

The Impact of *Diadema antillarum* Philippi on
the Spatial Microhabitat Structure, Survival, Population
Dynamics, and Evolutionary Strategies of Coral
Recruits to Post-Hurricane *Acropora cervicornis* rubble
in the *Acropora cervicornis* Zone at Discovery Bay,
Jamaica.

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March 8, 1983

Dartmouth Tropical Biology FSP

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Abstract:

Coral rubble was removed from a site 35 feet deep in the A. cervicornis zone and assessed for the number and sizes of coral recruits present on its' surfaces. All corals found were on the protective undersurface of the rubble. Of 80 coral recruits found 94% were Agaricia sp.

The rubble was returned to the site and exposed to Diadema antillarum philippi grazing for 5 nights & 4 days. Significant [damage and loss] rates (40%) were found, and the loss rate was significantly different for two size categories designated $< 5 \text{ mm}$ in diameter and $> 5 \text{ mm} < 45 \text{ mm}$ in diameter, indicating an "escape in size" by coral recruits. Ecological considerations of differential mortality, competition, response to abiotic factors, succession, and other factors were considered in the framework of this post-hurricane successional system.

Introduction

On August 6, 1980 Hurricane Allen passed Jamaica's North Coast, devastating the reefs at Discovery Bay. Those corals that suffered the most immediate damage were those in shallower areas ~~pos~~ with branching morphologies - Acropora palmata and Acropora cervicornis.

Today, from a depth of about 30 ft to a depth of about 60 ft. one finds a thick layer of partially fused A. cervicornis punctuated by occasional massive coral heads. Before the hurricane the most abundant species in this depth zone was A. cervicornis, but today little living A. cervicornis remains.

The hurricane provided researchers with an opportunity to examine recruitment and succession of corals on ~~new~~ newly opened substrate. As in terrestrial systems, the following questions come to mind:

- 1) What are the earliest and fastest recruits to the system? (pioneer species)
- 2) What biotic and abiotic factors affect survival of recruits and cause changes in the relative abundances ^{of species} approaching that found in the climax system?
- 3) How do these factors change over successional time as a result of modification of the environment by colonizing species?

and worms.

At this point I hypothesized that the Diadema were responsible for the cleaned upper rubble surfaces, and that cover found on the lower surface would soon be worn away if exposed to grazing by Diadema.

My third observation was that adult corals are exposed to Diadema, and do not seem to suffer great evident damage or mortality from them at this time, though some grazing scars are visible. In conclusion, at some stage in its ^(coral's) development Diadema is no longer a serious threat to a coral's existence. The question remains as to what coral stage of development yields a reasonable resistance to Diadema damage for each species.

The purpose of this experiment was to determine the density of young corals in the rubble zone, their species composition, and their relative sizes, and then to expose these formerly cryptic corals to Diadema grazing by turning the rubble over. Then the rate of damage and removal by Diadema could be determined as a function of the size and type of coral and time. It was thought that small corals would be more susceptible to destruction by Diadema, simply because if a Diadema does happen to graze over it ^{the urchin} it will have a higher likelihood of damaging a fatal proportion of the coral.

- 4) What ~~spet~~ specific aspects of competing species' differing morphologies and physiologies determine their differential mortality in the face of these ~~at~~ abiotic and biotic factors?

I became interested in one facet of this overall question after making several observations in the A. cervicornis rubble zone. The first observation was that there were almost no small corals (<5 cm. diameter) or algae growing on the upper surface of the coral rubble, even though the abiotic conditions are presumably more favorable on the upper surfaces, at least in terms of light intensity. The only young recruit corals encountered on upper surfaces appeared on vertical outcrops or promontories of rubble or dead massive coral skeleton, above the level of the reef floor.

My second observation was that there were numerous Diadema antillarum Phillipi on the surface of the rubble, apparently feeding on biomass on the rubble surface, though there was little present other than patches of crustose coralline algae or calcareous red algae.

On the lower surfaces of the rubble one finds an even layer of cover, composed of sparse filamentous green algae, crustose coralline and calcareous red algae, young corals, and ^{10th} occasional sessile invertebrates - foraminiferans, sponges,

(4)

The possibility that the coral's "escape in size" is effected at the planular stage of development (and settlement) was also considered, in which case corals exposed to Diadema grazing would survive, and lack of corals on upper surfaces would be a result of grazing the planulae before settlement occurs. ^(without different rules for different sizes)

It is not necessary to assume that Diadema actively consumes coral for this system to work. Diadema is a fairly generalized feeder which basically eats everything encountered in its path. As it grazes on algae on the surface of the coral rubble it incidentally removes young corals. "Is it possible for an organism associated with, but not included in, a defined trophic subweb to be as significantly affected by a predator or grazer as the prey?" (Sammarco, 1980.).

Methods and Materials

Site - The area I worked in was at a depth of 35 feet on the LTS reef at Discovery Bay's West Fore Reef. The location of the area was about 50 meters south of the mooring in the center of the LTS reef.

The LTS reef is an unbroken buttress about 50 meters

(5)

wide on the average which extends from the reef crest down to a steep vertical drop off at about 90 ft.

At a depth of 35 ft. the reef is in the A. cervicornis zone, and thus is basically rubble punctuated by massive coral heads of M. annularis, Siderastrea siderastrea, and M. cavernosa (to name several species) and smaller coral formations including gorgonians and Pontes.

Damselfish territories occur in places, and are separated spatially, though there is no visible difference between unoccupied and occupied areas of rubble, except of course the lush carpets of green algae within the territories. Very little live A. cervicornis can be found.

The fish here are numerous - algae feeders such as parrotfish and ^(p. odax) ~~wras~~ as well as planktivorous feeders like the blue chromis. But the most abundant algae feeder here is Diadema - it covers the rubble, the coral masses, and other available surface area. Unfortunately, I could not obtain a figure for Diadema densities here through sampling, but Chris Copeland obtained a value of $12/m^2$ here prior to the hurricane in 1980.

I chose the exact site used in the following manner - I swam from the center of the LTB hutress in a southerly direction looking for an area greater than $1/2 \times 1/2$ meter that contained rubble and young corals, without large corals or other large

sessile fauna. The site was thus conveniently close to the mooring and at a fairly shallow depth, which increased the time available to work with during each SCUBA dive. The area marked off with string was 60×70 cm.

Treatment

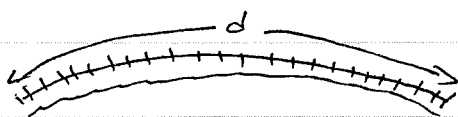
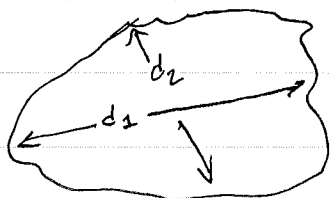
Having designated the area to be worked in I then removed all rubble A.enicornis in the upper, less amorphous levels of the rubble floor. The rubble layer is about $\frac{1}{3} \rightarrow \frac{1}{2}$ meter deep, below which it becomes much more fused and amorphous. By removing only the upper layers I could be fairly certain that I was only collecting post-hurricane rubble. Rubble was removed by hand and diving knife and placed carefully in a collection bucket.

The collected rubble was brought wet to the wet lab where it was carefully broken into smaller pieces about 120 cm long. Each piece was inspected for the presence of young coral colonies. I found that the smallest corals were about 1 mm in diameter; (diam of recruits immed. after settling $\sim 1-2$ mm (Borschwa 1929), (Edmondson 1929), via R.P.H. Baker & N.S. Engel, 1979), which could be seen with the naked eye if scrutinized closely. The diameter was recorded for each coral, and was obtained by measuring the smallest and largest diameters of the coral. Some of the

colonies have three dimensional relief, but this was accounted for by measuring diameters along the surface of the coral (see Figure 1). The diameter then equals the average of the two

Figure 1

TOP VIEW



SIDE VIEW

1) the diameter in all cases is the average of the smallest and largest diameters.

2) the diameters are measured along the surfaces of the coral with a flexible ruler to account for relief.

Figure 1: The drawings are schematics of how the diameter for a given individual coral is obtained, and beneath each is a verbal description of the process. The diameter recorded then, is $\frac{d_1 + d_2}{2}$.

diameters. Once all ^{recruit} corals had been measured on a given piece of coral rubble, and their sizes had been recorded, the piece of rubble was tagged with Nalgene paper and string. The tag was oriented so it would be on the bottom when the rubble fragment was placed "coral side up", thus reducing interference and facilitating placement. When I came across a very small coral (<3mm), a map of its position on the rubble fragment was recorded to facilitate finding it later on.

Many fragments had no coral on them at all, and

these were discarded. All fragments were measured for their total length. Branched fragments' lengths were considered the sum of the lengths of each branch.

It should be noted that during examination of the fragments I removed them from the water ~~for~~ for approximately two minutes to speed the examination process, but this is not expected to have harmed the corals in any way - K. Hylleberg (1980) in a similar experiment removed corals for 45 minutes without any harmful effect. At all times care was taken not to jar or scrape the young corals, though in transport a small amount of unavoidable jarring occurred.

The tagged rubble fragments were brought back to the same site they were taken from and placed on top of the remaining lower rubble layers, oriented "Coral side up", on the afternoon of 2/27/83. Because the fragments were placed in the depression created by removing the top layer of rubble, and because there was a massive coral head present to break the force of the mild surge, the fragments were not moved about and did not have to be tied down.

The next morning I checked the fragments to make sure they were maintaining their "Coral side

up "orientation". Due to a bout of Dengue fever no more field work was possible, and on March 4 '83 Harry Costanzo collected the tagged fragments for me, so that the corals were exposed to grazing by Diadema for 5 nights and 4 days. Each fragment was again examined to determine how many of the corals originally present had been removed by Diadema, and how many had suffered damage by Diadema. It was very easy to determine whether ^{or not} removal or damage was caused by Diadema due to the tell-tale markings it leaves on the rubble surface when it grazes.

Results

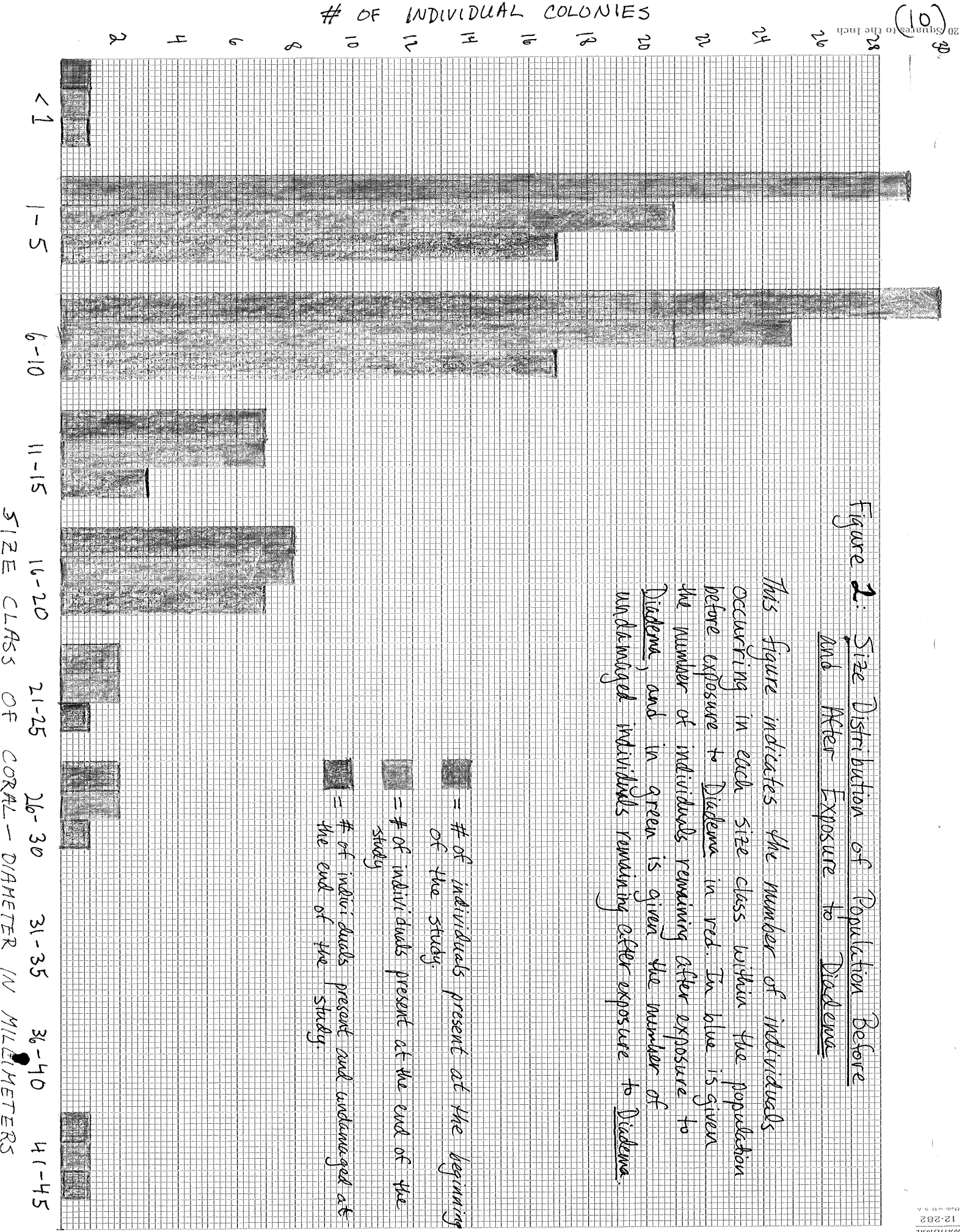
The raw data appears in histogram form in Figure 2. The number of individual colonies in each size class is indicated (size classes of <1, 1-5, 6-10, 11-15, 16-20, 21-25, 26-30, 31-35, 36-40, and 41-45 were considered within the error of measurement and reasonable - these are size classes similar to those used by Rylaarsdam 1980) for before exposure to Diadema and after exposure to Diadema. The corals remaining after exposure to Diadema are further categorized by being presented as those remaining with or without being damaged and those remaining completely ~~undamaged~~ undamaged. In all cases damage or removal was obviously caused by Diadema grazing - large scrape tracks

20 Squares to the Inch
(10)

Figure 2: Size Distribution of Population Before and After Exposure to *Diadema*

This figure indicates the number of individuals occurring in each size class within the population before exposure to *Diadema* in red. In blue is given the number of individuals remaining after exposure to *Diadema*, and in green is given the number of undamaged individuals remaining after exposure to *Diadema*.

■ = # of individuals present at the beginning of the study.
■ = # of individuals present at the end of the study.
■ = # of individuals present and undamaged at the end of the study.



could be seen along the exposed surface of the fragments, and often a small circular depression could be seen where the coral had formerly resided. The other sessile flora and fauna had also been scraped off, giving the rubble the "sand blasted appearance" found by Sammarco 1980. The damage to the coral ranged from abraded colline tissues in larger corals with more morphological relief, to abrasion of both polyp and colline in flatter, smaller corals, to the loss of part of the colony.

In cases of survival without damage what had occurred was that no Diadema happened to graze at the coral, though one may have grazed within millimeters of it.

Thus a 16.25% loss and a 39% damage or loss rate was obtained overall for the total of 80 corals followed after a 5 night, 4 day exposure to Diadema. Only 60% of the corals escaped any harm whatsoever, and it seems that if the exposure time had been doubled almost all corals would have suffered some level of damage. This rate of damage is comparable to that found by K. Rylaarsdam (1980) in a similar, laboratory, experiment - she found 12-52% of corals exposed to Diadema grazing visibly altered within 5 days.

To determine whether or not there is some escape

in size I divided the coral classes shown in Figure 2 into two size categories; those less than 6 millimeters in diameter, and those greater than 6 millimeters in diameter.

TABLE 2: DAMAGE AND LOSS RATES FOR THE TWO SIZE CATEGORIES OF CORAL

# of corals	①			②		
	< 1 mm → 5 mm	6-45 mm	Total	# of corals damaged or lost	< 1 → 5 mm	6-45 mm
lost	8	5	13	12	20	32
remain	22	45	67	unharmed	18	30
total	30	50	80	total	30	50
% loss	26.6%	10%	—	% loss or damage	40%	40%

① Fisher Exact:

$$\frac{13! 67! 30! 50!}{80! 8! 5! 22! 45!} = .0395 = p$$

② Fisher Exact

$$\frac{30! 50! 32! 48!}{12! 18! 20! 30! 80!} = .326 = p$$

Table 2: This table breaks down into numbers and percentages the data shown in Figure 2 for the two size categories 1-5 mm and 6-45 mm. The percent lost, and the percent either lost or damaged are presented for each size category, and then Fisher Exact Test Statistics are run for the frequencies to determine whether or not they are different for the size categories. The loss rate is significantly different to a level of $p = .04$ while the [damage or loss] rate is the same for both size categories and not significantly different.

As shown in Table 2, there is a significantly lower loss rate for the larger size category (10% vs 26.6%) while the [damage or loss] rate for the two classes are equal at about 40%. K. Rylaschun (1980) found a loss rate of ~25% for corals less than 3 mm

in diameter, so the loss rates obtained are reasonable.

If damage ultimately resulted in death of the individual colony in all cases then given enough time the death rate would be the same for both size ^{categories} ~~classes~~ - the removal rate would still be different, but all excess remaining damaged individuals would die, bringing the overall destruction rate to 40% for both size categories. However, damage does not necessarily result in death and the degree of damage inflicted was variable, with a ~~As~~ trend towards greater proportionate damage for smaller colonies. This would tend to increase the differences found between the two size categories.

In addition, there are values obtained for species distributions and densities on the rubble collected in the plot. The plot area was .42 meters, and there were 80 individual colonies found or $190/m^2$. K. Rylcaarsdam found $400/m^2$ in her survey at Upper Bvory Reef (1980). Her censusing was complete, while mine involved censusing only about half of the rubble layer - hence the values obtained may be comparable. Perhaps a more useful value for density is the number of corals found per meter rubble examined, which was 80 corals / 15.1 meters *A. cervicornis* rubble or 5.3/meter. This was not spread uniformly over the total length of rubble but often appeared in localized clumps, with several individual colonies appearing within a 110 millimeter

suggesting the possible existence of differentially adaptive microhabitats within the A. cernicornis rubble underside habitat.

Of the 80 corals found, all were agariciids except for one Porites.., and 4 colonies that were too small to be identified with certainty. In effect, 94% or higher of the corals examined were Agaricia, which is again comparable with more extensive data obtained by K. Rylaarsdam (1980) - she found 66-96% of all ^{recruit} species in a given transect were agariciids, with poritids a "distant second", and Agaricia becoming less important over time due to the differential mortality of species.

Along with this data base there are some important observations to be made. The first is that the algae on the rubble undersides, when exposed ^{to grazers} for feeding grazers, was obviously somewhat limiting - it vanished almost completely within 9 days, and as soon as the rubble was replaced at the site many fish immediately began feeding voraciously on the freshly exposed substrate - indeed, I had a school of parrotfish practically taking the rubble pieces from my hand as I laid them down on the substrate.

The next observation was that those corals which did survive exposure were those that either "got

reflects
rapidly
expanding
pop.

(15)

"lucky" or those that happened to be protected by a small depression or bump in the rubble surface. It seems that in the short run at least the smallest individuals have the highest likelihood of remaining "lucky" and are also most likely to be able to take advantage of topographic relief on the rubble surface since less relief is needed to protect a flat, tiny colony. In the same manner, one finds occasional small corals growing naturally on upper coral surfaces, where slight relief protects the coral as *Diadema* grazes over it.

As a final note one should refer to Figure 2 once again and note the population structure - most of the individuals are in the smaller size classes. This distribution is similar to that found by previous researchers (K. Rylands¹⁹⁸⁰, N. Sammarco 1980), and reflects a high mortality rate early on in recruiting coral colonies. Indeed, K. Rylands obtained a mortality rate of 95-99% for agariciids in their first 9 months of existence.

DISCUSSION

The most evident factor involving the coral recruit spatial distribution is the necessity for corals to reside on the undersides of the rubble, where protection is afforded from grazing *Diadema*. Sammarco (1980) performed a manipulation

involving controlled densities of Diadema, and found that with increasing Diadema density there was an increasing percentage of coral recruits occurring on the undersides of substrates. At a Diadema density of $100/m^2$ he found approximately 80% of the corals on the substrate underside. It is unlikely that the density of Diadema is that high in the study area, but the urchin may be a more effective predator in a naturally occurring situation than when a certain number are confined to a cage. Other researchers have found recruitment to underside of substrate more or less common though some attributed this pattern to different factors than others. Y. Loya (1976) found successful development of S. pistillata mainly on pipe undersides, and attributed this to surface grazing by Truchus dentatus, a gastropod, and Diadema setos, and to increased sedimentation on upper surfaces. In a five year study Charles Birkeland found that though growth rates are higher on upper surfaces, on plates left in the ocean for 70 days or more larger corals were on the undersides of the plates. This was attributed to an increased probability of survival, reduced algal growth rate, and less sedimentation. Unlike other authors that cite competition with algae as a factor and then do not specify the mechanism (i.e. Sammarco 1980),

Birkeland states that observed coral mortality on upper surfaces is due to smothering by sediment trapped by surrounding filamentous algae, and that overgrowth by filamentous algae is not a problem.

Landing on the underside of a substrate may be so essential for the survival of the planular larvae that there may be natural selection for larvae that land on the underside of substrates (K. Rylcaarsdam 1980). However, it may be that of the very few corals that survive a substantial number are from larvae that landed on an upper side piece of rubble, and that the microhabitat offers protection from Diadema. Also, Sammarco (1980) found that ^{at} a density of zero Diadema highest coral recruitment and diversity occurred, with planular larvae predominantly occurring in openly exposed habitats.

Obviously, landing on the underside does not guarantee survival. The ascertained population structure attests to that, assuming a constant recruitment rate. This is a safe assumption since Agaricia reproduce frequently (Duerden 1902 via K. Rylcaarsdam, 1980), and planulae are free swimming, released at full moon (K. Rylcaarsdam 1980).

Other factors than Diadema grazing are the responsible for the mortality evident in population

structure, and there are expected to be light; sedimentation; overgrowth by foraminiferous, Gypsina plana, and crustose coralline algae ((K. Ryland 1980), observations); accidental removal by grazing fish; predation by fish, Hermodice carunculata, and Coralliophila abbreviata; intercoral competition; and environmental disturbances.

Light is probably not that important once a planula has settled, assuming that it will not settle in a region which does not afford sufficient light for growth. The main effect of reduced light by being on the underside of a substrate is an ~~indirect~~ indirect one - the reduced growth rate increases the amount of time before an "escape in size" can be effected, which as this study has shown increases the likelihood of removal or higher proportionate damage.

It is likely that remaining small increases the likelihood of being overgrown by spatial competitors - in short being small for a longer time reduces overall competitive ability.

Sedimentation is probably the most important factor inducing early mortality, especially for Agaricia because its morphology is inefficient for the removal of sediment (R. P. M. Bak & M. S. Engel, 1979) - it's relatively flat. Furthermore, escape in size is again important - "because juvenile corals barely protrude above the

surface of their substratum and as such cannot rely on passive sediment clearing it is to be expected that sedimentation as well as sediment scouring will be a more significant parameter in survival of juveniles than it is in larger colonies (R.P.M. Bak & M.S. Engel, 1979)". Unlike for light, planulae cannot be "programmed" to move towards areas of favorable sedimentation levels because they are very variable on a very small scale, though some gross trends can be attributed to it, such as an increase near sediment sources (i.e. sand channels) and an increase with turbulence (i.e. in shallows).

Overgrowth (K. Rylaarsdam 1980), predation by fish (personal observations), Hermodice carunculata (K. Rylaarsdam 1980), and Coralliophila abbreviata (K. Rylaarsdam 1980), and internal competition (R.P.M. Bak & M.S. Engel) are probably very small factors for juvenile corals on rubble undersides. Of these, overgrowth is probably the most important. Once again, escape in size plays a role. Overgrowth is probably more a problem in terms of limiting growth than causing death. In 9 months, Bak & Engel (1979) found that $\frac{1}{3}$ of coral recruits remained normal, $\frac{1}{3}$ died or disappeared, and $\frac{1}{3}$ damaged or limited in growth by spatial competition. What essentially occurs is a stalemate - the neighbor

does not overgrow the coral, but the coral does not overgrow the neighbor.

Removal by grazing fish is a distinct possibility in affecting the population distribution found, especially since only smaller corals are likely to suffer significant damage from grazers like scarids. Scarids are known to bite corals, (Glynn '73, Frydl '77, via Bak & Engel 1979), but it is not known whether this is intended grazing or accidental. In either case, scarids are attracted to the relatively lush algae available on rubble undersides, and can be observed reaching underneath the rubble to obtain algae not reachable by Diodema. For this reason, and probably also due to reduced light levels, the amount of filamentous algae growing on the rubble undersides is much less than the amount found on rubble in damselfish territories. One study that suggests this grazing does not induce coral mortality is that of Birkeland ⁽¹⁹⁷⁷⁾ in which he found "small coral recruits on intensely grazed plates consistently avoided by herbivorous fishes, though corals were as small as 3mm in diameter." However, Bak and Engel (1979) found a high frequency of bites on juvenile skeletons which they attributed to fish grazing - "no evidence that grazing fish avoid small corals".

Environmental disturbances undoubtedly occur, and when they do, as with the above factors, smaller corals are probably more easily ~~disturbed~~ ^(fatally) damaged or destroyed. At the same time that a disturbance destroys the smaller corals it opens up new space for sessile recruitment, so that depending on the nature of the disturbance one finds different changes in observed abundance patterns.

At any rate, the abundance pattern obtained in this study for Agaricia is the one obtained in other studies, and it is one that characterizes an opportunistic, pioneer species. The coral reef should probably be divided into smaller units - zones or microhabitats - to allow differentiation between suboptimal and optimal environments for juvenile survival (RPM Bak & M.S. Engel 1979), and then we can more accurately predict the probability of survival for a settling planula of a given species.

Other species are often more resistant to grazing by Diodora - for example, Montastrea annularis actually regenerates better when it has had skeletal ~~to~~ tissue removed along with living tissue than if only living tissue is removed (K. Rylands 1980). M. annularis and A. cervicornis comprise less than 1% each of the coral recruits in the A. cervicornis zone (K. Rylands 1980), but are able to maintain a significant proportion of coral biomass.

This doesn't follow
from previous th.
Due to higher
recruitment?

(22)

One factor contributing to the success of A. cenicornis is its high growth rate and propensity for vegetative reproduction.

It seems, nevertheless, that Diadema plays a key role. With increasing Diadema density Agavecia becomes proportionately more abundant than the other recruiting species (Sammarco 1980), so that variations in Diadema density may directly affect community composition.

~~In conclusion, the scarcity of corals on the upper surfaces of rubble may be attributed~~

This system seems to work well within the framework of Connell's intermediate disturbance hypothesis. At a high level of disturbance by Diadema (i.e. upper rubble surface), no corals grow due to their being scraped off. At low Diadema densities (i.e. within damselfish territories), no corals grow because they are being outcompeted by dominant filamentous green algae through the prevention of planula settlement and death by sediment trapping. At an intermediate level of disturbance (i.e. coral rubble undersides), the corals flourish. This is consistent with R. Sammarco (1980), who found that with increasing Diadema densities algal percent cover decreases, and that more colonies occur at low grazing levels but the most growth occurs at moderate grazing levels due to reduced algal interference. Thus the highest diversity of sessile species is obtained at an intermediate level of disturbance.

A final aspect to this system is the shift in species abundances in the earliest stages to that found in the climax community of adult corals.

This is essentially due to the differential mortality of different species, which is due to their different morphological and physiological characteristics.

Agaricia is a strong reproducer and recycler, but it is not strong in regeneration, dominance interactions, or in abrasive environments. Other species settle less often but have a much greater capability for survival and success in competitive interactions — i.e. ^{and aforementioned A. cervicornis' vegetative reproduction, P. granulatus a forementioned resistance to tissue abrasion.} Judy Larg's dominance hierarchy.

In conclusion, the scarcity of corals on the upper surfaces of rubble may be attributed to grazing by Diadema, and there does seem to be an escape in size for coral colonies, so that given enough time undisturbed a coral will then have the a chance at persisting in the presence of Diadema. The importance of microhabitat should be emphasized in studying distribution and survival of corals and other sessile organisms, and the variation of abiotic & biotic factors on a microhabitat scale should be considered along with variation on a larger scale in examining successional, competitive, and other ecological coral reef interactions.

Author's Note:

This work could not have been done without the help and advice of Larry Castoraves, a researcher w/ Univ. of Georgia engaged in doctoral ^{thesis} research at Discovery Bay. It was through his inspiration, advice, and aid that this project was conceptualized, designed, and completed.

Special thanks also goes to Mark Durand for being a good dive buddy.

More field work would have been attempted in this research but for the unpreventable catching of Dengue fever.

Excellent study--from conception, design, data collection, analysis and presentation of results, to discussion.

References

- Bak, R.P.M. and M.S. Engel, 1979, Distribution, Abundance, & Survival of Juvenile Hermatypic Corals (Scleractinia) and the Importance of Life History Strategies in the Parent Coral Community Marine. Bio, 54: 341-352.
- Bak, R.P.M., and J.J.W.M. Brouns & F.M.L. Heys, Regeneration and Aspects of Spatial Competition in the Scleractinian Corals Agaricia agaricites and Montastrea annularis, Proc. 3rd Inter. Coral Reef Symp. Rosentiel School of Mar. & Atm. Sci., Univ. of Miami.
- Birkeland, Charles, The Importance of Rate of Biomass Accumulation in Early Successional Stages of Benthic Communities to the Survival of Coral Recruits, Proc. 3rd. Inter. Coral. Reef Symp. (see above ref)
- Borsschma, 1929 - via ^{Bak & Engel 1979} ~~K. Rylaarsdam 1980~~ On the postlarval development of the coral Meandrina areolata Rep. Tortugas Lab. 26: 129-147
- Duerden 1902 - via K. Rylaarsdam 1980
- Edmondson 1929 - via Bak & Engel '79 - Growth of Hawaiian Corals Bull. Bernice B. Bishop Mus. 58: 1-38
- Frydl, P., 1977 - via Bak & Engel '79 - The geological effects of grazing by parrotfish on a Barbados coral reef. McGill Univ., Dept. of Geological Sciences. Tech. Rep. Dep. geo. Sci. McGill Univ, 77(3): 1-136

Glynn, P.W. - via Bale & Engel '79 - Aspects of the Ecology of coral reefs in the Western Atlantic Region In: The biol. and geol. of coral reefs, Vol. 2 pp. 271-324 Ed. by O.A. Jones & R.A. Endean. New York: Academic Press.

Goreau, T.F., Goreau N.I., Goreau T.S., ¹⁹⁷⁹ Corals and Coral Reefs, Scientific American 241(2): 124-136.

Loya, Y., 1976, Settlement, Mortality & Recruitment of A Red Sea Scleractinian Coral Population, ^{From:} Coelenterate Ecol. and Beh. Edited by G.O. Mackie. New York: Plenum Pub. Corp.

Rydgarsdam K., 1980, Life Histories and Abundance Patterns of Some Common Caribbean Reef Corals, dissertation, John Hopkins Univ., Baltimore, Maryland - copy in DBML library.

Sammarco Paul W. ¹⁹⁸⁰ Diadema and its' Relationship to Coral Spat Mortality: Grazing, Competition, and Biological Disturbance, J. exp. mar. Biol. Ecol. 45: 245-272

Vine, P.J., 1974, Effects of Algal Grazing and Aggressive Behaviour of the Fishes Pomacentrus lividus and Acanthurus sobral on Coral Reef Ecology, Mar. Biol. 24(1): 131-136.

Woodley, J.D., E. Robinson 1977, Field Guidebook to the
Modern and Ancient Reefs of Jamaica,
3rd Internat'l Symp. on Coral Reefs 1977.

Chris Copeland - "The sea urchin is a voracious feeder -
always ready to eat", Dartmouth FSP
paper, 1980.