CHANGES IN CORAL COMMUNITY STRUCTURE IN BARBADOS: EFFECTS OF EUTROPHICATION AND REDUCED GRAZING PRESSURE

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Shortened version of title:

Effects of eutrophication and grazing on coral community changes

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ABSTRACT

Multivariate ordination techniques were used to characterize the direction and magnitude of coral community changes on west coast reefs in Barbados between 1982 and 1992, and to relate these changes to coastal eutrophication and variation in *Diadema antillarum* densities (grazing pressure). D. antillarum densities were substantially lower in 1992 than in 1982, reflecting the 1983 mass mortality event. Reductions in urchin density were greater on less eutrophic reefs than eutrophic reefs, since pic-mortality densities were higher on the former. Cover by macrophytic algae increased, cover by crustose coralline algae decreased, and the number of coral species decreased between 1982 and 1992. With the notable exception of the most eutrophic reef, coral cover decreased over the 10 year period. Changes in algal cover across reefs between 1982 and 1992 were strongly correlated with decreases in D. antillarum densities, and were therefore typically greater on less eutrophic reefs, indicating that reduced grazing pressure has more strongly influenced algal cover changes than prevailing eutrophication levels. Coral species composition changed at all sites between 1982 and 1992, and except at the most eutrophic site, the direction of change was directly related to reduced D. antillarum densities and associated algal cover changes. Moreover, for these reefs, the magnitude of changes in coral species composition over the 10 year period was directly proportional to the decrease in D. antillarum densities and changes in algal cover. Temporal change at the most eutrophic site was best explained by the prevailing high level of eutrophication, and resulted primarily from a substantial increase in the cover of one species, Porites porites P. porites is a branching coral, and eutrophication processes may facilitate asexual reproduction through fragmentation in this species. The decrease in coral cover that occurred on most of the study reefs in the face of the increasing cover by macrophytic algae was typically accompanied by an increase in the relative abundance of Type 1 (high recruitment, high natural juvenile mortality) to Type 2 (low recruitment, low natural

juvenile mortality) corals. This change in relative abundance would be expected if juvenile mortality rates become more similar between coral types under macroalgal stress, and/or if the typical recruitment dominance of Type 1 to Type 2 corals is magnified on such reefs.

RÉSUMÉ

Des méthodes d'ordination multivariées fürent utilisées afin de caractériser la direction et la magnitude des changements dans les communautés coralliennes de la côte ouest de la Barbade entre 1982 et 1992, ainsi que pour relier ces changements à l'eutrophisation côtière et aux variations de densités de Diadema antillarum (intensité de broutage) Les densités de D. antillarum étaient nettement réduites en 1992 comparativement à 1982, ceci résultant de la mortalité massive qui s'est produite en 1983. Les réductions de densité fûrent plus importantes sur les récifs moins eutrophes que sur les récifs plus eutrophes et ce, étant donné qu'avant la mortalité massive, les densités de D. antillarum étaient plus élevées sur les récifs moins eutrophes. Le couvert par les algues macrophytiques a augmenté tandis que celui des algues corallinacées a diminué et le nombre d'espèces coralliennes a diminué entre 1982 et 1992. À l'exception notable du récif le plus eutrophe, la couverture corallienne fût réduite au cours de ces 10 ans Les changements dans la couverture algale sur les récifs entre 1982 et 1992 étaient fortement corrélés avec les diminutions de densités de D. antillarum et furent donc généralement plus importants sur les récifs moins eutrophes. Ceci indique que l'effet de la réduction d'intensité de broutage a eu une influence plus grande sur les changements dans la couverture algale que les niveaux d'eutrophisation qui ont régnés sur les récifs durant les 10 années. La composition d'espèces coralliennes a changé sur tous les récifs entre 1982 et 1992. À l'exception du récif le plus eutrophe, la direction du changement était directement relié aux réductions de densités de D. antillarum et aux changements dans la couverture algale qui leur sont associés. De plus, pour ces récifs, la magnitude des changements dans la composition d'espèces coralliennes était directement proportionnelle au déclin des densités de D. antillarum et aux changements dans la couverture algale. Les changements temporels sur le récif le plus eutrophe étaient mieux expliqués par le niveau élevé d'eutrophisation qui régnait sur ce site, et résultent principalement d'une augmentation importante dans le couvert d'une espèce, *Porites porites*. *P.p.rites* est un corail branchant et les processus d'eutrophisation peuvent faciliter la reproduction asexuée par fragmentation dans cette espèce. La diminution de la couverture corallienne qui s'est produite sur la majorité des récifs, suite à l'augmentation du couvert par les algues macrophytiques, fût généralement accompagnée par une augmentation dans la dominance relative des coraux de Type 1 (recrutement élevé, mortalité naturelle juvénile élevée) par rapport aux coraux de Type 2 (recrutement peu élevé, mortalité naturelle juvénile peu élevé). Ce changement d'abondance relative serait attendu si les taux de mortalité juvenile deviennent comparables entre les deux types de coraux sous des conditions de stress macroalgal et/ou, si la dominance de recrutement des coraux de Type 1 par rapport aux coraux de Type 2 est accentuée sur de tels récifs.

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PREFACE

Statement of Contribution

The ideas for this research were developed by myself with input from my supervisors. I was responsible for sampling design, data collection, data analysis and initial drafting of the thesis. The final draft benefited considerably from editorial inputs by my supervisors.

Statement of Originality

This study is the first attempt to determine the relative contribution of coastal eutrophication and variation in grazing pressures to coral community dynamics when both processes are occurring simultaneously. It is the first study to use multivariate ordination techniques to quantify temporal changes in coral community structure and relate those changes to environmental factors.

Thesis Format

This thesis has been prepared for publication in a refereed scientific journal. The format corresponds to that required by the journal *Marine Biology*, to which the manuscript will be submitted.

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1.0 INTRODUCTION

Interpretations of temporal change in coral communities are often complicated by the simultaneous influence of abiotic and biotic factors related to anthropogenic and/or natural processes (Dahl, 1981; Dustan and Halas, 1987; Goreau, 1992; Porter and Meier, 1992). However, multivariate analyses can integrate the effects of abiotic and biotic factors and thereby facilitate interpretations of change by allowing the relative importance of the environmental factors to be appropriately weighted (Johnson and Wiederholm, 1989; Bakker et al., 1990; Kremen, 1992; Rodríguez et al., 1993). Typically, the long-term environmental impacts of coastal eutrophication and variation in grazing pressure have been assessed independently. When both processes are occurring simultaneously there has yet been no attempt to determine their relative contribution to coral community dynamics.

Increased nutrient and sediment loads associated with anthropogenic eutrophication can affect the distribution and abundance of corals by enhancing benthic algal biomass and water column primary production which in turn may reduce light penetration and contribute to elevated sedimentation rates (Pastorok and Bilyard, 1985; Grigg and Dollar, 1990; Rogers, 1990). Studies investigating the temporal effects of eutrophication on entire reef communities report major shifts in competitive advantage towards macrophytic algae and benthic filter-feeding invertebrates (Smith et al., 1981; Maragos et al., 1985; Hunter and Evans, 1993; Tomascik et al., 1993), presumably because the elevated nutrients disproportionately benefit the former, and the increased suspended particulate matter disproportionately benefits the latter. Eutrophication processes have been suggested to affect several coral life-history traits including adult growth (Maragos, 1972; Tomascik and Sander, 1985; Davies, 1990; Tomascik, 1990), reproduction (Tomascik and Sander, 1987b; Acosta, 1993), settlement (Tomascik, 1991; Hunte and Wittenberg, 1992; Mann, 1994), juvenile growth (Mann, 1994) and juvenile mortality (Wittenberg and Hunte, 1992; Mann, 1994). Moreover, corals with different life-history strategies may respond differently to changes in cutrophication processes and algal cover (Bak and Engel, 1979; Wittenberg and Hunte, 1992; Hughes, 1985, 1989, 1993), resulting in temporal changes in the relative abundance of coral species

Herbivore activity can strongly affect coral communities through mediation of competitive interactions between corals and algae (Berner, 1990; Cover et al., 1993). Although fish, mollusks and other micrograzers may have some effect, sea urchins, in particular Diadema antillarum, are considered the dominant herbivores in the Caribbean (Berner, 1990), particularly in shallow communities (Morrison, 1988) and on overfished reefs (Hay, 1984). Natural field studies and experimental manipulations have demonstrated an inverse relationship between D. antillarum densities and macrophytic algal abundance (Carpenter, 1981; Sammarco, 1982a). At low D. antillarum densities, macrophytic algae become dominant and inhibit settlement and survival of corals (Sammarco, 1980, 1982b). At higher D. antillarum densities, macrophytic algae are effectively removed by the urchins, and crustose coralline algae, which are more resistant to grazing, become more abundant (Benayahu and Loya, 1977; Littler and Littler, 1984; Berner, 1990). Although crustose coraline algae can outgrow corals and may therefore be a potential competitor (Littler and Littler, 1984), they can also have a positive effect by inducing settlement and metamorphosis in some corals (Morse et al., 1988; Van Moorsel, 1989; Morse and Morse, 1991). However, at extreme grazing pressures, coral recruitment and survival could be inhibited through direct consumption of recruits or increases in bioerosion/sedimentation; and optimal conditions for coral survival may therefore be at intermediate urchin densities (Sammarco, 1980).

During 1983, mass mortalities of *D. antillarum* were recorded throughout the Caribbean (Bak et al., 1984; Lessios et al., 1984; Hughes et al., 1985; Hunte et al., 1986), the event becoming the most widespread epidemic ever reported for a marine invertebrate (Lessios, 1988). The most plausible cause of the mortality is the spread of a host-specific

water-borne pathogen (Lessios, 1988). Short-term impacts on reef communities included immediate increases in macrophytic algae cover at the expense of crustose coralline algae, and severe reductions in coral cover (de Ruyter van Steveninck and Bak, 1986; Liddell and Ohlhorst, 1986; Hughes et al., 1987; Carpenter, 1985, 1988; Hughes, 1985, 1989). Although recovery of *D. antillarum* populations throughout the Caribbean appears to be slow or negligible (Hunte and Younglao, 1988; Lessios, 1988), long-term impacts of the reduced *D. antillarum* densities on coral communities have been infrequently documented (but see Hughes, 1993; Steneck, 1993).

The outcome of the competitive interactions between corals and algae may therefore be regulated by both grazing pressures and eutrophication levels (Littler and Littler, 1984, 1985; Berner, 1990; Littler et al., 1991; Knowlton, 1992), and the possibility that D. antillarum density is itself influenced by eutrophication processes is a confounding issue (Tomascik and Sander, 1987a; Wittenberg and Hunte, 1992; Mann, 1994). Eutrophication of coastal waters of Barbados has now been well documented (Lewis, 1985, 1987; Tomascik and Sander, 1985, 1987a,b; Snelgrove and Lewis, 1989; Davies, 1990; Tomascik 1990, 1991; Hunte and Wittenberg, 1992; Wittenberg and Hunte, 1992); and densities of D. antillarum were reduced by about 93.2% by the mass mortality event which occurred in early September 1983 in Barbados (Hunte et al., 1986; Hunte and Younglao, 1988). The objectives of this study are therefore to (1) characterize the direction and magnitude of changes in coral communities on the west coast of Barbados between 1982 and 1992, (2) determine how these changes relate to environmental factors at the study sites, specifically eutrophication levels, macrophytic and crustose coralline algae cover, and *D. antillarum* densities, and (3) comment on whether differences in the life-history strategies of corals appear to have influenced changes in their relative abundance on west coast reefs between 1982 and 1992.

2.0 METHODS

2.1 Study sites

The study sites were seven fringing reefs on the west coast of Barbados, namely Brighton (BR), Spring Garden (SG), Fitts Village (FV), Sandy Lane (SL), Bellairs Research Institute (BRI), Greensleeves (GS) and Sandridge (SR) (Fig. 1). In 1982, an extensive spatial study on the effects eutrophication on reef-building corals was conducted by Tomascik and Sander (1985, 1987a, b) at these seven sites. This provided the baseline data on water quality and reef community descriptors necessary for the present 1982-1992 study of temporal changes in the reef communities. Coastal development on the west coast of Barbados has resulted in the differential exposure of these reefs to sources of anthropogenic eutrophication. The major point sources of nutrients and suspended particulates are localized in the Bridgetown area and include a rum distillery outfall, a nitrate-enriched effluent from an electricity plant and domestic sewage effluent from the Bridgetown sewage treatment plant (secondary treatment). The contamination of freshwater runoff and groundwaters by agricultural waste and sewage originating from urban and tourism development also contributes substantially to the general eutrophication of coastal waters on the west coast of the island (Lewis, 1985, 1987). Most development along the west coast, north of Bridgetown, did not begin until the 1960's, and reached a peak in the early 1970's, with development centered around Holetown (BRI reef; Fig. 1) (Proctor and Redfern, 1984). There has been little further development along the west coast of Barbados during the 1980's (Ishmacl, 1993).

Figure 1. Locations of the study sites on the west coast of Barbados, West Indies. Abbreviations are: BR - Brighton, SG - Spring Garden, FV - Fitts Village, SL - Sandy Lane, BRI - Bellairs Research Institute, GS - Greensleeves, SR - Sandridge.



2.2 Reef community surveys

Prior to the resurvey of the seven study reefs in 1992, the linear transect method (LTR) used in 1982 by Tomascik and Sander (1987a) was compared with an alternate and faster method, the linear point intercept method (LPI; Kinzie and Snider, 1978; Loya, 1978; Dodge et al., 1982; Ohlhorst et al., 1988; Ohlhorst and Liddell, 1992). The methods were compared at the Greensleeves reef (GS), which was the site with the highest coral species diversity in the 1982 study. To compare the methods, twenty-one 20-m chain transects marked every 20cm were loosely draped over the reef (6 transects in the back reef, 6 in the reef flat zone, and 9 in the spur-groove zone; see Lewis 1960, Stearn et al. 1977, and Tomascik and Sander 1987a for zonation characteristics of west coast fringing reefs in Barbados). The sample size of 21 transects was chosen on the basis of species-area curves for the two census methods, which indicated that little further increase is expected in the cumulative number of new coral species with increasing number of transects surveyed beyond 21 (Fig. 2). The LTR method used is described by Tomascik and Sander (1987a). The LPI method consisted of identifying every substrate item (benthic organism) falling directly beneath each 20cm point along the 20-m transect, and giving each item so contacted a cover value of 1%. The organisms surveyed were all scleractinian corals, two hydrozoans (Millepora complanata Lamarck and M. squarrosa Lamarck), a colonial zoanthid (Palythoa mamillosa Ellis and Solander) and benthic algae. The benthic algae were identified as crustose coralline algae, turf algae (Lewis, 1986: a heterospecific assemblage of fleshy and filamentous algae < 2cm in height) and frondose macroalgae (Berner, 1990: plants >2cm in height). Total macrophytic algae was estimated by combining turf algae and frondose macroalgae. The census methods were executed simultaneously on the same transect lines to reduce the effect of chain movement, i.e. to reduce variation due to spatial differences on the reef instead of differences due to method. To reduce the possibility of making a type II error, the

Figure 2. The cumulative number of coral species as a function of the number of transects surveyed by the linear transect method (LTR) and the linear point intercept method (LPI). Data were collected at the Greensleeves reef (Fig. 1).



Number of transects

methods were considered as paired (Zar, 1984), and a Wilcoxon signed ranks test was used to investigate differences between methods. No significant differences (p>0.05) in the methods were found for any of the variables measured (d= mean difference LPI-LTR): total coral cover (d= 0.4%, p= 0.259), crustose coralline algae cover (d= 0.3%, p=0.732), macrophytic algae cover (d= -0.9%, p=0.237), cover by individual coral species (absolute and relative) (p= 0.10 is lowest value). Since the results of the comparison indicate no significant differences between the 2 methods in any of the variables, the LPI method was used to resurvey the study reefs in 1992.

For the resurveys, each reef was divided into three reference transects running perpendicular to the depth contour (see description by Tomascik and Sander, 1987a) The locations of these south, central and north reference transects were based on general reef morphology as determined by aerial photographs and drawings provided by Tomascik and Sander (1987a). The surveys were conducted along each of the reference transects, from beach edge to the seaward edge of the reef, by running the 20-m chain transects, perpendicular to the reference transects, at fixed intervals of 5 or 10m apart, depending on reef size (5m: FV, SL, GS; 10m: BR, SG, BRI, SR). The linear point intercept method was then used to quantify the benthic sessile fauna and flora as previously described. Densities of *Diadema antillarum* were also measured along each 20-m chain transect by holding a 1m rod perpendicular to the transect a few cm above the substrate, moving the rod along the transect, and recording all urchins observed beneath the rod. Urchin density was expressed as the number of individuals per m² of reef surface.

2.3 Water quality

Tomascik and Sander (1985) provided yearly means for several water quality variables measured at the seven sites between September 1981 and September 1982. To evaluate

water quality conditions in 1992, the same sampling methodology as that employed by Tomascik and Sander (1985) was used, and is described below. Between April and October, duplicate surface water samples (1m depth) were collected using a Van Dorn sampler on a bi-weekly basis to analyze for five variables, i.e. reactive phosphate, total inorganic nitrogen, suspended particulate matter, volatile particulate matter and chlorophyll-a. The samples were taken from permanent stations established at each site over the spur and groove zone (4-5m). The sampling schedule alternated between starting at sites north and south of the Bellairs Research Institute (BRI) (Fig. 1), and samples were taken between 10.00 and 13.00 hours at each station. The samples were transferred to 1-1 and 4-1 polyethylene bottles and transported to the laboratory in an insulated cooler. The 1-l samples were filtered through a GF/C glass fiber filter (previously washed, combusted and weighed), and stored in a freezer until analysis. Suspended particulate matter (SPM) was determined by drying the filters used for each sample to a constant weight at 60°C. Filters were then weighed to give SPM, combusted at 550°C for 15 min, and reweighed to obtain volatile particulate matter (VPM). Chlorophyll-a analyses were conducted using 3.51 of water (from the 4-1 bottles), while the stored water samples were used for the analyses of reactive phosphate (PO_4-P) and nitrate-nitrite-nitrogen (NO₃-NO₂-N). The three variables were analyzed according to the standard laboratory procedures described by Strickland and Parsons (1972). Monthly between April and October, duplicate sediment samples were taken with Ziploc[®] bags from the water-sediment interface between reef spurs at the study sites. The sediment samples (approximately 20 grams) were placed in pre-weighed aluminum tins, dried to constant weight at 60°C, weighed, and combusted at 550°C for 15 min to determine the percent organic matter.

Since little rainfall occurred during the sampling regime described above, a second sampling was conducted in January 1993 following heavy rainfall. For this, 10 water samples were collected at each of the sites on a single day and were analyzed for

four variables, i.e. reactive phosphate, total inorganic nitrogen, suspended particulate matter, and volatile particulate matter.

2.4 Data processing and analysis

2.4.1 Data processing

Individual reefs are the basic sampling unit for statistical analyses in this study, since water quality parameters were measured at one station per reef in both 1982 and 1992. The community variables used in the study are: total coral cover, cover by individual coral species, number of coral species, macrophytic and crustose coralline algae cover, and D. antillarum densities. Except for the number of coral species, the variables are presented as transect means per reef surface (hard substrate) for each site. Only coral species that were present in both the 1982 and 1992 surveys were considered for analysis (total of 19 species). To quantify changes in the reef communities over the 10 year period, the 1982 data obtained from Tomascik and Sander (1987a) was standardized to facilitate comparison with the 1992 data. The standardization involved: (1) Calculating a mean per reef (weighted by the number of transects used by Tomascik and Sander (1987a) in each of the 3 reef zones) for five variables, i.e. total coral cover, relative cover by individual coral species, macrophytic and crustose coralline algae cover, and D. antillarum densities, (2) Obtaining cover values for individual coral species by multiplying the relative cover values for individual coral species provided by Tomascik and Sander (1987a) by total coral cover, and (3) Re-presenting the values for total coral cover, cover by individual coral species and cover by macrophytic and crustose coralline algae derived from Tomascik and Sander (1987a) as means per unit of reef surface (hard substrate). The values for D. antillarum densities were originally presented by Tomascik and Sander (1987a) as number of individuals per m^2 of reef surface.

2.4.2 Data analysis

Principal component analysis (PCA) was used to characterize the direction and magnitude of temporal change in the coral communities. Prior to the analysis, cover values by the 19 coral species in 1982 and 1992 were arcsine $\sqrt{(x/100)}$ transformed to avoid very skewed distributions (Ter Braak, 1986). The principal component analysis was performed using the CANOCO program version 3.1 (Ter Braak, 1988, 1990). PCA is an indirect gradient analysis which ordinates sites based only on the distribution of the values of the descriptor variable (in this case, coral species cover) and thus requires no apriori assumptions about directions of underlying environmental gradients (Gauch, 1982). The ordination diagram (biplot) from the PCA (e.g. Fig. 8) is a graphical summary of the multivariate data (see Jongman et al., 1987). Scores of individual species are interpreted in relation to the origin (coordinates 0, 0) and to scores for other species. Specifically, the magnitude of response of a species to underlying environmental variables, whether abiotic or biotic, is indicated by the distance of the species score from the origin, and a difference between any two species in direction of response to underlying environmental variables is indicated by the angle between the scores for the 2 species and the origin (e.g. Fig. 8). Scores for sites (reefs) are arranged so that points which are close together indicate sites that are similar in species composition, and points that are far apart indicate sites that are dissimilar in species composition (e.g. Fig. 8). The time trajectories of the reefs (arrows; Fig. 8) indicate the magnitude (by arrow length) and direction (relative to other reefs) of changes in species composition of the reefs between 1982 and 1992.

Redundancy analysis (RDA) was used to determine the relationship between coral species and environmental variables in this study. The redundancy analysis was performed using the CANOCO program version 3.1 (Ter Braak, 1988, 1990). RDA is a

multivariate technique for direct gradient analysis in which the ordination of species and sites are constrained to lie along axes determined by the environmental variables. It can therefore be viewed as a constrained form of (multivariate) multiple regression (Ter Braak and Prentice, 1988). In the analysis, biplots are generated to illustrate the main patterns of variation in community composition as accounted for by the environmental variables, as well as to illustrate the species distributions along each environmental variable (e.g. Fig. 9). The interpretation of a RDA biplot is similar to that of a PCA, with the addition of environmental variables which are displayed as arrows pointing towards the maximum value of the variable, and with lengths proportional to their influence. Linear methods (i.e. PCA, RDA) were considered appropriate in this study since the range of ordination sample scores on the first axis obtained by a correspondence analysis was about 3 standard deviations (Jongman et al., 1987; Ter Braak and Prentice, 1988).

The environmental variables used in the redundancy analysis of coral species cover data were eutrophication levels, macrophytic and crustose coralline algae cover, and *D. antillarum* densities. Except for the eutrophication levels, the data for both 1982 and 1992 were arcsine $\sqrt{(x/100)}$ transformed prior to the analysis. The relationships between the environmental variables are provided in a Pearson correlation matrix as a first output of the redundancy analysis. The nominal variable "time" (1982 as "1" and 1992 as "2") was also included in the correlation matrix (but not in the redundancy analysis) to characterize changes in the environmental variables over time. Monte Carlo permutation tests (CANOCO program) were used to assess the significance of the relationships between coral species cover and the environmental variables.

The eutrophication levels used in the analysis were derived from the water quality parameters measured in 1982, 1992 and 1993. These were reactive phosphate, total inorganic nitrogen, suspended particulate matter, volatile particulate matter, chlorophyll-a and % organics in the sediments. Given that the seasonality of sampling was different in the different sampling years (e.g., yearly means for 1982, April-October means for 1992

and means for one day in January 1993), mean values for the parameters may not be directly comparable between years. However, the difference between reefs in any sampling period appears to have changed little, i.e. the eutrophication gradient has remained essentially the same (Table 1). This is consistent with the observation that further coastal development along the west coast of Barbados, and hence further changes in eutrophication sources, has been negligible during the 1980's (Ishmael, 1993). Data for each variable from the 3 sampling regimes were therefore combined (Table 1). A principal component analysis was then conducted with the log (x) of the combined values to reduce the highly correlated water quality variables to a single component (SYSTAT 5.2, Wilkinson, 1989). The first principal component (axis 1) accounted for 86% of the total variation in the water quality data and showed strong positive associations between the 6 water quality variables (Table 2). Site scores on the first principal component were therefore used as an index of the eutrophication levels which have prevailed at the study reefs over the 10 year period (Fig. 3).

General trends in reef community variables (i.e. total coral cover, number of coral species, macrophytic and crustose coralline algae cover, and *D. antillarum* densities) in relation to eutrophication levels were investigated in both 1982 and 1992 using simple linear regression analyses. Comparisons of the slopes of community variables on eutrophication levels between 1982 and 1992 were performed using analyses of covariance.

Table 1. Results of coastal water quality analyses since 1981 at 7 fringing reefs along the west coast of Barbados, West Indies (Fig. 1) Site abbreviationsas in Fig. 1. The data are presented as means and standard deviations (in parentheses) for each data set and as means only for the combined data setDatafrom 1981-82 are from Tomascik and Sander (1985). Data for 1992 and 1993 were collected in this study (see Methods).

Variables	BR	SG	FV	SL	BRI	GS	SR	N	YEAR
PO4-P (µg-at l ⁻¹)	0.10 (0.04)	0.21 (0.11)	0 09 (0.06)	0.08 (0 04)	0.11 (0.09)	0 06 (0 03)	0 06 (0 03)	45	1981-82
NO3-NO2-N (μ g-at l ⁻¹)	0 82 (0.43)	4.42 (2 65)	0.79 (0 50)	0 55 (0 39)	0 65 (0 39)	0 45 (0 23)	0 36 (0 21)	44	1981-82
SPM (mg l^{-1})	7 11 (4.08)	7.32 (2.86)	6.25 (3 92)	5 12 (3.46)	5 94 (3 41)	5.21 (3.29)	4 26 (1 98)	44	1981-82
$\frac{VPM}{VPM} (mg 1^{-1})$	3.26 (1.67)	3.10 (1 26)	2.71 (1.47)	1 94 (1 15)	2 49 (1.15)	2 00 (0.97)	1 85 (1.03)	43	1981-82
% Organics in sediments	8 30 (2.30)	10 90 (4.00)	4 90 (0.90)	2.50 (0.30)	5.10 (2 00)	2 30 (0.60)	2 90 (1 00)	10	1981-82
Chlorophyll a (mg m^{-3})	1 04 (0.54)	0 90 (0 41)	0 88 (0.33)	0 58 (0 29)	0.80 (0 47)	0 55 (0 27)	0.42 (0.16)	46	1981-82
PO4-P (µg-at 1 ⁻¹)	0 05 (0 03)	0 06 (0 03)	0 05 (0.03)	0.05 (0 04)	0 05 (0 04)	0 05 (0.04)	0 05 (0 03)	21	1992
NO ₃ -NO ₂ -N (μg-at l ⁻¹)	0.81 (0.69)	3.17 (2 50)	1 00 (0 60)	0.90 (0.45)	0.69 (0 38)	0 93 (1 28)	0 75 (0 56)	23	1992
SPM (mg l^{-1})	6.70 (4.37)	10 94 (20.48)	6 86 (4.96)	6.98 (4.81)	6 45 (5 22)	6 26 (4 66)	6 90 (5 60)	27	1992
VPM (mg l^{-1})	1.30 (0 58)	1 29 (0.64)	1 44 (0.84)	1 56 (0 87)	1.22 (0 76)	1 13 (0 66)	1 16 (0 62)	26	1992
% Organics in sediments	2.42 (0.43)	2.61 (0.44)	2 03 (0 43)	2.36 (0 54)	2 21 (0 34)	2 33 (0.47)	2 31 (0 62)	6	1992
Chlorophyll a (mg m $^{-3}$)	0.31 (0 07)	0.30 (0.18)	0.30 (0 17)	0.36 (0 13)	0.37 (0 17)	0 46 (0 29)	0 23 (0 07)	8	1992
······································									
PO ₄ -P (µg-at 1 ⁻¹)	0 09 (0 04)	0 13 (0.07)	0 08 (0 03)	0 09 (0 05)	0 09 (0 02)	0.08 (0 03)	0.10 (0 05)	10	1993
NO3-NO2-N (μ g-at l ⁻¹)	0.87 (0 26)	7 51 (2.65)	1 05 (0 30)	0 75 (0 21)	0 91 (0 18)	0.82 (0 30)	0 74 (0 27)	10	1993
SPM $(mg l^{-1})$	6 88 (0 75)	7 83 (2.91)	4 79 (0.58)	4 41 (1 49)	4 11 (1 10)	3.83 (0 82)	4 62 (1 14)	10	1993
$\frac{VPM}{VPM} (mg l^{-1})$	2 81 (0 38)	2 92 (0 90)	1 90 (0 62)	2 33 (0.72)	1 45 (0 78)	1 05 (0 56)	1 44 (0 78)	10	1993
		(,	,	,					
PO ₄ -P (µg-at l ⁻¹)	0 09	0 16	0.08	0 07	0.09	0 06	0 06	76	Combined
NO ₃ -NO ₂ -N (ug -at l^{-1})	0 82	4 45	0 89	0 68	0 69	0 64	0.52	77	Combined
SPM (mg l^{-1})	6 94	8.59	6 27	5 65	5 88	5 39	5 19	81	Combined
$\frac{VPM}{VPM}$	2 56	2.48	2 19	1 86	1 94	1 59	1 57	79	Combined
% Organics in sediments	6 09	7 79	3.82	2.45	4 01	2 31	2.68	16	Combined
Chlorophyll a (me m^{-3})	0.93	0 81	0 79	0 55	074	0 53	0 39	54	Combined
Successive a ting in the									

Table 2. Scores of the water quality variables on the first principal component of the PCA of water quality data for the 3 sampling regimes (i.e. 1982, 1992, 1993)

Water quality variables	Scores on principal component 1					
PO4-P (μg-at 1 ⁻¹)	0.959					
NO3-NO2-N (μ g-at 1^{-1})	0.874					
SPM (mg l^{-1})	0.982					
VPM (mg l^{-1})	0.924					
% Organics in sediments	0.965					
Chlorophyll a (mg m ⁻³)	0.850					

Figure 3. Eutrophication levels prevailing at the 7 study sites (from less eutrophic to more eutrophic), based on site scores on the first principal component of the PCA of water quality data for the 3 sampling regimes combined (i.e. 1982, 1992, 1993). Site abbreviations and locations as in Fig. 1.



3.0 RESULTS

3.1 General trends in reef community variables

Reef community variables for the 7 study reefs differing in the eutrophication levels prevailing over the 10 year period of the study, are shown for 1982 and 1992 in Table 3. Densities of *Diadema antillarum* were lower on more eutrophic than on less eutrophic reefs in both 1982 and 1992 (Table 3, Fig. 4; 1982, r^2 = 0.799, p= 0.007; 1992, r^2 = 0.656, p= 0.027). Densities were also substantially lower on all reefs in 1992 than in 1982, reflecting the mass mortality event that occurred in September 1983 in Barbados. The density reductions between 1982 and 1992 were greater on reefs where densities were higher (less eutrophic sites) than on reefs where densities were lower (more eutrophic sites) (Table 3, Fig. 4; 1982 slope > 1992 slope; ANCOVA, p= 0.004). However, the probability of an urchin dying during the mortality event (% reduction in density) was not correlated with the eutrophication level (nor urchin density) of the reefs at the time of the mortality (Fig. 5; r^2 = 0.023, p= 0.746; see also Hunte et al., 1986).

Cover by macrophytic algae was higher on the more eutrophic than on the less eutrophic reefs in 1982 but not in 1992 (Table 3, Fig. 6A; 1982, $r^2=0.539$, p=0.06; 1992, $r^2=0.001$, p=0.939). Macrophytic algae cover was substantially higher on all reefs in 1992 than in 1982, the increase in algae cover between years being greater on the less eutrophic than on the more eutrophic reefs (Table 3, Fig. 6A; 1982 slope > 1992 slope; ANCOVA, p=0.06). Cover by crustose coralline algae was lower on the more eutrophic than on the less eutrophic reefs in 1982 but not in 1992 (Table 3, Fig. 6B; 1982, $r^2=$ 0.485, p=0.082; 1992, $r^2=0.387$, p=0.136). Crustose coralline algae cover was substantially lower on all reefs in 1992 than in 1982, the decrease in cover between years tending to be greater on the less eutrophic than on the more eutrophic reefs (Table 3, Fig. 6B; 1982 slope Vs 1992 slope; ANCOVA, p=0.152).

Variable	BR		S	SG J		FV S		SL		RI	GS		SR	
	1982	1992	1982	1992	1982	1992	1982	1992	1982	1992	1982	1992	1982	1992
Diadema antillarum	3.17	0.27	4.99	0.64	6 48	1.46	12.73	2.33	9.79	0 76	16.45	2 13	14 64	1.83
Macrophytic algae	75.13	90.2	47.77	73.47	46 61	85.34	32.82	85 19	29.07	88.01	21 58	73 9 8	18.6	79.11
Crustose coralline algae	22.25	3.53	46.54	8.25	49.3	9.83	55.85	9.28	59.41	5.47	63 79	16 76	68 47	11.89
Number of coral species	9	7	11	11	13	11	21	15	20	13	28	16	22	17
Total coral cover	4.67	5.37	5.61	12 64	4.16	3.28	11 37	5.29	11.18	6 02	14.68	7.44	12 88	6.27
N	66	64	82	76	73	70	75	75	65	68	90	92	62	64

Table 3. Reef community variables for the 7 study reefs in 1982 and 1992. Data are means per reef surface for *Diadema antillarum* densities (x/m^2) , macrophytic algae cover (%), crustose coralline algae cover (%), number of coral species and total coral cover (%). The number of transects (N) surveyed per reef is presented. Site abbreviations and locations as in Fig. 1.

Figure 4. Densities of *Diadema antillarum* $(\#/m^2)$ in 1982 and 1992 at recf sites differing in the eutrophication levels prevailing over the 10 year period. Eutrophication levels as in Fig. 3



Eutrophication level
Figure 5. Percentage reduction in densities of *Diadema antillarum* ($\#/m^2$) between 1982 and 1992 at reef sites differing in eutrophication levels prevailing over the 10 year period. Eutrophication levels as in Fig. 3.



Figure 6. Algal cover (% cover) in 1982 and 1992 at reef sites differing in eutrophication levels prevailing over the 10 year period. Eutrophication levels as in Fig. 3. (A) Macrophytic algae. (B) Crustose coralline algae.



A







The number of coral species was lower on the more cutrophic than on the less eutrophic reefs in both 1982 and 1992 (Table 3, Fig. 7A; 1982, r^2 = 0.725; p= 0.015; 1992, r^2 = 0.647, p= 0.029). The number of species was lower in 1992 than in 1982, the decrease in coral species between years tending to be greater on the less eutrophic than on the more eutrophic reefs (Table 3, Fig. 7A; 1982 slope Vs 1992 slope; ANCOVA, p= 0.132). Total coral cover was higher on the less eutrophic reefs than on the more eutrophic reefs in 1982, although cover on the most eutrophic reef appeared higher than expected on the basis of the slope of the relationship between coral cover and eutrophication levels across sites (Table 3, Fig. 7B; r^2 = 0.656, p= 0.027). Coral cover also appeared to be higher on the less eutrophic reefs than on the more eutrophic reefs in 1992, with the notable exception of the most eutrophic reef, coral cover was typically higher in 1982 than in 1992, the decrease between years being greater on the less eutrophic reefs coral cover was typically higher in 1982 than in 1992, the decrease between years being greater on the less eutrophic than on the more eutrophic than on the more eutrophic reefs (Table 3, Fig. 7B; Fig. 7B; 1982 slope > 1992 slope; ANCOVA, p= 0.042).

3.2 Characterization of coral species changes and effects of environmental variables

3.2.1 Characterization of species changes

Species-specific coral cover values at the 7 study sites in 1982 and 1992, and percent changes in the values between the years, are presented in Table 4. These data were used in a principal component analysis to generate an ordination biplot that represents the similarities between reefs in space and time based on their coral assemblages (Fig. 8). The first two axes of the PCA accounted for 64.4% of the total variation in the coral species data. Figure 8 displays two main clusters of species, one where most corals are grouped and another where *Porites porites* is isolated. Isolation of a species can occur

Figure 7. The number of coral species and the total coral cover in 1982 and 1992 at reef sites differing in eutrophication levels prevailing over the 10 year period. Eutrophication levels as in Fig. 3. (A) Number of coral species (B) Total coral cover.







A

		1092	BR	(1	1093	SG	<i>C</i> 1	1083	FV	a	1093	SL 1002	a.	1097	BRI	7	1097	GS	0	1083	SR	
Coral species	Code	1982	1992	[%] Change	1982	1992	[%] Change	1982	1992	% Change	1982	1992	⁷ Change	1982	1992	Change	1982	1992	Thange	1982	1992	Thange
Acropora palmata	АР	0 00	0 00	0 00	0 00	0 00	0 00	0 00	0 00	0 00	0 00	0 03	А	0 00	0 00	0 00	0 21	0 00	в	0 03	0.00	в
Agaricia agaricites	AA	0 51	035	-31 77	0 70	0.06	-91 63	0 10	013	22 81	0 85	1 30	52 28	1 77	1 43	-18 80	0 48	0.38	-20 66	0 64	0.25	-60 53
Dendrogyra cylindrus	DY	0 00	0.00	0 00	0 00	0 02	Α	0 00	0 00	0 00	0 00	0.00	0 00	0 00	0 02	Α	0 19	015	-19 75	0 00	0.00	0 00
Diploria clivosa	DC	0 06	0 00	В	0 04	0 23	499 88	0 23	0 04	-83 99	1 08	0 03	-97 27	0 48	0 45	-6 24	0 65	0 22	-66 31	0 85	014	-83 90
Diploria labyrinthiformis	DL	0 00	0 00	0 00	0 01	0 00	В	0 00	0.00	0 00	010	0 00	В	0 01	0 03	200 25	015	0 00	В	0 22	0 00	В
Diploria strigosa	DS	0 00	0 00	0 00	0 13	0 02	-84 77	015	013	-12 01	0 32	0 01	-95 40	1 30	0 03	-97 42	0 35	017	-52 75	0 40	0 25	-36 38
Favia fragum	FF	0 00	0 00	0 00	0 06	0 08	25 86	0 09	0 09	4 77	0 05	0 04	-2 27	0 06	0 00	В	0 34	019	-43 24	018	0 02	-89 18
Madracis decactis	MD	0 00	0.00	0 00	0 00	0 00	0 00	0 01	0 00	В	0 03	0 00	B	0 02	0 00	В	015	0 04	-73 70	0 03	0.06	128 88
Madracıs mırabılıs	MM	0 00	0 00	0 00	00)	0.00	0 00	0 00	0 00	0 00	013	0 01	-88 30	0 73	0 00	В	015	0 00	В	014	0 10	-30 98
Meandrina meandrites	ME	0 00	0 00	0 00	0 00	0 00	0 00	0 00	0 00	0 00	0 06	0 00	В	0 01	0 00	В	0 10	0 00	В	0 22	012	-46 66
Millepora complanata	MCO	0 04	0 00	В	0 28	0 96	240 58	0 45	0 55	21 32	1 29	041	-67 85	021	0 38	80 46	2 57	1 29	-49 71	021	0 47	128 14
Millepora squarossa	MSQ	0 17	0 56	222 87	013	0 16	21 59	016	0 42	159 94	0 48	0 34	-28 76	0 85	0 32	-62 74	0 56	O 59	5 48	1 07	0 35	-67 07
Montastrea annularis	MA	0 62	1 22	95 04	0 28	0 25	-9 55	0 06	0 02	-70 44	0 57	0 27	-53 25	091	0 33	-63 16	1 37	0 40	-70 95	0 85	061	-28 71
Montastrea cavernosa	MC	0 00	0 00	0 00	0 00	0 00	0 00	0 13	0 00	B	015	0 01	-90 07	013	0 02	-87 62	0 25	0 26	2 68	0 88	0 59	-33 14
Palythoa mamillosa	PM	0 00	0 02	Α	0 00	0 00	0 00	0 00	0 00	0 00	0 20	0 00	В	0 25	1 27	414 40	018	0 26	45 34	0 23	0 47	101 86
Porites astreoides	PA	1 14	1 82	58 88	186	3 35	79 90	1 42	1 32	-6 90	4 09	2 23	-45 53	2 38	1 35	-43 28	4 14	2 38	-42 53	3 44	1 91	-44 30
Porites porites	PP	0 85	0 99	17 31	1 87	7 50	299 77	0 43	0 31	-27 42	0 27	0 19	-29 88	0 44	0 08	-80 91	1 29	0 59	-54 45	0 93	0 04	-95 78
Siderastrea radians	SR	0 99	0 41	-58 50	0 24	0 02	-91 85	0 68	0 26	-62 28	0 63	0 10	-83 51	0 12	0 00	В	0 28	0 05	-81 60	1 09	0 08	-92 87
Siderastrea siderea	SS	0 27	0 00	-100 00	0 00	0 00	0 00	0 24	0 02	-92 35	0 88	0 27	-69 60	1 27	0 30	-76 41	0 95	0 44	-54 36	1 42	0 76	-46 15

Table 4. Species-specific values of coral cover (%) at the 7 study sites in 1982 and 1992, and the percentage change for each coral species over the 10 year period. A indicates that the species was absent in 1982 but present in 1992, B indicates that the species was present in 1982 but absent in 1992. Site abbreviations as in Fig. 1

Figure 8. Principal component analysis (PCA) ordination biplot of coral species and reefs. Points are the species scores, arrows are the time trajectories of the reefs (reef score in 1982 to reef score (arrow head) in 1992) (see Methods for interpretation). Coral species codes as in Table 4; Sites abbreviations (bold) as in Fig. 1.



if, either the magnitude of response of the species to underlying environmental variables differs from the other species (as indicated by the distance of the species score from the origin), and/or, if the direction of response of the species differs from that of other species (as indicated by the angle between the score for the isolated species, the origin, and the scores for the other species). Figure 8 indicates that the isolation of *P. porites* has occurred primarily because its direction of response differs from that of other species, i.e. **P. porites** responded differently than other coral species to underlying environmental variables. The distribution of the reef scores in Fig. 8 indicates that the coral species composition of the most eutrophic reef (SG) differs considerably from that of the other reefs. The direction of change in species composition between 1982 and 1992 at SG is driven strongly by a substantial increase in the cover of *P. porites* (see time trajectory (arrows) for SG in relation to *P. porites* species score, Fig. 8; also Table 4) and, to a lesser extent, by increases in cover of P. astreoides, Millepora complanata and Favia fragum. (Fig. 8; Table 4). The trajectories of the other reefs are similar and are associated with reductions in cover for most of the coral species (Fig. 8; Table 4). Except for SG where the change in species composition is driven largely by the increase in the abundance of *P. porites*, the magnitude of change in species composition (arrow/vector length; Fig. 8) appears greater at the less eutrophic reefs (SR, GS, SL, BRI) than at the more eutrophic ones (BR, FV).

To determine if the arched distribution of the site scores observed on the first two axes of the PCA biplot in Figure 8 was related to an ecological phenomenon or was due to a mathematical artefact (the "arch-effect"; Hill and Gauch, 1980; Jongman et al., 1987; Peet et al., 1988), a second principal component analysis was performed on the coral species data but omitting *P. porites*. With *P. porites* removed, the time trajectory of SG was much less pronounced and was largely associated with slight increases in the cover of *P. astreoides* and *M. complanata*. This confirms that the arched distribution of reef scores in Figure 8 is not the consequence of a mathematical artefact.

3.2.2 Effects of environmental variables

The relationships between the environmental variables used to interpret the changes in coral communities (i.e. eutrophication levels, macrophytic and coralline algae cover, and D. antillarum densities) are presented as Pearson correlation coefficients in Table 5. Results of an investigation of temporal variations in the environmental variables through their correlations with the nominal variable "time" are also presented in Table 5. Since the eutrophication gradient appears not to have changed between 1982 and 1992, eutrophication levels and time are uncorrelated in the analysis (r = 0). Crustose coralline algae cover and D. antillarum densities showed strong negative correlations with time, while macrophytic algae cover showed a strong positive correlation (Table 5). The increase in macrophytic algae cover and the decrease in crustose coralline algae cover on a reef are highly correlated with the decrease in D. antillarum density on the reef over the 10 year period (Table 5). Neither the change in crustose coralline algae cover, in macrophytic algae cover, or in D. antillarum density on a reef were correlated with the eutrophication level prevailing at the reef over the 10 year study period (Table 5). Since the relationship between crustose coralline algae and macrophytic algae is essentially collinear (Table 5; variance inflation factor greater than 20; Ter Braak, 1988), only macrophytic algae was retained for the redundancy analysis. Since the effects of reduced crustose coralline algae cover can not be statistically distinguished from those of increased macrophytic algae cover, interpretation of their effects is made simultaneously hereafter.

The redundancy analysis was used to identify the major environmental processes that might underlie the changes in coral species composition observed on the study reefs. The first two axes in the redundancy analysis explained 91.9% of the variance in the coral species-environment relationship (Table 6). This suggests that discarding the third and

Crustose coralline algae cover	Macrophytic algae cover	D. antillarum densities	Eutrophication levels	Time
1.00				
-0.98 *	1 00			
0 96 *	-0.96 *	1.00		
-0.26	0.26	-0.43	1 00	
-0.91 *	0.85 *	-0 84 *	0 00	1.00
	Crustose coralline algae cover 1.00 -0.98 * 0.96 * -0.26 -0.91 *	Crustose coralline algae cover Macrophytic algae cover 1.00 -0.98 * 1 00 -0.98 * -0.96 * -0.96 * -0.26 0.26 -0.91 *	Crustose coralline algae cover Macrophytic algae cover D. antillarum densities 1.00 -0.98 * 1 00 -0.98 * 1 00 -0.96 * -0.26 0.26 -0.43 -0.91 * 0.85 * -0 84 *	Crustose coralline algae cover Macrophytic algae cover D. antillarum densities Eutrophication levels 1.00 -0.98 * 1 00 -0.96 * 1.00 0 96 * -0.96 * 1.00 -0.26 0.26 -0.43 1 00 -0.91 * 0.85 * -0.84 * 0 00 -0.90

Table 5. Pearson correlation coefficients between the environmental variables used to interpret changes in the coral communities on the study reefs. "*" indicates P< 0.001

Table 6. Results of the redundancy analysis (RDA) of environmental variables on coral species abundances, presented for the first 2 ordination axes Significance levels (p) are Monte Carlo probabilities based on 999 permutations First axis, p<0.01 and second axis, p<0.05 (with axis 1 as covariable)

	RI	DA
	Axis 1	Ax15 2
Summun total trai		
Summary statistics		
Eigenvalue	0.340	0.126
Cumulative % of		
variance explained	67 0	91.9
Species-environment correlation	0 952	0.753
Canonical coefficients of		
environmental variables		
Morronhutto algas sour	0.67	2.55
Macrophytic algae cover	-0.07	2.55
Diadema antillarum densities	-0 19	1 91
Eutrophication level	-0.79	-0.29

lower axes should not result in significant information loss. Although eigenvalues were not very high, the strength of the relationship between coral species and the environmental variables was confirmed by the high and statistically significant speciesenvironment correlations on axes 1 and 2 (Table 6) The standardized canonical coefficients for individual environmental variables indicate a strong influence of macrophytic algae cover (and by extension crustose coralline algae) on coral species composition along both ordination axes, a strong influence of eutrophication levels primarily along axis 1, and a strong influence of *D. antillarum* densities primarily along axis 2 (Table 6).

The relationships between the coral species and the environmental variables are presented as a redundancy analysis ordination biplot in Figure 9. As with the PCA ordination biplot (Fig. 7), two main clusters of species can be distinguished, one where most corals are grouped and another where *P. porites* is isolated (Fig. 9). The abundance of *P. porites* is higher at higher eutrophication levels (see location of *P. porites* score in relation to the direction of eutrophication increase; Fig. 9). By contrast, most coral species have lower abundances at higher eutrophication levels (compare locations of species scores with direction of eutrophication increase; Fig. 9). Moreover, most coral species are more abundant at lower values of macrophytic algae cover, and more abundant at higher *D. antillarum* densities and higher values of crustose coralline algae cover (Fig. 9).

The time trajectories for the 7 reefs based on their species composition in 1982 and 1992 are shown in relation to the environmental variables in Figure 10. The trajectories are very similar to those obtained with the principal component analysis (Fig.7). The similarity suggests that environmental variables not measured in the study have not had a major effect on changes in coral species composition (see Jongman et al.,1987; Kremen, 1992). Changes in the species composition at SG between 1982 and 1992 are being driven by the increased abundance of *P. porites*, and are associated with

Figure 9. Redundancy analysis (RDA) ordination biplot of coral species and environmental variables. Points are the species scores and arrows are the environmental variables (see Methods for interpretation). MA is macrophytic algae; CCA is crustose coralline algae. Since MA and CCA are essentially collinear (see text), interpretations of their inverse relationship are made simultaneously. Coral species codes as in Table 4.



Figure 10. Redundancy analysis (RDA) ordination biplot of reefs and environmental variables. Light arrows are the time trajectories of the reefs (reef score in 1982 to reef score in 1992); dark arrows are the environmental variables (see Methods for interpretation). MA is macrophytic algae; CCA is crustose coralline algae. Interpretations of the inverse relationship between MA and CCA are made simultaneously (see legend of Fig. 9). Sites abbreviations as in Fig. 1.



the higher eutrophication levels at that site (Fig. 10). The direction of change in the species composition at the other reefs between 1982 and 1992 is similar but differs from SG (Fig. 10). The change is accompanied by a reduction in the abundance of most coral species associated with decreases in *D. antillarum* densities, increases in macrophytic algae cover, and decreases in crustose coralline algae cover. For these 6 reefs, the magnitude of change in species composition at a site between 1982 and 1992 (vector length/arrow length; Fig. 10) is significantly correlated with the mean increase in macrophytic algae cover (r = 0.911, p= 0.011), mean decrease in crustose coralline algae cover (r = -0.867, p= 0.025) and mean decrease in *D. antillarum* density (r = -0.833, p= 0.04) over the 10 year period at the site (see Table 3 for data on changes in algal cover and *D. antillarum* densities between 1982 and 1992).

3.3 Coral species changes in relation to coral life history strategies

Scleractinian corals are often grouped into 3 types based on their life history strategies (see Bak and Engel, 1979; Hughes, 1985; Szmant, 1986; Smith, 1992; Wittenberg and Hunte, 1992). Type 1 corals brood planula larvae, and tend to have high recruitment rates and high natural juvenile mortality (e.g. Agaricia agaricites, Favia fragum, Meandrina meandrites, Porites astreoides, Siderastrea radians). Type 2 corals broadcast gametes, and tend to have low recruitment rates and low natural juvenile mortality (Dendrogyra cylindrus, Diploria clivosa, D. labyrinthiformis, D. strigosa, Montastrea annularis, M. cavernosa, Siderastrea siderea). Type 3 corals may either brood larvae or broadcast gametes. They typically have low recruitment rates, relying primarily on asexual reproduction (e.g. Acropora palmata, Madracis mirabilis, Porites porites).

The relative abundance of Type 1, Type 2 and Type 3 corals on the 7 study reefs is shown in Table 7. At BR, coral cover was low in both 1982 and 1992 with little change between years (Table 3). Species composition also changed little between years

Table 7. Mean relative abundance (%) of Type 1, Type 2 and Type 3 corals on the 7 study reefs in 1982 and 1992 Relative abundance is based on cover data (% cover per reef). Type 1 corals: brood larvae, high recruitment, high natural juvenile mortality: Type 2 corals. broadcast gametes, low recruitment, low natural juvenile mortality: Type 3 corals⁻ low recruitment, high asexual reproduction Relative abundance of Type 1 and Type 2 corals excluding Type 3 is also presented Site abbreviations as in Fig. 1; eutrophication levels as in Fig. 3.

strategy	BR		SG		FV		SL		BRI		GS		SR	
	1982	1992	1982	1992	1982	1992	1982	1992	1982	1992	1982	1992	1982	1992
Type 1	59.46	53 86	55.11	30 44	64.87	77.59	61 87	81.74	45.16	68.81	48.99	57 36	49 34	48 87
Type 2	21.40	25.47	8.86	4 51	22 95	9.05	33 77	13 14	42 66	29 21	35 87	31 36	40.92	48 25
Type 3	19.14	20.67	36.03	65.05	12 18	13.36	4.36	5 12	12 17	1 98	15 14	11 28	9.74	2 87
Type 1	73.54	67.89	86 14	87.10	73 87	89.55	64.69	86 15	51 42	70 20	57 73	64 66	54 66	50.32
Type 2	26.46	32.11	13.86	12 90	26.13	10.45	35.31	13 85	48 58	29 80	42.27	35 34	45 34	49 68

(Figs. 8, 10), with Type 1 corals being dominant in both 1982 and 1992 (Table 7). At SG, the major change is an increase in Type 3 corals (Table 7). This is the consequence of the increase in *P. porites* already documented (Table 4; Figs. 8 and 9). Excluding Type 3 corals, coral cover is low at SG, and Type 1 corals are strongly dominant to Type 2 corals in both years (Table 7). At FV, SL, BRI and GS, coral cover decreased between years (Table 3), and the decrease was accompanied by an increase in the relative abundance of Type 1 to Type 2 corals at all sites (Table 7). The sole exception to the pattern of an increase in the relative abundance of Type 1 to Type 2 corals were equivalently abundant, and relative abundance changed little between years (Table 7), although total cover was decreasing (Table 3).

4.0 DISCUSSION

Tourism, urban, agricultural and industrial developments on the west coast of Barbados over the past 30 years (Proctor and Redfern, 1984; Ishmael, 1993) have resulted in the differential exposure of the reefs to anthropogenic cutrophication. This has produced a eutrophication gradient along the west coast of the island which was first documented by Tomascik and Sander (1985) in 1982, but is likely to have been present prior to this. Water quality analyses indicate that the eutrophication gradient, has changed little between 1982 and 1992, and this is consistent with records indicating that development along the west coast peaked in the mid-1970's and has been negligible throughout the 1980's (Proctor and Redfern, 1984; Ishmael, 1993). Differences in coral communities at the study sites have therefore been interpreted in relation to the eutrophication levels prevailing at the sites over the 10 year period 1982-1992 (see Cramer and Hytteborn 1987, Wiegleb et al. 1989, and Kremen 1992 for examples of community monitoring in relation to established environmental gradients using ordination techniques). Note that the similarities between the ordination diagrams of the principal component analysis (indirect direct gradient) (Fig. 8) and that of the redundancy analysis (direct gradient analysis) (Figs. 9 and 10) in this study indicate that environmental variables not explicitly considered in the study have not had a major effect on temporal changes in coral community structure over the 10 year period (Jongman et al., 1987; Kremen, 1992).

A major change occurring in the reef communities on the west coast of Barbados between 1982 and 1992 was the sharp reduction in *Diadema antillarum* densities caused by the mass mortality event of September 1983 (mean 93.2%; Hunte et al., 1986). Prior to the mortality (i.e. 1982), densities of *D. antillarum* were lower on more cutrophic than on less eutrophic reefs. However, the probability of an urchin dying during the mortality event (% reduction in population size) did not differ with *D. antillarum* density on the reef (Hunte et al., 1986) nor with the eutrophication level of the reef (this study). One

consequence of this is that the negative correlation between *D. antillarum* densities and eutrophication levels on the reefs in 1982 was retained through the mortality event and to date (i.e. 1992). A second consequence is that density reductions during the mortality were greater where densities were higher, i.e. density reductions were greater on less eutrophic than on more eutrophic reefs. This difference between reefs in the magnitude of density reductions has been retained to date (1982-1992 comparison of *D. antillarum* densities).

The decrease in D. antillarum densities has strongly influenced other reef community variables. Specifically, the increase in macrophytic algae cover and decrease in crustose coralline algae cover on a reef between 1982 and 1992 are strongly correlated with the decrease in D. antillarum density on the reef between years, presumably reflecting the change in grazing pressure. Since reductions in D. antillarum densities were greater on less eutrophic reefs, changes in algal cover between 1982 and 1992 tended to be greater on less eutrophic than on more eutrophic reefs, i.e. changes in algal cover on Barbados west coast reefs between 1982 and 1992 have been more strongly influenced by the reduced grazing pressure following the 1983 mortality of D. antillarum than by prevailing eutrophication levels. These results imply that herbivorous fish have been unable to compensate for the reduced grazing pressure resulting from D. antillarum loss in the years following the mortality event. Inadequate compensation by herbivorous reef fish has previously been reported in areas of the Caribbean where fish stocks have been overfished (Liddell and Ohlhorst, 1986; Hughes et al., 1987; Hughes, 1993; Steneck, 1993). Low abundances of reef fish due to high fishing pressure on west coast fringing reefs in Barbados (Wilson, 1984) may therefore have magnified the importance of D. antillarum as a regulator of algal populations in these reef communities.

The spatial correlation between *D. antillarum* densities and eutrophication levels on west coast reefs in 1982, which has been retained to 1992 despite the 1983 mortality, is worthy of comment. *D. antillarum* preferentially recruits to clean substrates (Bak, 1985), and the grazing activities of adults may help to keep substrates free of macrophytic algae (Sammarco, 1980), thereby promoting recruitment. This may partly explain why *D. antillarum* recruitment is higher on reefs with higher adult densities (Hunte and Younglao, 1988). On less eutrophic reefs, grazing by *D. antillarum* may keep substrates relatively clean, thereby promoting recruitment and increasing densities and hence grazing pressure. On more eutrophic reefs, elevated nutrients may enhance growth of macrophytic algae, thereby overwhelming urchin grazing capabilities, inhibiting urchin recruitment and reducing densities. The reduced densities will lower grazing pressure and further inhibit recruitment. This positive feedback cycle, whereby *D. antillarum* grazing influences *D. antillarum* recruitment, could therefore explain the observed correlation between *D. antillarum* densities and eutrophication levels on west coast reefs (see also Wittenberg and Hunte, 1992; Mann, 1994).

The reduction in *D. antillarum* densities and consequent changes in algal cover between 1982 and 1992, have strongly influenced the coral communities on Barbados west coast reefs over the 10 year period. Except for the most eutrophic site SG, where the reduction in *D. antillarum* density was low, most of the reef sites lost coral cover between 1982 and 1992. The decrease in coral cover may result from changes in algal cover. Increased macrophytic algae cover may cause overgrowth and increased mortality of both recruits and established colonies (Sammarco, 1980, 1982b; Hughes, 1989). Reduced cover by crustose coralline algae may decrease coral settlement (Van Moorsel, 1989; Hunte and Wittenberg, 1992). Recent studies on *Favia fragum* in Barbados suggest that changes in algal cover may reduce coral cover primarily by affecting settlement and early post-settlement processes (Mann, 1994).

All reef sites changed in species composition over the 10 year period, and except for SG, the direction of change was directly related to the reduced *D. antillarum* densities and the associated changes in algal cover. Moreover, for these reefs, the magnitude of change in coral species composition between 1982 and 1992 was proportional to the

decrease in *D. antillarum* density, the increase in macrophytic algae cover and the decrease in crustose coralline algae cover on the reef between 1982 and 1992. Since reductions in *D. antillarum* densities, and consequently changes in algal cover were greater on less eutrophic than on more eutrophic reefs between 1982 and 1992, changes in coral communities on west coast reefs in Barbados over the 10 year period have been greater on less eutrophic than on more eutrophic reefs.

At the most eutrophic reef SG, where reduction in D. antillarum density was low, the change in coral community structure was best explained by the prevailing high level of eutrophication at the site. The change at SG results primarily from a substantial increase in the cover of one species, Porites porites, between 1982 and 1992. P. porites was already the most abundant species on this reef in 1982, and its abundance on west coast reefs follows the eutrophication gradient, i.e. is greatest where eutrophication is highest. It is of interest in this context that the abundance of *P. porites* decreased at all other sites between 1982 and 1992 except for BR, which ranks second to SG in eutrophication level. Several studies have suggested that the major mode of reproduction in branching corals such as P. porites is asexual reproduction through fragmentation (Bak and Engel, 1979; Highsmith, 1982; Szmant, 1986). Fragmentation may increase under eutrophic conditions through several processes that are not mutually exclusive. Increases in suspended particulate matter at eutrophic sites may favor benthic filter-feeding invertebrates, including borers, and hence may increase fragmentation (Highsmith et al., 1983; Tomascik et al., 1993). Eutrophication processes may reduce sexual reproduction in *P. porites* (Tomascik and Sander, 1987b), allowing more energy to be allocated to growth and hence fragmentation. Reduced light penetration may reduce calcification rates and thereby the strength of coral skeletons (Barnes and Chalker, 1990). Finally, fragments of *P. porites* usually consist of several minor branches, such that however the fragment comes to rest, some portion will be off the substrate. This may give fragments a competitive advantage over sexual recruits and juvenile corals by increasing the

probability that they will not be overgrown by benthic algae or smothered by sediments (Wittenberg and Hunte, 1992).

Reef morphology characteristics which affect the magnitude and distribution of wave energy at SG could have contributed to the high abundance of *P. porites* in 1982 at this site compared to other west coast reefs. The reef at SG appears well protected from incoming offshore waves by the presence of a shallow large buttress just offshore of the reef edge. These characteristics may have helped protect *P. porites* at SG from the effects of Hurricane Allen which impacted all reefs in Barbados in 1980 (Mah and Stearn, 1986). Recovery of *P. porites* at SG following 1980 could then have been facilitated by the effects of eutrophication on fragmentation previously discussed.

Species-specific life history strategies may influence the changes in species composition of coral communities that occur in response to changes in algal cover on reefs. Effects of eutrophication on Barbados west coast reefs have probably been in effect for 30 years, and a decade has now elapsed since the 1983 D. antillarum mortality. The present coral community composition of Barbados west coast fringing recfs may therefore allow insights into long-term effects of changes in macrophytic algae cover on corals, whether these be mediated through eutrophication processes or grazing pressure changes. The results of this study suggest that the relative abundance of Type 1 to Type 2 corals increases in the face of algal growth arising through cutrophication and/or reduced grazing pressure on reefs. At the two most eutrophic sites with highest algal cover (SG, BR), Type 1 corals are strongly dominant to Type 2 corals, and that situation has prevailed since at least 1982. At FV, SL, BRI and GS (but not at SR), coral cover decreased between 1982 and 1992 in the face of increasing cover by macrophytic algae, and the decrease was accompanied by an increase in the relative abundance of Type 1 to Type 2 corals at all sites. Wittenberg and Hunte (1992) have previously suggested that coral communities shift towards Type 1 corals under eutrophication stress, and Scoffin (1993) has reported a long-term shift towards Type 1 corals for the BRI reef in Barbados.

The shift towards Type 1 corals would be expected if natural juvenile mortality rates are essentially replaced with algal-driven juvenile mortality rates, with the difference between coral types in algal-driven mortality being less than the difference between types in natural mortality. The consequence would be that the strong dominance of Type 1 to Type 2 corals characteristic of juvenile communities, which results from higher recruitment in the former and which is typically reduced by their higher natural mortality, is maintained into and determines the species composition of adult communities under macroalgal stress. The shift towards Type 1 corals would be accelerated if the recruitment dominance of Type 1 to Type 2 corals is greater on reefs with high algal cover. This could occur if the typically smaller settlement size of Type 2 than Type 1 corals (Babcock, 1985) ensures that the immediate post-settlement mortality rates of the former are increased more than the latter on high algal reefs.

In contrast to the shift towards Type 1 corals observed on Barbados reefs, shifts towards Type 2 corals have been reported following the 1983 *D. antillarum* mortality on Jamaican reefs (Hughes, 1989, 1993). In contrast to Barbados reefs where coral recruitment still occurs (Tomascik, 1991; Hunte and Wittenberg, 1992), Hughes (1989, 1993) reports long-term recruitment failure on reefs in Jamaica. Algal cover may be higher on Jamaican than Barbados reefs because post-mortality *D. antillarum* densities have remained lower in Jamaica (average of 0.09 urchins/m²; Hughes, 1993) than in Barbados (average of 1.35 urchins/m²; this study). A shift to Type 2 corals may occur under complete recruitment failure, since changes in relative abundance of corals will exclusively reflect differences in mortality rates of adults. Type 1 corals being typically smaller than Type 2 corals as adults, may be more susceptible to algal overgrowth (see also Bak and Engel, 1979; Hughes, 1985, 1989).

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