THE EFFECTS OF EUTROPHICATION ON THE GROWTH RATES, REPRODUCTIVE POTENTIAL AND COMMUNITY STRUCTURE OF THE INSHORE REEF-BUILDING CORALS IN BARBADOS, WEST INDIES.

by

Tomas Tomascik

Institute of Oceanography

McGill University

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Abstract

Fourteen environmental variables were monitored at seven locations along the leeward coast of Barbados on a weekly basis over a one year period, 1981 to 1982. The physicochemical and biological data indicate that the environmental gradient detected along the leeward coast of the island is associated with eutrophication of the inshore water masses.

The response of scleractinian coral communities to various environmental conditions was determined by community structure and function analyses. The structure of scleractinian coral communities was studied along the environmental gradient with a quantitative sampling method (line transect) in terms of species composition, abundance, cover, trophic position, zonation and diversity patterns. The functional response of scleractinian corals to the various environmental conditions was analysed through coral growth rates and reproductive potential.

Statistically discernible and biologically significant differences in coral growth rates, reproductive potential, community structure, benthic algal cover, and *Diadema antillarum* Philippi densities were recorded among the seven fringing reefs. High correlations between environmental variables and biotic patterns indicate that eutrophication processes were directly and/or indirectly affecting both the community structure and function of the scleractinian coral assemblages.

Résumé

Quatorze variables du milieu furent contrôlées hebdomadairement pendant un an (1981-82) à sept endroits le long de la côte sous le vent de la Barbade. Les données physicochemeques et biologiques indiquent que le gradient du milieu décelé le long de la côte sous le vent de l'île est associée à une eutrophication des masses d'eau côtières.

La réponse des communautés de coraux scléractiniens à des conditions diverses du milieu fut déterminée par des analyses de la structure et des fonctions de la communauté. La structure des communautés de coraux scléractiniens fut étudiée le long du gradient du milieu avec une méthode d'échantillonnage quantitative (lignes de transect) en fonction de la composition spécifique, de l'abondance, de la couverture, du niveau trophique, de la zonation et des patrons de diversité. La réponse de la fonction des coraux scléractiniens à des conditions de milieu variées fut analysée par les taux de coralliens et la reproduction potentielle.

Des différences statistiquement décelables et biologiquement significatives des taux de croissance coralliens, de la reproduction potentielle, de la structure de la communauté, de la couverture d'algues benthiques et des densités de Diadema antillarum Philippi furent enregistrées parmi les sept récifs frangeants. Des corrélations élevées entre les variables du milieu et les patrons biologiques indiquent que les mécanismes d'eutrophication affectaient directement et/ou indirectement la structure et la fonction de la communauté d'assemblages de coraux scléractiniens.

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PREFACE

1.) Statement of Originality:

This study presents the first comprehensive comparative field investigation of the effects of eutrophication processes on the biological integrity of a series of fringing reef complexes lying along the leeward coast of Barbados, West Indies. The investigation is the first to incorporate, in a comparative framework, both the structural and functional analyses at the population and community levels to quantitatively discern differences among a number of scleractinian coral communities subjected to various environmental conditions associated with anthropogenic activities. The structural analysis approach (i.e. species composition, abundance, cover, trophic position and diversity) provided useful information on the ultimate effect of eutrophication upon the scleractinian coral communities, while the functional analysis approach (i.e. coral growth and reproduction) suggested possible causative relationships between coral community structure and the various environmental conditions. Each manuscript represents an original contribution to scientific knowledge in terms of study design, analyses and conclusions. Collectively, the three manuscrips provide a comprehensive data base for future environmental monitoring studies in Barbados.

2.) Historical background of previously relevant work:

An extensive historical background can be found in the General Introduction, and in the Introduction and text of each chapter.

3.) Declaration of assistance:

The candidate acknowledges the contribution of the co-author, Dr. Finn Sander, for his supervision, guidance and advice rendered during the study, his financial support and his critical review of the three manuscripts. In accordance with Section 7 of the Thesis Guidelines, the candidate declares that the study design, field and laboratory work, data analyses and interpretation, and writing of the manuscripts was done by the candidate alone, as is clearly reflected in the candidate's position as the senior author. The first person plural 'we' was used for publication purposes only.

4.) Thesis format:

In accordance with Section 7 of the Thesis Guidelines, this thesis has been prepared as a series of manuscripts suitable for submission to refereed scientific journals for publication. For this reason, each chapter contains its own

Abstract, Introduction, Materials and Methods, Results, Discussion and Conclusion, Literature cited, and understandably contains certain amount of repetition. The present thesis format has been approved by the thesis committee and by the Chairman of the Department.

The chapters in the present thesis have been written in the format required for publication in the journal *Marine Biology*. The manuscript in Chapter I has been published in the journal *Marine Biology 87(2)*, 143-155 (1985), and deals with the effects of eutrophication on the growth rates of a reef-building coral *Montastrea annularis*. The manuscript presented in Chapter II was accepted for publication in the journal *Marine Biology* on January 22, 1986. Chapter II deals with the effects of eutrophication on the reproduction of a reef-building coral *Porites porites*. The manuscript presented in Chapter III was accepted for publication in the journal *Marine Biology* on January 14, 1986. Chapter III deals with the response of scleractinian coral communities to various environmental conditions associated with eutrophication processes. The connections between the three chapters are implicit in the text.

TABLE OF CONTENTS

	Page
ABSTRACT	ii
RESUME	iii
ACKNOWLEDGEMENTS	iv
PREFACE	vi
GENERAL INTRODUCTION	1
LITERATURE CITED	8
CHAPTER I. Effects of Eutrophication on Reef Building Corals. Part I. Growth Rate of a Reef Building Coral *Montastrea annularis*.	
ABSTRACT	16
INTRODUCTION	17
MATERIALS AND METHODS	21
Environmental Assessment	21
Sampling and Determinations	21
Statistical Analyses	25
Coral Growth	27
Sampling and Measurements	27
Statistical Analyses	28
RESULTS	30
Environmental Study	30
Physical Variables	30
Chemical Variables	33
Biological Variables	36
Coral Growth	38
Effects of Environmental Variables on Growth	41
DISCUSSION AND CONCLUSIONS	47
ACKNOWLEDGEMENTS	66
LITERATURE CITED	67
CHAPTER II. Effects of Eutrophication on Reef Building Corals. Part III. Reproduction of the Reef Building Coral *Porites porites* (Pallas).	
ABSTRACT	74
INTRODUCTION	76
MATERIALS AND METHODS	81
Study Sites	81
Environmental Measurements	83
Histological Studies	83
Statistical Analyses	86
Environmental Data	86
Reproduction	87

RESULTS..... 89
Environmental Conditions..... 89
Reproductive Strategy..... 92
Gametogenesis..... 96
Oogenesis..... 96
Spermatogenesis..... 100
Embryonic Development..... 104
Reproductive Seasonality..... 108
Reproductive Activity..... 112
Average Number of Polyps..... 128
DISCUSSION AND CONCLUSIONS..... 130
ACKNOWLEDGEMENTS..... 142
LITERATURE CITED..... 143

CHAPTER III. Effects of Eutrophication on Reef Building Corals. Part II. Structure of Scleractinian Coral Communities on the Fringing Reefs of Barbados, West Indies.

ABSTRACT..... 153
INTRODUCTION..... 155
MATERIALS AND METHODS..... 158
Sampling..... 158
Environmental Assessment..... 165
Data Processing and Analyses..... 166
Data Processing..... 166
Data Analyses..... 171
RESULTS..... 175
General Species Distributions..... 175
Back Reef Zone..... 187
Faunal Comparisons..... 187
Community Descriptors..... 189
Diversity Indices..... 191
Reef Flat Zone..... 191
Faunal Comparisons..... 191
Community Descriptors..... 194
Diversity Indices..... 195
Spur and Groove Zone..... 198
Faunal Comparisons..... 198
Community Descriptors..... 199
Diversity Indices..... 200
Within Reef Zonation..... 202
Community Descriptors..... 202
Diversity Indices..... 202
Community and Environmental Interactions..... 206
DISCUSSION AND CONCLUSIONS..... 218
ACKNOWLEDGEMENTS..... 237
LITERATURE CITED..... 238

CONCLUDING REMARKS..... 247

General Introduction

The present study was initiated to test the hypothesis that the eutrophication of coastal water masses along the west coast of Barbados exerts a measurable impact on the structure (i.e. species composition, abundance, coverage, diversity) of scleractinian (zooxanthellate) coral communities, and directly or indirectly influences coral function (i,e. growth, reproduction) at the individual and population levels of organization. The term impact is used to describe changes in the reef system resulting from environmental changes initiated, magnified and/or accelerated by anthropogenic activities. The degradation of coral reef communities is becoming an increasing problem throughout the Caribbean and Indo-Pacific regions. During the last two decades the inshore waters of many Caribbean countries have become increasingly exposed to many environmental hazards directly and/or indirectly linked to urban, agricultural and industrial development. It is widely recognized that coral reefs are among the most biologically productive marine communities in the world (Lewis, 1977), and as such, they constitute an important natural resource in many developing nations which is being increasingly exploited in commercial activities such as fisheries and tourism. Scleractinian (zooxanthellate) corals are the ecological dominants on Caribbean reefs, because they are the key group of organisms which partake in the constructional framework of

reefs, thus providing and creating new habitats and environments for a great variety of reef organisms (Bak, 1983). Studies on the population explosion of *Acanthaster planci*, in the Indo-West Pacific region, have clearly demonstrated that high and selective mortality of scleractinian corals, as a result of excessive predation by *Acanthaster*, can have a profound effect on the associated coral reef fauna (Barnes, 1966; Chesher, 1969, 1970; Dana *et. al.*, 1972; Endean and Stablum, 1973a, b). To quote Johannes (1975), considering the central role of scleractinian corals to the integrity of the coral reef community as a whole, " the environmental tolerance of the reef community as a whole cannot exceed those of its corals." Indeed, the possible damaging effects of pollution and over-exploitation upon the coral reef ecosystems have in recent years increased the concern and research activities in the scientific community (Connell, 1970; Johannes, 1970, 1971, 1975; Straughan, 1970; Fishelson, 1973; Jokiel and Coles, 1974, 1977; Loya, 1975, 1976a, b; Dodge and Vaisnys, 1977; Bak, 1978; Dahl and Lamberts, 1978; Rogers, 1979; Loya and Rinkevich, 1980; Sheppard, 1980; Dahl, 1981; Dollar and Grigg, 1981; Hudson, 1981; Walker and Ormond, 1982; Tilmant and Schmahl, 1981; Howard and Brown, 1984). In the present study the Interogovernmental Oceanographic Commission's (IOC) definition of marine pollution is adopted: "Marine pollution is the introduction by man, directly or indirectly, of substances or energy into the marine environment (including estuaries), resulting in such deleterious effects as: harm to living

resources; hazards to human health; hindrance to marine activities including fishing; impairing the quality for use of seawater and reduction of amenities" (Gerlach, 1981).

Johannes (1975) in his extensive review on the effects of marine pollutants on coral reefs suggested that coral reefs are extremely sensitive to environmental perturbations associated with a wide spectrum of anthropogenic activities. This assertion was further supported by Loya (1976a), who showed that coral reefs subjected to chronic pollution may not return to their former states after being subjected to severe natural environmental perturbations. Rogers *et. al.* (1982) have also emphasized that while coral reefs may be adapted to natural catastrophes, such as hurricanes, they are highly susceptible to environmental perturbations associated with sewage discharge, oil pollution, and excessive sedimentation from dredging activities.

It is clear that scleractinian corals exhibit a wide range of responses to temporal and spatial heterogeneity of their environments (Bak, 1983), and therefore, assessing changes due to anthropogenic activities necessitates regular monitoring of coral reefs and their physicochemical environments. Recent reviews on the effects of pollution upon coral reefs (Brown and Howard, 1985; Pastorok and Bilyard, 1985) have stressed the need for comprehensive, long-term studies which should incorporate both the structural and functional responses of the coral communities to natural and anthropogenic perturbations. Recent suggestions that coral reefs are not as fragile as was

previously believed (Dollar and Grigg, 1981; Brown and Howard, 1985) clearly accentuate the lack of data and serious contradictions on this subject.

A significant number of studies have clearly demonstrated that sedimentation (Loya, 1976b; Dodge and Vaisnys, 1977; Lasker, 1980; Rogers, 1983; Cortez and Risk, 1985), nutrient enrichment (Clutter, 1972; Banner, 1974; Kinsey and Domm, 1974; Laws and Redalje, 1979; Smith *et. al.*, 1981; Walker and Ormond, 1982), toxicity (McCloskey and Chesher, 1971; Maragos, 1972; Maragos and Chave, 1973; Sorokin, 1973; Johannes, 1975; Kinsey and Davies, 1979) and oil pollution (Johannes, 1975; Loya, 1975; Birkeland *et. al.*, 1976; Rinkevich and Loya, 1977, 1979; see Loya and Rinkevich, 1980, for review), have direct and/or indirect effects on the integrity of coral reefs. The degree of impact upon the coral reef communities is directly related to the intensity and frequency of the perturbations, hydrography of the impact area, community composition and constructional qualities of the affected communities (Bak, 1983).

High suspended particulate matter concentrations and sedimentation associated with dredging, filling, blasting and coastal development activities produce a variety of direct and indirect effects at the individual, population and community levels. Sedimentation and related turbidity of the water column depress coral growth rates (Aller and Dodge, 1974; Dodge *et. al.*, 1974; Dodge and Vaisnys, 1977; Hudson and Robbin, 1980), and alter the community structure of scleractinian corals (Loya, 1976b) through reduced light levels, physical

interference with feeding, respiration, and through expenditure of energy in cleaning activities (Roy and Smith, 1971; Maragos, 1972; Dallmeyer *et. al.*, 1982).

The eutrophication of coastal marine waters is becoming a serious problem in many coastal areas (Cederwall and Elmgren, 1980; Larsson *et. al.*, 1985; Rosenberg, 1985). Eutrophication is here defined as a gradual accumulation of nutrients and increased sedimentation leading to organic biomass accumulation by increased levels of production (Rosenberg, 1985). Therefore, eutrophication as a result of anthropogenic activities (i.e. cultural eutrophication) is simply an unnatural acceleration of eutrophication processes (Laws, 1981). The problems associated with eutrophication processes vary with the biology, chemistry and hydrography of the affected coastal marine ecosystems. Most studies on the effects of eutrophication processes in tropical coastal regions have been generally restricted to estuaries and shallow embayments with restricted circulation (Goodbody, 1968, 1970a,b; Wade, 1971, 1972a, b, 1976; Wade *et. al.*, 1972; Banner, 1974; Smith, 1977; Smith *et. al.*, 1981; Dollar, 1983). Perhaps the most comprehensive study on the effects of eutrophication is from Kaneohe Bay, Hawaii (Smith and Kam, 1973; Maragos and Chave, 1973; Smith *et. al.*, 1981), which incorporated both the structural and functional analyses in assessing the impact of nutrient subsidy on the benthic community. The Kaneohe Bay study has provided some evidence that coral reefs damaged by anthropogenic activities may slowly recover to similar states upon the removal of stress (i.e.

sewage diversion). Recently Dollar (1983) emphasized the usefulness of integrating both the structural (i.e. species composition, abundance, diversity, trophic position and biomass) and functional (i.e. community metabolism, growth, reproduction) analysis in determining ecosystem or community response to environmental perturbations. The application of structural analysis in pollution related studies has provided much needed information of the general community response; however, the mechanisms through which the corals respond to environmental perturbations are still relatively unknown. As was clearly pointed out by Dollar (1983), structural analysis is aimed at assessing the ultimate effect of pollution, while little understanding can be obtained of the causative relationships between community structure and the perturbation.

Vezina (1975) provided the first detailed information on the effects of nutrient enrichment on phytoplankton associations and water conditions along the west coast of Barbados. However, most of the other detailed studies on the effects of eutrophication in Barbados were restricted to a shallow-water harbour located in the middle of Bridgetown, the capital of the island (Partlo, 1975; Turnbull, 1979).

The present comparative study was designed to integrate the structural and functional analysis, at the population and community levels, to determine the response of scleractinian coral communities to varying degrees of eutrophication along a well defined and characterized environmental gradient. The study presented here had three principal objectives; 1) To

define and characterize the physicochemical environment of the inshore waters along the leeward coast of Barbados. 2) To analyse the response of scleractinian coral communities along the leeward coast of Barbados to varying degrees of eutrophication through, a) coral growth rates; b) reproduction; and c) community structure (i.e. species composition, abundance, cover, diversity). 3) To provide an extensive data base to be used for future environmental monitoring studies in Barbados.

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CHAPTER I

Effects of eutrophication on reef-building corals. Part I. Growth rate of the reef-building coral *Montastrea annularis*.*

© Tomas Tomascik & Finn Sander

McGill University
Institute of Oceanography
3620 University St.
Montreal, PQ.
H3A 2B2

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* A contribution from the Bellairs Research Institute and the Institute of Oceanography, McGill University.

Abstract.

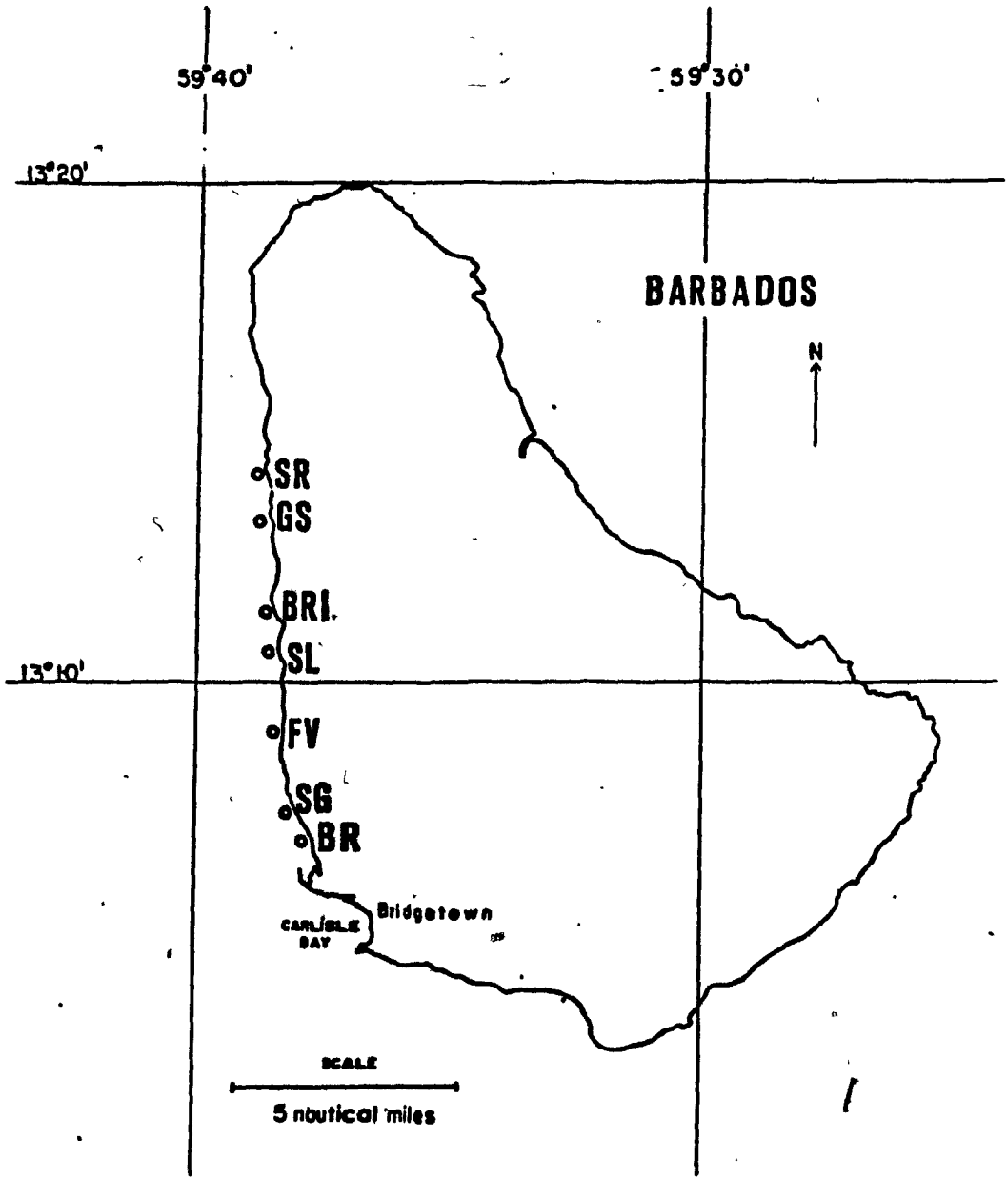
Fourteen environmental variables were monitored at seven locations along the west coast of Barbados on a weekly basis over a one year period, 1981 to 1982. The physicochemical and biological data indicate that an environmental gradient exists as a result of increased eutrophication of coastal waters. Growth rates (linear extension) of *Montastrea annularis* (Ellis and Solander), measured along the environmental gradient, exhibit high correlation with a number of environmental variables. Concentration of suspended particulate matter is the best univariate estimator of *M. annularis* skeletal extension rates (r^2= 0.79, $P<0.0001$). The results suggest that suspended particulate matter may be an energy source for reef corals, increasing growth up to a certain maximum concentration. After this, reduction of growth may occur due to smothering, reduced light levels and reduced zooxanthellae photosynthesis.

INTRODUCTION

One goal of coral reef ecologists it to predict the effects of changing environmental conditions (natural or man induced) on the integrity of scleractinian coral communities. In recent years skeletal extension rates, as determined by X-ray radiography (Dodge and Thompson 1974, Hudson *et al.* 1976), have been used by many workers as an index of coral growth in studies relating growth to a variety of environmental conditions (e.g. Aller and Dodge 1974; Dodge *et al.* 1974; Hudson 1981; Hudson *et al.* 1976). In the present study we define coral growth in terms of skeletal extension rates, unless stated otherwise. It is now well established that both temperature and light intensity are key environmental variables directly affecting coral growth rates (Highsmith, 1979). These factors have been used to explain both geographical and between-habitat variability in growth rates (Coles *et al.* 1976; Glynn 1977; Gladfelter *et al.* 1978; Foster 1980). We know of no attempt to investigate, in a comparative framework, the effects of water characteristics alone on the growth rates of scleractinian (zooxanthellate) corals.

Along the west coast of the Caribbean island of Barbados (Fig. 1) lie a series of fringing coral reefs previously described by Lewis (1960), Macintyre (1968), Stearn *et al.* (1977), and Scoffin *et al.* (1980). The present study documents the eutrophication of inshore water masses along the west coast of Barbados and investigates the effect of

Figure 1. Map of Barbados, West Indies. Collection sites are designated by ✪ . Station abbreviations: BR - Brighton; SG - Spring Gardens; FV - Fitts Village; SL - Sandy Lane; BRI - Bellairs Research Institute; GS - Greensleeves; SR - Sandridge.


59°40'
59°30'
13°20'
13°10'
BARBADOS
N
SR
GS
BRI.
SL
FV
SG
BR
Bridgetown
CARLISLE BAY
SCALE
5 nautical miles

eutrophication on coral growth rates. More specifically, it compares the relative power of several key environmental variables to discern changes statistically in the growth rates (skeletal extension rates) of *Montastrea annularis* (Ellis and Solander), a principal reef builder, among seven structurally similar fringing reef complexes which are under different environmental conditions associated with eutrophication of the inshore waters.

Throughout the island, sewage is usually dumped on land through dry toilets, suckwell systems and septic tanks. Prior to the construction of the Bridgetown sewage treatment plant in 1982, the city (population 95,000) was served by ten activated sludge sewage treatment plants. It has been estimated (Barbados Water Resources Study, 1978) that sewage flow on the west coast, including Bridgetown, is approximately 8.46 million liters per day, and 9% of this is discharged directly or indirectly into Carlisle Bay (Fig. 1). A dominant nearshore surface current with a mean recorded velocity of 24 cm/sec (Peck, 1978) carries the effluents in a north-northwesterly direction out of the bay. The coastal current regime north of the Carlisle Bay is not well documented. However, the effluents carried by the nearshore current may significantly contribute to the intensification of the eutrophication gradient through higher nutrient loading at the southernmost stations BR and SG (Fig. 1).

MATERIALS and METHODS

Environmental assessment

Sampling and determinations: Fourteen environmental variables were monitored at seven stations located over the fringing reefs (depth 4m) along the west coast of the island (Fig. 1). Since the water column is well mixed (Sander, 1981), surface water samples (1m) for nutrient analyses were collected from each station on a weekly basis, weather permitting, (from September 1981 to September 1982) using a Van Dorn sampler (7ℓ capacity). All stations were sampled on the same day between 10:00 and 13:00 hours. To minimize possible effects of diel cycles in nutrient concentrations, these seven stations were sampled in five different sequences (Table 1). The sampling sequence on each sampling day was chosen randomly from a table of random numbers (Snedecor, 1956). Water samples (5ℓ) collected at each station were placed in 5ℓ Nalgene polyethylene bottles and transported, in a cooler, to the laboratory. Prior to analysis, each water sample was filtered through a Whatman GF/C glass fiber filter (4.25cm in diameter; effective retention 1.2μm). Immediately after filtration, each water sample was analysed for reactive phosphate (PO_4-P), nitrate-nitrite nitrogen [NO_3 + NO_2-N), nitrite (NO_2-N), and ammonia (NH_3-N). Samples for chlorophyll *a* were treated according to the method outlined by Strickland and Parsons

Table 1. Sequence of stations sampled on each sampling day during the study. Sampling was initiated from the stations indicated in the first column.

Sampling sequence	Sequence of stations sampled on each sampling day.						
1	BR	SG	FV	SL	BRI	GS	SR
2	SR	GS	BRI	SL	FV	SG	BR
3	BRI	SL	FV	SG	BR	SR	GS
4	BRI	GS	SR	BR	SG	FV	SL
5	BRI	GS	SR	SL	FV	SG	BR

(1972) and stored in a freezer at -15°C for a maximum of five weeks. Samples for dissolved oxygen were fixed on site and transported to the laboratory for titration with a corresponding sample for the biological oxygen demand (BOD). All spectrophotometric determinations were performed using a Gilford spectrophotometer, Model 240. Standard methods for nutrient analysis, dissolved oxygen and chlorophyll *a* were used throughout the study (Strickland and Parsons 1972).

Surface water (1m) temperatures and salinities were measured *in-situ* using a YSI Model 33 S-C-T meter. At each station irradiance was measured 1m above the sea surface and at a depth of 4m using a QSI-140 Integrating Quantum Scalar Irradiance meter.

Total suspended particulate matter (SPM) was determined by filtering 1ℓ of sample through a pre-combusted, pre-washed and pre-weighed Whatman GF/C glass fiber filter (4.25cm in diameter; effective retention 1.2μm). Each filter was rinsed twice with 5ml of distilled water to remove salts (Strickland and Parsons, 1972). The filter was dried to constant weight at 100°C and, after weighing, combusted at 550°C for fifteen minutes to obtain volatile particulate matter (VPM) data (Turnbull, 1979).

To obtain a relative measure of the total downward flux of suspended particulate matter (DF-SPM), in the water column over the fringing reefs, sediment traps were placed at each station in the spur and groove zone (depth 5m) one meter above the bottom. The traps consisted of a concrete base and a T-bar

supporting two PVC tubes, painted with an antifouling paint, with a diameter of 3.8cm and a height of 49cm. These dimensions gave a resultant aspect ratio (height:mouth diameter) of 12.9. Previous studies on sediment trap collection efficiency by Gardner (1977) and Hargrave and Burns (1979) indicated that the most efficient traps had aspect ratios > 5. The PVC tubes were clamped (with an aid of SCUBA) to the T-bar and were retrieved, weather permitting, on a monthly basis over a sampling period of 11 months. Traps were sealed with a rubber stopper on collection, carefully brought upright to the surface and transported to the laboratory. Each trap was allowed to stand for one hour after which the water in the tubes was decanted. The settled contents were then transferred into glass bowls, the traps were rinsed with 200ml of distilled water and the sediments were allowed to settle. The water was decanted and an additional 200ml of distilled water was added into each glass bowl and mixed with the contents. After settlement the water was decanted. The rinsing procedure was repeated three times. The sediments were placed in a drying oven and dried at 60°C to constant weight.

Approximately top 2cm of surface sediment was analysed for organic content. At each station ten sediment samples were collected from the spur and groove zone (3 to 4m) with a small plastic scoop, placed into individual plastic bags (underwater), and transported to laboratory. The samples were allowed to dry to constant weight at 60°C and weighed. All samples were then combusted at 500°C for four hours and

reweighed (Hirota and Szyper, 1975).

Statistical analyses: To determine statistical differences in the various environmental variables among the stations, an SAS statistical package was used in all data analyses (Ray, 1982a; Ray,1982b). All linear model statistics, such as the analysis of variance (ANOVA), make the assumption that the underlying population from which the sample data are drawn is a normal distribution. To test this assumption the Shapiro-Wilk,W, statistic and normal probability plot were computed for all environmental data sets using the Univariate procedure in the SAS system. Examination of the normal probablity plots and the W statistic indicated violations of the above assumption. To determine an appropriate transformation, the method outlined by Box *et al.* 1978) was used on all data sets. Accordingly, the data were log(X+1) transformed. To test the success of the transformation, the Univariate procedure was applied to the transformed data sets to test the normality assumption and Fmax test (Zar, 1984) was performed to test the homogeneity of variance assumption. The results indicated violations of both assumptions, and therefore, tests for the additivity and independence assumptions were not performed. Since the transformed data did not meet basic assumptions of parametric ANOVA, a nonparametric ANOVA (NPAR1WAY procedure; Kruskal-Wallis Chi-square approximation) was used to test the null hypothesis; H_0: there are no differences in variable (x) among stations, against an alternate H_1: there are differences

in variable (x) among stations. Where the nonparametric ANOVA rejected the null hypothesis a nonparametric Tukey-type multiple comparison test (Zar, 1984) was used to determine between which of the stations significant differences occurred.

Coral growth

Sampling and measurements: Montastrea annularis colonies were collected from each station in August, 1983. To reduce within-station variation in growth (Foster, 1980), the ten specimens of *M. annularis* collected at each station were from within 10-15 m of the spur and groove zone at a depth of 5-7 m; and all coral specimens collected were of similar size and shape (round-lobate).

The coral specimens were cut, with a diamond blade, along the maximum growth axis parallel to the coralites to form 3-4 mm thick slabs. The slabs were X-rayed using a Minishot 2 X-ray unit set at 30 mKv with exposure of 15-25 seconds on a Kodak type AR X-ray film. To measure the annual growth increments of the high and low density couplets, techniques described by Dodge (1980) were used on all negatives. Two specimens were rejected from the analyses because of error in cutting. The recorded growth measurements were in the form of annual linear increments (cm / yr) measured over the entire life history of the coral specimens. However, it should be noted that the main thrust of this study is relating environmental conditions to extension rates during 1981 and 1982. It should also be made clear, that measurement of skeletal extension rates is only one of the methods available to measure skeletal growth of scleractinian corals. Coral calcification has received much attention in recent years (Goreau and Goreau, 1959; Barns and Taylor, 1978; Jokiel and

Coles, 1977; Coles and Jokiel, 1978; Fairbanks and Dodge, 1979), but the exact relationship between annual skeletal extension rates and calcification (mass addition) is not as yet clear. Dodge and Brass (1984) have shown that although annual extension rates and calcification rates of *M. annularis* were positively correlated, the correlations were not high. It was suggested that under certain environmental conditions (possibly pollution related) extension rates may remain unaffected (or possibly promoted) while calcification is depressed (Dodge and Brass, 1984).

Statistical analyses: The relationship between the mean and standard deviation (Box *et al. 1978)* implied logarithmic transformation of the coral growth data. Accordingly, the coral growth data were log(X+1) transformed. The transformed data sets were tested for the assumption of normality and homogeneity of variance. Univariate analysis on log transformed coral growth data showed no departures from the assumption of normality and the F max test (Zar, 1984) showed only slight heterogeneity of variance between two of the seven stations. Consequently, parametric single factor analysis of variance was performed, using the General Linear Model procedure, to test the null hypothesis H_0: there are no differences between the mean coral growth rates among stations, against an alternate H_1: there are differences in the mean coral growth rates among stations. Where tha ANOVA rejected the null hypothesis, the Tukey multiple comparison test was used to

determine between which of the stations significant differences occurred. A nested one-way analysis of variance was used to compare the amount of variation in coral growth rates among the stations to variation of coral growth rates within each station. To assess growth trends of corals for the past 15 years, index values were computed for each coral by dividing each linear increment by the mean growth rate of the entire coral. Index master chronologies were then computed by sequentially averaging by year the index series of each coral at each station to obtain information of life time growth trends within each station.

RESULTS

Environmental Study.

Table 2 presents the average values of all environmental variables monitored during the study. For ease of interpretation, the variables were subdivided into three categories - physical, chemical and biological.

Physical variables: Temperatures were generally higher at the southern stations (Fig. 1; Table 2). Table 3 shows the results of the nonparametric Tukey-type multiple comparison test (at the 0.05 level) for between-station comparisons. Station SG had a higher average temperature than any other station. However, differences in temperature among the remaining stations were not statistically discernible.

Total suspended particulate matter (SPM) has been classified as a physical variable since it contributes to reduction of available light. The southern stations had high SPM concentrations (Table 2 and 3). The SPM concentrations at stations BR and SG were greater than at the other stations. The SPM concentrations at stations FV and BRI were greater than those at SR, but were not discernibly different from those at SL and GS. The lowest light levels occurred at stations BR and SG. Among the northern stations, GS had statistically higher light levels than station BRI, but there were no statistical diferences between GS and SL or SR.

Table 2. Results of physicochemical and biological sea water analyses from the west coast of Barbados, West Indies. The variables are presented as mean yearly values with standard deviations in parentheses; N indicates number of samples collected at each station. Station initials are as shown in Fig. 1.

Variables	Stations							
	BR	SG	FV	SL	BRI	GS	SR	N
TEMPERATURE (°C)	28.08 (0.96)	28.55 (1.14)	27.98 (0.96)	27.96 (0.92)	27.94 (0.94)	27.88 (0.93)	27.83 (0.94)	47
SALINITY (‰)	33.32 (1.27)	32.22 (1.76)	33.37 (1.15)	33.48 (1.00)	33.43 (1.06)	33.28 (1.24)	33.24 (1.21)	46
Dissolved Oxygen (mg/ℓ)	6.70 (0.67)	6.46 (0.91)	7.03 (0.64)	6.86 (0.46)	6.78 (0.49)	6.79 (0.61)	6.75 (0.77)	38
BOD (mg/ℓ)	1.01 (0.54)	1.09 (0.58)	1.00 (0.50)	0.79 (0.40)	0.83 (0.49)	0.77 (0.54)	0.71 (0.41)	31
PO_4-P (µg-at/ℓ)	0.103 (.041)	0.214 (.106)	0.094 (.064)	0.081 (.036)	0.111 (.087)	0.060 (.030)	0.060 (.026)	45
NO_3+NO_2 -N (µg-at/ℓ)	0.816 (.426)	4.424 (2.649)	0.790 (.502)	0.546 (.393)	0.647 (.391)	0.452 (.232)	0.357 (.214)	44
NO_2-N (µg-at/ℓ)	0.098 (.033)	0.731 (.568)	0.066 (.030)	0.049 (.021)	0.048 (.018)	0.036 (.018)	0.035 (.021)	46
NH_3-N (µg-at/ℓ)	0.976 (.429)	2.695 (2.034)	0.896 (.506)	0.685 (.343)	0.736 (.414)	0.560 (.349)	0.542 (.270)	46
SPM (mg/ℓ)	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
VPM (mg/ℓ)	3.26 (1.67)	3.10 (1.26)	2.71 (1.47)	1.94 (1.15)	2.49 (1.43)	2.00 (0.97)	1.85 (1.03)	43
Chlorophyll a (mg/m^3)	1.040 (.537)	0.895 (.406)	0.876 (.331)	0.582 (.287)	0.799 (.470)	0.546 (.270)	0.420 (.157)	46
DF-SPM (mg/cm^2/day)	35.95 (40.17)	19.98 (17.42)	13.99 (10.24)	20.28 (29.56)	8.78 (7.07)	14.23 (17.61)	37.19 (53.15)	22
% Organics in sediments	8.3 (2.3)	10.9 (4.0)	4.9 (0.9)	2.5 (0.3)	5.1 (2.0)	2.3 (0.6)	2.9 (1.0)	10
% of surface illumination	27.10 (10.38)	28.82 (11.84)	35.62 (8.78)	37.08 (7.58)	34.52 (7.33)	40.45 (8.43)	37.52 (7.84)	28

Table 3. Nonparametric Tukey-type multiple comparison test (Zar, 1984) for significant ($P < 0.05$) differences between station means for temperature •, percentage of surface illumination 0, suspended particulate matter * and total downward flux of suspended particulate matter ■.

Stations	BR	SG	FV	SL	BRI	GS	SR
BR	-						
SG	•	-					
FV	0	• * 0	-				
SL	* 0	• * 0		-			
BRI	■	• * 0 ■	■		-		
GS	■ * 0	• * 0 ■	0		0	-	
SR	* 0	• * 0	*		*		-

The yearly average total downward flux of suspended particulate matter (DF-SPM), an integrated measure of turbidity and/or bottom instability, was not correlated with the yearly average SPM concentrations. Table 3 indicates that DF-SPM was statistically lower at station BRI than at stations BR, SG or FV, and that DF-SPM at station GS is lower than at stations BR and SG. During the rainy season (October-December) and periods of high swells (January-April) DF-SPM does not show any particular gradient between the northern and southern stations (Table 4). However, DF-SPM in summer (May-September) showed established gradient of decreasing rates in a northerly direction.

Chemical variables: Table 5 presents the results of the nonparametric Tukey-type multiple comparison test for between-station comparisons of the chemical variables. Station SG had statistically lower average salinity (32.3‰) than any other station, but there were no salinity differences among the remaining sites. With the exception of station BRI, PO_4-P concentrations tended to be higher for southern than northern sites (Table 2). Statistically higher PO_4-P concentrations occurred at station SG then at any other station. Lowest PO_4-P concentrations occurred at stations GS and SR with no discernible differences between them. There were no discernible differences in PO_4-P concentrations among stations FV, SL and BRI.

Trends in nitrogen concentrations (NO_3+NO_2-N, NO_2-N and

Table 4. Average total downward flux of suspended particulate matter (DF-SPM in mg/cm²/day) during summer months (May-September), periods of high swells (January-April), and the rainy season (October-December). First number: average DF-SPM rate; second number (in parentheses): standard deviation; third number: sample size. Duration of the periods as described in the text.

Stations	Summer	Swells	Rainy Season
BR	9.86 (5.16) 10	51.60 (28.55) 8	70.01 (66.51) 4
SG	11.52 (4.90) 10	20.06 (5.55) 8	40.91 (32.64) 4
FV	7.61 (4.39) 10	16.12 (1.26) 8	25.33 (17.72) 4
SL	4.17 (2.08) 10	21.26 (10.70) 8	58.79 (47.24) 4
BRI	5.50 (4.60) 10	9.42 (5.78) 8	15.24 (10.93) 4
GS	2.33 (1.75) 10	19.35 (6.01) 8	33.60 (30.61) 4
SR	2.54 (1.46) 10	55.18 (37.23) 8	88.52 (86.83) 4

Table 5. Nonparametric Tukey-type multiple comparison test (Zar, 1984) for significant ($P < 0.05$) differences between station means for inorganic phosphate *, nitrate-nitrite nitrogen 0, nitrite ■, ammonia • and salinity X.

Stations	BR	SG	FV	SL	BRI	GS	SR
BR	-						
SG	* 0 ■ •	-					
FV	* ■	* 0 • ■ X	-				
SL	* 0 ■ •	* 0 • ■ X	■ •	-			
BRI	0 ■ •	* 0 • ■ X	■		-		
GS	* 0 ■ •	* 0 • ■ X	* 0 ■ •	* ■	* 0 ■ •	-	
SR	* 0 ■ •	* 0 • ■ X	* 0 ■ •	* 0 ■ •	* 0 ■ •	0	-

NH_3-N) were similar to those in PO_4-P. Concentrations were highest at stations SG, BR and FV, and these were statistically greater than the nitrogen concentrations at northern reefs (stations BRI, SL, GS or SR). Intermediate nitrogen concentrations occurred at the BRI and SL sites, and these were statistically higher than the concentrations at GS and SR. Station GS had a statistically higher NO_3+NO_2-N concentration than SR.

Biological variables: The data on the biological variables (Table 2 and Table 6) clearly indicate a decrease in eutrophication from south (station BR) to north (station SR). A common indicator of eutrophication is an increase in phytoplankton biomass with increasing nutrient concentrations. Highest chlorophyll *a* concentrations occurred at stations BR, SG, and FV, with a gradual decrease in a northerly direction. There were no statistically discernible differences in chlorophyll *a* concentrations among the three southern stations, and these values were higher than those at the northern stations. Lowest chlorophyll *a* concentrations occurred at station SR and were lower than chlorophyll a concentrations at any other station. VPM and BOD concentrations showed a similar trend with concentrations decreasing in a northerly direction. However, dissolved oxygen concentrations were relatively constant along the west coast with slightly elevated concentrations at station FV that were greater than oxygen concentrations at stations BR, SG and SL.

Table 6. Nonparametric Tukey-type multiple comparison test (Zar, 1984) for significant ($P < 0.05$) differences between station means for dissolved oxygen O, chlorophyll *a* •, volatile particulate matter ■, and biological oxygen demand ★.

Stations	BR	SG	FV	SL	BRI	GS	SR
BR	-						
SG		-					
FV	O	O	-				
SL	• ■ ★	O • ■ ★	• ■	-			
BRI	• ■	■ ★	•	•	-		
GS	• ■ ★	• ■ ★	• ■ ★		•	-	
SR	• ■ ★	• ■ ★	• ■ ★	•	•	•	-

Coral growth

Table 7 presents the average growth rates of *Montastrea annularis* (for 1981 and 1982 separately and combined) for each of the seven reefs. Results from the ANOVA procedure indicate significant differences in mean coral growth rates among stations ($F = 14.92$, $P < 0.0001$). To evaluate specific site differences, the Tukey multiple comparison test was used (Table 8). Highest coral growth rates occurred at station SR (1.23 cm/yr) and were greater ($P < 0.05$) than growth rates at any other station. *M. annularis* at stations SL and GS grew faster than at station BR and SG ($P < 0.05$). Growth rates at station BRI were statistically indistinguishable from those at stations BR, SG, FV, SL and GS. In summary, *M. annularis* tended to grow faster at the less polluted northern stations.

To determine whether intrastation growth rates differed between 1981 and 1982, one-way analysis of variance was performed. Results showed that at stations BRI and SL, the growth rate of *M. annularis* in 1982 were lower then those in 1981 ($P < 0.05$). There were no between-year differences at the other stations. Note that growth rate varied among corals within sites (Nested one-way analysis of variance; $P<0.05$). Of the total model variability, 42.7% can be ascribed to among-site variability and 14.8% to within-site variability. This indicates that the proportion of growth rate variation between stations was high, relative to growth rate variation within sites.

Table 7. Linear growth information for *M. annularis* collected along the west coast of the island (sites are arranged from south to north; top to bottom).

Station	Year	Number of Corals	Mean Growth rate (cm/yr)	SD	Station Mean Growth Rates (cm/yr)	SD	Number of Corals
BR	1982	10	0.61	0.12	0.61	0.11	20
BR	1981	10	0.62	0.10			
SG	1982	10	0.63	0.21	0.58	0.18	20
SG	1981	10	0.52	0.14			
FV	1982	8	0.73	0.20	0.74	0.19	16
FV	1981	8	0.75	0.19			
SL	1982	10	0.71	0.24	0.93	0.45	20
SL	1981	10	1.05	0.43			
BRI	1982	10	0.69	0.15	0.77	0.16	20
BRI	1981	10	0.85	0.14			
GS	1982	10	0.86	0.16	0.94	0.22	20
GS	1981	10	1.02	0.24			
SR	1982	10	1.21	0.28	1.23	0.33	20
SR	1981	10	1.24	0.40			

ANOVA ; Comparison of mean growth rates among stations.
Data log transformed. Based on station mean growth rates.
H_o: There are no differences in the mean growth rates of corals among the stations.

Source	SS	df	MS	F value	PR > F
Model	6.0680	6	1.0113	14.92	0.0001
Error	8.7422	129	0.0678		
Total	14.8102	135	-		

$F = 14.92$ where $F_{0.05,6,129} = 2.18$
Therefore, reject H_o, $P < 0.0001$

Table 8. Tukey Test (Ray, 1982a). Results of the differences between station mean growth rates over the period 1981 - 1982. This test controls the experimentwise, Type 1, error rate.

Stations	BR	SG	FV	SL	BRI	GS	SR
BR	-						
SG	NS	-					
FV	NS	NS	-				
SL	*	*	NS	-			
BRI	NS	NS	NS	NS	-		
GS	*	*	NS	NS	NS	-	
SR	*	*	*	*	*	*	-

NS indicates no significant difference and * indicates significant ($P < 0.05$) difference.

To examine growth trends at each site, index master chronologies were plotted for each station over a ten to sixteen year period (Fig. 2). Except for stations BRI and SL, there was a general trend of decreasing growth rates from 1972 to 1982. To determine whether the growth trends among the stations were correlated, Kendall correlation coefficients were computed (Table 9). Strong correlations occurred between stations SL and BRI and among stations BR, SG, and GS.

Effects of environmental variables on growth

Table 10 presents simple linear regressions between the average coral growth rates and the environmental variables. Two simple linear regression models are possible to relate the rate of coral growth and the environmental variables measured in this study. The first model considers only 1982 growth rates as the dependent variable (i.e., regression without replication). However, since the environmental data were measured from September to December 1981 and from January to September 1982, it would be incorrect to state that the average environmental values are representative of the average environmental conditions during 1982 only. The second model, applied in the present study, uses both 1981 and 1982 coral growth rates in the regression model (Table 10). Although, this approach tended to lower the r^2 of the model, it did not affect the biological significance of the regression, since it takes into consideration the inherent variability of coral

Figure 2. *Montastrea annularis.* Three year moving average of index master chronologies of *M. annularis* at each study site. Station initials as designated in Figure 1. The numbers above the horizontal axis indicate the number of corals used in the chronology at the specified year.

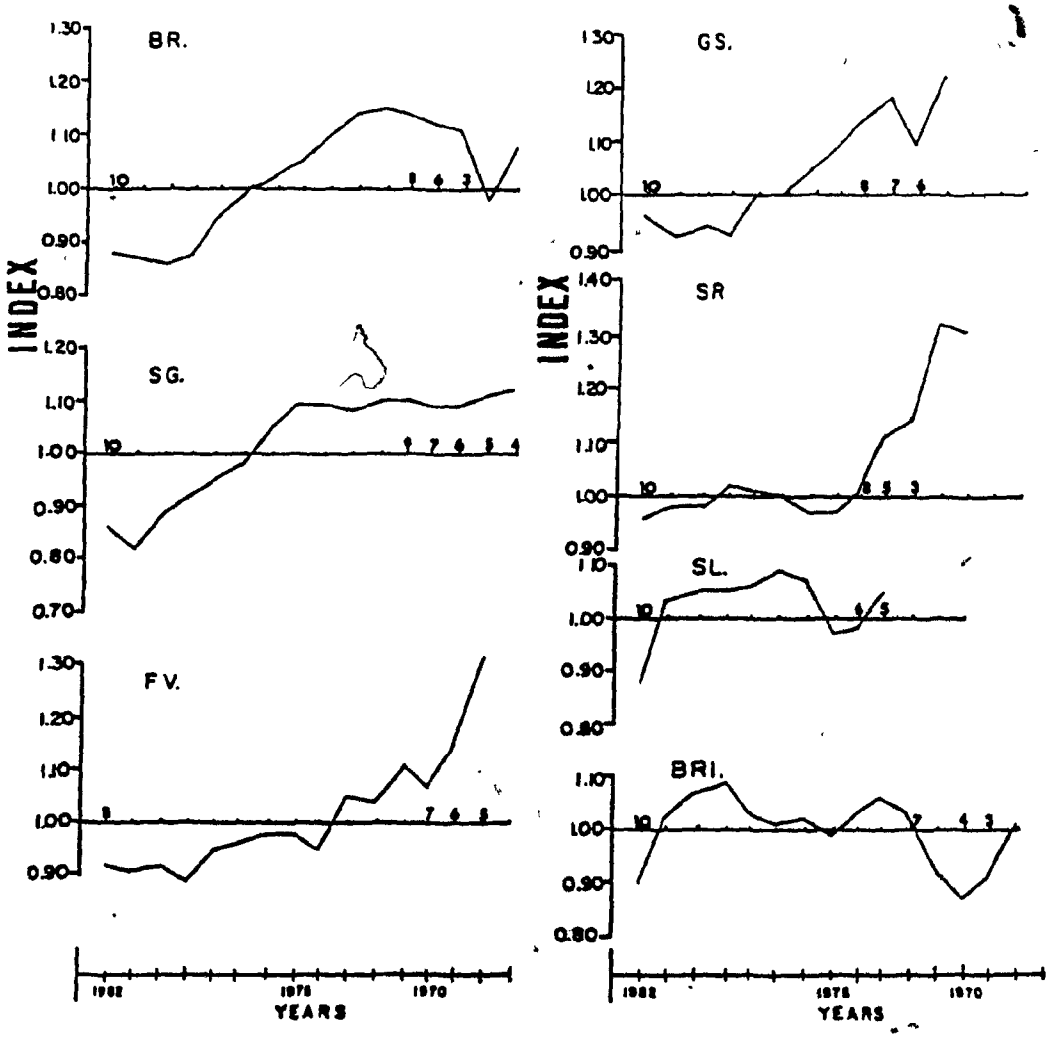

BR.
SG.
FV.
GS.
SR
SL.
BRI.
INDEX
INDEX
YEARS
YEARS
1982
1976
1970

Table 9. Kendall correlation coefficients between station index master chronologies over the period 1966 to 1982 (16 years). For r > 0.60, P > 0.05.

Station	BR	SG	FV	SL	BRI	GS	SR
BR	-						
SG	0.63	-					
FV	0.41	0.33	-				
SL	0.37	0.13	0.24				
BRI	0.04	0.24	0.08	0.74	-		
GS	0.73	0.64	0.22	0.29	0.11	-	
SR	0.41	0.11	0.19	0.40	0.41	0.09	-

Table 10. Regression equations for predicting coral growth rates (Y in cm/yr) from total suspended particulate matter concentration (SPM in mg/ℓ), volatile particulate matter concentration (VPM in mg/ℓ), chlorophyll a concentration (CHLA in mg/m³), biological oxygen demand (BOD in mg/ℓ), percentage of total organic content in sediments (ORG in %), percentage of surface illumination (IRR in %), inorganic phosphate concentration (PO4 in µg-at/ℓ), ammonia concentration (NH3 in µg-at/ℓ), nitrate - nitrite nitrogen concentration (NO3 in µg-at/ℓ), temperature (TEM in °C), salinity (SAL in ‰), total downward flux of suspended particulate matter (DF-SPM in mg/cm²/day), and current velocity (CUR in cm/sec).

Simple regressions	r^2	p^a	SE of slope
1. log Y = - 0.638 log SPM + 0.760	0.79	0.0001	0.096
2. log Y = - 0.340 log VPM + 1.670	0.79	0.0001	0.092
3. log Y = - 0.863 log CHLA + 0.452	0.75	0.0001	0.143
4. log Y = - 1.368 log BOD + 0.611	0.72	0.0001	0.245
5. log Y = - 0.169 log ORG + 0.367	0.63	0.0008	0.038
6. log Y = 0.619 log IRR - 0.701	0.56	0.002	0.159
7. log Y = - 1.940 log PO4 + 0.335	0.51	0.004	0.552
8. log Y = - 0.316 log NH3 + 0.339	0.48	0.006	0.096
9. log Y = - 0.183 log NO3 + 0.303	0.41	0.01	0.063
10. log Y = - 6.90 log TEM + 10.34	0.23	0.100	3.290
11. log Y = 3.76 log SAL - 5.5	0.16	0.1636	2.531
12. log Y = - 0.125 log DF-SPM + 0.392	0.13	0.200	-
13. log Y = - 0.38 log CUR + 0.67	0.06	0.200	-

[a] F-test.

growth rates. We suggest that this second approach is more robust and biologically more sound then the former.

Mean SPM and VPM concentrations were the strongest univariate estimators of growth rates, followed by chlorophyll *a* and BOD (see Table 10). Surprisingly, percentage of surface illumination showed a weaker relationship with growth (r^2 = 0.56, $P < 0.002$). Among the inorganic nutrients PO_4 - P showed the strongest negative relationship with growth (r^2 = 0.51, $P < 0.004$), followed by NH_3-N (r^2 = 0.48, $P < 0.006$) and NO_3+NO_2-N (r^2 = 0.41, $P < 0.01$).

Multiple regressions are not presented, since the environmental data showed a high degree of multicollinearity. It would therefore be difficult (if not impossible) to assess the unique effects of individual environmental variables on the rate of coral growth. Large correlation coefficients point to strong linear associations, thus suggesting that certain environmental variables may be correlates of others with little or no causal effects themselves.

DISCUSSION and CONCLUSIONS

The growth rates of *Montastrea annularis*, expressed as skeletal extension rates, were highly correlated with a number of environmental variables. Hudson (1981) has indicated that growth rates of *M. annularis* in the Key Largo Marine Sanctuary were correlated with three environmental factors; depth, distance from shore and water quality. Our sampling design minimized the effects of natural environmental factors, such as depth and distance from shore, in order to compare *M. annularis* growth rates with respect to water characteristics only.

Eight principal sources of pollution contribute directly and/or indirectly to the intensification of the eutrophication processes in the inshore waters (Table 11). The primary point sources of pollution on the west coast are industrial effluents from an electric power plant and a rum factory located between stations SG and BR (Fig.1). These two industrial plants may be directly responsible for the high nutrient concentrations measured in this area (Table 12). However, Lewis (in preparation) has recently demonstrated that groundwater discharge (Table 12) must also be considered as an important source of nutrients in the coastal waters. He found high concentrations of both PO_4-P and NO_3+NO_2-N in groundwater samples, indicating that past agricultural practices and urban development have affected the groundwater characteristics. Nutrient enrichment caused by, for example, internal waves have

Table 11. General summary of various pollution sources on the island of Barbados.

Pollution sources (industrial wastes)	Pollution parameters	System affected
Sugar factories	BOD, suspended solids, colour, nutrients, COD.	Groundwater
Rum refinery	BOD, pH, nutrients, suspended solids, COD.	West coast inshore waters
Power plant	Temperature, salinity, nutrients, BOD, suspended solids	West coast inshore waters
Beverage industries i.e. breweries, bottling, dairy	BOD, suspended solids, colour, COD, phosphates	Groundwater
Oil industry	BOD, suspended solids, phenols, heavy metals, ammonia, grease	Carlisle Bay
Domestic wastes (sewage effluents)	BOD, suspended solids, nutrients, bacteria, viruses	Groundwater South and West coast inshore waters
Solid waste disposal	BOD, suspended solids, nutrients, pesticides	Groundwater
Agriculture	Nutrients, herbicides, pesticides	Groundwater Coastal waters

Source: Barbados Water Resources Study (1978)

Table 12. Estimated nutrient loading capacity of various industrial and domestic effluents on the west coast of Barbados, including Carlisle Bay.

Pollution sources	Loading capacity (kg/year)	
	PO_4-P	NO_3+NO_2-N
Sewage effluents *	9.1×10^3	5.8×10^3
Power plant effluent	2.8×10^3	6.7×10^4
Rum refinery effluent	2.7×10^4	2.2×10^5
Groundwater ** discharge	3.0×10^4	6.0×10^4
TOTAL	6.9×10^4	3.5×10^5

Source * Barbados Water Resources Study (1978)
** Lewis (in preparation)

been shown to enhance productivity of coastal waters (Sander and Steven, 1973; Sander, 1981), however, additional data are needed to determine their contribution to the eutrophication processes.

The increase of nutrient and chlorophyll *a* concentrations at stations BR, SG and BRI during the last decade (Table 13) coincides with the construction of the power plant (directly affecting stations BR and SG), and a large tourist complex in the vicinity of station BRI. These data (Table 13) suggest that the eutrophication of the inshore water masses may be directly related to anthropogenic activities and not to natural processes. It is suggested that the proximate cause of the eutrophication gradient must necessarily be a combined function of circulation patterns (Emery, 1972), groundwater discharge (Lewis, in preparation) and differential inputs of domestic and industrial effluents.

Mayor (1914) showed that the temperature tolerance of *M. annularis* ranges between 14°C and 32°C. Seasonal temperature fluctuations in Barbados are between 26.2°C and 29.5°C, thus never exceeding known lethal limits. The average temperature at station SG is slightly higher than at other stations. However, since the difference is only 0.7°C, it is probably insignificant in affecting coral growth rates to any measurable degree. The results of a linear regression analysis showed no relationship between growth and temperature (r^2=0.23, $P > 0.100$).

Among the nutrient variables, PO_4-P ($r^2 = 0.51$), NH_3-N (r^2

Table 13. Average nutrient and chlorophyll *a* concentrations at stations BR, SG and BRI during 1972-1973 and 1981-1982. First number: average concentrations; second number(in parentheses): standard deviation; third number: total number of samples pooled for calculations.

	STATIONS								
	BR			SG			BRI		
	1972* to 1973	1981 to 1982	% change	1972* to 1973	1981 to 1982	% change	1972* to 1973	1981 to 1982	% change
PO_4-P µg-at/ℓ	0.060 (0.057) 96	0.103 (0.041) 45	54	0.049 (0.035) 95	0.214 (0.106) 46	336	0.055 (0.007) 54	0.111 (0.087) 45	102
NO_3-N µg-at/ℓ	0.781 (1.564) 24	0.818 (0.426) 45	5	0.771 (0.761) 23	4.424 (2.649) 45	474	0.402 (0.095) 15	0.647 (0.391) 44	61
Chl(a) mg/m³	0.407 (0.304) 92	1.040 (0.537) 47	151	0.396 (0.220) 91	0.895 (0.406) 47	126	0.273 (0.021) 52	0.799 (0.470) 46	193

* source Vezina (1975)

= 0.48) and NO_3+NO_2-N (r^2 = 0.48) showed strong inverse relationships with *M. annularis* growth rates. Kinsey and Davies (1979) have indicated that elevated nitrogen concentrations (20 µg-at/ℓ) probably did not have a significant effect on coral calcification rates, but high PO_4-P concentrations (2 µg-at/ℓ) have been implicated in reduction of calcification through interference in the formation of calcium carbonate (Simkis, 1964). The only location, in the present study, where the PO_4-P concentrations may be high enough to play a role in suppressing calcification rates, but not necessarily skeletal extension rates (Dodge and Brass 1984), is station SG where PO_4-P concentrations are 7 times higher (0.210 µg-at/ℓ) than oceanic levels (0.03 µg-at/ℓ, Sander 1971). However, even these concentrations are well below those used by Kinsey and Davies (1979). It is suggested that although both nitrogen and phosphate are negatively correlated with growth, they are surrogates of other environmental variables (i.e., chlorophyll *a*, SPM and VBM), having little or no direct causal effect on growth themselves.

Previous studies (Aller and Dodge, 1974; Dodge *et al.*, 1974; Dodge and Vaisnys, 1977; Hudson, 1981a) have implicated sedimentation and related turbidity of the water column to reduced growth rates in *M. annularis*. It is generally accepted that turbidity lowers growth because light is scattered by sediment particles in the water column, and hence illumination, a vital source of energy to the coral's symbiotic attendant zooxanthellae is reduced (Dodge and Vaisnys, 1977). Moreover,

in environments with high sedimentation and turbidity, cleaning by corals will require energy expenditure which could otherwise be used for biological activities such as growth.

If the DF-SPM was the main environmental factor affecting growth (skeletal extension rates) of *M. annularis*, we would expect growth rate to be a strong inverse function of DF-SPM; yet our data showed no significant relationship between average yearly DF-SPM and growth rates ($r^2 = 0.12$, $P > 0.200$). This could result either from the sampling design used in the measurement of DF-SPM rates, or from strong seasonal variations in resuspension rates independent of station location. Since the sediment traps were removed on a monthly basis, weather permitting, high resuspension rates of short duration would contribute to monthly DF-SPM values, but need not affect growth.

High turbidity observed during the periods of heavy swells was probably a direct result of resuspended bottom sediments. It is important to note that DF-SPM measured was an index of bottom instability over the collection period. Previous studies by Dodge and Vaisnis (1977); Bak (1978) and Sheppard (1980), suggested that corals may be more tolerent of short-term sediment loading than of chronic turbidity. Qualitative observations during the high swell periods indicated that the high turbidity lasted for only two to three days. During the swell period (January-April), highest DF-SPM rates occurred at station SR, which represented the area of highest coral growth in the present study. Furthermore, during the rainy season,

sediment traps located at the northern stations collected comparable amounts of sediment when compared to the southern stations (Table 4). It is suggested that during the rainy season the sediment trap data reflect the intensity of runoff, i.e. terrigenous sediment inputs, and not resuspension *per se*. We consider land runoff, associated with heavy rains, to be an important seasonal environmental factor affecting the coral community since it not only contributes to increased turbidity through high sediment loading, but also significantly lowers the salinity of the water column over the fringing reefs. It is important to consider that even though we have measured high DF-SPM rates during both the swell periods and rainy season, the disturbances are relatively short lived. Our data collected during the two seasons support the hypothesis that short-term sediment loading or high resuspension rates of short duration do not affect coral growth rates (skeletal extension) to the same extent as either low but persistant sediment loading or chronic turbidity. Indeed, if we regress the growth rates (skeletal extension) of *M. annularis* against the average DF-SPM rates during the summer months (Table 4), a strong inverse relationship becomes apparent ($r^2=0.71$, $P<0.001$). This stresses the importance of long term environmental monitoring in field studies, and also suggests that high resuspension rates of short-duration may have only limited effect on the yearly, as opposed to seasonal, growth rates of *M. annularis*.

The decrease of DF-SPM rates (mean and variance) indicates higher bottom sediment stability during the summer months and

reflects localized weather conditions. The south-north gradient of decreasing DF-SPM rates, during the summer months, may be ascribed to higher production of a benthic deposit-feeding community, in the polluted southern stations, which is directly linked to increased nutrient loading from anthropogenic sources (i.e. sewage, power plant effluent, rum factory effluent). Higher benthic production and/or nutrient loading are reflected in higher organic content of bottom sediments at the southern stations (Table 2). It is suggested that increased reworking of bottom sediments by macroinvertebrates, associated with high loading of organic material into the benthic community, further intensifies the instability of bottom sediments thus increasing resuspension rates in the southern stations.

A clear distinction must be maintained between SPM and DF-SPM measured in the present study. SPM concentrations represent an instantaneous measure of the concentration of particles suspended in the water column. DF-SPM, on the other hand, is a temporally integrated measure of the total downward flux of suspended particles in the water column. Both SPM and DF-SPM may be considered as measures of turbidity and/or bottom instablity. Note, that it is theoretically possible to measure low DF-SPM rates even though the water column may have high SPM concentrations. Sediment traps measure roughly only the downward movement of particles which may only be a small percentage of the total SPM in the water column. It is suggested that SPM may be the more meaningful index of stress

on corals, since it reflects the total concentration of suspended particles in the water column.

It is suggested that SPM is the main environmental variable affecting the growth rates of *M. annularis*, not only because it is involved in smothering and in reduction of calcification through reduction of available light for zooxanthellae photosynthesis, (Vandermeulen and Muscatine (1974) have demonstrated that decreased photosynthesis by zooxanthellae caused decrease in calcification of hermatypic corals), but also because it may have a positive effect as an energy source. For example, Lewis (1976) demonstrated that *M. annularis* can clear surrounding water of particulate matter, apparently to satisfy a need for an additional source of energy for growth. It has been estimated that the concentrations of organic matter necessary for corals to meet their daily maintainance requirements is approximately 0.29 mg/ℓ. According to Sander (1971) the average concentration of SPM in the surface waters at station BRI was 1.11 mg/ℓ, which represents 0.33 mg dry organic matter/ℓ (Lewis, 1977). Our data show that the concentration of organic particulate matter has increased since 1970 to 2.49 mg/ℓ, while the total suspended particulate matter has increased to 5.94 mg/ℓ.

The question is how have these increases affected the growth rates of *M. annularis*. The answer will depend on the relative importance of autotrophy to heterotrophy in *M. annularis*, and there is, of course, no *a priori* reason for assuming that the relationship between coral growth and SPM

should be linear or even monotonic. Foster (1980) suggested that the growth rates of *M. annularis* respond positively to light. There was a strong positive relationship ($r^2 = 0.56$, $P < 0.002$) between growth rates of *M. annularis* and percentage of surface illumination in the present study (Table 10). These results suggest that the species may be predominantly autotrophic. However, Yonge (1963), von Holt and von Holt (1968), Muscatine and Cernichiari (1969), and Goreau *et al.* (1971) suggested that zooxanthellae photosynthesis could only supply limited amounts of energy for corals and that additional sources are needed to satisfy their basic daily requirements.

If *M. annularis* uses the organic fraction of SPM as food, then a positive relationship should exist between SPM concentrations and *M. annularis* growth rates over some range of the former. However, the present results (Fig. 3) show an inverse relationship ($r^2 = 0.79$, $P < 0.0001$) over the range of values measured. It is of interest to note that using the 1982 average coral extension rates only in the regression model increases the r^2 value of the regression equation ($r^2=0.99$, $P<0.0001$). This would indicate that 99% of the variation in the coral extension rates is explained by the simple linear regression model based on the SPM concentrations. On the other hand, only 1% of the variability in coral extension rates can be explained by other factors such as chance and/or other variables that have not been considered. The results presented in Figure 3 indicate that 79% of the variation in coral extension rates is explained by the model, based on SPM

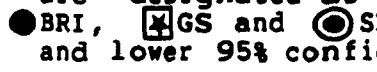
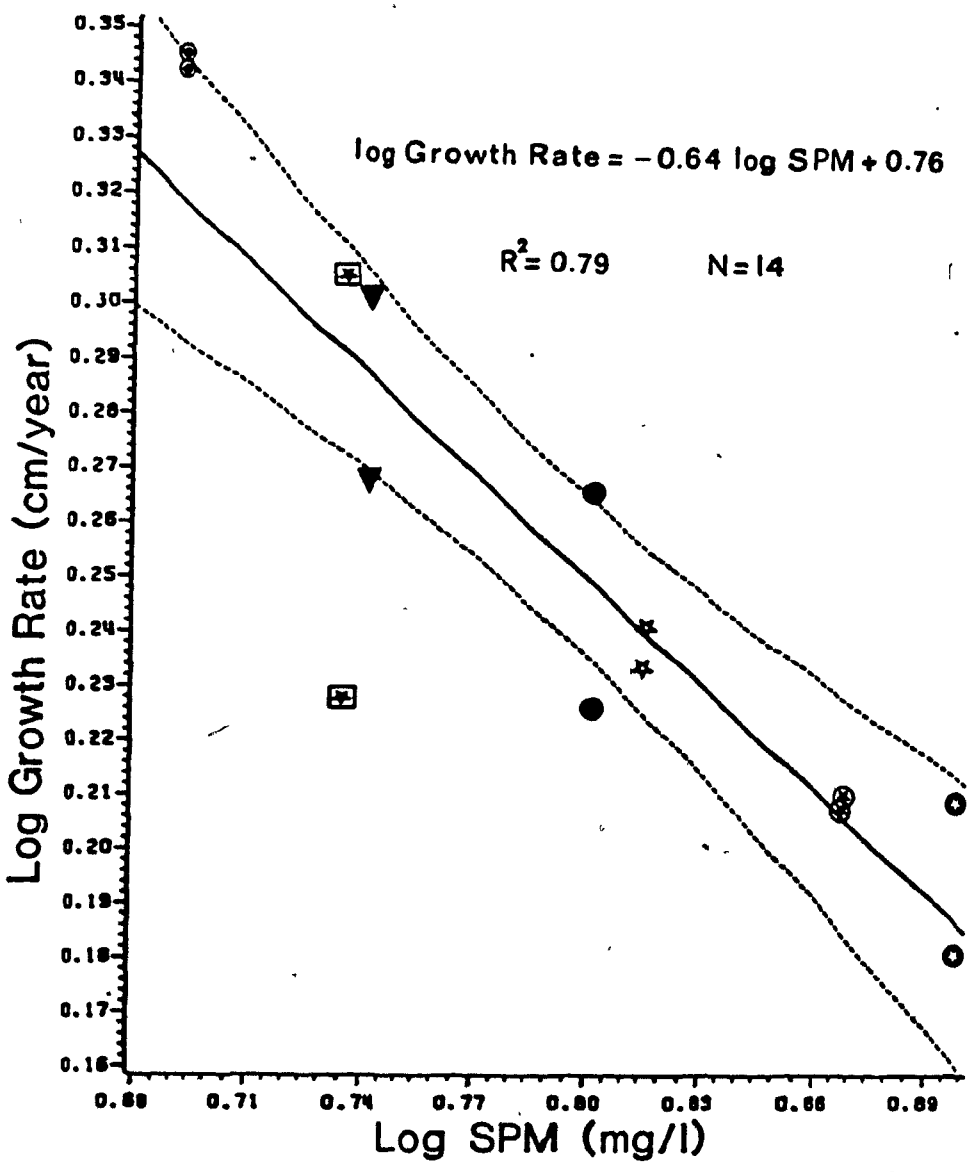


Figure 3. *Montastrea annularis.* Regression of *M. annularis* growth rate (Growth in cm/yr) on total suspended particulate matter concentration (SPM in mg/l). Stations are designated as follows; ⊕ BR, ⊙ SG, ✡ FV, ▼ SL, ● BRI, ⊠ GS and ◉ SR. The broken lines represent the upper and lower 95% confidence bands for the regression line.


log Growth Rate = −0.64 log SPM + 0.76
R² = 0.79
N = 14
Log Growth Rate (cm/year)
0.35
0.34
0.33
0.32
0.31
0.30
0.29
0.28
0.27
0.26
0.25
0.24
0.23
0.22
0.21
0.20
0.19
0.18
0.17
0.16
0.68
0.71
0.74
0.77
0.80
0.83
0.86
0.89
Log SPM (mg/l)

concentrations, leaving 21% to chance or other important variables that had not been considered in the model. Therefore, the equation presented in Figure 3 is considered to be a conservative (more robust) estimate of coral extension rates based on SPM concentrations.

To assess the relationship between coral growth and SPM concentrations more fully, we have measured *M. annularis* skeletal extension rates at stations BRI (1972-1973; 1975-1976), BR (1972-1973) and FV (1968-1969), when SPM concentrations were monitored by Vezina (1975), Kidd (1978) and Sander (1971) respectively (Table 14). Including the new data in the regression analysis (Fig. 4) indicates that the relationship between coral extension rates and SPM concentrations is a second-order polynomial (r^2=0.41, $P<0.005$). Even though the regression is highly significant the r^2 indicates that only 41% of the coral extension rate variation is explained by the model based on SPM concentrations. However, it is suggested that the low r^2 reflects the mathematical theory behind the regression model, and not necessarily the biological significance of the relationship between SPM concentrations and coral extension rates. Applying simple linear regression to these same data resulted in r^2 of 0.15, indicating that the polynomial model is a better estimator of coral extension rates over the range of SPM concentrations documented in this study. It is therefore proposed that in environments characterized by clear water, high light intensity and low SPM concentrations, autotrophy in

Table 14. Average skeletal extension rates of *Montastrea annularis* (cm/yr) with corresponding SPM concentrations (mg/ℓ) obtained from Sander (1971), Vezina (1975) and Kidd (1978). First number: average value; second number (in parentheses): standard deviation; third number: number of samples.

Station	Year	Average extension rates (cm/yr)	SPM (mg/ℓ)
FV *	1969	0.87 (0.30) 6	1.30 (1.06) 8
FV **	1972	0.74 (0.26) 8	4.12 (2.96) 44
	1973	0.87 (0.28) 8	
BR **	1972	0.81 (0.18) 10	3.90 (3.71) 45
	1973	0.80 (0.27) 10	
BRI **	1972	0.94 (0.27) 7	0.88 (0.77) 51
	1973	0.81 (0.29) 10	
BRI ***	1975	0.93 (0.28) 10	2.78 (2.22) 29
	1976	0.88 (0.30) 10	

source: * Sander (1971);
** Vezina (1975);
*** Kidd (1978);

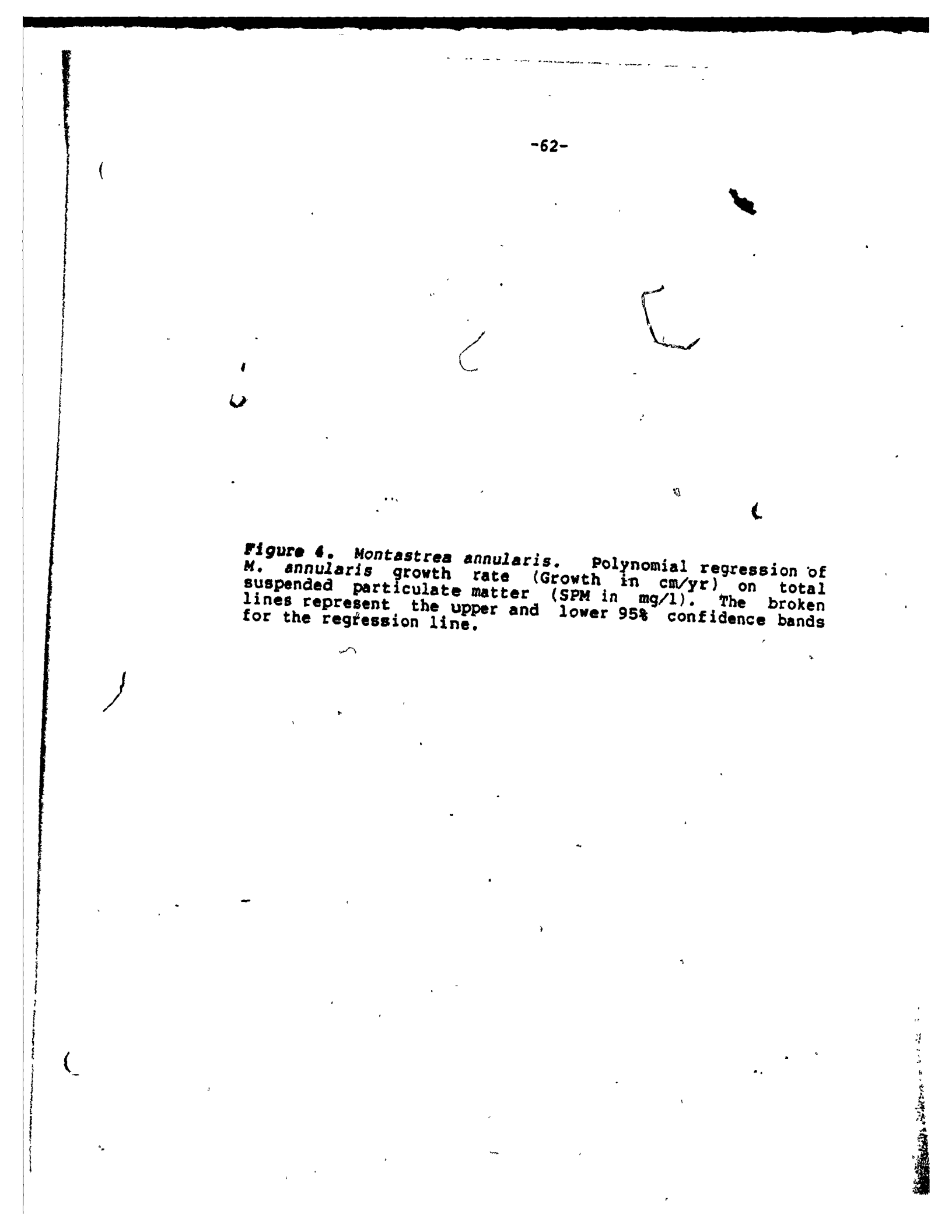
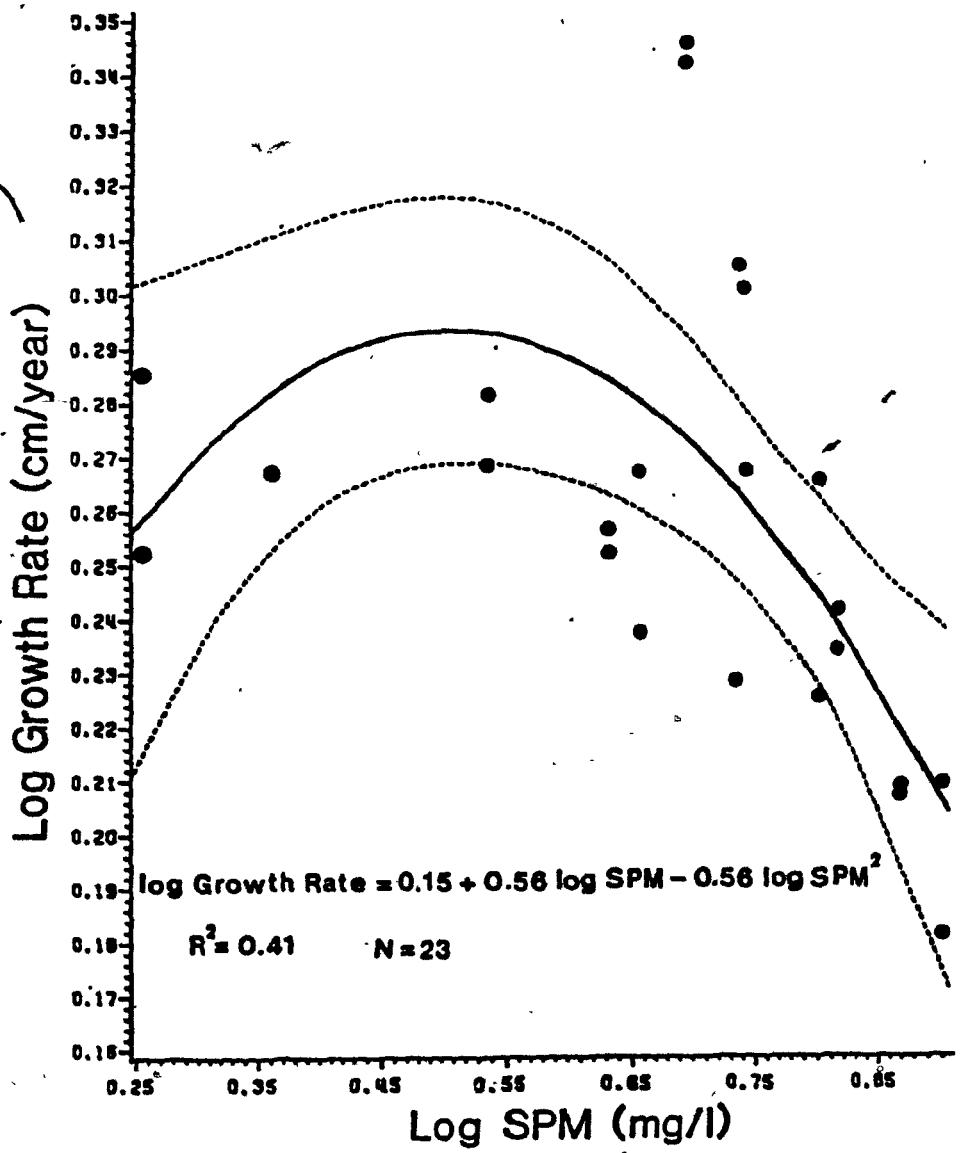


Figure 4. *Montastrea annularis.* Polynomial regression of *M. annularis* growth rate (Growth in cm/yr) on total suspended particulate matter (SPM in mg/l). The broken lines represent the upper and lower 95% confidence bands for the regression line.


Log Growth Rate (cm/year)
0.35
0.34
0.33
0.32
0.31
0.30
0.29
0.28
0.27
0.26
0.25
0.24
0.23
0.22
0.21
0.20
0.19
0.18
0.17
0.16
log Growth Rate = 0.15 + 0.56 log SPM – 0.56 log SPM²
R² = 0.41
N = 23
0.25
0.35
0.45
0.55
0.65
0.75
0.85
Log SPM (mg/l)

M. annularis may be relatively more important than heterotrophy as suggested by Foster (1980). However, with increasing eutrophication the corals use the additional organic fraction of SPM and skeletal extension rates increase, even though slight reduction in calcification (i.e. mass deposition) may occur (Dodge and Brass, 1984). At some point, presumably characteristic of the particular coral species or local gene pool, optimal growth (skeletal extension) will be attained, after which reduction of growth occurs because the negative effect of decreasing light intensity and physical smothering outweigh the positive effect of SPM as a food source.

Coupled with reduced growth rates is also reduction of growth variability as indicated by Dodge *et al.* (1974). This supports the view that in natural environments (unaffected by anthropogenic activities) several factors may be simultaneously affecting coral growth and consequently growth rate variation may be high. However, in polluted environments fewer factors may be having a statistically discernible and biologically significant effect on growth, consequently, growth rates vary less. It remains to be seen whether the observed differences in growth rates result from selective pressures acting on many generations, or whether resistance (through reduced growth) of *M. annularis* can be caused by physiological acclimatization to a gradual increase in SPM concentrations over a long time period.

The eutrophication gradient on the west coast is clearly a function of increased nutrient loading, best reflected in an

increase of phytoplankton biomass, as indicated by high chlorophyll *a* concentrations and in high organic content in the sediments. Chlorophyll a concentrations have increased by 318% since 1969, while SPM concentrations have increased by 555%. This dramatic increase in eutrophication during the past 15 years is clearly reflected in the growth rates of *M. annularis*, as shown by the index master chronologies (Fig. 2). It is suggested that the reduced growth rates of corals are a direct result of increased SPM concentrations brought about by the increased eutrophication processes; and that this is evident both temporally (1969 to 1982) and spatially along the present environmental gradient.

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CHAPTER II

Effects of eutrophication on reef-building corals. Part II. Reproduction of the reef building coral *Porites porites* (Pallas).*

© Tomas Tomascik & Finn Sander

McGill University
Institute of Oceanography
3620 University St.
Montreal, PQ.
H3A 2B2

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Abstract

The sexual reproduction of *Porites porites* (Pallas), a shallow water hermatypic coral, was studied over a one year period on three fringing reef complexes lying along an eutrophication gradient on the west coast of Barbados, W.I. The data suggest that *P. porites* is a gonochoric species with a brooding mode of reproduction, but a low incidence (2.7%) of hermaphroditism was detected in a population sampled from a reef subjected to urban and industrial pollution. Gonadal development occurs within the mesenteries between the retractor muscles and the mesenterial filaments. Gametogenesis occurs during nine to ten months of the year, with the peak reproductive activity occurring predominantly in the fall and winter (November to January). Gametogenesis was therefore loosely synchronized between colonies; however, gonads in all stages of development were present within colonies throughout the reproductive season. The reproductive season of two *P. porites* populations sampled from two polluted reefs began one to two months earlier than that of a *P. porites* population sampled from a less polluted reef. The simultaneous presence of ova and larvae within a colony between November and April suggests that larvae may be released repeatedly during an extended breeding season. No correlation was found between the average number of gonads and polyp size. However, the gonad index (average number of gonads based on the sum of male and female gonads) showed an inverse relationship with a number of

environmental variables. It is suggested that zooxanthellae in the maturing ova may play an important role in the reproductive success of *P. porites*. The reduction of zooxanthellae photosynthesis through reduced light levels may significantly lower the energy available from photosynthates to the maturing ova and/or embryos, thus depressing larval development and maturation. The 2:1 sex ratio observed in a *P. porites* population sampled from a polluted reef may result from rapid asexual reproduction (fragmentation), indicating that the mode of reproduction may be influenced by environmental conditions.

Introduction

Recent studies on the reproductive biology of scleractinian corals have provided much needed information on their sexuality and mode of reproduction (see Fadlallah, 1983, for review; Harrison *et al.*, 1983; Harrison *et al.*, 1984; Szmant-Froelich, 1984; Harrison, 1985; Willis *et al.*, 1985). The available information from the Great Barrier Reef Province suggests that the majority of scleractinian coral species in the Pacific region may be either hermaphroditic or gonochoric broadcasters (Kojis and Quinn, 1981a, b, 1982; Krupp, 1983; Harriott, 1983a; Harrison *et al.*, 1983; Babcock, 1984), and many may undertake mass spawning episodes (Harrison *et al.*, 1984; Willis *et al.*, 1985). These data provide a strong case against a previously held view that the majority of scleractinian coral species are viviparous, i.e. they brood their larvae (Hyman, 1940; Vaughan and Wells, 1948; Wells, 1956, 1966; Stimson, 1976). In contrast to information on Pacific corals, available data on the reproductive biology of Caribbean scleractinian corals are more scarce. A review of previous studies of sexual reproduction of Caribbean reef corals (Wilson, 1888; Duerden, 1902, 1904; Vaughan, 1908, 1909, 1910, 1914; Mavor, 1915; Moorsel, 1980, 1981, 1983; Szmant-Froelich, 1984; Wyers, 1984) revealed information on 17 of the 50 reef building coral species in Jamaica (Wells, 1973). However, the data show that 10 of the 17 coral species are

brooders while only seven are broadcasters. Furthermore, the mass spawning phenomena of coral species observed on the Great Barrier Reef Province (Willis *et al.*, 1985) has not been observed in the Caribbean region.

Recent research on sexual reproduction in scleractinian corals has been instrumental in reconsideration of a number of hypotheses which attempted to relate the mode of coral reproduction to habitat (Stimson, 1978), coral morphology (Rinkevich and Loya, 1979a) and ecology (Loya, 1976a). However, only a few workers have attempted to assess the effects of anthropogenic activities on coral reproduction (Loya, 1975, 1976b; Loya and Rinkevich, 1979) or to provide comparative data on natural variability of coral fecundity (Kojis and Quinn, 1984). Furthermore, most of these studies have been restricted to the effects of oil pollution (Rinkevich and Loya, 1977; Loya and Rinkevich, 1979; Rinkevich and Loya, 1979c; Peters *et al.*, 1981) and thermal stress (Jokiel and Guinther, 1978) on the reproductive biology of the corals. Given the high publicity of major oil spills, it is perhaps not surprising that eutrophication of coastal waters has received less attention, even though it may in the long term pose a more serious threat to many inshore coral reef habitats. Tomascik and Sander (1985a) have suggested that the eutrophication gradient along the west coast of Barbados, West Indies, is a result of differential inputs of domestic and industrial effluents, ground water discharge (Lewis, 1985) and coastal circulation patterns (Emery, 1972). Eutrophication processes have been

implicated in the reduction of skeletal extension rates of a reef building coral *Montastrea annularis* (Tomascik and Sander, 1985a).

Porites porites (Pallas) was chosen for the study, since it has been considered a dominant coral species on the leeward coast of Barbados (Lewis, 1960; Stearn *et al.*, 1977), and because little information is available on its reproductive biology (Duerden, 1902; Goreau *et al.*, 1981). *P. porites* has a wide distribution in the Caribbean region and is found on many fringing coral reefs, where it may be one of the most abundant species (Geister, 1977). Little is known about the reproductive biology of *P. porites*, other than that it may be a gonochoric species (Duerden, 1902) and it releases larvae (Duerden, 1902; Goreau *et al.*, 1981). *Porites* species often form large beds or mounds suggesting that asexual reproduction is common (Glynn, 1973; Highsmith, 1982).

This paper presents new data on reproduction in *P. porites*, including histological observations of gonad structure, gonad and larval abundance, and timing and cycle of gametogenesis. Three *P. porites* populations, from three fringing reefs (Fig. 1) lying along the eutrophication gradient on the leeward coast of Barbados, were used to compare the effects of eutrophication on the above aspects of sexual reproduction.

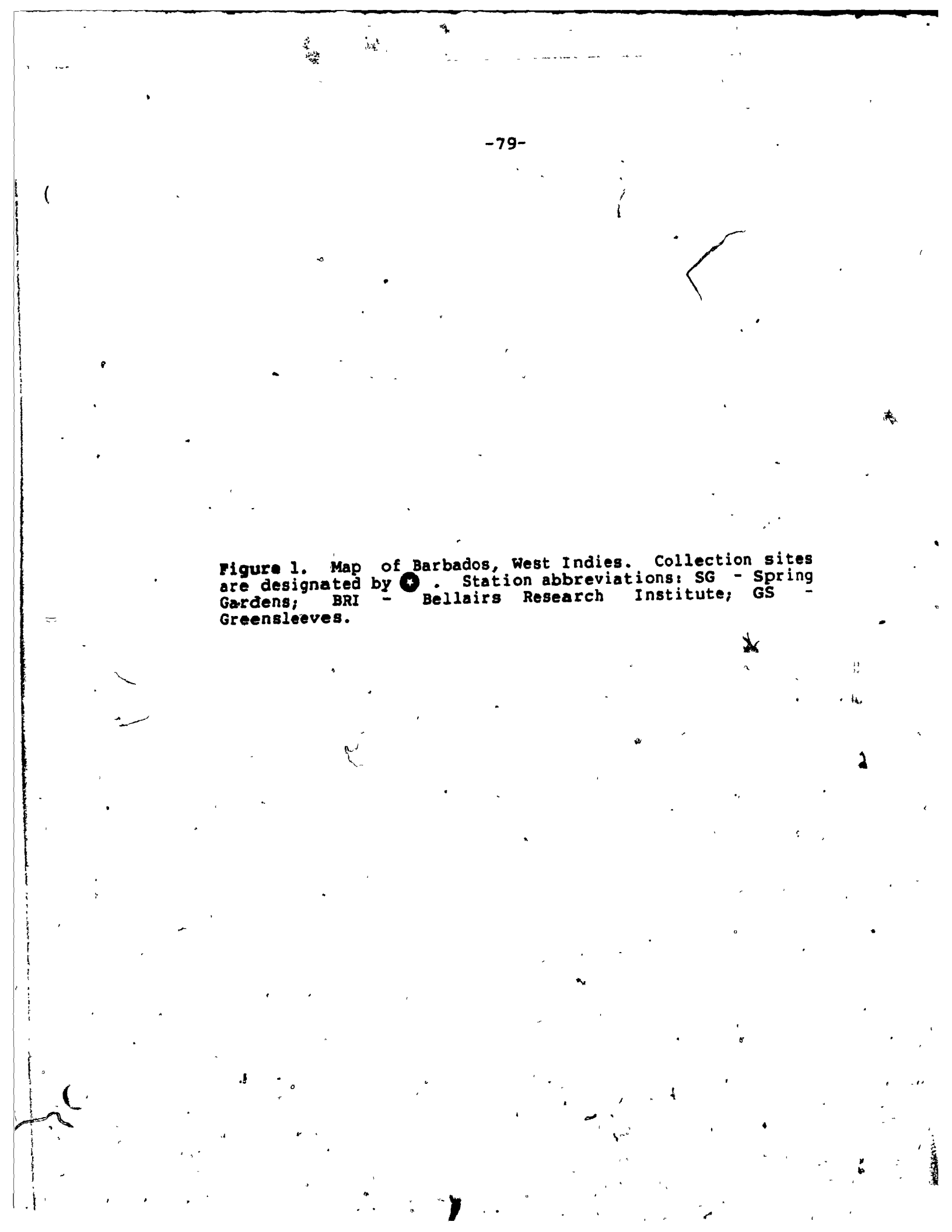
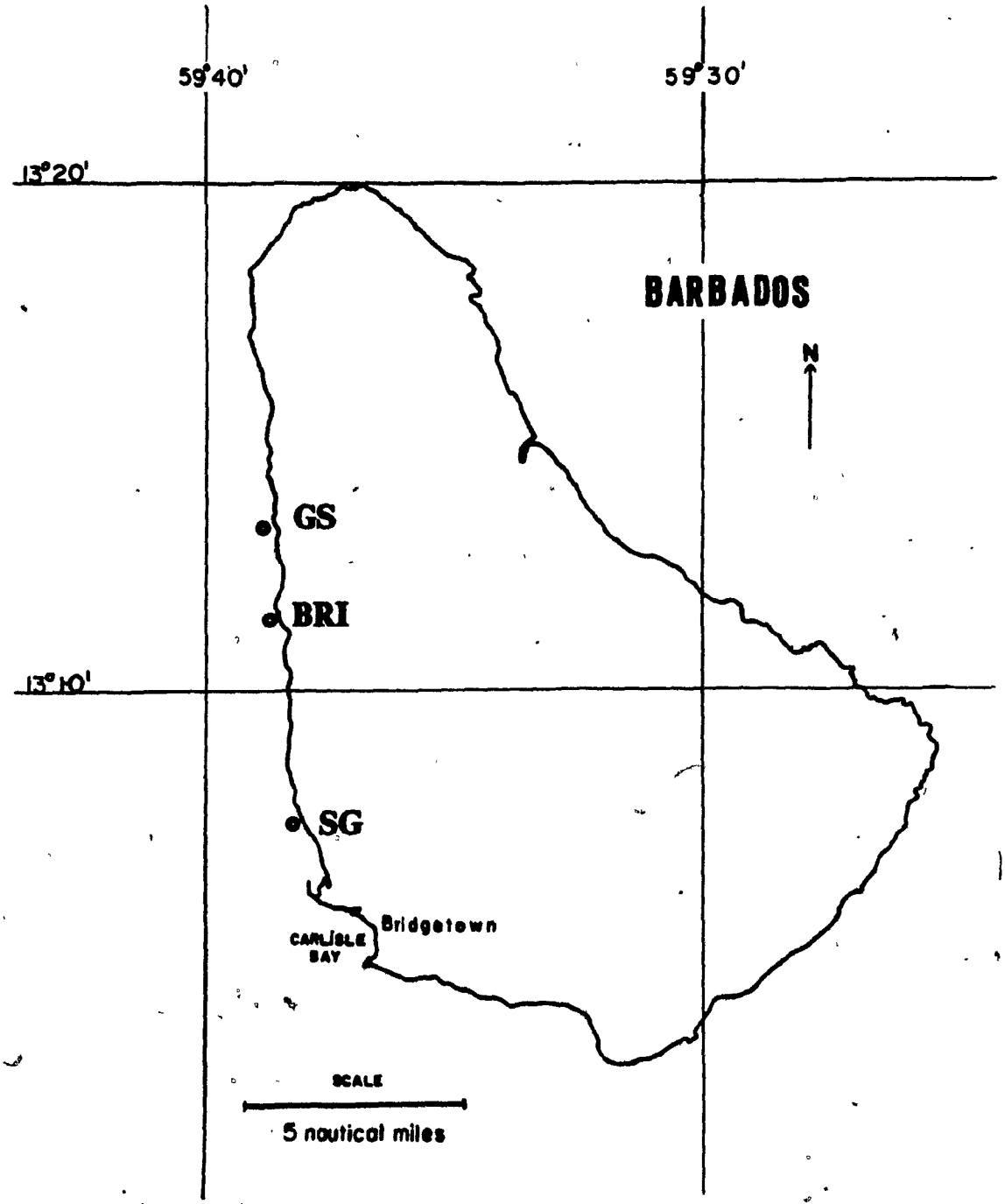


Figure 1. Map of Barbados, West Indies. Collection sites are designated by ✪. Station abbreviations: SG - Spring Gardens; BRI - Bellairs Research Institute; GS - Greensleeves.


59°40'
59°30'
13°20'
13°10'
BARBADOS
N
GS
BRI
SG
Bridgetown
CARLISLE BAY
SCALE
5 nautical miles

Materials and Methods

Study sites

Porites porites (Pallas) was studied on three fringing reef complexes on the leeward (West) coast of Barbados, W.I. (Fig. 1). The three fringing reefs lie along an eutrophication gradient previously described by Tomascik and Sander (1985a). It was suggested (Tomascik and Sander, 1985a) that the south-to-north gradient of decreasing nutrient, suspended particulate matter (SPM) and chlorophyll *a* concentrations is directly and/or indirectly related to the intensification and acceleration of eutrophication processes resulting from urban, agricultural and industrial development on the west coast of Barbados.

The most southern reef (SG) is located in an area that has been subjected to chronic pollution over the last 15 years by a number of anthropogenic activities (i.e. harbour and flour mill construction, rum distillery and power plant effluents). At the present, the main source of pollutants is a nutrient enriched thermal effluent from an electric power plant (Tomascik and Sander, 1985a) located adjacent to the fringing reef. Furthermore, the SG reef is also affected by an organic rich effluent from a rum distillery outfall situated approximately 900m west of the reef.

The central reef (BRI) is located directly in front of the

Bellairs Research Institute, 7km north of the SG reef. The surrounding land area has been extensively developed in the last 15 years and is the major tourist center on the west coast. The primary pollutants affecting the BRI reef are related to domestic effluents and heavy freshwater runoff during the rainy season (August - November). The effects of freshwater runoff have been intensified in this area through man-made modifications of natural drainage streams into major storm drains, which empty directly onto most of the fringing reefs.

The northern reef (GS) is situated 12 km north of the SG reef (Fig. 1), and is considered relatively unpolluted when compared to the two southern reefs (Tomascik and Sander, 1985a). The main source of pollutants is from freshwater runoff during the rainy season. However, qualitative analyses of aerial photographs indicated that the surrounding land area is more densely covered by vegetation than at the two southern locations, suggesting that the effects of freshwater runoff may be less severe.

The general morphological and ecological characteristics of Barbados fringing reefs are described by Lewis (1960), Macintyre (1968), Stearn *et al.* (1977), Scoffin *et al.* (1978), Mah (1984), Mah and Stearn (in press) and Tomascik and Sander (1985b).

Environmental measurements

Fourteen environmental variables were monitored on a weekly basis, on each study site, from September, 1981, to September, 1982. The environmental variables measured during the study were dissolved oxygen (DO mg/l), biological oxygen demand (BOD mg/l), percentage of surface illumination (PEN %), percentage of organic matter in sediments (ORG %), suspended particulate matter (SPM mg/l), volatile particulate matter (VPM mg/l), downward flux of SPM (DF-SPM mg/cm^2/day), chlorophyll a (Chla mg/m^3), inorganic phosphate (PO_4-P μg-at/l), nitrate-nitrite nitrogen (NO_3+NO_2-N μg-at/l), nitrite (NO_2-N μg-at/l), ammonia (NH_3-N μg-at/l), temperature (°C), and salinity ($^0/_{00}$). Note that both temperature and salinity were monitored on a monthly basis from September 1982 to June 1983 at each study site. Details of sampling procedures, laboratory analyses and statistical treatment of the environmental data are given elsewhere (Tomascik and Sander, 1985a).

Histological studies

Tissue samples from *P. porites* were obtained on a semimonthly basis from June, 1982, to June, 1983. Sampling involved breaking a branch from each colony. Because of the relatively small size of *P. porites*, it was not possible to sequentially sample the same colony, and therefore, 10 different colonies were sampled on each sampling day at each

study reef. To reduce possible within-reef variation in coral fecundity, all *P. porites* colonies collected were from the spur and groove zone at a depth of 2 to 3m; all coral specimens were of similar size. The sampling regime was design to minimize possible effects of natural environmental gradients (i.e. depth or wave action), as well as possible effects of colony size on the onset of gametogenesis and gonad abundance (Szmant-Froelich, 1985).

All coral specimens were fixed in 10% formalin for 24 hours within a few minutes after collection. To increase the rate of decalcification, each branch of *P. porites* was split in half with a chisel and decalcified in a solution of equal parts of 50% formic acid and 20% sodium citrate (Pearse, 1968; Rinkevich and Loya, 1979a), which was changed after six hours. After decalcification, all coral tissue samples were washed in running tap water for six hours and preserved in Bouin's solution (Humason, 1972).

For histological analyses, tissue samples (0.75 to 1.50 cm^2) were taken from mid-branch (Rinkevich and Loya, 1979b). All tissue samples were dehydrated in an ethanol series (Humason, 1972), cleared in toluene and embedded in TissuePrep. The prepared blocks were sectioned horizontally (i.e. parallel to the surface) at 10μm through two regions of the tissue 500μm apart. A number of tissue samples from each reef had previously been sectioned to locate the region of the polyp containing reproductive material. Thus, two slides with five to eight serial cross sections each were prepared from each

tissue sample. All tissue sections were stained with Harris hematoxylin (progressive method; 40 sec.) and counterstained with eosin (3 min.). For the quantitative analyses two cross sections (one from each slide) were chosen randomly. Maximum egg diameters were measured with a calibrated ocular micrometer.

The relative size of coral polyps was indirectly estimated by counting the number of polyps in a 0.25 cm^2 square hole placed under the slide containing a tissue cross section from the tentacular region of the polyps. The relative size index thus obtained was expressed as the number of polyps per 0.25 cm^2 of tissue. It has been demonstrated that the onset of gametogenesis in certain coral species is dependent on the number of polyps per colony, and the abundance of gametes seems to depend on colony size (Kojis and Quinn, 1984; Szmant-Froelich, 1985). Therefore, the gonad and larval abundances per polyp were transformed to abundance per 0.25 cm^2 of coral tissue, as suggested by Kojis and Quinn (1984). All tissue sections were examined under a compound light microscope, and a system of three sequential developmental stages, for spermaries and oocytes, was used to quantify the histological observations of gametogenesis. Note that no attempt was made to monitor gamete release, larval release or larval settlement (recruitment).

Statistical analyses

Environmental data. Temperature and salinity data were collected at each reef from September, 1981, to June, 1983. The temperature data were transformed ($\sqrt{X+1}$; X = temperature in °C) and tested for the basic assumptions of homogeneity of variance (Fmax test; Zar, 1984) and normality (Kolmogorov test; Ray, 1982a). Since the null hypothesis of normality and homogeneity of variance were accepted ($P < 0.05$) differences in average temperatures among the three reefs were tested by one-way ANOVA (Ray, 1982b). Specific among reef differences were determined using the Tukey's studentized range (HSD) test (at $P < 0.05$ level). Since a number of transformations were unsuccessful in normalizing the salinity data, the differences among the three reefs were determined by one-way ANOVA based on normalized rank scores (Blom technique; Ray, 1982b). The results of normality (Kolmogorov statistic) and homogeneity of variance (Fmax) tests on the normalized rank scores indicated no violations of the above assumptions. Parametric one-way ANOVA applied to normalized rank scores is equivalent to the Kruskal- Wallis K-sample test, and the F-test generated by the parametric procedure on ranks is often superior to the chi-squared approximation used by Kruskal-Wallis (Ray, 1982b). Specific differences were determined by the Tukey's test.

Reproduction. Prior to statistical analyses, all data sets were transformed ($\sqrt{X+3/8}$) and tested for the basic assumptions of normality (Kolmogorov statistic; normal probability plots) and homogeneity of variance (Fmax test). With the exception of the data sets containing the polyp size index and larval abundance, the null hypotheses of normality and homogeneity of variance were accepted ($P < 0.05$) for all transformed data.

A two-way ANOVA, using the General Linear Model (GLM) procedure for unbalanced design (Ray, 1982b), was used to test three null hypotheses; 1) H_0: There are no differences in the average gonad index among the three reefs; 2) H_0: There is no temporal variability in the average gonad index; and 3) H_0: There is no interaction of reef location and time of the year on gonad index. Since the aim of the two-way ANOVA was to demonstrate possible effects of eutrophication on the reproductive potential of *P. porites* colonies in reproductive state, coral colonies which did not contain reproductive material were excluded from this analysis. However, the null hypothesis that the relative frequencies of colonies in reproductive state are independent of location (i.e. reef) was tested using the 3 x 2 contingency table (Zar, 1984). Temporal variability in gonad index at each study reef was tested using parametric one-way ANOVA. In this analysis, all colonies sampled in each month (i.e. reproducing and non-reproducing) were used. Where ANOVA indicated discernible differences, a multiple comparison of means (at the $P < 0.05$ level) was carried out using the Tukey's studentized range (HSD) test. A

nonparametric ANOVA (Wilcoxon 2-sample test; chi-square approximation) was performed to test the null hypothesis that there were no differences in the average number of larvae among the three reefs. In this procedure samples not containing larvae were excluded from the analysis. Chi-square analysis was used to determine sex ratios among the coral colonies within each reef. To determine whether there were statistically discernible differences in polyp size index among the three reefs, one-way ANOVA was performed on the normalized rank scores and specific among reef differences were determined by the Tukey's test.

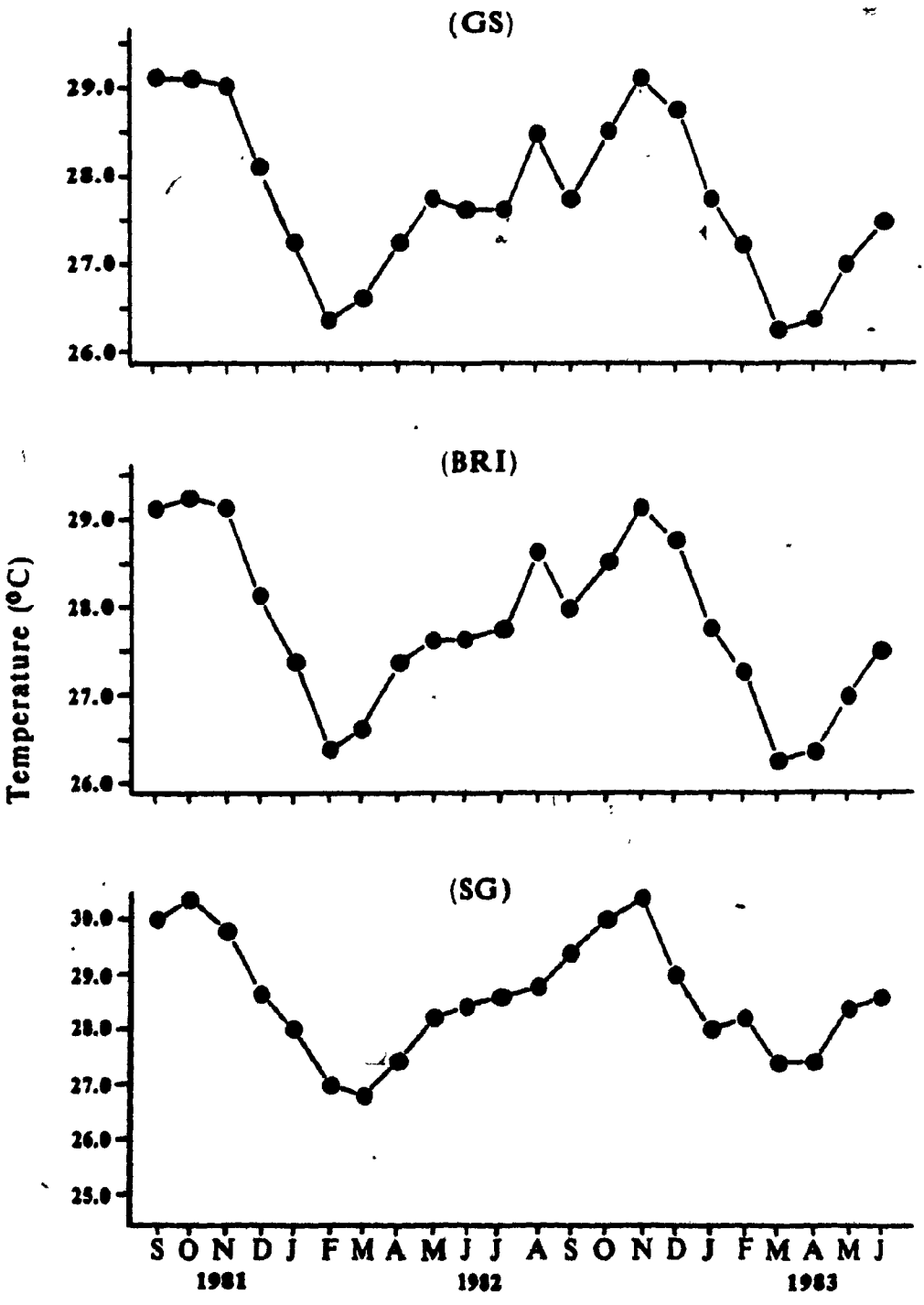
Results

Environmental conditions

Tomascik and Sander (1985a) demonstrated statistically discernible differences among the three reefs for a number of environmental variables. In general, statistically higher nutrient concentrations (i.e. PO_4-P; NO_3+NO_2-N; NO_2-N; NH_3-N) were measured at the SG reef than at the BRI or GS reefs. SPM concentrations, BOD levels and ORG% were statistically higher, while PEN% was statistically lower at the SG reef than at the two northern reefs BRI and GS. The only statistically discernible differences between the BRI and GS reefs were for PEN%, which was higher at the GS reef, and chlorophyll *a* concentrations, which were lower at the GS reef (Tomascik and Sander, 1985a).

Statistically higher temperatures ($P<0.05$) were measured at the SG reef ($\bar{X}$ = 28.56 ± 1.11; N = 57) than at the BRI reef ($\bar{X}$ = 27.89 ± 0.93; N = 57) and the GS reef ($\bar{X}$ = 27.82 ± 0.91; N = 57). Temperature differences between BRI and GS reefs were not statistically discernible. Highest temperatures generally occurred in September - November and gradually declined until February/March (Fig. 2). Salinities recorded at the SG reef ($\bar{X}$ = 32.26 9 1.67; N = 56) were statistically lower ($P < 0.05$) than at the BRI reef ($\bar{X}$ = 33.47 ± 1.11; N = 54) or at the GS reef ($\bar{X}$ = 33.35 ± 1.24; N = 56). However, there were no

Figure 2. Yearly temperature (°C) fluctuations at the GS, BRI and SG collection sites from September 1981 to June 1983.


(GS)
29.0
28.0
27.0
26.0
(BRI)
Temperature (°C)
29.0
28.0
27.0
26.0
(SG)
30.0
29.0
28.0
27.0
26.0
25.0
S O N D J F M A M J J A S O N D J F M A M J
1981
1982
1983

statistically discernible salinity differences between the BRI and GS reefs. Highest salinities occurred in January and progressively declined until June/July (Fig. 3). Seasonal patterns of salinity and temperature fluctuations were more similar between the BRI and GS reefs than between these reefs and the SG reef (Fig. 2, 3). These salinity and temperature differences can be attributed to the effects of thermal effluent released onto the back reef zone of the SG reef.

Reproductive strategy

Porites porites is gonochoric; i.e. each colony was either male or female. Hermaphroditism was detected in only ten colonies (2.7 %) ; and all of these were from the SG reef. Nine of the hermaphroditic colonies were predominantly male, with one to three ovaries, while one colony was predominantly female with one testis containing three spermaries. Both testes and ovaries develop within the mesenteries between the retractor muscle and the mesenterial filaments. Testes usually consist of one to six spermaries, each spermary is separated from the others by a thin membrane probably of mesogleal origin. The ovaries usually contain one ovum at maturation, which is surrounded by a thick endodermal layer during early oogenesis. Of the 620 colonies sampled throughout the year, 366 were in reproductive state, i.e. contained some reproductive material.

The sex ratio of colonies was 1:1 at the BRI and GS reefs, but 2:1 in favour of males at the SG reef (Table 1; $X^2=3.57$, P

Figure 3. Yearly salinity (‰) fluctuations at the GS, BRI and SG collection sites from September 1981 to June 1983.

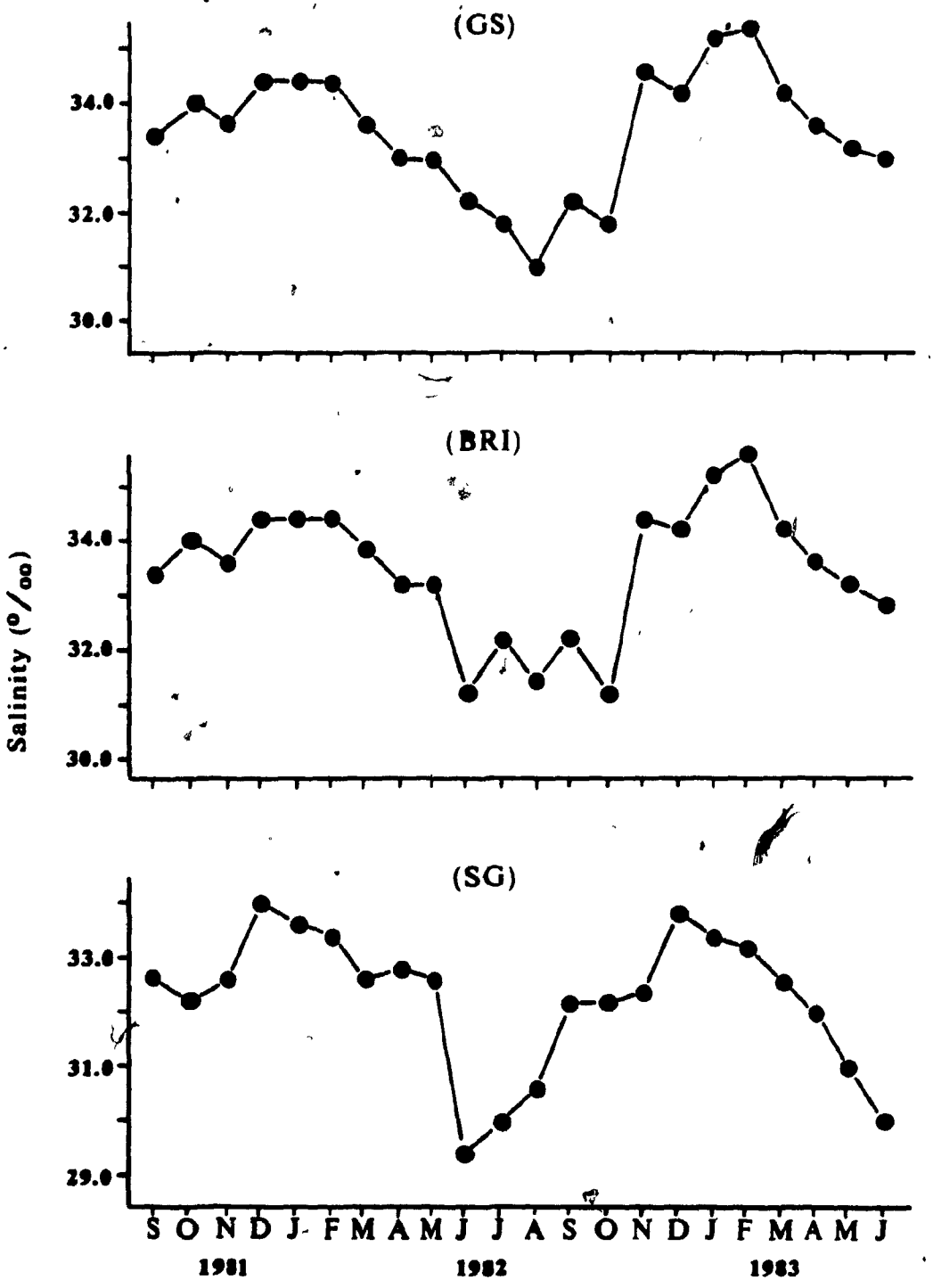

(GS)
34.0
32.0
30.0
(BRI)
Salinity (°/oo)
34.0
32.0
30.0
(SG)
33.0
31.0
29.0
S O N D J F M A M J J A S O N D J F M A M J
1981
1982
1983

Table 1. *Porites porites.* Chi-square analysis testing the null hypothesis; H_o: The sampled population of *P. porites* from the three reefs has a 1:1 sex ratio. Observed frequencies are listed, with the frequencies predicted by H_o in parentheses. N indicates number of colonies.

Reef	Male	Female	N	X^2	DF
SG	83 (68.5)	57 (68.5)	137	5.00*	1
BRI	55 (59.5)	64 (59.5)	119	0.68	1
GS	50 (55.0)	60 (55.0)	110	0.91	1
* Statistically significant					
Total of X^2				6.59	3
Pooled X^2	188 (184.5)	181 (184.5)	369	0.13	1
Heterogeneity X^2				6.46	2
				$0.025<P<0.05$	

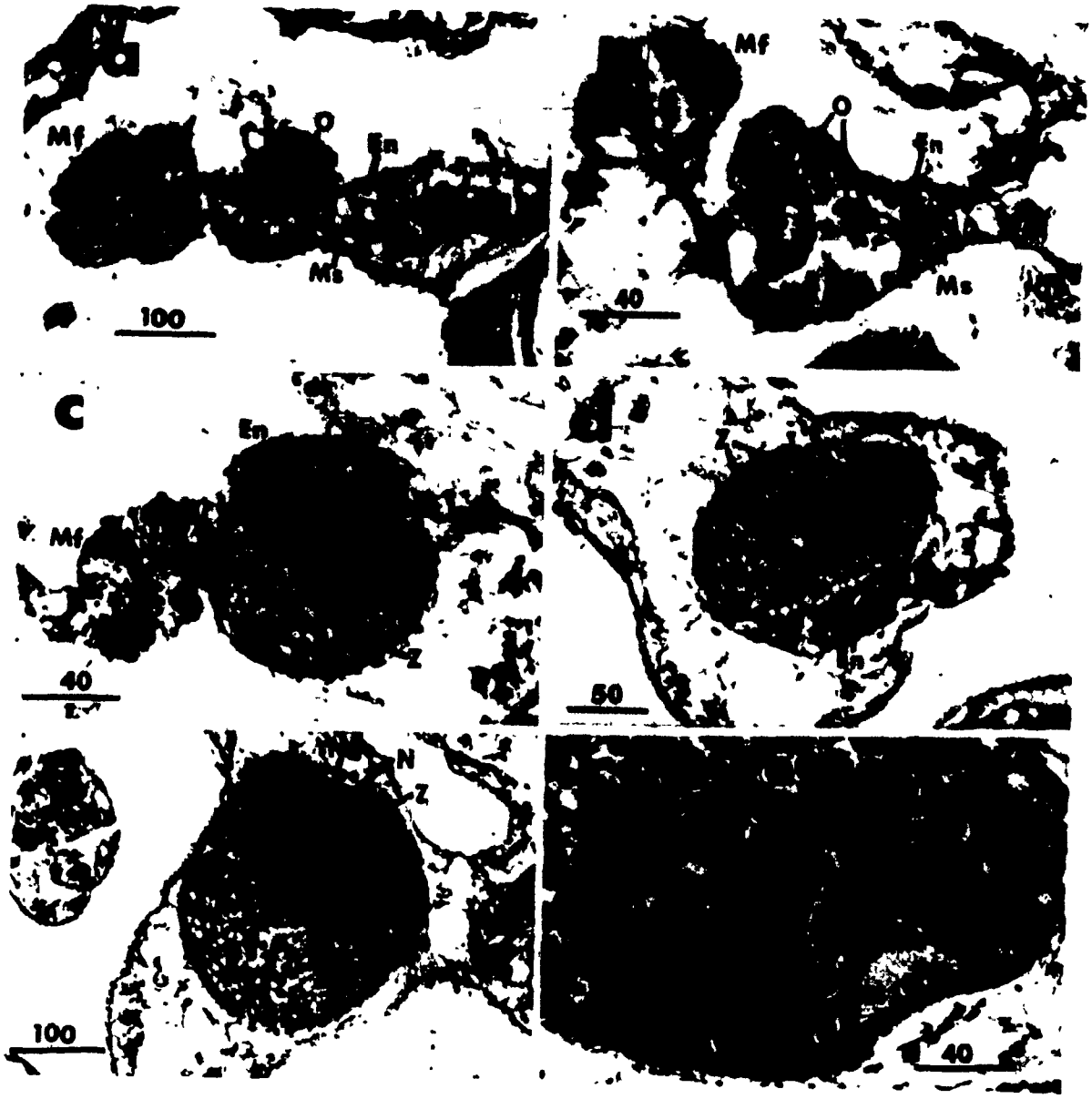
(χ^2) < 0.05). The probability that the samples collected at the three reefs came from more than one population is further supported by the results of the heterogeneity chi-square analysis (Zar, 1984); (Table 1).

Gametogenesis

Oogenesis. Oocyte development was characterized by three developmental stages separable by histological characteristics and relative size of the oocytes. The stages identified were, Stage I: early stage of oocyte development; Stage II: oocytes undergoing vitellogenesis; and Stage III: mature ova.

Stage I oocytes (Fig. 4a) were found in the mesoglea of the mesenteries and were distinguished by small size (< 70μm) and large nuclei (4-16 μm). Each immature ovary contained one oocyte; but in a few cases, two oocytes were present (Fig. 4b). Since the mature ovaries contained one mature ovum, any additional oocytes present during the early developmental stages are presumably resorbed during maturation of the successful oocyte (Rinkevich and Loya, 1979a; Harriot, 1983a, b; Stoddart and Black, 1985). The smallest oocytes, ovoid in shape, were approximately 10μm in diameter and consisted mostly of nuclei which contained distinct nucleoli. During this phase there was very little cytoplasm present. Subsequent changes of Stage I oocytes involved an increase of cytoplasm which was packed with clear vacuolated granules. This stage is characterized by an intense RNA synthesis (Giese and Pearse,

Figure 4 a-f. *Porites porites.* Photomicrographs of histological tissue cross sections showing structure of female gonads and the sequence of oogenesis. (a) Stage I oocyte located in the mesenterial endoderm; (b) Stage I - two oocytes located in the same mesentery, note the absence of zooxanthellae in the mesenterial endoderm; (c-d) Stage II oocytes located in the mesenterial mesoglea. Mesenterial endoderm contains numerous zooxanthellae. Yolk granules are apparent, but not differentiated. (e-f) Stage III - mature ova heavily impregnated with zooxanthellae. Note the dented structure of the nucleus and relative position of the nucleolus. Yolk granules are clearly differentiated from other ooplasmic material. Mature ova surrounded by thin egg membrane. Scale bars are in μm units. Abbreviations: O - oocyte; Mf - mesenterial filament; Rm - retractor muscle; En - endoderm; Ms - mesoglea; N - nucleus; Nu - nucleolus; Z - zooxanthellae; Y - yolk granules.


Mf
En
Ms
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40

1974), which was reflected in strongly basophilic cytoplasm that stained deep blue with Harris hematoxylin. Note that the endoderm of the mesentery surrounding the Stage I oocytes did not contain zooxanthellae. There were no observable histological differences in the structure of the Stage I oocytes among the three reefs.

Stage II oocytes (Fig. 4c) undergoing vitellogenesis were differentiated from the earlier Stage I oocytes by an eosin positive cytoplasm, which contained numerous cytoplasmic granules. The nuclei continued to enlarge during the vitellogensis, until they were approximately 30 to 50μm in diameter. During this phase, the ovaries contained one oocyte only (70 - 280μm in diameter). The cytoplasm of the smallest Stage II oocytes (70 - 100μm) contained mostly clear cytoplasmic granules, with only a few pink staining yolk granules present. Larger Stage II oocytes (100 - 280μm) were characterized by a large number of yolk granules in the cytoplasm (Fig. 4d). However, the yolk granules at this stage of vitellogenesis were not clearly delineated. Furthermore, the mesenterial endoderm surrounding the late STAGE II oocytes was impregnated with numerous zooxanthellae (Fig. 4d); but zooxanthellae were not observed in the ooplasm.

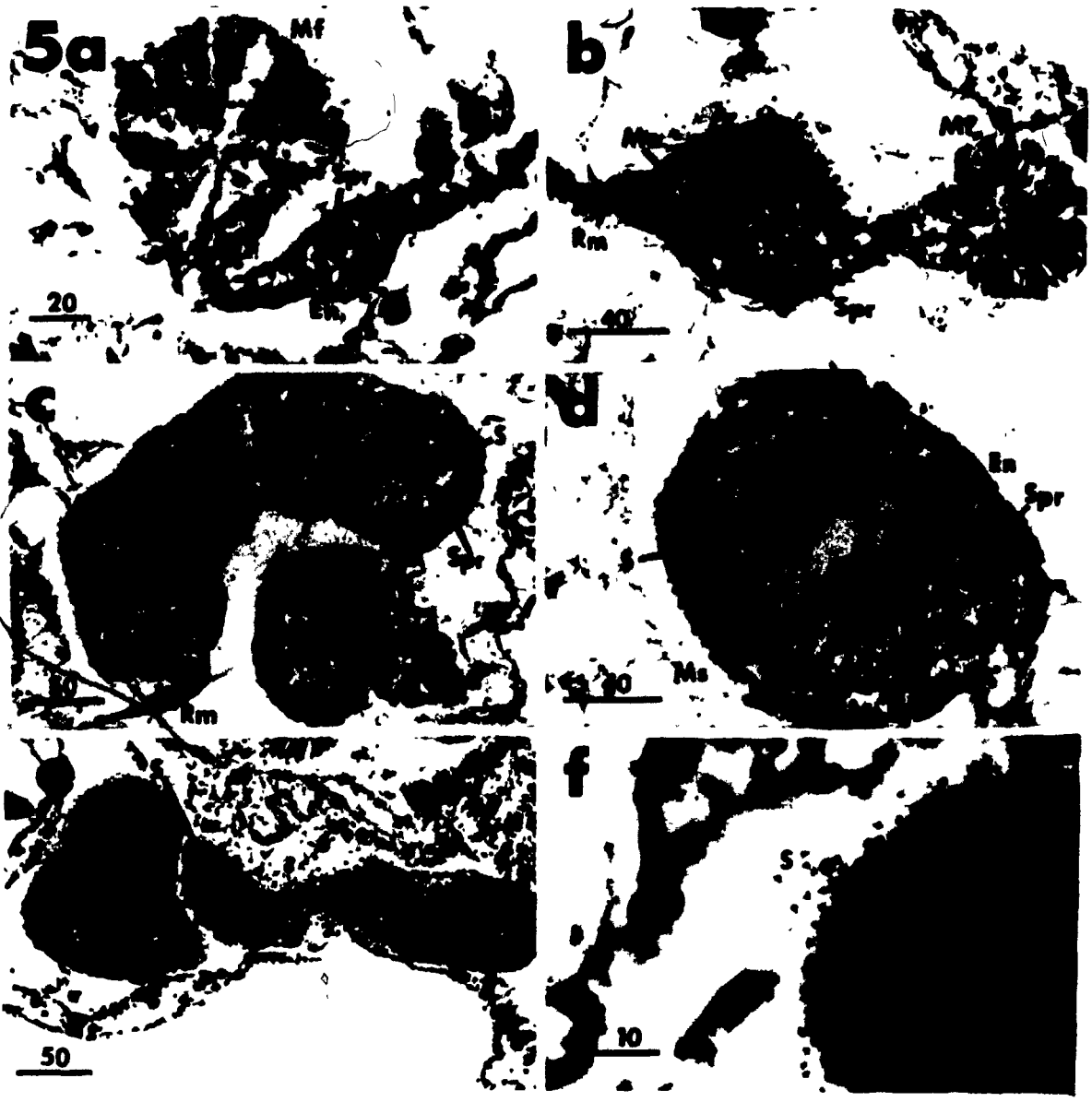
Stage III oocytes (Fig. 4e) were considered mature ova with a diameter of 280/490μm. The nuclei, approximately 30 to 50μm in diameter, have migrated towards the periphery of the ova and become characteristically dented at one side. The nucleoli were present and were usually located in the proximity

of the nuclear dent (Fig. 4f). The ooplasm contained distinct and deep staining yolk granules. Mesenterial endoderm surrounding the smaller Stage III oocytes (280μm) was heavily impregnated with zooxanthellae; however, as the oocytes matured, the endodermal layer became progressively thinner and the zooxanthellae migrated into the ooplasm of the mature ova (Fig. 4f). Thus, in *P. porites*, impregnation of mature ova by zooxanthellae seems to occur before fertilization.

Spermatogenesis

Three distinct stages of sperm development were identified based on the histological characteristics of the spermatocytes and spermaries. The earliest stages of *P. porites* spermatogenesis occurred in the swollen portion of mesenterial endoderm between the retractor muscles and the mesenterial filaments (Fig. 5a). However, with the technique used, it was not possible to identify the cells, which may range from interstitial germ cells to secondary spermatocytes (Giese and Pearse, 1974; Miller, 1983). In the later phase of development (Stage I) the spermatocytes were aggregated in clusters (spermaries), which were surrounded by mesogleal lining (Fig. 5b). The number of spermaries varied, usually with two to six spermaries per testes. The spermatocytes at this stage of development were large, deep staining and evenly distributed throughout the spermaries. The mesenterial endoderm surrounding the testes did not contain zooxanthellae throughout the

Figure 5 a-f. *Porites porites*. Photomicrographs of histological tissue cross sections showing structure of male gonads and the sequence of spermatogenesis. (a) Stage I - spermatocytes are located in the mesenterial endoderm, note the absence of zooxanthellae; (b) Stage I - early developmental stage of three spermaries contained by a single mesentery; (c) Stage II - six spermaries in a single mesentery, note all spermaries are at the same stage of development; (d) Stage II - single spermary illustrating the presence of maturing spermatozoa in the central region, with spermatocytes located towards the periphery, and the hollow central cavity. (e) Stage III - two spermaries packed with mature spermatozoa, note the absence of mesogleal lining; (f) Stage III - mature spermatozoa being released from a mature spermary into the coelenteron, note the conical shape of mature sperms. Scale bars are in μm units. Abbreviations: Mf - mesenterial filament; Rm - retractor muscle; En - endoderm; Ms - mesoglea; Spr - spermatocytes; S - mature spermatozoa.


5a
Mf
En
20
b
Mf
Mf
Rm
Spr
40
c
S
Rm
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d
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Ms
10
f
S
10

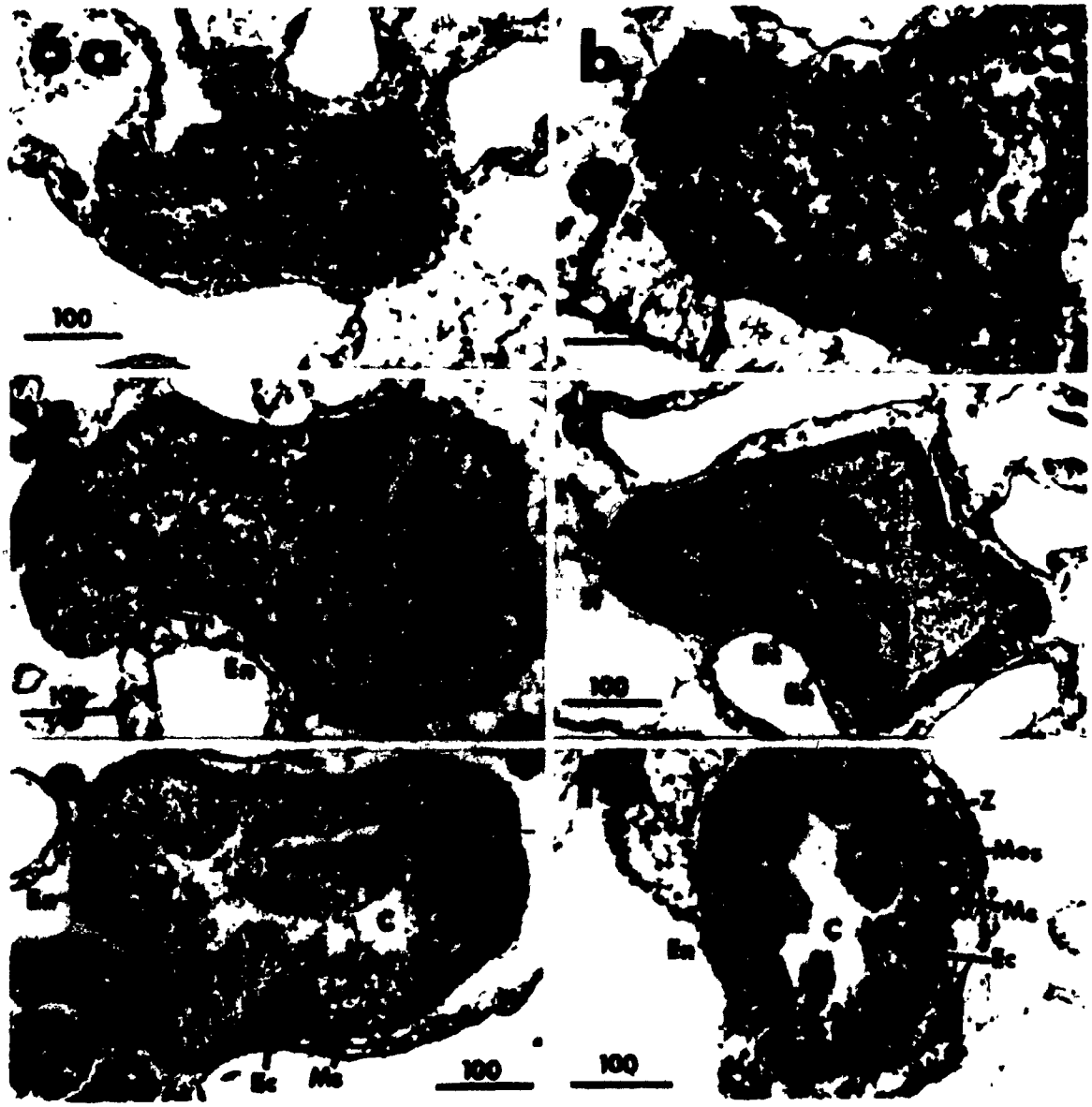
spermatogenesis.

In stage II (Fig.5c), the spermatocytes were located in the periphery of the spermaries and resembled the spermatocytes of Stage I. The central area of the spermaries was filled with much smaller spermatozoa (Fig. 5d) with a distinct, seemingly hollow space in the center of the spermaries. In stage III (Fig. 5e), the spermaries were densely packed with mature spermatozoa, and the mesogleal lining surrounding the mature testes was either much reduced or absent. The mature spermatozoa were conical in shape and contained a large triangular nucleus which was located at the tip of the cone (Fig. 5f).

Embryonic development

The earliest embryos detected resembled mature ova in their staining properties. However, unlike mature ova, the outer layer of the embryos was more irregular, rough and not clearly delineated from the inner yolky mass (Fig. 6a). In subsequent stages of development, the embryos had a distinct outer layer of columnar epithelial cells, impregnated with nematocysts (Fig. 6b), that resembled the ectodermal layer of mature larvae. It has been suggested that gastrulation in cnidarian embryos takes place by multipolar delamination (Campbell, 1974); however, this process is difficult to observe. Fig. 6c indicates two possible cleavage planes of the inner yolky layer, which may represent early stages of mesenterial differentiation. Subsequent stages of development involve formation of oral pore and stomodeum, which appears to form by ectodermal invagination (Fig. 6b) and the development of mesenteries (Fig. 6d). A cross section through a nearly mature larva (Fig. 6e) indicates well developed ectodermal, endodermal and mesogleal layers, as well as the presence of developing mesenteries that project into the coelenteron. Zooxanthellae were absent from the ectodermal layer. Ciliated larvae were not observed, indicating rapid development subsequent to the appearance of larvae with well developed mesenteries. The largest larvae measured in this study were 800μm (maximum diameter), while the smallest embryos were approximately 500μm, and thus very similar in size to mature

Figure 6 a-f. *Porites porites.* Photomicrographs of histological tissue cross sections showing various stages of larval development. (a) Early post fertilization stage gastrula; note presence of yolk granules, zooxanthellae and the irregular surface; (b) Differentiation of the ectodermal layer, note the absence of zooxanthellae. Development of stomodeum indicated by invagination of ectodermal layer; (c) Larva with two possible cleavage planes in the central mass; (d) Mesenterial and stomodeum development indicated, note the distinct ectodermal layer of columnar epithelial cells; (e) Larva near maturation showing distinct ectodermal and endodermal layers and coelenteron; (f) Larva with well developed mesenteries and coelenteron. Scale bars are in μm units. Abbreviations: En - endoderm; Ec - ectoderm; Ms - mesoglea; Mes - mesentery; Z - zooxanthellae; St - stomodeum; Cl - cleavage plane; Y - yolk granules; C - coelenteron.


a
b
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ova. The presence of larvae in colonies containing all stages of oocyte development indicates that larvae may develop and be released continuously during the peak reproductive period of November to February.

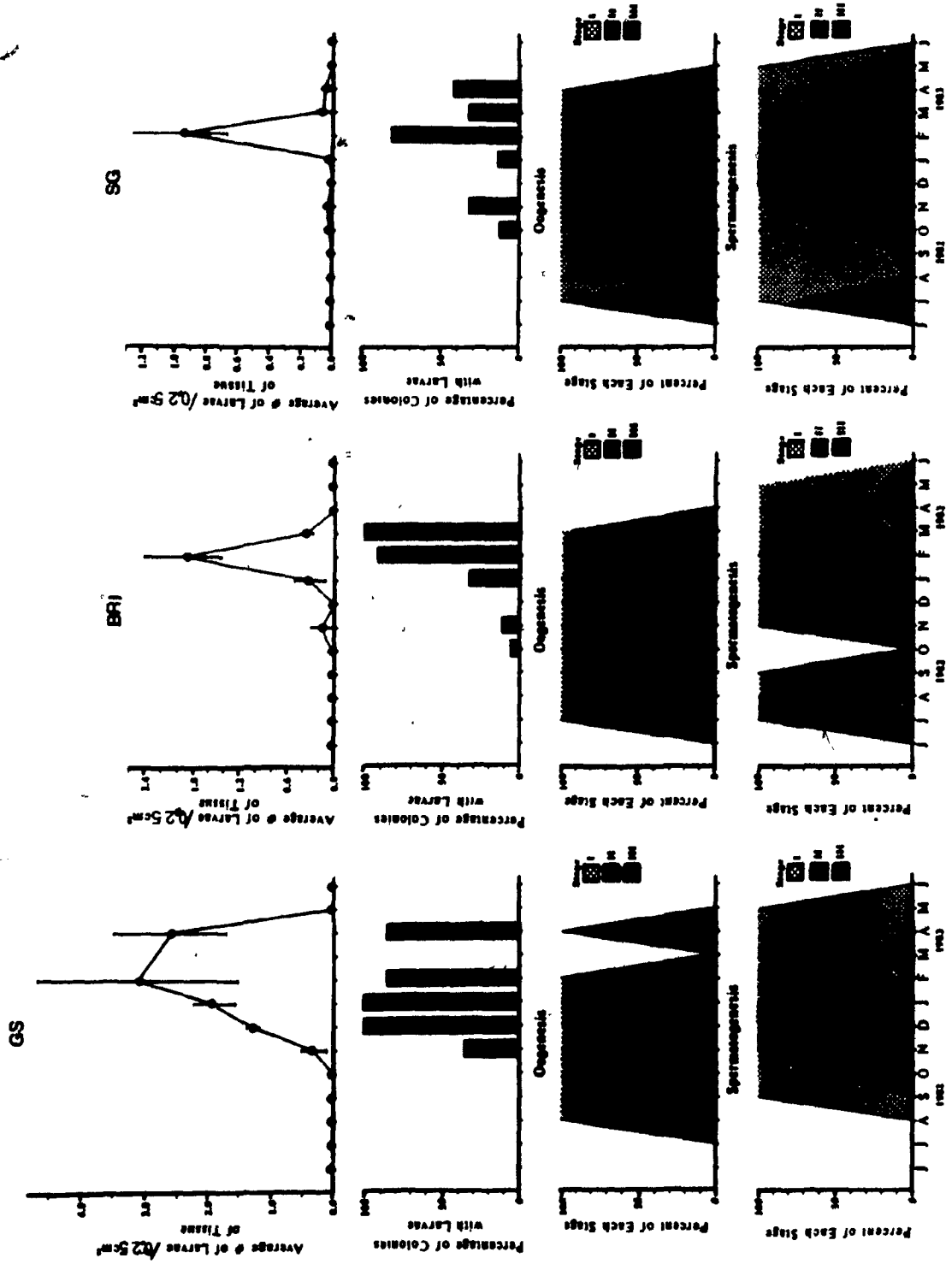
It is of interest to note that Stoddart (1983; 1984), using an electrophoretic technique, has demonstrated that production of larvae in *Pocillopora damicornis* (Linnaeus) may occur through yet unknown asexual processes. Stoddart and Black (1985) further point out that in *P. damicornis*, the developmental pathway leading to brooded larvae remains equivocal, since a developmental link between the gametes and larvae has not been demonstrated. In this study, the presence of large amounts of yolky material in the early embryonic stages of *Porites porites* strongly suggests a link between larval production and sexual reproduction.

Reproductive seasonality

The sequence of gametogenesis and larval appearance at the three reefs was compared by plotting the average relative frequencies of each developmental stage over each month of the year (Fig. 7). This type of comparison is qualitative, in that, the average abundance of each stage at the three reefs is not apparent. None of the coral colonies collected from the three reefs at the end of June, 1982, contained reproductive material. Therefore, it was surprising to find a high percentage of Stage I and II oocytes and spermaries in July/August, 1982, at the SG and BRI reefs (Fig. 7). From July to September the relative frequency of Stage I oocytes and spermaries increased, while Stage II and III oocytes and spermaries decreased at both SG and BRI reefs. Gametogenesis at the northern unpolluted reef GS lagged one to two months behind that at the SG and BRI reefs.

Oogenesis at the GS reef was initiated approximately one month before spermatogenesis. Colonies collected during August at the GS reef contained predominantly Stage I oocytes, with few Stage II and III oocytes; however, none of the colonies collected contained testes. Spermatogenesis at the GS reef was most likely initiated in early September, since all male colonies collected in September contained only Stage I spermaries (Fig.7). From November, 1982, to January, 1983, Stage III spermaries were most abundant, indicating that the

Figure 7. *Porites porites.* Temporal changes in the relative frequencies of the three developmental stages of spermatocytes and oocytes, percentage of colonies containing larvae, and the average number of larvae per 0.25cm² of tissue at the three study reefs GS, BRI and SG. Bars for the average number of larvae indicate standard deviations.


GS
BRi
SG
Percent of Each Stage
Spermatogenesis
Oogenesis
Percentage of Colonies with Larvae
Average # of Larvae /.02 Scm² of Tissue
J F M A M J J A S O N D J F M A M J
1982
1983

release of spermatozoa most likely occurred during these months. With the exception of SG reef, male colonies collected between February and March contained mostly Stage I spermaries. At the SG reef, there was a slight peak in the relative frequency of Stage III spermaries during April.

On all reefs, as the Stage I and II oocyte frequencies decreased from September to May, Stage III oocyte frequencies gradually increased until April - May. Depressing the production of new primary oocytes during the late stages of the reproductive cycle, may make more energy available for the maturing ova already present.

In summary, gametogenesis appears to be loosely synchronized, with mature ova and spermatozoa being present in most months, but the decrease in early developmental stages of oocytes and spermaries being accompanied by an increase in the relative frequencies of mature stages.

Larvae, at the SG and BRI reefs (Fig. 7), first appeared in October; but in only a few colonies and in low numbers. In contrast, larvae at the GS reef appeared in November, one month later than at the BRI and SG reefs (Fig. 7). From November the average abundance of larvae in the tissue cross sections gradually increased, and reached a peak during February.

Reproductive activity

The most widely used quantitative method for estimating reproductive activity in marine benthic invertebrates is the gonad index (Giese and Pearse, 1974). In the present study gonad index is expressed as the average number of gonads per 0.25cm² of coral tissue (based on the sum of all male and female gonads). The gonad index was used to quantify the reproductive activity of *P. porites*, and to relate the reproductive activity of *P. porites* to environmental conditions (Table 2). The average gonad index increased from the SG reef in a northerly direction towards the BRI and GS reefs by 12.5 % and 38.1 % respectively. Spatial and temporal differences in the average gonad indices of *P. porites* were statistically discernible (two-way ANOVA; Table 3). Average gonad index at the GS reef was statistically higher than at the SG and BRI reefs (Tukey's studentized range test; Table 2 and 3). There were no statistically discernible differences in the average gonad index between the SG and BRI reefs. The average gonad index had a significant temporal variability ($P < 0.0001$), suggesting strong seasonal patterns. Furthermore, the strong interaction effect (Table 3) suggests, that the average gonad index during the reproductive cycle is strongly dependent on both the time of year and the location (i.e. reef). Since all *P. porites* colonies were collected from similar ecological zones (spur and groove), similar depth (2 - 3m) and all were of similar size, the strong interaction effect in the two-way ANOVA (Table 3)

Table 2. *Porites porites*. The average gonad index of *P. porites* (sum of male and female gonads) at the three study reefs and the yearly means for temperature (Temp °C), salinity (Sal $^{o}/_{oo}$), suspended particulate matter (SPM mg/l), chlorophyll *a* (Chla mg/m^3) and percentage of surface illumination (Pen %). First number: average values; second number (in parentheses): standard deviation; third number: sample size.

Reef	Gonad Index	Temp (°C)	Sal ($^{o}/_{oo}$)	SPM (mg/l)	Chla (mg/m^3)	Pen (%)
SG	5.48 (5.22) 137	28.56 (1.11) 57	32.3 (1.7) 56	7.32 (2.86) 46	0.895 (0.406) 46	28.82 (11.84) 28
BRI	6.26 (6.65) 119	27.89 (0.94) 57	33.5 (1.1) 54	5.94 (3.41) 44	0.799 (0.470) 46	34.52 (7.32) 28
GS	8.85 (8.51) 110	27.82 (0.91) 57	33.4 (1.2) 56	5.21 (3.29) 44	0.546 (0.270) 46	40.45 (8.43) 28

Table 3. *Porites porites.* Parametric two-way ANOVA of the average gonad indices for *P. porites* at the SG, BRI and GS reefs over time.

Source	SS	df	MS	F value	PR>F
Model	32.726	31	1.056	12.41	0.0001
Error	28.411	334	0.085		
Total	61.137	365			
Reef	0.653	2	0.327	3.84	0.02
Time	26.539	10	2.654	31.20	0.0001
Reef X Time	5.534	19	0.291	3.42	0.0001

suggests that the observed differences in the average gonad indices were closely related to the environmental differences that exist among the three reefs (Tomascik and Sander, 1985a). The probability that the observed differences in the average gonad indices were related to the environmental differences between the reefs was further supported by the results of the 3 X 2 contingency table, using chi-square statistic (Zar, 1984), which rejected the null hypothesis that reproductive state of *P. porites* was independent of location (Table 4). However, it should be noted that the differences in the average gonad indices among the three *P. porites* populations may be also related to local genetic variability.

Since the release of larvae was not quantified or observed, the potential reproductive success of *P. porites* may be approximated by the average number of larvae in the tissue cross sections. The results of the nonparametric ANOVA demonstrated that the average number of larvae per tissue section at the northern reef GS ($\bar{X}$ = 1.2 ± 2.1; N = 60) was statistically higher ($P < 0.0002$) than at the SG reef ($\bar{X}$ = 0.1 ± 0.4; N = 54) and the BRI reef ($\bar{X}$ = 0.4 ± 1.1; N = 64; $P < 0.004$). There were no statistically discernible differences between the SG and BRI reefs ($P > 0.370$). In summary, even though the reproductive season at the SG and BRI reefs is one to two months longer than at the GS reef, the potential reproductive output (reflected by the average number of larvae per tissue section) was lower. However, the narrow larval peak at the two southern reefs (BRI and SG) also suggests a sudden

Table 4. *Porites porites.* A 3 X 2 contingency table for testing the independence of the reproductive state of *P. porites* and location. Colonies in reproductive state contain gonads.

Location (Reef)	No. of colonies with gonads	No. of colonies without gonads	Total
SG	137	73	210
BRI	119	81	200
GS	110	100	210
Total	366	254	620

$X^2 = 7.20$
$\nu = 2$
$X^2_{0.05,2} = 5.99$

$0.025 < P < 0.05$

larval release (Fig. 7). In contrast, the broader larval peak at the northern reef GS (Fig. 7) indicates longer larval release period, followed by a sudden drop in April.

Fig. 8a clearly demonstrates that *P. porites* colonies at the SG reef contain gonads throughout the year, with the exception of June. The percentage of colonies containing gonads increased from July to December and remained high until May. The sharp decline of colonies in a reproductive state in March was perhaps a result of sampling, since coral colonies collected in April contained gonads in all stages of development. Reproductive activity at the SG reef showed a well defined seasonal cycle, with peak reproductive activity (i.e. number of gonads per tissue section) occurring between October and January followed by a decline, even though the percentage of colonies with gonads remained high (Fig. 8a,b). The results of the one-way ANOVA indicated significant temporal variability for the average gonad index at the SG reef (Table 5). The results of Tukey's test indicated no statistically discernible differences in the average gonad indices among the four months of high reproductive activity, October to January, as well as February and April, however, the average gonad indices between November and January were statistically discernible (at the $P<0.05$ level) from other months (Table 5).

Seasonal variability in the average gonad index at the BRI reef was similar to the SG reef. Fig. 9a indicates that colonies of *P. porites* at the BRI reef were reproductively active throughout the year, however, the peak reproductive

Figure 8. *Porites porites*. Reproductive activity over a single breeding season for the population of *P. porites* collected at the SG reef. a) showing that colonies in reproductive state are present during 11 months of the year; b) showing that peak reproductive activity (expressed as the number of gonads per tissue section) occurs between November and January.

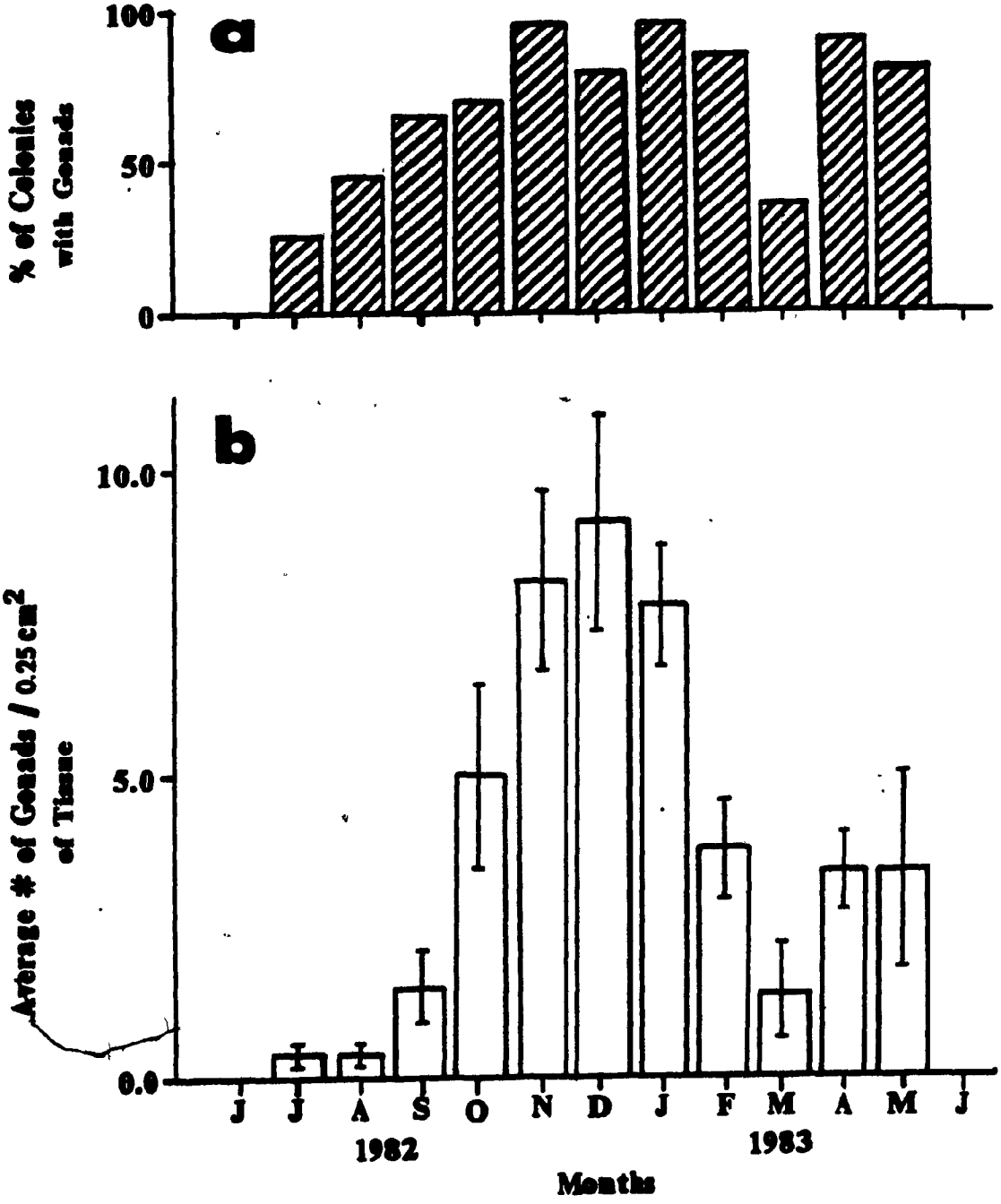

a
100
50
0
% of Colonies with Gonads
b
10.0
5.0
0.0
Average # of Gonads / 0.25 cm² of Tissue
J J A S O N D J F M A M J
1982
1983
Months

Table 5. *Porites porites.* A one-way ANOVA and Tukey's studentized range (HSD) test for the average gonad index of *P. porites* at the SG reef at different times of the year. Lines connecting different months indicate no statistically discernible differences (at least at the P < 0.05 level).

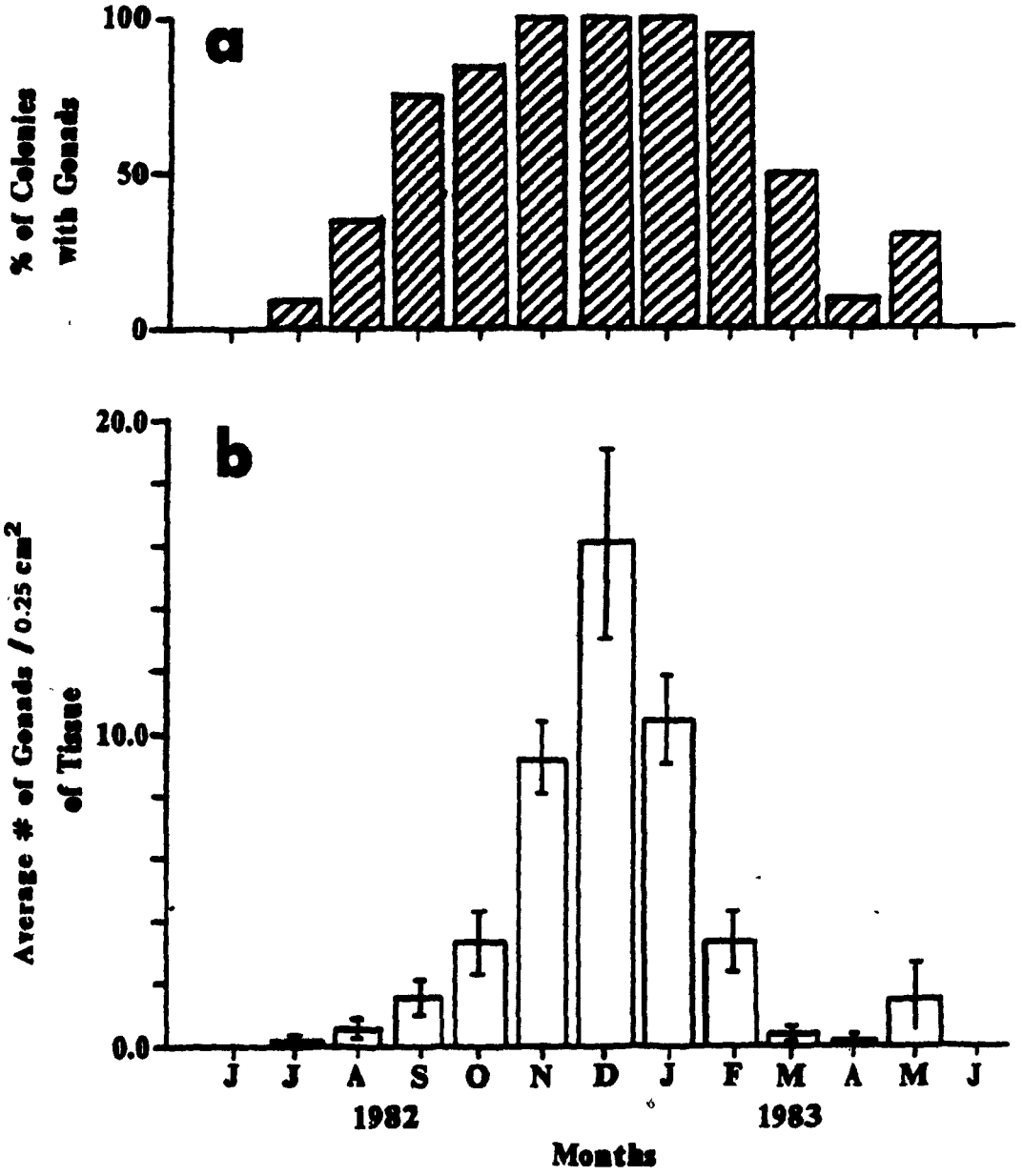
Source	SS	df	MS	F value	PR > F
Model	13.858	10	1.386	12.53	0.0001
Error	19.799	179	0.111		
Total	33.657	189			

Tukey's test:

Months

Dec Jan Nov Apr Oct Feb May Mar Sept Aug July

Figure 9. *Porites porites*. Reproductive activity over a single breeding season for the population of *P. porites* collected at the BRI reef. **a)** showing that colonies in reproductive state are present during 11 months of the year; **b)** showing that peak reproductive activity (expressed as the number of gonads per tissue section) occurs between November and January.


a
100
50
0
% of Colonies with Gonads
b
20.0
10.0
0.0
Average # of Gonads / 0.25 cm²
of Tissue
J J A S O N D J F M A M J
1982
1983
Months

period was more clearly defined (Fig. 9b) than at the SG reef. The average gonad index increased from July and peaked between November and January. The results of the one-way ANOVA indicated significant seasonal variability (Table 6), while the results of the Tukey's test showed that the average gonad indices between November and January were statistically discernible from other months (Table 6).

The seasonal variability in the average gonad index at the GS reef, with few exceptions, was similar to the two southern reefs SG and BRI. However, unlike at the two southern reefs, coral colonies in reproductive state were first observed in August, and represented 5% of the sampled population (Fig. 10a) compared to 35% and 45% at the SG and BRI reefs respectively. The percentage of colonies in reproductive state increased to 100% in December - January and subsequently declined (Fig. 10a). The average gonad index at the GS reef increased gradually from August to December (Fig. 10b). The results of the one-way ANOVA indicated that the seasonal variability in the average gonad index at the GS reef was significant (Table 7). Reproductive activity between November and January was statistically discernible from the other months of the year (Fig. 10b; Table 7), with the exception of March (Tukey's test).

Table 6. *Porites porites*. A one-way ANOVA and Tukey's studentized range (HSD) test for the average gonad index of *P. porites* at the BRI reef at different times of the year. Lines connecting different months indicate no statistically discernible differences (at least at the $P < 0.05$ level).

Source	SS	df	MS	F value	PR > F
Model	25.010	10	2.500	34.73	0.0001
Error	12.170	168	0.072		
Total	37.180	179			

Tukey's test:

Months

Dec	Jan	Nov	Feb	Oct	Sept	May	Aug	Mar	Apr	July
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Figure 10. *Porites porites*. Reproductive activity over a single breeding season for the population of *P. porites* collected at the GS reef. a) showing that colonies in reproductive state are present during 10 months of the year; b) showing that peak reproductive activity (expressed as the number of gonads per tissue section) occurs between November and January.

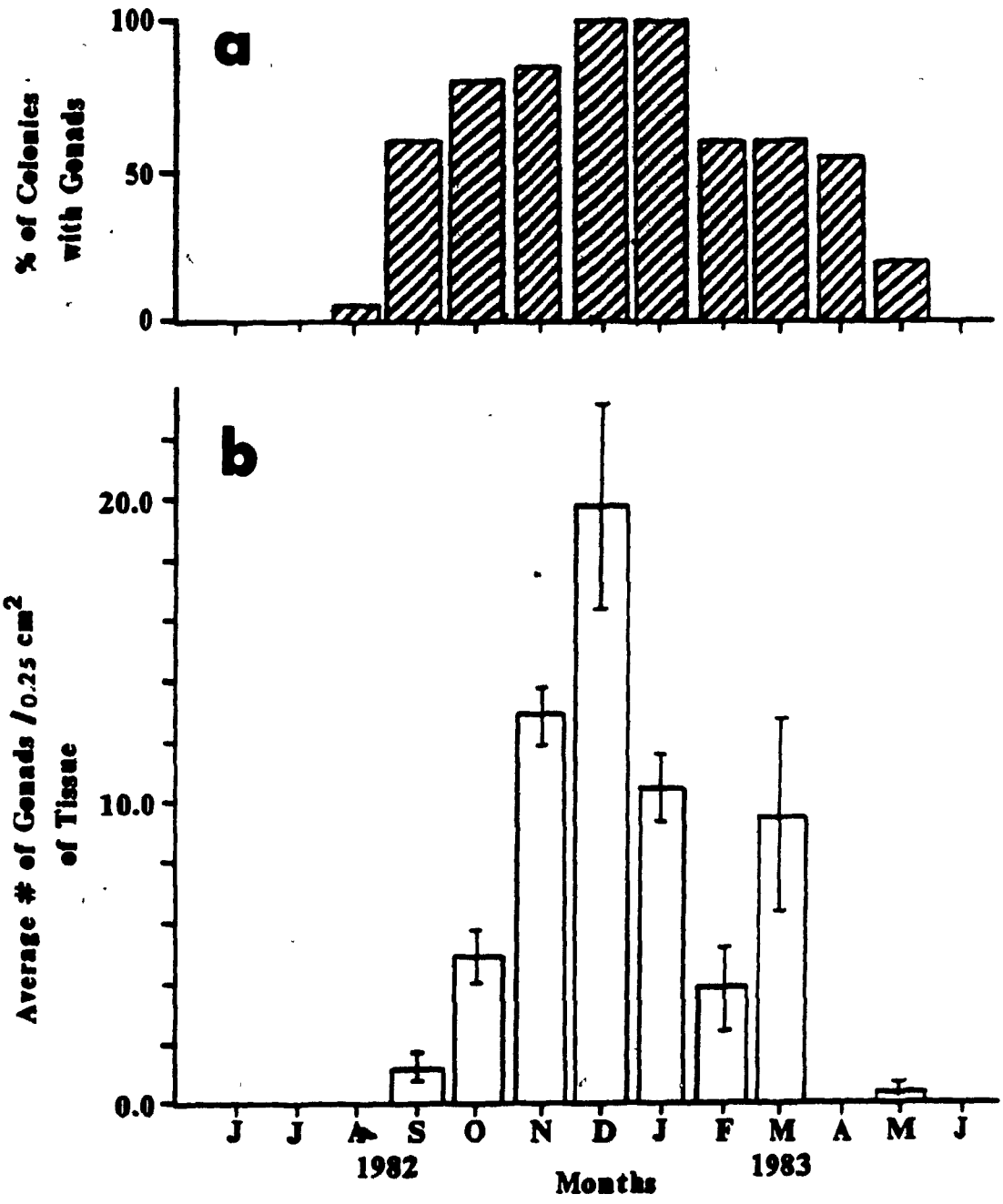
a
100
50
0
% of Colonies with Gonads
b
20.0
10.0
0.0
Average # of Gonads /0.25 cm²
of Tissue
J J A S O N D J F M A M J
1982
1983
Months

Table 7. *Porites porites*. A one-way ANOVA and Tukey's studentized range (HSD) test for the average gonad index of *P. porites* at the GS reef at different times of the year. Lines connecting different months indicate no statistically discernible differences (at least at the $P < 0.05$ level).

Source	SS	df	MS	F value	PR > F
Model	33.202	10	3.320	31.11	0.0001
Error	19.105	179	0.107		
Total	52.307	189			

Tukey's test

Months

Dec	Nov	Jan	Mar	Oct	Feb	Sept	May	Apr	Aug	July
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	---		---							

Average number of polyps

The results of one-way ANOVA (Table 8) based on the normalized rank scores (Ray, 1982b) indicated significant differences ($P < 0.0001$) for the average number of polyps per 0.25 cm^2 of tissue (i.e. polyp size index). The results of the Tukey's test showed that the polyp size index at the SG reef ($\bar{X}$ = 19.27 ± 4.73; N = 210) was statistically higher ($P<.05$) than at the BRI ($\bar{X}$ = 17.12 ± 3.95; N = 200) and GS ($\bar{X}$ = 14.17 ± 3.70; N = 210) reefs. Furthermore, the polyp size index at the BRI reef was statistically higher ($P<0.05$) than at the GS reef. Spearman rank correlation analysis between polyp size index and the average gonad index failed to demonstrate a statistical relationship ($r = -0.01$; $P > 0.81$; N = 366), indicating that the observed differences in the average gonad indices were not related to polyp size.

Table 8. *Porites porites.* A one-way ANOVA of the average polyp size index among the three reefs for *P. porites.*

Source	SS	df	MS	F value	PR > F
Model	122.283	2	61.141	76.84	0.0001
Error	490.936	617	0.796		
Total	613.219	619			

Discussion and Conclusions

Recent studies on the reproductive biology of *Porites* species in the Pacific have demonstrated two patterns of sexual reproduction. *Porites lutea* Edwards and Haime, *P. lobata* Dana, *P. andrewsii* Dana, and *P. australiensis* (Vaughan) spawn gametes and are gonochoric (Kojis and Quinn, 1981b; Harriott, 1983); while *P. murrayensis* Vaughan is a gonochoric brooder (Kojis and Quinn, 1981b). Thus, it has been suggested that gonochorism can be considered a general characteristic of the family Poritidae (Kojis and Quinn, 1981b).

Earlier accounts of the life history of the genus *Porites* in the Caribbean indicated that two species, *Porites astreoides* Lamarck and *P. clavaria* Lamarck, brooded their embryos to larval stage (Vaughan, 1908, 1909, 1910). Furthermore, Duerden (1902) indicated that *P. clavaria* (= *P. porites*; Roos, 1971; Cairns, 1981) may be a gonochoric species, since male and female gonads were not found in the same colony. However, this did not exclude the possibility that *P. porites* was a protandrous or protogynous hermaphrodite. Recently, it was demonstrated that *P. astreoides* is a hermaphroditic brooder (Szmant-Froelich, 1984).

The present study provides strong evidence that in natural environments (i.e. unaffected by anthropogenic activities) *P. porites* is a gonochoric brooder (colonies are either male or female) at least during each breeding season. In polluted environments *P. porites* may revert to hermaphroditism through

yet undetermined processes. Since the same *P. porites* colonies were not sampled sequentially throughout the breeding season, the possibility that *P. porites* is either protandrous or protogynous hermaphrodite needs further investigation. However, the data suggest that an earlier assumption that all Caribbean *Porites* species are hermaphrodites (Harrison, 1985) needs reevaluation. In view of the close morphological similarity of *P. porites* to *P. divaricata* Lesuer and *P. furcata* Lamarck (Roos, 1971; Cairns, 1981), it would be of interest to investigate whether these formae are similar to *P. porites* in terms of sexuality and mode of reproduction. In this context, note that two forms of *Agaricia agaricites* (Linnaeus), namely forma *purpurea* (Lesueur) and forma *humilis* Verrill (now considered separate species; Moorsel, 1983), are both hermaphroditic brooders (Fadlallah, 1983).

Note that the reproductive strategy of *P. porites* is more similar to its Pacific congener, *P. murrayensis*, than to its Caribbean congener, *P. astreoides*. Of equal interest is the similarity in timing of gametogenesis between *P. porites* and *P. murrayensis*. In both species gametogenesis is initiated from July to September. Release of larvae was not observed in this study, however, Goreau *et al.* (1981) have indicated that larval release in *P. porites* at Jamaica occurred during late November and subsequently declined. However, the study in Jamaica was conducted under laboratory conditions. The water temperature was maintained at a constant 21 °C which is well below the normal yearly range of 26.2 °C to 29.7 °C (Ohlhorst,

1980). The results of the present study (Fig. 7) indicate that, in Barbados, larval release in *P. porites* most likely occurs for five months of the year between November and April. Thus, the timing of larval release in *P. porites* is similar to *P. murrayensis* in the Pacific (Kojis and Quinn, 1981b). The available data on the breeding season of *P. astreoides* suggests that this species is reproductively active most of the year (Szmant-Froelich, 1984).

P. porites and *P. astreoides* are common Caribbean species found in all reef habitats: back reef, reef flat and spur and groove zone (Tomascik and Sander, 1985b). *P. astreoides* was the most abundant species in terms of the relative coral cover at the two northern reefs BRI and GS, while at the SG reef the relative percentage of coral cover of the two *Porites* species was the same (Tomascik and Sander, 1985b). Higher abundance of *P. porites* at the southern reef SG is perhaps a result of higher rates of asexual reproduction maintained by higher rates of fragmentation. Highsmith (1982) has indicated that reproduction by fragmentation in *P. furcata*, which is morphologically similar to *P. porites*, is an important mode of asexual reproduction responsible for recolonization of holes in *P. furcata* beds. It has been shown that higher water column productivity (i.e. eutrophication) may enhance production of filter and deposit feeding invertebrates including borers (Highsmith, 1980, Highsmith *et al.*, 1983). Thus, high boring intensity in *P. porites* colonies at the SG reef may result in higher fragmentation rates of mature colonies, and therefore,

result in higher abundance and cover of this species at the SG reef than at the two northern reefs BRI and GS. Lewis (1974a) has demonstrated that the contagious distribution of *P. astreoides* was a result of splitting of large colonies into clumps of smaller colonies, suggesting that this may be a type of asexual reproduction for this species. However, the environmental conditions at the SG reef are characterized by high water column turbidity associated with high SPM, nutrient and chlorophyll *a* concentrations (Tomascik and Sander, 1985a). Thus, under the measured environmental conditions at the SG reef, *P. porites*, because of its branching morphology, may be less susceptible to high sedimentation and/or SPM concentrations than the encrusting hemispherical *P. astreoides*. The apparent parity of these two coral species in terms of relative coverage, at the SG reef, could therefore result exclusively from better survivorship of *P. porites* than *P. astreoides*. High asexual reproduction rates, through fragmentation, may be one explanation for the 2:1 (male to female) sex ratio at the SG reef. Kojis and Quinn (1981b) have also suggested that higher local abundance of one sex (females) may be a result of high degree of asexual reproduction in *P. lutea* and *P. lobata*.

There is some evidence that the oogonia (Fig. 4a) and spermatogonia (Fig. 5a) of *P. porites* originate from interstitial cells of the endodermal layer in the mesenteries, as was suggested by a number of previous studies (Szmant-Froelich *et al.*, 1980; Rinkevich and Loya, 1979b). The

general features of *P. porites* gametogenesis are similar to those of other corals (Szmant-Froelich *et al.*, 1980; Fadlallah and Pearse, 1982a). Both male and female gametes develop within the mesoglea of mesenteries. It has been suggested that small branching species are more likely to produce gametes in the coelenteron (attached to mesenteries by stalks) and brood larvae (Rinkevich and Loya, 1979a). The mode of reproduction of *P. porites* supports the latter part of the hypothesis, while contradicting the former. In general, sexuality (Harrison, 1985) and gonadal development (Marshall and Stephenson, 1933; Kojis and Quinn, 1981b) of the family Poritidae are relatively consistent and predictable, however, the mode of reproduction (broadcasting versus brooding) is less consistent.

Gametogenesis of *P. porites*, at the three reefs, was continuous through most of the year. With the exception of the GS reef, gametogenesis was initiated in August and proceeded until April - May (Fig. 7). Both oogenesis and spermatogenesis were relatively synchronized, in the sense that mature ova and spermatozoa were present throughout the peak reproductive season. However, colonies collected throughout the year, with few exceptions (Fig. 7) contained all stages of oocyte and spermatocyte development. The high abundance of Stage II and III oocytes and spermaries in July and August, at the BRI and SG reefs, is surprising, since none of the colonies collected in June contained reproductive material. This may indicate rapid development of both oocytes and spermaries from Stage I to Stage II and III. In contrast, male colonies

collected at the GS reef in September had only Stage I spermaries; however, there were few Stage II and Stage III oocytes present in female colonies. Since colonies with embryos were not detected until October, the fate of the mature ova and spermatozoa observed in July and August is unknown. The appearance of embryos at the GS reef was more closely synchronized with gonad development than at the BRI and SG reefs (Fig. 7). The presence of mature ova and spermatozoa from November to January suggest that fertilization (i.e. male spawning) may occur repeatedly during this period. Additional data are needed to determine whether there is a lunar periodicity in sperm release. Histological evidence indicates that mature spermatozoa were released from spermaries into the coelenteron prior to spawning. In contrast, it has been shown that in some broadcasting species mature spermatozoa are released in clusters, which rise to the surface where they rupture releasing the spermatozoa (Kojis and Quinn, 1982). This mode of reproduction has not been observed in the Caribbean.

The available data in the literature indicate that few coral species release larvae containing zooxanthellae (Fadlallah, 1983) or larvae that become impregnated with zooxanthellae shortly after release (Szmant-Froelich *et al.*, 1980; Krupp, 1983). Hayes and Goreau (1977a, b) have suggested that larvae of *P. porites*, upon release, feed on particulate matter. This was substantiated by evidence that larvae deprived of zooplankton, mucus and particulate matter died presumably of starvation (Goreau *et al.*, 1981). Therefore, it is of interest

to note that mature ova in *P. porites* contain zooxanthellae before fertilization occurs (Fig. 4c, d). This condition has been observed previously in the Pacific *Porites* species only (Kojis and Quinn, 1981b). The presence of zooxanthellae in mature ova of other Caribbean species has not been reported (Szmant-Froelich, 1984; Wyers, 1984). As with other cnidarians, scleractinian corals lack accessory or nutritive cells that accompany oocyte development in other organisms (Campbell, 1974). Thus, it has been suggested that developing oocytes in some hydrozoan species are nourished at the expense of ectodermal or endodermal epithelial cells (Campbell, 1974). Rinkevich and Loya (1979a) suggested that in *Stylophora pistillata*, successful oocytes may absorb nutrients not only from surrounding endodermal cells, but also through phagocytosis on other oocytes. The extensive histological examination of the *P. porites* cross sections revealed only a few instances where more than one oocyte was present in a single ovary. Thus, resorption of other oocytes is most likely not an important source of nourishment for the developing oocytes in *P. porites*. With subsequent maturation of the oocytes, the endodermal layer surrounding the female gonads becomes progressively thinner, indicating that resorption of endodermal epithelial cells may be an important source of nutrients for the developing oocytes. However, the presence of zooxanthellae in the late developmental stages of oocyte maturation indicates that the symbionts may have an active nutritive role (i.e. transfer of photosynthate) during the

final maturation of the oocytes or early larval development. In this connection, Richmond (1981) demonstrated that translocation of photosynthate from zooxanthellae to larva occurs in *Pocillopora damicornis*.

Recent studies have clearly demonstrated that adverse environmental conditions (i.e. high sedimentation and/or turbidity) have a detrimental effect on coral growth (Aller and Dodge, 1974; Dodge *et al.*, 1974; Dodge and Vaisnys, 1977; Hudson, 1981; Rogers, 1983; Tomascik and Sander, 1985a), coral community structure (Loya, 1976c; Tomascik and Sander, 1985b) and coral survival (Marshall and Orr, 1931; Maragos, 1972). It is suggested that reduction in reproductive activity at the two southern reefs may be attributed to turbidity associated with eutrophication processes. Turbidity may affect the reproductive biology of *P. porites* through reduced light levels, and hence a reduction of zooxanthellae photosynthesis, and/or high SPM concentrations, which will require additional energy expenditure for cleaning at the expense of growth or reproduction. The extensive histological examination of *P. porites* failed to demonstrate any observable cellular degeneration or atrophy in the tissue samples.

The results of this study demonstrate that not only were there differences in gonad abundance, but that the potential larval output (expressed as the average number of larvae per 0.25 cm^2 of coral tissue) of *P. porites* was statistically higher at the GS reef than at the BRI and SG reefs. To determine whether these differences were a result of lower

reproductive activity of female colonies (i.e. number of oocytes per 0.25 cm^2 of coral tissue) at the SG and BRI reefs than at the GS reef, one-way ANOVA was performed on the data set containing gravid female colonies only. The results showed that the average oocyte abundance in female colonies, during the reproductive season, was not statistically discernible ($P < 0.107$) among the three reefs. This suggests that eutrophication may affect either the final developmental stages of oocyte maturation or early embryogenesis. These results also provide indirect evidence that the zooxanthellae associated with the mature ova may play a significant role in determining the success of reproduction in *P. porites*. Reduced light levels at the two southern reefs may significantly reduce the potosynthetic activity of the zooxanthellae, thus reducing potential source of nourishment derived from photosynthates. It is suggested that the observed differences in the seasonal pattern of larval abundance (Fig. 7), between the southern (SG and BRI) and northern (GS) *P. porites* populations, were related to adverse environmental conditions, local genetic variability or combined function of both. Alternatively, adverse environmental conditions may directly affect success of fertilization through direct toxicity or reduced viability of mature ova and/or spermatozoa. Kojis and Quinn (1984) have suggested that high sedimentation and turbidity may act synergistically to decrease the fecundity of *Acropora palifera* on a fringing reef in Papua by lowering light levels and increasing expenditure of energy for cleaning activities.

Clearly, more research is needed to determine the role of zooxanthellae in the oogenesis of *P. porites*.

Seasonal fluctuations in both water temperature and salinity (Fig. 2, 3) are relatively constant and predictable features of the inshore water masses off Barbados (see also Sander, 1971, 1981; Vezina, 1975). It is widely recognized that environmental changes exert proximate exogenous control on reproduction of marine organisms (Giese and Pearse, 1974). Changes in sea water temperatures have been shown to provide important clues or "zeitgebers" which may synchronize reproductive activities of many marine invertebrates with subsequent favourable environmental conditions (Kinne, 1963, 1964, 1970). Furthermore, Orton (1920) suggested that initiation of reproduction is triggered by a critical breeding temperature characteristic of each species and/or populations. A number of studies on the reproductive periodicities of tropical echinoids have demonstrated the general applicability of Orton's Rule to tropical marine environments characterized by slight temperature fluctuations (Lewis, 1966; Pearse, 1968, 1969, 1970). Whether reproduction of *P. porites* in Barbados is triggered by a certain water temperature (i.e. critical breeding temperature) needs further study through experimental manipulation. However, Harrison *et al.* (1984) have suggested that lower water temperatures at Orpheus Island on the Great Barrier Reef probably accounted for slower maturation and later spawning of corals, than at sites with higher water temperatures. Water temperature and salinity fluctuations in

Barbados may provide *P. porites* with important clues about subsequent environmental conditions and may serve to synchronize their reproduction; however, statistically discernible differences between the SG and BRI reefs in both water temperature and salinity suggest that the longer reproductive season at these reefs, than at the GS reef, is a response to eutrophication. The extended reproductive season of *P. porites* at the two southern reefs may be a direct response to altered physiological state induced by the eutrophication of the inshore water masses. Depressing gamete production may divert energy to other basic metabolic functions, necessary for coral's survival, which under stress may require additional energy expenditure. Thus, depressing gamete production and extending the breeding season under unfavourable environmental conditions may be considered either as a response to minimize the probability of exctinction, or to maximize the probability of reproductive success (i.e. successful release of larvae).

The reproductive activity of *P. porites*, on all reefs, was highest during November through January. Note that August to November is considered as a rainy season, in Barbados, characterized by high rainfall and cloud cover. The release of larvae at the end of the rainy season (late November) may, therefore, be of significance, since it allows for development of settled larvae under favourable environmental conditions, characterized by low turbidity and high irradiance. Whether food availability plays a significant role in the timing of

reproduction and release of larvae in *P. porites* is still undetermined, even though this study established no apparent correlation between chlorophyll *a* concentrations (i.e. phytoplankton biomass) and timing of larval maturation.

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CHAPTER III

Effects of eutrophication on reef-building corals. Part III. Structure of the scleractinian coral communities on the fringing reefs of Barbados, W.I. *

© Tomas Tomascik & Finn Sander

McGill University
Institute of Oceanography
3620 University St.
Montreal, PQ. .
H3A 2B2

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Abstract

Seven fringing reef complexes were chosen along the leeward coast (West) of Barbados, to study the effects of eutrophication processes upon the scleractinian coral assemblages. The structure of scleractinian coral communities was studied along an eutrophication gradient with a quantitative sampling method (line transect) in terms of species composition, zonation and diversity patterns. On the basis of these data the fringing reefs were divided into 3 ecological zones: back reef, reef flat, and spur and groove.

Statistically discernible and biologically significant differences in scleractinian community structure, benthic algal cover and *Diadema antillarum* Philippi densities were recorded among the seven fringing reefs. High correlations between environmental variables and biotic patterns indicate that the effects of eutrophication processes (nutrient enrichment, sedimentation, turbidity, toxicity and bacterial activity) were directly and/or indirectly affecting the community structure of scleractinian coral assemblages. In general, species diversity was most sensitive in delineating among-reef, and among-zone, differences which were attributed to intensification of eutrophication processes. *Porites astreoides* Lamarck, *P. porites* (Pallas), *Siderastrea radians* (Pallas), and *Agaricia agaricites* (Linnaeus) were the most abundant coral species in the polluted southern reefs. Coral species, previously

characterized as well adapted to high turbidity and sedimentation (i.e. *Montastrea cavernosa* Linnaeus), were either absent or present in low numbers. This study suggests that eutrophication processes appear to adversely affect coral species that were previously reported to be well adapted to high turbidity and sedimentation rates related to natural processes, or anthropogenic activities in relatively unpolluted environments that imitate natural perturbations. It is suggested that sediment rejection abilities combined with feeding and reproductive strategies are the primary biological proceses of scleractinian corals through which eutrophication processes directly and/or indirectly affect the structure of coral communities.

Introduction

Acceleration and intensification of eutrophication processes through anthropogenic activities cause major shifts in the physicochemical and biological environment of coral reef ecosystems. Eutrophication, considered here as a stress, is a combined function of nutrient enrichment, increased sedimentation and the introduction of toxins related directly and/or indirectly to human activities. The definition of 'stress' has generated much discussion (Odum *et al.*, 1979; Ivanovici and Wiebe, 1981; Franz, 1981; Pickering, 1981; Stebbing, 1981). Rosen (1982), considering scleractinian corals, stated that stress is difficult to define in absolute terms and suggested that stress may be taken to mean conditions that restrict growth and reproduction. For the purpose of this study Rosen's broader view of stress as a gradient between ideal conditions and the ultimate limits of survival will be adopted (see also Brown and Howard, 1985). Inherent in all definitions of stress is the basic concept that stress acting on a system will place that system at a disadvantage by exerting an energy cost, and interfering with the normal function of the system.

The distribution of scleractinian corals is determined by the net effect of many interrelated environmental factors that may be additive and/or synergistic in their action. Cummulative effects of long term exposure to adverse

environmental conditions can be studied in scleractinian coral communities because of their sedentary nature. Moreover, the immobility of scleractinian corals and other sessile organisms may make them more susceptible to environmental stress, in that they are unable to avoid local environmental perturbations. While a number of studies have demonstrated that coral communities are susceptible to environmental perturbations resulting from anthropogenic activities (Fishelson, 1973; Jokiel and Coles, 1974; Loya, 1975, 1976a,b; Dodge and Vaisnys, 1977; Bak, 1978; Walker and Ormond, 1982), others have failed to demonstrate serious damage (Sheppard, 1980; Dollar and Grigg, 1981; Brown and Holey, 1982). However, as was pointed out by Pastorok and Bilyard (1985), most pollution-related studies on coral reef ecosystems, specifically effects of sewage pollution, are short-term and limited in scope. Given these inadequate and conflicting reports, the concept that coral reefs are fragile ecosystems, and therefore, sensitive to environmental perturbations (Johannes, 1975; Loya, 1976b; Rogers *et al.*, 1983; Pastorok and Bilyard, 1985), needs reevaluation (Dollar and Grigg, 1981).

The initial response of corals to pollution is at the level of the individual, either through behavioural (Lasker, 1980; Dallmeyer *et al.*, 1982; Rogers, 1983) or physiological responses (Dallmeyer *et al.*, 1982; Krupp, 1984; Glynn *et al.*, 1985). Beyond this, changes in the community may occur through replacement of certain species or higher taxa. A useful first approach towards assessing the sensitivity of corals to an

environmental perturbation, such as eutrophication, can therefore be achieved by studying the distribution of coral populations lying along a spatial eutrophication gradient. The degree of eutrophication varies spatially along the fringing reefs of Barbados as a consequence of a number of interacting factors related to the hydrographic characteristics of the west coast (Murray *et al.*, 1977), and most likely to the nature and quantity of domestic and industrial effluents entering the coastal waters (Tomascik and Sander, 1985; Lewis, 1985).

The purpose of the present paper is (1) to provide a quantitative comparison of coral community structure on the fringing coral reefs along the west coast of Barbados (for earlier descriptions of coral communities see Lewis (1960); Macintyre (1968); Ott (1975a,b); Ott and Auclair (1977); Stearn *et al.* (1977); Scoffin *et al.* (1980); and Mah (1984)), (2) to quantitatively determine whether there is distinct within-reef zonation in coral distribution, (3) to determine whether differences exist in coral community structure along the eutrophication gradient (see Tomascik and Sander, 1985), and (4) to relate the characteristics of the coral communities to the environmental conditions along the gradient.

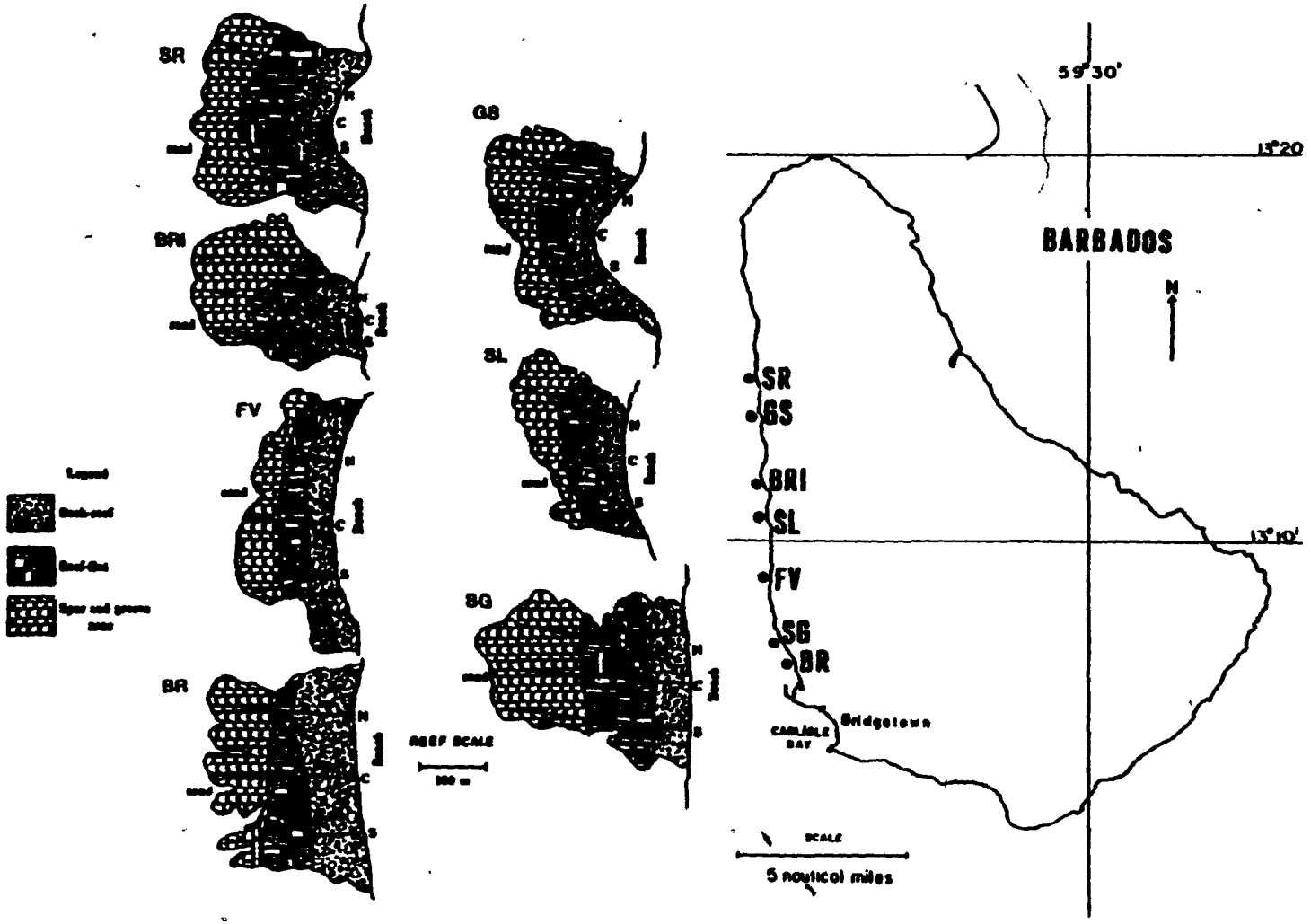
Materials and Methods

Sampling

Sampling methods in quantitative studies of scleractinian coral communities are divided into two main categories; the quadrat method (Goldberg, 1973; Maragos, 1974; Ott and Auclair, 1977), and the plotless method (Loya and Slobodkin, 1971; Loya, 1972, 1975, 1976a,b, 1978; Done, 1977). The literature indicates that there is a general lack of standardization in the sampling methodology, even though this problem has been addressed in a number of publications (Stoddart, 1972; Maragos, 1974; Loya, 1978). However, recent comparative studies on the relative efficiencies of the quadrat and plotless methods suggest that the results obtained by both methods are similar (Bouchon, 1981; Dodge *et al.*, 1982). The choice of method employed in any study is dictated primarily by local factors and objectives of the study. In the present study we have adopted the line transect method of Loya and Slobodkin (1971) and Loya (1978) inasmuch as this method was shown to be efficient in previous pollution related studies (Loya, 1975, 1976a).

Each study reef was divided by three reference transects (running perpendicular to the depth contour) into south, central and north sampling units (Fig. 1). The location of the reference transects was based on general reef morphology

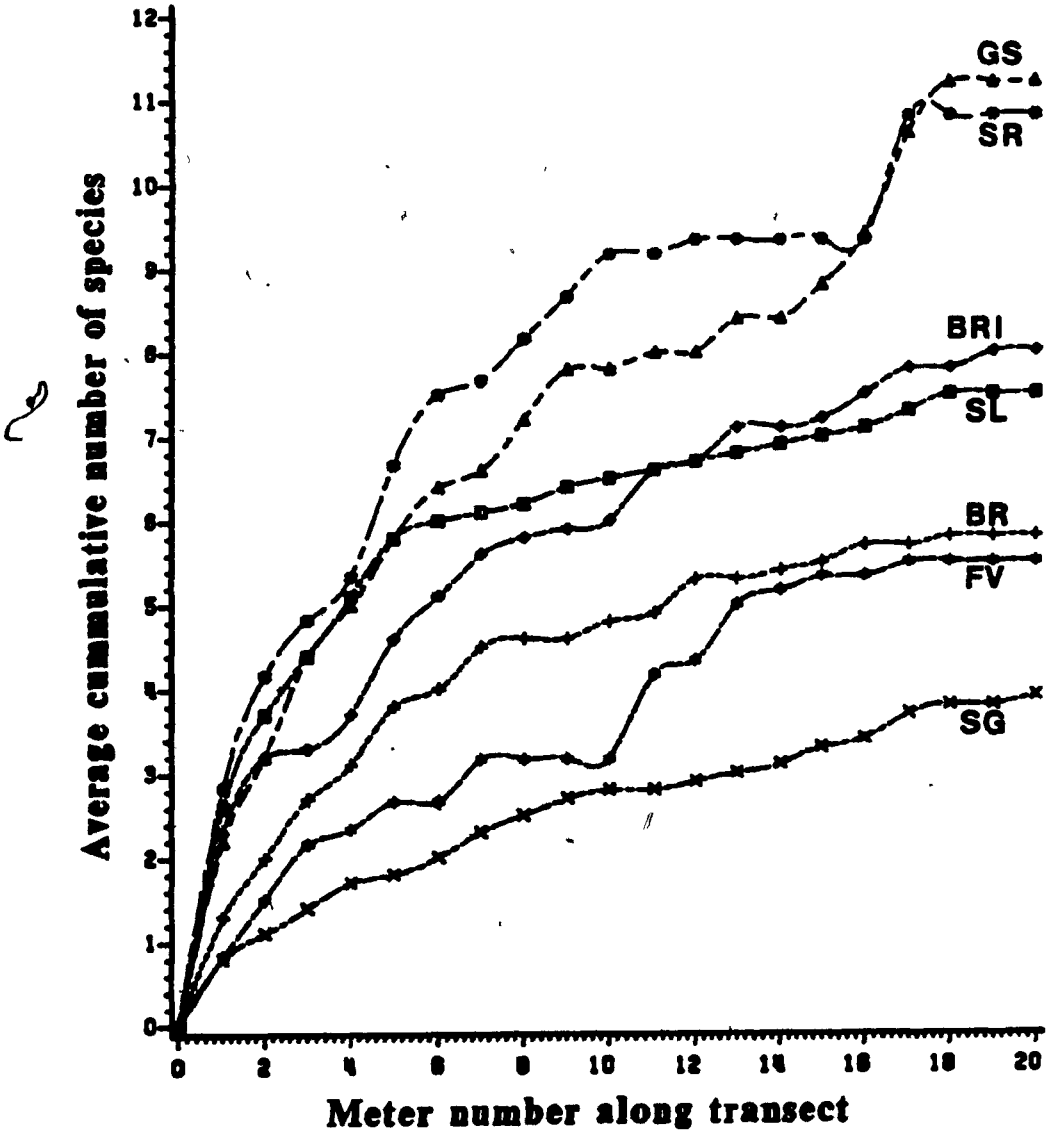
Figure 1. Map of Barbados, West Indies, indicating locations of study reefs and their main morphological and ecological features. Each fringing reef was divided into 3 sampling units: (N) north reference transect, (C) central reference transect, (S) south reference transec. Reef abbreviations: BR - Brighton; SG - Spring Gardens; FV - Fitts Village; SL - Sandy Lane; BRI - Bellairs Research Institute; GS - Greensleeves; SR - Sandridge. Reef zones as indicated in the legend.


SR
BRI
FV
BR
GS
SL
SG
Legend
REEF SCALE
59°30'
13°20
BARBADOS
N
SR
GS
BRI
SL
13°10'
FV
SG
BR
CARLISLE BAY
Bridgetown
SCALE
5 nautical miles

determined from aerial photographs. Sampling was conducted along each of the reference transects, from beach edge to the seaward edge of the reef, by running 20m line transects (perpendicular to the reference transect) with fixed intervals of 5 or 10m, depending on the size of the reef. The line transect consisted of a fine chain (1.5cm links) marked at 1m intervals. The sample size (i.e. the length of the line transect) for each reef was determined in a preliminary sampling study by randomly placing 10 line transects parallel to shore over the reef. From the data obtained, species-number versus transect-length curves were constructed (Loya, 1972; Dodge *et al.*, 1982) indicating that a 20m transect line was an appropriate sampling unit (Fig. 2).

During the study, any coral species intersected by the chain was recorded and the intersected length in plan view was measured to the nearest cm. A coral colony was defined as any colony growing independently of its neighbour (Loya, 1972, 1978). In cases where a single colony was divided into separate units by recent partial mortality of the colony (Hughes and Jackson, 1980) the separate units were considered as the same individual, and only the live tissue was measured and pooled for further analyses (Loya, 1978; Dodge *et al.*, 1982). In the few cases where two or more colonies were growing one above the other, only the intersected length of the largest colony was used for live coverage calculations, while the species and lengths of the underlying colonies were recorded for coral species diversity (Loya, 1978).

Figure 2. Average cumulative number of scleractinian species as a function of meter number along a line transect. Reef abbreviations as in Fig. 1.


Average cumulative number of species
Meter number along transect
GS
SR
BRI
SL
BR
FV
SG
0
1
2
3
4
5
6
7
8
9
10
11
12
0
2
4
6
8
10
12
14
16
18
20

Three hydrozoans, *Millepora alcicornis* Linnaeus, *M. squarrosa* Lamarck, *M. complanata* Lamarck, and a colonial zoanthid *Palythoa mamillosa* (Ellis and Solander) were included in the study, since they were considered to be an important component of the fringing reef community (Lewis, 1960; Stearn and Riding, 1973; Stearn *et al.*, 1977). The line transect technique was also used for the assessment of benthic algal cover. Benthic algae were divided into two main groups: 1) coralline encrusting algae, and 2) fleshy algae consisting of both frondose macroalgae and filamentous algae. Algal cover was recorded along each transect as percentage coverage per meter. Algae were not identified to lower taxa; however, all dominant forms were noted for qualitative comparisons.

In addition to the above substrate components, quantitative data were obtained on the population densities of the sea urchin *Diadema antillarum* Philippi along each line transect by a modified transect method (Hawkins, 1979). A one meter plastic rod, marked at midpoint, was held perpendicular to the line transect a few cms above the substrate. The rod was moved along the line and all urchins found beneath the rod were recorded. The population density was expressed as the number of individuals per m^2 of reef surface. A total of 513 line transects were measured during the study.

Environmental assessment

The environmental variables measured during the study were sea temperature (°C), salinity ($S^{o}/_{oo}$), dissolved oxygen (mg/l), biological oxygen demand (BOD mg/l), percentage of surface illumination (PEN %), percentage of organic matter in sediments (ORG %), suspended particulate matter (SPM mg/l), downward flux of SPM (DF-SPM $mg/cm^2/d$), chlorophyll a (Chl a mg/m^3), inorganic phosphate (PO_4-P μg-at/l), nitrate-nitrite nitrogen (NO_3+NO_2-N μg-at/l), nitrite (NO_2-N μg-at/l), and ammonia (NH_3-N μg-at/l). Discussion of the environmental data and full details of sampling procedure, laboratory analyses and statistical treatment are given elsewhere (Tomascik and Sander, 1985).

Data Processing and Analyses

Data processing

To describe and compare the scleractinian coral community structure among the seven fringing reefs a number of information indices were obtained from each transect line. The three basic descriptors of community structure on which all further analyses are based were: 1) species number per transect, 2) number of coral colonies per transect and 3) live coral coverage per transect. From the raw data four simple information indices were calculated directly:

1) Percent coral cover (PCC%), where

$$PCC\ \% = \frac{\textit{Total length of coral tissue / Transect}}{\textit{Transect length}} \textit{ X 100}$$

2) Relative coral coverage (RCC %), where

$$RCC\ \% = \frac{\textit{Total length of species A / Transect}}{\textit{Total length of all species / Transect}} \textit{ X 100}$$

RCC % represents the relative dominance of individual species with respect to total coral coverage;

3) Relative abundance of coral species (RAS %), where

$$RAS\ \% = \frac{\textit{Total number of colonies of species A / Transect}}{\textit{Total number of coral colonies / Transect}} \textit{ X 100}$$

RAS % represents the dominance of individuals of a particular species with respect to total number of individuals present; 4) Transect size index (TSI), where

$$TSI = \frac{\textit{Percentage coral cover / Transect}}{\textit{Total number of colonies / Transect}}$$

For the purpose of comparative analysis and to avoid possible loss of information (Loya, 1972), the coral community structure was characterized by three types of diversity measures: 1) number of species and individuals; 2) information-theory based diversity indices; and 3) Simpson's index of concentration. The simplest measure of species diversity is the species number S (Poole, 1974). In this study, S is expressed as the average number of species per transect (SP). Margalef (1958) proposed an alternative measure of diversity to incorporate both S and N, the total number of individuals in all the species where:

$$d = (S-1)\log_{10} N \qquad \textit{Equ. 1}$$

However, both S and d indices ignore the distribution of individuals among the species.

The diversity indices obtained from the information theory are a function of both the number of species present and the evenness with which the individuals are distributed among the species (Hurlbert, 1971). The Shannon function (Shannon and Weaver, 1949)

$$H' = -\sum_{j} pi \log pi \qquad Equ.\ 2$$

is the most frequently used diversity index in coral reef studies (Loya, 1972, 1975, 1976a,b; Porter, 1972a,b; Dana, 1979; Bouchon, 1981; Bull, 1982; Dodge *et al.*, 1982; Cortes and Risk, 1985). Shannon-Wiener's index was calculated using both coral abundance data (H'n) and coral coverage data (H'c). For H'n, $pi=ni/N$ is the proportion of the total number of colonies (N) belonging to the *ith* species (*ni*) and for H'c, $pi=ci/C$, where C is the total coral coverage and *ci* is the coverage of the *ith* species (Loya, 1972; Dodge *et al.*, 1982).

An alternative measure of diversity is Brillouin's (1962) function defined as:

$$H = (1/N) \log (N!/n_1!,n_2!...n_s!) \qquad Equ.\ 3$$

where *N* is the total number of individuals in the sample and $n_1,n_2,...ns$ are the numbers of individuals of the constituent species (Pielou, 1977). Brillouin's *H* was computed from coral abundance data only. It is important to note that Brillouin's index (Equ. 3) and not Shannon's index (Equ. 2) gives the actual diversity of a fully censused collection of organisms (Pielou, 1966a,b, 1977). In this study, each transect line can be considered as a fully-censused collection, and, therefore, *H* of Equ. 3 gives the exact diversity of the sample. Brillouin's index was therefore considered to be the most appropriate measure of diversity for the present study.

To assess the homogeneity of the scleractinian coral community Pielou's (1966b) evenness index was computed in conjunction with *H'n* as

$$J'n = H'n \text{ (observed)} / Hmax \qquad Equ.\ 4$$

and *H'c* as

$$J'c = H'c \text{ (observed)} / Hmax \qquad Equ.\ 5$$

In both eqn's 4 and 5 $Hmax = \log S$, where *S* is the total number of species encountered in the sample. The evenness indices thus express the observed diversity as a proportion of the maximum possible diversity. However, since *S* is typically an underestimate of the number of species in the population the sample evenness, *J'n* and *J'c*, are overestimates of the population evenness.

An unbiased estimate of dominance in a fully censused community is Simpson's (1949) measure of 'concentration', λ (Pielou, 1977) which was calculated from coral abundance data *(λ'n)* as:

$$\lambda'n = \frac{\Sigma ni(ni-1)}{N(N-1)} \qquad Equ.\ 6$$

where *ni* is the number of individuals of the *ith* species and *N* is the total number of individuals of all species in the sample. λ was also computed from coral coverage data *(λ'c)* as

$$\lambda'c = \frac{\Sigma\ ci\ (ci-1)}{C\ (C-1)} \qquad Equ.\ 7$$

where *ci* is the coverage of the *ith* species and *C* is the total coral coverage. The coral community will exhibit high dominance if two individuals, drawn at random and without

replacement from an S-species community containing N individuals, belong to the same species (Pielou, 1977).

Data analyses

All transects along each of the reference transects, within each reef, were subjected to Ward's agglomerative, hierarchical classification analysis using the SAS Cluster procedure (Ray, 1982a). The characters used in the classification analysis were log(x+0.05) transformed average species abundance and coverage values of all species present (Loya, 1972). The classification analysis was used to group all transects into relatively homogeneous groups that can be interpreted as specific reef zones as previously described by Lewis (1960) and Stearn *et al.* (1977). Since the basis for the classification analysis is to group transects which show high similarity with each other, it was possible that transects surveyed in different reef zones would cluster together. In all such cases the transects were placed into specific zones (groups) based on distance from shore criteria. To help identify specific reef groupings the classification analysis was also performed on the Reef x Species matrix using the transformed average abundance values.

Prior to the statistical analysis all raw data were tested for violation of the basic assumptions of normality and homogeneity of variance implied in all linear model statistics. To test the assumption of normality the Shapiro-Wilk, W, statistic and normal probability plot were computed for all ecological data sets using the Univariate procedure in the SAS system (Ray, 1982b); the Fmax test (Zar, 1984) was used to test

the homogeneity of variance assumption. Accordingly, appropriate transformations were applied to all data sets, as suggested by Box *et al.* (1978). The success of each transformation was tested, and the final transformations used in all data analyses are presented in Table 1.

A single factor one-way analysis of variance (ANOVA) was carried out on all ecological data sets to test two null hypotheses: 1) H_0 : there are no differences in the coral community structure among the seven fringing reefs within similar reef zones, and 2) H_0 : there are no differences in coral community structure among reef zones within each reef. Where ANOVA indicated significant differences, a multiple comparison of means (at P=0.05 level), for each of the ecological indices was carried out using the Tukey's studentized range (HSD) test procedure (Ray, 1982a). The Tukey's test is preferable to the more frequently used Student-Newman-Keuls (SNK) multiple range test (Dodge *et al.*, 1982; Russ, 1984a,b), since it controls the maximum experimentwise error rate under any complete or partial null hypothesis (Ray, 1982a). It should be stressed that the higher 'power' of the SNK test (it tends to conclude more significant differences than does the Tukey's test) is because of its higher Type I error rate, i.e. a false rejection of the null hypothesis (Zar, 1984).

To assess the relationship between the coral community structure and the environmental conditions, each fringing reef, rather than each reef zone, was considered as a sample.

Table 1. Variance stabilizing transformations for number of species and colonies, percent coral coverage (PCC %), *Simpson's index of concentration:* λ'n and λ'c, *Pielou's evenness index:* J'n and J'c and densities of *Diadema antillarum*. Note: variance stabilizing transformations were not necessary for *Shannon-Wiener's indices, Brillouin's index and Margalef's index*. SQRT = square root.

Ecological variables	Transformation
Number of species	SQRT(X+1)
Number of colonies	SQRT(SQRT(X+1))
Percent coral coverage (PCC %)	log(X+1)
Simpson's indices (λ'n and λ'c)	SQRT(SQRT(X+3/8)
Pielou's indices (J'n and J'c)	ARCSIN(SQRT(X))
Diadema antillarum density	SQRT(X+1)

Relating the environmental data to specific reef zones would have been inappropriate, since the environmental variables were sampled randomly over the reef throughout the study (Tomascik and Sander, 1985).

Spearman's rank correlation analysis was used to determine whether there were significant relationships between the various environmental variables and community descriptors. To simplify the interpretation of relationships between the environmental variables and the community descriptors, principal component analysis (PCA) procedure (Ray, 1982a) was used to transform the original sets of variables into smaller set of linear combinations that account for most of the variance of the original data sets. The principal components (PC), for both community descriptors and environmental variables, were computed from correlation matrices to remove differences due to both the mean and dispersion of the variables. Thus, the transformation makes the variables directly comparable (Dilon and Goldstein, 1984). The aim of the PCA was to delineate independent associations among the sets of environmental and community variables. To draw some inference about the general relationship between the environmental conditions and coral community structure, simple linear regression analysis was used to test the relationship between the PC scores of the environmental and community data sets. All statistical analyses were done at McGill University using the SAS statistical package (Ray, 1982a, b).

Results

General species distribution

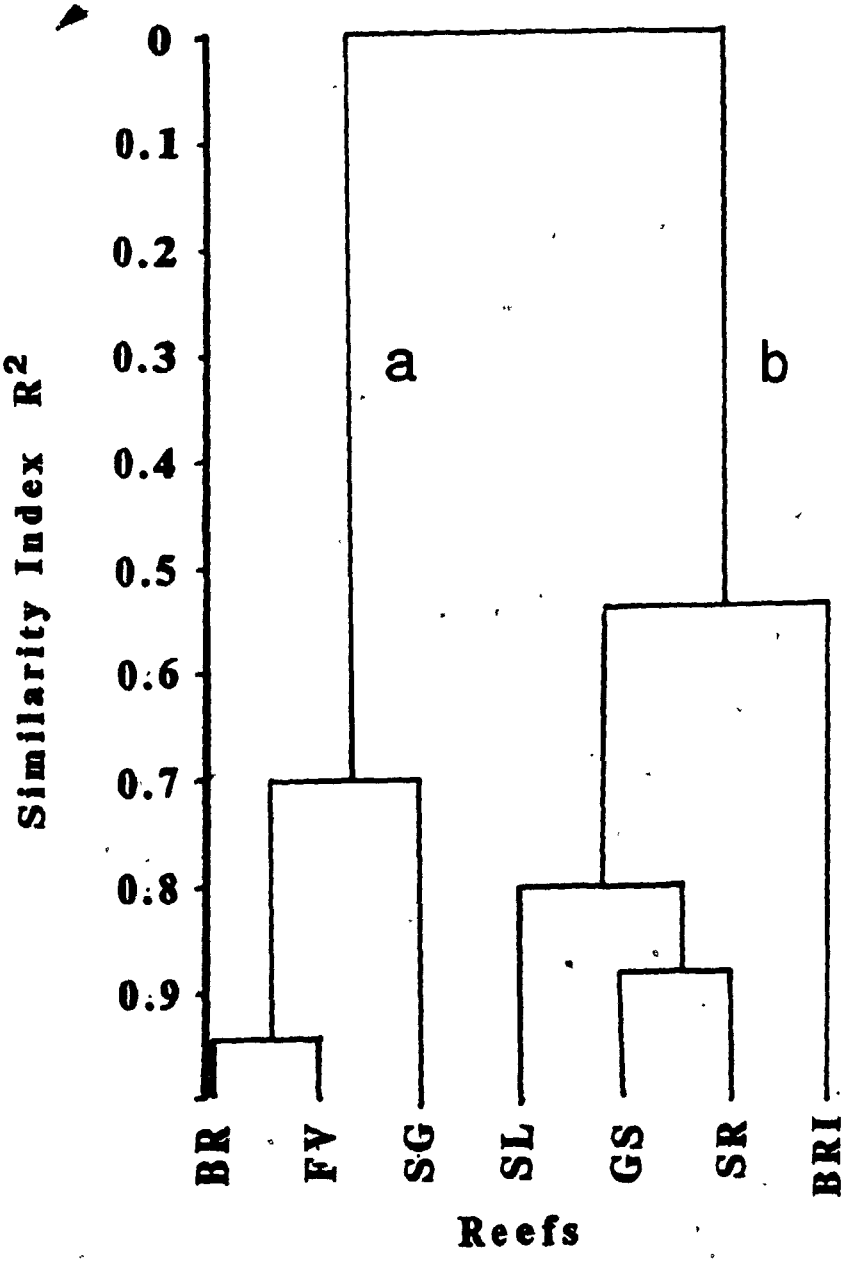
Table 2 illustrates the overall distribution and relative coverage of scleractinian corals among the seven fringing reefs along the west coast of Barbados. A total of 24 scleractinian species belonging to 16 genera were recorded on the reefs, as well as three species of the hermatypic hydrocoral *Millepora* and a single species of the colonial zoanthid *Palythoa*. Only eight species were found common to all the fringing reefs, these belonging to the genera *Porites*, *Siderastrea*, *Agaricia*, *Montastrea*, *Diploria* and *Millepora*. Three species of the genus *Mycetophyllia* and *Stephanocoenia michelinii* Milne Edwards and Haime, were found only on the northern reef GS. Of the eight common coral species the most abundant were *Porites astreoides*, *P. porites*, *Agaricia agaricites*, *Millepora squarrosa*, *M. complanata*, and *Montastrea annularis* (Ellis and Solander) which was more abundant at the four northern reefs SL, BRI, GS, and SR (Fig. 1), than on the three southern reefs BR, SG and FV. Table 2 indicates that there was a general increase in the absolute number of species recorded from the southern reef BR (9 species) to the most northern reef SR (22 species).

Fig. 3 is a dendrogram generated from the Ward's classification analysis using the Reef x Species data matrix based on the average abundance values of species on each reef. The first split in this dendrogram places the three southern

Table 2. Distribution and the average relative coverage (RCC % per transect) of scleractinian corals, *Millepora spp.*, and *Palythoa mamillosa* among the seven fringing reef complexes along the west coast of Barbados, West Indies. Reef abbreviations as in Fig. 1

	Reef						
Species	**BR**	**SG**	**FV**	**SL**	**BRI**	**GS**	**SR**
No. of transects	n=57	n=69	n=68	n=66	n=58	n=83	n=57
Porites porites	18.1	33.4	10.3	2.4	3.9	8.8	7.2
Porites astreoides	24.5	33.2	34.1	36.0	21.3	28.2	26.7
Siderastrea radians	21.3	4.3	16.4	5.5	1.1	1.9	8.5
Agaricia agaricites	11.0	12.5	2.5	7.5	15.8	3.3	5.0
Millepora squarrosa	3.7	2.3	3.9	4.2	7.6	3.8	8.3
Millepora complanata	0.9	5.0	10.9	11.3	1.9	17.5	1.6
Montastrea annularis	13.4	5.0	1.5	5.0	8.1	9.3	6.6
Diploria clivosa	1.3	0.7	5.5	9.5	4.3	4.4	6.6
Siderastrea siderea	5.9		5.8	7.7	11.4	6.5	11.0
Diploria strigosa		2.3	3.5	2.8	11.6	2.4	3.1
Favia fragum		1.1	2.1	0.4	0.5	2.3	1.4
Diploria labyrinthiformis		0.2		0.9	0.1	1.0	1.7
Madracis decactis			0.2	0.3	0.2	1.0	0.2
Montastrea cavernosa			3.2	1.3	1.2	1.7	6.8
Leptoseris cucullata				1.6	0.4	0.2	0.1
Millepora alcicornis				0.1	1.6	0.5	0.1
Madracis mirabilis				1.1	6.5	1.0	1.1
Meandrina meandrites				0.5	0.1	0.7	1.7
Dichocoenia stokesi				0.1	0.3	0.6	0.5
Palythoa mamillosa				1.8	2.2	1.2	1.8
Colpophyllia natans				0.1		0.4	0.5
Acropora palmata						1.4	0.2
Stephanocoenia michellini						0.4	
Mycetophyllia aliciae						0.04	
Mycetophyllia danaana						0.04	
Mycetophyllia ferox						0.04	
Isophyllia sinuosa						0.04	
Dendrogyra cylindrus						1.3	
Total no. of species	9	11	13	21	20	28	22

Figure 3. Dendrogram showing classification of 7 fringing reefs along the west coast of Barbados based on average species abundances of scleractinian corals. Abundances were log(X+0.05) transformed before comparing reefs using the Ward's agglomerative hierarchical clustering algorithm (Ray, 1982a). Two main groups (*a* and *b*) are distinguished at an arbitrary similarity level of R^2=0.5 (where R^2 is the sum of squares between all clusters divided by the corrected total sum of squares). Reef abbreviations as in Fig. 1.


Similarity Index R^2
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
a
b
BR
FV
SG
SL
GS
SR
BRI
Reefs

reefs (BR, SG, and FV) in a group distinct from the second group containing the four northern reefs (SL, BRI, GS and SR), suggesting that the coral community structure can be related to the eutrophication gradient present along the west coast of the island (Tomascik and Sander, 1985).

Three different reef zones were found on all the fringing reefs in this study, generally supporting the zonation pattern previously described by Lewis (1960) and Stearn *et al.*, (1977). Since the three zones are subdivisions of the coral community they can be defined on the basis of a number of ecological characteristics presented in Table 3 and 4. The dendrograms presented in Fig. 4 illustrate the subdivision of the line transects (samples) along each of the reference transects into three reef zones at the northern reef SR. The reef zones thus defined were back reef, reef flat, and spur and groove. Average relative coral coverage values by each species for each of the reef zones defined are presented in Table 5,6 and 7, the characteristics of the three zones will now be examined further.

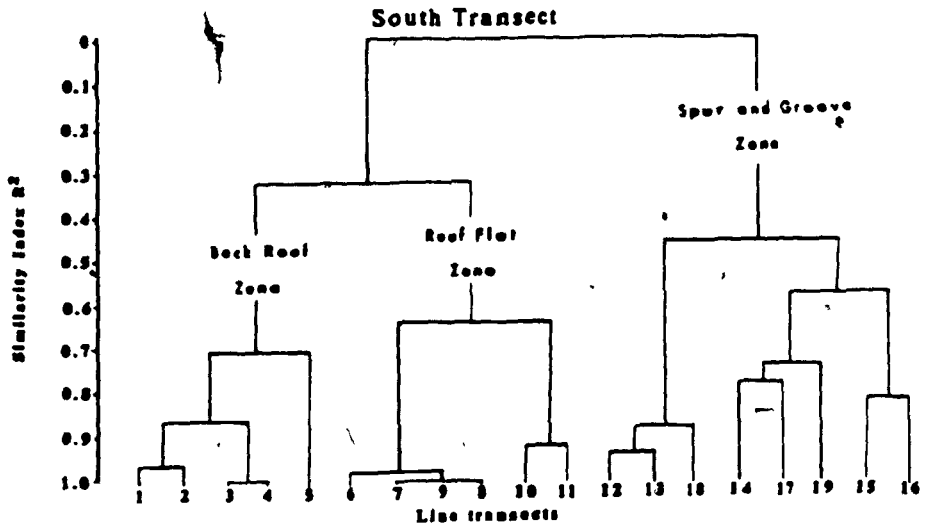
Table 3. Average depth (m), number of coral species and of colonies, percentage live coverage (PCC %), transect size index (TSI), densities of the sea urchin *Diadema antillarum*, % coverage of substrate by calcareous algae (% CAL) and fleshy algae (% FIL) calculated for each reef zone at seven fringing reef complexes along the west coast of Barbados. First number: average values; second number (in parentheses): standard deviation; third number: total number of transects used in the analysis. Zones: A = back reef, B = reef flat, C = spur and groove zone.

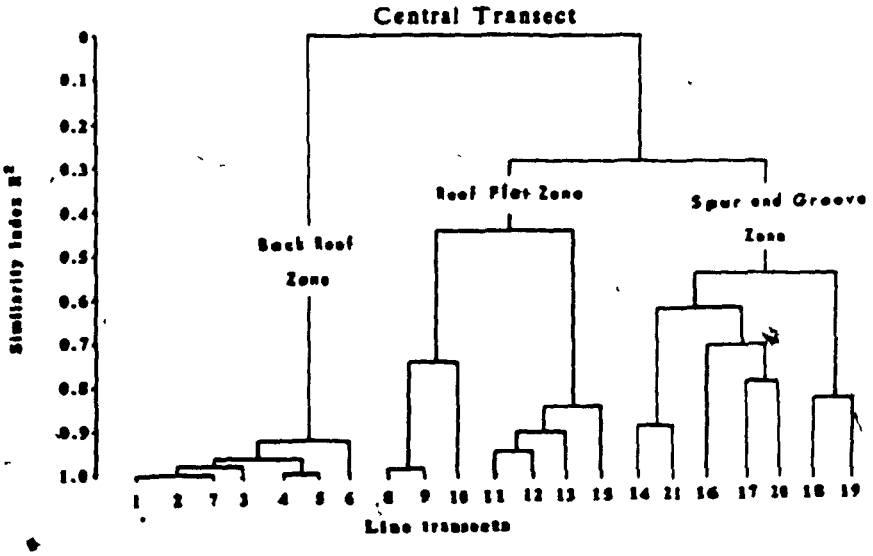
		Station attributes							
REEF	ZONE	Depth (m)	No. of Species	NO. of Colonies	PCC %	TSI Index	NO. of Urchins	% CAL	% FIL
	A	1.03	1.38	3.83	0.92	0.25	0.16	1.0	89.8
		(0.35)	(1.07)	(0.68)	(0.80)	(0.11)	(0.28)	(3.6)	(17.2)
		23	23	23	23	18	23	23	23
BR	B	2.69	3.88	13.00	8.21	0.46	4.88	21.9	31.1
		(0.77)	(1.27)	(10.6)	(4.91)	(0.23)	(3.71)	(23.1)	(28.9)
		20	20	20	20	19	20	20	20
	C	3.82	3.91	17.13	4.36	0.26	4.94	22.8	61.0
		(0.39)	(1.53)	(12.4)	(3.36)	(0.12)	(2.88)	(27.4)	(27.3)
		23	23	23	23	22	23	23	23
	A	1.39	0.44	0.69	0.13	0.24	0.04	0	61.4
		(0.44)	(0.73)	(1.20)	(0.23)	(0.26)	(0.07)		(37.2)
		16	16	16	16	5	16	16	16
BG	B	2.24	2.61	9.03	2.23	0.26	1.89	30.8	41.6
		(0.77)	(1.58)	(9.43)	(2.66)	(0.12)	(2.12)	(36.4)	(39.1)
		31	31	31	31	30	31	31	31
	C	4.20	3.81	29.37	6.18	0.28	10.00	40.8	4.7
		(1.44)	(1.40)	(25.25)	(4.87)	(0.17)	(7.04)	(35.7)	(13.0)
		35	35	35	35	34	35	35	35
	A	0.80	1.96	7.78	3.17	0.24	3.06	27.8	69.1
		(0.33)	(1.66)	(6.80)	(2.46)	(0.15)	(3.74)	(32.5)	(35.4)
		23	23	23	23	19	23	23	23
FY	B	2.12	3.92	10.40	3.08	0.31	11.96	56.6	20.4
		(0.82)	(1.50)	(4.18)	(1.48)	(0.14)	(7.16)	(34.5)	(35.5)
		25	25	25	25	24	25	25	25
	C	3.76	2.80	6.56	3.41	0.89	4.15	16.6	11.3
		(0.63)	(1.55)	(7.18)	(2.71)	(1.00)	(3.99)	(19.0)	(20.0)
		25	25	25	25	25	25	25	25
	A	0.87	1.22	2.78	1.17	0.42	0.99	13.3	85.6
		(0.21)	(1.20)	(3.67)	(1.80)	(0.26)	(2.28)	(23.9)	(24.5)
		23	23	23	23	14	23	23	23
SL	B	1.62	6.86	44.96	15.23	0.35	17.67	71.9	10.3
		(0.68)	(2.60)	(21.66)	(9.27)	(0.12)	(7.66)	(20.0)	(23.6)
		28	28	28	28	28	28	28	28
	C	3.85	7.67	39.88	13.69	0.42	18.23	63.4	0
		(0.89)	(1.71)	(22.98)	(4.78)	(0.21)	(8.20)	(23.4)	
		24	24	24	24	24	24	24	24
	A	1.21	1.71	3.71	3.01	0.70	2.28	11.4	74.0
		(0.58)	(1.35)	(4.14)	(4.95)	(0.60)	(3.76)	(21.4)	(32.8)
		21	21	21	21	15	21	21	21
MM	B	2.69	4.38	19.28	7.10	0.46	10.70	70.1	8.2
		(1.00)	(2.18)	(16.57)	(5.21)	(0.30)	(5.13)	(30.2)	(13.9)
		20	20	20	20	19	20	20	20
	C	3.82	7.13	67.83	18.82	0.31	18.64	72.8	0
		(1.58)	(3.11)	(35.87)	(12.69)	(0.24)	(7.49)	(21.7)	
		24	24	24	24	24	24	24	24
	A	0.82	2.82	8.76	3.41	0.34	4.89	29.9	62.1
		(0.33)	(2.12)	(9.79)	(4.49)	(0.14)	(7.23)	(31.5)	(37.1)
		25	25	25	25	18	25	25	25
GS	B	1.88	6.63	30.63	13.82	0.64	22.00	79.8	6.1
		(0.79)	(1.57)	(12.31)	(7.27)	(0.16)	(8.74)	(17.2)	(16.6)
		27	27	27	27	27	27	27	27
	C	4.78	9.66	40.18	18.90	0.80	20.12	87.4	0
		(1.41)	(2.64)	(20.24)	(8.21)	(0.16)	(7.61)	(27.1)	
		38	38	38	38	38	38	38	38
	A	0.63	2.17	7.22	2.45	0.31	2.38	26.3	47.3
		(0.29)	(1.62)	(6.89)	(2.68)	(0.11)	(3.58)	(38.1)	(44.3)
		18	18	18	18	14	18	18	18
SH	B	1.90	6.35	38.95	9.69	0.30	20.75	84.3	1.4
		(0.82)	(1.42)	(12.93)	(4.76)	(0.21)	(7.26)	(9.55)	(6.3)
		20	20	20	20	20	20	20	20
	C	5.47	8.79	27.79	18.46	0.60	18.75	66.9	0
		(1.63)	(1.47)	(11.30)	(6.57)	(0.25)	(8.60)	(27.9)	
		24	24	24	24	24	24	24	24

Table 4. Average species diversity indices calculated for each reef zone at seven fringing reef complexes along the west coast of Barbados. H'n and H'c: SHANNON - WIENER's index of diversity (Eq. 2); J'n and J'c: PIELOU's "evenness" index (Eq. 4,5); H: BRILLOUIN's index of diversity (Eq. 3); d: MARGALEF's diversity index (Eq. 1); λ'n and λ'c: SIMPSON's "measure of concentration" (Eq. 6,7). First number: average value; second number (in parentheses): standard deviation; third number: total number of transects used in the analysis. Zones: A = back reef, B = reef flat, C = spur and groove zone.

REEF	ZONE	Diversity indices H'n	H'c	J'n	J'c	H	d	λ'n	λ'c
BR	A	0.125 (0.173) 23	0.112 (0.167) 23	0.424 (0.443) 16	0.742 (0.230) 9	0.081 (0.114) 23	0.842 (1.229) 23	0.581 (0.392) 16	0.788 (0.258) 16
	B	0.345 (0.172) 20	0.286 (0.160) 20	0.738 (0.285) 19	0.686 (0.191) 17	0.272 (0.157) 20	1.909 (1.068) 20	0.641 (0.222) 19	0.881 (0.202) 19
	C	0.464 (0.217) 23	0.488 (0.233) 23	0.786 (0.264) 22	0.865 (0.201) 21	0.174 (0.191) 23	2.463 (1.047) 23	0.359 (0.232) 22	0.360 (0.200) 22
SG	A	0.034 (0.094) 16	0.032 (0.087) 16	0.367 (0.502) 5	0.861 (0.108) 2	0.020 (0.054) 16	0.262 (0.716) 16	0.333 (0.408) 5	0.803 (0.270) 5
	B	0.260 (0.223) 31	0.243 (0.215) 31	0.831 (0.399) 30	0.726 (0.210) 21	0.182 (0.159) 31	1.834 (1.526) 30	0.387 (0.336) 30	0.676 (0.261) 30
	C	0.362 (0.192) 35	0.337 (0.197) 35	0.610 (0.299) 34	0.686 (0.234) 31	0.277 (0.157) 35	1.875 (1.021) 35	0.488 (0.270) 34	0.589 (0.247) 34
FV	A	0.184 (0.216) 23	0.154 (0.184) 23	0.482 (0.418) 19	0.689 (0.180) 11	0.138 (0.162) 23	1.063 (1.331) 23	0.618 (0.346) 19	0.706 (0.290) 19
	B	0.489 (0.195) 25	0.423 (0.167) 25	0.830 (0.219) 24	0.782 (0.113) 23	0.348 (0.136) 25	2.963 (1.382) 25	0.303 (0.210) 24	0.484 (0.165) 24
	C	0.386 (0.234) 25	0.300 (0.248) 25	0.887 (0.282) 22	0.744 (0.288) 20	0.236 (0.177) 25	2.489 (1.608) 25	0.192 (0.227) 25	0.597 (0.305) 25
SL	A	0.136 (0.192) 23	0.110 (0.155) 23	0.545 (0.454) 14	0.722 (0.342) 9	0.088 (0.122) 23	0.946 (1.347) 23	0.417 (0.384) 14	0.741 (0.244) 14
	B	0.623 (0.174) 28	0.575 (0.185) 28	0.788 (0.093) 28	0.728 (0.157) 28	0.541 (0.109) 28	3.637 (0.981) 28	0.278 (0.122) 28	0.388 (0.164) 28
	C	0.790 (0.125) 24	0.702 (0.143) 24	0.889 (0.073) 24	0.801 (0.113) 24	0.623 (0.111) 24	4.418 (1.226) 24	0.196 (0.077) 24	0.268 (0.097) 24
BRI	A	0.211 (0.204) 21	0.168 (0.168) 21	0.682 (0.371) 15	0.681 (0.071) 12	0.140 (0.140) 21	1.683 (1.693) 21	0.313 (0.302) 15	0.604 (0.266) 15
	B	0.471 (0.175) 20	0.468 (0.199) 20	0.819 (0.120) 19	0.794 (0.154) 19	0.374 (0.164) 20	2.861 (1.119) 20	0.315 (0.127) 19	0.598 (0.156) 19
	C	0.807 (0.257) 24	0.883 (0.229) 24	0.889 (0.224) 24	0.893 (0.179) 24	0.667 (0.228) 24	3.660 (1.630) 24	0.674 (0.245) 24	0.883 (0.204) 24
OS	A	0.282 (0.262) 25	0.281 (0.2500 25	0.684 (0.341) 18	0.823 (0.106) 15	0.210 (0.205) 25	1.798 (1.664) 25	0.266 (0.210) 18	0.503 (0.246) 18
	B	0.630 (0.156) 27	0.861 (0.157) 27	0.778 (0.149) 27	0.688 (0.135) 27	0.528 (0.127) 27	3.839 (0.831) 27	0.276 (0.113) 27	0.376 (0.145) 27
	C	0.[illegible] (0.127) 38	0.783 (0.143) 38	0.836 (0.082) 38	0.774 (0.081) 38	0.666 (0.114) 38	5.530 (1.500) 38	0.192 (0.077) 38	0.230 (0.088) 38
SR	A	0.241 (0.199) 18	0.248 (0.210) 18	0.673 (0.325) 14	0.730 (0.296) 13	0.178 (0.158) 18	1.626 (1.219) 18	0.401 (0.272) 14	0.882 (0.244) 14
	B	0.648 (0.104) 20	0.619 (0.136) 20	0.821 (0.100) 20	0.781 (0.135) 20	0.588 (0.100) 20	3.628 (0.696) 20	0.266 (0.087) 20	0.382 (0.105) 20
	C	0.824 (0.109) 24	0.736 (0.166) 24	0.877 (0.079) 24	0.788 (0.088) 24	0.662 (0.096) 24	5.840 (0.996) 24	0.188 (0.079) 24	0.288 (0.103) 24

Figure 4. Reef SR. Dendrograms showing classification of line transects along each reference transect (south, central, north) based on average species abundance and live coverage of scleractinian corals. Abundance and coverage data were $\log(X+0.05)$ transformed before comparing line transects using the Ward's agglomerative hierarchical clustering algorithm (Ray, 1982a). Each reference transect splits into 3 main groups (back reef, reef flat and spur and groove zone) at an arbitrary similarity level of $R^2=0.4$ (where R^2 is the sum of squares between all clusters divided by the corrected total sum of squares).


South Transect
Similarity Index R²
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Back Reef Zone
Reef Flat Zone
Spur and Groove Zone
1 2 3 4 5 6 7 9 8 10 11 12 13 18 14 17 19 15 16
Line transects


Central Transect
Similarity Index R²
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Back Reef Zone
Reef Flat Zone
Spur and Groove Zone
1 2 7 3 4 5 6 8 9 10 11 12 13 15 14 21 16 17 20 18 19
Line transects

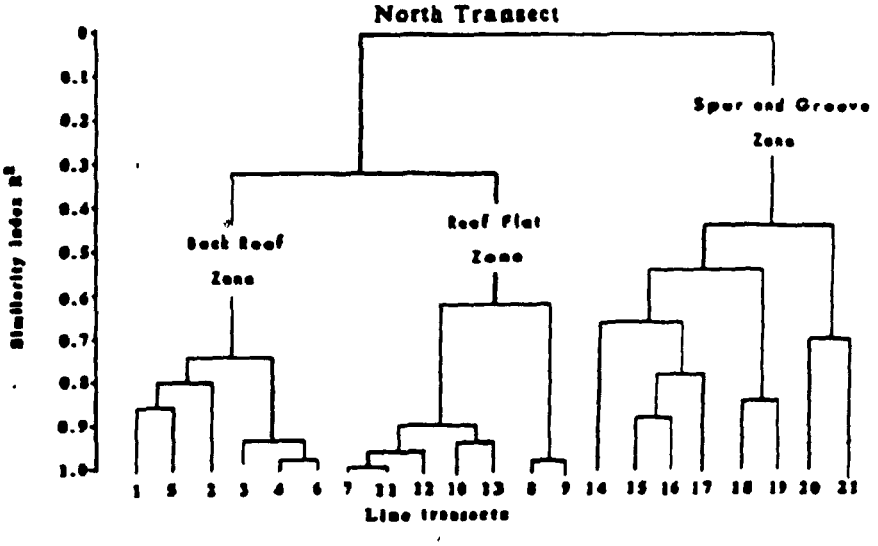

North Transect
Similarity Index R²
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Back Reef Zone
Reef Flat Zone
Spur and Groove Zone
1 5 2 3 4 6 7 11 12 10 13 8 9 14 15 16 17 18 19 20 21
Line transects

Table 5. Scleractinian corals, hydrozoans and zoanthids found on the *Back Reef* zone. Average relative coral coverage (%) by species (first number); standard deviation in parentheses.

	Reef						
	BR	SG	FV	SL	BRI	GS	SR
No. of transects	n=18	n=5	n=19	n=14	n=15	n=18	n=14
Species							
Porites porites	45.3 (6.5)	48.9 (20.6)	15.7 (5.8)	0.1 (0.1)	10.0 (6.8)	13.7 (3.3)	11.4 (3.0)
Porites astreoides	11.2 (5.2)	-	32.7 (8.6)	40.9 (10.7)	22.1 (6.9)	41.6 (6.9)	36.1 (9.6)
Siderastrea radians	68.2 (9.3)	44.4 (23.0)	42.6 (11.2)	25.1 (9.5)	3.7 (2.0)	7.3 (4.5)	22.7 (9.0)
Siderastrea siderea	-	-	-	-	6.7 (6.7)	-	-
Agaricia agaricites	1.2 (0.9)	-	0.8 (0.001)	-	8.6 (5.5)	1.2 (0.6)	-
Diploria clivosa	4.2 (4.2)	-	0.5 (0.5)	31.8 (10.7)	7.0 (5.6)	13.7 (6.0)	18.1 (6.2)
Diploria strigosa	-	-	-	1.1 (1.1)	35.5 (10.0)	-	1.1 (1.1)
Favia fragum	-	6.7 (6.7)	1.4 (0.8)	-	-	6.8 (4.5)	0.2 (0.2)
Montastrea annularis	-	-	-	-	0.7 (0.7)	-	0.3 (0.3)
Acropora palmata	-	-	-	-	-	4.5 (2.6)	-
Millepora squarrosa	-	-	0.2 (0.2)	-	2.9 (2.9)	0.9 (0.7)	7.9 (4.6)
Millepora complanata	-	-	6.1 (4.4)	1.1 (1.1)	-	13.4 (5.2)	1.5 (1.3)
Millepora alcicornis	-	-	-	-	0.5 (0.5)	-	-
Palythoa mamillosa	-	-	-	-	2.2 (2.2)	-	-

Table 6. Scleractinian corals, hydrozoans and zoanthids found on the *Reef Flat* zone. Average relative coral coverage (%) by species (first number); standard deviation in parentheses.

	Reef						
	BR	SG	FV	SL	BRI	GS	SR
No. of transects	n=19	n=30	n=24	n=28	n=19	n=27	n=19
Species							
Porites porites	14.5 (3.7)	23.0 (5.9)	8.2 (2.5)	3.6 (1.0)	1.1 (0.5)	6.7 (1.1)	11.5 (2.4)
Porites astreoides	45.7 (8.2)	54.0 (6.2)	49.6 (4.9)	40.1 (3.8)	34.8 (5.6)	33.0 (4.1)	33.0 (4.5)
Siderastrea radians	1.6 (1.1)	2.4 (1.4)	1.1 (1.1)	0.3 (0.2)	0.5 (0.5)	0.1 (0.1)	3.9 (2.0)
Siderastrea siderea	16.9 (7.3)	-	-	3.2 (1.3)	9.9 (4.7)	5.6 (3.3)	3.3 (3.3)
Agaricia agaricites	8.5 (2.5)	12.8 (5.5)	4.8 (1.3)	9.1 (1.6)	17.3 (3.8)	5.2 (1.0)	10.6 (1.8)
Leptoseris cucullata	-	-	-	1.6 (0.4)	0.4 (0.3)	-	-
Diploria clivosa	-	1.6 (1.2)	1.3 (1.3)	6.5 (2.9)	7.3 (4.0)	4.0 (1.8)	6.4 (2.9)
Diploria strigosa	-	2.2 (1.1)	2.8 (1.9)	3.4 (2.4)	3.6 (2.5)	1.9 (1.0)	1.4 (1.0)
Diploria labyrithiformis	-	-	-	0.3 (0.3)	-	-	-
Favia fragum	-	1.2 (0.6)	4.8 (1.5)	0.9 (0.3)	0.9 (0.4)	1.7 (0.3)	3.8 (1.1)
Montastrea annularis	9.5 (5.5)	-	3.4 (2.9)	3.4 (1.1)	4.1 (2.3)	3.3 (2.1)	4.1 (2.3)
Montastrea cavernosa	-	-	1.4 (1.4)	0.2 (0.1)	-	0.2 (0.2)	0.4 (0.4)
Acropora palmata	-	-	-	-	-	0.3 (0.3)	0.3 (0.3)
Madracis decactis	-	-	-	0.1 (0.1)	-	0.8 (0.6)	-
Madracis mirabilis	-	-	-	-	-	-	0.5 (0.5)
Isophyllia sinuosa	-	-	-	-	-	1.0 (0.8)	-
Millepora complanata	2.6 (2.6)	0.9 (0.9)	14.2 (4.2)	19.1 (3.8)	2.9 (1.6)	29.6 (4.8)	0.7 (0.5)
Millepora squarrosa	0.6 (0.6)	2.1 (1.0)	8.4 (2.0)	4.0 (1.2)	12.4 (4.4)	3.1 (0.5)	15.0 (3.6)
Millepora alcicornis	-	-	-	0.1 (0.1)	1.4 (0.7)	-	-
Palythoa mamillosa	-	-	-	4.2 (1.4)	3.6 (2.0)	3.3 (0.8)	5.3 (2.4)

Table 7. Scleractinian corals, hydrozoans and zoanthids found on the *Spur and Groove zone*. Average relative coral coverage (%) by species (first number); standard deviation in parentheses.

	Reef						
	BR	SG	FV	SL	BRI	GS	SR
No. of transects	n=22	n=34	n=25	n=24	n=24	n=38	n=24
Species							
Porites porites	23.5 (6.2)	40.3 (5.8)	8.2 (3.2)	2.4 (0.8)	2.4 (0.6)	9.3 (1.9)	1.7 (0.5)
Porites astreoides	16.9 (2.4)	19.6 (4.1)	20.2 (5.7)	28.4 (3.0)	10.1 (1.7)	18.4 (2.7)	14.1 (2.3)
Siderastrea siderea	1.3 (1.3)	-	15.8 (6.7)	17.5 (4.3)	15.6 (4.2)	10.2 (2.3)	23.7 (4.0)
Siderastrea radians	-	0.1 (0.1)	11.2 (5.6)	-	-	0.8 (0.8)	3.9 (1.5)
Agaricia agaricites	21.1 (3.7)	14.0 (4.0)	1.5 (0.6)	10.1 (1.7)	19.1 (3.6)	3.0 (0.5)	3.4 (0.6)
Leptoseris cucullata	-	-	-	2.4 (0.4)	0.7 (0.3)	0.5 (0.2)	0.2 (0.1)
Diploria clivosa	-	-	13.3 (6.0)	-	0.2 (0.2)	0.2 (0.2)	-
Diploria strigosa	-	3.2 (1.5)	6.9 (2.9)	2.3 (1.5)	2.9 (1.5)	3.9 (1.0)	5.7 (1.7)
Diploria labyrinthiformis	-	0.3 (0.3)	-	2.4 (2.4)	0.2 (0.2)	2.3 (0.7)	4.0 (1.7)
Favia fragum	-	0.2 (0.6)	-	0.1 (0.1)	0.6 (0.3)	0.5 (0.2)	0.2 (0.2)
Montastrea annularis	27.8 (4.9)	10.0 (4.3)	1.0 (1.0)	9.7 (2.3)	16.0 (5.1)	17.9 (2.9)	12.3 (4.0)
Montastrea cavernosa	-	-	7.6 (4.6)	3.4 (2.0)	2.9 (1.7)	3.7 (0.9)	15.9 (3.3)
Madracis decactis	-	-	0.7 (0.7)	0.6 (0.4)	0.5 (0.3)	1.7 (0.5)	0.4 (0.3)
Madracis mirabilis	-	-	-	3.1 (1.0)	15.3 (6.3)	2.2 (0.6)	2.1 (0.8)
Colpophyllia natans	-	-	-	0.3 (0.3)	-	0.9 (0.4)	1.1 (0.6)
Meandrina meandrites	-	-	-	1.2 (0.7)	0.2 (0.1)	1.6 (0.5)	4.1 (1.4)
Dychocoenia stokesi	-	-	-	0.4 (0.3)	0.6 (0.6)	1.4 (0.4)	1.3 (0.6)
Dendrogyra cylindrus	-	-	-	-	-	2.7 (1.4)	-
Stephanocoenia michelinii	-	-	-	-	-	0.4 (0.2)	-
Acropora palmata	-	-	-	-	-	-	0.2 (0.2)
Mycetophyllia alicea	-	-	-	-	-	0.1 (0.1)	-
Mycetophyllia danaana	-	-	-	-	-	0.1 (0.1)	-
Mycetophyllia ferox	-	-	-	-	-	0.2 (0.1)	-
Isophyllia sinuosa	-	-	-	-	-	0.1 (0.1)	-
Millepora squarrosa	9.5 (2.2)	3.0 (1.1)	2.4 (1.0)	6.9 (0.9)	6.7 (1.5)	5.7 (1.0)	3.3 (0.7)
Millepora complanata	-	9.3 (3.1)	11.5 (4.0)	8.2 (1.9)	2.3 (1.3)	10.9 (2.6)	2.4 (0.9)
Millepora alcicornis	-	-	-	0.2 (0.2)	2.5 (0.8)	1.1 (0.4)	0.1 (0.1)
Palythoa mamillosa	-	-	-	-	1.1 (0.7)	0.3 (0.3)	0.1 (0.1)

Back reef zone

Faunal comparison. The back reef zones, with an average depth of 0.5 to 1.4m, are characterized by high densities of fleshy algae covering a substrate primarily composed of movable sand and dead coral rubble (Table 3). At the BR reef *Thallasia testudinum* Koenig and Sims was a dominant macrophyte in a narrow zone 20m wide at the shore side of the back reef. The seaward edge of the back reef was dominated by *Dictyota sp., Padina sp.* and *Caulerpa spp.* In contrast, the shore side of the back reef at SG reef was dominated by *Ulva fasciata* Delile which underwent seasonal blooms (personal observation). Other species present in high numbers were *Padina sp.*, and *Caulerpa spp.* It should be pointed out that the back reef of the SG reef is directly affected by heated effluent from a power plant located next to the reef (Tomascik and Sander, 1985).

By comparison, the back reef zones of the four northern reefs (SL, BRI, GS and SR) were generally dominated by filamentous algae with a distinct absence of large macrophytes. Some of the filamentous algae identified include *Cladophoropsis membranacea* (C. Agardh) Borgesen, *Cladophora sp., Bryopsis sp.*, and *Chaetomorpha media* (C. Agardh) Kutzing. Hawkins and Lewis (1982) identified *Lyngbia sp.* and *Oscilatoria sp.* in the back reef as forming a thin veneer or turf on or within the shallow surface layers of the sediments. This study concentrated mainly on the more visible algal species. Another characteristic of the back reef zones were low densities of the

sea urchin *Diadema antillarum* (Table 3) during both day and night.

Ten coral species were found on the back reef zones of the fringing reefs (Table 5). In addition, *Palythoa mamillosa* was recorded on the seaward edge of the back reef at the BRI reef representing 2.2% of the total coral coverage.

Table 5 indicates that northern reefs had higher number of species recorded when compared to the southern reefs. The dominant species in terms of relative coral coverage on the three southern reefs (BR, SG, and FV) were *Porites porites*, *Siderastrea radians* and *Porites astreoides;* even though the latter was absent from the SG reef. These three coral species represent more than 90 % of the total coral coverage. *Agaricia agaricites* and *Diploria clivosa* (Ellis and Solander) were minor components, and were absent from the SG reef. The back reef zone at the SG reef contained only three species; note that *Favia fragum* (Esper) was rare (Table 5). These results indicate that *Porites porites* and *Siderastrea radians* can best tolerate the heated power plant effluent which impacts on the SG reef.

In comparison, the dominant coral species on the four northern reefs were *Porites porites, P. astreoides, Siderastrea radians* and *Diploria clivosa.* Note that *Diploria strigosa* (Dana) was the dominant species in terms of coral cover at the BRI reef (Table 5). *Millepora complanata* was an important component on the seaward edge of the back reef zone at the GS reef constituting 13.4 % of the total coral coverage. None of

the other species contributed more than 10 % to the total coverage values.

Community descriptors. The average values of the simple ecological indices were slightly higher at the northern reefs when compared to the southern reefs (Table 3). There were no statistically discernible differences in the average depth recorded in the back reef zones of the seven fringing reefs, indicating that differences in the community characteristics were independent of depth, and depth related environmental factors. The results of one-way multivariate ANOVA indicated significant differences for all community descriptors among the back reef zones. Table 8 presents the results of Tukey's multiple comparison test (at the 0.05 level) for among reef comparisons. Reef SG had the lowest average number of species when compared to other reefs; but, differences in the species number among the remaining reefs were not statistically discernible. Trends in the average number of colonies (abundance) and percentage coral coverage were similar to those of average species abundance. Values were statistically lower at the SG reef than at the other reefs. Highest transect size index (TSI) values occurred at BRI reef and these were statistically discernible from TSI values at the other reefs. TSI values were statistically indiscernible among the remaining reefs. Statistically lower densities of the sea urchin *Diadema antillarum* occurred at the two southern reefs BR and SG when compared to FV and GS reefs. Note that the percentage of

Table 8. Tukey's studentized range (HSD) test (Ray, 1982a) for significant ($P<0.05$) differences between station means for *Number of coral species* (V); *Number of colonies* (O); *Percentage coral coverage* (PCC%) (■); *Transect size index* (TSI) (•); and *Density* (#/m^2) *of Diadema antillarum* (•). Note: this test controls the Type 1 experimentwise error rate.

Back Reef

Reef	BR	BS	FV	SL	BRI	GS	SR
BR	-						
BS		-					
FV	•	V O ■ •	-				
SL				-			
BRI	•	V ■ •	•		-		
GS	•	V O ■ •			•	-	
SR		V O ■			•		-

Reef Flat

Reef	BR	BS	FV	SL	BRI	GS	SR
BR	-						
BS	■	-					
FV	•	•	-				
SL	V O ■ •	V O ■ •	V O ■	-			
BRI	•	V O ■ •	•	V O ■	-		
GS	V O ■ •	V O ■ •	V O ■ •	•	V O ■ •	-	
SR	V O ■ •	V O ■ •	V O ■ •	•	V O •	•	-

Spur and Groove Zone

Reef	BR	BS	FV	SL	BRI	GS	SR
BR	-						
BS		-					
FV	O •	O • •	-				
SL	V O ■ •	V ■ •	V O ■ • •	-			
BRI	V O ■ •	V O ■ •	V O ■ • •	O	-		
GS	V O ■ •	V O ■ •	V O ■ • •		V O	-	
SR	V O ■ •	V ■ • •	V O ■ •		V O		-

substrate cover by encrusting calcareous algae was low at the two southern reefs (Table 3). Higher urchin densities were recorded at the other reefs than at BR and SG; but statistical differences were not discernible (Table 8).

Diversity indices. Table 4 summarizes the average diversity values for the different diversity indices used. Multivariate one-way ANOVA revealed that significant differences occurred for *H'n*, *H'c*, *H* and *d*. The results of the Tukey's test (at 0.05 level) showed that diversity values were statistically lower at the SG reef than at GS and SR reefs (Table 9). There were no statistically discernible differences in species diversity among the other reefs. Neither Pielou's evenness indices nor Simpson's index of concentration showed statistically discernible differences among the back reef zones of the study reefs.

Reef flat zone

Faunal comparison. The reef flat zone defined in this study combines part of the reef crest and the coalesced spur zone previously described by Lewis (1960), Stearn *et al.*, (1977) and Lewis (1984). The reef flat extends from the seaward edge of the back reef zone seawards towards the spur and groove zone. The width of the reef flat varies among the study reefs from 40 to 100m (Fig. 1), with an average depth ranging from

Table 9. Tukey's studentized range (HSD) test (Ray, 1982a) for significant (P<0.05) differences between station means for *Shannon-Wiener's diversity index*: H'n (▼) and H'c (O); *Brillouin's diversity index*: H (▪); and *Margalef's diversity index*: d (*); for further explanation see "Materials and Methods" section. Note: this test controls the Type 1 experimentwise error rate.

Back Reef

Reef	BR	BG	FV	SL	BRI	OS	SR
BR	-						
BG		-					
FV			-				
SL				-			
BRI					-		
OS		▼ O ▪ *				-	
SR		▼ ▪ *					-

Reef Flat

Reef	BR	BG	FV	SL	BRI	OS	SR
BR	-						
BG		-					
FV	*	▼ O ▪ *	-				
SL	▼ O ▪ *	▼ O ▪ *	▪	-			
BRI	O	▼ O ▪ *		▪	-		
OS	▼ O ▪ *	▼ O ▪ *	▪		▼ ▪	-	
SR	▼ O ▪ *	▼ O ▪ *	▼ O ▪		▼ ▪		-

Spur and Groove Zone

Reef	BR	BG	FV	SL	BRI	OS	SR
BR	-						
BG		-					
FV	O *		-				
SL	▼ O ▪ *	▼ O ▪ *	▼ O ▪ *	-			
BRI		▼ O ▪ *	O ▪	▼ ▪	-		
OS	▼ O ▪ *	▼ O ▪ *	▼ O ▪ *	*	▼ O ▪ *	-	
SR	▼ O ▪ *	▼ O ▪ *	▼ O ▪ *	*	▼ ▪ *		-

1.6 to 2.7m (Table 3). The inshore portion of the reef flat is emerged in places at spring tides. The substrate is composed mainly of compacted coral rock with irregular surfaces. At the three southern reefs (BR, SG and FV) the substrate was covered by both encrusting coralline algae (predominantly *Porolithon sp.* and *Neogoniolithon sp.)* and macrophytes; the most visible being *Cladophora sp., Bryothamnion sp., Laurencia sp.,* and *Acanthophora spicifera* (Vahl) Borgesen. The macrophytes covered approximatly 20 to 40 % of the hard substrate. By comparison, the dead coral substrate at the four northern reefs (SL, BRI, GS and SR) was covered predominantly by encrusting coralline algae (i.e. *Porolithon sp.* and *Neogoniolithon sp.)* The coralline algae covered approximatly 70 to 80 % of the hard substrate, whereas filamentous algae covered only 1.4 to 10.3 % of the substrate (Table 3). The average densities of *Diadema antillarum* increase in a south to north direction (Table 3).

Sixteen species of scleractinian corals were recorded on the reef flat zones of the seven fringing reefs. Only four scleractinian species were common to all reef flats. The dominant species on the reef flats was *Porites astreoides* making up between 33 to 54 % of the live coral coverage (Table 6). *Siderastrea radians* represented a relatively small component of the coral coverage, whereas *Agaricia agaricites* constituted between 4.8 to 17.3 % of live coral cover, and *Porites porites* between 1.1 and 23.0 %. *Montastrea annularis,* considered to be a dominant reef builder in Barbados (Lewis, 1960; Macintyre, 1968; Stearn *et al.*, 1977), was absent only

from the SG reef flat. The colonies of *M. annularis* were small round and lobate, and were mainly restricted to the seaward edge. *Montastrea cavernosa* was present on four reef flats (Table 6), but in relatively low numbers. *Palythoa mamillosa* was absent from the three southern reef flats, but represented between 3 to 5 % of the coral coverage at the four northern reefs (Table 6). Both Lewis (1960) and Stearn *et al.* (1977) regarded *Palythoa* as a characteristic species of this zone, and Lewis (1960) named the *Diploria - Palythoa* zone based on the high abundance of *Diploria clivosa* and *Palythoa mamillosa*. The low abundance and coverage of both species in this study suggests that major changes have occurred within the coral community. *Millepora complanata* and *M. squarrosa* were present on all reef flats; with *M. complanata* forming a noteworthy feature at the seaward edge of SL and GS reef flats, and to a lesser extent at the FV reef flat. In general, the northern reef flats have a higher species complement when compared to the three southern reefs.

Community descriptors. The differences among the seven reef flats are evident in the simple community descriptors used in the study (Table 3). The results of multivariate one-way ANOVA indicated significant differences in all community descriptors (Table 3). No statistically discernible differences were found ($P > 0.05$) for the TSI index among the seven reefs. The results of Tukey's multiple comparison test (Table 8) indicated that the average number of species, number of

colonies, percentage coral coverage and *D. antillarum* densities all exhibited similar trends among the seven reefs. Tables 3 and 8 indicate that average values of the above descriptors were statistically higher at the four northern reefs (SL, BRI, GS and SR) than at the three southern reefs (BR, SG and FV); with lowest values occurring at the SG reef flat and BR reef flat. The only statistically discernible difference between the BR and SG reef flats was in the lower coral coverage values (Table 3) of the SG reef flat. The average values of the community descriptors (Table 3) at the BRI reef flat were not statistically discernible from the average values at BR and FV reef flats. However, the density of *D. antillarum* at the BRI reef flat was statistically higher than at the two southern reefs.

Diversity indices. Table 4 clearly indicates that the diversity of the coral community increased from the southern reef BR to the northern reef SR. The results of the multivariate one-way ANOVA indicated significant differences for all diversity indices. Tukey's multiple comparison test (Table 9) indicates that values of the four diversity indices *H'n*, *H'c*, *H* and *d* were statistically lower at SG reef than at the northern reefs, but were not statistically discernible from the diversity values at BR reef. Of the four northern reefs, BRI had the lowest *H'n* and *H* values and these were statistically discernible from the *H'n* and *H* values calculated for the GS and SR reefs. Margalef's diversity index *d* showed

lowest values at SG and BR reefs, which were statistically indiscernible from each other. However, the *d* values at the SG reef were statistically discernible from the other reefs. Note that the average *d* values at the BRI reef were statistically indiscernible from the BR reef. Table 9 clearly indicates that Brillouin's diversity index *H* showed a higher degree of differentiation among the reef flats when compared to the other diversity indices. The results of the multivariate one-way ANOVA have also indicated significant differences for *J'n* and λ'*c*. Statistically lower *J'n* values occurred at thr SG reef flat (Table 10), which was dominated by *Porites porites, P. astreoides* and *Agaricia agaricites*. Highest dominance values, λ'c, were observed at the two southern reefs (BR and SG), and these were statistically discernible from λ'c values measured at the four northern reefs (Table 10). Lowest λ'c values occurred at SR reef and these were statistically discernible from the other three northern reefs. The relatively lower dominance values at the four northern reefs result from the increased species number and reduced dominance of *Porites astreoides*.

Table 10. Tukey's studentized range (HSD) test (Ray, 1982a) for significant (P<0.05) differences between station means for *Simpson's index of concentration*: λ'n (▼) and λ'c (O); and *Pielou's evenness index*: J'n (■) and J'c (*); for further explanation see "Materials and Methods" section. No discernible differences were observed for the above indices at the Back Reef zone. Note: this test controls the Type 1 experimentwise error rate.

Reef Flat

Reef	RR	SG	FV	SL	RRI	OS	SR
RR	-						
SG		-					
FV		O ■	-				
SL	O	O ■		-			
RRI	O	O ■			-		
OS	O	O ■				-	
SR	O	O ■	O				-

Spur and Groove Zone

RR	-						
SG	O *	-					
FV	▼ O	▼ ■	-				
SL	▼	▼ O ■	O	-			
RRI	■ *	O	O ■	▼ ■	-		
OS	▼	▼ O ■	O		▼ O ■	-	
SR	▼	▼ O ■	O		▼ ■		-

Spur and groove zone

Faunal comparison. The spur and groove zone previously described by Lewis (1960) and Stearn *et al.*, (1977) is considered the most actively growing part of the fringing reef complex. The spur and groove configurations, generally running perpendicular to shore, vary in size from reef to reef. Stearn *et al.*, (1977) reported that the spurs at the seaward edge of the fringing reefs were dominated by *Porites porites*. The main characteristic of the spur and groove zones at the three southern reefs (BR, SG and FV), in the present study, was the high percent cover of substrate by fleshy algae. The spur and groove zone at the SG and BR reefs is being eroded, and in the case of the former, has almost collapsed. Similar erosion is occurring at the FV reef where the grooves are being filled with sand. The fleshy algae covering the collapsed spurs at the BR reef were dominated by *Acanthophora sp.*, *Dictyota sp.*, *Bryopsis sp.*, and *Cladophora sp.* This zone, at the SG and FV reefs, was heavily covered by filamentous algae; however, calcareous algae contributed more to the substrate cover at the SG reef (Table 3).

In contrast to the southern reefs, the spur and groove zones of the four northern reefs were almost devoid of fleshy algae. Some filamentous algae (endolithic algae; Hawkins and Lewis, 1982) were present on dead coral fragments and on the exposed skeletal framework of dead coral heads. The dominant encrusting coralline algae were *Porolithon sp.*, *Goniolithon*

sp., and *Neogoniolithon sp.*

Twenty three scleractinian species were recorded on the spur and groove zones of the seven fringing reefs. Of these, only *Porites porites*, *P. astreoides*, *Agaricia agaricites* and *Montastrea annularis* were common to all the reefs. Table 7 presents the average relative coverage of each species. In terms of abundance and percent coral coverage, the dominant species at the BR and SG reefs were *Porites porites*, *P. astreoides* and *Montastrea annularis* (Table 7). The abundance of *Porites porites* was greatly reduced on the FV reef and on the four northern reefs. The dominant species on the FV reef were *P. astreoides* and *Siderastrea siderea* (Ellis and Solander); and on the northern reefs, *P. astreoides*, *Agaricia agaricites*, *M. annularis*, and *S. siderea* (Table 7). The high dominance of *Madracis mirabilis* (Duchassaing and Michelotti) (15.3 % of coral cover) at the BRI reef is attributed to a large stand located at the southern seaward edge of the reef.

The colonial zoanthid *Palythoa mamillosa* was present on the three northern reefs (BRI, GS and SR); however, it was restricted to the inshore edge of the zone. *Millepora squarrosa* was common to all the reefs, while *M. complanata* was absent from the BR reef, and *M. alcicornis* was mainly restricted to the four northern reefs.

Community descriptors. There was a general increase in the average number of species, coral colonies, percent coral cover, TSI index and *D. antillarum* densities in a northerly

direction from the southern reef BR (Table 3). The increase in species number is primarily due to larger coral species which are absent from the three southern reefs (Table 7). Multivariate one-way ANOVA indicated significant differences among the spur and groove zones for all community descriptors. The results of the Tukey's multiple comparison test showed that the average number of species, number of colonies, percent coral cover and sea urchin densities were statistically lower at the three southern reefs when compared to the four northern reefs (Table 8). However, the average number of colonies at the southern reef SG was statistically indiscernible from that at the SL and SR reefs. The high value of the TSI index at the FV reef is attributed to the presence of large *S. siderea* colonies.

Diversity indices. The results of ANOVA also indicated significant differences for the diversity indices presented in Table 4. The values of all diversity indices (*H'n, H'c, H* and *d),* including the evenness indices *J'n* and *J'c,* increased in a northerly direction from the southern reef BR. The diversity of the coral community was statistically higher at the northern reefs (when compared to the southern reefs and BRI reef) as was indicated by the Tukey's test (Table 9). The average species diversity at BRI reef was statistically lower than at the SL, GS and SR reefs, but was statistically indiscernible from the BR reef. The northerly increase in species diversity is associated with an increase in evenness and coresponding

decrease in dominance (Table 4). High coral dominance, λ'n and λ'c, was characteristic of the three southern reefs, where only few species contribute to the abundance and coverage values. Higher dominance and lower evenness values at the three southern reefs were statistically discernible from those of the northern reefs (Table 10).

Within reef zonation

Community descriptors. The results of one-way ANOVA for within reef differences among the three zones indicated significant differences for all community descriptors. The specific differences among the three zones, for each reef, were tested by the Tukey's test (Table 11 and 12). Average number of species increased from the back reef zone seawards with highest numbers in the spur and groove zone. On all reefs the average number of species, number of colonies and live coral coverage were statistically lower on the back reef zones than on the reef flat and spur and groove zones. At the northern reefs, with the exception of the SL reef, average number of species was statistically higher on the spur and groove zone than on the reef flat zone (Table 11). By comparison, there were no statistically discernible differences in average number of species between the reef flat and the spur and groove zone at the three southern reefs (Table 11). Highest densities of *D. antillarum* were recorded on the reef flat and the spur and groove zone, and these were statistically discernible from densities on the back reef zone (Table 11). Coverage of substrate by calcareous algae was statistically higher on the reef flat and the spur and groove zone than on the back reef, while the coverage by fleshy algae was statistically higher on the back reef (Table 11).

Diversity indices. The results presented in Table 12

Table 11. Tukey's studentized range (HSD) test (Ray,1982a) for significant ($P < 0.05$) differences among the reef zones for average number of species, coral colonies, percent coral coverage (PCC %), densities of the sea urchin *Diadema antillarum*, depth, % coverage of substrate by calcareous algae (% CAL) and fleshy algae (% FIL). Zones: A = back reef, B = reef flat and C = spur and groove zone. Note: this test controls the Type 1 experimentwise error rate.

	Station attributes						
REEFS	No. of species	No. of colonies	PCC %	No. of urchins	Depth	% CAL	% FIL
BR	C,B>A	C,B>A	C,B>A	C,B>A	C>B>A	C,B>A	A>C,B
SG	C,B>A	C>B>A	C>B>A	C>B>A	C>B>A	C,B>A	A,B>C
FV	B>A	B>C	B>A	B>A,C	C>B>A	B>A,C	A>B,C
SL	C,B>A	C,B>A	C,B>A	C,B>A	C>B>A	C,B>A	A>B,C
BRI	C>B>A	C>B>A	C>B>A	C,B>A	C>B>A	C,B>A	A>B,C
GS	C>B>A	C,B>A	C,B>A	C,B>A	C>B>A	B>C>A	A>B,C
SR	C>B>A	C,B>A	C>B>A	C,B>A	C>B>A	B>C,A	A>B,C

Table 12. Tukey's studentized range (HSD) test (Ray, 1982a) for significant ($P<0.05$) differences among reef zones for *Shannon-Wiener's diversity index*: H'n and H'c; *Brillouin's diversity index*: H; *Margalef's diversity index*: d; *Pielou's evenness index*: J'n and J'c; and *Simpson's index of concentration*: λ'n and λ'c; Zones: A = back reef, B = reef flat and C = spur and groove zone; Note: this test controls the Type 1 experimentwise error rate.

	Diversity Indices							
Reefs	H'n	H'c	H	d	J'n	J'c	λ'n	λ'c
BR	C,B>A	C>B>A	C,B>A	C,B>A	C,B>A	A=B=C	A=B=C	A>B>C
SG	C,B>A	C,B>A	C,B>A	C,B>A	A=B=C	A=B=C	A=B=C	A=B=C
FV	C,B>A	C,B>A	B>C,A	C,B>A	C,B>A	A=B=C	A>B,C	A>B
SL	C>B>A	C>B>A	C>B>A	C>B>A	C,B>A	A=B=C	A>C	A>B,C
BRI	C,B>A	C,B>A	C,B>A	C,B>A	B>C	A=B=C	C>A	A>B,C
GS	C>B>A	C,B>A	C>B>A	C>B>A	A=B=C	A,C>B	A=B=C	A>B>C
SR	C>B>A	C,B>A	C>B>A	C>B>A	C>A	A=B=C	A,B>C	A>B,C

demonstrate that species diversity was statistically lower on the back reef when compared to reef flat or spur and groove zones. With the exception of the BRI reef, the zonation pattern at the northern reefs was well defined. The average values for the *H'n* at the GS and SR reef flats were statistically discernible from *H'n* values on the spur and groove zones (Table 12). In comparison, the reef flat and the spur and groove zones were similar in terms of *H'c*. In general, there was a progressive increase in coral diversity from the back reef to the spur and groove zone, however, the zonation was less pronounced at the three southern reefs. Pielou's evenness indices showed an increase towards the spur and groove zone (Table 4). Note that with the exception of the GS reef there were no statistically discernible differences among the three zones in *J'c*. By comparison, *J'n* was more sensitive (Table 12) in delineating within reef differences, suggesting that coral colonies are more evenly distributed among the species on the reef flat and the spur and groove zone than on the back reef. The dominance of few species on the back reef is also reflected in higher λ'n and λ'c values (Table 4). Lowest dominance values generally occurred on the spur and groove zone, however, few exceptions occurred (Table 12). In summary the data indicate that the scleractinian coral community is more diverse on the spur and groove zone than on the reef flat, and more diverse on the reef flat than the back reef.

Community and Environmental interactions

Table 13 presents Spearman's rank correlation coefficients between the various environmental variables and community descriptors. The results indicate that the structure of the scleractinian coral community is highly correlated with environmental conditions along the west coast of the island. In a previous study (Tomascik and Sander, 1985), it was demonstrated that dissolved oxygen, temperature and salinity differences among the seven fringing reefs were not biologically significant, and, therefore, are not included in the present analysis. Depth and downward flux of suspended particulate matter (DF-SPM) showed no correlation with any of the community descriptors (Table 13). It is interesting to note that both average number of colonies (COL) and Pielou's evenness index *J'c* failed to correlate with the environmental conditions, but since most environmental variables and community descriptors were strongly correlated it was not possible to clearly demonstrate which environmental factor or a combination of factors had the most significant effect on the structure of the coral community.

Table 14 presents the results of principal component analysis (PCA) for 11 environmental variables measured during the study. The first three principal components (PC) account for a total of 92.9 % of the variance in the data, the first component accounting for 68.5 % of the variance, the second for an additional 14.3 % and the third for the remaining 10.1 %.

Table 13. Spearman correlation coefficients between the environmental variables (SPM: suspended particulate matter; CHla: chlorophyll a; PEN: % of surface illumination; ORG: % of organic content in sediments; DF-SPM: downward flux of SPM; Depth; BOD: biological oxygen demand; PO_4-P: inorganic phosphate; NO_2+NO_3-N: nitrate-nitrite nitrogen; NO_2-N: nitrite nitrogen; NH_3-N: ammonia), and ecological descriptors (SP: species number; COL: number of colonies; PCC: % percentage coral coverage; TSI: transect size index; CAL: % substrate cover by calcareous algae; FIL: % substrate cover by fleshy algae; H'n and H'c: Shannon-Wiener's diversity index; H: Brillouin's diversity index; d: Margalef's diversity index; J'n and J'c: Pielou's evenness index; λ'n and λ'c: Simpson's index of concentration). For r>0.78, P>0.05; n=7.

	SPM	CHla	PEN	ORG	DF-SPM[1]	DF-SPM[2]	Depth	BOD	PO_4-P	NO_2+NO_3-N	NO_2-N	NH_3-N
SP	-0.89	-0.93	0.93	-0.96	-0.07	-1.00	-0.84	-0.96	-0.88	-0.96	-0 75	-0 96
COL	-0.84	-0.84	0.36	-0.38	-0.21	-0.84	0	-0.96	-0.13	-0.50	-0 64	-0 50
PCC	-0.71	-0.79	0.79	-0.76	0.14	-0.82	0.14	-0.75	-0.61	-0.79	-0 61	-0 75
TSI	-0.32	-0.36	0.43	-0.68	-0.64	-0.43	-0.32	-0.39	-0.31	-0.39	-0.68	-0.39
CAL	-0.79	-0.93	0.89	-0.83	-0.14	-0.93	0.21	-0.89	-0.79	-0.89	-0 75	-0 89
FIL	0.61	0.83	-0.68	0.50	-0.86	0.68	-0.64	0.71	0.46	0.71	0 35	0 71
H'n	-0.89	-0.93	0.93	-0.96	0.07	-1.00	-0.84	-0.96	-0.88	-0.96	-0.79	-0 96
H'c	-0.89	-0.93	0.93	-0.96	0.07	-1.00	-0.84	-0.96	-0.88	-0.96	-0 79	-0.96
H	-0.89	-0.93	0.93	-0.96	0.07	-1.00	-0.84	-0.96	-0.88	-0.96	-0.79	-0.96
d	-0.89	-0.93	0.93	-0.96	0.07	-1.00	-0.84	-0.96	-0.88	-0.96	-0.79	-0 96
J'n	-0.93	-0.93	0.93	-0.96	0.25	-0.93	-0.07	-0.96	-0.96	-0.96	-0.96	-0 96
J'c	-0.63	-0.18	0.14	-0.36	0.79	-0.32	-0.32	-0.39	-0.68	-0.39	0.07	-0 39
λ'n	0.82	0.93	-1.00	0.96	-0.04	0.93	-0.84	0.89	0.86	0.89	0.64	0 89
λ'c	0.84	0.84	-0.82	0.88	-0.21	0.96	0	0.93	0.86	0.93	0 68	0 93

[1] DF-SPM rates averaged over one year; [2] DF-SPM rates averaged over summer months only (see Tomascik and Sander, 1985).

Table 14. Eigenvector loadings and Spearman's rank correlation coefficients (r) for correlations between environmental variables and principal components 1,2 and 3; * indicates statistical significance (two-tailed test) at $P < 0.002$; ** $P < 0.01$; ▪ $P < 0.02$; • $P < 0.05$; n=7 reefs.

Environmental variables ▽	Principal component 1		2		3	
	Loading	r	Loading	r	Loading	r
SPM (mg/l)	0.346	0.96**	-0.208	-0.36	-0.050	-0.04
PEN (%)	-0.316	-0.89▪	0.181	0.46	-0.301	-0.25
DF-SPM (mg/cm²/d)	0.016	-0.21	0.155	0.18	0.920	0.92▪
Depth (m)	0.126	0	0.583	0.82•	-0.025	-0.07
ORG (%)	0.351	0.90▪	-0.121	-0.22	0.105	0.16
Chl(a) (mg/m³)	0.292	0.96**	-0.451	-0.61	-0.024	0.18
BOD (mg/l)	0.332	1.00*	-0.269	-0.43	0.022	0.07
NO_3+NO_2-N (µg-at/l)	0.334	1.00*	0.250	-0.43	0.129	0.07
NO_2-N (µg-at/l)	0.307	0.61	0.393	0.04	-0.025	0.68
NH_3-N (µg-at/l)	0.347	1.00*	0.177	-0.43	-0.057	0.07
PO_4-P (µg-at/l)	0.345	0.88•	0.148	-0.22	-0.146	-0.14

▽ Abbreviations used - SPM: suspended particulate matter; PEN: percentage of surface illumination; DF-SPM: downward flux of SPM; ORG: percentage of organic matter in sediments; Chl(a): chlorophyll a; BOD: biological oxygen demand.

High correlation between the PC1 and the environmental variables (Table 14) suggests that PC1 can be interpreted as a general index of environmental conditions. Thus reefs with high concentration of SPM, chlorophyll *a* and nutrients will have high scores on PC1; conversely reefs with low nutrient concentrations and high water clarity will have low scores on this component. As the PC1 accounts for the single largest proportion of variance in the data, it can be concluded that the major differences among the fringing reefs, in terms of environmental conditions, are related to water characteristics. It is of interest to note that both DF-SPM and depth score low on PC1. However, depth is highly correlated with PC2 indicating that PC2 is a function of depth, while DF-SPM is highly correlated with PC3 indicating that PC3 is a function of DF-SPM. Spearman rank correlations between the PC1 and the community descriptors (Table 15) indicate that species diversity is a more sensitive measure of eutrophication stress than coral abundance, coverage or TSI index. Furthermore, lack of correlation between the community descriptors and PC2 or PC3 indicates that neither depth nor DF-SPM are dominant environmental factors affecting the coral community.

Table 16 presents the results of PCA for 12 community descriptors used to characterize the structure of the coral community. The first PC accounts for 79.8 % of the variance in the data, while the second and third PC account for only 9.9 % and 6.5 % of the variance respectively. Note that with the exception of Pielou's evenness index *J'c*, all diversity indices

Table 15. Spearman's rank correlation coefficients between three principal components of environmental variables and community descriptors; * indicates statistical significance (two-tailed test) at $P < 0.01$; ** indicates $P < 0.05$; n=7 reefs.

	Principal components		
Community descriptors	1	2	3
Species abundance (SP)	-0.96 *	-0.39	-0.07
Colony abundance (COL)	-0.50	-0.29	-0.11
Percent coral cover (PCC)	-0.75	-0.57	-0.07
Transect size index (TSI)	-0.39	0.25	0.29
Shannon's diversity index (H'n)	-0.96 *	-0.39	-0.07
Shannon's diversity index (H'c)	-0.96 *	-0.39	-0.07
Brillouin's diversity index (H)	-0.96 *	-0.39	-0.07
Margalef's diversity index (d)	-0.96 *	-0.39	-0.07
Pielou's evenness index (J'n)	-0.96 *	-0.63	0
Pielou's evenness index (J'c)	-0.39	0.18	-0.54
Simpson's dominance index (λ'n)	0.89 **	0.54	-0.21
Simpson's dominance index (λ'c)	0.93 *	0.36	0.29

Table 16. Eigenvector loadings and Spearman's rank correlation coefficients (r) for correlations between community descriptors and principal components 1,2 and 3; * Indicates statistical significance (two-tailed test) at P < 0.002; ** P < 0.01; * P < 0.05; n=7 reefs.

	Principal component					
	1		2		3	
Community descriptors ▽	Loading	r	Loading	r	Loading	r
SP	0.318	1.00*	-0.135	0.11	0.036	-0.04
COL	0.239	0.54	-0.537	-0.64	-0.020	-0.07
PCC	0.230	0.82*	-0.306	-0.36	0.011	0.14
TSI	0.187	0.43	0.394	0.39	-0.725	-0.75
H'n	0.320	1.00*	0.042	0.11	0.056	-0.04
H'c	0.321	1.00*	-0.046	0.11	0.084	-0.04
H	0.320	1.00*	-0.024	0.11	0.123	-0.04
d	0.319	1.00*	0.004	0.11	-0.051	-0.04
J'n	0.290	0.93**	0.382	0.32	-0.093	0.04
J'c	0.175	0.32	0.536	0.61	0.629	0.75
λ'n	-0.301	-0.93**	-0.042	-0.11	0.179	0.18
λ'c	-0.320	-0.96**	0.065	-0.07	-0.082	-0.18

▽ Abbreviations as in Table 15.

have similar loading on PC1 irrespective of sign. Thus, reefs with higher species diversity and lower dominance will have higher scores on this component, while reefs with low species diversity and high dominance will have lower scores. High correlation between PC1 and the community descriptors suggest that PC1 can be interpreted as a general index of species diversity for the seven study reefs. The relationship between the PC1, or the general diversity index, and the environmental variables (Table 17) indicates that water characteristics are the dominant factors related to the structure of the coral community. Note that PC3 is highly correlated with DF-SPM, however since PC3 accounts for only 6.3 % of the variation in the data the relationship has no biological significance.

Fig. 5 presents the result of the linear regression between PC1 of the environmental data and PC1 of the community descriptors. Strong inverse relationship (r^2=0.88, P<0.002) clearly demonstrates the effect of eutrophication on the overall diversity of the coral community. Introduction of PC2 from the environmental data into the model, as a second independent variable, improved the r^2 (P<0.03) of the regression model (r^2=0.97, P<0.001). However, it should be noted that PC2, a function of depth, alone accounts for only 0.09 % of the total variance in the regression model (Fig. 6) and is a poor predictor of coral diversity in this study (r^2=0.09, P>0.52). This supports the hypothesis that depth in this study is not an important factor responsible for the measured differences in the structure of coral communities.

Table 17. Spearman's rank correlations between three principal components of community descriptors and environmental variables; * indicates statistical significance (two-tailed test) at $P < 0.01$; ** indicates $P < 0.05$; n=7 reefs. Abbreviations for environmental variables as in Table 14.

Environmental variables	Principal component 1	2	3
SPM (mg/l)	-0.89 **	-0.10	-0.14
PEN (%)	0.93 *	0.11	-0.18
DF-SPM (mg/cm²/d)	0.07	0.21	0.93 *
Depth (m)	-0.04	-0.43	0.11
ORG (%)	-0.95 *	-0.25	0.09
Chl a (mg/m³)	-0.93 *	0.04	0.04
BOD (mg/l)	-0.96 *	-0.14	-0.07
NO_3+NO_2-N (µg-at/l)	-0.96 *	-0.14	-0.07
NO_2-N (µg-at/l)	-0.75	0.04	0.50
NH_3-N (µg-at/l)	-0.96 *	-0.14	-0.07
PO_4-P (µg-at/l)	-0.88 **	-0.45	-0.16

Figure 5. Regression of PEC1 (first principal component of ecological data) on PEN1 (first principal component of environmental data). The arrow along the x-axis indicates the direction of deteriorating environmental conditions. The arrow along the y-axis indicates the direction of higher species diversity. The broken lines represent the upper and lower 95% confidence bands for the regression line. Symbols associated with each regression point are reef abbreviations.

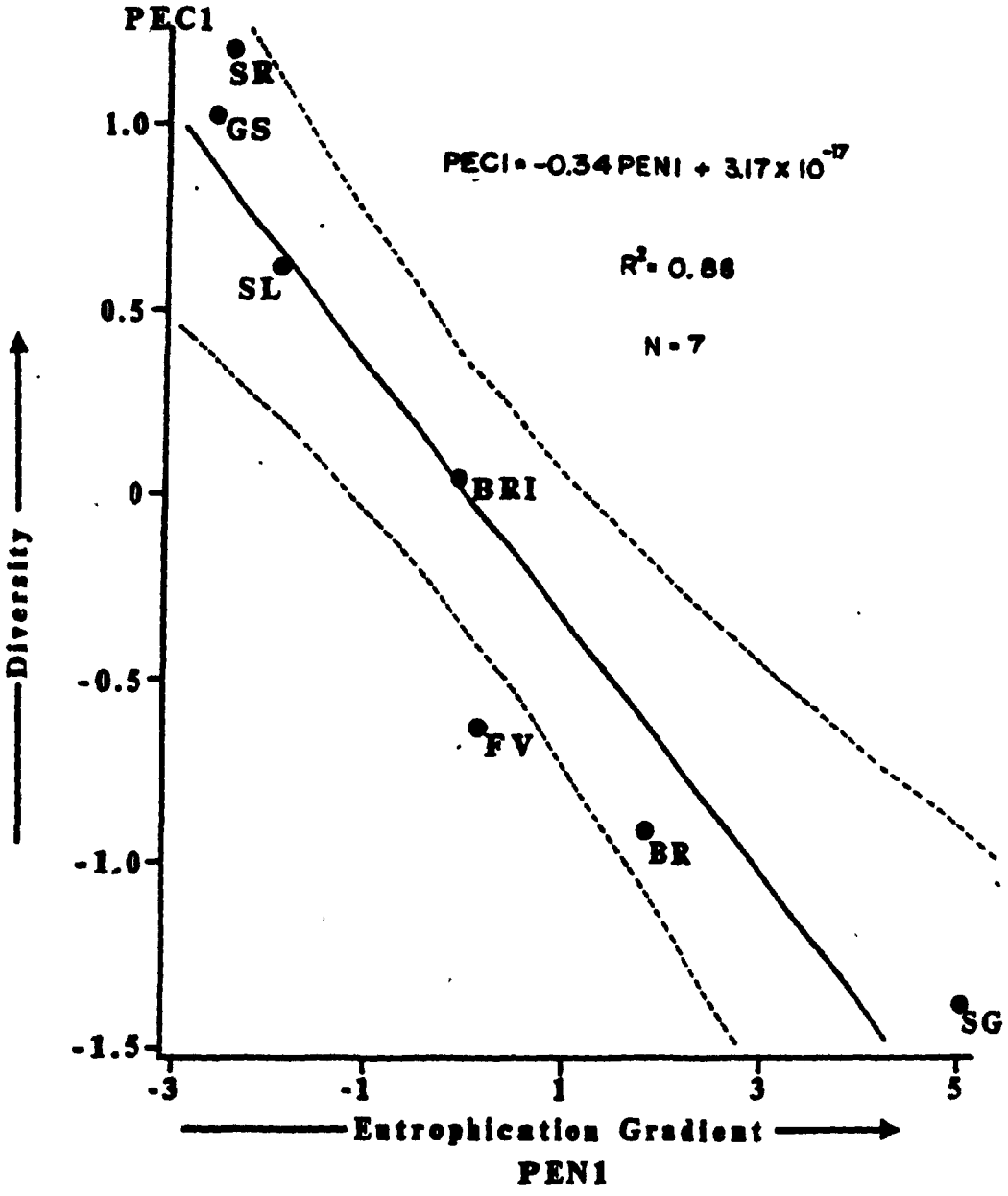
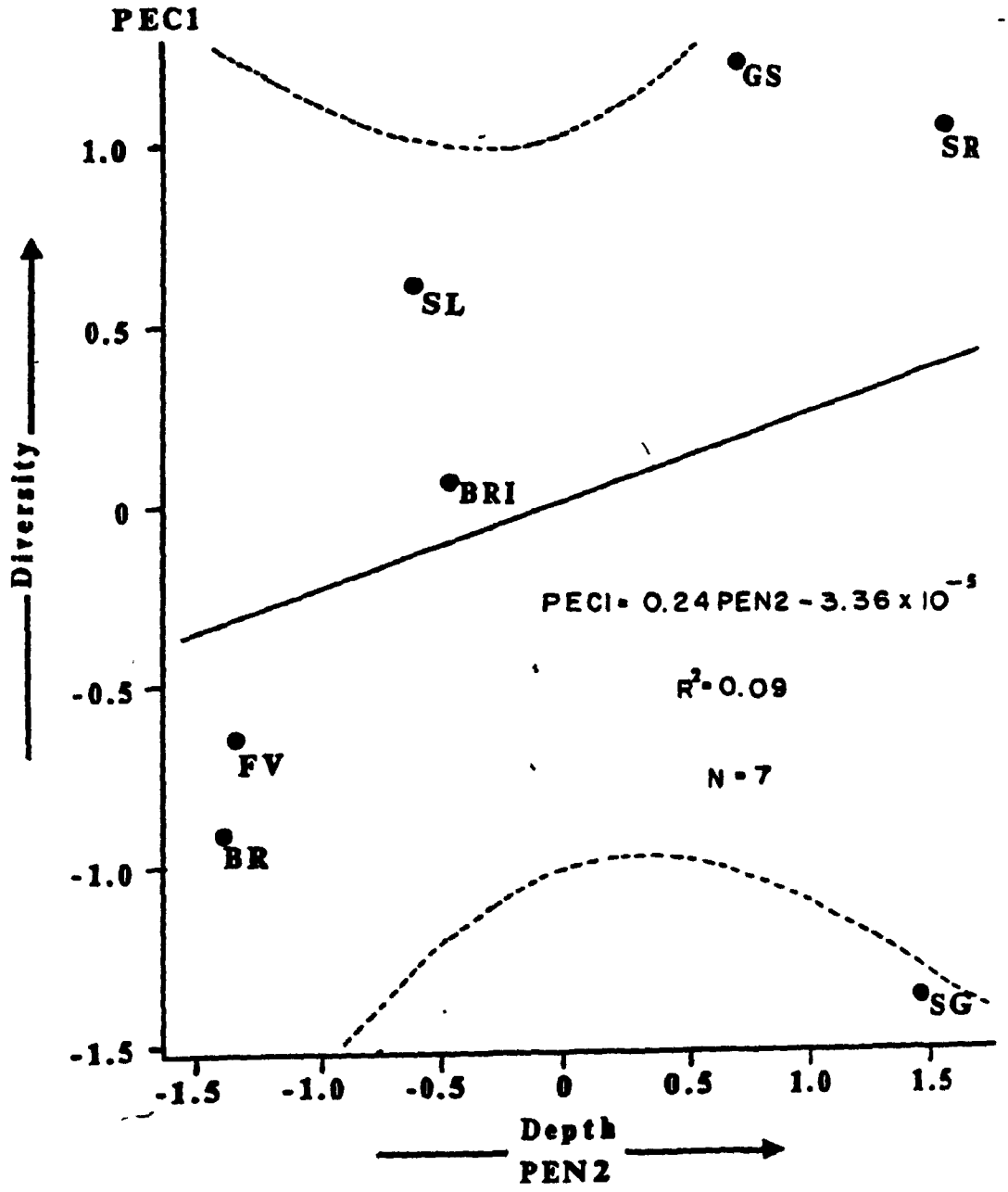

PEC1
SR
GS
SL
BRI
FV
BR
SG
1.0
0.5
0
-0.5
-1.0
-1.5
-3
-1
1
3
5
PEC1 = -0.34 PEN1 + 3.17 x 10^-17
R² = 0.88
N = 7
Diversity
Eutrophication Gradient
PEN1

Figure 6. Regression of PEC1 (first principal component of ecological data) on PEN2 (second principal component of environmental data). The arrow along the x-axis indicates increase in average reef depth. The arrow along the y-axis indicates the direction of higher species diversity. The broken lines represent the upper and lower 95 % confidence bands for the regression line. Symbols associated with each regression point are reef abbreviations.


PEC1
GS
SR
1.0
SL
0.5
Diversity
BRI
0
PECI = 0.24 PEN2 - 3.36 x 10⁻⁵
R² = 0.09
-0.5
FV
N = 7
BR
-1.0
SG
-1.5
-1.5
-1.0
-0.5
0
0.5
1.0
1.5
Depth
PEN2

Discussion and Conclusions

Eutrophication of the inshore water masses along the west coast of Barbados is regarded as a direct result of anthropogenic activities (Tomascik and Sander, 1985; Lewis, 1985). Anthropogenic eutrophication is a combined function of nutrient enrichment, sedimentation and toxicity associated with dumping of domestic and industrial wastes. A number of studies have demonstrated that nutrient enrichment (Clutter, 1972; Banner, 1974; Kinsey and Domm, 1974; Laws and Redalje, 1979; Smith *et al.*, 1981; Walker and Ormond, 1982), sedimentation (Loya, 1976b; Dodge and Vaisnys, 1977; Lasker, 1980; Rogers, 1983; Cortes and Risk, 1985) and toxicity (McCloskey and Chester, 1971; Maragos, 1972; Maragos and Chave, 1973; Sorokin, 1973; Johannes, 1975; Kinsey and Davies, 1979) have direct and/or indirect effects on the integrity of coral reefs. Tomascik and Sander (1985) showed that nutrient concentrations along the west coast of Barbados have increased substantially in the last 15 years. However, the nutrient concentrations are not high enough to have a direct toxic effect on individual coral colonies. Nutrient enrichment is therefore considered to be an indirect stress, affecting the structure of the coral communities through increased production at other trophic levels (Maragos, 1972; Maragos and Chave, 1973; Kinsey and Domm, 1974; Banner, 1974; Birkeland, 1977; Mahoney and McLaughlin, 1977; Laws and Redalje, 1979; Smith *et al.*, 1981). This in turn affects the coral community directly through

competition for space or indirectly through increased bioturbation or sediment trapping (Walker and Ormond, 1982).

High abundance of benthic macrophytes and filamentous algae at the three southern reefs (Table 3) may be a response to elevated influx of nutrients from domestic and industrial sources. However, macroalgal dominance can also be induced in coral reef habitats by exclusion of grazers (Ogden, 1976). The low densities of *Diadema antillarum* at the three southern reefs (Table 3) may therefore be contributing to the elevated algal biomass. In contrast to the present study, Walker and Ormond (1982) recorded higher densities of *Diadema setosum* (Leske) on reefs, with high algal standing crop, affected by sewage pollution. The difference may result from the fact that industrial effluents, rather than sewage, are primarily affecting the southern reefs in Barbados (Tomascik and Sander, 1985). Industrial effluents may inhibit and/or may increase mortality of urchins after recruitment. Note that overall grazing pressure may not be lower on the polluted reefs, where benthic herbivorous fishes are more abundant (Cotter, 1984). As the densities of sea urchins increase (i.e. SR reef), the dominance of the fish community shifts from benthic herbivores to planktivorous species (Cotter, 1984). Given these results, it is suggested that elevated nutrient levels, rather than reduced grazing pressure, are responsible for the high algal biomass on the southern reefs.

Elevated nutrient levels have resulted in high phytoplankton biomass (Tomascik and Sander, 1985) which may

affect the coral community indirectly through the reduction of light intensity and/or alteration of spectral quality; thus, affecting zooxanthellae photosynthesis essential for normal coral function (Vandermeulen and Muscatine, 1974). Elevated phytoplankton biomass combined with organic loading from anthropogenic sources (Tomascik and Sander, 1985) also promotes production of benthic macroinvertebrates. High influx of organic material to the benthic community is reflected in the high organic content of sediments, which ranges between 2.3 % at the northern reef GS and 10.9 % at the southern reef SG. Increased benthic production may be indirectly reflected in higher DF-SPM rates, caused by higher bioturbation, at the three southern reefs during calm summer months (Tomascik and Sander, 1985). Suchanek (1983) has demonstrated that *Callianassa* had a negative impact on *Thallasia testudinum* through bioturbation.

High SPM concentrations and DF-SPM rates associated with eutrophication processes are considered key environmental variables affecting the structure of the coral communities. The lack of significant relationship between the average yearly, as opposed to seasonal, DF-SPM rates and the community descriptors (Table 13) would imply that DF-SPM, which is a function of sedimentation, resuspension and current velocity, has no effect on the structure of the coral communities in this study. However, Tomascik and Sander (1985) showed that DF-SPM fluctuate sharply as a result of variation in swells and land run-off. Both the swells and land run-off may last only a few

days, and their occurrence wanes seasonally, but their impact is sufficient to mask the contribution of anthropogenic activities to the DF-SPM values. By using only DF-SPM values collected during the calm summer months and relating these to the community descriptors, an inverse relationship between DF-SPM rates and coral community structure materializes (Table 13).

Apart from problems resulting from short-term variations masking underlying patterns, there are problems associated with the measurement of sedimentation and/or resuspension rates and the interpretation of them in the context of coral function (Tomascik and Sander, 1985) or community structure. The wide variety of methods used to measure sedimentation and/or resuspension rates prevents meaningful comparisons between most studies. Moreover, since DF-SPM is a function of both current velocity and particle density, low DF-SPM rates do not necessarily imply low turbidity. Consequently, SPM in the water column is likely to be a more meaningful index of stress on corals than DF-SPM. Rogers (1979) has demonstrated that light reduction due to high SPM concentrations has a greater effect on some coral species than sedimentation rates. Measurement of both SPM concentrations and light intensity at standard depths during reef surveys would provide much needed comparative data on regional variations in environmental conditions.

SPM concentrations along the west coast of the island were clearly negatively correlated with all community descriptors (Table 13), with the exception of dominance indices λ'n and

λ'c. Similarly, high turbidity and sedimentation rates have been implicated in severely affecting coral diversity, cover, abundance and health (Bak and Elgershuizen, 1976; Loya, 1976a; Dodge and Vaisnys, 1977; Bull, 1982; Peters, 1984). Moreover, Tomascik and Sander (1985) suggested that elevated SPM concentrations may be responsible for reduced growth rates of *Montastrea annularis*. Recently, Kendall *et al.*, (1985) showed that stress related to elevated turbidity levels significantly reduces calcification rates and free amino acid (FAA) levels in the FAA pool in *Acropora cervicornis* (Lamarck) exposed to 200 ppm kaolin concentrations. Dallmeyer *et al.*, (1982) have also revealed that elevated peat concentrations reduced oxygen production in *Montastrea annularis*, through selective wavelength filtration and reduced light intensities.

Sedimentation can affect corals indirectly by contributing to turbidity or directly by physical smothering. Corals exhibit four mechanisms of sediment rejection: polyp distension, tentacular movement, ciliary action and mucus production (Hubbard and Pocock, 1972). A great deal of laboratory and field work has been done on the sub-lethal and lethal effects of sediments derived from terrestrial runoff (Cortes and Risk, 1985), dredging and filling activities (Brock *et al.*, 1965; Dodge and Vaisnys, 1977; Bak, 1978; Sheppard, 1980) and resuspension of bottom sediments (Aller and Dodge, 1974; Dodge *et al.*, 1974). A number of field studies in the Caribbean have demonstrated that areas associated with high sedimentation and/or resuspension have a characteristic coral

fauna (Lewis, 1960; Loya, 1976a), and these studies were in general agreement with the results of experimental studies on sediment rejection (Hubbard and Pocock, 1972; Lasker, 1980; Rogers, 1983). It is generally accepted that *Montastrea cavernosa*, *Diploria strigosa*, *D. labyrinthiformis* (Linnaeus), and *Siderastrea siderea* are efficient sediment rejectors (Hubbard and Pocock, 1972; Dodge and Vaisnys, 1977; Lasker, 1980; Rogers, 1983). *Montastrea cavernosa*, is perhaps the most efficient, being capable of removing approximately 14 mg/cm²/d of sediments (Lasker, 1980). It is the dominant coral species on turbid reefs in Puerto Rico (Loya, 1976a). The DF-SPM rates measured in this study fall within the range measured over extended periods in natural habitats in the Caribbean (0.3 to 32 mg/cm²/12 as reported by Pastorok and Bilyard, 1985).

The distribution and relative coverage by the different coral species (Table 2) indicates that coverage by large coral species such as *Diploria strigosa*, *D. clivosa*, *D. labyrinthiformis*, *Montastrea cavernosa*, *Colpophyllia natans* (Houttuyn), *Meandrina meandrites* (Linnaeus) and *Dichocoenia stokesi* Milne Edwards and Haime is significantly lower at the three southern reefs (BR,SG and FV). The general trend, towards the polluted southern reefs, is for higher abundance and dominance of coral species with smaller polyp size. *P. astreoides* is the dominant coral species on all the reefs in the study (Table 2), while *P. porites*, *A. agaricites* and *S. radians* show higher dominance at the three southern reefs. Based on sediment rejection efficiencies (Hubbard and Pocock,

1972), these results are somewhat surprising, since *Diploria strigosa*, *D. labyrinthiformis*, and *M. cavernosa* are considered good sediment rejectors while *P. astreoides*, *A. agaricites* are considered sensitive to sedimentation. However, it is important to appreciate that most sediment rejection studies have used sediments derived from natural sources and these may have quite different effect on corals than sediments derived from domestic or industrial effluents. Interestingly, most species that were absent from the southern reefs use mucus production as one means of sediment removal, and this could explain their sensitivity to elevated SPM concentrations or increased DF-SPM. Mucus is known to be a good energy source for resident coral bacteria (Antonius, 1981). Hence the high mucus production required for cleaning in polluted environments may make the corals susceptible to bacterial attack, particularly if the source of the pollution is domestic or industrial waste. This may be aggravated by high nutrient concentrations which also increase mucus production (Antonius, 1981).

To test these ideas coral species were divided into three groups based on their feeding strategies (Lewis and Price, 1975); and their average abundance values (Fig. 7) were related to environmental conditions (Table 18). The results clearly demonstrate that corals which feed by a combination of tentacle capture and mucus filament entanglement (Group III; Lewis and Price, 1975) show a significant negative correlation with the environmental conditions. The relatively low correlation between Group III and light intensity ($r=0.71$, $P<0.06$) further

Figure 7. General distribution of scleractinian coral species grouped on the basis of feeding strategies. Group I - tentacle capture only; Group II - mucus net and filament entanglement; Group III - tentacle capture and mucus entanglement. Numbers indicate average abundances. Reefs are arranged spatially along a gradient of improving water quality (left-to-right). Improving water quality implies a decrease in nutrient, SPM, and chlorophyll *a* concentrations, and an increase in water clarity. Reef abbreviations as in Fig. 1.

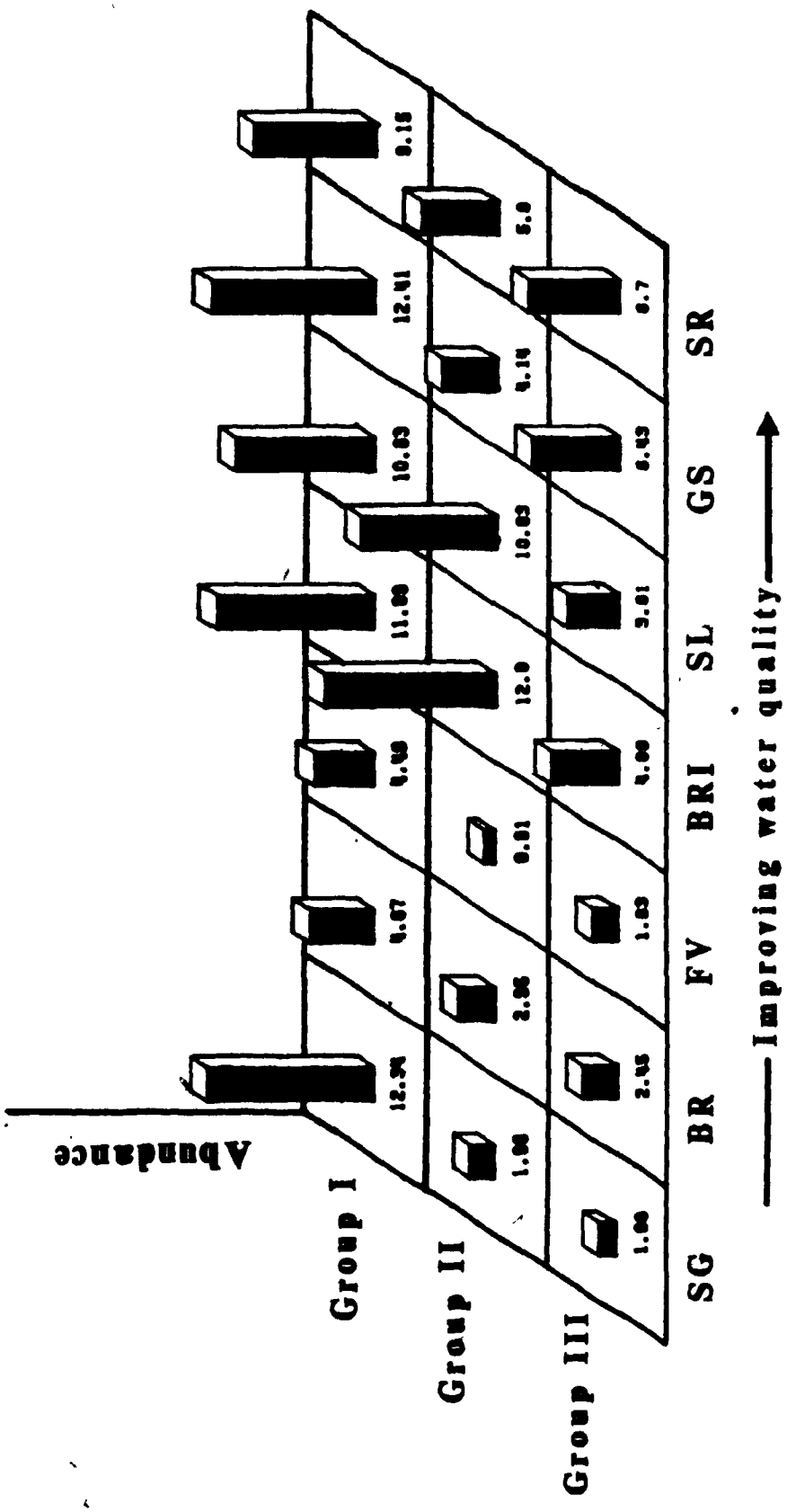

Abundance
Group I
Group II
Group III
SG
BR
FV
BRI
SL
GS
SR
Improving water quality

Table 18. Spearman's rank correlation coefficients for correlations between coral groups based on feeding strategies and environmental variables. Coral abundance used in the analysis; * Indicates statistical significance (two-tailed test) at $P < 0.01$; ** indicates $P < 0.05$; n=7 reefs.

Environmental variables	Feeding strategies •		
	Group I (tentacle capture)	*Group II* (mucus net and filament entanglement)	*Group III* (tentacle capture and mucus entanglement)
SPM (mg/l)	-0.04	-0.64	-0.86 **
DF-SMP (mg/cm²/d)¹	-0.25	0	0.21
DF-SPM (mg/cm²/d)²	-0.29	-0.54	-0.89 **
PEM (%)	0.29	0.29	0.71
ORG (%)	-0.16	-0.34	-0.74
BOD (mg/l)	-0.14	-0.57	-0.93 *
Chl a (mg/m³)	-0.29	-0.54	-0.86 **
PO_4-P (µg-at/l)	0.04	-0.20	-0.74
NO_3+NO_2-N (µg-at/l)	-0.14	-0.57	-0.93 *
NH_3-N (µg-at/l)	-0.14	-0.57	-0.93 *
Depth (m)	0.54	-0.11	0.14

¹ DF-SPM rates averaged over one year; ² DF-SPM rates averaged over summer months only (see Tomascik and Sander, 1985).
•: Source Lewis and Price (1975).

suggests that other factors than reduction in light are affecting the structure of the coral community. By contrast, the abundance of Group I and II corals is not correlated with the environmental variables. In summary, it appears that corals responding to sedimentation and/or feeding stimuli by producing mucus will be susceptible to bacterial attack, especially in areas directly affected by domestic and industrial effluents (Mitchell and Chet, 1975; Ducklow and Mitchell, 1979; Rublee *et al.*, 1980). Garrett and Ducklow (1975) demonstrated that, combined with oxygen depletion and hydrogen sulfide accumulation, bacterial infection will result in coral injury or death. It is suggested that the dominance of *Porites astreoides, P. porites* and *Siderastrea radians* in the southern polluted reefs may result from the secretion of bacterial resistant mucus envelopes which are not secreted by other coral species (Lewis, 1973; Ducklow and Mitchell, 1979).

Four of the dominant coral species on the three southern reefs reproduce by brooding larvae (Fadlallah, 1983), and this may be an additional factor contributing to their relative dominance and survival on the polluted reefs. It has been demonstrated that larval settlement near already established colonies is responsible for the contagious distribution of some brooding species (Lewis, 1974a; Goreau *et al.*, 1981). Since coral larvae are able to settle within hours after release (Lewis, 1974b; Goreau *et al.*, 1981), it is suggested that higher local recruitment of brooding species, than of broadcasting species, may be responsible for their numerical

dominance in the stressed environment.

The passage of Hurricane Allan in 1980 had a measurable effect on the structure of a fringing reef coral community on the west coast of Barbados (Mah, 1984). The species most severely affected by the wave action during the passage of Allan were *Porites porites* and *Madracis mirabilis*. In view of the possible damage to all the fringing reefs along the west coast and the lack of quantitative historical data on the structure of the coral communities, this study must necessarily be viewed in a comparative spatial context. However, because of the location and general morphology of the seven fringing reefs in the study, it is unlikely that the measured differences in the structure of the scleractinian communities were a result of differential impact of hurricane-generated waves. An exploratory survey of the fringing reef BRI after the passage of Allan showed none of the major physical destruction that was recorded in Jamaica (Woodley *et al.*, 1981). The main reason for the relatively low impact of the hurricane on the structure of the fringing reefs is related to lower energy waves generated in the rear left quarter of the cyclone. Qualitative observations during the passage of Allan indicated that the total energy absorbed by the fringing reefs was comparable to, if not lower than, annual periods of high winter swells (Tomascik and Sander, 1985). During the course of this study large intact stands of *Porites porites* were observed at the two southern reefs BR and SG. These were unaffected by the passage of the hurricane even though they were at a depth of 2 to 3m.

This suggests that if there was a differential effect of the hurricane generated waves along the west coast the northern reefs were affected to a greater extent than the southern reefs.

Species diversity proved to be a sensitive index in delineating major differences in the structure of the coral communities and in assessing the impact of pollution. With the exception of *J'c*, all measures of diversity were highly correlated with environmental conditions (Table 13). Thus, increased pollution resulted in the expected increase in dominance of certain species at the southern reefs. It could be argued that, since all diversity indices were highly correlated with environmental conditions (Table 13), the use of one index may be sufficient to demonstrate a pollution impact in future studies. Pielou (1977) has given an extensive treatment on the theories and use of diversity measures. Unfortunately, her suggestions are seldom implemented especially in coral reef studies. For theoretical reasons, the use of *H'n* or *H'c*, and the associated evenness indices *J'n* and *J'c*, are inappropriate in most studies using the line transect method. The implicit assumption of *H'n* is that the population, from which the sample was obtained, is infinitely large and homogeneous, and that all the species present in the parent population are present in the sample (Pielou, 1977). This assumption is clearly violated by the line transect method. It is suggested that Brillouin's index *H* is therefore more appropriate, since it directly measures the diversity of the

sample (transect line), is not an estimate, and therefore, is comparable to other samples. The correlation between *H'n* and *H* clearly demonstrates that *H'n* contains a consistent bias (Fig. 8). This relationship is also apparent in Loya's 1972 paper (Fig. 7, p., 110).

A number of studies have shown that diversity can be dependent on factors other than pollution stress (Loya, 1972; Bouchon, 1981; Dodge *et al.*, 1982), and it has been suggested that diversity indices are generally inappropriate in pollution related studies (Green, 1979; Green and Vascotto, 1978). However, for comparative purposes, the use of diversity indices is justified if the interpretation of results is restricted to the range of values measured, and no inference is attempted about the general assumption of a connection between high diversity and high environmental quality. In this study, the diversity indices were compared along an eutrophication gradient among similar ecological zones to minimize possible effects of natural environmental gradients (Fig. 9). The use of PCA has demonstrated that the effects of natural environmental factors (depth) on the structure of coral communities are masked by stresses related to eutrophication processes. The adverse effects of eutrophication processes are clearly demonstrated by high correlations between PC1 of the environmental data and diversity indices (Table 15).

In summary, the study has demonstrated statistically discernible and biologically significant differences in the structure of scleractinian coral communities among seven

Figure 8. Correlation between the Shannon's diversity index H'n, and Brillouin's diversity index H based on 513 line transects (samples). Spearman's rank correlation coefficient = 0.979.

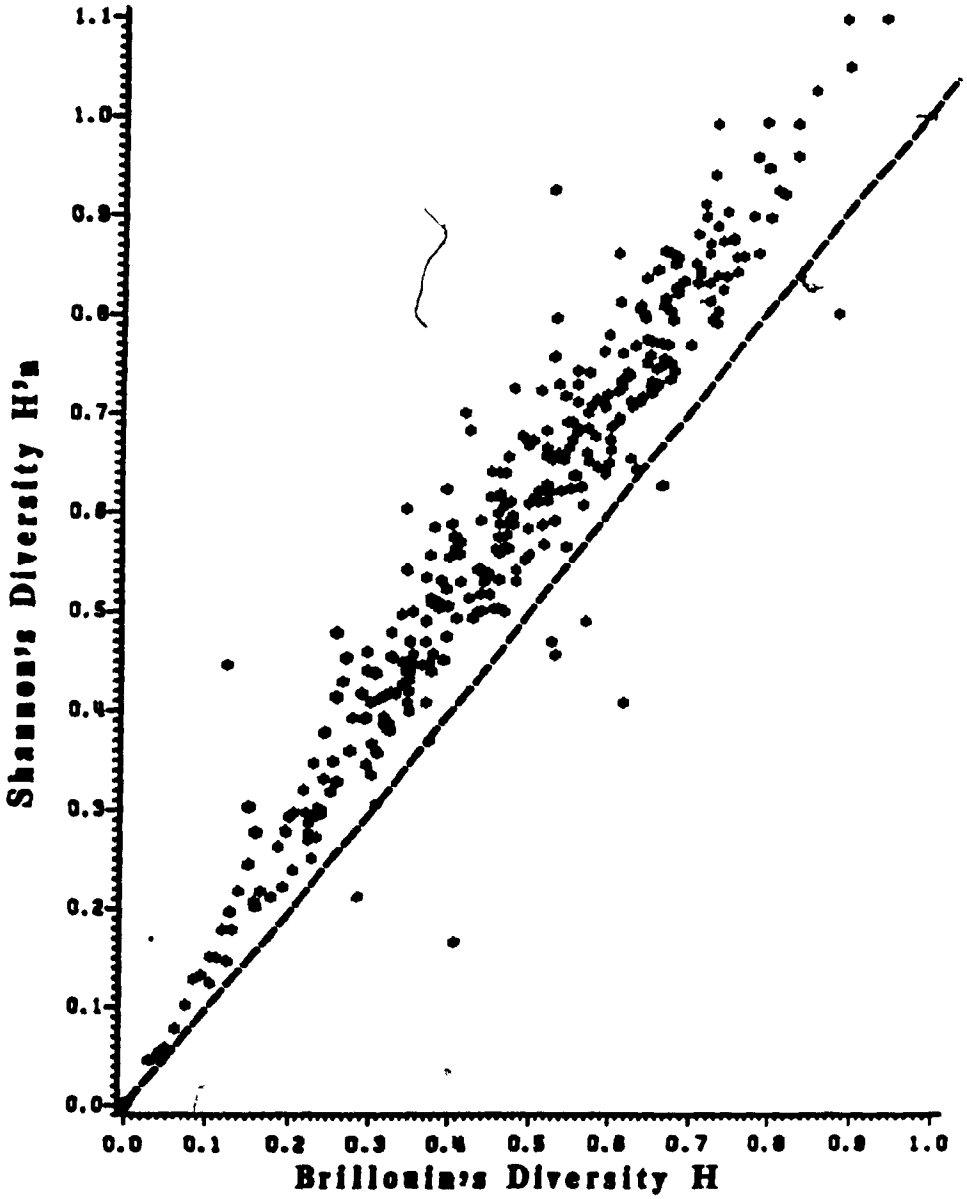
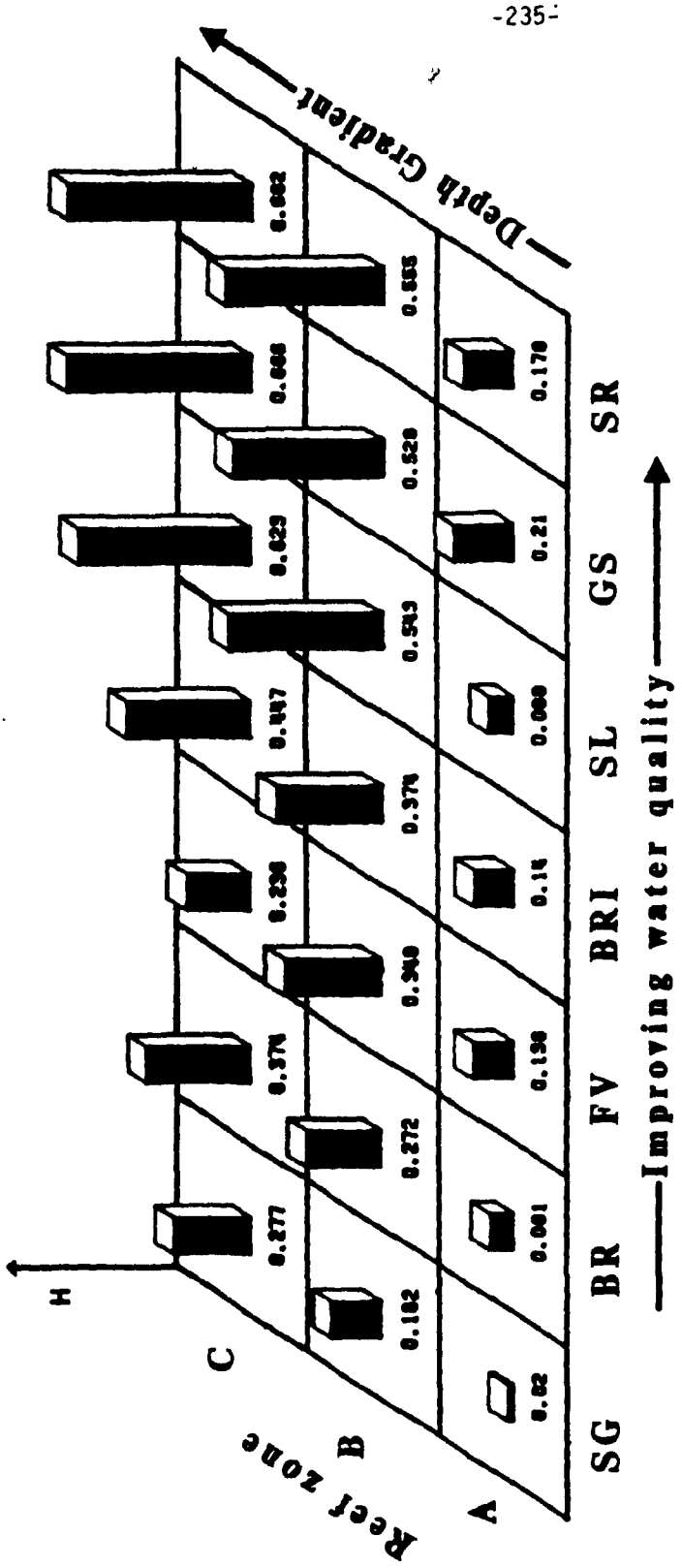

Shannon's Diversity H'n
Brillouin's Diversity H
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1

Figure 9. Variations, along 2 environmental gradients (horizontal axes), in Brillouin's diversity index H (vertical axis). Reefs are arranged spatially along an anthropogenic environmental gradient of improving water quality (left-to-right). Improving water quality implies a decrease in nutrient, SPM, and chlorophyll *a* concentrations, and an increase in water clarity. The natural environmental gradient is a function of depth and wave exposure extending through the reef zones. Numbers indicate average H values. Zone A - back reef; Zone B - reef flat; Zone C - spur and groove zone. Reef abbreviations as in Fig. 1.


Depth Gradient
Reef zone
A
B
C
H
SG
BR
FV
BRI
SL
GS
SR
Improving water quality
0.82
0.182
0.277
0.001
0.272
0.376
0.138
0.348
0.236
0.11
0.376
0.068
0.547
0.523
0.623
0.21
0.528
0.666
0.178
0.555
0.662

fringing reef complexes along the west coast of Barbados. High and significant correlations between various environmental variables and community descriptors (Table 13) suggest that the measured differences in coral community structure are directly and/or indirectly related to water conditions. Reduced species diversity, through direct elimination of certain species, results from the effects of eutrophication processes and responses of coral species to stress situations. Sediment rejection abilities combined with feeding and reproductive strategies of scleractinian corals are the main biological processes through which eutrophication affects the structure of the coral community. Furthermore, the study emphasizes the necessity of clearly defining the nature of the environmental stress when considering its effects on scleractinian corals. Characteristics which provide resistance to natural perturbations, such as swells or land run-off in natural environments (unaffected by pollution), may provide no resistance to stress arising from anthropogenic activities. Note too, that while apparently major perturbations, such as accidental spills of non-toxic substances, may have minimal impact on corals in natural environments (Dollar and Grigg, 1981) they may be lethal for corals already subjected to chronic pollution (Loya, 1976b).

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Concluding Remarks

This study supports the hypothesis that eutrophication of the coastal water masses along the west coast of Barbados exerts a measurable impact on the structure (i.e. species abundance, composition, coverage, diversity and trophic levels) of the scleractinian coral communities, and directly and/or indirectly affects coral growth and reproduction. Since an optimal impact study design (i.e. spatial-by-temporal framework) was not possible, because of the lack of baseline data, this study demonstrated and described the effects of environmental perturbation (eutrophication) upon the scleractinian coral communities from spatial patterns alone. Repeated collections were carried out at regular time intervals, from September 1981 to September 1982, to provide information on year-round levels of fourteen environmental variables at seven fringing reefs lying along the leeward coast of Barbados. High nutrient concentrations along the leeward coast of the island were attributed to domestic and industrial effluents, agricultural practices, groundwater discharge, and the circulation patterns of the inshore water masses.

The variations in the intensity of eutrophication (i.e. nutrient and organic inputs) are strongly implicated in changes in a complex of other environmental factors (biotic and abiotic) which had direct and/or indirect effects on the scleractinian coral communities. Nutrient enrichment of the inshore water masses has imposed a major environmental gradient

on the west coast of Barbados, and is implicated to be a significant factor related to the observed differences in the distributions of scleractinian corals. These differences were detected at different levels of organization (i.e. individual, population, community).

The ability of the scleractinian coral communities to withstand environmental perturbations depends primarily on the ability of individual corals to adapt to the new environmental conditions. Physiological responses of individual corals (implicit in coral growth and reproduction) to the stresses of the environmental changes, brought about by eutrophication, represent the first line of resistance of the coral community as a whole. Therefore, growth rates of *Montastrea annularis* and reproduction of *Porites porites* were used as quantitative measures of testing stresses, associated with eutrophication processes, not only because both parameters integrate a variety of physiological responses of individuals, but they may also provide a possible functional link between the community structure and the altered environment.

This study clearly demonstrated (Chapter I, II) that stresses associated with eutrophication processes are likely to be capable of exerting a significant effect on coral growth and reproductive processes. Over the range of environmental values measured during the study, both growth rates of *M. annularis* and reproductive potential of *P. porites* were directly related to water characteristics along the environmental gradient. Furthermore, *M. annularis* exhibited an optimum in growth

(skeletal extension) - unimodal distribution - along the SPM gradient (Chapter I). This suggested that SPM may be an energy source for reef corals up to a certain maximum concentration, characteristic of each species, after which reduction of growth occurs due to smothering, reduced light levels, reduced zooxanthellae photosynthesis or some other unidentified processes.

The ultimate effect of eutrophication stresses upon the scleractinian coral communities was reflected in their structural differences (i.e. species composition, abundance, cover, trophic position, and diversity) along the environmental gradient. The gradual decrease of water quality (i.e. increase in nutrient, chlorophyll *a*, and SPM concentrations) from north-to-south, resulted in a significant decrease in species numbers, abundance, cover, and diversity. Furthermore, the trophic position of the coral communities shifted towards species which are able to use tentacle capture as primary feeding mechanism. Coral species previously believed to be resistant to high turbidity and sedimentation (i.e. *Montastrea cavernosa, Diploria strigosa*) were characteristically absent from the southern stressed reefs. This discrepancy probably arises from the fact that most sediment rejection studies have involved unpolluted sediments which may differ considerably, from sediments affected by organic pollution, in their physicochemical properties, thus in their effect.

Reproduction and growth are two biotic factors that play an integral role in structuring of scleractinian coral

communities. Reduction in reproductive activity and growth rates, as a response to environmental stress, may contribute significantly to the measured differences in the structure of the coral communities. Reduced coral fecundity (i.e. number of eggs or larvae produced by an adult) may directly affect local recruitment patterns by reducing the number of potential recruits. Reduction in coral growth rates may also affect the structure of scleractinian coral communities. If the size of coral colonies determines whether some of its energy is to be diverted into production of gametes, then reduced growth may postpone reproduction until mature colony size is attained. Furthermore, reduced growth may place the coral colony at a disadvantage by reducing its ability to escape predation (through larger size), and decrease its interspecific competitiveness for resources (i.e. space and light). Since scleractinian corals are sessile they must necessarily experience passively the varying conditions in the water masses, and, therefore, the ultimate change in community structure in perturbed environments results from variations in rates of larval recruitment, growth and mortality in the adult population. The structure of scleractinian coral communities under pollution stress must, therefore, depend on the relative success of coral species which both as adults and larvae can tolerate reduced water quality (i.e. high nutrient and SPM concentrations) and secondary effects associated with eutrophication processes.