Acropora cervicornis populations 19 years after Hurricane Allen: Are they recovering?

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Abstract: Hurricane Allen hit Jamaica's north shore in 1980, destroying large thickets of *Acropora cervicornis* (Acroporidae) colonies. Before the hurricane, densities were as high as 11 colonies/m^2; immediately after the hurricane, densities declined sharply, to a maximum of 0.94 colonies/m^2. We examined whether staghorn coral densities have increased since the last survey in 1988, testing the hypothesis that the population is recovering. Instead of evidence of recovery, we found even lower densities of *A. cervicornis* at all sites. Dairy Bull was not surveyed previously, and we found the highest density there, perhaps due to the low algal cover and high degree of structural complexity there. Although populations appear almost extinct at most sites, Dairy Bull could prove to be a source population, allowing eventual recovery of *A. cervicornis*.

Keywords: *Staghorn coral, Discovery Bay, population dynamics*

INTRODUCTION

Prior to 1980, dense thickets of staghorn coral, *Acropora cervicornis* (Acroporidae), dominated the forereef at Discovery Bay, Jamaica, with densities up to 11 colonies/m^2 (Tunnicliffe 1983). *A. cervicornis* has extremely limited sexual reproduction, perhaps because resources are expended for rapid growth, and seems to reproduce primarily by vegetative propagation of broken fragments (Tunnicliffe 1983). Fragmentation occurs frequently, as *A. cervicornis* is brittle and is oriented perpendicular to wave flow. However, approximately 25% of fragments survive and are recemented to the substrate, either by the coral itself or by an encrusting organism (Tunnicliffe 1981, Tunnicliffe 1983). Vegetative propagation limits long distance dispersal and tends to produce large stands of genetically identical individuals, which may limit recovery from a major disturbance. Despite these shortcomings, vegetative reproduction affords *A. cervicornis* several important competitive advantages over other species: 1) a rapid growth rate that allows it to shade other corals and algae, 2) falling fragments that can damage organisms growing below, and 3) asexual reproduction throughout the year, in contrast to limited sexual reproduction seasonally.

Hurricane Allen, the strongest storm ever recorded in the Caribbean, passed Jamaica's north shore on 6 August 1980. At Discovery Bay, winds reached 110 km/hr, and waves over 12 m high broke in 15 m of water. Damage to corals occurred at depths up to 50 m (Woodley et al. 1981). Immediately after the hurricane, *A. cervicornis* densities were reduced to 40% of 1977 levels, and of 254 live fragments of *A. cervicornis* marked immediately after the hurricane, all but four were dead within five months (Knowlton et al. 1981). The extremely high post-hurricane mortality might have been due in part to the presence of white band disease, first noted in the region two months before the hurricane.

Another important source of staghorn coral mortality after the hurricane was predation. The main predators of *A. cervicornis* are *Diadema antillarum* (echinoid), *Coralliophila* sp. (gastropod), *Hermodice carunculata* (polychaete), and the three spot damselfish (*Stegastes planifrons*). Predation was low before the hurricane, and an insignificant source of mortality (Tunnicliffe 1983). However, within one year of the hurricane, *A. cervicornis* populations had fallen 100 fold while predator densities only decreased by 50%, creating a high predator to coral ratio. Thus, predation played an important role in staghorn coral decline during the 1980s (Knowlton et al. 1981; Knowlton et al. 1990).

Several population studies have been done since the hurricane to assess the recovery of *A. cervicornis*. The most recent study we found (Blechner, 1988) concluded that the population, although at lower densities than after the hurricane and 1984, was recovering. However, during orientation dives we observed very few staghorn colonies, prompting us to predict that *A. cervicornis* density has continued to decline. Spatial complexity and gradual slope of the ocean floor have been previously implicated as factors favoring *A. cervicornis* growth, while sedimentation and high algal cover may be deleterious to staghorn corals (Tunnicliffe 1983). Thus, we predicted that sites with high three-dimensional complexity and low slope would exhibit more pronounced regeneration than sites high in sediment and algal cover. Finally, we predicted that, due to its reproductive nature, recovery of *A. cervicornis*, if any, would be slow, and that current, live colonies would be clumped.

METHODS

A. cervicornis populations were surveyed using SCUBA on 6-12 March 1999. Transects (20 x 4 m) were located at 7 and 13 m by descending to the proper depth, swimming in a haphazardly chosen direction for 1 minute, and then randomly choosing a direction to drop a pre-measured rope. In a few cases (backreef), transects were run non-randomly along the contour gradient in order to ensure a constant depth (13 m). At least three (maximum of six) transects were run at each depth. Due to time constraints and a very high density of *A. cervicornis* at Dairy Bull 7 m, we sampled the third transect with 3 separate, randomly chosen 2 x 2 m plots within the transect.

For each *A. cervicornis* colony encountered in a transect we measured colony height, colony width, degree of branching, percent dead tissue, and mode of attachment. An individual colony was defined as all *A. cervicornis* polyps occurring on any number of branches arising from a single point of connection with the substrate. Colony height was taken as the distance between the substrate and the highest point of the colony. Colony width was measured between the widest two branches. Degree of branching was measured using the methodology described by Strahler (1957, as referenced in Tunnicliffe 1983) where the youngest branches have order 1, two 1st order branches join to make a branch of 2nd order, etc. The percent dead tissue was estimated visually. Mode of attachment was categorized as unbroken (developed from a larvae), broken and recemented, or broken and uncemented. We also noted if the colony was a larval recruit less than 1 yr old (<10 cm tall, unbroken attachment).

Site descriptions were written to relate sedimentation, slope, algal cover, and three-dimensional complexity between sites. Sedimentation and slope were not quantitatively measured, but rather ranked between sites. Sedimentation was categorized based on the sediment observed covering coral and algal. Algal cover was estimated visually at each site. Complexity was based primarily on the abundance of "haystacks"- mounds created by corals such as *Dendrogyra cylindrus*, *Montastrea annularis*, and *Montastrea covernosa*. Their abundance was ranked between sites.

As we did not have normal data, we analyzed our data using the Wilcoxon non-parametric test.

SITE DESCRIPTIONS

Dairy Bull, 7 m (11 March). This site had the highest coral cover of sites surveyed, and the lowest algal cover (10%). There were many large haystacks of coral, often within 1 m of each other, possibly providing shelter from wave action. Sedimentation was moderate, and the slope was very gradual.

Dairy Bull, 13 m (10, 11 March). After gradually sloping to 17 m, the slope gets considerably steeper. As at 7 m, there was a high abundance of living coral, especially haystacks. Algal cover was low (20%), as was sedimentation. The sand channels running perpendicular to the shore were much larger than at the other sites.

Dancing Lady, 7 m (11 March). Although this site had a minimal slope, there was considerable topographic variation due to the large haystack corals, which often grew taller than 1 m above the substrate. These haystacks occurred with moderate frequency, though there were large patches where they were noticeably absent. This site had high sedimentation, moderately low living coral cover, and high algal cover (70%).

Dancing Lady, 13 m (7 March). This site had high algal cover (65%) and a steeper slope than the other sites at 13 m. Sedimentation was low, although sand channels were common. Haystacks occurred less frequently than at Diary Bull, but were still relatively common.

Mooring #1, 7 m (10 March). This site was marked by high algal cover (85%). There was a moderate amount of sedimentation, and

haystacks were small but frequently encountered. There were many small sand channels running perpendicular to the reef crest.

Mooring #1, 13 m (6 March). This site had a gradual slope, large sand channels, and high algal cover (70%). Sedimentation was moderate, and three-dimensional complexity of the reef was low.

Long Term Survey, 7 m (12 March). This site had fewer and smaller haystacks than other sites. Particularly noticeable were patches without any haystacks present. LTS also seemed to have less sediment than the other 7 m sites, though overall sedimentation was still moderate. Sand channels were small and infrequent. Almost all of the available substrate was covered with living material, approximately 80% of which was algae.

Long Term Survey, 13 m (7 March). As at the 7 m site, the haystacks encountered here were all fairly low in height, and the topography was relatively uniform. This area had moderate sedimentation, and a low coral abundance. The algae covered 80% of the substrate. The slope was noticeably smaller and less steep between 20 and 13 m depths, though Tunnicliffe (1983) provides a more accurate description of slope. Green Buoy, backreef, 13 m (6 March) Most noticeable about this sight was the low visibility caused by the presence of suspended particulate matter. The turbidity may account for the low algal presence and the low cover of living coral. Most of the substrate was sand, interspersed with a large amount of *Acropora cervicornis* rubble. Sedimentation was extremely high. The reef was shallow, gently sloping from 7 m to 13 m and then falling off sharply to at least 27 m.

RESULTS

There was a significant difference in *A. cervicornis* density among sites (the two depths combined, Table 1, X^2=12.2, df = 4, P=0.016). As well, there was a trend for a difference in *A. cervicornis* density across sites and depths (Fig. 1, X^2=12.0, df = 7, P=0.08). Dairy Bull, 7 m, had the highest density of *A. cervicornis*. Dairy Bull, 7 m had a maximum density of 11 individuals/m^2. There was no significant difference in density between depths (all sites combined; X^2=1.65, df = 1, P=0.20). There were no significant differences in height, width, branching order, or percent dead tissue by site (all depths) (X^2=6.2, df = 4, P=0.18; X^2=8.18, df = 4, P=0.09; X^2=4.65, df = 4, P=0.37; X^2=7.2, df = 4, P=0.12 respectively). However, colony height and width were significantly greater at 7 m than 13 m (Fig 2, X^2=9.12, df = 1, P=0.0025; X^2=7.33, df = 1, P=0.0068).

A. cervicornis densities have declined sites since Hurricane Allen at all previously surveyed (Table 1). As well, at all sites where *A. cervicornis* was found, percent dead tissue had increased (Table 1). Height, width and branching order do not appear to have changed since the hurricane (Table 1). We found a lower proportion of corals that were unbroken than was found before the hurricane or in 1984 (Table 2), and only one larval recruit less than 1 yr old was found in our transects, at Dancing Lady 13 m.

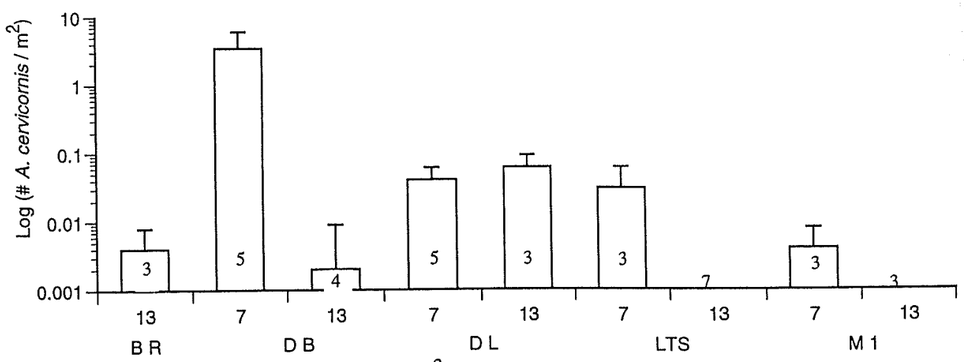

Fig. 1. Number of *A. cervicornis* colonies found per m^2 at all sites and depths (7 or 13 m) in Discovery Bay, Jamaica (mean ±SE; P=0.08). BR = Back Reef, DB = Dairy Bull, DL = Dancing Lady, LTS = Long Term Site, M 1 = Mooring 1. Numbers represent the number of transects run at each site.

Table 1. Population data of *A. cervicornis* before Hurricane Allen, after Hurricane Allen, and in 1999 (means ± SE). Pre-Hurricane data from Tunnicliffe 1981 and Tunnicliffe 1983. Post-Hurricane data from Knowlton et al. 1981, DeVaro and Rhee 1984, Williams 1984, Woodley 1981, and Blechner 1988.

Site	Backreef	Dairy Bull		Dancing Lady		Long Term Site		Mooring 1	
Depth (m)	13	7	13	7	13	7	13	7	13
DENSITY (COLONY/M^2)									
Pre-Hurricane	2.0					7.1	7.1		
Post-Hurricane				0.94	0.94			0.1	0.35
1999	0.004 (±0.004)	3.0 (±2.6)	0.02 (±0.008)	0.04 (±0.02)	0.06 (±0.03)	0.03 (±0.03)	0	0.004 (±0.004)	0
Dead Tissue (%)									
Pre-Hurricane	35.1						35.9		
Post-Hurricane								17.4	40.6
1999	50.0 (±0)	52.5 (±5.4)	74.1 (±7.4)	37.2 (±8.0)	36.5 (±9.4)	45.0 (±13.8)	-	30.0 (±0)	-
HEIGHT (CM)									
Pre-Hurricane	27.4						38.9		
Post-Hurricane								16.0	16.6
1999	20.0 (±0)	27.1 (±2.9)	19.6 (±3.9)	24.8 (±3.7)	13.6 (±2.8)	40.8 (±10.0)	-	12.0 (±0)	-
WIDTH (CM)									
PRE-HURRICANE	48.9						61.3		
POST-HURRICANE								24.2	20.1
1999	40.0 (±0)	38.0 (±3.5)	32.3 (±5.0)	37.3 (±5.2)	17.4 (±4.2)	45.8 (±5.2)	-	14.0 (±0)	-
BRANCHING ORDER									
Pre-Hurricane	3.1				5.0		4.8		
Post-Hurricane					2.0				
1999	2.0 (±0)	2.6 (±0.1)	2.7 (±0.2)	2.8 (±0.1)	2.6 (±0.22)	2.8 (±0.2)	-	2.0 (±0)	-

Table 2. Frequencies of basal breakage of *A. cervicornis* before and after Hurricane Allen Pre hurricane data from Tunnicliffe 1983, 1984 data from DeVaro and Rhee 1984.

	Pre-hurricane	1984	1999
Unbroken	0.22	0.43	0.10
Broken, recemented	0.52	0.46	0.63
Broken, uncemented	0.26	0.11	0.27

DISCUSSION

There was a significant difference in *A. cervicornis* densities between sites, suggesting that differences in algal cover, three-dimensional complexity, or other environmental factors may be important in the survival and colonization of this coral. Dairy Bull, 7 m, had the highest density of *A. cervicornis*, although the differences were not significant because of the large variance. The three-dimensional complexity at Dairy Bull might explain the high abundance of *A. cervicornis* there. The patches of high staghorn density were found nestled in "valleys" surrounded by large haystacks of coral, which may provide a cachement for fragments, allowing an aggregation of regrowing corals. The haystacks may also offer shelter from severe wave action, creating a

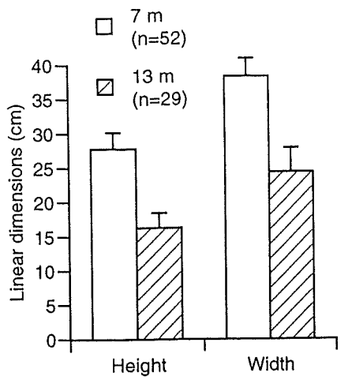

Fig. 2. Linear dimensions of *A. cervicornis* colonies at 7 m and 13 m. Height and width differ significantly with depth across all sites (P=0.003 and P=0.007 respectively).

relatively disturbance free microhabitat. As predicted, we found the dispersion of *A. cervicornis* to be clumped. At most sites, we found staghorns in only half of the transects, and all colonies usually occurred within a 2-3 m^2 area, generally in these sheltered "valleys". The sites with the lowest densities of *A. cervicornis* (LTS 40, M1 20 & 40) had the lowest three-dimensional complexity, and often had high algal cover. This further suggests that three-dimensional complexity may be an important factor for staghorn coral growth, and that high algal cover may reduce coral survivorship and recruitment. Unlike previous studies, depth was not an important variable determining staghorn coral density.

Individual colony dimensions, such as height, width, and branching order did not differ across sites, so environmental differences affected settlement and recruitment of larvae and fragment regeneration, but not growth. Height and width were significantly greater at 7 m, likely because of greater light than at 13 m (Tunnicliffe 1983).

As predicted, densities of *A. cervicornis* have declined at all sites since the most recent survey. As well, percent dead tissue has increased since Hurricane Allen. The mechanism for this increased mortality is unknown, though it is likely that predators have kept staghorn densities low, as suggested by Knowlton et al. (1990). White band disease was not observed at any of the sites in this study, suggesting that it is no longer a major cause of mortality. The fact that colony height and width did not differ between pre- and post-hurricane surveys indicates that perhaps the low density is not due to colony condition or growth but rather low reproduction or high mortality of young corals.

Hurricanes often break *A. cervicornis* at their bases. Because staghorns have a low larval recruitment rate, we expected to find very few unbroken colonies, and indeed most of the coral we found had been broken from its original attachment. Before the hurricane, Tunnicliffe (1983) found 100% more unbroken corals than we did. The presence of only one larval recruit established during the past year in 2372 m^2 of transects indicates that sexual reproduction is still extremely unsuccessful, and fragmentation is still the most important mode of reproduction for *A. cervicornis*.

A. cervicornis density has continued to decrease since 1988, and the percent dead tissue has increased, suggesting that *A. cervicornis* is still not recovering from Hurricane Allen in 1980. At only 1 site (Dairy Bull, 7 m) were densities greater than 1 colony/m^2, and all the others were less than 0.06 colonies/ m^2. Staghorn populations should continue to be surveyed periodically in Discovery Bay. Even though populations at other sites are all but extinct, Dairy Bull could prove to be a source population, from which fragments may slowly spread and repopulate Discovery Bay.

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