

INTERTIDAL MOSAICS: PATCH SIZE, PROPAGULE AVAILABILITY, AND SPATIALLY VARIABLE PATTERNS OF SUCCESSION¹

WAYNE P. SOUSA

Department of Zoology, University of California, Berkeley, California 94720 USA
and Bodega Marine Laboratory, Bodega Bay, California 94923 USA

Abstract. Localized disturbances transform most assemblages of sessile organisms into mosaics of patches differing in characteristics such as size and age (time since last disturbed). This mosaic nature of natural communities is especially evident on exposed intertidal shores along the northwest coast of North America, where the competitively dominant mussel, *Mytilus californianus*, occupies much of the space at mid-tidal levels. Nearly continuous beds of this species are interrupted by patches of open space generated mainly by the shearing forces of winter storm waves. These patches serve as foci for the recruitment, growth, and reproduction of many competitively inferior, "fugitive" species, including both algae and sessile invertebrates. These species are doomed to local extinction as the lateral encroachment of adult mussels closes the patch and excludes them from the area.

This study examined the dynamics of algal succession within experimental patches cleared in mussel beds. In particular, two potentially important sources of variation in successional dynamics were investigated: (1) the size of the patch when first created, and (2) the location of the patch with respect to potential sources of propagules.

The size of a cleared patch was found to influence strongly the course of algal succession. This effect was largely indirect, resulting from an interaction between patch size and grazing intensity. Small patches support higher densities of grazers, especially limpets, than do large patches. As a consequence, the assemblages of algae that develop within small and large patches differ markedly. The assemblage in small patches includes grazer-resistant but apparently competitively inferior species, whereas that in large patches is composed of grazer-vulnerable but competitively superior species. Small patches appear to serve as refuges from competition for grazer-resistant species.

Recruitment was variable among the experimental patches. Percent cover of several species was found to be highly correlated with the cover of epizoic conspecific adults within 1 m of the edge of the patch. This result suggests that a number of the species inhabiting patches within mussel beds may disperse their propagules over relatively short distances. For such species, patch dispersion may influence the regional dynamics of their populations.

Key words: algae; community structure; competition; dispersal; disturbance; grazing; mosaic; mussel beds; patch; recruitment; rocky intertidal; succession.

INTRODUCTION

Disturbances that create open space maintain the diversity of many natural communities for which such space is a limiting resource (Loucks 1970, Dayton 1971, Levin and Paine 1974, Grubb 1977, Whittaker and Levin 1977, Connell 1978, 1979, Sousa 1979a, White 1979, Paine and Levin 1981, and many others). The damage caused by most natural disturbances is localized, so the open space generated is usually in the form of more or less discrete patches or gaps within a preexisting background assemblage of organisms. If physical conditions are not too harsh, a patch begins to be recolonized soon after it is formed. In many space-limited assemblages, the sequence of species replacements that follows leads inevitably (in the absence of intervening disturbances) to the local extinction of all but a few dominant species (for possible exceptions see Osman 1977, Sutherland and Karlson 1977, Buss and Jackson 1979, Karlson and Jackson 1981, Kay and Keough 1981, Russ 1982). These species dominate by

virtue of being especially vigorous at interference competition or at preempting open space made available by the deaths of previous occupants and holding it against invasion (Sousa 1979b). Species whose populations go extinct locally are able to persist regionally by dispersing their propagules to other patches where conditions are more favorable for growth and reproduction. Regional persistence of these fugitives (sensu Hutchinson 1951) depends upon two interrelated features of such systems:

1) Localized disturbances are asynchronous in space, and their effects vary in intensity and areal extent. They transform an assemblage into a mosaic of patches varying in characteristics such as size and age (time since last disturbed).

2) The component species of the assemblage exhibit a range of life-history attributes that allows, to a degree, the differential exploitation of environmental heterogeneity afforded by the various phases of the mosaic. Some species may partition the temporal component of this heterogeneity by colonizing and growing to maturity during particular stages of succession. Other species may differentially exploit the purely spatial component of the heterogeneity (i.e., that component

¹ Manuscript received 27 September 1982; revised 11 September 1983; accepted 17 November 1983.

not attributable to asynchrony in patch formation). Such spatial variation results from variation in the characteristics of the patches themselves (e.g., their size or location). These characteristics directly or indirectly influence biological and physical environments within patches. Levin (1976) referred to these temporal and spatial components of heterogeneity as phase difference and local uniqueness, respectively. Undoubtedly, most species exploit some combination of these two forms of heterogeneity.

It should also be noted that an important element of randomness overlies the more deterministic sources of variation discussed above. Randomness occurs on a number of scales (Chesson 1978), and when associated with recruitment to open space, may promote diversity in some systems (Sale 1977, 1978, 1979, 1982, Chesson and Warner 1981).

Predictions of regional population dynamics within habitats subject to disturbance require detailed descriptions of: (1) the disturbance regime, including the size distribution of patches and the timing of their occurrence; and (2) the patterns of colonization and succession within patches. For very few natural communities is such detailed information available (e.g., Sousa 1979a, VanBlaricom 1982). The community characterizing the mid-intertidal zone of exposed sites along the Pacific northwest coast of North America is exceptional in this regard. Much of the space in this habitat is occupied by beds of the dominant competitor, the mussel *Mytilus californianus* (Paine 1966, 1974). Complete monopolization of space by this species is prevented by localized disturbances. The impact of drifting logs and, more commonly, the shearing forces of large winter waves (Dayton 1971, Paine and Levin 1981, W. Sousa, *personal observation*) clear patches of open space of differing sizes within the mussel bed matrix. These patches serve as foci for the recruitment, growth, and reproduction of many competitively inferior, fugitive species, including both algae and sessile invertebrates. These species are doomed to local extinction as *M. californianus* gradually invades and closes the patches.

The regime of disturbance in this habitat has been intensively studied. With the aid of a mathematical model (Levin and Paine 1974, 1975, Levin 1976, 1978, 1981), the "demography" of populations of disturbance-generated patches at several sites on the outer coast of Washington State has recently been described (Paine and Levin 1981). The predictions of the model (with some exceptions) were in good agreement with empirical observations of the age and size structure of natural patches. The biological processes that influence patch occupation are less well understood. What is much needed is information concerning the patterns of recruitment and succession within patches cleared in mussel beds, and the influence of patch size on these processes. Published information on the biology of patch occupation in this system is scant. Paine and Levin

(1981) described the sequences of colonization within two natural patches. Suchanek (1978, 1979) presented interesting but largely qualitative results of his experimental study of the effects of patch size on succession.

The study reported here gathered experimental evidence concerning the dynamics of algal succession within patches cleared in beds of the mussel *Mytilus californianus* on the coast of northern California. In particular, the study examined the influence of two potentially important sources of variation in these dynamics: (1) the size of the patch when first created, and (2) the location of the patch with respect to potential sources of propagules. The goal of this study was to enhance our understanding of the regional dynamics of populations both within this particular intertidal mosaic and in other patchy environments.

METHODS

Study site

The research was conducted in the rocky intertidal zone of Bodega Head, a small coastal peninsula in Sonoma County, California (38°18'N, 123°03'W), ≈105 km north of San Francisco. Much of the southwest-facing shoreline receives strong wave surge and may be classified as "exposed outer coast" (Ricketts et al. 1968). The intertidal zone consists of a bench of variable width and height, which is fragmented by deep fissures and pitted with shallow tidepools. This bench is composed of a very weathered, irregular granite. For detailed descriptions of the physical characteristics of the area, see Sutherland (1970) and Barbour et al. (1973).

The specific study site was a 10 m wide × 30 m long intertidal bench (mean tidal height = +2.18 m above mean lower low water) located within the Marine Life Refuge of the University of California's Bodega Marine Laboratory. The primary substratum of the top surface of the bench was monopolized by *Mytilus californianus* (mean cover at the start of the study in July 1979 = 85.2%; $n = 256$ quadrats, each 0.25 m²). However, the surfaces of the mussel valves were themselves covered (mean cover = 83.8%; $n = 256$ quadrats, each 0.25 m²) with attached macroalgae. Six species of macroalgae were especially common on the valves (Table 1). The presence of epizoic algae provided an opportunity to evaluate the influence of the local abundance of adult plants on the course of algal succession within patches of open space experimentally cleared in the mussel bed.

Experimental manipulations

Effects of patch size and grazers.—To evaluate the effects of clearing size (hereafter referred to as patch size) and grazing on the course of algal succession, a two-factorial experiment was begun in July 1979. Thirty-two square patches were cleared in the mussel bed; 16 were 50 × 50 cm and 16 were 25 × 25 cm. These sizes are within the range of sizes of natural patches at the tidal height of this study on Bodega Head (mean area: 2055 cm²; range: 75–11250 cm²; size distribution:

TABLE 1. Composition of the algal assemblage growing on the valves of *Mytilus californianus*. Data are means of 0.25-m² samples ($n = 256$) taken in July 1979. See Methods: Study Site for details of sampling methodology.

Species of algae	Mean cover of epizoites (%)
<i>Endocladia muricata</i>	40.7
<i>Pelvetiopsis limitata</i>	21.8
<i>Mastocarpus</i> (= <i>Gigartina</i>) <i>papillata</i> *	14.9
<i>Porphyra perforata</i>	9.9
<i>Iridaea flaccida</i>	5.1
<i>Fucus gardneri</i> (= <i>distichus</i>)	4.0
Other	3.6

* The nomenclature of the genus *Gigartina* has recently been revised. *Mastocarpus papillata* has been proposed as the new name for *Gigartina papillata* (Guiry et al. 1984). The name *Mastocarpus* is used in this paper.

47% were <625 cm², 33% were 625–2500 cm², 20% were >2500 cm²; $n = 30$; measured July 1982, created in winter 1981–1982). Mussels were pried from the substratum with a crowbar and a putty knife. The rock surface was then thoroughly scoured with a wire brush to remove most of the remaining byssal threads and accumulated sediment.

The immigration of limpets (*Collisella* spp.) from the surrounding mussel bed was greatly reduced in half of the patches of both sizes by applying a barrier of copper paint 3 cm wide along the edges of these patches (Cubit 1975). Previous studies that employed this method (Sousa 1979b, Lubchenco and Cubit 1980, Paine 1980, Slocum 1980, Robles and Cubit 1981, Robles 1982) reported little or no detrimental effects from the copper on algal recruitment or growth. The copper paint barrier reduced the access of limpets to the patches but did not prevent it. Juvenile limpets recruited from the plankton, and a few adult limpets crossed the barriers. The majority of the invading limpets were removed from the exclusion patches at each sampling date (usually at intervals of 1–3 mo). The chitons *Mopalia muscosa*, *Nuttallina californica*, and *Katharina tunicata* were very rare in the experimental area (see Results: Abundance of Grazers), but occasionally one was found inside an exclusion patch. These individuals were removed. Copper paint is ineffective as a barrier against coiled gastropods such as the grazers *Tegula funebralis*, *Littorina scutulata*, and *L. plena* (Mastro et al. 1982) and the predator *Thais* (= *Nucella*) *emarginata*. The densities of these species were not significantly different in patches with and without copper paint (see Results: Abundance of Grazers, Recruitment of mussels), and they were not otherwise manipulated. No attempt was made to assess the impacts of grazers such as amphipods, polychaetes, crabs, or fishes.

Although most natural patches are produced in the winter (Paine and Levin 1981, W. Sousa, *personal observation*), the experimental patches were created in the summer. This protocol was adopted for reasons of

safety and practicality. Large waves make prolonged fieldwork in the winter dangerous, and copper paint can only be applied to dry surfaces (a condition that is frustratingly difficult to achieve in winter). Seasonality in recruitment could potentially dictate the course of succession (Paine 1977, Sousa 1979b), causing the sequences observed in the experimental patches to differ from those occurring in natural ones; however, this did not appear to have been the case. Observations of natural patches suggest that the succession they undergo closely resembles that observed in the experimental clearings, though it may differ in rate.

The experimental patches were positioned to maximize variation in the composition of the epizoic algae surrounding them. Such placement facilitated correlative analyses of the influence of epizoic algae on patterns of recruitment (see below). Upon removal of mussels from what had appeared to be a homogeneous portion of the bed, the underlying substratum was sometimes found to be extremely irregular. In some instances, small tidepools were uncovered. Such clearings were abandoned and others established nearby on more homogeneous surfaces.

The study focused primarily on the dynamics and composition of the algal canopy within the experimental patches. The use of primary space was not examined in detail. Observations indicated that barnacles, especially *Chthamalus dalli* and *Balanus glandula*, were the most common occupants of the rock surface in clearings, comprising ≈ 25 –50% of the primary cover from January 1980 until the end of the study. Two other barnacle species, *Balanus cariosus* and *Pollicipes polymerus*, occurred only as scattered individuals and occupied $\ll 1\%$ of the primary substratum. The mussel *Mytilus edulis* was a temporary occupant of the patches. Though this species attained a maximum cover of only 6% in any one patch, its dynamics were examined in some detail because of its use of algae as a substratum for settlement (see Results).

The patches were sampled every 2–3 mo from July 1979 to July 1981. A final sample was taken in July 1982. To estimate the relative abundances of algal species in the canopy layer, a vinyl sheet quadrat (either 50 × 50 cm or 25 × 25 cm, depending on patch size) with 75 randomly placed 5-mm holes was positioned over each patch, and the number of holes through which the canopy layer of a particular species could be seen (at the center of the hole only) was recorded. The percentage of the 75 holes that fell on each species was an estimate of its cover. A different set of random points was used on each date. The holes (as opposed to dots) made sampling easier when moisture condensed on the underside of the vinyl sheet. When inclement weather and large storm waves reduced the time available for safe sampling in the field, the plots were photographed. Percent cover of the canopy was estimated in the laboratory from the projected 35-mm image by using a similar point-intercept method (Sousa 1979b). At each

sampling date extensive notes were taken on the composition of the understory. All percent cover data were normalized with an arcsine transformation before statistical analysis. The analysis most commonly used to detect the influence of limpet grazing and patch size on the composition of the algal canopy was two-way Model I analysis of variance (Sokal and Rohlf 1981: 202).

The densities of several species of invertebrates within the patches were also periodically sampled. The numbers of *Collisella* spp., *Tegula funebris*, and *Thais emarginata* were censused in each patch. Densities of *Mytilus edulis* and *Littorina* spp. were subsampled from several smaller quadrats (100 cm² and 25 cm², respectively) placed randomly within each patch.

Influence of surrounding adult plants on recruitment.—The influence of the local adult abundance of an alga on the recruitment of offspring to nearby disturbed sites depends, in part, on how far the parent plants disperse propagules. Unfortunately, only a few studies have attempted to experimentally determine the dispersal distances of marine macroalgae in the field (Anderson and North 1966, Dayton 1973, Paine 1979, Deysher and Norton 1982). These studies enumerated recruits at varying distances from either naturally occurring or experimentally transplanted adult isolates. This technique could not be used in the present investigation because of the large number of species involved and because of logistical difficulties in effectively isolating adult plants. I therefore adopted the less direct approach of testing for a statistical correlation between the recruitment of a species to an experimental patch and the epizoic cover of conspecific adults within various distances from the outer edge of the patch.

The cover of epizoic algae on the surrounding mussel bed within 10 cm, 50 cm, and 100 cm of the edge of each patch was estimated at the start of the experiment in July 1979. Vinyl sheet quadrats of the kind described earlier were used. The procedure for measuring cover within each of the three zones around a plot was as follows.

1) Cover within 10 cm: four 10 × 50 cm quadrats were placed immediately adjacent (one on each side) to each of the 2500-cm² patches. Similarly, four 10 × 25 cm² quadrats were placed around each of the 625-cm² patches. Cover was estimated as the percent of the combined 300 random holes (75 per quadrat) that fell on each species.

2) Cover within 50 cm: four 50 × 50 cm or 50 × 25 cm quadrats were placed, as above, around and immediately adjacent to each of the large and small patches, respectively. Cover was estimated as in (1).

3) Cover within 100 cm: an additional four 50 × 50 cm or 50 × 25 cm quadrats were placed in the zone between 50 and 100 cm from the edge of each large and small patch, respectively. Cover was estimated as the grand average of the four quadrats in (2) and these

additional four; 600 random holes in total (eight quadrats, 75 holes per quadrat).

Multiple linear regression was used to examine the relationship between recruitment and local abundance of adults. The dependent variable in each case was the maximum percent cover attained by the first generation to grow up in the patches following initial clearing. Since the estimates of epizoic cover within 10 cm (X_1), 50 cm (X_2), and 100 cm (X_3) of the edge of each patch were nested and therefore highly correlated, the values for the latter two distances were not entered directly as independent variables in the regression equation. Instead, two new variables (X_2' and X_3'), relatively free of collinearity with each other and with X_1 , were created. These variables are the residuals of the regressions of (1) X_2 on X_1 , and (2) X_3 on X_2 and X_1 , as symbolized in standard notation below.

$$X_2 = a_0 + a_1X_1 + \epsilon_2$$

$$X_2' = X_2 - \hat{a}_0 - \hat{a}_1X_1 = \hat{\epsilon}_2 \quad (1)$$

$$X_3 = b_0 + b_1X_1 + b_2X_2 + \epsilon_3$$

$$X_3' = X_3 - \hat{b}_0 - \hat{b}_1X_1 - \hat{b}_2X_2 = \hat{\epsilon}_3 \quad (2)$$

The independent variables were entered into the regression equation according to the criterion of forward (stepwise) inclusion; that is, in order of their respective contributions to the explained variance (Nie et al. 1975). Only in one analysis was it necessary to transform the variables to achieve linearity. The one exception was the analysis of *Fucus*. In this case the natural logarithms of the percent covers within the three distances were used. All other analyses employed the original values normalized with an arcsine transformation.

Since only the epizoic and recruited covers of erect thalli were measured (see below), meaningful correlations could, with one exception (*Mastocarpus* [= *Gigartina*] *papillata*), be calculated only for species that exhibit isomorphic life histories, all stages of which are macroscopic and erect. For such a species, the percent cover of epizoic plants was probably a reasonable relative measure of the abundance of propagule-releasing adults surrounding an experimental patch (assuming that the proportions of male to female, gametophytic to sporophytic, and fertile to infertile thalli were fairly homogeneous over the surface of the mussel bed). The relationship between recruitment and local adult abundance could not be examined for most colonizing algal species with heteromorphic life histories. In the life histories of such species (Abbott and Hollenberg 1976, Bold and Wynne 1978, Lubchenco and Cubit 1980), macroscopic erect phases alternate with inconspicuous crusts, filaments, or unicellular thalli (e.g., *Urospora*, *Porphyra*, *Colpomenia*, *Leathesia*, *Scytosiphon*). The abundances of the small alternate stages of heteromorphic algal species were not measured by the sampling method used in this investigation.

The only heteromorphic species for which a potentially meaningful correlation could be calculated was *Mastocarpus papillata*. In the life history of this species (West 1972, Polanshek and West 1977), haploid gametophytes alternate with a crustose diploid tetrasporophyte (*Petrocelis* sp.). The abundance of this crust, like the abundances of the minute alternate states of the species listed above, was not adequately assessed by the sampling method. However, alternation of erect and crustose forms is not obligate in this species. J. West (*personal communication*) has found that $\approx 60\%$ of the cystocarpic *Mastocarpus* collected in exposed areas on Bodega Head are apomictic. That is, carpospores released by erect carposporophytes develop directly into erect cystocarpic thalli, bypassing the crustose stage. Therefore, the cover of erect thalli of *Mastocarpus* (most of which are cystocarpic at Bodega; J. West, *personal communication*, W. Sousa, *personal observation*) might influence recruitment of erect thalli to nearby patches.

RESULTS

Abundances of grazers in patches of different size

The size of the patch clearly influenced the density of limpets. Colonization of the experimental clearings lacking a copper paint barrier began shortly after clearing (Fig. 1), and the rate of colonization was higher in small patches. Several species of limpets colonized the plots, including *Collisella scabra*, *C. digitalis*, *C. pelta*, and *C. limatula*. *C. scabra* was by far the most common, comprising 96.7% ($n = 60$), 86.5% ($n = 126$) and 95.4% ($n = 260$) of the limpets counted on the three sampling dates when limpets were identified to species. The first limpets to invade the plots were adults that had apparently immigrated from the surrounding mussel beds; recruitment from the plankton began shortly thereafter in the late summer and fall (see Sutherland 1970).

By October 1979, the density of limpets was significantly greater in the small patches (Fig. 1). This trend continued through the first year; densities in small patches were roughly twice those in large patches. By the middle of the second year after clearing, however, the densities of limpets in both large and small patches had dropped dramatically, so that they were no longer significantly different.

Three species of chitons, *Mopalia muscosa*, *Nuttallina californica*, and *Katharina tunicata*, were common in the study area but were rare in the experimental clearings. The maximum density of all three species pooled was 0.125 individuals/625 cm² (11 October 1981) and was the same in small ($SD = 0.35$) and large ($SD = 0.27$) control clearings.

The experimental treatments did not appear to affect the densities of grazing molluscs other than limpets and chitons. The maximum densities attained by *Littorina* spp. and *Tegula funebris* averaged over all

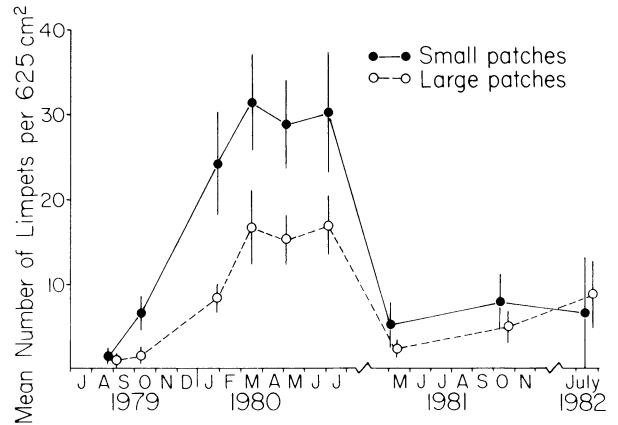


FIG. 1. Mean density of limpets in small and large experimental patches lacking copper barriers. Vertical bars indicate 95% confidence intervals.

treatments were 9.67 individuals/25 cm² ($SD = 9.59$, $n = 96$; 1 July 1980) and 1.56 individuals/625 cm² ($SD = 2.80$, $n = 32$; 1 July 1980), respectively. The densities of these species were influenced neither by the size of the patch nor by the presence of a copper paint barrier (two-way ANOVA, both species; $P > .05$ both for main effects and for two-way interaction).

Succession in patches with reduced grazing

Patch size, per se, under conditions of experimentally reduced grazing, had little influence on the patterns of macroalgal colonization and species replacement. For all but one of the common macroalgal species (Table 2), the mean percent covers in small vs. large patches with copper paint barriers were not significantly different (t tests on data from three to seven dates for each species; $P > .1$ in all cases, $df = 14$). The one exception, *Endocladia*, became significantly more abundant in large plots by February 1981 and remained so through July 1982 (see below).

The sequence of colonization in the 16 patches with reduced grazing (both sizes pooled) is illustrated in Fig. 2. Soon after clearing, the patches became coated with a mat of diatoms and the filamentous green alga *Urospora*. This mat was rapidly replaced by a turf of *Ulva* 1 cm high with some thalli of *Enteromorpha* mixed in. These two species are difficult to distinguish visually when in a dense mat, so for the purposes of this report, their abundances are pooled and treated as a single entity (*Ulva*) in all statistical analyses and figures. The *Ulva* turf dominated the patches by October 1979, holding $>90\%$ cover, but it declined precipitously during the winter of 1979–1980. This winter decline in the percent cover of *Ulva* was probably due, in part, to harsh physical conditions associated with daytime low tides and increased wave action. In the spring of 1980 the *Ulva* turf temporarily increased slightly in cover, but then continued to decline in extent as several

TABLE 2. Macroalgal species that colonized the experimental patches. Common species are those that attained an average of $\geq 5\%$ cover in any of the experimental treatments during the study.

Common species	Rare species
Chlorophyta	
<i>Urospora penicilliformis</i>	
<i>Ulva californica</i>	
<i>Enteromorpha intestinalis</i>	
<i>Cladophora columbiana</i>	
Phaeophyta	
<i>Pelvetiopsis limitata</i>	<i>Colpomenia bullosa</i>
<i>Fucus gardneri</i> (=distichus)	<i>Leathesia difformis</i>
<i>Analipus japonicus</i>	<i>Scytosiphon dotyi</i>
Rhodophyta	
<i>Mastocarpus</i> (=Gigartina)	<i>Polysiphonia hendryi</i>
<i>papillata</i>	<i>Ceramium eatonianum</i>
<i>Iridaea flaccida</i>	<i>Callithamnion pikeanum</i>
<i>Endocladia muricata</i>	<i>Microcladia borealis</i>
	<i>Cryptosiphonia woodii</i>
	<i>Odonthalia floccosa</i>
	<i>Neorhodomela</i> (=Odonthalia)
	<i>oregona</i>
	<i>Gelidium coulteri</i>
	<i>Porphyra perforata</i>

species of red and brown algae invaded the patches. Of the latter species, the brown furoid alga *Pelvetiopsis* and the red alga *Mastocarpus* were the first to appear, in the fall and winter of 1979–1980. The brown alga *Fucus* and the red alga *Iridaea* were not observed in the patches until the spring of 1980. *Pelvetiopsis* attained a mean cover of $\approx 40\%$ by the fall of 1980, which

it maintained with little change through July 1981. Large storm waves removed much of the otherwise healthy adult canopy of *Pelvetiopsis* in the winter of 1981–1982. This caused its cover to decline by $>50\%$ between July 1981 and July 1982. The mean cover of *Mastocarpus* reached a peak of 25% in the fall of 1980, then gradually declined. *Iridaea* held 9–15% of the canopy cover from July 1980 to July 1981, increasing to $\approx 17\%$ cover in July 1982. *Fucus* showed a gradual, but steady, increase to a maximum mean cover of slightly over 25% at the end of the study. *Endocladia*, *Analipus*, and *Cladophora* were persistent members of the algal assemblage, but they never became very abundant in patches from which limpets were excluded; they attained maximum covers of only 6.6%, 1.9%, and 0.7%, respectively.

The rare species listed in Table 2 were either seasonal ephemerals or perennials that are common lower in the intertidal zone. These species appeared to suffer differentially from seasonal exposures to harsh physical conditions. On several occasions in late winter, when daytime low tides coincided with clear skies, the thalli of these species bleached extensively. Subsequently, many plants died and decayed. The common perennials, discussed above, became dry and wizened, but recovered almost completely. Many of the individuals of species characteristic of lower tidal levels were growing beneath the canopy in the experimental patches. The upper distributions of these species are extended by this understory habit (Dayton 1975), which ameliorates the harsher physical conditions of the mid-shore.

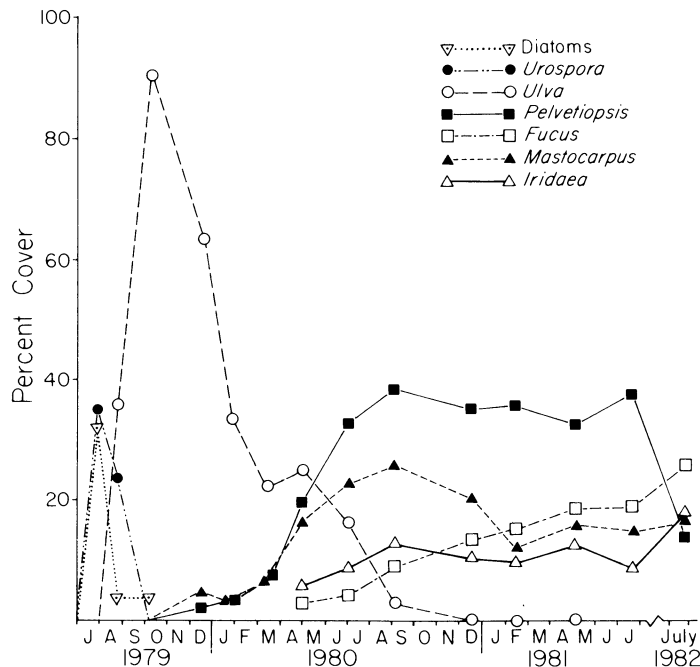


FIG. 2. Successional changes in the composition of the algal canopy in the 16 experimental patches from which limpets were excluded. Data are means for species that attained at least 10% cover on some sampling date.

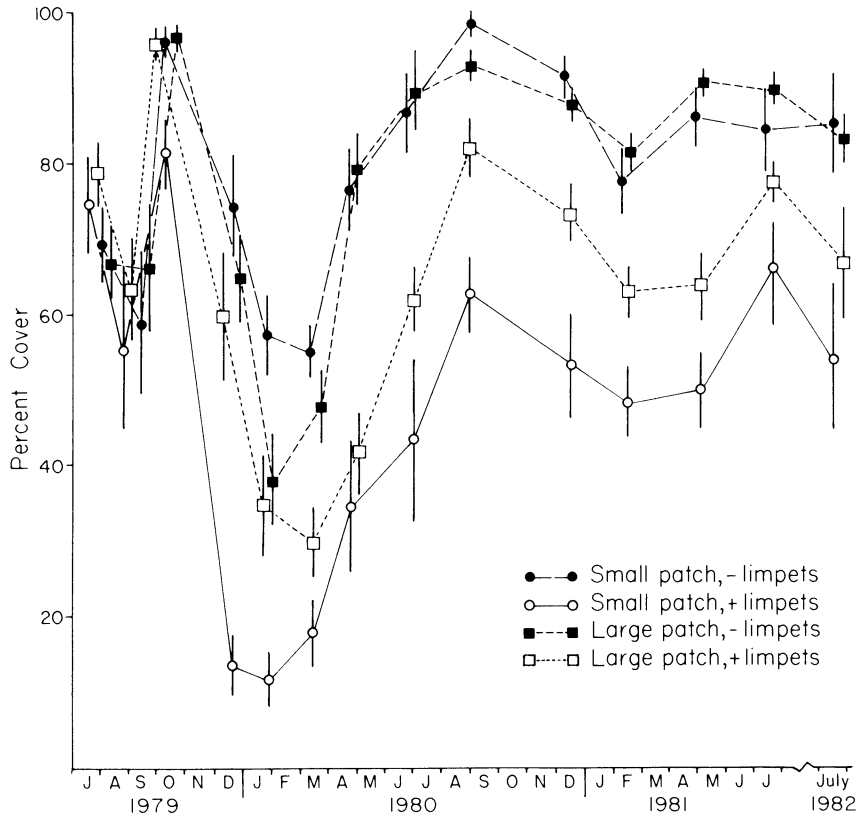


FIG. 3. Effects of patch size and limpet grazing on the extent of the total algal canopy. The mean percent cover (± 1 SE) in each of the two ungrazed treatments (- limpets) and two grazed controls (+ limpets) is indicated.

Effects of grazing and its interaction with patch size on algal populations

Limpet grazing and its interaction with patch size strongly affected the extent and the composition of the algal canopy. The influence of grazing on the total cover of algae was first apparent in October 1979, when the mean density of limpets in control plots had reached 3.8 individuals/625 cm² (Fig. 1). From that date on, algal cover was lower in grazed patches (Fig. 3, Table 3). On five sampling dates there was a significant interaction between patch size and grazing effects. Small patches accessible to limpets had a much lower canopy cover. Interaction effects were observed when limpets were significantly more abundant in small patches (late 1979 through 1980, Fig. 1). No interaction effect on total cover was observed in 1981 or 1982, when the densities of limpets in small vs. large patches were not significantly different. On two dates patch size had a barely significant effect on the total algal canopy, but had no concurrent interaction effect with grazing. In both instances, this effect of patch size was transient and appears to have been related to the development and dissolution of significant interaction between the effects of grazing and the effects of patch size in October 1979 and February 1981, respectively.

The individual species of algae exhibited a continuum of responses to the presence of limpets. Some species were more abundant when limpets were excluded, while others became most abundant in patches with limpets. *Ulva*, *Pelvetiopsis*, and *Fucus* were the species most vulnerable to grazing (Fig. 4, Table 3). From October 1979 to March 1980, there was an interaction between the effects of patch size and the effects of grazing on the canopy of *Ulva*; its canopy was reduced by grazing limpets much more quickly in small patches than in large ones.

Pelvetiopsis showed a similar response to the experimental treatments. It was significantly less abundant in the presence of limpets from September 1980 to July 1981. The alga was consistently least abundant in small patches subject to grazing until May 1981, by which time the densities of limpets in small vs. large patches were similar (Fig. 1). Large variation in the cover of *Pelvetiopsis* among replicates (discussed below) precluded the demonstration of a significant interaction effect. In July 1982, after the large decline in the canopy of *Pelvetiopsis*, no effects of the treatments were evident.

Limpet grazing also reduced the cover of *Fucus*. This reduction was statistically significant in February and

TABLE 3. Results of two-way analyses of variance for the effects of patch size and limpet exclusion on the percent cover of the algal canopy.

Dependent variable	Independent variable							
	Patch size		Limpet exclusion			Two-way interaction		
	$P < .05$	$P < .01$	$P < .05$	$P < .01$	$P < .001$	$P < .05$	$P < .01$	$P < .001$
Total algal canopy	3, 11*		3	13	7, 8, 11, 12, 14	6, 10	5	4, 9
Canopy of:								
<i>Ulva</i>					7, 8	3, 6		4, 5
<i>Mastocarpus</i>			7, 8	6				
<i>Pelvetiopsis</i>			13	9, 10, 12	11			
<i>Fucus</i>			11, 12					
<i>Iridaea</i>						14		
<i>Endocladia</i>	12, 13, 14	11			12, 13			
<i>Cladophora</i>					13			

* Entries are the sampling dates (coded by numerals) on which a statistically significant effect of patch size, limpet exclusion, or two-way interaction between these variables was observed. If a significant interaction effect was found on a particular date, no entries for the main effects on that date are made. The probability level of $F_{1,28}$ for each effect is indicated at the top of each column. The sampling dates were 7 July 1979 (1), 24 August 1979 (2), 9 October 1979 (3), 18 December 1979 (4), 27 January 1980 (5), 14 March 1980 (6), 2 May 1980 (7), 1 July 1980 (8), 5 September 1980 (9), 18 December 1980 (10), 18 February 1981 (11), 6 May 1981 (12), 23 July 1981 (13), and 24 July 1982 (14).

May 1981, despite large variation among replicates. There was, however, no evidence that the difference in the densities of limpets in small vs. large patches (without copper barriers) had any effect on the extent of the *Fucus* canopy. Apparently, even the density of limpets in the large patches was sufficient to limit *Fucus* to only 2–4% of the canopy cover. After May 1981, limpet densities were lower in general, and the canopy of *Fucus* in grazed patches of both sizes gradually increased.

The covers of the red algae *Iridaea* and *Mastocarpus* were less affected by limpet grazing than the covers either of *Ulva* or of the two furoid algae (Fig. 4, Table 3). *Iridaea* was slightly but not significantly less abundant in patches with limpets throughout the study. Again, variation among replicates was high. A weak interaction between the effects of patch size and the effects of grazing on the cover of *Iridaea* appeared in July 1982. This interaction effect was primarily attributable to the inexplicably high cover of *Iridaea* that developed in the small ungrazed patches. The cover of *Mastocarpus* was temporarily reduced in grazed patches from March to July 1980, but thereafter it was not different between patches with a copper barrier and patches without the barrier.

In contrast with the above results, the abundances of three relatively rare species appeared to be enhanced by limpet grazing (Fig. 4, Table 3). The brown alga *Analiplus* was consistently more common in grazed patches, and particularly so in small patches where limpets were most dense. Its rarity and variability among replicates prevented a statistically significant difference at the .05 level, but on two dates (11 February and 23 July 1981) the probability that the difference between the mean abundances in patches with and without grazing was due to chance alone was <0.1 . *Cladophora*, a green alga, showed the same pattern, becoming significantly more abundant in patches ac-

cessible to limpets, especially the small patches. The response of *Endocladia* to grazing was similar. The cover of this red alga became greater in patches open to limpets, as it did in similar experiments conducted higher on the shore within continuous stands of *Pelvetiopsis* (W. Sousa, personal observations).

All of the above species (*Analiplus*, *Cladophora*, and *Endocladia*) have low-lying, turf-like or crustose morphologies (see Discussion). If they had been common as understory species, the method of sampling employed in this study (which only estimated canopy cover) would have underestimated their abundances in patches supporting an extensive canopy of larger plants (i.e., those patches with fewer grazers). Such an underestimation would have created a nonconservative bias toward the conclusion that these three species are favored by grazing. This does not appear to be a significant problem in this study, since careful inspections on each sampling date indicated that adults of *Analiplus*, *Cladophora*, and *Endocladia* were rare in the understory. These algal species grew to maturity within gaps in the canopy of taller species. Whether these species persisted as suppressed juvenile stages in the understory of the canopy is unknown.

Recruitment of mussels to the experimental patches

In the winter of 1979–1980, large numbers of the mussel *Mytilus edulis* recruited to the experimental patches. Plantigrades were first noticed in the patches on 27 January 1980, when they were 2–5 mm long. The densities of *M. edulis* were first sampled on 15 March 1980, when the mean length of the mussels was 4.6 mm (SD = 1.6; range: 2–9 mm; $n = 98$). Data on spawning periodicity, length of larval life, and growth rates (Suchanek 1981) suggest that pediveligers first

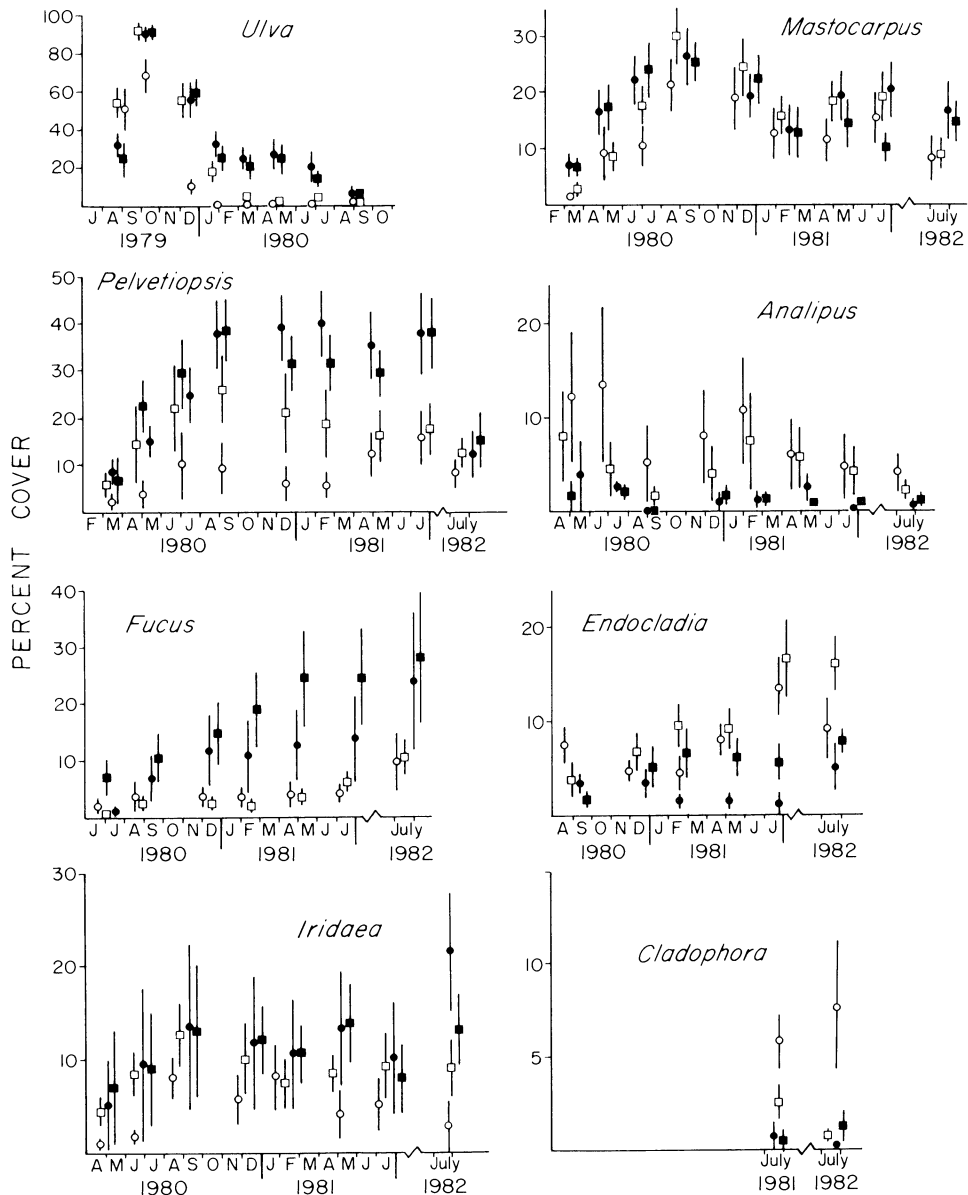


FIG. 4. Effects of patch size and limpet grazing on the abundances of the eight most common species to colonize the experimental patches. The mean percent cover (± 1 SE) of a species in each of the two treatments and two controls is indicated. See Fig. 3 for key to symbols.

recruited to the patches in December 1979, but were too small to be detected at the time. Pediveligers are believed to settle preferentially on filamentous substrata (De Blok and Geelen 1958, Bayne 1964, Seed 1969a, Dean and Hurd 1980, Dean 1981). In December 1979, when settlement probably occurred, such a substratum was provided by a turf of green algae. This turf varied significantly in cover among the experimental treatments, and was least extensive in small patches open to limpets (Fig. 4, Table 3). By March 1980, mussel densities were much lower in patches accessible to limpets and were lowest in small patches

without copper barriers (Table 4). The negative influence of limpets on the settlement and/or the survival of mussels could have been (1) a direct result of bulldozing by limpets (Dayton 1971, Suchanek 1978), and/or (2) an indirect result of their grazing, which reduced the availability of a suitable substratum (*Ulva*) for mussel settlement. Most of the mussels that were still present in March were restricted to crevices (54.4%, $n = 250$); others were attached to barnacles (22.4%) and bare exposed rock (15.6%), or were embedded in the algal turf (7.6%). *M. edulis* constituted only a small percentage of the cover in the patches (mean of small

TABLE 4. Mean density of *Mytilus edulis* in experimental patches with and without limpets on 15 March and 2 May 1980. Data are the mean numbers of mussels per 100 cm² (and SD) in the four treatments. Two-way analyses of variance in data collected on each date are presented. * $P < .05$, *** $P < .001$.

15 March 1980					2 May 1980				
Small patch		Large patch			Small patch		Large patch		
+ limpets	- limpets	+ limpets	- limpets		+ limpets	- limpets	+ limpets	- limpets	
6.1 (2.3)	32.7 (11.7)	15.9 (12.2)	27.6 (10.3)		0.9 (1.7)	2.4 (1.9)	1.8 (2.4)	2.2 (1.3)	
Source of variation	df	SS	MS	F	Source of variation	df	SS	MS	F
Patch size	1	43.94	43.94	0.44	Patch size	1	0.78	0.78	0.22
Limpet grazing	1	2954.88	2954.88	29.76***	Limpet grazing	1	7.03	7.03	2.02
Two-way interaction	1	446.26	446.26	4.49*	Two-way interaction	1	2.54	2.54	0.73
Within subgroups					Within subgroups				
(Error)	28	2780.47	99.30		(Error)	28	97.37	3.48	
Total	31	6225.55			Total	31	107.72		

patch, grazed (+ limpets) = 0.2%; mean of small patch, ungrazed (- limpets) = 2.7%; mean of large patch, (+ limpets) = 1.7%; and mean of large patch, (- limpets) = 2.0%). Patch size per se had no effect on the density of *M. edulis* (Table 4).

The density of *Mytilus edulis* in the patches dropped dramatically over the early spring (Table 4). On 2 May 1980, when the largest individuals had reached 12 mm, the mean density was <2 mussels/100 cm², and the experimental treatments no longer had a detectable effect. Predation was the likely cause of the decline in mussel density, since numerous *Thais emarginata* were observed feeding on small mussels in March and May 1980. On the latter date, the density of *T. emarginata* averaged over all treatments was 3.16 individuals/625 cm². Neither the size of the patch nor the presence of a copper paint barrier affected snail density (two-way ANOVA; $P > .05$ for both main effects and for two-way interaction). Since the densities of predatory snails were not experimentally manipulated, the conclusion that they caused the decline in mussel density remains speculative. However, it is consistent with the findings of other studies of the same system (Suchanek 1978). Only a few isolated *M. edulis* recruited to the patches in the winters of 1980-1981 and 1981-1982.

Mytilus californianus did not recruit to the patches from the plankton during the 3 yr of the study. Instead, the patches were colonized by adults that moved laterally into the open space from the edges. Given enough time and no intervening disturbances, the patches will be closed by this encroachment (Paine and Levin 1981). However, the rate of closure was quite slow (as well as variable) at the tidal height of this study. By June 1982, small patches without copper barriers had a 23% cover (SD = 24.2; range: 0-64%) of adult *M. californianus*, while large patches without copper barriers were 8.2% filled (SD = 6.0; range: 0-18%). As expected, small patches, whose ratio of perimeter to central area was twice that of the larger patches, shrank in size at a faster rate.

Local abundance of epizoic algae and recruitment to patches

There was considerable spatial variation in the recruitment of algae to the experimental patches. For four of the eight species of algae that were amenable to analysis, percent cover within the 16 ungrazed patches was highly correlated with the epizoic cover of conspecific adults surrounding them (Table 5). The epizoic cover within 10 cm of the edge of a patch explained most of the variation in recruited cover of *Fucus*, *Pelvetiopsis*, and *Mastocarpus*. Recruitment of *Iridaea* was more strongly correlated with its epizoic cover farther from the edge of a patch. Variation in recruited cover of the remaining four species (*Ulva*, *Endocladia*, *An-alipus*, and *Cladophora*) was not significantly correlated with their respective epizoic covers within 1 m of the ungrazed patches.

With one exception, grazing by limpets appeared to eliminate any correlation between epizoic cover and recruitment for the patch sizes studied. A significant amount of the variation in the cover of *Fucus* among large (but not small) grazed patches was explained by the variation in the epizoic cover of *Fucus* around these patches. This was not true for the remaining seven species in either small or large patches accessible to limpets. It should be noted, however, that since separate regressions were computed for small and large grazed patches, each regression was based on only eight data points. In contrast, the regressions computed for ungrazed patches were based on 16 data points. The small sample size for analyses of grazed patches reduces the likelihood of detecting significant correlations.

The tidal heights of the experimental patches ranged from 1.92 to 2.32 m. The variation in the maximum covers attained by *Fucus*, *Pelvetiopsis*, *Mastocarpus*, and *Iridaea* was not significantly correlated with the tidal heights of the 16 ungrazed patches (test of H_0 : $r = 0$, $P > .05$ in all cases). This was also true for the cover of *Fucus* in the eight large grazed patches. Thus, differences in tidal height did not significantly explain

TABLE 5. Results of the multiple linear regression analyses showing the terms included in the final fitted models and their statistical significance. * $P < .05$, ** $P < .01$, *** $P < .001$, NS = not significant.

Dependent variable†		Step no.	Independent variable†	Regressions‡		
Max. cover of	Patch type			<i>B</i>	SE	R^2 (full model)
<i>Fucus</i>	Ungrazed	1	X_1	.312***	.055	.770***
		2	X_3'	.312NS	.146	
		3	X_2'	.662NS	.750	
<i>Fucus</i>	Large grazed	1	X_2'	.158**	.034	.915**
		2	X_3'	.993*	.299	
		3	X_1	.110*	.033	
<i>Pelvetiopsis</i>	Ungrazed	1	X_1	1.215***	.245	.728***
		2	X_3'	2.703*	1.228	
		3	X_2'	.859NS	.525	
<i>Mastocarpus</i>	Ungrazed	1	X_1	1.509***	.355	.627**
		2	X_2'	.398NS	.360	
		3	X_3'	.719NS	.756	
<i>Iridaea</i>	Ungrazed	1	X_3'	2.657***	.605	.763**
		2	X_2'	1.531**	.467	
		3	X_1	1.200*	.410	

† The dependent variable in each case was the maximum percent cover attained by the first generation to grow up in the patches following initial clearing. Independent variables X_1 , X_2 , X_3 , are the epizoic covers of the species within 10, 50 and 100 cm, respectively, of the edge of a patch. X_2' and X_3' are the residuals of the regression of X_2 on X_1 , and of X_3 on X_2 and X_1 , respectively. For a more complete description of the regression variables, see Methods: Influence of surrounding adult plants on recruitment.

‡ Tabulated data include the regression coefficients (B) of each of the independent variables and their standard errors (SE). The squared correlation coefficients for the full models (R^2) are also presented.

the variation in recruitment among the experimental patches.

DISCUSSION

Effects of patch size on succession

Patch size strongly influenced succession within experimental clearings in mussel beds. For most potential algal colonists, however, it is neither the size of the patch itself nor its influence on the internal physical environment of the patch that affects their recruitment. Rather, the influence of patch size on the abundance of grazers determines recruitment success. As this study and previous investigations by Suchanek (1978, 1979) and Paine and Levin (1981) have demonstrated, small patches in mussel beds support higher densities of grazers (especially limpets) than do large patches. Suchanek (1979) has shown that peak limpet densities occur at the boundary between mussel bed and patch. Previous workers have hypothesized that this pattern obtains because the bed of mussels surrounding a patch serves as an important refuge for small grazers, possibly from desiccation and/or large waves. Limpets are also subject to predation by shorebirds, especially oystercatchers (*Haematopus bachmani*, Hartwick 1976, Frank 1981, 1982, W. Sousa, *personal observation*), and may be less vulnerable if living in or immediately adjacent to the matrix of the mussel bed. If the refuge explanation is correct, one would predict that 25×25 cm patches, which have twice as great a ratio of perimeter length to area as 50×50 cm² patches, would support twice the density of limpets. The densities of limpets

observed in patches during the first year of this study are in very close accord with this prediction (Fig. 1).

When a large natural patch is first created, grazers invade 10–20 cm from the periphery and maintain a “browse zone” around the edges of the patch (Fig. 5; also see Fig. 1 in Dayton 1973 and Fig. 4 in Suchanek 1978). Such zones were briefly visible in the larger experimental patches, but disappeared as limpets gradually invaded their centers (25 cm from the edge). Browse zones did not develop at all in the small patches (with centers only 12.5 cm from the edge). This interaction between patch size and grazing markedly influences the composition of the algal assemblage within a patch (also see Suchanek 1978, 1979, Paine and Levin 1981:172). Large patches accessible to limpets and patches with copper barriers (which presumably mimic patterns that would be observed in natural patches >2500 cm²) develop a dense algal canopy dominated by species that are particularly vulnerable to grazers. The composition of this canopy changes with time. Early dominance by green algae (i.e., *Ulva* and *Enteromorpha*) eventually gives way to dominance by larger furoid algae (i.e., *Fucus* and/or *Pelvetiopsis*). The experimental manipulation of limpets demonstrated that both ulvoid and furoid algae were vulnerable to grazing. The only difference is that furoids can escape the impact of grazers if they remain undetected long enough to grow to an invulnerable size (Lubchenco and Gaines 1981, Steneck and Watling 1982). In contrast, ulvoids appear to remain vulnerable to limpet grazing even as adults; they were completely eliminated from the control patches.

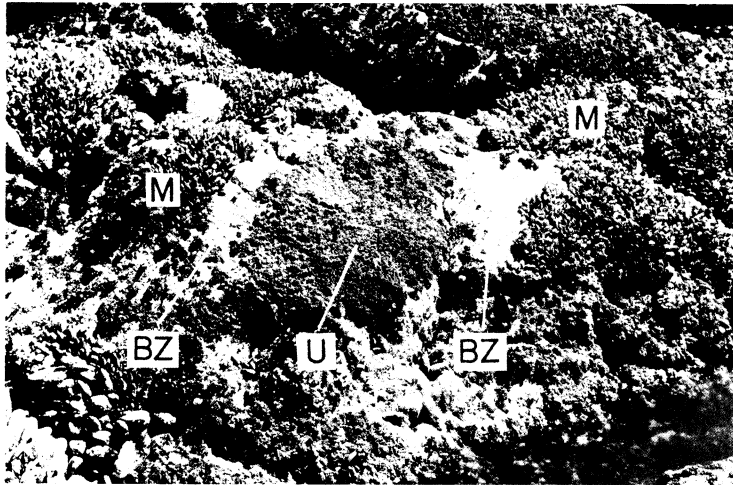


FIG. 5. Natural patch in a bed of *Mytilus californianus* (M) on Bodega Head. The patch is ≈ 1 m across and was probably created during the previous winter as indicated by the extensive cover of the early successional alga *Ulva* (U). Note the distinct browse zone (BZ) around the perimeter of the patch.

The densities of limpets in both the small and the large patches lacking copper barriers declined to low levels in the second year of the study. Similar declines in limpet density over the course of algal succession in mid- and low-intertidal zones have been observed in several recent studies (Dixon 1978, Sousa 1979b, Underwood and Jernakoff 1981). It is likely that limpets disappear because they are outcompeted for space by the developing stands of macroalgae. As juvenile plants, undetected or uneaten by grazers, grow to large invulnerable sizes they occupy or shade much of the primary substratum. This reduces the area available for limpet attachment and foraging, and probably decreases the rates of settlement and growth of microalgal foods (including juvenile stages of macroalgae). If undisturbed, the algal cover gradually grows dense enough to exclude limpets.

The mussel *Mytilus edulis* also became more abundant in patches with reduced grazing. This may have been because the ulvoid turf was a preferred substratum for larval settlement, and/or because the direct negative effects of limpet grazing on larval settlement, metamorphosis, and survival were less intense in large patches. Similar negative effects of limpet grazing on the recruitment of *M. edulis* have been observed by Seed (1969b) and Suchanek (1978, 1979). The rapid elimination of *M. edulis* by predators from even the large patches at Bodega may make patch size or availability relatively unimportant to the evolutionary dynamics of *M. edulis* populations in the study area. No data on size at first reproduction were gathered in this study, but *M. edulis* on the outer coast of Washington State are sexually mature when ≈ 15 –20 mm long (Suchanek 1981). Since nearly all of the mussels that colonized the experimental patches were eliminated before they had reached 12 mm, *M. edulis* that recruit

to patches in *M. californianus* beds may not contribute as much to the gene pool of populations in northern California as they do in Washington State. In the latter area, *M. edulis* can reach 28 mm (mid-intertidal) to 40 mm (low intertidal) in length, can occupy up to 80% of the interior of a patch (Suchanek 1978), and can persist for >2 yr (Paine and Levin 1981). *M. edulis* are very rare in natural patches on Bodega Head; the largest one observed during this study was 17 mm (W. Sousa, *personal observation*).

The cover of the three algal species, *Analipus*, *Endocladia*, and *Cladophora*, was enhanced by grazing. These species appear to be both grazer-resistant and grazer-dependent (Lubchenco and Gaines 1981). *Endocladia* and *Cladophora* grow as short, profusely branched turfs; *Analipus*, as a prostrate crust from which seasonal erect axes arise (Abbott and Hollenberg 1976, Bold and Wynne 1978). All three species can spread vegetatively over hard substrata (W. Sousa, *personal observation*). Crustose (and often calcified) or turf-like morphologies similar to those just described have been shown to effectively defend other species of algae against herbivory (Paine and Vadas 1969, Vine 1974, Dayton 1975, Littler and Doty 1975, Wanders 1977, Brock 1979, Lubchenco and Cubit 1980, Paine 1980, Slocum 1980, Brawley and Adey 1981, Dethier 1981, Hay 1981a, 1981b, Hixon and Brostoff 1981, Padilla 1981, Steneck 1982). In addition, epidermal cells of the crustose and upright portions of the *Analipus* thallus are rich in physodes, which contain phenolic compounds (Nelson 1982). These compounds may discourage grazing by limpets, as Geiselman (1980) has shown for littorine snails feeding on fucoid algae and Steinberg (1984) has demonstrated for turban snails feeding on laminarian kelp.

The observation that *Analipus*, *Endocladia*, and

Cladophora were rare in the understory of the taller canopy (i.e., in patches with reduced grazing) suggests that these three grazer-resistant species may have been outcompeted for light. In addition, when limpet densities declined in 1981 (Fig. 1), much of the *Analipus* crust was overgrown by a mixture of *Colpomenia*, *Leathesia*, *Mastocarpus*, *Endocladia*, and *Cladophora*. The overgrown crust decayed and sloughed off the rock, thereby contributing to the gradual decline in the cover of *Analipus* within the experimental patches (W. Sousa, personal observation; Fig. 4). The persistence of many species of grazer-resistant algae depends on the removal of competitively dominant species that are less resistant to herbivory (Lubchenco and Gaines 1981, and many of the references cited above). Some competition may still occur even in the presence of dense populations of herbivores. *Cladophora* occasionally overgrew *Analipus* in the small patches without copper barriers during the first year of the study. Such interactions among grazer-resistant species may reduce diversity to an even lower level than that caused by intense grazing alone (Lubchenco and Gaines 1981).

Iridaea and the erect stages of *Mastocarpus* showed an intermediate response to grazing. Grazing only temporarily reduced the recruitment of these two species to the experimental patches. As a result, the abundances of these species were also less affected by patch size. Although both *Iridaea* and *Mastocarpus* are erect algae, they also have discoid spreading holdfasts that may be relatively resistant to grazing. This latter feature likely explains the gradual invasion of grazed patches by these two species. Foster's (1982) study of zonation in *Iridaea* obtained results similar to this study. Molluscan grazers only temporarily reduced the recruitment of this species to his experimentally cleared plots.

Endocladia was the only species that seemed to respond to patch size irrespective of grazing. It developed greater cover in large patches than in small ones. The reasons for this difference are unknown. Greater density of settlement of its spores in large patches seems unlikely, because no mechanism by which its non-motile spores could actively select sites for settlement is known. Possibly, peculiarities of water flow allow the deposition of a greater number of spores in large patches, but such flow patterns should not influence the spores of *Endocladia* differentially. The influence of patch size on the cover of *Endocladia* more likely reflects a differential response in vegetative growth by established plants to differences in the microenvironment (i.e., to patterns of water motion, water drainage, humidity, regimes of light, etc.) in patches of different size.

Interactions between patch size and grazing intensity probably occur in many communities. Hawkins (1981) observed that green algae grew only in the centers of small areas cleared in stands of barnacles. He attributed this pattern to the grazing forays of small snails (*Littorina*), which apparently refuged (possibly from des-

iccation stress) amongst the barnacle tests. Presumably, large clearings in stands of barnacles would develop more extensive algal cover than small clearings. This phenomenon is likely in any assemblage where natural enemies prefer, or are forced, to live largely within the phases of the community mosaic that surround a patch, while their prey occupy the interior of the patch. Quite the opposite pattern of interaction between patch size and grazing may occur in some communities. For example, the introduced Klamath weed (*Hypericum perforatum*) grows best in open sunny sites (Huffaker and Kennett 1959, Huffaker 1967). Its introduced enemy, the beetle *Chrysolina quadrigemina*, prefers to lay its eggs in sunny areas. As a consequence, the leaf-eating beetle larvae have largely eliminated the weed from open areas. The weed is now more common in shady areas, where the introduced enemy is less abundant. Viewed from the perspective of a large-scale mosaic, the weed is probably more common in small open patches in the landscape than in large ones because of the interaction between patch size (and its influence on the light regime and the population dynamics of the introduced enemy). Cases of gap-size specialization by terrestrial plants are usually explained as adaptations to variations in the physical environment (e.g., light, humidity, soil type) with gap size (Richards 1952, Davis and Cantlon 1969, Whitmore 1975, 1978, Grubb 1977, Hartshorn 1978, 1980, Bormann and Likens 1979:Chapter 4, Denslow 1980, Gross 1980). Bazzaz and Pickett (1980), however, suggested that gap size may affect the abundances of animals that interact (negatively or positively) with plants in tropical forests. Further investigation of this latter phenomenon might prove fruitful.

Patch size and the regional dynamics of algal populations

One might infer from earlier comments that the persistence of populations of the algal species considered in this study depends on the predictable availability of open space within mussel beds. Such an inference would be incorrect. Many of these algal species live in areas outside of the tidal range over which *Mytilus californianus* does or could dominate in the absence of predation or physical disturbance (Paine 1974). *Pelvetiopsis*, *Mastocarpus*, and *Endocladia* are common at tidal heights above the apparent physiological limits (Paine 1976) of the mussel (W. Sousa, personal observation). In addition, most of the algal species examined in this investigation grow epizoically on mussel valves in the study area. The persistence of other species not considered in this study (for example the sea palm *Postelsia palmaeformis*) may indeed depend on regular physical and biological disturbance of *Mytilus californianus* beds (Dayton 1973, Paine 1979). This alga does not live above the upper limit of mussels on the shore, and only occasionally grows on mussel valves. The regional reproductive populations of all of the algae

examined in this study are nonetheless enhanced by the availability of patches generated by the disturbance of mussel beds. In addition, the size distribution of such patches probably has an important influence on the regional abundances of these species. Small patches provide grazer-resistant species with a refuge from competition. The competitively dominant but grazer-vulnerable species find refuge from high levels of grazing activity in larger patches, where grazers are less common. Although all of these algal species face local extinction as the lateral encroachment of *M. californianus* gradually closes a patch, the rate of closure is slow enough that one or more generations of algae will have released propagules, some of which will colonize younger patches of appropriate sizes nearby.

Studies of other marine communities have also concluded that patch size strongly affects community dynamics. For example, small, isolated substrata (i.e., artificial settling plates and shells of bivalves) can provide refuges for competitively inferior species in assemblages of colonial invertebrates (Jackson 1977, Karlson 1978, Kay and Keough 1981, Keough 1984). Fewer species colonize small, isolated patches, and variation in recruitment among such patches is higher than among large isolated patches. Therefore, individuals or colonies of a competitively inferior species that recruit to the former are less likely to encounter dominant competitors than are those that recruit to the latter. Jackson (1977) suggests that under these conditions the larvae of competitively inferior species may evolve the ability to settle selectively in small isolated patches of substratum. Data on bryozoan recruitment in Keough (1984) support this hypothesis. Quite the opposite patterns might be expected if the patches occur in continuous habitats (Kay and Keough 1981, Keough 1984). In such habitats, small patches are rapidly closed by the vegetative ingrowth of colonies of the dominant species that surround the patch, and inferior competitors will persist longer in large patches than in small ones.

The dynamics of patch occupation in mussel beds are analogous to the second situation described above, since encroaching mussels close small patches more rapidly than large ones (Paine and Levin 1981 and this study; also see Schoener and Schoener 1981). It would be incorrect, however, to conclude that only the availability of large patches need be considered when making predictions about the regional dynamics of algal species that colonize patches. The 25 × 25 cm patches considered in this study closed sufficiently slowly to serve as important refuges from interalgal competition. The refuge effect derives from (1) the influence of patch size on grazing intensity, and (2) the apparent tradeoff between grazer resistance and competitive ability in members of the algal assemblage. Since the rates of algal recruitment to small vs. large patches differed little when the density of grazers was reduced, the

mechanism proposed by Jackson (1977) and Kay and Keough (1981) does not appear to apply in this case.

Effect of patch location on recruitment

Clearly, the position of a patch of open space along some physical gradient (e.g., tidal height) may strongly influence the composition of its colonists and the outcome of their interactions. The importance of a patch's position with respect to other patches differing in successional age but occurring at the same point along a physical gradient is less apparent. The extent to which the position of patches relative to each other must be considered when attempting to predict the regional dynamics of a population will depend on the manner in which a patch is colonized. In the model of patch dynamics discussed earlier (Levin 1976, 1978), species may recruit to a patch (1) from a "bath" of propagules that originates in regions beyond the boundaries of the system of patches as defined by the investigator, and/or (2) from other patches within the system. The spatial scale of a study will determine the relative contributions of recruits from these two sources. At one extreme the system consists of a single patch, and all recruitment is from the "bath," while at the other extreme, one global system is envisioned that includes all patches, the process of recruitment being entirely internal to the system. (In essence the "bath" ceases to exist.) At any one spatial scale, the relative contributions of the two recruitment terms in the model are likely to be species-specific and dependent upon dispersal ability.

The recruitment and local adult abundance of several species of brown and red algae that are common in later successional stages were shown to be highly and positively correlated, suggesting that a majority of their propagules are dispersed relatively short distances. However, with the exception of *Fucus*, this correlation could be demonstrated only under conditions of artificially reduced grazing in the sizes of patches employed in this study. In the case of *Fucus*, the correlation persisted even under conditions of moderate grazing in the 50 × 50 cm patches without copper barriers. Under natural conditions, limpet density declines with increasing patch size, a consequence of the concomitant decline in the ratio of perimeter length to area. Therefore, the strength of the correlations between recruitment and local adult abundance for these species should increase with increasing patch size (assuming a constant patch shape). Dayton's (1973) and Paine's (1979) experimental studies of *Postelsia* provide further evidence of short-range dispersal of propagules by intertidal macroalgae. Their results indicate that spores are dispersed only 1–3 m from a stand of parent plants. Other species, including early successional green algae and competitively inferior grazer-resistant species, showed no correlation regardless of patch size or the abundance of grazers. Presumably, these species disperse their propagules relatively long

distances, thus taking advantage of short-lived and/or rare spatial refuges.

If indeed the propagules of many of the common species of algae inhabiting patches within mussel beds disperse only over short distances (< 1–2 m), important consequences for both experimental and theoretical investigations of the system's dynamics are implied. For such species, the idea that recruits to patches come from a "bath" of propagules originating outside of the system would be inappropriate (assuming the region of interest is that encompassed by most field studies: tens or hundreds of metres of shoreline). Almost all the colonizing propagules of these species with short-range dispersal would come from other patches within the region. In contrast, the notion of a "bath" might be appropriate for other species (e.g., early successional green algae and many sessile invertebrates) whose propagules appear to disperse over greater distances. However, it is likely that the distribution of such propagules in the water column is spatially and temporally heterogeneous (e.g., Hruby and Norton 1979), and, therefore, that the rates of settlement of these propagules into open patches varies considerably.

Short-range dispersal in algae may produce an analogous situation to that predicted for forests in which the recruitment of young trees is proportional to the local abundance of conspecific adults (Acevedo 1981, Horn 1981a, b). Different algal assemblages, initiated by accidents of history, may develop within adjacent patches along an otherwise homogeneous section of seashore. This seems to have occurred in the experimental patches created in this study. Only time will tell whether the observed variation in the relative abundances of species among patches is persistent.

For algal species whose propagules do not travel far, the dispersion of patches (as well as the age and size structure of patches) may affect the regional dynamics of their populations, especially in areas where these species do not grow on mussel valves. The degree to which the dispersion of patches must be considered may itself depend on their size distribution. If large patches predominate, the influence of grazers on algal populations will be minimized, recruitment will be related to local adult abundance, and patch dispersion will be important. On the other hand, if most patches are small, the influence of grazers on algal populations will be intensified, recruitment will be uncoupled from local adult abundance, and consideration of patch dispersion may be relatively unimportant.

ACKNOWLEDGMENTS

Many people assisted me in this study. To all of them, I am grateful. I especially thank the data recorders, wave watchers, and limpet pickers who worked with me in the field during the 4 yr of this study. They include V. Chow, A. Devreux, R. Lum, B. Okamura, D. Sousa, G. Sousa, and L. Sousa. For statistical consultation and computing I thank especially H.

Tsao as well as B. Yandell and C. Langhauser. T. DeCew and J. West kindly verified my identifications of algae and provided unpublished information regarding impending revisions of nomenclature. For valuable comments on earlier drafts of this paper I thank J. Cubit, P. Dayton, B. Okamura, R. Paine, J. Sutherland, T. Turner, J. Watanabe, and an anonymous reviewer.

Space in the Bodega Marine Laboratory and permission to work within the Marine Life Refuge were provided by the director, C. Hand, and the business managers, P. Connors and P. Siri. This research was supported by grants from the National Science Foundation Program in Biological Oceanography (OCE 80-08530) and the Faculty Committee on Research, University of California, Berkeley.

LITERATURE CITED

- Abbott, I. A., and G. J. Hollenberg. 1976. Marine algae of California. Stanford University Press, Stanford, California, USA.
- Acevedo, M. F. 1981. On Horn's Markovian model of forest dynamics with particular reference to tropical forests. *Theoretical Population Biology* 19:230–250.
- Anderson, E. K., and W. J. North. 1966. In situ studies of spore production and dispersal in the giant kelp *Macrocystis*. Pages 73–86 in E. G. Young and J. L. McLachlan, editors. Proceedings of the Fifth International Seaweed Symposium. Pergamon Press, New York, New York, USA.
- Barbour, M. G., R. B. Craig, F. R. Drysdale, and M. T. Ghiselin. 1973. Coastal ecology. University of California Press, Berkeley, California, USA.
- Bayne, B. L. 1964. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *Journal of Animal Ecology* 33:513–523.
- Bazzaz, F. A., and S. T. A. Pickett. 1980. Physiological ecology of tropical succession: a comparative review. *Annual Review of Ecology and Systematics* 11:287–310.
- Bold, H. C., and M. J. Wynne. 1978. Introduction to the algae. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
- Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York, New York, USA.
- Brawley, S. H., and W. H. Adey. 1981. The effects of micrograzers on algal community structure in a coral reef microcosm. *Marine Biology* 61:167–177.
- Brock, R. E. 1979. An experimental study on the effects of grazing by parrotfishes and the role of refuges in benthic community structure. *Marine Biology* 51:381–388.
- Buss, L. W., and J. B. C. Jackson. 1979. Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *American Naturalist* 113:223–234.
- Chesson, P. 1978. Predator-prey theory and variability. *Annual Review of Ecology and Systematics* 9:323–347.
- Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117:923–943.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.
- . 1979. Tropical rain forests and coral reefs as open nonequilibrium systems. Pages 141–163 in R. M. Anderson, B. D. Turner and L. R. Taylor, editors. Population dynamics. Blackwell Scientific Publications, Oxford, England.
- Cubit, J. 1975. Interactions of seasonally changing physical factors and grazing affecting high intertidal communities on a rocky shore. Dissertation. University of Oregon, Eugene, Oregon, USA.
- Davis, R. M., and J. E. Cantlon. 1969. Effect of size area open to colonization on species composition in early old-

- field succession. *Bulletin of the Torrey Botanical Club* **96**: 660–673.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41**:351–389.
- . 1973. Dispersion, dispersal, and persistence of the annual intertidal alga, *Postelsia palmaeformis* Ruprecht. *Ecology* **54**:433–438.
- . 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs* **45**:137–159.
- Dean, T. A. 1981. Structural aspects of sessile invertebrates as organizing forces in an estuarine fouling community. *Journal of Experimental Marine Biology and Ecology* **53**: 163–180.
- Dean, T. A., and L. E. Hurd. 1980. Development in an estuarine fouling community: the influence of early colonists on later arrivals. *Oecologia (Berlin)* **46**:295–301.
- De Blok, J. W., and H. F. M. Geelen. 1958. The substratum required to the settling of mussels (*Mytilus edulis* L.). *Archives Neerlandaises de Zoologie* **13**(supplement):446–460.
- Denslow, J. S. 1980. Gap partitioning among tropical rain-forest trees. *Biotropica* **12**(supplement):47–55.
- Dethier, M. N. 1981. Heteromorphic algal life histories: the seasonal pattern and response to herbivory of the brown crust, *Ralfsia californica*. *Oecologia (Berlin)* **49**:333–339.
- Deysher, L., and T. A. Norton. 1982. Dispersal and colonization in *Sargassum muticum* (Yendo) Fensholt. *Journal of Experimental Marine Biology and Ecology* **56**:179–195.
- 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.
- Foster, M. S. 1982. Factors controlling the intertidal zonation of *Iridaea flaccida* (Rhodophyta). *Journal of Phycology* **18**:285–294.
- Frank, P. W. 1981. A condition for a sessile strategy. *American Naturalist* **118**:288–290.
- . 1982. Effects of winter feeding on limpets by Black Oystercatchers, *Haematopus bachmani*. *Ecology* **63**:1352–1362.
- Geiselman, J. A. 1980. Ecology of chemical defenses of algae against the herbivorous snail, *Littorina littorea*, in the New England rocky intertidal community. Dissertation. Woods Hole Oceanographic Institution/Massachusetts Institute of Technology, Woods Hole, Massachusetts, and Cambridge, Massachusetts, USA.
- Gross, K. L. 1980. Colonization by *Verbascum thapsus* (Mullein) of an old-field in Michigan: experiments on the effects of vegetation. *Journal of Ecology* **68**:919–927.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews of the Cambridge Philosophical Society* **52**:107–145.
- Guiry, M. D., J. A. West, D. H. Kim, and M. Masuda. 1984. Reinstatement of the genus *Mastocarpus* Kützting (Rhodophyte). *Taxon* **33**:53–63.
- Hartshorn, G. S. 1978. Tree falls and tropical forest dynamics. Pages 617–638 in P. B. Tomlinson and M. H. Zimmermann, editors. *Tropical trees as living systems*. Cambridge University Press, London, England.
- . 1980. Neotropical forest dynamics. *Biotropica* **12**(supplement):23–30.
- Hartwick, E. B. 1976. Foraging strategy of the black oyster catcher (*Haematopus bachmani* Audubon). *Canadian Journal of Zoology* **54**:142–155.
- Hawkins, S. J. 1981. The influence of season and barnacles on the algal colonization of *Patella vulgata* exclusion areas. *Journal of the Marine Biological Association of the United Kingdom* **61**:1–15.
- Hay, M. E. 1981a. Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. *American Naturalist* **118**:520–540.
- . 1981b. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* **62**:739–750.
- Hixon, M. A., and W. N. Brostoff. 1981. Fish grazing and community structure of Hawaiian reef algae. Pages 507–514 in E. D. Gomez, C. E. Birkeland, R. W. Buddemeier, R. E. Johannes, J. A. Marsh, Jr., and R. T. Tsuda, editors. *Proceedings of the Fourth International Coral Reef Symposium, Manila, Philippines*. Marine Sciences Center, University of the Philippines, Quezon City, Philippines.
- Horn, H. S. 1981a. Succession. Pages 253–271 in R. M. May, editor. *Theoretical ecology*. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- . 1981b. Some causes of variety in patterns of secondary succession. Pages 24–35 in D. C. West, H. H. Sugart, and D. B. Botkin, editors. *Forest succession*. Springer-Verlag, New York, New York, USA.
- Hruby, T., and T. A. Norton. 1979. Algal colonization on rocky shores in the Firth of Clyde. *Journal of Ecology* **67**: 65–77.
- Huffaker, C. B. 1967. A comparison of the status of biological control of St. Johnswort in California and Australia. *Mushi* **39**(supplement):51–73.
- Huffaker, C. B., and C. E. Kennett. 1959. A ten-year study of vegetational changes associated with the biological control of Klamath weed. *Journal of Range Management* **12**: 69–82.
- Hutchinson, G. E. 1951. Copepodology for the ornithologist. *Ecology* **32**:571–577.
- Jackson, J. B. C. 1977. Habitat area, colonization, and development of epibenthic community structure. Pages 349–358 in B. F. Keegan et al., editors. *Biology of benthic organisms*. Pergamon Press, Oxford, England.
- Karlson, R. H. 1978. Predation and space utilization patterns in a marine epifaunal community. *Journal of Experimental Marine Biology and Ecology* **31**:225–240.
- Karlson, R. H., and J. B. C. Jackson. 1981. Competitive networks and community structure: a simulation study. *Ecology* **62**:670–678.
- Kay, A. M., and J. J. Keough. 1981. Occupation of patches in the epifaunal communities on pier pilings and the bivalve *Pinna bicolor* at Edithburgh, South Australia. *Oecologia (Berlin)* **48**:123–130.
- Keough, M. J. 1984. Effects of patch size on the abundance of sessile marine invertebrates. *Ecology* **65**:423–437.
- Levin, S. A. 1976. Population dynamic models in heterogeneous environments. *Annual Review of Ecology and Systematics* **7**:287–310.
- . 1978. Pattern formation in ecological communities. Pages 433–465 in J. H. Steele, editor. *Spatial pattern in plankton communities*. Plenum, New York, New York, USA.
- . 1981. The role of theoretical ecology in the description and understanding of populations in heterogeneous environments. *American Zoologist* **21**:865–875.
- Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation and community structure. *Proceedings of the National Academy of Sciences (USA)* **71**:2744–2747.
- Levin, S. A., and R. T. Paine. 1975. The role of disturbance in models of community structure. Pages 56–67 in S. A. Levin, editor. *Ecosystem analysis and prediction*. Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania, USA.
- Littler, M. M., and M. S. Doty. 1975. Ecological components structuring the seaward edges of tropical Pacific reefs: the distribution, communities and productivity of *Porolithon*. *Journal of Ecology* **63**:117–129.

- Loucks, O. L. 1970. Evolution of diversity, efficiency, and community stability. *American Zoologist* **10**:17–25.
- Lubchenco, J., and J. Cubitt. 1980. Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. *Ecology* **61**:676–687.
- Lubchenco, J., and S. D. Gaines. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. *Annual Review of Ecology and Systematics* **12**:405–437.
- Mastro, E., V. Chow, and D. Hedgecock. 1982. *Littorina scutulata* and *Littorina plena*: sibling species status of two prosobranch gastropod species confirmed by electrophoresis. *Veliger* **24**:239–246.
- Nelson, W. A. 1982. Development, anatomy and reproduction of *Analipus japonicus* (Harv.) Wynne (Phaeophyta, Heterochordariaceae). *Botanica Marina* **25**:357–369.
- 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.
- Osman, R. W. 1977. The establishment and development of a marine epifaunal community. *Ecological Monographs* **47**:37–63.
- Padilla, D. 1981. Selective agents influencing the morphology of coralline algae. Thesis. Oregon State University, Corvallis, Oregon, USA.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* **100**:65–75.
- . 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia (Berlin)* **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. *Academy of Natural Sciences of Philadelphia Special Publication* **12**:245–270.
- . 1979. Disaster, catastrophe and local persistence of the sea palm *Postelsia palmaeformis*. *Science* **205**:685–687.
- . 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* **49**:667–685.
- Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs* **51**:145–178.
- Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnology and Oceanography* **14**:710–719.
- Polanshek, A. R., and J. A. West. 1977. Culture and hybridization studies on *Gigartina papillata* (Rhodophyta). *Journal of Phycology* **13**:141–149.
- Richards, P. W. 1952. *The tropical rain forest*. Cambridge University Press, Cambridge, England.
- Ricketts, E. F., J. Calvin, and J. W. Hedgpeth. 1968. *Between Pacific tides*. Fourth edition. Stanford University Press, Stanford, California, USA.
- Robles, C. 1982. Disturbance and predation in an assemblage of herbivorous diptera and algae on rocky shores. *Oecologia (Berlin)* **54**:23–31.
- Robles, C. D., and J. Cubitt. 1981. Influence of biotic factors in an upper intertidal community: dipteran larvae grazing on algae. *Ecology* **62**:1536–1547.
- Russ, G. R. 1982. Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. *Oecologia (Berlin)* **53**:12–19.
- Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. *American Naturalist* **111**:337–359.
- . 1978. Coexistence of coral reef fishes—a lottery for living space. *Environmental Biology of Fishes* **3**:85–102.
- . 1979. Recruitment, loss, and coexistence in a guild of territorial coral reef fishes. *Oecologia (Berlin)* **42**:159–177.
- . 1982. Stock-recruitment relationships and regional coexistence in a lottery competitive system: a simulation study. *American Naturalist* **120**:139–159.
- Schoener, A., and T. W. Schoener. 1981. The dynamics of the species-area relationship in marine fouling systems. 1. Biological correlates of changes in the species-area slope. *American Naturalist* **118**:339–360.
- Seed, R. 1969a. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. 1. Breeding and settlement. *Oecologia (Berlin)* **3**:277–316.
- . 1969b. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. 2. Growth and mortality. *Oecologia (Berlin)* **3**:317–350.
- Slocum, C. J. 1980. Differential susceptibility to grazers in two phases of an intertidal alga: advantages of heteromorphic generations. *Journal of Experimental Marine Biology and Ecology* **46**:99–110.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. Second edition. W. H. Freeman, San Francisco, California, USA.
- Sousa, W. P. 1979a. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* **60**:1225–1239.
- . 1979b. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* **49**:227–254.
- Steinberg, P. D. 1984. Algal chemical defense against herbivores: allocation of phenolic compounds in the kelp *Alaria marginata*. *Science* **223**:405–407.
- Steneck, R. S. 1982. A limpet-coraline alga association: adaptations and defenses between a selective herbivore and its prey. *Ecology* **63**:507–522.
- Steneck, R. S., and L. Watling. 1982. Feeding capabilities and limitations of herbivorous molluscs: a functional group approach. *Marine Biology* **68**:299–319.
- Suchanek, T. H. 1978. The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* **31**:105–120.
- . 1979. The *Mytilus californianus* community: studies on the composition structure, organization, and dynamics of a mussel bed. Dissertation. University of Washington, Seattle, Washington, USA.
- . 1981. The role of disturbance in the evolution of life history strategies in the intertidal mussels *Mytilus edulis* and *Mytilus californianus*. *Oecologia (Berlin)* **50**:143–152.
- Sutherland, J. 1970. Dynamics of high and low populations of the limpet, *Acmaea scabra* (Gould). *Ecological Monographs* **40**:169–188.
- Sutherland, J. P., and R. H. Karlson. 1977. Development and stability of the fouling community at Beaufort, North Carolina. *Ecological Monographs* **47**:425–446.
- Underwood, A. J., and P. Jernakoff. 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. *Oecologia (Berlin)* **48**:221–233.
- VanBlaricom, G. R. 1982. Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. *Ecological Monographs* **52**:283–305.
- Vine, P. J. 1974. Effects of algal grazing and aggressive behavior of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral reef ecology. *Marine Biology* **24**:131–136.
- Wanders, J. B. W. 1977. The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles) III: the significance of grazing. *Aquatic Botany* **3**:357–390.
- West, J. A. 1972. The life history of *Petrocelis franciscana*. *British Phycological Journal* **7**:299–308.
- White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. *Botanical Review* **45**:229–299.
- Whitmore, T. C. 1975. *Tropical rain forests of the Far East*. Clarendon Press, Oxford, England.

- . 1978. Gaps in the forest canopy. Pages 639–655 in P. B. Tomlinson and M. H. Zimmermann, editors. *Tropical trees as living systems*. Cambridge University Press, London, England.
- Whittaker, R. H., and S. A. Levin. 1977. The role of mosaic phenomena in natural communities. *Theoretical Population Biology* 12:117–139.