

## A COMPARISON OF NUTRIENT-LIMITED PRODUCTIVITY IN MACROALGAE FROM A CARIBBEAN BARRIER REEF AND FROM A MANGROVE ECOSYSTEM

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### ABSTRACT

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Productivity-nutrient enrichment assays and tissue analysis of three dominant macroalgae at Carrie Bow Cay, Belize, suggest that the degree and type of nutrient limitation in tropical marine macroalgae are highly ecosystem and species dependent. In the frondose algae, *Dictyota divaricata* Lamouroux and *Acanthophora spicifera* Lamouroux, collected from a pristine barrier reef site, productivity increased significantly with enrichment by dissolved inorganic nitrogen (N, as  $\text{NH}_4^+$ ) and phosphorus ( $\text{P}_i$ , which accounted for more of the enhanced productivity), compared to insignificant or reduced effects of enrichment of these algae collected at a detritus-rich mangrove island. Tissue levels of total nitrogen and phosphorus were also generally higher in *D. divaricata* and *A. spicifera* collected at the mangrove site, compared to these species collected at the barrier reef site. Higher concentrations of N and  $\text{P}_i$  in seawater at the mangrove site, compared to the barrier reef site, appeared responsible for the above pattern. These results indicate that macroalgae in mangrove fringe areas may not always experience the severe nutrient limitation often associated with oligotrophic tropical reef ecosystems. In contrast to the above ecosystem-dependent pattern of nutrient limitation in the frondose algal forms, productivity of the calcareous *Halimeda opuntia* (L.) Lamouroux was enhanced at both sites only by N enrichment and the effects of  $\text{P}_i$  enrichment were insignificant. These different types of nutrient limitation between two frondose and one calcareous macroalgae suggest that algal community structure in tropical marine systems may be mediated by different resource limitations that are imposed on different populations within the community.

### INTRODUCTION

Dissolved nutrient concentrations in tropical coral reef environments are generally low and can, at times, limit productivity of dominant macroalgal species. Experimental nutrient enrichment of macroalgae on the Great Barrier

Reef ecosystem resulted in enhanced net production, as measured by  $O_2$  evolution (Kinsey and Domm, 1974) and change in biomass (Hatcher and Larkum, 1983). Reefs with large standing stocks of macroalgae usually receive elevated nutrient supplies (Adey et al., 1977), an observation consistent with the idea that growth rates of reef macroalgae are also nutrient limited. Lapointe (1987) found that in situ nutrient availability severely limited growth and productivity of the red alga, *Gracilaria tikvahiae* McLachlan, in oligotrophic waters of the Florida Keys.

The nutrient limitation often observed in tropical reef systems may not, however, be common in detritus-rich tropical mangrove systems that are characterized by elevated nutrient availability. For example, while detritus rarely develops to high levels on coral-dominated reefs because of intense herbivory and export, mangrove ecosystems are well known for their high levels of decomposing plant matter (Fell et al., 1980; Newell et al., 1984) that could result in relatively high concentrations of dissolved inorganic nitrogen (N, as  $NH_4^+$  and  $NO_3^-$ ) and phosphate ( $P_i$ ) (Snedaker and Brown, 1981). Considering that nutrient uptake kinetics in macroalgae are highly concentration dependent, productivity of mangrove macroalgae may be less nutrient limited compared to coral reef algae. To date, a comparison of macroalgae from coral-dominated reefs and mangrove ecosystems has not been considered with respect to nutrient limitation.

Furthermore, which nutrient — N or  $P_i$  — might limit macroalgal productivity in reef and/or mangrove ecosystems has not been experimentally addressed. Traditionally, N is considered the primary limiting nutrient in tropical marine waters (e.g., Parsons et al., 1977) although recent evidence from geochemical models (Smith, 1984) and in situ macroalgal bioassays (Lapointe, 1985, 1987) suggests that  $P_i$ , rather than N, may often be the more important growth-limiting nutrient in well-oxygenated carbonate-rich tropical marine waters where concentrations of  $P_i$  are often low due to equilibrium with carbonate fluorapatite (Gulbrandsen and Robertson, 1973). A greater knowledge of the limiting role of these two elements to macroalgal productivity would help eliminate current discrepancies regarding the relative importance of N versus  $P_i$  limitation in the marine environment (e.g., see Smith, 1984).

The present study was designed to determine the relative nutritional status, with regard to N versus  $P_i$  limitation, of dominant macroalgae collected from two different tropical marine ecosystems — one a coral-dominated reef and the other a nearby mangrove island. The study included nutrient enrichment-productivity bioassays and tissue analysis of dominant macroalgae as well as seawater nutrient analysis from the two different ecosystems.

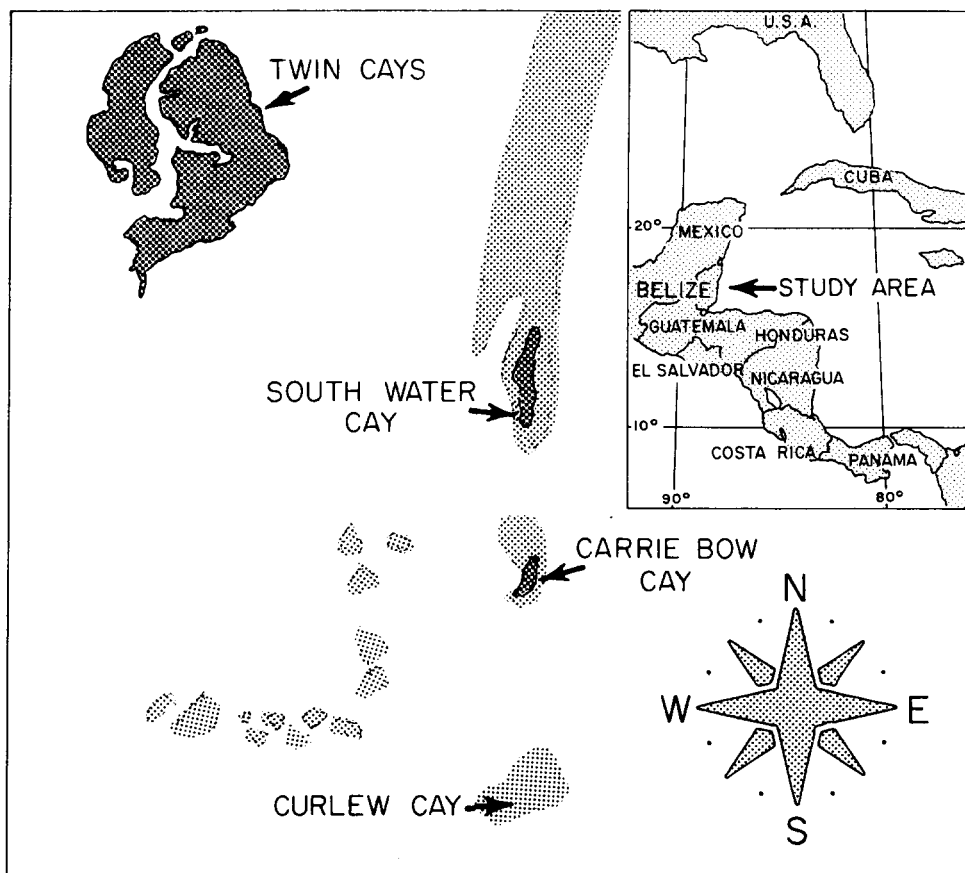


Fig. 1. Location of mangrove (Twin Cays) and barrier reef (Curlew Cay) study sites on the Belizean barrier reef system.

## MATERIALS AND METHODS

### *Study area*

The field studies reported here were conducted from Carrie Bow Cay (CBC), Belize ( $16^{\circ}48'N$ ,  $88^{\circ}05'W$ ) during 1–8 April 1985 in close proximity to Curlew Cay and Twin Cays (Fig. 1), which provided the actual study sites — a pristine barrier reef and mangrove ecosystem, respectively. Both cays are located within the Belizean barrier reef system, remote from anthropogenic influences. The geology, natural history and biology within the Carrie Bow Cay

environs are comparatively well known as a result of a decade of multidisciplinary investigations (Rützler and Macintyre, 1982).

### *Productivity-enrichment assays*

Three species of dominant macroalgae common to both habitats were chosen for the productivity-enrichment assays: a frondose red alga, *Acanthophora spicifera* Lamouroux, a frondose brown alga, *Dictyota divaricata* Lamouroux and a calcareous green alga, *Halimeda opuntia* (Linnaeus) Lamouroux. On the day prior to the productivity assays, samples of these macroalgae were hand-collected in shallow locations in full sunlight from Curlew Cay and Twin Cays, then carefully transported to Carrie Bow Cay, where they were cleaned of sediments, epiphytes and epizoa. Subsequently, aliquots of the algae were soaked in a factorial design enrichment of N ( $\text{NH}_4\text{Cl}$ ) and  $\text{P}_i$  ( $\text{NaH}_2\text{PO}_4$ ), which consisted of either +N, + $\text{P}_i$ , +N+ $\text{P}_i$  and a control (no enrichment). Initial concentrations of  $\text{NH}_4^+$  and  $\text{P}_i$  (measured as  $\text{PO}_4^{3-}$ ) in the enrichment were 200 and 20  $\mu\text{M}$ , respectively. Following the overnight (12 h) enrichment, the algae were flushed with fresh seawater 4 h prior to the incubation. This methodology for macroalgal photosynthetic bioassay has been field tested previously in the Florida Keys and the results indicate close correlation with a longer-term growth response (Lapointe, 1987); also, this relatively long-term  $\text{O}_2$  enrichment bioassay does not appear to suffer from the ambiguity that plagues the short-term  $^{14}\text{C}$  enrichment method (Healey, 1979; Lean and Pick, 1981).

For all productivity (net photosynthesis) measurements that followed the nutrient enrichment, four replicate incubations per species were conducted at ambient water temperatures (27.5–28.4 °C) between 09.00 and 14.30 h under a photon flux density of 900–1900  $\mu\text{E m}^{-2} \text{s}^{-1}$  of PAR. This was the range of natural photon flux in situ both at Curlew Cay and Twin Cays and within the range of light saturation values documented for other shallow water macroalgal species (King and Schramm, 1976; Arnold and Murray, 1980; Lapointe et al., 1984). Net productivity was measured using 1-l glass jars that received continuous cooling and stirring via water-driven magnetic stirrers. Dissolved oxygen was measured to within 0.01  $\text{mg l}^{-1}$  using an Orbisphere Model 2610 Oxygen Measurement System and converted to carbon fixed utilizing a photosynthetic quotient of 1.00. The methods concerning selection of material, handling, incubation and oxygen analysis were within the limits recommended by Littler (1979).

### *Tissue analysis*

Sub-samples of macroalgae were also taken from the nutrient enrichment-productivity studies for analysis of tissue carbon, nitrogen and phosphorus. Samples were rinsed briefly for 1–2 s in deionized water and dried to

constant weight (ca. 48 h at 60°C). After powdering with a mortar and pestle, carbon and nitrogen were determined using a Perkin-Elmer 240 Elemental Analyzer and phosphorus was measured by persulfate digestion of algal tissue, followed by the total phosphorus analysis (Menzel and Corwin, 1965). Preliminary studies indicated that this method recovered > 95% of total phosphorus from National Bureau of Standards' citrus leaves.

### *Seawater nutrient analysis*

Seawater samples for determination of dissolved inorganic nutrients ( $\text{NO}_3^-$ ,  $\text{NH}_4^+$ ,  $\text{PO}_4^{3-}$ ) were taken at the sites used for collection of the macroalgae at Curlew Cay and Twin Cays. Samples were collected in triplicate with acid-washed Nalgene bottles, filtered (0.45  $\mu\text{m}$ ) and preserved using a 1%  $\text{HgCl}_2$  solution. Subsequently, the samples were analyzed according to methods described in Strickland and Parsons (1977).

## RESULTS

### *Productivity-enrichment assays*

The productivity of *Acanthophora spicifera*, *Dictyota divaricata* and *Halimeda opuntia* in response to N and  $\text{P}_i$  enrichment was dependent on both the original location of the plants (i.e., ecosystem), as well as the species. For example, productivity of the frondose macroalgae, *A. spicifera* and *D. divaricata*, at Curlew Cay increased significantly (2–3-fold increase over controls) with either  $\text{P}_i$  or N +  $\text{P}_i$  enrichment, while N enrichment alone was insignificant (Figs. 2 and 3, Table I). However, the productivity response of these species from Twin Cays to N and  $\text{P}_i$  enrichment was either reduced (relative to controls) or insignificant (Figs. 2 and 3, Table I). In contrast to the above pattern, productivity of the calcareous macroalga, *H. opuntia*, from both Curlew Cay and Twin Cays increased significantly due to N, but not  $\text{P}_i$  enrichment (Fig. 4, Table I).

### *Tissue constituents*

Analysis of *Acanthophora spicifera*, *Dictyota divaricata* and *Halimeda opuntia* for total tissue nitrogen and phosphorus also suggested differences in levels of these nutrients between ecosystems and species. The greatest difference between the two ecosystems occurred in *A. spicifera*, which had ~2-fold higher levels of total nitrogen and phosphorus at Twin Cays, ~1.00 and 0.056% of dry weight, respectively, compared to levels of 0.48 and 0.030% for total nitrogen and phosphorus at Curlew Cay, respectively (Table II). Although not as dramatic, levels of tissue nitrogen and phosphorus were also generally higher

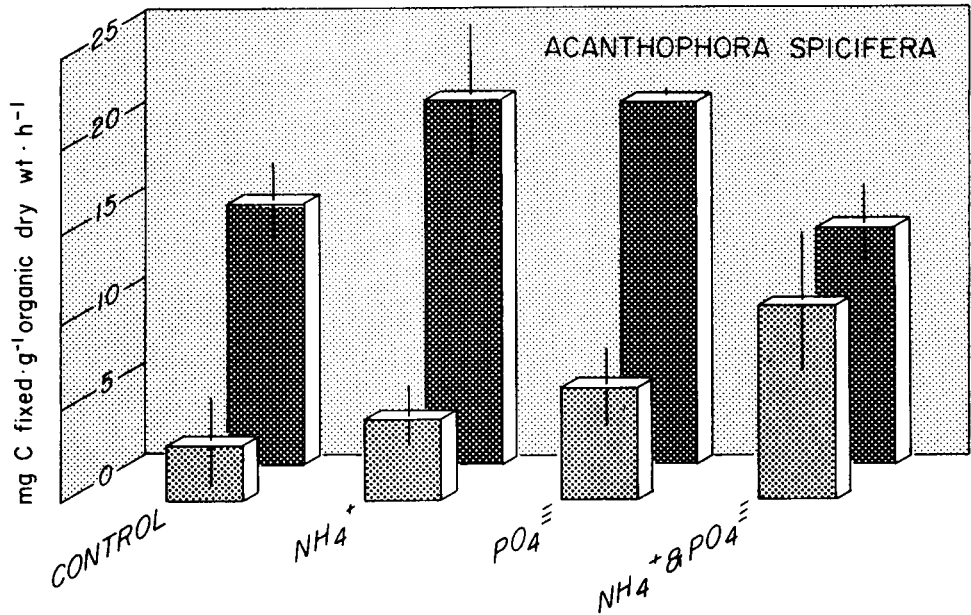


Fig. 2. Productivity (apparent photosynthesis) per gram ash-free dry weight of *Acanthophora spicifera* from Curlew Cay (light histograms in front) and Twin Cays (dark histograms in rear) as a function of N ( $\text{NH}_4^+$ ) and P<sub>i</sub> ( $\text{PO}_4^{3-}$ ) enrichment. Values represent means  $\pm 1$  S.D. (vertical lines at the top of each histogram,  $n = 4$ ).

in *D. divaricata* and *H. opuntia* collected at Twin Cays compared to Curlew Cay (Table II). The major differences among the species studied were the different responses of frondose versus calcareous forms to N and P<sub>i</sub> enrichment. For example, a 100% increase in total phosphorus content occurred in the frondose algae, *A. spicifera* and *D. divaricata*, from both Curlew Cay and Twin Cays in response to P<sub>i</sub> enrichment, compared to only a 10–30% increase for total nitrogen in these algae in response to N enrichment. In contrast, no significant increase in total phosphorus occurred in the calcareous *H. opuntia* in response to P<sub>i</sub> enrichment, although total tissue nitrogen increased significantly, ~10–40%, in response to N enrichment (Table II).

### Seawater chemistry

Concentrations of dissolved  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  were markedly different at the two ecosystems during the course of this study. Higher concentrations of  $\text{NH}_4^+$  and  $\text{PO}_4^{3-}$  consistently occurred at Twin Cays and ranged from 0.38 to 1.40  $\mu\text{M}$  and 0.08 to 0.10  $\mu\text{M}$ , respectively; lower concentrations of  $\text{NH}_4^+$  and  $\text{PO}_4^{3-}$  occurred at Curlew Cay and ranged from undetectable to 0.41  $\mu\text{M}$  and undetectable to 0.03  $\mu\text{M}$ , respectively. Concentrations of  $\text{NO}_3^-$

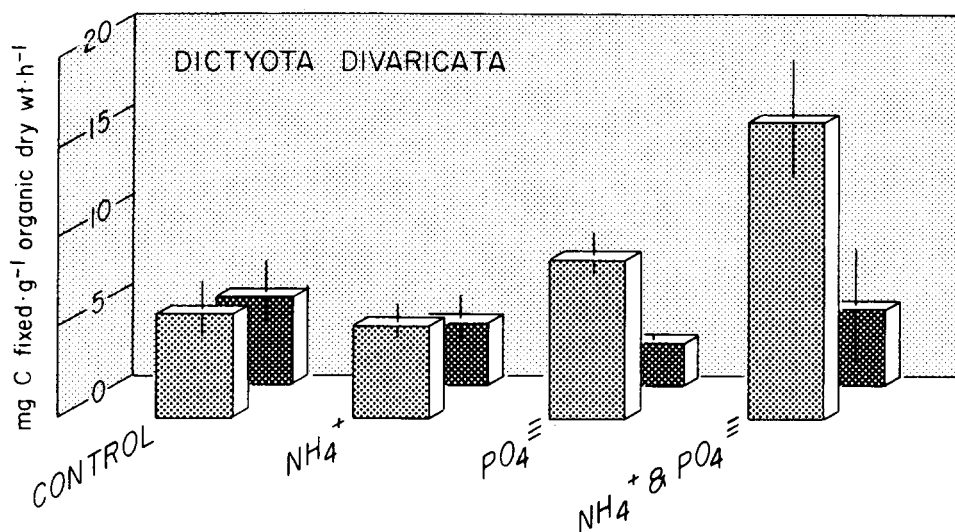


Fig. 3. Productivity (apparent photosynthesis) per gram ash-free dry weight of *Dictyota divaricata* from Curlew Cay (light histograms in front) and Twin Cays (dark histograms in rear) as a function of N ( $\text{NH}_4^+$ ) and  $\text{P}_i$  ( $\text{PO}_4^{3-}$ ) enrichment. Values represent means  $\pm 1$  S.D. (vertical lines at the top of each histogram,  $n=4$ ).

were low to undetectable and no significant differences between ecosystems were observed (Table III).

## DISCUSSION

Results of this study suggest that the type and degree of nutrient limitation to productivity of tropical marine macroalgae can be highly ecosystem dependent. Higher concentrations of dissolved seawater nutrients and macroalgal tissue nitrogen and phosphorus at the mangrove site (Twin Cays), compared to the barrier reef site (Curlew Cay), agree with the insignificant or reduced effects of N and  $\text{P}_i$  enrichment on productivity of *Dictyota divaricata* and *Acanthophora spicifera* from the mangrove site, compared to significant enrichment effects on productivity of these species at the barrier reef site. These findings support other observations of nutrient-limited productivity of benthic algae on tropical reefs (Kinsey and Domm, 1974; Kinsey and Davies, 1979; Smith et al., 1979; Hatcher and Larkum, 1983) and suggest that mangrove fringe areas might serve macroalgae not only by providing refuge habitats from intense herbivory (Taylor et al., 1986) associated with reef systems (e.g., Littler et al., 1985), but also by reducing the severe nutrient limitation that frequently occurs in reef ecosystems. Such ecosystem-level differences in nutritional state and productivity of macroalgae need to be considered in models of benthic productivity in tropical marine systems.

TABLE I

Summary of two-way ANOVA for the effects of N ( $\text{NH}_4^+$ ) and  $\text{P}_i$  ( $\text{PO}_4^{3-}$ ) enrichment on productivity of three macroalgae from Curlew Cay, a barrier reef and Twin Cays, a mangrove ecosystem, adjacent to the Belizean Barrier Reef

| Location   | Species                       | Factor           | % Variation accounted for by factor | F           |
|------------|-------------------------------|------------------|-------------------------------------|-------------|
| Curlew Cay | <i>Acanthophora spicifera</i> | $\text{P}_i$     | 20                                  | 8.76 *      |
|            |                               | N                | 3                                   | 2.03 (n.s.) |
|            |                               | N + $\text{P}_i$ | 64                                  | 16.80 **    |
|            | <i>Dictyota divaricata</i>    | $\text{P}_i$     | 30                                  | 13.56 **    |
|            |                               | N                | 3                                   | 2.08 (n.s.) |
|            |                               | N + $\text{P}_i$ | 50                                  | 59.02 **    |
|            | <i>Halimeda opuntia</i>       | $\text{P}_i$     | < 1                                 | 2.62 (n.s.) |
|            |                               | N                | 23                                  | 18.25 **    |
|            |                               | N + $\text{P}_i$ | 28                                  | 2.98 (n.s.) |
| Twin Cays  | <i>Acanthophora spicifera</i> | $\text{P}_i$     | 39                                  | 13.94 **    |
|            |                               | N                | 20                                  | 6.94 *      |
|            |                               | N + $\text{P}_i$ | 7                                   | 2.43 (n.s.) |
|            | <i>Dictyota divaricata</i>    | $\text{P}_i$     | 4                                   | 0.65 (n.s.) |
|            |                               | N                | 2                                   | 0.12 (n.s.) |
|            |                               | N + $\text{P}_i$ | 12                                  | 2.27 (n.s.) |
|            | <i>Halimeda opuntia</i>       | $\text{P}_i$     | 14                                  | 1.38 (n.s.) |
|            |                               | N                | 32                                  | 5.70 *      |
|            |                               | N + $\text{P}_i$ | 15                                  | 1.00 (n.s.) |

\* =  $P < 0.05$ ; \*\* =  $P < 0.01$ ; n.s. =  $P > 0.05$ .

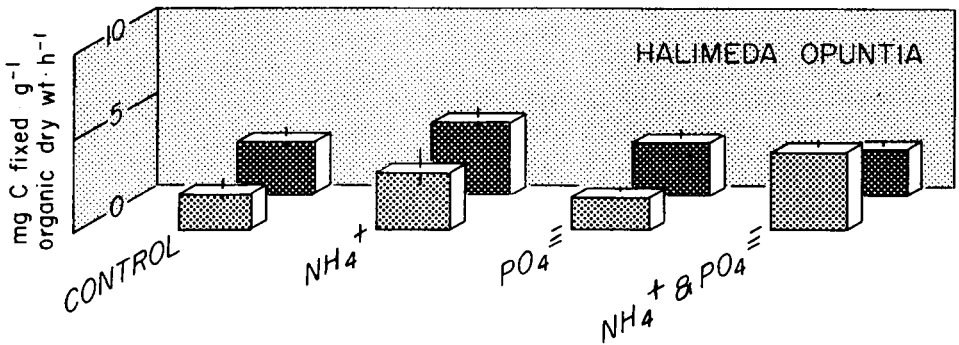


Fig. 4. Productivity (apparent photosynthesis) per gram ash-free dry weight of *Halimeda opuntia* from Curlew Cay (light histograms in front) and Twin Cays (dark histograms in rear) as a function of N ( $\text{NH}_4^+$ ) and  $\text{P}_i$  ( $\text{PO}_4^{3-}$ ) enrichment. Values represent means  $\pm$  1 S.D. (vertical lines at the top of each histogram,  $n = 4$ ).



TABLE II

Levels of tissue carbon (C), nitrogen (N) and phosphorus (P) in three macroalgae from Curlew Cay, a barrier reef and Twin Cays, a mangrove ecosystem, during 1-5 April 1985, in response to N and P<sub>i</sub> enrichment. The enrichment treatments consisted of a 12-h pulse of either N (NH<sub>4</sub><sup>+</sup>), P<sub>i</sub> (PO<sub>4</sub><sup>3-</sup>), or both N and P<sub>i</sub> at initial concentrations of 200 μM NH<sub>4</sub><sup>+</sup> and 20 μM PO<sub>4</sub><sup>3-</sup>. Values represent means ± 1 S.D. (in parentheses, n = 2)

| Species                       | Treatment          | Location      |                |                  |               |                |                  |
|-------------------------------|--------------------|---------------|----------------|------------------|---------------|----------------|------------------|
|                               |                    | Curlew Cay    |                |                  | Twin Cays     |                |                  |
|                               |                    | %C            | %N             | %P               | %C            | %N             | %P               |
| <i>Acanthophora spicifera</i> | Control            | 16.7<br>(0.6) | 0.48<br>(0.05) | 0.030<br>(0.007) | 13.3<br>(0.5) | 1.00<br>(0.07) | 0.056<br>(0.005) |
|                               | N                  | 15.8<br>(0.5) | 0.65<br>(0.07) | 0.030<br>(0.005) | 12.9<br>(0.4) | 1.20<br>(0.09) | 0.046<br>(0.006) |
|                               | P <sub>i</sub>     | 15.6<br>(0.5) | 0.46<br>(0.02) | 0.067<br>(0.009) | 13.4<br>(0.4) | 1.07<br>(0.05) | 0.127<br>(0.009) |
|                               | N + P <sub>i</sub> | 16.5<br>(0.4) | 0.69<br>(0.05) | 0.068<br>(0.008) | 13.3<br>(0.4) | 1.20<br>(0.10) | 0.122<br>(0.011) |
| <i>Dictyota divaricata</i>    | Control            | 24.0<br>(0.6) | 0.87<br>(0.06) | 0.040<br>(0.002) | 20.6<br>(0.6) | 0.97<br>(0.08) | 0.044<br>(0.015) |
|                               | N                  | 22.8<br>(0.4) | 1.02<br>(0.09) | 0.041<br>(0.003) | 20.5<br>(0.7) | 1.11<br>(0.11) | 0.042<br>(0.013) |
|                               | P <sub>i</sub>     | 23.3<br>(0.6) | 0.86<br>(0.06) | 0.074<br>(0.005) | 20.4<br>(0.8) | 1.00<br>(0.09) | 0.095<br>(0.006) |
|                               | N + P <sub>i</sub> | 22.4<br>(0.5) | 1.05<br>(0.04) | 0.068<br>(0.008) | 19.9<br>(0.6) | 1.11<br>(0.10) | 0.064<br>(0.005) |
| <i>Halimeda opuntia</i>       | Control            | 14.9<br>(0.7) | 0.44<br>(0.02) | 0.015<br>(0.003) | 14.8<br>(0.5) | 0.54<br>(0.06) | 0.036<br>(0.003) |
|                               | N                  | 15.2<br>(0.4) | 0.56<br>(0.03) | 0.020<br>(0.002) | 15.5<br>(0.6) | 0.79<br>(0.05) | 0.031<br>(0.006) |
|                               | P <sub>i</sub>     | 15.8<br>(0.6) | 0.44<br>(0.04) | 0.015<br>(0.001) | 15.2<br>(0.4) | 0.52<br>(0.03) | 0.027<br>(0.005) |
|                               | N + P <sub>i</sub> | 15.3<br>(0.5) | 0.61<br>(0.05) | 0.022<br>(0.003) | 14.8<br>(0.6) | 0.68<br>(0.02) | 0.033<br>(0.007) |

The elevated tissue nutrient levels and lack of severe nutrient limitation in *Dictyota divaricata* and *Acanthophora spicifera* from Twin Cays compared to Curlew Cay also illustrate the importance of dissolved nutrient concentration in seawater as an ecological factor regulating nutrient flux to macroalgae. Roughly 3-fold differences in seawater nutrient concentrations occurred between the two sites, which supports our findings of reduced nutrient limitation and generally higher tissue nutrients in macroalgae collected at Twin Cays compared to Curlew Cay. Considering that the nutrient concentrations at both sites were generally low (i.e., < 1.4 μM for NH<sub>4</sub><sup>+</sup>, < 0.10 μM for PO<sub>4</sub><sup>3-</sup>), nutrient uptake rates and, consequently, productivity of macroalgae may often be nutrient limited, especially at Curlew Cay. Half-saturation ( $K_s$ ) values for NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup> and PO<sub>4</sub><sup>3-</sup> uptake have not been studied for the macroalgal species in our study, but may resemble values for other related tropical seaweeds.

TABLE III

Concentrations of dissolved  $\text{NH}_4^+$ ,  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  at the two study locations — Curlew Cay, a barrier reef and Twin Cays, a mangrove ecosystem, during this study (4–7 April 1985). Values represent means  $\pm$  1 S.D. (in parentheses,  $n=3$ )

| Date       | Location | $\text{NH}_4^+$   | $\text{NO}_3^-$   | $\text{PO}_4^{3-}$ | N:P    |
|------------|----------|-------------------|-------------------|--------------------|--------|
| 4 April 85 | Twin     | 1.02              | 0.03              | 0.08               | 13.1   |
|            | Cays     | (0.23)            | (0.02)            | (0.02)             | (0.02) |
|            | Curlew   | 0.347             | 0.02              | 0.02               | 18.0   |
|            | Cay      | (0.06)            | (0.02)            | (0.03)             |        |
| 5 April 85 | Twin     | 0.38              | 0.17              | 0.10               | 5.5    |
|            | Cays     | (0.10)            | (0.10)            | (0.01)             |        |
|            | Curlew   | u.d. <sup>1</sup> | u.d. <sup>2</sup> | u.d. <sup>3</sup>  | —      |
|            | Cay      |                   |                   |                    |        |
| 6 April 85 | Twin     | 1.40              | u.d. <sup>2</sup> | 0.08               | 17.5   |
|            | Cays     | (0.25)            |                   | (0.02)             |        |
|            | Curlew   | 0.38              | 0.16              | u.d. <sup>3</sup>  | —      |
|            | Cay      | (0.02)            | (0.01)            |                    |        |
| 7 April 85 | Twin     | 1.40              | u.d. <sup>2</sup> | 0.09               | 15.5   |
|            | Cays     | (1.25)            |                   | (0.01)             |        |
|            | Curlew   | 0.41              | 0.16              | 0.03               | 19.0   |
|            | Cay      | (0.07)            | (0.04)            | (0.02)             |        |

u.d. = undetectable.

<sup>1</sup> < 0.10  $\mu\text{M}$ ; <sup>2</sup> < 0.05  $\mu\text{M}$ ; <sup>3</sup> < 0.03  $\mu\text{M}$ .

For example,  $K_s$  values for  $\text{NH}_4^+$  and  $\text{NO}_3^-$  uptake in the red alga, *Gracilaria tikvahiae*, range from 1.50 to 2.80  $\mu\text{M}$  and 1.90 to 3.60  $\mu\text{M}$ , respectively (D'Elia and De Boer, 1978);  $K_s$  values for  $\text{PO}_4^{3-}$  uptake in *G. tikvahiae* in the Florida Keys range from 2.50 to 5.62  $\mu\text{M}$  (depending on the degree of P limitation, B.E. Lapointe, unpublished, 1986). Because these  $K_s$  values for both N and  $\text{P}_i$  forms are well above the concentrations of these nutrients at the study sites, especially Curlew Cay, potential macroalgal N and  $\text{P}_i$  limitation is clearly suggested. This is particularly true for  $\text{P}_i$ , where the difference between estimated  $K_s$  values and ambient concentrations would be greatest. Considering the enhanced productivity we observed in *D. divaricata* and *A. spicifera* following N and  $\text{P}_i$  enrichment, these macroalgae must respond kinetically to transient increases in local N and  $\text{P}_i$  concentrations caused by fish excretion and microbial mineralization within the otherwise low range of ambient nutrient concentrations encountered in the oligotrophic Belizean marine environment. This may, in part, explain the frequent abundance of these algae not only in mangrove fringe areas that serve as potential sources of these limiting nutrients, but also in reef systems that receive elevated nutrient (especially  $\text{P}_i$ ) input from anthropogenic sources.

The different algal species we studied also appear to differ in their degree of N and  $\text{P}_i$  limitation. The frondose algae, *Dictyota divaricata* and *Acanthophora*

*spicifera*, at Curlew Cay appeared predominantly  $P_i$  limited, although N was an important secondary limiting nutrient. In contrast, the calcareous green alga, *Halimeda opuntia*, appeared only N limited at both locations and no degree of P limitation, or even uptake of  $P_i$  during the enrichment, occurred. This apparent difference between fleshy and calcareous macroalgae suggests that algal community structure in reef systems can be mediated by different resource limitations that are imposed on different populations within the community. Such resource partitioning among tropical marine algae may be facilitated by the divergent frondose and calcareous forms, which might differ in their growth strategy and nutrient requirements. This idea is supported by observations in several reef environments that receive elevated nutrient supply, where frondose algal forms flourish and outcompete slower-growing calcareous forms (Adey et al., 1977; Smith et al., 1979). More research is obviously needed to substantiate this hypothesis that functional form and nutrition are related in macroalgae (sensu Littler and Littler, 1983) and such studies are needed to more fully understand macroalgal competition during eutrophication of tropical marine ecosystems.

That frondose algal forms from Curlew Cay, the reef system, scavenged more  $P_i$  than N (compared to initial tissue levels) during the enrichment and resulted in greatly enhanced productivity, suggests that  $P_i$  may be more generally limiting to coral reef metabolism than previously thought. Studies have illustrated the effective recycling mechanisms for  $P_i$  in reef systems (Pilson and Betzer, 1973; Atkinson, 1982) and have engendered the view that N rather than  $P_i$  is more likely the major limiting nutrient (e.g., Hatcher and Larkum, 1983). While this view is in agreement with the view held by many biological oceanographers, that the oceans are predominantly N-limited systems (e.g., Ryther and Dunstan, 1971; Goldman et al., 1979), it contrasts with the opinion of most marine geochemists (e.g., Smith, 1984) that the oceans as a whole are  $P_i$ -limited systems. Our results support similar in situ macroalgal bioassays in the carbonate-rich waters of the Florida Keys, where  $P_i$  was also quantitatively more important than N in limiting both photosynthetic capacity and growth of *Gracilaria tikvahiae* during both summer and winter (Lapointe, 1987). Thus, future studies in oligotrophic, carbonate-rich tropical marine waters need to consider a full assessment of  $P_i$  as well as N availability to more fully understand mechanisms of nutrient limitation of benthic productivity.

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