

Modification of Tropical Reef Community Structure Due to Cultural Eutrophication: the Southwest Coast of Martinique

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Abstract. This study employed multifaceted techniques, including quantitative transects, nutrient-enrichment productivity experiments and alkaline phosphatase bioassays. These were conducted, in conjunction with water-column nutrient analyses, during May 1989 at a series of stations located at various distances from the large metropolitan area of Fort de France on the southwest coast of Martinique. Macroalgae were more dominant while species diversity decreased markedly as a function of nearness to the city, with coral-dominated systems giving way to *Sargassum*-dominated communities that in turn were epiphytized by the opportunistic chlorophyte *Enteromorpha chaetomorphoides*. Changes in standing stocks, photosynthetic nutrient-limitation responses, alkaline phosphatase activities and water-column nutrient patterns were indicative of widespread cultural eutrophication processes that parallel those occurring naturally on more localized scales.

Introduction

During an expedition in 1987 aboard the *R/V Columbus Islen* to study the coral/algal communities of southern Martinique, communities of large macroalgae were observed overgrowing pale, slightly eroded, dead skeletal remains of corals, which

formed the predominant substrata mainly to the south, but also slightly to the north, of Fort de France. This raised questions as to the possible causes of the obvious recent shift in these ecosystems from coral to algal domination. Because we had been developing a relative-dominance model (Littler and Littler 1984) that has potential to explain such changes, a subsequent expedition (May 1989) was focused on addressing possible causes of the shift.

The relative dominance of sessile photosynthetic organisms such as frondose macroalgae, crustose coralline algae, turf forming algae and corals has been predicted (see Fig. 1 of Littler and Littler 1984) 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 such as nutrient levels, wave action, sedimentation, irradiance, desiccation and temperature. Grazing is considered the more important direct controller of algal standing stocks on undisturbed reefs (Littler and Littler 1988), 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 (Littler et al. 1991a). Prior to our study, Bouchon and Laborel (1986) and Bouchon et al. (1987) pointed strongly to the degradation of Martinique reefs (see also Rogers 1985) which was attributed to the impacts of domestic sewage and siltation. 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

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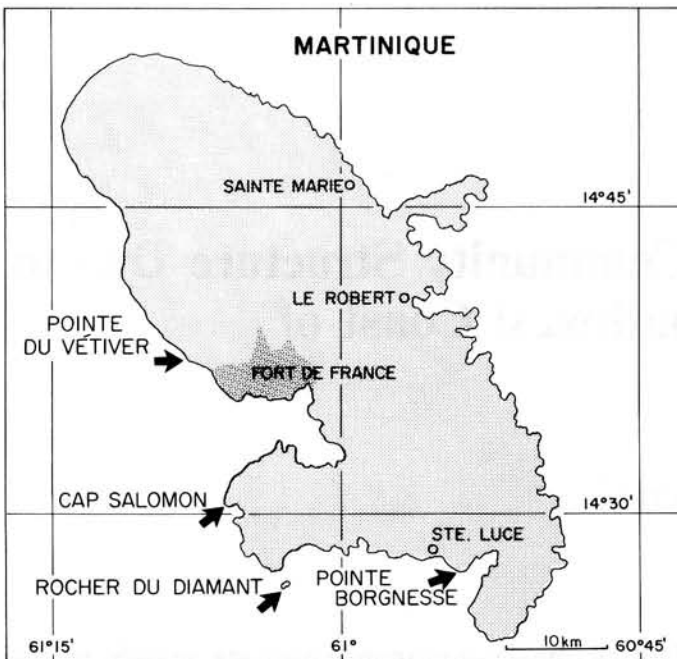


Fig. 1. Map showing the locations (arrows) of the four study areas.

fleshy algal dominance often have been associated with excessive nutrient increases, as in the cases of reefs off Venezuela (Weiss and Goddard 1977), the Florida reef tract (Lapointe 1989a), Kane'ohe Bay, Hawai'i (Banner 1974; Smith et al. 1981) and in the Seychelles Islands (Littler et al. 1991a).

A basic assumption is that increased nutrients from a major sewage source (Fort de France) are correlated with the observed recent alteration from coral- to algal-dominated systems. If so, then this apparent southeastward effect should be reflected by predictable changes in community structure and physiological responses in the presumed downcurrent direction, if the above municipal source is the important supplier of nutrients. The present study incorporated nutrient-enriched productivity and alkaline-phosphatase assays as well as water-column nutrient analyses, in conjunction with quantitative characterizations of the various ecosystems that were investigated. The *a priori* prediction tested was that the dominant macroalgal stocks should tend to be less nutrient limited overall on sites close to Fort de France due to elevated nutrient levels in the ambient seawater and this, in conjunction with the removal of herbivorous fishes by the human populations on Martinique, would tend to favor macroalgal domination over corals. Our findings also were tested with regard to the relative-dominance paradigm (Fig. 1 of Littler and Littler 1984; Littler et al. 1991a) whereby four major space-occupying groups of epilithic sessile photosynthetic organisms (corals, crustose coralline algae, fleshy macroalgae and microfilamentous algae) are pre-

dicted to shift in abundances as a function of changing nutrient histories.

Methods and Materials

Biological Surveys—This research was conducted from the *R/V Cape Hatteras* during an expedition throughout the Antilles from 13–27 May 1989. Four specific study sites, one to the north and three to the south of Fort de France (Fig. 1), were characterized by assessments of the overall biotic cover occupying the primary volcanic substratum. Specific study-site transect locations were preselected on navigational charts without prior specific knowledge of the biotas that would be encountered. Eight transects (two at each study site) at right angles to the shoreline for estimating percent cover were made by video from about 30 m to 4 m in depth using SCUBA and the methods detailed in Littler et al. (1991b). None of the transect areas was atypical, based on reconnaissance dives that extended several hundred meters along the shoreline at each site. Because the question addressed was what is the dominant cover of predominant sessile photosynthetic organisms at each site, it was not necessary to conduct high-resolution species-specific measurements. Instead, replicate video transects shot at right angles to the bottom were assessed to include the predominant populations. The video tapes were scored in stop action at random intervals (12 1.0 m quadrats per replicate transect) using a high-resolution monitor containing a transparent grid of randomized dots. Because wave surge moved upper-story plant life aside, it was possible to assess the underlying substrata. 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.

Physiological Assays—The productivity ($N=9$ per treatment per species) and alkaline phosphatase ($N=4$) assays focused on *Sargassum filipendula* and *Enteromorpha chaetomorphoides* (collected in full sunlight at 4 m) from 4 sites and were conducted during the period from 19–24 May 1989. Plants were incubated at saturating light levels (P_{max} , determined by PI curves) under four nutrient conditions, consisting of either +N ($NaNO_3$), +SRP (= soluble reactive phosphorus, NaH_2PO_4), both N+SRP or a control (no enrichment). Initial concentrations of N and SRP in the enrichment media were 160 and 16 μM , respectively. The concentrations were chosen in an attempt to saturate (Lapointe 1985) the uptake rates in the small vol-

umes used during nutrient pulsing (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 (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 demonstrates 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).

Sargassum filipendula from three sites was assayed for alkaline phosphatase activity both before and after pulsing with 16 μM SRP by the spectrophotometric method of Kuenzler and Parras (1965). The assays utilized about 3.0 g wet wt algae, 15 ml nitrophenyl phosphate (NPP) stock (1.0 g NPP substrate and 25.0 g MgSO_4 dissolved in 500 ml deionized water), 30 ml of Tris buffer and filtered seawater to make 500 ml of assay medium. Acid washed, 1.0-liter Wheaton wide-mouth glass bottles that received constant stirring via seawater-driven magnetic stirrers were used for the assay. A decrease in activity of the enzyme following spiking with SRP indicates that the nutrient is in short supply.

For all photosynthesis measurements that followed the 12-h nutrient enrichment period, 9 independent replicate thalli per species (per site) were incubated under each nutrient treatment in 1.0-liter glass jars at ambient water temperatures (28.2–29.4° C) under continuous cooling by a flow of 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 3000 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Light conditions did not vary from day to day and cloudy days were avoided for photosynthetic bioassays.

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 net carbon fixed utilizing

a photosynthetic quotient of 1.00 to facilitate comparisons. Photosynthesis was normalized to organic dry weight, which was determined by drying the samples to constant weight at 70° C and ashing them to constant weight at 500° C. The methods concerning selection of materials, handling, incubation and oxygen analysis were within the limits recommended by Littler (1979).

Water-Column Analyses—Time did not permit an exhaustive temporal/spatial study of nutrient variability at each study site. Consequently, only ancillary water-column samples were collected at two of the sites in an attempt to reveal large-scale tendencies between study areas. Nitrite plus nitrate and ammonium concentrations were measured on an Autoanalyzer II according to the methods of Slayk and MacIsaac (1972) and Technicon (1973). Phosphate was determined by the molybdenum blue method as soluble reactive phosphorus (Murphy and Riley 1962) and utilized a Baush and Lomb Spectronic 88 spectrophotometer fitted with a 10-cm cell for maximum sensitivity. Vertical water-column profiles of salinity and temperature from the surface to 50 m also were made on 15 May 1989 off Pointe de Vétiver and Rocher du Diamant to examine possible land-based freshwater inputs.

Because reef habitats are vertically zoned and patchy, one would expect considerable variability within the study areas in terms of the dominant cover organisms, physiological responses and water-column nutrients. Differences in coral and macroalgal percent cover (following arcsine transformation) between environments were analyzed independently by ANOVA (Sokal and Rohlf 1969). The Bonferoni *a posteriori* multiple classification analysis (SAS 1985) was used to identify significant groupings ($P < 0.05$). Statistical comparisons to assess nutrient effects on photosynthesis (P_{max}) and alkaline phosphatase activity were made by comparing each nutrient enrichment treatment to the appropriate controls by one-way ANOVA and *t*-tests to detect significant ($P < 0.05$) inhibitory, stimulatory or no responses to enrichment.

Results

Biological Surveys—Macroalgal cover for the sites to the southeast of Fort de France showed decreasing abundances, with the massive brown alga *Sargassum filipendula* (epiphytized by the large chlorophyte *Enteromorpha chaetomorphoides*) most dominant at sites closest to the city. For example, *S. filipendula* (with 55.9% mean cover, Fig. 2) was significantly ($P < 0.05$) more abundant at Cap Salomon than at the other sites, whereas it was sig-

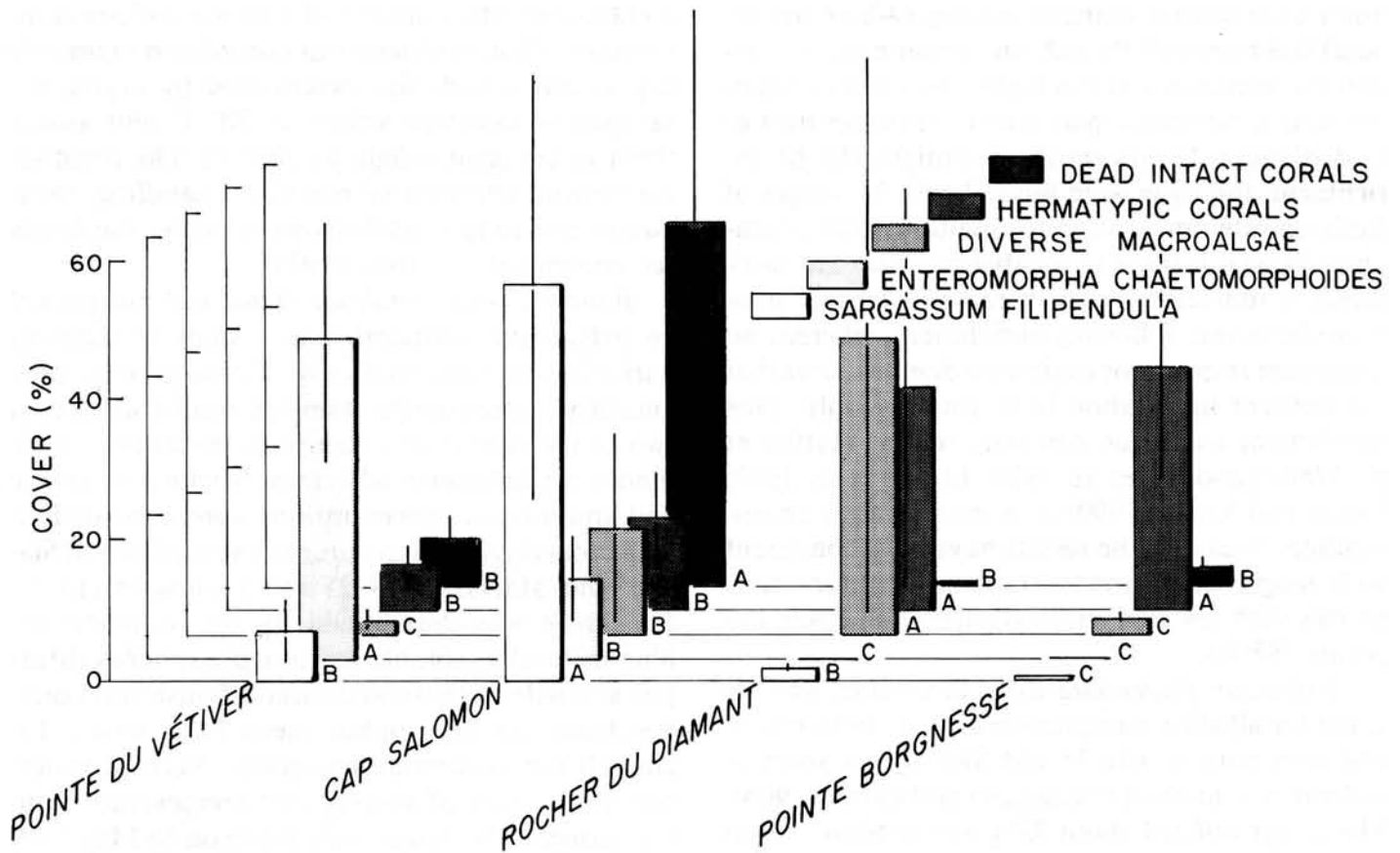


Fig. 2. Overall mean percent cover (vertical lines = ± 1 SD, N=12 quadrats per transect) of dominant taxa from the four study areas. Where letters differ (A,B,C), the means for that taxon are significantly different between study sites ($P < 0.05$, ANOVA using Bonferoni t-test of differences).

nificantly lower ($P < 0.05$) at Pointe Borgnesse (0.1% cover) than at the other sites. Cover of *S. filipendula* at Rocher du Diamant (1.8%) was lower than at Pointe du Vétiver (7.6%), but the difference was not significant ($P > 0.05$). The entangling opportunist *Enteromorpha chaetomorphoides* (Fig. 2), mostly epiphytic on *S. filipendula*, was significantly more abundant ($P < 0.05$) in quadrats just to the north of Fort de France at Pointe du Vétiver (45.0% cover), followed by Cap Salomon (12.1%) with significantly greater cover than at the two most remote sites (where it was absent from the samples). A considerable diversity of other frondose macroalgae (40 species combined) had by far the greatest combined cover at Rocher du Diamant (42.4%, $P < 0.05$) followed by less diverse macroalgal cover at Cap Salomon (15.2%) which was also significantly greater ($P < 0.05$) than at the other two sites.

Hermatypic coral coverages (Fig. 2) at the two most remote sites, Rocher du Diamant (32.9%) and Pointe Borgnesse (34.6%), were significantly greater ($P < 0.05$) than at the two study areas nearest Fort de France. Intact dead colonies of hermatypic corals (pale carbonate skeletons with little erosion) provided significantly more of the secondary substrata at Cap Salomon (51.7% cover) than at the other

three sites (Fig. 2). The variances (SD's) of the overall mean biotic coverages at some of the sites are exaggerated because of marked vertical zonation. For example, at Rocher du Diamant, corals dominated the lower portions (20–30m) of the transects while diverse algal assemblages characterized the upper regions (4–20m).

Photosynthetic Assays—At the site directly to the south of Fort de France (Cap Salomon), the productivity/nutrient bioassay using the biotic dominant (*Sargassum filipendula*) revealed either significant inhibition (N+SRP, $P < 0.05$) or no effect (N, SRP, $P > 0.05$) following pulses of nutrients relative to the controls (Fig. 3). Similarly, a lack of stimulation ($P > 0.05$) of the photosynthetic response by all combinations of nutrients was evident for *Enteromorpha chaetomorphoides* from Cap Salomon (Fig. 3). At the most remote southeastern coastal site (Pointe Borgnesse), *S. filipendula* also showed no photosynthetic stimulation by N alone ($P > 0.05$), however SRP and N+SRP combined resulted in significant ($P < 0.05$) increases in photosynthetic responses (Fig. 3). *Sargassum filipendula* from the offshore Rocher du Diamant (a highly diverse macroalgal community with 40 abundant species) demonstrated the strongest stimulatory re-

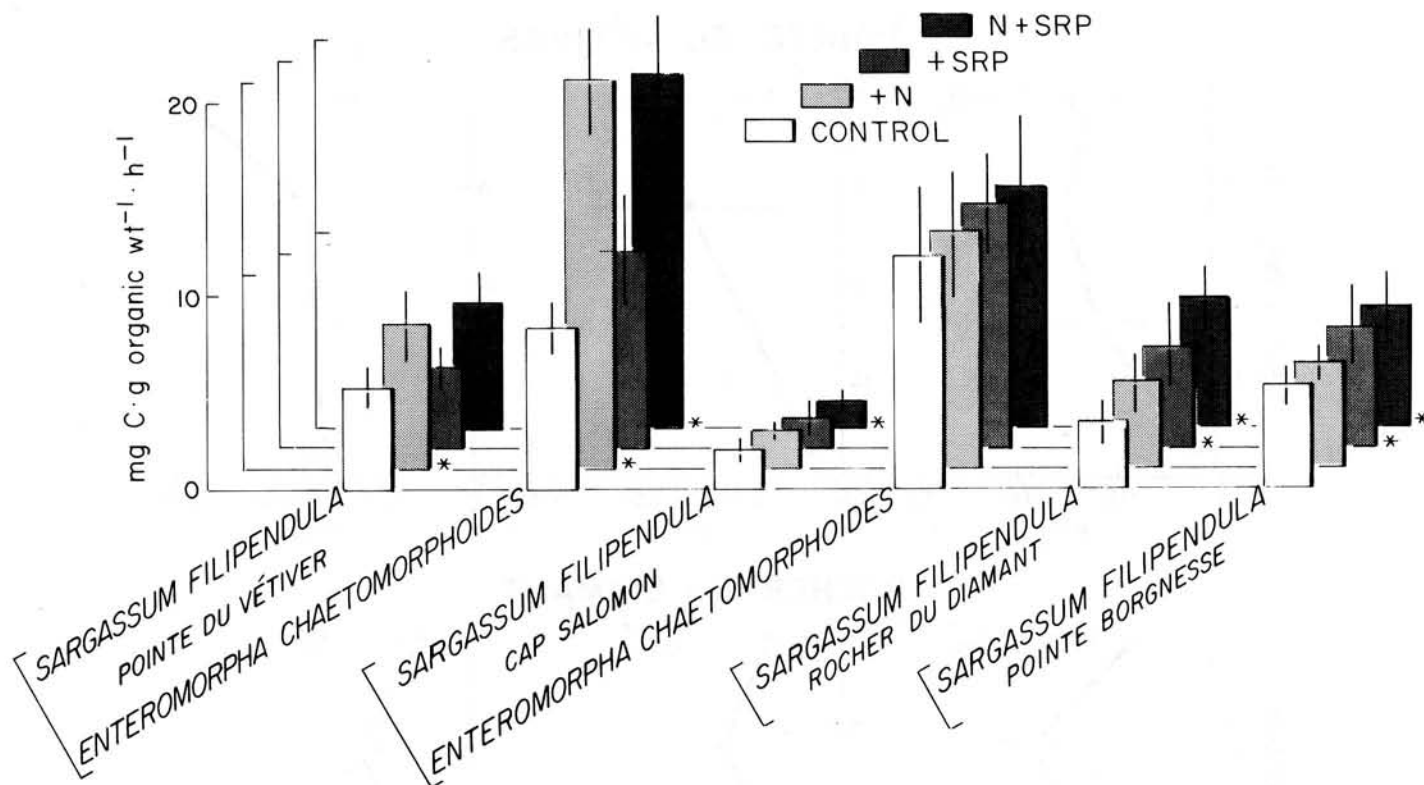


Fig. 3. Responses in apparent net photosynthesis for dominant macroalgae from the four study areas following NO_3^- (N) and soluble reactive phosphorus (SRP) nutrient pulses (vertical lines = ± 1 SD, $N=9$). Statistically significant differences ($P < 0.05$, one-way ANOVA, Bonferroni t-tests) between pulsed and control rates are indicated by asterisks.

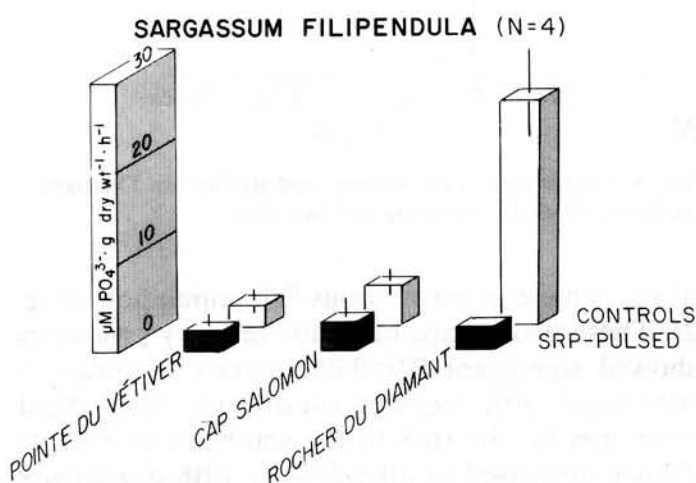


Fig. 4. Responses in alkaline phosphatase activity (vertical lines = ± 1 SD, $N=4$) for *Sargassum filipendula* from three study areas following pulses of soluble reactive phosphorus (SRP). Statistically significant differences (i.e., lower activity, $P < 0.05$, t-test) following pulsed vs control rates occurred only at Rocher du Diamant.

sponse following pulses of SRP as well as marked synergistic responses to N+SRP combined ($P < 0.05$). In contrast, both *S. filipendula* and *E. chaetomorphoides*, from the site just to the north of the sewage source (Pointe du Vétiver), exhibited pronounced photosynthetic stimulation by N alone, with the latter species also showing significant N+SRP stimulation ($P < 0.05$). *Enteromorpha chaetomorphoides*, with a photosynthetic rate of up

to $20 \text{ mg C fixed} \cdot \text{g organic wt}^{-1} \cdot \text{h}^{-1}$, ranks among the highest of marine primary producers.

Alkaline Phosphatase Assays—Significantly greater ($P < 0.05$) alkaline phosphatase activity was present (Fig. 4) in natural populations of *Sargassum filipendula* from Rocher du Diamant than from any of the other sites. However, a dramatic alteration of this pattern resulted following enrichment with SRP (Fig. 4), whereupon no differences ($P > 0.05$) in alkaline phosphatase activity occurred between *S. filipendula* plants at any of the sites. The result of SRP enrichment was to significantly ($P < 0.05$) reduce the high activity shown at Rocher du Diamant, convincingly documenting the dramatic SRP limitation for *S. filipendula* at this site.

Water-Column Analyses—The water-column nutrient profiles (Fig. 5) for Pointe du Vétiver contrasted markedly with those from Rocher du Diamant. The mean value for NO_3^- plus NO_2^- from 0–20 m for the former was $0.53 \mu\text{M}$, while NH_4^+ was $0.31 \mu\text{M}$ and SRP was $0.28 \mu\text{M}$. In comparison, the mean nutrient values for Rocher du Diamant were NO_3^- plus $\text{NO}_2^- = 0.62 \mu\text{M}$ (not significantly different), $\text{NH}_4^+ = 0.22 \mu\text{M}$ and SRP = only $0.10 \mu\text{M}$, which was significantly lower ($P < 0.05$, Fig. 5) than at Pointe du Vétiver. Peak values of all three nutrients occurred at a depth of 6.0 m in Rocher du Diamant samples (Fig. 5), with the difference at Pointe du Vétiver being that the peak values of

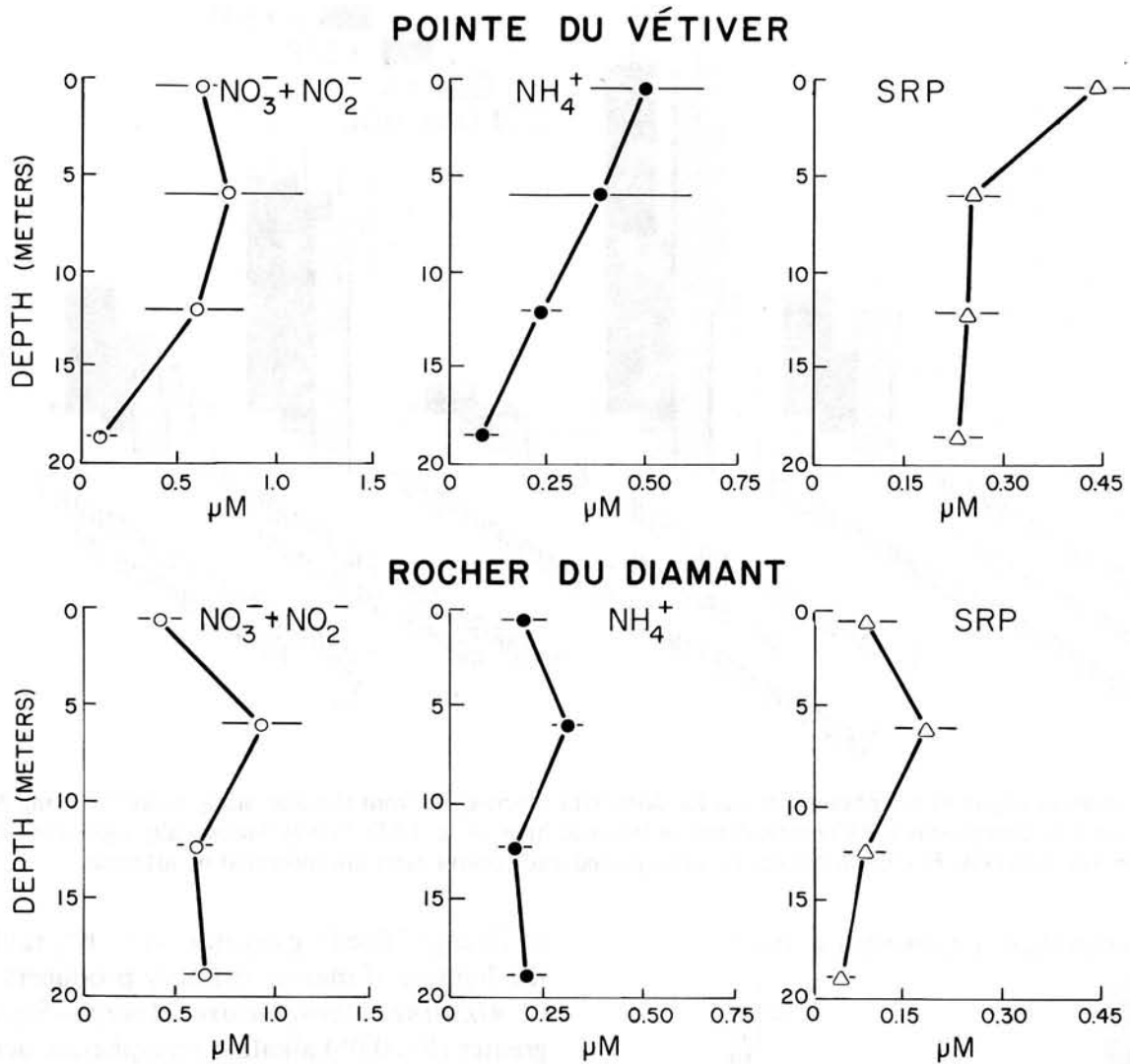


Fig. 5. Water-column nutrient profiles (horizontal lines = ± 1 SD, $N=2$) for Pointe du Vétiver and Rocher du Diamant. Mean soluble reactive phosphorus (SRP) values are significantly different ($P<0.05$) between the two sites.

NH_4^+ and SRP occurred just below the surface. Salinity and temperature profiles at the offshore Rocher du Diamant (Fig. 6) revealed no strong pycnocline, whereas those at Pointe du Vétiver showed a strong pycnocline between 25–30 m indicating a much more pronounced and deeper lens of freshwater influence at this coastal site that extended throughout the zone of study. Although no long-term data on current patterns have been published for the southwest coast of Martinique, we noticed a variable but persistent north to south current movement, which was more pronounced at Rocher du Diamant (0.5 km offshore).

Discussion

The findings are consistently parallel with the tests of the relative dominance paradigm as conducted by Littler et al. (1991a) in the Seychelles Archipelago. Coverages of reef building corals and frondose macroalgae provided the best indices to the status

of nutrients and herbivorous fish populations (Fig. 2). These two groups of sessile primary producers showed significant ($P<0.05$) inverse abundances correlated with nutrient conditions. Macroalgal coverages for the sites to the southeast of Fort de France decreased in abundances, with *Sargassum filipendula* covered by *Enteromorpha chaetomorpha* most dominant at sites closest to the city and highly diverse mixed algal assemblages or hermatypic corals dominant at the study areas most removed (Fig. 2). Sites near the city had primary substrata dominated by pale, slightly eroded, dead, reef-building coral skeletons suggesting recent mortality and subsequent shifts in community structure. Such recent mortality is further documented by the research of Bouchon and Laborel (1986), who only several years prior to the present investigation concluded that the ecological conditions along the southern coast of Martinique supported "abundant coral growth". At that time, the above workers also documented prolific hermatypic coral populations near Fort de France Bay.

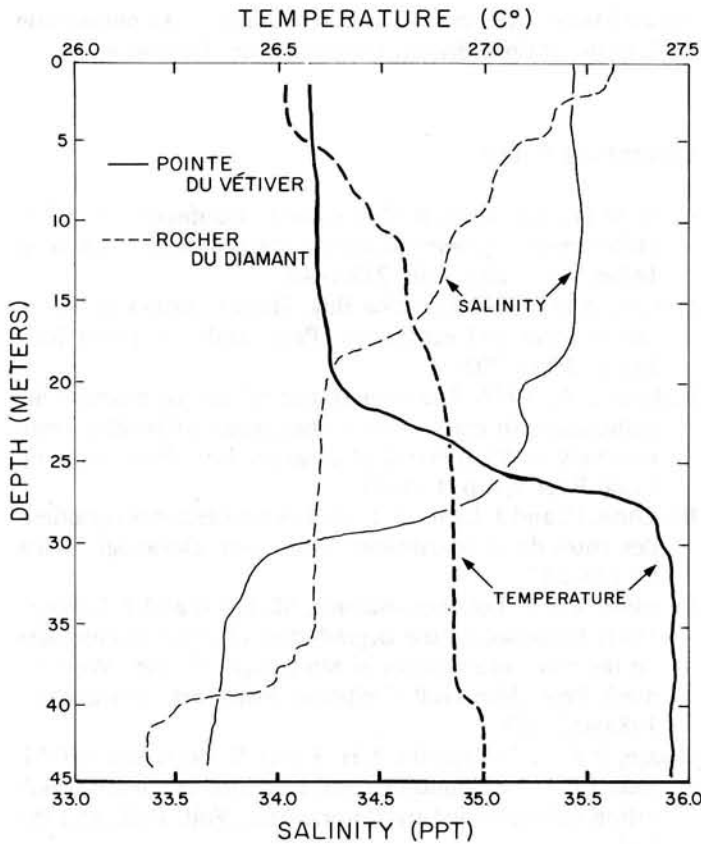


Fig. 6. Water-column profiles of temperature and salinity for Pointe du Vétiver and Rocher du Diamant.

At Pointe du Vétiver to the northwest, somewhat upcurrent from the municipal sewage source, but possibly impacted by the plume due to its close proximity to Fort de France, the community is dominated by both hard and soft corals invaded by scattered thalli of *S. filipendula* and *E. chaetomorpha*. Among the first investigations that attributed shifts from coral toward algal domination on reefs to the impact of urban sewage effluents is the study of Waikiki Reef, Hawai'i by Littler (1973) (cf. Pollock 1928). Others also have noted that tropical island habitats adjacent to urbanized areas support macroalgal communities dominated by populations of the large phaeophyte *Sargassum* [e.g., Hawai'i, Doty (1971); Seychelles Islands, Mshigeni et al. (1986), Littler et al. (1991a)].

We hypothesize that the reasons for the patterns of relative macroalgal domination in proximity to urban population centers could be twofold. The authors repeatedly noted more fish traps at sites closest to Fort de France. Such activity depletes the nearshore herbivorous fish stocks, particularly Scaridae and Acanthuridae, releasing certain macroalgal populations from predation controls (cf. observations in the Seychelles, Littler et al. 1991a). Several studies of tropical Caribbean algae have shown (reviewed in Littler et al. 1989) that ribbon-like ulvallean forms such as *Enteromorpha* and fucallean

forms such as *Sargassum* are highly to moderately palatable, respectively, to herbivorous fishes (see also Macintyre et al. 1987). Secondly, the large volume of sewage effluent, presumably with net movement to the southeast and, consequently, along the gradient of study sites (Fig. 1), would provide critical nutrients to large macroalgae such as *Sargassum* and *Enteromorpha*. Such nutrients increase the community productivity and carrying capacity thus elevating the upper limits for standing stocks of large algae. For example, the primary productivity of *E. chaetomorpha* under N enrichment approached the exceptionally high rate of 20 mg C fixed · g organic wt⁻¹ · h⁻¹, suggesting that the competitive growth potential of this alga poses a major threat to the remaining coastal communities if eutrophication continues to escalate.

Conversely, increased levels of SRP such as shown in Figure 5, are well documented to inhibit calcification and growth in hermatypic corals (e.g., Simkiss 1964; Fishelson 1973; Kinsey and Davies 1979; Walker and Ormond 1982; Dodge et al. 1984) while simultaneously favoring competitive dominance (shading, physical abrasion, smothering) by the faster growing large macrophytes (see Banner 1974; Birkeland 1977). This interpretation coincides with the observations of Doty (1973) who was the first to point out that *Sargassum* in the tropical Pacific is most abundant around high volcanic islands, which he attributed to elevated, but unknown, water quality parameters. High volcanic islands in the Caribbean, such as Martinique (Adey et al. 1977; also Curaçao, Wanders 1976) typically have large populations of *Sargassum*, but mainly on their wave-dashed windward coasts where the delivery rate of nutrients due to turbulence is obviously high. Low calcareous barrier reef islands removed from mainland coastal areas and impoverished in nutrient concentrations can also show localized patches of abundant *Sargassum* (e.g., see Macintyre et al. 1987) where herbivory is negligible and wave action and currents result in increased delivery rates.

The bioassay data offer support for the hypothesis concerning the shift in relative dominance between macroalgae and corals observed at sites proximal to Fort de France. At the site closest to the apparent downstream influence of municipal sewage effluent (Cap Salomon), the photosynthetic assays revealed either inhibition of photosynthesis (*Sargassum filipendula*, N+SRP) or no effect following pulses of nutrients. This finding is in accordance with the prediction that sites closest to the effluent source would be relatively rich in nutrients. At the remote southerly sites, nutrients were

shown to be progressively more limiting, particularly compelling are the data for both the photosynthetic and alkaline phosphatase assays at Rocher du Diamant where the most pronounced SRP limitation was documented.

The seawater nutrient and temperature/salinity profiles (Figs. 5 and 6) are in accordance with the hypothesis that sites closest to Fort de France are impacted by sewage-derived nutrient effects. The significantly lower water-column SRP values for Rocher du Diamant support the considerable evidence derived from both the photosynthetic (Fig. 3) and the alkaline phosphatase (Fig. 4) assays that SRP is more limiting to primary production and algal growth at sites farthest removed from the influences of Fort de France. Changes in standing stocks, photosynthetic nutrient-limitation responses, alkaline phosphatase activities and water-column nutrient patterns were indicative of widespread cultural eutrophication processes that parallel those occurring naturally on more localized scales (e.g., bird islands, Lapointe et al. 1993; high granitic islands, Littler et al. 1991a).

It is instructive to view the above findings from the perspective of coastal resources management. Many tropical reef systems are rapidly undergoing cultural eutrophication due to escalating human populational growth. Nearshore waters show continually increasing N and SRP loading from municipal and industrial sewage effluents and agricultural runoff (U.S. Environmental Protection Agency 1982, 1983). It is now well documented that advanced stages of eutrophication often lead to undesirable macroalgal blooms, e.g., as in the cases of coastal reefs of Venezuela (Weiss and Goddard 1977), the Florida reef tract (Lapointe 1989a) and Kāne'ohe Bay, Hawaii (Smith et al. 1981). Nutrient removal strategies need to be developed within the constraints of responsible development and existing economic limitations, which may dictate that only one or several elements can be removed by expensive tertiary treatment technologies. The bioassay results of this study suggest that SRP removal would appear to be most appropriate to protect the southwest coast of Martinique. Conversely, reduction of sources of N contamination might be most effective in the region to the north of Fort de France.

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sonian Marine Station at Link Port, Florida, and Contribution #991 of the Harbor Branch Oceanographic Institution.

Literature Cited

- Adey, W.H., P.J. Adey, R. Burke and L. Kaufman. 1977. The Holocene reef systems of eastern Martinique, French West Indies. *Atoll Res. Bull.* 218:1-40.
- Banner, A.H. 1974. Kaneohe Bay, Hawaii: urban pollution and a coral reef ecosystem. *Proc. 2nd Int. Coral Reef Symp.* 2:685-702.
- Birkeland, C. 1977. The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. *Proc. 3rd. Int. Coral Reef Symp.* 1:15-21.
- Bouchon, C. and J. Laborel. 1986. Les peuplements coralliens des côtes de la Martinique. *Ann. Inst. Océanogr., Paris* 62:199-237.
- Bouchon, C., Y. Bouchon-Navaro, M. Louis and J. Laborel. 1987. Influence of the degradation of coral assemblages on the fish communities of Martinique (French West Indies). *Proc. 38th Gulf Caribbean Fish. Inst., Martinique*, 1985:452-458.
- Dodge, R.E., T.D. Jickells, A.H. Knap, S. Boyd and R.P.M. Bak. 1984. Reef-building coral skeletons as chemical pollution (phosphorus) indicators. *Mar. Poll. Bull.* 15:178-187.
- Doty, M.S. 1971. Physical factors in the production of tropical benthic marine algae. In: J.D. Costlow, Jr. (ed.), *Fertility of the sea*, Vol. I. Gordon and Breach, New York, pp. 99-121.
- Doty, M.S. 1973. Marine organisms—tropical algal ecology and conservation. In: A.B. Costin and R.H. Groves (eds), *Nature conservation in the Pacific*. Australian National University Press, Canberra, pp. 183-196.
- Fishelson, L. 1973. Ecology of coral reefs in the Gulf of Aqaba (Red Sea) influenced by pollution. *Oecologia* 12:55-67.
- Kinsey, D.W. and P.J. Davies. 1979. Effects of elevated nitrogen and phosphorus on coral reef growth. *Limnol. Oceanogr.* 24:935-940.
- Kuenzler, E.J. and J.P. Perras. 1965. Phosphatases of marine algae. *Biol. Bull.* 128:271-284.
- Lapointe, B.E. 1985. Strategies for pulsed nutrient supply to *Gracilaria* cultures in the Florida Keys: interactions between concentration and frequency of nutrient pulses. *J. Exp. Mar. Biol. Ecol.* 93:211-222.
- Lapointe B.E. 1989a. Are we killing the reef? *Florida Keys Magazine* 12:19-28.
- Lapointe B.E. 1989b. Macroalgal production and nutrient relations in oligotrophic areas of Florida Bay. *Bull. Mar. Sci.* 44:312-323.
- Lapointe, B.E., M.M. Littler and D.S. Littler. 1987. A comparison of nutrient-limited productivity in macroalgae from a Caribbean barrier reef and from a mangrove ecosystem. *Aquat. Bot.* 28:243-255.
- Lapointe, B.E., M.M. Littler and D.S. Littler. (1994). Modification of benthic community structure by natural eutrophication: the Belize Barrier Reef. *Proc. 7th Int. Coral Reef Symp.*
- Littler, M.M. 1973. The population and community structure of Hawaiian fringing-reef crustose Corallinaceae (Rhodophyta, Cryptonemiales). *J. Exp. Mar. Biol. Ecol.* 11:103-120.
- Littler, M.M. 1979. The effects of bottle volume, thallus weight, oxygen saturation levels, and water movement on

- apparent photosynthetic rates in marine algae. *Aquat. Bot.* 7:21-34.
- Littler, M.M. and D. S. Littler. 1984. Models of tropical reef biogenesis: the contribution of algae. In: F.E. Round and D.J. Chapman (eds), *Progress in Phycological Research*, Vol. 3. Biopress, Bristol, pp. 323-364.
- Littler, M.M. and D.S. Littler. 1988. Structure and role of algae in tropical reef communities. In: C.A. Lembi and J.R. Waaland (eds), *Algae and human affairs*. Cambridge University Press, Cambridge, pp. 30-56.
- Littler, M.M. and D.S. Littler. 1990. Productivity and nutrient relationships in psammophytic versus epilithic forms of Bryopsidales (Chlorophyta): comparisons based on a short-term physiological assay. *Hydrobiologia* 204/205:73-77.
- Littler, M.M., D. S. Littler and B. E. Lapointe. 1986. Baseline studies of herbivory and eutrophication on dominant reef communities of Looe Key National Marine Sanctuary. National Oceanic and Atmospheric Administration, U.S. Department of Commerce, Washington, D.C.
- Littler, M.M., D.S. Littler and B.E. Lapointe. 1988. A comparison of nutrient- and light-limited photosynthesis in psammophytic versus epilithic forms of *Halimeda* (Caulerpales, Halimedaceae) from the Bahamas. *Coral Reefs* 6:219-225.
- Littler, M.M., P.R. Taylor and D.S. Littler. 1989. Complex interactions in the control of coral zonation on a Caribbean reef flat. *Oecologia* 80:331-340.
- Littler, M.M., D.S. Littler and E.A. Titlyanov. 1991a. 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. *Coral Reefs* 10:199-209.
- Littler, M.M., D.S. Littler and M.D. Hanisak. 1991b. Deep-water Rhodolith distribution, productivity, and growth history at sites of formation and subsequent degradation. *J. Exp. Mar. Biol. Ecol.* 150:163-182.
- Macintyre, I.G., R.R. Graus, P. Reinthal, M.M. Littler and D.S. Littler. 1987. The barrier reef sediment apron: Tobacco Reef, Belize. *Coral Reefs* 6:1-12.
- Mshigeni, K.E., V. Dhanjee and M.O. Jivan Shah. 1986. Marine algal resources of the Seychelles: a survey of the species occurring on the islands and an assessment of their potential for agriculture, commerce, phycocolloid industry and other uses. Commonwealth Science Council, London, pp. 1-75.
- Murphy, J. and J.P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta* 26:31-36
- Pollock, J. B. 1928. Fringing and fossil coral reefs of Oahu. *Bull. Bernice P. Bishop Mus.* 55:1-56.
- Rogers, C.S. 1985. Degradation of Caribbean and western Atlantic coral reefs and decline of associated fisheries. *Proc. 5th Int. Coral Reef Congr.* 6:491-496.
- SAS. 1985. SAS users guide: statistics, version 5 edition. SAS Institute Inc., Cary, N.C., pp. 1-956.
- Simkiss, K. 1964. Phosphates as crystal poisons of calcification. *Biol. Rev.* 39:487-505.
- Slawyk, G. and J.J. MacIsaac. 1972. Comparison of two automated ammonium methods in a region of coastal upwelling. *Deep-Sea Res.* 19:521-524.
- Smith, S.V., W.J. Kimmerer, E.A. Laws, R.E. Brock and T.W. Walsh. 1981 Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. *Pac. Sci.* 35:279-397.
- Sokal, R.R. and F.J. Rohlf. 1969. *Biometry*. Freeman, San Francisco.
- Technicon. 1973. *Technicon Autoanalyzer II, industrial methods*. Technicon Industrial Systems, Tarrytown, New York.
- U.S. Environmental Protection Agency. 1982. Chesapeake Bay program technical studies: a synthesis. U.S. Environmental Protection Agency, Chesapeake Bay Program, Annapolis, Maryland.
- U.S. Environmental Protection Agency. 1983. Ecological impacts of sewage discharges on coral reef communities. U.S. Environmental Protection Agency, Office of Water Program Operations, Washington, D.C.
- Walker, D.I. and R.F.G. Ormond. 1982. Coral death from sewage and phosphate pollution at Aqaba, Red Sea. *Mar. Pollut. Bull.* 13:21-25.
- Wanders, J.B.W. 1976. The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles). I: primary production in the coral reef. *Aquat. Bot.* 2:235-270.
- Weiss, M.P. and D.A. Goddard. 1977. Man's impact on coastal reefs: an example from Venezuela. *Amer. Assoc. Pet. Geol.Stud.Geol.* 4:111-24.