The relative importance of nutrient enrichment and herbivory on macroalgal communities near Norman's Pond Cay, Exumas Cays, Bahamas: a "natural" enrichment experiment

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Abstract

The simultaneous effects of grazing and nutrient enrichment on macroalgal communities were experimentally investigated using plastic mesh enclosure/exclosure cages along a natural nutrient (DIN, SRP) gradient from the discharge of a tidal mangrove creek on the west side of Norman's Pond Cay, Exumas Cays, Bahamas. Nutrient enrichment was the only factor affecting total biomass of macroalgae whereas selective herbivory moderated species composition. Biomass ranged from >2 kg dry weight m^{-2} at the DIN-enriched Waterfall to <600 g dry weight m^{-2} in the DIN-limited Algal Halo. Grazing by the queen conch *Strombus gigas* and the sea hare *Aplysia dactylomela* significantly reduced biomass of the epiphyte *Laurencia intricata*, but not its host *Digenea simplex* at the DIN-enriched Waterfall. These two rhodophytes dominated the macroalgal community at the DIN-enriched Waterfall and inner Algal Halo, whereas the chlorophytes *Microdictyon marinum* and *Cladophora catenata* dominated the relatively DIN-depleted outer Algal Halo. Higher grazing rates by *S. gigas*, *A. dactylomela*, and juvenile parrotfish and surgeonfish at the DIN-enriched Waterfall compared to the more oligotrophic Algal Halo suggested selective grazing on higher quality (nitrogen) diets by these herbivores. A pronounced increase in the carbon/nitrogen (C:N) ratios of *D. simplex* and *L. intricata* from the Waterfall to the Algal Halo indicated increased DIN-limitation of growth in the more offshore, lower DIN macroalgal communities. In contrast, only modest increases in C:N ratios of *M. marinum* and *C. catenata* between the Waterfall and Algal Halo suggested that these species are better

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adapted to growth in reef environments with lower levels of DIN enrichment. Low coral cover (< 2%) co-occurred with high macroalgal cover (>35%) at DIN-enriched reef sites around Norman's Pond Cay (Waterfall, Patch Reef, North Perry Reef) compared to relatively high coral cover (10–20%) and low macroalgal cover (< 20%) at the lower DIN reef sites (Rainbow Reef, Lang's Reef). These results support ecological theory that bottom-up control via nutrient enrichment is a primary factor regulating overall biomass and taxonomic assemblages of macroalgae on coral reefs, whereas grazing is more important in controlling relative species composition via dietary preferences.
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Keywords: Nitrogen; Phosphorus; Herbivores; Macroalgae; Coral; Groundwater

1. Introduction

Grazing and nutrient availability are important ecological factors regulating the structure of algal communities on coral reefs. The relative importance of these factors in supporting coral reef algal communities has become a subject of debate within the scientific literature. Stephenson and Searles (1960) first used experimental enclosures to demonstrate the importance of browsing herbivorous fishes to biotic structure of algal communities on Heron Island, Australia. From experiments in the Red Sea, Dart (1972) showed the importance of sea urchin grazing to competition between algal turf and reef coral colonization. Since then, a multitude of similar studies have followed, adding detailed and broad coverage of the importance of herbivores to the dynamics of coral reef communities. Alternatively, examples of alterations in bottom-up forcing provide evidence for changes in the dynamics of coral reef communities. The diversion of sewage from Kaneohe Bay, HI, in the 1970s resulted in a subsequent reduction in biomass of the green macroalga *Dictyosphaeria cavernosa*, which had previously overgrown and replaced coral-dominated reef communities from nutrient enrichment (Banner, 1974; Smith et al., 1981). More recent work has demonstrated the physiological and biophysical mechanisms by which macroalgal proliferation is controlled in nutrient-limited coral reef regions (e.g. Lapointe, 1987; Lapointe et al., 1987, 1992a,b; Larned and Stimson, 1996; Schaffelke, 1999). According to the Relative Dominance Model (RDM, Littler and Littler, 1984), the interaction of high grazing and low water column nutrient availability typically results in inconspicuous biomass and limited growth rates of macroalgae on oligotrophic, undisturbed coral reefs. In contrast, the views of Hughes (1994) and Hughes et al. (1999) suggest that macroalgal proliferation on coral reefs is exclusively controlled by reduced grazing pressure and biomass removal.

Several attempts have been made to experimentally analyze the simultaneous effects of nutrient enrichment and grazing on algal communities in coral reef regions. Hatcher and Larkum (1983), using experimental cages and nutrient diffusers in oligotrophic areas of the Great Barrier Reef, found significant effects of both nutrients and grazing on the productivity and biomass of algal turf communities. Recently, Smith et al. (2001) used grazer exclusion cages and artificial nutrient enrichment to experimentally manipulate algal growth on PVC settlement tiles on fringing reefs off Puako, Hawaii Island, HI. Despite the moderate background nutrient concentrations at their experimental site, Smith

et al. (2001) reported significant effects of both grazing and nutrient enrichment on algal biomass; the most significant overall effect was the growth of *Ulva fasciata* that resulted from the combination of reduced herbivory and nutrient enrichment. These results provided experimental evidence of simultaneous effects of both herbivory and nutrient availability, supporting the predictions of the RDM.

The shallow fringing reefs, patch reefs, and hard-bottom communities surrounding the Caribbean Marine Research Center (CMRC) on Lee Stocking Is., Exumas Cays, Bahamas, and the adjacent island of Norman's Pond Cay (NPC) have relatively low biomass of fleshy macroalgae (Stoner et al., 1992). However, at the "Waterfall" on the western side of NPC, a conspicuous and well-developed macroalgal community forms an Algal Halo in the outflow of a tidal mangrove channel. The mangrove channel was modified by the placement of limestone rocks at its outflow creating a dam with positive tidal outflow. Presumably, the Waterfall was designed to restrict tidal circulation of seawater into the mangrove channel to enhance evaporation and historical salt production in the upstream hypersaline ponds on NPC. Previous ecological surveys in this area of the Exumas have noted dense aggregations of juvenile queen conch, *Strombus gigas*, foraging at the Waterfall on NPC (Wicklund et al., 1988; Stoner et al., 1992).

Because of the potential for "point-source" nutrient enrichment from the outflows of the mangrove channel and its potential consequences upon macroalgal biomass, zonation and herbivory, we predicted that this site would provide a unique opportunity to examine the simultaneous effects of natural nutrient enrichment and grazing intensity on benthic community structure. In this report, we provide results of a multi-disciplinary study that included characterizing surface waters of the mangrove channel, Waterfall, Algal Halo, groundwaters of a karst cave system on NPC, and several adjacent coral reef sites for dissolved inorganic nitrogen and soluble reactive phosphorus to establish gradients and patterns of nutrient enrichment. In addition, we present results from an experimental enclosure/exclosure study and grazing assays that quantified the relative importance of herbivory and "natural" nutrient enrichment as a function of tissue nutrient biochemistry and physiology of predominant macroalgae located spatially along the gradient of nutrient enrichment.

2. Materials and methods

The field studies and experiments reported here were conducted between February 1997 and June 1999 at the Waterfall on NPC and several coral reef communities around Lee Stocking Island in the Exuma Cays, Bahamas (Fig. 1). The biology and ecology of queen conch, *S. gigas*, in proximity to NPC is particularly well known as a result of extensive research conducted at the nearby CMRC laboratory (Wicklund et al., 1988; Stoner, 1989; Stoner and Waite, 1990, 1991; Stoner et al., 1995).

2.1. Study sites

Field experiments to determine the relative importance of nutrient enrichment and herbivory were conducted at the Waterfall on the west side of NPC (Fig. 1). Here, outflows
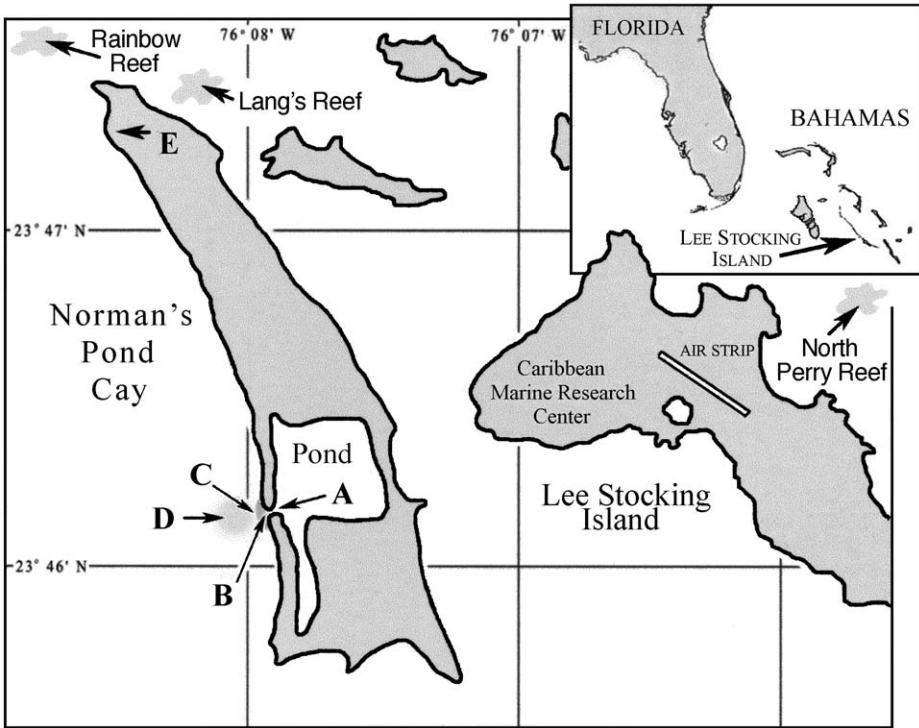
Fig. 1. Map of the Exumas Cays showing the spatial relationship of Norman's Pond Cay and Lee Stocking Island to study sites. (A) The tidal mangrove channel that connects the salt pond with coastal waters on the west side of Norman's Pond Cay. (B) The Waterfall. (C) The Algal Halo. (D) The Patch Reef. (E) The Blue Hole. Other sampling sites at Rainbow Reef, Lang's Reef, and North Perry Reef are shown.

from the salt pond–mangrove channel cascade down a man-made limestone rock formation (Waterfall, Fig. 2A) and into shallow (1–2 m depth) coastal waters where an Algal Halo contains unusually high biomass of several species of macroalgae (Fig. 2B). Between the Waterfall (shoreline) and the Algal Halo is a fluvial deposit of calcium carbonate sand that extends offshore for ~ 25 m. During the initial February 1997 survey, a 100-m transect was established from the Waterfall through the Algal Halo to an offshore patch reef comprised of *Porites astreoides* and *Siderastrea siderea* (Fig. 2C). This transect was used to guide the subsequent sampling for seawater nutrient analyses, collection of macroalgae for biomass and tissue carbon/nitrogen/phosphorus (C:N:P) contents, placement of experimental enclosures/exclosures, and digital video imagery of benthic biota. In addition to the Waterfall, Algal Halo, and Patch Reef, we examined other communities around NPC, including the Blue Hole (a karst cave system on the north end of NPC that is ~ 87 m deep, Fig. 2D), Rainbow Reef (a nearby patch reef in ~ 4–6 m water depth), Lang's Reef (a fringing reef on the northeast side of NPC in 2–3 m water depth), and North Perry Reef (a deep "spur-and-groove" limestone reef system offshore LSI in ~ 22 m water depth, Fig. 1).
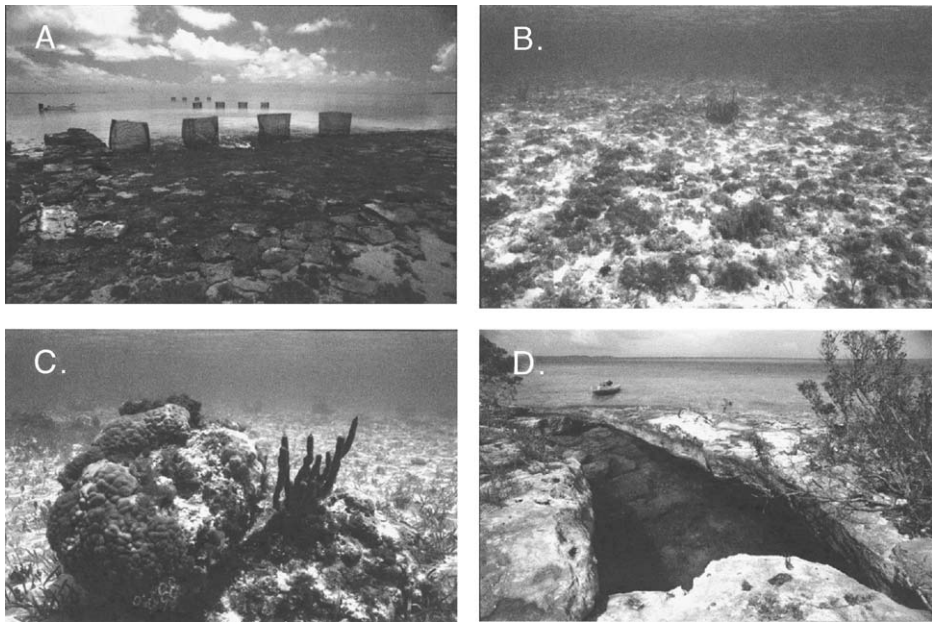
Fig. 2. Photographs illustrating the study sites. (A) The outflows of the mangrove channel discharging over the Waterfall that was dominated by the rhodophytes *D. simplex* and *L. intricata*; also shown are the Vexar cages used for the experimental studies. (B) The outer Algal Halo illustrating the abundant cover of the chlorophytes *M. marinum* and *C. catenata*. (C) The reef coral *P. astreoides* that dominated the patch reef at the outer Algal Halo. (D) The Blue Hole, a karst cave system on the north end of Norman's Pond Cay.

2.2. Sampling and analysis of seawater for dissolved inorganic nutrients

Water samples were collected in February 1997 ($n = 12$), July 1998 ($n = 13$), and May 1999 ($n = 41$) for measurement of dissolved inorganic nitrogen (DIN = NH_4^+ + NO_3^- + NO_2) and soluble reactive phosphorus (SRP) in the mangrove channel, Waterfall, Algal Halo, Blue Hole, Lang's Reef, Rainbow Reef, and North Perry Reef. Surface water samples (∼ 0.2 m below surface) were collected in the Blue Hole and the mangrove channel, Waterfall, Algal Halo (inner and outer), and a reference site adjacent to shore ∼ 0.5 km north on the Waterfall on NPC. In the Blue Hole, specialized cave diving methods (TRIMIX) were used to collect groundwater samples along a depth gradient from the surface to 87 m depth. At the three reef sites (Rainbow Reef, Lang's Reef, North Perry Reef), near-bottom (0.2 m above bottom) seawater samples were collected. The water samples were collected into clean 250-ml Nalgene bottles, filtered through 0.45 μm GF/F filters, and held on ice in the dark until return to either the CMRC lab or the R/V *Sea Diver* (May 1999) where they were frozen. The seawater samples were subsequently analyzed for NH_4^+, NO_3^- plus NO_2^-, and SRP on a Bran and Luebbe TRAACS Analytical Console at the HBOI Environmental Laboratory in Ft. Pierce, FL. The analytical detection limits were 0.08

μM for NH_4^+, 0.05 μM for NO_3^-, 0.003 μM for NO_2^-, and 0.009 μM for SRP. The methods used for collection, filtration, handling, and analysis followed a strict quality assurance/quality control protocol (certified by the US Environmental Protection Agency and Florida Department of Environmental Protection) to prevent contamination and ensure accurate and representative results.

2.3. Determination of macroalgal biomass, C:N:P, and alkaline phosphatase activity

We conducted quantitative sampling of macroalgal biomass and C:N:P ratios along the transect from the Waterfall through the Algal Halo in February 1997 following the end of the fall wet season and again in May 1999 at the end of the spring dry season. Replicate ($n = 5$) samples of macroalgae were collected at the Waterfall and at $\sim$ 7 m intervals through the Algal Halo (40 m to 93 m) with a 0.06-m^2 PVC quadrat. The macroalgae were placed in Zip-loc™ bags, returned to the lab, sorted, cleaned of sediment, epiphytes, epizoa, identified, and then wet-weighed on an Ohaus II Scout electronic balance. Subsamples ($n = 3$) of predominant macroalgal thalli collected at the Waterfall and different zones (inner Algal Halo, outer Algal Halo) along the transect were rinsed briefly in deionized water, damp-dried to remove excess water, wet-weighed, and dried in a laboratory oven (65 °C) to constant weight. The samples were then re-weighed to determine percent dry weight for calculation of biomass in g dry wt. m^{-2}. The dried subsamples of macroalgae were ground to a fine powder with a mortar and pestle and subsequently analyzed for C:N:P ratios at the University of Maryland's Analytical Services Laboratory in Solomons, MD. Alkaline phosphatase activity (APA) of macroalgae was measured on replicate samples ($n = 4$) of macroalgae collected at the Waterfall, Algal Halo, and reef sites during May 1999 by the spectrophotometric methods described in Lapointe et al. (1994).

2.4. Experimental analysis of grazing and nutrient enrichment

Preliminary measurements in February 1997 (Table 1) indicated a natural nutrient gradient with relatively high DIN and SRP concentrations in the mangrove channel and Waterfall and lower concentrations in the Algal Halo. To examine the effects of herbivory under "high" and "low" nutrient concentrations along this gradient, we constructed experimental enclosures/exclosures using 1.9-cm black plastic mesh (Vexar) to form square, 1-m^2 cages that were 1.2 m high. The topless cages (i.e. pens) were held in place and upright with vertical pieces of steel reinforcement (rebar) driven into the sediment and limestone rock with a slide hammer; the rebar was covered with PVC pipe to minimize metal contamination. Water depth varied from 0.2 to 0.5 m at the Waterfall and from 0.3 to 1.2 m at the Algal Halo. Both sites were subject to strong currents (50–100 cm s^{-1}) and mixing, particularly at the Waterfall where outflows from the mangrove channel resulted in considerable turbulence as water cascaded down the limestone rock formation.

A factorial, random-block design was used to examine the main effects and interactions of nutrients ("high" and "low") and herbivory ("high" and "low") on biomass of macroalgae. The design included a total of four treatments, with two

Table 1
Concentrations (mM) of dissolved ammonium, nitrate + nitrite, DIN (ammonium + nitrate + nitrite), soluble reactive phosphorus (SRP), and DIN:SRP ratio. ND = below detection limits

Location	Date	Ammonium	Nitrate – Nitrite	DIN	SRP	DIN:SRP
Mangrove Channel	Feb-97	0.91	0.31	1.22	0.017	
	Jul-98	1.01 ± 0.46	0.41 ± 0.13	1.43 ± 0.51	0.033 ± 0.032	
	May-99	0.58 ± 0.01	0.86 ± 0.03	1.45 ± 0.04	0.040 ± 0.002	
	May-99	0.68 ± 0.02	0.74 ± 0.05	1.41 ± 0.04	0.041 ± 0.001	
	Mean ± S.D.	0.80 ± 0.12	0.58 ± 0.22	1.38 ± 0.09	0.032 ± 0.011	42.5
Waterfall	Feb-97	0.74	0.51	1.25	0.016	
	Jul-98	1.13	0.57	1.7	0.06	
	May-99	0.43 ± 0.01	0.22 ± 0.01	0.65 ± 0.01	0.035 ± 0.005	
	May-99	0.45 ± 0.01	0.41 ± 0.15	0.87 ± 0.15	0.035 ± 0.005	
	Mean ± S.D.	0.69 ± 0.33	0.43 ± 0.15	1.12 ± 0.46	0.037 ± 0.054	30.3
Inner Algal Halo	Feb-97	0.26	0.27	0.52	ND	
	Jul-98	0.66	0.33	0.99	0.077	
	May-99	0.40 ± .04	0.39 ± 0.10	0.80 ± 0.14	0.01 ± 0.005	
	May-99	0.30 ± 0.08	0.27 ± 0.02	0.57 ± 0.07	ND	
	Mean ± S.D.	0.41 ± 0.23	0.32 ± 0.06	0.72 ± 0.22	0.026 ± 0.034	27.7
Outer Algal Halo	Feb-97	0.14	ND	0.14	ND	
	Jul-98	1.19	0.48	1.67	0.088	
	May-99	0.42 ± 0.02	0.09 ± 0.01	0.51 ± 0.03	0.005 ± 0.001	
	May-99	0.42 ± 0.03	0.04 ± 0.04	0.50 ± 0.02	0.025 ± 0.005	
	Mean ± S.D.	0.54 ± 0.05	0.15 ± 0.22	0.71 ± 0.66	0.032 ± 0.039	22.2
Blue Hole	Feb-97	0.21	4.13	4.34	0.025	
	Jul-98	0.89	3.48	4.37	0.115	
	May-99	0.42 ± 0.01	3.33 ± 0.47	3.75 ± 0.48	0.035 ± 0.025	
	May-99	0.42 ± 0.02	3.09 ± 0.52	3.51 ± 0.50	0.025 ± 0.030	
	Mean ± S.D.	0.48 ± 0.29	3.50 ± 0.45	3.99 ± 0.43	0.050 ± 0.044	79.8
Rainbow Reef	Feb-97	ND	0.26	0.26	ND	
	May-99	0.40 ± 0.02	0.31 ± 0.12	0.71 ± 0.14	0.019 ± 0.001	
	May-99	0.43 ± 0.01	0.24 ± 0.10	0.67 ± 0.09	0.014 ± 0.006	
	Mean ± S.D.	0.28 ± 0.21	0.27 ± 0.04	0.55 ± 0.25	0.014 ± 0.005	39.9
Lang's Reef	Feb-97	ND	0.15	0.15	ND	
	May-99	0.39 ± 0.06	0.27 ± 0.17	0.66 ± 0.23	0.018 ± 0.002	
	May-99	0.48 ± 0.002	0.30 ± 0.15	0.78 ± 0.14	ND	
	Mean ± S.D.	0.30 ± 0.24	0.24 ± 0.08	0.53 ± 0.33	0.011 ± 0.006	48.2
North Perry Reef	May-99	0.41 ± 0.02	0.39 ± 0.22	0.81 ± 0.24	0.010 ± 0.001	81

replicate cages per treatment. The "high" nutrient treatments were located in the Waterfall and the "low" nutrient treatments were 30 m from shore and within the inner portion of the Algal Halo. To experimentally manipulate levels of herbivory, gastropod mesograzers common at this site were enclosed in some cages at "high" densities and excluded from other cages to result in "low" densities of grazers.

Previous research in seagrass meadows near the Waterfall has shown that juvenile queen conch, S. gigas, commonly occur at densities of 2 S. gigas m^{-2} (Stoner et al., 1995). To increase grazing above this level, a density of 5 S. gigas m^{-2} was used for the "high" grazing treatments. Juvenile S. gigas were collected (mean size = 190 mm shell length) from the surrounding environs and randomly divided among the two

replicate cages at the Waterfall ("high" nutrient treatment) and two replicate cages in the Algal Halo ("low" nutrient treatment). During the experimental setup, we noticed abundant populations of the sea hare, *Aplysia dactylomela*, grazing on macroalgae at both the Waterfall and Algal Halo. We likewise collected this locally important herbivore and randomly placed them among the "high grazing" pens at densities of 2 *A. dactylomela* m^{-2}. Accordingly, the "high" grazing treatments included 5 *S. gigas* m^{-2} and 2 *A. dactylomella* m^{-2}. This level of grazing animal density is within the range we have observed at the Waterfall and also used by others in experimental field studies in the Exumas (Stoner, 1989). In addition to the factorial experimental design, controls were also employed and located at both the "high" nutrient Waterfall and the "low" nutrient Algal Halo. These uncaged sites, marked by upright PVC pipes adjacent to the cages, were open to the movements and grazing effects of juvenile *S. gigas*, *A. dactylomela*, and other sedentary and mobile, roving grazers (e.g. surgeonfish, parrotfish).

Following setup on May 20, 1999, the experiment was monitored visually and with digital underwater video (Sony VX-1000 with an Amphibico U/W housing) daily for 2 weeks to record the behavior of the grazers inside and outside of the cages. Water samples were collected at high and low tides during the experiment for determination of DIN and SRP concentrations. Upon termination of the experiment, a 0.06-m^2 PVC quadrat was used to collect random samples ($n = 5$) of macroalgae from within each of the eight pens and adjacent control plots and quantified for biomass as described above.

2.5. Quantifying herbivory by mobile icthyofauna

Herbivore grazing rates by mobile icthyofauna were quantified at the Waterfall, inner Algal Halo (40 m), and outer Algal Halo (70 m) using the bioassay method of Littler et al. (1986). The palatable macroalga *Padina* was used during morning (0600–1200 h) and afternoon (1200–1800 h) feeding trials to determine the mean number of bites by herbivorous fishes ($n = 12$).

2.6. Quantification of benthic biotic cover

We used digital underwater video (Sony VX-1000 with an Amphibico U/W housing) to quantify benthic biotic cover at various sites around NPC and LSI, including the NPC patch reef/Algal Halo, Lang's Reef, Rainbow Reef, and North Perry Reef. During May of 1999, the benthic biota at these sites were quantified by obtaining digital video imagery at right angles to the bottom along two 50-m belt transects. The video was obtained by a SCUBA diver swimming slowly along a transect line and carefully holding the camcorder 0.4 m off the bottom. A second oblique (45°) close-up video was also obtained to allow detailed identification of the biota along the transect. In the laboratory, 10 rectangular quadrats (~ 0.34 m^2 each) were randomly selected from each video transect and quantified for percent cover of various biotic elements using the randomized point-count method (Lapointe et al., 1997). The biotic elements included hard corals, turf algae (microfilamentous algae < 2 cm high), macroalgae (frondose algae >2 cm high), coralline algal crusts, sponges, and octocorals.

3. Results

3.1. Dissolved nutrients in surface waters and groundwaters

Surface water samples collected from around the Waterfall in February 1997 showed a significant offshore nutrient gradient. The highest DIN concentrations, ~ 1.25 μM, occurred in the mangrove channel and Waterfall, and decreased offshore to 0.52 μM at the inner Algal Halo (30 m) and 0.14 μM at the outer Algal Halo (Table 1). SRP concentrations in the mangrove channel and Waterfall were ~ 0.02 μM, higher than the undetectable concentrations (<0.008 μM) measured at the inner and outer Algal Halo (Table 1). Salinity and temperature ranged from 37.3 ppt and 28.1 °C in the mangrove channel to 37.1 ppt and 27.4 °C at the outer Algal Halo during this sampling. A similar spatial trend of decreasing DIN concentrations from the mangrove channel and Waterfall to the Algal Halo was measured in July 1998. DIN concentrations ranged from 1.1 to 1.7 μM at the channel and waterfall compared to values <1 μM at the inner and outer Algal Halo (Table 1). In July 1998, SRP concentrations ranged from 0.06 μM at the Waterfall to 0.09 μM in the inner Algal Halo (Table 1).

The lowest DIN and SRP concentrations of the study occurred at Rainbow Reef and Lang's Reef in February 1997. At that sampling, DIN concentrations were <0.26 μM with undetectable concentrations of NH_4^+ and SRP (Table 1). In May 1999, higher DIN and SRP concentrations occurred, ranging from 0.66 to 0.78 μM and from 0.011 to 0.019 μM, respectively (Table 1).

One-way ANOVA (Table 2) showed that the DIN concentrations in the surficial groundwaters of the Blue Hole (mean = 3.99 μM) were significantly higher than those of

Table 2

Results of one-way ANOVA for dissolved inorganic nitrogen (DIN) concentrations among study sites

Factor	df	SS	MS	F	P
Site	7	35.92	5.13	32.72	**<0.0001**
Error	20	3.14	0.16		
Fisher's multiple comparisons test					
MC vs. AH(i)					<0.0001
MC vs. AH(o)					0.0179
MC vs. BH					<0.0001
MC vs. RR					0.0086
MC vs. LR					0.0076
WF vs. BH					<0.0001
BH vs. AH(i)					<0.0001
BH vs. AH(o)					<0.0001
BH vs. RR					<0.0001
BH vs. LR					<0.0001
BH vs. PR					<0.0001

Significant Fisher's multiple comparisons test ($p < 0.05$) are presented for significant ANOVA comparisons ($p < 0.05$) in bold. MC = mangrove channel, AH = Algal Halo (i) = inner, (o) = outer, BH = Blue Hole, LR = Lang's Reef, RR = Rainbow Reef, WF = Waterfall, PR = Patch Reef.

all other surface waters sampled in the study. The mean DIN concentration of the mangrove channel was statistically similar to the mean DIN at the Waterfall, and the mangrove channel was significantly higher than both the inner and outer Algal Halo (Table 2). The mean DIN of the mangrove channel was also significantly higher than that of Lang's Reef and Rainbow Reef but not North Perry Reef. In contrast to DIN, a high degree
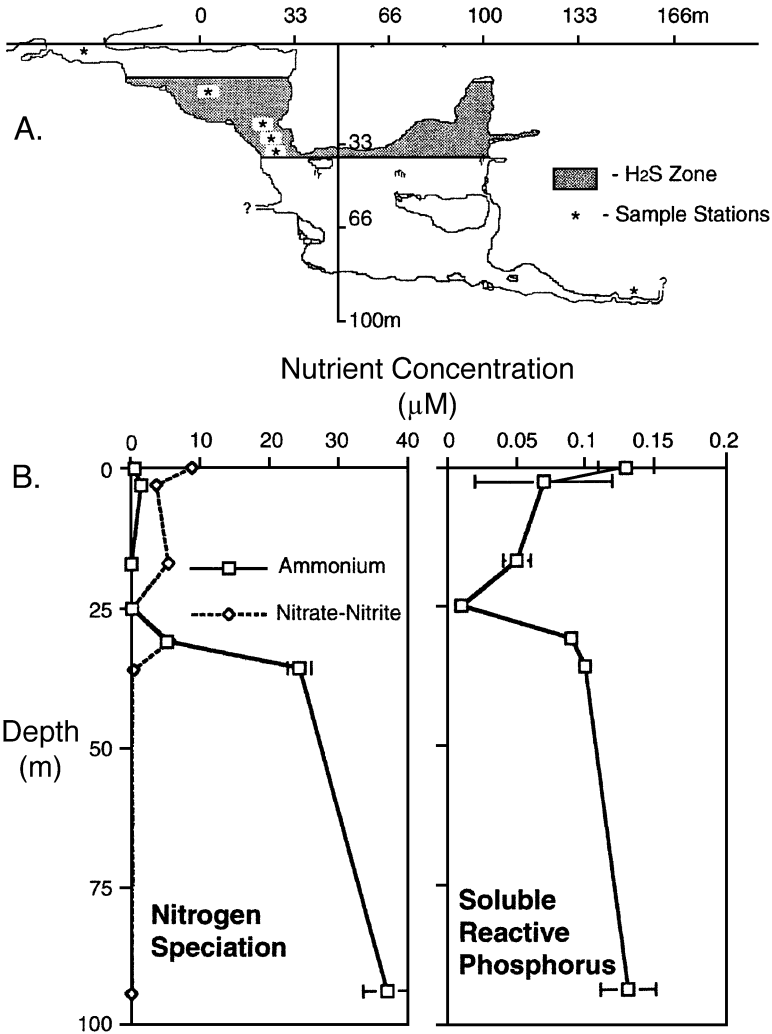

Fig. 3. (A) Diagram illustrating the configuration of the Blue Hole cave system on the north end of Norman's Pond Cay; note location of the hydrogen sulfide zone and sample stations. (B) Vertical profile of nutrient concentrations (ammonium, nitrate–nitrite, and soluble reactive phosphorus) in the Blue Hole. Values represent means ± 1 S.D. ($n = 2$).

of heterogeneity in SRP concentrations within the sites prevented statistical differences of SRP concentration vs. location.

The comprehensive sampling at seven depths in the Blue Hole cave system on April 30, 1997 (Fig. 3A) showed distinct vertical gradients in NH_4^+, NO_3^-, and SRP (Fig. 3B). Concentrations of NH_4^+ were relatively low (< 1 μM) at depths above 25 m and increased to maximum concentrations of ~ 36 μM at the bottom of the cave (87 m). In contrast, NO_3^- concentrations were highest (~ 9 μM) at the surface of the cave and decreased with depth to undetectable concentrations on the bottom (Fig. 3B). The highest SRP concentrations of ~ 0.15 μM occurred at the bottom of the cave and lowest concentrations occurred at depths between 15 and 33 m (Fig. 3B). Salinity ranged from a low of 35.4 ppt at the surface of the cave to 37 ppt at the bottom. Temperature and dissolved oxygen were also highest in the surface waters of the cave (29 °C and 6.0 mg/l, respectively) and decreased sharply with depth below 15 m to the lowest values at the bottom (25.8 °C and 0 mg/l, respectively).

The DIN:SRP ratios of surface waters and groundwaters sampled during this study ranged from 22 to 81 (Table 1). The lowest values of 22–30 occurred at the Waterfall and Algal Halo and increased at the more offshore shallow reefs (Rainbow Reef = 40, Lang's Reef = 48) with the highest values of ~ 80 in groundwaters of the Blue Hole and at the deepest reef at North Perry Reef (Table 1).
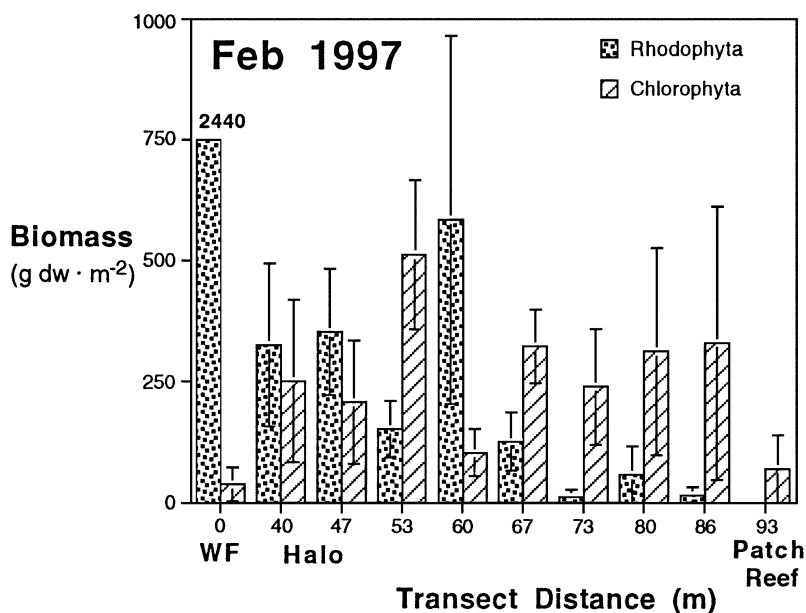

Fig. 4. Biomass (g dry wt. m^{-2}) of the dominant rhodophytes (*D. simplex*, *L. intricata*) and chlorophytes (*M. marinum*, *C. catenata*) along a transect extending from the Waterfall (WF) through the Algal Halo and terminating at the Patch Reef in February 1997. Values represent means ± 1 S.D. ($n = 5$).

3.2. Macroalgal biomass, C:N:P, and APA

In February 1997, a distinct zonation of fleshy, frondose macroalgae occurred at the Waterfall and Algal Halo. The Waterfall community was dominated by the rhodophyte *Digenea simplex*, which together with its epiphyte *Laurencia intricata*, had a mean biomass of 2440 g dry wt. m^{-2} (Fig. 4). These two rhodophytes generally dominated the macroalgal biomass from the Waterfall to 60 m offshore where their biomass diminished to levels of ∼ 200–600 g dry wt. m^{-2} (Fig. 4). Between 67 and 93 m from shore, the macroalgal community became dominated by two chlorophytes—*Microdictyon marinum* and *Cladophora catenata*—which occurred at levels >250 g dry wt. m^{-2}. In May 1999, the *D. simplex* and, to a lesser extent, *L. intricata*, again dominated the Waterfall community but at a much lower biomass, ∼ 600 g dry wt. m^{-2}, compared to the February 1997 sampling (Fig. 5). In May 1999, *D. simplex* and its epiphyte *L. intricata* extended offshore to only 47 m where the *M. marinum* and *C. catenata* became dominant.

Tissue % C, % N, and % P contents of macroalgae varied among the NPC salt pond, Waterfall, and Algal Halo sites (Table 3). One-way ANOVA revealed significant decreases in tissue % N and % P contents of all macroalgae from the Waterfall offshore to the inner and outer Algal Halo (Table 4). The mean % C of macroalgae decreased from maximum values at the Waterfall—24.1% of dry weight—to lower values of 22.1% at the inner Algal
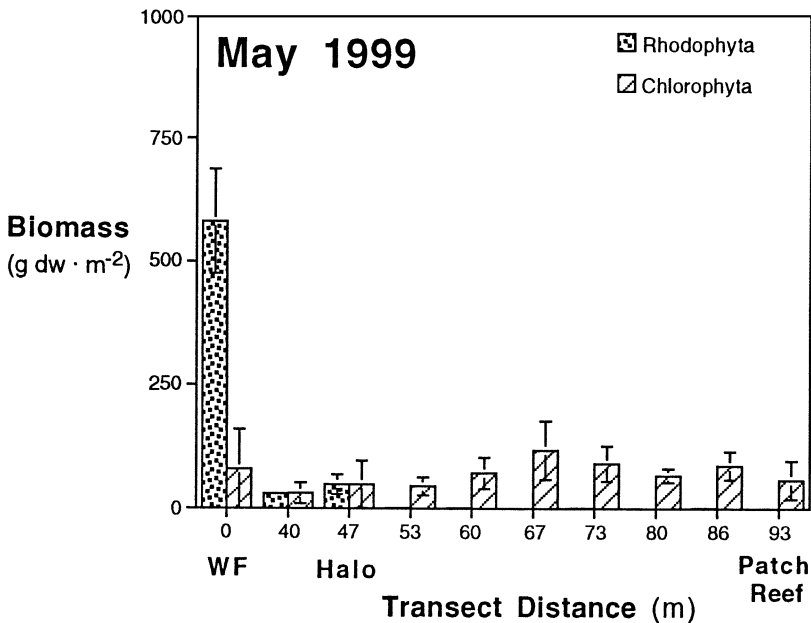

Fig. 5. Biomass (g dry wt. m^{-2}) of the dominant rhodophytes (*D. simplex*, *L. intricata*) and chlorophytes (*M. marinum*, *C. catenata*) along a transect extending from the Waterfall through the Algal Halo and terminating at the Patch Reef in May 1999. Values represent means ± 1 S.D. (*n* = 5).

Table 3
Carbon/nitrogen/phosphorus (C:N:P) contents and molar ratios in predominant macroalgae at various locations around Norman's Pond Cay

Location	Species	Date	% C	% N	% P	C:N	C:P	N:P
Salt Pond	*Hypnea musciformis*	25-May-99	23.6	1.40	0.01	19.6	6051	311
	Laurencia intricata	25-May-99	23.8	1.27	0.005	21.8	12,205	564
	Mean ± S.D.		23.7 ± 0.14	1.34 ± 0.09	0.007 ± 0.003	20.7 ± 1.55	9128 ± 4351	438 ± 179
Waterfall	*Digenea simplex*	25-May-99	30.5	2.00	0.05	17.7	1564	89
	Laurencia intricata	25-May-99	22.6	1.51	0.03	17.4	1931	112
	Cladophora catenata	25-May-99	20.1	1.04	0.03	22.5	1718	77
	Laurencia intricata	3-Feb-97	23.3	1.66	0.029	16.3	2060	127
	Mean ± S.D.		24.1 ± 4.46	1.55 ± 0.40	0.034 ± 0.01	18.5 ± 2.8	1818 ± 220	101 ± 22
Inner	*Digenea simplex*	25-May-99	20.3	0.62	0.01	38.1	5205	138
Algal Halo	*Laurencia intricata*	25-May-99	21.2	0.70	0.01	35.2	5436	156
(26–32 m)	*Microdictyon marinum*	25-May-99	24.0	1.14	0.03	24.5	2051	84
	Cladophora catenata	25-May-99	23.5	0.95	0.02	28.8	3013	106
	Laurencia intricata	3-Feb-97	21.4	0.82	0.013	30.3	4220	140
	Mean ± S.D.		22.1 ± 1.59	0.85 ± 0.21	0.017 ± 0.008	31.4 ± 5.4	3985 ± 1443	125 ± 29
Outer	*Digenea simplex*	25-May-99	21.6	0.53	0.01	47.4	5538	118
Algal Halo	*Microdictyon marinum*	25-May-99	16.1	0.46	0.03	40.7	1376	34.1
(66–80 m)	*Cladophora catenata*	25-May-99	16.8	0.44	0.01	44.4	4308	98
	Laurencia intricata	3-Feb-97	21.1	0.71	0.015	34.6	3607	105
	Mean ± S.D.		18.90 ± 2.85	0.54 ± 0.12	0.016 ± 0.009	41.8 ± 5.5	3707 ± 1747	89 ± 37
Reference Site	*Laurencia intricata*	3-Feb-97	22.7	0.79	0.015	33.4	3880	117
Rainbow Reef	*Laurencia intricata*	3-Feb-97	14.7	0.81	0.025	21.1	1508	72

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Table 4

Results of one-way ANOVA for macroalgal tissue contents: % nitrogen (N), % phosphorus (P), % carbon (C), nitrogen/phosphorus (N:P), carbon/nitrogen (C:N) and carbon/phosphorus (C:P) molar ratios

Factor	df	SS	MS	F	P
%N					
Site	3	2.4	0.8	12.7	**0.0007**
Error	11	0.7	0.1		
Fisher's multiple comparisons test					
SP vs. AH(i)					0.0408
SP vs. AH(o)					0.0037
WF vs. AH(i)					0.0016
WF vs. AH(o)					0.0001
%P					
Site	3	0.1	4.3×10^{-4}	5.4	**0.0159**
Error	11	0.1	8.0×10^{-5}		
Fisher's multiple comparisons test					
SP vs. WF					0.0049
WF vs. AH(i)					0.0117
WF vs. AH(o)					0.0139
%C					
Site	3	62.3	20.8	2.4	0.1212
Error	11	94.4	8.6		
N:P					
Site	2	3041.39	1520.70	1.67	0.2367
Error	10	9105.36	910.54		
C:N					
Site	2	1090.63	545.31	23.84	**0.0002**
Error	10	228.76	22.87		
Fisher's multiple comparisons test					
WF vs. AH(i)					<0.0024
WF vs. AH(o)					<0.0001
AH(i) vs. AH(o)					0.0089
C:P					
Site	2	11,733,242.19	5,866,621.10	3.326	0.0781
Error	10	17,637,337.50	1,763,733.75		

Significant Fisher's multiple comparisons test results ($p < 0.05$) are presented for significant ANOVA comparisons ($p < 0.05$) in bold. MC = mangrove channel, SP = salt pond, WF = Waterfall, AH = Algal Halo (i) = inner (o) = outer.

Halo and 18.9% at the outer Algal Halo—although these differences were insignificant. The mean % N content of macroalgae decreased significantly from a maximum value of 1.55% of dry weight at the Waterfall to 0.85% at the inner Algal Halo and 0.54% at the outer Algal Halo. The % N of the macroalgae from the salt pond averaged 1.34% of dry weight, a value similar to that at the Waterfall but significantly higher than that at both the

inner and outer Algal Halo. For tissue % P, mean values decreased significantly from 0.035% of dry weight at the Waterfall to 0.017% at the inner and 0.016% at the outer Algal Halo (Table 4).

The relatively large decreases in %N and %P relative to %C in macroalgae with increasing distance from the Waterfall (Table 3) resulted in significant increases in the C:N but not C:P or N:P ratios (Table 4). C:N ratios of macroalgae increased significantly from 18.5 at the Waterfall to 31.4 at the inner and 41.8 at the outer Algal Halo (Table 3). The mean C:P ratio of macroalgae increased from 1818 at the Waterfall to 3985 in the inner and 3707 at the outer Algal Halo, although this increase was marginally significant ($P = 0.078$, Table 4). Similarly, the N:P ratio did not vary significantly between the Waterfall and Algal Halo, averaging 101 at the Waterfall, 125 at the inner Algal Halo, and 89 at the outer Algal Halo. The highest mean C:P and N:P ratios of 9128 and 438, respectively, occurred in the rhodophytes *Hypnea musciformis* and *L. intricata* from the NPC salt pond (Table 3).

The APA of *L. intricata* sampled from five different sites around NPC ranged from a maximum mean value of 29.8 ± 15.9 μmol PO_4^{3}-g dry wt. h^{-1} at the Waterfall to a
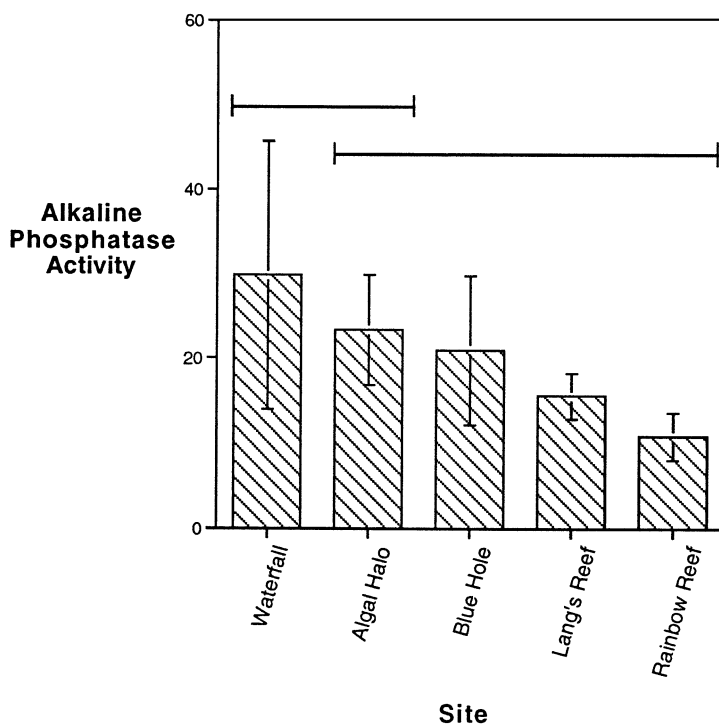

Fig. 6. Alkaline phosphatase activity (APA, μmol PO_4^{3}-g dry wt. h^{-1}) of *L. intricata* from the Waterfall, Algal Halo, Blue Hole, Lang's Reef, and Rainbow Reef. Shared bars denote a lack of significant difference at $p < 0.05$. Values represent means $\pm$ 1 S.D. ($n = 6-16$).

Table 5
Results of one-way ANOVA for alkaline phosphatase activity of macroalgal tissue among study sites

Factor	*df*	SS	MS	*F*	P
Site	4	1553.91	388.48	3.16	**0.0218**
Error	49	6025.19	122.97		
Fisher's multiple comparisons test					
WF vs. BH					0.0191
WF vs. LR					0.0097
WF vs. RR					0.0101

Significant Fisher's multiple comparisons test results ($p < 0.05$) are presented for significant ANOVA comparisons ($p < 0.05$) in bold. WF = Waterfall, BH = Blue Hole, LR = Lang's Reef, RR = Rainbow Reef.

minimum value of 10.8 ± 2.9 μmol PO_4^3-g dry wt. h^{-1} at Rainbow Reef (Fig. 6). One-way ANOVA indicated that mean APA of *L. intricata* at the Waterfall, Algal Halo, and Blue Hole was significantly greater than that of *L. intricata* at the more offshore reef sites at Lang's Reef and Rainbow Reef (Table 5).

3.3. Effects of grazing and nutrient enrichment on macroalgal biomass

Two-way ANOVA revealed insignificant effects of herbivory but highly significant effects of nutrient enrichment on the biomass of *D. simplex* in the factorial experiment

Table 6
Results of one- and two-way ANOVA for the main effects and interactions of nutrient enrichment and herbivory on biomass of *D. simplex* (A), *L. intricata* (B), and all macroalgae (C) from the manipulative experiment at the Waterfall at Norman's Pond Cay, Exumas Cays, Bahamas

Factor	DF	SS	%SS	MS	*F*	P
(A) D. simplex						
Nutrient enrichment	1	2,244,701.0	80	2,244,701.0	223.5	**< 0.0001**
Herbivory	2	49,442.1	2	24,721.1	2.5	0.0969
Interaction	2	55,582.4	2	27,791.2	2.8	0.0737
Error	44	44,1731.2	16	10,039.2		
(B) L. intricata						
Nutrient enrichment	1	9502.6	14	9502.6	12.4	**0.0010**
Herbivory	2	25,488.2	37	12,744.1	16.6	**< 0.0001**
Interaction	2	19,016.4	28	9508.2	12.4	**< 0.0001**
Error	44	33,788.7	49	767.9		
(C) All macroalgae						
Nutrient enrichment	1	1,273,151.6	33	1,273,151.6	235.6	**< 0.0001**
Herbivory	2	2172.7	< 1	1086.4	0.2	0.8183
Species	1	1,021,042.1	26	1,021,042.1	188.9	**< 0.0001**
Herbivory × Species	2	72,757.6	< 1	36,378.8	6.7	**0.0019**
Herbivory × Nutrients	2	6088.5	< 1	3044.2	0.6	0.5713
Species × Nutrients	1	981,052.0	25	981,052.0	181.5	**< 0.0001**
Herbivory × Species × Nutrients	2	68,510.4	< 1	34,255.2	6.4	**0.0027**
Error	88	47,5519.9	12	5403.6		

Significant effects ($p < 0.05$) in bold.

(Table 6A). At the "high nutrient" Waterfall, biomass of *D. simplex* ranged from ~ 400 to 600 g dry wt. m^{-2} among the experimental treatments and controls (Fig. 7). At the "low nutrient" Algal Halo, biomass of *D. simplex* was much lower, ranging from ~ 8 to 15 g dry wt. m^{-2} among the treatments and controls (Fig. 8).

In contrast to *D. simplex*, both herbivory and nutrient enrichment had significant effects on the biomass of *L. intricata* in the factorial experiment (Table 6B). At the Waterfall, biomass of *L. intricata* ranged from ~ 10 g dry wt. m^{-2} in the high grazing treatment and controls to ~ 100 g dry wt. m^{-2} in the low grazing treatment (Fig. 7). In the Algal Halo, biomass of *L. intricata* was significantly lower in the high grazing treatment compared to the low grazing treatment or controls (Fig. 8). Biomass of *L. intricata* decreased from ~ 10 g dry wt. m^{-2} in the low grazing treatment and controls to ~ 1 g dry wt. m^{-2} in the high grazing treatment over the 13-day period experimental period.

Overall, the effects of nutrient enrichment on total macroalgal biomass were highly significant compared to nonsignificant effects of herbivory (Table 6C). There were also significant effects of species, herbivory × species, species × nutrients, and herbivory × species × nutrients interaction effects (Table 6C).
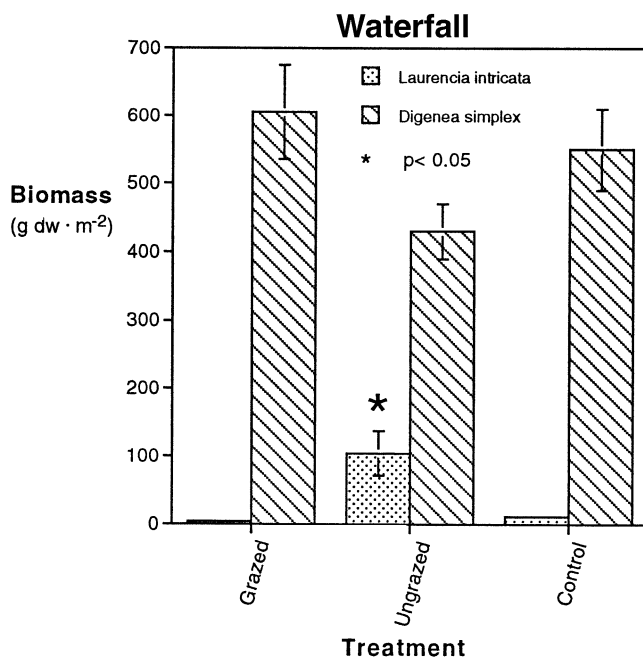

Fig. 7. Biomass (g dry wt. m^{-2}) of *L. intricata* and *D. simplex* in the grazed (*S. gigas* and *A. dactylomela* enclosed in pens), ungrazed (*S. gigas* and *A. dactylomela* excluded from pens), and control treatments at the Waterfall ("high nutrient") site. Two-way ANOVA revealed a significant ($p < 0.05$) increase in the biomass of *L. intricata* in the low grazing treatments over the 2-week experimental period; there were no significant effects of elevated grazing on *D. simplex*. Values represent means ± 1 S.D. ($n = 5$).
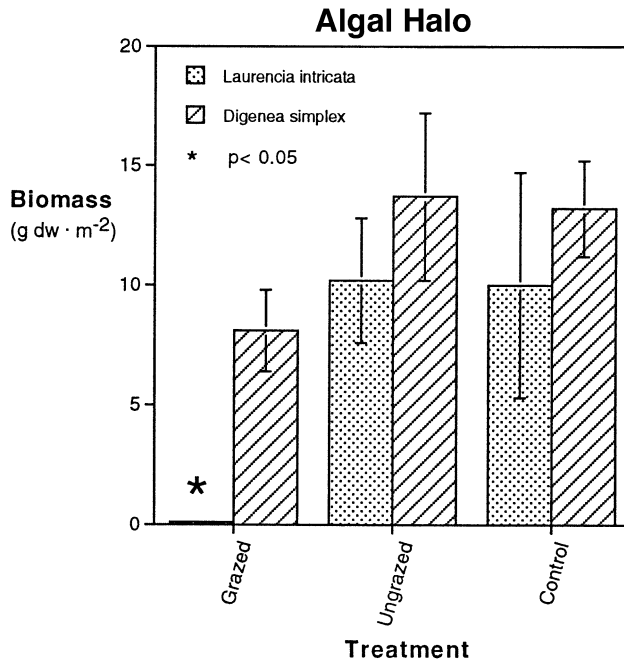
Fig. 8. Biomass (g dry wt. m^{-2}) of *L. intricata* and *D. simplex* in the grazed (*S. gigas* and *A. dactylomella* enclosed in pens), ungrazed (*S. gigas* and *A. dactylomella* excluded from pens), and control treatments at the Algal Halo ("low nutrient") site. Two-way ANOVA revealed a significant ($p < 0.05$) decrease in biomass of *L. intricata* in the high grazing treatment over the 2-week experimental period; there were no significant effects of elevated grazing on *D. simplex*. Values represent means ± 1 S.D. ($n = 5$).

The suspended line bioassay indicated that grazing intensity by juvenile parrotfishes and surgeonfishes was significant at the waterfall but not at either the inner or outer Algal Halo. In the morning bioassay (0600–1200 h), the mean number ($n = 12$) of bites on the palatable macroalga *Padina* was 25.2 at the Waterfall, 1.8 at the inner Algal Halo (40 m), and 1.0 at the outer Algal Halo (70 m). In the afternoon bioassay, the mean number of bites was 6.0 at the Waterfall, and 0 at both the inner and outer Algal Halo.

3.4. Biotic cover of coral reef communities

Biotic cover of hard corals, turf algae, macroalgae, and octocorals varied among the reef sites around Norman's Pond Cay (Fig. 9). The transect at the Algal Halo and patch reef on the west side of NPC had low coral cover (2%, *P. astreoides*, *S. siderea*) and was dominated by macroalgae (36% cover) and turf algae (26% cover, Fig. 9A). The deep reef at North Perry Reef had no significant hard coral cover and was dominated by macroalgae (76% cover, primarily *M. marinum* and *C. catenata*) with low cover of sponges (3%) and octocorals (7%, Fig. 9C). Higher coral cover occurred at Rainbow Reef and Lang's Reef (11% and 17% cover, respectively), where turf algae (30% and 25%, respectively) and
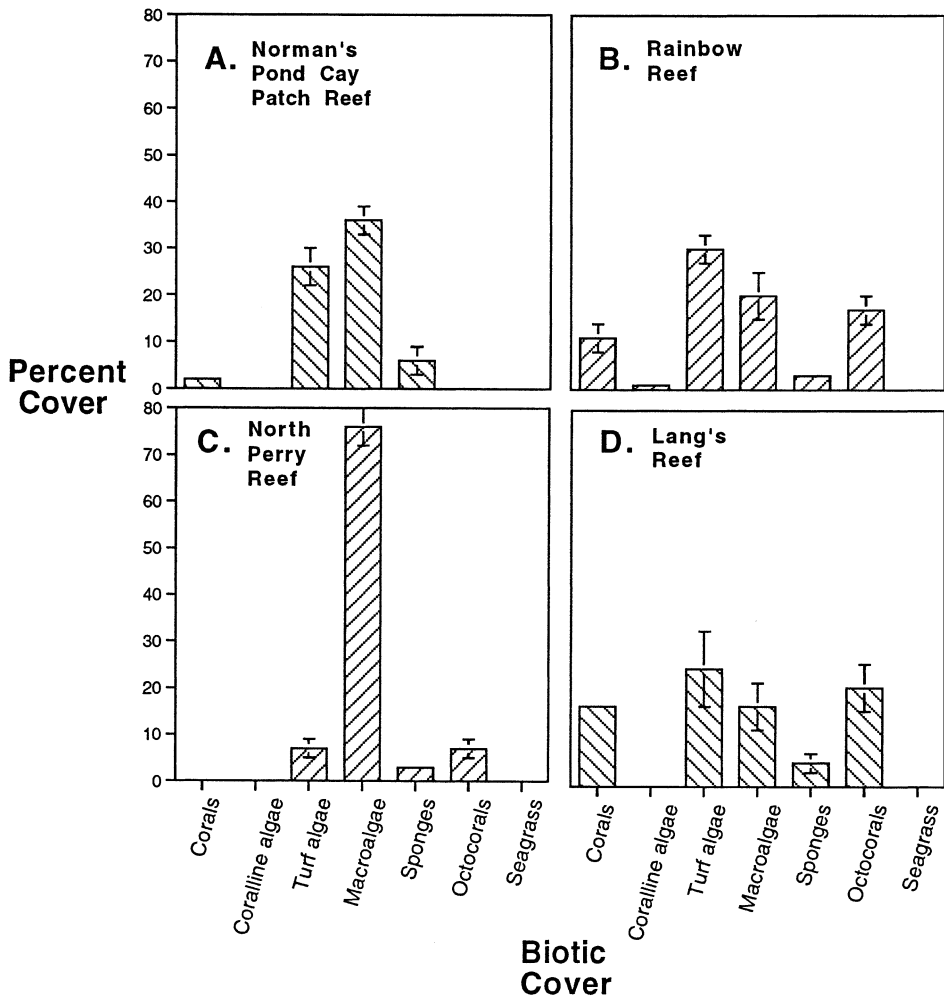
Fig. 9. Benthic biotic cover (based on digital video transects and the random point-count method) of (A) Norman Pond's Cay Patch Reef/Algal Halo study site, (B) Rainbow Reef, (C) North Perry Reef, and (D) Lang's Reef. Values represent means ± 1 S.D. ($n = 20$).

lower cover of macroalgae (20% and 17%, respectively) co-occurred with a higher cover of octocorals (17% and 21%, respectively, Fig. 9B and D).

4. Discussion

4.1. The simultaneous and interactive role of herbivory and nutrient enrichment

Many researchers studying "top-down" and "bottom-up" control of algal communities on coral reefs have viewed these forces as independent and unrelated (see Hughes et al.,

1999; Lapointe, 1999). In general, few examples exist in the marine ecological literature that provide a synthesis of how these forces interact (Menge, 1992). Our results clearly showed that the importance of herbivory as an ecological factor interacts simultaneously with nutrient enrichment. When compared as quantitative factors controlling total macro-algal biomass, nutrient enrichment rather than herbivory was the more important factor over the spatial scale (~ 100 m) of the nutrient gradient from the discharge of a small mangrove creek on Norman's Pond Cay. However, our experiment also clearly showed that the effect of herbivory was an important factor controlling macroalgal biomass—but only of specific prey items. Elevated biomass of macroalgae that are unpalatable to herbivores (Hay, 1981) can persist in high grazing, nutrient-enriched environments and this interaction appears to often define the expression of macroalgal blooms on coral reefs experiencing anthropogenic nutrient enrichment (Lapointe, 1997). In the present study, *D. simplex*, the dominant rhodophyte at the Waterfall and inner Algal Halo sites, was not significantly grazed under either high or low nutrient conditions, and achieved very high levels of biomass as a result. In contrast, grazing on the more palatable *L. intricata* was the more significant factor determining the biomass of this preferred prey item under both the high and low nutrient conditions. We describe below a variety of physiological and ecological mechanisms by which nutrient enrichment and herbivory interact to determine spatial patterns of macroalgal communities at Norman's Pond Cay.

4.2. Nutrient enrichment increases macroalgal biomass

The unusually high biomass (>2 kg dry wt. m^{-2}) of *D. simplex* at the Waterfall, compared to the Algal Halo and other coral reef communities around NPC were associated with the highest level of DIN enrichment. Water column DIN concentrations in the mangrove channel and Waterfall averaged at or above the threshold concentration of 1 μM, a level of enrichment noted to sustain macroalgal blooms in coral reef environments (Lapointe et al., 1992a,b; Lapointe, 1997, 1999; Larned and Stimson, 1996). The significantly lower water column DIN concentrations of ~ 0.5 μM (or less) in the Algal Halo and corresponding decrease in macroalgal biomass is consistent with laboratory and field studies that found DIN-limitation of growth at concentrations < 0.5 μM (Larned and Stimson, 1996; Lapointe, 1997, 1999). The decrease in DIN concentrations from the mangrove channel and Waterfall to the Algal Halo resulted not only from dilution in coastal waters with lower DIN, but also DIN uptake by the high biomass of *D. simplex* in the Waterfall. Despite limited water column nutrient sampling, significant decreases of tissue %N and increases in C:N ratios in macroalgae from the Waterfall to the Algal Halo corroborated the significance of this nutrient gradient. For example, the C:N ratio of the macroalgae increased from 18.5 at the Waterfall to values between 31 and 41 in the Algal Halo—levels indicative of N-limitation. In the rhodophyte *Gracilaria tikvahiae* grown experimentally with pulsed DIN in the Florida Keys, C:N ratios >18 resulted in strong DIN-limitation and decreased growth (Lapointe, 1985). Similarly, the high C:N ratios of the rhodophytes *D. simplex* and *L. intricata* in the Algal Halo reflect DIN-limitation and explain their lower biomass at that site. That increasing DIN-limitation was associated with decreasing tissue %C between the Waterfall and Algal Halo further suggests that this nitrogen limitation may directly

reduce growth, biomass, and ultimately persistence via decreased C-fixation in these N-depleted macroalgae.

The unusually high biomass of *D. simplex* at the DIN-rich Waterfall may also relate to various physical, chemical, and biological factors. The relatively high DIN:SRP ratio (30:1) at the Waterfall would have induced elevated APA in *D. simplex*, thereby compensating for potential SRP-limitation by mobilizing dissolved organic phosphorus pools to support algal growth (Lapointe et al., 1992a,b). Indeed, we found elevated APA values in *L. intricata* at the Waterfall that were higher than those at other sites with lower DIN concentrations. This pattern supports our previous findings of the importance of DIN enrichment to the evolution of SRP-limitation in macroalgae growing in carbonate-rich coastal waters (Lapointe et al., 1992a,b). Similarly high APA values of macroalgae on Jamaican reefs near Discovery Bay, Jamaica, were also related to high DIN concentrations that fueled high productivity and biomass (Lapointe, 1997, 1999; Lapointe et al., 1997). The shallow Waterfall habitat also experiences high levels of irradiance needed to sustain maximal photosynthesis and growth of *D. simplex*, especially in the thick mats where self-shading can attenuate light to growth-limiting levels. High seawater flow rates over the Waterfall during both ebbing and flooding tides increase turbulence that would reduce "diffusion transport limitation" around the coarse *D. simplex* thalli, increasing uptake of CO_2, DIN, and SRP to the levels needed to sustain rapid growth (Lapointe and Ryther, 1978). Lastly, selective grazing by abundant populations of *Strombus* (as well as *Aplysia* and juvenile parrotfish and surgeonfish) on *L. intricata* would minimize the shading and potential overgrowth of *D. simplex* by this relatively productive and opportunistic epiphyte.

The distinct zonation and shift in macroalgal dominance from rhodophytes at the DIN-rich Waterfall and inner Algal Halo habitats to chlorophytes at the relatively N-depleted outer Algal Halo suggests different strategies for uptake of a growth-limiting resource—DIN—in these different algal taxa. The rhodophytes are well known for their ability to assimilate DIN from turbulent water columns and their production of N-rich phycobili-protein pigments that have dual functions of light-harvesting and N-storage (Lapointe and Duke, 1984). Hence, in habitats like the Waterfall and inner Algal Halo that experience significant, but variable, DIN enrichment of the water column, growth of the rhodophytes *D. simplex* and *L. intricata* would be favored. In the Algal Halo, however, lower water column DIN concentrations and turbulence occur so that benthic DIN flux could be relatively more important to nutrient supply. The "cushion-like" morphology of the chlorophytes *M. marinum* and *C. catenata* may enable relatively efficient assimilation of benthic DIN fluxes compared to the filamentous and upright morphological forms of *D. simplex* and *L. intricata* that may be better adapted to habitats with elevated water column DIN concentrations. This hypothesis was supported by the May 1999 sampling where equally low tissue C:N ratios (17.4–22.5) occurred among the rhodophytes and chlorophytes at the Waterfall; however, in the lower DIN Algal Halo, significantly lower C:N ratios occurred in *M. marinum* and *C. catenata* (24.5–28.8) compared to *D. simplex* and *L. intricata* (35.2–38.1, Table 3). These data suggest that growth of these chlorophytes is favored in reef habitats that experience moderate water column DIN enrichment, as they can effectively augment their DIN requirements from benthic DIN fluxes, including groundwater discharges. Benthic nutrient efflux was suggested to be a key nitrogen source

to the chlorophyte ''bubble alga'' *D. cavernosa*, which remains abundant in parts of Kaneohe Bay with relatively low water column DIN concentrations following diversion of sewage from this bay (Larned and Stimson, 1996).

The ability of *M. marinum* and *C. catenata* to intercept benthic pore-water DIN fluxes may explain why they are favored in many Bahamian reef habitats—such as North Perry Reef in our study. Submarine groundwater discharge (SGD) is a recognized pathway by which DIN can be transported from land into adjacent coastal waters (Johannes, 1980), including relatively deep limestone coral reef formations over 2 km from shore in Jamaica (Lapointe and Thacker, 2002). The groundwaters in the Blue Hole had high DIN:SRP ratios of 80, which is typical of limestone groundwaters enriched by either natural or anthropogenic DIN (D'Elia et al., 1981; Lapointe et al., 1990). The karst geology of the Exumas is characterized by fractures and conduits that allow rapid horizontal and vertical groundwater transport and offshore SGD (Vacher, 1988). High DIN:SRP ratios in coastal waters and fringing reefs of the wider Caribbean are indicative of DIN-rich submarine groundwater discharges (D'Elia et al., 1981; Lapointe et al., 1990; Lapointe, 1997; Lapointe and Thacker, 2002). The high DIN:SRP ratio of 80 at North Perry Reef closely matched the value of 80 in groundwaters of the Blue Hole. Hence, DIN-enriched SGD may be an important source supporting high near-bottom DIN concentrations (0.80 μM) and blooms of *M. marinum* and *C. catenata* that now dominate (80% cover) these deep reef habitats.

4.3. Nitrogen enrichment increases herbivory

Significantly higher grazing activity of the mesogastropod *S. gigas* and mobile icthyofauna occurred at the DIN-rich Waterfall compared to the more nutrient-depleted Algal Halo. These results support the findings of McGlathery (1995) who reported a fourfold increase in grazing rate in nutrient-enriched experimental plots in a similar subtropical marine community in Bermuda. This pattern offers an alternative hypothesis to the conclusions of many reef biologists that attributed ''phase-shifts'' away from dominance by corals to macroalgae exclusively to reduced herbivory from overfishing or the die-off of the long-spined black sea urchin *Diadema antillarum* (Hughes, 1994; Hughes et al., 1999; Hughes and Connell, 1999; McCook, 1999; Miller et al., 1999; Jackson et al., 2001). Our findings of the importance of nitrogen enrichment to increased herbivory are consistent with results of recent monitoring in the Negril Marine Park, Jamaica, where sewage and agricultural runoff have resulted in DIN enrichment of shallow reefs that support higher biomass of fleshy macroalgae, higher tissue %N of macroalgae, higher densities of sea urchins, and lower cover of hard corals compared to the deep reefs where lower DIN concentrations occur (Lapointe and Thacker, 2002). Similar trophic alteration from sewage pollution was reported for coral reefs off northern Bahia, Brazil, where the high availability of wastewater nutrients resulted in increased abundance of macroalgae, sea urchins, and heterotrophic organisms, ultimately resulting in decreased coral cover (Costa et al., 2000).

Selective grazing behavior has been reported to be a critical factor structuring macro-algal communities in rocky intertidal and coral reef communities (Lubchenco and Gaines, 1981; Hay, 1991). The precept that nitrogen is a key element regulating feeding

preferences and growth rates of marine herbivores (Mattson, 1980; Sterner and Hessen, 1994) is supported by our findings of increased grazing by *S. gigas*, *A. dactylomela*, and juvenile parrotfish and surgeonfish at the DIN-enriched Waterfall. Our results clearly demonstrated that the high biomass of N-rich rhodophytes at the Waterfall provided specific prey sources for these herbivores at this site. The intensive, selective herbivory by *S. gigas* and *A. dactylomela* on *L. intricata* confirmed previous suggestions that these herbivores often prefer N-rich rhodophytes. Woon (1983) also found that adult queen conch preferred specific rhodophytes, such as *Laurencia papillosa*, *Liagora ceranoides*, and *Spyridea aculeata* when offered various combinations of macroalgae. Nitrogen-enriched diet availability appears to affect feeding selectivity in herbivorous fishes as well (Horn, 1989) and explains the increased grazing by icthyofauna at the N-enriched Waterfall in this study. Based on δ^{13}C evidence, Stoner and Waite (1991) concluded that *Laurencia* spp. and *Batophora oerstedi* were likely food sources for queen conch. Similarly, the sea hare is known to be oligophagous and responds to blooms of preferred prey items (Pennings, 1990; Rogers et al., 1995). Based upon laboratory feeding studies, Barile (2001) reported significantly greater feeding preferences and growth rate of *Aplysia californica* for the rhodophyte *Gracilaria ferox* containing high N contents (C:N = 7) compared to those with moderate (C:N = 13) or low N contents (C:N = 26). In temperate estuaries of Waquoit Bay, MA, Hauxwell et al. (1998) reported higher grazing rates by amphipods on macroalgae in sub-estuaries with the highest N-loading and %N of macroalgal tissue. Amphipod feeding preference studies in the laboratory using N-enriched macroalgae (Jimenez et al., 1996) supported the findings of Hauxwell et al. (1998).

Previous surveys in the Exumas documented unusually abundant populations of juvenile queen conch, *S. gigas*, in particular nursery areas around LSI and NPC—including the DIN-enriched Waterfall site (e.g. Stoner et al., 1992). Persistent aggregations were found south of NPC near Shark Rock, west of Children's Bay Cay, north of Pudding Point on the island of Barraterre, and several additional populations near NPC, including a population at the Waterfall (Wicklund et al., 1988; Stoner et al., 1992). Juvenile conch aggregations were all associated with tidal flow fields, a factor suggested to mediate the quality of the conch nursery areas through direct and indirect means. Observations in the Adderley Cut flow field indicated that macroalgal recruitment and productivity were greatest within the Shark Rock nursery area. Given that macroalgae are a primary carbon source for the queen conch juveniles, Stoner et al. (1992) suggested that such trophic interactions mediated by tidal circulation could have a strong influence on juvenile distributions. Alternatively, we suggest that the sites with higher flows could also produce macroalgae with higher tissue %N contents, providing a higher quality diet for *S. gigas* as we found at the Waterfall. Lapointe and Ryther (1978) experimentally showed that high seawater flow rates increased nitrogen flux (flow rate × nutrient concentration = flux) and tissue %N in the rhodophye *G. tikvahiae*, which increased its growth rate and yield. Presumably, if macroalgae in tidal flow fields have higher tissue %N contents and growth, then these localized areas could represent "high quality" habitats (Menge, 1992; Sterner and Hessen, 1994) that would attract herbivores such as juvenile queen conch.

Gastropod herbivores, such as *S. gigas* and *A. dactylomela,* may also preferentially choose sites with N-enriched macroalgae during larval settlement. Mianmanus (1988)

demonstrated in a laboratory study that *S. gigas* and *A. brasiliana* metamorphosed most significantly in response to pigments (phycobiliproteins) from the rhodophyte *Laurencia obtusa*. Members of the Aplysiidae are known to preferentially settle upon macroalgae that compose the primary diet of adults (Switzer-Dunlap and Hadfield, 1977). Indeed, feeding preference and consumption rates for rhodophytes with the highest protein and %N composition have been demonstrated in the laboratory with juvenile *A. californica* (Barile, 2001).

Alterations in primary tissue biochemistry may also affect herbivore feeding preference and palatability by altering the production of secondary metabolites, which act as chemical defenses. Both the rhodophytes *D. simplex* and *L. intricata* are known to produce halogenated compounds that can serve as anti-herbivore defense compounds (Fenical, 1975). A paradigm that addresses the role of chemical defenses on the persistence of macroalgal communities relative to "bottom-up" and "top-down" effects is the Carbon–Nutrient Balance (CNB) hypothesis. For terrestrial plants that produce nitrogen-based secondary metabolites (such as alkaloids), Bryant et al. (1983) found conditions that increased the C:N ratio increased the concentration of secondary metabolites but decreased growth rate; conversely, conditions that decreased the C:N ratio resulted in increased growth rate and decreased production of secondary metabolites. However, alterations of water column nutrients in land-based experimental trials using the rhodophyte *Portieria hornemannii* did not influence the production of monoterpene secondary metabolites (Puglisi and Paul, 1997).

4.4. Nutrient manipulation experiments in coral reef habitats

Manipulative studies of nutrient enrichment have become popular for elucidating the significance of anthropogenic nutrient enrichment in benthic ecology, particularly where nutrients have historically been growth-limiting (Worm et al., 2000). Coral reef environments provide an ideal system to experimentally compare the effects of water column nutrient enrichment vs. herbivory on the relative abundance of benthic biota (i.e. "top-down vs. bottom-up control") because of the typically low nutrient concentrations, tight biogeochemical cycling of nutrient pools, and well-described herbivorous feeding guilds. Artificial enrichment experiments suffer from the disadvantage of small scale and imprecision of fertilization effect (Worm et al., 2000). We suggest that artificial enrichment studies in coral reef environments can additionally suffer from an attempt to "enrich" ecosystems that have already exceeded known physiological thresholds for nutrient limitation of growth in test organisms (Lapointe et al., 1992a,b; Lapointe, 1997, 1999). In particular, recent experimental fertilization studies in the Florida Keys (Miller et al., 1999) and Guam (Thacker et al., 2001) were both performed in relatively DIN-rich (~ 1 μM) study sites that also had low coral cover and excessive macroalgal blooms. These studies reported marginal algal growth responses to nutrient enrichment and concluded that alterations in herbivory better explained the elevated macroalgal biomass.

The use of natural nutrient gradients, as presented in this study, appears to subvert the limitations of small spatial scale, imprecision of nutrient enrichment, and the establishment of definable nutrient gradients in the water column to compare with the efficacy of herbivores to control macroalgal biomass. Further, the inclusion of supporting data on

tissue nutrient biochemistry and physiology provides assurance of the establishment of biologically relevant nutrient gradients that are necessary to evaluate the significance of "top-down" vs. "bottom-up" forces. For example, the spatial pattern of resource limitation was particularly evident in the mean C:N ratios of macroalgae that "integrated" the more variable water column nutrient concentrations over time. These ratios increased from relatively nutrient-replete C:N ratios for macroalgae at the Waterfall (C:N = 18) to values indicative of N-limitation in the inner (31) and especially the outer (42) Algal Halo. In light of the growing recognition of the consequences of increasing nutrient pollution on ecosystems globally (Vitousek et al., 1997), especially coral reefs (NRC, 2000), we recommend similar multi-faceted approaches that include characterization of water column nutrient concentrations, algal tissue analysis for C:N:P ratios, and tests of algal physiological responses (growth rate, biomass, APA) to other researchers attempting to define ecological effects of land-based nutrient enrichment over space and time.

Acknowledgements

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