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

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ABSTRACT

Human alteration of nutrient cycling and the densities of important consumers have intensified the importance of understanding how nutrients and consumers influence the structure of ecological systems. We examined the effects of both grazing and nutrient enrichment on algal abundance and diversity in a high-intertidal limpet-macroalgal community on the South Island of New Zealand, a relatively nutrient-poor environment. We used a fully factorial design with three levels each of grazing (manipulations of limpet and snail densities) and nutrients (nutrient-diffusers attached to the rock). Top-down control by grazers appears to be the driving organizing mechanism for algal communities in this system, with strong negative effects of grazing on algal diversity and abundance across all levels of nutrient enrichment. However, in contrast to the conclusions drawn from the analysis of the whole algal community, there was an interactive effect of grazing and enrichment on foliose algae, an important component of the algal system. When herbivory was reduced to very low levels, enrichment generated increases in the abundance and biomass of foliose algae. As expected, top-down control was the primary determinant of algal community structure in this system, controlling abundance and diversity of macrophytes on the upper shore. Contrary to expectations, however, increased nutrients had no community-wide effects, although foliose algal abundance increases were greatest with high nutrients and reduced grazing. It seems likely that most of the corticated algal species have limited capacity to respond to nutrient pulses in this nutrient-poor environment.

1. Introduction

Understanding how nutrients and grazing influence the structure of ecological systems is both practically and conceptually important. The widespread use of nitrogenous fertilizers has significantly increased the amount of available nitrogen in global systems, with important implications for the structure and functioning of a wide array of ecosystems (Vitousek et al., 1997; Suding et al., 2005). Similarly, the reduction in abundance or complete removal of species that play key roles in systems can have dramatic effects on ecosystems (Paine, 1966; Power et al., 1996; Jackson et al., 2001; Myers and Worm, 2003). The effects of both top-down effects of consumers and bottom-up effects of nutrients have elicited a good deal of ecological inquiry, but an understanding of the conditions under which we expect each to reign remains elusive (McQueen et al., 1989; Hillebrand, 2002; Gruner, 2004; Schiel, 2004; Vinueza et al., 2006).

In marine systems, evidence that differences in productivity can lead to differences in the structure and dynamics of rocky intertidal communities comes primarily from examinations of the effects of large-scale oceanographic processes (Bosman et al., 1987; Bustamante et al., 1995; Menge et al., 1997, 2003; Nielsen and Navarrete, 2004; Vinueza et al., 2006). Experimental manipulations of nutrient availability in rocky intertidal systems are less prevalent—some have documented important effects (Bosman et al., 1986; Worm and Sommer, 2000; Nielsen, 2001; Worm et al., 2002; Kraufvelin et al., 2006), while others have seen little to no effect of enrichment (Wootton et al., 1996; Bokn et al., 2003; Pfister and Van Alstyne, 2003).

Grazing is a key determinant of algal community structure on rocky shores (reviewed by Lubchenco and Gaines, 1981; Hawkins and Hartnoll, 1983). Molluscan grazers, in particular, play key roles in determining algal distribution and abundance on intertidal rocky shores (Underwood, 1980; Lubchenco, 1983; Cubit, 1984; Underwood and Jernakoff, 1984; Freidenburg et al., 2007). Given the strength of top-down effects in these communities, an important question is: are there conditions under which bottom-up effects temper or alter the defining effects of grazers?

The effects of bottom-up and top-down control on primary producers are often co-dependent (Menge et al., 1997; Proulx and Mazumder, 1998; Menge, 2000; Lotze et al., 2001). Three meta-

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analyses of aquatic systems have examined how productivity affects the interactions of top-down and bottom-up forces (Hillebrand, 2002; Worm et al., 2002; Burkepile and Hay, 2006). One emerging synthetic result from these studies is that in nutrient-poor environments consumers appear to exert extremely strong control on primary producers but have less control in nutrient-rich environments. A second emerging result from these meta-analyses is that in nutrient-rich environments, enrichment tends to affect both abundance and diversity of primary producers, while in nutrient-poor environments enrichment increases diversity but not abundance.

Here, we examine the effects of experimentally manipulating both nutrient enrichment and grazing on the abundance and diversity of algal communities in a nutrient-poor system on the South Island of New Zealand. We tested two hypotheses:

H_1. at low (ambient) nutrient levels, consumers will depress both algal abundance and diversity

H_2. with enrichment, top-down control will weaken and algal diversity will be independent of, or enhanced by, consumers.

2. Methods

2.1. Study site

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

At Blue Duck, the low-zone is dominated by the large fucoids *Durvillaea antarctica* and *D. willana*, and encrusting coralline algae. The mid- to high-intertidal zone is dominated by the barnacles *Chamaesipho columna* and *Chamaesipho brunnea* interspersed with patches of bare rock. Algae occur in this zone, but are generally inconspicuous, occupying an average of 7% (±1.6 SE) of the space in all plots at the initiation of the experiment. Encrusting forms (such as *Hildenbrandia* spp., *Ralfsia verrucosa,* and coralline crusts) are the most common algae. Foliose *Porphyra* spp. are often present, with blooms in the winter. *Polysiphonia* spp., *Cladophoropsis* spp., and *Scytothamnus australis* also occur. Limpets of a variety of sizes and species are very abundant at this site, spanning 250-375 limpets /0.25 m^2. *Patelloidea corticata* is the most abundant limpet, although *Cellana ornata* and *Notoacmea* spp. are also common. *Siphonaria australis, C. denticulata*, and *C. radians* also occur. Chitons, primarily *Sypharochiton pelliserpentis,* are present but rare.

Satellite imagery, intertidal air and water temperatures, monthly and daily upwelling indices, and water-sampling data (chlorophyll-*a*, particulates, and nutrients) all indicate that although sites on the west coast of New Zealand experience upwelling, sites on the east coast predominantly experience downwelling (Menge et al., 2003 and references therein). In a global context, sites on the South Island of New Zealand are relatively nutrient-poor (Vincent et al., 1991; Chang et al., 1995).

2.2. Experimental design

We manipulated both grazers and nutrients in a fully factorial experimental design using randomized complete blocks. Both the grazer manipulation and the nutrient manipulation had three levels for a total of nine treatment combinations. With six replicates of each, there were 54 plots in total. To control for differences that might occur over 10s of meters along the shore, we set up the experiment using six blocks, with each block containing one replicate of each of the nine treatment combinations in close proximity (approximately 1 m apart). Treatments were assigned randomly within blocks. Each plot was 400 cm^2. The experiment began in October 2004 and ended in October 2005.

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

At the initiation of the experiment, the grazer manipulation consisted of (1) plots with a full complement of limpets (40-60 limpets), (2) plots with half of the limpets originally present (20-30 limpets), and (3) plots with all limpets removed. After three months (in December 2004), there was little algal growth in the plots without limpets. Concerned that a truly low grazing treatment was not being achieved, we began a process of counting and manually removing snails (primarily the small, but abundant *Austrolittorina cincta* and *Risselopsis varia*) at approximately 3-week intervals from the limpet-removal plots. Therefore, for most of the experiment, the grazing treatments were: "high grazing" plots with a full complement of limpets and snails, "intermediate grazing" plots with half of the limpets originally present and all of the snails, and 3) "low grazing" plots without limpets and from which all other grazers were removed periodically.

We maintained limpet densities by surrounding each plot with a barrier of Z-spar marine epoxy (Seattle Marine, Seattle, Washington, USA), flush with the rock and painted with copper anti-fouling paint, a deterrent to many molluscan herbivores including most limpets and chitons (but not snails) (Cubit, 1984; Freidenburg et al., 2007). Some prior studies using this method found no artifactual effect of paint (Menge et al., 1999; Menge, 2000), but others have demonstrated artifacts such as a positive effect of paint on the encrusting brown alga *Ralfsia verrucosa* (Benedetti-Cecchi and Cinelli, 1997). Since all of our experimental treatments were surrounded by paint and thus all comparisons would be made between plots with paint, we did not include any controls for potential artifacts of paint. Approximately every two months we counted all limpets in all plots and removed those that had recruited to or entered the low-grazing plots. We also removed limpets as necessary from the intermediate grazing plots to keep limpet numbers between 20 and 30. Occasionally the high-grazing plots lost limpets and we attempted to transplant limpets (though not *C. ornata* or *C. radians*) to them to increase their densities to the desired levels.

We manipulated nutrients using resin-coated, controlled-release fertilizer pellets (Worm et al., 2000; Nielsen, 2001). We used Nutricote (Chisso-Asahi Fertilizer,Tokyo Japan) in a 13-13-13 NPK formulation (oxide analysis). This formulation is similar to that used by Nielsen (2001). The nitrogen contributors in the fertilizer included Ammonium Nitrate (NH_4NO_3) and Potassium Nitrate (KNO_3) and the phosphate contributors included Ammonium Phosphate ($NH_4H_2PO_4$), Calcium Hypophosphate ($CaHPO_4$), and Dicalcium Phosphate $Ca_3(PO_4)_2$. Controlled-release fertilizer pellets such as Nutricote work by way of a resin coating that controls the rate of diffusion of nutrients to the environment as water is absorbed through the resin. We filled diffuser bags made from black plastic-coated fabric mesh (see Fig. 1) with approximately 1 mm mesh size with three types of filler: 200 g fertilizer pellets (high enrichment), 100 g fertilizer pellets and 42.5 g small plastic beads (low enrichment), or 85 g small plastic beads (no enrichment). Beads weigh less than pellets and the total volume of filler was the same in all three treatments. Diffuser bags for all treatments were 80 cm long and approximately 2.5 cm in diameter. The small plastic beads (of approximately the same size as the fertilizer granules) were used

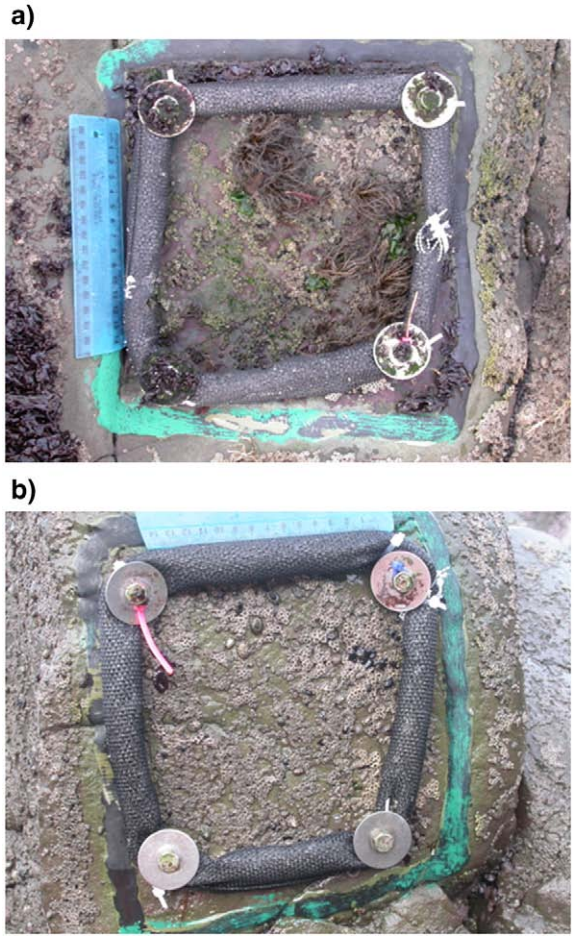

Fig. 1. Two experimental plots showing the tubular nutrient-diffuser bags affixed to the rock and surrounded by copper anti-fouling paint to control limpet densities. Both plots shown had high enrichment levels; the plot in panel *a* was a low-grazer plot, that in *b* was a high-grazer plot. Both photographs were taken June 23, 2005, after 8 months.

to control for any changes in the microclimate of the plots introduced by the fertilizer-filled diffuser bags, such as moisture retention and alteration of hydrodynamic forces. Nutricote pellets were replaced in the high- and low-enrichment treatments approximately every six weeks. Since emptying and refilling the nutrient diffuser bags in the field proved difficult and time-consuming, in March 2005 we began alternating between the original mesh bags and a second set of slightly wider bags (approximately 3 cm in diameter). These slightly larger bags allowed for 300 g of fertilizer pellets in the high-enrichment treatments, 150 g fertilizer pellets and 70 g beads in the low-enrichment treatments, and 140 g beads in the no-enrichment treatments.

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

The nutrient enrichment accomplished with this type of diffuser in a moderately wave-exposed environment is a pulse-type treatment (Bender et al., 1984). It is likely to be effective at some times (e.g. when the tide is just coming in or receding and water splashes into and sits on the plots or when the tide is in and the water is calm) and likely to be ineffective at other times (e.g. when plots are completely dry or when the water is very turbulent). Also, water temperature is likely to influence the rate of diffusion of nutrients from the pellets.

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

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

2.3. Monitoring and data collection

We visually estimated the percent cover of algae and sessile invertebrates (Meese and Tomich, 1992; Dethier et al., 1993) and counted mobile invertebrates in all plots after 54, 92, 133, 196, 253, and 351 days. All estimates of percent cover were conducted by one individual each visit, with a total of 2 individuals conducting assessments throughout the course of the experiment. We compared the estimates of these two individuals on several occasions and found them to be similar. We used the percent cover of the canopy as one response variable, so due to layering the total cover of a plot can sum to >100%. Algae were identified to the lowest taxonomic resolution possible (Adams, 1994; Schiel, 2006). This resulted in an inhomogeneous taxonomic resolution of our response variable "species richness," with some units identified to species, and others to morphological groups (Table 1). This approach has been widely used in these systems (e.g. Menge et al., 2005) and provides a conservative estimate of the diversity of the algal assemblage. Below, we refer to the diversity of algal taxonomic units as "algal species richness".

Because the same number of consumers can exert different amounts of pressure on their food resources depending on feeding rates and size (e.g., Menge, 1983), we examined potential differences in limpet growth with different levels of limpet densities and/or nutrient enrichment. In July 2005 we measured and tagged all *C. ornata* between 10 and 20 mm in all plots. Using superglue, we affixed a small plastic numbered tag (bee tags, "Opalith Plättchen", Graze, KG, Weinstadt-Endersbach, Germany) to each shell and then covered the tag with clear epoxy resin. At the end of the experiment, in October 2005, we again measured all tagged *C. ornata.* At that time we also collected all tagged limpets, weighed them, separated the tissue from the shell, weighed the shell, dried the tissue in a drying oven to constant mass and weighed the dry tissue.

Table 1
Algal taxonomic units occurring in the plots, morphological group assignments of each, and the Division to which each belongs

Taxonomic unit	Morphological group	Division
benthic diatom film	microalgae	Heterokontophyta
blue-green algae	microalgae	Cyanophyta
unidentified filamentous green	filamentous	Chlorophyta
unidentified filamentous brown	filamentous	Heterokontophyta
unidentified filamentous red	filamentous	Rhodophyta
Cladophoropsis herpestica	filamentous	Chlorophyta
Polysiphonia spp.	filamentous	Rhodophyta
Lophothamnion hirtum	filamentous	Rhodophyta
Porphyra spp.	foliose	Rhodophyta
Ulva spp. (blade form)	foliose	Chlorophyta
Ulva spp. (tubular form)	foliose	Chlorophyta
Scytosiphon lomentaria	foliose	Heterokontophyta
unidentified red blade	corticated foliose	Rhodophyta
Petalonia fascia	corticated foliose	Heterokontophyta
Scytothamnus australis	corticated	Heterokontophyta
Splachnidium rugosum	corticated	Heterokontophyta
Adenocystis utricularis	corticated	Heterokontophyta
Apophlea lyallii	corticated	Rhodophyta
unidentified branched red	corticated	Rhodophyta
Plocamium microcladioides	corticated	Rhodophyta
unidentified terete branched red	corticated	Rhodophyta
Caulacanthus ustulatus	corticated	Rhodophyta
Champia spp.	corticated	Rhodophyta
Laurencia thyrsifera	corticated	Rhodophyta
Gelidium caulacantheum	corticated	Rhodophyta
Colpomenia spp.	corticated	Heterokontophyta
unidentified branched feathery red	corticated	Rhodophyta
Mesogloia intestinalis	corticated	Heterokontophyta
unidentified green film	encrusting	Chlorophyta
unidentified green crust	encrusting	Chlorophyta
unidentified brown crust	encrusting	Heterokontophyta
unidentified thin red crust	encrusting	Rhodophyta
unidentified thick red crust	encrusting	Rhodophyta
unidentified encrusting coralline	encrusting coralline	Rhodophyta
unidentified erect coralline	erect coralline	Rhodophyta

At the end of the experiment, we collected algae for determination of biomass. We collected all non-encrusting algae, by species, from all plots and dried the samples to constant mass before weighing.

2.4. Data analysis

We used analysis of variance (ANOVA) to examine the effects of grazing and nutrient enrichment on algal species richness and abundance. We analyzed the mean response of each plot throughout the experiment. In all cases, we tested the effects of the grazing treatment, the nutrient treatment, and the interaction between grazing and nutrients. We also included the blocks as an independent variable to remove any environmental heterogeneity across blocks from the error term. The approach of analyzing the mean response over time is similar to that taken in a repeated-measures analysis but allows for better examination of the assumptions of the model and a more straightforward interpretation of results (Murtaugh, 2007). In fact, a repeated measures analysis of these data yielded qualitatively similar results. Because this experiment was initiated with established benthic communities, we also used similar ANOVAs to examine the mean differences in final – initial algal species richness and abundance. When necessary, we log-transformed data to meet assumptions of normality and equality of variance. In all analyses of percent-cover data, we used angular transformations (Sokal and Rohlf, 1995).

We used similar ANOVAs to examine the effects of grazing and nutrient enrichment on the mean abundance of different morphological groups of algae based on a functional group classification (Steneck and Dethier, 1994). The groups we used were microalgae, filamentous, foliose, corticated foliose, corticated, encrusting, erect coralline, and encrusting coralline algae (Table 1).

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

Because nutrient data were not normal, and could not be normalized using transformations, we used the nonparametric Kruskal-Wallis test to examine differences in nitrate+nitrite across the enrichment treatments. Similarly, given small sample sizes (n=6 from controls, 6 from low enrichment, and 4 from high enrichment) we pooled low and high enrichment and used a Mann-Whitney U test to examine the relationship between nutrient enrichment and C:N among the *Scytothamnus australis* specimens collected at the end of the experiment.

3. Results

3.1. Efficacy of treatments

The manipulation of limpet densities was successful (Table 2a). High grazing plots averaged (mean±SE; snail averages reported are after the snail removals began) 40.3±1.2 limpets and 42.5±6.5 snails, intermediate grazing plots averaged 26±0.9 limpets and 29.6±3.6 snails, and low grazing plots averaged 5.6±0.6 limpets and 15.1±1.5 snails. Throughout the experiment, there were more limpets in the high grazing treatment than there were in the intermediate grazing treatment. Although a few limpets invaded and/or recruited to the low grazing treatment, their densities were always lower than they were in the intermediate grazing treatment. Nutrient enrichment did not affect the number of limpets (Table 2a). The number of limpets varied in space (i.e., the block effect was significant, Table 2a), but this variation did not obscure the main effects of the limpet treatments, nor did it lead to variation in algal responses to the limpet treatments (Tables 3 and 4).

The removal of snails from the low-grazing treatment was also successful. The initial removal of snails from the low-grazing treatment (in December 2004) was by far the largest, with a mean of 83 snails removed from each of the low-grazing plots (SE=14.5). Subsequent removals resulted in fairly consistent and low numbers of snails removed (grand mean of 11 snails removed on 19 occasions with means for each removal ranging from 2-26 snails). Over time, the manipulation of snails resulted in lower numbers of snails in the low-grazing treatments (Table 2b). As with limpet numbers, there was spatial variation in the numbers of snails (block effect, Table 2b).

Table 2
ANOVAs of a) limpet abundance and b) snail abundance (ln(# snails+1) averaged over the course of the experiment

Source of variation	Sum of Squares	d.f.	Mean Square	F-ratio	*p-value*
a) R^2=*0.933*					
Limpet treatment	10917.847	2	5458.923	267.022	<**0.001**
Nutrient treatment	0.853	2	0.426	0.021	0.979
Block	320.455	5	64.091	3.135	**0.018**
Limpet×Nutrient	87.909	4	21.977	1.075	0.382
error	817.749	40	20.444		
b) R^2=*0.526*					
Limpet treatment	5.127	2	2.564	6.543	**0.003**
Nutrient treatment	0.239	2	0.120	0.305	0.739
Block	11.087	5	2.217	5.660	<**0.001**
Limpet×Nutrient	0.950	4	0.238	0.606	0.660
error	16.671	40	0.392		

Bold values represent significant effects at $p<0.05$.

Table 3
ANOVAs of a) algal species richness and b) abundance (percent cover, angular transformed) averaged over the course of the experiment

Source of variation	Sum of Squares	d.f.	Mean Square	F-ratio	*p-value*
a) R^2*=0.788*					
Limpet treatment	79.939	2	39.970	28.506	<**0.001**
Nutrient treatment	4.412	2	2.206	1.573	0.220
Block	1.868	5	0.374	0.266	0.929
Limpet×Nutrient	5.854	4	1.463	1.044	0.397
error	56.085	40	1.402		
b) R^2*=0.780*					
Limpet treatment	3.720	2	1.860	61.204	<**0.001**
Nutrient treatment	0.029	2	0.014	0.476	0.625
Block	0.371	5	0.074	2.440	0.051
Limpet×Nutrient	0.187	4	0.047	1.540	0.209
error	1.216	40	0.030		

Enrichment had a demonstrable effect on the nitrate+nitrite concentrations in water over the plots as the tide came in (Kruskal-Wallis test statistic=13.06, p=0.001; Fig. 2). It appears that after at least 19 days, nitrate+nitrite levels were still elevated in the high-enrichment treatments (Fig. 2). Average (±1SE) N+N concentrations were 1.13±0.11 μM, 1.54±0.37 μM, and 5.08±1.49 μM in no-enrichment, low-enrichment and high-enrichment treatments, with maxima of 2.12, 6.07, and 27.9 μM respectively. As expected, nutrient release rates were variable, with greater variability occurring in high enrichment treatments (Fig. 2).

C:N ratios of *Scytothamnus australis* did not vary with nutrient additions (Mann-Whitney U test statistic=43, p=0.16). However, *S. australis* tended to have slightly lower C:N in enriched treatments than it did in unenriched conditions (enrichment median=24.7; unenriched median=26.3).

3.2. Algal assemblages

Grazing decreased algal species richness irrespective of enrichment. A total of 35 taxa occurred in the plots over the course of the experiment (Table 1). Algal species richness and abundance were primarily determined by the intensity of grazing, with no community-wide effects of nutrient enrichment. Algal richness and abundance were greater in plots with low grazing than they were in plots with intermediate or high grazing; nutrient enrichment affected neither richness nor abundance of algae (Fig. 3; Table 3a and b). There is a suggestion (Fig. 4c) that in plots with low grazing, high enrichment increased algal species richness but not abundance after day 100.

Initial, pre-manipulation patterns of algal species richness and abundance in the plots did not influence observed patterns. The same patterns of algal species richness and abundance described above were apparent when examining the difference between initial algal species richness and abundance vs. final richness and abundance (data not shown). The plots were initially quite similar, with low diversity and very little algal cover (initial mean algal richness=2 species (±0.16 SE); mean algal cover=7.2% (±1.5 SE)).

Although there was little evidence of an effect of nutrient enrichment on the assemblage-wide metrics of algal richness and abundance, in the absence of grazing, the abundance of one morphological group, foliose algae, was greater in the high enrichment plots than it was in the low- or no-enrichment plots (Fig. 4f,

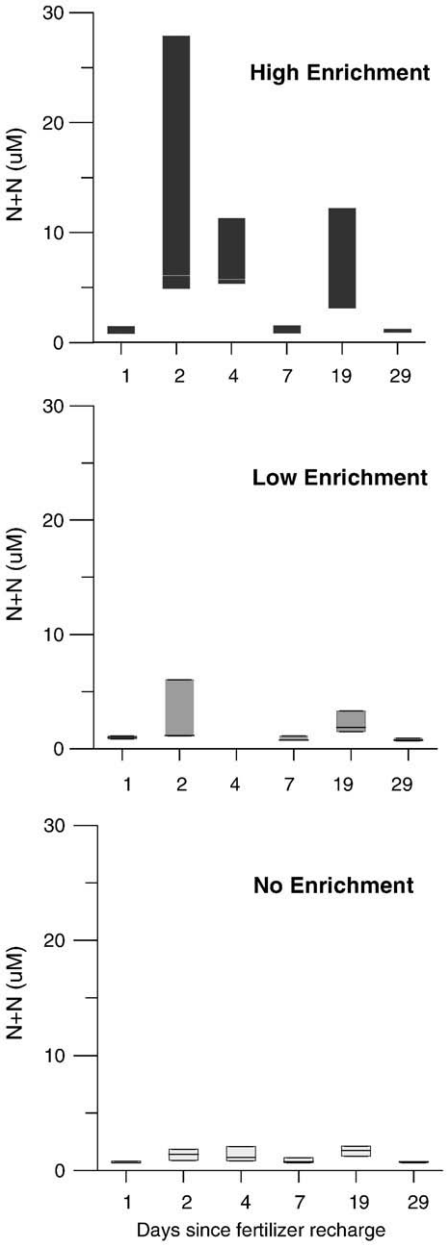

Fig. 2. Nitrate+nitrite concentrations (μM) in water sampled over the plots after 1,2,4,7,19, and 29 days had passed since recharging the nutrient-diffusing bags with slow-release fertilizer. The center line of each box represents the median, boxes represent the range of the data (n=3-4 points/enrichment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

Table 4
ANOVAs of a) foliose algal % cover (angular transformed) averaged over the course of the experiment, b) algal biomass (log10(biomass+1)) at the end of the experiment, and c) calculated foliose algal biomass averaged throughout the experiment

Source of variation	Sum of Squares	d.f.	Mean Square	F-ratio	*p-value*
a) R^2*=0.568*					
Limpet treatment	0.223	2	0.111	15.944	<**0.001**
Nutrient treatment	0.035	2	0.017	2.479	0.097
Block	0.016	5	0.003	0.467	0.798
Limpet×Nutrient	0.094	4	0.024	3.371	0.018
error	0.280	40	0.007		
b) R^2*=0.890*					
Limpet treatment	11.307	2	5.654	154.741	<**0.001**
Nutrient treatment	0.041	2	0.021	0.561	0.575
Block	0.264	5	0.053	1.446	0.229
Limpet×Nutrient	0.153	4	0.038	1.047	0.395
error	1.461	40	0.037		
c) R^2*=0.595*					
Limpet treatment	0.481	2	0.241	14.480	<**0.001**
Nutrient treatment	0.136	2	0.068	4.085	**0.024**
Block	0.053	5	0.011	0.644	0.668
Limpet×Nutrient	0.307	4	0.077	4.618	**0.004**
error	0.665	40	0.017		

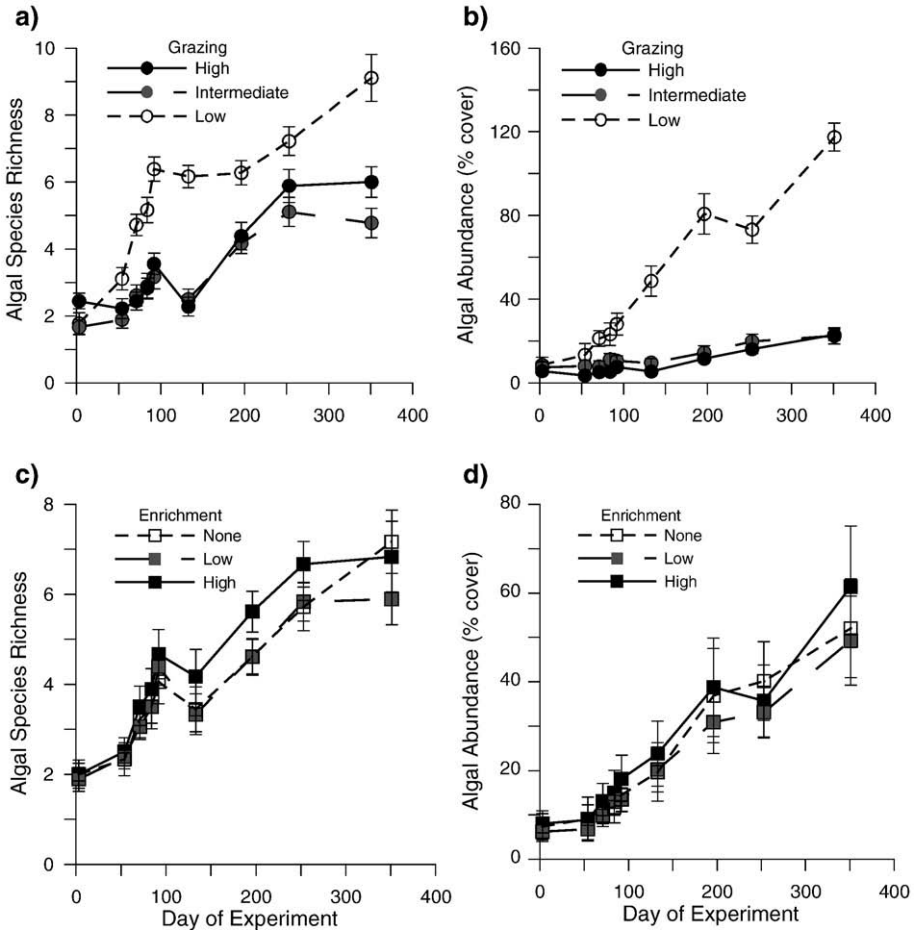

Fig. 3. Mean (±1 SE) algal species richness or percent cover over the course of the experiment. Panels a) and c) are collapsed across all enrichment levels (n=18 for each point) and allow for examination of differences in grazing treatments while panels b) and d) are collapsed across all grazing treatments (n=18 for each point) and show the lack of an enrichment effect.

Table 4a). Foliose algae common in these plots included *Ulva* spp., *Scytosiphon lomentaria* and *Porphyra* spp.

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

Although the response of algae was of primary interest in this experiment, marine algae interact—both positively and negatively—with sessile invertebrates. Thus, we also examined the responses of other elements of the benthic community to experimental manipulation. The percent cover and diversity of sessile invertebrates was independent of both grazing intensity and enrichment (ANOVA, $p>0.14$ in all cases).

3.3. Algal biomass

At the end of the experiment, the total algal biomass was approximately 20 times greater in the low-grazing plots than it was in the intermediate- or high-grazing plots (mean g±1SE: low grazing=13.1 ±1.6; intermediate grazing=0.3±0.1; high grazing=0.7±0.3). The intermediate- and high-grazing plots were not different from one another. Nutrient enrichment did not affect the final total biomass of algae (Table 4b).

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

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

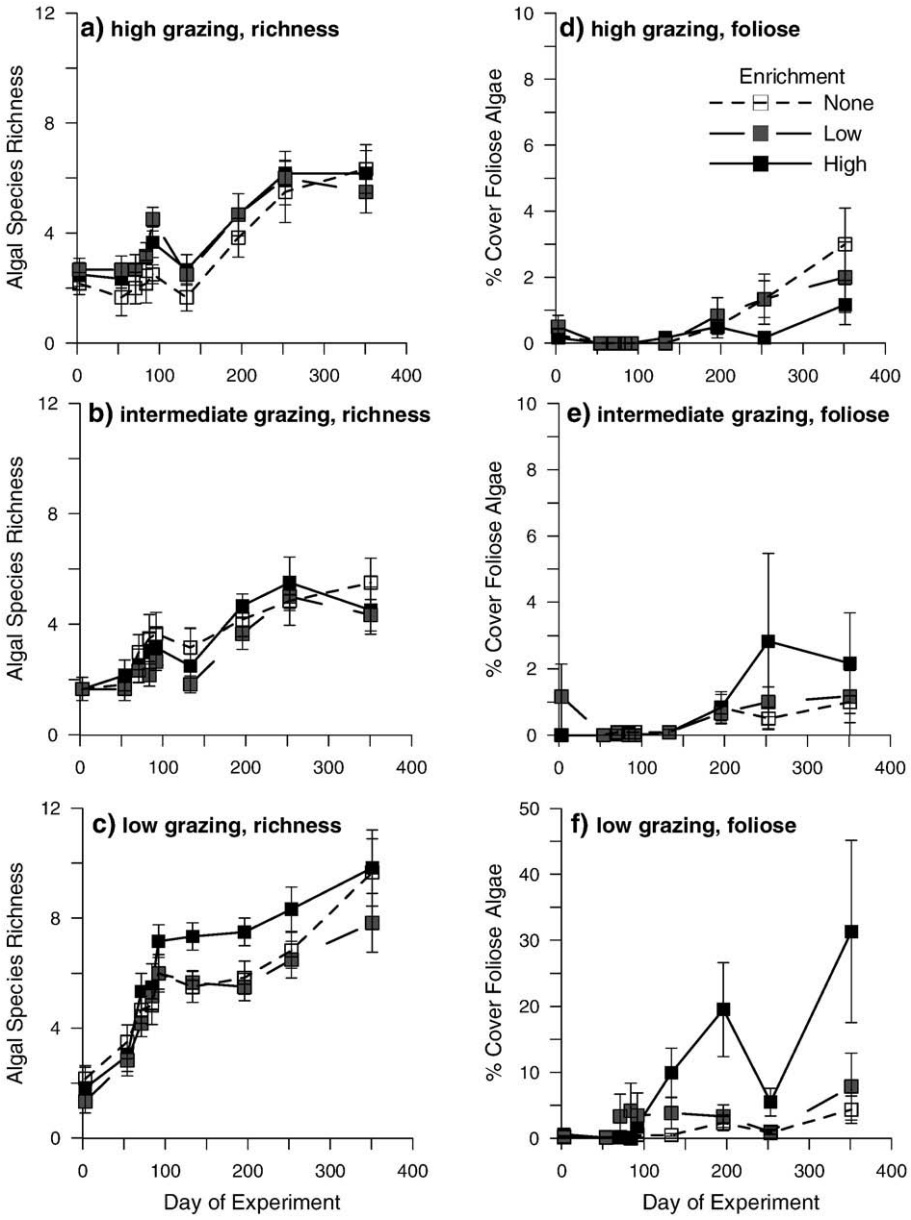

Fig. 4. (a-c) Mean algal species richness (±1 SE) in all 9 treatment combinations (n=6 for each point) and (d-f) mean (±1 SE) percent cover of foliose algae (n=6 for each point) throughout the duration of the experiment.

Using this relationship, we estimated the biomass of foliose algae throughout the experiment. This analysis reveals a strong and interactive effect of grazing and enrichment. Mean biomass of foliose algae throughout the experiment was approximately 1.5 times greater in plots with low grazing and high enrichment than it was in all other treatments (Fig. 5, Table 4c).

3.4. Limpet growth and biomass

We tagged a total of 62 *C. ornata* in 30 plots (9 plots had 1, 11 had 2, 9 had 3, and 1 had 4). There was no relationship between *C. ornata* growth, either in raw shell length or as a proportion of the initial length, and treatment (ANOVA, $p>0.45$ in all cases). However at the end of the experiment, tagged *C. ornata* were heavier in plots with intermediate grazing intensity (mean=0.59 g±0.08 SE) than they were in plots with high grazing (mean=0.34 g±0.03 SE) (ANOVA, limpet effect $p=0.016$). *C. ornata* weight did not appear to be influenced by nutrient enrichment (ANOVA, nutrient effect $p=0.457$). The differences in *C. ornata* weights was driven by differences in shell mass rather than by differences in tissue mass.

4. Discussion

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

The dominant structuring force of herbivory has been well documented in many temperate reef systems (reviewed by: Lubchenco and Gaines, 1981; Hawkins and Hartnoll, 1983). Similarly, the positive effect of enrichment on the biomass and abundance of foliose algae is consistent with the high N-affinity of these species (Lobban and Harrison, 1997). However, the lack of evidence for 1) a community-wide effect of enrichment and 2) for an interaction

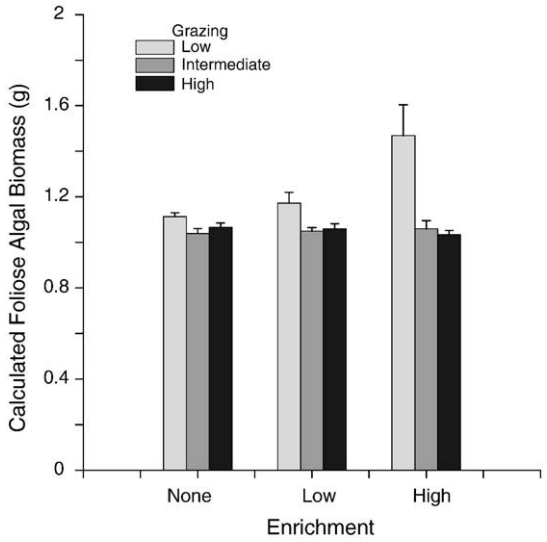

Fig. 5. Foliose algal biomass (±1 SE) averaged throughout the experiment. Values for each date were calculated using a regression of the biomass (g of dry weight) on the percent cover at the end of the experiment. See text for more details.

between grazing and enrichment in this nutrient-poor environment is surprising and contrasts with expectations (Worm et al., 2002; Burkepile and Hay, 2006).

4.1. Effectiveness of enrichment method

Quantification of nitrate and nitrite concentrations in water over the experimental plots showed that the treatments with fertilizer-filled diffusers were enriched compared to treatments with the control, plastic-bead-filled diffusers. The levels of enrichment achieved were, at times, comparable to nutrient-rich sites in New Zealand (on the order of 10 uM: Vincent et al., 1991; Chang et al., 1995) and to nutrient-rich sites in more productive temperate reef systems (e.g. Oregon, USA, on the order of 30 μM: (Dickson and Wheeler, 1995; Hill and Wheeler, 2002)). Although it was impossible to quantify nutrient concentrations under all possible environmental conditions, we had expected *a priori* that the enrichment treatment would be effective at some points in time, and not at others. This type of pulse enrichment has been shown to affect algal communities in other experiments (Miller and Hay, 1996; Nielsen, 2001). Also, it is possible that additional nutrients were still available under turbulent conditions; Worm et al. (2000) found that the benthic enrichment method used here worked similarly at a wave protected and a wave exposed site. The low N+N concentrations in unenriched plots indicate that the plots were spaced far enough apart for the enrichment treatments to be independent. Also, the increase in the abundance of foliose algae in high enrichment plots without grazers is another indication that the nutrient-diffuser bags successfully enriched the surrounding environment.

4.2. Response to grazer and nutrient manipulations

As expected (H_1), consumers depressed the abundance and diversity of primary producers in this nutrient-poor environment. However, contrary to expectations (H_2), top-down control remained strong—irrespective of enrichment. Enrichment had neither independent nor grazer-dependent effects on algal abundance and diversity.

In this system, when grazers were present, increased nutrients did not compensate for the overriding importance of grazers. Even with high enrichment, when grazers were allowed access to experimental plots, algal abundance and diversity remained low. When grazer densities were reduced by eliminating half of the limpets originally present in the plots, algal abundance and diversity remained as low as they were in the high grazing conditions. Despite this similarity in overall food abundance, we found increased individual weights of *C. ornata* in the intermediate vs. the high-density treatments. These findings corroborate those of previous workers who have demonstrated a negative relationship between limpet density and limpet growth and survival (Thompson et al., 2000; Boaventura et al., 2003; Dunmore and Schiel, 2003). Thus, even with reduced densities, limpets can compensate by increasing their intake and thus maintain very low abundance and diversity of algal assemblages.

Limpet densities in our "intermediate grazing" treatment, though intermediate relative to local ambient limpet densities, were still quite high. In an experiment conducted with *C. ornata* nearby, Dunmore and Schiel (2003) found that densities above 16 limpets/0.25 m^2 were sufficient to preclude macroalgal growth. Our intermediate grazing treatment used a mixed-species assemblage and a wide range of limpet sizes but had densities of 125-188 limpets/0.25 m^2. Thus, the lack of algal growth, with even half of the limpets removed, is consistent with previous findings. And though "intermediate" in this context, it still represents a substantial level of herbivory.

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

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

The lack of a difference in C:N in *Scytothamnus australis*, the most common corticated alga at this site, suggests that either the growth of *S. australis* was not limited by the background availability of N, or that it was not able to take advantage of increased N (either because the additional N was too ephemeral, the enrichment method inadequate, the emersion times too long, or competition with species (such as foliose algae) with higher uptake rates too fierce). Generally, C:N values above 10 are interpreted as an indication of N-limitation (D'Elia and DeBoer, 1978; Harrison and Druehl, 1982). The values seen in this experiment (18.9-29.0) are thus indicative of N-limitation. These values are quite similar to the range of values (18.5 to approximately 30) seen for the same species elsewhere in New Zealand (Phillips and Hurd, 2003). Based on laboratory experiments, Phillips and Hurd (2003, 2004) suggest that *S. australis* is often not N-limited but rather that it is adapted to maximizing N procurement from a variable supply.

In either the case of a lack of N-limitation or the case of an inability to utilize the added N, the similarity of C:N ratios in *Scytothamnus australis* across enrichment treatments may help explain the apparently contradictory main conclusions of this experiment. The algal community as a whole was not affected by nutrient enrichment because some species were apparently unable to take advantage of the increased N (for methodological or evolutionary reasons), instead, only the foliose algae (those with the fastest uptake-rates) demonstrated improved performance with enrichment in the absence of grazing. This result agrees with the findings of Worm and Sommer (2000), who found that a single short-term pulse of nutrients increased epiphyte growth on *Fucus* but had no direct effect on *Fucus*. In general, ephemeral algae can take up N quickly, but have limited storage capacity, while corticated species have slower uptake rates but higher storage capacities (Fujita, 1985). Burkepile and Hay (2006) suggest that ephemeral, filamentous algae are better able to respond to increased nutrients and are more prevalent in eutrophic environments, while larger perennial algae that are less responsive to nutrients dominate in more oligotrophic areas. Further exploration of the interaction between algal physiology and the size and duration of nutrient pulses will allow for a better understanding of the interactions between algal species under different eutrophication scenarios.

Another potential explanation for the lack of a community-wide response to nutrient enrichment is the duration of this study. Although we carried out the experiment for long enough for abundant and diverse algal assemblages to develop in the absence of grazing, the effects of nutrient enrichment may operate on longer timescales. For example, in a long-term mesocosm experiment, Kraufvelin et al. (2006) saw only very limited effects of nutrient enrichment for 3 years, then a dramatic response in years 4 and 5.

4.3. Community implications

Naturally, the mid- and high-zones of the intertidal at this site are relatively devoid of algae. Elucidating the factors that determine the vertical distribution of algae and macroinvertebrates on rocky-shores is essential to achieving a better mechanistic understanding of rocky-intertidal communities. The development and persistence of an abundant and diverse early-successional algal community in the absence of grazers on the upper shore suggests that grazers, not abiotic factors or propagule supply, limit the distribution of these algae in this system. In a mid-tidal, somewhat sheltered system in Australia, Underwood (1980) found that both grazing and abiotic factors combined to determine the distribution of algae. Similarly, in the low-zone in New Zealand, Hay (1979) found that both limpet grazing and desiccation determined the upper limit of the bull "kelp" *Durvillaea antarctica*. The findings reported here lend support to the notion that the top-down influence of grazers is of the utmost importance in this nutrient-poor system (Lotze et al., 2001; Burkepile and Hay, 2006). However, it is important to note that, even after one year, plots without grazers still were occupied by early-successional algae. The recruitment and survival of perennial species on the upper shore may be determined by physical factors and/or propagule supply.

4.4. Conclusion

As expected, top-down control by grazers appears to be the driving organizing mechanism for algal communities in this nutrient-poor system. However, contrary to expectations, experimentally increased nutrient availability had no community-wide effects. Yet, in contrast to the conclusions drawn from the analysis of the whole algal community, there was an important interactive effect of grazing and enrichment on foliose algae, a key component of the algal system. We conclude that grazing is the primary determinant of algal community structure on the upper shore in this system and that nutrients have only relatively minor effects, primarily on the abundance of ephemeral foliose species. It seems likely that most of the more perennial algal species have limited capacity to respond to nutrient pulses in this nutrient-poor environment.

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References

Adams, N.M., 1994. Seaweeds of New Zealand. Canterbury University Press, Christchurch, New Zealand.
Barr, N.G., Rees, T.A., 2003. Nitrogen status and metabolism in the green seaweed *Enteromorpha intestinalis*: an examination of three natural populations. Mar. Ecol. Prog. Ser. 249, 133–144.
Bender, E., Case, T.J., Gilpin, M., 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65, 1–13.
Benedetti-Cecchi, L., Cinelli, F., 1997. Confounding in field experiments; direct and indirect effects of artifacts due to the manipulation of limpets and macroalgae. J. Exp. Mar. Biol. Ecol. 209, 171–184.
Boaventura, D., Da Fonseca, L.C., Hawkins, S.J., 2003. Size matters: competition within populations of the limpet *Patella depressa*. J. Anim. Ecol. 72, 435–446.
Bokn, T.L., Duarte, C.M., Pedersen, M.F., Marba, N., Moy, F.E., Barron, C., Bjerkeng, B., Borum, J., Christie, H., Engelbert, S., Fotel, F.L., Hoell, E.E., Karez, R., Kersting, K., Kraufvelin, P., Lindblad, C., Olsen, M., Sanderud, K.A., Sommer, U., Sorensen, K., 2003. The response of experimental rocky shore communities to nutrient additions. Ecosystems 6, 577–594.
Bosman, A.L., Dutoit, J.T., Hockey, P.A.R., Branch, G.M., 1986. A field experiment demonstrating the influence of seabird guano on intertidal primary production. Estuar., Coast. Shelf Sci. 23, 283–294.
Bosman, A.L., Hockey, P.A.R., Siegfried, W.R., 1987. The influence of coastal upwelling on the functional structure of rocky intertidal communities. Oecologia 72, 226–232.
Boulding, E.G., Harper, F.M., 1998. Increasing precision in randomised field experiments: barnacle microtopography as a prediction of *Littorina* abundance. Hydrobiol. 378, 105–114.
Burkepile, D.E., Hay, M.E., 2006. Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87, 3128–3139.
Bustamante, R.H., Branch, G.M., Eekhout, S., Robertson, B., Zoutendyk, P., Schleyer, M., Dye, A., Hanekom, N., Keats, D., Jurd, M., Mcquaid, C., 1995. Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. Oecologia 102, 189–201.
Chang, F.H., Bradford-Grieve, J.M., Vincent, W.F., Woods, P.H., 1995. Nitrogen uptake by the summer size-fractionated phytoplankton assemblages in Westland, New Zealand, upwelling system. N.Z. J. Mar. Freshw. 29, 147–161.
Cubit, J.D., 1984. Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. Ecology 65, 1904–1917.
D'Elia, C.F., DeBoer, J.A., 1978. Nutritional studies of two red algae. II. Kinetics of ammonium and nitrate uptake. J. Phycol. 14, 197–211.
Dethier, M.N., Graham, E.S., Cohen, S., Tear, L.M., 1993. Visual versus random-point percent cover estimations: 'objective' is not always better. Mar. Ecol. Prog. Ser. 96, 93–100.
Dickson, M.L., Wheeler, P.A., 1995. Nitrate uptake rates in a coastal upwelling regime: a comparison of PN-specific, absolute, and Chl-a specific rates. Limnol. Oceanogr. 40, 533–543.
Dungan, M.L., 1986. Three-way interactions: barnacles, limpets, and algae in a sonoran desert rocky intertidal zone. Am. Nat. 127, 292–316.
Dunmore, R.A., Schiel, D.R., 2003. Demography, competitive interactions and grazing effects of intertidal limpets in southern New Zealand. J. Exp. Mar. Biol. Ecol. 288, 17–38.
Freidenburg, T.L., Menge, B.A., Halpin, P.M., Webster, M., Sutton-Grier, A., 2007. Cross-scale variation in top-down and bottom-up control of algal abundance. J. Exp. Mar. Biol. Ecol. 347, 8–29.
Fujita, R.M., 1985. The role of nitrogen status in regulating transient ammonium uptake and nitrogen storage by macroalgae. J. Exp. Mar. Biol. Ecol. 92, 283–301.
Gruner, D.S., 2004. Attenuation of top-down and bottom-up forces in a complex terrestrial community. Ecology 85, 3010–3022.
Harrison, P.J., Druehl, L.D., 1982. Nutrient uptake and growth in the Laminariales and other macrophytes: a consideration of methods. In: Srivastava, L.M. (Ed.), Synthetic and degradative processes in marine macrophytes. Walter de Gruyter, Berlin, pp. 99–120.

Hawkins, S.J., Hartnoll, R.G., 1983. Grazing of intertidal algae by marine invertebrates. Oceanogr. Mar. Biol. Ann. Rev. 21, 195–282.
Hay, C., 1979. Some factors affecting the upper limit of the bull kelp *Durvillea antarctica* (Chamisso) Hariot on two New Zealand shores. J. R. Soc. N.Z. 9, 279–289.
Hill, J.K., Wheeler, P.A., 2002. Organic carbon and nitrogen in the northern California current system: comparison of offshore, river plume, and coastally upwelled waters. Prog. Oceanogr. 53, 369–387.
Hillebrand, H., 2002. Top-down versus bottom-up control of autotrophic biomass–a meta-analysis on experiments with periphyton. J. N. Am. Benthol. Soc. 21, 349–369.
Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–638.
Jernakoff, P., 1985. An experimental evaluation of the influences of barnacles, crevices, and seasonal patterns of grazing on algal diversity and cover in an intertidal barnacle zone. J. Exp. Mar. Biol. Ecol. 88, 287–302.
Kraufvelin, P., Moy, F.E., Hartvig, C., Bokn, T.L., 2006. Nutrient addition to experimental rocky shore communities revisited: delayed responses, rapid recovery. Ecosystems 9, 1076–1093.
Lobban, C.S., Harrison, P.J., 1997. Seaweed Ecology and Physiology. Cambridge University Press, Cambridge.
Lotze, H.K., Worm, B., Sommer, U., 2001. Strong bottom-up and top-down control of early life stages of macroalgae. Limnol. Oceanogr. 46, 749–757.
Lubchenco, J., 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64 (5), 1116–1123.
Lubchenco, J., 1986. Relative importance of competition and predation: early colonization by seaweeds in New England. In: Diamond, J.M., Case, T.J. (Eds.), Community Ecology. Harper and Row, New York, pp. 537–555.
Lubchenco, J., Gaines, S.D., 1981. A unified approach to marine plant-herbivore interactions. I. Populations and Communities. Ann. Rev. Ecolog. Syst. 12, 405–437.
McQueen, D.J., Johannes, M.R.S., Post, J.R., Stewart, T.J., Lean, D.R.S., 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecol. Monogr. 59, 289–309.
Meese, R.J., Tomich, P.A., 1992. Dots on rocks: a comparison of percent cover estimation methods. J. Exp. Mar. Biol. Ecol. 165, 59–73.
Menge, B.A., 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. Oecologia (Berl.) 58, 141–155.
Menge, B.A., 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. J. Exp. Mar. Biol. Ecol. 250, 257–289.
Menge, B.A., Daley, B.A., Wheeler, P.A., Dahlhoff, Sanford, E., Strub, P.T., 1997. Benthic-pelagic links and rocky intertidal communities: bottom-up effects on top-down control? Proc. Natl. Acad. Sci. U. S. A. 94, 14530–14535.
Menge, B.A., Daley, B.A., Lubchenco, J., Sanford, E., Dalhoff, E., Halpin, P.M., Hudson, G., Burnaford, J., 1999. Top-down and bottom-up regulation of New Zealand rocky intertidal communities. Ecol. Monogr. 69, 297–330.
Menge, B.A., Lubchenco, J., Bracken, M.E.S., Chan, F., Foley, M.M., Freidenburg, T.L., Gaines, S.D., Hudson, G., Krenz, C., Leslie, H., Menge, D.N.L., Russell, R., Webster, M.S., 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. Proc. Natl. Acad. Sci. U. S. A. 100, 12229–12234.
Menge, B.A., Allison, G.W., Blanchette, C.A., Farrell, T.M., Olson, A.M., Turner, T.A., van Tamelen, P., 2005. Stasis or kinesis? Hidden dynamics of a rocky intertidal macrophyte mosaic revealed by a spatially explicit approach. J. Exp. Mar. Biol. Ecol. 314, 3–39.
Miller, M.W., Hay, M.E., 1996. Coral-seaweed-grazer-nutrient interactions on temperate reefs. Ecol. Monogr. 66, 323–344.
Murtaugh, P.A., 2007. Simplicity and complexity in ecological data analysis. Ecology 88, 56–62.
Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. Nature 423, 280–283.
Nielsen, K.J., 2001. Bottom-up and top-down forces in tide pools: test of a food chain model in an intertidal community. Ecol. Monogr. 71, 187–217.
Nielsen, K.J., Navarrete, S.A., 2004. Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. Ecol. Lett. 7, 31–41.
Paine, R.T., 1966. Food web complexity and species diversity. Am. Nat. 100, 65–75.
Pfister, C.A., Van Alstyne, K.L., 2003. An experimental assessment of the effects of nutrient enhancement on the intertidal kelp Hedophyllum sessile (Laminariales, Phaeophyceae). J. Phycol. 39, 285–290.
Phillips, J.C., Hurd, C.L., 2003. Nitrogen ecophysiology of intertidal seaweeds from New Zealand: N uptake, storage and utilisation in relation to shore position and season. Mar. Ecol. Prog. Ser. 264, 31–48.
Phillips, J.C., Hurd, C.L., 2004. Kinetics of nitrate, ammonium, and urea uptake by four intertidal seaweeds from New Zealand. J. Phycol. 40, 534–545.
Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the quest for keystones. BioScience 46, 609–620.
Proulx, M., Mazumder, A., 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. Ecology 79, 2581–2592.
Ryther, J.H., Dunstan, W.M., 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. Science 171, 1008–1013.
Schiel, D.R., 2004. The structure and replenishment of rocky shore intertidal communities and biogeographic comparisons. J. Exp. Mar. Biol. Ecol. 300, 309–342.
Schiel, D.R., Marine Ecology Research Group, 2006. Guide to common intertidal species of the South Island, New Zealand. University of Canterbury, Christchurch, New Zealand.
Schramm, W., 1999. Factors influencing seaweed responses to eutrophication: some results from EU-project EUMAC. J. Appl. Phycol. 11, 69–78.
Sokal, R.R., Rohlf, F.J., 1995. Biometry: The Principles and Practice of Statistics in Biological Research. W. H. Freeman and Company, New York.
Steneck, R.S., Watling, L., 1982. Feeding capabilities and limitations of herbivorous molluscs: a functional group approach. Mar. Biol. 68, 299–319.
Steneck, R.S., Dethier, M.N., 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69, 476–498.
Suding, K.N., Collins, S.L., Gough, L., Clark, C., Cleland, E.E., Gross, K.L., Milchunas, D.G., Pennings, S., 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proc. Natl. Acad. Sci. U. S. A. 102, 4387–4392.
Thompson, R.C., Roberts, M.F., Norton, T.A., Hawkins, S.J., 2000. Feast or famine for intertidal grazing molluscs: a mis-match between seasonal variations in grazing intensity and the abundance of microbial resources. Hydrobiol. 440, 357–367.
Underwood, A.J., 1980. The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. Oecologia 46, 201–213.
Underwood, A.J., Jernakoff, P., 1984. The effects of tidal height, wave-exposure, seasonality and rock-pools on grazing and the distribution of intertidal macroalgae in New South Wales. J. Exp. Mar. Biol. Ecol. 75, 71–96.
Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, D., Foreman, K., 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnol. Oceanogr. 42, 1105–1118.
Vincent, W.F., Howard-Williams, C., Tildesley, P., Butler, E., 1991. Distribution and biological properties of oceanic water masses around the South Island, New Zealand. N.Z. J. Mar. Freshw. 25, 21–42.
Vinueza, L.R., Branch, G.M., Branch, M.L., Bustamante, R.H., 2006. Top-down herbivory and bottom-up El Niño effects on Galapagos rocky-shore communities. Ecol. Monogr. 76, 111–131.
Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. Science 277, 494–499.
Wootton, J.T., Power, M.E., Paine, R.T., Pfister, C.A., 1996. Effects of productivity, consumers, competitor, and El Niño events on food chain patterns in a rocky intertidal community. Proc. Natl. Acad. Sci. U. S. A. 93, 13855–13858.
Worm, B., Sommer, U., 2000. Rapid direct and indirect effects of a single nutrient pulse in a seaweed-epiphyte-grazer system. Mar. Ecol. Prog. Ser. 202, 283–288.
Worm, B., Lotze, H.K., Bostrom, C., Engkvist, R., Labanauskas, V., Sommer, U., 1999. Marine diversity shift linked to interactions among grazers, nutrients and propagule banks. Mar. Ecol. Prog. Ser. 185, 309–314.
Worm, B., Reusch, T.B.H., Lotze, H.K., 2000. In situ nutrient enrichment: methods for marine benthic ecology. Int. Rev. Hydrobiol. 85, 359–375.
Worm, B., Lotze, H.K., Hillebrand, H., Sommer, U., 2002. Consumer versus resource control of species diversity and ecosystem functioning. Nature 417, 848–851.