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


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 (Glenn et al., 1964), Greta (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 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 Chiens, 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 year–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 (Grahn 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,
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; RYLAARS DAM, 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 (SCHMIDT 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; RAPPA PORT 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 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 m² 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 inter­
cepted (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
m² quadrat was flipped from E to W until no more live frag­
ments were found. The number of quadrats along each tran­
sect 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 test­
ed. 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) quad­
rats from the edge of the A. palmata patch. The second hy­
thesis 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 unce­
mented fragments.

In March 1993 (7 mo post-storm), approximately 80 Acro­
pora palmata fragments were marked in two different areas
of the reef where fragments had accumulated after the hur­
rricane. The substratum in one of these areas, located W of
the largest patch of standing A. palmata, was covered by piec­
es of dead coral rubble. The second set of fragments was lo­
cated 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-photo­
graphed 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 Ac­
ropora palmata that remained standing after the storm was
damaged to some extent (Table 1). Most colonies had many

<table>
<thead>
<tr>
<th>Acropora palmata</th>
<th>Fore-reef (n = 39)</th>
<th>Reef-flat (n = 29)</th>
<th>Bubble zone (n = 29)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standing colonies</td>
<td>0.0 (0.0)</td>
<td>18.2 (4.0)</td>
<td>5.4 (1.7)</td>
</tr>
<tr>
<td>Live fragments</td>
<td>0.0 (0.0)</td>
<td>17.9 (2.8)</td>
<td>11.1 (3.2)</td>
</tr>
<tr>
<td>Porites asastroides</td>
<td>4.8 (1.0)</td>
<td>11.3 (1.7)</td>
<td>2.6 (1.2)</td>
</tr>
<tr>
<td>Percent damaged</td>
<td>&lt;90</td>
<td>&lt;90</td>
<td>&lt;90</td>
</tr>
<tr>
<td>Percent damaged</td>
<td>0</td>
<td>&lt;5</td>
<td>0</td>
</tr>
<tr>
<td>Porites porites</td>
<td>20.5 (3.3)</td>
<td>2.1 (1.3)</td>
<td>0.3 (0.2)</td>
</tr>
<tr>
<td>Percent damaged</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Millepora spp.</td>
<td>5.9 (1.3)</td>
<td>5.5 (2.2)</td>
<td>1.9 (0.7)</td>
</tr>
<tr>
<td>Percent damaged</td>
<td>nd</td>
<td>nd</td>
<td>nd</td>
</tr>
<tr>
<td>Agaricia spp.</td>
<td>0.1 (0.02)</td>
<td>0.05 (0.01)</td>
<td>0.11 (0.03)</td>
</tr>
<tr>
<td>Percent damaged</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Massive corals</td>
<td>8.9 (1.5)</td>
<td>1.2 (0.5)</td>
<td>2.3 (0.9)</td>
</tr>
<tr>
<td>Percent damaged</td>
<td>0</td>
<td>&lt;5</td>
<td>&lt;5</td>
</tr>
</tbody>
</table>

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 Montastrea, 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.

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 cov­
ered by A. palmata fragments. The other dominant species of
coral in this zone, Porites asastroides, 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. pal­
mata 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 dam­
age observed.

Although the distribution of standing colonies and frag­
ments of Acropora palmata was patchy, there were three gen­
eral 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, sug­
gest that the force of the hurricane may have been dimin­
ished 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 differen­
tial transport and deposition during the storm, differential
removal after the storm, and differential survival after the
storm.

To determine whether larger fragments were transported
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 *Acropora 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 uncremented fragments close to a patch of standing colonies. To test whether there was differential removal after the storm, mean distance from the patch to uncremented and cemented fragments was compared. Mean distance to uncremented fragments was significantly less than for cemented fragments (t-test, p < 0.05), suggesting that standing colonies may protect uncremented fragments from removal from the reef.

In May 1993, 218 fragments in 48-1 m² 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 (r² = 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.

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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.
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 Cribbs (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 un-cemented 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


