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Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs (Reply to the comment by Hughes et al.)

In a recent article (Lapointe 1997), I reported a study of macroalgal blooms on coral reefs in Jamaica and southeast Florida that I hypothesized were related to simultaneous bottom-up (nutrient enrichment) and top-down (grazing) controls (relative-dominance model, RDM; Littler and Littler 1984). Hughes et al. (1999) argued that (1) an exclusive grazing hypothesis is a more parsimonious explanation for these blooms, (2) the nutrient threshold concept I used to calibrate the nutrient dimension of the RDM was not valid, and (3) the nutrient concentration, physiological, and biochemical assay data that I presented did not support my conclusions. I consider these topics in the above order and suggest that none of their arguments accurately accounts for or refutes the data, interpretation, or conclusions in Lapointe (1997) or the macroalgal bloom dynamics that have occurred in the two study areas in question. Nonetheless, I am grateful for this timely and important exchange, as it will hopefully provide a more refined and clear understanding of the potential cause(s) leading to the demise of coral reef ecosystems.

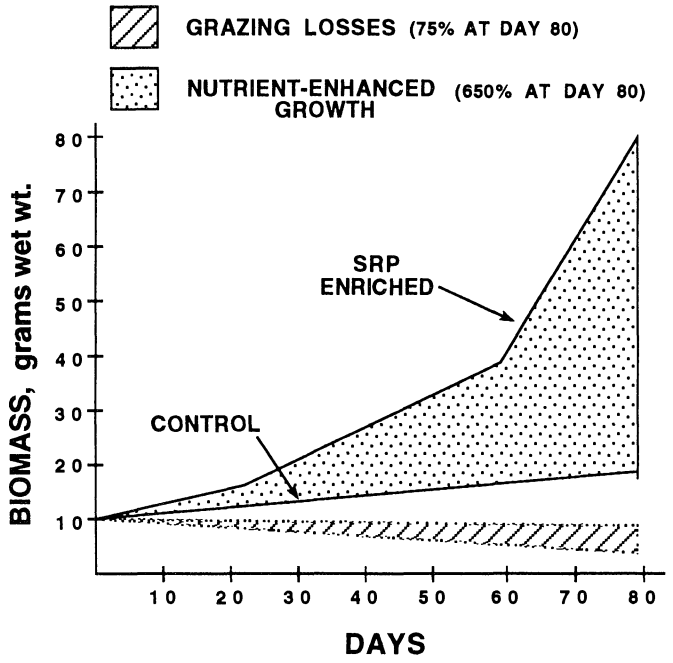

Fig. 1. Cumulative biomass production of *S. polyceratium* in DIN-rich (>1 μM) waters of the Florida Keys with and without (control) experimental SRP enrichment (data from Lapointe 1989). Also shown are the comparative cumulative grazing losses calculated from the data of Lewis (1986). Note that cumulative grazing losses are comparable to biomass production only in the control cultures that lack SRP enrichment; SRP-enrichment shifts macroalgal growth rates from linear to exponential, and the resulting biomass increase cannot be controlled by grazers.

(1) Top-down and bottom-up controls

Hughes et al. (1999) implied that I discounted the role of herbivory as a factor controlling macroalgal abundance on coral reefs. However, I explicitly recognized the contemporaneous effects of both grazing and nutrient availability as potential controllers of macroalgal blooms on coral reefs (*see Fig. 1,* RDM, and references in Lapointe 1997). While the term "macroalgal bloom" has been used loosely and is not defined in prior studies, I define this term to indicate an increase in abundance, above normal background levels, of a species in a geographic area or particular coral reef habitat. My article focused on the dynamics of the nutrient dimension of the RDM, a subject that has been largely unexplored on coral reefs compared to the wealth of studies that have examined herbivory but have largely ignored nutrient availability. For example, none of the "substantial number of experimental studies" of *Diadema* removal cited by Hughes et al. measured nutrient concentrations, so the claim that these experimental sites had "the same nutrient status" cannot be made. In his review of the *Diadema* die-off, Lessios (1988) did not consider the possible role of nutrient availability in explaining the variable pattern of macroalgal blooms in the Caribbean, despite the known importance of nutrients to growth and reproduction of macroalgae and the feeding preferences and growth of marine herbivores (Mattson 1980). My recognition of simultaneous grazing and nutrient controls was presented in my conclusion: "The importance of top-down control of macroalgal standings crops is much more compelling when combined with the synergistic effects of bottom-up control" (Lapointe 1997), an explanation that I believe to be general and robust.

In contrast to my interpretation, Hughes (1994) and Hughes et al. (1999) argued that macroalgal blooms on reefs in Jamaica and south Florida are controlled exclusively by declining herbivory from overfishing and the widespread die-off of the echinoid *Diadema.* Exclusive control of macroalgal blooms by decreased herbivory is not supported by grazer-reduction studies, e.g. Sammarco (1983), Lewis (1986), Carpenter (1988), and others, which reported relatively minor expansion of algal turfs (< 2 cm tall, Lewis 1986) and not macroalgal blooms. Data from Carpenter (1988) showed that the increase of algal turf biomass within 1 week of the sea urchin mass mortalities in St. Croix corresponded with an increase in turf height from 1.0 to 2.9 mm and a *61% decrease* of algal productivity per unit biomass, not the "*2-fold increase* in algal productivity" as claimed by Hughes et al. (1999). Lewis (1986) reported only a modest increase in algal turfs (28% over 10 weeks) and no significant increase in macroalgae (*Halimeda, Turbinaria*) following exclusion of grazing fishes on the Belize Barrier Reef. The RDM readily, and explicitly, predicts such increases in algal turf, not macroalgae, as a result of reduced grazing where nutrient availability is low. The distinction between algal turfs and macroalgae is important, and because Hughes et al. did not make this distinction, their argument as to the causes of "algal blooms" is confounded, at best.

The RDM readily predicts that decreased grazing on reefs with high nutrient availability, such as the reefs on Jamaica's north coast, will result in dominance by macroalgae rather than by algal turfs. This is supported by studies that have demonstrated dramatic increases in the growth of germlings and frondose macroalgae with increased nutrient availability, as well as case studies of eutrophication on coral reefs where macroalgae overgrew reef corals (references in Lapointe 1997). The relative importance of nutrient enrichment vs. grazing on macroalgal standing crops can be illustrated by comparing cumulative biomass of *Sargassum polyceratium* with and without enrichment of the growth-limiting nutrient—soluble reactive phosphorus (SRP)—vs. grazing losses based on the "high grazing" data of Lewis (1986) (Fig. 1).

Hughes et al. (1999) cited the work of Liddell and Olhorst (1992) as support for their exclusive grazing hypothesis for Jamaican reefs in stating that "immediately following the mass mortalities of sea urchins in 1983/84, algal biomass increased." However, the data of Liddell and Olhorst do not support that claim and actually show the reefs at 15 m off Discovery Bay began their shift from corals to macroalgae following Hurricane Allen in 1980, not following the *Diadema* die-off in 1983–1984. Liddell and Olhorst (1992) reported that "it is of interest to note that increases in noncrustose algae actually began several years *prior* to the mass mortality of *Diadema*" and that this trend was also "mirrored by shallower reef sites on Zingorro reef and other Jamaican localities." Reefs in the relatively oligotrophic waters of the Cayman Islands and other remote, low nutrient

Fig. 2. Bloom (up to 1.5 m deep, ~3-ha area) of macroalgae (*C. linum* and *Lyngbya* sp.) overgrowing fore reef communities on fringing reefs in the Negril Marine Park offshore Orange Bay, Jamaica, August 1998, following the onset of the summer wet season. During the past decade, macroalgal blooms like this have become increasingly common on Jamaican fringing reefs adjacent to nutrient inputs from sewage or agricultural runoff. Note the browsing sea urchin *Tripneustes ventricosus* that is normally found in more nutrient-rich seagrass meadows in the back reef along Jamaica's north coast. The recent expanded distribution of this urchin has followed the development of macroalgal blooms, suggesting cascading trophic responses to nutrient enrichment on these formerly coral-dominated fore reef communities.

areas of the Caribbean did not experience the macroalgal blooms and coral loss seen in Jamaica following *Diadema* die-off. Liddell and Olhorst (1992) concluded that a combination of reduced grazing and eutrophication was most likely fueling the increased macroalgal cover on shallow reefs in Jamaica, consistent with my previous conclusion (Lapointe 1997). That view is further supported by Goreau (1992), who reported that "algal overgrowth of corals is a seriously escalating problem in most Jamaican reefs . . . due to a combination of reduced herbivory and to increased fertilization by nutrients derived from inappropriate land and sewage management practices" (Fig. 2).

(2) The nutrient threshold concept

My study was not "a test of the hypothesis that reefs . . . had exceeded a threshold level of eutrophication" as stated by Hughes et al. (1999) but rather, a field test of the nutrient threshold model for macroalgal blooms. The onset of eutrophication and alteration of microbial populations, endolithic algae, and microfilamentous algal turfs would likely occur at nutrient concentrations lower than those of macroalgal blooms, the latter reflecting a more advanced stage of eutrophication. I specifically used this concept to calibrate the nutrient dimension of the RDM and quantify the approximate water-column concentrations of dissolved inorganic nitrogen (DIN) and SRP that can initiate and sustain macroalgal blooms on coral reefs in the wider Caribbean area. The nutrient threshold concept offers a functional framework for research and management of oligotrophic aquatic ecosystems and is being used in restoration efforts for South Florida's Everglades that are affected by agricultural runoff (*see* McCormick et al. 1996 for alteration of natural periphyton communities).

The nutrient threshold model is supported by studies that have shown the relationship between nutrient uptake/growth of macroalgae vs. concentration of the limiting nutrient to generally follow a rectangular hyperbolic function (e.g., Michaelis–Menten kinetics). Continuous-culture laboratory experiments and detailed field studies have quantified this relationship for DIN-limited growth, collectively showing a high affinity of macroalgae for DIN, with growth rates becoming maximal (i.e., exponential) at very low DIN concentrations in the range of ~0.5–1.0 μM (Fig. 3). Because water-column nutrient concentrations represent the net residual sum of internal nutrient cycling, algal assimilation, and external inputs, they offer the most direct method to assess nutrient sufficiency for growth of macroalgae. Inasmuch as algal nutrient uptake/growth rates are concentration-dependent, a nutrient threshold model based on nutrient concentrations (rather than on nutrient fluxes) is not only valid but is likely the best index of nutrient status on a reef relative to macroalgal growth demands. For example, despite overall high DIN fluxes associated with high flow rate waters on

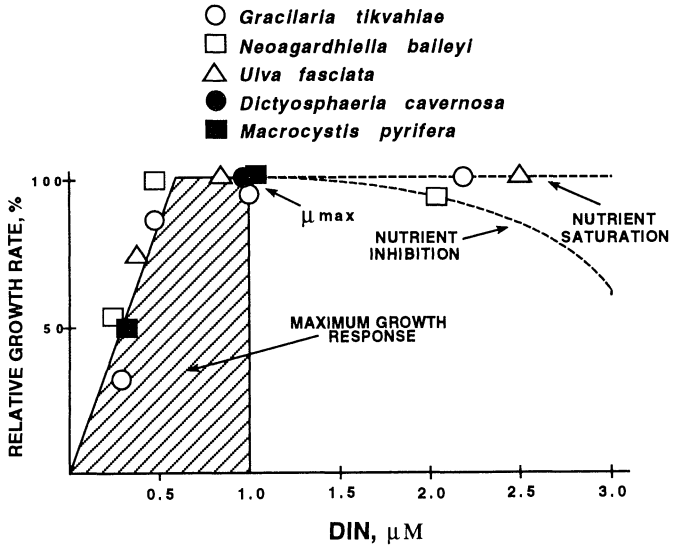

Fig. 3. Relationship of relative growth rates ($\mu : \mu_{max}$) in a variety of macroalgae to increasing DIN concentration. Data for the tropical macroalgae *Gracilaria foliifera* and *Neoagardhiella baileyi* are from DeBoer et al. (1978), *Ulva fasciata* data are from Lapointe and Tenore (1979), and *Dictyosphaeria cavernosa* data are from Larned and Stimpson (1996). Also shown are data for the giant kelp, *Macrocystis pyrifera,* from a temperate upwelling ecosystem in California (Zimmerman and Kremer 1982). These data show that the growth response region for DIN-limited macroalgal growth is between undetectable (zero growth) and 0.5–1.0 μM DIN. At DIN concentrations $> \sim 1$ μM, growth rates either become DIN-saturated or decrease due to epiphytic fouling or toxic effects.

oligotrophic reefs with very low DIN concentrations, such habitats would remain DIN-limited because the low DIN concentrations would restrict nutrient uptake and growth of macroalgae. Hence, when average DIN concentrations are below ~0.5 μM on coral reefs (Fig. 3), growth rates of macroalgae are strongly limited by DIN irrespective of flow rate; under these conditions, increased DIN concentrations can lead to increased productivity (i.e., P_{max}, α) and growth, initiating the macroalgal bloom, providing that irradiance, temperature, and other factors are favorable.

The validity of a nutrient threshold model for coral reefs was demonstrated by Bell (1992) in his critical analysis of eutrophication on reefs in Kaneohe Bay, Hawaii; Barbados; and the Great Barrier Reef lagoon. Despite these broad geographic differences, increased algal abundance and coral reef decline was apparent at average concentrations of ~1.0 μM DIN and 0.1–0.2 μM SRP. Very similar DIN and SRP thresholds were reported for macroalgal overgrowth of coral and seagrass habitats along natural nutrient gradients on the Belize Barrier Reef (Lapointe et al. 1992). These thresholds are further supported by a wide variety of macroalgal blooms reported for coral reef regions globally (*see* table 3 in Lapointe 1997), including macroalgal-dominated high-latitude reefs at the Houtman Abrolhos Islands, Western Australia (Crossland et al. 1984). Yentsch and Phinney (1989) showed that 1.0 μM DIN (as nitrate N) represents a value above which the dimensionless *f*-ratio and optical properties of the oceans (i.e., a*440) become saturated with respect to increasing DIN concentration. Thus, it appears that this level of nitrogenous fertility may represent a more general threshold for a broad range of algal-mediated benthic and pelagic biological processes in the marine environment.

Hughes et al. (1999) discounted the nutrient threshold concept by stating that "it is now widely accepted that (coral) reefs are not limited to low nutrient environments" and cited reviews by Hatcher (1997) and Szmant (1997) for supporting evidence. Hatcher (1997) presents no nutrient data to support that claim and, to the contrary, notes that "models that predict the response of reef production processes to local and global increases in nutrient supply are the most urgent requirement of ecosystem science." Szmant (1997) does not present a review of nutrient effects on coral reefs, either, but rather, proposes "a hypothesis on the importance of topographic and trophic complexity to reef nutrient dynamics." The few nutrient concentration data presented are not representative of published values for the locations; Szmant gives a value of 2 μM NO_3^- for reefs on the northern Great Barrier Reef, but that value exceeds the median DIN concentration reported for the outer coral-dominated reefs by more than one order of magnitude (0.13 μM DIN, Furnas et al. 1997).

Hughes et al. (1999) also cited Glynn (1993) as evidence that "coral reefs thrive in upwelling areas." However, Glynn (1993) concluded otherwise—"coral reefs are generally absent from the Arabian Sea coast of southern Oman, most likely a result of monsoon-induced upwelling" and noted that "nutrient pulses that accompany upwelling promote the growth of benthic algae which may interfere with coral growth and survivorship through increased competition." Hubbard (1997) noted that references to coral reefs preferring areas of upwelling, or other sources of nutrients, are a misconception.

(3) Nutrient concentration, physiological, and biochemical data

I did not use "a regression with only two points" to infer temporal trends in nutrient concentrations at Discovery Bay as asserted by Hughes et al.(1999) but rather, a time series comprised of three independent studies spanning from 1979 to 1989—the period during which the macroalgal blooms developed at this location. Hughes et al. cited D'Elia et al. (1981), the first study, as evidence of "an *exponential* decline in surface water nutrients and salinity within *a few meters* of the springs due to dilution." However, D'Elia et al. actually reported the relationship between salinity and NO_3^- as *linear or near-linear,* with the mixing zone extending all the way from the shoreline springs to the fore reef *> 400 m from shore,* consistent with my data from July 1987. Macfarlane's (1991) thesis data, collected between November 1987 and June 1989 in the same area, showed that while reduced salinity surface waters of the back reef had NO_3^- concentrations averaging ~13.2 μM, concentrations of higher salinity water at depth averaged >2.0 μM—still twofold over the DIN threshold. The NO_3^- concentrations I reported for Discovery Bay (four samples per station, not "two" as claimed by Hughes et al.) were bracketed within the range of NO_3^- concentrations reported by both D'Elia et al. (1981) and Macfarlane (1991) and were not "atypical"

as claimed. D'Elia et al. (1981) concluded "there appears to be a hydrographic mechanism for transporting NO_3^--rich water to the shallow reef," a statement inconsistent with Hughes et al.'s claim that "it is not known how much of these . . . nutrients were available to . . . the fore reef." Tissue analysis of the macroalga *Lobophora variegata* suggests that groundwater NO_3^- enriches the fore reef at Discovery Bay to depths of at least 24 m (Lapointe et al. 1997).

Contrary to the arguments of Hughes et al. (1999), a comparison of the three nutrient data sets does suggest that SRP concentrations increased at Discovery Bay during the 1980s. D'Elia et al. (1981) found no significant correlation between salinity and SRP (average = ~0.15 μM) and concluded that the groundwater discharges were "devoid of P." However, my SRP data in summer 1987 were significantly and negatively correlated with salinity (Lapointe 1997), suggesting that groundwaters were a source of SRP at the time of my sampling. Similarly, Macfarlane's (1991) more extensive SRP measurements from the same area, over a 19-month period, were significantly and negatively correlated with salinity but averaged 0.32 ± 0.19 μM ($n > 18$); this value is quite high for coral reefs and about twofold higher than the mean value of D'Elia et al. (1981). Maximum SRP concentrations reported by Macfarlane (1991)—1.01 μM in May 1989—were the highest recorded of all three studies and occurred in the same time frame when the blooms of *Chaetomorpha linum* and *S. polyceratium* expanded offshore from restricted areas of the back reef (not from "around the grottos," as attributed to me). Because of the additional evidence I presented that SRP was a primary nutrient limiting productivity of these two macroalgae at this site, this trend of increasing SRP could explain the development of macroalgal blooms in the late 1980s, irrespective of decreased grazing by *Diadema.* My conclusion is supported by observations at Dragon Bay in Portland, Jamaica, where SRP-rich sewage and laundry detergents from a resort led to the development of similar *C. linum* blooms in the adjacent bay; diversion of the SRP by the hotel managers led to a "rapid and dramatic improvement in the ecological condition of the bay," and "the weedy algae nearly vanished" (Goreau et al. 1997).

The evidence does not support the statements of Hughes et al. (1999) that the high C:N:P ratios of Jamaican macroalgae "do not indicate nutrient enrichment" or that the "high C:P ratios from Florida . . . are more suggestive of limitation by P than N." My reported average C:N ratio of the Jamaican macroalgae (22) was very close to the median (20) for benthic marine plants in general (Atkinson and Smith 1983), supporting the view that this reef experiences relatively high N availability. However, the C:P (973) and N:P (45) ratios of the Jamaican macroalgae were considerably higher than the median for marine plants (700 and 35, respectively), supporting the conclusion of SRP limitation. These high C:P and N:P ratios reflected the high DIN:SRP ratio of the groundwater inputs (~85:1), further evidence that these macroalgae were enriched by groundwater-borne nutrients. The importance of nutrient delivery by groundwaters was also supported by a significant linear regression of N:P ratios in the macroalgae vs. salinity ($F = 10.36$, $P = 0.032$), ranging from high N:P ratios (48–57.1) around the grottos to lower values (39.3–39.8) on the fore reef. In Florida, the average C:P (480) and N:P (37) ratios of *C. isthmocladum* were considerably lower than those in Jamaica and, in the case of the C:P ratio, lower than marine plants in general, reflecting a tendency toward DIN limitation. DIN limitation of *C. isthmocladum* was further supported by the low mean seawater DIN:SRP ratio (8.4) on the Floridian reefs.

Hughes et al. (1999) asserted that "no *Codium* blooms were documented during the summer [my] samples were collected" in Florida. However, as I noted (Lapointe 1997), the initial massive *C. isthmocladum* blooms that affected deep reefs (25–45 m) in southern Palm Beach County in the vicinity of sewage outfalls and agricultural discharges were mostly unattached plants and were physically disturbed by Hurricane Andrew in August 1992. Beginning in 1994, when my sampling began, *C. isthmocladum* populations spread to northern Palm Beach County where, for the first time, extensive attached populations began growing on reefs where they had not been reported previously (constituting a "bloom" by definition). This northern expansion was documented and reported in a Seagrant-funded research project (Lapointe and Hanisak 1997) and the local media. Since the development of annual *Codium* blooms, these reefs in northern Palm Beach County have been overgrown by extensive populations of *Caulerpa verticillata,* an attached macroalga typically found in relatively nutrient-rich mangrove habitats.

I was also criticized for not considering upwelling as a nutrient source to the *Codium* blooms and for the methods and interpretation regarding my $\delta^{15}N$ data. I specifically noted that "natural upwelling of deep offshore water potentially contributes nutrient inputs to the Florida study area" in my discussion. However, none of the three studies cited by Hughes et al. provided any nutrient or physical data for the Palm Beach County study area, so their claim that "upwelling is a major source of nutrients to these offshore reefs" is unsupported. The reference to Leichter et al. (1996) as evidence of upwelling is incorrect, as that study reported the phenomenon of internal tidal bores, not upwelling. The claim that $\delta^{15}N$ of "upwelled water from the North Atlantic can be in the +10 to +12‰ range" is also unsubstantiated by either data or citations to other work. During my studies at Jupiter Ledge in summer 1995, intrusions of cold, NO_3^--rich upwelled water were not apparent in the study area, and DIN measurements at this site showed higher concentrations of NH_4^+ compared to NO_3^- (a low *f*-ratio), evidence against the upwelling hypothesis. Even if episodic upwelling does occur at Jupiter Ledge, such transient nutrient inputs have not historically initiated or sustained blooms of *C. isthmocladum* (Lapointe 1997).

The correlation between increased summer rainfall and increased $\delta^{15}N$ to values between +10 and +12‰ in *C. isthmocladum* (the methods for collection of tissue, drying, and $\delta^{15}N$ analysis were described in the methods) during the summer bloom, together with high near-bottom concentrations of NH_4^+ and the supporting references I provided, collectively provided evidence that wastewater-enriched DIN pools may be contributing to growth of *C. isthmocladum* (Lapointe 1997). The $\delta^{15}N$ values I reported for *C. isthmocladum* during summer 1995 are typical of secondarily treated wastewater (greater than +10‰; Lindau et al. 1989) and

are similar to values measured downgradient of septic tank-contaminated groundwaters in the adjacent Town of Jupiter (greater than +7.3‰, unpubl. data). Approximately 400 million gallons per day of DIN-rich secondarily treated wastewater are disposed of by Class I injection wells in south Florida, which includes wells within miles of my study area. The $\delta^{15}N$ values I reported for *C. isthmocladum* are substantially higher than those reported for tropical macroalgae that rely on N fixation (+0.5‰) and are comparable to values for macroalgae from sewage-polluted sites such as Boston Harbor (+7‰, France et al. 1998).

The claim of Hughes et al. (1999) that "no evidence is provided to support this assertion" regarding the relationship between high alkaline phosphatase activity (APA) and SRP-limited productivity of the Jamaican macroalgae is inconsistent with the data I presented. That statement ignores the significant decreases in mean APA ($n = 4$) with SRP enrichment of *C. linum* ($F = 9.7$, $P = 0.05$) and *S. polyceratium* ($F = 23.7$, $P = 0.008$) I reported (Lapointe 1997), which confirmed SRP limitation in these two species. Hughes et al. claimed that "high levels of APA have been shown to be induced by low levels of PO_4 . . . but not of N enrichment." However, that opinion does not consider studies with *Cladophora prolifera,* where NO_3^- enrichment significantly increased APA ($P < 0.01$; Lapointe and O'Connell 1989) to the high levels characteristic of the Jamaican macroalgae. The high APA levels of the Jamaican macroalgae contrast sharply with the low APA levels of *C. isthmocladum* from Florida, supporting SRP limitation in the former but not in the latter. The suggestion that the APA should be reported as "μmol P" is incorrect (it could be expressed as μmol SRP or μmol PO_4^{3-} but not the element P) and irrelevant because the APA assay was used as a relative measure of SRP limitation (i.e., "units ml^{-1}").

I also reply to the criticisms of the nutrient-enrichment productivity bioassays with *C. linum* and *Codium isthmocladum.* Hughes et al. (1999) asserted that the nutrient concentrations I used in the nighttime pulses (which were administered over several days, not just one night) exceeded the ambient nutrient concentrations at the two sites by a factor of "10-fold" and were therefore not "ecologically relevant." The NO_3^- concentration (160 μM) used at Discovery Bay was about sixfold higher than the highest ambient DIN concentration (28 μM) measured in surface waters, and I used a similar enrichment factor in Florida, where lower concentrations of NH_4^+ (20 μM) were used because of lower ambient DIN concentrations on those reefs. The "pulsed" nutrient bioassays were never intended to represent ambient nutrient concentrations at the sites but rather, to saturate the nutrient uptake mechanisms of macroalgae and elicit physiological responses as a function of antecedent levels of DIN, SRP, or both nutrients. Previous work reported by myself and others has been published in peer-reviewed scientific journals and has demonstrated that this short-term method is a reliable assay for nutrient-limited productivity and reflects longer term growth rates of macroalgae.

Hughes et al. (1999) stated that "the most parsimonious interpretation of the results is that interactive effects of N and P were greater than those of P alone, which suggests nutrient limitation, contrary to Lapointe's interpretation." In fact, my interpretation did acknowledge nutrient limitation, albeit only "weak, N limitation of productivity" of *C. isthmocladum* compared to more significant SRP limitation of *C. linum.* My interpretation was based on a two-way ANOVA, which partitioned the overall variability within these experimental designs by assessment of the sums of squares and degrees of freedom, not just a visual comparison of treatment means, which can be misleading. The bioassay results are entirely consistent with the other corroborating evidence for the two study sites that included seawater DIN : SRP ratios, APA assays, and tissue C : N : P ratios. Primary SRP limitation of *C. linum* at Discovery Bay is consistent with the longer term macroalgal growth studies of Macfarlane (1991), who reported only significant SRP enrichment effects, concluding that "growth of *Gracilaria* in nitrate enriched habitats at Discovery Bay . . . is phosphate limited."

In summary, the multiple lines of evidence that I advanced in Lapointe (1997) supported my conclusions that nutrients, in addition to decreased herbivory, exert a significant and sometimes primary forcing mechanism underpinning macroalgal blooms on reefs in Jamaica and southeast Florida. The evidence included a large body of published data and information that collectively showed (1) macroalgal blooms on coral reefs are generally controlled by a complex interaction of simultaneous bottom-up and top-down controls, (2) nutrient uptake/growth studies, together with ecosystem studies of eutrophication along nutrient gradients, support the nutrient threshold concept for macroalgal blooms, (3) my data, and those of others, have demonstrated significant nutrient limitation of macroalgae on coral reefs, and (4) macroalgal blooms, such as those I described, are a logical and predictable response to the widely recognized phenomenon of increased nutrient inputs (especially nitrogen) to coastal waters that have occurred at local, regional, and global scales over the past several decades (Vitousek et al. 1998).

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