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# Top-down and bottom-up factors in tidepool communities

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## Abstract

Recent studies suggest that nutrient variation influences rocky intertidal community structure, however empirical evidence is rare. In the Gulf of Maine, tidepools that occur on seagull feeding roosts are potentially subjected to regular nutrient loading from seagull guano. The results of a survey conducted on Swan's Island, ME show that roost tidepools have very low macroinvertebrate and macroalgal diversity as well as very high phytoplankton biomass compared to non-roost tidepools. An experiment presented here tested basic food chain hypotheses in tidepool communities. These basic food chain models predict that in a tidepool with one trophic level (phytoplankton only), phytoplankton biomass will increase when nutrients are enriched. In contrast, these models predict that in two trophic level tidepools (phytoplankton and mussels) herbivory will prevent an increase in phytoplankton biomass when nutrients are enriched. A short term $2 \times 2$ factorially designed field experiment was used to test this basic conceptual model using herbivory by mussels and enrichment with nitrogen as the main effects. The results of this investigation are consistent with the predictions of basic food chain models, and indicate that over the short time interval of a few days, herbivory by mussels is sufficient to maintain low phytoplankton levels following enrichment with nitrogen. Experimental enrichment with phosphorus in this study had no effect on phytoplankton biomass. The results of this study suggest that periodic pulses of nitrogen into tidepools will have little effect on phytoplankton biomass when mussels are present and that longer-term chronic nitrogen influxes may be driving the patterns of community structure in tidepools occurring on roosts.

*Keywords:* Tidepool; Rocky intertidal; Community ecology; Nutrient enrichment; Top-down; Bottom-up

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## 1. Introduction

Models of trophic regulation predict either consumer control, resource control, or co-limitation by consumers and resources (for review, see Power, 1992). Proponents of strict consumer (top-down) control contend that all trophic levels are potentially predator-limited (Menge and Sutherland, 1976), whereas those who support control by resources (bottom-up control) propose that producers limit all upper levels (White, 1978). Most models, however, support co-limitation by consumers and resources (e.g. Hairston et al., 1960). The basic food chain models developed by Fretwell (1977) and Oksanen et al. (1981) predict that adjacent trophic levels will be controlled alternately by consumers or resources depending on the position of the trophic level of interest relative to the top level. These models make contrasting predictions for odd and even-numbered food chains (Fretwell, 1977; Oksanen et al., 1981). For example, these models predict that nutrient enrichment will cause an increase in primary producer biomass in a one trophic level food chain (primary producers only), whereas for a two trophic level food chain (primary producers and herbivores), these models predict that herbivory will prevent a significant change in primary producer biomass when nutrients are enriched (Fretwell, 1977; Oksanen et al., 1981). Other factors that may contribute to co-limitation include attenuation of top-down effects at lower trophic levels (McQueen et al., 1989), predator–predator interactions (Getz, 1984; Arditi and Ginzburg, 1989), changing resource requirements throughout the lifetime of the predator (Mittelbach et al., 1988), variation in prey edibility (Leibold, 1989), variability in the vulnerability of prey to predation and disease (Sinclair and Norton-Griffiths, 1979), spatial heterogeneity (Sih, 1982; Power, 1984; Mittelbach et al., 1988), functional heterogeneity among species (Hunter and Price, 1992), and species diversity (Strong, 1992) (see Power, 1992 for review of top-down and bottom-up control models).

In rocky intertidal communities, bottom-up control factors have received relatively little attention (Menge, 2000). However, accumulating evidence indicates that productivity is limited by nutrient availability in these systems. For example, elevated nutrient levels caused by near shore oceanographic conditions have been linked to increased intertidal primary and secondary production (Menge, 1992; Bustamante et al., 1995; Menge et al., 1997a,b, 1999). Nutrients that are translocated by seagulls from marine to terrestrial environments have also been shown to cause higher primary production and detritivorous beetle abundance on bird roosting islands in the Gulf of California (Polis and Hurd, 1996; Stapp et al., 1999; Sanchez-Piñero and Polis, 2000), and have also been associated with higher intertidal macroinvertebrate and algal abundance in South Africa (Bosman and Hockey, 1986). Despite this evidence for nutrient limitation in intertidal marine communities, few experiments have manipulated nutrient levels in the rocky intertidal due to problems associated with maintaining elevated nutrient levels in open systems. Instead, most experiments have focused on herbivory, predation, competition, and physical stress (Connell, 1961; Dayton, 1971; Lubchenco and Menge, 1978; Petraitis, 1983). However, some studies have shown that experimentally enriched nutrients can increase intertidal primary production (Bosman et al., 1986), but these effects have also been shown to vary with wave exposure intensity (Nielsen, 2001), seasonal climate fluctuations (Wootton et al., 1996), and treatment replicate (Metaxas and Scheibling, 1996).

Tidepools along rocky shores provide a novel setting in which to study top-down and bottom-up control factors. Unlike most hard-bottom marine communities, tidepools have well-defined boundaries, allowing nutrients as well as herbivores to be manipulated easily, and are commonly found along the shore, allowing treatments to be suitably replicated. Moreover, in the Gulf of Maine, there is a heterogeneous distribution of nutrients among tidepools caused by the disproportionately high rate of nutrient deposition into tidepools

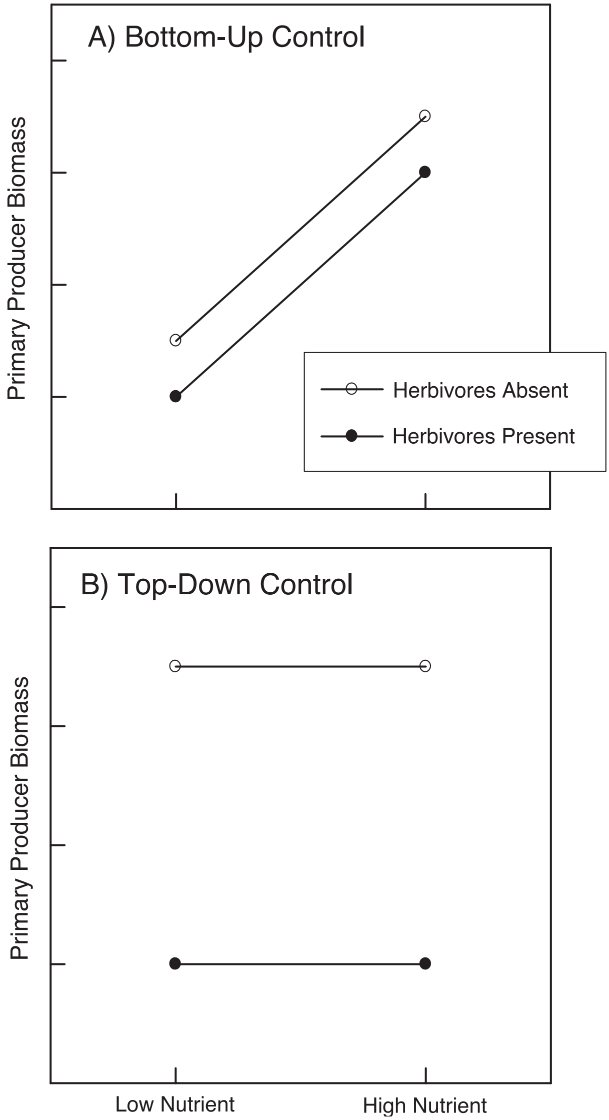

Fig. 1. Predictions of experimental outcome based on basic trophic interaction models for a (A) one trophic level system and for a (B) two trophic level system (Fretwell, 1977; Oksanen et al., 1981).

occurring on intertidal avian feeding roosts. Herring gulls (*Larus argentatus*) and great black-backed gulls (*Larus marinus*) use the hard substrate in the high intertidal zone like an anvil to break open hard shelled prey items collected from the low intertidal and subtidal zones. These high intertidal roosting sites are on the order of 100s of square meters in size and are characterized by guano-stained rocks, the presence of prey remains, and an orange lichen that grows exclusively in association with excreted bird guano (Petraitis, personal communication). Tidepools that occur on gull feeding roosts, hereafter referred to as roost pools, are potentially exposed to high rates of nutrient loading from seagull guano. Gulls, however, do not forage in tidepools (Methratta, personal observation). Nutrient enrichment (Bosman et al., 1986) and herbivory (Lubchenco, 1978; Benedetti-Cecchi and Cinelli, 1996) separately have been shown to have significant effects on the abundance and distribution of tidepool algae, but few studies have considered both factors (Nielsen, 2001; Metaxas and Scheibling, 1996).

To examine the effects of nutrient enrichment on high intertidal tidepool community structure, a survey of biological and chemical characteristics of roost and non-roost tidepools was conducted on Swan's Island, Maine (44°10′N, 68°25′W). Following this survey, a replicated, factorially designed field experiment was carried out in which nutrients (nitrogen or phosphorus) and herbivores (the blue mussel, *Mytilus edulis*) were manipulated to test the basic food chain models presented by Fretwell (1977) and Oksanen et al. (1981) for a one trophic level system (phytoplankton only) and for a two trophic level system (phytoplankton and mussels). These models predict that in the one trophic level system, phytoplankton biomass will increase when enriched with nutrients (Fig. 1A). However, when nutrients are enriched in the two trophic level system, the models predict that herbivory by mussels will prevent an increase in phytoplankton biomass (Fig. 1B). Because tidepools in this system are believed to receive nutrients in pulses from seagull guano, an ecologically relevant time period (56 h) was chosen for this experiment to evaluate the immediate response of tidepool phytoplankton biomass to a pulse nutrient enrichment event.

## 2. Methods

### 2.1. Tidepool surveys

Biological and chemical characteristics were surveyed in tidepools around Swan's Island during three separate surveys. Benthic macroalgal species richness, benthic macroinvertebrate species richness, and salinity were measured in 16 non-roost and 10 roost high intertidal pools in July 1998. In eight of the roost pools and eight of the non-roost pools, dissolved nutrient concentrations (nitrate, ammonium, and soluble reactive phosphorus or SRP) were sampled. Salinity of tidepool water was measured using an optical salinometer. Dissolved nutrient samples were collected in the field by filtering a known volume of tidepool water through a Whatman GF/F glass fiber filter and into an acid washed bottle. These filtered water samples were frozen immediately and transported back to the laboratory where dissolved nutrient concentrations were measured with an Alpkem autoanalyzer (RFA 300) (Strickland and Parsons, 1972). In August 1999, macroinvertebrate abundance and percent cover of macroalgae and barnacles (*Semibalanus balanoides*) were measured to quantify the community composition of 24 non-roost and eight roost pools at a site called East Point on Swan’s Island. Percent cover was measured by pushing a 100 cm$^2$ quadrat against the bottom surface of the tidepool, and counting the number of 1 cm$^2$ squares in the quadrat occupied by each species. The average of five replicate quadrat measures for each tidepool was used in statistical analyses. Macroinvertebrate abundance was determined by counting the total number of benthic macroinvertebrates in each tidepool. Phytoplankton biomass was estimated by measuring chlorophyll a concentrations in 15 non-roost and 8 roost high intertidal pools at East Point in August 2000. Chlorophyll *a* was measured by filtering a known volume of pool water through a Whatman GF/F glass fiber filter. These filters were then frozen in the dark immediately and returned to the laboratory. Chlorophyll a was extracted from the filters with 90% acetone and then the concentration of chlorophyll a in each sample was determined fluorometrically (Turner

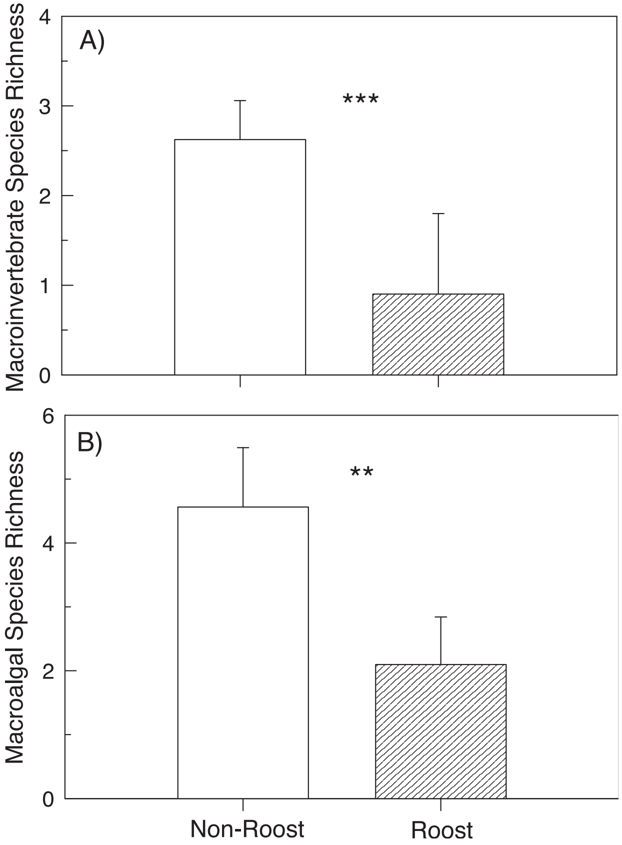

Fig. 2. Species Richness. (A) Macroinvertebrate species richness ($MS_{Error} = 1.2771$, $F = 14.3386$, $p = 0.0009$, ANOVA, $df = 1, 24$). (B) Macroalgal species richness ($F = 7.6676$, $MS_{Error} = 2.2697$, $p = 0.0109$, ANCOVA, $df = 1, 23$). Error bars represent 95% confidence intervals. Significance levels are indicated as follows: $*p \leq 0.05$, $**p \leq 0.01$, and $***p \leq 0.001$, $****p \leq 0.0001$.

Table 1
The percentage of surveyed roost and non-roost tidepools in which macroinvertebrate species were present

| | Frequency | |
|---|---|---|
| | Roost, % ($n=10$) | Non-roost, % ($n=16$) |
| *Littorina littorea* | 30 (3) | 93.75 (15) |
| *Mytilus edulis* | 0 (0) | 81.25 (13) |
| *Semibalanus balanoides* | 10 (1) | 75 (12) |
| *Tectura testudinalis* | 0 (0) | 18.75 (3) |
| *Littorina obtusata* | 10 (1) | 6.25 (1) |
| *Littorina rudis* | 0 (0) | 6.25 (1) |
| *Nucella lapillus* | 0 (0) | 6.25 (1) |

The number of pools in which each organism was present is given in parentheses.

fluorometer TD 700) using the acidification method (Strickland and Parsons, 1972). To maintain a clean work area both in the field and in the laboratory, gloves were always worn when handling nutrient and chlorophyll samples and all instruments were rinsed thoroughly with dilute acid and double-distilled water between samples.

During each of the three surveys, the physical dimensions of the tidepools were also measured. The length and width of each tidepool were measured by running a tape measure along the major axes of each tidepool dimension. Five measures of tidepool depth were taken by randomly placing the end of a meter stick on the bottom of the pool and

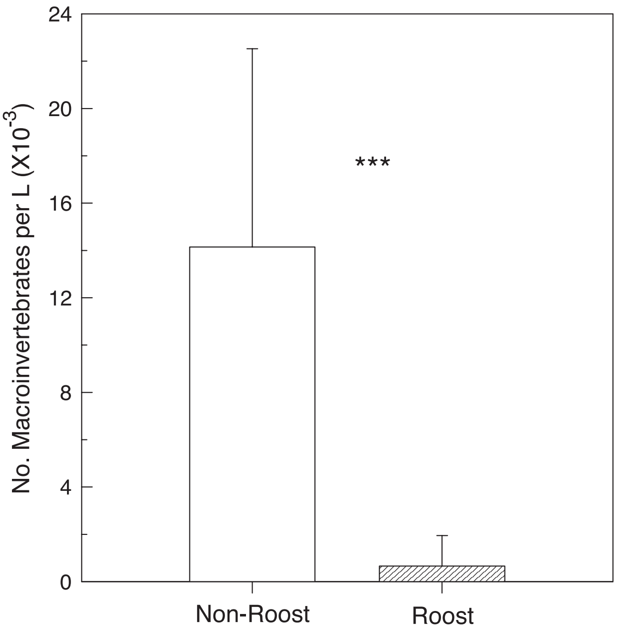

Fig. 3. Abundance of macroinvertebrates in surveyed tidepools ($F=12.8628$, $MS_{Error}=1192.59$, $p=0.0012$, ANCOVA, $df=1$, 29). See Table 1 for the species present. Error bars represent 95% confidence intervals. Significance is indicated as in Fig. 2.

recording the height of the water level. With this information and an estimate of the shape of the pools, the volume and surface area of each tidepool were estimated.

One-way analysis of variance (ANOVA) with nutrient level (roost vs. non-roost) as the main effect was used to analyze percent cover, benthic invertebrate species richness, dissolved nutrient, and salinity data. Macroalgal species richness and invertebrate abundance were both significantly correlated with tidepool surface area, so an analysis of covariance (ANCOVA) was used with surface area as the covariate and nutrient level as the main effect. Phytoplankton biomass was significantly correlated with the tidepool surface area to volume ratio (SA/V), and so the SA/V ratio was used as the covariate in an ANCOVA with nutrient level as the main effect.

### 2.2. Experimental design

A 2 × 2 factorial design in which the treatments were mussels only, nitrogen only, nitrogen + mussels, and control (no manipulation) was used to investigate the effects of herbivory by mussels and nutrient enrichment on tidepool phytoplankton biomass. A fifth

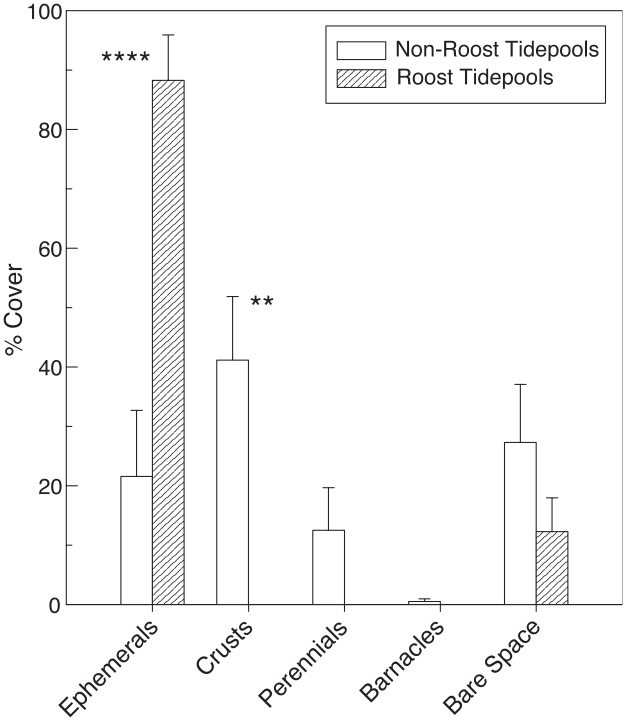

Fig. 4. Percent cover in surveyed tidepools. (Ephemerals: $F = 27.9743$, $MS_{Error} = 738.0$, $p < 0.0001$, ANOVA; Crusts: $F = 10.0783$, $MS_{Error} = 661.48$, $p = 0.0035$, ANOVA; Perennials: $F = 3.8032$, $MS_{Error} = 245.845$, $p = 0.0606$, ANOVA; Barnacles: $F = 1.5036$, $MS_{Error} = 0.9646$, $p = 0.2297$, ANOVA; Bare Space: $F = 2.9420$, $MS_{Error} = 476.89$, $p = 0.0966$, ANOVA). All tests had 1 and 30 degrees of freedom. Error bars represent 95% confidence intervals. Significance is indicated as in Fig. 2.

treatment of phosphorus enrichment only was used to investigate the effect of phosphorus enrichment on phytoplankton biomass. Each treatment was replicated in four individual non-roost tidepools. The tidepools used in this experiment were a subset of those surveyed during 1999 (see tidepool survey methods). Because the experimental tidepools occur so high in the intertidal (12.6 ± 0.4 ft, average ± 95% CI, measured using a surveying transit), they are infrequently flushed by the high tide, however some pools did receive tidal spray during the course of the study. The experiment was conducted during the second week of August 1999.

The consumer in this experiment was the suspension-feeding blue mussel, *M. edulis*. For treatments involving mussels, five medium-sized (5–7 cm in length) individuals were added to tidepools approximately 1 day before experiment initiation so that the mussels could attach to the substrate and orient themselves. The density of mussels used was chosen to approximate natural densities. Because the natural source of nutrient enrichment in this system is believed to be seagull guano (personal observation), nitrogen and phosphorus, the nutrients found in guano (Burger et al., 1978; Lindeboom, 1984; Loder et al., 1996), were manipulated in this experiment. Treatments involving nitrogen enrichment received $NH_4Cl$, and phosphorus addition treatments received $KH_2PO_4$. Nutrients were added with the intention of increasing dissolved ammonium and soluble reactive phosphorus (SRP) concentrations to the highest levels detected during preliminary surveys. Pools were stirred following nutrient addition to ensure an even distribution of nutrients. The time at which nutrients were added was considered to be the point of experiment initiation.

Chlorophyll a concentration, which was used as a measure of phytoplankton biomass, was sampled in all 20 pools before nutrients or mussels were added to any tidepools (pre-treatment) and then at 0.25, 6, 24, 32, 48, and 56 h following treatment addition. For each pool at each sampling interval, the average of duplicate chlorophyll a samples was used in

Table 2
The percentage of surveyed roost and non-roost tidepools in which macroalgal species were present

| | Frequency | |
|---|---|---|
| | Roost, % (*n* = 10) | Non-roost, % (*n* = 16) |
| *Ralfsia* spp. | 0 (0) | 93.75 (15) |
| *Hildenbrania* spp. | 0 (0) | 81.25 (13) |
| *Chondrus crispus* | 0 (0) | 62.5 (10) |
| *Fucus vesiculosus* | 0 (0) | 56.25 (9) |
| *Cladaphora* spp. | 20 (2) | 37.5 (6) |
| *Sytosiphon* spp. | 0 (0) | 37.5 (6) |
| *Ascophyllum nodosum* | 0 (0) | 31.25 (5) |
| *Rhizoclonium* spp. | 70 (7) | 18.75 (3) |
| *Clathromorphum* spp. | 0 (0) | 12.5 (2) |
| *Enteromorpha intestinalis* | 50 (5) | 12.5 (2) |
| *Halosaccion* spp. | 0 (0) | 12.5 (2) |
| *Petrocelis* spp. | 0 (0) | 12.5 (2) |
| *Laminaria* spp. | 0 (0) | 6.25 (1) |
| *Spongemorpha* spp. | 0 (0) | 6.25 (1) |

The number of pools in which each organism was present is given in parentheses.

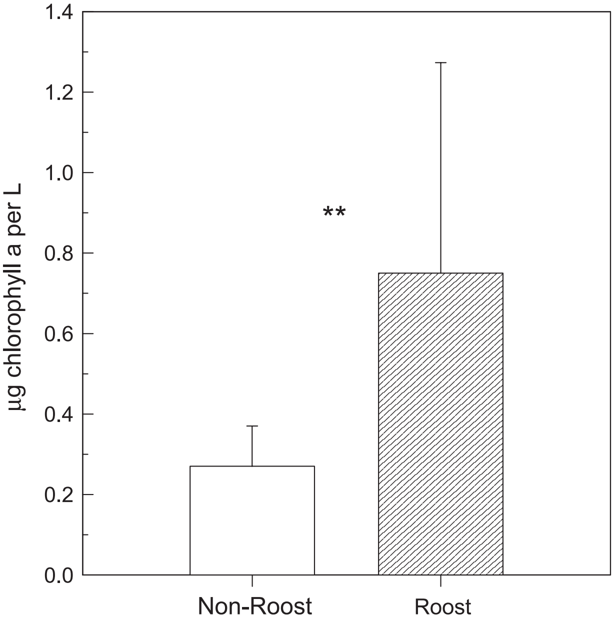

Fig. 5. Phytoplankton biomass (chlorophyll *a* concentration) in surveyed roost and non-roost tidepools. ($F = 10.3032$, $MS_{Error} = 0.15919$, $p = 0.0042$, ANCOVA, $df = 1, 20$). Significance is indicated as in Fig. 2.

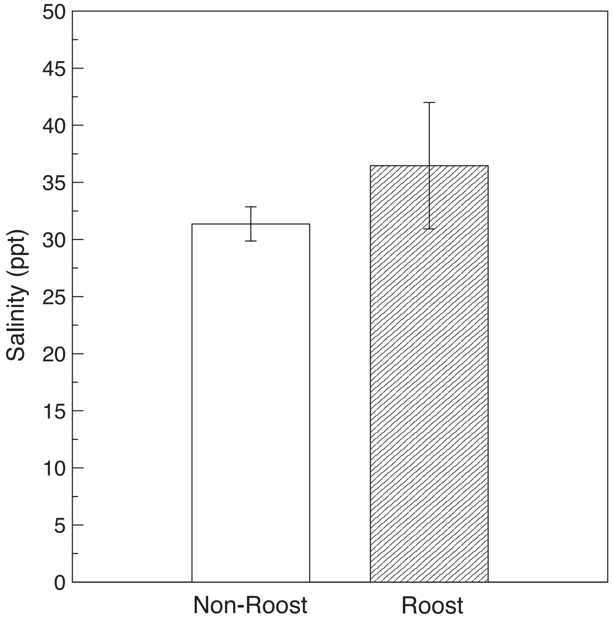

Fig. 6. Salinity of surveyed tidepools ($F = 2.9864$, $MS_{Error} = 160.297$, $p = 0.0968$, ANOVA, $df = 1, 24$).

statistical analyses. Dissolved nutrient concentrations (nitrate, ammonium, and SRP) were sampled at the 0, 0.25, and 24-h sampling intervals. Only one tidepool from each treatment was sampled during the 6 h sampling interval due to logistical constraints, so this timepoint was dropped from the analyses. One of the phosphorus addition pools was not sampled at the 24-h sampling interval, and so there are only three replicate tidepools for this treatment in all statistical analyses.

To sample phytoplankton biomass and nutrient concentrations, a syringe was used to filter a known volume of tidepool water through a Whatman GF/F glass fiber filter. Filtrates were collected in acid-washed bottles, frozen immediately, and then returned to the laboratory for dissolved nutrient analysis using an Alpkem autoanalyzer as before (Strickland and Parsons, 1972). The glass fiber filters from this filtration were frozen in the dark immediately and returned to the laboratory. Chlorophyll *a* was extracted from the filters with 90% acetone and then the concentration of pigment in each sample was measured fluorometrically as before (Strickland and Parsons, 1972). Care was taken to maintain a clean work area both in the field and in the laboratory as before.

Tidepools that had higher phytoplankton biomass prior to treatment additions showed a stronger response to treatment manipulations. To account for this, the response of phytoplankton biomass to treatments on each sampling date was analyzed using an ANCOVA with the pre-treatment phytoplankton biomass for each tidepool used as a covariate. Phytoplankton biomass was not significantly correlated with the surface area to volume ratio as it had been during the tidepool surveys, presumably because phytoplankton biomass was generally lower for all tidepools during the experiment than it had been during the surveys. The data were log-transformed to meet the assumptions of ANOVA.

Table 3
Dissolved nutrient concentrations from the 1998 tidepool survey

| | Nitrate (μM) | Ammonium (μM) | SRP (μM) | N/P |
|---|---|---|---|---|
| Nonroost tidpools | 0.571 | 22.9 | 5.19 | 4.53 |
| | 0.500 | 6.43 | 1.16 | 5.99 |
| | 0.500 | 27.7 | 3.81 | 7.40 |
| | 0.143 | 6.71 | 1.91 | 3.60 |
| | 0.071 | 5.43 | 0.813 | 6.77 |
| | 0.071 | 1.21 | 0.281 | 4.57 |
| | 0.214 | 1.71 | 0.469 | 4.11 |
| | 0.714 | 11.9 | 1.28 | 9.81 |
| Roost tidepools | 0.071 | 2.5 | 17.06 | 0.151 |
| | 0.357 | 2.36 | 1.34 | 2.02 |
| | 0.286 | 1.79 | 0.343 | 6.03 |
| | 0.286 | 1.79 | 0.594 | 3.49 |
| | 0.071 | 1.50 | 0.438 | 3.59 |
| | 68.5 | 23.1 | 31.5 | 2.90 |
| | 2.71 | 9.71 | 3.06 | 4.06 |
| | 0.214 | 2.50 | 2.28 | 1.19 |

For non-roost pools (average ± 95% CI): Nitrate: 0.348 ± 0.174; Ammonium: 10.5 ± 6.79; SRP: 1.86 ± 1.21; N:P: 5.85 ± 1.44; For roost pools: Nitrate: 9.06 ± 16.65; Ammonium: 5.65 ± 5.22; SRP: 7.08 ± 7.86; N:P: 2.93 ± 1.26. (Nitrate: $F=1.0517$, $p=$ns, ANOVA; Ammonium: $F=1.2296$, $p=$ns, ANOVA; SRP: $F=1.6535$, $p=$ns, ANOVA; N/P ratio: $F=8.9030$, $p<0.01$, ANOVA. All tests have 1 and 14 degrees of freedom. The notation ns indicates a non-significant result.

Planned contrasts were made among treatments to determine the effects of consumers (“mussels only” and “nitrogen + mussel” tidepools versus “control” and “nitrogen only” tidepools), nitrogen enrichment (“nitrogen only” and “nitrogen + mussel” tidepools versus “mussels only” and “control” tidepools), and the effect of the consumer × nitrogen itrogen interaction (“mussels only” and “nitrogen only” tidepools versus “control” and “nitrogen + mussels” tidepools). A contrast between “phosphorus only” tidepools and “control” tidepools was also performed to examine the effect of phosphorus enrichment. The dissolved nutrient concentrations of tidepool water (nitrate, ammonium, SRP, N/P) were analyzed using repeated-measures ANOVA to determine whether nutrient enrichment treatments were successful and whether mussel manipulations affected nutrient levels. All statistical calculations were carried out using either proc GLM in SAS or JMPin (SAS Institute, 1990, 1996).

## 3. Results

### 3.1. Tidepool survey results

Community structure differed between roost and non-roost tidepools. Benthic macroinvertebrates were rare in roost tidepools whereas in non-roost tidepools, a diverse community of benthic invertebrates was present (Fig. 2A, Table 1). Both macroinvertebrate abundance and species richness were significantly greater in non-roost tidepools

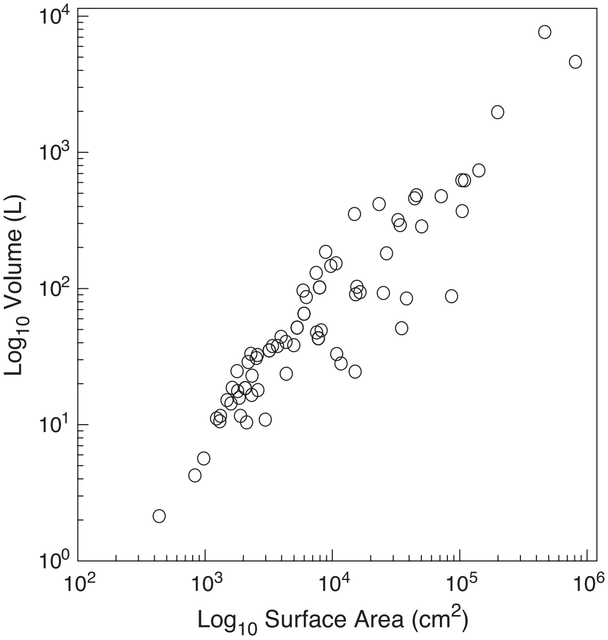

Fig. 7. Tidepool sizes. Surface area vs. volume of tidepools surveyed during 1998, 1999, and 2000.

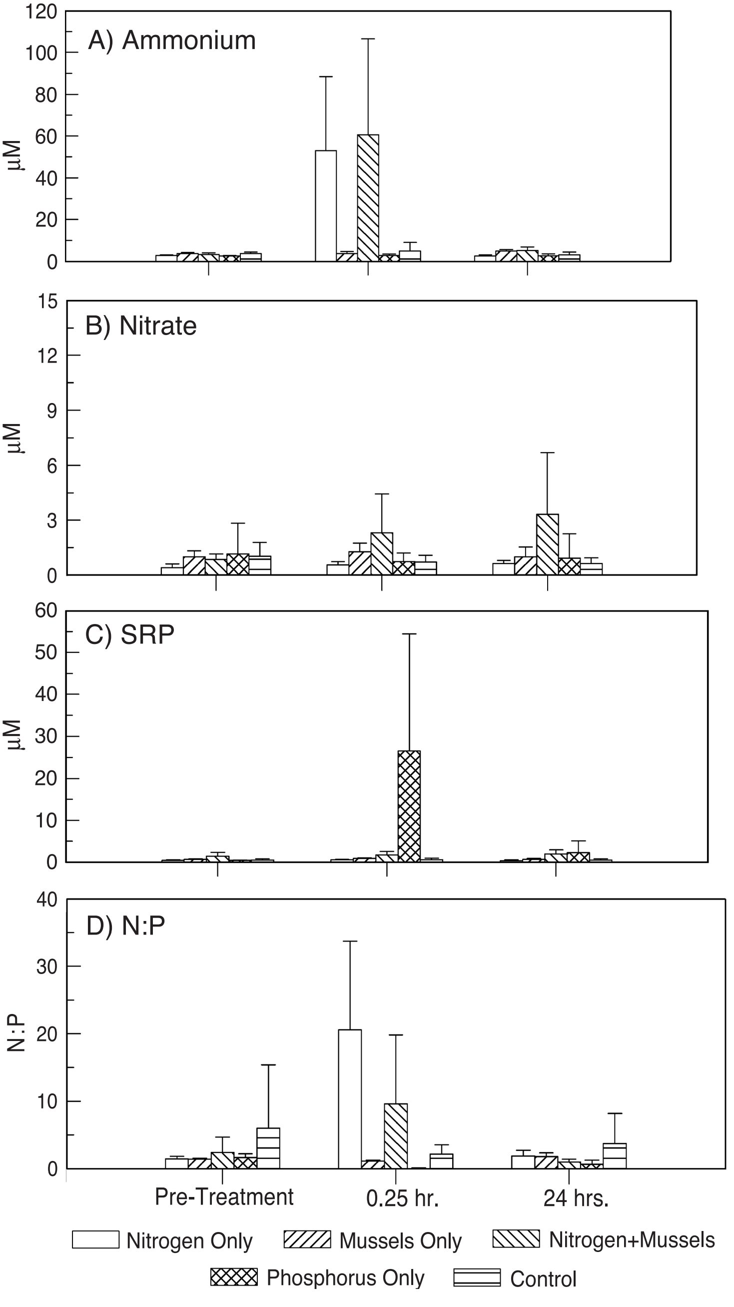

Fig. 8. Dissolved nutrient concentrations for all experimental tidepools throughout the experiment. Error bars represent the 95% confidence intervals.

(Figs. 2A and 3). The benthic macroalgal community also differed between tidepool types. Ephemeral species as well as the perennial species were present in non-roost tidepools (Fig. 4, Table 2). Roost tidepools, in contrast, contained primarily ephemeral green macroalgae and so species richness was significantly lower in roost tidepools (Fig. 2B). Percent cover of ephemeral and encrusting algae was also significantly greater in non-roost tidepools (Fig. 4). Phytoplankton biomass levels, however, were significantly higher in roost tidepools (Fig. 5). Salinity did not differ between roost and non-roost tidepools and both were well within the range of marine systems, suggesting that freshwater input (e.g. from rain) is insignificant compared to inputs of water from the open ocean (Fig. 6). Dissolved nutrient concentrations were not significantly different between roost and non-roost tidepools, although the nutrient levels were notably more variable in the roost tidepools, particularly for SRP (Table 3). The relatively low levels of ammonium and relatively high levels of SRP in roost tidepools contributed to the significantly lower N/P values in roost tidepools. The surface area and volume of all tidepools studied during the surveys and the experiment are shown in Fig. 7.

### 3.2. Experimental results

Nutrient enrichment treatments were successful (Fig. 8, Table 4). The dissolved ammonium concentration was significantly increased in tidepools that received nitrogen enrichment. There were also significant effects of time and the time × nitrogen interaction

Table 4
Results of the repeated-measures ANOVA for the responses of dissolved nutrient concentrations to experimental treatments

| Effect | *F* ratios | | | | |
|---|---|---|---|---|---|
| | *df* | Ammonium | Nitrate | SRP | N/P |
| *Between subjects* | | | | | |
| Treatment | 4 | 4.32* | 1.05 | 5.91** | 2.37 |
| Nitrogen | 1 | 14.00** | 1.12 | 0.08 | 3.75 |
| Consumer | 1 | 0.17 | 1.58 | 0.24 | 2.99 |
| Nitrogen × consumer | 1 | 0.13 | 1.32 | 0.12 | 0.10 |
| Phosphorus | 1 | 0.03 | 0.00 | 16.88*** | 1.36 |
| Error | 14 | | | | |
| *Within Subjects* | | | | | |
| Time | 2 | 11.65*** | 0.85 | 5.28** | 5.29** |
| Time × Treatment | 8 | 4.39* | 0.84 | 4.23** | 4.37** |
| Time × nitrogen | 2 | 15.00**** | 1.01 | 0.00 | 12.19*** |
| Time × consumer | 2 | 0.04 | 1.02 | 0.00 | 1.04 |
| Time × Nitrogen × Consumer | 2 | 0.09 | 1.18 | 0.00 | 2.57 |
| Time × phosphorus | 2 | 0.00 | 0.00 | 11.49*** | 0.09 |
| Error | 28 | | | | |

Significance levels are indicated as follows: $*p \leq 0.05$, $**p \leq 0.01$, and $***p \leq 0.001$, $****p \leq 0.0001$. (a) Between-subject MSError and (b) within-subject MSError terms are as follows: For ammonium: (a) MSError = 49724.052, (b) MSError = 48766.986; For nitrate: (a) MSError = 18531.933, (b) MSError = 11074.010; For SRP: (a) MSError = 26381.706, (b) MSError = 32099.718; For N/P (a) MSError = 38.322, (b) MSError = 24.690.

on both the dissolved ammonium concentration and N/P ratio, indicating that dissolved ammonium was elevated by the pulse nutrient enrichment initially, and that this effect diminished over time as the dissolved nitrogen was taken up by tidepool organisms. Similarly, the soluble reactive phosphorus (SRP) concentration increased significantly in tidepools that received phosphorus enrichments, and this effect also diminished over time as dissolved phosphorus was used by tidepool organisms. The N/P ratio was not significantly changed by phosphorus addition. Dissolved nitrate concentrations remained relatively unchanged in all treatments throughout the study.

Phytoplankton biomass was variable throughout the study. There was a trend of elevated phytoplankton biomass in tidepools that received nitrogen enrichment, but this effect was not significant (Fig. 9, Table 5). At the final sampling timepoint (56 h), there was a significant consumer effect indicating that herbivory by mussels was maintaining relatively low phytoplankton levels compared to tidepools where mussels were absent regardless of nutrient enrichment (Figs. 9 and 10, Table 5). The only other significant treatment effect was a consumer × nitrogen interaction effect at the first sampling timepoint (0.25 h.). This effect was driven by elevated phytoplankton biomass in the mussels + nitrogen tidepools compared to other treatments and by a relatively high level of phytoplankton in the control tidepools. The average phytoplankton biomass for the control treatment remained relatively high throughout the study, a pattern driven primarily

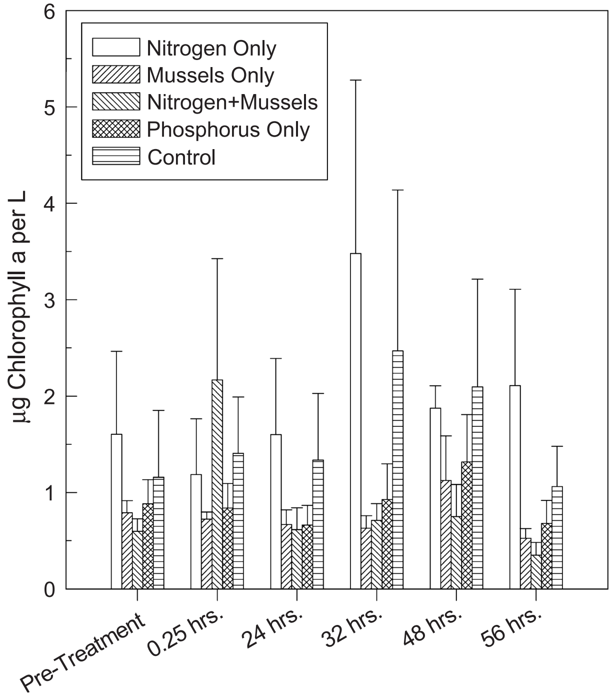

Fig. 9. The response of phytoplankton biomass (chlorophyll *a* concentration) in experimental tidepools. Error bars represent 95% confidence intervals.

Table 5
Results of the ANCOVAs for each sampling timepoint for the response of phytoplankton biomass (chlorophyll *a* concentrations) to experimental treatments

| | *F* ratios | | | | |
|---|---|---|---|---|---|
| Sampling timepoint (h) | 0.25 | 24 | 32 | 48 | 56 |
| $MS_{Error}$ | 0.39211 | 1.04813 | 0.58271 | 0.60349 | 0.26356 |
| Consumer | 1.28 | 0.00 | 3.10 | 3.49 | 10.85** |
| Nitrogen | 0.30 | 0.14 | 0.59 | 0.13 | 0.00 |
| Consumer × nitrogen | 4.98* | 0.01 | 0.03 | 0.38 | 1.25 |
| Phosphorus | 0.55 | 0.00 | 0.90 | 0.41 | 1.08 |
| Covariate | 24.35*** | 11.58** | 15.27** | 0.96 | 22.71*** |

The covariate in all tests was the pretreatment phytoplankton biomass. Significant results are indicated as in Table 4. For all tests, $df = 1$. For all $MS_{Error}$ terms, $df = 13$.

by one of the control pools that contained more planktonic primary production than expected. Phosphorus enrichment increased the concentration of dissolved phosphorus, but it had no significant effect on phytoplankton biomass. This suggests that either the phosphorus taken up by phytoplankton did not promote growth or that the phosphorus added was lost from the system (e.g. precipitation from solution). Pretreatment phytoplankton biomass was a significant covariate for all sampling timepoints except for one (48 h), indicating that initial phytoplankton levels strongly affected the response to treatments.

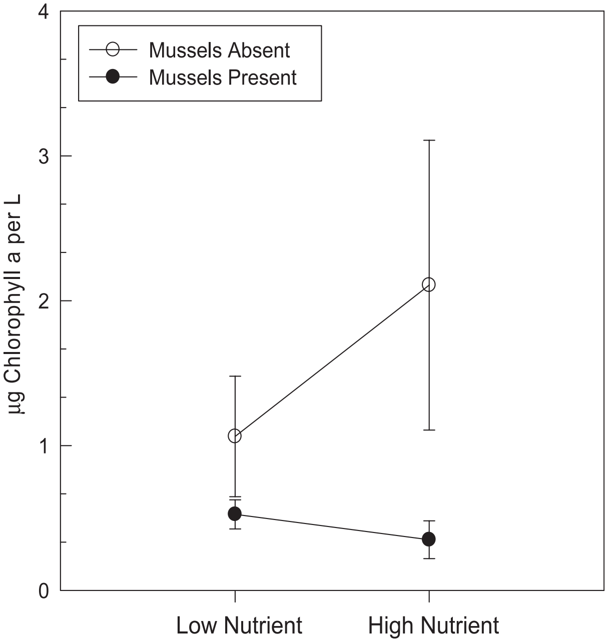

Fig. 10. Phytoplankton biomass at the final sampling interval (56 h). The data shown are the averages ± 1 S.E.

## 4. Discussion

Tidepool communities that occur on seagull roosts differ significantly from non-roost tidepool communities. Non-roost tidepools have more diverse communities of benthic macroalgae and benthic macroinvertebrates. In contrast, non-roost pools have very low diversity communities consisting primarily of ephemeral green macroalgae and high phytoplankton biomass. However, dissolved nutrient concentrations were not significantly different between roost and non-roost tidepools indicating that the nutrients pulsed into roost pools by seagulls are rapidly taken up by tidepool algae and retained in algal biomass. The large variation in the concentration of soluble reactive phosphorus in roost tidepools is another indication of guano deposition. Because marine algae take up nitrogen in greater amounts relative to phosphorus (Redfield, 1958), the nitrogen from the guano pulsed into tidepools is likely taken up quickly by producers leaving high levels of dissolved phosphorus from the guano remaining in the water column.

The results of the experiment presented here are consistent with the predictions of the basic food chain models for one and two trophic level communities presented by Fretwell (1977) and Oksanen et al. (1981). The reduction in phytoplankton biomass by the 56 h sampling interval in the mussels only tidepools and the nitrogen + mussel tidepools indicates that mussels are able to control phytoplankton biomass under both ambient nitrogen conditions and under pulse nitrogen enrichment conditions. Phosphorus enrichment had little effect on phytoplankton biomass at any sampling interval compared to control tidepools indicating that phosphorus alone does not limit phytoplankton biomass in tidepools. Nutrients added to the tidepools may have also been used by macroalgae present in experimental pool. However, phytoplankton have faster growth rates and were assumed to take up the nutrients more rapidly than macroalgae.

The results of this experiment may help to explain the differences in macrobenthic community structure observed between roost and non-roost tidepools. Nutrient-driven increases of phytoplankton biomass in infrequently flushed tidepools could increase the turbidity of the tidepool water, reducing light availability for the macrobenthic tidepool community and inhibiting the slower-growing species of benthic macroalgae. This experiment showed that the presence of suspension-feeding macroinvertebrates can prevent increases in phytoplankton biomass that may result immediately following a pulse nutrient enrichment event (e.g. from seagull guano). Mussels were rare or absent in surveyed roost tidepools. The lack of suspension-feeders to remove nutrient-driven increases of phytoplankton may help to explain why faster-growing phytoplankton and green macroalgae dominate roost tidepools, whereas non-roost tidepools support a much more diverse community of benthic macroalgae. However, the reasons why invertebrates are rare or absent from roost tidepools are less clear. It is possible that a chemical effect associated with nutrient enrichment such as periods of low dissolved oxygen concentrations or high acidity may inhibit the survival of invertebrates in roost tidepools, however this question requires more study. Chlorophyll *a* is known to provide a good estimate of phytoplankton biomass (Hobbie et al., 1972), however it does not give any information about species composition, cell numbers, or cell sizes of the phytoplankton. For these reasons, it is not known whether the changes in biomass observed in this experiment occurred because of changes in the number or size of phytoplankton cells or whether there was a shift in phytoplankton community structure.

Numerous mesocosm experiments have shown *M. edulis* be an effective regulator of phytoplankton biomass (Riemann et al., 1988; Olsson et al., 1992; Graneli et al., 1993; Prins et al., 1995). However, the few other field experiments involving both nutrient and consumer manipulations in rocky intertidal systems have produced mixed results (Metaxas and Scheibling, 1996; Nielsen, 2001; Wootton et al., 1996). Nielson (2001) used a blocked factorial experimental design of nutrient and herbivore levels (limpets, chiton, and snails) across a wave-exposure gradient and demonstrated that both herbivory and nutrients were important factors in benthic algal communities. However, these effects were mediated by the level of wave-exposure, suggesting that hydrodynamic variability should be incorporated into simple food chain models for this system. Wootton et al. (1996) placed flowerpots packed with nutrient-enriched agar into the intertidal zone both protected and unprotected from molluscan grazers, and then monitored benthic algal biomass and micrograzer abundance during El Niño and non-El Niño seasons. The top-down effect of molluscan grazing consistently decreased both micrograzer and algal abundance during all seasons of the experiment, while nutrient enrichment increased only micrograzer abundance during an El Niño summer. This study provides evidence for the prominence of top-down factors in an intertidal system through the using a replicated design ($n = 7$–8 flowerpots per treatment). However, the flowerpots used in this study were intended to produce gradual diffusion of nutrients, but direct measures of nutrient concentrations were not made, and so the role of bottom-up factors in this system remains unresolved. In Nielsen's (2001) experiment, nutrient enrichments were achieved using slow-releasing fertilizer pellets, and although three levels were intended (ambient, low, and high), the latter two levels were statistically indistinguishable from each other, illustrating the necessity of measuring nutrient concentrations following experimental enrichments. In a series of short (1–2 week) manipulative experiments, Metaxas and Scheibling (1996) studied the response of phytoplankton assemblages to different levels of planktonic micrograzers and nutrients (nitrate + phosphate + silicate solution) in plastic enclosures attached to the bottoms of tidepools. The structure of the phytoplankton assemblages varied between experiments, between weeks, within experiments, and among pools, showing the high level of spatial and temporal variation present in tidepool systems.

Studies of tidepool community dynamics involving only the manipulation of consumers have presented evidence for the strong role of top-down forces in these communities. Addition of the grazing snail, *Littorina littorea*, to two previously snail-free tidepools caused a significant decrease in percent cover of the green macroalga *Enteromorpha intestinalis*, while removing snails from two other pools showed a significant increase of the same algal species (Lubchenco, 1978). Similarly, Benedetti-Cecchi and Cinelli, (1996) demonstrated that excluding limpets and sea urchins from scraped plots within tidepools facilitated recolonization and percent cover of macroalgae. Rocky intertidal experiments involving only the manipulation of resources have likewise provided evidence for the importance of bottom-up factors in determining intertidal community structure. For example, natural nutrient enrichment by seabird guano is suspected to contribute to differences in marine invertebrate abundance as well as algal abundance and diversity along the South African coast (Bosman and Hockey, 1986). The addition of a liquid guano solution to grazer exclusion areas increased the growth rate of benthic algae compared to non-enriched treatments (Bosman et al., 1986).

The conclusions of these few intertidal studies indicate that variation in bottom-up as well as top-down factors may influence community structure, but the paucity of experimental work reveals the need for more manipulative studies with replication. Marine systems have traditionally been a difficult environment in which to manipulate nutrient levels. Intertidal pools, however, provide a novel system in which to conduct such experiments because their distinct boundaries prevent nutrient loss through diffusion. The study presented here investigated the immediate response of tidepool phytoplankton communities to pulse nutrient enrichment and helps to explain the observed differences in community structure between roost and non-roost tidepools. The results of this study suggest that periodic pulses of nitrogen into tidepools will have little effect on phytoplankton biomass when mussels are present and that longer-term chronic nitrogen influxes may be driving the patterns of community structure in tidepools occurring on roosts. Thus, a more complete understanding of this pattern will require longer-term experimental investigations.

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