Models and Mechanisms of Succession: An Example From a Rocky Intertidal Community

Article *in* Ecological Monographs · March 1991

DOI: 10.2307/1943001

Terence M Farrell
Stetson University

Models and Mechanisms of Succession: An Example From a Rocky Intertidal Community
Author(s): Terence M. Farrell
Source: *Ecological Monographs*, Vol. 61, No. 1 (Mar., 1991), pp. 95-113
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/1943001
Accessed: 10/02/2015 14:51

Ecological Monographs, 61(1), 1991, pp. 95–113

MODELS AND MECHANISMS OF SUCCESSION: AN EXAMPLE FROM A ROCKY INTERTIDAL COMMUNITY[1]

TERENCE M. FARRELL[2]
Department of Zoology, Oregon State University, Corvallis, Oregon 97331 USA

Abstract. An investigation of the processes that cause succession was performed in an intertidal community on the central Oregon coast. The community was dominated by barnacles and several species of macroalgae. The successional sequence was determined at three different sites by clearing sets of plots in a way that mimicked natural disturbance. Succession at each of these sites followed the same general sequence. A barnacle, *Chthamalus dalli,* first colonized the plots and was later replaced by a second barnacle, *Balanus glandula.* The macroalgae *Pelvetiopsis limitata, Fucus distichus,* and *Endocladia muricata* colonized the plots only after *Balanus* was established. While the order of species arrival and departure was consistent, the rate of succession varied greatly among sites. The sequence of community development that was observed at one site over a 36-mo period occurred in <12 mo in a nearby area. Differences in the rate of succession appeared to result from variation in the timing of successful *Balanus* recruitment.

The mechanisms of succession were investigated in a series of field experiments. An experiment with *Balanus*-removal, *Chthamalus*-removal, and control plots was used to assess the interactions between barnacles. A direct interaction, competition for space with *Balanus,* caused *Chthamalus* to decrease in abundance as succession proceeded. *Chthamalus* did not affect the establishment of *Balanus.* Successful *Balanus* recruitment depended on occasional periods of larval settlement followed by periods of favorable weather. At all three sites, algal colonization was dependent on the presence of barnacles. *Balanus* greatly facilitated algal colonization, while *Chthamalus* only weakly facilitated algal colonization. Facilitation of algal colonization by epoxy-filled barnacle tests indicated that facilitation resulted from barnacle tests altering the substrate, rather than the activities of the living animals. A factorial experiment involving manipulations of barnacle and consumer (limpet) abundances demonstrated that the facilitation of algae by barnacles is an indirect interaction that is mediated by limpets. Barnacles decreased limpet foraging activity and thereby increased algal abundance.

Succession in this community is complicated by several processes that are not included in traditional views of succession. (1) Not all early successional species have the same effect on the establishment of later successional species. This results in spatial variation in the rate of succession. (2) The model of succession is different in each step in the successional sequence. The *Chthamalus–Balanus* interaction is an example of the tolerance model, while the barnacle–algae interaction is an example of the facilitation model. (3) Both direct and indirect interactions between species determine the course of succession.

The results of this study support a general model that predicts the effect of consumers on the rate of succession. Consumers slowed succession in this community in two ways. First, limpets delayed the establishment of *Balanus* and the competitive exclusion of *Chthamalus.* Second, limpets delayed the establishment of macroalgae. Previous studies in marine and terrestrial habitats have found that consumers may slow, accelerate, or have no effect on the rate of succession and these observations are consistent with the predictions of this general model.

Key words: algae; barnacles; facilitation; herbivory; indirect interactions; interspecific competition; limpets; Oregon; rocky intertidal; succession.

INTRODUCTION

Ecological succession consists of the sequence of colonization and species replacement that occurs after a site is disturbed (Connell and Slatyer 1977). Disturbance can be defined as any process that removes much of the living biomass in a community. Recent investigations indicate that many, if not most, habitats are subject to frequent, patchy disturbances producing habitats that are a mosaic of different successional stages (reviewed by Pickett 1980, Sousa 1984, Pickett and White 1985). To understand these communities it is necessary to know the dynamics of succession.

To understand succession two general questions must

---

[1] Manuscript received 6 April 1989; revised 8 February 1990; accepted 20 March 1990.

[2] Present address: Box 8270, Biology Department, Stetson University, DeLand, Florida 32720 USA.

be answered: (1) What determines when each species becomes established after a disturbance, and (2) What determines when each species leaves the successional sequence? Species that are lost during the course of succession are often assumed to be victims of competitive exclusion by later successional species (Drury and Nisbet 1973, Connell and Slatyer 1977). Unfortunately, this assumption has rarely been experimentally tested (but see Menge 1976, Ellison 1987, Williams 1987).

There are two distinct answers to the question of what determines when a species becomes established in a successional sequence. If early colonists weakly interact with later successional species the appearance of a species will simply depend on when its propagules arrive in a disturbed area (Egler 1954, Connell and Slatyer 1977, Sousa 1979*a*). In this case, succession is simply a product of the life histories of the species in a community. Alternatively, if species interact strongly, the establishment of a species will be influenced by earlier colonists.

How do early colonists affect later successional species? Connell and Slatyer (1977) defined three models of succession by considering the net effect of early successional species on the establishment of later successional species (Connell et al. 1987). In the facilitation model, early successional species hasten the establishment of later colonists. In the tolerance model, the early successional species have little or no effect on the establishment of later colonists. In the inhibition model, early successional species slow the establishment of later colonists. Facilitation was thought to be the dominant model of succession in early studies of community development (Clements 1928, Egler 1954). More recent studies, however, have placed increasing emphasis on the inhibition model of succession (Drury and Nisbet 1973, Connell and Slatyer 1977, Sousa 1979*a*).

Understanding succession requires more than knowing just the model of succession. It is also important to determine the mechanism of succession, which is defined as the actual causal pathway that produces the net effect of the early colonists on the later successional species. A single model of succession may result from any one of a number of mechanisms. For example, facilitation can occur if the early arrivals increase the quality of soil (Clements 1928) or if early arrivals shield later colonists from herbivores (Lubchenco 1983, Harris et al. 1984, McAuliffe 1986).

The mechanisms involved in species interactions need to receive increasing attention (Tilman 1987). In particular, distinguishing between direct and indirect interactions is critical in developing an understanding of community dynamics (Bradley 1983, Bender et al. 1984). Indirect interactions occur when one species affects another by altering the abundance or behavior of a third species. Indirect interactions are known to affect competitive and predator–prey relationships (Levine 1976, Lawlor 1979, Vandermeer 1980), but have only recently been invoked as mechanisms of succession (Lubchenco and Menge 1978, Sousa 1979*a*, Lubchenco 1983, van Tamelen 1987).

Early views of succession focused on competitive interactions and the influence of colonists on the physical features of the environment. The influence of consumers on succession was largely ignored (Connell and Slatyer 1977). Several recent studies of succession have involved manipulations of consumers (reviewed by Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983). These studies indicate that consumers often have a strong influence on the rate of succession, but that succession may either be accelerated (Lubchenco and Menge 1978, Sousa 1979*a*, Day and Osman 1981, Robles and Cubit 1981, Lubchenco 1983), unaffected (Turner 1983*a*, Jernakoff 1985*a*), or slowed (Dayton 1975, Sousa et al. 1981, McBrien et al. 1983, Peer 1986). At present, however, no general predictive model of the influence of consumers on the rate of succession has been formulated.

A GENERAL MODEL OF THE EFFECT OF CONSUMERS ON THE RATE OF SUCCESSION

The qualitative effects of consumers on the rate of succession can be predicted from two factors: (1) the model of succession, and (2) the successional status of the species whose abundances are reduced by consumers (Fig. 1). The successional status of a species is determined by the order of colonization. Early successional species colonize soon after a disturbance, and their arrival is followed by the colonization of later successional species. For simplicity, consumers can be considered to remove mostly early successional species, equivalent amounts of early and later successional species, or mostly later successional species. In reality, both the consumer removal axis and the model of succession axis are continua. Predictions of this general model include the following. (1) If consumers remove mostly later successional species then succession will be slowed compared to succession in the absence of consumers regardless of the model of succession. (2) Equivalent removal in the inhibition model leads to no clear prediction. In this case, removal of the early colonists would hasten succession by decreasing inhibition, but this would be offset by consumption of later successional species, thereby slowing succession. (3) Equivalent removal in the tolerance model slows the rate of succession since removal of early colonists has no effect and removal of later successional species slows species replacement. (4) Equivalent removal in the facilitation model will greatly slow succession by both decreasing the facilitation provided by early successional species and by removing later successional species. (5) If consumers remove mostly early successional species the pace of succession is by definition dependent on the model of succession. In this case, consuming early successional species will either hasten succession in the inhibition model, have no effect on the rate of succession in the tolerance model, or slow succession in the facilitation model.

The intensity of consumption will influence the magnitude of the change in the rate of succession caused by the activities of consumers. If consumers have little influence on any species' abundance they will have little effect on the rate of succession regardless of the model of succession and the successional status of the species consumed. The expected difference in the rate of succession in the presence and absence of consumers is expected to be proportional to the intensity of consumption.

In this investigation, I examined the successional sequence in a high-zone rocky intertidal habitat, and determined the processes that controlled the establishment and loss of species during community development. This community exhibited complex successional processes. Two models of succession, tolerance and facilitation, occurred during succession. Furthermore, both direct and indirect interactions controlled key events in community development. Finally, the results supported the general model that predicts how consumers will affect the rate of succession.

The Study Sites

Experiments were done at three locations along the Oregon coast. The Fogarty Creek Point site (44°51′ N, 124°03′ W) was 19 km north of the two Yaquina Head sites (44°41′ N, 124°04′ W). The Yaquina Head sites were on the south side of a headland that extended 1.5 km seaward. These sites were therefore protected from oceanic waves coming from the north or northwest, but fully exposed to waves coming from the south or southwest. The Fogarty Creek Point site was on the seaward end of a smaller headland, and was directly exposed to waves coming from any direction. The experimental plots at both sites are located on horizontal or sloping (<45°) rock (basalt) surfaces. Mixed semidiurnal tides with an average daily range of ≈2.5 m occur along the Oregon coast. The study plots were in the high intertidal zone, ranging from 2.2 to 3.0 m above mean lower low water (MLLW). At this tidal height plots were occasionally not wetted at all during the daylight hours when a lower than average low high tide coincided with a period of very calm water and the higher high tide occurred at night.

A community of low diversity occurred at all sites. The two dominant species in this community were the fucoid alga *Pelvetiopsis limitata* and the barnacle *Balanus glandula*. The *Balanus–Pelvetiopsis* community occupies large areas of the high intertidal on exposed shores from central California to Vancouver Island, British Columbia (T. M. Farrell, *personal observation*). The only sessile animals commonly found in this community were *Balanus* and a smaller barnacle, *Chthamalus dalli*. In addition to *Pelvetiopsis*, three other species of macroalgae, the brown alga *Fucus distichus* and the red algae *Endocladia muricata* and *Mastocarpus papillatus* (=*Gigartina papillata*; Kim 1976), were common members of the community. These algae usually grew on the tests of *Balanus*. The most abundant herbivores were limpets, primarily *Lottia digitalis* and *L. strigatella* (formerly *Collisella digitalis* and *C. strigatella*; Lindberg 1986). Other common herbivores included *Littorina scutulata* and gammarid amphipods. Isopods, dipteran larvae, and grapsid crabs were rare. Sea stars and predatory snails are common lower in the intertidal zone at these sites but were usually not found in the high intertidal. Avian predators, including gulls (*Larus* spp.), American Black Oystercatchers (*Haematopus bachmani*), Surfbirds (*Aphriza virgata*), and Black Turnstones (*Arenaria melanocephala*), were abundant at these sites. Birds decrease limpet abundance at other sites on the Oregon coast (Frank 1982, Marsh 1986), and eat many of the other animals present in this community (Marsh 1984).

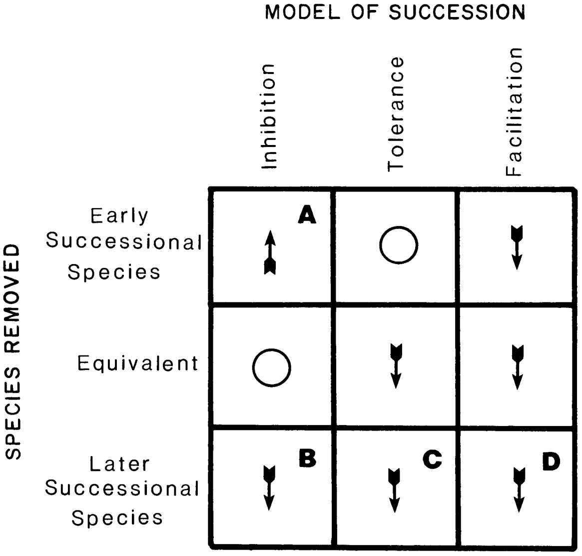


FIG. 1. A predictive model of the effect of consumers on the rate of succession (↑—consumers increase the rate of succession, ○—no effect, ↓—consumers decrease the rate of succession). Letters indicate examples of specific combinations of the two factors shown as dimensions of this contingency array (A: Lubchenco and Menge 1978, Sousa 1979*a*, Day and Osman 1981, Lubchenco 1983; B: Sousa et al. 1981; C: this study, the *Chthamalus–Balanus* interaction; D: this study, the barnacle–macroalgae interaction).

Although the *Balanus–Pelvetiopsis* community occurred at each of the study sites, they differed in subtle respects. The Fogarty Creek Point (Fogarty) site was the highest (2.4–3.0 m above MLLW). The Fogarty site covered the largest area, with plots spread along a 30 m length of shoreline. The plots were located along a wave-exposure gradient with the more seaward plots located at a higher tidal level. *Postelsia palmaeformis*, an alga that is found only in the most wave-exposed areas (Ricketts et al. 1985), grew near the plots at the seaward end of this site. *Fucus* was abundant only in the landward plots.

The Yaquina Head sites differed from each other in both tidal height and wave exposure. The Yaquina Head Low (Yaquina-low) site was an area ≈4 m in length with plots ranging from 2.2 to 2.6 m above MLLW. The plots were near the seaward edge of a basaltic platform and therefore slightly more exposed to wave action than the Yaquina Head High (Yaquina-high) site. The Yaquina-high plots were located on a 20 m length of shoreline that extended on both sides of the Yaquina-low site. The Yaquina-high plots ranged from 2.2 to 2.9 m above MLLW. Both Yaquina Head sites had higher barnacle cover than the Fogarty site. *Fucus* did not occur at the two Yaquina Head sites.

METHODS

Field experiments were used at all three sites to investigate succession in the *Balanus–Pelvetiopsis* community. The experimental design differed at each of the three sites. Some aspects of succession were investigated at all three sites to determine the generality of the experimental results. Other aspects of community development were investigated at a single site.

Experimental design: Yaquina-high

The Yaquina-high experiment was primarily designed to answer three questions: (1) What occurs in unmanipulated portions of the community? (2) What is the pattern of community development after a disturbance? (3) How do barnacles affect algae during succession?

In April 1983, I initiated an experiment near the upper edge of the *Balanus–Pelvetiopsis* zone to answer these questions. The experimental units were 21 square plots with 15 cm sides. The corners of each plot were marked with marine epoxy putty (splash zone compounds, Koppers Company, Los Angeles, California). These plots were used in a randomized block design consisting of seven blocks that contained a replicate of each of the three treatments. The treatments were totally unmanipulated plots, cleared plots, and cleared, barnacle-removal plots. The unmanipulated plots were not perturbed after the corners were marked. In the other two treatments the plots were scraped with a putty knife to remove upright organisms. Scraping, like natural disturbance, left large areas covered by the calcareous bases of *Balanus* and smaller areas covered by algal crusts (primarily the encrusting stage of *Mastocarpus papillatus*). The cleared plots used in all three experiments fell within the size range of the abundant, naturally occurring disturbances in this community (Farrell 1987, 1989). The cleared plots were not perturbed after scraping. In the cleared, barnacle-removal plots both species of barnacles were removed with a blunt probe during each visit.

Experimental design: Yaquina-low

The Yaquina-low experiment was primarily designed to answer five questions: (1) What is the pattern of community development after a disturbance? (2) How does *Chthamalus* affect *Balanus* during succession? (3) How does *Balanus* affect *Chthamalus* during succession? (4) How do barnacles affect macroalgae during succession? (5) Do nonliving barnacle tests have the same effect on macroalgae as live barnacles?

In September 1984 I initiated an experiment near the lower edge of the *Pelvetiopsis–Balanus* zone to answer these questions. The experimental units were 30 square plots with 6-cm sides. At the start of the experiment all plots were scraped with a putty knife and their corners marked with epoxy-putty. The plots were used in a randomized block design with six replicates of five treatments.

The five treatments were: (1) control, (2) barnacle-removal, (3) *Balanus*-removal, (4) *Chthamalus*-removal, and (5) *Balanus* test-addition. The control plots were not perturbed after the initial scraping. Barnacles of one or both species were removed as they settled in the *Balanus*-removal, *Chthamalus*-removal, and barnacle-removal plots. Adult *Balanus* shells were prepared for the test-addition plots by scraping them off the rock and heat-sterilizing them at 175°C for 0.5 h. The animal was removed from the test and the interior was filled with epoxy putty in a manner that left the tergum and scutum in place. These tests were then attached to the rock with epoxy putty until the plots were almost completely covered with tests.

I mistakenly removed all barnacles from one of the *Balanus*-removal plots early in the experiment. In all comparisons that include the *Balanus*-removal plots the sample size is therefore five, not six.

Experimental design: Fogarty

The Fogarty experiment was primarily designed to answer four questions: (1) What was the pattern of community development after a disturbance? (2) How do barnacles affect macroalgae during succession? (3) How does an abundant group of herbivores, limpets, affect succession? (4) Is the effect of barnacles on algae mediated by limpets?

The experiment was initiated at Fogarty in April 1984. The experimental units were square plots with 8-cm sides. At the start of the experiment all plots were scraped with a putty knife and their corners marked with small pieces of epoxy putty. The experiment consisted of a randomized block design with eight blocks. Each block contained a replicate of the following four treatments: (1) barnacles and limpets present, (2) barnacles present, limpets removed, (3) barnacles removed, limpets present, and (4) barnacles and limpets removed. These four treatments constituted a complete factorial design with barnacles and limpets removed singly and in combination. Limpets were excluded by 3 cm wide copper-paint barriers, which limpets did not cross (Cubit 1984). Since copper paint appears to have little or no effect on intertidal organisms, this method has been frequently used to exclude limpets from intertidal plots (Farrell 1988). The paint barrier was placed 10 cm beyond the edge of the experiment plot to produce a buffer zone of intact barnacles and algae between the paint and the plot. Any limpets found inside the paint barriers were removed manually.

Data collection

In all three experiments, the sites were visited approximately monthly to maintain the treatments and to observe changes in the experimental units. Data were collected at intervals of ≈4 mo. At each census period I determined the abundance and species composition of the macroscopic organisms occupying the plots. *Littorina* and algal thalli were counted in the entire plot. Individual *Endocladia* thalli were not always discernible because the filamentous thalli of adjacent individuals would grow together. A single clump of *Endocladia* was counted as an individual, leading to a conservative estimate of thallus density. At Yaquina-high, barnacles were counted in five, randomly chosen, 3 × 3 cm square subunits within each plot. At the other sites, barnacles were counted in four, randomly chosen, 2 × 2 cm (Fogarty) or 1.5 × 1.5 cm subunits (Yaquina-low).

In March 1986 barnacle size distributions were determined in the Yaquina-low experiment. Barnacle size was measured as the basal diameter along the rostral–carinal axis. Ten individuals of each species were measured in each control plot. Ten individuals of the only species present were measured in the single-species removal plots. Barnacles were chosen for measurement by finding the individuals whose aperture center was closest to 1 of 10 uniformly spaced dots on a vinyl sheet that was placed over the plot.

I estimated the percent of the rock surface that was covered by each species using two categories of cover: (1) primary percent cover, a measure of the portion of the plot to which a species is directly attached, and (2) secondary cover, a measure of the proportion of the plot that an alga overlies. Similar methods of quantification were used for these two types of cover. At Yaquina-high, I estimated percent cover using a Plexiglas table with a uniform array of holes. The legs of this table fit into holes drilled in the epoxy-putty plot corner markers, so the same locations were sampled at each census. Thirty-seven holes were used because the holes were arranged in a 7 × 7 array (49 holes), but the three holes closest to each corner marker (12 holes) were not used because they were often over the epoxy corner markers. The number of holes that was located above a species was divided by the total number of holes to calculate the estimated percent cover for that species. At Yaquina-high, I also estimated the proportion of the barnacle cover that had attached algae. Cover estimates at Yaquina-low and Fogarty were made using transparent vinyl sheets with a uniform array of 50 ink dots.

Data analysis

I used analysis of variance techniques (ANOVA) for randomized block designs in most of the statistical tests in this study. When F_{max} tests ($\alpha = .05$) indicated that raw data violated the assumption of homogeneity of variances, I transformed the data using log or arcsine transformations (Sokal and Rohlf 1981). The transformed data were analyzed with ANOVAs if the heteroscedasticity was reduced to nonsignificant levels. After performing ANOVAs, I made probability plots of the residuals to determine if error terms were normally distributed.

In some cases data transformation did not reduce heteroscedasticity. In these situations I chose one of the following three options. First, when only two treatment groups were being compared, I analyzed the data using the Wilcoxon signed-rank test, a nonparametric analog of the paired *t* test. The blocking factor was used as the pairing criterion in this test. Second, if several treatments were of interest and one of two treatments had an extreme variance, I removed these groups from the analysis and did an ANOVA on the groups with homogeneous variances. Extreme variances usually occurred when all or most replicates of a treatment group had zero values. Third, in a few cases I did no statistical analysis. When an ANOVA was statistically significant, I used a Student-Newman-Keuls (SNK) test to determine which means differed significantly.

Statistical tests were usually performed for each sampling period in a successional sequence. I used a Bonferroni correction to insure that performing several tests did not lead to an increased probability of Type I error. In the Bonferroni correction the P value of each test is divided by the number of tests being made in the time series. For example, if five statistical tests were performed on a time series, then each test would require a P value of $<.01$ to be significant at $\alpha = .05$. For time series with >5 data collections a statistical analysis was performed for every other sampling period. This reduced the number of tests made and thereby had the desirable effect of increasing the power of each individual test (Toft and Shea 1983).

RESULTS

Unmanipulated plots

Unmanipulated plots were monitored for 33 mo at Yaquina-high. The mean cover of both barnacle species remained stable during this period of time (Fig. 2A), with *Balanus* covering ≈80%, and *Chthamalus* covering ≈5% of the rock surface. The great majority

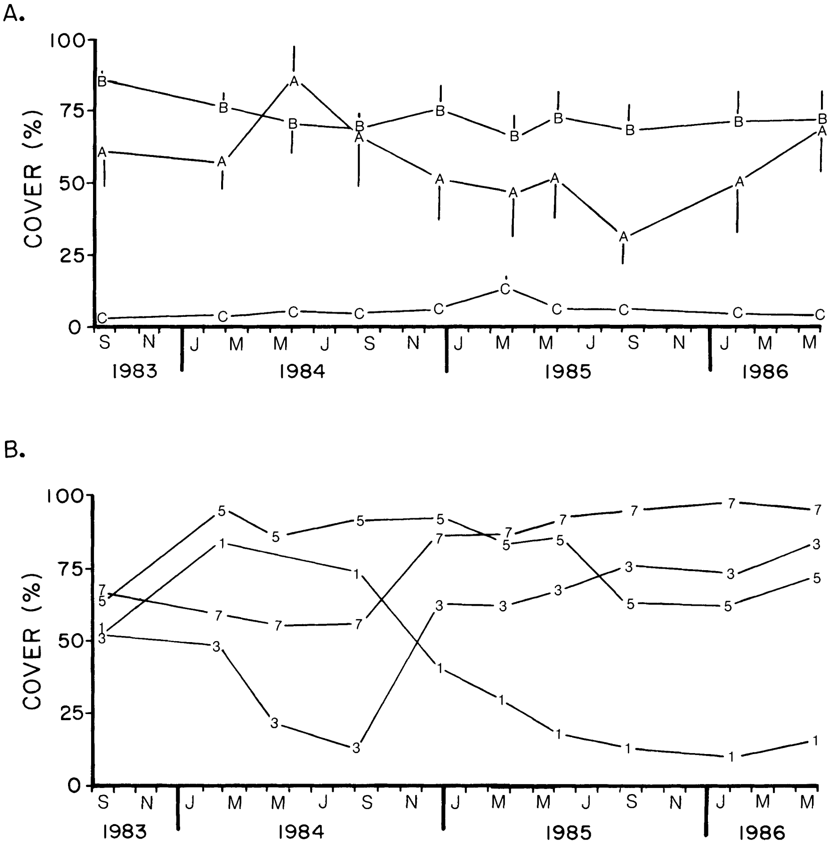


FIG. 2. (A) Substrate cover (mean ± 1 SE) in the unmanipulated plots at Yaquina-high (A = macroalgae, B = *Balanus,* C = *Chthamalus*). (B) *Balanus* cover in the four odd-numbered unmanipulated plots (other plots exhibit similar patterns but are not shown for clarity).

of the remaining 15% of the substrate was unoccupied by macroorganisms. Algal cover changed seasonally, with decreases in the summer and increases in the late winter and spring.

The constancy in mean barnacle cover masked the large changes in cover that occurred in several individual plots (Fig. 2B). Large disturbances decreased *Balanus* to <10% cover in several plots. Disturbance appeared to result from wave shear that removed clumps of barnacles and algae from the rock. Disturbance resulting from the impact of loose rocks or logs appeared to be uncommon. Loose objects were rarely observed at the study sites, and wood fibers and chipped substrate were not observed in recently disturbed areas. These disturbances were gradual. The size of open areas increased over a 6–12 mo period as patches of barnacles adjacent to disturbed patches washed off the rock. Recruitment and growth increased total barnacle cover. Since these changes did not occur synchronously in different plots the mean barnacle cover remained fairly constant.

Macroalgae usually grew on the tests of living barnacles. The proportion of *Balanus* with epizoic macroalgae varied between 10 and 35% (Fig. 3). Almost all of this cover was composed of the two most abundant algae, *Pelvetiopsis* and *Endocladia.*

The successional sequence

At each of the three sites, I cleared plots and followed the development of the *Balanus–Pelvetiopsis* community. These plots served as controls for the three experiments. At Yaquina-high, *Chthamalus* was abundant early in the successional sequence, but its cover decreased as *Balanus* became abundant (Fig. 4A). After 3 yr *Balanus* covered >70% of the rock surface. Macroalgae, primarily *Pelvetiopsis* and *Endocladia,* recruited to the plots after *Balanus* became established. The algae grew almost exclusively on the tests of *Balanus.*

At Yaquina-high, community structure in the cleared plots converged with the unmanipulated plots over 3 yr of succession (Figs. 2A and 4A). *Balanus* cover at the end of the study was almost identical in the cleared and unmanipulated plots. *Chthamalus* cover at the end of the study was significantly higher in the cleared plots than the unmanipulated plots (ANOVA, $n = 7$, $P = .013$), but was decreasing rapidly in the cleared plots. Algal cover was also significantly higher in the unmanipulated plots (ANOVA, $n = 7$, $P = .025$), but it

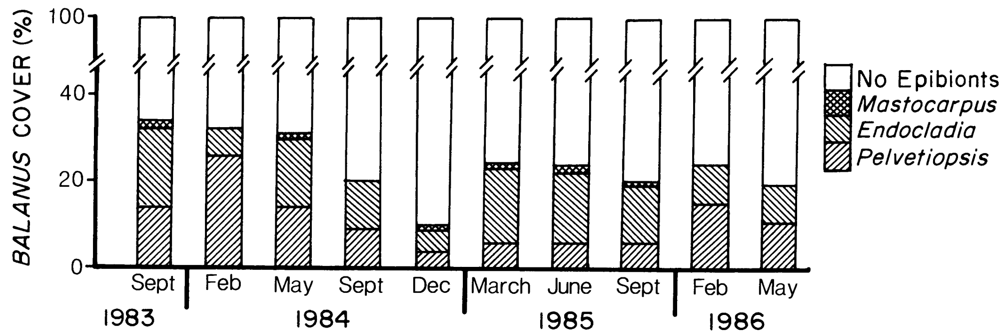
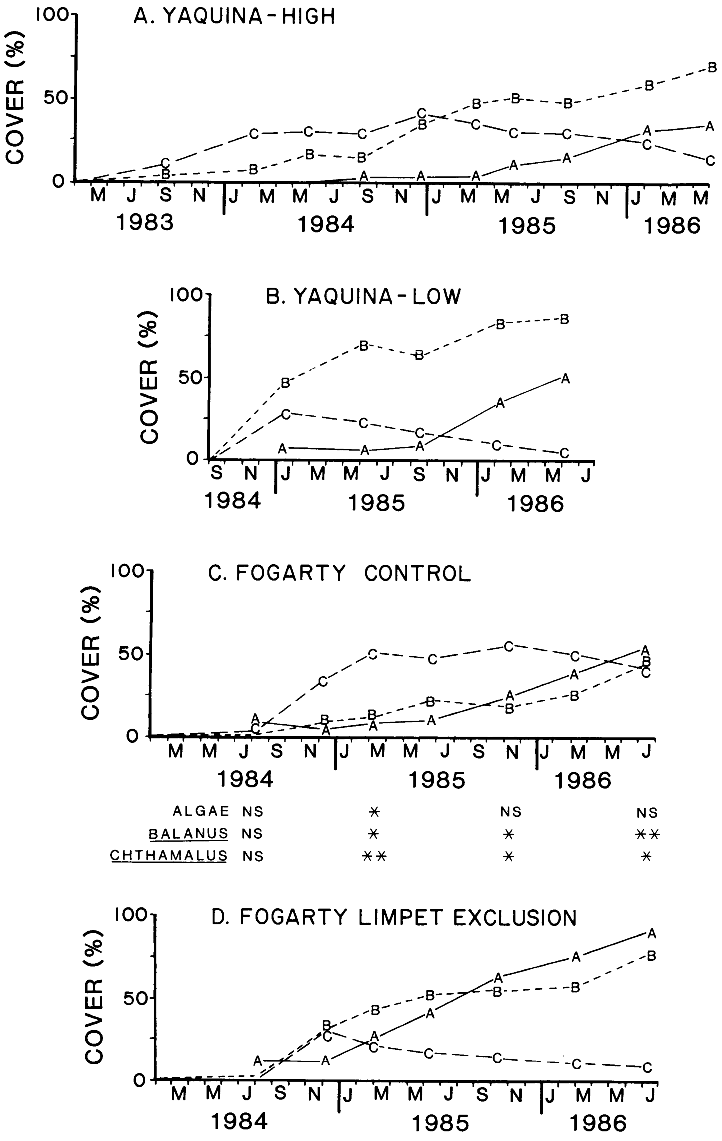


FIG. 3. Percent of *Balanus* test surface covered with epibionts in the unmanipulated plots at Yaquina-high.



ALGAE	NS	*	NS	NS
BALANUS	NS	*	*	**
CHTHAMALUS	NS	**	*	*

FIG. 4. Mean substrate cover in cleared plots at the three sites (A = macroalgae, B = *Balanus*, C = *Chthamalus*). For the Fogarty experiment, ANOVAs were used to compare the cover in control plots and limpet-removal plots at four sampling dates. The results of these statistical tests for algae and both barnacle species are shown between panels C and D (NS = not significant, * $P < .05$, ** $P < .01$).

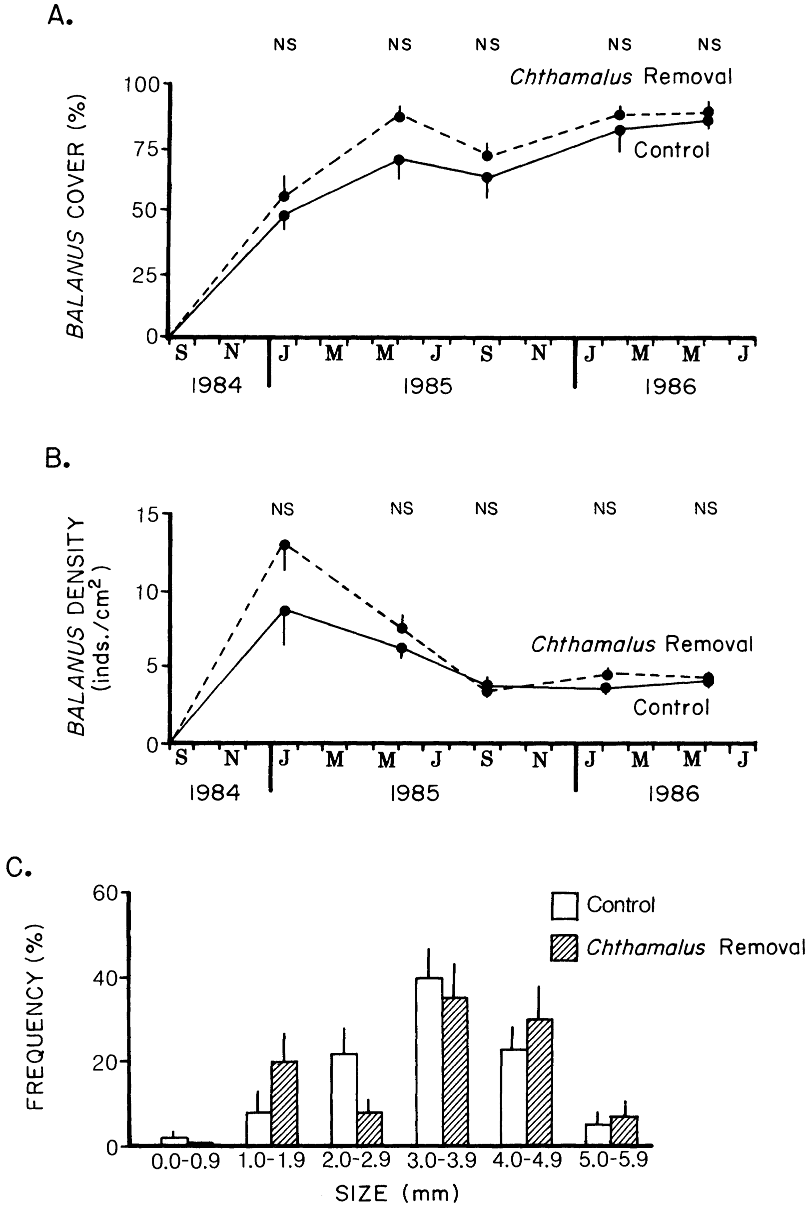


FIG. 5. The effects of *Chthamalus* on *Balanus* at Yaquina-low. In (A) and (B) plotted values are means (±1 SE) with significance levels shown (ANOVA, $n = 6$, NS = not significant). (C) Plotted values are mean proportion (±1 SE) of barnacles of each size class ($n = 6$ plots, 10 barnacles per plot).

was increasing rapidly in the cleared plots. Additionally, individuals of *Balanus, Chthamalus, Endocladia,* and *Pelvetiopsis* in the cleared plots were reproductive after 3 yr.

Although the rate of colonization varied, the basic sequence of succession at the other two sites was similar to that at Yaquina-high. At Fogarty, *Chthamalus* cover peaked 18 mo after scraping, and then declined as *Balanus* became more abundant (Fig. 4C). As at Yaquina-high, the algal cover increased only after *Balanus* had settled and algae recruited onto the tests. Succession at Yaquina-low was accelerated compared to the other sites (Fig. 4B). A dense settlement of *Balanus* and *Chthamalus* occurred soon after the plots were scraped (September 1985). The peak abundance of *Chthamalus* occurred only 4 mo after scraping, whereas peak *Chthamalus* abundance occurred after 25 and 36 mo at Fogarty and Yaquina-high, respectively. *Balanus* cover at Yaquina-low exceeded 70% after 10 mo, while at Yaquina-high comparable *Balanus* cover occurred after 36 mo and was not observed at Fogarty after >24 mo of succession. Early algal recruitment and the development of an algal canopy was associated with the rapid increase in *Balanus* cover at Yaquina-low, where

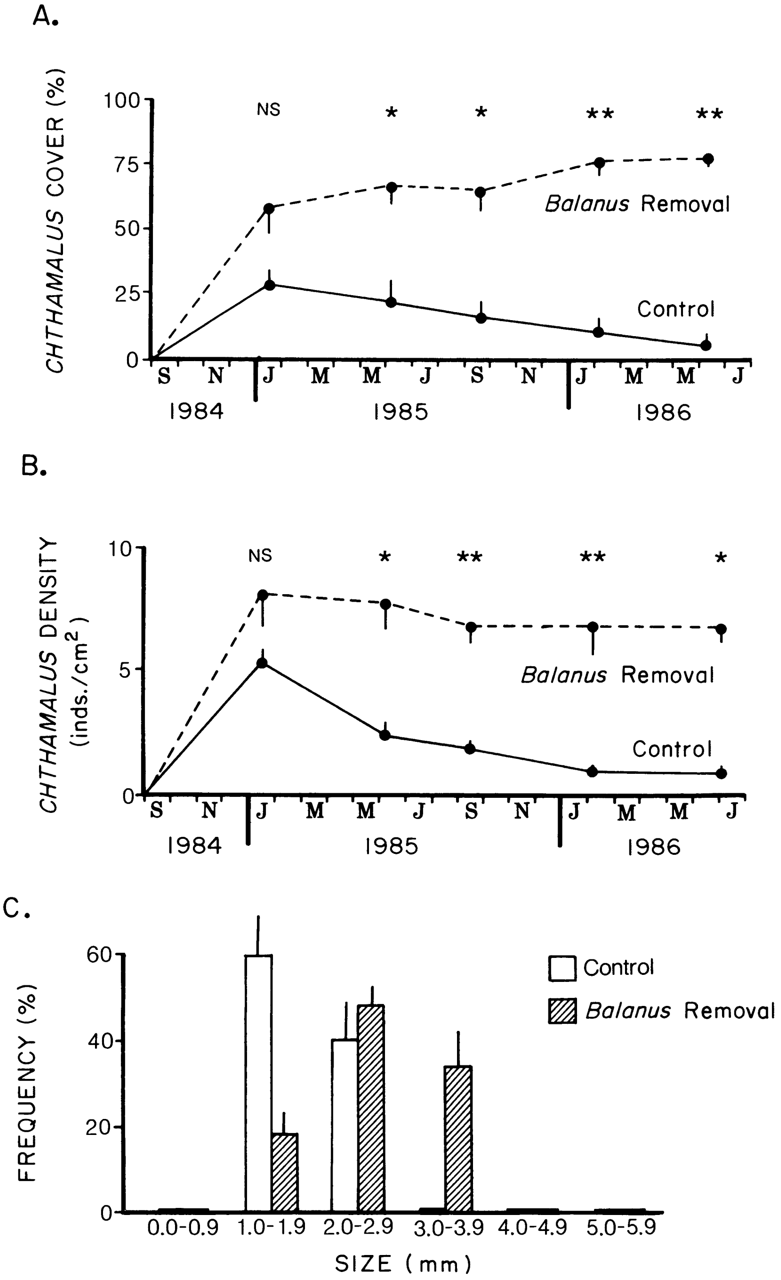


FIG. 6. The effects of *Balanus* on *Chthamalus.* Panels are as in Fig. 5 (except $n = 5$ plots). NS = not significant, * $P < .05$, ** $P < .01$.

algal cover reached 35% in 18 mo. Development of similar algal cover took 25 mo at Fogarty and 36 mo at Yaquina-high.

Thus, at all three sites, succession in the *Balanus–Pelvetiopsis* community was characterized by an early abundance of *Chthamalus,* a period of decreasing *Chthamalus* cover and increasing *Balanus* cover, and a third phase of increasing algal cover after the establishment of *Balanus.* Ephemeral algae never became abundant in this community. Three key questions about this successional sequence were investigated in greater detail: (1) How do interactions between the two barnacle species affect succession, (2) How do interactions between the barnacles and algae affect succession, and (3) How do herbivores affect succession?

Interactions between barnacles: the effect of Chthamalus *on* Balanus

Chthamalus had no observed effect on the percent cover, density, or size distribution of *Balanus* at Yaquina-low (Fig. 5). On each of the five sampling dates there was no significant difference between the control

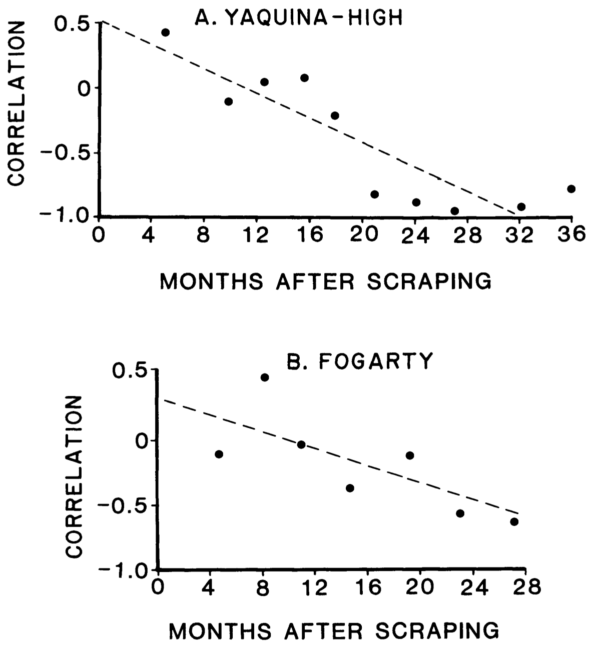


FIG. 7. The spatial association of *Chthamalus* and *Balanus* during succession. Plotted values are the correlation coefficients of the cover of the two species in the control plots. The coefficients are based on the seven (Yaquina-high) or eight (Fogarty) plots for each sampling date. For Yaquina-high the overall correlation between the barnacle association and the time since the plots were cleared is -0.89 ($n = 10$ sampling dates, $P = .001$). For Fogarty this overall correlation is -0.75 ($n = 7$ sampling dates, $P = .055$). The linear regression line is shown for both sites.

plots and the *Chthamalus*-removal plots in percent cover or density of *Balanus*. In March 1986, the only time when size distributions were measured, there was no significant difference between treatments in the mean size of *Balanus* (repeated-measures ANOVA, $n = 6$, $P = .94$).

The effect of Balanus *on* Chthamalus

In contrast to the above results, *Balanus* had large effects on the percent cover, density, and size of *Chthamalus* at Yaquina-low (Fig. 6). On the second sampling date, 9 mo after scraping, *Chthamalus* cover was significantly higher in the *Balanus*-removal plots than in the control plots. The difference in *Chthamalus* cover between treatments increased continually during the course of succession. These differences in cover were caused by decreases in both the density and size of *Chthamalus* in plots with *Balanus*. Nine months after scraping, *Chthamalus* densities were more than three times as great in the *Balanus*-removal plots as in the control plots. The difference in *Chthamalus* density between treatments continued to increase as succession proceeded. Mean *Chthamalus* size (2.8 mm) in the *Balanus*-removal plots was significantly greater than the mean size (1.7 mm) in the control plots (repeated-measures ANOVA, $n = 5$, $P = .014$).

The effect of *Balanus* on *Chthamalus* resulted from strong interspecific competition. Competition experiments were done only at Yaquina-low, but I observed *Balanus* crushing and undercutting *Chthamalus* at all three sites. This conclusion is also supported by the temporal shift from positive to strong negative correlation coefficients between the abundance of *Chthamalus* and *Balanus* in plots at both Yaquina-high and Fogarty (Fig. 7). The increased spatial segregation of the barnacle species in later successional stages is consistent with the notion that competition with *Balanus* decreases *Chthamalus* cover during the course of succession.

The effect of barnacles on algae

Barnacles strongly facilitated algal colonization at all three sites (Figs. 8–10). On the last sampling dates at Yaquina-high and Fogarty, the barnacle-removal plots had only 2% of the number of algal thalli found in the plots that were colonized by barnacles. At Yaquina-low, no plants grew in the barnacle-removal plots. Barnacles affected each algal species in the same manner. At Yaquina-high and Yaquina-low, *Pelvetiopsis* and *Endocladia* (which together constituted >90% of the algal thalli at each site) were facilitated to the same degree by barnacles (Figs. 8 and 9). At Fogarty, *Fucus, Pelvetiopsis,* and *Endocladia* were all facilitated by barnacles (Fig. 10). Comparisons of *Balanus*-removal plots (*Chthamalus* monocultures) and *Chthamalus*-removal plots (*Balanus* monocultures) indicated that *Balanus* enhanced algal colonization more than did *Chthamalus* (Fig. 9).

The mechanism of facilitation

Facilitation of algae by barnacles may have resulted from either the activities of living barnacles, such as excretion and feeding, or from the alteration of the substrate caused by the presence of barnacle tests. To determine which general hypothesis was correct, I used a test-addition treatment in the Yaquina-low experiment in which plots covered with epoxy-filled barnacle tests altered the substrate without the confounding factor of the activities of living barnacles. Addition of barnacle tests greatly increased algal colonization compared to the barnacle-removal plots (Fig. 9). This indicated that barnacles facilitated algal colonization by altering the substrate.

The test-addition plots also had higher algal colonization rates than the control plots that were colonized by barnacles. Either the activities of living barnacles had a deleterious effect on algae, or the size of the barnacles may have affected algal colonization. The barnacles used in the test-addition plots were larger than the recruiting barnacles in the other treatments. Since these two factors were confounded, the design of

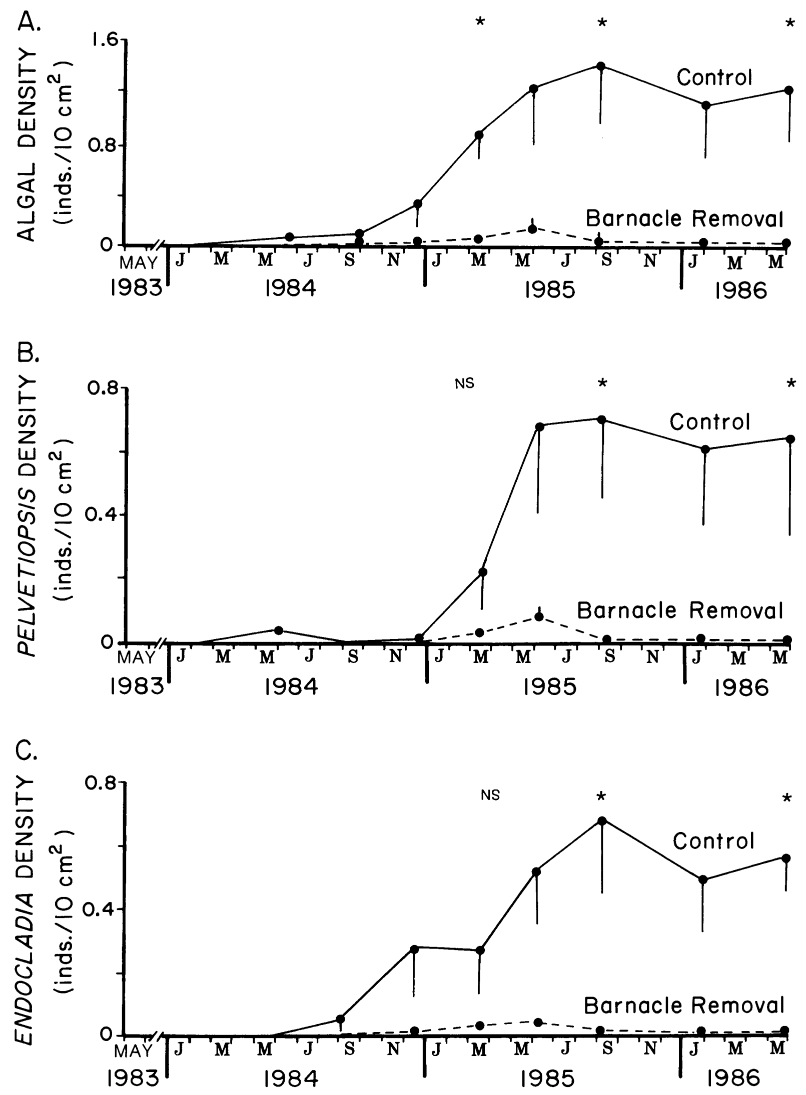


FIG. 8. Density of algal thalli (means ± 1 SE) in the Yaquina-high experiment for all macroalgae (A), *Pelvetiopsis* (B), and *Endocladia* (C). NS = not significant, *$P < .05$.

this experiment does not allow me to distinguish between these two alternatives.

The substrate-alteration hypothesis may explain why *Balanus* facilitated algal recruitment more than *Chthamalus*. *Balanus* tests were both larger and more rugose than *Chthamalus* tests. Increased substrate roughness could have caused facilitation in at least three ways: (1) the dispersal trap hypothesis: barnacles created a rough surface that collected more algal spores or zygotes than the smoother rock surface; (2) the desiccation protection hypothesis: the crevices on and between barnacles were shaded and retained moisture, and therefore were a favorable microhabitat for the growth and survival of newly recruited algae; (3) the herbivore protection hypothesis: algae growing in the crevices on and between barnacles were inaccessible to herbivores while they were small and vulnerable. These hypotheses are not mutually exclusive; facilitation could have resulted from two or more of these processes acting in concert.

The Fogarty experiment was, in part, designed to determine which, if any, of the listed hypotheses caused facilitation of algae by barnacles. In this experiment I manipulated the abundance of both barnacles and limpets, the dominant herbivores in this community. A prediction of the herbivore protection hypothesis is that algae will recruit to barnacle-removal plots in the absence of herbivores. In contrast, both the desiccation protection hypothesis and the dispersal trap hypothesis predict that algae will not recruit to areas without barnacles regardless of herbivore abundance. Limpet removal with and without barnacles should distinguish

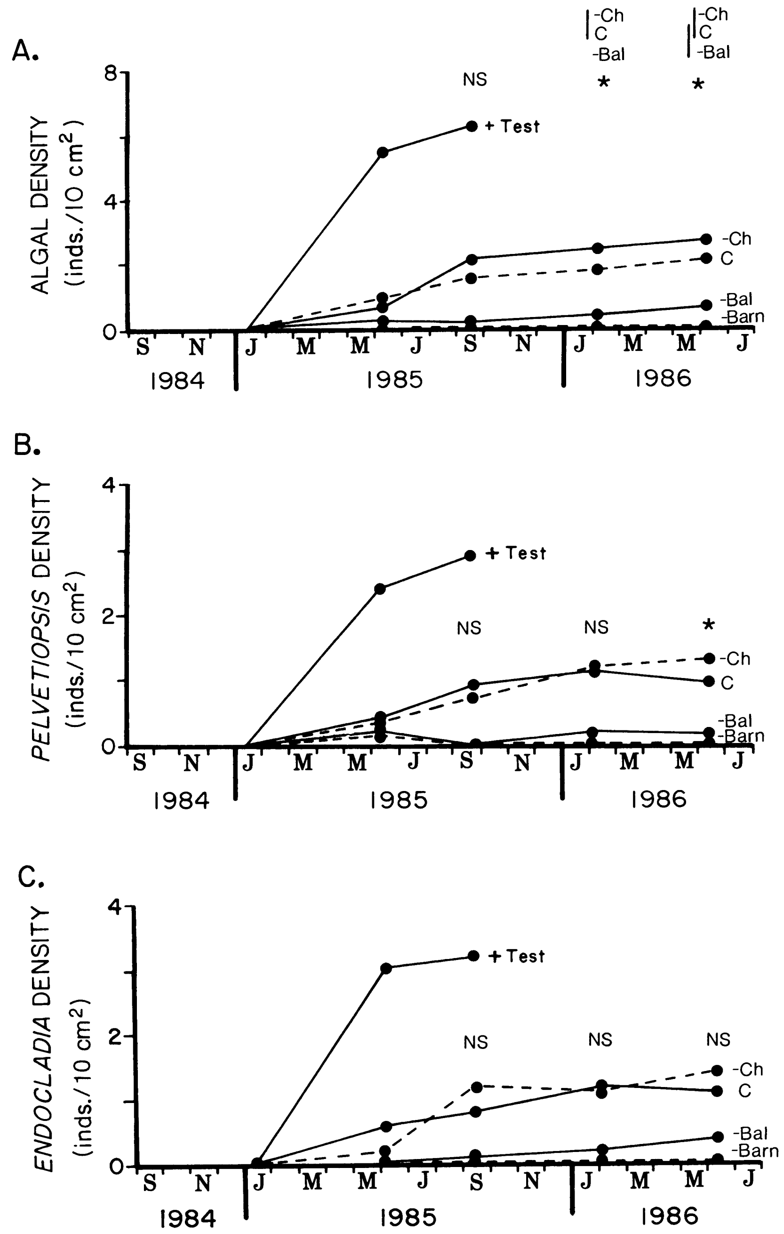


FIG. 9. Mean density of algal thalli in the Yaquina-low experiment. The five treatments are *Balanus*-test addition (+Test), *Chthamalus*-removal (−Ch), *Balanus*-removal (−Bal), barnacle-removal (−Barn), and control (C). Three of the treatments were analyzed by ANOVA ($n = 5$). At each sampling date, treatment means that did not significantly differ are connected by lines (Student-Newman-Keuls test). NS = not significant, * $P < .05$.

between alternatives 1 and 2 vs. 3. The results of this experiment show that algae did recruit into barnacle-removal plots when limpets were removed (Fig. 10). No statistically significant difference in algal density occurred between the +L+B (limpets and barnacles present) and the −L−B (limpets and barnacles removed) plots. This indicates that facilitation of algae by barnacles depended on limpets.

Algal recruitment was greater in the −L+B (limpets removed, barnacles present) plots than the −L−B plots. There are at least two possible explanations for this result. (1) Facilitation is the result of multiple causation. The dispersal trap hypothesis and/or the desiccation protection hypothesis acted in concert with the herbivore protection hypothesis to cause facilitation. (2) There were herbivores (amphipods, littorines, and a few limpets) present in the limpet exclusion plots. The barnacles protected the algae from these remaining herbivores. Since some herbivores remained in the limpet-removal plots it is impossible to determine from

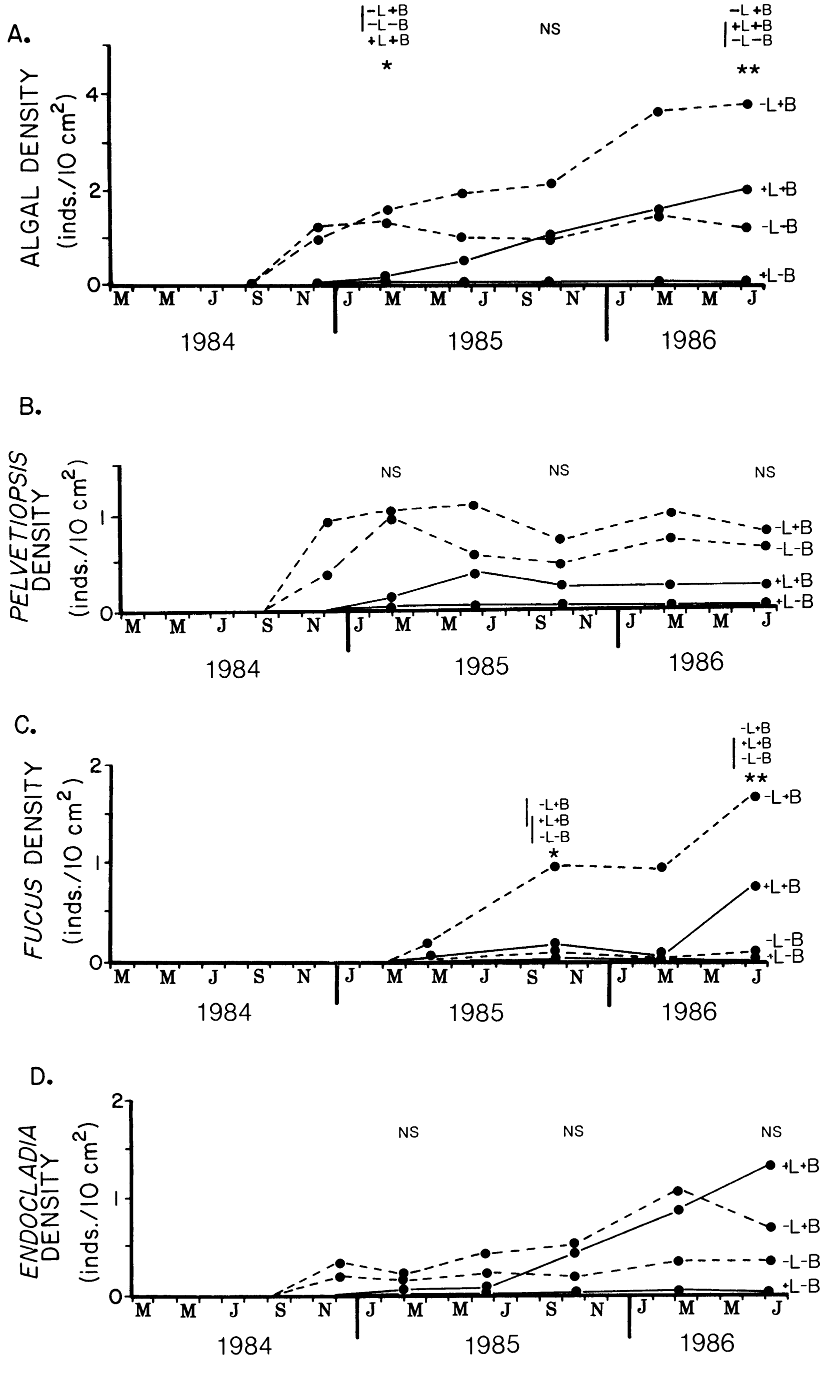


Fig. 10. Mean density of algal thalli in the Fogarty experiment. The four treatments are control (+L+B), limpet-removal (−L+B), barnacle-removal (+L−B), and limpet and barnacle removal (−L−B). Three of the treatments had homogeneous variances and were analyzed with ANOVA and Student-Newman-Keuls tests. ns = not significant, * $P < .05$.

this experiment if facilitation was caused only by the herbivore protection effect or if another process was also responsible.

The effect of herbivores on succession

Comparison of the control plots and the limpet-removal plots indicates that herbivores decreased the rate of succession at Fogarty (Fig. 4C, D). *Balanus* cover increased more rapidly in limpet-removal plots than control plots. Fifteen months after disturbance, *Balanus* covered more than half the removal plots whereas comparable *Balanus* cover was attained after 30 mo in the presence of limpets. In turn, *Chthamalus* cover decreased more rapidly in the limpet-removal plots because of increased competition with *Balanus*. Peak *Chthamalus* abundance occurred after only 11 mo in the removal plots compared to 22 mo in the control plots. The rate of algal colonization also was accelerated when limpets were removed. After 19 mo mean algal cover reached 50% in the limpet-removal plots, but similar algal cover took 30 mo to form in the control plots. Thus, limpet removal accelerated the timing of each major feature of the successional sequence.

DISCUSSION

In early views of succession, community development was thought to result in a stable climax state (Clements 1928, Odum 1969). The view that communities, even those in later stages of succession, are frequently disturbed has recently become much more prevalent (Sousa 1979*b*, 1984, Pickett and White 1985). The *Balanus–Pelvetiopsis* community is subject to frequent disturbances (Farrell 1989). Disturbance rates in this community may be increased by the algae growing on the tests of barnacles; epizoic algae may kill barnacles by overgrowing their apertures and by dislodging barnacles from the rock due to increased drag from water flow over the attached algal thalli. *Endocladia* sometimes appeared to kill the barnacles it overgrew. Its filaments grew in a dense turf that covered the apertures of the overgrown barnacles and collected sediment that occasionally became anoxic. *Pelvetiopsis* did not overgrow the apertures of barnacles and prevent feeding, but could have increased drag. Since algal cover increased during community development, the probability of disturbance probably increased as succession proceeded.

Similar conclusions have been recorded in other studies. Epibionts can cause mussels to be dislodged by waves (Witman and Suchanek 1984, Witman 1987). Sousa (1979*a*), Lubchenco (1983), and D'Antonio (1985) provide evidence that epiphytes can cause algae to become dislodged in intertidal habitats. In another intertidal community, Jernakoff (1985*b*) found that algal overgrowth did not increase barnacle mortality. Other workers, including Denley and Underwood (1979) and Farrell (1988), observed barnacle death after algal overgrowth. In terrestrial habitats, epibionts increased disturbance rates in tropical forests (Strong 1977, Putz 1984). The probability of disturbance also increased as succession proceeded in other marine (Paine and Levin 1981) and terrestrial habitats (Romme 1982). In these communities the most advanced successional stage is another transient stage of community development, not a stable climax state.

In early views of succession, community development was thought of as a highly deterministic and repeatable process (Clements 1928, Odum 1969). More recent models of succession have stressed the complexity and contingency involved in community development and predicted that successional sequences may not be repeatable (e.g., Cattelino et al. 1979). In the *Balanus–Pelvetiopsis* community the observed successional sequence was highly consistent. In three experiments, each performed at different places and times, the major features of succession occurred in the same sequence. In each case *Chthamalus* had an early peak in abundance and was replaced as the dominant space-utilizing organism by *Balanus*. At all three sites macroalgae invaded the disturbed plots only after *Balanus* became abundant. The predictability of succession may be a function of the species diversity of a community. Communities with low species diversity, such as the *Balanus–Pelvetiopsis* community, may have more predictable successional sequences than diverse communities simply because there are fewer possible paths of community development.

While the order of species appearance was repeatable, the rate of succession varied greatly between experiments. At the Yaquina-low site *Chthamalus* cover peaked 4 mo after disturbance, compared to 36 mo at Yaquina-high. Similarly, *Balanus* and algal cover developed much more slowly at Yaquina-high than Yaquina-low (Fig. 4A, B). In studies of algal succession in the low zone in Washington State, Dayton (1975) also found that the rate of succession varied between his study sites.

The timing and magnitude of successful barnacle recruitment appeared to cause much of the variation in the rate of succession. The same period (September 1984) of dense *Balanus* recruitment resulted in the rapid increase in space utilization by *Balanus* and the concomitant decrease in *Chthamalus* cover at both Yaquina-high and Yaquina-low. This event occurred immediately after disturbance at Yaquina-low, whereas it occurred 17 mo after disturbance at Yaquina-high. The difference in the successional trajectory of these two sites is largely the long initial period at Yaquina-high with low *Balanus* cover. The changes in species abundance are similar at Yaquina-high and Yaquina-low after the large recruitment event (Fig. 4A, B). The lack of early *Balanus* recruitment was not simply due to an absence of settling larvae. At all three sites, cyprids frequently settled in plots but were often killed by desiccation. For example, in early May 1985 at Yaquina-high, mean *Balanus* settlement densities exceeded 33 individuals/cm^2 of unoccupied space, but all died a few days later when hot, dry weather coincided with a midday low tide.

Models and mechanisms of succession

A fundamental question in ecology is what is the relative importance of the three models of succession? The limited evidence available at the time of Connell and Slatyer's review (1977) indicated that inhibition was the dominant model. Several more recent studies (Sousa 1979*a*, Dean and Hurd 1980, Breitburg 1984) also found inhibition to be the most frequent process. In the *Balanus–Pelvetiopsis* community, however, inhibition did not occur. Early successional species had either no effect, or facilitated the establishment of later colonists. Ephemeral algae often cause inhibition in rocky intertidal communities (Sousa 1979*a,* Robles and Cubit 1981, Lubchenco 1983, van Tamelen 1987). Ephemeral algae were rare in this community, probably because grazing amphipods and littorines removed them from the small clearings used as experimental units (Farrell 1989). While limpets did slow succession in the *Balanus–Pelvetiopsis* community, I do not consider this an example of the inhibition model since Connell and Slatyer explicitly used their models to describe interactions among the basal (sessile animals and plants) species in a community.

The tolerance model best describes the interaction between barnacles since *Chthamalus* has little or no effect on colonization by *Balanus.* The tolerance model of succession will be observed if there is either no interaction between early and later successional species, or if strongly asymmetric competition occurs with the later successional species being competitively superior. Since competition is usually asymmetric (Connell 1983), the tolerance model of succession may frequently occur. Connell and Slatyer (1977), however, found no examples of the tolerance model in their review. Breitburg (1984) found that the recruitment of only 2 of 15 taxa was not strongly affected by the presence of an early successional species. The *Balanus–Chthamalus* interaction is thus one of the first experimental demonstrations of the tolerance model (but also see Hils and Vankat 1982).

Barnacles, particularly *Balanus,* facilitate algal establishment by providing algae with refuges from their consumers. Barnacles have deleterious effects on herbivores in many intertidal communities (reviewed by Branch 1981, more recent studies include Hawkins 1981, Hawkins and Hartnoll 1983, Lubchenco 1983, Dungan 1986, Petratis and Sayigh 1987, Little et al. 1988), although this is not always the case (Creese 1982, Jernakoff 1983, 1985*a*). In several cases interference with herbivores results in barnacles facilitating algal establishment (Hawkins 1981, Lubchenco 1983). In other cases facilitation occurs when early colonists act as a substrate for recruitment of later successional species (Menge 1976, Suchanek 1978, Turner 1983*b*).

Facilitation was originally thought to result as early successional species altered the physical environment in ways favorable to later successional species (Drury and Nisbet 1973, Connell and Slatyer 1977). For this reason Connell and Slatyer suggested that facilitation might be more frequent in harsh physical environments. Recent studies show facilitation can occur when early successional species alter the biotic environment, specifically by decreasing consumer pressure (Lubchenco 1983, Harris et al. 1984). The refuges provided for a species by other organisms have been characterized as associational resistance (Tahvanainen and Root 1972) or associational defenses. Such defenses have been found in terrestrial (reviewed by Atsatt and O'Dowd 1976, Rausher 1981, Fuentes et al. 1986, McAuliffe 1986), intertidal (Lubchenco 1983), and subtidal communities (Russ 1980, Duggins 1981, Harris et al. 1984, Hay 1986, Littler et al. 1986, Pfister and Hay 1988). Given the apparent abundance of associational defenses, facilitation may occur both in physical harsh environments and also in areas with intense consumer pressure.

The model of succession is a continuum ranging from obligatory facilitation, where the early successional species is required for any establishment of the later successional species, to total inhibition, where the later successional species cannot become established in the presence of the early successional species. The interaction of barnacles and macroalgae in this study lies very close to the obligatory facilitation end of this continuum. In all three of the experiments the barnacle removal plots had $<2\%$ of the algal colonization observed in control plots. In a similar interaction between a fucoid alga (*Fucus vesiculosus*) and a balanoid barnacle (*Semibalanus balanoides*) in New England, Lubchenco (1983) found near-obligatory facilitation on very smooth rock surfaces, and weak facilitation on rougher rock surfaces. In Oregon, however, algae did not colonize even relatively rough surfaces. The difference in the strength of facilitation on rough rock surfaces between these two studies may result from differences in the feeding structures of the dominant herbivores, i.e., littorinid snails in New England and patellacean limpets in Oregon. The radulae of limpets can remove tough and encrusting algae more efficiently than the radulae of littorinids (Steneck and Watling 1982). Limpets may be better able than littorinids to eat algae in crevices and to eat large algal thalli, resulting in almost total algal removal in Oregon, even on rough rock surfaces.

In the simplest case, a group of early successional species would all have the same effect on the establishment of all later successional species. Studies examining interactions between individual species have revealed a much more complex view of succession (Dean and Hurd 1980, Turner 1983*a, b,* Breitburg 1984, 1985). An early successional species may not have the same effect on different later successional species. For example, Breitburg (1984) found coralline algae had little or no effect on a barnacle and one species of bryozoan, but inhibited many other species. In the present study, however, early successional species had consistent effects on later successional species. *Chthamalus* had little or no effect on *Balanus* and several species of macroalgae. Similarly, *Balanus* strongly facilitated all three common species of macroalgae.

Further complexity in succession will occur if different members of an assemblage of early successional species do not have the same effect on a later colonist. For example, Turner (1983*b*) found that some branched algae facilitated surfgrass recruitment, while algae of other morphologies had no effect on recruitment. In this study, *Chthamalus* weakly facilitated algal colonization while *Balanus* strongly facilitated colonization. Since there was spatial variation in the relative abundance of these barnacles, the strength of facilitation also varied. This promoted spatial variation in the rate of succession.

Turner (1983*a, b*) demonstrated in a low intertidal community that no single model of succession describes different periods in the successional sequence. Similarly, no single model described succession in the *Balanus–Pelvetiopsis* community. The *Chthamalus–Balanus* interaction follows the tolerance model, while the subsequent barnacle–macroalgae interaction follows the facilitation model. This study strengthens the conclusion that there is no reason to assume the same model of succession will be involved in each transition between seral stages.

The role of indirect interactions in determining the course of succession has been largely ignored (but see van Tamelen 1987). In the *Balanus–Pelvetiopsis* community direct and indirect interactions affected succession. Early in succession, *Chthamalus* was eliminated by a direct interaction: competition for space with *Balanus.* Later in succession, algal establishment resulted from an indirect interaction: the foraging activities of limpets were reduced by barnacles, allowing algal colonization. Limpets also indirectly affected *Chthamalus* abundance. Limpets decreased *Balanus* abundance and thereby slowed the competitive exclusion of *Chthamalus.* These results support earlier suggestions that the outcome of field experiments will be caused by a mixture of direct and indirect interactions (Bradley 1983, Bender et al. 1984). In the present study, indirect interactions were observed because the effect of herbivores on succession was investigated. As predicted by theory (Levine 1976, Vandermeer 1980), these indirect interactions were produced by chains of direct interactions between species on different trophic levels.

Competition between barnacles

Barnacles have frequently been the subject of investigations of interspecific competition. Stanley and Newman (1980) suggest that balanoid barnacles are generally superior competitors to chthamaloid barnacles. The punitive advantage of balanoids results from increased growth rates made possible by tubiferous (hollow) tests (Stanley and Newman 1980, Newman and Stanley 1981). This investigation, along with the studies of Connell (1961*b*) and Wethey (1984), support that generalization. Dungan (1985), however, found that a chthamaloid was competitively dominant to a tubiferous species (*Tetraclita*), and suggested recruitment density may be the key determinant of competitive ability. The present study does not support Dungan's idea since *Balanus* and *Chthamalus* recruited in approximately equal numbers at the start of the competition experiment, and *Balanus* quickly displayed its superior competitive ability.

Paine (1981) disagreed with Stanley and Newman's (1980) contention that competition with *Balanus* caused a reduction in the species diversity of chthamaloids over geologic time. Paine suggests that chthamaloids (particularly *Chthamalus* spp.) can coexist with balanoids since predation and disturbance frequently reduce the intensity of interspecific competition for space. The present study supports Paine's view. *Chthamalus* persists in this community by recruiting to recently disturbed patches. Additionally, *Chthamalus* is less susceptible to consumers, in this case limpets, than is *Balanus.* This result has also been observed in several other experiments involving limpet exclusions (Dayton 1971, Paine 1981, Farrell 1987, 1988).

Connell (1970) found that intraspecific competition did not normally occur in a high intertidal population of *Balanus glandula* on San Juan Island, Washington. He found that low rates of larval settlement and high mortality after settling prevented the establishment of dense populations. In Oregon, however, dense *Balanus* populations, covering almost 100% of the rock surface, developed and led to intense intraspecific and interspecific competition. Larval settlement densities were much higher in Oregon (132 individuals$\cdot$cm$^{-2}\cdot$yr^{-1}; T. M. Farrell, *personal observation*) than on San Juan Island (0.4–2.4 individuals$\cdot$cm$^{-2}\cdot$yr^{-1}; Connell 1985). Mortality rates are also likely to be lower in Oregon since limpets tend to be smaller and less abundant than on San Juan Island (T. M. Farrell, *personal observation*). The Oregon study sites have larval settlement rates close to those of Massachusetts (37–102 individuals$\cdot$cm$^{-2}\cdot$yr^{-1}; Wethey unpublished, cited by Connell 1985) and Scotland (37–143 individuals$\cdot$cm$^{-2}\cdot$yr^{-1}; Connell 1985), sites where barnacles were involved in intense competition (Connell 1961*a, b,* Wethey 1984).

The effects of herbivores on the rate of succession

A simplistic view of the model that predicts how consumers affect the rate of succession (Fig. 1) indicates consumers should usually slow succession since that is the result of six of the nine possible combinations, and that consumers should rarely hasten succession since that would result from only one of the nine combinations. In reality, prediction is more complex since not all the combinations of consumer removal and the model of succession are equally likely. Inhibition appears to occur more frequently than tolerance and facilitation in both marine (Connell and Slatyer 1977, Dean and Hurd 1980, Breitburg 1985) and terrestrial communities (Abul-Fatih and Bazzaz 1979, Hils and Vankat 1982, Walker and Chapin 1986). Similarly, consumers often appear to prefer early successional species over later successional species in both marine (reviewed by Day and Osman 1981, Lubchenco and Gaines 1981, Lubchenco 1986) and terrestrial communities (Cates and Orians 1975, Godfray 1985, Walker et al. 1986). The only combination of factors that results in consumers increasing the rate of succession (inhibition, early successional species removed) may occur most frequently in nature.

To determine the accuracy of this model in a community it is necessary to know three things: (1) the model of succession, (2) the successional status of the species most affected by consumers, and (3) the effect of consumers on the rate of succession. These three facts have been determined in several communities. In most cases, consumers removed primarily early successional species and the model of succession was inhibition. All of these studies found, as the general model predicts, that consumers increased the rate of succession (Lubchenco and Menge 1978, Sousa 1979*a*, Day and Osman 1981, Lubchenco 1983, Bryant 1987). Other combinations of the important parameters, however, have also occurred. Sousa et al. (1981), studying an algae-dominated community characterized by the inhibition model, found that herbivores preferentially removed later successional species. In that community, herbivores slowed the rate of succession, a result consistent with the model.

In this study consumers influenced the timing of the two major transitions in succession. The first transition was the replacement of *Chthamalus* by *Balanus,* and the second transition involved colonization by macroalgae (Fig. 4C, D). In this and other studies (Dayton 1971, Paine 1981, Farrell 1988), limpets reduced the abundance of *Balanus,* the later successional species, more than the abundance of *Chthamalus,* the early successional species. The tolerance model describes the interaction between the two barnacle species. As predicted by my model in this situation (Fig. 1), *Balanus* replaced *Chthamalus* more slowly in the presence of limpets (Fig. 4C, D). Limpets affected the abundance of barnacles, the early successional species, less than the abundance of macroalgae, the later successional species. Barnacles facilitated algal establishment. As predicted in this situation, macroalgae colonized more slowly in the presence of limpets (Fig. 4C, D).

The intensity of consumption will affect the magnitude of the consumer's influence on the rate of succession. In communities where consumers have little effect on species' abundances they are unlikely to affect the rate of succession regardless of the model of succession. For example, Turner (1983*a*) found herbivores had only a short-term influence on the abundance of an early successional alga and did not affect the rate of succession. In habitats where consumer pressure is extremely strong, succession may be halted at some early stage (Lubchenco and Gaines 1981, Robles and Cubit 1981, Sousa et al. 1981, Lubchenco et al. 1984, Menge et al. 1986).

The general model considers only the direct effect of a consumer feeding in a community. Herbivores may also affect environmental parameters, such as nutrient availability (Peer 1986, Inouye et al. 1987), and thereby influence the rate of succession. In these situations, successfully predicting the effects of consumers on the rate of succession may be beyond the capabilities of this model.

ACKNOWLEDGMENTS

I thank A. Brown, B. Ebberts, and J. Farrell for assistance in the field. This manuscript was greatly improved by the comments of J. Barry, J. Lubchenco, J. Leichter, B. Menge, A. Olson, C. Robles, W. Sousa, and T. Turner. I thank L. Weber for use of the facilities at the Mark O. Hatfield Marine Science Center. I received partial support from NSF grants OCE80-19020 (to B. Menge and J. Lubchenco) and OCE84-15609 (to B. Menge).

LITERATURE CITED

Abul-Fatih, H. A., and F. A. Bazzaz. 1979. The biology of *Ambrosia trifida* L. I. The influence of species removal on the organization of the plant community. New Phytologist **83**:813–816.

Atsatt, P. R., and D. J. O'Dowd. 1976. Plant defense guilds. Science **193**:24–29.

Bradley, R. A. 1983. Complex food webs and manipulative experiments in ecology. Oikos **41**:150–152.

Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology **65**:1–13.

Branch, G. M. 1981. The biology of limpets: physical factors, energy flow and ecological interactions. Oceanography and Marine Biological Annual Review **19**:235–379.

Breitburg, D. L. 1984. Residual effects of grazing: inhibition of competitor recruitment by encrusting coralline algae. Ecology **65**:1136–1143.

———. 1985. Development of a subtidal epibenthic community: factors affecting species composition and the mechanisms of succession. Oecologia (Berlin) **65**:173–184.

Bryant, J. P. 1987. Feltleaf willow–snowshoe hare interactions: plant carbon/nutrient balance and floodplain succession. Ecology **68**:1319–1327.

Cates, R. G., and G. H. Orians. 1975. Successional status and the palatability of plants to generalized herbivores. Ecology **56**:410–418.

Cattelino, P. J., I. R. Noble, O. R. Slatyer, and S. R. Kessell. 1979. Predicting multiple pathways of plant succession. Environmental Management **3**:41–50.

Clements, F. E. 1928. Plant succession and indicators. H. W. Wilson, New York, New York, USA.

Connell, J. H. 1961*a*. Effects of competition, predation by *Thais lapillus,* and other factors on natural populations of the barnacle *Balanus balanoides.* Ecological Monographs **31**:61–104.

———. 1961*b*. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus.* Ecology **42**:710–723.

———. 1970. A predator–prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais.* Ecological Monographs **40**:49–78.

———. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. American Naturalist **122**:661–696.

———. 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. Journal of Experimental Marine Biology and Ecology **93**:11–45.

Connell, J. H., I. R. Noble, and R. O. Slatyer. 1987. On the mechanisms producing successional change. Oikos **50**:136–137.

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**: 1119–1143.

Creese, R. G. 1982. Distribution and abundance of the acmaeid limpet, *Patelloida latistrigata,* and its interactions with barnacles. Oecologia (Berlin) **52**:85–96.

Cubit, J. D. 1984. Herbivory and the seasonal abundance of algae on a high rocky intertidal shore. Ecology **65**:1904–1917.

D'Antonio, C. 1985. Epiphytes on the rocky intertidal red algae *Rhodomela larix* (Turner) C. Agardh: negative effects on the host and food for herbivores? Journal of Experimental Marine Biology and Ecology **86**:197–218.

Day, R. W., and R. W. Osman. 1981. Predation by *Patiria miniata* (Asteroidea) on bryozoans: prey diversity may depend on the mechanism of succession. Oecologia (Berlin) **51**:300–309.

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.

———. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecological Monographs **45**:137–159.

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.

Denley, E. J., and A. J. Underwood. 1979. Experiments on factors influencing settlement, survival and growth of two species of barnacles in New South Wales. Journal of Experimental Marine Biology and Ecology **36**:269–293.

Drury, W. H., and I. C. T. Nisbet. 1973. Succession. Journal of the Arnold Arboretum **54**:331–368.

Duggins, D. O. 1981. Interspecific facilitation in a guild of benthic marine herbivores. Oecologia (Berlin) **48**:157–163.

Dungan, M. L. 1985. Competition and the morphology, ecology, and evolution of acorn barnacles: an experimental test. Paleobiology **11**:165–173.

———. 1986. Three-way interactions: barnacles, limpets, and algae in a Sonoran Desert rocky intertidal zone. American Naturalist **127**:292–316.

Egler, F. E. 1954. Vegetation science concepts 1. Initial floristic composition. A factor in old-field vegetation development. Vegetatio **4**:412–417.

Ellison, A. M. 1987. Effects of competition, disturbance, and herbivory on *Salicornia europaea.* Ecology **68**:576–586.

Farrell, T. M. 1987. Stability and succession in two rocky intertidal communities on the central Oregon coast. Dissertation. Oregon State University, Corvallis, Oregon, USA.

———. 1988. Community stability: effects of limpet removal and reintroduction in a rocky intertidal community. Oecologia (Berlin) **75**:190–197.

———. 1989. Succession in a rocky intertidal community: the importance of disturbance size and position within a disturbed patch. Journal of Experimental Marine Biology and Ecology **128**:57–73.

Frank, P. W. 1982. Effects of winter feeding on limpets by Black Oystercatchers *Haematopus bachmani.* Ecology **63**: 1352–1362.

Fuentes, E. R., A. J. Hoffman, A. Poiani, and M. C. Alliende. 1986. Vegetation changes in large clearings: patterns in the Chilean matorral. Oecologia (Berlin) **68**:358–366.

Godfray, H. C. J. 1985. The absolute abundance of leaf miners on plants of different successional stages. Oikos **45**: 17–25.

Harris, L. G., A. W. Ebeling, D. R. Laur, and R. J. Rowley. 1984. Community recovery after storm damage: a case of facilitation in primary succession. Science **224**:1336–1338.

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.

Hawkins, S. J., and R. G. Hartnoll. 1983. Grazing of intertidal algae by marine invertebrates. Oceanography and Marine Biology Annual Review **21**:195–282.

Hay, M. E. 1986. Associational plant defenses and the maintenance of species diversity: turning competitors into accomplices. American Naturalist **128**:617–641.

Hils, M. H., and J. L. Vankat. 1982. Species removals from a first-year old-field plant community. Ecology **63**:705–711.

Inouye, R. S., N. J. Huntly, D. Tilman, and J. R. Tester. 1987. Pocket gophers (*Geomys bursarius*), vegetation, and soil nitrogen along a successional sere in east central Minnesota. Oecologia (Berlin) **72**:178–184.

Jernakoff, P. 1983. Factors affecting the recruitment of algae in a midshore region dominated by barnacles. Journal of Experimental Marine Biology and Ecology **67**:17–31.

———. 1985*a*. An experimental evaluation of the influence of barnacles, crevices and seasonal patterns of grazing on algal diversity and cover in an intertidal barnacle zone. Journal of Experimental Marine Biology and Ecology **88**: 287–302.

———. 1985*b*. The effect of overgrowth by algae on the survival of the intertidal barnacle *Tesseropora rosea* Krauss. Journal of Marine Biology and Ecology **94**:89–97.

Kim, D. H. 1976. A study of the development of cystocarps and tetrasporangial sori in Gigartinaceae (Rhodophyta, Gigartinales). Nova Hedwigia **27**:1–145.

Lawlor, L. R. 1979. Direct and indirect effects of n-species competition. Oecologia (Berlin) **43**:355–364.

Levin, S. H. 1976. Competitive interactions in ecosystems. American Naturalist **110**:903–910.

Lindberg, D. R. 1986. Name changes in the "Acmaeidae." Veliger **29**:142–148.

Little, C., G. A. Williams, D. Morritt, J. M. Perrins, and P. Stirling. 1988. Foraging behavior of *Patella vulgata* L. in an Irish sea-lough. Journal of Experimental Marine Biology and Ecology **120**:1–21.

Littler, M. M., P. R. Taylor, and D. S. Littler. 1986. Plant defense associations in the marine environment. Coral Reefs **5**:63–71.

Lubchenco, J. 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology **64**:1116–1123.

———. 1986. Relative importance of competition and predation: early colonization by seaweeds in New England. Pages 537–555 *in* J. Diamond and T. J. Case, editors. Community ecology. Harper & Row, New York, New York, USA.

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.

Lubchenco, J., and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. Ecological Monographs **48**:67–94.

Lubchenco, J., B. A. Menge, S. D. Garrity, P. J. Lubchenco, L. R. Askenas, S. D. Gaines, R. Emlet, J. Lucas, and S. Strauss. 1984. Structure, persistence and role of consumers in a tropic rocky intertidal community (Taboguilla Island, Bay of Panama). Journal of Experimental Marine Biology and Ecology **77**:23–73.

Marsh, C. P. 1984. The role of avian predators in an Oregon rocky intertidal community. Dissertation. Oregon State University, Corvallis, Oregon, USA.

———. 1986. Impact of avian predators on high intertidal limpet populations. Journal of Experimental Marine Biology and Ecology **104**:185–201.

McAuliffe, J. R. 1986. Herbivore-limited establishment of a Sonoran Desert tree, *Cercidium microphyllum*. Ecology **67**:276–280.

McBrien, H., R. Harmsen, and A. Crowder. 1983. A case of insect grazing affecting plant succession. Ecology **64**:1035–1039.

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, B. A., J. Lubchenco, S. D. Gaines, and L. R. Askenas. 1986. A test of the Menge–Sutherland model of community organization in a tropical rocky intertidal food web. Oecologia (Berlin) **71**:75–89.

Newman, W. A., and S. M. Stanley. 1981. Competition wins out overall: reply to Paine. Paleobiology **7**:561–569.

Odum, E. P. 1969. The strategy of ecosystems development. Science **164**:262–270.

Paine, R. T. 1981. Barnacle ecology: is competition important? The forgotten roles of predation and disturbance. Paleobiology **7**:553–560.

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs **51**:145–178.

Petratis, P. S., and L. Sayigh. 1987. In situ measurements of radular movements of three species of *Littorina* (Gastropoda: Littorinidae). Veliger **29**:384–387.

Peer, R. L. 1986. The effects of microcrustaceans on succession and diversity of an algal microcosm community. Oecologia (Berlin) **68**:308–314.

Pfister, C. A., and M. E. Hay. 1988. Associational plant refuges: convergent patterns in marine and terrestrial communities result from different mechanisms. Oecologia (Berlin) **77**:118–129.

Pickett, S. T. A. 1980. Non-equilibrium coexistence of plants. Bulletin of the Torrey Botanical Club **107**:238–248.

Pickett, S. T. A., and P. S. White, editors. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Putz, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. Ecology **65**:1713–1724.

Rausher, M. D. 1981. The effect of native vegetation on the susceptibility of *Aristolochia reticulata* (Aristolochiaceae) to herbivore attack. Ecology **62**:1187–1195.

Ricketts, E. F., J. Calvin, and J. W. Hedgpeth. (Revised by D. W. Phillips.) 1985. Between Pacific tides. Stanford University Press, Stanford, California, USA.

Robles, C. D., and J. Cubit. 1981. Influence of biotic factors in an upper intertidal community: dipteran larvae grazing on algae. Ecology **62**:1536–1547.

Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs **52**:199–221.

Russ, G. R. 1980. Effects of predation by fishes, competition, and structural complexity of the substratum, on the establishment of a marine epifaunal community. Journal of Experimental Marine Biology and Ecology **42**:55–69.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, New York, New York, USA.

Sousa, W. P. 1979*a*. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecological Monographs **49**:227–254.

———. 1979*b*. Disturbance in marine intertidal boulder fields: the non-equilibrium maintenance of species diversity. Ecology **60**:1225–1239.

———. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics **15**:353–391.

Sousa, W. P., S. C. Schroeter, and S. D. Gaines. 1981. Latitudinal variation in intertidal algal community structure: the influence of grazing and vegetative propagation. Oecologia (Berlin) **48**:297–307.

Stanley, S. M., and W. A. Newman. 1980. Competitive exclusion in evolutionary time: the case of the acorn barnacles. Paleobiology **6**:173–183.

Steneck, R. S., and L. Watling. 1982. Feeding capabilities and limitation of herbivorous mollusks: a functional group approach. Marine Biology **68**:299–319.

Strong, D. R. 1977. Epiphyte loads, tree falls, and perennial forest disruption: a mechanism for maintaining higher tree species richness in the tropics without animals. Journal of Biography **4**:215–218.

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.

Tahvanainen, J. O., and R. B. Root. 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). Oecologia (Berlin) **10**:321–346.

Tilman, D. 1987. The importance of the mechanisms of interspecific competition. American Naturalist **129**:769–774.

Toft, C. A., and P. J. Shea. 1983. Detecting community wide patterns: estimating power strengthens statistical inference. American Naturalist **122**:618–625.

Turner, T. 1983*a*. Complexity of early and middle successional stages in a rocky intertidal surfgrass community. Oecologia (Berlin) **60**:56–65.

———. 1983*b*. Facilitation as a successional mechanism in a rocky intertidal community. American Naturalist **121**: 729–738.

Vandermeer, J. 1980. Indirect mutualism: variations on a theme by Stephen Levine. American Naturalist **116**:441–448.

van Tamelen, P. G. 1987. Early successional mechanisms in the rocky intertidal: the role of direct and indirect interactions. Journal of Experimental Marine Biology and Ecology **112**:39–48.

Walker, L. R., and F. S. Chapin, III. 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. Ecology **67**:1508–1523.

Walker, L. R., J. C. Zasada, and F. S. Chapin, III. 1986. The role of life history processes in primary succession on an Alaskan floodplain. Ecology **67**:1243–1253.

Wethey, D. S. 1984. Sun and shade mediate competition in the barnacles *Chthamalus* and *Semibalanus*: a field experiment. Biological Bulletin **167**:176–185.

Williams, S. L. 1987. Competition between the seagrasses *Thalassia testudinum* and *Syringodium filiforme* in a Caribbean lagoon. Marine Ecology Progress Series **35**:91–98.

Witman, J. D. 1987. Subtidal coexistence: storms, grazing, mutualism, and the zonation of kelps and mussels. Ecological Monographs **57**:167–187.

Witman, J. D., and T. H. Suchanek. 1984. Mussels in flow: drag and dislodgment by epizoans. Marine Ecology Progress Series **16**:259–268.