MACROALGAL OVERGROWTH OF FRINGING CORAL REEFS AT DISCOVERY BAY, JAMAICA: BOTTOM-UP VERSUS TOP-DOWN CONTROL

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ABSTRACT

Currently, a diverse multi-layered macroalgal community (*Lobophora variegata, Cladophoropsis sp., Halimeda spp., Dictyota spp., Sargassum spp.*) dominates the fore reef at Discovery Bay, Jamaica, in habitats that were covered mostly by corals prior to 1980. The macroalgal overgrowth of fringing coral reefs in Jamaica has been strongly correlated with reduced grazing due to overfishing coupled with die-offs of the sea urchin *Diadema antillarum* ("top-down" control). However, the potential role of nutrient enrichment ("bottom-up" control) in enhancing macroalgal biomass has not been adequately examined. The present study explored the additional hypothesis, as proposed in the relative dominance model, that because the phase shift involved mainly frondose macroalgae, nutrient enrichment must also be a causal factor. Our approach involved multi-faceted experiments and assessments including: nutrient-enrichment bioassays, alkaline phosphatase assays, water-column nutrient determinations, indicator species, biotic cover and tissue nitrogen levels. All approaches were consistent with the hypothesis of bottom-up control via increasing coastal eutrophication leading to superabundant macroalgal blooms. This finding offers an additional dimension of complexity and robustness toward fully understanding the phase shift.

INTRODUCTION

Ecologists studying the controls of aquatic food webs have used the concepts "bottom-up" and "top-down" to describe situations where either resource availability or the actions of consumers regulate the structure of food webs (e.g., Carpenter *et al.* 1985). A complex synergy of bottom-up and top-down controls are similarly important on coral reefs, where standing crops of benthic macroalgae are usually inconspicuous on undisturbed oligotrophic systems due to the combined effects of low nutrient availability and intense grazing by herbivorous fishes and invertebrates (i.e., the relative-dominance model, Fig. 1).

Despite recognition of the complex interactions of both bottom-up and top-down controls on coral reefs (Littler and Littler 1984), single-factor top-down interpretations still permeate the scientific literature concerning the causes of algal overgrowths. For example, the dramatic "phase shifts" on Jamaican coral reefs from >50% coral cover in the early 1970's to the current "spectacular algal bloom" was attributed simply to the effects of reduced grazing (overfishing, *Diadema* die-off) accelerated by the impact of Hurricane Allen in 1980 (Hughes 1994). The possible role of nutrient enrichment as a concomitant factor enhancing the growth rate and carrying capacity of the macroalgal standing crop was dismissed without supportive data.

Although herbivory is a significant factor in the benthic dynamics of coral reefs, its effects occur on relatively limited temporal and spatial scales (Hatcher and Larkum 1983). In contrast, exponentially expanding human populations are accelerating coastal eutrophication worldwide (Nixon 1995). Coral reefs are particularly susceptible to nutrient enrichment due to the very low thresholds for dissolved inorganic nitrogen (DIN; 1.0µM) and soluble reactive phosphorus (SRP; 0.1µM). These levels are the threshold concentrations noted (Bell 1992) for the decline of coral reefs from eutrophication and subsequent macroalgal blooms at Kaneohe Bay in Hawaii, fringing reefs of Barbados and inshore reefs within the Great Barrier Reef lagoon. These concentrations also represent nutrient thresholds experimentally determined by Lapointe *et al.* (1993) for macroalgal overgrowth of seagrass and coral reef communities along natural nutrient gradients on the Belize Barrier Reef.

As a test of the synergistic "nutrient enrichment" aspects of the model (Fig. 1) to explain the increasing macroalgal blooms on Jamaican reefs, the present study critically assessed relationships between water-column nutrient concentrations and the physiological status of macroalgae on the fringing reef system at Discovery Bay—one of the most intensively studied coral reefs in the world (Goreau 1992). Our approach involved multifaceted experiments including measurements of water-column nutrient concentrations, diversity of biotic cover from depths between 0 and 50m, tissue nitrogen levels from shore to the outer reef slope, nutrient-enrichment bioassays to assess the type and degree of nutrient-limited productivity of predominant reef macroalgae and alkaline phosphatase activity (APA) as a measure of the degree of P-limitation of productivity.

MATERIALS AND METHODS

The water quality, physiological and ecological research at Discovery Bay (Fig. 2) was performed during July 1987, a period within the "disease and algal blooms" phase in the transition from coral to macroalgal dominance (1983 to present; Hughes 1994). Discovery Bay is about 1.5km^2 in area and protected from the open ocean by a fringing reef flat (see Goreau 1959 for detailed description) that is exposed at extreme low tides. The adjacent upland drainage basin is porous limestone and contains numerous fissures and fractures that provide

HUMAN IMPACT

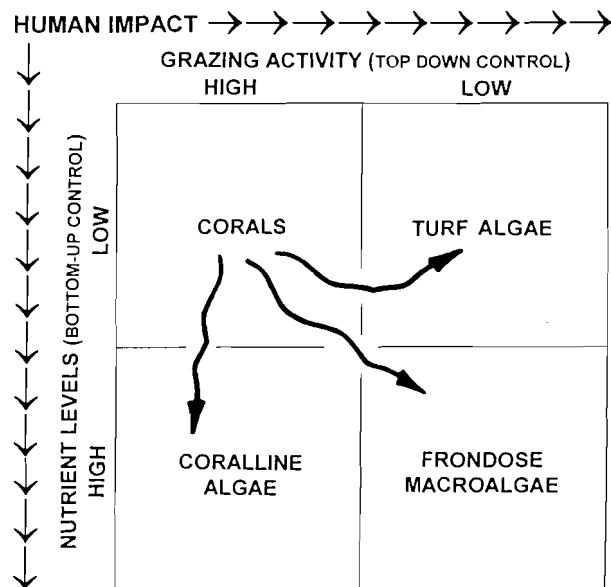GRAZING ACTIVITY (TOP DOWN CONTROL)

NUTRIENT LEVELS (BOTTOM-UP CONTROL)

Fig. 1: Diagrammatic representation of the relative-dominance paradigm (Littler and Littler 1984). Potential dominance of major space-occupying groups of photosynthetic reef organisms is predicted as a function of bottom-up control by long-term nutrient levels and top-down control by herbivory. Grazing is considered the more important direct controller of algal standing stocks on undisturbed oligotrophic reefs, whereas nutrients set the potential upper limits to biomass. Human activities inevitably reduce grazing animals and increase nutrient levels, which shifts reefs from coral to algal domination (arrows).

Fig. 2:   Location of the primary study site at Discovery Bay, Jamaica and the oligotrophic reference sites at Tobacco and Curlew Reefs, Belize.

of dominant Discovery Bay macroalgae by the spectro-photometric method described in Lapointe and O'Connell (1989). For comparison, APA was measured in predominant macroalgae at Curlew Reef, an oligotrophic system in Belize (Lapointe et al. 1993). APA of Chaetomorpha linum and Sargassum polyceratium from Discovery Bay was also measured following the overnight nutrient pulses (described above) to assess metabolic responses to DIN and SRP enrichment, which could potentially have different effects on the status of P-limited productivity.

To determine the offshore extent of N-enrichment, the widely-distributed, dominant phaeophyte Lobophora variegata was collected from the reef crest to the outer fore-reef slope. The algal tissue was returned to the laboratory, dried at 70°C in an oven, pulverized and duplicate samples analyzed for tissue percent N on a Carlo-Erba Elemental Analyzer.

During June 1996, the biota and substrata along the "Goreau transect" were videotaped at right angles in a continuous north-south belt transect beginning at a depth of 50m and continuing upwards to the crest of the back reef. Multi-layered communities were peeled away layer by layer and recorded to permit videoscoring of canopy, understory and encrusting layers. In the laboratory, five rectangular quadrats (~0.3m^2 each) were selected for each of 14 depth zones and quantified for percent cover by the methods detailed in Littler et al. (1991a).

Least-squares linear regression was used to determine significance between water-column nutrient concentrations vs. salinity, as well as tissue N content of Lobophora variegata vs. depth. The main effects and interactions of the Pmax and APA assays were analyzed by two-way ANOVA. Significance reported below indicates that the probability of the null hypothesis is P<0.05.

significant phreatic inputs of groundwater-borne NO3$^-$ (D'Elia et al. 1981). Sampling for dissolved inorganic nitrogen (DIN) and soluble reactive phosphorous (SRP) was conducted along a transect that extended from localized groundwater discharges (springs) near shore, through semi-enclosed grottos, over the back reef in 1-2m depths and across the reef crest to the fore reef. Duplicate water samples were collected from the surface and bottom of the water column in clean, high density, polyethylene bottles. For comparative purposes, DIN and SRP concentrations were measured from two well-studied oligotrophic reefs in Belize (Fig. 2) to ascertain threshold levels (Lapointe et al. 1993). The water samples were immediately filtered through combusted Gelman 0.45μM GF/F filters and placed on ice in the dark until analysis within 1-2 days. DIN (NH4$^-$ plus NO3$^-$ plus NO2$^-$) 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 was determined with a Bausch and Lomb hand-held refractometer.

The nutrient-enrichment bioassays (6 replicates • species^{-1}) involved analysis of macroalgal primary productivity measured by changes in dissolved oxygen using experimental procedures described by Lapointe (1995). These experiments determined the effects of DIN and SRP enrichment on Pmax (photosynthetic capacity at light saturation) for Chaetomorpha linum, Sargassum polyceratium and Lobophora variegata, which dominated shallow (1-2m) hard substrata on the back reef. Factorial enrichment treatments included overnight pulsing with NO3$^-$ (160μM), SRP (16.0μM), NO3$^-$ and SRP and a control (without added nutrients). These concentrations were high compared to ambient levels on most coral reefs but were only 2-fold greater than the NO3$^-$ concentrations in nearby spring waters (D'Elia et al. 1981). The assays were performed under natural irradiance on clear days between 1000 and 1400h. Irradiance ranged from 1400 to 2000μmol photons·m^{-2}·s^{-1} and temperature ranged from 27 to 29°C.

Alkaline phosphatase is an exoenzyme produced by P-deficient macroalgae that allows them to utilize ambient 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. APA (4 replicates) was measured on a variety

RESULTS

The surface waters at Discovery Bay during July 1987 were enriched substantially with groundwater NO3$^-$, evidenced by buoyant salinity and NO3$^-$ stratification and a significant negative correlation between salinity and NO3$^-$ (r=-0.96; P<0.0001) along the entire study transect. The highest concentrations (~28μM) occurred in the lowest salinity (28ppt) surface waters near the springs adjacent to the shore. NO3$^-$ concentrations >4μM were found at oceanic salinities (35-36ppt) on the shallow fore reef, indicating offshore dispersion, dilution and significant N enrichment from groundwater discharges. NH4$^-$ occurred at much lower concentrations than NO3$^-$ and was positively correlated (r=0.76, P=0.03) with salinity. The resulting DIN concentrations along the entire transect at Discovery Bay exceeded the eutrophication threshold for coral reefs, as evident when compared to
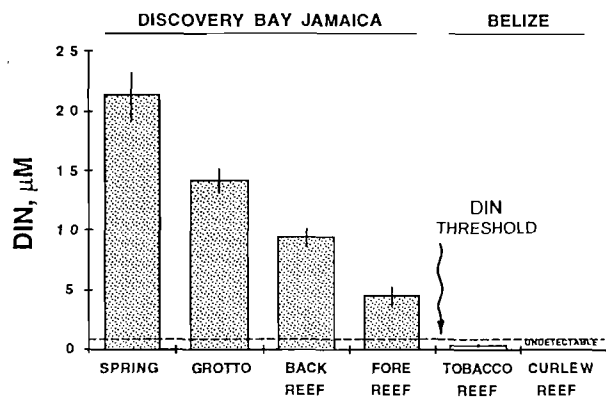

Fig. 3:   Water-column levels of dissolved inorganic nitrogen over the fringing-reef zones at Discovery Bay and the two oligotrophic reference sites in Belize (lines = ±1SD, n=4).   The dashed line indicates the threshold level for DIN limitation of macroalgal growth.
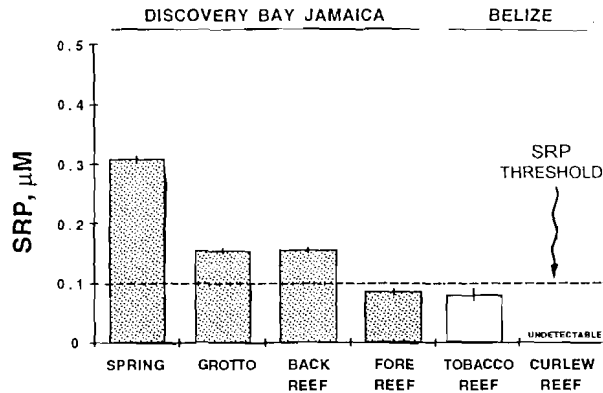
Fig. 4: Water-column levels of soluble reactive phosphorus over the fringing-reef zones at Discovery Bay and the two oligotrophic reference sites in Belize (lines = ±1SD, n=4). The dashed line indicates the threshold level for SRP limitation of macroalgal growth.

APA values averaged 72.8 ±13.6μM SRP released·g dry wt⁻¹·h⁻¹ in the Jamaican macroalgae, almost two-fold higher than the average value of 44.0 ±26.6μM SRP released·g dry wt⁻¹·h⁻¹ for macroalgae from Curlew Reef in Belize (Fig. 5). Two-way ANOVA revealed that SRP enrichment significantly decreased the mean APA of *Chaetomorpha linum* (F=9.7, P=0.05) and *Sargassum polyceratium* (F=23.7, P=0.008), whereas NO3⁻ enrichment increased mean APA values in these species, although the increases were not significant (P=0.07). The mean APA of the factorial enrichment treatments for *Chaetomorpha linum* ranged from 90.9μM SRP released·g dry wt⁻¹·h⁻¹ for the control, 56.6μM released for SRP, 124.7μM for NO3⁻ and 12.2μM for NO3⁻ + SRP. For *Sargassum polyceratium*, mean APA of the enrichment treatments ranged from 73.4μM SRP released·g dry wt⁻¹·h⁻¹ for the control, 30.1μM released for SRP, 81.1μM for NO3⁻ and 37.9μM for NO3⁻ + SRP enrichment.

Tissue N of the cover dominant, *Lobophora variegata* (Fig. 6) decreased with increasing depth on the fore reef at Discovery Bay. The N content ranged from a maximum value of ~0.8% at 3m on the shallow fore reef to a minimum of 0.45% at 36m (Fig. 6). Linear regression showed a highly significant and positive correlation (r=0.99, P<0.0001) between the tissue N and depth (correlated with distance offshore).

more oligotrophic waters of the Belize Barrier Reef (Fig. 3). A negative correlation (r=-0.93; P=0.0008) also was noted for SRP versus salinity, with concentrations ranging from ~0.33μM near the springs to near 0.10μM on the fore reef; thus, the SRP concentrations also exceeded the eutrophication threshold (Lapointe et al. 1993), in contrast to the oligotrophic waters of Tobacco Reef and Curlew Reef (Fig. 4). The high concentrations of NO3⁻ 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, which ranged from 103 in the grotto to 33 on the fore reef.

Pmax of back-reef macroalgae, including the phaeophytes *Sargassum polyceratium* and *Lobophora variegata* and the chlorophyte *Halimeda opuntia*, showed no effects of DIN and SRP enrichment. In contrast, Pmax of *Chaetomorpha linum* demonstrated significant effects of SRP enrichment (F=144, P<0.0001) although the effects of NO3⁻ and the NO3⁻ + SRP interaction were not significant. The mean Pmax values for the factorial enrichment treatments ranged from a low of 3.82mg C·g dry wt⁻¹·h⁻¹ for the control, to 5.94 for SRP, 4.64 for NO3⁻ and 6.74 for NO3⁻ + SRP.

Overall biotic cover (Table 1) was dominated by frondose phaeophytes and chlorophytes with mean cover of 83%, approaching or exceeding 100% cover above 24m. By comparison, hermatypic corals covered only 7% with two areas of peak abundance, i.e., the upper spur and groove zone and the reef ridge below the 30m-deep sand channel (Table 1). *Lobophora variegata* was the dominant single organism with 35% mean cover, relatively uniformly distributed over the entire depth range, followed by *Cladophoropsis* sp. (18%) and *Halimeda* spp. (16%). The last two reached peak abundances at shallow fore-reef depths (Table 1), along with *Dictyota* spp. (8%) and *Sargassum* spp. (2%). *Sargassum polyceratium* predominated on the upper spurs while *Sargassum hystrix* occurred in the deeper zone. Coralline algae were abundant (35% mean cover) but difficult to quantify accurately beneath the mostly multilayered frondose macroalgal canopies. Importantly, microscopic algae and algal turfs were not abundant relative to the predominant frondose macroalgal forms. Sponges, with 3% mean cover, reached maximal abundances below the lower spur zone. The shallow back-reef flat was mostly covered by the seagrass *Thalassia testudinum*; however, nearly all hard substrata were dominated by the hypereutrophic indicator species *Chaetomorpha linum* and *Dictyosphaeria cavernosa*.
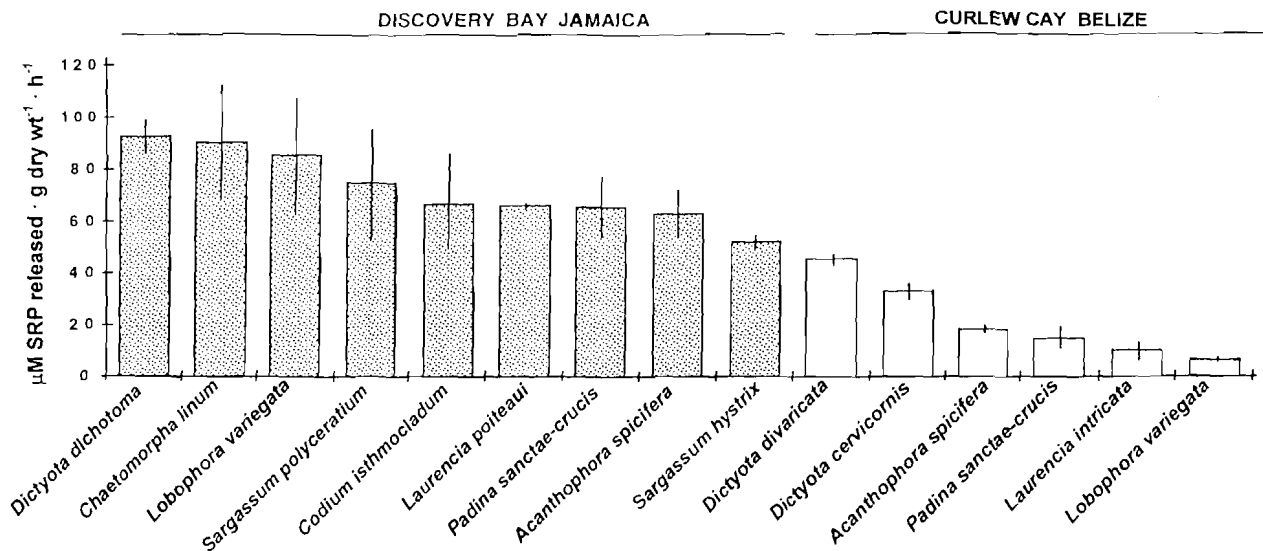

Fig. 5: Alkaline phosphatase activity of macroalgae from Discovery Bay and from the oligotrophic reference site at Curlew Cay, Belize. Values represent means ±1SD (n=4).

DISCUSSION

Results of this study did not falsify the hypothesis that nutrient enrichment was an important synergistic factor responsible for the increased productivities (growth rates) and standing crops of macroalgae on reefs at Discovery Bay. The DIN and SRP concentrations (Figs. 3 and 4) were at or exceeded ~1.0μM and 0.1μM, respectively, above which algal overgrowth begins to occur (Bell 1992; Lapointe et al. 1993). The DIN and SRP concentrations at Discovery Bay measured during this study rank among the highest concentrations reported for coral reefs worldwide and explain why such impressive macro-algal biomass now dominates this eutrophic reef system.

The potential for eutrophication at Discovery Bay was documented by widespread groundwater inputs of NO3⁻ in conjunction with predictions (D'Elia et al. 1981) of increased SRP enrichment associated with exponential human population growth and sewage pollution. Ironically, the NO3⁻ and SRP concentrations reported by D'Elia et al. (1981) for the back-reef habitats were all above 2.0 and 0.15μM, respectively; concentrations that already exceeded critical nutrient thresholds for eutrophication. This finding explains why the Jamaican macroalgal blooms began expanding in the early 1980's throughout the back-reef communities (T. J. Goreau, pers. comm.), prior to the die-off of Diadema in 1983.

Our nutrient data, in conjunction with those of D'Elia et al. (1981), suggest that nutrient concentrations increased in the back reef during the 1980's and spatially spread offshore, elevating DIN and SRP levels on the fore reef above critical thresholds. The SRP concentrations in groundwater-enriched seawater (28ppt) in the grotto reported by D'Elia et al. (1981) was ~0.25μM, a value lower than the average of 0.33μM during the present study in 1987. SRP concentrations were also ~0.10μM on the fore reef, indicating that this offshore habitat was at the SRP threshold in the late 1970's. The average NO3⁻ concentration for the outer back reef was ~2.0μM in the late 1970's (D'Elia et al. 1981), approximately half that measured on the fore reef during this study. More recent DIN and SRP measurements near our back-reef station averaged 7.27μM and 0.27μM between November 1987 and May 1988 and 5.67μM and 0.45μM between April and June 1989. Measurements following a rain event on 27 May 1989 at this station showed highly elevated DIN and SRP concentrations of 24.12μM and 1.01μM, respectively (Macfarlane 1991). The relatively high tissue N content of the dominant organism, Lobophora variegata, on the fore reef to 24m, confirmed the widespread impact of nearshore groundwater discharges on reef metabolism.
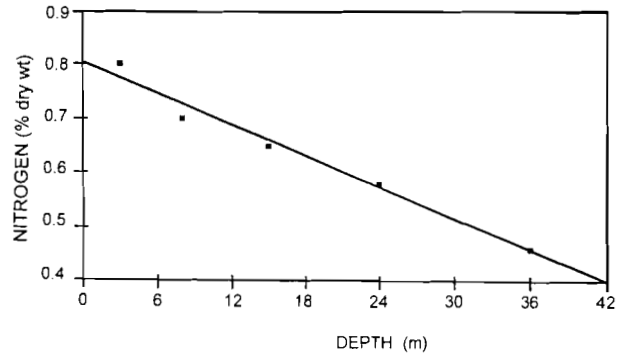

Fig. 6: Nitrogen content of Lobophora variegata versus depth showing the sequestering of high levels of N at offshore, light-limited depths on the Discovery Bay fringing reef; slope of N content (percent dry wt) = 0.80375-0.00088D, where D is the depth in meters (R=0.99, n=2).

The significant NO3⁻ and concomitant salinity stratification throughout the study area at Discovery Bay shows that nutrients derived from submarine groundwater discharges and springs along the shore are transported offshore as buoyant plumes. The groundwater-borne NO3⁻ was highly enriched in the reduced-salinity surface waters, which became progressively diluted as they mixed with more offshore, higher-salinity seawater lower in NO3⁻. Offshore dispersion and dilution clearly emphasize the open connection of this system with oceanic waters and explain the lack of planktonic food-web build-up (cf. Kaneohe Bay, Smith et al. 1981) and paucity of benthic filter feeders (e.g., sponges = only 3% cover). The effects of these N inputs from nearshore groundwater discharges were evident (Fig. 6) in the higher tissue N content of Lobophora variegata on the shallow fore reef (above 24m) compared to the deeper fore-reef slope populations. This trend of decreasing tissue N content with increasing depth and light attenuation is opposite predictions based on controlled physiological studies (Lapointe and Duke 1984) that showed increased tissue N associated with reduced irradiance and growth, further emphasizing the significant influence of DIN in promoting rapid growth offshore. In addition to offshore N dispersion via buoyant surface plumes, low-salinity high-NO3⁻ pore waters have been found (Pigott and Land

Table 1. Discovery Bay transect summary giving percent cover of dominant benthic organisms as a function of depth. Layering of populations resulted in >100% cover in the shallower communities (n=5 · depth interval⁻¹).

Taxa	Depth Intervals (m)													
	0.0-3.0	3.1-6.0 (upper spur)	6.1-9.0	9.1-12.0	12.1-15.0	15.1-18.0	18.1-21.0 (lower spur)	21.1-24.0 (sand channel)	24.1-30.0 (ridge)	30.1-33.0	33.1-36.0	36.1-43.0	43.1-46.0	46.1-50.0
Hermatypic corals	4	12	18	1	1	2	1	10	10	2	18	4	14	6
Sponges	1	0	2	0	1	0	3	2	9	1	2	8	6	6
Gorgonians	1	0	0	0	0	0	0	1	1	0	2	8	6	6
Crustose corallines	37	48	22	26	12	18	12	5	10	0	12	26	15	17
Frondose macroalgae														
Lobophora variegata	37	42	41	25	30	28	46	57	34	3	36	42	35	32
Sargassum spp.	12	8	4	0	0	0	0	4	0	0	0	0	0	0
Dictyota spp.	56	48	4	0	0	0	0	3	0	0	0	0	0	0
Halimeda spp.	29	27	26	22	29	32	16	10	2	0	10	2	7	6
Cladophoropsis sp.	34	43	28	47	37	32	25	8	0	0	0	0	0	0
Other macroalgae	12	2	3	9	2	7	12	8	4	2	2	2	1	0
Total frondose algae	180	170	106	103	98	99	99	90	40	5	48	46	44	32

1986) in fore-reef sediments at Discovery Bay, suggesting that NO3‾-rich groundwaters are seeping through the fore reef itself. These data, clearly showing that extensive areas of the Discovery Bay fringing reefs to depths of at least 24m are being affected by groundwater DIN enrichment, are therefore quite unequivocal.

The high concentrations of NO3‾ in combination with 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 and the pronounced P-limitation of macroalgal growth. The high APA values of all macroalgae assayed (Fig. 5), especially Chaetomorpha linum, Dictyota sp. and Lobophora variegata, represent physiological responses to this dystrophic N-rich environment; the high APA allows these species to utilize dissolved organophosphorus compounds as additional sources of P to achieve balanced growth. Light-saturated photosynthesis (Pmax) of the chlorophyte Chaetomorpha linum was enhanced by SRP enrichment, suggesting that P-enrichment of the back reef has enhanced blooms of this hypereutrophic indicator species (Lapointe et al. 1993), and another—Dictyosphaeria cavernosa ("green bubble weed")—that overgrew coral reefs in Kaneohe Bay, Hawaii, as a result of sewage and urban pollution (Banner 1974). Nutrient enrichment throughout the past decade has allowed such species to overgrow and smother massive hermatypic corals, e.g. Montastrea annularis, in the back reef (BEL, pers. obs.). The longer-lived forms, Sargassum polyceratium and Cladophoropsis sp., also have responded to increased SRP concentrations by expanding their offshore distribution and cover from nearshore spring and back-reef habitats in the early 1980's to more offshore fore-reef habitats now shared with blooms of Dictyota spp., Sargassum hystrix and Lobophora variegata (Table 1). The phaeophyte, S. filipendula, and the chlorophyte Enteromorpha chaetomorphoides, also overgrew fringing coral reefs on the southwest coast of Martinique during the late 1980's as a result of P-enrichment associated with cultural eutrophication (Littler et al. 1993). Rhodophyta are typically abundant components of the algal community on undisturbed oligotrophic coral reefs (Littler et al. 1987) and their paucity in the transect biota (Table 1) is a further indication of prolonged elevated nutrient levels, as is the predominance of macroalgal- vs. turf-algal forms (predicted in Fig. 1).

The evidence suggests that both DIN and SRP concentrations throughout the back reef had been above critical thresholds for over a decade when a major physical disturbance—Hurricane Allen—struck in 1980. This hurricane caused severe damage to the reef, especially the crest zone (0–6m) previously dominated by luxuriant stands of the elkhorn coral Acropora palmata (Woodley 1980). Although the physical disturbance was dramatic, it was not considered totally destructive and 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 levels were above critical threshold concentrations for maximum macroalgal growth, allowed the faster developing macroalgae to physically outcompete the corals and turf algae as predicted in Fig. 1. Eutrophication not only increases the biomass of 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 by eutrophication processes, provide a more robust explanation for the replacement of corals by macroalgae on reefs at Discovery Bay (cf. Hughes 1994).

In addition to the data supporting bottom-up control of macroalgal growth at Discovery Bay, further information exists to moderate the "top-down" interpretation of Hughes (1994). This evidence includes the fact that fish populations on the deep fore reef (below 15m) were overfished by intensive use of fish traps in the 1960's (Munro 1983), long before the widespread and massive blooms of Sargassum polyceratium developed on these reefs in the late 1980's. Fish and urchin grazing have never played a substantial role in the reef-crest area as well (Morrison 1988) due to the turbulent wave

action. Furthermore, the mass mortality of Diadema occurred in 1983, years prior to the expansion of Chaetomorpha linum and Sargassum polyceratium from restricted areas around grottos in the back reef onto the fore reef. Experimental studies during the 1980's at Discovery Bay (Morrison 1988) showed that while Diadema played a significant role in structuring the shallow (above 10m) communities on small spatial scales, this was not the case for communities below 15m; these studies were performed during a period of high Diadema densities when many habitats had high standing crops of macroalgae. Hence, there is inconsistency in the timeline between reduced herbivory from overfishing and massive macroalgal overgrowth in both shallow and deep habitats. These observations further reinforce the conclusion that reduced herbivory could not have been the only factor causing the massive macroalgal blooms that developed on reefs at Discovery Bay.

The evidence presented here adds a further dimension of complexity, augmenting Hughes (1994) conclusion that the algal blooms in Jamaica implicate loss of herbivory. The argument that reduced herbivory from overfishing and the Diadema die-off are correlated with the increased macroalgal biomass on Jamaican coral reefs is made more compelling by inclusion of the synergistic role of nutrient enrichment (Fig. 1). In addition, previous evidence of widespread nutrient enrichment at Discovery Bay (D'Elia et al. 1981) also leads to the obvious alternative hypothesis of the importance of bottom-up control on coral reefs (Littler and Littler 1984; Littler et al. 1991b). The locations of most of the macroalgal dominated habitats cited by Hughes (1994) suggest large-scale non-point-source nutrient loading associated with deforestation, sewage, agricultural and industrial development (Johannes 1975; Nixon 1995). All of these sources increased along Jamaica's coast over the past decades and, hypothetically, contributed to nutrient over-enrichment, giving rise to the macroalgal blooms that now dominate these degraded coral reefs.

In conclusion, this study affirms the need to adopt broad theoretical approaches to testing management-related hypotheses regarding the degradation of coral reefs. As pointed out by Dayton and Oliver (1982), scientists should constantly guard against preconceived concepts, research designed to verify rather than falsify hypotheses and narrow approaches that do not test multiple hypotheses, which can lead to accepting oversimplified hypotheses. While this is unhealthy for science in general, it can be devastating for coral reef conservation, especially in today's world when beaurocrats and resource managers often look for a politically expedient "quick fix". Hughes' (1994) conclusion that a ban on fish traps is needed to save Jamaican coral reefs from macroalgal overgrowth is extremely important, but, unfortunately, implies to managers that the effects of eutrophication are relatively minor. The evidence clearly indicates that eutrophication is an important and widespread problem, a conclusion recognized by a consensus of coral reef scientists (Ginsberg 1993). There is also considerable evidence that eutrophication, by itself, can lead to a reduction in reef fish populations (Johannes 1975). Thus, it is unlikely that simply controlling fishing practices will restore Jamaica's reefs, or other coral reefs being impacted by severe eutrophication. More importantly, the reality of large-scale coastal eutrophication needs to be vigorously confronted by scientists and resource managers alike, both in Jamaica and worldwide.

REFERENCES

Banner AH (1974) Kaneohe Bay, Hawaii: urban pollution and a coral reef ecosystem. Proc 2nd Inter Coral Reef Symp, Brisbane 2:685-702

Bell PRF (1992) Eutrophication and coral reefs: some examples in the Great Barrier Reef lagoon. Water Research 26:553-568

Birkeland C (1977) The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proc 3rd Inter Coral Reef Symp 1:15-21

Carpenter SR, Kitchell JF, Hodgson JR (1985) Cascading trophic interactions and lake productivity. BioScience 35:634-639

Dayton PK, Oliver JS (1982) An evaluation of experimental analyses of population and community patterns in benthic marine environments. Pages 93-120 in Tenore KR, Coull BC, eds. Marine Benthic Dynamics. University of South Carolina Press

D'Elia CF, Webb KL, Porter JW (1981) Nitrate-rich groundwater inputs to Discovery Bay, Jamaica: a significant source of N to local reefs? Bull Mar Sci 31:903-910

Goreau TF (1959) The ecology of Jamaican coral reefs: I. Species composition and zonation. Ecology 40:67-90

Goreau TJ (1992) Bleaching and reef community change in Jamaica: 1951-1991. Amer Zool 32:683-695

Hatcher BG, Larkum AWD (1983) An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. J Exp Mar Biol Ecol 113:39-59

Hughes TP (1994) Catastrophes, phase-shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547-1551

Johannes RE (1975) Pollution and the degradation of coral reef communities. Pages 13-51 in Wood E, Johannes RE, eds. Tropical Marine Pollution. Elsevier, New York

Lapointe BE (1995) A comparison of nutrient-limited productivity in Sargassum natans from neritic versus oceanic waters of the Western North Atlantic Ocean. Limnol Oceanogr 40:625-633

Lapointe BE, Duke CS (1984) Biochemical strategies for growth of Gracilaria tikvahiae (Gigartinales, Rhodophyta) in relation to light intensity and nitrogen availability. J Phycol 20:488-495

Lapointe BE, O'Connell JD (1989) Nutrient-enhanced growth of Cladophora prolifera in Harrington Sound, Bermuda: eutrophication of a confined, phosphorus-limited marine ecosystem. Est Coast Shelf Sci 28:347-360

Lapointe BE, Littler MM, Littler DS (1993) Modification of benthic community structure by natural eutrophication: the Belize Barrier Reef. Proc 7th Inter Coral Reef Symp, Guam 1:323-334

Littler MM, Littler DS (1984) Models of tropical reef biogenesis: the contribution of algae. Prog Phycol Res 3:323-364

Littler MM, Littler DS, Hanisak MD (1991a) Deep-water rhodolith distribution, productivity, and growth history at sites of formation and subsequent degradation. J Exp Mar Biol Ecol 150: 163-182

Littler MM, Littler DS, Lapointe BE (1993) Modification of tropical reef community structure due to cultural eutrophication: the southwest coast of Martinique. Proc 7th Inter Coral Reef Symp, Guam 1:335-343

Littler MM, Littler DS, Titlyanov EA (1991b) Comparisons of N- and P-limited productivity between high granitic islands versus low carbonate atolls in the Seychelles Archipelago: a test of the relative dominance paradigm. Coral Reefs 10:199-209

Littler MM, Taylor PR, Littler DS, Sims RH, Norris JN (1987) Dominant macrophyte standing stocks, productivity and community structure on a Belizean barrier-reef. Atoll Res Bull, No 302:1-24

Macfarlane AH (1991) The mariculture potential of Gracilaria species (Rhodophyta) in Jamaican nitrate-enriched back-reef habitats: growth, nutrient uptake and elemental composition., Ms thesis, Univ of Miami, pp xii + 96

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

Munro JL (1983) Jamaican fisheries trends. ICLARM Stud Rev 7:1

Nixon SW (1995) Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia 41:199-219

Pigott JD, Land LS (1986) Interstitial water chemistry of Jamaican reef sediment: sulfate reduction and submarine cementation. Mar Chem 19:355-378

Smith SV, Kimmerer WJ, Laws EA, Brock RE, Walsh TW (1981) Kaneohe Bay sewage diversion experiment: perspectives on ecosystem response to nutritional perturbation. Pac Sci 35:279-397

Tomascik T (1991) Settlement patterns of Caribbean scleractinian corals on artificial substrata along an eutrophication gradient, Barbados, West Indies. Mar Ecol Prog Ser 77:261-269

Woodley JD (1980) Hurricane Allen destroys Jamaican coral reefs. Nature 287:387