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# Nutrient Availability to Marine Macroalgae in Siliciclastic Versus Carbonate-Rich Coastal Waters

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**ABSTRACT: Abundant populations of frondose epilithic macroalgae from a variety of carbonate-rich tropical waters were significantly depleted in phosphorus relative to carbon and nitrogen when compared to macroalgae from temperate siliciclastic waters. Percent carbon (C) and percent nitrogen (N) dry weight contents were similar between tissues from the siliciclastic and carbonate environments (means of 22.6% vs. 20.1% and 1.0% vs. 1.2%, respectively), but phosphorus (P) levels were two-fold lower (0.15% vs. 0.07%) in the carbonate-rich systems. Accordingly, the molar C:N tissue ratios were comparable between macroalgae from the siliciclastic and carbonate sites (mean of 29.2 vs. 23.1), whereas large differences were observed for the C:P (mean of 430 vs. 976) and N:P ratios (mean of 14.9 vs. 43.4). In addition, alkaline phosphatase activity was low and often undetectable in the macroalgae from siliciclastic habitats (mean of 7.3 $\mu$M $PO_4^{3-}$ released g dry $wt^{-1}$ $h^{-1}$) compared to seven-fold higher rates (52.5 $\mu$M $PO_4^{3-}$ released g dry $wt^{-1}$ $h^{-1}$) observed in the macroalgae from carbonate systems. Seawater samples taken adjacent to benthic macroalgae from the carbonate-rich tropical waters contained relatively high levels of dissolved inorganic nitrogen with low concentrations of soluble reactive phosphorus (SRP), and showed elevated N:SRP ratios (mean = 36) compared to siliciclastic environments (mean <3). These data support the precept that availability of N limits the productivity of macroalgae in temperate siliciclastic waters but, conversely, suggest that availability of P, rather than N, may be of paramount importance in limiting primary production of macroalgae in carbonate-rich tropical waters.**

## Introduction

Primary production by marine macroalgae in coastal water is often limited by nutrient availability, particularly when irradiance and temperature are not critical (Lapointe and Tenore 1981; Lapointe et al. 1984). Nitrogen (N) is frequently the limiting nutrient to productivity of frondose macroalgae in temperate coastal waters (Topinka and Robbins 1976; Chapman and Craigie 1977; Hanisak 1979; Gerard 1982), in agreement with the precept that N rather than phosphorus (P) availability limits marine primary production in these environments (Ryther and Dunstan 1971; Vince and Valiela 1973). However, recent studies suggest that P may be of greater importance than N as a limiting nutrient for certain species, habitats, and/or seasons in the tropical/subtropical coastal waters of Bermuda (Lapointe and O'Connell 1989), Florida Keys (Lapointe 1987, 1989), Bahamas (Littler et al. 1988), and Belizian barrier reef (Lapointe et al. 1987).

The potential importance of P relative to N in limiting primary productivity of macroalgae has also been implicated by worldwide surveys of tissue carbon : nitrogen : phosphorus (C:N:P) data. Atkinson and Smith (1983) reported a mean C:N:P ratio of 700:35:1 in a survey of benthic marine plants from a wide variety of locations. Because N:P ratios < 10:1 indicate N-limitation while N:P ratios > 30:1 indicate P-limitation (Ryther and Dunstan 1971; Rhee 1978; Smith 1984), the mean N:P ratio of 35:1 for benthic marine plants suggests that marine macrophytes, in general, are in a nutritional state that tends toward P-limitation rather than N-limitation (Atkinson and Smith 1983).

Realizing that a high degree of variability exists in the type and degree of nutrient limitation on a worldwide basis, we predicted that significant geo-



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graphic patterns of nutrient limitation of macroalgal primary production occur as a function of contrasting biogeochemical environments. The contrast we studied was that between temperate siliciclastic and tropical carbonate-rich environments. Temperate siliciclastic environments are influenced by terrigenous organic matter and have characteristically low ratios of N:P regeneration (Nixon et al. 1980). Alternatively, tropical carbonate-rich environments lack such terrigenous input and generally have low concentrations of soluble reactive phosphate (SRP) (Berner 1974; Sander and Moore 1979; Hines and Lyons 1982).

As a partial test of this prediction, we compared tissue elemental composition and C:N:P ratios in a broad spectrum of temperate frondose algae from a well-studied siliciclastic environment (Woods Hole, Massachusetts) to those of tropical frondose macroalgae from a wide variety of sites in the tropical carbonate-rich Caribbean Sea and adjacent waters (Bermuda, Bahamas, Florida Keys, Belize, Jamaica). Dissolved seawater nutrient concentrations and alkaline phosphatase activities of the same array of macroalgae were also determined at the various sites.

## Methods

Samples of the predominant macroalgae were collected from shallow (<2 m) depths at the following locations (Fig. 1): Woods Hole (Waquoit Bay, Nobska Point); Bahamas (Spanish Wells, Egg Island); Bermuda (Harrington Sound, Castle Harbor); Florida Keys (Pine Channel, Looe Key National Marine Sanctuary); Belize (Curlew Cay and Twin Cays, adjacent to Carrie Bow Cay); Jamaica (Discovery Bay). All plants were collected during active growth in spring and summer 1986–1987. A special effort was made to collect plants that were not shaded (i.e., light limited), either by dense growths of neighboring macroalgae or by rocks, ledges, and mangrove trees, as light limitation uncouples the relationship between tissue nutrient ratios and productivity (Lapointe and Tenore 1981). At least six different individual plants per species were collected, macroscopic epiphytes removed, and the plants pooled into one composite sample.

The composite macroalgal samples were quickly rinsed in deionized water prior to drying in a laboratory oven at 70°C for 48 h and grinding to a powder. Total C and N were determined using a Carlo Erba CHN analyzer. Total P was determined by digesting preweighed samples with persulfate (Menzel and Corwin 1965) followed by analysis for SRP (Murphy and Riley 1962).

Macroalgae from the various sites were assayed for alkaline phosphatase activity by the spectrophotometric method of Kuenzler and Perras (1965). The assays utilized about 3.0 g wet wt algae, 15 ml nitrophenyl phosphate (NPP) stock (1.0 g NPP substrate and 25.0 g $MgSO_4$ dissolved in 500 ml deionized water), 30 ml of Tris buffer, and filtered seawater to make 500 ml of assay medium. Acid-washed, 1.0-l Wheaton wide-mouth glass bottles that received constant stirring via seawater-driven magnetic stirrers were used for the assay. Natural irradiance during the incubations ranged from 1,200 $\mu$mol $m^{-2}$ $s^{-1}$ to 2,100 $\mu$mol $m^{-2}$ $s^{-1}$ and temperature ranged from a low of 19°C (Woods Hole) to 23–29°C at the carbonate-rich sites.


Fig. 1. Locations of the six general study areas containing the 12 specific habitats and 41 macroalgal species sampled.

Water samples were collected at each location for determination of ammonium, nitrate plus nitrite, and SRP. Syringes fitted with sipper tubes were used to collect seawater closely adjacent to macroalgae (within 1 cm) at the sediment-seawater interface. The samples were placed in acid-washed Nalgene bottles, spiked with $HgCl_2$ (10 mg $l^{-1}$), and frozen until analysis. Ammonium, as well as nitrate plus nitrite, concentrations were determined on an Autoanalyzer II according to the methods of Slawyk and MacIsaac (1972) and Technicon (1973), respectively. Concentrations of SRP were determined by the molybdenum-blue method (Murphy

TABLE 1. Tissue levels (as percent dry weight) of carbon (C), nitrogen (N), phosphorus (P), and alkaline phosphatase activity ($\mu M$ $PO_4^{3-}$ g dry $wt^{-1}$ $h^{-1}$) in frondose marine macroalgae from siliciclastic (Woods Hole) and carbonate-rich (Bermuda, Bahamas, Florida Keys, Belize, Jamaica) coastal waters.

| Location | Species | % C | % N | % P | C:N | C:P | N:P | Alkaline Phosphatase Activity |
|---|---|---|---|---|---|---|---|---|
| Woods Hole | *Gracilaria tikvahiae* | 16.3 | 0.64 | 0.12 | 29.6 | 346 | 11.8 | 3.2 ± 0.8 |
| | *Neoagardhiella bayleyi* | 12.2 | 0.74 | 0.16 | 19.1 | 196 | 10.3 | 6.0 ± 1.8 |
| | *Chondrus crispus* | 25.6 | 1.33 | 0.29 | 22.4 | 224 | 10.0 | 9.7 ± 0.6 |
| | *Hypnea musciformis* | 21.2 | 1.50 | 0.19 | 15.9 | 286 | 7.9 | 5.8 ± 1.8 |
| | *Ceramium rubrum* | 16.3 | 1.76 | 0.19 | 10.8 | 216 | 20.2 | 19.4 ± 3.5 |
| | *Sargassum filipendula* | 21.8 | 0.85 | 0.17 | 29.8 | 327 | 11.1 | 9.0 ± 0.6 |
| | *Fucus vesiculosus* | 30.0 | 0.68 | 0.11 | 51.3 | 699 | 13.7 | 4.1 ± 0.3 |
| | *Fucus spiralis* | 34.7 | 1.33 | 0.13 | 30.4 | 679 | 22.6 | 3.4 ± 0.9 |
| | *Ascophyllum nodosum* | 37.6 | 0.56 | 0.12 | 67.1 | 811 | 10.4 | 3.8 ± 0.6 |
| | *Codium fragile* | 17.9 | 0.67 | 0.08 | 31.2 | 576 | 18.6 | 2.8 ± 1.4 |
| | *Codium decorticatum* | 14.5 | 0.64 | 0.09 | 26.4 | 429 | 16.4 | 3.7 ± 1.2 |
| | *Ulva lactuca* | 23.5 | 0.88 | 0.14 | 31.0 | 433 | 14.1 | 5.2 ± 1.2 |
| | *Enteromorpha intestinalis* | 22.8 | 1.88 | 0.16 | 14.1 | 366 | 26.1 | 18.6 ± 5.4 |
| Bermuda | *Laurencia obtusa* | 16.8 | 1.07 | 0.06 | 17.6 | 718 | 39.6 | 34.4 ± 4.6 |
| | *Cladophora prolifera* | 17.7 | 0.98 | 0.05 | 20.9 | 942 | 45.3 | 45.3 ± 5.1 |
| | *Codium decorticatum* | 12.9 | 1.00 | 0.04 | 14.6 | 830 | 56.0 | 4.4 ± 0.8 |
| Florida Keys | *Gracilaria tikvahiae* | 28.4 | 2.23 | 0.04 | 15.6 | 1,817 | 124.0 | 11.4 ± 7.7 |
| | *Chondria tenuissima* | 20.3 | 1.95 | 0.12 | 11.6 | 433 | 36.1 | N/A |
| | *Laurencia poitei* | 21.0 | 2.05 | 0.14 | 11.5 | 384 | 32.5 | 101.0 ± 53.3 |
| | *Laurencia intricata* | 20.1 | 1.71 | 0.05 | 13.7 | 1,080 | 74.8 | 52.8 ± 17.8 |
| | *Meristiella gelidium* | 22.1 | 0.78 | 0.07 | 31.7 | 809 | 24.8 | N/A |
| | *Liagora mucosa* | 15.7 | 0.61 | 0.06 | 28.9 | 672 | 22.6 | 53.4 ± 3.9 |
| | *Padina jamaicensis* | 22.0 | 1.02 | 0.10 | 24.3 | 564 | 22.7 | 58.2 ± 11.3 |
| | *Stypopodium zonale* | 35.3 | 1.53 | 0.12 | 25.9 | 754 | 28.4 | 22.1 ± 3.4 |
| | *Dictyota divaricata* | 23.9 | 1.64 | 0.10 | 16.3 | 612 | 36.4 | 186.0 ± 26.3 |
| | *Sargassum pteropleuron* | 27.8 | 0.80 | 0.06 | 41.1 | 1,307 | 23.4 | 35.5 ± 3.2 |
| | *Sargassum polyceratium* | 26.0 | 1.31 | 0.13 | 23.1 | 550 | 24.9 | 27.8 ± 8.3 |
| Bahamas | *Sargassum hystrix* | 22.6 | 1.81 | 0.07 | 14.0 | 827 | 57.5 | 25.1 ± 6.1 |
| | *Lobophora variegata* | 28.0 | 0.63 | 0.03 | 49.9 | 2,393 | 46.7 | 37.7 ± 14.9 |
| | *Codium isthmocladum* | 13.8 | 1.08 | 0.11 | 14.4 | 321 | 21.8 | 3.0 ± 2.4 |
| | *Bryopsis pennata* | 15.7 | 2.29 | 0.12 | 7.7 | 335 | 42.4 | 1.3 ± 0.8 |
| | *Microdictyon marinum* | 16.1 | 0.74 | 0.03 | 24.4 | 1,376 | 54.8 | 27.8 ± 13.4 |
| Belize | *Acanthophora spicifera* | 16.7 | 0.48 | 0.03 | 39.1 | 1,427 | 35.6 | 65.4 ± 6.4 |
| | *Dictyota divaricata* | 24.0 | 0.87 | 0.04 | 30.9 | 1,538 | 48.3 | 78.4 ± 6.2 |
| | *Halimeda opuntia* | 14.9 | 0.44 | 0.02 | 38.0 | 1,910 | 48.9 | 5.3 ± 2.2 |
| Jamaica | *Gracilaria ferox* | 20.6 | 1.52 | 0.07 | 15.7 | 712 | 45.7 | 47.1 ± 15.6 |
| | *Dictyota dichotoma* | 17.7 | 0.89 | 0.05 | 23.2 | 842 | 36.6 | 226.0 ± 82.1 |
| | *Sargassum polyceratium* | 11.9 | 0.64 | 0.03 | 21.6 | 984 | 45.8 | 99.3 ± 42.6 |
| | *Lobophora variegata* | 25.0 | 0.71 | 0.04 | 41.0 | 1,690 | 41.5 | 84.7 ± 32.3 |
| | *Chaetomorpha linum* | 18.4 | 1.29 | 0.05 | 16.5 | 871 | 53.1 | 21.1 ± 11.6 |
| | *Halimeda opuntia* | 6.8 | 0.54 | 0.03 | 14.6 | 642 | 44.4 | 11.1 ± 4.9 |

and Riley 1962) and utilized a Bausch and Lomb Spectronic 88 fitted with a 10-cm cell for maximum sensitivity.

Parametric statistics were used for the tissue C:N:P, alkaline phosphatase, and seawater nutrient data within each site. Comparisons between siliciclastic versus carbonate environments utilized data pooled from the spectrum of sites that were analyzed by the nonparametric Mann-Whitney U-test.

## Results and Discussion

The C, N, and P composition and alkaline phosphatase activity of macroalgae collected during this study are presented in Table 1. These data, as mean (±1 standard deviation) % C, % N, % P, C:N, C:P, N:P, and alkaline phosphastase activity, are summarized for the single siliciclastic site and the five carbonate-rich sites in Figs. 2–4.

Macroalgal tissue from the siliciclastic and carbonate sites (Fig. 2) had similar % C (mean of 22.6 ± 7.7 vs. 20.1 ± 6.0, % dry wt, $p > 0.05$) and % N contents (1.04 ± 0.45 vs. 1.17 ± 0.55, % dry wt, $p > 0.05$) compared to significantly lower % P values in macroalgae from the carbonate-rich environments (0.15 ± 0.05 vs. 0.07 ± 0.03, % dry wt, $p = 0.004$). The molar C:N ratios were not

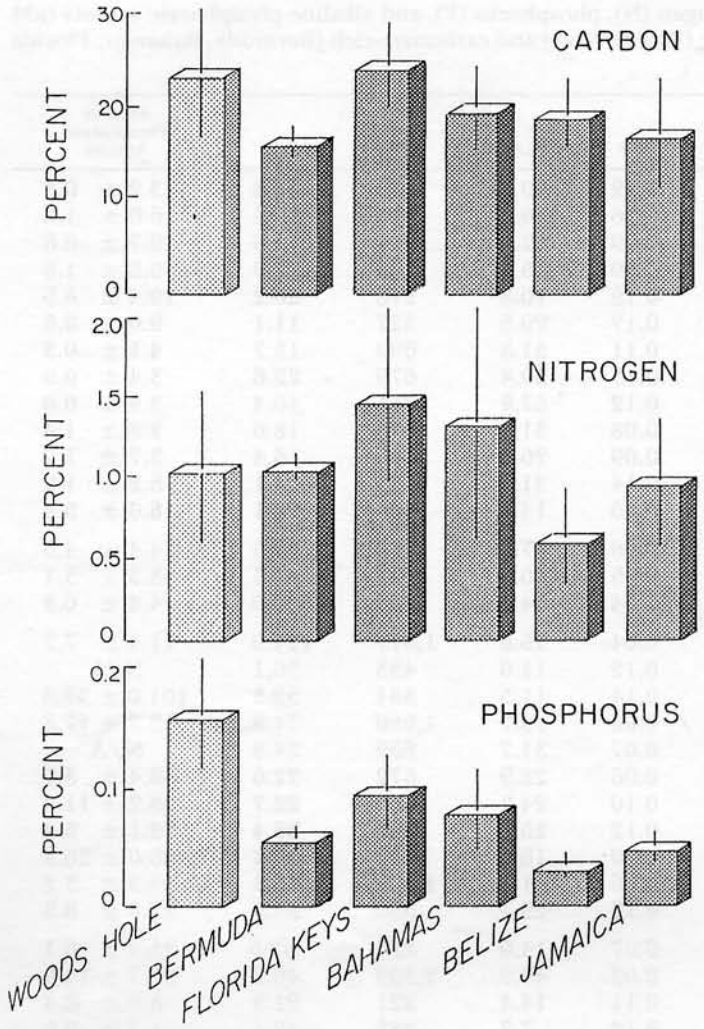


Fig. 2. Mean percentage dry weight (±1 SD) of tissue carbon, nitrogen, and phosphorus in frondose macroalgae from siliciclastic (n = 13) versus carbonate (n = 28) sites. The overall means are not significantly different ($p > 0.05$) for carbon and nitrogen, but are significantly different ($p = 0.004$) for phosphorus between the two environments.

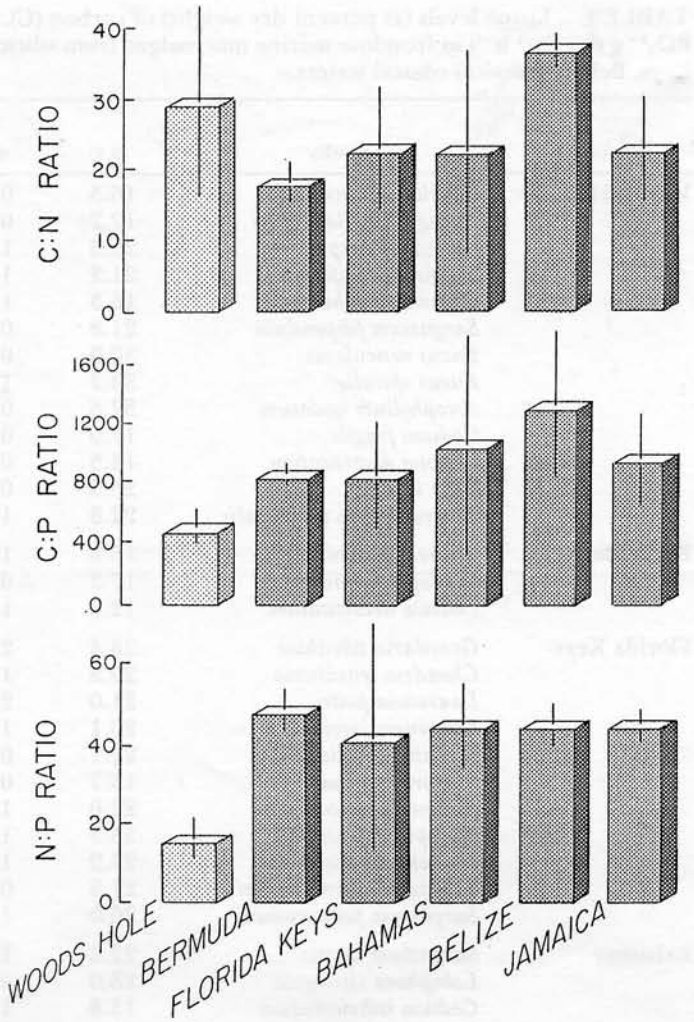


Fig. 3. Mean (±1 SD) carbon : nitrogen, carbon : phosphorus, and nitrogen : phosphorus ratios of frondose macroalgae from siliciclastic (n = 13) versus carbonate (n = 28) sites. The overall means between the two environments are not significantly different ($p > 0.05$) for C:N, but are significantly different ($p < 0.001$) for C:P and N:P.

significantly different between the two environments (29.2 ± 15.4 vs. 23.1 ± 10.8, $p > 0.05$; Fig. 3) compared to significantly elevated C:P (429 ± 201 vs. 976 ± 42, $p = 0.001$) and N:P (14.9 ± 5.5 vs. 43.4 ± 20.3, $p < 0.001$) ratios in macroalgae from the carbonate-rich sites (Fig. 3). Alkaline phosphatase activity was also significantly lower in macroalgae from siliciclastic compared to carbonate environments (7.3 ± 5.6 vs. 52.5 ± 40.5, $\mu M$ $PO_4^{3-}$ released g dry $wt^{-1}$ $h^{-1}$, $p = 0.005$; Fig. 4).

Concentrations of dissolved ammonium and nitrate plus nitrite also were similar among the siliciclastic and carbonate-rich seawater samples, with the exception of elevated ammonium in Belize and high levels of nitrate plus nitrite in the Florida Keys and Jamaica (Table 2). Mean concentrations of SRP (±1 SD) were about four-fold higher in the Woods Hole water samples (0.42 ± 0.05 $\mu M$) compared to those from the carbonate-rich locations (0.10 ± 0.05 $\mu M$). Seawater N:SRP ratios averaged <3 in Woods Hole waters compared to 36 for the carbonate-rich waters.

This study demonstrates significant shifts in N:P availability to marine macroalgae in contrasting biogeochemical environments. Previous studies have shown that C:N and C:P ratios of macroalgae are elevated in low nutrient environments and that these elevated ratios reflect increased limitation of net productivity by N, P, or both (e.g., Lapointe 1987; Lapointe et al. 1987). C:N:P ratios of macroalgae also vary as a function of taxonomic affinity (Niell 1976; Faganeli et al. 1986) and seasonality in nutrient availability (Chapman and Craigie 1977; Kornfeldt 1982; Lapointe 1987, 1989). Because this study was conducted during spring and summer periods of active growth, productivity of the

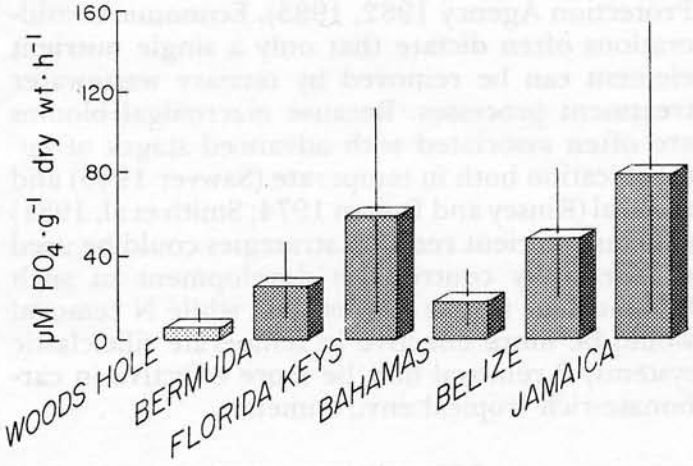


Fig. 4. Mean alkaline phosphatase activity (±1 SD) of frondose macroalgae from siliciclastic (n = 13) versus carbonate (n = 26) sites. The overall means are significantly different ($p < 0.005$) between the two environments.

macroalgae sampled appeared to be nutrient-limited. For example, the % N values of the Woods Hole macroalgae were low compared to values from adjacent waters at other times of the year (e.g., see Hanisak 1979). Inasmuch as the study included frondose forms from the three major macroalgal phyla (Table 1), the geographic differences in the mean composite N:P and C:P ratios were apparently great enough to overcome whatever small-scale spatial and species-specific variability in N:P status existed within each location.

Low seawater N:SRP ratios (<3) combined with low alkaline phosphatase activity, and C:P (430) and N:P (14.9) tissue ratios in the Woods Hole macroalgae support the precept that primary production in the temperate system was N-limited. These ratios were considerably lower than corresponding values (700 and 35) reported by Atkinson and Smith (1983), but were similar to the low N:P ratios (mean = 19) reported for *Cladophora glomerata* from Baltic coastal waters (Wallentinus 1976) known to be N-limited (Graneli 1978). Nixon et al. (1980) have shown that nutrient cycling in coastal environments similar to those of Woods Hole is dominated by sediment-water exchanges and that nutrient regeneration produces low N:P ratios (e.g., <7). Such low N:P regeneration ratios result not only from efficient P regeneration in organic-rich siliciclastic sediments (e.g., Nixon et al. 1980) but possibly from relatively large losses of N via denitrification. Seitzinger and Nixon (1985) additionally found that benthic denitrification was proportional to inorganic nutrient loading and eutrophication in Narragansett Bay, Rhode Island. However, they indicated that the ratio of N loss to input was the same or smaller in the temperate eutrophic habitat, suggesting that the increased N loss may be overshadowed by organic-rich loading.

TABLE 2. Concentrations (μM) of dissolved ammonium, nitrate plus nitrite, soluble reactive phosphorus (SRP), and the N:P ratio of seawater associated with benthic macroalgae in siliciclastic (Woods Hole) versus carbonate-rich coastal waters (Bermuda, Florida Keys, Bahamas, Belize, Jamaica).

| Location | Ammonium | Nitrate Plus Nitrite | SRP | N:P |
|---|---|---|---|---|
| Woods Hole | 0.25 | 0.14 | 0.46 | 1.0 |
| | 0.23 | 0.14 | 0.47 | 1.0 |
| | 0.46 | 0.24 | 0.38 | 2.0 |
| | 0.41 | 0.18 | 0.38 | 1.0 |
| | 0.47 | 0.20 | 0.43 | 2.0 |
| Bermuda | 0.53 | 1.13 | 0.14 | 11.9 |
| | 0.69 | 0.64 | 0.13 | 10.2 |
| | 0.79 | 0.54 | 0.11 | 12.1 |
| | 0.67 | 0.59 | 0.09 | 14.0 |
| Florida Keys | 0.62 | 1.23 | 0.10 | 18.5 |
| | 0.47 | 1.37 | 0.13 | 14.2 |
| | 0.54 | 2.10 | 0.10 | 26.4 |
| | 0.20 | 3.40 | 0.12 | 30.0 |
| Bahamas | 0.35 | 0.19 | 0.04 | 13.5 |
| | 0.44 | 0.22 | 0.04 | 16.5 |
| | 0.32 | 0.26 | 0.05 | 11.6 |
| | 0.51 | 0.20 | 0.04 | 17.8 |
| Belize | 1.02 | 0.15 | 0.08 | 14.6 |
| | 0.35 | 0.15 | 0.02 | 25.0 |
| | 0.38 | 0.17 | 0.03 | 18.3 |
| | 1.40 | 0.11 | 0.08 | 18.9 |
| | 0.38 | 0.16 | 0.03 | 18.0 |
| | 1.40 | 0.10 | 0.09 | 16.7 |
| | 0.41 | 0.16 | 0.03 | 19.0 |
| Jamaica | 0.79 | 8.85 | 0.14 | 68.9 |
| | 0.53 | 8.85 | 0.11 | 85.3 |
| | 0.68 | 9.20 | 0.13 | 76.0 |
| | 0.34 | 20.69 | 0.20 | 105.2 |
| | 0.38 | 20.46 | 0.17 | 122.6 |
| | 0.15 | 19.10 | 0.18 | 114.2 |

In contrast, elevated seawater N:SRP ratios, higher alkaline phosphatase activity, and greater macroalgal C:P and N:P ratios from the carbonate-rich tropical environments suggest P-limitation of benthic primary production. Sander and Moore (1979) also reported elevated N:P ratios (29) in seawater off Barbados and suggested that P, rather than N, was the primary nutrient limiting production in these waters. The mean C:P and N:P ratios of macroalgae in the present study (976 and 43.4, respectively) were higher than the corresponding values reported by Atkinson and Smith (700 and 35, respectively; 1983), strongly reflecting P-limitation in the carbonate-rich environments of this study. Similarly, C:P and N:P ratios were elevated (1,390 and 47, respectively) in the blade tissues of the seagrass *Syringodium filiforme* from carbonate-rich sediments of San Salvador Island, Bahamas (Short et al. 1985), a plant subsequently shown to be P-limited by both long-term and short-term experiments (Short et al. 1990).

Several factors may contribute to P-limitation in

carbonate-rich tropical environments. First, carbonate sediments adsorb $PO_4^{3-}$ onto surfaces (Berner 1974; De Kanel and Morse 1978; Dodge et al. 1984), which must be largely responsible for the low rates of P regeneration from these sediments (Hines and Lyons 1982). Additionally, carbonate sediments derived from skeletons of the calcareous marine plants and corals that predominate in tropical oligotrophic waters are relatively low in organic matter compared to siliciclastic sediments derived in part from terrigenous organic matter. If one were to posit similar sediment production rates in both geological systems, and thus different organic loading rates, the result would not only produce a lower mass of P to be regenerated in the carbonate habitats, but could also substantially lower the potential denitrification rate, thereby elevating the N:P regeneration ratio. Such an hypothesis is based on the Seitzinger and Nixon (1985) finding mentioned above, that less organic matter results in reductions in the denitrification process.

Furthermore, rates of benthic nitrogen fixation by epiphytic Cyanophyta associated with macroalgae in tropical carbonate-rich waters are quite high (Mague and Holm-Hansen 1975; Webb et al. 1975; Wiebe et al. 1975; Capone 1977; Penhale and Capone 1981) relative to temperate coastal systems (Howarth and Cole 1985). Inasmuch as N-fixation is usually P-limited (Redfield et al. 1963; Stewart et al. 1970; Bone 1971; Doremus 1982), the stoichiometry of nutrient uptake during fixation could further deplete available P and increase seawater N:P ratios (however, see Rueter 1982; Howarth and Cole 1985; and Paerl 1985, who have shown examples of N-fixation limitation by Fe, Mo, and dissolved organic matter, respectively).

Despite the significant differences in N:P availability between the coastal systems studied here, a suite of natural and anthropogenic factors could rapidly shift N:P availability within any of these biogeochemical environments. Transitions between N and P limitation occur seasonally in temperate (McComb et al. 1981; D'Elia et al. 1986) and tropical (Marsh 1977; Lapointe 1989) coastal waters and could alter N:P availability and patterns of nutrient limitation from those observed during this study. Land-use characteristics in the watershed, wastewater discharges, and species-specific nutritional requirements can also initiate transitions in N:P availablilty within any particular environment.

These findings are relevant to estuarine resources management for control of cultural eutrophication. Many temperate and tropical coastal waters are receiving increased N and P loading from sewage, industrial wastes, agricultural runoff, and a variety of other land uses (US Environmental Protection Agency 1982, 1983). Economic considerations often dictate that only a single nutrient element can be removed by tertiary wastewater treatment processes. Because macroalgal blooms are often associated with advanced stages of eutrophication both in temperate (Sawyer 1965) and tropical (Kinsey and Domm 1974; Smith et al. 1981) systems, nutrient removal strategies could be used to effectively control the development of such blooms. Our results suggest that while N removal would be more effective in temperate siliciclastic systems, P removal may be more effective in carbonate-rich tropical environments.

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