AN ABSTRACT OF THE THESIS OF

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Title: Succession and Stability in Two Rocky Intertidal Communities on the Central Oregon Coast

Abstract approved: Redacted for Privacy
Bruce Menge

The stability of a limpet-dominated community was assessed in a experiment in which an consumer was temporarily removed. Compared to unmanipulated plots, the limpet-exclusion plots developed greater algal abundance and altered species composition of both algae and barnacles. The community was not perturbed beyond its capacity to recover, since the community structure of the limpet-removal plots converged on the structure of the unmanipulated plots after limpet reintroduction. Different components of the community recovered at different rates, depending on whether a species had a size-related escape from limpets. The length of the limpet-removal period did not affect community recovery.

The mechanisms of succession were investigated in a community dominated by the barnacle *Balanus glandula* and the alga *Pelvetiopsis limitata*. Competition for space with *Balanus* excluded the barnacle, *Chthamalus dalli*, as succession proceeded. *Chthamalus* did not affect *Balanus*. Algal colonization was strongly facilitated by *Balanus*, but not *Chthamalus*. Algal recruitment to epoxy-filled barnacle tests indicated that facilitation resulted from barnacle tests altering the substrate, not from the activities of the living animal. Manipulations of barnacle and herbivore abundances demonstrated that facilitation was an mediated by limpets. Consumers decreased the rate of succession, supporting a model of how consumers affect the rate of succession as a function of both the model of succession and the successional status of the species consumed. Both gap size and position within a gap influenced algal cover, limpet density and species composition, but not total barnacle cover or the density and species composition of algal recruits. The results supported the prediction that the effects on succession of increasing gap size are similar to the effects of moving towards the center of a gap.

SUCCESSION AND STABILITY IN TWO ROCKY INTERTIDAL COMMUNITIES ON THE CENTRAL OREGON COAST

by

Terence M. Farrell

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Dean of the Graduate School

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Chapter I

GENERAL INTRODUCTION: STABILITY AND SUCCESSION

A traditional view holds that natural communities are stable (Egerton 1973). Stable communities will both resist being altered and, once altered, rapidly return to their initial state. The widely used phrase "the balance of nature" is an indication of how deeply this equilibrium view of communities is ingrained in our society. Recent empirical studies (e.g. Pianka 1986) are often based on the assumption that communities exist in a stable equilibrium (Travis 1987). Theoreticians also frequently assume that natural communities are stable. Pimm (1982), for example, proposes that several attributes that increase the stability of model communities will, therefore, also be found in real communities. While the assumption that communities are stable is frequently made, it is rarely tested.

Discussions of community stability have been complicated by jargon that is partially redundant and often used inconsistently (Connell and Sousa 1983). I will use the terminology adopted by Connell and Sousa (1983) in which community stability involves three components--resistance, amplitude, and elasticity. Together these components determine the response of a community to a perturbation. Resistance is the ability of a community to maintain its current state when subjected to a perturbation (Boesch 1974). A past perturbation can affect current community structure only if it exceeded the resistance of the system. Once a community is altered, the amplitude of the system will determine if it will return to its original state. Perturbations that exceed the amplitude of a community will produce a persistent alternative state (Orians 1974). The present structure of systems with persistent alternative states will depend strongly on the types of perturbations that have occurred in the past. If a perturbation exceeds the resistance of a community, but not its amplitude, the elasticity of the community will determine the rate of return to its initial configuration (Orians 1974). Communities with high elasticity will be influenced by perturbations for a shorter time than communities with low elasticity.

The process of succession has a strong effect on the stability of a community. Succession is composed of the "changes observed following a perturbation that opens up a relatively large space (Connell and Slatyer 1977)". Succession will determine the stability of a community after it has been perturbed in a manner that removes all or most of the organisms in an area. The amplitude and elasticity of a community will be controlled by succession (Connell and Slatyer 1977). If succession always leads to a single endpoint than the amplitude of a community will be large. The outcome of more complex successional sequences may depend on a variety of factors and therefore result in any one of several endpoints (Cattelino et al. 1979). In this case, the amplitude of the community would be low, resulting in the possibility of persistent alternative states. The rate of succession is by definition the elasticity of a community. Attributes that speed the successional process will increase the elasticity of a community.

This thesis includes three manuscripts (chapters 2-4) that deal with specific aspects of succession or stability in two different rocky intertidal communities. In chapter two, I describe an experimental investigation of community stability. In this experiment I perturbed a community by temporarily removing limpets, the dominant group of consumers. The response of the community to both limpet removal and reintroduction was assessed. In chapter three, I report on an investigation of a second intertidal community. In a set of field experiments I examined the processes that caused succession. In chapter four I describe the effect of two factors--the size of a disturbance and position within a disturbed area, on community development. In the final chapter I examine the results of my field experiments in a continuation of the discussion of stability and succession.

Chapter II

COMMUNITY STABILITY: THE EFFECTS OF LIMPET REMOVAL AND REINTRODUCTION IN A ROCKY INTERTIDAL COMMUNITY

INTRODUCTION

Temporal variation in the population density of consumers (herbivores and predators) is a common perturbation in communities. In terrestrial systems, cyclical changes in population density occur in many consumer populations (i.e. Krebs et al. 1973, Keith et al. 1983, Potts et al. 1984). Extreme drought and cold can also cause temporary reductions in consumer abundance (i.e. Stafford 1971, Boag and Grant 1981). Consumers in marine communities may also suffer large and rapid decreases in abundance. Disease-caused reductions in sea urchin populations have occurred in many parts of the world (reviewed by Scheibling 1986). Similar events have been observed in sea star populations (Menge 1979, Dungan et al. 1982). Catastrophic mortality caused by extreme weather affects limpets (Frank 1965, Sutherland 1970), snails (Dayton 1971), seabirds (Schreiber and Schreiber 1984), and fish (Idyll 1973). Human exploitation and pollution have also caused reductions in marine consumer abundance (Simenstad et al. 1978, Southward and Southward 1978, Beddington and May 1982).

Decreases in consumer abundance often affect lower trophic levels. Both observation of naturally occurring consumer reductions and controlled field experiments involving the removal of consumers demonstrate that predators and herbivores influence the abundance and species composition of organisms in natural communities (reviews in Connell 1975, Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983, Sih et al. 1985, Hughes 1986). These studies indicate that many prey species assemblages are not resistant to the removal of consumers. The effect on community structure of a temporary reduction in a consumer population depends on two factors--1) the magnitude of the change in community structure that occurs during the absence of the consumers; and 2) the period of time these changes persist after consumers recolonize an area. While many studies have determined the first factor, far fewer have investigated the second factor (exceptions include Paine 1976, Paine et al. 1985, Southward and Southward 1978, and Sebens and Lewis 1985). Even rare temporal escapes from consumer pressure will be an important determinant of community structure if they cause persistent changes in prey abundance. Connell and Sousa (1983) found little evidence for persistent alternative states (but see Peterson 1984). Lubchenco (1978) and Paine et al.

(1985), however, demonstrated that persistent changes in community structure can occur after temporary removal of consumers.

Following a temporary reduction in consumer abundance, prey species are likely to respond in one of three ways to reintroduction of the consumer:

1) Prey populations are quickly reduced to pre-removal levels.

2) Prey populations gradually decrease to pre-removal levels over a period of time that corresponds with the maximum life span of the prey species.

3) Prey populations remain above pre-removal densities.

Which of these occurs depends on size- or age-related escapes from predators. The first response is expected if the prey lack an age or size class that cannot be eaten, or prey do not have time to grow to the invulnerable size before reintroduction of the consumer. In this case, the amplitude of the community is not exceeded and elasticity is high, resulting in short-lived changes in community structure. The second response is expected if the consumer eats new recruits of the prey population, but cannot eat the individuals that colonized and grew to an invulnerable stage in its absence (Sebens and Lewis 1985). In this case, the amplitude of the community is not exceeded but elasticity is low, resulting in long-lived changes in community structure. The third response is expected only when the prey has both an escape to a invulnerable stage and the presence of adults protects new recruits from the consumer (Paine et al. 1985). In this case, the amplitude of the community is exceeded, resulting in a persistent change in community structure.

Size-related escapes from predation occur in many habitats. In aquatic communities, the probability of being eaten may decrease with growth in fish (Werner 1986), amphibians (Wilbur 1984), and zooplankton (reviewed by Zaret 1980). Many epibenthic marine organisms have size-related escapes from predation. Paine (1976) found large mussels were invulnerable to a sea star. Birds cannot consume the larger size classes of limpets (Frank 1982; Hockey and Branch 1984, cited in Feare and Summers 1986) and snails (Feare 1970). Snails cannot consume the larger individuals in species of barnacles (Sebens and Lewis 1985) and algae (Lubchenco 1983). While size-related escapes often occur, their consequences in communities are not fully understood. The frequency of size-related escapes may affect community stability, and therefore determine the effects of temporary reductions in consumer abundance.

In this study I experimentally examined the three components of stability in a rocky intertidal community.

I perturbed the community by temporarily removing limpets, the most abundant group of herbivores. I determined if this perturbation exceeded the resistance of the community by comparing the abundances of the prey species in the consumer-removal plots with their abundances in unperturbed plots. I determined if the amplitude of the community was exceeded by reintroducing the consumers and observing if the community converged with the unperturbed plots or persisted in an alternative state. I determined the elasticity of the community by observing the rate with which the perturbed plots converged with the unperturbed plots after the reintroduction of consumers. The relationship between size-related prey escapes and elasticity was also investigated.

Temporary reductions in limpet populations may have important effects on intertidal communites for two reasons. First, limpets strongly affect the abundance and species composition of algae and barnacles in many epibenthic communities (reviewed by Branch 1981, 1986). Second, limpet population reductions may be fairly common perturbations in high intertidal communities. These reductions are caused by extreme weather (Frank 1965, Sutherland 1970), oil spills (Southward and Southward 1978), and seasonally active predators (Frank 1982, Marsh 1986). I determined if the period of time that consumers were absent affected the response of the prey species to reintroduction by removing limpets for approximately one year in one set of plots, and by removing limpets for over two years in a second set of plots.

STUDY SITE

This investigation was done in Boiler Bay (44° 50' N, 124° 03'W) on the Oregon coast, USA. The area is moderately exposed to oceanic waves and would be defined as protected outer coast in the scheme of Ricketts et al. (1985). Since the site is near the base of a north-facing cliff, it receives direct sunlight for only a few hours a day in the spring and summer. The substrate is composed of a rapidly eroding sandstone that is part of the Astoria formation (Snavely and Macleod 1971). Mixed semidiurnal tides occur on the Oregon coast with an extreme tidal range of approximately 3.8 m. Experimental plots were located from 2.0-2.8 m above mean lower low water.

The rock surface is normally barren, with less than 15 percent of its surface covered by sessile organisms. Most of this cover is composed of the barnacles, _Balanus glandula_ and _Chthamalus dalli_, and the encrusting tetrasporic stage (petrocelis) of the alga _Mastocarpus papillatus_ (=_Gigartina papillata_; Kim 1976). An erect alga, *Cumagloia andersonii*, appears in the late spring and summer. Limpets are extremely abundant, with densities exceeding 2,000 individuals per square meter. Approximately 65 percent of the limpets were *Lottia digitalis* (=*Collisella digitalis*, Lindberg 1986), 35 percent were *L. strigatella*; occasional individuals of *L. pelta* and *Tectura scutum* (=*Notoacmea scutum*, Lindberg 1986) were found. Frank (1965) discusses the life history characteristics of these limpets. Other herbivores, including the snail, *Littorina scutulata*, and the isopod, *Ligia pallasii*, were present in low densities. Predators were rarely observed. The black oystercatcher (*Haematopus bachmani*), which may control limpet populations on the Oregon coast (Frank 1982; Marsh 1986), was locally abundant, but could not forage on the vertical face where the study plots were situated. Both water temperature (Tabata 1984) and sea level (Huyer et al. 1983) were elevated in early 1983 by an extrememly strong El Nino event. Paine (1986), however, observed no effect of this event on several species of intertidal organisms. This site is similar to those described by Castenholz (1961), Frank (1965), and Cubit (1984).

METHODS

Experimental Design

The experimental units were square plots with 15 cm sides. In April 1983 all plots were scraped with a wire brush to remove visible organisms. The corners of the plots were marked by drilling holes in the rock and filling them with marine epoxy putty (Z-spar splash zone compound, Koppers Company, Los Angeles, California). Thirty-two plots were established along a horizontal, 16.5 meter transect on the vertical rock face. These plots were used in a completely randomized experimental design consisting of eight replicates of four treatments.

The four treatments were unmanipulated plots, paint controls, short-term limpet removals, and long-term limpet removals. The unmanipulated plots were not experimentally perturbed after initiation. Limpets were excluded by a barrier of copper-based paint (Cubit 1975, 1984). The plot edges were dried with a propane torch before painting a 2-3 cm wide band around the entire plot. There was a 5-10 cm wide buffer zone between the paint and the edge of the experimental plot. At monthly intervals, I manually removed limpets that settled or moved into the exclusion plots. In the short-term exclusion plots the paint was chiseled off the rock in August 1984 (16 months after their initiation) and limpets were allowed to reinvade the plots. In the long-term exclusion plots the paint was chiseled off the rock in July 1985 (28 months after they were initiated). Paint control plots had a 2-3 cm wide strip painted 5-10 cm above the plot on the rock face. This treatment allowed limpets to move in and out of the bottom and sides of the plot, but the area still received the water which washed down over the paint and any chemicals that may have leached out of the paint.

Data Collection and Analysis

Between April 1983 and May 1986, at intervals of approximately four months, I determined the abundance and species composition of macroscopic organisms in the experimental plots. Barnacle densities were determined by counting individuals in five randomly chosen 3 by 3 cm squares within each plot. Other species were counted in the entire plot. Limpets were removed from exclusion plots more frequently than data were collected for the entire experiment. The average limpet density in an exclusion plot between two sampling periods (L) was calculated using the formula:

$$L = \sum_{i=1}^{n} (Pi/T)Di;$$

where Pi is the period of time between the ith limpet removal and the previous removal, T is the total amount of time between sampling dates, Di is the density of limpets in the plot at the ith removal, and n is the number of removals that were done between sampling dates.

I estimated the percent of the rock surface covered by a species by counting the number of dots (out of 50 randomly placed dots) painted on a clear vinyl sheet that were directly above a species. Two categories of percent cover, primary and secondary, were estimated. Primary percent cover measures the percent of the substrate on which a species is directly attached. Attachment space is a resource that is often limiting in intertidal communities. Secondary percent cover estimates the percent of the rock surface that an alga overlays (it does not have to be attached at that particular point). This measure of abundance is a better estimate of biomass and the amount of light an alga intercepts than primary space occupancy.

Data from each sampling period were analyzed separately to detect when statistically significant differences between treatments first began or ended. Raw data frequently exhibited significant between-treatment differences in variances (F-max tests, $\alpha = 0.05$). When necessary, I reduced this heteroscedasticity by using either the arcsin, log, or squareroot transformation (Sokal and Rohlf 1981). No one transformation consistently removed significant heteroscedasticity, so different transformations were used at different dates or for different types of data.

One-way analysis of variance (ANOVA) was used to test for significant differences between treatments. Probability plots were made of residuals to determine if error terms were normally distributed. If an ANOVA test was significant (α=0.05), I used a Student-Newmen-Keuls (SNK) test to determine which treatment means differed significantly. In cases where no transformation would reduce heteroscedasticity to a nonsignificant level I used the Kruskal-Wallis test (Sokal and Rohlf 1981). If a Kruskal-Wallis test was significant (α=0.05), I determined which treatment distributions were significantly different using a STP test (Sokal and Rohlf 1981). Statistical analyses were performed by hand or on a microcomputer using the SYSTAT statistical package (Systat Inc., Evanston, IL).

Special attention was given to two types of comparisons between treatment means. Comparisons between unmanipulated plots and the paint control plots were made to determine the direct effect of copper-based paint on the community. In the absence of paint effects, the comparison between unmanipulated plots and limpet exclusion plots were made to determine the effects of limpets on the community.

RESULTS

Limpet Densities

Limpets were classified either as small (less than 0.5 cm in shell length), or large (greater than 0.5 cm in shell length). Maximum length was approximately 1.5 cm. Separate analyses were performed for different size classes of limpets for two reasons. First, large limpets presumably eat more than smaller limpets. Second, the abundances the two size classes may change for different reasons. Large limpets will appear in plots through immigration or growth of smaller limpets. Small limpets recruit to plots through immigration or settlement of planktonic larvae. The copper-paint barriers greatly reduce immigration but may have little or no affect on larval settlement. The density of both large and small limpets displayed great variation over the course of this study in the unmanipulated plots (Fig. 1). Small limpet density tended to increase with time, while large limpet density displayed no clear trends. The changes in density occurred rapidly, with almost as much variation seen in periods of several months as observed in the entire three years of observation.

No significant differences were observed between small limpet densities in the unmanipulated plots and in the paint controls (Fig. 1). In two of the first three sampling dates, significantly fewer large limpets were found in the paint control plots than the unmanipulated plots. Evidently large limpets moved more rapidly into the unmanipulated plots than into the paint controls immediately after the experiment started. In the final 2.5 years of the experiment the density of large limpets differed from the unmanipulated plots only once, in May 1986.

Both large and small limpet densities were greatly reduced in the exclusion plots (Fig. 1). Significantly fewer limpets were found in the short-term exclusions than the unmanipulated plots on five (large limpets) or six (small limpets) sampling dates before the paint barrier was removed. Similarly, there were significantly fewer limpets in the long-term exclusions than in the unmanipulated plots in seven (large limpets) or six (small limpets) of ten sampling periods before limpets were allowed to reinvade.

After paint barriers were removed, both large and small limpets rapidly increased in numbers to densities similiar to those in unmanipulated plots. Limpet densities did not differ significantly from the unmanipulated plots within 24 days (short-term exclusion) or 15 days (long-term exclusion) after the barriers were removed, and remained similar for the rest of the experiment.

Figure 1. Mean limpet densities in experimental plots (U, unmanipulated controls; P, paint controls; S, short-term limpet exclusions; L, long-term limpet exclusions). The time that limpet removals stopped in the short-term limpet exclusions (*), and the long-term limpet exclusions (**) are marked below the x-axis. At each sampling date, the symbols above the graphs that are not joined by a line indicate treatment means that are statistically different ($\alpha = 0.05$). Fig. 1A. Small (<0.5 cm) limpet density. Fig. 1B. Large (>0.5 cm) limpet density.

Figure 1

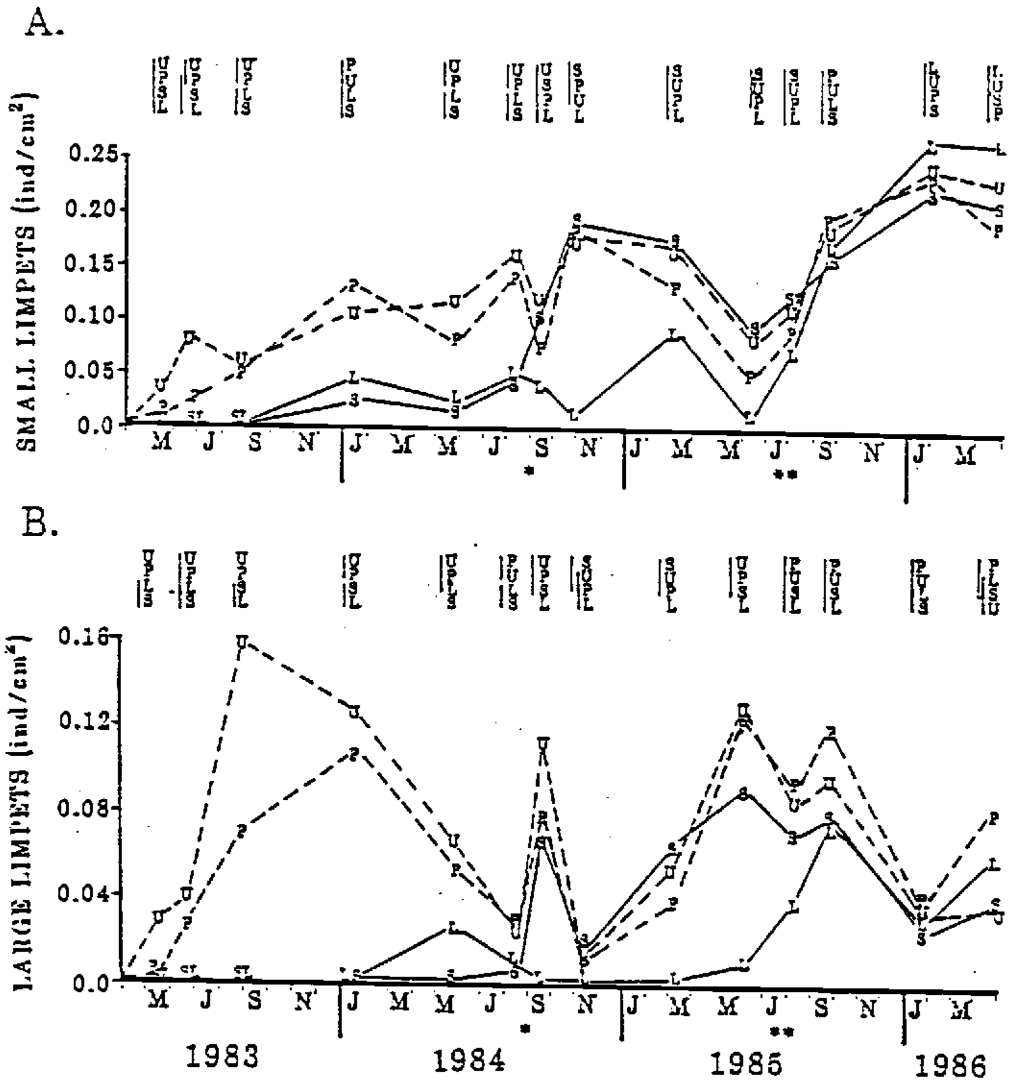
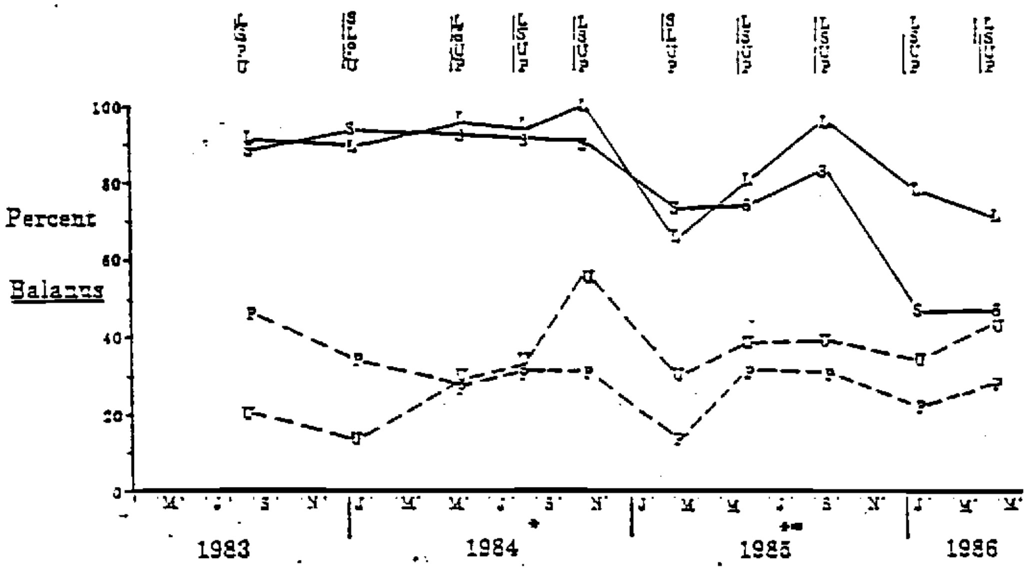

A.
SMALL LIMPETS (ind/cm²)
0.25
0.20
0.15
0.10
0.05
0.0
M J S N J M M J S N J M M J S N J M
*
**
B.
LARGE LIMPETS (ind/cm²)
0.16
0.12
0.08
0.04
0.0
M J S N J M M J S N J M M J S N J M
*
**
1983
1984
1985
1986
U
P
L
S

Figure 2. Mean barnacle species composition in the experimental plots. Symbol definitions are as in the caption of figure 1.

Figure 2


100
80
60
40
20
0
Percent
Balanus
L
S
P
U
M
J
S
N
J
M
M
J
S
N
J
M
M
J
S
N
J
M
M
1983
1984
1985
1986

Barnacle Abundance and Species Composition

Barnacle abundance decreased along the horizontal transect where the experimental plots were located. The seaward plots had much higher larval settlement densities than the landward plots. Similar gradients in larval settlement density have been observed in California (Gaines et al. 1985). This settlement gradient overwhelmed the effects of the individual treatments on barnacle abundance.

Species composition of barnacles (the number of *Balanus* divided by the number of *Balanus* plus *Chthamalus*), however, was not influenced by plot position. Copper-paint appears to have little effect on the species composition of barnacles (Fig. 2). There was a statistically significant difference in species composition on only two of ten sampling dates. On one of these dates (September 1983) the relative abundance of *Balanus* was higher in the paint control plots than in the unmanipulated plots, while on the other date (March 1985) the relative abundance of *Balanus* was lower in the paint control plots than in the unmanipulated plots.

In contrast, limpets had strong and consistent effects on barnacle species composition (Fig. 2). *Balanus* was the most abundant barnacle in the exclusion plots, while *Chthamalus* was more abundant in the unmanipulated plots. After limpets recolonized the short-term limpet exclusion plots it took 17 months for barnacle species composition to converge with the unmanipulated plots. In the long-term exclusion plots the relative abundance of Balanus was still significantly higher than in the unmanipulated plots at the end of the experiment, nine months after limpet removal ended.

Primary Space Utilization

The total primary cover of all organisms in the paint control plots differed significantly from the unmanipulated plots only on the first sampling date (Fig. 3A). This difference resulted from a microalgal film that covered approximately 10 percent of the rock surface in the paint controls, but was absent from the unmanipulated plots (Fig. 4). Other studies involving limpet reductions produced similar microalgal films that were composed primarily of diatoms and blue-green algae (Castenholz 1961; Nicotri 1977). Limpet exclusion resulted in a large and rapid increase in the cover of sessile organisms. In the unmanipulated plots mean primary space utilization never exceeded 18 percent, while total cover in limpet exclusions always exceeded 38 percent. The difference between the unmanipulated plots and both the short-term and long-term exclusions were statistically significant on all sampling dates when limpets were excluded. Primary cover decreased in both sets of exclusion plots soon after reinvasion by limpets, and in approximately six months total primary space occupied did not differ significantly among the treatments.

Treatments not only differed in the total amount of primary space occupied, but also in the species composition of that cover (Fig. 4). In the unmanipulated plots encrusting algae and barnacles were most abundant, with *Cumagloia* contributing to the cover in the late spring and summer. In the first months of the experiment, the exclusion plots had more ephemeral algae and microalgal film than the unmanipulated plots. The ephemeral algae included *Enteromorpha linza*, *E. intestinalis*, and small amounts of *Porphyra* sp. and *Urospora wormskioldii*. At later dates a thick, mixed growth of *Petalonia fascia* and *Scytosiphon dotyi* (*Scytosiphon*-*Petalonia* turf) was abundant in the exclusions but completely absent in the unmanipulated plots. *Cumagloia* comprised relatively less of the primary cover in the exclusion plots in the summer of 1984 than in the unmanipulated plots. After limpet reintroduction, in both the short- and long-term exclusions the abundance of the *Scytosiphon*-*Petalonia* turf decreased rapidly, while barnacle and encrusting algal abundances decreased more slowly. The algal crusts consisted primarily of Mastocarpus papillatus and the ralfsioid crusts of Petalonia and Scytosiphon. A smaller fraction of the crusts consisted of Corallina vancouveriensis, Ralfsia fungiformis, and Analipus japonicus.

Secondary Space Utilization

There were no significant differences in upright algal cover between the unmanipulated plots and the paint control plots. More secondary algal cover occurred in the limpet exclusion plots than the unmanipulated plots (Fig. 3B). The largest differences occurred in the late spring and summer when algal cover was most abundant. The exclusion plots had significantly more secondary cover than the unmanipulated controls on four of the five dates (short-term exclusions) or seven of the eight dates (long-term exclusions) while limpets were excluded. In both the short- and long-term exclusions significantly higher levels of algal cover did not occur after the reintroduction of limpets.

The species composition of the secondary cover differed greatly between unmanipulated plots and exclusion plots (Fig. 5). Almost all of the canopy in control plots consisted of Cumagloia. In the exclusions algal cover was more diverse with ephemeral algae, *Cumagloia*, *Scytosiphon*, and *Petalonia* all achieving high relative abundance at some time. Many other species, including *Odonthalia lyallii*, *Endocladia muricata*, *Iridaea cordata*, *Corallina vancouveriensis*, *Cladophora* sp., *Halosaccion glandiforme*, *Analipus japonicus*, and *Mastocarpus papillatus* were found in low abundances in the exclusions, but were never present in the unmanipulated plots.

Figure 3. Mean percentage of space occupied by organisms. Symbol definitions are as in the caption of figure 1. Figure 3A--Total primary space occupancy. Figure 3B--Total secondary space occupancy.

Figure 3

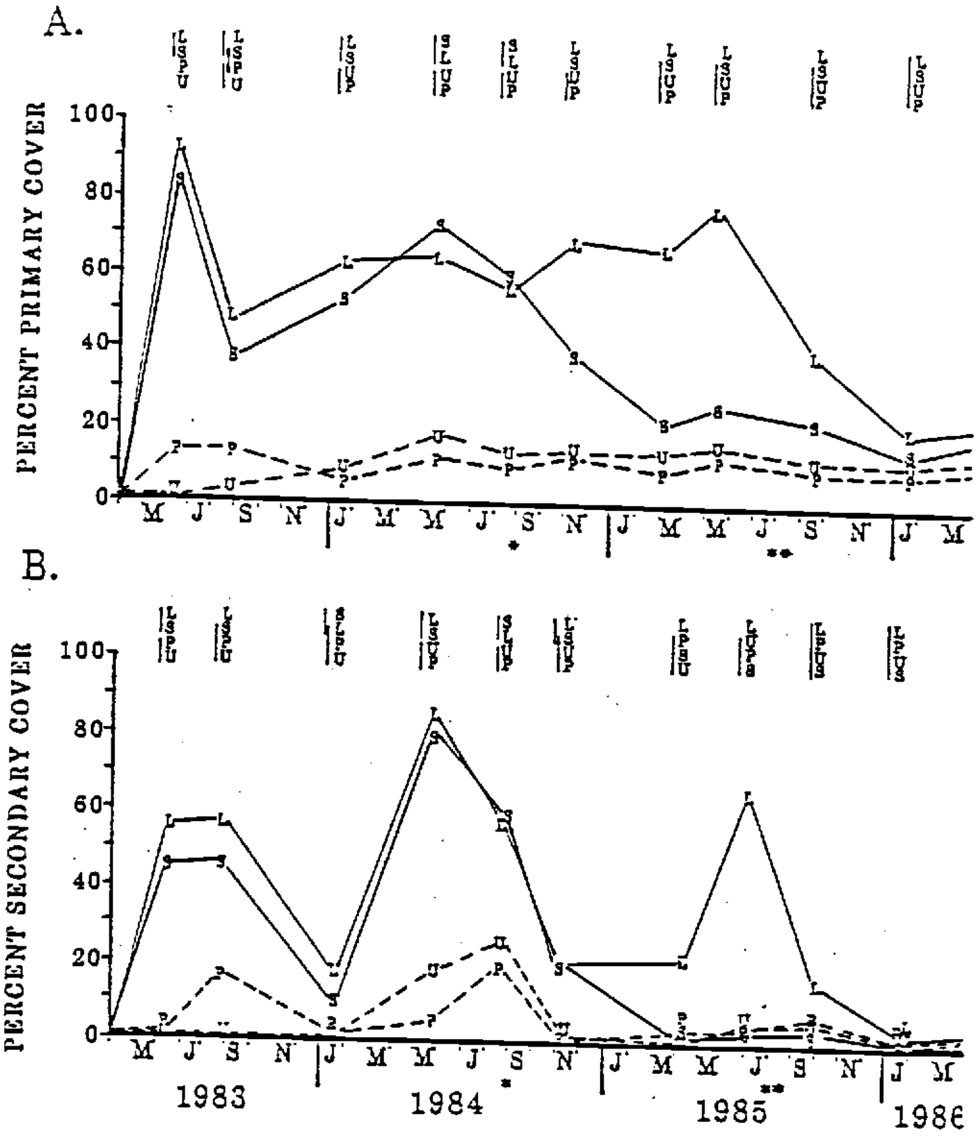

A.
PERCENT PRIMARY COVER
100
80
60
40
20
0
M J S N J M M J S N J M M J S N J M
*
**
L
S
P
U
B.
PERCENT SECONDARY COVER
100
80
60
40
20
0
M J S N J M M J S N J M M J S N J M
1983
1984
*
1985
**
1986

Figure 4. Mean species composition of organisms occupying primary space. The time that limpet removals stopped in the exclusion plots are marked (*) above the x-axis.

Figure 4

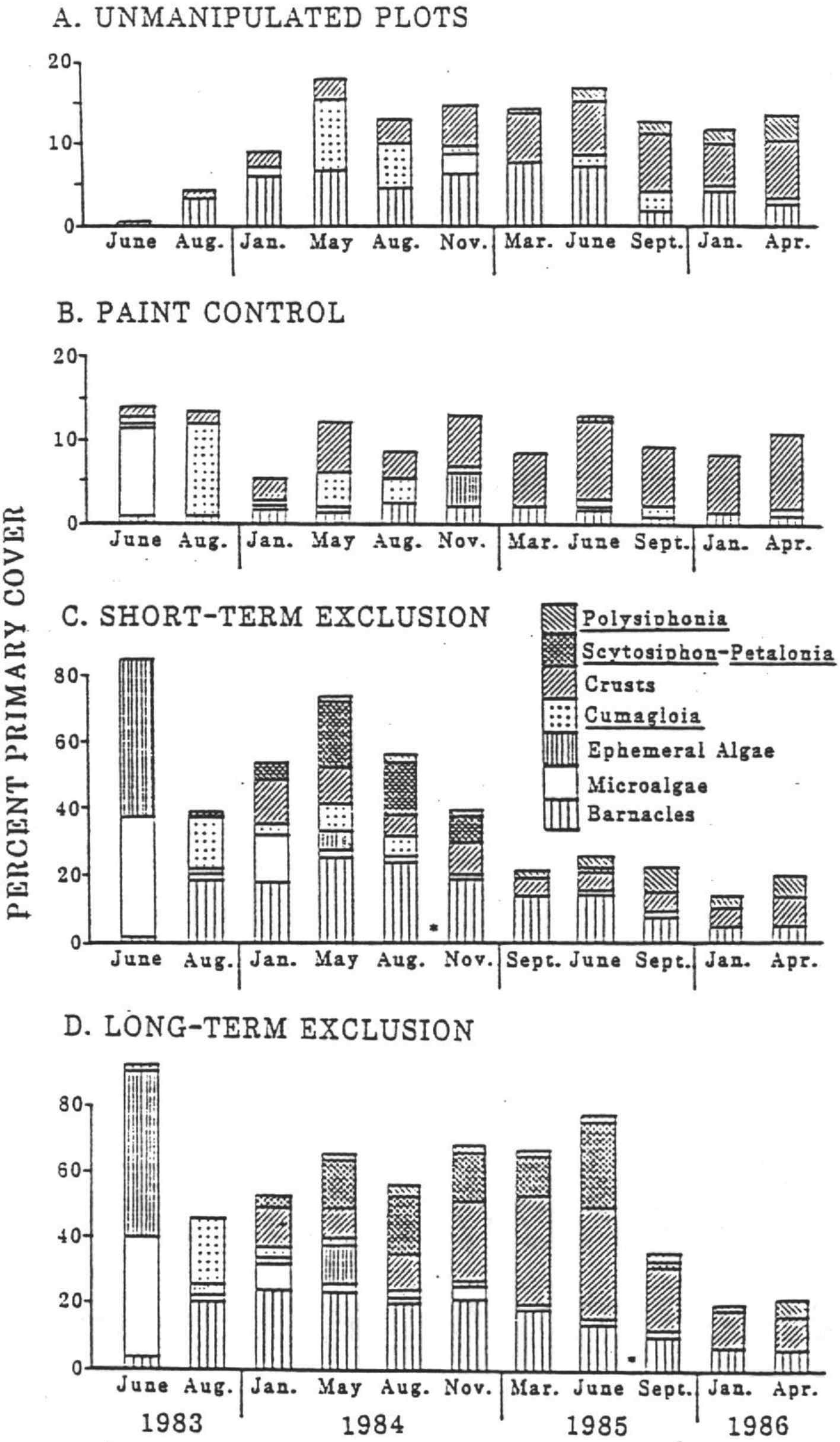
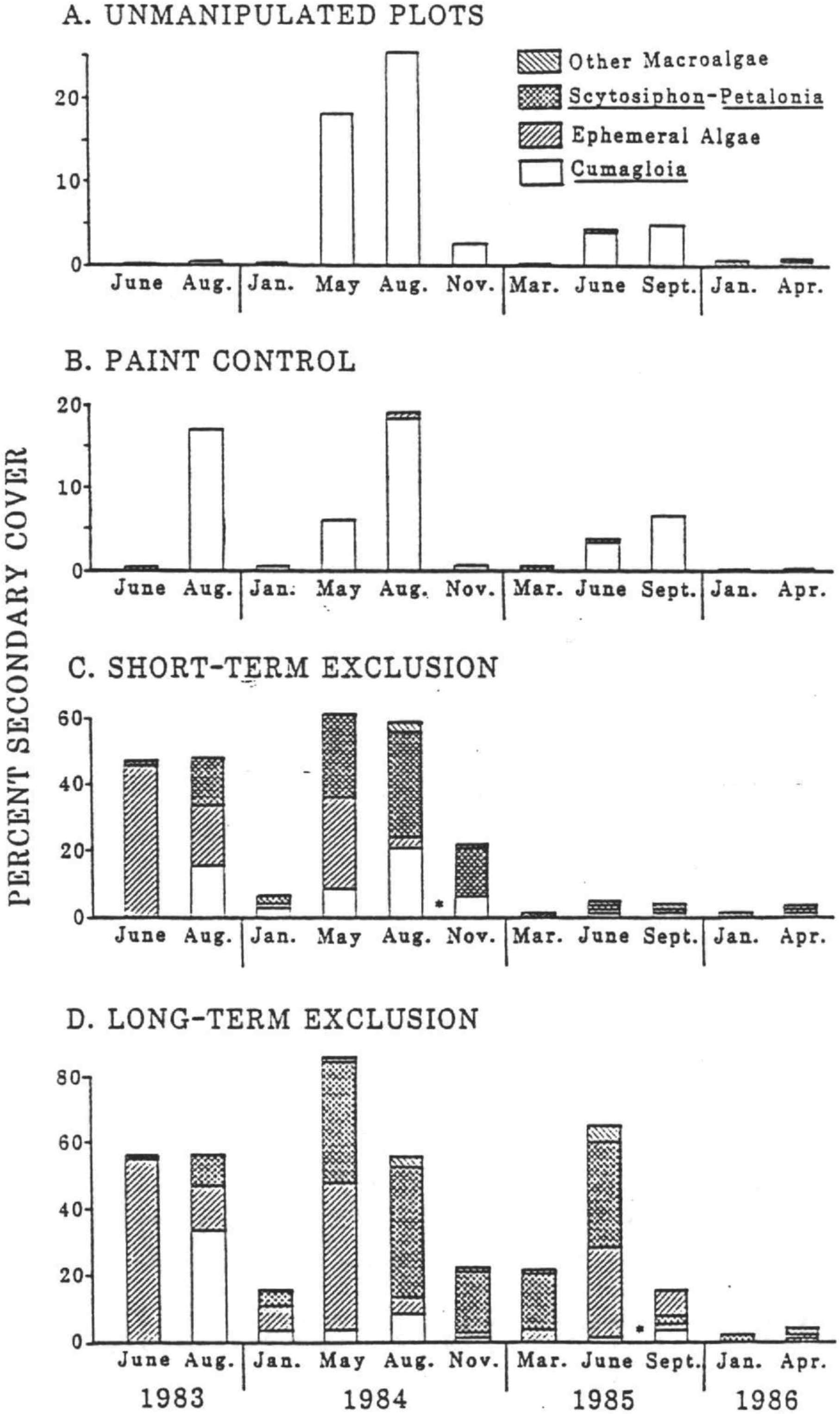

A. UNMANIPULATED PLOTS
20
10
0
June
Aug.
Jan.
May
Aug.
Nov.
Mar.
June
Sept.
Jan.
Apr.
B. PAINT CONTROL
20
10
0
June
Aug.
Jan.
May
Aug.
Nov.
Mar.
June
Sept.
Jan.
Apr.
PERCENT PRIMARY COVER
C. SHORT-TERM EXCLUSION
Polysiphonia
Scytosiphon-Petalonia
Crusts
Cumagloia
Ephemeral Algae
Microalgae
Barnacles
80
60
40
20
0
*
June
Aug.
Jan.
May
Aug.
Nov.
Sept.
June
Sept.
Jan.
Apr.
D. LONG-TERM EXCLUSION
80
60
40
20
0
*
June
Aug.
Jan.
May
Aug.
Nov.
Mar.
June
Sept.
Jan.
Apr.
1983
1984
1985
1986

Figure 5. Mean species composition of algae occupying secondary space. The time that limpet removals stopped in the exclusion plots are marked (*) above the x-axis.

Figure 5


A. UNMANIPULATED PLOTS
Other Macroalgae
Scytosiphon-Petalonia
Ephemeral Algae
Cumagloia
B. PAINT CONTROL
C. SHORT-TERM EXCLUSION
D. LONG-TERM EXCLUSION
PERCENT SECONDARY COVER
0
10
20
40
60
80
June
Aug.
Jan.
May
Aug.
Nov.
Mar.
June
Sept.
Jan.
Apr.
*
1983
1984
1985
1986

DISCUSSION

Effectiveness of the Treatments

Copper-based paint has been used to exclude limpets in a large number of studies (e.g. Cubit 1975, 1984, Sousa 1979a, 1984b, Little and Smith 1980, Lubchenco and Cubit 1980, Slocum 1980, Paine 1980, 1981, 1984, Robles and Cubit 1981, Robles 1982). Few of these studies have tried to determine if copper paint directly affects organisms. Robles (1982) and Cubit (1984) used control plots with discontinuous paint barriers. Robles (1982) observed no obvious differences in algal growth between areas with complete and discontinuous barriers. No previous study, however, has compared plots partially enclosed by copper paint with plots with no adjacent paint to determine if copper paint directly affects organisms. Early in this experiment, significant differences were observed between unmanipulated plots and paint control plots in large limpet density, primary cover, and barnacle species composition. This difference in large limpet density resulted from limpets immigrating more slowly into the partially enclosed paint control plots than into the unmanipulated plots. The differences in barnacle species composition and primary cover could have been caused by either the reduced density of limpets in the paint controls or by a direct effect of the copper paint.

Two factors suggest that the differences in barnacle species composition between the unmanipulated and paint control treatments were caused by the change in limpet abundance and not a direct paint effect: 1) As limpet densities converged in the unmanipulated plots and the paint control plots the differences in primary cover and barnacle species composition ended. 2) The differences in barnacle species composition and algal film cover are those expected to occur under reduced limpet densities but not due to proximity to copper paint. Working with the same species as in this study, Dayton (1971) found that removing limpets (without the use of copper paint) increased the relative abundance of Chthamalus. Many studies have shown that removing limpets results in a microalgal bloom (reviewed by Branch 1981, 1986). These studies include several investigations of Lottia digitalis, the most abundant limpet in this community (Castenholz 1961, Dayton 1971, Cubit 1984). There is no reason to predict that proximity to copper paint would increase the relative abundance of Chthamalus or cause a microalgal bloom. In another study on the Oregon coast (Olson 1985), both fewer limpets and increased algal cover occurred in the paint controls than in unmanipulated plots. In my experiment the problem in interpretating comparisons of paint controls and unmanipulated plots caused by different limpet densities probably could have been avoided by moving limpets into the plots at the start of the experiment, instead of allowing them to colonize on their own.

The large and rapid changes in limpet density in the control plots do not seem to be caused by mortality or recruitment. Limpets appeared to move into crevices located outside the plots during stressful periods. Small limpets, which are less vagile than large limpets, showed smaller changes in density over short time periods than large limpets. Vertical seasonal migrations of limpets (Frank 1965, Breen 1972) may have also affected the abundance of limpets in the experimental plots.

Effects of Limpet Exclusion

The increase in the relative abundance of _Balanus_ that occurred when limpets were removed is consistent with the results of other studies involving these species (Dayton 1971, Paine 1981). _Chthamalus_ is more resistant than _Balanus_ to mortality caused by limpet grazing activity, probably because of its smaller size and lower profile (Paine 1981). Dayton (1971) found that interspecific competition with _Balanus_ reduced the abundance of _Chthamalus_ in the limpet exclusion plots. In the present experiment, interspecific competition for space was slight since barnacles never covered more than 25 percent of the rock surface. Overgrowth by algae may have been a major source of mortality for Chthamalus in limpet exclusion plots. Many small, dead Chthamalus were observed covered with ephemeral algae and Scytosiphon-Petalonia turf soon after the start of the experiment. Balanus, however, did not appear to be harmed by this overgrowth. On Australian shores, Denley and Underwood (1979) found that algal overgrowth killed barnacles, although Jernakoff (1985b) demonstrated adult barnacles were not adversely affected by algal overgrowth for periods as long as one year.

The removal of limpets produced a rapid increase in algal abundance. As in other studies (Southward and Southward 1978, Robles 1982), the limpet removals caused a bloom of microalgae and ulvoids. The abundance of these algae decreased as Petalonia and Scytosiphon became established. A thick growth of the upright morphs of Petalonia and Scytosiphon occurred in the exclusion plots and not in the plots with limpets. This supports Lubchenco and Cubit's (1980) hypothesis that these morphs are an adaptation to habitats with low grazing pressure. Upright thalli of Petalonia and Scytosiphon are usually found in the winter (Abbott and Hollenberg 1976, Bold and Wynne 1978, Clayton 1981). The prostrate morphs produce upright thalli in response to daylength cues indicating the coming of winter (Roeleveld et al. 1974). In this study, however, the upright thalli were found in all seasons in the exclusions and were most abundant in the summer months.

Effects of Limpet Reintroduction

In both short- and long-term limpet exclusions algal cover declined rapidly after the reintroduction of herbivores. The most abundant species of algae in the removal plots, *Petalonia*, *Scytosiphon*, and *Enteromorpha*, appear to have no defenses that prevented limpets from consuming them. The species of algae that appeared unpalatable to the limpets, such as *Analipus*, *Mastocarpus*, *Iridaea*, and *Corallina*, were too rare to have much influence on community structure. These algae appeared to be more slow growing than the palatable species, and may not have been able to maintain large populations because the rock surface eroded rapidly during this study. The erosion rates around the epoxy-putty plot markers (n=168) averaged 0.05 cm/year. I often observed large barnacles and algal thalli in the process of peeling off the rock. Similar disturbances were observed by Frank (1965) after below-freezing air temperatures. The formation of unoccupied space by exfoliation of the rock may prevent competitive exclusion and maintain the high algal diversity that occurred in the limpet exclusion plots.

Barnacle species composition in the exclusion plots, unlike algal abundance and species composition, did not converge rapidly with the unmanipulated plots after the reintroduction of limpets. The relative abundance of Balanus in comparisons with the unmanipulated plots remained higher for 17 months in the short-term exclusions and for more than nine months after reintroduction in the long-term exclusions. The changes in barnacle species composition in the exclusion plots persisted only as long as the barnacles that recruited to the plots during limpet exclusion survived in large numbers. Other studies have observed that only recently settled barnacles are susceptible to limpet bulldozing (reviewed by Branch 1986). Algal abundance, however, was not significantly different in the exclusions six months after Lottia reintroduction.

The Effects of Spatial and Temporal Scale

The results of a field experiment may be influenced by the size of the area manipulated and the length of time the treatments are imposed (Wiens et al. 1986). In consumer-removal experiments increasing the period of exclusion could influence the response of the community to consumer reintroduction in several ways. First, longer removal periods would give individuals additional time to grow to invulnerable sizes. Second, longer removal periods could allow the colonization of new species with different characteristics than those of the early colonists. Neither of these events appeared likely to occur in this community. The individuals of the species present in the exclusion plots grew to their maximum sizes before the reintroduction of Lottia. New species also did not appear to be successfully invading the exclusion plots. Nearby horizontal intertidal areas in which limpets have been effectively removed by birds for many years have a similiar species composition to that of the exclusion plots. The fact that the communities in the short-term and long-term limpet exclusion plots reacted almost identically to the reintroduction of limpets indicates that the results of this experiment were not strongly dependent on the length of the exclusion period.

Changing the size of the area from which limpets were removed may have also affected the outcome of this study. If much larger areas were cleared of limpets recolonization would result primarily from the recruitment of planktonic larvae, not from the immigration of adults from adjacent substrate as was the case here. Many new recruits were observed settling in the exclusion plots, indicating recruitment would probably rapidly replace the limpet population. Lottia probably has a long planktonic period, like the only member of the Lottiidae studied in this respect (Kessel 1964). If this is the case, recruitment rates are not dependent on the presence of nearby adult populations. The changes in community structure that occur after limpet reinvasion might be delayed until after recruitment events, which, for Lottia, occur in both the spring and fall (Fritchman 1961, Morris et al. 1980), and subsequent growth of the limpets. Southward and Southward (1978) have documented the changes that occurred following the removal and recolonization of limpets from large areas of the English shore after an oil spill. They concluded that the results of these large scale limpet removals were similar to those observed in small-scale field experiments.

Community Stability

The large changes in community structure that occurred in the limpet exclusion plots indicate that the original community was not resistant to a large decrease in consumer abundance. Alternative states occur in many communities after the removal of consumers (see reviews by Connell 1975; Lubchenco and Gaines 1981; Sih et al. 1985). The changes occurring after consumer removal often result from both the direct effect of decreased predation and the indirect effect of increased competition among members of the prey assemblage (Sih et al. 1985).

The community that developed while limpets were excluded was not a persistent alternative state. After reintroduction of limpets this community converged with the community in the plots that were not perturbed. This convergence indicates that limpet removal is a perturbation that did not exceed the amplitude of the original community; the alternative state could only persist while limpets were removed. Connell and Sousa (1983) discuss similar situations in aquatic and grassland communities where human intervention appears to be necessary to maintain alternative states. As in this study, other investigations demonstrate that the alternative communities with increased algal abundance that resulted from temporary herbivore exclusion were unstable (Castenholz 1961, Lamberti and Resh 1983, Paine 1984, Sebens 1986). Herbivore reintroductions lead to rapid decreases in algal abundance and a return to the pre-removal state.

Insight on the formation of alternative stable states is provided by experimental removals of sea stars in several geographic locations (Paine et al. 1985). In these communities, alternative stable states formed after temporary consumer removal if the prey (mussels) had both a size-related escape from predation and if adult mussels protected young from predators. In Chile, the mussels studied were too small to attain a size escape from a sea star and therefore did not persist after the reintroduction of the predator. In New Zealand and Washington State (USA), however, mussels did attain escapes through growth to large size and therefore persisted after the reintroduction of sea stars. Additionally, the large mussels formed dense beds that protected young mussels from consumers, causing changes in community structure that persisted longer than the life span of the mussels that became established during sea star exclusion. In these intertidal areas, sea star removal was a perturbation that exceeded the amplitude of the community and resulted in a persistent alternative state. In Oregon, barnacles had a size-related escape from limpet-caused mortality. Barnacle-covered substrate, however, is structurally less complex than mussel beds. Small mussels can grow beneath the byssal threads and shells of adults where they are protected from predators. In contrast, groups of barnacles do not produce a comparable refugia for recruits, and therefore do not produce an alternative stable state. Size-related escapes of prey that occur after reductions in consumer abundance decreased the elasticity of the community. The barnacles that settled and grew to an invulnerable size while limpets were removed persisted after limpet reintroduction and decreased the rate of return to the initial state. Because the algae did not have a size-related escape from limpets they had higher elasticity than the barnacles. Algae in many other communities also do not appear to have size-related escapes from herbivores (Castenholtz 1961, Lamberti and Resh 1983, Paine 1984, Sebens 1986). The rapid decline in algal cover after the herbivore reintroductions observed in these studies indicate that the communites had high elasticity. Size-related escapes do occur in some algae-herbivore interactions. Several species of fucoid algae (Southward and Southward 1978, Lubchenco 1983) and kelp (Harris et al. 1984) can escape from their consumers through growth to large size. The long recovery period (9-10 years) of an English intertidal community after a large decrease in limpet abundance may have been caused, in part, by a size-related escape of the dominant alga (Southward and Southward 1978). The encrusting portions of algal thalli may also be an invulnerable life history stage. Algal crusts are more resistant than upright portions of the thalli to grazers and physical disturbance (Lubchenco and Menge 1978, Lubchenco and Cubit 1980, Sousa 1980).

The effect of invulnerable life history stages on the elasticity of a community may depend on the type of perturbation to which it is exposed. The presence of invulnerable stages can increase the elasticity of a community if it is perturbed by an increase in consumer abundance. Sousa (1980) found that surviving algal crusts quickened community recovery after a large temporary increase in sea urchin grazing.

Community stability influences how past events affect the present distribution and abundance of organisms. Recent studies (Menge and Lubchenco 1981, Hawkins and Hartnoll 1983, Jernakoff 1983, Petraitis 1983) indicate that the patchy distribution of organisms in many rocky intertidal communities is caused by past spatial variation in the abundance of consumers. This study indicates the effects of variation in limpet abundance will not be similar for all community members. Experimental limpet population reductions caused relatively long lasting changes in barnacle species composition. This indicates that past variation in consumer abundances may affect present barnacle distributions. The experiments, however, indicate that past variation in limpet abundance will not lead to long-lasting changes in the algal assemblage.

Chapter III

DIRECT AND INDIRECT INTERACTIONS AS MECHANISMS OF SUCCESSION: AN EXAMPLE FROM A ROCKY INTERTIDAL COMMUNITY

INTRODUCTION

Ecological succession consists of the sequence of colonization and species replacement that occurs after a site is disturbed (Connell and Sousa 1977). A community will tend to exist in a climax state if the average period between disturbances is much longer than the time needed to complete succession. A community will be characterized by preclimax stages if the average period between disturbances is near or less than the time needed to complete succession. 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 1979, Sousa 1984, Pickett and White 1985). To understand such communities it is necessary to know the dynamics of succession.

Two general questions must be answered to understand succession--1) What factors determine when each species becomes established after a disturbance, and 2) What factors determine when species are eliminated from 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).

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 1979a). 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 depend on earlier colonists.

How do early colonists affect later successional species? Connell and Slatyer (1977) pointed out that there are three possible modes of succession. First, in the facilitation model early successional species hasten the establishment of later colonists. Second, in the tolerance model the early successional species have little or no effect on the establishment of later colonists. Third, in the inhibition model early successional species slow the establishment of later colonists. In early studies of community development, facilitation was thought to be the dominant mode of succession (Clements 1928, Egler 1954). More recent studies, however, have shown the importance of the inhibition mode of succession (Drury and Nisbet 1973, Connell and Slatyer 1977, Sousa 1979a).

The mode of succession, defined as the net effect of the early successional species on later successional species, is not identical to the mechanism of succession, defined as the actual causal pathway that produces that net effect. A single mode 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).

The mechanisms involved in species interactions need to receive increasing attention (Tilman 1987). In particular, distinguishing between direct and indirect interactions is critical for 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 (Fig. 6). 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 1979a, Lubchenco 1983, Van Tamelen 1987).

Traditional views of succession have focused on competitive interactions and the influence of colonists on the physical features of the environment. The role of consumers in succession has been largely ignored (Connell and Slatyer, 1977). Some more recent studies of succession, however, 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 1979a, Lubchenco 1983) or slowed (Dayton 1975, Sousa et al. 1981, 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 effects of consumers on the rate of succession can be based on two factors: 1) the mode of succession, and 2) the successional status of the species whose abundances are reduced by consumers (Fig. 7). For simplicity, consumers can be considered to remove mostly early succession species, equivalent amounts of early and later successional species, or mostly later successional species. In reality, both the consumer removal axis and the mode of succession axis are a continuum.

Predictions of the model include the following: (1) If consumers remove mostly later successional species then succession will be slowed regardless of the mode 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 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 facilitation and removing later successional species. (5) if consumers remove mostly early successional species the pace of succession is by definition dependent on the mode of succession. In this case, consuming early successional species will--a) hasten succession in the inhibition model, b) have no effect on the rate of succession in the tolerance model, or c) slow succession in the facilitation model.

In this investigation, I examined the successional sequence in a rocky intertidal habitat, and sought to determine the processes that controlled the establishment and loss of species during community development. Finally, I used the results of this study to test a general model that predicts how consumers will affect the rate of succession as a function of the mode of succession and the successional status of the species consumed.

Figure 6. A comparison of direct and indirect interactions. Interpretation A--Probabilities of correct prediction (Pc) of direct (solid lines) and indirect interactions (dashed lines) in a hypothetical interaction web. The probability of correct prediction is assumed to be 0.75 for direct interactions and calculated for indirect interactions as the product of the probabilities of the component direct interactions. Direct interactions are more predicatable than indirect interactions. Interpretation B--Pc is the probability that an interaction remains the same from one area (or time) to another. The probability of consistency is assumed to be 0.75 for direct interactions and calculated as above for indirect interactions. Direct interactions are more likely to remain the same than indirect interactions.

Figure 6

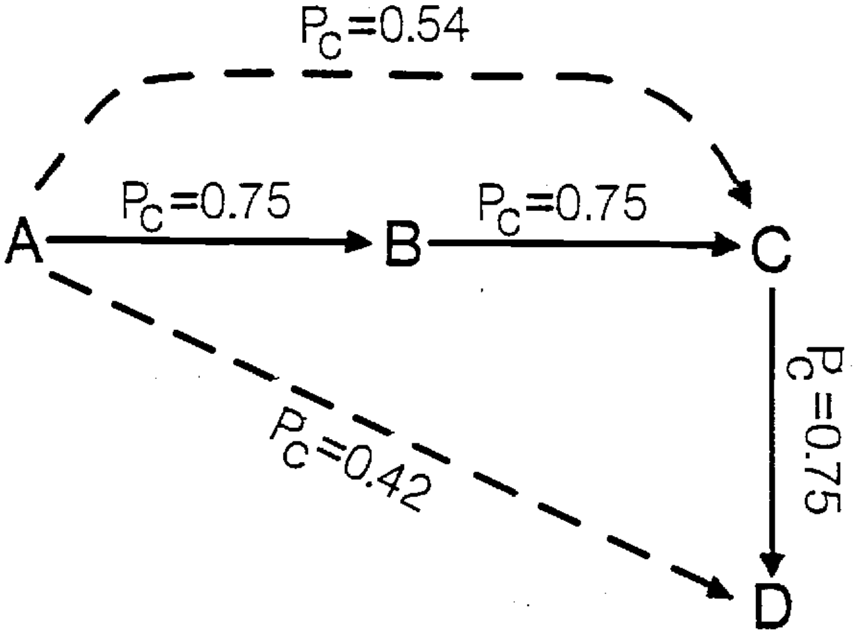
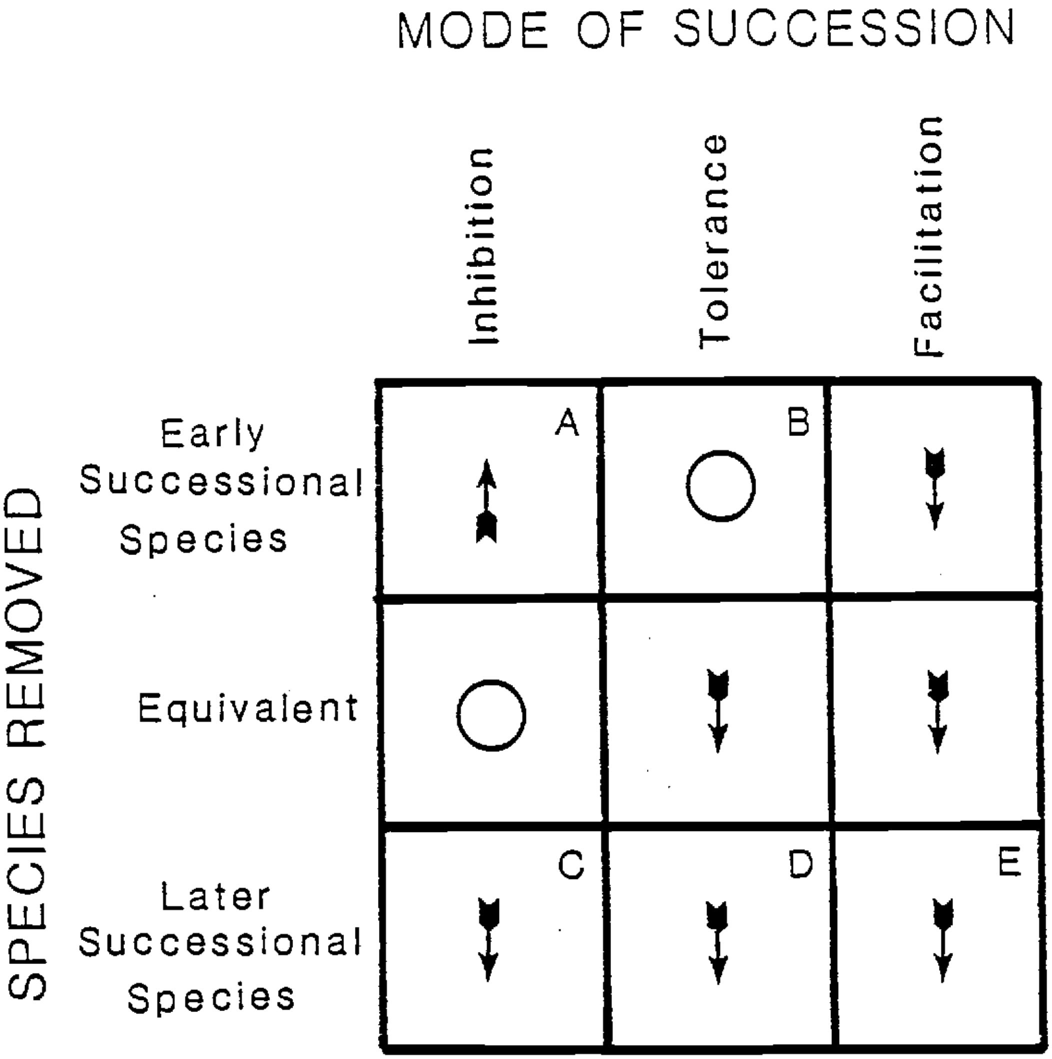


Figure 7. A predictive model of the effect of consumers on the rate of succession. ↑--consumers increase the rate of succession, 0--no effect, ↓--consumers decrease the rate of succession. Letters indicate possible examples of specific combinations of the two factors (A--Lubchenco and Menge, 1978; Sousa, 1979; Lubchenco, 1983; B--Jernakoff, 1985; C--Sousa et al. 1981; D--this study, the *Chthamalus*-*Balanus* interaction; E--this study, the barnacle-macroalgae interaction).

Figure 7



MODE OF SUCCESSION

SPECIES REMOVED

	Inhibition	Tolerance	Facilitation
Early Successional Species	A ↑	B ○	↓
Equivalent	○	↓	↓
Later Successional Species	C ↓	D ↓	E ↓

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 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 were directly exposed to oceanic waves coming from any direction. The experimental plots at both sites are located on horizontal or sloping (< 45°) rock surfaces. Mixed semi-diurnal tides with an average daily range of approximately 2.5 m occur along the Oregon coast. The study plots were in the high intertidal zone, ranging from 2.2-3.0 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. The rock at all sites was basalt.

A community of low diversity occurred at the study sites. The two dominant species in this community were the fucoid algae Pelvetiopsis limitata, and the barnacle

Balanus glandula. This *Balanus*-*Pelvetiopsis* community occupies large areas of the high intertidal zone on exposed shores from central California to Vancouver Island, British Columbia (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--*Fucus distichus*, *Endocladia muricata*, and *Mastocarpus papillatus*, were common members of the community. The algae usually grew on the tests of *Balanus*. The most abundant herbivores were limpets, primarily *Lottia digitalis* and *L. strigatella*. Other herbivores included *Littorina scutulata*, and gammarid amphipods. Predatory invertebrates were rare. Seastars and predatory snails are common lower in the intertidal zone at these sites but were 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).

Though each of the study sites was occupied by the *Balanus*-*Pelvetiopsis* community, they differed in more subtle respects. The Fogarty Creek Point (FCP) site was the highest, with plots located between 2.4-3.0 m above MLLW. The FCP site covered the largest area, with plots spread along a 30 m length of shoreline. The plots were located along a wave-exposure gradient. The more seaward plots were located higher in the intertidal. Postelsia palmaeformis, a algae 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 (YHL) site was an area about 4 m in length. The YHL plots ranged from 2.2-2.6 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 (YHH) site. The YHH plots were located on a 20 m length of shoreline that extended on both sides of the YHL site. The YHH plots ranged from 2.2-2.9 m above MLLW. Both Yaquina Head sites had higher barnacle cover than the FCP site. Fucus did not occur at the two Yaquina Head sites.

METHODS

Quantification of Disturbance

I monitored plots at YHH and FCP to determine the rate and size distribution of disturbances. A dense settlement of barnacles occurred at YHH in the second week of September 1984. After this recruitment period all the patches in the community were occupied by barnacles. No successful barnacle recruitment occurred between late September 1984 and the fall of 1985 (unpublished data). A dense settlement of barnacles did occur in May 1985, but all these recruits were soon killed by desiccation during a period of calm, clear weather. In June 1985, I recorded the number and size of patches without barnacles in ten 0.5 square m plots. These barnacle-free areas were disturbed since the previous September becausee they were occupied at that time. Furthermore, since no successful recruitment occurred between September and June all patches disturbed in that period would have remained unoccupied and were therefore counted in the June census. Barren areas smaller than 2 square cm were not counted. At FCP, I monitored twelve 0.5 square m plots. I determined the disturbance rate during the period from October 1985 (immediately after a period of dense barnacle recruitment) to July 1986. Some barnacles successfully recruited in May and June, so patches that were completely barren or had only very young barnacles were counted as being disturbed in the census period.

Experimental Design: YHH

In April 1983, I initiated an experiment near the upper edge of the *Balanus*-*Pelvetiopsis* zone. The experimental units were square plots with 15 cm sides. The corners of each plot were marked with a rounded knob (aproximately 3 cm in diameter) of marine epoxy-putty. Twenty-one plots were established in seven groups of three plots. These plots were used in a randomized block design consisting of seven replicates of 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. This scraping mimicked natural disturbance. 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 were not perturbed after scraping. In the cleared, barnacle-removal plots both species of barnacles were removed with a blunt probe as they settled.

Experimental Design: YHL

In September 1984 I initiated an experiment near the lower edge of the *Pelvetiopsis*-*Balanus* zone. The experimental units were 30 square plots with 6 cm sides. These plots were about one-sixth the area of the YHH plots. At the start of the experiment all plots were scraped with a putty knife and their corners marked with small (less then 1 cm in diameter) pieces of 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 hours. I then removed the animal from the test and filled the interior with epoxy-putty leaving 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: FCP

In April 1984 an experiment was initiated at FCP. 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 experimental design was a randomized block design with eight groups of plots. Each of these groups consisted of one replicate of the following treatments--1) barnacles and limpets present, 2) barnacles present, limpets removed, 3) barnacles removed, limpet present, 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 copper-paint barriers painted on the rock. Limpets refuse to move across areas covered with copper paint (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 (references in Chapter 2, Farrell

1987). A 3 cm wide strip was scraped to remove organisms and dried with a propane torch before painting. This 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 that moved or recruited inside the paint barriers were removed manually.

Data Collection

In all three experiments, data were collected approximately every four months. 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 discernable 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. Limpets were observed to nestle among the larger barnacles near the edge of the recently cleared plots during the day, and then moved into the plots to forage at night or while the plots were awash. I therefore included all limpets within two cm of a plot when estimating limpet density. At YHH, barnacles were counted in five, randomly choosen, 3X3 cm square subunits within each plot. At the other sites, barnacles were counted in four, randomly choosen, 2X2 cm (FCP) or 1.5X1.5 cm subunits (YHL).

In March 1986 barnacle size distributions were determined in the YHL experiment. Barnacle size was measured as the basal diameter along the rostral-carinal axis (as in Dungan 1986). 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 choosen for measurement by finding the individuals whose aperture center was closest to one of ten 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. Two catagories of cover were recognized: 1) Primary percent cover is a measure of the portion of the plot to which a species is directly attached, 2) Secondary cover is 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 YHH, I estimated percent cover using a plexiglass 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 seven by seven 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 were located above a species was divided by the total number of holes to calculate the estimated percent cover for that species. At YHH, I also estimated the proportion of the barnacle cover that had algae growing on their tests. Estimates at YHL and FCP were obtained 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. F-max tests (α=0.05) often indicated that raw data violated the assumption of homogeneity of variances. When this was the case, I transformed the data using log or arcsin transformations (Sokal and Rohlf 1981). The transformed data were analyzed with ANOVA's if the heteroscedasticity was reduced to nonsignificant levels. After performing ANOVA's, 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 choose one of the following three options. First, when only two treatment groups were being compared, I analyzed the data using the Wilcoxon's 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 a single treatment had an extreme variance, I removed this group 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-Neuman-Kuels (SNK) test to determine which means differed significantly. The statistical analysis were performed by hand or on a microcomputer using the SYSTAT statistical package (SYSTAT Inc., Evanston, IL).

RESULTS

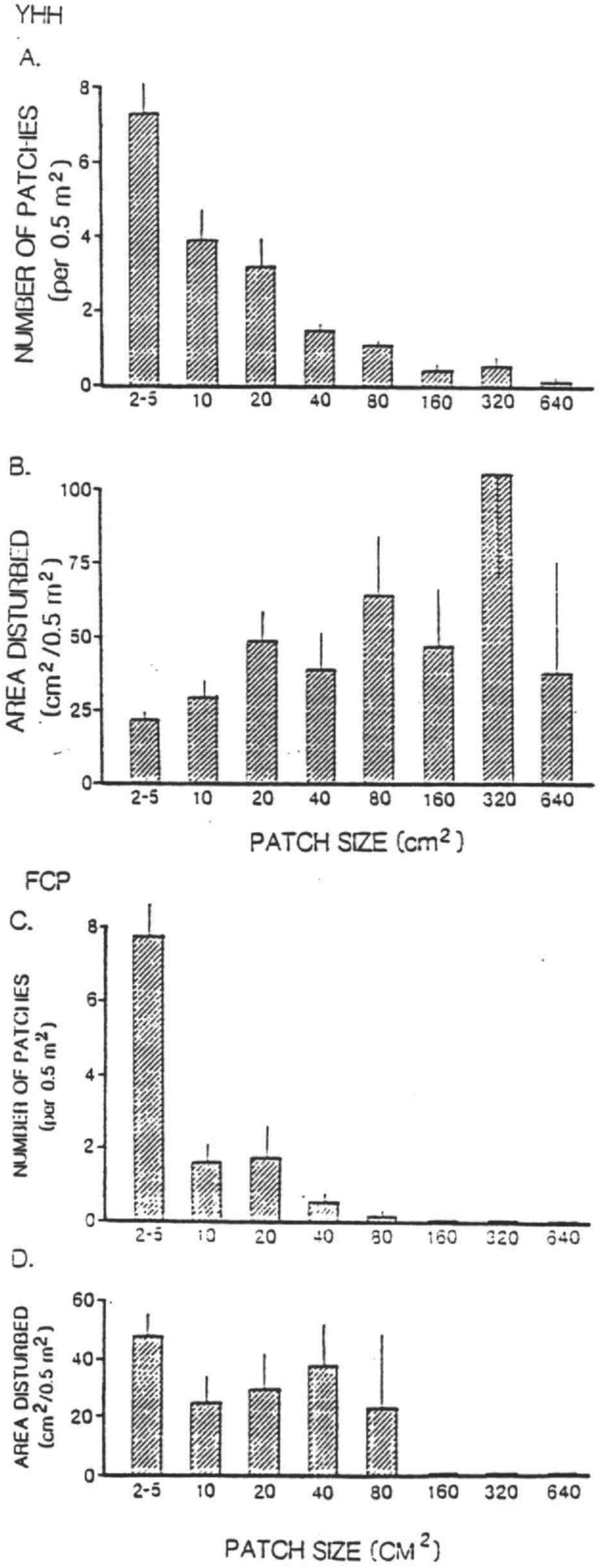
The Disturbance Regime

At YHH smaller disturbed patches were much more common than larger disturbances (Fig. 8A). Large disturbances, however, are probably just as important as smaller disturbances since their larger area compensates for their relative rarity (Fig. 8B). If the disturbance rate for the nine month census period is extrapolated to a one year period then 10.6 percent of the area was disturbed per year. The reciprocal of the proportion of the area disturbed per year, 9.5 years, is an estimate of the turnover time of patches in this habitat. Turnover time is the average period of time between successive disturbances at a site (Sousa 1984a).

At FCP, smaller disturbances were also more common than larger disturbances (Fig. 8C). As at YHH, the greater area of the larger patches resulted in approximately equal areas of the habitat occurred in over a range of patch sizes (Fig. 8D). Approximately 2.2 percent of the habitat was disturbed per year at FCP, leading to an estimated turnover time of 45.5 years. This difference between FCP and YHH was due to a total lack of disturbances larger than 80 square cm at FCP.

Figure 8. Patch size distributions by number of patches (A and C) and disturbed area per plot (B and D). The upper limit of each patch size class is given under each bar. Plotted values are means (+1.0 S.E.) for 10 plots (YHH) or 12 plots (FCP).

Figure 8


YHH
A.
NUMBER OF PATCHES (per 0.5 m²)
0
2
4
6
8
2-5
10
20
40
80
160
320
640
B.
AREA DISTURBED (cm² /0.5 m²)
0
25
50
75
100
2-5
10
20
40
80
160
320
640
PATCH SIZE (cm²)
FCP
C.
NUMBER OF PATCHES (per 0.5 m²)
0
2
4
6
8
2-5
10
20
40
80
160
320
640
D.
AREA DISTURBED (cm²/0.5 m²)
0
20
40
60
2-5
10
20
40
80
160
320
640
PATCH SIZE (CM²)

Unmanipulated Plots

Unmanipulated plots were monitored for 33 months at YHH. The mean cover of both barnacle species remained stable during this period of time (Fig. 9A). *Balanus* covered approximately 80, but *Chthamalus* covered only about 5 percent of the rock surface. The great majority of the remaining 15 percent of the substrate was unoccupied. In contrast to barnacles, algal cover changed seasonally (Fig. 9A). Algal abundance tended to decrease in the summer, and increase in the late winter and spring.

The constancy in mean barnacle cover masked the large changes in cover that occured in several individual plots (Fig. 9B). Large disturbances decreased *Balanus* to less than ten percent cover in several plots. These disturbances were gradual. Disturbed areas grew over a 6-12 month period as patches of barnacles adjacent to a disturbed patch 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. That proportion of *Balanus* with epizooic macroalgae varied between 10 and 35 percent (Fig. 10).

Almost all of this cover was composed of the two most abundant algae, *Pelvetiopsis* and *Endocladia*.

Figure 9. A. Mean substrate cover (+1.0 S.E.) in the unmanipulated plots (A=macroalgae, B=*Balanus*, C=*Chthamalus*). B. *Balanus* cover in the four odd-numbered unmanipulated plots.

Figure 9

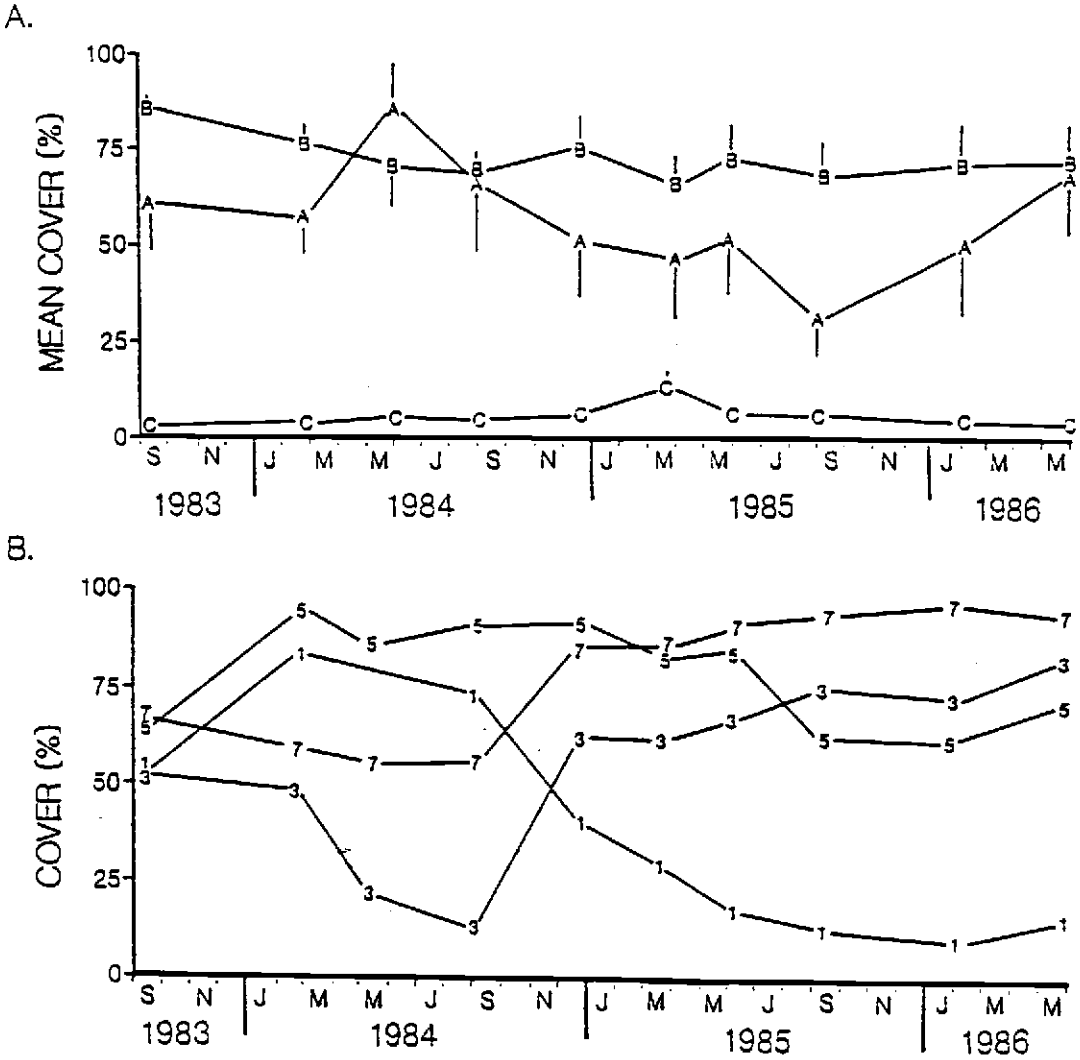
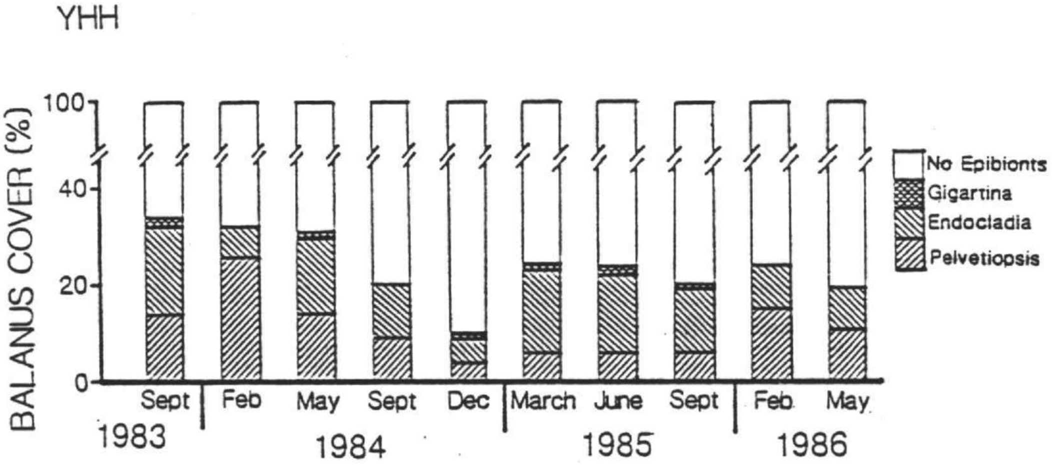

A.
MEAN COVER (%)
100
75
50
25
0
S N J M M J S N J M M J S N J M M
1983
1984
1985
1986
A
B
C
B.
COVER (%)
100
75
50
25
0
S N J M M J S N J M M J S N J M M
1983
1984
1985
1986
1
3
5
7

Figure 10. Percent of *Balanus* cover with epibionts in the unmanipulated plots.

Figure 10


YHH
BALANUS COVER (%)
100
40
20
0
Sept
Feb
May
Sept
Dec
March
June
Sept
Feb
May
1983
1984
1985
1986
No Epibionts
Gigartina
Endocladia
Pelvetiopsis

The Successional Sequence

At each of the three sites, I cleared plots and followed the development of the *Balanus*-*Pelvetiopsis* community. At YHH, *Chthamalus* was abundant early in the successional sequence (Fig. 11A). *Chthamalus* cover decreased, however, later in succession as *Balanus* occupied an increasing proportion of the substrate. After three years *Balanus* covered more than 70 percent 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*.

Community structure in the cleared plots was converging with the unmanipulated plots after three years of succession (Figs. 9A and 11A). *Balanus* cover was almost identical in the cleared and unmanipulated plots. *Chthamalus* cover was significantly higher in the cleared plots than the unmanipulated plots (ANOVA, n=7, p=0.013), but was decreasing rapidly in the cleared plots. Similarly, algal cover was significantly higher in the unmanipulated plots (ANOVA, n=7, p=0.025), but algal cover was rapidly increasing in the cleared plots. Additionally, individuals of *Balanus*, *Chthamalus*, *Endocladia* and *Pelvetiopsis* in the cleared plots were reproductive after three years.

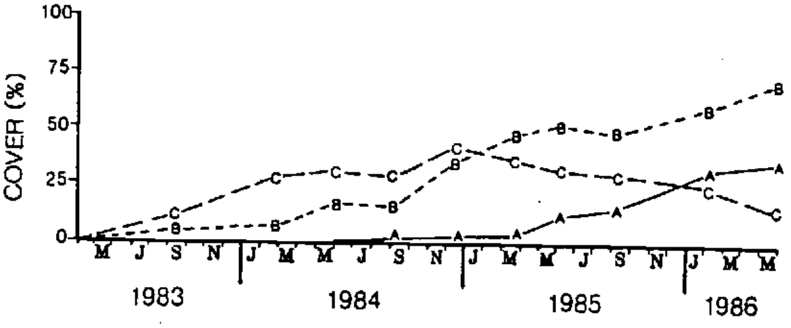
The pattern of succession observed at the other two sites was similar to the successional sequence at YHH. At FCP, Chthamalus cover peaked 18 months after scraping, and then it declined as Balanus became increasingly abundant (Fig. 11C). As at YHH, the algae cover increased only after Balanus had settled and algae recruited among the tests. Succession at YHL was accelerated compared to the other sites (Fig. 11B). A dense settlement of Balanus and Chthamalus occurred in September 1985 soon after the plots were scraped. The peak abundance of Chthamalus occurred only four months after scraping, whereas peak Chthamalus abundance occurred after 25 and 36 months at FCP and YHH, repectively. Balanus cover at YHL exceeded 70 percent after ten months, while at YHH comparable Balanus cover occurred after 36 months and was not observed at FCP after more than 24 months of succession. Early algal recruitment and the development of a canopy was associated with this rapid increase in Balanus cover. Algal cover reached 35 percent in 18 months. Development of similar algal cover took 25 months at FCP and 36 months at YHH.

While the rate of succession differed between sites, the general patterns of succession were similar. Succession in the Balanus-Pelvetiopsis community was characterized by an early abundance of Chthamalus, followed by a period of decreasing Chthamalus cover and increasing *Balanus* cover. At all the sites, algal cover increased late in the successional sequence, after *Balanus* became established. 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?

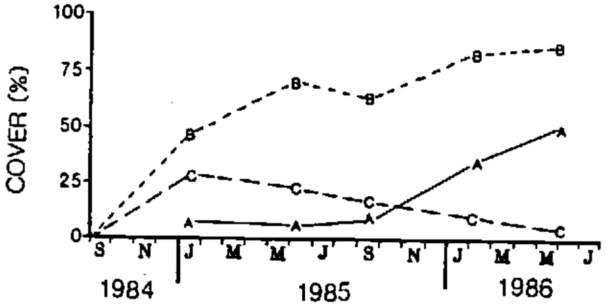
Figure 11. Mean substrate cover in cleared plots at three sites (A=macroalgae, B=*Balanus*, C=*Chthamalus*). For the FCP experiment, ANOVA's were used to compare the cover in control plots and limpet-removal plots at each sampling data. The results of these tests for algae and both barnacle species are shown between panels C and D (NS=not significant, *=p<0.05, **=p<0.01).

Figure 11

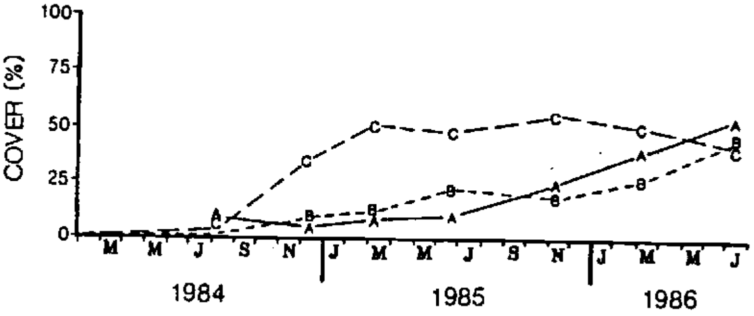
A. YHH



B. YHL

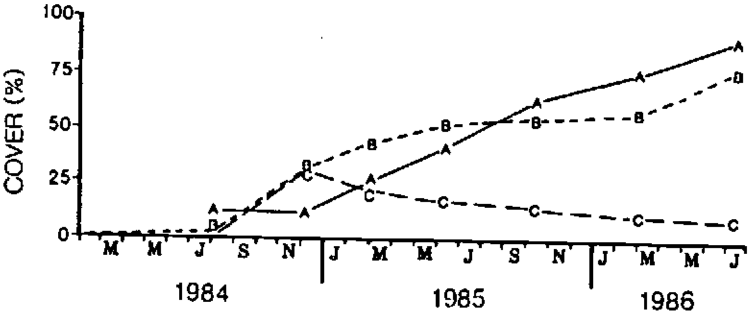


C. FCP: CONTROL



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

D. FCP: Limpet Exclusion



Interactions Between Barnacles

The YHL experiment was designed, in part, to determine how each species of barnacle affected the other. Three of the treatments (the cleared plots, cleared *Balanus*-removal plots, and cleared *Chthamalus*-removal plots) together form an experiment in which the effect of each species on the other was assessed during the course of succession.

The Effect of *Chthamalus* on *Balanus*

Chthamalus had no apparent effect on the percent cover, density, or size distribution of *Balanus* (Fig. 12). On all five sampling dates there were no significant differences between the cleared plots and the cleared *Chthamalus*-removal plots in the 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* (ANOVA, n=6, p=0.94).

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* (Fig. 13). On the second sampling date, nine months after scraping, *Chthamalus* cover was significantly higher in the cleared *Balanus*-removal plots than in the cleared plots. The difference in *Chthamalus* cover between treatments continually increased 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 time greater in the *Balanus*-removal plots than in the cleared plots. The difference in *Chthamalus* density between treatments continued to increase as succession proceeded. The mean *Chthamalus* size of 2.8 mm in the *Balanus*-removal plots was significantly greater than the mean size of 1.7 mm in the cleared plots (ANOVA, n=5, p=0.014).

The effect of *Balanus* on *Chthamalus* resulted from strong interspecific competition. While competition experiments were done only at YHL, 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 *Chthtamalus* and *Balanus* at both YHH and FCP (Fig. 14). 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.

Figure 12. The effects of Chthamalus on Balanus. In A and B plotted values are means (+1.0 S.E.) with significance levels shown (ANOVA, n=6, symbols as in fig. 4). C. Plotted values are mean proportion (+1.0 S.E.) of barnacles of each size class (n=6 plots, 10 barnacles per plot).

Figure 12

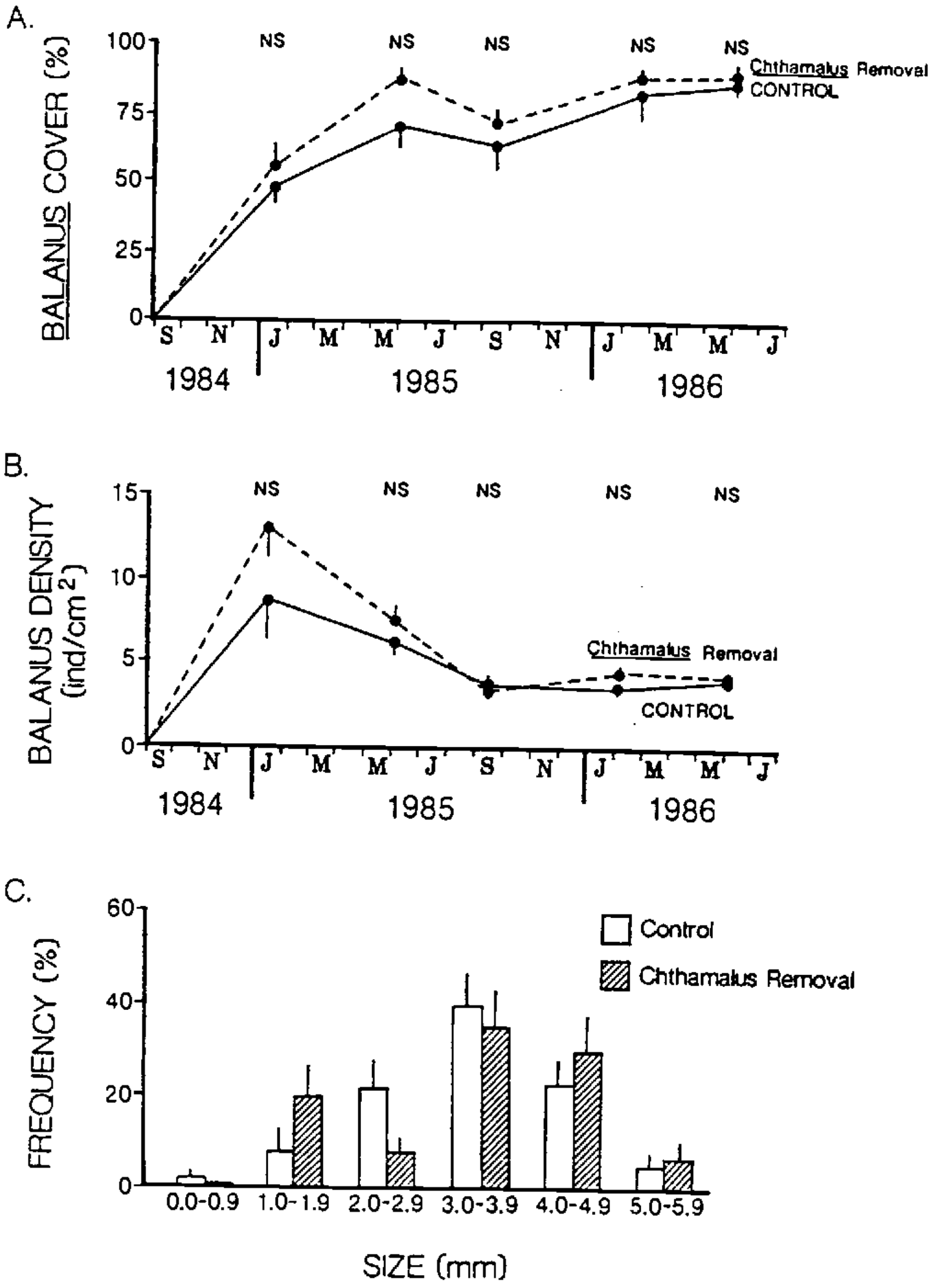

A.
BALANUS COVER (%)
100
75
50
25
0
NS
NS
NS
NS
NS
Chthamalus Removal
CONTROL
S
N
J
M
M
J
S
N
J
M
M
J
1984
1985
1986
B.
BALANUS DENSITY (ind/cm²)
15
10
5
0
NS
NS
NS
NS
NS
Chthamalus Removal
CONTROL
S
N
J
M
M
J
S
N
J
M
M
J
1984
1985
1986
C.
FREQUENCY (%)
60
40
20
0
□ Control
▨ Chthamalus Removal
0.0-0.9
1.0-1.9
2.0-2.9
3.0-3.9
4.0-4.9
5.0-5.9
SIZE (mm)

Figure 13. The effects of Balanus on Chthamalus. Panels are as in figure 12 except n=5.

Figure 13

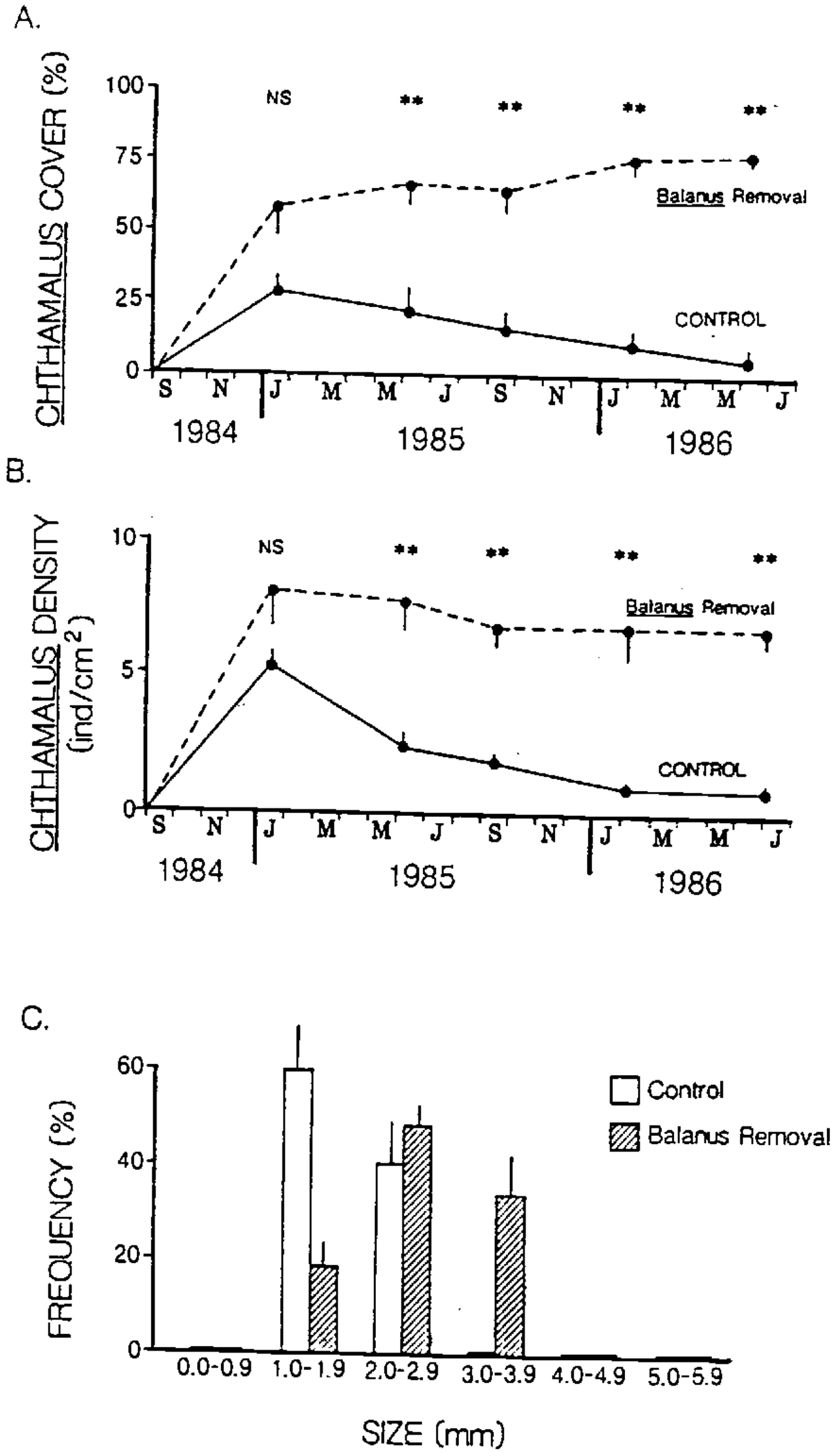
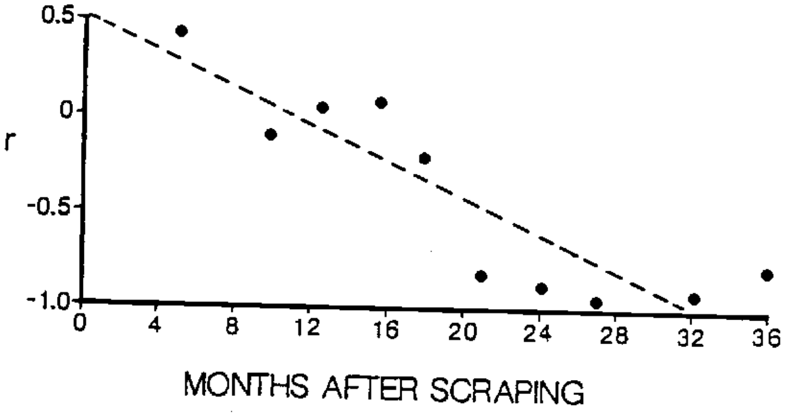

A.
CHTHAMALUS COVER (%)
100
75
50
25
0
NS
**
**
**
**
Balanus Removal
CONTROL
S N J M M J S N J M M J
1984
1985
1986
B.
CHTHAMALUS DENSITY (ind/cm²)
10
5
0
NS
**
**
**
**
Balanus Removal
CONTROL
S N J M M J S N J M M J
1984
1985
1986
C.
FREQUENCY (%)
60
40
20
0
Control
Balanus Removal
0.0-0.9
1.0-1.9
2.0-2.9
3.0-3.9
4.0-4.9
5.0-5.9
SIZE (mm)

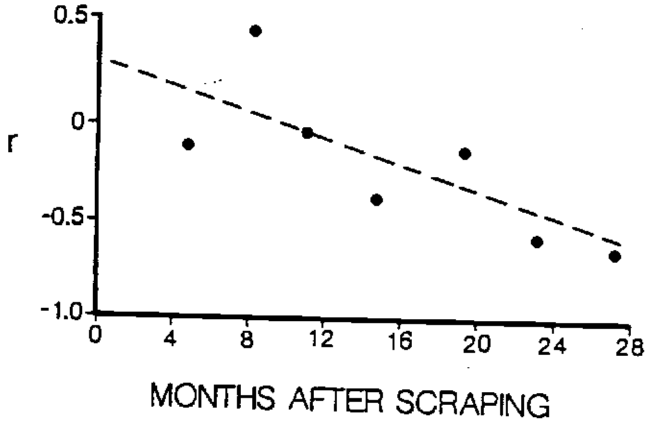
Figure 14. The association of *Chthamalus* and *Balanus* during succession. Plotted values are the correlation coefficients (r) of the two species in the cleared plots. The coefficients are based on the seven (YHH) or eight (FCP) plots for each sampling date. For YHH the overall correlation between the barnacle association and the time since the plots were cleared is -0.89 (n=10 sampling dates, p=0.001). For FCP this overall correlation is -0.75 (n=7 sampling dates, p=0.055). The linear regression line is shown for both sites.

Figure 14

A. YHH



B. FCP



The Effect of Barnacles on Algae

Barnacles strongly facilitated algal colonization at all three sites (Figs. 15-17). On the last sampling dates at YHH and FCP, the barnacle-removal plots had only two percent of the number of algal thalli found in the plots that were colonized by barnacles. At YHL, no plants grew in the barnacle-removal plots. Barnacles affected each algal species in the same manner. At YHH and YHL, *Pelvetiopsis* and *Endocladia* (which together constituted more than 90 percent of the algal thalli at these sites) were facilitated to the same degree by barnacles (Figs. 15-16). At FCP, *Fucus*, *Pelvetiopsis*, and *Endocladia* were all facilitiated by barnacles (Fig. 17).

The two species of barnacle did not facilitate algal recruitment equally. The YHL experiment included *Balanus*-removal plots (*Chthamalus* monocultures) and *Chthamalus*-removal plots (*Balanus* monocultures). Comparisons of these plots indicate that *Balanus* enhanced algal colonization more than *Chthamalus* (Fig. 15).

Figure 15. Mean algal thalli density (+1.0 S.E.) in the YHH experiment. Significance levels were generated by Wilcoxon's signed-rank test (n=7).

Figure 15

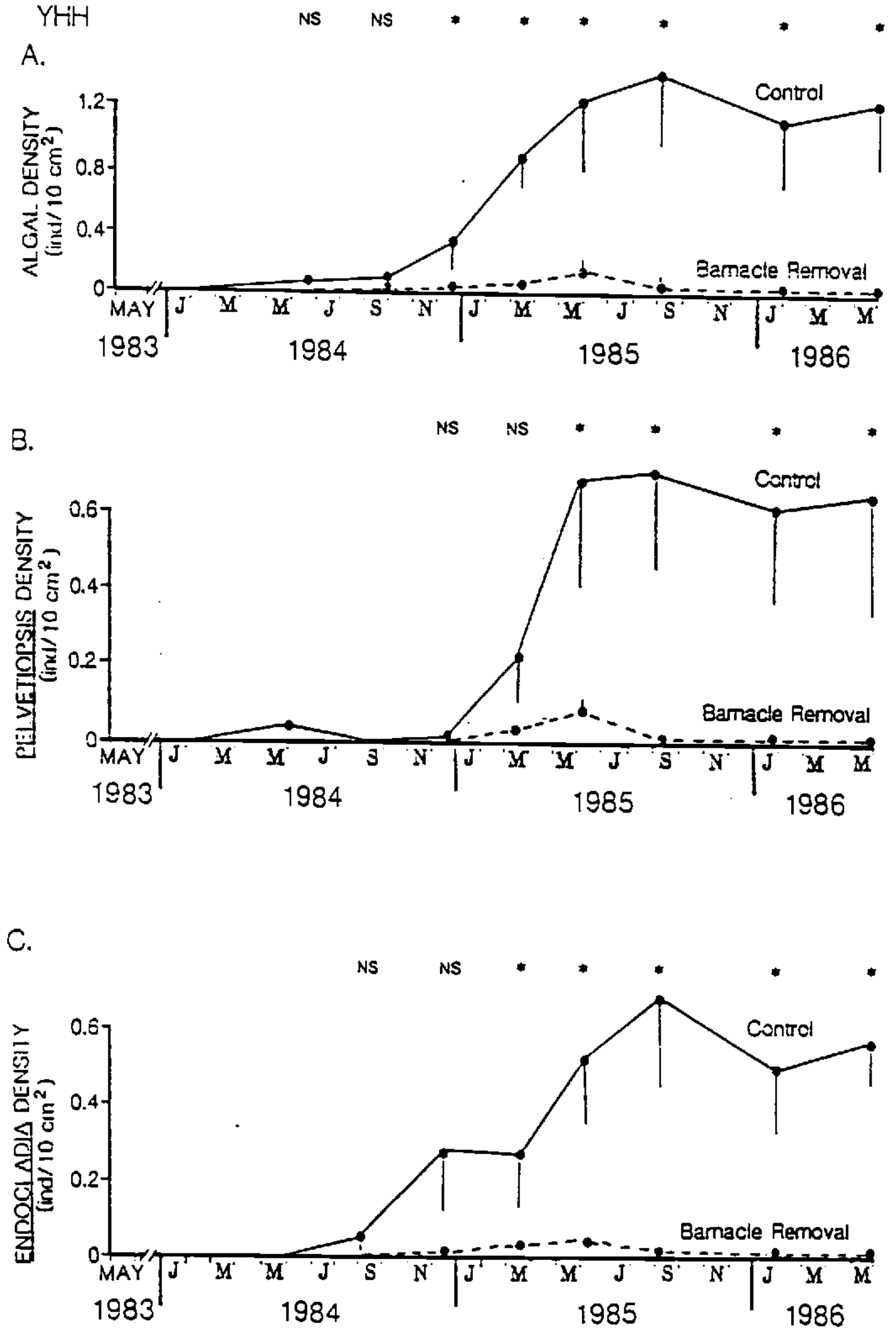

YHH
A.
NS NS * * * * * *
ALGAL DENSITY (ind/10 cm^2)
1.2
0.8
0.4
0
Control
Barnacle Removal
MAY J M M J S N J M M J S N J M M
1983 1984 1985 1986
B.
NS NS * * * *
PELVETIOPSIS DENSITY (ind/10 cm^2)
0.6
0.4
0.2
0
Control
Barnacle Removal
MAY J M M J S N J M M J S N J M M
1983 1984 1985 1986
C.
NS NS * * * * *
ENDOCLADIA DENSITY (ind/10 cm^2)
0.6
0.4
0.2
0
Control
Barnacle Removal
MAY J M M J S N J M M J S N J M M
1983 1984 1985 1986

Figure 16. Mean algal thalli density in the YHL 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, ND=no test done). At each sampling date, means that did not significantly differ are connected by lines (SNK test).

Figure 16

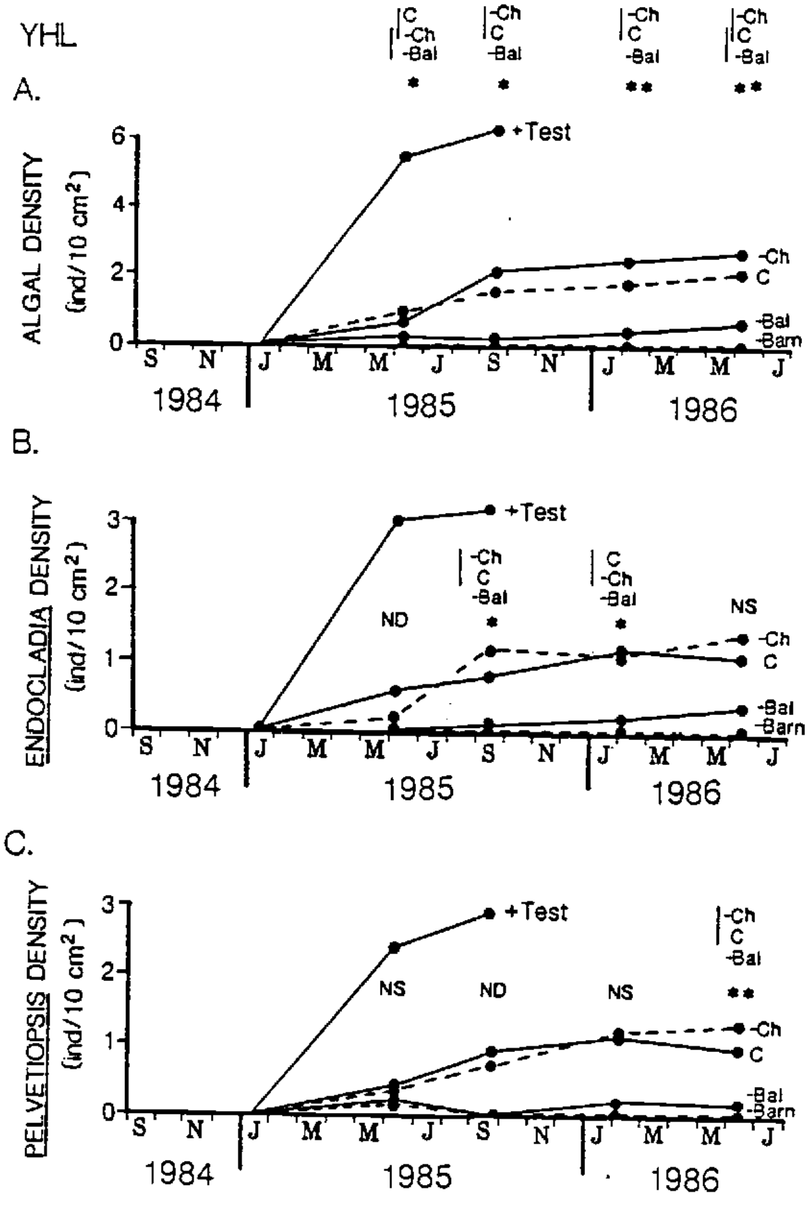
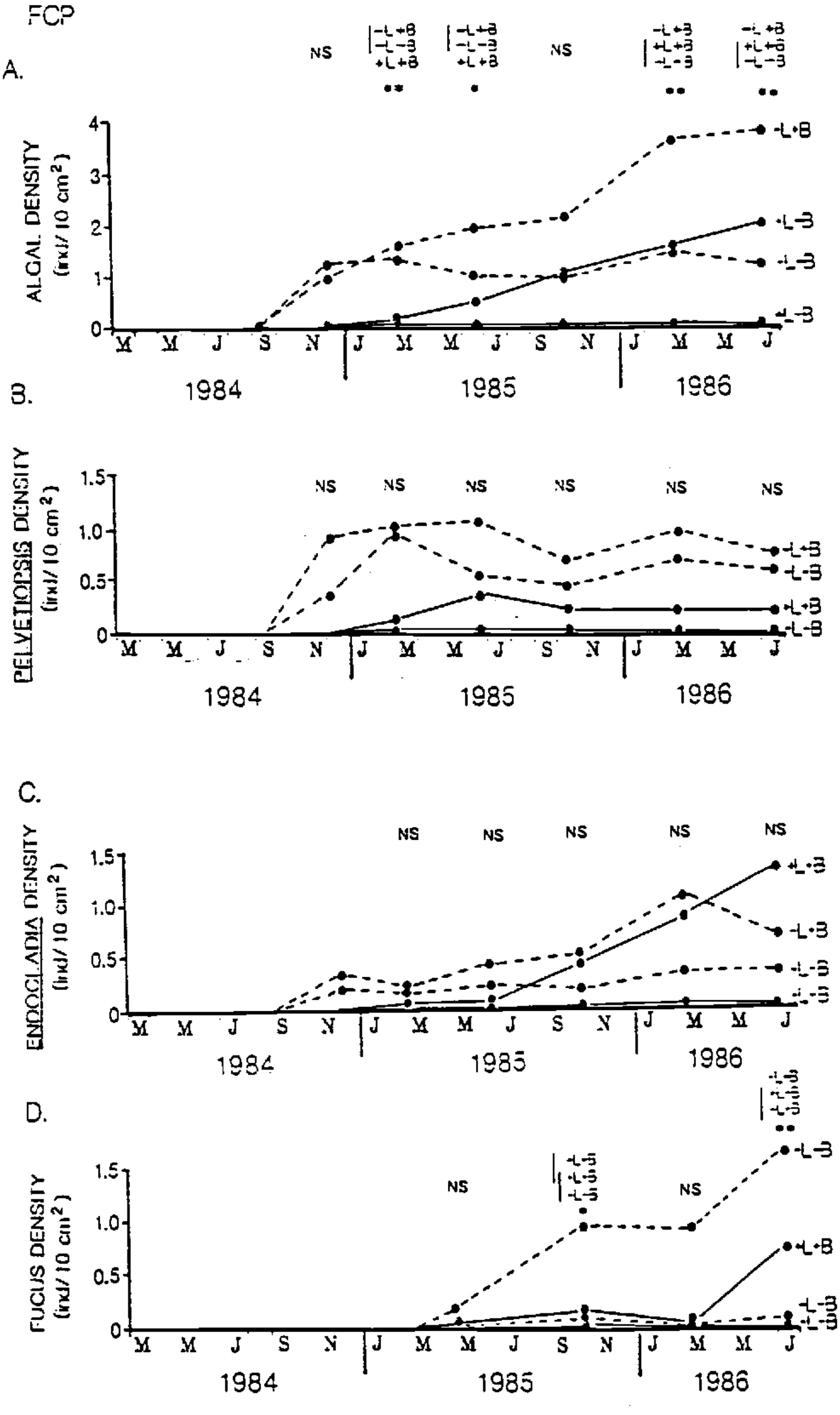

YHL
A.
C
-Ch
-Bal
*
-Ch
C
-Bal
*
-Ch
C
-Bal
**
-Ch
C
-Bal
**
ALGAL DENSITY (ind/10 cm^2)
6
4
2
0
+Test
-Ch
C
-Bal
-Barn
S N J M M J S N J M M J
1984
1985
1986
B.
ENDOCLADIA DENSITY (ind/10 cm^2)
3
2
1
0
+Test
ND
-Ch
C
-Bal
*
C
-Ch
-Bal
*
NS
-Ch
C
-Bal
-Barn
S N J M M J S N J M M J
1984
1985
1986
C.
PELVETIOPSIS DENSITY (ind/10 cm^2)
3
2
1
0
+Test
NS
ND
NS
-Ch
C
-Bal
**
-Ch
C
-Bal
-Barn
S N J M M J S N J M M J
1984
1985
1986

Figure 17. Mean algal thalli density in the FCP 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 were analyzed with ANOVA and SNK tests. Symbols as in figure 16.

Figure 17


FCP
A.
NS
-L+B
-L-B
+L+B
**
-L+B
-L-B
+L+B
*
NS
-L+B
+L+B
-L-B
**
-L+B
+L+B
-L-B
**
ALGAL DENSITY (ind/10 cm²)
4
3
2
1
0
-L+B
+L-B
-L-B
+L+B
M M J S N J M M J S N J M M J
1984
1985
1986
B.
PELVETIOPSIS DENSITY (ind/10 cm²)
1.5
1.0
0.5
0
NS NS NS NS NS NS
-L+B
-L-B
+L+B
+L-B
M M J S N J M M J S N J M M J
1984
1985
1986
C.
ENDOCLADIA DENSITY (ind/10 cm²)
1.5
1.0
0.5
0
NS NS NS NS NS
+L-B
-L-B
-L+B
+L+B
M M J S N J M M J S N J M M J
1984
1985
1986
D.
FUCUS DENSITY (ind/10 cm²)
1.5
1.0
0.5
0
NS
+L-B
+L+B
-L-B
*
NS
-L-B
+L+B
-L+B
**
-L-B
+L+B
-L+B
+L-B
M M J S N J M M J S N J M M J
1984
1985
1986

The Mechanism of Facilitation

Comparisons of cleared plots with cleared barnacle-removal plots indicated that barnacles facilitate algal colonization but did not indicate the mechanism of facilitation. Two general types of mechanism may have caused facilitation: 1) The animal hypothesis--facilitation results from the activities of living barnacles such as excretion and feeding. 2) The substrate hypothesis--facilititation results 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 YHL experiment. 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. 16). This indicated that barnacles facilitated algal colonization by altering the substrate.

The test-addition plots also had higher colonization rates than the cleared plots that were colonized by barnacles. This difference may have resulted from two factors: 1) the activities of living barnacles have a deleterious affect on algae, or 2) the size of the barnacles may affect 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 this experiment does not allow me to distinquish between these two alternatives.

The subtrate 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 create a rough surface that collects more algal spores or zygotes than the smoother rock surface.
2) The desiccation protection hypothesis--the crevices on and between barnacles are shaded and retain moisture, and therefore are 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 are inaccessable to herbivores while they are small and vulnerable.

These hypotheses are not mutually exclusive, since two or more of these processes could have acted in concert to produce facilitation.

The FCP experiment was designed, in part, to determine which, if any, of the listed hypotheses caused facilitation. 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, in their extreme forms both the desiccation protection hypothesis and the dispersal trap hypothesis predict that algae will not recruit to areas without barnacles regardless of whether herbivores are present. Limpet removal with and without barnacles should distinquish between alternatives 1 and 2 versus 3. The results of this experiment show that algae did recruit into barnacle-removal plots when limpets were removed (Fig. 17). No statistically significant difference in algal density occured between the +L+B (limpets and barnacles present) and the -L-B (limpets and barnacles removed) plots. This indicates facilitation of algae by barnacles was dependent on limpets.

There was greater algal recruitment in the -L+B (limpets removed, barnacles present) plots than the -L-B plots. There are at least two 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, littorine, 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 this experiment if facilitation is caused by only the herbivore protection effect or if another process is also causing facilitation.

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 FCP (Fig. 1C-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 while comparable Balanus cover was attained after 30 months 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 months in the removal plots compared to 22 months in the control plots. The rate of algal colonization was also accelerated when limpets were removed. After 19 months mean algal cover reached 50 percent in the limpet-removal plots while similar algal cover formed after 30 months in the control plots. The timing of each major feature of the successional sequence was accelerated by the removal of limpets.

DISCUSSION

In early views of succession, community development was though 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 1979b 1984a, Pickett and White 1985). The *Balanus-Pelvetiopsis* community is subject to frequent disturbances (Fig. 8). Disturbance rates in this community may be increased by the algae growing on the tests of barnacles. Two possible mechanisms of disturbance are 1) death of barnacles due to overgrowth of the apertures by algae, and 2) dislodgement of 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 rhizomatous fashion over groups of barnacles, forming a dense turf. This turf 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 the drag induced by epizoic algal thalli may have increased the rate that barnacles were dislodged from the substrate by waves. Since algal cover increased during community development, the probability of disturbance probably increased as succession proceeded in the Balanus-Pelvetiopsis community.

Similar conclusions have been recorded in other studies. Epibionts can cause mussels to be dislodged by waves (Witman and Suchanek 1984, Witman 1987). Sousa (1979a), Lubchenco (1983) and D'Antonio (1985) provide evidence that epiphytes can cause algae to become dislodged in intertidal habitats. In another intertidal community, Jernakoff (1985b) found that algal overgrowth did not increase barnacle mortality. Other studies, including Denley and Underwood (1979) and Farrell (1987), observed barnacle death after algal overgrowth. In terrestrial habitats, Strong (1977) has suggested that epibionts accumulate increase disturbance rates in tropical forests. The probability of disturbance also increases 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 a 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.

While the order of species appearance was repeatable, the rate of succession varied greatly between experiments. At the YHL site Chthamalus cover peaked four months after disturbance, compared to 36 months at YHH. Similarly, Balanus and algal cover developed much more slowly at YHH than YHL (Fig. 11). 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 caused 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 YHH and YHL. This event occurred immediately after disturbance at YHL, whereas it occurred 17 months after disturbance at YHH. The difference in the successional trajectory of these two sites is largely the long initial period at YHH with low *Balanus* cover. The changes in species abundance are similar at YHH and YHL after the large recruitment event (Fig. 11). 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 YHH, mean *Balanus* settlement densities exceeded 33 individuals per square cm of unoccupied space but all died a few days later when hot, dry weather coincided with a mid-day low tide.

The Mode and Mechanisms of Succession

A fundamental question in ecology is what is the relative importance of the three modes of succession--

facilitation, tolerance, and inhibition? The limited evidence available at the time of of Connell and Slatyer's review (1977) indicated that inhibition was the dominant mode of succession. Several more recent studies (Sousa, 1979a; 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.

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 two 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.

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 1982, Lubchenco 1983, Dungan 1986), although this is not always the case (Creese 1982, Jernakoff 1983, 1985a). In several communities the interference with herbivores results in barnacles facilitating algal establishment (Lubchenco 1983, Hawkins 1981). Inhibition of herbivores by early successional species also results in facilitation in subtidal communities (Harris et al. 1984) and deserts (McAuliffe 1986). In other cases facilitation occurs when early colonists act as a substrate for recruiting later successional species (Menge 1976, Suchanek 1978, Turner 1983b).

Facilitation was originally though 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, this study). Given these results, facilitation may occur both in physically harsh environments and areas with intense consumer pressure.

The mode 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 less than 2 percent of the algal colonization observed in control plots. In a similar interaction between a fucoid alga (Fucus vesiculosus) and a balanoid barnacle (Semibalanus balanoides), 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 in this study. The difference in the stength 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). The limpets may be able to eat both algae in crevices and larger algal thalli than the littorinids, resulting in more complete algal removal on rough rock surfaces in Oregon than in New England.

In the simplest possible situation a group of early successional species would all have the same effect on the establishment of all later successional species. Studies that examined interactions between individual species have revealed a much more complex view of succession (Dean and Hurd, 1980; Turner, 1983a, 1983b; Breitburg, 1984, 1985). An early successional species may not have the same affect 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 this 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. Similiarly, *Balanus* strongly facilitated all three common species of macroalgae.

Further complexity in succession will occur if different members of an assemblage of early succession species do not have the same effect on a later colonist. For example, Turner (1983b) 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 (1983a, 1983b) demonstrated that succession may be characterized by different processes at different points along the successional sequence. The Balanus-Pelvetiopsis community is not characterized by a single model of succession. The Chthamalus-Balanus interaction follows the tolerance model, while the subsequent barnacle-macroalgae interaction follows the facilitation model. In sequences with several seral stages there is no reason to assume the same model of succession may be involved in each transition from one stage to the next.

The question of how early successional species effect later successional species has received much attention, while much less interest has been expressed in its converse--How do later successional species affect early successional species? There may be several reasons for this lack of information. First, determining how later successional species affect earlier colonists may require longer periods of experimentally manipulating successional sequences than determining how early successional species affect later colonists. Second, there is less controversy concerning the affect of later successional species on early successional species than visa versa. Later successional species are frequently assumed to competively exclude early successional species (Drury and Nisbet 1973, Connell and Slatyer 1977). Additionally, early successional species are thought to alter the habitat in a manner that makes the habitat less suitable for their own offspring. These assumptions have rarely been tested. In this community *Balanus*, a late successional species, does competively exclude *Chthamalus*, an early successional species. *Chthamalus*, however, is able to replace itself in the absence of *Balanus* (Fig. 13A-B).

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 punative advantage of balanoids results from increased growth rates made possible by tubiferous (hollow) tests (Stanley and Newman 1980, Newman and Stanley 1981). The studies of Connell (1961b), Wethey (1984) and this investigation support this generalization. Dungan (1985), however, found that a chthamaloid was competitively dominant to a tubiferous species (Tetraclita), and suggests that recruitment density may be the key determinant of competitive ability. This idea is not supported by this study 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 quickly 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).

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 one hundred percent of the rock surface, developed and lead to intense intraspecific and interspecific competition. Larval settlement densities were much higher in Oregon (132 individuals/cm2/year Farrell, unpublished data) than on San Juan Island (0.4-2.4 ind./cm2/year 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 (personal observation). The Oregon study sites had larval settlement rates similar to sites in Massachusetts (37-102 ind./cm2/year; Wethey unpublished, cited by Connell 1985) and Scotland (37-143 ind./cm2/year; Connell 1985) where barnacles were involved in intense competition (Connell 1961b, Wethey 1984).

The Effects of Herbivores on Succession

Herbivores slow the rate of succession in the

Balanus-Pelvetiopsis community by delaying two major steps in community development--1) the replacement of Chthamalus by Balanus, and 2) the colonization of macroalgae (Fig. 11C-D). Limpets reduced the abundance of Balanus, the later successional species, more than the abundance of Chthamalus, the early successional species. The interaction between the two barnacle species is characterized by the tolerance mode of succession. As is predicted by my model, Chthamalus is replaced by Balanus more slowly in the presence of limpets (Fig. 7). Barnacles, the early successional species, are affected by limpets less than macroalgae, the later successional species. The interaction between barnacles and algae is characterized by the facilitation mode of succession. As predicted, macroalgae colonize more slowly in the presence of limpets. Sousa et al. (1981), studying an algae-dominanted community characterized by the inhibition mode of succession, also found that herbivores preferentially removed later successional species. In this community, herbivores slowed the rate of succession, a result consistent with my model.

A simplistic view of this model would predict that consumers usually slow succession since that is the result of six of the nine possible combinations (Fig. 7). Similarly, herbivores would be predicted to rarely hasten succession since that results from only one of the nine combinations. In reality, prediction is more complex since not all the combinations of consumer removal and mode of succession are equally likely. Inhibition appears to occur more frequently than tolerance and facilitation (Connell and Slatyer 1977, Dean and Hurd 1980). Consumers often appear to prefer early successional species over later successional species (reviewed by Lubchenco and Gaines 1981). Herbivores may commonly accelerate succession since the combination that produces that result (inhibition, removal of early successional species) probably occurs most frequently (i.e., Lubchenco and Menge 1978, Sousa 1979a, Lubchenco 1983). Jernakoff (1985a) found that early successional species were preferred by consumers but unfortunately did not determine the mode of succession. In that community he found herbivores had little or no effect on the rate of succession, a result that would be consistent with my model only if the mode of succession was tolerance. Peer (1986) found that consumers preferred early successional species and slowed succession in microcosms. Unfortunately the mode of succession was not known in this system, and the nutrient dynamics in such closed systems may lead to unexpected interactions between grazers and plants (Peer 1986).

The intensity of consumption will affect the magnitude of the consumer's influence on the rate of succession. In communities where consumers have little affect on species abundances they are unlikely to affect the rate of succession regardless of the mode of succession. For example, Turner (1983a) found herbivores had only a short-term influence 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 (Sousa et al. 1981, Lubchenco anGaines 1981, Lubchenco et al. 1984, Menge et al. 1986, Farrell 1987).

Direct and Indirect Interactions

The role of both direct and 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 affect succession at different stages. Early in succession, *Chthamalus* is eliminated by a direct interaction--competition for space with *Balanus*. Later in succession, algal establishment results from an indirect interaction--the foraging activities of limpets are reduced by barnacles allowing algal colonization. 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).

Successional sequences that are controlled by indirect interactions are likely to be less predictable and consistent than sequences controlled by direct interactions. Decreased predictability results from the fact that indirect interactions are composed of chains of direct interactions. Assume we can predict direct interactions (based on a knowledge of resource utilization, life history, closely related species, etc.) with a certain accuracy. The probability of correctly predicting indirect interactions will necessarily be lower than the probability of correctly predicting direct interactions. Decreased accuracy occurs because the probability of correctly predicting an indirect interaction will be the product of the probabilities of at least two direct interactions (Fig. 1). Successional sequences that are controlled by indirect interactions are likely to contain more surprises than sequences controlled by direct interactions.

Not only are indirect interactions less predictible than direct interactions, indirect effects are also likely to be less spatially and temporally consistent. This also results from the fact that indirect interactions are composed of chains of direct interactions. If any of the links in the chain of direct interactions is altered, then the indirect interaction will change. Successional sequences that are controlled by indirect interactions will be more likely to vary in space and time than sequences that are controlled by direct interactions.

Studies of intertidal herbivores provide an example of spatial inconsistency an indirect interaction. Dethier and Duggins (1984) found that the presence of a chiton, *Katharina tunicata*, increased the abundance of a limpet, *Lottia pelta*, on the shores of San Juan Island. This interaction is an indirect interaction--*Katharina* removes macroalgae which allows the microalgae consumed by *Lottia* to increase in abundance. On the outer coast of Washington and Oregon, however, the presence of *Katharina* decreases the abundance of limpets (Paine 1980, Gaines 1985). The differences in the interactions between the herbivores probably results from variation in the intensity of competition between macroalgae and microalgae at these sites. In the absence of *Katharina*, macroalgae form a dense canopy on San Juan Island that greatly reduces microalgal abundance. On the outer coast, however, the macroalgal canopy is less dense and microalgae may persist (Dethier and Duggins 1984). On the outer coast, the algal canopy may also provide shelter from avian predators (Dethier and Duggins 1984). In the *Balanus*-*Pelvetiopsis* community, however, the indirect interaction between barnacles and macroalgae was consistent. The consistency of this indirect interaction may result from consistency of two component direct interactions. In experiments at three different sites, each initiated at different times, barnacles always increased the abundance of all common species of macroalgae.

Chapter IV

SUCCESSION IN A ROCKY INTERTIDAL COMMUNITY: THE INFLUENCES OF GAP SIZE AND POSITION WITHIN A GAP

INTRODUCTION

The abundance and species composition of many communities is strongly influenced by disturbances (reviewed by Pickett 1980, Sousa 1984a). Early studies primarily considered the rate of disturbance (Connell 1978, Huston 1979), but investigations have recently included several other attributes of disturbance regimes. The seasonality (Hawkins 1981, Foster 1975a, Lubchenco 1986), intensity (Sousa 1980, Armesto and Pickett 1985), temporal distribution (Abugov 1982), and location (Palumbi and Jackson 1982, Sousa 1984b, Connell and Keough 1985) of disturbance can all influence community structure.

Succession may also be influenced by the position within a disturbed patch. Areas near the edge of a gap may be affected by their proximity to the intact community. The undisturbed community may provide shading (Runkle 1985), propagules (Sousa 1984b), competition for nutrients, or act as a refuge for animals that forage in the gap (Suchanek 1978, Sousa 1984b). Vegetative growth of undisturbed organisms will also have a greater effect on the perimeter than the center of a gap (Miller 1982, Connell and Keough 1985). Unfortunately, reports of edge effects are often anecdotal (e.g. Suchanek 1978, Paine and Levin 1981, Sousa 1984b) since data are rarely collected separately in the perimeter and central portions of gaps (but see Foster 1975b).

If proximity to the intact community affects succession then both gap shape and size will also influence community development. Elongate disturbances will have more of their area near the gap boundary than more circular disturbances of equal size (Sousa 1984a). Similarly, small disturbances will have more of their area near the gap boundary than larger disturbances of the same shape. Experimental tests in terrestrial (Davis and Cantlon 1969, Goldberg and Werner 1983, McConnaughay and Bazzaz 1987) and marine (Osman 1977, Sousa 1979, 1984b, Palumbi and Jackson 1982, Keough 1984) systems indicate that gap size can have large effects on the abundance and species composition of colonists. When proximity to the intact community influences succession, the differences in community structure observed between the edge and central regions of gaps should also be observed between small and large gaps.

In this study, I determined the effects of gap size on succession in a rocky intertidal community. The influence of position in a gap was assessed by collecting data separately in the perimeter and central portions of the largest gaps. Furthermore, I tested the prediction that increasing gap size would influence succession in the same manner as moving towards the center of a gap.

METHODS

The Study Site

This investigation was done at Fogarty Creek Point (FCP) study site that is described in chapter 3.

Experimental Design

The experimental units consisted of square plots of three different sizes--4X4 cm, 8X8 cm, and 16X16 cm. These plot sizes span the usual range of naturally occurring disturbed patches in the *Balanus*-*Pelvetiopsis* community (Chapter 3--Fig. 8). These three treatments were part of a larger experiment. The 8X8 cm plots served as controls in an investigation of the effects of limpets and barnacles on succession (Chapter 3). The treatments were arranged in a randomized block design. Each treatment was present once in each block, and there were eight blocks. The experiment was initiated by scraping the plots with a putty-knife. Like natural disturbance, scraping produces gaps that are barren except for the bases of barnacles and small areas of encrusting algae. The corners of the gaps were marked with small pieces of epoxy-putty.

Data Collection

The abundance of all macroscopic organisms was determined at 3-4 month intervals. In the large gaps, abundances were determined in two areas--1) the edge, a four cm wide band area on the perimeter of the plots, and 2) the center, the remaining 8X8 cm area in the interior of the plots. Barnacles became too numerous to count in the entire plot so subunits were censused. In the center area four randomly chosen, 2X2 cm areas were censused. In the edge area, either four or eight randomly chosen, 2X2 cm areas were censused. Limpet and algal densities were counted in the entire plot. Individual thalli of *Pelvetiopsis* and *Fucus* were easily discerned. *Endocladia* and *Mastocarpus*, however, had less discrete holdfasts. For these algae, clumps were counted as single individuals, leading to conservative estimates of density since a single clump may have resulted from several propagules.

The abundances of sessile species were also estimated by determining the proportion of the rock surface each species covered. Algal cover included algal thalli that lay over a plot, not just those thalli with their holdfasts in the plot. To estimate cover, a clear vinyl sheet with a uniform array of ink dots was placed over a plot. The cover of a species was estimated by determining the percentage of the dots that were located directly above a species. I used sheets with 94 dots to estimate cover in the edge portion of the large gaps, and used sheets with 50 dots in the relatively smaller central areas.

To determine how gap area affected succession, I observed the abundances of organisms in the three different-sized plots every 3-4 months. The total abundance (density or cover) of a species in the large gaps was calculated as the weighted mean of the abundances in the edge and center regions (total abundance = 0.25 center abundance + 0.75 edge abundance). In the medium gaps, barnacle densities were estimated by censusing four 2X2 cm subunits in each plot. In the small gaps, barnacle densities were found by censusing the entire plot. To estimate cover, I used vinyl sheets with 40 or 50 dots in the small and medium gaps, respectively.

In September 1984, I censused a 2 cm wide band around the perimeter of the medium gaps to determine if algal canopy affected barnacle densities. This area was divided into 12 2X2 cm subunits. Each subunit was classified as either: 1) canopied--if most of the subunit could be covered by an algal thalli, or 2) uncovered--if most of the subunit could not be covered by an algal thalli.

Data Analysis

The data were analysed using analysis of variance (ANOVA's) for a randomized block designs. After an ANOVA was performed, a probability plot of the residuals was examined to determine if error terms were normally distributed. I used the Student-Newman-Kuels (SNK) test to determine which treatment means significantly differed. If significant heterogeneity in variances occurred (F-max test, $\alpha = 0.05$; Sokal and Rohlf 1981) the data were log transformed to reduce this heterogeneity. In a few cases, transformations did not reduce this heterogeneity to non-significant levels so ANOVA's were not performed. In the within gap comparisons, the Wilcoxon's rank-sum test, a nonparametric analog of the paired t-test, could be used since there were only two classification groups (center and edge). Block number was used as the pairing criterion in this test. The Wilcoxon's test was used only three times; once on the limpet density data (September, 1984) and twice on the total algal cover data (September and December 1984). In the gap-size comparisons, no statistical tests were done on data that maintained significant heterogeneity of variances after transformation.

A separate analysis was used on the barnacle density data collected in the canopied and uncovered areas of the medium patches. For this ANOVA, each patch served as a block that contained the two classification groups (canopied and uncovered). One plot had no algal canopy so the sample size was seven. Since I did not manipulate algal cover, this portion of the study was not experimental, but simply correlational.

RESULTS

Limpet Density

Limpet densities were higher in the edge than the center area of the large gaps (Fig. 18A). The magnitude of this difference decreased as succession advanced, and was statistically significant on only one of the last three sampling dates. On the majority of sampling dates, mean limpet densities was significantly higher in the small gaps than in the medium and large gaps (Fig. 18B). The medium gaps had higher limpet densities than large gaps, though this difference was statistically significant on only one sampling date (October 1985).

Barnacle Abundance and Species Composition

Position in the large gaps had no detectable influence on the total amount of barnacle cover (Fig. 19A). Similarly, gap size did not significantly affect barnacle cover except on one sampling date (Fig. 19B). At that time (June 1985), the small gaps had significantly lower barnacle cover than the medium and large gaps.

The species composition of barnacles was influenced by position in the large gaps. The relative abundance of <u>Balanus</u> was higher in the center than the edge area on three of the first four sampling dates (Fig. 20A). As succession advanced this position effect diminished and significant differences did not occur on the last three sampling dates.

The species composition of barnacles was also affected by gap size. Large gaps had a higher relative abundance of <u>Balanus</u> than medium or small gaps on all sampling dates, and this difference was significant on three of the seven sampling dates (Fig. 20B). Medium and small gaps were more similar to each other than to the large gaps, but on two of seven dates the relative abundance of <u>Balanus</u> was higher in the medium gaps than the small gaps.

An algal canopy did not appear to influence total barnacle density (September 1984 data, ANOVA, n=7, p=0.64). The density of barnacles in the canopied areas (1.98 individuals/cm2) of the medium gaps was similar to the density in uncovered areas (1.81 individuals/cm2). The species composition of barnacles, however, did appear to be influenced by an algal canopy. There was a significantly higher relative density of Balanus in the canopied portion (22.9%) than the uncovered portion (14.2%) of the medium gaps (ANOVA, $n=7$, $p=.001$).

Figure 18. A. Mean limpet density in the center (C) and edge (E) areas of the large plots. B. Mean limpet density in the small (S), medium (M), and large (L) plots. The results of significance tests for each sampling date are shown above each graph (00--no test done, NS--no significant difference, *--$p<0.05$, **--$p<0.01$). For the patch size comparison, the means that did not significantly differ are connected by lines.

Figure 18

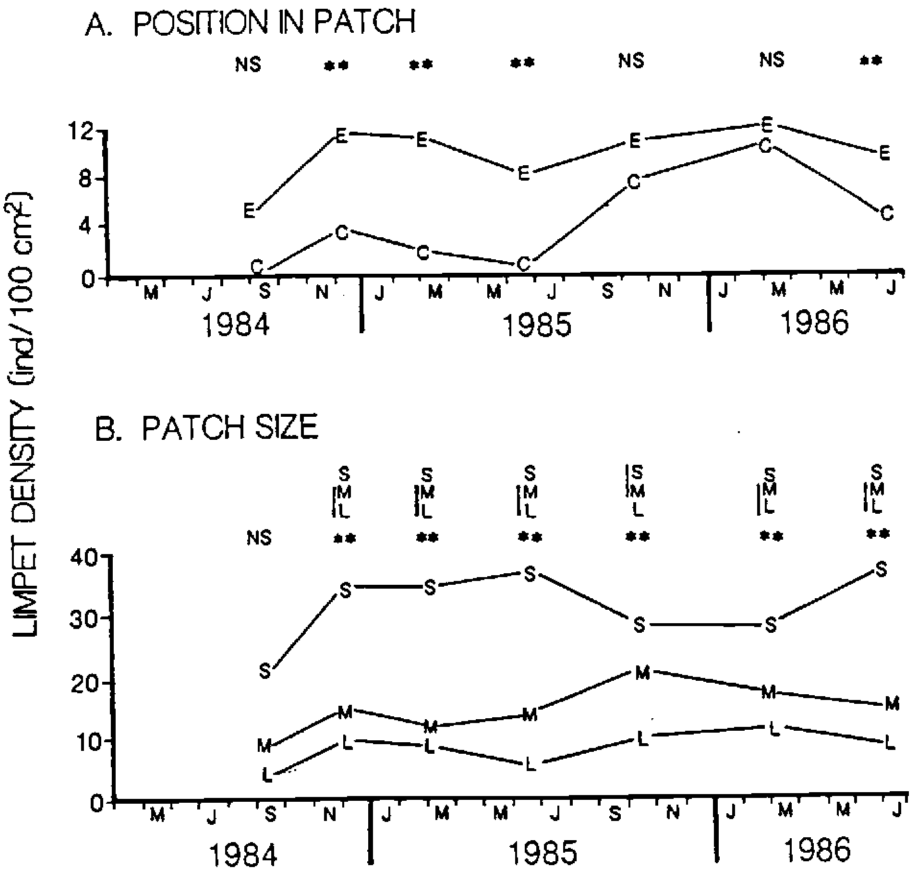
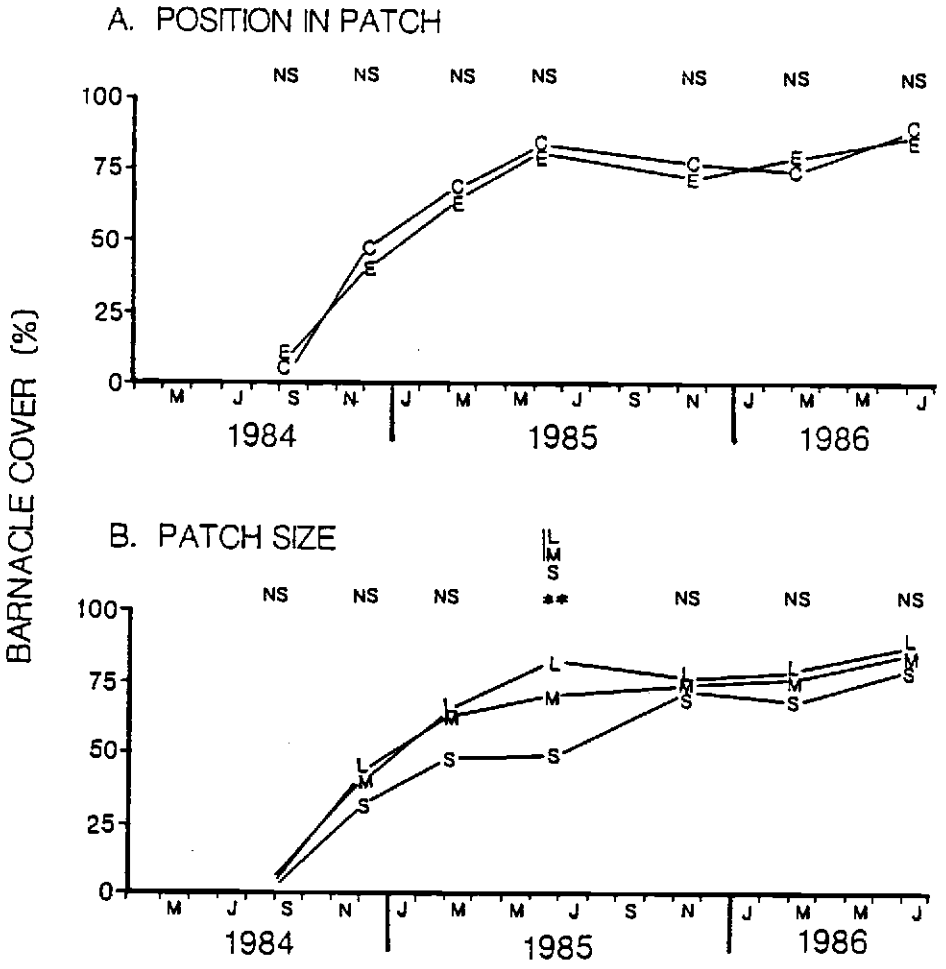

A. POSITION IN PATCH
NS
**
**
**
NS
NS
**
12
8
4
0
E
C
M
J
S
N
J
M
M
J
S
N
J
M
M
J
1984
1985
1986
LIMPET DENSITY (ind/100 cm^2)
B. PATCH SIZE
S M L
NS
**
40
30
20
10
0
S
M
L
1984
1985
1986

Figure 19. Mean barnacle cover with respect to position in the large patches (A) and patch size (B). Symbols as in figure 18.

Figure 19


A. POSITION IN PATCH
NS NS NS NS NS NS NS
100
75
50
25
0
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M J S N J M M J S N J M M J
1984
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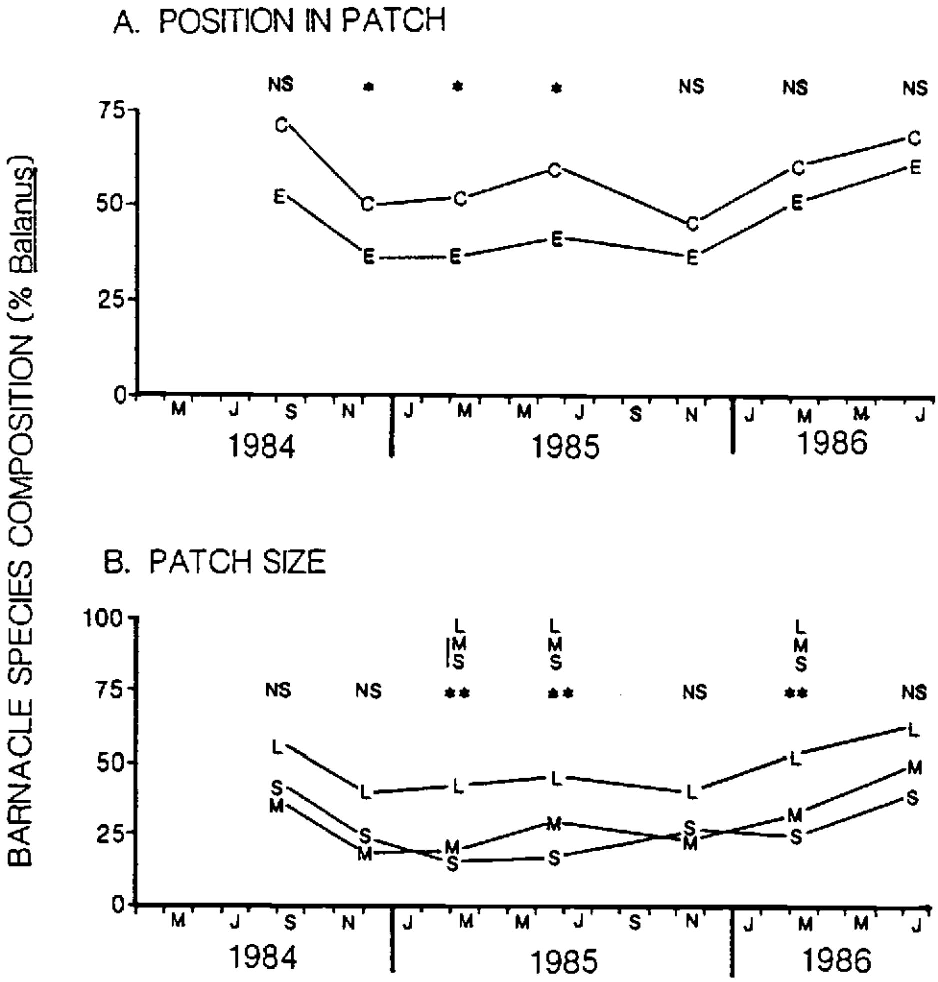
1986
BARNACLE COVER (%)
B. PATCH SIZE
L
M
S
**
NS NS NS NS NS NS
100
75
50
25
0
L
M
S
M J S N J M M J S N J M M J
1984
1985
1986

Figure 20. Mean barnacle species composition (100 X _Balanus_ cover / the cover of _Balanus_ plus _Chthamalus_) with respect to position in the large plots (A) and patch size (B). Symbols as in figure 18.

Figure 20


A. POSITION IN PATCH
NS
*
*
*
NS
NS
NS
75
50
25
0
C
E
M J S N J M M J S N J M M J
1984
1985
1986
BARNACLE SPECIES COMPOSITION (% Balanus)
B. PATCH SIZE
100
75
50
25
0
L
M
S
NS
NS
**
**
NS
**
NS
L M S
L M S
L M S
M J S N J M M J S N J M M J
1984
1985
1986

Algal Cover

Total algal cover was higher in the edge than the center of the large gaps (Fig. 21A). As succession advanced, however, algal cover rapidly increased in the interior of the gaps resulting in non-significant differences between the edge and center on the last two sampling dates.

The species composition of the algal cover was also dependent on position within the large gaps (Fig. 22A). On the last two sampling dates, the relative cover of _Pelvetiopsis_ (the cover of _Pelvetiopsis_ divided by the total algal cover) was significantly higher in the edge than in the center areas (March 1986--ANOVA, n=7, p=0.005; July 1986--ANOVA, n=7, p=0.01). _Endocladia_, however, was more abundant in the center than the edge areas.

Gap size may have influnced total algal cover. On all sampling dates, the small gaps had higher mean algal cover than the medium gaps, which, in turn, had higher mean algal cover than the large gaps (Fig. 21B). These differences in algal cover were not, however, statistically different on any sampling date.

Gap size had no significant effect on the relative abundance of _Pelvetiopsis_ or _Endocladia_ on the last two sampling dates (Fig. 22B). The relative cover of _Pelvetiopsis_ increased with decreasing gap size, while the relative cover of *Endocladia* increased with increasing gap size.

Figure 21. Mean algal cover with respect in position in the large plots (A) and patch size (B). Symbols as in figure 18.

Figure 21

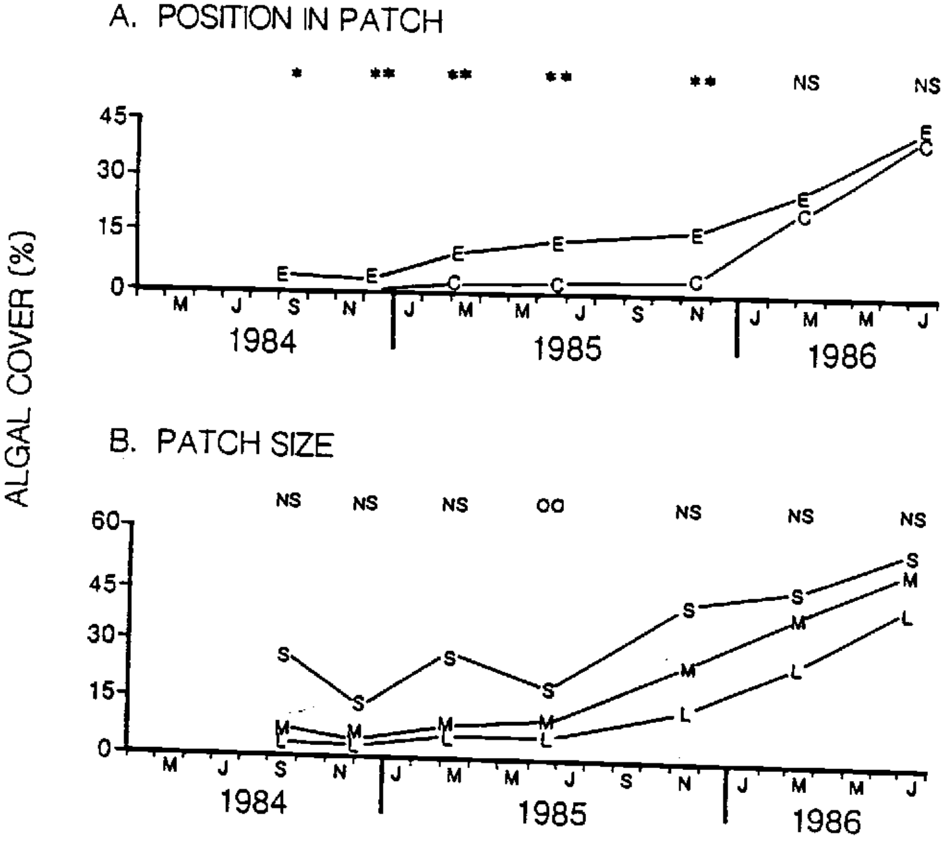
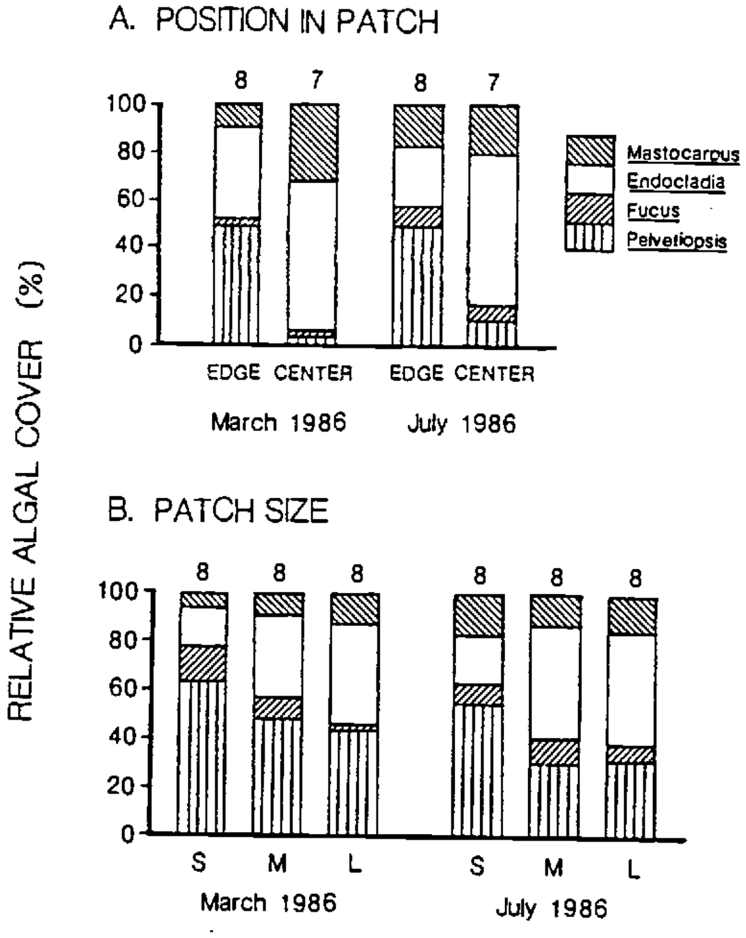

A. POSITION IN PATCH
*
**
**
**
**
NS
NS
ALGAL COVER (%)
45
30
15
0
E
C
M
J
S
N
J
M
M
J
S
N
J
M
M
J
1984
1985
1986
B. PATCH SIZE
NS
NS
NS
OO
NS
NS
NS
60
45
30
15
0
S
M
L
1984
1985
1986

Figure 22. Mean relative cover of the four most abundant species of algae on the last two sampling dates. The number above each bar indicate the number of replicates with any algal cover.

Figure 22


A. POSITION IN PATCH
RELATIVE ALGAL COVER (%)
100
80
60
40
20
0
8
7
8
7
EDGE
CENTER
EDGE
CENTER
March 1986
July 1986
Mastocarpus
Endocladia
Fucus
Pelvetiopsis
B. PATCH SIZE
8
8
8
8
8
8
S
M
L
S
M
L
March 1986
July 1986

Algal Density

The density of algal thalli in the large patches did not depend on location within a gap. There were no significant differences in mean algal density between the edge and center portions on any sampling date (Fig. 23A). Similarly, gap size had a significant influence on algal density on only one sampling date (March 1986). At that time, the medium gaps had significantly higher algal density than the small gaps (Fig. 23B).

The species composition of the algal thalli also appeared not to be affected by position within the large gaps. The mean relative abundances of the four most common algae were almost identical in the edge and center portions of the large gaps on the last two sampling dates (Fig 24A). Gap size had no clear effect on algal species composition (Fig. 24B). The small gaps had both lower algal densities and smaller areas resulting in low total numbers of thalli in these plots. On the last three sampling dates, three or four of the small gaps had no algal thalli. The relative abundance data in the small gaps was therefore based on a few highly variable replicates.

Figure 23. Mean density of algal thalli with respect to position in the large plots (A) and patch size (B). Symbols as in figure 18.

Figure 23

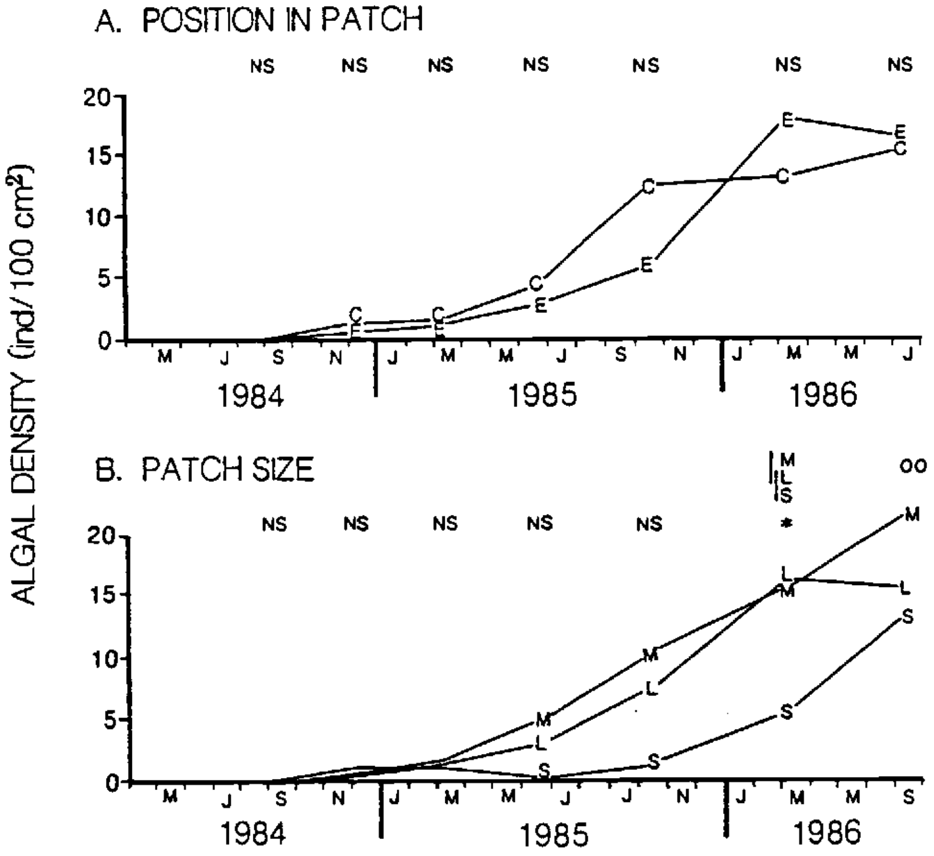
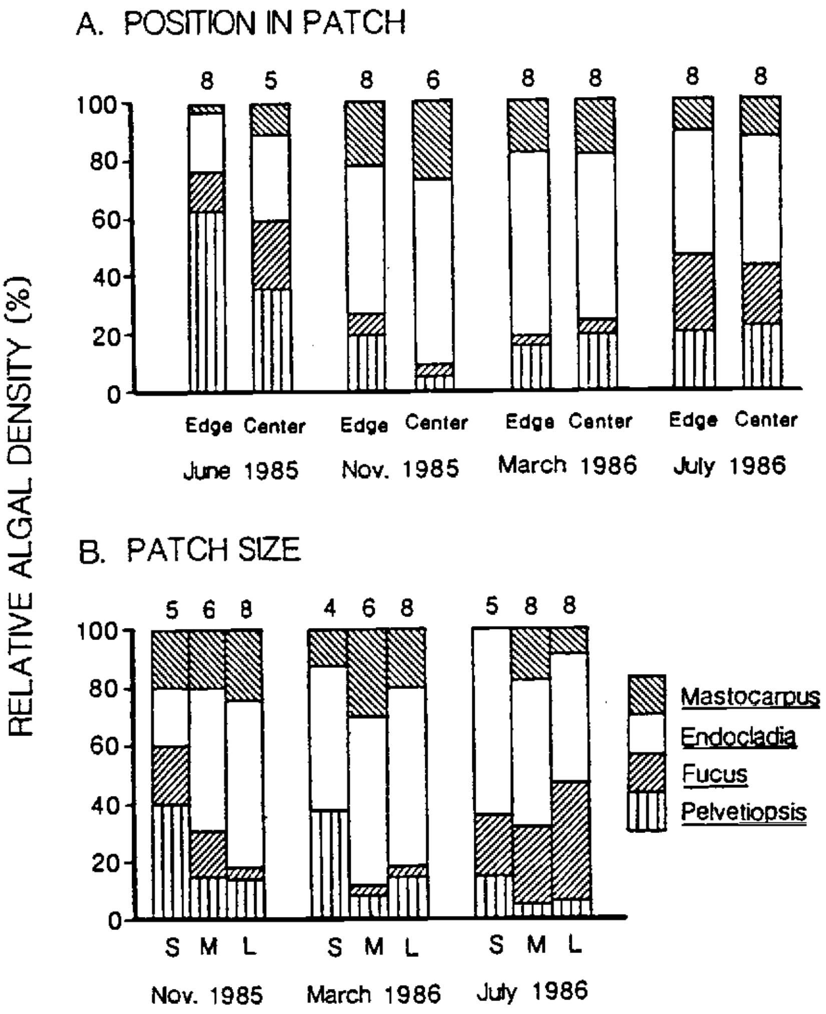

A. POSITION IN PATCH
NS NS NS NS NS NS NS
ALGAL DENSITY (ind/100 cm²)
0
5
10
15
20
C
E
M J S N J M M J S N J M M J
1984
1985
1986
B. PATCH SIZE
NS NS NS NS NS
*
M
L
S
oo
M
L
S
M J S N J M M J J N J M M S
1984
1985
1986

Figure 24. Relative density of the four most abundant species of algae on the last three sampling dates. The number above each bar indicates the number of replicates with any attached algae.

Figure 24


A. POSITION IN PATCH
8 5 8 6 8 8 8 8
100
80
60
40
20
0
Edge Center
June 1985
Edge Center
Nov. 1985
Edge Center
March 1986
Edge Center
July 1986
RELATIVE ALGAL DENSITY (%)
B. PATCH SIZE
5 6 8 4 6 8 5 8 8
100
80
60
40
20
0
S M L
Nov. 1985
S M L
March 1986
S M L
July 1986
Mastocarpus
Endocladia
Fucus
Pelvetiopsis

DISCUSSION

The abundance of limpets, the dominant herbivore in this community, was influenced by both position within a gap and gap size. Limpet densities were higher in the edge than center areas of the large gaps. Soon after scraping, the limpets tended to nestle against the barnacles at the edge of the gap or cluster under algae hanging over the patch boundary. This behavior may protect them from avian predators since they are less conspicuous when under algae or next to barnacles (Mercurio et al. 1985). Limpets moved into the gaps to forage at night or while the plots were awash. The limpets took up residence in the interior of the gaps after barnacles and macroalgae colonized the plots. Limpet density decreased as gap size increased. Limpets aggregated at the gap boundaries in all plots. The amount of boundary per unit gap area decreased as gap size increased, leading to the higher densities observed in the smaller gaps. Similarly, several studies have found that limpet densities decreased with increasing gap size in mussel beds (Suchanek 1978; Sousa 1984b).

Early in succession, algal cover was higher in the edge than the center of the large gaps. This algal cover in the edge region was primarily composed of individual thalli whose holdfasts were located outside the boundary of the gaps. The algal thalli were not large enough to shade the center region of the large gaps. At the end of the experiment, the majority of algal cover in the edge areas, and all of the cover in the center areas, was composed of individuals that had recruited to the gaps. Small disturbances, with their large perimeter/area ratio, also had higher algal cover than the medium and large disturbances. Sousa (1979a) also found that small gaps initially had more algal canopy than large gaps. Shading also decreases as gap size increases in forests (reviewed by Runkle 1985).

Unlike this study, dense growths of ephemeral algae occur in the interior of gaps in mussel beds, while a barren zone 10-20 cm wide is maintained by limpets around the perimeter of the gap (Suchanek 1978, Paine and Levin 1981, Sousa 1984b). This difference may have resulted from the small size of the gaps used in this study. The distance from the boundary to the center of the largest patches I created was eight cm. The centers of even the largest gaps were therefore within the foraging range of the limpets that aggregated near the edge of the gap. The small sizes of the gaps normally produced in the Balanus-Pelvetiopsis community (Chapter 3--Fig. 8) precludes the formation of the complete refugia from limpets that are formed by the large disturbances normally observed in mussel beds (Suchanek 1978, Paine and Levin 1981, Sousa 1984b).

The species composition of algal cover was influenced by position within a gap and disturbance size. *Pelvetiopsis* was the dominant source of cover in the edge of the large gaps, while *Endocladia* was the dominant source of cover in the center areas. Similarly, *Pelvetiopsis* was the major component of cover in the small gaps, while *Endocladia* was the major component of cover in the medium and large gaps. *Endocladia* is a shorter (2-3 cm) alga than *Pelvetiopsis* (5-8 cm). This difference in length allowed *Pelvetiopsis* thalli with holdfasts located outside the gsp boundaries, but not *Endocladia*, to cover much of the small gaps and edges of the larger gaps. Sousa (1984b) found *Endocladia* had high cover in large gaps both in the presence and absence of grazers. He suggested that the higher water flow and light levels in large gaps caused this pattern of distribution. This explanation is consistent with my observation of high *Endocladia* cover in both the large disturbances and gap centers.

Algal recruitment is greatly reduced by limpets in the *Balanus*-*Pelvetiopsis* community (Chapter 3--Fig. 17). Although the edges had higher limpet densities than the gap centers, the rate of algal recruitment was not higher in the plot interiors. The lower grazer higher in the plot interiors. The lower grazer abundance in the center of the gaps may have been compensated for by several factors that increased algal abundance in the perimeters of the plots. First, algal mortality caused by heat stress and desiccation may have been reduced near the plot boundaries by shading and water draining out of the mature community. Second, Pelvetiopsis and Fucus have extremely limited dispersal distances (Sousa 1984b, Farrell, manuscript in preparation), which could have caused higher propagule settlement near the boundaries than the gap centers. As would be expected from limpet densities, algal establishment was several times higher in the medium and large gaps than in the small gaps mid-way through the experiment. The patchy pattern of algal establishment, however, led to high within-treatment variation and so algal densities only significantly differed among the gap sizes on a single date.

Barnacle species composition was influenced by both position in a gap and gap size. The relative abundance of Balanus was higher both in the center than the edges of gaps and in the larger gaps. This pattern of distribution would have occurred if Chthtamalus is less susceptible than Balanus to deleterious effects of algal canopy. Many studies have found that algal cover reduces settlement or decreases barnacle survival by

Hawkins 1983). In this study, however, the relative abundance of _Balanus_ was higher in portions of the gaps covered by algae than in uncovered areas. As in Dayton's (1971) study, _Balanus_ density was higher under algal cover, possibly because desiccation-caused mortality was reduced beneath the canopy. The species of algae in this community may not have been massive enough to kill barnacles (Grant 1977, Hawkins 1983). The relative abundance of _Balanus_ is lower in smaller gaps and the edges of gaps not as a result of, but despite, the algal canopy in those areas.

The pattern of barnacle species composition may result from the distribution of limpets. Several studies have shown that _Balanus_ is more susceptible than _Chthamalus_ to limpet-caused mortality (Dayton 1971, Paine 1981, Farrell 1987, Chapter 2--Fig. 2), and this is also the case in this community (Chapter 3--Fig. 11). The lower relative abundance of _Balanus_ in the smaller gaps and near the edges of gaps may be caused by the high limpet densities in those areas.

As predicted, the differences between small versus large gaps were also observed in the gap edge versus center comparisons (Table 1). The differences in limpet density and the abundance and species composition of algal cover appear directly related to proximity of the boundary in the disturbed plots. Vegetative growth of the longer algae could cover large areas of the smaller gaps and the edge portions of gaps because of the nearness of undisturbed individuals. Limpets were also associated with the boundary of the intact community and, in turn, appear to affect barnacle species composition. The similarity between small gaps and the edges of larger gaps is likely to be observed in any situation where proximity to the undisturbed community has either a direct or indirect influence on the colonization of a disturbed patch.

Table 1. A summary of the effects of patch size and position within a patch (*=statistically significant effect, NS=trend but not statistically significant).

COMMUNITY ATTRIBUTE	POSITION IN PATCH	SIZE OF PATCH
Limpet Density	EDGE > CENTER*	SMALL > LARGE*
Total Barnacle Cover	No Effect	No Effect
Relative Abundance of *Balanus*	CENTER > EDGE*	LARGE > CENTER*
Total Algal Cover	EDGE > CENTER*	SMALL > LARGE^{NS}
Relative Cover of *Pelvetiopsis*	EDGE > CENTER*	SMALL > LARGE^{NS}
Algal Recruit Density	No Effect	No Effect
Species Composition of Algal Recruits	No Effect	No Effect

Several models predict that the size distribution of disturbed patches will influence the species composition of communities (Miller 1982, Malanson 1985). These models predict that early successional species will be more rapidly excluded from small gaps than larger gaps since competitive dominants tend to slowly encroach or disperse inward from the edge of a disturbed area (e.g. Sousa 1979, Paine and Levin 1981, Palumbi and Jackson 1982, Keough 1984). In this study, however, a later successional species, _Balanus_ became established more slowly in small than large gaps. _Balanus_ does not have either short distance dispersal or fast vegetative growth, the two characteristics that cause many later successional species to dominate small gaps more rapidly than large gaps (Miller 1981, Connell and Keough 1985). _Chthamalus_, the early successional species, therefore will persist longer and in greater abundance in smaller gaps. This result indicates that the models of Miller (1982) and Malanson (1985) have limited applicability.

Chapter V

CONCLUSIONS: COMMUNITY STABILITY AND SUCCESSION

In this thesis two types of perturbations were investigated. The limpet-dominated community (Chapter II) was perturbed by removing a group of consumers. The *Balanus*-*Pelvetiopsis* community (Chapters III and IV) was perturbed by removing all macroscopic organisms from plots. Succession played strong, but different, roles in the stability of these two communities.

The resistance of both communities was influenced by succession. In the limpet-dominated community, succession occurred while limpets were removed. At the start of limpet exclusion the previously-barren plots were invaded by a succession of species. Micoalgae (primarily diatoms) were the first colonists. They were followed by weedy green algae (primarily *Enteromorpha linza*), that in turn were replaced by brown (*Scytosiphon*) and red (*Polysiphonia*) algae. That succession occurred during the perturbation (limpet removal) indicated the resistance of the community was overcome. Succession usually results in community structure converging with its predisturbance state (Connell and Slatyer 1977). In this case, however, succession resulted in community structure diverging from its predisturbance state.

The resistance of the _Balanus_-_Pelvetiopsis_ community was also influenced by community development. As succession advanced, algae grew on the _Balanus_ tests, increasing their wave-induced drag. Furthermore, _Balanus_ acquired tall, thin morphologies as a result of crowding. These successional changes resulted in the community that was more susceptible to wave-induced disturbance. This result is directly opposed to Odum's (1969) belief that the resistance of a community increases as succession proceeds.

The amplitudes of the two communities were not exceeded by the experimental perturturbations. In the limpet-dominated community, prey species that increased in abundance during the period of limpet exclusion could not manitain their abundance after limpet reintroduction. The amplitude of the _Balanus_-_Pelvetiopsis_ community was not exceeded in any of the three experiments, even though the disturbances were performed at three different sites, at different seasons, and the clearings were of several different sizes. In each experiment succession followed a similar path and community structure converged with the predisturbance state.

Different factors influenced the elasticity of the two communities. In the limpet-dominated community, elasticity was determined, in part, by whether prey had size-related escapes from limpets. For species with size-related escapes (*Balanus* and *Chthtamalus*) the life span of the individuals that recruited during limpet removals also influenced elasticity. In the *Balanus-Pelvetiopsis* community, elasticity was determined by the rate of succession, or more specifically, the factors that influenced the successful recruitment of barnacles and algae. Herbivores decreased the elasticity of the community by decreasing the recruitment rate of both barnacles and algae. Elasticity differed among the three experiments in this community, in part, because dense recruitment of *Balanus* rarely occurred. At the Yaquina Head low site (YHL) a dense cohort of *Balanus* recruited almost immediately after scraping, leading to a rapid rate of succession. At the Yaquina Head high site (YHH), however, this recruitment event occurred 17 months after scaping, leading to a slow rate of succession. The timing of *Balanus* recruitment influences other taxa. *Chthamalus* abundance decreased and macroalgae abundance increased only after *Balanus* became established. These interactions caused the timing of *Balanus* recruitment to influence the elasticity of all major components of the community. The major difference between the two study communities is that in the limpet-dominated community elasticity depended on factors that removed established individuals and decreased the biomass of the community, whereas in the *Balanus*-*Pelvetiopsis* community, elasticity depended on factors that influenced the colonization and growth of individuals.

The results of my investigations indicate that community stability was strongly linked to succession. Different components of stability, however, were influenced by succession in each community. In the limpet-dominated community, succession affected resistance, but not amplitude or elasticity. In the *Balanus*-*Pelvetiopsis* community succession affected resistance, amplitude, and elasticity. While succession and stability are strongly linked, they are not united by a simple relationship. Rather, this relationship will depend both on aspects of the study community and on the nature of the perturbation

Chapter VI

BIBLIOGRAPHY

Abbott I.A., and G. J. Hollenberg. 1976. Marine algae of California. Stanford University Press, California, USA.

Abugov, R. 1982. Species diversity and phasing of disturbance. Ecology 63:289-293.

Armesto, J. J., and S. T. A. Pickett. 1985. Experiments on disturbance in old-field plant communities: impact on species richness and abundance. Ecology 66:230-240.

Beddington J. R., and R. M. May. 1982. The harvesting of interacting species in a natural ecosystem. Scientific American 247:62-69.

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

Boag P.T., and P. R. Grant. 1981. Intense natural selection on a population of Darwin's finches (Geospizinae) in the Galapagos. Science 214:82-85.

Boesch, D. F. 1974. Diversity, stability and response to human disturbance in estuarine ecosystems. Pages 109-114 in A. J. Cave, editor. Structure, functioning and management of ecosystems. Proceedings of the

First International Congress of Ecology. Pudoc, Wageningen, Netherlands.

Bold, H.C., and Wynne. 1978. Introduction to the algae. Prentice-Hall, New Jersey.

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

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

------. 1986. Limpets: their role in littoral and sublittoral community dynamics. Pages 97-116 in P. G. Moore and R. Seed, editors. The ecology of rocky coasts. Columbia University Press, New York, New York, USA.

Breen, P. A. 1972. Seasonal migration and population regulation in the limpet _Acmaea_ (_Collisella_) _digitalis_. Veliger 14:177-183.

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.

Castenholz, R. W. 1961. The effect of grazing on marine littoral diatom populations. Ecology 42:783-794.

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

Clayton, M. N. 1981. Experimental analysis of the life history of the complanate form of *Scytosiphon* (Scytosiphonaceae, Phaeophyta) in southern Australia. Phycologia 20:358-364.

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

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

------. 1961b. 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. 1. *Balanus glandula* and several predatory species of *Thais*. Ecological Monographs 40:49-78.

------. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460-490 in M. L. Cody and J. M.

Diamond, editors. Ecology and evolution of communities. Belknap Press, Cambridge, Massachusetts, USA.

------. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

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

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.

Connell, J. H., and W. P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. American Naturalist 122:661-696.

Connell, J. H., and M. J. Keough. 1985. Disturbance and patch dynamics of subtidal marine animals on hard substrates. Pages 125-151 in S.T.A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

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. 1975. Interactions of seasonally changing physical factors and grazing affecting high intertidal communities on a rocky shore. Ph.D. thesis. University of Oregon, Eugene, USA.

------. 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 alga _Rhodomela_ _larix_ (Turner) C. Agardh: negative effects on the host and food for herbivores? Journal of Experimental Marine Biology and Ecology 86:197-218.

Davis, R. M., and J. E. Cantlon. 1969. Effects 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.

------. 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.

Dethier, M. N., and D. O. Duggins. 1984. An "indirect commensalism" between marine herbivores and the importance of competitive hierarchies. American Naturalist 124:205-219.

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

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.

Dungan, M. L., T. E. Miller, and D. A. Thomson. 1982. Catastrophic decline of a top carnivore in the Gulf of California rocky intertidal zone. Science 216:989-991.

Egerton, F. N. 1973. Changing concepts of the balance of nature. Quarterly Review of Biology 48:322-350.

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

Farrell, T. M. 1987. Community stability: the effects of limpet removal and reintroduction in an intertidal community. Oecologia (Berlin) In Press.

Feare, C. J. 1970. Aspects of the ecology of an exposed shore population of dogwhelks Nucella lapillus (L.). Oecologia (Berlin) 5:1-18.

Feare, C. J., and R. W. Summers. 1986. Birds as predators on rocky shores. Pages 249-264 in P. G. Moore and R. Seed, editors. The ecology of rocky coasts. Columbia University Press, New York, New York, USA.

Foster, M. S. 1975a. Algal Succession in a Macrocystis pyrifera forest. Marine Biology 32:313-329.

------. 1975b. Regulation of algal community development in a Macrocystis pyrifera forest. Marine Biology 32:331-342.

Frank, P.W. 1965. The biodemography of an intertidal snail population. Ecology 46:831-844.

------. 1982. Effects of winter feeding on limpets by black oystercatchers Haematopus bachmani. Ecology 63:1352-1362.

Fritchman, H. K. 1961. A study of the reproductive cycle in the California Acmaeidae (Gastropoda). Part 3. Veliger 4:41-47.

Gaines, S. D. 1985. Herbivory and between-habitat diversity: the differential effectiveness of defenses in a marine plant. Ecology 66:473-485.

Gaines, S., S. Brown, and J. Roughgarden. 1985. Spatial variation in larval concentrations as a cause of spatial variation for the barnacle, Balanus glandula. Oecologia (Berlin) 67:267-272.

Goldberg, D. E., and P. A. Werner. 1983. The effects of size of opening in vegetation and liter cover on seedling establishment of goldenrods (Solidago spp.). Oecologia (Berlin) 60:149-155.

Grant, W. S. 1977. High intertidal community organization on a rocky headland in Maine, U.S.A. Marine Biology 44:15-25.

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.

------. 1983. Interactions of Patella and macroalgae with settling Semibalanus balanoides (L.). Journal of Experimental Marine Biology and Ecology 71:55-72.

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

Hughes, R. N. 1986. Rocky shore communities: catalysts to understanding predation. Pages 223-233 in P. G. Moore and R. Seed, editors. The ecology of rocky coasts. Columbia University Press, New York, New York, USA.

Huston, M. 1979. A general hypothesis of species diversity. American Naturalist 113:81-101.

Huyer, A., W.E. Gilbert, and H. L Pittock. 1983. Anomalous sea levels at Newport, Oregon, during the 1982-83 El Nino. Coastal Ocean Climatological Newsletter 5:37-39.

Idyll, C. P. 1973. The anchovy crisis. Scientific American 228:22-29.

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.

------. 1985a. 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.

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

Keith, L. B. 1983. Role of food in hare population cycles. Oikos 40:385-395.

Keough, M. J. 1984. Effects of patch size on the abundance of sessile marine invertebrates. Ecology 65:423-437.

Kessel, M. M. 1964. Reproduction and larval development of *Acmaea testudinalis*. Biological Bulletin 127:294-303.

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

Krebs, C. J., M. S. Gaines, B. L. Keller, J. M. Myers, and R. H. Tamarin. 1973. Population cycles in small rodents. Science 179:35-41.

Lamberti, G. A., and V. H. Resh. 1983. Stream periphyton and insect herbivores: an experimental study of grazing by a caddisfly population. Ecology 64:1124-1135.

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

Levine, S. H. 1976. Competitve interactions in ecosystems. American Naturalist 110:903-910.

Lindberg, D. R. 1986. Name changes in the "acmaeidae".

Veliger 29:142-148.

Little, C., and L. P. Smith. 1980. Vertical zonation on rocky shores in the Severn Estuary. Estuarine and Coastal Marine Science 11:651-669.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. American Naturalist 112:23-39.

------. 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 and Row, New York, New York, USA.

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

Lubchenco, J., and J. D. Cubit. 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. 1. Populations and communities. Annual Review of Ecology and Systamatics 12:405-437.

Lubchenco, J., 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.

Malanson, G. P. 1985. Intensity as a third factor of disturbance and its effect on species diversity. Oikos 43:411-413.

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

Marsh, C. P. 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.

McConnaughay, K. D. M., and F. A. Bazzaz. 1987. The relationship between gap size and performance of several colonizing annuals. Ecology 68:411-416.

Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecological Monographs 46:355-393.

------. 1979. Coexistence between the seastars Asterias vulgaris and A. forbesi in a heterogeneous environment: a non-equilibrium explanation. Oecologia (Berlin) 41:245-272.

Menge, B. A., and J. Lubchenco. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. Ecological Monographs 51:429-450.

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.

Mercurio, K. S., A. R. Palmer, and R. B. Lowell. 1985. Predator-mediated microhabitat partitioning by two species of visually cryptic, intertidal limpets. Ecology 66:1417-1425.

Miller, T. E. 1982. Community diversity and interactions between size and frequency of disturbance. American Naturalist 120:533-536.

Morris, R. H., D. P. Abbott, and E. C. Haderlie. 1980. Intertidal invertebrates of California. Stanford University Press, California, USA.

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

Nicotri, M. E. 1977. Grazing effects of four marine intertidal herbivores on the microflora. Ecology 58:1020-1032.

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

Olson, A. M. 1985. Early succession in beds of the red alga _Iridaea_ _cornucopiae_ Post. & Rupr. (Gigartinaceae). M.S. Thesis, Oregon State University, Corvallis, Oregon, USA.

Orians, G. H. 1974. Diversity, stability and maturity in natural ecosystems. Pages 139-150 in W. H. van Dobben and R. H. Lowe-McConnell, editors. Unifying concepts in ecology. Junk, The Hague, Netherlands.

Osman, R. S. 1977. The establishment and development of a marine epifaunal community. Ecological Monographs 47:37-63.

Paine, R. T. 1976. Size limited predation: an observational and experimental approach with the _Mytilus_-_Pisaster_ interaction. Ecology 57:858-873.

------. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49:667-685.

------. 1981. Barnacle ecology: is competition important? The forgotten roles of predation and disturbance. Paleobiology 7:553-560.

------. 1984. Ecological determinism in the competition for space. Ecology 65:1339-1348.

------. 1986. Benthic community-water column coupling during the 1982-1983 El Nino. Are community changes at high latitudes attributable to cause or coincidence? Limnology and Oceanography 31:351-360.

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

Paine, R. T., J. C. Castilla, and J. Cancino. 1985. Perturbation and recovery patterns in starfish dominated intertidal assemblages in Chile, New Zealand, and Washington State. American Naturalist 125:679-691.

Palumbi, S. R., and J. B. C. Jackson. 1982. Ecology of cryptic coral reef communities. 2. Recovery from small disturbance events by encrusting bryozoa: the influence of "host" species and lesion size. Journal of Experimental Marine Biology and Ecology 64:103-115.

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

Peterson, C. H. 1984. Does a rigorous criterion for environmental identity preclude the existence of multiple stable points? American Naturalist 124:127-133.

Petraitis, P. S. 1983. Grazing patterns of the periwinkle and their effect on sessile intertidal organisms. Ecology 64:522-533.

Pianka, E. R. 1986. Ecology and natural history of desert lizards. Princeton University Press, Princeton, New Jersey, USA.

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.

Pimm, S. L. 1982. Food webs. Chapman and Hall, New York, New York, USA.

Potts, G. R., S. C. Tapper, and P. J. Hudson. 1984. Population fluctuations in red grouse: analysis of bag records and a simulation model. Journal of Animal Ecology 53:21-36.

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. 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. D. Cubit. 1981. The influence of biotic factors in an upper intertidal community: dipteran larvae grazing on algae. Ecology 62:1536-1547.

Roeleveld, J. G., M. Duisterhof, and M. Vroman. 1974.

On the year cycle of Petalonia fascia in the Netherlands. Netherlands Journal of Sea Research 8:410-426.

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

Runkle, J. R. 1985. Disturbance regimes in temperate forests. Pages 17-33 in S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Scheibling, R. 1986. Increased macroalgal abundance following mass mortality of sea urchins (Strongylocentrotus droebachiensis) along the Atlantic coast of Nova Scotia. Oecologia (Berlin) 68:186-198.

Schreiber, R. W., and E. H. Schrieber. 1984. Central Pacific seabirds and the El Nino/Southern Oscillation: 1982-1983 perspectives. Science 225:713-716.

Sebens, K. P. 1986. Community ecology of vertical rock walls in the Gulf of Maine, USA: small scale processes and alternative community states. Pages 346-371 in P. G. Moore and R. Seed, editors. The ecology of rocky coasts. Columbia University Press, New York, New York, USA.

Sebens, K. P., and J. R. Lewis. 1985. Rare events and population structure of the barnacle Semibalanus cariosus (Pallas, 1788). Journal of Experimental Marine Biology and Ecology 87:55-65.

Sih, A., P. Crowley, M. McPeek, J. Petranka, and K. Strohmeier. 1985. Predation, competition and prey communities: a review of field experiments. Annual Review Ecology and Systamatics 16:269-312.

Simenstad, C. A., J. A. Estes, and K. K. Kenyon. 1978. Aluets, sea otters, and alternative stable state communities. Science 200:403-411.

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.

Snavely, P. D., and N. S. Macleod. 1971. Visitor's guide to the geology of the coastal area near Beverly Beach State Park, Oregon. Ore Bin 33:85-105.

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

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

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

------. 1980. The responses of a community to disturbance: the importance of successional age and species' life histories. Oecologia (Berlin) 45:72-81.

------. 1984a. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353-391.

------. 1984b. Intertidal mosaics: patch size, propagule availability and spatially variable patterns of succession. Ecology 65:1918-1935.

------. 1985. Disturbance and patch dynamics on rocky intertidal shores. Pages 101-124 in S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

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 molluscs: 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 Biogeography 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.

Southward, A. J., and E. C. Southward. 1978. Recolonisation of rocky shores in Cornwall after use of toxic dispersants to clean up the Torrey Canyon spill. Journal of the Fisheries Resource Board of Canada 35:682-706.

Stafford, J. 1971. Heron populations of England and Wales 1928-70. Bird Study 18:218-221.

Sutherland, J. P. 1970. Dynamics of high and low populations of the limpet *Acmaea scabra* (Gould). Ecological Monographs 40:169-188.

Tabata, S. 1984. Anomalously warm water of the Pacific coast of Canada during the 1982-83 El NIno. Tropical Ocean-Atmosphere Newsletter 24:7-9

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

Travis, J. 1987. Comparative ecology. Science 235:492-493.

Turner, T. 1983a. Complexity of early and middle successional stages in a rocky intertidal surfgrass community. Oecologia (Berlin) 60:6-65.

------. 1983b. 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, In Press.

Werner, E. E. 1986. Species interactions in freshwater fish communities. Pages 344-358 in J. Diamond and T. J. Case, editors. Community ecology. Harper & Row, New York, New York, USA.

Wethey, D. S. 1984. Sun and Shade mediate competion in the barnacles _Chthamalus_ and _Semibalanus_: a field experiment. Biological Bulletin 167:176-185.

Wiens, J. A., J. F. Addicott, T. J. Case, and J. Diamond. 1986. Overview: the importance of spatial and temporal scale in ecological investigations. Pages 145-153 in J. Diamond and T. J. Case, editors. Community ecology. Harper & Row, New York, New York, USA.

Wilbur, H. M. 1984. Complex life cycles and community organization in amphibians. Pages 195-224 in P. W. Price, C. N. Slobodchikoff and W. S. Gand, editors. A new ecology: novel approaches to interacting systems. Wiley, New York, New York, USA.

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 Suchanek, T. H. 1984. Mussels in flow: drag and dislodgement by epizoans. Marine Ecology-Progress Series 16:259-268.

Zaret, T. M. 1980. Predation and Freshwater Communities. Edwards Brothers Inc, Ann Arbor, Michigan, USA.