ECHINOID GRAZING AS A STRUCTURING FORCE IN CORAL COMMUNITIES: WHOLE REEF MANIPULATIONS

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Abstract: To examine the effects of echinoid grazing on shallow water coral community structure, the entire Diadema antillarum Philippi population (> 3000 individuals) was eliminated from a patch reef in Discovery Bay, Jamaica, W.I. in January 1974. All remaining regular echinoids, notably including Echinometra viridis A. Agassiz (> 7000 individuals), were removed from one-half of the same reef 6 months later. Where Echinometra was present, its grazing was highly patchy, even at densities of up to 50/m². On the other hand, the effects of grazing by Diadema were more uniformly distributed at equivalent or lower densities.

Percent-cover of adult corals was enhanced in the presence of Echinometra viridis; however, it was greatly reduced in the absence of all echinoid grazing as a result of massive overgrowth by algae. Success of coral recruitment (density of coral spat) increased in the absence of Diadema due to the alleviation of biological disturbance imposed by this urchin's feeding activities. The presence of Echinometra viridis, even at the high densities naturally present on the reef, did not deter coral settlement.

Coral diversity was highest in the presence of all echinoids, intermediate in the presence of E. viridis (without Diadema), and lowest in the absence of all echinoids. This was due to the disproportionately successful recruitment and resultant high relative abundance of Agaricia at low echinoid densities. Favia, Millepora, Helioseris, and Acropora all exhibited universally low recruitment levels. Predation by Diadema and Echinometra is responsible for damaging larger coral colonies, particularly Porites.

As echinoid species composition and density was altered, the species composition of benthic algae and associated invertebrates shifted. In this way, the array of species competing for space with coral spat shifted as did their competitive relationships. Major epifaunal competitors included spirorbid polychaetes, various foraminifera (particularly Gypsina), and sponges. Algal competitors included filamentous chlorophytes, corallines (e.g. Jania), and numerous other red algae; the species composition of algal competitors shifted through time. Competitive success in corals varied as echinoid density changed and was species-specific with respect to coral genus. Interspecific competition between coral spat (i.e., interspecific aggression via extracoelenteric digestion) was negligible under all treatments.

The presence of Echinometra viridis in high densities (in the absence of Diadema) created conditions where growth and fusion in Agaricia spat were optimized. Under these conditions, fusion allows a young coral colony to attain a large enough size to survive damage incurred from grazing or from competitive overgrowth, decreasing the probability of whole-colony mortality during the early stages of development.

INTRODUCTION

An increasing amount of data is accumulating on the effects of echinoid grazing, particularly in tropical waters (Ogden et al., 1973a,b; Ogden, 1976; Benayahu & Loya, 1982). This study was supported by N.S.F. Biological Oceanography Predoctoral Grant No. 31848A with supplementary support from the Department of Ecology and Evolution, Overseas Academic Program, and the Graduate School, State University of New York at Stony Brook. Contribution No. 396, Ecology and Evolution; No. 238, Discovery Bay Marine Laboratory.

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Grazing in the marine environment by echinoids can contribute to the control of benthic community structure, particularly on hard substrata (reviewed in Lawrence & Sammarco, in press). This control results from their rasping activities and, on coral reefs, is manifested in several ways including direct alteration of distribution and abundance of sessile prey (Sammarco et al., 1974; Lawrence, 1975; Ogden, 1976; and others) and biological disturbance of coral spat (Schuhmacher, 1974; Sammarco, 1977, 1980). Here biological disturbance is defined as incidental alteration of or damage inflicted upon members of a community by the movements or activities of another organism or group of organisms (see Laws, 1970; Dayton, 1971).

By altering the composition, distribution, and abundance of sessile prey, grazing also alters the array of species with which a sessile organism must compete for space. Under primary succession conditions (Odum, 1971), intermediate densities of *Diadema antillarum* Philippi created optimal conditions for settlement and survival of coral spat (Sammarco, 1980). Under post-primary conditions, the effects of grazing on epibenthic community structure appeared to be more complex. Many population and community variables exhibited high variances, including coral cover, abundance, and species diversity.

The genus *Echinometra* is almost as abundant and ubiquitous in tropical and subtropical waters as *Diadema* and usually occurs sympatrically with it. Its habits have been studied predominantly in *Echinometra lucunter* (Abbott et al., 1974; Ogden et al., 1975; Grunbaum et al., 1978; and others) and *E. mathaei* (Kelso, 1970; Khamala, 1971; Russo, 1977). *E. viridis* A. Agassiz is a major but little studied inhabitant of Jamaican reefs.

The object of this study was to assess the differential effects of grazing by *Diadema antillarum* and *Echinometra viridis* on shallow-water coral community structure by means of manipulations of echinoid populations over a whole reef. Here I demonstrate that changes in echinoid density can affect distribution, abundance, species composition, and diversity of corals. Other factors also affected include survival, growth, competitive success, and frequency of fusion in corals.

In caging experiments on reefs, very large coral colonies are usually not included within enclosures. In this experiment cages are not used. The response of juvenile and adult corals will be considered together, allowing the evaluation of effects of echinoid removal in the natural presence of fish without side-effects normally associated with enclosures.

**Materials and Methods**

**Study Site and Treatments**

All experiments were performed on two patch reefs at the southern end of Discovery Bay, Jamaica, W.I. (77°24′W : 18°28′N), chosen because of their abundant echinoid...
<table>
<thead>
<tr>
<th>Activity</th>
<th>1973</th>
<th>1974</th>
<th>1975</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initiation of Treatment 1</td>
<td></td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>(elimination of Diadema)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Initiation of Treatment 2</td>
<td></td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>(elimination of Echinometra viridis and other echinoids)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Echinoid density adjustments</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(minimum 1/month)</td>
<td>x x x x x x x x x x x x x x x x x x x x x x x x</td>
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<td></td>
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<tr>
<td>Sampling</td>
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</tr>
<tr>
<td>Echinoid transects</td>
<td>x</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>Quadrats</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Chain transects</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

TABLE I
Summary of treatments and sampling procedures utilized in this study and the times at which they were executed.
populations. They were Crosby and Stills Reefs, estimated to be 760 and 230 m² in area, respectively, and ranging from 2 to 6 m in depth (Fig. 1). Each reef was divided by two nylon transect lines marked in meters and oriented orthogonally, partitioning each reef into four quadrants.

Densities of regular echinoids were estimated with the aid of quadrats laid along linear transects. The timing of treatments and frequencies with which samples were collected are summarized in Table I. Regions of the reef being utilized for concurrent experiments were avoided during all sampling.

Utilizing an experimental design originally conceived by Ogden et al. (1973b), I eliminated the entire *Diadema antillarum* population of > 3000 urchins from Stills Reef; this will herein be referred to as Treatment 1. Six months later, it became apparent that *Echinometra viridis* was keeping some areas of the treatment reef clear of algae. In order to determine the effects of greatly reduced echinoid grazing on the benthic community and knowing that nearby patch reefs differed in size and depth from the experimental reefs, I eliminated all remaining echinoids (~7000 individuals) from one-half of the same treatment reef (quadrants II and III; Fig. 1). This will be referred to as Treatment 2. (This treatment is confounded with both time and the earlier treatments; thus assessment of the effects of seasonality will not be attempted. The results of the

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Fig. 1. Left, aerial photograph of Discovery Bay, Jamaica, W.I., c.1966; right, illustrations of Crosby and Stills Reefs at southern end of bay, each divided into four quadrants; Crosby Reef, non-treatment area; Stills I/IV, Treatment 1, *Diadema antillarum* population eliminated; and Stills II/III, Treatment 2, elimination of *Diadema* followed by that of all echinoids.
treatment were, however, robust enough to provide insight into effects of negligible echinoid densities on the reef.)

A third area, Crosby Reef, was left undisturbed for comparative purposes; this will be referred to as “the non-treatment”.

Echinoid densities were monitored and adjusted once or twice per month for 15 months to maintain experimental conditions.

**SAMPLING**

Quadrats 0.25 m² in area were selected from each treatment area with the aid of a random numbers table and a cartesian coordinate system which was superimposed on the reefs. The reef surface within each was excised with the aid of hammer and chisel. The cumulative area sampled throughout the experiment was limited to < 2% of any treatment area to minimize potential confounding effects due to sampling.

Samples were labelled, frozen, and later thawed and examined under a dissecting microscope. All algae were removed with forceps and placed in a pre-weighed Petri dish. They were then decalcified in dilute (5%) HCl solution for up to 24 h, oven-dried for ≥ 24 h, and weighed for determination of biomass (g decalcified dry wt).

The samples were then examined for coral spat (> 500 µm in diameter) as well as larger juveniles and adult colonies. Each colony was identified to species and measured for size (estimated by two-dimensional ellipsoidal area; see Sammarco, 1980, for further details on spat processing techniques).

Shortly after initiation of the study, additional measurements of certain characters in coral spat were recorded. Coral condition was assessed as follows: (1) tissue and skeleton intact; (2) overgrown by another sessile organism; (3) skeleton physically damaged; (4) both overgrown and damaged; and (5) complete colony mortality.

Each sessile organism within 8 mm of the colony was recorded and assessed for competitive state. Competition between corals and all other sessile organisms was judged from the coral’s perspective: (1) coral competitively successful, overgrowing neighbor(s); (2) coral competitively unsuccessful, being overgrown by neighbor(s); (3) simultaneous competitive success and loss (with several individuals of the same species or over different portions of the same colony); (4) fusion between coral spat; or (5) lack of contact, associated only.

Techniques of sample processing were further developed and refined as the study progressed. Coral spat became easier to locate and identify, mainly as a result of drying samples prior to processing. This technical artifact has been accounted for in the interpretation of estimated population and community parameters, and care has been taken in making comparisons through time.

Coral cover on the reef was estimated with the aid of chain transects (Porter, 1972; Risk, 1972). A 10-m chain consisting of 507 2-cm links was placed along a transect line and the number of links contacting or occurring within 5 mm of a sessile organism was recorded. Organisms <1 cm were not included in the census estimating coral cover. Four transects were taken per treatment and corals were identified to species.
RESULTS

THE ECHINOIDS AND ALGAE

The non-treatment reef possessed high natural echinoid densities, particularly in comparison to those reported for Tague Bay, St. Croix, U.S. Virgin Islands \((\approx 10/m^2; \text{Sammarco et al., 1974})\). Mean densities here were 71.0/m² for *Diadema antillarum*, 25.5/m² for *Echinometra viridis*, and 99.5/m² for all echinoids combined (Table II).

TABLE II

<table>
<thead>
<tr>
<th>Echinoid species</th>
<th>Crosby Reef</th>
<th>Stills Reef</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diadema antillarum</td>
<td>(\bar{X}) 71.0 72.8 60.7</td>
<td>33.5 1.0*</td>
</tr>
<tr>
<td></td>
<td>(s) 19.45 21.93 22.89</td>
<td>16.69 1.70</td>
</tr>
<tr>
<td></td>
<td>(n) 8 20 20</td>
<td>8 14</td>
</tr>
<tr>
<td>Echinometra viridis</td>
<td>(\bar{X}) 25.5 21.8 24.6</td>
<td>49.5 25.4 45.2</td>
</tr>
<tr>
<td></td>
<td>(s) 27.46 9.83 13.62</td>
<td>17.62 13.37 17.82</td>
</tr>
<tr>
<td></td>
<td>(n) 8 20 20</td>
<td>8 20 20</td>
</tr>
<tr>
<td>Lytechinus williamsi</td>
<td>(\bar{X}) 2.0 2.2 4.1</td>
<td>4.5 5.3 5.1</td>
</tr>
<tr>
<td></td>
<td>(s) 0.53 2.61 2.66</td>
<td>6.52 3.85 3.92</td>
</tr>
<tr>
<td></td>
<td>(n) 8 20 20</td>
<td>8 20 20</td>
</tr>
<tr>
<td>Eucidaris tribuloides</td>
<td>(\bar{X}) 1.0 0.1 0.1</td>
<td>0.0 0.1 0.2</td>
</tr>
<tr>
<td></td>
<td>(s) 2.83 0.81 0.31</td>
<td>0.0 0.31 0.41</td>
</tr>
<tr>
<td></td>
<td>(n) 8 20 20</td>
<td>8 20 20</td>
</tr>
<tr>
<td>Total</td>
<td>(\bar{X}) 99.5 96.9 89.6</td>
<td>87.5 30.8 50.5</td>
</tr>
<tr>
<td></td>
<td>(s) 24.79 22.84 24.88</td>
<td>19.76 16.00 16.11</td>
</tr>
<tr>
<td></td>
<td>(n) 8 20 20</td>
<td>8 20 20</td>
</tr>
</tbody>
</table>

Stills Reef also possessed high densities – 33.5/m² for *Diadema* and 49.5/m² for *Echinometra*. *Lytechinus williamsi* Chesler and *Eucidaris tribuloides* Lamarck were also present on both reefs, but in much lower abundances. Earlier studies have demonstrated that the effects of grazing by *Diadema antillarum* on algal and coral community structure are very similar above densities of 16/m² (Sammarco, 1977, 1980). Thus, the densities encountered here are considered to be sufficiently similar to justify between-reef comparisons.

*D. antillarum* densities in Treatment 1 were kept down to an average of 1.0/m² \((s = 1.70, n = 14)\). Total echinoid density in Treatment 2 was depressed to 2.0 individ-
uals/m² ($s = 2.43, n = 16$). The reasons for the apparent decrease in the density of *Echinometra viridis* 6 months after the elimination of *Diadema* are not understood.

Algal biomass increased as echinoid grazing pressure decreased. Treatment and non-treatment areas were equivalent prior to experimentation (Table III). After

<table>
<thead>
<tr>
<th>Reef</th>
<th>Treatment</th>
<th>1973</th>
<th>1974</th>
<th>1975</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crosby</td>
<td>Control</td>
<td>$\bar{x}$ 1.4961</td>
<td>2.7566</td>
<td>7.1445</td>
</tr>
<tr>
<td></td>
<td></td>
<td>s 2.42847</td>
<td>3.26781</td>
<td>6.43365</td>
</tr>
<tr>
<td></td>
<td></td>
<td>n 4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Stills</td>
<td>(1)</td>
<td>$\bar{x}$ 1.3800</td>
<td>8.2174</td>
<td>14.7359</td>
</tr>
<tr>
<td></td>
<td></td>
<td>s 0.23481</td>
<td>2.29406</td>
<td>15.52355</td>
</tr>
<tr>
<td></td>
<td></td>
<td>n 4</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>(2)</td>
<td>$\bar{x}$</td>
<td>27.2373</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>s 5.89210</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>n 4</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

8 months, algal biomass increased significantly in Treatment 1. Biomass in Treatment 2 was greater than in the non-treatment at completion of the experiment. Biomass in Treatment 1 had a high variance, overlapping with both Treatment 2 and the non-treatment. Although the patchy distribution of *Peyssonnelia* sp. caused a high variance in algal biomass within the non-treatment, there were no significant changes in biomass on that reef through time.

**THE CORALS**

*Density, species composition, and diversity*

Success of coral settlement in both treatments was higher than in the non-treatment 14 to 15 months after initiation of the experiment. There was no significant difference in spatfall of coral between the two treatment areas. The apparent increase observed in coral density under all conditions after 5 months is not considered here, due to the technical artifact described above (see p. 35). No significant differences between conditions were noted after 5 months.
The density of *Agaricia* increased in both treatments (Fig. 3a). It was initially second in dominance to *Porites*, but became dominant only 5 months after the removal of *Diadema* (Fig. 3b). After 15 months, it represented 85% of all corals in Treatment 1 and 81% in Treatment 2 (compared to 69% in the non-treatment). *Agaricia* dominated the non-treatment reef throughout the study.

*Porites* initially occurred in densities equivalent to that of *Agaricia* and subsequently dropped in relative abundance in the area of Treatment 1 (Table IV). After 15 months, *Porites* fell to a clear second rank in both treatments. It consistently ranked second in abundance in the non-treatment.

The density of *Favia fragum* was low under all conditions. In Treatment 2 its relative abundance declined significantly from 2 to 0.1% after 15 months; this was a result of highly successful recruitment in *Agaricia*. Rarer juveniles such as *Millepora*, *Helioseris*, and *Acropora* dropped similarly in relative abundance. The position of *Favia* as third in rank remained constant in the non-treatment area.

Generic coral diversity in Treatment 1 fell significantly below that in the non-treatment after 15 months, whether estimated by cumulative ($P < 0.05$, two-way ANOVA) or mean $H'$ (Fig. 4a; see Pielou, 1969). Generic evenness ($J'$) followed a similar pattern (Fig. 4b).
Fig. 3. a, density of *Agaricia* in no./0.25 m² through time under varying echinoid densities: ●, Treatment 1. *Diadema*-elimination treatment; △, ▲, Treatment 2, complete echinoid elimination; ○, non-treatment; closed circles also refer to treatment reef prior to initiation of experiment in 1973; data derived from 0.25 m² quadrats; density under *Diadema* only elimination conditions significantly higher than non-treatment in 1975 (P < 0.05, Kruskal-Wallis test); b, relative abundance of *Agaricia* in percent through time with 95% confidence limits; confidence limits for first and second treatments contiguous but non-overlapping; arcsine transformation used for purposes of normalization (see Sokal & Rohlf, 1969); arrows represent initiation times of treatments, respectively.
Species composition and relative abundances of corals under echinoid elimination treatment and non-treatment conditions through time: data derived from three (*) or four 0.25-m² quadrats per treatment per sampling period; arrows represent initiation times of treatments, respectively.

<table>
<thead>
<tr>
<th>Species</th>
<th>Crosby Reef Non-treatment</th>
<th>Stille Reef Treatment 1</th>
<th>Stille Reef Treatment 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acropora sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. cervicornis</td>
<td>1.5</td>
<td>0.4</td>
<td>0.9</td>
</tr>
<tr>
<td>A. palmata</td>
<td>0.18</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Agaricia sp.</td>
<td>31.1</td>
<td>54.4</td>
<td>51.4</td>
</tr>
<tr>
<td>A. agaricites</td>
<td>26.5</td>
<td>15.3</td>
<td>11.1</td>
</tr>
<tr>
<td>A. fragilis</td>
<td>7.8</td>
<td>5.9</td>
<td></td>
</tr>
<tr>
<td>A. 33</td>
<td>2.7</td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td>A. 34</td>
<td>2.2</td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td>Eusimilia fastigiata</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Favia fragum</td>
<td>12.1</td>
<td>1.8</td>
<td>4.3</td>
</tr>
<tr>
<td>Helioseris cucullata</td>
<td></td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>Isophyllia sp.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Millepora sp.</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>M. alcicornis</td>
<td>0.8</td>
<td>1.0</td>
<td>7.0</td>
</tr>
<tr>
<td>M. complanata</td>
<td>2.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Porites sp.</td>
<td>12.1</td>
<td>8.0</td>
<td>9.9</td>
</tr>
<tr>
<td>P. astreoides</td>
<td>9.8</td>
<td>4.0</td>
<td>4.0</td>
</tr>
<tr>
<td>P. furcata</td>
<td>0.8</td>
<td>1.3</td>
<td>1.9</td>
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<td>P. porites</td>
<td>0.2</td>
<td>3.3</td>
<td>5.8</td>
</tr>
<tr>
<td>P. 64</td>
<td>1.3</td>
<td>1.0</td>
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</tr>
<tr>
<td>Siderastrea radians</td>
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<td></td>
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<tr>
<td>S. siderea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Solenastrea hyoides</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Stephanovencia sp.</td>
<td>0.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Others</td>
<td>0.8</td>
<td>0.2</td>
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</tr>
<tr>
<td><strong>Summary of major genera</strong></td>
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<tr>
<td>Acropora</td>
<td>1.51</td>
<td>0.4</td>
<td>1.4</td>
</tr>
<tr>
<td>Agaricia</td>
<td>57.6</td>
<td>82.5</td>
<td>69.1</td>
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<td>1.8</td>
<td>4.3</td>
</tr>
<tr>
<td>Helioseris</td>
<td>0.2</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>Porites</td>
<td>22.7</td>
<td>14.8</td>
<td>20.1</td>
</tr>
<tr>
<td>Millepora</td>
<td>3.0</td>
<td>1.2</td>
<td>9.3</td>
</tr>
<tr>
<td><strong>Total no. colonies</strong></td>
<td>132</td>
<td>548</td>
<td>576</td>
</tr>
</tbody>
</table>
Fig. 4. a. generic diversity ($H'$) of corals, including juveniles and adults, as a function of time: ●, Treatment 1, Diadema-only elimination; ▲, Treatment 2, complete echinoid elimination; ○, non-treatment; closed circles also refer to treatment reef prior to initiation of experiment in 1973; significant difference between Diadema-elimination treatment and non-treatment in 1975 ($P < 0.05$, two-way ANOVA); no significant difference between elimination treatments ($P > 0.05$, one way ANOVA); b, generic evenness of corals ($J'$) as a function of time; Diadema-elimination treatment significantly lower than non-treatment in 1975 ($P < 0.05$, two-way ANOVA); arrows represent initiation times of treatments, respectively.
The number of coral genera and species in Treatment 1 was significantly higher than the non-treatment ($P < 0.05$, one-way ANOVA). This was predominantly a result of the addition of rare corals such as *Eusimilia fastigiata*, *Isophyllia* sp., and *Solenastrea hyoides*. The two elimination treatment areas were equivalent in diversity, irrespective of the diversity index considered ($P > 0.05$).

**Cover and growth**

Coral cover decreased significantly in Treatment 2 from 41 (5 months) to 24% (15 months; Fig. 5). This was well below levels estimated in the other areas and was a direct result of losses in competition with algae for space. In Treatment 1, coral cover increased significantly from 36 to 48%. Cover decreased in the non-treatment area from 47 to 39%.

![CORAL COVER](image)

Fig. 5. Percent cover of live coral through time: 95% confidence limits also shown; ●, Treatment 1, *Diadema*-only elimination; ▲, Treatment 2, complete echinoid elimination; ○, non-treatment; data derived from chain transects; percent transformed by arcsine for purposes of normalization (see Sokal & Rohlf, 1969); arrows represent initiation time of treatments, respectively.

The size-frequency distributions of *Agaricia* on the two reefs were equivalent prior to initiation of the experiment. After 5 months, the area of Treatment 1 possessed a significantly higher proportion of large colonies ($P < 0.05$, three-way contingency analysis); 42% of the colonies were >16 mm² compared to 32% in the control. This difference disappeared after 15 months. *Agaricia* colonies in the area of Treatment 2 were smaller than those of Treatment 1 ($P < 0.05$), but were statistically indistinguishable from those in the area of non-treatment ($P > 0.05$).

The size-frequency distribution of *Porites* shifted noticeably after 15 months. The average colony size in Treatment 2 dropped well below those in Treatment 1 and the non-treatment (Fig. 6).
Fig. 6. Size-frequency distributions of *Porites* under non-treatment conditions (Crosby Reef), *Diadema*-elimination conditions (Treatment 1), and complete echinoid elimination conditions (Treatment 2) through time; in latter years, darkened areas represent proportion of corals in excellent condition; open areas represent all other states combined; significantly lower proportion of large colonies found in second treatment in 1975 ($P < 0.005$, 3-way contingency analysis); also significantly higher survival in larger colonies in first treatment at this time ($P < 0.005$).
Condition, competition, and fusion

After 14 to 15 months, the proportion of *Agaricia* colonies found in excellent condition (state 1) increased in Treatment 1 (Table V). No net change was detectable in Treatment 2 (*P* > 0.05, three-way contingency analysis), but the larger colonies (> 152 mm²) were found to suffer significantly higher levels of overgrowth and mortality than the smaller ones (*P* < 0.005).

The condition of *Porites* in Treatment 1 changed in a manner similar to that of *Agaricia*, but a significant increase in the proportion of *Porites* colonies in excellent condition also increased in Treatment 2. The larger *Porites* colonies (> 38 mm²) of Treatment 1 were in better condition on the average than those in Treatment 2 or the non-treatment (Fig. 6).

Physical damage sustained by colonies of *Porites* and *Agaricia* was highest in the non-treatment area. Damage was significantly lower in Treatment 1 and negligible in Treatment 2. *Porites* consistently exhibited the highest levels of damage under all conditions.

The competition variable was defined as the proportion of competitive wins in corals of a particular taxon observed to be in physical contact with some other sessile epibiote. A total of over 3000 competitive interactions were observed in samples representing 4.75 m² of reef. Competitive success in *Agaricia* generally decreased as density of echinoids decreased (Table VI). This was most pronounced in the absence of all echinoids. By contrast, the highest degree of mortality in *Porites* occurred at the highest echinoid density, as was clearly evident at the completion of the study.

Major epifaunal competitors of corals after 5 months were spirorbid polychaetes, various foraminifera (particularly *Gypsina*), and several sponges (Table VII). Major algal competitors in the first treatment were unidentifiable filamentous chlorophytes, *Peyssonnelia* sp., encrusting corallines, and *Herposiphonia secunda*. In both treatments, the array of competitors varied through time. Near the end of the experiment, numerous other rhodophytes became major contenders for space in both elimination treatments.

Interspecific competition between coral spat via extracoelenteric digestion was among the most infrequent of events, accounting for < 1% of all competitive interactions.

*Agaricia* spat were commonly found in aggregations (Table VII), and the usually rare phenomenon of natural fusion between spat became relatively common in Treatment 1. Fusion is the result of two conspecific corals growing into contact and jointly accreting CaCO₃ (Fig. 7). A similar action in two heterospecifics (and some conspecifics) can trigger extracoelenteric digestion in one against the other (Lang, 1971, 1973; Hildemann et al., 1977; Sheppard, 1979), even in spat (Fig. 8).

The frequency of fusion in *Agaricia* increased from 0 to 5% in Treatment 1 (Table VIII). Negligible levels of fusion were characteristic of Treatment 2, despite a similar increase in *Agaricia*’s density. Fusion was negligible in the non-treatment. *Porites* exhibited universally low frequencies of fusion.
Coral condition in *Agaricia* and *Porites*; data presented are percent of colonies found in excellent or damaged condition; data derived from three to four 0.25-m² samples per treatment per sampling period; proportion of *Agaricia* in excellent condition in Treatment 1 increased significantly in 1975 ($P < 0.005$, three-way contingency analysis); significantly higher than non-treatment ($P < 0.05$); condition in *Porites* increased significantly in both treatments in 1975 ($P < 0.05$); in all cases, proportion of damaged coral colonies in non-treatment significantly higher than treatments, 1974 and 1975; Treatment 2 significantly lower than Treatment 1; higher levels of damage in *Porites* in all cases ($P < 0.005$, two- and three-way contingency analyses); 95% confidence limits also shown.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Reef</th>
<th>Treatment</th>
<th>Excellent (1)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>%</td>
</tr>
<tr>
<td><em>Agaricia</em></td>
<td>Crosby</td>
<td>Non-treatment</td>
<td>64.1</td>
</tr>
<tr>
<td></td>
<td>Stills</td>
<td>(1)</td>
<td>64.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(2)</td>
<td>-</td>
</tr>
<tr>
<td><em>Porites</em></td>
<td>Crosby</td>
<td>Non-treatment</td>
<td>60.08</td>
</tr>
<tr>
<td></td>
<td>Stills</td>
<td>(1)</td>
<td>63.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(2)</td>
<td>-</td>
</tr>
</tbody>
</table>
Competitive success in *Agaricia* and *Porites* under *Diadema*-elimination (Treatment 1), total echinoid elimination (Treatment 2), and non-treatment conditions through time: competition index represents percent of colonies overgrowing another sessile epibenthic organism if involved in competitive encounter; 95% confidence limits also shown; estimates derived from three to four 0.25-m² quadrats per treatment per sampling period.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Crosby</td>
<td>Control</td>
<td>60.0</td>
<td>(55.59-65.54)</td>
<td>371</td>
<td>62.1</td>
<td>(56.72-67.22)</td>
<td>327</td>
</tr>
<tr>
<td></td>
<td>(1)</td>
<td>47.7</td>
<td>(41.75-53.79)</td>
<td>266</td>
<td>60.5</td>
<td>(57.42-63.56)</td>
<td>1193</td>
</tr>
<tr>
<td></td>
<td>(2)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Table VI
Fig. 7. Fusion between two *Agaricia* spat resulting from contact through growth after settlement: scale in mm.

Fig. 8. Scanning electron micrograph of intraspecific aggression between two *Porites* spat: in this case, fusion has not occurred.
Competition and association matrix for *Agaricia* under varying echinoid densities through time: data presented are total number of competitive wins, losses, or simple associations, respectively: 1, competitive win via overgrowth; 2, competitive loss via overgrowth; 5, associated only; data derived from three to four 0.25-m² quadrats per treatment per sampling period.

<table>
<thead>
<tr>
<th>Competitors and associates of <em>Agaricia</em> (Competitive state)</th>
<th>Crosby Reef</th>
<th>Stills Reef</th>
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<tr>
<td></td>
<td>Non-treatment</td>
<td>Treatment 1</td>
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<tr>
<td><strong>Corals</strong></td>
<td></td>
<td></td>
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<tr>
<td><em>Agaricia</em> sp.</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td><em>A. agaricites</em></td>
<td>1</td>
<td>17</td>
</tr>
<tr>
<td><em>A. fragilis</em></td>
<td>16</td>
<td>5</td>
</tr>
<tr>
<td><em>A. 33</em></td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td><em>Porites</em> sp.</td>
<td>10</td>
<td>5</td>
</tr>
<tr>
<td><em>P. astreoides</em></td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td><em>Asfarangia</em> solitaria</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Other corals</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td><strong>Other epifauna</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spirobranchus polychaetes</td>
<td>23</td>
<td>4</td>
</tr>
<tr>
<td>Foraminifera</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Gypsina</em> 521</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td><em>Gypsina</em> 522</td>
<td>22</td>
<td>8</td>
</tr>
<tr>
<td><em>Homotrema rubrum</em></td>
<td>15</td>
<td>32</td>
</tr>
<tr>
<td>Other Forams</td>
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<td>2</td>
</tr>
<tr>
<td>Porifera</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cliona</em> apica</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>Other sponges</td>
<td>20</td>
<td>3</td>
</tr>
<tr>
<td>Ectoproct, Unident.</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Encrusting forms</td>
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<td>1</td>
</tr>
<tr>
<td>Other epifauna</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Algae</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>---------------------------</td>
<td>----</td>
<td>----</td>
</tr>
<tr>
<td>Amphiroa sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ceramium spp.</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Champia parvula</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Cladophora sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. brasiliana</td>
<td>7</td>
<td>10</td>
</tr>
<tr>
<td>C. crispata</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>C. crassifolia</td>
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<td></td>
</tr>
<tr>
<td>Other Cladophora spp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coelothrix irregularis</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Corallines, encrusting</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unident.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1471</td>
<td>29</td>
<td>32</td>
</tr>
<tr>
<td>1472</td>
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<td>41</td>
</tr>
<tr>
<td>1473</td>
<td>10</td>
<td>5</td>
</tr>
<tr>
<td>Gelidium pusillum</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>G. caribaea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Herposiphonia secunda</td>
<td>2</td>
<td>12</td>
</tr>
<tr>
<td>H. tenella</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jania adhaerens</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>J. capillacea</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Kallymenia spp.</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Padina sp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Peyssonnelia sp.</td>
<td>12</td>
<td>35</td>
</tr>
<tr>
<td>Polyphorina spp.</td>
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<tr>
<td>P. exilis</td>
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<td>1</td>
</tr>
<tr>
<td>Unident. filamentous</td>
<td></td>
<td></td>
</tr>
<tr>
<td>chlorophytes</td>
<td></td>
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</tr>
<tr>
<td>Unident. rhodophytes</td>
<td>7</td>
<td>11</td>
</tr>
<tr>
<td>Valonia ocellata</td>
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<td>1</td>
</tr>
<tr>
<td>V. ventricosa</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Other algae</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>225</td>
<td>146</td>
</tr>
</tbody>
</table>
Table VIII

Percent of intraspecific colony fusion in spat of *Agaricia* under *Diadema*-elimination (Treatment 1), total echinoid elimination (Treatment 2), and non-treatment conditions through time: 95% confidence limits also shown; significant increase in *Agaricia* in *Diadema*-only elimination treatment in 1975 (*P* < 0.05, two-way contingency analysis).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>1974</th>
<th>1975</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>% Fused</td>
<td>95% C.L.</td>
<td>N</td>
<td>% Fused</td>
<td>95% C.L.</td>
<td>N</td>
</tr>
<tr>
<td>(1)</td>
<td>0.0</td>
<td>(0.0–0.85)</td>
<td>436</td>
<td>4.9</td>
<td>(3.68–6.46)</td>
<td>993</td>
</tr>
<tr>
<td>(2)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0.9</td>
<td>(0.39–1.85)</td>
<td>765</td>
</tr>
<tr>
<td>Non-treatment</td>
<td>0.9</td>
<td>(0.27–2.22)</td>
<td>452</td>
<td>2.0</td>
<td>(0.98–3.82)</td>
<td>398</td>
</tr>
</tbody>
</table>

**DISCUSSION**

Echinoid grazing affects numerous community characteristics of the reef but in a species-specific manner. The effects of grazing by *Diadema* appear to be more uniformly distributed than those of *Echinometra viridis*. Individual estimates for algal biomass in the absence of *Diadema* overlapped both the non-grazed and overgrazed conditions, despite a density of *Echinometra viridis* of nearly 50/m² (Table III). This high variance suggests that *E. viridis*, even in high densities, grazes locally creating numerous small algae-free patches on the reef. *Diadema*, on the other hand, appears to be a more efficient grazer, being capable of clearing algae from the reef at densities of > 16/m² (Sammarco, 1977, 1980).

Coral cover is clearly depressed in the absence of echinoids. Many corals characteristic of shallow water were unable to survive extensive overgrowth by algae (Table IV). The visual appearance of the experimental area changed from a shallow water patch-reef to that of an algae-dominated back-reef, despite the presence of other grazers such as fish (scarids and acanthurids) and gastropods (cerithiids). Echinoid grazing contributes to the maintenance of sustained growth in large corals. The presence of high densities of *Echinometra viridis* in the absence of *Diadema antillarum* creates favourable conditions for coral growth, as is evidenced by the increase in coral cover under these conditions.

**CORAL RECRUITMENT, BIOLOGICAL DISTURBANCE, AND DIVERSITY**

Dart (1972) predicted that increased echinoid grazing would decrease competition between corals and algae, providing additional free space for coral settlement. Others have also claimed that algae inhibit the settlement of sessile invertebrates, including corals (Stephenson, 1930; Bakus, 1969; Vine, 1974; Potts, 1977). Concurrent studies (Sammarco, 1980) demonstrated that algae do not inhibit coral settlement in the absence of grazing; rather, an important factor limiting success of settlement is bio-
logical disturbance. Schuhmacher (1974) and Day (1977) reached similar conclusions. Additional supporting evidence has been presented here and lends further insight into the problem. The removal of *D. antillarum* alone resulted in increased success of coral settlement. High densities of *Echinometra viridis* and the presence of herbivorous fish did little to deter it (Fig. 2). Strong evidence of a species-specific interaction has emerged and may apply to coral reefs wherever *Diadema antillarum* (and perhaps other species of *Diadema*) occur in high densities.

The two major coral genera affected were *Agaricia* and *Porites*. These genera produce planulae which settle in great numbers (Bak & Engel, 1979), but the presence of their spat becomes conspicuous only at relatively low *Diadema* densities. In general, these genera appear to be more sensitive to the grazing activities of *Diadema* than to those of *Echinometra viridis* or other grazers.

Most other corals exhibited characteristically low recruitment rates. *Favia fragum*, however, can be prolific, colonizing in great numbers in the absence of fish and regular echinoids under primary succession conditions (Sammarco, 1980). Here, under post-primary conditions, its recruitment remained universally low under all conditions. It is possible that *Favia* planulae exhibit a settlement preference for primary substratum at low grazing pressures, but this remains to be conclusively demonstrated.

Very few *Acropora* spat (≈1.5% of all spat) were observed in the samples. This is similar to the 1% level observed in the concurrent study. It is possible that this genus is less dependent on larval dispersal than some other corals. Storm surge and wave shock are already known to be important means of vegetative dispersal for *Acropora*, especially in the Caribbean (Gilmore & Hall, 1976; Bak & Engel, 1979; Tunnicliffe, 1979; Highsmith *et al.*, 1980).

The frequency and extent of damage incurred by corals varied greatly between the treatments. Apparently, predation on corals by both *Diadema* and *Echinometra viridis* is at least genus-specific, as *Porites* consistently sustained higher levels of damage than *Agaricia* (Table V). This concurs with observations made recently on Britomart Reef, Great Barrier Reef where *Porites* also exhibits proportionally higher degrees of damage than other sympatric corals as a result of fish predation (pers. obs.; Loya & Lovell, pers. comm.). Physical damage suffered by large *Porites* and *Agaricia* colonies was most likely a result of directed predation (Bak & Van Eys, 1975). The incidental ingestion of or damage imparted to newly settled spat is most likely non-directed as a result of the spat's minute size (500 μm to several mm), and this may mark an important distinction between the process of predation and biological disturbance.

The observed decline of coral diversity (*H'* and *J'* ) as a response to reduced echinoid density does not agree with the response exhibited by coral spat in a concurrent experiment where *Diadema* density alone was altered (Sammarco, 1980). The drop in diversity here may be attributed predominantly to lack of recruitment by *Favia* and the disproportionate increase in *Agaricia* recruitment under conditions of reduced echinoid grazing (Table IV). This points to differences in the predictability of responses within the coral community to changes in echinoid density, depending on the stage of suc-
cession at which the treatment is imposed and on the response of the individual coral species to that treatment.

Reduction in grazing activities by *Diadema* not only caused an increase in overall coral settlement but also allowed a greater number of coral genera to recruit successfully and survive. These included rare species such as *Eusimilia fastigiata*, *Isophyllia* sp., and *Solenastrea hyoides*. Although these species do not account for a large proportion of the coral cover, they do contribute in an important way to overall coral diversity on Jamaican reefs (Goreau & Wells, 1967; Wells, 1973).

**COMPETITION FOR SPACE, CORAL GROWTH, AND FUSION IN SPAT**

The removal of key competitors for space and the lack of urchin predation on adult colonies apparently aided the survival of *Agaricia* at high urchin densities. The drop in the competitive success of *Porites* was correlated with an increase in predation upon it by urchins at high urchin densities. *Porites* is highly susceptible to overgrowth by algae, and the lesions resulting from urchin predation would provide excellent sites for colonization by algae and other competitors. This would hinder regeneration and depress overall competitive success. These findings concur with those of Fishelson (1973) and Bak *et al.* (1977).

*Diadema* regulated the success of coral recruitment but optimal conditions for growth, at least in *Agaricia*, occurred in the presence of *Echinometra viridis*. This was due to alleviation of competition for space, allowing many of the young colonies to grow to a large enough size to survive injuries sustained from grazing (also see Birkeland, 1977).

The high frequency of successful fusion in *Agaricia* was a function of both increased density and optimal conditions for growth. The density of *Agaricia* was high in both treatments but the frequency of fusion in Treatment 2 was as negligible as in the non-treatment. Successful fusion appeared to be enhanced by a combination of high spat density, aggregated settlement patterns (as has also been reported by Lewis, 1974), and moderately low levels of competition for space. All of these were characteristic of Treatment 1 (i.e., the absence of *Diadema* and the presence of *Echinometra*).

If two conspecific spat fuse, their functional size is increased as is their chance of survival. This has been suggested by Knight-Jones & Moyse (1961) and Hamilton (1971) for fusion within certain algae, ascidians, and other colonial organisms. It is suggested here that this concept may be extended to juvenile corals.

In conclusion, the control by echinoid grazing of community characteristics such as algal biomass is an obvious first-order effect. Echinoids can also, however, act as a source of disturbance and predation on coral reefs, influencing competition for space between corals and associated epibiota at all stages of development. The presence of *Echinometra viridis* can enhance coral growth, while the absence of all echinoids, including *Diadema antillarum*, can result in massive coral mortality due to algal overgrowth. Echinoid grazing clearly contributes to the control of shallow-water coral
community structure, and this control varies in character with the urchin species in question.

ACKNOWLEDGEMENTS

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REFERENCES


PAUL W. SAMMARCO


