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Patterns of Damage to the Branching Coral *Acropora palmata* Following Hurricane Andrew: Damage and Survivorship of Hurricane-generated Asexual Recruits

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ABSTRACT

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Hurricane Andrew caused widespread damage to the *Acropora palmata* population on a patch reef on the Florida Reef Tract. After the storm, more than 50% of the *A. palmata* cover in the rubble and reef-flat zones was comprised of live fragments. Other species of coral were minimally damaged. Most fragments were distributed within or adjacent to the remaining patches of standing elkhorn colonies. Neither distribution nor mortality rate of fragments was dependent on initial fragment size. However, rate of stabilization of fragments was related to substrate type and distance from a patch of mature colonies, suggesting that standing colonies may protect regenerating fragments from removal from the reef. Differences in the substrate type (hard *vs.* unconsolidated rubble) where fragments landed, affected removal, total mortality, and partial mortality rates of hurricane-generated fragments. Rubble substrate favored stabilization and survival of hurricane-generated asexual recruits.

ADDITIONAL INDEX WORDS: *Hurricane damage, coastal storm, coral reef, elkhorn coral.*

INTRODUCTION

Elkhorn coral (*Acropora palmata*) is a branching, tree-like coral that forms densely aggregated patches on the shallow portions of reefs in the Florida Reef Tract and throughout the Caribbean (GOREAU, 1959; GEISTER, 1977; GLADFELTER *et al.*, 1978; ROGERS *et al.*, 1982). Although it is adapted to high wave and surge zones of reefs (SCHUHMACHER and PLEWKA, 1981), it is very susceptible to the intensity of physical forces generated by a hurricane (WOODLEY *et al.*, 1981). Significant dislodgment and fragmentation of this species were reported after Hurricanes Edith (GLYNN *et al.*, 1964), Gerta (HIGHSMITH *et al.*, 1980), Allen (WOODLEY *et al.*, 1981), David and Frederic (ROGERS *et al.*, 1982), Hugo (GLADFELTER, 1991), and Andrew (FONG and LIRMAN, 1994). In some cases, up to 95% of the existing *A. palmata* cover was lost (WOODLEY *et al.*, 1981; GLADFELTER, 1991). This susceptibility has been related to *A. palmata*'s high surface-area-to-volume ratio that results from the upright branching form, as massive and encrusting corals with a low profile seem to be more resistant to damage (WOODLEY et al., 1981; ROGERS *et al.*, 1982, 1983; STODDART, 1985; EDMUNDS and WITMAN, 1991; BYTHELL *et al.*, 1993).

Although highly susceptible to storms and many other physical (PORTER *et al.*, 1982; DALLMEYER *et al.*, 1982; DUSTAN, 1985), chemical (BAK, 1987) and biological (BAK and CRIENS, 1981; GLADFELTER, 1982; JAAP, 1984) stresses, *Acropora palmata* persists as a dominant component of shallow, high energy reef areas. Many scientists believe that local dominance of this species is achieved by fast growth rates (4.7–9.9 cm·yr^{-1}) and high regeneration potential (BAK, 1976; GLADFELTER *et al.*, 1978; HIGHSMITH, 1982; HUSTON, 1985). Additionally, *A. palmata* has several morphological adaptations to wave stress. A thick stem composed of skeletal material with unusual structural strength anchors the colonies to the reef (SCHUHMACHER and PLEWKA, 1981). Each colony aligns branches parallel to the prevailing water flow presumably to reduce the force exerted on them by waves and currents (GRAUS *et al.*, 1977; SCHUHMACHER and PLEWKA, 1981).

Unlike acroporid species in the Indo-Pacific Province that exhibit high sexual recruitment rates (WALLACE, 1985), the main propagation mode of *A. palmata* in the Caribbean is by means of colony fragmentation (BAK and ENGEL, 1979; HIGHSMITH, 1982; RYLAARSDAM, 1983; JORDAN-DAHLGREN, 1992), enabling this species to re-cover and re-populate areas disturbed by intense physical disturbances (HIGHSMITH *et al.*, 1980; ROGERS *et al.*, 1982; LIRMAN and FONG, *unpublished data*). Some researchers believe the ability to produce asexual recruits readily from wave generated fragments is also an adaptation to wave stress (HIGHSMITH, 1982). Fast growth rates, the ability to regenerate lesions (ROGERS *et al.*, 1982;

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BAK, 1983; FONG and LIRMAN, 1994), and the ability of broken branches to cement to the substratum (TUNNICLIFFE, 1983), are all characteristics that enhance the probability of fragment survival following mechanical disturbances.

The recovery of mechanically damaged reefs is highly dependent on the continued growth of those colonies that remained upright after a disturbance, colonization by newly produced coral planulae, and the stabilization and growth of coral fragments (ENDEAN, 1976; PEARSON, 1981). Due to the low recruitment success of sexually produced planulae in this species (DUSTAN, 1977; RYLAARSDAM, 1983; ROSESMYTH, 1984), the survivorship of damaged adults and asexual recruitment by coral fragments may play significant roles in the recovery process. In this paper, we accomplish three objectives. First, we document spatial patterns of hurricane-generated damage to *A. palmata* by recording the distribution of damaged adult colonies and fragments. Second, we measure rates of early survivorship of new recruits derived from fragments. Third, several hypotheses about factors affecting survivorship of *Acropora palmata* fragments are tested, including the effect of distance from an existing *A. palmata* patch, initial size of each fragment, and substrate characteristics of the area where a fragment landed.

METHODS

Study Site

Elkhorn Reef (25°21.766′N, 80°0.9.961′W) is an isolated reef in the northern region of the Florida Reef Tract (Figure 1). It is approximately 4.5 hectares and surrounded by sand plains and seagrass beds. Although it is a mid-shelf formation located 2.5 km from the outer reef, it is afforded little protection from wave action because to the E and S-E, the direction of the prevailing wind, the fore-reef is discontinuous (SHINN *et al.*, 1989). The long axis of the reef is oriented N and S and there is no typical reef crest formation; rather there is a relatively wide and shallow reef flat. A Principal Component Analysis performed on the abundance of all coral species on Elkhorn Reef (LIRMAN and FONG, 1995) revealed that the coral community can be statistically divided into three major zones: rubble zone (mean depth = 1.7 m), reef-flat (1.2 m), and fore-reef (3.1 m).

Storm Description

Hurricane Andrew was a compact and quickly moving storm that crossed South Florida on August 24, 1992 (Figure 1). Maximum sustained winds of 225 km·hr^{-1} with gusts of up to 285 km·hr^{-1} were measured 15 km N of our study site (POWELL and HOUSTON, 1993; RAPPAPORT and SHEETS, 1993). This storm ranked as a Category 4 storm on the Saffir-Simpson hurricane damage-potential scale (AHRENS, 1993), making Hurricane Andrew the strongest storm to hit South Florida in at least 50 yr.

Field Methods

Visual surveys of the reef community on Elkhorn Reef were performed 3 wk after Hurricane Andrew. To quantify the relative damage to different coral species among reef zones, we

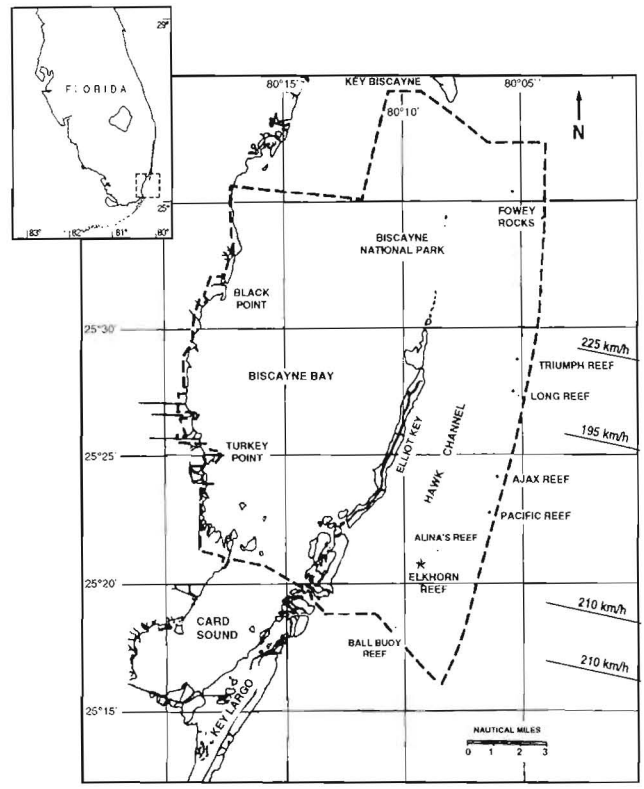

Figure 1. Map of South Florida including the path of Hurricane Andrew with demarcations indicating bands of approximate maximum sustained winds, the boundaries of Biscayne National Park, and several of the larger reefs of northern Florida Reef Tract. The star shows the location of the study site, Elkhorn Reef.

surveyed a belt transect that crossed all three reef zones. Planar percentages of cover by each species were estimated *in situ* with SCUBA in March 1993 by placing a 1 m^2 quadrat along a transect bisecting the reef from W to E. Along with cover, we estimated the percentage of colonies of each species that had sustained any physical damage during the hurricane. *Acropora palmata* was divided into standing colonies and live fragments that were broken from colonies and deposited on the benthos. We defined as standing *A. palmata* those colonies that remained upright and had a visible attachment to the bottom through the characteristic stalk (SCHUHMACHER and PLEWKA, 1981). We defined as fragments those broken branches of *A. palmata* covered by live tissue lying on the substratum and lacking an obvious stalk. Fragments become new asexual recruits when they attach to the bottom. It was not possible to estimate the damage that might have occurred to *Millepora* spp., because it was not always apparent when fine branches may have been removed. Although we found skeletal remains of fine branches in the rubble field, we saw few obvious scars where removal occurred. It is possible that these small wounds were already healed by our sampling time as *Millepora* spp. is often very fast-growing.

To determine the large-scale distribution patterns of both

standing colonies and fragments of *A. palmata,* we surveyed three line-intercept transects along the E–W axis of the reef in April and May 1993. These transects were 10 m apart, running parallel to each other. The cover of fragments and standing colonies was estimated at every meter-interval by calculating the fraction of the length of the line these intercepted (LOYA, 1978).

The distribution and abundance of fragments in relation to a patch of damaged *Acropora palmata* colonies that may have been the fragment source was measured. Five parallel belt transects 5 m apart were surveyed. These transects bisected the largest fragment field on the reef, starting at the edge of a large standing *A. palmata* patch. Along each transect, a 1 m^2 quadrat was flipped from E to W until no more live fragments were found. The number of quadrats along each transect ranged from 8 to 12. Within each quadrat, we counted the number of fragments, measured the size of each fragment as longest length and widest width, and noted whether the fragment was loose or cemented to the substrate. This survey was done in May 1993, 9 mo after the storm. Two hypotheses about the spatial patterns of fragment abundance were tested. The first hypothesis was that larger fragments traveled shorter distances. To test this, we compared average size of fragments in the closest (1–3 m) and furthest (10–12 m) quadrats from the edge of the *A. palmata* patch. The second hypothesis was that more unattached fragments were closer to the source patch. This was based on the assumption that proximity to an *A. palmata* patch reduced wave action and removal of fragments. To test this, we compared the mean distance from the center of a patch for cemented and uncemented fragments.

In March 1993 (7 mo post-storm), approximately 80 *Acropora palmata* fragments were marked in two different areas of the reef where fragments had accumulated after the hurricane. The substratum in one of these areas, located W of the largest patch of standing *A. palmata,* was covered by pieces of dead coral rubble. The second set of fragments was located E of the large *A. palmata* patch on a hard, consolidated substratum. Each fragment was individually labeled with a metal tag and photographed with a fixed framer quadropod in June 1993. The fragment fields were surveyed again in May 1994, and those fragments bearing tags were re-photographed using similar methods. The resulting photographs were digitized, and the area covered by live coral tissue was estimated for each fragment. The hypothesis that initial size of fragments affected the survivorship of coral fragments was tested with linear regression. The hypothesis that substrate type affected fragment removal, rates of partial mortality, and fragment stabilization (cementation to substrate) was tested with t-tests.

RESULTS

The percentage of the benthos of Elkhorn Reef covered by corals was very patchy, ranging from 0–100%. Mean coral cover for the whole reef was 42.3% (S.E. = 2.8). Cover was highest on the reef-flat, where approximately 90% of the *Acropora palmata* that remained standing after the storm was damaged to some extent (Table 1). Most colonies had many missing branches easily detected by the presence of a circular to oval area of exposed white skeleton. Standing *A. palmata* covered over 18% of the reef-flat, and an equal area was covered by *A. palmata* fragments. The other dominant species of coral in this zone, *Porites astreoides,* was almost undamaged, only a few colonies showing signs of surface scouring. None of the other species or species groups were damaged in this zone. Total cover of hard corals was low in the rubble zone, an area dominated by *Acropora palmata* forming discrete and densely aggregated clumps. Here, cover of standing *A. palmata* was lower than cover of fragments (Table 1). In this zone where massive corals are rare, a few small colonies (<30 cm in diameter) had been dislodged and overturned during the storm. No other types of coral were damaged in this zone. On the deeper fore-reef, an area dominated by the branching coral *Porites porites,* there was no apparent hurricane damage observed.

Table 1. *Percent coral cover (±S.E.) and percentage of coral colonies that was damaged within each major zone on Elkhorn Reef. Massive corals include species in the genera* Montastraea, Siderastrea, *and* Diploria. *nd = no data available. We were unable to quantify damage to colonies of* Millepora *spp. that may have had finely branching sections removed.*

	Fore-reef (n = 39)	Reef-flat (n = 29)	Rubble zone (n = 28)
Acropora palmata			
Standing colonies	0.0 (0.0	18.2 (4.0)	5.4 (1.7)
Percent damaged	—	>90	>90
Live fragments	0.0 (0.0)	17.9 (2.8)	11.1 (3.2)
Porites astreoides	4.8 (1.0)	11.3 (1.7)	2.6 (1.2)
Percent damaged	0	<5	0
Porites porites	20.5 (3.3)	2.1 (1.3)	0.3 (0.2)
Percent damaged	0	0	0
Millepora spp.	5.9 (1.3)	5.5 (2.2)	1.9 (0.7)
Percent damaged	nd	nd	nd
Agaricia spp.	0.1 (0.02)	0.05 (0.01)	0.1 (0.03)
Percent damaged	0	0	0
Massive corals	8.9 (1.5)	1.2 (0.5)	2.3 (0.9)
Percent damaged	0	0	<5

Although the distribution of standing colonies and fragments of *Acropora palmata* was patchy, there were three general patterns observed (Figure 2). First, there were fewer fragments and more standing colonies of *A. palmata* in the northern section of the reef than in the center or the S, suggesting that the force of the hurricane may have been diminished in the northern part of the reef. Second, patches of standing colonies seemed to fall into two categories. Either colonies within a patch were lightly damaged and surrounded by few fragments (as in interval 35–50 and 85–100 in Figure 2a and 32–50 in Figure 2c), or there were only a few standing colonies remaining and most were reduced to fragments (as in interval 15–40 and 85–100 in Figure 2b). Last, many of the *A. palmata* fragments that survived through the 7 mo after the hurricane were distributed within or adjacent to the remaining patches of standing colonies. There are several possible explanations for this distribution, including differential transport and deposition during the storm, differential removal after the storm, and differential survival after the storm.

To determine whether larger fragments were transported

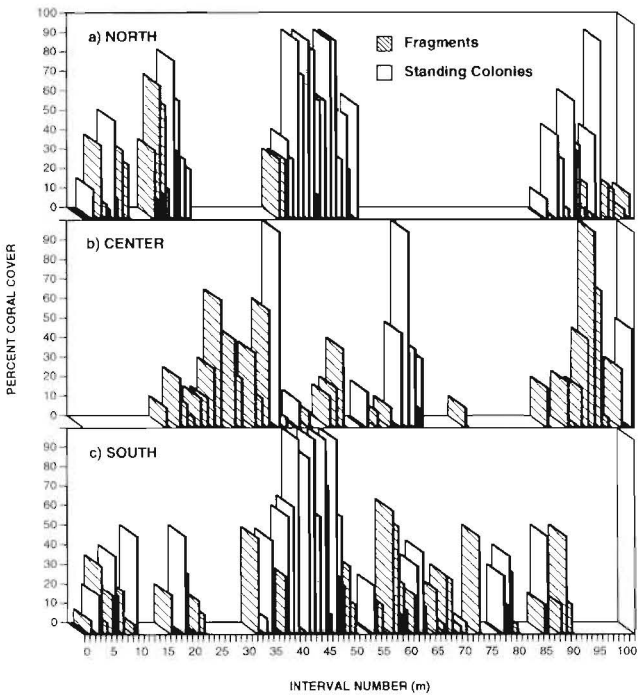

Figure 2. Distribution of standing *Acropora palmata* colonies and fragments along three parallel E-W transects bisecting Elkhorn Reef. Transects were surveyed with the line-intercept method, recording the length of each 1 m interval that was covered by either standing or fragmented *A. palmata*.

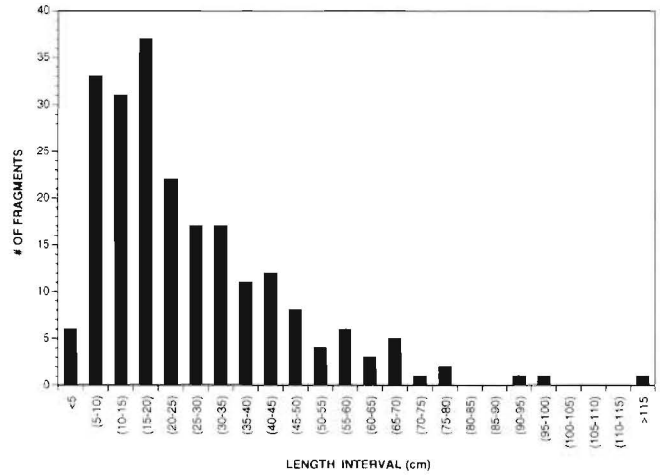

Figure 3. Size frequency distribution of fragments of *Acropora palmata* in the largest fragment field. Size of each fragment was measured as the longest length of living tissue.

shorter distances, we compared the average size of fragments close to and distant from the edge of a patch of standing colonies. There was no difference in mean size of fragments in the closest (1–3 m) and the farthest (10–12 m) intervals (t-test, $p > 0.05$). Thus, our data indicate that the distribution of fragments is not directly dependent on size. One possible explanation of this distribution is that fragmentation may have occurred in several stages, first from the hurricane and then through several winter storms. Alternatively, clusters of large fragments away from standing colonies may represent the shattered remnants of isolated colonies.

Proximity to a patch of *A. palmata* may limit removal of fragments by reducing wave and current action. If loose fragments are removed more rapidly away from a patch than next to it, then there should be fewer uncemented fragments close to a patch of standing colonies. To test whether there was differential removal after the storm, mean distance from the patch to uncemented and cemented fragments was compared. Mean distance to uncemented fragments was significantly less than for cemented fragments (t-test, $p < 0.05$), suggesting that standing colonies may protect uncemented fragments from removal from the reef.

In May 1993, 218 fragments in 48-1 m^2 quadrats within the hurricane generated field of fragments were measured (Figure 3), for a mean of 4.56 fragments·m^{-2} (S.E. = 0.54). There are two lines of evidence that suggest that survivorship of fragments may not have been dependent on initial fragment size. Although there were few fragments with a longest length less than 5 cm, a large proportion of fragments were within the next three smallest size classes (5–20 cm). This indicates that mortality may not be directly dependent on size above a 5 cm threshold. In addition, there was no significant relationship between initial fragment size and survivorship of the 80 marked fragments ($r^2 = 0.048$, $p > 0.05$).

Differences in substrate type affected removal, total mortality, and partial mortality rates of hurricane-generated fragments. In the rubble zone, only 34% of the fragments that were marked were removed from the reef during the 11 mo interval between sampling dates, while 57% of the fragments were removed from the hard-bottom area. Thus cementation, an important process in the transformation of a fragment to a recruit, may be slower or less efficient in the hard bottom area. Total mortality, or complete loss of live tissue was also higher in the hard bottom (50%) than the rubble (4%) substrate. In addition, many of the marked fragments (73%) lost tissue over the 11 mo of the study. Average partial mortality rates of surviving fragments was significantly higher for fragments in the hard bottom area (t-test, $p < 0.05$). Fragments in the hard bottom area lost 61% of their live tissue area (S.E. = 15.5, n = 23), whereas fragments in the rubble areas lost 31% of their live tissue area (S.E. = 6.9, n = 10).

Only a few fragments increased the area covered by tissue (6 in the rubble zone and only 2 in the hard bottom area) over the 11 mo of the study; for these fragments mean increase in tissue area was 15.5% (S.E. = 2.2). During the summer of 1993, the marked fragments started developing vertical growth features on their upper surfaces. The rapid upward growth of these features (3.65 ± 0.04 cm/yr, FONG and LIRMAN, *unpublished data*) sharply contrasts with the planar tissue loss shown by the fragments. This seems to indicate that after the fragments have re-cemented to the substratum, most of the energy allocated for growth is dedicated to the upward extension of these vertical growth features.

DISCUSSION

Hurricane damage to Elkhorn Reef was extremely patchy. However, there were three general patterns observed. First, almost all the coral damage that occurred was to colonies of *Acropora palmata*. Damage to this species was extensive; we found very few undamaged colonies of *A. palmata* in all of our surveys. Destruction of *A. palmata* colonies is commonly reported after hurricanes (WOODLEY *et al.*, 1981; and many others), and may be attributed to colony shape (GRAUS *et al.*, 1977) and the location of most colonies in high energy reef zones (GOREAU, 1959; GEISTER, 1977; ROBERTS *et al.*, 1977). Second, damage was variable among patches of *A. palmata*. We attribute this difference to a downcurrent "domino effect", where if one colony is shattered, its fragments can cause a cascade of damage to nearby colonies before coming to rest on the benthos. Thus, the probability of sustaining damage increases with the amount of damage to neighbours. Third, many surviving fragments were retained within or adjacent to standing *A. palmata* colonies. Fragment retention within patches was also observed after Hurricane Gerta in Belize (HIGHSMITH *et al.*, 1980). One explanation may be that contact with standing colonies of the same species enhances the re-cementation process and therefore decreases the probability of a fragment being removed from the reef by subsequent wave action. BAK and CRIENS (1981) found that *A. palmata* fragments fuse to other elkhorn fragments faster than to any other type of substrate. Additionally, proximity to standing *A. palmata* colonies may produce a baffling effect on waves and currents that prevents or delays the removal of uncemented fragments from the reef.

The most important factor affecting the ability of fragments to become new recruits was the substrate type where the fragment landed after the storm. To become a recruit, a fragment must preserve live tissue area (survive), stabilize itself on the reef by cementation, and begin to grow upward so that it can compete for light. Fragments on rubble substrate suffered less partial or total mortality, and more fragments cemented to the bottom than those on hard, consolidated substrate. It will be important to determine if these differences are complemented by differences in rates of upward growth through time. The first signs of upward growth on hurricane-generated fragments were observed in the summer of 1993.

Due to the lack of success of sexual recruitment in *Acropora palmata*, the recovery of *palmata*-dominated reefs after mechanical disturbances (*e.g.*, hurricanes, groundings) will be highly dependent on the survivorship and growth of asexual recruits. The effects of initial size on the survivorship of hurricane-generated *Acropora palmata* fragments has been studied previously with conflicting results. HIGHSMITH *et al.* (1980) found a significant positive correlation between fragment size and survivorship after Hurricane Gerta. In contrast, ROGERS *et al.* (1982) found that fragments that died were larger than fragments that survived after Hurricanes David and Frederic. In our study, we did not find a significant relationship between fragment size and survivorship. Nevertheless, we determined that the early survivorship of hurricane-generated fragments can be influenced by substrate type and distance from standing coral colonies.

CONCLUSIONS

Tropical storms are undoubtedly major shaping forces acting on coral community structure. The damage caused by Hurricane Andrew, although significant, was not as devastating as may have been predicted given the magnitude of the storm. The *Acropora palmata* population on Elkhorn Reef exhibited remarkable recovery capabilities even though most of the colonies experienced some degree of fragmentation due to waves and coral projectiles. This coral species, with limited sexual recruitment capabilities, was able to increase its distribution due to the asexual recruitment of hurricane-generated fragments. The survival of these fragments was shown to be size-independent, but affected by substrate type and distance from standing colonies. Only the continued study of the survivorship and growth of these recruits as well as the healing of standing colonies will enable us to fully evaluate the long-term effects of Hurricane Andrew on this coral community.

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LITERATURE CITED

AHRENS, C.D., 1993. *Essentials of Meterology*. Minneapolis: W. Publishing Co.

BAK, R.P.M., 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. *Netherlands Journal of Sea Research*, 10, 285–337.

BAK, R.P.M., 1983. Neoplasia, regeneration and growth in the reef-building coral *Acropora palmata*. *Marine Biology*, 77, 221–227.

BAK, R.P.M., 1987. Effects of chronic oil pollution on a Caribbean coral reef. *Marine Pollution Bulletin*, 18, 534–539.

BAK, R.P.M. and CRIENS, S.R., 1981. Survival after fragmentation of colonies of *Madracis mirabilis*, *Acropora palmata*, and *A. cervicornis* (Sclerectinia) and the subsequent impact of a coral disease. *Proceedings Fourth International Coral Reef Symposium*, 2, 221–228.

BAK, R.P.M. and ENGEL, M.S., 1979. Distribution, abundance and survival of juvenile hermatypic corals (Sclerectinia) and the importance of life history strategies in the parent coral community. *Marine Biology*, 54, 341–352.

BYTHELL, J.C.,; GLADFELTER E.H., and BYTHELL, M., 1993. Chronic and catastrophic natural mortality of three common Caribbean corals. *Coral Reefs*, 12, 143–152.

DALLMEYER, D.G.; PORTER, J.W., and SMITH, G.J., 1982. Effects of peat on the behavior and physiology of the Jamaican reef building coral *Montastrea annularis*. *Marine Biology*, 68, 229–233.

DUSTAN, P., 1977. Vitality of reef coral populations off Key Largo,

Florida: Recruitment and mortality. *Environmental Geology*, 2, 51–58.

DUSTAN, P., 1985. Community structure of reef-building corals in the Florida Keys: Carysfort Reef, Key Largo and Long Key Reef, Dry Tortugas. *Atoll Research Bulletin*, 288, 1–29.

EDMUNDS, P.J. and WITMAN, J.D., 1991. Effect of Hurricane Hugo on the primary framework of a reef along the S. shore of St. John, USVI. *Marine Ecology Progress Series*, 78, 201–204.

ENDEAN, R., 1976. Destruction and recovery of coral reef communities. *In:* JONES and ENDEAN (eds.), *Biology and Geology of Coral Reefs, Vol. III. Biology 2.* New York: Academic, pp. 215–254.

FONG, P. and LIRMAN, D., 1994. Damage and recovery on a coral reef following Hurricane Andrew. *National Geographic Research and Exploration*, 10, 116–131.

GEISTER, J., 1977. The influence of wave exposure on the ecological zonation of Caribbean coral reefs. *Proceedings Third International Coral Reef Symposium*, 1, 23–30.

GLADFELTER, E.H.; MONAHAN, R.K., and GLADFELTER, W.B., 1978. Growth rates of five reef-building corals in the northeastern Caribbean. *Bulletin of Marine Science*, 28, 728–734.

GLADFELTER, W.B., 1982. White-band disease in *Acropora palmata*: Implications for the structure and growth of shallow water reefs. *Bulletin of Marine Science*, 32, 639–643.

GLADFELTER, W.B., 1991. Population structure of *Acropora palmata* on the windward forereef, Buck Island National Monument: Seasonal and catastrophic changes 1988–1989. Chapter 5. *In: Ecological Studies of Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands.* U.S. Department of the Interior, National Park Service, U.S. Virgin Islands.

GLYNN, P.W.; ALMODOVAR, L.R., and GONZALEZ, J.G., 1964. Effects of hurricane Edith on marine life in La Parguera, Puerto Rico. *Caribbean Journal of Science*, 4, 335–345.

GOREAU, T.F., 1959. The ecology of Jamaican coral reefs. I. Species composition and zonation. *Ecology*, 40, 67–90.

GRAUS, R.R.; CHAMBERLAIN JR., J.A., and BOKER, A.M., 1977. Structural modification of corals in relation to waves and currents. *American Association of Petrology Geology, Studies in Geology*, 4, 135–153.

HIGHSMITH, R.C., 1982. Reproduction by fragmentation in corals. *Marine Ecology Progress Series*, 7, 207–226.

HIGHSMITH, R.C.; RIGGS, A.C., and D'ANTONIO, C.M., 1980. Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. *Oecologia*, 46, 322–329.

HUSTON, M.A., 1985. Patterns of species diversity on coral reefs. *Annual Review of Ecology and Systematics*, 16, 149–177.

JAAP, W.C., 1984. The ecology of the south Florida coral reefs: A community profile. *U.S. Fish. Wildlife Service FWS/OBS-82/08.* 138p.

JORDAN-DAHLGREN, E., 1992. Recolonization patterns of *Acropora palmata* in a marginal environment. *Bulletin of Marine Science*, 51, 104–117.

LIRMAN, D. and FONG, P., 1995. Hurricane Andrew causes zone-specific damage to a coral reef community. *Florida Scientist* (in press).

LOYA, Y., 1978. Plotles and transect methods. *In:* STODDART, D.R. and JOHANNESS, R.F. (eds.), *Coral Reefs: Research Methods.* Paris: UNESCO, pp. 197–217.

PEARSON, R.G., 1981. Recovery and recolonization of coral reefs. *Marine Ecology Progress Series*, 4, 105–122.

PORTER, J.W.; BATTEY, J., and SMITH, G.J., 1982. Perturbation and change in coral reef communities. *Proceedings of the National Academy of Science*, 79, 1678–1681.

POWELL, M.D. and HOUSTON, S.H., 1993. Surface wind field analyses in Hurricane Andrew. *Seventh U.S. Conference on Wind Engineering*, pp. 523–532.

RAPPAPORT, E.N. and SHEETS, R.C., 1993. A meteorological analysis of Hurricane Andrew. *15th Annual National Hurricane Conference*, pp. 1–18.

ROBERTS, H.H.; MURRAY, S.P., and SUHAYDA, J.N., 1977. Physical processes in a fore-reef shelf environment. *Proceedings Third International Coral Reef Symposium*, Miami, 1, 507–515.

ROGERS, C.S.; GILNACK, M., and FITZ, H.C., 1983. Monitoring of coral reefs with linear transects: A study of storm damage. *Journal of Experimental Marine Biology and Ecology*, 66, 285–300.

ROGERS, C.S.; SUCHANECK, T.H., and PECORA, F.A., 1982. Effects of hurricanes David and Frederic (1979) on shallow *Acropora palmata* reef communities: St. Croix, U.S. Virgin Islands. *Bulletin of Marine Science*, 32, 532–548.

ROSESMYTH, M.C., 1984. Growth and survival of sexually produced *Acropora* recruits: A post-hurricane study at Discovery Bay, Jamaica (extended abstract). *In: Advances in Reef Science*, University of Miami, Florida, pp. 105–106.

RYLAARSDAM, K.M., 1983. Life histories and abundance patterns of colonial corals on Jamaican reefs. *Marine Ecology Progress Series*, 13, 249–260.

SCHUHMACHER, H. and PLEWKA, M., 1981. The adaptive significance of mechanical properties versus morphological adjustments in skeletons of *Acropora palmata* and *Acropora cervicornis* (Cnidaria, Sclerectinia). *Proceedings Fourth International Coral Reef Symposium*, 2, 121–128.

SHINN, E.A.; LIDZ, B.H.; KINDINGER, J.L.; HUDSON, J.H., and HALLEY, R.B., 1989. *Reefs of Florida and the Dry Tortugas* (Field Trip Guidebook T176), American Geophysics Union, Washington, DC, 1989, 53p.

STODDART, D.R., 1985. Hurricane effects on coral reefs. *Proceedings Fifth International Coral Reef Congress*, 3, 349–351.

TUNNICLIFFE, V., 1983. Caribbean staghorn coral populations: Pre-hurricane Allen conditions in Discovery Bay, Jamaica. *Bulletin of Marine Science*, 33, 132–151.

WALLACE, C.C., 1985. Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. *Marine Biology*, 88, 217–233.

WOODLEY, J.D.; CHORNESKY, E.A.; CLIFFORD, P.A.; JACKSON, J.B.C.; KAUFMAN, L.S.; KNOWLTON, N.; LANG, J.C.; PEARSON, M.P.; PORTER, J.W.; ROONEY, M.C.; RYLAARSDAM, K.W.; TUNNICLIFFE, V.J.; WAHLE, C.M.; WULFF, J.L.; CURTIS, A.S.G.; DALLMEYER, M.D.; JUPP, B.D.; KOEHL, M.A.R.; NIEGEL, J., and SIDES, E.M., 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science*, 214, 749–755.