

Harmful algae on tropical coral reefs: Bottom-up eutrophication and top-down herbivory

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Abstract

A conceptual paradigm, the “Relative Dominance Model”, provides the perspective to assess the interactive external forcing-mechanisms controlling phase shifts among the dominant benthic functional groups on tropical coral reefs [i.e., microalgal turfs and frondose macroalgae (often harmful) versus reef-building corals and calcareous coralline algae (mostly beneficial due to accretion of calcareous reef framework)]. Manipulative experiments, analyses of existing communities and bioassays tested hypotheses that the relative dominances of these functional groups are mediated by two principal controlling factors: nutrients (i.e., bottom-up control) and herbivory (i.e., top-down control). The results show that reduced nutrients alone do not preclude fleshy algal growth when herbivory is low, and high herbivory alone does not prevent fleshy algal growth when nutrients are elevated. However, reduced nutrients in combination with high herbivory virtually eliminate all forms of fleshy micro- and macro-algae. The findings reveal considerable complexity in that increases in bottom-up nutrient controls and their interactions *stimulate* harmful fleshy algal blooms (that can alter the abundance patterns among functional groups, even under intense herbivory); conversely, elevated nutrients *inhibit* the growth of ecologically beneficial reef-building corals. The results show even further complexity in that nutrients also act *directly* as either *limiting* factors (e.g., physiological stresses) or as *stimulatory* mechanisms (e.g., growth enhancing factors), as well as functioning *indirectly* by influencing competitive outcomes. Herbivory *directly* reduces fleshy-algal biomass, which *indirectly* (via competitive release) favors the expansion of grazer-resistant reef-building corals and coralline algae. Because of the sensitive nature of *direct/indirect* and *stimulating/limiting* interacting factors, coral reefs are particularly vulnerable to anthropogenic reversal effects that decrease top-down controls and, concomitantly, increase bottom-up controls, dramatically altering ecosystem resiliencies.

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1. Introduction

Coral-reef ecosystems are adapted to conditions far removed from human influences, such as eutrophication

and destructive fishing. It would appear that in regard to nutrients (NH_4^+ , NO_3^- , NO_2^- and PO_4^{3-}), the fewer the better; with the opposite being the case for herbivores (parrotfishes, surgeonfishes, rudderfishes), where more are usually better. Under such conditions, coral reefs have evolved impressive levels of biological diversity, including many uniquely specialized photo-synthetic symbionts and benthic algae. Four major functional groups of benthic photosynthetic organisms

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are responsible for the bulk of coral-reef primary production: microalgal turfs (defined here as fleshy filamentous and prostrate forms <2 cm high), frondose macroalgae, calcareous crustose coralline algae and reef-building corals (containing symbiotic algae). Of these, cnidarian corals and coralline algae are the most desirable due to their accretion of the CaCO₃ matrix that comprises the reef framework, which is responsible for the spatial heterogeneity/complexity that supports the remarkable diversity of associated biota.

The concepts “top-down” and “bottom-up” controls have long been used (e.g., Atkinson and Grigg, 1984; Carpenter et al., 1985) to describe mechanisms where either the actions of predators or resource availability regulate the structure of aquatic communities; these opposing concepts can be particularly useful in understanding complex coral-reef ecosystems. The Relative Dominance Model (RDM, Fig. 1, first

proposed by Littler and Littler, 1984a) predicts that the competitive outcomes determining the relative abundances of corals, crustose coralline algae, microalgal turfs and frondose macroalgae on coral reefs are most often controlled by the complex interactions of environmental factors (bottom-up controls such as nutrient levels) and biological factors (top-down controls such as grazing).

Before any model can be useful, its predictions must accurately reflect the biological relationships in the target ecosystems. The previous evidence relevant to the RDM consists of several short-term experiments (e.g., Miller et al., 1999; Thacker et al., 2001; Belliveau and Paul, 2002), in the case of bottom-up versus top-down effects, as well as considerable circumstantial evidence (e.g., Hallock et al., 1993; Hughes, 1994) and correlative biogeographic surveys (Littler et al., 1991; Verheij, 1993). Using a longer-term manipulative approach on an

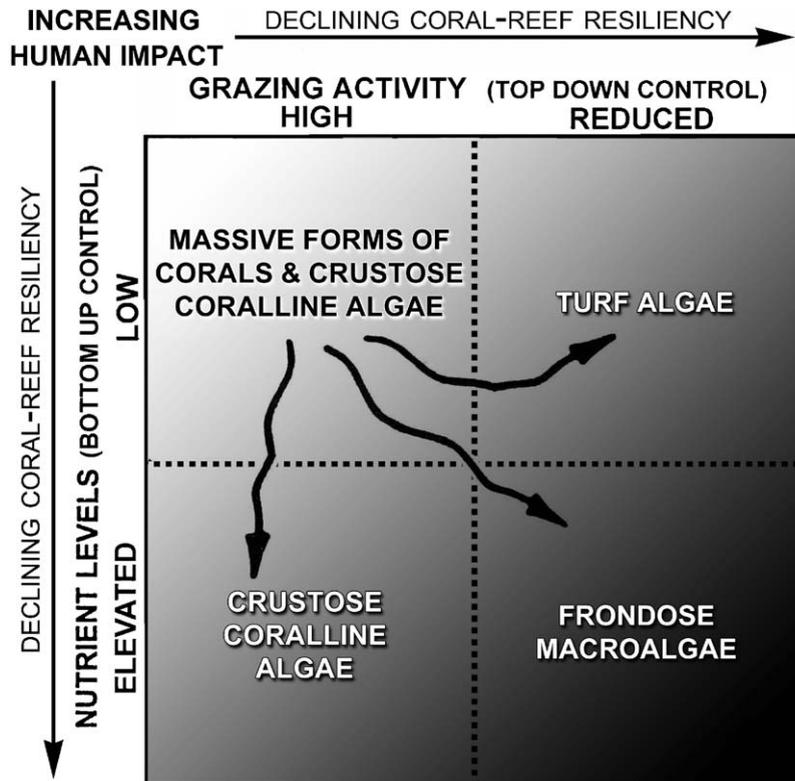


Fig. 1. The Relative Dominance Model. All of the four sessile functional groups depicted occur under the conditions in every compartment of the model; however, the RDM predicts which groups will be predominant under the complex interacting vectors of eutrophication and declining herbivory (most often anthropogenically derived). Crustose coralline algae are posited to be competitively inferior and dominate mainly by default; where frondose algae are removed by herbivores and corals are inhibited by nutrients. The dotted lines represent tipping points where the external forcing functions of increasing nutrients and declining herbivory reach critical levels that reduce resiliency to phase shifts. Light to dark shading indicates declining desirability of each functional group from a management perspective. Hypothetically, one vector can partially offset the other (e.g., high herbivory may delay the impact of elevated nutrients, or low nutrients may offset the impact of reduced herbivory). We further posit that such latent trajectories can be activated or accelerated by large-scale stochastic disturbances such as tropical storms, cold fronts, warming events, diseases and predator outbreaks; events from which coral reefs have recovered for millions of years in the absence of humans.

appropriately oligotrophic coral-dominated reef, Smith et al. (2001) provide the most relevant experimental evidence in support of the RDM to date.

Top-down control by abundant populations of large mobile herbivores has been shown repeatedly since the time of Stephenson and Searles (1960) for coral reefs. As noteworthy examples, Carpenter (1986), Lewis (1986), Morrisson (1988) and many other workers (reviewed in Steneck, 1989; McCook, 1999; Bellwood et al., 2004) have unanimously reported that lowering herbivory without changing nutrient inputs often results in rapid increases in fleshy algae on coral reefs. However, in most of the few studies that manipulated both herbivores and nutrients (e.g., Thacker et al., 2001; McClanahan et al., 2002; Belliveau and Paul, 2002), the duration was too short and adequate nutrient data were lacking, or ambient nutrient background concentrations already exceeded levels limiting to macroalgal growth (e.g., Miller et al., 1999).

Despite many advocates, herbivory patterns alone do not consistently explain the distributions and abundances of benthic algae on coral reefs (Adey et al., 1977; Hay, 1981; Hatcher and Larkum, 1983; Hatcher, 1983; Carpenter, 1986). For example, several studies (e.g., Hatcher, 1981; Schmitt, 1997; Lirman and Biber, 2000) found no significant correlation between grazing intensity and frondose algal biomass. A dramatic increase in fleshy algal biomass due to eutrophication was reported (Fishelson, 1973) without any concomitant reduction in herbivore populations. As noted by Lewis (1986), frondose macroalgae occur in healthy reef areas of low herbivory (see also Littler et al., 1986); many such areas generate increased current acceleration, like the reef crest and tops of patch-reef rocks, implicating higher nutrient fluxes (e.g., see Atkinson and Bilger, 1992; Bilger and Atkinson, 1995). Further considerations are the widespread abundance of nitrogen-fixing Cyanobacteria and the now-ubiquitous presence of substantial anthropogenic nitrogen sources (from burning fossil fuels) in rainfall worldwide (Vitousek et al., 1997)—making the terms “pristine” or “nutrient-limited” relative, at best.

Coral reef ecosystems have evolved in the most oligotrophic of warm ocean waters and are sensitive to low level increases in the concentrations of dissolved inorganic nitrogen ($\text{DIN} = \text{NH}_4^+ + \text{NO}_3^- + \text{NO}_2^-$) and soluble reactive phosphorus ($\text{SRP} = \text{PO}_4^{3-}$) associated with human eutrophication (Johannes, 1975; Tomascik and Sander, 1987a,b; Bell, 1992; NRC, 1995; Dubinsky and Stambler, 1996). Nutrient enrichment of coral reefs has many direct and indirect effects that, over time, can result in alternative stable states dominated by fleshy,

non-calcifying macroalgae (Birkeland, 1987; Done, 1992; Lapointe et al., 1993, 1997; Lapointe, 1997; NRC, 2000; Bellwood et al., 2004). Growth and reproduction of macroalgae are nutrient limited in oligotrophic coral-reef waters (Lapointe, 1987, 1997, 1999; Larned and Stimson, 1996; Schaffelke and Klumpp, 1998; Lapointe et al., 2004) where low-nutrient concentrations and high herbivory favor the dominance of calcareous, hermatypic corals (Adey, 1998; McConnaughey et al., 2000). Case studies in Kaneohe Bay, Hawaii, USA (Banner, 1974; Smith et al., 1981) and, more recently, the Negril Marine Park, Jamaica (Goreau, 1992; Lapointe and Thacker, 2002) have demonstrated the pivotal role of low-level nutrient enrichment to the development of excessive macroalgal biomass (ECO HAB, 1997) on coral reefs. Macroalgae can inhibit the survival of coral recruits (Birkeland, 1977; Sammarco, 1980, 1982) and because of enhanced growth and reproduction in the presence of elevated nutrients, they can quickly overgrow the slower-growing hermatypic corals (NRC, 1995).

Spatial and temporal patterns of nutrients also have been shown (Adey et al., 1977; Hatcher and Hatcher, 1981; Hatcher and Larkum, 1983) to co-vary with algal biomass. The decrease in coral cover (Pollock, 1928), relative to frondose algae (Doty, 1971) and coralline algae (Littler, 1971), on the reef flat at Waikiki, Hawaii was the first phase shift from coral to macroalgal domination that was postulated (Littler, 1973) as due to increases in eutrophication (bottom-up control). Shifts from coral dominance to algal dominance that suggest linkages with chronic nutrient loading are exemplified by case studies in Hawaii (Littler, 1973; Banner, 1974; Smith et al., 1981), Venezuela (Weiss and Goddard, 1977), the Red Sea (Mergener, 1981), Barbados (Tomascik and Sander, 1985, 1987a,b), Reunion Island (Cuet et al., 1988), Bermuda (Lapointe and O'Connell, 1989), the Great Barrier Reef (Bell, 1992), mainland southeast Florida (Lapointe et al., 2005a,b), the Florida Keys (Lapointe et al., 1994), Martinique (Littler et al., 1993) and Jamaica (Goreau et al., 1997; Lapointe et al., 1997). The very low nutrient levels involved in limiting macroalgal growth (tipping points are the critical nutrient levels that reduce resiliency to phase shifts), either natural or anthropogenic, have been proposed (Bell, 1992; Lapointe et al., 1997) regarding the enabling of undesirable transitions from coral dominance toward algal stable states. Therefore, understanding both the processes of productivity (bottom-up) and those of disturbance (top-down) are critical to the elucidation of mechanisms that mediate algal/herbivore interactions.

The present 24-month investigation combines in situ experiments with field bioassays and descriptive surveys to provide predictive information regarding the relative importance of bottom-up versus top-down controls on the dominant benthic functional groups on coral reefs. The study includes: (1) characterization of environmental parameters (i.e., nutrient analyses, herbivory assays and nutrient-limitation bioassays); (2) distribution and abundance patterns of indicator-groups and their palatability to herbivores; and (3) controlled manipulations of nutrient concentrations in areas of both high and low herbivory. We believe that the strongest approach is to test multiple hypotheses using multifaceted experiments. Both environmental and bioassay data are essential to characterize the ambient nutrient/herbivory environments and antecedent nutrient history of the two Study Sites (A and B, Fig. 2). The nutrient-limitation bioassays provide physiological tests of the assumption that both Study Sites A and B have had an oligotrophic history. This type of assay furnishes a powerful index to the long-term integration of the ambient nutrient concentrations by the naturally occurring functional producer groups prior to and following experimental enrichment. In the palatability assays, natural populations of reef fishes are

used to assess the herbivore resistances of predominant functional groups, including the massive reef-building corals, as an independent test of the RDM's efficacy. The controlled manipulative experiments examine the importance of nutrient regime on long-term recruitment, colonization and competition patterns that influence coral-reef community structure in habitats with contrasting levels of herbivory. Transplant studies test the growth/inhibition responses of reef-building corals to elevated nutrients under natural levels of high herbivory.

In healthy tropical reefs, nutrient concentrations are extremely low and attachment space is pre-empted by a broad diversity of sessile benthic organisms. Given these conditions, competition between attached organisms should be severe. We posit that competition for space and light is not only important in determining the relative abundances of major functional groups, but also that the outcome of competition for these resources on coral reefs is often controlled by differential nutrient and grazing effects. Controlled nutrient-enrichment experiments, utilized in conjunction with closely juxtaposed habitats of high versus low herbivores, test hypotheses concerning the colonization and competitive interactions of harmful blooms of microalgal turfs

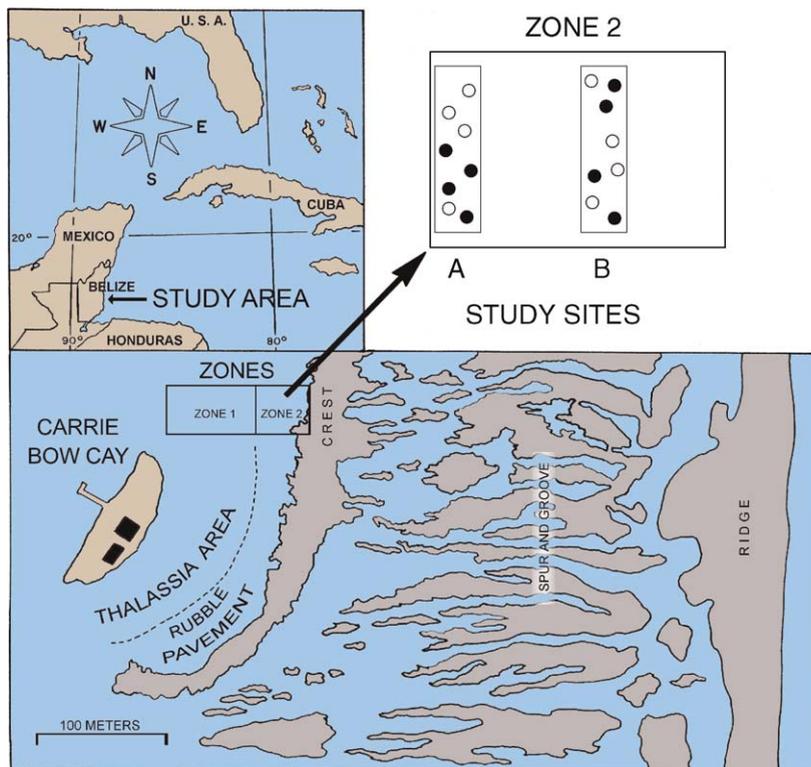


Fig. 2. Location of the two main reef-flat Zones and the two Study Sites (A = low herbivory, B = high herbivory) and diffuser arrays (open = reduced nutrients, closed = elevated nutrients) at CBC.

and frondose macroalgae versus beneficial reef-building corals and crustose coralline algae on a healthy barrier-reef system. The RDM (Fig. 1) provides the perspective for advancing hypotheses and is examined by the following four central predictions: In the high-herbivory Study Site B (Fig. 2): (1) reduced nutrients should favor the development of calcareous coralline algae and corals relative to frondose macroalgae and microalgal turfs; and (2) elevated nutrients should result in high coverage of coralline algae; whereas in the low-herbivory Study Site A; (3) elevated nutrients should lead to the dominance of frondose macroalgae; and (4) reduced nutrients should lead to an abundance of turf microalgae.

2. Materials and methods

2.1. Study areas

The Belize Barrier Reef complex is the largest coral-reef tract in the western hemisphere (over 250 km in length and from 10 to 32 km wide), consisting of an almost unbroken barrier reef containing hundreds of patch reefs and mangrove islands. Within back-reef habitats, such as the one studied here (Fig. 2), assemblages of framework-building corals and calcareous algae have the same general taxonomic composition along the entire barrier reef (Burke, 1982, personal observations). Carrie Bow Cay (CBC) reef habitats and surrounding environs comprise a well-developed, representative, barrier-reef system remote from major human influences. Offshore Secchi disc depths in excess of 43 m are typical, indicating Jerlov Type I oceanic waters. Most importantly, nutrient levels above the tipping-point concentrations noted (Bell, 1992) to potentially enable macroalgal overgrowth (i.e., $>0.1 \mu\text{M}$ phosphorus and $>1.0 \mu\text{M}$ nitrogen) have seldom been recorded (Lapointe et al., 1987, 1993) from coral reefs of this system.

The topography, geology and general biology of CBC are well known due to over a quarter century of study (see Ruetzler and Macintyre, 1982). Herbivory has been extensively investigated for many of the CBC reef habitats (Hay, 1981; Littler et al., 1983b, 1986, 1987a, 1989, 1995; Lewis and Wainwright, 1985; Lewis, 1986; Lewis et al., 1987; Macintyre et al., 1987; Reinthal and Macintyre, 1994), including the sites studied here. The two experimental Study Sites (A and B, Fig. 2), located directly shoreward of the intertidal and spatially complex reef crest on the northeast side of CBC ($16^{\circ}48'N$, $88^{\circ}05'W$), are typical of the back-reef systems found throughout much of the Belizean barrier

tract (James et al., 1976; Burke, 1982; personal observations). The community composition and zonal patterns of the CBC region are also representative of much of the entire barrier reef platform (Littler et al., 1989, 1995). Furthermore, distinct similarities exist between the Belize Barrier Reef's biological/geological zonation and the barrier reefs of the north coast of Jamaica (Goreau, 1959; Goreau and Land, 1974), the north coast of Haiti (Burke, 1982), the southeastern coast of Alarcran (Burke, 1982) and the offshore reefs of the Bahamas, Puerto Rico, the Lesser Antilles, Panama's San Blas Islands, Mexico's Yucatan Peninsula and the Bay Islands of Honduras (Littler and Littler, 2000, personal observations).

The bottom characteristics exhibit a shoreward (i.e., westward, downstream) transition from the smooth flat pavement zone adjacent to the crest to a rubble-pavement zone (Fig. 2). These are followed by a thin overlying veneer zone of rubble and gravel-sized fragments (Littler et al., 1987b; Macintyre et al., 1987), finally grading to an epilithic *Thalassia*-bed. The *Thalassia* plants on this reef flat are firmly anchored directly to the pavement and secondarily entrap a thin layer of gravel and coarse sand.

The back-reef pavement zone and rubble-pavement zone (Fig. 2) contain numerous coral colonies (Lewis, 1986; Littler et al., 1989) and are characterized by high densities of transient herbivorous fishes (Hay, 1981; Lewis and Wainwright, 1985). Sea urchins and territorial damselfishes are uncommon in the CBC back-reef areas studied (Lewis, 1986; personal observations). The most common herbivorous fish species in the outer Study Site B are: the surgeonfishes *Acanthurus bahianus* and *A. coeruleus*, and the parrotfishes *Scarus inserti*, *Sparisoma chrysopterum*, *Sparisoma viride* and *Sparisoma rupripinne*. Repeated censuses from April 1982 to March 1983 (see Table 2 of Lewis, 1986) indicated reasonably stable herbivorous fish populations and this pattern has continued to the present.

2.2. Environmental data

To characterize the nutrient environment of CBC, water samples were collected from each of the two Study Sites (designated A and B, Fig. 2) in 100 ml acid-washed polyethylene bottles. Each sample was taken as three separate replicates (to increase coverage) and pooled (to reduce analytical costs). Samples were obtained once yearly from 3 cm above the surface (i.e., top) of individual clay-pot diffusers (see description below) 3 weeks following the addition of fertilizer (N = 12 separate samples of three pooled replicates each) in

each Study Site during midday. At the same time, an additional 12 concurrent samples were taken from 3 cm above non-enriched (control) diffusers to compare both natural and enriched levels of nutrients. The samples were immediately filtered through combusted Gelman 0.45 μm GF/F filters, placed in a cooler of ice and frozen in the laboratory until analysis. Dissolved inorganic nitrogen ($\text{DIN} = \text{NH}_4^+ + \text{NO}_3^- + \text{NO}_2^-$) and soluble reactive phosphorus ($\text{SRP} = \text{PO}_4^{3-}$) concentrations were determined by the Nutrient Analytical Services Laboratory, Chesapeake Biological Laboratory, Solomons, MD. SRP and NO_3^- were measured with a Technicon Autoanalyzer II. NH_4^+ and NO_2^- were measured using a Technicon TRAACS 800. The detection limits for NH_4^+ , NO_3^- plus NO_2^- and SRP were 0.21, 0.01 and 0.02 μM , respectively.

The current speeds at both sites were measured sporadically under typical non-storm wind and wave conditions on 12 separate days during the 24-month study by fluorescent dye injected next to the nutrient diffusers on the bottom and timing the movement over a horizontal distance of 2.0 m. To further characterize water quality (light penetration), Secchi disc depths were determined just to the east of the study areas in the deeper waters bathing the reef flat, between 1000 and 1100 h on 10 separate occasions.

2.3. Herbivory assays

Natural levels of herbivory close to the experimental arrays at the eastern transitional margin of Study Site A (Fig. 2, relatively remote from structural shelter) and Study Site B (relatively closer to the shelter of the crest structure, see diffuser locations in Fig. 2) were assayed using the palatable test alga, *Acanthophora spicifera*. This ubiquitous red alga is a highly preferred food item by both parrotfishes and surgeonfishes (Lewis and Wainwright, 1985), as well as by sea urchins (Littler et al., 1983b). The alga was cut into 7.0-cm lengths and attached to $\sim 3 \times 10$ -cm dead coral-rubble fragments by thin (1-mm thick \times 5-cm long), dull-beige, rubber bands. Fifteen replicates were placed haphazardly in each Study Site for 3 h. Additionally, 15 replicates of the seagrass *Thalassia testudinum* were placed (using the above methods) in Study Site A to augment the data that Hay (1981) collected only for Study Site B. This technique avoided both pseudo-replication (non-independence) and novelty effects (i.e., artifactual conspicuousness) that could bias grazing patterns and rates. We have personally observed that gaudy markers, or devices such as colored rope and surveyor's tape, alarm herbivorous fishes in areas where they are intensively

harvested and, conversely, attract them in protected (no-fishing) reserves. Percent eaten was determined by re-measuring the algal segments and the results were analyzed using one-way ANOVA followed by the Bonferroni (Dunn) *t*-test (SAS, 2003). Herbivorous fish abundances were enumerated by counting numbers of individuals (by species), from mid-morning to mid-day throughout a typical spring day, 1 m on either side of 15, 10-m long, north-south, transect lines. Historical values from previous literature (Hay, 1981; Lewis and Wainwright, 1985) in the same locations were also re-examined and tabulated with the current data set.

2.4. Biotic distribution patterns

A cluster analysis of the coral and macrophyte cover was used to test the hypothesis that grazing intensity and algal characteristics that resist herbivory (e.g., calcification) are related to the natural distribution patterns of the dominant functional groups. A single transect on compass heading 90° magnetic was established beginning next to shore on the CBC reef flat in 0.2 m of water and extending eastward to the reef crest at a distance of 111 m. Quantitative samples were obtained by photographing (perpendicular to the substrate) 0.15-m² quadrats centered at every third meter mark from 0 to 100, and at every meter mark thereafter. Due to the patchy nature of the biota, uniformly spaced quadrat arrays produced a more representative sampling than would patchy (i.e., randomized) hit-or-miss arrays (see discussion in Littler and Littler, 1985). Simultaneously, voucher specimens of dominant macrophytes and turf microalgae were taken for taxonomic purposes. In the laboratory, the images were scored using a randomized grid of 100 dots (see Littler and Littler, 1985).

To describe the natural species assemblages along the transect in an unbiased manner, the cover data of each species for all quadrats (those without organisms were excluded) were subjected to hierarchical cluster analysis (flexible sorting, unweighted pair-group method) using the Bray and Curtis (1957) coefficient of similarity. The resultant dendrogram of similar quadrat groupings was based on the dominant biota and environmental affinities and used to characterize zones that were predicted (a priori) to correlate with herbivory levels.

2.5. Nutrient-enrichment assays

Nutrient-enrichment bioassays tested the hypothesis that both Study Sites had an oligotrophic antecedent history. This procedure assayed the light-saturated net

photosynthetic rates (P_{\max}) of the most widespread macroalga (*Dictyota pulchella*) in the CBC study area. The P_{\max} response to DIN and SRP enrichment (detailed in Littler and Littler, 1990) was used as an index to its long-term integration of the ambient nutrient concentrations prior to the experimental enrichment manipulations. Factorial experiments (6 replicate-plants treatment⁻¹) included overnight (dark) pulsing with DIN (as NH_4^+ , 16.0 μM), SRP (as PO_4^{3-} , 1.6 μM), both DIN + SRP and a control (no nutrients added). The above concentrations were chosen to saturate the uptake rates (see Lapointe, 1987) in the small volumes used during nutrient pulsing (4-l freezer bags). These concentrations represent realistic levels encountered in eutrophic reef environments (e.g., near bird islands, Lapointe et al., 1993), and are an order of magnitude below levels characteristic of reef interstitial pore waters used by rhizophytic macrophytes (i.e., 120–200 μM , Williams and Fisher, 1985). The bioassays were performed at 12 month intervals in 1.0 l incubation jars containing ambient seawater under natural saturating irradiance levels (between 1000 and 1300 h, 1400–2200 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 27–29 °C water temperatures), while vigorously mixed by water-driven magnetic turbines to eliminate diffusion boundary layers.

2.6. Palatability experiment

Natural populations of reef fishes were used to assess the herbivore resistances of eight predominant macrophytes representing five morphological form groups as well as two species of massive corals (to test the following prediction and document how the herbivory component of the model works). Sea urchins are no longer common in the CBC environs. If corals and members of the calcified-crustose and jointed-calcareous algal forms have evolved anti-herbivore defenses (e.g., toughness, structural inhibition, low calorific content or toxicity), then they should show the greatest resistance to herbivory by generalist fish grazers with a gradient of increasing palatability toward the more fleshy thick-leathery, coarsely-branched and sheet-like algal form groups (see Littler et al. (1983a) for morphological characterization).

Experiments were run in the rubble-pavement zone (Study Site B, 95 and 100 m) of high herbivory (Fig. 2, Reinthal and Macintyre, 1994) just shoreward of the reef crest. The algae and corals were collected while submerged and separated into approximately 10-cm² clumps to avoid bias arising from a size-based differential attractiveness to visual feeders. The 10-

cm² clumps were attached to independent rubble fragments by thin dull-beige rubber bands and deployed at ~0.5 m intervals in a randomized pattern (12 replicate clumps per each of the 10 species). Surgeonfishes and parrotfishes showed no wariness and began feeding immediately, moving from clump to clump and feeding persistently as they located a particularly palatable species. The clumps were photographed immediately after deployment and 6.0 h later. Quantification of losses was determined digitally from the photographs. Published values from a similar study near the same location (Littler et al., 1983b) also were re-examined and graphically included to augment the present data set.

2.7. Top-down versus bottom-up experiments

To test the RDM, two sites [Study Sites A (72–77 m) and B (92–97 m), Fig. 2] were established in the same structureless rubble-pavement Zone 2 but differing primarily in the levels of herbivorous fish activity; as determined by the patterns of biotic cover (see Fig. 3, Table 3) and palatability (Fig. 4), as well as by herbivorous fish densities and assays of herbivory (Table 2). Nutrients were manipulated in these same environments using 4-l clay diffusers. Data were assessed within functional groups (i.e., relative abundances) as well as at the community level (i.e., relative dominances). The goal of these manipulative experiments was to provide direct experimental tests of the nutrient mediated interactions posited from the RDM. Proximity to seaward reef-crest shelters (Fig. 2) also provided a high level of fish herbivory that was further manipulated for 24 months with nutrient diffusers containing coral transplants (see below).

The low-herbivory Study Site A is not regularly frequented by herbivorous fishes [because of the lack of both large- and small-scale structural shelter from carnivorous fishes (e.g., barracudas, sharks, jacks, snappers) and birds (e.g., ospreys, herons, cormorants, pelicans), which forage daily on the back reef (personal observations)]. Proximity to shelter has been long recognized (Randall, 1965; Ogden et al., 1973) as an important factor determining herbivorous fish foraging ranges. Study Site B, established 15-m seaward (92–97 m) in the same rubble-pavement zone but closer to the shelter of the reef crest, is characterized by exceptionally high fish herbivory (Macintyre et al., 1987; Littler et al., 1989; Reinthal and Macintyre, 1994). Because of the close juxtaposition of the two Study Sites, and otherwise physical/chemical/geomorphic similarity (see Table 1, Lewis, 1986), the

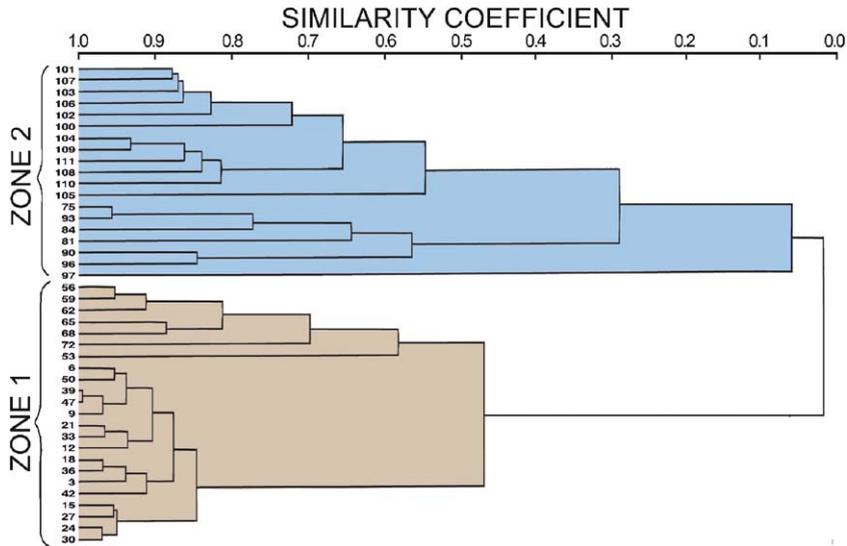


Fig. 3. Dendrogram display showing differential cluster analysis (using the Bray and Curtis (1957) Similarity Coefficient) for the percent cover of dominant taxa, including all quadrats (labeled by distance from CBC shore) except those devoid of biota. Two major zones are indicated (see Table 3, Fig. 2).

degree of fish herbivory is the overriding ecological variable (supported by the herbivory assays, extensive nighttime/daytime observations over a 25-year period and the biotic zonal patterns, see Tables 2 and 3 and Figs. 3 and 4). Both of these experimental sites are in the structurally homogeneous rubble-pavement zone that does not support damselfish or other potentially confounding organisms. Based on earlier work (Dayton and Oliver, 1980; Littler et al., 1989), cages were not used as a method of choice due to well-known problems

with cage artifacts (e.g., shading, alteration of current flow, etc.) and the necessity for cage controls. Furthermore, the exclusion of fish grazers by cages has been shown to promote fouling and also shelter benthic invertebrates from predation. Such potential artifactual increases in the density of mesograzers and fouling organisms (Dayton and Oliver, 1980) would have been undesirable during the 2-year experiment.

Within each of the two Study Sites (A and B, Fig. 2), eight, independent, terra-cotta, clay-pot, nutrient diffu-

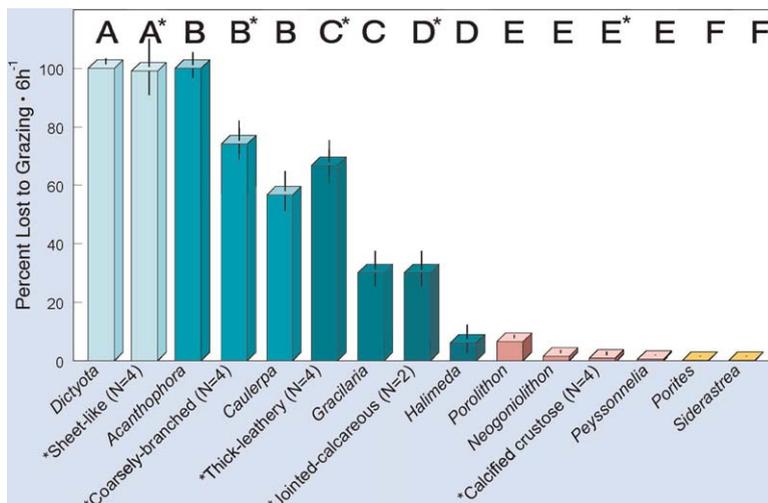


Fig. 4. Susceptibility to fish grazing for species representing five macroalgal form groups ($N = 12\text{-species}^{-1}$). A = sheet-like, B = coarsely-branched, C = thick-leathery, D = jointed-calcareous, E = calcified-crustose. The corals (=F) *Siderastrea radians* and *Porites astreoides* showed zero losses during this experiment. Mean data ($N = \text{species-group}^{-1}$) on CBC form-group palatability values included from Littler et al. (1983b) are indicated by asterisks. All form-group differences are significant ($P < 0.05$, Duncan's Multiple Range Test), vertical lines = $\pm 1\text{S.E.}$

Table 1
Environmental data for the Study Sites on the CBC back-reef flat (means \pm 1 S.D., $N = 24$ (12-year⁻¹))

Sites	Current speed (cm·s ⁻¹)	Depth range (m)	Natural DIN levels (μ M)	Enriched DIN levels (μ M)	Natural SRP levels (μ M)	Enriched SRP levels (μ M)	Distance from shore (m)
Site B	~3.0–4.7 (mean = 3.6 ± 0.5)	0.4–0.6	UD to 0.51 (0.37 ± 0.06)	1.9–7.1 (3.8 ± 0.62)	UD to 0.07 (0.03 ± 0.02)	0.18–0.76 (0.39 ± 0.03)	92–97
Site A	~3.0–5.7 (mean = 4.9 ± 0.8)	0.3–0.4	UD to 0.61 (0.44 ± 0.03)	1.9–5.7 (3.8 ± 0.86)	UD to 0.06 (0.03 ± 0.02)	0.18–0.88 (0.39 ± 0.06)	72–77

DIN = dissolved inorganic nitrogen, SRP = soluble reactive phosphorous, UD = undetectable (not used in means).

fers (4-l volume, 15.5-cm high, 22-cm mouth diameter) were cemented upside down to the reef substrate at >1.5 m distances from each other using marine epoxy cement to completely seal the rims. These porous clay diffusers had 1235 cm² of total surface area, but only the 220-cm² flat top was sampled. Osmocote (Sierra Chemical Co., California, USA) slow-release (9 months) fertilizer containing 18% N (as ammonium nitrate and ammonium phosphate) and 6% P (as ammonium phosphate and calcium phosphate) was poured into four elevated-nutrient diffusers (randomly selected for treatment) from each of the two Study Sites until each diffuser was completely full, and the hole was then stoppered. The fertilizer was replenished at ~3-month intervals to assure ample delivery. The remaining four low-nutrient diffusers (ambient controls) in each Study Site were filled with seawater and stoppered. Consequently, the eight diffusers (four reduced nutrients and four elevated nutrients in each Study Site) provided two experimental arrays that included randomly selected independent nutrient treatments exposed in two closely juxtaposed Study Sites chosen for their extremes of herbivory. This design yielded the following four combinations ($N = 4$) of experimental conditions: (1) reduced nutrients/high herbivory and (2) elevated nutrients/high herbivory in Study Site B, in addition to (3) reduced nutrients/low herbivory and (4) elevated nutrients/low herbivory in Study Site A.

Abundances of each colonizing group were determined 24 months following initial set-up by making detailed field estimates through magnifying lenses followed by taking macro-images of the top (center 108-cm², 9 cm \times 12 cm framer) of each diffuser. The images were scored for percent cover of predominant taxa (see details in Littler and Littler, 1985). The high magnification afforded by macro-photography of the 108-cm² plots enhanced the resolution and, in conjunction with the field notes, facilitated discrimination of microscopic turf species and crusts. Comparisons were made between treatments to detect changes in the relative abundances of the benthic groups that recruited, colonized and persisted over the 24-month

study period. To test the null hypothesis that the percent cover differences of functional groups under elevated versus reduced nutrients were not statistically different (at $\alpha = P > 0.05$), we used one-way ANOVA followed by Bonferroni (Dunn), a posteriori, multiple classification analysis (SAS, 2003). All percent cover data were arcsine transformed prior to analysis. The same statistics were used separately to compare patterns between the two different Study Sites.

2.8. Coral transplant experiment

We concurrently conducted long-term (24-month duration) transplant studies ($N = 8$) of the two massive coral species, *Siderastrea radians* and *Porites astreoides*, to assess their performances in the high-herbivory Study Site B under the two levels of nutrients used in the colonization/competition experiments. Specimens were cut underwater into approximately 2-cm² “nubbins”. Individual 2-cm² samples of each coral species were transplanted (12 cm apart) using marine epoxy cement onto the tops of an additional 16 haphazardly arrayed nutrient diffusers (>1.5 m separation), all in the Study Site B rubble-pavement zone of high herbivory (Lewis, 1986). Eight diffusers were randomly selected to remain nutrient-free, while the interspersed remaining eight were filled with slow-release Osmocote fertilizer that was replenished every 3 months. The transplanted nubbins were initially photographed and then re-photographed after 24 months from the same distance and orientation so that changes in two-dimensional area could be scored and compared between the treatments (one-way ANOVA, Bonferroni).

3. Results

3.1. Environmental data

The DIN and SRP concentrations next to the non-enriched diffusers (Table 1) are barely detectable in both Study Sites (i.e., Study Site B, means = 0.37 ± 0.06 S.D.

μM DIN and $0.03 \pm 0.02 \mu\text{M}$ SRP; Study Site A, means = $0.44 \pm 0.03 \mu\text{M}$ DIN and $0.03 \pm 0.02 \mu\text{M}$ SRP), indicating oligotrophic conditions. Conversely in both Study Sites B and A, the nutrient diffusers filled with slow-release fertilizer show nearly identical results (Table 1), significantly increasing DIN by 10-fold to means of 3.80 ± 0.62 and $3.80 \pm 0.86 \mu\text{M}$ and SRP by 13-fold to means of 0.39 ± 0.03 and $0.39 \pm 0.06 \mu\text{M}$ at about 3 cm above the experimental substrates. These enriched values (Table 1) exceed the kinetic levels (tipping points), noted by Bell (1992) and Lapointe et al. (1993) for releasing inhibition of algal growth on coral reefs, by approximately 3- to 4-fold.

Predominant current speeds are reasonably constant in a northwesterly direction (340° magnetic, Table 1), ranging from 3.0 to $5.7 \text{ cm}\cdot\text{s}^{-1}$ (mean = 4.9 ± 0.8 S.D.) in Study Site A and 3.0 to $4.7 \text{ cm}\cdot\text{s}^{-1}$ (mean = 3.6 ± 0.5 S.D.) in Study Site B. These currents are driven by the pumping action of offshore waves breaking over the reef crest and slowly flowing westward through the Study Sites and Zones (Fig. 2), exiting around the northern tip of the island. Secchi disc depths seaward of CBC average 43 ± 3 S.D. m ($N = 10$, range = 38–47 m), indicating exceptionally clear, Type I (Jerlov, 1976), oceanic waters consistently cascading onshore over the study area.

3.2. Herbivory assays

Large and significant ($P < 0.0001$, $F = 53.28$, d.f. = 14, Bonferroni) differences in herbivory are present (Table 2) within Zone 2 between 72 and 77 m (Study Site A, just beyond the outer transitional edges of

Zone 1) and 15 m nearer the reef crest at 92 and 97 m (Study Site B) on the CBC back-reef flat. The assay using the palatable seaweed *A. spicifera* shows grazing rates that are 17 times greater in Study Site B than in Study Site A. In agreement, Study Site B on the outer reef flat contains 145-fold more surgeonfish and 148-fold more parrotfish than Study Site A (Table 2). In support of these differences, experimental assays of herbivory by others (Table 2) prior to this study show 15 times greater loss of *A. spicifera* in Study Site B than in Study Site A ($P < 0.01$, Kruskal–Wallis), and 62 times greater loss of the palatable seagrass *T. testudinum* ($P < 0.01$, Table 2).

3.3. Biotic distribution patterns

Cluster analysis of the percent cover transects (Fig. 3) establishes the existence of two major biotic zones on the back-reef flat at CBC (Table 3), dominated by benthic indicator groups corresponding to gradients in herbivory and prey palatability (Table 2, Fig. 4). The landward Zone 1 (Fig. 3) on the back-reef flat between 0 and 72 m from the shoreline, remote from herbivorous fish activity (see Macintyre et al., 1987; Reinthal and Macintyre, 1994) and extending over a carbonate pavement substrate (thinly covered by sand and gravel) from 0.2 to 0.5 m in water depth (mean = 0.3 m), includes a discrete grouping of quadrats with a high level of similarity (Bray–Curtis Index). Total plant cover averages 70.3% and the palatable macrophyte *T. testudinum* (Table 2) is dominant (Table 3, average cover 60%, with maxima $>100\%$ due to layering). Sediments in this shallow grass-bed system (i.e.,

Table 2

Herbivorous fish densities and grazing intensity for the Carrie Bow Cay outer *Thalassia* zone (Study Site A, 72–77 m) and rubble-pavement zone (Study Site B, 92–97 m) Study Sites (see Fig. 2)

Study and taxa	Study Site A		Study Site B	
	$\text{N}\cdot\text{m}^{-2}$	Percentage loss $\cdot\text{h}^{-1}$	$\text{N}\cdot\text{m}^{-2}$	Percentage loss $\cdot\text{h}^{-1}$
Present investigation				
<i>Acanthophora spicifera</i>	–	1.0	–	16.5
Scaridae	0.001	–	0.180	–
Acanthuridae	0.001	–	0.164	–
Lewis and Wainwright (1985)				
<i>Acanthophora spicifera</i>	–	0.7	–	10.2
Scaridae	0.001	–	0.115	–
Acanthuridae	0.001	–	0.126	–
Hay (1981)				
<i>Thalassia testudinum</i>	–	0.5 ^a	–	30.9

All percentage loss values ($N = 15$) between Study Sites are significantly different ($P < 0.01$ for previous studies, Kruskal–Wallis; $P = 0.0001$, $F = 53.28$ for the present study, Bonferroni).

^a Additional data from the present investigation.

Table 3

Mean percent cover (\pm standard error) of the dominant macrophyte and massive coral taxa in reef-flat habitats of low (Zone 1) and high (Zone 2) herbivory (see Table 2)

Dominant taxa	Zones	
	1 (N = 25)	2 (N = 28)
	0–72 ^a	73–111 ^a
	0.2–0.4 ^b	0.1–0.8 ^b
Massive corals	0.03 \pm 0.03	16.60 \pm 2.75
Corallines and other calcified algae (totals)	8.86	46.70
<i>Porolithon pachydermum</i> (Fosl.) Fosl.	1.27 \pm 0.81	19.95 \pm 3.99
<i>Hydrolithon boergesenii</i> (Fosl.) Fosl.	0.20 \pm 0.08	16.77 \pm 2.93
<i>Amphiroa rigida</i> var. <i>antillana</i> Børg.	6.55 \pm 1.64	0.00
<i>Halimeda opuntia</i> (L.) Lamour.	0.33 \pm 0.26	4.31 \pm 1.02
<i>Jania capillacea</i> Harvey	0.10 \pm 0.10	2.94 \pm 0.84
<i>Jania adhaerens</i> Lamour.	0.25 \pm 0.07	2.68 \pm 1.01
<i>Peyssonnelia</i> sp.	0.01 \pm 0.01	0.05 \pm 0.05
<i>Neogoniolithon strictum</i> (Fosl.) Setch. et Mason	0.15 \pm 0.10	0.00
Fleshy macrophytes (totals)	61.43	0.59
<i>Thalassia testudinum</i> Banks ex Koenig	60.10 \pm 5.50	0.00
<i>Caulerpa racemosa</i> (Forssk.) J. Ag.	0.60 \pm 0.31	0.46 \pm 0.21
<i>Dictyota pulchella</i> Lamour.	0.42 \pm 0.09	0.00
<i>Lobophora variegata</i> (Lamour.) Womersley	0.15 \pm 0.15	0.00
<i>Dictyota</i> sp.	0.14 \pm 0.10	0.10 \pm 0.10
<i>Neomeris annulata</i> Dickie	0.02 \pm 0.01	0.03 \pm 0.01

^a Distance from shore (m).

^b Depth range (m).

Landward Zone 1, Table 3) are, hypothetically, more an effect of *T. testudinum* abundance, rather than a cause, since the rhizomes are anchored directly to reef pavement. Massive corals average only 0.03% cover in the Landward Zone 1.

Seaward Zone 2, between 73 and 111 m (Fig. 1, depth range 0.1–0.8 m, mean = 0.3 m), includes the rubble-pavement zone (containing Study Sites A and B), the deeper (0.8 m) pavement zone and the inner slope of the reef crest and is dominated by grazer-resistant calcareous macroalgae and reef-building corals. Total plant cover averages 47.3% (almost all calcareous forms, Table 3) with the primary species being the crustose corallines *Porolithon pachydermum* (19.9%) and *Hydrolithon boergesenii* (16.8%). The grazer-resistant, calcareous, green alga *Halimeda opuntia* (4.3%) is conspicuous in patches on the shallow leeward (inner) slope of the reef-crest area. Also abundant in Seaward Zone 2 are the massive corals (16.6% cover).

3.4. Nutrient-enrichment assays

The P_{\max} of the common reef-flat macroalga *D. pulchella* (Fig. 5) shows significant ($P < 0.05$, Bonferroni) effects of DIN and SRP enrichment during two assays conducted 12 months apart, with a greater overall effect in the second year. These results, in conjunction

with comparable assays of other species on the Belize Barrier Reef (Lapointe et al., 1987), suggest severe antecedent nutrient limitation in the two CBC Study Sites. In the first year, SRP was most limiting with significant ($P < 0.05$) positive interactions of both nutrients combined, whereas during the second year, DIN was most limiting.

3.5. Palatability experiment

The palatability assay reveals a consistent pattern (also noted by Littler et al., 1983a,b) regarding grazer resistances of coral and algal form groups as follows (Fig. 4). The algal sheet forms are less resistant (100% lost 6 h^{-1}) than the coarsely-branched forms (76% lost), the thick-leathery forms (30%), the jointed-calcareous forms (6%), the calcified-crustose forms (3%) and massive corals (0%). All of the differences between form groups are significant ($P < 0.05$, Duncan's Multiple Range Test).

3.6. Bottom-up manipulations in sites of high and low herbivory

In these experiments, algal recruitment and subsequent encroachment interactions were rapid, with multi-layered cover values approaching or exceeding

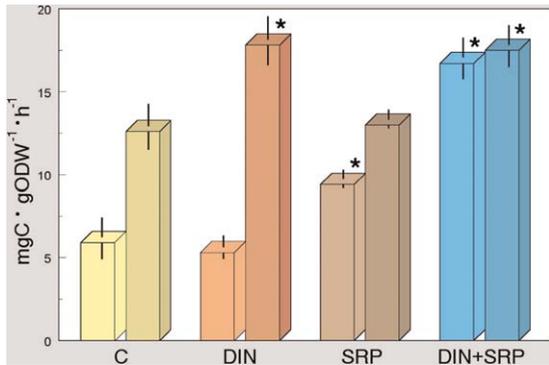


Fig. 5. Productivity assays (net photosynthesis g organic dry weight⁻¹ h⁻¹, $N = 6$) of the predominant macrophyte *Dictyota pulchella* as a function of dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) enrichment initially (unshaded histograms) and 12 months later (shaded histograms). Differences significant from non-enriched controls (C, $P < 0.05$, Bonferroni) are indicated by asterisks, vertical lines = ± 1 S.E.

100% under most treatment combinations (three out of four; Table 4, A–D). Under elevated nutrients in the low herbivory Study Site A (Table 4), the frondose macroalgae (mostly *D. pulchella*, along with *Gelidiopsis* spp., *Coelothrix irregularis*, *Padina jamaicensis*, *Turbinaria turbinata* and *Laurencia papillosa*) with 64% cover became predominant (significant at $P = 0.004$, $F = 5.14$, d.f. = 3). Turf microalgae (mostly Cyanobacteria, small *Digenea simplex*, *Jania capillacea*, *J. adhaerens*, Vaughaniella-stage of *Padina*, *Centroceras clavulatum* and *Heterosiphonia* spp.) attained their cover maxima (37% cover) following 24 months of reduced nutrient concentrations in the low herbivory Study Site A, although crustose corallines were slightly more abundant at 41% cover. Conversely, in the high-herbivory Study Site B, the elevated-nutrient conditions resulted in dominant cover values for crustose coralline algae with 72% cover (significant at $P = 0.0001$, $F = 89.74$, d.f. = 3; mostly *H. boerge-*

senii and *P. pachydermum*). However, elevated nutrients partially offset the effects of high herbivory, with 16% more frondose macroalgal cover and 22% more microalgal turf cover (both significant at $P = 0.0001$) than in the reduced nutrient treatment. All three of the above abundance peaks (Table 4) were statistically greater ($P < 0.05$, Bonferroni) under the conditions inferred by the RDM. Colonization on the reduced-nutrient treatments in the high-herbivory Study Site B consisted of only trace patches of microalgal turfs and coralline crusts, with frondose macroalgae being only slightly more conspicuous (all values significantly lower than in other treatments, Table 4). Corals did not colonize any of the diffusers during the study, but were investigated by the separate coral transplant experiment below.

All of the cover maxima within each functional group were greater under the conditions predicted by the model (Table 4, A–D). In terms of relative dominance between groups, there was only a single case that was contrary to the predicted RDM patterns (see Fig. 6 and Table 4); i.e., crustose corallines were slightly more prevalent (insignificant at $P > 0.05$, Table 4, column A) than algal turfs under low nutrients in the low-herbivory Study Site A.

3.7. Coral transplant experiment

The *S. radians* and *P. astreoides* transplanted to 16 additional independent nutrient diffusers (in the rubble-pavement zone between 90 and 97 m, where high grazing restricted fleshy algae to trace quantities) showed significantly reduced ($P = 0.0001$, $F = 49.09$, d.f. = 7 and $P = 0.0001$, $F = 11.68$, d.f. = 7, respectively) cover increases in the elevated-nutrient treatments versus the reduced-nutrient treatments (Fig. 6), consistent with the model. Interestingly, *S. radians* experienced significant inhibition (=net losses, $P = 0.0001$) under elevated nutrients.

Table 4

Mean percent cover (\pm standard error) of benthic functional groups colonizing clay diffusers following 24 months under reduced and elevated nutrients in low- and high-herbivory Study Sites ($N = 4$)

Functional groups	Study Site A (low herbivory)		Study Site B (high herbivory)		Significant differences ($P < 0.05$)
	Nutrients		Nutrients		
	Reduced	Elevated	Reduced	Elevated	
	A	B	C	D	
Crustose corallines	41.2 \pm 4.6	1.8 \pm 1.8	<0.1	71.7 \pm 3.0	D > A > B, C
Frondose macroalgae	20.8 \pm 4.3	63.7 \pm 8.2	0.6 \pm 0.3	16.9 \pm 4.1	B > A, D > C
Algal turfs	37.1 \pm 3.9	14.5 \pm 4.7	<0.1	22.1 \pm 2.9	A > D > B > C
Predicted dominants	Turfs	Macroalgae	Corals	Corallines	

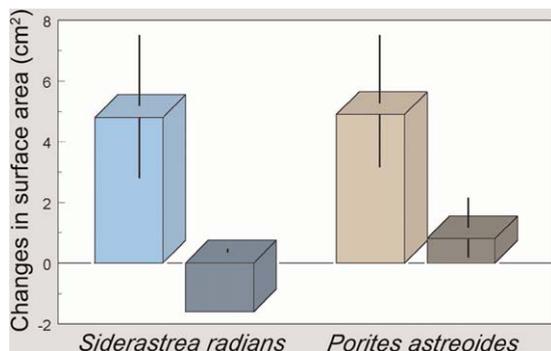


Fig. 6. Increases and decreases (cm²) in living surface area of nubbins ($N = 8$) of *Siderastrea radians* and *Porites astreoides*, transplanted onto clay diffusers under reduced (unshaded) and elevated (shaded) levels of nutrient enrichment, after 24 months between 90 and 97 m in the rubble-pavement zone fully exposed to high herbivory. Differences within species are significant ($P = 0.0001$, Bonferroni), vertical lines $s = \pm 1$ S.E.

4. Discussion—functional groups as indicators of reef health

4.1. Reef-building corals

Cnidarian corals, the architects of structural dimensionality, while preyed upon by a few omnivorous fishes and specialist invertebrates (e.g., crown-of-thorns sea star, corallivorous gastropods), generally achieve dominance under the control of intense herbivory (Lewis, 1986) and extremely low nutrient concentrations (Bell, 1992; Lapointe et al., 1993). Massive corals consistently prove to be the most resistant to grazing at the highest levels of herbivory (Figs. 4 and 6). *S. radians* and *P. astreoides*, hard mound-shaped forms, show little colony mortality under high grazing pressure (Fig. 6), even though occasionally rasped by parrotfishes (see also Littler et al., 1989). Contrastingly, some delicately branched corals such as *Porites porites* are quite palatable and readily eaten by parrotfishes (e.g., *S. viride*, Littler et al., 1989; Miller and Hay, 1998). However, many hermatypic corals are inhibited by increases in nitrate (e.g., *Montastrea annularis* and *P. porites*, Marubini and Davies, 1996), ammonia (e.g., *Pocillopora damicornis*, Stambler et al., 1991; Muller-Parker et al., 1994) and orthophosphate (e.g., *Porites compressa*, Townsley cited in Doty, 1969; *P. damicornis* and *Stylophora pistillata*, Hoegh-Guldberg et al., 1997). Nutrient inhibition of coral larval settlement also is known for *Acropora longicyathis* (Ward and Harrison, 1997). Nutrient poisoning is probably the case for *S. radians* in this study where growth inhibition is apparent (Fig. 6); whereas, *P. astreoides* was severely

inhibited. Orthophosphate is known (Simkiss, 1964) to inhibit CaCO₃ crystal formation at concentrations above 0.01 μM and can block deposition of external skeletal materials in some marine animals. The 50% suppression of community calcification and stimulation of algal overgrowth (Kinsey and Domm, 1974; Kinsey and Davies, 1979) subsequent to the experimental fertilization of a patch reef at One Tree Island on the Great Barrier Reef, Australia is partly attributable to phosphate poisoning. A sophisticated experiment on a larger and more carefully controlled scale (Larkum and Koop, 1997; ENCORE Program) did not produce supporting results because: (1) ambient nutrient levels within the lagoon at One Tree Island are now well above tipping-point concentrations that are inhibitory to some corals, while being more than sufficient to support the existing luxuriant frondose macroalgal community (Bell, 1992; Larkum and Koop, 1997) and (2) the experimental organisms were isolated on raised grids, precluding natural encroachment, overgrowth or other key competitive interactions crucial to testing the RDM. The challenge now is to rigorously conduct this type of large-scale manipulation in an extreme oligotrophic coral-reef setting (e.g., Smith et al., 2001), in conjunction with staged competitive bouts among the major functional groups, to determine how herbivore/nutrient interactions affect relative dominances over a long time scale.

4.2. Crustose coralline algae

In contrast to the corals (and fleshy algae), crustose coralline algae tend to be slow-growing competitively inferior understory taxa that are abundant in most coral-reef systems (Littler, 1972); although the group includes forms ranging from thin early-successional flat sheets to long-lived massive branched heads. Their critical roles in coral reefs is to form the protective algal ridge/reef crest, cement the dead coral and other carbonate fragments into a stable framework and, by sloughing (Littler and Littler, 1997), prevent propagules of fouling organisms from colonizing. Crustose corallines, because of their slow growth rates, tolerate reduced nutrient levels and generally are conspicuous, but not dominant, at low concentrations of nutrients and high levels of herbivory (Littler et al., 1991). Accordingly, they do well under both low and elevated nutrients (i.e., most are not inhibited by nutrient stress and many are maintained competitor-free by surface cell-layer shedding (Johnson and Mann, 1986; Keats et al., 1994), even at lower levels of grazing (Littler and Littler, 1997). Their ability to dominate is largely controlled indirectly

by the factors influencing the abundances of the other groups, primarily corals and fleshy algae. In this study, crustose corallines were shown to predominate mainly by default (i.e., under conditions of minimal competition), where either corals were inhibited by elevated nutrients (Fig. 6) or fleshy algae were removed by intense herbivory (Table 2, Fig. 4). In independent corroborations of the RDM, a gradient from frondose- to turf- to coralline-algal groups correlated closely with escalating herbivory (Steneck, 1989); and increased sea urchin populations under elevated nutrients (Lapointe et al., 1997) at Discovery Bay, Jamaica resulted in a dramatic frondose macroalgal to crustose coralline algal phase shift (Aronson and Precht, 2000).

4.3. Turf microalgae

Low-stature turf microalgae tend to become dominant under minimal inhibitory top-down and stimulatory bottom-up controls (Table 4). Their relatively small size and rapid regeneration/perennation results in moderate losses to herbivory at low grazing pressures. Turf microalgae have opportunistic life-history characteristics, including the ability to maintain substantial nutrient uptake and growth rates under low-nutrient conditions (Rosenberg and Ramus, 1984). Convincing evidence also is afforded by large-scale mesocosms with controlled low-herbivory and reduced water-column nutrient regimes (McConnaughey et al., 2000), where turf algae invariably dominate due to the inclusion of low-lying, microscopic, nitrogen-fixing Cyanobacteria as a source of within-turf nutrients. In agreement, algal turfs have been shown to be favored under reduced nutrient-loading rates (Fong et al., 1987) or episodic nutrient pulses (Fujita et al., 1988) and this can lead to extensive, two-dimensional, horizontal mats. Numerous other studies have shown the expansion of algal turfs, not macroalgae, resulting from the removal of fish or echinoid grazers in a wide variety of oligotrophic sites worldwide, including the Red Sea (Vine, 1974), Fiji (Littler and Littler, 1997), Belize (Lewis, 1986), the Great Barrier Reef (Sammarco, 1983; Hatcher and Larkum, 1983; Klumpp et al., 1987) and Saint Croix (Carpenter, 1986). In the study of Lewis (1986) on the same reef flat studied here, increases in an algal turf form with its upright *Padina* blades, not blooms of mixed macroalgae, followed short-term (11-wk) reductions of herbivorous fish grazing under conditions of low nutrient levels. Lewis' (1986) Table 4 shows statistically significant, although relatively small, increases (28%) in algal turfs such as the above *Vaughaniella*-stage and its frondose form *Padina*;

however, contrary to several literature citations, no significant increases occurred in any of the major macroalgal species such as *Turbinaria turbinata* and *Halimeda* spp.

4.4. Frondose macroalgae

Terrestrial plant abundances and evolutionary strategies theoretically (Grime, 1979) are controlled by physiological stresses (external factors that limit production) coupled with disturbances (factors that physically remove biomass); a concept expanded to apply to marine macroalgae (Littler and Littler, 1984b; Steneck and Dethier, 1994). In the RDM (Fig. 1), nutrients (bottom-up) control production and grazing (top-down) physically reduces biomass of undesirable fleshy algal overgrowth. We demonstrate experimentally that distributions and abundances of functional groups on tropical coral reefs result from bottom-up forces that affect metabolic production and growth (i.e., nutrients—mainly SRP and DIN); however, as shown (Table 2), patterns vary between habitats (i.e., Study Site B) having beneficial counterbalancing top-down forces that limit or remove detrimental algal biomass (i.e., herbivores—mainly Scaridae, Acanthuridae and Kyphosidae).

Most importantly, we found a complexity of *stimulation/inhibition* interactions acting either *directly* or *indirectly* (see also McCook, 1999). For example, our data reveal that insufficient nutrients act *directly* to *inhibit* (limit) fleshy-algal domination (via physiological stress, Fig. 5); conversely, abundant nutrients *stimulate* (enhance) fleshy-algal growth, with the opposite effect on reef-building corals (via toxic *inhibition?* (Fig. 6), see Marubini and Davies, 1996). Furthermore, the effects of controls also can be *indirect* by influencing competition. Even this seemingly *indirect* control can have further levels of complexity because competition between algae and corals can be *direct* (e.g., overgrowth) or *indirect* (e.g., pre-emption of substrate). Low nutrients and high herbivory (via physical removal) also act *indirectly* on fleshy algae through reduced competitive abilities; whereas, lowered herbivory and elevated nutrients also *indirectly inhibit* (limit) corals (e.g., Banner, 1974; Birkeland, 1977) and coralline algae (e.g., Littler and Doty, 1975; Wanders, 1976) by *directly stimulating* (enhancing) fleshy-algal competition. With an increase in nutrients, the growth of fleshy algae is favored over the slower-growing corals (Table 4, Genin et al., 1995; Miller and Hay, 1996; Lapointe et al., 1997) and the latter can become *inhibited* by either poisoning (*direct* effect, Fig. 6) or, as

mentioned, by competition for space and light (*indirect* effect, Jompa and McCook, 2002). Other ecologically important factors, such as light regime, abrasion, allelopathy and sediment smothering (e.g., Littler et al., 1983c; Ruyter van Steveninck, 1984; Chadwick, 1988; Coen, 1988; Coles, 1988; Keats et al., 1997; Littler and Littler, 1997), also can *indirectly* influence further outcomes of competition.

On healthy oligotrophic coral-reefs, even very low nutrient increases (Tables 1 and 4) may exceed critical tipping-point levels that can shift relative dominances by releasing macroalgal production from nutrient limitation. Birkeland (1977) also noted that filamentous and frondose algae can outcompete corals, some of which are inhibited under elevated nutrient levels (reviewed in Marubini and Davies, 1996, Fig. 6). Fast-growing algae are not just opportunists that depend on disturbances to release space resources from established longer-lived populations (cf. McCook, 1999), but, hypothetically, become the superior competitors when provided with abundant nutrients. Macroalgae, such as *Halimeda*, also gain competitive advantage by serving as carriers of coral disease (Nugues et al., 2004). Potential competitive dominance of fast-growing macroalgae is inferred from their overshadowing canopy heights, as well as from inverse correlations in abundances between algae and the other benthic functional groups (Lewis, 1986; Bellwood et al., 2004), particularly at the higher nutrient concentrations (e.g., Littler et al., 1993; Lapointe et al., 1997). Turbulent water motion driven by wind and wave action can be sufficient to reduce oligotrophic boundary-layer diffusion gradients and increase delivery rates to support considerable macroalgal biomass (e.g., Atkinson and Bilger, 1992), but the abundant herbivores may mask these effects. The fleshy algal form groups (both micro- and macro-) are particularly vulnerable to herbivory (Table 4, see also Hay, 1981; Littler et al., 1983a,b) and, in accordance with the predictions of the RDM, only become abundant in habitats where grazing is low. Such over-compensation by herbivory may explain some of the reported cases (e.g., Crossland et al., 1984; Szmant, 1997; Glynn and Ault, 2000) of specific corals surviving in high-nutrient reef environments.

The complex interactions of herbivory and nutrients can change gradually with no apparent effects to induce subtle declines in resiliencies of coral/coralline-dominated reef systems (Scheffer et al., 2001). These systems then become vulnerable to catastrophic impacts by large-scale stochastic disturbances such as tropical storms (e.g., Done, 1992), warming events (e.g., Macintyre and Glynn, 1990; Lough, 1994), cold fronts

(Precht and Miller, in press), diseases (e.g., Littler and Littler, 1997; Santavy and Peters, 1997; Nugues et al., 2004) and predator outbreaks (e.g., Cameron, 1977), which typically trigger or accelerate such low-resilience reef systems (Scheffer et al., 2001; Bellwood et al., 2004) toward the long-term externally-mediated phase-shifts postulated in the RDM. For completeness, we also point out the obvious devastating effects of sedimentation (land-based and dredging), toxic spills, carbonate mining and landfill. Such catastrophic events selectively eliminate the longer-lived organisms in favor of fast-growing early-successional macroalgae (Littler and Littler, 1984b), which can prevent settlement of coral planulae and become competitively superior (Birkeland, 1977; Lewis, 1986) to persist as alternative stable states.

The macroalgal overgrowth recorded under the elevated-nutrient treatments in the low herbivory Study Site A (Table 4) demonstrates that the tipping-point nutrient concentrations needed to support substantial primary production are quite low, but comparable to those reported for other tropical marine algae. For example, several controlled, high-flux, continuous-culture laboratory experiments and detailed field studies have demonstrated the physiological basis for low-nutrient tipping-points (i.e., $\sim 0.5\text{--}1.0\ \mu\text{M}$ DIN) leading to macroalgal blooms. The tropical rhodophytes *Gracilaria foliifera* and *Neoagardiella baileyi* (DeBoer et al., 1978) and the chlorophyte *Ulva fasciata* (Lapointe and Tenore, 1981) all achieved maximal growth rates in continuous cultures at DIN levels of approximately $0.5\text{--}0.8\ \mu\text{M}$. Comparable low nutrient levels (i.e., $\sim 0.10\ \mu\text{M}$ SRP, $\sim 1.0\ \mu\text{M}$ DIN) have been correlated with macroalgal blooms and the subsequent decline of coral reefs from eutrophication at Kaneohe Bay in Hawaii, fringing reefs of Barbados and inshore reefs within the Great Barrier Reef lagoon (Bell, 1992), as well as the macroalgal-dominated reefs of the Houtman Abrolhos Islands off Western Australia (Crossland et al., 1984). These low nutrient concentrations were also experimentally corroborated (Lapointe et al., 1993) for macroalgal overgrowth of seagrass and coral reef communities along natural nutrient gradients on the Belize Barrier Reef. We recognize that coral reef organisms can tolerate higher levels of DIN and SRP; however, these nutritional levels represent tipping-point concentrations that reduce resiliency to a point at which coral-reef ecosystems can potentially shift towards dominance by fleshy algae.

Tropical reefs in different geological systems have contrasting patterns of photosynthetic nutrient limitation in regard to nitrogen and phosphorus availability

(Littler et al., 1991; Lapointe et al., 1992). Such patterns of nutrient limitation have been correlated (Littler et al., 1991) with the biogeographic distributions of major groups of epilithic photosynthetic organisms that were consistent with the RDM (see also Verheij, 1993). Long-term ecological studies coincide in reporting general worldwide declines in live coral cover and concomitant increases in macroalgal abundances (Ginsberg, 1993; Birkeland, 1997). These kinds of biotic phase shifts have been steadfastly attributed solely to over-fishing and diseases of herbivore stocks (e.g., see Hughes, 1994 on trends in Jamaican reefs over the past 20 years, Hughes et al., 1999); however, such shifts more-often-than-not occur in concert with cultural eutrophication (Goreau et al., 1997; Lapointe et al., 1997, 2005a,b). The spatial/temporal changes in the patterns of algal dominance with regard to local nutrient inputs in Jamaica and reefs around the world (Goreau, 1992, 2003; Goreau and Thacker, 1994) undermine the sea-urchin demise and overfishing explanations, while lending further empirical support to the RDM.

It is encouraging that the critical role of excess nutrients on coral reefs has begun to receive appropriate recognition in recent review papers (Scheffer et al., 2001; Hughes et al., 2003; Bellwood et al., 2004; Pandolfi et al., 2005). Although, some scientists (e.g., Preech and Miller, in press) continue to downplay human-induced declining resiliency issues, instead invoking unmanageable stochastic factors like upwellings, hurricanes and cold fronts (see Fig. 1 caption); events from which coral reefs have recovered for millions of years. Also, nutrient/herbivory models similar to the RDM are receiving considerable attention (cf. Fig. 1 this paper and Fig. 2a in Bellwood et al., 2004). The coral-reef community needs a broader biological perspective to further the recognition of the role played by chronic nutrient enrichment in the coral reef health/resilience paradigm. Hopefully, the well-intended plea (Pandolfi et al., 2005) for scientists to . . . “stop arguing about the relative importance of different causes of coral reef decline” . . . , will not discourage much-needed insightful research on nutrification.

Unfortunately, the recurrent role of modern human-kind on coral reefs will continue to be to elevate nutrients via sewage and agricultural eutrophication (i.e., increasing bottom-up controls, Littler et al., 1991, 1993; Goreau et al., 1997; Lapointe et al., 1997), while simultaneously decreasing herbivorous fishes (Littler et al., 1991, 1993; Hughes, 1994) through trapping, netting, poisoning and blasting (i.e., reducing top-down controls). Unless curbed, such anthropogenically

induced shifts (long predicted by the RDM—see also Fig. 2a in Bellwood et al., 2004 and anticipated by Nixon, 1995) will expand geographically at an accelerated pace.

5. Conclusions

By simultaneously using multifaceted descriptive and experimental approaches, conducted for a sufficient duration on a healthy coral-dominated reef, this study provides the critically-needed long-term data to begin to close the historically-polarized intellectual rift involving the importance of eutrophication versus herbivore overfishing in causing coral to algal phase shifts. We found (Table 4), as have others, that reduced nutrients alone do not prohibit fleshy algal growth when herbivory is low, and that high herbivory alone does not prevent fleshy algal growth when nutrients are elevated. However, reduced nutrients in combination with high herbivory virtually eliminate all forms of harmful micro- and macro-algae. It is our opinion that on the few remaining undisturbed, oligotrophic, coral-reef systems, the effects of top-down inhibitory controls via intense herbivory prevail; whereas, bottom-up stimulatory controls are less prevalent, due to the lack of nutrient availability and over-compensatory consumption by grazers. However, eutrophic systems may lose their resiliency to inundation by macroalgae, with herbivores becoming swamped by bottom-up (nutrient-induced) harmful algal blooms. We show that the growth of reef-building corals can be inhibited under elevated nutrients relative to low nutrients (Fig. 6), even though herbivory remains high.

Changes in bottom-up controls and their interactions not only alter the dominance patterns of the major benthic functional groups on coral reefs, but, hypothetically, could have profound long-term consequences mediated through structural transformations and chemical modifications to reef systems and their herbivorous fish populations. In other words, excessive nutrient enrichment not only increases the productivity and biomass of weedy macroalgae via bottom-up controls that alter patterns of competitive dominance (Littler et al., 1993), but, over the long term, may lead to coral habitat degradation through: (1) reduced spatial heterogeneity by overgrowth (Johannes, 1975; Pastorok and Bilyard, 1985; Szmant, 1997); and (2) nighttime anoxic conditions (tolerated by macroalgae, but not by coral competitors and herbivorous predators, Lapointe and Matzie, 1996) that could indirectly reduce top-down grazer effects. Furthermore, eutrophication-induced macroalgal blooms decrease the growth and

reproductive capacity of the more structurally complex reef-building corals (Tanner, 1995; Miller and Hay, 1996), as well as inhibit coral larval recruitment (Birkeland, 1977; Tomascik, 1991; Ward and Harrison, 1997) and survival (Lewis, 1986; Hughes et al., 1987; Hughes, 1989; Wittenberg and Hunte, 1992). Such complicated feedback loops following eutrophication are known to occur in seagrass meadows (Sand-Jensen and Borum, 1991; Duarte, 1995) and could also explain decreases in fish populations on coral reefs with long-term histories of eutrophication (Johannes, 1975).

Healthy coral-reef ecosystems are composed of diverse and highly productive communities. In natural reef ecosystems, much of the overall diversity at the primary-producer functional-group level is afforded by the intricate interaction of opposing herbivory/nutrient *stimulating/limiting* controls with the local physical/spatial variability. This results in a mosaic of continually changing environmental conditions in close proximity. Because of the sensitive nature of *direct/indirect* and *stimulating/limiting* interacting factors, coral reefs are particularly vulnerable to anthropogenic reversal effects that decrease top-down controls and, concomitantly, increase bottom-up controls, dramatically altering ecosystem resiliencies.

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