Distribution, abundance and life history of the reef coral *Favia fragum* (Esper) in Barbados: effects of eutrophication and of the black sea urchin *Diadema antillarum* (Philippi)

by

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Effects of eutrophication and of grazing on *Favia fragum* in Barbados

ABSTRACT

Effects of variation in eutrophication and in *Diadema antillarum* densities (grazing pressure) on the abundance and life history characteristics of *Favia fragum* on seven reefs along the [illegible] of Barbados were investigated. Densities of *D. antillarum* were negatively [illegible] with eutrophication levels, and interpretations of their effects have been made simultaneously. Abundance of *F. fragum* was lower on more eutrophic reefs with lower *D. antillarum* densities. This may result from effects of eutrophication and of *D. antillarum* on algal cover on reefs. Macrophytic algae were more abundant, and crustose coralline [illegible] abundant, on eutrophic reefs with lower *D. antillarum* densities; and [illegible] cover was negatively correlated with crustose coralline algal cover [illegible] abundance was positively correlated with crustose coralline algal [illegible] occurred less frequently on reef areas where macrophytic algae were abundant. High eutrophication and low *D. antillarum* density (grazing pressure) may therefore reduce *F. fragum* abundance by increasing the cover of macrophytic algae relative to crustose coralline algae on reefs. Neither planulation periodicity, colony fecundity, nor polyp fecundity in *F. fragum* differed at different eutrophication levels and *D. antillarum* densities. Moreover, adult growth and adult mortality did not differ with eutrophication levels and *D. antillarum* densities on reefs. However, growth of juveniles appeared slower and mortality higher on eutrophic reefs with low *D. antillarum* densities. Moreover, larvae of *F. fragum* preferred to settle on crustose coralline algae than on turf algae (macrophytic algae), and the former are comparatively scarce on eutrophic reefs with low *D. antillarum* densities. The results suggest that the negative correlation between adult abundance of *F. fragum* and eutrophication levels/grazing pressure (*D. antillarum* densities) on Barbados reefs are caused primarily by effects of these processes on settlement and early post-settlement stages of *F. fragum*.

RÉSUMÉ

Les effets de variation d'eutrophisation et de la densité de *Diadema antillarum* sur l'abondance et les characteristiques du cycle biologique de *Favia fragum* sur sept récifs de la côte ouest de la Barbade furent examinés. Les densités de *D. antillarum* étaient négativement correlés avec les niveaux d'eutrophisation et l'interprétation de leurs effets fût donc réalisé simultanément. *F. fragum* était moins abondant sur les récifs plus eutrophes et possédant de faibles densités de *D. antillarum*. Ceci peut être le résultat des effets de l'eutrophisation et de *D. antillarum* sur la couverture des algues récifales. Les algues macrophytiques étaient plus abondantes, par contre les algues corallinacées étaient moins abondantes sur les récifs plus eutrophes et possédant de faibles densités de *D. antillarum*; et la couverture des algues macrophytiques étaient négativement correlée avec la couverture des algues corallinacées sur tous les récifs. L'abondance de *F. fragum* était positivement correlée avec la couverture des algues corallinacées, et la présence de *F. fragum* était moins fréquent sur les récifs òu les algues macrophytiques étaient abondantes. De haut niveau d'eutrophisation combinés de faibles densités de *D. antillarum* pourrait donc alors réduire l'abondance de *F. fragum* en augmentant la couverture des algues macrophytiques relativement aux algues corallinacées sur les récifs. Ni la périodicité de planulation, ni la fécondité colonale, ni la fécondité polypale de *F. fragum* ne différaient pas à différents niveaux d'eutrophisation et de densité de *D. antillarum*. De plus, la croissance des adultes et la mortalité des adultes ne différaient pas avec les niveaux d'eutrophication et les densités de *D. antillarum* sur les récifs. Cependant, la croissance des juvéniles paraissait plus lente et la mortalité plus élevée sur les récifs plus eutrophes et possédant de faibles densités de *D. antillarum*. De plus, les larves du *F. fragum* préféraient se fixer sur les algues corallinacées plutôt que sur un gazon d' algues macrophytiques, et les algues corallinacées sont comparativement plus rare sur les récifs plus eutrophes et possédant de faibles densités de *D. antillarum*. Les résultats suggèrent que la corrélation négative entre l'abondance de *F. fragum* et les niveaux d'eutrophisation/d'intensité de broutage (densité de *D. antillarum*) sur les récifs de la Barbade sont causés principalement par les effets de ces processus sur la fixation et le début du stage de post-fixation de *F. fragum*.

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PREFACE

1.) Statement of contribution:

The ideas for this research were developed by myself, with the aid of a wide body of literature and input from my supervisor. I was responsible for the experimental design, data collection and analysis, as well as writing initial drafts of each chapter. The final draft of this thesis benefited considerably from editorial inputs by my supervisor.

2.) Statement of originality:

To the best of my knowledge, the material presented in this thesis is an original contribution to knowledge of the effects of anthropogenic eutrophication and of grazing by the black sea urchin *Diadema antillarum* on the abundance and life history of the hermatypic coral *Favia fragum*. Several of the life history traits have never been documented for *Favia fragum* in the field (adult growth and mortality, fecundity, early juvenile growth and mortality, larval settlement choice), and others have never been reported for Barbadian populations (reproductive periodicity).

3.) Historical statement of relevant work:

An historical review of relevant work may be found in the general introduction to the thesis, and is supplemented by more extensive background material in the introduction and text of individual chapters.

4.) Thesis format:

This thesis has been prepared as a series of manuscripts to be submitted for publication in refereed scientific journals. The format of each chapter corresponds to that required by the journal Marine Biology, to which they will be submitted.

ACKNOWLEDGEMENTS

Trying to write this section of the thesis was not a simple task, especially under the bone shattering pressure of an August 30 deadline for submission. Given these conditions, I will be quite open about the likelihood of forgetting to mention people who aided me in my quest. For those of you who were unfortunately omitted, I give my sincerest thanks and apologies.

My supervisor, Wayne Hunte, always gave me the freedom to proceed on my own volition. This thesis would not have been possible without his generous support, which ranged from personal, financial, theoretical, and editorial, to downright comical. I hope that he can eventually catch up on the sleep he lost making sure that this thesis met the aforementioned deadline (knock on wood).

My field and lab assistants during the summer of 1992 were absolutely incredible. Francois Landry and Isabelle Gagnon provided stoic support in the sea. Toni Johnson and Rob Bateson gave expert instruction and assistance with the water quality analysis. The Bellairs Research Institute staff provided help in a variety of ways. Pierrette MacLean aided in constructing the settlement domes.

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This thesis is dedicated to my grandmother (Claire) and my parents (Bob and Lolah), who made it possible for me to fall in love with the ocean, and to Suzanne, whose courage and strength has been truly inspiring.

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GENERAL INTRODUCTION

Eutrophication is stressing coastal marine ecosystems globally. While not directly toxic as persistent chlorinated compounds, heavy metals, residual nuclear wastes, and petroleum products may be, eutrophication typically occurs on a larger scale, and may therefore have greater overall impact. Rosenberg (1985) defined eutrophication as an increase in nutrients leading to increased growth of algae and plants. It is often associated with increased sedimentation (Bell, 1991; Wittenberg and Hunte, 1992). Nutrient enrichment may result from natural causes on a local scale, but generally becomes a chronic large-scale problem only under anthropogenic influences, such as industrialization, urbanisation, coastal development and modern agricultural practices.

Coral reefs are characteristic of oligotrophic tropical water. Hermatypic corals are the dominant benthic fauna on most reefs. As a result of intricate nutrient recycling mechanisms (see review by D'Elia and Wiebe, 1990), corals can maintain high productivity at low nutrient levels, and may therefore be particularly sensitive to eutrophication (Johannes, 1975). Low levels of eutrophication may enhance algal production without affecting the biomass, species composition, or trophic structure of coral reefs (Kinsey and Domm, 1974). However, moderate to heavy levels of eutrophication cause a substantial increase in algal populations (Laws and Redalje, 1979; Smith *et al.*, 1981) and have major implications for the biological, chemical and physical environment of corals and coral reef communities (Maragos, 1972; Banner, 1974; Kinsey and Domm, 1974; Loya, 1975; 1976; Kinsey and Davies, 1979; Smith *et al.*, 1981; Pastorok and Bilyard, 1985; Tomascik and Sander, 1985; 1987a; 1987b; Rogers, 1990; Wittenberg and Hunte, 1992; Hunte and Wittenberg, 1992). Increased algal production affects corals by decreasing available light and increasing the sediment load, particularly the organic fraction (Bell, 1991). The higher sedimentation rates associated with the elevated nutrient levels favour filter-feeders such as sponges, bryozoans and tunicates. These filter feeders and the benthic algae whose growth is directly affected by the eutrophication, may outcompete corals for space on the reef

(Maragos, 1972; Birkeland, 1977; Wittenberg and Hunte, 1992). Maragos (1972) describes the elimination of coral cover by the production of dense mats of benthic algae in response to eutrophication. The growth of benthic algae may be further enhanced on eutrophic reefs if the abundance of important herbivores is reduced (Sammarco *et al.*, 1974, Littler and Littler, 1984; Lewis, 1986; Wittenberg and Hunte, 1992).

Herbivory is the most influential biotic factor affecting algal distribution and abundance (Berner, 1990). Fish are generally considered the dominant grazers in most reef systems (Gaines and Lubchenco, 1982), but urchins become more important as herbivorous fish densities decline. In the Caribbean, the black sea urchin *Diadema antillarum* is a key herbivore, and may be the dominant grazer on shallow reefs (Morrison, 1988) experiencing heavy fishing pressure (Hay, 1984). Density manipulation experiments have demonstrated that the removal of urchins from patch reefs in the Caribbean results in a rapid accumulation of benthic algal biomass, which can gradually displace corals (Sammarco *et al.*, 1974; Sammarco, 1982). Accumulation of benthic algae has also been reported following the 1983 mass-mortality of *D. antillarum*, in which densities were reduced by more than 90 percent throughout the Caribbean by a water borne pathogen (Lessios, 1988 for mass mortality; Carpenter, 1985; de Ruyter van Steveninck and Bak, 1986; Hughes *et al.*, 1987 for algal accumulation).

Changes in algal biomass on reefs can ultimately alter coral community structure only by influencing responses of the constituent coral species. Several studies have now suggested that eutrophication and sedimentation can affect the abundance (Maragos, 1972; Walker and Ormond, 1982; Tomascik and Sander, 1987a; Wittenberg and Hunte, 1992), mortality (Maragos, 1972; Wittenberg and Hunte, 1992), growth (Maragos, 1972; Kinsey and Davies, 1979; Smith *et al.*, 1981; Tomascik and Sander, 1985; Davies, 1990; Tomascik, 1990), reproduction (Tomascik and Sander, 1987b), and settlement rates (Tomascik, 1991; Hunte and Wittenberg, 1992) of corals. However, the number of species studied in this context remains relatively small. Moreover, few studies simultaneously investigate effects of eutrophication on several aspects of the life history of a single species. To fully understand the impact of eutrophication on corals, effects on all life history traits should be simultaneously considered.

Many studies have documented eutrophication and its effects on the fringing reefs off the west coast of Barbados (Lewis, 1985; 1987; Tomascik and Sander, 1985; 1987a; 1987b; Snelgrove and Lewis, 1989; Davies, 1990; Wittenberg and Hunte, 1992; Hunte and Wittenberg, 1992). Barbados has been extensively developed as a major tourist center over the last three decades. The associated urban and industrial expansion, coupled with modern agricultural practices, has led to increased pollution of inshore waters, especially near the capital of Bridgetown. The major point sources of pollution are the organic and/or nutrient enriched effluents of a rum distillery, electricity plant, and a sewage treatment plant. The more diffuse sources are nutrient-enriched surface and groundwater runoff, the volumes of which vary spatially due to differences in vegetation clearance and geomorphology.

This study investigates the effects of eutrophication and of reduced grazing pressure on the abundance and life-history characteristics of *Favia fragum* on the west coast of Barbados. *F. fragum* is a small (10 cm maximum diameter) hermatypic coral found throughout the tropical western Atlantic. Lewis described its distribution on reefs (1960; 1970; 1974a), early growth (1974b), and larval settlement behaviour (1974c). The reproductive biology and general ecology of *F. fragum* have been documented by Duerden (1902), Szmant-Froelich *et al.* (1985), Szmant (1986), and Soong (1991). In contrast to most corals, *F. fragum* has year-round reproductive cycle and broods its larvae until the planula stage. *F. fragum* was chosen for this study because it occurs across the full range of eutrophication and grazing pressure levels prevailing along the west coast of Barbados.

The primary objectives of the present study were to (1) investigate effects of eutrophication and of variation in *Diadema antillarum* density on the distribution and abundance of *Favia fragum* on seven fringing-reef complexes along the west coast of Barbados, and (2) to determine possible mechanisms responsible for the spatial variation in abundance by examining effects of eutrophication and *D.antillarum* density on several life history characteristics of *F. fragum.*

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CHAPTER 1

Distribution and abundance of the reef coral *Favia fragum* (Esper) in Barbados: effects of eutrophication and of the black sea urchin *Diadema antillarum* (Philippi)

1.1 Abstract

Effects of variation in eutrophication levels and in *Diadema antillarum* densities on abundance of the hermatypic coral *Favia fragum* were investigated at seven reefs along the west coast of Barbados. An index of eutrophication was established for each site using a principal component analysis of a suite of water quality variables including reactive phosphate, total inorganic nitrogen, suspended particulate matter, volatile particulate matter, and chlorophyll-a. *F. fragum* abundance was measured in a total of 210 quadrats (5 x 5 m) over 3 depth zones on the seven reefs. Cover by crustose coralline algae and macrophytic algae were recorded for each quadrat, and *D. antillarum* densities were surveyed by transects. *D. antillarum* densities were negatively correlated with eutrophication levels on the study reefs, and their effects on *F. fragum* abundance are therefore interpreted simultaneously. The abundance of *F. fragum* was negatively correlated with eutrophication levels and positively correlated with *D. antillarum* densities (grazing pressure) on the reefs. Effects of these processes on *F. fragum* abundance may be mediated by their effect on algal cover. Macrophytic algal cover was higher, and crustose coralline algae lower, on more eutrophic reefs with lower *D. antillarum* density; and macrophytic algal cover was negatively correlated with crustose coralline algal cover across the study reefs. Cover by crustose coralline algae was higher, and cover by macrophytic algae lower, on reef areas where *F. fragum* was present, and cover by crustose coralline algae was positively correlated with *F. fragum* abundance across the reefs. These results suggest that high eutrophication and low grazing pressure (*D. antillarum* density) reduce *F. fragum* abundance by increasing the cover of macrophytic algae relative to crustose coralline algae on reefs. Increasing coastal eutrophication, and a sharp reduction in *D. antillarum* densities accompanying a mass mortality event in 1983, may be primarily responsible for the apparent temporal decline in *F. fragum* abundance on Barbados west coast reefs over the past few decades.

1.2 Introduction

Anthropogenic eutrophication affects reefs by increasing their nutrient and sediment loads. Elevated nutrient levels may be directly toxic to corals (e.g. Simkiss, 1964; Kinsey and Davies, 1979), but generally affect corals indirectly through increased primary productivity. Nutrient enrichment can promote the growth of phytoplankton in the reef environment. The increased phytoplankton biomass and the elevated concentrations of suspended particulate matter reduce light availability for zooxanthellae photosynthesis and increase sedimentation, and may therefore alter the energy budget of corals (Edmunds and Davies, 1989; Rogers, 1990). The ability of corals to compete with other reef organisms is dependent on prevailing nutrient levels (Littler and Littler, 1984; 1985). Benthic algae and filter-feeding invertebrates benefit more than corals from the increased nutrients and particulates, and their rapid growth results in the displacement of corals from the reef (Birkeland, 1977; Hunte and Wittenberg, 1992). Maragos (1972) describes the elimination of coral cover by the production of dense mats of benthic algae in response to eutrophication. The increase in benthic algae biomass under increased nutrient levels may also depend on grazing pressure on the reef.

Herbivory is the most influential biotic factor affecting benthic algal abundance (Berner, 1990). While fish are generally considered the dominant grazers in most reef systems (Gaines and Lubchenco, 1982), sea urchins become more important as herbivorous fish densities decline. In the Caribbean, the black sea urchin *Diadema antillarum* is generally considered a key herbivore, and may be the dominant grazer on shallow reefs (Morrison, 1988) experiencing heavy fishing pressure (Hay, 1984). Effects of *D. antillarum* density on benthic algal distribution have been demonstrated by both experimental and natural reductions in *D. antillarum* density. The experimental removal of *D. antillarum* from reefs has been shown to result in a substantial increase in benthic algal biomass, which dominated available space at the expense of coral populations (Sammarco *et al.*, 1974; Sammarco, 1982). Studies examining the impacts of the 1983 mass-mortality of *D. antillarum*, in which densities were reduced by more than 90 percent throughout the Caribbean (Lessios, 1988), have generally supported the experimental results (Carpenter, 1985; de Ruyter van Steveninck and Bak, 1986; Hughes *et al.*, 1987).

It is now well documented that eutrophication is occurring on the fringing reefs along the west coast of Barbados (Lewis, 1985; 1987; Tomascik and Sander, 1985; 1987a; 1987b; Snelgrove and Lewis, 1989; Davies, 1990; Tomascik, 1991; Hunte and Wittenberg, 1992; Wittenberg and Hunte, 1992). Over the last three decades, Barbados has developed as a major tourist center. The associated urban and industrial expansion, coupled with modern agricultural practices, has led to increased pollution of inshore waters, especially near the capital, Bridgetown. The major point sources of pollution are the organic and/or nutrient enriched effluents of a rum distillery, electricity plant, and a sewage treatment plant. Non-point sources include nutrient-enriched surface and groundwater runoff, the volumes of which vary spatially due to differences in vegetation clearance and geomorphology.

This chapter examines the distribution and abundance of *Favia fragum* along the west coast of Barbados. *F. fragum* is a small (10 cm maximum diameter) hermatypic coral found throughout the tropical western Atlantic. Lewis described its general distribution on reefs (1960; 1970; 1974a), early growth (1974b), and settlement behaviour (1974c). The reproductive biology and ecology of *F. fragum* have been documented by Duerden (1902), Vaughan (1908; 1910), Szmant-Froelich *et al.* (1985), Szmant (1986), and Soong (1991).

The primary objective of this chapter is to investigate effects of variation in eutrophication and in *D. antillarum* densities, and hence grazing pressure, on the distribution and abundance of *F. fragum* at seven fringing-reef complexes along the west coast of Barbados. Specifically, the objectives are (1) to establish water quality characteristics at 7 fringing reef complexes along the west coast of Barbados, (2) to quantify basic reef morphology and dominant organisms (*D. antillarum*, macrophytic algae, crustose coralline algae, other corals) as habitat characteristics that might influence *F. fragum* abundance at these sites, (3) to document the abundance of *F. fragum* at each site, and (4) to correlate the presence and abundance of *F. fragum* with the habitat characteristics and water quality characteristics at the 7 sites.

1.3 Methods

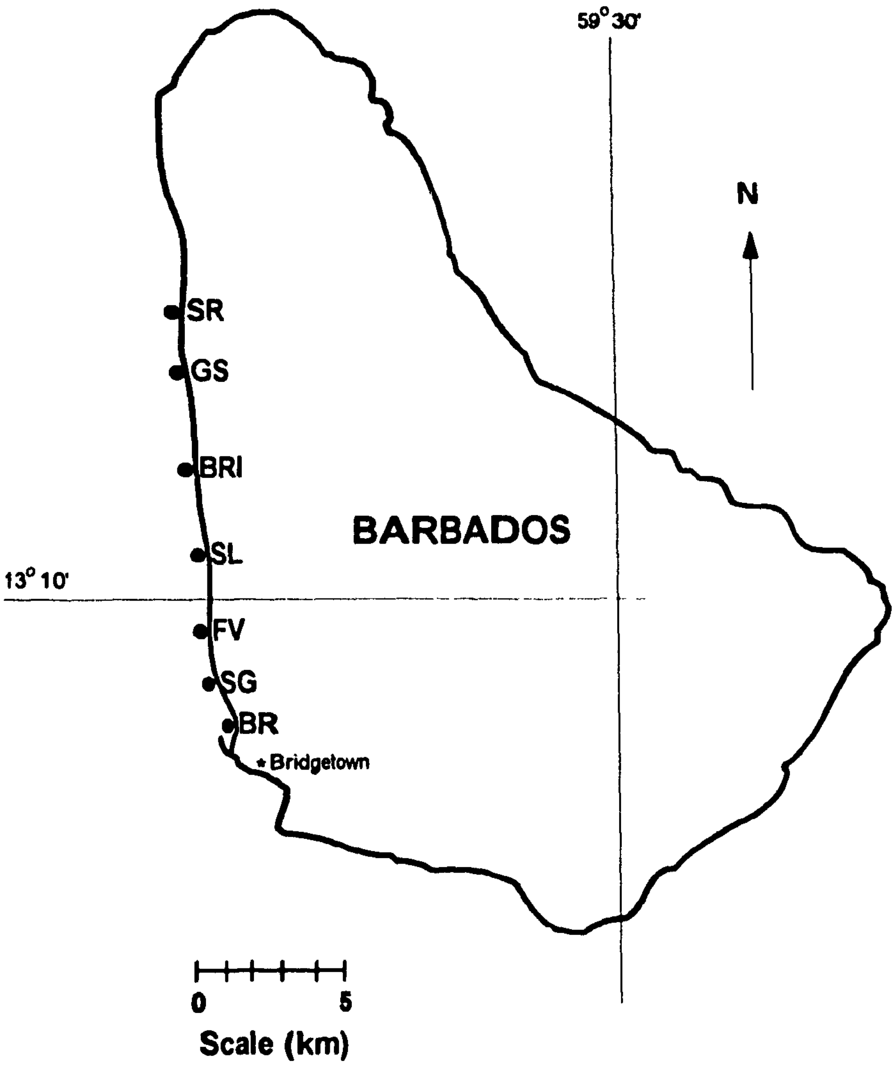
1.3.1 Study Sites

Seven fringing reefs along the west coast of Barbados, West Indies (13°15'N, 50°30'W) were selected for study. The basic structure of Barbados west coast fringing reefs is described by Lewis (1970). Data for several water quality indices of eutrophication exist for the seven sites from a previous study (Tomascik and Sander, 1985). Tomascik and Sander (1985) describe inter-reef differences in morphology as small. The sites, from south to north, are: Brighton (BR), Spring Garden (SG), Fitts Village (FV), Sandy Lane (SL), Bellairs Research Institute (BRI), Greensleeves (GS), and Sandridge (SR) (Fig. 1).

1.3.2 Distribution and abundance of *Favia fragum*

The abundance of *F. fragum* was assessed in its preferred habitat on west coast fringing reefs (Lewis, 1960; 1970; 1974a; Tomascik and Sander, 1987a) from June to August, 1992. On each reef, three 100-m reference transects were placed parallel to shore; one in the reef crest zone (1-2m depth), one in the shallow spur and groove zone (2-3m depth), and one in the mid spur and groove zone (3-4m depth). The transects were marked at 5-m intervals. Ten quadrats (25 m^2) were randomly placed along each transect, providing a total of 30 quadrats per reef and 210 quadrats for the study. Each study zone covered $1000m^2$ of reef, while $250m^2$ was actually sampled with quadrats. Each of the quadrats was systematically searched for *F. fragum* by divers using SCUBA. The quadrat size (5 x 5 m) was chosen on the basis of preliminary work on North Bellairs reef. Smaller quadrats ($1m^2$, $5m^2$, and $10m^2$) sampled too few specimens of *F. fragum*, while larger quadrats were cumbersome and may have caused reef damage.

Figure 1. Locations of the study sites alonog the west coast of Barbados, West Indies. Study site abbreviations: BR - Brighton; SG - Spring Garden; FV - Fitts Village; SL - Sandy Lane; BRI - Bellairs Research Institute; GS - Greensleeves; SR - Sand Ridge.


59° 30'
N
SR
GS
BRI
BARBADOS
SL
13° 10'
FV
SG
BR
Bridgetown
0
5
Scale (km)

1.3.3 Environmental variables

1.3.3.1 *Habitat characteristics*

To quantify the habitat characteristics of ***F. fragum***, a 100-point grid system was used in each quadrat. The grid consisted of ten lines in each direction (parallel and perpendicular to the reference transect), starting 0.25m from the edge of the quadrat and spaced at 0.5m intervals. The intersections of the lines formed 100 points over the quadrat. A two-layer point-contact sampling method was then used to assess the bottom composition. Twenty points were randomly selected for each quadrat, with each point representing 1.25m^2 of the quadrat area. To sample under the points, a diver pushed the intersection of the two lines (corresponding to the randomly selected point) down until it touched the substrate. The first layer determined whether a point was above sand, rubble, or reef. Rubble was defined as hard substrate that could be moved by a diver. Reef was defined as hard substrate that could not be moved. When the point was above reef, a second layer was sampled to determine the organism present at that point. Reef flora (turf, frondose, crustose coralline algae) and fauna (species of coral, sponge, other invertebrates) were recorded for each point above reef. Turf algae consisted of a heterospecific assemblage of fleshy and filamentous algae less than 2cm in height (Lewis, 1986), and frondose macroalgae consisted of those plants greater than 2cm in height (Berner, 1990). Total macrophytic algae was estimated by grouping frondose macroalgae and turf algae. The percent cover data of the second-layer habitat characteristics were recorded relative to the area of reef in each quadrat.

The depth of each quadrat was determined by taking the mean value of the depths of the two corners of the quadrat that rested on the reference transect. Distance from shore and rugosity were measured for each of the reference transects.

Densities of *Diadema antillarum* per transect were calculated using data from a concurrent field study (Allard, 1993). All urchins within a 1-m wide area along 20-m transects running parallel to shore were counted. Only transects that corresponded to the zones sampled in this study were used to estimate *D. antillarum* densities. This was generally between 40 and 60 transects per reef.

1.3.3.2 *Water quality*

The sampling methodology was based on that of Tomascik and Sander (1985) to facilitate comparisons between studies. Reactive phosphate, nitrate-nitrite nitrogen, suspended particulate matter, volatile particulate matter, and chlorophyll-a were monitored every two weeks from April to October, 1992 (8 samples for chlorophyll-a, 21-27 samples for the others at each site). Percent organic matter in the sediment was measured every four weeks (6 samples) during this same period. The sampling schedule alternated between starting at sites north and south of Bellairs Research Institute. Since there was relatively little rainfall during the original sampling period, sampling was also conducted in January, 1993, during a period of heavy rainfall. The January sampling consisted of ten samples for reactive phosphate, total inorganic nitrogen, suspended particulate matter, volatile particulate matter from each site collected on a single day.

A permanent sampling station was established at each site over the spur and groove zone (depth 4 m). During each sediment sampling session, two samples were taken from the water-sediment interface between spurs (depth 4-5m) at each site with Ziploc® bags. At each sampling session for water quality, two surface water samples (depth 1 m) were taken between 10.00 and 13.00 hours using a Van Dorn bottle. Water samples were transferred into 1-l and 4-l polyethylene bottles and transported to the laboratory in an insulated cooler. The 1-l samples were filtered through a GF/C glass fibre filter (washed, combusted and weighed beforehand), and stored in a freezer until analysis. Suspended particulate matter (SPM) was determined by drying each filter to a constant weight at 60°C. The dried filters were weighed to give SPM, combusted at 550°C for 15 min, then reweighed to obtain volatile particulate matter (VPM) (dry weight - combusted weight). Chlorophyll-a analyses were conducted using 3.5 l of water (from the 4-l bottles) following Strickland and Parsons (1972). Sediment samples (approximately 20 grams) were placed in pre-weighed aluminum tins, dried to constant weight at 60°C, weighed, then combusted at 550°C for 15 min to determine the percent organic material. Stored water samples were thawed to room temperature before being analyzed for reactive phosphate (PO_4-P) and nitrate-nitrite nitrogen (NO_3- NO_2- N) using standard methods (Strickland and Parsons, 1972).

1.3.4 Data treatment and analyses

Prior to analyses, *F. fragum* abundance was transformed to number of colonies/m^2 of reef substrate to control for differences in reef substrate area between sites.

All data were tested for normality (one sample Kolmogorov-Smirnov test) and homogeneity of variance (visual or Bartlett's test) using SYSTAT (Wilkinson, 1990). Transformations were applied to all data violating these assumptions (Zar, 1984). All percent cover data were transformed using arcsine $\sqrt{x}$, while density variables were treated with log $(x+1)$. Any variables remaining non-normal after transformation were analyzed non-parametrically using a Kruskal-Wallis test.

A principal component analysis (PCA, correlation matrix) was used to reduce the highly autocorrelated, log-transformed water quality variables to a single linear combination of the variables. The principal component score for each site was used as the index of eutrophication.

A discriminant function analysis was used to investigate the effects of habitat characteristics on *F. fragum*. The habitat variables were combined into a composite linear function that maximized differences between quadrats where *F. fragum* was present and those where it was absent (Tabachnick and Fidell, 1983). The loadings of habitat variables onto that function determines the relative importance of habitat characteristics in predicting the presence or absence of *F. fragum* in a quadrat.

Simple linear regression analyses were used to test relationships between the principal component eutrophication index, *D. antillarum* density, *F. fragum* density, and the habitat characteristics measured.

1.4 Results

1.4.1 Environmental Variables

1.4.1.1 *Water Quality*

The mean values for the water quality variables for 1981-82 (Tomascik and Sander, 1985), 1992, and 1993 are shown in Table 1. The combined data are used in all subsequent discussions and analyses. SG, located directly offshore from the national power plant outfall, had consistently high values for all eutrophication/sedimentation variables (Table 1). BR, located in the vicinity of a rum refinery effluent outfall and the Barbados Deep Water Harbour, also had high values for the eutrophication variables. FV and BRI generally had intermediate values, and SL, GS, and SR had the lowest values for the variables.

The six eutrophication/sedimentation variables were reduced to one significant principal component (PC1) using PCA. PC1 accounted for 85.9% of the variation in the data. The eigenvector loadings of these variables onto PC1 is shown in Table 2. The high loadings of the eutrophication/sedimentation variables on PC1 suggest that PC1 is a good index of eutrophication/sedimentation. Principal component scores (eutrophication/sedimentation indices) for the seven study reefs are shown in Fig. 2.

1.4.1.2 *Habitat Characteristics*

The habitat characteristics of each study site are summarized in Table 3. The sites differed significantly (ANOVA, $P<0.05$) in hard substrate (reef), rubble, sand, macrophytic algae, crustose coralline algae, and rugosity; but the difference in coral cover was not statistically significant ($P=0.069$). Tukey's tests indicated that BR and SG did not differ significantly from each other in any habitat characteristic, but had less cover by hard substrate than all other sites (Tables 3, 4). BR had significantly more sand cover than SL and BRI, and both BR and SG were significantly less rugose than several of the other sites (Tables 3, 4). These results suggest that BR and SG are being eroded

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

Variables	Study Sites								
	BR	SG	FV	SL	BRI	GS	SR	*N*	Year
PO_4-P (μg-at l^{-1})	0.10 (0.04)	0.21 (0.11)	0.09 (0.06)	0.08 (0.04)	0.11 (0.09)	0.06 (0.03)	0.06 (0.03)	45	1981-82
NO_3-NO_2-N (μg-at l^{-1})	0.82 (0.43)	4.42 (2.65)	0.79 (0.50)	0.55 (0.39)	0.65 (0.39)	0.45 (0.23)	0.36 (0.21)	44	1981-82
SPM (mg l^{-1})	7.11 (4.08)	7.32 (2.86)	6.25 (3.92)	5.12 (3.46)	5.94 (3.41)	5.21 (3.29)	4.26 (1.98)	44	1981-82
VPM (mg l^{-1})	3.26 (1.67)	3.10 (1.26)	2.71 (1.47)	1.94 (1.15)	2.49 (1.15)	2.00 (0.97)	1.85 (1.03)	43	1981-82
% Organics in sediments	8.30 (2.30)	10.90 (4.00)	4.90 (0.90)	2.50 (0.30)	5.10 (2.00)	2.30 (0.60)	2.90 (1.00)	10	1981-82
Chlorophyll-a (mg m^{-3})	1.04 (0.54)	0.90 (0.41)	0.88 (0.33)	0.58 (0.29)	0.80 (0.47)	0.55 (0.27)	0.42 (0.16)	46	1981-82
PO_4-P (μg-at l^{-1})	0.05 (0.03)	0.06 (0.03)	0.05 (0.03)	0.05 (0.04)	0.05 (0.04)	0.05 (0.04)	0.05 (0.03)	21	1992
NO_3-NO_2-N (μg-at l^{-1})	0.81 (0.69)	3.17 (2.50)	1.00 (0.60)	0.90 (0.45)	0.69 (0.38)	0.93 (1.28)	0.75 (0.56)	23	1992
SPM (mg l^{-1})	6.70 (4.37)	10.94 (20.48)	6.86 (4.96)	6.98 (4.81)	6.45 (5.22)	6.26 (4.66)	6.90 (5.60)	27	1992
VPM (mg l^{-1})	1.30 (0.58)	1.29 (0.64)	1.44 (0.84)	1.56 (0.87)	1.22 (0.76)	1.13 (0.66)	1.16 (0.62)	26	1992
% Organics in sediments	2.42 (0.43)	2.61 (0.44)	2.03 (0.43)	2.36 (0.54)	2.21 (0.34)	2.33 (0.47)	2.31 (0.62)	6	1992
Chlorophyll-a (mg m^{-3})	0.31 (0.07)	0.30 (0.18)	0.30 (0.17)	0.36 (0.13)	0.37 (0.17)	0.46 (0.29)	0.23 (0.07)	8	1992
PO_4-P (μg-at l^{-1})	0.09 (0.04)	0.13 (0.07)	0.08 (0.03)	0.09 (0.05)	0.09 (0.02)	0.08 (0.03)	0.10 (0.05)	10	1993
NO_3-NO_2-N (μg-at l^{-1})	0.87 (0.26)	7.51 (2.65)	1.05 (0.30)	0.75 (0.21)	0.91 (0.18)	0.82 (0.30)	0.74 (0.27)	10	1993
SPM (mg l^{-1})	6.88 (0.75)	7.83 (2.91)	4.79 (0.58)	4.41 (1.49)	4.11 (1.10)	3.83 (0.82)	4.62 (1.14)	10	1993
VPM (mg l^{-1})	2.81 (0.38)	2.92 (0.90)	1.90 (0.62)	2.33 (0.72)	1.45 (0.78)	1.05 (0.56)	1.44 (0.78)	10	1993
PO_4-P (μg-at l^{-1})	0.09	0.16	0.08	0.07	0.09	0.06	0.06	76	Combined
NO_3-NO_2-N (μg-at l^{-1})	0.82	4.45	0.89	0.68	0.69	0.64	0.52	77	Combined
SPM (mg l^{-1})	6.94	8.59	6.27	5.65	5.88	5.39	5.19	81	Combined
VPM (mg l^{-1})	2.56	2.48	2.19	1.86	1.94	1.59	1.57	79	Combined
% Organics in sediments	6.09	7.79	3.82	2.45	4.01	2.31	2.68	16	Combined
Chlorophyll-a (mg m^{-3})	0.93	0.81	0.79	0.55	0.74	0.53	0.39	54	Combined

Table 2. Water quality variable loadings on principal component 1 (PC1). N=7 sites.

Water quality variables	Component Loading
PO_4-P (μg-at l^{-1})	0.959
NO_3-NO_2-N (μg-at l^{-1})	0.874
SPM (mg l^{-1})	0.982
VPM (mg l^{-1})	0.924
Organics in sediment (%)	0.965
Chlorophyll-*a* (mg m^{-3})	0.850

Figure 2. Principal component scores, as eutrophication/sedimentation indices, at each of the seven study sites. Site abbreviations as in Fig. 1.

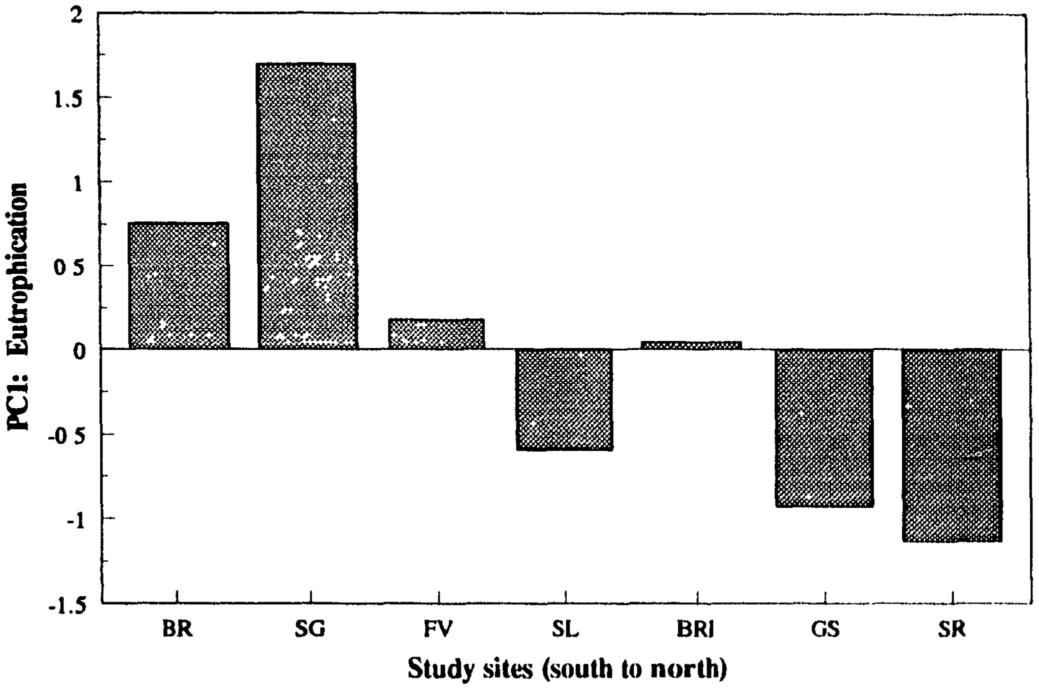

2
1.5
1
0 5
0
-0 5
-1
-1.5
PC1: Eutrophication
BR
SG
FV
SL
BRI
GS
SR
Study sites (south to north)

Table 3. Mean (SD) depth (m), density of *Diadema antillarum* , rugosity of reference transect (RUG) (100m substrate profile/linear distance above line), mean density of *Favia fragum* per m^2 quadrat, percent cover sand (Sand %), % cover rubble (Rubble %), % cover by hard substate (Reef %), % cover crustose coralline algae (CCA), % cover frondose macroalgae (FRON), % cover turf algae (TURF), % cover total macrophytic algae (MACRO), % cover coral (CORAL), % cover of other invertebrates (OTHER) calculated for each study site (SITE), and presented by each transect (TRANS) separately (1,2,3) and all three combined (Mean) Layer 1 and 2 as described in Methods. Site abbreviations as in Fig. 1.

Site	Trans					Layer 1			Layer 2					
		Depth (m)	DIAD (#/m^2)	RUG	FAVIA (#/m^2)	SAND %	RUBBLE %	REEF %	CCA %	FRON %	TURF %	MACRO %	CORAL %	OTHER %
BR	1	1.9(0.4)	0.5	1.05	0.6(0.8)	24.0(22.3)	29.0(20.4)	47.5(26.5)	22.4(17.9)	20.8(15.1)	46.6(21.6)	67.4(23.7)	10.3(11.1)	0.0(0.0)
	2	3.1(0.6)	0.1	1.06	0.1(0.2)	29.5(22.4)	31.5(18.7)	39.0(29.5)	11.6(12.5)	44.5(27.1)	28.8(20.5)	73.3(33.4)	15.1(21.6)	0.0(0.0)
	3	4.1(0.4)	0.4	1.03	0.0(0.1)	20.5(12.8)	35.5(13.6)	44.0(11.7)	8.2(17.2)	40.0(31.7)	29.6(28.0)	69.6(31.0)	22.2(17.5)	0.0(0.0)
	MEAN	3.0(1.0)	0.3(0.2)	1.05	0.2(0.5)	24.7(19.4)	32.0(17.4)	43.5(23.3)	14.1(16.6)	35.1(26.3)	35.1(24.4)	70.2(28.7)	15.8(7.1)	0.0(0.0)
SG	1	1.7(0.3)	0.4	1.06	0.1(0.2)	27.5(18.0)	49.5(23.6)	23.0(21.5)	8.9(14.5)	1.8(3.9)	63.2(41.1)	65.0(42.7)	26.1(26.3)	0.0(0.0)
	2	2.5(0.4)	0.4	1.05	0.1(0.3)	6.0(7.0)	23.5(16.8)	71.1(19.1)	26.0(11.0)	20.0(24.8)	29.8(21.6)	49.8(17.9)	24.1(14.1)	0.0(0.0)
	3	3.7(0.8)	0.7	1.04	0.4(1.0)	15.0(22.2)	36.0(25.1)	49.0(30.6)	7.7(12.6)	48.6(37.0)	20.7(19.8)	69.3(29.5)	22.9(26.4)	0.0(0.0)
	MEAN	2.6(1.0)	0.5(0.2)	1.05	0.2(0.6)	16.2(18.7)	36.3(24.0)	47.7(30.8)	14.2(15.1)	23.5(31.1)	37.9(29.5)	61.4(32.1)	24.4(22.4)	0.0(0.0)
FV	1	1.9(0.3)	2.5	1.10	0.4(0.2)	7.5(10.1)	14.5(12.1)	78.0(18.0)	34.3(20.1)	0.0(0.0)	56.0(19.3)	56.0(19.3)	9.7(6.4)	0.0(0.0)
	2	2.3(0.4)	2.1	1.15	0.5(0.4)	18.0(10.6)	5.5(6.4)	76.5(15.3)	63.2(10.4)	0.0(0.0)	25.8(15.8)	25.8(15.8)	11.0(9.7)	0.0(0.0)
	3	2.8(0.3)	1.1	1.08	0.4(0.5)	25.0(13.7)	3.0(2.6)	72.0(13.8)	32.7(22.3)	0.0(0.0)	61.3(23.5)	61.3(23.5)	6.0(4.5)	0.0(0.0)
	MEAN	2.3(0.5)	1.9(0.7)	1.11	0.4(0.4)	16.8(13.4)	7.7(9.3)	75.5(15.4)	43.4(22.6)	0.0(0.0)	47.7(24.7)	47.7(24.7)	8.9(7.3)	0.0(0.0)
SL	1	2.0(0.5)	1.8	1.18	0.9(0.5)	9.0(11.0)	9.0(13.3)	82.0(17.8)	48.1(17.9)	0.0(0.0)	33.4(16.9)	33.4(16.9)	17.5(13.2)	1.0(2.1)
	2	2.7(0.6)	4.9	1.23	0.6(0.4)	13.5(19.4)	5.0(7.5)	80.5(21.9)	42.0(14.2)	0.0(0.0)	35.8(14.1)	35.8(14.1)	22.2(15.4)	0.0(0.0)
	3	3.2(0.6)	4.0	1.16	0.2(0.1)	16.5(10.3)	18.0(16.2)	65.5(14.4)	37.2(15.9)	1.0(3.1)	45.5(20.9)	46.5(22.8)	16.3(11.4)	0.0(0.0)
	MEAN	2.6(0.7)	3.5(1.6)	1.19	0.6(0.5)	13.0(14.1)	10.7(13.6)	76.0(19.2)	42.4(16.2)	0.3(1.8)	38.2(17.7)	38.5(18.5)	18.7(13.2)	0.3(1.3)
BRI	1	1.9(0.4)	0.9	1.27	0.3(0.2)	9.5(9.0)	11.0(10.7)	80.0(14.1)	26.2(11.1)	0.0(0.0)	58.6(11.6)	58.6(11.6)	10.2(8.0)	5.0(5.8)
	2	1.9(0.4)	1.6	1.27	0.2(0.3)	8.5(12.7)	12.5(12.1)	79.0(18.2)	25.4(13.4)	0.0(0.0)	54.8(15.8)	54.8(15.8)	17.1(8.8)	2.6(4.2)
	3	3.7(0.3)	1.1	1.22	0.1(0.1)	11.0(7.7)	15.5(17.1)	73.5(15.1)	24.6(9.7)	0.6(1.8)	42.3(20.9)	42.9(21.3)	32.5(17.2)	0.0(0.0)
	MEAN	2.5(1.0)	1.2(0.4)	1.25	0.2(0.2)	9.7(9.7)	13.0(13.2)	77.5(15.6)	25.4(11.1)	0.2(1.1)	51.6(17.4)	51.8(17.4)	19.9(14.9)	2.6(4.2)
GS	1	1.6(0.3)	2.6	1.15	1.4(1.1)	6.0(5.7)	8.0(11.4)	86.0(15.8)	33.5(16.3)	0.0(0.0)	43.5(14.7)	43.5(14.7)	15.1(9.1)	7.8(9.9)
	2	2.1(0.4)	3.5	1.18	2.1(2.0)	13.0(6.7)	13.5(17.3)	74.5(19.5)	33.6(13.3)	0.0(0.0)	45.9(21.1)	45.9(21.1)	19.9(14.5)	0.6(1.9)
	3	3.8(0.5)	2.8	1.11	1.1(0.7)	22.5(13.4)	14.0(9.7)	63.5(15.3)	29.8(18.7)	0.0(0.0)	50.1(15.5)	50.1(15.5)	20.1(18.1)	0.0(0.0)
	MEAN	2.5(1.0)	3.0(0.4)	1.15	1.5(1.4)	13.8(11.3)	11.8(13.0)	74.7(18.8)	32.3(15.8)	0.0(0.0)	46.5(17.0)	46.5(17.0)	18.4(14.1)	2.8(6.7)
SR	1	1.6(0.3)	3.0	1.25	1.3(0.8)	11.0(5.7)	10.5(11.9)	78.5(11.8)	26.4(13.1)	0.0(0.0)	61.0(17.4)	61.0(17.4)	10.9(7.6)	1.8(2.9)
	2	2.5(0.6)	3.5	1.18	1.0(0.7)	10.0(9.4)	16.5(10.8)	73.5(16.7)	20.8(10.5)	0.0(0.0)	60.9(19.4)	60.8(19.4)	17.0(19.0)	1.4(3.0)
	3	4.0(0.5)	1.3	1.33	0.8(0.6)	18.5(7.8)	14.5(14.6)	67.0(19.5)	12.5(14.7)	0.0(0.0)	52.8(26.3)	52.8(26.3)	32.2(20.4)	2.5(5.9)
	MEAN	2.7(1.1)	2.6(1.2)	1.25	1.0(0.7)	13.2(8.5)	13.8(12.4)	73.0(16.4)	19.9(13.8)	0.0(0.0)	58.2(21.0)	58.2(21.0)	20.0(18.4)	1.9(4.0)

Table 4. Results of Tukey's tests for differences in habitat characteristics between study sites. Symbols indicate differences at $P<0.05$. Site abbreviations as in Figure 1. Reef (□), rubble (◇), sand (○), total macrophytic algae (■), crustose coralline algae (◆), and rugosity (★).

Site	BR	SG	FV	SL	BRI	GS	SR
BR	–		■ ◆	■ ◆	◆ ★	■ ◆	★
SG		–	◆	◆ ★	◆ ★	◆	★
FV	□ ◇	□ ◇	–		◆ ★		◆ ★
SL	□ ◇ ○	□ ◇		–	◆		■ ◆
BRI	□ ◇ ○	□ ◇			–		
GS	□ ◇	□ ◇				–	
SR	□ ◇	□ ◇					–

(see Tomascik and Sander, 1987a for similar suggestion), and this is also supported by significantly higher amounts of rubble at BR and SG compared to most other sites. BR had significantly more macrophytic algal cover than several other sites, and both BR and SG had significantly less cover by crustose coralline algae than most other sites (Tables 3, 4).

The density of *Diadema antillarum* differed significantly between sites (Table 3; Kruskal Wallis test, KW test statistic=41.241, $P<0.001$, df=6). SG, BR, and BRI did not differ significantly in *D. antillarum* density, but had lower density than the other sites (Tables 3, 5). SR, GS, FV, and SL did not differ significantly in density (Tables 3, 5).

1.4.2 Abundance of *Favia fragum*

The abundance of *F. fragum* differed significantly between sites (Table 3; Kruskal Wallis test, KW test statistic=46.272, $P<0.001$, df=6). Abundance at SG, BR, and BRI did not differ, but was significantly lower at these sites that at most other sites (exception FV for BR; Tables 3, 5). Abundance at GS was significantly higher than at all sites except SR (Tables 3, 5).

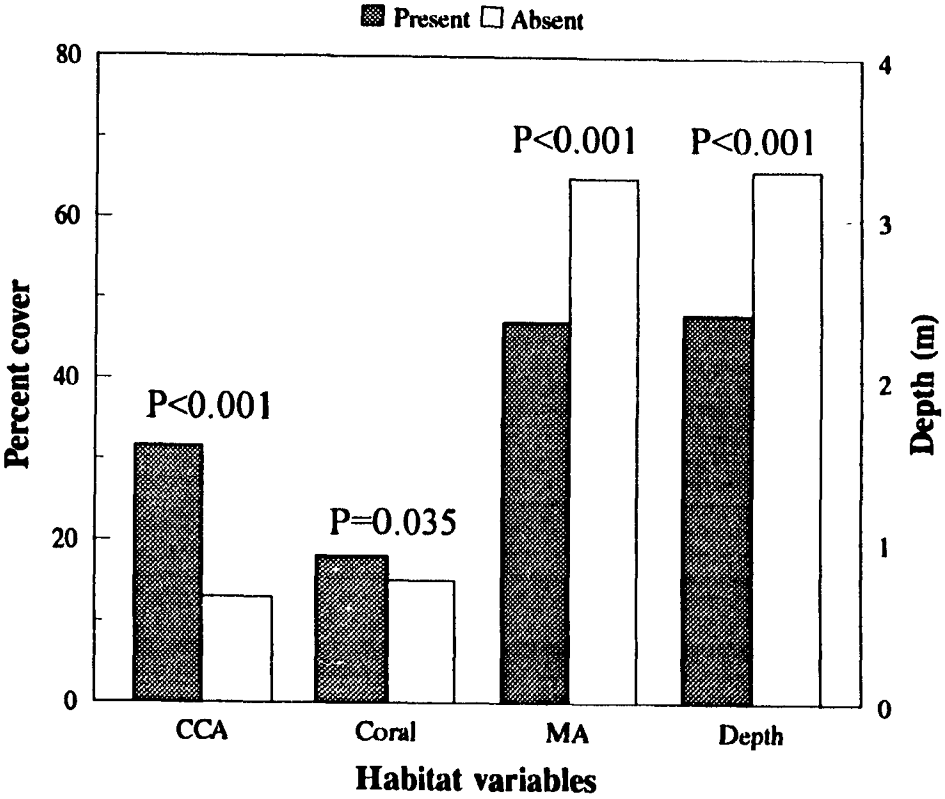
1.4.3 Effects of habitat characteristics on *Favia fragum* distribution and abundance

The distribution of *F. fragum*, based on presence and absence within surveyed quadrats, was significantly related to crustose coralline algal cover, coral cover, total macrophytic algal cover, and depth (Fig. 3). Discriminant function analysis allowed the testing of the predictive value of the habitat variables in determining the distribution of *F. fragum* to be tested. The linear composite function discriminated significantly ($P<0.001$) between *F. fragum* presence/absence based on these variables. The canonical correlation, a multiple correlation between the habitat variables (predictors) and the discriminant function, was 0.56. The canonical loadings of the habitat variables on the discriminant

Table 5. Results of Tukey's (non-parametric) tests for differences in *Favia fragum* abundance and *Diadema antillarum* density between study sites. Symbols indicate differences at $P<0.05$. Site abbreviations as in Figure 1. *Favia fragum* (*) and *D. antillarum* (#).

Site	BR	SG	FV	SL	BRI	GS	SR
BR	–		#	#		#	#
SG		–		#		#	
FV		*	–				
SL	*	*		–			
BRI			*	*	–	#	
GS	*	*	*	*	*	–	
SR	*	*	*		*		–

Figure 3. Mean values of habitat variables in quadrats with (N=158) or without (N=52) *Favia fragum* along the west coast of Barbados. Data were analysed using ANOVA. Significance (P) values from paired comparisons are presented above each variable tested. CCA is crustose coralline algae; MA is macrophytic algae.



▨ Present ☐ Absent
80
60
40
20
0
Percent cover
4
3
2
1
0
Depth (m)
P<0.001
P=0.035
P<0.001
P<0.001
CCA
Coral
MA
Depth
Habitat variables

Table 6. Canonical loadings for habitat variables on the discriminant function. N=7 sites.

Habitat variables	Principal component loading
Crustose coralline algae	+0.760
Coral	+0.218
Macrophytic algae	-0.435
Depth	-0.625

function are shown in Table 6. Based on these loadings, crustose coralline algae and depth are the most important predictors of *F. fragum* presence/absence in a quadrat. *D. antillarum* was not included in the presence/absence analyses because its abundance was not measured in each quadrat.

To ensure that possible correlations between the biotic variables (crustose coralline algae, macrophytic algae, coral cover) and depth were not confounding the results, Tukey's tests were performed for each habitat variable to investigate differences between depth zones (reference transects). While there were significant differences between zones, none of the habitat variables showed the same response as *F. fragum* to depth (Fig. 4).

Relationships between the biotic variables were examined using simple regressions, based on mean values per transect (Fig. 5). Macrophytic algae and crustose coralline algae were negatively correlated (Fig. 5A). Moreover, the density of *Diadema antillarum* was positively correlated with crustose coralline algae (Fig. 5B) and negatively correlated with macrophytic algae (Fig. 5C). The abundance of *F. fragum* was positively correlated with both crustose coralline algal cover (Fig. 5D) and *Diadema antillarum* density (Fig. 5E). The abundance of *F. fragum* was negatively correlated with macrophytic algal cover, but the correlation was not statistically significant ($r^2=0.03$, $P=0.211$).

1.4.4 Effects of Water quality on habitat variables, *D. antillarum*, and *F. fragum* abundance

Based on the mean values for each site (n=7), *D. antillarum* density was negatively correlated with PC1 (Fig. 6A). *F. fragum* density was also negatively correlated with the PC1 (Fig. 6B). None of the habitat variables was significantly correlated with PC1.

Figure 4. Mean values of habitat variables in different depth zones (transects) on fringing reefs along the west coast of Barbados. N=70 for each zone. Transect 1 (1-2 m), Transect 2 (2-3 m), Transect 3 (3-4 m). Data analysed using Tukey's test ($P<0.05$).

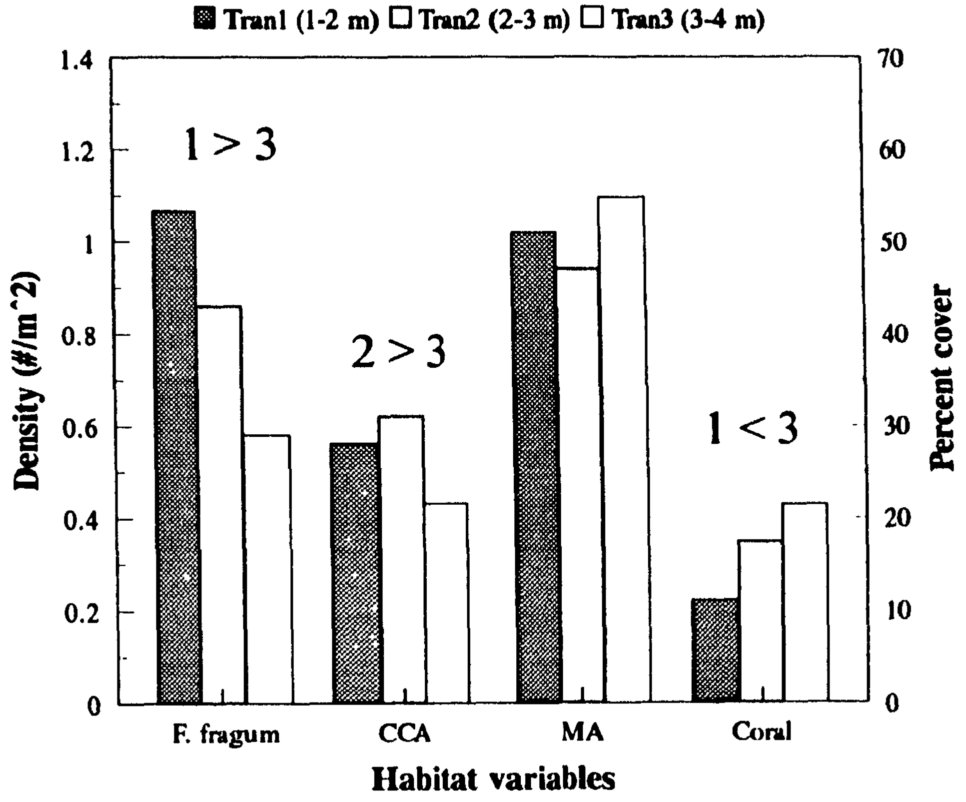

▨ Tran1 (1-2 m) ☐ Tran2 (2-3 m) ☐ Tran3 (3-4 m)
Density (#/m^2)
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Percent cover
70
60
50
40
30
20
10
0
1 > 3
2 > 3
1 < 3
F. fragum
CCA
MA
Coral
Habitat variables

Figure 5. Relationships between dominant benthic colonizers, *Diadema antillarum*, and *Favia fragum* based on transect means (N=21). Linear regressions A) macrophytic algal cover on crustose coralline algal cover, B) *Diadema antillarum* density on crustose coralline algal cover, C) *Diadema antillarum* density on macrophytic algal cover, D) *Favia fragum* density on crustose coralline algal cover, and E) *Favia fragum* density on *Diadema antillarum* density. Cover = arcsine $\sqrt{\%}$; Density = Log (#/m^2).

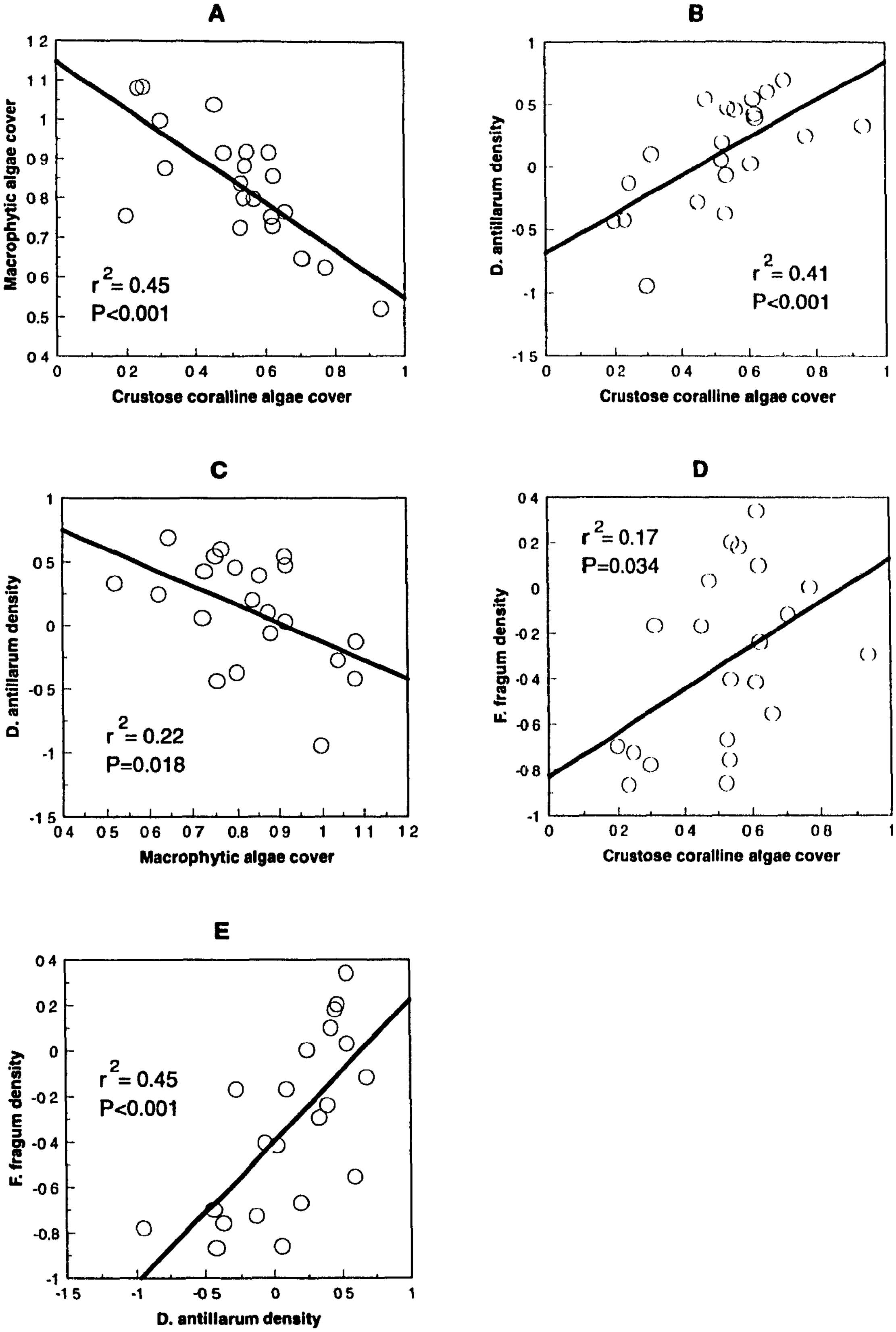
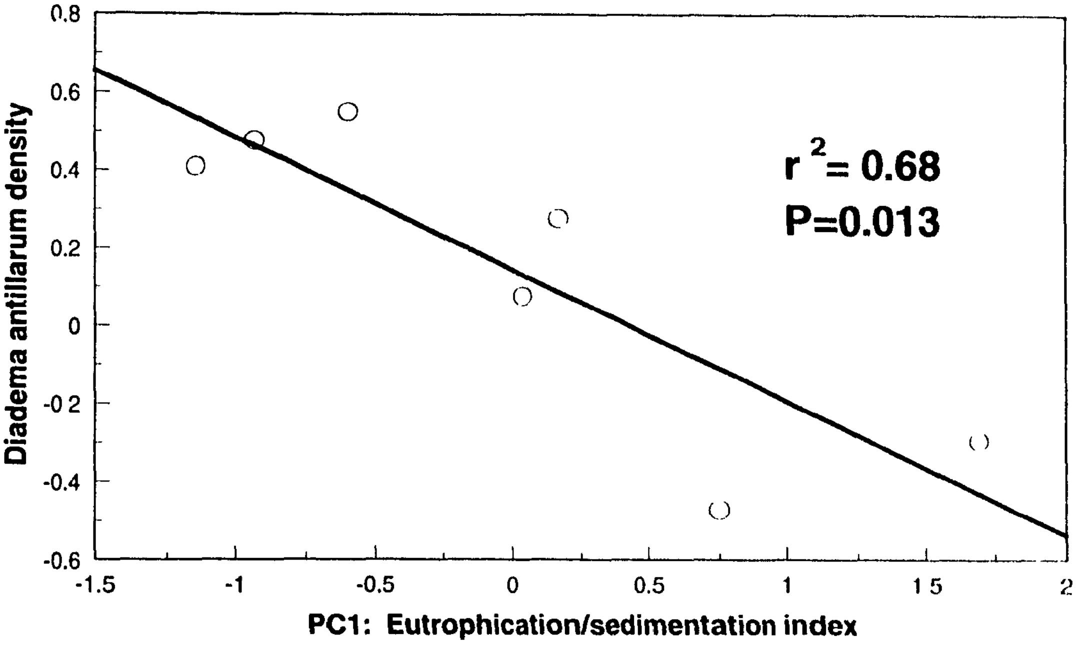

A
Macrophytic algae cover
Crustose coralline algae cover
r^2 = 0.45
P<0.001
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0
0.2
0.4
0.6
0.8
1
B
D. antillarum density
Crustose coralline algae cover
r^2 = 0.41
P<0.001
1
0.5
0
-0.5
-1
-1.5
C
D. antillarum density
Macrophytic algae cover
r^2 = 0.22
P=0.018
0.4
0.5
0.6
0.7
0.8
0.9
1
1.1
1.2
D
F. fragum density
Crustose coralline algae cover
r^2 = 0.17
P=0.034
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
E
F. fragum density
D. antillarum density
r^2 = 0.45
P<0.001
-1.5
-1
-0.5
0
0.5
1

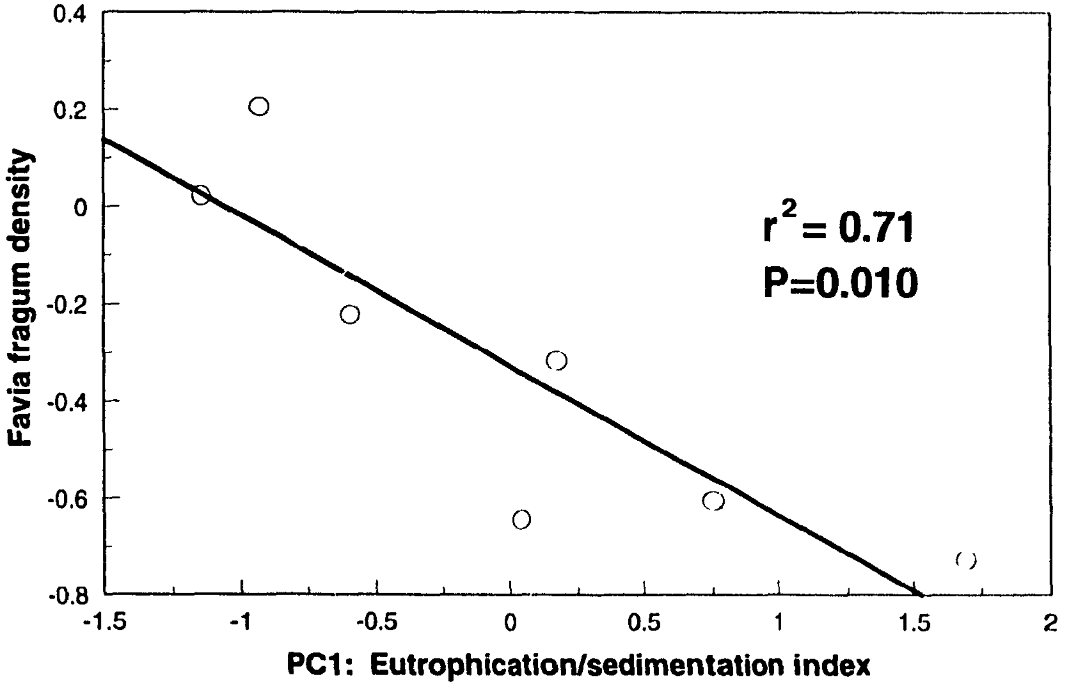
Figure 6. Relationships between *Diadema antillarum* and *Favia fragum* densities and PC1 (eutrophication index) based on site means (N=7). Linear regressions of a) *Diadema antillarum* density on eutrophication/sedimentation index (PC1), and b) *Favia fragum* density on eutrophication/sedimentation index (PC1). Density = Log (#/m^2).

A



r² = 0.68
P=0.013
Diadema antillarum density
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-1.5
-1
-0.5
0
0.5
1
1.5
2
PC1: Eutrophication/sedimentation index

B



r² = 0.71
P=0.010
Favia fragum density
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
-1.5
-1
-0.5
0
0.5
1
1.5
2
PC1: Eutrophication/sedimentation index

1.5 Discussion

Favia fragum was more common at shallower than deeper locations. This may be due to increased water motion in shallower areas. As *F. fragum* feeds both autotrophically and heterotrophically (Lewis, 1974b; Lewis, 1977; Lewis and Price, 1975) increased water motion could lead to higher encounter rates with zooplankton prey and with suspended particulate matter. Furthermore, high water motion is likely to reduce sediment accumulation, which could be critical to the survival of juveniles.

The abundance of *F. fragum* on the study reefs was negatively correlated with eutrophication levels (PC1) on reefs in this study. Elevated nutrient levels may be toxic to corals, but this is only likely at high concentrations (Simkiss, 1964; Kinsey and Davies, 1979); i.e. at concentrations higher than characteristic of the Barbados west coast (Tomascik and Sander, 1985). Pastorok and Bilyard (1985) suggest that hermatypic corals are generally affected indirectly through the increased primary productivity that accompanies eutrophication. Phytoplankton blooms can lower the amount of light available to corals for photosynthesis, and increase the sediment load (Bell, 1991). Coral energy budgets may also be altered because more resources are diverted to sediment rejection, and this may seriously affect coral maintenance costs (Edmunds and Davies, 1989). Perhaps most importantly, freed from the restraint of nutrient limitation, macrophytic algal biomass may rapidly rise until it is the dominant component of the reef community (Maragos, 1972; Birkeland, 1977).

Benthic macroalgae has long been considered to inhibit coral recruitment by monopolizing available substrate (Bakus, 1966; Vine, 1974; Potts, 1977). Competition for space between coral planulae and juveniles and macrophytic algae may decrease settlement and/or increase post-settlement mortality. Lewis (1974c) has shown that *F. fragum* planulae prefer a clean settlement surface, and Hunte and Wittenberg found coral settlement to be lower on more eutrophic reefs in Barbados, probably because of non-availability of suitable settlement surface. By contrast, Sammarco (1980) suggested that coral settlement was not significantly reduced by heavier algal growth, but that post-settlement mortality was higher. Similarly, Harriott (1983) reported higher settlement rates of *Pocillopora damicornis* on algal covered than clean plates, but higher subsequent mortality from smothering through algae. Mortality of juvenile corals in Barbados is reported to be higher on more eutrophic reefs with higher macrophytic algal biomass (Wittenberg and Hunte, 1992). In this study, macrophytic algae abundance was lower in areas where *F. fragum* occurred than in areas where it did not, and frondose macroalgae was the dominant benthic organism at the more eutrophic study sites, where *F. fragum* densities were low.

Macrophytic algae may also affect *F. fragum* abundance by decreasing crustose coralline algal cover; macrophytic algal cover and crustose coralline algal cover were negatively correlated in this study. The distribution and abundance of *F. fragum* was strongly dependent on crustose coralline algal cover. Crustose coralline algae was the best predictor of *F. fragum* presence and absence on the reefs, and was positively correlated with the abundance of *F. fragum* across reefs. This correlation may occur through shared environmental preferences, or because coralline algae is an appropriate settlement substrate for *F. fragum*. A crustose coralline algae-associated chemical cue has been postulated to induce larval metamorphosis in many invertebrate groups (soft corals: Sebens, 1983; polychaetes: Gee, 1965; abalone: Morse *et al.*, 1979; Morse and Morse, 1984; limpets: Steneck, 1982; chitons: Barnes and Gonor, 1973; Rumrill and Cameron, 1983; asteroids: Yamaguchi, 1973; Barker, 1977; Johnson *et al.*, 1991; sea urchins: Pearse and Scheibling, 1988; Rowley, 1989), and specifically in agariciid planulae (Morse *et al.*, 1988; Morse and Morse, 1991).

D. antillarum density was negatively correlated with eutrophication levels on the reefs in this study, and was positively correlated with *F. fragum* abundance. Given the correlation between urchin abundance and eutrophication, it is not possible to separate their effects on *F. fragum* abundance. It is likely that they are both important, since both may affect macrophytic algal cover. *D. antillarum* density was negatively correlated with macrophytic algal cover in this study, suggesting that grazing by the urchins may control algal abundance. Sammarco *et al.* (1974) found that algal biomass when urchins were removed from reefs was more than tenfold higher than when urchins were present. However, Sammarco (1980) manipulated *D. antillarum* densities in enclosures, and suggested that optimal conditions for corals occurred at relatively low (4 and 6 m^{-2}) densities due to a balance between negative effects of macrophytic algae and disturbance from abrasive urchin grazing. Mean densities of *D. antillarum* on reefs in the present study ranged from 0.34 m^{-2} to 3.54 m^{-2}.

The question of why *D. antillarum* density is negatively correlated with eutrophication levels (PC1) in this study merits comment. Bak (1985) showed that *D. antillarum* larvae settle more readily on a clean substrate devoid of macrophytic algae. Hunte and Younglao (1988) showed that recruitment of *D. antillarum* was higher on reefs with higher adult abundance, and suggested that this was the consequence of cleaner substrates resulting from heavier grazing by adults. Wittenberg and Hunte (1992) suggested that a positive feedback cycle may exist whereby *D. antillarum* influences its own density, and that the cycle may be sensitive to the eutrophication status of the reef. On a non-eutrophic reef, high *D. antillarum* abundance reduces benthic macroalgal cover, and the resulting clean substrate promotes successful recruitment. If elevated nutrient levels increase benthic macroalgal growth to the point where it overwhelms *D. antillarum*'s grazing capabilities, recruitment will decrease due to the lack of suitable settlement substrate. This results in reduced adult abundance and a further increase in macrophytic algae abundance. High benthic algal production has previously been suggested to compromise the ability of grazers to control macrophytic algae (Birkeland, 1977; Hatcher, 1984; Knowlton, 1992). A decrease in *D. antillarum* abundance at higher nutrient levels should therefore result in a more rapid change in benthic community structure than would occur from nutrient elevation alone (Littler and Littler, 1984; 1985; Knowlton, 1992). In contrast to the situation with *D. antillarum*, densities of *D. setosum* were found to be positively correlated to sewage pollution in the Red Sea (Walker and Ormond, 1982).

Not only is the abundance of *F. fragum* presently lower on the more eutrophic Barbados west coast reefs, but its abundance may also have declined on all reefs over the past few decades. Lewis (1970) reported a mean density of *F. fragum* of 23 m^{-2}, but the highest density found in a quadrat in this study was 7.4 m^{-2}. This decline coincides with increased land clearing and development of the west coast of Barbados, and with a presumed corresponding decrease in water quality (Tomascik and Sander, 1985). However, it also coincides with a sharp reduction in *D. antillarum* on west coast reefs in the past decade, caused by the mass mortality of *D. antillarum* in Barbados (mean mortality 93.2%; Hunte *et al.*, 1986) and throughout the Caribbean in 1983 (Lessios, 1988). This again makes separating the effects of eutrophication and reduced *D. antillarum* on *F. fragum* abundance in Barbados difficult. However, the reduction in *D. antillarum* densities following the mass mortality event is known to have caused increases in algal biomass on reefs throughout the Caribbean (de Ruyter van Steveninck and Bak, 1986; Liddell and Ohlhorst, 1986; Hughes *et al.*, 1987; Levitan, 1988; Carpenter, 1985; 1988; 1990; Allard, 1993).

Phenomena other than eutrophication and reduced *D. antillarum* grazing pressure may have contributed to the temporal decline in *F. fragum* abundance in Barbados. One possibility is the impact of Hurricane Allen in 1980 (Mah and Stearn, 1986). A second is a temporal decline in abundance of herbivorous fish on west coast reefs. Several studies have documented impacts of grazing by fish (Stephenson and Searles, 1960; Randall, 1961; Bakus, 1966; Miller, 1982; Meyer *et al.*, 1983; Lewis, 1985; 1986; Lewis and Wainwright, 1985; Carpenter, 1986; Morrison, 1988) on macrophytic algal biomass on reefs, but fishing has led to a substantial decrease in abundance of reef fish in Barbados (Wilson, 1984).

In summary, the results of this study suggest that spatial variation in the distribution and abundance of *F. fragum* on Barbados west coast reefs is influenced by variation in exposure to anthropogenic eutrophication and by variation in *D. antillarum* densities and hence in grazing pressure. These factors can also explain the apparent temporal decrease in abundance of *F. fragum* in Barbados. The two factors will work synergistically if the abundance of *D. antillarum*, or any key grazer, is itself negatively affected by eutrophication, since this will further increase the dominance of macrophytic algae relative to crustose coralline algae on eutrophic reefs. The negative correlation detected between *D. antillarum* and eutrophication levels in this study suggest that this effect is occurring on Barbados reefs. A better understanding of the mechanisms of impact of eutrophication and *D. antillarum* density on *F. fragum* requires a study of the effects of these factors on the life history characteristics of *F. fragum* (Chapter 2).

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CHAPTER 2

Life history of the reef coral *Favia fragum* (Esper) in Barbados: effects of eutrophication and of the black sea urchin *Diadema antillarum* (Philippi)

2.1 Abstract

The abundance of *Favia fragum* is negatively correlated with eutrophication levels and positively correlated with densities of *Diadema antillarum* (grazing pressure) on Barbados west coast reefs. The variation in abundance was explored by investigating effects of eutrophication and of variation in *D. antillarum* densities on life-history characteristics of *F. fragum*. Planulation in *F. fragum* peaked between days 8 - 12 following New Moon, but planulation periodicity was not affected by eutrophication levels. Colony surface area was a strong predictor of both colony fecundity and mean polyp fecundity, but neither coral fecundity, polyp fecundity nor the relationships between fecundity and colony surface area differed at different eutrophication levels and *D. antillarum* densities. Neither adult growth nor adult mortality of *F. fragum* differed with eutrophication levels and *D. antillarum* densities in this study. By contrast, growth rates of juveniles appeared slower and mortality rates higher on more eutrophic reefs with lower *D. antillarum* densities. Moreover, larvae of *F. fragum* preferred to settle on crustose coralline algae than on turf algae, and the former is comparatively scarce on eutrophic reefs with low *D. antillarum* densities. These results suggest that the negative correlation between adult abundance of *F. fragum* and eutrophication levels/grazing pressure levels on Barbados west coast reefs is primarily driven by the effects of these processes on settlement and early post-settlement stages of *F. fragum*.

2.2 Introduction

Eutrophication, viewed here as increased nutrient and sediment loads, has been implicated as a major factor causing community changes in coral reefs (Walker and Ormond, 1982; Maragos *et al.*, 1985; Tomascik and Sander, 1987a; Hunte and Wittenberg, 1992; Wittenberg and Hunte, 1992; Tomascik *et al.*, 1993). Experimental and natural reductions in grazing pressure have also been shown to influence coral community structure (Sammarco, 1980; 1982; Lessios, 1988). Both factors may change community structure by enabling macrophytic algae to outcompete corals and crustose coralline algae for space on the reef (Littler and Littler, 1984; 1985 Pastorok and Bilyard, 1985; de Ruyter van Steveninck, 1986; Carpenter, 1990; Wittenberg and Hunte, 1992). Eutrophication may further affect corals by increasing phytoplankton biomass. This may increase sedimentation and lead to elevated turbidity levels that reduce light availability for zooxanthellae photosynthesis (Rogers, 1979; 1990).

Diadema antillarum is a key herbivore in the Caribbean (Berner, 1990), especially on shallow reefs (Morrison, 1988) subjected to heavy fishing pressure (Hay, 1984). The massive mortality experienced by *D. antillarum* in the Caribbean in 1983 (e.g. Lessios, 1984; Hunte *et al.*, 1986), aggravated by its relatively slow recovery (Hunte and Younglao, 1988; Lessios, 1988), has presumably resulted in a major reduction in grazing pressure on Caribbean reefs. On Barbados reefs, densities of *D. antillarum* are negatively correlated with eutrophication, and the relative dominance of macrophytic and crustose coralline algae on the reefs appears to be mediated by grazing of *D. antillarum* (Chapter 1). The lower grazing pressure at sites with high eutrophication has generally resulted in high macrophytic algal cover at the expense of crustose coralline algae and coral cover (Tomascik and Sander, 1987a; Wittenberg and Hunte, 1992; Chapter 1). However, the strong spatial correlation between eutrophication and *D. antillarum* densities in Barbados precludes the separation of their individual effects, and their impact on corals and coral community structure must therefore be viewed as a simultaneous effect.

Hughes (1993) suggests that community monitoring techniques alone often fail to uncover the mechanisms responsible for changes in species composition, and that parallel experimental work, and demographic and life history studies, should be used to clarify mechanisms of change. Differential susceptibilities of fundamental coral life history traits to environmental perturbations should provide valuable information on mechanisms of community change. Documented responses of life history traits to eutrophication include increased mortality of adults (Maragos, 1972) and juveniles (Wittenberg and Hunte, 1992), reduced growth (Maragos, 1972; Kinsey and Davies, 1979; Tomascik and Sander, 1985; Davies, 1990; Tomascik, 1990), reduced fecundity (Tomascik and Sander, 1987b; Acosta, 1993) and reduced settlement/recruitment rates (Tomascik, 1991; Hunte and Wittenberg, 1992). Most of these studies have been restricted to a single aspect of a coral's life history, and can not be used to assess variation in susceptibility of life history stages to eutrophication stresses and reduced grazing pressure.

Increased competition with macrophytic algae, resulting from changes in nutrient levels and grazing pressure, could affect corals at all life stages. However, the substrate changes envisaged may be particularly deleterious for corals during settlement and early post-settlement periods. For example, the low relief of juveniles in relation to the reef surface may make them more sensitive to overgrowth and smothering from macrophytic algae and sediment (Birkeland, 1977; Bak and Engel, 1979; Wittenberg and Hunte, 1992). The microscopic size of newly settled juveniles makes *in situ* work difficult, and most studies are therefore of visible recruits that may be several months old depending on growth rates (Harrison and Wallace, 1990). This constraint has been countered by using artificial plates to monitor settlement, (Tomascik, 1991; Hunte and Wittenberg, 1992), but the use of plates to investigate juvenile growth and mortality is difficult, since natural settlement is often intermittent, and the number of settlers on plates is typically low. Following a specific cohort from planulae to juveniles would clearly facilitate the assessment of early growth and mortality (Harriott, 1983; Babcock, 1985; Sato, 1985).

Favia fragum (Esper) is a small (10 cm maximum diameter), brooding, hermaphroditic coral (Duerden, 1902; Vaughan, 1908; 1910) which planulates with year-round lunar periodicity (Szmant-Froelich *et al.*, 1985). Lewis (1974a, 1974b) described its settlement behaviour and early ontogeny. The abundance of *F. fragum* in Barbados is positively correlated with the abundance of *D. antillarum* and crustose coralline algae, and negatively correlated with eutrophication; and *F. fragum* is more likely to occur in areas where macrophytic algal cover is low (Chapter 1). These results suggest that at least one of the life history traits of *F. fragum* influencing its abundance is affected by elevated eutrophication levels and reduced *D. antillarum* densities. The objectives of this chapter are to (1) characterise the life history of *F. fragum* in Barbados, and (2) investigate inter-reef variation in the life history traits of *F. fragum* in relation to eutrophication levels and densities of *D. antillarum*. Specifically, fecundity, periodicity of larval release (planulation), adult growth, adult mortality, juvenile growth, juvenile mortality, and larval settlement choice of *F. fragum* were examined on reefs along the west coast of Barbados varying in eutrophication levels and in *D. antillarum* densities.

2.3 Methods

2.3.1 Study sites

Seven fringing reefs were selected along the west coast of Barbados based on prior knowledge of differences in exposure to eutrophication over the past decade (Fig. 1) (Tomascik and Sander, 1985; Chapter 1). An index of eutrophication was derived from a principal components analysis based on reactive phosphate (PO_4-P), nitrate-nitrite nitrogen (NO_3-NO_2-N), chlorophyll-a, suspended particulate matter (SPM), volatile particulate matter (VPM), and percent of organic matter in sediment (see Chapter 1). Densities of *D. antillarum* are negatively correlated with eutrophication levels across the study sites (Chapter 1). Site scores on the eutrophication index and *D. antillarum* densities for each site are shown in Figures 2A and 2B respectively. A subset of two eutrophic (low *D. antillarum* density) reefs (Spring Garden: E_1; and Brighton: E_2) and two less eutrophic (high *D. antillarum* density) reefs (Sandy Lane: LE_1; and Greensleeves: LE_2) were used for several aspects of the study (Fig. 1). The eutrophication sources on the west coast of Barbados are described by Tomascik and Sander (1985) and in Chapter 1 of this thesis.

2.3.2 Planulation and fecundity

Sixteen adult colonies ranging in size from 1.2 cm to 5.1 cm in diameter were collected from each of four study sites (E_1, E_2, LE_1, LE_2; Fig. 1) on July 27, 1992, two days before new moon. The timing of sampling ensured that the stress of collection did not cause premature planulation (Szmant-Froelich *et al.*, 1985). Healthy colonies were chiselled off each reef and transported to the laboratory in an insulated cooler. The colonies were measured for maximum length, width, and height using vernier calipers. Polyp number was estimated for each colony as the mean value of three independent counts. Surface area was measured after the study by covering each colony with a single

Figure 1. Locations of the study sites along the west coast of Barbados, West Indies. Study site Abbreviations: BR (E_1) - Brighton; SG (E_2) - Spring Garden; FV - Fitts Village; SL (LE_1) - Sandy Lane; BRI - Bellairs Research Institute; GS (LE_2) - Greensleeves; SR - Sandridge.

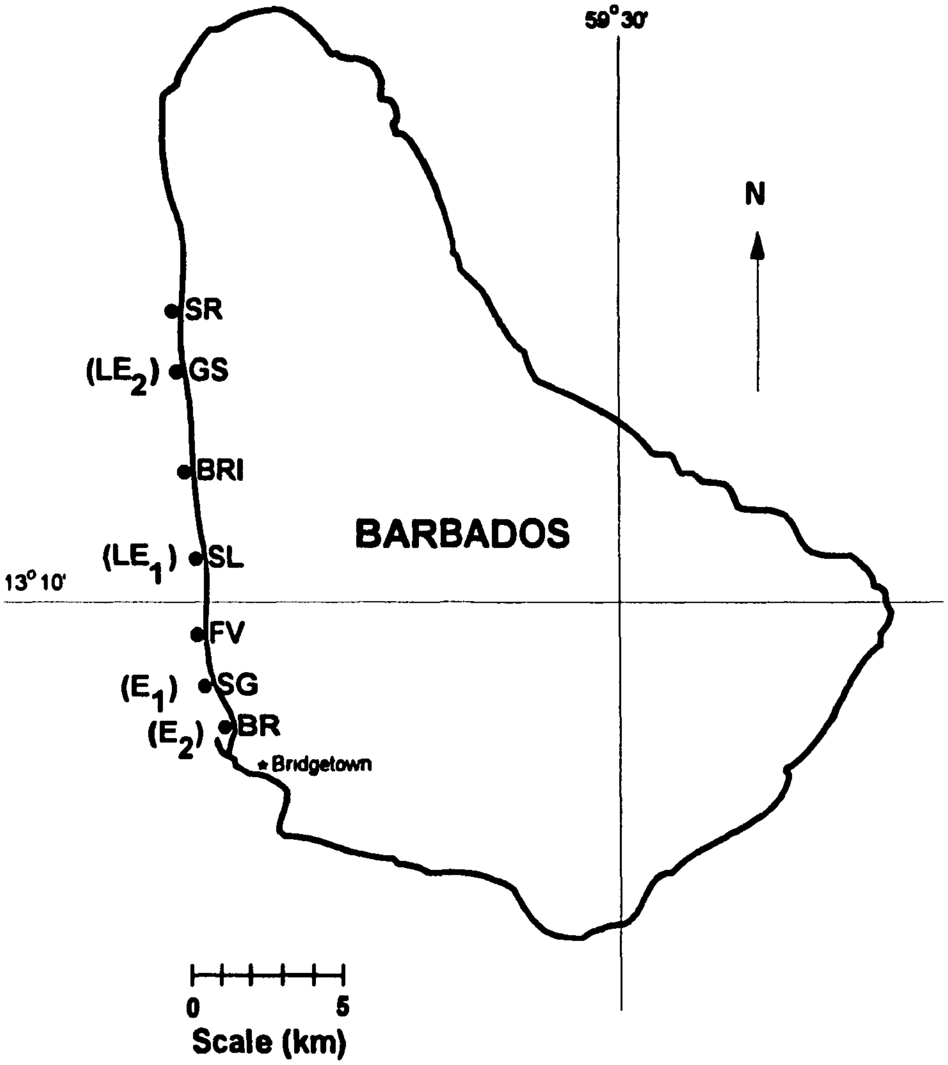
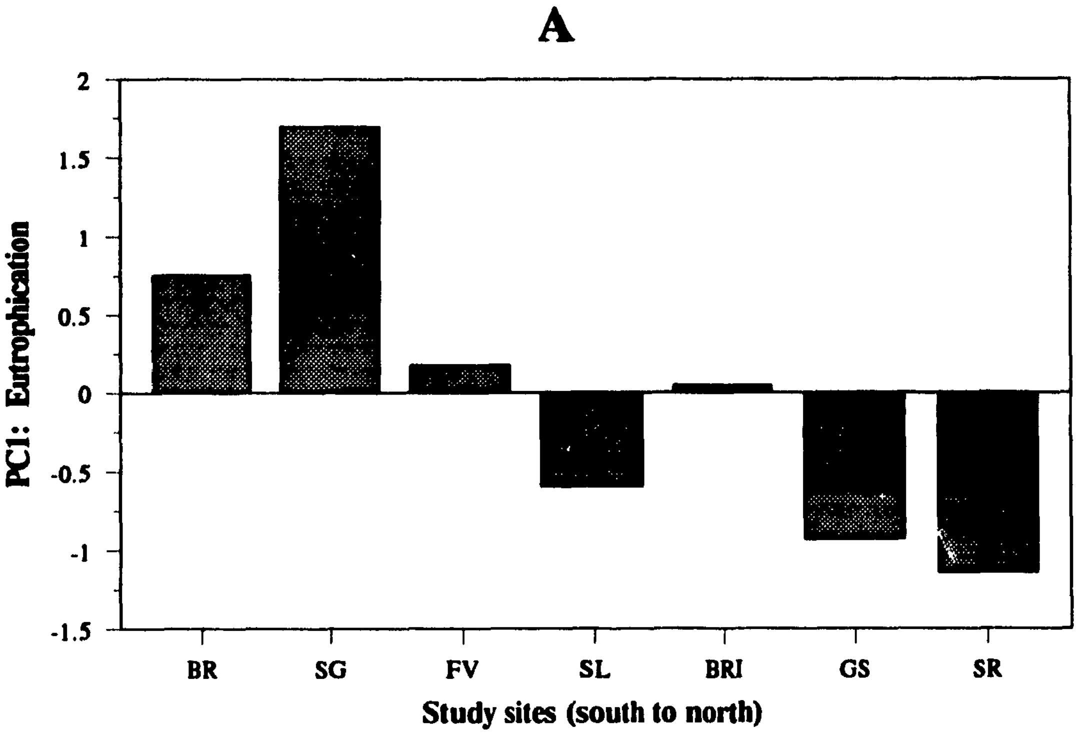
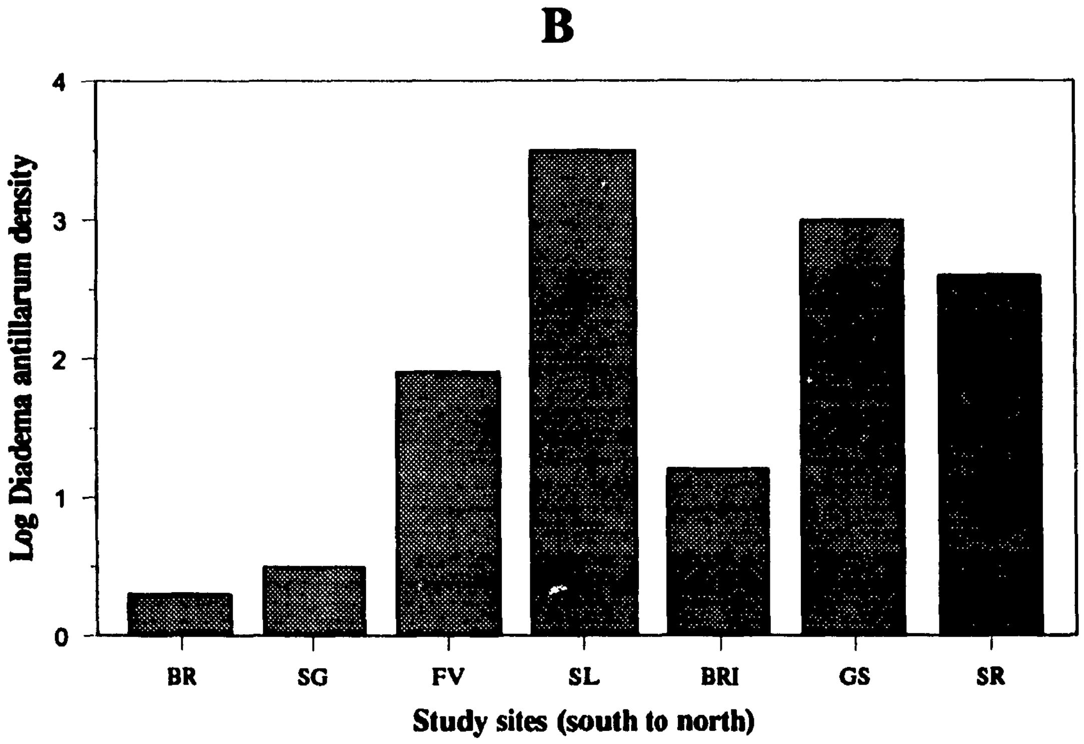

59° 30'
N
SR
(LE2) GS
BRI
BARBADOS
(LE1) SL
13° 10'
FV
(E1) SG
(E2) BR
Bridgetown
0
5
Scale (km)

Figure 2. Site scores on the eutrophication/sedimentation index (PC1) derived from principal component analysis of water quality variables (A), and density (#/m^2) of *Diadema antillarum* (B) at each of the seven sites (see Section 2.3.1).


A
PC1: Eutrophication
2
1.5
1
0.5
0
-0.5
-1
-1.5
BR
SG
FV
SL
BRI
GS
SR
Study sites (south to north)


B
Log Diadema antillarum density
4
3
2
1
0
BR
SG
FV
SL
BRI
GS
SR
Study sites (south to north)

layer of aluminum foil. The foil was then dried and weighed, and the surface area calculated using a known area/weight ratio of foil. The colonies were placed in individual Nitex® (202 μm mesh size) compartments in a continuous-flow water table during the day, and in 350 ml finger bowls at dusk. Planulation occurred at night in the finger bowls. Each morning all larvae in each finger bowl were collected and counted using a 10 ml pipette, taking care to clean the base of each colony and finger bowl with a weak stream of water using a WaterPik®. The larvae were collected daily until all the colonies had stopped planulating. The dates of larval collection were converted to a lunar month, with new moon as the origin and subsequent days reported sequentially after new moon (ANM). Colony fecundity is defined here as the total number of larvae released by a colony in a given lunar reproductive cycle. Mean polyp fecundity was also calculated for each colony by dividing colony fecundity by the number of polyps in the colony.

It was necessary to maintain colony health in the laboratory in order to accurately discern planulation periodicity and colony fecundity, and the health status of each colony was therefore recorded throughout the study. Colonies suspected of incipient bacterial infection were treated by soaking the exposed bases in an antibiotic solution (0.1133g penicillin and 0.05g streptomycin in 100 ml seawater) for 1 minute each day. Most infections were minor and the colonies recovered completely in 24 to 48 hours. Colonies which did not respond immediately to treatment were not considered in the analyses.

2.3.3 Adult growth and mortality

2.3.3.1 *Short-term growth*

The buoyant weight technique (Davies, 1989) was used to assess whether short-term differences in growth rate occurred among four study sites (E_1, E_2, LE_1, LE_2). Colonies of *F. fragum* were collected from North Bellairs Reef and prepared for mounting onto perspex tiles (30 x 30 x 3 mm). Colonies were ground into a hemispherical shape and fixed to the tiles with Krazy Glue®. The nubbins (mounted corals) were then placed on racks which were bolted onto cement blocks in a nursery area located on North Bellairs Reef. The blocks were enclosed in chicken wire to prevent large grazers from damaging the corals. The corals were left in the nursery area for three weeks, with the tiles being cleaned each week. The purpose of the nursery area was to allow the corals to recover from the stress of the mounting process, and to allow the regeneration of tissue over any exposed skeleton.

After retrieval from the nursery area, the coral nubbins were carefully cleaned of all encrusting organisms and filamentous algae, ensuring that the tiles were clean but not scratched. The buoyant weighing technique is described by Davies (1989). Briefly, an Ohaus® scale was equipped with a Sartorious® Density Kit to enable the weighing of objects in seawater. Water temperature was continuously measured so that sea water density could be recalculated. A reference weight was used to recalibrate the sea water density for every 0.02 °C temperature increase. The seawater in the weighing pan was replaced each time the total rise in temperature reached 1 °C. The apparatus was kept away from direct sunlight and drafts. The buoyant weight of the corals was recorded along with the weight of the reference object. The air weight of the skeleton could then be calculated using several constants (see Davies, 1989; density of reference object = 2.225, air weight of reference object = 11.237g, density of skeletal material = 2.82, density of tile = 1.186, density of tubes = 1.408).

Following the weighing procedure, the nubbins were randomly assigned to one of four racks so that equal numbers would be present at each study site (one rack per site). The racks were then carefully transported to the study sites (E_1, E_2, LE_1, LE_2) in an insulated cooler filled with seawater and were bolted into place on the pre-positioned cement blocks in the same depth zone on each reef. The coral nubbins were left at each study site for three weeks, with the tiles being cleaned each week. At the end of the 3 weeks, the nubbins were transported back to the laboratory and reweighed.

2.3.3.2 *Long-term growth*

Twenty-five adult colonies ranging in size from approximately 1 cm - 5 cm (diameter) were selected at each of the seven study reefs (Fig. 1) in June and July, 1992. The colonies were measured (maximum length and width), and their positions marked with numbered plastic tags nailed into the adjacent reef. Growth rates were standardized to radial extension in cm/yr. The health status of each colony was also recorded. In contrast to "healthy" colonies, "partial mortality" colonies showed partial tissue loss which left the skeleton open to colonization by filamentous and coralline algae. The size of colonies was re-assessed in February 1993, and again in June 1993. Colonies which were originally classified healthy, but showed tissue loss during the study were re-classified as "partial mortality." Colonies which were not relocated were not included in the analyses.

2.3.3.3 *Mortality*

The colonies used in the long-term growth study were used to estimate mortality rates at the seven sites. The number of colonies showing complete mortality was recorded during each size re-assessment period (i.e. after 8 months; after 12 months). Mortality rates were calculated for each site over the entire study period as % dead/yr. The apparent cause of mortality was noted when possible.

2.3.4 Juvenile growth and mortality

Post-settlement growth and mortality of *F. fragum* was investigated at four study sites (E_1, E_2, LE_1, LE_2) over the 19 day period following settlement. To do so, glass plates were used as artificial settlement substrates. The choice of glass plates was based on prior experiments comparing settlement on these plates with settlement on glazed and unglazed ceramic tiles. The plates (10 cm x 10 cm) were mounted on PVC racks and placed directly on the reef at each of the four study sites for a conditioning period of three months. This allowed the settlement plates to be colonized primarily by crustose coralline and turf algae, but also by other early successional species.

After the conditioning period, 16 randomly selected plates from each site were place in 4 Nitex domes (inner dimensions 40 x 40 x 10 cm; mesh 202 μm) installed at each site, i.e. 4 plates per dome, 4 domes per site. Each dome was then injected with 400 larvae obtained by planulation in the laboratory and randomly mixed to minimise possible differences in size at settlement within domes. After 5 days to allow for settlement, the plates were carefully removed from the domes and placed directly on the reef. Two weeks later, the plates were transferred to the laboratory in coolers filled with seawater and examined for settlers under a dissecting microscope. The maximum diameter of each settler was measured with an ocular micrometer at 40x magnification to calculate growth at each site; and the number of settlers dead and alive was recorded to calculate mortality rates. A brief period of heavy swells disrupted the domes at site E_1, preventing the acquisition of juvenile growth or mortality data for that site.

2.3.5 Larval settlement patterns

To determine whether larvae of *F. fragum* exhibited non-random settlement patterns with respect to crustose coralline algae and turf algae, the cover of these substrate components was measured on artificial settlement plates after 3 months of conditioning in the field. The plates were placed in Nitex domes and larvae injected inside as described in section 2.3.4. The number of settlers on each substrate type on each settlement plate was counted immediately after the initial 5 day settlement period. If the proportion of settlers on a given substrate did not differ significantly from the percent cover of that substrate, settlement was defined as random.

2.4 Results

2.4.1 Planulation and fecundity

2.4.1.1 *Planulation periodicity*

Planulation by colonies of *Favia fragum* peaked between days 10 - 12 after new moon (ANM) (Fig. 3). Since fecundity is positively correlated with colony size (Section 2.4.1.2), the planulation periodicity observed could have been driven by a few large colonies with peak planulation between days 10 - 12 ANM. The peak release day for each colony was therefore calculated to give each colony the same contribution to planulation periodicity regardless of colony size. The peak release day for most colonies of *F. fragum* occurred between days 8 - 12 ANM, with a mean of 10.4 and a median of 10.5 (Fig. 4). There was a weak tendency for peak release day to be earlier for smaller colonies (Linear regression of peak release day on colony surface area; $r^2 = 0.06$, $P=0.086$). Peak planulation of colonies from eutrophic sites was slightly later (mean = 10.56 ANM) than those from less eutrophic sites (mean = 10.31 ANM), but the difference was not statistically significant (ANOVA, $P=0.711$).

2.4.1.2 *Fecundity*

Colony surface area was the best univariate predictor of colony fecundity (Fig. 5), followed by the number of polyps in the colony and colony length (Table 1). Colony width and height were the poorest predictors of colony fecundity, but the relationships were still highly significant (Table 1). Multiple regressions are not presented, as the colony parameter data are highly collinear.

Colony fecundity did not differ significantly between sites or eutrophic levels (E_1 E_2 vs LE_1 LE_2) (ANOVA; sites, $P=0.488$; levels, $P=0.936$). The possibility that the relationship between colony fecundity and colony surface area differed at the two eutrophic levels (E, LE) was investigated. Neither the slopes (ANCOVA, $P=0.380$) nor the intercepts (ANCOVA, $P=0.286$) of the regressions of colony fecundity on colony

Figure 3. Lunar periodictiy of larval release by *Favia fragum* colonies during the lunar month beginning July 29, 1992. Colonies collected from the west coast of Barbados. N=54 colonies. Total larval release = 30,247.

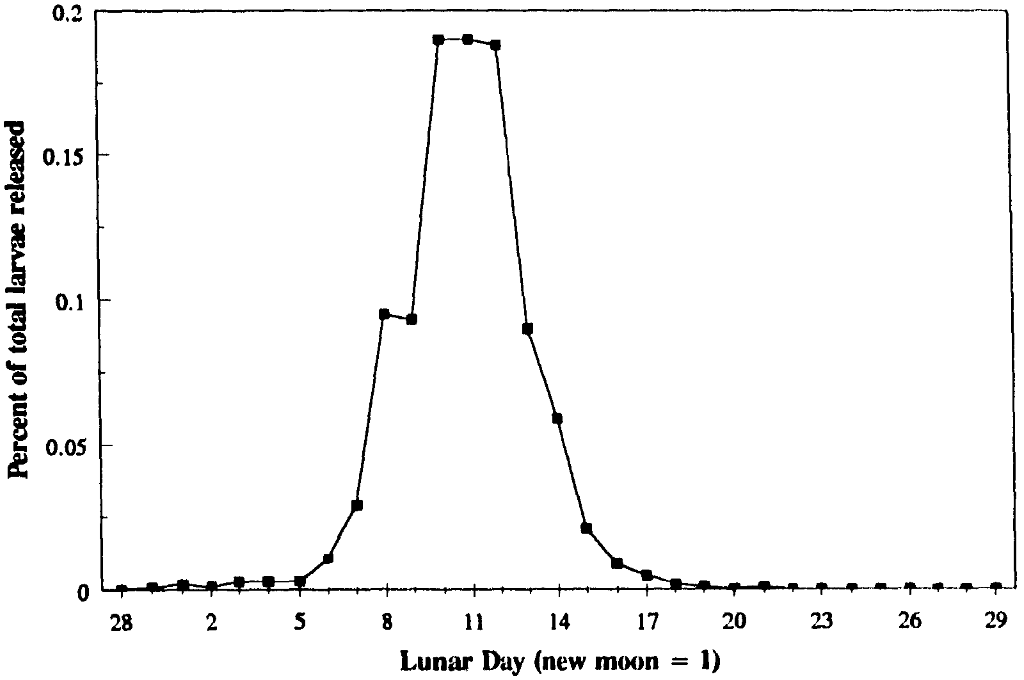
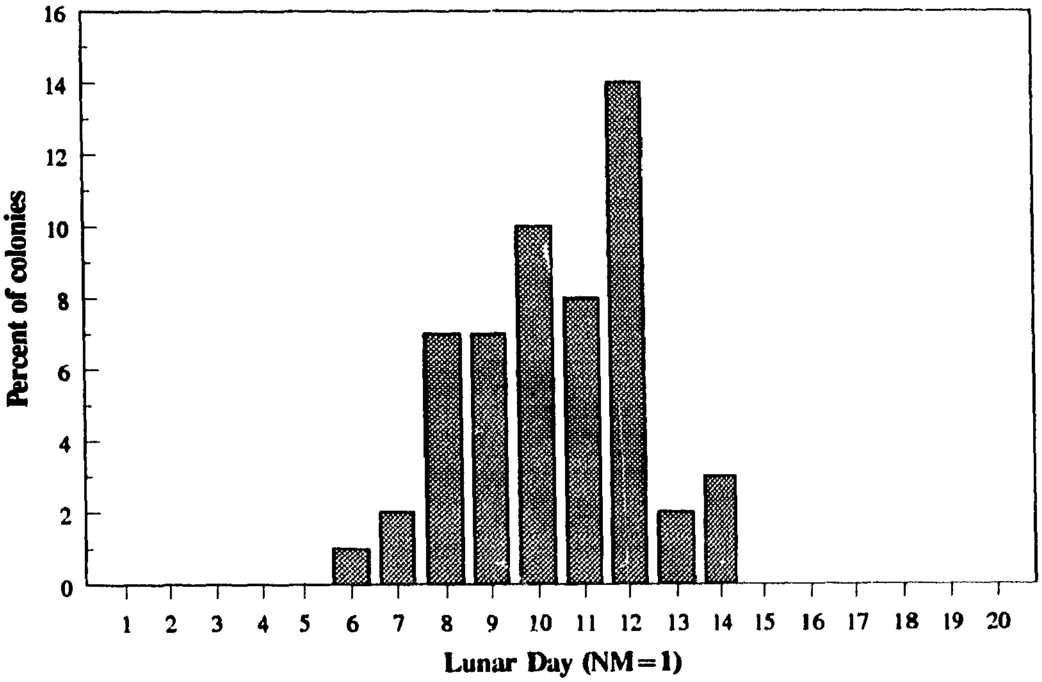

0.2
0.15
0.1
0.05
0
Percent of total larvae released
28
2
5
8
11
14
17
20
23
26
29
Lunar Day (new moon = 1)

Figure 4. The distribution of peak release days by lunar day for colonies of *Favia fragum* from all study sites along the west coast of Barbados. N=54 colonies.



16
14
12
10
8
6
4
2
0
Percent of colonies
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
Lunar Day (NM=1)

Figure 5. Linear regression of colony fecundity on colony surface area (cm^2) for ***Favia fragum*** from the west coast of Barbados. N=54 colonies. Colony fecundity defined in Section 2.3.2.

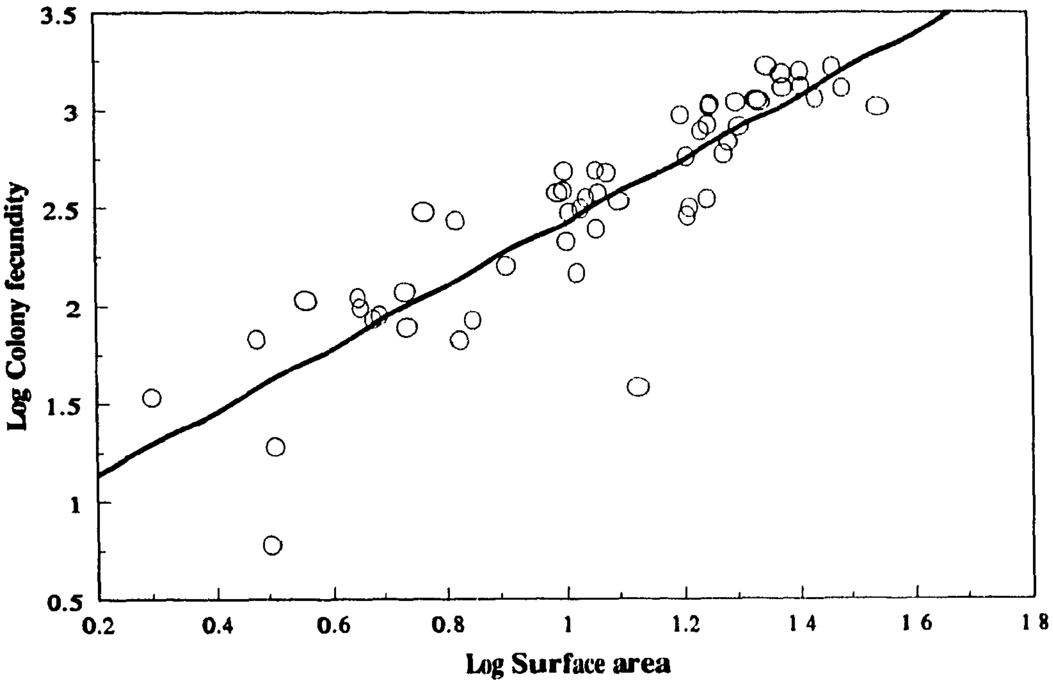

3.5
3
2.5
2
1.5
1
0.5
Log Colony fecundity
0.2
0.4
0.6
0.8
1
1.2
1 4
1 6
1 8
Log Surface area

Table 1. Regression equations for predicting (A) colony fecundity (CF in number of planulae released per reproductive cycle per colony) and (B) polyp fecundity (PF in mean number of planulae released per polyp per reproductive cycle per colony) from length (maximum colony diameter, L in cm), width (maximum colony diameter perpendicular to length, W in cm), height (maximum colony height perpendicular to substrate, H in cm), number of polyps (P), and surface area (SA in cm^2).

A

Simple regressions	r^2	P	SE of Slope
1. $\log CF = 0.884 + 3.310 \log L$	0.71	<0.001	0.288
2. $\log CF = 1.128 + 3.311 \log W$	0.68	<0.001	0.312
3. $\log CF = 1.766 + 3.145 \log H$	0.60	<0.001	0.353
4. $\log CF = -0.218 + 1.695 \log P$	0.71	<0.001	0.147
5. $\log CF = 0.812 + 1.601 \log SA$	0.77	<0.001	0.120

B

Simple regressions	r^2	P	SE of Slope
1. $\log PF = 0.419 + 3.372 \log L$	0.34	<0.001	0.651
2. $\log PF = 0.687 + 3.324 \log W$	0.31	<0.001	0.663
3. $\log PF = 1.298 + 3.289 \log H$	0.30	<0.001	0.670
4. $\log PF = -0.502 + 1.601 \log P$	0.29	<0.001	0.675
5. $\log PF = 0.301 + 1.673 \log SA$	0.39	<0.001	0.626

surface area differed between the 2 eutrophic levels. This indicates that neither the increment in fecundity for an increment in colony size, nor fecundity at a given colony size, differed at the different eutrophic levels. Finally, a multiple regression of colony fecundity with site scores on the eutrophication index (Fig. 2) and colony size was insignificant ($P=0.683$), further confirming that eutrophication ($P=0.683$) does not affect colony fecundity in *F. fragum*.

Colony surface area was the best univariate predictor of mean polyp fecundity (Table 1; Fig. 6), but polyp fecundity was positively correlated with all the colony parameters (Table 1). Mean polyp fecundity did not differ significantly between sites or eutrophication levels (ANOVA; sites, $P=0.163$; levels, $P=0.445$); and the relationship between polyp fecundity and colony surface area did not differ in either slope or elevation between eutrophication levels (ANCOVA; slope, $P=0.430$; levels, $P=0.775$). These results confirm that eutrophication does not affect mean polyp fecundity in *F. fragum*.

2.4.2 Adult growth and mortality

2.4.2.1 *Short term growth*

Growth rates of *F. fragum* as detected by the buoyant weight technique over a three week period at four sites differing in exposure to eutrophication (E_1, E_2,, LE_1, LE_2) are shown in Table 2. Mean growth was higher at the less eutrophic site LE_1 than at the other sites, but the differences in growth were not statistically significant (Table 2; ANOVA, $P=0.465$).

2.4.2.2 *Long term growth*

Growth rates of *F. fragum* as detected by radial extension rates over a 12-month period at seven sites differing in eutrophication levels along the west coast of Barbados (Fig.s 1, 2) are shown for three time periods (0 - 8 months; 8 - 12 months; 0 - 12 months) in Table 3. Only "healthy" colonies (Section 2.3.3.2) were included in the analysis of

Figure 6. Linear regression of polyp fecundity on colony surface area (cm^2) for *Favia fragum* from the west coast of Barbados. N=54 colonies. Polyp fecundity defined in Section 2.3.2.

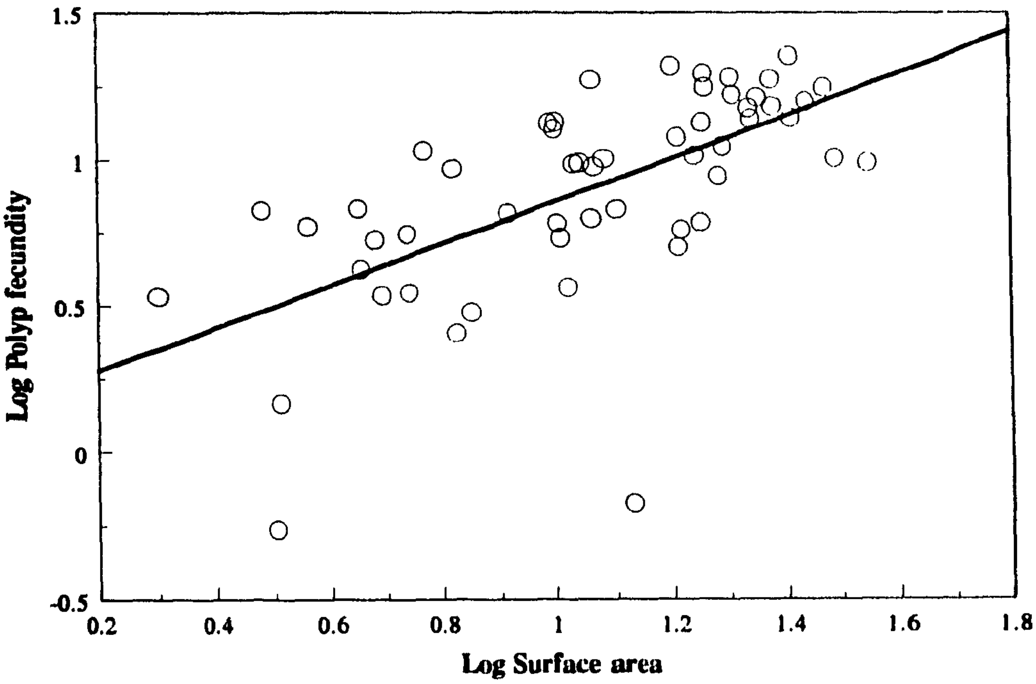

1.5
1
0.5
0
-0.5
Log Polyp fecundity
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
Log Surface area

Table 2. Short term adult growth (over 3 weeks), and juvenile growth and mortality (over 19 days), of *Favia fragum* at four sites differing in eutrophication levels and in *D. antillarum* density along the west coast of Barbados. E_1 and E_2 are eutrophic (low *D. antillarum*) sites; LE_1 and LE_2 are less eutrophic (high *D. antillarum*) sites. Adult growth rates are reported as percent increase in skeletal mass per day. Juvenile growth rates are reported as the final size of settlers at the end of the growth period, and juvenile mortality as the % of settlers dying over the growth period. Standard deviations are in parentheses. * No data available; N is number of adult colonies; n is number of settlers. Site abbreviations as in Fig. 1.

Site	Adult growth (%/d)	N	Juvenile growth (mm)	Juvenile mortality %	n
SG (E_1)	0.35 (0.11)	10	*	*	*
BR (E_2)	0.34 (0.14)	10	1.19 (0.21)	43.8	51
SL (LE_1)	0.41 (0.12)	10	1.45 (0.35)	5.9	17
GS (LE_2)	0.35 (0.08)	10	1.24 (0.25)	24.2	57
E (Mean)	0.35 (0.12)	20	1.19 (0.21)	43.8	51
LE (Mean)	0.38 (0.11)	20	1.29 (0.29)	15.3	74
Mean	0.36 (0.11)	40	1.25 (0.26)	28.0	125

growth rate differences between sites. Growth rates of healthy colonies over the year ranged from 0.16 cm/yr at BRI to 0.33 cm/yr at BR, but the range was wider over shorter periods (0.49 cm/yr for the first 8 months at BR to 0.12 cm/yr for the last 4 months at SL; Table 3). The mean growth rate for all healthy colonies at all sites was 0.23 cm/yr over the year (Table 3). Mean growth rates of healthy colonies did not differ significantly between sites over the one year period (Table 3; ANOVA, P=0.284).

Thirty colonies (28.3%) changed status from "healthy" at the start of the study to "partial mortality" after the first 8 months (Section 2.3.3.2). Colonies which were classified as "partial mortality" status at the start of the study, as well as those which acquired "partial mortality" status during the study, are presented as "partial mortality" colonies in Table 3. Colonies with partial mortality showed highly variable tissue loss rates over the study year, mean tissue loss ranging from -0.58 cm/yr at BR to -0.13 cm/yr at SL (Table 3). The range was even wider over shorter periods (-0.80 cm/yr for the last 4 months at BR to -0.12 cm/yr for the first 8 months at SL). The mean rate of tissue loss in partial mortality colonies did not differ significantly between sites over the year (Table 3; ANOVA, P=0.076).

Net growth or loss of tissue at each site is shown by the combined values (Total) for healthy and partial mortality colonies in Table 3. There was a net increase in tissue over the year (range 0.01 to 0.10 cm/yr) at all sites except GS, where there was no net change in tissue over the year. Since the colonies were originally selected to include both "healthy" and "partial mortality" colonies (i.e. selection was non-random), the net tissue changes presented in Table 3 are relevant only to the corals selected, and can not be extrapolated to represent net tissue changes in the coral populations at the study sites.

2.4.2.3 *Mortality*

Mortality rates of adults of *F. fragum* at the seven sites are shown in Table 3. Mortality ranged from 0.0 %/yr at FV and SR to 40.0 %/yr at BRI, but no relationship is evident between mortality rates and eutrophication levels (*D. antillarum* densities) at the study sites (Table 3). The principal apparent causes of adult mortality were overgrowth by turf algae and crustose coralline algae, the two major substrate components on the reef (Table

Table 3. Long term adult growth and mortality rates (over a 12 month period) of *Favia fragum* at seven sites differing in eutrophication levels and in *D. antillarum* densities (Fig. 2) along the west coast of Barbados. Data are presented separately for healthy (H) colonies, partial mortality (PM) colonies, and the two combined (Total). Growth rates are reported over three time periods (0-8 months, 8-12 months, 0-12 months) as mean radial extension in cm per year. Standard deviations are in parentheses. Mortality rates are reported as the percent of colonies dying over the study period. N is number of colonies. Site abbreviations as in Fig. 1.

Site		Growth						Mortality
	Colony Status	0 to 8 mths N	0 to 8 mths (cm/yr)	8 to 12 mths N	8 to 12 mths (cm/yr)	0 to 12 mths N	0 to 12 mths (cm/yr)	(%/yr)
BR	H	12	0.49 (0.47)	11	0.21 (0.16)	12	0.33 (0.28)	20.0
	PM	7	-0.62 (0.44)	5	-0.80(1.064)	4	-0.58 (0.37)	
	Total	19	0.09 (0.71)	16	-0.10 (0.74)	16	0.10 (0.50)	
SG	H	19	0.29 (0.20)	13	0.16 (0.13)	18	0.21 (0.11)	12.0
	PM	4	-0.58 (0.46)	9	-0.34 (0.26)	4	-0.52 (0.37)	
	Total	23	0.08 (0.42)	22	-0.04 (0.31)	22	0.07 (0.33)	
FV	H	18	0.25 (0.17)	17	0.23 (0.16)	16	0.23 (0.15)	0.0
	PM	6	-0.30 (0.36)	7	-0.25 (0.20)	8	-0.15 (0.20)	
	Total	24	0.08 (0.33)	24	0.09 (0.28)	24	0.10 (0.25)	
SL	H	15	0.20 (0.13)	13	0.12 (0.10)	13	0.17 (0.11)	8.7
	PM	7	-0.12 (0.07)	8	-0.23 (0.28)	8	-0.13 (0.13)	
	Total	22	0.09 (0.19)	22	-0.01 (0.26)	22	0.06 (0.19)	
BRI	H	6	0.22 (0.11)	4	0.17 (0.12)	5	0.16 (0.13)	40.0
	PM	6	-0.51 (0.52)	5	-0.32 (0.15)	4	-0.17 (0.07)	
	Total	12	0.12 (0.52)	9	-0.10 (0.29)	9	0.01 (0.20)	
GS	H	17	0.27 (0.20)	7	0.17 (0.20)	11	0.26 (0.18)	13.0
	PM	3	-0.17 (0.15)	13	-0.68 (0.85)	9	-0.31 (0.35)	
	Total	20	0.09 (0.25)	20	-0.38 (0.80)	20	0.00 (0.39)	
SR	H	19	0.27 (0.22)	11	0.17 (0.14)	15	0.21 (0.15)	0.0
	PM	3	-0.21 (0.17)	11	-0.50 (0.74)	7	-0.26 (0.31)	
	Total	22	0.09 (0.27)	22	-0.17 (0.62)	22	0.06 (0.30)	
MEAN	H	106	0.28 (0.24)	76	0.18 (0.14)	90	0.23 (0.16)	11.8
	PM	36	-0.37 (0.39)	58	-0.46 (0.62)	44	-0.27 (0.30)	
	Total	142	0.12 (0.41)	134	-0.10 (0.53)	134	0.06 (0.32)	

4). Exposed skeleton on colonies that suffered tissue loss through injury or disease was rapidly colonized by either turf or crustose coralline algae. Growth of the colonizing algae then took advantage of further tissue recessions until the entire colony was dead. Although the number of dead colonies is small, the type of algae covering dead colonies differed significantly at different eutrophication levels/*D. antillarum* densities; more colonies were covered by turf algae at higher eutrophication/lower *D. antillarum* density and more by crustose coralline algae at lower eutrophication/higher *D. antillarum* density (Table 4; $\chi^2=7.021$, df=2, $P<0.05$).

2.4.3 Juvenile growth and mortality

2.4.3.1 *Growth*

The mean size of all juveniles of *F. fragum* at the end of the 19 day growth study was 1.25 mm (Table 2). Juvenile size differed significantly between sites (Table 2; ANOVA, $P<0.05$). Juveniles at the eutrophic/low *D. antillarum* site E_2 were significantly smaller (1.19 mm) than those at the less eutrophic/high *D. antillarum* site LE_1 (1.45 mm) (Tukey's test, $P<0.05$). E_2 juveniles were also smaller than those at the less eutrophic/high *D. antillarum* site LE_2 (1.24 mm), but the difference was not statistically significant (Tukey's test, $P>0.05$). Juveniles at LE_1 were larger than at LE_2 (Tukey's test, $P<0.05$).

2.4.3.2 *Mortality*

The mean mortality rate for all juvenile corals over the 19 days following settlement was 28 %, mortality ranging from 5.9% at the less eutrophic/high *D. antillarum* site LE_1 to 43.8% at the eutrophic/low *D. antillarum* site E_2 (Table 2). The proportion of dead to living juveniles after 19 days differed significantly between sites ($\chi^2=11.857$, df=2, $P<0.005$), with mortality being high at the eutrophic/low *D. antillarum* site (E_2), moderate at the less eutrophic site LE_2, and low at the less eutrophic/high *D. antillarum* site LE_1 (Table 2). The mortality difference between E_2 and LE_2 was statistically

Table 4. The type of algae overgrowing the adult colonies of *Favia fragum* which died during the study, presented separately for three levels of eutrophication (*D. antillarum* densities) on Barbados west coast reefs. The levels were determined from the eutrophication index scores and *D. antillarum* densities in Fig. 2. Site names are in parentheses; abbreviations as in Fig. 1.

Eutrophication Level	*D. antillarum* density	Crustose coralline algae	Turf algae
High (BR, SG)	Low	0	2
Medium (FV, BRI)	Medium	2	3
Low (SL, GS, SR)	High	5	0

significant (χ^2=4.862, df=1, $P<0.05$). While the causes of mortality were not quantified, qualitative observations suggested that the main source of mortality was smothering by turf algae and sediment.

2.4.4 Larval settlement choice

The settlement pattern of ***F. fragum*** on glass plates colonized primarily by crustose coralline and turf algae is shown in Table 5. Coralline algae occupied 7.8% of the surface of the plates. The rest of the surface was occupied by turf algae infrequently interspersed with other colonizers. Random settlement would predict that 7.8% (26) of the 339 larvae which settled should be on crustose coralline algae. The number of settlers observed on crustose coralline algae was 77 (22.7%), was significantly more than predicted by random settlement (Table 5; χ^2=98.087, df=1, $P<0.001$).

Table 5. The distribution of settlers of *Favia fragum* on artificial (glass) settlement plates primarily covered by crustose coralline algae and turf algae following 3 months of conditioning in the field. N_E is the number of settlers expected by random settlement across substrate types; N_O is the number of settlers observed.

Substrate	% cover of plates by substrate	N_E	N_O
Crustose coralline algae	7.8	26	77
Turf algae	92.2	313	262

2.5 Discussion

Planulation by individual colonies of *F. fragum* peaked between days 8 - 12 after new moon in Barbados. A similar periodicity has been reported for *F. fragum* in Puerto Rico (planulation peaked 9-11 days after new moon; Szmant-Froelich *et al.* (1985). Nocturnal irradiance has been proposed as the primary proximate factor influencing the synchrony of planula release in corals (Jokiel *et al.*, 1985). Several authors have suggested that the lunar periodicity of planulation is adaptive, release occurring when environmental conditions are optimal for local larval survival (Richmond and Jokiel, 1984; Jokiel, 1985; Jokiel *et al.*, 1985). Differences between habitats in the lunar periodicity of planulation have been documented for *Pocillopora damicornis* in the Indo-Pacific (Richmond and Jokiel, 1984). The similarity in planulation periodicity of *F. fragum* in Barbados and Puerto Rico may therefore suggest little variation between these locations in the lunar periodicity of environmental conditions influencing larval survival. Planulation periodicity did not vary with eutrophication levels on Barbados reefs, suggesting either that the optimal time of larval release is not influenced by eutrophication, and/or that there is little phenotypic flexibility in planulation periodicity in response to prevailing environmental conditions.

Scott (unpublished data cited in Harrison and Wallace, 1990) reported that planulation in *F. fragum* varied with colony size, peak release in smaller colonies occurring at the first-quarter moon phase and in larger colonies at full moon. Peak release in the present study was only marginally earlier for smaller colonies. It is unclear what advantage smaller colonies could have in earlier planulation. Earlier release may therefore be the simple consequence of faster development resulting from the energetics of producing fewer planulae per polyp (lower polyp fecundity in smaller colonies; this study).

Colony surface area was the best univariate predictor of colony fecundity among the colony parameters measured in this study, i.e. larger colonies produced more larvae. Soong (1991) found that colonies of *F. fragum* in Panama had one egg in each of 20 ovaries per polyp. However, polyp fecundity was positively correlated with colony surface area in this study, suggesting that the number of larvae per polyp in *F. fragum* can vary, and that proportionately more energy may be allocated to reproduction as colonies grow (age). Other Faviidae are known to augment polyp fecundity by increasing the number of eggs per mesentery (*Goniastrea favulus*, Kojis and Quinn, 1981; *G. aspera*, Babcock, 1984; *Platygyra sinensis*, Babcock, 1986 in Harrison and Wallace, 1990). Scott (pers. comm. in Harrison and Wallace, 1990) claimed to have observed reproductive senescence in larger colonies of *F. fragum*. This was not detected in the present study, both colony fecundity and polyp fecundity increasing with colony size (age). All colonies collected in this study were reproductively active. This included a colony only 1.3 mm in diameter (10 polyps, 3.02 cm^2 surface area). *F. fragum* has been known to planulate at the three-polyp stage (6 to 12 months old; Szmant, pers. comm.). High adult mortality rates are typically expected to select for early reproduction (e.g. MacArthur and Wilson, 1967). Given its early onset of reproduction, *F. fragum* may therefore be expected to have high natural adult mortality. Mean adult mortality of *F. fragum* in this study was high (11.8% per year), suggesting that *F. fragum* could be grouped among corals with high natural mortality (Bak and Engel, 1979; Hughes, 1985).

Although reproduction is often considered to have a narrower tolerance to stress than other life functions (Harrison and Wallace, 1990), eutrophication levels did not influence either colony or polyp fecundity of *I. fragum* in this study. However, it should be noted that only a few studies have reported eutrophication-induced inhibition of reproduction in corals. Acosta (1993) reported that gonad production in *Montastrea annularis* was lower near a possible contamination source than at a site further away; and Tomascik and Sander (1987b) have suggested that eutrophication-associated turbidity and sedimentation caused a reduction in gonad production of *Porites porites* on polluted reefs in Barbados. However, asexual reproduction through fragmentation may have been a confounding factor in the latter study. *P. porites* at the most polluted site of Tomascik and Sander (1987b) (Spring Garden; Fig. 1 this study) appears to primarily reproduce by fragmentation (Wittenberg and Hunte, 1992), and newly formed fragments are generally less fecund than older fragments of similar size in corals (Kojis and Quinn 1981; 1985; Szmant-Froelich, 1985).

Neither short-term nor long-term studies of growth rates in *F. fragum* along the west coast of Barbados detected any effects of eutrophication levels on adult growth. Growth is considered a good quantitative measure of assessing stress in corals as it integrates several physiological processes (Brown and Howard, 1985), and eutrophication has been linked to reduced growth rates in *Montastrea annularis* in Barbados (Tomascik and Sander, 1985; Davies, 1990; Tomascik, 1990). Tomascik and Sander (1985) suggested that suspended particulate matter, through its smothering and its reduction of light intensity for zooxanthellae photosynthesis, was the primary cause of the reduced growth observed. However, they also suggested that particulate matter may serve as an energy source for corals. The extent to which coral growth is affected by eutrophication and sedimentation may therefore depend on the relative importance of particulate matter in the coral's energy budget. This is not known for any coral, but *F. fragum* is believed to utilise particulate matter as an energy source (Lewis, 1977), and may therefore be less susceptible to growth reduction under sediment stress.

As true for adult growth, mortality rates of adult colonies were not correlated with eutrophication levels along the west coast of Barbados, and it was difficult to verify precise causes of mortality. Exposed skeleton on colonies was rapidly colonized by algae, and the algae continued to take advantage of further tissue recessions to spread over the colony until the colony was dead. However, the extent to which the colonizing algae was the cause of further tissue recessions is difficult to determine. Interestingly, the colonizing algae was turf algae at sites with high eutrophication levels and low *D. antillarum* density, and crustose coralline algae at sites with low eutrophication levels and higher *D. antillarum* density. Maragos (1972) described the elimination of coral cover by the production of dense mats of benthic algae in response to eutrophication in Kaneohe Bay, Hawaii.

In summary, no effects of eutrophication or variation in *D. antillarum* densities on reproduction, growth or mortality of adults of *F. fragum* were detected in this study. This apparent resistance of *F. fragum* adults to eutrophication may partly be due to the physical conditions in the reef crest zone to which *F. fragum* is adapted. Sediment resuspension caused by the high wave energy in this zone creates very turbid conditions, and spatial variation in turbidity resulting from eutrophication may be minor relative to these turbidity levels. Moreover, the shallow depth of the reef crest zone (1-2 m) may allow high photosynthetic rates in spite of eutrophic water, particularly if photoadaptation capabilities are high.

In contrast to adults, growth and survival rates of juveniles of *F. fragum* appeared to be higher at less eutrophic sites with high *D. antillarum* densities. Wittenberg and Hunte (1992) also reported higher mortality rates of juvenile corals at eutrophic sites with low *D. antillarum* densities in Barbados, although their colonies were older than those used in the present study. Sato (1985) found that juveniles of *Pocillopora damicornis* survived better and grew faster on experimentally manipulated surfaces not affected by high sediment and turf algal growth. The main causes of juvenile mortality of *F. fragum* in the present study were overgrowth by turf and crustose coralline algae, and smothering by sediment, although the cause of many deaths could not be verified. Interestingly, juvenile growth and mortality rates follow the same spatial pattern, i.e. juveniles at LE_1 had the fastest growth and best survival, those at LE_2 had intermediate growth and intermediate survival, and those at E_2 had slowest growth and poorest survival. Growth and mortality may be independently affected by eutrophication levels and differences in *D. antillarum* densities, but the spatial pattern observed may imply an interaction between growth and mortality. Many studies suggest that coral mortality decreases with increasing size (Connell, 1973; Rylaarsdam, 1983; Hughes, 1984; Babcock, 1985; Hughes and Jackson, 1985; Hughes and Connell, 1987; Babcock, 1991). Consequently, faster growth and hence larger size may be a refuge from algal overgrowth and sediment smothering. An interaction between juvenile growth and juvenile mortality will tend to magnify differences in coral abundance between reefs differing in the processes inhibiting juvenile growth and survival.

Invertebrate larvae of benthic marine organisms display complex settlement behaviours enabling them to distinguish between potential settlement substrates (Crisp, 1974; Doyle, 1975; 1976; Underwood, 1979; Hunte *et al.*, 1990a; 1990b; Marsden *et al.*, 1990). Morphogens associated with crustose coralline algae may be instrumental in such behaviours in many organisms (e.g. Gee, 1965; Barnes and Gonor, 1973; Yamaguchi, 1973; Steneck, 1982; Pearse and Scheibling, 1988; Rowley, 1989; Johnson *et al.*, 1991). Larvae of *F. fragum* preferred to settle on crustose coralline algae than on turf algae in this study. This is consistent with the positive correlation between adult abundance of *F. fragum* and abundance of crustose coralline algae observed on Barbados reefs (Chapter 1). Pearson (1981) suggested that the clean, firm surface of crustose coralline algae provides a more suitable settlement surface for corals than turf algal mats; and Lewis (1974a) demonstrated that *F. fragum* preferred to settle on clean surfaces than on surfaces covered with biological slime. Agariciid corals have shown a settlement preference for crustose coralline algae in both the field (Van Moorsel, 1989) and the laboratory (Morse *et al.*, 1988), and Morse and Morse (1991) have characterized the structural elements of the morphogen recognized by *Agaricia humilis*, and controlling the distribution of recruits in the field. These results suggest that crustose coralline algae is an appropriate settlement substrate for corals, but it could also be a spatial competitor (Littler and Littler, 1984; 1985); and overgrowth of both juvenile and adult corals by crustose coralline algae was observed in this study. However, several studies suggest that corals are better competitors against crustose coralline algae than against macroalgae (Sammarco, 1980; Rylaarsdam, 1983; Van Moorsel, 1985).

Settlement rates of coral larvae in Barbados are lower on more eutrophic reefs with lower *D. antillarum* densities than on less eutrophic reefs with higher *D. antillarum* densities (Tomascik, 1991; Hunte and Wittenberg, 1992). Suggested reasons for reduced settlement include a lower level of larval abundance and a lower probability of larvae settling when present, possibly because of limited availability of appropriate settlement substrate (Hunte and Wittenberg, 1992). Local abundance of larvae may be low on eutrophic reefs if reefs are primarily self-seeding (Black *et al.*, 1991) and adult abundance and/or reproduction is lower on eutrophic reefs. Self-seeding may be more likely for bro[illegible]g corals (Richmond, 1987; 1988) such as *F. fragum*, in which planulae can settle wit[illegible]ours of release (Lewis, 1974a; this study). Hunte and Wittenberg (1992) [illegible]ed that the lower settlement on eutrophic reefs in Barbados was unlikely to be sole[illegible]e to lower adult abundance, but could not eliminate the possibility that it resulted from lower larval abundance through reduced local reproduction. The present results suggest that reduced reproduction on eutrophic reefs is not a characteristic of all corals, and h[illegible]n not be contributing to reduced settlement on eutrophic reefs in all species [illegible]bility of suitable settlement substrate may be a more general cause of re[illegible] eutrophic reefs. This is supported by the present results demonstr[illegible]*fragum* prefer to settle on crustose coralline algae than on turf algae, [illegible]er is less common than the latter on eutrophic reefs with low *D. antillarum* de[illegible]

The results of this study suggest that the lower abundance of adults of *F. fragum* on eutrophic reefs (Chapter 1) does not result from effects of eutrophication and lower *D. antillarum* densities on adults, but rather from their effects on settlement and early post-settlement stages. Settlement is lower on eutrophic reefs with low *D. antillarum* densities because crustose coralline algae, a preferred settlement substrate, is largely replaced by turf algae on these reefs. The abundance of adults is further lowered because growth and survival of *F. fragum* juveniles is lower on eutrophic reefs with low *D. antillarum* density. The principal cause of mortality on these reefs may be overgrowth by turf algae and sediment smothering; and susceptibility to these factors may be increased by slower growth and hence smaller juvenile size. The interaction of eutrophication with *D. antillarum* densities can clearly magnify effects of eutrophication on coral abundance. *D. antillarum* is less abundant on more eutrophic reefs, probably because eutrophication processes inhibit its recruitment (Hunte and Wittenberg, 1992; Chapter 1). Turf algae will replace crustose coralline algae and corals on eutrophic reefs, but the rate of replacement will be substantially accelerated by reduced grazing pressure resulting from lower *D. antillarum* density. Finally, it seems likely that the impact of eutrophication and *D. antillarum* density on coral abundance will differ between corals with different life histories. Broadcasting species are typically smaller at settlement and have slower growth rates than brooding species (Babcock, 1985). This may make broadcasters more susceptible than brooders to turf algal smothering following settlement, and may thereby ensure that successful recruitment is reduced more for broadcasters than brooders on eutrophic reefs with reduced grazing pressure. Brooding corals, such as *F. fragum*, may therefore retain their abundance better than broadcasting corals on such reefs; and a shift in community structure towards dominance of brooding corals has recently been reported for eutrophic reefs with low grazing pressure in Barbados (Wittenberg and Hunte, 1992; Allard, 1993).

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GENERAL SUMMARY

Effects of variation in eutrophication and in densities of the black sea urchin *Diadema antillarum* (grazing pressure) on the abundance of *Favia fragum* on seven fringing reefs on the west coast of Barbados were investigated in Chapter 1. Eutrophication was assessed by measuring reactive phosphate, total inorganic nitrogen, suspended particulate matter, volatile particulate matter, and chlorophyll-a concentrations at the seven sites, and using a principal component analysis to reduce the variables to a single eutrophication index at each site. *F. fragum* abundance was surveyed in a total of 210 quadrats (5 x 5 m) of three depth zones of the seven reefs. Cover by crustose coralline algae and macrophytic algae was recorded for each quadrat, and *D. antillarum* densities were surveyed by transect method of each site. Densities of *D. antillarum* were negatively correlated with eutrophication levels across reefs, perhaps because urchin recruitment is inhibited by eutrophication processes. Given the negative correlation between eutrophication and *D. antillarum* density, interpretations of their effects on the abundance of *F. fragum* were made simultaneously thereafter. *F. fragum* was less abundant on more eutrophic reefs with lower *D. antillarum* density (grazing pressure) than on less eutrophic reefs with higher *D. antillarum* density. Effects of eutrophication and grazing pressure on *F. fragum* abundance may occur through their effects on algal cover on reefs. Macrophytic algal cover was cover was higher, and crustose coralline algae lower, on more eutrophic reefs with lower *D. antillarum* density, and macrophytic algal cover was negatively correlated with crustose coralline algal cover across reefs. This suggests that eutrophication and reduced grazing pressure may effect reef communities by increasing the abundance of macrophytic algae relative to crustose coralline algae on reefs. The changes in algal cover may in turn affect *F. fragum* abundance. On areas of a reef where *F. fragum* was present, cover by crustose coralline algae was higher and cover by macrophytic algae was lower, than on areas of the reef where *F. fragum* was absent; and *F. fragum* abundance was positively with crustose coralline algal cover across reefs. A comparison of the present abundance of *F. fragum* with values from previous studies suggests that *F. fragum* abundance of Barbados west coast reefs has declined over the past few decades. Increased coastal eutrophication, and a sharp reduction in *D. antillarum* densities following the mass mortality of this species in Barbados in 1983, may be responsible for the apparent temporal decline in *F. fragum* abundance.

In Chapter 2, effects of eutrophication and of variation in *D. antillarum* densities on life history characteristics of *F. fragum* were investigated to explore possible mechanisms for the reduced abundance of *F. fragum* on more eutrophic reefs with lower *D. antillarum* densities reported in Chapter 1. Planulation in *F. fragum* peaked 8 - 12 days after new moon, but planulation periodicity was not affected by eutrophication levels. Colony fecundity and mean polyp fecundity was positively correlated with colony surface area in *F. fragum*. However, neither coral fecundity, polyp fecundity, nor the relationships between coral and polyp fecundity and coral surface differed at different eutrophication levels and *D. antillarum* densities. As indicated by short-term growth studies using a buoyant weight technique and long-term growth studies based on radial extensions, growth of adults of *F. fragum* did not differ with eutrophication levels and *D. antillarum* densities. Moreover, adult mortality of *F. fragum* did not differ on reefs differing in eutrophication levels and *D. antillarum* densities in this study. By contrast, growth rates of juveniles appeared slower and mortality rates higher on more eutrophic reefs with lower *D. antillarum* densities. In addition, settlement of *F. fragum* may be lower on more eutrophic reefs with lower urchin densities, since suitable settlement space may limiting. Larvae of *F. fragum* preferred to settle on crustose coralline algae than on turf algae in this study; and eutrophication and reduced grazing pressure reduced the abundance of the former and increased the abundance of the latter on the study reefs. The results of this study suggest that the reduced abundance of *F. fragum* adults on eutrophic reefs with low *D. antillarum* densities is primarily caused by effects of these processes on settlement and early post-settlement stages of *F. fragum*.