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ABSTRACT

The effects of grazers on the biomass of algae and coral recruitment have been investigated extensively in shallow water, yet the dynamics of this interaction in deeper water have received, by comparison, relatively little attention. Fifteen cement artificial reefs were established at a depth of 20m in Salt River Canyon on the north coast of St. Croix. One third of the reefs were exposed to all grazing organisms, one third were protected from macrograzers by exclusion cages, and one third had partial cages (controls). After a year-long immersion, 267 corals of two genera were found, and comparisons were made between the three reef treatments. Numbers of newest coral recruits (3mm diameter and less) were similar on all types of reefs, indicating similar rates of settlement. However, caged reefs, with visibly greater algal biomass, had significantly fewer of the larger juveniles than those that were uncaged and exposed to (primarily fish) grazers. Though relatively few herbivores occur at these depths, herbivory nevertheless appears to indirectly control the survival of coral recruits, and hence determines the structure of coral communities on moderately deep reefs.

INTRODUCTION

Coral reefs and their primary structural component, scleractinian corals, have been the focus of intensive study, with numerous investigators analyzing some aspect of the ecology of the corals. Yet an understanding of the factors influencing coral distribution is far from complete. The present study attempts to elucidate the effects of fish (and echinoid) grazing on the settlement and survival of scleractinian corals at intermediate (20m) depths.

The effects of competition for space between algae and coral planulae or settled corals has received some attention (e.g.,Dart 1972, Vine 1974, Kaufman 1977, Potts 1977, and others cited below), particularly in shallow water. Sammarco (1980) manipulated densities of the echinoid *Diadema antillarum* in shallow water, finding that ungrazed areas of high algal biomass (free from predation or disturbance by *Diadema*) allowed the highest rates of coral settlement. Subsequent survival, however, was highest in areas subject to moderate grazing pressures: competition from algae in ungrazed areas -- and predation/disturbance in heavily grazed areas -- reduced coral survivorship. Certain fishes also crop the algae and/or prey on small corals. Brock's (1979) microcosm study revealed low rates of coral recruitment in areas exposed to grazing scarids. Given adequate spatial refuges for the corals, however,

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the highest recruitment was then found in the presence of the fishes, which cropped the algal competitor without harming the corals. Also, damselfishes, maintaining territories that form algal mats, can have either positive or negative effects on corals, depending upon the location of the coral relative to the territory (see Vine 1974, Kaufman 1977, Wellington 1982).

Observing the browsing activities of Caribbean acanthurid and scarid fishes, Birkeland (1977) found evidence that fishes avoided corals as small as 3mm; yet Bak and Engel (1979) saw no such avoidance. Moreover, Neudecker (1977, 1979) observed fishes selectively preying on corals transplanted to different areas on Pacific reefs. The extent to which urchins and fishes prey upon corals may depend to a great extent on the availability of the preferred food resource. Diadema, for instance, shift to feeding on corals as the preferred algal food is diminished through grazing (Carpenter 1981). The differing observations reported above may be a reflection of different grazer densities and/or algal biomass in the various study sites. Manipulative studies such as Sammarco's (1980) and Brock's (1979) indicate the existence of optimal levels of grazing for coral survival, with these grazer densities apparently being closer to those commonly found on the reefs.

We sought to determine the influence that grazers naturally present at intermediate depths have on populations of juvenile corals. As a large number of cement artificial reefs were constructed and censused, extensive underwater time was required and the work would not have been feasible without the saturation diving facilities of NOAA's underwater habitat, NULS 1 (Hydrolab).

The study area is off the north coast of St. Croix, US Virgin Islands, in Salt River Submarine Canyon. The canyon extends seaward from a small estuary, with the canyon walls being variously covered by hard corals and coral rubble, sponges, gorgonians, etc. (see Rogers et al. 1983). The artificial reefs were established on the sandy floor of the canyon, well removed from the reef complex of the walls. This is an area of shifting sand uncolonized by benthic macroflora; during periods of heavy swells on this exposed coastline, sand scouring around the reefs is evident.

METHODS

Artificial reefs were established during NOAA Hydrolab Mission #81-1 in January 1981. Each reef structure was identical, consisting of 11 cement cinder blocks stacked and lashed together in three layers of 6, 4, and 1 block per layer. Total censused surface area of each reef was $0.93m^2$ vertical and $0.46m^2$ horizontal substrate. Corals inside the holes of the cinder blocks were not censused. Cage enclosures were composed of 2.5 X 5cm wire mesh over a 1.5 X 3 X 1.5m frame.

A total of fifteen reefs were constructed at a depth of 20m on the canyon floor along a line a constant 15m distance from the junction of the sandy floor and the east coral wall. The reefs were divided equally into three treatment types, with each reef along the line being an alternate treatment. Uncaged reefs were exposed completely to fishes and invertebrates; caged reefs were totally enclosed by cages; and cage controls had cages with two sides and the top partly-open, allowing access by macrofauna.

In January 1982 during Hydrolab Mission #82-1, all of the reefs were censused in situ for juvenile scleractinian corals. Maps of each reef were employed to record the location of the corals, its identification to genus and sometimes species, and its length and width (± 0.5-1mm). Deterioration of all the cages during storms in February 1982 did not allow repeat censuses of the corals on the caged reefs.

After initial establishment of the reefs, periodic fish censuses were performed to quantify the number of resident fishes on the reefs. Transient fishes (including herbivorous fishes around the reefs) were not quantified. Numbers of Diadema antillarum, being low, were recorded during only one census in February 1982.

Analyses of variance (ANOVA), both completely randomized and randomized block design, and Student's t-tests were employed for statistical analysis as was appropriate. Where the ANOVA indicated significant differences ($p<0.05$), Tukey's Studentized Range Test was used to determine which cells differed significantly ($p<0.05$).

RESULTS

Cage effects: corals

After the year-long immersion, a total of 267 corals were found on the fifteen reefs, all being on vertical edges. This included only two genera of corals: *Porites* and *Agaricia* formed 19% and 81% of the total number of corals, respectively. Difficulty with *in situ* identification of corals less than approximately 6mm in diameter prevented assigning species to the smallest corals. However, of the larger *Agaricia* sp., approximately 2/3 were *A. agaricites* and 1/3 *A. lamarki*. All *Porites* were *P. astreoides*.

A Student's t-test indicated no significant differences in the numbers of *Porites* vs. *Agaricia* on any reef treatment; thus all further analyses pooled both genera. Substantially more corals settled on uncaged and cage control reefs (totals of 123 and 90 respectively) than on caged reefs (54 total). However, a one-way ANOVA showed that the mean number of corals on the three reef types was not significantly different, nor was the mean diameter (Table 1).

Table 1. Number of corals on each reef; total number and mean for each treatment type; mean diameter of corals for each treatment type. Numbers in parentheses are standard deviations; n.s. = not significant ($p<0.05$).

	Caged		Uncaged		Cage Control
Rep.#1	10		12		14
Rep.#2	19		26		28
Rep.#3	9		41		20
Rep.#4	1		34		10
Rep.#5	15		10		18
Total	54		123		90
Mean number	10.8 (±6.8)	n.s.	24.6 (±13.5)	n.s.	18.0 (±6.8)
Mean diameter (mm)	5.3 (±3.0)	n.s.	6.8 (±3.0)	n.s.	5.4 (±2.6)

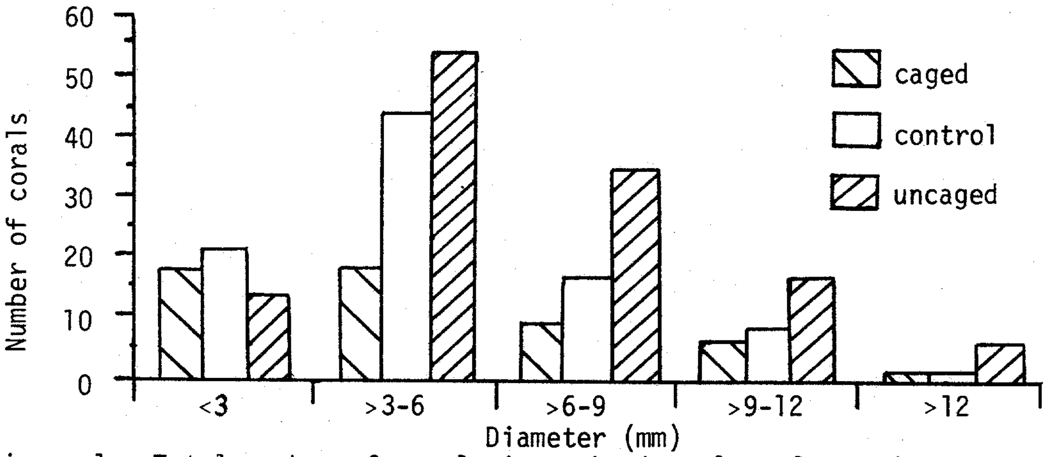
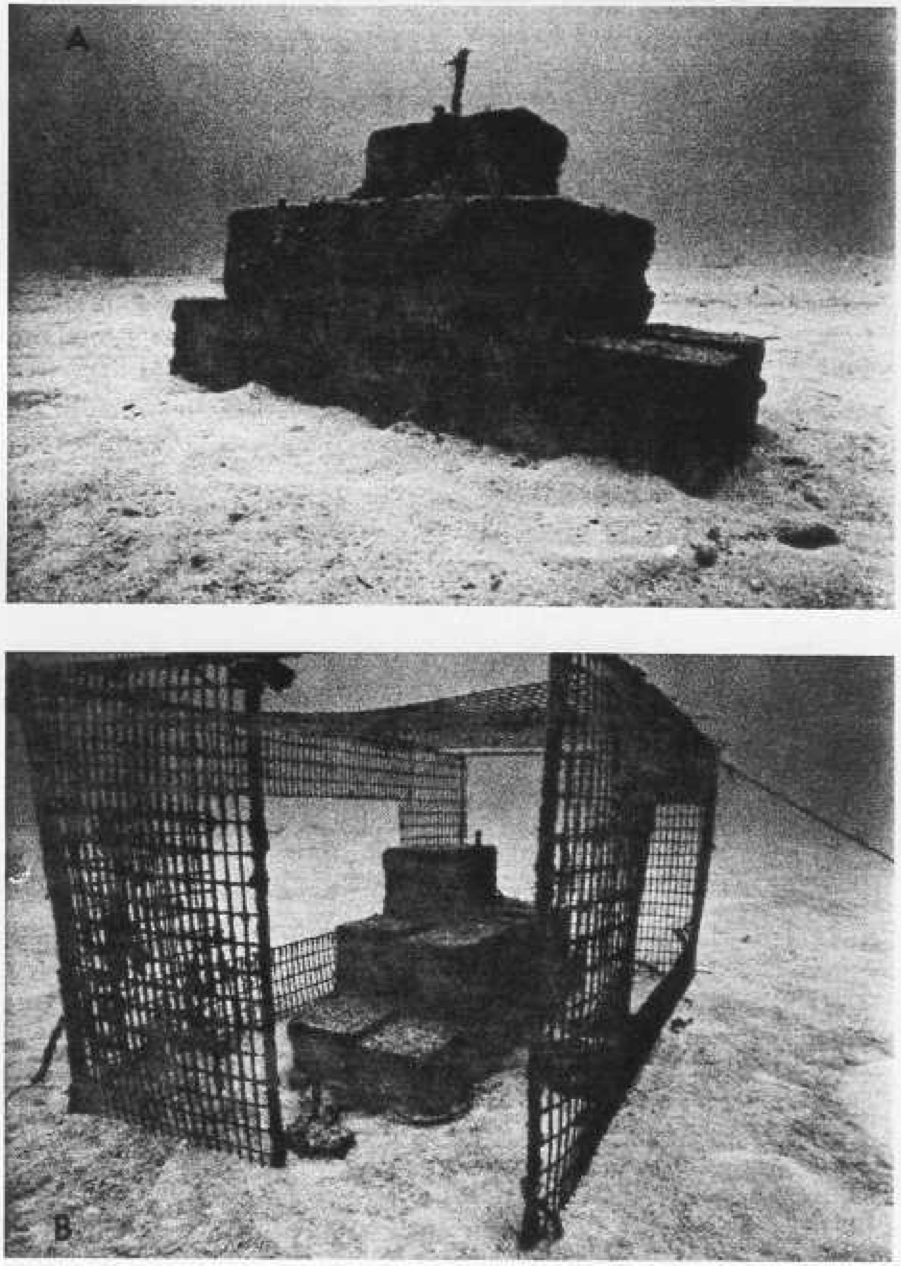
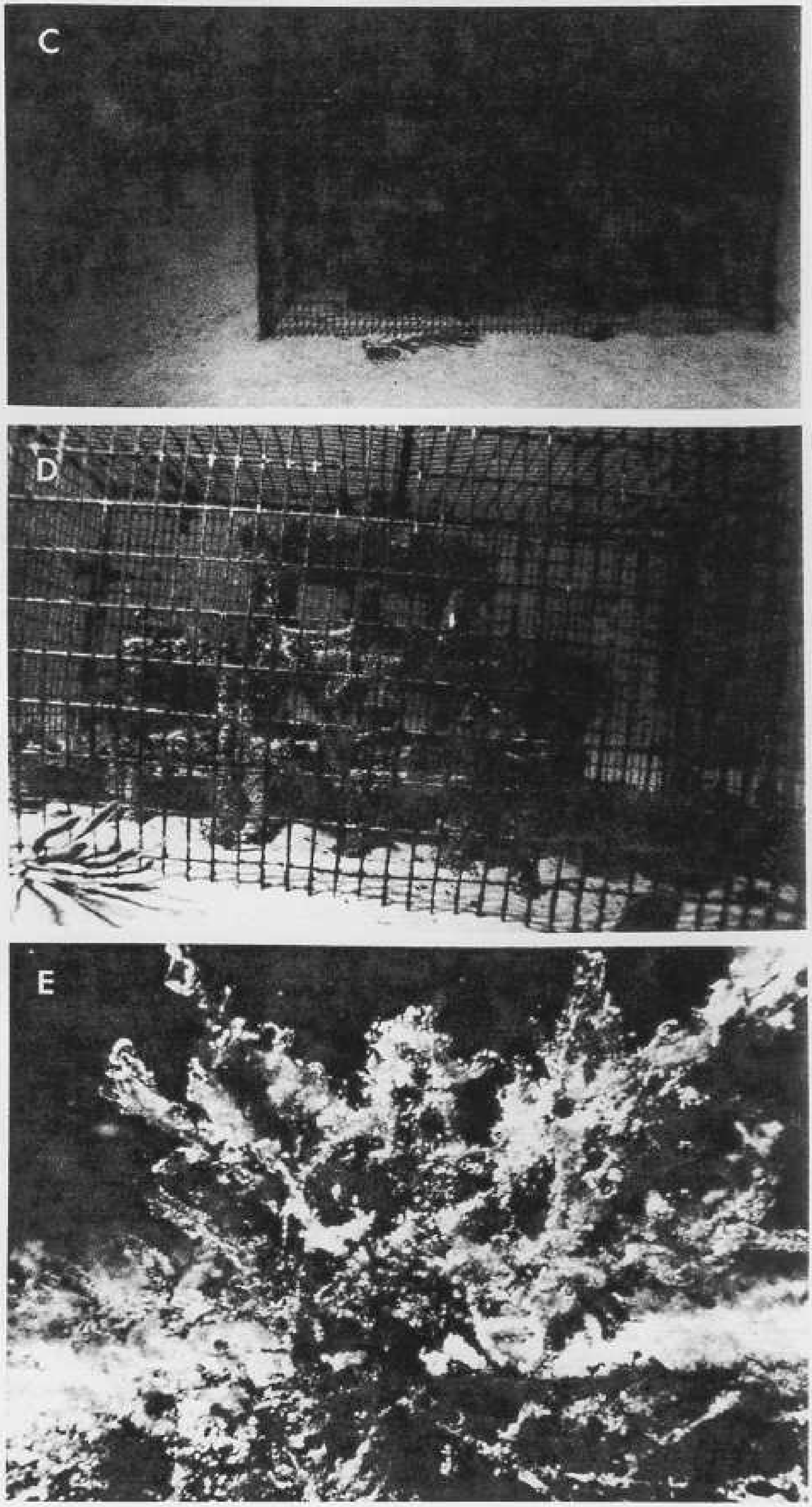


Figure 1. Total number of corals in each size class for each treatment type.

Figure 2. A. Open artificial reefs built of cinder blocks as described in the text. B. Cage control. C. Caged artificial reef. D. Closer view of caged artificial reef, showing extensive algal growth about 3 months after initiation of the experiment. E. Close-up view of fleshy algal growth on the edge of a cinder block in a caged reef.

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Though no overall differences in numbers of corals existed between types of reefs, the size (age) structure of corals on the reef types was dissimilar. Corals on each type of reef were divided into five size classes at 3mm intervals. The total number of corals in each size class for the combined five reefs of each type are depicted in Figure 1; the general trend of similar numbers of newest (≤3mm) recruits and differing numbers of older corals between types of reefs is evident.

A two-way ANOVA indicated a significant effect of type of reef treatment (blocked over size classes) on the mean number of corals per reef. With this knowlege, a one-way ANOVA on each size class was used to determine which size class(es) had different mean numbers of corals between the reef types. The only significant difference was found in the >6-9mm class, with a Tukey's Studentized Range Test indicating that the caged reefs had significantly fewer corals than the uncaged reefs (Table 2). Shading by cages was insignificant, as the cage control did not differ from the uncaged reefs.

Table 2. Mean number of corals in each size class for each treatment type. Five replicates in each cell, numbers in parentheses are standard deviations, asterisk indicates significant difference ($p<0.05$).

	Caged		Uncaged	Cage control
≤3mm	3.8(±2.6)		2.6(±2.0)	4.4(±4.0)
>3-6mm	3.8(±2.6)		10.6(±7.2)	8.6(±4.6)
>6-9mm	1.8(±1.9)	*	7.0(±3.7)	3.2(±2.5)
>9-12mm	1.2(±1.3)		3.4(±4.0)	1.6(±1.1)
>12mm	0.0(±0.5)		1.0(±1.2)	0.0(±0.5)

Grazing fishes and invertebrates

Diadema antillarum was an uncommon echinoid on these reefs, well removed from the hard substratum of the East Wall of the canyon. One complete census showed an occasional Diadema on the ten uncaged and cage control reefs for a mean of 0.4 per reef. Total available surface area (including 12X12cm holes uncensused for corals) was $3.4m^2$.

The herbivorous fishes around the reefs were acanthurids, scarids and pomacentrids. Bicolor damselfish (Eupomacentrus partitus) were common residents on the reefs, along with occasional juvenile blue tangs (Acanthurus coeruleus). Schools of roaming doctorfish (A. chirurgus) and ocean surgeons (A. banianus) were common but, due to their transient nature, difficult to quantify (see Wolf et al. 1983 for the results of the fish censuses). Princess parrotfish (Scarus taeniopterus) were seen occasionally, again roaming about between different reefs.

The cages effectively excluded these larger macrograzers, as evidenced by the very noticable difference in cover of filamentous algae. The algal 'turf' on the exposed reefs was cropped extremely short, whereas thick, long tufts of filamentous algae and some fleshy algae were present on the completely caged reefs (see Figure 2).

DISCUSSION

Recruitment to these reefs, as evidenced by numbers of the smallest corals, was similar in both ungrazed and grazed situations. Though algal biomass was visibly greater on ungrazed reefs, space for coral settlement was apparently adequate in either type of habitat.

Large differences in numbers of >6-9mm corals between caged and uncaged reefs indicate that coral survivorship had been greater in areas subject to some grazing pressure. Thus, any incidental predation on corals by the fishes (and echinoids) was more than offset by the reduction in competition with the algae. Though differences between the types of reefs are suggestive in the >3-6mm class, the lack of statistical significance is indicative of the time required for competitive effects to become evident and of the patchy nature of recruitment. The very small sample sizes of corals larger than 9mm prevents thorough statistical treatment of differences in corals of this size. It seems unlikely that the trends toward greater survival in the corals of intermediate size on the exposed reefs would cease to be significant statistically as the community matures. For Agaricia spp. and Porites astreoides, Fitz (unpublished data) measured mean linear growth rates of 0.6 (±0.2)mm/mo for corals 5-10mm diameter, 0.9 (±0.3)mm/mo for corals 10-15mm diameter, and 1.3 (±0.3)mm/mo for corals 15-20mm diameter (n=45, 41 and 17, respectively). Few corals would be expected, therefore, to attain sizes greater than 9mm in the year-long immersion period.

Some manipulations of the coral reef community are feasible and provide insights into the processes shaping that community. This caging experiment implies that the herbivores present at moderate depths play a crucial role in the survival of juvenile corals. As has been shown in shallow water areas (e.g., Sammarco 1980), herbivory can reduce the deleterious effects of the algae on the corals by reducing the biomass of the algal competitor. Though not as abundant in deeper as in shallow waters, herbivores nevertheless appear to control the survival of coral recruits and determine the structure of this epibenthic sessile community.

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