Recovery patterns of *Acropora cervicornis* after Hurricane Allen

ABSTRACT

In August 1980, Hurricane Allen devastated the dense monotypic stands of staghorn corals (*Acropora cervicornis*) at Discovery Bay, Jamaica. A comparison was made between pre and post hurricane *cervicornis* population characteristics in order to assess the recovery patterns after the disturbance. Recovery has been slow thus far (11 corals/m^2 before and 0.57 corals/m^2 3.5 years after the hurricane) and while many of the growth patterns of *A. cervicornis* resemble those from pre-hurricane conditions, the overall distribution of the corals has changed dramatically. The distribution has shifted from one that was even throughout the *cervicornis* zone (15'–65') before the hurricane to one which shows the most extensive and rapid recovery occurring at an intermediate depth within this previous range (~40 feet).

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Introduction

The staghorn coral, *Acropora cervicornis* is a common reef-building coral in the Caribbean. In Jamaica, these corals often form very dense monotypic stands which dominate over other coral communities (Goreau and Goreau, 1973). It is a fragile coral and can easily be fractured in high wave activity and thus is limited in distribution to areas and depths which do not experience extraordinary turbulence (Tunnicliffe, 1981). She found the greatest abundance of *A. cervicornis* to be between 5 and 20 meters depth where up to 11 corals per m^2 produced a maximum of 10m of branches (Tunnicliffe, 1983). It has been hypothesized that *A. cervicornis* also experiences a lower limit to growth (Hughes, 1983). Being primarily an autotroph and thus relying heavily on the photosynthetic processes of its zooanthallae for its nutritional requirements, *A. cervicornis* cannot venture beyond a limiting maximum depth of ~95 feet (Tunnicliffe, 1983). Hence in essence the observed distribution of these corals reflects an optimization of its probability of survival.

Before Hurricane Allen, there existed no variation in coral height and density with increasing depth within these extensive monotypic stands (Tunnicliffe, 1983). This result is surprising in light of the two limitations discussed above. The limiting forces, turbulence and light availability ought to have shaped the distribution in such a way as to concentrate the corals at an optimal depth. What she found instead was a relatively homogeneous "climax" fauna composed chiefly of A. cervicornis from 20' to 60'.

In August 1980, Hurricane Allen caused catastrophic damage to the coral reefs of north Jamaica (Woodley et al, 1981). At Discovery Bay, the A. cervicornis beds were leveled and mortality of this coral during and after the storm was over 95% (Knowlton et.al. 1981). Consequently, the huge monotypic stands of A. cervicornis were literally wiped out throughout the fore reef regions. The effects of this hurricane will be felt by the coral reef systems of Discovery Bay for years to come. Especially hard hit were the staghorn corals, for these corals propagate primarily by fragmentation and produce very few recruits (Tunnicliffe, 1981). On the other hand, the hurricane's destructive path left a "clean" slate of coral reef upon which recolonization and recovery could occur. This natural stochastic disaster offers a unique opportunity to observe and study the various patterns of recovery in A. cervicornis.

The goal of this study was to quantify and describe some of the growth patterns of A. cervicornis after Hurricane Allen. Pre-hurricane studies, such as that of Verena Tunnicliffe on the West Fore Reef (Discovery Bay) from 1977-1979 were used to compare many of the observed trends. This type of study is valuable in that one can evaluate the relative importance of rare environmental processes, such as Hurricane Allen, on the distributions, growth rates and meristics of a very common coral system (Woodley et al., 1981).

We expected to find that the post-hurricane _A. cervicornis_ fauna would no longer exhibit the same population characteristics as the pre-hurricane climax community that Tunnicliffe studied. Some of the new trends one might predict are the following: ① Turbulence and light intensity (availability) may play a more significant role in recolonization and/or recovery processes. ② Mortality of new recruits? will be greatest at shallower depths because thickets of staghorn coral no longer exist to protect newly established individuals. ③ Due to the onset of adverse conditions, asexually reproducing organisms such as _A. cervicornis_ may have suddenly released more larva (Marshall + Stephenson, 1933). Thus juvenile recruits may be more common after the hurricane.

why?

While new trends such as these may be evident in the recovery patterns of post-hurricane _A. cervicornis_, it is equally probable that those colonies that have successfully established themselves will exhibit at least some of the same growth patterns shown by those before the storm.

Furthermore, in order to assess the overall recovery pattern, this study investigated many of the other factors which may have influenced growth. For instance, damselfish have been known to predate on the polyps of _A. cervicornis_ and subsequently convert the dead regions into algal lawns (Potts, 1977). Also, boring sponges, such as _Cliona aprica_ have been known to weaken the integrity of the coral structure by drilling holes at the base of the colony (Tunnicliffe, 1979). Before the storm, these two agents played a role in coral mortality and propagation via fragmentation, respectively. We wished to see if their roles had changed (increase, decrease or adapting) within the new recovery stand of _A. cervicornis_.

How long does this take?

STUDY SITE

FIELD AND LABORATORY STUDIES WERE CONDUCTED BETWEEN 25 FEBRUARY AND 4 MARCH 1984 AT THE DISCOVERY BAY MARINE LABORATORY IN DISCOVERY BAY, JAMAICA. THE STUDY SITE WAS LOCATED AT MOORING #1 ON THE WEST FORE REEF AT DEPTHS BETWEEN 15' AND 65'. THE REEF AT THIS SITE, ORIENTED IN A NORTH-SOUTH DIRECTION, WAS LONG AND RELATIVELY NARROW, EXTENDING (WITH SEVERAL INTERRUPTIONS BY SAND CHANNELS) FROM THE REEF CREST TO A DEPTH OF ABOUT 65', WHERE IT SLOPES DOWNWARD TO A SAND FLAT. IT PROVIDED LARGE AREAS AT DEPTHS OF 20', 40', AND 60' ON WHICH TO SURVEY *Acropora cervicornis*. WHILE *cervicornis* WAS PRESENT AT ALL ~~DEPTHS~~ THREE DEPTHS, VARIATIONS IN TOPOGRAPHY AND SPECIES COMPOSITION WERE OBSERVED BETWEEN THEM (see also Figure 6.):

a) 20 feet: LARGE VARIATIONS IN TOPOGRAPHY RESULTED FROM MANY LARGE (SOME > 1m TALL) MOUNDS OF *Montastrea annularis* AND THE RESULTING "VALLEYS" WHICH OCCURRED BETWEEN THEM. *Acropora palmata* BARELY EXTENDED INTO THIS ZONE, USUALLY GROWING ON THE TOPS OF DEAD CORAL MOUNDS (GIVING IT AN EFFECTIVELY SHALLOWER DEPTH). SMALLER MOUNDS OF *Agaricia* spp. AND *Diploria* spp., *Millepora*, and BRANCHING CORAL STANDS OF *Porites* spp AND *Madracis mirabilis* WERE COMMON.

b) 40 feet: THIS DEPTH HAD AN INTERMEDIATE TOPOGRAPHY, WITH *Montastrea* MOUNDS USUALLY ABOUT 0.5 m IN HEIGHT. THIS STILL PROVIDED VALLEYS IN WHICH REATTACHED *cervicornis* HAD ESTABLISHED THEMSELVES, YET HERE THERE WERE WIDER AREAS OF FLAT

BOTTOM SURFACE (OFTEN COVERED WITH BRANCHING CORAL RUBBLE FROM HURRICANE ALLEN) WHICH CONTAINED *cervicornis* COLONIES. LARGE STANDS OF *Madracis mirabilis* AND *Porites* spp. WERE ALSO COMMON ON THESE FLATS, WHILE THE OMNIPRESENT *Millepora* OCCURRED MOSTLY ON DEAD CORAL MOUNDS. SMALLER MOUNDS OF *Diploria* spp., *Meandrina meandrites*, AND *Agaricia* spp., AS WELL AS *Gorgonia* spp. WERE SCATTERED THROUGHOUT THE AREA.

c) *60 feet*: THE TOPOGRAPHY HERE WAS FLAT IN TERMS OF VARIATIONS IN CORAL HEIGHT, SINCE THE SURFACE WAS DOMINATED BY PLATE-LIKE MOUNDS OF *Montastrea* AND *Agaricia*, WITH *Porites* AND *Madracis* FORMING SMALL MATS BETWEEN THEM. FLAT ENCRUSTING BRAIN CORALS WERE ALSO PRESENT. HOWEVER, THE REEF AT 60' SLOPED FAIRLY SHARPLY (~30°) TOWARD THE SAND FLAT BELOW, AND THUS *cervicornis* WAS ONLY FOUND IN CLUMPS ON SMALL FLAT AREAS WHERE A PORTION OF THE REEF WOULD LEVEL OFF BEFORE SLOPING DOWNWARD AGAIN.

OBVIOUSLY, THE EFFECT OF WAVE ACTION DECREASED WITH INCREASING DEPTH; LIGHT INTENSITY (MEASURED AS % SURFACE LIGHT) DROPPED IN A RATIO OF 4 : 3 : 2 AT DEPTHS OF 20', 40', AND 60', RESPECTIVELY. (*Figure* 6.)

MATERIALS AND METHODS

AT EACH DEPTH (20', 40', AND 60'), THREE 10m × 2m TRANSECT BELTS WERE TAKEN IN AN EAST-WEST DIRECTION ACROSS THE REEF AT MOORING #1. TWO ADDITIONAL TRANSECTS WERE LATER TAKEN AT 20' AFTER A STORM ON 29 FEB 84 TO ASSESS ANY POSSIBLE RECENT DAMAGE AT SHALLOW DEPTHS DUE TO THIS DISTURBANCE. FOR EACH TRANSECT BELT, A TEN-METER NYLON CORD WAS EXTENDED AND ALL CORALS LYING WITHIN ONE METER TO EITHER SIDE WERE SURVEYED. FOR EACH CORAL WE NOTED LOCATION ON THE TRANSECT, MAXIMUM HEIGHT AND WIDTH, NUMBER OF FRACTURES, BRANCH WIDTH AT THE SITE OF ATTACHMENT ("BASAL WIDTH"), TYPE OF ATTACHMENT (BASAL = juvenile recruit; REATTACHED; or UNATTACHED = no attachment at the present time), PERCENT OF ALGAL COVER AND TISSUE DEATH, AND DEGREE OF BRANCHING. THIS LAST CATEGORY WAS ASSESSED BY COUNTING THE NUMBER OF BRANCHES PER COLONY IN EACH BRANCHING ORDER (WITH PRIMARY (1°) BRANCHES BEING THE YOUNGEST, SECONDARY (2°) BRANCHES ~~BEG~~ BEING THE SECOND YOUNGEST BELOW THEM, AND SO ON). AN INDEX OF OVERALL GROWTH, THE GROWTH INDEX, COULD THEN BE FORMULATED TO RELATE THIS DENSITY WITH CORAL SIZE:

$$\text{GROWTH INDEX} = \frac{\text{BRANCH DENSITY}}{\text{CORAL SIZE}} \times 100$$

Does this assume that 1°, 2° and 3° branches grow at same rate?

WHERE BRANCH DENSITY = [1 × (number of 1° branches) + 2 × (number of 2° branches) + 3 × (number of 3° branches) + ...]

AND CORAL SIZE = (maximum height) × (maximum width).

SINCE *cervicornis* GENERALLY BRANCHES AT SPECIFIC

TIMES DURING THE YEAR (Tunnicliffe 1983), A MEASURE OF RELATIVE GROWTH RATE WAS DETERMINED AT EACH DEPTH BY MEASURING THE LENGTH OF THE 1° BRANCHES ON SELECTED CORALS.

IN ADDITION, THE SURROUNDING AREA AND SUBSTRATE WERE EXAMINED FOR CORAL SPECIES COMPOSITION, TOPOGRAPHY, AND PRESENCE OF DAMSELFISH TERRITORIES IN AND AROUND EACH *cervicornis* COLONY.

A STUDY OF POLYP DISTRIBUTION, DENSITY, AND SIZE ON BRANCHES FROM THE THREE DIFFERENT DEPTHS WAS ACCOMPLISHED BY COLLECTING 3 SAMPLE 1° BRANCHES FROM EACH DEPTH. POLYP DENSITIES WERE CALCULATED BY COUNTING THE NUMBER OF POLYPS ON THE TOP (FACING WATER SURFACE) AND BOTTOM (FACING SUBSTRATE) HALVES ALONG A 2-cm SEGMENT OF EACH SAMPLE BRANCH. NUMBER OF POLYPS PER SURFACE AREA (cm^2) COULD THEN BE DETERMINED ($n=3$). TO DETERMINE POLYP SIZE, THE DIAMETERS OF FIVE RANDOMLY CHOSEN POLYPS ON EACH SIDE (TOP + BOTTOM) OF THE 2-cm SEGMENTS WERE MEASURED USING AN OCULAR MICROMETER ON THE DISSECTING MICROSCOPE (3 BRANCHES FOR EACH DEPTH $\rightarrow n = 15$).

THE DATA WERE QUANTIFIED, TABULATED, AND TESTED FOR STATISTICAL SIGNIFICANCE USING NON-PARAMETRIC TESTS.

Results

Meristics

A. cervicornis height remained constant throughout the three depths (Kruskal-Wallis test $H = 2.68$ $p > .05$). The growth rate of the primary branches also remained relatively constant (Kruskal-Wallis test $H = 1.07$ $p > .05$). However, the basal diameter of coral decreased significantly with increasing depth (Kruskal-Wallis test $H = 5.32$ $p < .029$). The Growth Index revealed no significant difference with increasing depth in the overall growth of the individual colonies (Kruskal Wallis test $H = 1.81$ $p > .1$); but it was noticeably greater at 20 feet (Table 1).

Distributions

The number of *A. cervicornis* colonies found per 20 m^2 transect varied significantly with depth (Kruskal-Wallis test $H = 8.97$ $p < .009$). Greatest number of colonies per m^2 was found at depth of 40 feet (Table 1). The distribution of the colonies at each depth was clumped (X^2 test with expected Poisson distribution, all three with $p < .005$). The degree of "clumpness" was a function of increasing depth i.e. the distribution at 60' was more clumped than at 20' with p values of $< .0001$ and $< .005$ respectively.

Topographical Locality

The location of the corals on substrate at the three depths differed significantly (Kruskal-Wallis $H = 4.6$ $p \cong 0.10$). There was an increase in the use of flat surfaces by *A. cervicornis* in the deeper regions of the reef while the use of "valleys" decreased with increasing depth (Figure 1).

Nature of Attachment

The type of attachment to substrate at the three depths did not differ significantly ($\chi^2 = 3.31$ $df = 4$ $p > .05$). Juvenile recruits did not show any preference for a particular depth (Figure 2). The total number of fractures per coral decreased with increasing depth (Kruskal-Wallis test $H = 7.03$ $p < .01$).

Coral Mortality

The greatest % dead tissue per coral was found at 40 feet, at 24.5%. This was somewhat related to the greatest % algal cover, which was also at 40' at 19.3%. Damselfish territories did not significantly dominate one region ($\chi^2 = 5.98$ $df = 4$ $p > .05$). However, at 40' there seems to be the greatest damselfish presence (D1+D2, Figure 3). The percentages of corals surveyed with one or more boring sponges attached differed significantly with varying depth ($\chi^2 = 10.1$ $df = 2$ $p < .01$).

When 20' and 40' corals were lumped and compared to the 60' corals, there was a significantly higher % boring sponge attachment at the shallower depths (20', 40') ($x^2 = 9.79$ df = 1 $p < .05$). Indeed no corals found at 60' exhibited sponge attachment.

Coral Polyp Characteristics

Both polyp densities (Figure 4) and polyp diameters (Figure 5) showed significant differences between top and bottom branch surfaces at depths of 20' and 40' (Mann-Whitney U test, $p \leq 0.1$ for densities $p \leq 0.05$ for diameters). However, densities and diameters were not significantly different at 60' (Mann-Whitney U test $p > 0.1$).

In addition, polyp densities on both surfaces were significantly greater at 20' and 40' than at 60' (Mann-Whitney U test $p \leq 0.1$). While polyp density did not vary between 20' and 40', polyp diameters were almost twice as large at 20' as at 40' (significant, Mann-Whitney U test, $p < .10$), causing polyps to seem twice as "packed" on the top surfaces of branches from 20' when compared to those at 40'. Bottom polyp diameters showed no significant difference between these two depths (Mann-Whitney U test, $p > 0.1$).

Effect of minor storm (Feb 29, 1984) on *A. cervicornis* in shallow depths (20')

No significant differences in coral structure, numbers or fragmentation were observed between transects taken before and after the storm. Thus the data (all 5 transects) were consolidated and analyzed as one lumped data set.

Table 1: Coral Meristics, Distributions, Growth Rates, and other characteristics.

Depth (feet)	20			40			60		
	n	$\bar{x}$ ±	SE	n	$\bar{x}$ ±	SE	n	$\bar{x}$ ±	SE
CORAL DISTRIBUTION (colonies / transect)	5	2.40	0.678	3	11.3	2.40	3	6.00	0
CORAL DENSITY (colonies / m^2)	5	0.12		3	0.57		3	0.30	
Maximum height (cm)	12	16.9	3.46	34	15.6	1.82	17	13.0	1.58
Maximum width (cm)	12	24.2	6.50	34	20.7	2.69	17	14.8	1.43
Basal diameter (cm)	6	1.48	0.106	24	1.15	0.0823	17	1.04	0.0618
Growth Rate[1]	15	11.5	0.960	15	15.9	1.45	15	12.3	0.586
Growth Index[2]	12	13.2	3.03	33	9.53	1.23	18	9.88	2.05
% algal cover	12	16.9	7.88	34	19.3	5.14	17	2.06	0.863
% dead	12	18.8	8.46	34	24.5	5.57	17	2.06	0.863
# of fractures	12	2.42	0.828	34	1.56	0.301	17	0.235	0.0570
% with boring sponges[3]	12	33		34	41		18	0	

[1] Lengths of primary branches (cm) (with similar ages) from tip to base.

[2] Measure of density of branching per colony, calculated by (degree of branching) ÷ (area of colony), as described in methods.

[3] % of individuals surveyed with some form of sponge cover, usually at the base of the coral.

Table 2. Comparison of growth patterns in *A. cervicornis* before Hurricane Allen (from Tunnicliffe 1983) and at present time.

	Before Hurricane Allen	Present
Coral Distribution	Clumps evenly distributed from 15' to 65'	Clumped, but greatest number of individuals occurs at ~ 40'
Coral density (#corals/m^2)	11 corals/m^2	20' < 40' > 60' 0.12 0.57 0.30
GROWTH RATE	20' > 40' > 60'	(not significantly different) ($p > .1$) 20' < 40' > 60' 11.5 15.9 12.3
GROWTH INDEX (density of branching)	20' > 40' > 60'	greatest @ 20' ($p > .1$) but 40' ≈ 60'
BRANCH THICKNESS (cm)	20' > 40' > 60'	20' > 40' > 60'
MAXIMUM HEIGHT OF COLONY.	no significant diff. $\bar{x} \approx 1.0$ m	no significant diff. $\bar{x} < 0.17$ m
% TISSUE DEATH	33%	20' < 40' > 60' 19% 25% 2%
Type of attachment:		
BASAL ATTACHMENT (juvenile recruit)	20%	43%
REATTACHED	68%	46%
UNATTACHED	12%	11%

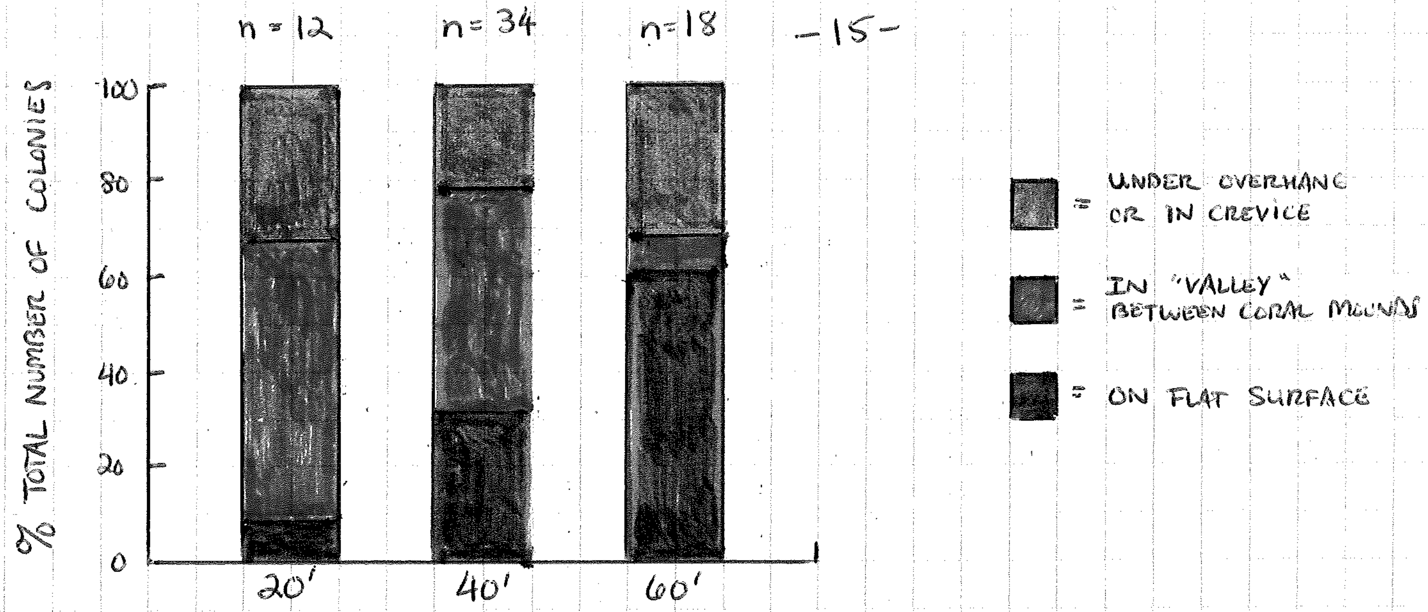

Figure 1. Topographical locality of corals at 3 depths, in percentages of total number of corals surveyed.

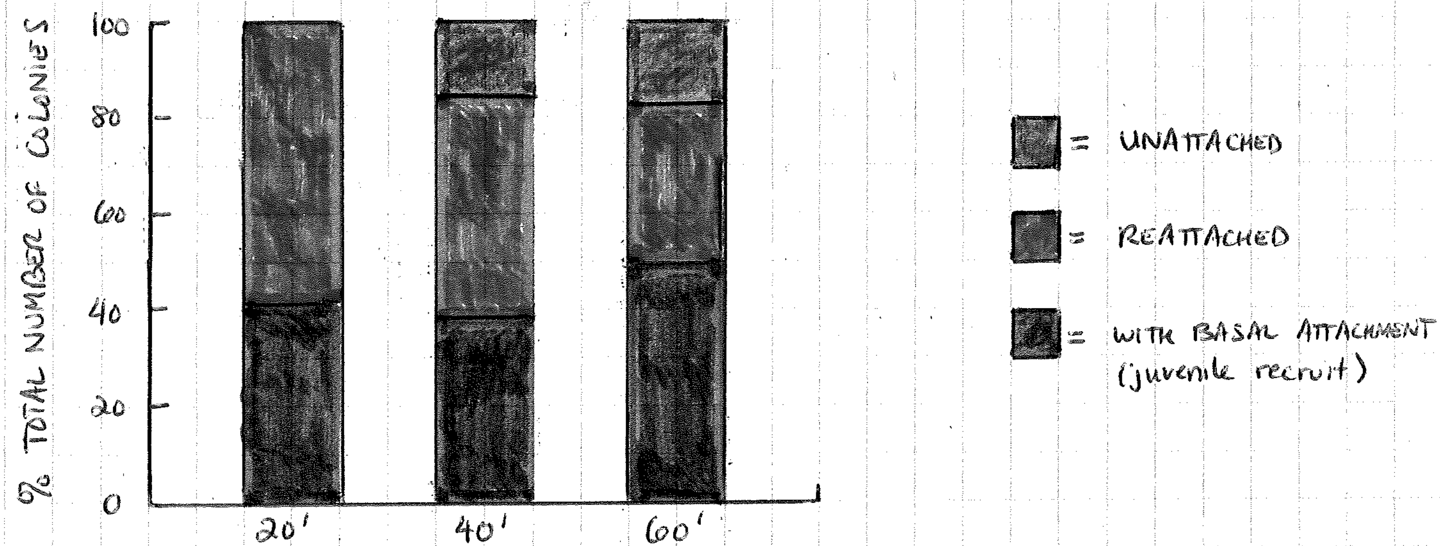

Figure 2. Type of attachment to substrate at 3 depths, in percentages of total number of corals surveyed.

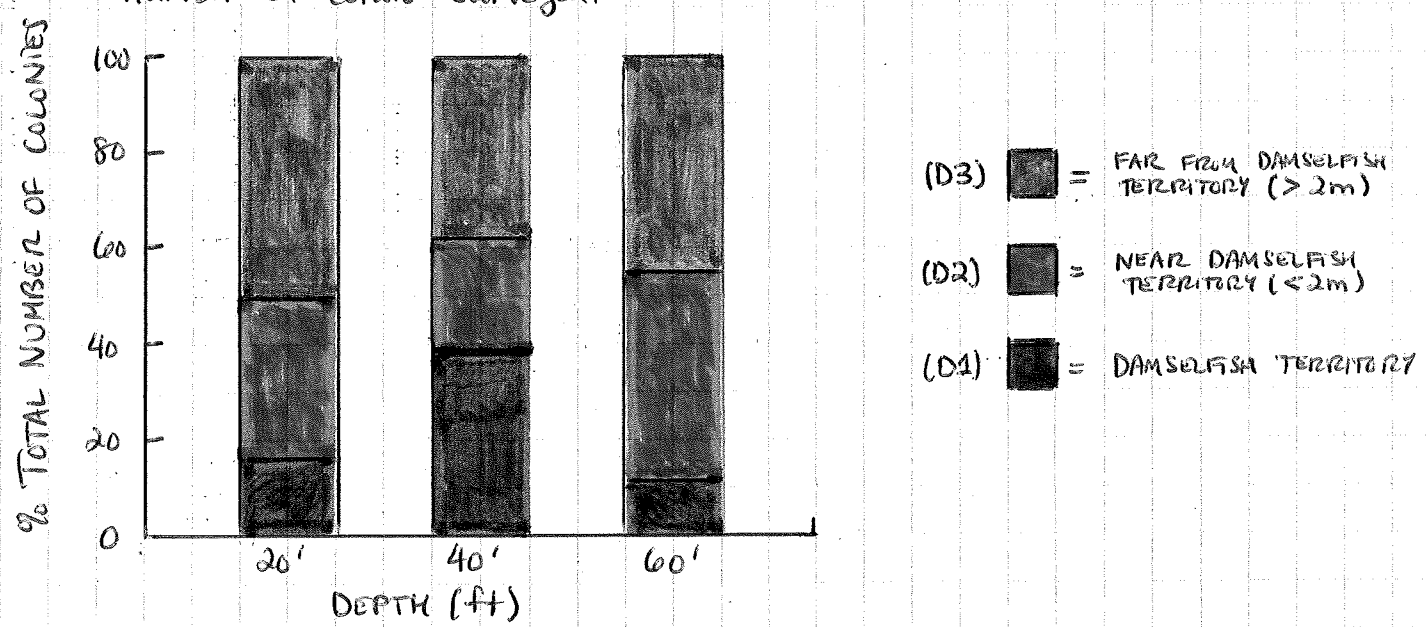

Figure 3. Relationship between coral locality and damselfish territories at 3 depths, in percentages of total number of corals surveyed.

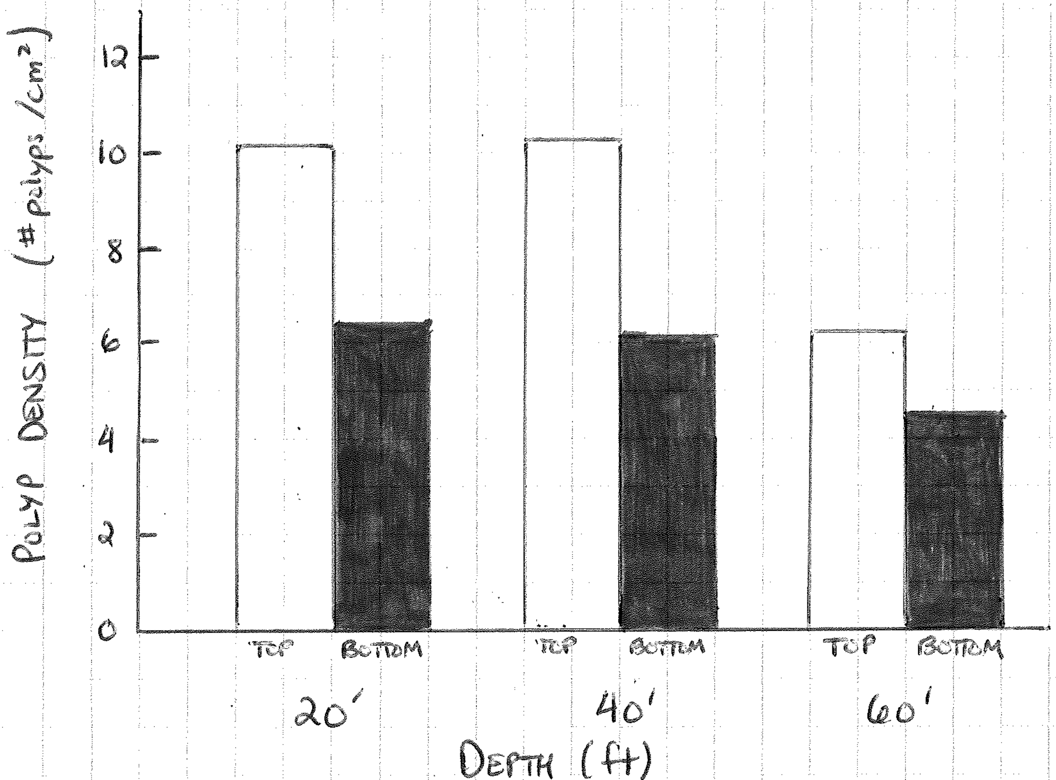

Figure 4. Variations in polyp densities on tops and bottoms of branches of *A. cervicornis* with increasing depth. (n = 3).

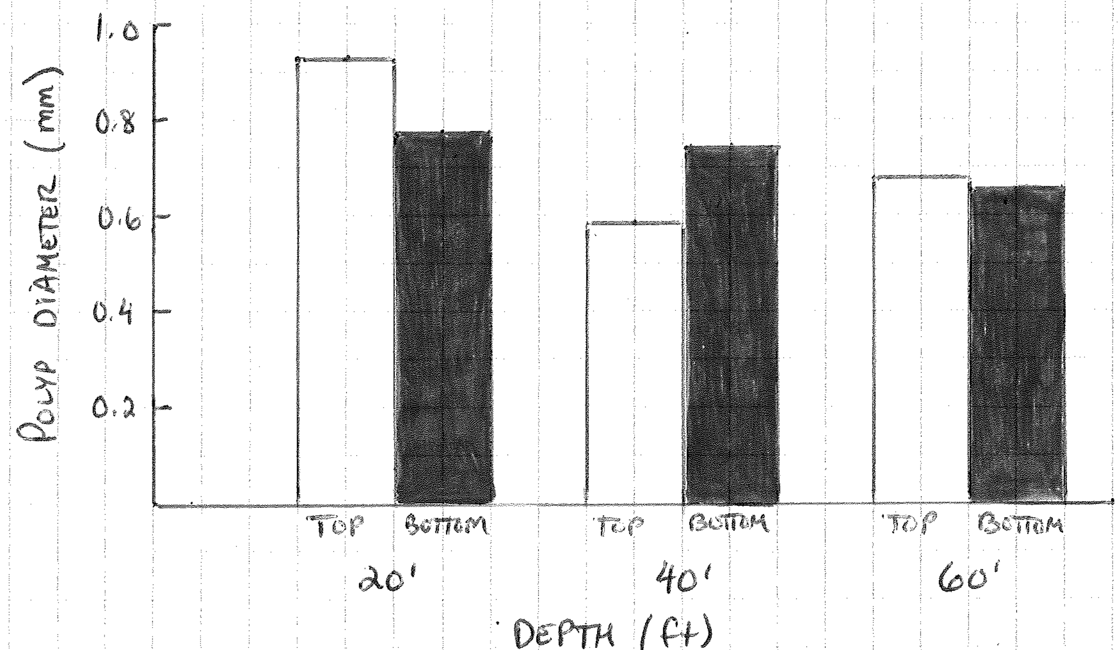

Figure 5. Variations in polyp diameter on tops and bottoms of branches of *A. cervicornis* with increasing depth. (n = 15).

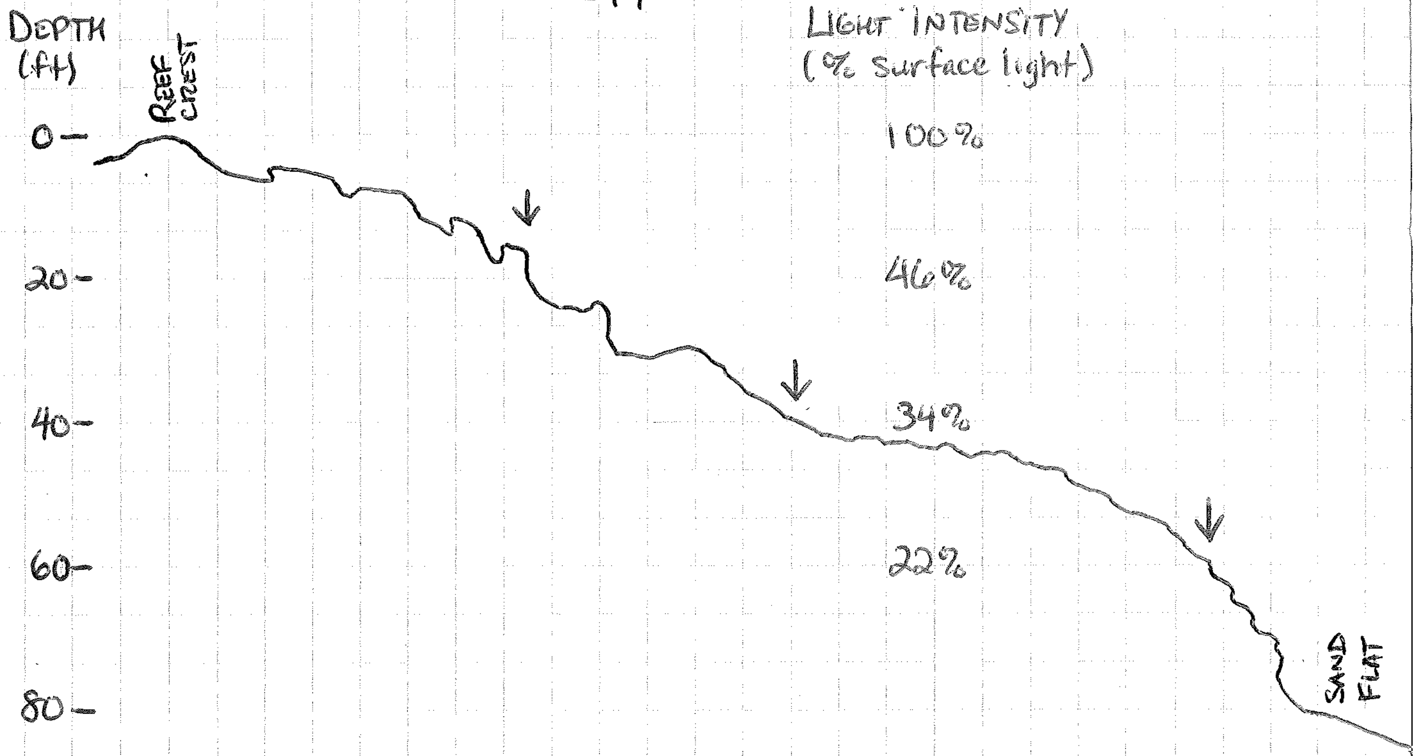

Figure 6. Schematic topographical depiction of Mooring #1 reef study site. (↓ = three depth study sites). (light intensity values from Brakel, 1976).

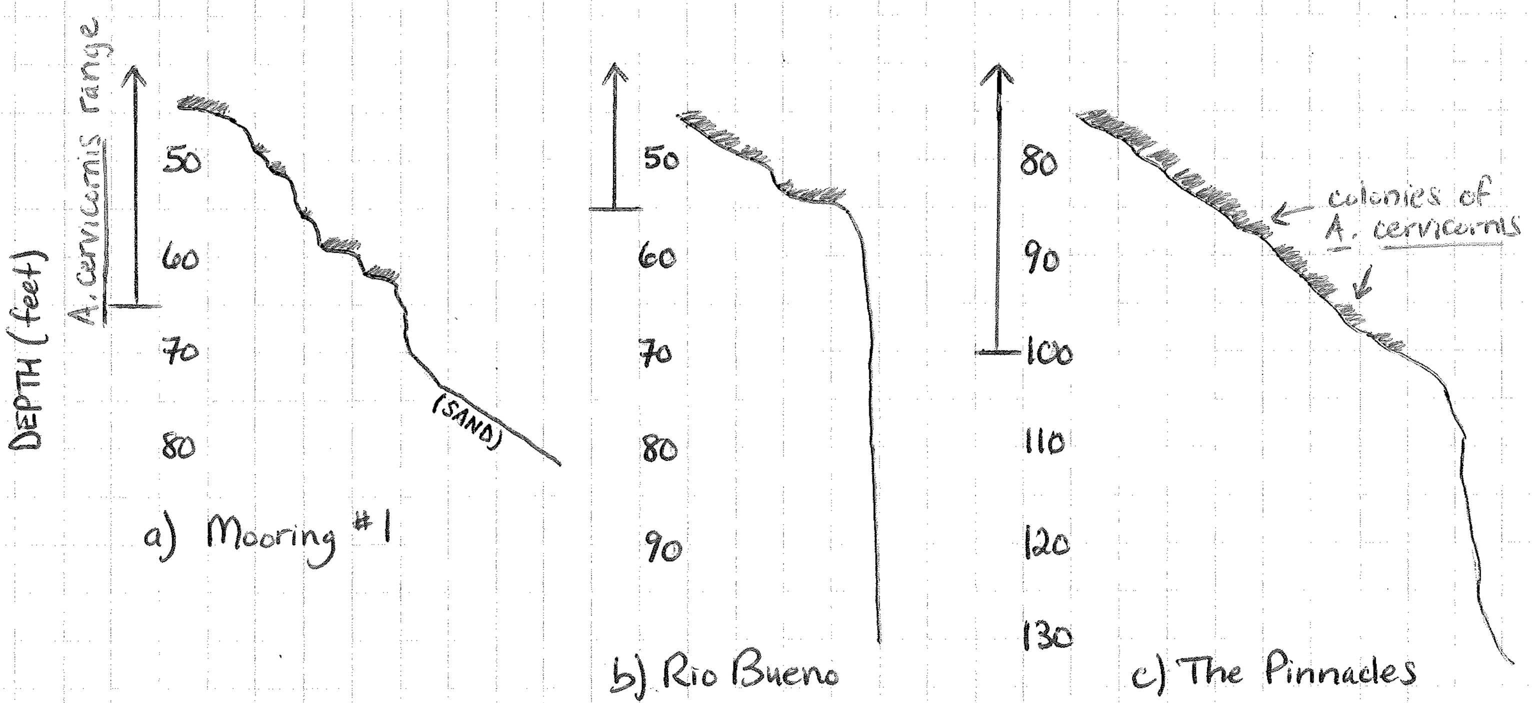

Figure 7. Observational study of maximum depth range of *A. cervicornis* at 3 different locations: variations of maximum depth in relation to local topography.

Discussion

While many of the growth patterns of individual colonies of *Acropora cervicornis* resemble those seen by Tunnicliffe before Hurricane Allen, the overall distribution of the coral has changed dramatically. Trends in maximum height of colonies, density of branching (Growth Index), branch thickness, and rate of ~~Brea~~ fragmentation (measured in terms of % corals unattached to substrate) were similar to those found before the hurricane (Table 2).

Tunnicliffe (1983) showed that before Hurricane Allen, *A. cervicornis* was evenly distributed between 15' and 65'. However, our study shows that there now exists a significantly uneven distribution with depth; highest densities were recorded at the 40' study site (Table 1). Growth rate was also greatest at this depth (although insignificantly: Kruskal-Wallis test, $p > 0.05$), indicating the possibility that 40' could be an optimal depth for recovery by *cervicornis*. Of the three depths surveyed, this depth represents an "ideal" combination of decreased wave action at greater depths with increased light intensity at shallower ones. At this depth, we also noted the greatest amount of tissue death, % algal cover, % individuals with boring sponge, and numbers of damselfish territories associated with staghorn corals (Table 1). All of these trends point to the conclusion that *A. cervicornis* has been successfully reestablished at depths around 40' for the longest period of time since Hurricane Allen. (In fact, 4° branches,

THE OLDEST BRANCHES FOUND IN OUR SURVEY, WERE ONLY FOUND AT A DEPTH OF 40'.). THUS THE CORAL IS RECOVERING AT AN UNEVEN RATE OVER DIFFERENT DEPTHS, PRODUCING THE UNEVEN DISTRIBUTION WHICH WE OBSERVED.

THE GREATER AMOUNT OF TIME THAT *A. cervicornis* HAS BEEN ESTABLISHED AT 40' HAS ALLOWED THE GREATEST NUMBER OF DAMSELFISH TERRITORIES TO APPEAR ON STAGHORNS AT THIS DEPTH (Figure 3). BECAUSE DAMSELFISH ARE KNOWN TO MAINTAIN TERRITORIAL ALGAL "LAWNS" ON *A. cervicornis* (Tunnicliffe 1983), IT SEEMS LOGICAL THAT THE % ALGAL COVER ON *cervicornis* IS ALSO GREATEST AT 40' (Table 1). IT IS IMPORTANT TO NOTE THAT OTHER FACTORS SUCH AS GRAZING BY THE GASTROPOD *Coralliophila* AND *Diadema* COULD PRODUCE INCREASES IN ALGAL COVER (Tunnicliffe 1983), BUT THEIR RELATIVE EFFECTS SHOULD ALSO CORRESPOND TO AREAS WHERE *cervicornis* IS MOST ABUNDANT.

Is clumping due entirely to dist'n of optimum substrate?

BEFORE THE HURRICANE, TUNNICLIFFE FOUND THE COLONIES TO BE CLUMPED AT ALL DEPTHS. OUR STUDY FOUND SIMILAR CLUMPING AT ALL THREE DEPTHS, WITH THE GREATEST DEGREE OF CLUMPING OCCURRING AT 60'; THIS IS ALSO THE DEPTH WHERE THE LEAST NUMBER OF FLAT SURFACES WERE AVAILABLE TO *cervicornis* FOR COLONIZATION. Figure 7 SHOWS THAT DEPTH IS NOT AS GREAT A LIMITING FACTOR TO THE RANGE OF *cervicornis* AS IS THE ANGLE WHICH THE SUBSTRATE MAKES WITH THE WATER SURFACE ABOVE. *A. cervicornis* cannot SURVIVE ON A STEEP SLOPE (AS NOTED ALONG THE STEEPER SLOPES OF THE FORE REEF AT MOORING #1, Figure 7a) OR ON A VERTICAL WALL (AS AT RIO BUENO, Figure 7b) AT

DEPTHS OF EVEN 60', YET IT CAN SURVIVE TO DEPTHS OF UP TO 100' IF IT IS ON A GENTLY SLOPING, RELATIVELY FLAT REEF SURFACE (AS AT THE PINNACLES, Figure 7c). ACCESS TO DIRECT LIGHTING BECOMES MORE IMPORTANT WITH INCREASING DEPTH, AS REFLECTING LIGHT RAYS ARE INCREASINGLY FILTERED OUT (Hughes 1983). THE LIGHT STRIKING AN OBJECT WILL OBVIOUSLY BE GREATEST AT ANY DEPTH IF IT IS HORIZONTAL, ie PARALLEL TO THE WATER SURFACE. THUS, THE cervicornis THAT CAN FIND THE MOST HORIZONTAL SUBSTRATE WILL BE THE MOST SUCCESSFUL. THIS PHENOMENON BECOMES INCREASINGLY IMPORTANT AT GREATER DEPTHS.

ADDITIONALLY, THE SUBSTRATE ON WHICH THE DETACHED cervicornis FRAGMENTS CAN REESTABLISH THEMSELVES AND THEREBY PROPAGATE THE SPECIES (Tunnicliffe 1981) HAS CHANGED DRAMATICALLY AS A RESULT OF HURRICANE ALLEN. BEFORE THE HURRICANE, THE DENSE THICKET OF STAGHORNS PROVIDED A LARGE AREA OVER WHICH A FRAGMENT COULD ANCHOR AND REESTABLISH ITSELF (Tunnicliffe 1983). PRESENTLY, THIS THICKET IS GONE, AND FRAGMENTS MUST REATTACH TO SUBSTRATE IN "VALLEYS" OR DEPRESSIONS IN CORAL ROCK IN ORDER TO SURVIVE, ESPECIALLY IN SHALLOWER WATERS WHERE WAVE ACTION IS MOST INFLUENTIAL AND DAMAGING TO UNATTACHED CORALS. IN FACT, WE SEE THAT "VALLEYS" ARE THE MOST POPULAR CHOICE OF SUBSTRATE AT 20', WHILE FLAT SURFACES ARE MOST POPULAR AT 60'. (Figure 1).

or next to existing colonies

INTERESTINGLY, JUVENILE RECRUITS (FROM PLANULAR

LARVAE) SEEM TO IGNORE BOTH OF THE ABOVE TRENDS, ESTABLISHING THEMSELVES IN CREVICES OR OVERHANGS (Figure 1) WHERE LIGHT INTENSITY IS LOW, FAIRLY EVENLY AT ALL DEPTHS (Figure 2). THUS THEY ARE

perhaps

FAVORING PROTECTION OVER LIGHT INTENSITY FOR THE INITIAL BASAL ATTACHMENT, AND WILL SUBSEQUENTLY BRANCH OUT INTO THE LIGHT AS THEY GROW. THEN, TOO, JUVENILES OCCUR AT A MUCH HIGHER FREQUENCY NOW THAN THEY DID BEFORE THE STORM (Table 2). THIS RELATES TO MARSHALL'S AND STEPHENSON'S (1933) THEORY THAT *cervicornis* MAY SUDDENLY RELEASE A LARGE NUMBER OF EMBRYOS AT THE ONSET OF ADVERSE CONDITIONS. THE HURRICANE COULD HAVE CAUSED SUCH A RELEASE, THE EFFECTS OF WHICH WE NOW SEE IN THE INCREASED NUMBER OF BASALLY ATTACHED JUVENILES AT ALL DEPTHS.

did you measure these?

LIGHT LEVELS ALSO SEEMED TO HAVE AN EFFECT ON POLYP DISTRIBUTION AND SIZE AROUND THE BRANCH. IN ALL CASES, POLYP AND ZOOXANTHELLAE DENSITIES WERE GREATER ON THE TOPS OF BRANCHES THAN ON THE BOTTOMS. (Figures 4+5). IT APPEARS THAT THE POLYPS ARE MORE USEFUL TO THE COLONY IF THEY CAN RECEIVE DIRECT LIGHTING AND HAVE MAXIMAL PHOTOSYNTHETIC PRODUCTION, SO THE CORAL DIRECTS ITS ENERGY INTO THE PRODUCTION OF AS MANY CORALS AS POSSIBLE ON THE ILLUMINATED TOP SURFACE. THIS IS ESPECIALLY TRUE AT 20', WHERE LIGHT INTENSITIES ARE GREATEST. *A. cervicornis* ALSO ALLOCATES IT ENERGY IN POLYP PRODUCTION IN ANOTHER WAY: OVER DEPTH. THE LARGEST POLYPS OCCUR IN HIGH DENSITIES AT 20', WHILE SMALLER ~~POLP~~ POLYPS ARE PRESENT IN

EQUAL DENSITIES AT 40'. RECALL THAT GROWTH RATE WAS HIGHEST AT 40'. IT COULD BE THAT WHILE CORALS AT 20' WOULD HAVE MORE TO GAIN BY PRODUCING LARGER POLYPS ON A SHORTER, THICKER BRANCH (SINCE LONGER, MORE FRAGILE BRANCHES WOULD BE BROKEN OFF BY WAVE TURBULENCE), THOSE AT 40' CAN INVEST MORE ENERGY IN SKELETAL GROWTH, SINCE (1) THE BRANCHES ARE LIKELY TO BE BROKEN OFF BY WAVE ACTION, AND (2) SMALLER POLYPS HAVE A SMALLER SURFACE AREA TO VOLUME RATIO WHICH ~~WOULD~~ WOULD REQUIRE LESS ENERGY TO OPERATE. (Hughes 1983). THIS TREND IS ALSO REPEATED AT 60', WHERE POLYPS ARE AGAIN SMALLER. HOWEVER, POLYP DENSITIES ALSO DECREASE HERE, WHICH COULD SIMPLY POINT TO THE DECREASED GROWTH LEVELS AT ~~LOW~~ GREATER DEPTHS (Table 1). INTERESTINGLY, AT 60', POLYP DENSITY AND SIZE NO LONGER DIFFER SIGNIFICANTLY BETWEEN TOP AND BOTTOM BRANCH SURFACES. THIS MAY BE AN INDICATION OF THE DECREASING LIGHT LEVELS, BUT IT MAY ALSO BE TRUE THAT SIMILAR-SIZED POLYPS EVENLY SPACED AROUND THE BRANCH COULD INDICATE AN INCREASED RELIANCE ON ZOOPLANKTON AS A DIETARY SUPPLEMENT AT DEPTHS WHERE PHOTOSYNTHETIC PRODUCTION CAN ONLY BE A FRACTION OF WHAT IT IS IN SHALLOWER WATERS.

IN SUMMARY, THE CHARACTERISTIC PRE-HURRICANE WEST FORE REEF HAD AN EXPENSIVE cervicornis ZONE FROM 15'-65' WHICH WAS MARKED BY A DENSE THICKET OF STAGHORN CORAL. HURRICANE ALLEN WIPED OUT THIS THICKET, CREATING A CLEAN SLATE ON WHICH NEW CORALS COULD COLONIZE AND ESTABLISH THEMSELVES

IN AN AREA ONCE DOMINATED BY Acropora cervicornis AND SCATTERED MOUNDS OF Montastrea annularis. IN ESSENCE, THE HURRICANE WAS A DISTURBANCE WHICH PRODUCED A CHANGE IN SPECIES COMPOSITION AND AN ~~IN ORDER TO~~ INCREASE IN SPECIES DIVERSITY. ACCORDING TO Connell (1978), THE INTERMEDIATE DISTURBANCE HYPOTHESIS STATES THAT, "DIVERSITY IS HIGHER WHEN DISTURBANCES ARE INTERMEDIATE ON THE SCALES OF FREQUENCY AND INTENSITY." WHILE IT CAN BE ARGUED THAT HURRICANE ALLEN WAS BY NO MEANS A SMALL DISTURBANCE, ITS EFFECT ON THE FORE REEF AT DISCOVERY BAY HAS BEEN TO INCREASE THE DIVERSITY OF CORAL SPECIES BY DESTROYING THE ONCE-DOMINANT SPECIES, A. cervicornis. SMALLER STORMS ACTUALLY HELP THE STAGHORNS TO PROPAGATE INTO NEW AREAS: "THE STAGHORN STRUCTURE ... IS DESIGNED TO BE BROKEN; ITS SUCCESS IS DUE TO, RATHER THAN IN SPITE OF, THE LARGER NUMBER OF FRACTURES PRESENT." (Tunnicliffe 1981). Thus it WOULD TAKE A MAJOR STORM, INDEED, TO ALTER THE DOMINANCE OF A. cervicornis PRESENT BEFORE AUGUST 1980. (NOTE THAT A MINOR STORM ON 29 FEB 84 SEEMED TO HAVE NO EFFECT ~~WHATSOVR~~ WHATSOEVER ON THE STAGHORNS, EVEN AT 20' DEPTHS ON THE FORE REEF!).

THE PRESENT SITUATION AT DISCOVERY BAY PROVIDES AN EXCELLENT OPPORTUNITY IN WHICH TO STUDY THE RECOVERY AND GROWTH PATTERNS OF A FAST-GROWING, SLOW-COLONIZING CORAL THAT ONCE DOMINATED THE REEF COMMUNITY. THE RESULTS OF THIS STUDY SHOW THAT ONE CANNOT CONFIDENTLY PREDICT THE COLONIZATION AND RECOVERY PATTERNS THAT WILL OCCUR

IN SUCH A SITUATION SIMPLY BY STUDYING THE CLIMAX COMMUNITY THAT EXISTED BEFORE THE DISTURBANCE. WHETHER OR NOT *Acropora cervicornis* WILL EVER RECOVER TO ITS PRE-HURRICANE LEVELS, AND HOW THE EMERGENCE ~~ON~~ OF NEW DIVERSE CORAL SPECIES IN THE PREVIOUS *cervicornis* ZONE WILL AFFECT ITS RECOVERY PATTERNS, REMAIN TO BE SEEN.

Excellent study. Results nicely presented, discussed, and compared with published studies.

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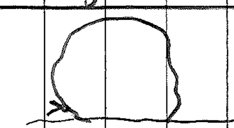
Appendix : Raw Data Sheets

1- 20' transects ×2 #1, #2
2- " " ×3 #3, #4, #5
3- 40' #1
4- " " #2
5- " " #3
6- 60' #1
7- " " #2
8- " " #3

20' transects (post-storm) 3/3/84 AM Mooring 1

location	max ht	max wd	# fracs	branching 1°	2°	3°	% algae	% dead	Sponge damaged	B/R juv adult	Basal width	Comments
transect 1												
2	33	55	9	33	17	7	20	25	Sponge 01	R	1.9	large; in valley; Mont. annul. + Agaricia mounds around it. Also, Agaricia mound, Mont. asteroides (encrust) underneath it, cervicornis is dying?
7	10	15	0	18	10	5	5	5	— D3	B juv.	1.4	much smaller; under "shadow" of Mont. annularis in rel. open valley
10	15	12	0	2	-	-	0	0	— D2	B juv.	1.2	tiny juvenile, basal attachment under Montastrea annularis mound, now branches growing out 
transect 2												
4	5	6	0	5	1	—	<5	0	— D2	B juv	1.3	on edge of large crevice ("cave") under large mound of M. annularis. tiny juvenile
2	14	13	5	19	9	3	93	100	Sponge D2	R	1.4	all dead
1	11	10	0	8	3	-	0	0	— D3	B juv.	1.7	on flat area. 0.5 from M. annularis mound in relatively open area

evidence of increased fractures on several large individuals. No fragments were noticed in exceeding numbers, although Marianne reported them at deeper (40') depths. Could storm have moved them down?

20' transects #1, 2, 3   2/27/84   PM   MOORING I

location	max ht	max wid	# fracs	branching 1°	2°	3°	% algae	% dead	Sponge or damsel	(B/R) juv adult	Comments
Transect #3											
4	48	81	5	47	17	6	35	40	$\overline{D3}$	adult R	in valley ~~????~~ betw high coral mounds – Montastrea annularis et al
4	14	21	2	17	8	3	10	10	$\overline{D3}$	adult R	Same spot, much smaller than first. large amt of Acropora hurricanehurrican brains, stars, Agaricia – all mounds up to 1m high much Fire coral
1	~~??~~ 17.5	35	4	9	5	3	35	35	$\overline{D3}$	R (adult)	tiny } in crevice on outcrop of coral rock
1	9	10.5	0	5	1	–	0	~0	$\overline{D3}$	juv B	tiny, same area as above }
Transect #4											
3	17	21	3	16	6	2	0	5-10	Sponge D2	R (adult)	great variety of corals + sponge purple tube sponge: Haliclona hogarthi mounds of M. annularis – up to 1m high
2	9	10.5	1	8	3	1	0	~0	Sponge Di	R (adult)	
Transect #3											

No. Corals / ~~ϕ~~ 10 m²

A. cervicornis often in "valleys" btw. these mounds
Porites porites
Meandrina meandrites – encrusting large + flat
Agaricia
Gorgonians – sea rods
✱ rubble is much thicker here from hurricane than at 40'

Wave action fairly strong here: fewer damselfish!

notes: A. cervicornis rubble has branches of much thicker ϕ than new corals
A. cervicornis rubble from hurricane much greater (thicker) at 20' than 40'
we could see beginnings of A. palmata zone just 10-20 m further up reef slope (@ 10-15' deep)

40' transect #1 2/27/84 AM MOORING I n = 10

D1 - Damsel terr
D2 - near damsel
D3 - no damsel

location (section)	(cm) max height	(cm) max wid	frac	branching 1°	2°	3°	% algae	% dead	~~dame~~ sponge or damsel	juv or adult / reattached (B or R)	comments
1	8	26	2	10	7	7	90	100	D2 sponge	adult R	ALL DEAD Porites all over, too Madracis ~~mounds~~ growing under dead Acrop. Montastrea* mounds, Agaricia mounds + plates
1	4	5	2	2	-	-	0	~0	sponge D1	juv B	" " very tiny, near above
1	20	43	NA	34	NA	8	100	100	sponge D1	adult R	ALL DEAD - many Agaricia mounds, 1 Montastrea* mound.
8	4.5	5	0	5	4	2	0	~0	D2	~~adult~~ ? B juv	tiny, in crevice of Montastrea annularis*
8	18	22	0	24	12	3	0	~0	sponge D1	adult B	in "valley" between two large (.5m) mounds of mixed coral spp.
6	13	18	0	31	10	4	0	0	D1	juv B	Madracis mirab, Porcupine sponge
4	4	13	2	4	1	-	0	5	D3	adult R	growing (horizontal orientation) on outcrop in semi-crevice (on a ledge?)
3	12	8	1	3	1	-	10	10	D3	juv B	dead basal attachment; in valley (~flat) in betw. mounds
4	24	25	NA	9	3	-	5	10	D3	adult R	very large, but few branches same type substrate
3	17	27	2	6	3	-	5	10	D3	no attached	completely detached, but living - fallen from one of corals in section 4? laying on Acropora rubble from hurricane

note: lots of covered Acropora rubble from ~~[illegible]~~ hurricane - dead branches are much wider in ∅

40' transect #2 3/2/84 AM Mooring I n=8

location	max ht	max wd	fracs	1°	2°	3°	%alg	% dead	sponge damsel	B/R juv adult	Basal width	Comments
10	15	11.5	1	5	3	1	30	30	Sponge D2	R	.8	(detached) "hiding" (protected) where landed between .3-.5 m high mounds of dead coral *Agaricia* mounds, (black) encrust sponge
9	22*	40*	2	16	4	2	50	55	— D1	R	1.0	only ½ of coral within transect belt boundary — much of reef was dead w/algae / has overgrown dead coral mounds. Fighting w/ BRANCHING FIRE CORAL (beginning to take over *cervicornis*)
7	16	19	0	8	2	–	0	40	Sponge D2	R	1.3	on flat area → no protection less damsel protection → algae all grazed away
4	16	21	1	9	4	3	5	5	— D3	juv B	1.0	growing under (where it started?) and now over *Agaricia* mound
3	14.5	13	2	5	3	1	0	0	— D3	R (but detached)	1.2	
3	4.0	6.0	0	5	1	0	0	0	— D2	juv B	0.75	tiny juv. growing in indentation on top of coral mound (*Agaricia*)
1	12.	19.	0	6	3	1	10	10	— D2	R	1.2	Reattached to top of mound
1	48	44	3	11	5	4 4° 1* dead	50	50	— D1	R adult	1.6	Sitting in flat valley but protected by damsel .5 m mounds all around

close together

40' transect #3 3/2/84 PM Mooring I n = 16

location	max ht	max wd	# fracs	1°	2°	3° (4°)	% alg	% dead	Sponge damsel	B/R juv adult	Base width	Comments
10	8.5	7.0	0	3	–	–	0	5 →	Sponge D3	B juv	0.5	all three on a flat between Coral mounds including Mont. annulars and Madr. mirab.
10	22	29	2	(30)	11	6	10	15	— D3	R	1.6	
10	43	64	3	51	18	8 (1)	10	10	D1* —	R	1.8	4° branch ½ living ½ covered w/ algae
10	10	5	0	2	1	–	0	0	D1* —	B juv	0.8	tiny juv. directly underneath Coral #3 above
9	23	28	5	13	7	3	15	20	sponge* D1	R (detached)	1.2	adjacent to and under brain coral mound
9	8	3	0	3	1	–	<5	0	D1 Sponge	B juv	1.3	on other side of this Same flat
9	33	20	3	9	4	2	10	10	Sponge D1	R (semi)	2.3	on top of coral mound w/ one branch in crevice – attachment site
8	8	8	0	9	2	–	0	0	— D2	B juv.	1.0	two recruits near each other
7	9	7	0	6	2	–	0	0	— D3	B juv.	0.8	
7	2	7	0	1	–	–	0	0	— D3	reattach R	0.7	Broken single fragment in Coral "cave": Totally protected by surrounding rock
7	13	19.5	0	7	3	–	0	5	— D3	B juv	1.0	
5	14.5	14.5	4	7	2	1	80	90	Sponge D3	R (detached)	1.2	pretty dead – abandoned terr? on flats w/ next two
5	16	33	6	20	10	5	45	50	Sponge D2	R	1.5	on flat "
4	32	65	5	53	29	12	60	70	Sponge D1	R	1.0	in process of dying due to damsel terr. fire coral (branch) and Agaricia mound growing beneath it.
2	9	11	2	6	2	–	75	85	Sponge D3	detached	0.8	fragment never successfully attached → dying?
2	16	17.5	2	11	5	1	0	0	— D1	R	1.3	on flat.

60' transect #1 3/1/84 AM Mooring I (after storm, 2/29/84)

location	(cm) max ht	(cm) max wd	no. fracs	branching 1°	2°	3°	% algae	% dead	sponge damsel	B/R juv adult	cm Basal width	Comments
Transect #1												
1	5.5	11.5	0	3	1	1	0	0	$\overline{D}3$	R	1.5	much Madr. mirab, Agaricia plates on edge of overhanging coral mound. - fairly in open
1	1	10.2	0	1	0	0	0	0	$\overline{D}3$	tiny R Fragmt	1.0	reattached in sed^{mt} w/in 0.5 m of above - broken off
3	18.9	17.5	0*	15	6	3	5	5	$\overline{D}3$	R	1.2	Small, but ~~$~~ many branches on sandy "flat" under Mont. annul. mound, Agaricia plate Porites, tube sponges below
4	12.	16.5	0	10	5	2	10	10	$\overline{D}3$	Detached Adult fragmt	0.8	in crevice under overhanging coral w/ Porites, Madr. mirab all around, Detached.
6	2.0	6.0	0	3	1	-	0	0	$\overline{D}3$	B juv.	0.6	Tiny ~~[illegible]~~ juv. under overhang w/ Por. por., Madr. mirab.
10	8.2	8.5	1	4	1	-	~0	~0	$\overline{D}2$	R	0.7	On overhang facing sand ~ protected, Madr. mirab. + Porites around (as usual)

Very little algae @ this depth
Very few fractures, Corals are relatively small + rare.

60 m transect #2 3 MAR 84 PM Mooring 1

location	cm max ht	cm max wd	# fracs	branching 1°	2°	3°	% algae	% dead	sponge damsel	(B/R) juv/adult	cm Basal width	Comment
10	16	23	0	8	4	2	5	10	$\overline{D2}$	detach	1.0	all of these are in a single clump on a flat area between
10	26.5	9.5	0	7	2	1	0	5	$\overline{D2}$	R	1.4	Coral mounds (.5 m high) on slope of reef edge leading to
10	14	13	0	10	3	2	0	0	$\overline{D2}$	R	1.3	sand @ 65'
10	–	2	–	–	–	–	–	–	"	juv B	–	juvenile was just a lump w/ no branches yet (a new recruit!)
7	15	16.5	0	13	3	2	5	5	D2	juv B	1.3	juvenile in crevice
2	7.5	6	0	4	–	–	0	0		juv B	.8	tiny juvenile within territory of a spotted drum fish (8"). protected under overhanging coral ledge.

60' transect #3 3/3/84 PM Mooring I

location	max hgt	max wid	# fracs	1°	2°	3°	% algae	% dead	sponge/ damsel	(B/N) juv/ adult	basal width	Comments	* outside of trans. belt
10	16	15	0	7	3	-	0	0	— D3	B juv	1.0	in valley between M. annularis and dead coral mounds. Near (.5m) another cervicornis of similar size*	
6	19	25	1	14	5	2	10* Dictyota on live coral	0	— D2	B juv	1.2	encrusted on Porites (club) in 2 places. On flat along slope (as w/above). M. mirabilis below cf. down slope	
3	16	18	0	11	5	2	0	0	— D1	B juv	1.0	large "juvenile"	
2	13	23	0	4	2	-	0	0	— D1	B juv	0.9	basally attached to branch to Porites porites (purple club finger) growing over dense mat of finger corals.	
2	14.5	13	0	11	3	1	0	0	— D2	B juv	0.8	on substrate below Porites	
2	16	20	2	6	2	1	0	0	— D2	detached	1.1	fragment fallen from above? 0.5 m below previous 2 on slope	