



Macroalgal blooms on southeast Florida coral reefs I. Nutrient stoichiometry of the invasive green alga *Codium isthmocladum* in the wider Caribbean indicates nutrient enrichment

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Abstract

Invasive blooms of the siphonaceous green algae *Codium* spp. have been considered a symptom of coastal eutrophication but, to date, only limited biochemical evidence supports a linkage to land-based nutrient pollution. Beginning in the summer of 1990, spectacular blooms of unattached *Codium isthmocladum* developed on deep coral reef habitats in southern Palm Beach County and northern Broward County, and in subsequent years, attached populations formed on reefs in northern Palm Beach County.

To better understand the nutrition of these HABs, we collected *C. isthmocladum* and other reef macroalgae from various locations in southeast Florida as well as the wider Caribbean region for tissue C:N:P analysis in order to gauge variability in the type and degree of N- and/or P-limited growth. Widespread nutrient enrichment in floridian *C. isthmocladum* populations was evidenced by significantly higher tissue P (0.06% versus 0.04% of dry weight) and lower C:N (12 versus 19), C:P (425 versus 980), and N:P (35 versus 50) ratios compared to more nutrient-depleted Caribbean populations. To determine nutrient availability on southeast Florida's reefs, we sampled near-bottom waters at a variety of locations for DIN ($=\text{NH}_4^+ + \text{NO}_3^- + \text{NO}_2^-$) and SRP analysis. In general, concentrations of NH_4^+ , NO_3^- and SRP were all high on southeast Florida's reefs compared to values reported for Caribbean coral reefs. Although summertime upwelling provides episodic NO_3^- and SRP enrichment to reefs in southeast Florida, these transient nutrient pulses have not historically supported *C. isthmocladum* blooms.

We suggest that the widespread P enrichment of *C. isthmocladum* tissue and water column DIN:SRP ratios <16:1 in southeast Florida drive this system toward N limitation where low level NH_4^+ enrichment becomes of paramount importance. Hence, the recent *C. isthmocladum* blooms appear to be supported by increasing land-based nutrient pollution, particularly,

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sewage that is enriched in NH_4^+ and SRP at a low N:P ratio (<10:1) critical to sustaining balanced growth during bloom formation.

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1. Introduction

Coral reef ecosystems are adapted to oligotrophic tropical and subtropical waters and are sensitive to low level increases in the concentrations of dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) associated with cultural eutrophication (Johannes, 1975; Tomascik and Sander, 1987; 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 an alternative stable state 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 turbulence favors the dominance of calcifying, hermatypic corals (Adey, 1998; McConnaughey et al., 2000). Case studies in Kaneohe Bay, HI, USA (Banner, 1974; Smith et al., 1981), and more recently, the Negril Marine Park, Jamaica (Lapointe and Thacker, 2002) have demonstrated the pivotal role of low level nutrient enrichment to the development of excessive macroalgal biomass—harmful algal blooms (HABs; ECOHAB, 1997)—on coral reefs. Macroalgal HABs 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, macroalgae can quickly overgrow and replace the slower growing reef-forming (hermatypic) corals (NRC, 1995). Additionally, increases in macroalgal biomass typically result in elevated sea urchin densities and the subsequent bioerosion of reefs (Sammarco, 1982; Lapointe and Thacker, 2002).

Macroalgal HABs have developed in many tropical/subtropical coral reef communities in recent decades as a result of increasing land-based nutrient

pollution (UNEP, 1994; ECOHAB, 1997; NRC, 2000). During the summer of 1990, coral reefs off southern Palm Beach and northern Broward counties in southeast Florida experienced an unprecedented succession of macroalgal blooms first evidenced by unattached populations of the green alga *Codium isthmocladum* on deep (>30 m) reefs. Historically, *C. isthmocladum* occurred at low standing crops in these deep reef communities (24–58 m) in the 1970s (Hanisak and Blair, 1988). However, the more recent blooms resulted in biomass accumulations up to 2 m thick over the reef surface, which resulted in an emigration of reef fish populations from the impacted areas and die-offs of sponges, hard corals and soft corals via physical smothering and hypoxia/anoxia (Lapointe, 1997; Lapointe and Hanisak, 1997). By the mid-1990s, blooms of attached populations of *C. isthmocladum* spread to reefs in northern Palm Beach County, which were followed by extensive blooms of *Caulerpa* spp. (see Lapointe et al., 2005).

Species in the green algal genus *Codium* are widely known as invaders of coastal waters (Ramus, 1971; Fralick and Mathieson, 1973; Carlton and Scanlon, 1985; Trowbridge, 1998) and their abundance in certain tropical/subtropical habitats also suggests they may be ecological indicators of nutrient enrichment. Blooms of invasive *Codium fragile* occurred in the northwestern (Fralick and Mathieson, 1973; Carlton and Scanlon, 1985) and northeastern (Silva, 1957) Atlantic decades ago. In the Niantic River estuary, CT, USA, the invasion of *C. fragile* was related to DIN availability (Malinowski and Ramus, 1973), although no evidence of anthropogenic nutrient sources was reported. Whereas *Codium* spp. are not conspicuous in oligotrophic coral reef communities in the wider Caribbean region (Littler and Littler, 2000), they commonly form blooms in nutrient replete habitats. For example, in guano enriched waters surrounding White Cay north of San Salvador, Bahamas, *C. isthmocladum* formed extensive populations in a

nutrient enriched inner zone around the small island (Urnezis, 1995). A human induced simulation of this enrichment effect followed the maritime shipwreck of the *Arimora* and its cargo of fertilizer (guano) off Egg Island near Spanish Wells, Bahamas. Downstream of the wreck, a halo of macroalgae developed that included *C. isthmocladum* (Lapointe et al., 1992).

Both natural and anthropogenic nutrient sources may be important to *C. isthmocladum* blooms on reefs in southeast Florida. Episodic summertime upwelling has historically occurred in this area (Green, 1944; Taylor and Stewart, 1958) but, because these HABs developed only recently, we hypothesized that land-based nutrient enrichment resulting from increasing urbanization and associated nutrient pollution from the watershed is a significant factor. The human population in the southeast Florida area is now ~ 7 million, with over 12,000 metric tonnes/year of sewage nitrogen discharged directly into coastal waters from six ocean outfalls between Dade and Palm Beach counties (see Lapointe et al., 2005). In addition, Palm Beach and Broward counties have an estimated 183,645 septic tanks (www.doh.state.fl.us) and nearly 30 Class I injection well facilities that dispose of secondarily treated wastewater under pressure to depths of ~ 1100 m (USEPA, 2003). Land-based sewage effluent and stormwater runoff can enter coastal waters either via submarine groundwater discharges (SGD, Finkl and Charlier, 2003) or surface water discharges via the Port Everglades, Hillsboro, Boynton, Lake Worth, and Jupiter inlets.

To better understand the nutritional status of the summertime *C. isthmocladum* blooms, we performed tissue carbon (C), nitrogen (N), and phosphorus (P) analyses on *C. isthmocladum* populations and other abundant taxa from a variety of reef sites off southeast Florida to compare with those of *C. isthmocladum* populations collected around the wider Caribbean region. We used this information to gauge the type and degree of N-limited versus P-limited growth of the Florida HABs relative to Caribbean populations and to quantify any effects of anthropogenic nutrient enrichment on C:N:P contents and molar ratios of *C. isthmocladum* tissue. In addition, we collected near-bottom water samples to determine the availability of DIN and SRP to these HABs at a variety of sites on southeast Florida's reefs.

2. Materials and methods

2.1. Collection sites for C:N:P analysis of macroalgae: 1994–1998

To assess variability in tissue C:N:P ratios of *C. isthmocladum* over the wider Caribbean region (Fig. 1), we collected plants by SCUBA from a variety of reef sites in depths of 15–40 m in the Greater Antilles (Isla de Culebra, PR; Dominican Republic; Discovery Bay, Jamaica) and Lesser Antilles (Bird Island, Antigua; Prickley Pear Cays, St. Martin; Point Perces, Guadeloupe; Ile Perle, Martinique; Diamond Rock, Martinique; Dark Head, St. Vincent) in May/June of 1995 and 1996 during research cruises aboard the R/V *Sea Diver*. Additional collections of *C. isthmocladum* were made on reefs in the Abacos, Bahamas (Powell Cay, Munjack Cay; 7–10 m depths) in July of 1995 and at several locations in the Negril Marine Park, Jamaica (Little Bay, Ironshore, South Negril, and Davis Cove, 5–23 m depths; Lapointe and Thacker, 2002) during 1998.

In southeast Florida, *C. isthmocladum* was collected for C:N:P analysis between 1994 and 1996 on reefs in Palm Beach and Broward counties (26–43 m depths; Lapointe and Hanisak, 1997). We collected *C. isthmocladum* tissue from four sites in Palm Beach and Martin counties in August 1994 (Princess Anne, North Colonel's Ledge, Jupiter Ledge, Hobe Sound; Lapointe, 1997); from Jupiter Ledge, off northern Palm Beach County, monthly between May and August, 1995; and from several sites in northern Broward (Deerfield Reef) and Palm Beach counties (Jupiter Ledge, Hopper Barge, Hole in the Wall, North Colonel's Ledge, Spadefish Point, Juno Ball, South Double Ledges, Princess Anne, Boca Raton near the sewage outfall, and Spanish River Reef) between June and August, 1996. In addition, other abundant macroalgae (Chlorophyta, Rhodophyta, and Phaeophyta) were collected from several reef sites in Broward and Palm Beach counties in 1996 and analyzed to allow broader assessments of phylogenetic variability in C:N:P contents.

2.2. Analysis of macroalgae for C:N:P

The collections of macroalgae were processed and analyzed for tissue C:N:P contents. The Caribbean samples (Fig. 1) were prepared aboard the R/V *Sea*

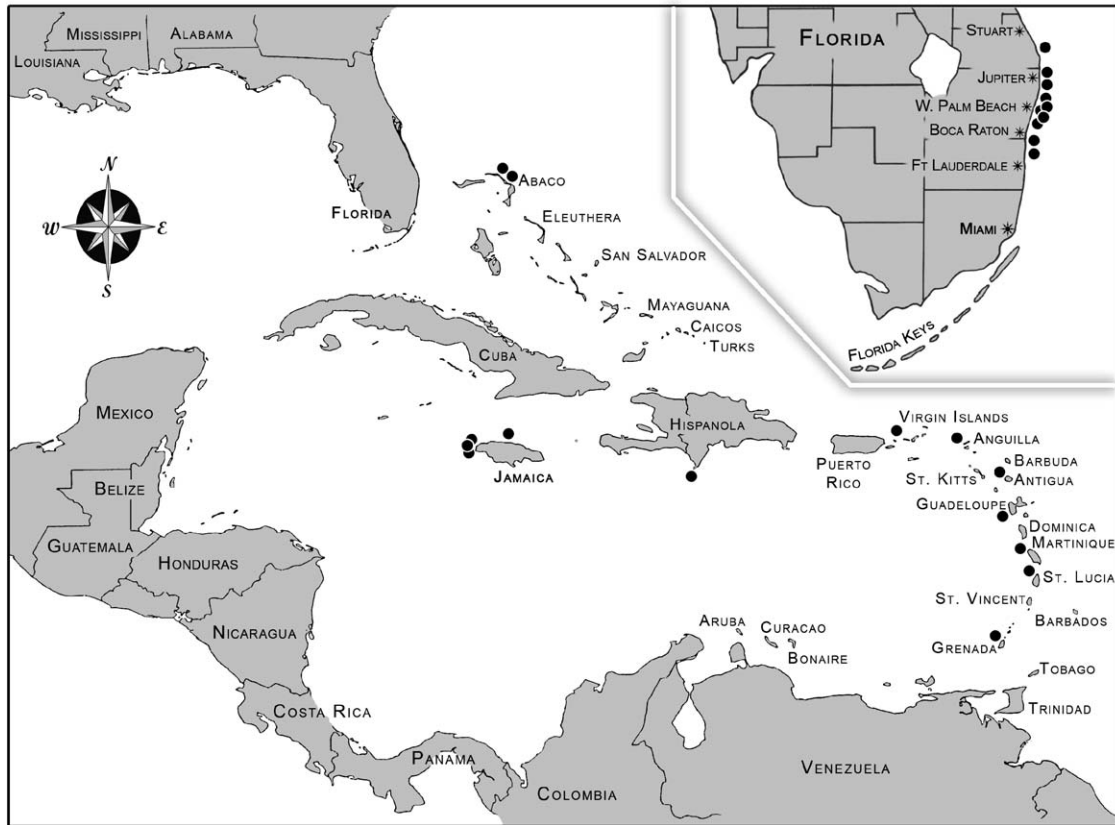


Fig. 1. Map showing location of study sites in the wider Caribbean region and southeast Florida (*inset*).

Diver, whereas the Florida samples were processed in the Marine Nutrient Dynamics Laboratory at HBOI in Ft Pierce, FL. In both cases, composite samples (thalli from five to eight different plants) of freshly collected macroalgae were immediately sorted, cleaned of visible epiphytes and sediments, and rinsed briefly (3–5 s) in deionized water to remove salt and debris. The cleaned, composite samples were dried in a Fisher Scientific Isotemp™ oven at 65 °C for 48 h. The dried macroalgae were ground to a fine powder using a mortar and pestle and stored in plastic vials in a dessicator. Samples of the dried, powdered macroalgae were analyzed for C:N:P contents at the Nutrient Analytical Services Laboratory, University of Maryland, Solomons, MD. Tissue C and N were measured on an Exeter Analytical, Inc. (EAI) CE-440 Elemental Analyzer, whereas P was measured following the methodology of Asplia et al. (1976) using a Technicon Autoanalyzer II with a IBM compatible Labtronics

Inc. DP500 software data collection system (D'Elia et al., 1997).

2.3. Seawater nutrient analyses

To quantify DIN ($=\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N} + \text{NO}_2^-\text{-N}$) and SRP ($\text{PO}_4^{3-}\text{-P}$) availability on southeast Florida's reefs, SCUBA divers collected near-bottom water samples for low level nutrient analysis from a variety of reef sites in Palm Beach and Broward counties in summer 1996 (June–August). Replicate ($n = 3\text{--}6$) water samples were collected by divers from the near-bottom layer (5 cm above reef surface) into clean, HDPE bottles. The water samples were held on ice in a cooler and subsequently filtered through a Gelman 0.45 μm GF/F filter and frozen until analysis. Within 28 days of collection, the samples were analyzed for $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, $\text{NO}_2^-\text{-N}$, and $\text{PO}_4^{3-}\text{-P}$ on either a Bran and Luebbe TRAACS 2000

Table 1

Tissue levels (% dry wt.) of carbon (C), nitrogen (N), phosphorus (P), and C:N, C:P, and N:P molar ratios of *Codium isthmocladum* from southeast Florida and the wider Caribbean

Location	Site	Date	%C	%N	%P	C:N	C:P	N:P	
Florida									
Martin Co.	Hobe Sound	8/7/94	11.71	1.07	0.06	13	503	39	
Palm Beach Co.	Jupiter Ledge	8/7/94	11.93	1.00	0.05	14	615	44	
		5/29/95	10.50	0.57	0.05	21	542	25	
		6/30/95	6.03	0.52	0.03	14	518	38	
		7/27/95	10.30	0.72	0.03	17	885	53	
		8/12/95	9.65	0.74	0.04	15	622	41	
	Hole in the Wall	8/16/96	10.80	1.23	0.07	10	398	39	
		7/15/96	8.34	1.44	0.11	7	196	29	
		Spadefish Point	7/15/96	8.85	1.01	0.07	10	326	32
		Juno Ball	7/21/96	9.59	0.77	0.05	15	495	34
		N. Colonel's Ledge	8/7/94	9.74	1.06	0.07	11	359	33
	Princess Anne	8/16/96	10.70	1.11	0.15	11	184	16	
		8/7/94	10.68	0.97	0.06	13	459	36	
		6/18/96	9.21	1.12	0.08	10	297	31	
		7/20/96	10.90	1.10	0.07	12	402	35	
		S. Double Ledges	7/21/96	9.45	0.85	0.06	13	406	31
Broward Co.	Boca Raton Outfall	8/27/96	8.79	1.17	0.06	9	378	43	
	Deerfield Reef	8/27/96	12.00	1.33	0.07	11	442	42	
Florida mean \pm 1S.D.			9.95 \pm 1.41	0.99 \pm 0.24	0.07 \pm 0.03	12.4 \pm 3.2	446 \pm 160	35.7 \pm 7.9	
Caribbean									
Puerto Rico	Isla de Culebra	6/2/95	12.90	0.74	0.03	20	1109	55	
St. Martin	Prickly Pear Cays	6/6/95	17.00	0.61	0.09	33	487	15	
Antigua	Bird Island	6/9/95	14.90	0.91	0.04	19	961	50	
Guadeloupe	Pointe Perces	6/11/95	12.60	0.64	0.04	23	812	35	
Martinique	Rocher de la Perle 1	6/13/95	13.50	1.01	0.06	16	580	37	
	Rocher de la Perle 2	6/13/95	12.30	0.78	0.05	18	634	34	
	Rocher du Diamant	6/15/95	10.60	0.72	0.05	17	547	32	
Little St. Vincent	Dark Head	6/19/95	15.00	0.99	0.05	18	774	44	
Powell Cay	Powell Channel 1	7/4/95	16.00	0.95	0.04	20	1032	53	
	Powell Channel 2	7/4/95	12.70	0.60	0.02	25	1638	66	
Munjack Cay	Munjack Cave 1	7/5/95	16.10	1.02	0.03	18	1384	75	
	Munjack Cave 2	7/6/95	13.60	1.06	0.04	15	877	59	
	Munjack Reef 1	7/7/95	15.10	1.04	0.03	17	1298	77	
	Munjack Reef 2	7/7/95	14.80	1.06	0.03	16	1272	78	
Dominican Rep.	St. Cruz de Barahona	5/30/96	14.30	0.49	0.03	34	1229	36	
Jamaica	Discovery Bay	6/2/96	14.47	0.88	0.04	19	933	49	
	Davis Cove, Deep	8/98	15.60	0.80	0.04	23	1006	44	
	South Negril, Deep	8/98	16.30	1.02	0.05	19	841	45	
	Ironshore	8/98	17.40	1.18	0.05	17	897	52	
	Little Bay, Shallow	8/98	21.20	1.26	0.04	20	1367	70	
	Little Bay, Deep	8/98	15.70	0.76	0.03	24	1350	56	
Caribbean Mean \pm 1S.D.			14.86 \pm 2.18	0.88 \pm 0.20	0.04 \pm 0.01	20.5 \pm 4.9	1001 \pm 306	50.6 \pm 16.0	
Grand Mean \pm 1S.D.			12.60 \pm 3.08	0.93 \pm 0.23	0.05 \pm 0.02	16.7 \pm 5.8	745 \pm 372	43.7 \pm 14.9	

Table 2

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

Phylum	Site	Date	Species	%C	%N	%P	C:N	C:P	N:P
Chlorophyta	Jupiter Ledge	8/16/96	<i>Codium isthmocladum</i>	10.80	1.23	0.07	10	398	39
	Hole in the Wall	7/15/96	<i>Anadyomene stellata</i>	23.30	2.38	0.14	11	429	38
			<i>Codium decorticatedum</i>	6.09	0.66	0.07	11	224	21
			<i>Codium isthmocladum</i>	8.34	1.44	0.11	7	196	29
			<i>Codium repens</i>	11.60	1.34	0.07	10	427	42
			<i>Ulva lactuca</i>	20.20	2.26	0.10	10	521	50
	Spadefish Point	7/15/96	<i>Anadyomene stellata</i>	21.70	1.78	0.10	14	560	39
			<i>Codium isthmocladum</i>	8.85	1.01	0.07	10	326	32
	Juno Ball	7/21/96	<i>Codium isthmocladum</i>	9.59	0.77	0.05	15	495	34
			<i>Codium repens</i>	12.00	0.94	0.06	15	516	35
	N. Colonel's Ledge	8/16/96	<i>Codium isthmocladum</i>	10.70	1.11	0.15	11	184	16
	Princess Anne	6/18/96	<i>Codium isthmocladum</i>	9.21	1.12	0.08	10	297	31
			<i>Ulva lactuca</i>	18.70	1.96	0.10	11	482	43
			7/20/96	<i>Codium isthmocladum</i>	11.10	1.09	0.07	12	409
	S. Double Ledge	7/21/96	<i>Codium isthmocladum</i>	10.70	1.11	0.06	11	460	41
			<i>Codium decorticatedum</i>	8.48	0.66	0.05	15	437	29
			<i>Codium isthmocladum</i>	9.45	0.85	0.06	13	406	31
	Hopper Barge	8/16/96	<i>Codium repens</i>	9.18	0.65	0.05	16	473	29
			<i>Codium decorticatedum</i>	9.03	1.11	0.10	9	233	25
			<i>Codium isthmocladum</i>	8.79	1.17	0.06	9	378	43
Boca Raton Outfall	8/27/96	<i>Caulerpa racemosa</i>	14.30	1.55	0.07	11	527	49	
		<i>Codium isthmocladum</i>	10.20	1.23	0.06	10	438	45	
		<i>Codium isthmocladum</i>	12.00	1.33	0.07	11	442	42	
Chlorophyta mean \pm 1 S.D.				11.93 \pm 4.5	1.25 \pm 0.46	0.08 \pm 0.03	11.4 \pm 2.22	403 \pm 107	35.5 \pm 8.41
	Rhodophyta	Hole in the Wall	7/15/96	<i>Chrysiomenia</i> sp.	6.18	0.98	0.08	7	199
<i>Gracilaria mammillaris</i>				18.70	2.21	0.15	10	321	33
<i>Halymenia floridana</i>				11.20	1.26	0.08	10	361	35
<i>Scinaia complanata</i>				7.22	1.48	0.13	6	143	25
Spadefish Point		7/15/96	<i>Chrysiomenia</i> sp.	8.43	1.02	0.07	11	224	21
S. Double Ledge		7/21/96	<i>Botryocladia occidentalis</i>	10.70	1.24	0.12	10	230	23
			<i>Bryothamnion</i> sp.	19.20	2.00	0.13	11	381	34
			<i>Chrysiomenia</i> sp.	3.09	0.30	0.03	12	266	22
			<i>Halymenia floridana</i>	11.10	0.88	0.06	15	477	32
Spanish River		8/15/96	<i>Grateloupia</i> sp.	13.80	1.14	0.10	14	356	25
			<i>Halymenia floresia</i>	8.96	0.89	0.06	12	385	33
Boca Raton Outfall		8/27/96	<i>Halymenia floridana</i>	11.70	1.44	0.10	9	302	32
Deerfield Reef		8/15/96	<i>Grateloupia</i> sp.	13.40	1.03	0.09	15	384	25
			<i>Halymenia floresia</i>	10.80	1.18	0.08	11	348	33
Rhodophyta Mean \pm 1 S.D.					11.03 \pm 4.24	1.22 \pm 0.46	0.09 \pm 0.03	10.9 \pm 2.55	313 \pm 87
	Phaeophyta	Hole in the Wall	7/15/96	<i>Styopodium zonale</i>	20.0	1.50	0.08	16	645
Spadefish Point				7/15/96	<i>Dictyota divaricata</i>	19.30	1.68	0.13	13
Juno Ball		7/21/96	<i>Styopodium zonale</i>	26.90	1.64	0.07	19	991	52
			<i>Lobophora variagata</i>	34.80	1.50	0.09	27	997	37
			<i>Styopodium zonale</i>	28.30	1.65	0.07	20	1043	52
Phaeophyta Mean \pm 1 S.D.				25.86 \pm 5.73	1.59 \pm 0.08	0.09 \pm 0.02	19.0 \pm 4.69	812 \pm 258	42.2 \pm 8.89
	Grand Mean \pm 1 S.D.			13.29 \pm 6.52	1.28 \pm 0.45	0.08 \pm 0.03	12.1 \pm 3.73	421 \pm 197	34.0 \pm 8.66

Analytical Console or an Alpkem nutrient autoanalyzer at the HBOI Environmental Laboratory (HBEL) in Ft. Pierce, FL. The analytical detection limits for these analyses were $0.08 \mu\text{M}$ for NH_4^+ , $0.05 \mu\text{M}$ for $\text{NO}_3^- + \text{NO}_2^-$, $0.003 \mu\text{M}$ for NO_2^- , and $0.009 \mu\text{M}$ for SRP. The methods for collection, handling, and processing of the water samples for low level nutrient analysis followed a quality assurance/quality control protocol designed to prevent problems associated with sample contamination and excessive holding times in order to provide accurate and reliable data (Gunsalus, 1997).

2.4. Statistical analyses

Analysis of tissue C:N:P contents between the Caribbean region and southeast Florida and nutrient data from southeast Florida involved both parametric (ANOVA) and non-parametric tests. We utilized non-parametric tests (e.g., Kruskal–Wallis H -test, Mann–Whitney U -test) when assumptions of homogeneity of variance and sample distribution normality were not met. Summary statistics are provided in the results below; reports of significance imply that the probability of the null hypothesis (p) is <0.05 .

3. Results

3.1. C:N:P analyses of macroalgae

The mean tissue C:N:P composition of *C. isthmocladum* sampled from reefs in southeast Florida in 1996 was markedly different than in populations from the Bahamas, Greater Antilles, and Lesser Antilles sampled between 1995 and 1998 (Table 1; Fig. 2). Although the mean %N of *C. isthmocladum* from southeast Florida (0.99 ± 0.25) was statistically similar (Mann–Whitney, $p = 0.179$) to that from the wider Caribbean region (0.89 ± 0.21), the mean %P of the Florida populations (0.06 ± 0.03) was significantly higher than the Caribbean populations (0.04 ± 0.01 ; Mann–Whitney, $p < 0.001$). The floridian *C. isthmocladum* population had lower %C (9.83 ± 1.56 versus 14.83 ± 2.21 ; $p < 0.001$), C:N (12.22 ± 3.07 versus 19.15 ± 5.21 ; $p < 0.001$), C:P (425 ± 146 versus 980 ± 278 ; $p < 0.001$), and N:P ratios (35.0 ± 8.2 versus 50.1 ± 15.0 ; $p < 0.001$) compared to the Caribbean populations (Table 1). These regional

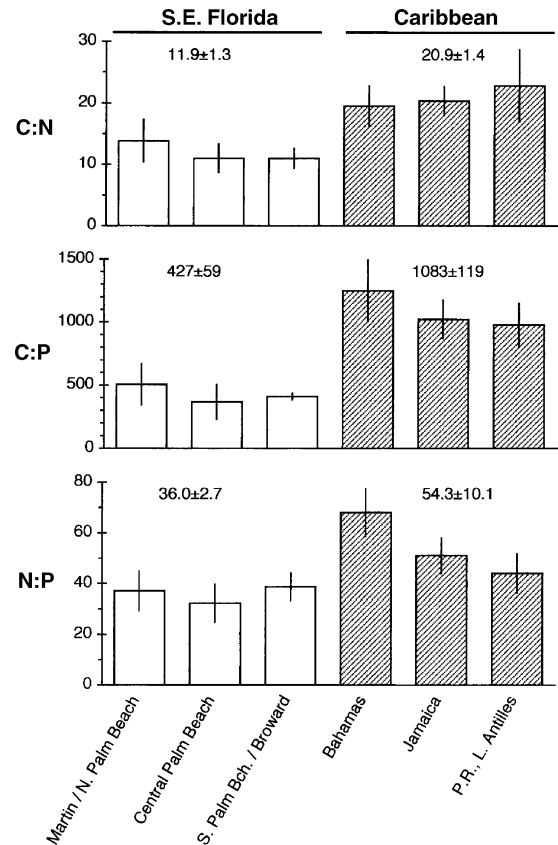


Fig. 2. Tissue carbon:nitrogen (C:N), carbon:phosphorus (C:P), and N:P molar ratios of *Codium isthmocladum* at sites in southeast Florida vs. the wider Caribbean region (locations sampled near urbanized areas of the Caribbean are omitted from this plot). Values represent means \pm S.D. ($n = 3$ –12).

differences become even more apparent when urbanized sites from the Caribbean (e.g., sites around Fort-de-France, Martinique; see Littler et al., 1993) are removed from the comparison (Fig. 2).

Significant phylogenetic differences in mean C:N:P composition among species of Chlorophyta, Rhodophyta and Phaeophyta were detected (Kruskal–Wallis test) on reefs in southeast Florida in 1996 (Table 2). Although the overall mean %P of the three groups were statistically similar ($p = 0.267$), significant differences were observed for %C (Kruskal–Wallis, $p = 0.003$), C:N ($p = 0.004$), C:P ($p = 0.001$), and N:P ($p = 0.008$). Differences in %N were only marginally significant ($p = 0.063$). With the exception of %P, which was similar among the three phyla, most of the significant differences in other tissue variables resulted

from large differences between species of Phaeophyta and the Chlorophyta/Rhodophyta. For example, the mean %C was over two-fold higher in the Phaeophyta (25.86 ± 5.73) compared to either the Chlorophyta (11.93 ± 4.5) or Rhodophyta (11.03 ± 4.24). Likewise, differences between the Phaeophyta and the Chlorophyta/Rhodophyta occurred for %N (1.59 ± 0.08 versus $1.25 \pm 0.46/1.22 \pm 0.46$), C:N (19.0 ± 4.69 versus $11.4 \pm 2.22/10.9 \pm 2.55$), C:P (812 ± 258 versus $403 \pm 107/313 \pm 87$), and N:P ratios (42.2 ± 8.89 versus $35.5 \pm 8.41/28.6 \pm 4.82$).

3.2. Water column nutrient concentrations

Concentrations of NO_3^- and NH_4^+ in near-bottom reef waters in Palm Beach and Broward counties ranged from 0.07 to 8.91 μM and from undetectable ($<0.05 \mu\text{M}$) to 2.99 μM , respectively, between June and August 1996 (Fig. 3). The highest NH_4^+ concen-

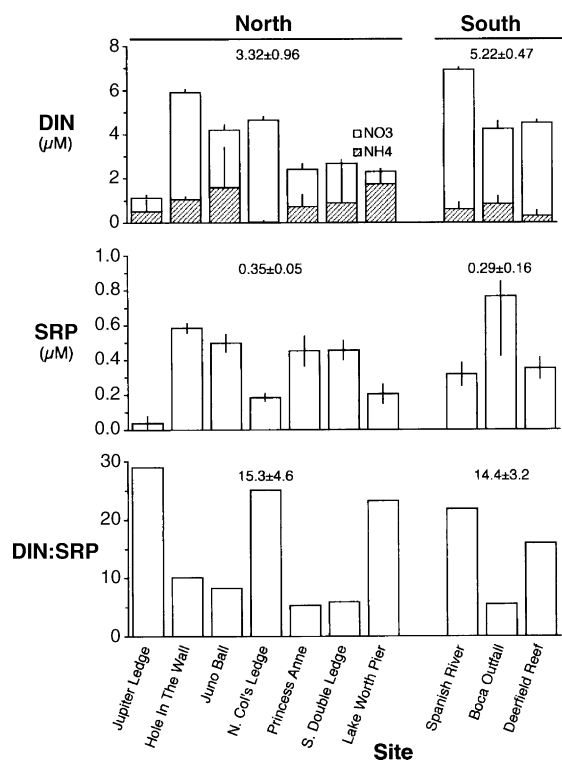


Fig. 3. Concentrations (μM) of dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), and the DIN:SRP ratio for north vs. south regions of the southeast Florida study area from June to August of 1996. Values represent means \pm S.D. ($n = 3-6$).

trations occurred on shallow reefs (e.g., 4 m, Lake Worth Pier, Fig. 3) compared to the highest NO_3^- concentrations that occurred on the deepest reefs during upwelling events (e.g., August 1996 at Hole in the Wall, North Colonel's Ledge, Spanish River, Fig. 3). This depth-related pattern was apparent in August 1996 off Spanish River (Boca Raton) during an upwelling event when NO_3^- concentrations increased with increasing depth; whereas, NH_4^+ concentrations decreased with increasing depth (Fig. 4A and B).

Significant differences occurred in mean DIN concentrations between the northern and southern regions of the study area during summer 1996. Overall, DIN concentrations were significantly (ANOVA, $F = 9.01$, $p = 0.0073$) greater in the southern ($5.22 \pm 0.48 \mu\text{M}$) compared to the northern region ($3.23 \pm 0.35 \mu\text{M}$, Fig. 3). This difference was largely the result

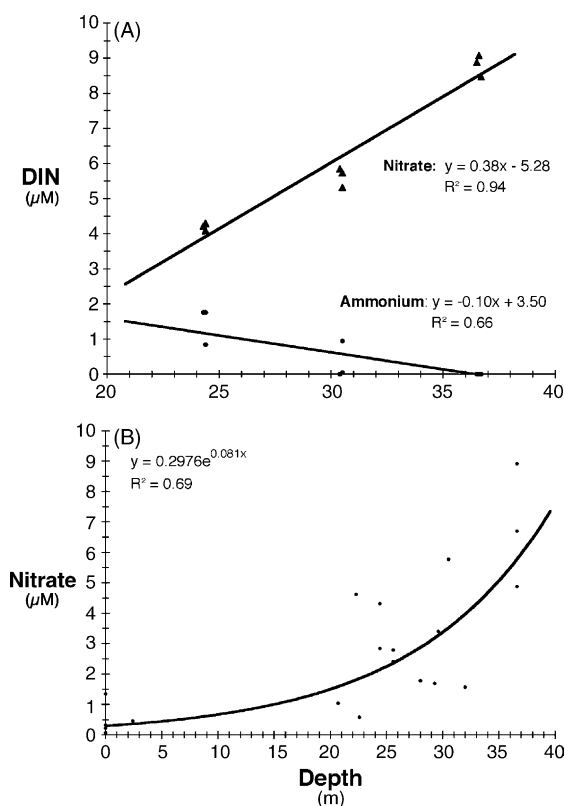


Fig. 4. Regressions for: (A) dissolved inorganic nitrogen (DIN = $\text{NH}_4^+\text{-N} + \text{NO}_3^-\text{-N} + \text{NO}_2^-\text{-N}$) concentrations (μM) vs. depth (m), and (B) NO_3^- concentrations (μM) vs. depth (m). Samples were collected from reefs off Spanish River, Boca Raton, August 15, 1996.

of higher concentrations of NO_3^- (ANOVA, $F = 13.92$, $p = 0.0014$) in the southern compared to the northern region during the 1996 sampling. Concentrations of NH_4^+ were not significantly ($p > 0.05$) different between the two regions and averaged $0.82 \mu\text{M}$ throughout the study area.

SRP concentrations ranged from 0.066 to $0.766 \mu\text{M}$ during the summer 1996 sampling with the highest concentrations at the site nearest the Boca Raton sewage outfall (Fig. 3). The mean SRP concentration in the northern region ($0.35 \pm 0.05 \mu\text{M}$) was lower, but not significantly ($p > 0.05$) different than that of the southern region ($0.48 \pm 0.07 \mu\text{M}$; Fig. 2). The DIN:SRP ratio averaged 15.3 in the northern region and 14.4 in the southern region with peak values >20 associated with low SRP concentrations (Fig. 3).

4. Discussion

4.1. Importance of P-availability to bloom development and species composition

Our comparative studies of C:N:P contents in *C. isthmocladum* among a broad spectrum of sites support previous findings (Lapointe, 1997) of reduced P limitation in coastal waters of southeast Florida compared to stronger P limitation in carbonate-rich Caribbean waters. Lapointe et al. (1992) sampled a wide variety of taxa, including Chlorophyta, Phaeophyta and Rhodophyta, from several carbonate-rich environments throughout the Caribbean and from a temperate, siliciclastic environment at Woods Hole, MA, USA. Whereas %C and %N were similar in macroalgal tissue between these regions (22.6% versus 20.1% and 1.0% versus 1.2% , respectively), P levels were two-fold lower (0.15% versus 0.07%) in the carbonate-rich sites of the Caribbean region. We found parallel results for *C. isthmocladum* in the present study, which had similar tissue %N values between southeast Florida and the Caribbean region, but elevated levels of %C and depleted levels of %P in the Caribbean region. The relatively low C:P and N:P ratios of *C. isthmocladum* in southeast Florida versus the Caribbean region indicate P enrichment in southeast Florida compared to strong P limitation throughout the Caribbean sites. The strong P limitation in the Caribbean region may explain the higher %C levels

of *C. isthmocladum*, which would result from accumulation of photosynthetic products in the absence of rapid growth under P limitation. Conversely, reduced P limitation in the floridian *C. isthmocladum* populations suggests that this P enrichment is a primary physiological factor supporting excessive biomass development of HABs characterized by rapid growth and relatively low %C contents. The highest SRP concentrations in the 1996 nutrient survey in southeast Florida were near the Boca Raton outfall and off Juno Beach during a strong upwelling event, suggesting the importance of P enrichment from both chronic sewage inputs as well as from natural episodic inputs. More broadly, the limestone platform of the southeast Florida study area has been covered with siliciclastic sediments transported southwards from Piedmont and coastal plain rivers over geologic time (Meade, 1969; Hine, 1997). This would provide naturally higher background SRP concentrations compared to those in carbonate-rich waters of the Caribbean (Lapointe et al., 1992).

Our findings also indicate that strong P limitation resulting from reduced SRP availability is a major factor limiting bloom formation of *C. isthmocladum* in the Caribbean region. Land-based nutrient discharges from carbonate-rich islands around the Caribbean region typically have low SRP concentrations and high N:P ratios (D'Elia et al., 1981; Lapointe and Clark, 1992; Lapointe and Thacker, 2002), resulting in depleted SRP concentrations and strong P limitation in coastal waters. SRP concentrations in southeast Florida averaged $>0.29 \mu\text{M}$ during the summer 1996 studies, a value that is an order-of-magnitude higher than the SRP concentrations reported for shallow and deep reefs in the Negril Marine Park, Jamaica, and the Belize Barrier Reef (Lapointe and Thacker, 2002; Lapointe et al., 1997; Lapointe, 2004). This regional pattern of depleted SRP in the Caribbean parallels observations of \sim five-fold higher alkaline phosphatase activity (APA) in *C. isthmocladum* at Discovery Bay, Jamaica, compared to southeast Florida (Lapointe, 1997), demonstrating the strong P limitation in Jamaica. The primary P limitation at Discovery Bay was further evidenced by nutrient enrichment assays where SRP significantly increased P_{max} of the green filamentous alga *Chaetomorpha linum* compared to insignificant effects of NO_3^- (Lapointe, 1997). The higher water column SRP concentrations and reduced P limitation in southeast

Florida can support blooms of chlorophyte “SRP indicators” like *C. isthmocladum*. This species is abundant with other SRP indicators (e.g., *Ulva*, *Chaetomorpha*, *Enteromorpha*) surrounding seabird rookeries or sewage-impacted waters where elevated SRP concentrations and low N:P ratios occur (Lapointe et al., 1993).

The relatively low SRP concentrations on many carbonate-rich Caribbean reefs would make DOP cycling an adaptive strategy for macroalgal growth in these environments. Several phaeophyte genera, including *Dictyota*, *Sargassum*, and *Lobophora*, have high capacities for APA and would be favored in waters with low SRP concentrations. Klausmeier et al. (2004), using a stoichiometrically explicit model, suggested that competitive equilibrium favors greater allocation to biochemical pathways for SRP-poor resource acquisition (e.g., APA), and therefore, a higher optimal N:P ratio; exponential growth favors greater allocation to P-rich assembly processes, and therefore, a lower N:P ratio. This physiological mechanism may explain why phaeophytes such as *Dictyota* spp. have become dominant bloom species on reefs formerly dominated by live coral cover in the nutrient enriched (high N:P) coastal waters of the Florida Keys (Lapointe and Clark, 1992; Lirman and Biber, 2000; Lapointe et al., 2004). Similarly, lush meadows of the phaeophytes *Sargassum polyceratum* and *Sargassum hystrix*, with an extensive understory of *Lobophora variegata* (Lapointe, 1997; Lapointe and Thacker, 2002), have replaced the hermatypic (reef-forming) coral genera that historically dominated shallow and deep reefs on Jamaica’s north coast (Goreau, 1959). These Jamaican reefs have also experienced high N:P ratios associated with human activities from the upland watershed (D’Elia et al., 1981; Lapointe, 1997; Lapointe and Thacker, 2002).

Tropical phaeophytes typically have higher %C content, C:N and C:P ratios than chlorophytes and rhodophytes (Table 2), indicating their greater ability for storage of structural C under nutrient limited growth. This physiological characteristic allows for the production of C-rich secondary compounds known to be important for chemical defense from herbivores in the Phaeophyta. For example, a decrease in chemical defense production under elevated nitrogen conditions has been demonstrated in the field for the temperate *Fucus vesiculosus* (Yates and Peckol, 1993)

and in laboratory conditions for the tropical *Lobophora variegata* (Arnold et al., 1995). For phaeophytes, plant phenols tend to accumulate under environmental conditions where plants have excess C above the level needed for balanced growth and where phenylalanine, the substrate of phenylpropanoid synthesis, accumulates due to suppressed protein synthesis (Ilvessalo and Tuomi, 1989). While phaeophytes have not formed widespread HABs on the northern portion of the Florida Reef Tract (Palm Beach County), they have formed conspicuous blooms on reefs in the Florida Keys where considerable grazing activity occurs (Lapointe and Clark, 1992; Lirman and Biber, 2000). The extensive meadows of phaeophytes that have developed on Jamaica’s north coast have elevated tissue C:N ratios (~28; Lapointe et al., 1992), suggesting that these populations likewise benefit from the production of anti-herbivore secondary compounds (e.g., polyphenolics).

4.2. The role of NH_4^+ in bloom nutrition in southeast Florida

The lower N:P ratios of *C. isthmocladum* in southeast Florida compared to the Caribbean populations would not only reduce P limitation, but would also increase the potential for N limitation on southeast Florida’s reefs. Enrichment assays with NH_4^+ significantly increased α , the initial slope of the P versus I curve, of *C. isthmocladum* compared to insignificant effects of SRP (Lapointe, 1997). The mean C:N ratio of *C. isthmocladum* in southeast Florida (12.2) was lower than that of Caribbean populations (19.2), suggesting that the floridian populations were relatively N enriched relative to C demands. The chronically elevated NH_4^+ concentrations reported for this study area (see Fig. 3) suggest that the availability of NH_4^+ would increase photosynthetic efficiency under low light, leading to nitrogen saturation of growth and bloom formation (see Lapointe, 1999).

During summer months, episodic upwelling with high NO_3^- concentrations occur in the study area (Atkinson, 1985; Lapointe et al., 2005) and provide additional enrichment to the NH_4^+ and NO_3^- derived from land-based nutrient inputs. In the Niantic River estuary, CT, USA, the invasion of *C. fragile* was related to NH_4^+ enrichment in addition to the available NO_3^- in that system (Malinowski and Ramus, 1973).

Nutrient kinetic studies with macroalgae provide evidence as to why episodic, upwelled NO_3^- , by itself, could not have historically supported bloom formation of *C. isthmocladum* in southeast Florida. In controlled laboratory studies, Hanisak and Harlin (1978) reported that uptake of DIN by *C. fragile* subsp. *tomentosoides* was highly dependant upon light, temperature, and the source of DIN (i.e., NO_3^- versus NH_4^+). At temperatures of 20–25 °C, the uptake rate of NH_4^+ was ~seven-fold greater than that of NO_3^- and the presence of NH_4^+ inhibited uptake of NO_3^- . Similar preferences for NH_4^+ over NO_3^- have been reported in other kinetic studies with macroalgae (D'Elia and DeBoer, 1978) as well as for natural phytoplankton communities (Conway, 1977). Because an average of 0.82 μM NH_4^+ was present in the near-bottom waters during the summer 1996 upwellings, it is unlikely that NO_3^- was a major DIN source supporting the *C. isthmocladum* blooms. In a seasonal upwelling system similar to that of southeast Florida, Fujita et al. (1989) found that relatively low concentrations of NH_4^+ (1.22 μM) supplied >100% of the N required for maximum growth of the chlorophyte *Ulva rigida*, even in the presence of much higher NO_3^- concentrations (10.8 μM).

4.3. Understanding nutrient enrichment and eutrophication on coral reefs

Within the past decade, many coral reef biologists and managers have not fully appreciated the severity of nutrient enrichment and eutrophication problems facing coral reefs (Risk, 1999). We suggest that this has led to the use of inadequate analytical methods and concomitant misinterpretations of nutrient data. For example, in the Great Barrier Reef lagoon, the effects of “water quality” on biomass of *Sargassum* spp. transplants from an inshore fringing reef to a mid-shelf reef (Otter Reef) were assessed (McCook, 1996). Although no water samples were actually analyzed for nutrients, McCook (1996) concluded that the “tissue analyses indicate that mid-shelf *Sargassum* transplants were not limited by nitrogen or phosphorus supplies”. However, his reported C:N ratio of 32:1 and C:P ratio of 1261:1 indicated significant N limitation and severe P limitation, even higher than that of pelagic *Sargassum* in nutrient-depleted surface waters of the Sargasso Sea (C:P = 877; Lapointe, 1995). McCook's

study (1996) was cited by Fong et al. (2003) as evidence that calls into question whether macroalgae in tropical systems are ever limited by nutrients. Fong et al. (2003) collected water samples from two sites on the southwest coast of Puerto Rico. However, their analytical methods were not sensitive enough (detection limits of 3.57 μM for NH_4^+ and NO_3^- , and 1.61 μM for P) to assess nutrient availability in that oligotrophic environment. Because the resulting nutrient data of Fong et al. (2003) were below detection limits, inferences regarding water column nutrient availability in those studies could not reasonably be made. Similar problems with inadequate detection limits plagued another recent study at Glover's Reef offshore the Belize Barrier Reef that reported background SRP concentrations of 0.36–1.0 μM (McClanahan et al., 2002). Those values are some 20-fold higher than the typical SRP concentrations reported for this location (~0.05 μM , Lapointe, 2004) and for offshore waters of the Caribbean Sea (Rajendran et al., 1991). For the coral reefs off southeast Florida, failure to establish reasonable background concentrations for NH_4^+ have confounded the SEFLOE II (Hazen and Sawyer, 1994) dilution model for the discharge of partially-treated sewage from ocean outfalls (see Lapointe et al., 2005).

Although macroalgal HABs on coral reefs have long been attributed to nutrient enrichment and eutrophication (e.g., Littler, 1973; Banner, 1974; Johannes, 1975; Smith et al., 1981; Lapointe, 1997), some reef biologists have concluded that such changes in benthic community structure on Caribbean coral reefs result solely from overfishing of herbivorous fish stocks (Hughes, 1994) and/or loss of keystone grazers, such as the long-spined sea urchin *Diadema antillarum* (Jackson et al., 2001). However, these conclusions are not supported by numerous grazer reduction experiments that generally report an expansion of algal turfs (<2 cm high) rather than macroalgal blooms (>2 cm high, see Lapointe, 1999) in oligotrophic environments. These include studies in the Red Sea (Vine, 1974), Fiji (Littler and Littler, 1997), Belize (Lewis, 1986), the Great Barrier Reef (Sammarco, 1983), and St. Croix (Carpenter, 1988). The widely cited study by Lewis (1986) on the Belize Barrier Reef reported a statistically significant though relatively small increase (28% over 10 weeks) in algal

turfs and no significant increase in the macroalgae *Halimeda* sp. and *Turbinaria turbinata*. These particular macroalgae have both overgrown coral reefs in the Negril Marine Park, Jamaica, following decades of nutrient enrichment from sewage pollution associated with tourism development and from use of fertilizers for agriculture (Lapointe and Thacker, 2002). Another confounding issue is that many invasive, bloom-forming macroalgae (such as *Codium* spp.) on reefs are not preferred by generalist grazers (Ramus, 1971; Malinowski and Ramus, 1973; Hanisak, 1980; Trowbridge, 1995). Overfishing of herbivorous fishes and other keystone grazers has been implicated as the sole cause of macroalgal HABs on reefs in southeast Florida and Jamaica (Hughes et al., 1999) without recognition of the escalating rate and scale of anthropogenic nutrient pollution and its consequences to coral reefs (Lapointe, 1999). This explanation for the decline of coastal ecosystems (see Jackson et al., 2001), including the emergence of macroalgal HABs, has been noted and criticized by Boesch et al. (2001). We encourage coral reef biologists and managers to consider more broadly the complex role that escalating nutrient enrichment plays in the regulation of macroalgal HABs in coral reef ecosystems.

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