AN ABSTRACT OF THE DISSERTATION OF

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Title: Linking Marine Communities and Ecosystems: Invertebrates Mediate Nutrient Availability in Intertidal Communities.

Abstract approved

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Bruce A. Menge and Jane Lubchenco

While community ecologists have traditionally focused on local-scale processes, it has become apparent that a broader perspective, which explores the community-level ramifications of material fluxes within and between ecosystems, is necessary to effectively evaluate bottom-up influences on community structure and dynamics. In this dissertation, I employed ecosystem principles to understand these processes in rocky intertidal communities. I specifically examined the roles of sessile invertebrates in mediating the transfers and transformations of carbon and nitrogen in intertidal ecosystems.

First, I quantified the links between nearshore pelagic and rocky intertidal systems. By assimilating suspended particulate organic material (seston), mussels and other sessile invertebrates serve as mediators of material exchange from pelagic to

benthic ecosystems. I evaluated these trophic linkages along productivity gradients on the coasts of New Zealand and Oregon, which allowed me to address the influences of seston quality and quantity on the growth and ammonium excretion rates of mussels. My results highlight the necessity of simultaneously considering both seston quantity (total organic particulates) and quality (phytoplankton availability) in evaluating benthic-pelagic coupling.

Second, I assessed the utilization of invertebrate-excreted ammonium by macroalgae in high-intertidal pools. Sessile invertebrates not only serve as mediators of material transfer into intertidal ecosystems, they also chemically transform that material, converting particulate organic nitrogen, which is unusable by macroalgae, into ammonium, which algae readily assimilate. I showed that especially in high-zone pools, which are isolated from the ocean for 80% of the time, invertebrate-excreted ammonium is an important nitrogen source for macroalgae. Ammonium accumulated in tide pools and was subsequently taken up by algae. This novel positive interaction influenced community structure: macroalgal species richness increased with the rate of invertebrate-mediated ammonium loading in pools.

Finally, by experimentally manipulating macroalgae and invertebrates in laboratory mesocosms, I quantified the effect of ammonium loading on algal growth. I demonstrated that algal nitrogen assimilation rates increased with the rate of ammonium accumulation in tide pools, which resulted in enhanced growth when invertebrates were present. Together, these studies suggest that by merging community and ecosystem perspectives we can gain unique and important insights into the bottom-up processes influencing intertidal systems.

Linking Marine Communities and Ecosystems: Invertebrates Mediate Nutrient Availability in Intertidal Communities

by

Matthew E. Bracken

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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.

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Matthew E. Bracken, Author

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Bruce A. Menge, Melissa M. Foley, David R. Schiel, and Jane Lubchenco assisted with data collection, analyses, logistical support, and writing for Chapter 2, and are therefore included as authors.

Karina J. Nielsen provided important insights into nutrient dynamics in tide pools. She assisted with data collection, analyses, and writing for Chapter 3, and is included as an author.

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DEDICATION

To Jack Eddy: friend, teacher, coach, and inspiration.

Linking Marine Communities and Ecosystems: Invertebrates Mediate Nutrient Availability in Intertidal Communities

CHAPTER 1

GENERAL INTRODUCTION

In examining factors influencing biological communities, benthic marine ecologists historically focused on local-scale processes such as competition (Connell 1961), consumption (Paine 1966, Lubchenco 1978), and physical stress (Lewis 1954, Dayton 1971). While these studies documented important effectors of organisms' diversity, abundances, and distributions, they ignored the possibility that processes varying on larger scales, such as nutrient availability, could influence benthic communities (Menge 1992). More recent evidence, however, suggests that local-scale processes are insufficient to explain variation in key attributes of benthic systems (Menge *et al.* 1996, Menge 2000b), and that a broader perspective, which explicitly explores the community-level implications of material fluxes within and between ecosystems, is necessary in order to evaluate community structure and dynamics (Grover and Loreau 1996, Polis *et al.* 1997).

Similarly, while ecosystem ecologists have traditionally ignored individual species in measuring fluxes and transformations of materials and energy (Likens 1992), it has become increasingly clear that species possess unique traits and therefore play important roles in mediating ecosystem functions (Lawton 1994, Chapin *et al.*

1995, Chapin *et al.* 1997). For example, species affect ecosystems by acting as consumers (transferring stored energy or materials from lower trophic levels), engineers (influencing flows of materials and energy by altering physical structures in the system), and transformers (chemically converting materials from one form into another form) (Ernest and Brown 2001).

These interactions all involve the transformation or transfer of energy or materials, thereby providing a common currency linking communities and ecosystems. They include both familiar interactions viewed in new ways (consumers as mediators of material and energy fluxes) and novel interaction mechanisms, such as chemical and physical alteration of the environment. Ecological processes, both at the community level and at the ecosystem level, can be viewed in terms of their impacts on material pools, fluxes, and transformations (Shachak and Jones 1995). This perspective blurs the lines between communities and ecosystems, allowing community ecologists to effectively address the influences of large-scale phenomena (*e.g.,* nutrient availability and cycling) and ecosystem ecologists to evaluate the disparate roles of individual species.

The importance of incorporating large-scale processes into assessments of community structure and dynamics is illustrated by studies conducted at the interfaces between ecosystems. For example, Gary Polis and his colleagues (Polis and Hurd 1995, Polis *et al.* 1998) demonstrated that terrestrial island ecosystems in the Gulf of California are largely subsidized by marine inputs. On these desert islands, *in situ*

productivity is incredibly low, and inputs of marine macroalgal detritus, carrion, and seabird guano strongly influence patterns of community structure and dynamics.

Another ecosystem-interface habitat based predominantly on external subsidies occurs on rocky shorelines. Rocky intertidal ecosystems are a well-studied model system in community ecology (Paine 1994). In these systems, *in situ* primary productivity (*e.g.*, macroalgal growth) is largely regulated by concentrations of nutrients in an adjacent ecosystem, the nearshore ocean (Dayton *et al.* 1999, Blanchette *et al.* 2002). Secondary productivity also relies on oceanic subsidies. The majority of biomass on rocky reefs often consists of benthic filter feeders such as mussels and barnacles (Bustamante *et al.* 1995). These organisms assimilate suspended particulate organic material (*e.g.*, phytoplankton and detritus) from the seston, thereby serving as mediators of material exchange from pelagic to benthic systems (Menge *et al.* 1997a). Because these consumers receive the majority of their resources from outside the local system, they have been termed "basal species," and from the standpoints of space use on the shore and resource acquisition from the surrounding milieu, serve functionally as primary producers (Menge 1995).

By assimilating organic particulates, sessile invertebrates not only serve as mediators of material inputs into benthic systems, they also chemically transform that material in the process. An appreciable fraction of the nitrogen in nearshore waters is in the form of particulate organic material. In Oregon coastal waters, the concentration of particulate organic nitrogen can equal or exceed that of inorganic nitrogen (Menge *et al.* 1997a, Menge *et al.* 1997b, M. Bracken, unpublished data). However, particulate

nitrogen cannot be utilized by algae, which require inorganic nitrogen for growth (Lobban and Harrison 1994). The primary excretory product of sessile invertebrates is ammonium (Bayne and Scullard 1977, Williamson and Rees 1994), a reduced form of inorganic nitrogen that is readily taken up and assimilated by algae. Thus, by converting particulate organic nitrogen into ammonium, invertebrates provide intertidal macroalgae with access to an otherwise unavailable nitrogen source.

The goal of my doctoral research was to evaluate the roles that sessile invertebrates play in mediating fluxes of materials into and within rocky intertidal ecosystems. In Chapter 2, I examine the factors influencing the transfer of carbon and nitrogen between nearshore and intertidal ecosystems. I evaluated the trophic linkages between pelagic and intertidal systems on temperate rocky reefs in two geographic regions with independently evolved assemblages of species: the coasts of New Zealand's South Island and Oregon. Variation in nearshore oceanographic conditions, both within and between New Zealand and Oregon, allowed me to address the influences of seston quality and quantity on the growth and ammonium excretion rates of intertidal mussels (*Mytilus galloprovincialis* in New Zealand and *M. californianus* in Oregon). I also used a novel technique, the analyses of seston and mussel carbon-stable-isotope ratios, to explicitly evaluate fluxes of carbon from the nearshore ocean to intertidal ecosystems along gradients of seston quality and quantity. My results highlight the importance of considering both seston quality and quantity in evaluating the links between pelagic and benthic ecosystems.

In Chapters 3 and 4, I evaluate the utilization of invertebrate-excreted ammonium by tide pool macroalgae. In Chapter 3, I assess this interaction, the excretion of ammonium by invertebrates and its subsequent uptake by macroalgae, in high-intertidal pools on the Oregon coast. I demonstrate that because high-zone tide pools are isolated from the ocean for approximately 80% of the time, the macroalgae in those pools are subjected to severe nitrate limitation. In many pools, ammonium excretion by invertebrates ameliorated this stress, and more macroalgal species were found in pools with higher rates of ammonium loading by invertebrates. Furthermore, biomass-specific ammonium uptake rates were higher in pools with more macroalgal species, suggesting that macrophyte diversity influences ecosystem functioning.

In Chapter 4, I used laboratory mesocosms to experimentally quantify the influence of invertebrate-excreted ammonium on macroalgal growth. In Oregon coast high-intertidal pools, the macroalga *Odonthalia floccosa* often grows epizoically on the shells of *M. californianus*. I monitored growth of *O. floccosa* in the presence and absence of mussels and demonstrated that assimilation of nitrogen into algal tissue was closely associated with the rate of invertebrate-excreted ammonium accumulation in the mesocosms. Increases in nitrogen assimilation were associated with increased macroalgal growth: *O. floccosa* individuals added 41% more biomass when mussels were present. Together, the studies described in Chapters 3 and 4 provide convincing evidence for a positive nontrophic interaction between intertidal invertebrates and macroalgae based on nitrogen excretion by invertebrates.

These studies demonstrate the effectiveness of merging community and ecosystem perspectives in exploring linkages between nearshore and intertidal ecosystems. They illustrate the novel species interactions revealed by simultaneously considering community-level and ecosystem-level processes. Finally, they suggest that ecosystem approaches to the science of ecology, which evaluate material transfers and transformations within and between systems, can provide unique insights into the bottom-up processes influencing rocky intertidal communities.

CHAPTER 2

VARIATION IN BENTHIC-PELAGIC COUPLING ALONG PRODUCTIVITY GRADIENTS

Abstract

Quantifying the links between nearshore and intertidal productivity is fundamental to understanding the structure and dynamics of rocky-shore communities. Because filter-feeding invertebrates consume phytoplankton and detritus from the seston, they serve as important mediators for the exchange of materials from nearshore pelagic to intertidal benthic ecosystems. In this study, we compare and contrast the trophic linkages between pelagic and intertidal systems on temperate rocky reefs in two geographic regions: the coasts of New Zealand's South Island and the coast of Oregon. We exploited mesoscale oceanographic differences in nearshore productivity within each of those regions and more substantial differences between New Zealand and Oregon to evaluate the influences of seston quality and quantity on the growth and ammonium excretion rates of intertidal mussels (*Mytilus galloprovincialis* in New Zealand and *M. californianus* in Oregon). We also analyzed the carbon stable-isotope ratios of nearshore organic particulates and mussel tissues to explicitly evaluate material fluxes from pelagic systems to benthic systems along gradients of seston quality and quantity. These analyses suggested that as seston carbon-to-chlorophyll ratios increased, terrestrial detritus became an increasingly important component of

the seston. We found that after accounting for total organic particulates, increases in nearshore phytoplankton availability were associated with increased mussel growth and decreased ammonium excretion, suggesting that phytoplankton carbon and nitrogen were readily assimilated by mussels. Conversely, after accounting for phytoplankton, increases in total particulates were associated with decreased growth and increased ammonium excretion, indicating that detrital carbon and nitrogen were less readily assimilated. Especially in nearshore systems, where a significant fraction of the particulate biomass can consist of refractory terrigenous material, it is necessary to simultaneously consider both seston quality and quantity in evaluating benthic-pelagic coupling.

Introduction

The productivity of an ecosystem is based on a combination of internal material transfers (*e.g., via* consumption, regeneration, and assimilation) and external material inputs (*e.g.,* of nutrients, detritus, and organisms) (Polis *et al.* 1997). Historically, marine community ecologists have focused on local-scale autochthonous processes, especially "top-down" trophic interactions, influencing the structure and dynamics of benthic communities (Menge 1992). However, more recent evaluations of "bottom-up" processes, including inputs of propagules, nutrients, and prey, suggest that allochthonous inputs also influence benthic communities in important ways (Menge *et al.* 1997a, Worm *et al.* 2002).

For example, phytoplankton and detritus in nearshore waters are consumed by benthic filter-feeding invertebrates. Those invertebrates (*e.g.*, mussels and barnacles) thereby serve as mediators of particulate organic material fluxes from the seston into the benthic food web (Duggins *et al.* 1989). In open-coast ecosystems, variation in nearshore pelagic primary productivity can have profound bottom-up influences on benthic community structure. Differences in nearshore phytoplankton availability, associated with variation in oceanographic processes such as upwelling and coastal hydrodynamics, correspond with differences in the biomass and growth rates of filter-feeding invertebrates in adjacent intertidal communities (Bustamante *et al.* 1995, Menge *et al.* 1997a). Because filter-feeding invertebrates comprise a large fraction of the biomass in temperate intertidal ecosystems (Menge 2000b), these differences in nearshore oceanography can propagate up the benthic food web, influencing the average sizes, abundances, and consumption rates of predators (Menge *et al.* 1994, 1997a, 1999).

Therefore, in order to understand benthic community structure and dynamics, it is necessary to quantify the material fluxes into benthic systems from adjacent nearshore pelagic systems. The ubiquity of congeneric mussels (*Mytilus* spp.) on temperate rocky shores worldwide allowed us to compare this benthic-pelagic coupling in two similar, but independently evolved, intertidal ecosystems: the rocky reefs of the Oregon coast and New Zealand's South Island.

The Oregon coast, located within the California Current upwelling system of the northeastern Pacific, is characterized by high nearshore productivity; during the

upwelling season, nitrate concentrations can exceed 30 μmol L^{-1} (M. Bracken, unpubl.), and chlorophyll *a* (Chl *a*) concentrations are occasionally in excess of 60 μg L^{-1} (Menge *et al.* 1997a). However, within this highly productive system, mesoscale hydrodynamic differences associated with gyres and meanders in the upwelling-front jet create substantial variation in phytoplankton availability between intertidal sites (Strub *et al.* 1991, Menge *et al.* 1997a).

The coastal waters off New Zealand's South Island, although not generally considered an upwelling region, do exhibit variability in primary productivity associated with nearshore hydrodynamics (Menge *et al.* 1999). The Tasman Current, which flows eastward across the Tasman Sea, impinges upon the west coast of the South Island in a broad front. The current's major flow is directed southward by the continental-shelf topography, forming the Southland Current, which, guided by the Subantarctic Convergence, wraps around the south end of the island and flows northward along the east coast (Stanton 1976, Vincent *et al.* 1991). However, a wind-driven northward current, the Westland Current, splits from the main body of the Tasman/Southland Current and follows the west coast northward. Because Ekman transport is to the left of the wind-stress in the southern hemisphere, intermittent upwelling occurs along the South Island's northwest coast (Vincent *et al.* 1991, Stanton and Moore 1992). In contrast, downwelling is more persistent along the east coast of the South Island.

In this study, we exploited the differences in nearshore productivity within each of those geographic regions (Oregon and New Zealand) and more substantial

productivity differences between Oregon and New Zealand to address the influences of seston quality and quantity on the growth and ammonium excretion rates of intertidal mussels. We also analyzed the carbon stable-isotope ratios of nearshore organic particulates and mussel tissues to evaluate the trophic linkages between pelagic and benthic systems along gradients of nearshore productivity and seston quality. This suite of ecological, physiological, and biogeochemical indices, along with the comparisons and contrasts between geographic regions, suggest that it is necessary to simultaneously examine both phytoplankton and total particulate availability in order to describe benthic-pelagic links.

Materials and Methods

Study Sites

Identical measurements were conducted at four sites each in New Zealand and Oregon (Fig. 2.1). Sites in New Zealand included Woodpecker Bay (42°01.3'S, 171°22.7'E; hereafter WB) and Twelve Mile (42°19.1'S, 171°16.2'E; TM) on the South Island's west coast and Raramai (42°35.7'S, 173°33.0'E; RR) and Box Thumb (43°35.0'S, 172°47.8'E; BT) on the South Island's east coast. Two of the New Zealand sites, TM and BT, are described elsewhere (Menge *et al.* 1999, Menge *et al.* 2002). WB was ~35 km north of TM. RR was located just south of the Kaikoura Peninsula, while BT was located ~125 km south of RR on Godley Head.

Oregon sites included Boiler Bay (44°50.0'N, 124°03.7'W; BB), Strawberry

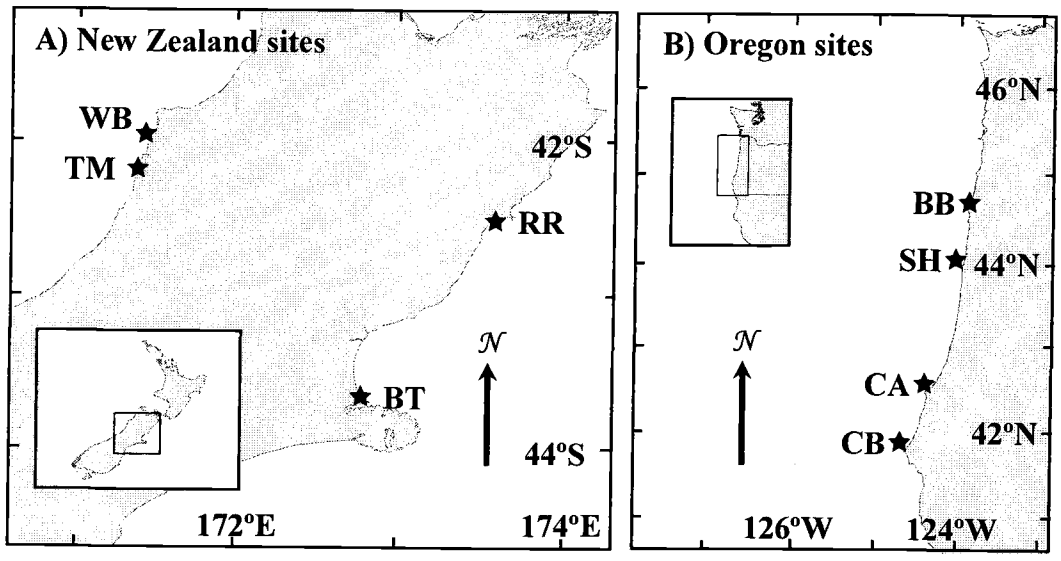

Figure 2.1. Sampling locations. (A) New Zealand sites included Woodpecker Bay (WB) and Twelve Mile (TM) on the west coast of the South Island and Raramai (RR) and Box Thumb (BT) on the east coast. (B) Oregon sites were Boiler Bay (BB), Strawberry Hill (SH), Cape Arago (CA), and Cape Blanco (CB).

Hill (44°15.3'N, 124°06.7'W; SH), Cape Arago (43°18.4'N, 124°23.5'W; CA), and Cape Blanco (42°50.3'N, 124°33.7'W; CB). BB and SH, located ~65 km apart on the central Oregon coast, have been described elsewhere (Menge *et al.* 1997b, Menge 2000b). CA and CB were on the southern Oregon coast; CA was ~100 km south of SH, and CB was ~55 km south of CA (Connolly and Roughgarden 1998, Freidenburg 2002, respectively).

All sites, both in New Zealand and Oregon, were characterized by extensive mid-intertidal-zone mussel beds on rocky intertidal reefs. These sites were selected because previous research suggested that variation in nearshore oceanographic conditions, both within and between New Zealand and Oregon, was associated with differences in nearshore phytoplankton and particulate concentrations at those sites. In

New Zealand, two sites were located in the Westland Current intermittent upwelling system (WB and TM), and two sites were located in the Southland Current downwelling system (RR and BT) (Menge *et al.* 1999, Menge *et al.* 2002). Although all four Oregon sites were located in the California Current upwelling system, we predicted that latitudinal changes in upwelling intensity and mesoscale coastal hydrodynamic differences due to variation in the continental-shelf width would be associated with differences among sites in the supply of phytoplankton and particulates to intertidal mussels (Menge *et al.* 1997b, Connolly and Roughgarden 1998, Menge 2000b).

Seston quality and quantity

Water samples for quantifying particulate organic material and Chl *a* were collected from wave-exposed rocky intertidal reefs, just below the mussel bed at each site. Samples (n=5 per collection) were taken by filling acid-washed opaque plastic (HDPE) brown bottles at the water's edge at low tide. Bottles were clamped to the end of a 3-m-long pole, rinsed in seawater three times, and plunged to a depth of 20-40 cm below the surface to collect the sample.

From each 500 ml sample bottle, two subsamples (200 ml each) were filtered through combusted, pre-weighed 25-mm Whatman GF/F filters (pore size 0.7 μm). The filters, with trapped particulates, were then transported to the laboratory on ice and stored at -20°C prior to analyses of particulates. Filters were dried (50°C for 72 h) and weighed. One filter was then combusted (450°C for 8 h) and re-weighed; the

difference between the pre-combusted and post-combusted masses was used as an index of total particulate organic biomass. The second filter was acid-fumed to remove carbonate, then analyzed for total organic carbon, ^{13}C, and ^{12}C using a Carlo Erba NC2500 elemental analyser coupled to a Finnigan MAT Delta plus gas isotope ratio mass spectrometer at the University of Texas Marine Science Institute (Port Aransas, Texas). The resulting carbon-isotopic signatures of the seston were expressed as $\delta^{13}C$ values in units of 'per mil' (‰), defined as $\delta^{13}C = [R(sample)/R(standard) - 1] \times 1000$, where R was $^{13}C : ^{12}C$ and the standard was Pee Dee Belemnite (PDB) limestone.

An additional 50 ml subsample was filtered through a 25-mm Whatman GF/F filter, and the filter was then transported to the laboratory on ice and frozen prior to Chl *a* analysis. Chl *a* was quantified using a Turner Designs benchtop fluorometer (model TD-700) after extraction in 90% HPLC acetone for 12 h at -20°C.

In New Zealand, seston attributes were quantified three times at each site during the austral spring and summer (December and January) of 2001-2002. In Oregon, Chl *a* and total particulates were quantified three times at each site (at approximately monthly intervals) during the boreal summer (June through August) of 2001. Additionally, Chl *a*, particulates, total carbon, and carbon-isotopic ratios were quantified three times during the boreal summer of 2002.

Attributes of benthic filter feeders

Growth rates, ammonium excretion rates, and carbon stable-isotope signatures ($\delta^{13}C$) were measured for congeneric mussels in New Zealand (*Mytilus*

galloprovincialis Lamarck) and Oregon (*M. californianus* Conrad). Growth rates were calculated by notching the posterior growing margins of mussel shells at each site with a file and harvesting the notched mussels ~1 year later. New shell material was added beyond the mark, but the notch was still visible, allowing calculation of growth based on initial and final shell lengths. Final length (from the umbo to the posterior shell edge) and initial length (from the umbo to the notch) were measured for each mussel. The tissue was then dissected out of each shell and weighed (wet tissue mass). A subset of the tissue samples was dried for 72 h at 50°C, and weighed again (dry tissue mass). Regressions relating shell length to wet tissue mass (New Zealand: wet tissue mass = $[5 \times 10^{-5}] \times \text{length}^{2.877}$, r^2=0.83; Oregon: wet tissue mass = $[1 \times 10^{-5}] \times \text{length}^{3.284}$, r^2=0.78) and wet tissue mass to dry tissue mass (New Zealand: dry tissue mass = 0.1906 x wet tissue mass, r^2=0.96; Oregon: dry tissue mass = 0.1204 x wet tissue mass, r^2=0.83) were used to calculate growth in dry tissue mass, normalized by the initial dry tissue mass (mg d^{-1} g^{-1}). In New Zealand, between 6 and 108 mussels at each site were notched in October 2001 and harvested in October 2002. In Oregon, between 68 and 187 mussels at each site were notched in May 2001 and harvested in May 2002.

Mussels' ammonium excretion rates are influenced by seston quality and quantity (Bayne and Scullard 1977), so we used the rate of ammonium excretion at each site as a physiological index of benthic-pelagic coupling. Ammonium excretion rates were measured by collecting 20 mussels from each site, simultaneous with the seston measurements described above. Live mussels were transported to the laboratory

in a cooler and allowed to recover overnight in running seawater tanks. Each mussel was placed in a 100 mL plastic chamber containing 60 mL of 4 μm-filtered seawater. Water samples (1 ml) were taken from each chamber at 0, 0.75, and 1.5 h and analyzed for ammonium using the phenol-hypochlorite method (Solórzano 1969). The tissue from each mussel was then dried (50°C for 72 h) and weighed. The rate of ammonium accumulation in each chamber was normalized by the dry tissue mass of each mussel to calculate the ammonium excretion rate (μmol h^{-1} g^{-1}). While excretion rates were determined for Oregon mussels during the summers of both 2001 and 2002, only the 2001 data are presented below, to parallel the growth data, which are currently only available for 2001-2002. Overall site-mean ammonium excretion rates were virtually identical in 2001 and 2002, and our conclusions were not altered by excluding the 2002 ammonium data.

Tissue samples from five randomly selected mussels were collected on each sampling date during the austral spring and summer of 2001-2002 (New Zealand) and the boreal summer of 2002 (Oregon). Samples were oven-dried, powdered, and analyzed for carbon stable isotopes (^{13}C and ^{12}C) using a Carlo Erba 1108 elemental analyser coupled to a Finnigan MAT Delta S isotope ratio mass spectrometer at the Stable Isotope Facility for Environmental Research at the University of Utah (Salt Lake City, Utah). The resulting carbon-isotopic signatures of the mussels were expressed as $\delta^{13}C$ values in units of 'per mil' (‰), defined as $\delta^{13}C$ = [R(sample)/R(standard) - 1] x 1000, where R was ^{13}C : ^{12}C and the standard was Pee Dee Belemnite (PDB) limestone.

Statistical analyses

Analyses were preformed using general linear models procedures in the SAS System for Windows v. 8 (SAS Institute, Inc., Cary, North Carolina). These included analyses of variance (ANOVA) and covariance (ANCOVA). The assumptions of normality and homogeneity of variances were verified for each model by visually examining residual plots and normal probability plots of the residuals. In many cases, it was necessary to log transform ($ln[x + 1]$) the data to meet these assumptions.

Analyses of seston particulate and Chl *a* concentrations and mussel growth and ammonium excretion rates were based on least-squares means. These were appropriate given the unbalanced nature of the data, especially for the mussel growth rates. Additionally, SAS incorporates covariates into the calculated least-squares means, so that where it was necessary to include a covariate (*i.e.,* for analyses of growth and ammonium excretion rates), the values shown are least-squares means after accounting for the covariate.

General linear models were used to evaluate the effects of Chl *a* and total organic particulate availability on the growth and ammonium excretion rates of mussels:

$$\text{Growth} = \beta_0 + \beta_1(\text{mass}) + \beta_2(\text{Chl } a) + \beta_3 \text{ (organic particulates)}$$

and

$$NH_4^+ \text{ excretion} = \beta_0 + \beta_1(\text{mass}) + \beta_2(\text{Chl } a) + \beta_3 \text{ (organic particulates)}$$

Mass was included as a covariate in these models, as physiological rates, including growth and ammonium excretion rates, decline as an individual's mass increases. Each individual mussel was treated as a replicate, and its growth rate or ammonium excretion rate was evaluated as a function of the mean Chl *a* and organic particulate concentrations associated with that site. Growth rates were evaluated as a function of overall mean seston attributes, while ammonium excretion rates were evaluated as a function of the Chl *a* and organic particulate concentrations measured when individuals were collected.

Because the effects of Chl *a* and particulates could not be determined at the level of the individual mussel, we also analyzed the mean growth and ammonium excretion rates measured at each site as a function of phytoplankton and organic particulate availability. This resulted in a severe decrease in statistical power (a reduction in the sample size from >200 to 4), and a consequent failure to detect statistically significant relationships between seston attributes and mussel growth and ammonium excretion rates. However, these models were more statistically appropriate, given the nature of the data.

Results

Seston Quality and Quantity

Mean concentrations of total particulate organic material were similar in Oregon and New Zealand nearshore waters. While sites within each geographic region

(Oregon vs. New Zealand) differed in particulate availability (New Zealand: $F_{3,54}$=29.86, P<0.0001; Oregon: $F_{3,49}$=9.36, P<0.0001; Fig. 2.2), they varied over similar ranges. For example, the mean particulate concentration at TM in New Zealand was statistically indistinguishable from that at SH in Oregon, and particulate concentrations at BB and CA in Oregon were comparable to those at BT and RR in

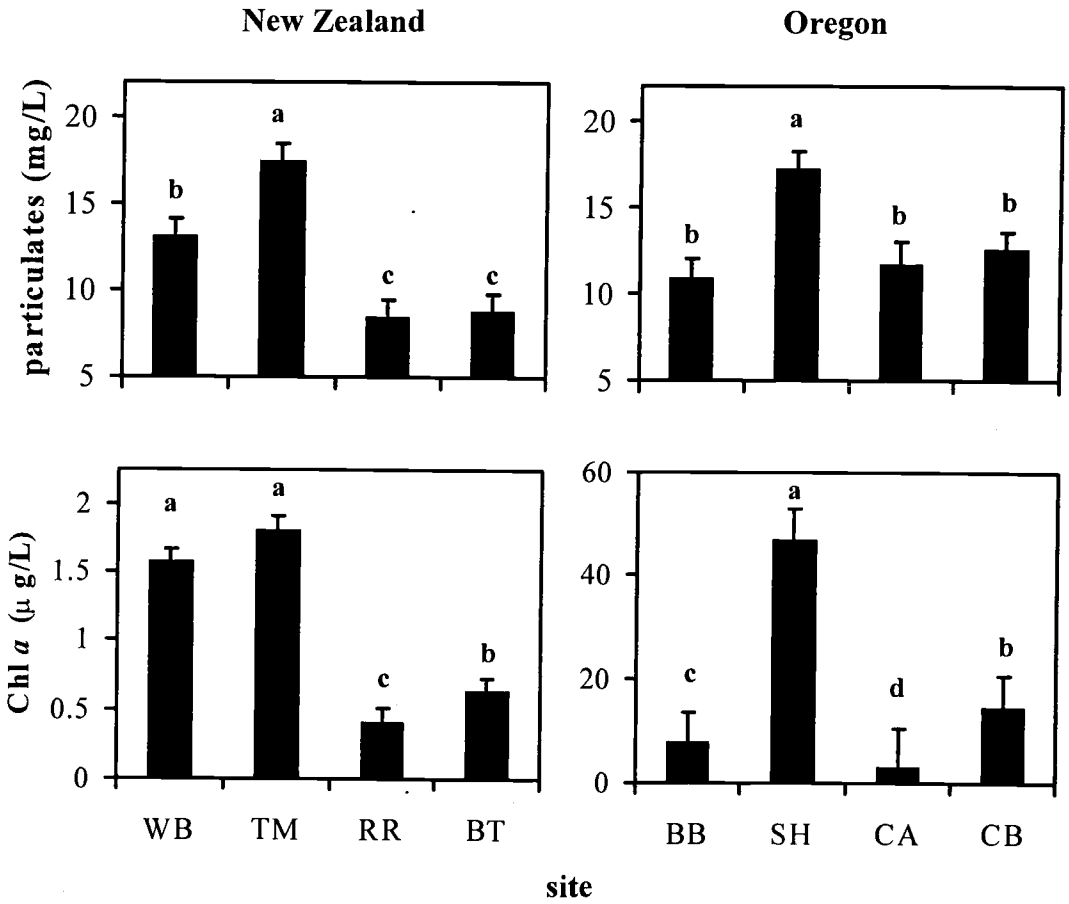

Figure 2.2. Particulate biomass and Chl *a* concentrations in water samples collected at sites in New Zealand and Oregon. Values are least-squares means (+1 SE) of all samples (n=15/site) taken during the austral summer of 2001-02 (New Zealand) and the boreal summer of 2001 (Oregon). Note that scales of the Chl *a* axes differ greatly between Oregon and New Zealand panels. Letters indicate significant differences among site least-squares means ($P < 0.05$) after Bonferroni adjustment.

New Zealand (ANOVA: Bonferroni-adjusted $P>>0.05$).

Despite these similarities in total organic particulate concentrations, there were major differences between New Zealand and Oregon in seston quality. Whereas sites within each geographic region differed in nearshore phytoplankton availability (New Zealand: $F_{3,54}=98.69$, $P<0.0001$; Oregon: $F_{3,49}=67.93$, $P<0.0001$; Fig. 2.2), Chl *a* concentrations were considerably higher in Oregon. The site with the lowest mean Chl *a* concentration in Oregon (CA) was comparable to the site with the highest mean Chl *a* concentration in New Zealand (TM) (ANOVA: Bonferroni-adjusted $P>>0.05$), and the highest mean Chl *a* concentration measured in Oregon (SH) was an order of magnitude higher than the highest in New Zealand (ANOVA: Bonferroni-adjusted $P<0.0001$).

Thus, while particulate biomass concentrations were positively associated with Chl *a* concentrations in both New Zealand and Oregon, the slope of this relationship was significantly steeper in New Zealand ('geographic location x Chl *a*' interaction: $F_{1,161}=127.69$, $P<0.0001$; Fig. 2.3). Similarly, analyses of the relationships between particulate organic carbon and Chl *a* concentrations indicated that there was significantly more carbon per unit Chl *a* in the New Zealand seston than in the Oregon seston ('geographic location x Chl *a*' interaction: $F_{1,110}=283.85$, $P<0.0001$) and that carbon-to-chlorophyll ratios (C:Chl *a*) were higher in New Zealand than in Oregon ($F_{1,113}=418.74$, $P<0.0001$) (Table 2.1; Fig. 2.4).

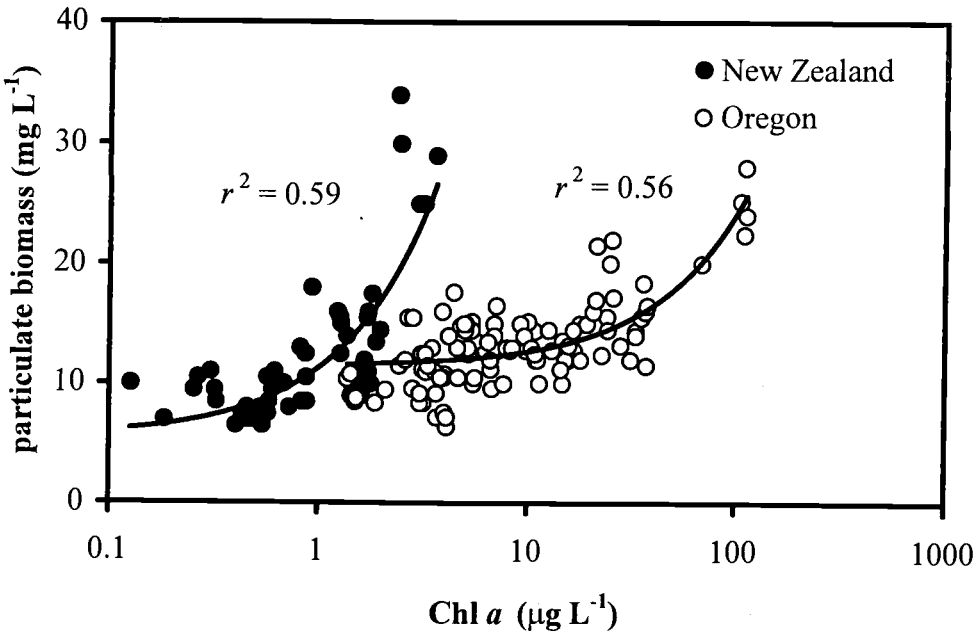

Figure 2.3. Particulate biomass associated with Chl a at sites in New Zealand and Oregon. Each datum represents particulate and Chl a analyses from a single water bottle. Because maximum Chl a concentrations at Oregon-coast sites were two orders of magnitude higher than maximum concentrations in New Zealand, the x-axis is presented on a logarithmic scale. This makes the linear regressions of particulates on Chl a appear curved.

Mussel Growth and Ammonium Excretion Rates

After accounting for mussel initial mass, growth rates varied with site in both New Zealand ($F_{3,247}$=44.31, P<0.0001) and Oregon ($F_{3,547}$=97.12, P<0.0001) (Fig. 2.5). Highest growth rates occurred at WB in New Zealand and at SH in Oregon, while lowest growth rates were measured at TM in New Zealand and at CB in Oregon. These results did not agree with simple patterns of phytoplankton or particulate availability. In New Zealand, for example, TM (where the lowest growth rates were measured) was the site with highest Chl *a* and particulate concentrations (Fig. 2.2).

Table 2.1. Attributes of the seston at sites in New Zealand and Oregon.

Site	C:Chl a ($\mu g\ \mu g^{-1}$)		$\delta^{13}C$ (‰)	
	Mean (±SE)	Range	Mean (±SE)	Range
New Zealand				
Woodpecker Bay	1226 (±133)	718 to 2258	-25.6 (±0.4)	-27.8 to -22.9
Twelve Mile	1852 (±190)	756 to 3288	-26.9 (±0.1)	-28.0 to -26.1
Raramai	1122 (±127)	607 to 2320	-23.1 (±0.4)	-24.7 to -20.7
Box Thumb	719 (±59)	415 to 1174	-23.5 (±0.2)	-24.6 to -22.1
Oregon				
Boiler Bay	138 (±14)	70 to 272	-22.0 (±0.2)	-23.6 to -20.5
Strawberry Hill	133 (±25)	58 to 401	-19.6 (±0.4)	-22.6 to -18.0
Cape Arago	159 (±21)	86 to 282	-22.5 (±0.1)	-23.3 to -22.0
Cape Blanco	147 (±24)	69 to 332	-20.6 (±0.3)	-22.8 to -19.4

Similarly, in Oregon, CB had relatively high Chl *a* and particulate concentrations and low rates of mussel growth.

This conundrum was resolved by evaluating the simultaneous influences of particulate and Chl *a* concentrations on mussel growth rates (Table 2.2). This analysis allowed us to consider the effects of phytoplankton availability, after accounting for initial mussel mass and organic particulate concentrations. It similarly allowed us to address the influences of increasing particulate concentrations, after accounting for mass and Chl *a*. In both New Zealand and Oregon, growth rates increased with increasing phytoplankton availability (New Zealand: $F_{1,248}$=51.21, P<0.0001; Oregon: $F_{1,548}$=34.30, P<0.0001) and decreased with increasing particulate concentrations (New Zealand: $F_{1,248}$=79.95, P<0.0001; Oregon: $F_{1,548}$=18.09, P<0.0001). This

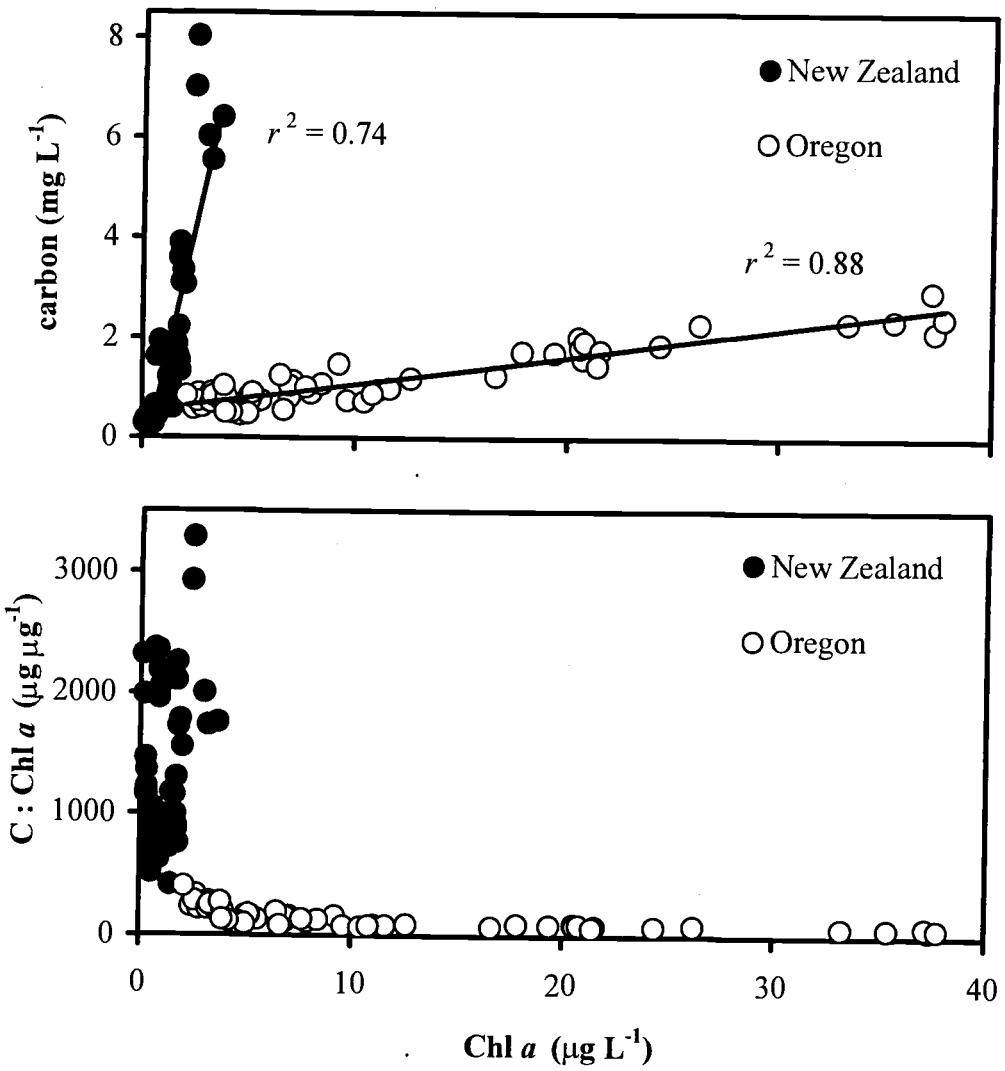

Figure 2.4. Relationships between Chl *a* and particulate organic carbon (POC) in New Zealand and Oregon. Each datum represents POC and Chl *a* analyses from a single water bottle. New Zealand waters were relatively low in Chl *a* and high in POC, while Oregon waters were relatively high in Chl *a* and low in POC.

contrasting influence of phytoplankton and particulate availability on mussel growth is suggested by the estimates of parameters in the general linear model (Table 2.2). These indicate the direction and magnitude of the effect on the growth rate associated

with a unit increase in the corresponding explanatory variable. This model suggests that sites with relatively higher Chl *a* concentrations can have relatively lower growth rates, if the sites differ sufficiently in total particulate concentrations. For example, while the mean Chl *a* concentration was higher at CB (14.5 μg L^{-1}) than at BB (7.8 μg L^{-1}), the model predicts a lower mussel growth rate at CB because of the negative influence of particulates.

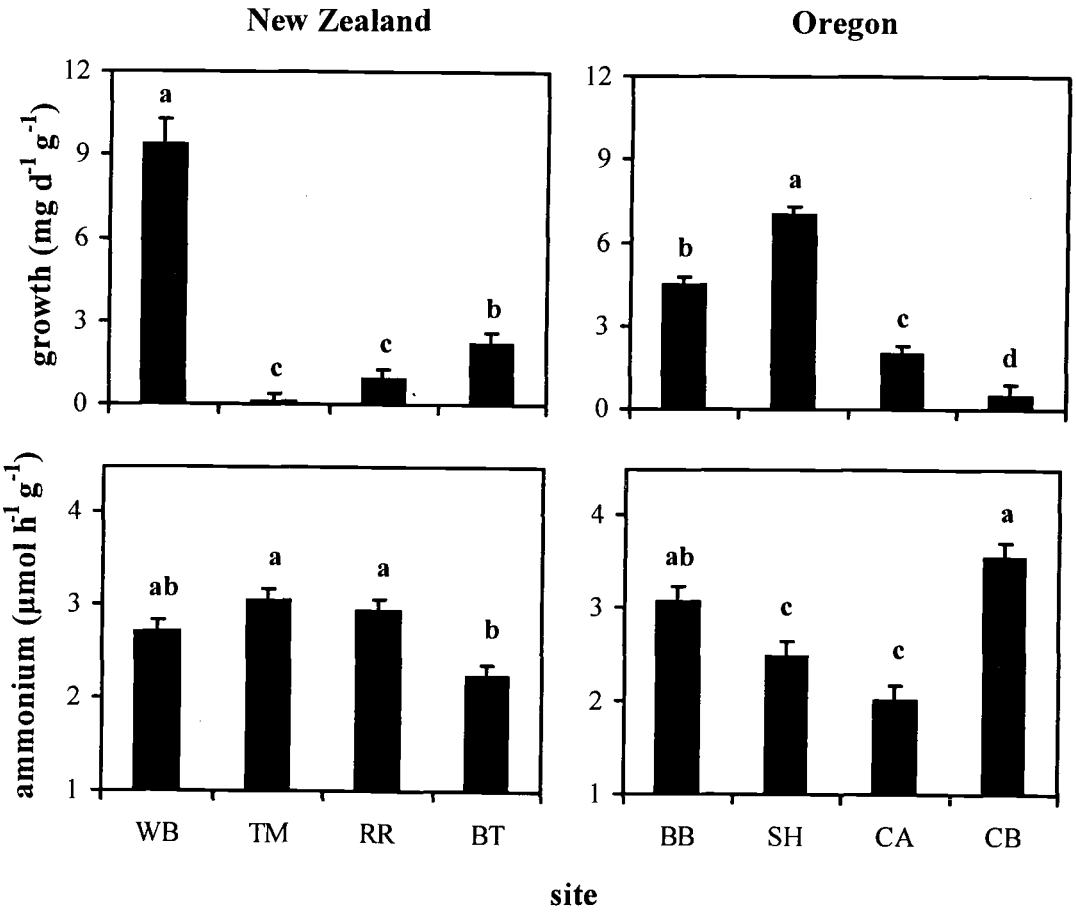

Figure 2.5. Growth and ammonium excretion rates of mussels at sites in New Zealand and Oregon. Values are least-squares means (+1 SE), after accounting for mussel mass, of all samples taken during the austral summer of 2001-02 (New Zealand) and the boreal summer of 2001 (Oregon). Letters indicate significant differences among site least-squares means ($P < 0.05$) after Bonferroni adjustment.

Table 2.2. Influences of nearshore particulate and Chl *a* concentrations on mussel growth rates in New Zealand and Oregon.

(a) New Zealand

Source of Variation	df	MS	Parameter Estimates	*F*	*P*
Mass	1	23.85	-3.04	97.44	<0.0001
Chl *a*	1	12.54	+0.76	51.21	<0.0001
Particulates	1	19.57	-1.04	79.95	<0.0001
Error	248	0.24			

(b) Oregon

Source of Variation	df	MS	Parameter Estimates	*F*	*P*
Mass	1	11.47	-1.30	27.75	<0.0001
Chl *a*	1	14.17	+0.04	34.30	<0.0001
Particulates	1	7.47	-0.22	18.09	<0.0001
Error	548	0.41			

A similar analysis, using site mean growth rates instead of individual growth rates, supported these trends. After accounting for particulates, increases in phytoplankton availability were associated with increased growth, though the low sample size (n=4 sites) and consequent lack of statistical power prohibited statistical significance (New Zealand: $F_{1,2}$=0.46, P=0.57; Oregon: $F_{1,2}$=5.61, P=0.14). After accounting for Chl *a*, increases in particulates were associated with declines in mussel growth. However, these reductions in growth were also not statistically significant, due to low sample size (New Zealand: $F_{1,2}$=0.14, P=0.74; Oregon: $F_{1,2}$=0.08, P=0.80).

Mussel ammonium excretion rates also varied with site (New Zealand: $F_{3,231}$=8.63, P<0.0001; Oregon: $F_{3,257}$=16.47, P<0.0001; Fig. 2.5), and they were similarly unrelated to simple patterns of phytoplankton and organic particulate availability (Fig. 2.2). For example, while mussels at both TM and RR (in New Zealand) had high ammonium excretion rates, those sites had contrasting patterns of particulate and phytoplankton availability. Both Chl *a* and particulates were high at TM and low at RR. In Oregon, mussels at CA and SH had similar ammonium excretion rates, but differing patterns of nearshore Chl *a* and particulates.

As in the previous analysis of growth, this situation was clarified by simultaneously analyzing the influences of particulates and Chl *a* on ammonium excretion rates (Table 2.3). After accounting for mussel mass, ammonium excretion rates decreased with increasing Chl *a* concentrations (New Zealand: $F_{1,232}$=30.31, P<0.0001; Oregon: $F_{1,258}$=31.07, P<0.0001) and increased with increasing particulate concentrations (New Zealand: $F_{1,232}$=18.05, P<0.0001; Oregon: $F_{1,258}$=69.75). Thus, after accounting for mussel mass and Chl *a*, sites with higher concentrations of particulate biomass had higher ammonium excretion rates and lower growth rates. Conversely, after accounting for mussel mass and particulate biomass, sites with higher concentrations of Chl *a* had lower ammonium excretion rates and higher growth rates.

We verified these patterns by evaluating the relationship between overall mean ammonium excretion rates and corresponding mean seston attributes. As in the above analysis of growth, low sample sizes (n=4) usually resulted in a failure to show

Table 2.3. Influences of nearshore particulate and Chl *a* concentrations on mussel ammonium excretion rates in New Zealand and Oregon.

(a) New Zealand

Source of Variation	df	MS	Parameter Estimates	*F*	*P*
Mass	1	111.49	-6.74	162.40	<0.0001
Chl *a*	1	20.81	-0.74	30.31	<0.0001
Particulates	1	12.39	+0.07	18.05	<0.0001
Error	232	0.69			

(b) Oregon

Source of Variation	df	MS	Parameter Estimates	*F*	*P*
Mass	1	65.32	-4.17	33.94	<0.0001
Chl *a*	1	59.80	-0.22	31.07	<0.0001
Particulates	1	134.24	+0.24	69.75	<0.0001
Error	258	1.92			

statistically significant results, but a similar pattern was observed. After accounting for total organic particulates, increases in Chl *a* were associated with decreases in the ammonium excretion rate (New Zealand: $F_{1,2}$=1.60, P=0.33; Oregon: $F_{1,2}$=2.28, P=0.27). Conversely, after accounting for Chl *a*, increases in particulates were associated with increases in the ammonium excretion rate (New Zealand: $F_{1,2}$=13.19, P=0.07; Oregon: $F_{1,2}$=21.46, P=0.04).

Stable Isotope Analyses

Mean carbon isotopic signatures of mussels ranged from -18.7‰ to -17.8‰ in New Zealand and from -17.5‰ to -16.9‰ in Oregon. While New Zealand mussels were more ^{13}C-depleted than Oregon mussels ($F_{1,16}$=143.28, P<0.0001), the isotopic signatures of the two geographic regions overlapped, so that the signatures of RR (in New Zealand) and BB (in Oregon) were statistically indistinguishable (ANOVA: Bonferroni-adjusted P>>0.05). Seston mean isotopic signatures were more variable than those of mussels (ranging from -26.9‰ to -23.1‰ in New Zealand and from -22.4‰ to -19.6‰ in Oregon; Table 2.1), and a similar pattern emerged: seston organic particulates were more ^{13}C-depleted in New Zealand than in Oregon ($F_{1,16}$=76.14, P<0.0001).

Because the carbon isotopic signature of a consumer reflects the signature of its food, we used these data to evaluate consumption of the seston by benthic filter feeders. While the isotopic signatures of the mussels varied with those of the seston ($\delta^{13}C$ mussels = [0.23 x $\delta^{13}C$ seston] - 12.42; $F_{1,6}$=10.57, P=0.0174, r^2=0.64), the slope (0.23) was significantly shallower than the 1:1 relationship predicted if the mussels were integrating all organic carbon in the seston (ANCOVA test of actual vs. predicted slope: $F_{1,12}$=115.86, P<0.0001). This suggested that the mussels were selecting for a more isotopically enriched food source as the seston $\delta^{13}C$ became more depleted.

We evaluated this possibility by examining the changes in the isotopic signatures of the seston and mussels as seston quality decreased (Fig. 2.6). We used

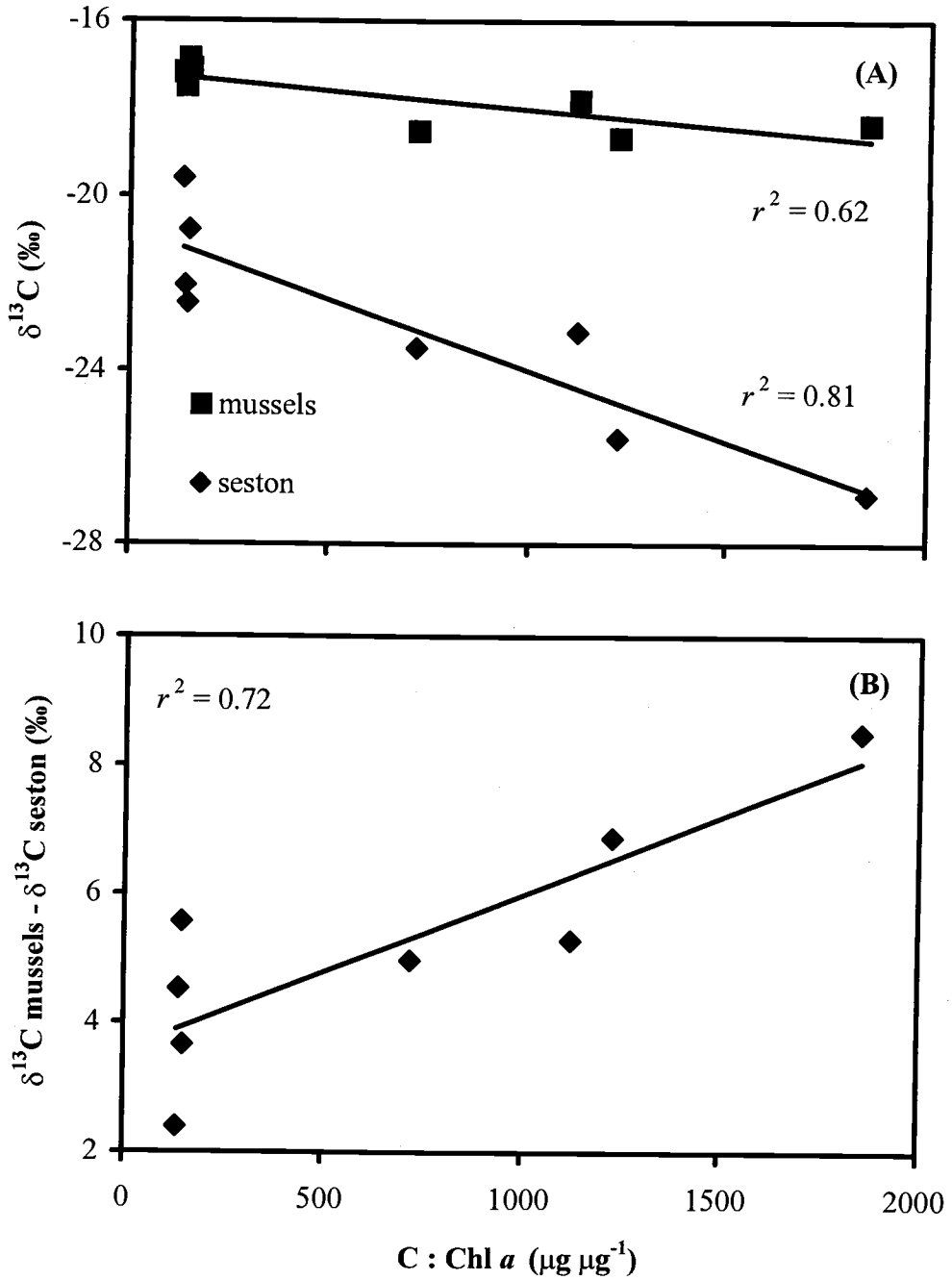

Figure 2.6. Dietary selectivity by *Mytilus* spp. As the carbon-to-chlorophyll ratio increases, seston quality decreases. This decrease in quality was associated with deviation of the carbon isotopic signature ($\delta^{13}C$) of the mussels from that of the seston. (A) As C:Chl *a* increased, the $\delta^{13}C$ of the seston decreased more quickly than that of the mussels. (B) Similarly, as C:Chl *a* increased, the difference between the mussel and seston isotopic signatures increased. Values are overall site means.

the carbon-to-chlorophyll ratio (C:Chl *a*) as a proxy for seston quality; as C:Chl *a* increases, more of the seston is dominated by detritus, a lower-quality food source for benthic filter-feeding invertebrates. As C:Chl *a* increased, the $\delta^{13}C$ of the seston decreased. This trend was consistent in Oregon ($F_{1,52}$=11.39, P=0.0014), in New Zealand ($F_{1,58}$=45.56, P<0.0001), and overall ($F_{1,111}$=108.87, P<0.0001). To address benthic-pelagic coupling, we compared the mean stable-isotope signatures of the mussels and seston collected at each site. As C:Chl *a* increased, the $\delta^{13}C$ of both the mussels ($F_{1,6}$=9.97, P=0.0196) and the seston ($F_{1,6}$=25.66, P=0.0023) decreased. However, the difference between the $\delta^{13}C$ signatures of the mussels and seston increased as C:Chl *a* increased. Similarly, the slope of the relationship between $\delta^{13}C$ and C:Chl *a* for the seston was significantly steeper than the slope for the mussels ('C:Chl *a* x sample type' interaction: $F_{1,12}$=12.19, P=0.0045; Table 2.4), indicating deviation of the carbon isotopic signature of the seston from that of the mussels as seston quality decreased.

Table 2.4. General linear model evaluating the effects of food quality (C:Chl *a*) on mussel and seston carbon stable-isotope ($\delta^{13}C$) signatures.

Source of Variation	df	MS	*F*	*P*
C:Chl *a*	1	25.23	34.63	<0.0001
Sample type (mussels, seston)	1	22.68	31.12	0.0001
C:Chl *a* x Sample type	1	8.88	12.19	0.0045
Error	12	0.73		

Discussion

Seston Quality and Quantity

As predicted, large-scale oceanographic differences were associated with major disparities in nearshore productivity. In this study, we evaluated pelagic phytoplankton availability along three coastlines with contrasting oceanographic regimes: the California Current system off the Oregon coast (strong, intermittent upwelling), the Westland Current system off the west coast of New Zealand's South Island (weak, intermittent upwelling), and the Southland Current system off the South Island's east coast (persistent downwelling). During the boreal upwelling season of April through October 2001, California Current sites were characterized by mean monthly Bakun indices (obtained from the Pacific Fisheries Environmental Laboratory, Pacific Grove, California; http://www.pfeg.noaa.gov) ranging from +60.1 to +163.2 $m^3 s^{-1} 100 m^{-1}$, indicating net offshore transport of water at all sites. During the austral upwelling season of October 2001 through April 2002, monthly Bakun indices at Westland Current sites ranged from -42.2 to +74.3 $m^3 s^{-1} 100 m^{-1}$, suggesting transitions between upwelling and downwelling. Finally, at Southland Current sites, upwelling indices during the same period (October 2001 through April 2002) were uniformly indicative of downwelling, ranging from -7.4 to -45.4 $m^3 s^{-1} 100 m^{-1}$. Mean Chl *a* concentrations were associated with upwelling intensity: highest concentrations were measured along the Oregon coast (~19.5 $\mu g L^{-1}$), lower concentrations along the west coast of the South Island (WB and TM; ~1.7 $\mu g L^{-1}$),

and lowest concentrations along the east coast of the South Island (RR and BT; ~0.5 $\mu g\ L^{-1}$) (Fig. 2.2).

Within those large-scale oceanographic regimes, sites (~65 to 220 km apart) differed in nearshore phytoplankton concentrations, likely due to mesoscale hydrographic variation associated with continental-shelf and coastline topography. For example, in New Zealand, Chl *a* concentrations were consistently higher at BT than at RR, though both sites were within the Southland Current downwelling region (Fig. 2.2). This difference, which has persisted since our sampling at those sites began in 1999 (B. Menge et al., *unpublished data*), appears to be associated with an eddy in the Southland Current, which forms in the lee of the Banks Peninsula, a large headland just to the south of the BT site (Carter and Herzer 1979). In Oregon, all four sites differed with respect to Chl *a* concentrations: lowest concentrations were measured at CA, followed by BB, CB, and SH, respectively (Fig. 2.2). In general, these differences have persisted since 1994 (Menge *et al.* 1997a), and support the assertions that (1) an onshore meander associated with increasing continental-shelf width creates a phytoplankton-retention region in the nearshore ocean adjacent to SH (Menge *et al.* 1997a) and (2) the formation of an offshore jet at CB results in enhanced upwelling at that site (Strub *et al.* 1991, Dale and Barth 2001).

Although differences were more subtle than those observed with respect to Chl *a* concentrations, mesoscale variation was also apparent in the availability of total organic particulates at the sites (Fig. 2.2). In New Zealand, particulate concentrations were higher at TM than at WB, though no differences were observed between east-

coast sites. In Oregon, total mean particulate concentrations were indistinguishable at BB, CA, and CB; the only significant variation was associated with relatively higher particulate concentrations at SH. What is striking about our measurements of particulate biomass is the overlap between oceanographic regimes: TM in the Westland Current system was equivalent to the most productive site (SH) in Oregon, and BT and RR in the Southland Current downwelling regime were comparable to BB and CA in Oregon. Thus, while phytoplankton concentrations appeared to be associated with large-scale oceanographic differences, total particulate concentrations were not.

To address this disparity, we evaluated differences between Oregon and New Zealand seston quality. First, while total particulate biomass was associated with phytoplankton concentrations in both Oregon and New Zealand, the slopes of that relationship differed between the two: there was considerably more particulate biomass associated with a given quantity of phytoplankton in the waters off New Zealand (Fig. 2.3). Second, the carbon-to-chlorophyll ratios measured at New Zealand sites were incredibly high, averaging 1229.8 (±173.9 SE) $\mu g\ \mu g^{-1}$ and ranging from about 400 to 3300 $\mu g\ \mu g^{-1}$ (Fig. 2.4; Table 2.1). Carbon-to-chlorophyll ratios for phytoplankton range from approximately 25 to 250 $\mu g\ \mu g^{-1}$ (Parsons *et al.* 1977). Taken together, these characteristics suggest that the New Zealand seston was largely dominated by detritus.

What was the origin of this detrital material? There are three distinct possibilities: (1) dead phytoplankton material, (2) macroalgal particulates, and (3)

terrestrial inputs. Each of these possible sources has a distinct carbon stable-isotope ($\delta^{13}C$) signature: literature values for phytoplankton in temperate coastal waters range from approximately -22.7‰ to -19.1‰ (Richard *et al.* 1997, Maksymowska *et al.* 2000), signatures for laminarian kelps and kelp detritus range from -17.7‰ to -12.0‰ (Duggins *et al.* 1989, Bustamante and Branch 1996), and signatures for terrestrially derived particulate organic material range from -31.3‰ to -25.5‰ (Richard *et al.* 1997, Maksymowska *et al.* 2000). The high C:Chl *a* of the New Zealand seston samples, their relatively depleted $\delta^{13}C$ signatures (-24.7‰ ± 0.3‰ SE; Table 2.1), and the steep decline in the seston $\delta^{13}C$ with increasing C:Chl *a* (Fig. 2.6) all point to terrestrial detritus as an important constituent of New Zealand's nearshore seston.

In contrast, our Oregon seston samples, with their relatively lower carbon-to-chlorophyll ratios (50 to 400 $\mu g\ \mu g^{-1}$; Table 2.1) and enriched carbon stable-isotope signatures (-21.1‰ ± 0.2‰ SE; Table 2.1) suggest that the Oregon nearshore seston was more phytoplankton-dominated. While the absolute quantity of organic material in the Oregon and New Zealand seston was similar, the constituents of the seston in Oregon and New Zealand were very different. However, even in Oregon, periodic measurements of C:Chl *a* >250 $\mu g\ \mu g^{-1}$ and a decline in the seston $\delta^{13}C$ with increasing C:Chl *a* suggest that terrestrial detritus is occasionally an important component of the seston.

Mussel Growth and Ammonium Excretion Rates

We exploited these geographic differences in seston quality (Oregon vs. New Zealand) and mesoscale differences in both seston quantity and quality to evaluate the influences of seston quantity and quality on benthic-pelagic coupling in temperate coastal ecosystems. We accomplished this by correlating aspects of mussel physiology (growth and ammonium excretion rates) with the above-described qualitative and quantitative attributes of the seston.

While there was clear mesoscale variation in both growth and ammonium excretion rates of mussels (Fig. 2.5), this variation did not correspond with simple patterns of particulate and phytoplankton availability. Therefore, we employed general linear models, which evaluated the simultaneous influences of mussel mass (a necessary covariate), total particulate concentration, and Chl *a* concentration on mussel growth and ammonium excretion rates. This allowed us to evaluate the influences of total particulate availability, after accounting for the effects of mussel mass and Chl *a* and, similarly, to examine the influences of phytoplankton availability, after accounting for mussel mass and particulates.

In both Oregon and New Zealand, after accounting for mass, mussel growth rates increased with increasing phytoplankton concentrations and decreased with increasing particulate concentrations (Table 2.2). Thus, this model predicts that if particulate concentrations remain constant, increasing Chl *a* will increase mussel growth. Conversely, if Chl *a* remains constant, increasing organic particulates will decrease mussel growth. It is important to note, however, that statistically significant

results were only observed when individual mussels were treated as the experimental units. Because Chl *a* and organic particulates could only be measured at the site scale, the most appropriate dependent variable in this model is the mean growth rate from each site. This analysis resulted in a severe loss of statistical power, and a consequent failure to show statistically significant results. However, the same trends were evident, suggesting that increasing the number of sites could allow us to make inferences at that scale.

While the positive association between phytoplankton availability and mussel growth is intuitive, reflecting mussels' dietary preference for phytoplankton (Ward *et al.* 1997), the reasons for the decline in growth associated with increasing total organic particulate concentrations are less obvious. As they filter-feed, mussels actively select from suspended particles, preferentially retaining high-quality phytoplankton and rejecting lower-quality refractory and inorganic material (Ward *et al.* 1997, Hawkins *et al.* 1998). However, this process is not perfect; mussels feeding on lower-quality food have reduced efficiency in the digestion and absorption of ingested particles. For example, net absorption efficiencies of *Mytilus edulis* vary from -56% to +54%, becoming negative (more organics are lost in the feces than are absorbed) when phytoplankton make up <10% of the seston, by mass (Bayne and Hawkins 1990). The reduction in growth associated with increasing total particulates, after accounting for Chl *a*, may reflect increased metabolic costs associated with selective feeding and the reduced absorption efficiency of lower-quality food.

An opposite pattern emerged with respect to the influences of Chl *a* and organic particulates on mussel ammonium excretion rates: after accounting for mass, ammonium excretion decreased with increasing phytoplankton concentrations and increased with increasing organic particulate concentrations (Table 2.3). Again, we verified these trends by examining the effects of mean Chl *a* and organic particulates on mean ammonium excretion rates. While the reduced sample size (n=4) resulted in statistically insignificant results, we observed the same patterns with respect to the influences of phytoplankton and detritus, suggesting that expanding the number of sites could allow us to make stronger inferences at that scale.

Increases in Chl *a* (after accounting for total organic particulates) are associated with increases in growth and reductions in ammonium excretion, while increases in particulates (after accounting for Chl *a*) are associated with decreases in growth and increases in ammonium excretion. This appears to reflect a trade-off between assimilation and excretion: phytoplankton carbon and nitrogen are readily assimilated, promoting growth, while detrital carbon and nitrogen are less readily assimilated, resulting in increased ammonium excretion rates. The decline in the $\delta^{13}C$ as C:Chl *a* increased, which we observed in both New Zealand and Oregon, suggests that as seston quality decreased, terrestrial detritus became an increasingly important component of the seston in both geographic regions. Terrestrially derived detrital material is composed largely of lignin and cellulose, and is therefore indigestible by benthic filter feeders (Mann 1988). However, terrestrial detritus is readily colonized by bacteria, and this bacterial "coating" is an important source of protein for mussels

and other filter feeders (Newell and Field 1983). Use of protein as an energy source (*e.g.,* when labile carbon is limiting) is associated with increased rates of ammonium excretion by *Mytilus* (Bayne and Scullard 1977). We hypothesize that as the seston became increasingly dominated by detritus (*i.e.,* the concentration of total particulates increased, after accounting for Chl *a*), mussels increasingly relied on catabolism of bacterial protein for energy, resulting in increased ammonium excretion rates.

Stable Isotope Analyses

We used carbon stable-isotope signatures of mussels and seston collected at each site to explicitly evaluate the trophic linkages between pelagic and benthic systems. Because there is little carbon-isotopic fractionation (<1‰) associated with trophic level, examining the relationship between the $\delta^{13}C$ signatures of a consumer and its putative prey can give an indication of the actual consumption of that prey resource (Peterson and Fry 1987). In our case, while the isotopic signatures of the mussels and seston were correlated, the slope of the relationship between them (0.23) was significantly less than 1, which suggested that the mussels were selecting for a more isotopically enriched food source as the seston $\delta^{13}C$ became more depleted.

This was clarified by our evaluation of the relationship between food quality (C:Chl *a*) and the carbon-isotopic signatures of the mussels and seston. The difference between the $\delta^{13}C$ signatures of the mussels and seston increased as the food became more dominated by detritus (Fig. 2.6; Table 2.4). While New Zealand mussels were more depleted than Oregon mussels, the overall range of mussel $\delta^{13}C$ signatures

(-18.7‰ to -16.9‰) was consistent with a combination of phytoplankton (-22.7‰ to -19.1‰) (Richard *et al.* 1997, Maksymowska *et al.* 2000) and macroalgal detritus (-17.7‰ to -12.0‰) (Duggins *et al.* 1989, Bustamante and Branch 1996). As C:Chl *a* increased, and the seston was more dominated by refractory terrigenous particulates, mussel diets universally reflected more edible food sources: phytoplankton and macroalgal detritus.

Summary

Especially in nearshore ecosystems, where refractory terrigenous material can be an important constituent of the seston, the total concentrations of either organic particulates or Chl *a* may not independently predict trophic linkages between pelagic and benthic systems. Instead, it is necessary to simultaneously address both phytoplankton and total particulate availability to understand the fluxes of materials from the nearshore ocean into benthic communities. Thus, our results highlight the necessity of considering both the quantity and the quality of the seston in evaluating benthic-pelagic coupling.

CHAPTER 3

DIVERSITY OF INTERTIDAL MACROALGAE INCREASES WITH NITROGEN LOADING BY INVERTEBRATES

Abstract

Understanding the relationship between productivity and diversity is a fundamental issue in ecology. Evidence suggests that the relationship is scale-dependent: diversity is a unimodal function of productivity at large scales, but local-scale nutrient enrichment generally results in decreased diversity due to displacement of subordinate species by aggressive competitors. Unlike most studies, where nutrients are added in excess of ambient levels, we examined the effects of reduced nutrients and their subsequent replacement *via* local-scale nutrient loading. Macroalgae in Oregon-coast tide pools have evolved in a nitrate-replete upwelling ecosystem, but instead of settling on low-zone reefs (where algae are often immersed in nutrient-rich nearshore waters) those individuals have colonized high-zone pools, where they are isolated from the ocean for nearly 80% of the time and are thus subjected to severe nitrate limitation. While high-intertidal pools were typically emersed for nearly 13 hours during each tidal cycle, oceanic nitrate was completely eliminated from pools *via* uptake after only 7 hours of isolation. In many pools, this nutrient stress was ameliorated by a positive interaction: the excretion of ammonium as a waste product

by invertebrates. Variation in the volumes of tide pools and the biomasses of invertebrates in those pools created a gradient of local-scale nutrient inputs, allowing us to address the relationship between nitrogen loading and diversity. A four-fold increase in the rate of ammonium loading was associated with a doubling in the number of macroalgal species in pools as slow-growing species tolerant of low nitrogen availability were supplemented by fast-growing species with higher nitrogen requirements. Our data suggest that the effect of enrichment on diversity is context-dependent. Each ecosystem has a critical level of nutrient availability, determined by the level of nutrients typically available in that system. Below this critical level, adding nutrients increases diversity, but above it, diversity declines with enrichment.

Introduction

Humans impact both the productivity of ecosystems and the diversity of species in those systems. The rate of anthropogenic nitrogen fixation is more than twice that of natural processes (Vitousek 1994), and extinction rates are increasing worldwide, primarily as a result of habitat destruction (Pimm *et al.* 1995). Given evidence suggesting that the relationship between productivity and diversity is reciprocal—that diversity both affects and is affected by productivity (Naeem 2002)—understanding diversity, productivity, and their relationship is both a scientific and a societal concern.

However, the influence of increasing productivity on the diversity of organisms in an ecosystem is unclear. Both theory and experimental evidence suggest that diversity can be an increasing (Connell and Orias 1964, Hall *et al.* 2000), a decreasing (Riebesell 1974, Tilman 1987), or a unimodal (Leibold 1999, Kassen *et al.* 2000, Chase and Leibold 2002) function of productivity. Most experimental increases in productivity (*via* addition of limiting nutrients) result in declines in macrophyte diversity, due to domination by aggressive competitors (Gough *et al.* 2000). Rosenzweig (1995) argues that this "paradox of enrichment" occurs because the assemblage of autotrophs inhabiting an ecosystem are adapted to coexist at that system's typical level of productivity. Adding nutrients to the system predictably destabilizes this coexistence, reducing the number of species. How can this be reconciled with the intuitive fact that a nutrient-poor environment cannot meet the needs of certain rare species and should therefore have lower diversity (Wright *et al.* 1993)? Ideally, this question could be addressed by experimentally reducing nutrient availability to levels below the norm. However, while it is relatively simple to add nutrients to natural assemblages of species, it is far more difficult to remove them.

Intertidal pools provide a unique solution to this dilemma. On the Oregon coast, where we conducted our research, tide pools contain assemblages of macroalgae adapted to a high productivity ecosystem: nitrate levels in the adjacent coastal ocean often exceed 20 μmol/L (Fujita *et al.* 1989, Menge *et al.* 1997a). However, instead of settling on low-intertidal reefs, where macroalgae are frequently immersed in nutrient-rich water, tide pool algae have colonized the upper reaches of the intertidal zone,

where they are isolated from oceanic inputs of new nitrogen (sensu Dugdale and Goering 1967) for extended periods of time. High-zone pools contain many of the same species found lower in the intertidal zone (Johnson and Skutch 1928, M. Bracken, personal observation), but individuals in the pools live in a much less productive microhabitat. Because high-intertidal pools are nutrient-poor microhabitats within a nutrient-replete ecosystem, we were functionally able to quantify the influences of reduced nutrient availability on diversity.

Invertebrates also live in tide pools, and their nitrogenous excretory products provide a potential local-scale nutrient source for macroalgae (Jensen and Muller-Parker 1994). Invertebrates may thereby have a positive effect on macroalgae by reducing the stress associated with nutrient limitation in high-intertidal pools. Variation in both the volumes of Oregon-coast tide pools and the biomasses of invertebrates in them created a natural gradient of local-scale nutrient inputs into pools.

Below, we describe manipulations and measurements that quantified the excretion of ammonium by invertebrates in tide pools, the utilization of that excreted ammonium as a nitrogen source by macroalgae, and the consequent association between ammonium loading and algal diversity. Based on these experiments, we propose a general hypothesis for the relationship between nutrient availability and macroalgal diversity.

Materials and Methods

Site and Tide Pool Characteristics

Studies were conducted at three sites on the coast of Oregon, USA: Boiler Bay (44°50.0'N, 124°03.7'W; hereafter BB), Strawberry Hill (44°15.3'N, 124°06.7'W; SH), and Bob Creek (44°14.7'N, 124°06.7'W; BC). BB is characterized by broad mudstone reefs in which tide pools were chiseled for a previous experiment (Nielsen 2001). Because of the pools' recent origin and the rapidly eroding mudstone substrate, they were not colonized by mussels (K. Nielsen, *unpublished data*), and experimental removals of herbivores resulted in low overall invertebrate biomasses. At SH and BC, flat reefs extended into the high-intertidal zone. Natural tide pools in the reefs contained substantial biomasses of both invertebrates (primarily *Mytilus californianus* Conrad) and macroalgae.

The volume of each pool at SH and BC (n=10 at each site) was determined by siphoning its water into a graduated bucket. A flexible mesh 'quadrat' (Foulweather Trawl Supply, Newport, Oregon) was spread over the bottom of each pool and used to calculate surface area, and all macroalgae were identified to species. Censuses, water sampling, and experimental manipulations were conducted in June 2000 at SH and in July 2002 at BC.

Nitrogen Limitation in High-Zone Tide Pools

Because the presence of invertebrates can confound measurement of nitrate depletion due to oxidation of invertebrate-excreted ammonium by nitrifying bacteria (M. Bracken, *unpublished data*), in June 1996 we evaluated macroalgal depletion of nitrate in six pools at BB which had low ratios of invertebrate biomass to pool volume (g/L). Water samples were collected from each pool at 0.0, 2.6, and 5.4 h after isolation by the receding tide. Samples were filtered through a Whatman GF/F glass-fiber filter, transported to the laboratory on ice, and stored at -20°C prior to analysis. Nitrate concentrations were determined on a spectrophotometer after reduction with cadmium and addition of sulfanilamide and NEDA to form an azo dye (Parsons *et al.* 1984).

Emersion durations of tide pools at SH and BC were calculated by determining, by observation, the time at which the ebbing tide isolated the pools, then using tide-prediction software (Tides & Currents for Windows™ v. 2.5b, Nautical Software, Inc., Beaverton, Oregon) to determine the heights of the pools above mean lower-low water. The same software was used to calculate the duration of each time those pools were emersed between January 1, 2000 and December 31, 2002.

Ammonium Fluxes in High-Zone Tide Pools

Water samples (1 ml) were taken from each SH and BC tide pool at intervals after the receding tide isolated the pools, and the concentration of ammonium in each

sample was determined using the phenol-hypochlorite method (Solórzano 1969). SH pools were emersed 2.3 to 3.8 h before sunrise (depending on the day), and samples were taken at -1, 0, 1, and 2 h before and after sunrise. Additionally, a sample was collected from each SH pool as it was isolated by the falling tide. At BC, pools were isolated during the afternoon, and samples were taken 0, 1, 2, and 4 h after pool emersion. Sampling and manipulations were conducted over the course of three days at each site. On day one, we measured ammonium fluxes in intact pools. Then we removed all macroalgal biomass from each pool. On day two, we again measured ammonium fluxes in each pool. We then removed all invertebrates from the pools. Finally, on day three, we measured ammonium concentrations in the absence of both invertebrates and macroalgae. The ash-free dry masses of all invertebrate and macroalgal tissues from each pool were determined for calculation of mass-normalized ammonium excretion and uptake rates based on the measurements described above. Based on these measurements, the rate of ammonium loading into the pools was defined as the ammonium accumulation rate ($\mu mol\ L^{-1}\ h^{-1}$) in the absence of macroalgae.

Ammonium Uptake Experiments

Individuals of two algal species, *Prionitis lanceolata* Harvey and *Ulva californica* Wille (n=15 each), were collected from a single high-intertidal pool at BC. They were rinsed with seawater to remove sediment and epiphytes and maintained

overnight in a 40 μm-filtered running seawater system on a simulated sunrise and sunset cycle prior to uptake measurements.

Each algal thallus was placed in an acid-washed glass beaker containing 100 ml of filtered seawater. Ammonium (NH_4Cl) was added to each beaker so that individual seaweeds were supplied with initial concentrations of ammonium ranging from 2 to 60 μmol/L. While most protocols indicate that water circulation is necessary (Harlin and Wheeler 1985), our beakers were not stirred, to simulate the still-water conditions in tide pools. Beakers were illuminated by full-spectrum fluorescent lamps, which provided 77.4 (±1.2 SE) μmol quanta m^{-2} s^{-1} photosynthetically active radiation. Water samples (1 ml) were collected from each beaker at 0.0 and 0.5 h and analyzed for ammonium using the phenol-hypochlorite method (Solórzano 1969). Each thallus was then removed and dried to constant mass at 50°C. The change in each beaker's ammonium concentration over the 30-minute incubation period was divided by the dry tissue mass to evaluate the biomass-specific uptake rate of each individual (μmol h^{-1} g^{-1}) as a function of the initial ammonium concentration.

Statistical Analyses

Analyses were performed using general linear models and *t*-tests in the SAS System for Windows v. 8 (SAS Institute, Inc., Cary, North Carolina). General linear models included analyses of variance (ANOVA) and repeated-measures ANOVA. The assumption of normality was verified for *t*-tests by calculating the Shapiro-Wilk and Kolmogorov-Smirnov statistics for each distribution. The assumptions of normality

and homogeneity of variances were verified for each general linear model by visually examining residual plots and normal probability plots of the residuals. In many cases, it was necessary to log-transform ($\log_{10}[x]$ or $\log_{10}[x + 1]$) the data to meet the ANOVA assumptions. We used $\log_{10}$-transformations for consistency with the Arrhenius equation ($\log_{10}S = z\log_{10}A + \log_{10}c$) generally used to evaluate species-area relationships (Arrhenius 1921, Preston 1960).

Results

Nitrogen Limitation in High-Intertidal Pools

We evaluated the potential for nitrogen limitation in tide pools by measuring the depletion of nitrate in six pools at BB which contained low biomasses of invertebrates (0.5±0.1 SE g/L). Nitrate concentrations in the nearshore ocean were high (27.2±2.7 SE μmol/L), but macroalgal uptake reduced nitrate concentrations at a rate of 4.1 (±0.3 SE) μmol L^{-1} h^{-1}, so nitrate was completely exhausted from the pools 7.2 (±0.9 SE) hours after isolation by the receding tide. The pools at SH and BC, which are at a height of 2.1 (±0.2 SE) m above mean lower-low water, were isolated from the ocean for an average duration of 12.8 (±0.2 SE) hours during each emersion, with occasional isolations of up to 4.7 days during neap-tide periods. Algal biomasses (g/L) in the SH and BC pools were similar to those at BB ($F_{2,23}$=2.43, P=0.1105), so we assumed that depletion of nitrate from those pools would occur by approximately 7.2 h after isolation. Therefore, in the absence of invertebrates, macroalgae in high-

zone pools at SH and BC would be without nitrogen for 5.6 (±0.2 SE) hours during each emersion. They would therefore spend an appreciable fraction (~35%) of time in a severely nitrogen-depleted environment.

Ammonium Fluxes in Tide Pools

Sequential removals of macroalgae and invertebrates affected the concentrations of ammonium in tide pools at SH (Fig. 3.1); similar patterns were

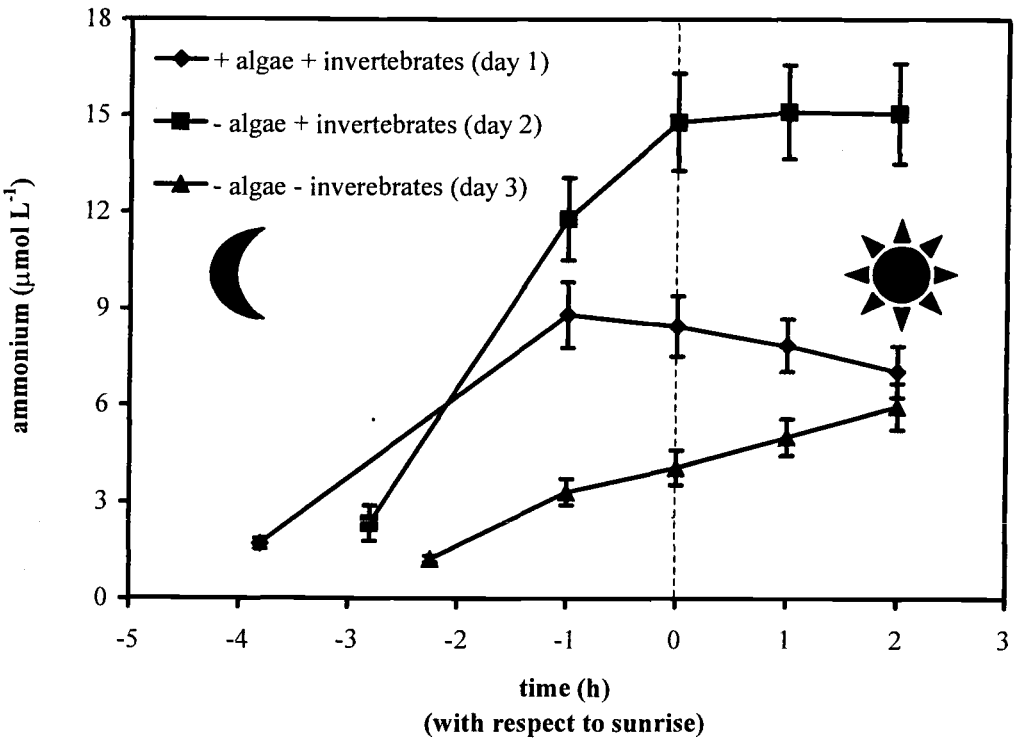

Figure 3.1. Sequential removals of macroalgae and invertebrates influenced ammonium concentrations in SH tide pools (n=10). Mean ammonium concentrations (±SE) were determined at -1, 0, 1, and 2 hours before and after sunrise, and an initial sample was taken as the receding tide isolated each pool. Removals were conducted after each day's measurements, and treatments consisted of +algae, +invertebrates (day 1); -algae, +invertebrates (day 2); and -algae, -invertebrates (day 3). The accumulation of ammonium in the -algae, -invertebrates treatment was associated with a failure to completely remove invertebrates from those treatments.

observed at BC. After accounting for site differences, removal of macroalgae increased ammonium accumulation rates by 3.8 (±0.6 SE) μmol L^{-1} h^{-1} (repeated-measures ANOVA: $F_{1,18}$=99.76, P<0.0001), and subsequent removal of invertebrates decreased ammonium accumulation rates by 3.4 (±0.6 SE) μmol L^{-1} h^{-1} (repeated-measures ANOVA $F_{1,18}$=81.24, P<0.0001). We used these ammonium fluxes and the biomasses of macroalgae and invertebrates removed from the pools to calculate biomass-specific excretion and uptake rates. Invertebrates excreted ammonium into the pools at a rate of 0.5 (±0.1 SE) μmol h^{-1} g^{-1} (t=4.4, df=19, P=0.0003), and macroalgae took up that excreted ammonium at a rate of 1.8 (±0.3 SE) μmol h^{-1} g^{-1} (t=5.4, df=19, P<0.0001). Ammonium loading in tide pools increased with increasing invertebrate biomass per volume (g/L) ($F_{1,17}$=5.70, P=0.0289).

Ammonium Loading and Macroalgal Diversity

Our surveys of macroalgal species in those pools allowed us to address the relationship between ammonium loading and macroalgal diversity. Eleven species of macroalgae were present: six Rhodophytes (*Farlowia mollis*, *Mastocarpus papillatus*, *Mazzaella splendens*, *Odonthalia floccosa*, *Polysiphonia hendryi*, and *Prionitis lanceolata*); three Heterokontophytes (*Fucus gardneri*, *Pelvetiopsis limitata*, and *Soranthera ulvoidea*); and two Chlorophytes (*Cladophora columbiana* and *Ulva californica*) (see Scagel et al. 1993 for authorities).

More macroalgal species were found in pools with higher rates of ammonium loading (Fig. 3.2a). After accounting for site differences and the potential influence of

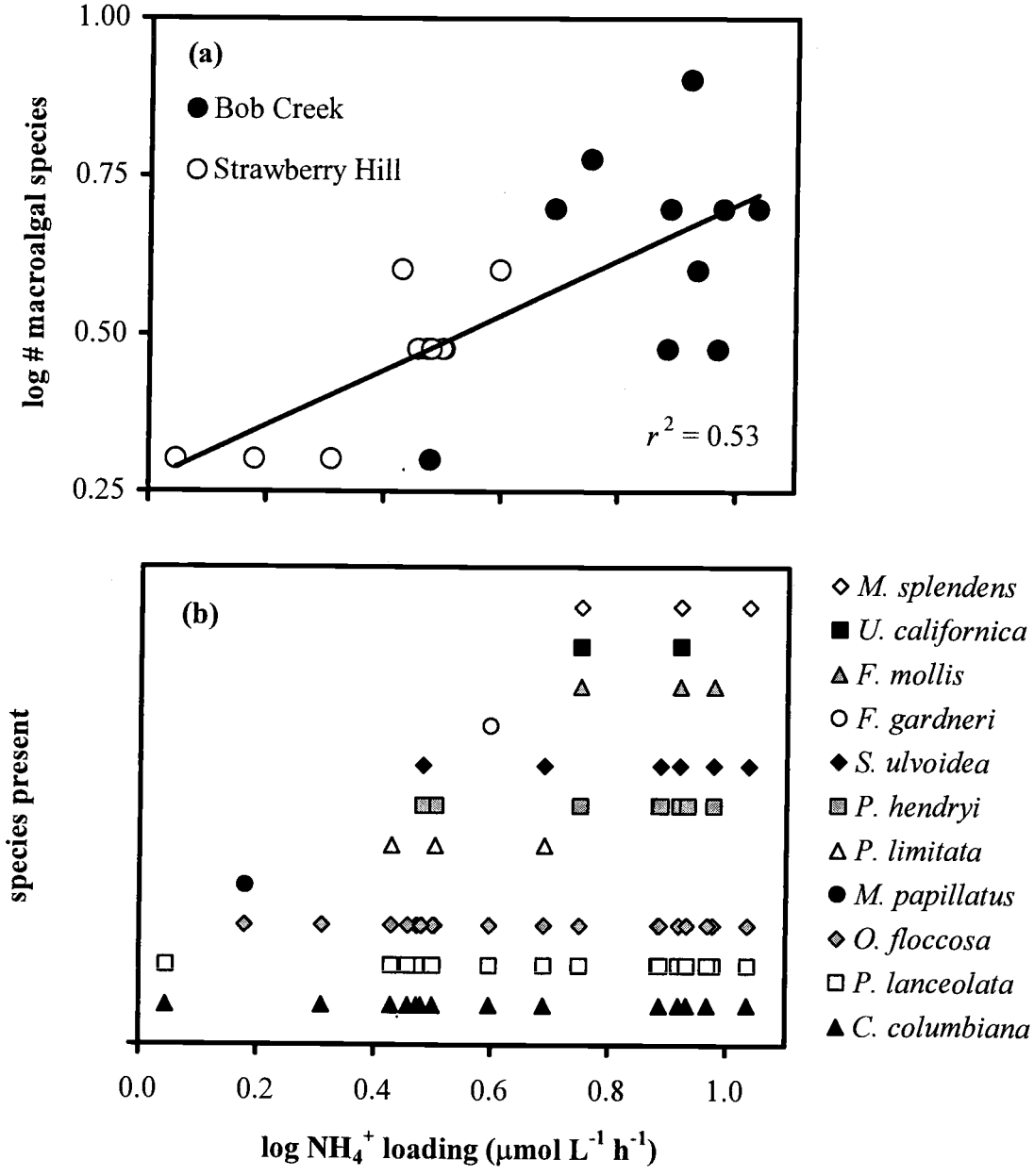

Figure 3.2. The number of macroalgal species increased with ammonium loading in tide pools. (a) More species were found in pools with higher rates of ammonium accumulation. (b) This increase in species richness with ammonium loading was primarily associated with the presence of additional species in pools with higher ammonium accumulation rates.

Table 3.1. Ammonium loading influences the number of macroalgal species in tide pools.

Source of Variation	df	MS	Parameter Estimates	*F*	*P*
Site	1	0.02	-0.11	0.22	0.6453
Surface area	1	0.03	0.20	0.37	0.5490
Ammonium loading	1	0.64	0.49	7.70	0.0135
Error	16	0.08			

pool surface area on species richness, a four-fold increase in the rate of ammonium loading was associated with a doubling in the number of macroalgal species (P=0.0135; Table 3.1). This increase in species richness was primarily additive: species present in pools with low ammonium loading rates (*e.g., C. columbiana*, *P. lanceolata*, and *O. floccosa*) were also present in pools with high ammonium loading rates, and new species (*e.g., P. hendryi*, *S. ulvoidea*, *F. mollis*, *U. californica*, and *M. splendens*) occurred as ammonium loading rates increased (Fig. 3.2b).

As the number of macroalgal species increased in tide pools, the ammonium uptake rate of their combined biomass increased (Fig. 3.3). After accounting for differences between SH and BC, a two-fold increase in the number of species was associated with a 50% increase in the biomass-specific ammonium uptake rate (ANOVA: $F_{1,17}$=6.61, P=0.0199). This suggested that the additional species present at high nitrogen loading rates might have a greater capacity for uptake. We investigated this possibility by comparing the ammonium uptake rates of *U. californica*, which was found only in pools with high rates of ammonium accumulation, and *P. lanceolata*,

which occurred in pools with both low and high ammonium loading rates (Fig 3.4). Both species' biomass-specific uptake rates increased with increasing ammonium concentrations ($P<0.0001$), but the uptake rate of *U. californica* increased 3.6 times more rapidly than that of *P. lanceolata* ('ammonium x species' interaction: $P=0.0001$; Table 3.2), indicating that *U. californica* was capable of higher uptake rates than *P. lanceolata* at higher ammonium concentrations.

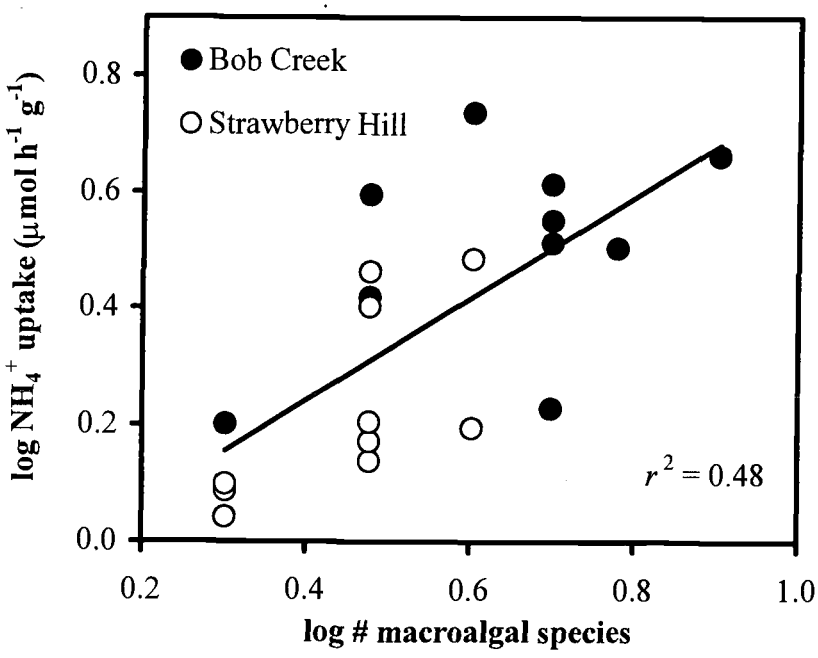

Figure 3.3. The efficiency of ammonium uptake increased with the number of macroalgal species in tide pools. Biomass-specific ammonium uptake rates were higher in pools with more species.

Discussion

Nitrogen Limitation in High-Intertidal Pools

Rocky intertidal ecosystems in the northeastern Pacific are remarkably productive. During the summer months, coastal upwelling transports nitrate-rich water to the surface, resulting in mean daily nitrate concentrations of 16.1 (±1.3 SE) μmol/L in the nearshore ocean immediately adjacent to SH and BC, with maximum concentrations in excess of 30 μmol/L (K. Nielsen and B. Menge, *unpublished data*). However, high-zone tide pools are nutrient-poor microhabitats within the nutrient-replete Oregon coast intertidal ecosystem.

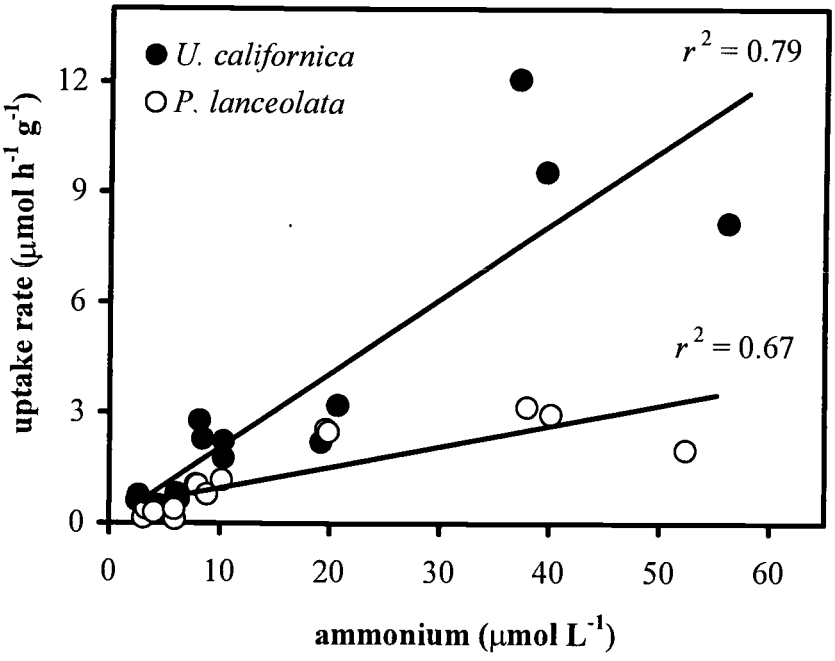

Figure 3.4. Ammonium uptake rates of tide pool macroalgae. Biomass-specific uptake rates of *Ulva californica* and *Prionitis lanceolata* were measured across a range of ammonium concentrations. As the ammonium concentration increased, the uptake rate of *U. californica* increased more quickly than that of *P. lanceolata*.

Table 3.2. Analysis of variance in ammonium uptake by *U. californica* and *P. lanceolata*.

Source of Variation	df	MS	Parameter Estimates	*F*	*P*
Species	1	0.51	0.38	0.28	0.5986
Ammonium	1	114.82	0.20	63.18	<0.0001
Species x ammonium	1	37.05	-0.15	20.39	0.0001
Error	25	1.82			

Oceanic nitrate is rapidly depleted from pools during tidal emersion. We evaluated the uptake of nitrate by macroalgae in BB pools, and found that nitrate concentrations declined linearly with time, becoming exhausted after about seven hours of isolation from the ocean. High-zone pools at SH and BC were typically emersed for 12.8 (±0.2 SE) hours at a time, substantially longer than the estimated time required for complete draw-down of all oceanic nitrate. Thus, macroalgae living in high-intertidal pools are subjected to extended periods of nitrogen limitation. This contrasts sharply with the nitrogen environment experienced by the same species living on emergent surfaces lower on the shore, where macroalgae are isolated from their nitrogen supply for an average of only one to four hours per day.

Ammonium Fluxes in Tide Pools

Nutrient stress in high-zone pools was ameliorated by a positive interaction: the excretion of ammonium by invertebrates living in the tide pools and the utilization of that ammonium as a nitrogen source by macroalgae (Fig. 3.1). Positive interactions

between species, where one or both participants benefit, tend to occur when biotic or abiotic conditions are stressful (Bertness and Callaway 1994). One species modifies the conditions responsible for the stress, allowing the other species to persist in an environment where it would not have thrived without the intervention of its benefactor. These interactions are particularly important in the rocky intertidal zone, where organisms are subjected to stresses such as heat, desiccation, and nutrient limitation during tidal emersion (Thomas *et al.* 1987, Bertness and Leonard 1997). In the case of high-zone pools, retention of seawater eliminates desiccation stress, allowing low-zone macroalgae to exist higher on the shore. However, those algae are then susceptible to nutrient stress, which can be reduced by local-scale ammonium excretion. A gradient in ammonium loading ranging from 1.1 to 10.9 $\mu mol\ L^{-1}\ h^{-1}$, associated with variation in pool volume and invertebrate biomass, allowed us to quantify the positive influence of invertebrates on macroalgal diversity.

Ammonium Loading and Macroalgal Diversity

More macroalgal species occurred in pools with higher rates of invertebrate-excreted ammonium loading (Fig. 3.2). This pattern contrasts with the results of most local-scale studies of nutrient enrichment, especially in terrestrial systems, where adding nutrients generally decreases the number of macrophyte species (Tilman 1987, Gough *et al.* 2000). We suggest that this disparity reflects a unimodal relationship between diversity and productivity, which is usually only seen on regional scales (200-4000 km): increasing productivity is associated with increasing diversity to a point,

after which diversity declines as productivity continues to increase (Tilman and Pacala 1993, Mittelbach *et al.* 2001). Nutrient enrichments of intact communities often begin at the hump's peak, because the assemblage of species at a particular location has adapted to coexist at that location's level of productivity. Adding nutrients perturbs this coexistence, promoting the growth of aggressive competitors and leading to declines in diversity (Rosenzweig 1995).

High-intertidal pools, on the other hand, are nitrate-limited microhabitats within a nitrate-rich ecosystem. The species found in high-zone pools represent only a subset of the species found on emergent substrata lower on the shore, where more frequent immersion is associated with increased nutrient availability. Thus, in moving from low-intertidal reefs to high-intertidal pools, macroalgae are subjected to a reduction in nutrient availability, and we see an associated decline in diversity. In effect, this natural experiment illustrates the effect of local-scale nutrient depletion on diversity.

Surveys of low- and mid- intertidal macroalgae at SH and BC suggest that approximately 15 species can coexist in the nutrient-rich low-shore environment (G. Allison, M. Kavanaugh, S. Wood & S. Etchemendy, *unpublished data*). The number of species in high-zone pools at SH and BC ranged from 2 to 8, depending on the rate of ammonium loading. We hypothesize that as nutrient availability increases in the pools, the number of species has the potential (in the absence of strong herbivory; see Worm 2002) to increase until it approximates the richness observed lower in the intertidal zone. Beyond a certain point, however, nutrient availability will exceed the

maximum natural level of the system, and the addition of nutrients will lead to domination by fast-growing ephemeral species, resulting in declines in richness (Duarte 1995).

At higher rates of ammonium loading, polysiphonous and thin foliose species such as *Polysiphonia hendryi*, *Farlowia mollis*, and *Ulva californica* occurred in pools (Fig 2b). The addition of these species, which are characterized by high ammonium uptake rates (Pedersen and Borum 1997, Campbell 2001), was associated with increases in the rates of biomass-specific nitrogen uptake by the macroalgal assemblages in the pools (Fig. 3.3). Especially in pools characterized by high rates of ammonium accumulation, where ammonium concentrations reached ~25 μmol/L, uptake rates of ephemeral, fast-growing species such as *U. californica* could be nearly three times higher than uptake rates of slow-growing species such as *Prionitis lanceolata* (Fig. 3.4). However, at lower ammonium concentrations (<14.6 μmol/L), the biomass-specific uptake rates of *U. californica* and *P. lanceolata* were indistinguishable. While *P. lanceolata* occurred in pools spanning the observed range of ammonium loading rates and concentrations, *U. californica* was only found in pools where ammonium concentrations exceeded ~15 μmol/L.

In general, increases in nutrient availability result in shifts from communities dominated by slow-growing macroalgal species, which are tolerant of low nutrient levels, to communities characterized by fast-growing species, which require high nutrient concentrations (Pedersen and Borum 1997, Middelboe and Sand-Jensen 2000). Imagine a two-species system composed of one slow-growing species and one

fast-growing species. At low levels of nutrient availability, only the slow-growing species can occur. As nutrient availability increases, both species coexist for a time, but eventually the higher growth and uptake rates of the fast-growing species lead to its dominance and the local extinction of the slow-growing species. This simple heuristic model, supported by our data (the shift from slow-growing species to a mixed assemblage of slow- and fast-growing species) and typical ecosystem responses to eutrophication (the shift from a mixed assemblage of species to one dominated by fast-growing ephemeral macroalgae) (reviewed in Duarte 1995), produces a unimodal relationship between nutrient loading and species richness.

Thus, the effects of local-scale nutrient additions on diversity appear to be context-dependent. When nutrients are limiting, nutrient additions can increase diversity. However, adding nutrients to a nutrient-replete system promotes the growth of aggressive competitors, reducing diversity. This is analogous to the unimodal relationship between consumer abundance and diversity demonstrated by Lubchenco (1978), which resolved contradictions between experiments suggesting that removing consumers could increase (e.g., Paine and Vadas 1969, Hillebrand 2003) or decrease (e.g., Paine 1966, Porter 1972) the diversity of resource species. In the case of consumer-mediated diversity patterns, the unimodal relationship requires selective consumption of the competitively dominant prey: resource-species diversity is highest at intermediate consumer densities because consumers are abundant enough to prevent overgrowth by competitive dominants, but not so abundant as to eliminate them. Similarly, the unimodal relationship between nutrient loading and macroalgal diversity

relies on species' differences in growth and nutrient uptake. Diversity peaks at intermediate nutrient availability because nutrient levels are sufficient to permit existence of fast-growing species with high nutrient requirements, but low enough to prohibit their domination.

Summary

In high-zone tide pools, the excretion of ammonium by invertebrates ameliorated nutrient limitation, and was associated with increases in the number of macrophyte species. This contrasts with most local-scale descriptions of the productivity-diversity relationship (but see Chase and Leibold 2002), where experimental nutrient additions lead to declines in richness, because nutrient availability exceeds the level to which the macrophyte assemblage is accustomed. Together, these patterns support our hypothesis that the unimodal relationship between productivity and diversity, widely observed at the regional level, can also occur at smaller scales, if local-scale heterogeneity in nutrient availability creates nutrient-limited microhabitats within an ecosystem.

CHAPTER 4

NITROGEN LOADING BY INVERTEBRATES INCREASES GROWTH OF INTERTIDAL MACROALGAE

Abstract

Even within nitrogen-replete ecosystems, microhabitats exist where local-scale nutrient limitation occurs. For example, coastal waters of the northeastern Pacific Ocean are characterized by high nitrate concentrations associated with upwelling. However, macroalgae living in high-intertidal zone pools on adjacent rocky shores are isolated from that upwelled nitrate for extended periods of time, leading to nutrient limitation. When high-intertidal pools are isolated during low tide, invertebrate-excreted ammonium accumulates, providing a potential nitrogen source for macroalgae. I quantified the influence of mussels (*Mytilus californianus* Conrad) on ammonium accumulation rates in tide pools. I then evaluated the effects of ammonium loading by mussels on nitrogen assimilation and growth rates of *Odonthalia floccosa* (Esp.) Falkenb., a common red algal inhabitant of pools on northeastern Pacific rocky shores. *Odonthalia* was grown in artificial tide pool mesocosms in the presence and absence of mussels. Mesocosms were subjected to a simulated tidal cycle mimicking emersion and immersion patterns of high-intertidal pools on the central Oregon coast. In the presence of mussels, ammonium accumulated more quickly in the mesocosms, resulting in increased rates of nitrogen assimilation into algal tissues. These increased

nitrogen assimilation rates were primarily associated with higher growth rates: in mesocosms containing mussels, *Odonthalia* individuals added 41% more biomass than in mesocosms without mussels. This direct positive effect of mussels on macroalgal biomass represents a novel interaction between macroalgae and invertebrates. In nutrient-limited microhabitats, such as high-intertidal pools, invertebrate-excreted ammonium is likely an important local-scale contributor to macroalgal productivity.

Introduction

Bottom-up factors, such as nutrient availability, have received comparatively little attention from benthic marine ecologists (Menge 1992). However, by influencing macroalgal abundances, nutrients can have important effects on the structure and dynamics of nearshore and intertidal marine communities (Bosman *et al.* 1987, Wootton *et al.* 1996, Nielsen 2001, Worm *et al.* 2002). Understanding the sources and variability of nutrients is crucial to understanding the distributions and abundances of macroalgae, which can account for the majority of primary productivity in temperate coastal ecosystems (Newell 1984).

Inorganic nitrogen, a primary growth-limiting nutrient for algae in nearshore marine systems (Ryther and Dunstan 1971, Howarth 1988), exists in two forms: nitrate and ammonium. Most studies addressing the influence of nitrogen on open-coast macroalgae have focused on nitrate, because that is the form of nitrogen associated with oceanographic processes, such as upwelling, that transport nutrient-

rich water above the nutricline and make it available to algae in the photic zone. However, especially in oligotrophic waters, ammonium, excreted as a waste product by heterotrophs, is also an important nitrogen source for autotrophs (Eppley *et al.* 1973).

Biological oceanographers differentiate between "new production," primary production associated with nitrate upwelled or advected from beneath the nutricline, and "regenerated production," primary production that utilizes locally recycled nitrogen in the form of ammonium (Dugdale and Goering 1967). Whereas the majority of phytoplankton production in the world's oceanic and coastal ecosystems is fueled by regenerated nitrogen (Eppley and Peterson 1979), it is only recently that benthic ecologists have begun to address the influence of local-scale ammonium excretion on macroalgal productivity. Emerging evidence suggests that ammonium is an important nitrogen resource for temperate open-coast macroalgae (Fujita *et al.* 1989, Wheeler and Björnsäter 1992) and that sessile invertebrates, which often live in close association with macroalgae, can influence algal C:N ratios and growth (Hurd *et al.* 1994, Williamson and Rees 1994). However, many of the studies that link invertebrate-excreted ammonium and macroalgal growth have been conducted in oligotrophic regions, where nitrogen concentrations are low and ammonium makes up a large fraction of the available nitrogen. The question therefore remains: Is there an effect of invertebrate ammonium excretion on macroalgal growth in systems where nitrogen concentrations are not generally considered limiting?

In regions characterized by seasonal upwelling, including the northeastern Pacific's California Current system, the growth season of some macroalgal species occurs during the nitrate-limited winter and spring, not during the nitrate-replete May-to-October upwelling season (Lubchenco and Cubit 1980, Ruesink 1998). Even on the Oregon coast, where seasonal upwelling periodically elevates summer nitrate levels to >20 μmol L^{-1} (Fujita *et al.* 1989, Menge *et al.* 1997a), macroalgal growth can be nitrogen-limited (Fujita *et al.* 1989, Wheeler and Björnsäter 1992) and nitrate can be severely depleted from the water column (<2 μmol L^{-1}) for periods of several days (K. Nielsen and B. Menge, *unpublished data*).

Additionally, within the larger context of an upwelling ecosystem like the Oregon nearshore environment, there are nitrate-limited microhabitats. For example, macroalgae inhabiting high-intertidal pools are isolated from oceanic nitrate inputs for extensive periods of time, which may result in local-scale nutrient depletion. By experimentally adding nutrients (nitrogen and phosphorus) to Oregon-coast tide pools, Nielsen (2001) effected increases in macroalgal biomass, indicating that algae in those pools were potentially nutrient limited. By excreting ammonium into tide pools, invertebrates may ameliorate this nutrient limitation. Substantial biomasses of both macroalgae and sessile invertebrates typically inhabit high-intertidal pools on the Oregon coast, and invertebrate-excreted ammonium may be an important nitrogen source for the algae in these pools.

A common association in Oregon's high-intertidal pools consists of the branching red alga *Odonthalia floccosa* (Esp.) Falkenb. (Rhodophyta) (hereafter

Odonthalia) growing epizoically on shells of mussels (*Mytilus californianus* Conrad). This alga-invertebrate pairing provided a convenient unit for experimental evaluation of ammonium excretion by invertebrates and its assimilation by macroalgae. By manipulating the presence and absence of mussels in laboratory mesocosms, I quantified the influence of invertebrate-excreted ammonium on nitrogen assimilation and growth of *Odonthalia*.

Materials and Methods

Laboratory Mesocosms

I constructed an array of 32 tide pool mesocosms in four running seawater tanks (91 cm wide x 96 cm long x 15 cm deep) using eight 2.5 L plastic tubs per tank. To mimic the low-tide accumulation and high-tide flushing of ammonium in high-intertidal pools on the Oregon coast, I simulated a tidal cycle in the running seawater tables (Fig. 4.1). This was accomplished by using an overflow outlet just below the top of each tank and a controllable drain valve (Toro® 252-20 3.8 cm Pin-Type Hydraulic Valve) in the bottom of each tank. The valves were attached to a vacuum pump *via* a hydraulic line. Power to the vacuum pump was controlled by a digital timer programmed to mimic daily tidal fluctuations experienced at 2.25 m above mean-lower-low water on the central Oregon coast. The digital timer stored a one-week simulated tidal cycle, and it was programmed weekly according to the tidal model in

Tides & Currents for Windows™ v. 2.5b (Nautical Software, Inc., Beaverton, Oregon).

Each seawater tank was illuminated by eight 1.22 m full-spectrum fluorescent lamps. A combination of Hagen Power-Glo high-intensity aquarium lamps (Rolf C. Hagen Corp., Mansfield, Massachusetts) and GE wide-spectrum plant and aquarium

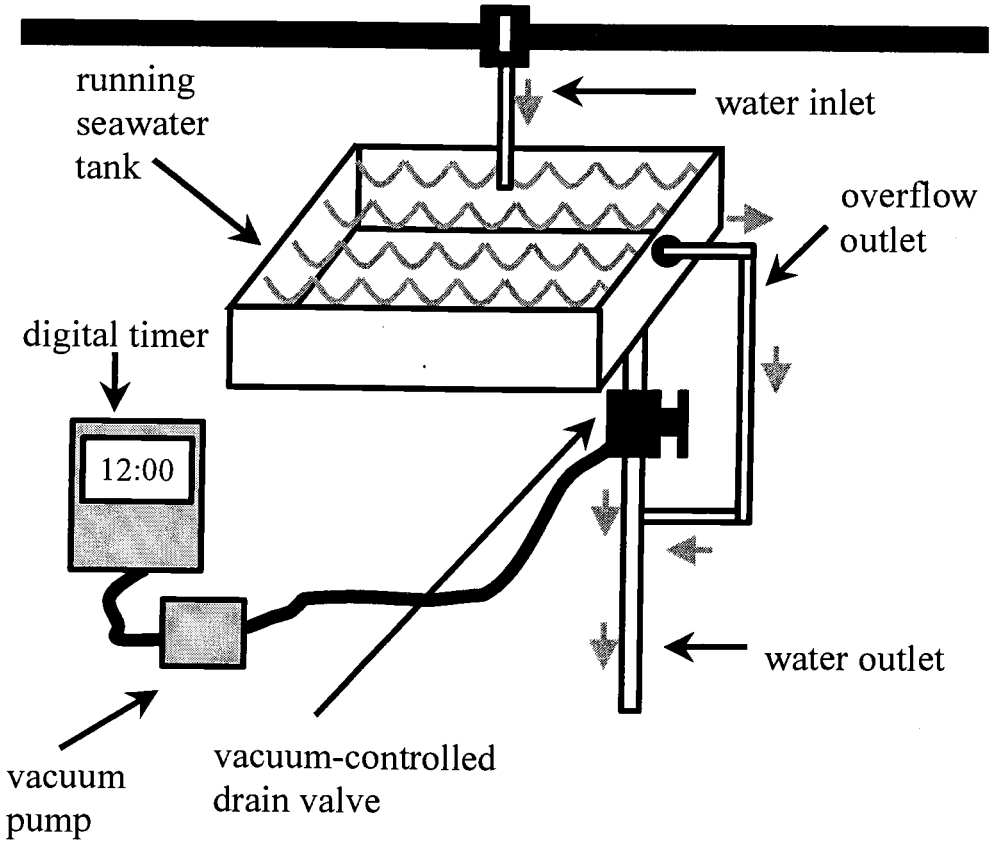

Figure 4.1. Simulating a tidal cycle in a running seawater tank. Filtered seawater enters the tank *via* the water inlet: When the vacuum-controlled drain valve is closed (vacuum off), water fills the tank and exits through the overflow outlet, simulating high tide. When the drain valve is open (vacuum on), water drains out of the tank, simulating low tide.

lamps (General Electric Co., Cleveland, Ohio) provided 77.4 ± 1.2 (mean±SE) μmol quanta m^{-2} s^{-1} photosynthetically active radiation. The entire apparatus (tanks and light fixtures) was shrouded in black plastic lined with reflective mylar to exclude outside light and decrease light loss. Lights were attached to a timer set to approximate a natural sunrise and sunset cycle, as growth of *Odonthalia* is highly dependent on season (Ruesink 1998).

Experimental Treatments

To evaluate the influence of mussel-excreted ammonium on growth and nitrogen assimilation of *Odonthalia*, mussels (*M. californianus*) with substantial epizoic biomasses of *Odonthalia* (2.6 ± 0.2 SE g dry algal tissue mass per mussel) were collected from tide pools ~2.25 m above mean-lower-low water at Neptune State Park on the central Oregon coast, U.S.A. (44°15'41"N, 124°03'57"W). Algae and mussels were rinsed with seawater to remove sediment and epiphytes and were maintained in the laboratory in a 40 μm-filtered running seawater system on a simulated natural sunrise and sunset cycle prior to experimental manipulations.

Three mussels were randomly assigned to each pool, and pools were randomly assigned (within each tank) to the following treatments: (a) +mussels, +phytoplankton; (b) +mussels, -phytoplankton; (c) -mussels, +phytoplankton; and (d) -mussels, -phytoplankton. *Odonthalia* were present in all treatments, attached to either live mussels or empty mussel shells. Treatments without mussels (-mussels) were prepared by dissecting the mussel tissue out of each shell. Phytoplankton were added to

+phytoplankton treatments to test the effects of feeding on mussel ammonium excretion and macroalgal growth. The phytoplankton consisted of cultured *Chaetoceros calcitrans* (Paulsen) Takano (Heterokontophyta, Bacillariophyceae) (courtesy of C. Langdon, Hatfield Marine Science Center, Newport, Oregon).

Introduction of nitrate from the f/2 culture medium into the experimental treatments was avoided by centrifuging phytoplankton in the culture medium, discarding the supernatant, and re-suspending the pellet in filtered seawater. *C. calcitrans* abundances in the re-suspended pellet were then quantified using a Coulter Counter and Coulter Channelyzer 256 (Coulter Electronics, Hialeah, Florida). Phytoplankton were added once each day to +phytoplankton treatments to bring the phytoplankton concentration to 10^5 cells ml^{-1} in each mesocosm.

Ammonium Concentrations and Fluxes

Ammonium fluxes in each experimental treatment were quantified at the experiment's beginning and end. Water samples (1 ml) were taken from each mesocosm at 0, 1, 2, and 4 h after emersion by the simulated receding tide, and the concentration of ammonium was determined using the phenol-hypochlorite method (Solórzano 1969). Ammonium loading into the mesocosms, defined as the rate of ammonium accumulation ($\mu mol\ L^{-1}\ h^{-1}$) in the absence of *Odonthalia*, was determined by removing the macroalgae from each pool at the end of the experiment. First, I measured ammonium concentrations in +*Odonthalia* pools, as described above. Then I removed the *Odonthalia* from each pool. On the following day, I measured changes in

ammonium concentrations after pool emersion. I then removed the live mussels (from +mussel treatments) and the empty mussel shells (from -mussel treatments). Finally, on the third day, I measured changes in ammonium concentration in the absence of both mussels and macroalgae. The mussel and macroalgal tissues from each mesocosm were dried to constant mass at 50°C for calculation of mass-normalized ammonium excretion and uptake rates based on the measurements described above.

The ammonium concentrations determined in the sequential removals were not statistically independent (they represented repeated samples in the same mesocosms over three days). Therefore, patterns of ammonium uptake and excretion were verified by collecting additional *Odonthalia* growing on mussels (as above) and preparing fully-factorial manipulations of seaweeds and invertebrates in the mesocosms. Mesocosms within each running seawater tank were randomly assigned to the following treatments: (1) +*Odonthalia*, +mussels; (2) +*Odonthalia*, -mussels; (3) -*Odonthalia*, +mussels; and (4) -*Odonthalia*, -mussels, for a total of n=8 mesocosms per treatment. As in the sequential removals, water samples were taken at 0, 1, 2, and 4 h after emersion by the simulated receding tide, and the ammonium concentration of each sample was determined.

Measurement of Algal Growth

The experiment was initiated on 10 April 2002, to coincide with *Odonthalia*'s natural growth cycle; thalli grow from January to June on northeastern Pacific shores (Ruesink 1998). At the beginning of the experiment I removed two *Odonthalia* thalli

from each mesocosm. One of these was randomly selected for determination of initial nitrogen content and frozen at -20°C. The other was weighed (blotted wet tissue mass), labeled by placing its base in a numbered clamp, and returned to the mesocosm. Blotted wet tissue masses of all labeled *Odonthalia* individuals were determined every two days for 24 days. At the termination of the experiment, both thalli from each pool (the one frozen on day 0 and the one monitored throughout) were dried to constant mass at 50°C. After the dry tissue mass of each thallus had been measured, samples were frozen in liquid nitrogen and powdered using a mortar and pestle. They were then analyzed for percent tissue nitrogen using a CHN Organic Elemental Analyzer (Exeter Analytical, North Chelmsford, Massachusetts) at the Analytical Laboratory, Marine Science Institute, University of California, Santa Barbara.

Nitrogen Assimilation by Odonthalia

Nitrogen accumulation in the algal tissues was calculated based on the percent tissue nitrogen values from each treatment (days 0 and 24) and the dry masses (dm) of each labeled individual on days 0 and 24. A regression relating blotted wet tissue mass and dry tissue mass for day 24 (dry tissue mass = 0.1646 x wet tissue mass; r^2=0.98) was used to back-calculate the dry tissue mass of each individual at day 0. Then, the per-mass nitrogen assimilation rate (μg h^{-1} g dm^{-1}) was calculated according to Eq. 4.1:

$$\text{N assimilation rate} = (10^6 \text{ mg g}^{-1}) \frac{\left(\left(M_{24}\frac{\%N_{24}}{100}\right)-\left(M_0\frac{\%N_0}{100}\right)\right)}{576\text{h}}(M_{24})^{-1} \quad (4.1)$$

where M_0 and M_{24} are the initial and final biomass (g dm), respectively, and $\%N_0$ and $\%N_{24}$ are the initial and final values for percent tissue nitrogen.

Statistical Analyses

Analyses were performed using the SAS System for Windows v. 8 (SAS Institute, Inc., Cary, North Carolina). Data were analyzed with general linear models, including analysis of variance (ANOVA) and repeated-measures ANOVA. The ANOVA assumptions of normality and homogeneity of variances were verified for each model by visually examining residual plots and normal probability plots of the residuals.

Five labeled *Odonthalia* individuals lost biomass during the course of the experiment and were statistical outliers, based on a regression of algal tissue nitrogen assimilation rates on rates of ammonium loading by mussels. These were therefore excluded from all analyses, giving final sample sizes of n=8 for the +mussels, +phytoplankton treatment; n=7 for the +mussels, -phytoplankton treatment; n=6 for the -mussels, +phytoplankton treatment; and n=6 for the -mussels, -phytoplankton treatment. Because the majority (4/5) of the algae which lost biomass were from -mussel treatments, excluding those samples actually provided a more conservative evaluation of the influence of mussels on *Odonthalia* growth.

Results

Experimental Treatments and Ammonium Fluxes

The presence of mussels was associated with increased ammonium accumulation rates in mesocosms, both at the beginning (day 0) and the end (day 24) of the experiment (repeated-measures ANOVA: 'time x mussels' interaction; $F_{3,60}$=60.76, p<0.0001 for day 0 and $F_{3,60}$=7.56, p=0.0002 for day 24; Table 4.1, Fig. 4.2). Ammonium accumulation rates at the beginning of the experiment were 3.96 (±0.44 SE) μmol L^{-1} h^{-1} higher when mussels were present, and accumulation rates at the end of the experiment were 1.21 (±0.65 SE) μmol L^{-1} h^{-1} higher when mussels were present. There was no influence of phytoplankton on ammonium accumulation rates ('time x phytoplankton' interaction; $F_{3,60}$=0.04, p=0.9647 for day 0 and $F_{3,60}$=0.6102, p=0.6102 for day 24; Table 4.1).

Phytoplankton did, however, influence overall ammonium concentrations at the experiment's end. The significant 'mussels x phytoplankton' interaction term ($F_{1,20}$=5.97, p=0.0239; Table 4.1b) indicates that when mussels were present, ammonium concentrations were higher when phytoplankton were also present. Conversely, when mussels were absent from mesocosms, ammonium concentrations were lower when phytoplankton were present.

Since phytoplankton had no effect on ammonium accumulation rates, ammonium fluxes in mesocosms were associated primarily with excretion by mussels and uptake by *Odonthalia*. Sequential removals of *Odonthalia* and mussels in +mussel

Table 4.1. Repeated-measures analysis of variance evaluating the effect of mussels and phytoplankton on ammonium accumulation in experimental mesocosms.

(a) Day 0

Source of Variation	df	MS	*F*	*P*
Between Subjects				
Mussels (+,-)	1	2,003.08	98.14	<0.0001
Phytoplankton (+,-)	1	0.34	0.02	0.8988
Mussels x Phytoplankton	1	1.12	0.05	0.8172
Tank[1]	3	106.48	5.22	0.0048
Error	20	20.41		
Within Subjects				
Time	3	677.85	134.86	<0.0001
Time x Mussels	3	305.40	60.76	<0.0001
Time x Phytoplankton	3	0.22	0.04	0.9647
Time x Mussels x Phytoplankton	3	1.27	0.25	0.7209
Time x Tank	9	19.47	4.19	0.0003
Error (Time)	60	5.03		

(b) Day 24

Source of Variation	df	MS	*F*	*P*
Between Subjects				
Mussels (+,-)	1	292.76	29.17	<0.0001
Phytoplankton (+,-)	1	5.35	0.53	0.4738
Mussels x Phytoplankton	1	59.93	5.97	0.0239
Tank[1]	3	56.44	5.62	0.0058
Error	20	10.03		
Within Subjects				
Time	3	131.59	30.08	<0.0001
Time x Mussels	3	33.06	7.56	0.0002
Time x Phytoplankton	3	2.68	0.61	0.6102
Time x Mussels x Phytoplankton	3	11.03	2.52	0.0662
Time x Tank	9	11.13	2.55	0.0151
Error (Time)	60	4.37		

[1]Because treatments were randomized within the running seawater tanks, "Tank" is included in the models.

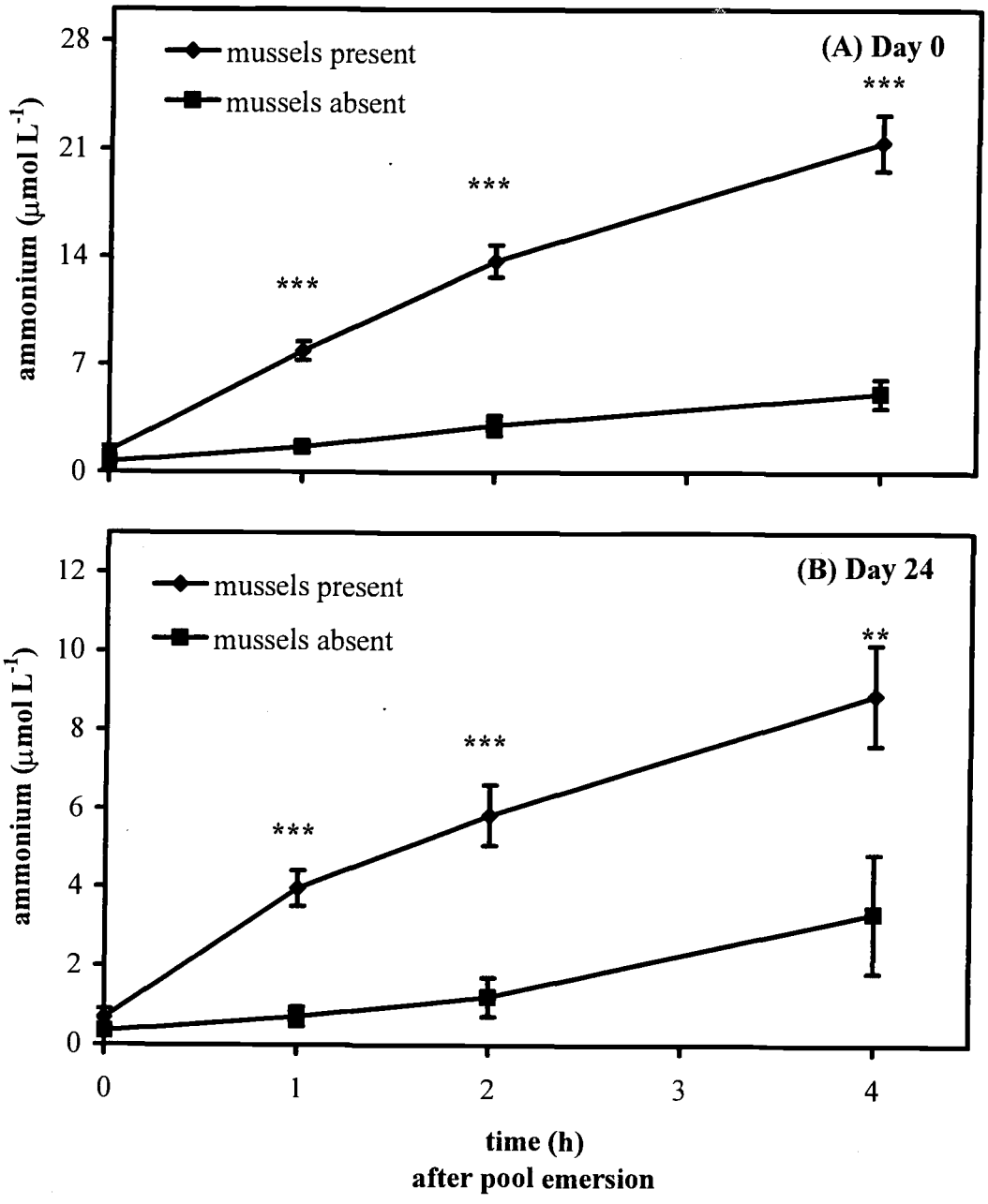

Figure 4.2. Influence of mussels on ammonium concentrations in mesocosms. While ammonium concentrations were higher at the beginning of the experiment (A) than at the end of the experiment (B), in both cases, the presence of mussels resulted in a significant increase in ammonium concentrations. Values are means (±SE), and asterisks indicate significant differences in ammonium concentrations at $P<0.01$ (**) and $P<0.001$ (***).

mesocosms revealed differences in ammonium accumulation rates associated with the presence and absence of macroalgae and invertebrates (ANOVA: $F_{2,39}$=115.41, p<0.0001; Fig. 4.3). Removal of *Odonthalia* increased the mean (±SE) ammonium accumulation rate by 2.38 (±0.31) μmol L^{-1} h^{-1} (ANOVA: Bonferroni-adjusted P<0.0001), and subsequent removal of mussels reduced the ammonium accumulation rate by 4.16 (±0.31) μmol L^{-1} h^{-1} (ANOVA: Bonferroni-adjusted P<0.0001). These differences in ammonium concentrations were associated with the removal of known

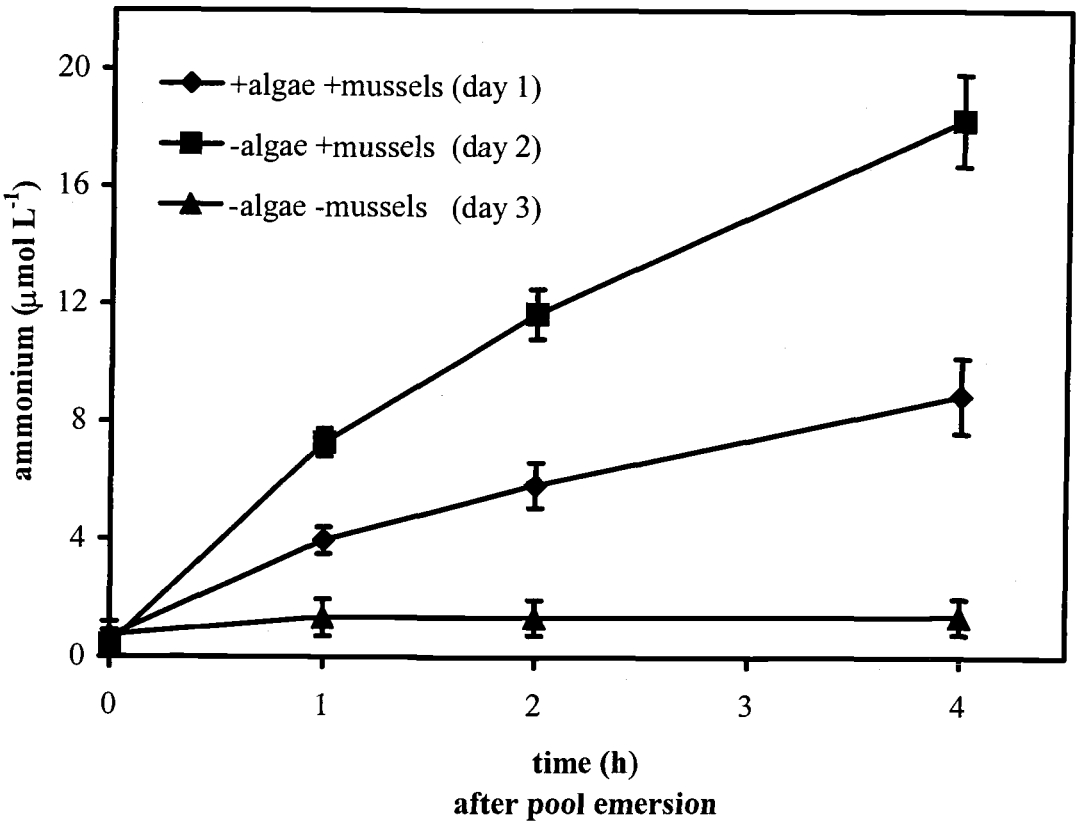

Figure 4.3. Ammonium fluxes in mescosms based on sequential removals of *Odonthalia* and mussels. Values are mean (±SE) ammonium concentrations (n=8 mesocosms), determined 0, 1, 2, and 4 hours after pool emersion. Removals were conducted after each day's trial, and treatments consisted of +algae, +mussels (day 1); -algae, +mussels (day 2); and -algae, -mussels (day 3).

quantities of *Odonthalia* and mussel biomass. Therefore, it was possible to calculate mass-specific uptake and excretion rates, based on changes in the ammonium fluxes (μmol h^{-1}) and on the dry tissue masses of *Odonthalia* and mussels. Thus, at the end of the experiment, mussels excreted ammonium into +mussel mesocosms at 0.31 (±0.02 SE) μmol h^{-1} g dm^{-1} (one-sample *t*-test: t=13.53, P<0.0001, df=14), and *Odonthalia* reduced the ammonium in those mesocosms *via* uptake at -0.76 (±0.07 SE) μmol h^{-1} g dm^{-1} (one-sample *t*-test: t=-10.19, P<0.0001, df=14).

Simultaneous manipulations of seaweeds and invertebrates revealed similar patterns to the sequential removals (Fig. 4.4). Ammonium accumulation rates were affected by the presence and absence of macroalgae and mussels (repeated-measures ANOVA: 'time x manipulation' interaction; $F_{9,75}$=68.31, P<0.0001). Highest accumulation rates occurred in the -algae, +mussels treatment (3.94 ± 0.19 SE μmol L^{-1} h^{-1}), followed by the +algae, +mussels treatment (2.40 ± 0.19 SE μmol L^{-1} h^{-1}). These treatments differed from each other and from every other treatment (ANOVA: Bonferroni-adjusted P<0.0001 for all comparisons with both treatments). However, the other two treatments differed neither from each other nor from zero (-algae, -mussels: P=0.6602; +algae, -mussels: P=0.1897).

Ammonium Loading and Algal N Assimilation

Ammonium loading rates, defined as the change in ammonium concentration per time (μmol L^{-1} h^{-1}) in the absence of *Odonthalia*, were primarily associated with

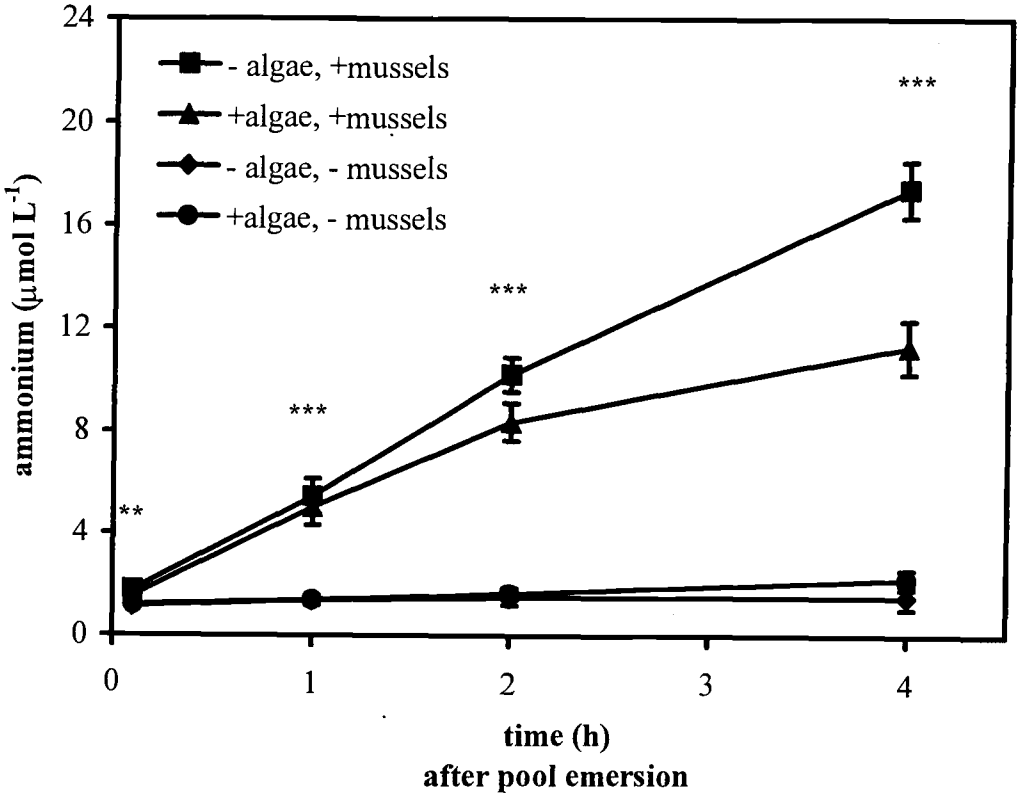

Figure 4.4. Ammonium fluxes in mesocosms based on simultaneous manipulations of *Odonthalia* and mussels. Values are mean (±SE) ammonium concentrations, determined 0, 1, 2, and 4 hours after pool emersion. Manipulations consisted of n=8 pools each of the following four treatments: -algae, +mussels; +algae, +mussels; -algae, -mussels; and +algae, -mussels. Asterisks indicate significant differences in ammonium concentrations at P<0.01 (**) and P<0.001 (***).

the presence of mussels in mesocosms: the mean ammonium loading rate was 3.69 (±0.42 SE) µmol L^{-1} h^{-1} higher when mussels were present (ANOVA: $F_{1,21}$=77.90, P<0.0001).

Using the changes in biomass (g dm) of labeled *Odonthalia* individuals and in the nitrogen content of *Odonthalia* tissue, I calculated the rate of macroalgal nitrogen assimilation (µg h^{-1} g dm^{-1}) for each mesocosm. Mussels primarily influenced algal biomasses: over the course of the experiment, labeled thalli added 123.7 (±16.3 SE)

mg dm in +mussel mesocosms and only 42.6 (±18.4 SE) mg dm in -mussel mesocosms (ANOVA: $F_{1,22}$=10.90, P=0.0032). Tissue nitrogen content was not influenced by the presence of mussels (ANOVA: $F_{1,22}$=1.39, P=0.2502) and did not change over the course of the experiment (paired t-test: t=1.26, P=0.2181, df=26). At the start of the experiment, the mean percentage of nitrogen in dried *Odonthalia* tissue was 3.96 (±0.05 SE), and at the end of the experiment it was 4.07 (±0.07 SE). Algal C:N ratios ranged from 5.9 to 7.0 at the start of the experiment and from 6.7 to 9.1 at the end of the experiment.

Thus, primarily due to changes in biomass associated with nitrogen loading by mussels, nitrogen assimilation rates were higher when mussels were present (ANOVA: $F_{1,22}$=17.66, P=0.0004). Similarly, nitrogen assimilation by *Odonthalia* reflected rates of ammonium loading into the mesocosms (ANOVA: $F_{1,22}$=40.38, P<0.0001; Fig. 4.5).

Ammonium Loading and Algal Growth

While mussels increased the percent growth of macroalgae (ANOVA: $F_{1,20}$=8.19, P=0.0097), neither phytoplankton ($F_{1,20}$=0.06, P=0.8019) nor the interaction between mussels and phytoplankton ($F_{1,20}$=0.45, P=0.5105) explained significant variation in growth (Table 4.2a). When mussels were present, growth was slightly higher when phytoplankton were present, and when mussels were absent, growth was slightly higher when phytoplankton were absent, which corresponded to

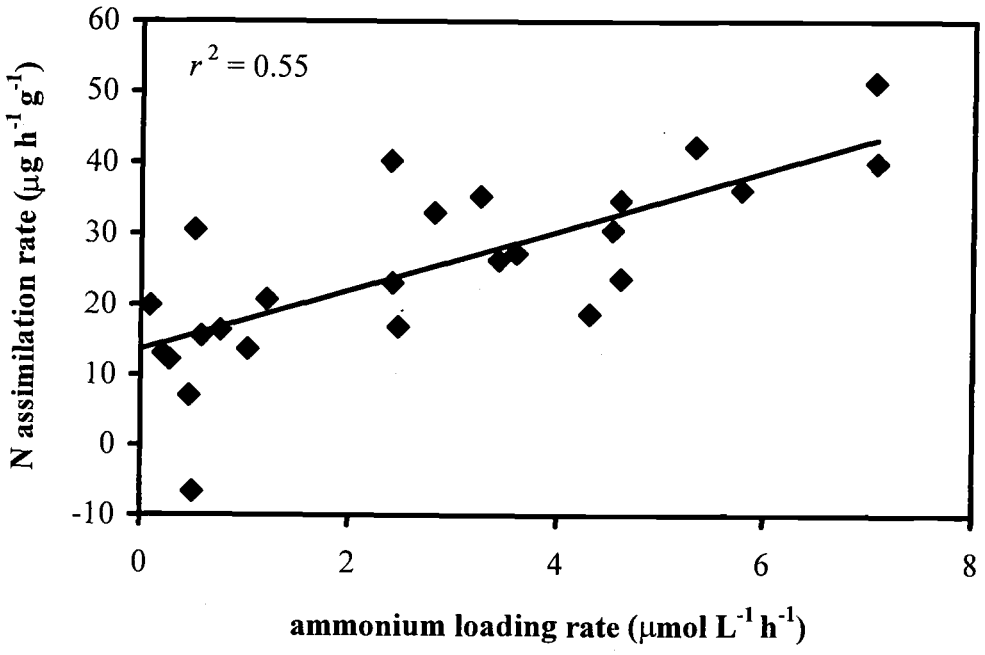

Figure 4.5. Nitrogen assimilation rates, based on elemental analysis of tissue nitrogen and growth of individual *Odonthalia* thalli, increased with ammonium loading by mussels in tidepool mesocosms.

the between-subjects 'mussels x phytoplankton' interaction associated with overall differences in ammonium concentration (Table 4.1b).

In evaluating growth of *Odonthalia* over time, I used a reduced model, which addressed the influence of mussels on percent growth (Table 4.2b). Based on this model, macroalgae grew in both +mussel and -mussel treatments, adding 74.9 (±9.3 SE; $P<0.0001$) percent wet tissue mass when mussels were present and 33.6 (±10.5 SE; $P=0.0041$) percent when mussels were absent. However, after 24 days, *Odonthalia* in treatments where mussels were present grew 41.3 (±14.0 SE) percent more than those in treatments without mussels (ANOVA: $F_{1,22}=8.66$, $P=0.0075$).

Measurements of labeled individual *Odonthalia* in each mesocosm were taken every 2 days over the 24-day experimental trial. I therefore used a repeated-measures

analysis of variance to evaluate the influence of mussels on *Odonthalia* growth (Table 4.3, Fig. 4.6). Overall, macroalgae added biomass over the 24 days (repeated-measures ANOVA: $F_{11,242}$=45.46, P<0.0001 for time). However, the change in percent growth of *Odonthalia* over time was higher when mussels were present (repeated-measures ANOVA: 'time x mussels' interaction; F=7.13, P<0.0001).

Table 4.2. Analysis of variance in percent growth (wet tissue mass) after 24 days of experimental treatments.

(a) Full model

Source of Variation	df	Mean Square	*F*	*P*
Model	6	2,933	2.13	0.0948
Mussels (+,-)	1	11,274	8.19	0.0097
Phytoplankton (+,-)	1	89	0.06	0.8019
Mussels x Phytoplankton	1	618	0.45	0.5105
Tank[1]	3	1,872	1.36	0.2836
Error	20	1,377		
Corrected Total	26	45,145		

(b) Reduced model

Source of Variation	df	Mean Square	*F*	*P*
Model	4	4,196	3.26	0.0306
Mussels (+,-)	1	11,166	8.66	0.0075
Tank[1]	3	1,873	1.45	0.2547
Error	22	1,289		
Corrected Total	26	45,145		

[1]Because treatments were randomized within the running seawater tanks, "Tank" is included in the models.

Discussion

Ammonium Fluxes in Mesocosms

Ammonium uptake rates of macroalgae in still water are very low; *Odonthalia* in this study reduced the concentration of ammonium in tide pool mesocosms by only 0.76 μmol h^{-1} g dm^{-1}. Most studies of macroalgal nutrient uptake are conducted in moving water, where maximum non-surge ammonium uptake rates range from 22 μmol h^{-1} g dm^{-1} (*Fucus vesiculosis*) to 72 μmol h^{-1} g dm^{-1} (*Ulva lactuca*) (Pedersen and Borum 1997). Furthermore, in still water, the rate of ammonium uptake by *Odonthalia* increases slowly and linearly with increasing ammonium concentration

Table 4.3. Repeated-measures analysis of variance in percent growth (wet tissue mass) over time when mussels were present and absent.

Source of Variation	df	MS	*F*	*P*
Between Subjects				
Mussels (+,-)	1	20,353	5.84	0.0244
Tank[1]	3	3,556	1.02	0.4029
Error	22	3,487		
Within Subjects				
Time	11	8,492	45.46	<0.0001
Time x Mussels	11	1,332	7.13	<0.0001
Time x Tank	33	191	1.02	0.4381
Error (Time)	242	187		

[1]Because treatments were randomized within the running seawater tanks, "Tank" is included in the models.

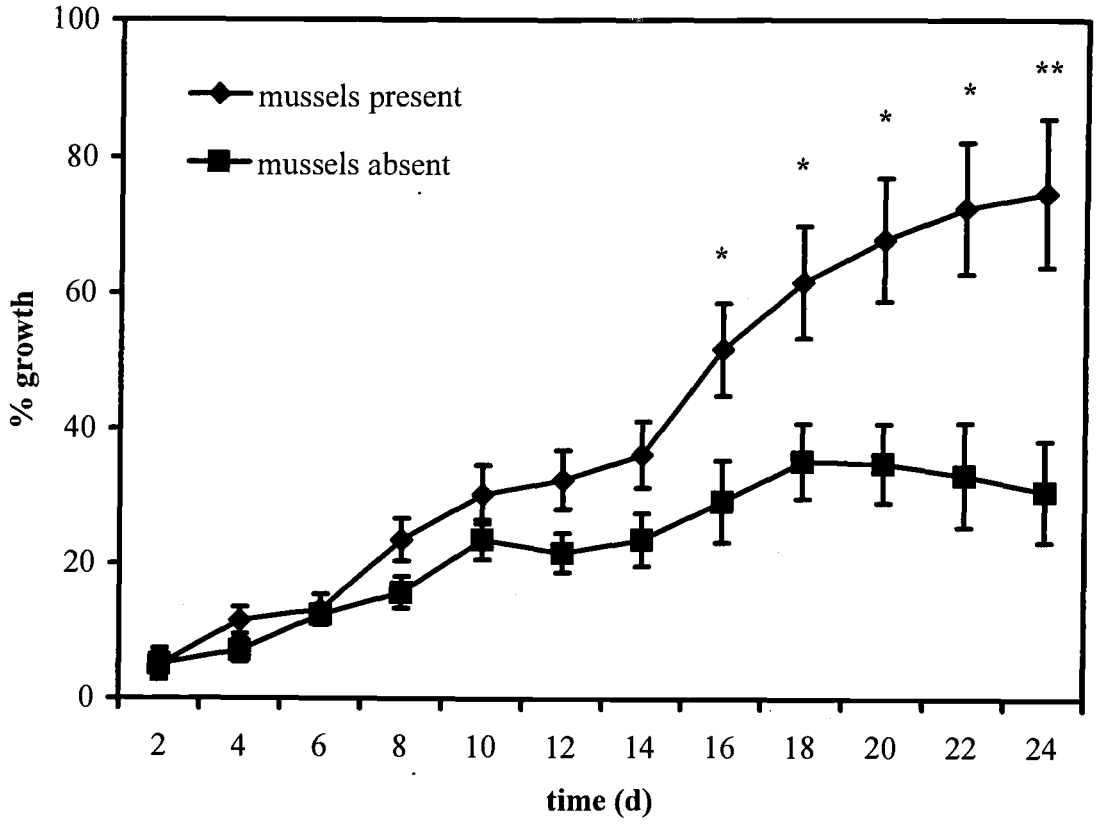

Figure 4.6. Growth of *Odonthalia* in the presence and absence of mussels. Values are mean (±SE) percent growth in blotted wet tissue mass in the presence and absence of mussels. Asterisks indicate significant differences in growth between treatments at $p<0.05$ (*) and $p<0.01$ (**). By the experiment's end (day 24), *Odonthalia* in mesocosms where mussels were present exhibited 41% more growth than when mussels were absent.

(M. Bracken, *unpublished data*). The lack of saturation and the low overall uptake rates suggest that diffusion is the likely mechanism of ammonium acquisition by *Odonthalia* when pools are emersed, probably due to the formation of boundary layers in the still water (Hurd 2000). Especially high in the intertidal zone, where tide pool macroalgae are isolated from oceanic nitrate and subject to still water for extensive periods of time, nitrogen limitation is a potential stress. Due to the direct relationship

between ammonium concentration and uptake by *Odonthalia*, increasing the ammonium concentration in tide pools would increase uptake, and could ameliorate this stress. Invertebrates excrete substantial amounts of ammonium into tide pools (Table 4.1, Fig. 4.2), and can therefore help alleviate the nutrient limitation characteristic of high-intertidal pools.

In this experiment, I quantified the influence of a dominant intertidal invertebrate, the mussel *Mytilus californianus*, on ammonium fluxes in tide pool mesocosms. At the experiment's end, when I sequentially removed *Odonthalia* and mussels to quantify excretion by *Mytilus* and uptake by *Odonthalia*, mussels excreted 0.31 μmol h^{-1} g dm^{-1} ammonium into the mesocosms, raising mean ammonium concentrations to >8.9 μmol L^{-1} when algae were present and >18.3 μmol L^{-1} when algae were absent. The contribution of mussels was even more pronounced at the beginning of the experiment, when ammonium concentrations increased to >21.4 μmol L^{-1} in mesocosms where both *Odonthalia* and mussels were present.

Why did mussel ammonium-excretion rates decrease over the 24-day experimental period, even when mussels in +phytoplankton treatments were being fed? While 10^5 cells ml^{-1} was experimentally determined to be the ration that maximized ammonium excretion rates (M. Bracken, *unpublished data*), feeding the mussels only once a day may not have been sufficient to maintain natural excretion rates. Furthermore, there is evidence that starved mussels may actually excrete at higher rates than fed mussels due to catabolism of protein (Bayne and Scullard 1977). The factors influencing the assimilation of ingested particulate organic nitrogen into

new growth versus its excretion as ammonium are complex, and involve both the quantity and quality of food (Chapter 2). However, it is clear that the presence of mussels was the primary factor influencing ammonium fluxes in the experimental mesocosms (Table 4.1).

The only notable effect of phytoplankton on ammonium concentrations involved their interaction with the presence of mussels ('mussels x phytoplankton', Table 4.1b). While this did not translate to an equivalent effect on *Odonthalia* growth ('mussels x phytoplankton' interaction; F=0.45, p=0.5105; Table 4.2a), it suggests that mussels may play a dual role in their positive interaction with macroalgae. It is clear that mussels' excretion of ammonium increases macroalgal abundance (Fig. 4.6). Mussels also remove phytoplankton, which can reach high abundances in tide pools (Metaxas and Scheibling 1994) and may therefore compete with macroalgae for inorganic nitrogen. Thus, mussels may influence macroalgal growth both directly, by excreting a nutrient necessary for growth, and indirectly, by ingesting their microalgal competitors.

Ammonium Loading and Algal N Assimilation

The long-term rate of nitrogen assimilation (its incorporation into algal tissue) is a function of changes both in the nitrogen content of the tissue and in the mass of the algal thallus. Rates of nitrogen assimilation into the thalli of labeled individuals ($\mu g\ h^{-1}\ g\ dm^{-1}$) increased with the rates of ammonium accumulation in the mesocosms containing those individuals (Fig. 4.5). This increase in nitrogen assimilation was

primarily associated with addition of new biomass. Mussels did not affect tissue nitrogen content, nor did tissue nitrogen content change over the course of the experiment. Tissue nitrogen percentages in algal thalli were never less than 3.3%. In no case was an alga below the critical concentration for maximum growth rates, which ranges from <0.9 to 3.1%, depending on the species (Table 4.4).

Odonthalia individuals were never nutrient limited; C:N ratios ranged from 5.9 to 9.1, far less than the approximate ratio of 19 that Atkinson and Smith (1983)

Table 4.4. Critical tissue nitrogen concentrations for maximum growth of macroalgae.

Species	Critical N concentration (% of dry tissue mass)	Source
Chlorophyta		
Chaetomorpha linum	1.2%	Pedersen and Borum 1997
Cladophora serica	2.1%	Pedersen and Borum 1997
Ulva lactuca	2.2%	Pedersen and Borum 1997
Ulva rigida	3.0%	Fujita et al. 1989
Rhodophyta		
Ceramium rubrum	3.1%	Pedersen and Borum 1997
Gelidiella acerosa	1.9 to 2.5%	Mairh et al. 1990
Polysiphonia decipiens	2.4 to 2.9%	Campbell 2001
Phaeophyceae		
Fucus vesiculosis	1.7%	Pedersen and Borum 1997
Hincksia sordida	2.1%	Campbell 2001
Pelvetiopsis limitata	<0.9%	Fujita et al. 1989
Sargassum baccularia	0.9%	Schaffelke and Klumpp 1998

associate with macroalgal nutrient limitation. The potential for *Odonthalia* to grow does not appear to be a function of the nitrogen stored in their tissues. While most macroalgal species deplete stores of tissue nitrogen to support additional growth (Hanisak 1983, Pedersen and Borum 1997), *Odonthalia* maintains a high, constant level of tissue nitrogen, translating external nitrogen inputs directly into new growth instead of depleting internal stores.

Ammonium Loading and Algal Growth

By excreting ammonium into the tide pool mesocosms, mussels increased *Odonthalia* growth: when mussels were present, algal thalli added 41% more mass than when mussels were absent (Fig. 4.6). It is likely that a similar interaction occurs in natural tidepools; Nielsen (2001) demonstrated that artificially adding nitrogen and phosphorus to Oregon-coast tide pools increased both macroalgal biomass and productivity. However, a positive influence of nutrients was apparent only in pools where herbivore abundances were experimentally reduced. If herbivore consumption rates equal or exceed macroalgal growth rates, the bottom-up influence of nutrients on tide pool community structure may be masked by top-down regulation by herbivores. Wootton et al. (1996) conducted a similar nutrient-enrichment study on rocky intertidal reefs. During an El Niño period of low nitrate availability, their addition of slow-release nitrate and phosphorus to intertidal plots increased herbivore biomasses but had no influence on algae. Thus, while nutrient additions have demonstrable effects on macroalgal growth, the magnitude and fate of those increases in primary

productivity, and the consequent influences on community structure and dynamics, depend on the relative strengths of both bottom-up nutrient loading and top-down herbivory.

Summary

Regenerated nitrogen increased the growth of *Odonthalia*, an abundant macroalga in high-intertidal pools. Even within the nitrate-replete upwelling ecosystem of the northeastern Pacific, there are nutrient-limited microhabitats, like tide pools, where local depletion of nitrate during pool emersion can result in nutrient stress. This stress is ameliorated by the excretion of ammonium by invertebrates. Based on the results of this study, I suggest that local-scale nutrient availability, mediated by processes such as localized nitrogen limitation and regeneration, can play an important and previously overlooked role in determining the structure and dynamics of intertidal communities.

CHAPTER 5

GENERAL CONCLUSIONS

Each of the studies presented above illustrates the community-level implications of ecosystem-level processes in rocky intertidal habitats. I specifically examined the functional role of invertebrates as mediators of material exchange into and within intertidal systems. In those systems, filter-feeding invertebrates both assimilate and chemically transform organic particulates, making nearshore particulate organic carbon and nitrogen available to intertidal consumers and macroalgae.

In Chapter 2, I evaluated processes influencing the assimilation and transformation of seston carbon and nitrogen by intertidal mussels. Both assimilation (growth rates) and transformation (ammonium excretion rates) were affected by the quality and quantity of seston in the adjacent nearshore ocean. Growth rates increased with increasing phytoplankton availability, but declined as concentrations of total organic particulates increased. Conversely, ammonium excretion rates increased with increasing total concentrations of particulate organic material, but declined with increasing phytoplankton availability. These results suggest that mussels' efficiency as mediators of energy and nitrogen fluxes in intertidal ecosystems change with seston composition. Carbon stable-isotope analyses of seston and mussels supported this assertion, indicating that the ability of mussels to assimilate particulate organic carbon declines as seston quality decreases.

These measurements of benthic-pelagic coupling highlight two important aspects of species' roles in ecosystem functioning. First, the impact of a species on a given ecosystem-level process is not necessarily constant. Instead, it may be context-dependent. In this case, for example, the efficiency of mussels' transfer and transformation of nearshore particulates changed with seston quality and quantity. This is not surprising: the roles of species in effecting ecosystem functioning are emergent properties of their individual traits (MacGillivray *et al.* 1995, Chapin *et al.* 1997, Grime 1997), and those traits (*e.g.,* interactions, physiological rates) change depending on environmental conditions (Sanford 1999, Brown *et al.* 2001).

Second, when species play multiple functional roles in ecosystems, changes in environmental conditions can have different (and in this case, opposite) effects on the species' different roles. I simultaneously considered two ecosystem functions of mussels: their transfer of materials from pelagic to benthic systems and their chemical transformation of particulate organic nitrogen into ammonium. Increases in phytoplankton concentrations increased growth rates, but decreased ammonium excretion rates. Associated increases in total organic particulate concentrations decreased growth rates, but increased ammonium excretion rates.

In Chapters 3 and 4, I examined the role of sessile invertebrates, particularly mussels, as transformers of particulate organic nitrogen into ammonium. This is a potentially important ecosystem function: while the concentration of particulate organic nitrogen can equal or exceed the concentration of inorganic nitrogen in temperate nearshore waters (Menge *et al.* 1997a, Menge *et al.* 1997b, M. Bracken,

unpublished data), only inorganic forms of nitrogen, such as nitrate and ammonium, are usable by macroalgae (Lobban and Harrison 1994). I focused on high-zone tide pools, which are isolated from oceanic inputs of new nitrogen (sensu Dugdale and Goering 1967) for 80% of the time. In those pools, macroalgae can deplete the available nitrate, leading to severe nutrient limitation during pool emersion. I demonstrated that local-scale nitrogen regeneration by invertebrates can ameliorate this limitation, increasing macroalgal growth and diversity.

This positive interaction—the excretion of ammonium by invertebrates and its subsequent uptake by macroalgae—illustrates an important consequence of jointly considering community and ecosystem-level processes. This perspective allows community ecologists to think beyond the traditional set of community-level interactions (*e.g.*, competition, consumption) and consider a broader suite of possibilities. Species' ecosystem functions certainly include traditional interactions (*e.g.*, energy transfer *via* consumption), but they also include novel interactions such as ecosystem engineering (physical modification of habitat) and chemical transformation (Lawton and Jones 1995, Shachak and Jones 1995, Ernest and Brown 2001). It also exemplifies two aspects of positive interactions: their importance in ameliorating harsh physical conditions and their links to both ecosystem functioning and diversity.

Positive interactions are predicted to occur under physically stressful conditions (Bertness and Callaway 1994). Under those conditions, "facilitator" species, whose ecosystem functions (*e.g.*, habitat modifications, chemical

transformations) reduce physical stress, can increase the abundances of other individuals or species (Stachowicz 2001, Chapter 4). Positive interactions can also influence diversity. The intermediate disturbance hypothesis predicts that diversity is a unimodal function of physical stress (Connell 1978). When physical stress is low, diversity is also low, due to monopolization of space and resources by competitive dominants. Initially, as stress increases, those dominant species are supplemented by stress-tolerant species, and diversity increases. However, at very high levels of physical stress, only the stress-tolerant species can survive, and diversity declines. Hacker and Gaines (1997) suggest that by reducing physical stress and facilitating the occurrence of less stress-resistant species, positive interactions can increase diversity in stressful habitats. My research supports this hypothesis: few macroalgal species occurred in tide pools with low rates of invertebrate-mediated nitrogen loading. As ammonium accumulated more rapidly, species tolerant of low nitrogen availability were supplemented by fast-growing species with high nitrogen requirements, and macroalgal richness increased.

However, despite the obvious influences of positive interactions on the structure and dynamics of biological communities, their importance relative to negative interactions is not well understood and probably underappreciated (Menge 2000a, Stachowicz 2001, Bruno *et al.* 2003). This is partly due to the novel nature of many of these interactions. While negative interactions, including consumption and competition, are well-studied and amenable to established experimental methods, positive interactions often involve aspects of ecosystem functioning, including habitat

modification and chemical transformation. Applying ecosystem perspectives to community ecology, as I have done here, will help ecologists to understand, quantify, and judge the importance of positive interactions.

These perspectives will also improve our understanding of the relationship between diversity and ecosystem functioning. While the effects of consumption and disturbance on diversity are appreciated and understood (Paine 1966, Menge and Sutherland 1976, Connell 1978, Lubchenco 1978), the influences of ecosystem functions and positive interactions on diversity remain unclear (Rosenzweig and Abramsky 1993, Mittelbach *et al.* 2001). While large-scale patterns suggest that the relationship between diversity and productivity is unimodal, experimental nutrient additions often result in local-scale declines in diversity due to overgrowth by competitive dominants (Rosenzweig 1995). In Chapter 3, I attempt to clarify this relationship by addressing the relationship between invertebrate-mediated nitrogen loading and macroalgal species richness in high-intertidal pools. In those pools, which are nitrate-poor microhabitats within a nitrate-replete ecosystem, macrophyte richness increased with nutrient loading. Based on these results, I hypothesize that the local-scale relationship between nutrient loading and diversity is unimodal and that oft-observed declines in diversity with enrichment represent the decrease phase of the unimodal function.

Identifying ecosystem-level processes and evaluating the relationships between those processes and diversity are fundamental issues in ecology. Given dramatic anthropogenic impacts on both biodiversity and ecosystem functioning (Pimm *et al.*

1995, Vitousek *et al.* 1997), understanding diversity, ecosystem functioning, and their relationship is both a scientific and a societal concern. Emerging evidence suggests that this relationship is reciprocal: not only do ecosystem functions such as chemical transformation influence diversity, but the diversity of ecosystems influences ecosystem functioning (Naeem 2002). My research suggests that not only does invertebrate-excreted nitrogen loading increase the number of macroalgal species in tide pools, but more species-rich pools are characterized by higher nitrogen use efficiency (Chapter 3).

Applying ecosystem perspectives to community ecology helps us address the effects of ecosystem functioning on diversity, but that is only half of the story. The other half—evaluation of the impacts of diversity on ecosystem functioning—requires ecologists to apply community perspectives to ecosystem ecology. In this dissertation, I have shown that by linking communities and ecosystems, we can gain unique and necessary insights into processes influencing ecological systems at multiple scales: "the distribution and abundance of organisms, the interaction among organisms, and the interaction between organisms and the transformation and flux of energy and matter" (Likens 1992).

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