Fragmentation in the branching coral *Acropora palmata* (Lamarck): growth, survivorship, and reproduction of colonies and fragments

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**Abstract**

*Acropora palmata*, a branching coral abundant on shallow reef environments throughout the Caribbean, is susceptible to physical disturbance caused by storms. Accordingly, the survivorship and propagation of this species are tied to its capability to recover after fragmentation. Fragments of *A. palmata* comprised 40% of ramets within populations that had experienced recent storms. While the survivorship of *A. palmata* fragments was not directly related to the size of fragments, removal of fragments from areas where they settled was influenced by size. Survivorship of fragments was also affected by type of substratum; the greatest mortality (58% loss within the first month) was observed on sand, whereas fragments placed on top of live colonies of *A. palmata* fused to the underlying tissue and did not experience any losses. Fragments created by Hurricane Andrew on a Florida reef in August 1992 began developing new growth (proto-branches) 7 months after the storm. The number of proto-branches on fragments was dependent on size, but growth was not affected by the size of fragments. Growth-rates of proto-branches increased exponentially with time (1.7 cm year$^{-1}$ for 1993–1994, 2.7 cm year$^{-1}$ for 1994–1995, 4.2 cm year$^{-1}$ for 1995–1996, and 6.5 cm year$^{-1}$ for 1996–1997), taking over 4 years for proto-branches to achieve rates comparable to those of adult colonies on the same reef (6.9 cm year$^{-1}$). In addition to the initial mortality and reduced growth-rates, fragmentation resulted in a loss of reproductive potential. Neither colonies that experienced severe fragmentation nor fragments contained gametes until 4 years after the initial damage. Although *A. palmata* may survive periodic fragmentation, the long-term effects of this process will depend ultimately on the balance between the benefits and costs of this process.

**Keywords:** Asexual reproduction; Coral fragmentation; Fragment survivorship; Hurricanes

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1. Introduction

Coral colonies are made up of modules (ramets) capable of surviving alone or in small groups. The sum of all ramets derived from a single zygote constitutes the coral’s genet, and, unlike acausal organisms, a coral’s genotype can exist as independent units that may experience diverse environmental conditions (Coates and Jackson, 1985; Harper, 1985; Heyward and Collins, 1985). The population dynamics of several reef-building corals in the Caribbean are largely determined by the formation and death of ramets as the recruitment of new genets through the sexual recruitment of planula larvae is often limited. For example, sexual recruits of Acropora palmata and Montastraea spp. were absent, or present in very low numbers, in several settlement studies (e.g. Dustan, 1977; Bak and Engel, 1979; Hughes and Jackson, 1980, 1985; Rylaarsdam, 1983; Rosesmyth, 1984).

For Acropora palmata, a species with documented limited sexual recruitment, asexual reproduction by tissue fission or fragmentation can have a significant influence on its survivorship and propagation. The main goal of this study is to describe the incidence of fragmentation within populations of A. palmata, determine the survivorship and growth of fragments, and evaluate some of the costs and benefits of fragmentation for this reef-building species.

Several benefits of asexual reproduction have been described for clonal organisms. The organization of coral colonies into modules allows the biomass of a genotype to increase beyond the mechanical limits of individual colonies by the formation of fragments (Jackson, 1977; Hughes et al., 1992). Moreover, where growth-rates decline with increasing colony size (e.g. Maragos, 1974; Loya, 1976; Hughes and Jackson, 1985), fragmentation may help maintain high growth-rates. The larger size of fragments compared to planulae may result in higher survivorship after recruitment (Jackson, 1977) and the colonization of areas not suitable for larval development, such as soft-bottom habitats (Highsmith, 1982; Heyward and Collins, 1985). Also, unlike sexual reproduction, which is restricted seasonally for Acropora palmata (Szmant, 1986), fragmentation can take place year-round.

Despite these potential benefits of fragmentation, there are disadvantages associated with this process that have to be considered. The final outcome of fragmentation may be a total increase in biomass after a period of growth (Clark and Edwards, 1995), but tissue losses and the initial reduction in colony size can produce negative consequences as colony size in cnidarians has been directly associated with survivorship, growth, and reproduction (e.g. Connell, 1973; Loya, 1976; Highsmith, 1982; Jackson, 1985; Karlson, 1986, 1988; Hughes and Connell, 1987; Lasker, 1990; Babcock, 1991; Hughes et al., 1992).

Severe fragmentation, as commonly observed after storms, may limit future sexual reproduction by reducing the biomass of colonies and shifting the energy allocation of damaged colonies from reproduction to regeneration (Van Veghel and Bak, 1994; Van Veghel and Hoetjes, 1995; Hall and Hughes, 1996). Also, the size and weight of fragments may limit their dispersal range (Williams, 1975; Wulff, 1985; Jackson, 1986), slowing the recovery of damaged areas where the cover of adult colonies has been reduced significantly. In such cases, recovery will depend on the recruitment of sexual propagules produced in distant, undisturbed areas (Connell and Keough, 1985).
In this study, I examine fragmentation of the branching coral *Acropora palmata* to document some of the costs and benefits of this process. Specifically, I document: (1) abundance and percent cover of fragments within several *A. palmata* populations, (2) survivorship of fragments with respect to size and substrate type, and (3) effects of fragmentation on the growth and reproduction of colonies and fragments.

2. Methods

2.1. Study species

*Acropora palmata* forms tree-like colonies on shallow, high-energy reef environments throughout the Florida Reef Tract and Caribbean (e.g. Goreau, 1959; Geister, 1977; Gladfelter et al., 1978; Highsmith, 1982; Rogers et al., 1982; Wells, 1988). It is one of the most important reef-building corals in the region because of fast growth-rates (up to 10 cm year$^{-1}$, Gladfelter et al., 1978), high reef-accretion rates (7–15 kg CaCO$_3$ m$^{-2}$ year$^{-1}$, Gladfelter and Gladfelter, 1979), and rapid C-fixation rates (gross C fixation = 84–109 mg C cm$^{-2}$ day$^{-1}$, Bythell, 1988). Populations of *A. palmata* have undergone a recent regional decline attributed to their susceptibility to diseases such as White Band Disease and physical disturbance (e.g. Bak et al., 1981; Davis, 1982; Gladfelter, 1982; Bythell and Bythell, 1991; Tunnell, 1992; Bythell and Sheppard, 1993; Jaap and Sargent, 1993). Fragmentation and dislodgment of this species were reported after Hurricanes Hattie (Stoddart, 1963, 1965), 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), Gilbert (Kobluk and Lysenko, 1992; Jordan-Dahlgren and Rodriguez-Martinez, 1998), and Andrew (Lirman and Fong, 1996, 1997a), as well as after Tropical Storms Bret (Van Vechel and Hoetjes, 1995) and Gordon (Lirman and Fong, 1995, 1997a,b).

2.2. Study sites

Two reefs with dense populations of *A. palmata* were studied within Biscayne National Park in the northern Florida Reef Tract, Elkhorn Reef (25° 21.766′ N, 80° 09.961′ W, depth of *A. palmata* population = 1–3 m) and Ball Buoy Reef (25° 18.524′ N, 80° 11.996′ W, 2–5 m, Fig. 1). These reefs were damaged by two storms: Hurricane Andrew (24 August 1992, maximum sustained winds = 225 kph, Powell and Houston, 1993; Rappaport and Sheets, 1993) and Tropical Storm Gordon (14–17 November 1994, maximum sustained winds = 84 kph; NOAA, 1994; Rappaport and Avila, 1995; Lirman and Fong, 1997a).

Additional populations of *A. palmata* were surveyed along the Florida Reef Tract at Key Largo Dry Rocks (2–4 m), Little Grecian Reef (2–5 m), French Reef (2–7 m), Pickles Reef (2–5 m), and Dry Tortugas (2–4 m), and in the US Virgin Islands at Saba Island, St. Thomas (1–3 m), Hawksnest Bay, St. John (0.5–3 m), and Buck Island, St. Croix (2–8 m) (Fig. 1).
2.3. Abundance and percent cover of fragments

Coral populations are commonly described in terms of coral abundance and percent cover. Given the numerous reports of storm damage to *A. palmata*, it was hypothesized that populations that experienced recent storm damage may be dominated in both abundance and percent cover by fragments as opposed to standing colonies. The percentage of ramets within populations that was comprised of fragments was determined with belt transects (25 × 1 m) on ten reefs with abundant *A. palmata*.
populations (seven in the Florida Keys and three in the USVI). On each reef, the location of A. palmata was established and a meter tape was positioned bisecting the population. The position of the belt transects \((n = 4\) per reef), which were run perpendicular to the main line, was determined from a set of random numbers previously drawn. All colonies and fragments within these transects were counted. Standing A. palmata were defined as those colonies that remained upright and had a single attachment to the bottom through the characteristic stalk. Fragments were defined as broken branches of A. palmata covered by live tissue lying on the substratum and lacking an obvious stalk.

Also, to determine the percent cover of colonies and fragments after storms, three 100-m long line-intercept transects (LITs, Loya, 1972, 1978) were surveyed on two reefs of the northern Florida Reef Tract. The LITs, placed parallel to each other on an E-W direction (the general direction of the storm paths), were separated by a distance of 15 m. Elkhorn Reef was surveyed in March, 1993, 7 months after Hurricane Andrew, and Ball Buoy Reef was surveyed before (August, 1994) and after (January, 1995) Tropical Storm Gordon (November, 1994). The cover of fragments and standing colonies was estimated at 1-m intervals by calculating the fraction of the length of the line these intercepted.

2.4. Survivorship of fragments and colonies

In a previous study, the survivorship of A. palmata fragments was monitored starting 7 months after Hurricane Andrew (Lirman and Fong, 1997b). Because these fragments were not marked until 7 months after fragmentation, no information was obtained on early survivorship (0–6 months). In the present study, the hypothesis that early survivorship will be affected by the size of fragments and type of substratum was evaluated using a transplant experiment.

Fifty fragments of A. palmata created by a ship grounding on Elkhorn Reef were collected within 24 h of fragmentation and assigned haphazardly to one of the following four types of substratum \((n = 12–13\) fragments per group): (1) hard-bottom (consolidated carbonate framework), (2) rubble (loose, dead pieces of A. palmata and A. cervicornis), (3) sand, and (4) live coral. All transplant sites were located in the back-reef area of Elkhorn Reef at a depth of 2 m. Maximum distance between transplant sites was 50 m. Each fragment was labeled with a metal tag, photographed with a fixed-distance framer and transported to the transplant sites where they were placed individually on the bottom separated from each other by at least 50 cm. Fragments transplanted onto live coral were placed on top of A. palmata colonies. Photographs of each fragment were taken at monthly intervals starting in June, 1994; size was determined by digitizing the developed prints using NIH Image Analysis Software.

Mean percent tissue mortality for fragments was estimated as:

\[
\frac{1}{n} \sum_{i=1}^{n} \left( \frac{IA - FA}{IA} \right) \times 100
\]
where \( IA \) = initial live tissue area (cm\(^2\)), \( FA \) = final live tissue area (cm\(^2\)), \( n \) = number of fragments.

To test the hypothesis that fragmentation will affect the survivorship of fragmented colonies, fragmented and unfragmented colonies were surveyed on Elkhorn and Ball Buoy Reefs between 1993 and 1997 (\( n = 25 \) fragmented and 25 unfragmented colonies per reef). Fragmented colonies had one to three branches recently removed as evidenced by the presence of skeletal lesions (Fong and Lirman, 1995).

2.5. Growth of fragments and colonies

Starting on May 1993, many of the fragments of \( A. \) palmata generated by Hurricane Andrew on Elkhorn Reef began developing new vertical growth features (‘proto-branches’) on their upper surfaces. A previous study documented a direct relationship between the size of fragments (mean size = 4752 cm\(^2\)) and the number of proto-branches formed, but no significant relationship between size and mean height of proto-branches after 5 months (Fong and Lirman, 1995).

Here, the size-range of fragments surveyed was expanded to include smaller units (mean size = 651 cm\(^2\), \( n = 30 \) fragments), to re-test the hypothesis that size will determine the number of proto-branches growing on a fragment as well as their growth-rates. Also, the growth of proto-branches was followed over a longer period of 4 years (1993–1997) to document the development of the branching patterns leading to the tree-like morphology seen on adult colonies. All of the fragments studied were originated during Hurricane Andrew in August, 1992 and found in the back-reef area of Elkhorn Reef. Over 100 of these fragments were labelled with numbered metal tags after the hurricane and a subset of 30 was chosen at random for this study by their tag number. The growth of proto-branches was averaged within fragments.

The linear extension of branches on 30 colonies of \( A. \) palmata was measured over a 6-month period between May–November, 1996 at Elkhorn Reef. Three branches were marked per colony and an average extension-rate was obtained for each colony. Growth-rates of proto-branches were compared to the growth-rates of standing colonies.

2.6. Fragmentation and sexual reproduction

The reproductive state of colonies and fragments was determined 1 week prior to the predicted spawning dates in 1995–1997 to test the hypothesis that fragmentation will have negative effects on sexual reproduction as resources are directed away from this process and into repair and re-growth. Tissue samples were collected from: (1) small fragments (longest dimension = 20–50 cm), (2) medium fragments (51–80 cm), (3) large fragments (81–145 cm), (4) colonies damaged by storms (three or more branches missing), and (5) undamaged colonies (no signs of fragmentation). All of the samples were collected from units that had been identified after Hurricane Andrew on Elkhorn Reef and after Tropical Storm Gordon on Ball Buoy Reef, establishing their disturbance history. Tissue samples (10–15 cm\(^2\)) were fixed with Zenker’s solution within 30 min of collection, decalcified in 10% HCl within 24 h (Szmant, 1991), and inspected under a dissecting microscope for the presence or absence of gametes.
3. Results

3.1. Abundance and cover of fragments

Both the abundance and percent cover of fragments within *A. palmata* populations can be high, especially in reefs that experienced recent storms such as Elkhorn and Ball Buoy Reefs, where fragments comprised 40% of the total number of ramets (Fig. 2). Fragments occupied 14.8% (S.E. = 2.1, n = 3 transects) of the bottom on Elkhorn Reef after Hurricane Andrew, while standing colonies occupied 12.1% (±2.4). On Ball Buoy Reef, the cover of fragments increased from 2.3 (±0.8) to 10.0% (±2.6) after Tropical Storm Gordon.

Nevertheless, surveys at other reefs showed that fragmentation may be prevalent even in the absence of hurricane damage as evidenced by the large proportion of fragments within *A. palmata* populations on Little Grecian Reef (35%) and the Dry Tortugas (43%), two areas with no significant storm activity reported in the recent past.

3.2. Survivorship of fragments

No significant relationships were found between size and the survivorship of fragments (regression, *P* = 0.52). However, there was a significant difference between

![Graph showing relative abundance of colonies and fragments on different reefs](image-url)
the size of those fragments that remained within transplant sites and those that were carried away; fragments removed from the reef by waves and currents were significantly smaller (mean size = 77.6 (±13.4) cm², n = 10) than those fragments that remained (289.3 (±16.1) cm², n = 40, Mann–Whitney U-test, P < 0.05). Non-parametric tests were used to compare size of fragments in this case because even though variances were homogeneous (Bartlett’s test, P > 0.1), the size-distribution of those fragments that were removed from the reef was not normal (Shapiro–Wilk test, P < 0.05) and no data transformations were successful in achieving normality (Sokal and Rohlf, 1981).

Partial mortality on fragments was high initially as 35.5% (±6.5) of live tissue was lost within the first month. Although mortality continued, subsequent losses were not as high as those recorded during the first month (38.4 (±6.4), 45.7 (±6.9), and 47.1% (±3.4) after 2, 3, and 4 months, respectively). Fragments placed on sand were covered by sediments and showed signs of bleaching within a week. Fragments placed on live A. palmata colonies fused to the underlying tissue without any apparent tissue rejection within 3 weeks.

Survivorship of transplanted fragments was significantly affected by type of substratum (Fig. 3). Fragments transplanted to rubble (n = 12), hard (n = 13), or sandy bottoms (n = 12) experienced high mortality during the first month. In contrast, fragments placed on live adult A. palmata colonies (n = 13) did not experience any tissue losses. Mortality during the first month was significantly greater in the sandy bottom than on rubble or hard-bottom areas (ANOVA, P < 0.05, Tukey’s a posteriori comparisons).

![Fig. 3. Mean tissue mortality (±S.E.) of A. palmata fragments transplanted to different types of substratum on the back reef of Elkhorn Reef, Florida. n = 12 fragments for transplants onto rubble and sand, n = 13 for transplants onto live and hard substrata.](image-url)
Table 1
Height of proto-branches (PB) on fragments of *Acropora palmata* generated by Hurricane Andrew (24 August 1992) at Elkhorn Reef (*n* = 267 PB on 35 fragments; a mean PB height was obtained for each fragment)

<table>
<thead>
<tr>
<th></th>
<th>7/93</th>
<th>6/94</th>
<th>5/95</th>
<th>9/96</th>
<th>4/97</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean PB height (±1 S.E.) (cm)</td>
<td>2.6 (0.1)</td>
<td>4.5 (0.2)</td>
<td>7.64 (0.3)</td>
<td>14.1 (0.5)</td>
<td>16.9 (0.6)</td>
</tr>
<tr>
<td>Maximum PB height (cm)</td>
<td>9</td>
<td>13</td>
<td>18</td>
<td>30</td>
<td>38</td>
</tr>
<tr>
<td>Mean # PB/m² of live tissue (±1 S.E.)</td>
<td>11.1 (1.9)</td>
<td>11.8 (2.1)</td>
<td>10.2 (2.4)</td>
<td>9.1 (1.1)</td>
<td>6.4 (0.8)</td>
</tr>
</tbody>
</table>

3.3. Growth of fragments

Most proto-branches were formed on the upper surfaces of fragments within the first year after fragmentation, with only a few additional proto-branches formed subsequently. The number of proto-branches was directly related to the surface area of fragments (*r*² = 0.64, *P* < 0.05). Mean density of proto-branches on fragments decreased with time as some partial mortality occurred and some proto-branches fused to each other (Table 1).

Proto-branches reached a mean height of 2.6 (±0.1) cm within 1 year. After this initial growth, growth-rate of proto-branches increased exponentially with time (Fig. 4). Growth-rates calculated from regression were 1.7 cm year⁻¹ for 1993–1994, 2.7 cm year⁻¹ for 1994–1995, 4.2 cm year⁻¹ for 1995–1996, and 6.5 cm year⁻¹ for 1996–

![Fig. 4. Relationship between mean proto-branch height and time from fragment formation (24 August 1992). *n* = 267 proto-branches in 35 fragments.](image)
Fig. 5. Photographs of *A. palmata* proto-branches at different times of development on fragments created by Hurricane Andrew on Elkhorn Reef on August 1992. (a) December 1993, (b) July 1994, (c) July 1995, (d) August 1996. Depth = 1.5–2.0 m.
1997. A regression of size and mean proto-branch height showed no significant relationships in 1995, 1996, and 1997 ($r^2 = 0.07–0.48$, $P = 0.10–0.33$).

After formation, proto-branches grew upwards with a cylindrical shape until they reached a height of 4–5 cm (Fig. 5a), when a mushroom-type cap developed (Fig. 5b). The first branching pattern was observed as proto-branches reached 6–10 cm and began developing the typical tree-like morphology seen in adult colonies (Fig. 5c). Secondary branching patterns were observed in 1996 on the tallest proto-branches (Fig. 5d).

3.4. Survivorship and growth of colonies

Survivorship of adult colonies was high on both Elkhorn and Ball Buoy Reefs. Partial mortality attributed to competition with algae or feeding activities of corallivores was observed, but none of the adult colonies surveyed, fragmented or unfragmented, exhibited complete tissue mortality between 1992 and 1996 ($n = 100$). The linear growth-rate of $A. \text{palmata}$ colonies was 6.9 ($\pm 0.3$) cm year$^{-1}$ ($n = 30$).

3.5. Fragmentation and sexual reproduction

Production of gametes in $A. \text{palmata}$ was affected by size and previous disturbance history (Table 2). In August, 1995, 3 years after Hurricane Andrew, none of the $A.$

<table>
<thead>
<tr>
<th>Date</th>
<th>Type</th>
<th>Reef</th>
<th>Mean size (cm)</th>
<th>$n$</th>
<th>% With gametes</th>
</tr>
</thead>
<tbody>
<tr>
<td>8/95</td>
<td>Fragment/small</td>
<td>ER</td>
<td>28.8 (4.8)</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>8/95</td>
<td>Fragment/medium</td>
<td>ER</td>
<td>63.4 (2.5)</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>8/95</td>
<td>Fragment/large</td>
<td>ER</td>
<td>131.0 (12.1)</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>8/95</td>
<td>Colony/damaged</td>
<td>ER</td>
<td>193.0 (27.4)</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>8/95</td>
<td>Colony/undamaged</td>
<td>ER</td>
<td>161.0 (49.0)</td>
<td>5</td>
<td>80</td>
</tr>
<tr>
<td>8/95</td>
<td>Fragment</td>
<td>BBR</td>
<td>48.6 (9.9)</td>
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<td>0</td>
</tr>
<tr>
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<td>BBR</td>
<td>91.0 (23.8)</td>
<td>11</td>
<td>18</td>
</tr>
<tr>
<td>8/96</td>
<td>Fragment/small</td>
<td>ER</td>
<td>35.8 (7.2)</td>
<td>6</td>
<td>0</td>
</tr>
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<td>Fragment/medium</td>
<td>ER</td>
<td>62.4 (5.6)</td>
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</tr>
<tr>
<td>8/96</td>
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<td>140.7 (11.1)</td>
<td>6</td>
<td>33</td>
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<tr>
<td>8/96</td>
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<td>167.0 (18.9)</td>
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<td>50</td>
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<tr>
<td>8/96</td>
<td>Colony/undamaged</td>
<td>ER</td>
<td>185.0 (33.3)</td>
<td>6</td>
<td>67</td>
</tr>
<tr>
<td>8/96</td>
<td>Fragment</td>
<td>BBR</td>
<td>52.3 (12.6)</td>
<td>6</td>
<td>67</td>
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<tr>
<td>8/96</td>
<td>Colony/damaged</td>
<td>BBR</td>
<td>120.0 (13.5)</td>
<td>9</td>
<td>67</td>
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<tr>
<td>7/97</td>
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<td>27.3 (3.8)</td>
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<td>0</td>
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<tr>
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<td>55.8 (3.6)</td>
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<td>127.2 (10.2)</td>
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<td>72</td>
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<tr>
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<td>170.5 (16.5)</td>
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<td>78</td>
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<td>7/97</td>
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<td>ER</td>
<td>179.3 (22.5)</td>
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<td>78</td>
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<td>BBR</td>
<td>44.7 (6.9)</td>
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<tr>
<td>7/97</td>
<td>Colony/damaged</td>
<td>BBR</td>
<td>156.3 (32.1)</td>
<td>8</td>
<td>62</td>
</tr>
</tbody>
</table>

*Colonies on Elkhorn Reef (ER) were fragmented during Hurricane Andrew (August 1992). Colonies on Ball Buoy Reef (BBR) were fragmented during Tropical Storm Gordon (November 1994). Mean size ($\pm$1 S.E.) was estimated as longest length of live tissue on fragments and maximum canopy diameter on colonies.
palmata fragments sampled at Elkhorn Reef had gametes, irrespective of size. A lack of gametes also occurred in adult colonies that had been damaged by the hurricane. The only samples that contained gametes in 1995 were taken from undamaged colonies. In August, 1996, neither small nor medium fragments had any gametes, but two of six large fragments sampled were reproductive. Colonies, both damaged and undamaged, had gametes at this time. In July, 1997, a high proportion of both damaged and undamaged colonies had gametes (seven of nine colonies sampled from each group). Also, three of seven medium fragments and five of seven large fragments had gametes. In contrast, none of the small fragments surveyed had gametes in 1997.

At Ball Buoy Reef, fragments did not have any gametes in August, 1995, 8 months after Tropical Storm Gordon. However, two of eleven damaged colonies had gametes at this time. In August, 1996, four of six fragments and six of nine damaged colonies had gametes. Finally, four of six fragments and five of eight damaged colonies had gametes in July, 1997.

4. Discussion

Fragmentation is prevalent within populations of Acropora palmata. Surveys conducted at different locations revealed that, especially within populations that experienced recent storms, fragments can comprise a large percentage of ramets as well as cover a large percentage of the bottom (Lirman and Fong, 1997a). This is consistent with a previous study by Highsmith (1982) where an average of 69% of all A. palmata colonies were derived from fragments on several reefs in Panama.

The effects of storms on coral populations can extend beyond the direct physical disturbance that causes significant tissue mortality (reviewed by Harmelin-Vivien, 1994 and Connell, 1997). A secondary effect documented for A. palmata is the shift in biomass from ramets with low mortality probabilities (i.e. colonies) to units with higher mortality probabilities (i.e. fragments). This secondary effect highlights the importance of fragment survivorship and regrowth in the recovery and persistence of damaged A. palmata populations.

Survivorship of fragments of A. palmata can be influenced by the type of substratum where fragments land. Highest survivorship was observed for those fragments placed on top of live A. palmata colonies. These fragments fused to the underlying tissue and showed no signs of mortality. In contrast, fragments placed on sand lost 58% of their tissue within the first month and 71% after 4 months. Similar effects of substratum or location within reefs on fragment survivorship were documented for other coral species (e.g. Yap and Gomez, 1984, 1985; Heyward and Collins, 1985; Wallace, 1985; Bruno, 1998)

The relationship between the size of fragments and survivorship is not consistent. Although there is a general indication that survivorship increases with size (Loya, 1976; Highsmith et al., 1980; Heyward and Collins, 1985; Liddle and Kay, 1987; Lasker, 1990), several exceptions have been reported. Results from the transplant experiment support findings from previous studies where no relationship between the size of fragments and survivorship was found (Kobayashi, 1984; Lewis, 1991; Lirman and
Fong, 1997b; Bruno, 1998). However, even if survivorship was not directly related to size, size may still affect the long-term survivorship of fragments indirectly through its effect on rates of removal. Here, fragments that remained within transplant sites were larger than those removed by waves or currents. Thus, if smaller fragments are removed more easily from reefs, size may still influence their long-term survivorship.

The transport of fragments away from reefs can provide a mechanism for the creation of additional primary space and reef expansion as suggested by Highsmith (1982). Patch reefs on the Florida Reef Tract are commonly surrounded by sand and seagrass beds that are not optimal habitats for coral recruitment and survivorship (Jaap, 1984). Although mortality of transplanted fragments was high on sand, those fragments placed on rubble substrate showed high survivorship. Thus, even if fragments experience high mortality on sand, the rubble produced by these fragments can increase the survivorship of fragments created by subsequent storms, expanding the potential settlement area around a reef, and resulting ultimately in reef expansion.

Fragments of *A. palmata* showed rapid regrowth through the formation of proto-branches less than a year after fragmentation. The number of proto-branches was directly related to the size of fragments, as can be predicted based on limited resource availability (Fong and Lirman, 1995). The growth of proto-branches was slow initially, but increased with time, showing an exponential behavior. As proto-branches first develop, growth would be supported by the tissue on the upper surface of the fragments as the translocation of resources from the central portions of colonies often support the growth of the distal portions of branches (Pearse and Muscatine, 1971; Taylor, 1977; Gladfelter et al., 1989). This may limit initial growth-rates as several proto-branches can be found even in small fragments. As proto-branches grow in size and complexity, they would no longer rely on resources produced by the fragment, and their growth-rates would be expected to increase as a function of their own surface area. On average, it took more than 4 years for proto-branches to achieve linear growth-rates comparable to those measured for *A. palmata* colonies on the same reef. Slower growth-rates of fragments and coral transplants compared to undamaged colonies were also observed by Kobayashi (1984) and Cox (1992).

The success of asexual propagation in *A. palmata* contrasts with the limited sexual recruitment reported for this species (Dustan, 1977; Bak and Engel, 1979; Rylaarsdam, 1983; Rosesmyth, 1984). In this study, it was shown that fragmentation can have long-term effects on gamete production in *A. palmata*. Three years after Hurricane Andrew, gametes were present only in large *A. palmata* colonies that had not experienced direct fragmentation during the storm. Neither those colonies that were damaged by the hurricane nor any of the hurricane-generated fragments had produced gametes at this time. These results are in contrast to those reported by Ward (1995) who found that fragmented colonies of *Pocillopora damicornis* had a higher reproductive output than non-damaged colonies.

The cessation in gamete production in fragments and recently fragmented colonies suggests a differential allocation of energy towards stabilization, lesion repair, and growth. Reproduction may only resume after a certain size and/or level of repair or growth has been achieved. A similar trade-off between reproduction and regeneration was observed for the coral *Montastraea annularis* (Van Veghel and Bak, 1994), and
differential allocation of resources to repair and growth at small colony sizes has been noted for other hard corals (Kojis and Quinn, 1985; Szmant, 1986; Hughes et al., 1992) and zoanthids (Karson, 1988).

The combination of high frequency of fragmentation and the apparent lack of sexual reproductive success has been considered as evidence of the adaptive value of fragmentation for several coral species (Bak and Engel, 1979; Highsmith et al., 1980; Tunnilliffe, 1980, 1981; Bothwell, 1981; Highsmith, 1982). The emerging picture of fragmentation in *Acropora palmata* seems to fit well within the conceptual framework proposed in previous studies. *A. palmata* fragments often and, except in cases of widespread mortality (e.g. Woodley et al., 1981), populations can recover and propagate as fragments and damaged colonies regrow (Fong and Lirman, 1995). However, as remarked by Hughes et al. (1992), claims on the adaptive value of fragmentation should be made with caution since the potential costs of this process may be significant and have not been well-documented. Such indirect costs of fragmentation were observed in the present study, as both reduced growth and loss of reproductive potential were documented. This evidence suggests that the ultimate fate of coral populations damaged by storms can only be predicted after the potential indirect costs of fragmentation have been carefully considered.

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