



# Comparisons of N- and P-limited productivity between high granitic islands versus low carbonate atolls in the Seychelles Archipelago: a test of the relative-dominance paradigm

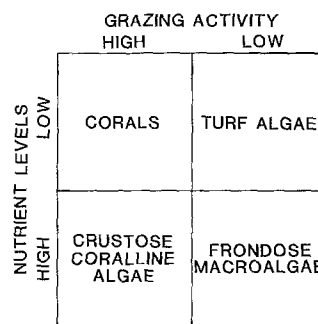
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**Abstract.** This exploratory study suggests that different geological systems (carbonate vs. granitic) in tropical waters have contrasting patterns of photosynthetic nutrient limitation correlated with inorganic nitrogen (N) and phosphorus (P) availability. Physiological assays for 21 predominant macrophyte species show that inorganic N and P are much less limiting to photosynthesis on granitic islands than is the case on carbonate islands and that, of the two, P is more likely to limit production in carbonate-rich tropical waters. Patterns of nutrient limitation in turn are reflected by differences in the relative dominance of functional groups of sessile, epilithic, photosynthetic organisms. Surveys at 33 sites on 10 islands revealed that nearshore waters on high granitic islands tend to be characterized by large and species-rich standing stocks of frondose macroalgae, often dominated by *Sargassum* spp., whereas waters around low carbonate islands tend to be dominated by hermatypic corals. Macrophyte tissue and seawater analyses also indicate a possible trend toward higher levels of N and P in granitic vs. carbonate islands. Pagode Island, a low carbonate island influenced by guano from seabird colonies, is an exception, with few corals, relatively high levels of tissue and seawater N and P, and a predominance of macroalgae (mostly *Dictyosphaeria cavernosa*).



**Fig. 1.** Diagrammatic representation of the relative dominance paradigm modified from Littler and Littler (1984). Potentially predominant space-occupying groups of photosynthetic reef organisms are emphasized as a function of long-term nutrient levels and disturbance by herbivores. Hermatypic corals are hypothesized to be the competitive dominants on pristine reefs (because of their size potential) and macroalgae are posited as potential dominants on reefs where macronutrient levels are elevated. Grazing is considered the more important direct controller of algal standing stocks on undisturbed reefs, whereas nutrients set the potential upper limits to biomass. Human activities tend to reduce grazing animals and increase nutrient levels, which shifts reefs from coral to algal domination

## Introduction

Calcareous and non-calcareous algae and corals tend to predominate within defined reef habitats, although with some specific exceptions. The relative dominance (Fig. 1, Littler and Littler 1984) of sessile photosynthetic organisms such as frondose macroalgae, crustose coralline algae, turf forming algae, and corals is predicted to be regulated most directly by complex biological interactions (Littler et al. 1989) between competition and grazing, the outcomes of which are influenced indirectly by abiotic factors, including nutrient levels, wave action, sedimentation, irradiance, desiccation, and temperature.

Where nutrient levels are elevated as a consequence of human activities (Littler and Littler 1988), biotic reefs tend to shift from coral to algal domination (Fig. 1). Numerous studies (e.g., Simkiss 1964; Fishelson 1973; Kinsey and Davies 1979; Walker and Ormond 1982; Dodge et al. 1984) have demonstrated the detrimental effects of elevated phosphate concentrations on coral survival. Alterations from coral dominance to fleshy algal dominance often have been associated with excessive nutrient increases, as in the cases of reefs of Venezuela (Weiss and Goddard 1977), the Florida reef tract (Lapointe 1989a), and in Kaneohe Bay, Hawaii (Banner 1974; Smith et al. 1981).

Dissolved nutrient concentrations in pristine tropical reef systems are typically very low and can limit the primary productivity of dominant macroalgal species (Lapointe 1989b). Unusually large macroalgal stocks on

reefs often correlate with elevated nutrient levels (Adey et al. 1977), supporting the concept that growth rates of tropical reef algae are characteristically nutrient limited. Experimental manipulations involving nutrient enrichments of macroalgae on the Great Barrier Reef resulted in increased net production (Kinsey and Domm 1974) and, under conditions of herbivore exclusion, increases in biomass (Hatcher and Larkum 1983). In agreement, nutrient pulse experiments have resulted in increased growth rates (Littler et al. 1986; Lapointe 1989b), and productivity (Littler et al. 1988; Littler and Littler 1990) for tropical macroalgae.

The invitation to participate in the First Joint USSR-USA Expedition in Marine Biology provided an opportunity to test the predictive capability of aspects of the relative dominance model (Fig. 1) and to study photosynthetic responses to phosphorus (P-orthophosphate) and nitrogen (N-nitrate) for a variety of macrophyte species and habitats from the geochemically diverse Seychelles island systems. A knowledge of such responses could prove useful to clarify present uncertainties (Smith 1984) concerning the relative importances of N and P limitation to algal stocks in tropical marine environments. The present study was designed to examine the relative nutritional status, with regard to N vs. P limitation, of dominant macrophytes collected from high (up to 1000 m) granitic vs. low (< 10 m) atoll islands and guano-rich vs. nutrient-poor carbonate islands throughout the Seychelles Archipelago.

A basic assumption is that increased rainfall and terrestrial runoff due to greater adiabatic cooling of monsoonal winds on high rain-forested islands (Procter 1984; Walsh 1984), should lead to an increase in organically-derived nutrient availability in nearshore waters (Littler 1976). The climate is dominated (Taylor and Lewis 1970) by the south-east monsoon, that blows from late April to early November while the north-west monsoon prevails from December to March, which results in a shift in the rain-shadow/watershed patterns around all high islands. The detailed geomorphology of Seychelles island groups, including all those studied here, has been characterized in Stoddart (1984a). Seawater temperatures vary between 27° C and 31° C and the salinity ranges from 34.5‰ to 35.5‰ (Taylor and Lewis 1970). Because carbonate sediments in the seas around high islands are relatively less abundant than around low carbonate atolls (Braithwaite 1984), we predicted also that P levels would be higher due to reduced geochemical scrubbing action (Gulbrandsen and Robertson 1973; DeKanel and Morse 1978; Gaudette and Lyons 1980; Berner 1984; Lapointe et al. in press) by carbonate precipitates. As a related example, about 86% of the available P is removed per day by the carbonate sediments surrounding pore waters on San Salvador Island, Bahamas (Short et al. 1989). Nutrient input into low island systems is mainly from normal oceanic water throughput, presumed episodic upwelling, and nitrogen fixation. However, some of the low atoll islands receive considerable enrichment from terrestrial erosion of both modern and fossil guano deposits.

The present study incorporated nutrient-enriched productivity assays, determinations of nutrients in algal tis-

ues, and seawater-nutrient analyses, in conjunction with detailed characterizations of the various ecosystems that were investigated. Several a priori predictions were tested. (1) Macroalgal stocks should tend to be less nutrient limited overall on granitic islands due to elevated nutrient levels in the ambient seawater and this, in conjunction with the removal of herbivorous fishes by the greater human populations on high islands, would tend to favor macroalgal domination over corals. (2) P should be more limiting than N to productivity on most low carbonate atolls due to the physical/chemical binding affinities of carbonate sediments for P. (3) Low atoll islands with guano enrichment should tend to show nutrient levels, algal physiological responses, and macroalgal standing stocks comparable to those associated with high granitic islands. (4) Finally, our findings were tested with regard to a relative-dominance paradigm (Fig. 1, Littler and Littler 1984) whereby four major space-occupying groups of epilithic sessile photosynthetic organisms (corals, crustose coralline algae, fleshy macroalgae, and microfilamentous algae) are predicted to shift in abundances as a function of long-term nutrient histories. This exploratory study was not expected to produce unequivocal conclusions without exception, but rather to reveal overall mean data trends and general tendencies that would be useful in further refining or falsifying the hypotheses proposed.

## Methods and materials

This research was conducted from the Soviet research vessel *R/V Nesmeyanov* during an expedition throughout the Republic of the Seychelles (Fig. 2) from 6 February – 15 March 1989. Thirty three specific study sites on 10 islands were characterized by detailed assessments of the overall biotic cover occupying the primary substrata. Study site locations were preselected on navigational charts without prior knowledge of the biotas that would be encountered. Transects for estimating percent cover (33) were made at right angles to the shoreline from about 35 m to < 4 m in depth at each study site using a combination of SCUBA and snorkeling. Because the question addressed was what is the estimated cover of predominant sessile photosynthetic organisms at each island reef system, it was not necessary to conduct high-resolution quantitative surveys such as those undertaken earlier by Mshigeni et al. (1986). Multiple transects were assessed to include the predominant communities observed at each island. While swimming the cover transects, attempts were made to rank the numerical abundance of Scaridae (parrotfishes) and Acanthuridae (surgefishes) on a relative scale of low to moderate to high. Voucher materials of all species were collected and preserved in 4% buffered paraformaldehyde and deposited in the US National Herbarium, National Museum of Natural History, Smithsonian Institution, Washington, DC.

The physiological assays were exhaustive and involved 21 species (collected between 4–10 m deep) from 8 islands conducted over the period from 7 February 1989–11 March 1989. A total of 968 separate plants were incubated at saturating light levels ( $P_{max}$ , determined by PI curves) under four nutrient conditions, consisting of either +N ( $NaNO_3$ ), +P ( $NaH_2PO_4$ ), +N + P, or a control (no enrichment). Initial concentrations of N and P in the enrichment media were 160 and 16  $\mu M$ , respectively. The concentrations were chosen in an attempt to saturate (Lapointe 1985) the uptake rates in the small volumes used (4-liter freezer bags) and represent the extreme upper range of natural levels encountered in highly enriched environments (e.g., sediment pore waters, seawater next to bird islands). Following the overnight (12 h) enrichment, the algae were flushed with 3 changes of fresh seawater under shaded conditions

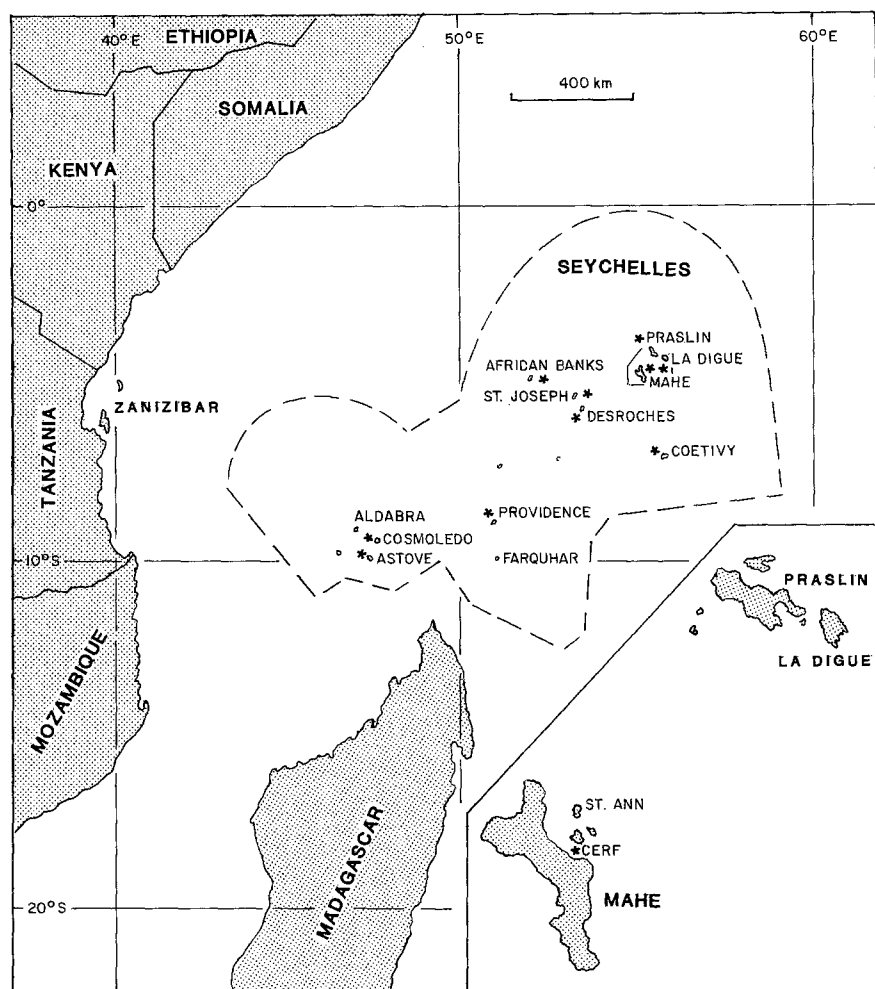


Fig. 2. Map showing the locations (asterisks) of the island groups studied. Inset shows the group of high granitic islands in larger detail

(50% of ambient light) 4 h prior to incubation. Nutrient limitation is indicated by an increase in the net photosynthetic rate following enrichment, whereas no significant response or inhibition demonstrate that the nutrient in question is in ample supply. This enrichment technique has been refined (Littler et al. 1986; Lapointe et al. 1987; Littler et al. 1988; Littler and Littler 1990) as a marine algal photosynthetic bioassay; the results have been consistent with longer-term growth responses in numerous species with few exceptions (Littler et al. 1986; Lapointe 1989b).

For all photosynthesis measurements that followed the 12-h nutrient enrichment period, 10 to 12 independent replicate thalli per species (per island) were incubated under each nutrient treatment in one-liter glass jars at ambient water temperatures ( $28.2\text{--}29.4^\circ\text{C}$ ) under continuous cooling by a flow of ambient seawater and continuous mixing by water-driven magnetic stirrers. Photon-flux densities (PFD) were measured in full sunlight throughout the experimental time series with two integrating 4- $\pi$  sensors (Li-Cor Model LI-1000 DataLogger). Incubations lasted about 4 h and occurred between 1000 and 1530 hours under an average daily PFD of  $2185\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  of photosynthetically active radiation (PAR), with short-term fluctuations ranging from a minimum of 1500 to a maximum of  $3,000\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . Light conditions did not vary from day to day near the low islands and cloudy days were avoided for photosynthetic bioassays near high islands.

Dissolved oxygen was measured to  $0.01\ \text{mg}\cdot\text{l}^{-1}$  with a 5-channel Orbisphere Model 2610 oxygen analyzer and converted to carbon fixed utilizing a photosynthetic quotient of 1.00 to facilitate comparisons. Photosynthesis and respiration were normalized to organic dry weight, which was determined by drying the samples to constant weight at  $70^\circ\text{C}$  and ashing them to constant weight at  $500^\circ\text{C}$ . A t-test was used to compare +N, +P, and +N+P with

the controls to detect significant ( $P < 0.05$ ) inhibitory, stimulatory, or no responses to enrichment. The methods concerning selection of materials, handling, incubation, and oxygen analysis were within the limits recommended by Littler (1979).

Samples were taken for intensive tissue nutrient analysis from the same materials used for the photosynthesis/nutrient assays. Four different thalli per taxon (per island), were maintained separately to provide replicate samples. The individual plants were taken from unshaded habitats at depths that ranged from 4–10 m, returned to the ship submerged in darkened plastic buckets, cleaned of all visible sediments and epiphytes, and rinsed in distilled water prior to drying to constant weight at  $70^\circ\text{C}$  (48 h). The four separate replicate samples were milled in a tissue grinder and analyzed for N using a Control Equipment Corporation Model 240-XA Elemental Analyzer. Total P was determined from the milled samples using the semiautomated method of Aspila et al. (1976).

Time did not permit an exhaustive temporal/spatial study of nutrient variability at each study site. Consequently only ancillary seawater samples were collected during midday at each island group next to the algal thalli used in the photosynthesis/nutrient assays (4–10 m deep) in an attempt to reveal large scale tendencies between island types. Wave action usually overshadowed the small tidal variations experienced by the subtidal macrophytes we studied. Acid-washed nalgene squeeze bottles were filled just above the substratum and returned to the ship where they were filtered and analyzed. Nitrite, nitrate, and ammonium were measured for a total of 30 samples according to the methods of Strickland and Parsons (1972). Phosphate was determined for 10 samples by the molybdenum blue method as soluble reactive phosphate (Murphy and Riley 1962).

Because island reef habitats are extremely patchy, one would expect considerable variability within the island types in terms of dom-

inant macrophyte abundances, physiological responses, tissue nutrients, and seawater nutrients. This variation is magnified by the fact that a given species seldom dominated more than a single habitat and with the exception of *Avrainvillea* sp., high-island dominants were always different from those on low islands. The philosophical approach taken here involved searching for divergent ecological/physiological patterns between geologically different systems, taking advantage of natural experiments. Statistical comparisons to assess nutrient effects on photosynthesis ( $P_{max}$ ) were made by comparing each nutrient enrichment treatment to the appropriate control by t-test with significance levels reported at a probability of  $<0.05$ . We analyzed differences in coral and macroalgal percent cover (following arcsine transformation) and total net productivity of macrophytes under each of the four nutrient pretreatments between geochemical environments independently by unbalanced nested ANOVA (Sokal and Rohlf 1969). The type III sums of squares (SOS) as well as the Bonferroni a posteriori multiple classification analysis (General Linear Models, SAS 1985) were used to identify significant groupings ( $P < 0.05$ ). In the case of *Avrainvillea* sp., which was the only predominant species at both a granitic and carbonate island, one-way ANOVA and Bonferroni tests were used for both tissue nutrients and physiological nutrient-limitation comparisons.

## Results

### Biological surveys

Macroalgal cover for the 16 sites studied on the four high granitic islands (mean of 70%, dominated by *Sargassum*

spp., *Turbinaria* spp., and geniculate corallines) averaged nearly nine times greater than that (8% cover) for the 16 sites assessed on five of the low carbonate islands (significantly different at  $P < 0.05$ , type III SOS, Bonferroni analysis, Table 1). The guano-containing low island, Pagode (Cosmoledo Atoll), showed total macroalgal cover comparable ( $P < 0.05$ ) to high granitic islands with 54% cover (40% *Dictyosphaeria cavernosa*), which was significantly higher ( $P > 0.05$ ) than mean macrophyte cover on low islands. Crustose coralline algae, turf algae, and corals, with only 1% mean cover each, were significantly reduced ( $P < 0.05$ ) on Pagode Island (Table 1). Conversely, the other five low carbonate islands showed a significant ( $P < 0.05$ ) overall predominance of corals (53% mean cover at 16 sites, mostly *Porites*, *Acropora*, *Pocillopora*), which was over seven and one half times the mean coral cover (7%) for the four granitic islands. Crustose coralline algal cover was about the same ( $P > 0.05$ ) for high islands (24%) as for low islands (28%). Observations of herbivorous fish stocks (Table 2) indicates relatively low abundances of both Scaridae and Acanthuridae on 80% of the 16 high granitic sites, and high abundances on 80% of the 16 low islands sites lacking input of guano. The island containing guano had small populations of grazing fishes, but only in undercut ledges just beneath the intertidal shoreline. Herbivorous

**Table 1.** Summation of descriptive transect (33) estimates of overall mean epilithic cover (%) dominants between 4–35 m depth ranges for 4 high granitic islands and 6 low carbonate atolls

Dominant taxa	High granitic islands				Low carbonate islands					Guano islands
	Cerf (2 sites)	La Digue (2 sites)	Mahe (9 sites)	Praslin (3 sites)	African Banks (2 sites)	Astove (6 sites)	Desroches (2 sites)	Grand (1 sites)	St. Joseph (5 sites)	Pagode (1 site)
<b>Large macroalgae</b>										
<i>Geniculate corallines</i>	2		6	9					1	
<i>Caulerpa</i> spp.			2		1	5				3
<i>Dictyosphaeria cavernosa</i>			1			1			1	40
<i>Halimeda</i> spp.			1	3	2	5	6		1	10
<i>Lobophora variegata</i>			1	21						
<i>Sargassum</i> spp.	38	33	64	60						
<i>Turbinaria</i> spp.	10		7			1			1	
<i>Other macroalgae</i>	6	1	9	8	3	4	1	1	5	1
<b>Totals</b>	<b>56</b>	<b>34</b>	<b>91</b>	<b>101</b>	<b>6</b>	<b>16</b>	<b>7</b>	<b>1</b>	<b>9</b>	<b>54</b>
<b>Microalgae</b>										
Turf formers	1	30	9	4	5	5	1	1	1	1
<b>Nongeniculate corallines</b>										
<i>Lithophyllum</i> spp.			1	8		1				
<i>Porolithon</i> spp.				17		25				
<i>Other crustose corallines</i>	1	42	29		90		5	1	19	1
<b>Totals</b>	<b>1</b>	<b>42</b>	<b>30</b>	<b>25</b>	<b>90</b>	<b>26</b>	<b>5</b>	<b>1</b>	<b>19</b>	<b>1</b>
<b>Hermatypic corals</b>										
<i>Acropora</i> spp.							30			
<i>Millepora</i> spp.	1									
<i>Pocillopora</i> spp.			2							
<i>Porites</i> spp.						7		41		
<i>Octocorals</i>			5					20	1	
<i>Other hermatypic corals</i>	10	2	7	1	42	25	20	22	55	1
<b>Totals</b>	<b>11</b>	<b>2</b>	<b>14</b>	<b>1</b>	<b>42</b>	<b>32</b>	<b>50</b>	<b>83</b>	<b>56</b>	<b>1</b>

**Table 2.** Environmental features of the 10 island systems studied

Study areas	Seawater nutrients ( $\mu\text{M}$ )				Herbivorous fish abundances	Nutrient sources
	N-NO <sub>2</sub>	N-NO <sub>3</sub>	N-NH <sub>4</sub>	P-PO <sub>4</sub>		
High granitic islands						
Cerf Island (near Mahe)	0.00	0.63	0.66	0.12	Low	Victoria Harbor
La Digue Island	0.00	0.78	0.20	0.14	Moderate	Terrestrial runoff
Mahe Island	0.08	0.20	0.49	0.22	Low	Anthropogenic and terrestrial runoff
Praslin Island	0.15	0.14	6.50	0.00	Low	Anthropogenic and terrestrial runoff
Means	0.06	0.44	1.96	0.12		
Low carbonate islands						
African Banks, Amirantes Group	0.06	0.37	0.00	0.00	Moderate	None
Astove Atoll	0.00	0.50	0.85	0.00	High	None
Desroches Island, Amirantes Group	0.00	0.24	0.00	0.08	High	None
Grand Island, Cosmoledo Group	0.00	0.63	0.20	0.00	High	None
Saint Joseph Atoll, Amirantes Group	0.00	0.44	0.20	0.11	High	None
Means	0.01	0.44	0.25	0.04		
Carbonate island with guano						
Ile Pagode, Cosmoledo Group	0.24	3.34	1.90	0.50	Low	Bird Guano

fishes were much larger on low islands and, in this regard, we observed mostly juvenile (under 30 cm long) parrotfish and surgeonfish being sold in the open-air-markets of the capital (Victoria, Mahe).

#### Photosynthetic assays

All of the macrophytes from high granitic islands (Table 3, Figs. 3 and 4) except one exhibited either photosynthetic inhibition (1 species),  $P < 0.05$ ,  $t$ -test, or showed no effect (7 species,  $P > 0.05$ ) following pulses of either N, P, or N+P relative to the controls. In accordance with our predictions that high granitic islands would be relatively nutrient rich, photosynthesis in *Gracilaria crassa* from Mahe was significantly inhibited ( $P < 0.05$ ,  $t$ -test) by N, P, and N+P relative to the controls (Fig. 3 A), whereas *Lobophora variegata* (Fig. 3 B) showed no significant changes due to nutrient enrichment. Similarly, *Microdictyon montagne* (Fig. 3 C), *Caulerpa cupressoides* (Fig. 3 D), and the seagrass *Thalassodendron ciliata* (Fig. 3 E) from Cerf Island and *Avrainvillea* sp. (Fig. 3 F), *Halimeda macroloba* (Fig. 3 G), and *L. variegata* (Fig. 3 H) from Praslin Island showed no significant effects ( $P > 0.05$ ,  $t$ -test) of nutrients on photosynthetic rate. The only exception to our prediction was *Halymenia* sp. (Fig. 3 I) from the relatively unpopulated high island La Digue, which showed photosynthetic enhancement by P ( $P < 0.05$ ,  $t$ -test).

In marked contrast, all 12 of the macrophytes from low carbonate atolls demonstrated significant ( $P < 0.05$ ,  $t$ -test) photosynthetic enhancement following nutrient pulses (Table 3): 7 following N, 10 with P added and 6 due to N+P pulses. From Astove Atoll, *Rhipilia* sp. (Fig. 4 A) showed P enhancement of photosynthesis ( $P < 0.05$ ,  $t$ -test). Isle Desroches macroalgae gave mixed responses ( $P < 0.05$ ), with N enhancement and P inhibition (but stimulation by both) in *Rhipilia orientalis*

**Table 3.** Stimulating (+), inhibitory (−), or no (0) effects of phosphorus (P) and nitrogen (N) enrichment on photosynthesis of dominant algal species from high granitic islands and low coralline atoll (all + and − responses significant at  $P < 0.05$ ,  $t$ -test)

Habitat	Species	N	P	N+P
High granitic islands				
Mahe	<i>Gracilaria crassa</i>	−	−	−
	<i>Lobophora variegata</i>	0	0	0
Cerf	<i>Microdictyon montagne</i>	0	0	0
	<i>Caulerpa cupressoides</i>	0	0	0
	<i>Thalassodendron ciliata</i>	0	0	0
Praslin	<i>Avrainvillea</i> sp.	0	0	0
	<i>Halimeda macroloba</i>	0	0	0
	<i>Lobophora variegata</i>	0	0	0
La Digue	<i>Halymenia</i> sp.	0	+	0
Low carbonate islands				
Astove	<i>Rhipilia</i> sp.	0	+	0
	<i>Caulerpa</i> sp.	0	+	0
Desroches	<i>Rhipilia orientalis</i>	+	−	+
	<i>Halimeda micronesica</i>	0	+	0
	<i>Halimeda opuntia</i>	+	0	0
Saint Joseph	<i>Udotea orientalis</i>	+	+	+
	<i>Codium</i> sp.	+	+	+
	<i>Avrainvillea</i> sp.	+	+	+
	<i>Udotea argentea</i>	+	+	+
	<i>Udotea palmata</i>	+	+	+
	<i>Udotea</i> sp.	0	+	0
	<i>Halimeda micronesica</i>	0	+	0
Carbonate island with Guano				
Pagode	<i>Dictyosphaeria cavernosa</i>	−	−	−

(Fig. 4 B), P enhancement in *Halimeda micronesica* (Fig. 4 C), and N stimulation in *H. opuntia* (Fig. 4 D). From Saint Joseph Atoll, *Udotea* sp. (Fig. 4 E) and *H. micronesica* (Fig. 4 F) had P enhancement ( $P < 0.05$ ). Stimulation by P, N, and N+P ( $P < 0.05$ ) was shown for *U. orientalis* (Fig. 4 G), *Codium* sp. (Fig. 4 H), *Avrainvillea*

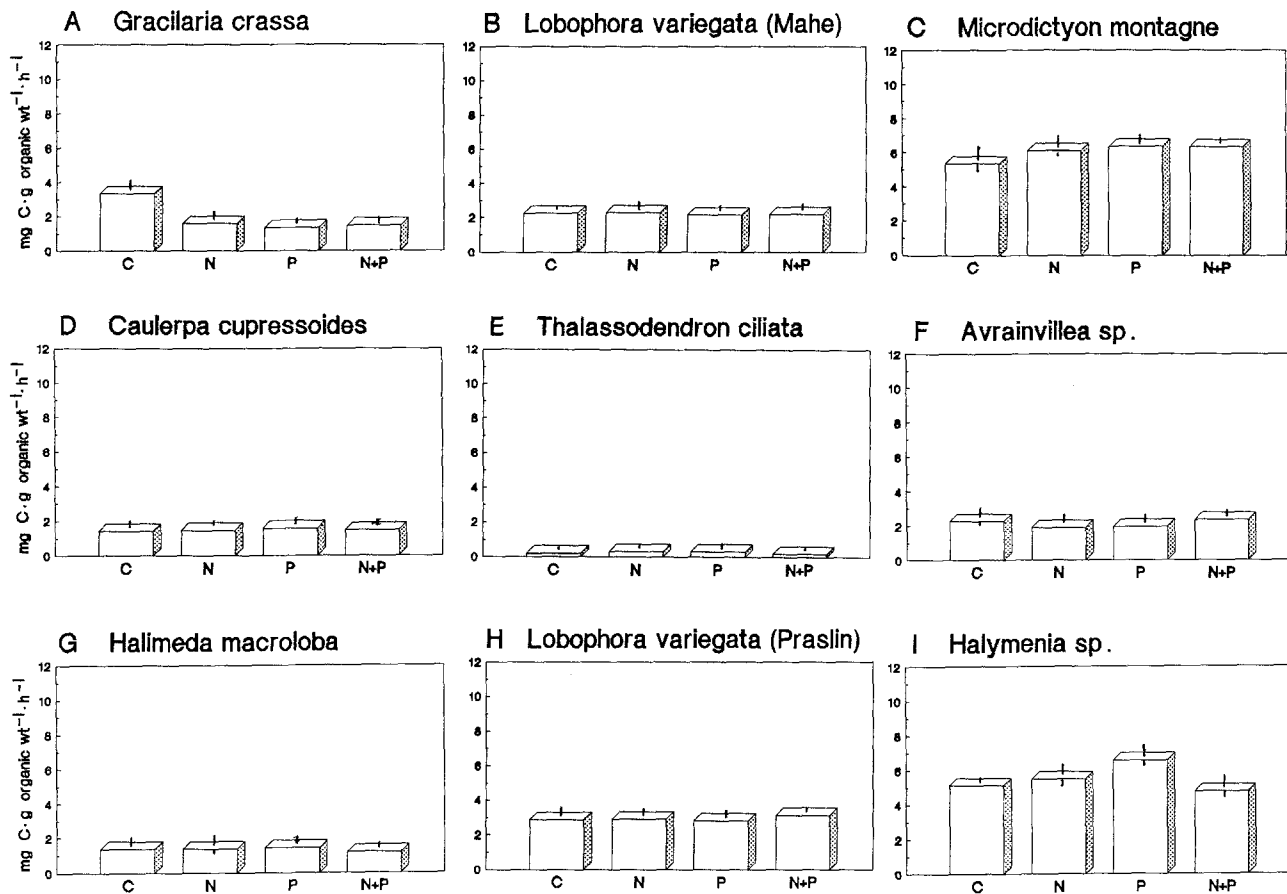


Fig. 3. Responses in apparent photosynthetic rates for macroalgae from high granitic islands following nutrient pulses. Standard deviations are shown by the vertical lines. Statistically significant differ-

ences ( $P < 0.05$ ,  $t$ -test,  $n = 10$  to  $12$ ) from control rates are indicated by + and - signs in Table 3

sp. (Fig. 4I), *U. argentea* (Fig. 4J), and *U. palmata* (Fig. 4K).

Conversely, significant ( $P < 0.05$ ,  $t$ -test) inhibition occurred under all three nutrient-pulse conditions in *Dictyosphaeria cavernosa* (Fig. 4L, Table 3) from Pagode Island in the Cosmoledo Group, a low island habitat dominated by colonies of nesting sea birds and influenced by their substantial guano deposits.

In the case of both P- and N+P-pulsed samples, in accordance with the prediction, the mean net photosynthetic rates did not differ significantly ( $P > 0.05$ , type III SOS, Bonferroni analysis) between the high granitic islands and the guano enriched low island; however, mean P- and N+P-pulsed rates were significantly different ( $P < 0.05$ ) between high islands and low islands, as well as low islands and the guano-enriched island. The mean net photosynthetic rates for macroalgal samples pulsed with N were significantly different ( $P < 0.05$ , type III SOS, Bonferroni) only between high granitic islands and low carbonate atolls, while N-pulsed samples from the guano-enriched island did not differ significantly ( $P > 0.05$ ) between those from either high or low islands. The mean net photosynthetic rates for the control macrophyte samples from high granitic islands collectively did not differ significantly ( $P > 0.05$ ) from those of the low

carbonate atolls, whereas the rate for the guano enriched dominant was significantly greater ( $P < 0.05$ ) than the mean rates for either granitic islands or carbonate atolls.

#### Tissue nutrients

Because the same species, except in the case of *Avrainvillea* sp., did not dominate both high and low island study sites, a spectrum of different algal species was used for the tissue analyses. Consequently, we do not believe that the different algal morphologies, in light of the published variations in nutrient content of different algal species, would allow rigorous statistical comparisons between the three island groups. However, the trends for means are suggestive of overall higher N and P patterns for granitic and guano-enriched islands and are presented as such. For example, the mean percentage total N · thallus by dry weight<sup>-1</sup> for the macrophytes we sampled from the high granitic islands (1.477%, Table 4) was more than double that (0.632%) for the carbonate islands. In the case of percent of P · dry weight<sup>-1</sup> (Table 4), the mean value for granitic island species that we analyzed (0.141%) was almost triple that for those species sampled from low carbonate islands (0.052%). This pattern is borne out for the

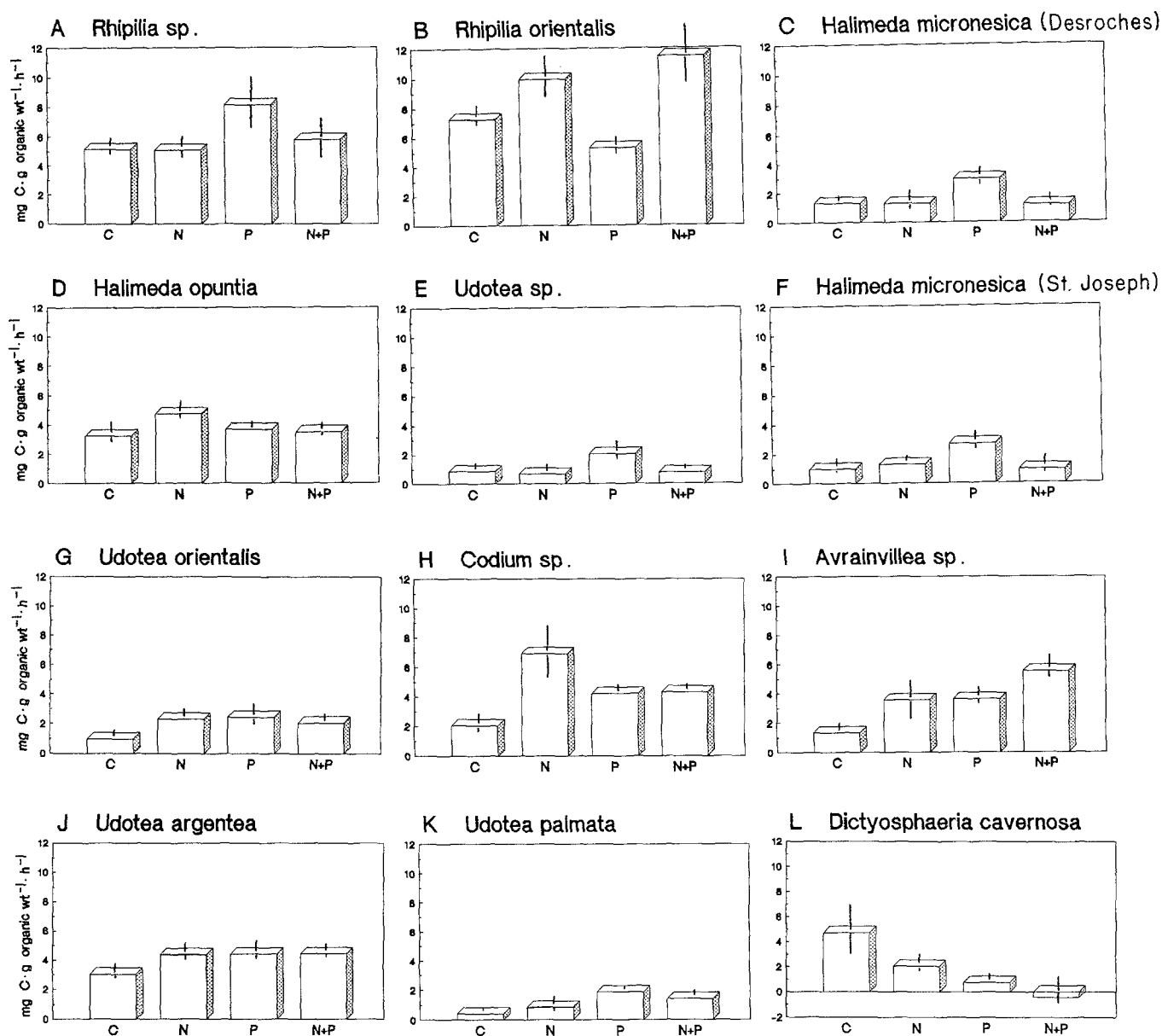


Fig. 4. Responses in apparent photosynthetic rates for macroalgae from low carbonate islands following nutrient pulses. Features are the same as those indicated in Fig. 3

only predominant species (i.e., *Avrainvillea* sp.) found at a high-island site (Praslin) as well as at a low-island site (Saint Joseph), where both N and P levels were significantly elevated ( $P < 0.05$ , Bonferroni analysis) at the former. The dominant alga from the guano-enriched Pagode Island, *Dictyosphaeria cavernosa*, had double the mean P and total N content of the macrophytes sampled from the other low carbonate islands. Mean N and P levels in tissue samples from the high island macrophytes were comparable to values for the dominant macrophyte of the guano-enriched low island.

#### Seawater nutrients

Seawater nutrient samples were ancillary because of lack of shipboard resources and, due to lack of replication,

can only be used to suggest tendencies circumstantial to the questions posed. However, the differences in mean values for the 40 separate analyses between granitic and carbonate islands may be indicative of a general trend (Table 2). For example, the mean concentration of  $\text{PO}_4 - \text{P}$  in our samples for high granitic islands (Table 2) was triple that for low calcareous atolls. The highest value  $\text{PO}_4 - \text{P}$  (12.5 times the mean for the other low islands) was recorded (Table 2) for the atoll island with extensive seabird colonies, Pagode Island of the Cosmoledo Group. The  $\text{NO}_3 - \text{N}$  values that we obtained were about equal between granitic and carbonate islands, whereas  $\text{NH}_4 - \text{N}$  and  $\text{NO}_2 - \text{N}$  were considerably elevated in granitic vs. carbonate islands. The seawater sample from Pagode Island also was by far the most N-rich (7.8 times the mean total N value for other low islands).

**Table 4.** Tissue nutrient levels (percent dry weight  $\pm$  standard deviation, N=4) from granitic islands and carbonate atolls. Where SD<sub>x</sub> is missing, only one sample was run

	Total N (%)	Total P (%)
<b>Granitic Island Species</b>		
<i>Avrainvillea</i> sp. (Praslin)	3.263 $\pm$ 0.731	0.107 $\pm$ 0.011
<i>Caulerpa cupressoides</i> (Cerf)	1.595 $\pm$ 0.771	0.159 $\pm$ 0.020
<i>Gracilaria crassa</i> (Mahe)	1.140	0.126
<i>Gracilaria multifurcata</i> (Mahe)	1.478 $\pm$ 0.417	0.230 $\pm$ 0.033
<i>Halymenia</i> sp. (La Digue)	0.893 $\pm$ 0.092	0.144 $\pm$ 0.023
<i>Lobophora variegata</i> (Mahe)	1.362 $\pm$ 0.402	0.109 $\pm$ 0.015
<i>Lobophora variegata</i> (Praslin)	1.325 $\pm$ 0.054	0.090 $\pm$ 0.007
<i>Thalassodendron ciliata</i> (Cerf)	0.760 $\pm$ 0.013	0.165 $\pm$ 0.045
Means	1.477	0.141
<b>Carbonate Island Species</b>		
<i>Avrainvillea</i> sp. (Saint Joseph)	1.243 $\pm$ 0.226	0.089 $\pm$ 0.007
<i>Caulerpa</i> sp. (Astove)	0.645 $\pm$ 0.068	0.080 $\pm$ 0.015
<i>Codium</i> sp. (Saint Joseph)	0.938 $\pm$ 0.095	0.069 $\pm$ 0.005
<i>Halimeda micronesica</i> (Desroches)	0.553 $\pm$ 0.252	0.031 $\pm$ 0.002
<i>Halimeda micronesica</i> deep (Desroches)	0.323 $\pm$ 0.057	0.034 $\pm$ 0.004
<i>Halimeda micronesica</i> (Saint Joseph)	0.414 $\pm$ 0.035	0.029 $\pm$ 0.003
<i>Halimeda tuna</i> (Desroches)	0.315 $\pm$ 0.041	0.029 $\pm$ 0.002
<i>Halimeda opuntia</i> (Desroches)	0.258 $\pm$ 0.068	0.027 $\pm$ 0.006
<i>Halimeda stuposa</i> (Desroches)	0.488 $\pm$ 0.044	0.027 $\pm$ 0.002
<i>Udotea argentea</i> (Saint Joseph)	0.755 $\pm$ 0.146	0.064 $\pm$ 0.013
<i>Udotea orientalis</i> (Saint Joseph)	0.865 $\pm$ 0.090	0.066 $\pm$ 0.008
<i>Udotea palmata</i> (Saint Joseph)	0.783 $\pm$ 0.111	0.079 $\pm$ 0.007
Means	0.632	0.052
<b>Carbonate Island with Guano</b>		
<i>Dictyosphaeria cavernosa</i> (Pagode)	1.472 $\pm$ 0.193	0.109 $\pm$ 0.007

## Discussion

In general, our data are consistent with the relative dominance paradigm (Fig. 1), with site-specific exceptions. Frondose macroalgae and hermatypic coral stocks (Table 1) proved to be the best indicators of nutrient and herbivore status and showed significant ( $P < 0.05$ , type III SOS, Bonferroni analysis) inverse responses correlated with island type. Macroalgae provide a greater biomass (Mshigeni et al. 1986) and cover (Table 1) than corals on the high granitic island groups. Macrophytes also are more conspicuously species rich (36% greater) on high islands (mean = 147 taxa) than on the carbonate atolls (mean = 94 taxa) studied here (Kalugina-Gutnik et al. in press). Throughout both monsoonal seasons, it has been noted (Mshigeni et al. 1986) that the various shorelines of Mahe, Praslin, Cerf, and La Digue Islands have "relatively rich marine algal floras and support huge populations of attached seaweeds, particularly *Sargassum*, *Turbinaria*, and *Gracilaria*".

We posit that the reasons for such macroalgal domination could be twofold. First, the granitic islands contain larger human populations (Benedict 1984) and fish

trapping is much more extensive (personal observations), thus depleting the nearshore herbivorous fish populations (Table 2, particularly parrotfishes and surgeonfishes which also tend to be subadults, personal observations). Secondly, the granitic islands contain steeply elevated slopes that promote adiabatic cooling of warm moist air, which increases rainfall (Walsh 1984), supporting densely vegetated ecosystems (Proctor 1984) with concomitant terrestrial runoff. Terrestrial runoff in large quantities would probably inhibit coral growth (Hallock and Schlager 1986) yet provide critical nutrients essential for the predominant macroalgae such as the large brown algal genera *Sargassum*, *Turbinaria*, and *Lobophora*. *Sargassum* in turn, contributes much of the year-round community biomass and three-dimensional structure promoting the establishment of a diversity of epiphytic and understory macrophytes (Mshigeni et al. 1986). On low atoll islands, we observed no *Sargassum*; despite hundreds of person hours of searching, none was located on Desroches, African Banks, St. Joseph Atoll, Cosmoledo Group, Astove Atoll, and Coetivy during the period from 26 February to 12 March 1989. Conversely, all of the high granitic island sites examined (Praslin, Mahe, Cerf, and La Digue) contain dominant communities of *Sargassum* on the shallow reef flats where herbivorous fish populations are reduced. This agrees with the observations of Doty (1973) who was the first to point out that *Sargassum* in the tropical Pacific is typically absent from pristine low carbonate atolls and appears to be present around all high volcanic islands, attributed to some unknown water quality parameter(s). High volcanic islands in the Caribbean, such as Martinique (Adey et al. 1977; personal observations) and the wave-dashed north-east coast of Curaçao (Wanders 1976), likewise are characterized by remarkably dense stands of *Sargassum* and other macroalgae. Low carbonate barrier reef islands off mainland coasts can also develop patches of abundant *Sargassum*, but these tend to be localized exceptions (personal observations). The green algal genus *Ulva*, which is also common to abundant on high granitic islands, was not found by us on carbonate atolls, although the related genus *Enteromorpha* was found (but rare).

For the most part, macroalgal stocks and diversity are higher on all island types where refuges from herbivorous fishes exist. Such refuges include: (1) shallow areas with high wave energy that inhibit efficient feeding, (2) vertical reef faces that are dominated by large pelagic and benthic carnivorous fishes (e.g., Cosmoledo Group and Astove Atoll), and (3) regions lacking spatial heterogeneity, and thus shelter from predation for herbivorous fishes, such as found in deeper waters (below 35 m) on most islands. The greatest biomass and species richness of algae on any of the low atoll sites is in the Gueule Bras Channel of the guano-containing Astove Atoll, a high-nutrient shallow habitat that drains the lagoon. The waters off the bird colonies on Pagode Island, Cosmoledo Group are dominated by the green alga *Dictyosphaeria cavernosa* (40% cover), a widespread species of considerable notoriety that has been documented throughout Kaneohe Bay, Hawaii (Banner 1974; Smith et al. 1981) to overgrow and kill corals under elevated nutrient conditions.



Our bioassay data show multiple examples of both P and/or N limitation (significant at  $P < 0.05$ ,  $t$ -test, Table 3) in the carbonate-rich atoll environments in support of our hypothesis. In the case of both P- and N+P-pulsed samples, the mean net photosynthetic rates did not differ significantly ( $P > 0.05$ , type III SOS, Bonferroni analysis) between the high granitic islands and the guano-enriched low island; however, mean P- and N+P-pulsed rates were significantly different ( $P < 0.05$ ) between high islands and low islands, as well as low islands and the guano-enriched island. Seawater  $\text{PO}_4 - \text{P}$  data in conjunction with total inorganic N values, although very limited, are consistent with our prediction that non-calcareous high granitic islands should be richer in dissolved macronutrients than low carbonate islands. For example, the seawater nutrient data are indicative of probable elevated  $\text{PO}_4 - \text{P}$  and  $\text{NH}_4 - \text{N}$  concentrations on granitic islands. This apparent difference, hypothetically, is due to the increased rainfall and concomitant accumulation of organic matter and its subsequent decomposition releasing inorganic nutrients near high islands. Crossland (1983) has also pointed out the nutrient differences between low oceanic islands and high islands due to possible input variables such as ground water (Marsh 1977) and surface run-off (Wade 1976) in high islands. For example, nutrient levels in waters surrounding Lizard Island, a moated high island, are somewhat greater than those associated with tropical low reefs (Crossland 1983). Also, there are some minor anthropogenic nutrient sources from sewage and agriculture on the granitic islands of the Seychelles (see Stoddart 1984b), although the human population in the Republic is quite low. Benedict (1984) notes that 98% of the 62 000 people (1977 census) live on Mahe (88%), Praslin (7%), and La Digue (3%). The overall result is that sediments from the high rain-forested islands contain relatively abundant organic components, compared to the carbonate sediments derived from calcareous marine plants and corals, which results in a greater mass of potential nutrients for regeneration. Littler (1976) predicted a similar tendency of algal domination over corals would be shown for older rain-forested vs. geologically younger volcanic islands and we agree, since the critical factor would seem to be organically derived nutrients and not substrate type in the case of non-calcareous materials such as basalt or granite.

Levels of N and P in macroalgal tissues are thought to be indicative of general nutrient limitation (e.g., Lapointe 1987; Lapointe et al. 1987), but also vary among taxonomic groups (Niell 1976; Fagineli et al. 1986; Lapointe 1989b) and time of year (Chapman and Craigie 1977; Kornfeldt 1982; Lapointe 1987). Nevertheless, the overall tendencies for mean macroalgal tissue levels of both N and P to be substantially greater for high granitic islands in comparison with low carbonate atolls (more than two-fold) were not overshadowed by taxonomic and site-specific sources of variation (although unquestionably present, Table 4). *Avrainvillea* sp., the only species common to both a high- and low-island site, showed significantly elevated N and P levels at the high island site ( $P < 0.05$ , Bonferroni analysis). As expected, the guano-enriched dominant macroalga from Pagode Island represents an

exception among the carbonate islands with values of total N and P intermediate between the means for the other low islands and the high islands. Therefore, we conclude that the nutrient-limitation bioassays (Table 3, Figs. 3 and 4) provide considerable support for the hypothesis that macroalgal stocks should be relatively more limited by macronutrients on low carbonate islands, with the data for tissue analyses (Table 4) and the seawater nutrient analyses (Table 2) lending further circumstantial support.

The multiple tests of the hypothesis that P-limitation should be more pronounced than N-limitation in carbonate systems, for the most part, also tended to be supportive. Nitrogen traditionally has been considered to be the macronutrient that most limits productivity in tropical marine waters (e.g., Parsons et al. 1977). Conversely, geochemical evidence (Broecker and Peng 1982; Smith 1984; Lapointe et al. in press) and more-recent in situ macrophyte bioassays (Lapointe 1985; 1987; Littler et al. 1986; Short et al. 1989) implicate P as the more important growth limiting nutrient on well-oxygenated carbonate-rich tropical reefs. Our limited seawater nutrient samples generated N:P ratios of 20:1 and 18:1 for granitic and carbonate islands, respectively, which are above the Redfield ratio of 16:1 and consistent with P-limitation. The fact that both mean P- and N+P-pulsed photosynthetic rates were significantly different ( $P < 0.05$ , type III SOS, Bonferroni analysis) between high islands and low islands, as well as between low islands and the guano-enriched islands, and the observation that P- and N+P-pulsed rates did not differ significantly ( $P > 0.05$ ) between high islands and the guano-enriched island, also supports the hypothesis. The mean net photosynthetic rates for macroalgal samples pulsed with N were significantly different ( $P < 0.05$ ) only between high granitic islands and low carbonate atolls, while N-pulsed samples from the guano-enriched island did not differ significantly ( $P > 0.05$ ) between those from either high or low islands. The individual photosynthetic assays indicated only a slight tendency (significant at  $P < 0.05$ ) toward P-limitation as shown in more cases (10 species) than N-limitation (7 species) in the macroalgae from low calcareous islands (Table 3).

The somewhat higher mean tissue N:P ratio for the carbonate atolls (mean molar ratio of 27:1, Table 4) provides additional evidence of relatively greater P-limitation compared to that for granitic islands (23:1 molar ratio). Low N:P ratios such as found for *Cladophora glomerata* in the northern Baltic (mean of 20:1, Wallentinus 1976) correspond with the known (Graneli 1978) N-limitation in that system. In contrast, elevated N:P ratios (29:1) suggest (Sander and Moore 1979) that P, rather than N, is the major limiting nutrient to phytoplankton productivity in the carbonate-dominated waters off Barbados. Exceptionally high N:P ratios averaging 47:1 were found (Short et al. 1985) in the tissues of the seagrass *Syringodium filiforme* attached in low-island carbonate sediments; subsequent enrichment experiments (Short et al. 1989) confirmed P-limitation in this plant. The mean N:P ratio of 92 benthic marine plants from five phyla and nine locations worldwide (Atkinson and

Smith 1983) averaged about 35:1, strongly implicating P as the most frequent major limiting nutrient.

This study is the first to show that geologically different tropical reef systems (i.e., carbonate vs. granitic) have contrasting patterns of biotic cover and photosynthetic nutrient limitation. Also, observations of herbivorous fish populations and trapping activities, while unquantified, are not counter to the relative-dominance paradigm. Productivity-nutrient enrichment assays in Belize (Lapointe et al. 1987), the Bahamas (Littler et al. 1988), and the Florida Keys (Littler et al. 1986; Lapointe 1989b; Littler and Littler 1990), and in temperate systems (Lapointe et al. in press) have shown that the degree and type of nutrient limitation in marine macroalgae are usually related to the nutrient regimes of the ecosystems under study, but, as mentioned, can be markedly different among sympatric species as well. While alternative hypotheses, e.g. regarding trace elements, dissolved organic nutrients, or taxonomic specificity, can not be ruled out pending further manipulative experimental approaches; nevertheless, *when overall tendencies are considered*, the differences in Seychelles geochemical environments (and antecedent nutrient histories) appear substantial enough on a geological scale to not be obscured by meso- and micro-scale spatial and species-specific variability. The combination of biological surveys and nutrient-limitation assay data, (in conjunction with the more limited tissue N and P composition and seawater analyses) suggest marked tendencies between island groups of the Seychelles Archipelago that are likely to be applicable to other geochemically distinct ecosystems.

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