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Settlement patterns of Caribbean scleractinian corals on artificial substrata along a eutrophication gradient, Barbados, West Indies

Tomas Tomascik*

Bellairs Research Institute of McGill University, St. James, Barbados, W.I.

ABSTRACT: Artificial substrate settlement plates (terracotta tiles) were set out on 3 fringing reefs for a period of 12 mo to study settlement patterns of juvenile scleractinian corals along a eutrophication gradient on the west coast of Barbados, W.I. A total of 716 coral planulae settled on 120 experimental plates after 12 mo of exposure. Statistically higher ($p < 0.05$) average number of juvenile corals per plate ($\overline{X}$= 9.2 ± 3.3; N = 40) was recorded on a less eutrophic reef compared to 2 more eutrophic reefs ($\overline{X}$ = 6.9 ± 3.1; N = 40 and $\overline{X}$ = 1.9 ± 1.3; N = 40). Differences in juvenile coral settlement between reef zones, within each reef, were dependent on the reef's position along the eutrophication gradient. Statistically higher number of coral planulae ($\overline{X}$ = 7.2 ± 4.5; N = 60) successfully settled on vertical plates compared to horizontal plates ($\overline{X}$ = 4.8 ± 3.3; N = 60). Coral planulae did not settle on upper surfaces of horizontal plates. In terms of relative abundance, the most common coral species in the juvenile population on the experimental plates were *Porites astreoides* Lamarck which accounted for 42% of the settled planulae, followed by *Agaricia* spp. (23%); and *P. porites* (Pallas) (19%). Juveniles of *Montastrea annularis* (Ellis & Solander), *Siderastrea* spp. and *Diploria* spp., while present at 2 northern reefs, were absent from the most eutrophic reef.

INTRODUCTION

Sampling methods in quantitative studies of coral settlement patterns are divided into 2 categories: (1) the use of artificial substrates such as terracotta tiles, PVC surfaces or cement blocks (Birkeland 1977, Brock 1979, Sammarco & Carleton 1982, Wallace & Bull 1982, Alino et al. 1985, Harriott 1985, Babcock 1988, Gittings et al. 1988), and (2) the use of natural substrata (Birkeland 1977, Bak & Engel 1979, Rylaarsdam 1983, Sakai & Yamazato 1984, Wallace 1985a, Sammarco 1991). A study based on the comparison of settlement plate types, for experiments on the settlement of scleractinian corals, demonstrated that coral settlement patterns are dependent on the type of settlement plates used (Harriott & Fisk 1987). This information is in addition to other factors that must be considered in designing coral settlement studies, e.g. depth, reef habitat and plate orientation (Birkeland 1977, Birkeland et al. 1982, Neudecker 1982, Wallace & Bull 1982, Sammarco 1983, Wallace 1985a,b). Carleton & Sammarco (1987) demonstrated that substrate irregularity plays a significant role in dispersion patterns and generic diversity of juvenile scleractinian corals. They showed a positive correlation between juvenile coral abundance and the surface irregularity of the substrates.

Previous coral settlement studies were designed to compare coral settlement patterns with respect to natural environmental conditions or habitats (Birkeland 1977, Bak & Engel 1979, Birkeland et al. 1982, Wallace & Bull 1982, Rogers et al. 1984, Baggett & Bright 1985, Sammarco 1991) or temporal variability (Bothwell 1982, Wallace & Bull 1982, Rogers et al. 1984), and to determine the role of competitors (Birkeland 1977), grazers (Sammarco & Carleton 1982), and predators (Sammarco 1980a) in the settlement of scleractinian corals.

Natural environmental factors, both abiotic (e.g. temperature, light, depth, water circulation) and biotic (e.g. competition, predation, grazing), play an important role in determining spatial heterogeneity of

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* Present address: Environmental Management Development in Indonesia (EMDI) Project, Kantor Menteri Negara, Kependudukan & Lingkungan Hidup, Jl. Medan Merdeka Barat 15, Jakarta 10110, Indonesia

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benthic communities (Dart 1972, Harger & Tustin 1973, Bak & van Eys 1975, Sammarco 1975, 1980a, b, Birkeland 1977, Brock 1979, Russ 1980, Dean 1981, Wellington 1982, Hughes & Jackson 1985, Sammarco 1991). Distribution and relative abundance of scleractinian corals reflect patterns of larval settlement, recruitment, mortality, asexual reproduction and aggressive interactions between coral species (Rogers et al. 1984). However, the pattern of successful recruitment on available substrate, which is a function of dispersal and post-settlement selection, is probably more important in shaping the spatial complexity of coral reef communities than competitive interactions among coral species which, as suggested by Birkeland et al. (1982), 'proceed no faster than the growth of colonies at their overlapping margins'. Although successful coral recruitment is a function of complex interactions between competition for space and disturbances by grazers (Wellington 1982, Hughes & Jackson 1985, Rogers et al. 1984), few studies have documented coral recruitment patterns with respect to abiotic environmental factors; e.g. nutrient enrichment resulting from upwelling events (Birkeland 1977), or from anthropogenic activities (Maragos 1972, 1974, Banner 1974, Coles 1985, Fitzhardinge 1985).

Coral reefs are among the most biologically diverse and productive benthic communities in the world (Lewis 1977), and as such, they constitute an important natural resource in many developing countries which is being increasingly exploited in commercial activities. The application of structural analysis in pollution-related studies has provided much needed information on the general community response; however, the mechanisms through which scleractinian corals respond to environmental perturbations are still relatively unknown. Since scleractinian corals are sessile, they must necessarily experience the varying conditions in the water masses. Therefore, the ultimate change in community structure in perturbed environments results from variations in rates of larval recruitment, growth, and mortality in adult populations. The structure of scleractinian coral communities under eutrophic conditions must, therefore, depend on the relative success of coral species which both as adults and larvae can tolerate reduced water quality and secondary effects associated with eutrophication processes. Indeed, a number of studies have demonstrated that eutrophication of water masses, as a result of anthropogenic activities, over coral reefs may have adverse effects on the structure and function of coral reef communities (Maragos 1972, 1974, Banner 1974, Smith et al. 1981, Walker & Ormond 1982, Dollar 1983, Maragos et al. 1985, Tomascik & Sander 1985, 1987a, b).

The main objective of the present study was to test the hypothesis that eutrophication (i.e. nutrient enrichment associated with elevated concentrations of suspended particulate matter), as a result of anthropogenic activities, has a measurable effect on the recruitment patterns of juvenile scleractinian corals. The use and selective deployment (i.e. similar depth, distance from shore, and reef habitat) of unglazed terracotta tiles was chosen to allow for a concurrent comparison of juvenile coral recruitment rates, among 3 fringing reef complexes situated along a eutrophication gradient on the west coast of Barbados, with respect to water quality only. Thus, the present study will address spatial variability of coral recruitment patterns.

MATERIALS AND METHODS

Study sites. This study was carried out from September 16, 1986 to September 17, 1987 along the west coast of Barbados. Three fringing reef complexes were chosen for the study, based on their relative positions along a previously described eutrophication gradient (Tomascik & Sander 1985). The southernmost reef, BR,

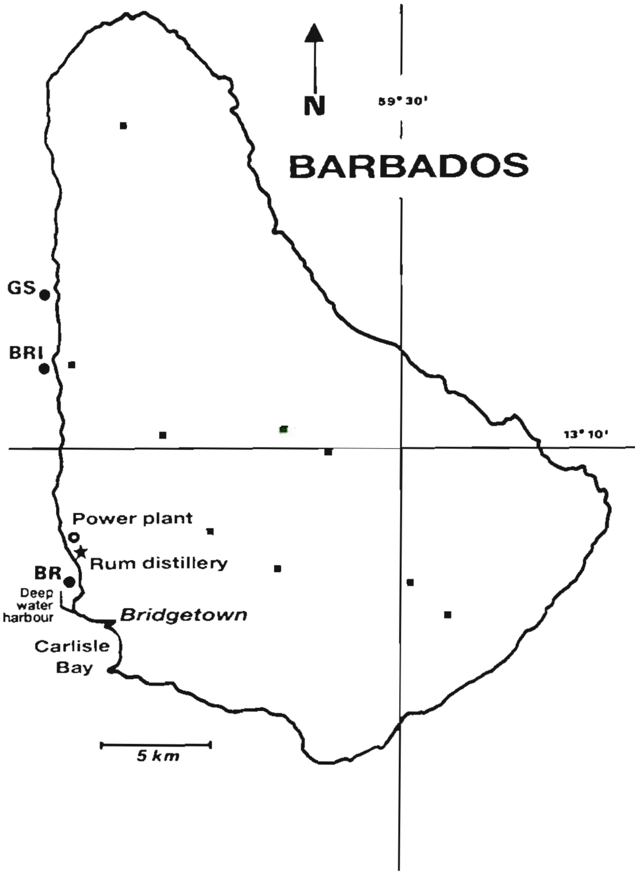

Fig. 1. Map of Barbados, West Indies, showing the general location of the 3 sampling stations, rum distillery, power plant, and the location of sugar mills (■). Station abbreviations: BR, Brighton; BRI, Bellairs Research Institute; GS, Greensleeves

(Fig. 1) represents a fringing reef under eutrophic conditions (i.e. high suspended particulate matter and nutrient concentrations, low light intensity, and high phytoplankton biomass). The reef is located in an area that has been subjected to chronic pollution from urban and industrial sources over the past 15 yr. The major sources of pollution are related to deep water harbour activities, and to rum distillery and power plant effluents that are discharged in close proximity to the reef.

The second fringing reef, BRI, is located 8 km north of BR (Fig. 1). The land area close to the reef has undergone extensive urban development, and is currently a major tourist center. The reef is primarily affected by domestic and hotel effluents, and by severe freshwater runoff during the rainy season between June and December (runoff from agricultural and urban areas has been greatly intensified through modification of natural drainage streams).

The northernmost reef, GS, is situated 13 km north of BR (Fig. 1), and is considered to be relatively unpolluted (Tomascik & Sander 1985). Hotel effluents and freshwater runoff are the main sources of pollutants; however, the freshwater runoff events are less severe (Tomascik unpubl.) as a result of higher vegetation density in the area.

For qualitative and quantitative descriptions of the reef crest and spur and groove zones see Lewis (1960), Macintyre (1968), Stearn et al. (1977), and Tomascik & Sander (1987a).

Coral settlement. Sampling was designed to cover 2 major reef zones on each fringing reef that contained highest coral abundance and cover. The zones chosen were the reef crest (depth 1.5 to 2.0 m) and the spur and groove (depth 4 m).

The settling plates, made of unglazed terracotta tiles (20 × 7 cm), were placed in each zone at the 3 reefs. The tiles were suspended from a stand which consisted of a cement block (1 m × 1 m × 0.25 m) into which 6 iron bars (1 cm diameter and 45 cm high) were embedded as support rods. Each stand supported 10 terracotta tiles: 5 positioned along a horizontal plane and 5 positioned along a vertical plane. Each tile was suspended 15 cm above the cement base with a nylon line which ran through holes drilled at each corner of the tile. The space separating each tile was approximately 10 cm in width. Two stands (replicates) were deployed in each reef zone within 2 m of each other. The stands within each zone were placed into as similar an environment as possible. Even though this was accomplished subjectively, it was deemed important to have the replicates in similar environments, since the main objective of the study was to assess among-reef differences in coral recruitment with respect to water quality only. All tiles were preconditioned before being placed on the reefs by keeping them submerged in a running seawater system (100 μm filter) for a period of 10 d. On January 16, 1987, all tiles were examined underwater with the aid of a magnifying glass (ca 20 × magnification). On September 17, 1987, all plates were removed and fixed, in the field, in 7% buffered formalin. All tiles were analyzed within 2 d of collection. Each plate was examined using a dissection microscope (120 × magnification) and all juvenile corals were counted and identified to species level if possible. Coral planulae recruitment was recorded as number of juvenile corals per tile.

Statistical analysis. Prior to statistical analysis, the data were tested for violations of the basic assumptions of normality and homogeneity of variance implied in all linear model statistics. The assumption of normality was tested using the probability plot procedure in Statgraphics (1985), while the Bartlett's test (Statgraphics 1985) and the F_{max} test (Zar 1984) were used to test the homogeneity of variance assumption. The results of the exploratory data analysis revealed major violations of normality and homogeneity of variance. Accordingly, the data were transformed using the SQRT(SQRT(X+3/8)) transformation (SQRT = square root). The success of the transformation was tested again with results indicating no violations of the basic assumptions of normality and homogeneity of variance. Three-factor analysis of variance (ANOVA) for balanced design (Statgraphics 1985) was carried out on the transformed data set. The 3 factors in the analysis were location along the eutrophication gradient (reefs: BR, BRI and GS), zones within reefs (reef crest and spur and groove), and orientation (vertical and horizontal). Multiple comparison of means for significant ($p < 0.05$) differences were carried out using the Tukey's multiple comparison (HSD) test (Zar 1984). A nested analysis of variance (Statgraphics 1985) was carried out to assess within reef and within zone variations.

RESULTS

The first examination of the settling plates on January 16, 1987, revealed no coral recruitment during the first 4 mo of the study. At the end of the experiment (September 17, 1987) a total of 716 juvenile corals were counted on 120 settling plates.

Table 1 presents the abundance and distribution of 6 coral genera which are represented in the coral recruitment data. The highest overall settlement was shown by *Porites astreoides* which represents 42% of the total juvenile coral count, followed by *Agaricia* spp. and *P. porites* which accounted for 23% and 19% of the total juvenile coral abundance respectively. *Montastrea annularis*, *Siderastrea* spp., and *Diploria* spp. were

Table 1. Abundance (number of juvenile corals), and relative abundance (percentage of total within each reef) of juvenile corals at each reef. First number: number of juvenile corals; second number (in parenthesis): relative abundance

Species	Reef			Total
	BR	BRI	GS	
Porites astreoides	29 (39)	125 (45)	149 (41)	303 (42)
Agaricia spp.	19 (25)	68 (25)	81 (22)	168 (23)
Porites porites	26 (35)	54 (20)	59 (16)	139 (19)
Favia fragum	1 (1)	7 (3)	10 (3)	18 (7)
Montastrea annularis	0	10 (4)	40 (11)	50 (7)
Siderastrea spp.	0	7 (3)	25 (7)	32 (4)
Diploria spp.	0	4 (2)	2 (1)	6 (1)
Total	75	275	366	716

Table 2. Parametric 3-factorial analysis of variance (ANOVA) (Statgraphics 1985) for average juvenile coral numbers per tile. First factor: reef (BR, BRI and GS); second factor: zone (reef crest and spur and groove); third factor: tile orientation (vertical and horizontal)

Source of variation	df	MS	*F*-value	PR > *F*
Reef (Factor A)	2	2.9899	170.43	0.0000
Zone (Factor B)	1	0.0026	0.15	0.7044
Orientation (Factor C)	1	0.6657	37.95	0.0000
Interactions				
A × B	2	0.4529	25.82	0.0000
A × C	2	0.0353	2.01	0.1386
B × C	1	0.0001	0.01	0.9287
A × B × C	2	0.0818	4.67	0.0114
Error	108	0.1754		

absent from the most eutrophic reef BR, while *P. astreoides* was the dominant colonizing species on all reefs. Note that the relative abundances of the 3 major groups present on reef BR were more evenly distributed when compared to the 2 northern reefs BRI and GS.

The results of a 3-factorial analysis of variance (ANOVA) indicated that there were statistically significant differences in the average number of juvenile corals per settling plate among the 3 reefs in the study (Table 2). Statistically higher ($p < 0.05$) recruitment of juvenile corals occurred on the northernmost reef GS (Table 3) when compared to the southern reefs BRI and BR. The lowest number of juvenile corals was recorded on BR which is the most eutrophic reef in the study (Table 3).

Table 2 also indicates that, while there were no statistically significant differences in coral recruitment between the reef crest and the spur and groove zones, there was a significant ($p < 0.0001$) interaction effect between reef and zone. This means that the differences in coral recruitment between the 2 zones are strongly dependent on the location of the reef. The data presented in Table 3 demonstrate that, while there were no statistically discernible differences in coral recruitment between the 2 reef zones at BR, a statistically higher number of juvenile corals was recorded in the reef crest zone (compared to the spur and groove zone) on the central reef BRI. On the northernmost reef GS, statistically higher number of juvenile corals settled on plates in the spur and groove zone compared to the reef crest. The data in Table 3 do not indicate any clear pattern for within-reef variability among the 3 study reefs. However, the data in Table 4 demonstrate that there were statistically discernible differences in coral planulae recruitment among the same reef zones among the 3 reefs. The highest recruitment of coral planulae in the reef crest zone occurred on reef BRI; however, this was not statistically discernible from the abundance of juvenile corals in the reef crest zone on the northernmost reef GS. The lowest number of coral planulae in the reef crest zone settled on plates at the southernmost reef BR (Tables 3 & 4). Coral planulae recruitment in the spur and groove zone showed a general pattern of increased abundance with improving water conditions. Statistically higher number of coral planulae settled on the northernmost reef GS than on the 2 southern reefs BRI and BR, while the lowest number of coral planulae settled on BR (Tables 3 & 4).

Table 3. Average number of juvenile corals per tile calculated for each reef and each reef zone within reef. First number: average values; second number (in parentheses): standard deviation; third number: total number of tiles used in the analysis. NS: no statistically discernible differences between reefs, and between zones; * statistically discernible ($p < 0.05$) differences based on a 3-factorial analysis of variance (Statgraphics 1985) and Tukey's studentized range (HSD) test (Zar 1984)

Reef	Total	Reef crest		Spur and groove
BR	1.9	1.6		2.2
	(1.3)	(1.4)	NS	(1.2)
	40	20		20
	*			
BRI	6.9	8.9		4.9
	(3.1)	(2.2)	*	(2.5)
	40	20		20
	*			
GS	9.2	7.7		10.7
	(3.3)	(2.2)	*	(3.5)
	40	20		20

Table 4. Tukey's studentized range (HSD) test (Zar 1984) for significant ($p < 0.05$) differences in average number of juvenile corals per tile for each reef zone among the 3 reefs. * Statistically discernible differences ($p < 0.05$); NS: no statistically discernible differences. Note: this test controls the Type 1 experimentwise error rate

Reef	Reef crest			Spur and groove		
	BR	BRI	GS	BR	BRI	GS
BR	–			–		
BRI	*	–		*	–	
GS	*	NS	–	*	*	–

The results of the 3-factorial ANOVA also indicated that there were significant differences in juvenile coral abundance between the 2 plate orientations (i.e. horizontal and vertical). Throughout the study there was no coral planulae recruitment on the top of the horizontal plates. All counts for the horizontal orientation represent coral recruitment on the bottom of the horizontal plates.

The 3-factorial ANOVA also indicated a strong interaction effect among reef, zone and orientation suggesting that coral planulae recruitment, in terms of plate orientation, was dependent on both reef zone and location of the reef. Table 5 presents the coral recruitment data in terms of plate orientation within each reef zone for each reef in the study. The data suggest that, in this study, coral planulae had a tendency to colonize vertical surfaces in greater numbers compared to horizontal surfaces. However, this generalization does not hold for planulae recruitment in the reef crest zone of reef GS, and in the spur and groove zone of reef BR (Table 5).

Table 5. Average number of juvenile corals per tile at each reef calculated for the 2 reef zones and each orientation of settlement tiles. First number: average value; second number (in parentheses): standard deviation; third number: number of tiles analyzed in the study. NS: no statistically discernible differences; * Statistically discernible ($p < 0.05$) difference based on 3-factor analysis of variance (Statgraphics 1985), followed by Tukey's studentized range (HSD) test (Zar 1984)

Reef	Reef crest			Spur and groove		
	Horizontal		Vertical	Horizontal		Vertical
BR	0.8		2.4	2.1		2.2
	(0.8)	*	(1.5)	(0.9)	NS	(1.4)
	10		10	10		10
BRI	7.2		10.6	3.1		6.6
	(1.5)	*	(1.4)	(1.7)	*	(1.9)
	10		10	10		10
GS	6.9		8.4	8.6		12.7
	(1.9)	NS	(2.4)	(1.9)	*	(3.7)
	10		10	10		10

Nested analysis of variance was used to test for major sources of variability in the data. Of the total model variability, 63.3% can be ascribed to among-reef differences, 11.5% to within-zone variability, and only 3.5% to within-replicate (i.e. stand) variability. Therefore, in this study, the variability in juvenile coral abundance among the 3 reefs is the major source of variation.

DISCUSSION

The present study supports the hypothesis that eutrophication of the coastal water masses along the west coast of Barbados exerts a measurable effect on the settlement rates of scleractinian corals. The results indicate that eutrophication may alter scleractinian coral reef communities through reduction of coral recruitment rates. A number of studies have demonstrated that larvae of benthic organisms exhibit complex behaviours that enable them to distinguish potentially suitable settlement substrates (Crisp 1974, Gray 1974, Underwood 1979, Caffey 1982, Woodin 1986). Substrate composition under eutrophic conditions may generate a complex set of physical, chemical and/or biological signals that may stimulate coral planulae to remain in the water column, and thus be carried by the currents to a more favourable environment. Alternatively, environmental conditions in the water column under eutrophic conditions may generate negative cues which are detected by the planktonic coral planulae thus inhibiting their settlement.

The concentration of total suspended particulate matter (SPM – organic and inorganic) in the water column and the associated reduction in light intensity are 2 environmental factors that may play a significant role in the early pre-settlement behaviour of planktonic coral planulae. Sedimentation and associated turbidity are known to negatively affect coral settlement rates (Sammarco 1980a, 1991, P.R.F. Bell & S.R. van Woesik pers. comm.). Tomascik & Sander (1985) have demonstrated quantitatively that significant differences in these 2 environmental parameters occur among the 3 reefs in the study. High concentrations of SPM may directly influence planulae settlement behaviour through direct physical action (e.g. abrasion), thus producing cues that delay planulae settlement. Furthermore, reduced light intensity in the water column may add a physiological component to the overall response through reduction of zooxanthellae photosynthesis in coral planulae. Reduction of zooxanthellae photosynthesis in coral planulae, under turbid conditions, may generate specific physiological cues that may delay planulae settlement. Tomascik & Sander (1987b) demonstrated that the planulae of *Porites porites* contain zooxanthellae when released.

Nutrient concentrations in the water column are not high enough (Tomascik & Sander 1985) to affect coral planulae directly through toxic effects, and thus to have a measurable effect on coral recruitment rates. However, the possibility of direct toxic effects by pollutants other than nutrients cannot be excluded.

Bell & Gabric (1990) have suggested that a release of toxic substances by marine benthic cyanobacteria may reduce coral reproduction and inhibit coral recruitment. The relatively high phosphate concentrations found on reefs BR and BRI, 0.103 µg-at. l^{-1} and 0.111 µg-at. l^{-1} respectively (Tomascik & Sander 1985), could promote growth and biomass accumulation of benthic cyanobacteria thus affecting recruitment of coral planulae either through direct toxic effects or through overgrowth and smothering.

Qualitative observations of the settling plates revealed that while the settling plates at the most eutrophic reef, BR, were covered by a dense turf of algae (with upper surfaces of horizontal plates covered with a layer of sediment 5 to 10 mm deep), the settling plates at the 2 less eutrophic reefs were covered by an invertebrate community consisting mostly of hydroids, colonial tunicates, bryozoans, and sponges. These observations support the general conclusions of other recruitment studies (Birkeland 1977, Goreau et al. 1981), suggesting that an increase in nutrient concentrations promotes growth of benthic filamentous algae, macrophytes, and benthic heterotrophic invertebrate assemblages that can out-compete coral recruits directly through smothering, and/or by acting as sediment traps (Walker & Ormond 1982).

Nevertheless, a number of indirect effects may explain reduced coral recruitment in eutrophic environments. In a sequence of events, eutrophication may produce a powerful environmental stress that, on an individual and/or species level, may first precipitate a stress response characterized by the reduction of reproductive output of coral colonies in the affected area (Tomascik & Sander 1987b). Low coral recruitment rates at the most eutrophic reef may be directly related to a general reduction of reproductive output by the local coral community (Tomascik & Sander 1987b). This hypothesis assumes that coral seeding from adjacent fringing reefs and the bank reef is negligible, which, considering the coastal current patterns (Peck 1978, Cotter 1984), may not be realistic. However, 4 coral species recruited at the southernmost reef are brooders, and are the dominant constituents of the adult coral community (Tomascik & Sander 1987a). There is some evidence (Lewis 1974, Goreau et al. 1981) that planulae from brooding species settle very shortly after release and this may in part explain the dominance of *Porites astreoides*, *P. porites* and *Agaricia agaricites*.

The settlement patterns of juvenile corals varied with reef zone. Under natural conditions the spur and groove zone is a relatively stable environment with higher coral diversity and abundance (Tomascik & Sander 1987a), compared to the reef crest where diurnal and annual temperature differences and wave energies provide more dynamic and variable environmental conditions. Therefore, it is suggested that in the case of the northern reef GS, higher recruitment rates of juvenile corals in the spur and groove zone, when compared to the reef crest, are a function of natural environmental conditions. In comparison, on the central reef BRI higher recruitment rates in the reef crest zone, compared to the spur and groove zone, may be attributed to differences in water characteristics. BRI is located near a natural freshwater stream that has been extensively modified to accommodate increased freshwater runoff from adjacent urban and agricultural areas. During the rainy season high quantities of fine sediments and nutrients are released into the coastal waters (Tomascik unpubl.). Since the prevailing current direction during the rainy season is in a north-northwest direction, most of the sediments settle on the southern edge of the reef (Tomascik unpubl.). During the dry season most of the sediments are resuspended through wave action and/or bioturbation, and as a result, light intensities are reduced over the spur and groove zone. Therefore, the differences in water quality characteristics between the 2 habitats may override the effects of natural environmental factors associated with natural environmental gradients such as wave energy, distance from shore and depth.

The lack of statistically significant differences in settlement rates between the reef crest and the spur and groove zones on the most eutrophic reef BR may be attributed to the relatively homogeneous environmental conditions of the water column, over the reef, brought about by high inputs of industrial and domestic effluents. Thus, the environmental conditions imposed by anthropogenic activities may override and/or mask the effects of natural environmental gradients.

Eutrophication of coastal marine ecosystems has been recognized as 'the Future Marine Coastal Nuisance' (Rosenberg 1985) in many northern European temperate marine coastal waters. However, with few exceptions (Maragos 1972, Banner 1974, Smith et al. 1981, Walker & Ormond 1982, Tomascik & Sander 1985, 1987a,b, Bell & Gabric 1990, R. van Woesik pers. comm., Bell 1991), research on eutrophication in tropical coral reef ecosystems has received relatively little attention. In an elegant synthesis of the effects of eutrophication on the demise of coral reefs and carbonate platforms, Hallock & Schlager (1986) proposed that the drowning of carbonate platforms in the geologic record may be related to (other than to subsidence and/or sea level rise) the sensitivity of scleractinian corals and other hermatypic organisms to nutrient enrichment of their environment. Hallock & Schlager (1986) proposed that reduction of water clarity, phosphate inhibition of calcium carbonate crystal formation, biotic disruption, and increased rates of bioerosion may elucidate why excess nutrients are detrimental to hermatypic coral reef communities and to calcium carbonate productivity in general.

While there is sufficient evidence to demonstrate that massive nutrient loading into coral reef ecosystems will cause measurable changes in the benthic coral communities (Smith & Kinsey 1976, Smith et al. 1981, Pastorok & Bilyard 1985, van Woesik et al. 1990), there still is little experimental evidence to demonstrate a cause-and-effect relationship and the mechanisms through which structural and functional changes occur.

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