

Modification of Benthic Community Structure by Natural Eutrophication: the Belize Barrier Reef

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Abstract. Opportunistic macroalgae adjacent to a mangrove bird rookery (Man-of-War Cay) on the Belize Barrier Reef were significantly enriched with phosphorus, but not nitrogen, compared to macroalgae on an unenriched control mangrove island (Twin Cays) and two pristine coral reef lagoons (Tobacco Reef and Curlew Cay). Macroalgal C:N ratios were statistically similar among all the sites, whereas macroalgae receiving guano enrichment at Man-of-War Cay had lower C:P and N:P ratios compared to macroalgae at the unenriched sites. Opportunistic macroalgae at Man-of-War Cay also had lower alkaline phosphatase activities compared to those at the unenriched sites, corroborating elevated P-availability and reduced P-limitation at the bird rookery. Water column concentrations of dissolved inorganic nitrogen (DIN = ammonium + nitrate + nitrite) and soluble reactive phosphorus (SRP) were highest at Man-of-War Cay (4.84 and 1.56 μM , respectively), which was followed by Twin Cays > Tobacco Reef > Curlew Cay. The highest nutrient concentrations occurred on the lee (west) side of Man-of-War Cay where extensive populations of the sheet-like and filamentous macroalgae *Ulva lactuca*, *Chaetomorpha linum*, *Rosenvingia intricata*, *Padina sanctae-crucis*, and *Acanthophora spicifera* dominated the benthos; the windward (east) side had lower water column nutrient concentrations and the benthos was dominated by turtle grass (*Thalassia testudinum*) and

contained populations of reef corals growing within 100 m of the island. Our findings suggest that: 1) phosphorus, rather than nitrogen, is the primary nutrient mediating competition among benthic primary producers along trophic gradients in these shallow, carbonate-rich tropical waters and 2) similar benthic communities having water column SRP concentrations $> \sim 0.10 \mu\text{M}$ and DIN concentrations $> \sim 1.0 \mu\text{M}$ will tend toward dominance by macroalgae rather than seagrasses and corals.

Introduction

The relative dominance of sessile primary producers in tropical marine ecosystems is controlled by complex biological interactions between competition and grazing (Littler and Littler 1984), the outcomes of which are mediated by abiotic factors including nutrient availability (Birkeland 1987, 1988). The productivity of benthic macroalgae is often nutrient-limited in tropical coral reef and seagrass ecosystems (Lapointe 1987; Lapointe et al. 1987); nutrient inputs from small-scale experimental enrichment (Kinsey and Domm 1974; Hatcher and Larkum 1983) and larger-scale cultural eutrophication (Smith et al. 1981; Lapointe and O'Connell 1989) increases the productivity and standing crops of benthic macroalgae. Sustained nutrient inputs from cultural eutrophication causes mortality of corals via macroalgal overgrowth (Fishelson 1973; Banner 1974) resulting in the long-term decline in biotic diversity and fisheries production of coral reefs (Johannes 1975). Excessive nutrient inputs to tropical seagrass meadows also increase ma-

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croalgal epiphyte loads on seagrass blades (Silberstein et al. 1986; Tomasko and Lapointe 1991), decreasing irradiance, lowering seagrass productivity (Sand-Jensen 1977) and ultimately causing seagrass die-off (Cambridge and McComb 1984). Considerable debate still exists as to the threshold concentrations of dissolved inorganic nitrogen (N) and phosphorus (P) triggering macroalgal overgrowth of tropical coral reefs and seagrass meadows and the relative importance of N and P in regulating primary productivity in tropical waters (Smith 1984; Howarth 1988)

During our earlier research in the vicinity of the Smithsonian Institution field station on Carrie Bow Cay, Belize, we became intrigued with the distribution of filamentous and sheet-like macroalgae, seagrasses, and corals around Man-of-War Cay, a seabird mangrove rookery. Colonial piscivorous birds concentrate nutrient inputs around roost islands and shorelines by foraging in adjacent waters and returning to the colonies where they defecate, thereby enriching local waters (Golovkin 1967). Onuf et al. (1977) showed that mangrove islands colonized by pelicans and egrets had higher productivity and leaf tissue N compared to a control island lacking significant bird nutrient input. Such nutrient enrichment from bird guano enhances the production of intertidal foliose algae, resulting in the formation of permanent algal mats around bird islands (Bosman and Hockey 1986, 1988). Because opportunistic forms of macroalgae dominated an innermost halo around Man-of-War Cay, we posited that shifts in competitive advantage, relative dominance and distributional patterns among these macroalgae, seagrasses and corals are mediated by nutrient availability (assumed hereafter to vary directly with water column concentrations of dissolved inorganic N and P) in the absence of unusual stresses or physical disturbances.

We present here a modification of the relative dominance model (Littler and Littler 1984) for tropical reef corals, seagrasses, and macroalgae that addresses nutrient mediation of their distributional patterns. The *a priori* prediction tested was that the dominant macroalgal stocks should be less nutrient-limited at sites in close proximity to Man-of-War Cay due to elevated nutrient availability. As a corollary, we hypothesized that nutrient enrichment from bird guano would significantly modify the benthic community structure by enhancing the productivity of opportunistic, fleshy macroalgae that overgrow seagrasses and corals. A nearby mangrove island lacking guano enrichment (Twin Cays), and two coral reef lagoons (Tobacco Reef, Curlew Cay) at different distances from Man-of-

War Cay and Twin Cays were selected for comparative purposes to provide a gradient of nutrient availability. We also hypothesized that P, rather than N, would be the more important nutrient regulating productivity and benthic community structure in carbonate-rich tropical waters of Belize (see Lapointe et al. 1992).

We used a spectrum of multidisciplinary approaches to test these hypotheses, including: 1) benthic community structure, 2) macroalgal tissue C:N:P ratios, 3) alkaline phosphatase activity as a measure of macroalgal P-limitation, and 4) water column concentrations of dissolved inorganic nitrogen (DIN; ammonium + nitrate + nitrite) and soluble reactive phosphorus (SRP). We performed these studies along a nutrient gradient that included a guano-enriched mangrove island, an unenriched mangrove island, and two coral reef lagoons on the 250 km long Belize Barrier Reef, the world's second largest continuous reef system (Smith 1948).

Materials and Methods

This research was performed from the Smithsonian Institution field station on Carrie Bow Cay, Belize, Central America (16° 48'N, 88° 05'W; Fig. 1) during 20 to 25 February 1988 and 20 to 27 June 1989. Additional studies were performed during research expeditions aboard the R/V *Calanus* during 14 to 18 May 1987 and the R/V *Cape Hatteras* during 27 to 30 May 1990. Our study sites included a seabird mangrove roost island, Man-of-War Cay (colonized by several hundred frigate birds and brown boobies) as well as a "control" mangrove island lacking significant bird enrichment (Twin Cays) and two pristine coral reef lagoons (Tobacco Reef and Curlew Cay, Fig. 1). All these sites are located along the 120 km long central province of the Belize Barrier Reef system (Burke 1982), and is remote from large-scale anthropogenic influences on water quality. The geology, natural history and biology of the marine communities around the Carrie Bow Cay environs are relatively well-known due to over two decades of multidisciplinary investigations (Ruetzler and Macintire 1982).

Benthic Community Structure—Transect locations at the various sites were selected from navigational charts without prior knowledge of the biotas to be encountered. Transects for estimating the percent cover of Man-of-War Cay were made perpendicular to the shoreline on the east and west sides of the island from about 0.1 m to 2.0 m depth using SCUBA and the non-destructive methods detailed in Littler and Littler (1985). Because our intent was to determine the percent cover of predom-

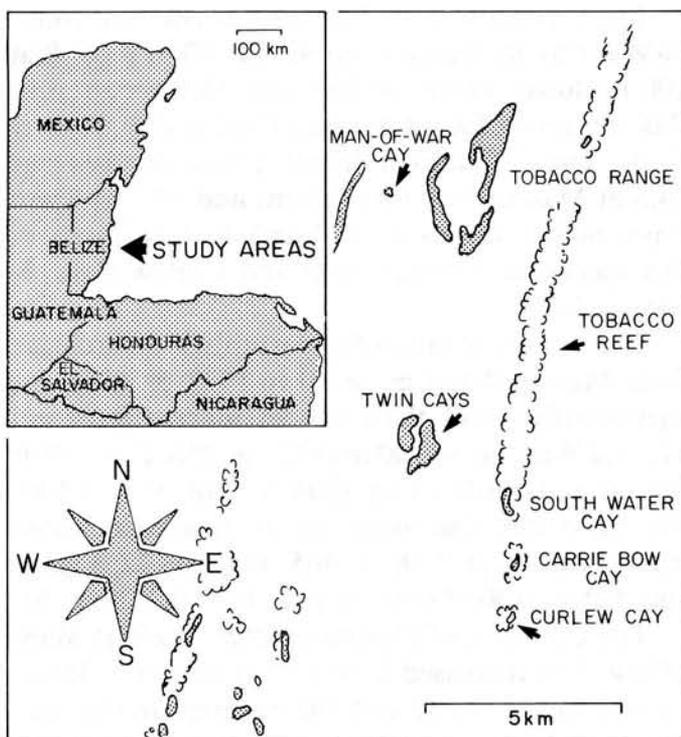


Fig. 1. Location of the general study areas showing Man-of-War Cay, Twin Cays, Tobacco Reef, and Curlew Cay on the Belize Barrier Reef.

inant sessile photosynthetic organisms at each study site, it was not necessary to conduct high-resolution species-specific measurements. Instead, replicate measurements were assessed to include the predominant populations observed at each site. For Man-of-War Cay, video footage was scored in stop-action at random intervals using a high-resolution monitor containing a grid of randomized dots. For the other study areas, the photographic method (Littler and Littler 1985) was used whereby photographic transparencies were scored by a random grid of dots to estimate percent cover. Voucher materials of all species were collected, preserved in 4% buffered paraformaldehyde, mounted on herbarium paper and deposited in the U. S. National Herbarium, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Macroalgal Tissue Analysis—Samples of the predominant macroalgae were collected at shallow depths (< 2 m) at the different sites for determination of C:N:P contents. Samples collected at the west side of Man-of-War Cay were stratified into two zones: an inner zone (10 m) received direct nutrient enrichment from guano inputs while an outer zone (100 m) was spatially removed from direct inputs. At least four 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 oven-drying 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 pre-weighed samples with persulfate (Menzel and Corwin 1965) followed by analysis for soluble reactive phosphorus (Murphy and Riley 1962).

Alkaline Phosphatase Activity (APA)—Macroalgae were collected at all sites within 1.5 hours of each other and immediately assayed side-by-side for APA. Samples collected at Man-of-War Cay were stratified into 10m and 100m zones as described above for tissue analysis. The APA assays were a modification of the spectrophotometric method of Kuenzler and Perras (1965) and were performed deckboard on the R/V *Calanus* under a light flux of 1,000–1,500 $\mu\text{mol m}^{-2} \text{sec}^{-1}$; the assays used 1-liter Wheaton jars held in flowing seawater for temperature control and are described in detail in Lapointe et al. (1992).

Water Column Nutrient Concentrations—Replicate water samples were collected into 250 ml polyethylene bottles at all four sites on several sampling dates for determination of DIN and SRP. Water samples at Man-of-War Cay and Twin Cays were collected from north, south, east, and west sides of the islands to determine spatial variability in enrichment around these mangrove islands. Samples collected at Man-of-War Cay were also stratified into inner (10 m) and outer (100 m) zones on each side of the island to determine the spatial distribution of guano nutrient enrichment. Immediately following collection, the water samples were spiked with HgCl_2 (10 mg/l) and kept either on ice or frozen (and in the dark) until analysis. Concentrations of ammonium (NH_4^+) and nitrate/nitrite ($\text{NO}_3^- + \text{NO}_2^-$) were determined on an Autoanalyzer II according to the methods of Slawk and MacIsaac (1972) and Technicon (1973), respectively. Concentrations of SRP were determined by the molybdenum-blue method (Murphy and Riley 1962) and utilized a Bausch and Lomb Spectronic 88 fitted with a 10-cm cell for maximum sensitivity. The detection limits for NH_4^+ , NO_3^- plus NO_2^- , and SRP were 0.08, 0.08, and 0.03 μM , respectively.

Significant differences in tissue C:N:P ratios, alkaline phosphatase activity, and community structure among the various strata and sites were determined using one-way ANOVA and paired T-tests. Significance reported below implies that the probability of the null hypothesis is < 0.05.

Results

Benthic Community Structure—The biota of Man-of-War Cay showed pronounced patterns of zonal-

tion as a function of distance from the island (Table 1) Cover of the seagrass *Thalassia testudinum* was significantly greater (more than an order-of-magnitude) at 90–100 m from the island than next to the overhanging treeline. Sheet-like and filamentous opportunistic forms of macroalgae dominated the inner halo from 0–10 m on the east transect but extended to 20 m on the west transect beyond which *T. testudinum* became dominant. Of the opportunistic macroalgae, *Ulva lactuca* (> 21.5 % cover), *Acanthophora spicifera* (> 9.4 % cover), *Enteromorpha* sp. (> 5.3 % cover), and *Padina sanctae-crucis* (> 0.7 % cover) all had significantly greater cover near the island on both transects than at 90–100 m. The filamentous *Chaetomorpha linum* (8.7 % cover) was significantly greater in cover on the east transect from 0–10 m, whereas *Rosenvingia intricata* (18.4 %) and *Dictyota divaricata* (1.2 %) occurred on the west transect within 20 m of the island (Table 1).

The nearby Twin Cays (Table 1) was dominated by the calcareous green *Halimeda opuntia* (36.1 %) dispersed among *T. testudinum* (25.6 %) along with epiphytic populations of *Dictyota dichotoma* (12.4 %), *Caulerpa verticillata* (11.2 %) and the geniculate coralline *Amphiroa fragilissima* (10.0 %).

At the carbonate-rich Tobacco Reef site, cover of *T. testudinum* (19.0 %) was considerably reduced (Table 1) and the macroalgal cover was dominated by the long-lived perennial forms *Turbinaria turbinata* (5.0 %) and *Sargassum polyceratum* (2.0 %) in combination with epiphytic *Dictyota divaricata* (3.3 %). The carbonate-rich Curlew Cay site showed the least *T. testudinum* cover (10.0 %), with most of the additional plant cover consisting of *Acanthophora spicifera* (3.2 %) and *Dictyota divaricata* (2.4 %).

Reef-building corals were most abundant on the east (windward) transect at Man-of-War Cay between 90–100 m (10.7 % mean cover, significantly greater than the west transect and the nearshore transects), followed by Curlew Cay (2.0 %) and Tobacco Reef (1.9 %). Corals were absent in habitats exposed to bird guano at Man-of-War Cay and in the short transect on the margin of Twin Cays.

Macroalgal Tissue Analysis—The mean C:N ratio of opportunistic sheet-like and filamentous macroalgae from Man-of-War Cay at 10 m (29.9 ± 7.1) was not significantly different from that of longer-lived macroalgae at 100 m (42.2 ± 11.9 ; $P = 0.115$; Fig. 2) or that of predominant macroalgae at Twin Cays (25.8 ± 9.7 ; $P = 0.075$; Fig. 2), Tobacco Reef (37.8 ± 16.1 ; $P = 0.79$; Fig. 3), or Curlew Cay (36.0 ± 9.1 ; $P = 0.995$; Fig. 3).

The C:N ratio of *Padina sanctae-crucis* at Man-of-War Cay increased from 42.8 at 10 m to 59.8 at 100 m; lower values of 29.9 and 33.5 occurred in this species at Twin Cays and Curlew Cay, respectively. The C:N ratio of *Acanthophora spicifera* was 24.3 at Man-of-War Cay (10 m) and 14.2 at Twin Cays; higher values of 35.7 and 39.3 occurred in this species at Tobacco Reef and Curlew Cay, respectively.

The mean C:P ratio of opportunistic macroalgae from Man-of-War Cay at 10 m (522 ± 166) was significantly lower than that of macroalgae from Man-of-War Cay at 100 m (1327 ± 256 , $P = 0.001$; Fig. 4) and Curlew Cay (804 ± 198 , $P = 0.049$; Fig. 5); it was also lower, on average, than those from Twin Cays (916 ± 465 , $P = 0.122$; Fig. 4) and Tobacco Reef (986 ± 522 , $P = 0.79$, Fig. 5).

The C:P ratio of *Padina sanctae-crucis* at Man-of-War Cay increased from 679 at 10 m to 1354 at 100 m; values of 641 and 792 occurred in this species at Twin Cays and Curlew Cay, respectively. The C:P ratio of *Acanthophora spicifera* was 500 at Man-of-War Cay (10 m) and 510 at Twin Cays; higher values of 813 and 828 occurred in this species at Tobacco Reef and Curlew Cay, respectively.

The mean N:P ratio of opportunistic macroalgae from Man-of-War Cay at 10 m (17.5 ± 4.1) was also significantly lower than that of macroalgae from Man-of-War Cay at 100 m (33.3 ± 5.6 , $P = 0.002$; Fig. 6), Twin Cays (36.0 ± 11.1 , $P = 0.007$, Fig. 6), Tobacco Reef (27.1 ± 7.3 , $P = 0.023$, Fig. 7), and Curlew Cay (22.1 ± 1.4 , $P = 0.040$, Fig. 7).

The N:P ratio of *Padina sanctae-crucis* at Man-of-War Cay increased from 16.0 at 10 m to 25.0 at 100 m; values of 21.4 and 24.1 occurred in this species at Twin Cays and Curlew Cay, respectively. The N:P ratio of *Acanthophora spicifera* was 20.7 at Man-of-War (10 m) and 34.8 at Twin Cays; values of 22.9 and 21.3 occurred in this species at Tobacco Reef and Curlew Cay, respectively.

Alkaline Phosphatase Activity—The sheet-like and filamentous macroalgae from Man-of-War Cay at 10 m had mean APA values ($6.6 \pm 6.4 \mu\text{M PO}_4^{3-}$ released g dry wt⁻¹ h⁻¹) significantly lower than those of macroalgae from Man-of-War Cay at 100 m ($75.3 \pm 49.5 \mu\text{M PO}_4^{3-}$ released g dry wt⁻¹ h⁻¹, $P = 0.001$, Fig. 8), Twin Cays ($68.7 \pm 72.4 \mu\text{M PO}_4^{3-}$ released g dry wt⁻¹ h⁻¹, $P = 0.005$, Fig. 8), Curlew Cay ($44.0 \pm 23.6 \mu\text{M PO}_4^{3-}$ released g dry wt⁻¹ h⁻¹, $P = 0.001$, Fig. 9), and Tobacco Reef ($43.2 \pm 23.3 \mu\text{M PO}_4^{3-}$ released g dry wt⁻¹ h⁻¹, $P = 0.001$, Fig. 9). The opportunistic green algae *Chaetomorpha linum* and *Ulva lactuca* and the opportunistic brown alga *Rosenvingia intricata*, all of which were abundant

Table 1. Mean percent cover of dominant frondose macrophytes from seven transect areas at four study sites. For the Man-of-War Cay transects, means with no letters in common (parentheses, A, B, C) are significantly different ($P < 0.05$, ANOVA using Boneferoni t test of differences, $N = 21$). Statistical analysis was not performed for the other three study sites.

Species	Man of War Cay				Twin Cay (North) (0–6.5m)	Tobacco Reef (Back Reef) (0–160m)	Curlew Cay (Back Reef) (0–150m)
	East (0–10m)	West (0–20m)	East (90–100m)	West (90–100m)			
Seagrasses							
<i>Thalassia testudinum</i>	4.2(B)	6.2(B)	92.5(A)	90.2(A)	25.6	19.0	10.8
Macroalgae							
Chlorophyta							
<i>Ulva lactuca</i>	21.5(B)	32.1(A)	0.0(C)	0.0(C)	0.0	0.0	0.0
<i>Enteromorpha</i> sp.	10.0(A)	5.3(A)	0.0(B)	0.0(B)	0.0	0.0	0.0
<i>Chaetomorpha linum</i>	8.7(A)	0.0(B)	0.0(B)	0.0(B)	0.0	0.0	0.0
<i>Caulerpa verticillata</i>	0.0	0.0	0.0	0.0	11.2	0.0	0.0
<i>Caulerpa mexicana</i>	0.0(A)	0.0(A)	0.0(A)	1.1(A)	0.0	0.0	0.0
<i>Dictyosphaeria cavernosa</i>	0.0	0.0	0.0	0.0	0.1	0.1	0.0
<i>Halimeda opuntia</i>	0.0	0.0	0.0	0.0	36.1	0.4	0.0
Rhodophyta							
<i>Acanthophora spicifera</i>	18.7(A)	9.4(A)	0.0(B)	0.0(B)	0.0	0.7	3.2
<i>Rosenvingia intricata</i>	4.9(AB)	18.4(A)	0.0(B)	0.0(B)	0.0	0.0	0.0
<i>Amphiroa fragilissima</i>	0.0	0.0	0.0	0.0	10.0	0.1	0.0
<i>Laurencia intricata</i>	0.0	0.0	0.0	0.0	0.0	1.2	0.4
<i>Laurencia papillosa</i>	0.0	0.0	0.0	0.0	0.0	1.0	0.0
<i>Laurencia poiteaui</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.2
<i>Liagora mucosa</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.1
<i>Polycavernosa debilis</i>	0.0	0.0	0.0	0.0	0.0	0.1	0.0
<i>Spyridia filamentosa</i>	0.0	0.0	0.0	0.0	0.0	0.2	0.0
Phaeophyta							
<i>Dictyota divaricata</i>	1.1(AB)	1.2(A)	0.0(B)	0.0(B)	0.0	3.3	2.4
<i>Padina sanctae-crucis</i>	0.7(A)	0.9(A)	0.0(B)	0.0(B)	0.0	0.0	0.1
<i>Dictyota cervicornis</i>	0.0	0.0	0.0	0.0	0.0	0.1	0.1
<i>Dictyota dichotoma</i>	0.0	0.0	0.0	0.0	12.4	0.0	0.0
<i>Dictyota linearis</i>	0.0	0.0	0.0	0.0	0.0	0.1	0.1
<i>Lobophora variegata</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.4
<i>Sargassum polyceratium</i>	0.0	0.0	0.0	0.0	0.0	2.0	0.0
<i>Turbinaria turbinata</i>	0.0	0.0	0.0	0.0	0.0	5.0	0.0
Corals							
	0.0(B)	0.0(B)	10.7(A)	0.0(B)	0.0	1.9	2.0

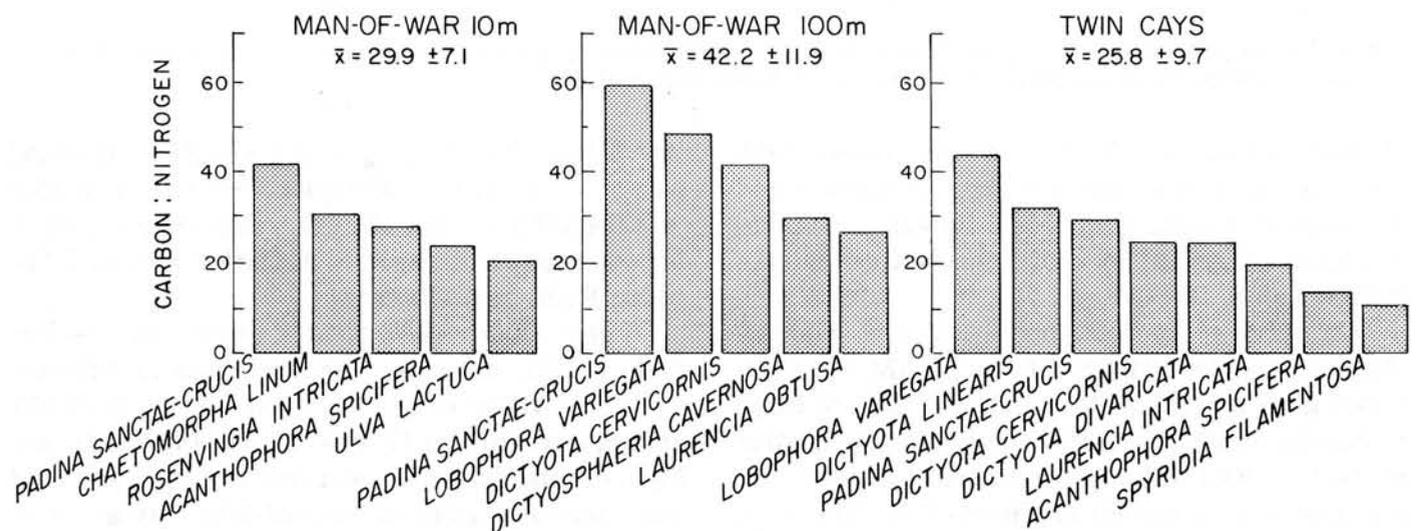


Fig. 2. Carbon:nitrogen ratios of macroalgae from the seabird mangrove rookery Man-of-War Cay (10 m and 100 m) and the unenriched mangrove island Twin Cays on the Belize Barrier Reef.

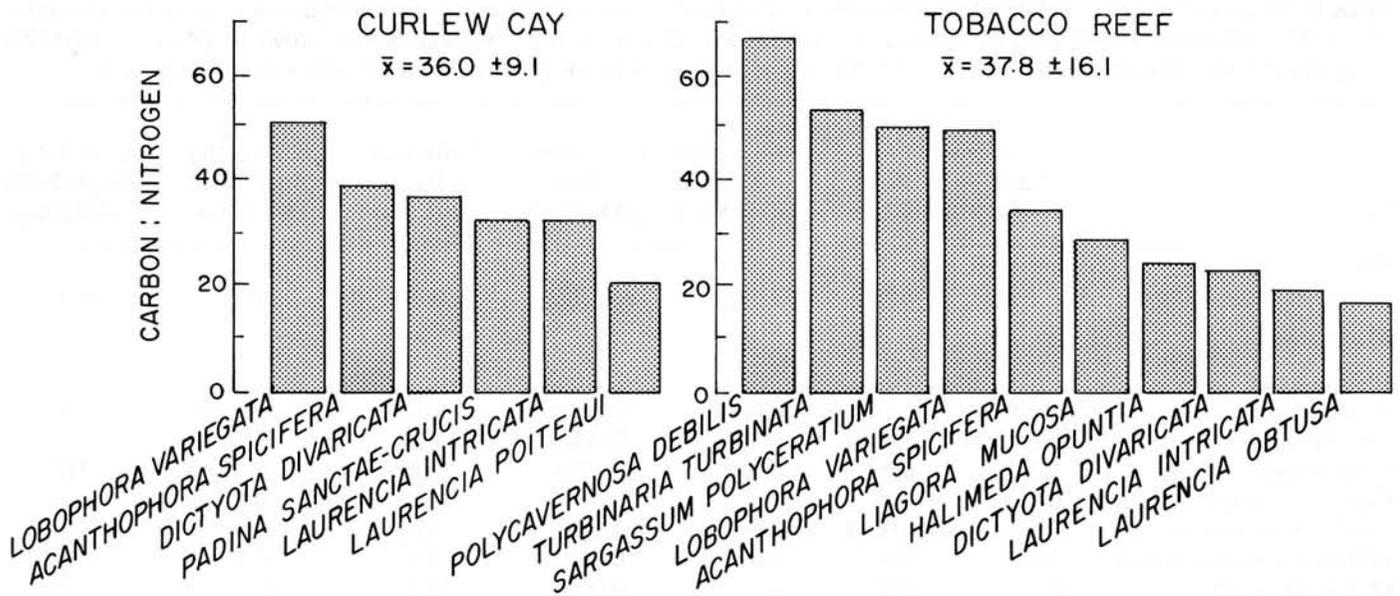


Fig. 3. Carbon:nitrogen ratios of macroalgae from the lagoon of two coral reef ecosystems—Tobacco Reef and Curlew Cay—on the Belize Barrier Reef.

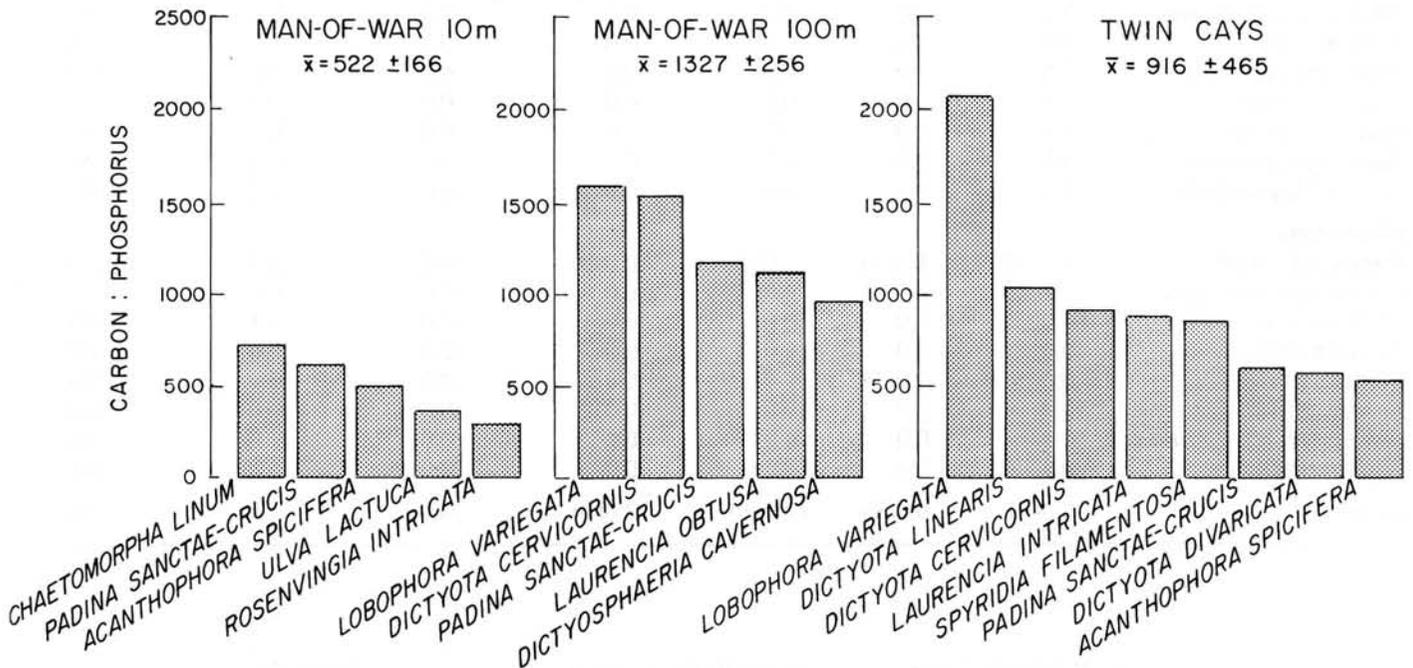


Fig. 4. Carbon:phosphorus ratios of macroalgae from the seabird mangrove rookery Man-of-War Cay (10 m and 100 m) and the unenriched mangrove island Twin Cays on the Belize Barrier Reef.

at Man-of-War at 10 m, had the lowest APA whereas the brown algae *Dictyota cervicornis* and *Dictyota divaricata* from Man-of-War at 100 m, Twin Cays, Curlew Cay, and Tobacco Reef had the highest values (Figs. 8 and 9).

The APA of *Padina sanctae-crucis* at Man-of-War Cay increased from $6.6 \pm 1.3 \mu\text{M PO}_4^{3-}$ released $\text{g dry wt}^{-1} \text{h}^{-1}$ at 10 m to $27.9 \pm 8.1 \mu\text{M PO}_4^{3-}$ released $\text{g dry wt}^{-1} \text{h}^{-1}$ at 100 m; a higher mean value of $34.7 \pm 10.3 \mu\text{M PO}_4^{3-}$ released $\text{g dry wt}^{-1} \text{h}^{-1}$ occurred in this species at Curlew Cay. The APA of *Acanthophora spicifera* at Man-of-War Cay increased from $6.4 \pm 1.3 \mu\text{M PO}_4^{3-}$ released g dry

$\text{wt}^{-1} \text{h}^{-1}$ at 10 m to $23.3 \pm 2.8 \mu\text{M PO}_4^{3-}$ released $\text{g dry wt}^{-1} \text{h}^{-1}$ at 100 m; higher APA values of 35.5 ± 1.0 and $65.4 \pm 6.4 \mu\text{M PO}_4^{3-}$ released $\text{g dry wt}^{-1} \text{h}^{-1}$ occurred in this species at Curlew Cay and Tobacco Reef, respectively.

Water Column Nutrient Concentrations—The highest NH_4^+ concentrations occurred at Man-of-War Cay where values averaged $1.21 \pm 0.26 \mu\text{M}$ and ranged from 0.17 to $4.08 \mu\text{M}$ (Table 2); the highest concentrations occurred on the north and west (leeward) sides of Man-of-War Cay at 10 m (Table 2). Lower NH_4^+ concentrations—averaging $0.41 \pm 0.10 \mu\text{M}$ —occurred at Twin Cays outside

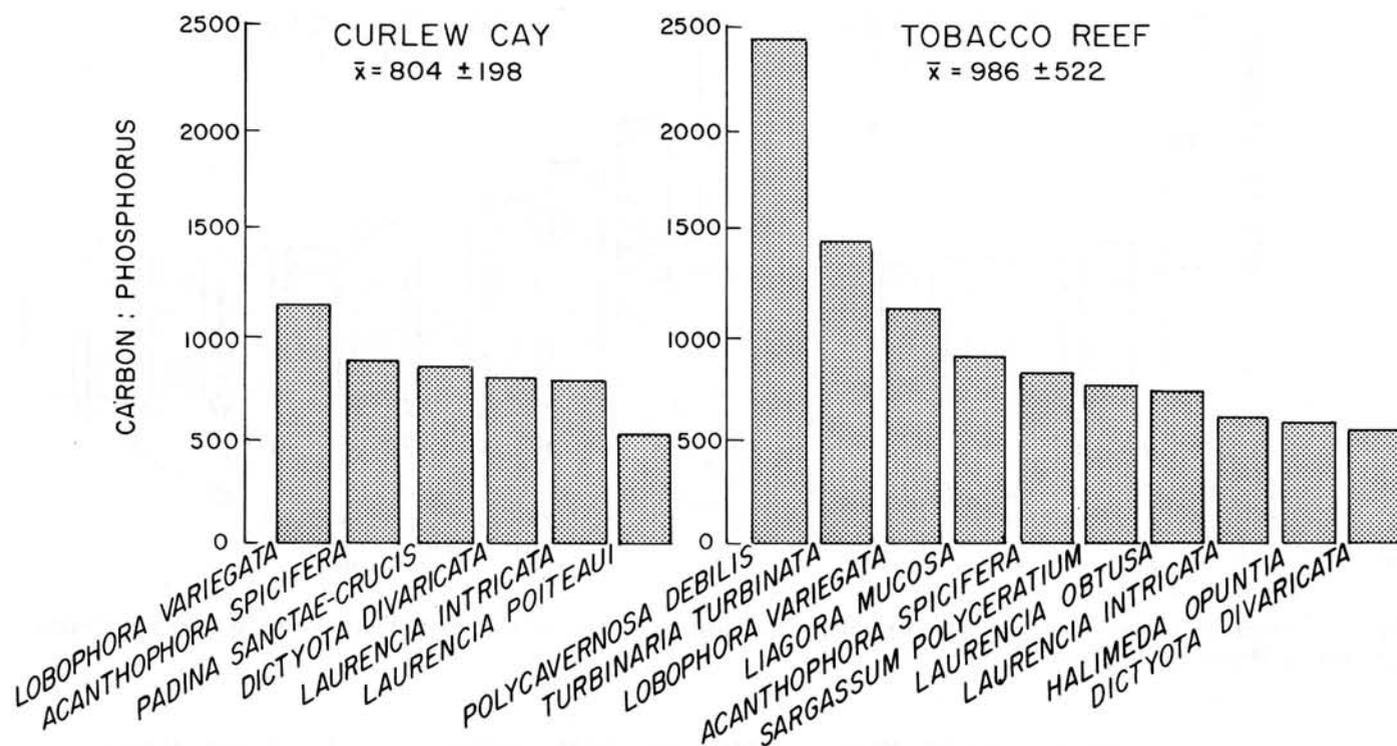


Fig. 5. Carbon:phosphorus ratios of macroalgae from the lagoon of two coral reef ecosystems—Tobacco Reef and Curlew Cay—on the Belize Barrier Reef.

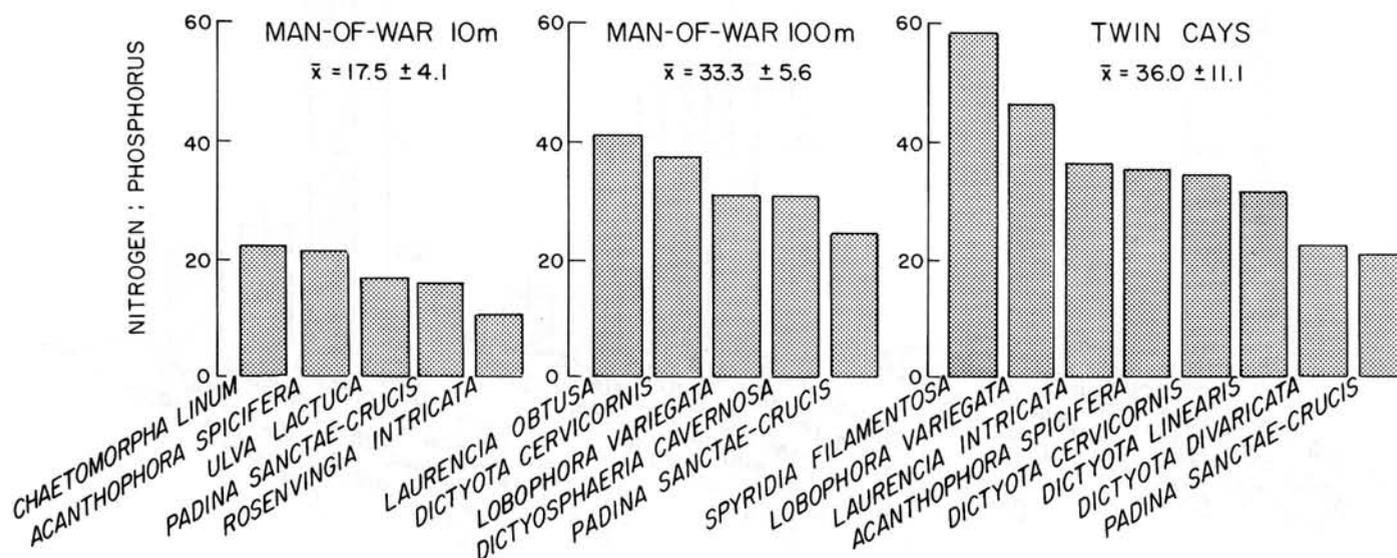


Fig. 6. Nitrogen:phosphorus ratios of macroalgae from the seabird mangrove rookery Man-of-War Cay (10 m and 100 m) and the unenriched mangrove island Twin Cays on the Belize Barrier Reef.

the mangrove channels and around the periphery of the islands (Table 2). The lowest NH_4^+ concentrations occurred at the Tobacco Reef and Curlew Cay lagoons where concentrations averaged 0.43 ± 0.09 and $<0.10 \pm 0.01 \mu\text{M}$, respectively (Table 2).

Concentrations of NO_3^- and NO_2^- were also highest at Man-of-War Cay where values averaged $3.63 \pm 1.31 \mu\text{M}$ and ranged from 0.16 to $20.1 \mu\text{M}$; the highest concentrations occurred on the north and west sides at 10 m with lower values at 100 m (Table 2). Lower concentrations of NO_3^- and NO_2^- —averaging 0.36 ± 0.02 —occurred at Twin Cays within the man-

grove channels and around the periphery of the island (Table 2). Concentrations of NO_3^- and NO_2^- at the Tobacco Reef and Curlew Cay lagoons were undetectable ($<0.08 \mu\text{M}$; Table 2).

SRP concentrations were also highest at Man-of-War Cay where values averaged $1.56 \pm 0.48 \mu\text{M}$ and ranged from 0.06 to $7.18 \mu\text{M}$; the highest SRP concentrations occurred on the north and west sides at 10 m with lower values at 100 m (Table 2). Lower SRP concentrations—averaging $0.14 \pm 0.03 \mu\text{M}$ —occurred at Twin Cays within the mangrove channels and around the periphery of the island (Table

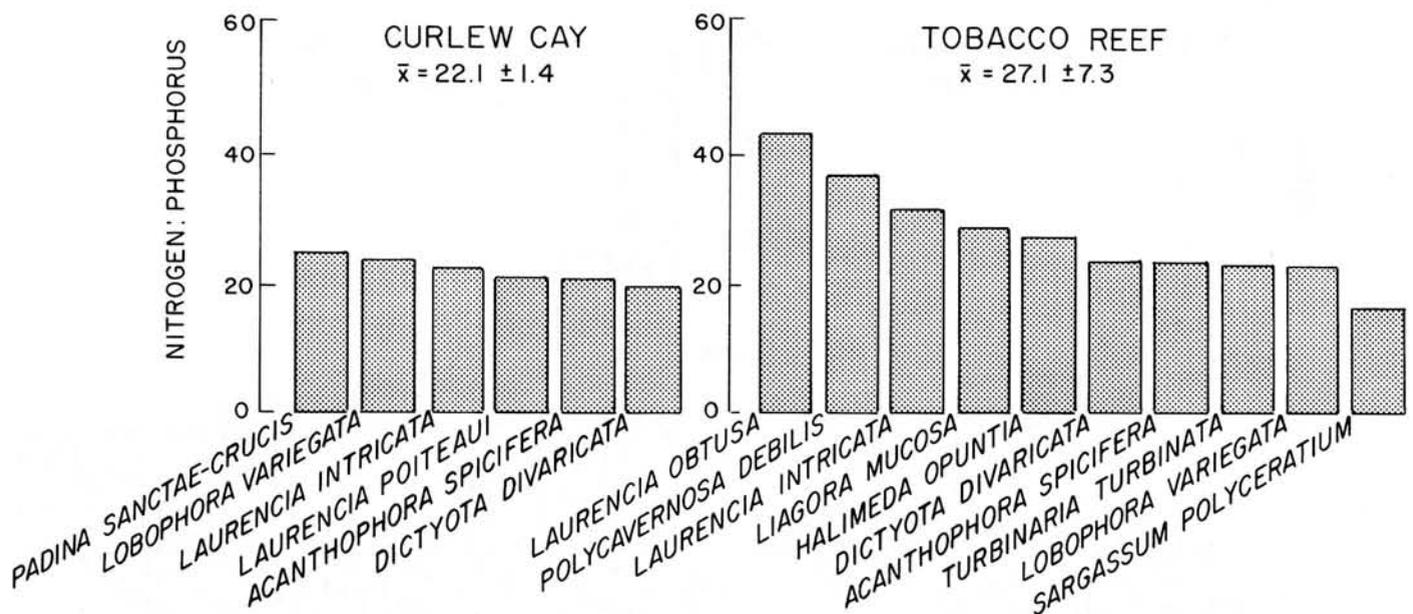


Fig. 7. Nitrogen:phosphorus ratios of macroalgae from the lagoon of two coral reef ecosystems—Tobacco Reef and Curlew Cay—on the Belize Barrier Reef.

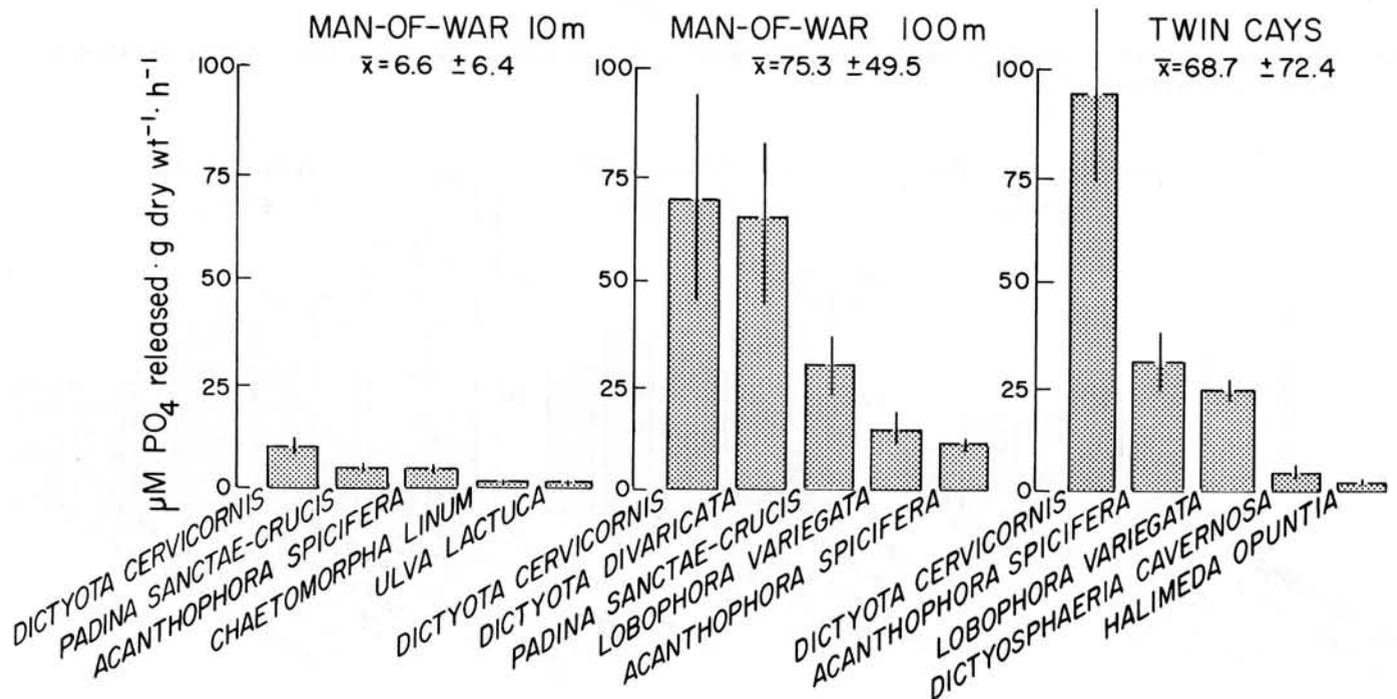


Fig. 8. Alkaline phosphatase activity of macroalgae from the seabird mangrove rookery Man-of-War Cay (10 m and 100 m) and the unenriched mangrove island Twin Cays on the Belize Barrier Reef. Values represent means \pm 1 SD ($n=3$).

2). The lowest SRP concentrations occurred at Tobacco Reef and Curlew Cay where concentrations averaged $0.08 \pm 0.01 \mu\text{M}$ and undetectable, respectively (Table 2).

Discussion

Our results support the trends predicted by the relative dominance paradigm (Littler and Littler 1984) with few specific exceptions. The distribution of opportunistic and long-lived macroalgae, seagrasses and corals proved to be good indicators of water

column nutrient availability. Opportunistic sheet-like and filamentous forms of macroalgae (*Ulva lactuca*, *Chaetomorpha linum*, *Rosenvingia intricata*) with low alkaline phosphatase activities dominated the nutrient-enriched, hypereutrophic habitats at Man-of-War Cay whereas longer-lived, perennial macroalgae (e.g. *Polycavernosa debilis*, *Turbinaria turbinata*, *Sargassum polyceratium*), seagrasses and corals tended to be most abundant under nutrient-poor conditions at the reef sites. Sheet-like and filamentous macroalgal forms are highly productive (Littler et al. 1983) and flourish in high nutrient

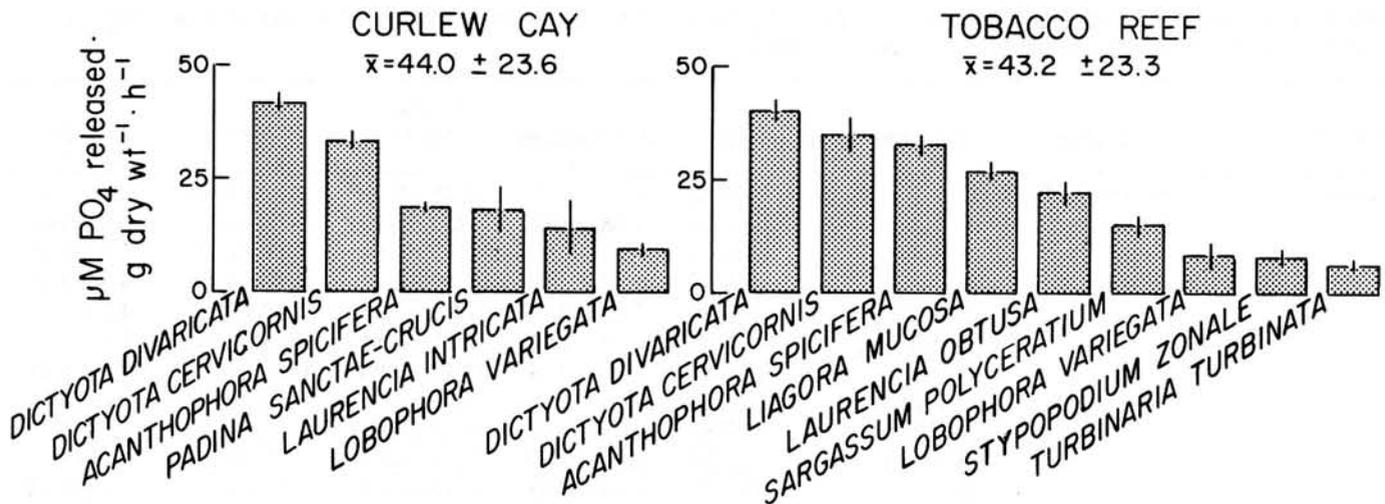


Fig. 9. Alkaline phosphatase activity of macroalgae from the back reef of two coral reef ecosystems—Tobacco Reef and Curlew Cay—on the Belize Barrier Reef. Values represent means \pm 1 SD ($n=3$).

waters (e.g. *Ulva* spp. in Boston Harbor, Sawyer 1965) where nutrient availability can balance high rates of carbon fixation. Under nutrient-replete conditions, opportunistic species can double their biomass in short periods of time (e.g. $< 3-4$ days; Lapointe and Tenore 1981) leading to overgrowth of more slowly growing seagrasses and corals. The perennial macroalgae appear to dominate under moderate levels of nutrient availability and can do well in environments with low nutrient concentrations provided that they have high delivery rates due to currents and turbulence (e.g. Tobacco Reef).

Shifts in tissue C:N:P ratios of macroalgae among the various sites suggests that availability of P, rather than N, is the proximal nutrient regulating the productivity and relative dominance in these habitats. The lack of a significant shift in C:N ratios of macroalgae among the enriched and unenriched sites suggests that N is not critically limiting the productivity of these algal populations nor their community structure. Significant decreases in C:P and N:P ratios between the unenriched reef and mangrove sites and the enriched mangrove site suggests that P availability is critically limiting the productivity of opportunistic macroalgae in these waters. This finding is in close agreement with our earlier nutrient enrichment-productivity research at Twin Cays and Curlew Cay (Lapointe et al. 1987) where P-enrichment was quantitatively more important than N-enrichment in enhancing the productivity of *Acanthophora spicifera* and *Dictyota divaricata*. Similar enrichment studies also indicated that P rather than N limits the productivity of the seagrass *Syringodium filiforme* in the carbonate-rich waters of San Salvador Island in the Bahamas (Short et al. 1991). The mean N:P and C:P ratios of macroalgae at our unenriched sites

were elevated—29.6 and 1008—similar to worldwide mean values of 35 and 700 for marine plants that indicates P-limitation of productivity (Atkinson and Smith 1983).

That P-enrichment from bird guano relieves P-limitation of macroalgae is directly supported by our APA data. APA of the opportunistic macroalgae (e.g. *Ulva lactuca*, *Chaetomorpha linum*, and *Rosenvingia intricata*) at Man-of-War Cay was significantly reduced compared to that of macroalgae at the other sites. This pattern is clearly related to guano P-enrichment and the resulting high SRP concentrations at Man-of-War Cay (SRP concentrations up to $7.18 \mu\text{M}$) that relieves P-limitation of algal productivity in these waters (Lapointe et al. 1987) as well as APA of P-limited macroalgae (Lapointe 1989). This pattern also suggests that the highly productive macroalgae adjacent to Man-of-War Cay may lack adequate APA to sustain balanced growth under more oligotrophic, P-limited conditions at unenriched mangrove and reef sites. Species of brown macroalgae, including *Dictyota cervicornis* and *Dictyota linearis*, as well as the red alga *Acanthophora spicifera*, had relatively high capacities of APA during these studies and would be competitively superior in environments with low water column SRP; indeed, these species were common at all the unenriched sites during this study. APA of *Padina sanctae-crucis* and *Acanthophora spicifera* increased with decreasing SRP concentrations between the most enriched site—Man-of-War Cay (10 m)—and the most nutrient-poor site—Curlew Cay. Higher APA provides these species an increased ability to hydrolyze organic phosphorus monoesters as a source of SRP (Kuenzler and Perras 1965), clearly a trait of adaptive value to growth

Table 2. Water column nutrient concentrations (μM) at four sites on the Belizean Barrier Reef. Values represent means \pm 1 SE ($n = 2$). U.D. = Undetectable; N/A = Not Available.

Location	System	Sampling Area	Date	Ammonium	Nitrate/ Nitrite	SRP	N:P		
<i>Man-of-War Cay</i>	Mangrove Bird Rookery	W	2/24/88	1.26 \pm 0.08	2.25 \pm 0.25	1.29 \pm 0.01	2.8 \pm 0.21		
		N	2/24/88	4.08 \pm 0.18	16.2 \pm 0.25	7.18 \pm 0.12	2.8 \pm 0.00		
		S	2/24/88	1.92 \pm 0.10	1.17 \pm 0.02	1.18 \pm 0.01	2.6 \pm 0.00		
		E	2/24/88	0.60 \pm 0.01	0.69 \pm 0.06	0.30 \pm 0.01	4.3 \pm 0.10		
		W 10m	6/27/89	2.99 \pm 0.27	14.6 \pm 2.05	3.95 \pm 0.16	4.5 \pm 0.31		
		N 10m	6/27/89	3.74 \pm 0.34	20.1 \pm 2.81	4.45 \pm 0.18	5.4 \pm 0.37		
		S 10m	6/27/89	1.56 \pm 0.14	0.46 \pm 0.06	0.10 \pm 0.00	21.0 \pm 1.47		
		E 10m	6/27/89	1.02 \pm 0.09	0.35 \pm 0.05	U.D.	N/A		
		W 100m	6/27/89	0.25 \pm 0.02	0.19 \pm 0.03	U.D.	N/A		
		N 100m	6/27/89	0.22 \pm 0.02	0.26 \pm 0.04	U.D.	N/A		
		S 100m	6/27/89	0.33 \pm 0.03	0.17 \pm 0.02	0.28 \pm 0.01	1.8 \pm 0.13		
		E 100m	6/28/89	0.17 \pm 0.02	0.20 \pm 0.03	0.37 \pm 0.01	1.0 \pm 0.07		
		W	5/30/90	0.36 \pm 0.02	0.21 \pm 0.15	0.09 \pm 0.02	6.3 \pm 0.11		
		N	5/30/90	0.58 \pm 0.30	0.67 \pm 0.00	0.24 \pm 0.00	6.4 \pm 0.00		
		S	5/30/90	0.18 \pm 0.11	0.84 \pm 0.11	0.09 \pm 0.01	11.9 \pm 0.70		
		E	5/30/90	0.45 \pm 0.17	0.16 \pm 0.00	0.06 \pm 0.00	7.3 \pm 0.00		
				Mean		1.21	3.63	1.56	5.7
		Std. Error		0.26	1.31	0.48	1.0		
<i>Twin Cays</i>	Mangrove	W	2/20/88	0.83 \pm 0.07	0.74 \pm 0.10	0.17 \pm 0.01	9.3 \pm 0.65		
		N	2/20/88	0.26 \pm 0.02	0.16 \pm 0.02	0.17 \pm 0.01	2.5 \pm 0.18		
		S	2/20/88	0.44 \pm 0.04	0.27 \pm 0.04	0.08 \pm 0.01	8.8 \pm 0.08		
		E	2/20/88	0.69 \pm 0.06	0.74 \pm 0.10	0.09 \pm 0.01	15.8 \pm 1.9		
		W	6/27/89	U.D.	0.38 \pm 0.05	0.19 \pm 0.0	N/A		
		N	6/27/89	U.D.	0.15 \pm 0.02	0.15 \pm 0.0	N/A		
		S	6/27/89	0.12 \pm 0.01	U.D.	U.D.	N/A		
		E	6/27/89	0.14 \pm 0.01	0.08 \pm 0.01	U.D.	N/A		
				Mean		0.41	0.36	0.14	9.1
				Std. Error		0.10	0.02	0.03	2.4
<i>Tobacco Reef</i>	Coral Reef	W	6/27/89	0.22 \pm 0.02	U.D.	0.09 \pm 0.00	N/A		
		N	6/27/89	0.60 \pm 0.05	U.D.	0.09 \pm 0.00	N/A		
		S	6/27/89	0.60 \pm 0.05	U.D.	0.06	N/A		
		E	6/27/89	0.30 \pm 0.03	U.D.	0.08 \pm 0.00	N/A		
				Mean		0.43	U.D.	0.08	N/A
		Std. Error		0.09	U.D.	0.01	N/A		
<i>Curlew Cay</i>	Coral Reef	W	5/30/90	U.D.	U.D.	U.D.	N/A		
		N	5/30/90	U.D.	U.D.	U.D.	N/A		
		S	5/30/90	0.14 \pm 0.01	U.D.	U.D.	N/A		
		E	5/30/90	U.D.	U.D.	U.D.	N/A		
		W	5/30/90	U.D.	U.D.	U.D.	N/A		
		N	5/30/90	U.D.	U.D.	U.D.	N/A		
		S	5/30/90	0.18 \pm 0.02	U.D.	U.D.	N/A		
		E	5/30/90	U.D.	U.D.	U.D.	N/A		
				Mean		<0.10	U.D.	U.D.	N/A
		Std. Error		0.04	U.D.	U.D.	N/A		

in tropical carbonate-rich waters having low SRP concentrations (Atkinson 1987).

The P-enrichment at Man-of-War Cay is also evident from the reduced N:P and C:P ratios of predominant macroalgal tissue. The elevated water column DIN and SRP concentrations were present at low N:P ratios (< 6 , Table 2) at the bird rookery compared to the N:P stoichiometric demand of 15–30 for most algae (Rhee 1978); thus, the P-rich guano relieves P-limitation otherwise affecting macroalgae in these waters (Lapointe et al. 1987) and

allows highly productive opportunistic species to dominate the benthos in the nutrient wake of the bird island. The mean N:P and C:P ratios of macroalgae receiving guano-enrichment were 17.5 and 522—significantly lower than mean values of 29.6 and 1008 for P-limited macroalgae from the unenriched sites. These low values in enriched macroalgae from Man-of-War Cay are similar to the mean values of 14.9 and 430 for macroalgae from N-limited siliciclastic environments in temperate latitudes (Lapointe et al. 1992).

These results suggest that the concentrations of DIN and SRP representing approximate thresholds for eutrophication and macroalgal overgrowth of coral reefs may be quite low. DIN and SRP concentrations averaged ~ 0.80 and $0.14 \mu\text{M}$ at Twin Cays, a detritus-rich but pristine mangrove island with extensive macroalgal and seagrass cover but virtually no coral development. These concentrations at Twin Cays are significantly elevated compared to the undetectable DIN and SRP concentrations at Curlew Cay, clearly the most offshore and oligotrophic site in our study. Considering the evidence of primary P-limitation in these waters and the nutrient concentration gradient measured between sites, we suggest that DIN and SRP concentrations of ~ 1.0 and $0.10 \mu\text{M}$, respectively, represent threshold water column concentrations for nutrient-replete growth of macroalgae in these carbonate-rich coral reef environments. These DIN concentrations are similar to those that sustain maximal growth rates of highly productive, opportunistic red (DeBoer et al. 1978) and green macroalgae (Lapointe and Tenore 1978). Our findings are consistent with studies in Kaneohe Bay, Hawaii (Smith et al. 1981) and Barbados, West Indies (Tomascik and Sander 1985) in which DIN and SRP concentrations of $\sim 1.0 \mu\text{M}$ and $0.10 \mu\text{M}$, respectively, represented threshold values for the onset of cultural eutrophication (Bell 1992)

The source and loadings of nutrient inputs to tropical coastal waters will determine the ultimate spatial extent of nutrient distributions, macroalgal productivity, and benthic community structure. Because piscivorous seabirds forage in waters adjacent to roost islands where they defecate, these nutrients are autochthonous and are recycled within the ecosystem. In contrast, human activities are introducing orders-of-magnitude greater nutrient loadings to coastal waters (Peierls et al. 1991) from allochthonous sources—sewage, agricultural runoff, and deforestation—all of which represent “new” nutrients rather than recycled nutrients (sensu Dugdale and Goering 1967). Unlike the limited mass and spatial effects of guano enrichment on nutrient concentrations at Man-of-War Cay, anthropogenic nutrient inputs can lead to much larger-scale eutrophication and elevated nutrient concentrations in coastal waters (Smith et al. 1981; Tomascik and Sander 1985). Increased dominance of macroalgae relative to corals has been observed on reefs impacted by cultural eutrophication, including *Dictyosphaeria cavernosa* in Kaneohe Bay, Hawaii (Smith et al. 1981), *Cladophora prolifera* in Bermuda (Lapointe and O’Connell 1979), and *Sargassum filipendula* in Martinique (Littler et al. 1994); increased nutrient

concentrations also increase macroalgal epiphytes on seagrass blades (Silberstein et al. 1986), decreasing seagrass productivity via light-limitation (Sand-Jensen 1977) and ultimately causing seagrass die-off (Cambridge and McComb 1984). Macroalgal blooms can be undesirable as they not only inhibit reef coral recruitment and growth (Birkeland 1988), but also have negative cascading effects on coral reef food webs (Johannes 1975). Our results suggest that P-removal from wastewaters and land-based runoff will be a cost-effective strategy to control cultural eutrophication in carbonate-rich waters of the Belize Barrier Reef and similar reef systems worldwide.

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