

EXPERIMENTAL INVESTIGATIONS OF DISTURBANCE AND ECOLOGICAL SUCCESSION IN A ROCKY INTERTIDAL ALGAL COMMUNITY¹

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Abstract. Mechanisms of ecological succession were investigated by field experiments in a rocky intertidal algal community in southern California. The study site was an algal-dominated boulder field in the low intertidal zone. The major form of natural disturbance which clears space in this system is the overturning of boulders by wave action. Algal populations recolonize cleared surfaces either through vegetative regrowth of surviving individuals or by recruitment from spores.

Boulders which are experimentally cleared and concrete blocks are colonized within the first month by a mat of the green alga, *Ulva*. In the fall and winter of the first year after clearing, several species of perennial red algae including *Gelidium coulteri*, *Gigartina leptorhynchos*, *Rhodoglossum affine*, and *Gigartina canaliculata* colonize the surface. If there is no intervening disturbance, *Gigartina canaliculata* gradually dominates the community holding 60-90% of the cover after a period of 2 to 3 years. If undisturbed, this monoculture persists through vegetative reproduction, resisting invasion by all other species. During succession diversity increases initially as species colonize a bare surface but declines later as one species monopolizes the space.

Several contemporary theories concerning the mechanisms of ecological succession were tested. The early successional alga, *Ulva*, was found to inhibit the recruitment of perennial red algae. This competition for settling space is an important feature of the successional process. *Ulva* is the best competitor for this space; it reproduces throughout the year and quickly becomes established on newly cleared substrates. As long as these early colonists remain healthy and undamaged, they preempt colonization by perennial red algae which have highly seasonal recruitment and slower growth.

Selective grazing on *Ulva* by the crab, *Pachygrapsus crassipes*, breaks this inhibition and accelerates succession to a community of long-lived red algae. Grazing by small molluscs, especially limpets, has no long-term effect on the successional sequence. Their grazing temporarily enhances the recruitment of the barnacle, *Chthamalus fissus*, by clearing space in the mat of algal sporelings and diatoms which develops on recently denuded rock surfaces.

Where locally abundant, middle successional red algae also slow the invasion and growth of the late successional dominant, *Gigartina canaliculata*. This alga replaces middle successional species because it is less susceptible to damage by desiccation and overgrowth by epiphytes.

The results of this study do not support either the classical facilitation model or the tolerance (competitive) model of ecological succession. Once early colonists secure the available space/light, they resist rather than facilitate the invasion of subsequent colonists. Early colonists are not killed by direct interference competition with late successional species which grow up through their canopy; rather, early colonists can successfully inhibit the recruitment and growth of these species. Successional sequences occur because species which dominate early in a succession are more susceptible to the rigors of the physical environment and to attacks by natural enemies than late successional species. Late species colonize and grow to maturity when early species are killed and space is opened. Only late in a successional sequence, when large clearings become a mosaic of small openings, does direct competition with surrounding adult plants of late successional species contribute to the decline in cover of the remaining early species. Studies of succession in a number of terrestrial and marine communities lend support to this inhibition model.

Key words: algae, community structure, competition, desiccation, disturbance, diversity, dominance, epiphytes, grazing, rocky intertidal, succession.

INTRODUCTION

The study of temporal changes in the structure of communities began with North American plant ecologists at the turn of the twentieth century (Cowles 1899, Cooper 1913, Clements 1916). Clements (1916) interpreted "community development" as an emergent property of the community analogous to the em-

bryological development of an organism. With some noted exceptions (Gleason 1926, 1927, Egler 1954), his view was widely accepted and as a result succession has historically been viewed as a closed-system deterministic process (Drury and Nisbet 1973). This led to a series of generalizations about successional trends and mechanisms (summarized in Odum 1969) which were based on the tenuous assumption of a homology between a spatial sequence of zones of vegetation visible at one time in a landscape and a long-term se-

¹ Manuscript received 24 May 1978; revised 28 October 1978; accepted 10 January 1979.

quence of vegetation types on a single site (Gleason 1927, pp. 320–324). Little evidence exists to support these generalizations, especially when patterns of succession are viewed in the context of the life histories of individual species (Drury and Nisbet 1973, Horn 1974, Connell and Slatyer 1977).

Many of the mechanisms proposed to account for the observed changes in ecological communities following a perturbation remain untested. Most of the research on succession has been conducted in terrestrial communities, mainly in forests and abandoned old-fields. In these situations, only the earliest stages dominated by short-lived species are amenable to experimentation. Sequences of species replacements later in succession and the mechanisms which produce them have never been observed directly because later-appearing species, especially forest trees, persist for a much longer time than any ecological study. Until recently, few tests of successional theory have been carried out in communities in which the time-course of succession from bare space to climax is relatively short. The marine rocky intertidal is one such system where experimental manipulations can elucidate successional mechanisms and trends (Dayton 1971, 1975, Menge 1975, Lubchenco and Menge 1978).

This is the first of two papers (see Sousa 1979) on the dynamics of algal-dominated communities in marine intertidal boulder fields. The sessile species of this system are distributed in a patchwork of successional states. The top surface of each boulder is a patch of habitat which differs in size and age from that of neighboring boulders. Together they form a mosaic analogous to the patch structure of intertidal mussel beds modelled by Levin and Paine (1974). Small boulders are more susceptible to disturbance (i.e., being overturned) by wave impact than larger boulders. Such disturbances act to renew space in an otherwise space-limited system. Boulder fields are excellent systems in which to investigate experimentally the interactions between species in patches of habitat which have remained undisturbed for relatively long periods of time, and the role of disturbance in maintaining diversity within and between patches.

Most studies of algal succession on denuded surfaces in the rocky intertidal reveal several common features of recolonization. Those algal species which arrive first on a large opened patch of space do so as a result of evolved life history characteristics. Their propagules are produced in large numbers during most seasons of the year and have a high vagility. Young recently germinated plants grow rapidly to maturity but populations of these plants are relatively short-lived. The cosmopolitan "weedy" species of the seashore include members of the green algal genera, *Ulva* and *Enteromorpha*. These species possess flagellated motile spores and are usually the first algal species (after an initial cover of colonial diatoms) to colonize denuded surfaces in the marine rocky intertidal (Hat-

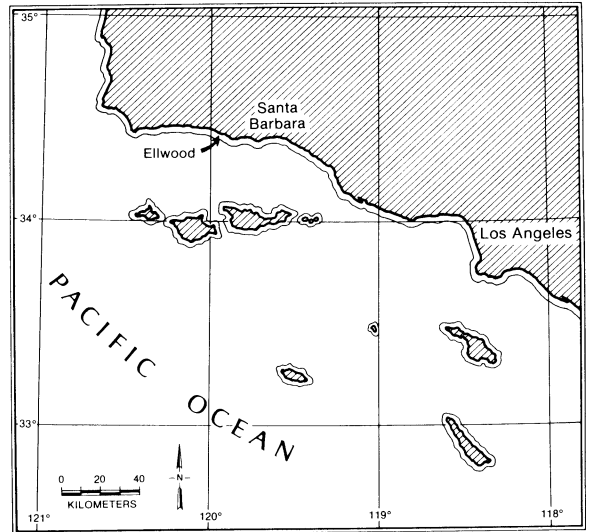


FIG. 1. Map of south coast of California from Point Conception to Los Angeles showing the location of the study site at Ellwood. The Channel Islands are also indicated.

ton 1938, Rees 1940, Northcraft 1948, Castenholz 1961, Menge 1975, and others). These pioneer species settle densely and grow quickly, securing most of the available canopy space. Sometime later, large perennial brown or red algae, which tend to have larger and less motile spores, become established, replacing the earlier colonists. Reproduction and recruitment in these perennial species is usually more seasonal than in the green algae. This group is composed of both the species which will eventually come to dominate the space as well as others which will not persist in the climax community in the absence of disturbance.

Here, I present data on the patterns of algal recolonization following a disturbance and the results of experimental investigations of the mechanisms which drive these successional changes. In a companion paper (Sousa 1979) I present correlative data and experimental corroboration of the role of disturbance in maintaining diversity in this system.

STUDY SITE

Intertidal boulder fields comprise much of the rocky shore of southern California. They often occur near points where rocks have been deposited at the mouths of creek beds. The study site was established in one of these areas at Ellwood Beach, California (34°25'N, 119°41'W) located within the Santa Barbara Channel approximately 9 km west of the University of California, Santa Barbara (Fig. 1). Sandstone boulders overlie a gently sloping shale platform which extends into the low intertidal zone (from -0.30 m to +0.30 m above mean lower low water, hereafter MLLW). This habitat is bordered on the landward side by a sand beach and on the other sides, at lower tidal levels, by beds of the surf grass, *Phyllospadix torreyi*, in sand

areas and patches of the brown alga, *Egregia laevigata*, on rock substrates.

After large winter rainstorms, freshwater runoff from a nearby intermittent stream flows across the beach and out into the rocky intertidal to the east of the main study area. Though the latter area appeared unaffected, the density of grazers, particularly of sea urchins and crabs, was much reduced in an adjacent boulder field. This is presumably a result of these periodic inundations. There was no observable difference in the algal species composition in these two areas.

Wave exposure and disturbance of boulders

Ellwood is protected from the effects of large summer swells by the Channel Islands located approximately 35–40 km offshore. Little boulder movement occurs here during summer months (May through October). However, winter storms (November through April) out of the northwest frequently produce mid-channel wind waves in excess of 2.4 m in height or swells greater than 1.5 m in height which overturn many boulders (Sousa 1979). When a boulder is overturned, the algae and sessile invertebrates on its top surface are killed in whole or part by a combination of sea urchin grazing (if urchins are present), anoxia, light levels below compensation intensity, and mechanical damage caused by abrasion. The length of time that a boulder remains overturned determines the intensity of disturbance and thus the amount of space renewed. If this time is relatively short, the residents may simply be damaged, and open space is recolonized primarily by vegetative regrowth of surviving individuals. At the opposite extreme, if boulders remain overturned a long time, all the algae may be killed and recolonization accomplished completely by propagules from the outside.

Tidal exposure and desiccation stress

Climatological stress is highly seasonal because most winter low tides at or below 0.0 m MLLW occur in the late morning and afternoon between the months of October and March. The actual number of hours of exposure is sometimes reduced when high seas are generated by storm conditions but this does not substantially change the general pattern of daytime exposure to air during winter months.

Strong winds and intense sunlight often coincide with late morning and afternoon low tides causing severe desiccation and death of both plants and animals. In the early winter (October–January) several red algal species, including important canopy species in this zone, are defoliated by a combination of this desiccation stress and simultaneous attack by large numbers of the small herbivorous snail, *Lacuna unifasciata* (W. P. Sousa, *personal observation*). The effect of *Lacuna* will be described in more detail later. As a

consequence, during winter months, algal abundances are reduced and free primary space (i.e., space not covered by the algal canopy) increases. Populations of most herbivores are also reduced during winter months.

Most summer (April–September) low tides at or below 0.0 m MLLW occur in the early morning and during the night when physical conditions are benign. Algal growth is most rapid and herbivores most abundant during this period. Algae which defoliated during the winter regrow from a low tuft of short branches or a perennating holdfast in the spring. Available free space is less than during winter months. Data on these trends will be presented later.

Animal and plant communities

The area of the boulder field between 0.0 and +0.30 m above MLLW (approximately 1500 m²) is covered by an algal association dominated by the red alga, *Gigartina canaliculata*, on stable substrates (Table 1). This association contains about 30 species of macro-algae but this study was limited to those which comprised at least 5% of the cover on the substrates sampled. Smaller (less stable) boulders contain various mixtures of *Gigartina canaliculata*, *Gigartina leptorhynchus*, *Gelidium coulteri*, *Rhodoglossum affine*, *Ulva* spp., *Centroceros clavulatum*, *Corallina vancouveriensis*, and the barnacle, *Chthamalus fissus*. During benign summer months, *Laurencia pacifica* and *Gastroclonium coulteri* may also be present. The anemone, *Anthopleura elegantissima*, never covered more than 5% of the space on boulders in this habitat and was not studied in any detail. The mussel, *Mytilus californianus*, is the potential competitive dominant at this level (Paine 1974). However, it is absent from this site due presumably to intense predation by octopuses, starfishes, and predatory snails.

At or below 0.0 m MLLW, this algal association grades into one which is dominated by the red algal species, *Gastroclonium coulteri* and *Laurencia pacifica* (Table 1). This zone is not extensive in area, ending abruptly at the lower edge of the boulder habitat (approximately –0.45 m below MLLW) where a bench of soft shale sparsely covered with encrusting coralline algae, *Phyllospadix torreyi* and *Egregia laevigata* extends into the subtidal. Hereafter, sessile species will be referred to by their generic names, except for the two species of *Gigartina* for which both genus and species names will be used.

Large herbivores present in the Ellwood boulder field include the sea urchin, *Strongylocentrotus purpuratus*, the sea hare, *Aplysia californica*, the lined shore crab, *Pachygrapsus crassipes*, and several species of fish including the adult opaleye, *Girella nigricans*, the monkey-face eel, *Cebidichthys violaceus*, and the top smelt, *Atherinops affinis*. Small grazers include the limpets, *Notoacmea fenestrata*, *Collisella strigatella*, and *Collisella scabra*, the chiton, *Mopalia*

TABLE 1. Relative abundance of sessile organisms on stable boulders at two tidal levels at Ellwood. Data are from 40 boulders (mean top surface area of 0.15 m², SD = .06), 20 in each zone. Boulders were sampled at random along horizontal transects on 15 February 1977. Value in parentheses is one standard deviation of the mean. Four determinations of tidal height (meters above mean lower low water, MLLW) were made in each zone.

Dominant species	Tidal level	Per-cent bare space	Mean percent cover					Species with <1% cover
			<i>Gigartina canaliculata</i>	<i>Gelidium coulteri</i>	<i>Gigartina leptorhynchos</i>	<i>Rhodoglossum affine</i>	<i>Gastroclonium coulteri</i>	
<i>Gigartina canaliculata</i>	+.145 (.01)	7.8 (7.2)	80.6 (11.6)	5.3 (6.3)	2.6 (3.5)	1.6 (3.0)	1.1 (2.1)	<i>Laurencia pacifica</i> <i>Centroceros clavulatum</i> <i>Ulva</i> spp. <i>Anthopleura elegantissima</i> <i>Chthamalus fissus</i>
<i>Gastroclonium coulteri</i>	+.013 (.05)	5.2 (8.4)	59.4 (25.1)	12.6 (16.6)	12.1 (13.1)	8.1 (12.8)	1.4 (3.8)	<i>Laurencia pacifica</i> <i>Gigartina leptorhynchos</i> <i>Gigartina spinosa</i> <i>Corallina vancouveriensis</i> <i>Prionitis lanceolata</i> <i>Anthopleura elegantissima</i> <i>Chthamalus fissus</i>

muscosa, the volcano limpet, *Fissurella volcano*, hermit crabs, *Pagurus* spp., and the snail, *Lacuna unifasciata*. Juveniles of the herbivorous snail, *Tegula fenebralis*, recruit to this zone but are completely eliminated by predators (Fawcett 1979).

Densities of the more abundant of these herbivores were sampled cooperatively with M. Fawcett and S. Schroeter, whose studies on populations of herbivores at the Ellwood site coincided with this study of the algal community (Fawcett 1979). A uniform grid (25 × 60 m in area) of 28 permanently marked 0.25-m² quadrats was established across the boulder field. The quadrats were sampled for limpets and chitons in January 1975, May 1975, November 1975, and January 1976. The number of sea urchins in the same quadrats was counted on the January 1975 and May 1975 dates. Accurate estimates of the densities of the crab, *Pachygrapsus crassipes*, are difficult to make. Crude estimates which undoubtedly underestimate their abundance were obtained by carefully searching randomly

laid 1-m² quadrats in August 1976 (four quadrats) and January 1977 (15 quadrats). Sea hares, mostly *Aplysia californica*, in the 1500-m² grid area were periodically counted between April 1975 and February 1977. Only a single pair of mating *Aplysia vaccaria* was observed in August 1975. The abundance of all these grazers except for sea urchins and sea hares (Table 2) was greatest at the spring and summer sampling dates. Sea urchin densities were nearly identical in the two seasons in which they were sampled. The abundance of sea hares fluctuated erratically with no clear seasonal trends. The greatest number of sea hares was recorded in April 1975 while the number in April 1976 was one of the lowest of that year. Mating in these hermaphrodites began in May of each year and egg masses laid on algae were found between May and December. Small juveniles (2–5 cm long) were very rare until the winter and spring of 1977 when a large number could be located with relatively little searching effort.

The snail, *Lacuna unifasciata*, was not sampled

TABLE 2. Mean densities of common grazers at Ellwood. Data are mean numbers of individuals for all sampling dates per 0.25 m² except where noted. Range of average densities is also presented (range for the sea hare *A. californica* is of absolute density rather than average).

Species	Number of sample dates	Mean density	Range
<i>Notoacmea fenestrata</i>	4	12.9	5.9–29.9
<i>Collisella strigatella</i>	4	4.5	1.1–12.9
<i>Collisella scabra</i>	4	2.6	1.4–5.5
<i>Fissurella volcano</i>	4	1.3	.7–2.0
<i>Mopalia muscosa</i>	4	.6	.3–1.3
<i>Strongylocentrotus purpuratus</i>	2	22.9	22.2–23.6
<i>Pachygrapsus crassipes</i>	2	2.9/m ²	1.3–4.5
<i>Aplysia californica</i>	17	50.7/1500 m ²	1–155

quantitatively. I observed snails laying egg masses on *Gigartina canaliculata* in May and June of 1975 and 1976. Their populations became very dense between September and December of each year, inflicting heavy grazing damage to most of the algal species I studied. This damage does not kill perennials, which regrow the following spring. The snails graze small holes in the thallus; the weakened branches are torn off and carried away by waves. Shortly after winter defoliation, the snails largely disappeared.

GENERAL METHODS

A number of experimental techniques used repeatedly during the course of this study are described below. The designs of experiments are detailed in the appropriate sections in the text followed by presentations of the results.

Settling surfaces

One method of documenting the seasonal patterns of recolonization of boulders denuded by disturbances is to overturn large numbers of "replicate" boulders at different times of the year and monitor subsequent colonization. This approach has two important drawbacks. It would be extremely destructive to the habitat, which was rather small in area to begin with. Secondly, it was difficult to find a sufficient number of boulders similar enough in size, surface texture, and composition to act as true replicates. To satisfy these latter requirements, I used 165-cm² concrete blocks as settling surfaces. Though some previous workers (MacGinitie and MacGinitie 1968, p. 91) have warned of the potentially lethal nature of chemicals which leach from concrete, I saw no evidence of this during the study. As will be seen later, the successional patterns observed on concrete blocks did not differ in any obvious way from those which occur on natural boulder surfaces.

Most experiments using the surface of natural boulders were conducted in 100-cm² clearings in beds of algae. These plots were cleared by removing as much algae as possible with a putty knife, then burning off the remainder with a propane torch. Subsequent observations revealed no vegetative regrowth of algae within the plots, indicating that the burning had been effective. The corners of all plots were marked with stainless steel screws or Sea-Goin Epoxy Putty (Permalite Plastics Corporation, Newport Beach, California 92668).

Estimation of percent cover and numbers of plants

The percent cover of a sessile species is a measure of its relative abundance and use of space. Two methods were used to estimate cover. Concrete blocks and experimental plots on boulders were photographed periodically and the percentage covers of each macroalgal species and of the barnacle, *Chthamalus*, were estimated by a point sampling technique using 100 uni-

formly positioned points superimposed on the projected image. The number of points which hit each species is an estimate of its cover.

A systematic sampling design often gives an estimate of percentage cover which has a smaller variance than if a random pattern were used (Greig-Smith 1964, Snedecor and Cochran 1967). It does, however, have two potential disadvantages. If there is some periodic variation in the spatial pattern of the cover being estimated which matches that of the sample spacing, then bias will be introduced. I did not observe any pattern in the algal canopy which was likely to induce bias in this manner. Second, there is no reliable way of estimating the standard error of the mean of a systematic sample, although in most cases it will be smaller than that for a random sample. Approximate values were calculated by applying the usual formula for the standard error of a random sample to the cover estimates obtained with the uniform grid of points. The positioning of the points over the projected image was shifted haphazardly each time a slide was analyzed to reduce any potential serial correlations in the data from successive sampling dates.

When inclement weather or a dense overlying canopy precluded photography of the cleared plots or concrete blocks, the percent cover was estimated visually in the field with the aid of plexiglass quadrats subdivided into 100 squares. By simultaneously using both techniques on the same sampling date I found that the two estimates differed by less than 5%. Dayton (1971, 1975) using similar methods reported the same precision in his visual estimates of percent cover. All statistical comparisons of percent cover data were performed on values normalized with an arcsine transformation (Sokal and Rohlf 1969).

Since plants of the species studied often have many basal branches making it difficult to enumerate individuals, I counted distinct holdfasts as separate plants. This method probably underestimates the actual number of individuals as adjacent holdfasts may fuse into one. There is no bias between treatments in this respect as all were conducted in 100-cm² areas over the same period of time.

Manipulations of algae

To study interactions between different species of algae, I performed a number of selective removals. Plants were removed from the experimental plots using forceps or a scalpel. Because of rapid recruitment of some species and/or regrowth of plants from portions of surviving holdfasts, removals had to be repeated on each sampling date.

When plants had to be marked individually, I cemented color-coded, numbered Brady Wire Markers (W. H. Brady Company, Milwaukee, Wisconsin 53201) to the dried rock surface near the holdfast of each plant with Loctite 404 epoxy adhesive (Loctite Corporation, Newington, Connecticut 06111). I experi-

mentally transplanted algal sporelings by chipping off small pieces of rock to which they were attached and cementing these chips to the surface of other boulders with Sea-Goin Epoxy Putty.

Manipulations of grazers

To assess the effects of grazing on patterns of algal succession I experimentally manipulated the densities of herbivores. Grazing by the limpets, *Notoacmea fenestrata*, *Collisella strigatella*, and *Collisella scabra*, was prevented using a technique devised by Cubit (1974). A 3-cm-wide ring of copper paint was applied to four sides of each concrete block from which limpets were to be excluded. Limpets do not cross the barrier because of the toxic and/or electrolytic properties of the copper. In addition, I painted strips of copper on two sides of a second group of blocks to which limpets were allowed access. This partial application was intended to serve as a control for any influence the presence of copper ions might have on the recruitment or growth of algae. See Cubit (1974) for details concerning the components of the paint mixture.

The effects of larger grazers were studied by using cages. I used cages either to exclude herbivores and thus prevent their grazing on experimental plots, or to enclose them and thus ensure that the plots were grazed. To control for the effects of shading by the cage roofs I constructed cages with openings in the sides allowing access to all grazers. Possible cage effects will be discussed later. The cages were 0.6 m on a side and 0.45 m high. They were constructed of 1.25-cm-wide Vexar mesh (DuPont Corporation) wired to a 5 × 10 cm mesh vinyl-coated hardware cloth frame with stainless steel wire. Cages were secured in place and supported by 1.25-cm-diameter reinforcing bars driven into the soft shale platform underlying the boulder field at Ellwood.

PATTERNS OF RECOLONIZATION FOLLOWING A DISTURBANCE

Disturbances in boulder fields create openings which vary in size from small holes in the algal canopy to entire surfaces of boulders being wholly or partially cleared. Recolonization usually begins soon after space is cleared. The resultant patterns and mechanisms of change in species composition depend in part on the size of the initial clearing and whether adult plants surround the opening or not.

Recolonization of large clearings

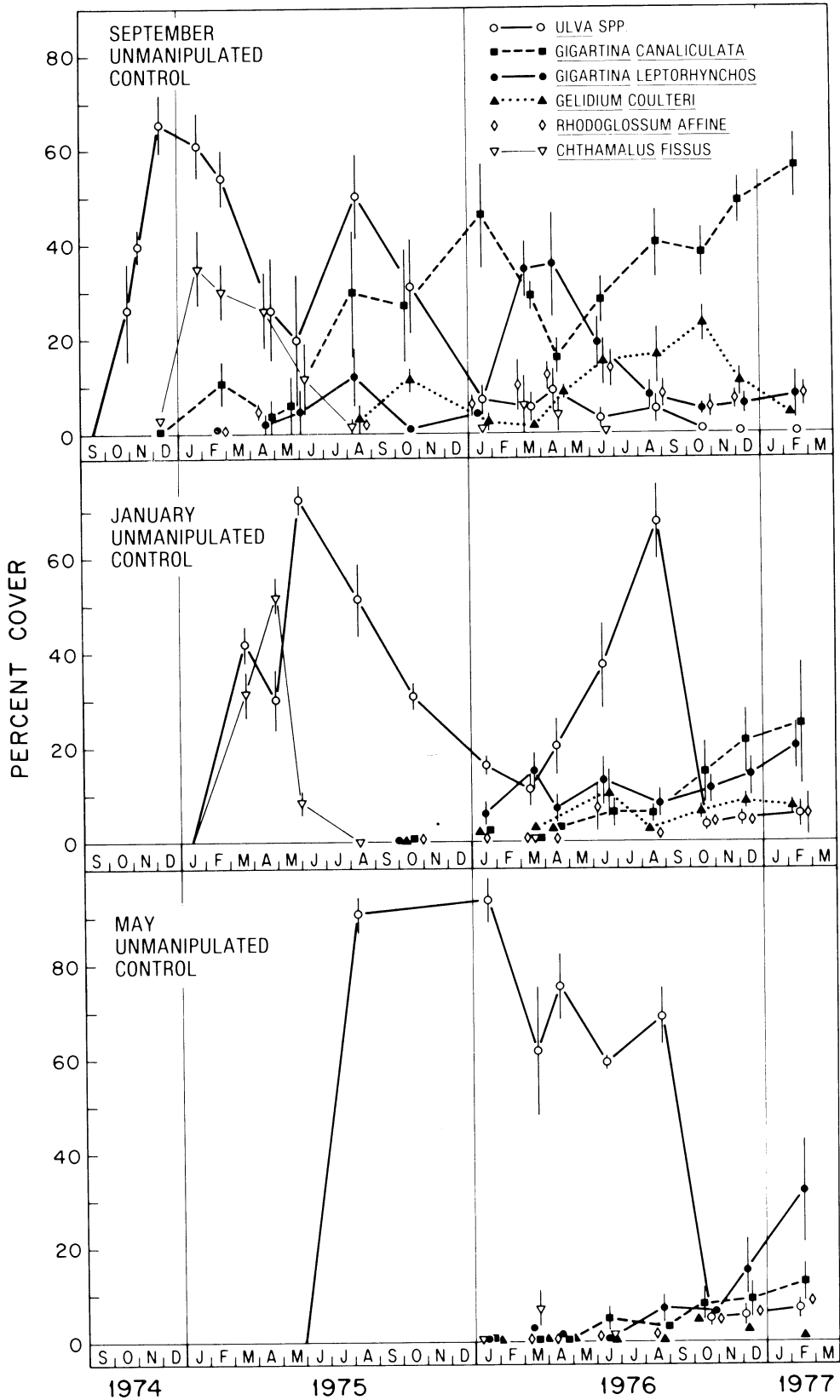
When a boulder remains overturned for a long period of time (i.e., more than 2 mo), all of the sessile organisms on what used to be its upper surface are killed. When the boulder is reflipped and stabilized, the entire surface is bare and recolonization begins. I documented the seasonal recruitment patterns of algae and sessile invertebrates and examined the species interactions which influence the sequence of colonization on bare surfaces by establishing a series of concrete blocks in the Ellwood boulder field at approximately +0.15 m above MLLW tidal level. Replicated sets of concrete blocks were placed in the intertidal on 16 September 1974, 15 January 1975, and 31 May 1975. While all sets began with six replicate blocks, some were lost or damaged during winter storms, reducing the minimum number of replicates to four at later sampling dates.

The percentage covers of all sessile species which averaged at least 5% cover on a set of blocks are plotted in Fig. 2. These plots are for unmanipulated blocks set out on the September 1974, January 1975, and May 1975 dates, respectively. Though a cover of diatoms dominated by *Navicula* spp. and *Licmophora* spp. usually developed first on a block or cleared boulder, I did not study this phenomenon in any detail.

In each set of blocks, the green alga, *Ulva*, recruited and grew to dominate soon after the blocks were established. On the September blocks, the cover of *Ulva* declined during the physically harsh months of January through May 1975 when the lowest tides occurred in the afternoon. Surviving *Ulva* plants form a 1-cm-high turf during harsh winter months while the same thalli can grow to be 20 cm long during the summer. As tides shifted to night and early morning hours in the summer, and physical conditions became more benign, *Ulva* rerecruited and grew rapidly, holding 50% of the cover on the September blocks in August 1975. This cover gradually declined again until *Ulva* had essentially disappeared from these blocks by October 1976. By this time, four species of perennial red algae had recruited and grown to cover most of the space on the blocks. *Ulva* dominated the January blocks during the early summer of 1975 (June–August) but declined to about 15% cover by March 1976. It then underwent a second increase in abundance between June and August 1976 and disappeared by the late fall, 1976. There was no corresponding increase in *Ulva* on the September blocks, indicating that the canopy of red algae probably interfered with the re-

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FIG. 2. Mean percent cover of algae and barnacles which colonized unmanipulated concrete blocks at Ellwood. Sets of blocks were established in September 1974, January 1975, and May 1975. The mean ± one standard error of the mean of four to six blocks in each set are indicated (see text for details). Only species which held an average of at least 5% cover at some sampling date over the period are included.



recruitment and growth of *Ulva*. *Ulva* covered nearly 90% of the space on the May blocks between August 1975 and January 1976. It declined somewhat in the winter of 1975–76 and disappeared during the late fall of 1976.

On the September and January blocks, the barnacle, *Chthamalus*, held approximately 35% and 50% of the space, respectively, during the winter months of 1974–75. These barnacles settled into small openings in the cover of *Ulva* and diatoms created by the grazing activities of limpets. This effect of limpet grazing will be discussed in greater detail later. By August 1975, the cover of barnacles had disappeared from both block sets. Only the empty tests of dead barnacles remained. Barnacles did not recruit to the May blocks during 1975 and held less than 10% of the space on those blocks in March of the winter of 1976.

During the fall and early winter months of 1974–75 four species of perennial red algae, *Gigartina canaliculata*, *Gigartina leptorhynchos*, *Gelidium*, and *Rhodoglossum* recruited to the September blocks. Their settlement is far more restricted seasonally than that of either *Chthamalus* or *Ulva*. Settlement occurs in the fall and early winter when space is available for colonization due to the defoliation of the algal canopy. Blocks exposed for settlement in January and May 1975 were not colonized by any of these red algae during the late winter of 1975. Not until the fall and early winter of 1975–76 did these species recruit to the January and May blocks. By February 1977, these four species had grown to comprise most of the algal cover on these blocks, but strong dominance by any one species had not developed by the time the study was ended.

Strong dominance by *G. canaliculata* did develop slowly on the unmanipulated September blocks. The *G. canaliculata* canopy increased in cover during the benign summer months when the thalli grew rapidly but declined in the harsh winter months (February through April of 1975 and 1976) when its branches defoliated. There was almost no decline in the cover of this plant, however, in the fall and winter of 1976–77 as it had by that time secured 55% of the primary space on the blocks. Though the recruitment of this species to the blocks was predominantly from spores, I did see several instances in which branches from plants on neighboring boulders became attached at their distal ends to the sides of a concrete block. These branches became detached from their parent plants and developed into new individuals. This form of colonization may be relatively common under natural conditions. It should be noted that a crustose *Petrocelis* stage has not been identified for any of the red algal species in this study; all have erect tetrasporic plants (West 1972, W. P. Sousa, *personal observation*).

The three other species of perennial red algae which recruited to the September blocks in the fall and winter

of 1974–75 underwent seasonal fluctuations in abundance throughout the 2½ yr study, eventually declining to less than an average of 10% cover by February 1977. After recruiting to the September blocks in the fall–winter 1974–75, *G. leptorhynchos* increased slightly to more than 10% cover by August 1975. It then declined in cover to near zero in late October 1975, but rerecruited in the winter of 1976. These plants grew to cover nearly 40% of the space on the September blocks in April 1976. This cover declined again throughout the summer of 1976, remaining near 10% cover into February of the 1977 settlement season when strong dominance by *G. canaliculata* was developing. *Gelidium* showed seasonal fluctuations in abundance which differed somewhat from those of *G. leptorhynchos*. *Gelidium* covered nearly 10% of the space on the September blocks by October 1975. By March 1976, most of this cover had disappeared but the growth of surviving and newly recruited plants during the next summer resulted in an average of 20% cover of *Gelidium* in October 1976. Once again this cover declined dramatically to about 5% by February 1977 as *G. canaliculata* dominated the surfaces of the blocks. The seasonal decline in abundance of *G. leptorhynchos* and *Gelidium* coincided with their overgrowth by various species of epiphytes. This phenomenon will be discussed in detail later. *Rhodoglossum* never increased above an average of 10% cover throughout the study and I could not detect any marked consistent fluctuation in its abundance.

In summary, shortly after a block is established in the low intertidal it is colonized (independent of season) and dominated by the early successional species, *Ulva*. The barnacle, *Chthamalus*, may also be abundant, depending upon what season the block is established and whether limpets are present. These early species gradually disappear from the blocks after undergoing several seasonal pulses in recruitment and growth. In the first fall and winter, the block is colonized by four species of perennial red algae, three of which fluctuate in abundance seasonally, reaching their peak abundances in the middle of the successional sequence (hereafter referred to as middle successional species), while the fourth, *Gigartina canaliculata* (late successional species), gradually increases in cover and dominates, holding 55% of the space after 30 mo.

Recolonization of small clearings

Small bare patches in a bed of the dominant algal species, *Gigartina canaliculata*, are sometimes cleared when a loose rock is lifted by waves and strikes the surface of a larger, more stable boulder. Small openings may also be created when a large boulder overturns for a short period of time so that when it is re-flipped, most of the canopy recovers vegetatively except for small areas where intense urchin grazing or abrasion occurred. Late in a successional sequence,

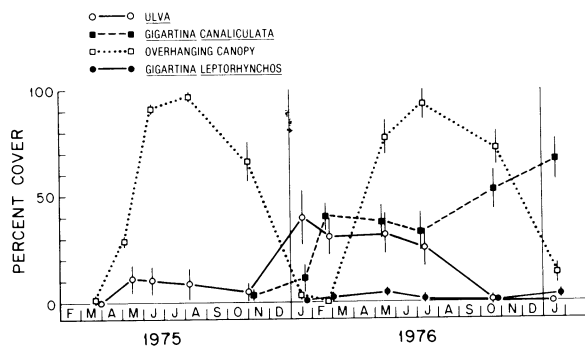


FIG. 3. Mean percent covers of algae which colonized four 100-cm² clearings in beds of *Gigartina canaliculata*. The mean percent of the plots covered by an overhanging canopy of surrounding adult plants is also plotted. Plots were cleared in February 1975 and sampled periodically until January 1977. The mean \pm one standard error of the mean are indicated. All limpets and chitons which recruited into the plots were removed at each sampling date.

large clearings become a mosaic of small openings. Some are filled with early or middle successional species, others are bare, and all are surrounded by adults of the late successional algae.

The successional processes which occur in small openings in a canopy of adult plants are qualitatively different from those which operate when a completely denuded boulder is recolonized. In small openings, the canopy of surrounding plants grows long and covers the cleared patch during summer months. In the winter the surrounding plants defoliate, opening the patch to sunlight and colonization. In addition to colonization from planktonic propagules, vegetative reproduction occurs. Adult plants of *Gigartina canaliculata* have the capacity to spread vegetatively across the rock surface by rhizoid-like basal branches that can attach to the surface at their distal ends and then sprout branches at the point of contact, creating an entirely new plant. In this way, surrounding plants slowly encroach into and eventually fill the opening.

To study the dynamics of colonization within small openings, I cleared a number of 100-cm² plots in solid beds of *G. canaliculata* on a group of large stable boulders in February 1975. To examine mainly plant-plant interactions, all small molluscan grazers, including limpets and chitons, were removed at each sampling date from all plots.

Patterns of recolonization of small clearings in beds of *Gigartina canaliculata* are shown in Fig. 3. An important feature of small clearings is the fluctuating canopy of surrounding *G. canaliculata* plants, which during the summer months of 1975 and 1976 covered nearly 100% of the space in the plots. *Ulva* recruited to the plots in March 1975 shortly after clearing. Its abundance remained low, an average of approximately 10% cover, until January 1976 when the *G. canaliculata* canopy defoliated, opening the plots to the

light. Subsequent recolonization and growth of newly recruited and surviving *Ulva* plants caused its cover to increase to 30–40% in the plots. This cover of *Ulva* gradually disappeared by November 1976 as the canopy of *G. canaliculata* redeveloped. The middle successional red algae, *G. leptorhynchos*, recruited into the plots in the fall and winter of 1975–76, but never comprised more than 10% cover throughout the study. For unknown reasons, recruitment of *Gelidium*, *Rhodoglossum*, and of the barnacle, *Chthamalus*, to these plots was very low and none of these species reached an average of 5% cover in any treatment.

Gradually, beginning in November 1975, the plots were filled by plants of the dominant red algal species, *G. canaliculata*. These plants were predominantly of vegetative origin, spreading inward from adult plants which surrounded the plot. By January 1977, 24 months after initial clearing, *G. canaliculata* held 70% of the space in the plots. By contrast, *G. canaliculata* covered 55% of the space after 30 mo of succession on the concrete blocks where almost all the initial recruitment of algae was from spores.

MECHANISMS OF SPECIES REPLACEMENTS DURING SUCCESSION

What mechanisms account for the relatively predictable patterns of ecological succession observed in this intertidal algal community? More specifically, what mechanisms alter the relative abundances of species within the community from an almost pure stand of green algae with some barnacles, shortly after a severe disturbance, to a mixed assemblage of green and red algae sometime later, and finally, to a community dominated by a single species of perennial red algae?

Three alternative mechanisms might account for these patterns. First, the species in each stage of the successional sequence may modify local environmental conditions so as to facilitate the recruitment and growth of species which appear later in the sequence. The community would continue to change until the species which dominates the site creates local conditions under which no other species can become established. Alternately, late species may replace early ones by growing up through their canopy and casting a shade which kills them. The species which casts a shade so deep that no other species can grow will eventually dominate. Finally, late species may be less susceptible to sources of mortality including desiccation stress, grazing, and overgrowth by epiphytes than early species and replace them as they die. The climax will consist of the best-protected and most long-lived species.

To decide between these alternative mechanisms I experimentally investigated interactions between algae and the effects of grazing and other sources of mortality on successional patterns. Both large and

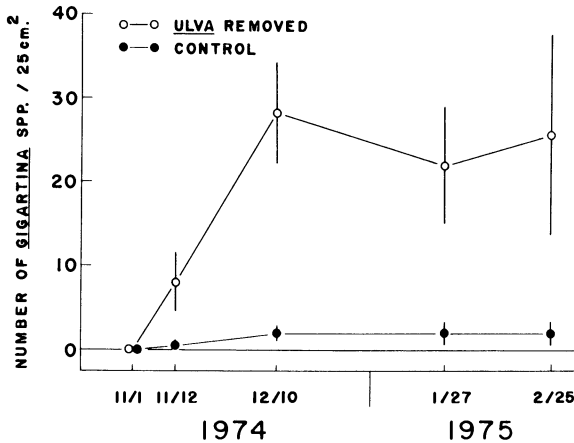


FIG. 4. Effect of manually removing the early successional species, *Ulva*, on the recruitment of *Gigartina* spp. over a 4-mo period from 15 October 1974 to 25 February 1975. Data are mean numbers of *Gigartina leptorhynchos* and *Gigartina canaliculata* sporelings which recruited to four 25-cm² plots on concrete blocks from which *Ulva* was removed and four on which it was left undisturbed. The two species of *Gigartina* are indistinguishable to the unaided eye when less than 0.5-cm tall. The mean \pm one standard error of the mean are indicated.

small clearings were studied as observations indicated some differences in the mechanisms operating in each.

Mechanisms operating in large clearings

Effect of early and middle successional species of algae on subsequent recruitment.—There are two major points of transition in the successional sequence on concrete blocks. The first point is where early dominance by *Ulva* gives way to a community composed almost entirely of perennial red algae including both middle and late successional species. The second major replacement occurs when the late successional species, *Gigartina canaliculata*, replaces the middle successional algae, *Gigartina leptorhynchos*, *Gelidium*, and *Rhodoglossum*, and the early green alga, *Ulva*, and dominates after approximately three years.

To determine which mechanism of replacement might be acting at each of these two major steps, I conducted a series of selective removals of algal species with appropriate controls. In one series of experiments I selectively removed the early species, *Ulva*, in order to determine its effects on the recruitment of the later-appearing red algae. Using a replicated design, four plots were kept cleared of *Ulva* while four control plots were allowed to develop a dense canopy (90–100% cover) of the plant. This experiment was conducted between September 1974 and February 1975 in small 25-cm² plots on the top surfaces of concrete blocks. It was later repeated in cleared plots on boulders as discussed in a later section.

In a second series of selective removals, the middle successional species, *Gigartina leptorhynchos* and

Gelidium, were similarly manipulated with controls in 100-cm² plots on stable boulders in July 1976. In both of these removal experiments there were four replicates of treatments and controls. I removed these species in order to determine what effect their presence had on both the development of dominance by *Gigartina canaliculata* and the reinvasion of *Ulva* which they would naturally have replaced. At Ellwood, solid 100-cm² patches of these plants are uncommon; such patches were used in order to detect if any effect existed. It was assumed that smaller more isolated clumps of these species would have a similar but proportionately smaller effect on the rate of replacement by *G. canaliculata*. The middle successional species, *Rhodoglossum*, never formed monospecific patches over an area large enough to manipulate.

The plots on concrete blocks which were kept cleared of *Ulva* had a much greater recruitment of perennial red algae than those plots which had a dense cover of the early successional species (Fig. 4). There was significantly higher recruitment of *G. leptorhynchos* and *G. canaliculata* sporelings when *Ulva* was removed (on 10 December 1974: $t = 4.37$, $P < .0025$). For unknown reasons there was negligible recruitment of *Gelidium* or *Rhodoglossum* in both treatment and control plots in this experiment.

Selective removal of the middle successional species, *G. leptorhynchos* and *Gelidium* (Figs. 5 and 6, respectively), resulted in significantly greater recruitment and growth of the late successional species, *G. canaliculata*, as compared to controls (*G. leptorhynchos* removal on 21 November 1976: $t = 2.86$, $P < .05$; *Gelidium* removal on 21 November 1976: $t = 3.05$, $P < .05$, on 19 January 1977: $t = 3.54$, $P < .02$). Most of the increase in cover of this plant was a result of vegetative growth of previously suppressed individuals which were present in the experimental plots from the beginning, or of adult plants which surrounded the plots and grew into them from the edges. In addition, shortly after both middle successional species were removed, there was rapid colonization and growth of *Ulva* which resulted in significantly greater cover of this plant in removal plots (*G. leptorhynchos* removal on 24 August 1976: $t = 2.59$, $P < .05$; *Gelidium* removal on 24 August 1976: $t = 6.13$, $P < .001$). This was also true in the *G. leptorhynchos* removal plots for the ephemeral sporelings of the red alga, *Laurencia*, which recruit to this zone from lower areas during summer and fall months but are killed by desiccation during the harsh winter months (on 23 September 1976: $t = 2.60$, $P < .05$). I did not find any statistically significant inhibition between the middle successional species, *Gigartina leptorhynchos* and *Gelidium*, though each showed a greater increase in cover when the other was removed. If the experiment was repeated during the season of peak recruitment of these species, inhibition might be demonstrated.

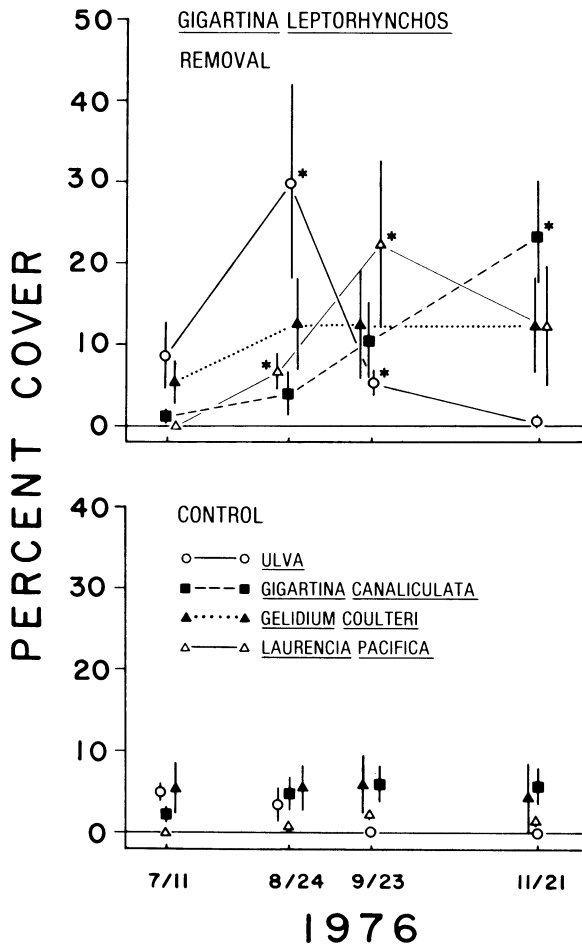


FIG. 5. Effect of manually removing the middle successional species, *Gigartina leptorhynchos*, on the recruitment and growth of other species of algae over a 4-mo period from 11 July to 21 November 1976. Data are the mean percent covers of algae in four 100-cm² plots from which the alga was removed and four in which it was left undisturbed. The mean \pm one standard error of the mean are indicated. Asterisks indicate means for the removal plots which were significantly greater than those for the controls on the same date ($P < .05$) using a one-tailed t test. The mean percent covers of *G. leptorhynchos* on the control plots on the four sampling dates were 81.8%, 74.5%, 82.0%, and 83.7%.

In summary, the early successional green alga, *Ulva*, inhibits rather than facilitates the recruitment and growth of more long-lived red algae (both middle and late successional) which usually replace it in the sequence described earlier. Similarly, the middle successional red algal species, *Gigartina leptorhynchos* and *Gelidium*, inhibit the invasion and growth of the late successional dominant red alga, *Gigartina canaliculata*. In addition, once these middle successional species are established, they inhibit the reinvasion of early successional green algae. In neither case was there any evidence that species which normally appear

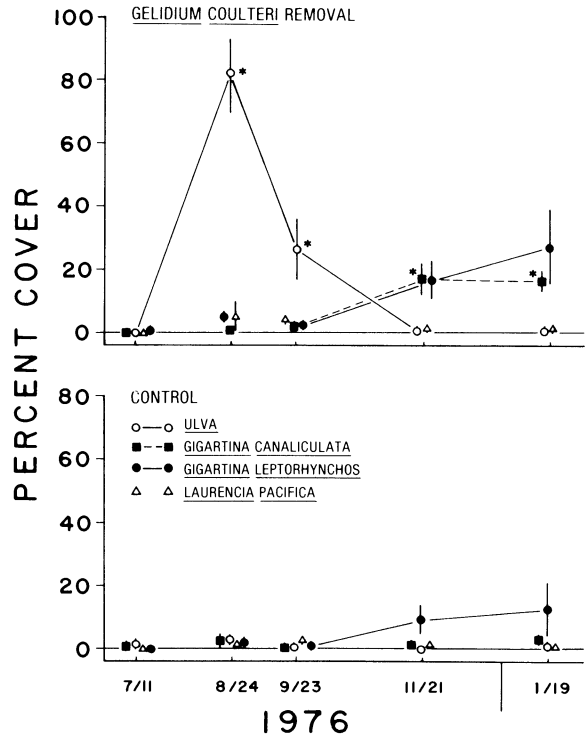


FIG. 6. Effect of manually removing the middle successional species, *Gelidium coulteri*, on the recruitment and growth of other species of algae over a 6-mo period from 11 July 1976 to 19 January 1977. Data are the mean percent covers of algae in four 100-cm² plots from which the alga was removed and four in which it was left undisturbed. The mean \pm one standard error of the mean are indicated. Asterisks indicate means for the removal plots which were significantly greater than those for the controls on the same date ($P < .05$) using a one-tailed t test. The mean percent covers of *G. coulteri* on the control plots at the five sampling dates were 97.6%, 90.3%, 62.5%, 45.2%, and 21.3%.

later in the sequence could grow through the canopy of early species and outcompete them for light.

Relative susceptibility of early, middle and late successional species to sources of mortality.—If the successional sequence is characterized by inhibition of successive invasions, what causes one species to replace another? A successional sequence will occur if early successional green algae are more susceptible to the rigors of the physical environment and to attack by natural enemies including grazers and epiphytes than middle and late successional red algae. In turn, the same relationship must exist between middle successional red algae and the late successional red alga which eventually dominates.

1. *Relative susceptibility to physical stress.*—An important source of mortality in intertidal marine algae is simultaneous exposure to air, intense sunlight, and drying winds. To determine if there was any relationship between the stage of succession at which a species of alga was most abundant and its relative sus-

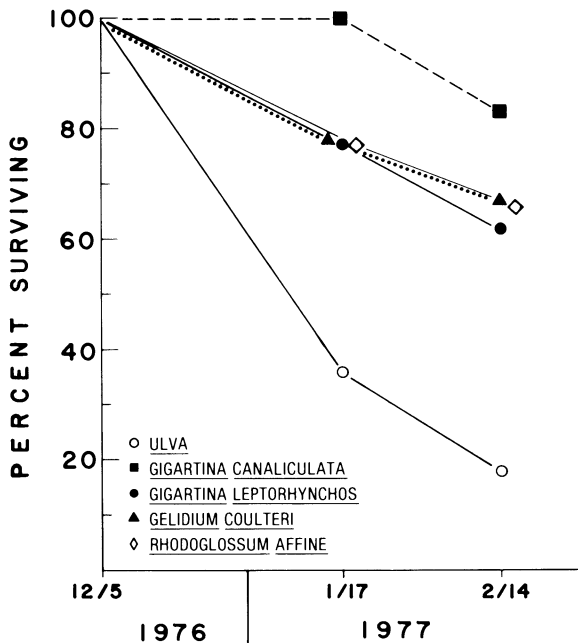


FIG. 7. Survival curves for five species of algae over a 2-mo period from 5 December 1976 to 14 February 1977, when low tides occurred in the afternoon, creating harsh physical conditions. Thirty plants of each species were tagged on the initial date.

ceptibility to desiccation stress, I gathered survivorship data on each of the five predominant species in the successional sequence. I tagged 30 randomly selected plants of each species (i.e., *Ulva*, *Gigartina leptorhynchos*, *Gelidium*, *Rhodoglossum*, and *Gigartina canaliculata*) at the beginning of the period of physically harsh afternoon low tides in December 1976. I monitored the survival of these tagged plants for a little over 2 mo. The results, in the form of survivorship curves, are plotted in Fig. 7. The early successional green alga, *Ulva*, suffered a greater mortality during this period than did either the middle or late successional perennial red algae species. The three middle successional red algae also did not survive as well as the late successional red alga, *Gigartina canaliculata*. Populations of the latter species grow in low-lying turfs, making individual plants less susceptible to desiccation stress. Plants of the middle successional species are more exposed to stress; they occur as isolated individuals or in small clumps.

2. *Relative palatability to herbivores and resistance to being grazed.*—Though undoubtedly important, relative susceptibility to desiccation stress is not the only source of mortality which might more strongly affect species which appear earlier in a successional sequence. If herbivores grazed more heavily on early species this would also contribute to the pattern seen in Fig. 7. To see if selective grazing on early species played an important role in dictating patterns of

species replacements, I examined the food preferences of two of the larger intertidal grazers in the laboratory. The grazers I tested were the sea hare, *Aplysia californica*, and the lined shore crab, *Pachygrapsus crassipes*. Using several individuals of each species of herbivore as replicates, I measured preference by offering each animal 5 g blotted damp weight of each species of alga being tested. Selectivity was determined by comparing statistically the mean blotted damp weight consumed of each alga. Group means were compared by testing at the $P = .01$ level using multiple Welch-Aspin tests (Snedecor and Cochran 1967, p. 115). This method of testing was used in order to take account of heterogeneity in the group variances which violated the assumptions of the one-way analysis of variance model. Each animal was simultaneously presented with nine different species of algae, all of which were relatively common at the Ellwood site. Only plants which were free of epiphytes were used.

During the experiments, individual crabs (average carapace width 26.1 mm, $SD = 3.4$) were enclosed in $8 \times 30 \times 36$ -cm plastic freezer boxes through which flowed unfiltered aerated seawater (16.1 – 17.5°C). Individual sea hares (average wet weight = 104.6 g, $SD = 39.1$) were tested in 18.92-l aquaria, also with running seawater and aeration. The experiments were run for approximately 40 h until it was clear that the animals in all of the replicates had been feeding on the enclosed plants. To help ensure feeding, all animals were starved for approximately 1 wk before the start of the trials. One drawback to this procedure is that it probably underestimates differences in preference since hungry animals might be expected to be less selective.

To correct for algal weight losses due to respiration rather than feeding, I maintained two complete sets of algae (i.e., 5 g each) under the same conditions for the same length of time without grazers. Average weights lost by these plants were assumed to have been respired away and were subtracted from weight losses of plants in the presence of grazers to get true estimates of the weights of algae consumed.

The mean blotted weights of each alga consumed by the two herbivores tested are presented in Table 3. The sea hare showed a marked preference for the early successional green alga, *Ulva*, and the red alga, *Laurencia pacifica*, which is a codominant in the -0.30 -m to 0.0 -m MLLW tidal level just below the height at which I conducted the study. Though *Aplysia* consumed significantly more of the middle successional red alga, *Rhodoglossum*, than of the brown alga, *Cystoseira osmundacea*, the middle successional red alga, *Gelidium*, or the late successional red alga, *Gigartina canaliculata*, there was little absolute difference in *Aplysia*'s preference for either of the two species of brown algae or the middle and late successional red algae species tested. All are much less preferred than

TABLE 3. Results of laboratory food preference experiments. Data are mean blotted weights in grams of algae consumed over the time period that the experiment was run. Underlines indicate means which are not significantly different at $P \leq .01$ using multiple Welch-Aspin tests where sample variances are not assumed equal. Species of algae tested were *Cystoseira osmundacea* (C.o.), *Egria laevigata* (E.l.), *Gelidium coulteri* (G.c.), *Gigartina canaliculata* (G.c.), *Gigartina leptorhynchos* (G.l.), *Laurencia pacifica* (L.p.), *Macrocystis pyrifera* (M.p.), *Rhodoglossum affine* (R.a.), and *Ulva* spp. (U.).

Herbivore	Weight of each alga offered (grams)	Length of time offered (hours)	Number of replicates	Mean weights consumed*								
				<i>Ge.c.</i>	<i>G.c.</i>	<i>C.o.</i>	<i>E.l.</i>	<i>M.p.</i>	<i>G.l.</i>	<i>R.a.</i>	<i>L.p.</i>	<i>U.</i>
Sea hare:				<i>Ge.c.</i>	<i>G.c.</i>	<i>C.o.</i>	<i>E.l.</i>	<i>M.p.</i>	<i>G.l.</i>	<i>R.a.</i>	<i>L.p.</i>	<i>U.</i>
<i>Aplysia californica</i>	5.0	39	12	<u>.06</u>	<u>.07</u>	.11	<u>.12</u>	.19	<u>.97</u>	.85	4.42	4.61
Lined shore crab:				<i>Ge.c.</i>	<i>R.a.</i>	<i>G.l.</i>	<i>G.c.</i>	<i>L.p.</i>	<i>C.o.</i>	<i>E.l.</i>	<i>M.p.</i>	<i>U.</i>
<i>Pachygrapsus crassipes</i>	5.0	40	8	<u>0</u>	<u>0</u>	<u>0</u>	<u>.01</u>	.03	.05	.08	.11	<u>.55</u>

* Corrected for weight loss due to respiration.

either *Ulva* or *Laurencia*. Other workers have also reported preference for *Ulva* and *Laurencia* in the same or closely related species of *Aplysia* (Saito and Nakamura 1961, Frings and Frings 1965, Carefoot 1967, 1970).

The crab, *Pachygrapsus*, also preferred *Ulva*. Crabs consumed more grams of *Ulva* than of any species of brown or red algae. There was essentially

no difference in the amounts of brown algae or middle and late successional red algae consumed. *Pachygrapsus* is commonly observed grazing on early successional green algae in the field (Hiatt 1948, W. P. Sousa, personal observation).

To see if selective grazing by *Pachygrapsus* on the early successional green algae, *Ulva*, would accelerate rates of succession to a red algae-dominated commu-

TABLE 4. Effects of grazing by *Pachygrapsus* alone and by all grazers on algal succession on denuded boulders. Experiments were started on 6 September 1975. There were three replicates of each treatment except for the grazer exclusion which had six. Data from censuses taken on 7 November 1976, 17 January 1976, and 12 March 1976 are presented. Data are percent cover of *Ulva*, *Gigartina canaliculata* (G.c.) and *Gelidium coulteri* (G.c.). The initial number of settled *Gigartina canaliculata* sporelings is enclosed in parentheses following its percent cover on the November date. + = <1% cover. - = none present.

Replicate	Percent cover							
	Four crabs enclosed			Open to all grazers		All grazers (>1 cm) excluded		
	<i>Ulva</i>	<i>G.c.</i>	<i>Ge.c.</i>	<i>Ulva</i>	<i>G.c.</i>	<i>Ulva</i>	<i>G.c.</i>	
November								
1	7.0	1.0 (24)	-	2.0	+(8)	14.0	-(0)	
2	-	4.0 (10)	-	9.0	-(0)	48.0	-(0)	
3	-	5.0 (2)	-	4.0	+(2)	82.0	-(0)	
4						8.0	-(0)	
5						20.0	-(0)	
6						13.0	-(0)	
January								
1	12.0	17.0	-	85.0	11.0	90.0	-	
2	21.0	9.0	-	93.0	-	95.0	-	
3	18.0	14.0	-	80.0	1.0	91.0	-	
4						99.0	-	
5						100.0	-	
6						99.0	-	
March								
1	8.0	20.0	1.0	97.0	1.0	84.0	-	
2	26.0	8.0	-	98.0	-	95.0	-	
3	17.0	19.0	1.0	88.0	2.0	97.0	-	
4						100.0	-	
5						100.0	-	
6						100.0	-	

TABLE 5. Effects of grazing by *Pachygrapsus* alone and by all grazers on algal succession on concrete blocks. The experiment was begun on 20 November 1976. There were six replicate blocks per treatment except for the crab enclosure which had nine. Data are the percent cover of *Gigartina canaliculata* (*G.c.*), *Gelidium coulteri* (*Ge.c.*), *Rhodoglossum affine* (*R.a.*), *Gigartina leptorhynchus* (*G.l.*), and *Ulva* (*U.*) on each block on 4 June 1977. + = <1% cover. - = none present.

Replicate	Percent cover														
	Four crabs enclosed					Open to all grazers					All grazers (>1 cm) excluded				
	<i>G.c.</i>	<i>Ge.c.</i>	<i>R.a.</i>	<i>G.l.</i>	<i>U.</i>	<i>G.c.</i>	<i>Ge.c.</i>	<i>R.a.</i>	<i>G.l.</i>	<i>U.</i>	<i>G.c.</i>	<i>Ge.c.</i>	<i>R.a.</i>	<i>G.l.</i>	<i>U.</i>
1	1.0	1.0	-	-	-	30.0	-	-	-	-	-	-	-	-	-
2	10.0	1.0	-	-	+	20.0	1.0	-	-	-	-	-	-	-	+
3	5.0	2.0	-	-	+	+	2.0	-	-	-	-	+	-	-	5.0
4	35.0	1.0	-	-	+	15.0	-	-	-	+	+	-	-	-	+
5	25.0	1.0	+	-	2.0	15.0	-	-	+	5.0	+	-	-	-	+
6	40.0	-	+	+	-	20.0	-	-	2.0	-	+	-	-	-	-
7	45.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	15.0	+	+	-	+	-	-	-	-	-	-	-	-	-	-
9	30.0	+	+	-	+	-	-	-	-	-	-	-	-	-	-

nity, I manipulated the densities of these grazers in the field. I protected some denuded boulders, on each of which I marked a 100-cm² plot, from all grazing in a cage, placed four crabs (i.e., roughly natural density) inside another cage with similar boulders, and had a control cage with the boulders enclosed but open to entry of all grazers. The experiment originally had a sea hare enclosure treatment but these animals repeatedly disappeared from the cages either because they squeezed through the cage walls or died and disintegrated inside. Attempts to manipulate them were abandoned. The first of two such experiments was run during the fall and winter of 1975-76 when the perennial red algae were fruiting and any inhibitory effect of an *Ulva* mat would be most evident.

Grazing by *Pachygrapsus* not only reduced the percent cover of *Ulva* but dramatically increased the recruitment of *Gigartina canaliculata* (Table 4). There was a noticeably greater set of this red alga when all herbivores were allowed access but not as great as under the intense grazing of the enclosed crabs. The relatively low recruitment of red algae in the control cage was probably a result of low natural densities of grazers in the area where the experiment was run. As mentioned earlier, this area (to the east of the main study site) was occasionally subjected to freshwater runoff from a nearby creek bed which could account for the low densities of grazers observed.

The persistence of *Ulva* in the total exclusion cage is probably due to the shading of the cage roof that affords *Ulva* some protection from desiccation. Usually, most plants which are not removed by grazers are killed by desiccation as indicated by the survivorship data in Fig. 7. This result also points out, however, that when early species are protected from grazers and desiccation, they persist for long periods and resist all invasion by species of red algae.

I repeated this experiment using 20 × 20 × 10-cm concrete blocks as settling surfaces in the winter of

1976-77. It was rerun in the main study area where grazers were generally more abundant. The treatments were established on 20 November 1976, but the experiment was not sampled until the termination date on 4 June 1977 (Table 5). The results are essentially the same as those in the first experiment. Blocks exposed to grazing by crabs enclosed in cages and those open to all grazers showed a much higher recruitment of perennial red algae, particularly *Gigartina canaliculata*, than blocks from which all grazers were excluded. Because of a greater abundance of herbivores in the new area, recruitment of red algae to blocks in the control cages open to all grazers was not different ($t = .86, P > .4$) from that on blocks grazed only by crabs. Unlike the first experiment, *Ulva* did not persist until June 1977 in the exclusion cages. This may be due in part to the later starting date of the second experiment which did not allow for the development of a dense mat of *Ulva* before winter desiccation took its toll. In addition, juvenile sea hares invaded all of the cages in this experiment, including the total exclusion cages, in the spring of 1977 and may have grazed away the *Ulva* which earlier in the winter had inhibited red algae recruitment. A dense mat of *Ulva* and *Chthamalus* which developed on the cage roofs by June 1977 may have shaded out any *Ulva* which remained on the blocks below.

The laboratory preference experiments and accounts in the literature indicate that the sea hare, *Aplysia* (see references above), and various herbivorous fishes, notably the adult opaleye, *Girella nigricans* (Williams 1955), also show strong preferences for the early successional species, *Ulva*. The stomachs of several opaleyes, monkey-face eels (*Cebidichthys violaceus*), and top smelt (*Atherinops affinis*) caught at high tide in the intertidal at Ellwood were filled with *Ulva*. I have also observed hermit crabs (*Pagurus* spp.) grazing on mats of *Ulva*. Though I found it impossible to manipulate the densities of these grazers experimentally, I presume that they have the

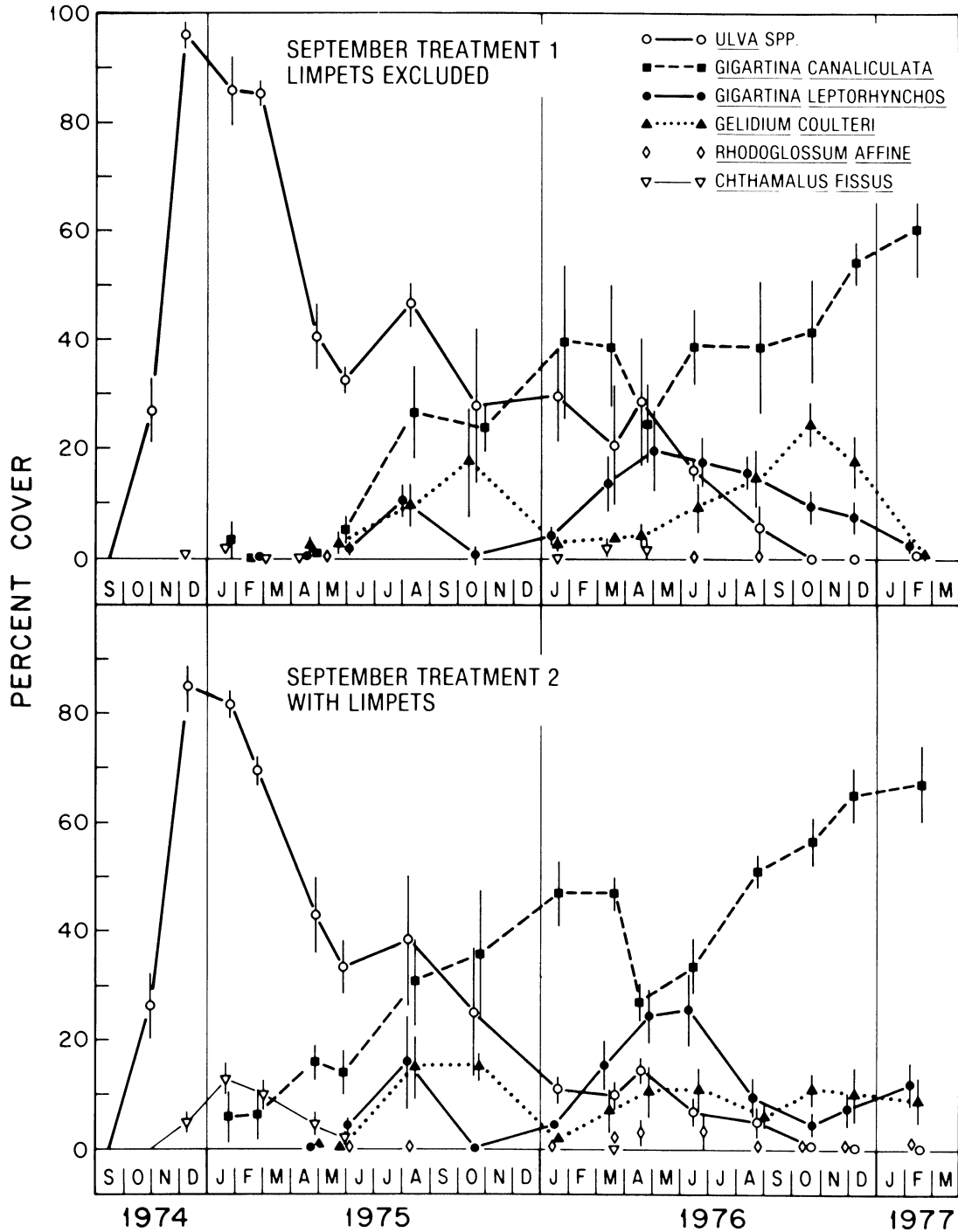


FIG. 8. Effects of excluding limpets on the recruitment of algae and barnacles to concrete blocks established at Ellwood in September 1974. Data are mean percent covers of species which held at least 5% cover on some sampling date between 16 September 1974 and 16 February 1977. The mean \pm one standard error of the mean for four to six blocks sampled on each date are indicated (see text for details). The density of limpets on control blocks ranged from 0-7 individuals.

same effect as the crabs on the pattern of species replacements.

In addition to manipulating crabs, I also manipulated the densities of limpets by excluding them from

some blocks within each of the three sets of concrete blocks established at Ellwood, while allowing them to colonize and graze on others. The September, January, and May sets were first established with six rep-

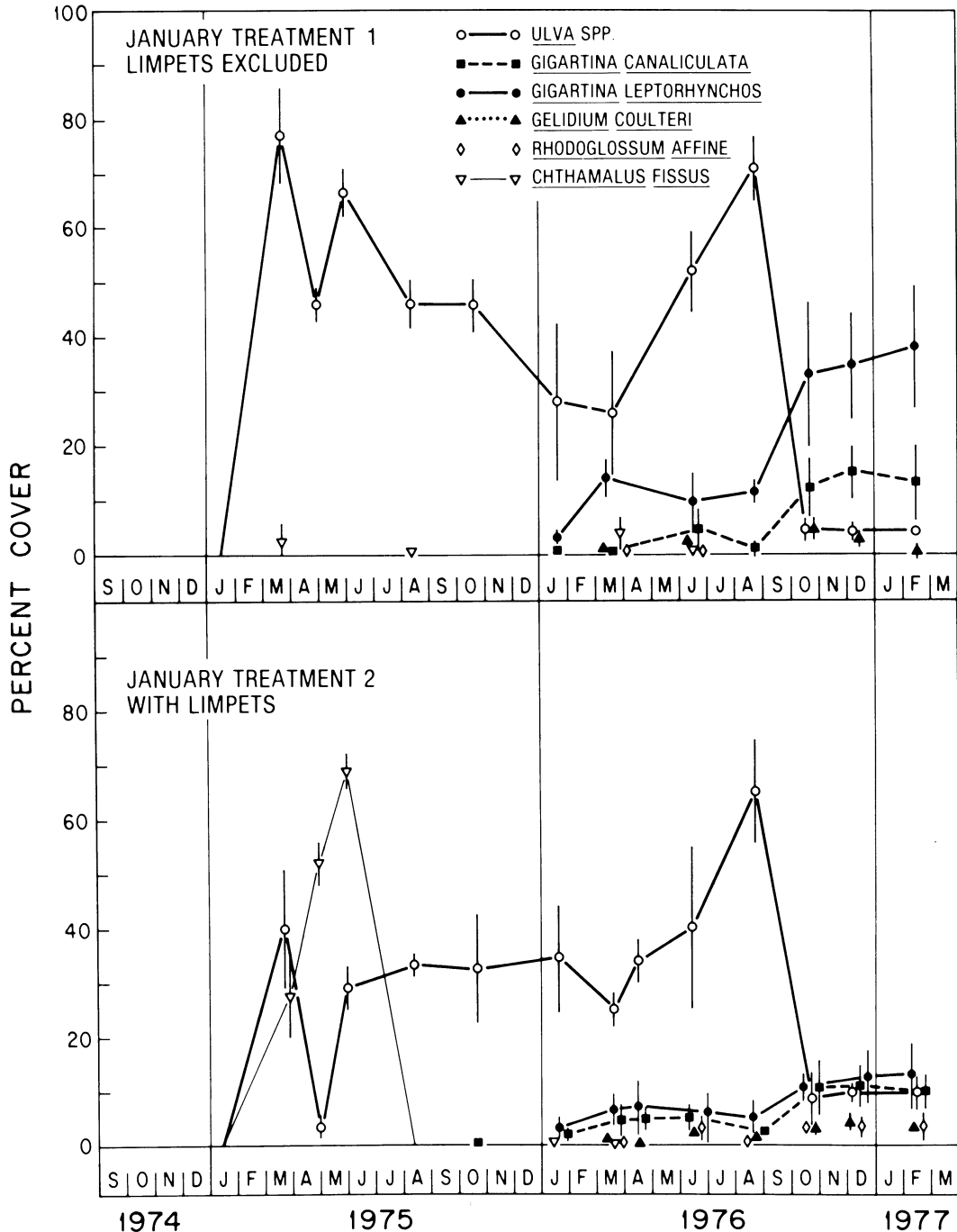


FIG. 9. Effects of excluding limpets on the recruitment of algae and barnacles to concrete blocks established at Ellwood in January 1975. Data are mean percent covers of species which held at least 5% cover on some sampling date between 15 January 1975 and 16 February 1977. The mean \pm one standard error of the mean for four to six blocks sampled on each date are indicated (see text for details). The density of limpets on control blocks ranged from 0–8 individuals.

licates of both the limpet exclusion treatment and its control. Some blocks within each set were lost during winter storms, reducing the number of replicates to a minimum of four each. All replicates of the May controls were lost in April 1976; these results are omitted here.

The effects of excluding limpets from concrete blocks are shown in Figs. 8 and 9. The only significant effect of limpets was to decrease temporarily the abundance of *Ulva* and increase the recruitment and thus the percent cover of the barnacle, *Chthamalus*, on blocks on which they grazed. The mean percent cover

of *Chthamalus* was significantly greater on the September (on 27 January 1975, $t = 2.84$, $.01 < P < .025$) and January (on 30 May 1975, $t = 24.91$, $P < .001$) blocks on which limpets were allowed to graze than on those from which they were excluded. Most limpets colonized the September and January control blocks as adults which migrated onto them from adjacent boulders rather than recruiting from the plankton. These limpets grazed predominantly on the outside edges of the developing mat of algae, removing young sporelings of *Ulva* and diatoms. These cleared areas were then colonized during fall and winter months by barnacles. Uncleared mats of early successional green algae and diatoms accumulate sediment in the interstices and form impenetrable barriers to barnacle recruitment. This seasonal enhancement of barnacle recruitment by limpet grazing in the low intertidal seems to have little if any long-term effect on subsequent development of the algal community. There was no significant difference in the percentage covers of any of the algal species including *Ulva*, on the September and January limpet exclusion blocks, as compared to controls after this initial effect. Colonization of red algae on these blocks was essentially identical to that on unmanipulated blocks (Fig. 2). The barnacles which settled on blocks during the fall and winter of 1974–75 were overgrown by algae during the following summer. Presumably the combination of overgrowth and accumulation of sediment in the algal mat killed the barnacles. Predation by the snail, *Acanthina spirata*, during this period also contributed to their decline. In addition, shortly after initial colonization, limpets disappeared from the blocks, thus eliminating their effect on barnacle recruitment.

Sea urchins (*Strongylocentrotus purpuratus*), though common in the boulder field, never graze the tops of boulders. Presumably wave shock and desiccation stress prevent them from doing so. As a result, they have no direct effect on the course of succession on stable substrates. They are important, however, in clearing space on boulders which are overturned during storms (Sousa 1977, 1979).

3. *Relative susceptibility to overgrowth by epiphytes.*—Selective herbivory does not seem to explain how the middle successional species, *Gigartina leptorhynchos*, *Gelidium*, and *Rhodoglossum*, are replaced by the eventual dominant, *Gigartina canaliculata*, on stable substrates. The herbivores tested did not show any substantial differences in preference between middle and late successional red algae. *Aplysia* consumed a significantly greater amount of *Rhodoglossum* than of the other three species of perennial red algae, but the magnitude of this difference was rather small.

Another potential source of differential mortality between species of intertidal algae is overgrowth by epiphytes. During certain seasons, plants often become covered with one to several times their own

weight in epiphytes. A cover of epiphytes may greatly increase the resistance of the thallus of the host plant to water flow, block incident sunlight, and thus interfere with photosynthesis, or extract metabolites from the host plant (Harlin 1973). During storms I have observed that plants with heavy loads of epiphytes are frequently torn off rocks while those without epiphytes remain attached. Menge (1975) has observed the same phenomenon in the New England intertidal.

To determine if the three species of middle successional red algae were more susceptible to overgrowth by epiphytes than the late successional red alga, *G. canaliculata*, I collected at random 30 individuals of each species during each month of 1976. Each plant was inspected for the presence of epiphytes. If at least 20% of the thallus of a plant was covered with epiphytes it was classified as overgrown. The choice of 20% as a significant level of overgrowth is comparable to the maximum level which was observed being supported by host plants before they began to disappear during storms or large wave swells. The plants were further subdivided into those overgrown by colonies of blue-green algae and those covered with macro-algae. Macro-algal epiphytes were generally sporelings of species which also occupied significant amounts of primary space elsewhere in the intertidal or shallow subtidal. These included *Ulva*, *Centroceros clavulatum*, *Laurencia pacifica*, *Gastroclonium coulteri*, and *Plocamium coccineum* var. *pacificum*. While *Ulva* and *Centroceros* appear to be ephemerals, *Laurencia*, *Gastroclonium*, and *Plocamium* are perennials at lower tidal levels. The latter species recruit to higher levels during the benign summer months but die back during afternoon low tides in the winter. The monthly percentages of the plants of each species which were classified as overgrown by either type of epiphytes are shown in Fig. 10.

The percentages of plants of the two middle successional species, *G. leptorhynchos* and *Gelidium*, which were overgrown by epiphytes of any kind were much greater than the same percentages for either the late successional species, *G. canaliculata*, or the other middle successional species, *Rhodoglossum*. Between approximately 30% and 70% of the *G. leptorhynchos* plants collected between July and October were overgrown by macro-algal epiphytes. By November it was very difficult to find adult plants of this species; most plants I collected were new recruits of that year. Presumably most of the adult plants which had recruited the previous year became overgrown with epiphytes and were then lost. The same general phenomenon seems to occur with *Gelidium*. It becomes overgrown, predominantly by blue-green algae in the late fall and winter, and older individuals disappear by January or February. Most of the remaining plants of this species appear to be new recruits from the fall–winter settlement season. The seasonal disappearance of these species both on the concrete blocks and in experi-

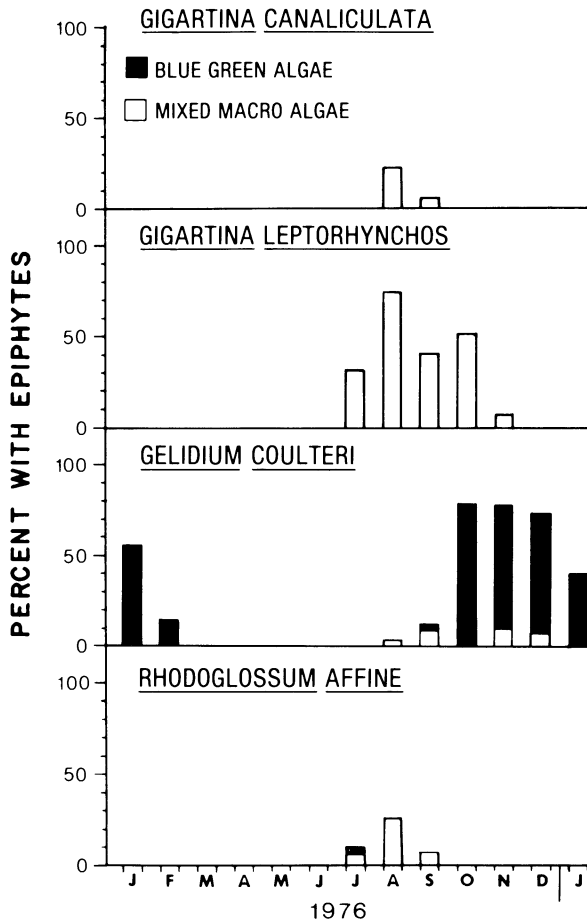


FIG. 10. Percents of random samples of 30 plants of each of four species which were overgrown by epiphytes. Plants were collected monthly from January 1976 to January 1977. A plant was considered to be overgrown if at least 20% of its thallus was covered with either blue-green algae or mixed macro-algae.

ments on boulder surfaces which I will discuss later, coincided with these seasonal peaks in epiphyte overgrowth.

Neither *Rhodoglossum* nor *G. canaliculata* were heavily overgrown by epiphytes. At most, 20–30% of the plants of either species collected had epiphytes. This amount of overgrowth occurred during only the single month of August for each species. This difference in epiphyte load is probably a result of differences in the surface texture of the thalli of these four species. *G. leptorhynchos* and *Gelidium* have highly branched thalli and a spiny surface providing good sites for the attachment of epiphytes. The thalli of *Rhodoglossum* and *G. canaliculata* are comparatively smooth, making it difficult for epiphytes to attach. I do not know if these plants possess any chemical defenses against epiphyte overgrowth.

Although I was not able to verify experimentally that epiphytes cause differential mortality, my obser-

vations indicate that two of the three middle successional species studied are more susceptible than the late successional species to overgrowth by epiphytes. These epiphytes appear to be directly or indirectly responsible for the death of individuals of these species and in part, for their replacement in time by the late successional species, *G. canaliculata*.

Mechanism operating in small clearings

As described earlier, a number of 100-cm² plots were cleared in solid beds of the dominant alga, *Gigartina canaliculata*, in order to study the processes by which small clearings are recolonized. I randomly assigned several treatments to these cleared areas and monitored six uncleared plots as well. In four of the cleared plots, the canopy of surrounding *G. canaliculata* plants was kept cut back. As previously described, these surrounding plants grow long during summer months and cover the cleared patches, shading and/or abrading other algae which have settled into the plot either shortly after it was cleared or during the winter months when surrounding plants defoliate and the plot becomes open for colonization. In another four cleared plots, I removed both this overhanging canopy and the *Ulva* which settled and grew up in the plots. Eight other cleared plots were not manipulated after initial clearing and served as controls for the manipulations performed. Recolonization of these control plots has already been discussed. Six more plots were cleared on nearby boulders in July 1976 in order to determine if the algae which recruited and grew up in the plots cleared in February 1975 would interfere with subsequent recruitment during the next settlement season, and to control for differences between years in the levels of algal recruitment. These plots had no canopy of surrounding *G. canaliculata* plants and correspond to the minus canopy plus *Ulva* treatments in February 1975.

By comparing changes in plots which were not manipulated after initial clearing and which were seasonally covered by a canopy of *G. canaliculata*, with changes in plots from which this canopy was removed throughout the study, the influence of the canopy could be determined. By comparing changes in algal populations in cleared plots from which the canopy from surrounding plants was removed, allowing a dense cover of *Ulva* to develop, with changes in similar plots from which both the canopy and *Ulva* were removed, I was able to test the effects of the early species, *Ulva*, on the subsequent recruitment of algae to small clearings. Finally, by monitoring changes in the uncleared plots it was possible to determine the resistance to invasion of solid beds of the dominant species, *G. canaliculata*, once they are established. Changes in algal populations in these treatments from February 1975 to January 1977 are plotted in Fig. 11. The graph of the unmanipulated clearings (Fig. 3) is redrawn here (Fig. 11B) for comparative purposes.

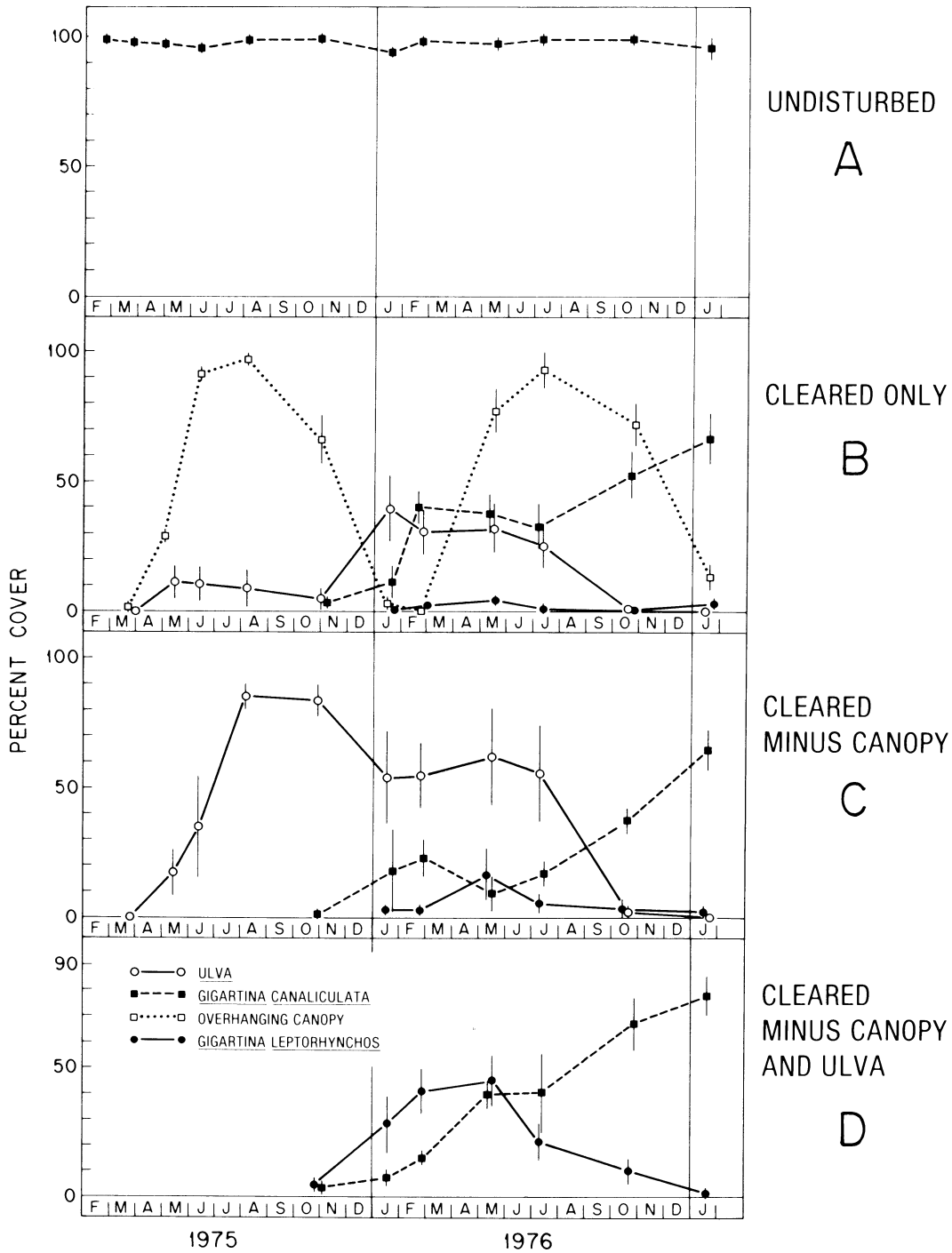


FIG. 11. Effects of various manipulations on the recruitment and growth of algae in 100-cm² plots cleared in solid beds of *Gigartina canaliculata*. Sixteen plots were cleared in February 1975 and five others were left undisturbed. All were monitored periodically until the end of the experiment in January 1977. Eight of the cleared plots were not further manipulated, in four others the overhanging canopy of surrounding adult *Gigartina canaliculata* plants was kept cut back, and in the remaining four, both this canopy and the *Ulva* which recruited into the plots were removed. Data are mean percent covers of algae in the plots and of the overhanging canopy. The mean \pm one standard error of the mean are indicated. All limpets and chitons which recruited into the plots were removed at each sampling date.

TABLE 6. Numbers of *Gigartina leptorhynchos* plants present in experimental *Gigartina canaliculata* clearings. Sixteen 100-cm² plots were cleared in February 1975 and six more in July 1976. Various treatments were assigned to these plots as noted below. Mean percent closure of plots due to vegetative ingrowth of surrounding *G. canaliculata* adults is also presented. A boulder on which two of the July 1976 quadrats were established was lost in a storm in March 1977.

Treatment	Plot	1 Nov. 1975	19 Jan. 1976	26 Feb. 1976	17 May 1976	13 Jul. 1976	23 Oct. 1976	20 Jan. 1977	20 May 1977
Number of plants									
A. Cleared Feb. 1975									
- Canopy	1	0	1	1	0	0	1	0	0
+ <i>Ulva</i>	2	0	15	4	3	3	0	3	2
	3	0	1	0	0	0	1	1	1
	4	0	3	9	8	4	3	3	0
		Mean percent closure							
		1.3	18.0	22.9	9.8	19.5	37.8	64.3	93.3
Number of plants									
- Canopy									
- <i>Ulva</i>	1	16	42	35	25	7	0	0	0
	2	3	20	14	10	8	3	0	2
	3	5	22	20	18	11	8	8	2
	4	3	15	11	8	6	5	0	0
		Mean percent closure							
		3.8	7.8	14.8	39.5	40.5	66.3	77.6	97.5
Number of plants									
+ Canopy									
+ <i>Ulva</i>	1	0	0	13	8	6	9	7	1
	2	0	0	0	0	5	0	0	0
	3	0	0	2	1	1	1	0	1
	4	0	11	17	3	3	0	0	3
	5	0	4	4	1	1	0	0	0
	6	0	3	4	4	1	8	5	1
	7	0	1	2	2	0	8	7	4
	8	0	0	11	3	1	1	1	2
		Mean percent closure							
		2.9	11.5	40.3	37.7	32.6	52.3	66.4	93.0
Number of plants									
B. Cleared July 1976									
- Canopy	1							6	lost
+ <i>Ulva</i>	2							3	lost
	3							1	9
	4							4	5
	5							8	12
	6							3	12
		Mean percent closure							
								3.8	23.0
C. Not cleared									
Number of plants									
1-5	None invaded solid bed of <i>Gigartina canaliculata</i> between Feb. 1975 and May 1977								

In small clearings, the canopy of surrounding *G. canaliculata* plants seasonally shaded and reduced the cover of *Ulva* which had recruited to the opening (Fig. 11B vs. 11C). When the *G. canaliculata* canopy disappeared on the control clearings (Fig. 11B) due to natural defoliation in the fall and winter of 1975-76, new *Ulva* recruited and surviving plants grew up, reaching an average of 40% cover in the canopy removal plots in January 1976. *Ulva* gradually disappeared from both treatments by October 1976. This is presumably due to desiccation caused by the onset of afternoon low tides in October and to grazing by large grazers including crabs, sea hares, and fish.

The presence of a dense bed of *Ulva* inhibited the

recruitment of the middle successional species, *G. leptorhynchos*, as it did in the concrete block experiment. While *G. leptorhynchos* recruited to all cleared plots between October 1975 and January 1976, its percent cover was greatest when both the surrounding *G. canaliculata* canopy and *Ulva* were removed (Fig. 11D). The cover of this plant was less in the canopy removal plots with a dense cover of *Ulva* ($t = 3.01$, $P < .0125$) and in the control clearings which were seasonally covered by a *G. canaliculata* canopy and had some *Ulva* ($t = 5.59$, $P < .001$).

The *G. leptorhynchos* plants in all treatments became overgrown with macro-epiphytes during the summer months (May through September) of 1976 and

TABLE 7. Mean growth of transplanted algal sporelings with and without an overlying canopy of the dominant alga, *Gigartina canaliculata*. Data are mean growth increments (and SE) in 120 d between 18 January and 17 May 1976. Two-way analysis of covariance is presented below. Because the design is not orthogonal, the sums of squares of the main effects and two-way interactions do not sum to the corresponding subtotals for each category (Nie et al. 1975).

Species	<i>G. canaliculata</i> canopy removed		With <i>G. canaliculata</i> canopy		Mean reduction of growth by canopy (cm)
	N	Growth in cm (SE)	N	Growth in cm (SE)	
<i>G. canaliculata</i>	8	5.8 (.8)	9	4.9 (1.1)	.9
<i>Rhodoglossum affine</i>	6	3.1 (.6)	8	1.5 (.4)	1.6
<i>G. leptorhynchos</i>	5	9.1 (2.6)	7	6.2 (2.9)	2.9
<i>Gelidium coulteri</i>	8	3.5 (.6)	10	.6 (.3)	2.9

Source of variation	Sum of squares	df	Mean square	F	Significance level
Covariates					
Initial size	228.882	1	228.882	18.534	0.001
Main effects	180.321	4	45.080	3.651	0.011
Canopy	72.559	1	72.559	5.876	0.018
Species	102.671	3	34.224	2.771	0.050
Two-way interactions					
Canopy-species	31.270	3	10.423	0.844	0.999
Explained	440.473	8	55.059	4.459	0.001
Residual	642.149	52	12.439		
Total	1082.622	60	18.044		

most had disappeared from the cleared plots by January 1977. The numbers of individuals of this plant in all treatments at each sampling date from November 1975 to May 1977 are shown in Table 6.

Gigartina canaliculata grew into all cleared plots, filling over 90% of the space in all clearing treatments by the end of the experiment in May 1977 (Table 6). As mentioned before, this growth was predominantly vegetative; less than 10 plants in all the clearings grew from settled spores. There was no significant difference between treatments in the rate at which *G. canaliculata* grew into the plots. While a bed of *Ulva* inhibits the recruitment of this plant from spores, as demonstrated in the concrete block experiments, I could not detect any significant effects of *Ulva* on the vegetative spread of adult *G. canaliculata* plants. The significance of any effect, either negative or positive, would be dubious in any case; it could be argued that cropping the *G. canaliculata* canopy, which allowed for a dense cover of *Ulva*, might either enhance or retard the vegetative spread of *G. canaliculata*.

Once a solid bed of *G. canaliculata* is established as in the uncleared plots, it resists invasion by all other species. There was no recruitment of early or middle successional species into these plots (Fig. 11A).

The closure of the February 1975 clearings by the vegetative spread of *G. canaliculata* inhibited the recruitment of *G. leptorhynchos*. The mean number of *G. leptorhynchos* plants which recruited to and survived in the July 1976 clearings until May 1977 (or until January 1977 in the case of the two quadrats which were lost) was greater ($\bar{x} = 7.8$, $SD = 3.8$) than

the mean number of new surviving recruits to the February 1975 clearings ($\bar{x} = .75$, $SD = .96$) during the same period (Table 6; $t = 3.62$, $P < .005$). Recruitment of other species was too low to detect any inhibition by the spreading cover of *G. canaliculata*.

To determine if the presence of a canopy of *Gigartina canaliculata* has a negative effect on the growth of its own sporelings and those of middle successional species which are already established in small clearings, I transplanted sporelings of each of the perennial red algae into 3-cm-diameter clearings in an otherwise solid bed of *G. canaliculata*. The canopy over about half of the sporelings of each species was cut off while an intact canopy shaded the others. The net growth of each transplanted sporeling was measured over a 120-day period from 18 January to 17 May 1976. I analyzed for differences in these data between treatments and between species of sporelings using a two-way analysis of covariance with initial length as a covariate.

A canopy of *G. canaliculata* significantly reduced the growth of all perennial red algae sporelings including its own (Table 7). There seems to be a tendency for it to inhibit the growth of its own sporelings less than those of other species, though this trend was not significant. There was a barely significant difference in the growth rates of the different species over this period. *G. leptorhynchos* grew most rapidly, followed by *G. canaliculata*. *Rhodoglossum* and *Gelidium* grew most slowly. The effect of the canopy might well have been more marked if the experiment had been conducted during summer months when algal growth is most rapid.

DISCUSSION

The experimental results presented here indicate that when a space is cleared in the low intertidal, most species in the area have the capacity to colonize immediately if spores are available. Certain species, in this case green algae, will usually be the first to colonize and dominate because of evolved life history characteristics such as the production of large numbers of motile propagules (less seasonal than other algae) which grow rapidly to maturity. Once these early colonists have become established, they resist the invasion of subsequent red algal colonists or suppress the growth of those already on the site. This inhibition appears to last as long as the earlier species remain healthy and undamaged. Middle successional red algae have a similar inhibitory effect on the late successional red alga which eventually dominates.

In a comprehensive review of successional theory and field work, Connell and Slatyer (1977) have delineated three alternative models of ecological succession. These are the facilitation model, the tolerance model, and the inhibition model.

Three models of ecological succession

The facilitation model assumes that only certain early successional species are able to colonize the site under the conditions that occur immediately after a disturbance which opens space. The tolerance and inhibition models assume that any species, including those which usually appear later, can colonize at the beginning. All models agree, however, that certain species will usually appear first because they have evolved colonizing characteristics such as the ability to produce large numbers of propagules which are dispersed over relatively large areas. These propagules grow rapidly to maturity shortly after colonizing the open space or can remain dormant for long periods of time until conditions become favorable for successful growth and reproduction. An important difference in the models lies in the mechanisms which are assumed to determine which species appear later in a successional sequence. In the facilitation model, the early successional species modify the environment so that it is more suitable for late successional species to invade and grow to maturity, while making the site less suitable for their own offspring. This sequence continues until the resident species which dominates the site no longer modifies it in ways that facilitate the invasion and growth of a different species.

According to the tolerance model, the modifications in the environment caused by the presence of early successional species neither increase nor decrease the rates of recruitment or growth to maturity of later colonists. Species which appear later may colonize either at the very beginning or at some later time and then grow slowly. These later species are more efficient competitors for limited resources than early species. They are able to survive and grow despite the pres-

ence of early species which, while healthy and undamaged, reduce the available resources of light and space which can be used by later colonists. The end point of the sequence is reached when the most shade-tolerant species available occupies the site and casts shade so deep that no other species can invade. This shade is often so deep that even the resident species' own offspring cannot survive. In both the facilitation and tolerance models, early species are killed by competition with later colonists which can utilize the limiting resource more efficiently. The latter grow up and shade or otherwise deprive the former of resources.

In contrast to the facilitation model in particular, the inhibition model holds that once early colonists secure most of the available space/light, they resist the invasion of subsequent colonists or suppress the growth of those which are present from the beginning. Early colonists are not killed by competition with late successional species as predicted by the tolerance model. Rather, early colonists can successfully resist invasion as long as they remain healthy and undamaged. At this point the inhibition of subsequent recruitment by early species would tend to truncate successional sequences at an early stage.

The Ellwood algal community: inhibition by early colonists

Clearly the classical facilitation model does not apply to this algal community. There is also little evidence to support the tolerance model. I have demonstrated that early successional species, usually assumed to be competitively inferior to later successional species, can successfully hold space against their invasion. This pattern of inhibition by early colonists is relatively common in communities of sessile organisms, both terrestrial and marine. Analogous terrestrial examples have been reviewed by Drury and Nisbet (1973) and Connell and Slatyer (1977). Niering and Egler (1955) and Niering and Goodwin (1974) have documented the 45-yr resistance of *Viburnum* thickets to invasion by trees. Marine examples in which the establishment of sessile species is inhibited directly by other species that arrive first include: barnacles, hydroids, and bryozoans by the tunicate, *Styela* (Sutherland 1974, 1978, Sutherland and Karlson 1977, see Dean 1977 for other epifaunal examples); larvae of infaunal species by dense adult assemblages (Woodin 1976); coralline algae and the brown alga, *Hedophyllum sessile*, by a cover of *Ulva* and other ephemeral algal species (Dayton 1975, Paine 1977); the brown alga, *Fucus serratus*, and the red alga, *Chondrus crispus*, by the green alga, *Enteromorpha* (Menge 1975, Lubchenco and Menge 1978); and invertebrate fouling organisms by a cover of filamentous algae (Pyefinch 1950). In all of these examples the seasonality of recruitment is crucial in determining the sequence in which species colonize newly cleared space. The species which is least seasonal in its recruitment will

usually become established first, particularly if it is very fecund and grows rapidly. Its early dominance of the site has a large effect on the rates and patterns of subsequent successional changes.

Most studies of intertidal and subtidal algal succession have found little or no evidence that the facilitation model plays a role in the observed temporal changes in community structure (Lee 1965, Huvé 1969, Chapman 1974, Dayton 1975, Foster 1975, Kain 1975, Menge 1975, Harlin and Lindbergh 1977, Lubchenco and Menge 1978). One possible exception comes from a study of high intertidal algal communities on the Atlantic coast of France. Hatton (1938) reported that a mat of the early successional green alga, *Enteromorpha*, increased the successful recruitment of the dominant brown alga, *Ascophyllum*. Extremes of light intensity, heat, and desiccation encountered in the high intertidal may have to be ameliorated by the presence of a mat of early successional species before any other species can colonize and survive. As pointed out above, however, Menge (1975, also see Lubchenco and Menge 1978) working in a very similar community on the Atlantic coast of New England experimentally demonstrated that a mat of *Enteromorpha* inhibited the successive invasion of red and brown algae. If Hatton's observation is a true case of facilitation, this situation is analogous to successional patterns on glacial till in Alaska. There too, though no experimental evidence is available, early colonists appear to modify extreme conditions which exist on a site following glacial recession (i.e., extreme pH and soil nitrogen levels) and thus allow for the successful recruitment of various tree species (Crocker and Major 1955).

While many successional sequences seem to be characterized by the inhibition of successive invasions, it is usually true that the species which colonize first are replaced by other species through time on a site. The mechanism proposed by Connell and Slatyer (1977) seems to account for species replacements during succession in the intertidal algal community which I studied. Certain species characteristically dominate late in a successional sequence because they survive for a long time; that is, they withstand the suppression of species which dominate early in a successional sequence and then grow to maturity when the death of an early individual frees space. For this mechanism to produce the vegetational sequences commonly observed, species which dominate early in succession must be more susceptible, both to the rigors of the physical environment and to grazers, predators and/or parasites, than late successional species. If so, there is no need to evoke the facilitation model of Clements (1916) and Odum (1969) or the tolerance model which suggests that predictable sequences result from the successive invasion of increasingly efficient competitors as proposed by MacArthur and Connell (1966) and Horn (1974). Early successional species may be just

as efficient as long-lived species at utilizing the available space, particularly if the length of time that it is held, which is a measure of this ability, is scaled to the generation time of the species.

Early successional green algae are short-lived because they are killed by desiccation stress and grazers. If protected against these sources of mortality, *Ulva* appears to live for long periods, resisting the invasion of red algae. If unprotected, however, it is replaced by perennial red algae which are less susceptible to these rigors and can regrow from very persistent holdfasts if damaged. In all four of these species of red algae, recruitment from spores is restricted to a 3–4 mo period in the fall and early winter. Only during this period can these species become established in openings in the *Ulva* canopy. All four colonize during the first recruitment season following initial clearing and grow to adult size over the next summer. Of the three middle successional species, *Gigartina leptorhynchos* and *Gelidium* developed sufficient cover to slow the development of dominance by *Gigartina canaliculata*. *Rhodoglossum* never became common enough to exert this effect.

Through vigorous vegetative spreading *Gigartina canaliculata* gradually takes over the space held by these middle successional species as they are overgrown by epiphytes or killed by desiccation stress and removed by waves. The developing monoculture of *G. canaliculata* resists the reinvasion of both early and middle successional species. This dominance develops much more slowly if, as on the concrete blocks, all the initial recruitment to the substrate is from spores. Dominance is hastened if surrounding adult plants or survivors within the patch can begin to fill it vegetatively from the start, as occurred in the small clearings. Both situations occur naturally in this system (Sousa 1977). If a large boulder is overturned by waves it remains so for long periods and all sessile macroorganisms are killed. When righted, recolonization is entirely from dispersed propagules. On smaller boulders which do not remain overturned for as long a time, some individuals survive and regrow vegetatively. Dominance by a species develops much more rapidly with this initial advantage.

This observation seems especially relevant to the interpretation of developmental studies of marine fouling communities. In contrast to the commonly observed monopolization of space by a few species in the rocky intertidal, studies of fouling communities often reveal no clear dominants (Sutherland and Karlsson 1977). This difference in the observed behavior of the two systems may be attributable in part to the use, in most fouling studies, of spatially-isolated artificial settling surfaces which eliminate the potential for vegetative colonization of the sort described above. Vegetative colonization and regrowth are very important to the acquisition and dominance of space in the rocky intertidal. The present study and others (Lubchenco

and Menge 1978) have demonstrated this fact for low intertidal algae; Paine (1974) has shown that much of the spread of dominant mussel beds into cleared spaces is caused by the lateral movements of adults as the clumps expand.

The persistence and coexistence of early and middle successional species are dependent upon localized disturbances which open space in the system (Sousa 1979). While dominance is developing on some boulders, others are being overturned by waves. These newly cleared surfaces are colonized by the offspring of adult populations which are going locally extinct on undisturbed boulders.

Most successional theory to date has ignored the role of grazers in accounting for patterns of species replacements during succession in plant communities. Instead, workers have concentrated mainly on plant-plant interactions with the result that competition for limited resources (e.g., light, nutrients, space) has assumed overwhelming importance (see, for example, Horn 1974). This oversight emphasizes the important distinction between the tolerance and inhibition models of ecological succession, in terms of the relative importance of different selective pressures which the models predict to be acting on individuals of sessile species in natural communities.

The tolerance model argues that competition for limited resources is a major selective agent, calling for increasingly efficient use of resources. The inhibition model, on the other hand, predicts that an individual will be most successful if it can resist death by local physical disturbances and attack by natural enemies. Unfortunately in terms of testability, both models predict similar continua of adaptations. The tolerance model predicts a continuum, from species which grow rapidly to maturity, produce many vagile offspring, and are short-lived as a result of energetic tradeoffs, to species which grow slowly and produce fewer offspring but over a long period of time. The former are postulated to be inefficient in the utilization of resources, relying on migration to local areas of high resource abundance (e.g., areas cleared by disturbances) in order to persist (Hutchinson's fugitive species, 1951); the latter can survive, grow, and reproduce effectively at lower resource levels. This interpretation has prompted the formulation of large numbers of models to explain various life history strategies (see Stearns 1976, 1977 for recent reviews).

The range of adaptations predicted by the inhibition model of succession is surprisingly similar to those outlined above, though caused by quite different selective forces. At one end of the continuum are species which are poorly defended against damage or death by local disturbances or natural enemies and thus do not live a long time. These species produce many vagile offspring which grow rapidly to maturity and rely on an escape in space from these sources of mortality. At the other end of the continuum are species which pro-

duce protective or toxic chemicals to defend against natural enemies (Feeny 1970, 1975, Irvine 1973, Levin 1976) and/or develop defensive structures to resist damage by physical disturbances (e.g., hard wood in late successional trees to resist blowdowns; perennating holdfasts in algae), grazers (e.g., thorns or spines on some terrestrial plants; dense thallus structure of some marine algae) or predators (e.g., thick tests in barnacles, Dayton 1971; large body size in mussels, Paine 1976). These species grow slowly and live a long time. Cates and Orians (1975) and Feeny (1975) present a more thorough discussion of this idea as it relates to terrestrial plant communities. Undoubtedly, species are subjected to all three selective forces: competition, attack by natural enemies, and damage by physical disturbances. In question is the relative importance of each in different communities (Connell 1975).

This study and others have demonstrated that natural enemies and local physical disturbances are often very important in determining temporal patterns of species replacements. Menge (1975, also see Lubchenco and Menge 1978) working in a New England intertidal system, found that selective grazing by littorine snails on an early successional species of green alga, *Enteromorpha*, accelerated the invasion of eventual dominant species of brown and red algae. Cates and Orians (1975) found that generalist herbivorous slugs ate early successional species in preference to species that occurred in late successional stages in the coniferous forests of the northwestern United States. Snowshoe hare grazing suppresses the growth of birch seedlings, allowing balsam fir to dominate regenerating forests in northern New England (Sprugel 1974). Eastern tent caterpillars inflict heavy defoliation damage on black cherry seedlings in young hardwood stands in central Massachusetts. The fast-growing cherries are defoliated year after year, soon becoming overtopped by oak and maple that are apparently more resistant to insect attack (Spurr and Barnes 1973, p. 300).

Some sessile animal communities show the same pattern. Species replacements in marine fouling communities appear to be a result of differential susceptibility to periodic inundations by freshwater during storms and selective predation by fish (Sutherland 1974). Connell (1973) has evidence that the faster-growing species of corals on the Great Barrier Reef are more heavily attacked by destructive boring organisms. Fishelson (1973) and Glynn (1976) have shown that fast-growing branched corals are more susceptible to desiccation stress than more slow-growing, massive, brain-like corals. Dart (1972) has suggested that urchins graze away mats of filamentous algae allowing corals to recruit.

In other communities of sessile organisms, species replace others through direct interference competition. Mechanisms include direct crushing or undercutting (e.g., barnacles, Connell 1961a, b); overgrowth

of competitors, which smothers or shades them to death (e.g., mussels over barnacles, Dayton 1971; in corals, Connell 1973, 1976; in bryozoans, Stebbing 1972, 1973; in sponges, Rützler 1965, 1970; Dayton et al. 1974; in epifaunal marine invertebrate communities, Osman 1977); exocoelenteric digestion of competitors (e.g., in corals, Connell 1973, 1976, Lang 1973); and the killing of competitors with toxic exudates (e.g., allelopathy in terrestrial plant communities, Muller 1966, McPherson and Muller 1969; allelopathy in cryptic invertebrate communities under coral heads, Jackson and Buss 1975). What distinguishes these communities from those mentioned above in which direct competition does not seem as important, is a question which remains to be answered.

In the algal community I studied, some direct interference competition does seem to occur in small clearings. Adult *Gigartina canaliculata* plants which grow long during benign summer months form a nearly closed canopy over small clearings. This canopy shades or, through whiplash, abrades off *Ulva* plants which recruited when the plot was more open. It also slows the growth of red algal sporelings. Since large clearings eventually become a mosaic of small openings as long-lived red algae colonize and grow, this form of competition is probably important in eliminating remaining individuals of early and middle species late in a successional sequence. This late stage is when grazers and physical stress are likely to be less important sources of mortality. Plants which surround small openings probably ameliorate harsh physical conditions which would ordinarily kill early species, and small patches of early successional species may be difficult for searching grazers to locate. Desiccation stress and certain species of grazers were demonstrated to be important in eliminating early species in the younger stages of succession when these species were more abundant and site conditions more open.

It would be misleading, however, to label *Gigartina canaliculata* a competitive dominant in the usual sense, since direct competition with earlier colonists plays a relatively small role in its establishment. It does not kill a large proportion of the individuals of the species it replaces by shading, overgrowth, or whiplash as the term competitive dominant implies. *G. canaliculata* dominates because of what might be called its "grab and hold open space" strategy, its ability to secure open space made available by the death of individuals of other species and to hold it against potential invaders. It maintains and expands this occupancy by vegetative propagation. I suggest that the use of the term "competitive dominant" be restricted to species which dominate by virtue of having monopolized the limiting resource through direct interference competition (e.g., mussels competitively dominate exposed mid-intertidal sites by overgrowing

algae and barnacles; Dayton 1971, Paine 1974, Lubchenco and Menge 1978).

Some grazers do not appear to be very important in altering or accelerating succession in the algal community I studied. The limpet exclusion experiments showed that limpets may temporarily enhance the recruitment of barnacles on newly cleared surfaces by grazing off algal sporelings and diatoms which inhibit their recruitment. However, the presence of limpets has little long-term effect on the development of the algal community. Though I did not manipulate the density of the chiton, *Mopalia muscosa*, it was relatively rare at Ellwood (Table 2) and I did not observe any strong effects of its grazing activities. Dayton (1975) working in the low intertidal in the Pacific Northwest also claimed that molluscan herbivores were ineffective at controlling their algal resources. One reason for the apparent ineffectiveness of these herbivores in controlling algal populations in the lower intertidal both there and in southern California is that predation on these small molluscs by starfishes, octopuses, and fishes reduces the density and average body size of their populations (Fawcett 1979). The algae which settle densely and grow rapidly in these lower zones swamp the ability of these herbivores to control them. The algae quickly grow to a size invulnerable to the grazing activities of those grazers which are most likely to affect the settling algal spores and sporelings (Dayton 1970, Nicotri 1974, 1977). This is in contrast to large herbivores such as the crab, *Pachygrapsus*, the sea hare, *Aplysia*, the fish, *Girella*, and the urchin, *Strongylocentrotus purpuratus*, which can graze effectively on the thalli of adult sporophytes and gametophytes. In addition to losses caused by predation, limpets may actually be out-competed for space by sessile invertebrates and algae which have grown invulnerable to their grazing (Dayton 1971, Choat 1977, Dixon 1978, W. P. Sousa, *personal observation*).

These patterns differ markedly from those found in the mid to high intertidal. There, experiments have shown that grazing by small molluscs including limpets and littorine snails has a strong effect on the distribution and abundance of algae (Jones 1948, Lodge 1948, Burrows and Lodge 1950, Southward 1956, 1964, Castenholz 1961, Haven 1973, Cubit 1974, Menge 1975). In the absence of predation, limpets are generally larger and more dense in the mid to high intertidal (Frank 1965; Nicotri 1974, for two species; Dixon 1978) so that the control of algae which grow more slowly at these tidal levels is possible. Also in contrast to my findings in the low intertidal, manipulations of limpet densities in the high intertidal (Hatton 1938, Connell 1961b, Dayton 1971, Menge 1976) have shown that these larger animals bulldoze barnacles off the surfaces of rocks, reducing their abundance locally rather than increasing it.

The successional mechanisms operating in marine

intertidal algal communities are not those which would be predicted by more traditional models of this process. Changes in this community following a disturbance are largely the result of the life history characteristics of individual species, in particular, differential susceptibility to physical stress and attack by natural enemies. Future experimental investigations of successional patterns are bound to yield results which will challenge our preconceptions about the forces which structure natural communities.

ACKNOWLEDGMENTS

This paper is based on a dissertation submitted in partial fulfillment of the requirements for the Ph.D. in the Department of Biological Sciences, University of California, Santa Barbara. I thank my major advisor, Joseph H. Connell, for his friendship, sense of humor, criticisms, and generous support. His sharing of ideas about natural communities and ways of testing them has been and will continue to be a most stimulating and enjoyable experience. The other members of my thesis committee, William W. Murdoch, Allan Oaten, and Paul K. Dayton, provided constructive criticism and encouragement throughout my research program. Discussion with S. Arnold, A. Blaustein, J. Dixon, P. Ebsworth, M. Fawcett, S. Holbrook, G. Irvine, J. Kastendiek, A. Kuris, D. Landenberger, S. Levin, J. Lubchenco, C. Onuf, R. Osman, C. H. Peterson, M. Quammen, P. Sale, S. Schroeter, A. Sih, R. Slatyer, R. Warner, and J. Watanabe have helped to clarify my thinking and improve the manuscript.

Many people have helped with the field work: in particular I thank V. Berg, L. Chavez, K. Davis, J. Dixon, M. Fawcett, W. Kajimura, W. Muchenje, S. Schroeter, D. Spiller, and J. Norris who helped with algal taxonomy. R. Strange of North American Weather Consultants, Goleta, California, supplied unpublished data on wave heights in the Santa Barbara Channel. Signal Oil, Burmah Oil, and Aminoil Companies kindly provided access to the seashore at Ellwood.

Research support was provided by the National Science Foundation Doctoral Dissertation Research Grant #OCE 75-23635 and a grant from the Ford Foundation to Drs. Connell and Murdoch to support graduate education in ecology.

LITERATURE CITED

- Burrows, E. M., and S. M. Lodge. 1950. A note on the inter-relationships of *Patella*, *Balanus* and *Fucus* on a semi-exposed coast. Annual Report of the Marine Biological Station, Point Erin, Isle of Man 62:30-34.
- Carefoot, T. H. 1967. Growth and nutrition of *Aplysia punctata* feeding on a variety of marine algae. Journal of the Marine Biological Association of the United Kingdom 47:565-589.
- . 1970. A comparison of absorption and utilization of food energy in two species of tropical *Aplysia*. Journal of Experimental Marine Biology and Ecology 5:47-62.
- Castenholz, R. W. 1961. The effects of grazing on marine littoral diatom populations. Ecology 42:783-794.
- Cates, R. G., and G. H. Orians. 1975. Successional status and the palatability of plants to generalized herbivores. Ecology 56:410-418.
- Chapman, A. R. O. 1974. The ecology of macroscopic marine algae. Annual Review of Ecology and Systematics 5:65-80.
- Choat, J. H. 1977. The influence of sessile organisms on the biology of three species of acmaeid limpets. Journal of Experimental Marine Biology and Ecology 26:1-26.
- Clements, F. E. 1916. Plant succession. Publication 242, Carnegie Institute of Washington, Washington, District of Columbia, USA.
- Connell, J. H. 1961a. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42:710-723.
- . 1961b. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecological Monographs 31:61-104.
- . 1973. Population ecology of reef-building corals. Pages 205-245 in O. A. Jones and R. Endean, editors. Biology and geology of coral reefs. Biology 1, Volume 2. Academic Press, New York, New York, USA.
- . 1975. Some mechanisms producing structure in natural communities: A model and evidence from field experiments. Pages 460-490 in M. L. Cody and J. Diamond, editors. Ecology and evolution of communities. Belknap Press, Cambridge, Massachusetts, USA.
- . 1976. Competitive interactions and the species diversity of corals. Pages 51-58 in G. P. Mackie, editor. Coelenterate ecology and behavior. Plenum Press, New York, New York, USA.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111:1119-1144.
- Cooper, W. S. 1913. The climax forest of Isle Royale, Lake Superior, and its development. Botanical Gazette 55:1-44, 115-140, 189-235.
- Cowles, H. C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Botanical Gazette 27:97-117, 167-202, 281-308, 361-391.
- Crocker, R. L., and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. Journal of Ecology 43:427-488.
- Cubit, J. D. 1974. Interactions of seasonally changing physical factors and grazing affecting high intertidal communities on a rocky shore. Dissertation. University of Oregon, Eugene, Oregon, USA.
- Dart, J. K. G. 1972. Echinoids, algal lawn and coral recolonization. Nature 239:50-51.
- Dayton, P. K. 1970. Competition, disturbance, and community structure: The allocation and subsequent utilization of space in a rocky intertidal community. Dissertation. University of Washington, Seattle, Washington, USA.
- . 1971. Competition, disturbance and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41:351-389.
- . 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecological Monographs 45:137-159.
- Dayton, P. K., G. A. Robilliard, R. T. Paine, and L. B. Dayton. 1974. Biological accommodation in the benthic community at McMurdo Sound, Antarctica. Ecological Monographs 44:105-128.
- Dean, T. A. 1977. Succession in a marine fouling community: changes in community structure and mechanisms of development. Dissertation. University of Delaware, Newark, Delaware, USA.
- Dixon, J. D. 1978. Determinants of the local distribution of four closely-related species of herbivorous marine snails. Dissertation. University of California, Santa Barbara, California, USA.
- Drury, W. B., and I. C. T. Nisbet. 1973. Succession. Journal of the Arnold Arboretum 54:331-368.
- Egler, F. E. 1954. Vegetation science concepts. I. Initial floristic composition—a factor in old-field vegetation development. Vegetatio 4:412-417.
- Fawcett, M. H. 1979. The consequences of latitudinal variation in predation for some marine intertidal herbivores. Dissertation. University of California, Santa Barbara, California, USA.

- Feeny, P. P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* **51**:565–581.
- . 1975. Biochemical coevolution between plants and their insect herbivores. Pages 3–19 in L. E. Gilbert and P. H. Raven, editors. *Coevolution of plants and animals*. University of Texas Press, Austin, Texas, USA.
- Fishelson, L. 1973. Ecological and biological phenomena influencing coral-species composition on the reef tables at Eilat (Gulf of Aqaba, Red Sea). *Marine Biology* **19**:183–196.
- Foster, M. S. 1975. Algal succession in a *Macrocystis pyrifera* forest. *Marine Biology* **32**:313–329.
- Frank, P. W. 1965. The biodemography of an intertidal snail population. *Ecology* **46**:831–844.
- Frings, H., and C. Frings. 1965. Chemosensory bases of food-finding and feeding in *Aplysia juliana* (Mollusca, Opisthobranchia). *Biological Bulletin* **128**:211–217.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* **53**:7–26.
- . 1927. Further views of the succession concept. *Ecology* **8**:299–326.
- Glynn, P. W. 1976. Some physical and biological determinants of coral community structure in the eastern Pacific. *Ecological Monographs* **46**:431–456.
- Greig-Smith, P. 1964. *Quantitative plant ecology*. Second edition. Plenum Press, New York, New York, USA.
- Harlin, M. M. 1973. Transfer of products between epiphytic marine algae and host plants. *Journal of Phycology* **9**:243–248.
- Harlin, M. M., and J. M. Lindbergh. 1977. Selection of substrata by seaweeds: optimal surface relief. *Marine Biology* **40**:33–40.
- Hatton, H. 1938. Essais de biologie explicative sur quelques especes intercotidales d'algues et d'animaux. *Annales de l'Institut Océanographique*, Monaco **17**:241–348.
- Haven, S. B. 1973. Competition for food between the intertidal gastropods *Acmaea scabra* and *Acmaea digitalis*. *Ecology* **54**:143–151.
- Hiatt, R. M. 1948. The biology of the lined shore crab, *Pachygrapsus crassipes*. *Pacific Science* **2**:135–213.
- Horn, H. S. 1974. The ecology of secondary succession. *Annual Review of Ecology and Systematics* **5**:25–37.
- Hutchinson, G. E. 1951. Copepodology for the ornithologist. *Ecology* **32**:571–577.
- Huvé, P. 1969. Le stade initial et son importance réelle dans le peuplement algal des surfaces rocheuses du littoral marin. *Proceedings of the International Seaweed Symposium* **6**:201–211.
- Irvine, G. V. 1973. The effect of selective feeding by two species of sea urchins on the structuring of algal communities. Thesis. University of Washington, Seattle, Washington, USA.
- Jackson, J. B. C., and L. Buss. 1975. Allelopathy and spatial competition among coral reef invertebrates. *Proceedings of the National Academy of Science of the USA* **72**:5160–5163.
- Jones, N. S. 1948. Observations and experiments on the biology of *Patella vulgata* at Port St. Mary, Isle of Man. *Proceedings and Transactions of the Liverpool Biological Society* **56**:60–77.
- Kain, J. M. 1975. Algal recolonization of some cleared subtidal areas. *Journal of Ecology* **63**:739–766.
- Lang, J. 1973. Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift. *Bulletin of Marine Science* **23**:260–279.
- Lee, R. K. S. 1965. Development of marine benthic algal communities on Vancouver Island, British Columbia. Pages 100–120 in R. L. Taylor and R. A. Ludwig, editors. *The evolution of Canada's flora*. University of Toronto Press, Toronto, Canada.
- Levin, D. A. 1976. The chemical defenses of plants to pathogens and herbivores. *Annual Review of Ecology and Systematics* **7**:121–160.
- Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Science of the USA* **71**:2744–2747.
- Lodge, S. M. 1948. Algal growth in the absence of *Patella* on an experimental strip of foreshore, Port St. Mary, Isle of Man. *Proceedings and Transactions of the Liverpool Biological Society* **56**:78–85.
- Lubchenco, J., and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. *Ecological Monographs* **48**:67–94.
- MacArthur, R. H., and J. H. Connell. 1966. *The biology of populations*. John Wiley and Sons, New York, New York, USA.
- MacGinitie, G. E., and N. MacGinitie. 1968. *Natural history of marine animals*. Second edition. McGraw-Hill, New York, New York, USA.
- McPherson, J. K., and C. H. Muller. 1969. Allelopathic effect of *Adenostoma fasciculatum*, "chamise," in the California chaparral. *Ecological Monographs* **39**:177–198.
- Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs* **46**:355–393.
- Menge, J. L. 1975. Effect of herbivores on community structure of the New England rocky intertidal region: Distribution, abundance, and diversity of algae. Dissertation. Harvard University, Cambridge, Massachusetts, USA.
- Muller, C. H. 1966. The role of chemical inhibition (allelopathy) in vegetational composition. *Bulletin of the Torrey Botanical Club* **93**:332–351.
- Nicotri, M. E. 1974. Resource partitioning, grazing activities, and influence on the microflora by intertidal limpets. Dissertation. University of Washington, Seattle, Washington, USA.
- . 1977. Grazing effects of four marine intertidal herbivores on the microflora. *Ecology* **58**:1020–1032.
- Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. *Statistical package for the social sciences*. Second edition. McGraw-Hill, New York, New York, USA.
- Niering, W. A., and R. H. Goodwin. 1974. Creation of relatively stable shrublands with herbicides: Arresting "succession" on rights-of-way and pastureland. *Ecology* **55**:784–795.
- Niering, W. A., and F. E. Egler. 1955. A shrub community of *Viburnum lentago*, stable for twenty-five years. *Ecology* **36**:356–360.
- Northcraft, R. D. 1948. Marine algal colonization on the Monterey Peninsula, California. *American Journal of Botany* **35**:396–404.
- Odum, E. P. 1969. The strategy of ecosystem development. *Science* **164**:262–270.
- Osman, R. W. 1977. The establishment and development of a marine epifaunal community. *Ecological Monographs* **47**:37–63.
- Paine, R. T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principle predator. *Oecologia* **15**:93–120.
- . 1976. Size-limited predation: An observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* **57**:858–873.
- . 1977. Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory. Pages 245–270 in *The changing scenes in natural sciences, 1776–1976*. Special publication 12, Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA.

- Pyefinch, K. A. 1950. Notes on the ecology of ship fouling organisms. *Journal of Animal Ecology* **19**:29–35.
- Rees, T. 1940. Algal colonization at Mumbles Head. *Journal of Ecology* **28**:403–437.
- Rützler, K. 1965. Substratstabilität im marinen Benthos als ökologischer Faktor, dargestellt am Beispiel adriatischer Porifer. *Internationale Revue der gesamten Hydrobiologie* **50**:818–827.
- . 1970. Spatial competition among Porifera: solution by epizooism. *Oecologia* **5**:85–95.
- Saito, Y., and N. Nakamura. 1961. Biology of the sea hare, *Aplysia juliana*, as a predator on the brown seaweed, *Undaria pinnatifida*. I. The feeding habit. *Bulletin of the Japanese Society of Scientific Fisheries* **27**:395–400.
- Snedecor, G. W., and W. G. Cochran. 1967. *Statistical methods*. Sixth edition. Iowa State University Press, Ames, Iowa, USA.
- Sokal, R. R., and F. J. Rohlf. 1969. *Biometry*. W. H. Freeman, San Francisco, California, USA.
- Sousa, W. P. 1977. Disturbance and ecological succession in marine intertidal boulder fields. Dissertation. University of California, Santa Barbara, California, USA.
- . 1979. *in press*. Disturbance in marine intertidal boulder fields: The non-equilibrium maintenance of species diversity. *Ecology* **60**.
- Southward, A. J. 1956. The population balance between limpets and seaweeds on wave-beaten rocky shores. *Annual Report of the Marine Biological Station, Point Erin, Isle of Man* **68**:20–29.
- . 1964. Limpet grazing and the control of vegetation on rocky shores. Pages 265–273 in O. J. Crisp, editor. *Grazing in terrestrial and marine environments*. Symposium Number 4, British Ecological Society, Blackwell Scientific Publication, Oxford, England.
- Sprugel, D. G. 1974. Natural disturbance and ecosystem responses in wave-regenerated *Abies balsamea* forests. Dissertation. Yale University, New Haven, Connecticut, USA.
- Spurr, S. H., and B. V. Barnes. 1973. *Forest ecology*. Ronald Press, New York, New York, USA.
- Stearns, S. C. 1976. Life-history tactics: a review of the ideas. *Quarterly Review of Biology* **51**:3–47.
- . 1977. The evolution of life history traits. *Annual Review of Ecology and Systematics* **8**:145–172.
- Stebbing, A. R. D. 1972. Observations on colony overgrowth and spatial competition. Pages 173–183 in G. P. Larwood, editor. *Living and fossil Bryozoa*. Proceedings of the Second International Conference on Bryozoa. Academic Press, New York, New York, USA.
- . 1973. Competition for space between the epiphytes of *Fucus serratus* L. *Journal of the Marine Biological Association of the United Kingdom* **53**:247–261.
- Sutherland, J. P. 1974. Multiple stable points in natural communities. *American Naturalist* **108**:859–873.
- . 1978. Functional roles of *Schizoporella* and *Styela* in the fouling community at Beaufort, North Carolina. *Ecology* **59**:257–264.
- Sutherland, J. P., and R. H. Karlson. 1977. Development and stability of the fouling community at Beaufort, North Carolina. *Ecological Monographs* **47**:425–446.
- West, J. A. 1972. The life history of *Petrocelis franciscana*. *British Phycological Journal* **7**:299–308.
- Williams, G. C. 1955. Observations on the feeding habits of the opaleye, *Girella nigricans*. *California Fish and Game* **41**:203–208.
- Woodin, S. A. 1976. Adult-larval interactions in dense infaunal assemblages: patterns of abundance. *Journal of Marine Research* **34**:25–41.