

Effects of eutrophication and sedimentation on juvenile corals

I. Abundance, mortality and community structure

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Abstract. This study investigated effects of eutrophication and sedimentation on juvenile abundance, juvenile mortality and community structure of scleractinian corals on fringing reefs on the west coast of Barbados, West Indies, in 1989. Juvenile abundance was lower on eutrophic/high-sediment reefs than less eutrophic/low-sediment reefs, but juvenile size was larger on the former. The larger size could result from size-selective mortality against smaller juveniles on the eutrophic reefs, from lower recruitment to the eutrophic reefs, or from faster growth on the eutrophic reefs. Juvenile mortality was higher on the eutrophic reefs than the less eutrophic reefs and may result from increased smothering of corals by algae and sediment. Algae were more abundant on the eutrophic reefs, probably in response to elevated nutrients and/or because grazers (*Diadema antillarum*; herbivorous fish) were less common on eutrophic reefs. Juvenile community structure on all reefs was dominated by Type 1 corals (high recruitment, high natural mortality), but Type 2 corals (low recruitment, low natural mortality) became more common in adult communities on the less eutrophic reefs. This transition in community structure did not occur on the eutrophic reefs, adult community structure continuing to be dominated by Type 1 corals. The fact that the pattern of relative abundance of species in the juvenile community is maintained in the adult community on the eutrophic reefs suggests that juvenile mortality rates of different species are similar on eutrophic reefs, and hence that differences in adult community structure between eutrophic and less eutrophic reefs may be largely explained by interspecific differences in juvenile mortality becoming smaller on eutrophic reefs.

Introduction

Anthropogenic eutrophication can result from sewage, agricultural and industrial pollution (Laws 1981), and is often accompanied by increased sediment load. The combination can cause major changes in the biological, chem-

ical and physical environment of coral reef ecosystems (Pastorock and Bilyard 1985, Rogers 1990). A number of studies have shown that eutrophication and sedimentation affect growth rates (Maragos 1972, Kinsey and Davies 1979, Smith et al. 1981, Tomascik and Sander 1985), reproduction (Tomascik and Sander 1987b) and community structure (Maragos 1972, Loya 1975, 1976, Tomascik and Sander 1987a) of scleractinian corals. Birkeland (1977) showed that, under nutrient enrichment from upwelling waters, juvenile scleractinian corals were out-competed for space by opportunistic algae and tunicates, resulting in reduced survivorship. However, there is little information on the effects of anthropogenic eutrophication on the abundance and survival of juvenile corals, and the implications of this for adult community structure have not been specifically addressed.

Many processes other than anthropogenic eutrophication and sedimentation may influence coral community structure. For example, recent studies have shown that community structure may be strongly affected by the grazing activities of both fishes (Sammarco and Carleton 1981) and urchins (Dart 1972, Sammarco 1980). These authors suggest that corals settle more readily when grazing by urchins and fish is rapid enough to prevent filamentous non-coralline algae from monopolizing available space. However, if urchins (e. g. *Diadema antillarum*) are particularly abundant, they may decrease coral recruitment through direct consumption of coral recruits. Interpretation of differences in coral community structure is therefore facilitated by information on the abundance of urchins and reef fish.

Recruitment and juvenile mortality are fundamental life-history characteristics and have been used to divide Caribbean corals into three groups: (1) high recruitment, high mortality; (2) low recruitment, low mortality; (3) low recruitment, high level of asexual reproduction (Bak and Engel 1979, Hughes 1985). Corals with different life-history strategies may respond differently to eutrophication stress. The objective of this study was to clarify the processes leading to changes in adult coral reef community structure under eutrophication stress. The approach

was to compare juvenile abundance, mortality and community structure of scleractinian corals on eutrophic/high-sediment reefs and less eutrophic/low-sediment reefs, and to ascertain whether the relative success of different coral species under eutrophication and sediment stress can be predicted by the recruitment/mortality group to which the corals belong.

Methods

Study sites

The study sites were four fringing reefs on the west coast of Barbados (13°15'N, 50°30'W). These were Fitts Village (E₁), Spring Garden (E₂), Kings Beach (LE₁), and Drift Wood (LE₂). Eutrophication is more extreme towards the south than north of this coast (Tomascik and Sander 1985, Seakem 1989, Snelgrove and Lewis 1989, Davies 1990) such that highly eutrophic water [high nutrients, chlorophyll *a* and suspended particulate matter (SPM), and low water clarity] is characteristic of E₁ and E₂ and less eutrophic water (lower nutrients, chlorophyll *a* and SPM, and higher water clarity) is characteristic of LE₁ and LE₂ (see Table 1 for water quality characteristics). The southern reefs (E₁, E₂) have been subjected to eutrophication pollution for over 20 yr. The principal sources are

an organic and nutrient-enriched effluent from a rum distillery, an ammonia-enriched effluent from an electricity plant, domestic sewage effluent from a sewage treatment plant, and increased freshwater land-runoff following vegetation clearance and heavy urbanization in the area (Tomascik and Sander 1987b). The main eutrophication source on the northern reefs (LE₁, LE₂) is freshwater land-runoff. However, the surrounding land area is more densely vegetated than is the case for the two southern reefs, suggesting a lower rate of freshwater land-runoff (Tomascik and Sander 1987b).

Juvenile abundance and community structure

During April and May 1989, two 100-m reference transects were laid across each study reef perpendicular to the depth contour from the seaward edge of the spur and groove zone in towards the back reef zone (see Lewis 1960 and Stearn et al. 1977 for zonation on Barbados fringing reefs). The locations of the reference transects were chosen so as to minimise variation in water depth and topography between reefs. Along each transect, the abundance of juvenile corals was determined by censusing 20 randomly selected 1-m² quadrats within each of two depth zones (4 to 6 m, 1 to 2 m). These depth zones correspond to the spur and groove zone and the reef flat zone respectively. Within each quadrat, all juvenile corals were identified, counted and the greatest diameter of each juvenile measured to the nearest 1 mm with Vernier callipers. A juvenile coral was defined as any primary polyp or colony with a maximum diameter less than 40 mm (see Bak and Engel 1979). Juveniles of the hydrozoans *Millepora* spp. were also counted and measured within each quadrat since they are an abundant member of the fringing reef community in Barbados (Lewis 1960). Juveniles of *Millepora squarrosa*, *M. alcicornis* and *M. complanata* can only be identified to genus in the field (Bak and Engel 1979), and were consequently grouped as *Millepora* spp.

Community structure was characterized by calculating relative abundances (by number of colonies) of the species and Simpson's Diversity Indices (*D_n*) for each study site. Simpson's Diversity Index was used since it carries as much information but is less subject to biases than most other diversity indices (Southwood 1978, Green 1979). It was calculated as $D_n = N(N-1)/\sum n_i(n_i-1)$, where *N* is the total number of individuals of all species and *n_i* is the number of individuals of the *i*th species in the sample.

Juvenile mortality

Juvenile mortality was investigated in *Porites astreoides* and *Agaricia agaricites*, and the rarer *Diploria strigosa* and *D. labyrinthiformis*. One-hundred and sixty 20 × 20 cm permanent quadrats were established on the spur and groove zones of each of the study reefs during February 1989. Juvenile corals of the above species (15 to 25 mm maximum diameter) were measured and monitored for signs of damage or death for 6 mo. Juveniles of *A. agaricites* and *P. astreoides* were monitored on all four reefs. Juveniles of *D. strigosa* and *D. labyrinthiformis* were not found at E₁ and E₂, and were therefore monitored only at LE₁ and LE₂.

Adult community structure

At each site, ten 20-m transects were run perpendicular to each reference transect at randomly chosen intervals. Any coral colony intersected by the transect line and having a maximum diameter greater than 40 mm was identified, and the intersected length in planar view as well as the maximum diameter were measured to the nearest cm. For each site, adult cover (mean % cover per transect) and Simpson's Diversity Index by cover (*D_c*) were calculated. Filamentous and frondose macroalgal cover was also recorded along each line transect as percentage cover per meter.

Table 1. Water quality characteristics at the four study reefs (LE₁, LE₂, E₁, E₂). Data for 1981 are from Tomascik and Sander (1985), for 1985 from Snelgrove and Lewis (1989), for 1988 from Seakem (1989), for 1989 from Davies (1990). Values for 1981 and 1988 are annual means; those for 1985 and 1989 are means over a single month. When available, SDs are given in parentheses. SPM: suspended particulate matter; Chl *a*: chlorophyll *a*

Characteristic	Year	LE ₁	LE ₂	E ₁	E ₂
PO ₄ -P (µg-at. l ⁻¹)	1981	0.06 (0.03)	0.06 (0.03)	0.09 (0.06)	0.21 (0.11)
	1985	0.12 (0.03)	0.11 (0.04)	0.15 (0.04)	0.31 (0.09)
	1988	0.08 (0.03)	0.08 (0.03)	0.40 (0.15)	0.64 (0.22)
	1989	–	0.07	–	0.17
	Mean	0.09	0.08	0.21	0.33
(NO ₃ + NO ₂)-N (µg-at. l ⁻¹)	1981	0.36 (0.21)	0.45 (0.23)	0.79 (0.50)	4.42 (2.64)
	1985	0.02 (0.01)	0.03 (0.01)	0.10 (0.05)	0.12 (0.04)
	1988	0.40 (0.24)	0.10 (0.06)	0.70 (0.42)	3.50 (1.82)
	1989	–	0.74	–	4.90
	Mean	0.26	0.33	0.53	3.24
SPM (mg l ⁻¹)	1981	4.26 (1.98)	5.21 (3.29)	6.25 (3.92)	7.32 (2.86)
	1985	5.58 (0.64)	6.33 (0.85)	6.52 (0.97)	6.58 (0.68)
	1988	1.97 (0.52)	3.22 (0.92)	4.00 (1.21)	4.97 (1.36)
	1989	–	4.93	–	5.93
	Mean	3.94	4.92	5.59	6.20
Chl <i>a</i> (mg m ⁻³)	1981	0.42 (0.16)	0.55 (0.27)	0.88 (0.33)	0.90 (0.41)

Rare corals

To obtain more information on rare corals, an area of 100 × 100 m around each reference transect line on each reef was searched by two divers for 1 h. Any coral species which had not previously been found during either the quadrat (juvenile) or transect (adult) surveys was identified and measured.

Grazing organisms

The population density of *Diadema antillarum* was determined for each line transect by a modified transect method (Hawkins 1979). A 1-m plastic rod, marked at midpoint, was held perpendicular to

a transect line above the substratum. The rod was moved along the line and all urchins found beneath the rod were counted. This was repeated for each of the ten 20-m transects at each site.

The abundance of fish in the spur and groove zone at each site was estimated by visual counts along each reference transect. A diver swam slowly above the transect line recording all the fish observed between the substrate and the diver in a 1-m corridor bisected by the transect line (see Miller and Hunte 1987 for methodology).

Statistical analysis

Prior to statistical analysis all data were tested for normality (Shapiro-Wilk; *W* statistic) and homogeneity of variance (graphical methods; Zar 1984). Data violating the assumptions were transformed [(*x* + 0.5)^{1/2} for data on maximum diameter of juveniles and on Simpson's Index; log (*x* + 1) for adult coral cover and *Diadema antillarum* densities.] The success of each transformation was tested and any data sets remaining non-normal (data on algal cover) were analyzed nonparametrically (Kruskal-Wallis test). All normal data were analyzed using ANOVA (analysis of variance for balanced data) and GLM (general linear models procedure for unbalanced data) (SAS 1985). The proportion data on juvenile mortality were analyzed for variation between reefs using normal approximation testing for more than two proportions (Zar 1984), followed by Tukey's test to detect pair-wise difference.

Table 2. Results of a two-way ANOVA (mean square values) for effects of study reef (E₁, E₂, LE₁, LE₂) and reef zone (spur and groove, reef flat) on juvenile coral density (mean no./m²), juvenile coral diversity (mean Simpson's D_c), adult coral cover (mean % cover), adult coral diversity (mean Simpson's D_c), size of juveniles of *Agaricia agaricites* and *Porites astreoides* (mean maximum diameter in mm), and density of *Diadema antillarum* (mean no./20 m²). Degrees of freedom in parentheses

Variable	Source of variation:			
	Study reef	Reef zone	Interaction	Residual
Juvenile density	6775** (3)	2496* (1)	1412* (3)	246 (152)
Juvenile diversity	0.05 (3)	0.03 (1)	0.19* (3)	0.07 (129)
Adult cover	18.78** (3)	0.71 (1)	0.45 (3)	0.36 (72)
Adult diversity	0.51** (3)	0.12 (1)	0.08 (3)	0.06 (68)
Size of <i>A. agaricites</i>	15.87** (3)	11.74** (1)	1.69 (3)	0.75 (1227)
Size of <i>P. astreoides</i>	17.77** (3)	24.85** (1)	0.87 (3)	0.96 (1091)
Density of <i>D. antillarum</i>	15.35** (3)	32.67** (1)	4.9** (3)	0.75 (71)

* *P* < 0.05, ** *P* < 0.001

Table 3. Juvenile density (mean no./m²), juvenile diversity (mean Simpson's D_n), adult cover (mean % cover), and adult diversity (mean Simpson's D_c) for scleractinian corals and *Millepora* spp. at each study reef. LE₁ and LE₂ are less eutrophic reefs, E₁ and E₂

Variable	LE ₁			LE ₂			E ₁			E ₂		
	Zone: 1	2	3	1	2	3	1	2	3	1	2	3
Juvenile density	33.8 (26.1)	23.4 (20.4)	28.7 (23.6)	43.7 (16.6)	20.3 (13.6)	32.0 (19.1)	7.1 (4.1)	10.7 (14.4)	8.9 (11.2)	7.7 (9.8)	6.3 (6.3)	7.0 (8.1)
Juvenile diversity	2.47 (0.55)	1.92 (0.67)	2.21 (0.65)	2.62 (0.51)	2.11 (0.82)	2.36 (0.87)	1.40 (0.50)	3.16 (1.61)	2.16 (1.41)	2.01 (0.53)	2.13 (0.70)	2.08 (0.67)
Adult cover	9.2 (5.7)	9.1 (3.6)	9.2 (4.6)	24.9 (11.7)	22.2 (11.2)	23.6 (11.2)	2.0 (2.3)	1.4 (0.9)	1.7 (1.7)	11.3 (16.5)	3.0 (1.6)	7.1 (12.2)
Adult diversity	2.72 (0.69)	2.53 (0.84)	2.62 (0.76)	3.27 (0.99)	2.36 (0.89)	2.82 (1.02)	2.22 (1.42)	1.97 (0.77)	2.08 (1.06)	1.58 (0.67)	1.73 (0.66)	1.66 (0.65)

Results

Juvenile abundance and community structure

The density of juvenile corals differed significantly between study reefs and reef zones (Tables 2 and 3). The effect of reef on juvenile density differed between reef zones (Table 2; significant interaction effect). However, in both zones, density was greater on the less eutrophic reefs than the eutrophic reefs (Table 3; Tukey's tests, *P* < 0.003 for all pair-wise comparisons).

More species were present on the less eutrophic reefs than on the eutrophic reefs in both zones (Table 4). Notably, juveniles of the massive corals such as *Montastrea annularis*, *Diploria labyrinthiformis*, *D. clivosa* and *Siderastrea siderea* were absent from the eutrophic reefs. The most common juveniles in both zones on all reefs were *Agaricia agaricities* and *Porites astreoides* (Table 4).

eutrophic (see Table 1). Zone 1 is spur and groove zone; Zone 2 is reef flat zone; Zone 3 is whole reef (Zones 1 and 2 combined). SDs in parentheses

Table 4. Relative number of juveniles of different coral species (% of total numbers) and total number of species in the spur and groove zone (Zone 1) and reef flat zone (Zone 2), at each study reef. LE₁ and LE₂ are less eutrophic reefs, E₁ and E₂ eutrophic (see Table 1). No. of colonies observed shown in parentheses

Species	LE ₁		LE ₂		E ₁		E ₂	
	Zone: 1	2	1	2	1	2	1	2
<i>Agaricia agaricites</i>	44.0	61.4	49.8	66.5	20.0	46.0	61.0	57.9
<i>Porites astreoides</i>	41.7	19.6	31.3	20.7	62.5	23.7	27.3	29.4
<i>Porites porites</i>	5.5	4.8	3.3	3.5	2.5	15.3	(10) ^a	3.2
<i>Favia fragum</i>	0.3	3.8	0.2	3.2	0.8	2.8	1.9	8.7
<i>Millepora</i> spp.	7.5	10.0	14.4	5.9	(5) ^a	10.7	9.1	0.8
<i>Diploria strigosa</i>	0.3	(1) ^a	0.1	(1) ^a	(2) ^a		(1) ^a	
<i>Diploria labyrinthiformis</i>	(6) ^a		0.1					
<i>Diploria clivosa</i>	(6) ^a	(1) ^a	(6) ^a	(1) ^a				
<i>Montastrea annularis</i>	0.2		0.1					
<i>Siderastrea siderea</i>	0.3		0.1					
<i>Siderastrea radians</i>	0.3	(4)			14.6	1.4	0.7	0.8
<i>Madracis decactis</i>	(3) ^a	(3) ^a	0.2	(2) ^a				
<i>Isophyllastrea sinuosa</i>			0.1					
<i>Stephanocoenia michelini</i>	(2) ^a		(1) ^a					
<i>Meandrina meandrites</i>	(1) ^a		(1) ^a					
<i>Dichocoenia stokesii</i>	(1) ^a							
No. of juveniles	667	469	875	406	142	215	154	126
No. of species	15	9	14	8	7	6	7	6

^a Juveniles observed outside of quadrat

Table 5. Mean relative abundance (% cover per transect) of adults of the different coral species in the spur and groove zone (Zone 1) and the reef flat zone (Zone 2) at each study site. LE₁ and LE₂ are less eutrophic reefs, E₁ and E₂ eutrophic (see Table 1). No. of colonies observed shown in parentheses

Species	LE ₁		LE ₂		E ₁		E ₂	
	Zone: 1	2	1	2	1	2	1	2
<i>Porites astreoides</i>	33.7	26.9	18.7	31.4	22.1	19.6	38.3	55.9
<i>Porites porites</i>	29.8	55.5	39.0	46.2	4.1	52.8	63.7	39.6
<i>Millepora complanata</i>	3.2	1.9	3.9	1.4	10.0	5.2	3.1	(4) ^a
<i>Millepora alcicornis</i>	1	1.1	1.1	2.8	15.3	13.8	(1) ^a	(1) ^a
<i>Millepora squarosa</i>	1.9	8.9	0.5	3.3	10.6	30	0.1	(2) ^a
<i>Agaricia agaricites</i>	0.1	0.1	0.1	0.1	0.2	0.4	0.1	0.6
<i>Diploria strigosa</i>	9.6	0.8	1.6	2.4	9.9		(3) ^a	
<i>Diploria labyrinthiformis</i>	(13) ^a	0.4	0.6		(1) ^a		(2) ^a	
<i>Diploria clivosa</i>	(5) ^a	(3) ^a	(8) ^a	(4) ^a	(4) ^a	1.1	(1) ^a	(1) ^a
<i>Montastrea annularis</i>	(3) ^a		(4) ^a	0.2			1.1	
<i>Montastrea cavernosa</i>	(3) ^a	1.6	17.9	4.4				
<i>Siderastrea siderea</i>	12.5	2.2	4.4	14.1	(4) ^a	2.9	(3) ^a	(1) ^a
<i>Siderastrea radians</i>					7.5		(1) ^a	
<i>Madracis decactis</i>	(4) ^a		2.8					
<i>Dichocoenia stokesii</i>	9.9		0.6		(1) ^a		(1) ^a	
<i>Meandrina meandrites</i>	(5) ^a		0.1					
<i>Dendrogyra cylindrus</i>			5.2		(1) ^a			
<i>Stephanocoenia michelini</i>	(3) ^a		(4) ^a		(2) ^a		(2) ^a	
No. of species	16	11	17	11	14	8	14	8

^a Adults observed outside of quadrat

The species diversity of juvenile corals did not differ either between study reefs or between reef zones (Tables 2 and 3).

Adult abundance and community structure

Percent of the substrate covered by live coral differed significantly between study reefs but not between reef

zones (Tables 2 and 3). Data from zones were therefore pooled for pair-wise comparisons between reefs. Percent cover was significantly higher on less eutrophic than eutrophic reefs (Table 3; Tukey's test, $P < 0.02$ for all pair-wise comparisons except LE₁ vs LE₂, where $P = 0.20$).

More species were present on the less eutrophic reefs than on the eutrophic reefs in both zones (Table 5). Notably, most massive corals (e.g. *Montastrea cavernosa*,

Table 6. *Agaricia agaricites* and *Porites astreoides*. Mean maximum diameter (mm) of juveniles corals at each study reef. Zone 1 is spur and groove zone; Zone 2 is reef flat zone; LE₁ and LE₂ are less eutrophic reefs, E₁ and E₂ eutrophic (see Table 1). SDs in parentheses

Species	LE ₁		LE ₂		E ₁		E ₂	
	Zone: 1	2	1	2	1	2	1	2
<i>A. agaricites</i>	16.2 (7.1)	16.9 (6.9)	16.3 (7.1)	18.9 (6.65)	21.8 (9.5)	22.5 (9.0)	20.8 (7.4)	21.4 (8.3)
<i>P. astreoides</i>	19.1 (9.7)	21.5 (8.7)	19.1 (8.6)	23.0 (8.6)	24.9 (7.1)	24.9 (7.1)	23.21 (8.18)	24.8 (9.2)

Diploria labyrinthiformis, *D. clivosa*, *Siderastrea siderea*) were rare or absent on eutrophic reefs (Table 5).

Species diversity of adult corals differed significantly between study reefs but not between reef zones (Tables 2 and 3). Data from zones were therefore pooled for pair-wise comparisons between reefs. Species diversity was significantly higher on the less eutrophic reefs than the eutrophic reefs (Table 3; Tukey's tests, $P < 0.05$ for all pair-wise comparisons).

Juvenile size and mortality

Mean maximum diameter of *Agaricia agaricites* juveniles differed significantly between study reefs and reef zones (Tables 2 and 6). Juvenile diameter was larger on eutrophic reefs than less eutrophic reefs in both zones (Table 6; Tukey's tests, $P < 0.01$ for all pair-wise comparisons except LE₂ vs E₂ in Zone 2, where $P = 0.26$). Mean maximum diameter of *Porites astreoides* juveniles differed significantly between study reefs and reef zones (Tables 2 and 6). As with *A. agaricites*, juvenile diameter of *P. astreoides* was larger on eutrophic than less eutrophic reefs in both zones (Table 6; Tukey's tests, $P < 0.01$ for all pair-wise comparisons).

Since juveniles on all reefs are defined as individuals < 40 mm in maximum diameter, a larger mean size on a given reef suggests fewer smaller juveniles on that reef.

Across all zones at all sites, the mean maximum diameter of juveniles was negatively correlated with the abundance of juveniles for both *Agaricia agaricites* (Spearman rank-correlation; $n = 8$, $r_s = 0.819$; $P = 0.03$) and *Porites astreoides* (Spearman rank-correlation; $n = 8$, $r_s = 0.855$; $P = 0.02$).

Mortality rates of juveniles of *Porites astreoides* differed significantly between reefs (Chi-square; $\chi^2 = 9.29$, $P = 0.026$), mortality being higher on the eutrophic reefs than the less eutrophic reefs (Tukey's tests: $P < 0.02$ for all pair-wise comparisons; Table 7). Mortality rates of juveniles of *Agaricia agaricites* were also higher on the eutrophic reefs than the less eutrophic reefs (Table 7), but the differences were not statistically significant (Chi-square; $\chi^2 = 2.07$, $P = 0.72$). When data for *A. agaricites* and *P. astreoides* were combined, significant differences were again found between reefs (Chi-square; $\chi^2 = 11.12$, $P = 0.01$), mortality being higher on the eutrophic than less eutrophic reefs (Tukey's tests; $P < 0.04$ for all pair-

Table 7. Mortality rates (% dying over 6 mo) of juvenile corals in the spur and groove zone at each study reef, presented separately by species and mortality cause. LE₁ and LE₂ are less eutrophic reefs, E₁ and E₂ eutrophic (see Table 1). Number of corals at start of study is given in parentheses

Species	LE ₁	LE ₂	E ₁	E ₂
<i>Agaricia agaricites</i>	32 (31)	29 (17)	43 (14)	50 (16)
<i>Porites astreoides</i>	12 (31)	6 (33)	31 (16)	48 (27)
<i>Diploria strigosa</i>	0 (12)	0 (15)		
<i>Diploria clivosa</i>	0 (2)	0 (2)		
<i>Agaricia agaricites</i> <i>Porites astreoides</i> }	22 (62)	16 (50)	37 (30)	48 (43)
Mortality causes (%):				
Burial by sediment/sand	12.5	0	18.2	0
Algal overgrowth	0	0	18.2	27.3
Unknown	87.5	100	63.6	72.7

wise comparisons). The causes of mortality are largely unknown for each reef. However, mortality of several juveniles at the eutrophic reefs was identified as resulting from overgrowth by algae (Table 7).

Grazing organisms and algal cover

Density of *Diadema antillarum* differed significantly between study reefs and between reef zones (Tables 2 and 8). Although there was a significant interaction effect between reef and zone (Table 8), density was significantly higher on the less eutrophic than eutrophic reefs (Table 8; Tukey's tests, $P < 0.05$ for all pair-wise comparisons except for LE₁ vs E₂ in Zone 1, where $P = 0.50$).

The density of herbivorous fish in the spur and groove zone differed significantly between reefs (Table 8; ANOVA, $F = 4.88$, $P < 0.05$). The difference was generated by the fish density on one of the less eutrophic reefs (LE₂), only LE₂ having a significantly higher fish density than the eutrophic reefs in pair-wise comparisons (Table 8; Tukey's tests, $P < 0.05$ in both cases).

Percent algal cover differed significantly between reefs (Table 8; Kruskal-Wallis test; for spur and groove zones, $\chi^2 = 35.49$, $P < 0.0001$; for reef flat zones, $\chi^2 = 16.29$, $P < 0.001$). Algal cover was higher on the eutrophic than less eutrophic reefs in both zones (Table 8; Tukey's tests, $P < 0.003$ for all pair-wise comparisons).

Table 8. Mean % algal cover, mean density of *Diadema antillarum* (per 20 m²) and mean density of herbivorous reef fish (per 40 m²) (Acanthuridae, Scaridae, Pomacentridae) on the spur and groove zone (Zone 1) and the reef flat zone (Zone 2) of each study reef. LE₁ and LE₂ are less eutrophic reefs, E₁ and E₂ eutrophic (see Table 1). SDs in parentheses

Species	LE ₁		LE ₂		E ₁		E ₂	
	Zone: 1	2	1	2	1	2	1	2
<i>D. antillarum</i> density	9.9 (9.9)	58.7 (29.3)	18.8 (14.2)	75.8 (35.7)	1.3 (2.1)	23.6 (21.0)	10.6 (7.0)	11.1 (9.3)
Fish density	31.3 (20.5)		60.7 (16.8)		18.3 (7.8)		31.7 (12.2)	
% Algal cover	5.3 (6.2)	0.3 (1.2)	2.3 (1.4)	0.1 (1.4)	50.2 (30.3)	20.9 (35.2)	60.7 (49.1)	26.7 (19.1)

Table 9. Mean relative abundance (%) of Types 1, 2 and 3 corals as juveniles (no. of colonies per quadrat) and adults (% cover per transect) on the spur and groove zone (Zone 1) and the reef flat zone (Zone 2) at each study reef. LE₁ and LE₂ are less eutrophic reefs, E₁ and E₂ eutrophic (see Table 1). Type 1 corals: high recruitment, high mortality; Type 2 corals: low recruitment, low mortality; Type 3 corals: low recruitment, high asexual reproduction

Zone Reef	Juveniles			Adults		
	Type 1	Type 2	Type 3	Type 1	Type 2	Type 3
Zone 1						
LE ₁	91.0	1.7	6.4	33.3	40.0	28.3
LE ₂	95.9	0.8	3.4	26.6	31.1	41.8
E ₁	98.5	0.0	1.6	46.8	12.2	0.4
E ₂	100.0	0.0	0.0	40.7	1.2	58.6
Zone 2						
LE ₁	96.3	0.0	4.8	38.8	5.7	55.5
LE ₂	96.0	0.1	3.8	39.0	9.3	53.3
E ₁	90.6	0.0	3.7	76.1	2.3	18.7
E ₂	91.8	0.0	3.1	64.6	0.0	34.3

Changes in community structure

Type 1 corals are those with high recruitment and hence high juvenile abundance (e. g. *Agaricia agaricites*, *Porites astreoides*); Type 2 corals are those with low recruitment and hence low juvenile abundance (e. g. *Diploria strigosa*, *D. clivosa*, *D. labyrinthiformis*, *Montastrea annularis*, *Siderastrea siderea*, *Stephanocoenia michelini*, *Meandrina meandrites*, *Dichocoenia stokesii*, *Montastrea cavernosa*, *Dendrogyra cylindrus*); and Type 3 corals are those with low recruitment but frequent asexual reproduction (e. g. *Porites porites*).

Juvenile community structure was dominated by Type 1 corals on both zones of all four reefs, with Types 2 and 3 being either absent or rare (Table 9). However, adult community structure differed between eutrophic and less eutrophic reefs. On the latter, the dominance by Type 1 corals characteristic of the juvenile community disappeared, Type 2 and 3 corals becoming relatively more common. This transition in structure as the community matures is presumably characteristic of all non-stressed coral communities. It reflects the fact that species with high recruitment have high juvenile mortality, and those

with low recruitment have low juvenile mortality. In contrast, the adult community structure on the eutrophic reefs remained dominated by Type 1 corals, particularly relative to Type 2 (Table 9). Note that eutrophic reefs can have high relative abundances of Type 3 corals in the adult community (i. e. asexual reproducers, for example at E₂).

Discussion

On both the spur and groove and reef flat zones, juvenile coral abundance was higher on the less eutrophic/low-sediment reefs than on the eutrophic/high-sediment reefs. This could result from higher juvenile mortality and/or lower juvenile recruitment on the eutrophic reefs. Our results suggest that it is caused at least partly by higher juvenile mortality, since juveniles of *Agaricia agaricites* and *Porites astreoides* had higher mortality on the eutrophic reefs. Hunte and Wittenberg (submitted) have shown lower settlement rates of corals on eutrophic/high-sediment reefs than less eutrophic/low-sediment reefs. This suggests that lower recruitment also contributes to lower abundance of juvenile corals on the eutrophic reefs. Previous studies on adult corals have inferred higher mortality under eutrophic conditions, suggesting that it results either directly or indirectly from increased algal production and sedimentation (e. g. Pastorok and Bilyard 1985, Tomascik and Sander 1987a).

In this study, the eutrophic reefs had higher algal cover than the less eutrophic reefs. This may have resulted either from elevated nutrients or from a reduction in the number of grazing organisms, since both *Diadema antillarum* and herbivorous fish were less abundant on the eutrophic reefs.

Nutrient enrichment is known to increase production of both benthic and planktonic algal populations (Smith et al. 1981). Maragos (1972) found that high benthic algal growth under eutrophic conditions smothered corals; and Birkeland (1977) termed benthic algae "r-selected" opportunists that out-compete juvenile corals for space, preventing "K-selected" corals from becoming established. Hughes (1985) found that the mortality of juvenile corals rose sharply following an algal bloom caused by the 1983–84 mass mortality of *D. antillarum* in Jamaica.

Bak (1986) showed that larvae of *Diadema antillarum* prefer to settle on clean rather than fouled substrata. Grazing by adults of *D. antillarum* may typically keep substrata clean, and thereby facilitate settlement. This may partly explain the positive correlation between adult density and recruitment strength observed in *D. antillarum* (Hunte and Younglao 1988). High algal cover under eutrophic conditions may therefore decrease *D. antillarum* abundance by reducing recruitment strength, and the lower *D. antillarum* abundance may in turn promote higher algal cover by decreasing grazing pressure. Sedimentation will also result in fouled substrata, and may therefore directly reduce *D. antillarum* recruitment. In contrast to this study, Walker and Ormond (1982) recorded high densities of *Diadema setosum* on eutrophic reefs with a high algal standing crop.

Sedimentation is known to decrease coral growth (Aller and Dodge 1974, Dodge and Vaisnys 1977) and reduce reproduction (Aller and Dodge 1974, Tomascik and Sander 1987a). Juvenile corals may be particularly sensitive to sedimentation, since they barely protrude above the surface. Consequently, they are more likely to be smothered by sediment than are larger coral colonies (Bak and Elgershuizen 1976). Hughes (1984) and Hughes and Jackson (1985) have shown that smaller individuals often have higher mortality than larger individuals but the difference may be particularly marked on eutrophic reefs. The mean diameter of juvenile corals was greater on our eutrophic than on less eutrophic reefs, supporting the suggestion of heavier mortality of smaller individuals on eutrophic reefs. However, the size difference could also result from lower recruitment or faster growth on eutrophic reefs. The negative correlation between juvenile abundance and juvenile size is consistent with all three explanations for the juvenile size difference between eutrophic and less eutrophic reefs, and none of the explanations are mutually exclusive. Moreover, Hunte and Wittenberg (submitted) have shown lower settlement rates of corals on eutrophic/high-sediment reefs than on less eutrophic/low-sediment reefs.

The juvenile coral community on both the eutrophic and less eutrophic reefs was dominated by *Agaricia agaricites* and *Porites astreoides*, i.e. Type 1 corals (high recruitment, high natural mortality; see Bak and Engel 1979, Hughes 1985). Type 2 corals (i.e. low recruitment, low mortality; for example, *Diploria strigosa*, *D. labyrinthiformis*, *Montastrea annularis*) and Type 3 corals (i.e. low recruitment, high asexual reproduction; for example, *Porites porites*) were rare members of the juvenile coral community on both the eutrophic and less eutrophic reefs. The consequence of species with high recruitment having high mortality is that the dominance characteristic of such species in the juvenile community should be much less marked in the adult community. This transition was observed on the less eutrophic reefs but not on the eutrophic reefs. Instead, with the exception of *Porites porites* on one reef (E₂), Type 1 corals remained dominant in the adult community on the eutrophic reefs.

Differences in the species composition of adult coral communities on eutrophic and less eutrophic reefs have been typically explained through differences in suscepti-

bility of different corals to eutrophication and sediment stress (e.g. Maragos 1972, Tomascik and Sander 1987a). However, the changes observed in species composition need not imply differences in susceptibility of different corals. Indeed, changes in species composition under eutrophication and sedimentation would be expected if juvenile mortality become more similar for all species on eutrophic reefs. Similar mortality rates for all corals on eutrophic/high-sediment reefs would ensure that the pattern of relative abundance of species characteristic of the juvenile community is retained in the adult community on eutrophic reefs. This was observed in the present study.

Juveniles of *Porites porites* were relatively rare on all four study reefs, but the species was well represented in all of the adult communities, particularly on eutrophic reef E₂. The scarcity of juveniles (Bak and Engel 1979, Rogers et al. 1984) and histocompatibility studies (Nigel and Avise 1983) indicate that the major mode of reproduction in branching corals such as *P. porites* is asexual reproduction through fragmentation. The high abundance of *P. porites* at E₂, despite its low juvenile recruitment, suggests increased fragmentation. This may result from increased boring by filter-feeding invertebrates, since the latter are reported to be more abundant under eutrophic conditions (Tomascik and Sander 1987a); or from effects of reduced light penetration on skeletal formation under eutrophic conditions. A branch of *P. porites* usually consists of several minor branches. Consequently, however the branch comes to rest, some portion will be off the substratum. Under eutrophic/high-sediment conditions, this could give a fragment a competitive advantage over juvenile corals by increasing the probability that it will not be smothered by benthic algae or sediment (Highsmith 1983). It may therefore be possible to view reproduction through fragmentation as both a consequence of, and a functional response to, eutrophication and sedimentation.

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Literature cited

- Aller, R. C., Dodge, R. E. (1974). Animal-sediment relations in a tropical lagoon – Discovery Bay, Jamaica. *J. mar. Res.* 32: 209–232
- Bak, R. P. M. (1986). Recruitment patterns and mass mortalities in the sea urchin *Diadema antillarum*. *Proc. 5th int. Coral Reef Congr.* 5: 267–272 [Gabri , C. et al. (eds.) Antenne Museum – EPHE, Moorea, French Polynesia]
- Bak, R. P. M., Elgershuizen, J. H. B. W. (1976) Patterns of oil-sediment rejection in corals. *Mar. Biol.* 37: 105–113
- Bak, R. P. M., Engel, M. S. (1979). Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. *Mar. Biol.* 54: 341–352
- 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 [Taylor, D.L. (ed.) Rosenstiel School of Marine and Atmospheric Science, University of Miami]
- Dart, J.K.G. (1972). Echinoids, algal lawn and coral recolonization. Nature, Lond. 239: 50–51
- Davies, P.S. (1990). A rapid method for assessing growth rates of corals in relation to water pollution. Mar. Pollut. Bull. 21: 346–348
- Dodge, R.E., Vaisnys, J.R. (1977). Coral populations and growth patterns response to sedimentation and turbidity associated with dredging. J. mar. Res. 35: 715–730
- Green, R.H. (1979). Sampling design and statistical methods for environmental biologists. John Wiley and Sons, Toronto
- Hawkins, C.M. (1979). Ecological energetics of the tropical sea urchin *Diadema antillarum Phillipi* in Barbados, West Indies. Ph.D. thesis. McGill University, Quebec
- Highsmith, R.C. (1983). Reproduction by fragmentation in corals. Mar. Ecol. Prog. Ser. 7: 207–226
- Hughes, T.P. (1984). Population dynamics based on individual size rather than age: a general model with a reef coral example. Am. Nat. 123: 778–795
- Hughes, T.P. (1985). Life histories and population dynamics of early successional corals. Proc. 5th int. Coral Reef Cong. 4: 101–106 [Gabri , C. et al. (eds.) Antenne Museum – EPHE, Moorea, French Polynesia]
- Hughes, T.P., Jackson, J.B.C. (1985). Population dynamics and life histories of foliaceous corals. Ecol. Monogr. 55: 141–166
- Hunte, W., Wittenberg, M. (submitted). Effects of eutrophication on juvenile corals. II. Settlement. Mar. Biol.
- Hunte, W., Younglao, D. (1988). Recruitment and population recovery in the black sea urchin *Diadema antillarum* in Barbados. Mar. Ecol. Prog. Ser. 45: 109–119
- Kinsey, D.W., Davies, P.J. (1979). Effects of elevated nitrogen and phosphorus on coral reef growth. Limnol. Oceanogr. 24: 935–940
- Laws, E.A. (1981). Aquatic pollution. An introductory text. John Wiley and Sons, Toronto
- Lewis, J.B. (1960). The coral reefs and coral communities of Barbados West Indies. Can. J. Zool. 38: 1133–1145
- Loya, Y. (1975). Possible effects of water pollution on the community structure of Red Sea corals. Mar. Biol. 29: 177–185
- Loya, Y. (1976). Recolonization of Red Sea corals affected by natural catastrophes and man-made perturbations. Ecology 57: 278–289
- Maragos, J.E. (1972). A study of the ecology of the Hawaiian reef corals. Ph.D. thesis. University of Hawaii, Honolulu
- Miller, R.J., Hunte, W. (1987). Effective area fished by Antillean fish traps. Bull. mar. Sci. 40(3): 484–493
- Nigel, J.E., Avise, J.C. (1983). Colonial diversity and population structure in a reef building coral, *Acropora cervicornis*: self-recognition analysis and demographic interpretation. Evolution 37: 437–453
- Pastorok, R.A., Bilyard, G.R. (1985). Effects of sewage pollution on coral-reef communities. Mar. Ecol. Prog. Ser. 21: 175–189
- Rogers, C.S. (1990). Responses of coral reefs and reef organisms to sedimentation. Mar. Ecol. Prog. Ser. 62: 185–202
- Rogers, C.S., Fitz, H.C. III, Gilnack, M., Beets, J., Hardin J. (1984). Scleractinian coral recruitment patterns at Salt River Submarine Canyon, St. Broix, U.S. Virgin Islands. Coral Reefs 3: 69–76
- Sammarco, P.W. (1980). *Diadema* and its relationship to coral spat mortality: grazing, competition, and biological disturbance. J. exp. mar. Biol. Ecol. 45: 245–272
- Sammarco, P.W., Carleton, J.H. (1981). Damselfish territoriality and coral community structure: reduced grazing and effects on coral spat. Proc. 4th int. Coral Reef Symp. 2: 339–344 [Gomez, E.D. et al. (eds.) Marine Sciences Center, University of the Philippines, Manila]
- Sas (1985). SAS/STAT guide for personal computers, Version 6 edition. SAS Institute, Inc., Cary, North Carolina
- Seakem (1989). Government of Barbados South and West Coast Sewage Project. Technical memoranda 2(a). Government of Barbados, Bridgetown
- Smith, S.V., Kimmerer, W.J., Laws, A.A., Brock, R.E., Walsh, T.W. (1981). Kaneohe Bay sewage diversion experiment. Perspectives on ecosystem responses to nutritional perturbation. Pacif. Sci. 35: 279–407
- Snelgrove, P.V.R., Lewis, J.B. (1989). Response of a coral associated crustacean community to eutrophication. Mar. Biol. 101: 249–257
- Southwood, T.R.E. (1978). Ecological methods. ELBS/Chapman and Hall, London
- Stearn, C.W., Scoffin, T.P., Martindale, W. (1977). Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part I. Zonation and productivity. Bull. mar. Sci. 84: 479–510
- Tomascik, T., Sander, F. (1985). Effects of eutrophication on reef-building corals. I. Growth rate of the reef-building coral *Montastrea annularis*. Mar. Biol. 87: 143–155
- Tomascik, T., Sander, F. (1987 a). Effects of eutrophication on reef-building corals. II. Structure of scleractinian coral communities on fringing reefs, Barbados, West Indies. Mar. Biol. 94: 53–75
- Tomascik, T., Sander, F. (1987 b). Effects of eutrophication on reef-building corals. III. Reproduction of the reef-building coral *Porites porites*. Mar. Biol. 94: 77–94
- Walker, D.I., Ormond, R.F.G. (1982). Coral death from sewage and phosphate pollution at Aquaba, Red Sea. Mar. Pollut. Bull. 13: 21–25
- Zar, J.H. (1984). Biostatistical analysis. Prentice-Hall, Englewood Cliffs