increased algal cover and diversity. Thus, the preemptive

ability of surfgrass is a major factor organizing this community. If surfgrass is removed by wave action, the community is profoundly altered, because surfgrass recovers very slowly: high plant diversity should continue for >3 yr. The slow vegetative growth of surfgrass plants largely controls recovery.

In contrast to the dramatic invasion into 0.25 m^2 bare patches in surfgrass beds, no algae invaded 400 cm^2 bare patches shaded by surfgrass blades (Table 6). This suggests that small, shaded, bare patches have little influence on community structure. Other studies have also shown that small openings (relative to the size of nearby canopy cover) experience little successional change (Connell and Slatyer 1977, Sousa 1979).

The differences between Squaw Island and Boiler Bay can be explained by combining the above results with the differences in substratum stability. Squaw Island has a hard sandstone substratum, and surfgrass dominates space (Figs. 3 and 4, Table 1). Boiler Bay has a soft mudstone substratum, which is more easily bored by organisms and commonly exfoliates (pers. obs.), and surfgrass is a less abundant, co-dominant space occupier. I suggest the susceptibility of mudstone to exfoliation produces a higher disturbance rate. Disturbance produces free space, which is rapidly colonized by algae. These algae are slowly replaced by surfgrass. Disturbance thus prevents surfgrass from occupying as much space at Boiler Bay as it does at Squaw Island. Rates of disturbance will not have to be large to have this effect, because surfgrass recovers slowly. Conclusive demonstration of this hypothesis will require quantification of disturbance rates for several years. At

Squaw Island, spatial heterogeneity partly accounts for the failure of surfgrass to occupy 100% of the space, because surfgrass evidently cannot live on vertical surfaces (Black 1974, pers. obs.). Consequently, ridges, dips, and drop-offs can increase algal diversity.

Sand scour and sand burial are other structuring agents in these communities. (Fig. 4 and Table 1 document extensive sand cover.) Extreme sand scour may have prevented algae from invading a few of the surfgrass removal replicates (Table 2). Moreover, some of the plants in these communities appear adapted to sand scour. For example, both R. larix and Phaeostrophion irregulare regrow from a crustose perennial holdfast if the erect thallus is removed by sand scour (Mathieson 1965, Abbott and Hollenberg 1976, C. D'Antonio pers. comm.). In addition, sand may have a variety of indirect effects. For example, herbivores, such as urchins, may not be able to withstand sand scour (C. D'Antonio pers. comm.). Several authors have suggested that sand scour and sand burial can influence the structure of marine hard substratum communities (e.g., Stephenson and Stephenson 1972, Markham 1973, Cimberg et al. 1973, Foster 1975, Daly and Mathieson 1977, Taylor and Littler 1982). Phinney (1977) even suggests greater sand scour in Oregon causes the discontinuous distributions of many algae. Ninety-three species of algae found in California and Washington have not been recorded in Oregon. These species may be unable to withstand sand scour.

Although my data suggest surfgrass preempts other species, specific mechanisms of preemption are not known. Possible mechanisms include whiplash of blades (Dayton 1975a, Menge 1976), physical barriers that

blades present to spores (Menge 1976, Lubchenco and Menge 1978, Hruby and Norton 1979, Lubchenco 1980, Deysher and Norton 1982), shading (Rosenthal et al. 1974), sand that tends to accumulate around surfgrass (pers. obs.), and allelopathy (Sieburth and Conover 1965). Surfgrass blades apparently create deep shade: I have observed colorless anemones underneath them, presumably because the photosynthetic zooxanthellae that normally give anemones a green color cannot live in this shade. Although the clipping experiment did not result in the strong invasion that might have occurred in other seasons, it does suggest that surfgrass blades alone do not account for its preemptive ability (Table 6). The phenolic compounds that surfgrass contains (Zapata and McMillan 1979, Fishlyn and Phillips 1980, McMillan et al. 1980) may have an allelopathic effect on other species similar to the effects in terrestrial plants.

One further caveat concerning the characterization of surfgrass beds presented here is that stability of ecological systems must be considered with respect to the life span of the organisms (Frank 1968). Three years is probably a small portion of the life span of surfgrass. Similar slow rhizome growth occurs in other seagrasses (Zieman 1976). Growth of surfgrass rhizomes and surfgrass seed settlement vary from year to year (Chapter 4). Thus, as in most communities, the role of episodic events (sensu Dayton and Oliver 1980) in surfgrass beds is unknown.

Studies in other geographic areas suggest that the characteristics described here for surfgrasses (most authors do not differentiate between the two species) in Oregon, are found throughout their range.

For example, surfgrasses dominate space as far south as San Diego and Baja California (Stewart and Myers 1980, Littler and Littler 1981). They preempt the kelps Egregia menziesii (Black 1974) and Sargassum muticum (Deysher and Norton 1982) in southern California and the red alga Gastroclonium coulteri in central California (Hodgson 1980). Furthermore, in tide pools in Washington, surfgrass preempts a variety of species including the crustose alga Ralfsia, barnacles, and the erect coralline alga Corallina vancouveriensis (Dethier 1981).

Comparisons with other communities

A review of other investigations suggests some, but not all, communities are organized like surfgrass beds. That is, some other communities are dominated by species that have high persistence ability, high preemptive ability, and low recovery ability. Species that resemble surfgrass on this conceptual level often have the ability to capture space by vegetative growth, large size, and escapes from herbivores.

Persistence ability varies greatly among communities even if consideration is restricted to marine communities. Both Lubchenco and Menge (1978) and Ortega (1981) report striking seasonal mortality of mussels in wave exposed areas. Wilson (1971), moreover, reports that cover of worms building sand tubes varies dramatically over a 5-yr period as a result of variability in wave action and in larval recruitment. Other communities are highly persistent over the time scales that have been studied (Lubchenco and Menge 1978, Hoare and

Peattie 1979). Ultimately, persistence will depend on the physical environment and the adaptations of the organisms.

In many communities preemptive ability alone does not account for spatial dominance by a particular species. Physical conditions and consumers often play key roles. Alaskan subtidal kelp beds, for example, are dominated by Agarum at certain depths, because urchins prefer to eat other species (Dayton 1975b). In other communities a combination of factors may be important. The dominance of Adenostoma fasciculatum in chaparral communities, for instance, appears to be caused both by its allelopathic effects through its association with soil microbes (Kaminsky 1981) (indirect preemption) and by seed foraging of herbivores associated with the shrub cover (Halligan 1973, 1976). Another combination of factors may explain the spatial dominance of the anemone Anthopleura elegantissima in southern California. It both preempts space from opportunistic algae and withstands up to three months of sand burial (Taylor and Littler 1982).

Recovery rate also varies greatly among marine communities (see Kain 1975 for a review). At one extreme, Lee (1966) documented that an algal community in British Columbia recovered in just 9 mo. At another extreme, Boney (1979) documented that an intertidal lichen did not return in 24 yr after removal. Slow recovery (or low adjustment stability) and high persistence stability appear to be generally correlated (Menge 1975). The correlation between these life history characteristics may be caused by a trade-off between preemptive ability and recruitment ability (e.g., Grime 1977, 1979). However, the

existence of such a trade-off has not been conclusively demonstrated, and its genetic and physiological basis remains unclear.

Of the communities that have been studied, surfgrass beds most closely resemble eastern Pacific mussel beds (Paine and Levin 1981 and references therein). Like surfgrass, mussels dominate space in large areas and persist for years. Both organisms preempt space. Recovery from the disturbance requires many years for both species. Hence, the structure of both communities is determined by the pattern of disturbance. For these reasons, the model developed by Paine and Levin (1981) to describe mussel bed dynamics may also apply to surfgrass beds. The two communities resemble each other conceptually even though the extent of disturbance appears to be much greater in mussel beds.

The ability to capture space by vegetative growth, as surfgrass does, should enhance persistence ability, preemption ability, and invasion ability (Jackson 1977). Disturbances often simply damage organisms with such vegetative growth and do not cause mortality. Vegetative growth might therefore allow for quicker recovery (Jackson 1977, Jackson and Palumbi 1978, Kay and Keough 1981, Shepherd 1981, Taylor and Littler 1982), making the effects of small disturbances slight or unmeasurable. Because vegetative growth occurs commonly in marine and terrestrial organisms (Harper 1977, Sousa et al. 1981), it may influence the organization of many communities. Even mussels, although they do not invade space vegetatively in the same way that colonial organisms do, act similarly. Mature mussel beds have several layers; when a hole appears adult mussels can move into the bare space (Paine and Levin 1981).

Sousa et al. (1981) tentatively propose that communities of marine plants with vegetative growth might be more common in southern California than in more northern areas on the Pacific coast of North America. They describe red algae that grow vegetatively, persist well, preempt space, and invade space occupied by other organisms. My data suggest that their generalization is incorrect, because similar communities occur at higher latitudes. Both surfgrass beds and R. larix beds have these same characteristics and are common along the Oregon coast (Table 1, C. D'Antonio pers. comm.).

Large size, such as that of surfgrass plants, should also enhance preemption and invasion (e.g., Buss 1980). One example of the benefits of large size is the dominance hierarchy of rocky intertidal animals in the northeast Pacific (Dayton 1971): small barnacles can be overgrown by larger barnacles, which in turn can be overgrown by mussels. Large size likewise determines many competitive relationships among terrestrial plants (Grime 1979) and even among mobile animals (e.g., Grant 1972). Vegetative growth might also be important in this context, because it allows organisms to attain large sizes horizontally.

Current ecological theory predicts preemption will not occur unless space occupiers have escaped their consumers (Connell 1975, Menge and Sutherland 1976). Although these hypotheses need to be tested, surfgrass may escape the herbivorous snails with which it occurs -- Tegula funebris and Lacuna marmorata (Best 1964, Fishlyn and Phillips 1980 showed that they eat some surfgrass) -- by virtue of its phenolic compounds (Zapata and McMillan 1979, Fishlyn and Phillips, 1980, and McMillan et al. 1980 described these compounds but did not demonstrate

their effectiveness), its large size, or its toughness. Urchins, larger herbivores which usually do not co-occur with surfgrass, appear to control it when they do occur together (pers. obs.). Thus, some surfgrass beds may owe their existence to sand, to freshwater run-off (Sousa et al. 1981), or to other features that exclude urchins. That is, surfgrass may enjoy a refuge from a dominant grazer like the high intertidal refuge that mussels have from their starfish predators.

In conclusion, the organization of surfgrass communities is strongly influenced by the interaction of three biological features of surfgrass -- its persistence ability, its preemptive ability, and its recovery ability. Because surfgrass recovers slowly from disturbance, it would not dominate space if it did not both persist through most potential disturbances and preempt space from potential invaders. Its strong preemptive and persistence ability mean that the removal of surfgrass profoundly alters the community. Because surfgrass recovers slowly, even very low rates of disturbance can produce a mosaic of surfgrass and algae. Some other communities have a similar organization in being dominated by organisms with large size, vegetative growth, and escapes from herbivores.

Table 1. Community structure in the low intertidal zone in winter and summer at two sites on the Oregon coast. Only species with more than 1% cover or 0.5 individuals/0.25 m² at one site and time are included. See Appendix 1 for other species in the community. Data are presented as means (percent covers retransformed from degrees) followed by one standard error. Standard errors in parentheses are in degrees.

Species	Sites			
	Squaw Island		Boiler Bay	
	Aug 1980	Mar 1981	Aug 1980	Jan 1979
Canopy Cover				
<u>Phyllospadix scouleri</u>	79.6 (2.9)	79.1 (2.8)	20.7 (2.9)	14.4 (3.1)
<u>Phyllospadix torreyi</u>	0.3 (0.9)	0.4 (1.1)	11.0 (3.4)	12.8 (3.8)
Macrophytic epiphytes on canopy species				
<u>Monostroma zostericola</u> (G)*	5.9 (5.0)	0	0	0
Understory cover				
<u>Ulva</u> spp. (G)	2.2 (3.3)	0.1 (0.7)	12.8 (7.9)	0.8 (1.7)
<u>Rhodomela larix</u> (R)	2.0 (1.3)	0.9 (1.2)	17.4 (2.0)	8.7 (1.3)
<u>Bossiella plumosa</u> (R)	1.6 (1.4)	0.4 (1.4)	0.8 (0.7)	0.7 (1.6)
<u>Corallina vancouveriensis</u> (R)	1.1 (0.5)	0.6 (1.3)	0	0
<u>Phaeostrophion irregulare</u> (B)	0.7 (1.4)	1.5 (3.0)	0.3 (1.4)	7.7 (5.4)
<u>Odonthalia lyalli</u> (R)	0.6 (4.4)	0.1 (2.1)	0	0
polysiphonous algae (R)	0.4 (2.3)	0	9.4 (6.8)†	1.1 (2.8)
<u>Odonthalia floccosa</u> (R)	0.3 (1.6)	0.6 (0.8)	1.6 (2.1)	0.7 (1.5)
<u>Cryptosiphonia woodii</u> (R)	0.3 (1.8)	0	1.4 (1.4)	0.3 (1.1)
<u>Iridaea</u> spp. (R)††	0.2 (1.3)	0	2.0 (0.9)	1.8 (2.2)
<u>Dilsea californica</u> (R)	0	0	1.7 (3.1)	0
Primary Cover				
<u>Phyllospadix scouleri</u> roots + rhizomes	43.7 (1.6)	47.6 (1.8)	14.5 (2.4)	5.3 (2.0)
sand	11.9 (0.8)	25.5 (8.6)	19.4 (1.6)	38.1 (1.1)
algal holdfasts (R, B, G)	10.2 (1.1)	4.2 (1.1)	27.2 (2.2)	20.2 (1.5)
fleshy crustose algae (R, B)	10.0 (2.7)	1.3 (1.6)	1.4 (1.7)	1.0 (4.5)
bare rock	4.1 (2.3)	2.6 (2.3)	1.1 (1.9)	7.1 (2.0)
barnacles ‡	1.5 (3.4)	1.4 (3.5)	0	0
<u>Anthopleura elegantissima</u> (anemone)	1.3 (2.8)	1.7 (4.1)	0.3 (1.0)	0.4 (1.3)
coralline crustose algae (R)	1.2 (1.8)	0.1 (1.1)	1.0 (2.0)	3.4 (2.2)
<u>Phyllospadix torreyi</u> roots + rhizomes	0.3 (0.9)	0.4 (1.1)	11.1 (3.5)	3.0 (1.1)

Table 1. (continued)

Species	Sites							
	Squaw Island				Boiler Bay			
	Aug 1980		Mar 1981		Aug 1980		Jan 1979	
Densities (Number/0.25 m ²)								
<u>Collisella</u> spp.	51.7	26.3	7.5	3.4	2.5	1.7	0.7	0.5
<u>Tegula funebris</u> (colled snails)	11.6	4.4	10.9	4.5	0.4	0.3	0.9	0.4
<u>Pagurus</u> spp. (hermit crabs)	2.2	0.7	1.2	0.7	1.7	0.7	2.2	0.9
<u>Searlesia dira</u> (colled snail)	1.5	0.5	0.8	0.5	0		0.2	0.2
<u>Thais emarginata</u> (colled snail)	0.6	0.6	0.1	0.1	0		0	
<u>Pugettia producta</u> (kelp crab)	0.4	0.2	0		0.7	0.4	0	

*G = green algae, R = red algae, B = brown algae. Plant species designations follow Abbott and Hollenberg (1976), and animals follow Smith and Carlton (1975).

† matted with sand and diatoms

++ L. flaccida, L. heterocarpa, and L. cordata

§ Balanus glandula, Balanus cariosus, and Chthamalus dalli

" C. strigatella and C. pelta

Table 2. Percent cover of erect algae (canopy and understory cover combined yielding over 100% cover in some cases) in control quadrats and quadrats from which surfgrass was removed at various dates. Each treatment had four replicates. At both sites all treatments had initially similar algal cover ($p > 0.05$, Kruskal-Wallis test), then algal cover increased significantly when surfgrass was removed ($p < 0.05$, Kruskal-Wallis test).

Treatment	Initial Cover		Spring 1981 Cover	
	\bar{x}	Range	\bar{x}	Range
Squaw Island				
Control (Initial values - Summer 1978)	13.0	4 - 33	6.0	4-9
Removed Summer 1978	15.0	4 - 31	71.5	41 - 101
Removed Fall 1978	11.3	1 - 35	120.0	88 - 162
Removed Winter 1979	13.8	4 - 21	115.3	105 - 141
Removed Spring 1979	7.3	3 - 14	120.0	83 - 146
Boiler Bay				
Control (Initiated - Fall 1978)	No data		12.8	4 - 26
Removed Fall 1978	12.5	0 - 20	76.5	50 - 83
Removed Winter 1979	5.0	1 - 11	85.8	3 - 122
Removed Spring 1979	No data		93.8	64 - 133

Table 3. Diversity (H' , Shannon and Weaver 1949) of erect plants (understory and canopy combined) in control quadrats and quadrats from which surfgrass was removed at each treatment. Each treatment had four replicates. Initially all treatments had similar diversity ($p > 0.05$, Kruskal-Wallis test). By Spring 1981 Squaw Island removal plots were significantly more diverse than control plots ($p < 0.05$, Kruskal-Wallis test), but Boiler Bay differences were not significant ($p > 0.05$, Kruskal-Wallis test).

Treatment	Initial H' values		Spring 1981 H' values	
	\bar{x}	Range	\bar{x}	Range
Squaw Island				
Control	0.4	(0.3 - 0.6)	1.2	(1.1 - 1.4)
Removed Summer 1978	1.3	(0.9 - 1.7)	1.8	(1.5 - 2.2)
Removed Fall 1978	0.4	(0.1 - 1.1)	2.4	(1.3 - 2.9)
Removed Winter 1979	0.8	(0.3 - 1.2)	2.5	(1.5 - 3.1)
Removed Spring 1979	1.0	(0.4 - 1.6)	2.4	(2.2 - 2.8)
Boiler Bay				
Control		no data	0.7	(0.4 - 1.0)
Removed Fall 1978	0.7	(0.2 - 0.9)	2.0	(1.2 - 2.7)
Removed Winter 1979	0.4	(0.1 - 0.6)	1.8	(0.6 - 2.5)
Removed Spring 1979		no data	2.0	(1.7 - 2.3)

Table 4. Understory space utilization in plots with and without surfgrass in spring 1981 at Squaw Island. Surfgrass had been removed in spring 1979. Each treatment had four replicates. Only those species occupying over 1% cover in any treatment are included.* Data are presented as mean % cover with one standard error in degrees in parenthesis. The plus signifies a very rare species, less than 0.1% cover.

Species	Surfgrass Removed		Control
<u>Rhodomela larix</u>	32.6	(2.7)	+
<u>Cryptosiphonia woodii</u>	18.3	(1.3)	0
<u>Phaeostrophion irregulare</u>	16.0	(2.2)	0.9 (0.5)
<u>Ulva spp.</u>	7.0	(1.3)	0.1 (0.2)
<u>Odonthalia floccosa</u>	3.3	(1.0)	0.1 (0.2)
<u>Microcladia borealis</u>	3.2	(0.7)	+
<u>Fucus distichus</u>	2.3	(0.7)	0
<u>Porphyra sp.</u>	1.2	(0.9)	+
<u>Iridaea heterocarpa</u>	1.0	(0.7)	0
<u>Bostelia plumosa</u>	0.9	(0.3)	3.5 (0.6)

* Other species that colonized surfgrass removals but not controls include Gigartina papillata, Odonthalia lyalli, Iridaea flaccida, Iridaea cordata, Laurencia spectabilis and Anallpus japonicus.

Table 5. Density of herbivores (nos./0.25 m²) at Squaw Island in spring 1981 in plots from which surfgrass had been removed (16 plots) and controls (four plots). Data are presented as mean \pm one standard error. Differences are not significant (T test), with the exception of T. funebris which was significantly more abundant in surfgrass removals ($p < 0.01$).

Species	Surfgrass removed	Control
Limpets - <u>Collisella</u> spp. (mainly <u>C. strigatella</u>)	17.0 \pm 8.0	2.8 \pm 2.1
Turban snail - <u>Tegula funebris</u>	13.8 \pm 4.1	7.5 \pm 2.7
Chiton - <u>Mopalia</u> spp. (mainly <u>M. muscosa</u>)	0.7 \pm 0.3	0.3 \pm 0.3
Other chitons (mainly <u>Cyanoplax dentiens</u>)	1.3 \pm 0.5	0.3 \pm 0.3

Table 6. Mean density (nos./0.25 m²) of newly settled *Ulva* spp. plants in plots with and without shade from surfgrass blades and roots (Table 2). All values underlined with the same line are not significantly different using the Student-Newman-Keuls test. There are four replicates for each treatment. The experiment was conducted near Squaw Island.

Control		Shaded surfgrass removal (0.04 m ²)		Surfgrass clipped to 5 cm long (2.25 m ²)		Unshaded surfgrass grass removal (2.25 m ²)	
+R*	+B	-R	+B	+R	-B	-R	-B
0		0		3.0		20.3	

*R = rhizomes and roots, B = blades, + and - indicate presence and absence.

Table 7. Recovery of primary space by surfgrass rhizomes growing vegetatively from areas surrounding experimental removals at Squaw Island. Data are expressed as the mean of the untransformed percent cover of roots and rhizomes and the range recorded in spring 1981. Each experiment was initiated at a different date and had four replicates (Table 1).

Age of experiments in months	\bar{x} % primary surfgrass cover	Range
24	4.8	1-9
27	4.3	1-9
31	2.3	0-6
34	15.0	2-22

Table 8. Change in length of longest rhizome of small surfgrass plants (2.5 - 17.0 cm in diameter) at Boiler Bay over 11 mo (Aug. 1980 - July 1981) with and without surrounding Rhodomela larix plants. Initially eight plants were traced for each treatment. Seven control plants survived, but only three plants from which Rhodomela had been removed survived. Broken rhizomes produced negative values, because the plants became smaller.

Treatment	\bar{x} change in rhizome length (cm)	Range of changes (cm)
<u>Rhodomela</u> removal	-5.2	-10.5 - -0.5
Control	-2.5	-5.0 - +2.5

Figure 1. Study sites at (a) Squaw Island and (b) Boiler Bay, both dominated by surfgrass.

Figure 1a.



Figure 1b.



Figure 2. Location of study sites in Oregon.

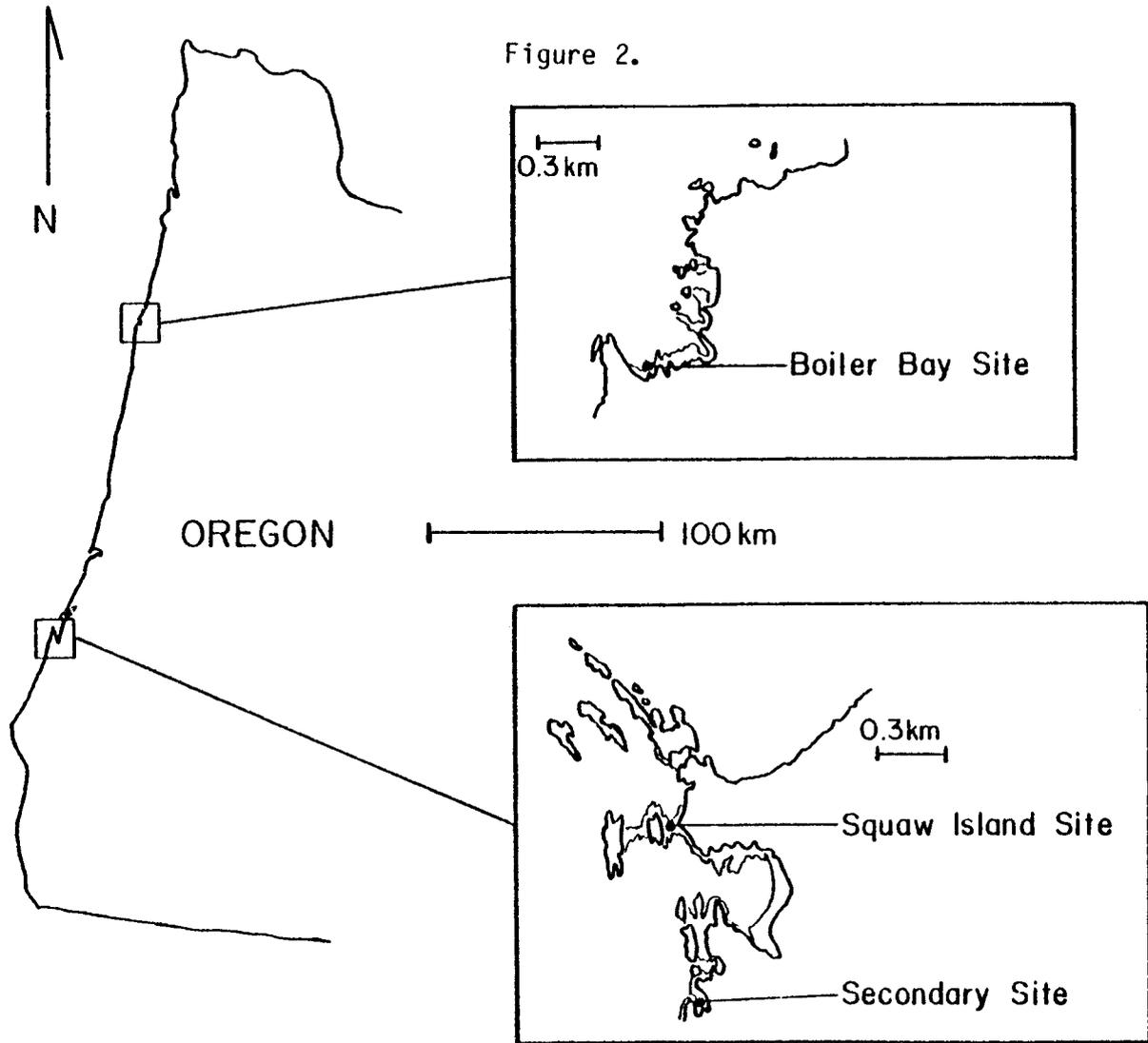


Figure 3. Utilization of canopy and understory space along permanent transect lines at (a) Squaw Island and (b) Boiler Bay. Breaks in axis signify seasons in which no data were taken.

Figure 3.

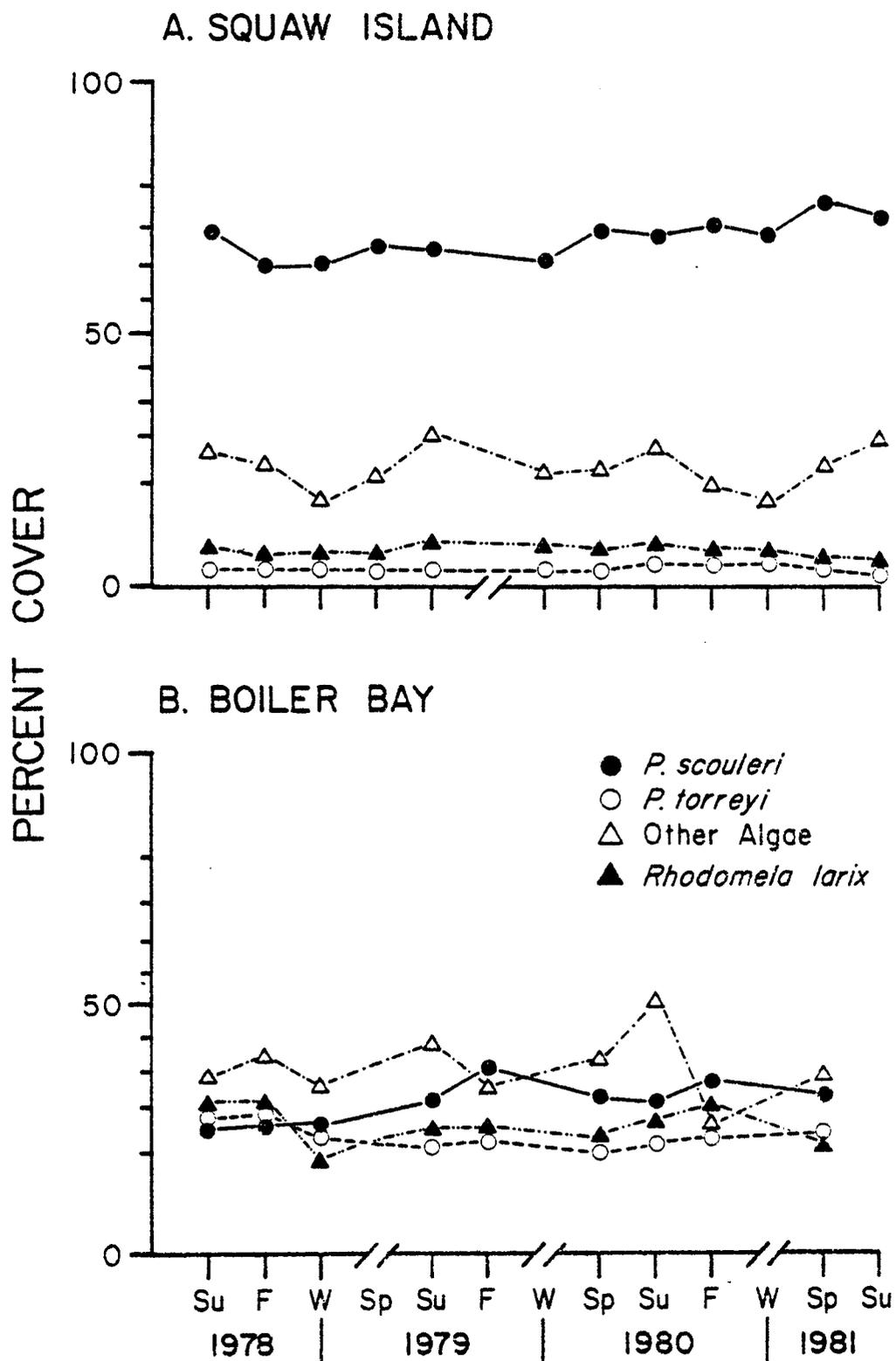
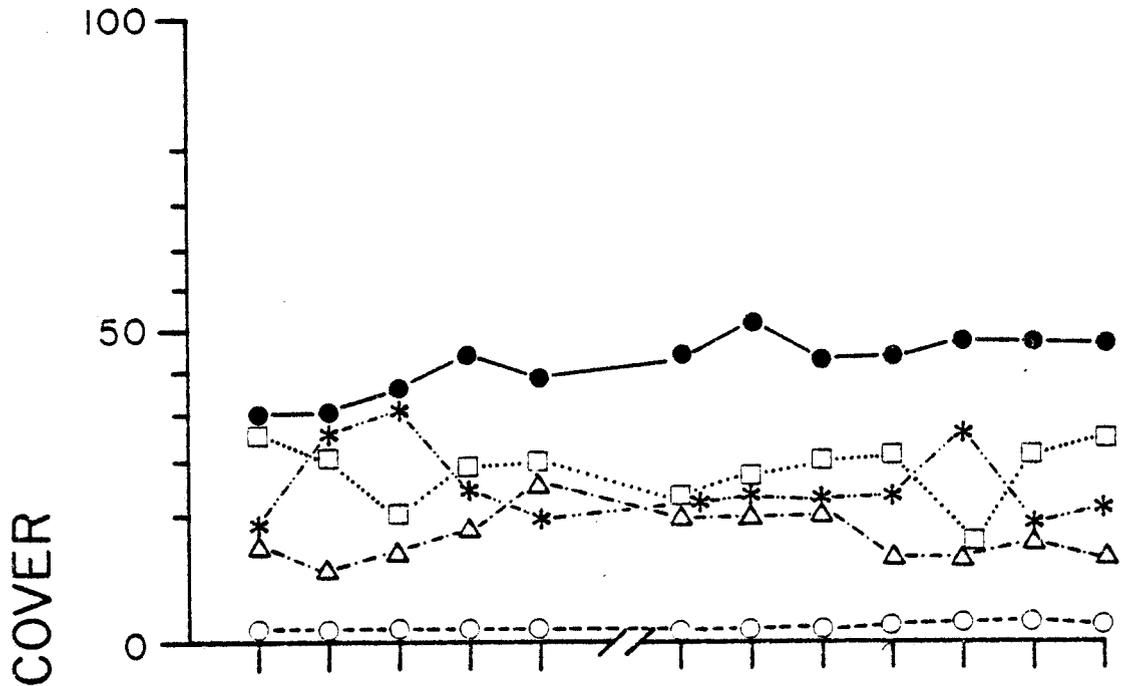


Figure 4. Utilization of primary space along permanent transect lines at (a) Squaw Island and (b) Boiler Bay. Breaks in axis signify seasons in which no data were taken.

Figure 4.
A. SQUAW ISLAND



B. BOILER BAY

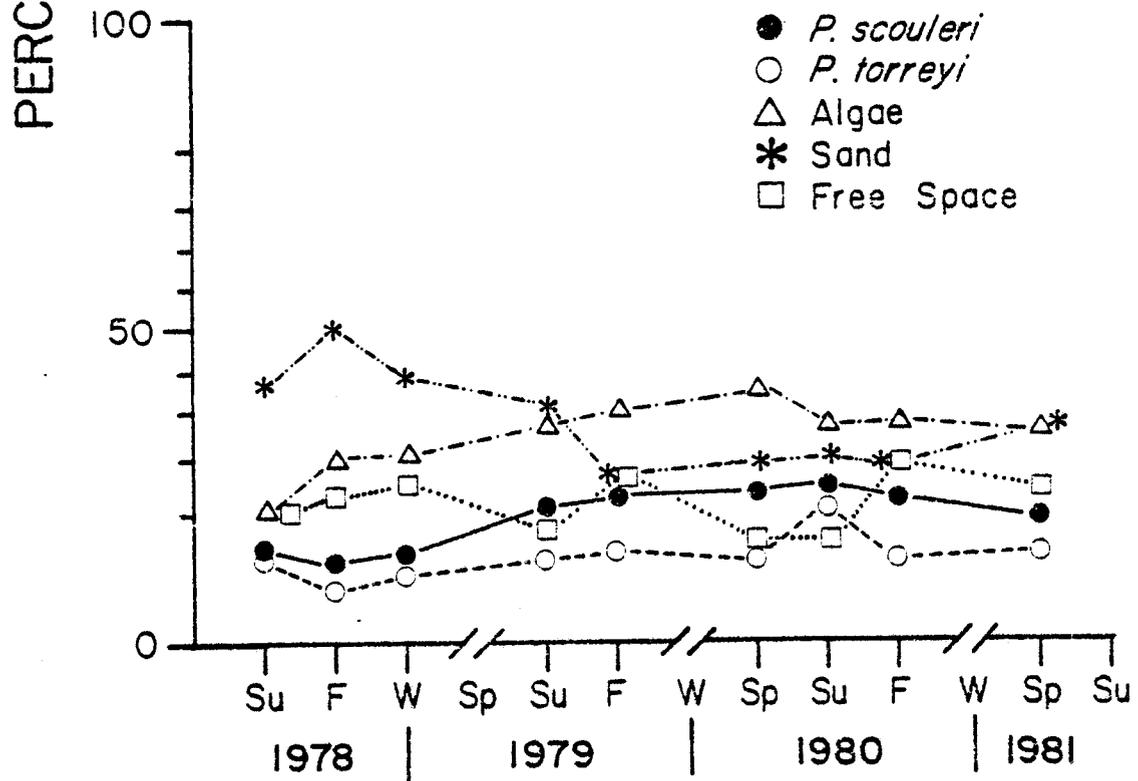
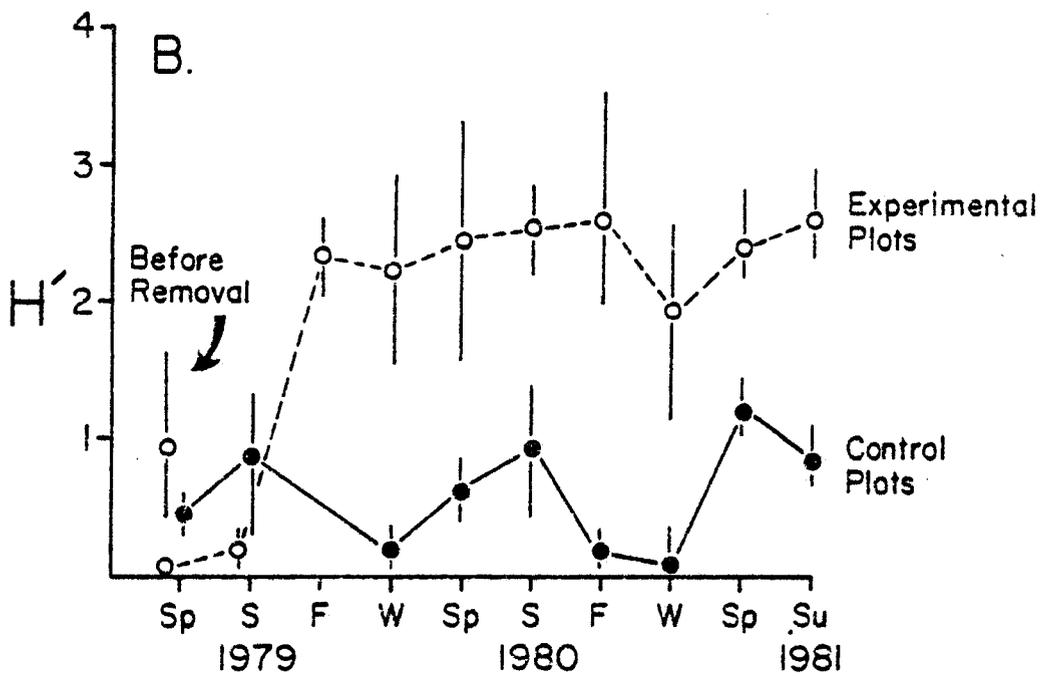
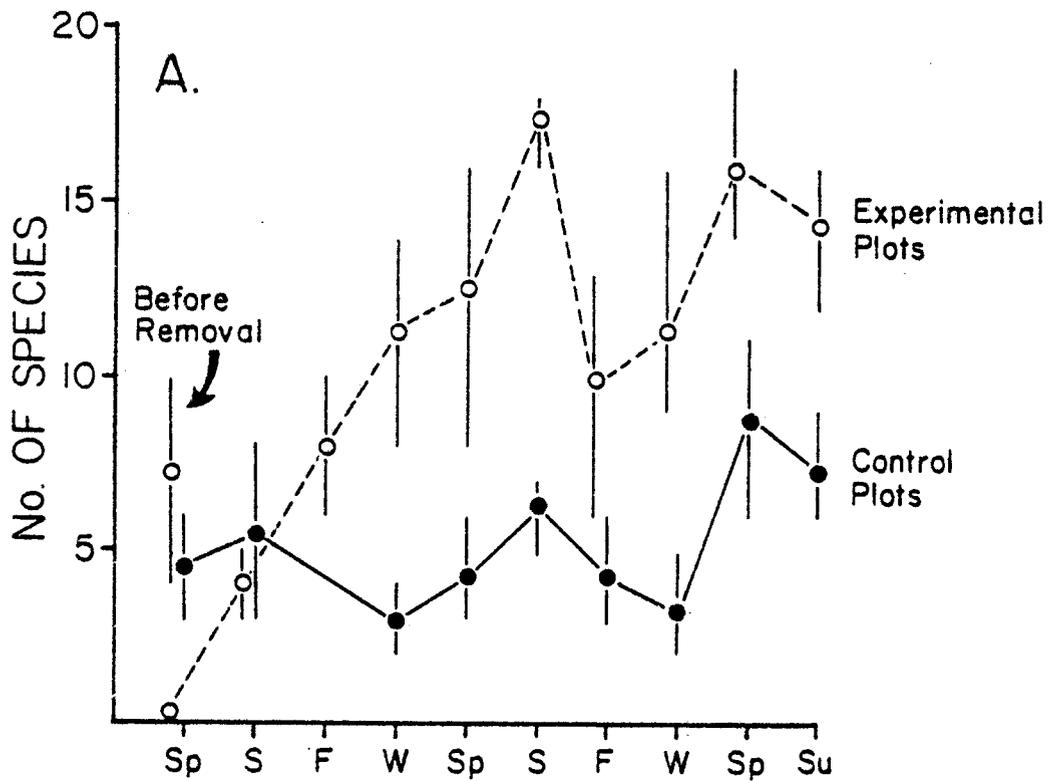


Figure 5. Diversity of upright plants in controls and surfgrass removals initiated at Squaw Island in Spring 1979, (a) number of species, and (b) H' , Shannon-Weiner diversity (Shannon and Weaver 1949). Points indicate means and bars indicate ranges. Each treatment has four replicates; therefore, when the range bars do not overlap the treatments are significantly different using a Mann-Whitney U test.

Figure 5.



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CHAPTER III.
COMPLEXITY OF EARLY AND MIDDLE
SUCCESIONAL STAGES IN A ROCKY INTERTIDAL SURFGRASS COMMUNITY

SUMMARY

The successional sequence in low zone rocky intertidal surfgrass beds on the Oregon coast is more complex than predicted by any of the simple models proposed by Connell and Slatyer (1977), because of variation in time, in space, and in the species replacement mechanism. Succession experiments initiated in different seasons at two sites and herbivore exclusions documented this complexity. At both sites (Boiler Bay and Squaw Island) experimental plots in which succession was initiated in the spring were first colonized by the green alga Ulva sp., but those initiated in other seasons were first colonized by the brown alga Phaeostrophion irregulare. Ulva appears adapted to take advantage of space made available by winter storms, whereas Phaeostrophion takes advantage of space made available by sand movement in the fall. Regardless of the season of initiation, most of the early and middle successional algal species occupied the maximum amount of space in the summer. Total algal cover sharply declined in the fall, when wave action increased. At Squaw Island, the presence of Phaeostrophion established in fall and winter significantly inhibited the summer establishment of Ulva, though Ulva occupied some space epiphytically. At Boiler Bay, Phaeostrophion totally inhibited the establishment of filamentous diatoms. Herbivores significantly decreased the cover of

Ulva in the summer, but Ulva cover declined in the fall in both herbivore exclusions and controls, suggesting that herbivores were not solely responsible for its replacement. By the end of the experiment, replicate plots often differed. The early colonists, Phaeostrophion and Ulva, dominated some plots the entire three years; in others they were replaced by middle successional species, including the branched red algae Cryptosiphonia woodii and Odonthalia floccosa. In still other plots the slowly growing red alga Rhodomela larix replaced other species. The presence of Rhodomela larix in the understory before surfgrass removal influenced the species composition 3 years later, because Rhodomela regrows from its holdfast (even if scraped with a putty knife) and captures space by horizontal vegetative growth, but it seldom recruits from spores. Similar complexity occurs during succession in many natural communities. Thus, simple models do not always have predictive value.

INTRODUCTION

Scientists often propose simple models to explain complex phenomena. Although models can never include the complexity of the natural world, they often capture the salient features and often have predictive value. Even when simple models fail, they can serve an important purpose, because they can generate hypotheses and thereby direct investigations (see Pielou 1981 for a review of the role of models in ecology). Thus, empirical workers must determine whether

simple models are predictive and the conditions that reduce their predictive value.

Models describing succession fall into four categories. (1) Successional changes may result solely from differences in life histories. Rapidly growing species dominate early in the successional sequence; slowly growing species dominate later. No interactions occur (Connell and Slatyer 1977). (2) Successional changes may result from early space occupiers preparing the way (facilitation) for later species. This is the traditional view of succession (Clements 1916). (3) Successional changes may result from natural enemies or physical conditions that kill early colonists, allowing later species to predominate. This view supposes that early species inhibit later ones. As a result, without this mortality late successionalists would not replace early successionalists or at least would replace them much more slowly (Connell and Slatyer 1977, Sousa 1979). (4) Successional changes may result from later species outcompeting early colonists. This view also supposes that early successionalists inhibit later ones. If early space occupiers were not present, later species would grow faster, because they would not pay the energetic costs of competition (Horn 1981). In their simplest form all four models predict little variation in the timing of successional changes and the species composition in each successional change (but see Horn 1981 for a model incorporating some causes of successional variation). In this paper I describe succession in one community, examine how well simple models predict successional changes, and discuss the cause of the discrepancies between the models and this community.

Several studies suggest agents that increase the complexity of succession. The season in which a succession experiment is initiated, for instance, can profoundly influence the species composition and the sequence of changes (e.g., Keever 1950, 1979; Sutherland 1974; Foster 1975; Kain 1975; Paine 1977; Emerson and Zedler 1978; Hay and South 1979; Sousa et al. 1981). This effect could have several causes. Many species recruit only in certain seasons, and physical conditions influencing growth and predation pressure may change seasonally. Because temporal variation is common in natural systems, it may influence many communities.

Experimental studies indicate that variation in the mechanisms of species replacement make succession more complex. Succession within one community can be characterized by either facilitation, inhibition, both, or neither (e.g., Dean and Hurd 1980; Hils and Vankat 1982; Chapter 4). Variation in the strength of these interactions between species also increases the complexity of succession. For example, at two ends of the spectrum, an early species might either totally prevent a later species from invading or only slightly decrease its invasion. The causes of these differences are just beginning to be understood (e.g., Connell and Slatyer 1977; Sousa 1979; Chapter 4; Lubchenco in prep.).

Many models of succession also ignore consumers. Depending on their feeding preferences, herbivores might either enhance or arrest successional changes (see Lubchenco and Gaines 1981 for a review), or they might have more subtle effects, influencing the biomass of a particular species at a particular stage. Higher order consumers might also influence succession by removing sessile animals that compete with

algae (Lubchenco and Menge 1978). The changes in species composition during succession might in turn influence the density of consumers. Some plants may attract herbivores; others may compete with herbivores for space and actually crowd them out (e.g., Southward and Southward 1978; Underwood and Jernakoff 1981). Thus, consumers could also increase the complexity of successional changes.

Local variation further increases the complexity of succession. Replicate plots of a succession experiment always differ to some extent. Often this variation can be ignored and mean values can be considered, but in some communities variation among replicates is large. The species composition of replicates can differ completely (e.g., Sutherland 1974; Robles and Cubit 1981; Lubchenco in prep.). Differences among replicates may result from variability in the species composition before disturbance, in recruitment, in the organisms surrounding the experimental replicates, or in the abiotic environment. The interactions between species (i.e., the degree of variation in inhibition or facilitation for different species pairs) should determine whether divergent replicates will converge to the same last successional stage. The importance of this type of local variation is being realized more and more. As Simberloff (1980) wrote, "what physicists view as noise is music to the ecologist."

Here I describe the early and middle successional stages in a rocky intertidal community normally dominated by surfgrass. A variety of factors influence these sequences, producing complex patterns. I designed observations and experiments to address four questions:

- (1) In which seasons do particular species recruit and in which seasons are the different algal species most abundant?
- (2) Does the presence of established species inhibit or facilitate the recruitment of later colonizing species?
- (3) Do herbivores influence early succession?
- (4) How different is the species composition of replicates of succession experiments and will these differences persist as alternative equilibria?

COMMUNITY AND STUDY SITES

I studied successional complexity in surfgrass beds (the seagrass Phyllospadix scouleri Hook) on the Oregon coast in the low zone (+0.6-0 m) of rocky intertidal areas. On horizontal benches in areas with little disturbance, surfgrass can form a virtual monoculture (Chapter 2). It persists in all seasons for many years and prevents other species from invading. Thus, on a conceptual level, surfgrass beds resemble the mussel beds described by Paine and Levin (1981). Disturbances (wave action or wave-borne logs) prevent monopolization of space in both communities and are the primary agents producing the mosaic of different successional stages in the communities. In this study I experimentally simulated these natural disturbances by removing surfgrass and other macroscopic organisms from the rock. I present data for 3 years on the resultant early and middle colonizing stages. Elsewhere I describe the undisturbed community (Chapter 2) and the

initiation of the last successional stage, surfgrass recruitment (Chapter 4).

This study was carried out at two main sites and one secondary site (fully described in Chapter 2). The main sites differ primarily in substratum; Squaw Island (43° 19' N, 124° 23' W) has sandstone, Boiler Bay (44° 50' N, 124° 03' W) has mudstone. All experimental plots were on horizontal benches at approximately + 0.3 m. Both sites experience moderate wave action and sand scour. I observed occasional pockets of sand up to 2 cm deep in experimental plots at both sites. A herbivore exclusion experiment was conducted at a third site 0.7 km south of Squaw Island. This site was similar both physically and biologically to the Squaw Island site.

METHODS

To determine the effect of temporal and spatial variation on successional sequences, I initiated succession experiments in four seasons at Squaw Island and in three seasons at Boiler Bay. In each season at each site I removed surfgrass with a wrecking bar and putty knife from four replicate 0.25 m² areas, each selected to have a surfgrass canopy cover >90%. Four nearby unmanipulated plots served as controls. At Squaw Island the plots are all within a 300 m² area; at Boiler Bay within a 900 m² area. Because surfgrass beds are less extensive at Boiler Bay, the replicate plots had to be spread over a larger area. A putty knife does not remove all encrusting algae, but encrusting plants are rare (<10% cover) under a surfgrass canopy, and

they often die from desiccation when the canopy is removed. Further, when natural disturbances like wave action remove surfgrass, encrusting algae remain. The experimental plots were permanently marked with concrete nails and Sea Goin' Poxy Putty®. I recorded patterns of space utilization by plants and density of herbivores in these plots generally four times a year for 3 years. Surfgrass plants surrounding the experimental removals grew slightly into the plots, and a few surfgrass seeds recruited (Chapters 2 and 4), but this slow recovery did not appear to influence the other species.

To quantify patterns of space utilization within these experimental plots, I chose methods similar to those in other studies (Menge 1976; Lubchenco and Menge 1978). I estimated percent cover of sessile invertebrates and plants using a flexible vinyl quadrat marked with 100 randomly placed dots: I counted the number of dots above each species. I counted those species present but not under any dots as 0.5% cover. Densities of limpets and the coiled snail Tegula funebris were also recorded, but some herbivores were too small to be accurately counted; these include amphipods, isopods, and the gastropod Lacuna marmorata.

I recorded four categories of space utilization. These are (1) primary space, defined as space on the rock surface (e.g., mussels, barnacles, and encrusting algae), (2) understory space, defined as the space volume from the rock surface to a height ≤ 10 cm, (3) canopy space, defined as the space volume >10 cm from the surface, and (4) epiphytic space, defined as space on the surface of plants. Occasional overlap within these layers caused some layers to add up to more than

100% cover. That is, if one understory plant laid on top of another under a dot, each species had 1% cover. In this respect, my methods differed from those of Menge (1976) and resembled those of Littler and Littler (1980). To compute parametric statistics, I made an arcsine transformation of the percent cover data (Sokal and Rohlf 1969). Replicate plots were compared with this percentage similarity index (Whittaker 1975):

$$\text{Percentage Similarity} = \sum \text{minimum } (p_a \text{ or } p_b)$$

Where p_a is the proportion of the total plant cover occupied by a given species in sample A, and p_b is the proportion of the total plant cover occupied by the same species in sample B. It ranges from 0, when the two samples have no species in common, to 1.0, when the two samples are identical.

To determine the effect of herbivores on early succession, I excluded herbivores from four 25 cm x 25 cm quadrats with stainless steel mesh fences at a site 0.7 km south of Squaw Island. The fences were 5 cm high with a 2 cm lip projecting outward at the top with a 0.5 cm mesh size. The experiment ran from May 4, 1980, when the surfgrass (100% canopy cover) was removed, to October 23, 1980. During the experiment, I removed herbivores that entered the exclusions and cleaned the fences at least twice a month. Because the fences were not completely effective, herbivory was only reduced, not eliminated. The design included two control treatments. The unmanipulated control consisted of four replicate plots located randomly at least 1 m from any exclusion fences. These experienced the natural successional changes after surfgrass removal. The fence control consisted of four plots

immediately seaward of the four fences (i.e., with a fence along one side). These were presumably accessible to herbivores but experienced some of the artifacts of the fences, such as changes in water movement and inoculation by the spores of drift algae entangled on the fences. I removed surfgrass from a 0.5 m buffer zone around each of the plots to eliminate the influence of shading by adjacent surfgrass. Algal cover was estimated in these plots with the same methods as above, except that only 25 randomly placed dots were used.

RESULTS

The removal of surfgrass completely changes the community; within 3 months algal cover increased significantly (Chapter 2) and many species invaded (Appendix 2). In broad outline the sequence runs thus: at Squaw Island, depending on the season, one of two species colonized abundantly within 3 months, the brown blade Phaeostrophion irregulare or the green blade Ulva sp. Members of the genus Ulva are generally annuals with a perennial holdfast of small rhizoidal processes (Abbott and Hollenberg 1976). Phaeostrophion has an encrusting perennial holdfast and annual blades. At Boiler Bay, in addition to these two species, filamentous diatoms sometimes formed thick mats on bare space in the summer. In some plots Phaeostrophion and Ulva continued to dominate for the entire 3 years; in others they were replaced by a suite of middle successional algae including mats of polysiphonous red algae, the red blades Iridaea spp. and Gigartina papillata, and the branching red algae Cryptosiphonia woodii and Odonthalia floccosa. In other plots

the slowest growing middle successional species, Rhodomela larix, another branched red alga, was apparently in the process of replacing other middle successional species after 3 years. Presumably, surfgrass will eventually replace all these middle successional species. The results of this study suggest the complexity of succession in this community is caused by temporal and spatial variation as well as from variation in the species replacement mechanisms.

Seasonal Patterns

Most of the species colonizing experimental plots after surfgrass removal had distinct seasonal patterns in recruitment, cover, or both. The early colonists at Squaw Island illustrate the trends (Fig. 6). I could find only a few tiny blades of Ulva spp. in the late fall and winter. Over the summer, however, Ulva settled densely and grew very rapidly in all cases. This rapid growth forced abandonment of an Ulva removal experiment, originally included in this study. Hand removal of Ulva from a 25 x 25 cm² area proved unfeasible, because Ulva regrew rapidly and occupied 100% cover in less than 2 weeks. The brown blade Phaeostrophion irregulare also had a striking seasonal pattern (Fig. 6). It settled in the late fall, grew to occupy its maximum cover in winter, and declined as the blades became small and desiccated in the spring and summer. At Boiler Bay these two early colonists had abundance and recruitment patterns generally similar to those at Squaw Island (Fig. 7).

Middle successional algae at Squaw Island also had seasonal patterns of abundance. Gigartina papillata, for example, colonized three replicates the first spring and reached peak cover that summer (Fig. 8) with a maximum cover of 52% in one replicate. Its cover declined dramatically in the fall (a similar pattern to that observed by Slocum 1980). Although phycologists have not described any perennial tissues in Gigartina papillata (Abbott and Hollenberg 1976), its cover increased in these same plots again in spring and summer 1980, and again in spring 1981 as if it had regrown from perennial cells. Iridaea spp. (I. heterocarpa, I. flaccida, and I. cordata) exhibited a similar pattern. These species have annual blades and a perennial crustose holdfast (Hruby 1975; Hansen and Doyle 1976; Hansen 1977; Foster 1982; Gaines in prep.). They often colonize within 3 months but do not reach peak cover until summer (Fig. 9). In summer 1979 one replicate (initiated in fall 1978) had the maximum cover, 81%. Cover declines severely in fall and winter, but usually rebounds in the spring and summer.

A few species invaded plots every spring and summer at both sites. They usually did not occupy over 5% cover and often grew epiphytically. These included the red algae Halosaccion glandiforme and Porphyra sp., filamentous diatoms, and the brown algae Leathesia difformis and Leathesia nana. Mainly because of these rarer species, erect algal species diversity (measured as number of species) also peaked in summer in some replicates (Chapter 2).

Algal cover as a whole also exhibited seasonal patterns. At Squaw Island, because most individual algal species peaked in the summer, total algal cover peaked in the summer (Fig. 10) despite the opposite

trend in Phaeostrophion cover (Fig. 6). At Boiler Bay, algal cover peaked in the summer in most replicates (Fig. 11), but replicates initiated in fall 1978 did not exhibit a fall decline until the second year. The data demonstrate strong seasonal patterns in this community.

Inhibition: Variation in the Species Replacement Mechanism

Because some species recruit seasonally and space was cleared each season, comparisons between treatments in these experiments reveals the effect of established species on later colonizers. These comparisons are not as ideal as species removal experiments, because other factors might vary along with the presence of established species. Time since initiation is the most likely confounding factor. One might expect a greater cover of a species in plots exposed to propagules for a longer time. Nonetheless, if cover is less in plots exposed longer -- the opposite of the result expected from this confounding factor -- then established species clearly inhibit later colonizers.

At Squaw Island, Phaeostrophion appears to inhibit the establishment of Ulva. In summer 1979 Ulva invaded all the treatments, but it occupied significantly more space in plots initiated in spring 1979 than in plots initiated in summer or fall 1978 (Fig. 6; $p < 0.05$, Mann-Whitney U-test). The winter colonist Phaeostrophion apparently preempted some space, but the inhibition was not strong, because Ulva occupied 64.6% cover in the presence of Phaeostrophion versus 98.5% in its absence. Ulva was thus able to invade despite a high Phaeostrophion cover,

because it grew epiphytically on the small, desiccated Phaeostrophion blades. Ulva occupied only a little less cover as an epiphyte than as a saxicolous alga. At Boiler Bay both filamentous diatoms and Ulva invaded plots initiated in spring 1979. Diatoms generally invaded depressions in the plots, whereas Ulva generally invaded emergent areas. Differences between plots initiated in fall and spring by summer 1979 suggest Phaeostrophion completely preempts filamentous diatoms, which do not become epiphytic on Phaeostrophion. Diatoms occupied a mean of 59.0% cover in plots without Phaeostrophion, but did not invade plots in which it was present ($p < 0.05$, Mann-Whitney U-test). Reductions in Ulva cover in the presence of Phaeostrophion were not significant at Boiler Bay, suggesting that strength of interspecific interactions varies in space.

Herbivores

Densities of herbivores varied greatly between replicates, but the removal of surfgrass evidently increased their densities somewhat above control densities. Limpets (mainly Collisella strigatella) had similar densities in control and experimental plots before the experiment was initiated in summer 1978 (Fig. 12). As algal cover increased, limpet densities increased, remaining significantly above control densities from winter 1979 through summer 1979 ($p < 0.05$, Mann-Whitney U test). As early successional algae decreased in abundance, limpet densities fell to control levels. Tegula funebris densities were also initially similar in control and experimental plots (Fig. 13). Although Tegula

was usually more abundant in experimental plots, the difference was significant only in winter 1979 ($p < 0.05$, Mann-Whitney U-test). Less abundant herbivores, such as chitons, did not increase after surfgrass removal (Chapter 2). The sizes of all herbivores appeared similar in experimental and control plots. Thus, removal of surfgrass mainly influenced limpet densities early in the successional sequence.

An exclusion experiment suggests herbivores could influence the cover of Ulva during the summer. I initiated the experiment May 4, 1980. By August 10, Ulva occupied 94.3% of the understory space in the exclusions but only 29.0% and 30.0% in the fence controls and unmanipulated controls respectively, a highly significant difference ($p < 0.01$, ANOVA). By October 23, Ulva still occupied more space in the exclusions than in the fence controls and unmanipulated controls (55.5% vs. 15.4% and 22.2% respectively). However, the difference was no longer significant ($p > 0.05$, ANOVA). Ulva may have decreased in cover because of physical conditions in the fall despite the low level of herbivory in the exclusions. I terminated the experiment in October 1980, because the fences could not have withstood late fall and winter storms. From this experiment, I conclude that herbivores could depress the cover of Ulva early in succession, but they apparently are not solely responsible for the decline of Ulva.

Middle Successional Stages: Local Variation Among Replicate Plots

As succession proceeded, replicate plots began to differ in their species composition. The four replicates at Squaw Island initiated in

spring 1979 illustrate how greatly replicates can differ (Fig. 14). Before the experiment all four replicates were similar with a 100% canopy cover of surfgrass and a small cover (<15%) of understory plants. By summer 1979 Ulva dominated all four replicates (88-98% cover), and by fall 1979 Ulva cover declined in all four. By the second summer (1980) the replicates had important differences. Replicate 1 (in Fig. 14) consistently had the greatest number of limpets and the greatest density of barnacles. Perhaps as a consequence, algal cover was never as great in replicate 1 as in others. Ulva was the most abundant species all three summers, and Iridaea spp. and polysiphonous red algae were also abundant in some summers. In replicate 2 the branched red alga Cryptosiphonia woodii dominated during summer 1980 (87% cover), but when Cryptosiphonia declined in fall 1980, early successional species, Ulva and Phaeostrophion, again captured most of the space. In contrast, in replicate 3 although Cryptosiphonia invaded, it never occupied as high a cover as in replicate 2, possibly because another branched red alga Rhodomela larix occupied 48% cover in summer 1980. This high cover of Rhodomela relatively early in succession might have been caused by regrowth from cells not completely removed when the experiment was initiated (see below). Replicate 3 had a 2% cover of Rhodomela in the understory of the initial surfgrass bed, but none of the other replicates in this treatment had initial Rhodomela cover. In replicate 4 Cryptosiphonia replaced Ulva and dominated the next summer (1980). Rhodomela invaded replicate 4 in winter 1980, grew slowly, and replaced Cryptosiphonia as the most abundant species by spring 1981.

Thus, the four replicates experienced entirely different successional sequences.

Similar differences among replicates occurred in several treatments at both sites. At Squaw Island at the end of the experiment in spring 1981 six species occupied over 20% in at least one plot (Table 9). The replicates initiated in summer 1978 were fairly similar. Phaeostrophion invaded these plots the first winter and maintained a high cover in all plots throughout the experiment (Fig. 6). Epiphytic Ulva had a high cover in some plots. In contrast, replicates of the other three treatments did not resemble each other any more closely than they resembled non-replicate plots initiated in different seasons (Table 9). In many plots early successional species still maintained a high cover, but in others Iridaea flaccida, Cryptosiphonia, and Rhodomela had established a high cover. At Boiler Bay the replicates initiated in fall 1978 resembled each other fairly closely (Table 10). Rhodomela was the most abundant species in all four. In the other two treatments, however, replicates hardly resembled each other at all. A variety of species were abundant, including Phaeostrophion, Cryptosiphonia, polysiphonous red algae, and Odonthalia.

The percentage similarity values make the same point. If local variation among replicates were not important, one would expect that treatment effects would make replicate plots far more similar than non-replicate plots. At Boiler Bay, replicates initiated in fall 1978 are indeed more similar than non-replicates (Table 11). For the other two treatments, however, average pairwise similarity between replicates is hardly greater than average pairwise similarity between non-

replicates. At Squaw Island replicates initiated in summer 1978 were more similar than non-replicates. These plots all had a fairly high cover of Phaeostrophion (43-66%). Nonetheless, the replicates of the other three treatments at Squaw Island were no more similar than non-replicates. In fact, the two most similar plots at Squaw Island were non-replicates, replicate 3 initiated summer 1978 and replicate 4 initiated winter 1979 (similarity index = .90).

One cause of this local variation among replicates appears to be small variations in the initial surfgrass understory. The mean cover of Rhodomela at the end of the experiment in plots that had had some initial cover was 38.7%, but the mean cover in plots that had had no initial cover was 10.7% (see footnotes in Tables 9 and 10). This highly significant difference ($p < 0.005$; Mann-Whitney U-test) may have been caused by the thin crustose holdfast of Rhodomela, which is very difficult to completely remove (C. D'Antonio per. comm.). Upright branches regrow from the holdfast. Apparently, my scraping with a putty knife did not completely remove the holdfasts, and the plants regrew vegetatively. This vegetative regrowth was crucial, because Rhodomela rarely recruits (C. D'Antonio, pers. comm.).

Another possible cause of local variation among replicates is the preemptive ability of Phaeostrophion, which settles densely during the fall and winter when few other species recruit. Its crustose holdfast occupies almost as much space on the rock as the blades occupy in the understory. Such a form might result in higher preemptive ability than an alga such as Iridaea flaccida, whose holdfast occupies as little as 1/20 of the area of occupied by the blades in understory or canopy

space. Most importantly, Phaeostrophion is a long-lived perennial. If surfgrass is removed in August, Phaeostrophion invades and attains a high cover for at least 3 years. If two replicates are excluded from the analysis (Boiler Bay, winter initiated replicate 3 and Squaw Island, fall initiated replicate 4), then the final cover of branched algal species (Rhodomela, Cryptosiphonia, and Odonthalia) is negatively correlated with the final cover of Phaeostrophion ($p > 0.01$, Hotelling-Pabst test, Conover 1971). Exclusion of two replicates is warranted, because none of the species of interest attained over 3% cover in either replicate. Further evidence of competition between Phaeostrophion and branched algae is provided by Rhodomela removals (Chapter 4). September Rhodomela removals were dominated by Phaeostrophion by March. Thus, if Phaeostrophion invades plots uniformly, they are likely to remain similar for years. If Phaeostrophion recruitment varies, local variation among replicates is likely to persist for years.

DISCUSSION

Early and middle stages of succession in these surfgrass beds are complex. Because of this complexity, none of the simple models of succession predicts the changes in species composition that occur. Complexity in this community apparently results from three types of variation: (1) in time, (2) in species replacement mechanisms, and (3) in space. Below I discuss the possible causes of each aspect of complexity in turn and compare surfgrass beds to other communities.

The seasonal patterns of growth and recruitment by Ulva and Phaeostrophion documented in this study appear to illustrate adaptations to different types of disturbance. Along the Oregon coast space can be made available in two ways at two different times: either "winter" storms (November-April) can remove space occupants (e.g., Paine and Levin 1981) or the first storm in the fall can remove the sand that totally buries some areas in the summer (e.g., Markham 1973). The distribution of Phaeostrophion (limited to sand-influenced areas), the ability of its blades to regrow if they are removed by sand scour, and its fall and winter recruitment suggest that it is adapted to take advantage of space made available by sand movement (Mathieson 1965). On the other hand, Ulva, a thinner, more fragile blade, appears adapted to take advantage of space made available by wave removal of organisms later in the year. At Squaw Island and Boiler Bay both processes make space available, and both algae occur. In other communities, organisms are also thought to be closely adapted to the disturbance regime (e.g., Paine and Levin 1981).

The other distinct seasonal pattern documented in this study, dramatic fall declines in algal cover, could have a variety of causes. In Oregon the changes occurring in the fall include shorter days (= reduced time for photosynthesis), lower temperatures (night low tides mean algae may experience freezing temperatures), larger waves, increased freshwater from heavy rains, and perhaps increased sand scour due to increased water movement. Hansen (1977) believed that large waves and shorter days, which could reduce growth to the point where it does not compensate for tissue removed by waves, correlated best with

declines in the cover of Iridaea cordata. Gaines (in prep.), however, showed that blade loss in I. cordata occurs at the same time the plants lose their cuticle. Without this cuticle, I. cordata is much more susceptible to herbivores. Thus, fall declines in algae might be due to a complex of interacting factors.

Regardless of its cause, this seasonal decline in algal cover plays a central role in the community by reducing the cover of dominant algal species. For example, the deaths of Ulva individuals in the fall might allow Cryptosiphonia to replace them. Similarly, the deaths of Cryptosiphonia individuals in the fall might allow Rhodomela or even Phaeostrophion to replace them. Therefore, the strong seasonal variation in this community adds to its complexity.

Variation in the species replacement mechanism (= all types of interspecific interaction; Connell and Slatyer 1977) also increases the complexity of succession in this community. One example of such variation is in the ability of Phaeostrophion to inhibit Ulva and diatoms. Diatoms were completely inhibited, but Ulva was only slightly inhibited, because it grew epiphytically on Phaeostrophion. The variation may result from the different competitive abilities of Ulva and diatoms, if the ability to grow epiphytically is considered a component of competitive ability. The result is puzzling, however, because filamentous diatoms do grow epiphytically on other species. It suggests that the host-epiphyte interaction is fairly specific. Without further experiments, the precise interaction between Ulva and Phaeostrophion is unclear. Phaeostrophion may not be greatly harmed by

Ulva, because its blades become small and desiccated in the summer in any case.

A more striking example of variability in the species replacement mechanism is the occurrence of both inhibition, demonstrated here, and facilitation (Chapter 4) in the successional sequence in surfgrass beds. Surfgrass is an angiosperm with barbed seeds (Gibbs 1902). Surfgrass seeds must recruit by attachment to algae with a specific morphology or they will be dislodged (Chapter 4). The form of the seeds complements the form of branched algae with a central axis 1 mm in diameter, such as Rhodomela, Odonthalia, Cryptosiphonia, and some erect coralline algae. Therefore, the step from middle to late successional species is classified as obligate facilitation. None of the simple models predicts such different species replacement mechanisms in one successional sequence.

The successional sequence of the plants observed in this study influences the herbivores. The increased limpet densities early in succession might have two causes. (1) Early successional plants are generally more attractive to marine herbivores than late successional plants (Lubchenco and Gaines 1981). (2) Early successional plants are smaller and therefore less likely to crowd out herbivores (e.g., Southward and Southward 1978; Underwood and Jernakoff 1981). The slight increases in Tegula densities throughout the successional sequence might have similar causes. Tegula seems to prefer algae to surfgrass (Best 1964) and might be attracted to algae.

The influence of herbivores on succession as a whole is not known, but the experiments reported here suggest that they have only a subtle

effect on the early stages. Herbivore exclusions produced a significant increase in Ulva, but in some places, Ulva can attain almost 100% cover, even with herbivore access (spring 1979 removals, Squaw Island, Fig. 6). In addition, the reduced Ulva cover produced by herbivores in the experiment did not result in a significant increase in other algal species. Finally, fall declines in algal cover occurred both in the presence and absence of herbivores.

Spatial variation among replicates is perhaps the most unpredictable aspect of succession in surfgrass beds. One cause of variation suggested by the data is an historical effect, the presence or absence of Rhodomela in the initial surfgrass bed. Two other possible causes of variation among replicates are spatial differences in recruitment magnitude and surrounding organisms. Rhodomela and surfgrass itself are examples of species with particularly variable recruitment. The ability to capture space by vegetative growth can amplify these chance differences, because one propagule might grow to occupy a large patch. The organisms surrounding a successional plot could influence the sequence in four ways: (1) they could provide a source of propagules; (2) they could invade the plot themselves by vegetative growth, (3) they could produce variability in conditions near the edge of the plot by shading, whiplash, or allelopathy, or (4) they could harbor different species of herbivores. Although few algal dispersal patterns are known, some species do not disperse more than a few meters (Dayton 1973; Deysher and Norton 1981). If this pattern is common, differences in surrounding plants could produce high local variability (Horn 1981). Surrounding organisms might also invade plots by vegetative growth of

adults. In my experiments, for instance, vegetative growth by Rhodomela plants at the borders of some plots accelerated its dominance of the plots. Variations in conditions created by surrounding plants have not been documented in the present study, but they appear to exist. I noticed, for example, that Ulva did not colonize the edges of plots shaded by surfgrass at low tide. An alternate hypothesis, that the replicates are not true replicates but differ in their abiotic characteristics or in their microscopic biotic characteristics, also merits consideration. Further experimentation could evaluate how each of these effects contributes to divergence of replicate plots.

Despite the variety of middle successional stages, all my replicates will probably have the same last successional stage dominated by surfgrass. I expect the replicates to become similar again because of some specific characteristics of this system. Surfgrass plants surrounding the plots slowly invade by horizontal vegetative growth (Chapter 2). Even if surfgrass plants did not surround the plots, they would probably still form surfgrass beds, though much more slowly, as surfgrass recruited from seeds. The only condition that might preclude surfgrass invasion is a persistent monoculture of blade-like species such as Phaeostrophion that cannot facilitate surfgrass (Chapter 4). Although an indefinitely persisting monoculture of any species seems improbable, Phaeostrophion has dominated several experimental plots for 3 years. In addition, Phaeostrophion forms large monocultures at Strawberry Hill and Seal Rock, sand-influenced areas on the Oregon coast (C. D'Antonio pers. comm.). Such abundant Phaeostrophion could clearly delay surfgrass establishment. Hence, the initial season could

influence the long term course of succession by determining the abundance of perennial Phaeostrophion.

Comparisons of the dynamics of low zone rocky intertidal algal associations in different areas provide further insights into the process of succession. Sousa's (1979) study in Santa Barbara, California, for example, was similar in design to this study, but in contrast to my results, Sousa found that Ulva sp. colonized first throughout the year. Northcraft (1948) made a similar observation in Monterey, California. Ulva may only recruit in one season in Oregon, because the physical environment changes more there. Day length, temperature, and wave action (B. Menge pers. comm.) vary less in Santa Barbara. Whether this difference represents a latitudinal difference or a difference between sites unrelated to latitude is not clear.

Sousa's (1979) results also differ from the present study in the role of herbivores. When Sousa excluded herbivores, Ulva persisted through the winter and middle successional red algae did not invade. In the presence of herbivores, however, Ulva was removed, its inhibition broken, and red algae invaded. By contrast, in Oregon Ulva declines in the fall even in herbivore exclusions. Two possible explanations could account for this difference. First, Oregon appears to experience greater changes in the physical environment that could remove Ulva. Second, the large herbivores most important in California, the crab Pachygrapsus crassipes and the sea hare Aplysia californica, are absent in Oregon. In California, limpets temporarily reduced the abundance of Ulva but did not effect its replacement. Since limpets and other molluscan herbivores were the main herbivores excluded by my

experiments, these type of consumers appear to play similar roles in the two communities.

The seasonal variation, the variation in species replacement mechanisms, and the spatial variation that add complexity to succession in surfgrass beds are not unusual features in natural communities. In marine fouling communities, for example, abilities of different species to invade space and to resist invasion vary greatly (Sutherland and Karlson 1977). Stochastic spatial variation in the intensity of recruitment influences both marine and terrestrial communities (e.g., Sutherland 1974, 1980; Robles and Cubit 1981; Hils and Vankat 1982). Historical effects analogous to Rhodomela cells remaining after a disturbance may occur in many communities, because most natural disturbances do not remove all parts of all organisms. Other algae or simple colonial organisms like sponges may be able to recover from just a few cells, and terrestrial plants can resprout or grow from a seed bank, which may reflect the history of the site (Marks 1974; Harper 1977; Van Hulst 1980). Surrounding organisms are known to influence succession in a fouling community (Kay and Keough 1981), where sponges rapidly invade newly available space adjacent to them. Thus, in many situations simple models can not predict successional change. This complexity should challenge ecologists to work towards the development of general theory explaining why different processes occur in different communities.

Table 9. Abundant erect plant species in each replicate of surfgrass removal experiments from data taken in June 1981 at Squaw Island. Numbers preceding each species name in parentheses are percent covers, canopy, understory, and epiphytic cover combined.

Treatment (date succession initiated)	Replicate #	Species with greatest % cover	Other abundant species (> 20% cover)
Summer 1978	1 ^b	(68) <u>Ulva</u>	(55) <u>Phaeostrophion</u>
	2 ^b	(66) <u>Phaeostrophion</u>	none
	3 ^b	(48) <u>Phaeostrophion</u>	(27) <u>Ulva</u>
	4 ^a	(43) <u>Phaeostrophion</u>	none
Fall 1978	1 ^b	(41) <u>Phaeostrophion</u>	(32) <u>Ulva</u> , (24) polysiphonous red algae
	2 ^a	(51) <u>Rhodomela</u>	(27) <u>Iridaea flaccida</u>
	3 ^b	(51) <u>Phaeostrophion</u>	none
	4 ^b	(73) <u>Ulva</u>	none
Winter 1979	1 ^a	(56) <u>Phaeostrophion</u>	(38) <u>Rhodomela</u>
	2 ^b	(29) <u>Iridaea flaccida</u>	(23) <u>Phaeostrophion</u>
	3 ^a	(30) <u>Rhodomela</u>	(24) <u>Ulva</u>
	4 ^b	(61) <u>Phaeostrophion</u>	(41) <u>Ulva</u>
Spring 1979	1 ^b	(29) <u>Ulva</u>	none
	2 ^b	(53) <u>Phaeostrophion</u>	(35) <u>Cryptosiphonia</u>
	3 ^a	(72) <u>Rhodomela</u>	(35) <u>Phaeostrophion</u>
	4 ^b	(68) <u>Rhodomela</u>	(34) <u>Cryptosiphonia</u>

^a Rhodomela present as an understory species in the surfgrass bed before the experiment was initiated.

^b Rhodomela absent before the experiment was initiated.

Table 10. Abundant erect plant species in each replicate of surfgrass removal experiments from data taken in April 1981 at Boiler Bay. Numbers preceding each species name in parentheses are percent covers, canopy, understory, and epiphytic covers combined.

Treatment (date succession initiated)	Replicate #	Species with greatest % cover	Other abundant species (> 20% cover)
Fall 1978	1 ^a	(17) <u>Rhodomela</u>	none
	2 ^a	(61) <u>Rhodomela</u>	none
	3 ^a	(66) <u>Rhodomela</u>	(23) <u>Phaeostrophion</u>
	4 ^b	(39) <u>Rhodomela</u>	(29) <u>Odonthalia</u>
Winter 1979	1 ^b	(82) <u>Cryptosiphonia</u>	none
	2 ^a	(42) <u>Rhodomela</u>	(32) polysiphonous red algae
	3 ^a	(3) <u>Phaeostrophion</u>	none
	4 ^b	(34) <u>Cryptosiphonia</u>	(30) <u>Phaeostrophion</u>
Spring 1979 ^c	1	(30) polysiphonous red algae	none
	2	(41) <u>Phaeostrophion</u>	none
	3	(57) <u>Phaeostrophion</u>	(53) <u>Rhodomela</u> (23) <u>Odonthalia</u>
	4	(49) <u>Odonthalia</u>	(33) polysiphonous red algae

^a Rhodomela present as an understory species in the surfgrass bed before the experiment was initiated.

^b Rhodomela absent before the experiment was initiated.

^c Data on the initial presence or absence of Rhodomela in this treatment are unavailable.

Table 11. Comparisons of percentage similarity (Whittaker 1975) of replicate plots of surfgrass removals and of plots initiated in different seasons. Similarity was calculated using the percent of total upright plant cover occupied by each species in spring 1981.

Plots compared		Average similarity of all pairwise comparisons	Range of similarity values
Boiler Bay:	Replicates initiated fall 1978	.55	.23 - .69
	Replicates initiated winter 1979	.33	.01 - .54
	Replicates initiated spring 1979	.35	.08 - .56
	All pairwise comparisons between non-replicates	.32	0 - .73
Squaw Island:	Replicates initiated summer 1978	.63	.47 - .74
	Replicates initiated fall 1978	.41	.26 - .62
	Replicates initiated winter 1979	.44	.30 - .52
	Replicates initiated spring 1979	.38	.14 - .69
	All pairwise comparisons between non-replicates	.44	.03 - .90

Figure 6. Seasonal cover of two early colonizing species, Ulva sp. (dark bars) and Phaeostrophion irregulare (light bars), at Squaw Island following surfgrass removal in four seasons. I initiated four replicates in each season. Bars represent means, and lines represent standard errors, which are symmetrical about the means. Both epiphytic and epilithic cover are included. Ulva cover in summer 1979 is significantly higher in the spring removals, without Phaeostrophion, than in the fall and winter removals, with Phaeostrophion ($p < 0.05$, Mann-Whitney U-test).

Figure 6.

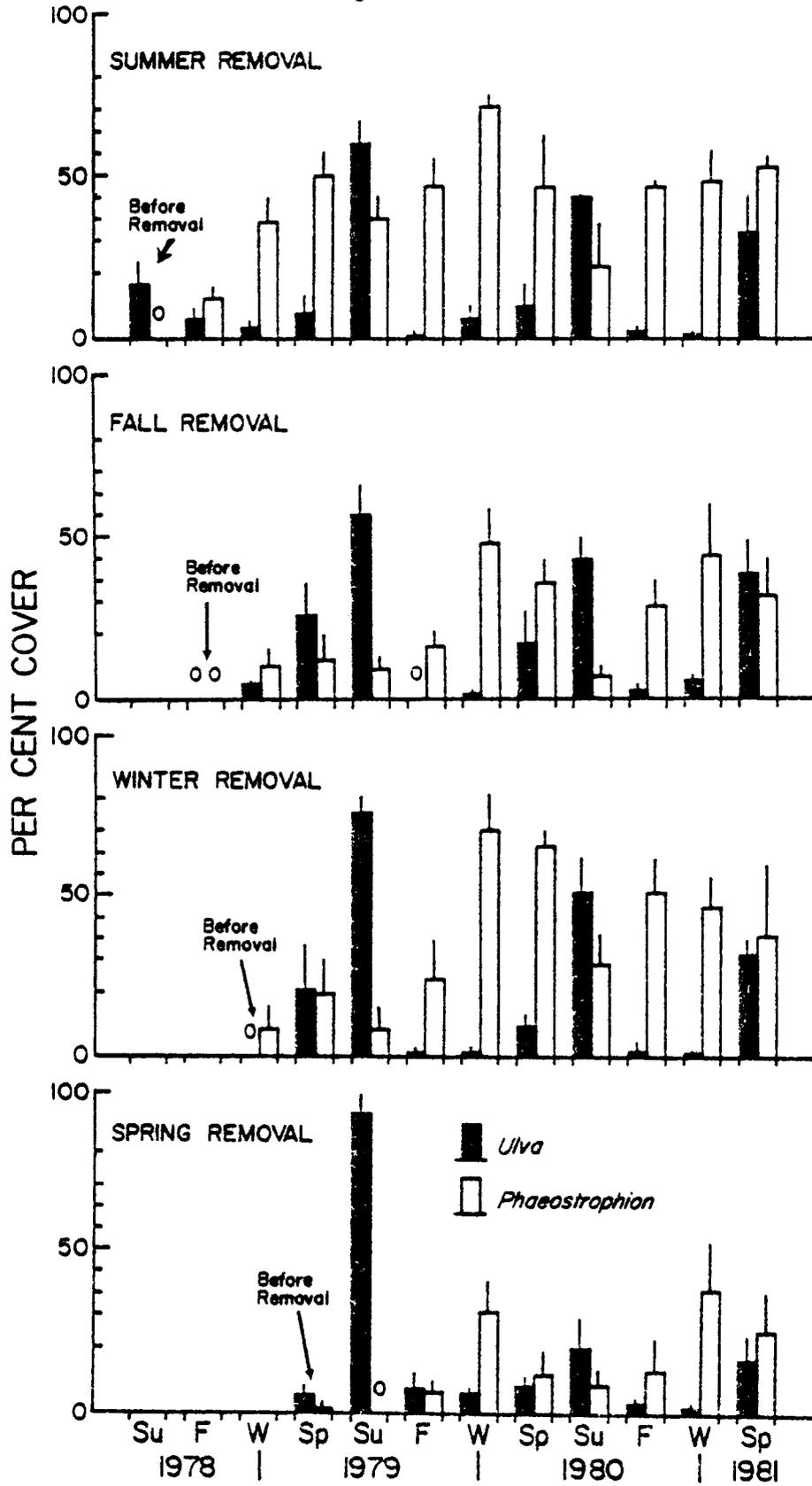


Figure 7. Seasonal cover of two early colonizing species, Ulva sp. and Phaeostrophion irregulare, at Boiler Bay following surfgrass removal in three seasons. I initiated four replicates in each season. Bars represent means, and lines represent standard errors, which are symmetrical about the mean. Both epiphytic and epilithic cover are included. Breaks in the axis indicate dates for which no data were taken. The asterisk indicates data were only taken for one replicate.

Figure 7.

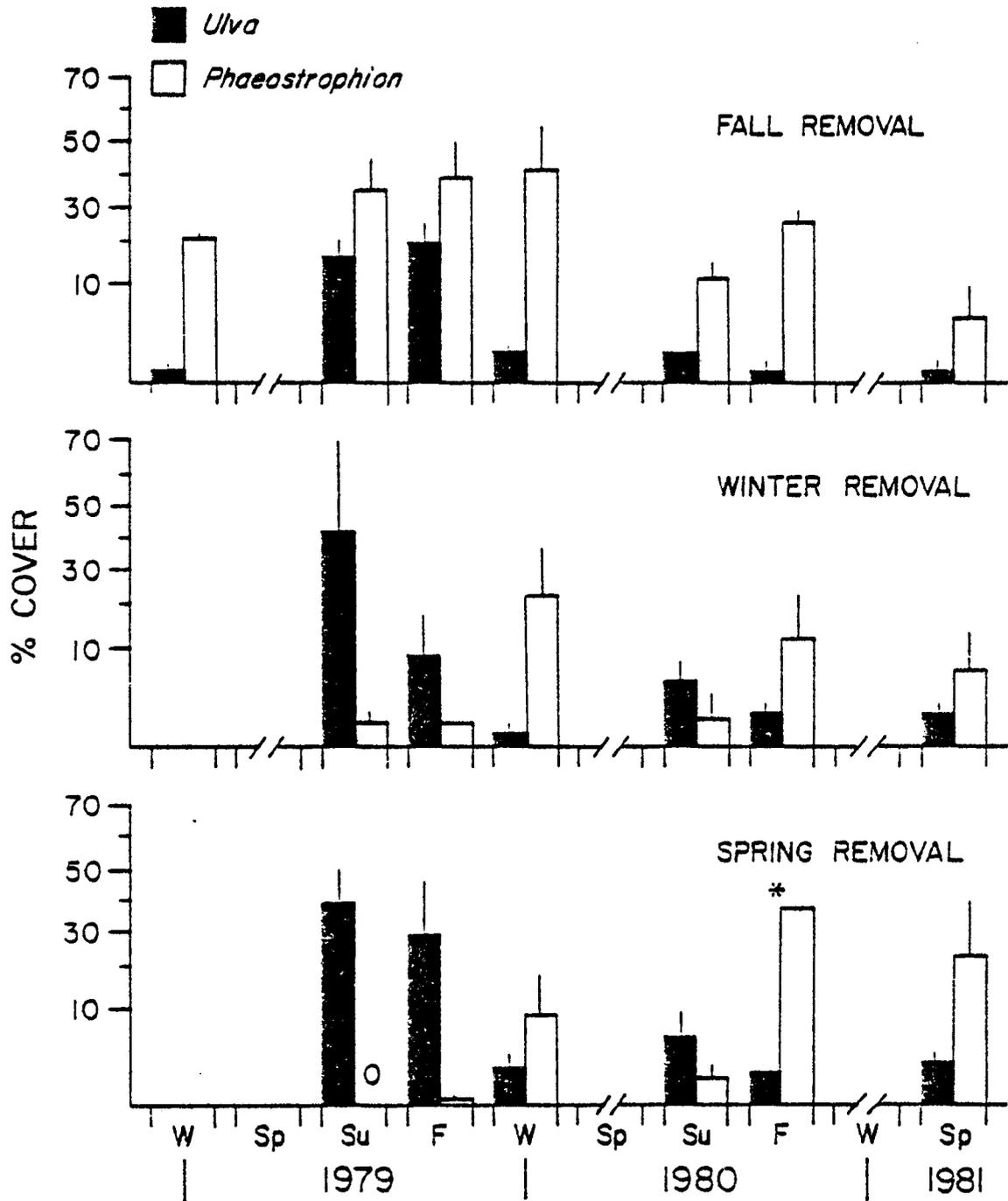


Figure 8. Seasonal cover of Gigartina papillata in the three replicates it invaded at Squaw Island. It did not invade Boiler Bay. For each replicate, I expressed the combined canopy and understory percent cover for each sampling date as a percentage of the maximum observed in that replicate. Maxima ranged from 17 to 52 percent cover. These percentages were arcsine transformed, and the bars represent means, the line standard errors, which are symmetrical about the means.

Figure 8.

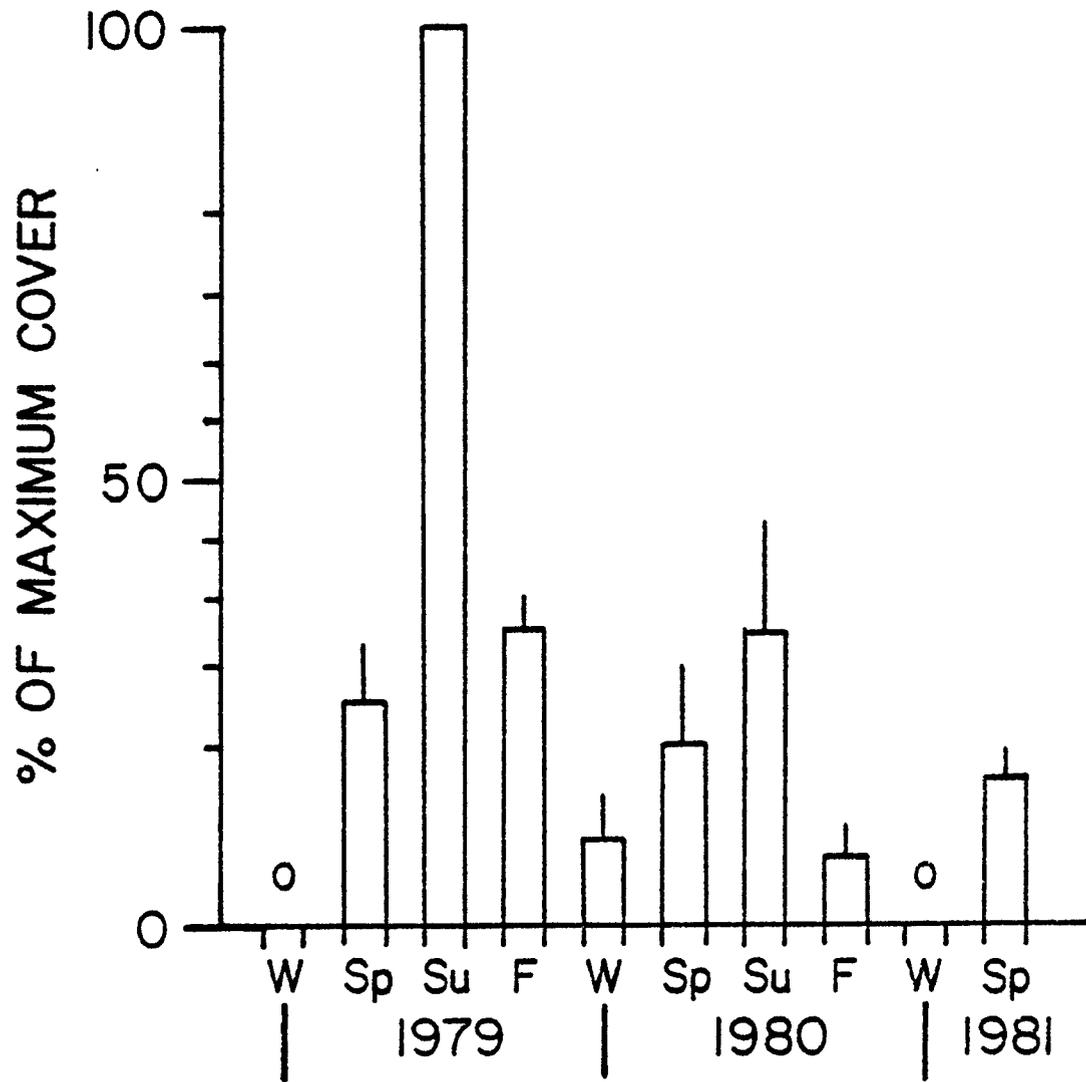


Figure 9. Seasonal cover of Iridaea spp. (I. flaccida, I. heterocarpa and I. cordata combined) in the replicates it colonized at Squaw Island: four replicates of the treatments initiated in summer, fall, and spring, and three replicates initiated in winter. These species were not as abundant at Boiler Bay. For each replicate, I expressed the combined canopy and understory percent cover for each sampling date as a percentage of the maximum observed in that replicate. Maxima ranged from 5 to 81 percent cover. These percentages were arcsine transformed, and the bars represent means, the lines standard errors, which are symmetrical about the means.

Figure 9.

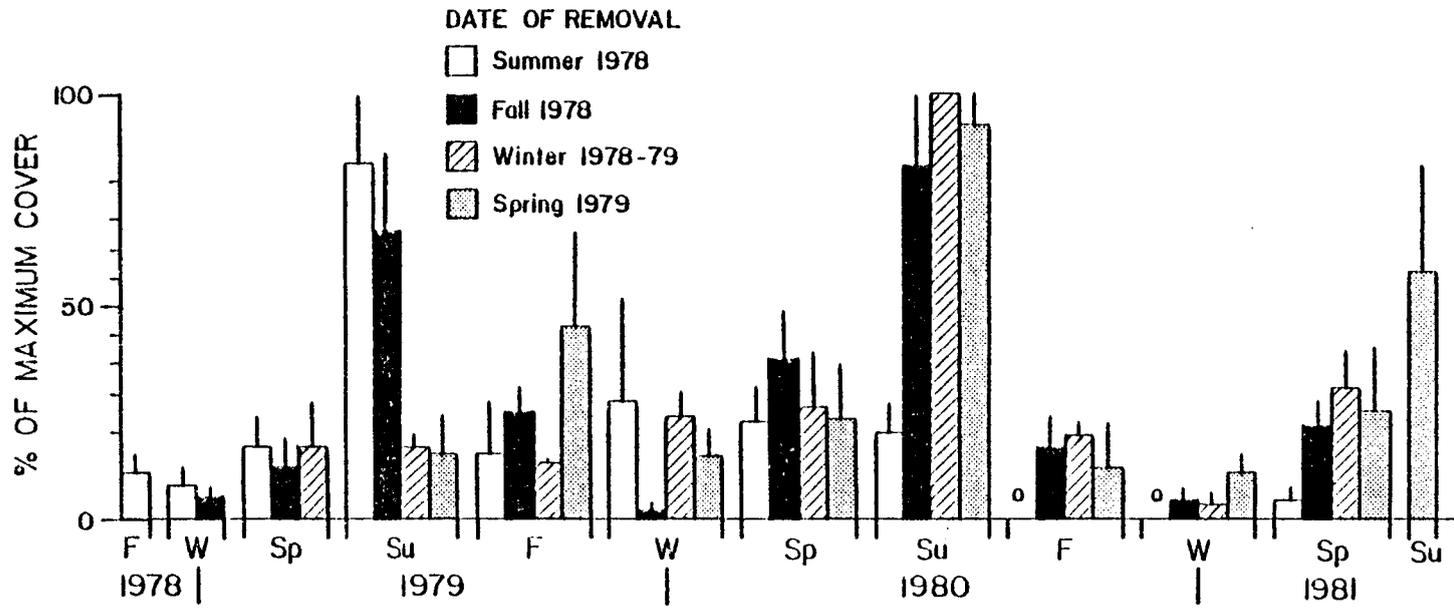


Figure 10. Seasonal cover of all upright algae, understory, canopy, and epiphyte cover combined, illustrating the consequences of four different seasons of initiation at Squaw Island. All values over 100% were considered as 100%. Points represent means; lines standard errors.

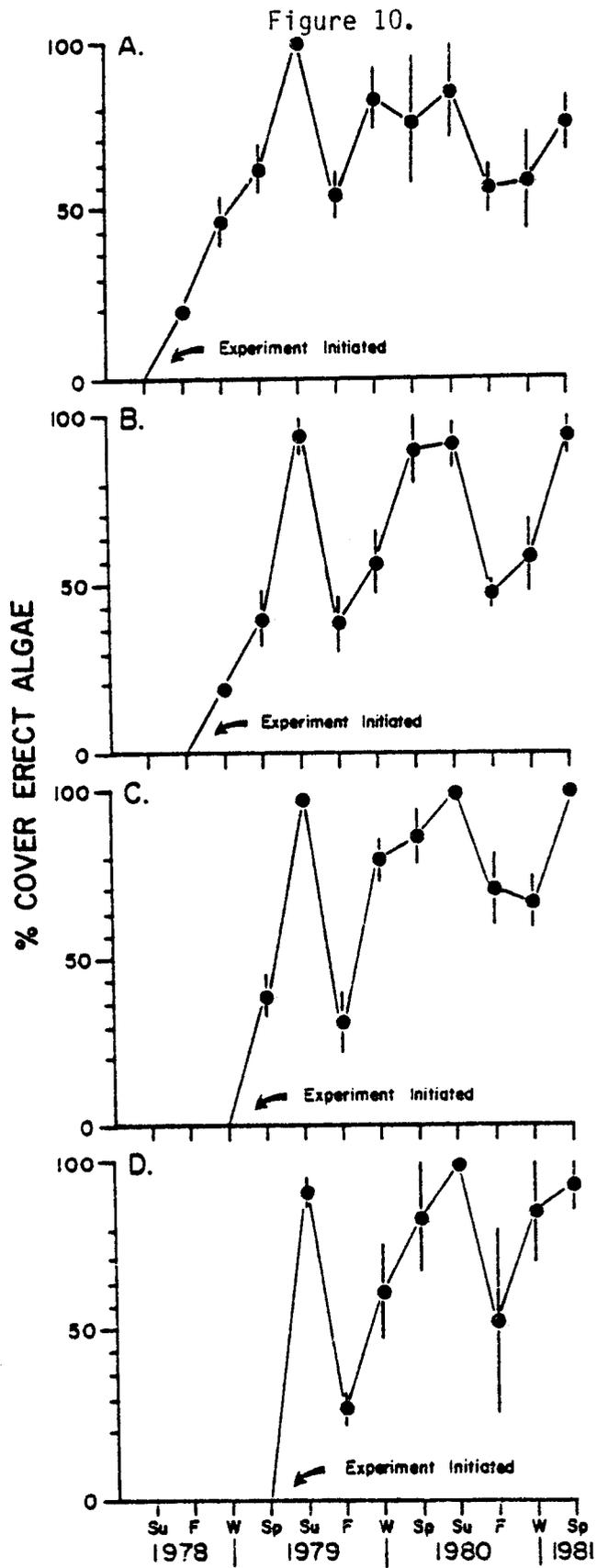


Figure 11. Seasonal cover of all upright algae, understory, epiphytic, and canopy cover combined, in three seasons at Boiler Bay. All values over 100% were considered as 100%. Bars represent means; lines standard errors. Breaks in the axis indicate dates for which no data were taken. The asterisk indicates data were only taken for one replicate.

DATE OF REMOVAL

□ Fall 1978

■ Winter 1978-79

▨ Spring 1979

Figure 11.

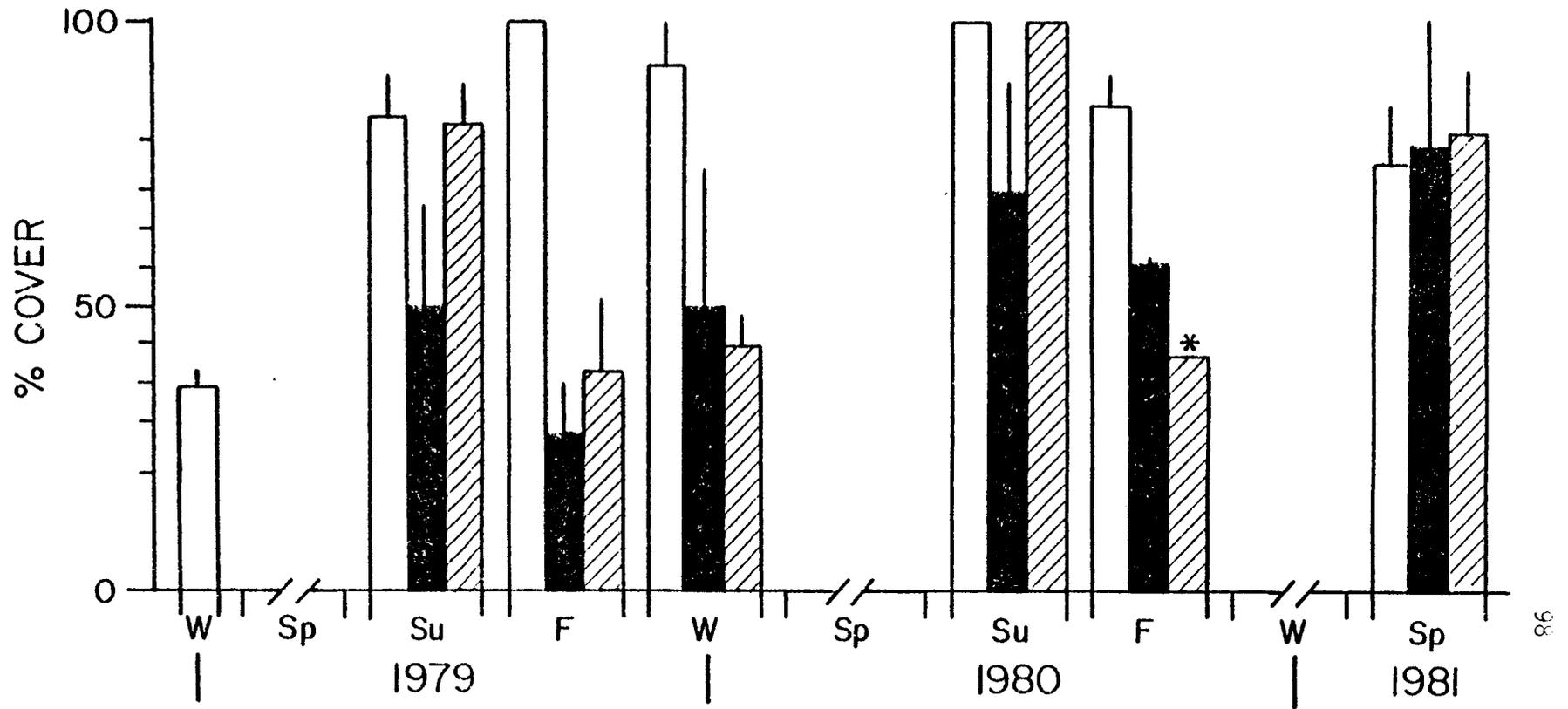


Figure 12. Limpet densities (mainly Collisella strigatella) in surfgrass removal plots and unmanipulated control plots at Squaw Island. Dots represent means; lines standard errors. Lines are missing when the standard error is the size of the dot. Gaps represent dates when no data were taken. Experimental limpet densities were significantly above control densities from winter 1979 through summer 1979 ($p < 0.05$, Mann-Whitney U-test).

Figure 12.

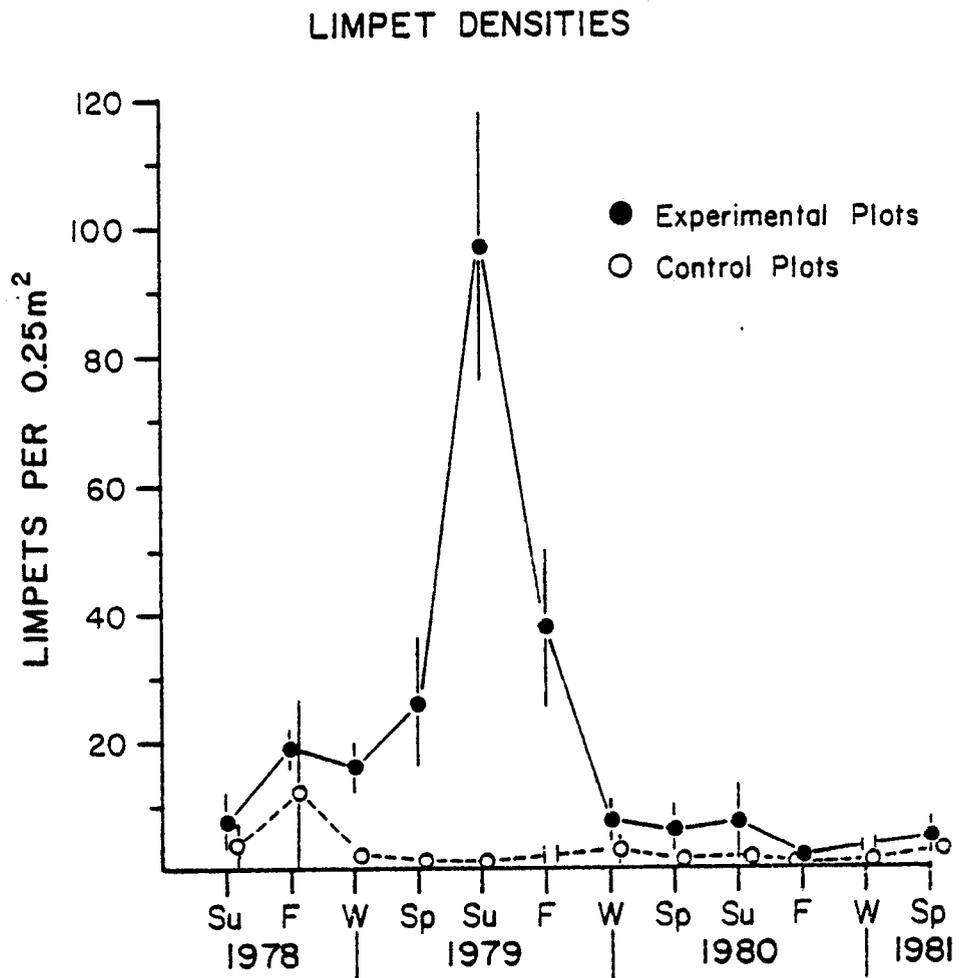


Figure 13. Tegula funebris densities in surfgrass removal plots and unmanipulated control plots at Squaw Island. Dots represent means; lines standard errors. Standard errors are not represented if they are the size of the dot. Gaps represent dates when no data were taken. Experimental densities were significantly above control densities only in winter 1979 ($p < 0.05$ Mann-Whitney U-test).

Figure 13.

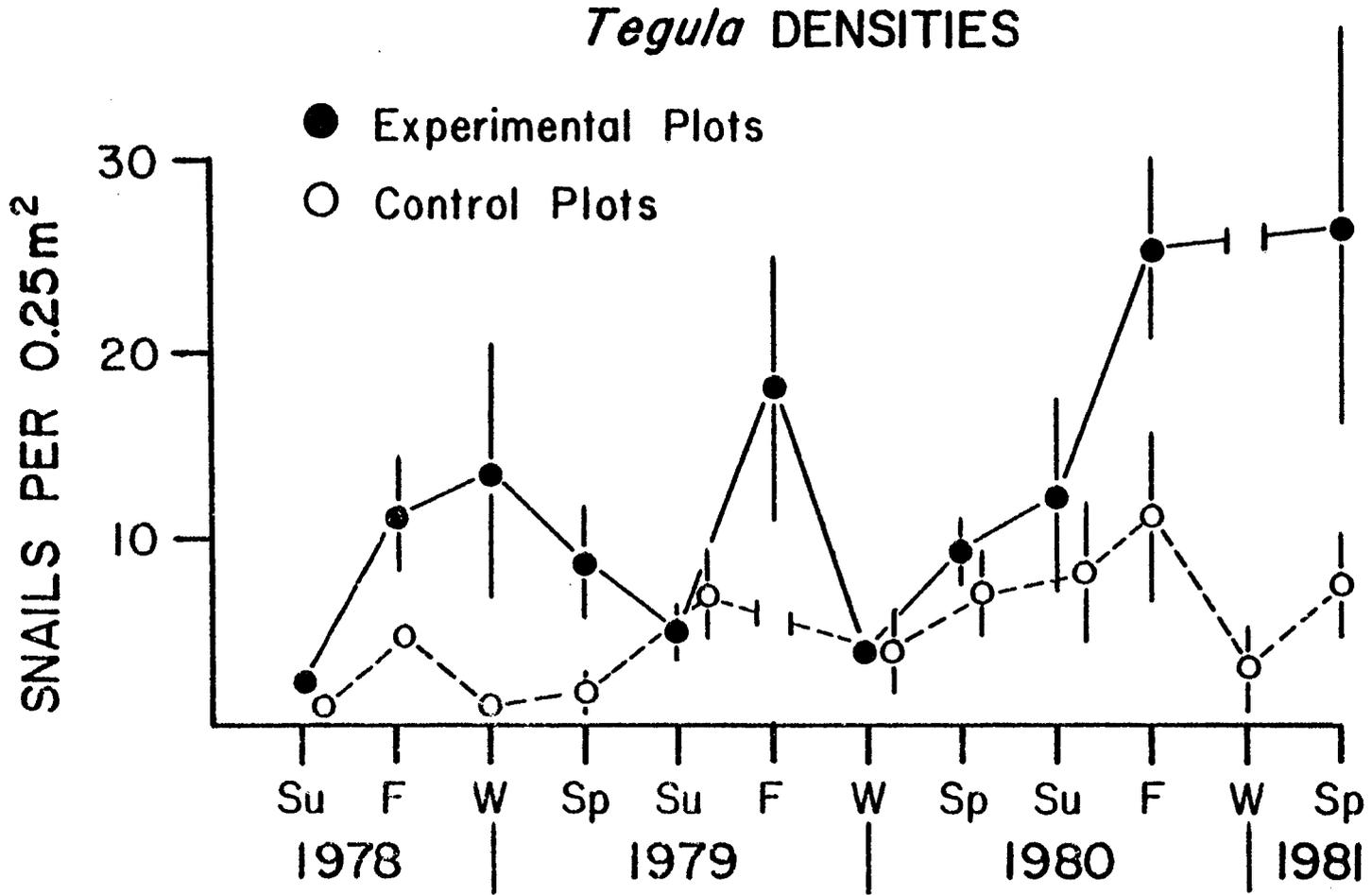
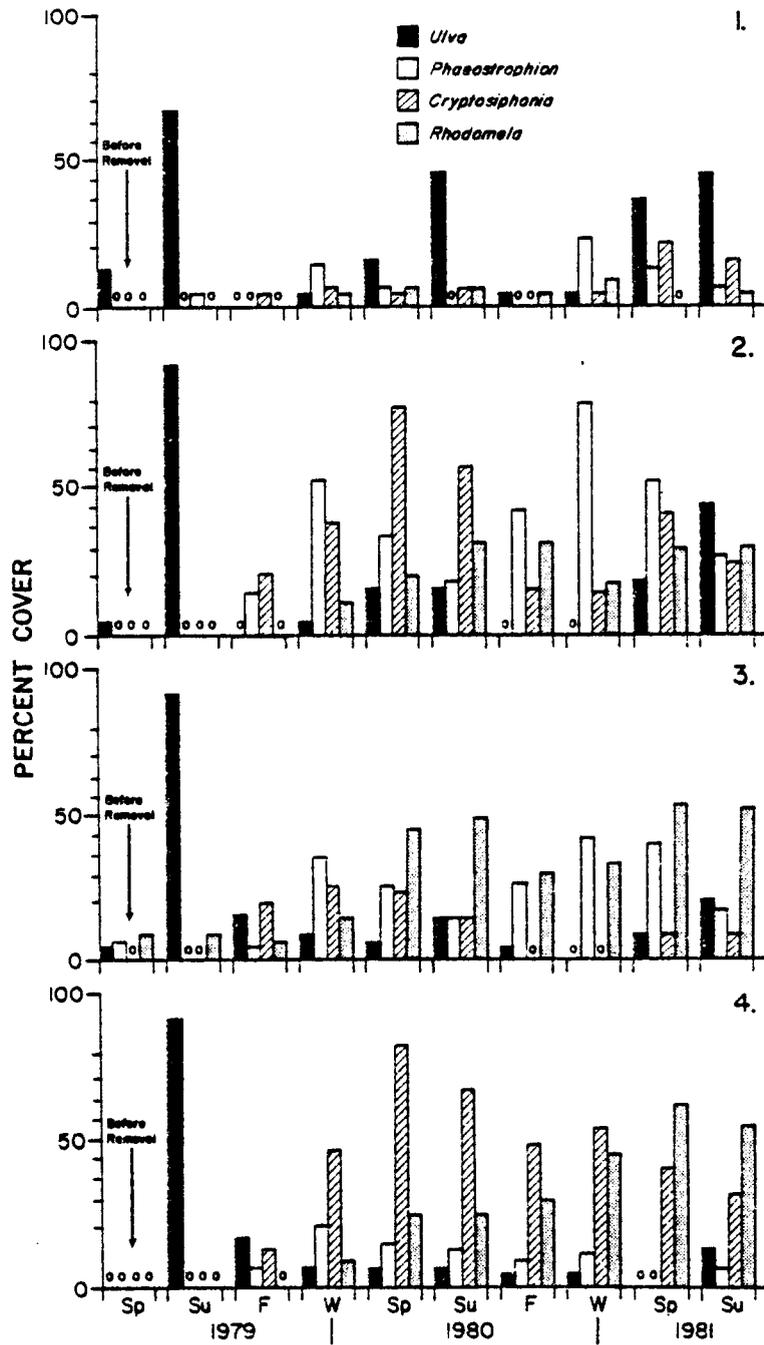


Figure 14. Cover of four most abundant species, Ulva sp., Phaeostrophion irregulare, Cryptosiphonia woodii, and Rhodomela larix, in each of four replicate plots numbered one to four at Squaw Island initiated in spring 1979. Both epiphytic and epilithic cover are included. The algal cover before removal was beneath a 100% cover surfgrass canopy.

Figure 14.



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CHAPTER IV.

FACILITATION AS A SUCCESSIONAL MECHANISM
IN A ROCKY INTERTIDAL COMMUNITY

INTRODUCTION

Succession, or species replacement during community development, is one of the oldest and most fundamental concepts of ecology (e.g., Clements 1916; Drury and Nisbet 1973; Horn 1976; Golley 1977; Whittaker and Levin 1977; McIntosh 1981). Each step in a successional sequence proceeds by one of three possible mechanisms (Connell and Slatyer 1977). The earlier species may (1) facilitate, (2) inhibit, or (3) have no effect on the establishment of subsequent species. Despite the importance and the age of the concept of succession, studies which definitively distinguish between these alternatives are relatively rare. Field experiments can both differentiate these three mechanisms and determine the magnitude of inhibition or facilitation. The facilitation model describes the traditional view of succession (Clements 1916; Odum 1969). However, recent experimental investigations suggest that inhibition occurs more frequently in many communities, particularly in marine environments (Standing 1976; Connell and Slatyer 1977; Sutherland and Karlson 1977; Lubchenco and Menge 1978; Sousa 1979; Dean and Hurd 1980; Botkin 1981; Day and Osman 1981; Dean 1981; Schoener and Schoener 1981). In the few experiments suggesting the facilitation model, facilitation is not obligate. That is, although later species

establish faster in the presence of earlier species, they can also colonize areas devoid of earlier species (Menge 1976; Standing 1976; Dean and Hurd 1980; Dean 1981). Here I report the results of a two-part investigation of secondary succession: (1) experimental evidence of obligate facilitation in the recruitment of a dominant plant and (2) observations describing the importance of different middle successional species to this recruitment. Then I discuss the differences between the facilitation in this system and the traditional view, the limitations of this study, the possible influence of this mechanism on successional predictability, the previous studies in marine systems, and the conditions under which facilitation might occur. This investigation is part of a larger study of succession within beds of the surfgrass Phyllospadix scouleri Hook in the low zone of the rocky intertidal Oregon coast, U.S.A.

Surfgrass is a perennial angiosperm with grass-like blades, 2-4 mm wide and approximately 0.5 m long, borne on a branched rhizome with adventitious roots securing the plant to the rock (Dudley 1893, 1894; Chrysler 1907; den Hartog 1970; Phillips 1979; Tomlinson 1980). Experimental studies suggest that surfgrass maintains a striking numerical and functional dominance in the low intertidal zone along many rocky shores of western North America (Black 1974; Hodgson 1980; Dethier 1981; Chapter 2). Space is made available in surfgrass beds by wave action during winter storms (Chapter 2). A three-year study (Chapters 2 and 3) has revealed that the successional pattern in these bare patches is variable, but can be summarized as follows: in May, newly opened space is invaded by Ulva sp., a blade-like ephemeral green

alga. By October, Ulva is replaced by a suite of middle successional species, the three most abundant being the red algae Rhodomela larix, Cryptosiphonia woodii, and Odonthalia floccosa. These middle successional species are replaced by surfgrass in either of two ways: (1) rhizomes of surrounding surfgrass plants invade the patch by vegetative growth, or (2) surfgrass seeds recruit into the patch. In experimentally created 0.25 m² bare patches, recovery by vegetative growth is much faster than recovery by seed recruitment (Chapter 2). Nevertheless, seed recruitment is necessarily important when large, bare patches without surrounding surfgrass plants occur. This paper addresses the recruitment by seeds.

Unlike the microscopic recruiting stages of marine algae, surfgrass seeds are relatively large (fig. 15) -- readily detected by careful visual searches of the plant-covered substratum. Perhaps the most unusual feature of these seeds is their barbs, which allow them to become attached to algae. The seeds germinate soon after attachment, producing first blades and then roots which eventually anchor the plant to the rock (Gibbs 1902). The plant then continues to invade space by vegetative growth. I can find seeds up to one year after they first become attached. Thus, I can determine the alga to which a seed attached even after the seedling has produced roots and a rhizome.

METHODS AND RESULTS

To quantify the seasonal dispersal of surfgrass seeds and to provide baseline information for the study, I constructed seed traps from Vexar

plastic mesh with 1 mm plastic strands and 3 mm openings. Each trap was a 12 x 15 cm rectangle nailed to the rock at all four corners so that the center was 6 cm high. These traps showed that seeds disperse from September to March (fig. 16). The number of available seeds appears to vary greatly from year to year.

To ascertain the mechanism by which a middle successional species is replaced by surfgrass, I compared the recruitment of surfgrass in control (unmanipulated) plots and plots from which the alga R. larix had been removed. I manipulated R. larix because (1) it often dominates middle successional plots, (2) surfgrass seeds attach to it, and (3) it forms large beds by vegetative growth, such that replicate monocultures could be manipulated. In September 1980 I chose eight experimental and eight control 0.25m² quadrats in an area of 100% cover of R. larix at Boiler Bay (44°50'N, 124°03'W), 1 km north of Depoe Bay, Oregon. All surfgrass seeds were removed by hand from the control quadrats, which were otherwise undisturbed. All upright Rhodomela (and attached surfgrass seeds) were removed from the experimental quadrats with a putty knife. I monitored the experiment in March 1981 after the fall period of seed dispersal. By this time (March 1981) the blade-like brown alga Phaeostrophion irregulare dominated the experimental quadrats. All 48 seeds that recruited during this experiment attached to Rhodomela larix; 46 seeds attached in control quadrats, and the two seeds that attached in the experimental quadrats were attached to isolated sprigs of R. larix that regenerated from persistent holdfasts. The magnitude of the interaction was 5.6 seeds recruited per 0.25 m² of R. larix (s.e. = 0.3). This difference between experimental

and control quadrats is highly significant ($p < 0.001$, Mann-Whitney U test), suggesting that the recruitment of surfgrass is facilitated by the prior establishment of R. larix. In fact, during three years of study all of 298 surfgrass seeds that recruited were attached to an alga. I have systematically searched over 200 m² of low zone habitat, including crevices and both organic and inorganic substrates. My data suggest the facilitation of surfgrass seeds is obligate. As far as I am aware, this is the first experimental evidence of obligate facilitation in any system.

To define the characteristics of the algae to which surfgrass seeds attach, I determined the relative importance of different algal species by comparing the proportion of surfgrass seeds attached to each species to the relative abundance of each species. Data were collected by mapping the seeds and seedlings within 1 m of either side along a 14 m long transect line (=28 m²) in an area lacking large surfgrass plants but with a high cover of algae. (I specifically chose an area lacking adult surfgrass plants to increase the number of seeds mapped, because seeds were never found attached to adult surfgrass plants.) To quantify algal cover, a vinyl quadrat with a hundred randomly placed dots was used in ten 0.25 m² quadrats placed randomly along this transect. The number of dots covering each species estimates percent cover of that species (Menge 1976). Seeds and seedlings were censused January 17-February 3, 1981, so they recruited in fall and winter 1980 to 1981. (I was certain that these were new recruits, because I censused and mapped seeds in this area previously in June 1980). In February 1981, 117 out of 131 seeds had germinated. Of these juveniles, the longest blade

measured was 4.5 cm. The substrate, tidal height and other habitat characteristics were homogeneous along the transect.

The data suggest the pattern of seed attachment is related to the form of the algae. Significantly more seeds attached to turf-forming algal species with a central axis approximately 1 mm in diameter and bushy side branches (Bossiella plumosa, Corallina vancouveriensis, O. floccosa, and R. larix) than would be expected from their abundance (Table 12). In contrast, seeds did not attach to blade-like algae such as Iridaea heterocarpa or Dilsea californica or to the thick strap-like kelp Egregia menziesii. This result is a consequence of the complementary structures of surfgrass seeds and branching algae (fig. 15). Blade-like algae do not provide a purchase for seeds. Therefore, not all species of algae can equally facilitate surfgrass recruitment. The importance of form is further illustrated by surfgrass seed attachment to different species with similar shapes in California, such as Lithothrix aspergillum and Gigartina canaliculata (pers. obs.). Seeds will even attach to and germinate on plastic mesh (fig. 16) further suggesting that form determines which species facilitate surfgrass recruitment: plastic mesh is biologically inert but has the correct form.

To determine whether any branched species was differentially important to the establishment of surfgrass, I followed seedlings for seven months. During this time 90% of the seedlings died (fig. 17A), but the seeds attached to each algal species died in about the same proportion (fig. 17B). These results suggest that all the branched species facilitate surfgrass and that the magnitude of the facilitation

is proportional to the number of seeds originally attached to the alga.

I probably overestimated the mortality rate, because I assumed that all seedlings not in their mapped position had died, but seedlings can be broken from one alga and subsequently become attached to another alga. I have seen seeds on algae and on plastic traps with pieces of other algal species caught in their barbs. The number of moved seeds can be estimated from the repeated censuses. In June 1981, in addition to the 31 seeds that I had mapped previously, I found 13 seeds in new positions. These seeds probably had become reattached in a different spot between February and June 1981, because few seeds recruit during this time (fig. 16).

To understand the population dynamics related to the recruitment and establishment of surfgrass, I recorded the probable mortality sources and the growth rates of seedlings. The probable sources of seedling mortality include wave action, desiccation, and herbivory by the snails Lacuna spp. (pers. obs.; Fishlyn and Phillips 1980). Mortality was observed in both newly attached and firmly rooted seedlings. When seedlings died of desiccation they lost their chlorophyll and became tattered. All the seeds attached to the seed traps in fall and winter 1980-1981 desiccated during the daylight low tides of the spring. Unlike the naturally attached seeds, algal turf did not surround the seeds attached to traps. These results suggest that algae may further facilitate seedling survivorship by protecting seedlings from desiccation. Seedlings grew at an extremely variable rate. The fastest growing seedling had a longest blade that grew 11.5 cm in seven months

and a rhizome that grew 2 cm. By contrast, two of the 14 seedlings surviving until September 1981 decreased in size from February. These results suggest that the replacement of middle successional species by surfgrass may require many years or perhaps an occasional very good year and will be influenced by adult seed set, water movement, desiccation, and herbivores.

DISCUSSION

The results of this study suggest that obligate facilitation occurs in surfgrass beds, but that succession in this community differs from the traditional paradigm (Clements 1916) in several respects: (1) Facilitation does not occur in a way strictly analogous to soil development, although middle successional species do increase spatial heterogeneity. (2) Not all middle successional species act to facilitate surfgrass; the extent of the facilitation appears to vary with the morphology of the species. (3) This study does not document facilitation at every point in the successional sequence. In fact, evidence presented elsewhere suggests elements of inhibition at an earlier point in the same successional sequence (Chapter 2). (4) Surfgrass does not act as a "climax" species in a strict sense, because surfgrass itself is apparently not the correct form for seed attachment. Surfgrass cannot perpetuate itself in an area with seed recruitment, though it may with vegetative recruitment. Thus, this successional mechanism appears to have several unique features not included in any theory or model. Our understanding of succession will

be enhanced by examining this system and similar systems carefully. Below I discuss the limitations of this study, the possible influence of this mechanism on successional predictability, the previous studies of recruitment in marine systems and successional mechanisms, and the conditions under which facilitation might occur.

Since most late successional species take years to reach reproductive maturity, ecologists rarely follow a sequence of species replacement to its conclusion. Nevertheless, many features of late successional sequences can be illuminated by focussing on propagules, recruitment, and juveniles (e.g., Horn 1976; Connell and Slatyer 1977). In the case of surfgrass, this study of seeds and seedlings strongly suggests obligate facilitation is the mechanism by which this late successional species replaces earlier species. Despite the fact that obligate facilitation has not been unequivocally proven in this system, the evidence suggests that attachment to algae is vastly more important than attachment to any inorganic substrates, both in the development of communities and in the evolution of seed morphology. I have never found a seedling on a natural inorganic substrate, and the form of surfgrass seeds seems clearly adapted for attachment to algae with a specific form (fig. 15).

This successional mechanism could influence the timing and the species composition of the successional sequence. For example, an isolated patch of a blade-like algal species (i.e., in a tide pool or on a boulder) could not be invaded by surfgrass seeds. If this blade-like species were able to continually replace itself, the isolated patch would exist as an alternate stable state (Sutherland 1974). In all

patches the presence of blade-like species could slow the successional sequence. These considerations illustrate the importance of understanding the natural history of a system when performing the experiments outlined by Connell and Slatyer (1977). For example, if one removed a blade-like algal species from a recovering surfgrass bed, this manipulation might increase abundance of a branched species released from competition and consequently increase surfgrass recruitment. Using Connell and Slatyer's (1977) scheme one would conclude the blade-like species inhibits surfgrass, and indeed it does. However, the indirect inhibition in this example differs from the direct inhibition Connell and Slatyer (1977) envisioned.

Natural history observations suggest recruitment by entanglement in turf-like plants may be common in marine systems. The Australian seagrass Amphibolis, for instance, also recruits by barbed propagules that become attached to plants (den Hartog 1970). McMillan (1981) reports that the seedlings of other seagrasses, though not so obviously adapted for entanglement, can also recruit in this way. A further example may be Clokie and Boney's (1980) observation of drift red algae, Gigartina and Gelidium, becoming tangled in mats of Enteromorpha and Blindingia and then releasing spores. Additionally, Mshigeni (1978) reports that adult drift algae, Acanthopora and Hypnea, can become entangled and then reattach during succession experiments.

A review of the other experimental successional studies as well as the work reported here reveals that no one model fully describes succession in the marine environment. Other studies conducted in habitats very similar to that described here suggest very different

successional mechanisms, such as inhibition (Standing 1976; Sutherland and Karlson 1977; Lubchenco and Menge 1978; Sousa 1979; Dean and Hurd 1980; Day and Osman 1981; Dean 1981; Schoener and Schoener 1981; Lubchenco in prep.; Chapter 2) or non-obligate facilitation (Menge 1976; Standing 1976; Dean and Hurd 1980; Dean 1981). Of course, in some cases non-obligate facilitation is very strong and perhaps functionally similar to obligate facilitation. The magnitude of inhibition can also vary greatly between different marine communities.

When should facilitation occur? I suggest this question can be rephrased thus: when should recruitment problems that are likely to be ameliorated by biotic factors occur? Such recruitment difficulties can be caused by both abiotic and biotic factors. Some desert plants, for example, do not survive unless they germinate in the shade of other species, "nurse plants" (Niering et al. 1963; Jordan and Nobel 1979). Recruitment of the brown alga Fucus on smooth rocks is low, because snails eat juvenile plants unless they grow in heterogeneities provided by early successional barnacles (Lubchenco in prep.). Experimental removals demonstrate that barnacles facilitate Fucus on smooth rock, but on rocks with crevices barnacles are not necessary for high recruitment. A priori, one might expect recruitment difficulties in "harsh" environments (Connell and Slatyer 1977). The facilitation of surfgrass would fit this generalization in the sense that wave-swept, rocky intertidal habitats might be harsh for an angiosperm recently derived from terrestrial plants. In fact, no other seagrass genus occupies this habitat (den Hartog 1970). In general, predictions concerning the harshness of an environment and possible recruitment

problems will require a good understanding of relevant natural history.

Recruitment problems and facilitation of recruitment will not always translate into a net facilitation, because inhibition later in the life cycle might be stronger. If an early space occupier is removed experimentally to determine the successional mechanism, a species that recruits by entanglement, for example, might still become dominant faster in the absence of the earlier species if the early species inhibits growth more strongly than it facilitates recruitment. Facilitation of recruitment will be the key to the overall nature of the interaction only if the facilitation is obligate. In fact, facilitation might be expected to be rare, since there should be strong selective pressure against characteristics of an early successional species acting to hasten its own death.

I suggest facilitation will only evolve if the early space occupier is not harmed by the species it facilitates (e.g., if the early species is short-lived, dying even if it is not replaced) or if counter-balancing selective pressure favors the very characteristics that enhance the recruitment of another species. The successional sequence described here apparently exemplifies such counter-balancing selective pressure. Surfgrass seeds evidently become established by overgrowing the algae that facilitate their recruitment. Since the branched algae appear to be long-lived, this overgrowth should reduce their fitness. Though one might expect such mortality to select against a bushy, branched algal morphology, I suggest the plants retain their morphology for at least two reasons: (1) few surfgrass seeds successfully

establish, reducing selective pressure (fig. 17); (2) this bushy, branched morphology has other advantages, such as water retention during low tides and increased reproductive or photosynthetic surface (Hay 1981; Padilla 1982; see also Littler and Littler 1980 for a discussion of selective pressures and algal form.) These hypotheses require testing. Of course, some characteristics that facilitate later species are unavoidable. Desert plants, for example, must create shade, despite the facilitation that this shade might provide for competitors. Thus, facilitation could occur under a variety of conditions.

In summary, this study presents the first experimental evidence for obligate facilitation in any system as well as the first evidence of the possible complexities if more than one species is present during a successional stage. This work also illustrates that no one model describes succession, even within the restricted domain of rocky intertidal communities. I suggest facilitation is most likely to occur in harsh environments that create recruitment problems. Furthermore, facilitation might be limited to situations in which either later species do not lower the fitness of earlier ones or the lowered fitness is counter-balanced by other selective pressures. It is unclear how many other natural systems will exhibit these characteristics. Hence, further experimental investigations are necessary to refine our understanding of succession.

TABLE 12.
RELATIVE IMPORTANCE OF ALGAL SPECIES OF VARIOUS MORPHOLOGIES
TO SURFGRASS SEED ATTACHMENT

Algal Species	% Cover	% of Attached Seeds	No. of Attached Seeds
Branched Species (central axis approx. 1 mm in diameter)			
<u>Bossiella plumosa</u>	28.5	50.4	66
<u>Corallina vancouveriensis</u>	15.7	21.4	28
<u>Odonthalia floccosa</u>	15.3	13.0	17
<u>Rhodomela larix</u>	12.9	13.0	17
<u>Ptilota filicina</u>	1.8	0.8	1
<u>Cryptosiphonia woodii</u>	0.5	1.5	2
Total... ..	72.0	100.0*	131
Other Morphologies†			
<u>Egrelia menziesii</u>	9.2	0	0
<u>Iridaea heterocarpa</u>	8.0	0	0
<u>Dilsea californica</u>	6.0	0	0
Rare Species ‡.....	4.8	0	0
Total	28.0	0	0

* $P < 0.001$, differences in percentages test comparing % cover and % attached seeds in the two classes (Sokal and Rohlf, 1969).

† blade-like species and branched species with a very large or very small central axis.

‡ Includes Ulva sp., Microcladia borealis, Phaeostrophion irregulare, Hedophyllum sessile, Gigartina papillata, Laurencia spectabilis, and Constantinea simplex.

Figure 15. a. Seed of the surfgrass Phyllospadix scouleri as it is dispersed. Note the barbs. b. The barbs allow seeds to become attached to algae. This seed is attached to an erect coralline alga and has germinated (from Gibbs 1902).

Figure 15.

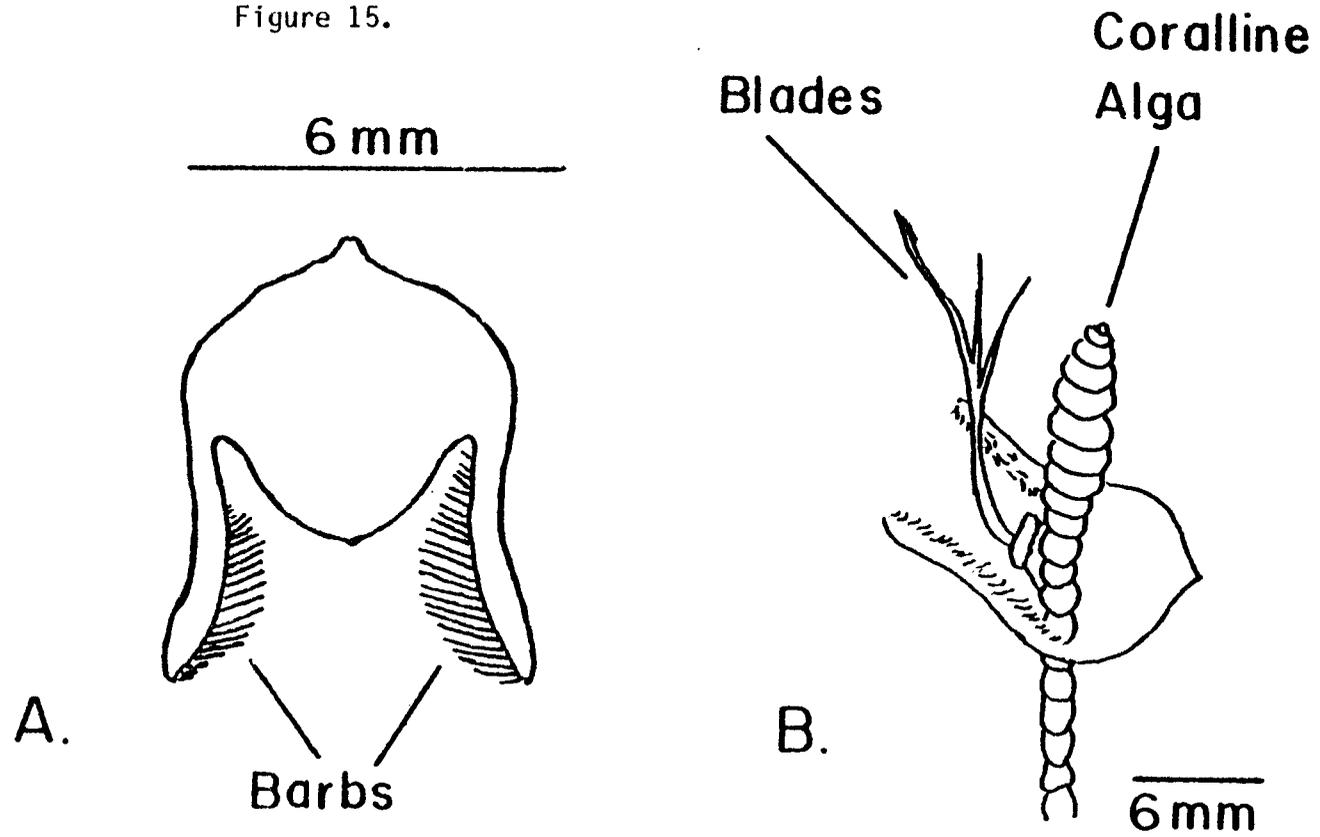


Figure 16. Number of new seeds attached each month to 19 Vexar mesh seed traps (described in text). Total trap area is 3,420 cm². Exact number of seeds appears above each bar in the histogram.

Figure 16.

MONTHLY SEED SETTLEMENT ON TRAPS

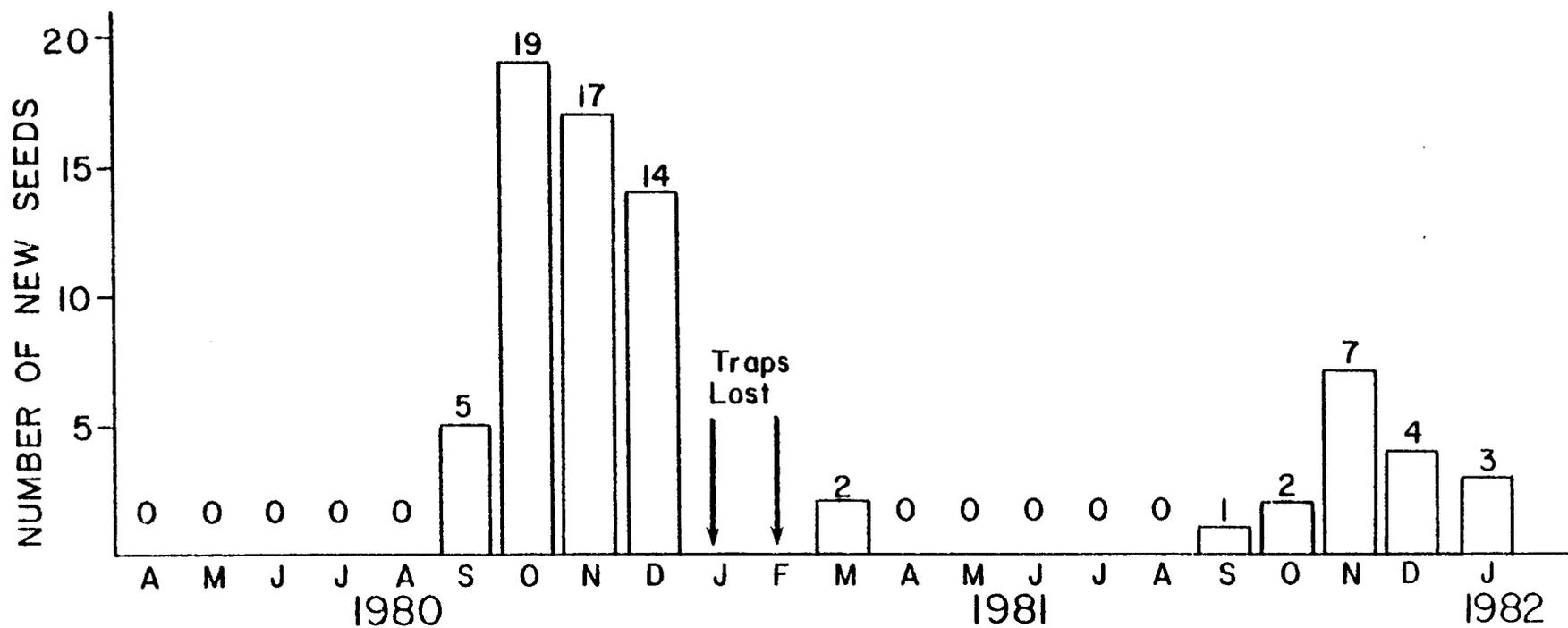
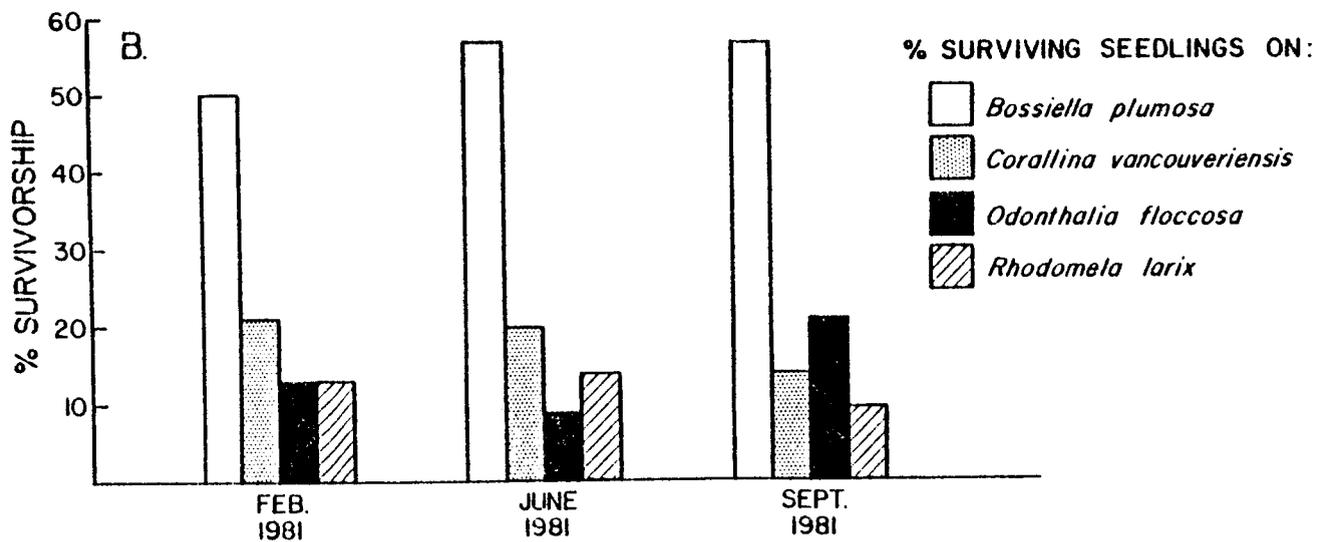
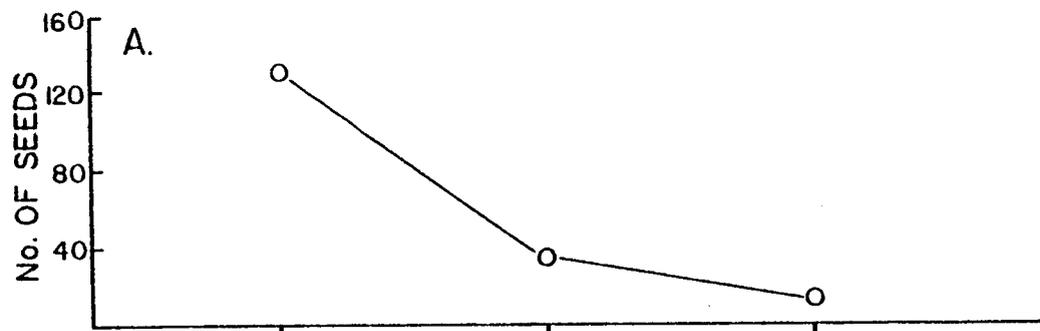


Figure 17. a. Number of mapped surfgrass seeds surviving over time.
b. Percentage of the surviving seeds attached to each algal species at each date. Three seeds attached to rare species are not included in the February histograms.

Figure 17.

SEEDLING MORTALITY



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CHAPTER V.
GENERAL CONCLUSIONS

My results contribute to the understanding of two interrelated concepts, community organization and succession. The organization of communities dominated by surfgrass is strongly influenced by the interaction of three phenomena; high persistence ability, high preemptive ability, and only slow recovery ability. Permanently marked plots demonstrate that surfgrass is highly persistent. Differences between experimental removal and control plots demonstrate that its preemptive ability is also high. The slow growth of rhizomes and the slower recruitment of seeds are responsible for the poor recovery ability of surfgrass. The interaction of these phenomena makes even small amounts of disturbance important. Undisturbed surfgrass beds have low diversity and resist invasion, but disturbed areas have higher diversity, which continues for many years. Differences in disturbance rates, such as the differences between Boiler Bay and Squaw Island, apparently produce differences in the extent of surfgrass dominance.

Experiments mimicking natural disturbances in surfgrass beds illustrate the complexity of succession. Complexity is caused by both spatial and temporal variation. Early successional species are seasonal. The winter colonist inhibits the summer colonists, and the magnitude of the inhibition varies with the species. Throughout succession, algal cover and diversity fall drastically when day length decreases and wave action increases in the fall. Herbivores decrease cover of early colonists the first summer but are not solely responsible

for the fall declines. After the first year, stochastic factors become important, and replicate plots have divergent successional pathways. Rhodomela, a species sometimes present in the understory of the mature surfgrass bed, regrows from its holdfast after disturbance and dominates some replicates. These divergent replicates will probably all eventually become surfgrass beds through vegetative growth or seed recruitment.

Unlike the inhibition early in succession, several middle successional species actually facilitate the recruitment of surfgrass seeds. Bushy, turf-forming algal species with a central axis 1 mm in diameter, a shape complementary to that of surfgrass seeds, apparently are necessary for seed recruitment. This study is the first experimental evidence of obligate facilitation. Taken together, these results indicate that no simple model describes succession in this community. Thus, one goal of ecological research must be a more complex theory that explains when different types of interactions occur. Comparative studies seem to be the best research strategy to accomplish this goal.

Comparison of this study with others suggests why surfgrass beds are organized this way. The life history characteristics and morphology of the species appear especially important. Surfgrass, for example, apparently owes its dominance to its large size and its ability to capture space by vegetative growth. Unlike mussel beds (described in Paine and Levin 1981), surfgrass beds do not become more susceptible to removal as they mature. Their high persistence -- compared to mussel beds -- may have precluded the evolution of a specialist that lives only

in the holes in surfgrass beds, similar to the brown alga Postelsia palmaeformis, a specialist in mussel beds (Paine 1979). The facilitation of surfgrass seemed to be a result of two factors. (1) Wave-swept, rocky intertidal habitats are a harsh environment for an angiosperm, and branched algae can ameliorate this harshness by providing a purchase for seeds and perhaps by decreasing desiccation. (2) Selection against a branched algal morphology from surfgrass-caused mortality is counterbalanced by selection in favor of this morphology resulting from other factors. The complexity of succession in surfgrass beds seems to have a variety of causes. The extreme seasonality of my study sites on the Oregon coast, for instance, apparently precludes an aseasonal early successional species. The two different types of disturbance, wave action and sand movement, may allow two different early successional species with different adaptations to coexist. The magnitude of inhibition apparently differs with the competitive ability of the species. Variations among replicates undoubtedly has several causes, but slight differences before manipulation (as little as 0.5% cover of Rhodomela) are important. Seasonal abiotic conditions on the Oregon coast outweigh the effects of small molluscan herbivores, because large waves remove plants every fall. Also, large herbivores with an important role in other communities are absent from the Oregon coast. These hypotheses can be stated in general terms and tested experimentally.

In general philosophy, if not in specifics, both Clements (1916) and Gleason (1926) appear to have been correct. Ecology can be advanced by studying both the traits of individual species and the interactions of species within communities. Further research can fill in the specifics with predictive theories.

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APPENDICES

Appendix 1. Organisms found in permanently marked quadrats in the low intertidal zone on the Oregon coast. These species do not occupy enough space or are not abundant enough to be listed in the text, but they have been found consistently in the permanently marked quadrats. This does not represent a complete checklist. All species occur at both sites, with the exception of the surfgrass epiphyte S. naiadum, which occurs only at Squaw Island.

Chlorophyta

Cladophora sp.

Phaeophyta

Analipus japonicus
Egregia menziesii
Fucus distichus
Hedophyllum sessile
Leathesia nana
Petalonia fascia

Rhodophyta

Ceramium sp.
Corallina officinalis var. chilensis
Endocladia muricata
Farlowia mollis
Gigartina papillata
Halosaccion glandiforme
Laurencia spectabilis
Melobesia mediocris
Microcladia borealis
Plocamium cartilageum
Plocamium tenue
Porphyra sp.
Ptilota filicina
Smithora naiadum

Annelida

Pista elongata

Mollusca

Amphissa columbiana
Bittium eschrichtii
Mopalia muscosa
Thais lamellosa
Tonicella lineata

Arthropoda

Cancer sp.

Echinodermata

Pisaster ochraceus

Appendix 2. Species that colonized experimental plots but are not listed in text. Species designations follow Abbott and Hollenberg (1976). Unless noted, species occurred at both sites.

 Rhodophyta

Bossiella plumosa
Callithamnion pikeanum^a
Ceramium sp.
Corallina officinalis^a
Corallina vancouveriensis
 coralline crusts
Cryptopleura violacea
Endocladia muricata^a
Farlowia mollis
Laurencia spectabilis
Microcladia borealis
Odonthallia lyalli^a
Odonthallia washingtoniensis^b
Plocamium cartilageum
Plocamium tenue
Ptilota filicina^b

Animalia

Anthopleura elegantissima
Balanus cariosus
Balanus glandula
 Bryozoa^a
Chthamalus dalli
Mytilus sp.^a

Phaeophyta

Analipus japonicus
Costaria costata^b
Egregia menziesii
Fucus distichus^a
Haplogloia andersonii^b
Hedophyllum sessile
Petalonia fascia
Ralfsia sp.
Scytosiphon sp.

Chlorophyta

Bryopsis sp. ^a
Cladophora sp.
Monostroma oxyspermum
Rhizoclonium riparium^a
Spongomorpha sp.^a

^a occurred only at Squaw Island

^b occurred only at Boiler Bay