AN ABSTRACT OF THE THESIS OF

Deborah M. Brosnan for the degree of Doctor of
Philosophy in Zoology presented on August 19, 1994.

Title: Environmental Factors and Plant-Animal
Interactions on Rocky Shores along the Oregon Coast

Abstract Approved: _____

Bruce A. Menge

Factors affecting the persistence of mussels (Mytilus
californianus) and their associated epibiont species were
studied along the central Oregon coast. Interactions
between mussels and their algal epibionts (Endocladia
muricata) varied in sign and strength with environmental
conditions. In extreme temperatures mussel-epibiont
interactions determined survival of individual mussels,
and persistence of the mussel-bed assemblage.

Under normal conditions Endocladia had weak negative
effects on mussels. Mussels colonized by Endocladia had
lower body weight, produced more byssal threads, and
experienced increased drag. However, in the field,
dislodgment of mussels with Endocladia epibionts was
higher only when mortality in the mussel bed was >25%. By
contrast under freezing conditions, Endocladia appeared to

insulate mussels, and protect them from freeze-induced mortality. Historical temperature records suggested that freezing temperatures may be important in the ecology of mussel-epibiont interactions. Short-term negative interactions between mussels and algal epibionts are balanced by occasional, but important positive interactions which affect the persistence of mussels and their associated assemblage.

Factors affecting the development of the epibiont community on mussels were experimentally studied. The epibiont assemblage on mussels consisted primarily of barnacles, and the alga E. muricata. Barnacles colonized mussels, but no algal species successfully recruited directly onto mussels. Barnacles facilitated Endocladia. Limpets reduced diatom and algal abundance, except for Endocladia, and reduced barnacle abundance at low and moderate recruitment intensity only.

The effect of human trampling on mussels, and the uppershore barnacle-algal assemblage was experimentally studied. Trampling reduced the abundance of canopy-forming algae, and mussels, and their epibionts. Continued trampling inhibited succession. After trampling stoppep, the algal assemblage recovered within a year, but mussels loss continued in previously trampled plots. This suggests that trampling may increase susceptibility to natural disturbance.

Environmental Factors and Plant-Animal
Interactions on Rocky Shores along the Oregon Coast

by

Deborah M. Brosnan

A THESIS

submitted to

Oregon State University

in partial fulfillment
of the requirements for
the degree of

Doctor of Philosophy

Completed August 19, 1994

Commencement June 1995

APPROVED

Bruce Menge

Bruce A. Menge, Professor of Zoology, in charge of major

John Morris, Chairperson, Department of Zoology

Dean of Graduate School

Date thesis is presented _____ August 19, 1994

Typed by _Deborah M. Brosnan_ , Author

ACKNOWLEDGMENTS

I thank my parents for giving me many hours of fun in tidepools while growing-up in Ireland. Thanks for providing me with opportunities to pursue my interests. My extended family encouraged my interests in marine ecology: At an impressionable age, my older cousins convinced me that red sea-anemones were vampire bloodsuckers.

My doctoral advisor Bruce Menge contributed greatly to my understanding of science, as did Jane Lubchenco. I thank Bruce and Jane for patiently letting me explore my ideas, discover my interests, and especially for being supportive when I needed help. In different ways, both contributed much to my personal and professional growth. I am especially grateful to Jane for her help in developing a conceptual framework for this thesis, and to Bruce for help with analysis. Stimulating discussions, and advice from Mark Hixon, Stan Gregory, and Fred Menino helped me develop my interests, and helped me to appreciate the broader field of ecology. Annette Olson, Terry Farrell, and Peter van Tamelen helped me form my ideas, and ensured that I got wet on the shore at an early point. Their friendship, and support made a difference to graduate school. Their intellectual caliber contributed greatly to my thesis. Discussions with Brian Tissot, Dave Booth, Liz Walsh, Denise Idler, Andrea Larson, Claire Fuller, Eric

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ENVIRONMENTAL FACTORS AND PLANT-ANIMAL INTERACTIONS ON ROCKY SHORES ALONG THE OREGON COAST.

CHAPTER I
INTRODUCTION

The effects of environmental variation on the outcome of species interactions, and the persistence of communities is still relatively unknown, although it has been long appreciated that variations in environmental factors affect the importance of species interactions (e.g., Connell 1961, Grime 1979, Huston 1979, Menge and Sutherland 1976, 1987). This thesis examines the occurrence of variations in interaction outcomes, and their potential effects on a marine community. The study focuses on how changes in temperature can affect the outcome of mussel-epibiont interactions, and how this in turn can affect the persistence of a diverse mussel-bed assemblage. I also consider the factors that affect the establishment of the epibiont community itself. The effects of trampling (a physical stress) on the persistence of a mussel and algal community is also examined. This includes the effects of trampling on the ability of mussels and other species to recover from disturbance.

The ecology of mussels had been much studied. Mussel abundance, and distribution can be determined by predation (Paine 1966, 1974, 1980, Lubchenco and Menge 1979, Menge 1976, 1978a), competition (Harger 1972, Suchanek 1978, Petersen 1984b), and disturbance (Harger 1970, Harger and Landenberger 1971, Dayton 1973, Paine 1979, Paine and Levin 1981). The relative importance of these interactions can vary along an exposure gradient (Lubchenco and Menge 1978, Menge 1976, 1978b). Mussel-epibiont relationships have not been studied under different conditions. Evidence suggests that epibionts, growing on mussels, harm mussels by increasing their risk of mortality (Suchanek 1979, Witman and Suchanek 1984, Dittman and Robles 1991). However, there is little information on the strength and overall importance of this interaction to mussels, and to the species living associated with mussels (termed matrix species; Suchanek 1979).

Environmental conditions can impose stress on species and communities. Below I define stress, and discuss its potential impacts on species interactions, and communities.

Gradients in environmental factors occur in all communities and habitats (Menge and Sutherland 1987,

Stephens and Bertness 1989). At some point, an environmental factor imposes stress on a particular species. At the individual or species level, stress is defined by its adverse effects on physiological functioning, or ability to persist. Stress is often quantified by its effects on growth, reproduction or survival rates. In community ecology, environmental stress is usually described in relative terms. There is rarely an absolute definition of stress in a community because individual species respond differently. In addition, there is no quantitative measure of stress that can be applied across communities.

One way to understand the effects of environmental stress would be to carry out transplant studies of each species, and species combinations under the entire range of individual and combined stresses. However, this is not practical. As a result we are often faced with defining stressful conditions in terms of their effects on the dominant or most abundant species in a community, or on a trophic level (e.g., Oksanen et al. 1981, Menge and Sutherland 1987). Differential responses among species to the same level of a particular environmental factor (e.g., wave force) can lead to different patterns of community structure and regulation.

In this thesis I consider that stress results from variation in physical or physiological conditions which affect physiological responses, and survival abilities of individual species. In turn, differential responses to environmental factors among species can affect the occurrence and outcome of species interactions.

Broadly speaking, environmental factors can cause two main types of stress (Menge and Sutherland 1987): Physical stress is caused by physical factors in the environment. These include wave force, wind velocity, floods and debris flows in streams, and avalanches. Physical factors can have either no effect on a species, impose a sublethal stress which can be energetically costly (e.g., in wave exposed areas mussels produce more byssal threads to anchor themselves to the substrate (Price 1980, 1982)), or result in death (e.g., the dislodgment, and subsequent death of organisms). Physiological stresses are caused by environmental conditions such as temperature, moisture, and salinity. As with physical factors, physiological effects range from negligible to lethal. The overall effects of variations in physical and physiological factors in communities depend on the magnitude and frequency of deviations from normal conditions.

Environmental factors can affect the occurrence and relative importance of particular interactions in communities (e.g., Levitan and Kohn 1980, Ortega 1985, Wiens 1986, 1988, Louda 1988). Extreme weather patterns can cause catastrophic mortality of consumers with resulting changes in the abundance and distribution of prey (Frank 1965, Sutherland 1970, Idyll 1973, Schreiber and Schreiber 1984). The relative importance of competition and predation as a function of stress has been explored in the models of Menge and Sutherland (1976, 1987). The Menge-Sutherland model (1987) predicts that a low diversity assemblage will persist towards the extremes of an environmental gradient. This assemblage will be composed mainly of stress-resistant, sessile species, whose composition is regulated by environmental factors. As environmental factors become less stressful, competition and predation are predicted to regulate intermediate and basal species, while competition regulates top consumers. Some empirical evidence supports these predictions (Menge and Farrell 1989).

Gradients in environmental factors can affect the outcome of species interactions (c.f. interaction norms of evolutionary studies, defined as the range of interaction

outcomes among environments (Thompson 1982, 1988)). In marine intertidal communities, interactions between adjacent populations of barnacles and mussels can range from exclusion of barnacles by mussels (negative interaction), to protection of barnacles from heat stress by mussels (positive interaction) (Stephens and Bertness 1991). Changes in interaction outcomes between two species have been noted, or suggested in marine and terrestrial habitats in response to moisture (Pickett et al 1979, Rice and Menke 1985), nutrients and light (Lewis 1973, Muscatine and Porter 1977, Holl 1983, Bowen 1980, Martinez et al 1983, Boryslawski and Bentley, 1985, Tilman 1982, 1987, Wilkinson 1987), and CO_2 concentration (Bazzaz and Carlson 1984).

Although the evolutionary consequences of varying interaction outcomes have been explored (Thompson 1982, 1985 a, b 1988), ecological consequences have received far less attention. Few studies in interaction reversals, or changes in outcomes along gradients have been carried out in the field (Thompson 1988). Furthermore, the community-wide implications of changes in interactions outcomes have rarely been explored. The importance of these changes in interactions will depend on the strength of the interaction, and the frequency of its occurrence (which is

in turn affected by the frequency, and magnitude of environmental changes).

One species can mediate the effects of environmental stress on another species (Bertness and Callaway 1994). Species interactions could potentially increase or decrease the perceived stress on the interacting species. For example, Witman and Suchanek (1984) noted that algal epibionts, growing on mussels, increase drag on mussels. As a result, wave forces that do not dislodge an uncolonized mussel, can dislodge a mussel colonized by epibionts. Similarly Strong (1977) suggested that lianas increase the risk of uprooting of tropical trees in wind-storms.

In other situations, a species can buffer another species against environmental stress. For instance barnacles provide a less physiologically stressful environment for algal spores, and this interaction can be an important factor in the development of an algal assemblage (Farrell 1989, 1991, Johnson 1989). Depending on the frequency and magnitude of environmental changes, all these types of mediating-interactions (which increase or decrease stress), may have important community

consequences, particularly if they affect dominant species.

One consequence of stress in communities may be disturbance, defined as a loss of biomass (Sousa 1984). Disturbance can affect community composition, and start a successional process (Connell and Slatyer 1977, Connell 1978, Pickett and White 1985). Some early successional environments are stressful for intermediate and late successional species. In these circumstances, facilitation by early successional species (Connell and Slatyer 1977, Sousa 1979, Farrell 1989, 1991) or habitat alteration (Connell and Slatyer 1977, Bertness and Callaway 1994) may be key elements in succession.

This thesis focuses on the role of environmental factors (physical and physiological) on species interactions and community structure. Chapter II is a study of interaction outcomes between a mussel and its algal epibiont, under both extreme weather and normal weather patterns.

Chapter III describes an experimental study on the development of the epibiont community on mussels. Many of the species that occur as epibionts on mussels also occur

on rock substrate. Mussels, because they have a smooth surface, and are elevated from the surrounding substrate, represent a different type of habitat and environment.

Chapter IV reports experimental study on the effect of trampling on the persistence of mussel and algal communities. These communities are subject to natural disturbance from physical forces such as wave shear (Dayton 1971, 1973, Sousa 1979, Paine 1979, Paine and Levin 1981). Trampling, because it imposes an additional physical stress, may alter the pattern of natural disturbance and community structure. This chapter has been recently published: Brosnan, D. M. and L. L. Crumrine. 1994. Effects of human trampling on marine rocky shore communities. Journal of Experimental Marine Biology and Ecology, 177:79-97.

CHAPTER II
EFFECTS OF ENVIRONMENTAL STRESS ON THE OUTCOME OF
INTERACTIONS BETWEEN ALGAL EPIBIONTS AND MUSSELS

ABSTRACT

Models of community dynamics predict that
environmental conditions can affect the relative
importance of different interactions in communities. In
addition, the outcome of the interaction between two
species may change as environmental conditions alter. This
study focuses on the relative importance, and nature of
the interaction between a mussel (Mytilus californianus),
and its algal epibiont (Endocladia muricata).

Under normal conditions, Endocladia had weak negative
effects on mussels. Endocladia increased drag on mussels
by about 50%. In the field, high neighborhood mortality
and winter storms significantly increased the dislodgment
of mussels colonized by Endocladia (termed + epibiont
mussels). + epibiont mussels had significantly lower
length-weight ratios than mussels without Endocladia
(termed -epibiont mussels). In laboratory experiments +
epibiont mussels produced more byssal threads.

The beneficial effects of Endocladia on mussels were
also investigated. Positive effects of Endocladia on

mussels were observed in 1989 and 1990/1, when northerly storms resulted in sub-freezing temperatures at the coast. In both years, mortality of - epibiont mussels was high (up to 97% on some shores), while mortality of + epibiont mussels was significantly lower (approximately 20-30%). Laboratory studies suggested that Endocladia insulated mussels and protected them from freezing conditions. Analysis of historical temperature and tidal data, from 1931 to 1994, suggested that there have been thirteen occurrences of comparable weather conditions. These cold conditions are suspected of causing comparable large scale mortality, especially in those mussels lacking Endocladia. The frequency of conditions likely to cause mussel mortality is sufficient to be important to the ecology of mussels, which can live for at least 15 years.

In the short-term epibionts appear to have weak harmful effects on mussels, but in the long-term these are balanced by occasional strong positive effects which are important to mussels. In freezing conditions, - epibiont mussels may be lost and this can affect diversity on the shore. Under non-freezing conditions, the weak negative effect of epibionts on mussels may reduce growth rates of individual mussels, but they are unlikely to affect diversity patterns.

INTRODUCTION

The role of biological interactions in community
dynamics has been the center of much ecological research.
Throughout the 1950s and 1960s an emphasis on density-
dependence in populations led to explanations of community
structure based on competition and predation (e.g.,
MacArthur and MacArthur 1961, MacArthur et al. 1966, Paine
1966). As ecological knowledge and theory progressed,
emphasis shifted to defining the conditions under which
competition or predation would be more important
(MacArthur et al 1966, Lubchenco 1983, 1986, Sih et al
1985). At the same time, ecologists began to acknowledge a
greater role in communities for non-equilibrial factors
including disturbance (Connell 1978, Talbot et al. 1978,
Buss and Jackson 1979, Paine and Levin 1981).

Models such as those by Menge and Sutherland (1976,
1987), Connell (1978), and Sale (1978) have been
influential in our understanding of how the relative
importance of biological interactions are influenced by
environmental conditions. While predation and competition
have been the focus of much attention in studies of
biological interactions, other species interactions such
as direct facilitation, and mutualism have received far
less attention in community ecology (Bronstein 1994),

despite the strong evolutionary theory that exists for these types of interactions (e.g., Thompson, 1982, 1989, Boucher 1985, Bronstein 1994). There is no all-encompassing theory or general framework for predicting the importance of all these types of interactions in communities. However, recently Bertness and Callaway (1994) proposed that two types of positive interactions will be important under conditions of physical stress. These are neighborhood amelioration, where individuals of one species protect adjacent individuals of a second species from environmental stress, and associational defenses (e.g., a toxic plant provides a habitat for, and thereby defends a palatable prey item).

The outcome of non-trophic interactions, such as neighborhood amelioration may depend on environmental conditions (e.g., conditional-outcome interactions; Bronstein 1994). For instance, mussels protect adjacent barnacles on primary substrate from heat stress (Bertness 1989), a positive outcome for barnacles. However under less stressful temperatures, mussels may have no effect on barnacles (0 outcome), or may outcompete barnacles for space (- outcome). Thus we need to understand not only when non-trophic interactions will be important in

communities, but also the likely outcomes of these interactions.

I studied direct interactions between algal epibionts and mussels, with a focus on the importance of the nature and outcome of interactions between these species under different environmental conditions. The aim of this study was to explore the nature of interactions between species that are direct but neither competitive nor consumptive.

BACKGROUND

Mussels are one of the most studied species of mid-intertidal rocky shores in temperate regions (e.g., Bayne 1976, Gosling 1992 and references therein). They are often dominant competitors, and occupy much of the available primary substrate on many exposed rocky shores (Kitching et al 1959, Ebling et al 1964, Dayton 1971, 1973, Menge 1976, 1983, Paine et al 1985, Suchanek 1985, Seed and Suchanek 1992, and references in Gosling 1992). On the west coast of North America, Mytilus californianus is the dominant species. Its competitive interactions with other mussels (M. trossulus, previously M. edulis) and other species (notably barnacles and algae) have been extensively studied (Paine 1966, 1980, 1984, Dayton 1975, Suchanek 1980, 1981, 1985, Petersen 1984a, b, Seed and Suchanek 1992, and references therein). Likewise the importance of predation and disturbance in the ecology of Mytilus has received much attention (Paine 1966, 1974, 1979, 1980, 1984, Harger 1970, 1972, Harger and Landenberger 1971, Dayton 1971, 1973, Levin and Paine 1974, Paine and Levin 1981, Suchanek 1981, 1985, Witman and Suchanek 1984, Marsh 1986, Wootton 1993, 1994). Less studied are the species' direct interactions that do not fall within the realms of competition, predation or disturbance (but see Suchanek 1979, Witman and Suchanek

1984). For instance, mussels provide a habitat for over 300 associated species which live either directly attached to mussel shells (e.g., barnacle and algal epibionts) or within the mussel matrix (small mobile invertebrates) (Suchanek 1979).

Because mussels act as a substrate for many associated species, they often play an important and beneficial role in the ecology of these species (Dayton 1973, Laihonen and Furman 1986, Sebens 1982, Paine 1979, Lee and Ambrose 1989, Lohse 1993a, b). In turn, at least some of these species affect mussels. For instance, epibionts increase drag (Dayton 1973, Paine 1979, Witman and Suchanek 1984, Dittman and Robles 1991), and grazers living in the mussel matrix potentially benefit mussels by consuming epibionts (Suchanek 1979). However, how important these effects are to mussels, and to the ecology of mid-intertidal communities is not fully known.

This study focused on the epibionts that live attached to the valves of living mussels. Mytilus californianus is colonized by a variety of algal and barnacles species (Suchanek 1979, Sousa 1984, Witman and Suchanek 1984, Dittman and Robles 1991, Lohse 1993a, b). Previous studies indicate that these epibionts have a

harmful effect on mussels. For instance increased drag from epibionts can increase the dislodgment rate of mussels (see above). Similarly epibionts can interfere with feeding, growth, and reproduction in mussels (Paine 1976, Dittman and Robles 1991).

It is also possible that epibionts may benefit mussels. Potential beneficial effects could include protection against environmental stress. Algal epiphytes can protect seagrass against desiccation stress (Penhale and Smith 1977). In corals and subtidal bivalves, associated species often facilitate the survival of their host (by reducing their risk of predation) (Bloom 1975, Vance 1978, Barkai and Branch 1988). On primary substrate mussels can protect adjacent sessile species from environmental stress (Santelices and Martinez 1988, Bertness 1991) through neighborhood amelioration (Bertness and Callaway 1994).

This study examined the effect of algal epibionts on drag, dislodgment, byssal production and weight of mussels. It also focused on how epibionts affect mussels under harsh environmental conditions. Two periods of freezing temperatures, caused by storms of Arctic origin, that moved through the Pacific Northwest coast, allowed

for study of this effect in the field. Historical
temperature and tidal records for the Oregon coast were
examined, in an effort to determine the frequency of
severe freezes, and predict their importance in mussel-
epibiont interactions. These studies focused on the
interaction between mussels and the red alga _Endocladia_
muricata. _Endocladia_ is the dominant algal-epibiont on
mussels on many Oregon shores (Brosnan and Crumrine 1994;
and personal observation), and also on mussels in areas of
northern and central California (Sousa 1984, personal
observation).

STUDY SITES

Studies were carried out at fourteen rocky shores on the Oregon coast USA ranging from Cape Meares (45°30'N 124°02.0'W) south to Strawberry Hill (44°15'N 124°06.5'W) (Figure II.1). All shores are characterized by extensive flat or sloping benches, mainly basaltic (except for Otter Crest which is composed of sandstone benches). The marine community at each of these sites, is typical of outer-coast rocky shore assemblages (as described by Kozloff 1983). Mussels (<u>Mytilus californianus</u>) dominate the mid-intertidal zone. Gooseneck barnacles (<u>Pollicipes polymerus</u>), acorn barnacles (<u>Balanus glandula</u> and <u>Chthamalus dalli</u>), and a variety of algal species are found in patches interspersed among mussel beds. Predatory starfish (<u>Pisaster ochraceus</u>) and whelks (<u>Nucella emarginata</u>) are common, and shorebirds sometimes feed among the mussel beds. For a more complete description of these sites see Turner 1985, Marsh 1986, Farrell 1989, McCrae and Osis 1989, Menge et al 1994.

METHODS

Effect of epibionts on drag and dislodgment

In this study effect of drag on mussels at different water velocities were measured in the laboratory. This study was carried out as part of ongoing work on dislodgment in the field, and also in collaboration with C.A. Blanchette, and formed part of her class project on thermal stress in mussels at Friday Harbor Laboratories, Washington (Blanchette 1990). Results were then related to hydrodynamic forces acting on mussels in the field. I measured the forces required to dislodge mussels to determine if the presence of <u>Endocladia</u> can affect the dislodgement of a mussel. I subsequently conducted a series of experiments to study dislodgment rates of mussels.

Drag

We measured drag forces in a flow tank by attaching mussels to a strain gauge connected to a voltage output. A force applied parallel to the strain gauge deflected the force beam, and this in turn caused a change in electrical resistance which was recorded as a voltage signal

Figure II.1 Location of study sites

Figure II.1

46 N

Cape Meares
Maxwell Point

Fogarty Creek
45 N Boiler Bay
Whale Cove
Otter Crest
Yaquina Head ● Newport

Seal Rock

N. Headland Yachats
Yachats South Park
Devils Churn
Neptune
44 N
Strawberry Hill
Bob Creek

Pacific Ocean
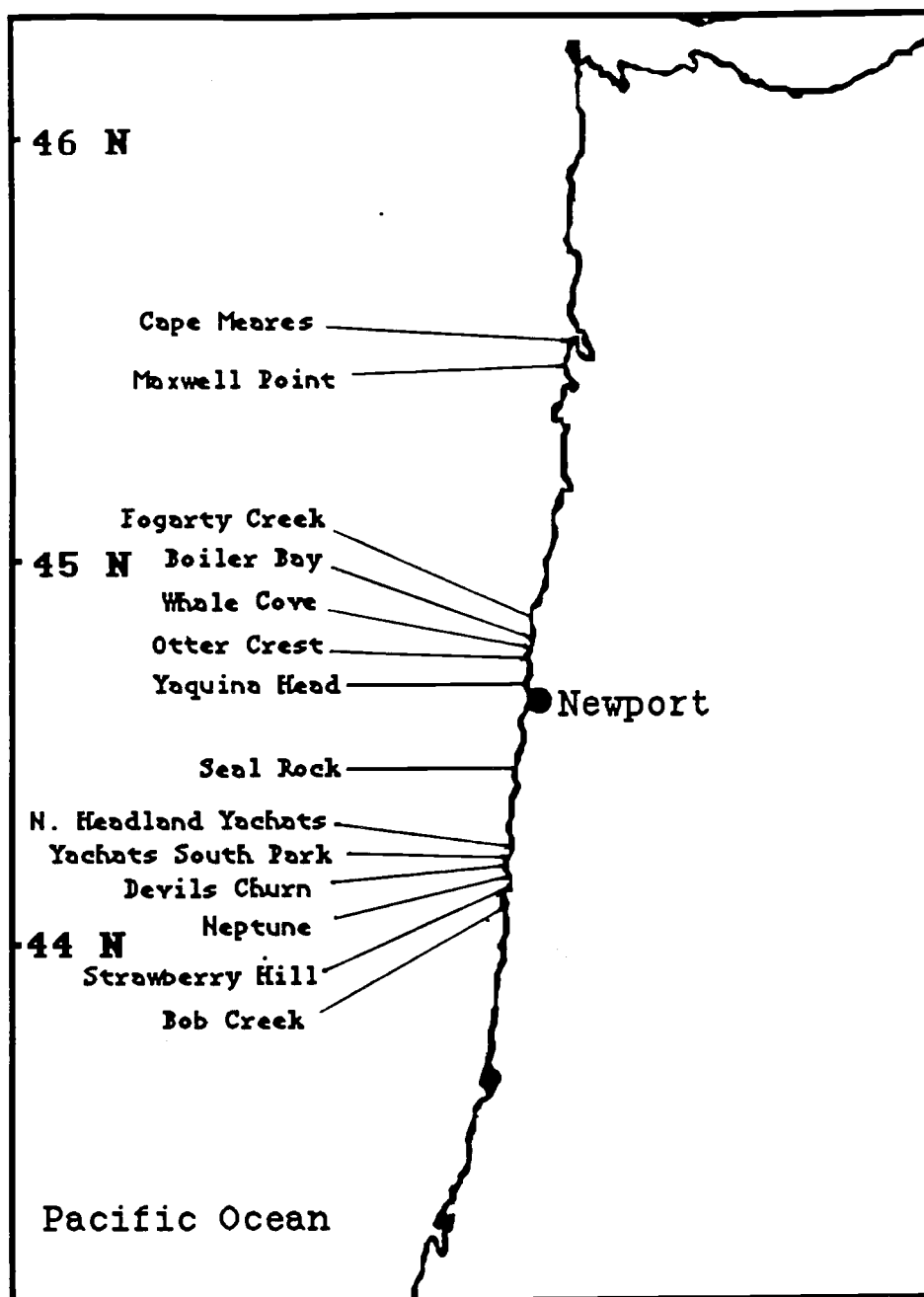
proportional to the force applied to the transducer. The force beam was calibrated by hanging known weights from the beam. Drag forces on individual mussels were measured by attaching a mussel covered with <u>Endocladia</u> to the force beam with a rubber band (Figure II.2). Drag forces on the mussel were then measured at four velocities: 0.091 m.s^{-1}, 0.29 m.s^{-1}, 0.49 m.s^{-1}, and 0.58 m.s^{-1}. Tank water velocities were recorded using a Marsh-McBirney electromagnetic flowmeter. At each velocity, drag measurements were recorded four times for each mussel and the average value for each velocity was calculated. The mussel was removed from the tank, and <u>Endocladia</u> scraped off its shell. Drag forces were then re-measured on the same mussel without <u>Endocladia</u> using the same procedure.

Analysis

Regression analysis (Systat, Wilkinson 1991) was used to describe the relationship between velocity and drag for mussels with and without <u>Endocladia</u>, and to test for the effect of <u>Endocladia</u> on drag forces.

Mussel Dislodgment.

This study measured the total force required to
dislodge individual mussels from mussel beds at Little
Whale Cove (N=38) in August 1990, and at Boiler Bay (N=52)
in June 1991. At each site, mussels were randomly chosen
by tossing a coin onto the mussel bed, and choosing the
mussel underneath the coin. A small hole was drilled at
the edge of the posterior end of one of the valves, and a
fish-hook inserted through the hole. The hook was attached
to a spring-balance. The mussel was then pulled in one
direction horizontal to the substrate. The main
hydrodynamic forces act on mussels in a horizontal
direction (M. Denny, Hopkins Marine Laboratory, personal
communication). The amount of force required to dislodge
the mussel, as measured by the spring balance, was
recorded, and shell length of the dislodged mussel was
also noted. Length was subsequently regressed against the
force required to dislodge a mussel at each site, to
 determine if size affected attachment strength (e.g.,
Harger and Landenberger 1971).

Mussel Dislodgment: Effect of Epibionts and Mortality

Storms and logs dislodge mussels and create patches
within mussel beds (Dayton 1971, Harger and Landenberger

Figure II.2 Experimental set-up for measuring drag forces on mussels in a laboratory flow tank. Individual mussels (colonized by <u>Endocladia</u>) were attached to a force beam. Water flowed in a unidirectional path across the tank. Drag caused the force beam to deflect in proportion to the total drag forces acting on the mussel. Drag measurements were made at four different velocities. <u>Endocladia</u> was subsequently removed, and drag forces re-measured on mussels without <u>Endocladia</u> at the same four velocities.

Figure II.2

To Voltage Outlet

Force Beam

Mussel

Endocladia

Direction of flow
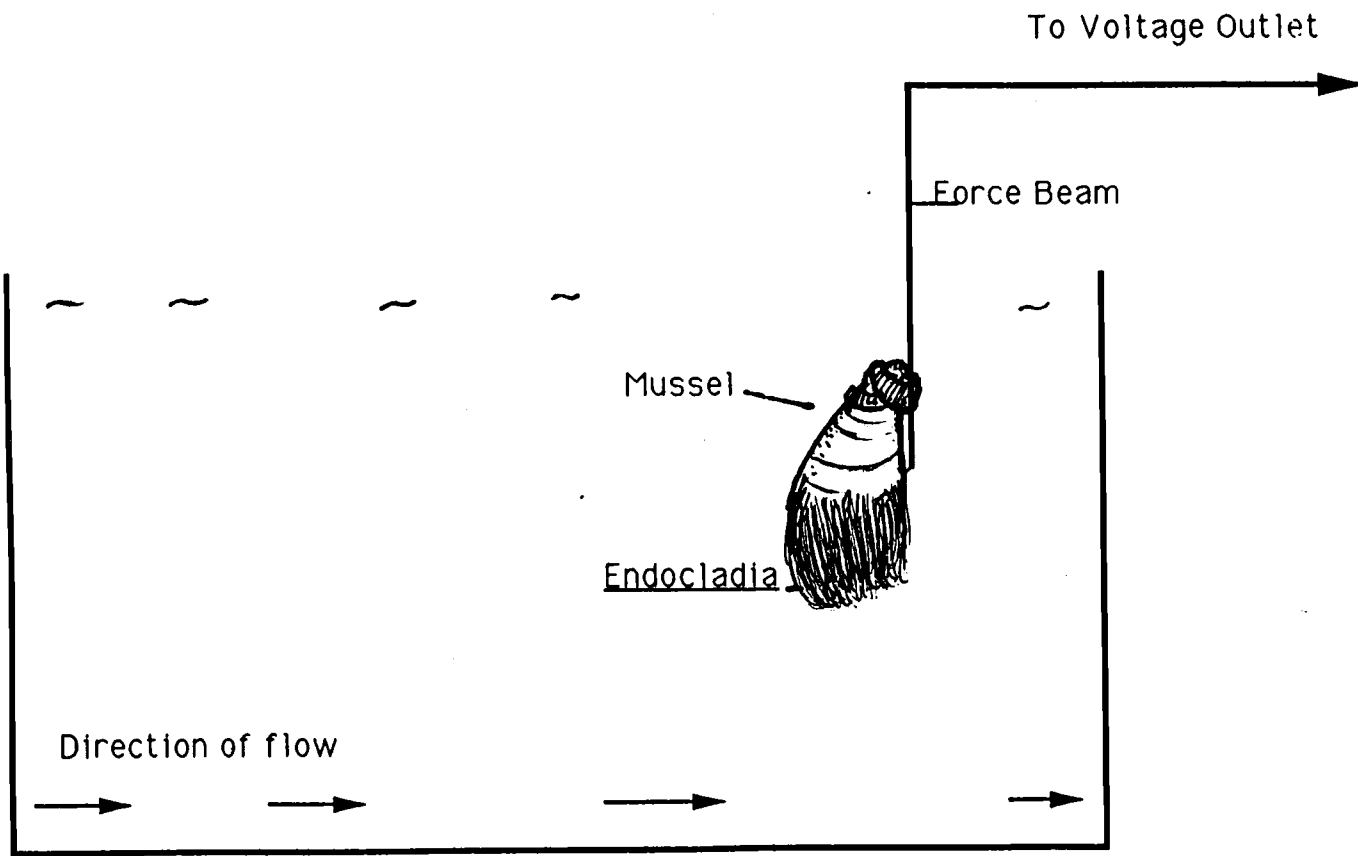
1971, Paine and Levin 1981). Inherent weakness in a mussel bed can increase the risk of dislodgment (e.g., multi-layered beds, poor attachment strength, the presence of empty shells, and small gaps caused by predation) (Harger 1970, Paine and Levin 1981). In addition, the presence of epibionts can also increase the risk of dislodgment (references above). Few studies have directly studied the effect of epibionts on dislodgment rates in the field (but see Dittman and Robles 1991). There have been no reports on how the effect of epibionts might vary with the condition of a mussel bed, specifically how epibiont cover and integrity of a mussel bed interact to affect dislodgment rate.

This series of experiments, compared the rate of dislodgment of + epibiont mussels, and - epibiont mussels from natural (undisturbed beds), and beds where the degree of mortality in the mussel bed was manipulated.

A factorial experimental was chosen to study the effect of two factors on dislodgment: the effect of mortality level, and the effect of colonization by Endocladia. Groups of one-hundred mussels were randomly selected within existing mussel beds. To create variation in mortality, mortality was manipulated in each group as

follows: by randomly (using random numbers) killing, but
not removing, 0%, 10%, 25%, 50%, 75%, or 90% of mussels in
each group of one-hundred mussels (Figure II.3). Mussels
were killed by inserting a knife through the adductor
muscle so that the shells gaped-open. This mimics natural
mortality, which does not involve removal of the mussel
from the bed, an event that occurs commonly, judging from
the regular occurrence of gaping mussel shells still
present in mussel beds. Higher mortality levels were
intended to mimic the effect of harsh environmental
factors on mussels, such as freezing or heat stress
(Suchanek 1978, Peterson 1979, Tsuchiya 1983).

To create differences in epibiont cover, Endocladia
was removed from mussels in one set of replicate plots,
and left on living, but not dead, mussels in another set
of plots. This experiment was repeated three times, twice
at Fogarty Creek, and once at Boiler Bay further to the
south. In experiment one, which ran from June to October
1990, at Boiler Bay, there were ten replicates each for
0%, 10%, 25%, 50% and 75% mortality, and 20 replicates for
90% mortality (because the number of living mussels in
each group at 90% mortality was low) (Total number of
mussels used in experiment one was 14,000). Each mussel
was marked using non-toxic model paint (Testers).

Different colors were used for living and dead mussels. In each plot the number of live mussels remaining was recorded after 14 days, 30 days, and 90 days, to calculate the dislodgment rate under different mortality levels. Experiment two began in February 1991, and used 0%, 10%, 50%, and 90% mortality levels, with the same number of replicates per treatment as above (Total number of mussels used in this experiment was 10,000). Experiment two was monitored at 18 days, 35 days and 50 days after initiation. Experiment three was carried out at Boiler Bay, and began in July 1991 using 0% and 90% mortality levels only (Total number of mussels used in experiment three was 6,000). Experiment three was monitored after 14 days and 28 days.

Analysis

Data from each experiment were analyzed separately. Raw data were analyzed for normality using probability plots. Data were analyzed by two-way repeated measures ANOVA (RMANOVA). If the RMANOVA was significant, tests for homogeneity of variances were carried out (Bartlett's test) (Sokal and Rohlf 1981). If variances were not homogenous, data were transformed using arcsin or

squareroot transformations to reduce heterogeneity
(Underwood 1981).

Effect of algal epibionts on byssal thread production and body weight

Byssal Thread Production

Mussels anchor themselves to the substrate by producing byssal threads which they attach to the substrate. Mytilus detects and responds to increased wave energy and drag forces by producing more byssal threads (Pieters et al 1978, Price 1980, 1982, Young 1985, Gardener and Skibinski 1991, Suchanek unpublished data, cited in Seed and Suchanek 1992). Additional drag from epibionts is thus likely to result in + epibiont mussels producing more byssal threads than − epibiont mussels in the same environment. Byssal thread production is costly, and often represents a significant part of the total nitrogen budget of an individual mussel (Hawkins and Bayne 1985).

The hypothesis that + epibiont mussels produce more byssal threads than − epibiont mussels was tested under laboratory conditions. Byssal thread production was measured in the laboratory. Both exposure and mussel size

Figure II.3 Experimental design to test the effects of <u>Endocladia</u> and mortality on dislodgment rates in the field. Groups of one-hundred mussels within a mussel bed were randomly chosen. Each group received one of the following mortality treatments; no mortality, 10% 25% 50% 75% or 90% mortality. Filled circles = dead mussels; open circles = live mussels. In the + epibiont groups, live mussels were colonized by <u>Endocladia</u>. In the - epibiont groups live mussels were without algal epibionts.10% = 10% mortality, etc.

Figure II.3

% Mortality

% Mortality

0%
(10
reps)

10%
(10
reps)

25%
(10
reps)

50%
(10
reps)

75%
(10
reps)

90%
(20
reps)
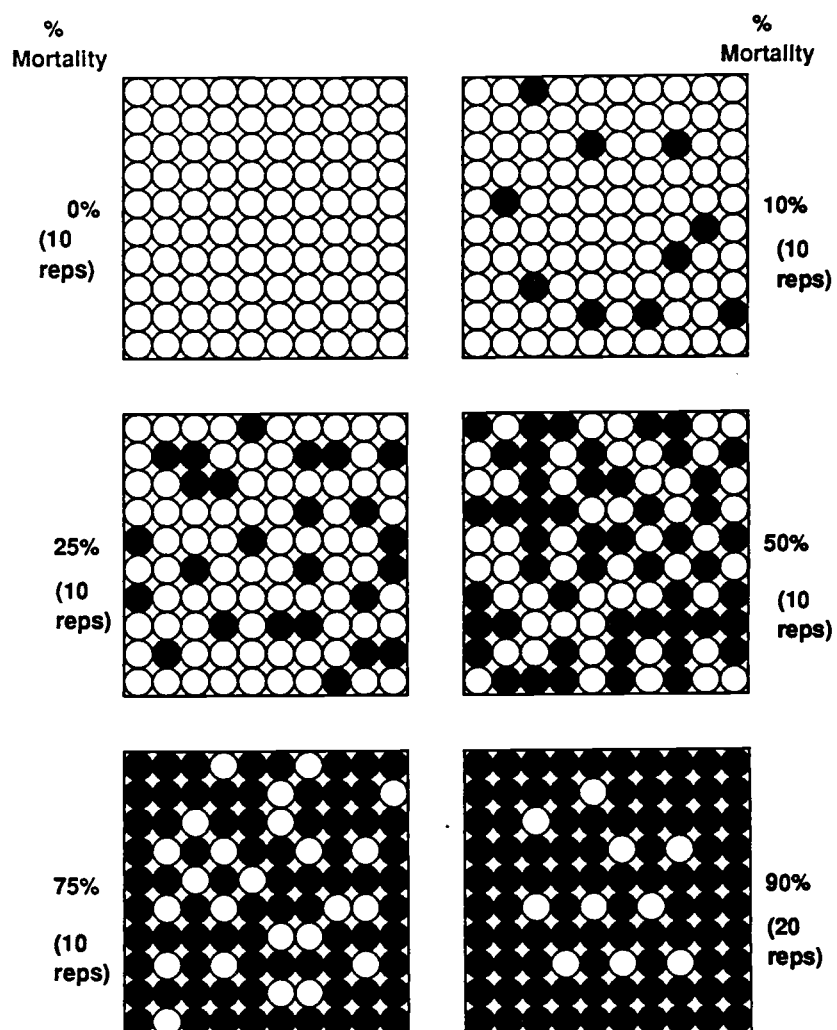
can influence byssal thread production (Price 1980, 1982). Therefore in an effort to standardize pre-experiment conditions, similarly sized mussels were collected from the same 0.25 x 0.25 m plot in the same bed. Mussels were randomly placed in a glass flow tank at a water velocity of 0.25 m.s^{-1}. The number of byssal threads produced by + epibiont mussels and - epibiont mussels were counted over twelve hours. This experiment was carried out twice. The first trial used 27 mussels ranging from 54-60 mm in length. The experiment was subsequently repeated using 50 freshly collected mussels, ranging in size from 50-56 mm.

Effect of epibionts on body weight of mussels

Previous studies indicate that epibionts reduce the growth of mussels (Paine 1976, Dittman and Robles 1991) Epibionts may interfere with feeding (Paine 1976, Seed and Suchanek 1992), and, because + epibiont mussels need to anchor themselves more firmly to the substrate, epibionts may limit energy available for somatic and reproductive growth. In both cases a + epibiont mussel is predicted to have lower body weight than a comparable - epibiont mussel. Paine (1976), for instance, found that the body weight of mussels colonized by sessile invertebrates was

generally lower than - epibiont mussels in a subtidal
population. I tested this hypothesis in my study, by
comparing the body weight of - epibiont and + epibiont
mussels of the same size, and from the same habitat.

Mussels were collected from Boiler Bay and Little
Whale Cove in January 1990 and from Fogarty Creek in
February 1990 (Figure II.1). At each site, mussels were
collected from a 30 x 30 cm area in an existing mussel
bed. Mussels were collected in pairs, i.e., a + epibiont
mussel and an adjacent - epibiont mussel of the same size.
The surface of each + epibiont mussel was 40%-50% covered
by <u>Endocladia</u>, and <u>Endocladia</u> overgrew the posterior
margins of the shell to a height of 1.5-2 cm above the rim
of the mussel. In the laboratory, shell length of each
mussel was measured. Mussels were subsequently dried to a
constant dry weight (24-48 hours at 60°C).

Analysis

Least squares regression analysis was carried out on
shell length to dry weight ratio for + epibiont and for -
epibiont mussels. Covariance analysis was subsequently
carried out on dry weight using presence/absence of
<u>Endocladia</u> as the independent variable, and shell length
as the covariate. Before analysis of covariance, tests for

heterogeneity of slopes were made between the covariate (length) and treatment (presence/absence of <u>Endocladia</u>) to determine if there was an interaction between length and presence of epibionts. Analysis was carried out using SYSTAT (Wilkinson 1990).

Mussel Survival After Freezing: Field Studies

In general the effect of algal epibionts on mussel growth and survivorship is considered to be negative (Suchanek 1979, Paine 1979, Dayton 1973, Witman and Suchanek 1984, Dittman and Robles 1991). However, algal epibionts may also protect mussels from environmental stress. The potential facilitative effect of algal epibionts on mussels was observed in the field during two severe winters. This effect was also tested under laboratory conditions.

In February 1989, and in January 1991 severe storms occurred on the coast of the Pacific Northwest USA. Temperatures fell to $-12^{\circ}C$ in 1989, and to $-14^{\circ}C$ in 1991. During this time snow lay on the shore for over 7 days in Washington, Oregon, and Northern California (personal observation, S. Rumrill, Oregon Institute of Marine Biology, personal communication). On the central Oregon

coast, temperatures on the shore fell to below freezing for ten to fourteen consecutive nights (US Department of Commerce, 1989, 1991). These periods of freezing temperatures coincided with evening spring low tides and calm seas.

Within three weeks of the storm, I monitored survivorship of + epibiont and – epibiont mussels on the shore. Because the most common algal epibiont on mussels was the red alga _Endocladia muricata_, results refer mostly to the effects of _Endocladia_ on mussels.

1989 Storm

During February and March 1989, mortality and overgrowth patterns were recorded at fourteen shores on the Oregon coast (from Cape Meares to Bob Creek, Figure II.1). To estimate the percentage of mussels on a shore colonized by algal epibionts, mussels were sampled in ten to fifteen 0.25 m^2 quadrats at each site. Quadrats were placed at 1.0 m (Boiler Bay) or 0.5 m intervals (all other sites) along two transect lines, extending from the upper to the lower limit of the mussel bed. Each mussel in the quadrats was scored as + epibiont or – epibiont, and as dead or alive. These data were used to determine the

extent of mussel mortality resulting from freezing
conditions. The relationship between the percentage of the
mussel population colonized by <u>Endocladia</u>, and the
mortality rate for each shore was also analyzed.

At three shores, + epibiont and - epibiont mussels
were randomly collected (by collecting all mussels from
within four randomly placed 0.25 m^2 quadrats at each
shore), Fogarty Creek (276 + epibiont, 481 - epibiont),
Boiler Bay (200 + epibiont, 200 - epibiont), and Otter
Crest (110 + epibiont, 89 - epibiont). On the same day,
and in the laboratory, the number of dead and alive
mussels in each group were counted.

1991 Storm

During January and February 1991, I surveyed mussels
on twelve shores for mortality and overgrowth patterns.
The technique used was similar to that described above.
However, rather than collecting mussels for analysis in
the laboratory, mussels in ten to twenty 0.25 m^2 randomly
placed quadrats were counted. Each mussel was scored as +
epibiont or - epibiont, and as dead or alive.

Analysis

Least square regression analysis (Sokal and Rohlf 1981) was used to test whether the relationship between percent epibiont cover and mussel survivorship was significant in 1989 and in 1991. To test the hypothesis that mortality of + epibiont mussels differed from - epibiont mussels within a shore, data from each shore were analyzed, in 1989 and in 1991, using a G test with Williams q correction factor (Sokal and Rohlf 1981).

Mussel Survival After Freezing: Laboratory Studies

The effect of _Endocladia_ on mussel survivorship under laboratory conditions was experimentally tested to determine whether the presence of _Endocladia_ protected mussels from freeze-induced mortality. In February 1990, 500 + epibiont mussels, and 400 - epibiont mussels were collected from Little Whale Cove. Mussel length ranged between 58-70 mm. Mussels were held in a seawater tank for one day prior to the experiment. Seawater was pumped directly from Yaquina Bay through the tanks, thus mussels received seawater at ambient temperature (ranging from $9.0-10.1^{\circ}C$ during the experimental period) and salinity (approx. $31.5^{\circ}/oo$) (i.e., approximately the same seawater conditions as they would have experienced on the shore).

Mussels, + epibiont, and − epibiont, were randomly assigned to one of two treatments; a control group (N=200), or an experimental group (N=200). The experimental group was subjected to freezing conditions. To control for possible confounding effects (e.g., genetic differences associated with presence of Endocladia), 100 + epibiont mussels were subjected to freezing conditions after removing Endocladia. Experimental mussels were placed in twelve plastic trays (each tray contained 50 mussels).

Mussels were covered in ice, and placed in a freezer at an initial temperature of 4°C which dropped to −12°C within 3 hours. Mussels were left in the freezer for a total of six hours, the approximate time they would be out of water at low tide. After six hours exposure, mussels were re-immersed in sea water in the flow tanks for a further six hour period. This procedure was repeated twice more. The control group were treated similarly, except that they were exposed to ambient air temperatures, not freezing temperatures. During the six hour periods that experimental mussels were in the freezer, water was drained from the tanks to expose the control mussels to air, and I followed this with six hours immersion. This

replicated the tidal immersion-emersion cycle that mussels experience in the field. After treatment, mussels were held in flow tanks, and mortality in control and experimental groups was monitored for a further ten days.

Analysis

G test with Williams q correction (Sokal and Rohlf 1981) was used to test for differences in mortality among groups.

Insulatory effects of **Endocladia**

Algal epibionts may protect mussels from freezing conditions by insulation. If so, then + epibiont mussels would be expected to have higher (or lower) body temperatures during cold (or warm) conditions than - epibiont mussels. These predictions were tested in the laboratory (for cold conditions) and in the field (in hot weather).

To test the effect of Endocladia on mussel body temperature, + epibiont, and - epibiont mussels, ranging in length from 48 to 71 mm. were collected from Fogarty Creek in March 1990. One hundred and fifteen mussels were

placed in trays in a freezer at -10°C for 6 hours. Body
temperatures were measured after 40 min., 80 min., 120
min., and 360 min. Body temperature was monitored using an
Infra-red thermometer (Everest Co. Illinois), by
destructively subsampling from each group. The valves were
separated, and the average of four body temperature
measurements was recorded for each mussel. Mussels were
not replaced in the freezer after monitoring, and thus
different mussels were used at each time period. 36
mussels were sampled after 40 min., 40 mussels after 80
min., 20 mussels after 120 min. and 18 mussels after 360
min.

In a second experiment I compared body temperatures
of -epibiont mussels (N=27), mussels colonized by
Endocladia (N=26), and mussels colonized by Mastocarpus
(N=18) under freezing conditions. These mussels were
placed in trays in a freezer at -12°C. The body
temperature of each mussel was recorded after 60 min.,
using the method described above.

Field studies

On three sunny days in May, July, and August 1990,
internal body temperatures of -epibiont and + epibiont
mussels were recorded at three sites, Fogarty Creek,
Boiler Bay and Otter Crest. Temperatures were measured as
described above for a total of 210 mussels. Temperatures
were monitored between 11.00 a.m. and 2.00 p.m., (i.e., 2
- 3 hours after low tide). Air temperatures on the shore
ranged from 20-21.5^{0}C in the sun. Substrate temperature at
the edges of the mussel bed was also noted at the same
time.

Frequency of occurrence of positive interactions

To understand the importance of positive interactions
to the ecology of mussels, I attempted to determine the
frequency of conditions that could result in positive
interaction outcomes between epibionts and mussels.
Because the sign of interaction is apparently affected by
temperature conditions, daily tidal predictions and
temperature records gathered from 1931 at South Beach
Oregon (US Department of Commerce, 1931-1994) were
analyzed. The criteria for determining the conditions that
affect the sign of the interaction between epibionts and
mussels, were based on results from experiments carried

out in this study (i.e., which temperature conditions
cause mussel mortality), and are described more fully in
the appropriate results section.

RESULTS

Drag and dislodgment

Drag forces on mussels colonized by Endocladia were significantly higher at all four velocities (F=14.9, p=0.001). Endocladia increased drag forces on a mussel by approximately 50% (Figure II.4). Based on regression analysis from laboratory results (see Figure II.4 legend for regression equations), results of laboratory studies were extrapolated to estimate drag forces in the field at water velocities of 10 m.s^{-1} (M. Denny, Hopkins Marine Laboratory, personal communication). Velocities of this magnitude are not uncommon on exposed shores in the Pacific Northwest (Denny 1988). At 10 m.s^{-1}, drag forces on + epibiont mussels will exceed 29 N compared to 18.5 N on − epibiont mussels. These values are within the range of forces required to dislodge mussels from the shore (see data below).

Based on attachment strengths, drag forces at much lower velocities (e.g., 5 m.s^{-1}) could result in dislodgment. In studies on attachment strength of mussels at Little Whale Cove and Boiler Bay, dislodgment forces ranged from <5 N to 135 N.(Figure II.5). At Little Whale Cove larger mussels were more firmly attached than smaller

ones (F=19.76, p=0.01) (Figure II.5). However the
relationship between size and attachment strength was not
significant at Boiler Bay (F=2.1, p=0.12) (Figure II.5).
In many cases, when a mussel was dislodged two to three
neighboring mussels that were anchored to it were also
ripped out. This observation combined with the wide
variability of attachment strengths of mussels in the same
bed, suggests that the spatial arrangement of mussels in
the mussel bed has an important effect on dislodgment
rates.

Dislodgment of + epibiont and - epibiont mussels in the
field.

Endocladia increased the dislodgment rate of
mussels in all three experiments. However, the effect of
Endocladia was different at high and low mortalities
(interaction term Table II.1). More live + epibiont
mussels were lost at higher mortalities than at lower
mortality. (Figures II.6-II.8). For example, in beds where
mortality was high (e.g.,, 75% or 90% mortality rate),
more living mussels were lost from the bed within two
months than in beds with lower mortality (Figures II.6,
II.7. Table II.1). This is predictable because an
individual mussel is exposed to stronger wave action at
higher mortalities as dead shells are lost. In addition,

Figure II.4 Drag forces on mussels, with and without algal epibionts (<u>Endocladia</u>), measured in a laboratory flow tank. Mussels ranged in length from 30-90mm. <u>Endocladia</u> significantly increased drag (F=14.17 p=0.001 N=13 mussels) (Regression equation for + epibiont mussels Y=0.267+2.932X r^2=0.768, for - epibiont mussels Y=0.15+1.844X r^2=0.787). Error bars are standard errors.

Figure II.4
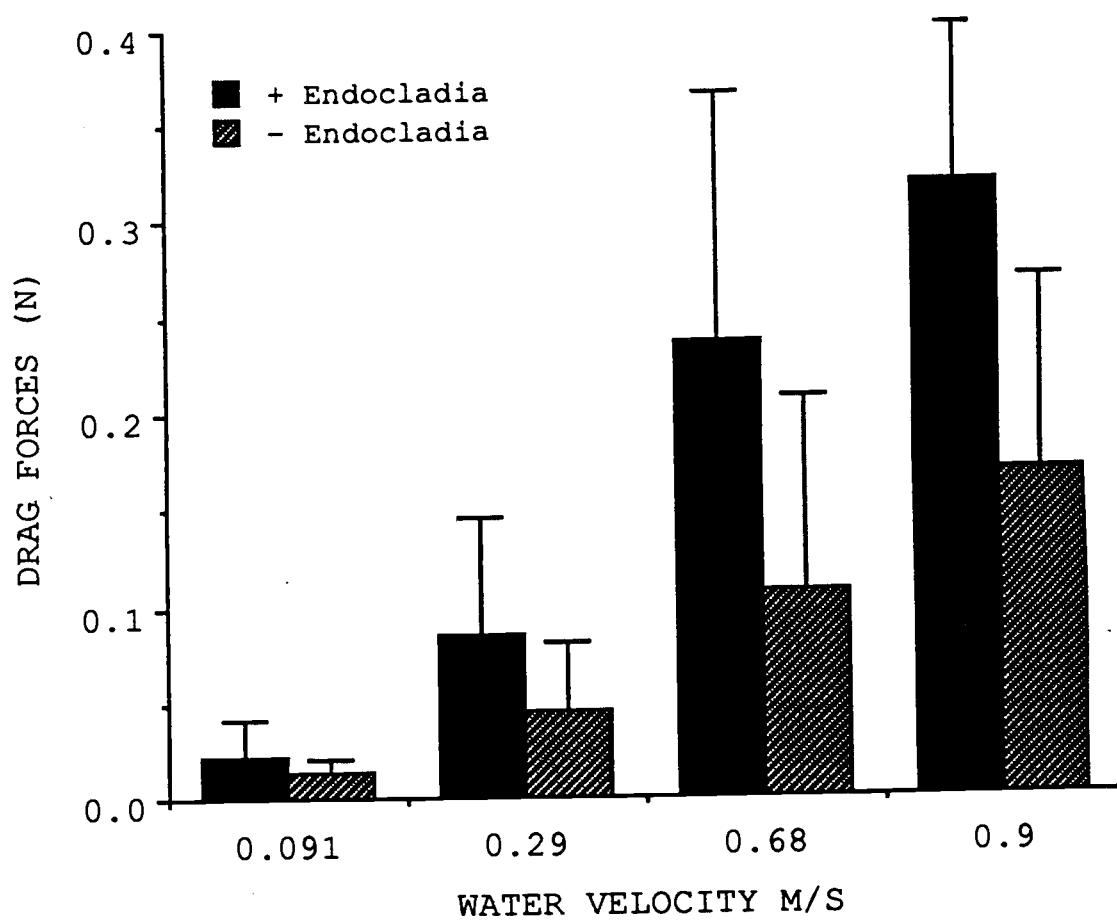
Figure II.5 Force required to dislodge mussels from the substrate. a. Little Whale Cove (August 1990). Larger mussels were more firmly attached (F=19.76, p=0.01 r^2=0.35 N=38). b. Boiler Bay (June 1991). At this site the regression was not significant, indicating that shell length was not an important factor determining attachment strength (F=2.47, p=0.12 r^2=0.04, N=57).

Figure II.5

a.

b.

DISLODGMENT FORCE (N)

SHELL LENGTH
(MM)
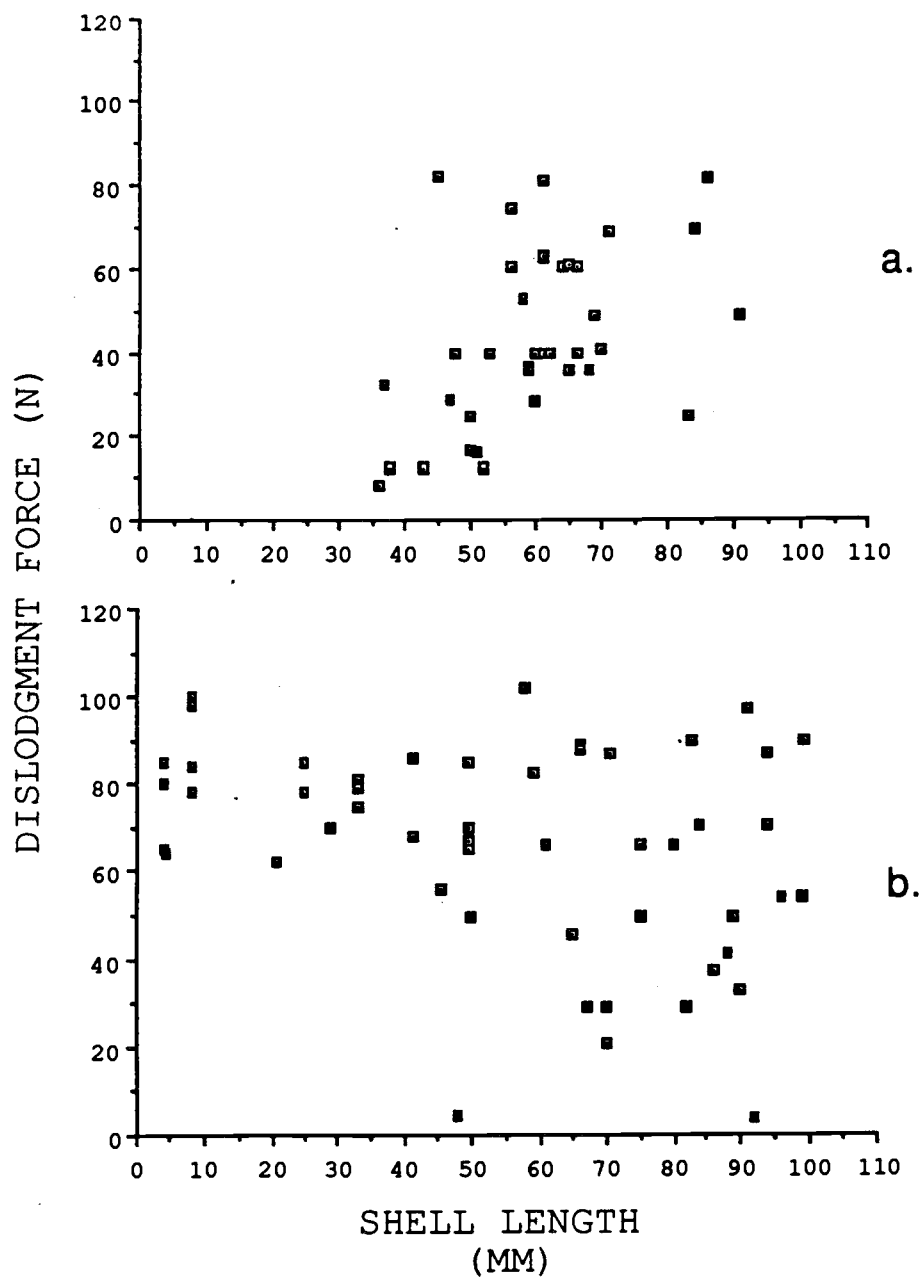
more mussels are likely to be attached to dead mussels. No mussels were lost from control beds and Endocladia had no effect on dislodgment of live mussels in relatively undisturbed beds where mortality was low (i.e., 10% mortality (p=0.23) in the first experiment (Figure II.6f); and 10% and 25% mortalities in the second experiment (p=0.9 and p=0.89 respectively) Figure II.7b, c). In the remaining treatments, where mortality was higher, Endocladia increased the rate of dislodgment of live mussels (p<0.05). This suggests that following small disturbances to a mussel bed, the presence of Endocladia does not impose additional dislodgment risk. However, if conditions in the mussel bed change, for instance, if many mussels die from environmental stress, or if clumps of mussels are removed by predation, or log damage, then + epibiont mussels are more likely to be dislodged by subsequent wave action.

Seasonality did not appear to change the overall effect of Endocladia on dislodgment risk of mussels, although it may have affected the rate of mussel loss in beds with higher mortality (50%-90%). A week after the second experiment was set up (in February 1991), there was a winter storm on the coast (with accompanying high winds and seas, but normal temperatures). The rate of

dislodgment was higher in this experiment. For instance in beds with 90% mortality, 79% of + epibiont, and 63% of - epibiont mussels were dislodged within 18 days (Figure II.7a). By comparison 39% of + epibiont and 4% of - epibiont mussels were dislodged within 14 days from 90% mortality treatments when conditions were calmer, in the June-Oct. experiment (Figure II.6a).

No evidence suggested that dislodged mussels reattach. In surveys of nearby crevices and tide pools we did not find any live marked mussels. We did however find several now dead and empty shells of mussels, which were not killed in initiating the experiment, in nearby tidepools, where the anemone (_A. xanthogrammica_), which traps and consumes dislodged mussels (Sebens 1983), were abundant.

Byssal Thread Production

In the laboratory flow tank, + epibiont mussels produced significantly more byssal threads in a twelve hour period (Figure II.9a, b). In the first experiment + epibiont mussels produced close to twice as many threads (an average of 5.2 compared to 2.8 (t=2.4, p=0.03, 26 df)). This general pattern was repeated by mussels in the

Table II.1 Summary of RMANOVA table (on transformed data) on the effect of Endocladia and mortality on dislodgment rate of live mussels.

Experiment 1. from June-October 1991 (Mortality Levels 90% 75% 50% 25% 10%).

SOURCE	SS	DF	MS	F	P	G-G	H-H
Between Subjects							
Endocladia	1.74	1	1.74	48.75	0.001		
Mortality	4.97	4	1.24	34.97	0.001		
Endocladia* Mortality	1.84	4	0.29	5.86	0.001		
Error	3.95	111	0.036				
Within treatments							
Date	2.87	2	1.45	40.51	0.001	0.001	0.001
Date* Endocladia	0.009	2	0.005	0.13	0.88	0.81	0.82
Date *Mortality	1.15	8	0.14	4.06	0.001	0.001	0.001
Date*Endocladia* Mortality	0.09	8	0.01	0.32	0.96	0.93	0.92
Error	7.86	222	0.035				

Table II.1 continued

Greenhouse-Geiser episilon = 0.72. Huynh-Feldt episilon= 0.78

Multivariate repeated-measures analysis (error df=110 for time, time*mortality, and df=220 for remaining tests)

Effect	Wilks' Lambda	hypothesis df	F	P
Time	0.62	2	33.78	0.001
Time*Endocladia	0.80	8	3.27	0.002
Time*Mortality	0.99	2	0.35	0.70
Time*Endocladia* Mortality	0.96	8	0.56	0.80

Experiment 2. February-May 1991 (Mortality Levels 90% 50% and 10%)

SOURCE	SS	DF	MS	F	P	G-G	H-H
Between Subjects							
Endocladia	1.81	1	0.81	7.42	0.008		
Mortality	39.99	2	19.99	182.6	0.001		

Table II.1 continued

Endocladia*Mortality	1.09	2	0.55	4.99	0.009		
Error	9.54	87	0.11				

Within treatments

Date	1.21	2	0.61	10.56	0.001	0.001	0.001
Date* Endocladia	0.015	2	0.007	0.13	0.79	0.78	0.78
Date *Mortality	0.09	4	0.24	0.43	0.87	0.87	0.88
Date*Endocladia* Mortality	0.03	4	0.009	0.15	0.96	0.95	0.96
Error	9.96	174	0.056				

Greenhouse-Geisser episilon=0.97. Huynh-Feldt episilon=1.0

Multivariate repeated-measures analysis (error df=86 for time, time*mortality, and df=172 for remaining tests).

Effect	Wilks' Lambda	hypothesis df	F	P
Time	0.78	2	12.06	0.001
Time*Endocladia	0.98	4	0.42	0.790
Time*Mortality	0.99	2	0.16	0.86

Table II.1   continued.

Time*<u>Endocladia</u>*	0.99	4		0.17	0.95

Mortality

Experiment 3. July-Setpember 1991. (90% mortality only)

SOURCE	SS	DF	MS	F	P	G-G	H-H
<u>Between Subjects</u>							
<u>Endocladia</u>	42.08	1	42.08	13.66	0.001		
Error	113.98	37	3.08				
<u>Within treatments</u>							
Date	6.38	1	6.38	2.80	0.13	0.12	0.13
Date* <u>Endocladia</u>	0.01	1	0.01	0.01	0.94	0.93	0.93
Error	84.25	37	2.28				

Figure II.6 Effect of mortality and epibionts on
dislodgment rate of live mussels. Experiment 1. (June-Oct.
1991). No mussels were lost from beds with zero mortality.
+ epibiont mussels; living mussels in each bed were
colonized by <u>Endocladia</u>. - epibiont mussels: living
mussels in the bed had no algal epibionts. a. 90%
mortality; b 75% mortality; c 50% mortality; d 25%
mortality; e 10% mortality.

Figure II.6
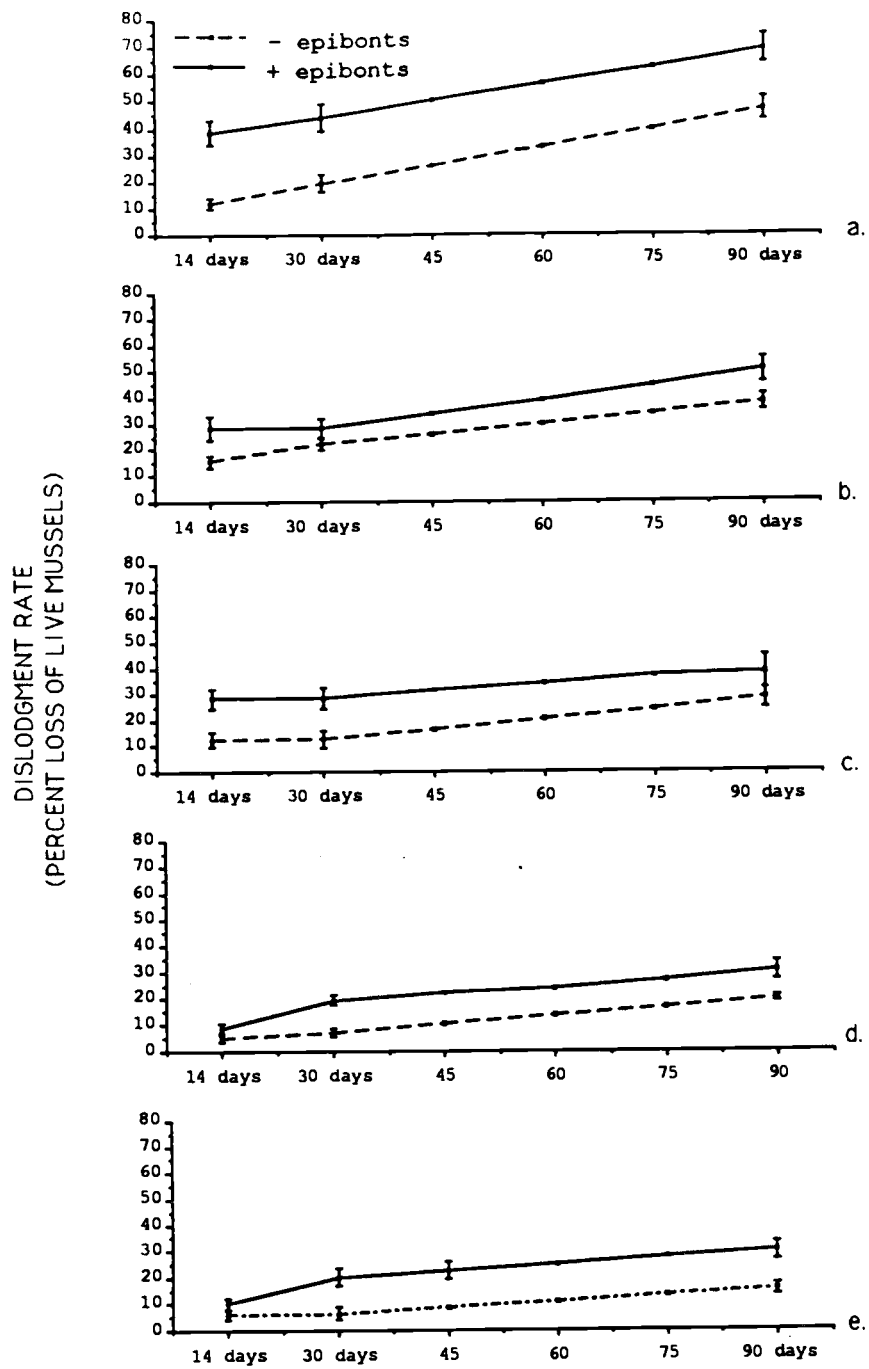
Figure II.7 Effect of mortality and epibionts on dislodgment rate of live mussels. Experiment 2. (Feb.-May 1991).No mussels were lost from beds with zero mortality. a 90% mortality; b 50% mortality; c 10% mortality.

Figure II.7
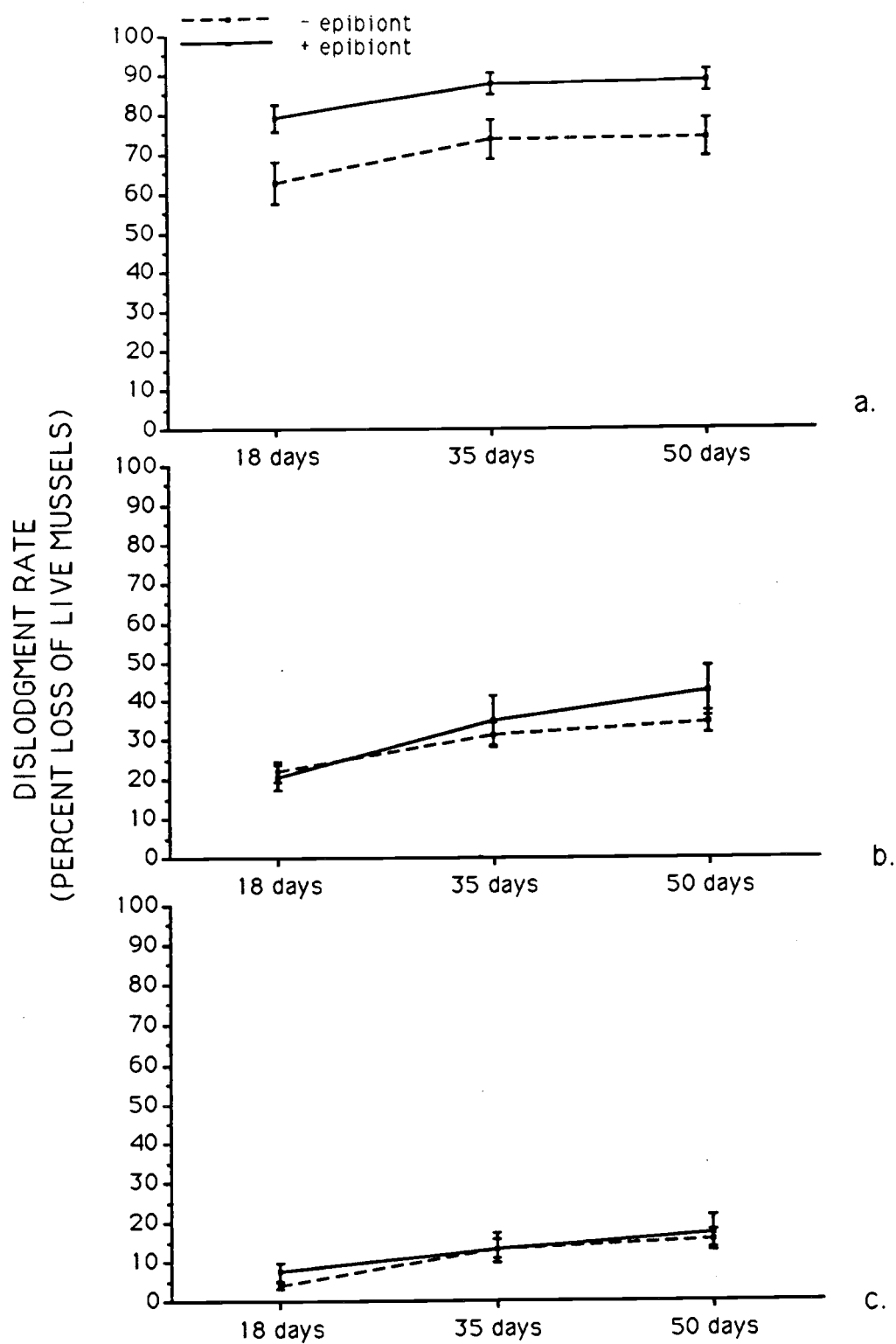
Figure II.8 Effect of epibionts on dislodgment rate of live mussels under conditions of high mortality (90% mortality). Experiment 3. July-Sept. 1991. No mussels were lost from beds with zero mortality.

Figure II.8
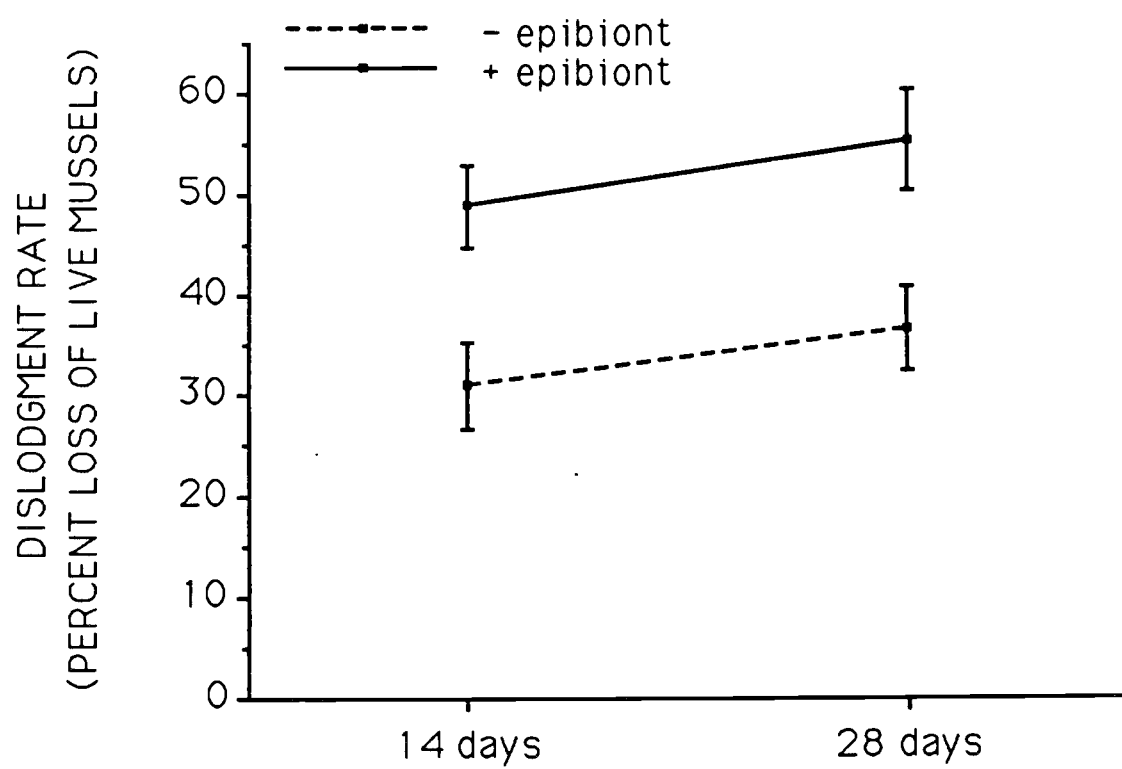
Figure II.9 Byssal thread production in a 12 hour period by - epibiont and + epibiont mussels in a laboratory flow tank at $0.25ms^{-1}$ water velocity. + epibiont mussels were 40% covered by <u>Endocladia</u> a. First trial. b. Second trial. Error bars are standard errors of the mean.

Figure II.9

a.

b.
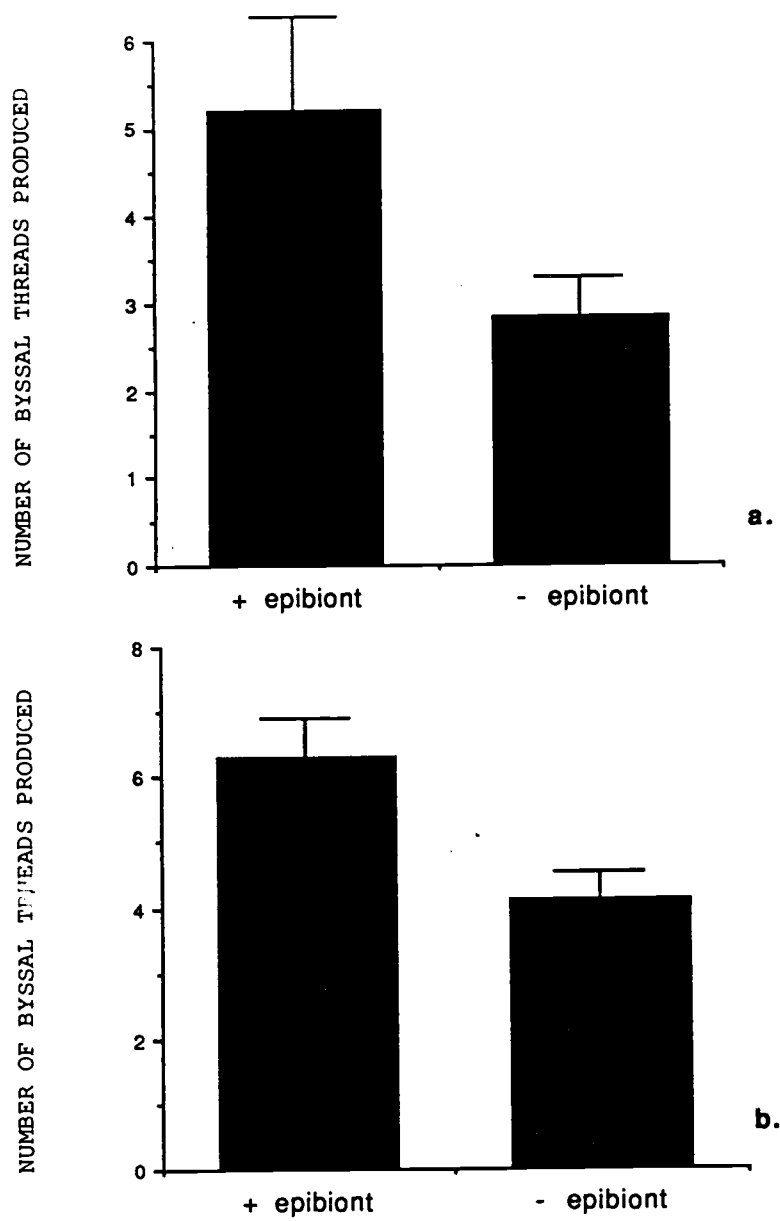
second set of experiments, where + epibiont mussels produced about 33% more byssal threads (6.4 compared to 4.1 (t=2.5, p=0.02, 49df).

Body Weight

Tests for heterogeneity of slopes were non-significant at all three sites (Table II.2), indicating that ANCOVA was an appropriate test for the effect of epibionts on dry weight. Shell length was a significant predictor of dry weight (Table II.2), and a polynomial equation best described the relationship between length and dry weight (Figure II.10 a, b, c) However at all three sites, the body weight of a + epibiont mussel was significantly lower than that of a - epibiont mussel of the same size (Table II.2). The effect of _Endocladia_ on body weight of mussels seemed to vary with shore. For instance at Fogarty Creek + epibiont mussels weighed 30-50% less than - epibiont mussels of the same size. At Boiler Bay and Little Whale Cove the differences were 15%-23% less and 82%-86% less respectively. This is not too surprising as environmental conditions (e.g., wave exposure and food availability) can vary considerably within mussel beds and among shores.

Epibionts as Insulation

In early 1989, and late 1990 to early 1991, Arctic storms evidently caused high mussel mortality (up to 97%) on all shores sampled. However, mussels colonized by Endocladia were largely protected from the effects of freezing, and had a significantly lower mortality rate than - epibiont mussels. This was true both in 1989 and 1990-91 (Table II.3). For instance, in 1989, at Fogarty Creek, 62.5% of - epibiont mussels died compared to 19.5% of + epibiont mussels. Mussel mortality was highest in the upper distribution of the mussel bed (i.e., the region exposed for longest during low tide), and gradually declined with decreasing tidal height (Table II.4). On sloping surfaces (>45°), highest mortality was recorded in the upper 3 meters of the mussel bed. No mussels sampled at the lower distribution of the bed (>6m down) were colonized by Endocladia. At Bob Creek, mortality in a narrow upper band of small mussels was relatively low (18.5%) compared to 0.5 m down (81%)(Table II.4). This is probably because these mussels were Mytilus trossulus which often form a narrow upper band at Bob Creek (S. Yamada, Oregon State University, personal communication). M trossulus is capable of surviving freezing conditions which are lethal to M. californianus (Suchanek 1985).

Table II.2 Summary of ANCOVA table on the effect of
Endocladia on mussel weight. The covariate was shell
length. Tests for homogeneity of slopes indicated that the
effects of length and _Endocladia_ were independent (Boiler
Bay F=0.16, p=0.69; Fogarty Creek F=1.82, p=0.18; Little
Whale Cove F=4.69, p=0.057). Regression equations: Boiler
Bay +epibiont mussels. $Y=-1.074 + 4.083e-2X - 2.354e-4X^2$
$r^2=0.24$. -epibiont mussels. $Y=1.039 - 4.024e-2X + 5.596e-4X^2$ $r^2=0.52$): Fogarty Creek + epibiont mussels. $Y=-0.289 + 7.75e-3X + 1.51e-4X^2$ $r^2=0.82$. - epibiont mussels. $Y=-0.55 + 1.79e-2X + 1.06e-4X^2$ $r^2=0.83$: Little Whale Cove. +
epibiont mussels $Y=0.69 - 1.81e-2X + 2.87e-4X^2$ $r^2=0.27$. -
epibiont mussels $Y=1.01 - 2.91e-2X + 4.11e-4X^2$ $r^2=0.65$.

SOURCE	SS	DF	MS	F	P
Boiler Bay					
Endocladia	0.25	1	0.25	6.07	0.018
Error	1.76	43	0.04		
Fogarty Creek					
Endocladia	0.39	1	0.39	11.59	0.002
Error	1.26	37	0.03		
Little Whale Cove					
Endocladia	0.27	1	0.27	7.86	0.007
Error	1.71	49	0.35		

Figure II.10 Length:dry weight relationship of +
epibiont and - epibiont mussels at three shores on the
Oregon coast. a. Boiler Bay, b. Fogarty Creek, and c.
Little Whale Cove. (See Table II.2 for regression
equations) At each site, - epibiont mussels had a
significantly higher length to weight relationship,
indicating that the presence of <u>Endocladia</u> decreases
growth rates in mussels.

Figure II.10

a.

b.

c.

DRY WEIGHT (GRMS)

SHELL LENGTH (MM)
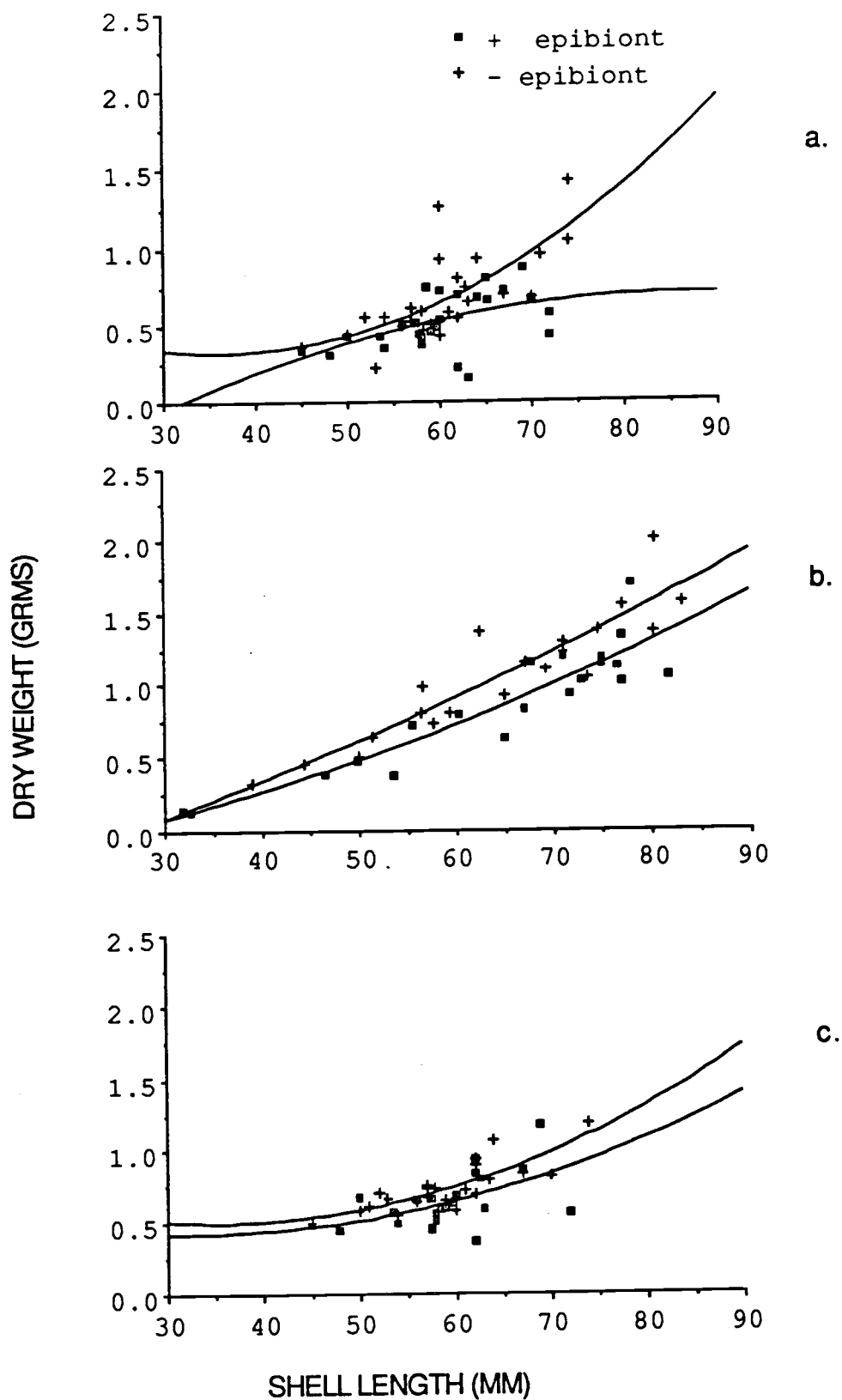
■ + epibiont
+ - epibiont

Among shores, mussel mortality was strongly correlated with the overall percentage of mussels that were colonized by epibiont algae (Figure II.11). This relationship was significant in both 1989 (F=74.82, p=0.003, r^2=.87), and 1991 (F=18.16, p=0.004, r^2=0.66). The relationship allows broad predictions of the effects of freezing on mussel mortality, based on overgrowth rates at that shore. At Little Whale Cove, 98% of mussels in the upper distribution of the bed were colonized by algae, and mortality was 0.5%. By contrast at the North Headland in Yachats less than 1% of mussels were colonized by algae, and mortality at this site was 97.5% (Figure II.11).

Although conditions were more severe in 1991,(i.e., temperatures were lower and for longer), mortality was lower (Figure II.11). For example, at Bob Creek, <1% of mussels were colonized by algae, and mortality was 95% in 1989, but was 55.8% in 1991. This is probably because on many shores, particularly those where epibiont cover was low, mussel mortality and dislodgment of dead shells after February 1989 lowered the upper limit of distribution by 1-3 meters. Thus the upper limit of the mussel bed was not at the same tidal heights in 1989 and 1991. In years when temperatures do not fall below freezing, overall mussel mortality on the shore is considerably lower, and can

range from 3-12% (Brosnan unpublished data for March 1990 and March 1992).

Mussel Survival After Freezing: Laboratory studies

When exposed to freezing conditions in the laboratory, the mortality of + epibiont mussels was significantly lower than for - epibiont mussels (Figure II.12). 18.5 % of + epibiont mussels died compared to 41.2% of - epibiont mussels (G/q = 22.62, 1df, N=400, p<0.001). Low mortality in the + epibiont group appeared to be due to the presence of Endocladia, rather than to confounding factors associated with Endocladia. This is supported by results from the Endocladia-removal group (Endocladia removed from mussels before freezing). Mortality in this group was 43%. This was significantly higher than the + epibiont group (G/q=16.84, 1 df, N=300, p<0.001), but was not different from the - epibiont-mussel group (G/q = 0.03, 1df, N=300, p>0.05 ns). No mussels in the control groups (- epibiont and + epibiont) died during the experiment.

Insulating effects of <u>Endocladia</u>

As expected, <u>Endocladia</u> appeared to insulate mussels (Figure II.13). In laboratory experiments carried out over a 6 hour period, + epibiont mussels were significantly warmer than − epibiont mussels after 40 min. ($t=2.05$, $P=0.02$, $N=36$), 80min. ($t=1.75$, $p=0.04$, $N=39$) and 120 min. ($t=2.80$, $p=0.01$, $N=20$). However after 360 min. there was no difference between body temperature of − epibiont and + epibiont mussels ($t=0.64$, $p=0.07$, 18 df), and both groups of mussels were completely frozen. The second study confirmed the above result ($F=15.31$, $p=<0.001$, 2df) (Figure II.14). However, <u>Mastocarpus</u> was less effective than <u>Endocladia</u> at insulating mussels ($F=0.865$, $p=0.04$).

Table II.3 Mortality of + <u>Endocladia</u> and − <u>Endocladia</u> mussels at three shores on the Oregon coast in February and March 1989. Mussels were collected from randomly placed 0.25 m² quadrats. G-test with Williams q corection tested the effect of <u>Endocladia</u> cover on mortality levels. **=significant at p<0.01 level, *=significant at p<0.05 level.

Site	+ epibiont mussels	− epibiont mussels	Total number sampled N	G/q
Fogarty Creek			667	99.8
number dead	238	70		**
number alive	143	216		
Boiler Bay			555	62.6
number dead	98	17		**
number alive	202	238		
Yachats			200	18.2
number dead	24	6		**
number alive	65	105		

Table II.3 continued. Mortality in January and February 1991. Mussels were sampled using 10 to 20 randomly placed 0.25 m^2 quadrats at each site.

Site	+ epibiont mussels	- epibiont mussels	Total number sampled N	G/q
Boiler Bay			3777	346.6
number dead	1464	146		**
number alive	1434	733		
Otter Crest			2445	333.9
number dead	1224	86		**
number alive	799	366		
Fogarty Creek			3707	648.5
number dead	1578	86		**
number alive	1255	789		
Little Whale Cove (north bench)			543	4.98 *
number dead	10	5		
number alive	254	274		
Yachats			1401	19.27
number dead	359	5		**
number alive	996	71		
Strawberry Hill (north bench)			493	5.51 *
number dead	189	2		
number alive	291	14		

Table II.3 continued. Mortality in January and February 1991. Mussels were sampled using 10 to 20 randomly placed 0.25 m^2 quadrats at each site.

Site	+ epibiont mussels	- epibiont mussels	Total number sampled N	G/q
Yaquina Head (north shore)			484	77.7 **
number dead	200	3		
number alive	200	81		
Devils Churn (south bench)			420	34.3 **
number dead	50	5		
number alive	169	156		
Bob Creek (north bench)			405	23.2 **
number dead	260	5		
number alive	120	20		

Table II.4 Changes in mortality rate on sloping substrates (>45°) at 0.5 m intervals from the upper limit of the mussel bed to the lower limit. Data were collected in February and March 1989. Mortality rate was estimated from 0.25m^2 quadrats placed at 0.5 m intervals (1m at Boiler Bay) along a transect line. -- indicates a break in the distribution of the mussel bed. ** At Bob Creek mortality in a narrow upper band of mussels was low. These mussels were probably <u>Mytilus trossulus</u> which is more resistant to freezing conditions (see text).

Distance from upper limit of mussel bed	Fogarty Creek % mortality	Boiler Bay %	Bob Creek %	Strawberry Hill %	Devils Churn %	Cape Meares %	Seal Rock %
Upper Limit of mussel bed	81.8	44	18.5**	87.5	86.5	92	87
-0.5	58.6		81	--	57.5	88	59
-1	40	45	14	86.5	18.5	47.5	24
-1.5	37.		14	86.0		42.5	21
-2	17	29	2	--		21	6
-2.5	0		0	--		5	--
-3		22	0	27		0	1
-3.5				--			
-4		16		--			
-4.5				--			
-5		16		1.5			
-5.5							

Table II.4   continued

-6	3
-6.5	
-7	1
-7.5	

Figure II.11. The relationship between percent mortality on the shore, and the percent of mussels colonized by algae. Each point represents the data from one shore. Data were collected at 0.5 m intervals between 0 and 3 m from the upper limit of a mussel bed. a. 1989. (y=93.33-1.03x. R^2=0.87) The regression was significant (F=74.82, p=0.003, N=14 shores). (Bob Creek, Strawberry Hill, Neptune, Devils Churn, Yachats (south park), Yachats (north headland), Seal Rock, Yaquina Head, Otter Crest, Little Whale Cove, Boiler Bay, Fogarty Creek, Maxwell Point, Cape Meares). b. 1991.(y=51.64-0.59x. R^2=0.66). The regression was significant (F=18.16, p=0.004, N=12 shores) (Bob Creek (shore south bench), Bob Creek (north Creek), Strawberry Hill, Neptune, Devils Churn, Yachats (south park), Yaquina Head (marine gardens), Yaquina (North Headland), Otter Crest, Little Whale Cove, Boiler Bay, and Fogarty Creek).

Figure II.11
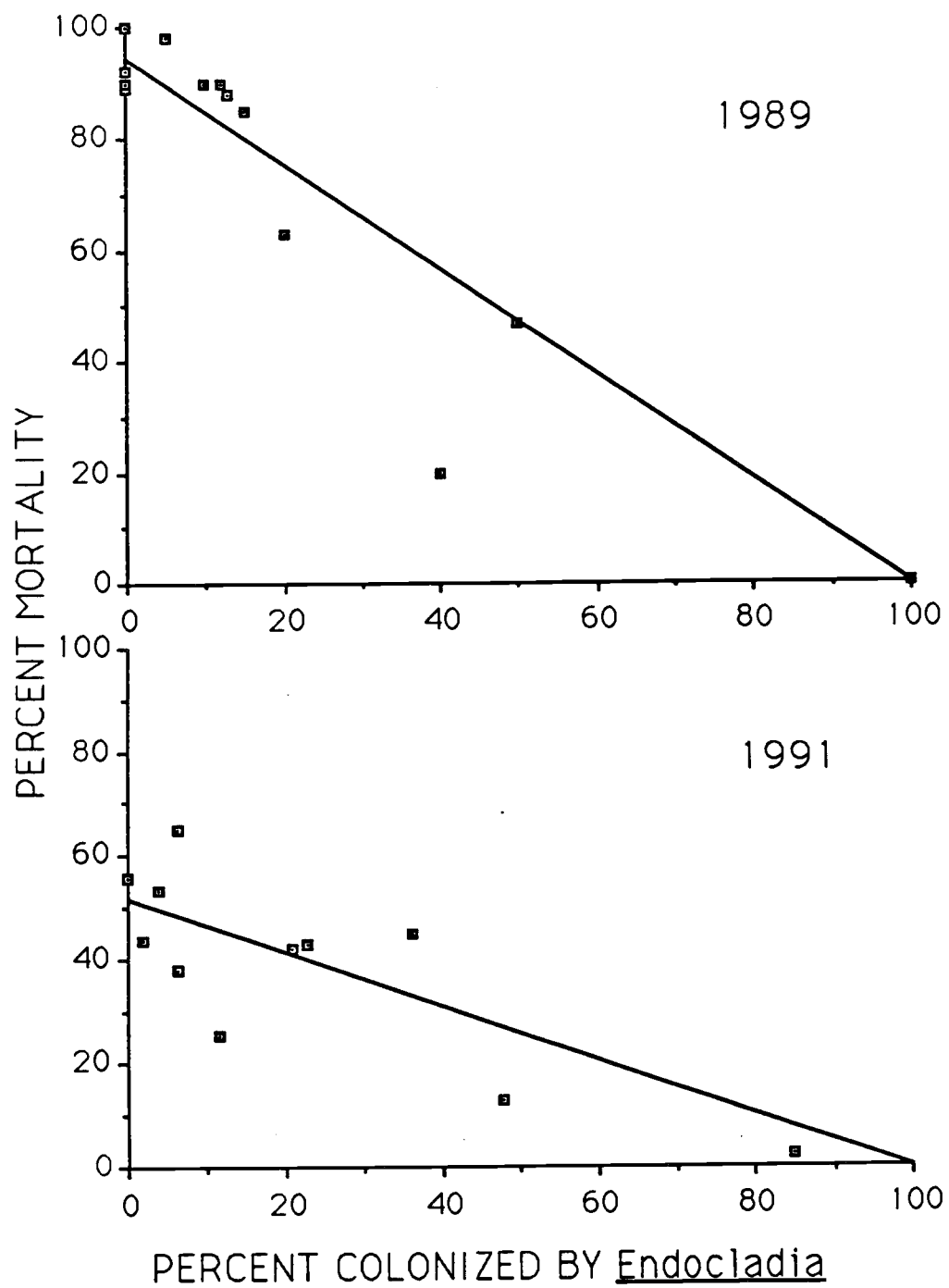
Figure II.12 Effect of algal epibionts (<u>Endocladia</u>) on mussel mortality under laboratory conditions. Graph shows the mortality rate 10 days after freezing conditions. See text for experimental details. No mussels in the control group suffered any mortality. Standard error of the means.

Figure II.12
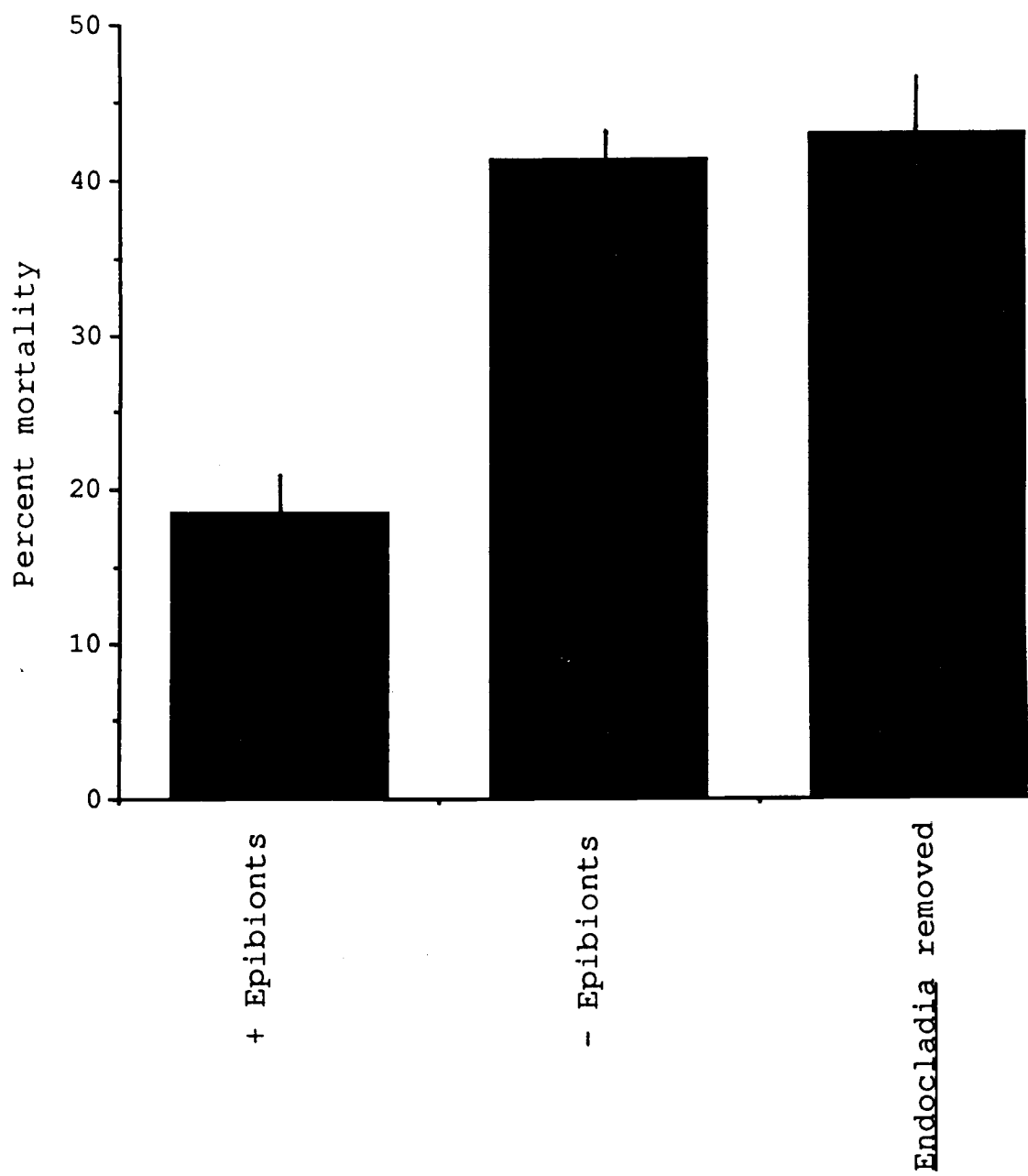
Field studies

On warm sunny days, <u>Endocladia</u> appeared to insulate mussels. Between two and three hours after low tide, the body temperatures of + epibiont mussels were significantly lower than - epibiont mussels. (Table II.5)

Frequency of positive interactions between mussels and epibionts.

Daily tidal predictions and temperature records, collected at South Beach central Oregon coast from 1931 to 1994, were analyzed. The goal was to estimate the frequency of conditions which could produce positive effects of algae on mussels. Large scale mussel (and invertebrate) mortality was recorded in the Pacific Northwest in 1974, and 1978 (W. B. Wick, personal communication; R. Starr, Oregon Department of Fish and Wildlife personal communication), in 1983-4 (Paine 1986), in 1989 (this study and Dethier 1990), and in 1990-1 (this study). Tidal and temperature records for these dates were analyzed in an attempt to determine what conditions result in large scale mortality.

Figure II.13 The effect of _Endocladia_ on internal body temperature of mussels under laboratory conditions. + epibiont and − epibiont mussels were placed in a freezer at −12°C. Mussels were sampled after 40 min., 80 min., 120 min. and 360 min.

Figure II.13

84
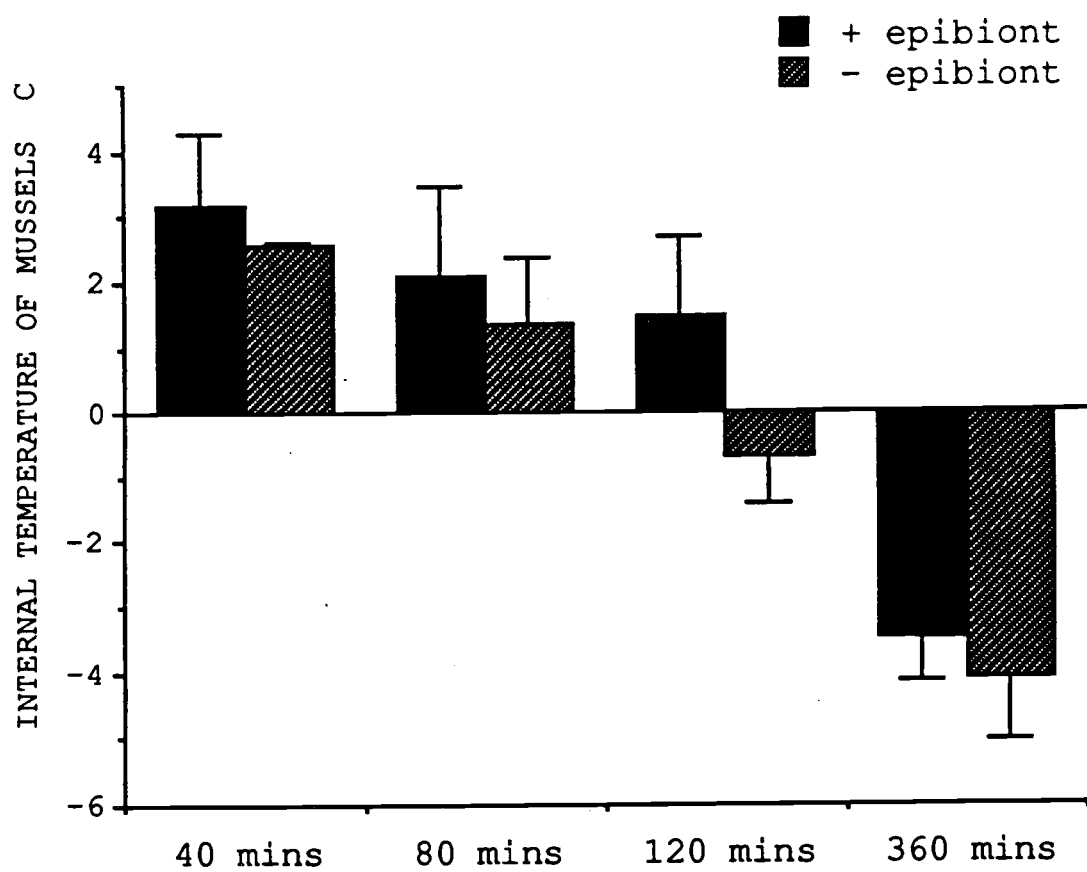
Figure II.14 Effect of <u>Endocladia</u> on internal body temperatures of mussels after 1 hour at freezing conditions. Mussels colonized by <u>Endocladia</u> were significantly warmer than mussels + epibiont by <u>Mastocarpus</u> and - epibiont mussels.

Figure II.14
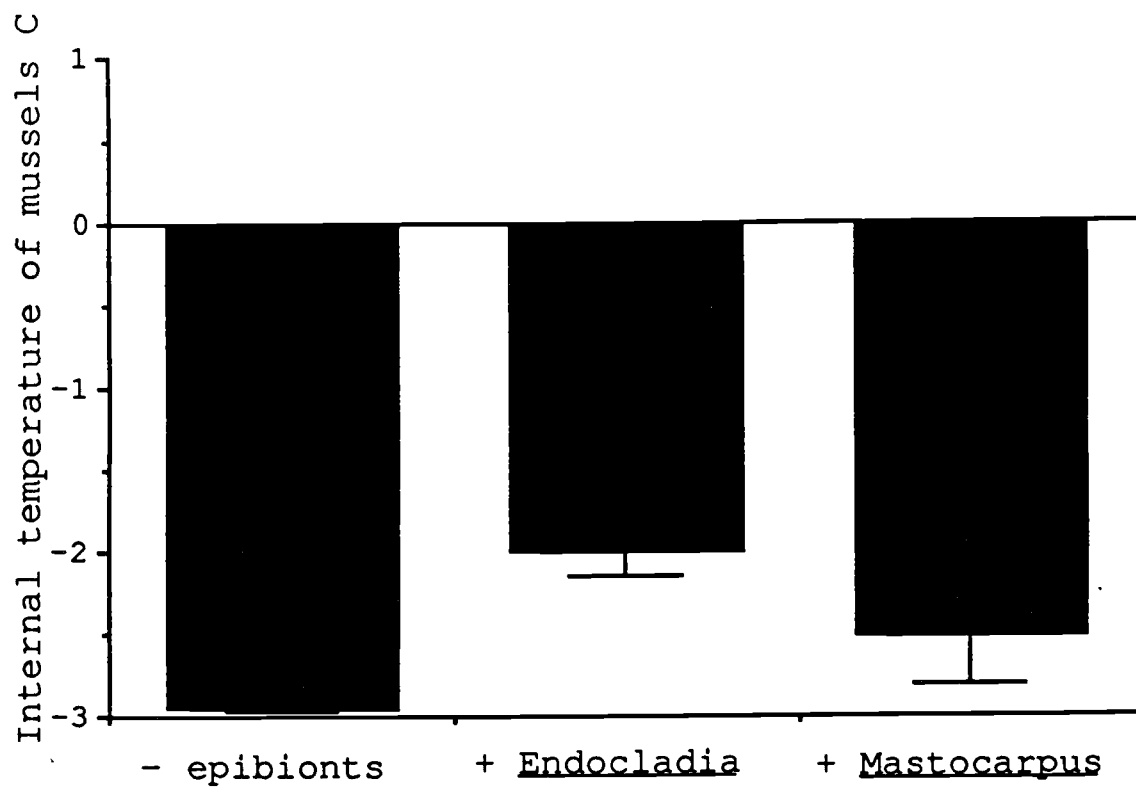
Table II.5 Field measurements of internal temperatures of + epibiont and - epibiont mussels. Temperatures were recorded on sunny days (air temperature on the shore 21-21.5°C), and 2-3 hours after low tide between 11.00 a.m. and 1:30 p.m. ** indicates significant at p=0.001.

Month	+ epibiont mussels $^{\circ}$C (s.e)	- epibiont mussels $^{\circ}$C (s.e)	F	N	Substrate temperature ($^{\circ}$C)
May	19.59	24.99	65.1	111	23.6
1990	(0.90)	(0.80)	**		
July	20.74	22.5	38.7	80	20.0
1990	(0.37)	(0.31)	**		
Aug	19.80	22.84	20.4	20	21.94
1990	(0.53)	(0.41)	**		

During all five events low temperatures were at least
-6.0°C for a minimum of three consecutive nights. Lowest
low tides occurred from mid-afternoons to late evenings:
Low tide height ranged from +0.3 m (+1.0 ft) (in 1983), to
-0.66 m (-2.2 ft) (in 1978) on days when subzero
temperatures were recorded. For dates before 1974, I
determined when conditions equaled or exceeded (lower
temperatures, for longer periods) those above, and judged
that these were times of probable large scale mortality.
Based on these criteria, there were thirteen probable
"freeze-events" on the Oregon coast between 1931 and 1994.
(Table II.6) (Note that, apart from Jan. 1937, pre-1978
conditions are more severe (i.e., longer periods of lower
temperatures), which suggests that this is a conservative
estimate of mortality). Temperature data were not
collected from May 1932-May 1933, and Nov. 1950-July 1951,
and there were occasional days when equipment failure
prevented data collection, and so these periods are not
included in the analysis. Periods of freezing temperatures
were more common beginning in the 1950s, while there were
no freezing conditions recorded for over ten years during
the late 1930s and 1940s (Figure II.15).

Severe weather leading to large scale mortality is important to shore invertebrates. However, I also tried to estimate the frequency of smaller-scale mortality events. These are times when environmental conditions may be stressful enough that a few individuals die. Environmental stress frequently limits the upper distribution of intertidal plants and animals (e.g., Connell 1972; Underwood 1980, Menge and Lubchenco 1981). Under low temperatures, mussels in the upper part of the shore, mussels at the edge of mussel beds, and mussels without algal cover are likely to have a higher mortality rate. This would not be recorded as a mass mortality of mussels on a shore, but it may affect distributions, alter the frequency of epibiont cover, and affect subsequent dislodgment (see above).

I attempted to estimate the frequency of these events based on the following criteria. My observations from laboratory studies indicated that after 2 hours at 0°C the tissues of - epibiont mussels are usually completely frozen, and that some mussels die after such exposure (personal observation). To be conservative, I estimated that if temperatures fell below -4°C for more than three consecutive nights, and if this coincided with evening low tides below -0.06 m, then it is probable that some mussel

mortality can occur. Under these tidal conditions mussel beds may be exposed for three to four hours on some shores (This is based on the number of hours that mussel beds are accessible on shores used in this study).

Daily temperature and tidal records were reanalyzed and 14 more dates met these additional criteria (Figure II.15). On thirteen of those dates temperatures ranged from -6°C to -8°C (exception was January 1969) and tidal height at lowest low tide ranged from -0.06 m to -0.57 m. Although this estimate is based on less stringent conditions than above, these conditions are still severe. Conservatively, these temperatures probably reflect periods of individual mussel mortality from environmental stress.

Table II.6 Environmental conditions (range of daily temperatures and tidal heights) that led to large-scale mussel mortality (from 1974) and periods estimated to have resulted in large scale mortality on the shore (pre-1974). Estimated dates were included if temperatures were <-6°C for at least three consecutive days, and if lowest low tides were less than 0.3 m

Year	Month and duration of freeze (i.e. period when temperatures were -3°C or below for consecutive nights)	Temperature range °C	Range of lowest low tides (meters)	Times of low tide (to nearest hour)	Mortality recorded
1937	Jan 2-11	-9.4 to -3	.3 to -.15	1700-2100	
1937	Jan 19-21	-7.2 to-6.1	-.15 to -.3	1100-1500	
1949	Jan 9-11	-7 to-5.5	.3 to -.15	1500-1900	
1950	Jan 29- Feb 23	-10.1 to -3	.3 to -.3	1600-2000	
1955	Nov 13-17	-9.4 to-6	-.06 to-.15	1700-2000	
1957	Jan 24-30	-11.6 to -8.3	0 to -.36	1400-1800	
1962	Jan 19-23	-10 to -4	.06 to -.15	1800-2000	

Table II.6   continued.

1964	Dec 16-19	-10.1 to -7	-.12 to -.15	1800-2200	
1972	Dec. 4-12	-17.2 to -9.4	.06 to-.12	1500-1700	
1974	Jan 4-10	-11.1 to -9	-.06 to -.66	1600-2100	ODFW
1978/9	Dec 28- Jan 2	-12.5 to -5	.06 to -.57	1800-2200	W. B. Wick (pers comm); ODFW
1983	Dec 20-25	-9.4 to-5.5	.3 to -.51	1600-1700	Paine 1986
1989	Feb 1-10	-12 to -6	.06 to -.48	1600-1900	Dethier 1990;this study
1990/1	Dec 19-24 and Dec 29 -Jan 1	-14 to -6	0 to -.43	1600-2100	this study

Figure II.15 ● Frequency of "major freeze events" which are known (from 1972-94) or estimated to have resulted in large scale mussel mortality (pre 1974). See text and Table II.6 for details of conditions and criteria used for including pre-1974 conditions. ◆ Frequency of "small scale" freeze events. These are estimated to have resulted in small scale mussel mortality, where only a few individuals died. (See text for details of criteria and rationale used in including these conditions).

Figure II.15

DISCUSSION

Negative effects of epibionts on mussels included increased drag, and dislodgment under harsh physical conditions. Hydrodynamic forces on individual mussels are greater when mussel beds are disturbed, and mussels are weakly attached. This suggests that the importance of the interactions between mussels and epibionts can, to some extent, be decreased or increased by the structure of the mussel bed. <u>Endocladia</u> insulated mussels against freezing conditions. However unless more that 10% of mussels in the bed are colonized by epibionts, the chances of dislodgment of an + epibiont survivor are high, because the bed will be weakened by the presence of dead conspecifics. Conversely, a - epibiont mussel, in a bed where most other mussels are colonized by algae, and which survives freezing conditions, will be unlikely to suffer dislodgment.

The outcome of interactions between mussels and algal epibionts can vary in sign (positive or negative), and strength, depending on environmental conditions. Under normal conditions, the negative effects of <u>Endocladia</u> on mussels are weak. Increased drag and energetic costs may reduce the growth and reproductive output of individual mussels. However they may have little effect on

persistence of mussels on the shore. Under harsh environmental conditions, both negative and positive interactions between mussels and epibionts are relatively more important. In high wave action, the added drag can increase dislodgment. Similarly insulation can be important to survivorship, and to persistence of mussel beds under conditions of extreme temperature stress.

Mussels colonized by Endocladia trade-off increased physical stress for a reduction in physiological stress under extreme temperatures. Costs to mussels colonized by algal epibionts (which include lower growth rates, and a potentially higher mortality risk), appear to be balanced in the long-term, by occasional strong positive interactions, that are important to the survival of individual mussels and to the persistence of the mussel bed itself. The overall outcome of the interaction between mussels and algal epibionts may depend on a long-term association between the species.

Weak interactions between mussels and epibionts may have little effects on species diversity because they do not change the patterns of space occupancy on rock substrate. However, strong positive and negative interactions may affect diversity patterns. The nature of

this effect depends on whether the species affected occupy rock substrate (primary substrate), or whether they use mussels as a habitat (i.e., plants and invertebrates living in the mussel matrix). During winter storms, dislodgment of + epibiont mussels may be higher. This creates patches of bare space, on rock surfaces, which are subsequently colonized by other species, (notably pioneer species of barnacles, and algae). The result is a spatial-temporal mosaic, with high diversity on primary substrate (Paine and Levin 1981). Note however, that when mussel beds are dislodged, the associated matrix species assemblage is also lost. This may result in a lower diversity of species that do not occupy primary substrate.

Strong insulatory effects by algal epibionts can increase survivorship of mussels and prevent loss of the mussel bed. The frequency of major freeze events suggests that they can have significant effects on the ecology of mussels and associated species, particularly in upper levels of the bed. Major freezes occur on average every 5 years (range 1- over 10 years). As mussels can live for at least 15 years (Suchanek 1979; P. Frank, University of Oregon, personal communication), they are likely to experience an average of three major freeze events (and

perhaps 3-4 additional smaller freezes). By insulating mussels, algal epibionts also indirectly benefit other associated species that depend on mussels for habitat.

Under what conditions are non-trophic interactions (such as insulation, or increased drag) likely to be important in regulating diversity? Bertness and Callaway (1994) have suggested that positive non-trophic interactions are likely to be important in physically stressful environments. This study supports their prediction. In addition, my results suggest that negative non-trophic interactions are also likely to be important under stressful conditions. In this study, the effect of epibionts on mussel dislodgment was greater when mortality was high, and when wave action was severe.

Other interactions between algal epibionts and mussels

This study focused on interactions between the epibiont Endocladia and adult mussels, and how these interactions varied with environmental stress. However, there are other interactions between epibionts and mussels (Figure II.16). For instance, algal epibionts including Endocladia, also settle on primary substrate, where they eventually lose in direct competition for space with

mussels. In addition, algae, particularly Endocladia, are the preferred settlement substrate for plantigrade mussels (Bayne 1964, Paine 1976, Petersen 1984a, b, Brosnan and Crumrine unpublished). Young mussels will settle onto algae on rock substrate, and onto algal epibionts on mussels (Petersen 1984a, b, and Brosnan and Crumrine unpublished). Thus, there are at least five different types of direct, non-trophic interactions between mussels and Endocladia, only one of which is competition. The outcome of these interactions is conditional on the life-stage (e.g., algal epibionts provide a habitat for plantigrades, but may dislodge adult mussels), and environmental conditions (Figure II.16).

Endocladia is not present on all mussels: Factors affecting the abundance of Endocladia on mussels include the presence of barnacles (which proved a suitable settlement habitat for Endocladia), and limpets (Chapter II).

In conclusion, mussel-epibiont relationships are characterized by interactions that range from weak to strong, and positive to negative. The outcome of these interactions can affect distribution patterns of mussels, and also species diversity on the shore.

Figure II.16 Nature and outcome of interactions between _Endocladia_ and mussels. a. On primary substrate mussels outcompete _Endocladia_, and _Endocladia_ provides a settlement substrate for young mussels. On secondary substrate,(b-d), _Endocladia_ persists as an epibiont on mussels. Mussels provide a habitat for _Endocladia_ under all physical conditions (b-d). In addition _Endocladia_ also provides a habitat for mussels, although the importance of this is low under conditions of physical stress (b), because here _Endocladia_ increases dislodgment rate of mussels. In c. _Endocladia_ protects mussels from temperature stress. In benign conditions, _Endocladia_ has weak negative effects on mussels by reducing growth rates of individual mussels.

Figure II.16

PRIMARY SUBSTRATE
a. Interactions on
   Rock Substrate

MUSSELS   ENDOCLADIA
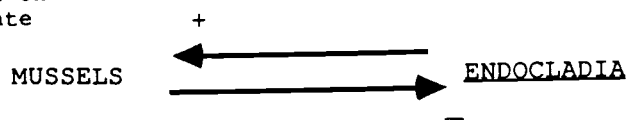
SECONDARY SUBSTRATE

b. Harsh Physical
   Conditions

MUSSELS   ENDOCLADIA

c. Extreme
   Temperatures

MUSSELS   ENDOCLADIA
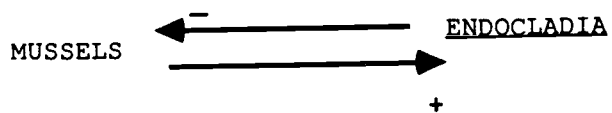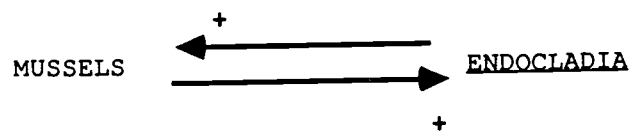
d. Benign
   Conditions

MUSSELS   ENDOCLADIA
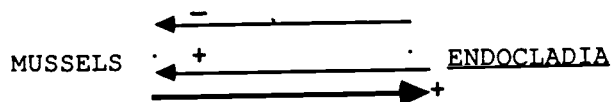
CHAPTER III

FACTORS AFFECTING RECRUITMENT AND SUCCESSION IN AN EPIBIONT
ASSEMBLAGE ON MUSSELS, <u>Mytilus californianus</u>

ABSTRACT

Epibionts have important effects on the survival of
mussels, and the persistence of the mussel bed assemblage. I
investigated some of the factors regulating epibiont
community structure, by experimental manipulations of the
barnacle-algal epibiont assemblage. The species in this
assemblage occur on both rock and mussel shells (<u>Mytilus
californianus</u>); I was interested in determining if the same
factors regulate the community on rock and mussel
substrates. The experiment tested the effects of mussel
substrate, barnacles, and limpets on epibionts.

Limpets reduced barnacle abundance, except when barnacle
settlement was very high. Although barnacles generally
facilitated algae, only one species (<u>Endocladia muricata</u>)
persisted longer than three months. Limpets enhanced
<u>Endocladia</u> abundance, but reduced cover of other algae and
diatoms. These results suggest that facilitation by
barnacles, bulldozing by limpets, and unsuitability of

mussel shells as algal-recruitment sites are the main factors regulating the epibiont community on mussels.

In contrast, when these same species occur on rock substrate, they are often affected by a richer variety of direct and indirect interactions. On rock substrate herbivory, and competition between barnacles and algae, can often be important factors in regulating this assemblage.

INTRODUCTION

Understanding the processes that lead to the development and maintenance of communities is a fundamental goal of ecology. Effects of direct and indirect biological interactions can have important consequences for community structure and diversity (Paine 1966, Schoener 1983, 1993, Connell 1983, and Sih et al. 1985, Bender et al. 1984, Dethier and Duggins 1984, Dungan 1986; Abrams 1987, Yodzis 1988, Wootton 1994, Menge in press).

The relative importance of biological interactions may be affected by environmental factors. For instance, under harsh physical conditions, competition and predation can be relatively unimportant in community regulation (e.g., Connell 1985, Menge and Sutherland 1976, 1987, McNaughton 1983, Peckarsky 1983). Environmental gradients may therefore alter the occurrence and importance interactions in a particular species assemblage. As a result of varying environmental conditions, there may be spatial and temporal variation in both abiotic and biotic factors regulating a particular species assemblage.

In mussel-bed assemblages, epibionts can have important effects on growth, and survival of individual mussels (Paine 1976, Chapter II), and on the persistence of the mussel bed

itself (Chapter II). However the biological or environmental factors that regulate the epibiont community are relatively unknown. Epibionts are patchily distributed both among shores, and within mussel-beds (Chapter II). Previous studies have concentrated on the effects of epibionts on mussels (e.g., Dayton 1973, Paine 1979, Suchanek 1979, Witman and Suchanek 1984, Dittman and Robles 1991). Few studies have explored the conditions leading to the development of an epibiont assemblage, although Suchanek (1979) suggested that grazers in the mussel matrix keep mussels free of epibionts.

Epibiont species also occur on rock substrate. Do the same factors that regulate this community on rock substrate, also affect the epibiont community? Alternatively, mussels because of their smooth and elevated surface, may be a physiologically stressful habitat. If this is so, then biological factors may be less important in regulating the epibiont community on mussels. In addition, the relative abundance of species may differ between mussel substrate and rock substrate.

The aim of this study was to examine some of the main factors affecting the distribution of epibionts on mussels. The experiments consider the relative roles of biological

processes (competition, herbivory, recruitment, and facilitation) in the development of the epibiont assemblage. The primary goal of this study was to determine which, if any, of these processes were important in this environment.

BACKGROUND

On exposed rocky shores of the Pacific coast of North America, mussels, <u>Mytilus</u> <u>californianus</u>, are dominant competitors for space (Paine 1966). However, once established, mussels provide a habitat for these barnacles and algae, which persist as epibionts on mussels (Suchanek 1979, Lee and Ambrose 1989, Sousa 1984, Dittman and Robles 1991, Lohse 1993a, b). In addition, mobile invertebrates, including limpets, live within the matrix of mussel beds, and forage on the surface of mussel shells (Craig 1968, Jode 1968, Suchanek 1979).

Barnacle and algal epibionts, and limpets also occur on bare rock, where interactions among these species have been well studied (Figure III.1). Mussels are dominant competitors and outcompete barnacles and algae (Paine 1966, 1974, Harger 1970, 1972, Dayton 1971, Menge 1976, but see Underwood and Denley 1984). Algae and barnacles compete for primary space (e.g., Dayton 1971, Menge 1978, Underwood et al. 1983). However algae also establish on barnacle tests (Burrows and Lodge 1950, Southward 1964, Lubchenco 1980, Hawkins 1981, Hawkins and Hartnoll 1983, Farrell 1989, 1991). Limpets are known to affect recruitment of algae and barnacles by bulldozing barnacles (Dayton 1985, Denley and Underwood 1979, Branch 1975, 1981, Underwood et al. 1983,

Levings and Garrity 1984, Farrell 1989, 1991) and consuming algal sporelings (e.g., Southward 1964, Lubchenco 1978, 1980, 1983, 1985; Lubchenco and Cubit 1980, Underwood 1980, Underwood and Jernakoff 1981, Jernakoff 1983, Dethier and Duggins 1984, Sousa 1984, Farrell 1989, 1991). However, limpets can also indirectly facilitate barnacles by grazing algae from the rock surface (Hawkins and Hartnoll 1983, Underwood et al. 1983). In addition limpets can also indirectly facilitate unpalatable algae (Sousa 1984). Thus a range of direct (e.g., competition for space, facilitation) and indirect (enhancement through removal of competitors) interactions determine species composition and abundance on rock substrate.

To determine if the same factors regulate community structure on rock and mussel substrate, I conducted an experiment to study effects of direct and indirect species interactions on establishment of epibionts on mussels. For instance, based on studies on rock substrate, competition for limited space (i.e., the surface of a mussel) is likely to be an important factor regulating the relative abundance of barnacle and algal epibionts. Note that algae may recruit onto mussels directly or onto barnacles on mussels. Thus interactions between barnacles and algae may differ depending on whether algae colonize mussel shells directly,

or are facilitated by barnacle epibionts. Consequently, in this experiment, I distinguished between algal recruitment onto mussel shells (secondary substrate) and algal recruitment onto barnacle epibionts (tertiary substrate).

Figure III.1. Main interactions between limpets, barnacles, and algae on rock substrate (____ denotes direct effect) (--- denotes indirect effect). Barnacles and algae (palatable and unpalatable species) compete for space (-). Barnacles facilitate algae (+). Limpets bulldoze barnacles (-) but also indirectly benefit them by grazing algae (+). Limpets graze palatable algae (-) and indirectly benefit unpalatable species (+). Limpets also indirectly benefit algae by bulldozing barnacles (+).

Figure III.1
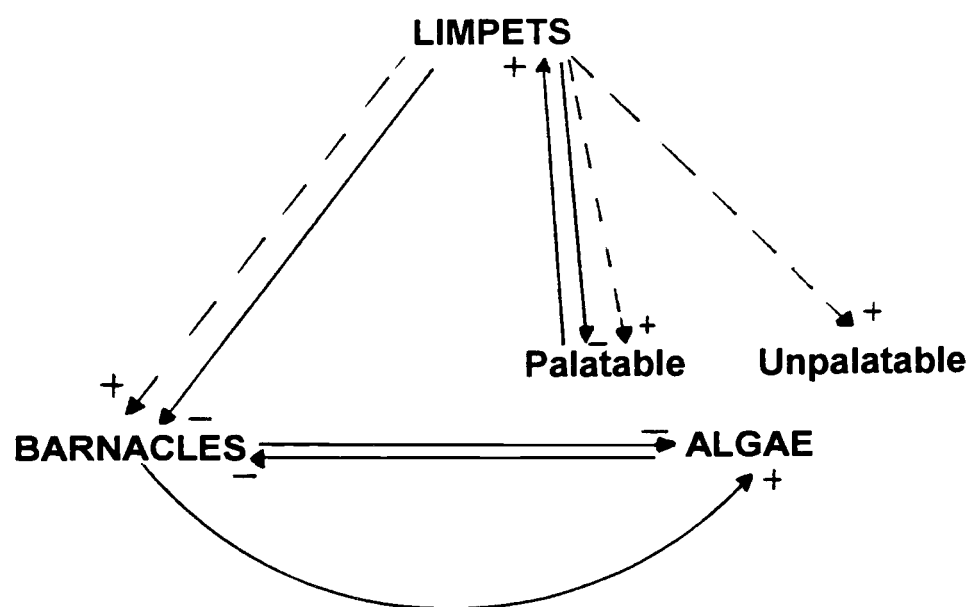
STUDY SITES

Experiments were carried out in the mid-intertidal zone
at two sites on the Oregon coast, Fogarty Creek (44°51'
N:124°03' W) and Boiler Bay (44° 53'N; 124.04'W). Both
shores consist of extensive basaltic platforms. The mid-
intertidal zone at both sites was dominated by extensive
beds of mussels (Mytilus californianus). Barnacle epibionts
(Balanus glandula) are common on mussel shells at both
sites. Algal epibionts were mainly Endocladia muricata, but
also included Mastocarpus papillatus, Ulva sp. and
Pelvetiopsis limitata. These species are also common on rock
substrate at both sites. The most common invertebrates
living in the mussel matrix at both sites included limpets
(mainly Lottia pelta), crabs (Petrolisthes spp), predatory
whelks (Nucella emarginata), and anemones (Anthopleura
xanthogrammica and A. elegantissima). Mobile herbivores, and
predators in the vicinity of the experimental plots included
limpets (Lottia pelta, and littorines Littorina scutulata),
and occasionally seastars (Pisaster ochraceus) (see Turner
1985, Farrell 1989, and Menge et al. 1994, for more complete
site descriptions).

METHODS

Experimental design

In August 1989, I set up an experiment to test the
effects of barnacles, limpets, and barnacle-limpet
interactions on epibiont colonization of mussels. Plots
consisted of small mussel beds with an initial density of
12-15 single-layer mussels each. Mussels ranged in size from
4-8 cm. These mussel beds were created by clearing a space
within existing mussel beds at Fogarty Creek and Boiler Bay.
I cleared space around a central group of 12-15 mussels.

To exclude mobile grazers and invertebrate predators a
stainless-steel mesh fence was placed around each
experimental bed. Plot size averaged 14 x 15 cm. The mesh
was anchored in place using 4-6 stainless-steel screws. The
top of the mesh was folded down facing outwards (Dayton
1971). To ensure that grazers or predators could not crawl
under the mesh, the base of the mesh was embedded in Z-spar
marine epoxy putty. Plots were 2-6 m from the nearest algal
beds.

A randomized block design was used, with six treatments
and four blocks at the two sites, making a total of forty-
eight experimental units (Figure III.2). Treatments were

designed to test the hypotheses outlined above (Table III.1). For instance, comparisons between +L and -L treatments tested the effects of limpets on barnacle recruitment. Treatments with and without barnacles tested the effects of barnacles on algae. My design was not orthogonal (there was no "adult only" treatment), because I focused on the effects of the presence of absence of barnacles (+B and -B) and on their role in epibiont community development. Treatments where barnacles were removed initially only (-B+R) examined succession on mussels.

Existing barnacles were removed from mussels in barnacle absent (-B-R), and no adult (-B+R) treatments at the beginning of the experiment, by scraping the mussel shell clean using a metal scraper and a wire brush. There were no algae present on any of the epibiont barnacles in the +B treatments (1 and 2). However, barnacles were scraped with a wire brush and a small metal scraper and the exposed surfaces of mussel shells were also scraped in an effort to remove any spores. Other organisms were removed from the matrix of the experimental beds (including limpets, thaids and crabs).

Six limpets (<u>Lottia pelta</u>) per mussel were added to +L treatments (1, 3, and 5). <u>Lottia pelta</u> is the most abundant limpet living on mussel shells at Fogarty Creek and Boiler Bay (n=160 mussels). Six limpets is slightly more that the average density per mussel (mean=4.3, s.e.=1.7, n=160), but within the normal range. These limpets were carefully removed from nearby mussels with a pair of forceps, and immediately placed on the lower anterior region of each mussel, as this is where most limpets are found on mussels (personal observation).

Monitoring Protocol

Data were collected on initial percent cover of barnacles on mussel shells in +B treatments (1 and 2). Subsequently, at each sampling period, data were collected on (1) percent cover of barnacle epibionts on mussel shells (barnacles on secondary space), (2) algal epibionts on mussel shells (algae on secondary space), and (3) algal epibionts on barnacle epibionts (algae on tertiary space). Data were collected at the beginning of the experiment (August 1988), and monthly from October 1989 until November 1990 when an unusually hard freeze killed most of the mussels in the experimental plots.

Percent cover was estimated using the random dot-method (Connell 1961) on "vinyl mussels". I estimated cover for individuals using mussel-shaped vinyl overlays ranging in size from the smallest to the largest mussel in the plots. Each overlay had 50 evenly spaced dots on it. To estimate percent cover of barnacle and algal epibionts, I placed an overlay of the appropriate size over an experimental mussel and counted the number of dots which covered barnacles or algae. At each sampling period, data were collected from four randomly chosen mussels in each plot. On each sampling date, plots were carefully checked for limpets, whelks and other species. When necessary these species were removed or added, as appropriate for the treatment. Densities of limpets in each plot were recorded in October 1989, and February, June, July, September, and November 1990.

Figure III.2 Experimental design used to test the effects of barnacles and limpets on the recruitment of epibionts. Design consisted of a 3x2 factorial design with three barnacle treatments, +B+R (adult and recruit barnacles), -B+R (barnacle recruits, that settled onto bare mussels), -B-R (barnacles absent); and two limpet treatments, +L (grazers present), -L (grazers absent). The design was repeated in four blocks at each site (Fogarty Creek and Boiler Bay).

Figure III.2
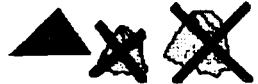
Barnacle epibionts Present (adult and recruits) (+B+R)	Barnacle recruit epibionts (no barnacles present initially) (-B+R)	Mussels without barnacle epibionts: Barnacles Removed (-B-R)
(+B+R+L) Tmt 1	(-B+R+L) Tmt 3	(-B-R+L) Tmt 5
(+B+R-L) Tmt 2	(-B+R-L) Tmt 4	(-B-R-L) Tmt 6

Table III.1. Experimental treatments and effects tested by each combination.

Treatment	Tests	Adult barnacles	Barnacle recruits	Limpets
1.(+B+R+L)	Control.	+	+	+
2.(+B+R-L)	Effects of grazers in the presence of barnacles.	+	+	-
3.(-B+R+L)	Development of a barnacle-algal epibiont assemblage in the presence of barnacles and grazers.	-	+	+
4.(-B+R-L)	Role of grazers in the development of a barnacle-algal epibiont assemblage.	-	+	-
5.(-B-R+L)	Development of algal epibiont assemblage in the presence of barnacles and grazers.	-	-	+

Table III.1. continued.

Treatment	Tests	Adult barnacles	Barnacle recruits	Limpets
6.(-B-R-L)	Effect of grazers on the development of algal epibiont assemblage.	-	-	-

DATA ANALYSIS

Data were analyzed using Systat (Wilkinson 1990).
Raw data always violated the assumption of homogeneity of
variances, and they were transformed using either arcsin or
log transformations (Sokal and Rohlf 1981). Replicates,
blocks and sites were measured repeatedly over time and so
results from each date were not independent. However,
mussels were randomly subsampled with replication. Therefore
I analyzed transformed data using a 3x2 mixed-design,
nested, repeated measures ANOVA, with blocks nested within
site. Probability plots of residuals were made to determine
if error terms were normally distributed. Bartlett's test
was used to test for homogeneity of variances (Sokal and
Rohlf 1981). If only main effects were significant, all
treatment means were compared. However, when main effects
and interaction terms were significant, I compared within-
factor means only (Sokal and Rohlf 1981). Means were
compared using Tukey's test (Day and Quinn 1990). In
barnacle-absent (-B-R) treatments, barnacles were removed
monthly.

Occasionally, barnacles settled onto mussels in these
treatments (i.e., -B-R) in the intervening period between
removals. This allowed for testing the effects of limpets on
new barnacle recruits. Therefore I also analyzed these data

separately to test for grazer effects on recruitment to secondary substrate. For some algal species, recruitment was low and patchy, and transformations did not reduce heteroscedasticity to acceptable levels (Underwood 1981). Therefore I analyzed these data using a G test with Williams q correction to test for differences in the frequency of occurrence among different treatments.

RESULTS

Recruitment onto Mussels

Barnacle recruitment

Barnacles were abundant on unmanipulated mussels at both sites. There was a strong settlement pulse of <u>Balanus</u> in September 1989 (Figure III.3, III.4, reflected in October 1989 data). Recruitment and overall barnacle abundance was lower at Fogarty Creek (Table III.2 "site" was significant). At Boiler Bay, barnacles occupied 60%-70% of available space on mussels in all plots (Figure III.4). <u>Balanus</u> continued to recruit in occasional small pulses during the course of the study (Figure III.3c, III.4c). Recruitment occurred into all treatments at these times (Figure III.3, III.4). However, in unmanipulated treatments (+B+R and -B+R) changes in barnacle cover were confounded by effects of resident barnacles (e.g., growth or death of individuals from previously settled cohorts). In general, barnacle abundance did not appear limited by recruitment at either site.

Limpet Effects

Fences were generally successful at excluding grazers. Limpets were always significantly higher in limpet inclusion

plots (t=37.32, p<0.001, n=48), and ranged in density from 63 to 67 per plot. There was some recruitment into limpet exclusion plots, up to 15 limpets <2mm were recorded in one plot.

Limpets reduced barnacle abundance, but their effect was related to barnacle settlement intensity (Figure III.3, III.4 and Table III.2). In RMANOVA analysis, "Limpet" was significant, both in univariate (within subject), and multivariate interaction terms. As suggested by results at Boiler Bay, when barnacle settlement was high, limpets were swamped and did not affect recruitment (Figure III.4b. In October 1989, limpets did not reduce barnacle cover in any treatment). At low to moderate barnacle settlement, limpet bulldozing reduced barnacle recruitment (Figure III.4b). For instance, at Fogarty Creek barnacle settlement was lower than at Boiler Bay in October 1989, and barnacle cover was lower in limpet inclusion treatments. I continued to monitor the effects of limpets on barnacle recruitment by removing barnacles in -B treatments. At both sites additional barnacle settlement was low or moderate, and the presence of limpets decreased barnacle recruitment (Figure III.3c, III.4c). In summary, limpets inhibited barnacles but only when recruitment was low to moderate.

Algal and diatom recruitment

Few algae recruited directly onto mussel shells during the experiment (Table III.3). Only 13 of 48 observations showed algae recruiting directly onto mussels. Recruitment was low at Fogarty Creek, to non-existent at Boiler Bay. Algae rarely persisted on mussels, and had often disappeared from the plots after two or three months. Barnacles did not affect algal recruitment. Of those species that colonized mussel shells, equal numbers recruited onto mussels in the presence of barnacles (+B+R and -B+R) as in the absence of barnacles (-B-R) ($G/q=0.19$, $p>0.05$, $n=20$). By contrast diatom recruitment was inhibited by barnacles ($F=5.88$, $p=0.015$, 1df. Figure III.5). However, competition between barnacles and diatoms may be sporadic, because even in the absence of barnacles, diatoms did not persist beyond two months. (Figure III.5).

Limpet Effects

Limpets reduced the overall abundance of algae (species listed in Table III.3) settling directly onto mussels ($G/q=4.1$, $p<0.05$, $n=48$. Algae were grouped for analysis).

Figure III.3 Barnacle recruitment and abundance on mussels at Fogarty Creek. * denotes a significant limpet effect on barnacle abundance (p<0.05). a. effects of limpets on adult and new recruits (+B+R+L, +B+R-L), b. effects of limpets on recruitment and post-recruitment barnacle abundance (-B+R+L, -B+R-L). c. effect of limpets on barnacle recruitment (-B-R+L, -B-R-L, barnacles were removed monthly from mussels).

Figure III.3
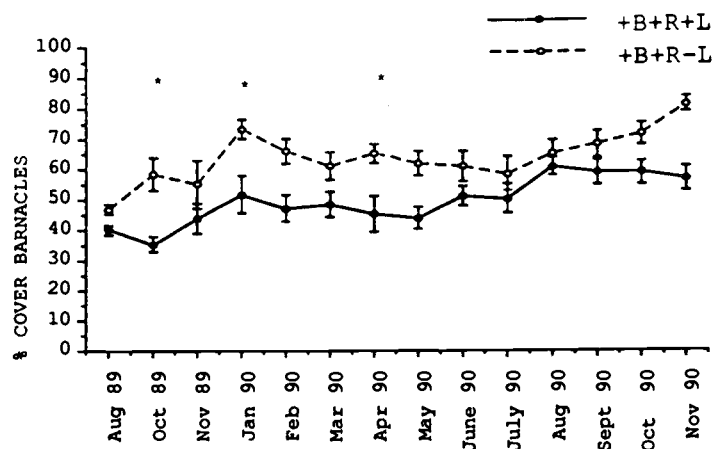
a.
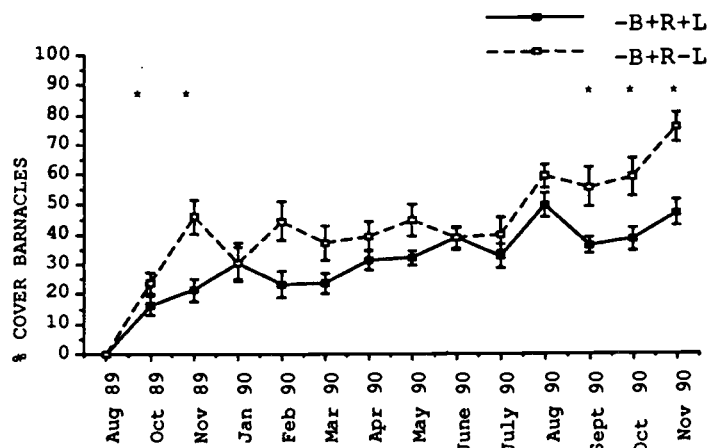
b.
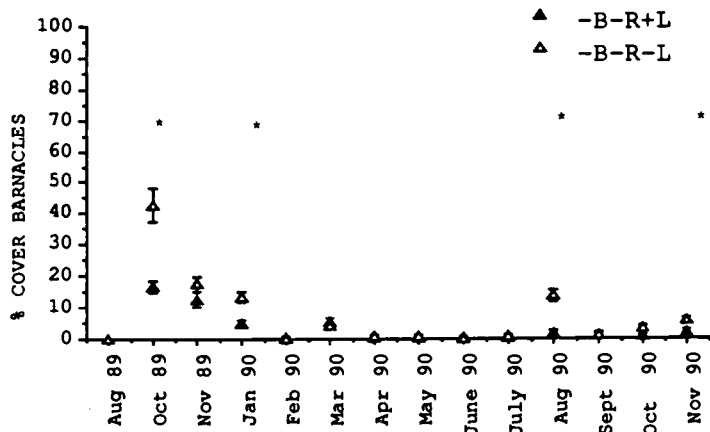
c.

Figure III.4 Barnacle recruitment and abundance on mussels at Boiler Bay. * denotes a significant limpet effect on barnacle abundance ($p < 0.05$). See figure III.3 for caption codes.

Figure III.4
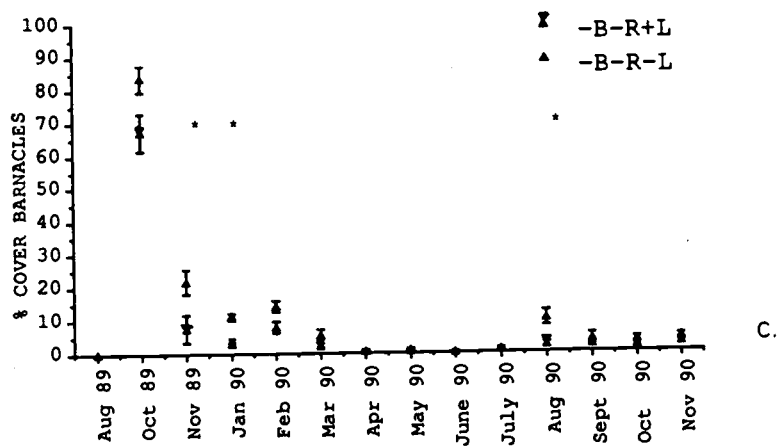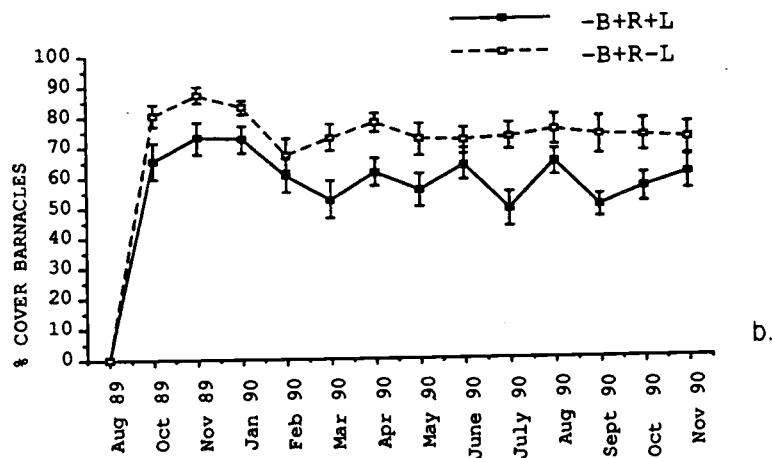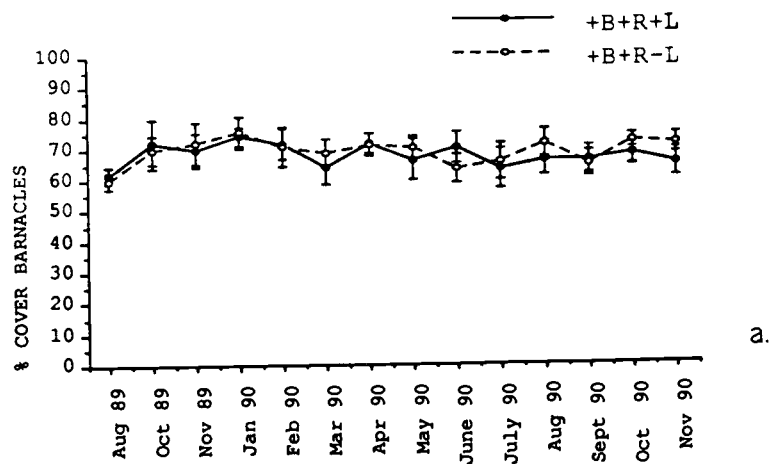
Figure III.5. Diatom abundance on mussels at a. Fogarty Creek, and B. Boiler Bay. See figure III.3 for caption codes.

Figure III.5
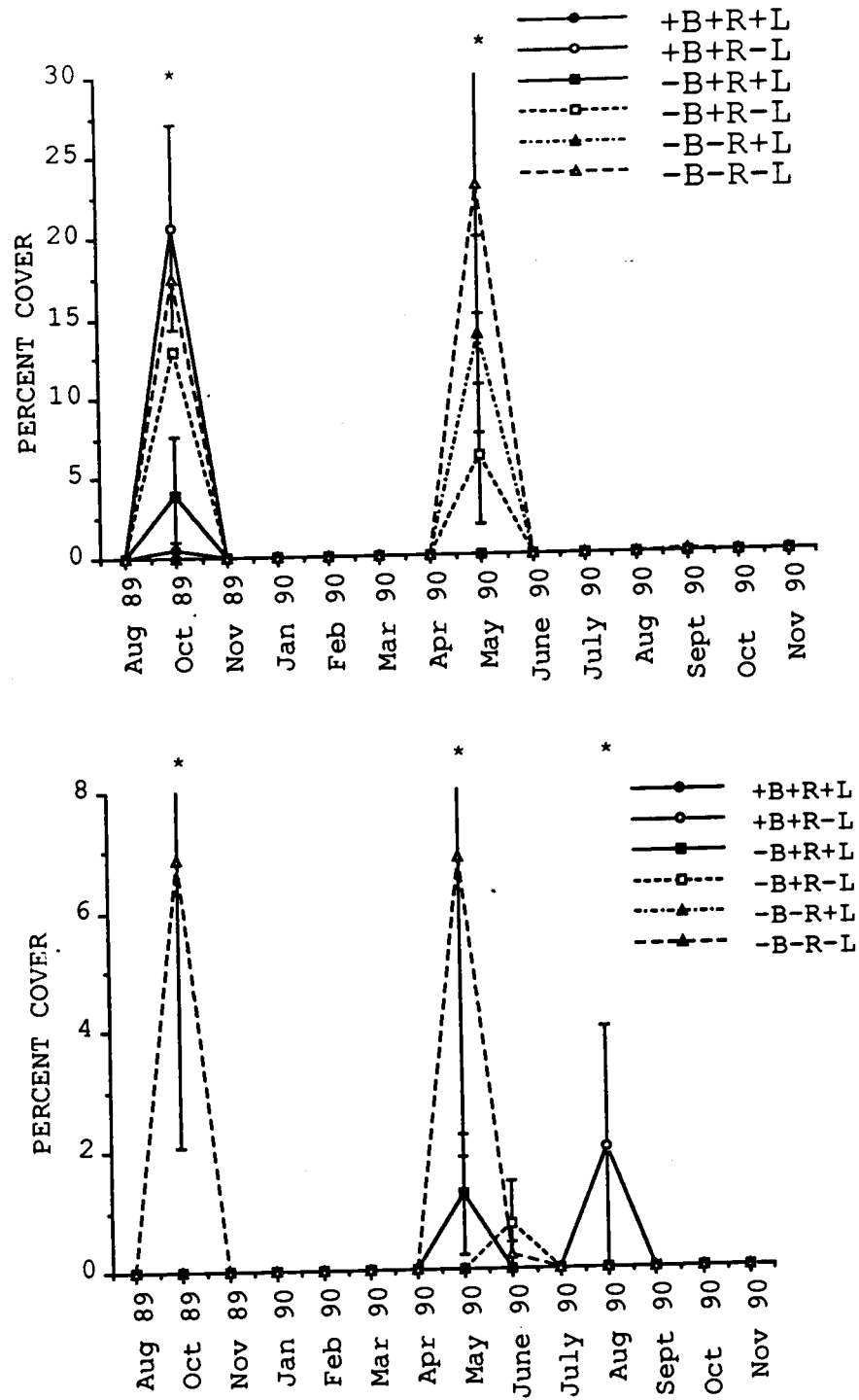
Table III.2 Summary of RMANOVA on abundance of barnacles (<u>Balanus glandula</u>) on mussels. Data were log-transformed prior to analysis.

Between treatments

SOURCE	DF	MS	F	P		
Site	1	3632.4	10.15	0.003		
Barnacle	2	71889	201.03	0.001		
Limpet	1	3242.9	9.07	0.005		
Barnacle*Limpet	2	617.07	1.73	0.19		
Site*Barnacle	2	1413.5	3.95	0.03		
Site*Limpet	1	114.17	0.32	0.57		
Site*Barnacle* Limpet	2	172.2	0.48	0.62		
Error	30	357.59				

Within treatments					G-G	H-F
Date	12	18485	384.33	0.001	0.001	0.001
Date*Site	12	325.37	6.76	0.001	0.001	0.001
Date*Barnacle	24	4555.3	94.71	0.001	0.001	0.001
Date*Limpet	12	266.46	5.54	0.001	0.002	0.001
Date*Barnacle* Limpet	24	87.37	1.72	0.012	0.10	0.06
Date*Site*Barnacle	24	128.78	2.67	0.001	0.021	0.001
Date*Site*Limpet	12	41.34	0.86	0.58	0.46	0.51
Date*Site*Barnacle* Limpet	24	33.13	0.69	0.96	0.65	0.73
Error	30	48.09				

Table III.2 continued.

Greenhouse-Geisser Epsilon: 0.242: Huyn-Feldt Episilon: 0.422

MULTIVARIATE RMANOVA

	Hypoth.	df	Error df	F	P
Date					
Wilks-Lambda	0.01	12	19	108.8	0.001
Pillai Trace	0.98			108.8	0.001
H-L Trace	68.72			108.8	0.001
Date*Site					
Wilks-Lambda	0.13	12	19	10.52	0.001
Pillai Trace	0.87			10.52	0.001
H-L Trace	6.65			10.52	0.001
Date*Barnacle					
Wilks-Lambda	0.01	24	38	14.30	0.001
Pillai Trace	1.35		40	3.43	0.001
H-L Trace	63.02		36	47.29	0.001
Date*Limpet					
Wilks-Lambda	0.32	12	19	3.35	0.009
Pillai Trace	0.68			3.35	0.009
H-L Trace	2.12			3.35	0.009

Table III. 2 continued.

Date*Barnacle*Limpet

Wilks-Lambda	0.15	24	38	2.39	0.008
Pillai Trace	1.15		40	2.25	0.011
H-L Trace	3.37		36	2.52	0.006

Date*Site*Barnacle*
Limpet

Wilks-Lambda	0.29	24	38	1.38	0.186
Pillai Trace	0.90		40	1.37	0.183
H-L Trace	1.83		36	1.37	0.191

Table III.3. Species composition and abundance of algae (other than <u>Endocladia</u>), that recruited onto mussels and barnacles.

Species	maximum percent cover
<u>Mastocarpus</u> <u>papillatus</u>	24
<u>Ulva</u> sp	4
<u>Porphyra</u> sp	10
<u>Pelvetiopsis</u> <u>limitata</u>	10
<u>Iridaea</u> <u>cornucopiae</u>	8
red crust	10

Limpets also reduced the abundance of diatoms ($F=7.52$, $p=0.006$, 1df). However, even in limpet exclusion plots, neither diatoms nor other algal species persisted beyond three months.

Algal recruitment onto barnacle epibionts (tertiary substrate)

Barnacles facilitated algal colonization (RMANOVA for all algal species, $F=26.35$, $p=0.001$, 2df). Algae settled almost exclusively onto the side walls of barnacles on mussels. Algal recruitment was higher at Fogarty Creek than Boiler Bay (Table III.4). In RMANOVA analysis "site" was a significant main effect in univariate (between subjects), and in multivariate tests. Endocladia was by far the most abundant alga to settle on barnacles. At Fogarty Creek percent cover reached an average of 21% (Figure III.6) on barnacles compared to <2% on mussels. In addition Endocladia persisted on barnacles throughout the experiment, while few plants growing directly on mussels survived beyond three months.

Because of the generally low occurrence of other algal species (listed in Table III.3), I grouped them together for analysis. These species recruited more frequently onto

barnacles than onto mussels (G/q=11.0, p<0.01, n=48). In addition there was no difference between algal recruitment onto +B+R (adult and recruit) and -B+R (recruit only) treatments (G/q=0.20, p>0.05, n=45).

Limpet Effects

When all algal species were analyzed together, the overall effect of limpets was to increase algal abundance (F=9.5, p=0.002, 1df). However, because few species other than <u>Endocladia</u> persisted on barnacles, and only <u>Endocladia</u> recruited at Boiler Bay, this result is largely due to limpet effects on <u>Endocladia</u>. The effect of limpets on <u>Endocladia</u> was analyzed separately by RMANOVA. However, because other algal species were scarce, I did not analyze other species separately. Limpets appeared to enhance <u>Endocladia</u> abundance (Figures III.6, III.7). In RMANOVA analysis, "Limpet" was significant as a main effect in univariate tests. However it was not significant in multivariate tests, and so results must be interpreted with caution (Table III.4).

On primary substrate, limpets can indirectly inhibit algae by bulldozing barnacles. In this experiment, this indirect interaction appeared to be largely unimportant. It

was, in fact, evident only once during the experiment. In July 1990, at Fogarty Creek barnacles settled onto mussels. Limpets prevented barnacle recruitment in -B-R+L treatments. However barnacles successfully recruited in the absence of limpets (-B-R-L). Before these barnacles were removed by monthly scraping, <u>Endocladia</u> had settled onto barnacles (in the absence of limpets) (Figure III.6c). There was no algal recruitment in the +L plots.

Figure III.6. <u>Endocladia</u> recruitment and abundance at Fogarty Creek. Results show <u>Endocladia</u> recruitment onto barnacle epibionts (tertiary substrate). * denotes a significant limpet effect on <u>Endocladia</u> abundance (p<0.05). See Figure III.3 for caption codes.

Figure III.6

a.

b.

c.
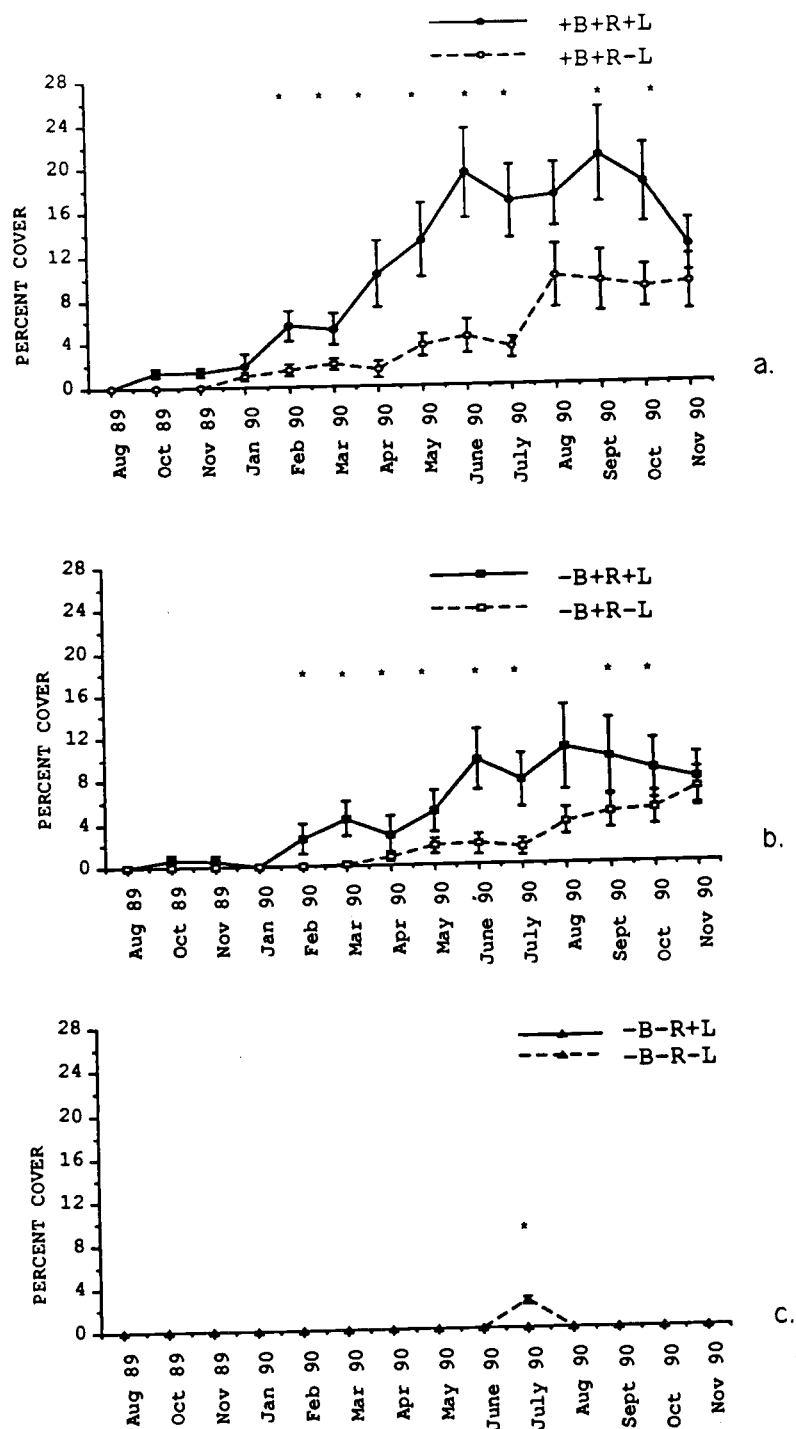
Figure III.7. <u>Endocladia</u> recruitment and abundance at Boiler Bay. <u>Endocladia</u> did not recruit directly onto mussels (secondary substrate). * denotes a significant limpet effect on <u>Endocladia</u> abundance (p<0.05). See Figure III.3 for caption codes.

Figure III.7
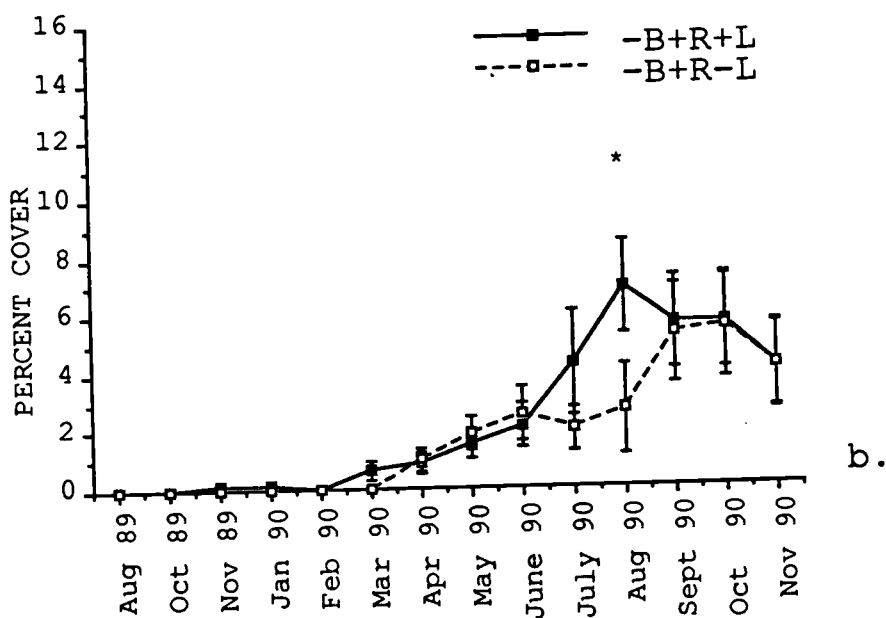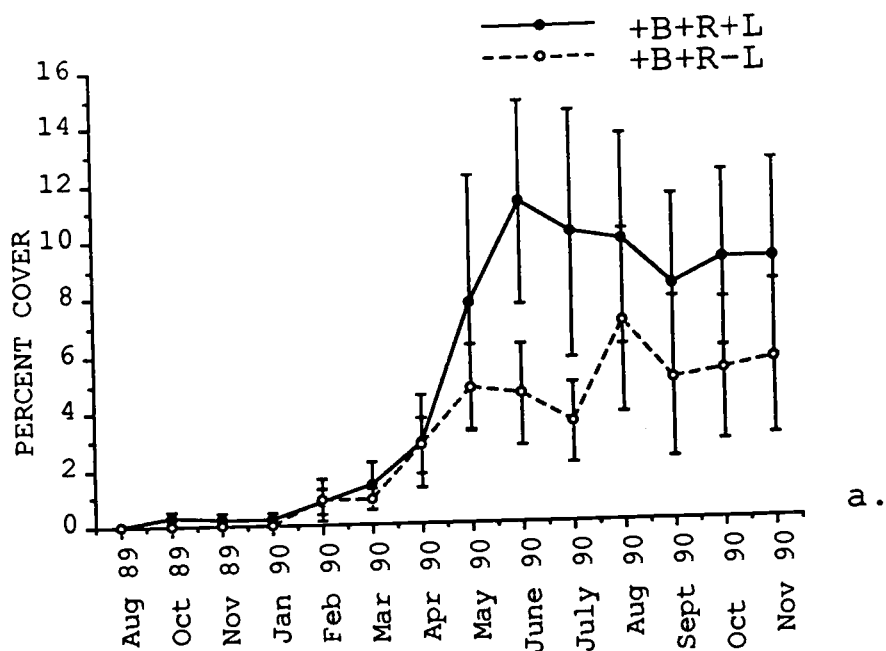
Table III.4 Summary of RMANOVA on abundance of <u>Endocladia</u> on barnacle epibionts. Data were arcsin transformed prior to analysis.

<u>Between treatments</u>

SOURCE	DF	MS	F	P		
Site	1	0.04	3.90	0.05		
Barnacle	2	0.19	17.33	0.001		
Limpet	1	0.078	7.16	0.012		
Barnacle*Limpet	2	0.03	2.68	0.85		
Site*Barnacle	2	0.015	1.37	0.27		
Site*Limpet	1	0.23	2.16	0.15		
Site*Barnacle* Limpet	2	0.007	0.617	0.546		
Error	30	0.001				
<u>Within treatments</u>					G-G	H-F
Date	12	0.025	27.76	0.000	0.001	0.001
Date*Site	12	0.001	1.34	0.19	0.27	0.25
Date*Barnacle	24	0.008	8.76	0.001	0.001	0.001
Date*Limpet	12	0.003	3.60	0.001	0.02	0.001
Date*Barnacle* Limpet	24	0.002	0.36	0.998	0.889	0.95
Date*Site*Barnacle	24	0.001	0.78	0.77	0.58	0.64
Date*Site*Limpet	12	0.001	0.98	0.47	0.40	0.42
Date*Site*Barnacle* Limpet	24	0.001	0.36	0.998	0.89	0.95
Error	360	0.001				

Table III.4 continued.

Greenhouse-Geisser Epsilon: 0.228: Huyn-Feldt Episilon: 0.395

MULTIVARIATE RMANOVA

	Hypoth.	df	Error df	F	P
Date					
Wilks-Lambda	0.16	12	19	8.26	0.001
Pillai Trace	0.83			8.26	0.001
H-L Trace	5.21			8.26	0.001
Date*Site					
Wilks-Lambda	0.38	12	19	2.54	0.003
Pillai Trace	0.61			2.54	0.003
H-L Trace	1.61			2.51	0.003
Date*Barnacle					
Wilks-Lambda	0.14	24	38	2.69	0.003
Pillai Trace	1.13		40	2.18	0.014
H-L Trace	4.32		36	3.23	0.001
Date*Limpet					
Wilks-Lambda	0.43	12	19	2.08	0.07
Pillai Trace	0.56			2.08	0.07
H-L Trace	1.31			2.08	0.07

Table III. 4 continued.

Date*Barnacle*Limpet

Wilks-Lambda	0.32	24	38	1.21	0.29
Pillai Trace	0.81		40	1.14	0.34
H-L Trace	1.70		36	1.27	0.25

Date*Site*Barnacle*

Limpet

Wilks-Lambda	0.49	24	38	0.78	0.73
Pillai Trace	0.65		40	0.81	0.70
H-L Trace	1.00		36	0.75	0.76

DISCUSSION

Of the direct and indirect interactions among algae, barnacles, and limpets which have been shown to be important on rock substrate (Figure III.1), only two were relatively important in this study. These were bulldozing by limpets (which depended on barnacle recruitment), and algal facilitation by barnacles (Figure III.8). Herbivory was generally unimportant (except for limpet effects on diatoms). Interspecific competition was not detected, and indirect interactions were largely unimportant in this assemblage. One reason for this result may be that environmental factors limit algal abundance on mussels (see below), and as a result interspecific interactions are less important (as predicted by Menge and Sutherland 1987).

Limpets seemed to have relatively little effect on algal recruitment. However, some limpets did recruit into the limpet exclusion plots, and it is possible that a few recruits could have had large effects. However, it seems unlikely that these recruits alone accounted for the overall low abundance of algae in limpet exclusion plots. Most limpet recruits were found on rock substrate within

Figure III.8. Main interactions between limpets, barnacles, and algal epibionts on mussel substrate (____ denotes direct effect). In contrast to interactions on rock substrate (see figure III.1), only direct effects were demonstrated, Limpets bulldozed barnacles (-) (except at high barnacle recruitment). Barnacles facilitated _Endocladia_ (+), but had little effect on other algal species. Limpets enhanced _Endocladia_ abundance (+).

Figure III.8
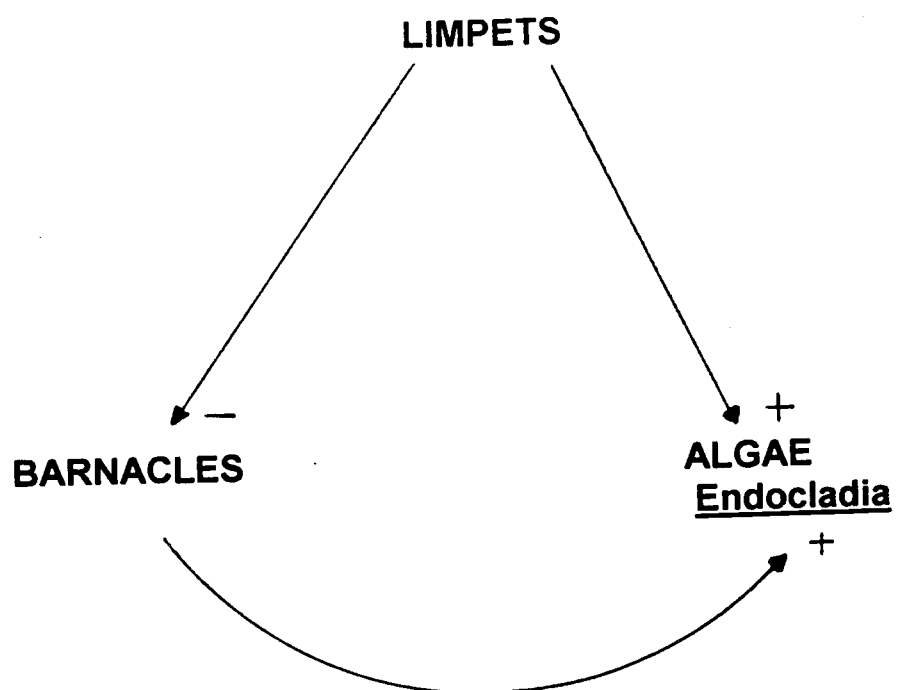
the plot area, and not on mussel shells. In addition, algal species (including Mastocarpus, Gigartina, and Fucus) recruited successfully on rock substrate within the fenced exclusion plots, and not on mussels. Nevertheless, the potential impact of other grazers, which could have migrated into the plots, is unknown.

Recruitment onto mussels and barnacle epibionts

Barnacles were always abundant on unmanipulated mussels at both sites, and recruitment did not appear to limit Balanus. Interestingly Chthamalus did not successfully establish on mussels. This species is an uncommon epibiont on mussels at many sites on the Oregon coast (Lee and Ambrose 1989; author's personal observation). At high recruitment intensity, barnacles swamped limpets. This is similar to the results of Sutherland and Ortega (1986) who found no effect of limpets (Siphonaria gigas) on barnacle (Chthamalus fissus) abundance during periods of high barnacle recruitment.

In this study, few algae recruited directly onto mussels, and most algal recruitment was onto barnacle epibionts. In an earlier study, Dayton (1973) also observed a similar pattern of recruitment for Postelsia palmaeformis

These results suggest that mussel shells may be an unsuitable settlement substrate for algae. More variable temperatures, and a smoother surface may result in physical conditions that are too harsh for sporeling survival (see below). The low algal recruitment levels recorded here, even at low limpet densities, contrast with Suchanek's (1979) study. Suchanek found that, in the absence of grazers, fouling species on mussels increased. However, Suchanek did not distinguish between settlement directly onto mussels, and onto barnacles on mussels. In addition, much of the fouling on mussels resulted from increased barnacle cover in the absence of grazers. It is possible that increased algal cover in Suchanek's study was due to an initial increase in barnacles followed by subsequent algal settlement onto barnacles. However, it is not possible to determine which factor was most important in that study based on the published data.

One puzzling result of this study is that limpets appeared to enhance the abundance of Endocladia. This is despite earlier results showing that Endocladia forms a substantial part of limpet's (Lottia pelta) diet (Craig 1968). Other studies on rock substrate have noted that Endocladia is more abundant in the presence of limpets (Sousa 1984, Farrell 1991, Grubba and Brosnan in prep).

Sousa suggested that <u>Endocladia</u> is dependent on grazers removing competitively superior, but palatable, algal species. However, in this study there were few, or no other algal species present, and so this indirect positive effect does not explain its increased abundance. Other explanations include the suggestion that fertilization by limpet wastes can increase algal growth rates and abundance. Additionally some authors have suggested that grazers can increase the abundance and distribution of algal species, by egesting undigested fragments, that subsequently germinate (e.g., Santelices et al. 1983, Santelices and Ugarte 1987, Santelices and Martinez 1988). The mechanism here is unknown and deserves further attention.

Factors affecting assemblages on rock and mussel substrate.

An aim of this study was to determine which factors affect epibiont colonization, and whether the same factors are equally important on rock and mussel substrates. On rock substrate, barnacles are important in facilitating the recruitment of many algal species (Lubchenco 1978, Farrell 1991). However, in this study only <u>Endocladia</u> recruited in any abundance onto barnacles. Other algal species did not persist. <u>Endocladia</u> is a turf species (growing in upright

and prostrate forms), and seems to be resistant to harsh
conditions (e.g., Hay 1981, Sousa 1984, Farrell 1989, 1991).
On some shores, it is more abundant than many other algal
species in the high intertidal zone (Glynn 1964). Thus,
Endocladia may persist in harsh conditions on barnacles on
mussels, that are lethal to other algal species.

It is likely that mussels are a more physiologically
stressful habitat for newly settled propagules. Temperature
data collected on 14 mussels at Boiler Bay in May 1990
showed that temperatures on the surface of a mussel was up
to $4^{o}C$ higher than on basalt substrate approximately 0.5 m
away (t=5.25, p<0.01, 32df). Other factors, such as
desiccation, may also be important. The distribution of
other algal epibionts tends to support the suggestion that
environmental stress limits the composition of algae on
mussels. Species such as Mastocarpus, Fucus and Pelvetiopsis
are more abundant on large mussel beds that are shaded, and
on sloping surfaces that remain moist (e.g., at Little Whale
Cove, personal observation). These conditions may offer more
favorable micro-climates. In this study, experimental plots
were set up in small mussel beds, and on horizontal
surfaces. Thus more stressful environmental conditions in
these beds may partially explain the low algal recruitment
in experimental plots.

These results are consistent with predictions of the environmental stress model (Menge and Sutherland 1987), which predicts that, under harsh conditions, diversity will be low and competition relatively unimportant.

The main interaction between mussels and barnacles on primary substrate is competitive: mussels outcompete barnacles (Paine 1966, 1973, Dayton 1971). However, because mussels can subsequently facilitate barnacles, the net effect of mussels may be beneficial to barnacles. For instance Lee and Ambrose (1989) found that, on average, barnacle population density on mussels was 128% the density on primary substrate. In addition barnacles on mussels may grow faster (Laihman and Furman 1986), and have higher survivorship and recruitment rates (Lohse 1993b).

On primary substrates, algae may outcompete barnacles and inhibit their recruitment (e.g., Dayton 1971, Menge 1978, Hawkins 1981, Hawkins and Hartnoll 1983, Underwood et al. 1983). However, the lack of algae on most mussels implies that barnacles generally do not compete with algae for space on mussels. The overall effect of mussels on barnacle epibionts may be to provide them with competitor-free space. Lohse (1993b), for instance, noted that some

algal species that overgrow barnacles were less abundant on mussel shells.

The outcome of algal interactions may vary between primary and secondary substrate. For instance, on rock surfaces, Endocladia is often a minor component of the algal assemblage, rarely exceeding 10% cover in mixed algal groups (Paine 1974, Sousa 1984, Farrell 1989, 1991, Brosnan and Crumrine 1992a). However, in Oregon, Washington and Northern California, Endocladia is usually the dominant algal-epibiont on mussels (Sousa 1984, Brosnan and Crumrine 1994). In Northern California, this alga covers an average of 40.7% of mussel-shell surface, and only a maximum of 6.6% on primary substrate (Sousa 1984). Endocladia may cover up to 80% of mussel-shell surface in Oregon (Brosnan and Crumrine 1994), and reached a maximum of 40% cover on some mussels in this study. Other algal species are less common on mussels (Sousa 1984, Brosnan and Crumrine 1992a), although they are often abundant on primary substrate on the same shore (Brosnan and Crumrine 1992a).

Sousa (1984) characterized Endocladia as both grazer-resistant and grazer-dependent (sensu Gaines and Lubchenco 1980). He suggested that, on primary space, Endocladia is a competitively inferior species, outcompeted for light by

other algae, and consequently grazer-dependent. On primary substrate, its distribution reflects both indirect facilitation, and the presence of favorable microenvironments where it can establish and subsequently spread vegetatively (Sousa 1984, Farrell 1991). The dominance of Endocladia on mussel shells seems less grazer-dependent, although it is apparently grazer-enhanced. Rather, the dominance of Endocladia on mussels shells may be due primarily to an ability to withstand harsh environmental conditions (see above). Thus the overall effect of mussels on Endocladia may be to provide it with a "competitor-free habitat"

Ultimately Endocladia smothers barnacles and spreads vegetatively onto the mussel shells. I examined Endocladia on mussels at all sites and always found either an intact barnacle, or remains of barnacle tests at the base of the plant. This was also often true for other algal species, including Mastocarpus, Fucus and Pelvetiopsis. Barnacle mortality caused by algal overgrowth has frequently been observed (Burrows and Lodge 1950, Dayton 1971, Lewis and Bowman 1975, Underwood and Denley 1979, Farrell 1991, but see Jernakoff 1983).

Unlike the results of many studies on rock substrate (references above), I found relatively little evidence of indirect effects. The relative unimportance of indirect effects may stem from three factors. Firstly, the epibiont community on mussels is species-poor when compared to adjacent rock. Competitive interactions are largely absent in this species-poor assemblage. Secondly the algae appear to be recruitment limited. As predicted by Sutherland (1990), competition is less intense and indirect effects less important when recruitment limits abundance.

Finally, high barnacle densities may reduce the importance of interspecific interactions. In effect, barnacles swamp competitors and grazers, which do not exert significant negative effects. In my study, high densities of barnacle recruits were immune to limpet bulldozing. This, in effect, weakened the interaction between limpets and barnacles. Thus any other factors which affect limpet density (e.g., shorebird predation; Frank 1965, 1981, Marsh 1986a, b, Wootton 1992, 1993), are not expected to affect barnacle density, or other interactions in the epibiont community. In this case, high recruitment leads to weaker interactions, in contrast to the predictions of Sutherland (1990). We may therefore expect fewer indirect interactions with high recruitment, in this special case.

The net outcome of all these interactions is that indirect effects are relatively unimportant in this epibiont assemblage. This result gives only partial support to the predictions of Sutherland (1990), that indirect effects are more important at high recruitment levels. The result does however support the underlying assumption of Sutherland's work, that indirect effects are more important in communities with strong interactions, a prediction also made by other researchers (e.g., Bender et al. 1984, Dethier and Duggins 1984, Dungan 1986, Schoener 1993, 1994, Menge in press).

Conclusion

In this study three sets of interactions appeared to be the most important. Facilitation of algae by barnacles, bulldozing by limpets, and enhancement of Endocladia in the presence of limpets. However the importance of these interactions depended on barnacle recruitment. In the absence of barnacles, bulldozing did not occur. On mussels (secondary substrate), barnacles appear to be the key species that determine whether an algal epibiont assemblage will develop. Thus, the presence or absence of barnacles can indirectly affect mussel growth, and mussel survival under extreme conditions, by determining algal colonization. This successional pathway is similar to succession on rock substrate, where barnacles facilitate algae (Farrell 1991). However, it appears that in some mussel beds, environmental stress may regulate algal recruitment, and barnacle facilitation may be less important.

Contrary to studies of Suchanek (1979), grazers alone did not control the abundance of algae on mussels. This study demonstrated that a combination of environmental factors, and interspecific interactions determined algal cover. Santelices and Martinez (1988) also found that small grazers alone were not important in determining algal abundance in mussel beds. Instead environmental conditions,

especially desiccation, algal life history, and filtration by mussels affected algal composition and abundance. Algal epibionts can have strong effects on mussels (Paine 1974 1979, Suchanek 1979, Witman and Suchanek 1984, Dittman and Robles 1991, Chapter II). However whether these interactions occur depends on the effects of at least two other groups, barnacles and limpets.

CHAPTER IV

EFFECTS OF HUMAN TRAMPLING ON MARINE ROCKY SHORE
COMMUNITIES

Deborah M. Brosnan
Department of Zoology
Oregon State University
Corvallis OR 97331
and
Lana L. Crumrine
Department of Biology
University of Oregon
Eugene OR 97403

ABSTRACT

The effects of human trampling on two marine intertidal communities were experimentally tested (the upper-shore algal-barnacle assemblage, and mid-shore mussel bed communities). On two shores, experimental plots were trampled 250 times every month for a year, and then plots were allowed to recover for a further year.

Results from the upper shore community showed that canopy-forming algae were susceptible to trampling, and suffered significant declines shortly after trampling started. Canopy cover remained high in untrampled control plots. Barnacles were crushed and removed by trampling. Algal turf was resistant to trampling, and increased in

relative abundance in trampled plots. In general the algal-barnacle community recovered in the year following trampling.

In the mussel bed community, mussels from a single layer bed were removed by trampling, By contrast, mussels at a second site were in two-layers, and only the top layer was removed during the trampling phase. However, mussel patches continued to enlarge during the recovery phase, so that by the end of the second year, experimental plots at both sites had lost mussels and bare space remained. Mussel beds did not recover in the 2 years following cessation of trampling. Control plots lost no mussels during the trampling and recovery phase. Barnacle and algal epibionts on mussels were significantly reduced by tramping.

Overall, trampling can shift community composition to an alternate state dominated by low profile algae, and fewer mussels.

INTRODUCTION

The last decade has seen increased interest in human impact on intertidal areas. Studies have focused on harvesting (e.g., Moreno 1984, Castilla and Duran 1985, Olivia and Castilla 1986, Ortega 1987, Castilla and Bustamente 1989, Duran and Castilla 1989, Godoy and Moreno 1989, Underwood and Kennelly 1990), and more recently on trampling (Zedler 1976, 1978, Beauchamp and Gowing 1982, Ghazanshai et al. 1983, Cole et al. 1990, Kingsford et al. 1991, Povey and Keough 1991, Brosnan and Crumrine 1992a, b, Brosnan 1993). Trampling is an important ecological phenomenon on many shores, and its effects are likely to increase as use of shore areas increase.

Effects of trampling have been studied in terrestrial systems since 1917 (Jeffreys 1917, Shantz 1917). Bates (1934, 1935) began the systematic study of trampling effects on terrestrial habitats. Since then numerous studies have shown trampling to be detrimental in alpine meadows, forests, and sand dunes (e.g., Nickerson and Thibodeau 1983, Burden and Randerson 1971, Liddle 1975, Hylgaard and Liddle 1981). In marine systems, repeated surveys of rocky intertidal communities near areas of dense human population indicated that marine communities had changed as population density increased (Widdowson

1971, Boalche et al. 1974, Thom and Widdowson 1978). More recent studies have confirmed that human impact can affect marine communities. For example, certain algal and bivalve species normally common on rocky shores have been found to be rare at heavily visited sites (Beauchamp and Gowing 1982, Povey and Keough 1991, Brosnan and Crumrine, 1992a, b, Brosnan 1993).

In this paper we address the effect of human trampling on rocky intertidal areas on the Oregon coast U.S.A. I carried out an experimental study of trampling and looked at post-trampling recovery. Our interest in this is twofold. Trampling may change community composition and diversity, and hence is of concern to ecologists, conservation biologists, and managers of shore areas. Secondly, Pacific rocky shores are well studied, and abiotic disturbance is an important structuring force in this community (Harger 1968, Harger and Landenberger 1970, Dayton 1971, Sousa 1979, 1984a, b, 1985, Paine and Levin 1981). Trampling, because it removes biomass and creates space, is a disturbance. We compare the effects of trampling with other disturbances such as log damage and wave shear.

Trampling affects marine organisms in a variety of ways:

1. Directly, by removing all or part of an individual through crushing and dislodgment, or by weakening attachment strength, which increases the risk of dislodgment during storms.

2. Indirectly, by removing other species that interact through competition, predation, or habitat provision. For instance, mussels <u>Mytilus</u> <u>californianus</u> Conrad provide a habitat for more that 300 matrix species (Suchanek 1979). We hypothesized that these effects would cause changes in both community composition and susceptibility to storm damage.

The effects of human trampling were studied in two exposed rocky intertidal communities: the upper shore barnacle-algal assemblage, and mussel beds in the mid intertidal zone. In mussel beds trampling effects on organisms occupying primary space, (mussels and gooseneck barnacles), and also epibionts on mussels were investigated.

BACKGROUND

Uppershore algal-barnacle assemblage

Rock surface on the upper shore is occupied by a variety of sessile invertebrates and algae. These include acorn barnacles (<u>Balanus glandula</u> Darwin and <u>Chthamalus dalli</u> Pilsbry), small mussels (<u>M. californianus</u>, and <u>M. trossulus</u> Gould), mussel recruits, and a variety of algal species including fucoids, <u>Pelvetiopsis limitata</u> (Setchell) Gardner; <u>Fucus distichus</u> Linnaeus; and red algae <u>Iridaea cornucopiae</u> Setchell and Gardner, <u>Mastocarpus papillatus</u> Kutzing, and <u>Endocladia muricata</u> (Postels and Ruprecht) J. Agardh). In this part of the shore, no one algal species was dominant. <u>E. muricata</u> grew as both a canopy (tall and upright growth form) and a turf-like species. The remaining algae are canopy forming species. Mobile herbivores such as limpets (<u>Lottia digitalis</u> Lindberg, <u>L. strigatella</u> Eschoscholtz, and <u>L. pelta</u> Eschoscholtz), and snails (<u>Littorina scutulata</u> Gould) are common; but were not studied in this experiment.

Mussel bed community

Primary substrate

Primary substrate in the mid-intertidal zone is
dominated by mussels M. californianus. Mussels form dense
beds of one to many layers which provide habitat for many
invertebrate and algal species (Suchanek 1978). Logs and
winter storms dislodge mussels and create patches of bare
space (e.g., Harger, 1968, Dayton, 1971, Harger and
Landenberger, 1979, Sousa, 1979, 1984b, 1985, Paine and
Levin, 1981). In our study areas, mussels occupied about
95% of the primary space and gooseneck barnacles
(Pollicipes polymerus Sowerby) covered the remaining 5%
(there was no bare space). The Fogarty Creek experimental
mussel bed was two layers thick; mussels were tightly
packed, and it was difficult to move any individual
mussel. The mussel bed at Little Whale Cove was a
monolayer, and mussels were less tightly packed than at
Fogarty Creek.

Epibionts on mussel shells

Mussels outcompete algae and other sessile
invertebrates for primary space on rocky shores (Paine,
1966, 1974, Dayton, 1971, Paine and Levin, 1981). Many of

these competitively subordinate species subsequently settle on mussel shells and persist as epibionts (Lee and Ambrose, 1989). Because these epibionts protrude from the bed, they may be more vulnerable to the effect of trampling. Barnacles <u>B.</u> <u>glandula</u>, and <u>C.</u> <u>dalli</u> are the main invertebrate epibionts on mussel shells. These were abundant on mussels at both sites. <u>E.</u> <u>muricata,</u> a common algal epibiont on mussel shells in Oregon (Brosnan and Crumrine 1992a), was common on Little Whale Cove mussels but was rare on mussels in Fogarty Creek plots.

METHODS

Study sites

Trampling experiments were conducted at two sites on the Oregon coast: Fogarty Creek ($44.51^{O}N:124.03^{O}W$) and Little Whale Cove ($44.20^{O}N:124.05^{O}W$). Both sites consist of exposed rocky (basalt) platforms. Algal-barnacle and mussel communities were found on slightly sloping surfaces. We chose these sites because human access to them is restricted, and we did not want existing trampling to confound the results. It is necessary to cross private property to reach the shore from land, and heavy surf prevents access by boat. In addition, these sites are similar in exposure and substrate to other shores on the Oregon coast where trampling is more intense (Brosnan and Crumrine, 1992a, b). Apart from other marine biologists, humans were rarely present when we visited these sites. At each site we set up experiments to study the effect of human trampling on two assemblages.

Experimental design

The effects of trampling on intertidal communities were tested using a randomized block design. At each site four blocks were set-up in the algal-barnacle assemblage

(from about + 2 to + 2.5 m above mean low water (MLLW)),
and four blocks were set-up in the mussel bed community
(from about + 1 to + 1.5 m above MLLW). There were two
treatments per block, trampled and non-trampled controls.
These were randomly assigned to plots within each block.
Trampled and non-trampled plots within a block were
separated by 0.5 m. Algal-barnacle plots measured 20 x 20
cm and plots in the mussel bed were 20 x 30 cm. The
corners of each plot were marked with unleaded model
paint. Mussels in each plot were individually marked with
a spot of non-toxic paint, and counted at the beginning of
the experiment. We trampled the experimental "trampled"
plots 250 steps on one day every month, from March 1990 to
March 1991. Trampling consisted of walking across an
experimental plot. This intensity was selected based on
studies of humans visiting nearby shores, where up to 228
steps per hr. were recorded (Brosnan and Crumrine, 1992a,
b). Compared to these visited sites, two hundred and fifty
steps per month represents a relatively low trampling
intensity at these two shores.

Recovery

Recovery of experimental plots was monitored in July
1991, September 1991 (6 months after trampling stopped)
and again in April 1992 (1 year after trampling).

STATISTICAL ANALYSIS

Data were collected on percent cover of primary space, secondary substrate (epibionts), and canopy species. Percent cover of each species was estimated by placing a clear vinyl sheet, marked with 100 randomly placed dots, directly over the plot. The number of dots directly over a species was counted. For algae and barnacles, primary percent cover was defined as the percent of the substrate on which a species is directly attached. Algal canopy was defined as the percent of the rock surface that a non-encrusting alga covers, although it may not be attached at that particular point. For mussels and goose-neck barnacles, percent cover was defined as the percent of rock surface covered by a species. We did not distinguish between the two species of acorn barnacle (C. dalli and B. glandula) since many individuals were too small to be identified. I collected data on epibiont abundance by estimating the percent cover of epibionts on 10 randomly chosen mussels in each plot. For each mussel the number of dots on a mussel-shaped vinyl sheet that were directly above a species were counted. Data on epibionts on all plots were collected prior to trampling. Subsequently data were collected monthly from April to July 1990 only, because mussels were lost due to trampling after July

1990. Initial pre-trampling data were collected from all plots.

Data were arcsine or log transformed to reduce heteroscedasticity (Sokal and Rohlf 1981) and analyzed by ANOVA using SYSTAT (Wilkinson 1990). Probability plots of the data were made to test for normality, and Bartlett's test was used to test for homoscedasticity of variances. Transformed data were analyzed by ANOVA. Transformations did not reduce heteroscedasticity to acceptable levels in primary mussel cover data. Consequently these data were analyzed using a non-parametric Kruskal-Wallis test. Initial pre-trampling data were analyzed to check for statistically significant differences between treatment and control plots prior to trampling. Data from each sampling period were analyzed separately.

RESULTS

Algal-Barnacle Assemblage

Algae

Algal canopy was high at both sites at the start of the experiment (Figure IV.1). For both sites combined, there was no difference between algal cover in trampled versus untrampled plots at the beginning of the experiment (F=0.014, p=0.091, df=1). Total canopy was similar on all trampled plots (mean=81.7%, se=3.6) and on all control plots (mean=80.2%, se=4.7) (Figure IV.1). Canopy cover in trampled plots declined rapidly at both sites after the onset of trampling, and remained at a consistently low level of 13% to 22% for the remainder of the trampling period (Figure IV.2). Control plots did not show such a decline; canopy cover remained high but tended to fluctuate more than in the trampled plots, and ranged from 60% to 97% (Figure IV.2).

At each site trampling significantly reduced algal cover within 1 month of trampling. At Fogarty Creek, algal cover in trampled plots decreased from 83.3% (se=2.5) in March 1990 to 22.5% (se=5.3) in April 1990. While canopy in control plots was 60% (se=6.6) in April (ANOVA for

April 1990, F=17.6, p=0.006, df=1). After that algal cover remained low in trampled plots for the remainder of the experimental trampling period, and ranged from 5% to 9.5%. By contrast canopy cover in control plots ranged from 58.4% to 87% in the same period. At Little Whale Cove, algal cover in trampled plots fell from 80% (se=7.1) in March 1990 to 33% (se=5.1) in April 1990. Canopy in control plots was 79.3% (se=3.6) in April 1990 (ANOVA for April 1990 F=45.24, p=0.001, df=1). During the remainder of the trampling period canopy remained low on trampled plots and ranged from 19% to 35%. Canopy in control plots ranged from 63% to 92% in the same period.

Canopy-forming, foliose algae were more susceptible to trampling, and when grouped together, mean cover decreased in trampled plots from 75% (se=3.5), to 9.1% (se=3.2) by August 1990. By contrast, foliose algal cover in control plots averaged 70% (se=8.1) in August 1990 (ANOVA for August 1990, F=12.45, p=0.001, df=1). Fucoids and M. papillatus showed large declines in trampled plots (from 9% to 1%) (Figure IV.2). In control plots, M. papillatus increased from 11% to 15% during summer 1990, and subsequently declined over winter.

_F._ _distichus_ cover decreased in both trampled and control plots in spring 1990 (Figure IV.2). However, in control plots, it gradually rebounded through summer 1990 and declined again during the following winter. By contrast in trampled plots, _F._ _distichus_ remained low throughout the summer and winter (cover ranged from 1% to 3%). _P._ _limitata_ declined rapidly from 16% to 1.5% in trampled plots. Cover in control plot ranged from 6% to 12.5% from March 1990 to March 1991. In winter 1991, cover was low in all plots (Figure IV.2).

_I._ _cornucopiae_ showed a large decrease in response to trampling (from an initial 38% to 14% in the first month). _I._ _cornucopiae_ canopy continued to decline in trampled plots until February 1991 when it rose from 4% to 8%. Percent cover in control plots remained high throughout the experiment, ranging from 29% to 52% (Figure IV.2).

_E._ _muricata_ showed the least changes in percent cover as a result of trampling. Initial cover in trampled plots was 5% (se = 1.5) and cover remained at 3% to 5% for the experimental period. Cover in control plots started at 11% (se=0.7) and declined gradually until August when it rose to 13.5% (se=1.3). By March 1991 cover was again 11%. _E._ _muricata_'s decline in trampled plots was due to the loss

of canopy cover of upright forms: low profile turf forms persisted near 4.5% (se=0.9) in trampled plots throughout the trampling phase (Figure IV.2).

Total canopy cover in control plots increased gradually from 69% in April to 85% in August, due to increased abundance of all species. Canopy declined during fall and winter. Settlement and growth of I. cornucopiae caused the large rise in canopy cover between January and February, 1991 (60% to 87%). All other canopy species declined slightly during this period, except for E. muricata. The decrease in March was also due primarily to I. cornucopiae loss, although the reason for this is unknown. Canopy cover in trampled plots did not show the same pattern as control plots except for a rise in February 1991. This increase again reflected an increase in I. cornucopiae from 4% to 8%. In contrast to control plots, the subsequent drop in canopy cover was due to declines in F. distichus, P. limitata, and I. cornucopiae

Recovery

Algal cover steadily increased after trampling stopped (Figure IV.1). Species recovering rapidly included I. cornucopiae, M. papillatus and E. muricata (Figure IV.2)

In the case of E. muricata, trampled plots increased in cover from 5.6% (se=1) in April 1991 to 19.5% (se=3) in April, 1992, (higher than the initial pre-trampling cover of 5% (se=1.5)).

Sessile Invertebrates

Barnacles

Initial barnacle cover differed between sites (F=81.78, p=0.0001, df=1), and sites were analyzed separately. Fogarty Creek trampled and control sites initially contained 66.6% (se=3.3) and 71% (se=7.7) respectively. At Little Whale Cove barnacles covered 21.3% (se=3.1) of primary substratum in trampled plots and 15% (se= 2.3) in control plots. At each site there was no initial difference in barnacle cover between control and trampled plots.(Fogarty Creek, F=0.38, p=0.56, df=1; Little Whale Cove F=2.88, p=0.14, df=1). Trampling significantly reduced barnacle cover at both sites (Figure IV.3). Barnacle cover declined from 66.6% to 7.2% in 4 months at Fogarty Creek. At Little Whale Cove cover fell from 21.3% to 5.5% in 6 months. Barnacle cover in control plots did not vary much from initial levels. Barnacle cover on trampled plots was significantly lower than

Figure IV.1. Percent cover of algal canopy at Fogarty Creek (a) and Little Whale Cove (b), during trampling March (1990-March 1991), and recovery (April 1991-April 1992) phases of the experiment. * and ** indicates significant difference between trampled and control plots at p=0.05 and p=0.01 levels respectively; error bars are standard error.

Figure IV.1

a.

b.
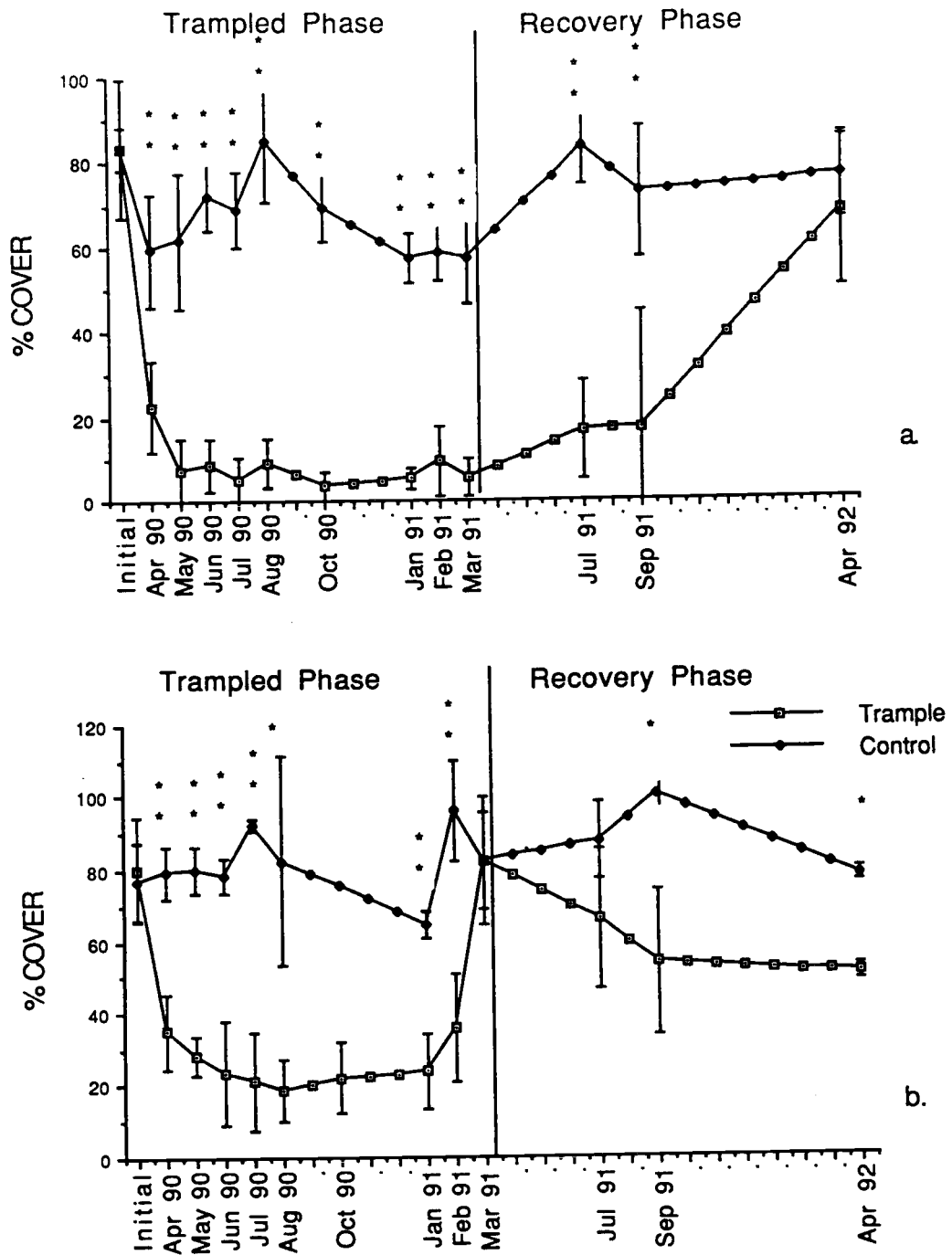
Figure IV.2. Canopy percent cover of individual algal species in trampled and control plots during trampling and the recovery phases. Results from Fogarty Creek and Little Whale Cove are combined.

Figure IV.2
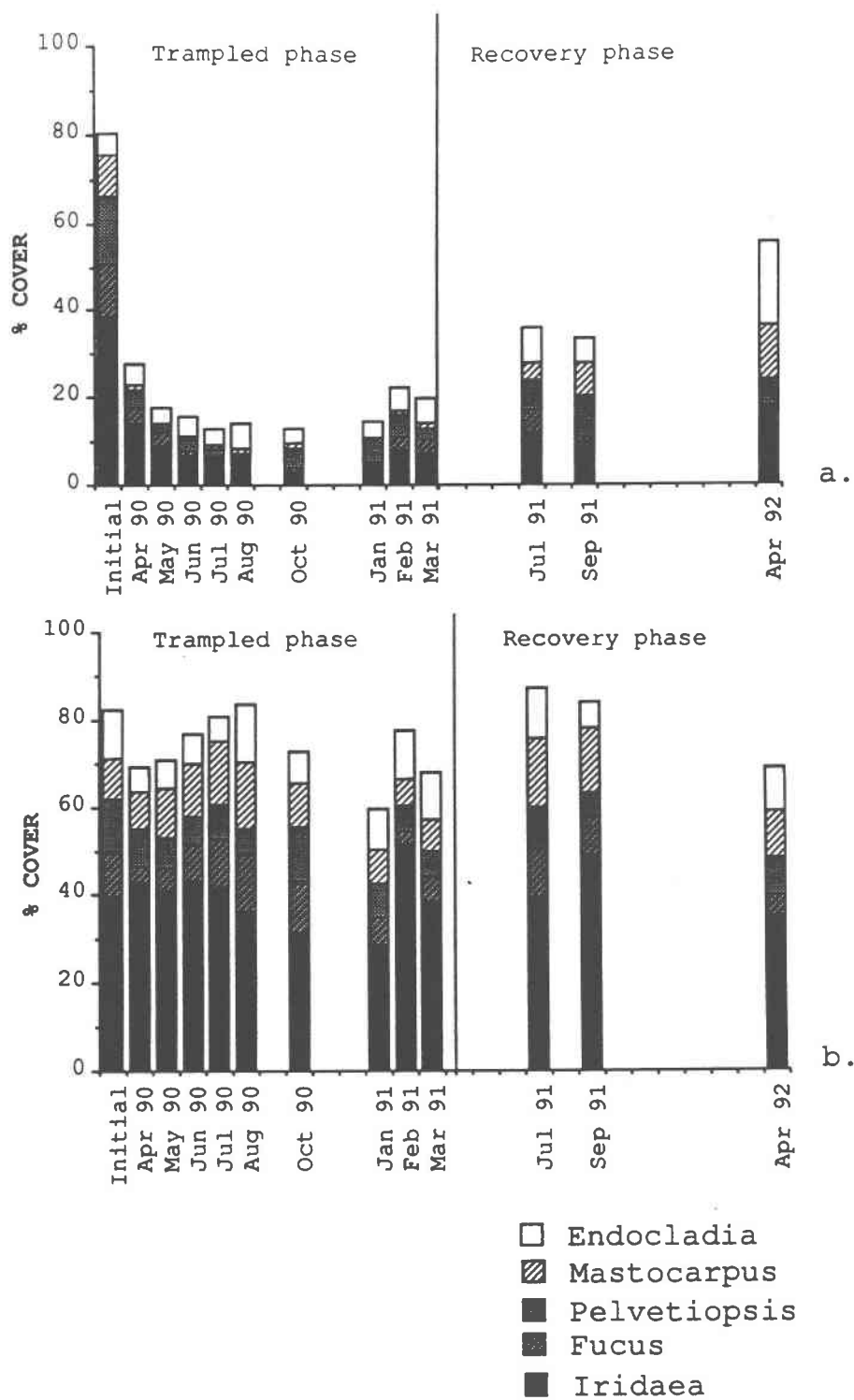
control plots until recruitment increased cover on trampled plots in March 1991. Barnacle density did not increase as much in control plots, because there was little available bare space.

Mussels

Small mussels (_Mytilus_ spp.) occupying primary space were scarce in all plots. Cover ranged from 1% to 3.5% in control plots during the study. Trampled plots initially had 2.5% (se=0.9) mussel cover. Within four months mussels were absent in all trampled plots and did not reappear.

Mussel-bed Community

Primary Substrate.

There was no difference between mussel cover in control and trampled plots at the beginning of the experiment (Fogarty Creek F=0.679, p=0.441, df=1); Little Whale Cove F=0.028, p=0.872, df=1); mussel cover averaged 97% (se=2.8) at both sites. Because of the differences in mussel bed structure sites were analyzed separately.

Figure IV.3. Primary cover of barnacles in trampled
and control plots at Fogarty Creek (a) and Little Whale
Cove (b) during trampling and recovery phases * and **
indicates significant difference between trampled and
control plots at p=0.05 and p=0.01 levels respectively;
error bars are standard error.

Figure IV.3
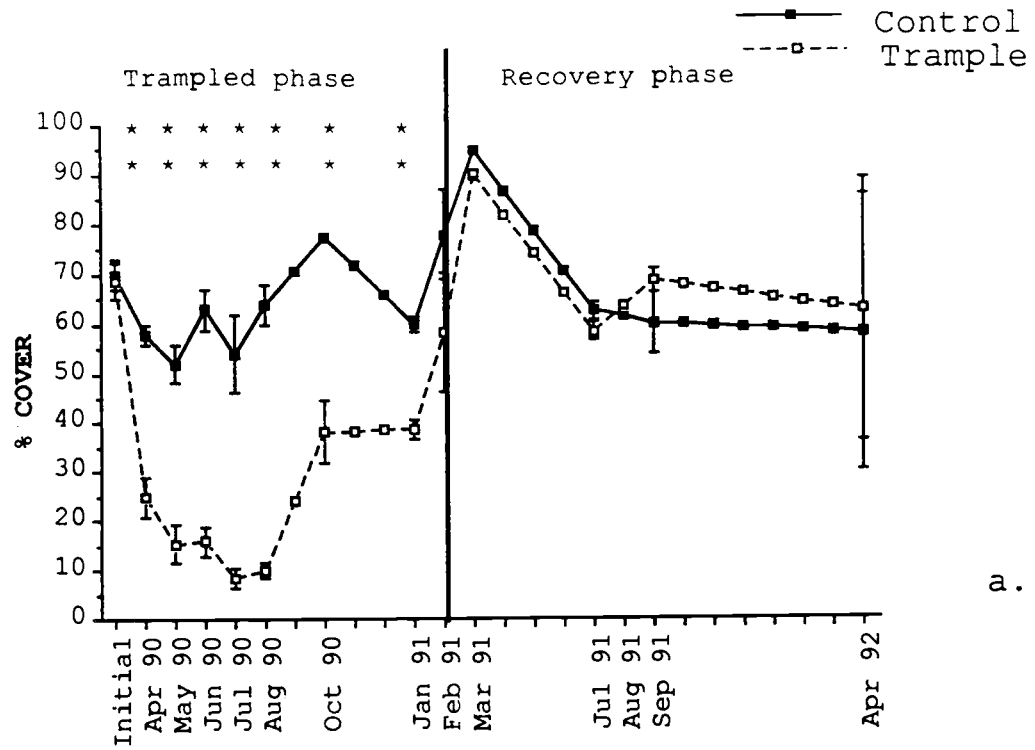
a.
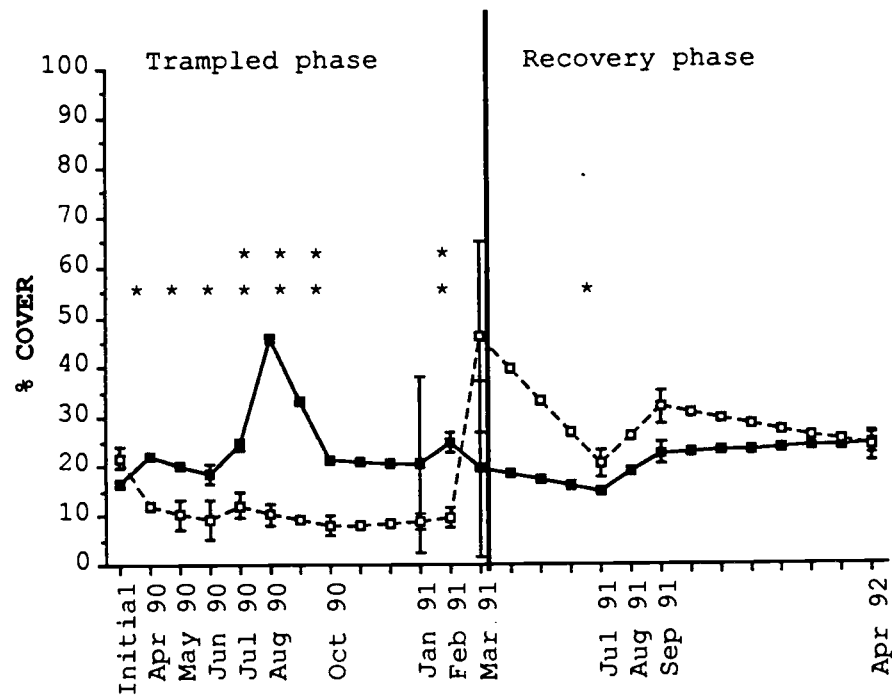
b.

At Little Whale Cove, there were large declines in mussel cover in trampled plots in April and May 1990 (Figure IV.4). This was due mainly to mussel loss from one plot: on a single day, 54% of the mussels were lost from one trampled plot. By May, a second trampled plot had begun to lose mussels. Mussel loss continued throughout the experimental period, so that by January 1991 two large patches had been created, one measuring 2700 cm^2 and the second measuring 450 cm^2. These patches were much larger than our original plot size. A third small patch had formed in another trampled plot by this stage, and 1% of the mussels were lost. Bare space occupied these patches. In August 1990 mean cover of mussels in trampled plots was 48% (se=28.0). Control plots lost no mussels during this period.

Trampled plots at Fogarty Creek also lost mussels (Figure IV.4). However, Fogarty Creek has a two-layer mussel bed, and loss of the top layer did not create bare space as it did in Little Whale Cove. Consequently, primary percent cover remained high (97% (se=1.6)) on all plots. However, based on marked mussel counts taken through July 1990, We estimated that trampled plots lost at least 14.2% of the initially marked mussels between April and July 1990. Mussel loss after July 1990 could not

be reliably measured, because some paint was lost from mussels in the plot. But byssal threads attached to matrix mussels (which were visible in trampled plots) indicate that top layer mussels continued to be lost from trampled plots.

Recovery

Mussel beds did not show marked recovery during the year following trampling (Figure IV.4). In fact, mussels continued to be lost from trampled plots at both sites. At Little Whale Cove, bare patch continued to expand in all three trampled plots. By April 1992 mussel cover averaged 33.2% (se=23.5) in trampled plots (this does not include the large mussel loss peripheral to the plots) and mussel cover was unchanged in control plots (mean=98%, se=1.6) (ANOVA for April 1992, F=9.83, p=0.02, df = 1). By May 1993, patches were still visible, and patch size had enlarged in two of the plots. No mussels had recruited to the patches. At the same time, mussel beds were still intact in the control plots. (D. M. Brosnan, personal observation)

By April 1992, 1 year after trampling had stopped, trampled plots in Fogarty Creek had lost mussels to a

point where patches of bare space were visible in two of
the trampled plots, indicating that two layers of mussels
had been removed. Control plots did not lose mussels
during the recovery year. In May, 1993, 2 years after
trampling ceased, patch size had increased further; one
patch in a previously-trampled plot measured 1 x 0.5 m, no
mussels had recruited into the patch. Between 1992 and
1993 control plots did not lose mussels (personal
observation).

Epibionts

Trampling significantly affected epibiont cover.
Epibiont cover was measured until July 1990, and included
barnacles and the red alga E. muricata. Barnacle epibionts
per mussel were significantly more abundant at Fogarty
Creek than at Little Whale Cove, while the opposite was
true for E. muricata, This alga was rare at Fogarty Creek,
but abundant on Little Whale Cove mussels.

At both sites, barnacle cover decreased significantly
in the first month in response to trampling (Fogarty Creek
F=25.95, p=0.0001, df=1; Little Whale Cove F=4.902,
p=0.034, df= 1) (Figure IV.5). At Fogarty Creek,

Figure IV.4. Primary cover of mussels <u>M californianus</u> at a. Fogarty Creek and b. Little Whale Cove during trampling and recovery phases. * indicates significant difference between trampled and control plots at p=0.05; error bars are standard error.

Figure IV.4
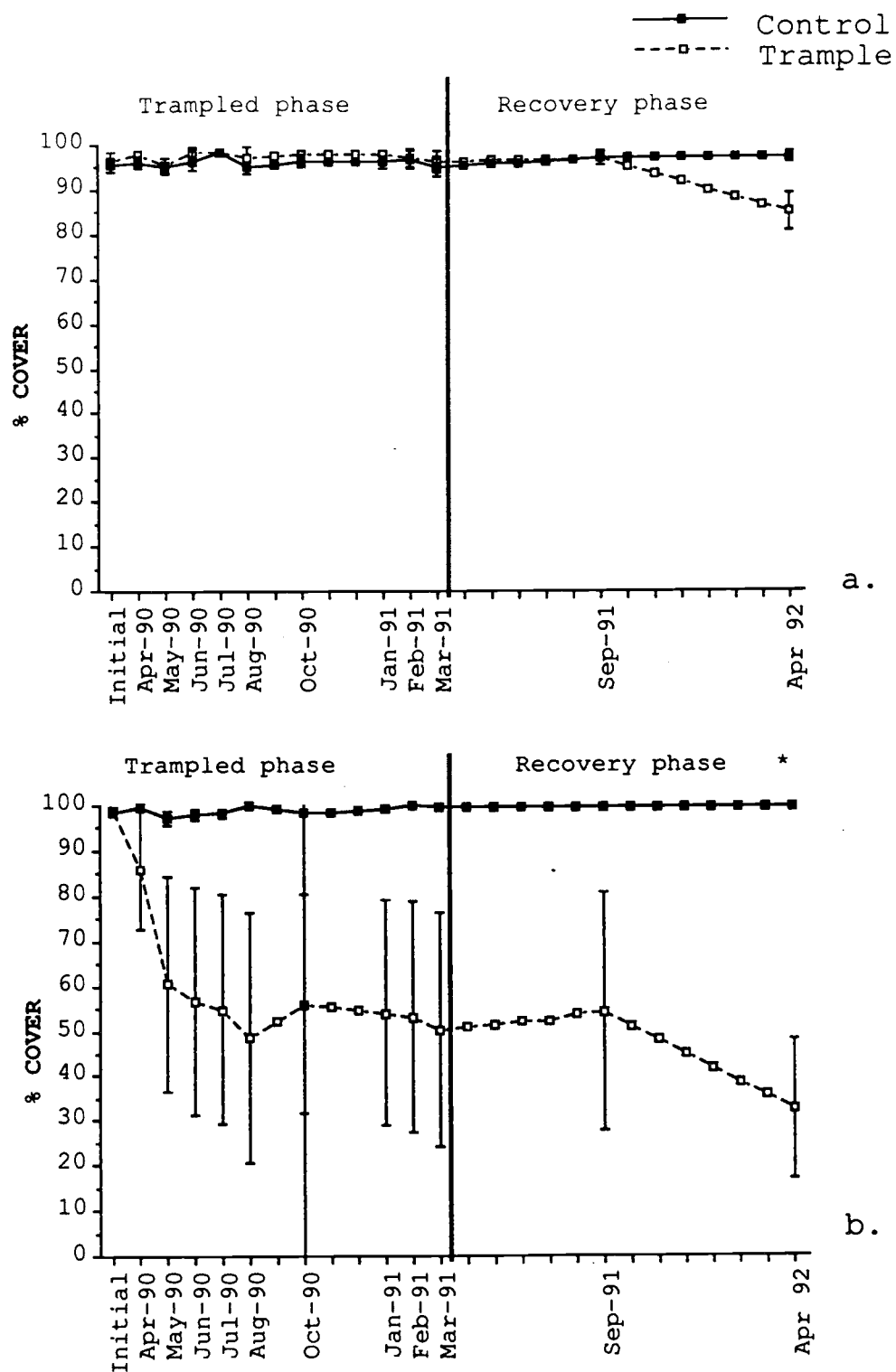
cover in trampled plots reached a minimum of 17.8%
(se=2.8) in July. At the same time barnacles increased to
58% (se=6.1) in control plots. Although there were fewer
barnacles at Little Whale Cove, barnacle cover also
declined in the trampled plots. These differences were
significantly lower on 2 of 4 dates.

The epibiont _E. muricata_ decreased steadily on
trampled plots at Little Whale Cove, from an initial cover
of 15% (se=2.9) to 4% (se=1.5) in July (Figure IV.6). _E.
muricata_ cover on control plots increased slightly from
13.6% (se=2.8) in early April to 14.5 % (se=4.0) in July.
Cover on trampled plots was significantly lower than that
of control plots in July (F=5.76, p=0.02, df=1). Recovery
data for epibionts were not recorded.

Figure IV.5. Percent cover of barnacle epibionts per mussel at a. Fogarty Creek and b. Little Whale Cove during the trampling phase from March-July 1990, Mussel loss from trampled plots prevented us from gathering further data. * and ** indicates significant difference between trampled and control plots at p=0.05 and p=0.01 levels respectively; error bars are standard error.

Figure IV.5
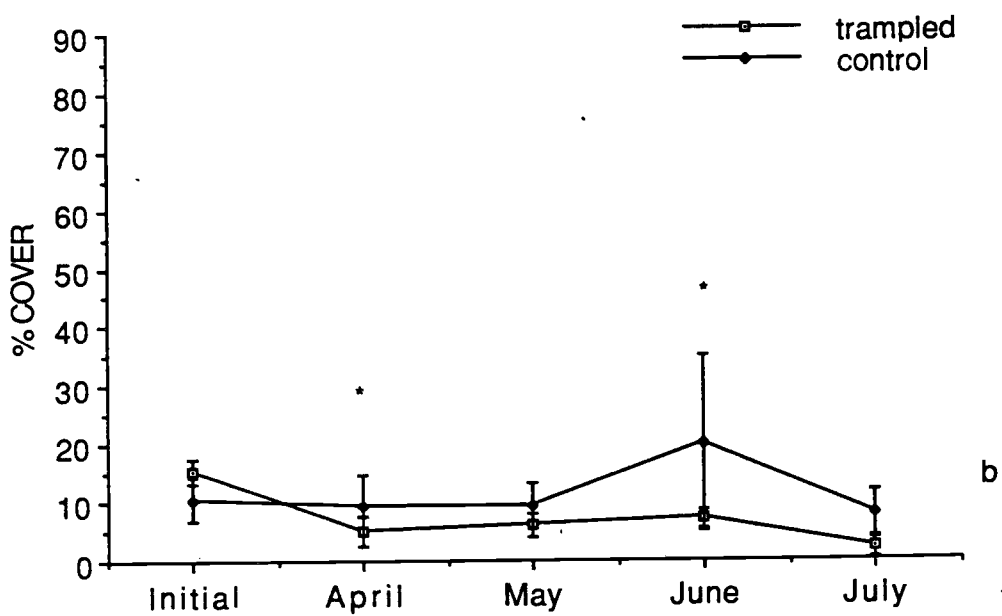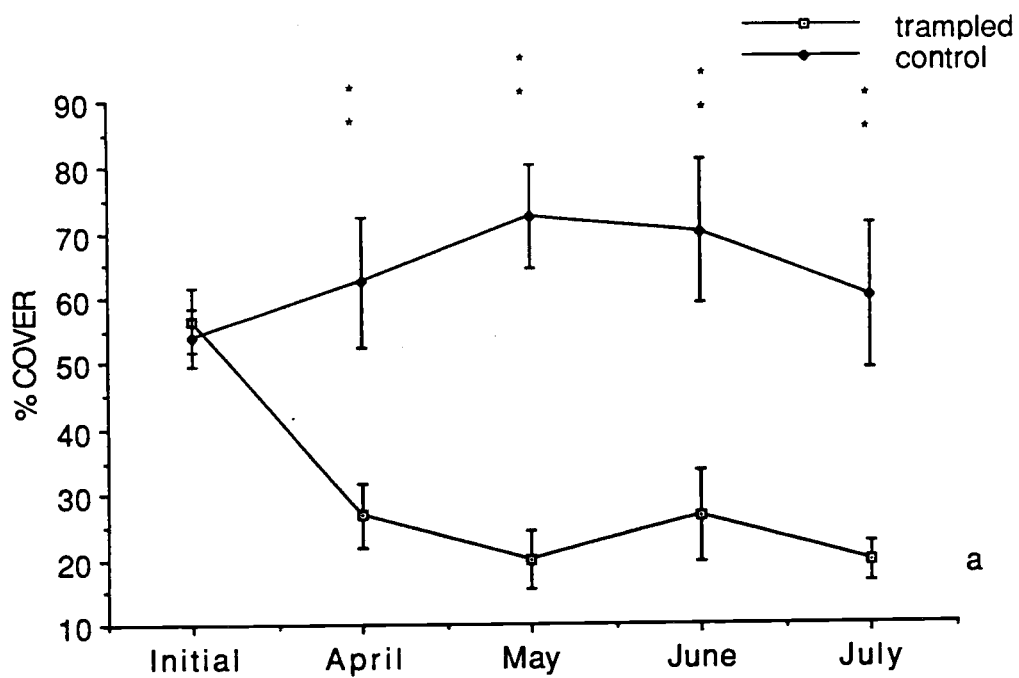
Figure IV.6. Percent cover of the red algal epibiont
E. muricata per mussel during the trampling phase from
March-July 1990, Mussel loss from trampled plots prevented
us from gathering further data. * and ** indicates
significant difference between trampled and control plots
at p=0.05 and p=0.01 levels respectively; error bars are
standard error.

Figure IV.6
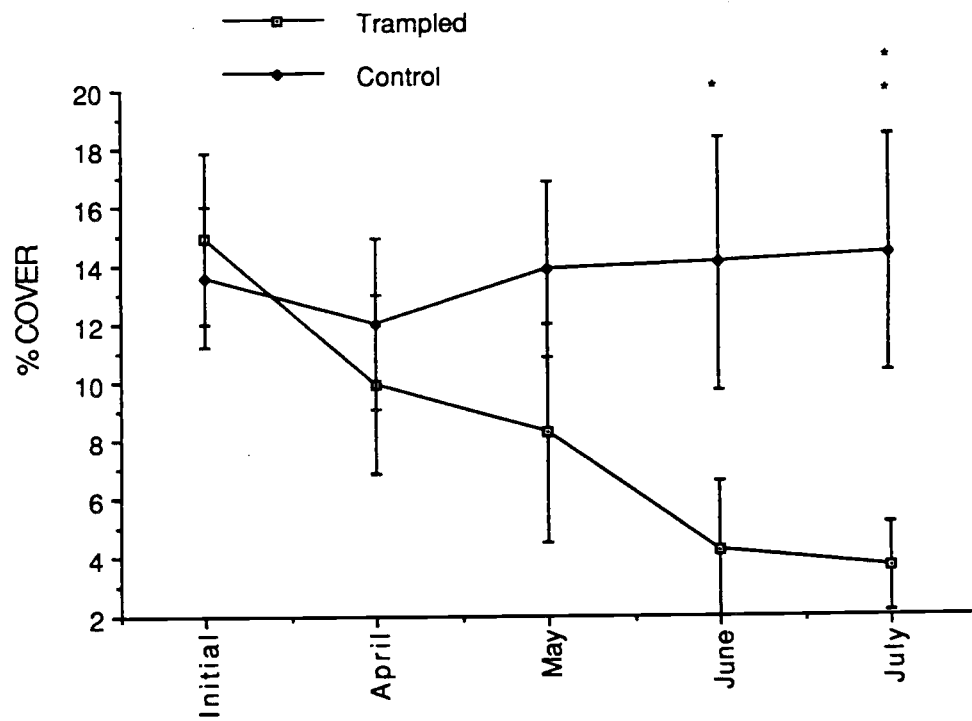
DISCUSSION

Trampling affects both the uppershore algal-barnacle assemblage and the midshore mussel community by dislodging individuals and weakening their attachment strengths, making them vulnerable to wave shock. We did not study trampling effects on the low intertidal community, but expect these to be minimal. At a heavily visited site, there was no difference in low tide communities in trampled and isolated areas (Brosnan and Crumrine 1992a).

Effect of Trampling on the Upper Shore Algal-Barnacle Assemblage

These results show that foliose algae are susceptible to trampling and that turf forms (mainly E. muricata) are more resistant. This suggests that turf or low profile (e.g., crusts) species will dominate areas subjected to heavy trampling. Data from Yaquina Head, a heavily visited marine garden 10 km south of Little Whale Cove support this idea: Trampled areas at Yaquina Head are dominated by algal turf (E. muricata and Gelidium spp.). Turf was replaced by foliose species (mainly Iridaea cordata and F. distichus) when trampling was prevented in experimental plots (Brosnan and Crumrine 1992a, b, Brosnan 1993).

Why are foliose forms more susceptible to trampling?
Many foliose canopy species are attached at a single point
or over a small area, e.g., the discoid holdfasts of some
red algae and fucoids. Kicking off one discoid holdfast
can result in significant canopy loss. In addition,
because erect canopy protrudes more from the substrate
than turf, it is more likely to be removed by foot
traffic. In contrast, the turf form of E. muricata is
short and profusely branched; it spreads vegetatively over
rocky substrata (Sousa 1984), and is attached at many
points. These characteristics are likely to make turf, and
possibly some crustose algae (e.g., petrocelis crust),
resistant to trampling, and dominant on heavily trampled
shores. Other authors have also noted that certain species
appear susceptible to trampling in marine intertidal
communities. For example, Povey and Keough, (1991), noted
that foliose species are more readily removed than crusts
or turf. Zedler (1976, 1987), and Beauchamp and Gowing
(1982) found that foliose species, notably P. limitata,
were less abundant at a heavily visited site in
California. Boalche et al. (1974) noted that the large
canopy forming species Ascophyllum nodosum became
significantly rarer at a shore in SW England after
construction of a parking lot, and an increase in
visitors. They attributed this loss to trampling impact.

Interestingly, growth forms that are reasonably resistant
to wave shock provide poor defense against foot traffic
disturbance: A flexible stipe attached by a single point
can allow a species to persist in areas of high wave
action, but not in heavily trampled sites for reasons
noted above. Species differences in trampling resistance
has also been noticed in reef flat communities (Woodland
and Hooper 1977, Liddle and Kay 1987, Kay and Liddle
1989).

Barnacles on primary and secondary substrate were
crushed by trampling. We noticed that after trampled plots
lost algal canopy, barnacles recruited heavily into bare
space. Control plots did not show large concurrent
increases in primary barnacle cover. Though canopy can
provide protection against desiccation, it can also
prevent barnacle settlement through whiplash or space
occupancy (Dayton 1971, Menge 1978). Individuals settling
into trampled space eventually reach a size large enough
to be susceptible to trampling. The net effect of
trampling will depend on the timing of the disturbance. If
trampling removes barnacles prior to sexual maturity, the
population will suffer a steady decline. Therefore, the
benefit in recruitment to primary surfaces may be offset
by direct crushing mortality.

Mussels did not recruit into uppershore trampled plots during the experimental period, although they did recruit into non-trampled plots. Mussel recruitment tends to be sporadic along the Oregon coast (Petersen 1983, B. A. Menge personal communication). Trampling can indirectly prevent mussel settlement. For example, mussels settle preferentially among algal fronds and holdfasts and onto barnacle tests, but rarely onto bare rock (Paine 1974, Suchanek 1979, Paine and Levin 1981, Petersen 1983). By removing algae and large barnacles, trampling will reduce settlement space. Trampling can also directly dislodge or kill mussels after settlement, as shown in this experiment.

Effect of Trampling on the Mussel-Bed Community

Trampling removed mussels and disturbed the surrounding mussel bed. We cannot account for initial differences in numbers of layers of mussels between Fogarty Creek and Little Whale Cove. Wave exposure is similar at both sites, and substrate type does not seem to vary in irregularities, which might allow for stronger attachment at Fogarty Creek. One possible explanation is that recruitment may be higher at Fogarty Creek. In a

separate study, barnacle recruitment was higher at Fogarty Creek than Little Whale Cove (Brosnan, unpublished data). Differential predation may also be a factor, but we did not noticed more predators at Little Whale Cove.

Tightly packed mussels, such as the plots in the Fogarty Creek study, were less susceptible to trampling-induced loss. However the top mussel layer was lost from the bed, suggesting that on some trampled shores mussel beds may be restricted to a monolayer, or that trampling may first reduce a multi-layered bed to a single layer, and continued loss may lead to disappearance of the mussel-bed. In a separate study at a heavily trampled site, (Brosnan and Crumrine 1992a, b, Brosnan 1993), mussels were not common, and were confined to crevices. This suggests that the presence of crevices and depressions in the rock surface is likely to be important to the persistence of mussels on trampled shores. Mussels aggregated into a loose monolayer are highly susceptible to trampling, as at Little Whale Cove.

Once a patch had been created, natural forces (e.g., the edges of the holes and the patches expanded beyond the area that was trampled. This effect contrasts with the observations of Paine and Levin (1981) who noted

that patches formed by storms did not enlarge. These
results may indicate that trampling weakens areas of
mussel beds that would normally not be affected by storms.
Thus trampling makes mussels more susceptible to winter
disturbances.

Once bare space has been created, continued trampling
appears to prevent colonization and succession. There was
little mussel recruitment on patches in mussel plots until
experimental trampling had stopped. Even then, it may take
many years for mussels to recolonize the area; Paine and
Levin (1981), estimate that it would take at least 7 years
for large patches to recover to a stage where natural
disturbances would once again affect them. Loss of mussel
bed also includes the loss of species dependent on mussels
(Suchanek 1979) and therefore results in a decrease in
diversity of the site.

Epibionts seem particularly susceptible to trampling.
Even E. muricata, which is resistant when it grows on
primary substratum, was significantly affected. Epibionts
on mussel shells protrude above the surface, and are the
first organisms to be hit by foot-traffic. This may
account for their susceptibility. Initially, barnacle
epibionts were more abundant at Fogarty Creek than at

Little Whale Cove. E. muricata, which is known to smother
and kill barnacles (Farrell 1989, 1991), is common at the
latter site and may be partially responsible for the low
barnacle abundance there. In a study carried out in
Oregon, Lee and Ambrose (1989) showed that barnacles are
more abundant as epibionts than on bare rock. Trampling
removes barnacle epibionts and therefore may have major
consequences for barnacle populations on frequently
visited shores.

The effect of algal epibonts on mussels varies with
environmental conditions. In cold weather, algal epibionts
reduce mortality rates in mussels by insulating them
(Chapter 2). Trampling, by removing epibionts, may thus
increase mussel mortality rate under harsh environmental
conditions. Epibionts also increase drag and the risk of
mussel dislodgment (Witman and Suchanek 1983, Chapter 2).
By removing epibionts, trampling decreases drag on
mussels. However, this effect may be small compared to the
increased risk of dislodgment from trampling.

Trampling as a Disturbance

Storms and waveswept logs create disturbance in the
rocky intertidal which results in patches of bare space

(Harger 1968, Harger and Landenberger 1970, Dayton 1971, Sousa 1979, 1984b, 1985, Paine and Levin 1981). Such disturbances are generally seasonal (winter) and localized. Trampling also removes individuals and creates patches of bare space and can therefore be defined as a disturbance (sensu Sousa 1985). However, unlike natural disturbances such as storms and logs, trampling is more likely to be chronic in nature. Trampling may also be more frequent during spring and summer, and less common in winter.

Many species have evolved in response to the natural disturbance regime. For instance, fugitive species (sensu Sousa 1985) may time their reproduction to take advantage of bare space created by these winter storms. Changes in the frequency and intensity of disturbance can change the species composition and diversity of a community (Connell 1979). On the Oregon shore, trampling is concentrated in the spring and summer months, at a time of peak algal and barnacle settlement and growth. Hence these species that have evolved to take advantage of bare space at these times, are now subject to a new disturbance.

Some species are resistant to trampling (Liddle 1991). Resistant species such as E. muricata appear to benefit

from chronic trampling. On untrampled shores this alga is often present as an understory species and covers about 10% of space (personal observation). Consequently, trampling may initiate a shift in community structure. Historic evidence of such changes has been noted not only in terrestrial systems (Liddle 1975) but also on rocky shores in the U.S. and England (Boalche et al. 1974, Widdowson 1971, Thom and Widdowson 1978, Brosnan and Crumrine 1992, Brosnan 1993).

Trampling interacts with natural forces, such as storms, to increase the extent of the disturbance. For example, in our plots, trampling created the initial disturbance by removing mussels and weakening the beds; patches subsequently continued to expand as more mussels were lost through wave action. Similarly, trampling damages algal holdfasts and thalli, and damaged plants are more susceptible to wave dislodgment (personal observation).

Recovery from trampling depends on the community involved. Algal abundance on the upper shore reached nearly control-level a year after trampling stopped. Similarly high barnacle recruitment aided recovery of these organisms. The relative abundances of certain

species differed between the initial pre-trampling level and recovery period. But in general, the upper shore algal-barnacle community seemed to be resilient. However, chronic trampling for many years might alter this conclusion. Shores that have low recruitment will also have slower recovery. The mussel community did not recover in the year following trampling, and did not show mussel recruitment by April 1993 (personal observation), 2 years after trampling stopped. In fact some of the patches had enlarged further (personal observation). Paine and Levin (1981) found that recovery in some mussel bed patches did not begin until 26 months after a natural disturbance. Chronic trampling will most likely prevent recovery.

In conclusion, trampling affects community structure on rocky shores and may shift the community to an alternate state. Based on these and other studies, I predict that at similar sites, trampled shores will be dominated by algal turf or crust, and that cover of canopy-forming species will be low. I also predict that mussels will be infrequent or at most in densely packed monolayers. In contrast, where trampling intensity is low, mussels and foliose algae will be more common. Because it mimics some aspects of natural disturbance, communities can recover from the effects of trampling; however, its

frequency and intensity make it a particularly severe stress. Trampling also interacts with natural disturbance to increase the rate of dislodgment of organisms.

Marine parks and reserves have been set up in many areas of the world to protect sensitive areas of high diversity. A designated reserve in a biologically rich area is a prime attraction to visitors. Ironically this increased use may degrade the very resource that the reserve was set up to protect. Human impact on marine ecosystems will continue to increase and its effects will need to be factored into any reserve or conservation design.

CHAPTER V

CONCLUSIONS

This thesis focused mainly on the factors that affect
the survival of mussels, and the persistence of mussel
beds. The ecology of mussels (<u>Mytilus californianus</u>) has
been well studied. Predation plays an important role in
their recruitment, distribution, and abundance (Paine
1966, 1974, 1980, Dayton 1971, Petersen 1984, Marsh 1986a,
b, Dayton 1971, Wootton 1992, Menge et al 1994). However,
large mussels have a size refuge from predation.
Disturbance (e.g., wave shear and log damage) dislodges
clumps of mussels, leaving patches of bare space, which
are subsequently colonized by other species (Harger 1970,
Paine and Levin 1981). This thesis demonstrated that, in
addition to predation and disturbance, epibionts and
trampling can affect the abundance of mussels, and the
persistence of the mussel-bed assemblage.

In Chapter II, I studied the nature of the interaction
between epibionts and mussels. Results demonstrated that
the sign and strength of mussel-epibiont interactions can
vary along an environmental gradient. Changing outcomes
are likely to be important only if they are sufficiently

strong, and frequent enough to affect survival, growth and
reproduction of the interacting species. Mussel-epibiont
interactions seemed to meet these criteria. Under normal
conditions, algal epibionts had weak negative effects on
mussels. However, in freezing conditions, algal epibionts
had strong positive effects on mussels, by protecting them
from freeze-induced mortality. Freezing conditions occur
frequently enough to be important to the survival of
individual mussels, and to the persistence of the mussel-
bed assemblage. For mussels colonized by algal epibionts,
there is a trade-off between additional physical stress
and reduced growth, and the benefit of protection against
severe physiological stress. These constant negative
effects seem to be balanced by occasional strong positive
effects. Any potential costs to _Endocladia_ from its
association with mussels are unknown. The benefits to
Endocladia seem to be the provision of a competitor-free
habitat.

Changing interaction-outcomes are likely to have a
greater effect on community structure and diversity, if
one of the interacting species is a dominant or abundant
species. Mussels are dominant competitors on rock
substrate (Paine 1966, 1980, Dayton 1971, 1975).
Predation and disturbance can increase diversity on rock
substrate by removing mussels, and allowing other species

to colonize (Paine and Levin 1981). Depending on
environmental conditions, mussel-epibiont interactions may
also have strong effects of diversity. Chapter II
demonstrated that waves could dislodge mussels colonized
by _Endocladia_, when the mussel bed was weakly attached.
Under freezing conditions, mussel mortality was high in
mussel beds with little _Endocladia_. Whenever large numbers
of mussels were removed from rocks, large patches of bare
space became available for colonization by other species
(because mussels do not recruit onto bare rock (Petersen
1984a,b)). By contrast, in mussel beds where many mussels
were colonized by _Endocladia_, mortality was generally low
under freezing conditions, and no new space was created.
Here, the positive effects of _Endocladia_ on mussels may
result in the maintenance of existing diversity, and
species distributions on rock substrate.

Not all species on the shore are occupants of primary
substrate. Many species exist on the surface of, or in
association with other species. Mussel-epibiont
interactions may have strong influences on the diversity
of such organisms, such as those within the mussel bed
matrix. Mussel beds are structurally complex, and provide
a habitat for over 300 associated species (Suchanek 1979,
Lohse 1993a,b.), and a nursery ground for juveniles of

many species (Sebens 1982). Factors leading to mussel dislodgment will result in the loss of these associated species. The positive effects of Endocladia on mussels in freezing conditions maintained the mussel bed assemblage, and this in turn maintained existing patterns of diversity and species distributions. The contribution of matrix, and epibiont species to overall diversity has received little attention. For instance, the intermediate disturbance hypothesis (Connell 1978) and the predation hypothesis (Paine 1966) focus on the species on rock substrate only. Ecological theories of diversity should be expanded to incorporate epibiotic and matrix species.

The frequency of changes in interaction outcomes, and their effects on communities have also received little attention. We do not yet know their general importance in other communities. However, it seems likely that other host-epibiont interactions may be characterized by changes in the outcome of interactions. For instance, epibionts often increase the rate of dislodgment of host algae (Sousa 1979, 1984, D'Antonio, 1985), trees (Strong 1977), and invertebrates (Dayton 1973, Paine 1979, Witman and Suchanek 1984, Hardwick-Witman 1991) (negative effects). However, studies show that epiphytes can also reduce herbivory on some plants (Lubchenco 1983, but see Emmett-Duffy 1987), and protect seagrasses from sunlight (Penhale

and Smith 1977) (positive effects). Whether there are important tradeoffs to the host species, or whether these interactions are strong enough to be important to community dynamics is unknown. However, these systems could be used for further study of changes in interaction outcomes.

The effects of barnacles and limpets on the establishment of the epibiont community on mussels were examined in Chapter III. Results showed that barnacles successfully colonized directly onto mussels. Few algae successfully recruited onto mussels, but they recruited onto barnacles on mussels. <u>Endocladia</u> was the most abundant alga in the experimental plots. <u>Endocladia</u> has strong effects on mussels, and facilitation by barnacles appears to be the main factor controlling its abundance on mussels. Limpets bulldozed barnacles, except at high barnacle recruitment density. Limpets also reduced the abundance of diatoms and other algal species, but only <u>Endocladia</u> persisted, even when few limpets were present. These results suggest that mussels are a stressful habitat for many algal species. <u>Endocladia</u> may be an abundant epibiont species because it can withstand harsh physical conditions, which may be lethal to other species (Sousa 1984). In contrast to mussel substrate, the same assemblage on rock substrate is regulated by other factors

including predation and competition. These results are consistent with Environmental Stress Models (Menge and Sutherland 1987, Menge and Olson 1990) that predict a low diversity assemblage of resistant species in stressful environments.

Chapter IV examined the effects of trampling on the persistence of mussels, and epibionts. Results showed that trampling is a severe physical stress, which can remove dominant species and prevent succession. Trampling dislodged epibionts, and this can have significant effects for mussels in extreme temperatures. However, trampling also had negative effects on the persistence of mussel beds by directly dislodging mussels, and increasing the frequency and intensity of normal disturbances. During winter storms more mussels were lost from trampled plots: A year after trampling had stopped, mussels continued to be lost from previously trampled plots. Continued trampling prevented recovery on bare space, previously occupied by mussels.

In conclusion, environmental factors such as temperature and physical stress can have important effects on the persistence of mussel beds. These factors operate through direct effects on individual mussels, and by affecting the interaction between species. In

physiologically harsh environments, protection from stress may be an important interaction in communities (Bertness and Callaway 1994). However, in physically harsh environments, a species may also increase the stress on another species (e.g., by increasing drag). In the mussel-bed assemblage, persistence of mussels seems to be due in part, to a balance between the negative effects of epibionts and the strong positive of epibionts in extreme temperatures.

BIBLIOGRAPHY

Abrams, P. 1987. Indirect interactions between species
that share a predator; varieties of indirect effects. In
Predation: direct and indirect effects. edited by W. C.
Kerfoot and A. Sih. University Press of New England, N. H.
pp. 38-54.

Arrontes, J. 1990. Competition, distribution on host, and
seasonality of epiphytes on three marine intertidal algae.
Botanica Marina 33:205-211.

Barkai, A., and G. M. Branch. 1988. The influence of
predation and substratal complexity on recruitment to
settlement plates: a test of the theory of alternative
states. Journal of Experimental Marine Biology and Ecology
124:215-237.

Bates, G.H., 1934. The relation of leaf size to root
structure in Trifolium repens. Journal of Ecology 22:271-
278.

Bates, G.H., 1935. The vegetation of footpaths, sidewalks,
cart-tracks and gateways. Journal of Ecology 23:470-487.

Bayne, B. L. 1964. Primary and secondary settlement in
Mytilus edulis L. (Mollusca). Journal of Animal Ecology
33:513-523.

Bayne, B. L. editor 1976. Marine Mussels. Cambridge
University Press, Cambridge, U.K.

Bazzaz, F. A. and R. W. Carlson 1984. The response of
plants to elevated CO_2 I. Competition among assemblages of
annuals at two levels of soil moisture. Oecologia 62:196-
8.

Beauchamp, K. A. and M. M. Gowing, 1982. A quantitative
assessment of human trampling effects on a rocky
intertidal community. Marine Environmental Research 7:279-
83.

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

Bertness, M.D. 1989. Intraspecific competition and facilitation in a northern acorn barnacle. Ecology 70:257-268.

Bertness, M.D. 1992. The ecology of a New England salt marsh. American Scientist 80:260-268

Bertness, M.D., and R. Callaway 1994. Positive interactions in communities. Trends in Ecology and Evolution 9:191-194.

Beukema, J. J. 1991. The abundance of shore crabs Carcinus maenas (L.) on a tidal flat in the Wadden Sea after cold and mild winters. Journal of Experimental Marine Biology and Ecology 153:97-113.

Blanchette, C. A. 1990. Mechanical and thermal interactions between an algal epizoan, Endocladia muricata and its host Mytilus californianus Class report, Biomechanics Summer Course, Friday Harbor Laboratories, University of Washington.

Bloom, S. A. 1975. The mobile escape response of a sessile prey: a sponge-scallop mutualism. Journal of Experimental Marine Biology and Ecology 17:311-321.

Boalche, G.T., N.A. Holme, N.A. Jephson and J.M. Sidwell 1974. A resurvey of Colemans intertidal traverse at Wembury, South Devon. Journal of the Marine Biological Association UK 54:551-3.

Boryslawski, Z and B. L. Bentley 1985. The effect of nitrogen and clipping on interference between C3 and C4 grasses. Journal of Ecology. 73:113-121.

Boucher, D. H. editor 1985. The Biology of Mutualism. Croom Helm Publisher.

Bowen, G. D. 1980. Mycorrhizal roles in tropical plants and ecosystems. In Tropical mycorrhiza research. edited by P. Mikola. Clarendon Press Oxford pp116-190.

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

Branch, G. M. 1975. Ecology of Patella species from the Cape peninsula, South Africa. IV. Desiccation. Marine Biology 32:179-200.

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

Bronstein, J. L. 1994. Conditional outcomes in mutualistic interactions. Trends in Ecology and Evolution. 9:214-217.

Brosnan, D.M. 1992. Ecology of tropical rocky shores: Plant-animal interactions in tropical and temperate latitudes. In: Plant-animal interactions in the marine benthos. D.M. John, S.J. Hawkins, and J.H. Price, editors. Clarendon Press Oxford. pp. 101-131

Brosnan, D.M., 1993. The effect of human trampling on biodiversity of rocky shores: monitoring and management strategies. Recent Advances in Marine Science and Technology 1992. 333-341.

Brosnan, D. M. and L.L. Crumrine, 1992a. Human impact and a management strategy for Yaquina Head Outstanding Natural Area. A report to the Bureau of Land Management Dept. of the Interior. Salem, Oregon. 105 pp.

Brosnan, D.M. and L.L. Crumrine, 1992b. A study of human impact on four shores on the Oregon coast: Results and recommendations for management and development. Report to the Oregon State Department of Land Conservation and Development. 36 pp.

Brosnan, D.M., and L. C. Crumrine. 1994. Effects of human trampling on marine rocky shore communities. Journal of Experimental Marine Biology and Ecology, 177:79097.

Burden, R. F. and P.F. Randerson, 1972. Quantitative studies of the effects of human trampling on vegetation as an aid to the management of semi-natural areas. Journal of Applied Ecology 9:439-458.

Burrows, E. M., and S. M. Lodge. 1950. A note on the inter-relationships of Patella, Balanus and Fucus on a semi-exposed coast. Annual Report for 1949, Marine Biology Station, Port Erin 62:30-34.

Buss, L. W., and J.B.C. Jackson 1979. Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. American Naturalist 113:223-234.

Calow, P. and R. J. Berry editors 1989. Evolution, ecology and environmental stress. Academic Press.

Castilla J.C. and L.R. Duran. 1985. Human exclusion from the rocky intertidal zone of central Chile: the effects on Concholepis concholepis (Gastropoda) Oikos 45:391-9.

Castilla, J.C. and R.H. Bustamente, 1989. Human exclusion from rocky intertidal of Las Cruces, central Chile: effects on Durvillea antarctica (Phaeophyta, Durvilleales) Marine Ecology Progress Series 50:203-214.

Choat, J.H. 1977. The influence of sessile organisms on the population biology of three species of acmaeid limpets. Journal of Experimental Marine Biology and Ecology 26:1-26.

Cole, R.C., A.M. Ayling, and R.G. Creese, 1990. Effects of marine reserve protection at Goat Island, northern New Zealand. New Zealand Journal of Marine and Freshwater Research 24:197-210.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle <u>Chthamalus stellatus</u>. Ecology 42:710-723.

Connell, J.H. 1972. Community interactions on marine rocky intertidal shores. Annual Review of Ecology and Systematics 3: 169-192.

Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Ecology and evolution of communities. edited by M. L. Cody, and J. Diamond

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 189:1302-1310.

Connell, J. H. 1979. Tropical rain forests and coral reefs as open noneqilibrium systems. Pages 141-163 in R. M. Anderson, B. D. Turner, and L. R. Taylor, editors. Population dynamics. Blackwell Scientific Publications, Oxford, England.

Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35:131-138.

Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. American Naturalist 122:661-696.

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

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111:1119-1143.

Craig, P. C. 1968. The activity pattern and food habits of the limpet <u>Acmaea</u> <u>pelta</u>. Veliger 11:13-19.

Crisp, D. J. editor 1964. The effects of the severe winter of 1962/3 on marine life in Britain. Journal of Animal Ecology 33:165-210.

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

D'Antonio, C. 1985. Epiphytes on the rocky intertidal red 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.

Darwin, C. R. 1859. The Origin of Species by Natural Selection. John Murray. London.

Day R.W., and G. P. Quinn 1990. Comparison of treatments after analysis of variance in ecology. Ecological Monographs 59: 433-463.

Dayton, P. K. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41:351-89.

Dayton, P. K. 1973. Dispersion, dispersal and persistence of the annual intertidal alga, Postelsia palmaeformis Rurprecht. Ecology 54:433-438.

Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecological Monographs 45:137-159.

Dayton, P. K. 1985. Ecology of kelp communities. Annual Review of Ecology and Systematics 16:2415-245.

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.

Denny M. 1988. Biology and the mechanics of the wave -
swept environment. Princeton University Press, Princeton
New Jersey.

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

Dethier M. N. 1990. A report to Washington Deptartment of
Natural Resources.

Dittman, D., and C. Robles. 1991. Effect of algal
epiphytes on the mussel Mytilus californianus. Ecology 72:
286-296.

Doherty, P. J. 1981. Coral reef fish: Recruitment-limited
assemblages? Proceedings of International Coral Reef
Symposium (4th) 2:465-470.

Duggins, D. O., and M. N. Dethier. 1988. Variation in
strong interactions in the intertidal zone along a
geographical gradient: a Washington, Alaska comparison.
Marine Ecology Progress Series 50:97-105.

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

Duran, L.R. and J.C. Castilla, 1989. Variation and
persistence of the middle rocky intertidal community of
central Chile, with and without human harvesting. Marine
Biology 103:555-562

Ebling, F. J., J. A. Kitching, L. Muntz, and C. M. Taylor.
1964. The ecology of Lough Ine xiii. Experimental
observations of the destruction of Mytilus edulis and
Nucella lapillus by crabs. Journal of Animal Ecology
33:73-82.

Farrell, T.M. 1989. Succession in a rocky intertidal
community: the importance of disturbance, size, and

position within a disturbed patch. Journal of Experimental Marine Biology and Ecology 128:57-73.

Farrell, T. M., 1991. Models and mechanisms of succession: an example from a rocky intertidal community. Ecological Monographs 61:95-113.

Farrell, T. M. , D. Bracher, and J. Roughgarden. 1991. Cross-shelf transport causes recruitment to intertidal populations in central California. Limnology and Oceanography 36:279-288.

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

Foster, M. S. 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.

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

Fretwell, S. D. 1977. The regulation of plant communities by food chains exploiting them. Perspectives in Biology and Medicine 20: 169-185.

Gaines, S.D., and J. Lubchenco. 1982. A unified approach to marine plant-herbivore interactions II. Biogeography. Annual Review of Ecology and Systematics. 13:111-138.

Gaines, S. D., and J. Roughgarden. 1987. Fish predation in offshore kelp forests affect recruitment to intertidal barnacle populations. Science 235:479-481.

Gaines, S. D., and M. Bertness. 1993. The dynamics of juvenile dispersal: why field ecologists must integrate. Ecology 74(8):2430-2435

Gardner, J. P. A., and D. O. F. Skibinski. 1991.
Biological and physical factors influencing genotype-
dependent mortality in hybrid mussel populations. Marine
Ecology Progress Series 71:235-243.

Garrity, S. D., and S. C. Levings. 1984. Aggregation in a
tropical neritid. Veliger 27:1-6.

Gause, G. F. 1934. The struggle for existence. Williams
and Wilkins, Baltimore. (reprinted in 1964 by Hafner, New
York).

Ghazanshahi, J., T. D. Huchel, and J.S. Devinney, 1983.
Alteration of Southern California rocky shore ecosystems
by public and recreational use. Journal of Environmental
Management 16:379-394.

Glynn, P. W. 1965. Community composition, structure, and
inter-relationships in the marine intertidal Endocladia
muricata-Balanus glandula association in Monterey Bay,
California. Beaufortia 12:1-198.

Godoy, C. and C.A. Moreno, 1989. Indirect effects of human
exclusion from the rocky intertidal in southern Chile: a
case of cross-linkage between herbivores. Oikos 54:101-6.

Gosling, E. editor 1992. The mussel Mytilus: Ecology,
Physiology, Genetics, and Culture. Elsevier Amsterdam.

Gray, J. S. 1989. Effects of environmental stress on
species rich assembalges. Biological Journal of the
Linnean Society 37:19-32.

Grime, J. P. 1979. Vegetation classification by reference
to srategies Nature 250:26-31.

Grime, J. P. 1979. Plant strategies and vegetation
processes: Wiley Chichester England.

Hardwick-Witman, M, N. 1985. Biological consequences of ice rafting in a New England salt marsh community. Journal of Experimental Marine Biology and Ecology 87:283-298.

Harger, J. R. E. 1970. The effect of wave impact on some aspects of the biology of mussels. Veliger 12:401-414.

Harger, J. R. E. 1972. Competitive coexistence: Maintenance of interacting associations of the sea mussels Mytilus edulis and Mytilus californianus. Veliger 14:387-410.

Harger, J. R. E., and D. E. Landenberger. 1971. The effects of storms as a density dependent mortality factor on populations of sea mussels. Veliger 14:195-201.

Hartnoll, R. G., and S. J. Hawkins. 1985. Patchiness and fluctuations on a moderately exposed shore. Ophelia 24:53-63.

Hawkins, A. J. S., and B. L. Bayne. 1985. Seasonal variation in the relative utilization of carbon and nitrogen by mussel Mytilus edulis: budgets, conversion efficiencies and maintenance requirements. Marine Ecology Progress Series 25:181-188.

Hawkins, S. J. 1981. The influence of season and barnacles on the algal colonization of Patella vulgata exclusion areas. Journal of the Marine Biological Association of the United Kingdom 61:1-15.

Hawkins, S. J., and R. G. Hartnoll. 1982. Settlement patterns of Semibalanus balanoides L.in the Isle of Man. Journal of Experimental Marine Biology and Ecology 62:271-283.

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

Hawkins, S. J., and R. G. Hartnoll. 1985. Factors determining the upper limits of intertidal canopy-forming algae. Marine Ecology Progress Series 20:265-271.

Hay, M. E. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical. Ecology 65:446-454.

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

Holl, W. 1983. Interactions between plants and animals in marine systems. Physiological Plant Ecology 3:469-88.

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

Hylgaard, T. and M.J. Liddle, 1981. The effect of human trampling on a sand dune ecosystem dominated by _Empetrum nigrum._ Journal of Applied Ecology 18:559-569.

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.

Jernakoff, P. 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.

Jernakoff, P. 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.

Johnson, L. E. 1989. Spatial and temporal influences on the recruitment of intertidal red algae. Ph. D. dissertation University of Washington. 186pp.

Kay, A.M. and M.J. Liddle, 1989. Impact of human trampling in different zones of a coral reef. Environmental Management 13:509-520.

Keough, M. J. 1983. Patterns of recruitment of sessile invertebrates in two subtidal habitats. Journal of Experimental Marine Biology and Ecology 66:213-245.

Keough, M. J. 1984b. The dynamics of the epifauna of Pinna bicolor: interactions between recruitment, predation, and competition. Ecology. 65:677-688.

Keough, M. J. and A. J. Butler, 1983. Temporal changes in species number in an assemblage of sessile marine invertebrates. Journal of Biogeography 10:317-330.

Keough, M. J., and B. J. Downes. 1982. Recruitment of marine invertebrates: the role of active larval choice and early mortality. Oecologia (Berlin) 54:348-352.

Kingsford, M.J., A.J. Underwood, S.J. Kennelly. 1991. Humans as predators on rocky reefs in New South Wales, Australia. Marine Ecology Progress Series 22:1-14.

Kitching, J. A., J. F. Sloane, and F. J. Ebling. 1959. The ecology of Lough Ine VIII. Mussels and their predators. Journal of Animal Ecology 28:331-341.

Laihonen, P. and E. R. Furman. 1986. The site of settlement indicates commensalism between blue mussel and its epibionts. Oceologia (Berlin) 71:38-40.

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

Lee, H., and W. H. Ambrose, 1989. Life after competitive exclusion: an effective strategy for an inferior competitor. Oikos 56:424-427.

Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation and community structure. Proceedings of the National Academy of Sciences (USA) 71:2744-2747.

Levings, S. C., and S. D. Garrity. 1984. Grazing patterns in _Siphonaria gigas_ (Mollusca, Pulmonata) on the rocky Pacific coast of Panama. Oecologia (Berlin) 64:152-159.

Levitan, P. J. and A .J. Kohn 1980. Microhabitat resource use, activity patterns and episodic catastrophe: _Conus_ on tropical intertidal reef rock benches. Ecological Monographs 50: 55-75.

Lewis, D. H. 1973. The relevance of symbiosis to taxonomy ad ecology with particular reference to mutualistic symbioses and the exploitation of marginal habitats. American Naturalist 110:903-10.

Lewis, J. R., and R. S. Bowman. 1975. Local habitat-induced variations in the population dynamics of _Patella vulgata_ L. Journal of Experimental Marine Biology and Ecology 17:165-204.

Liddle, M.J., 1975. A selective review of the ecological effects of human trampling on natural ecosystems. Biological Conservation 7:17-36.

Liddle, M.J., 1991. Recreation Ecology: Effects of trampling on plants and corals. Trends in Ecology and Evolution 6:13-16.

Liddle, M.J. and M.M. Kay 1987. Resistance, survival and recovery of trampled corals on the Great Barrier Reef. Biological Conservation 42:1-18.

Lohse, D. P. 1993a. The importance of secondary substratum in a rocky intertidal community Journal of Experimental Marine Biology and Ecology 166:1-17.

Lohse, D. P. 1993b. The effects of substratum type on the population dynamics of three common intertidal animals. Journal of Experimental Marine Biology and Ecology 173:133-154.

Louda, S. M. 1988. IN: Rehabilitation of damaged ecosystems edited by J. Cairns. CRC Press.

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.

Lubchenco, J. 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. Ecology 61:333-344.

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

Lubchenco, J. 1986. In Community Ecology edited by J. Diamond and T. Case. Harper and Row New York.

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.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

MacArthur, R. H., H. Recher, and M. Cody. 1966. ON the relation between habitat selection and species diversity. American Naturalist. 100:319-332.

Marsh, C. P. 1986a. Impact of avian predators on high intertidal limpet populations. Journal of Experimental Marine Biology and Ecology 104:185-201.

Marsh, C. P. 1986b. Rocky intertidal community organization: the impact of avian predators on mussel recruitment. Ecology 67:771-786.

Martinez, L., M. Silver, M.W. King, J. M. Aldredge. 1983. Nitrogen fixation by floating diatom mats: a source of new nitrogen to oligotrophic ocean waters. Science 221:152-54.

May, R. M. 1974. Biological populations with nonoverlapping generations: Stable points, stable cycles, and chaos. Science 186:645- 647.

McCook, L. J. and A.R.O. Chapman 1991. Community succession following massive ice-scour on an exposed rocky shore: effects of Fucus canopy algae and of mussels during late succession. Journal of Experimental Marine Biology and Ecology 154:137-169.

McCrae, J. and L Osis. 1989. Plants and animals of Oregon's rocky intertidal habitat. Oregon Department of Fish and Wildlife. Newport Oregon USA.

McQuaid, D., and P. W. Fronman. 1993. Mutualism between the territorial intertidal limpet Patella longicosta and the crustose alga Ralfsia verrucosa. Oecologia 93:128-133.

McNaughton, S. J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. Ecological Monographs 53:291-320.

Meese, R. J. 1992. Effects of bird predation on rocky intertidal community structure (Mytilus californianus, Colisella, Mopalia mucosa) Ph. D. thesis University of California at Davis,. 150pp

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

Menge, B. A. 1978a. Predation intensity in a rocky intertidal community: relation between foraging activity and environmental harshness. Oecologia (Berlin) 34:1-16.

Menge, B. A. 1978b. Predation intensity in a rocky intertidal community effect of an algal canopy, wave

action and desiccation on predator feeding rates. Oecologia (Berlin) 34:17-35.

Menge, B. A. 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. Oecologia (Berlin) 58:141-155.

Menge, B. A. 1991. Relative importance of recruitment and other causes of variation in rocky intertidal community structure. Journal of Experimental Marine Biology and Ecology 146:69-100.

Menge, B. A., and J. P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. 110:351-369.

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, L. R. Ashkenas, and F. Ramsey. 1986. Experimental separation of effects of consumers on sessile prey in the low zone of a rocky shore in the Bay of Panama: direct and indirect consequences of food web complexity. Journal of Experimental Marine Biology and Ecology 100:225-269.

Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. 130:730-757.

Menge, B. A., and T. Farrell. 1989. Community structure and interaction webs in shallow marine hard bottom communities: tests of an environmental stress model. Advances in Ecological Research 19:189-262.

Menge, B. A. and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. Trends in Ecology and Evolution 5:52-57.

Menge, B. A. T. M. Farrell, A. M. Olson, P. van Tamelen, and T. Turner. 1993. Algal recruitment and the maintenance of a plant mosaic in the low intertidal region on the Oregon coast. Journal of Experimental Marine Biology and Ecology 170:91-161.

Menge B, A., E. L. Berlow, C.A. Blanchette, S.A. Navarrete, and S.B. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecological Monographs 64:249-286.

Moreno, C.A., J. P. Sutherland, and F.H. Jara. 1984. Man as a predator in the intertidal zone of central Chile. Oikos 42:155-60.

Muscatine, L., and J.W. Porter 1977. Reef corals: mutualistic symbioses adapted to nutrient-poor environments. BioScience 27:454-60.

Nickerson, N.H. and F.R. Thibodeau, 1983. Destruction of Ammophila breviligulata by pedestrian traffic: quantification and control. Biological Conservation 27:277-287.

NOAA, 1994. US Dept. of Commerce Temperature Records for South Beach Oregon 1930-1994.

Oksanen, L, S. D. Fretwell, J. Arruda, and P. Niemela, 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240-261.

Olivia, D. and J.C. Castilla, 1986. The effects of human exclusion on the population structure of key-hole limpets Fissurella crassa and F. limbata on the coast of central Chile. PSZNI Marine Ecology 7:201-217.

Orth, R. J., and J. Van Montfrons. 1984. Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. Aquatic Botany 18: 43-69.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65-75.

Paine, R. T. 1971. Energy flow in a natural population of the herbivorous gastropod *Tequla* *funebralis*. Limnology and Oceanography 16(1):86-98.

Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia (Berlin) 15:93-120.

Paine, R. T. 1976. Biological observations on a subtidal *Mytilus californianus* bed Veliger 19:125-130.

Paine, R. T. 1979. Disaster, catastrophe and local persistence of the sea palm *Postelsia* *palmaeformis*. Science 205:685-687.

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

Paine, R. T. 1984. Ecological determinism in the competition for space. Ecology 65:1339-1348.

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

Paine, R. T., and T. H. Suchanek. 1983. Convergence of ecological processes between independently evolved competitive dominants: A tunicate-mussel comparison. Evolution 37:821-831.

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.

Peckarsky, B. L. 1983. In Dynamics of lotic ecosystems edited by T.D. Fontaine III and S. M. Bartell. Ann Arbor Science pp303-323.

Penhale, P. A., and W. O. Jr. Smith. 1977. Excretion of dissolved organic carbon by eelgrass (_Zostera marina_) and its epiphytes. Limnology and Oceanography 22:400-407.

Petersen, J. H. 1984a. Establishment of mussel beds; attachment behavior and distribution of recently settled mussels (_Mytilus californianus_) Veliger 27:7-13.

Petersen, J. H. 1984b. Larval settlement behavior in competing species: _Mytilus californianus_ Conrad and _M. edulis_ L. Journal of Experimental Marine Biology and Ecology 82:147-159.

Pickett, S.T.A., and F.A. Bazzaz 1978. Organization of an assemblage of early successional species on a soil moisture gradient. Ecology 59:1248-55.

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

Pieters H., J. H. Kluytmans, W. Zurburg, and D. I. Zandee. 1978. The influence of seasonal changes on energy metabolism in _Mytilus edulis_ (L>) I. Growth rate and biochemical composition in relation to environmental parameters and spawning. In: Cyclic phenomena in marine plants and animals. Proceedings of 13th European Marine Biology Symposium. edited by E. Naylor and R. G. Hartnoll. Pergamon Press.

Povey, A., and M.J. Keough 1991. Effects of trampling on plant and animal populations on rocky shores. Oikos 61:355-368.

Price, H. A. 1980. Seasonal variation in the strength of attachment of the common mussel _Mytilus edulis_ L. Journal of the Marine Biological Association of the U.K. 60:1035-1037.

Price, H. A. 1982. An analysis of factors determining seasonal variation in the byssal attachment strength of _Mytilus edulis_. Journal of Experimental Marine Biology Association, United Kingdom 62:147-155.

Raimonidi, P. T. 1988. Rock type affects settlement, and zonation of the barnacle <u>Balanus</u> <u>anisopoma</u> Pilsbry. Journal of Experimental Marine Biology and Ecology 123:253-267.

Reed, D. C., D. R. Laur, and A. W. Ebling. 1988. Variation in algal dispersal and recruitment: the importance of episodic events. Ecological Monographs 58:321-335.

Rice, K. J., and J. W. Menke. 1985. Competitive reversals and environment-dependent resource partitioning in <u>Erodium</u>. Oecologia 67:430-34.

Rosenzweig, M. L. 1973. Exploitation in three trophic levels. American Naturalist 107: 275-294.

Roughgarden, J., Y. Iwasa, and C. Baxter. 1985. Demographic theory for an open marine population with space-limited recruitment. Ecology 66:54-67.

Sale, P. F. 1978. Coexistence of coral reef-a lottery for living space. Environmental Biology and fisheries 3:85-102.

Sand-Jensen, K. 1977. Effect of epiphytes on eelgrass photosynthesis. Aquatic Botany 3:55-63.

Santelices, B. 1990. Patterns of reproduction, dispersal and recruitment in seaweeds. Oceanography and Marine Biology Annual Review 28: 177-276.

Santelices, B., and J. Correa. 1985. Differential survival of macroalgae to digestion by intertidal herbivore molluscs. Journal of Experimental Marine Biology and Ecology 38:183-191.

Santelices, B., J. Correa, and M. Avila. 1983. Benthic algal spores surviving digestion by sea urchins. Journal of Experimental Marine Biology and Ecology 70:263-270.

Santelices, B. and R. Ugarte. 1987. Algal life-history strategies and resistance to digestion. Marine Ecology - Progress Series 35:267-275.

Santelices, B. and E. Martinez 1988. Effects of filter-feeders and grazers on algal settlement and growth in mussel beds. Journal of Experimental Marine Biology and Ecology 188: 281-306.

Savage, R. E. 1956. The great spatfall of mussels in the River Conway Estuary in spring 1940. Fisheries Investigation of the Ministry of Agriculture Fisheries and Food London. UK Series ii 20:1-21

Schlosser, I. J. 1987. In Community and evolutionary ecology of North American stream fish. edited by W. J. Mathews and D. C. Heinz. Oklahoma University Press pp17-26.

Schoener, T. W. 1983. Field experiments in interspecific competition. American Naturalist. 122:240-285.

Schoener, T. W. 1989. Food webs from the small to the large. Ecology 70:1559-89.

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

Sebens, K. P. 1982. Recruitment and habitat selection in the intertidal sea anemones, Anthopleura elegantissima (Brandt) and A. xanthogrammica (Brandt). Journal of Experimental Marine Biology and Ecology 59:103-124.

Sebens, K. P. 1983. Population dynamics and habitat suitability of the intertidal sea anemones, Anthopleura elegantissima and A. xanthogrammica. Ecological Monographs 53:405-433.

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

Seed, R. and T. H. Suchanek 1992. Population and community ecology of <u>Mytilus</u> In: The mussel Mytilus: Ecology, Physiology, Genetics, and Culture. E. Gosling editor, Chapter 4 pp87-169 Elsevier Amsterdam.

Shantz, H.L., 1917. Plant succession on abandoned roads in eastern Colorado. Journal of Ecology 5:19-34.

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

Sokal, R.R. and F.J. Rohlf. 1981. <u>Biometry</u> W.H. Freeman and Co,. New York USA., second edition 859 pp.

Sousa, W.P., 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60:1225-1239.

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

Sousa, W.P. 1985. Disturbance and patch dynamics on rocky intertidal shores. in Pickett, S.T.A. and P.S. White, editors. The Ecology of natural disturbance and patch dynamics. Academic Press New York U.S.A. pp.101-124.

Southward, A. J. 1964. Limpet grazing and the control of vegetation on rocky shores. In grazing in terrestrial and marine environments. D. J. Crisp editor, pp 265-276. Blackwell, Oxford.

Southward, A. J. 1967. Recent changes in abundance of intertidal barnacles in S.W. England: a possible effect of climatic deterioration. Journal of Marine Biological Association of the UK. 47:81-95.

Stephens, E. G. and M. D. Bertness. 1991. Mussel facilitation of barnacle survival in a sheltered bay

habitat. Journal of Experimental Marine Biology and Ecology 145:33-48.

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.

Suchanek, T. H. 1979. The community: studies on the composition, structure, organization, and dynamics of a mussel bed. Ph.D. dissertation, Department of Zoology, University of Washington, Seattle. 286 pp.

Suchanek, T. H. 1980. Diversity in natural and artificial mussel bed communities of Mytilus californianus. American Zoology 20:807.

Suchanek, T. H. 1981. The role of disturbance in the evolution of life history strategies in the intertidal mussels Mytilus edulis and Mytilus californianus. Oecologia (Berlin) 50:143-152.

Suchanek, T. H. 1985. Mussels and their role in structuring rocky shore communities. In the ecology of rocky coasts. P. G. Moore and R. Seed editor, pp 70-96. Hodder and Stoughton, Sevenoaks, U.K.

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

Sutherland, J. P. 1987. Recruitment limitation in a tropical intertidal barnacle: Tetraclita panamensis (Pilsbry) on the Pacific coast of Costa Rica. Journal of Experimental Marine Biology and Ecology 113:267-282.

Sutherland, J. P. 1990. Recruitment regulates demographic variation in a tropical intertidal barnacle. Ecology 71:955-972.

Sutherland, J. P., and S. Ortega. 1986. Competition conditional on recruitment and temporary escape from predators on a tropical rocky shore. Journal of Experimental Marine Biology and Ecology 95:155-166.

Talbot, F. H., B. C. Russell, and G. R. V. Anderson. 1978. Coral reef fish communities: unstable, high-diversity systems? Ecological Monographs 48:425-440.

Tansley, A. G. 1917. On competition between *Gallium saxatile* L. (*G. hercynium* Weig.) and *Gallium sylvistre* (*G. asperum* Scheib) on different types of soil. Journal of Ecology 5:173-197

Thom, R.M. and T.B. Widdowson, 1978. A resurvey of E. Yale Dawson's '42 intertidal algal transects on the southern California mainland after 15 years. Bulletin of the Southern California Academy of Science 77:1-13.

Thompson, J. N. 1982. Interaction and Coevolution. Wiley and Sons USA.

Thompson, J. N. 1988. Variation in interspecific interactions. Annual Review of Ecology and Systematics 19:65-87.

Thompson, J. N. 1989. Concepts of coevolution. Trends in Ecology and Evolution. 4:179-183.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press.

Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecological Monographs 57:189-214.

Tsuchiya, M. 1983. Mass mortality in a population of the mussel *Mytilus edulis* L. caused by high temperature on rocky shores. Journal of Experimental Marine Biology and ecology 66:101-111.

Tsuchiya, M., and M. Nishihira. 1985. Islands of _Mytilus_ as habitat for small intertidal animals: effects of island size on community structure Marine Ecology Progress Series 25:71-81.

Tsuchiya, M., and M. Nishihira. 1986. Islands of _Mytilus_ as habitat for small intertidal animals: effect of _Mytilus_ age structure on the species composition of the associated fauna and community organization. Marine Ecology Progress Series 31:171-178.

Turner, T. 1985. Stability of rocky intertidal surfgrass beds: persistence, preemption, and recovery. Ecology 66:83-92.

Underwood, A. J. 1980. The effect of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. Oecologia (Berlin) 46:201-213.

Underwood, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanography and Marine Biology Annual Reviews 19:513-605.

Underwood, A. J. 1989. The analysis of stress in natural populations. Biological Journal of the Linnean Society 34:51-78.

Underwood, A. J., and E. J. Denley 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. In: Ecological communities: conceptual issues and the evidence. D.R. Strong Jr., D. Simberloff, L.G. Abele, and A.B. Thistle editors., pp151-180. Princeton University Press, Princeton New Jersey.

Underwood, A. J., and P. Jernakoff. 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. Oecologia (Berlin) 48:221-233.

Underwood, A. J., E. J. Denley, and M. J. Moran. 1983. Experimental analyses of the structure and dynamics of

mid-shore rocky intertidal communities in New South Wales.
Oecologia (Berlin) 56:202-219.

Underwood, A.J. and S.J. Kennelly 1990. Pilot studies for
designs of surveys of human disturbance of intertidal
habitats in New South Wales. Australian Journal of Marine
and Freshwater Research 41:165-173.

Vance, R. R. 1978. A mutualistic interaction between a
sessile marine clam and its epibionts. Ecology 59:679-685.

Weins, J. A. 1986. Spatial scale and temporal variation in
studies of shrubsteppe birds. In Community ecology (edited
by J. Diamond and T. J. Case. Harper and Row pp 154-172.

Weins, J. A. 1989 The ecology of bird communities Vol. 2.
processes and variations. Cambridge University Press.

Wethey, D. 1985. Catastrophe, extinction, and species
diversity: a rocky intertidal example. Ecology 445-456.

Widdowson, T.B. 1971. Changes in the intertidal algal
flora of the L.A. area since the survey of E. Yale Dawson
in 1956-1959. Bulletin of the Southern California Academy
of Science 70:2-16.

Wilkinson, C. R. 1987. Interocean differences in size and
nutrition of coral reef sponge populations. Science
236:1645-57.

Wilkinson, L. 1990. SYSTAT: The system for statistics.
Evanston LL. Systat Inc.

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

Woodland, D.J. and J.N. Hooper, 1977. The effects of human
trampling on coral reefs. Biological Conservation 11:1-4.

Wootton, J. T. 1992. Indirect effects, prey susceptibility, and habitat selection: impacts of birds on limpets and algae. Ecology 73:981-91.

Wootton, J. T. 1993. Indirect effects and habitat use in an intertidal e community: interaction chains and interaction modifications (bird predation of Lottia limpets affects the acorn barnacle). American Naturalist 141:71-89.

Wootton, J. T. 1994. Predicting direct and indirect effects: an integrated approach using experiments and path analysis. Ecology 75:151-65.

Wulff, J. L., and L. W. Buss 1979. Do sponges help hold coral reefs together? Nature London 281:474-5.

Yodiz P. 1988 The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology 69:508-15.

Young, G. A. 1985. Byssus-thread formation by the mussel Mytilus edulis: effects of environmental factors. Marine Ecology Progress Series 24:261-271.

Zedler, J. B., 1976. Ecological resource inventory of the Cabrillo National Monument intertidal zone. Project report of the U.S. dept. of Interior National Park Service. 69pp.

Zedler, J. B., 1978. Public use effects in the Cabrillo National Monument intertidal zone. Project report of the U.S. dept. of Interior National Park Service. 52pp.