Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida

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Abstract

During the past two decades coral reefs in the greater Caribbean area have been altered by phase shifts away from corals and toward macroalgae or algal turfs. This study tested the hypothesis that because the phase shift on reefs in Jamaica and southeast Florida involved frondose macroalgae, bottom-up control via nutrient enrichment must be a causal factor. The approach was multifaceted and included measurement of near-bottom nutrient concentrations, salinity, nutrient enrichment bioassays, alkaline phosphatase assays, tissue $C:N:P$ ratios, and tissue ^{15}N: ^{14}N ($\delta^{15}N$) ratios. In both locations, concentrations of dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) exceeded nutrient thresholds ($\sim$1.0 μM DIN, 0.1 μM SRP) noted to sustain macroalgal blooms on Caribbean coral reefs. High seawater $DIN:SRP$ ratios, alkaline phosphatase activity, and tissue $C:P$ and $N:P$ ratios of macroalgae on the carbonate-rich Jamaican reef suggested SRP limitation of productivity compared to lower values of these variables on siliciclastic reefs in Florida that suggested DIN limitation. This pattern was corroborated experimentally when SRP enrichment increased P_{max} (photosynthetic capacity at light saturation) of the chlorophyte *Chaetomorpha linum* in Jamaica compared to DIN enrichment that increased α (the photosynthetic efficiency under low irradiance) of the deeper growing chlorophyte *Codium isthmocladum* in southeast Florida. Increased DIN concentrations were associated with reduced salinity on both reefs, indicating submarine groundwater discharge was a significant source of DIN. Elevated $\delta^{15}N$ values of *C. isthmocladum* tissue further pointed to wastewater DIN as a source of nitrogen contributing to the blooms in southeast Florida.

A basic objective in marine ecology is to understand the mechanisms by which various natural and anthropogenic factors maintain and alter structure in biotic communities. Coral reefs are the most diverse and complex of all marine ecosystems yet flourish in shallow tropical waters with very low and often undetectable concentrations of dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP, *see* Lewis 1977). Coral reefs are noted for their fragile ecological balance, high rates of gross productivity, and unique ability to accrete massive limestone formations over geological time (Goreau et al. 1979). Ecologists studying the controls of aquatic food webs have used the concepts "bottom up" and "top down" to describe how resource availability or the actions of consumers regulate the structure of food webs (Carpenter et al. 1985). A complex interaction of bottom-up and top-down controls are similarly important on coral reefs (Littler and Littler 1984), where standing crops of benthic macroalgae are usually inconspicuous on undisturbed coral reefs due to the combined effects of low nutrient

availability and grazing by herbivorous fish and invertebrates (i.e. relative-dominance model, Fig. 1).

The very low or undetectable concentrations of dissolved inorganic nutrients in the water column of undisturbed coral reefs results in nutrient-limited productivity of epilithic algae and sets the upper limit to algal standing crops. The term "nutrient-limited productivity" is defined here as a condition where an increase in the concentration (or flux) of a nutrient increases a metabolic response, such as net photosynthesis or other physiological processes related to growth (Droop 1983). The epilithic algal community on coral reefs includes small microfilamentous forms referred to as "turfs," larger frondose macroalgae including both fleshy and calcareous forms, and coralline algae that form crusts on exposed reef substrata (Littler and Littler 1984). The productivity or standing crop of algal turfs (Hatcher and Larkum 1983; Williams and Carpenter 1988), frondose macroalgae (Lapointe 1987; Lapointe et al. 1987), and coralline algae (Littler 1973) increase with increased nutrient availability on coral reefs, confirming their nutrient-limited status. This nutrient-limited status is most pronounced in the larger, rapidly growing macroalgae, and it greatly restricts their ability to favorably compete with corals and turf algae in low nutrient environments (Atkinson 1988; Littler and Littler 1984; Fig. 1).

Accordingly, increases in water-column nutrient concentrations associated with exponentially expanding human populations and coastal eutrophication can lead to increased productivity and biomass of frondose macroalgae. The first well-documented example of a coral reef shifting to a macroalgal-dominated reef occurred almost 25 yr ago in Kaneohe Bay, Hawaii, where nutrient enrichment from domestic sewage led to overgrowth of corals by the green bubble alga *Dictyosphaeria cavernosa* (Banner 1974). Since then, case studies from Reunion Island (Cuet et al. 1988; Naim

GRAZING ACTIVITY

HIGH   LOW

NUTRIENT AVAILABILITY

LOW

CORALS → TURF ALGAE
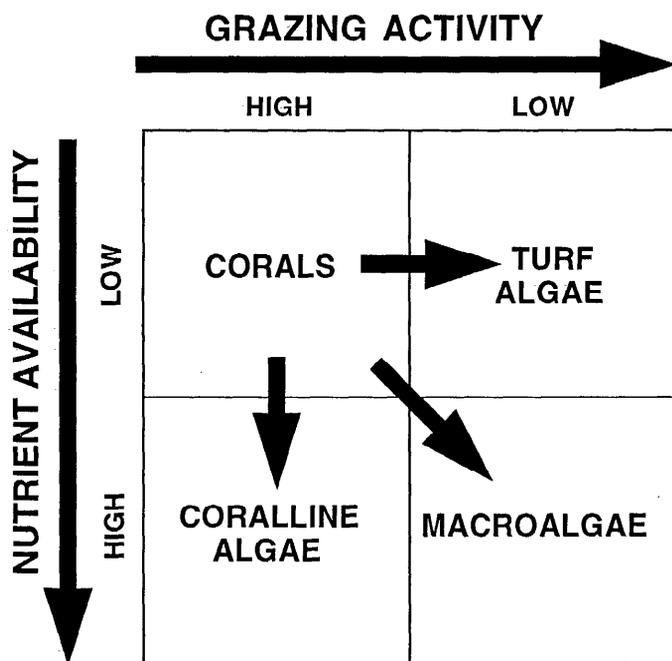
HIGH

CORALLINE ALGAE   MACROALGAE

Fig. 1. Diagram illustrating the relative dominance of major space-occupying primary producers on tropical and subtropical reefs. The relative dominance is predicted to be a function of bottom-up control by nutrient availability and top-down control by herbivory. Human activities inevitably reduce grazing animals and increase nutrient availability, which shifts reefs from coral to macroalgal dominance.

1993), Bermuda (Lapointe and O'Connell 1989), Barbados (Tomascik and Sander 1985, 1987), Martinique (Littler et al. 1993), Venezuela (Weiss and Goddard 1977), the Florida Keys (Lapointe et al. 1994), Belize (Lapointe et al. 1993), the Seychelles (Littler et al. 1991), the Red Sea (Mergener 1981), and the Great Barrier Reef (Bell 1992) have affirmed linkages between nutrient enrichment and increased algal dominance in coral reef regions. The most recent evidence of nutrient regulation of macroalgal blooms on coral reefs is from the Gulf of Eilat where atmospheric cooling following the eruption of Mt. Pinatubo led to vertical mixing, nutrient enrichment, and large-scale macroalgal overgrowth that directly caused coral death (Genin et al. 1995).

Despite research demonstrating bottom-up control of macroalgal standing crops on coral reefs that extends back more than 20 yr, single-factor top-down interpretations concerning the cause of macroalgal blooms on coral reefs are still found in the literature. For example, Hughes (1994) concluded that dramatic phase shifts on Jamaican coral reefs from >50% coral cover in the early 1970s to the current <5% resulted from a "spectacular algal bloom" due to reduced grazing from overfishing coupled with die-offs of the sea urchin *Diadema antillarum*; the possible role of nutrient enrichment as a factor enhancing macroalgal productivity and standing crop was dismissed without supportive data. Although herbivory is a significant factor in the benthic dynamics of coral reefs, its effects occur on limited temporal and spatial scales (Hatcher and Larkum 1983). Thus, studies addressing macroalgal blooms on coral reefs need to examine the potential

for bottom-up control via nutrient enrichment, especially considering that eutrophication associated with exponentially expanding human populations is a major mechanism altering coastal ecosystems world-wide (GESAMP 1990; Natl. Acal. Sci. 1994; Duarte 1995; Nixon 1995).

As a test of the alternative nutrient enrichment hypothesis to explain the increasing macroalgal blooms on Caribbean reefs, my study critically assessed relationships between water-column nutrient concentrations and the type and degree of nutrient-limited productivity of macroalgae on two different coral reef systems recently affected by macroalgal blooms. One was a carbonate-rich fringing reef system located on the north coast of Jamaica at Discovery Bay—a site monitored by Hughes (1994) and also one of the most intensively studied coral reefs in the world (Goreau 1992). The other, a siliciclastic reef system located offshore Palm Beach County, Florida, represents the northern limit of coral growth in the southeastern U.S. Studies in both locations involved a multifaceted approach that included determination of water-column nutrient concentrations, limiting-nutrient bioassays, alkaline phosphatase activity (APA) as a measure of P limitation of productivity, and tissue $C:N:P$ ratios to assess the type and degree of nutrient-limited productivity of predominant reef macroalgae. In Florida, natural abundances of stable isotopic $^{15}N:^{14}N$ ratios in macroalgal tissue were also used to discriminate between natural and anthropogenic nitrogen sources that could potentially enhance the macroalgal blooms.

Methods

Study areas—The research at Discovery Bay began in July 1987—a period within the transition of these reefs from coral to macroalgal dominance (Goreau 1992). Discovery Bay is ~1.5 km² in area and protected from the open ocean by a typical Jamaican fringing reef system (Goreau 1959) that is exposed at extreme low tides (Fig. 2). The adjacent upland drainage basin is porous limestone and contains numerous fissures and fractures that provide for significant phreatic inputs of groundwater-borne NO_3 (D'Elia et al. 1981). The water and macroalgal sampling was conducted along a transect that extended from localized groundwater discharges from springs (SP) near shore, through semi-enclosed grottos (GR), across the back reef (BR) in 1–2 m of water, and beyond the reef crest to the fore reef (FR, Fig. 2). Surveys along this transect in July 1987, November 1992, and June 1996 indicated that the chlorophyte *Chaetomorpha linum*, a eutrophic indicator species (Lapointe et al. 1993), expanded from the spring and grotto habitats in 1987 offshore to the fore reef in the 1992 and 1996 surveys. During the same period, the pheophyte *Lobophora variegata* became unusually abundant on the fore reef as coral cover decreased; by 1992, the large perennial pheophyte *Sargassum polyceratium* and the chlorophyte *Cladophoropsis* sp. also expanded their distribution from the back reef to the fore reef, which they now share with *Sargassum hystrix*, *Dictyota* spp., and *L. variegata*. Currently, a diverse multilayered macroalgal community dominates the fore reef that was dominated by corals prior to 1980.
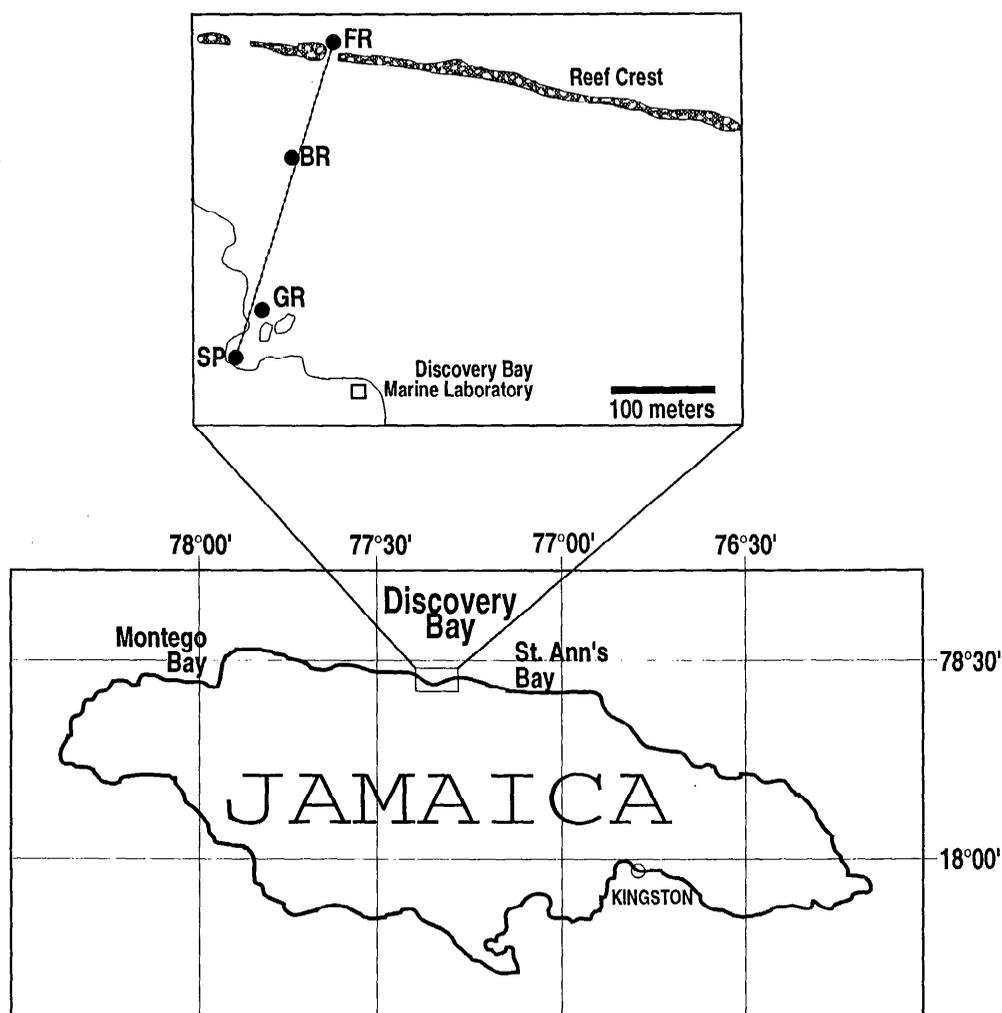
Fig. 2.   Map showing sampling sites at springs (SP), grotto (GR), back reef (BR), and fore reef (FR) at Discovery Bay.

Studies on the Floridian reefs were performed during summer 1994 and 1995 at four sites between West Palm Beach and Hobe Sound (Princess Anne, North Colonel's Ledge, Jupiter Ledge and Hobe Sound), ~2–3 km offshore (Fig. 3). Between 1989 and 1992, the coenocytic chlorophyte *Codium isthmocladum* formed spectacular blooms on reefs offshore southern Palm Beach County during the summer wet season. This alga previously occurred in deep reef communities (24–58 m) at low standing crops along this coastline (Hanisak and Blair 1988), but these recent blooms were in relatively shallow depths (24–33 m) where the macroalgae developed to >100% cover over large areas and accumulated in unattached drift mats up to 2 m thick. The *C. isthmocladum* blooms represent the most dramatic change on these reefs in recorded history. In the impacted reef habitats, *C. isthmocladum* smothered sponges, hard corals, octocorals, and other reef organisms; the blooms also caused hypoxia-anoxia on the reef surface (evidenced by the presence of H_2S within the mats of *C. isthmocladum*) along with a dramatic decline of reef fish populations in the impacted areas. The *C. isthmocladum* blooms in southern Palm Beach County were

physically disturbed during late August 1992 by Hurricane Andrew; as a result, growth of *C. isthmocladum* between 1993 and 1995 was restricted primarily to northern Palm Beach County where my study took place.

Water sampling and analysis—Water samples were collected by SCUBA divers from the surface and bottom of the water column (0.5–3-m depth in Jamaica; 0.5–28-m depth in Florida) into clean, high-density polyethylene Nalgene bottles. The water samples were immediately passed through combusted Gelman 0.45-μm GF/F filters and placed on ice in the dark (or frozen) until analysis. DIN (NH_4^+ + NO_3^- + NO_2^-) concentrations were determined with a Technicon AutoAnalyzer II and SRP concentrations were measured with a Bausch and Lomb Spectronic 88 fitted with a 10-cm cell for increased sensitivity. Salinity of the Jamaican samples was measured with a Bausch and Lomb hand-held refractometer and those of the Florida samples with a Hydrolab Data Sonde 3.

Nutrient-enrichment assays—In both locations, the nutrient enrichment assays involved critical analysis of macroal-
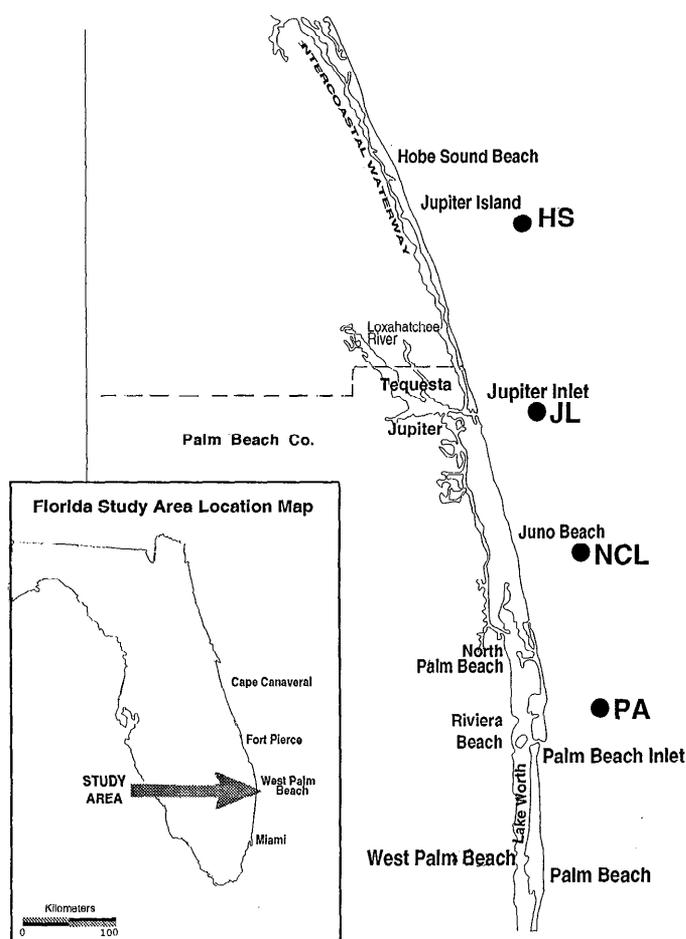
Fig. 3. Map showing sampling sites at Princess Anne (PA), North Colonel's Ledge (NCL), Jupiter Ledge (JL), and Hobe Sound (HS) along offshore reefs.

gal P vs. I curves measured by changes in dissolved oxygen with an Orbisphere (model 2610) oxygen measurement system. In Jamaica, the P vs. I experiments were conducted with the chlorophytes *C. linum* and *Halimeda opuntia* and the pheophytes *S. polyceratium* and *L. variegata* collected from shallow (1 m) waters of the grotto and back reef. In Florida, *C. isthmocladum* from 28-m depth on North Colonel's Ledge was used. Following collection, small (<1 g wet wt) apical portions were excised and exposed to overnight (12 h) nutrient pulses in polycarbonate aquaria. During the overnight pulses, the macroalgae were gently aerated to provide mixing to facilitate nutrient uptake. The factorial enrichment treatments included NO_3^- (160 μM), SRP (16.0 μM), NO_3^- and SRP, and an unenriched control. These NO_3^- concentrations are high compared to ambient concentrations on most coral reefs but are only 2× the NO_3 concentrations in undiluted spring water at Discovery Bay (D'Elia et al. 1981). The Florida experiments utilized lower nutrient concentrations and NH_4^+ rather than NO_3^- as the DIN source, because preliminary sampling indicated higher concentrations of NH_4^+ compared to NO_3 and generally lower DIN concentrations on these reefs; accordingly, treatments in-

cluded NH_4^+ (20 μM), SRP (2.0 μM), NH_4^+ and SRP, and an unenriched control.

Following the overnight pulses in both Jamaica and Florida, thalli were held in clean polycarbonate aquaria that received ambient flowing seawater prior to incubation in clean, 1-liter Wheaton widemouth bottles that received mixing and cooling via seawater-driven magnetic stirrers. The P vs. I assays were performed under full natural irradiance (I_0) on clear, sunny days between 1000 and 1400 hours. Irradiance was measured continuously throughout the incubations with a 4π spherical quantum sensor submerged in the flowing seawater bath and coupled to a LiCor LI-1000 data logger. Photosynthesis (at seven irradiance levels) was determined in triplicate by methods described by Lapointe and O'Connell (1989). Nutrient pulsing assays with tropical macroalgae (Lapointe 1987; McGlathery et al. 1992) have demonstrated that short-term (1 d) enrichment effects on photosynthesis accurately represent longer term (1–3 weeks) effects on growth rate. Temperature ranged from 27 to 29°C during these studies.

Photosynthetic capacity (net P_{max}) was estimated for the various macroalgae from the six highest photosynthetic rates in a particular P vs. I curve, which occurred between 0.60 I_0 and I_0 for *C. linum* and 0.10 I_0 and 0.20 I_0 for *C. isthmocladum*. The initial slope of the P vs. I curve, α, was estimated by least-squares linear regression of the linear portion of the P vs. I curve at low irradiance (i.e. <100 μmol photons m^{-2} s^{-1}).

Alkaline phosphatase activity and tissue $C:N:P$—Alkaline phosphatase is an exo-enzyme produced by P-deficient macroalgae that allows them to utilize dissolved organic phosphorus (DOP) pools as a source of SRP for growth; accordingly, it is useful as a means to gauge the degree of P-limited productivity of coral reef macroalgae (Lapointe and O'Connell 1989). APA was measured in a variety of macroalgae from Discovery Bay and *C. isthmocladum* from Florida to assess between-reef and between-species variability in P-limited productivity. APA of *C. isthmocladum* from Florida and *C. linum* and *S. polyceratium* from Discovery Bay was also measured following the overnight nutrient pulses (described above) to assess the metabolic responses of these macroalgae to N and P enrichment, which could have different effects on the status of P-limited productivity. APA was measured by the spectrophotometric method of Lapointe and O'Connell (1989).

Tissue analysis for $C:N:P$ ratios was also used to assess the type and degree of N- vs. P-limited productivity. Composite samples (~6–10 apical thalli each) of fresh macroalgae were cleaned of macroscopic epizoa and epiphytes, rinsed briefly (3 s) in deionized water, oven-dried at 60°C for 48 h, powdered, and frozen until tissue analysis in triplicate. Total C and N were determined on a Carlo-Erba CHN analyzer, and total P was determined by persulfate digestion followed by analysis for SRP (Menzel and Corwin 1965).

Natural abundance of stable nitrogen isotopes—Natural abundances of stable nitrogen isotope ratios ($^{15}N:^{14}N$ = $\delta^{15}N$, ‰) have been used to discriminate between natural and wastewater nitrogen sources in groundwaters (Kreitler

Table 1. Salinity (S, ‰), concentrations (μM) of dissolved ammonium (NH_4^+), nitrate plus nitrite ($NO_3^- + NO_2^-$), dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), and the DIN:SRP ratio of the water column. Values for nutrient concentrations represent means ± 1 SD (Jamaica, $n = 2$; Florida, $n = 4$).

Location	Site	Depth, m	S	NH_4^+	$NO_3^- + NO_2^-$	DIN	SRP	DIN:SRP
Jamaica								
Discovery Bay	Spring	0.1	28.0	0.22±0.07	27.86±5.80	28.10	0.33±0.06	85.2
	Spring	1.0	30.0	0.19±0.06	13.50±3.70	13.70	0.20±0.05	68.5
	Grotto	0.5	29.0	0.26±0.10	18.20±3.00	18.50	0.18±0.06	103
	Grotto	1.0	32.0	0.40±0.09	7.79±1.32	8.20	0.11±0.04	74.5
	Back reef	0.5	33.0	0.30±0.08	9.84±2.30	10.10	0.19±0.05	53.4
	Back reef	2.0	36.0	0.47±0.12	6.52±1.80	8.99	0.10±0.03	69.9
	Fore reef	0.5	35.0	0.37±0.23	4.25±1.20	4.62	0.14±0.01	33.0
	Fore reef	2.0	36.0	0.49±0.33	4.96±1.58	5.45	0.12±0.03	45.4
Florida								
Princess Anne	Surface	0.5	34.6	0.20±0.01	0.62±0.29	0.80	0.14±0.01	3.1
	Bottom	28.0	34.6	0.63±0.44	0.38±0.05	1.00	0.32±0.11	5.9
North Colonel's Ledge	Surface	0.5	34.6	0.76±0.47	0.83±0.25	1.60	0.20±0.04	8.0
	Bottom	29.0	34.4	1.73±0.97	1.22±0.01	2.94	0.21±0.04	14.3
Jupiter Ledge	Surface	0.5	34.7	1.05±0.70	0.50±0.07	1.55	0.13±0.01	11.9
	Bottom	26.0	34.4	2.42±1.23	1.02±0.27	3.44	0.24±0.03	14.1
Hobe Sound	Surface	0.5	33.4	0.44±0.26	0.37±0.21	0.81	0.15±0.04	5.2
	Bottom	25.0	33.8	0.41±0.26	0.35±0.21	0.75	0.15±0.04	5.0

1979; Kreitler and Browning 1983) and estuarine primary producers (McClelland et al. in press). Natural abundances of $\delta^{15}N$ were measured in dried *C. isthmocladum* tissue from Jupiter Ledge monthly between May and September 1995, the period from the beginning of the spring growth of *C. isthmocladum* (May) to the peak biomass in late summer (August–September). This period also marks the seasonal transition from the dry season (February–May) to the wet season (June–October); because rainfall is an important forcing mechanism causing nutrient discharges from watersheds to coastal waters (Lapointe et al. 1990), rainfall data were obtained from the Loxahatchee River Environmental Control District in Jupiter, Florida. Analyses for total N and ^{15}N atom% were performed by Isotope Analytical Services, Inc. (Los Alamos, New Mexico). The samples were processed through a Carlo-Erba N/A 1500 elemental analyzer using Dumas combustion. The purified nitrogen gas was then measured by a VG Isomass mass spectrometer.

Statistical analysis—Least-squares linear regression was used to determine significance among relationships between water-column nutrient concentrations and salinity. The main effects and interactions of the nutrient enrichment assays on the P vs. I parameters (P_{max} and α) and APA were analyzed by two-way ANOVA. Significance reported below indicates that the probability of the null hypothesis is <0.05.

Results

Nutrient-salinity relationships—Groundwater inputs enriched the water column of the fringing reef at Discovery Bay as evidenced by the increased nutrient concentrations in areas directly receiving groundwater discharges. This was most pronounced for NO_3^-, indicated by the buoyant salinity

and NO_3^- stratification and a significant negative correlation between salinity and NO_3^- ($r = -0.96$; $P < 0.0001$) along the entire study transect. Concentrations (~ 28 μM) were highest in the lowest salinity (28‰) surface waters near the springs along shore (Table 1). NO_3^- concentrations >4 μM occurred at oceanic salinities (35–36‰) on the shallow fore reef, indicating offshore dispersion and dilution but significant N enrichment of the fore reef from groundwater discharges. There was a similar negative correlation ($r = -0.93$; $P = 0.0008$) for SRP, with concentrations ranging from ~ 0.33 μM near the springs to 0.12 μM on the fore reef (Table 1). NH_4^+ occurred at much lower concentrations than NO_3 and was positively correlated ($r = 0.76$; $P = 0.03$) with salinity (Table 1). The high concentrations of NO_3^- relative to SRP, especially near the springs, resulted in a significant negative correlation ($r = -0.96$; $P = 0.0001$) of the DIN:SRP ratio with salinity along the transect (Table 1).

There was also evidence of groundwater nutrient inputs on reefs in southeastern Florida. Water-column concentrations of NO_3, NH_4^+, and SRP correlated negatively with salinity at two (North Colonel's Ledge and Jupiter Ledge) of the four Florida sites. In contrast to Discovery Bay, higher concentrations of NH_4^+, NO_3^-, and SRP were present in the near-bottom waters compared to lower concentrations in surface waters at North Colonel's Ledge and Jupiter Ledge but not at Hobe Sound or Princess Anne (Table 1). Because of lower (~ 0.3‰) salinity in near-bottom waters compared to surface waters at North Colonel's Ledge and Jupiter Ledge, significant negative correlations were found between salinity and NH_4^+ ($r = -0.71$; $P = 0.017$), NO_3^- ($r = -0.72$; $P = 0.016$), and SRP ($r = -0.73$; $P = 0.015$). The DIN:SRP ratios ranged from 3.1 to 14.3 at the four study sites (Table 1).
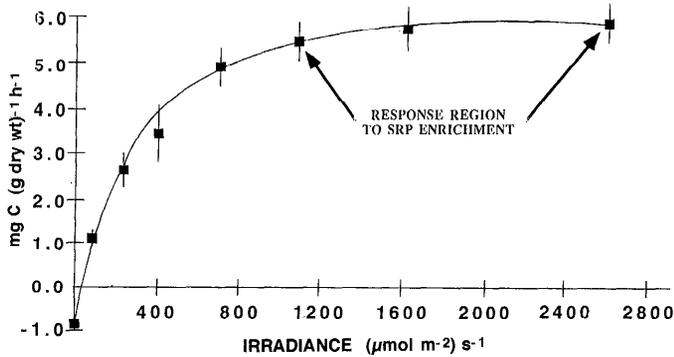
Fig. 4. Photosynthesis vs. irradiance curve of the chlorophyte *Chaetomorpha linum* collected from shallow (1 m) nearshore waters in the grotto at Discovery Bay. Values represent means ±1 SD (n = 3). Note region of significant response at high irradiance (P_{max}) to SRP enrichment.

Effects of nutrient enrichment on productivity and APA—Enrichment with SRP significantly increased the productivity of the fast-growing eutrophic indicator species *C. linum.* The *P* vs. *I* curve for *C. linum* from Discovery Bay indicated that photosynthesis was light saturated at irradiances >1,000 μmol photons m^{-2} s^{-1} (Fig. 4). Two-way ANOVA revealed significant main effects of the factorial SRP enrichment treatments on P_{max} (F = 144; P < 0.0001) compared to insignificant effects of NO_3^- and the NO_3^- + SRP interaction. The mean P_{max} values for the factorial enrichment treatments with *C. linum* ranged from a low of 3.82 mg C (g dry wt)$^{-1}$ h^{-1} for the control to 5.94 for SRP, 4.64 for NO_3^-, and 6.74 for NO_3^- + SRP. Parallel assays with *S. polyceratium, L. variegata,* and *H. opuntia* all showed high rates of productivity and appeared to be nonnutrient limited owing to insignificant effects of NO_3^- or SRP enrichment on P_{max} of these species.

The nutrient enrichment assays with *C. isthmocladum* in southeastern Florida suggested significant, but weak, N limitation of productivity. The *P* vs. *I* curve of the deeper growing *C. isthmocladum* from North Colonel's Ledge indicated that photosynthesis was light saturated at relatively low irradiances of ~50–100 μmol photons m^{-2} s^{-1} and became photoinhibited at higher irradiance (Fig. 5). Two-way ANOVA of the enrichment assay results showed significant (F = 7.12; P = 0.028) main effects of NH_4^+ on α, the initial slope of the *P* vs. *I* curve, compared with insignificant effects of SRP and the NH_4^+ + SRP enrichment interaction. The mean α values for the enriched treatments ranged from a low of 0.026 mg C (g dry wt)$^{-1}$ h^{-1} μmol m^{-2} s^{-1} for the control (unenriched) to 0.032 for SRP, 0.038 for NH_4^+, and 0.053 for the NH_4^+ + SRP interaction.

The mean APA values of macroalgae from Discovery Bay were considerably higher than the low values found for the Floridian *C. isthmocladum,* indicating a greater degree of P limitation of productivity in Jamaican macroalgae (Fig. 6). For the Discovery Bay enrichment assays, two-way ANOVA revealed that SRP enrichment significantly decreased the mean APA of *C. linum* (F = 9.7; P = 0.05) and *S. polyceratium* (F = 23.7; P = 0.008), confirming some degree of P limitation in these species. In contrast, NO_3^- enrichment
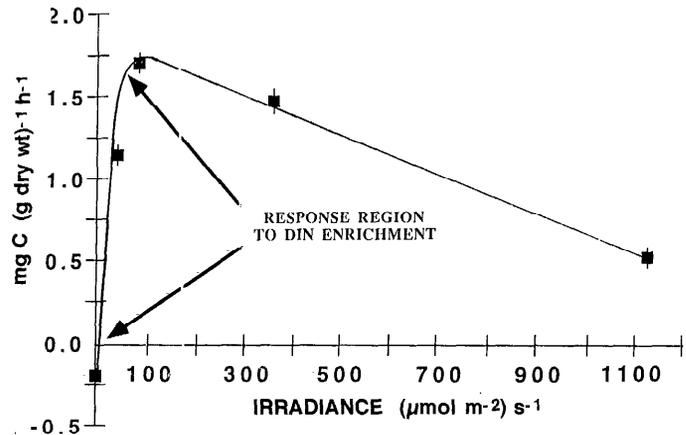

Fig. 5. Photosynthesis vs. irradiance curve of *Codium isthmocladum* from a deep reef (28 m) population on North Colonel's Ledge, Florida. Values represent means ±1 SD (n = 3). Note region of significant response at low irradiance (α) to DIN enrichment and photoinhibition at high irradiance.

increased mean APA values, although the increases were not significant (P = 0.07). The mean APA of the factorial enrichment treatments for *C. linum* ranged from 90.9 μM SRP released (g dry wt)$^{-1}$ h^{-1} for the control to 56.6 for SRP, 124.7 for NO_3^-, and 12.2 for NO_3^- + SRP. For *S. polyceratium,* mean APA of the enrichment treatments ranged from 73.4 μM SRP released (g dry wt)$^{-1}$ h^{-1} for the control to 30.1 for SRP, 81.1 for NO_3^-, and 37.9 for the NO_3^- + SRP enrichment.

Tissue C:N:P and $\delta^{15}N$—Tissue levels (% dry wt) of C, N, P, and C:N:P molar ratios of Discovery Bay macroalgae and *C. isthmocladum* provided further evidence of P limitation in Jamaica compared to N limitation of macroalgal productivity in southeast Florida. Mean tissue levels of %N and %P were similar between Jamaican macroalgae and *C. isthmocladum,* compared to significantly higher tissue %C in the shallower growing Jamaican macroalgae (16.7 vs. 10.9%, Table 2). These low %C values in *C. isthmocladum* resulted in low C:N ratios compared to the Jamaican macroalgae, suggesting a higher N requirement for growth of *C. isthmocladum* under low irradiance. The C:P and N:P ratios were higher in Jamaican macroalgae compared to *C. isthmocladum* in Florida (Table 2), supporting the concept of greater P limitation of productivity in the Jamaican macroalgae.

Tissue analysis of *C. isthmocladum* sampled monthly through the summer bloom at Jupiter Ledge showed significant increases in tissue $\delta^{15}N$ values with the onset of the wet season. In May, $\delta^{15}N$ values averaged 7.11±0.15‰ and increased to 11.4±0.26‰ by late June; values remained >10.50‰ throughout the peak bloom period in July and August and then decreased to 2.53±0.32‰ in September as rainfall decreased and the bloom waned. Over this 5-month period, $\delta^{15}N$ values correlated significantly (r = 0.81; P = 0.001) with rainfall (Fig. 7).

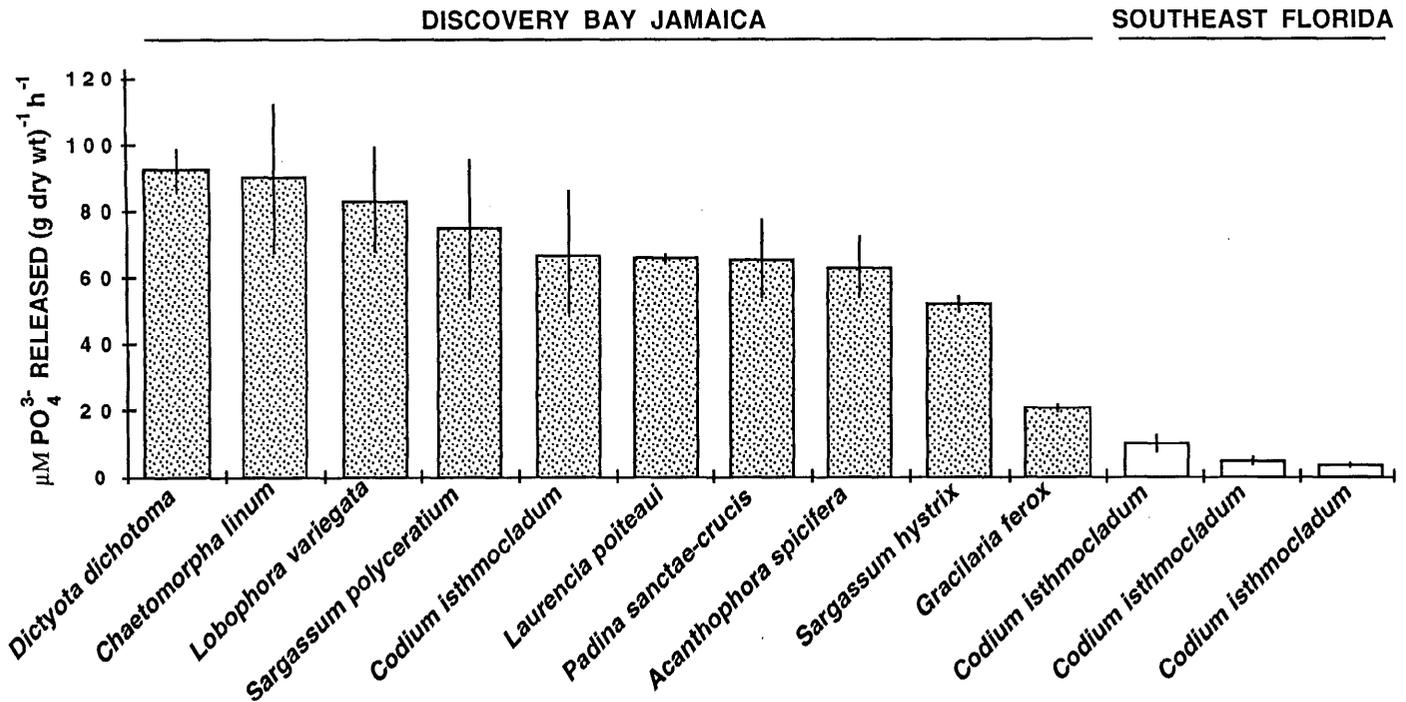**DISCOVERY BAY JAMAICA** **SOUTHEAST FLORIDA**

Fig. 6. Alkaline phosphatase activity of predominant macroalgae from Discovery Bay and *Codium isthmocladum* from three Florida reefs (North Colonel's Ledge, Jupiter Ledge, Princess Anne, left to right). Values represent means ±1 SD (Jamaica, $n = 4$; Florida, $n = 8$).

Discussion

Results of this study support the hypothesis that nutrient enrichment and bottom-up control were major factors causing increased productivity and standing crops of macroalgae on reefs in Jamaica and southeastern Florida. The DIN and SRP concentrations on both reef systems were at or above ~ 1.0 μM, and 0.1 μM, respectively—threshold concentrations noted for macroalgal overgrowth of seagrass and coral reef communities along natural nutrient gradients around seabird mangrove rookeries on the Belize Barrier Reef (Lapointe et al. 1993). The DIN and SRP concentrations on

corals reefs impacted by macroalgal blooms globally all seem to be above these thresholds (Table 3), suggesting that increased nutrient concentrations associated with coastal eutrophication exert a significant kinetic control leading to the development of macroalgal blooms. The nutrient concentrations I measured at Discovery Bay are some of the highest reported for coral reefs world-wide and explain why such impressive standing stocks of macroalgae have developed on this fertile reef system (Table 3).

The utility of the DIN threshold was validated during the massive blooms of *Enteromorpha* in the Gulf of Eilat during 1992 when DIN concentrations increased from a normal

Table 2. Tissue levels (% dry wt) of carbon (C), nitrogen (N), phosphorus (P), and molar C:N, C:P, and N:P ratios in macroalgae.

| Location	Habitat		%C	%N	%P	C:N	C:P	N:P
Jamaica								
Discovery Bay	Grotto	*Gracilaria ferox*	20.6	1.52	0.07	15.8	759	48.0
	Grotto	*Chaetomorpha linum*	18.4	1.29	0.05	16.6	949	57.1
	Back reef	*Sargassum polyceratium*	11.9	0.64	0.03	21.7	1023	47.2
	Back reef	*Halimeda opuntia*	6.8	0.54	0.03	14.7	584	39.8
	Fore reef	*Lobophora variegata*	25.0	0.71	0.04	41.1	1612	39.3
	Fore reef	*Dictyota dichotoma*	17.7	0.89	0.05	23.2	913	39.4
Mean ±1 SD			16.7±6.5	0.93±0.39	0.05±0.02	22.2±9.0	973±319	45.1±6.5
Florida								
Princess Anne	Deep reef	*Codium isthmocladum*	10.7	0.93	0.06	13.4	460	34.3
North Colonel's Ledge	Deep reef	*Codium isthmocladum*	9.74	1.06	0.07	10.7	359	33.5
Jupiter Ledge	Deep reef	*Codium isthmocladum*	11.6	0.99	0.05	13.7	598	43.8
Hobe Sound	Deep reef	*Codium isthmocladum*	11.7	1.07	0.06	12.8	503	39.4
Mean ±1 SD			10.9±0.91	1.01±0.07	0.06±0.01	12.6±1.2	480±86	37.7±4.2
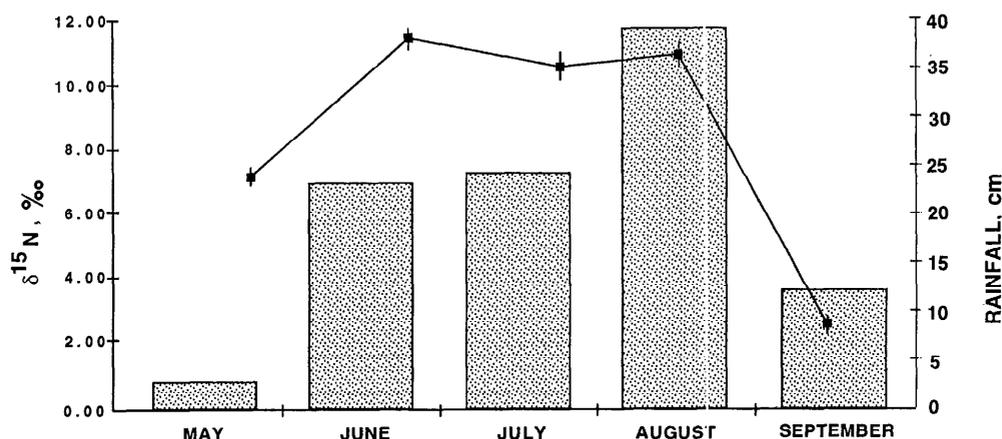
Fig. 7.   Natural abundance of stable isotopic $^{15}N:^{14}N$ ratios ($\delta^{15}N$, ‰) in *Codium isthmocladum* and rainfall between May and September 1995 at Jupiter Ledge in southeast Florida. Values for $\delta^{15}N$ (lines) are given as means ± 1 SD ($n = 3$) for date sampled, rainfall (bars) is shown as monthly total.

range of <0.4 μM to 1.2 μM as a result of an anomalous large-scale upwelling event (Genin et al. 1995). Blooms of the macroalgae *Hypnea musciformis* and *Ulva fasciata* have also recently impacted coastal waters of west Maui, Hawaii, another situation where DIN and SRP concentrations have risen above these thresholds. Monitoring efforts indicate that these blooms are linked to enrichment from surface water and groundwaters discharges from the upland Maui watershed, which has undergone urban, agricultural, and industrial development in recent decades (Hodges unpubl.). These nutrient thresholds for the onset of macroalgal blooms are similar to those noted for the decline of coral reefs from cultural eutrophication in Kaneohe Bay, Hawaii, fringing reefs in Barbados, and inshore reefs of the Great Barrier Reef lagoon (Bell 1992).

Nutrient thresholds for macroalgal booms on coral reefs—The findings of low nutrient threshold concentrations for overgrowth of Floridian and Jamaican coral reefs by macroalgae demonstrate that the half-saturation constants (K_s) needed to support near-maximal productivity (i.e. growth rate) of macroalgae are quite low and similar to those reported for phytoplankton. Thomas and Dodson (1968) reported K_s values of ~0.1 μM for SRP-limited growth in the diatom *Chaetoceros gracilis* isolated from tropical Pacific waters. Caperon et al. (1971) found similar K_s values of ~0.2–0.4 μM for NH_4^+- and NO_3-limited growth of Kaneohe Bay phytoplankton. In comparison, the tropical red macroalgae *Gracilaria foliifera* and *Neoagardhiella bayieyi* (DeBoer et al. 1978) and the sheetlike green alga *U. fasciata* (Lapointe and Tenore 1981) all achieved maximum growth rates at DIN concentrations of ~0.5–0.8 μM. Nutrient-limited productivity of tropical macroalgae along a nutrient gradient from a guano-enriched seabird rookery to nearby pristine coral reefs on the Belize Barrier Reef showed decreased P limitation of productivity at SRP concentrations >0.1 μM (Lapointe et al. 1993). Although macroalgal productivity and growth rates become saturated at these low nutrient concen-

Table 3.   Macroalgal blooms reported for coral reef regions with mean concentrations (μM) of dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), and the DIN:SRP ratio.

Location	Macroalgae	DIN	SRP	DIN:SRP	Reference
Hawaii, Kaneohe Bay (before sewage diversion)	*Dictyosphaeria cavernosa, Acanthophora spicifera, Gracilaria* sp.	1.13	0.36	3.1	Banner 1974; Smith et al. 1981
Hawaii, west Maui	*Ulva fasciata, Hypnea musciformis*	4.70	0.29	16.2	Hodges unpubl.
Red Sea, Gulf of Eilat	*Enteromorpha* sp.	1.20			Genin et al. 1995
Martinique	*Sargassum filipendula, Enteromorpha chaetomorphoides*	1.20	0.25	4.8	Littler et al. 1993
Bermuda, Harrington Sound	*Cladophora prolifera*	1.66	0.14	11.9	Lapointe and O'Connell 1989
Southeast Florida	*Codium isthmocladum*	1.61	0.19	8.5	This study
Jamaica, Discovery Bay	*Lobophora variegata, Dictyota* spp., *Sargassum* spp., *Chaetomorpha linum, Cladophoropsis* sp.	12.21	0.17	71.8	This study
Belize Barrier Reef, Man-O-War Cay (Guano island)	*Ulva lactuca, C. linum, A. spicifera*	4.84	1.56	5.7	Lapointe et al. 1993

trations, nutrient uptake does not (e.g. D'Elia and DeBoer 1978) and results in luxury consumption of nutrients—a well-known mechanism that provides surplus nutrient storage in macroalgae that can support growth when water-column nutrient concentrations are low.

Thus, in warm and clear tropical waters, both phytoplankton and macroalgae can respond simultaneously to slight increases in water-column nutrient concentrations. This is consistent with field observations of macroalgal blooms developing concurrently with phytoplankton biomass in tropical coral reef regions experiencing eutrophication and increased nutrient concentrations. For example, in central Kaneohe Bay during the 1960s, the chlorophyte bubble alga *D. cavernosa* overgrew the reef coral *Porites compressa* as phytoplankton biomass increased due to eutrophication from sewage inputs (Banner 1974). During the same period in the southern sector of the bay, praised as the "coral gardens" in the early 1900s, sewage enrichment caused blooms of the rhodophyte macroalgae *Gracilaria* and *Acanthophora* and the pheophyte macroalga *Hydroclathrus* to overgrow reef flats previously dominated by the corals *P. compressa* and *Montipora verrucosa* (Maragos 1972). Cause-and-effect linkages between the macroalgal blooms and eutrophication were demonstrated following sewage diversion in the mid-1970s when nutrient concentrations, biomass of *D. cavernosa*, and phytoplankton populations all decreased in the central bay (Laws and Redalje 1979; Smith et al. 1981).

Macroalgal blooms at Discovery Bay—The potential for eutrophication at Discovery Bay was noted by D'Elia et al. (1981) who documented groundwater inputs of NO_3^- and concluded that increased SRP enrichment associated with increased population growth and sewage pollution could lead to eutrophication on these reefs. In fact, NO_3^- and SRP concentrations >2.0 and ~0.15 μM, respectively, were reported for the back-reef habitats (D'Elia et al. 1981), concentrations that were already above thresholds found to sustain maximum productivity of macroalgae on Caribbean coral reefs (Lapointe et al. 1993). This finding explains why nutrient enrichment did not increase the already nutrient-replete, high productivities observed in three of the four back-reef macroalgae in this study—*S. polyceratium, L. variegata,* and *H. opuntia*—and why the back-reef macroalgae were abundant in the late 1970s and early 1980s prior to the die-off of *Diadema* in 1983 (Goreau 1992).

Comparison of the nutrient data from the present study with those of D'Elia et al. (1981) suggests that nutrient concentrations further increased in the back reef during the 1980s and spatially spread offshore, elevating DIN and SRP concentrations on the fore reef above threshold concentrations. The SRP concentrations in groundwater-enriched seawater (28‰) in the grotto reported by D'Elia et al. was ~0.25 μM, a value lower than the average of 0.33 μM reported for this salinity in the grottos in 1987. SRP concentrations were >0.10 μM on the fore reef, indicating that this habitat was at or above the SRP threshold noted for SRP-replete productivity of tropical macroalgae (Lapointe et al. 1993); the DOP pool, which was not measured in my study, can provide additional SRP to macroalgae via alkaline phosphatase hydrolosis. The average NO_3^- concentration for the offshore side of the back reef was ~2.0 μM in the late 1970s (D'Elia et al. 1981), ~50% of the concentration measured in this area during my study. DIN and SRP measurements near the back-reef station of my study averaged 7.27 μM and 0.27 μM between November 1987 and May 1988 and 5.67 μM and 0.45 μM between April and June 1989; measurements following rain on 27 May 1989 at this station showed highly elevated DIN and SRP concentrations of 24.12 μM and 1.01 μM, respectively (Macfarlane 1991). These data suggest a trend of increasing NO_3^- and SRP concentrations at Discovery Bay concurrent with escalation of the macroalgal blooms on the fore reef, indicating that the phase shift from corals to macroalgae was directly linked to nutrient concentrations and underscoring the fundamental kinetic control of the eutrophication process. This finding explains why shifts in biotic stable states of coastal ecosystems cannot always be related directly to loading rates alone but rather occur as step functions (Duarte 1995) that are concentration-dependent. Many factors interact in the expression of nutrient loads and the buildup of nutrient concentrations in coastal ecosystems, including microbial processes such as denitrification, assimilation, biotic storage of nutrients, rates of P adsorption and cycling, residence time and dilution potential of the system, and other factors. The source(s) of the groundwater NO_3^- have not been discriminated at Discovery Bay, but naturally high concentrations and flows of groundwater NO_3^- in Jamaica have almost certainly been increased by human influences, including deforestation, agricultural-industrial development, and sewage contamination. P inputs to Discovery Bay reefs have also not been examined but would include sewage-contaminated groundwaters, atmospheric particulate P from bauxite (red dust from a nearby loading facility is visible throughout the study area) that contains 5–10% P (Comer 1974), and coastal rivers and streams that contribute fluvial P inputs.

The significant nutrient-salinity stratification throughout the study area at Discovery Bay shows that nutrients derived from submarine groundwater discharge from springs along the shore are transported by buoyant plumes across the back-reef to fore-reef communities. The groundwater-borne NO_3^- was highly enriched in the reduced salinity surface waters, which became progressively diluted as they mixed with offshore, higher salinity seawater lower in NO_3^-. Relatively low concentrations of SRP in these groundwaters (D'Elia et al. 1981) resulted in the high DIN:SRP ratios (~100:1) of the discharges, causing the observed P limitation of macroalgal productivity. The offshore dispersion and rapid nutrient dilution in this system emphasizes the open connection and low residence time of this coastal system and explains the lack of planktonic development in longer residence time systems experiencing eutrophication (e.g. Kaneohe Bay, Smith et al. 1981). In addition to the offshore nutrient dispersion via buoyant surface plumes, low-salinity, high-NO_3^- pore waters have been found in fore-reef sediments at Discovery Bay (Pigott and Land 1986), suggesting that NO_3^--rich groundwaters are discharging directly through fore-reef sediments.

The high N:P ratios (~100:1) of the groundwater discharges resulted in pronounced P-limited productivity of macroalgae at Discovery Bay. High tissue C:P and N:P

ratios of all macroalgae assayed reflected the P limitation, as did the significantly higher APA, especially in the productive and abundant species *C. linum, L. variegata, S. polyceratium,* and *Dictyota* spp. The high APA allows these species to hydrolyze DOP pools as a source of P under conditions of limiting SRP concentrations to achieve balanced growth. These high APA values could provide the considerable P availability needed to support high macroalgal productivity in the low SRP waters of the fore-reef community. Light-saturated productivity (P_{max}) of the macroalga *C. linum* was enhanced by SRP enrichment, indicating that P enrichment of the back reef over the past decade has triggered blooms of this indicator species that were observed smothering hermatypic corals, e.g. *Montastrea annularis,* in the back reef. The longer lived forms, including *S. polyceratium* and *Cladophoropsis* sp., also have responded to increasing SRP concentrations by expanding their distribution from nearshore spring and back-reef habitats into more offshore fore-reef habitats now shared with blooms of *Dictyota* spp., *S. hystrix,* and *L. variegata.* The pheophyte *Sargassum filipendula,* together with the chlorophyte *Enteromorpha chaetomorphoides,* also overgrew fringing coral reefs on the southwest coast of Martinique during the late 1980s as a result of nutrient enrichment associated with cultural eutrophication (Littler et al. 1993).

The evidence suggests that both DIN and SRP concentrations throughout the back reef were above critical thresholds in the late 1970s and early 1980s when a major physical disturbance—Hurricane Allen—hit this coast in 1980. This hurricane caused severe physical disturbance to the reef, especially the crest zone (0–6 m) previously dominated by luxuriant stands of the elkhorn coral *Acropora palmata*; branching corals were smashed, massive corals toppled or split, and plate corals fractured or torn from reef slopes to depths of 50 m (Woodley 1980). Although the physical disturbance on this reef was dramatic, it was not considered totally destructive and reef recovery was expected to occur "in a few years" despite the massive blooms of various green turf algae (Woodley 1980). Corals compete for space with macroalgae and turf algae and the competitive outcomes are influenced by relative growth rates and nutrient availability (Fig. 1). The reduction of upright corals to rubble at a time when nutrient concentrations were at or above critical threshold concentrations for maximum macroalgal growth rates allowed the faster growing macroalgae to physically overgrow and out-compete the corals and turf algae. Eutrophication not only increases the biomass of reef macroalgae but also reduces the reproductive capacity of hermatypic reef corals (Tomascik 1991) and inhibits coral larval settlement and survival (Birkeland 1977). All of these factors, driven simply by eutrophication processes, provide a more robust explanation for the replacement of corals by macroalgae on reefs at Discovery Bay (cf. Hughes 1994).

Macroalgal blooms in southeastern Florida—As in Discovery Bay, the blooms of *C. isthmocladum* on southeast Florida reefs are related to bottom-up control, evidenced by concentrations of DIN and SRP above thresholds for blooms of macroalgae in the Caribbean (Lapointe et al. 1993). The blooms of this opportunistic genus in Florida are not sur-

prising considering that Malinowski and Ramus (1973) documented blooms of the related species *C. fragile* in a Connecticut estuary where DIN and SRP concentrations were ~3 μM and 0.5 μM—concentrations similar to those measured on the Florida reefs during my study.

However, several features of the Florida *Codium* blooms contrast with the macroalgal blooms at Discovery Bay. For example, the productivity of *C. isthmocladum* in Florida was N rather than P limited, evidenced by low seawater DIN: SRP ratios (<1.5:1) and low tissue N:P (35:1), C:P (479:1), and APA values of *C. isthmocladum.* These geographic differences in N vs. P availability are consistent with biogeochemical models of nutrient regulation of macroalgal productivity in which N is of primary importance in siliciclastic systems compared to P in carbonate-rich systems (Lapointe et al. 1992). Experimental nutrient enrichment assays also supported this pattern of N- vs. P-limited productivity; N enrichment increased the initial slope (α) of the deep-water *C. isthmocladum,* compared with P enrichment that increased P_{max} of the shallow-growing *C. linum* in Jamaica. Hanisak (1979) also used tissue nutrient analysis to demonstrate N-limited growth of the related *Codium fragile* subsp. *tomentosoides* in coastal waters of Rhode Island.

The differences between the Jamaican and Floridian blooms illustrate various physiological strategies that macroalgae can utilize to optimize productivity under different levels of irradiance and conditions of N- vs. P-limited growth. For example, increased photosynthetic efficiency would be more advantageous to *C. isthmocladum* growing at depth under low irradiance in Florida compared with increased photosynthetic capacity for *C. linum* growing in shallow depths under high irradiance in Jamaican back-reef habitats. Although not addressed in this study, N fixation by endophytic cyanobacteria could potentially compensate for N limitation in *C. isthmocladum* in Florida, a phenomenon noted by Rosenberg and Paerl (1981) for the related *Codium decorticatum* in North Carolina coastal waters. In contrast, macroalgae in the high N waters of Jamaica utilize APA to compensate for severe P limitation, compared to the low APA in *C. isthmocladum* in the relatively P-rich siliciclastic waters on reefs in southeastern Florida.

Although natural upwelling of deep offshore water and outwelling of land-based stormwater runoff via the Palm Beach and Jupiter Inlets potentially contribute nutrient inputs to the Florida study area, submarine groundwater discharges of DIN and SRP seem to be an important route of nutrient enrichment to *C. isthmocladum* blooms on these reefs. Kohout (1965) first hypothesized the importance of deep geothermal convection to the cyclic flow of deep groundwater from the Floridan Aquifer System to reef development in south Florida. Finkl et al. (unpubl.) calculated that annual discharges of groundwater beneath reefs in southeastern Florida are ~4×10^8 m^3 but suggested that discharges probably were larger during times of lowered sea level. Elevated concentrations of NH$_4^+$, NO$_3^-$, and SRP were associated with reduced salinity in near-bottom waters of reefs at Jupiter Ledge and North Colonel's Ledge in my study, providing evidence of groundwater as a nutrient source for these reefs. Submarine groundwater discharge was further indicated as a nutrient source by high (1,000 dpm m^{-3}) near-

bottom ^{226}Ra concentrations at Jupiter Ledge during my study—values characteristic of regional groundwaters (W. Burnett pers. comm.)

The increase in δ^{15}N values in *C. isthmocladum* to >10‰ with onset of the rainy season suggests that N derived from wastewater enrichment of groundwaters is a significant source of N contributing to these blooms. The major sources of N enrichment to surface waters and groundwaters in southeast Florida include atmospheric deposition, nitrogenous fertilizers, and human and animal wastes, all which have distinguishable δ^{15}N values. Groundwater influenced only by atmospheric deposition typically has δ^{15}N values ranging from +2 to +8‰ (McClelland et al. in press); that derived from human or animal wastes is more enriched in ^{15}N, bearing δ^{15}N values >+10‰ (Lindau et al. 1989). N from fertilizers is depleted in ^{15}N, having δ^{15}N values between −3 and +3‰ (Fryer and Aly 1974). The upland watershed of this reef system has experienced extensive human development during the past several decades, including enrichment of shallow groundwaters by septic tanks, wastewater reuse for irrigation, and agriculture.

Deeper groundwaters (>900 m) are enriched by Class 1 injection wells for wastewater disposal and vertical upward migration of effluents can occur as a result of natural fractures or vertical channels in the carbonate formations of the Floridan Aquifer System. Swayze and Miller (1984) showed a highly permeable surficial aquifer unit between 20- and 33-m depth, which could also be enriched by the use of septic tanks. This unit extends offshore to the reef outcrops where the *C. isthmocladum* blooms occur. The >4‰ increase in δ^{15}N values of *C. isthmocladum* correlated directly with rainfall, suggesting that increased water-table height and hydraulic head of the coastal aquifer increases the offshore flux of wastewater N in groundwaters to coastal reefs. This finding is consistent with studies in the Florida Keys where rainfall caused increases in the offshore fluxes of groundwater contaminated with septic tank N (Lapointe et al. 1990). McClelland et al. (in press), who also used δ^{15}N tracing techniques, found that septic tank N loads contributed significantly to blooms of the macroalgae *Cladophora vagabunda, Enteromorpha* sp., and *Gracilaria tikvahiae* in the Waquoit Bay estuary, Cape Cod.

Top-down control not the primary cause of macroalgal blooms—In addition to the data supporting bottom-up control of macroalgal biomass at Discovery Bay, further evidence exists to moderate the top-down interpretation of Hughes (1994). This evidence includes the fact that fish populations on the deep fore reef (>15 m) were overfished by intensive use of fish traps in the 1960s (Munro 1983)—long before the widespread blooms of *L. variegata* and *S. polyceratium* developed on these reefs in the 1980s. Fish and urchin grazing do not play a substantial role in the reef crest area (Morrison 1988) due to turbulent wave action. Similarly, the mass mortality of *Diadema* occurred in 1983, years before expansion of *C. linum* and *S. polyceratium* from restricted areas in the back reef to the fore reef. Experimental studies during the 1980s at Discovery Bay showed that although *Diadema* played a significant role in structuring the shallow (above 10 m) fore-reef communities on small spatial

scales, this was not true for deep (15 m) fore-reef communities; these studies were performed during a period of high *Diadema* densities when many reef habitats had high standing crops of macroalgae (Morrison 1988). Hence, the inconsistency in the timeline between reduced herbivory from overfishing, *Diadema* die-offs, and macroalgal overgrowth in both shallow and deep reef habitats argues against strict control of the blooms by only the grazers. These observations further reinforce the conclusion that reduced herbivory by itself could not have been the only factor causing the massive macroalgal blooms that developed on reefs at Discovery Bay.

Evidence also suggests that reduced herbivory from overfishing and the *Diadema* die-off was not the primary cause of the *C. isthmocladum* blooms in Florida. Unlike Jamaica, the reefs impacted by the *C. isthmocladum* blooms have been protected from intensive fishing pressure via fish traps by State of Florida fishing regulations. Although other commercial and sport fishing practices have reduced the abundances of larger fish such as groupers and snappers, these reefs still contain significant populations of grazers, including parrotfish, surgeonfish, damselfish, and chubs. Like the deep reef slope in Jamaica, these deep reefs also never had large populations of *Diadema* so that the die-off in 1983 would not have had major effects. Furthermore, observations by divers during the blooms indicated that few invertebrates or fish seem to graze directly on *C. isthmocladum*—a characteristic that could make this species particularly susceptible to bloom development.

Implications for science and management—The importance of groundwater discharges to the ecology of reefs in both Jamaica and southeast Florida underscores the earlier work of Johannes (1980) who noted the growing evidence for the role of groundwaters as a nutrient source in shallow coastal waters. The evidence presented here adds a further dimension of complexity to Hughes' (1994) conclusion that macroalgal blooms in Jamaica resulted only from loss of herbivory. The importance of top-down control of macroalgal standing crops is much more compelling when combined with the larger scale, synergistic effects of bottom-up control via groundwater nutrient enrichment. Previous evidence of widespread nutrient enrichment at Discovery Bay via groundwater discharges (D'Elia et al. 1981) also leads to the obvious alternative hypothesis of bottom-up control on reefs at Discovery Bay. The locations of the macroalgal-dominated habitats around Jamaica cited by Hughes (1994) implicate large-scale coastal enrichment not only from groundwater discharges but also from river discharges exporting nonpoint-source nutrient loading associated with deforestation, agriculture, sewage, and industry (Gabric and Bell 1993; Nixon 1995).

This study affirms the need to adopt broad theoretical approaches to testing management-related hypotheses regarding the deterioration of coral reefs. As pointed out by Dayton and Oliver (1982), all scientists should constantly guard against preconceived concepts, research designed to verify rather than falsify hypotheses, and narrow single-factor approaches that do not test multiple factors. While oversimplification and biased perspectives are unhealthy for science

in general, they can undermine coral reef conservation, especially in today's world where bureaucrats often look for a politically expedient "quick fix." Hughes' (1994) conclusion that a ban on fish traps is needed to save Jamaican reefs from macroalgal overgrowth is certainly important but could also be used to argue that the effects of eutrophication are relatively minor. The available data indicate that eutrophication is an important and widespread problem—a conclusion already recognized by coral reef scientists world-wide (Ginsberg 1994). There is also evidence that eutrophication, by itself, leads to a significant reduction in reef fish populations (Johannes 1975; Naim 1993) and other grazers as well via a positive feedback loop that would further accelerate macroalgal blooms (Duarte 1995). Thus, it seems unlikely that simply controlling fishing practices will restore Jamaica's coral reefs or other coral reefs being impacted by severe eutrophication. The reality of large-scale coastal eutrophication needs to be rigorously confronted by scientists and resource managers alike, both in Jamaica, the U.S., and world-wide.

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