AN ABSTRACT OF THE DISSERTATION OF

Anne D. Guerry for the degree of Doctor of Philosophy in Zoology presented on March 10, 2006.
Title: Grazing, Nutrients, and Marine Benthic Algae: Insights into the Drivers and Protection of Diversity

Abstract approved:

Bruce A. Menge   Jane Lubchenco

Two of the most powerful ways in which humans have altered ecosystems are by increasing productivity and changing the densities of important consumers. The bottom-up effects of productivity and the top-down effects of consumers have been identified as primary determinants of biological diversity, though the links between them remain unclear. Understanding how consumers and productivity act and interact to yield differences in diversity is of both conceptual and pragmatic importance. Here, I describe three experiments designed to examine the links between grazing, productivity, and diversity in rocky intertidal systems in Oregon and New Zealand. In two experiments I used fully-factorial designs in which I manipulated both grazing and nutrients. Both experiments revealed the primary importance of grazing as a structuring force of algal assemblages. In the Oregon experiment, I also document an interaction between grazing and productivity, with nutrient enrichment decreasing algal diversity at low grazer densities and increasing algal diversity at high grazer densities. This interaction was not apparent in the New Zealand experiment. In the absence of grazers, nutrient addition led to increased abundance of foliose algae at this site but had no net effect on algal diversity. In the third experiment, also conducted in New Zealand, I used natural variation in nearshore productivity as a backdrop against which I manipulated the access of grazers. In this experiment, I found that grazers had negative impacts on benthic algal diversity and abundance at sites with lower productivity and negligible impacts on benthic algal assemblages at sites with higher productivity. Overall these three studies suggest that in these intertidal grazer-dominated communities, the strong top-down effects often documented in such systems can be modified by more subtle bottom-up effects. Together, results from these experiments elucidate factors that determine algal diversity in these systems and underscore the importance of the evolutionary context in which experiments are conducted. Finally, I conclude with a synthesis of the literature in which I put these and other findings to work by exploring the ways in which basic marine ecological research can inform the management of human activities that affect the marine environment.

Grazing, Nutrients, and Marine Benthic Algae: Insights into the Drivers and Protection of Diversity

by
Anne D. Guerry

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APPROVED:

Co-Major Professor, representing Zoology

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Chair of the Department of Zoology

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Anne D. Guerry, Author

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PREFACE

The Peace of Wild Things

When despair for the world grows in me
and I wake at night at the least sound
in fear of what my life and my children's lives may be,
I go and lie down where the wood drake
rests in his beauty on the water, and the great heron feeds.
I come into the peace of wild things
who do not tax their lives with forethought
of grief. I come into the presence of still water.
And I feel above me the day-blind stars
waiting with their light. For a time
I rest in the grace of the world, and am free.

--Wendell Berry (1998)

Grazing, Nutrients, and Marine Benthic Algae: Insights into the Drivers and Protection of Diversity

Chapter One: General Introduction

Humans have profoundly altered, and continue to alter, the ecosystems on which we depend. Two of the ways in which humans impact ecosystems are through the addition of nutrients and the alteration of the densities of important consumers. The widespread use of nitrogenous fertilizers and other anthropogenic factors have significantly increased the amount of available nitrogen in global systems, with important implications for the structure and functioning of a range of ecosystems (Vitousek et al. 1997, Suding et al. 2005). Similarly, the reduction in abundance or complete removal of species that play key roles in systems can have dramatic effects on the systems from which they are deleted (Paine 1966, Power et al. 1996, Jackson et al. 2001, Myers and Worm 2003).

These factors are not only important because they represent significant anthropogenic impacts on ecosystems, but also they have been hypothesized to play important roles in determining diversity. Both productivity and consumers (and other forms of disturbance) play central roles in ecological theory aimed at understanding the defining question of the field of ecology: “what determines the distribution and abundance of species.”

The link between productivity and diversity has generated a great deal of theoretical and empirical research. However, both the shape and the underlying mechanisms of this relationship remain controversial. Numerous authors have hypothesized and demonstrated a unimodal relationship between productivity and diversity (e.g., Grime 1973a, Huston 1979, Tilman and Pacala 1993, Dodson et al. 2000). Others have maintained that competition, the primary mechanism thought to underlie the decreasing portion of the unimodal relationship at high productivity, can instead produce a monotonically increasing relationship between productivity and diversity (Abrams 1995). Empirical, positive relationships between productivity and diversity have been demonstrated (Brown 1973, Phillips et al. 1994). Recent reviews of this subject have concluded that unimodal relationships were either the predominant pattern (Grace 1999), or were relatively common but that other relationships—particularly monotonically increasing relationships—were not infrequent (Waide et al. 1999, Mittelbach et al. 2001). A number of factors contribute to the lack of consensus on the nature of the relationship between productivity and diversity. Studies conducted to date use different metrics of diversity (e.g. richness, evenness) and productivity (e.g. nutrient availability, evapotranspiration, plant biomass), are conducted over a wide range of spatial scales, examine different ranges of productivity, and often fail to account for confounding factors such as disturbance.

The intermediate disturbance hypothesis (Grime 1973a, b, Horn 1975, Connell 1978) predicts a unimodal relationship between disturbance and diversity. The conceptually similar intermediate predation hypothesis (Paine 1966) also predicts a unimodal diversity relationship, with predation or grazing rather than disturbance as the underlying mechanism. These models have been supported by theoretical and empirical evidence (Lubchenco 1978, Sousa 1979). The intermediate disturbance hypothesis has been claimed to be "one of the best-accepted principles in ecology" (Hoopes and Harrison 1998). However, this hypothesis has been criticized for its oversimplification (McGuinness 1987, Shiel and Burslem 2003) and lack of generality (Mackey and Currie 2001). Also, difficulties in quantifying disturbance (Reynolds et al. 1993) and the inherent circularity in some empirical tests (Shea et al. 2004) have been cited as indications of a potential lack of testability.

The dynamic equilibrium model (Huston 1979, 1994) is a conceptual model that simultaneously examines the effects of productivity and disturbance on diversity. This model assumes that factors that influence the rate of competitive displacement (i.e., disturbance [defined broadly to include biotic and abiotic disturbance and predation/grazing] and productivity) are primary determinants of the number of coexisting species within a given functional group. At its simplest, the model suggests that disturbance decreases diversity when productivity is low, is unimodally related to diversity at intermediate levels of productivity, and increases diversity when productivity is high. Similarly, increasing productivity decreases diversity when disturbance is low, is unimodally related to diversity at intermediate levels of disturbance, and increases diversity when disturbance is high. A simpler version of this model, the “grazer-reversal-hypothesis” (Proulx and Mazumder 1998) suggests that grazing decreases the species richness of primary producers in nutrient-poor environments and increases or has no effect on the species richness of nutrient-rich or experimentally enriched environments.

Here, I present three experiments that examine the relationships between productivity, grazing, and diversity. I use limpet-algal communities on rocky shores in Oregon and the South Island of New Zealand as systems in which to examine these relationships. Oregon and the South Island of New Zealand span similar latitudes in their respective hemispheres (OR: 43′-46′ N; S.I. N.Z.: 42′-44′ S), have similar taxonomic compositions (above the Genus level), and display similar biological zonation patterns on wave-exposed rocky shores (Menge et al. 1999 and citations therein). However, nearshore waters off the coast of Oregon yield temperate reef environments that rank among the most nutrient rich globally, with nitrogen concentrations often reaching values of 30μM or higher (Dickson and Wheeler 1995, Hill and Wheeler 2002, F. Chan, unpublished data). In contrast, the South Island of New Zealand is nutrient-poor, with nitrogen concentrations rarely above 10μM (Vincent et al. 1991, Chang et al. 1995, F. Chan, unpublished data). Thus, the two systems provide a unique opportunity to compare and contrast the effects of nutrients and grazing on benthic algal assemblages.

In Chapter Two, I report the results of a fully-factorial experiment in which I manipulated both the availability of nutrients (namely nitrogen (N) and phosphorous (P)) and the density of consumers (limpets, the dominant grazers) in a high intertidal limpet-macroalgal community on the Oregon coast. In this nutrient-rich environment, I demonstrate that grazing is of primary importance, with strong negative effects on algal diversity, likely acting partially through effects on algal abundance. I also document an interaction between grazing and enrichment, with nutrient enrichment increasing algal diversity at high grazer densities. I discuss these results in the context of the dynamic equilibrium model and conclude that although some of the patterns documented are consistent with the conceptual model, some of the mechanisms expected to operate do not appear to be primary drivers in this system. I argue that the careful consideration of the contexts in which models are expected to operate will further advance the understanding of the drivers of biological diversity.

In Chapter Three, I present a similar experiment conducted on the South Island of New Zealand. Despite differences in methodology necessitated by differences in the two systems, the experimental design was similar to that used in Oregon. I used a fully-factorial design in which I manipulated both levels of enrichment and densities of grazers. Similar to the results of the Oregon experiment, grazing was of primary importance in this community, with strong negative effects on algal abundance and diversity. Unlike the Oregon experiment, there was no interaction between grazing and enrichment; grazers acted to reduce the abundance and diversity of the overall algal assemblage regardless of enrichment level. However, I found an interactive effect of grazing and enrichment on the abundance and biomass of foliose algae, an important component of the algal system. Thus, the effects of bottom-up inputs in this experimental system in a low-nutrient environment were weaker that they were in a similar system in a high-nutrient environment. This finding contrasts with the expectations of both the dynamic equilibrium model and the grazer-reversal hypothesis.

In Chapter Four, I describe the results of an experiment in which I manipulated the presence or absence of limpets at sites with naturally varying levels of background productivity. For this experiment, I used sites on the east and west coasts of the South Island of New Zealand. Upwelling, the delivery of cold, nutrient-rich water from depth to the sea surface is the combined result of the Coriolis effect and equatorward winds that push surface waters offshore. Satellite imagery, intertidal air and water temperatures, monthly and daily upwelling indices, and water-sampling data (chlorophyll-*a*, particulates, and nutrients) indicate that sites on the west coast of New Zealand are characterized by intermittent upwelling, while sites on the east coast predominantly experience downwelling (Menge et al. 2003 and references therein). Thus, productivity is generally higher on the west coast than it is on the east coast. I found that limpets had a negative effect on algal species richness and biomass at nutrient-poor sites and little effect at nutrient-rich sites. This result supports the predictions of the grazer-reversal hypothesis, although the mechanism behind the pattern appears linked to differences in grazing intensity between nutrient-poor and nutrient-rich sites. Also, these findings provide further evidence for the links between nearshore oceanography and rocky-intertidal community structure and dynamics.

In Chapter Five, I attempt to put the results from these and other basic marine ecological experiments to work informing the management of human activities that affect marine systems. In the past few years, two major national commissions have concluded that the oceans are increasingly being affected by human activities and that new approaches to managing those activities are needed. Both commissions highlight the fragmented governance of US oceans today and the importance of taking an ecosystem-based approach to managing human activities that affect the oceans (Pew Oceans Commission 2003, U.S. Commission on Ocean Policy 2004). I examine some of the ways in which principles from ecological research in nearshore marine systems can help both the generators and users of ecological science to further integrate the management of human impacts on marine ecosystems. For ecologists, I provide examples of the relevance of basic research for shaping the concepts of ecosystem-based management. Recognizing that ecological theory, experiments, principles, and tools are important for the management of marine systems is easy. Communicating their utility and ensuring that their power is brought to bear on real-world problems is not. For practitioners, I aim to distill some of the lessons learned from work in nearshore systems and discuss some of the ways they can help provide different perspectives for thinking about management.

Finally, in Chapter Six, I compare and contrast the results of the three experiments and interpret their collective messages in light of ecological theory. Together these experiments can help us to understand the factors that determine the abundance and diversity of algae in these systems. Differences in the results across the experiments highlight the importance of the evolutionary context in which experiments are conducted, the effect of the spatial and temporal scales over which experiments are conducted, and the utility—and limitations—of conceptual models for structuring our thinking about the ways in which ecological systems work. I close with a plea to continue to strengthen the links between basic ecological research and the policies that govern the human activities within the ecological systems that provide the ecosystem services necessary for life on this planet.

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Chapter Two:

Interactive effects of grazing and enrichment on benthic algal diversity in a rocky intertidal community

Abstract

Understanding the ways in which disturbance and productivity act and interact to yield differences in diversity is of primary conceptual and pragmatic importance in a world in which humans are simultaneously changing disturbance regimes and responsible for substantially altering the availability of nutrients. The dynamic equilibrium model predicts the effects of each of these factors and their interactions in ecological communities, but empirical evidence remains inconclusive. In this experiment, I used macroalgal communities on rocky reefs to examine the effects of both limpet grazing and nutrient enrichment on macrophyte diversity. The experimental design included three levels each of grazing and nutrients, with unglazed terracotta pots attached to the rock as replicate plots in a high intertidal limpet-macroalgal community. Grazing was of primary importance in this experiment, with strong negative effects on algal diversity, likely acting primarily through effects on algal abundance. I also document an interaction between grazing and enrichment, with nutrient enrichment increasing algal diversity at high grazer densities. Although this pattern appears consistent with predictions of the dynamic equilibrium model, some of the mechanisms expected to operate in this model do not appear to be primary drivers in these algal communities. In particular, I propose that the absence of competitive exclusion and low settlement rates of late-successional species suggest that the dynamic equilibrium model can not adequately explain patterns of diversity in this system. Careful consideration

of the contexts in which models are expected to apply to real ecological systems and the adaptation of models to better apply in particular cases will yield further advances in our understanding of the drivers of biological diversity.

Introduction

In a world where humans are increasingly becoming dominant ecosystem engineers, the time-honored ecological quest to understand the causes and consequences of biological diversity becomes increasingly important. Two primary ways in which humans have altered ecosystems are by increasing productivity—through the addition of nitrogen (N) and phosphorous (P) (Vitousek et al. 1997b) —and by altering disturbance regimes—e.g., through the reduction in abundance or complete removal of species that play key roles (Jackson et al. 2001, Myers and Worm 2003) and the large-scale conversion of ecosystems through land transformation and the equivalent in the oceans (Sala et al. 2000). Both productivity and disturbance (biotic and abiotic) have been identified as primary drivers of biological diversity.

The link between productivity and diversity has elicited a great deal of ecological inquiry, although both the shape and the underlying mechanisms of this relationship remain controversial. Numerous authors have hypothesized and demonstrated a unimodal relationship between productivity and diversity (e.g., Grime 1973a, Huston 1979, Tilman and Pacala 1993, Dodson et al. 2000). But others have maintained that competition, the primary mechanism proposed to underlie the decreasing portion of the unimodal relationship at high productivity, can alternatively produce a monotonically increasing relationship between productivity and diversity (Abrams 1995). Empirical, positive relationships between productivity and diversity have been demonstrated (Brown 1973, Phillips et al. 1994). Recent reviews have reported that unimodal relationships were either the predominant pattern (Grace 1999), or relatively common but that other relationships—particularly monotonically increasing relationships—were not infrequent (Waide et al. 1999, Mittelbach et al. 2001). A number of factors contribute to the lack of consensus on the nature of the relationship between productivity and diversity. Studies conducted to date use different metrics of diversity (e.g. richness, evenness) and productivity (e.g. nutrient availability, evapotranspiration, plant biomass), are conducted over a wide range of spatial scales, examine different ranges of productivity, and often fail to account for confounding factors such as disturbance.

The intermediate disturbance hypothesis (Grime 1973a, b, Horn 1975, Connell 1978) predicts a unimodal relationship between disturbance and diversity. It has been supported by theoretical and empirical evidence (Lubchenco 1978, Sousa 1979) and has been touted as "one of the best-accepted principles in ecology" (Hoopes and Harrison 1998). However, this hypothesis has been criticized for its oversimplification (McGuinness 1987, Shiel and Burslem 2003) and lack of generality (Mackey and Currie 2001). Also, difficulties in quantifying disturbance (Reynolds et al. 1993) and the inherent circularity in some empirical tests (Shea et al. 2004) have been cited as indications of a potential lack of testability.

The dynamic equilibrium model (Huston 1979, 1994) (Fig. 2.1) is a conceptual model that simultaneously examines the effects of productivity and disturbance on diversity. This model assumes that factors that influence the rate of competitive displacement (i.e., disturbance and productivity) are primary determinants of the number of species that can coexist. At its simplest,

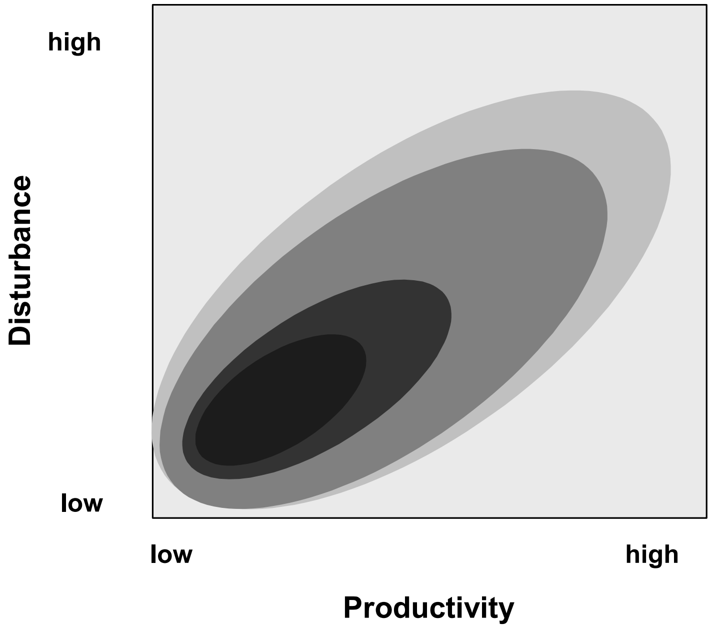

Figure 2.1. A graphic depiction of the predictions of the dynamic-equilibrium model, re-drawn from Huston (1994). Darker shades represent higher levels of diversity.

the model suggests that disturbance decreases diversity when productivity is low, is unimodally related to diversity at intermediate levels of productivity, and increases diversity when productivity is high. Similarly, increasing productivity decreases diversity when disturbance is low, is unimodally related to diversity at intermediate levels of disturbance, and increases diversity when disturbance is high.

A number of recent experimental studies have simultaneously examined the effects of productivity and disturbance on diversity. Several of these have documented important interactive effects of biotic disturbance by grazers and nutrient levels on diversity (Gough and Grace 1998, Wilson and Tilman 2002, Worm et al. 2002). Worm et al. (2002) performed a factorial meta-analysis of studies of these factors in aquatic environments and concluded that peak diversity shifts from low to high productivity as grazing levels increase. This conclusion is consistent with the predictions of the dynamic equilibrium model. However, other empirical work has documented important, antagonistic, but generally non-interacting effects of these factors (e.g. Hillebrand 2003, Nielsen 2003). Hillebrand (2003) found that grazers (primarily gastropods and trichopteran larvae) and nutrients had contrasting effects on the diversity of periphyton in lakes, but that the two factors acted independently. Similarly, Nielsen reported contrasting, but independent effects of grazing and nutrient-addition on macroalgal diversity in tide pools.

Disturbance can be physical or biological and is defined broadly as any major agent of biomass removal (Grime 1977, Lubchenco and Gaines 1981, Huston 1994). Herbivory is a primary structuring force of algal communities on rocky shores (Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983) and is arguably the most important cause of algal biomass loss in these environments (Steneck and Dethier 1994). Molluscan grazers are particularly important drivers of algal distribution and abundance on intertidal rocky shores (e.g. Underwood 1980, Lubchenco 1983, Cubit 1984, Underwood and Jernakoff 1984), and they can also have profound impacts on the structure of the benthic community through non-trophic interactions, such as by bulldozing newly-settled barnacles from the rocks while grazing (Underwood et al. 1983, Dethier and Duggins 1984, Menge et al. 1986). Grazing by limpets, of course, acts in concert with physical disturbances such as dislodgement by waves.

Here, I examine the effects of both productivity and grazing on diversity in experimental algal communities. I used nutrient availability as a proxy for productivity and limpet grazing as the dominant disturbance. I used the number of species within a trophic level (therefore likely to compete for resources) as a metric of diversity. I conducted a fully-factorial experiment in which I experimentally enriched benthic algal communities with N and P and manipulated the density of limpets. I used three levels of enrichment and three levels of limpet density to examine not only the extremes, but also intermediate levels. I examined both short-term (days to months) and longer-term (>1.5 years) responses in algal species richness.

Methods

Study site

I conducted this experiment on a limpet-dominated mudstone vertical wall at Boiler Bay, Oregon, USA (44°50′ N, 124°03′ W). A vertical wall was used to eliminate bird-predation on experimental limpets (e.g. Frank 1982, Marsh 1986). The intertidal zone at Boiler Bay is topographically and geologically diverse; horizontal reefs made up of basaltic and conglomerate rock predominate at the more wave-exposed locations, while horizontal and vertical reefs composed of mudstone are common at more wave-sheltered areas. Although much of the mudstone is bare, isolated patches of mussels (*Mytilus californianus* and *Mytilus trossulus*), barnacles (*Balanus glandula, Chthamalus dalli*), and algae were present. The latter consisted mostly of mats of benthic diatoms and filamentous green algae, some foliose algae (e.g., *Ulva* spp., *Enteromorpha* spp., *Porphyra* spp.), and the occasional corticated alga (e.g. *Mastocarpus papilatus, Analipus japonica, Endocladia muricata*). The wall faces southwest, is nearly vertical in aspect, and is approximately 50m north of the well-studied wave-exposed basaltic and conglomerate reef at this site (Menge 1992, Menge et al. 1994, Menge et al. 1997a).

Experimental design

Nitrogen is often the limiting macronutrient in marine systems (Ryther and Dunstan 1971). Summertime coastal upwelling of cold, nutrient-rich water from depth as a result of equatorward winds and the Coriolis effect results in high levels of productivity along the coast of Oregon (e.g. Huyer 1983, Dickson and Wheeler 1995, Menge et al. 1997b, Hill and Wheeler 2002). Data from 100 sampling days from 1993-2004 in the months of May through September show that mean summer nitrate concentrations at Fogarty Creek (a rocky reef <1 km north of Boiler Bay) have been 12.7 μM (± 0.8 SE). The maximum value seen was 32.3 μM, with 20 days (20% of samples) with concentrations >20 μM and 43 days (43% of samples) with concentrations <10 μM (F. Chan, unpublished data). Although ecosystems in many marine environments, such as bays, estuaries, and inland seas, have been dramatically altered through the addition of anthropogenic nitrogen (Vitousek et al. 1997a), open, upwelling-dominated coastlines such as Oregon's are thought to be less susceptible to the effects of additional nitrogen (Walsh 1991, Nixon et al. 1996). However, recent work in tidepools in Oregon has documented effects of enrichment on macroalgal communities (Nielsen 2001, 2003, Bracken and Nielsen 2004). Also, half-saturation constants for some macroalgae suggest that N-limitation is possible for some common species in Oregon much of the time (Lobban and Harrison 1997).

I manipulated nutrients using a modified nutrient-diffusing terracotta flowerpot technique (Fig. 2.2) (Fairchild et al. 1985, Wootton et al. 1996). When submerged, nutrients in agar within the inverted flowerpot diffuse slowly through the agar and the terracotta to become available to the benthic community that establishes on the surface of the pot. Using Z-spar marine epoxy (Seattle Marine, Seattle, Washington, USA), I cemented inverted terracotta flowerpot saucers (13 cm diameter, 2.5 cm tall) to custom-made PVC plates with a large (10 cm) hole in the center, and three holes for screws (Fig. 2.2). Before installation, I inserted a rubber gasket (10.16 cm outside diameter, 8.26 cm inside diameter, 0.48 cm thick) into the saucer, and poured a warm agar solution to the level of the gasket (30 mls). I then filled a plastic Petri-dish (9 cm diameter, 1.5 cm tall) with warm agar (84 mls). When the agar had solidified, I

Figure 2.2. An experimental plate without limpets at the end of the experiment in August 2005. For scale, the terracotta pot saucer is 13 cm in diameter.

placed the rim of the Petri-dish (through the large hole in the PVC plate) against the gasket. In the field, I placed pieces of neoprene fabric between the rock surface and the back of the Petri-dish to prevent breakage of the dish, and then tightened three stainless-steel lag screws through the holes in the PVC plate and into pre-drilled holes in the rock (fitted with plastic wall-anchors) to ensure a seal of the Petri-dish against the gasket. This modification of the technique allowed for the regular exchange of agar-filled Petri-dishes (and disks of agar to fit within the gaskets) approximately every 6-8 weeks throughout the duration of the experiment. Also, I scored the surface of the terracotta saucers with a hand-held engraving tool to provide a more rugose substrate for the attachment of algae.

Each Petri-dish of agar contained one of three levels of nutrients: one third were filled with a high enrichment solution (.67M N (42.5g $NaNO_3$/L), .04M P (3.75g NaH_2PO_4/L), 20g agar/L), one third with a low enrichment solution (.34M N (21.25g $NaNO_3$/L), .02M P (1.88g NaH_2PO_4/L, 20g agar/L), and one third without enrichment (20g agar/L). The 16:1 N:P ratio was chosen to be consistent with the Redfield ratio (Redfield 1958). The high enrichment level approximates that employed by Fairchild et al. (1985) and Wootton et al. (1996). Fairchild et al. (1985) examined the nutrient-releasing behavior of similarly-designed diffusers in the laboratory and found that although nutrient release rates declined over a 23-day period, an average of 7% of stored N and 4% of stored P were released per day in 8.8-cm x 8-cm pots with similar initial concentrations. To estimate nutrient release-rates in the field and to ensure that nutrients were in fact being released, I melted and diluted a weighed portion of the agar from Petri-dishes that had been deployed for 10, 15, and 25 days and determined the concentrations of N remaining. I melted and diluted weighed pieces of solidified agar from deployed pots and determined the concentrations of N (nitrate + nitrite) by colorimetry on a Shimadzu UV-1201 UV-vis spectrophotometer.

I manipulated limpet densities by painting the ring of Z-spar marine epoxy that cemented the terracotta saucer to the PVC plate with copper-based antifouling paint, a deterrent to many molluscan herbivores including most limpets (Cubit 1984). I then stocked the saucers with 6, 3, or 0 *Lottia digitalis*, 1-2 cm in length (3.4, 1.7, and 0 limpets/10 cm^2). The highest stocking density was chosen to reflect ambient densities.

Both 3-level treatments were applied in a fully factorial design with 6 replicates of each treatment combination, for a total of 54 experimental units (hereafter plates). Plates were placed at least 0.5m apart in randomly determined positions in the mid-high zone (5-6.8 feet [1.5-2.1 m] above mean-lower-low water) in January 2004. Plates were placed in a horizontal line to minimize tidal height differences among them.

Monitoring

The experiment was initiated in January 2004 and ran for 576 days. Throughout the duration of the experiment I monitored—and restored—limpet densities on the plates approximately every two weeks. I surveyed the benthic community on the plates every 20-60 days, with more frequent surveys during the first year of the experiment. Surveys involved visually estimating the percent cover of all sessile invertebrates and algae and counting all mobile invertebrates. Algae were identified to the lowest taxonomic resolution possible without destructive sampling. The final sampling in August 2005 (day 576) involved scraping all of the biomass from the pates in order to calculate dry weights of each taxonomic unit. Dry weight was determined by placing each sample into a pre-weighed aluminum foil packet and drying it to constant mass at 60°C.

Background nutrient concentrations were monitored periodically during the course of the experiment as part of my research group's monitoring activities. Water samples were collected from shore by filling acid-washed collection bottles at approximately 0.5 to 1 meter below the surface. Samples were collected by filtration (50ml to 100ml) with pre-combusted (450°C for 4 hrs) 25mm Whatman GF/F glass fiber filters. Filtrates were collected in acid-washed polyethylene vials and frozen for later analysis of nitrate + nitrite (N+N), soluble reactive phosphate (SRP), soluble reactive silicate (SRSi) and total dissolved nitrogen. Water samples were typically filtered in the field within 30 minutes of collection and transported on ice back to the lab. Nitrate + nitrite, SRP, SRSi were analyzed by colorimetry on a Lachat QuikChem 8000 autoanalyzer at the analytical laboratory of the Marine Sciences Institute, University of California, Santa Barbara. Water sampling was conducted more frequently at Fogarty Creek, a rocky reef <1 km north of Boiler Bay than it was at the Boiler Bay site. Given the proximity of the two sites, I examined the relationship between nutrient concentrations at the two sites over the period from 1995-2004 (n=34 sampling days where water was collected at both sites) and found them to be highly correlated (N+N, R^2=0.90; SRP, R^2=0.78; SRSi R^2=0.91). Therefore, I report background nutrient values from the more intensively sampled Fogarty Creek site.

A number of plates were lost to wave action: 15 were lost in the first year and 3 more were lost in the second. By the end of the experiment, 36 plates remained and no treatment combination had fewer than 3 replicates.

Statistical analysis

I used analysis of variance (ANOVA) to examine the effects of nutrient enrichment and limpet density on algal species richness and abundance. I analyzed the data for 3 time-periods: 1) overall patterns for which I modeled the mean response of each plate throughout the experiment, 2) year one for which I modeled the mean response of each plate during the first year of the experiment, and 3) year two for which I modeled the mean response of each plate during the second year of the experiment. This approach is similar to that taken in a repeated-measures analysis but allows for better examination of the assumptions of the model, the use of data from plates that were lost, and a more straightforward interpretation of results.

Of the 15 plates that were lost in the first year, only two were lost in the first 80 days. These were dropped from all analyses. The remaining 13 lost plates remained in place until at least day 202 for a total of ≥ 12 sample dates. Thus, all analyses of overall or early-successional patterns represent results from 52 plates. The second year began with 39 plates. Of the three plates that were lost in the second year, two were lost after day 381 (the first sample date of the second year) and were therefore dropped from all year two analyses. Year two analyses therefore represent results from 37 plates. In all analyses of percent cover data, I used angular transformations (Sokal and Rohlf 1995). When an ANOVA indicated significant effects, I used Tukey's HSD to perform post-hoc tests corrected for multiple comparisons.

To examine the rate of accumulation of species, for each plate I plotted species richness over time and examined the shape of the LOESS smoother (Cleveland and Devlin 1988). Almost all plates showed increases to an initial maximum at approximately day 150. I then performed a piecewise regression for each plate regressing the number of species against day for the first 150 days only. The slope of the line represents the initial rate of species accumulation for each plate. I then modeled the effects of limpets and enrichment on these slopes using an analysis of variance.

I classified the algae into morphological groups based on the "functional group" classification of Steneck and Dethier (1994) (Table 2.1). Given the lack of normality of much of these data, I examined each enrichment level separately and used the non-parametric Kruskal-Wallis test to examine the effects of limpets on morphololgical groups.

Table 2.1. Morphological group assignments of algae that colonized the plates. Groups were based on "functional groups" of Steneck and Dethier (1994) that represent increasing susceptibility to herbivory.

Morphological group	Taxon
microalgae	diatom film
filamentous	green filamentous (likely *Urospora* spp.)
	Bangia spp.
	Acrosiphonia spp.
	Cladophora spp.
	Polysiphonia spp.
foliose	*Porphyra* spp.
	Enteromorpha spp.
	Ulva spp.
corticated foliose	*Mastocarpus papillatus*
	Petalonia fascia
	Mazzaella parksii
	unidentified red blade
corticated macrophyte	*Endocladia muricata*
	Analipus japonicus
	Melanosiphon intestinalis
	Pelvetiopsis limitata
	unidentified terete red
	unidentified corticated brown
crustose	Red crust (likely *Hildenbrandia* spp.)
	Brown crust (likely *Ralfsia* spp.)
	unidentified black crust

Results

Efficacy of treatments

Although limpets are deterred from crossing barriers of copper paint, limpets occasionally invaded the plates from the surrounding area or (more commonly) were lost from plates on which they were stocked. Recorded limpet numbers from the bi-monthly assessments of limpet numbers indicated that zero-limpet plates had an average of 0.86 limpets (SE=0.13), three-limpet plates had an average of 2.84 limpets (SE=0.13), and six-limpet plates had an average of 4.45 limpets (SE=0.13). These are likely to be underestimates for the three- and six-limpet plates because the counts were performed on each date just before re-stocking to the desired levels and thus likely represent the lowest number of limpets present during the time period between sampling events.

Melting down the agar from plates that had been in the field for 10, 15, and 25 days (4 plates/time period/nutrient treatment) yielded mean nitrate concentrations of 0.54 (± 0.10 SE), 0.22 (±0.08 SE), and 0.32 (± 0.07 SE) M for high-enrichment plates and 0.23 (± 0.02 SE), 0.15 (± 0.03), and 0.17 (± 0.05) M for low-enrichment plates. An average of 4% of stored N was released/day throughout the trial period of 25 days.

Background nutrient levels

We sampled water from Fogarty Creek on 19 different days from early May 2004 until late August 2005. The mean N+N concentration during this time period was 10.3 μM (±1.7 SE). The minimum value was 1.0 μM and the maximum was 22.1 μM, with 7/19 values less than 5 μM and only 3/19 values above 20 μM. SRP ranged from 0.22 to 2.13 μM, with a mean of 1.13 μM (± 0.15

SE). SRSi ranged from 2.8 to 40.9 µM with a mean of 17.68 µM (±2.78 SE) (F. Chan, unpublished data).

Algal communities

Both grazing and productivity affected algal diversity. Limpets strongly affected algal species richness throughout the experiment. The effect of nutrient enrichment depended on limpet density overall and specifically during the first year of the study (nutrient x limpet interaction; Table 2.2a, Fig. 2.3a & b). Enrichment tended to decrease algal species richness at low and intermediate limpet densities, while high levels of enrichment increased richness at high limpet densities. During the second year of the study, limpets and enrichment affected algal species richness independently, with increasing limpets and high enrichment levels decreasing species richness (Table 2.2a, Fig. 2.3c).

Throughout the experiment, limpets also had a very strong negative effect on algal abundance. Plates without limpets had an average of seven times higher percent cover than those with six limpets (Table 2.2b; Fig. 2.3d). The same was true for the first year, in which I saw even stronger effects of limpets (Table 2.2b). However, in the second year, the effect of limpets on algal abundance had weakened. In contrast to its effects on richness, the addition of nutrients did not affect the abundance of algae either throughout the experiment or when looking separately at the first or second year of the experiment (Table 2.2b, Fig. 2.3d-f).

The effect of limpets weakened as time progressed, with differences in diversity persisting through the second year, but not differences in abundance. In fact, neither percent cover (Fig. 2.3f, Table 2.2b) nor algal biomass (ANOVA;

Table 2.2. ANOVA results for a) algal species richness and b) percent cover over the duration of the experiment (“overall”), during the first year, and during the second year. Bolded probabilities indicate those effects that were significant at $p < 0.05$.

a. Algal Species Richness

	Source of variation	d.f.	Mean Square	F-ratio	*p*-value	R^2
Overall	Nutrients	2	0.525	2.597	0.086	0.729
	Limpets	2	9.524	47.127	**<0.001**	
	Nutrients x Limpets	4	0.715	3.537	**0.014**	
	error	43	0.202			
Year One	Nutrients	2	0.278	1.564	0.221	0.741
	Limpets	2	9.047	50.904	**<0.001**	
	Nutrients x Limpets	4	0.728	4.097	**0.007**	
	error	43	0.178			
Year Two	Nutrients	2	5.248	5.114	**0.013**	0.553
	Limpets	2	12.223	11.909	**<0.001**	
	Nutrients x Limpets	4	1.010	0.985	0.432	
	error	28	1.026			

b. Percent Cover

	Source of variation	d.f.	Mean Square	F-ratio	*p*-value	R^2
Overall	Nutrients	2	0.011	0.376	0.689	0.753
	Limpets	2	1.800	62.014	**<0.001**	
	Nutrients x Limpets	4	0.043	1.467	0.229	
	error	43	0.029			
Year One	Nutrients	2	0.016	0.473	0.626	0.770
	Limpets	2	2.344	70.045	**<0.001**	
	Nutrients x Limpets	4	0.035	1.057	0.389	
	error	43	0.033			
Year Two	Nutrients	2	0.008	0.076	0.927	0.286
	Limpets	2	0.318	2.934	0.070	
	Nutrients x Limpets	4	0.110	1.016	0.416	
	error	28	0.109			

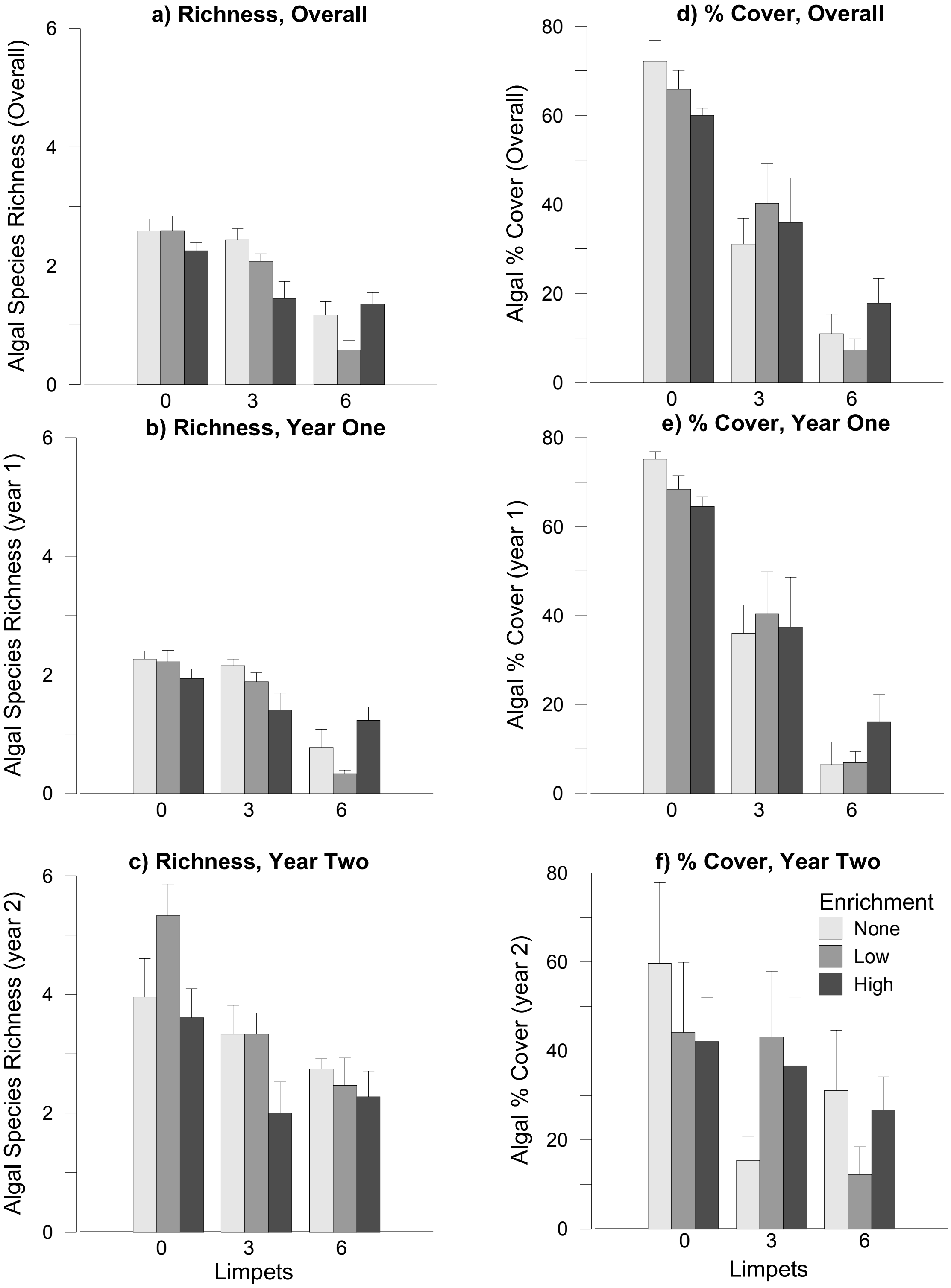

Figure 2.3. Algal species richness (a-c) and percent cover (d-f) throughout the duration of the experiment (a,d), during the first year (b,e), and during the second year (c,f).

nutrient effect, $F_{2,27}$=1.554, p=0.230, limpet effect, $F_{2,27}$=0.975, p=0.390, interaction, $F_{4,27}$=1.196, p=0.335) differed in relation to limpets or nutrients at the end of the experiment.

There were two peaks of algal abundance and species richness in most treatment combinations. Algal abundance initially increased until September 2004 (day 248), decreased until February 2005 (day 381), and then increased or remained the same until the end of the experiment in August 2005 (day 576) (Fig. 2.4a). An initial bloom of benthic diatoms was followed by a dramatic increase of filamentous algae (primarily filamentous green algae such as *Urospora spp.*). This was followed by foliose algae (primarily *Porphyra* spp., *Enteromorpha* spp., and *Ulva* spp.) that dominated the community until they senesced in late summer 2004. Corticated macroalgae colonized the plates in the second year, but never became dominant (the maximum percent cover of corticated algae on any plate was 32%). Algal species richness initially peaked in June 2004 (day 130), decreased until September 2004 (day 245 or 248) (while abundance remained high), increased again until February 2005 (day 381) and then either remained the same or decreased until the end of the experiment (Fig. 2.4b).

Given the significant interaction between limpets and enrichment in most cases, I examined patterns of different morphological groups of algae separately for each limpet density. Limpets affected the occurrence and abundance of different morphological groups of algae in different ways (Fig. 2.5). Without enrichment, filamentous and foliose algae were less abundant at higher limpet densities (Kruskal-Wallis, 2 d.f., filamentous:10.635, p=0.005, foliose: 13.071, p=0.001), and corticated foliose and macroalgae were absent

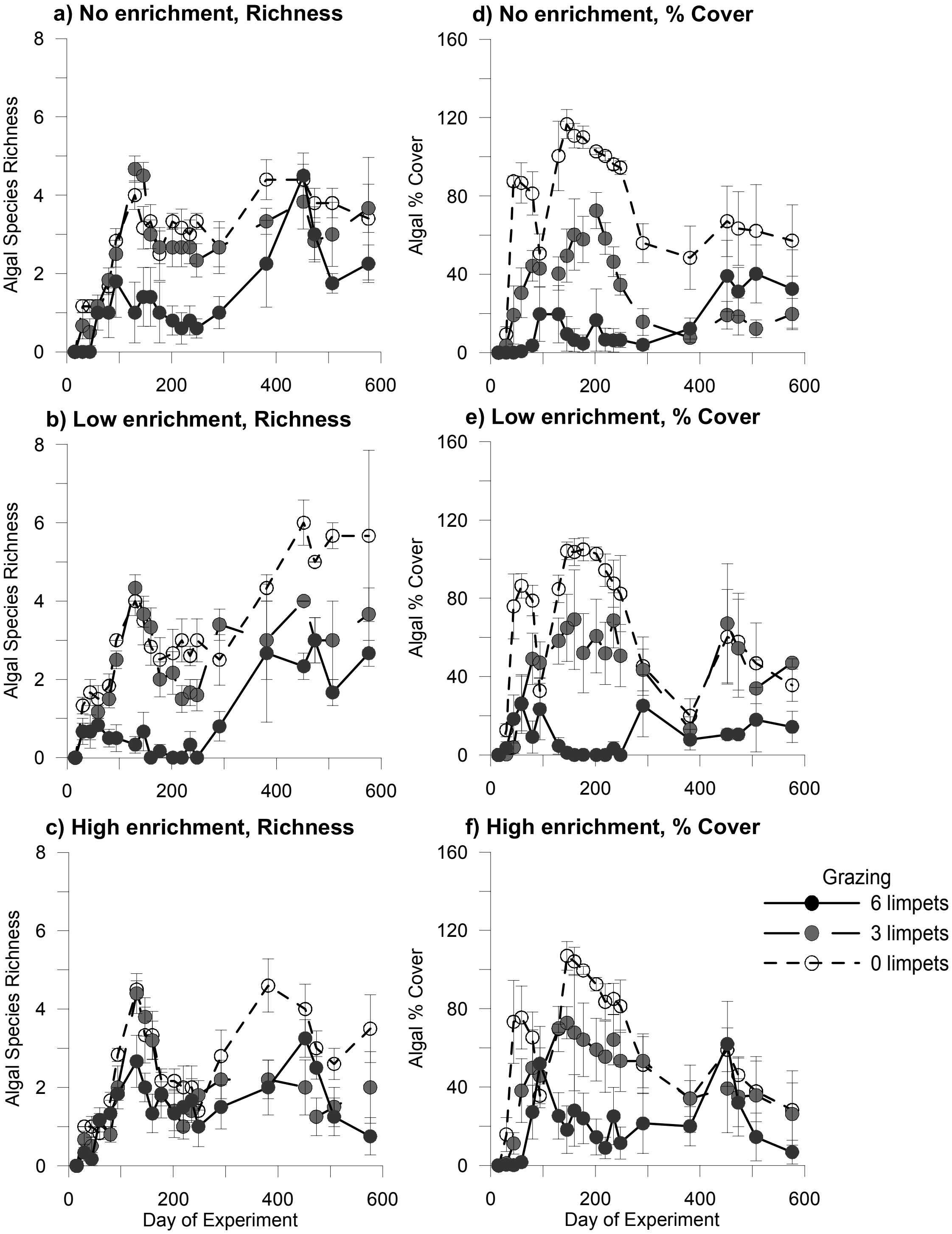

Figure 2.4. Mean (± 1 SE) algal species richness (a-c) and abundance (d-f) over the duration of the experiment. Day 0 is January 20, 2004.

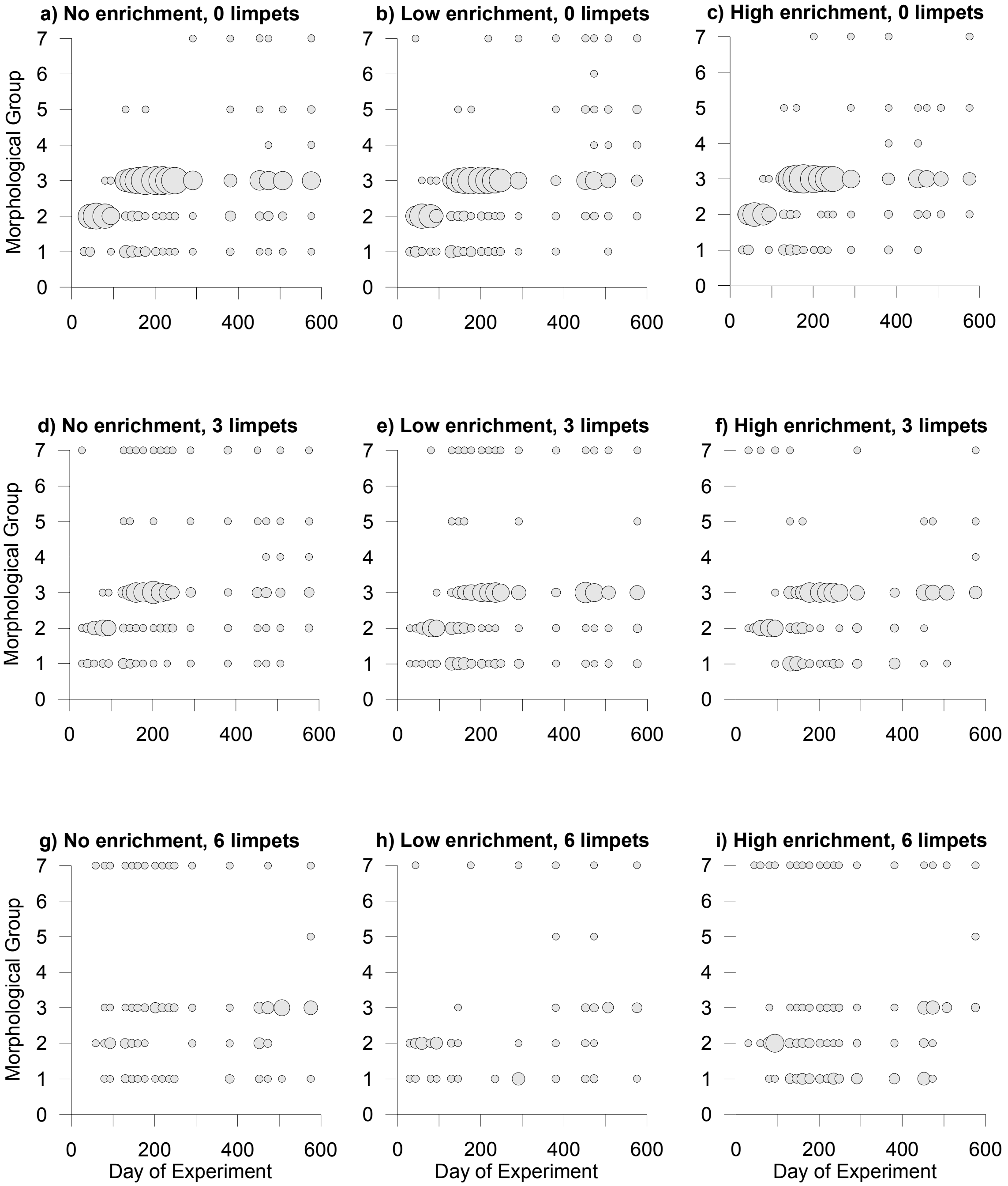

Figure 2.5. Bubble plots representing the mean percent cover (maximum = 98%) of the 7 morphological groups of algae for each of the plates in each treatment combination throughout the duration of the experiment. 1=microalgae, 2=filamentous algae, 3=foliose algae, 4=corticated foliose algae, 5=corticated macroalgae, 6=corticated leathery macroalgae, and 7=crustose algae.

from plates with high limpet densities (Fig. 2.5 a,d,g). With low enrichment, foliose algae were almost completely absent from early succession in plates with high limpet densities (Kruskal-Wallis, 2 d.f., 13.328, p=0.001) (Fig. 2.5h). Corticated foliose algae were absent from plates with limpets (Fig. 2.5 e & h), and corticated macroalgae were marginally less prevalent on plates with high densities of limpets (Kruskal-Wallis, 2 d.f., 5.915, p=0.052) (Fig. 2.5 b, e, h). On plates with high enrichment, foliose algae were less abundant on plates with high densities of limpets in early succession (Kruskal-Wallis, 2 d.f., 13.087, p=0.001) (Fig. 2.5 c, f, i). Corticated foliose algae were absent from plates with high densities of limpets (Fig. 2.5i). Across all enrichment levels, crustose algae were absent or less abundant without limpets in early succession (Kruskal-Wallis, 2 d.f., 7.687, p=0.021) (Fig. 2.5, all panels).

Grazing slowed the rate of species accumulation. The initial rate of accumulation of species on plates with six limpets was slower than that on plates with zero or three limpets without enrichment and with intermediate enrichment (Table 2.3, Fig. 2.6). However, high enrichment sped the initial rate of species accumulation on the six-limpet plates such that it was no longer distinguishable from the rates on plates with zero or three limpets (Fig. 2.6).

Table 2.3. ANOVA results for the rate of accumulation of species (slope of the regression of species richness vs. day for the first 150 days of the experiment).

Source of variation	d.f.	Mean Square	F-ratio	*p*-value	R^2
Nutrients	2	0.00015	2.447	0.098	0.695
Limpets	2	0.00234	39.473	**<0.001**	
Nutrients x Limpets	4	0.00020	3.406	**0.017**	
error	43	0.00006			

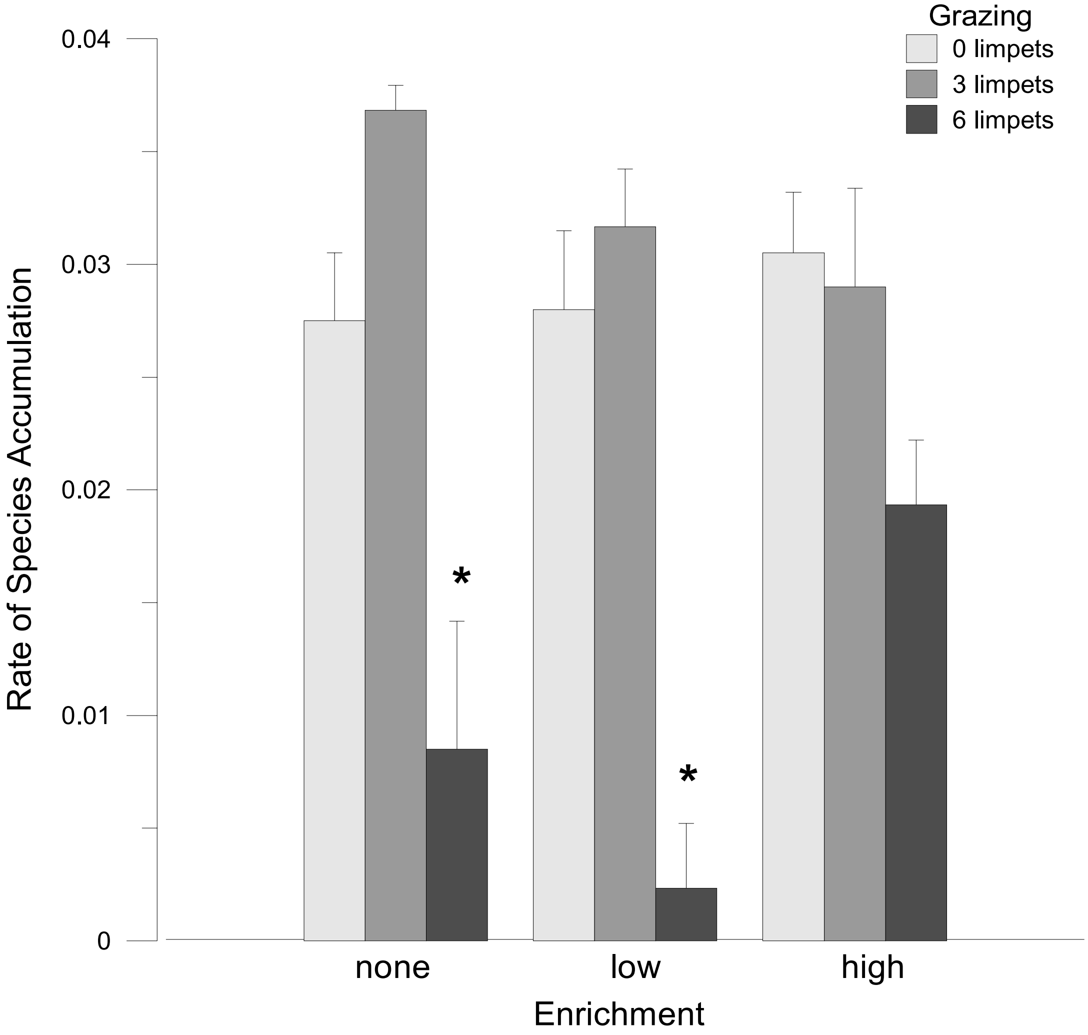

Figure 2.6. Mean rates of accumulation (+ 1 SE) of species for the nine treatment combinations over the first 150 days of the experiment. Values for each plate were calculated by regressing the number of species present against time. *'s represent significant differences at $p<0.05$ (ANOVA post-hoc Tukey's HSD).

Fauna

Although algae were of primary interest in this experiment, marine algae live in a world in which interactions with both sessile invertebrates, micrograzers, and other mobile invertebrates can play important roles. Thus, I also examined the responses of other elements of the benthic community to experimental manipulation. Barnacles, the dominant sessile invertebrates that colonized these plates, were more abundant on plates with fewer limpets. These differences occurred during year one (ANOVA, year one limpet effect $F_{2,43}=30.939$, $p<0.0001$), but not during year two (year two limpet effect $F_{2,43}=2.118$, $p=0.139$). In contrast, barnacle abundance was not affected by enrichment. Barnacle cover was positively correlated with algal cover in both years (linear regression; year one $R^2=0.382$, $p<0.0001$, year two $R^2=0.169$, $p=0.009$).

The density of other mobile invertebrates (primarily littorinid snails) was negatively associated with limpet density during both years of the experiment (ANOVA; year one $F_{2,43}=4.957$, $p=0.012$, year two $F_{2,28}=10.094$, $p=0.001$), but enrichment had no effect on mobile invertebrate density.

At the end of the experiment, biomass of both sessile and mobile invertebrates differed on plates stocked with different numbers of limpets. Higher limpet densities were associated with less biomass of other invertebrates (sessile invertebrate ANOVA; limpet effect, $F_{2,27}=5.436$, $p=0.01$; mobile invertebrate ANOVA; limpet effect, $F_{2,27}=15.627$, $p<0.0001$). Enrichment, however, had no effect on the biomass of either type of invertebrate, whether as a main effect (sessile invertebrate ANOVA; $F_{2,27}=0.743$, $p=0.485$; mobile invertebrate ANOVA; $F_{2,27}=2.302$, $p=0.119$), or through an interaction with limpet density (sessile invertebrate ANOVA; $F_{4,27}$=1.375, p=0.269; mobile invertebrate ANOVA; $F_{4,27}$=2.253, p=0.09).

Bare space

Competition for space is an important factor in many marine benthic environments. Overall, the pattern of the availability of bare space mirrors the pattern of algal abundance—with the same factors driving its prevalence, but in opposite directions (ANOVA; nutrient effect $F_{2,43}$=3.210, p=0.05, limpet effect, $F_{2,43}$=128.941, p<0.0001, interaction, $F_{4,43}$=4.587, p=0.004). Generally, the patterns for both years were similar. The amount of bare space increased with increasing limpet density, and was context-dependent (limpet x nutrient interaction) with enrichment increasing the amount of bare space with low limpet densities but decreasing the amount of bare space with high limpet densities.

Discussion

These results demonstrate that grazing can interact with productivity to affect diversity in the Boiler Bay rock wall system. During year one, at low limpet densities, nutrient enrichment tended to decrease algal diversity; at high limpet densities high enrichment increased algal diversity. These findings are in agreement with earlier empirical work (e.g., Gough and Grace 1998 (though the effect in that case was on longer-term results)), and appear to lend support to the dynamic equilibrium model (Huston 1979, 1994). However the primacy of the role of grazing by limpets in this system—and their overarching negative effect on abundance and diversity—demonstrates that in this system at least, no level of increased productivity can compensate for such intense grazing.

The two peaks of algal abundance through time (Fig. 2.4 a-c) showed the effects of both successional and seasonal patterns. With some exceptions, these patterns reflect our understanding of the development of algal communities on rocky intertidal shores (Dayton 1975, Sousa 1984). The early-successional sequence of microalgae→ filamentous algae → foliose algae generally fits with our understanding of early succession in similar systems (Dayton 1975, Hawkins 1981, Sousa 1984, Dean and Connell 1987, McCook and Chapman 1997). However, later in succession, there were some departures from the expected pattern. Often, particularly in the presence of grazers, longer-lived corticated algae replace foliose algae (Lubchenco 1983, Worm et al. 1999). Although some longer-lived corticated algae did colonize these plates, they never became abundant. Therefore, despite the duration (>1.5 years) of this experiment, most of the algae—even in the second year—are early-successional species. Thus, the results of this experiment shed light on the effects of grazing and productivity within the context of early succession.

Given the differences observed between patterns in year one and year two, I discuss each of these in turn below. I then address the response of (non-manipulated) invertebrates in this experiment and their potential impact on algal distribution and abundance. Finally, I relate these results to expectations from conceptual models, examine key assumptions inherent in those models, and suggest additional factors to consider when determining their applicability.

Year one

Although the intermediate disturbance hypothesis is generally applied to the long-term coexistence of species, it should apply during the early stages of succession if its assumptions are met. Intermediate disturbance is expected to increase diversity when competition operates within the community and when disturbance acts to re-set succession (Chesson and Huntly 1997, Shea et al. 2004).

Although limpet grazing clearly re-set the successional process in my experiment, competitive exclusion was not apparent. Only those species adapted to highly disturbed environments persisted on the plates with high levels of limpet grazing. Furthermore, these highly disturbed plates had large amounts of unoccupied space. Plates with intermediate numbers of limpets had a mixture of both very early- and early-successional species as the intermediate disturbance hypothesis would predict for this early successional system. However, despite the fact that zero-limpet plates generally had 100% algal cover, competitive exclusion did not appear to be occurring. Like the plates with intermediate numbers of limpets, the zero-limpet plates also had a mixture of very early- and early-successional species. Because richness decreased initially on both zero- and three-limpet plates (without and with bare space respectively), we can assume that competitive exclusion (by early-successional species of very early-successional species) was unlikely to be occurring in the experiment. The coexistence of very early- and early-successional species on these plates contrasts with the findings of Lubchenco (1978), who found that *Enteromorpha* spp., an early-successional species, was able to outcompete the later-successional, corticated species *Chondrus crispus* and suggests that the pre-emptive exclusion that occurred in that system was not occurring here.

The most parsimonious explanation for the increase in species richness with decreases in limpet density is that limpets control the proportion of the surface that is inhabited by algae, and that plates with more algal cover have more species. This pattern matches the predictions of Lubchenco and Gaines (1981) for the effects of herbivory on species richness without strict competitive hierarchies.

Competitive exclusion is also an important mechanism in the dynamic equilibrium model, although this model deals more explicitly with rates of competitive exclusion. In this context, it is interesting that the observed interactive effects of limpets and enrichment on algal species richness are generally consistent with the dynamic equilibrium model. As observed in this experiment, the model predicts that at low levels of grazing, increased productivity decreases diversity, and at high levels of grazing increased productivity increases diversity (Fig. 2.1). However because competitive exclusion does not appear to be important in this experiment, it appears as though the right predictions are being made for the wrong reasons (e.g. Dayton 1973). Low levels of grazing are the only conditions under which relatively complex and speciose algal assemblages are able to develop. At these levels, enrichment tends to decrease richness, but given the lack of evidence for competitive exclusion, the mechanism driving this pattern is unclear. At the other end of the herbivory-spectrum, few species can survive in the heavily grazed treatments, but enrichment increases the numbers of species that persist on the plates. Also, plates with high levels of limpets and high enrichment had rates of species accumulation that were essentially equivalent to plates with fewer limpets and lower levels of enrichment. This suggests that enrichment allows algae to grow (or turnover) quickly enough to be more likely to escape herbivory.

Year two

Despite the nearly two-year duration of my experiment, a truly late-successional community, that is, one dominated by leathery corticated macroalgae, did not develop. One potential mechanism is that early-successional species inhibited colonization by later-successional species (Connell and Slatyer 1977, Lubchenco 1978). This mechanism could operate to slow the rate of succession, but in my experimental system, it is unlikely that early species pre-empted late species given the high availability of bare space and relatively low cover of algae in most treatments during most time periods.

Grazers can have complicated effects on succession (Lubchenco and Gaines 1981, Lubchenco 1983, Farrell 1991, Anderson and Underwood 1997). Although limpets feed on the adults of the early-successional species but generally little or not at all on the adults of the late-successional species (Lubchenco 1983, Steneck and Dethier 1994), they are likely to stall succession because they eat the germlings of both early- and late-successional species (Dayton 1971). In the presence of herbivores, late-successional species need refugia, such as rock crevices not present on smooth plates, to grow to a size at which they are impervious to grazing (Lubchenco 1983). In this experiment, generally only early-successional species (those with both high growth rates and high recruitment rates) persisted on the plates with limpets. However, this does not explain the rarity of late-successional species on plates without limpets.

Much of the theory about succession relies on a trade-off between colonization rate and competitive ability (Connell and Slatyer 1977, Grime 1977). Early-successional species are considered to have high colonization rates and low competitive ability, while late-successional species are thought to have low colonization rates and high competitive ability. Scales of dispersal vary widely in marine systems, but macroalgae are among the shortest dispersers, with estimates ranging from 5 m to 5 km (Kinlan and Gaines 2003). Although isolated corticated macroalgal individuals were present near the plates and extensive beds of corticated macroalgae (at the same tidal height) were approximately 50 m from this experiment, it is possible that late-successional species did not colonize these plates because the supply of propagules was too low. Evidence for the potential limiting effects of algal propagules on community development in a similar system comes from Sousa (1984). He documented that, for some algae (including some of the corticated macroalgae that colonized the plates in this experiment such as *Pelvetiopsis, Mastocarpus,* and *Mazzaella*), the percent cover of macroalgae recruiting to ungrazed patches in the mid-zone of the rocky intertidal was highly correlated with the cover of conspecific adults nearby. He also found that recruitment and subsequent cover of the more ephemeral *Ulva,* and *Cladophora* were not correlated with their cover within 1 m of experimental patches. However, neither the variation in the cover of the corticated *Endocladia* nor *Analipus* was explained by the cover of adult plants within 1 m of experimental patches.

The hypothesized relationships between disturbance and productivity and diversity generally assume that recruitment (or propagule supply) is not limiting. In fact, as predicted by Gaines and Roughgarden (1985) and Dial and Roughgarden (1998), at sufficiently low settlement rates the coexistence of a relatively large number of species is possible even without disturbance. Recent work in terrestrial plant communities (e.g. Foster 2001, Henry et al. 2004) and intertidal marine communities (e.g. Worm et al. 1999, Worm et al. 2001) has begun to explore the co-occurring effects of disturbance, productivity, and propagule supply on diversity at fine scales. The results of this experiment support the prediction (Gaines and Roughgarden 1985) that when colonization rates of late-successional species are low, increasing disturbance negatively affects diversity regardless of the strength of interspecific competition.

Finally, it is important to note that differences in diversity across limpet-treatments persisted during the second year of the experiment, while differences in abundance did not (Table 2.2). Thus, the effect of limpets on algal abundance does not entirely explain differences in diversity across limpet treatments.

Fauna

Because recently settled barnacles are often bull-dozed from the rocks by feeding limpets (Dayton 1971, Foley et al. in prep) the limpet treatments in my experiment were likely directly reducing barnacle cover. Hence, the effect of barnacles on algal communities cannot be examined independently of the effects of limpets on algae. However, given the strong positive relationship between barnacle and algal cover there was no evidence of competition for space between algae and barnacles. Instead, the results suggest that barnacles facilitate algae by providing heterogeneous surfaces on which to settle, a pattern demonstrated previously in this system (Farrell 1991).

My results corroborate earlier work suggesting critical roles for limpets in the development and persistence of patterns of diversity and abundance of benthic communities (Farrell 1988, Anderson and Underwood 1997). Limpets directly affect algal abundance and diversity and the abundance and biomass of sessile invertebrates. Although the effect of limpets on the percent cover of barnacles was weaker in the second year of the experiment, limpet densities did affect barnacle biomass at the end of the experiment. Indirectly, limpets negatively affect the biomass of other mobile invertebrates, probably through competition for food and by reducing habitat complexity.

Conclusion

This experiment adds to the growing body of evidence that suggests that grazing and productivity can have interactive effects on diversity. Grazing by limpets had strong negative effects on algal diversity, likely acting partially through effects on algal abundance. The effects of nutrients on diversity were more subtle; the effects of enrichment depended on the level of herbivory.

It is critical that we carefully consider the contexts in which we expect models—such as the intermediate disturbance hypothesis and the dynamic equilibrium model—to apply to real ecological systems. Attention solely to the patterns that are predicted by theory without examining whether or not the expected mechanisms are operating is counter-productive. I have shown here that although it was reasonable to expect the intermediate disturbance hypothesis and the dynamic equilibrium model to operate in this well-studied system, the lack of evidence of competitive exclusion and low settlement rates of middle- and late-successional algae suggest that some key mechanisms behind these models will not operate in certain systems. Further work elucidating the conditions under which we expect conceptual models to operate will significantly advance our understanding of the factors that drive the diversity of ecological communities.

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Chapter Three:

Effects of consumers and enrichment on abundance and diversity of benthic algae in a rocky intertidal community

Abstract

Human alteration of nutrient cycling and the densities of important consumers have intensified the importance of understanding how productivity and consumers determine the diversity of ecological systems. Conceptual and empirical work examining the links between productivity, consumption (or disturbance), and diversity remain inconclusive. In this experiment, I examined the effects of both grazing and nutrient enrichment on algal abundance and diversity in a rocky intertidal community in New Zealand. I used a fully-factorial design with three levels each of grazing and nutrients, with nutrient-diffusers attached to the rock in replicate plots in a mid- to high-intertidal limpet-macroalgal community. Top-down control by grazers appears to be the driving organizing mechanism for algal communities in this system. I found strong negative effects of grazing on algal diversity and abundance across all levels of nutrient enrichment. However, in contrast to the conclusions drawn from the analysis of the whole algal community, there was an important interactive effect of grazing and enrichment on the abundance and biomass of foliose algae, an important component of the algal system. Thus, these results suggest that both grazing and nutrients have an impact in this system, but that the impact of grazing is by far the strongest effect.

Introduction

Understanding the relationships among productivity, disturbance, and diversity is of both conceptual and pragmatic importance. The widespread use of nitrogenous fertilizers in recent years has significantly increased the amount of available nitrogen in global systems, with important implications for the structure and functioning of a wide array of ecosystems (Vitousek et al. 1997, Suding et al. 2005). Similarly, the reduction in abundance or complete removal of species that play key roles in systems can have dramatic effects on the systems from which they are deleted (Paine 1966, Power et al. 1996, Jackson et al. 2001, Myers and Worm 2003). Alterations of nutrients and species composition (introduction of non-natives and deletions, especially of keystone species) are primary ways in which humans have altered, and continue to alter, the environment (Sala et al. 2000, Millennium Ecosystem Assessment 2005). Both are also hypothesized to be primary determinants of biological diversity.

The links among productivity, disturbance, and diversity have elicited a great deal of ecological inquiry, although mechanisms that link the three and the form of their relationships remain controversial. The dynamic equilibrium model (Huston 1979, 1994) examines the effects of both productivity and disturbance on diversity. This conceptual model suggests that disturbance (biotic or abiotic) decreases diversity when productivity is low, is unimodally related to diversity at intermediate levels of productivity, and increases diversity when productivity is high. Similarly, increasing productivity decreases diversity when disturbance is low, is unimodally related to diversity at intermediate levels of disturbance, and increases diversity when disturbance is high. A simpler version of this model, the “grazer-reversal-hypothesis” (Proulx and Mazumder 1998) suggests that grazing decreases the species richness of primary producers in nutrient-poor environments and increases or has no effect on the species richness of nutrient-rich or experimentally enriched environments.

Empirical work examining the relationships between productivity, disturbance, and diversity has yielded conflicting results. In some systems, as predicted, there appear to be important interactive effects of biotic disturbance by grazers and nutrients on diversity (Gough and Grace 1998, Wilson and Tilman 2002, Worm et al. 2002). In others, antagonistic, but generally non-interacting effects of these factors have been demonstrated (Hillebrand 2003, Nielsen 2003).

Disturbance can be physical or biological and is defined broadly as any major agent of biomass removal (Grime 1977, Huston 1994). Grazing is an important disturbance that helps to define algal communities on rocky shores (reviewed by Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983). It is arguably the most important agent of biomass removal in these systems (Steneck and Dethier 1994). Molluscan grazers, in particular, play key roles in determining algal distribution and abundance on intertidal rocky shores (Underwood 1980, Lubchenco 1983, Cubit 1984, Underwood and Jernakoff 1984).

Productivity, though it can have multiple meanings, is used here to signify resource-availability and thus the capacity for an environment to support biomass. In marine systems, evidence that differences in productivity can lead to differences in the structure and dynamics of rocky intertidal communities comes both from examinations of the effects of large-scale oceanographic processes (Bustamante et al. 1995, Menge et al. 1997, Menge et al.

2003, Nielsen and Navarrete 2004) and, more recently, from experimental manipulations of nutrient availability (e.g. Worm et al. 2002, Nielsen 2003).

Here, I examine the effects of both productivity and grazing on diversity (measured as species-richness) in algal communities by manipulating both factors simultaneously. I conducted a fully-factorial experiment in which I enriched benthic algal communities with nitrogen (N) and phosphorous (P) and manipulated the densities of important grazers. This approach allows for a comparison of the effects of nutrients and grazing on the abundance and diversity of algal communities and allows for testing of the hypotheses of the dynamic equilibrium model and the grazer-reversal hypothesis.

Methods

Study site

I conducted this experiment in the mid- to high-intertidal zone at Blue Duck, a rocky reef north of Kaikoura (42°25'S, 173°42'E), on the northeast coast of the South Island of New Zealand. The reef is composed of greywacke bedrock and some large, immobile boulders. The rock is extremely hard and relatively smooth. The site is moderately wave exposed, with a wide range of wave action throughout the year.

At Blue Duck, the low-zone is dominated by large kelp-like *Durvillaea* spp. and encrusting coralline algae. The mid- to high-intertidal zone is dominated by the barnacles *Chamaesipho columna* and *Chamaesipho brunnea* interspersed with variably-sized patches of bare rock. The barnacle *Epopella plicata* and the mussel *Xenostrobus pulex* also occur. Algae occurs in this zone, but is generally inconspicuous. Encrusting forms (such as *Hildenbrandia* spp., *Ralfsia verrucosa,* coralline crusts, and thin tars) are the most common algae. The foliose *Porphyra* spp. is often present, with blooms in the winter. *Polysiphonia* spp., *Cladophora* spp., and *Scytothamnus australis* also occur. Limpets are very abundant at this site. *Patelloidea corticata* are the most abundant limpets, although *Cellana ornata* and *Notoacmea* spp. are also common. *Siphonaria* spp., *C. denticulata*, and *C. radians* also occur. Chitons, primarily *Sypharochiton pelliserpentis,* are rare.

Differences in the productivity of temperate reef environments are often the result of nearshore oceanographic processes. Upwelling, the delivery of cold, nutrient-rich water from depth to the sea surface is the combined result of the Coriolis effect and equatorward winds that push surface waters offshore. In New Zealand, as the eastward-flowing Tasman Current contacts the island, it is split into northeastward and southward components. The southward component, the Southland Current, flows around the southern portion of the island, is influenced by the Subantarctic Convergence, and heads northeast along the east coast of the island. Satellite imagery, intertidal air and water temperatures, monthly and daily upwelling indices, and water-sampling data (chlorophyll-*a*, particulates, and nutrients) indicate that although sites on the west coast of New Zealand experience upwelling, sites on the east coast predominantly experience downwelling (Menge et al. 2003 and references therein). Globally, sites on the South Island of New Zealand are relatively nutrient-poor (Vincent et al. 1991, Chang et al. 1995), making them ideal candidates for experimental nutrient enrichment.

Experimental design

I manipulated both grazers and nutrients in a fully factorial experimental design using randomized complete blocks. Both the grazer manipulation and the nutrient manipulation had three levels for a total of nine treatment combinations. With six replicates of each, there were 54 plots in total. In order to control for differences that might occur over 10's of meters along the shore, I set up the experiment using six blocks, with each block containing one replicate of each of the nine treatment combinations in close proximity. Treatments were assigned randomly within blocks. Each plot was 400 cm^2. The experiment began in October 2004 and ended in October 2005.

Earlier experience with limpets common at the site (specifically *C. ornata* and *C. radians*) indicated that transplanting limpets to achieve desired densities was not feasible; transplanted limpets were almost always lost within a few days. Therefore, rather than clearing plots of all algae and invertebrates and then stocking them with the desired densities of limpets, I allowed the established benthic community to remain and removed limpets to achieve desired densities. From a sample of 575 experimental limpets, limpets ranged from 1-25mm, with a mean of 7.7mm and a standard deviation of 4.3mm. I surveyed the plots at the beginning of the experiment, recording the percent cover of all algae and sessile invertebrates.

At the initiation of the experiment, the grazer manipulation consisted of 1) plots with a full complement of limpets (40-60 limpets), 2) plots with half of the limpets originally present (20-30 limpets), and 3) plots with all limpets removed. After three months (in December 2004), there was little algal growth in the plots without limpets. In previous experiments manipulating limpets in similar habitats, algal cover was noticeably higher in exclusions than in control plots after 1-2 months (Menge et al. 1999). Concerned that manipulation of grazers by excluding limpets was not severe enough to allow for algal growth, I began a process of counting and manually removing snails (primarily the small, but abundant *Austrolittorina cincta* and *Risselopsis varia*) at approximately 3-week intervals from the limpet-removal plots. Therefore, for most of the experiment, the grazing treatments were: "high grazing" plots with a full complement of limpets and snails, "intermediate grazing" plots with half of the limpets originally present and all of the snails, and 3) "low grazing" plots without limpets and from which all other grazers were removed periodically.

I maintained limpet densities by surrounding each plot with a barrier of Z-spar marine epoxy (Seattle Marine, Seattle, Washington, USA) painted with copper anti-fouling paint, a deterrent to many molluscan herbivores including most limpets and chitons (but not snails) (Cubit 1984). All plots were surrounded by painted Z-spar; since all comparisons would be made between plots with paint, I did not include any controls for potential artifacts of paint. Approximately every two months I counted all limpets in all plots and removed those that had recruited to or entered the low grazing plots. I also removed limpets as necessary from the intermediate grazing plots to keep limpet numbers between 20 and 30. Occasionally the high grazing plots lost limpets and I attempted to transplant limpets (though not *C. ornata* or *C. radians*) to them to increase their densities to the desired levels.

I manipulated nutrients using resin-coated, controlled-release fertilizer pellets (Worm et al. 2000b, Nielsen 2001). I used Nutricote (Chisso-Asahi Fertilizer,Tokyo Japan) in a13-13-13 NPK formulation (oxide analysis). This formulation is similar to that used by Nielsen (2001). The nitrogen contributors in the fertilizer include Ammonium Nitrate (NH_4NO) and Potassium Nitrate (KNO_3) and the phosphate contributors include Ammonium Phosphate ($NH_4H_2PO_4$), Calcium Hypophosphate ($CaHPO_4$), and Dicalcium Phosphate $Ca_3(PO_4)_2$. Controlled-release fertilizer pellets such as Nutricote work by way of a resin coating that controls the rate of diffusion of nutrients to the environment as water is absorbed through the resin. I filled diffuser bags made from black plastic-coated fabric mesh with approximately 1mm mesh size with three types of filler: 200g fertilizer pellets (high enrichment), 100g fertilizer pellets and 42.5g small plastic beads (low enrichment), or 85g small plastic beads (no enrichment). Diffuser bags for all treatments were 80 cm long and approximately 8 cm wide. The small plastic beads (of approximately the same size as the fertilizer granules) were used in order to control for any changes in the microclimate of the plots introduced by the fertilizer-filled diffuser bags, such as moisture retention. Nutricote pellets were replaced in the high and low enrichment treatments approximately every six weeks. In March 2005 I used a second set of slightly wider bags (approximately 9cm diameter); these slightly larger bags allowed for 300g of fertilizer pellets in the high enrichment treatments, 150g fertilizer pellets and 70g beads in the low enrichment treatments, and 140g beads in the no enrichment treatments. After the introduction of these larger bags, the two sets of diffuser bags were alternately deployed for approximately six-week periods.

The tubular diffuser bags ran along the perimeter of the plots, just inside the barrier of Z-spar and copper anti-fouling paint (Fig. 3.1). They were wrapped around stainless steel screws in the four corners of the plots and fastened to the screws (with large washers above them) by plastic cable ties. Plots were spaced at least 1m apart to decrease the likelihood of added nutrients flowing between them.

The nutrient enrichment accomplished with this type of diffuser in a moderately wave-exposed environment is a pulse-type treatment. It is likely to be effective at some times (e.g. when the tide is just coming in or receding and

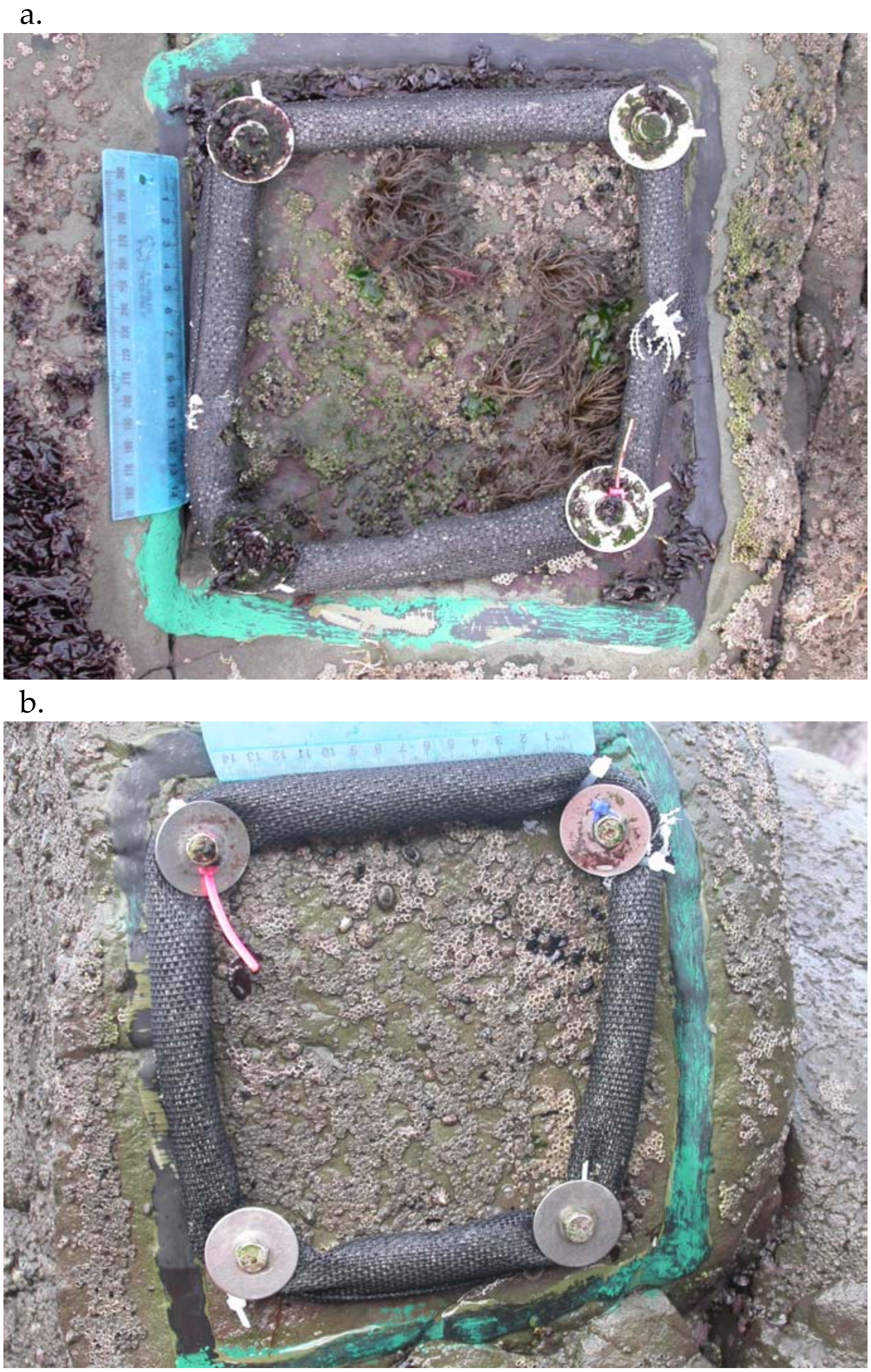

Figure 3.1. Two experimental plots showing the tubular nutrient-diffuser bags affixed to the rock and surrounded by copper anti-fouling paint to control limpet densities. Both plots shown had high enrichment levels; the plot in panel *a* was a low-grazer plot, that in *b* was a high-grazer plot. Both photographs were taken June 23, 2005, after 8 months.

water splashes into and sits on the plots or when the tide is in and the water is calm) and likely to be ineffective at other times (e.g. when plots are completely dry or when the water is very turbulent).

Because nitrogen is often the limiting macronutrient in marine systems (Ryther and Dunstan 1971), I monitored nitrate and nitrite (N+N) levels in the water above the plots as the tide came in or receded on 6 different days. I used a syringe to draw up water from the plots, approximately 5 cm from the diffuser. On calm days, this involved wading to plots that were covered by approximately 30-40 cm of water. On rougher days it involved sampling water that splashed into the plots by incoming waves. On each day that I sampled water, I recorded the number of days since the fertilizer pellets had been replenished. I sampled water (3 50-ml syringe draws from each of 3 plots per nutrient enrichment level) 1, 2, 4, 7, 19, and 29 days after replenishing the fertilizer granules. Water samples were filtered through pre-combusted (450°C for 4 hrs) 25mm Whatman GF/F glass fiber filters. Filtrates were collected in acid-washed polyethylene vials and frozen for later analysis of N+N. Water samples were filtered in the field within 30 minutes of collection and transported on ice back to the lab, where they were frozen. N+N was analyzed by colorimetry on a Shimadzu UV-1201 UV-vis spectrophotometer.

At the end of the experiment, I collected specimens of the most common species, the corticated *Scytothamnus australis* for analysis of carbon to nitrogen ratios (C:N). Plants with more access to N should have decreased C:N compared to those in unenriched conditions. I collected *S. australis* from 4 high enrichment plots, 6 low enrichment plots, and 6 no enrichment plots. Specimens were cleaned of any debris, rinsed with de-ionized water, and frozen. They remained frozen until they were ground to a fine powder using a mechanical grinder. Cellular carbon and nitrogen quotas were obtained on the dried and homogenized tissue using an Exeter Analytical CE-440 CHN analyzer. Carbon and nitrogen were calculated against a standard curve generated from acetanilide standards.

Monitoring and data collection

I monitored the percent cover of algae and sessile invertebrates and counted mobile invertebrates in all plots after 54, 92, 133, 196, 253, and 351 days (December 2004, January 2005, March 2005, May 2005, July 2005, and October 2005).

In order to examine potential differences in limpet growth with different levels of limpet densities and/or nutrient enrichment, in July 2005 I measured and tagged all *C. ornata* between 10 and 20mm in all plots. Using superglue, I affixed a small plastic numbered tag (bee tags, "Opalith plattchen", Graze, KG, Weinstadt-Endersbach, Germany) to each shell and then covered the tag with clear epoxy resin. At the end of the experiment, in October 2005, I again measured all tagged *C. ornata.* At that time I also collected all tagged limpets, weighed them, separated the tissue from the shell, weighed the shell, dried the tissue in a drying oven to constant mass and weighed the dry tissue.

At the end of the experiment, I collected algae for determination of biomass. I collected all non-encrusting algae, by species, from all plots. I placed each sample in a pre-weighed aluminum foil packet and dried it to constant mass before weighing.

Data analysis

I used analyses of variance (ANOVA) to examine the effects of grazing and nutrient enrichment on algal species richness and abundance. I analyzed the mean response of each plot throughout the experiment. In all cases, I tested the effects of the grazing treatment, the nutrient treatment, and the interaction between grazing and nutrients. I also included the blocks as an independent variable to remove any environmental heterogeneity across blocks from the error term. The approach of analyzing the mean response over time is similar to that taken in a repeated-measures analysis but allows for better examination of the assumptions of the model and a more straightforward interpretation of results. In fact, a repeated measures analysis of these data yielded qualitatively similar results. Because this experiment was initiated with established benthic communities, I also used similar ANOVAs to examine the mean differences in algal species richness and abundance from the initial conditions. When necessary, I log-transformed data to meet assumptions of normality. In all analyses of percent-cover data, I used angular transformations (Sokal and Rohlf 1995).

I used similar ANOVAs to examine the effects of grazing and nutrient enrichment on the mean abundance of different morphological groups of algae based on a functional group classification (Steneck and Dethier 1994). The groups I used included: microalgae, filamentous, foliose, corticated foliose, corticated, thin encrusting, thick encrusting, erect coralline, and encrusting algae.

I also used ANOVAs to examine the effects of the treatments on the growth of tagged *C. ornatas*, on *C. ornata* biomass, and on algal biomass. Because the growth of limpets in the same plots may not have been independent, I analyzed the mean growth, proportional growth (growth/initial length), and final weights of all tagged limpets in each plot. For algal biomass, I analyzed the total dry weight of algae in each plot as well as the weight of all morphological groups collected based on the same functional group classification used for the abundance data.

I used the nonparametric Kruskal-Wallis test to examine differences in N+N across the enrichment treatments. These data were not normal and transformations did not yield approximations of normality.

I used a simple one-way ANOVA to test for a relationship between nutrient enrichment and C:N among the *Scytothamnus australis* specimens collected at the end of the experiment.

Results

Efficacy of treatments

The manipulation of limpet densities was successful (ANOVA of mean limpet abundance over time; limpet treatment $F_{2,40}=267.02$, $p<0.0001$, Table 3.1a). Throughout the experiment, there were more limpets in the high grazing treatment than there were in the intermediate grazing treatment. Although a few limpets invaded and/or recruited to the low grazing treatment, their densities were lower than they were in the intermediate grazing treatment (Fig. 3.2). Nutrient enrichment did not affect the numbers of limpets (ANOVA of mean limpet abundance over time; nutrient treatment $F_{2,40}=0.02$, $p=0.98$, Table 3.1a).

Table 3.1. ANOVAs of a) limpet abundance and b) snail abundance (ln(# snails + 1) averaged over the course of the experiment. Bold values represent significant effects at $p<0.05$.

a) $R^2=0.933$

Source of variation	Sum of Squares	d.f.	Mean Square	F-ratio	*p*-value
Limpet treatment	10917.847	2	5458.923	267.022	**<0.001**
Nutrient treatment	0.853	2	0.426	0.021	0.979
Block	320.455	5	64.091	3.135	**0.018**
Limpet x Nutrient	87.909	4	21.977	1.075	0.382
error	817.749	40	20.444		

b) $R^2=0.526$

Source of variation	Sum of Squares	d.f.	Mean Square	F-ratio	*p*-value
Limpet treatment	5.127	2	2.564	6.543	**0.003**
Nutrient treatment	0.239	2	0.120	0.305	0.739
Block	11.087	5	2.217	5.660	**<0.001**
Limpet x Nutrient	0.950	4	0.238	0.606	0.660
error	16.671	40	0.392		

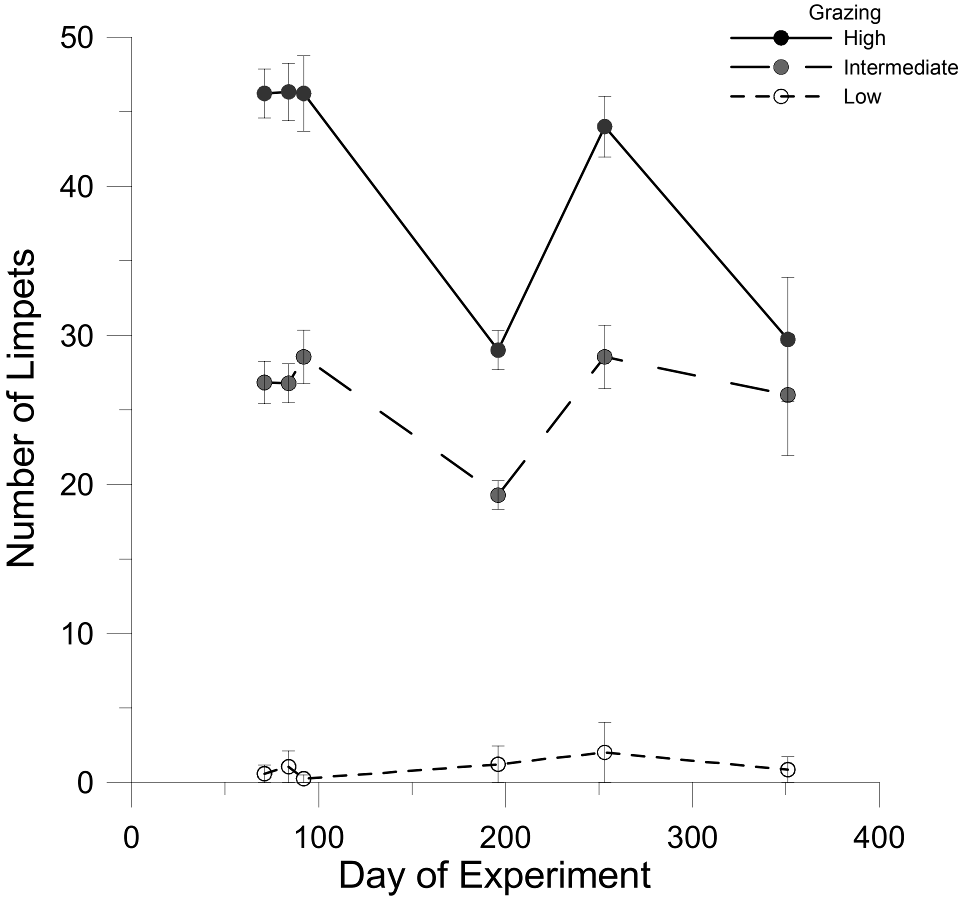

Figure 3.2. Mean (± 1 SE) number of limpets in each of the three grazing treatments over the course of the experiment. Data are lumped across the three nutrient treatments.

The removal of snails from the low grazing treatment was also successful. The initial removal of snails from the low grazing treatment (in December 2004) was by far the largest; subsequent removals resulted in fairly consistent numbers of snails removed (Fig. 3.3). Over time, the manipulation of snails resulted in lower numbers of snails in the low grazing treatments (ANOVA of mean snail abundance (ln(snail abundance +1) over time; limpet treatment $F_{2,40}=6.54$, p=0.003; Fig. 3.4, Table 3.1b).

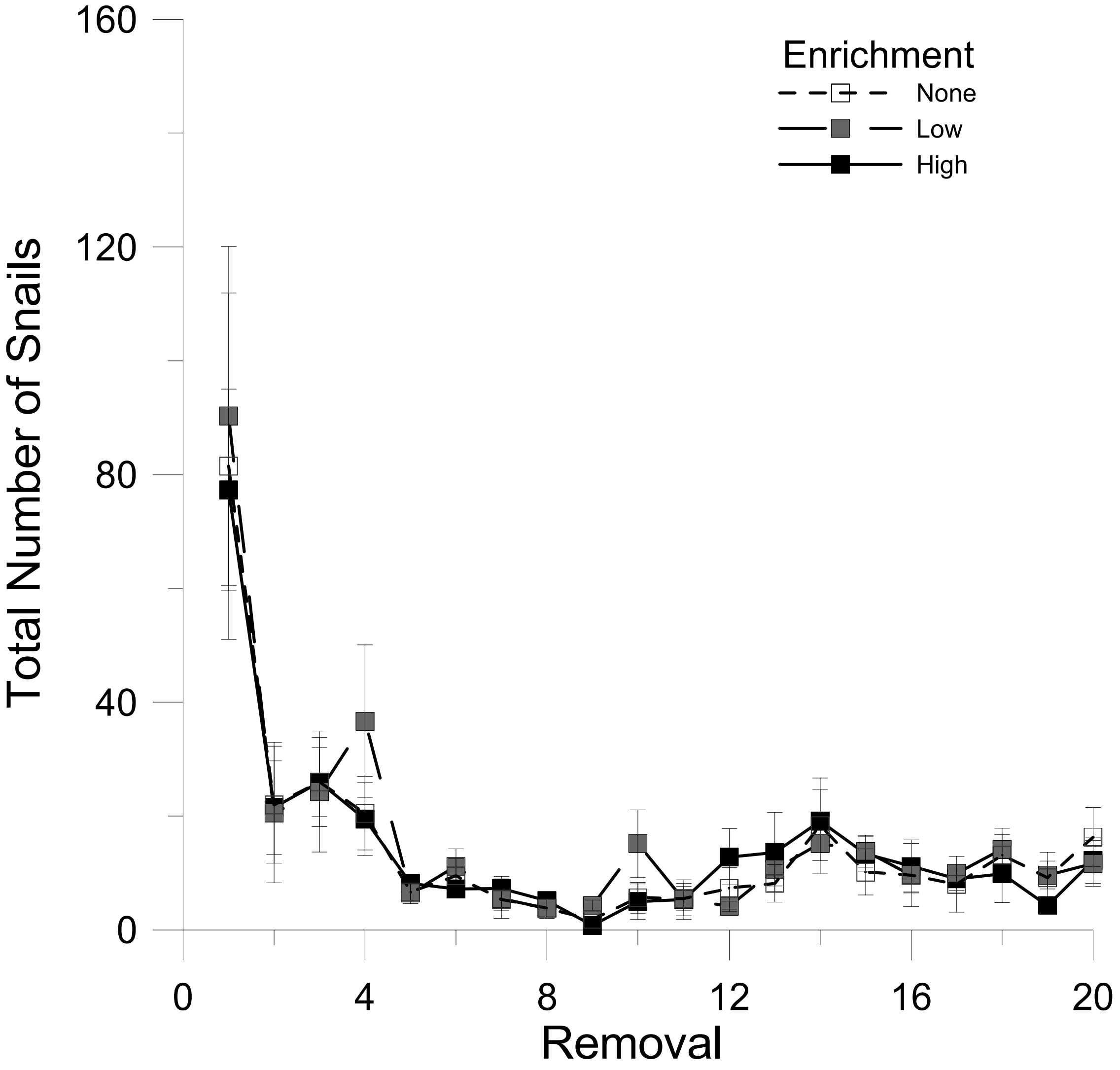

Figure 3.3. Mean (± 1 SE) number of snails removed from the low grazing plots throughout the course of the experiment. Removals were conducted approximately every 3 weeks and were numbered consecutively.

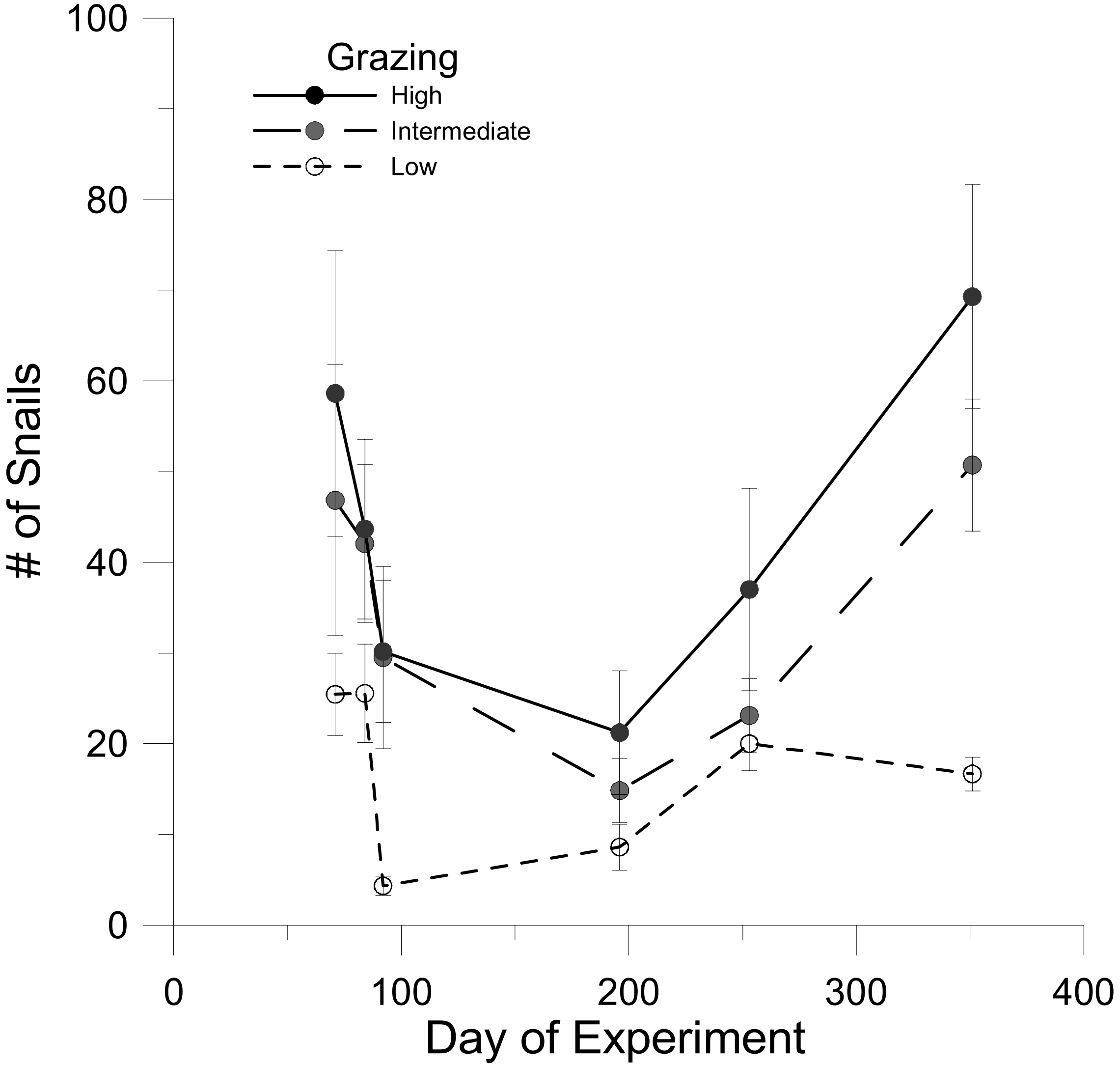

Figure 3.4. Mean (+ 1 SE) numbers of snails (primarily *Risselopsis varia* and *Austrolittorina cincta*) counted in all plots and counted and removed from low-grazing plots throughout the course of the experiment.

Enrichment had a demonstrable effect on the N+N concentrations in water over the plots as the tide came in (Kruskal-Wallis test statistic=13.06, p=0.001; Fig. 3.5). It appears that after at least 19 days, N+N levels were still elevated in the high enrichment treatments (Fig. 3.5). Without enrichment, N+N concentrations averaged 1.13 μM (± 0.11 SE), with a maximum of 2.12 μM. With low enrichment, N+N concentrations averaged 1.54 μM (± 0.37 SE), with a maximum of 6.07 μM. With high enrichment, N+N concentrations averaged 5.08 μM (± 1.49 SE), with a maximum of 27.9 μM. As expected, the nutrient release rates were variable, with greater variability occurring in the high enrichment treatments. Concentrations of N+N in the water above the plots decreased over the length of the deployment of the fertilizer-filled diffusers. The variation around this temporal decline is likely explained by varying wave conditions among the different sampling days (Fig. 3.5).

There was no statistically significant difference in the C:N of the collected *Scytothamnus australis* (ANOVA, nutrient treatment $F_{2,13}$=0.80, p=0.47). However, it did appear that this alga had slightly lower and more variable C:N in enriched treatments than it did in unenriched conditions (high enrichment mean = 24.6 ± 2.1 SE; low enrichment mean = 24.2 ± 1.4 SE; unenriched mean = 26.4 ± 0.6 SE).

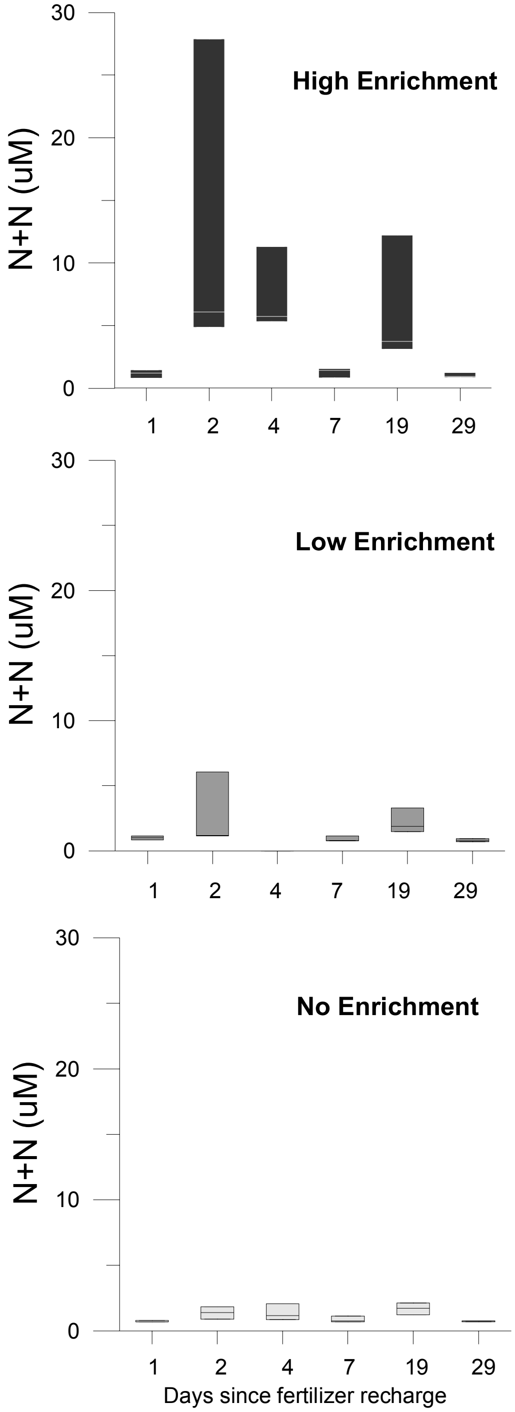

Figure 3.5. Nitrate + nitrite concentrations (μM) in water sampled over the plots after 1,2,4,7,19, and 29 days had passed since recharging the nutrient-diffusing bags with slow-release fertilizer. The center line of each box represents the median, boxes represent the range of the data (n=3-4 points/enrichment treatment/sample day).

Algal assemblages

Algal species richness and abundance were primarily determined by the intensity of grazing, with no community-wide effects of nutrient enrichment. Algal richness and abundance were greater in plots with low grazing than they were in plots with intermediate or high grazing; nutrient enrichment neither affected richness nor abundance of algae (Fig. 3.6; Tables 3.2a&b). There is a suggestion (Fig. 3.7) that in plots with low grazing, high enrichment increased algal species richness but not abundance.

Initial patterns of algal species richness and abundance in the plots did not influence the patterns I saw. The same patterns of algal species richness and abundance described above were apparent when examining the change in algal species richness and abundance from the initial survey. The plots were initially quite similar, with low diversity and very little algal cover (initial mean algal richness = 2 species (± 0.16 SE); mean algal cover=7.2 % (± 1.5 SE)). Although there was little evidence of an effect of nutrient enrichment on the assemblage-wide metrics of algal richness and abundance, there was evidence that in the absence of grazing, the abundance of one morphological group, foliose algae, was greater in the high enrichment plots than it was in the low- or no-enrichment plots (Fig. 3.8, Table 3.3). Foliose algae common in these plots included *Ulva lactuca, Enteromorpha* spp., *Scytosiphon lomentaria* and *Porphyra* spp.

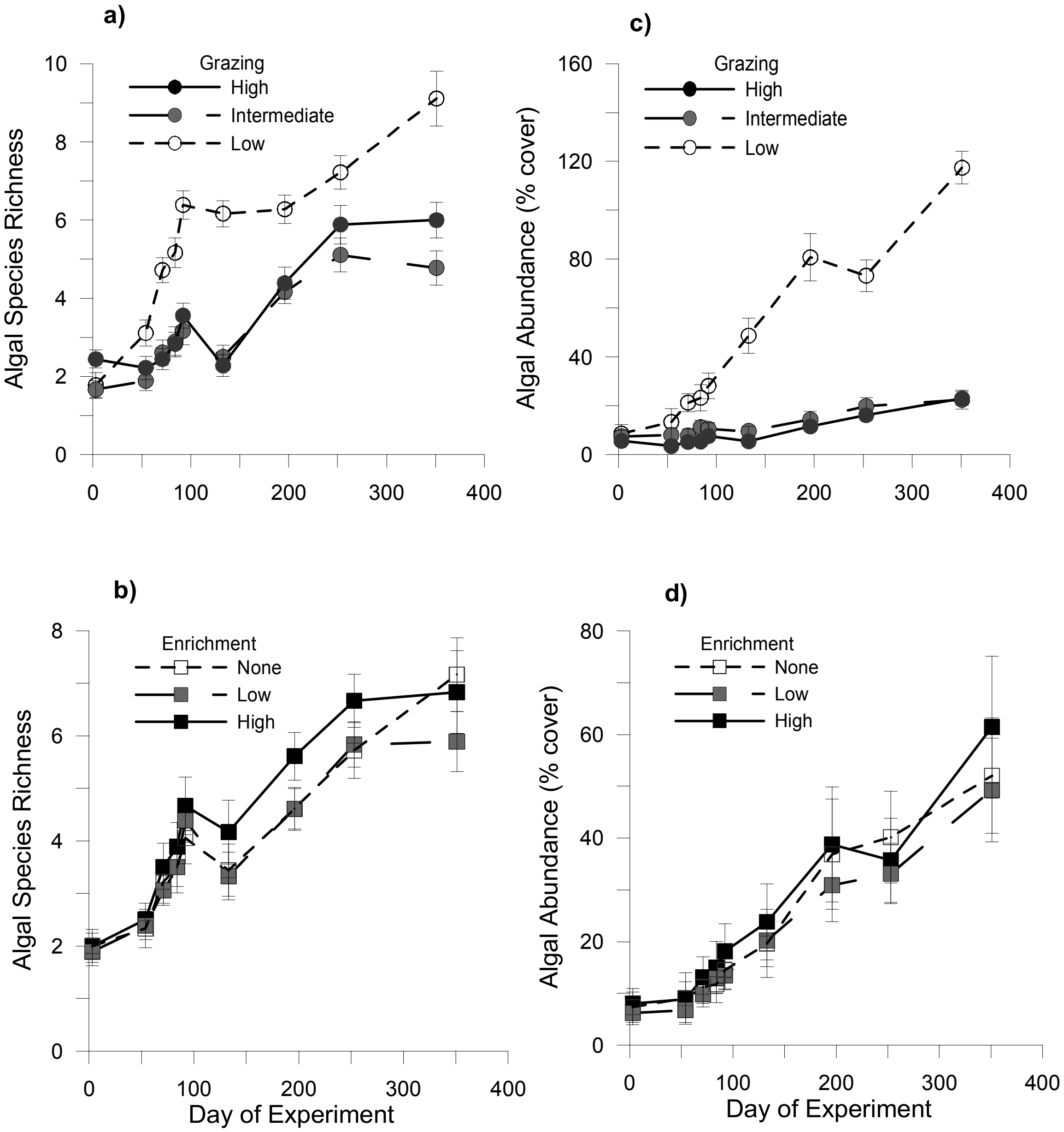

Figure 3.6. Mean (± 1 SE) algal species richness (a&b) or percent cover (c&d) over the course of the experiment. Panels a) and c) allow for examination of differences in grazing treatments while panels b) and d) allow for examination of enrichment.

Table 3.2. ANOVAs of a) algal species richness and b) abundance (percent cover, angular transformed) averaged over the course of the experiment.

a) R^2=0.788

Source of variation	Sum of Squares	d.f.	Mean Square	F-ratio	*p*-value
Limpet treatment	79.939	2	39.970	28.506	**<0.001**
Nutrient treatment	4.412	2	2.206	1.573	0.220
Block	1.868	5	0.374	0.266	0.929
Limpet x Nutrient	5.854	4	1.463	1.044	0.397
error	56.085	40	1.402		

b) R^2=0.780

Source of variation	Sum of Squares	d.f.	Mean Square	F-ratio	*p*-value
Limpet treatment	3.720	2	1.860	61.204	**<0.001**
Nutrient treatment	0.029	2	0.014	0.476	0.625
Block	0.371	5	0.074	2.440	0.051
Limpet x Nutrient	0.187	4	0.047	1.540	0.209
error	1.216	40	0.030		

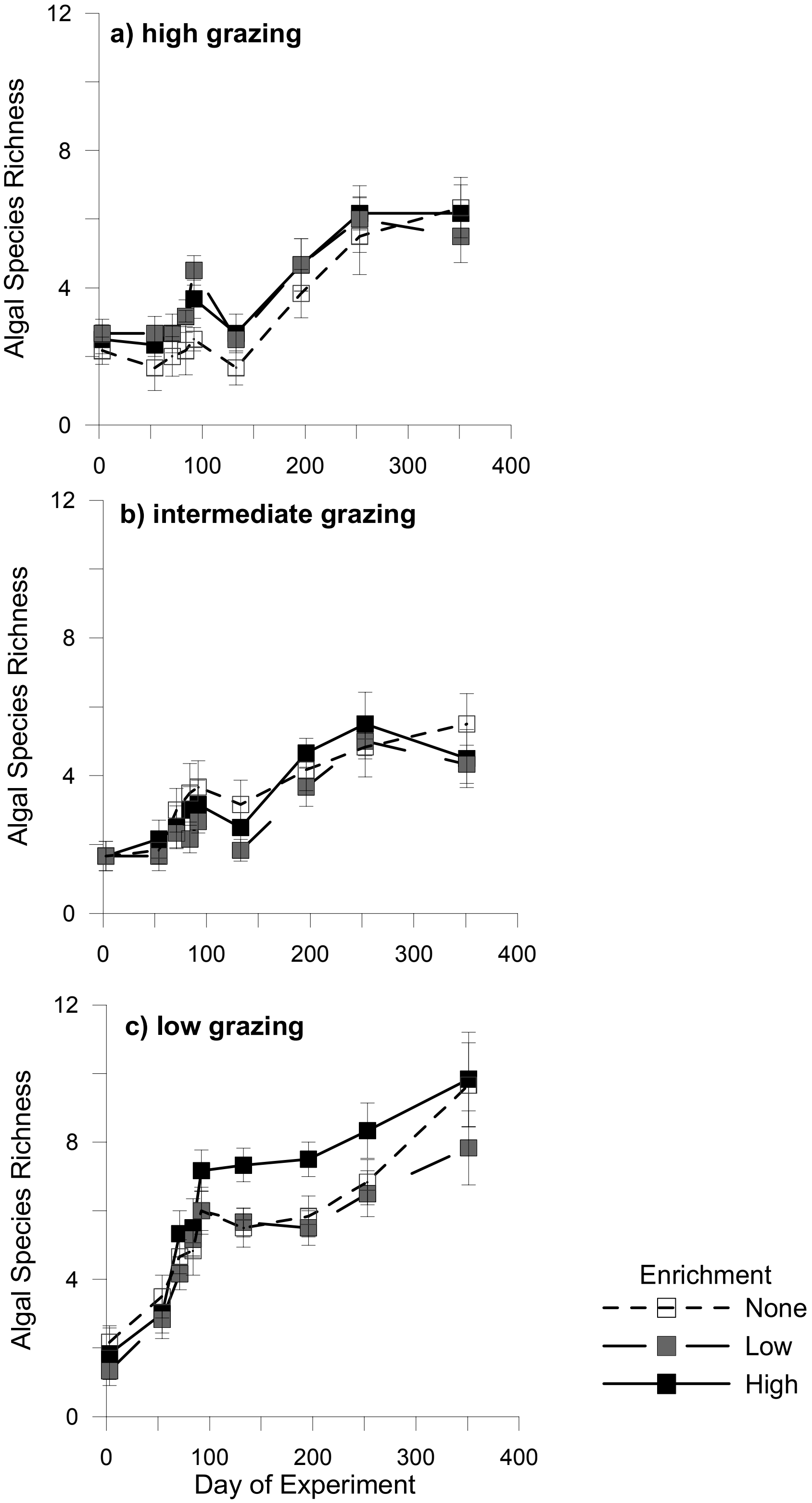

Figure 3.7. Algal species richness (± 1 SE) at a) high, b) intermediate, and c) low grazing throughout the duration of the experiment.

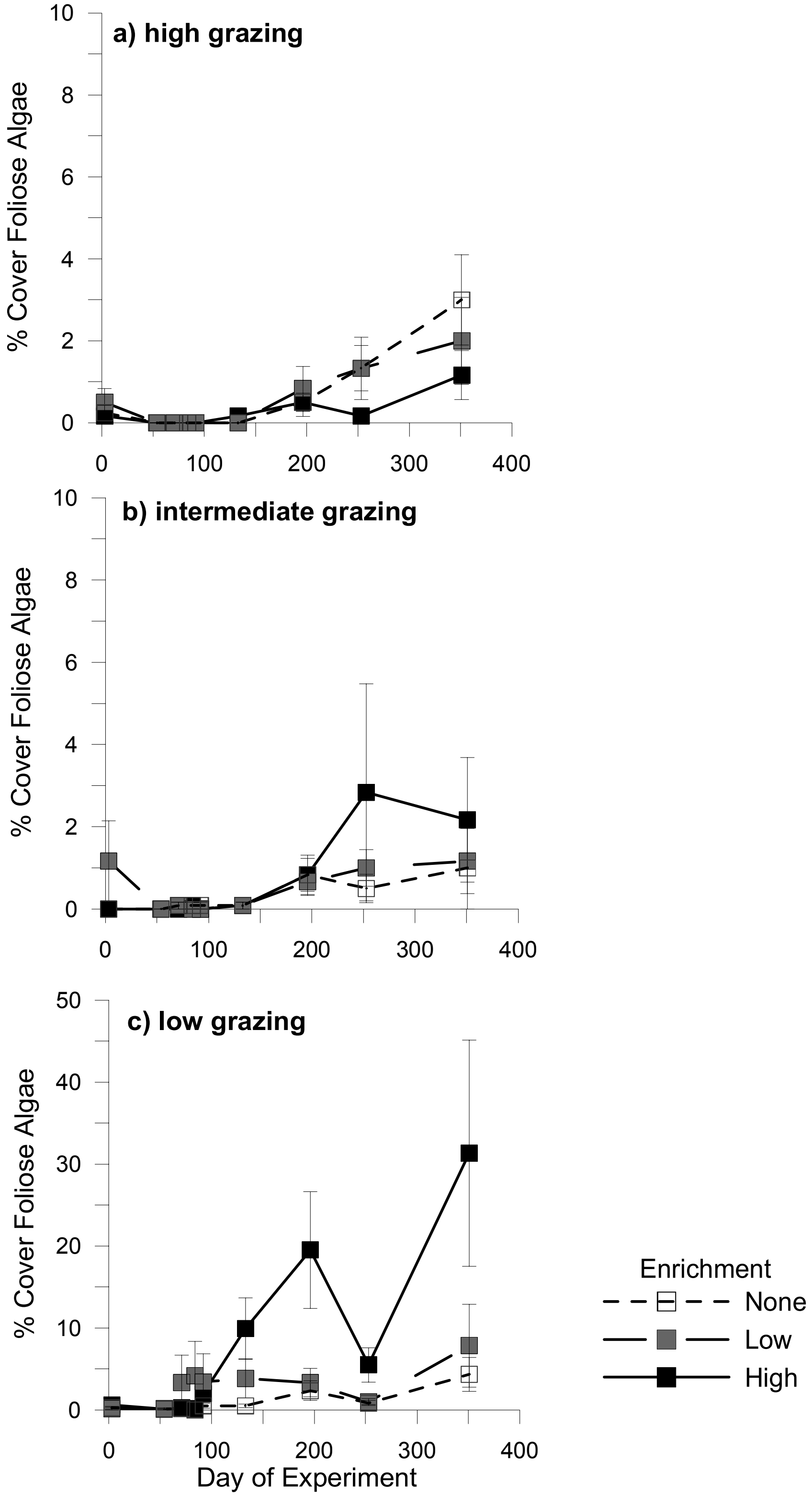

Figure 3.8. Mean (± 1 SE) percent cover of foliose algae across all treatments throughout the course of the experiment.

Table 3.3. ANOVA of foliose algal percent cover (angular transformed) averaged over the course of the experiment.

R^2=0.568

Source of variation	**Sum of Squares**	**d.f.**	**Mean Square**	**F-ratio**	***p*-value**
Limpet treatment	0.223	2	0.111	15.944	**<0.001**
Nutrient treatment	0.035	2	0.017	2.479	0.097
Block	0.016	5	0.003	0.467	0.798
Limpet x Nutrient	0.094	4	0.024	3.371	0.018
error	0.280	40	0.007		

Almost all other morphological groups performed similarly to one another (in terms of their abundance) with respect to the experimental treatments—with increased abundance in the absence of grazing and no effect of enrichment. Microalgae, filamentous algae, corticated algae, thin crusts, and thick crusts were all more abundant in the low-grazing treatments (ANOVAs, $p<0.01$ for grazing effect in all cases); corticated foliose and erect coralline algae were too rare to analyze. Encrusting coralline algae were the only morphological group examined that were unaffected by grazing (ANOVA, $p=0.291$ for grazing effect). No morphological group, except foliose algae, as discussed above, was affected by enrichment or the interaction between grazing and enrichment ($p>0.1$ in all cases).

Algal biomass

At the end of the experiment, the total algal biomass was approximately 20 times greater in the low grazing plots than it was in the intermediate or high grazing plots (low grazing, mean=13.1g ± 1.6 SE; intermediate grazing, mean=0.3g ± 0.1 SE; high grazing, mean=0.7g, ± 0.3 SE). The intermediate and high grazing plots were not different from one another. Nutrient enrichment did not affect the final biomass of algae (Table 3.4).

Table 3.4. ANOVA of algal biomass (log10(biomass + 1)) at the end of the experiment.

$R^2=0.890$

Source of variation	Sum of Squares	d.f.	Mean Square	F-ratio	*p*-value
Limpet treatment	11.307	2	5.654	154.741	**<0.001**
Nutrient treatment	0.041	2	0.021	0.561	0.575
Block	0.264	5	0.053	1.446	0.229
Limpet x Nutrient	0.153	4	0.038	1.047	0.395
error	1.461	40	0.037		

Grazing clearly affected the total biomass of algae present at the end of the experiment, and similarly affected the various morphological groups of algae examined. Foliose and corticated algae both achieved greater biomass in the absence of limpets (Kruskal-Wallis $p<0.005$ for both). Filamentous algae achieved a similar total biomass across all grazing treatments (Kruskal-Wallis $p=0.08$). Because I did not collect encrusting forms, it is not possible to compare their biomass. As with total biomass of algae, nutrient enrichment did not appear to alter the final biomass of any of the morphological groups examined (Kruskal-Wallis $p>0.76$ in all cases).

The constraints of the study allowed direct estimation of biomass only on the final sample date. Since seasonal changes and other factors are likely to cause variation in biomass through time, an estimate at a single time might provide misleading results about the response of algal biomass to the treatments. Further, the documented effect of enrichment on the terminal abundance of foliose algae in the plots with low grazing, suggested that further exploration of the abundance data for this group was warranted. I therefore performed a regression on the abundance of foliose algae and its biomass (where percent cover was angular transformed and biomass was transformed using log base 10) to estimate the biomass of foliose algae during the earlier surveys. I forced the regression through the origin, since 0% cover must lead to 0 g biomass. Percent cover of foliose algae was a strong predictor of the biomass of foliose algae ($R^2 = 0.879$, log10(foliose algal weight) = 0.538*(arcsine(square-root(percent cover foliose algae/100))).

Using this relationship, I estimated the biomass of foliose algae throughout the experiment. This analysis reveals a strong and interactive effect of grazing and enrichment. Mean biomass of foliose algae throughout the experiment was approximately 1.5 times greater in plots with low grazing and high enrichment than it was in all other treatments (Fig. 3.9, Table 3.5).

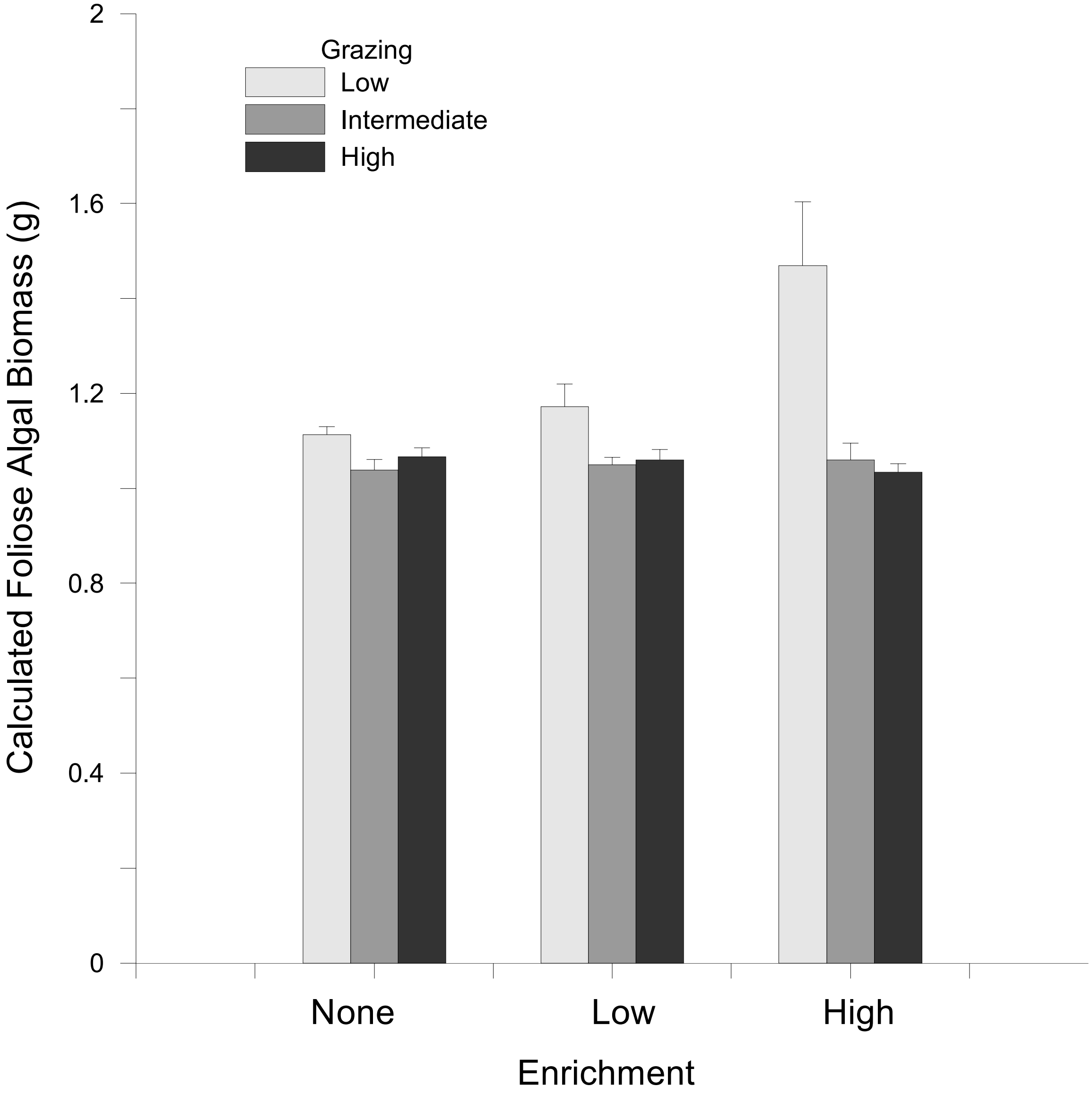

Figure 3.9. Foliose algal biomass (± 1 SE) averaged throughout the experiment. Values for each date were calculated using a regression of the biomass (g of dry weight) on the percent cover at the end of the experiment. See text for more details.

Table 3.5. ANOVA of calculated foliose algal biomass averaged throughout the course of the experiment.

R^2=0.595

Source of variation	Sum of Squares	d.f.	Mean Square	F-ratio	*p*-value
Limpet treatment	0.481	2	0.241	14.480	**<0.001**
Nutrient treatment	0.136	2	0.068	4.085	**0.024**
Block	0.053	5	0.011	0.644	0.668
Limpet x Nutrient	0.307	4	0.077	4.618	**0.004**
error	0.665	40	0.017		

Limpet growth and biomass

I tagged a total of 62 *C. ornata* in 30 plots (9 plots had 1, 11 had 2, 9 had 3, and 1 had 4). There was no relationship between *C. ornata* growth, either in raw shell length or as a proportion of the initial length, and treatment (Tables 3.6a & b). However at the end of the experiment, tagged *C. ornata* were heavier in plots with intermediate grazing intensity than they were in plots with high grazing but *C. ornata* weight did not appear to be influenced by nutrient enrichment (Fig. 3.10, Table 3.6c). The differences in *C. ornata* weights appear to be driven by differences in shell mass rather than by differences in tissue mass (Tables 3.6d & e).

Table 3.6. ANOVAs of *C. ornata* lengths and weights at the end of the experiment.

a) growth (mm)

R^2=0.679

Source of variation	Sum of Squares	d.f.	Mean Square	F-ratio	*p*-value
Limpet treatment	0.072	1	0.072	0.305	0.587
Nutrient treatment	0.316	2	0.158	0.667	0.525
Block	8.701	5	1.740	7.340	**0.001**
Limpet x Nutrient	0.254	2	0.127	0.535	0.594
error	4.504	19	0.237		

b) proportional growth (growth/initial length)

R^2=0.682

Source of variation	Sum of Squares	d.f.	Mean Square	F-ratio	*p*-value
Limpet treatment	0.001	1	0.001	0.586	0.453
Nutrient treatment	0.003	2	0.001	0.828	0.452
Block	0.064	5	0.013	7.142	**0.001**
Limpet x Nutrient	0.002	2	0.001	0.664	0.526
error	0.034	19	0.002		

c) total (visceral mass + shell) weight

R^2=0.508

Source of variation	Sum of Squares	d.f.	Mean Square	F-ratio	*p*-value
Limpet treatment	0.352	1	0.352	7.812	**0.012**
Nutrient treatment	0.071	2	0.036	0.793	0.469
Block	0.211	5	0.042	0.935	0.483
Limpet x Nutrient	0.120	2	0.060	1.330	0.291
error	0.766	17	0.045		

d) Visceral mass weight ((ln(weight + 1)).

R^2=0.510

Source of variation	Sum of Squares	d.f.	Mean Square	F-ratio	*p*-value
Limpet treatment	0.030	1	0.030	0.079	0.781
Nutrient treatment	0.082	2	0.041	0.108	0.898
Block	1.572	5	0.314	0.824	0.548
Limpet x Nutrient	0.746	2	0.373	0.978	0.394
error	7.249	19	0.382		

Table 3.6 (continued)

e) Shell weight

$R^2=0.493$

Source of variation	Sum of Squares	d.f.	Mean Square	F-ratio	*p*-value
Limpet treatment	0.308	1	0.308	7.138	**0.016**
Nutrient treatment	0.071	2	0.035	0.820	0.457
Block	0.179	5	0.036	0.831	0.545
Limpet x Nutrient	0.116	2	0.058	1.347	0.286
error	0.734	17	0.043		

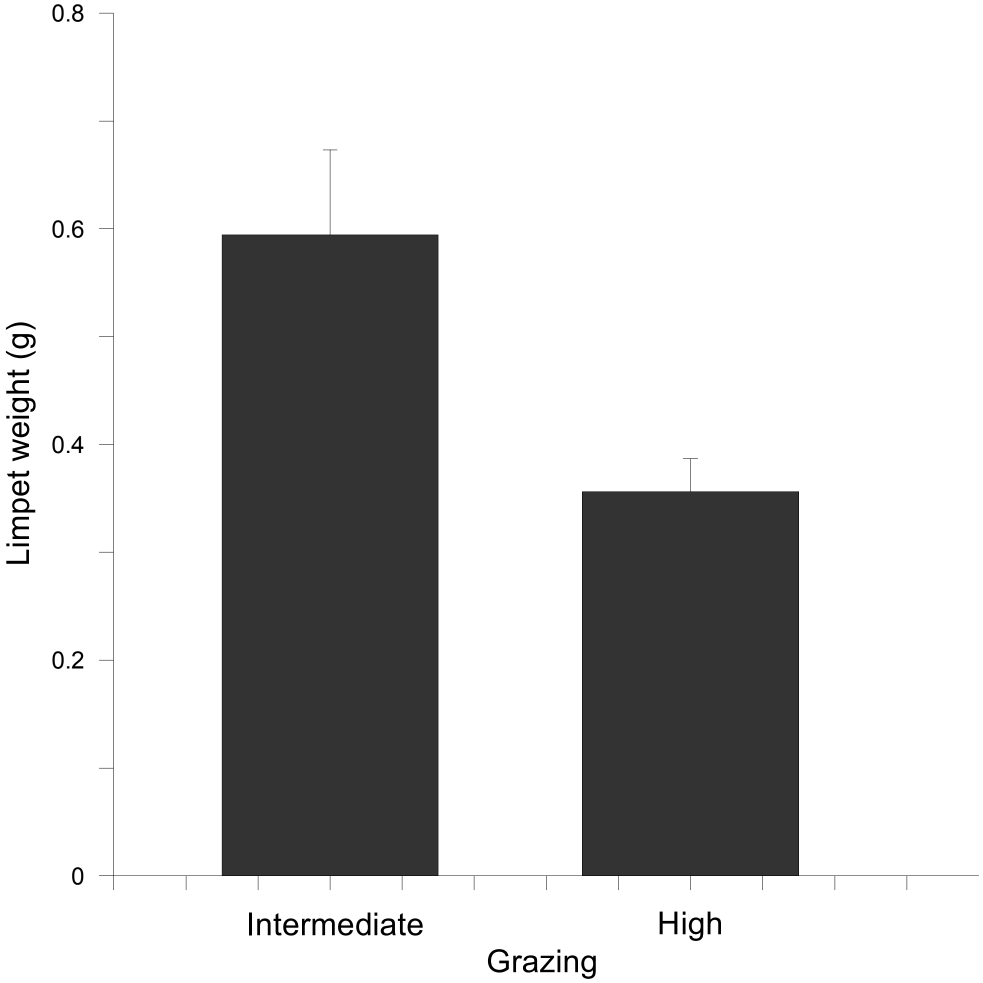

Figure 3.10. Mean total (visceral mass + shell) dry weight (+ 1 SE) of tagged *C. ornata* in the intermediate and high grazing treatments.

Discussion

This experiment had two major, somewhat contrasting results. First, at the level of the overall community, herbivory, but not nutrient enrichment, had consistent and strong effects on the abundance and diversity of algae in this system. Second, at the level of foliose algae, a major but not the dominant component of the community, grazing and nutrients interactively influenced algal abundance and biomass.

The dominant structuring force of herbivory has been well-documented in many temperate reef systems (reviewed by: Lubchenco and Gaines 1981, Hawkins and Hartnoll 1983). Similarly, the positive effect of enrichment on the biomass and abundance of foliose algae is consistent with the high N-affinity of these species (Lobban and Harrison 1997). However, the lack of evidence for a community-wide effect of enrichment in this nutrient-poor environment is surprising and contrasts with evidence for shifts in macroalgal diversity and loss of consumer control with increased N loading (Worm et al. 1999, Worm et al. 2000a, Nielsen 2003). Also, I found no evidence of an interaction between grazing and enrichment at the community-level, a finding that contrasts with the predictions of the dynamic equilibrium model and the grazer-reversal hypothesis (Huston 1979, 1994, Proulx and Mazumder 1998) and contrasts with empirical patterns seen in other systems (Gough and Grace 1998, Wilson and Tilman 2002, Worm et al. 2002, Guerry Chapter 2). However, this is not the first study to find little to no effects of nutrient enrichment on algal communities in a marine benthic environment (Wootton et al. 1996, Miller et al. 1999, Bokn et al. 2003). It appears that in this system, although nutrient enrichment increases the abundance of foliose algae in the absence of grazers, herbivory—more so than nutrient availability—is a primary force structuring algal assemblages.

Effectiveness of enrichment method

Quantification of nitrate and nitrite concentrations in water over the experimental plots showed that the treatments with fertilizer-filled diffusers were enriched compared to treatments with the control, plastic-bead-filled diffusers. Although it was impossible to quantify nutrient concentrations under all possible environmental conditions, I had expected prior to the experiment that the enrichment treatment would be effective at some points in time, and not at others. This type of pulse enrichment has been shown to affect algal communities in other experiments (Miller and Hay 1996, Nielsen 2001). Also, it is possible that additional nutrients were still available under turbulent conditions; Worm et al. (2000b) found that the benthic enrichment method used here worked similarly at a wave protected and a wave exposed site.

Although there were no apparent community-wide effects of nutrient enrichment, the increase in the abundance of foliose algae in high enrichment plots without grazers is another indication that the nutrient-diffuser bags successfully enriched the surrounding environment.

Response to grazer and nutrient manipulations

With grazers present, it appears that in this system, no level of increased productivity can compensate for the overriding importance of grazers. Even with high enrichment, when grazers were allowed access to experimental plots, algal abundance and diversity remained low. When grazer densities were reduced by eliminating half of the limpets originally present in the plots, algal abundance and diversity remained as low as they were in the high grazing conditions. In an experiment conducted with *C. ornata* nearby, Dunmore and

Schiel (2003) found that densities above 16 limpets/.25 m^2 were sufficient to preclude macroalgal growth. My intermediate grazing treatment used a mixed-species assemblage and a wide range of limpet sizes but had densities of 125-188 limpets/.25m^2. Thus, the lack of algal growth, with even half of the limpets removed, is consistent with previous findings.

Because I removed both limpets and snails from the low grazing treatment it is not possible to effectively separate the effects of these two types of grazers. However, the lack of a response of algal growth in the low grazing plots before snails were removed and the immediate response of algae once snails were removed suggests that snails play an important role in this system. The most abundant snails in this system, *Austrolittorina cincta* and *Risselopsis varia*, are generally smaller than limpets (<20mm). Small snails tend to graze primarily on microalgae and filamentous algae, while the larger-bodied limpets can graze more deeply with their larger and functionally different radulae and can handle larger food items (Steneck and Watling 1982). A barnacle-laden substrate can favor the smaller snails by providing refugia—and surfaces for foraging—inside and between barnacle tests (Jernakoff 1985, Boulding and Harper 1998), while hampering the foraging activities of larger limpets (Dungan 1986). Given the design of this experiment, I cannot separate the effects of these two types of grazers, but can conclude that the two of them, in concert, have significant effects on the abundance and diversity of macrophytes.

In the absence of grazing, diverse, abundant blooms of benthic macroalgae developed and persisted, regardless of nutrient enrichment. This is inconsistent with the predictions of the grazer-reversal hypothesis (Proulx and Mazumder 1998), which suggests that grazing decreases species richness when productivity is low or unenriched and increases or has no effect on species richness when productivity is high or enriched. In this experiment, grazing decreased abundance and diversity of algae regardless of productivity.

In conceptual models (Huston 1979, 1994, Proulx and Mazumder 1998), the postulated mechanism for the expected decreases in species richness in the absence of grazing (or other forms of disturbance) is competitive exclusion. Without grazers or abiotic disturbance, dominant species are expected to outcompete subordinates, thereby reducing diversity. In marine benthic communities, in the presence of grazers, it is often the later-successional, corticated species that are competitively superior to early-successional ephemeral algae such as microalgae, filamentous and foliose macroalgae (Lubchenco 1983, Worm et al. 1999). Marine benthic algae compete for nutrients, light, and space. By adding to the pool of available nutrients, I expected to increase algal growth-rates and thereby intensify competition for all three limiting factors.

In this experiment, I did not see evidence for non-encrusting corticated species outcompeting ephemeral algae (i.e. replacing them in the algal assemblage). In fact, although it was not statistically significant, there was a suggestion that the low-grazing treatments with high enrichment had slightly higher diversity (but not abundance) throughout the experiment, the opposite of what was expected. Also, at the end of the experiment, ephemeral algae occurred in 50 of 54 plots, indicating that, even after one year, these ephemeral species remain part of the algal community. Erect forms of corticated algae were present in all low-grazing treatments (18 of 18 plots), suggesting that, regardless of nutrient enrichment, corticated algae and ephemeral algae coexist in this system even when grazing is severely limited for a year.

The increase in abundance of ephemeral foliose algae with high enrichment and without grazers did not appear to come at the expense of other groups of algae. Only 2 plots with erect corticated forms did not also have ephemeral algae. With strong competition, in the absence of grazing we would expect to see erect corticated forms exclude ephemeral foliose algae. Thus, even in the near-absence of grazing, competitive exclusion does not appear to be occurring; without grazing, species richness remains high at all tested levels of productivity.

On the other end of the grazing spectrum, conceptual models (Huston 1979, 1994, Proulx and Mazumder 1998) hold that grazing or other forms of disturbance should decrease species richness because few species are able to tolerate high levels of disturbance (biotic or abiotic). This predicted decrease in diversity with increases in disturbance is expected to be most evident in nutrient-poor environments where the number of species in the community is also likely to be limited by resource availability. Although I did not see the predicted interaction between grazing and productivity, at least at the overall community level, in this resource-poor environment, grazers did have a negative impact on algal abundance and diversity. The most parsimonious explanation for the effect of grazers on richness is through effects on plant biomass and abundance (Proulx and Mazumder 1998, Hall et al. 2000). In this system, with grazers, algae did not achieve high abundance and without much algae there are not many species of algae. It is only without grazers that algae are released from top-down control; higher abundance—and therefore higher diversity—was achieved.

The differences in the abundance of foliose algae without grazers and with high enrichment and the calculated differences in the biomass of foliose algae throughout the experiment make sense in light of algal physiology. Foliose algae such as *Ulva* spp., *Enteromorpha* spp., and *Porphyra* spp. have high surface area to volume ratios and some of the highest half-saturation constants for N among all investigated algal species (Lobban and Harrison 1997), and are thus most likely to do better in enriched conditions. In an experiment in New Zealand, at an ammonium-enriched site, *Enteromorpha intestinalis* displayed high rates of ammonium uptake rates with approximately 10% of the total nitrogen content of the alga taken up during a 90 minute immersion period (Barr and Rees 2003). Foliose algae have previously been shown to flourish in eutrophic or enriched conditions (Lubchenco 1986, Worm et al. 1999). In some cases, increased nitrogen loading in coastal systems resulted not only in increased growth of these species, but also in decreases in algal diversity (e.g. Valiela et al. 1997, Schramm 1999).

The lack of a difference in C:N in *Scytothamnus australis*, the most common corticated alga at this site, suggests that either the growth of *S. australis* was not limited by the background availability of N, or that it was not able to take advantage of increased N (either because the additional N was too ephemeral, the enrichment method was inadequate, the emersion times were too long, or because of competition with species (such as foliose algae) with higher uptake rates). Generally, C:N values above 10 are interpreted as an indication of N-limitation (D'Elia and DeBoer 1978, Harrison and Druehl 1982). The values seen in this experiment (18.9-29.0) are thus indicative of N-limitation. These values are quite similar to the range of values (18.5 to approximately 30) seen for the same species elsewhere in New Zealand (Phillips and Hurd 2003). Phillips and Hurd (2003) also found that *S. australis* rarely had tissue N levels above 2% and interpret that as an indication of N-limitation or lower N requirements. However, Phillips and Hurd (2003) suggest that constant uptake rates of nitrate (NO_3^-) over 90 minutes in *S. australis* (and the other three high-shore species they examined) indicate an adaptation to maximizing nitrate uptake in a variable, but generally N-poor environment. Also, *S. australis* was one of two species in their experiment that displayed rapid ammonium uptake when exposed to experimentally enriched (2-12 times ambient) ammonium levels. They conclude that *S. australis* (among others) is not necessarily N-limited and that it is adapted to maximizing N procurement from a variable supply (Phillips and Hurd 2003, 2004). However, although informative, uptake rates under experimental conditions do not necessarily represent uptake rates under natural conditions (or under enriched conditions *in situ*).

In either the case of a lack of N-limitation or the case of an inability to utilize the added N, the similarity of C:N ratios in *Scytothamnus australis* across enrichment treatments may help explain the apparently contradictory main conclusions of this experiment. The algal community as a whole was not affected by nutrient enrichment because some species were apparently unable to take advantage of the increased N (for methodological or evolutionary reasons), instead, only the foliose algae (those with the fastest uptake-rates) demonstrated improved performance with enrichment in the absence of grazing. This result agrees with the findings of Worm and Sommer (2000), who found that a single short-term pulse of nutrients increased epiphyte growth on *Fucus* but had no direct effect on *Fucus* itself (though there was a suggestion of a negative indirect effect of enrichment on *Fucus* through competition from epiphytes). In general, microalgae and filamentous algae can take up N quickly, but have limited storage capacity, while corticated species have slower uptake rates but higher storage capacities (Fujita 1985). Further exploration of the interaction between algal physiology and the size and duration of nutrient pulses will allow for a better understanding of the interactions between algal species under different eutrophication scenarios.

Community implications

Naturally, the mid- high-zone of the intertidal at this site is relatively devoid of algae. Elucidating the factors that determine the vertical distribution of algae and macroinvertebrates on rocky-shores is essential to achieving a better mechanistic understanding of rocky-intertidal communities. The development and persistence of an abundant and diverse algal community in the absence of grazers suggests that grazers, not abiotic factors or propagule supply, limit the distribution of macroalgae in this system. In a mid-tidal, somewhat sheltered system in Australia, Underwood (1980) found that both grazing and abiotic factors combined to determine the distribution of algae. Similarly, in the low-zone in New Zealand, Hay (1979) found that both limpet grazing and desiccation determined the upper limit of the bull kelp *Durvillaea antarctica*. The findings reported here lend support to the notion that the top-down influence of grazers is of the utmost importance in this system (reviewed by Creese 1988).

Limpet growth and biomass

The response of limpets to the grazer density treatment in this experiment suggests that at lower densities, limpets are partially released from competition for food and consume more food. For example, algal communities were similarly scarce (both in terms of both abundance and diversity) in the high and intermediate grazing treatments. Despite this similarity in overall food abundance, I found increased individual weights of limpets (*C. ornata*) in the intermediate vs. the high-density treatments. These findings corroborate those of previous workers who have demonstrated a negative relationship between limpet density and limpet growth and survival (Thompson et al. 2000, Boaventura et al. 2003, Dunmore and Schiel 2003). Thus, even with reduced densities, limpets and snails presumably can compensate by increasing their intake and thus maintain very low abundance and diversity of algal assemblages.

Conclusion

Top-down control by grazers appears to be the driving organizing mechanism for algal communities in this system. Both the dynamic equilibrium model (Huston 1979, 1994) and the grazer-reversal hypothesis (Proulx and Mazumder 1998) correctly predicted that, at low levels of productivity, disturbance by grazers would decrease the diversity of algal assemblages. However, contrary to the expectations of both models, with experimentally increased nutrient availability, grazing continued to decrease both algal abundance and diversity. Despite the nutrient-poor background conditions in which this experiment was conducted, it appears to be grazing—and not nutrient availability—that structures algal communities in this system. However, in contrast to the conclusions drawn from the analysis of the whole algal community, there was an important interactive effect of grazing and enrichment on foliose algae, an important component of the algal system.

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Chapter Four:

The effect of limpets on benthic algal diversity; a link between nearshore oceanography and rocky intertidal community structure

Abstract

Community dynamics are often influenced by processes operating at large spatial scales. For example, the structure and dynamics of rocky intertidal communities depend not only on local factors, but also on the nearshore oceanographic processes that affect the delivery of nutrients, propagules, and food particles. Conceptual models such as the grazer-reversal hypothesis predict that grazers will decrease the diversity of primary producers in nutrient-poor environments and increase diversity in nutrient-rich environments. In this experiment, I used natural variation in the productivity of nearshore waters around the South Island of New Zealand as a backdrop against which I experimentally manipulated the occurrence of limpets, the dominant consumers. I either excluded or allowed limpets access to replicate plots at five sites, two of high productivity and three of low productivity. Limpets had a negative effect on algal species richness and biomass at the nutrient-poor sites and little effect at the nutrient-rich sites. This finding supports the predictions of the grazer-reversal hypothesis. Also, surprisingly, the results from this experiment suggest that in the high zone of the rocky intertidal, and over a relatively long time period, stronger bottom up effects (higher productivity) don't necessarily yield stronger top-down effects (greater effects of limpets). This finding contrasts with the results of previous studies and highlights the importance research aimed at understanding the ways in

which the top-down forces of consumers and the bottom-up forces of nutrients are linked.

Introduction

Ecologists have only relatively recently expanded their scale of inquiry to address linkages between adjacent ecosystems. These studies are concluding that the supply of resources (Bustamante et al. 1995a, Polis and Hurd 1996) and propagules (Gaines and Roughgarden 1985) from one system can profoundly affect another. Clarifying the role of subsidies from adjacent systems is an important step toward understanding large-scale variation in the abundance of and interactions between species.

Rocky intertidal communities are inherently linked to the larger oceanographic context in which they occur. Although much attention has been focused on the effects of top-down processes such as predation and grazing on structuring rocky intertidal communities (Paine 1966, Dayton 1971, Lubchenco 1978, Fairweather 1985), there is growing evidence from around the world that large-scale oceanographic processes can influence the structure and dynamics of these communities (South Africa: Bustamante et al. 1995b, USA: Menge et al. 1997, New Zealand: Menge et al. 2003, Chile: Nielsen and Navarrete 2004). Clearly, both top-down and bottom-up factors are important in marine (Menge 1992) as well as terrestrial and freshwater communities (Hunter and Price 1992, Power 1992).

Top-down and bottom-up factors can interact in a number of ways. Theoretical and empirical work suggests that higher levels of nutrients support higher consumer biomass and/or more trophic levels (Fretwell 1977, Neill and Peacock 1980, Oksanen et al. 1981, Bohannan and Lenski 2000). Menge (2000) summarized the roles of top-down and bottom-up effects in rocky intertidal habitats and concluded that these two forces are tightly linked, with high levels of nutrients leading to greater effects of consumers. Much of the work in this area has focused on understanding the effects of top-down and bottom-up factors on the abundance, biomass, or survival of benthic primary producers (algae) and/or prey (e.g. barnacles, mussels). However, these factors can also interact to yield different levels of diversity within ecological communities.

Productivity (a bottom-up force) and consumer pressure (a top-down force) have been hypothesized to interact to drive species diversity within functional groups (Huston 1979, 1994). Proulx and Mazumder (1998) specifically examine the effects of grazers on the diversity of primary producers in environments of varying productivity. They proposed the "grazer-reversal hypothesis" which states that grazing decreases the species richness of primary producers in nutrient-poor environments and increases or has no effect on the species richness of nutrient-rich or experimentally enriched environments. The objective of the study presented here was to test the grazer-reversal hypothesis by experimentally manipulating grazers against a backdrop of natural variation in the productivity of nearshore waters of the South Island of New Zealand.

Previous work has documented dramatic differences in rocky shore communities on the east and west coasts of the South Island of New Zealand. These differences have been attributed to differences in nearshore oceanography—specifically between upwelling and downwelling regions (Menge et al. 1999, Menge et al. 2003). Upwelling, the delivery of cold, nutrient-rich water from depth to the sea surface is the combined result of the Coriolis effect and equatorward winds that push surface waters offshore. In New Zealand, as the eastward-flowing Tasman Current contacts the island, it is split into northeastward and southward components. The southward component, the Southland Current, flows around the southern portion of the island, is influenced by the Subantarctic Convergence, and heads northeast along the east coast of the island. Satellite imagery, intertidal air and water temperatures, monthly and daily upwelling indices, and water-sampling data (chlorophyll-*a*, particulates, and nutrients) indicate that sites on the west coast are characterized by intermittent upwelling, while sites on the east coast predominantly experience downwelling (Menge et al. 2003 and references therein). Thus, productivity is generally higher on the west coast than on the east coast.

Menge et al. (2003) documented dramatic differences in the rates of key ecological processes between sites characterized by intermittent upwelling and those with persistent downwelling on the South Island of New Zealand. They hypothesized that decreased upwelling would lead to fewer subsidies (nutrients, food, larvae), which would result in lower abundances of both predators and prey, which would ultimately lead to decreased impacts of predators on prey. As predicted, they found that the rates of key ecological processes such as recruitment and predation were higher at the upwelling-dominated west-coast sites than they were at the downwelling-dominated east-coast sites.

Results linking nearshore oceanographic conditions to the impacts of grazers on algae have been less clear. By excluding limpets in the mid to high zone on the South Island of New Zealand, Menge et al. (1999) demonstrated that, unlike the patterns seen with predation, the longer-term (4 months) effect of limpets was similar at upwelling- and downwelling-dominated sites.

However, their results indicated that in the short-term (<4 months), grazing was more intense at the upwelling-dominated sites.

Here, I use the "comparative-experimental approach" (e.g. Dayton 1971, McPeek 1998, Menge et al. 2002) to examine the effects of limpets in the high zone at five sites on the South Island of New Zealand. I used two sites on the upwelling-dominated, more productive west coast and three sites on the downwelling-dominated, less-productive east coast. I used the natural variation in productivity as a backdrop against which to conduct identical experiments in which I either excluded or allowed access to plots by limpets. This work builds upon the previous work of Menge et al. (1999, 2003) by examining the effects of limpets higher on the shore, by examining longer-term effects (>1.5 years), and by examining how the composition of algal communities changes in relation to grazing. More broadly, it examines the role of the top-down force of grazing at sites with differing levels of subsidies from the nearshore ocean and tests the predictions of the grazer-reversal hypothesis. If this hypothesis is supported, limpets should have positive or no effects on algal diversity at the more productive west-coast sites, but negative effects at the less productive east-coast sites.

Methods

Study sites and experimental design

I conducted this experiment on vertical walls in the barnacle-dominated high zone at five sites on the south island of New Zealand. Three sites were on the east coast and two were on the west coast. The east coast sites include Raramai (RR) and Bird Rock (BR) (200m apart, 43.5° S, 175.5° E) just south of the Kaikoura peninsula, and Box Thumb (BT) (45.5° S, 173.5° E) on the north side of the Banks peninsula (approximately 150 km south of RR and BR). The two west coast sites, Woodpecker Bay (WB) (41.5° S, 171.5° E), and Jackson Head (JH) (44.5° S, 167.5° E) are approximately 350 km apart. These sites were chosen because all of them, except for BR, have been the focus of previous work elucidating the link between nearshore oceanographic conditions and community dynamics (Menge et al. 1999, Menge et al. 2003). All sites are moderately wave-exposed rocky reefs. The aspect of the vertical surfaces used for the experiment at each site are varied; the wall at BR faces north, RR faces south, BT faces east, WB faces northwest, and JH faces southeast

Depending on the availability of appropriate habitat, I placed five (RR, BT, JH) or six (BR, WB) sets of experimental plots at each of the field sites. Each experimental set consisted of a limpet exclusion plot, a paint control-plot and a marked plot. All plots were 175 cm^2. I created the exclusion plots using a barrier of Z-spar marine epoxy (Seattle Marine, Seattle, Washington, USA) painted with copper-based anti-fouling paint to exclude limpets (and other molluscan herbivores such as chitons) (Cubit 1984). I allowed limpets access to the two control plots in each set of plots. Paint controls were bounded by an incomplete barrier of Z-spar and anti-fouling paint to control for possible artifacts of paint while allowing grazers to enter. The marked plots were bounded by only the inert Z-spar—this allowed all grazers free access to the plots.

At the start of the experiment, in October 2003, I removed all algae and invertebrates from the plots. The limpets *Cellana radians* and *Siphonaria australis* were present on all walls. *C. ornata*, *C. denticulata*, and *Notoacmea spp*. were also present in varying densities on most walls. Chitons, primarily *Sypharochiton pelliserpentis,* and the limpet *Patelloidea corticata* were rare.

Monitoring

I surveyed the experiment at each site after 5, 12, 14, 15, 17, and 20 months (from March 2005 to June 2005). Surveys involved visually estimating the percent cover of all algae and sessile invertebrates and counting all mobile invertebrates. Algae were identified to the lowest taxonomic resolution possible without destructive sampling. Limpets were identified (if >5mm) and counted in all plots, and then removed from any exclusion plots they had entered. After the final survey at 20 months (June 2005), I scraped all of the sessile organisms from each plot in order to calculate dry weights of each taxonomic unit. This involved some sub-sampling of encrusting forms that were difficult to remove from the rock-surface. Dry weight was determined by placing each sample into a pre-weighed aluminum foil packet, drying it to constant mass at 60°C, re-weighing the packet, and subtracting the weight of the foil.

At the beginning of the experiment (October 2004), I surveyed the ambient densities of limpets at each site by randomly placing 12 to 30 175 cm^2 quadrats along a transect line parallel to the water's edge and through the middle of the area in which the experiment was set up and counting all limpets in each quadrat. In March 2005 (17 months), I conducted a similar survey of 10 plots at each site. At this time, I also measured the size-structure of the limpet population at each site by recording the size of the first approximately 100 limpets encountered in a 10-cm wide belt-transect through the area around the experiment.

In order to account for differences in limpet densities, sizes, composition, and behavior at the various sites, I used wax disks embedded in the rock to record grazing marks, using a modified version of a technique developed by

Thompson et al. (1997). I filled the bottom half of screw-end caps (14 mm diameter) with melted dental wax. To deploy them in the field (40/site), I drilled shallow depressions, filled them partially with Z-spar, and pressed the wax-filled caps into the soft Z-spar, taking care to ensure that the surface of the disk was flush with the Z-spar and rock surface. The radulae of limpets and chitons leave distinctive marks on the wax as the animals move across the substrate in search of food. Grazing pressure can thus be estimated by scoring the percent of each disk that has been scraped by mollusks or by recording the proportion of disks that were scraped. In order to yield information about the relative strength of grazing intensity, the disks must be deployed for long enough to have some, but not all disks scraped. Although Thompson et al. (1997) found that the optimal period of deployment on the Isle of Man was 1-14 days, I found that even after 30 days, many disks remained untouched. I therefore removed the disks after 76-90 days; at this time, many disks were still untouched and all disks were <100% scraped. To score grazing activity, I examined the disks in the laboratory using a dissecting microscope.

Recruitment of sessile invertebrates

The recruitment of sessile invertebrates was quantified to provide part of the ecological context for the algal communities at each site. Barnacle recruitment was quantified by using a dissecting scope to count the cyprids and metamorphs that settled on polyvinylchloride plates coated with a rubbery, textured surface (Farrell et al. 1991, Menge et al. 2003). Mussel recruitment was measured by deploying plastic mesh collectors (“Tuffys”) that mimic the structure of benthic algae to which mussels recruit; in the laboratory, recruits were detached from the collectors and counted using a dissecting scope (Menge et al. 1994, Menge et al. 1999). Recruitment collectors (five plates, five tuffys) were replaced at each visit to the sites (month 5, 12, 14, 15, 17, and 20); results are expressed as the number of recruits/day. I sampled recruitment at all sites except for BR, which is close enough to RR (200m) that I assume levels of recruitment to be similar.

Algal/sessile invertebrate interactions

Benthic algal communities often live within the context of sessile invertebrates. To examine the potential importance of interactions of the algal assemblages in this experiment with sessile invertebrates, I looked first at the maximum percent cover of sessile invertebrates in any plot at each site at the last sampling period. At sites where the percent cover of sessile invertebrates reached >10% in any plot, I examined the correlation between the percent cover of algae and invertebrates at that site. As is appropriate for percent cover data, I used angular transformations before calculating correlation coefficients and probabilities (Sokal and Rohlf 1995).

Productivity levels

To ensure that the previously documented differences in productivity persisted during the course of this experiment, background nutrient concentrations were monitored periodically through my research group's monitoring program. We sampled water (3 replicates/site/sample day) from a depth of approximately 1m using a sampling pole affixed to a 250-ml acid-washed brown high-density polyethylene bottle while standing onshore. Nutrient samples (50 ml) were filtered through 25-mm combusted Whatman glass-fiber filters with a pore size of 0.7 μm. The filtrate was transported to the laboratory on ice and frozen for later quantification of nitrate, nitrite, phosphate, and silicate on a Lachat autoanalyzer (Atlas et al. 1971). As with the sampling of recruitment rates of sessile invertebrates, BR and RR are treated as one site.

Data analysis

To examine whether or not there were differences between the paint-control and the marked plots, I used separate non-parametric Kruskal-Wallis tests to compare the algal species richness and percent cover of each set of plots at each site during each month. I used non-parametric statistics in this instance because of non-normal data that could not be transformed to approximate normality. This method yielded 30 different tests (six time periods x five sites). Although adjusting p-values accordingly, such as through the use of a Bonferroni correction, would lower the p-value required to identify significant differences between these two types of controls, I did not adjust p-values. This approach is conservative because it inflates the possibility that differences will be identified where none in fact exists. For species richness (on four different occasions) and percent cover (on two occasions) the two types of control plots at one site (JH) appeared to differ (Kruskal-Wallis, $p<0.05$). Therefore, in order to be conservative and consistent across all sites, I used the paint-control plots rather than the marked plots for all comparisons with exclosures.

I used nested analysis of variance (ANOVA) to examine the effects of upwelling regime (upwelling or downwelling) on algal abundance (% cover and biomass) and diversity (species richness). For all nested ANOVAs I used the mean square value for the subgroups (sites) to test for significance of groups (upwelling regime) (Sokal and Rohlf 1995). For analyses of algal assemblages, I used the proportional difference between the exclosure and the paint-control ((exclosure - paint-control)/exclosure) for each replicate as a metric of the effect of limpets. For these analyses, I used only the data at the end of the experiment. Because a number of replicates did not have any sessile invertebrates in the exclosures, it was not meaningful to use the same metric for limpet effect as I did for the algal assemblages. Limpet effects on invertebrates are therefore not expressed as a proportion of the value in the exclosure but purely as the difference between the exclosure and the paint-control plots.

I also used nested ANOVA to determine whether or not the concentrations of nutrients in the water at each site varied as expected according to the described upwelling regimes. I used ANOVA to examine differences between abundance, size-structure, and grazing-intensity of limpets at each site and to examine differences between sites with respect to the recruitment of sessile invertebrates.

In order to examine the types of algae that colonized and persisted in the experiment, I used morphological groups based on the algal functional groups of Steneck and Dethier (1994). Groups present in this experiment included microalgae (benthic diatoms), and filamentous (e.g. *Cladophora spp.*), foliose (e.g. *Porphyra* spp., *Ulva* spp., *Enteromorpha* spp.), corticated (e.g. *Scytothamnus australis, Caulacanthus ustulatus, Stictosiphonia gracilis, Gelidium caulacantheum*), and encrusting forms (e.g. *Ralfsia verrucosa, Hildenbrandia* spp., coralline crusts).

Results

Productivity

Although we sampled water at various times throughout the experiment, data are currently only available from the sampling events between the beginning of the experiment (October 2003) and January 2004 (4 sampling dates/site; F. Chan, unpublished data). Although these data only represent the initial time-period of this experiment, they are consistent with previous results for these sites and are likely to be representative of the relative values.

On average, west coast sites had nearly 4 times more N (nitrate + nitrite) than east coast sites, but sites within coasts were not different from one another (nested ANOVA; upwelling regime $F_{1,2}$=55.9, p=0.017, site within upwelling regime $F_{2,12}$=0.12, p=0.89, Fig. 4.1). Also, west coast sites had an average of 1.5 times more P (phosphate) than east coast sites. Again, sites within coasts were not different from one another (nested ANOVA; upwelling regime $F_{1,2}$=36.7, p=0.026, site within upwelling regime $F_{2,12}$=0.07, p=0.93, Fig. 4.1). Neither coasts nor sites differed with respect to Si (silicate) concentrations: (nested ANOVA; upwelling regime $F_{1,2}$=1.11, p=0.4, site within upwelling regime $F_{2,12}$=0.63, p=0.55, Fig. 4.1).

Algal assemblages

In general, limpets had a greater effect on algal communities at the downwelling-dominated east coast sites than they did at the intermittent-upwelling characterized west coast sites. At the east coast sites, on all sampling dates, benthic algae were more abundant and more speciose in the plots from which limpets were excluded (Fig.'s 4.2 & 4.3, east coast panels). At the west coast sites, although there were differences in algal abundance between plots with and without limpets on the first 1-2 sampling dates (month 5 and/or month 12), these differences did not persist throughout the experiment. At JH, plots without limpets were more speciose than plots with limpets until the 15th month, but at WB there were never differences in species richness between

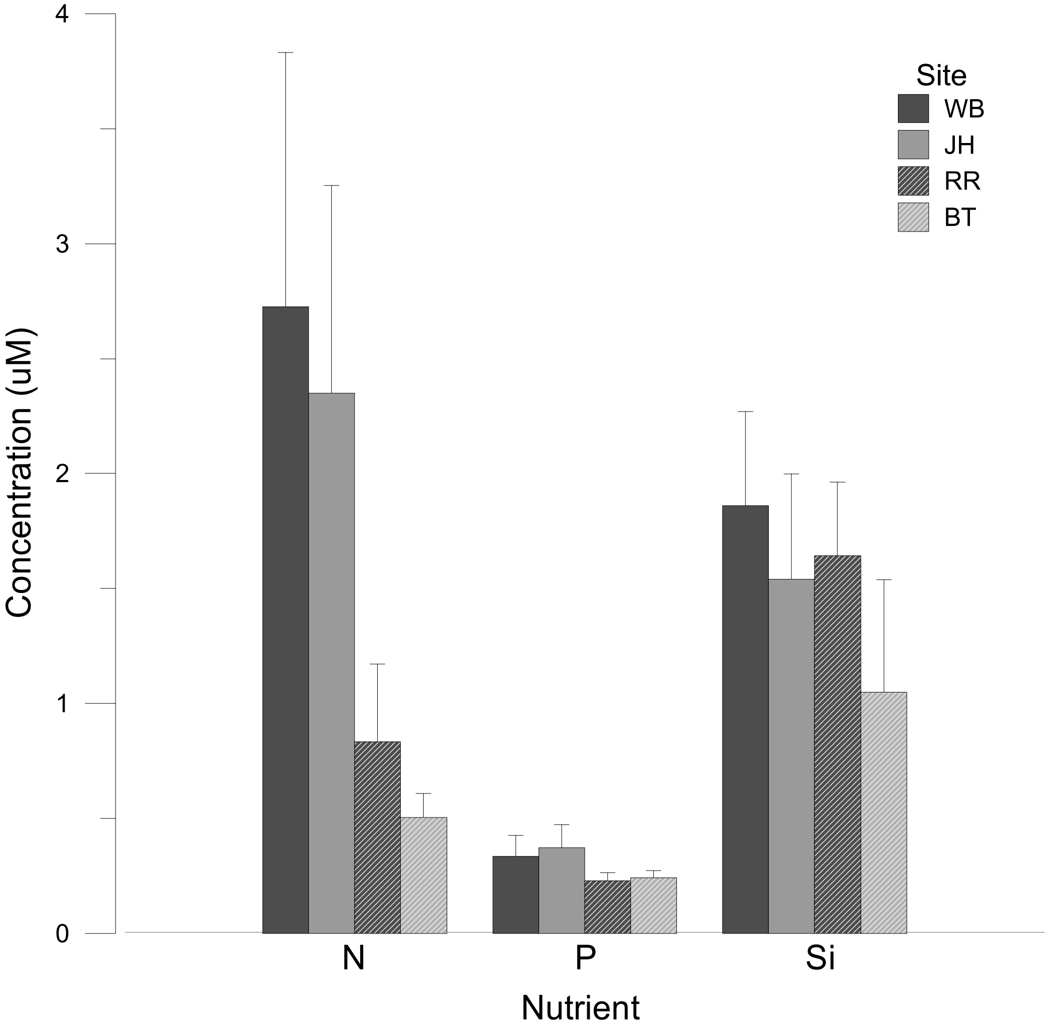

Figure 4.1. Average nutrient concentrations at 4 sites during October 2003-January 2004 (4 sampling events/site). Values are mean + 1 SE. Upwelling-dominated west coast sites (WB and JH) are shown in solid colors; downwelling-dominated east coast sites (RR and BT) are hatched.

plots with and without limpets (Fig.'s 4.2 & 4.3, west coast panels). At the visit to BT after 5 months limpets had heavily recruited to all plots such that the densities of limpets in the exclosures and controls were similar. I did not conduct a survey at that point in time, but instead removed limpets from the exclosures. Therefore, data from the month 5 survey is missing for BT (Fig.'s

4.2 & 4.3, BT panel). Thereafter, limpet densities in the exclosures at BT were more consistent with the experimental design.

At the end of the experiment, limpet effects (the proportional difference between treatments with and without limpets (exclosure – paint-control)/exclosure, as described above) on species richness and biomass varied by upwelling regime but not by site within upwelling regime, whereas limpet effects on the percent cover of algae did differ by site but not by upwelling regime. The effect of limpets on species richness was, on average, six times larger at east coast sites than it was at west coast sites (Fig. 4.4a; nested ANOVA; upwelling regime $F_{1,3}$=149.3, p=0.001, site within upwelling regime $F_{3,22}$=0.22, p=0.88). Similarly, limpets affected the biomass of algae more on the east coast than they did on the west coast (Fig. 4.4b, nested ANOVA; upwelling regime $F_{1,3}$=27.7, p=0.007, site within upwelling regime $F_{3,22}$=1.89, p=0.61). Differences in the effects of limpets on algal percent cover were not explained by upwelling regime, but rather by site, with limpets at JH having even a positive effect on algal cover (Fig. 4.4c, nested ANOVA; upwelling regime $F_{1,3}$=3.48, p=0.16, site within upwelling regime $F_{3,22}$=18.452, p<0.0001).

Differences in limpet effects by coast appeared to be driven not only by differences in the cover of algae in the exclosures, but also by the relative abundance of algae in the plots to which limpets were allowed access. The large differences between the exclosures and the paint controls on the east coast were driven by the high percent cover of algae in the plots without limpets and the negligible cover of algae in the paint controls (which were similar to the marked plots) (Fig. 4.5). On the west coast, the exclosures generally have lower coverage of algae than the east coast sites but, unlike the east coast sites, there was significant algal coverage in the plots that were accessible to limpets. Most

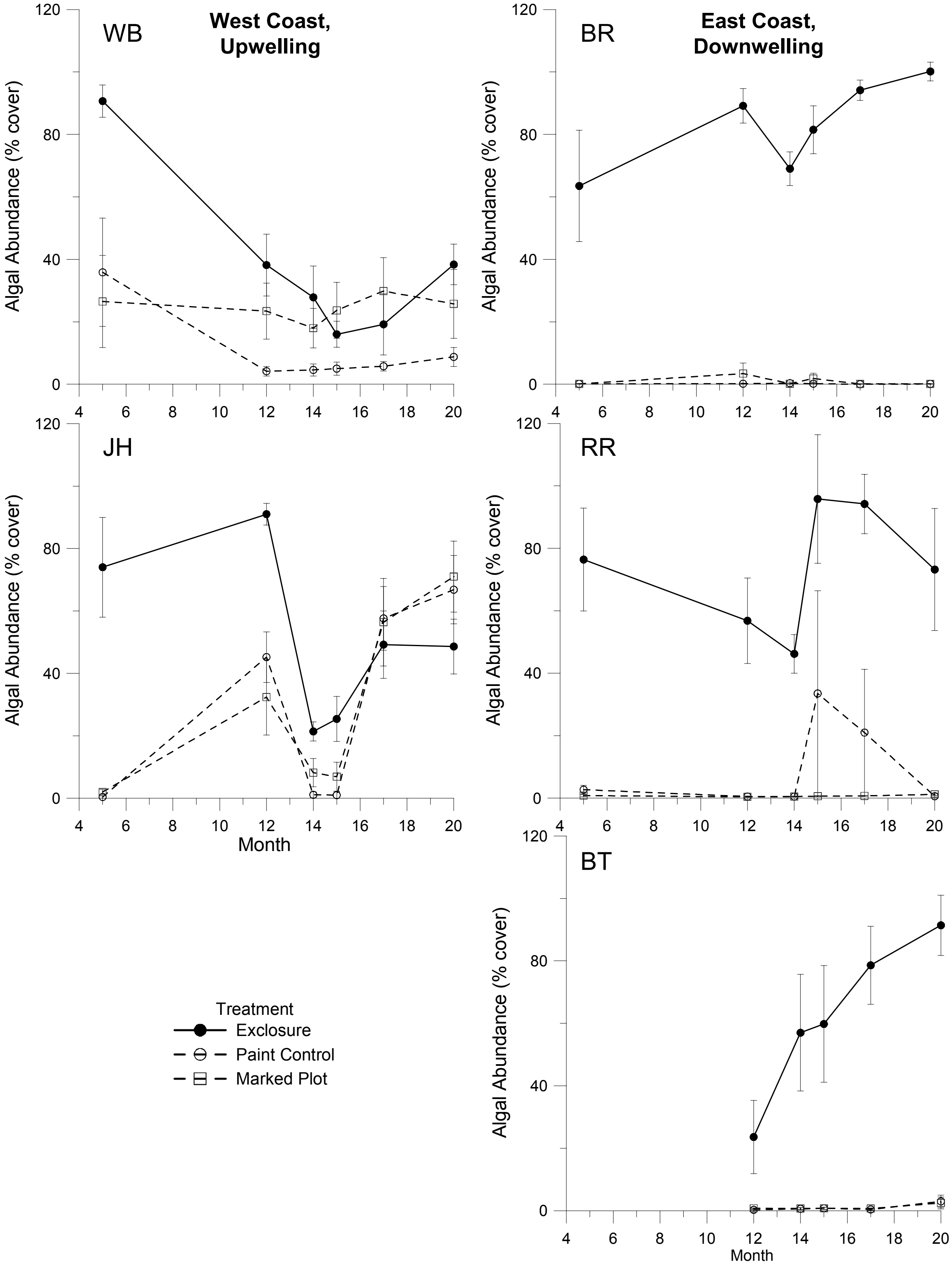

Figure 4.2. Algal percent cover in the three treatments at each site over the 20-month duration of the experiment. Values represent means (± 1 SE).

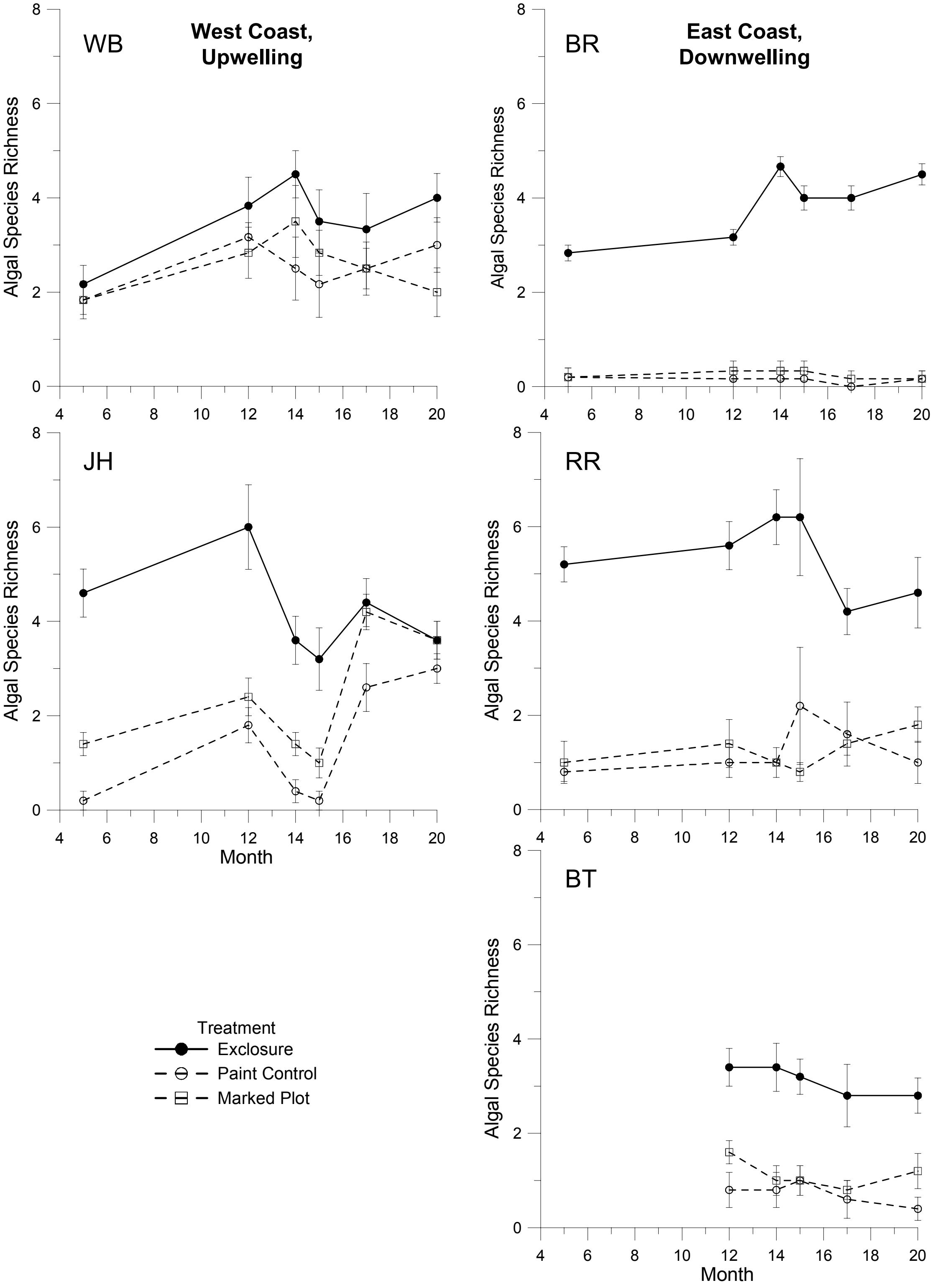

Figure 4.3. Algal species richness in the 3 treatments at each site over the 20-month duration of the experiment. Values represent means (± 1 SE).

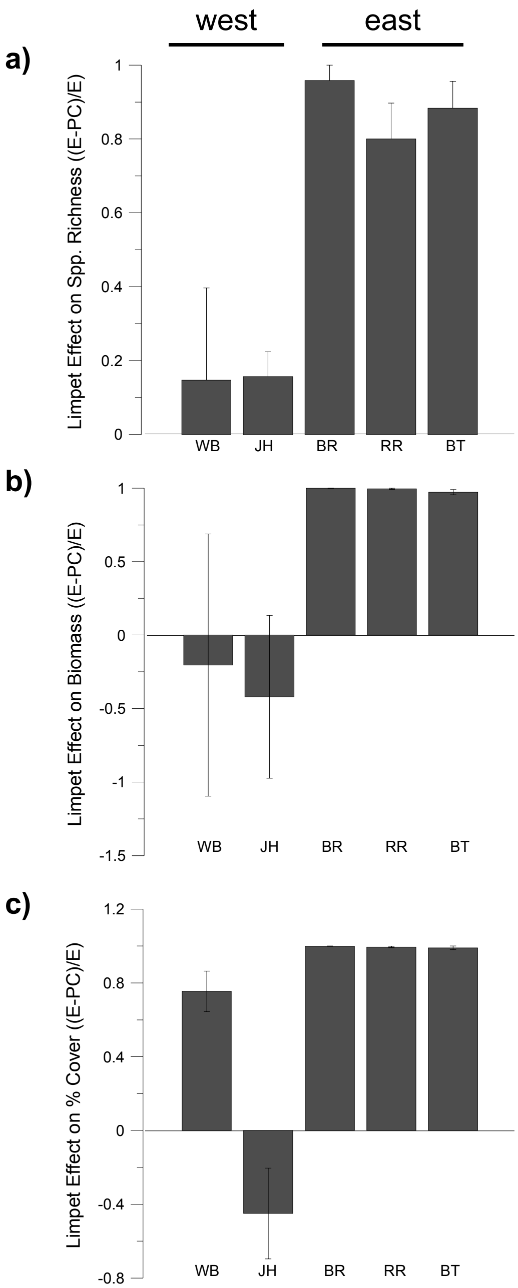

Figure 4.4. Limpet effects on a) algal species richness, b) biomass, and c) abundance. Values represent means ± 1 SE. See text for details.

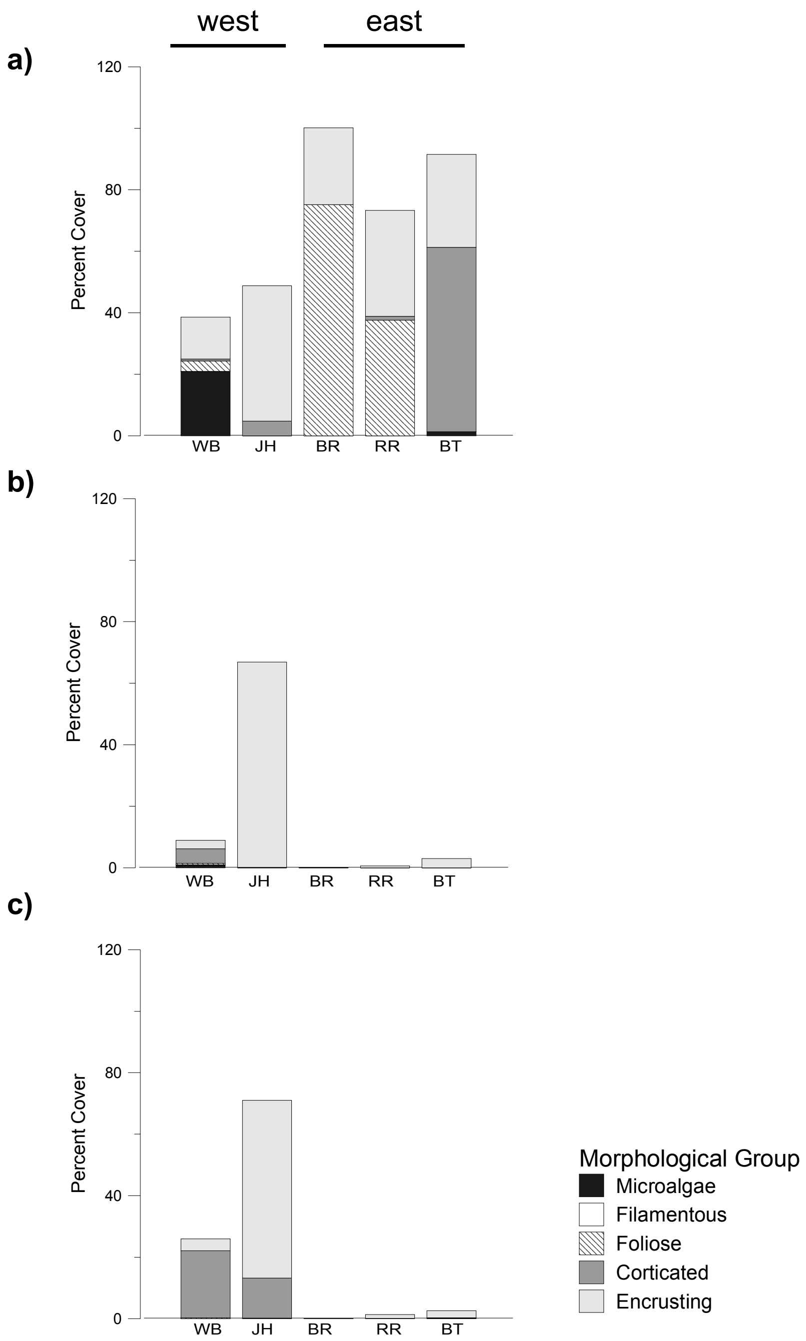

Figure 4.5. Mean abundance of morphological groups of algae at the end of the experiment (month 20) in a) exclosures, b) paint-control plots, and c) marked plots.

of the algae that persisted in the plots grazed by limpets was encrusting algae, though microalgae and corticated algae also occurred (Fig. 4.5).

Sessile invertebrates

Limpet effects on the percent cover of sessile invertebrates differed by site but not by upwelling regime (Fig. 4.6, nested ANOVA; upwelling regime $F_{1,3}$=0.012, p=0.92, site within upwelling regime $F_{3,22}$=3.995, p=0.02, Fig. 4.6). In fact, two groups of sites are apparent that appear independent of upwelling

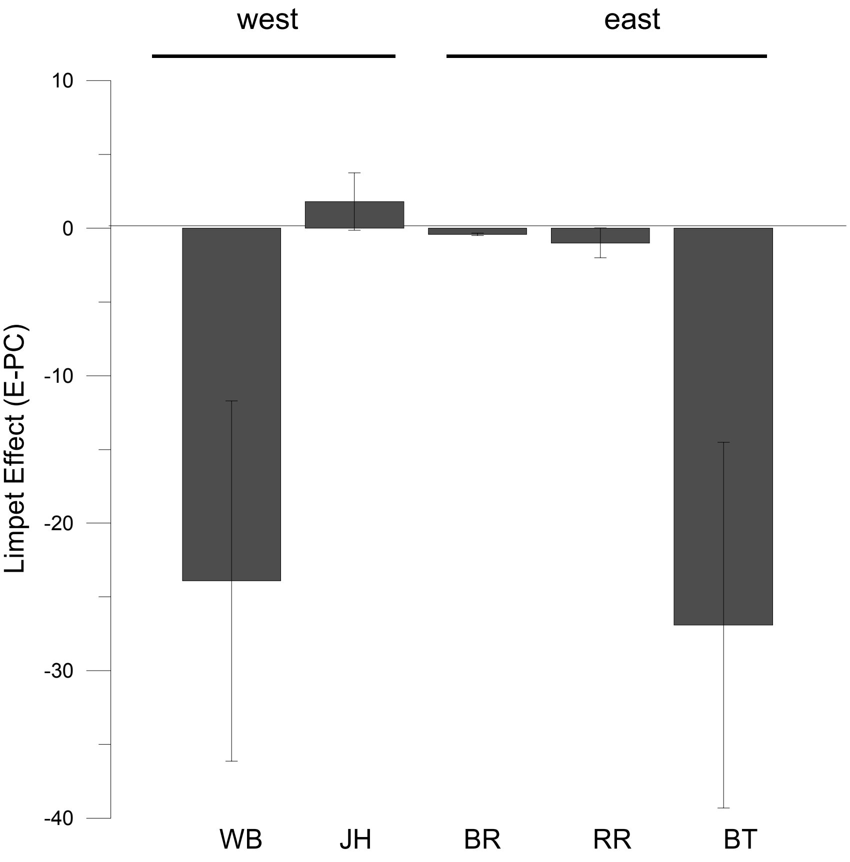

Figure 4.6. Limpet effect on sessile invertebrate abundance (% cover). Values are means ± 1 SE.

regime. WB (west coast) and BT (east coast) had more abundant sessile invertebrates (primarily mussels at WB and barnacles at BT) in all treatments than did any other sites. Sessile invertebrates were more abundant in the paint-controls than in the exclosures, with mean differences between the two of –23.9% (± 7.4) and –26.9% (± 8.3), at WB and BT respectively. At the other three sites, cover of sessile invertebrates was very low in general and therefore there was little difference in their cover between treatments. Differences ranged from –1.0% to +1.8%.

Limpet effects on the biomass of sessile invertebrates follows the same pattern as described above for percent cover (nested ANOVA; upwelling regime $F_{1,3}$=0.57, p=0.51, site within upwelling regime $F_{3,22}$=3.37, p=0.04). Again, there is no apparent effect of upwelling regime on the biomass of sessile invertebrates. Instead, biomass differs by site with WB and BT having considerable biomass of sessile invertebrates and the other three sites having negligible sessile invertebrates.

Barnacle recruitment differed by site but not by upwelling regime (nested ANOVA; upwelling regime $F_{1,2}$=0.69, p=0.49, site within upwelling regime $F_{2,22}$=13.61, p<0.001). Recruitment was greatest at WB and lowest at JH and RR (Fig. 4.7). Although not significantly different from JH and RR, recruitment appears to be slightly higher at BT than at JH or RR.

Mussel recruitment at WB was approximately two orders of magnitude greater than it was at JH, RR, or BT (Fig. 4.8). Among the 3 sites with similarly low recruitment in comparison to WB, there were differences in mussel recruitment by site (ANOVA, site $F_{2,20}$=11.17, p=0.001), with RR experiencing lower recruitment than JH and BT (Fig. 4.8).

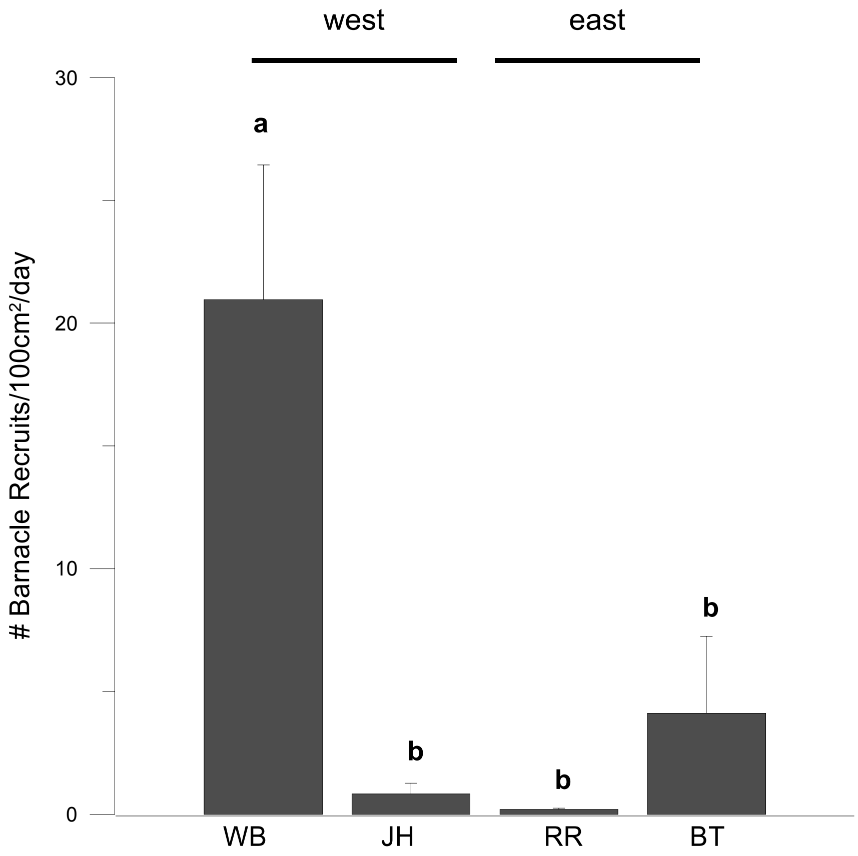

Figure 4.7. Barnacle recruitment over the course of the experiment. Values are means + 1 SE across all sampling periods. Letters represent significant differences or lack thereof (Tukey's HSD).

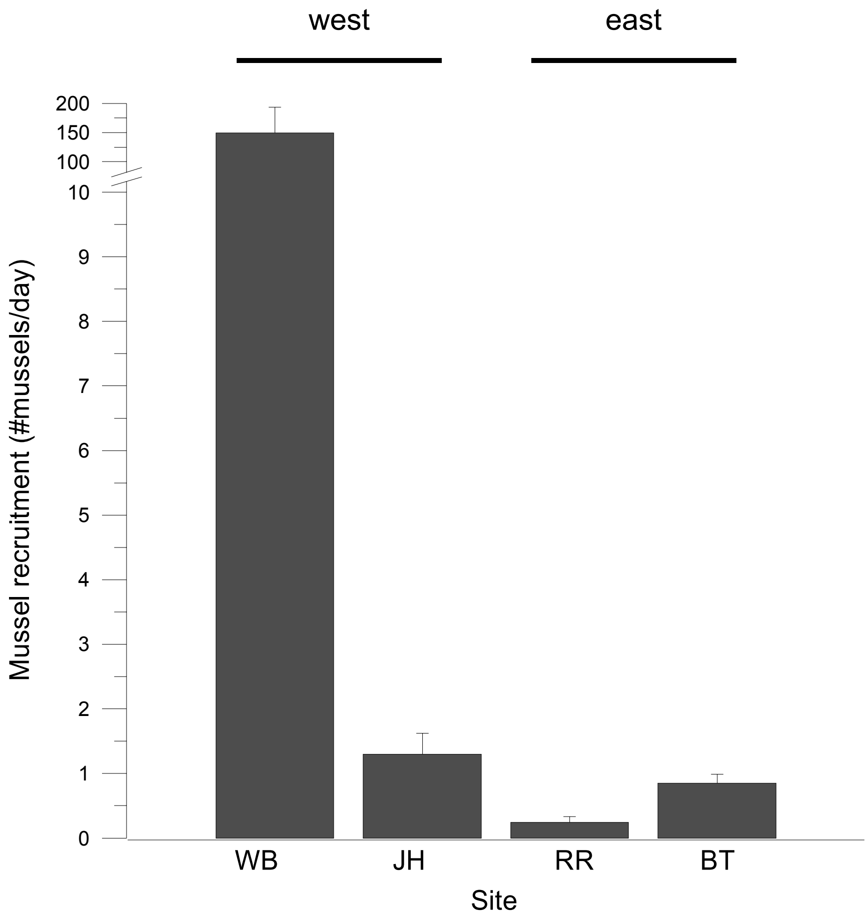

Figure 4.8. Mussel recruitment over the duration of the experiment. Values are means across all sampling periods. Note the broken axis in order to show WB on the same figure as the other three sites.

Algal/sessile invertebrate interactions

At 20 months, sessile invertebrates were an important part of the community at WB and BT (maxima of 95% and 80.5% respectively), but they were of little numerical importance at BR, RR, and JH (maxima of 1%, 5%, and 10% respectively). At both WB and BT, the abundance of sessile invertebrates was inversely correlated to the abundance of algae (WB: R= -0.71, p=0.001; BT: R= -0.68, p=0.005).

Limpet densities, size-structure, grazing intensity, and species composition

At the initiation of the experiment, limpets were approximately twice as dense at BT as they were at JH and RR and five times as dense as they were at WB and BR (Fig. 4.9a). Toward the end of the experiment, in March 2005, the same general pattern of relative abundance was apparent, except that densities at WB had increased such that they were no longer equivalent to those of BR, the least dense site, but rather to JH and RR, the sites of intermediate densities (Fig. 4.9b).

Counts of limpets in the paint control and Z-spar control plots from each monitoring date have the potential to provide an integrated measure of limpet densities at each site. This integrated measure again indicates that limpet densities were greatest at BT and least at BR; densities at the remaining sites were intermediate—limpets at JH and WB were less dense than at BT but more dense than at RR (Fig. 4.9c).

Although BR had the fewest limpets, on average, it had the largest limpets. BT, the site with the highest densities of limpets, had relatively small limpets. The sites with intermediate densities had intermediate sizes, except for WB, which had the smallest limpets (Fig. 4.9d).

Grazing intensity, as measured by radulae-scrapings on the wax disks, was greater at the downwelling-dominated east coast sites than it was at the upwelling-dominated west coast sites (nested ANOVA; upwelling regime $F_{1,3}$=19.56, p=0.02, site within upwelling regime $F_{3,20}$=1.34, p=0.27, Fig. 4.9e & f).

The compositions of the limpet assemblages at each site were varied, with no apparent differences with respect to coast (east vs. west) (Fig. 4.10). BR was the least diverse, with only 3 limpet species occurring in the plots throughout the course of the experiment. RR was the most diverse, with 6 limpet species and one chiton species occurring. *Cellana denticulata* was by far the most common limpet at BR. *Siphonaria australis* was the most common limpet at JH and RR, though *C. radians, C. ornata, Notoacmea spp*., and *C. denticulata* were also fairly common. *Notoacmea spp.* were the most common at WB and BT. WB also had relatively large numbers of *C. radians*; at BT *C. radians, C. ornata*, and *S. australis* were also common.

Figure 4.9. Limpet densities, sizes, and grazing intensity at the 5 sites. a) Densities at the beginning of the experiment, values are means + 1 SE. Letters above bars indicate significant differences or lack thereof (post-hoc tests using Tukey's HSD). (ANOVA, site effect $F_{4,106}$=28.94, p<0.001). b) Densities in March 2005. Figure follows panel a. (ANOVA, site effect $F_{4,47}$=16.89, p<0.001). c) Densities in the paint-control and marked plots throughout the experiment. Values are means ± 1 SE. An ANOVA on the long-term averages of each site throughout the experiment with post-hoc Tukey's HSD showed that BT>JH=WB>RR>BR (ANOVA, site effect $F_{4,49}$=99.9, p<0.001). d) Mean ± 1 SE limpet sizes at each site. (ANOVA, site effect $F_{4,543}$=59.8, p<0.001). e) Grazing intensity as measured by wax disks. The height of bars represents the mean number of disks grazed/replicate at each site (n=8 disks/replicate, 40/site). f) Box plot of grazing intensity measured by the percent of the surface of all disks grazed at each site. The center line of each box represents the median, boxes represent 50% of the data, and the whiskers show the range of the data that fall within 1.5x the inner-quartile range. Circles represent outliers.

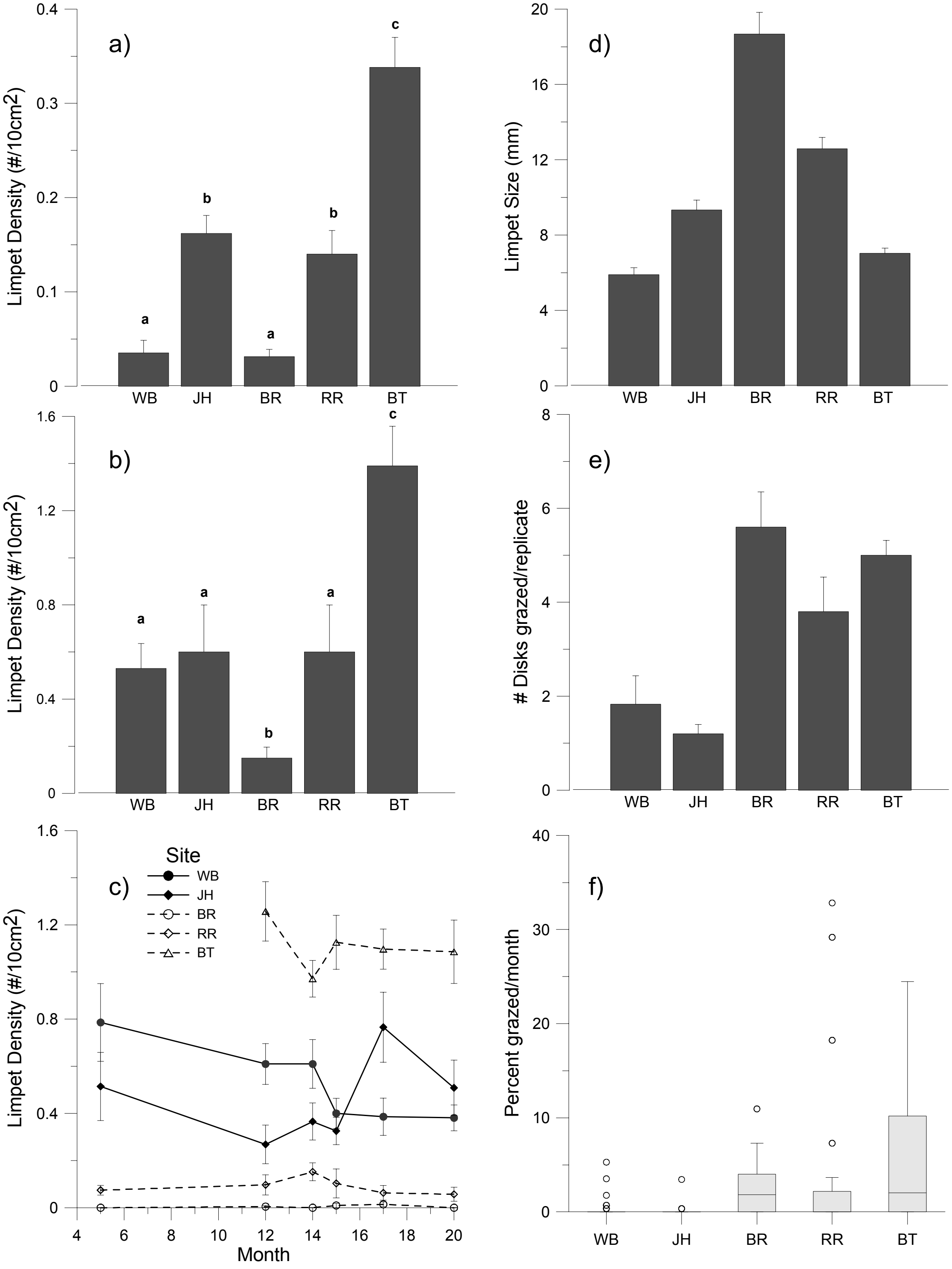
a)
Limpet Density (#/10cm2)
0
0.1
0.2
0.3
0.4
a
b
a
b
c
WB
JH
BR
RR
BT
d)
Limpet Size (mm)
0
4
8
12
16
20
WB
JH
BR
RR
BT
b)
Limpet Density (#/10cm2)
0
0.4
0.8
1.2
1.6
a
a
b
a
c
WB
JH
BR
RR
BT
e)
Disks grazed/replicate
0
2
4
6
8
WB
JH
BR
RR
BT
c)
Site
WB
JH
BR
RR
BT
Limpet Density (#/10cm2)
0
0.4
0.8
1.2
1.6
4
6
8
10
12
14
16
18
20
Month
f)
Percent grazed/month
0
10
20
30
40
WB
JH
BR
RR
BT

Figure 4.9

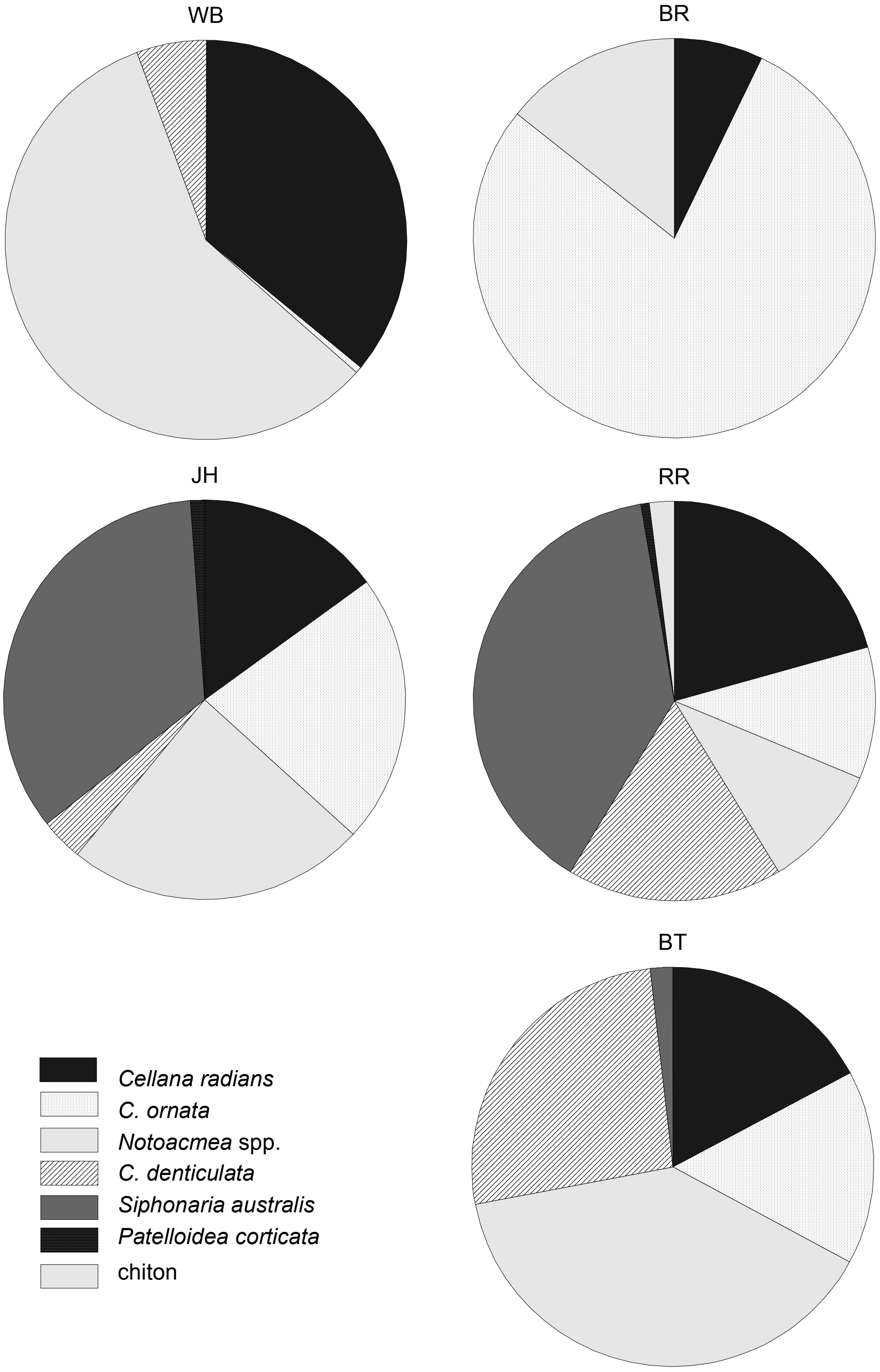

Figure 4.10. Limpet species composition (with chitons) at the 5 sites. Values are the percent of the total number of limpets (>5mm) observed in all plots at each site throughout the duration of the experiment.

Discussion

The effect of limpets on the species richness of benthic algal communities in the high intertidal zone of the South Island of New Zealand appears to be linked to nearshore oceanographic conditions. In this experiment, limpets had a greater effect on algal species richness and biomass at the downwelling-dominated east coast sites than they did at the upwelling-dominated west coast sites. At the east coast sites, grazers decreased species richness, whereas at the west coast sites, grazers had little effect on species richness. This finding matches the predictions of the grazer-reversal hypothesis (Proulx and Mazumder 1998), which suggests that grazing decreases species richness when productivity is low and increases or has no effect on species richness when productivity is high.

The most parsimonious explanation for the effect of grazers on richness is through effects on plant biomass and abundance (Proulx and Mazumder 1998, Hall et al. 2000). An examination of the effects of limpets on algal biomass (Fig. 4.4b) suggests that this mechanism is operating here. At the east coast sites, algal biomass in the paint-control plots is negligible. With negligible biomass, it is not surprising that few species occurred. At the west coast sites, the limpet effect on algal biomass was not distinguishable from zero, indicating that the biomass of algae in the plots with and without limpets was similar. This parity is also reflected in the species richness data. However, an examination of the effects of limpets on algal percent cover is less clear. The pattern on the east coast is the same as that for biomass. But on the west cost, the effect of limpets on algal percent cover at WB is similar to that at the east coast sites, with higher algal abundance in the exclosures than in the paint controls. Furthermore, at JH, limpets appear to be having a positive effect on algal abundance, with higher algal coverage in the paint-controls than in the exclosures (Figs. 4.2, 4.4c). Neither of these patterns is reflected in the species richness data (Fig. 4.4a).

A potential explanation for the differing effect of grazers on algal richness and biomass is the apparent difference in grazing intensity among the upwelling regimes. The upwelling-dominated west coast sites had lower grazing-intensity, as measured by radulae marks on the wax disks, than did the downwelling-dominated east coast sites. This difference in grazing intensity cannot be explained by differences in limpet abundance or size-structure because differences amongst the sites with respect to abundance and limpet-sizes were not explained by differences in upwelling regime (Fig. 4.9). Also, although the composition of limpet assemblages varied across sites, this variation does not appear to be linked to upwelling regime (Fig. 4.10). One potential explanation for this pattern lies in the feeding methods of limpets; limpets crawl over the rock, scraping the substrate with their radulae in search of food as they go. Their primary food source is microalgae, which can include benthic diatoms as well as the spores and sporelings of benthic macroalgae (Lodge 1948, Dayton 1971, Castenholz 1973, Dayton 1975, Nicotri 1977). At more productive sites, the production and/or turnover of benthic microalgae may be greater, such that limpets can achieve the same level of intake by grazing over a smaller surface area. Although I did not measure limpet activity directly, grazing intensity, as measured by the wax disks may provide an indication of limpet activity—which was greater at the less productive, east-coast sites. Further investigation of this possibility will help to elucidate this potential mechanism for explaining the observed differences in limpet grazing intensity that appear to lead to differences in limpet effects on algal species richness and biomass.

Contrary to these results, Nielsen and Navarette (2004), in a similar experiment in Chile, found that herbivores were less dense and achieved lower biomass at sites of high upwelling, but that the *per capita* effects of herbivores were greater at sites with high upwelling. An interesting similarity between the Chilean study and that reported here is that, as seen in New Zealand, there were differences in algal biomass at the end of the experiment (1 year) between plots with and without herbivores at the low upwelling sites, but no differences in algal biomass between plots with and without herbivores at the high upwelling sites. Although this is an intriguing pattern, further work aimed at understanding the interactions between the productivity of nearshore waters and the effects of consumers on the structure and dynamics of intertidal communities is necessary to determine the mechanisms underlying these results.

After 20 months, there were no systematic differences in the types of algae that occurred in the experiment between the two upwelling regimes. This is contrary to the experimental and observational patterns seen by Nielsen and Navarette (2004) and Broitman et al. (2001) in which corticated algae were more abundant at sites of high upwelling intensity and ephemeral algae were more abundant at sites of low upwelling intensity. My examination of morphological groups (Fig. 4.5) did show that, while algae were scarce in the plots to which limpets were allowed access on the east coast, when they did occur, they were almost always the more herbivore-resistant encrusting forms (Steneck and Dethier 1994). On the west coast, the plots to which limpets were allowed access were often dominated by encrusting algae, although microalgae and corticated and foliose macroalgae did occur (Fig. 4.5).

Productivity

In general, our measurements of nutrient concentrations (N and P but not Si) matched the *a priori* designation of sites within upwelling regimes and are thus consistent with the oceanographic context of these sites described by Menge et al. (1999, 2003). Nitrogen is often the limiting macronutrient in marine systems (Ryther and Dunstan 1971). Nearshore waters along New Zealand's coastlines are among the most N-poor temperate systems globally (Vincent et al. 1991, Chang et al. 1995). For comparison with the west coast average of 2.5 μM and east coast average of <1 μM in this study, summertime concentrations in Oregon, USA (a relatively nutrient-rich temperate system (Dickson and Wheeler 1995, Hill and Wheeler 2002)) can reach as high as 30 μM (F. Chan, unpublished data). At such low levels of nearshore productivity, the nearly four-fold difference in N concentrations observed among upwelling regimes is likely to affect algal success.

Sessile invertebrates and interactions with limpets and algae

Sessile invertebrates appeared to be an important component of the benthic community at only two sites, WB (on the west coast) and BT (on the east coast). This pattern is partially explained by the differences in recruitment among the sites. Mussel recruitment was two orders of magnitude higher at WB than it was at other sites. Also, barnacle recruitment was higher at WB than it was elsewhere. Although mean barnacle recruitment over the course of the experiment at BT was not significantly higher than it was at RR, BR, or JH, it does appear to be slightly higher. Also, there was one pulse of barnacle recruitment at BT during February and March of 2005 that yielded densities of recruits similar to those at WB (data not shown). In general, these patterns of recruitment match those seen in previous years at these sites (Menge et al. 2003).

At WB and BT, the sites with significant sessile invertebrate components of the benthic community, sessile invertebrates were more abundant and achieved a higher biomass in the plots to which limpets had access than they did in the exclosures, indicating a positive interaction between sessile invertebrates and limpets. Limpets have often been shown to have negative effects on sessile invertebrates through bulldozing of these animals during feeding activity (Dayton 1971, Foley et al. in prep), and densities of the two are often negatively correlated (Underwood et al. 1983). However, limpets have also been shown to have positive effects on sessile invertebrates by decreasing competition for space with benthic algae (Dungan 1986).

The negative correlation between algal abundance and sessile invertebrate abundance at WB and BT suggests that, in this system, where abundant, barnacles and mussels compete with algae for space on the rock. Although this pattern is seen in some intertidal work (e.g. Dungan 1986), barnacles have also been shown to have no effect on algal recruitment (Jernakoff 1983), or to play an important role in facilitating algal colonization (Farrell 1991). Because the two sites in this experiment at which sessile invertebrates were important components of the community were on different coasts, interactions with sessile invertebrates do not explain the observed differences in limpet effects on algal communities.

In a similar experiment excluding limpets at many of the same sites studied here, the findings of Menge et al. (1999) contrast with these. They found that after 4 months the total impact of limpets was similar at upwelling- and downwelling-dominated sites. However, shorter-term results (<4 months) indicated that grazing was more intense at the upwelling-dominated sites, the opposite of what was seen here. Two primary differences in the experiments may explain this contrast. First, the present experiment was conducted for nearly 1.5 years, while the earlier study focused only on early dynamics. Second, this study was conducted higher in the intertidal zone than the previous work. It is not surprising that the complex interplay of top-down and bottom-up forces may change throughout time and in different environmental contexts.

Conclusion

The results from this experiment suggest that in the high zone, and over a relatively long time period, stronger bottom up effects (increased productivity) don't necessarily yield stronger top-down effects, at least for limpets grazing on algae. In fact, the opposite was true in this case; the sites with lower productivity had the most dramatic top-down effect of limpets on algal abundance. This is contrary to the expected pattern of tight linkages between bottom-up and top-down effects (Menge 2000). Also, in this study, the lower-productivity sites have more dramatic top-down effects of limpets on algal diversity. This finding is consistent with the grazer-reversal hypothesis (Proulx and Mazumder 1998), though the mechanism driving this pattern may be explained by differences in grazing intensity that co-varied with differences in upwelling regimes. Clearly, further research aimed at understanding the contexts in which the strengths of bottom-up and top-down forces are likely to be tightly linked—and in which they are likely to act in concert or inversely—will provide critical information about the ways in which ecological communities are structured. More broadly, these results provide further evidence for the impact of nearshore oceanographic conditions on the ecology of rocky shores and add to the growing body of evidence that suggests that subsidies from adjacent systems can have profound effects on the structure and functioning of ecological systems.

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Icarus and Daedalus: conceptual and tactical lessons for marine ecosystem-based management

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Chapter Five:

Icarus and Daedalus: conceptual and tactical lessons for marine ecosystem-based management

Abstract

A growing realization that the oceans are being degraded has led to calls for a fundamental shift in the management of activities that affect marine ecosystems. Insights from research in coastal marine ecosystems will help shape policies that consider interactions between ecosystem components. The concept of connections is central to coastal marine ecology, connections between: (1) ecosystem structure and functioning; (2) land and sea; (3) marine habitats; (4) species; (5) diverse stressors; and (6) knowledge and uncertainty are of particular importance. These linkages provide conceptual and tactical guidance to inform the transition to ecosystem-based management for the oceans. Conceptual guidance includes recognition of linkages, expectation of surprises, and an avoidance of hubris in management. Tactical guidance includes managing coastal systems at watershed scales, emphasizing monitoring, using area-based management, and incorporating the recognition of uncertainties into decision-making. Ultimately, successful management of human activities that affect the oceans will require integrating these conceptual and tactical approaches.

Introduction

The first two major commissions to review the status and governance of the oceans in 30 years, the Pew Oceans Commission (2003) and the US Commission on Ocean Policy (2004), recently concluded that the oceans are increasingly being affected by human activities and that new approaches to managing those activities are needed. Both highlight the importance of moving from the current fragmented system of governance to an ecosystem-based approach to management of these activities (Fig. 5.1).

Figure 5.1. Indications of the status of marine ecosystems and their current governance. Ecosystem-based management involves streamlining fragmented governance structures to better address the degradation of marine environments.

Signs of degradation of marine environments:

- The 2005 National Coastal Condition Report classified only 21% of US estuarine environments as unimpaired; the rest were identified as threatened or impaired for human use and/or aquatic life. (Environmental Protection Agency 2004).
- In 2003, the National Marine Fisheries Service was able to determine the status of 25% of 932 fish stocks examined. Of these, 38% were classified as experiencing overfishing, overfished, or both (National Marine Fisheries Service 2004).
- The rate of introductions of invasive species to coastal environments has risen exponentially over the past 200 years (Ruiz et al. 2000).
- The population density in coastal counties is greater than 5 times that of non-coastal counties—and growing. In addition, land is being developed at more than twice the rate of population growth (Beach 2002).

Signs of fragmented governance of U.S. marine environments:

- More than 60 congressional committees and subcommittees oversee agencies that manage activities in the marine environment.
- Approximately 20 federal agencies and permanent commissions are charged with implementing marine-related statutes.
- At least 140 federal ocean-related statutes are in force.
- 35 coastal states, commonwealths, and territories are responsible for the management of nearshore waters.

New information and new syntheses of extant information will be insufficient to fundamentally change the ways in which we manage human activities that affect the marine environment. A change in perspective is also required. The myth of Icarus and Daedalus offers some useful ways to think about the challenges of ecosystem-based management for the oceans (Fig. 5.2).

Figure 5.2. Daedalus and his son Icarus were captives on the island of Crete. In order to escape, Daedalus made two pairs of wings and warned Icarus not to fly too high. However, Icarus felt the power of flight and climbed higher and higher. Ultimately, his wings melted and he plummeted to his death. In this story, Daedalus is not only intelligent and innovative, but also he recognizes the limits of his own cleverness. Icarus possesses the tragic fatal flaw of hubris, or too much faith in his own abilities. Painting by C. Saraceni, image used courtesy of Art Source.

Marine community ecology provides both conceptual and tactical insights that are relevant to a shift to ecosystem-based management. Conceptual lessons can help change the way we think about managing human activities that affect the oceans, encouraging avoidance of Icarus-like hubris. Tactical lessons challenge us to emulate Daedalus' cleverness and point to ways in which we can reform the management of activities that affect marine systems to reflect these changing perspectives.

Ecosystem-based management is fundamentally about perceiving the big picture, recognizing connections, and striving to maintain the elements of ecosystems and the processes that link them. Ecosystem-based management is often misconstrued as the management of an entire ecosystem. More accurately, it is a coordinated effort to manage the diverse human impacts that affect an ecosystem to ensure the sustainability of the ecosystem services it provides. Ecosystem-based management was used in ancient societies, is still used in some non-Western cultures (Berkes et al. 1998), and has been described in the scientific and management literature for almost a century (Grumbine 1994). Work on the science, policy, and implementation of ecosystem-based management in terrestrial systems has yielded important advances (e.g. Christensen et al. 1996). The application of the same concept to marine systems is more recent and has, to date, been primarily focused on fisheries management (e.g. Ecosystem Principles Advisory Panel 1999, Babcock and Pikitch 2004, Browman and Stergiou 2004). Evolving from a single-species approach to an ecosystem-based approach in marine fisheries is an important step toward more holistic management. However, ecosystem-based management of fisheries represents only one component of the larger governance changes needed for the oceans. At this interface between marine science and policy, scientists and managers continue to reshape perspectives and tools for ecosystem-based management. Coastal marine ecology offers many lessons that are timely and relevant for developing these approaches to management (Fig. 5.3).

Figure 5.3. Research in coastal systems has formed the basis for much knowledge about the structure and functioning of marine ecosystems. Unlike the deep sea and open ocean, intertidal and shallow subtidal systems are relatively accessible and are therefore amenable to experimentation and long-term monitoring. Lessons from coastal systems thus have the potential to inform ecosystem-based management for the oceans. (Photographs by A. Guerry, L. Ahlgren, B. Menge, and M. Webster).

At the core of ecosystem-based management is the recognition of connections between: (1) ecosystem structure, functioning, and services; (2) land and sea; (3) marine habitats; (4) species; (5) diverse stressors; and (6) knowledge and uncertainty. The lessons learned about these connections in nearshore marine systems can inform the shift towards more ecosystem-based approaches (Table 5.1). Here, I examine some of the ways in which principles from nearshore marine research can help both the generators and users of ecological science to further integrate the management of human impacts on marine ecosystems by providing examples of ways in which basic research can inform ecosystem-based management. Recognizing that ecological theory, experiments, principles, and tools are important for the management of marine systems is easy. Communicating their utility and ensuring that their influence is brought to bear on real-world problems is not.

Table 5.1. Lessons learned from nearshore marine systems that can help inform ecosystem-based approaches in the oceans.

CONNECTION	LESSONS	CONCEPTUAL GUIDANCE	TACTICAL GUIDANCE
1. Ecosystem structure, functioning, and services	• provisioning of goods and services depends upon ecosystem functioning • ecosystem functioning depends on ecosystem structure	• provides the foundation for shifting from a single-species to an ecosystem-based approach • strive to maintain all of the parts of ecological systems and the processes that link them	• research the connections between structure, functioning, and services; with a focus on maintaining services • tighten linkages between systems theory and application to management
2. Land and sea	• actions on land can have important ramifications for coastal marine ecosystems • coastal systems can be resilient	• think big: be cognizant of linkages • scales of management should be matched with scales of systems	• manage coastal oceans and bays at a watershed scale • link terrestrial and marine conservation efforts • emphasize monitoring of the status and trends of coastal systems, and impacts of human activities on them
3. Marine Environments	• organisms, energy, and nutrients flow between habitats • the pelagic environment plays an important role in determining community structure of the benthos	• recognize the importance of context • acknowledge the uniqueness of places	• identify and protect key habitats such as nurseries • consider the juxtaposition of marine habitats in conservation strategies • use regional management

Table 5.1 (continued)

4. Species	• species are embedded in complex communities • indirect effects of species interactions can cause unexpected consequences • effects of perturbations can be delayed	• expect surprises • use precaution • expect time-lags • recognize the impossibility of managing each piece of a system in isolation • keep all the players to maintain the natural range of interactions	• monitor • research conditions under which different interaction types are likely to play key roles • use marine protected areas and marine reserves
5. Diverse stressors	• no stressor operates in a vacuum	• consider how stresses interact in natural systems • take precautions	• research cumulative effects of stressors • manage multiple stressors in tandem
6. Knowledge and uncertainty	• marine ecosystems are complex; there are significant uncertainties in their future states	• avoid hubris • do not expect precise predictions of future states	• be explicit about uncertainties; incorporate them into decision-making; develop probable scenarios • use insurance policies • manage for resilience

Connections between ecosystem structure, functioning, and services

The Millennium Ecosystem Assessment (2005) classifies ecosystem services into four categories: (1) provisioning services that produce goods such as food and fresh water; (2) regulating services that modulate ecosystem processes, such as disease control and climate regulation; (3) cultural services that provide nonmaterial benefits such as education and recreation; and (4) supporting services such as nutrient cycling and primary production that are necessary for the generation of all other ecosystem services. Marine ecosystems provide all of these services.

The functioning of an ecological system, like all systems, depends on its structure. There is a long history of debate about the functional role of biological diversity in ecosystems; sometimes it results in stability, sometimes instability, sometimes increased productivity, sometimes decreased productivity. Establishing the relative importance of key species compared to diversity *per se* remains an active area of inquiry. In either case, we know that the number of species and/or the identities and abundances of species in systems can affect ecosystem properties (Jones et al. 1997, Loreau et al. 2001). Although most research on this topic has been conducted in terrestrial systems, ecosystem functioning has also been linked to diversity and structure of marine communities (Stachowicz et al. 2002, Worm et al. 2002).

Humans have altered the structure and functioning of the earth's ecosystems in far-reaching and dramatic ways (Millennium Ecosystem Assessment 2005). One of the essential contributions of the field of ecology will be to help shape a future in which humans and the natural systems on which they depend can sustainably coexist (Palmer et al. 2004). Economic arguments for conservation that incorporate ecosystem services suggest that the benefit to cost ratio of an effective global conservation program is approximately equal to or greater than 100:1 (Balmford et al. 2002).

Both conceptual and tactical guidance can be gained from the connections between ecosystem structure, functioning, and services. The increasing realization that human activities have the potential to compromise marine ecosystem services provides an impetus for shifting to a more holistic, ecosystem-based approach to managing human activities. Because the provisioning of goods and services depends on ecosystem functioning, which in turn depends on ecosystem structure, careful attention to maintaining both the components of systems and the processes that link them is essential.

Tactically, insights from ecological theory, case studies of coupled social–ecological systems, and work on indicators of ecosystem properties are useful as management becomes more integrative. Current theoretical work, such as the study of complex adaptive systems, is synthetic in nature and can reveal emergent properties of systems (Levin 1999). Case studies of coupled social–ecological systems are yielding important insights into key ecosystem properties such as multiple stable states and resilience (e.g. Elmqvist et al. 2003). One of the challenges to implementing marine ecosystem-based management is the identification of indicators with which to assess the state of ecosystems and the effectiveness of management, though progress has been made (Link et al. 2002). For example, the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) uses selected prey populations that play key roles in the ecosystem and predator populations that are likely to be responsive to changes in prey availability as indicators of ecosystem performance (Agnew 1997).

Connections between land and sea

Human activities on land can have major impacts on marine systems. When more than 10% of a watershed is converted to impervious surfaces such as roads and rooftops, the water quality of associated aquatic systems is degraded (Beach 2002). More than 60% of the coastal rivers and bays in the continental US are moderately to severely degraded by nutrient pollution as a result of terrestrial-based human-driven changes in nutrient cycling (Howarth et al. 2000). Human-derived sources of nitrogen (including wastewater, agricultural fertilizers, and fossil-fuel combustion) have increased nitrogen fluxes into the coastal waters of the northeastern US six- to eightfold (Howarth et al. 2000). Alterations of nutrient availability have been shown to stimulate phytoplankton growth; the development of hypoxia and anoxia; changes in the biomass and community composition of phytoplankton, macroalgae, and invertebrates; increases in the frequency of toxic algal blooms; and more subtle effects such as the alteration of growth and reproductive rates of invertebrates and changes in the seasonality of productivity (Cloern 2001). Pollution is not the only link between actions on land and conditions offshore. Changes in seawater temperature, potential harbingers of ocean warming through anthropogenic climate change, have been shown to cause dramatic shifts in marine benthic communities (Schiel et al. 2004). However, the most well-known examples of the land-sea connection are hypoxic areas, so-called “dead zones”, that occur as a result of increased nutrient loading from growing human populations, agriculture, and food and energy consumption (Rabalais et al. 2002).

Bays are particularly instructive for understanding the linkages between land and sea. Their proximity to land and distinct geographical boundaries create tight feedbacks, causing bays to be heavily impacted by human activities but also providing practical opportunities for holistic management. Tampa Bay, Florida, and the Chesapeake Bay provide prime examples of these linkages (both the generation and mitigation of human impacts). In the 1970s, the Hillsborough Bay section of Tampa Bay exhibited numerous symptoms of nutrient pollution. Efficient treatment of municipal wastes and the abatement of pollution at agricultural fertilizer production plants in the early 1980s decreased the annual wastewater loading of total nitrogen tenfold, halved chlorophyll levels and turbidity, decreased noxious blooms of cyanobacteria, and allowed for the recolonization of seagrasses and their associated communities (Pribble et al. 2003). Land-use changes, overfishing, the introduction of exotic species, and other factors have combined to greatly diminish oyster and seagrass populations and water quality in the Chesapeake Bay (Boesch and Greer 2003, Chesapeake Bay Program 2004).

There has been some progress towards managing bays within an ecosystem framework. The Tampa Bay Estuary Program has continued to improve water quality by addressing non-point source pollution in the watersheds that drain to the bay (Pribble et al. 2003). Emphasis on the connection between land and sea, monitoring, data management, and adaptive management have been essential to this success. The Chesapeake Bay Program is also guided by the necessity to mitigate diverse human impacts. Although significant challenges remain, increases in migratory fish habitat, declining phosphorous and nitrogen loads, and increases in streamside forests are a few indicators of progress toward restoration (Chesapeake Bay Program 2004). The Scientific and Technical Committee of the Chesapeake Bay has modeled the outcomes of various scenarios of land use and development, forest management, agriculture, and fisheries within Chesapeake Bay watersheds (Boesch and Greer 2003). The integration and synthesis of these factors exemplifies the ecosystem-based approach.

There is both conceptual and tactical guidance to be gained from this connection between land and sea. On the conceptual side, recognition of the large-scale connections between marine and terrestrial systems will lead to management that better matches the scales at which ecological systems operate. Management structures and scientific disciplines often treat upland and coastal areas as separate systems. Overcoming these distinctions and recognizing the links between the two is an important component of ecosystem-based management. On the tactical side, land–sea connections highlight the importance of: (1) managing coastal oceans and bays at watershed scales; (2) linking marine and terrestrial conservation efforts; and (3) monitoring the status of coastal systems. Focusing ecosystem-based management on one geographical area, such as a bay, has the advantage of highlighting the human impacts that require consideration, thereby making a broad concept like ecosystem-based management more feasible.

Connections among marine environments

Marine environments are connected by the flow of organisms, energy, and nutrients. Many marine species use different habitats at different stages in their lifecycles. Most benthic invertebrates in the rocky intertidal zone have pelagic larvae, while seagrass beds, mangrove forests, and other coastal wetlands frequently serve as nursery areas for juveniles of many species whose adults reside elsewhere. Carbon subsidies from sub-tidal kelps are important determinants of the structure of intertidal communities and growth rates of organisms within them (Duggins et al. 1989, Bustamante et al. 1995). Given the movement of organisms and resources between systems, what happens in one habitat will likely affect neighboring systems.

The larger oceanographic context in which habitats are embedded provides the mechanism by which connectivity of marine environments occurs and plays an important role in structuring ecological communities. Nearshore oceanographic features influence recruitment, competition, predation, and resource supply (Menge 2003). Thus, the community dynamics of one patch of habitat, such as a rocky reef, may be quite different from those of another, similar patch. Understanding the oceanographic context of a particular region helps in tailoring management to that area. For instance, some sites may produce relatively more larvae, owing to local oceanographic conditions, and could therefore serve as larval sources for nearby areas (Leslie 2004). Although the determination of sources and sinks has proven difficult in many marine systems, genetic techniques (Sotka et al. 2004) and mapping of habitat patches and surface currents can yield information about the connectivity of marine habitats (Roberts 1997). A better understanding of the flow of materials between these habitats, and the spatial scales most appropriate for thinking about particular systems, are key areas of ongoing research.

Conceptually, connections among marine environments highlight the importance of context and the recognition of the uniqueness of places. Tactically, the flow of organisms, energy, and resources indicates that conserving mosaics of habitat types linked by larval dispersal and other processes will be an important facet of effective management. Although guidelines at the national scale will be necessary, regional input and flexibility are essential. This echoes the recommendation of both the U.S. Commission on Ocean Policy (2004) and the Pew Oceans Commission (2003), calling for enhanced regional coordination.

Interspecific connections

There are at least three different types of connections between species that can inform ecosystem-based management: (1) top predators and other species in the community; (2) weak connections among species; and (3) indirect interactions between species.

In communities with keystone predators such as sea otters and some sea stars, one species can have an extraordinary impact on the rest of the community (e.g. Paine 1966, Estes and Palmisano 1974). Maintenance of keystone species is therefore an important component of a systems perspective. In an ocean where top predators have been fished to 10% of their pre-industrial levels (Myers and Worm 2003), and where coastal systems have been drastically altered by the top-down effects of fisheries (Jackson et al. 2001), it is important to consider the ecosystem-wide effects of the removal of top predators.

Intermediate-sized consumers and weak interactions may also play important roles in structuring marine communities (Neutel et al. 2002, Sala and Graham 2002). Berlow (1999) showed that species that have the weakest average interaction strengths (the *per capita* effect of one species on another) also tend to have the greatest variability in those strengths. Similarly, Harley (2003) showed that the interaction strength between two species in one context explained only 37% of the variation in the interaction strength between those species in another context. Therefore, a species that is not important to community dynamics at one point in time or space may be very important at a different time or place.

A number of different kinds of indirect effects can be critical in shaping communities (Wootton 1994). Menge (1995) showed that, on average, in rocky intertidal communities indirect effects accounted for approximately 40% of the changes in species abundances observed after experimental removals. In some situations, the effects of a perturbation on a community can be predicted with reasonable success (Menge 2003). However, in other cases, indirect effects can cause disturbances to have unexpected consequences over both short and long timeframes (Peterson et al. 2003). Given the complexity of communities and the prevalence of indirect effects, we should not expect particular actions or disturbances to have simple effects.

Area-based management, including the creation of marine reserves and other types of marine protected areas, can be used to address the challenge of managing systems in the face of interspecific connections. Marine protected areas are regions of the ocean where destructive and/or extractive activities are limited; marine reserves, also called no-take areas, are regions where all extractive and destructive activities are prohibited. Marine protected areas can be valuable tools for ecosystem-based management because their use stems from the goal of protecting entire systems rather than managing individual parts. Such areas allow complicated interactions between species to play out in relatively intact systems. Reserves can also serve as reference points from which we can learn about human impacts (Castilla 1999), and if they maintain the full complement of species and their interactions, they can also act as insurance against management failures in other areas (National Research Council 2001). However, marine protected areas are not a panacea. They are often small, so that attention to management actions in the broader matrix in which they are embedded is essential, as is flexibility for adaptation. Just as with any other management tool, they should be employed in conjunction with monitoring programs.

Conceptually, connections between species highlight the importance of expecting surprises (e.g. indirect effects); taking precautions (because it is impossible to predict all indirect effects); recognizing the impossibility of managing each piece of a system in isolation; and striving to maintain all the components of a system. Tactically, these lessons emphasize the importance of setting management targets with built-in buffers, monitoring over long timeframes, continuing research efforts to better understand where and when different types of interactions are important, and considering the use of area-based management.

Connections among diverse stressors

Our understanding of the effects of stressors on biological systems comes, predominately, from laboratory examinations of individual stressors on particular species. In nature, no stressor operates in isolation, but the importance of context and the synergistic effects of stressors are not well understood. One area of research that has been explored is the connection between disease and other stressors. For example, both increased nutrient concentrations and increased temperatures have been linked to disease severity and susceptibility in Gorgonian sea fans and reef-building corals (Cerrano et al. 2000, Bruno et al. 2003).

The degradation of the Black Sea provides a striking example of a system impacted by the synergistic effects of multiple stressors and the need for ecosystem-based management. In the past three decades, the effects of eutrophication, oil pollution, over-fishing, inadequate coastal zone management, and the invasion of the exotic ctenophore, *Mnemiopsis leidyi,* have combined to cause a dramatic shift to a profoundly different phytoplankton community, frequent outbreaks of *Mnemiopsis*, and the collapse of commercial fish stocks such as anchovy, sprat, and horse mackerel (Rass 1992, Black Sea Environmental Program 1999). Although some attempts are being made to address these stressors in an ecosystem context, the political and economic climate in many of the countries bordering the Black Sea compound the challenges of restoration (Acar 2001).

On the conceptual side, the potential for stressors to interact highlights the importance of recognizing multiple stressors such as pollution and climate change and of using precaution in their management. In a tactical sense, the connections between diverse stressors not only underline the importance of examining multiple stressors in the laboratory, but also the need to examine cumulative impacts on ecological systems and to manage multiple stressors in tandem. An ecosystem-based approach makes this possible. For example, the Pew Oceans Commission (2003) recommendations for a watershed-based approach to managing coastal development and non-point source pollution are based on taking the broad view rather than looking at each development project and each pollutant in isolation. The Chesapeake Bay and Tampa Bay Programs provide examples of attempts to manage multiple stressors in tandem.

Connections between knowledge and uncertainty

We know a lot about community structure and functioning at fine scales (i.e. those of 1-m^2 quadrats) and at coarse scales (i.e. general themes describing the way things work), but precise predictions of specific outcomes are difficult in complex ecological systems. In general, an emphasis on precise predictions reflects a reductionist view that is inappropriate for complex systems. A more reasonable framework describes possible scenarios, often with attached probabilities. This approach reflects a more synthetic view, is more appropriate for complex systems, and can provide useful guidance for decision-making.

Allison et al. (2003) recognized the linkage between knowledge and uncertainty in their analysis of marine reserve design under various disturbance regimes. They acknowledged that severe disturbances such as hurricanes and oil spills are common across long temporal and large spatial scales. They used the frequency of past catastrophic events to calculate "insurance factors", the extent to which the size of a marine reserve would need to be increased in order to achieve the desired objectives. Essentially, they were planning for resilience in the face of inevitable disturbances. This kind of thinking is also applicable when establishing acceptable levels of pollutants and other stressors. Using scientific knowledge to predict probable outcomes of particular actions and then adding an insurance factor may be a useful way to approach marine policy.

Another tactic for explicitly incorporating uncertainty into decision-making is the use of Bayes' theorem in decision analysis to examine the potential outcomes of a decision based on uncertainty and knowledge of past events (Ellison 1996). Bayesian inference has been successfully used in fisheries management (e.g. Punt and Hilborn 1997, McAllister and Kirchner 2002), but further work on this interface between scientific uncertainty and decision-making is needed (McAllister and Kirchner 2002). More generally, the incorporation and communication of uncertainty is essential to science-based decision-making (Kinzig et al. 2003).

The connection between knowledge and uncertainty is instructive; although we have a long history of attempting to manage ecological systems to look a certain way or to produce a particular level of resources, we have had limited success. Even if such efforts had been more successful in the short term, stasis may not be optimal in the long term. Because the reduction of natural variability through management for stasis can create a less resilient system, external perturbations are more likely to result in drastic changes in ecosystem states (Holling and Meffe 1996). Thus, even if management for precise endpoints were feasible, striving to retain the natural ranges of variation in ecological systems appears to be a better long-term strategy in order to avoid catastrophic shifts (Holling and Meffe 1996, Folke et al. 2002). Ecosystem-based management incorporates the idea of managing with environmental variability in mind. Recognizing uncertainty in management endeavors is an important step, but recognizing the certainty of variability at multiple spatial and temporal scales is essential to the maintenance of functioning systems.

From a conceptual standpoint, the recognition of uncertainty instructs us to avoid hubris by recognizing the limits of our understanding of ecological systems and our ability to manage them. From a tactical standpoint, the limits of our knowledge about complex ecological systems underscore the importance of incorporating uncertainties into decision-making processes; using insurance policies in management activities; and managing for resilience, rather than for desired endpoints.

Progress towards ecosystem-based management of marine systems

The concept of ecosystem-based management provides an overarching goal of integrated management of human activities that affect the oceans and represents one end of a spectrum from piecemeal to holistic management.

Dramatic declines in cod and bluefin tuna provide well-known examples of social and ecological failures of single-species fisheries management (Pauly and Maclean 2002). Precipitous declines in species such as sea turtles that are primarily taken as by-catch in fisheries targeting other species also provide evidence that a piecemeal approach to management has not worked (National Research Council 1990). In some respects, substantial progress towards ecosystem-based management of fisheries has occurred, including requirements to identify essential fish habitat within fishery management plans, and the inclusion of language relevant to an ecosystem-based approach in key policy documents such as the Magnuson-Stevens Fishery Conservation and Management Act. Nevertheless, fisheries management often continues to focus on single species.

One example of a more comprehensive approach to fisheries is provided by the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). CCAMLR's approach is fundamentally ecosystem-based, developed to prevent over-exploitation of Antarctic krill, which was considered essential to the recovery of over-fished whale and seal populations (Constable et al. 2000). By setting catch limits for krill at a higher level than would be set for single-species management, CCAMLR aims to allow krill populations to recover to levels that will support their predators (Constable et al. 2000). CCAMLR's ecosystem-based approach to fisheries management involves taking precautions. For example, recognizing that "reactive management (the practice of taking management action when the need for it has become apparent) is not a viable long-term strategy for the krill fishery" (CCAMLR, cited in Constable et al. 2000), CCAMLR has incorporated the connections between ecosystem structure and functioning, species, and knowledge and uncertainty into their management framework.

While CCAMLR's approach is a pioneering attempt at ecosystem-based fishery management, fishing is the only human impact that is managed. The South Florida Ecosystem Restoration Task Force (SFERTF) is a congressionallymandated effort to coordinate the restoration of the 47,000 km^2 South Florida ecosystem by addressing a diversity of human impacts. In this historically mis-managed system of uplands, wetlands, and coral reefs, restoration efforts are founded upon three primary goals: (1) restoring hydrology and water quality, (2) restoring, preserving, and protecting natural habitats and species, and (3) fostering compatibility of management activities (South Florida Ecosystem Restoration Task Force 2000). These goals exemplify an ecosystem-based approach to managing human impacts on an entire region.

Conclusions

Scientists, managers, decision-makers, and stakeholders of marine resources are beginning to realize that although some components of marine systems are well understood, it is impossible to manage each piece of an ecological system in isolation. Too much faith in the feasibility of managing individual components yields complicated, fragmented, sometimes contradictory, and often bewildering regulations, an inability to achieve management targets, and, most importantly, damage to ecosystems. Ecosystem-based management provides a recourse from the trap of trying to manage each piece until the whole is managed. Key elements of ecosystem-based management include recognizing the intrinsic limits to our current – and potential – understanding of and ability to manipulate ecosystems, the profound impacts of human activities on marine systems, and an attendant requirement to take precautions when managing diverse human impacts.

Ecosystem-based management requires a shift in the philosophy of governance. Lessons from research in coastal marine systems remind us to recognize connections, to expect surprises, and to take precautions. They also emphasize the importance of striving to maintain the full range of components and processes within systems in order to maintain the full range of ecological interactions, of aiming for resilience rather than for desired endpoints, and, overall, of avoiding hubris by recognizing our own limitations. Tactically, this translates into managing at ecologically relevant scales such as watersheds, monitoring the status and trends of systems over long time periods, and incorporating marine protected areas and marine reserves into management frameworks. These connections also highlight the importance of incorporating uncertainties into decision-making, using insurance policies, and enhancing our understanding of marine systems in order to better understand the effects of human actions. Ultimately, better managing human activities that affect the oceans will require a combination of both cleverness and humility.

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Chapter Six: General Conclusion

The research presented in this thesis was motivated by my interest in understanding the factors that determine variation in species diversity. Specifically, I wondered whether or not general conceptual models such as the dynamic-equilibrium model (Huston 1979, 1994) and the grazer-reversal hypothesis (Proulx and Mazumder 1998) provided adequate descriptors of the ways in which grazing and nutrients interact to produce variation in algal diversity in rocky intertidal communities. Previous studies at sites on the Oregon coast demonstrated that in the low zone, grazing impacts varied on the "headland" scale, or on scales of tens of kilometers (Menge 2000, Freidenberg 2002). Nutrients have also been shown to vary along the Oregon coast at the headland scale (e.g., F. Chan et al. unpublished data), suggesting the hypothesis that the variation in grazing pressure might be related to nutrient impacts on algal communities. Furthermore, Nielsen (2001, 2003) showed that in tide pool communities at Boiler Bay, Oregon, nutrient-limitation of algal abundance occurred in wave-sheltered but not wave-exposed habitats. These and similar results in other rocky intertidal habitats (e.g. Worm et al. 2002, Hillebrand 2003, Nielsen and Navarrete 2004) suggested that an understanding of algal diversity patterns might depend on examination of the simultaneous role of both grazers and nutrients.

Individually, each of the experiments presented here illuminates some of the ways in which grazing and nutrients affect the diversity and abundance of algal assemblages in the middle to high-intertidal zone of rocky shores. Together, they can shed light on: 1) the importance of the evolutionary context in which experiments are conducted, 2) the effect of the spatial and temporal scales over which experiments are conducted, 3) the utility—and limitations—of conceptual models for structuring our thinking about the ways in which ecological systems work, and, most importantly, 4) factors that determine the abundance and diversity of algae in these systems. These and other experiments in nearshore marine ecology can inform a shift toward an ecosystem-based approach to managing human activities that affect marine systems.

A review of each experiment

In Chapter Two, grazing by limpets was of primary importance on the Oregon shore, with strong negative effects on algal diversity and abundance. However, in this experiment, there was also an interaction between grazing and enrichment, such that high levels of nutrient enrichment partially compensated for the negative effects of dense grazers by allowing more algae and more species of algae to persist. Low settlement rates of late-successional species in this experiment suggest that the diversity of algal communities in this system may be limited by the supply of propagules.

In Chapter Three, grazing by limpets was again of primary importance, this time on the New Zealand shore. Limpets and snails strongly negatively affected the diversity and abundance of algae, regardless of the level of nutrient enrichment. Despite the low background nutrient levels in New Zealand waters, enrichment had no appreciable effect on the abundance or diversity of the overall algal community. However, in the absence of grazers, nutrient enrichment increased the abundance and biomass of foliose algae, an important component of this algal assemblage. This suggests not only that the method of enrichment was effective, but also that these foliose species with high nitrogen affinities were the only species that were able to take advantage of the artificially increased nutrients.

In Chapter Four, grazing by limpets had a negative impact on algal abundance and diversity at the nutrient-poor sites on the east coast of the South Island of New Zealand and little impact at the richer sites on the west coast. These findings are generally consistent with the grazer-reversal hypothesis, but contrast with the New Zealand nutrient-addition experiment in Chapter Three.

A synthesis of the three experiments

The importance of evolutionary context

It is interesting to note that, in the two nutrient-addition experiments, I found more of a signal of nutrient effects in the nutrient-rich environment of Oregon than I did on the nutrient-poor shores of New Zealand. It seemed reasonable to assume that in New Zealand, where background nutrient levels were low, nutrients were more likely to be limiting than they were in Oregon. However, as my experiments show, the importance of the local suite of species and their unique evolutionary histories cannot be underestimated. One cannot take the low background nutrient levels in New Zealand, add nutrients—even to ecologically relevant levels seen elsewhere—and expect to see Oregon-like conditions. Generally, species in New Zealand are likely adapted to low-nutrient conditions and cannot necessarily take advantage of artificially increased concentrations. For example, the lack of a difference across nutrient treatments in C:N of *Scytothamnus australis*, a dominant alga in the nutrient addition experiment in New Zealand, reflects the apparent inability of this species to utilize the experimentally-added nitrogen.

Although I was not able to conduct identical experiments using identical methodologies in Oregon and New Zealand, I think that it is important to point out that these two experiments are far more similar than any other two experiments that might be selected from the literature that attempt to address the same questions in different systems. Conducted by the same researcher, with similar designs, asking similar questions, and using similar metrics, these two experiments provide a particularly informative comparison. The differences in the results between the two experiments highlight the importance of evolutionary histories in determining a system's response to an experimental manipulation.

The effect of the spatial and temporal scales of experiments

For many years, ecologists have been grappling with understanding the effects of the spatial and temporal scales at which we conduct experiments on our interpretations of the results of those experiments (Wiens 1989). Also, in experimental ecology, one must examine whether or not the experimental conditions employed truly reflect the reality of ecological systems and thus shed light on the processes that drive them. The contrast between the experiment in which I added nutrients in New Zealand (Chapter Three) and that in which I used natural variation in nutrient levels at sites on different coasts of the South Island (Chapter Four) is emblematic of this challenge. The experiment with natural variation suggested that differences in productivity affect the strength of the top-down effects of limpets. Limpets had a lower impact at sites with higher productivity. The nutrient-enrichment experiment conducted on the less-productive east coast did not corroborate these results; limpets had overwhelming impacts on the algal communities regardless of enrichment.

Several factors could be responsible for this discord. First, the differences observed between sites on the east and west coasts of New Zealand that I attribute to differences in productivity may be driven by factors that co-vary with the documented differences in productivity. For example, recruitment of sessile invertebrates has been linked to upwelling-regime (Roughgarden et al. 1988) and interactions with sessile invertebrates can impact algal communities (Chapter Four). However, I examined the recruitment of barnacles and mussels and found that while recruitment for both groups differed by site, it did not differ by upwelling regime (coast). Another potential difference was the suite of limpet species resident on each coast, but again, I did not see differences by coast with respect to limpet species composition. However, other, unexplored factors could be varying and should be the focus of further study. For example, the effect of environmental stress could vary by coast or by intertidal zone or both. Differing stress regimes might help to explain the contradiction between the results of my east vs. west coast experiments, in which grazing strength differed between coasts, and those of Menge et al. (1999) in which no between-coast difference was observed. My experiments were done in the upper, and probably more stressful, zone of these areas while those of Menge et al. (1999) were done in the lower, and probably less stressful, zones. Stress could have inhibited grazers in the west coast high zone, helping to account for the differences I have documented.

Second, there are obvious differences in the temporal and spatial scales at which nutrients varied—or were varied experimentally. Naturally (in

Chapter Four) nutrient concentrations vary over tens of kilometers and have been doing so for centuries; experimentally (in Chapter Three), nutrient concentrations varied over centimeters, in pulses, over the course of one year. Although my experiments enriching marine benthic communities and those of other authors (e.g. Nielsen 2001, Worm et al. 2002, Hillebrand 2003, Nielsen 2003) are important first steps toward clarifying our understanding of the effects of productivity on these systems, they are best viewed as the initial stages of research in this arena.

The utility—and limitations—of conceptual models

Conceptual models such as the dynamic equilibrium model (Huston 1979, 1994) are, without a doubt, useful for helping to structure our thinking about the ways in which ecological systems work. However, although deceptively simple, the use of relative terms such as “high” and “low” productivity can render them unfalsifiable. As seen in these experiments, variation in productivity within the spectrum of natural variation within the South Island of New Zealand resulted in patterns that appeared to be consistent with the dynamic equilibrium model and the grazer-reversal hypothesis—if one considers the east coast of New Zealand to represent low productivity and the west coast to represent high productivity. However, by global standards, the west cost of New Zealand is relatively nutrient-poor, and thus one could consider these findings to run counter to the expectations of the models. Careful consideration of the contexts in which we expect a model to apply (for example, within a system? globally?) will help to strengthen the utility of these synthetic tools.

What affects the abundance and diversity of algae in these systems?

Grazing—particularly by limpets—is a primary determinant of the abundance and diversity of algal assemblages in the systems I studied. Beyond a threshold density of limpets, few algae escape grazing (Chapters Two and Three), and those species that do tend to be the more grazer-resistant species, such as encrusting forms (Chapter Four). The importance of grazing documented here is consistent with the findings of previous work in several intertidal systems from around the globe (e.g. Underwood 1980, Lubchenco 1983, Cubit 1984, Underwood and Jernakoff 1984). I have added to this body of work with the experiments described here by examining the role of these important grazers while changing the nutrient context of the systems. Although there were subtle effects of nutrient-enrichment, the overall dominance of grazing remains clear. An exception to this pattern is the striking difference in the effect of limpets at sites on the east and west coasts of New Zealand (Chapter Four).

The supply of algal propagules also appears to play a key role in structuring algal assemblages in these systems. The results of Chapter Two, in particular, suggest that the proximity of adult fronds affects the likelihood of settlement of late-successional algal species. This suggests that the regional pool of species from which individuals are drawn during community assembly may be considerably smaller for algae than one might expect.

Both nutrients and competition for space were less important than I predicted *a priori*. Neither of the nutrient-enrichment experiments suggested a main-effect of nutrients. The effects of enrichment, when evident, were always dependent on the level of grazing. In Oregon (Chapter Two) nutrients appeared to play a role only when limpet densities were at their highest, with conditions of high enrichment allowing for some algal growth despite heavy grazing. In New Zealand (Chapter Three), nutrients played a role only when grazers were excluded; in the absence of grazers, high enrichment favored the growth of foliose algae. When comparing sites on the east and west coasts of the South Island of New Zealand (Chapter Four), nutrients appear to play a larger role, with the effect of limpets being linked to the upwelling regime at the site.

Marine benthic algae compete for space, nutrients, and light. By adding to the pool of available nutrients, I expected to increase algal growth-rates and thereby intensify competition for all three limiting factors. Competition for space, exemplified by Connell's (1961) classic paper establishing competition as a primary determinant of the distributions of intertidal barnacles, is particularly well-documented in rocky-intertidal systems (e.g. Lubchenco 1980, Branch 1984). However, competition for space appeared to be relatively weak in my studies. Competition for a limiting resource underlies the hypothesized decrease in diversity with increased productivity (and decreasing biotic or abiotic disturbance) in the dynamic-equilibrium model and some diversity-productivity theory (Grime 1973, Huston 1979, Huston 1994). The apparent weakness of competition in these systems suggests that a re-evaluation of the assumption of its importance is warranted.

How experiments in marine ecology can inform management

Recently, the U.S. Commission on Ocean Policy (2004) and the Pew Oceans Commission (2003) concluded that the oceans are increasingly being affected by human activities and recommended a shift toward ecosystem-based management of marine systems. Ecosystem-based management is fundamentally about perceiving the big picture, recognizing connections, and striving to maintain the elements of ecosystems and the processes that link them (Chapter Five). I believe that insights from coastal marine ecology—such as from the kinds of experiments described here—will be instrumental in structuring ecosystem-based management of marine systems. In order to better manage the interactions between humans and the ecosystems of which we are a part, we need to have and communicate a reasonable understanding of how those ecosystems work. In Chapter Five, I reviewed some of the ways in which research in nearshore marine systems can help inform a shift toward ecosystem-based management, discussed necessary shifts in both conceptual frameworks and tactics, and provided examples of regional programs that are making progress toward ecosystem-based management that demonstrate the feasibility of more comprehensive management of human impacts on marine systems. Ultimately, successful management of human activities that affect ecosystems will require integrating new conceptual and tactical approaches and will depend upon tighter linkages between ecological research and the policies that govern human activities.

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