SEPARATE AND INTERACTIVE EFFECTS OF CONSUMERS AND NUTRIENT ENRICHMENT ON THE STRUCTURE OF BENTHIC MARINE COMMUNITIES

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SEPARATE AND INTERACTIVE EFFECTS OF CONSUMERS AND NUTRIENT ENRICHMENT ON THE STRUCTURE OF BENTHIC MARINE COMMUNITIES

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For Allison

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SUMMARY

Determining the relative roles of top-down vs. bottom-up forces in controlling the structure of ecological communities is of primary importance because anthropogenic nutrient loading, overharvesting of consumers, and potential interactions of these bottom-up and top-down forces are pervasively changing ecosystems throughout the world. In my dissertation, I take advantage of both field experimentation and meta-analyses of existing data to address the top-down and bottom-up forces that control the structure of benthic marine communities. Specifically, I investigate the role of predators in controlling community composition, the relative roles of herbivores vs. nutrient enrichment in controlling the abundance of benthic primary producers, and the influence of herbivore diversity on the community structure of coral reefs.

In Chapter 1, I show that release from predation by large fishes and invertebrates via exclusion cages allows population increases in the gorgonian-eating gastropod *Cyphoma gibbosum*. Increased densities of *C. gibbosum* lead to more intense grazing on gorgonian corals consistent with other studies showing cascading effects of removing top predators from communities. Chapter 2 tests the role of herbivores vs. nutrient enrichment in controlling the abundance of primary producers in benthic marine communities. I used factorial meta-analysis of 54 field experiments that orthogonally manipulated herbivore pressure and nutrient loading to quantify consumer and nutrient effects on primary producers in benthic marine habitats. Herbivores consistently had stronger effects than did nutrient enrichment for both tropical macroalgae and seagrasses. For temperate macroalgae and benthic microalgae, the effects of top-down and bottom-up

forces were context dependant, varying as a function of the inherent productivity of the ecosystem. Overall, I show that the influence of herbivory and nutrients on marine primary producers is context dependant, varying with latitude, the type of primary producer, and the nutrient status of the system.

In Chapters 3 and 4, I address how herbivore diversity influences the role of top-down pressure on coral reef communities. In Chapter 3, I use manipulative field experiments to show that Caribbean reefs change dramatically as a function of herbivorous fish diversity. Higher herbivore diversity caused lowered macroalgal abundance, reduced coral mortality, and increased coral growth when compared to treatments with lower herbivore diversity. Complementary feeding by different fishes drove these patterns because macroalgae were unable to effectively deter feeding by fishes with different attack strategies. To further address the role of herbivore diversity in affecting coral reef communities, Chapter 4 addresses the effects of two separate years of experiments manipulating herbivore diversity on a coral reef. In Year 1, I used the redband parrotfish (*Sparisoma aurofrenatum*) and the ocean surgeonfish (*Acanthurus bahianus*) to generate the treatments while in Year 2 I used the redband parrotfish and the princess parrotfish (*Scarus taeniopterus*). I show strong effects of herbivore diversity on community structure due to feeding differences among herbivores both years of the experiment. In Year 1, ocean surgeonfish and redband parrotfish synergistically suppressed upright macroalgae by feeding on dissimilar species thereby decreasing facilitating crustose coralline algae and coral cover while decreasing coral mortality. In Year 2, redband parrotfish and princess parrotfish fed on different algal functional groups

in that redband parrotfish fed mostly on upright macroalgae while princess parrotfish fed mostly on filamentous, turf algae thus facilitating crustose coralline algae when these fishes were combined. When all treatments were compared across both years of the experiment, despite being morphologically and taxonomically distinct, princess parrotfish and ocean surgeonfish had more similar effects on macroalgal community structure than did the two morphologically and taxonomically similar species of parrotfish. These data suggest that these three fishes play functionally diverse roles in the herbivore guild and that their complementary effects of algal communities are important to the structure and function of coral reefs.

CHAPTER 1

PREDATOR RELEASE OF THE GASTROPOD *CYPHOMA GIBBOSUM* RESULTS IN INCREASED PREDATION ON GORGONIANS

Abstract

The gastropod *Cypohoma gibbosum* is a principle predator of gorgonian corals on Caribbean coral reefs. However, little is known about how *C. gibbosum* populations are regulated or about how *C. gibbosum* affects gorgonian populations. We used 4 m^2 cages to exclude large, predatory fishes and invertebrates from natural areas of a coral reef in the Florida Keys and assessed the role of predators in affecting *C. gibbosum* densities and their damage to gorgonians. After 10 months, *C. gibbosum* was up to 50X more abundant in predator exclosures than in uncaged areas. Gorgonians in predator exclosures were grazed 2.5X as often and exhibited 8.4X more recent damage from *C. gibbosum* predation than gorgonians in uncaged areas where gastropod predators were not excluded. The most abundant gorgonian, *Pseudopterogorgia americana*, had 8.6X more grazing damage inside predator exclosures than in uncaged areas. These data suggest that predators suppress populations of *C. gibbosum* and that overfishing of gastropod predators such as the hogfish, *Lachnolaimus maximus*, or Caribbean spiny lobster, *Panuliris argus*, could lead to release of *C. gibbosum* and increased predation on gorgonians.

Introduction

Gorgonian corals are common on most Caribbean coral reefs and are often the dominant benthic invertebrate in some areas (Lasker & Coffroth 1983, Yoshioka &

Yoshioka 1989). Predation on gorgonians is assumed to be minimal because gorgonians are poor food due to their effective chemical and morphological defenses (Pawlik et al. 1987, Van Alstyne & Paul 1992, O'Neal & Pawlik 2002). Consequently, little emphasis has been placed on predation as an important force structuring populations of gorgonians, and more emphasis has been placed on reproduction (Lasker 1991, Lasker et al. 1996), recruitment (Yoshioka 1996, Lasker et al. 1998), disturbance (Yoshioka & Yoshioka 1987, Witman 1992), and disease (Jolles et al. 2002, Kim & Harvell 2004) as key factors regulating the dynamics of gorgonian populations. The majority of work on the relationships between gorgonians and their predators has focused on identifying patterns of gorgonian anti-predator defenses (Pawlik et al. 1987, Harvell et al. 1993, O'Neal & Pawlik 2002).

The gastropod *Cyphoma gibbosum* is often the primary consumer of gorgonians on Caribbean coral reefs (Birkeland & Gregory 1975, Gerhart 1986) with the polychaete worm *Hermodie carunculata* (Vreeland & Lasker 1989) and some butterflyfishes (Chaetodontidae) (Lasker 1985) also feeding on gorgonians. Although *C. gibbosum* feeds on a wide range of gorgonian species (Lasker et al. 1988), most studies have focused on the distribution and movement of *C. gibbosum* among gorgonians (Gerhart 1986, Lasker & Coffroth 1988, Gerhart 1989) with less emphasis on the effects of *C. gibbosum* on gorgonian populations in the field.

There are few investigations of predator effects on *Cyphoma gibbosum* populations. The mantle tissue of *C. gibbosum* is unpalatable to some fishes (Gerhart 1986) suggesting that *C. gibbosum* may sequester secondary metabolites from its gorgonian prey, thus using host defenses to deter its own predators as do other gastropods

(Sammarco et al. 1983), but no work has documented patterns of predation on *C. gibbosum* or their response to being released from predation. However, a large-scale survey of *C. gibbosum* abundance in the Florida Keys suggests that *C. gibbosum* may be more abundant in areas where large, molluscivorous fishes have been extensively harvested (Chiappone et al. 2003). Removal of top predators often results in the release of their prey (i.e. herbivores or mid-level predators) and can have cascading indirect effects on plants or other animals two links away in the food chain (i.e. a trophic cascade or mesopredator release) (Hairston et al. 1960, Paine 1980, Crooks & Soule 1999, Silliman & Bertness 2002). If predators have strong top-down effects on *C. gibbosum* populations, then removal of these predators may allow increases in *C. gibbosum* abundance and thus increased predation on gorgonians. Here we report results from a caging experiment that excluded large predators from areas of a Caribbean coral reef to test the effects of releasing *C. gibbosum* from predation and the subsequent effects of *C. gibbosum* predation on gorgonians.

Materials and Methods

Experimental setup and maintenance

In November 2003, we used NOAA's Aquarius, a self-sufficient underwater research laboratory offshore of Key Largo, FL to perform an experiment on Conch Reef (24°57'N/80°27'W) designed to test the effects of herbivorous fish diversity on the community structure of coral reefs. As part of the experiment we constructed 32 cages (2.5 cm mesh size) measuring 2 m x 2 m x 1 m tall (covering 4 m^2 of the reef bottom). Different combinations of herbivorous fishes were maintained within these

cages to test for the effects of herbivore diversity on coral reef community structure; however, the cages also excluded large gastropod predators such as fishes, lobsters, and large crabs that could not pass through the 2.5 cm mesh. Cages thus served as a refuge from predation for gastropods such as *Cyphoma gibbosum.*

The experiment was located at depths of 16-18 m on a spur and groove reef formation with the spurs rising 1-2 m from a sandy bottom. Cages were made of 0.6 cm steel bar and covered with PVC-coated, galvanized chicken wire attached to the cage frame with cable ties. We attached the cages to the reef by wiring the frames to 30 cm galvanized nails that had been hammered into the reef substrate. A 30 cm flange of chicken wire extended from the base of the cage and was conformed to the reef substrate and affixed using galvanized fencing nails. This barrier prevented larger fishes and invertebrates from escaping or entering the cage, but the mesh size allowed small fishes and invertebrates to enter and exit at will. Zinc anodes attached to the chicken wire and the cage frame prevented corrosion.

The benthic community inside the cages consisted of unmanipulated populations of macroalgae, corals, sponges, gorgonians, and other common reef invertebrates. Treatments within the cages for the herbivore diversity experiment consisted of: (1) two redband parrotfish, *Sparisoma aurofrenatum*, (2) two ocean surgeonfish, *Acanthurus bahianus*, (3) one redband parrotfish and one ocean surgeonfish, or (4) no large fish (n = 8 for each treatment and n = 32 total for the caged areas). We also monitored uncaged areas of equal size as controls (n = 8). Four cages and an uncaged area were blocked as closely as the reef configuration allowed in one general area, and the fish treatments were allocated randomly among each of the four cages. Thus, we had eight blocks each

containing one replicate each of the five experimental treatments. Cages were scrubbed inside and out every 4-6 weeks to remove fouling organisms and prevent shading. Grazing by fishes (surgeonfishes and juvenile parrotfishes) kept cages relatively free of fouling organisms between scrubbings.

Data collection and analysis

We surveyed each caged and uncaged area for the presence of *Cyphoma gibbosum* in August 2004 (after 10 months of caging). We identified all gorgonians in each caged and uncaged area to genus or species as was practical under field conditions, and noted which gorgonians hosted *C. gibbosum*. To assess *C. gibbosum* predation on gorgonians, we sampled the gorgonians in each uncaged area and in one caged area chosen from the same block of treatments as each uncaged area ($n = 8$ for uncaged and caged areas). We chose the caged area within each block of treatments at random. To quantify *C. gibbosum* damage to each gorgonian in the uncaged and caged areas, we measured the total length of the live main axes of each gorgonian and then measured the total length of the main axes that had been stripped of its coenenchyme by *C. gibbosum* feeding. For estimates of damage by *C. gibbosum*, we measured only those areas where the gorgonian skeleton was not fouled by epiphytic algae or invertebrates and did not include areas of exposed gorgonian skeleton that had been fouled. Although these areas were probably also the result of previous grazing by *C. gibbosum* that subsequently had been colonized by fouling organisms (Gerhart 1990), we did not include them in our analysis as they could not be unambiguously attributed to predation by *C. gibbosum*. We did not include gorgonians that were within 10 cm of the cage in the estimates of grazing

damage as these gorgonians could have been damaged by wave action abrading them against the cage.

We tested for differences in the abundance of gorgonians between caged and uncaged areas using *t*-tests and for differences in *Cyphoma gibbosum* abundance between caged and uncaged areas using a Mann-Whitney U-test which is a non-parametric equivalent to a *t*-test (Sokal & Rohlf 1995). We analyzed the percentage of gorgonians damaged by *C. gibbosum* in each treatment and the average grazing damage per gorgonian scaled to main axis length in each treatment using paired one-tailed, *t*-tests that paired each caged and uncaged area from an experimental block. We used one-tailed *t*-tests based on the hypothesis that caged areas that had more *C. gibbosum* would also have more damage to gorgonians from *C. gibbosum*. Data for average grazing damage per gorgonian were log transformed to achieve homogeneity of variances as evaluated with Cochran's test (Underwood 1997).

Results

Pseudopterogorgia americana was the most abundant gorgonian in caged and uncaged areas (Table 1.1; Figure 1.1) representing 83% of gorgonians in the caged areas and 84% of gorgonians in the uncaged areas. *Briareum asbestinum*, *Eunicea* spp., and *Pseudoplexaura* spp. were also common in both the caged and uncaged areas (Figure 1.1), each representing $\leq$ 7% of the total gorgonian density. *Gorgonia* spp., *Pseudopterogorgia acerosa*, and *Plexaurella* spp. were present but rare. Densities did not differ between caged and uncaged areas for any of the gorgonian species (Figure 1.1).

Table 1.1. *Cyphoma gibbosum.* Their abundance and the abundance of their gorgonian hosts within the cages. The distribution of *C. gibbosum* on the gorgonians differed significantly from what would be expected given the gorgonian abundance data ($P < 0.001$, $G = 83.909$; G-test).

Gorgonian	**# indiv.**	**% of total gorgonians**	**# *C. gibbosum***	**% of total *C. gibbosum***	***C. gibbosum* per gorgonian**
Pseudopterogorgia americana	553	82.9	21	40.5	0.04
Briareum asbestinum	33	4.9	0	0	0
Eunicea spp.	32	4.8	20	38.6	0.63
Pseudoplexaura spp.	31	4.7	9	17.4	0.29
Pseudopterogorgia acerosa	10	1.5	2	3.5	0.20
Gorgonia ventalina	5	0.8	0	0	0
Plexaurella spp.	3	0.4	0	0	0
Total	667	100	52	100	0.08

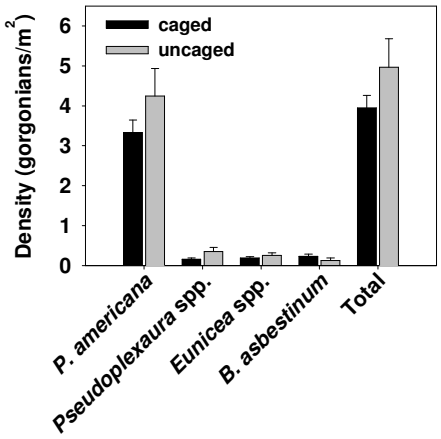


Figure 1.1. Density of gorgonians (means ± SE) for caged (black bars; n =32) and uncaged areas (gray bars; n = 8). There were no differences in gorgonian densities between caged and uncaged areas for total gorgonians or for any gorgonian species or genus as evaluated with *t*-tests.

Cyphoma gibbosum were more abundant in the caged areas than in uncaged areas when scaled to either area (0.61 ± 0.14 vs. 0.03 ± 0.03 snails/m^2 [mean ± SE] respectively; $P < 0.001$; Figure 2.2A) or to gorgonian abundance (0.21 ± 0.07 vs. 0.004 ± 0.004 snails/gorgonian respectively; $P < 0.001$; Figure 2.2B). Of the 52 *C. gibbosum* found in the caged areas, 41% of individuals were found on the most abundant gorgonian, *Pseudopterogorgia americana* (Table 1.1). The remaining *C. gibbosum* were found on *Eunicea* spp. (39% of individuals), *Pseudoplexaura* spp. (17%) and *Pseudopterogorgia acerosa* (4%) (Table 1.1). The distribution of *C. gibbosum* on gorgonian hosts differed significantly from what would have been expected given the abundances of the different gorgonians ($P < 0.001$, $G = 83.9$; Table 1.1). The single *C. gibbosum* found in the uncaged areas was on *P. americana*.

Cyphoma gibbosum could be observed feeding on gorgonians and were often at or near areas stripped of tissue. The damaged areas of gorgonian we observed were consistent with those previously described as due to *C. gibbosum* feeding (Gerhart 1984, Harvell & Suchanek 1987) and inconsistent with damage done by *Hermodice carunculata* (Vreeland & Lasker 1989), the only other major gorgonian predator that could have been present in the caged areas. Further, *H. carunculata* was rarely observed inside the caged areas and was never observed feeding on gorgonians. Thus, all indications are that the damage we found was due to *C. gibbosum* feeding. The vast majority of grazing damage removed all soft tissue and exposed the gorgonian skeleton;

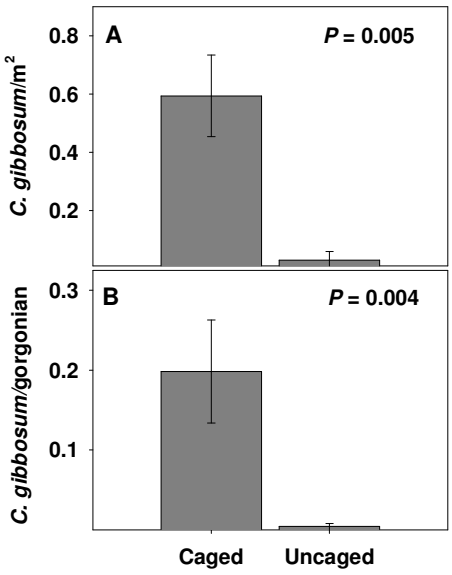


Figure 1.2. *Cyphoma gibbosum.* Individuals (means ± SE) (A) per m^2 or (B) per gorgonian in caged and uncaged areas. $n = 32$ for caged and $n = 8$ for uncaged areas. *P*-values are from Mann-Whitney *U*-tests.

superficial removal of gorgonian tissue was rare but occurred on species with a thicker coenenochyme (i.e. *Pseudoplexaura* spp.).

The percentage of all gorgonians with grazing scars was greater in the caged vs. the uncaged areas ($P = 0.043$; Figure 1.3A). The same trend was evident for the most abundant gorgonian *Pseudopterogorgia americana* ($P = 0.085$; Figure 1.3B). The amount of grazing damage per gorgonian showed dramatic differences between the caged and uncaged areas. When gorgonians were considered as a group, 8.9 ± 2.6% (mean ± SE) of the main axes of each gorgonian in the caged areas had been damaged by *Cyphoma gibbosum* vs. 1.1 ± 0.7% in the uncaged areas ($P = 0.004$; Figure 1.3C). The most abundant gorgonian species, *P. americana*, had 11.5 ± 4.2% of its main axes damaged per individual in the caged areas vs. 1.3 ± 0.8% damage per individual in the uncaged areas ($P = 0.001$; Figure 1.3D). When we considered only those gorgonians that had grazing damage, the gorgonians that had been grazed in the caged areas had 2.5X more damage than the gorgonians that had been grazed in uncaged areas (58.1 ± 6.8% vs. 23.7 ± 7.8% [mean ± SE] respectively; $P = 0.01$, *t*-test).

Discussion

Exclusion of predatory fishes and invertebrates led to a 50X increase in the abundance of *Cyphoma gibbosum* and a >8X increase in damage to gorgonians by *C. gibbosum* (Figures 1.2 & 1.3). Gorgonians in predator exclusions were 2.5X more likely to be grazed by *C. gibbosum* than gorgonians in uncaged areas (Figure 1.3A). Damage to individual gorgonians from *C. gibbosum* was 8.4X greater in caged as opposed to uncaged areas (Figure 1.3C) when averaged across all gorgonian species. Damage to the

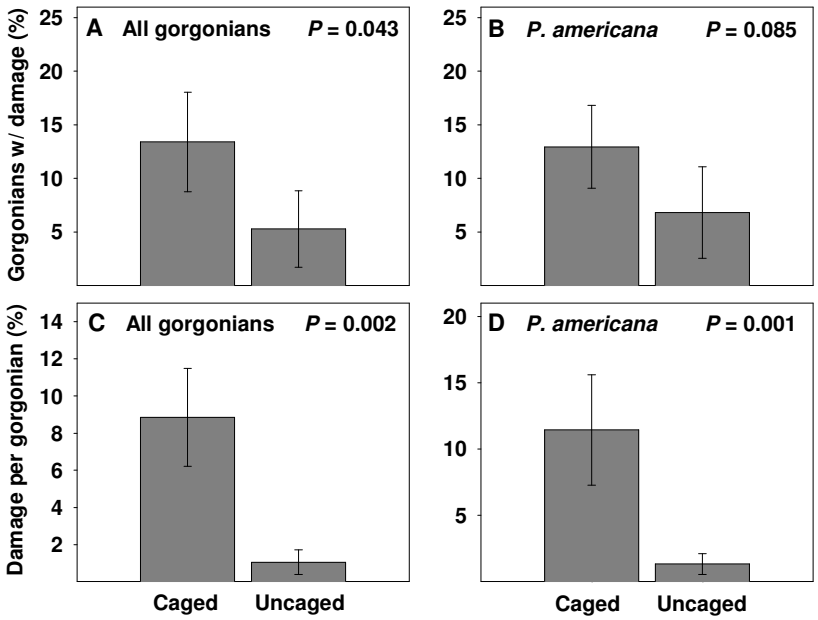


Figure 1.3. *Cyphoma gibbosum* and *Pseudoterogorgia americana.* Percentage (means ± SE) of (A) all gorgonians or (B) *P. americana* with grazing scars or percentage of each gorgonian's main axes damaged by *C. gibbosum* (means ± SE) for (C) all gorgonians or (D) *P. americana* in caged and uncaged areas (n = 8 for all comparisons). P-values are from paired t-tests.

most abundant gorgonian, *Pseudopterogorgia americana*, was 8.6X greater in the caged as opposed to uncaged areas (Figure 1.3D). Thus, predators typically keep *C. gibbosum* populations in check and prevent heavy grazing on gorgonians.

The average density of *Cyphoma gibbosum* in the caged areas, 0.61 ± 0.14 snails/m^2, was 10X greater than the maximum density found in the Florida Keys by Chiappone et al. (2003) (which was in a subset of the actively fished areas that they surveyed) and >2X the maximum density found in Panama by Lasker and Coffroth (1988). Fish predation on *C. gibbosum* at our field site could be high as it is part of a Special Protection Area within the Florida Keys National Marine Sanctuary. Commercial and recreational fishing is prohibited, but enforcement is less than complete and we commonly found fishing gear hooked in, and broken off on, our cages and the adjacent coral formations. So fishing does occur. However, we commonly observed predators such as hogfish (*Lachnolaimus maximus*), pufferfishes (Tetraodontidae), and Caribbean spiny lobsters (*Panulirus argus*) that commonly consume gastropods (Randall & Warmke 1967, Turingan 1994, Cox et al. 1997). On one occasion we witnessed a hogfish consume a *C. gibbosum* (D.E.B. pers. obs.). At the end of the experiment (August 2004), the caging material was removed from all cages, which allowed gastropod predators full access to the previously caged areas. When the formerly caged and uncaged areas were surveyed for *C. gibbosum* eight weeks later, none were found. Thus, *C. gibbosum* were either consumed after cages were removed or they dispersed so widely that none were evident when the areas were resurveyed (40 areas of 4 m^2 or 160 m^2 total).

Given our data, we cannot differentiate between a demographic response of *Cyphoma gibbosum* as a result of predator release or the aggregation of individuals to

predator-free areas. However, we did notice the presence of several juvenile *C. gibbosum* in the caged areas, suggesting an increase in population size as a result of escaping predation. Feeding by the increased density of *C. gibbosum* in cages did not change gorgonian desnsity during the 10 month experiment (Figure 1.1), but gorgonians in predator exclusions were attacked more frequently (Figure 1.3A) and more damage was done to them when attacked (Figures 1.3C & 1.3D). Over longer periods, *C. gibbosum* densities may have increased further and their grazing damage may have accumulated to change gorgonian density rather than just extent of damage.

Most *Cyphoma gibbosum* were found on the gorgonians *Pseudopterogorgia americana* and *Eunicea* spp. (>75% of the individuals). However, when corrected for gorgonian density, *C. gibbosum* was found less often on *P. americana* but more often on both *Eunicea* spp. and *Pseudoplexaura* spp. than would be expected given their abundance (Table 1.1). Data from Harvell and Suchanek (1987) generally supported this pattern, but Lasker et al. (1988) found that *Pseudopterogoria* spp. was among the most preferred and *Eunicea* spp. among the least preferred hosts for *C. gibbosum* (Lasker et al. 1988). Lasker et al. (1988) also suggested that *C. gibbosum* fed less intensely on *P. americana* than on several other gorgonians species, yet the most extensive damage in our study was on *P. americana* (Figure 1.3D) and *Eunicea* spp. (D.E.B. pers. obs.).

Predation by *Cyphoma gibbosum* typically results in only partial consumption of the gorgonian colony possibly due to physical defenses (i.e. spicules) or induced chemical defenses in the gorgonians (Gerhart 1986, Harvell & Suchanek 1987). However, *C. gibbosum* completely removed all of the tissue from several small (~0.2 m in height) *Pseudopterogorgia americana* and ~75% of the tissue from a 0.8 m tall

Eunicea calyculata (this individual was completely dead two months later). Thus, the intense feeding from high densities of *C. gibbosum* that resulted from predator release may have overwhelmed gorgonians' capacities to mount effective induced defenses that may usually keep predation to low levels and prevent runaway consumption of the host. These data suggest that *C. gibbosum* could have strong effects on the population structure of gorgonians if released from predators as they can completely kill both small and large colonies.

Our estimates of *Cyphoma gibbosum* damage to gorgonians are conservative in that we only quantified *C. gibbosum* damage that was recent (i.e. not overgrown with fouling organisms). Yet, fouling of the exposed gorgonian skeleton following *C. gibbosum* predation is common (Gerhart 1990), happens within only a few weeks, and would have increased the estimates of *C. gibbosum* damage had such damage been included. Gorgonians that are fragmented as a result of being fouled often have reduced fecundity (Wahle 1983). Thus, damaging effects to the gorgonians by *C. gibbosum* in our study probably exceeded the mere removal of tissue and also impacted the reproductive capacity of damaged colonies.

Although gorgonian diseases were not noticed at our field site, *Cyphoma gibbosum* could potentially act as a vector for the spread of diseases such as the fungal epizootic aspergillosis (Smith et al. 1996, Kim & Harvell 2004) as they feed on multiple species of gorgonians (Birkeland and Gregorgy 1975, Lasker et al. 1988, this study) and frequently move among different colonies (Gerhart 1986). Although the potential of *C. gibbosum* as a vector for aspergillosis has not been investigated in depth, *C. gibbosum* were shown to be more abundant on diseased *Gorgonia* spp. than on healthy ones

(Nagelkerken et al. 1997) suggesting a link between *C. gibbosum* and disease. Similarly, the corallivorous gastropod *Coralliophila abbreviata* is a vector for the transmission of white band disease among individuals of the coral *Acropora cervicornis* in the Caribbean (Williams & Miller 2005). If the same relationship exists between *C. gibbosum* and gorgonians, increases in the abundance of *C. gibbosum* following overfishing of gastropod predators potentially could increase the prevalence of aspergillosis.

Predators often exert strong top-down control on communities (Terborgh et al. 1999), and their removal frequently results in cascading, indirect effects on these communities (Crooks & Soule 1999, Duffy & Hay 2000, Silliman & Bertness 2002). Removing predators from coral reefs often results in large cascading effects such as increases in coral-eating starfish and decreases in coral cover (Dulvy et al. 2004) or increases in sea urchins and the erosion of reef structure (McClanahan & Muthiga 1989). Here we show that releasing the gastropod *Cyphoma gibbosum* from large predators allows an increase in their abundance which increases their predation on gorgonians. Thus, overfishing of gastropod predators could have large cascading effects on Caribbean coral reefs by releasing *C. gibbosum* from predator control, allowing it to heavily damage gorgonians, and thus potentially altering the structure and abundance of gorgonian populations.

CHAPTER 2

HERBIVORE VS. NUTRIENT CONTROL OF MARINE PRIMARY PRODUCERS: CONTEXT-DEPENDANT EFFECTS

Abstract

We know little about how the strength of bottom-up versus top-down forces differs across different types of habitats, ecosystems, or primary producers. However, understanding such context-dependency is becoming critical due to anthropogenic nutrient loading, overharvesting of consumers, and potential interactions of these bottom-up and top-down forces. We used factorial meta-analysis of 54 field experiments that orthogonally manipulated herbivore pressure and nutrient loading to quantify consumer and nutrient effects on primary producers in benthic marine habitats. Across all experiments and producer types, herbivory and nutrient enrichment both significantly affected primary producer abundance and also interacted to create greater nutrient effects in the absence of herbivores. The significant interaction suggests that a decrease in herbivore populations can result in more dramatic effects of nutrient loading on marine ecosystems. Herbivores consistently had stronger effects than did nutrient enrichment for both tropical macroalgae and seagrasses. The strong effects of herbivory but limited effects of nutrient enrichment on tropical macroalgae suggest that suppression of herbivore populations has played a larger role than eutrophication in driving the phase shift from coral- to macroalgal-dominated reefs in many areas, especially the Caribbean. For temperate macroalgae and benthic microalgae, the effects of top-down and bottom-up forces were context dependant, varying as a function of the inherent productivity of the

ecosystem. For these algal groups, nutrient enrichment enhanced producer abundance in both low and high productivity systems, but herbivores exerted a top-down force only in low productivity systems. Effects of herbivores vs. nutrients also varied among algal functional groups (crustose coralline algae, upright macroalgae, and filamentous algae) and also varied within a functional group between temperate and tropical systems. The influence of herbivory and nutrients on marine primary producers is context dependant, varying with latitude, the type of primary producer, and the nutrient status of the system.

Introduction

A key question regarding the forces structuring communities is the relative influence of consumers (top-down) versus resources (bottom-up) in controlling community composition, structure, and function (Hairston et al. 1960, Oksanen et al. 1981, Leibold et al. 1997). Understanding the relative effects of these forces is becoming increasingly important as humans alter ecosystems by removing consumers (Jackson et al. 2001, Duffy 2003) and increasing nutrients (Smith *et al.* 1999) over large spatial scales. For example, the recent switch from coral-dominated to algal-dominated reefs in many areas, especially the Caribbean, may be via an interaction of decreased herbivore pressure and increased nutrient loading that reduces the ability of coral reefs to rebound in the face of disturbance (McCook 1999, Hughes et al. 2003, Bellwood et al. 2004). Such large scale changes in community structure and in top-down and bottom-up forces are now widespread in many marine ecosystems (Valiela et al. 1997, Estes et al. 1998,

Smith et al. 1999, Steneck et al. 2004), making it critical to understand how alterations to these top-down and bottom-up forces cascades through the community.

Many marine ecosystems are typified by primary producers like kelps and seagrasses that are the foundation species that facilitate whole ecosystems (Bertness et al. 2001). Other primary producers, such as coral reef macroalgae that can overgrow and kill corals (McCook et al. 2001), are pivotal interactors that strongly impact foundation species fundamentally changing the physical and ecological structure of the entire ecosystem. Thus, knowing how consumers and resource availability affect primary producers is critical for understanding how marine ecosystems function. Benthic marine communities are commonly regulated by consumers (Estes et al. 1998, Duffy and Hay 2001). However, broad-scale oceanographic features such as nutrient availability and larval recruitment are influential bottom-up forces that also influence benthic communities (Menge et al. 1997, Nielsen and Navarrete 2004). These multiple forces are not mutually exclusive and may rarely act in isolation (Leibold et al. 1997), making it important to identify when and where they interact (or fail to interact) as drivers of community organization. Given the context-dependent nature of most ecological interactions (Hay et al. 2004), it is unlikely that any single experiment can address this general question. A quantitative synthesis of the experimental data investigating the interactions of herbivores and nutrient loading on the abundance of primary producers (e.g. Miller et al. 1999, Smith et al. 2001, Thacker et al. 2001, McClanahan et al. 2003) is needed to critically evaluate the relative roles of herbivores vs. nutrients in controlling the abundance of primary producers and mediating phase shifts.

Recent meta-analyses have shown complex interactions between herbivores and nutrients in controlling the species diversity of primary producers (Worm et al. 2002) and in affecting periphyton abundance (Hillebrand 2002) suggesting that these interactions might be important for controlling primary producer abundance across a variety marine ecosystems and environmental conditions and for different types of producers. We used factorial meta-analysis (Gurevitch *et al.* 2000) to synthesize the results of 54 field experiments that orthogonally manipulated nutrient availability and herbivore pressure in benthic marine ecosystems representing a wide diversity of habitats and primary producer types. This approach allowed us to quantitatively assess the effects of herbivore removal, nutrient enrichment, and their interaction on the abundance of primary producers. We assessed the effects of herbivore removal and nutrient enrichment on: (1) marine primary producers pooled across all habitats and producer types, (2) different types of producers (i.e. macroalgae vs. seagrasses vs. microalgae), (3) producers in different habitats (i.e. oligotrophic vs. eutrophic environments or temperate vs. tropical systems), and (4) producers in different functional groups (i.e. encrusting coralline algae vs. upright macroalgae). Instead of debating the role of bottom-up vs. top-down forces, we focus instead on the types of primary producers responding to these forces and the conditions under which their relative roles change – i.e. the context-dependant nature of the answer to this debate.

Materials and Methods

We found studies by searching the ISI Web of Science database (1945-2005; search terms included herbiv* and marine, herbiv* and nutrient, nutrient and marine, etc.) for field experiments manipulating both herbivory and nutrients. We also searched the reference lists of papers identified by this search. Studies had to satisfy three criteria to be included in our analyses: (1) experimentally manipulate nutrient availability and herbivore presence orthogonally in a field setting, (2) measure the abundance of primary producers in response to these treatments, and (3) report abundance means, error measurements, and sample sizes for experimental treatments. All studies that satisfied criteria 1 and 2 also satisfied criterion 3.

We found 23 published studies with a total of 50 experiments and also included three unpublished studies for a total of 26 studies with 54 experiments (Table 2.1). Twenty-one experiments were on benthic microalgae, 15 on tropical macroalgae, 14 on temperate macroalgae, 3 on seagrasses, and 1 on the marsh grass *Spartina alterniflora*. Benthic microalgae consisted primarily of diatoms and cyanobacteria. Common species in the tropical macroalgal communities were *Dictyota* spp. *Lobophora variegata*, *Sargassum* spp. *Dasycladus vermicularis*, *Jania* spp., *Amphiroa* spp., and several species of cyanobacteria. Filamentous turf algae and crustose coralline algae were rarely identified to genus or species. In temperate macroalgal communities, the common perennial algae were *Fucus* spp., *Ascophyllum nodosum*, and *Sargassum* spp., whereas the common annual algae were *Pilayella littoralis*, *Enteromorpha intestinalis*, *Ulothrix flacca*, *Callithamnion tetragonum*, and *Cladophora* spp. *Thalassia testudinum* and

Table 2.1. Details of studies used in meta-analysis

Note:
One experiment was excluded from the McGlathery (1995) study on seagrasses because non-target herbivores (fishes) fed preferentially on a subset of the treatments confounding the herbivore and nutrient effects.

Abbreviations: Exp # - Experiment number in that study
Day - Experimental duration in days
Biovol. - Biovolume

Authors	**Year**	**Primary producers**	**Location**	**Major herbivores**	**Exp #**	**Day**	**Size (m^2)**	**Nutrient status**	**Metric**
Armitage and Fong	2003	Microalgae	California, USA	Snails	1	56	0.250	NA	Chl. a
Armitage and Fong	2003	Microalgae	California, USA	Snails	2	56	0.250	NA	Chl. a
Armitage and Fong	2003	Microalgae	California, USA	Snails	3	56	0.250	NA	Chl. a
Armitage and Fong	2003	Microalgae	California, USA	Snails	4	56	0.250	NA	Chl. a
Armitage and Fong	2003	Microalgae	California, USA	Snails	5	56	0.250	NA	Chl. a
Armitage and Fong	2003	Microalgae	California, USA	Snails	6	56	0.250	NA	Chl. a
Armitage *et al.*	2006	Seagrass	Florida, USA	Fishes Urchins	1	90	0.250	NA	Biomass
Belleveau and Paul	2002	Tropical macroalgae	Guam	Fishes	1	35	0.026	NA	Biomass
Belleveau and Paul	2002	Tropical macroalgae	Guam	Fishes	2	35	0.026	NA	Biomass
Burkepile and Hay	unpub	Tropical macroalgae	Florida Keys USA	Fishes	1	280	0.080	NA	% cover
Burkepile and Hay	unpub	Tropical macroalgae	Florida Keys USA	Fishes	1	180	0.080	NA	% cover
Diaz and McCook	2003	Tropical macroalgae	Australia Barrier Reef	Fishes	1	40	0.160	NA	Density
Hatcher and Larkum	1983	Tropical macroalgae	Australia Barrier Reef	Fishes	1	20	0.025	NA	Biomass
Hatcher and Larkum	1983	Tropical macroalgae	Australia Barrier Reef	Fishes	2	12	0.025	NA	Biomass

Authors	**Year**	**Primary producers**	**Location**	**Major herbivores**	**Exp #**	**Day**	**Size (m^2)**	**Nutrient status**	**Metric**
Hatcher and Larkum	1983	Tropical macroalgae	Australia Barrier Reef	Fishes	3	20	0.025	NA	Biomass
Hatcher and Larkum	1983	Tropical macroalgae	Australia Barrier Reef	Fishes	4	12	0.025	NA	Biomass
Hatcher and Larkum	1983	Tropical macroalgae	Australia Barrier Reef	Fishes	5	150	0.025	NA	Biomass
Hillebrand and Kahlert	2001	Microalgae	Sweden Baltic Sea	Molluscs Amphipods Isopods	1	31	0.023	low	Biovol.
Hillebrand and Kahlert	2001	Microalgae	Sweden Baltic Sea	Molluscs Amphipods Isopods	2	38	0.023	low	Biovol.
Hillebrand and Kahlert	2001	Microalgae	Sweden Baltic Sea	Molluscs Amphipods Isopods	3	28	0.023	low	Biovol.
Hillebrand and Kahlert	2001	Microalgae	Sweden Baltic Sea	Molluscs Amphipods Isopods	4	36	0.023	low	Biovol.
Hillebrand *et al.*	2000	Microalgae	Germany Baltic Sea	Molluscs, crustaceans	1	23	0.063	high	Biovol.
Hillebrand	2002	Microalgae	Nova Scotia NW Atlantic	Molluscs Amphipods Isopods	1	21	0.063	low	Biovol.
Hillebrand	2002	Microalgae	Nova Scotia NW Atlantic	Molluscs Amphipods Isopods	2	21	0.063	low	Biovol.
Hillebrand	2002	Microalgae	Nova Scotia NW Atlantic	Molluscs Amphipods Isopods	3	21	0.063	low	Biovol.
Hillebrand	2002	Microalgae	Nova Scotia NW Atlantic	Molluscs Amphipods Isopods	4	21	0.063	low	Biovol.
Lever and Valiela	2005	Microalgae	Mass. USA	Snails Shrimp	1	300	0.053	low	Chl. a
Lever and Valiela	2005	Microalgae	Mass. USA	Snails Shrimp	2	300	0.053	high	Chl. a
Lever and Valiela	2005	Microalgae	Mass. USA	Snails Shrimp	3	300	0.053	high	Chl. a
Lotze *et al.*	2000	Temperate macroalgae	Germany Baltic Sea	Molluscs Amphipods Isopods	1	330	0.063	high	Density
Lotze *et al.*	2000	Temperate macroalgae	Germany Baltic Sea	Molluscs Amphipods Isopods	2	330	0.063	high	Density
Lotze *et al.*	2001	Temperate macroalgae	Germany Baltic Sea	Molluscs Amphipods Isopods	1	30	0.063	high	Density
Lotze *et al.*	2001	Temperate macroalgae	Nova Scotia NW Atlantic	Molluscs Amphipods Isopods	2	30	0.063	low	Density
Lotze *et al.*	2001	Temperate macroalgae	Nova Scotia NW Atlantic	Molluscs Amphipods Isopods	3	30	0.063	low	Density

Authors	**Year**	**Primary producers**	**Location**	**Major herbivores**	**Exp #**	**Day**	**Size (m^2)**	**Nutrient status**	**Metric**
Lotze *et al.*	2001	Temperate macroalgae	Nova Scotia NW Atlantic	Molluscs Amphipods Isopods	4	30	0.063	low	Density
Lotze *et al.*	2001	Temperate macroalgae	Nova Scotia NW Atlantic	Molluscs Amphipods Isopods	5	30	0.063	low	Density
McClanahan *et al.*	2003	Tropical macroalgae	Belize	Fishes	1	49	0.250	NA	Biomass
McGlathery	1995	Seagrass	Bermuda	Urchins	2	70	0.785	NA	Biomass
Miller and Hay	1996	Temperate macroalgae	N. Carolina USA	Fishes Urchins	1	83	0.075	low	Biomass
Miller *et al.*	1999	Tropical macroalgae	Florida Keys USA	Fishes	1	60	0.045	NA	% cover
Nielsen	2001	Temperate macroalgae	Oregon USA	Molluscs	1	540	0.126	low	Biomass
Nielsen	2001	Temperate macroalgae	Oregon USA	Molluscs	2	540	0.126	low	Biomass
Russell and Connell	2005	Temperate macroalgae	S. Australia	Molluscs	1	76	0.360	low	% cover
Silliman and Ziemann	2001	*Spartina*	Virginia USA	Snails	1	120	1.000	NA	Biomass
Smith *et al.*	2001	Tropical macroalgae	Hawaii USA	Fishes	1	180	0.120	NA	Biomass
Sotka and Hay	unpub	Tropical macroalgae	Florida Keys USA	Fishes	1	142	0.045	NA	% cover
Thacker *et al.*	2001	Tropical macroalgae	Guam	Fishes	1	120	0.250	NA	Biomass
Valentine and Heck	2001	Seagrass	Florida USA	Urchins	1	116	1.000	NA	Biomass
Wootton *et al.*	1996	Microalgae	Washington USA	Molluscs	1	85	0.018	low	Biomass
Wootton *et al.*	1996	Microalgae	Washington USA	Molluscs	2	135	0.018	low	Biomass
Wootton *et al.*	1996	Microalgae	Washington USA	Molluscs	3	50	0.018	low	Biomass
Worm *et al.*	2002	Temperate macroalgae	Nova Scotia NW Atlantic	Molluscs Amphipods Isopods	1	330	0.063	low	% cover
Worm *et al.*	2002	Temperate macroalgae	Germany Baltic Sea	Molluscs Amphipods Isopods	2	330	0.063	high	% cover
Worm *et al.*	2000	Temperate macroalgae	Germany Baltic Sea	Molluscs Amphipods Isopods	1	250	0.063	high	% cover

Halodule wrightii were the primary seagrasses. Experiments in tropical macroalgal communities typically manipulated herbivorous fishes, and experiments in seagrass beds manipulated fishes and urchins. Gastropods and crustaceans were the dominant herbivores in temperate macroalgal, benthic microalgal, and *Spartina* communities (Table 2.1). Urchins were common in only one of the experiments in temperate macroalgal communities.

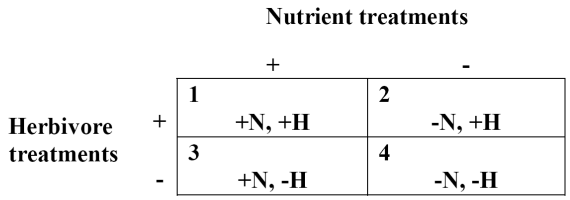
Herbivore removal was typically accomplished via physical barriers preventing access to experimental plots (i.e. cages or anti-fouling paint). Nutrient enrichment was generally accomplished via nutrient reservoirs that continually released nutrients to the water-column except for two studies that used reservoirs to enrich sediment pore water. The most common nutrient treatment was combined nitrogen + phosphorus enrichment although some experiments enriched with nitrogen alone. When a single study enriched at multiple nutrient concentrations or with both a nitrogen + phosphorus and a nitrogen-only treatment, we used data from the nitrogen + phosphorus treatment at the highest concentration tested; this maximized our ability to detect a nutrient enrichment effect. The majority of studies monitored nutrient levels to ensure significant nutrient enrichment of the water column or sediment pore water. When data were reported as a time series, we used the data from the final sampling period. Primary producer abundance was measured as biomass (20 experiments), absorbance of chlorophyll *a* (a proxy for microalgal biomass) (9 experiments), biovolume (9 experiments), primary producer density (8 experiments), or percent cover (8 experiments). We did not analyze effects on species diversity or richness because such metrics were rarely reported.

We performed meta-analyses on the total, pooled data set and then separately on tropical macroalgae, temperate macroalgae, benthic microalgae, and seagrasses. Because effects of herbivory and nutrient availability may differ depending on the inherent productivity of the ecosystem (Hillebrand 2002, Worm et al. 2002, Nielsen and Navarrete 2004), we divided the studies on temperate macroalgae and benthic microalgae into those conducted in either low vs. high productivity habitats (Table 2.1). The nutrient status of the system (productivity) was often reported in different measure (i.e. dissolved vs. total nutrients or nitrogen vs. phosphorus) making thresholds for classification difficult to define. Consequently, we used designations by the authors or in other publications related to the study area to classify the experiments into low or high productivity categories in the convention of Worm et al. (2002). Studies where productivity designations could not be obtained were excluded from these analyses. We did not divide tropical macroalgal or seagrass studies into low vs. high productivity studies because all studies were performed in areas of similar productivity.

Because different algae may respond differently to experimental treatments (Pedersen and Borum 1996), we used functional group designations from Steneck and Dethier (1994) to lump algae from tropical and temperate macroalgal studies into three categories: (1) crustose coralline algae, (2) filamentous turf algae, and (3) upright macroalgae. Too few studies reported enough data to perform analyses on each functional group as listed by Steneck and Dethier (1994). The crustose coralline algae category includes the functional group crustose algae (i.e. *Lithothamnion*, *Neogonolithon*, *Peyssonnella*, etc.). The filamentous turf algae include the functional groups (1)

filamentous algae (i.e. *Cladophora, Ectocarpus,* and *Piayella*) and (2) foliose algae (i.e. *Ulva* and *Porphyra*). The upright macroalgae include the functional groups (1) corticated foliose algae (i.e. *Dictyota*, *Padina,* and *Lobophora)*, (2) corticated macrophytes (i.e. *Chondrus*, *Acanthophora*, *Sargassum*, and *Gigartina*), (3) leathery macrophytes (i.e. *Fucus* and *Ecklonia*), and (4) articulated calcareous algae (i.e. *Halimeda* and *Amphiroa*). Not all studies reported data for the abundance of specific algal functional groups so our sample sizes were not consistent for all analyses across functional groups.

We used factorial meta-analysis (Gurevitch *et al.* 2000) that calculates the mean effect of the major factors as well as how the two main factors interact to determine the response variable (conceptually similar to a two-factor ANOVA). This allowed us to compare the mean effects of herbivore removal, nutrient addition, and their interaction. In addition, we calculated the individual effects of herbivore removal under ambient and enriched nutrient status and of nutrient enrichment in the presence and absence of herbivores (See Figure 2.1 for an outline of experimental treatments and their use in computing effect sizes). These calculations are based on Hedges' *d* (Gurevitch and Hedges 1993), which measures the difference between treatment and control means divided by a pooled standard deviation from the treatment and control and multiplied by a correction factor to account for differences in sample size among studies. For the analyses of algal functional groups from temperate vs. tropical habitats, we used the response ratio [$rr = \ln(x_t/x_c)$ where x_t is the treatment mean and x_c is the control mean] (Hedges *et al.* 1999) as the metric because it does not require error measurements for its calculation (as does Hedges' *d*), and many studies did not report error measurements for



Meta-analysis calculations:

Mean effects

Nutrient Enrichment: (1 + 3) – (2 + 4)

Herbivore removal: (3 + 4) – (1 + 2)

Interaction: (3 – 4) – (1 – 2)

Individual effects

Enrichment w/ herbivores [E (w/ H)]: (1 – 2)

Enrichment w/o herbivores [E (w/o H)]: (3 – 4)

Herbivore removal w/o enrichment [No H (w/o E)]: (4 – 2)

Herbivore removal w/ enrichment [No H (w/ E)]: (3 – 1)

Figure 2.1. The figure shows the four treatments present in all orthogonal manipulations of herbivore pressure and nutrient availability. Mean effects refer to the average effect of herbivore removal or nutrient addition. Individual effects refer to the effects of nutrient enrichment in the absence and presence of herbivores and the effects of herbivore removal in the absence and presence of nutrient enrichment. The effect size calculations are represented by the addition or subtraction of the number labels for each treatment in the figure. These equations represent the numerator in the effect size calculation equations as in Gurevitch *et al*. (2000).

functional group response variables. However, using the response ratio precluded using factorial meta-analysis, allowing us to calculate only the individual effects for the analyses of functional groups.

Means, error measurements, and sample sizes used to calculate effect sizes were obtained from tables or extracted from graphs using Grab It! XP (Datatrend Software, Raleigh, NC). Error measurements reported as standard errors were converted to standard deviation for use in effect size calculations. Calculations of effect sizes were performed as outlined in Gurevitch et al. (2000) for factorial analysis with Hedges' *d*, and Hedges *et al.* (1999) for the response ratio using workbooks in Microsoft Excel. We performed unweighted, mixed effect model meta-analyses with MetaWin 2.0 (Rosenberg *et al.* 2000). Confidence intervals (95%) were calculated using a bias-corrected bootstrapping technique with 9999 sampling iterations (Adams *et al.* 1997). Effect sizes were considered significant if 95% confidence intervals did not cross zero. Effect sizes within analyses (e.g. herbivore removal effect vs. nutrient enrichment effect) were considered different from each other if their 95% confidence intervals did not overlap.

To facilitate comparison of treatment effect sizes, we constructed our calculations so that the effects of both nutrient enrichment and herbivore removal were positive. Thus, we tested (1) the effect of removing herbivores from the system, not the effect of adding herbivores to the system and (2) the effect of nutrient enrichment. A positive effect size for herbivore removal or nutrient enrichment means that these manipulations enhance the abundance of primary producers. A positive effect size for the interaction term means that nutrient enrichment has a larger effect in the absence of herbivores than

in their presence. For factorial analyses, mean effect sizes are designated d^{++} whereas individual effect sizes are designated d^{+}. Response ratio effect sizes in the analyses of algal functional groups are designated *rr*.

To determine if effect sizes were either negatively or positively correlated with experimental duration or experimental plot size, we used least squares linear regression to compare effect sizes with the log-transformed duration (in days) or the log-transformed experimental plot size (in m^2) of each experiment. Regressions were performed only for mean effects and were performed for all studies pooled and for each primary producer type except for seagrasses due to low sample size ($n = 3$).

Results

Factorial meta-analysis across all experiments showed that both nutrient enrichment ($d^{++} = 0.98$) and herbivore removal ($d^{++} = 1.55$) strongly affected abundance of primary producers (Figure 2.2A). There was also a significant interaction ($d^{++} = 0.42$), indicating that nutrient enrichment had a greater effect in the absence of herbivores. Further, herbivore removal in the presence of enrichment ($d^{+} = 1.84$) had a much greater effect than enrichment when herbivores were not removed ($d^{+} = 0.51$) (Figure 2.2B).

For tropical macroalgae (Figure 2.2C), nutrient enrichment ($d^{++} = 0.90$), herbivore removal ($d^{++} = 2.84$), and their interaction ($d^{++} = 0.60$) were all positive. Nutrient enrichment enhanced tropical macroalgae in the absence of herbivores ($d^{+} = 1.37$) but not in their presence ($d^{+} = 0.28$) (Figure 2.2D). In contrast, herbivore removal had a strong, positive effect both with ($d^{+} = 3.23$) and without ($d^{+} = 2.15$) enrichment; the effects of

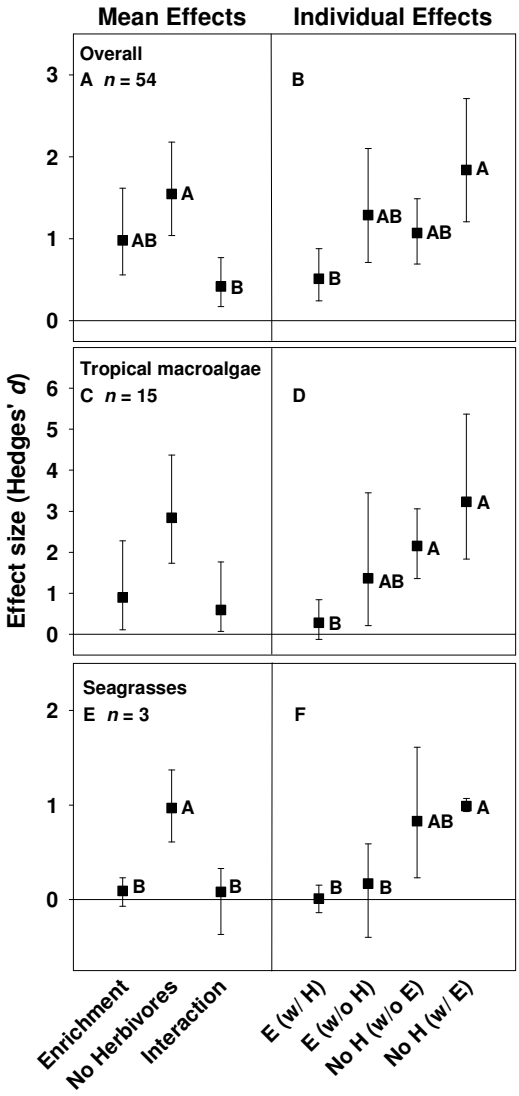


Figure 2.2. Results of meta-analyses on mean and individual effects (left panel and right panel respectively) for all primary producers (A&B), tropical macroalgae (C&D), and seagrasses (E&F). Effect sizes are Hedges' $d \pm 95\%$ confidence intervals. Effects are statistically significant ($P < 0.05$) if confidence intervals do not overlap $d = 0$. A positive d indicates an increase and a negative d a decrease in primary producer abundance. Letters designate differences among categories within an analysis as based on 95% confidence intervals, i.e. data points with different letters do not have overlapping confidence intervals. Graphs with no letters had no significant differences among data points. Note different scales on Y-axes.

herbivore removal were greater under either nutrient regime than were the effects of nutrients in the presence of herbivores (Figure 2.2D).

Seagrass communities (Figure 2.2E) showed no effect of nutrient enrichment (d^{++} = 0.09), a positive effect of herbivore removal (d^{++} = 0.97), and no interaction (d^{++} = 0.08). Nutrient enrichment did not affect seagrass abundance either in the presence (d^{+} = 0.01) or absence (d^{+} = 0.17) of herbivores (Figure 2.2F). In contrast, herbivore removal strongly affected seagrass abundance both in the absence (d^{+} = 0.83) and presence (d^{+} = 0.99) of added nutrients. These analyses suggest that herbivores have strong effects while nutrients have limited effects on seagrass abundance, but the low sample size (n = 3) constrains these conclusions.

Temperate macroalgae (Figure 2.3A) were positively affected by both nutrient enrichment (d^{++} = 1.06) and herbivore removal (d^{++} = 1.27). The effect size for the interaction term was positive (d^{++} = 0.40, CI = -0.03/0.93) but not significant (the confidence intervals slightly overlapped zero). The nutrient enrichment effect was significant both in the presence (d^{+} = 0.61) and absence (d^{+} = 1.37) of herbivores (Figure 2.3B). Herbivore removal had a significant positive effect in the presence of added nutrients (d^{+} = 1.56), but without added nutrients the effect size was smaller (d^{+} = 0.80) and slightly overlapped zero, making the effect non-significant.

Herbivore removal and nutrient enrichment differentially affected temperate macroalgae as a consequence of the background nutrient status of the ecosystem. In low productivity environments, both nutrient enrichment (d^{++}=0.75) and herbivore removal (d^{++} = 2.06) had positive effects (Figure 2.3C). The interaction effect was marginally

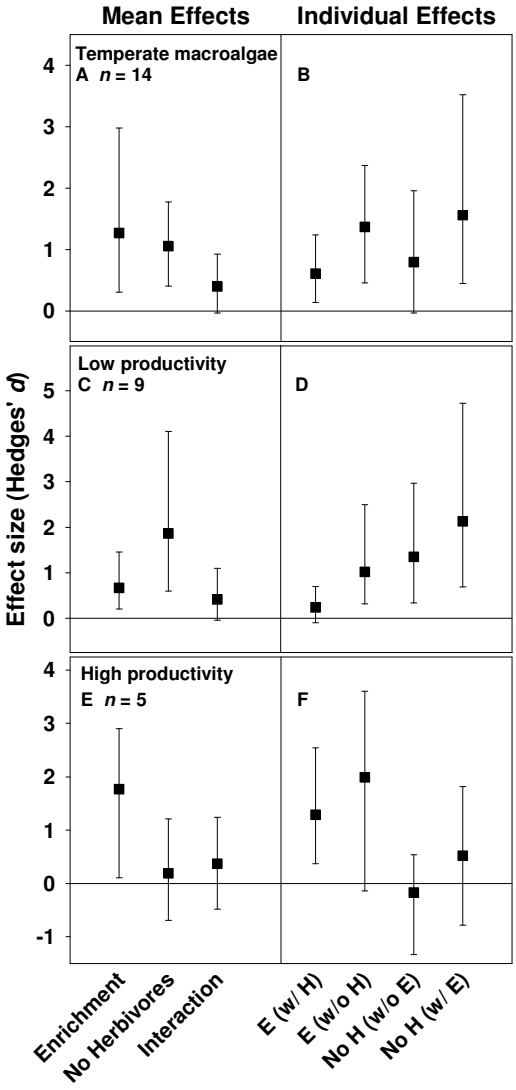


Figure 2.3. Results of meta-analyses on mean and individual effects for temperate macroalgae all studies (A&B), studies in low productivity areas (C&D), and studies in high productivity areas (E&F). Symbols and analyses as in Figure 2.2.

non-significant (d^{++}=0.42, CI = -0.03/1.10). However, analyses of individual effects showed that nutrient enrichment significantly enhanced algal abundance only in the absence of herbivores (d^{+} = 1.10; Figure 2.3D). Herbivore removal effects were strong in the absence (d^{+}=1.52) and presence (d^{+} = 2.31) of enrichment. In high productivity areas, there was a positive nutrient enrichment effect (d^{++} = 1.48) but no herbivore removal effect (d^{++} = 0.22) or interaction (d^{++} = 0.37; Figure 2.3E). The enrichment effect appeared strong in both the presence and absence of herbivores (d^{+} = 1.29 and 1.99 respectively; Figure 2.3F) but was statistically significant only with herbivores present despite the effect size being larger without herbivores.

For benthic microalgae, the nutrient enrichment (d^{++} = 0.64), herbivore removal (d^{++} = 0.76), and interaction effects (d^{++} = 0.21) were positive (Figure 2.4A). Additionally, nutrient enrichment was significant in the presence (d^{+}=0.40) and absence (d^{+} = 0.80) of herbivores, and herbivore removal was significant both in the absence (d^{+} = 0.51) and presence (d^{+} = 0.91) of nutrient enrichment (Figure 2.4B). In low productivity areas, the effects of nutrient enrichment (d^{++} = 0.35), herbivore removal (d^{++} = 1.01), and their interaction (d^{++} = 0.28) were significant (Figure 2.4C). Individual effects showed significant nutrient enrichment effects only in the absence of herbivores (d^{+} = 0.59), but herbivore removal effects were significant both with (d^{+} = 1.21) and without (d^{+} = 0.68) nutrient additions (Figure 2.4D). Studies in high productivity areas showed a strong nutrient enrichment response (d^{++} = 1.33) but no herbivore removal response (d^{++} = 0.47) or interaction (d^{++} = 0.32; Figure 2.4E). Individual effects for high productivity areas showed a positive response to enrichment in both the presence (d^{+} = 0.95) and absence

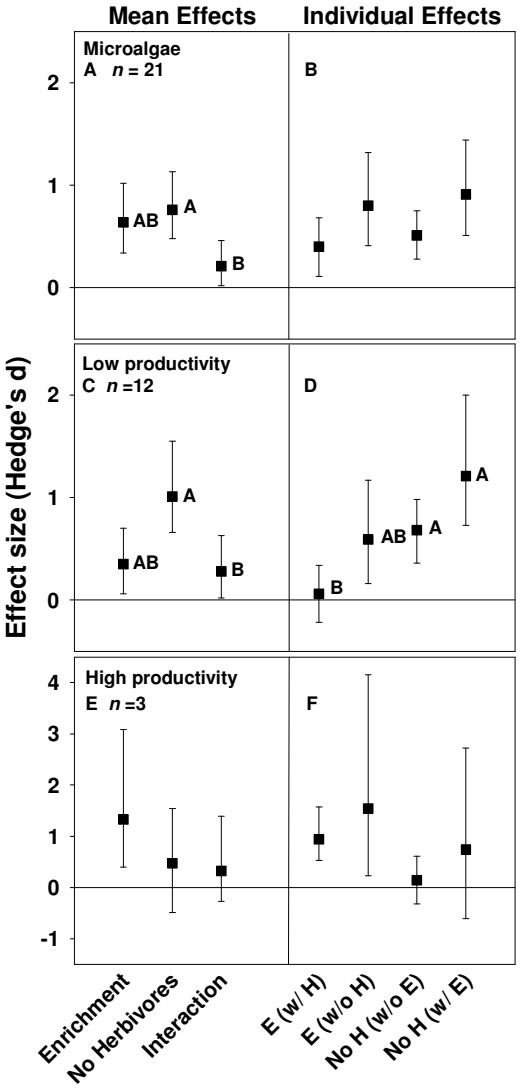


Figure 2.4. Results of meta-analyses on mean and individual effects for benthic microalgae all studies (A&B), studies in low productivity areas (C&D), and studies in high productivity areas (E&F). Symbols and analyses as in Figure 2.2.

(d^+ = 1.54) of herbivores, but no herbivore removal effect regardless of nutrient enrichment (Figure 2.4F).

When we divided temperate and tropical macroalgae into functional groups, effects of herbivore removal and nutrient enrichment depended on algal type and latitude. For crustose coralline algae in temperate systems (Figure 2.5A), enrichment in the presence of herbivores decreased abundance, but this was the only significant result and should be viewed with caution due to very low sample size (n = 2). Crustose corallines in tropical systems (Figure 2.5B) were modestly enhanced by nutrient enrichment, with this being significant in the absence of herbivores (rr = 0.57). However, herbivore removal strongly decreased crustose corallines in the absence (rr = -2.36) and presence (rr = -2.23) of nutrient enrichment.

For upright macroalgae, nutrient enrichment had no effect in either temperate or tropical habitats (Figures 2.5C & 2.5D), but herbivore removal increased macroalgal abundance in both temperate (rr = 0.60 in the absence of nutrient enrichment; Figure 2.5C) and tropical communities (rr = 3.13 and rr = 2.81 in the absence and presence of nutrient enrichment; Figure 2.5D). Filamentous algae in temperate systems were enhanced by nutrient enrichment (rr = 1.22 and rr = 1.11 in the presence and absence of herbivores, respectively) but not by herbivore removal (Figure 2.5E). In tropical systems, nutrient enrichment decreased abundance of filamentous algae in the presence of herbivores (rr = -1.02) (Figure 2.5F) while other treatments had no significant effects.

Regressions comparing effect sizes and experiment duration showed relationships for only 2 of the 12 comparisons (i.e. the herbivore removal and interaction effects for

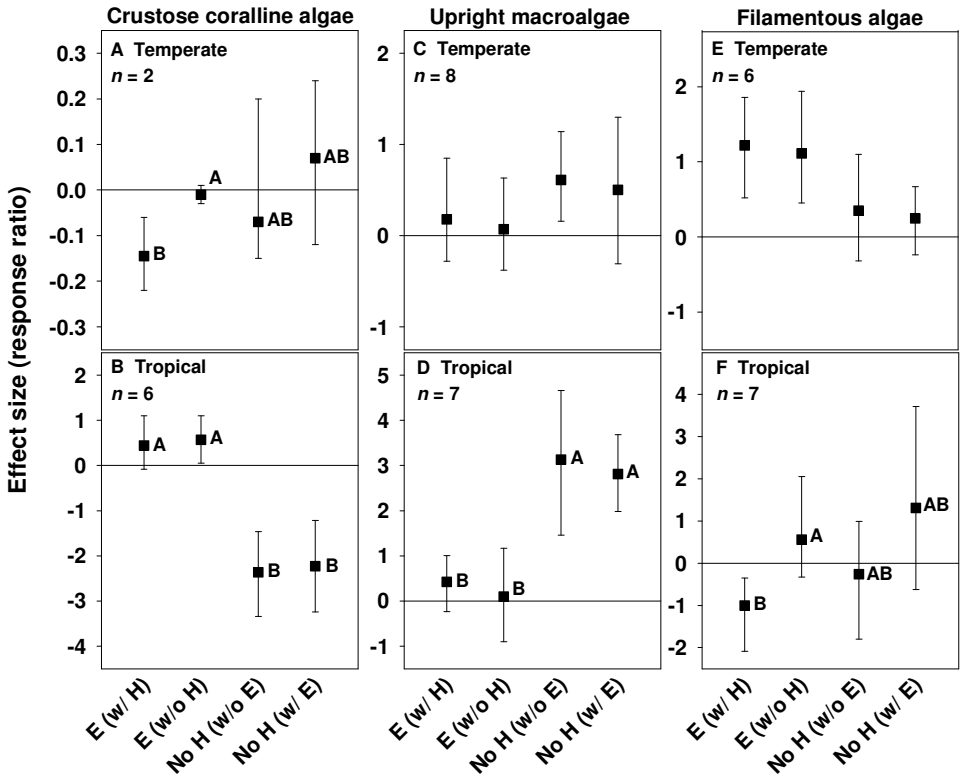


Figure 2.5. Results of meta-analyses on individual effects for crustose coralline algae, upright macroalgae, and filamentous algae in temperate and tropical ecosystems. Effect sizes are response ratio ± 95% confidence intervals. Symbols and analyses as in Figure 2.2.

benthic microalgae) (Table 2.2). Experiments lasted on average 119.2 ± 17.8 d (mean ± SE) with a range of 12-540 d. Regressions comparing effect sizes and experimental plot size showed no significant relationships for any of the comparisons (Table 2.3). Mean experimental plot size was 0.14 ± 0.03 m^2 (mean ± SE) with a range of 0.023-1 m^2. Therefore, combining experiments of different durations and sizes rarely confounded effect size with experimental characteristics and would have had little effect on most analyses.

Discussion

When averaged across all the benthic marine systems in our study, herbivore pressure and nutrient availability both played significant roles in determining abundance of primary producers (Figures 2.2A & 2.2B). The positive interaction terms for the overall analysis (Figure 2.2A), for tropical macroalgae (Figure 2.2C), and for benthic microalgae (Figure 2.4A) demonstrate that effects of nutrient enrichment are magnified in the absence of herbivores and that simultaneous alterations to biotic and abiotic forces can have synergistic effects on communities (Scheffer et al. 2001, Worm et al. 2002). Further, context-dependent patterns of top-down and bottom-up regulation were evident when comparing temperate vs. tropical macroalgae (Figures 2.2D & 2.3B), low vs. high productivity systems (Figures 2.3 & 2.4), and different algal functional groups (Figure 2.5).

Table 2.2. Results of regression analyses testing for relationships between mean effect size and experimental duration. Seagrasses were not included due to low sample size (n = 3).

Primary producer	Effect type	*n*	slope	r^2	*P*
Overall	Herbivore	54	-0.026	0.001	0.972
Overall	Nutrient	54	-0.157	0.001	0.812
Overall	Interaction	54	0.778	0.017	0.817
Tropical macroalgae	Herbivore	15	0.008	0.0	0.634
Tropical macroalgae	Nutrient	15	-1.093	0.051	0.482
Tropical macroalgae	Interaction	15	-2.609	0.120	0.202
Temperate macroalgae	Herbivore	14	0.323	0.005	0.820
Temperate macroalgae	Nutrient	14	0.315	0.015	0.679
Temperate macroalgae	Interaction	14	1.790	0.251	0.068
Microalgae	Herbivore	21	-1.070	0.270	0.015
Microalgae	Nutrient	21	-0.698	0.109	0.145
Microalgae	Interaction	21	-1.500	0.285	0.013

Table 2.3. Results of regression analyses testing for relationships between mean effect size and experimental plot size. Seagrasses were not included due to low sample size (n = 3).

Primary producer	Effect type	*n*	slope	r^2	*P*
Overall	Herbivore	54	-0.184	<0.001	0.783
Overall	Nutrient	54	0.766	0.012	0.208
Overall	Interaction	54	-0.010	<0.001	0.977
Tropical macroalgae	Herbivore	15	0.480	<0.001	0.805
Tropical macroalgae	Nutrient	15	-1.280	<0.001	0.404
Tropical macroalgae	Interaction	15	-1.060	<0.001	0.381
Temperate macroalgae	Herbivore	14	-2.700	<0.001	0.427
Temperate macroalgae	Nutrient	14	-2.230	0.053	0.213
Temperate macroalgae	Interaction	14	-0.440	<0.001	0.732
Microalgae	Herbivore	21	-0.375	<0.001	0.366
Microalgae	Nutrient	21	0.691	0.091	0.099
Microalgae	Interaction	21	-0.028	<0.001	0.922

The analyses of tropical macroalgae show a modest effect of nutrient enrichment only when herbivores are first excluded but a consistently strong effect of removing herbivores regardless of nutrient enrichment (Figure 2.2D). Although both the decline of herbivores (Hughes 1994, Hughes et al. 1999) and eutrophication (Lapointe 1997, 1999) have been emphasized as the primary mechanism driving the transition of many reefs from coral- to macroalgal-dominated ecosystems, our analyses suggest that reduced herbivory is the primary factor driving increased macroalgal abundance but that nutrient enrichment significantly interacts with reduced herbivory to magnify these effects (Figures 2.2C & 2.2D). This interaction between herbivory and nutrient availability in driving macroalgal abundance has been emphasized in recent conceptual models of the decline of coral reef health (McCook 1999, Bellwood et al. 2004) as well as experimental manipulations addressing this problem (e.g. Miller et al. 1999, McClanahan et al. 2003). These interactions likely make reefs less resilient and less likely to recover from the effects of climate change and disturbance (Hughes et al. 2003) as reduced herbivore populations would be less likely to keep open space caused by coral bleaching, hurricanes, and disease epidemics free of algae and allow recolonization of corals (Aronson et al. 2005), and eutrophication would likely accelerate the transition from coral- to algal-dominated communities via increased growth rates of algae. Additionally, excess nutrients also increase the severity of coral diseases (Bruno et al. 2003), decrease coral growth rates (Koop et al. 2001), and increase bioerosion of reef substrate (Carreiro-Silva et al. 2005), all of which decrease the resilience of reefs.

Removal of herbivores on reefs dramatically depressed the abundance of crustose corallines (Figure 2.5B) but dramatically increased the abundance of upright macroalgae (Figure 2.5D). Many corals preferentially recruit to crustose coralline algae (Heyward and Negri 1999) but have their recruitment and survival suppressed by upright macroalgae (Lewis 1986, McCook et al. 2001) making herbivores crucial to reef health because they indirectly facilitate coral recruitment and survival by promoting crustose corallines and by suppressing upright macroalgae. However, the effects of herbivores on tropical crustose coralline algae (Figure 2.5B) and nutrients on temperate crustose algae (Figure 2.5A) may not reflect actual changes in crustose coralline abundance but in apparency as crustose corallines are often overgrown but not killed by macroalgae (Steneck and Dethier 1994). Because these studies measured percent cover of crustose coralline algae instead of biomass, crustose algae may have been present but obscured by a fleshy algal canopy making them less visible and decreasing their relative abundance but not decreasing their absolute abundance. However, this decrease in apparency in response to herbivore removal still would be significant for coral reefs in that the preferred settlement sites for corals (i.e. crustose coralline algae), would be obscured by turf or upright macroalgae thereby decreasing recruitment success of corals and the regenerative capacity of reefs.

Although we showed little effect of scale on the experimental effect sizes (Table 2.3), the maximum plot size for these experiments was 1 m^2 which is far smaller than the kilometer-wide scale that may represent anthropogenic effects on ecosystems. This smaller scale may diminish the effects of nutrients but magnify the effects of herbivores

on producer communities. For example, nutrient enrichment in the presence of herbivores did not show an effect for tropical systems which could be the result of highly mobile fishes concentrating their feeding efforts on a small patch of very nutritious algae (Burkepile and Hay unpub. data). This interaction could explain the depression of turf algae under nutrient enrichment in the presence of herbivores (Figure 2.5F). Yet, experimental nutrient enrichment on coral patch reefs averaging 253 m^2 also showed no effect of enrichment on algal abundance in the presence of fish (Koop et al. 2001) while exclusions of herbivores on reefs of 50-230 m^2 (Sammarco 1982, Lewis 1986) have shown dramatic increases in macroalgal abundance similar to our analyses (Figures 2.2C & 2.5B). Although, these "large-scale" experiments are still far smaller than what might be expected from overfishing of herbivores or anthropogenic eutrophication, their results suggest that the processes regulating tropical macroalgae on the scale of $<1m^2$ are similar to those on the scale of 100's of m^2.

For temperate macroalgae and benthic microalgae the relative importance of herbivores and nutrients differed between areas of low vs. high productivity. In low productivity areas, both herbivore removal and nutrient enrichment were significantly positive (Figures 2.3C & 2.4C), but nutrient enrichment was significant only when herbivores were absent (Figures 2.3D & 2.4D). In contrast, for high productivity areas, the effects of nutrient enrichment were significant whereas the effects of herbivore removal were not (Figures 2.3E, 2.3F, 2.4E, & 2.4F). However, all of the studies for temperate macroalgae in high productivity systems were conducted in the same area of the Baltic Sea, and the analyses of benthic microalgae in high productivity areas had a

low sample size (n = 3) meaning that this effect could be a region-specific pattern rather than a general phenomenon. Yet, Hillebrand (2002) also showed that varying the level of background productivity in the system alters the interaction between herbivore vs. nutrient control of benthic microalgae in freshwater and marine systems, although the differences among areas of differing productivity were modest. Worm et al. (2002) showed even more dramatic effects of background productivity on the role of herbivores vs. nutrient availability in controlling species diversity in aquatic communities. Nutrient enrichment in low productivity systems increased diversity but herbivores decreased diversity, whereas nutrients in high productivity systems decreased diversity and herbivores increased diversity. Further, the comparison of our analyses with those of Worm et al. (2002) suggests that the effects of herbivores and nutrients are more complex than merely changing overall abundance of primary producers. For example, herbivores could facilitate the replacement of palatable macroalgae with unpalatable macroalgae with little effect on actual primary producer abundance (Lubchenco and Gaines 1981, Lotze et al. 2001). Thus, our measure of producer abundance almost certainly overlooked important changes in species composition in response to herbivores and nutrients. Further comparison of these three meta-analyses (Hillebrand 2002, Worm et al. 2002, this study) suggest that consumers in high productivity areas have little effect on the overall abundance of primary producers but a large effect on community composition whereas nutrient enrichment increases abundance and decreases diversity. In low productivity areas consumers depress both the abundance and diversity of producers while nutrient enrichment increases diversity but not abundance.

For temperate macroalgal communities, these patterns for low and high productivity studies may stem, in part, from the types of algae present in these systems. Large, perennial macroalgae tend to dominate low productivity intertidal areas, while ephemeral, filamentous macroalgae become more abundant as productivity increases (Worm et al. 2000, Bracken and Nielsen 2004). Studies of nutrient uptake dynamics indicate that perennial macroalgae absorb nutrients more slowly than filamentous algae (Pedersen and Borum 1996), suggesting that perennial macroalgae may respond less quickly to nutrient pulses than would filamentous algae. Our analyses agree with these physiological studies and show that upright macroalgae in temperate systems are more strongly affected by herbivores than by nutrient availability (Figure 2.5C) while the abundance of filamentous algae is more strongly affected by nutrient availability with herbivores having minimal influence (Figure 2.5E). Thus, primary producer abundance in high productivity areas may show strong responses to nutrient enrichment because dominant, filamentous algae rapidly respond to nutrient pulses and more easily compensate for losses to herbivores with rapid growth. Similarly, laboratory studies have shown that the same density of grazers has a smaller effect on the recruitment of the annual alga *Enteromoprha intestinalis* as nutrient enrichment increases (Lotze and Worm 2002). Producer abundance in low productivity areas may be more strongly affected by herbivores because upright macroalgae are less influenced by fluctuations in nutrient availability (Pfister and Van Alstyne 2003) and grow more slowly making them more susceptible to herbivores than are fast-growing filamentous algae in high productivity areas even though these perennial macroalgae may be less preferred food than annual

algae. Further, these patterns could be confounded if herbivores were consistently less abundant in high as opposed to low productivity areas. Although few studies in our analysis measured herbivore abundance making quantitative comparisons difficult, Lotze et al (2001) found the highest herbivore densities at their high productivity site but showed little effect of herbivore removal on producer abundance further suggesting that algae in high productivity areas can grow fast enough that they essentially escape control by grazers.

A limitation of the analyses for temperate macroalgae is that all of the studies come from rocky intertidal or shallow subtidal systems where herbivores may be large (i.e. urchins or gastropods) relative to the primary producers (filamentous algae and small to medium-sized macroalgae). Our dataset did not included experiments from large kelp communities (i.e. *Macrocystis* spp.). These large, perennial macroalgae can respond strongly to pulsed inputs of nutrients (Dean and Jacobsen 1986) and suffer extensive die-offs when faced with nutrient-poor water for extended periods (Dayton et al. 1992) showing that nutrient availability plays a strong role in affecting their abundance, a pattern contrary to the one we show for perennial macroalgae (Figure 2.5C). Further, herbivores can have effects on kelp communities that range from weak (Sala and Graham 2002) to strong (Estes et al. 1998) emphasizing the need for more in depth experimental work addressing the relative roles of herbivores and nutrient availability in affecting kelp communities.

Nutrient enrichment in the presence of herbivores significantly suppressed both temperate crustose corallines (Figure 2.5A) and tropical filamentous algae (Figure 2.5F).

Nutrients never suppressed any other primary producers in our other analyses (Figures 2.2-2.5). The studies we analyzed did not address these effects and our analyses cannot rigorously assess the mechanisms involved, but herbivores are commonly nitrogen limited (Mattson 1980) suggesting that dominant herbivores in these systems selectively attack algae with enriched levels of nitrogen. Fishes on tropical reefs will selectively attack filamentous algae growing on plots with elevated nutrients (Burkepile and Hay unpub. data) and individual macroalgae that have been subjected to nutrient enrichment (Boyer et al. 2004). This aspect of nutrition and fish behavior could explain why filamentous algae in temperate areas with few herbivorous fishes are enhanced by nutrients while those in tropical areas with abundant fishes are significantly suppressed by nutrient additions only when herbivores are present (Figure 2.5F). Similarly, gastropods in the temperate intertidal commonly enhance coralline abundance by grazing competing filaments and microalgae more heavily than encrusting corallines (Steneck and Dethier 1994), but increased nutrients may enhance the value of crustose corallines and result in them being targeted by these grazers. However, as discussed earlier, the pattern for crustose coralline algae may reflect changes in relative as opposed to absolute abundance and not result directly from grazing by herbivores.

Conclusions

Both herbivores and nutrients significantly affected the abundance of primary producers across all habitats we examined. These data suggest that human alteration of food webs and nutrient availability will have demonstrable, often compounded, effects on

primary producers but that the effects will depend on context and vary among latitudes, primary producers, and the inherent productivity of ecosystems. Further, herbivory and nutrient availability have complex and interactive effects on both overall abundance and diversity of primary producers making the mechanisms that drive these patterns fruitful areas of future research. The small scale of most of these experiments underscores to the need for creative experimentation that analyzes the effects of top-down and bottom-up forces on larger spatial and temporal scales that more closely resemble the effects of anthropogenic stressors on these ecosystems. Further, tests on how the patterns from these small-scale experiments extrapolate at larger scales are required to continue to address productively the effects of top-down and bottom-up forces on marine communities.

CHAPTER 3

REVIVING CARIBBEAN REEFS: THE CRITICAL ROLE OF HERBIVORE DIVERSITY

Abstract

Herbivory is crucial for healthy coral reefs, but reef function may depend as much on herbivore diversity as on the intensity of herbivory. Using manipulative field experiments, we show that Caribbean reefs change dramatically as a function of changing herbivorous fish diversity. Higher herbivore diversity caused lowered macroalgal abundance, reduced coral mortality, and increased coral growth when compared to treatments with lower herbivore diversity. Complementary feeding by different fishes drove these patterns because macroalgae were unable to effectively deter feeding by fishes with different attack strategies. Maintaining diversity of herbivorous fishes is critical for conserving and restoring healthy coral reefs.

Introduction

Coral reefs are imperiled worldwide because of the compounding effects of multiple stressors (Hughes et al. 2003a, Bellwood et al. 2004). The decline of reefs is particularly evident in the Caribbean where coral cover has decreased by 80% in recent decades (Gardner et al. 2003) and may drop further as reefs fail to rebound from increased coral bleaching and disturbances (Gardner et al. 2005, McWilliams et al. 2005). During this decline there has been considerable scientific focus on determining and debating causes of coral loss (Aronson et al. 2003, Hughes et al. 2003a, Hughes et al.

2003b, Pandolfi et al. 2003a, 2003b), but minimal focus on ecologically sustainable solutions to enhance reef recovery (Pandolfi et al. 2005). Here, we focus on a prescription for reef recovery by demonstrating that herbivorous fish diversity positively impacts Caribbean reef function and could serve as a management tool for reviving coral reefs.

At previous historic densities, herbivorous fishes and urchins kept reefs free of macroalgae that can overgrow and kill established corals (Lewis 1986) as well as prevent coral recruitment (McCook et al. 2001). The removal of these herbivores via overfishing and disease led to macroalgal blooms and dramatic loss of corals on many reefs (Hughes 1994, Jackson et al. 2001). Despite the clear role of herbivory as a critical process for maintaining reef health, we know little about the effects of herbivore diversity on the function of coral reefs. Herbivore diversity should benefit reefs as a more diverse herbivore assemblage should include herbivores with varied attack strategies, which in turn should increase the efficiency of macroalgal removal because particular macroalgal species are unlikely to be well defended against all types of herbivores (Lubchenco and Gaines 1981, Schupp and Paul 1994).

To address the role of herbivore diversity on coral reefs, we enclosed equal densities of single species and mixed species groups of herbivorous fishes in large, replicate cages on a reef in the Florida Keys, USA. We used the redband parrotfish, *Sparisoma aurofrenatum*, and the ocean surgeonfish, *Acanthurus bahianus* to generate our experimental treatments. We chose these two fishes because videotaping of reef macroalgae showed that these were the major grazers of macroalgal species that commonly overgrow coral reefs (M.E. Hay unpub. data). Additionally, these two fishes

also differ in their adaptations for herbivory as redband parrotfish have robust mouthparts, a pharyngeal mill that mechanically breaks algal cells, and no differentiated stomach, while ocean surgeonfish lack robust mouthparts and a pharyngeal mill, but have an acidic stomach that lyses algal cells (Horn 1989). Over the 10 month duration of the experiment, we monitored changes to macroalgal abundance and species composition and to coral health and cover in response to the treatments and assessed feeding preferences of the herbivores for common macroalgae.

Materials and Methods

Experimental setup and maintenance

In November 2003, we used NOAA's Aquarius, a self-sufficient underwater research laboratory at a depth of 16 m offshore of Key Largo, FL to set up the experiment. The experiment was located on a spur and groove reef formation at depths of 16-18 m on Conch Reef (24°57'N/80°27'W). The cage frames were constructed from 0.6 cm steel bar and covered with PVC-coated, galvanized chicken wire (2.5 cm mesh size) attached to the cage frame with cable ties. Chicken wire of this mesh size has been used in previous experiments and imparts minimal caging artifacts (Miller et al. 1999). Cages measured 2 m X 2 m X 1 m tall and covered 4 m^2 of the reef bottom. We attached the cages to the reef by wiring the frames to 30 cm galvanized nails that had been hammered into the reef substrate. A 30 cm flange of chicken wire extended from the base of the cage and was conformed to the reef substrate and affixed using galvanized fencing nails. This barrier prevented larger fishes from escaping or entering the cage, but the mesh size allowed small fishes to enter and exit at will. One half of the cage top was

secured with bungee cords instead of cable ties to allow easy access to the inside of the cages for routine maintenance and data collection. Zinc anodes were attached to the chicken wire and the cage frame to prevent corrosion. Two 25 cm X 10 cm PVC tubes were attached to the inside of the cage frame as refuges for the enclosed fish.

The benthic community inside the cages consisted of unmanipulated populations of macroalgae, corals, sponges, gorgonians, and other common reef invertebrates. Treatments within the cages consisted of: (1) two redband parrotfish, (2) two ocean surgeonfish, (3) one redband parrotfish and one ocean surgeonfish, and (4) no enclosed fish. We also monitored uncaged areas of equal size with $n = 8$ for each treatment and for the uncaged areas. Our treatments achieved equal density of grazers within the cages (0.5 fish/m^2) and also did not differ in fish biomass as parrotfish and surgeonfish within treatments did not differ in biomass (142.7 ± 11 g vs. 137.4 ± 4.6 g respectively [mean ± SE]; $t = 0.45$, $P = 0.66$, $df = 13$). Four cages and an uncaged area were blocked as closely as the reef configuration allowed in one general area and treatments were allocated randomly among each of the four cages. Thus, we had eight blocks each containing all five experimental treatments. We caught fishes with hand nets and barrier nets and placed them inside the cages. Every 4-6 weeks, we surveyed fishes inside the cages and replaced missing fishes to maintain treatments. Four replicates were not included in the data analyses due to persistent predation on the treatment fishes by moray eels resulting in $n = 6$ for the parrotfish-only and the parrotfish/surgeonfish treatments. We scrubbed the cages inside and out roughly every 4-6 weeks to remove fouling organisms and prevent shading. Between scrubbings, grazing by reef fishes (especially surgeonfishes and juvenile parrotfishes feeding on filamentous algae) kept the cages relatively clean of

fouling organisms. Macroalgal abundance and community structure at the start of our experiment did not differ among our treatments (Table 3.1). The experiment ran for 10 months between November 2003 and August 2004.

Data collection and analysis

Every 8-10 weeks, we monitored macroalgal cover and species composition on the benthos inside the cages and in uncaged areas. Using a 1.5 m X 0.75 m quadrat containing 50 stratified random points, we sampled two areas within each cage for a total of 100 points and identified the organisms under each point to the lowest taxonomic level possible under field conditions. For some species that grew as easily identifiable separate individuals (i.e. *Halimeda tuna* and *Sargassum* spp.), we counted numbers within each cage as well as recording percent cover. We avoided taking data from the outer 10cm border within each cage to minimize cage effects because the cage itself could have impeded fish from feeding in close proximity to the edges. Cover or density data from the end of the experiment (August 2004) were used for all analyses. We used one-factor analysis of variance (ANOVA) followed by Tukey's multiple comparisons to determine differences among treatments within an analysis. Even though our experiment was designed with eight blocks each containing a replicate of each treatment, we did not use a blocking factor in our ANOVA's because eel predation on the treatment fish necessitated the removal of four cages from the experiment resulting in $n = 6$ for the parrotfish-only and the parrotfish/surgeonfish treatments. The loss of these replicates invalidated our blocked design. Data were subjected to Cochran's test for homogeneity of variance (Sokal and Rohlf 1995) and transformed when necessary to meet the variance

Table 3.1. One-way ANOVAs assessing differences among treatments in macroalgal cover at the beginning of the experiment.

Macroalgal type	***F***	***P***
Dictyota spp.	1.24	0.315
Halimeda tuna	0.89	0.415
Lobophora variegata	0.79	0.539
Articulted coralline algae	0.68	0.611
Turf algae	0.74	0.571
Coralline algae	1.41	0.252
Upright macroalgae	2.01	0.115

homogeneity assumptions of ANOVA. We used the nonparametric Kruskal-Wallis test followed by multiple comparisons for *Sargassum* spp. because no transformation satisfied the data assumptions for ANOVA.

To more completely address the effects of herbivore diversity on the abundance of upright macroalgae as a group, as well as specific groups or species of macroalgae, we calculated a difference metric (D) comparing single species treatments to the diversity treatment. To calculate D, we used the formula $D = (O_i - E)/E$ where E is the average of the two single species treatments combined (the expected value) and O_i is the observed value for one of the replicates in the diversity treatment. D was calculated for each diversity treatment replicate. This metric is similar to D_{max} that is used to detect overyielding in studies of how plant diversity affects ecosystem function (Loreau 1998). If $D < 0$, then abundance of that macroalgal group is lower in the diversity treatment than the average single species treatment; if $D > 0$ then the diversity treatment facilitates that macroalgal group.

We monitored the condition and growth of corals within the treatments using digital photography. We took digital photographs of each coral colony *in situ* within each replicate of all treatments at the beginning (November 2003) and end (August 2004) of the experiment. The camera was mounted on a quadrapod frame to allow consistent positioning of the camera above each coral. Corals were individually mapped onto detailed drawings of the benthos of each treatment. We did not include corals that were growing in areas that were difficult to photograph such as on the tops of large coral aggregates or vertical reef structure. To measure loss or gain of live area for each colony, we used the computer imaging program Image J to outline each coral in the photographs and calculate colony area. We did this for each coral at the beginning and end of the experiment. To calculate the change in coral area over the course of the experiment, we used the following formula: (end coral area - beginning coral area)*100/beginning coral area. Measuring coral colony area using photographs is a good method for estimating coral growth when corals are mounding or encrusting (Tanner 1995). Since this photographic method does not work well for branching corals such as *Porites porites*, they were not included in the analysis, but branching corals represented <5% of colonies within the cages so our sample size was not significantly diminished by excluding them. The most common mounding and encrusting corals found in the treatments were *Siderastrea siderea* (45% of all corals), *Porites astreoides* (19%), *Agaricia* spp. (16%), and *Stephanocoenia michelini* (10%).

To assess coral mortality for each treatment, we calculated the percentage of corals from each replicate that died and tested for significant mortality in each treatment by testing for difference from zero using a one-tailed, t-test. Change in coral area was

analyzed using a nested, one-way ANOVA on the rank transformed data with individual corals nested within a fish treatment replicate followed by Tukey's test for multiple comparisons. Additionally, we used linear least squares regression to investigate the relationship between total macroalgal abundance in each replicate for each treatment and change in coral area for that replicate. For regression analysis, the average change in coral area was regressed against total macroalgal cover.

Fish feeding preferences for common macroalgae

To determine feeding preferences of redband parrotfish and ocean surgeonfish for macroalgae that were present in the various treatments, we offered macroalgae to the parrotfish and surgeonfish housed in the single species treatments. We used *Dictyota menstrualis*, *Halimeda tuna*, *Sargassum fillipendula*, *Lobophora variegata*, *Kallymenia westii*, and *Haloplegma duperryi* as these species were common in some of the treatments. In the lab, pieces of macroalgae (3.0 ± 0.3 g pieces for *H. tuna* and 2.0 ± 0.2 g pieces for other macroalgae) were blotted dry with a paper towel, weighed to the nearest 1 mg, and then entwined into a three-stranded polypropylene rope (one species per rope). Ropes of each macroalgal species were placed in the parrotfish-only, surgeonfish-only, and exclosure cages. Fish were allowed to feed on the macroalgae for 24-30 h before the ropes were collected. Remaining pieces of macroalgae were then blotted dry and weighed to the nearest 1 mg to get the final weight. The beginning and final weights were used to calculate the percent of the macroalgae removed. To determine if the parrotfish and surgeonfish consumed significant quantities of these macroalgae, change in mass of the macroalgae in the parrotfish and surgeonfish

treatments were compared individually to changes in mass in the exclosures using one-tailed t-tests. We used one-tailed t-tests based on the prediction that more macroalgal biomass would be removed in cages enclosing large herbivores than cages excluding large herbivores.

Analyses of possible confounding factors

To determine if the patterns of macroalgal abundance and coral growth could have been the result of factors that were confounded with the experimental treatments, we quantified the weight:length ratios of enclosed treatment fishes, the feeding rates of enclosed treatments fishes, and the use of different treatments by small fishes that could pass through the mesh (i.e. damselfishes and juvenile parrotfishes). If caged fish weighed less per unit length than free-roaming fish it would suggest that caging these species had reduced their food intake potentially biasing our results. To determine weight:length ratios for redband parrotfish and ocean surgeonfish, all fish were removed from the cages at the end of the experiment, their standard length was measured to the nearest 0.1 cm, and each fish was weighed to the nearest 1 g using a spring scale. Several fish were lost during the underwater transfer and weighing process. This decreased our sample size of caged fish. We also caught free-roaming redband parrotfish and ocean surgeonfish in the vicinity of our cages and measured their weight and length as described. We compared the weight:length relationships of caged to free-roaming fishes using t-tests.

Small fish (i.e., damselfish and juvenile parrotfish) could easily pass through our cages and could potentially graze preferentially within different treatments and alter community composition, potentially confounding our treatments. In order to quantify

small fish abundance inside our treatments, divers swam above a cage, picked one of the four 1 m^2 sections of the cage (as delineated by the cage frame when looking down on the cage from above), and identified the number and species of small fishes present within that section of cage. These counts were repeated 10 times for each cage to get an average small fish density for each replicate. Small fish abundances were log transformed and analyzed using one-way ANOVA followed by Tukey's multiple comparison test.

To determine bite rates within treatments, we monitored fish feeding by hovering in the water column 3-4 m above each cage and counting the bites the treatment fish took from the benthos within the cage and from the surface of the cage itself over 10 minutes. In uncaged controls, bites by all adult fishes were counted. Bites by juvenile fishes were excluded from the uncaged controls to facilitate direct comparison of grazing rates by adult fishes within treatments. Bite rates were also determined on a nearby shallow reef site to compare bite rates within our cages to feeding rates on a shallow reef as fish herbivory is often more intense on shallow reefs than on deeper reefs (Hay 1984, Morrison 1988) where our experiments were located. Bite rates were analyzed with one-way ANOVA followed by Tukey's multiple comparisons.

Results and Discussion

At the end of the experiment, cover of upright macroalgae was a significant 2.7-5.9X higher in the single species treatments than in the diversity treatment (Figure 3.1A). Parrotfish depressed the abundance of *Lobophora variegata*, articulated coralline algae, and *Halimeda tuna* relative to the surgeonfish-only treatment (Figures 3.1C – 3.1E). Parrotfish also depressed *Sargassum* spp. relative to the exclosure while surgeonfish did

not (Figure 1F). Surgeonfish depressed the abundance of *Haloplegma duperreyi* (Figure 3.1G) as compared to the parrotfish-only treatment and completely eliminated *Kallymenia westii* (Figure 3.1H). Our results underestimate the cover of upright macroalgae in the parrotfish-only and exclosure treatments because wave action from Hurricane Charley (early August 2004) removed most of the large, bladed, but poorly attached macroalgae such as *K. westii* which had reached up to ~15% cover in these treatments before the storm (data not shown). Thus, herbivore diversity directly depressed upright macroalgal abundance.

When we calculated the *D* statistic as a further measure of the effect of herbivore diversity, increasing herbivore diversity significantly affected the majority of common macroalgal types in our study (Figure 3.2). Herbivore diversity depressed upright macroalgae as a group as well as the common species *Lobophora variegata*, *Dictyota* spp., articulate coralline algae, *Halimeda tuna*, *Haloplegma duperreyi,* and *Sargassum* spp.; herbivore diversity facilitated crustose coralline algae and filamentous turf algae (Figure 3.2). Of particular interest are the results for upright macroalgae, crustose coralline algae, and turf algae. On coral reefs with healthy herbivore communities and intense grazing, the primary producer community is typically dominated by crustose coralline and turf algae, while upright macroalgae are rare (Steneck 1988, Hay 1997). Turf algae are preferred food for many reef herbivores and their high productivity fuels much of the herbivore production on coral reefs (Carpenter 1986). Crustose coralline algae are important to the health of coral reefs as many coral larvae recruit preferentially to crustose coralline algae (Heyward and Negri 1999). However, both turf algae and crustose coralline algae are poor competitors and are often replaced by upright

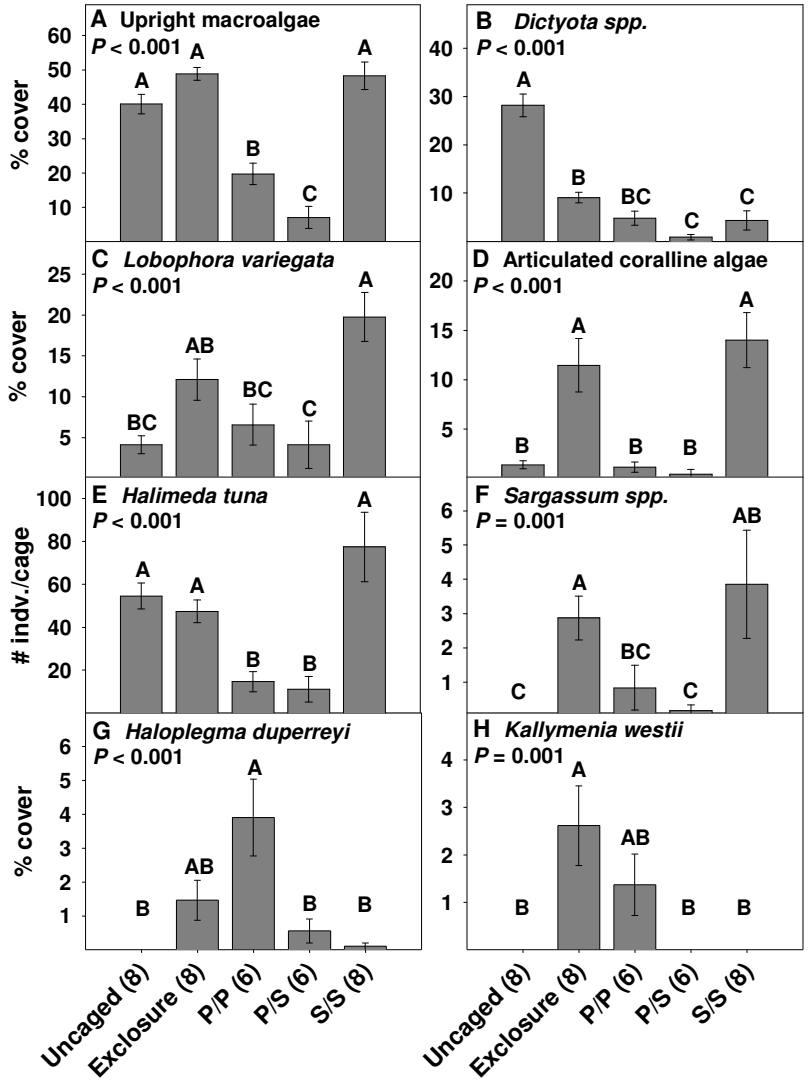


Figure 3.1. Percent cover or density (mean ± SE) of (A) total upright macroalgae and (B-H) macroalgal types. *P*-values are from one-way ANOVA. Letters above bars designate significant groupings according to Tukey's multiple comparison test. P = parrotfish, S = surgeonfish. *n* is designated in brackets next to each treatment's label on the X-axis. Note different scales for Y-axes.

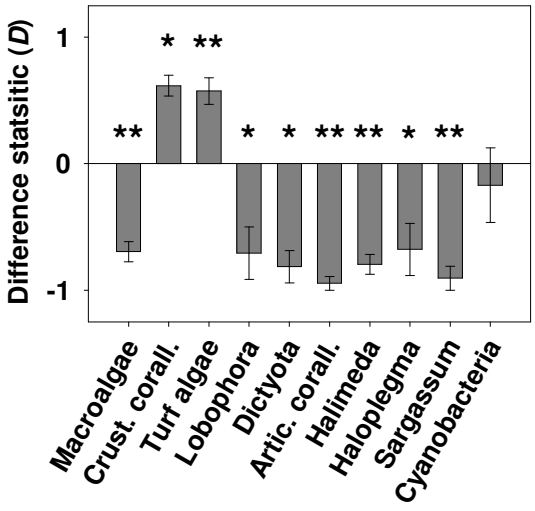


Figure 3.2. Difference statistic (D) (mean ± SE) for total macroalgae and different macroalgal types. D measures the difference between the diversity treatment and the average of the single species treatments. If $D < 0$ then abundance is lower in the diversity treatment than the average single species treatment; if $D > 0$ then the diversity treatment facilitates that macroalga. $^{*}P < 0.05$, $^{**}P < 0.01$. P-values are from t-tests. $n = 6$ for all comparisons.

macroalgae when rates of herbivory are low (Steneck 1988). Thus, herbivore diversity generates a macroalgal community that most resembles that found on a healthy coral reef.

The patterns of abundance for macroalgae in the diversity and single-species treatments can be explained by the complementary feeding preferences of redband parrotfish and ocean surgeonfish. When common macroalgae were fed directly to the fishes, parrotfish consumed *Dictyota menstrualis, Halimeda tuna*, *Lobophora variegata*, and *Sargassum filipendula* while surgeonfish ate *Dictyota menstrualis*, *Kallymenia westii* and *Haloplegma duperryei* (Figure 3.3). Thus, complementarity in diet breadth for these two herbivores led to near elimination of upright macroalgae and facilitation of crustose coralline and filamentous algae in the treatment with increased herbivore diversity.

Although herbivore diversity strongly suppressed macroalgae (Figures 3.1 & 3.2), it is critical to determine whether macroalgal suppression enhanced coral health. When we assessed coral cover and mortality using digital photographs from the beginning and end of the experiment, significant coral mortality occurred in the exclosure and in the single species treatments (Figure 3.4A), but no mortality occurred in the uncaged areas or in the diversity treatment. The exclosure and single-species treatments all experienced mean losses of coral cover (Figure 3.4B). In contrast, the diversity treatment experienced a net 20% increase in coral cover in only 10 months. This change was significantly greater than in either single-species treatment. This increase did not differ significantly from the change in the uncaged areas to which all herbivores had access, but the mean growth was 20% as opposed to 10% in uncaged areas, suggesting that reef management to enhance these two herbivorous fishes might enhance coral growth and recovery in

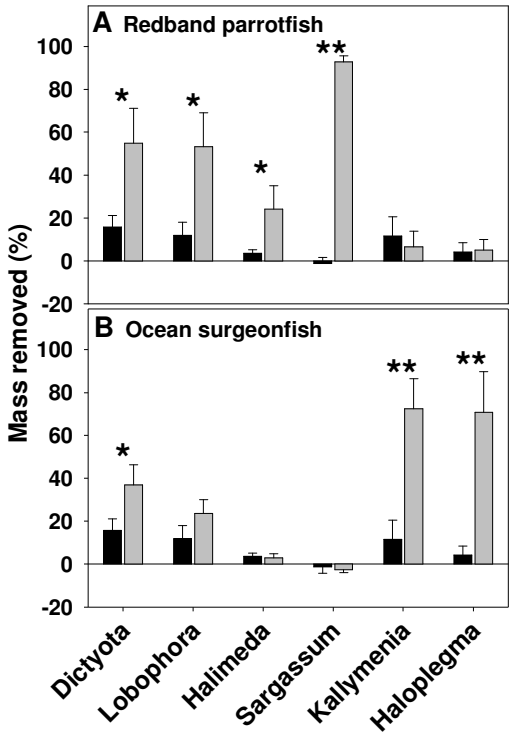


Figure 3.3. Percentage (mean ± SE) of the mass of macroalgae removed when placed into cages with (A) redband parrotfish and (B) ocean surgeonfish or into the exclosures in the field. $*P < 0.05$ and $**P < 0.01$ as determined using one-tailed, t-tests. A significant difference between treatment and control shows that more macroalgal mass was removed in the cages with herbivores (gray bars) as compared to the exclosure cages without large herbivores (black bars).

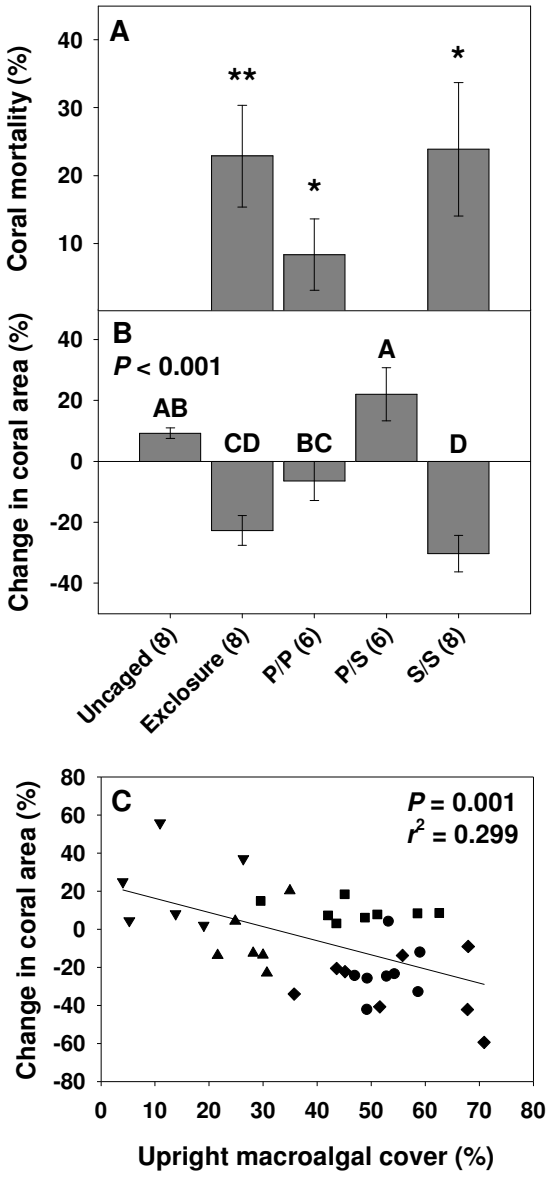


Figure 3.4. Results of experimental treatments on (A) coral mortality (mean ± SE), (B) coral growth (mean ± SE), and (C) the relationship between macroalgal cover and coral cover. Statistical analyses were via (A) *t*-tests testing for a difference from zero * $P < 0.05$, ** $P < 0.01$, (B) one-way ANOVA as in Fig. 1, and (C) linear least squares regression. For (C) symbols are ■ Uncaged, ● Exclosure, ▲P/P, ▼ P/S, and ♦ S/S.

areas dominated by upright macroalgae. Further, coral cover decreased as macroalgal cover increased when examined over all treatments ($P = 0.001$, $r^2 = 0.299$) (Figure 3.4C). Together, these data show that having a diverse herbivore assemblage not only depressed macroalgal abundance but also decreased coral mortality and increased coral cover.

Analyses of potential confounding factors show that these factors do not explain the experimental patterns that we show and that suppression of macroalgae and facilitation of crustose coralline algae and corals is driven by changing herbivore diversity and complementary feeding between fishes. The weight:length ratios of fishes within our treatments at the end of the experiment did not differ from those of free-roaming fishes (Figure 3.5), suggesting that the fishes in our cages grew as well as uncaged fishes that were free-roaming and thus free to graze from a wider variety of habitats, surfaces, or species. Small fishes in general and juvenile parrotfishes in particular were most abundant in uncaged controls but there were no differences in fish density among other treatments (Figures 3.6A & 3.6B, respectively). Furthermore, small fishes such as juvenile parrotfish that entered the cages typically fed on fouling organisms that were growing on the cages themselves as opposed to organisms growing on the benthos. There were also no differences among treatments in damselfish density (Figure 3.6C) which could have confounded our treatments as they are territorial herbivores that can have strong effects on macroalgal communities (Hixon and Brostoff 1996). These data suggest that differences in small or juvenile fish abundance were not driving the patterns of macroalgal abundance within our treatments. Finally our estimates of bite rates inside the cages show that the bite rate in the diversity treatment did not differ from the single species treatments (Figure 3.7). Although the bite rates in

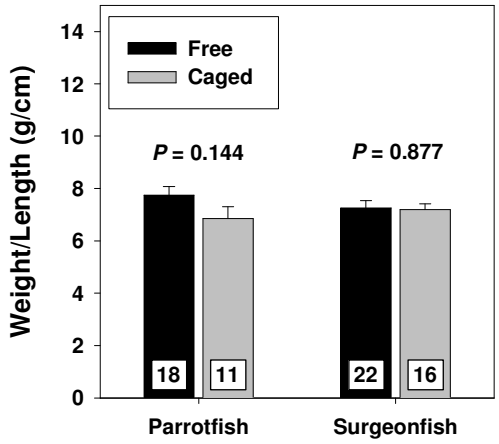


Figure 3.5. Weight:length ratios (mean + SE) for free-ranging and caged redband parrotfish and ocean surgeonfish at the end of the experiment. *P*-values are from t-tests. Inset boxes give sample sizes.

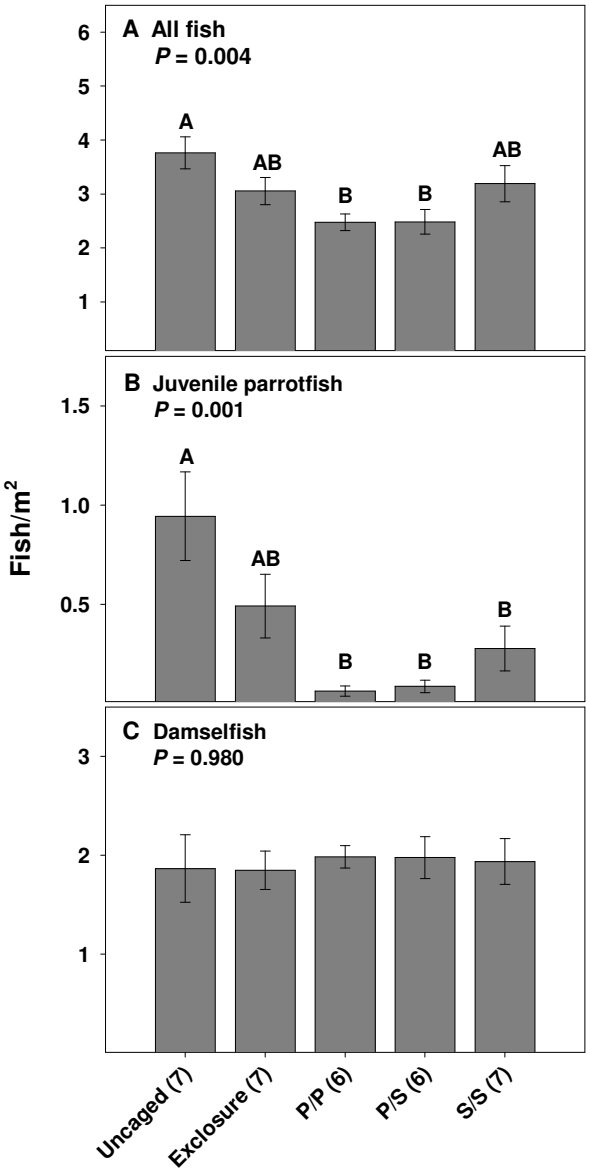


Figure 3.6. Abundance (mean ± SE) for (A) all small fish, (B) juvenile parrotfish, and (C) damselfish within each treatment. *P*-values are from one-way ANOVA. Letters above bars designate significant groupings according to Tukey's multiple comparison test. P = parrotfish, S = surgeonfish. *n* for each treatment is designated in brackets next to each treatment label on the X-axis. Note different scales for Y-axes.

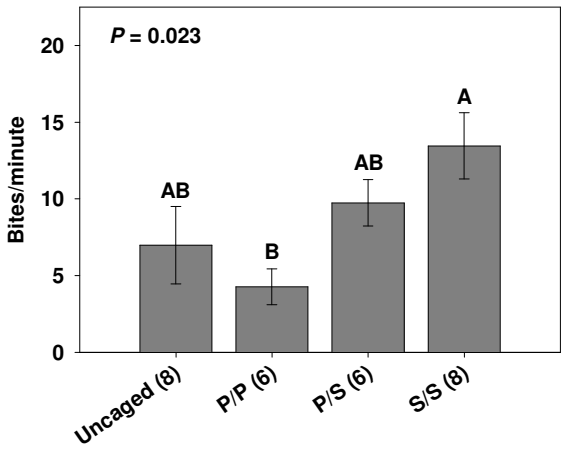


Figure 3.7. Bite rates for adult fishes (mean ± SE) inside treatments at Conch Reef and for uncaged areas nearby. *P*-value is from one-way ANOVA. Letters above bars designate significant groupings according to Tukey's multiple comparison test. X-axis as in Figure 3.6.

some of the treatments may be higher than those on our study reef (although we could not detect significant differences in post-hoc tests), the bite rate on a shallow reef (6-8 m) in the Upper Florida Keys was 1.6 - 5.1X greater than those inside any of our treatments on Conch Reef. These data suggest that the bite rates inside our treatments are well within the levels normally seen on shallow reefs in the Florida Keys. The fact that the surgeonfish-only treatments had grazing rates over 2X that of the parrotfish-only treatments (Figure 3.7) yet had over 2X as much upright macroalgae (Figure 3.1A) indicates that bite rates *per se* do not equal overall grazing, or impact, for these two species. Both visual observations of algal length removed per bite (ME Hay, *personal observation*) and the more robust mouthparts of redband parrotfish, indicate that they remove considerably more macroalgal biomass per bite than do ocean surgeonfish. Given this difference, the lower bite rates in the parrotfish-only treatments will not necessarily reflect lower rates of macroalgal consumption. In sum, we are confident that our results reflect the effects of herbivore diversity and not some other covariate.

Herbivores are critical drivers of ecosystem function on coral reefs because they keep reefs free of macroalgae and facilitate the recruitment, growth, and resilience of corals (Lewis 1986, Hughes 1994, Hay 1997, McCook et al. 2001, Bellwood et al. 2004), the foundation species that support the entire ecosystem. We experimentally show that herbivore diversity is crucial for ecosystem health because complementary feeding by herbivorous fishes suppresses upright macroalgae (Figures 3.1 & 3.2), facilitates crustose corallines and turfs (Figure 3.2), and promotes coral growth (Figure 3.4). Practical constraints of erecting large enclosures at depth constrained our test of herbivore diversity effects to only two species. However, our results should be conservative in that

the 3 species of surgeonfishes and 12 species of parrotfishes in the Caribbean should have even more complementarity in diet overlap thereby enhancing the effect of diversity on macroalgae. Yet, the redband parrotfish vs. ocean surgeonfish contrast may have focused on a contrast producing a striking diversity effect. If so, the contrast is nonetheless ecologically important because these two fishes are among the most common species of herbivorous fishes at many sites in the Caribbean (Lewis and Wainwright 1985, Lewis 1986, Mumby and Wabnitz 2002) and have been identified as important consumers of many macroalgae (Lewis 1985). Furthermore, the differential effects we documented were strong despite caging fishes in restricted areas, which could have forced them to eat some macroalgae that they might normally avoid. In addition, ongoing experiments comparing multiple species of parrotfish show similar, though less dramatic, effects of herbivore diversity on macroalgal communities (Burkepile and Hay, unpub. data).

As food webs become simplified via human-mediated extinction of strongly interacting consumers (Jackson et al. 2001, Duffy 2003), understanding the role of consumer diversity in driving ecosystem function will become increasingly imperative (Duffy 2002). This understanding is critical on coral reefs where widespread overfishing and removal of important trophic linkages has caused reef collapse in some areas (Hughes 1994, Jackson et al. 2001) and threatens the collapse of reefs world-wide (Bellwood et al. 2004). The dismal state of many Caribbean reefs may require proactive measures to facilitate coral reef recovery rather than simply creating marine preserves (Pandolfi et al. 2005). We suggest that maintaining or restoring herbivore diversity is a critical step in attaining healthy reefs as it promotes a coral-dominated rather than a macroalgal-dominated system. Thus, the establishment of marine reserves coupled with

proactive enhancement of particular herbivorous fish populations may be a more effective restoration technique than the attempt to conserve without proactive management focused on herbivore diversity. Further appreciation for the roles of consumers and consumer diversity in ecosystem function will not only allow us to better protect the important drivers of ecosystems but also to identify ways to proactively manage degraded ecosystems back to health via consumer-driven restoration (Soule et al. 2003).

CHAPTER 4

FUNCTIONAL DIVERSITY OF HERBIVOROUS FISHES ON A CARIBBEAN CORAL REEF

Abstract

Consumers commonly drive community patterns and ecosystem processes, yet we know far less about the role of consumer diversity as opposed to producer diversity in ecosystem function. This understanding is critical on coral reefs where consumers, particularly herbivores, are strong drivers of ecosystem function but are under imminent threat of overharvesting worldwide. In two experiments, over the course of two years, we enclosed equal densities of single-species and mixed-species groups of herbivorous fishes in large (4 m^2), replicate cages on a reef in the Florida Keys, USA to evaluate the effects of herbivore diversity on community composition. In Year 1, we used the redband parrotfish (*Sparisoma aurofrenatum*) and the ocean surgeonfish (*Acanthurus bahianus*) to generate the treatments while in Year 2 we used the redband parrotfish and the princess parrotfish (*Scarus taeniopterus*). We show strong effects of herbivore diversity on community structure due to feeding differences among herbivores both years of the experiment. In Year 1, ocean surgeonfish and redband parrotfish synergistically suppressed upright macroalgae by feeding on dissimilar species thereby decreasing facilitating crustose coralline algae and coral cover while decreasing coral mortality. In Year 2, redband parrotfish and princess parrotfish fed on different algal functional groups in that redband parrotfish fed mostly on upright macroalgae while princess parrotfish fed mostly on filamentous, turf algae. Consequently, turf algae dominated redband-only treatments while upright macroalgae dominated princess-only treatments. In both years,

increasing herbivore diversity facilitated crustose coralline algae, which is crucial for coral recruitment on reefs. Feeding assays with common macroalgae corroborated the community patterns in the cages showing that redband parrotfish and ocean surgeonfish had complementary feeding preferences for upright macroalgae while princess parrotfish fed on hardly any upright macroalgae. When all treatments were compared across both years of the experiment, despite being morphologically and taxonomically distinct, princess parrotfish and ocean surgeonfish had more similar effects on macroalgal community structure than did the two morphologically and taxonomically similar species of parrotfish. Our data suggest that these three fishes play functionally diverse roles in the herbivore guild and that their complementary effects of algal communities are important to the structure and function of coral reefs.

Introduction

Widespread overfishing and the alteration of important trophic linkages has caused severe degradation of coral reefs world-wide (Jackson et al. 2001, Pandolfi et al. 2003, Bellwood et al. 2004). Herbivores, in particular, are crucial to reef health because their intense grazing removes the majority of upright macroalgae that can directly overgrow and kill corals (Lewis 1986, Jompa and McCook 2002), prevent recruitment of juvenile corals (McCook et al. 2001), and facilitate coral disease (Nugues et al. 2004). Herbivores also provide ecosystem resilience in the face of disturbances such as hurricanes or outbreaks of coral disease by keeping disturbed areas free of macroalgae and allowing corals to reestablish (Aronson et al. 2005). Macroalgae become abundant and the health of coral reefs declines when herbivores are removed from the system via

caging (Carpenter 1986, Lewis 1986, Morrison 1988), disease (Carpenter 1988, Lessios 1988), or overfishing (Hughes 1994).

Because consumers drive community and ecosystem processes on coral reefs (Glynn 1990, Hay 1997, Bellwood et al. 2003, Burkepile and Hay in press), consumer diversity may play a large role in ecosystem function. Yet, the effects of consumer diversity *per se* have rarely been experimentally addressed for coral reefs, and, in general, we know far less about the effects of consumer diversity than of producer diversity on ecosystem function (Duffy 2002, Hooper et al. 2005). This disparity should be redressed given the critical role of consumers in community organization and ecosystem function (Naiman 1988, Paine 2000, Duffy and Hay 2001) and the disproportionate impact that humans have on upper trophic levels (Pauly et al. 1998, Jackson et al. 2001, Duffy 2003). Understanding the role of consumer diversity will not only allow a better plan to conserve ecosystems by protecting crucial biotic interactions (Soule et al. 2003) but will also allow scientists and conservation practitioners to identify particularly useful species or mixes of species that could be used to leverage degraded ecosystems to desired states of health or function. This research is critical for coral reefs, especially Caribbean reefs, where reef health continues to decline (Gardner et al. 2003, McWilliams et al. 2005) and food webs are degraded because strongly interacting consumers have been removed and are at continued high risk of exploitation (Bascompte et al. 2005).

Fishes and sea urchins are typically the dominant herbivores on coral reefs (Ogden and Lobel 1978). In the Caribbean, several studies have examined the differential effects of herbivory by fishes and the urchin *Diadema antillarum* (Hay 1984a, Carpenter 1986, Morrison 1988) and their potential competition for resources (Hay and

Taylor 1985, Carpenter 1988, 1990, Robertson 1991). However, herbivorous fishes became the single, dominant herbivore group on most reefs (Carpenter 1990) after the Caribbean-wide mass mortality of *D. antillarum* in the early 1980's (Lessios 1988). Yet, there has been little research on the differential effects of different species of large herbivorous fishes on reef community structure in the Caribbean. Observational studies have revealed differences in foraging patterns among different species of herbivorous fishes (Bruggemann et al. 1994, McAfee and Morgan 1996) and important impacts of particular species of herbivorous fish by comparing reefs with differential fishing pressure (Mumby et al. 2006). However, controlled experiments have not been employed to investigate the role of herbivore diversity in driving reef health or the species-specific effects of different herbivorous fishes on reef community structure. Herbivore diversity should benefit reefs because a more diverse herbivore assemblage should include herbivores with varied attack strategies, which in turn should increase the efficiency of macroalgal removal because particular macroalgae are unlikely to be well defended against all types of herbivores (Lubchenco and Gaines 1981, Hay 1984b, Schupp and Paul 1994).

Instead of focusing on the effects of herbivorous fishes as a group, we asked specific questions about how herbivore diversity, and particular common species of herbivores, impacts the structure and function of Caribbean coral reefs. In two experiments, over the course of two years, we enclosed equal densities of single-species and mixed-species groups of herbivorous fishes in large, replicate cages on a reef in the Florida Keys, USA. In Year 1, we used the redband parrotfish (*Sparisoma aurofrenatum*) and the ocean surgeonfish (*Acanthurus bahianus*) to generate experimental treatments

with equal densities but different diversity of herbivores (Burkepile et al. in review). In Year 2 we used the redband parrotfish and princess parrotfish (*Scarus taeniopterus*) to produce similar treatments. Over the 7-10 month duration of each experiment, we: (1) monitored changes to macroalgal abundance and species composition and coral health and cover in response to the treatments, (2) assessed feeding preferences of the herbivores for common macroalgae, and (3) documented differential resource use by free-ranging herbivorous fishes by removing the cages in Year 1 and allowing herbivorous fishes access to the macroalgal communities that had been generated by the experimental treatments. These experiments allowed us to address: (1) the effects of herbivore diversity on coral reef communities, (2) the differential effects of parrotfishes vs. surgeonfishes on community structure, and (3) the functional overlap of different herbivore species we investigated.

Materials and Methods

Experimental setup and maintenance

In November 2003, we used NOAA's Aquarius, a self-sufficient underwater research laboratory at a depth of 16m offshore of Key Largo, FL to set-up Year 1 of the experiment. The experiment was located on a spur and groove reef formation at depths of 16-18m on Conch Reef (24°57'N/80°27'W), approximately 5km off the coast of the upper Florida Keys. The reef is a spur and groove formation with the spurs rising 1-2 m from a sandy bottom. We constructed 32, 4 m^2 cages made of steel bar and plastic coated chicken wire to house the different fish treatments. In Year 1, we tested the effects of herbivore diversity on community structure using redband parrotfish (*Sparisoma*

aurofrenatum) and ocean surgeonfish (*Acanthurus bahianus*) to generate the treatments: (1) two redband parrotfish (R/R), (2) two ocean surgeonfish (S/S), (3) one redband parrotfish and one ocean surgeonfish (R/S), (4) no enclosed fish, and (5) an uncaged control. We monitored changes in macroalgal abundance and species composition as well as coral mortality and change in coral cover in response to the different treatments.

The Year 1 experiment with redband parrotfish and ocean surgeonfish showed dramatic effects of herbivore diversity on macroalgal abundance and coral health (Burkepile et al. in review). However, the redband parrotfish vs. ocean surgeonfish contrast may have focused on a contrast producing a striking diversity effect given that the two species differ considerably in their adaptations for herbivory (Horn 1989). In Year 2 of the study, we chose redband parrotfish and princess parrotfish (*Scarus taeniopterus*) for experimental manipulations because they have similar adaptations to herbivory (Horn 1989, Bellwood 1994), but preliminary data from videotaping consumption of macroalgae in the field suggested that princess parrotfish feed primarily on turf and crustose coralline algae while redband parrotfish feed primarily on upright macroalgae (D. Burkepile unpub. data).

In November 2004, we again used NOAA's Aquarius to set up Year 2 of the experiment at the same location on Conch Reef. We used the same experimental setup, cage construction, and cage locations as in Year 1 to enclose the different fish treatments. We constructed 32, 2 m X 2 m X 1m tall cages made of 0.6 cm steel bar and covered with PVC-coated galvanized chicken wire (2.5 cm mesh size). Chicken wire of this mesh size has been used in previous experiments near this site and imparts minimal caging artifacts (Miller et al. 1999). We attached the cages to the reef by wiring the frames to 30 cm

galvanized nails that had been hammered into the reef substrate. A 30 cm flange of chicken wire extended from the base of the cage and was conformed to the reef substrate and affixed using galvanized fencing nails. This barrier prevented larger fishes from escaping or entering the cage, but the mesh size allowed small fishes to enter and exit at will (i.e. juveniles of many species as well as adult wrasses and many damselfishes). Zinc anodes were attached to the chicken wire and the cage frame to prevent corrosion. The benthic community inside the cages consisted of the natural assemblage of macroalgae, corals, sponges, gorgonians, and other common reef invertebrates.

Treatments in Year 2 consisted of: (1) two princess parrotfish (P/P), (2) two redband parrotfish (R/R), (3) one princess parrotfish and one redband parrotfish (P/R), and (4) no enclosed fish. We also monitored uncaged areas of equal size (n = 8 for each treatment and uncaged areas). We did not use partially caged treatments to test for the effects of the cages themselves because partial cages often attract large predators (i.e. groupers) that alter the use of the partial cages by herbivorous fishes. Thus, using partial cages to test for cage artifacts may confound the effect of the cages with the effect of having large predators present. Four cages and an uncaged area were blocked as closely as the reef configuration allowed in one general area and treatments were allocated randomly among each of the four cages. Thus, we had eight blocks of the five experimental treatments. We caught fishes with hand nets and barrier nets and placed them inside the cages.

Princess parrotfish can attain larger size (35 cm total length) than redband parrotfish (28 cm total length) and adult princess parrotfish on Conch Reef appeared to be larger on average than adult redband parrotfish. For our treatments, we used fishes

approximately 15-22 cm (standard length). However, adult princess parrotfishes were less abundant than redband parrotfish at our field site, and at the beginning of the experiment (November 2004-February 2005) we used some princess parrotfish that were approximately 22-26 cm (these lengths are estimations as we did not measure each fish that was used in the treatments). Over the course of the experiment, these larger princess parrotfish were replaced with ones that fell within the 15-22 cm range. To determine if we were potentially confounding fish treatments with biomass of fish, we determined the weight:length ratios for free-ranging redband parrotfish and princess parrotfish in the size class that we were using in our cages. We caught free-ranging, adult redband parrotfish and princess parrotfish in the vicinity of our cages and measured their standard length to the nearest 0.1 cm and their weight to the nearest 1 g using a spring scale. We compared the weight:length relationships of redband and princess parrotfish using a t-test. We did not measure the weight:length ratio of the fishes inside our cages at the end of Year 2 of the experiment in order to compare them to free-ranging fishes because Hurricane Dennis destroyed the experiment before these data could be obtained.

The size range of fishes we used in the experiment included smaller terminal phase males for the redband parrotfish, but not for the princess parrotfish. We did use terminal phase male redband parrotfish in the experiment, but rarely noticed aggressive interactions between redband parrotfish in the same cage. We removed terminal phase males that became aggressive when placed inside the cages and replaced them with an intermediate phase fish. Aggressive interactions between princess parrotfish individuals or between princess parrotfish and redband parrotfish within the cages were rarely observed.

We surveyed fishes inside the cages every 4-6 weeks and replaced missing fishes to maintain treatments. Cages were scrubbed inside and out every 4-6 weeks to remove fouling organisms and prevent shading. Between scrubbings, grazing by reef fishes (especially surgeonfishes and juvenile parrotfishes feeding on filamentous algae) kept the cages relatively clean of fouling organisms.

We are confident that there were no lasting treatment effects from Year 1 that biased the community patterns at the beginning of Year 2. At the end of the Year 1 experiment (August 2004), we removed the mesh from each cage allowing access to all herbivorous fishes which rapidly fed upon the macroalgae within the previously caged areas. All experimental plots had open access to all grazing fishes for >10 weeks before setting up Year 2 of the study, and treatments for Year 2 were assigned at random to cages within each block of treatments. Analysis of variance (ANOVA) showed no differences in macroalgal abundance among the treatments at the inception of the experiment (Table 4.1).

Data collection and analysis

The experiment in Year 1 ran from November 2003 until August 2004 when we took final data points and removed the mesh from the cage frames. In Year 2, the experiment ran from November 2004 until July 2005 when wave surge from Hurricane Dennis destroyed the cages and ended the experiment. In both years, we used the same methods to monitor macroalgal cover and species composition on the benthos inside the cages and uncaged control. Every 6-10 weeks we used a 1.5 m X 0.75 m quadrat containing 50 stratified random points to sample two areas within each cage for a total of

Table 1. One-factor ANOVAs assessing among treatment differences in macroalgal cover at the beginning of Year 2 of the experiment.

Macroalgal type	***df***	***F***	***P***
Dictyota spp.	4, 35	0.63	0.642
Halimeda tuna	4, 35	1.50	0.223
Lobophora variegata	4, 35	1.91	0.131
Articulated corallines	4, 35	0.48	0.753
Turf algae	4, 35	2.21	0.088
Cyanobacteria	4, 35	0.96	0.444
Coralline algae	4, 35	0.07	0.990
Upright macroalgae	4, 35	0.35	0.842

100 points. We identified the organisms under each point to the lowest taxonomic level possible under field conditions. For some species that grew as easily identifiable, separate individuals (i.e. *Sargassum* spp.), we counted numbers of individuals within each cage as well as recording percent cover. We avoided taking data from the outer 10 cm border within each cage to minimize cage effects because the cage itself could have impeded fish from feeding in close proximity to the edges.

One-factor ANOVA followed by Tukey's multiple comparisons were used to determine differences in macroalgal abundance among treatments within an analysis. Moray eel predation on the treatment fish necessitated the removal of four cages from Year 2 of the experiment resulting in $n = 7$ for the princess/redband treatment and $n = 5$ for the redband-only treatment. Thus, we did not use a blocking factor in the ANOVA's. Data were transformed when necessary to meet the variance homogeneity assumptions of ANOVA as examined with Cochran's test (Underwood 1997).

We assessed fish bite rates within treatments vs. uncaged areas to see if fishes confined to cages were feeding differently than free-ranging fishes. We monitored fish feeding by hovering in the water column 3-4 m above each cage and counting the bites the treatment fish took from the benthos inside the cage and from the surface of the cage itself over 10 minutes. In uncaged areas, bites by all adult fishes were counted. Bites by juvenile fishes were excluded from the uncaged areas to facilitate direct comparison of grazing rates by adult fishes within treatments. Bite rates were also determined on a nearby shallow reef site to compare bite rates within our cages and in our uncaged treatment on this deeper reef to feeding rates on a shallow reef, as herbivory by fishes is often more intense on shallow than on deeper reefs (Hay 1984a) where our experiments were located. We also quantified bite rates for free-ranging fishes for redband parrotfish, princess parrotfish, and ocean surgeonfish on Conch Reef to determine natural feeding rates. A diver haphazardly selected an adult fish of one of the three species and followed that fish for five minutes counting the number of bites the fish took from the benthos. If fishes were lost while following them, the time at which the fish was lost was recorded and the bite rate was scaled to the amount of time that fish was followed. Bite rates for caged and free-ranging fishes were log transformed and analyzed with one-factor ANOVA followed by Tukey's multiple comparisons.

To further analyze the effects of herbivore diversity on the abundance of total upright macroalgae, as well as specific macroalgal species or groups, we calculated a difference metric (D) comparing the average of the single species treatments to the diversity treatment. To calculate D, we used the formula $D = (O_i - E)/E$ where E is the average of the two single species treatments combined (the expected value) and O_i is the

observed value for one of the replicates in the diversity treatment. D was calculated for each diversity treatment replicate. This metric is similar to D_{max} that is used to detect overyielding in studies of how plant diversity affects ecosystem function (Loreau 1998). If $D < 0$, then abundance of that macroalgal group is lower in the diversity treatment than the average single species treatment; if $D > 0$ then the diversity treatment facilitates that macroalgal group. We used one-sample *t*-tests to determine if D was significantly different from zero for each macroalgal group in both Year 1 and Year 2. In addition, we took an average value for D for each macroalgal group across both years of the experiment. We also compared richness of macroalgal genera in each treatment for Year 1, Year 2, and for the uncaged, exclosure, single-species, and diversity treatments as averaged across both years of the study using one-factor ANOVA.

We also assessed the effects of herbivore treatments on the health and growth of corals. In Year 1, we monitored the condition and growth of corals within the treatments using digital photography (Burkepile et al. in review). At the beginning (November 2003) and end (August 2004) of the experiment, we took *in situ* digital photographs of each coral colony within each replicate of all treatments and analyzed the area of each coral at the beginning and end of the experiment using the computer imaging program Image J. We assessed coral mortality, change in coral cover, and the relationship between total macroalgal abundance and change in coral cover for all treatments. For Year 2, comparisons of the effects of fish treatments on coral survivorship and growth were planned, but Hurricane Dennis removed the markers used to identify corals for photographic documentation thus eliminating the possibility of evaluating effects of the treatments on coral growth as had been done in Year 1.

Fish feeding preferences for common macroalgae

In both years of the experiment we determined feeding preferences of the treatment fishes by offering macroalgae to the parrotfish and surgeonfish housed in the single species treatments. To redband parrotfish and ocean surgeonfish in Year 1, we offered *Dictyota menstrualis*, *Halimeda tuna*, *Sargassum fillipendula*, *Lobophora variegata*, *Codium taylori, Kallymenia westii*, and *Haloplegma duperryi* because these species were common in some of the treatments. In Year 2, for redband parrotfish and princess parrotfish, we used *D. menstrualis*, *H. tuna*, *S. fillipendula*, *L. variegata*, and *C. taylori*. *K. westii* and *H. duperryi* were not used in Year 2 because they were rare in all treatments. In the lab, pieces of macroalgae (3.0 ± 0.3 g pieces for *H. tuna* and 2.0 ± 0.2 g pieces for other macroalgae) were blotted dry with a paper towel, weighed to the nearest 1mg, and then entwined into a three-stranded polypropylene rope (one species per rope). Ropes of each macroalgal species were placed in the single-species and exclosure cages. Fish were allowed to feed on the macroalgae for 24-30 h before the ropes were collected. The beginning and final weights were used to calculate the percent of the macroalgae removed. To determine if the fishes consumed significant quantities of these macroalgae, change in mass of the macroalgae in the fish treatments were compared individually to changes in mass in the exclosures using one-tailed *t*-tests because we were predicting that more biomass would be removed in cages enclosing large herbivores than cages excluding large herbivores. For Year 2, we directly compared feeding by redband parrotfish and princess parrotfish on each macroalgal species using a two-tailed t-test.

Comparisons between Year 1 and Year 2

To compare the effects of the fish treatments across both years of the experiment, we combined data from the both Year 1 and 2 for analyses. Comparing treatment effects during Year 1 with those from Year 2 potentially confounds treatment effects with temporal effects (i.e. differences between years due to differences in macroalgal recruitment, physical conditions, or other parameters). We tested for effects of year for the exclosure, uncaged, and redband-only treatments using MANOVA since these treatments were present in both years of the study. If MANOVA detected significant differences between years, we used t-tests to test for differences between years for each macroalgal group within each fish treatment. For these post-hoc t-tests, we used the Dunn-Sidak method (Sokal and Rohlf 1995) to control for the experimentwise error rate which yielded a significance level of $\alpha = 0.005$ for each between-year macroalgal comparison.

Although MANOVA did detect significant differences between years of the experiment, we felt that the value of comparing the effects of fish treatments across years offset some of the potential difficulties, such as confounding temporal differences with treatment effects, especially due to the labor-intensive nature of conducting these studies. We used cluster analysis to quantify similarities between treatments to compare macroalgal community structure in response to the experimental treatments across both years of the study. We used the average linkage unweighted pair-group method using arithmetic means (UPGMA) that is one of the most common methods for cluster analysis (McGarigal et al. 2000) and has been used to assess similarities of the effects of different predators on prey communities (Kurzava and Morin 1998). For the cluster analysis, we

used the mean percent cover for each macroalgal species or group (i.e. crustose coralline algae) as the variables used to describe similarity of the macroalgal community. For treatments that were present in both years of the experiment, data were averaged across both years. Given the significant differences between years of the study, the results from the cluster analysis should be interpreted with caution.

Responses of herbivorous fishes to experimental macroalgal communities

To compare differences in resource use among different species of free-ranging fishes, we removed the mesh from the cages at the termination of Year 1 of the experiment (August 2004) and videotaped the free-ranging fishes feeding on the macroalgae inside the cages. This analysis could not be done for Year 2 as Hurricane Dennis destroyed the cages before these data could be gathered. We videotaped fish feeding after mesh removal for only the five blocks of cages that had all four fish treatments intact [(1) two redband parrotfish (R/R), (2) two ocean surgeonfish (S/S), (3) one redband parrotfish and one ocean surgeonfish (R/S), (4) no enclosed fish] in an attempt to control for spatial differences in fish abundance and feeding intensity. We did not include data from the uncaged areas as fish rarely fed in these plots when the previously caged areas were available. After we removed the mesh from each cage, we placed a 1 m X 1 m quadrat on the benthos inside the cage frame and focused a super hi-8 video camera, mounted on a tripod on the quadrat. We then started the camera and removed the quadrat from the area being filmed. The video cameras ran for 1.25-2 h to record feeding behavior of herbivorous fishes in response to the macroalgal communities that had previously been enclosed inside the cages.

To quantify fish feeding, we played the videos on a television monitor. We used a dry erase marker to trace the outline of the quadrat on the monitor screen. When an herbivorous fish took bites from the benthos within the area delineated by the quadrat, we recorded the species of fish and number of bites taken by that fish. We counted only bites by adult fishes as juvenile fishes were often obscured by corals and sponges which made their behavior and bite rates difficult to quantify. We did not quantify the number of visits by herbivorous fishes to the cage because there were often 10-20 fishes in the frame at the same time for the cage removal videos making it difficult to identify individual fishes and determine when they left and entered the frame. Data on bite rates were transformed when necessary to meet assumptions of ANOVA and analyzed using a blocked, one-factor ANOVA followed by Tukey's multiple comparisons to determine differences among treatments within an analysis. We also performed cluster analysis to quantify similarities in herbivorous fish feeding among the experimental fish treatments. The analysis was run using the mean values of bites per hour by common herbivorous fish species after removal of the cage mesh.

Results

At the end of Year 2 of the experiment, cover of upright macroalgae was 66% greater in the fish exclosures than in uncaged areas (Figure 4.1A). Upright macroalgae in both the redband-only and diversity treatments was significantly lower than in the princess-only treatment which did not differ significantly from either the exclosure or the uncaged treatments (Figure 4.1A). Relative to the exclosure, redband parrotfish depressed articulated coralline algae (Figure 4.1D), *Lobophora variagata* (Figure 4.1E),

Halimeda tuna (Figure 4.1F), and *Sargassum* spp. (Figure 4.1H), but facilitated turf algae (Figure 4.1C). Princess parrotfish tended to depress turf algae significantly relative to the uncaged areas but not relative to the exclosure (Figure 4.1C); they also tended to increase crustose coralline algae significantly relative to the exclosure but not to the uncaged areas (Figure 4.1B). *L. variegata*, *Sargassum* spp. and *Codium* spp. were abundant in the princess-only treatment, with princess parrotfish facilitating *Codium* spp. when compared to the exclosure (Figure 4.1G). The diversity treatment facilitated the abundance of crustose coralline algae when compared to any of the other treatments (Figure 4.1B).

Analyses of fish bite rates showed no differences among the treatments (Figure 4.2A), but this was probably a result of low statistical power as the bite rates in the princess-only treatment had a mean that was >2.3X higher than either the redband-only treatment or the diversity treatment. Further, when we compared the bite rates of free-ranging fishes, princess parrotfish bit the bottom 2.9X more often per minute than redband parrotfish and in similar frequency to ocean surgeonfish (Figure 4.2B) suggesting that the higher feeding rates of princess parrotfishes in the cages reflect their natural feeding behavior and is not an artifact of being caged. Bite rates for ocean surgeonfish were also greater than those for redband parrotfish. The bite rates of fishes inside the cages were slower than those of free-ranging fishes because the caged fishes also fed on algae that grew on the cages so they bit the benthos less frequently than did free-ranging fishes. Although the bite rates in some of the treatments may be higher than those on our study reef (although we could not detect significant differences in post-hoc tests), the bite rate on a shallow reef (6-8 m) in the Upper Florida Keys (21.9 bites/min in 4 m^2) was 1.9 – 4.6X greater than those inside any of our treatments on Conch Reef.

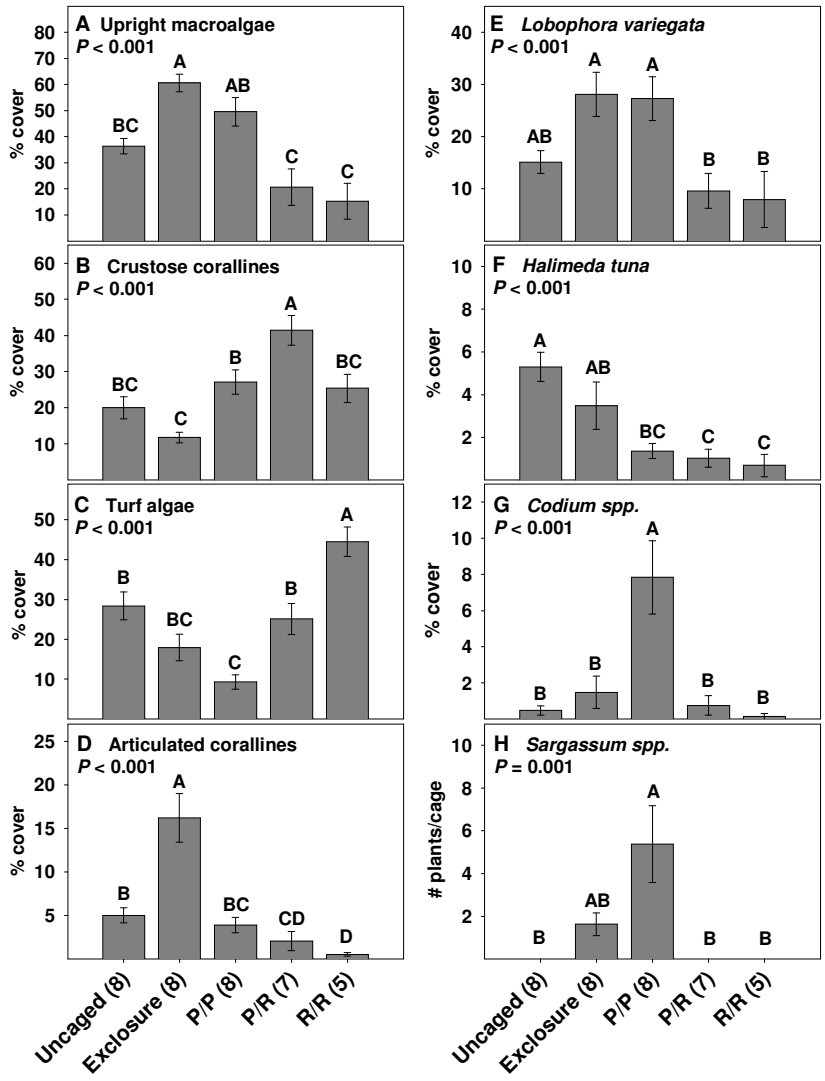


Figure 4.1. Percent cover or density (mean ± SE) at the end of Year 2 of the experiment for (A) total upright macroalgae and (B-H) macroalgal species or groups. *P*-values are from one-factor ANOVA. Letters above bars designate significant groupings according to Tukey's multiple comparison test. P = princess parrotfish, R = redband parrotfish. *n* for each treatment is designated in brackets next to each treatment label on the X-axis. Note different scales for Y-axes.

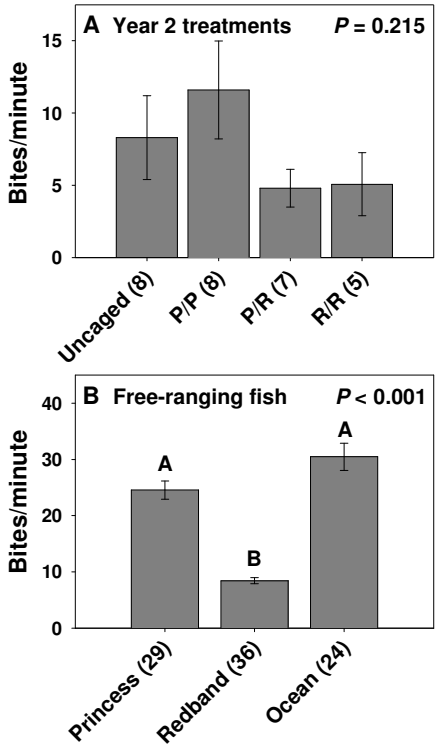


Figure 4.2. Bite rates (mean ± SE) for (A) adult fishes inside treatments and in the uncaged area at Conch Reef and (B) free-ranging princess parrotfish, redband parrotfish, and ocean surgeonfish on Conch Reef. *P*-values are from one-factor ANOVA. Letters above bars designate significant groupings according to Tukey's multiple comparison test. P = princess parrotfish, R = redband parrotfish. *n* for each treatment is designated in brackets next to each treatment label on the X-axis.

These data suggest that the bite rates inside our treatments are well within the levels normally seen on shallow reefs in the Florida Keys.

When we calculated the weight:length ratios for princess parrotfish and redband parrotfish, we found no difference between the two fishes (9.34 ± 0.76 vs. 8.66 ± 0.43 g/cm for princess and redband parrotfish respectively; $P = 0.450$, $df = 14$; t-test). Therefore, it is unlikely that we systematically biased our results by using fish of differing size in the treatments. Additionally, had there been an undetected bias, it would most likely be due to greater biomass in the princess-only vs. redband-only treatments, but the redband-only treatment tended to decrease algae to a greater extent (Figure 4.1). Thus, the differences between fish treatments should be due to the effects of feeding by the different fishes and not to differences in intensity as a result of having larger fishes in a subset of the treatments.

Herbivore diversity significantly affected the majority of common macroalgal types as assessed with the *D* statistic. In year 1, herbivore diversity depressed upright macroalgae as a group as well as the common species *Lobophora variegata*, *Dictyota* spp., articulate coralline algae, *Halimeda tuna*, *Haloplegma duperreyi,* and *Sargassum* spp.; herbivore diversity facilitated crustose coralline algae and filamentous turf algae (Figure 4.3A). In Year 2, the effect of diversity was significant only for crustose coralline algae, *L. variegata*, and *Sargassum* spp. (Figure 4.3B). Overall macroalgal cover, *Dictyota* spp., *H. tuna*, articulated coralline algae, or turf algae were not significantly affected by herbivore diversity. However, the trends for Year 2 were the same as Year 1, and the effect for overall macroalgal cover was marginally non-significant at $P = 0.067$. The overall pattern represented by pooling the *D* statistic across

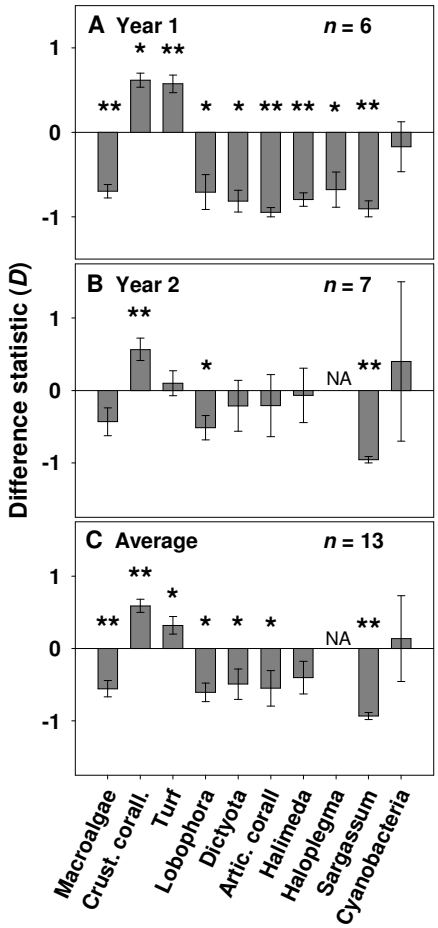


Figure 4.3. Difference statistic (D) (mean ± SE) for all upright macroalgae and different macroalgal species or groups for (A) Year 1, (B) Year 2, or (C) average of Year 1 and Year 2. D measures the difference between the diversity treatment and the average of the single species treatments. If $D < 0$ then abundance of that macroalga is lower in the diversity treatment than the average single species treatment; if $D > 0$ then the diversity treatment facilitates that macroalga. *$P < 0.05$, **$P < 0.01$. P-values are from t-tests. NA designates that this macroalga was not abundant enough to calculate the statistic.

both years of the study, resembled the pattern for Year 1; upright macroalgae as a group and all common species except *H. tuna* and cyanobacteria were significantly affected by herbivore diversity (Figure 4.3C).

Analyses of the richness of macroalgal genera showed that there were fewer genera present when large herbivorous fishes were present than in their absence (Figure 4.4). In Year 1, both single-species treatments had higher richness than the diversity treatment, but the redband-only and surgeonfish-only treatments did not differ from each other (Figure 4.4A). This same pattern was not evident for the diversity treatment in Year 2 of the study as there were no significant differences between the single-species and diversity treatments (Figure 4.4B). But, when the single-species and diversity treatments were averaged across both years of the study, the diversity treatment had lower generic richness of macroalgae than the single-species treatments (Figure 4.4C).

When offered common macroalgae inside the cages, redband parrotfish consumed *Dictyota menstrualis*, *Halimeda tuna*, *Sargassum fillipendula*, *Lobophora variegata*, and *Codium taylori* (Figure 4.5A). Princess parrotfish could be demonstrated to feed only on *H. tuna* (Figure 4.5B). Further, redband parrotfish ate significantly more of each macroalgal species than did princess parrotfish, including *H. tuna* which was the only macroalgal species that princess parrotfish significantly consumed (data not shown). When approximately the same suite of macroalgae was offered to ocean surgeonfish during Year 1 of the experiment, they consumed *D. menstrualis, C. taylori, Kallymenia westii, and Haloplegma duperryi* but not *H. tuna*, *S. fillipendula*, or *L. variegata* (Figure 4.5C). Redband parrotfish did not consume *K. westii* or *H. duperryi* when offered during

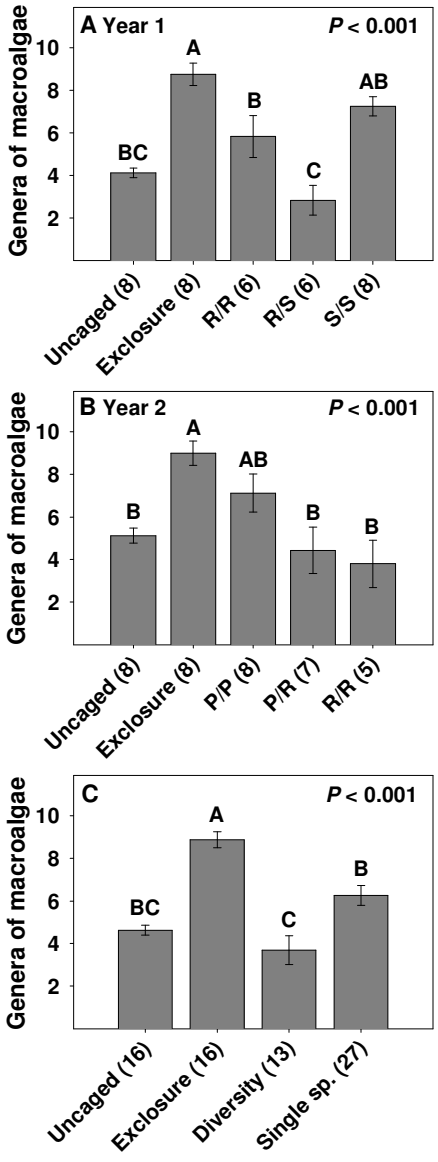


Figure 4.4. Genera of upright macroalgae (mean ± SE) for (A) Year 1, (B) Year 2, and (C) the uncaged, exclosure, single-species, and diversity treatments averaged across both years of the study. *P*-values are from one-factor ANOVA. Letters above bars designate significant groupings according to Tukey's multiple comparison test. P = princess parrotfish, R = redband parrotfish, S = ocean surgeonfish. *n* for each treatment is designated in brackets next to each treatment label on the X-axis.

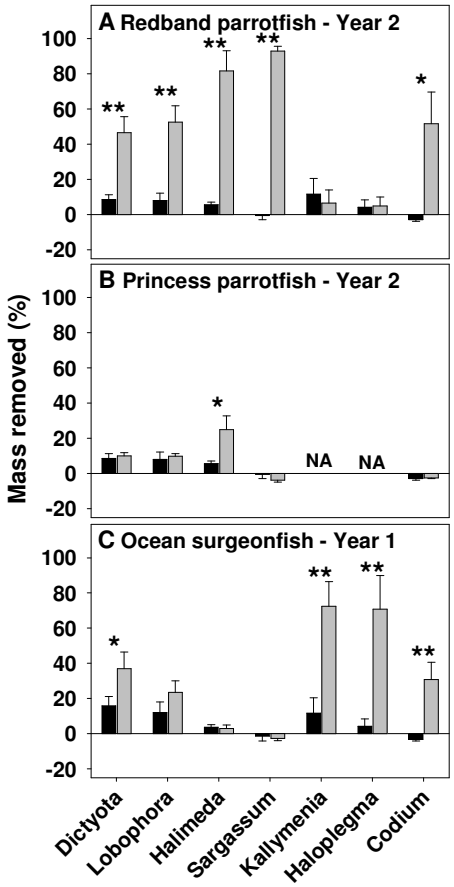


Figure 4.5. Mass (mean ± SE) of macroalgae removed by (A) redband parrotfish, (B) princess parrotfish, or (C) ocean surgeonfish. *$P < 0.05$ and **$P < 0.01$ as determined t-test. A significant difference between treatment and control shows that more macroalgal mass was removed in the cages with herbivores (gray bars) as compared to the control cages without large herbivores (black bars). n = 5-8 for each comparison. NA designates that this macroalga was not offered to this fish species. *Kallymenia westii* and *Haloplegma duperyii* were offered to redband parrotfish in Year 1 not Year 2 but are included here to facilitate comparisons with ocean surgeonfish.

Year 1 (Figure 4.5A). We did not offer *K. westii* or *H. duperryi* directly to princess parrotfish inside the cages since neither alga was common during Year 2.

MANOVA showed that there were significant effects of year on experimental treatments for both the exclosure and uncaged treatments but not for the redband-only treatment (Figure 4.6). For the exclosure, post-hoc t-tests showed that crustose coralline algae and cyanobacteria were more abundant in Year 1 while *Lobophora variegata* was more abundant in Year 2 (Figure 4.6A). For the uncaged treatment, *Dictyota* spp. and cyanobacteria were more abundant in Year 1 while *L. variegata* and articulated corallines were more abundant in Year 2 (Figure 4.6B).

When we combined data from both years (Figure 4.7) and used cluster linkage analysis to compare the similarities in macroalgal community structure among treatments, the analysis showed that the three fish species created different macroalgal communities (Figure 4.8). The princess parrotfish treatment was more similar to the ocean surgeonfish treatment than to the redband parrotfish treatment. The ocean surgeonfish treatment most closely resembled the exclosure. The three treatments that included redband parrotfish (redband/ocean surgeonfish, redband/princess parrotfish, and redband/redband) clustered more closely to each other than to any of the other treatments. The uncaged treatment clustered most closely to the princess parrotfish treatment, but similarity was very low indicating that none of our 1-2 species experimental treatments resulted in macroalgal communities that closely resembled the natural community, which is impacted by many more herbivore species.

When we analyzed data on fish feeding following cage removal in Year 1 in order to assess differences in resource use among species, herbivorous fishes took 1.8-2.6X

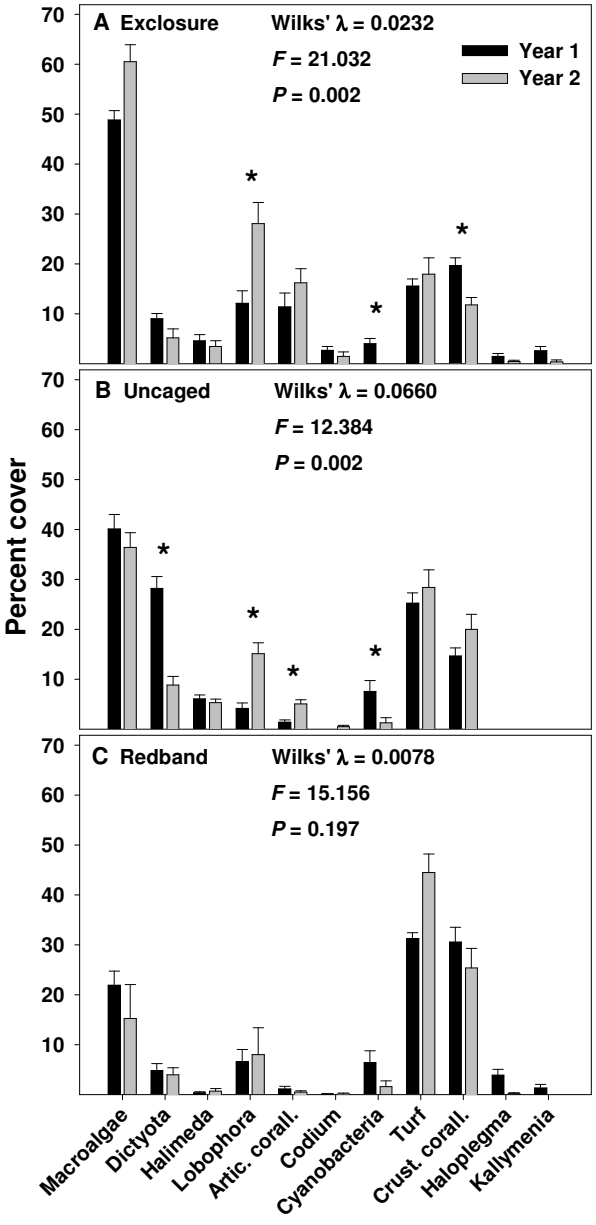


Figure 4.6. Percent cover (mean ± SE) of upright macroalgae and macroalgal types for (A) exclosure, (B) uncaged, and (C) redband parrotfish only treatments across both years of the experiment. Results of MANOVA for each treatment type comparing effects for Year 1 and Year 2 are inset for each treatment. Significant *P*-values show that the macroalgal communities were different between years for that treatment. The upright macroalgal category was not used in the MANOVA as it encompasses the majority of the algal species but is provided in the graph only as reference. For MANVOA's that showed significant between year effects, we performed post-hoc ANOVA's testing for between year differences for each macroalgal category within a fish treatment. * denotes a significant difference between years for a specific macroalgal group test that was significant (at $P = 0.005$ as determined using the Dunn-Sidak method for controlling experimentwise error rate).

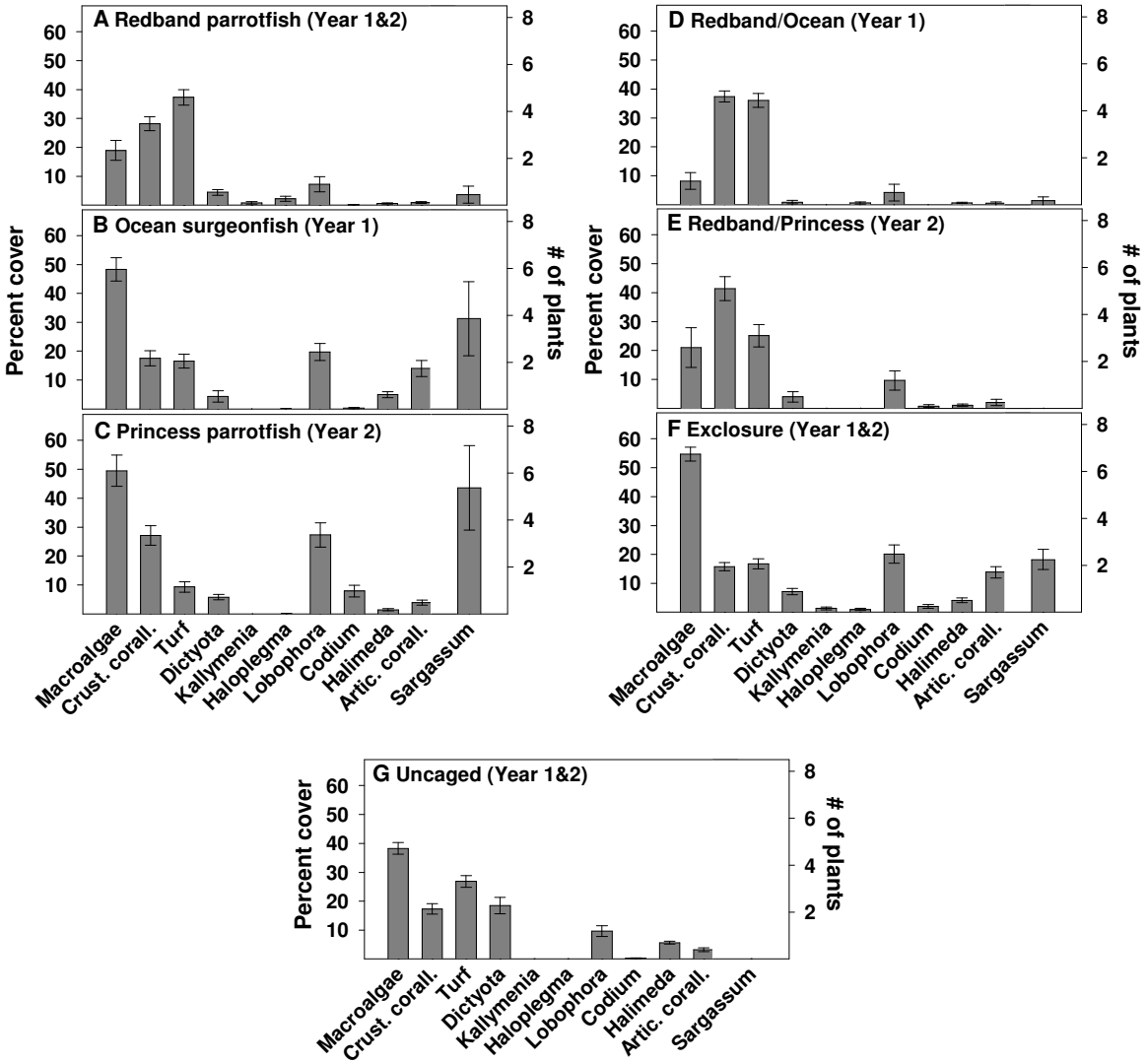


Figure 4.7. Percent cover, or number of plants for *Sargassum* spp. (mean ± SE) of all macroalgal groups for (A) redband parrotfish, (B) ocean surgeonfish (C) princess parrotfish, (D) redband parrotfish/ocean surgeonfish, (E) redband parrotfish/princess parrotfish, (F) fish exclosure, or (G) uncaged treatments. For treatments that were in both years of the experiment (i.e. redband-only, fish exclosure, and uncaged treatments), means represent data averaged across both years. Means for each macroalgal species or group from these graphs were used for the cluster linkage analysis in Figure 8 except for the macroalgae category which encompasses the majority of the upright macroalgal species and is provided in the graph only as reference.

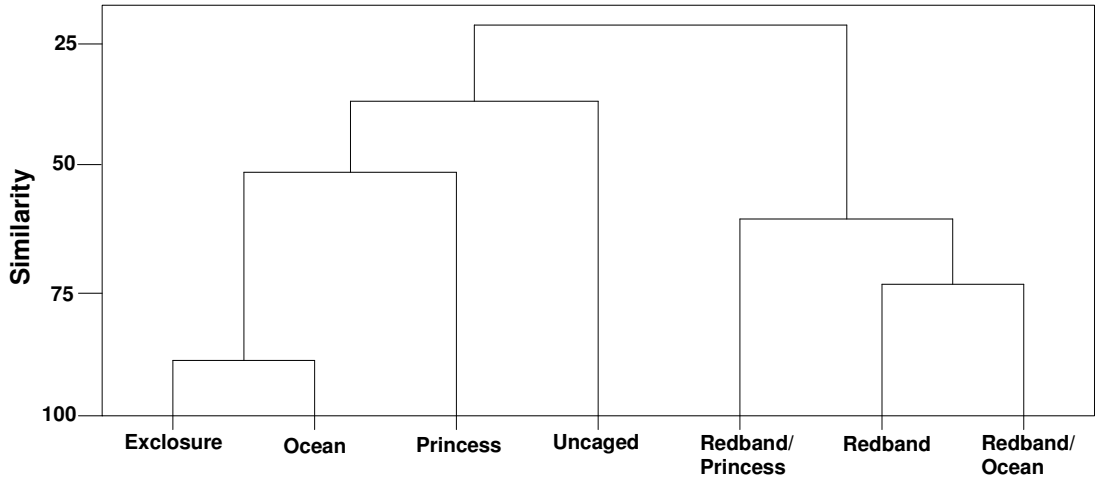


Figure 4.8. An average linkage cluster analysis using the mean values of abundance for macroalgal species or groups in the different herbivore treatments to describe the similarity of effects of herbivores on macroalgal community structure. Abundance data for the Exclosure, Uncaged, and Redband treatments were averaged across both years of the experiment. See Figure 7 for data used in this analysis.

more bites per hour in the exclosures than in the other fish treatments (Figure 4.9A). When averaged across all species, parrotfish fed more in the exclosure than in either of the treatments holding redband parrotfish while the exclosure and the surgeonfish-only treatment did not differ (Figure 4.9B). Parrotfish in the genus *Sparisoma* fed 4.8-6.1X faster in the exclosures and surgeonfish-only treatments than in either treatment including redband parrotfish (Figure 4.9C). Similar patterns were evident for the three common species in the genus *Sparisoma*: (1) redband parrotfish (*Sp. aurofrenatum*), (2) redtail parrotfish (*Sp. chrysopterum*), and (3) stoplight parrotfish (*Sp. viride*) (Figures 4.9D-F). Parrotfish in the genus *Scarus* fed up to 2.8X faster in the exclosures and in the parrotfish-only treatments as compared to the surgeonfish-only treatment, but neither differed from the diversity treatment (Figure 4.9G). Feeding by princess parrotfish (*Sc. taeniopterus*) drove this pattern, as this species comprised ~80% of all bites by *Scarus* spp. (Figure 4.9H). No pattern was evident for striped parrotfish (*Sc. croisensus*) (Figure 4.9I). When averaged across all species, surgeonfishes (*Acanthurus* spp.) fed 2.2-5.3X more rapidly on the exclosures than on either treatment that included an ocean surgeonfish (Figure 4.9J). Feeding by *Acanthurus* spp. was also lower in the surgeonfish-only treatment than in the parrotfish-only treatment but not the diversity treatment. These patterns were driven by feeding patterns of ocean surgeonfish (*A. bahianus*) (Figure 4.9K) as there were no differences in feeding by the blue tang (*Acanthurus coerelus*) (Figure 4.9L), the other abundant acanthurid at our field site.

Cluster analysis testing for similarities in fish feeding among treatments following cage removal after Year 1 showed significant separation among the treatments (Figure 4.10). The redband-only and the diversity treatments clustered most closely, showing the

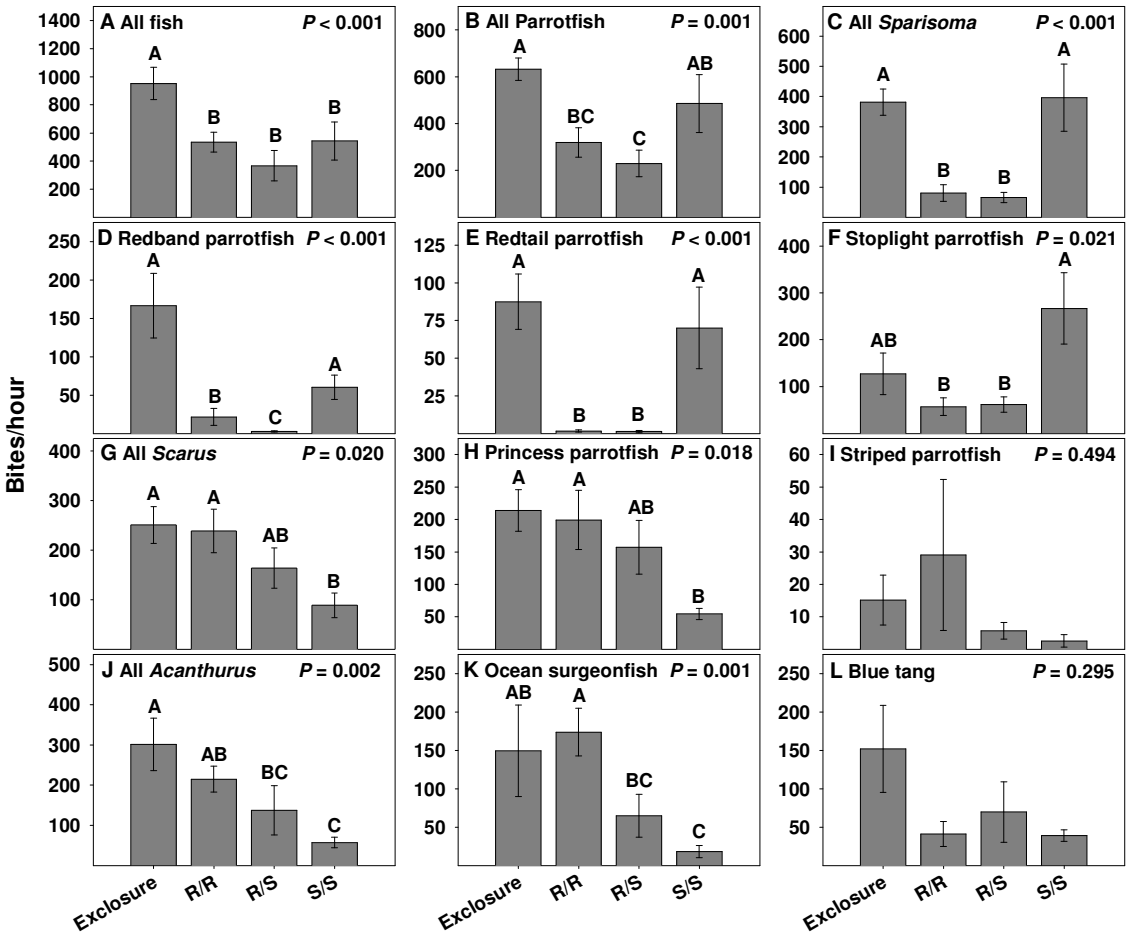


Figure 4.9. Bites per hour (mean ± SE) by common herbivorous fishes after removal of the cage mesh at the end of Year 1. *P*-values are from blocked, one-factor ANOVA. Letters above bars designate significant groupings according to Tukey's multiple comparison test. R = redband parrotfish, S = ocean surgeonfish. *n = 5* for each graph. Note different scales for Y-axes.

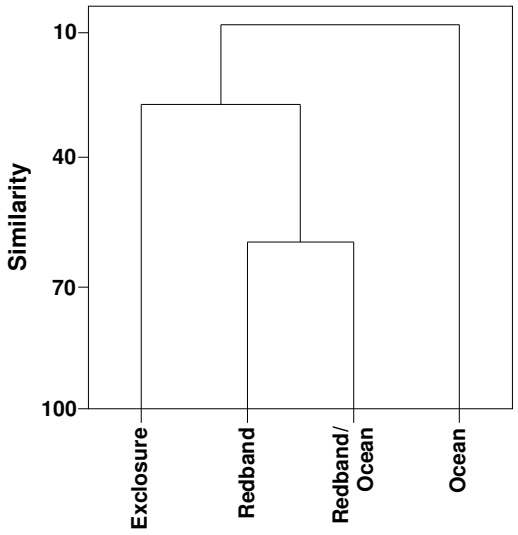


Figure 4.10. An average linkage cluster analysis to describe the similarity of herbivorous fish feeding on the macroalgal communities inside the experimental fish treatments at the end of Year 1. The analysis was run using the mean values of bites per hour by common herbivorous fish species after removal of the cage mesh.

most similarity in fish feeding. The fish exclosure clustered next showing low similarity to the redband-only and the diversity treatments. The ocean surgeonfish treatment clustered last showing little similarity to any of the other treatments.

Discussion

Herbivory is critical to coral reef health as it keeps reefs free of most upright macroalgae (Steneck 1988, Hay 1997), facilitates corals (McCook et al. 2001, Jompa and McCook 2002) and provides ecosystem resilience in the face of disturbance (Nystrom and Folke 2001, Hughes et al. 2003, Aronson et al. 2005). Using manipulative field experiments, we show that diversity of herbivores is important for this ecosystem process because increasing herbivore diversity depresses upright macroalgae (Figures 4.3 & 4.4) and facilitates both crustose coralline algae (Figures 4.1B & 4.3) and coral cover (Burkepile et al. in review) as compared to low diversity treatments. The effects of diversity were strong across both years of the study despite caging fishes in restricted areas, which could have forced them to eat some macroalgae that they might normally avoid. In fact, the diversity treatments in both years generated macroalgal communities that closely resembled those of Caribbean reefs with abundant herbivorous fishes in that they were dominated by crustose coralline algae and algal turfs with low cover of upright macroalgae (Lewis and Wainwright 1985, Lewis 1986, Williams and Polunin 2001, Mumby et al. 2006).

Consumer diversity can have significant effects on communities by changing the abundance and species composition of primary producers (Sommer et al. 2004), facilitating primary and secondary production (Naeem et al. 2000, Duffy et al. 2003), and

altering the strength of trophic cascades (Finke and Denno 2004, Bruno and O'Connor 2005). These effects of diversity often stem from complementary resource use by consumers (Naeem et al. 2000, Duffy et al. 2003, Sommer et al. 2004) or differential susceptibility to predation (Duffy et al. 2005). Both years of the experiment showed effects of herbivore diversity due to differential feeding between the major herbivores. When we used the difference statistic (*D*) to quantify the effect of herbivore diversity on different macroalgal groups, the abundance of upright macroalgae and most macroalgae species or groups were significantly affected by increasing herbivore diversity in Year 1 (Figure 4.3A; Burkepile et al. in review). However in Year 2, the effect of herbivore diversity was less striking as *D* showed significant effects for only facilitation of crustose coralline algae and suppression of *Lobophora variegata* and *Sargassum* spp. (Figure 4.3B). *D* was negative and marginally non-significant (P =0.067) for upright macroalgae in Year 2. When *D* was pooled across both years, the effect of herbivore diversity was evident for upright macroalgae and for most macroalgal species or groups (Figure 4.3C). Analyses of generic richness of macroalgae across both years of the experiment showed similar patterns to those for the *D* statistic (Figure 4.4). The stronger effect of herbivore diversity on upright macroalgal abundance and generic richness in Year 1 probably stems from the strong diet complementarity of redband parrotfish and ocean surgeonfish (Figure 4.5). However, redband parrotfish feed primarily on upright macroalgae (Figure 4.5A) while princess parrotfish feed primarily on filamentous turf algae (Figure 4.1C & 4.5B), and we saw no overall effect of diversity in reducing the richness of macroalgae for the Year 2 contrast (Figure 4.4B). Thus, the redband parrotfish and ocean surgeonfish showed complementary feeding on different species of upright macroalgae while redband

parrotfish and princess parrotfish showed complementary feeding on different functional groups of algae (i.e. upright macroalgae vs. turf algae).

Differences in feeding preferences between fishes showed the potential for strong indirect effects on the reef community. In both years, increasing herbivore diversity facilitated crustose coralline algae (Figure 4.1B & 4.3). Since the larvae of many corals preferentially recruit to crustose coralline algae (Heyward and Negri 1999), its facilitation could have positive impacts on the rates of coral recruitment and survival. Further, in Year 1, herbivore diversity prevented coral mortality and facilitated a net 20% increase in coral cover as compared to the single-species treatments which had significant coral morality and net decreases in coral cover (Burkepile et al. in review). Although Hurricane Dennis prevented us from quantifying the effects of the different fish treatments on corals during Year 2, we suggest that the same pattern for the single-species vs. diversity treatments may have existed had the experiment run its course. The princess-only treatment was dominated by upright macroalgae such as *Lobophora variegata*, *Sargassum* spp., and *Codium* spp. (Figure 4.1) which commonly overgrow and harm corals (Lewis 1986, Tanner 1995, Lirman 2001, Jompa and McCook 2002). The redband-only treatment was dominated by filamentous turf algae (Figure 4.1C) which can also directly overgrow corals as well as trap sediment next to coral tissue exacerbating the effect of overgrowth (Nugues and Roberts 2003). In contrast, the diversity treatment was dominated by crustose coralline algae (Figure 4.1B) and had low levels of both upright macroalgae (Figure 4.1A) and filamentous turf algae (Figure 4.1C); high cover of crustose corallines and small filamentous algae are associated with healthy reefs supporting active coral growth (Steneck 1988). Thus, corals in the diversity treatment

would have been relatively free from competing upright macroalgae and filamentous algae which should have increased their growth rates and reduced colony mortality. The strong direct and indirect effects of increasing herbivore diversity in both years of the experiment suggests that this is a robust pattern. The positive effects of feeding complementarity that we show suggests that further research is needed on these groups of Caribbean herbivores to determine how much functional diversity or redundancy exists within the genera *Sparisoma*, *Scarus*, and *Acanthurus* not only for use of resources but also for life history traits that influence response diversity in the face of disturbances such as overfishing or habitat destruction (Folke et al. 2004).

Most studies of how herbivores affect Caribbean reefs have focused on the role of herbivores as a group or on comparing herbivory by fishes and urchins (Hay 1984a, Hay and Taylor 1985, Carpenter 1986, Foster 1987, Morrison 1988) rather than the differential role of different species or functional groups of herbivores (Bellwood et al. 2004). Our study is unique in that it uses experimental manipulations of fishes to address the effects of different herbivore species on reef communities as opposed to previous mensurative studies of herbivore feeding behavior (Bellwood and Choat 1990, Bruggemann et al. 1994) or comparisons of reefs with and without different herbivore species (Bellwood et al. 2003, Mumby et al. 2006). Although mensurative and comparative studies provide insight on the community-wide effects of large-scale processes such as overfishing that are hard to manipulate experimentally, manipulative studies allow clearer assessment of the effects of different species (and diversity of species) and allow more rigorous assessment of the ecological mechanisms affecting the structure and function of communities.

Large herbivorous fishes on Caribbean reefs are generally limited to parrotfishes and surgeonfishes which are often considered as functionally different groups. Parrotfishes have robust mouthparts and scrape the benthos whereas surgeonfish have weaker mouthparts and crop algae but do not scrape the benthos (Steneck 1988). However, the parrotfishes can be further divided into excavators, scrapers, and browsers based on jaw morphology and feeding habits (Bellwood and Choat 1990, Bellwood 1994, Streelman et al. 2002). Excavators typically have robust jaws with heavy musculature, feed on epilithic algal turfs, and scar the substrate as they remove (excavate) portions of the reef matrix with each bite. Scrapers have less robust jaws and more gracile musculature than do excavators, but they also feed on algal turfs removing little inorganic reef matrix during feeding. Browsers exhibit jaws that have more well defined teeth than either browsers or scrapers and typically feed on turf algae, upright macroalgae and seagrasses without scarring or scraping the substrate. However, these groups are somewhat plastic as species can exhibit traits of multiple groups as do some species in the genus *Sparisoma* that browse upright macroalgae and seagrasses but also excavate live coral (Bernardi et al. 2000).

The two parrotfishes used in this study, the redband parrotfish and princess parrotfish, would be considered a browser and a scraper, respectively. Although they have similar feeding morphologies (i.e. both have robust jaws and a pharyngeal mill), there are interesting differences in jaw structure. In princess parrotfish (and *Scarus* spp. in general), the upper jaw closes over the lower jaw while in redband parrotfish (and *Sparisoma* spp. in general) the lower jaw closes over the upper jaw (Bellwood 1994). For princess parrotfish, the upper and lower jaws have teeth coalesced into uniform

cutting edges while redband parrotfish have obvious individual teeth on both upper and lower jaws. The two species also have different foraging behaviors. Princess parrotfish take small, quick bites in rapid succession from the benthos while redband parrotfish take fewer bites in a given time period resulting in princess parrotfish having a bite rate that is 2.9X higher than redband parrotfish (Figure 4.2B). Princess parrotfish also take more bites per feeding foray while redband parrotfish often take only one or two bites per foray before moving to a different patch (D. Burkepile pers. obs.).

Although princess and redband parrotfish have somewhat different jaw morphologies and feeding behaviors, both species can, and will feed, on tough, calcified macroalgae such as *Halimeda tuna* (Figures 4.5A & B), and both species depressed articulated coralline algae and *H. tuna* to similarly low levels but with redband parrotfish suppressing articulated corallines significantly more than princess parrotfish (Figures 4.1D & F). Yet, overall, princess parrotfish and redband parrotfish had significantly different diet preferences (Figure 4.5) and different effects on macroalgal communities (Figures 4.1 & 4.8). When offered macroalgae directly, princess parrotfish consumed the tough calcified macroalgae, but would not eat softer macroalgae that redband parrotfish would normally consume such as *Dictyota menstrualis*, *Lobophora variegata*, *Sargassum fillipendula*, and *Codium taylorii* (Figure 4.5B). The patterns from the macroalgal communities also differed significantly with the redband-only treatment suppressing upright macroalgae and facilitating filamentous, turf algae while the princess-only treatment suppressed turf algae but had an abundance of upright macroalgae, specifically *L. variegata*, *Codium* spp. and *Sargassum* spp. (Figure 4.1). Thus, redband parrotfish and

princess parrotfish have different effects on the macroalgal community despite their obvious morphological similarities.

In contrast to redband parrotfish, ocean surgeonfish have different feeding morphologies but similar feeding behavior to princess parrotfish. Ocean surgeonfish lack the robust jaws of parrotfishes and generally avoid calcified and tough macroalgae (Figure 4.5C). However, free-ranging individuals of princess parrotfish and ocean surgeonfish showed similar feeding behavior in that they both took small, successive bites in rapidity from the benthos (Figure 4.2B). Despite their contrasting morphology, these two fishes generated similar macroalgal communities in the single-species treatments (Figure 4.8). Princess parrotfish and ocean surgeonfish had similar overall levels of upright macroalgae (49.5 ± 5.4% vs. 48.3 ± 4.0% respectively), *Lobophora variegata* (27.3 ± 4.2% vs. 19.7 ± 3.0% respectively), and *Sargassum* spp. (5.4 ± 1.8 vs. 3.9 ± 1.6 plants/cage respectively) (Figures 4.7B & C). Thus, these taxonomically and morphologically distinct fishes generated macroalgal communities that were more similar to one another than were those generated by two taxonomically and morphologically similar species, the redband parrotfish and princess parrotfish. These patterns suggest that consumers with similar traits or taxonomic relationships can have more dissimilar effects on prey communities than do consumers with limited functional or taxonomic relatedness (Purcell and Bellwood 1993, Chalcraft and Resetarits 2003, this study).

The MANOVA of effects between years showed significant differences for the exclosure and uncaged treatments but not for the redband-only treatment. The between-year difference for crustose coralline algae in the exclosure (Figure 4.6A) may reflect an artifact of Hurricane Charley (early August 2004) which passed within 150 miles of the

field site before final data were collected for Year 1. Wave action from the hurricane removed some of the large, but poorly attached macroalgae, such as *Kallymenia westii*, *Dictyota menstrualis*, and some *L. variegata*, from the exclosure treatment exposing crustose coralline algae that had been overgrown by these upright macroalgae. This hurricane effect also resulted in an underestimate of the effect of removing large herbivorous fishes on upright macroalgae in Year 1 (i.e. compare the upright macroalgal data for the exclosure vs. uncaged treatments in both years; Figures 4.6A & B). The lack of a between-year difference in *Dictyota* spp. and the greater abundance of *L. variegata* in Year 2 for the exclosure may also partially reflect artifacts of Hurricane Charley. However, *L. variegata* was the most abundant upright macroalga in the uncaged treatment in Year 2 suggesting that *L. variegata* was more abundant overall in Year 2 vs. Year 1. Further, dominance by *L. variegata* in Year 2 represented a shift in the dominant macroalga as *Dictyota* spp. was the most common upright macroalgae in Year 1 (Figure 4.6B). However, the between-year differences in the dominant species did not appear to change the overall abundance of the major macroalgal groups (i.e. upright macroalgae, turf algae, and crustose coralline algae) which were similar across years in the uncaged areas (Figure 4.6B). Despite the between-year differences in species composition for the exclosure and uncaged areas, there were no detectable differences in community structure for the redband-only treatment suggesting that the effects of redband parrotfish were similar in both years despite differences in the dynamics of the macroalgal community at the site itself. Thus, the differences seen among fish treatments (i.e. redband parrotfish vs. princess parrotfish vs. ocean surgeonfish) in the cluster analysis may be less

influenced by inherent differences in the macroalgal community between years than are differences seen for the exclosure or uncaged treatments.

Videotaping of fishes feeding on the macroalgal communities generated by the Year 1 treatments showed significant separation in resource use among parrotfishes and surgeonfishes. On average, parrotfishes in the genus *Sparisoma* fed more slowly in cages that had previously held redband parrotfish as opposed to those that did not (Figure 4.9C). This pattern held for the three common *Sparisoma* spp. at our field site (Figures 4.9D-F). As redband parrotfish appear to have the broadest diets of species in the genus *Sparisoma* (McAfee and Morgan 1996), they probably exhausted most of the macroalgae that would have been attractive to other *Sparisoma* spp. If other *Sparisoma* species with different feeding modes would have been used in the treatments instead of redband parrotfish [e.g. *Sparisoma viride* is an excavator which includes more live coral and turf algae in its diet (Bruggemann et al. 1994)], this pattern may not have been as striking because different *Sparisoma* sp. may have generated a different macroalgal community. Use of macroalgal resources following cage removal in Year 1 suggests that princess parrotfish and ocean surgeonfish may have significant dietary overlap because: (1) both species fed rapidly in the redband-only treatment (Figures 4.9H & K), (2) princess parrotfish fed more slowly in the surgeonfish-only treatments than in other treatments (Figures 4.9H), and (3) princess parrotfish and ocean surgeonfish generated similar macroalgal communities inside the cages (Figures 4.7B, 4.7C, 4.8). Further, macroalgal composition in the exclosure and the surgeonfish-only treatments were very similar (Figures 4.7B, 4.7F, 4.8), but princess parrotfish fed more rapidly in the exclosures than in the surgeonfish-only treatments (Figure 4.9H) suggesting that surgeonfish lower the

abundance of algae that are attractive to princess parrotfish. Feeding assays show, however, that ocean surgeonfish feed on upright macroalgae that princess parrotfish avoid (Figures 4.5B & C) which may moderate competition between these two herbivores. Blue tangs (*Acanthurus coereleus*), the other common acanthurid at our field site, showed no distinct patterns of preferred grazing after cage removal (Figure 4.9L) possibly due to low numbers of blue tangs feeding in the experiment and the resulting low power to rigorously document preference patterns. But, the higher mean in the exclosure suggests that this species focused on treatments that had not previously held fishes and that both redband parrotfish and ocean surgeonfish may remove algae that blue tangs prefer.

When we analyzed the similarity of fish feeding in the different experimental treatments following cage removal in Year 1, cluster analysis showed that the redband-only and diversity treatment were the most similar among the treatments (Figure 4.10). The exclosure clustered next with the redband-only and diversity group while the ocean surgeonfish treatment showed little similarity to the other treatments. This result is somewhat surprising given that the exclosure and surgeonfish-only treatments showed high similarity in terms of macroalgal community structure (Figures 4.7B, 4.7F, 4.8). However, the feeding rate by all fishes was 75% higher in the exclosure than in the surgeonfish-only treatment. In addition, two of the herbivores that exhibited the highest feeding rates, the princess parrotfish and the ocean surgeonfish, fed more in the exclosure than the surgeonfish only treatment (Figures 4.9H & K). The redband parrotfish showed the same pattern but the two treatments were not different statistically (Figure 4.9D). The *Sparisoma* species that fed most intensely after cage removal, the stoplight parrotfish,

showed the opposite pattern by feeding more in the surgeonfish-only treatment than in the exclosure, although there was no statistical difference (Figure 4.9F).

The differences in feeding preferences and effects on community structure seen among these three herbivores may be especially useful for managing fish populations as a method for reviving Caribbean reefs. For reefs that are heavily overgrown with macroalgae, *Sparisoma* spp. seem important for denuding stands of macroalgae and thus opening substrate for crustose coralline algae and coral recruitment; clearly, adding princess parrotfish to a reef overgrown by macroalgae will have little positive effect relative to adding redband parrotfish. In both years of this study, when redband parrotfish were present in the treatments they appeared to control macroalgal community composition relative to the other fishes present (Figures 4.7 & 4.8). Thus, they may be particularly influential herbivores for reefs with an abundance of macroalgae. For reefs that are dominated by filamentous turf algae such as reefs with high sedimentation, *Scarus* spp. such as princess parrotfish will be important to graze down thick turfs to prevent them from hindering coral recruitment and survival. The complementary feeding of redband parrotfish and ocean surgeonfish suggests that surgeonfishes will be important for decreasing overall upright macroalgal cover as they remove species that may be avoided by other herbivores (Figure 4.5C). However, parrotfishes may have stronger overall effects on macroalgal abundance than do surgeonfishes (Ogden and Lobel 1978, Steneck 1988). Williams and Polunin (2001) showed that for nineteen areas throughout the Caribbean biomass of both parrotfishes and surgeonfishes was negatively correlated with macroalgal abundance (i.e. as grazer biomass increases macroalgae decrease) but that the correlation for parrotfishes appeared stronger. Further, Mumby et at. (2006)

showed that recovery of large parrotfish (*Scarus* spp.) in protected areas of the Bahamas dramatically reduced macroalgal abundance. Thus, efforts to facilitate parrotfish may have strong impacts on macroalgal abundance but promoting herbivore diversity should benefit overall macroalgal removal.

Given that biotic interactions strongly influence the structure and dynamics of ecosystems (Naiman 1988, Chapin et al. 1997), the conservation of strongly interacting species may be critical to preserving natural areas (Soule et al. 2003). Because fishes are numerous, have high metabolic rates, can rapidly move to areas with increased algal production, and are the most abundant herbivores in many areas of the Caribbean (but see Carpenter and Edmunds (2006) for a description of *Diadema antillarum* recovery in the Caribbean), developing conservation strategies that directly involve the enhancement of critical species of herbivorous fishes with an emphasis on promoting herbivore diversity should facilitate the management and restoration of reef health. Although the establishment of marine protected areas has resulted in an increase in large predatory fishes and herbivorous fishes and a reversal of coral reef decline in some areas (Mumby et al. 2006), many reefs may be so impacted that the mere establishment of protected areas may not be sufficient to reverse the downward spiral of reefs (Pandolfi et al. 2005). Thus, the combination of protected areas and active management of herbivorous fish stocks may be a step in the right direction of reestablishing the herbivores and herbivore diversity that is a critical part of the resiliency of coral reef ecosystems.

REFERENCES

Adams, D. C., J. Gurevitch, and M. S. Rosenberg. 1997. Resampling tests for meta-analysis of ecological data. Ecology **78**:1277-1283.

Armitage, A. R., and P. Fong. 2004. Upward cascading effects of nutrients: shifts in a benthic microalgal community and a negative herbivore response. Oecologia **139**:560-567.

Armitage, A. R., and J. W. Fourqurean. In press. The short-term influence of herbivory near patch reefs varies between seagrass species. Journal of Experimental Marine Biology and Ecology.

Aronson, R. B., J. F. Bruno, W. F. Precht, P. W. Glynn, C. D. Harvell, L. Kaufman, C. S. Rogers, E. A. Shinn, and J. F. Valentine. 2003. Causes of coral reef degradation. Science **302**:1502-1502.

Aronson, R. B., I. G. Macintyre, S. A. Lewis, and N. L. Hilbun. 2005. Emergent zonation and geographic convergence of coral reefs. Ecology **86**:2586-2600.

Bascompte, J., C. J. Melian, and E. Sala. 2005. Interaction strength combinations and the overfishing of a marine food web. Proceedings of the National Academy of Sciences of the United States of America **102**:5443-5447.

Belliveau, S. A., and V. J. Paul. 2002. Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. Marine Ecology-Progress Series **232**:105-114.

Bellwood, D. R. 1994. A phylogenetic study of the parrotfishes family Scaridae (Pisces: Labroidei), with a revision of genera. Records of the Australian Museum **20**:1-84.

Bellwood, D. R., and J. H. Choat. 1990. A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. Environmental Biology of Fishes **28**:189-214.

Bellwood, D. R., A. S. Hoey, and J. H. Choat. 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecology Letters **6**:281-285.

Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nystrom. 2004. Confronting the coral reef crisis. Nature **429**:827-833.

Bernardi, G., D. R. Robertson, K. E. Clifton, and E. Azzurro. 2000. Molecular systematics, zoogeography, and evolutionary ecology of the Atlantic parrotfish genus *Sparisoma*. Molecular Phylogenetics and Evolution **15**:292-300.

Bertness, M. D., S. D. Gaines, and M. E. Hay, editors. 2001. Marine Community Ecology. Sinauer, Sunderland, MA.

Birkeland, C., and B. Gregory. 1975. Foraging behavior and rates of feeding of the gatropod, *Cyphoma gibbosum* (Linnaeus). Bulletin of the Natural History Museum of Los Angeles County **20**:57-67.

Boyer, K. E., P. Fong, A. R. Armitage, and R. A. Cohen. 2004. Elevated nutrient content of tropical macroalgae increases rates of herbivory in coral, seagrass, and mangrove habitats. Coral Reefs **23**:530-538.

Bracken, M. E. S., and K. J. Nielsen. 2004. Diversity of intertidal macroalgae increases with nitrogen loading by invertebrates. Ecology **85**:2828-2836.

Bruggemann, J. H., M. W. M. Kuyper, and A. M. Breeman. 1994. Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). Marine Ecology-Progress Series **112**:51-66.

Bruno, J. F., and M. I. O'Connor. 2005. Cascading effects of predator diversity and omnivory in a marine food web. Ecology Letters **8**:1048-1056.

Bruno, J. F., L. E. Petes, C. D. Harvell, and A. Hettinger. 2003. Nutrient enrichment can increase the severity of coral diseases. Ecology Letters **6**:1056-1061.

Burkepile, D. E., A. D. Chequer, and M. E. Hay. in review. Reviving Caribbean reefs: the critical role of herbivore diversity. Science.

Burkepile, D. E., and M. E. Hay. in press. Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology.

Carpenter, R. C. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecological Monographs **56**:345-363.

Carpenter, R. C. 1988. Mass mortality of a Caribbean sea urchin - immediate effects on community metabolism and other herbivores. Proceedings of the National Academy of Sciences of the United States of America **85**:511-514.

Carpenter, R. C. 1990. Mass mortality of *Diadema antillarum* II: effects on population densities and grazing intensity of parrotfishes and surgeonfishes. Marine Biology **104**:79-86.

Carpenter, R. C., and P. J. Edmunds. 2006. Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals. Ecology Letters **9**:271-280.

Carreiro-Silva, M., T. R. McClanahan, and W. E. Kiene. 2005. The role of inorganic nutrients and herbivory in controlling microbioerosion of carbonate substratum. Coral Reefs **24**:214-221.

Chalcraft, D. R., and W. J. Resetarits. 2003. Mapping functional similarity of predators on the basis of trait similarities. American Naturalist **162**:390-402.

Chapin, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science **277**:500-504.

Chiappone, M., H. Dienes, D. W. Swanson, and S. L. Miller. 2003. Density and gorgonian host-occupation patterns by flamingo tongue snails (*Cyphoma gibbosum*) in the Florida Keys. Caribbean Journal of Science **39**:116-127.

Cox, C., J. H. Hunt, W. G. Lyons, and G. E. Davis. 1997. Nocturnal foraging of the Caribbean spiny lobster (*Panulirus argus*) on offshore reefs of Florida, USA. Marine and Freshwater Research **48**:671-679.

Crooks, K. R., and M. E. Soule. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature **400**:563-566.

Dayton, P. K., M. J. Tegner, P. E. Parnell, and P. B. Edwards. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecological Monographs **62**:421-445.

Dean, T. A., and F. R. Jacobsen. 1986. Nutrient-limited growth of juvenile kelp, *Macrocystis pyrifera*, during the 1982-1984 El-Nino in Southern California. Marine Biology **90**:597-601.

Diaz-Pulido, G., and L. J. McCook. 2003. Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. Ecology **84**:2026-2033.

Duffy, J. E. 2002. Biodiversity and ecosystem function: the consumer connection. Oikos **99**:201-219.

Duffy, J. E. 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecology Letters **6**:680-687.

Duffy, J. E., and M. E. Hay. 2000. Strong impacts of grazing amphipods on the organization of a benthic community. Ecological Monographs **70**:237-263.

Duffy, J. E., and M. E. Hay. 2001. The ecology and evolution of marine consumer-prey interactions. Pages 131-157 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine Community Ecology. Sinauer, Sunderland, MA.

Duffy, J. E., J. P. Richardson, and E. A. Canuel. 2003. Grazer diversity effects on ecosystem functioning in seagrass beds. Ecology Letters **6**:637-645.

Duffy, J. E., J. P. Richardson, and K. E. France. 2005. Ecosystem consequences of diveristy depend on food chain length in estuarine vegetation. Ecology Letters **8**:301-309.

Dulvy, N. K., R. P. Freckleton, and N. V. C. Polunin. 2004. Coral reef cascade and the indirect effects of predator removal by exploitation. Ecology Letters **7**:410-416.

Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science **282**:473-476.

Finke, D. L., and R. F. Denno. 2004. Predator diversity dampens trophic cascades. Nature **429**:407-410.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology Evolution and Systematics **35**:557-581.

Foster, S. A. 1987. The relative impacts of grazing by Caribbean coral reef fishes and *Diadema*: effects of habitat and surge. Journal of Experimental Marine Biology and Ecology **105**:1-20.

Gardner, T. A., I. M. Cote, J. A. Gill, A. Grant, and A. R. Watkinson. 2003. Long-term region-wide declines in Caribbean corals. Science **301**:958-960.

Gardner, T. A., I. M. Cote, J. A. Gill, A. Grant, and A. R. Watkinson. 2005. Hurricanes and Caribbean coral reefs: Impacts, recovery patterns, and role in long-term decline. Ecology **86**:174-184.

Gerhart, D. J. 1984. Prostaglandin-A2 - an Agent of Chemical Defense in the Caribbean Gorgonian Plexaura-Homomalla. Marine Ecology-Progress Series **19**:181-187.

Gerhart, D. J. 1986. Gregariousness in the gorgonian-eating gastropod *Cyphoma gibbosum*: tests of several possible causes. Marine Ecology-Progress Series **31**:255-263.

Gerhart, D. J. 1989. Movements of the tropical gorgonian-eating gastropod *Cyphoma gibbosum* (Linnaeus): association with wave surge. Marine Behaviour and Physiology **15**:207-215.

Gerhart, D. J. 1990. Fouling and gastropod predation: consequences of grazing for a tropical octocoral. Marine Ecology-Progress Series **62**:103-108.

Glynn, P. W. 1990. Feeding ecology of selected coral-reef macroconsumers: patterns and effects on coral community structure. Pages 365-400 *in* Z. Dubinsky, editor. Ecosystems of the World 25: Coral Reefs. Elsevier, Amsterdam.

Gurevitch, J., and L. V. Hedges. 1993. Meta-analysis: combining the results of independent experiments. Pages 378-398 *in* S. Scheiner and J. Gurevitch, editors. Design and analysis of experiments. Chapman and Hall, New York.

Gurevitch, J., J. A. Morrison, and L. V. Hedges. 2000. The interaction between competition and predation: A meta-analysis of field experiments. American Naturalist **155**:435-453.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **94**:421-425.

Harvell, C. D., W. Fenical, V. Roussis, J. L. Ruesink, C. C. Griggs, and C. H. Greene. 1993. Local and geographic variation in the defensive chemistry of a West Indian gorgonian coral (*Briareum asbestinum*). Marine Ecology-Progress Series **93**:165-173.

Harvell, C. D., and T. H. Suchanek. 1987. Partial predation on tropical gorgonians by *Cyphoma gibbosum* (Gastropoda). Marine Ecology-Progress Series **38**:37-44.

Hatcher, B. G., and A. W. D. Larkum. 1983. An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. Journal of Experimental Marine Biology and Ecology **69**:61-84.

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

Hay, M. E. 1984b. Predictable spatial escapes from herbivory: how do these affect the evolution of herbivore resistance in tropical marine communities. Oecologia **64**:396-407.

Hay, M. E. 1997. The ecology and evolution of seaweed-herbivore interactions on coral reefs. Coral Reefs **16**:S67-S76.

Hay, M. E., J. D. Parker, D. E. Burkepile, C. C. Caudill, A. E. Wilson, Z. P. Hallinan, and A. D. Chequer. 2004. Mutualisms and aquatic community structure: The enemy of my enemy is my friend. Annual Review of Ecology Evolution and Systematics **35**:175-197.

Hay, M. E., and P. R. Taylor. 1985. Competition between herbivorous fishes and urchins on Caribbean reefs. Oecologia **65**:591-598.

Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. Ecology **80**:1150-1156.

Heyward, A. J., and A. P. Negri. 1999. Natural inducers for coral larval metamorphosis. Coral Reefs **18**:273-279.

Hillebrand, H. 2002. Top-down versus bottom-up control of autotrophic biomass - a meta-analysis on experiments with periphyton. Journal of the North American Benthological Society **21**:349-369.

Hillebrand, H., and M. Kahlert. 2001. Effect of grazing and nutrient supply on periphyton biomass and nutrient stoichiometry in habitats of different productivity. Limnology and Oceanography **46**:1881-1898.

Hillebrand, H., B. Worm, and H. K. Lotze. 2000. Marine microbenthic community structure regulated by nitrogen loading and grazing pressure. Marine Ecology-Progress Series **204**:27-38.

Hixon, M. A., and W. N. Brostoff. 1996. Succession and herbivory: Effects of differential fish grazing on Hawaiian coral-reef algae. Ecological Monographs **66**:67-90.

Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setala, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecological Monographs **75**:3-35.

Horn, M. H. 1989. Biology of marine herbivorous fishes. Oceanography and Marine Biology **27**:167-272.

Hughes, T., A. M. Szmant, R. Steneck, R. Carpenter, and S. Miller. 1999. Algal blooms on coral reefs: What are the causes? Limnology and Oceanography **44**:1583-1586.

Hughes, T. P. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science **265**:1547-1551.

Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M. Nystrom, S. R. Palumbi, J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003a. Climate change, human impacts, and the resilience of coral reefs. Science **301**:929-933.

Hughes, T. P., A. H. Baird, D. R. Bellwood, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M.

Nystrom, S. R. Palumbi, J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003b. Causes of coral reef degradation - Response. Science **302**:1503-1504.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science **293**:629-638.

Jolles, A. E., P. Sullivan, A. P. Alker, and C. D. Harvell. 2002. Disease transmission of aspergillosis in sea fans: Inferring process from spatial pattern. Ecology **83**:2373-2378.

Jompa, J., and L. J. McCook. 2002. Effects of competition and herbivory on interactions between a hard coral and a brown alga. Journal of Experimental Marine Biology and Ecology **271**:25-39.

Kim, K., and C. D. Harvell. 2004. The rise and fall of a six-year coral-fungal epizootic. American Naturalist **164**:S52-S63.

Koop, K., D. Booth, A. Broadbent, J. Brodie, D. Bucher, D. Capone, J. Coll, W. Dennison, M. Erdmann, P. Harrison, O. Hoegh-Guldberg, P. Hutchings, G. B. Jones, A. W. D. Larkum, J. O'Neil, A. Steven, E. Tentori, S. Ward, J. Williamson, and D. Yellowlees. 2001. ENCORE: The effect of nutrient enrichment on coral reefs. Synthesis of results and conclusions. Marine Pollution Bulletin **42**:91-120.

Kurzava, L. M., and P. J. Morin. 1998. Tests of functional equivalence: complementary roles of salamanders and fish in community organization. Ecology **79**:477-489.

Lapointe, B. E. 1997. Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. Limnology and Oceanography **42**:1119-1131.

Lapointe, B. E. 1999. Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs. Limnology and Oceanography **44**:1586-1592.

Lasker, H. R. 1985. Prey preferences and browsing pressure of the butterflyfish *Chaetodon capistratus* on Caribbean gorgonians. Marine Ecology-Progress Series **21**:213-220.

Lasker, H. R. 1991. Population growth of a gorgonian coral: equilibrium and nonequilibrium sensitivity to changes in life history variables. Oecologia **86**:503-509.

Lasker, H. R., D. A. Brazeau, J. Calderon, M. A. Coffroth, R. Coma, and K. Kim. 1996. In situ rates of fertilization among broadcast spawning gorgonian corals. Biological Bulletin **190**:45-55.

Lasker, H. R., and M. A. Coffroth. 1983. Octocoral distributions at Carrie Bow Cay, Belize. Marine Ecology-Progress Series **13**:21-28.

Lasker, H. R., and M. A. Coffroth. 1988. Temporal and spatial variability among grazers: variability in the distribution of the gastropod *Cyphoma gibbosum* on octocorals. Marine Ecology-Progress Series **43**:285-295.

Lasker, H. R., M. A. Coffroth, and L. M. Fitzgerald. 1988. Foraging patterns of *Cyphoma gibbosum* on octocorals: the roles of host choice and feeding preference. Biological Bulletin **174**:254-266.

Lasker, H. R., K. Kim, and M. A. Coffroth. 1998. Production, settlement, and survival of plexaurid gorgonian recruits. Marine Ecology-Progress Series **162**:111-123.

Leibold, M. A., J. M. Chase, J. B. Shurin, and A. L. Downing. 1997. Species turnover and the regulation of trophic structure. Annual Review of Ecology and Systematics **28**:467-494.

Lessios, H. A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned. Annual Review of Ecology and Systematics **19**:371-393.

Lever, M. A., and I. Valiela. 2005. Response of microphytobenthic biomass to experimental nutrient enrichment and grazer exclusion at different land-derived nitrogen loads. Marine Ecology-Progress Series **294**:117-129.

Lewis, S. M. 1985. Herbivory on coral reefs: algal susceptibility ot herbivorous fishes. Oecologia **65**:370-375.

Lewis, S. M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef communitiy. Ecological Monographs **56**:183-200.

Lewis, S. M., and P. C. Wainwright. 1985. Herbivore abundance and grazing intensity on a Caribbean coral reef. Journal of Experimental Marine Biology and Ecology **87**:215-228.

Lirman, D. 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. Coral Reefs **19**:392-399.

Loreau, M. 1998. Separating sampling and other effects in biodiversity experiments. Oikos **82**:600-602.

Lotze, H. K., and B. Worm. 2002. Complex interactions of climatic and ecological controls on macroalgal recruitment. Limnology and Oceanography **47**:1734-1741.

Lotze, H. K., B. Worm, and U. Sommer. 2000. Propagule banks, herbivory and nutrient supply control population development and dominance patterns in macroalgal blooms. Oikos **89**:46-58.

Lotze, H. K., B. Worm, and U. Sommer. 2001. Strong bottom-up and top-down control of early life stages of macroalgae. Limnology and Oceanography **46**:749-757.

Lubchenco, J., and S. D. Gaines. 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. Annual Review of Ecology and Systematics **12**:405-437.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics **11**:119-161.

McAfee, S. T., and S. G. Morgan. 1996. Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama. Marine Biology **125**:427-437.

McClanahan, T. R., and N. A. Muthiga. 1989. Patterns of predation on a sea urchin, *Echinometra mathaei* (Deblainville), on Kenyan coral reefs. Journal of Experimental Marine Biology and Ecology **126**:77-94.

McClanahan, T. R., E. Sala, P. A. Stickels, B. A. Cokos, A. C. Baker, C. J. Starger, and S. H. Jones. 2003. Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. Marine Ecology-Progress Series **261**:135-147.

McCook, L. J. 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral Reefs **18**:357-367.

McCook, L. J., J. Jompa, and G. Diaz-Pulido. 2001. Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs **19**:400-417.

McGarigal, K., S. Chushman, and S. Stafford. 2000. Multivariate Statistics for Wildlife and Ecology Research. Springer-Verlag, New York.

McGlathery, K. J. 1995. Nutrient and grazing influences on a subtropical seagrass community. Marine Ecology-Progress Series **122**:239-252.

McWilliams, J. P., I. M. Cote, J. A. Gill, W. J. Sutherland, and A. R. Watkinson. 2005. Accelerating impacts of temperature-induced coral bleaching in the Caribbean. Ecology **86**:2055-2060.

Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997. Benthic-pelagic links and rocky intertidal communities: Bottom- up effects on top-down control? Proceedings of the National Academy of Sciences of the United States of America **94**:14530-14535.

Miller, M. W., and M. E. Hay. 1996. Coral-seaweed-grazer-nutrient interactions on temperate reefs. Ecological Monographs **66**:323-344.

Miller, M. W., M. E. Hay, S. L. Miller, D. Malone, E. E. Sotka, and A. M. Szmant. 1999. Effects of nutrients versus herbivores on reef algae: A new method for manipulating nutrients on coral reefs. Limnology and Oceanography **44**:1847-1861.

Morrison, D. 1988. Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. Ecology **69**:1367-1382.

Mumby, P. J., C. P. Dahlgren, A. R. Harborne, C. V. Kappel, F. Micheli, D. R. Brumbaugh, K. E. Holmes, J. M. Mendes, K. Broad, J. N. Sanchirico, K. Buch, S. Box, R. W. Stoffle, and A. B. Gill. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science **311**:98-101.

Mumby, P. J., and C. C. C. Wabnitz. 2002. Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species. Environmental Biology of Fishes **63**:265-279.

Naeem, S., D. R. Hahn, and G. Schuurman. 2000. Producer-decomposer co-dependency influences biodiversity effects. Nature **403**:762-764.

Nagelkerken, I., K. Buchan, G. W. Smith, K. Bonair, P. Bush, J. Garzon-Ferreira, L. Botero, P. Gayle, C. D. Harvell, C. Heberer, K. Kim, C. Petrovic, L. Pors, and P. Yoshioka. 1997. Widespread disease in Caribbean sea fans: II. Patterns of infection and tissue loss. Marine Ecology-Progress Series **160**:255-263.

Naiman, R. J. 1988. Animal influences on ecosystem dynamics. Bioscience **38**:750-752.

Nielsen, K. J. 2001. Bottom-up and top-down forces in tide pools: Test of a food chain model in an intertidal community. Ecological Monographs **71**:187-217.

Nielsen, K. J., and S. A. Navarrete. 2004. Mesoscale regulation comes from the bottom-up: intertidal interactions between consumers and upwelling. Ecology Letters **7**:31-41.

Nugues, M. M., and C. M. Roberts. 2003. Coral mortality and interaction with algae in relation to sedimentation. Coral Reefs **22**:507-516.

Nugues, M. M., G. W. Smith, R. J. van Hooidonk, M. I. Seabra, and R. P. M. Bak. 2004. Algal contact as a trigger for coral disease. Ecology Letters **7**:919-923.

Nystrom, M., and C. Folke. 2001. Spatial resilience of coral reefs. Ecosystems **4**:406-417.

O'Neal, W., and J. R. Pawlik. 2002. A reappraisal of the chemical and physical defenses of Caribbean gorgonian corals against predatory fishes. Marine Ecology-Progress Series **240**:117-126.

Ogden, J. C., and P. S. Lobel. 1978. The role of herbivorous fishes and urchins in coral reef communities. Environmental Biology of Fishes **3**:49-63.

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

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

Paine, R. T. 2000. Phycology for the mammalogist: marine rocky shores and mammal-dominated communities - how different are the structuring processes? Journal of Mammalogy **81**:637-648.

Pandolfi, J. M., R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. H. Newman, G. Paredes, R. R. Warner, and J. B. C. Jackson. 2003a. Causes of coral reef degradation - Response. Science **302**:1502-1503.

Pandolfi, J. M., R. H. Bradbury, E. Sala, T. P. Hughes, K. A. Bjorndal, R. G. Cooke, D. McArdle, L. McClenachan, M. J. H. Newman, G. Paredes, R. R. Warner, and J. B. C. Jackson. 2003b. Global trajectories of the long-term decline of coral reef ecosystems. Science **301**:955-958.

Pandolfi, J. M., J. B. C. Jackson, N. Baron, R. H. Bradbury, H. M. Guzman, T. P. Hughes, C. V. Kappel, F. Micheli, J. C. Ogden, H. P. Possingham, and E. Sala. 2005. Ecology - Are US coral reefs on the slippery slope to slime? Science **307**:1725-1726.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres. 1998. Fishing down marine food webs. Science **279**:860-863.

Pawlik, J. R., M. T. Burch, and W. Fenical. 1987. Patterns of chemical defense among Caribbean gorgonian corals: a preliminary survey. Journal of Experimental Marine Biology and Ecology **108**:55-66.

Pedersen, M. F., and J. Borum. 1996. Nutrient control of algal growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen

storage among phytoplankton and species of macroalgae. Marine Ecology-Progress Series **142**:261-272.

Pfister, C. A., and K. L. Van Alstyne. 2003. An experimental assessment of the effects of nutrient enhancement on the intertidal kelp *Hedophyllum sessile* (Laminariales, Phaeophyceae). Journal of Phycology **39**:285-290.

Purcell, S. W., and D. R. Bellwood. 1993. A functional analysis of food procurement in two surgeonfish species, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (Acanthuridae). Environmental Biology of Fishes **37**:139-159.

Randall, J. E., and G. L. Warmke. 1967. The food habits of the hogfish (*Lachnolaimus maximus*), a labrid fish from the western Atlantic. Caribbean Journal of Science **7**:141-144.

Robertson, D. R. 1991. Increases in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panama indicate food limitation. Marine Biology **11**:437-444.

Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 2000. MetaWin: statistical software for meta-analysis Version 2.0. *in*. Sinauer Associates, Sunderland, MA.

Russell, B. D., and S. D. Connell. 2005. A novel interaction between nutrients and grazers alters relative dominance of marine habitats. Marine Ecology-Progress Series **289**:5-11.

Sala, E., and M. H. Graham. 2002. Community-wide distribution of predatory-prey interaction strength in kelp forests. Proceedings of the National Academy of Sciences of the United States of America **99**:3678-3683.

Sammarco, P. W. 1982. Echinoid grazing as a structuring force in coral communities: whole reef manipulations. Journal of Experimental Marine Biology and Ecology **61**:31-55.

Sammarco, P. W., J. C. Coll, S. La Barre, and B. Willis. 1983. Competitive strategies of soft corals (Coelenterata: Octocorallia): allelopathic effects on selected scleratinian corals. Coral Reefs **1**:173-178.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature **413**:591-596.

Schupp, P. J., and V. J. Paul. 1994. Calcium carbonate and secondary metabolites in tropical seaweeds - variable effects on herbivorous fishes. Ecology **75**:1172-1185.

Silliman, B. R., and M. D. Bertness. 2002. A trophic cascade regulates salt marsh primary production. Proceedings of the National Academy of Sciences of the United States of America **99**:10500-10505.

Silliman, B. R., and J. C. Zieman. 2001. Top-down control of Spartina alterniflora production by periwinkle grazing in a Virginia salt marsh. Ecology **82**:2830-2845.

Smith, G. W., L. D. Ives, I. A. Nagelkerken, and K. B. Ritchie. 1996. Caribbean sea-fan mortalities. Nature **383**:487-487.

Smith, J. E., C. M. Smith, and C. L. Hunter. 2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs **19**:332-342.

Smith, V. H., G. D. Tilman, and J. C. Nekola. 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. Environmental Pollution **100**:179-196.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. W.H. Freeman and Company, New York.

Sommer, U., F. Sommer, B. Santer, C. Jamieson, M. Boersma, C. Becker, and T. Hansen. 2004. Complementary impact of copepods and cladocerans on phytoplankton. Ecology Letters **4**:545-550.

Soule, M. E., J. A. Estes, J. Berger, and C. M. Del Rio. 2003. Ecological effectiveness: conservation goals for interactive species. Conservation Biology **17**:1238-1250.

Steneck, R. S. 1988. Herbivory on coral reefs: a synthesis. Proceedings of the 6th International Coral Reef Symposium **1**:37-49.

Steneck, R. S., and M. N. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. Oikos **69**:476-498.

Steneck, R. S., J. Vavrinec, and A. V. Leland. 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the western North Atlantic. Ecosystems **7**:323-332.

Streelman, J. T., M. Alfaro, M. W. Westneat, D. R. Bellwood, and S. A. Karl. 2002. Evolutionary history of the parrotfishes: biogeography, ecomorphology, and comparative diversity. Evolution **56**:961-971.

Tanner, J. E. 1995. Competition between scleractinian corals and macroalgae - an experimental investigation of coral growth, survival and reproduction. Journal of Experimental Marine Biology and Ecology **190**:151-168.

Terborgh, J., E. J.A., P. Paquet, K. Ralls, D. Boyd-Heger, B. J. Miller, and R. F. Noss. 1999. The role of top carnivores in regulating terrestrial ecosystems. Pages 39-64 *in* M. E. Soule and J. Terborgh, editors. Continental Conservation. Island Press, Washington, DC.

Thacker, R. W., D. W. Ginsburg, and V. J. Paul. 2001. Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. Coral Reefs **19**:318-329.

Turingan, R. G. 1994. Ecomorphological relationships among Caribbean tetraodontiform fishes. Journal of Zoology **233**:493-521.

Underwood, A. J. 1997. Experiments in Ecology. Cambridge University Press.

Valentine, J. F., and K. L. Heck. 2001. The role of leaf nitrogen content in determining turtlegrass (Thalassia testudinum) grazing by a generalized herbivore in the northeastern Gulf of Mexico. Journal of Experimental Marine Biology and Ecology **258**:65-86.

Valiela, I., J. McClelland, J. Hauxwell, P. J. Behr, D. Hersh, and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: Controls and ecophysiological and ecosystem consequences. Limnology and Oceanography **42**:1105-1118.

Van Alstyne, K. L., and V. J. Paul. 1992. Chemical and structural defenses in the sea fan *Gorgonia ventalina*: effects against generalist and specialist predators. Coral Reefs **11**:155-159.

Vreeland, H. V., and H. R. Lasker. 1989. Selective feeding of the polychaete *Hermodice carunculata* Pallas on Caribbean gorgonians. Journal of Experimental Marine Biology and Ecology **129**:265-277.

Wahle, C. M. 1983. The role of age, size, and injury in sexual reproduction among Jamaican gorgonians. American Zoologist **23**:961.

Williams, D. E., and M. W. Miller. 2005. Coral disease outbreak: pattern, prevalence and transmission in *Acropora cervicornis*. Marine Ecology-Progress Series **301**:119-128.

Williams, I. D., and N. V. C. Polunin. 2001. Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. Coral Reefs **19**:358-366.

Witman, J. D. 1992. Physical disturbance and community structure of exposed and protected reefs - a case study from St. John, United States Virgin Islands. American Zoologist **32**:641-654.

Wootton, J. T., M. E. Power, R. T. Paine, and C. A. Pfister. 1996. Effects of productivity, consumers, competitors, and El Nino events on food chain patterns in a rocky intertidal community. Proceedings of the National Academy of Sciences of the United States of America **93**:13855-13858.

Worm, B., H. K. Lotze, H. Hillebrand, and U. Sommer. 2002. Consumer versus resource control of species diversity and ecosystem functioning. Nature **417**:848-851.

Worm, B., H. K. Lotze, and U. Sommer. 2000. Coastal food web structure, carbon storage, and nitrogen retention regulated by consumer pressure and nutrient loading. Limnology and Oceanography **45**:339-349.

Worm, B., H. K. Lotze, and U. Sommer. 2001. Algal propagule banks modify competition, consumer and resource control on Baltic rocky shores. Oecologia **128**:281-293.

Yoshioka, P. M. 1996. Variable recruitment and its effects on the population and community structure of shallow-water gorgonians. Bulletin of Marine Science **59**:433-443.

Yoshioka, P. M., and B. B. Yoshioka. 1987. Variable effects of Hurricane David on the shallow water gorgonians of Puerto Rico. Bulletin of Marine Science **40**:132-144.

Yoshioka, P. M., and B. B. Yoshioka. 1989. A multispecies, multiscale analysis of spatial patterns and its application to a shallow-water gorgonian community. Marine Ecology-Progress Series **54**:257-264.