

COSTS AND BENEFITS OF FRAGMENTATION IN THE BRANCHING CORAL
ACROPORA PALMATA

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MBF

Chapter 1. Draft

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ABSTRACT

Acropora palmata (elkhorn coral) is a branching coral that dominates shallow reef environments throughout Caribbean. Recently, elkhorn populations have undergone a region-wide decline attributed in part to its susceptibility to diseases and physical disturbance caused by storms. In this study, I examine fragmentation of elkhorn coral to determine the costs and benefits of this important process, and the role that asexual reproduction plays in the survivorship and propagation of this species.

Fragmentation is a common phenomenon for *A. palmata*, and elkhorn fragments can comprise up to 40% of all units within populations that experienced recent storms. The survivorship of elkhorn fragments can be affected by location within the reef, bottom type, and the presence of adults. Highest mortality was observed on sand, whereas those fragments that landed on top of live elkhorn colonies showed the highest survivorship. Fragment size does not have an effect on survivorship. The removal of fragments from settlement areas is affected by bottom type and fragment size.

Fragments created by Hurricane Andrew on August 1992 began developing new growth features (proto-branches) on their top surfaces seven months after the storm. The number of proto-branches on fragments was determined by fragment size, but growth of proto-branches was not affected by fragment size. The growth rate of proto-branches increased with time. Average growth rates were 1.4 cm.yr⁻¹ for 1992-1993, 2.2 cm.yr⁻¹ for 1993-1994, 3.4 cm.yr⁻¹ for 1994-1995, and 5.3 cm.yr⁻¹ for 1995-1996. It takes more than four years for proto-branches on fragments to achieve growth rates comparable to those of colonies on the same reef.

The benefits of fragmentation determined for *A. palmata* include: High propagation and colonization potential, high competitive advantage, increase in abundance and biomass, and year-round reproduction. However, significant costs can be associated with this process. These costs include: initial loss of tissue, decreased growth rates, increased susceptibility, and loss of sexual reproduction. Coral colonies that experienced severe fragmentation did not become sexually reproductive until four years after the initial damage.

Although elkhorn populations can clearly benefit from periodic fragmentation, the long-term effects of this process will depend on the balance between these benefits and associated costs. The decrease in growth rates and sexual reproduction potential caused by severe fragmentation can have significant consequences on the persistence of this important reef-building species.



Dear Committee Members:

I am enclosing for review the first two chapters of my dissertation. These chapters on coral lesions and coral fragmentation were reviewed already by Mark harwell and Peggy Fong.

After you've had time to review these manuscripts please let me know so I can set up a committee meeting to discuss my dissertation defense.

As it stands today, my dissertation will have a total of five chapters. The remaining chapters will be as follows:

Ch3) SUSCEPTIBILITY OF CORAL COMMUNITIES TO STORM INTENSITY, DURATION, AND FREQUENCY: THE ROLE OF DISTURBANCE HISTORY.

Ch4) RELATIONSHIP BETWEEN CORAL COVER, DIVERSITY AND TOPOGRAPHICAL RELIEF ON THE ABUNDANCE AND DIVERSITY OF ASSOCIATED MACROINVERTEBRATE- AND FISH POPULATIONS.

CH5) LOOKING FOR A DISTURBANCE SIGNAL: A SIMULATION MODEL OF POPULATION STRUCTURE OF THE BRANCHING CORAL *ACROPORA PALMATA*.

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INTRODUCTION

"The breaking of a branch is no serious injury to a zoophyte... The fragment broken off, dropping in a favorable place, would become the germ of another coral plant, its base cementing by means of new coral secretions to the rock on which it might rest; or, if still in contact with any part of the parent tree, it would be reunited and continue growth as before... The coral zoophyte may be leveled by transported masses swept over it by the waves; yet, like the trodden soil, it sprouts again, and continues to grow and flourish as before." Dana, 1872

Coral colonies are made up of modules (ramets) that can survive alone or in small groups. The sum of all ramets derived from the same zygote constitutes the coral's genet (Coates and Jackson, 1985; Heyward and Collins, 1985). Unlike aclonal organisms, a coral's genotype can exist as disjunct, independent units that may experience diverse environmental conditions and evolutionary pressures (Harper, 1985). The survivorship, growth, and propagation of these ramets will ultimately determine the persistence of the genet.

The population dynamics of many coral species are largely determined by the formation and death of ramets; the recruitment of new genets through the sexual recruitment of planula larvae is often limited. In the Caribbean, the success of sexual recruitment appears to be limited for most reef-building corals, with the notable exception of some agaricids. Sexual recruits of the two major reef-building corals in this region, *Acropora palmata* and *Montastraea* spp., were notably absent, or present in very low numbers, in several settlement experiments (Dustan, 1977; Bak and Engel, 1979; Hughes and Jackson, 1980; 1985; Rylaarsdam, 1983; Rosesmyth, 1984).

In such cases where sexual recruitment is limited, asexual reproduction will play a significant role in the survivorship and propagation of the species. Asexual recruitment (or the formation of new ramets) can take place through tissue fission or fragmentation. Colony fission can be caused by sedimentation, abrasion, diseases,

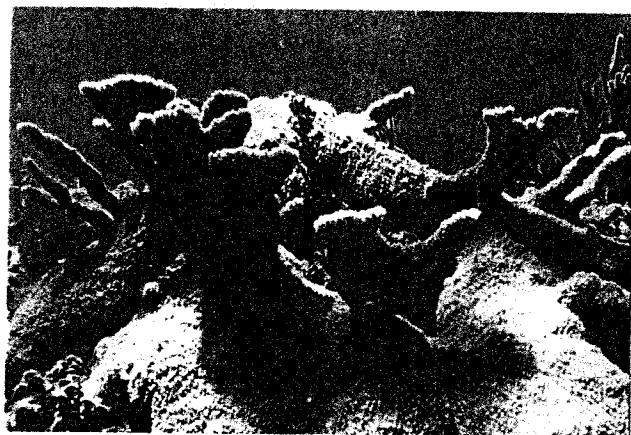
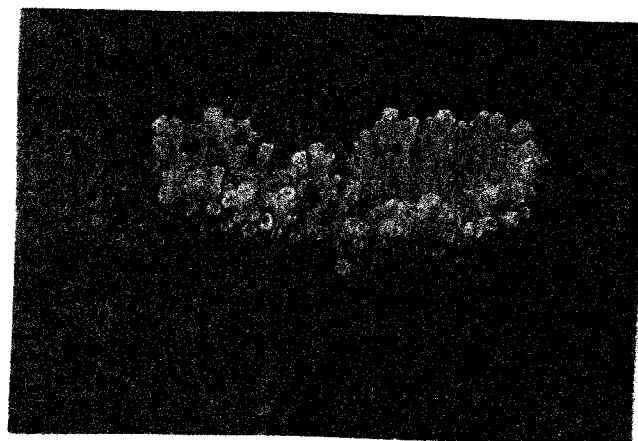
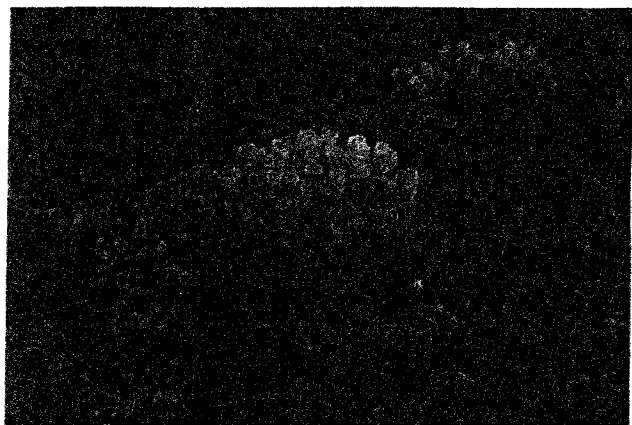


Figure 16. Photographs of *Acropora palmata* proto-branches at different times of development. All of these features were found on elkhorn fragments created by Hurricane Andrew on Elkhorn Reef on 24 August 1992. A) December 1993, B) July 1994, C) July 1995, D) August 1996.

predation, grazing activities, or algal overgrowth (Knowlton et al., 1981, 1988). Similarly, colony fragmentation can be a result of both physical (e.g., storms, ship groundings, anchor damage) and biological (e.g., bioerosion, predation, feeding activities of associated fauna) processes (Highsmith, 1982).

Many coral species have clearly incorporated fragmentation into their life-histories. By reviewing life-histories of fragmenting and non-fragmenting corals, Highsmith (1982) concluded that many of the characteristics exhibited by fragmenting corals appear to be in fact adaptive features selected by evolutionary forces. However, Hughes et al. (1992) cautioned against postulating such conclusions until the real costs and benefits of fragmentation have been assessed properly. In this study I conduct a comprehensive assessment of asexual recruitment in the branching coral *Acropora palmata* to determine the adaptive value of this process. Here I examine the costs and benefits of fragmentation, including the possible trade-offs between sexual and asexual reproduction.

Several advantages of asexual reproduction have been described for clonal organisms. In the absence of other limitations, the growth of coral colonies may be mechanically constrained, specially those of branching species such as *Acropora palmata* that achieve great colony height and complexity. The organization of coral colonies into different modules allows the biomass of a genotype to increase beyond mechanical limits by the constant formation of fragments (Jackson, 1977; 1979; Hughes et al., 1992). The periodic self-pruning of *A. palmata*, where large colonies lose their understory branches, may be an example of this (Porter and Meier, 1992). Moreover, in corals where growth rates decline with increasing colony size (Maragos, 1974; Loya, 1976; Hughes and Jackson, 1985), fragmentation may help maintain high growth rates. Clonality may also be a way of circumventing the genotype senescence usually observed in aclonal organisms (Jackson, 1985).

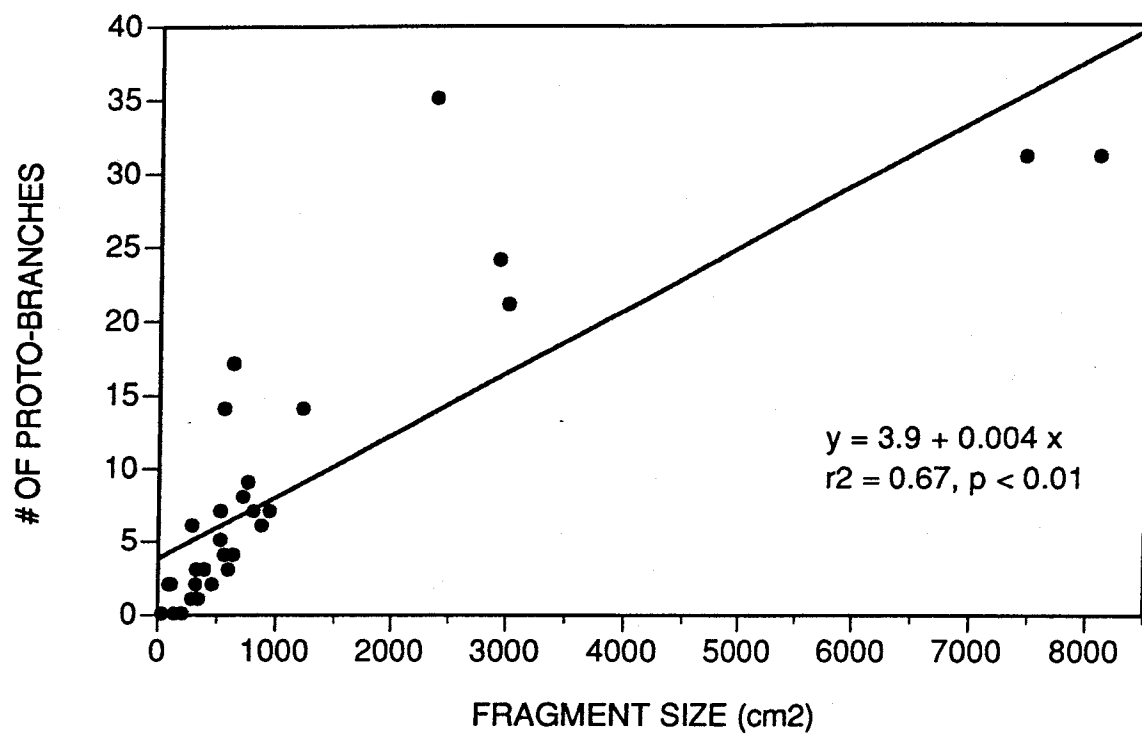


Figure 15. Relationship between number of proto-branches and fragment size in July 1993.

Asexually produced modules are usually larger than sexually produced planulae and may have higher survivorship after recruitment (Jackson, 1977). Larger size may enable fragments to colonize areas not suitable for larval development such as soft-bottom habitats (Highsmith, 1982; Heyward and Collins, 1985). Since mating is not required, a colonizing unit may continue propagation in isolation after a period of growth (Hughes and Cancino, 1985). Unlike sexual reproduction, which is often restricted seasonally (Wallace, 1985; Szmant, 1985), the production of asexual propagules can occur year-round. The constant production of propagules can take advantage of an unpredictable or episodic availability of suitable space, increasing local dispersal and enhancing genotype persistence.

The capacity of ramets to survive localized mortality through the functional independence among units can be enhanced by the spatial separation of units (Hughes and Cancino, 1985). Those fragments that encounter favorable conditions can survive and grow, whereas those that do not only suffer the consequences locally (Waller and Steingraeber, 1985). The spreading of fragments over a wide area may enhance genet survival even if a large portion of the habitat is destroyed. This way, the risk of genet mortality is spread among many daughter colonies and over a wide spatial scale, making the fitness of a genet less variable (Waller and Steingraeber, 1985; Hughes et al., 1992).

Although asexual reproduction by fission and/or fragmentation may be advantageous for corals allowing rapid genet multiplication, adaptation to local environments, space monopolization, and short-range dispersal and colonization, there are also disadvantages associated with these mechanisms that have to be considered.

Even though the final outcome of fission and fragmentation may be a total increase in biomass after a period of growth (Clark and Edwards, 1995), there may be initial tissue losses and a reduction in size that may produce negative consequences.

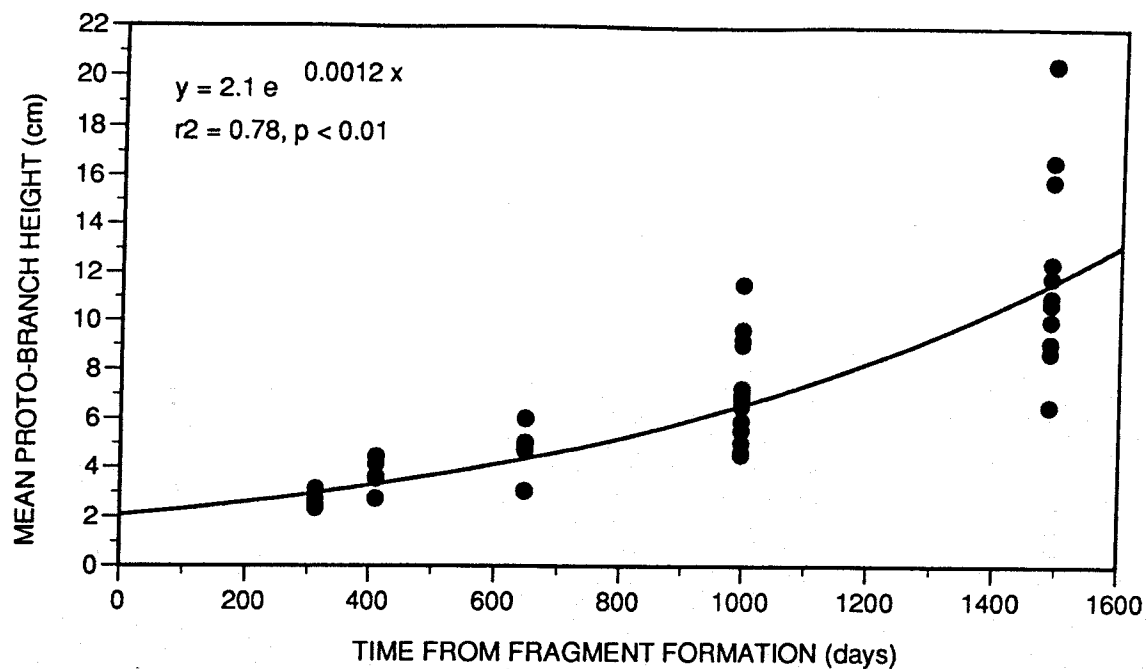


Figure 13. Relationship between mean proto-branch height and time from fragment formation (24 August 1992). Regression equations were calculated for the complete data set even though only mean proto-branch height for each fragment is plotted here.

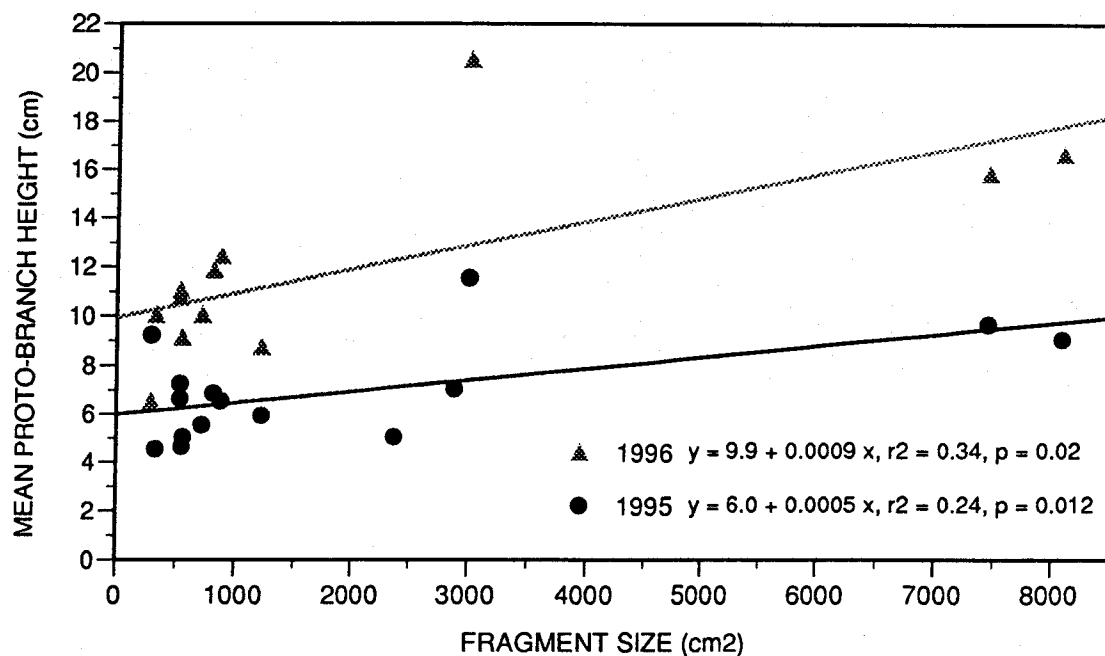


Figure 14. Relationship between mean proto-branch height and fragment size. Regression equations were calculated for the complete data set even though only mean proto-branch height for each fragment is plotted here.

Colony size in cnidarians is directly associated with growth, reproduction, and mortality (Connell, 1973; Loya, 1976; Highsmith, 1982; Jackson, 1985; Karlson, 1986; 1988; Hughes and Connell, 1987; Babcock, 1991; Hughes et al., 1992). In general, smaller colonies have a higher probability of experiencing complete mortality (Connell, 1973; Highsmith et al., 1980; Hughes and Jackson, 1980; 1985; Jackson, 1985; Babcock, 1991). After asexual division, daughter colonies may stop reproduction, resuming breeding only after corals have regenerated damaged tissues and regained a certain size (Szmant, 1985; Kojis and Quinn, 1985; Karlson, 1988; Hughes et al., 1992).

In plants, there can be a competition for resources between sexual and asexual reproduction (Williams, 1975; Cook, 1985). A similar competition seems to take place in corals that reproduce by both means (Highsmith, 1982). Severe fragmentation, as commonly observed after storms, may limit future sexual reproduction by reducing the biomass of colonies or by shifting the energy allocation of damaged colonies from reproduction to regeneration and regrowth (Van Veghel and Bak, 1994; Van Veghel and Hoetjes, 1995; Hall and Hughes, 1996). In addition, fragmentation may have negative effects on the growth rates of damaged colonies. Liddle and Kay (1987) showed that the growth rates of damaged branches on *Pocillopora damicornis* colonies were significantly lower than growth rates of branches within intact colonies.

Both fragmentation and fission result in the exposure of skeleton void of living tissue. Such areas are rapidly colonized by algae, boring organisms, and other coral competitors that may smother the remaining live tissue and weaken the structure of the colony, making it more susceptible to further damage (Hernandez-Ávila et al., 1977; Chamberlain, 1978; Tunnicliffe 1978; 1979; Rogers et al., 1982; Mitchell-Tapping, 1983).

Asexual propagation may be a superior mechanism for maintaining populations and colonizing nearby habitats (Highsmith, 1982; Jackson, 1985). Nevertheless, the

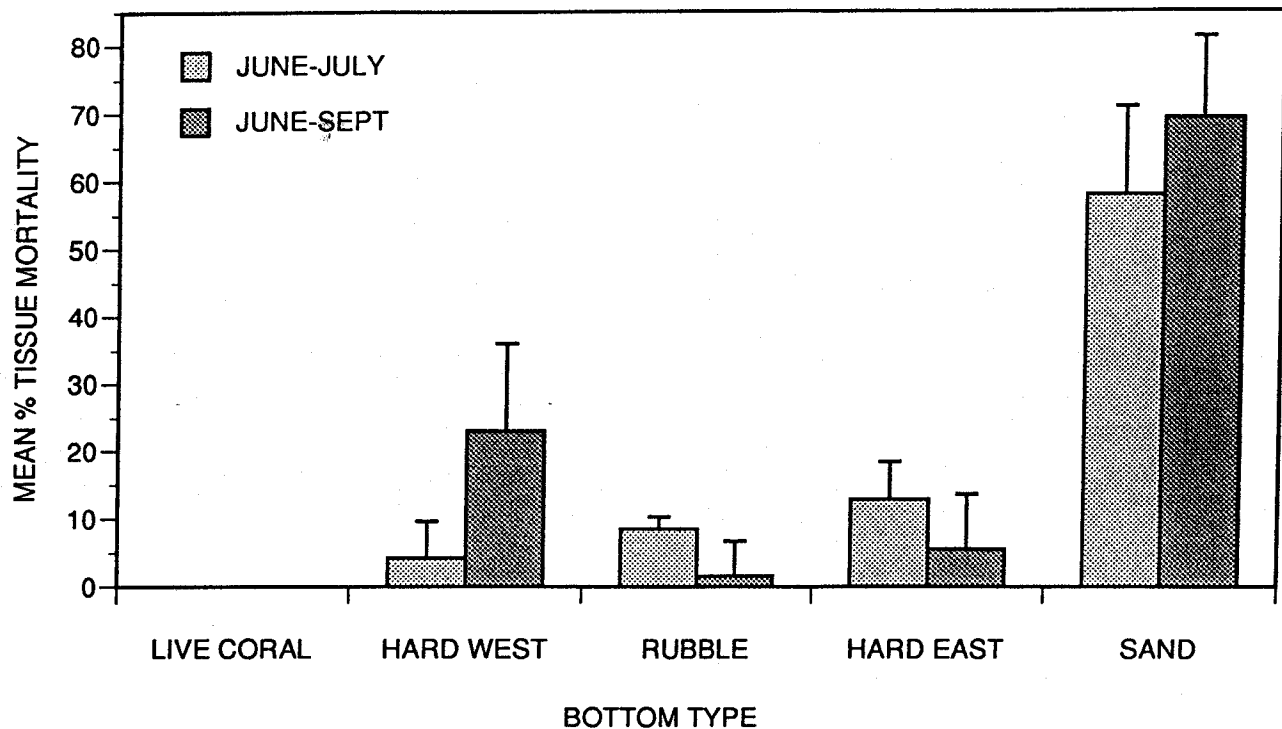


Figure 12. Mean partial tissue mortality of elkhorn fragments transplanted to different reef locations and bottom types. Light shaded bars represent tissue mortality during the first month of the study and dark shaded bars represent the total change in live tissue area over the duration of this study. Whereas further mortality was observed between July and September in the Hard West and Sand areas, fragments in the Rubble and Hard East areas grew during this same time period. Error bars are S.E.

larger size and weight of asexual propagules restrict and limit their long-range dispersal (Williams, 1975; Silander, 1985; Wulff, 1985; Jackson, 1986). This may delay or even prevent the recovery of severely 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).

Acropora palmata (elkhorn coral) forms tree-like colonies that dominate shallow, high-energy reef environments throughout the Florida Reef Tract and Caribbean (Goreau, 1959; Geister, 1977; Gladfelter et al., 1978; Highsmith, 1982; Rogers et al., 1982; Wells, 1988; and many others). It is one of the most important reef-building corals in the region because of fast upward growth rates (up to 10 cm yr^{-1} ; Gladfelter et al., 1978), high productivity, high reef accretion rates (7-15 kg $\text{CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$; Gladfelter and Gladfelter, 1979) and rapid C fixation rates (gross C fixation = 84-109 mgC $\text{cm}^{-2} \text{ day}^{-1}$; Bythell, 1988).

Elkhorn populations have undergone a recent decline throughout the Atlantic province (Bythell et al., 1991; Tunnell, 1992; Jaap, 1993; and many others). The two major sources of mortality of *Acropora palmata* are diseases and physical disturbance caused by storms. White Band Disease has resulted in the demise of several *A. palmata* populations throughout the Caribbean (Bak and Criens, 1981; Gladfelter, 1982; Jaap, 1984; Bythell and Sheppard, 1993). Significant fragmentation and dislodgment of this species were reported after Hurricanes Hattie (Stoddart 1963, 1965), Edith (Glynn et al., 1964), Gerta (Highsmith et al., 1981), Allen (Woodley et al., 1981), David and Frederic (Rogers et al., 1982), Hugo (Gladfelter, 1991), and Andrew (Lirman and Fong, 1996), as well as after Tropical Storms Bret (Van Veghel and Hoetjes, 1995) and Gordon (Lirman and Fong, 1996). In some cases, up to 95% of the existing *A. palmata* cover was lost (Stoddart 1963; Woodley et al., 1981; Gladfelter, 1991).

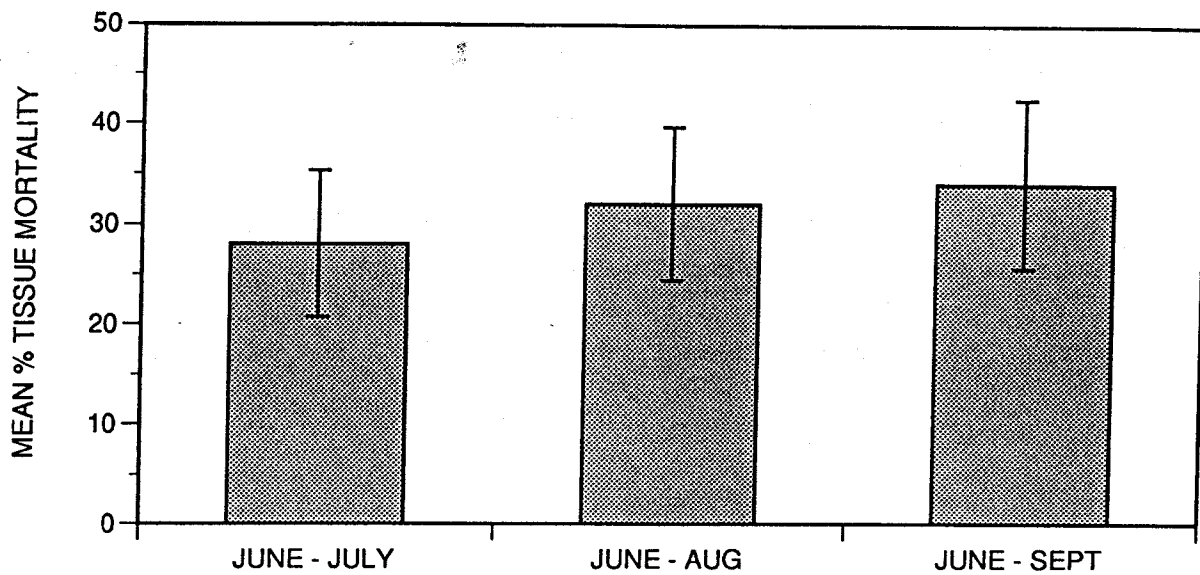


Figure 11. Mean partial tissue mortality of transplanted elkhorn fragments from time of transplantation. Data include all fragments in all transplant sites ($n = 50$). Error bars are S.E.

The high susceptibility of this species to fragmentation under extreme conditions can give a false impression of fragility that has been contradicted in several studies of morphological adaptations and structural strength of this species. *A. palmata* is known to combine several mechanisms to prevent fragmentation. Colonies in exposed environments undergo a general reduction in the number and/or size of lateral branches, branches become thicker, shorter, and more cylindrical, branches tend to point into the incoming current and waves, and colony shape in plan view becomes more eccentric (Graus et al., 1977; Vosburgh, 1982).

Elkhorn skeletons are less porous and stronger than those of more massive corals such as *Montastraea annularis* and *Siderastrea siderea* (Chamberlain, 1978). Within an elkhorn colony, porosity is lower towards the stalk, and higher at the branch tips (Schuhmacher and Plewka, 1981). Branches become thicker and rounder towards the stalk, and the stalks of elkhorn colonies are very resistant to breakage, and hurricane-force winds are required to fracture them (Mitchell-Tapping, 1978). The strength of elkhorn stalks was evidenced after Hurricane Andrew, when more than 80% of all *A. palmata* colonies on Elkhorn Reef had broken branches, but less than 10% of colonies were uprooted or overturned (Lirman and Fong, 1996).

The combination of skeletal strength, differential carbonate deposition, low porosity, and morphological plasticity present in *A. palmata* indicate that this species is well-adapted to survive in high-energy zones, and that considerable resources are spent to avoid fragmentation under the normal environmental conditions encountered in the *palmata* zone (Geister, 1977).

Adaptations are features of organisms that have come about by natural selection because they serve certain functions and thus increase the reproductive success of the carriers (Dobzhansky et al., 1977). The mere presence or success of a feature or behavior in an organism is not necessarily evidence that these features are adaptive (Lasker, 1984). The combination of the high frequency of fragmentation and the

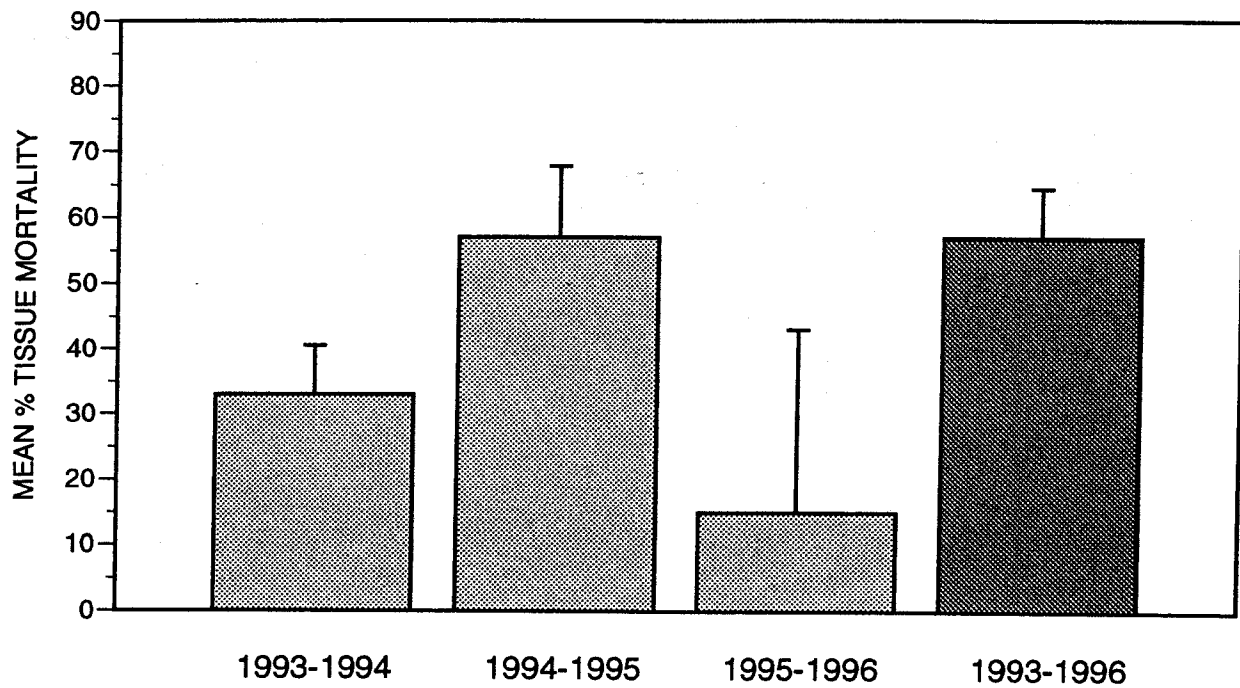


Figure 10. Average partial tissue mortality of marked fragments on Elkhorn Reef at different time intervals. Only fragments that remained in the settlement areas between surveys were considered here. $n = 9$ fragments in each area. Error bars are S.E.

apparent lack of sexual reproductive success have been considered as evidence of the adaptive value of fragmentation in corals (Bak and Engel, 1979; Highsmith et al., 1980; Tunnicliffe, 1980; 1981; Bothwell, 1981; Highsmith, 1982). However, extreme caution should be exercised when making such claims, as fragmentation can represent significant costs that have not been quantified in the past (Hughes et al., 1992). The answer to whether fragmentation may have been selected for as an adaptive trait that increases the reproductive contribution of fragmenting corals clearly lies on the balance between the costs and benefits of fragmentation for a coral species within a particular environment. Alternatively, fragmentation may just be a consequence of the interaction between coral morphology and the environment, and fragmenting corals may have developed survival mechanisms to make "the best of a bad situation".

In this study, I examine fragmentation of the branching coral *Acropora palmata* to determine the costs and benefits of this process in an important reef-building, Caribbean coral. Several of the benefits predicted by previous studies of asexual reproduction in clonal organisms that will be tested here include: increase in coral cover and biomass after fragmentation, increased growth, high survivorship of propagules, and high competitive advantage of fragments. The costs of asexual propagation that will be tested in this study include: loss of biomass, increased susceptibility, reduced growth, and loss of sexual reproduction.

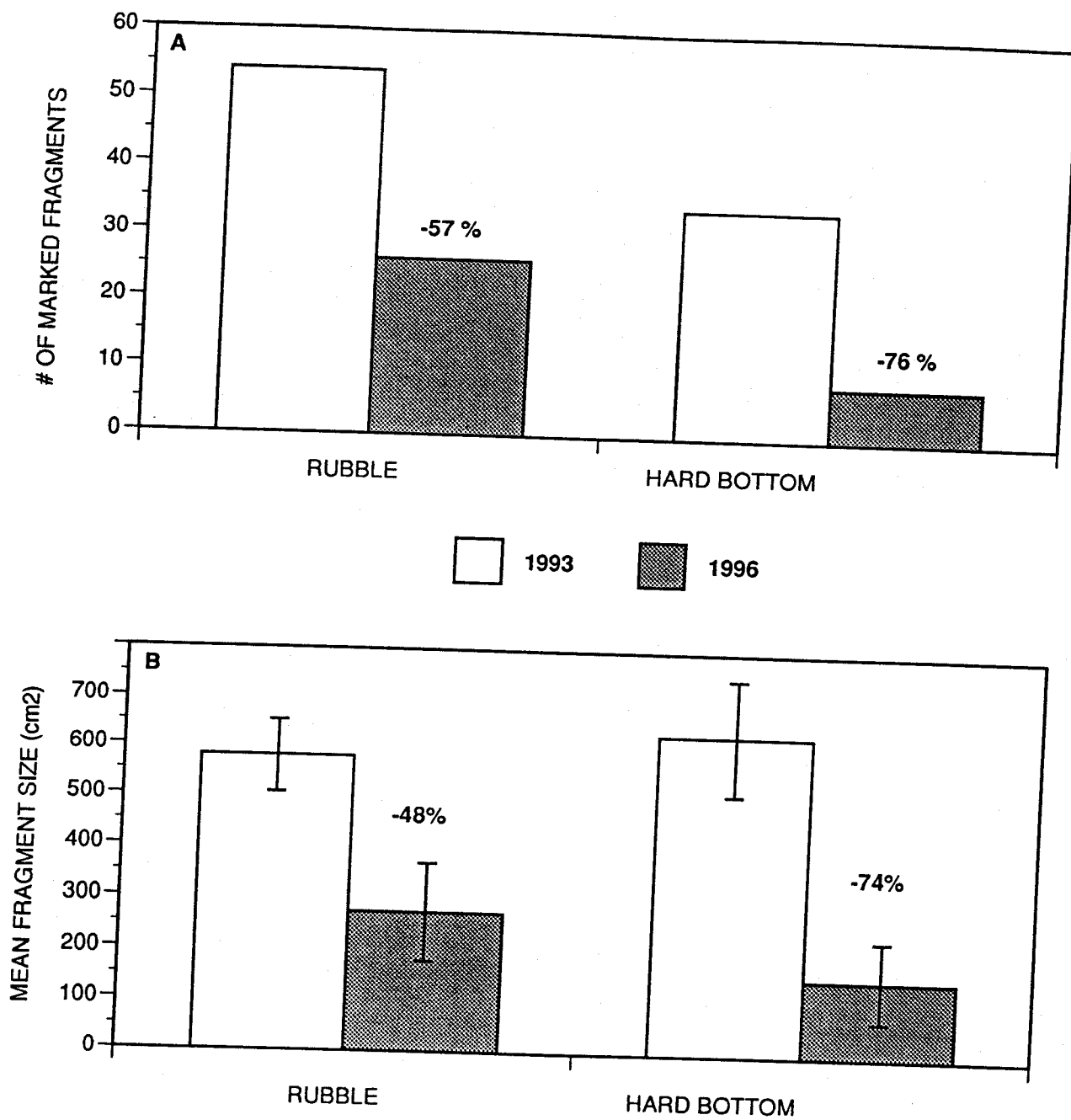


Figure 9. Changes in A) number of marked fragments and B) mean size of marked fragments on the rubble and hard-bottom areas of Elkhorn Reef between 1993 and 1996. Bold numbers represent percent change between samples. Error bars are S.E.

METHODS

Study Sites

The main site for this study, Elkhorn Reef (25° 21.766' N, 80° 09.961' W), is an isolated patch reef in the northern region of the Florida Reef Tract (Figure 1). Jaap (1984) characterized this reef as a transitional or embryonic bank reef that has not reached full development. It is approximately 4.5 ha and surrounded by sand plains and seagrass beds.

A Principal Component Analysis performed on the cover of all coral species on Elkhorn Reef revealed that the coral community can be divided into three major zones: back-reef (mean depth = 1.7 m), reef-flat (1.2 m), and fore-reef (3.1 m). The shallowest areas of this reef, the back-reef and reef-flat, are dominated by standing colonies and fragments of elkhorn coral (Lirman and Fong, 1996).

Elkhorn Reef is a mid-shelf formation located 2.5 km from the outer reef and it is afforded little protection from wave action because to the E and SE, the direction of the prevailing winds, the fore-reef is discontinuous (Shinn et al., 1989). Seas higher than 1.5 m result in waves breaking on the shallowest area of the reef, the reef-flat. Much of the wave energy is dissipated within this zone, and the back-reef area remains unaffected by waves, except during storms.

A second reef in the northern Florida Reef Tract was sampled. Ball Buoy Reef (25° 18.524' N, 80° 11.996' W) is a high-profile reef of approximately 7 ha, with a well-developed *Acropora palmata* population dominating shallow zones (2.5 m). Mean hard coral cover for this reef is 12.9% (Weil and Miller, unpublished results).

The reefs of this region were exposed to three severe storms in a period of 27 months: Hurricane Andrew (24 August 1992; maximum sustained winds = 225 kph; Powell and Houston, 1993; Rappaport and Sheets, 1993), the Storm of the Century (12-13 March 1993; maximum sustained winds = 75 kph; Storm Data, 1993), and

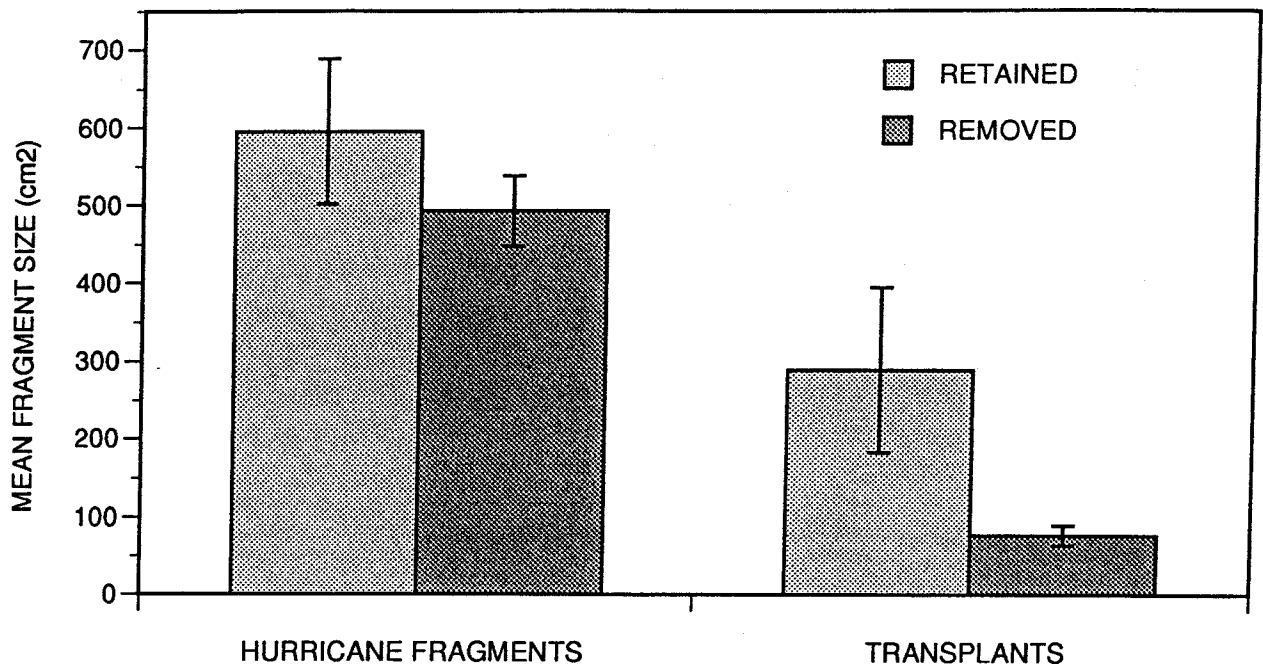


Figure 8. Comparison of mean size of *Acropora palmata* fragments retained and removed from settlement and transplant areas

Tropical Storm Gordon (14-17 November 1994; maximum sustained winds = 84 kph; Storm Data, 1994; Rappaport and Avila, 1995).

The relative abundance of standing colonies and fragments of *Acropora palmata* were also determined in the following reefs: Pickles Reef, (depth 2-5 m), French Reef (depth 2-7 m), and the Dry Tortugas (depth 2-4 m) in the Florida Keys, and Saba Island, St. Thomas (depth 1-3 m), Hawksnest Bay, St. John (depth 0.5-3 m), and Buck Island, St. Croix (depth 2-8 m) in the U.S. Virgin Islands.

Sampling methods

Spatial distribution and abundance of elkhorn colonies and fragments:

I performed counts of standing colonies and fragments on different reefs to document and compare the incidence of fragmentation in areas with different disturbance histories. At each site, 25m² transects were positioned at random over the elkhorn coral populations. A total of five to eight such transects were performed in each site, depending on the total area covered by *A. palmata*. All colonies and fragments were counted within these transects.

To determine the large-scale distribution patterns of both standing colonies and fragments of *A. palmata* after Hurricane Andrew on Elkhorn Reef, I surveyed three 100m-long line-intercept transects (LITs; Loya, 1972; 1978) along the E-W axis of the reef in April-May 1993 (Figure 2). These transects were parallel and 10 m apart. The cover of fragments and standing colonies was estimated at one meter intervals by calculating the fraction of the length of the line these intercepted. I defined as standing *A. palmata* those colonies that remained upright and had a visible attachment to the bottom through the characteristic stalk. I 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.

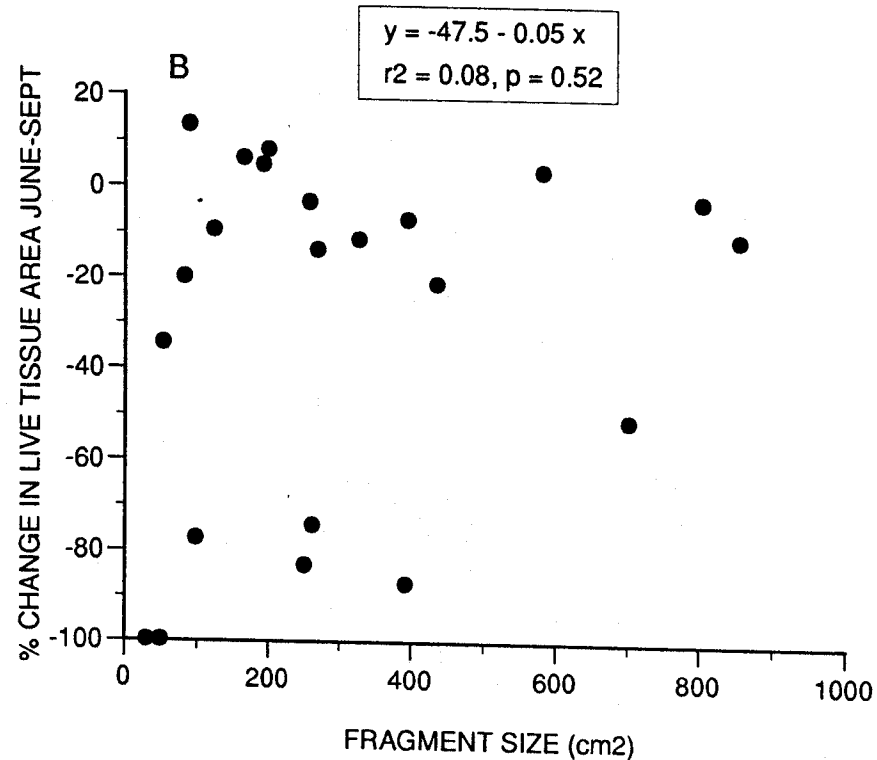
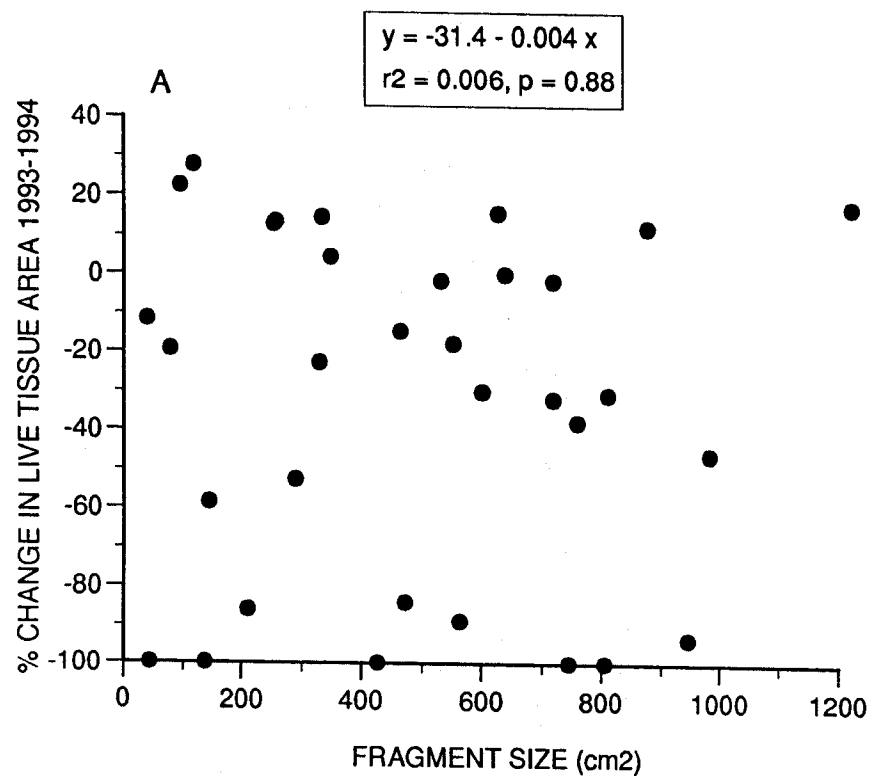


Figure 7. Relationship between mortality expressed as percent change in live tissue cover and fragment size for: A) hurricane-generated elkhorn fragments between 1993 and 1994, and B) transplanted elkhorn fragments between June and September.

In addition, three similar LITs 50m-long were performed on Ball Buoy Reef on January 1995, two months after Tropical Storm Gordon damaged the elkhorn population on this reef.

Fragment size distribution and cementation to the bottom:

In March 1993, I established five permanent belt transects to determine the size distribution of elkhorn fragments generated during Hurricane Andrew on Elkhorn Reef. The transects, which were placed 5 m apart, bisect a large fragment field created on the back-reef after the storm. Starting at the edge of a large *A. palmata* patch (the likely source of these fragments), a 1 m² quadrat was flipped from E to W until no more live fragments were found (Figure 2). The number of quadrats along each transect ranged from 8 to 12. Within each quadrat, I counted the number of fragments, measured the length of each fragment, and noted whether the fragment was loose or cemented to the substrate. These transects were resurveyed at yearly intervals from 1993-1996.

Using the data collected within these transects, I tested two hypotheses about the spatial distribution and stabilization of fragments. First, I tested whether fragment size affected the transport of fragments away from the reef during storms by comparing the 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 the presence of standing colonies may prevent the removal of fragments by modifying water flow. To test this I compared the proportion of uncemented fragments in relation to distance from the standing elkhorn patch, as well as the average distance from the origin of the transects for cemented and uncemented fragments.

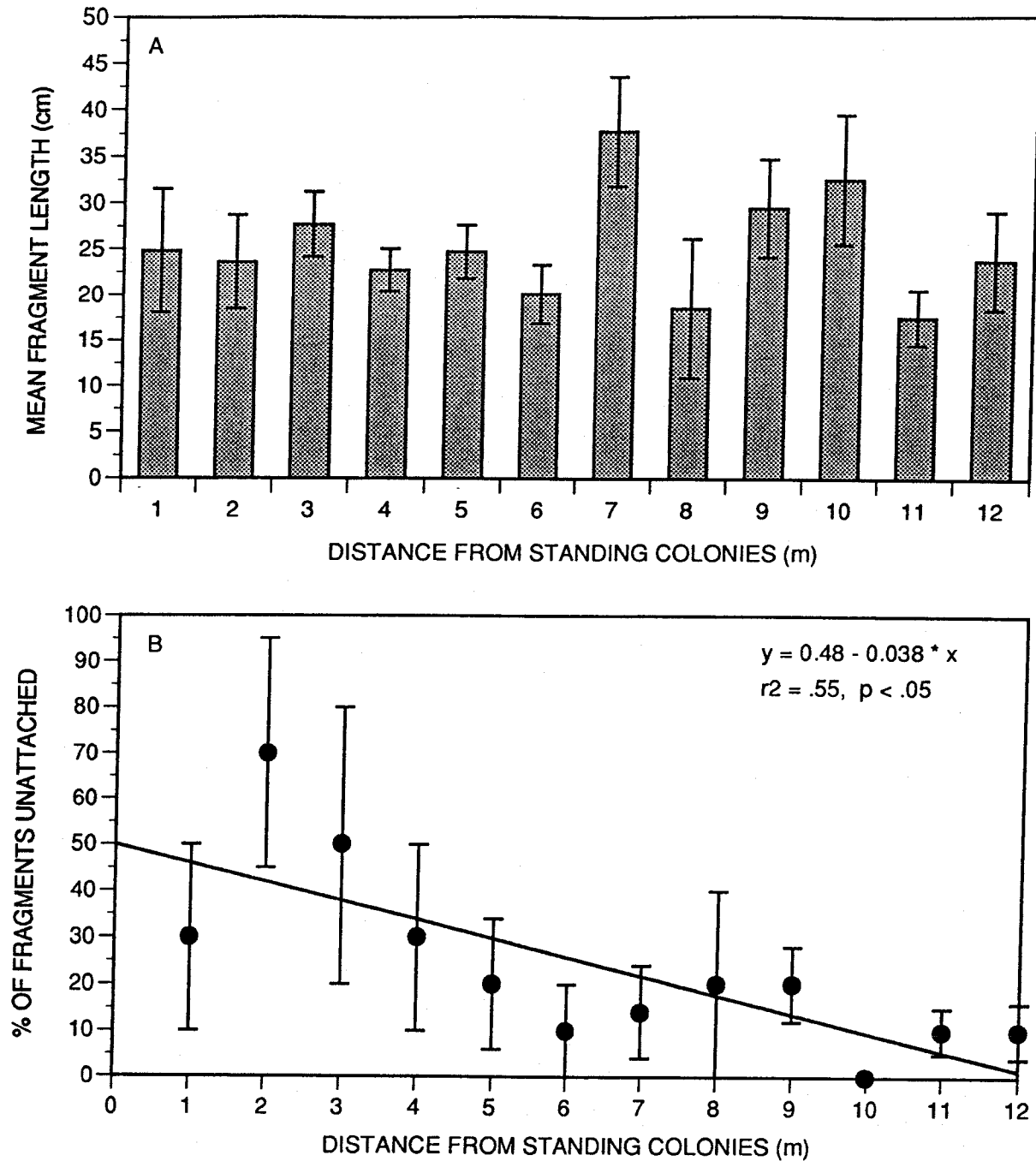


Figure 6. A) Mean length of *Acropora palmata* fragments in relationship to distance from a standing patch of colonies (the likely source of these fragments) on the back-reef of Elkhorn Reef. B) Relationship between percent of total number of fragments that were unattached to the bottom and distance from standing colonies. Although the regression analysis was performed on the complete data set, only the means for the five belt transects are plotted here for simplicity. Error bars are S.E.

Survivorship and permanence of fragments:

In March 1993, 7 months after Hurricane Andrew, I marked 80 *Acropora palmata* fragments in two different areas on Elkhorn Reef where fragments had accumulated after the storm (Figure 2). 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 group of fragments was located E of the large *A. palmata* patch on hard, consolidated substrate. Each fragment was labeled with a metal tag and photographed with a fixed-frame quadropod in June 1993. The fragment fields were surveyed at yearly intervals from 1993-1996, 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.

Since the elkhorn fragments produced by Hurricane Andrew were not labeled until March 1993, I was not able to quantify the early survivorship of newly formed fragments. To examine the survivorship of fragments during the first few months after fragmentation, and to determine the effects of bottom type and location within the reef on fragment survivorship, I performed a transplant experiment on Elkhorn Reef.

For this experiment I used elkhorn fragments created by a small ship grounding on Elkhorn Reef on June 1994. Fifty fragments were collected within 24 hours of fragmentation and assigned to one of six groups at random. Each fragment was labeled with a metal tag and photographed to determine initial size. The fragments were then transported underwater to the transplant sites and placed on the bottom without the aid of any attachment method (e.g., cement, line). Each fragment was

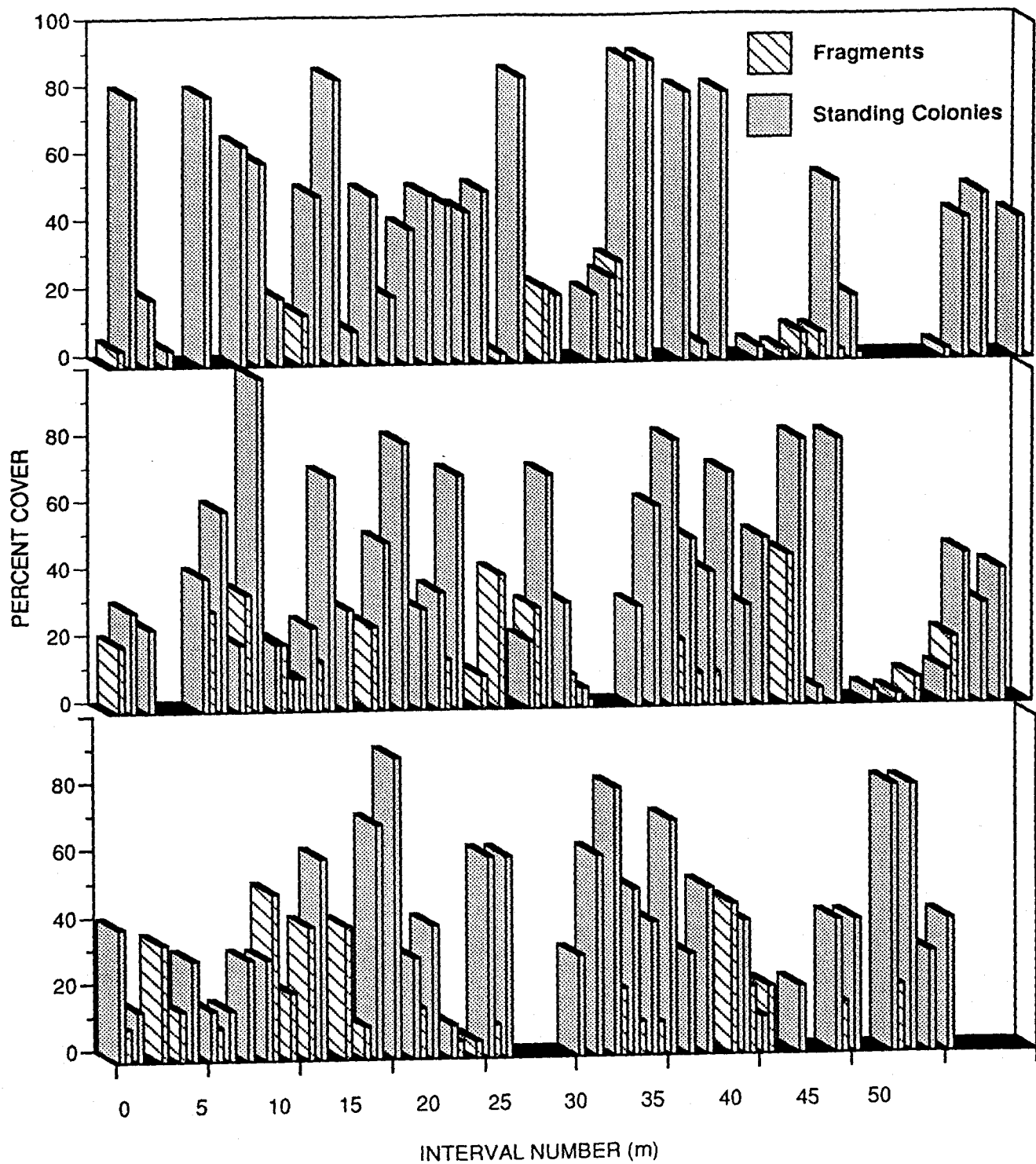


Figure 5. Percent cover of standing colonies and fragments of *Acropora palmata* along three line-intercept transects on Ball Buoy Reef after Tropical Storm Gordon.

photographed at monthly intervals starting in June 1994. Fragment size was determined by digitizing the developed prints.

Eight to nine fragments were assigned to one of the following bottom types and locations within the reef: 1) hard bottom/exposed area of the reef (E of the reef-flat); 2) hard bottom/protected area of the reef (back-reef); 3) rubble/exposed; 4) rubble/protected; 5) live coral(*Acropora palmata* colony)/exposed; and 6) live coral/protected (Figure 2). All the fragments from the two groups transplanted onto live *A. palmata* were placed on a single colony at each location.

Growth of fragments:

Starting on May 1993, many of the elkhorn fragments generated by Hurricane Andrew on Elkhorn Reef began developing new vertical growth features on their upper surfaces. I monitored the growth of these features that I named proto-branches on the fragments already marked for survivorship (mean fragment size = 642 cm²). For each fragment I noted the number of proto-branches and measured their height. Each proto-branch was assigned a number to be able to follow their individual development through time. Proto-branches on these fragments were surveyed at yearly intervals from 1993-1996.

In addition, I mapped the distribution of proto-branches on six large fragments (mean fragment size = 4762 cm²). Proto-branches were measured on May 1993 and October 1993 to determine their initial growth rates. These large fragments were subsequently surveyed at yearly intervals from 1994-1996.

By following the growth of individual proto-branches, I was able to determine the early branching patterns of these features as the recruits developed the typical, tree-like morphology seen on adult elkhorn colonies. I also tested the hypothesis that, based on the assumption of limited resources, both the number and growth rates of proto-branches would be affected by the size of fragments.

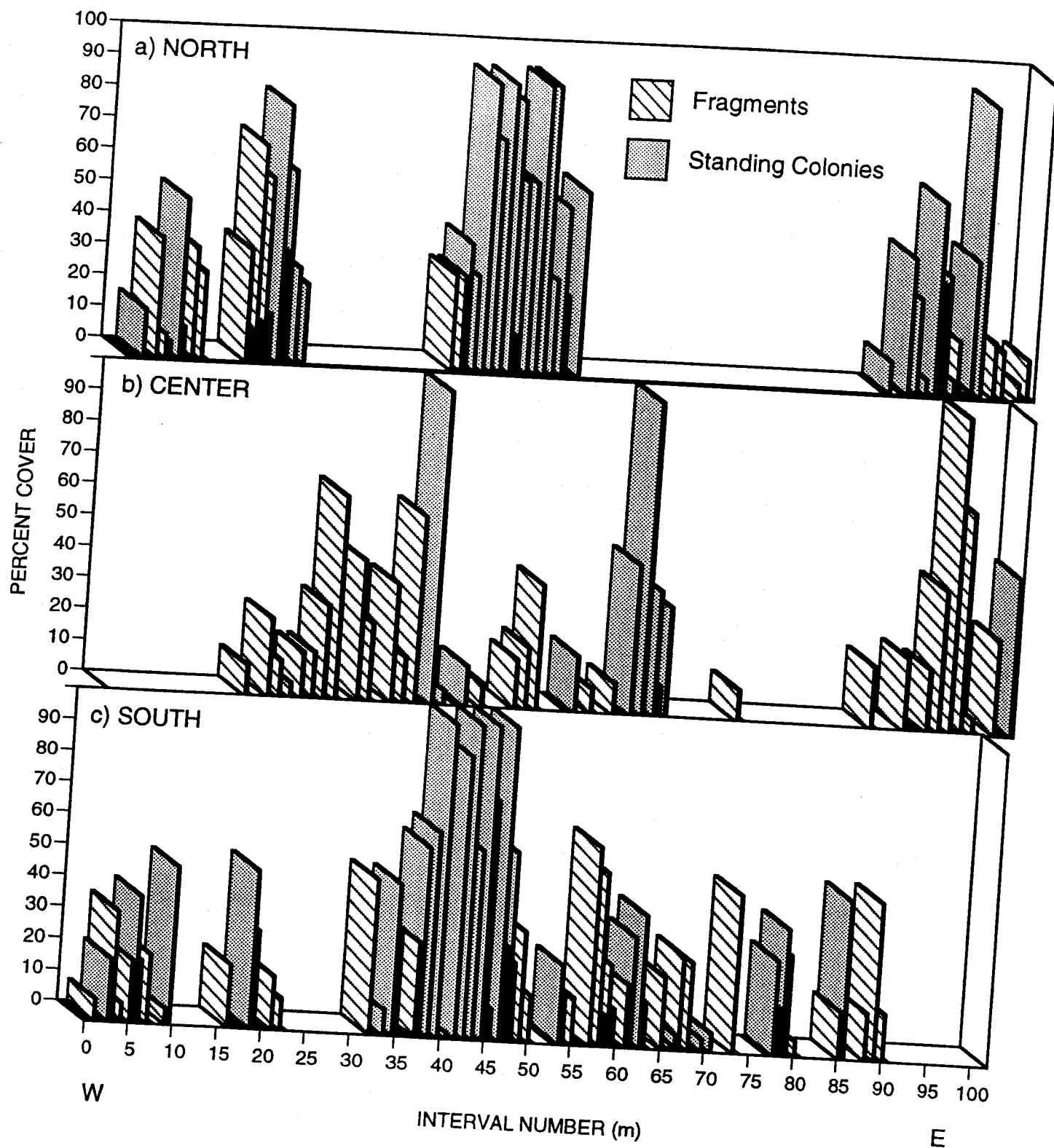


Figure 4. Percent cover of standing colonies and fragments of *Acropora palmata* along three line-intercept transects on Elkhorn Reef after Hurricane Andrew.

Survivorship and growth of adult colonies:

To determine the possible effects of fragmentation on the parent colonies, I surveyed more than 100 fragmented and unfragmented elkhorn colonies on Elkhorn and Ball Buoy Reefs between 1992 and 1996. In this case, only total mortality of colonies was considered; partial mortality and colony fission were noted but not quantified.

To quantify the linear extension rates of adult colonies, I marked 50 branches on 10 *Acropora palmata* colonies on Elkhorn Reef. To determine whether growth rates are correlated with colony size, I marked branches on five small (50-70 cm in canopy diameter) and five large (150-200 cm in canopy diameter) elkhorn colonies. Branches were marked with plastic ties at 5 cm from the branch tip. The linear extension of these branches was measured after 5 months.

Bioerosion and Fragmentation:

Several researchers have emphasized the role of bioerosion in fragmentation of coral colonies (Chamberlain, 1978; Tunnicliffe, 1981; Mitchell-Tapping, 1983). To determine if bioerosion played a significant role in the fragmentation of *Acropora palmata* colonies during storms, I surveyed 120 lesions on elkhorn colonies and fragments on Elkhorn and Ball Buoy Reefs after Hurricane Andrew and Tropical Storm Gordon for signs of bioerosion by organisms such as sponges and bivalves.

Reproduction:

To determine the possible effects of fragmentation on sexual reproduction of *Acropora palmata*, I collected tissue samples from individual colonies and fragments on Elkhorn and Ball Buoy Reef one week prior to the predicted spawning date in 1995 and 1996. Tissue samples 10-15 cm² were obtained with a hammer and chisel from

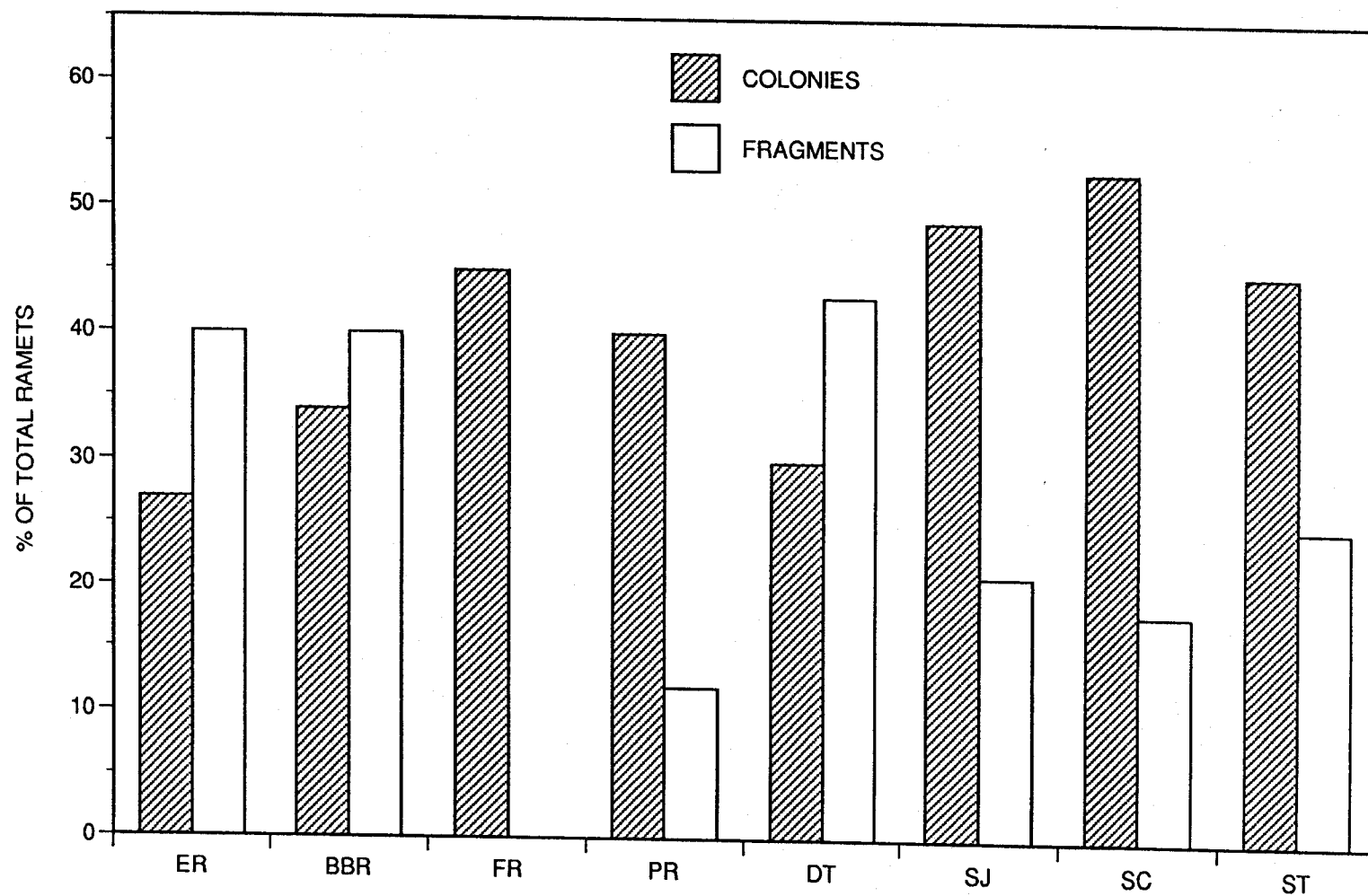


Figure 3. Relative abundance of *Acropora palmata* colonies and fragments on different reefs expressed as the percentage of total ramets (isolated units) in a population. A third category, crusts, is not represented here. Florida Reefs: ER = Elkhorn Reef (7/95), BBR = Ball Buoy Reef (6/95), FR = French Reef (8/96), PR = Pickles Reef (8/96), DT = Dry Tortugas (3/96). U.S. Virgin Islands: SJ = St. John (7/95), SC = St. Croix (7/95), ST = St. Thomas (7/95).

the center of colonies and fragments. Tissue samples were fixed with Zenker's solution within 30 minutes of collection. The samples were decalcified in 10% HCl within 24 hours, following the procedures outlined in Szmant (1991). Each tissue sample was inspected under a dissecting microscope and the presence or absence of gametes noted.

Samples were collected from five individuals of each of the following groups: 1) small fragments (20 - 50 cm), medium fragments (51 - 80 cm), large fragments (81 - 145 cm), colonies damaged by storms, and undamaged colonies.

Statistics

The data were examined for normality (Shapiro Wilk W test) and conformity to the assumptions of each statistical test prior to analysis. When assumptions were not met, non-parametric tests were used. Comparisons between means of two groups were made with t tests (or Mann Whitney U test), and for > 2 groups with ANOVA with a *posteriori* Tukey tests (or Kruskal Wallis test). Regression analysis was used to determine relationships between variables. Statistical analyses were performed on JMP and SYSTAT software packages.

Mean percent partial mortality of elkhorn fragments was estimated with the following formula:

$$\frac{\sum_{i=1}^n \left(\frac{IA - FA}{IA} \right)}{n} * 100,$$

where IA = Initial live tissue area (cm²), FA = Final live tissue area (cm²), and n = number of fragments.

Figure 2. Map of Elkhorn Reef showing the general location of belt transcets (BT), permanent fragment transects (FT), and fragment translocation sites. H/E = hard bottom/exposed area, H/P = hard bottom/protected, SB = sandy bottom, R/E = rubble bottom/exposed, R/P = rubble bottom/protected, L/P = live coral/protected, L/E = live coral/exposed. Not drawn to scale..

RESULTS AND DISCUSSION

My surveys of elkhorn populations on different reefs in the Caribbean show that fragmentation is a common phenomenon in this species (Figure 3). The number of fragments can be high, especially in reefs that experienced recent storms such as Elkhorn and Ball Buoy Reefs where fragments comprised up to 40% of the total number of ramets in the populations. Highsmith (1982) observed that an average of 69% of all elkhorn colonies were derived from fragments in several reefs in Panama.

Bioerosion and fragmentation. A survey of 120 skeletal lesions created by fragmentation of elkhorn colonies after Hurricane Andrew and Tropical Storm Gordon revealed that only 10% of these lesions showed signs of bioerosion by boring organisms on their surfaces. Thus, although bioerosion may facilitate breakage, it is not required for fragmentation to take place during severe storm events.

Recruitment of fragments. The percent bottom cover of hurricane-generated fragments was high in certain areas, reaching up to 60% on the back-reef of Elkhorn Reef. Piles of elkhorn fragments in this area smothered smaller colonies of other coral species such as *Porites astreoides* and *Siderastrea* spp. that had survived the impact of the storm. In March 1993, 218 fragments in 48-1 m² quadrats were measured on the back-reef, for a mean of 4.5 fragments m⁻² (S.E. = 0.54). Mean fragment length at this time was 25.7 cm (S.E. = 1.3).

The size frequency distribution of fragments showed a very low proportion of fragments < 5 cm (Table 1). This indicates that either small fragments were not generated during the storm, or that small fragments experienced very high mortality during the first few months after the storm. A survey of the coral rubble in the area also indicated that very few fragments < 5 cm were created by Hurricane Andrew.

Figure 1. Aerial view of coral zonation on Elkhorn Reef. Scale = 1:1800. FR = Fore-reef, RF = Reef-flat, RZ = Rubble-zone.

Spatial distribution of fragments. Although the distribution of *Acropora palmata* colonies and fragments on Elkhorn Reef after Hurricane Andrew was very patchy, several general patterns were detected (Figure 4). First, high variability in coral damage can be observed even at this small scale. Transects that were separated by only 10 m show significantly different damage patterns. The spatial distribution of fragments, especially within the center transect that lost many of its standing colonies, suggests a general shoreward transport in the forward direction of the hurricane. Last, many of the *A. palmata* fragments that survived through the seven months after the hurricane were retained within or landed adjacent to the remaining patches of standing colonies. The retention of elkhorn fragments within standing patches of elkhorn colonies was also evident on Ball Buoy Reef two months after Tropical Storm Gordon (Figure 5). There are several possible explanations for this distribution, including differential transport and deposition during the storm, differential removal after the storm, and differential survival of fragments.

To test the effects of fragment size on transport, I compared the average size of fragments at different distances from the shoreward edge of the 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, these data indicate that the distribution of elkhorn fragments is not directly dependent on size, and that storms of Hurricane Andrew's intensity can easily transport large fragments long distances (Figure 6a). One possible explanation for this distribution is that fragmentation may have occurred in several stages, first from the hurricane and then through subsequent 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 and increase survivorship of fragments by reducing wave and current action. Fragments that are able to cement to

Table 5. Costs and benefits of fragmentation in *Acropora palmata* as determined in this study

COSTS	BENEFITS
• TISSUE LOSS/BIOMASS REDUCTION	• PROPAGATION/COLONIZATION
• DECREASED GROWTH RATES	• INCREASE IN ABUNDANCE
• LESIONS	• INCREASE IN BIOMASS
• LOSS OF SEXUAL REPRODUCTION	• COMPETITIVE ADVANTAGE
• INCREASED SUSCEPTIBILITY	• YEAR-ROUND REPRODUCTION

the bottom rapidly will be less likely to be carried away from the reef by subsequent storms. If the presence of standing elkhorn colonies delays or prevents the removal of uncemented fragments, there should be a higher proportion of uncemented fragments closer to standing colonies than further away from the reef (Figure 6b). This was true for fragments surveyed within five permanent transects on the back-reef of Elkhorn Reef. The proportion of unattached fragments was highest within the first three meters of these transects and diminished with distance from the reef. Also, mean distance from the origin of the transects to uncemented fragments was significantly less than for cemented fragments (t-test, $p < 0.05$), suggesting that standing colonies may indeed protect uncemented fragments from removal from the reef.

Fragment survivorship. Stabilization. The stabilization of elkhorn fragments by cementation to the bottom was very rapid. Within 7 months after Hurricane Andrew, 72% of the fragments surveyed had cemented to the rubble bottom, becoming new recruits (Table 2). Stabilization took place by two mechanisms: cementation through the growth of algae, and the growth of coral tissue over the substrate. In 1994, the percentage of cemented fragments increased to 94, reaching 95 % by 1995.

Some of the factors that may affect the cementation of fragments to the bottom include fragment size, location, and bottom type. I tested the hypothesis that fragment size affects cementation and found no difference in the mean length of cemented (25.9 cm, S.E. = 1.3) and uncemented fragments (25.1 cm, S.E. = 0.9; t-test, $p > 0.1$).

The flat morphology of elkhorn branches ensures that a large portion of the tissue on one surface of the branch will be in direct contact with the benthos as the fragment comes to lie horizontally on the bottom. The lack of light, contact with sediments, and the scouring effects of the bottom can kill the coral tissue within one week. Therefore, unless the fragment is wedged in a crevice or has a three-dimensional structure that lifts it from the bottom, the initial tissue loss can amount to one-half of the live tissue

Table 4. Reproductive state of *Acropora palmata* colonies and fragments on Elkhorn and Ball Buoy Reefs in 1995 and 1996. Damaged colonies on Elkhorn Reef experienced severe fragmentation during Hurricane Andrew (August 1992). Size was estimated as longest length of live tissue on fragments and maximum canopy diameter on colonies.

DATE	TYPE	MEAN SIZE (cm)	REEF	# SAMPLED	# WITH GAMETES
8-95	FRAGMENT/SMALL	28.8 (4.8)	ELKHORN	5	0
8-95	FRAGMENT/MEDIUM	63.4 (2.5)	ELKHORN	5	0
8-95	FRAGMENT/LARGE	131.0 (12.1)	ELKHORN	5	0
8-95	COLONY/DAMAGED	193.0 (27.4)	ELKHORN	5	0
8-95	COLONY/UNDAMAGED	161.0 (49.0)	ELKHORN	5	4
8-95	FRAGMENT	48.6 (9.9)	BALL BUOY	6	0
8-95	COLONY	91.0 (23.8)	BALL BUOY	11	2
8-96	FRAGMENT/SMALL	35.8 (7.2)	ELKHORN	6	0
8-96	FRAGMENT/MEDIUM	62.4 (5.6)	ELKHORN	6	0
8-96	FRAGMENT/LARGE	140.7 (11.1)	ELKHORN	6	2
8-96	COLONY/DAMAGED	167.0 (18.9)	ELKHORN	6	3
8-96	COLONY/UNDAMAGED	185.0 (33.3)	ELKHORN	6	4
8-96	COLONY	120 (13.5)	BALL BUOY	9	6

present originally. Also, after a fragment has been lying on one side for over a week, it would only take a single flip to completely kill it. Several of the fragments marked in this study had complete tissue loss by this mechanism. This highlights the importance of fragment stabilization to avoid being flipped by subsequent disturbances.

Fragment survivorship. Size effects. Initial fragment size did not have an effect on fragment survivorship as demonstrated by several lines of evidence. Most fragments created by Hurricane Andrew on Elkhorn Reef were small to medium-size (5-50 cm), and few very small or very large fragments were produced. The relative distribution of fragments of different lengths remained constant over the duration of this study (Table 1), indicating that fragment mortality was not size-dependent, and that tissue growth and partial mortality offset each other. Reduction in fragment size took place through partial mortality, fission, and further fragmentation, whereas increase in fragment size took place through growth and fusion. Some of the larger fragments (> 75 cm) were formed by the fusion of two or more smaller fragments.

Regression analysis showed that the initial size of the hurricane-generated fragments did not appear to affect survivorship significantly during the first year (regression analysis, $p > 0.05$; Figure 7a). In addition, no significant relationships were found between the initial size of the transplanted fragments and survivorship (regression, $p > 0.1$; Figure 7b). However, there was a significant difference between the size of those fragments that remained within transplant sites and those that were removed (Figure 8). Fragments that were removed from transplant sites by waves and currents were significantly smaller than those fragments that remained (t test, $p < 0.05$).

A review of coral fragmentation studies reveals that the relationship between fragment size and survivorship is not always consistent. There is a general indication that fragment survivorship increases with fragment size (Highsmith et al., 1980; Heyward and Collins, 1985; Liddle and Kay, 1987), but there are some exceptions.

Table 3. Height of proto-branches (PB) on large (n = 5) and medium-size (n = 17) *Acropora palmata* fragments generated by Hurricane Andrew on Elkhorn Reef. Heights of proto-branches on medium fragments were not estimated until 1995.

LARGE FRAGMENTS (3000-8000 cm ²)	7-01-93	6-01-94	5-17-95	9-19-96
Mean PB height (cm) (S.E.)	2.6 (0.1)	4.5 (0.2)	8.3 (0.4)	17.5 (0.7)
Maximum PB height (cm)	9	13	18	30
# of proto-branches	163	150	147	157
MEDIUM FRAGMENTS (200-1200 cm ²)			5-15-95	4-25-96
Mean PB height (cm) (S.E.)			6.1 (0.3)	9.1 (0.6)
Maximum PB height (cm)			11	19
# of proto-branches			64	65

Kobayashi (1984) found no relationship between fragment size and survivorship for two Acroporid species. Rogers et al. (1982) found the opposite results for the survivorship of *Acropora palmata* fragments after storms in the U.S. Virgin Islands. In this case, survivorship was lower for larger fragments.

Although results from the present study indicate that elkhorn fragment survivorship is not dependent on initial fragment size, the size of fragments may influence survivorship indirectly through its effect on fragment removal from settlement areas (Figure 8). As most reefs are surrounded by sand, and fragment survivorship is very low in high sediment areas, fragment survivorship can be expected to decrease with distance from the reef. If smaller fragments are removed from the reef more easily, this will ultimately affect their long-term survivorship.

Fragment survivorship. Bottom type and location effects. Differences in substrate type can affect removal, total mortality, and partial mortality rates of hurricane-generated fragments. In the rubble zone of Elkhorn Reef, only 34 % of marked fragments were removed from the reef in the 11-month interval between 1993 and 1994 surveys, whereas 57 % of the fragments were removed from the hard-bottom area. The proportion of fragments removed from the original settlement areas increased to 57 % in the rubble and 76 % in the hard-bottom areas between 1993 and 1996 (Figure 9a).

The physical environment of the area where a fragment lands can determine fragment retention. The hard-bottom area where fragments were marked lies E of the reef-flat in an area exposed to the incoming seas (Figure 2). In comparison, fragments marked on the rubble bottom lie in the protected back-reef area. Also, the bottom type where a fragment lands may affect the cementation process. In this case, a combination of location within the reef and bottom type resulted in a higher loss of fragments in the hard-bottom area of Elkhorn Reef.

Table 1. Percentage of *Acropora palmata* fragments within permanent belt transects on the back-reef of Elkhorn Reef belonging to different length interval categories from 1993 to 1996.

LENGTH INTERVAL	1993	1994	1995	1996
0-5 cm	3	4	8	2
5-30 cm	64	65	64	65
30-50 cm	22	16	16	15
50-75 cm	9	9	7	11
>75 cm	2	6	5	6

Table 2. Results from five permanent belt transects sampled yearly on a rubble field on the back-reef of Elkhorn Reef following Hurricane Andrew. All *Acropora palmata* fragments within these transects were counted and measured.

	1993	1994	1995	1996
# FRAGMENTS	218	271	178	206
# QUADRATS	48	51	45	49
# FRAGMENTS/m ²	4.5	5.3	3.7	4.2
% CEMENTED	72	94	95	95
MEAN LENGTH cm (SEM)	25.8 (1.3)	25.6 (1.4)	24.4 (1.8)	27.7 (1.7)

Total mortality was also higher on the hard-bottom, where 50 % of the marked fragments died compared to only 4 % of the fragments on the rubble substrate. Those fragments that survived within the settlement areas between 1993 and 1996 lost 48 % of their live tissue area on the rubble substrate compared to 74 % on the hard-bottom (Figure 9b). Partial mortality was significantly higher in the hard-bottom over this period (Mann-Whitney U, $p < 0.01$). Mortality rates for all fragments combined were not constant throughout this study, being relatively low during the first year (31 %, S.E. = 7.5), but increasing significantly between 1994 and 1995 (57 %, S.E. = 10.8; Mann-Whitney U, $p < 0.05$; Figure 10). This high mortality was a direct result of Tropical Storm Gordon in November 1994.

Overall partial mortality for the duration of this study (1993 - 1996) was 57% (S.E. = 12.5). During the first year of this study (1993-1994), only four fragments (total $n = 89$) increased in tissue area; the remaining 95 % lost tissue cover. Over the duration of this study (1993-1996), only five fragments exhibited increases in planar tissue area. This contrasts sharply with the rapid upward growth of proto-branches that began to develop in June 1993 on the same fragments. After stabilization, fragments seem to allocate all of their energy to upward growth instead of increasing their planar area and attachment to the substratum.

Fragment Transplants. Results from the transplant experiments further confirm the conclusions drawn from the fragment monitoring study: survivorship of elkhorn fragments is not dependent on initial fragment size, but is highly dependent on location within the reef and the bottom type.

When data are combined for all fragments, there was a 28% reduction in the area covered by live tissue within the first month after transplantation (Figure 11). Although partial mortality continued, subsequent decreases in live tissue cover were not as significant (4% and 6%) as those recorded during the first month.

Mechanisms that enhance or favor fragmentation, such as those described in the previous studies, are not found in elkhorn corals. In fact, the complex structural and morphological adaptations of this species indicate that elkhorn colonies go to great lengths to avoid fragmentation under normal environmental conditions. In addition, I found significant costs to fragmentation that have not been determined in previous studies. The high susceptibility to breakage under episodic storm conditions and subsequent asexual recruitment can not be considered as sole evidence for adaptive fragmentation in this species. However, this study shows that elkhorn coral is well-suited to cope with episodic fragmentation events and even benefit from them under certain conditions. When fragmentation is not severe or frequent enough as to cause high mortality of both colonies and fragments, elkhorn populations can increase in abundance and biomass.

Transplant survivorship was affected by location and bottom type (Figure 12). Fragments transplanted to rubble, hard, or sandy bottoms experienced significant partial mortality during the first month. In contrast, those fragments placed on live adult elkhorn colonies did not experience any mortality. Tissue mortality was significantly higher in the sandy bottom than in the rubble or hard-bottom zones, which were not different from each other (ANOVA, $p < 0.05$; Tukey's *a posteriori* comparisons). Those fragments placed on sand were covered by sediments and showed signs of bleaching within a week; mean tissue mortality reached 69% within this area in September. The differences in fragment survivorship observed between the rubble and hard-bottom areas in the post-hurricane surveys were not observed for the transplants. This may be a result of the small sample size used in the transplant experiment. Substrate effects on transplant mortality were also observed in other studies (Yap and Gomez, 1984; 1985). Heyward and Collins (1985) reported higher mortality of fragments placed on sand for *Montipora ramosa*.

Fragments in the exposed, hard-bottom area E of the reef-flat lost a higher percentage of their live tissue cover than those fragments placed on the more protected hard-bottom area W of the reef-flat. Fragments in the rubble and hard-bottom areas started showing signs of tissue recovery two months after transplantation (Figure 12). Fragments placed on live elkhorn colonies fused to these within 3 weeks and showed no signs of tissue mortality. The fusion of the transplants without tissue rejection indicates that colonies on Elkhorn Reef may be clones originated from one or a few colonies.

This experiment was interrupted because Tropical Storm Gordon (November 1994) removed or buried all of the transplanted fragments except those that had cemented to live *Acropora palmata* colonies. Nevertheless, the data collected provide important information on the survivorship of elkhorn fragments immediately following detachment. Such estimates were missing from the monitoring study of hurricane-

In all organisms, the energy allocated to reproduction is just a portion of the total energy available, the remainder being dedicated to growth, repair, and maintenance. The fact that energy may be limited and has to be shared by different processes is evidenced by the cessation in gamete production in fragments and recently fragmented colonies; most of the energy in such cases seems to be allocated to stabilization, lesion repair, and growth. Reproduction can resume after a certain size and/or level of repair or growth has been achieved. A trade-off between reproduction and regeneration was also observed for the coral *Montastraea annularis* (Van Veghel and Bak, 1994). The differential allocation of resources to repair and growth at small colony sizes has been observed for other hard corals (Szmant, 1985; Kojis and Quinn, 1985; Hughes et al., 1992) and zoanthids (Karlson, 1988).

Highsmith (1982) predicted that if fragmentation in corals were adaptive (e.g., selected traits incorporated into the life history of corals), corals should have evolved skeletal features to enhance fragmentation under specific conditions. Such features have been described for a reduced number of organisms. The gorgonian *Junceella fragilis* produces fragments by resorbing tissue below the branch tips, creating a weak point that favors fragmentation (Walker and Bull, 1983). Colonies of the gorgonian *Plexaura A* are brittle and possess skeletal constrictions at the branch points that facilitate detachment (Lasker, 1984). Among hard corals, genetically determined methods of asexual reproduction or fragment formation seem to be restricted to solitary corals (for a review see Cairns, 1988). For example, *Diastrea fragilis* propagates asexually by natural autotomy (Yamashiro et al., 1989), and *Goniopora stokesi* forms small polyp aggregations that break off from the parent colony (Rosen and Taylor, 1969). These species appear to have evolved mechanisms to promote fission and fragmentation, suggesting these mechanisms may have been selected through evolutionary time.

generated fragments that were marked seven months after Hurricane Andrew. These data show that mortality of newly formed fragments can be high initially, but that provided no other significant disturbances take place, the growth of fragments in favorable locations and substrate type can make up for the tissue lost initially (Figure 10, 12).

Fragment growth. Proto-branches on elkhorn fragments reached a mean height of 2.6 cm (S.E. = 0.1) within one year. The growth rate of proto-branches increased with time (Figure 13). Average growth rates calculated from regression were 1.4 cm.yr⁻¹ for 1992-1993, 2.2 cm.yr⁻¹ for 1993-1994, 3.4 cm.yr⁻¹ for 1994-1995, and 5.3 cm.yr⁻¹ for 1995-1996. This shows that it takes more than four years for proto-branches on fragments to achieve linear growth rates comparable to those measured for standing elkhorn 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).

As it has been shown for several coral species, the translocation of resources from the more central portions of a colony supports the rapid growth rates observed at the tips of branches (Pearse and Muscatine, 1971; Taylor, 1977; Gladfelter et al., 1989). As proto-branches first develop, they must compete for the resources harvested by the fragment across its surface area. This may limit initial growth rates as several proto-branches can be found in even the smallest 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 biomass. Although growth rates may continue to increase exponentially, an upper limit for growth may be imposed by other factors such as nutrients or food availability.

Although large fragments tend to have taller proto-branches (Table 3), fragment size does not appear to have a major effect on mean proto-branch height as estimated

Meesters and Bak, 1995; Fong and Lirman, 1996). Similarly, the growth rates of coral fragments can be adversely affected (Kobayashi, 1984; Cox, 1992). After detachment, it took approximately seven months for elkhorn fragments to start developing new vertical growth features, and the initial growth rates of these proto-branches were slow. The linear growth of proto-branches on fragments was slower than the growth rates measured for standing colonies on the same reef even four years after being developed. Moreover, planar extension of fragments was rare throughout this study.

The lesions created by fragmentation can be colonized by bioeroders and compromise the structural strength of the surviving colonies. Even though I did not find any correlation between the presence of bioeroders and fragmentation in this study, other researchers reported that the action of bioeroders can severely reduce the skeletal strength of elkhorn colonies (Hernandez-Ávila et al., 1977; Mitchell-Tapping, 1978).

A survey of the reproductive state of *Acropora palmata* colonies and fragments revealed that both colony size and disturbance history can affect gamete production in corals. On Elkhorn Reef gametes were present only in large elkhorn colonies that had not experienced direct fragmentation during Hurricane Andrew. Neither those colonies that were damaged by the hurricane nor any of the hurricane-generated fragments had any gametes three years after the storm. One year later, a larger proportion of the colonies sampled contained gametes. In 1996, both damaged and undamaged colonies had produced gametes, and some of the larger fragments were now showing signs of reproductive activity. Only the small and medium size elkhorn fragments were not producing gametes at this time. This shows that fragmentation can have significant, long-term effects on the sexual reproduction of corals.

from regression in 1995 and 1996 ($r^2 = 0.24 - 0.34$, $p = 0.012 - 0.02$; Figure 14). This is another indication that after a certain height is attained, the growth of proto-branches no longer depends on resources procured by the polyps on the original fragment.

The effects of fragment size on the number of proto-branches was tested with regression. The number of proto-branches developing on the upper surfaces of fragments less than a year after fragmentation was directly related to the fragments' surface area, as can be predicted based on limited resource availability (regression, $p < 0.01$; Figure 15). Most proto-branches are formed at the same time, and only a few additional proto-branches are formed subsequently indicating a shift in energy allocation from proto-branch formation to proto-branch growth (Table 3).

Most proto-branches were formed on the top surfaces of fragments between March and June 1993. Proto-branches grew upwards with a cylindrical shape until they reached a height of 4-5 cm (Figure 16a). At this time, a mushroom-type cap developed (Figure 16b). The first branching pattern was observed as proto-branches reached 6-10 cm (Figure 16c). At this point, proto-branches began developing the typical tree-like morphology seen in adult elkhorn colonies. Secondary branching patterns were observed in 1996 on the tallest proto-branches (Figure 16d).

Survivorship and growth of colonies. Survivorship of adult *Acropora palmata* colonies was high on both Elkhorn and Ball Buoy Reefs from 1992 to 1996. Partial mortality associated with colony fission, competition with algae, or feeding activities of corallivores was observed, but none of the adult colonies surveyed exhibited total tissue mortality. The yearly growth of elkhorn colonies was 6.7 cm.yr^{-1} for small colonies (50-70 cm in canopy diameter) and 6.9 cm.yr^{-1} for large colonies (150-200 cm in canopy diameter). No significant differences in linear growth were found between small and large colonies (t test, $p > 0.1$).

Acropora palmata fragments produced by storms were transported shoreward where they landed on rubble and sandy bottoms. Mortality of elkhorn fragments was very high on sand, but those fragments that landed on rubble areas showed high survivorship and cementation capabilities. Thus, even if storm-generated fragments landing on sand experience high mortality, 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.

Costs of fragmentation

The costs of fragmentation, as determined in this study, can be considerable (Table 5). The most significant immediate cost documented here is the loss of tissue that can occur on both colonies and fragments. Partial tissue mortality on storm-generated fragments ranged from 50 to 74% from 1993-1996.

Fragmentation has the general effect of reducing the average size of ramets within a population, and this can have significant negative effects on clonal populations. Survivorship, reproduction, growth, and regeneration of clonal organisms have all been directly related to colony size (Connell, 1973; Harper and White, 1974; Williams, 1975; Loya, 1976; Buss, 1980; Hughes and Jackson, 1980; 1985; Highsmith, 1982; Rogers et al., 1982; Hughes, 1984; Jackson, 1985; Karlson, 1986; 1988; Hughes and Connell, 1987; Babcock, 1991; Hughes et al., 1992; Hall and Hughes, 1996). Also, populations composed of smaller individuals may more susceptible to subsequent disturbances (Babcock, 1991).

Previous studies have shown that fragmentation can have negative effects on the growth rates of damaged colonies (Gladfelter et al., 1977; Bak, 1983; Kobayashi, 1984). Adult elkhorn colonies have to repair skeletal lesions before linear extension can proceed (Lirman, unp. results), and depending on the size and shape of the lesions, regeneration can take from several weeks to several months (Bak, 1983;

Reproduction. Effects of fragmentation. The production of gametes in *Acropora palmata* appears to be affected by size and previous disturbance history. In 1995, three years after Hurricane Andrew and nine months after Tropical Storm Gordon, none of the *A. palmata* fragments on Elkhorn Reefs had any gametes, irrespective of size. A lack of gametes was also observed in adult colonies that were damaged by the hurricane. The only samples that contained gametes in 1995 were taken from colonies that were not damaged by the storm (Table 4). In Ball Buoy Reef, neither the colonies nor the fragments had any gametes in 1995. In 1996, neither small nor medium fragments on Elkhorn Reef had any gametes, but two of the six large fragments sampled were reproductive. Both colonies damaged and undamaged by Hurricane Andrew in 1992 had gametes at this time. In Ball Buoy Reef, six of the nine colonies sampled had gametes (Table 6).

A reduced investment in sexual reproduction predicted for species that propagate mainly by asexual means (Williams, 1975; Highsmith, 1982) does not appear to be present in *Acropora palmata*. Although the success of asexual propagation in *A. palmata* contrasts sharply with the minimal sexual recruitment reported for this species (Dustan, 1977; Bak and Engel, 1979; Rylaarsdam, 1983; Rosesmyth, 1984), it is clear that the low sexual recruitment observed does not result from a lack of investment in gamete production, as spawning in this species occurs on a yearly basis (Szmant, 1986), and even colonies damaged by storms and storm-generated fragments become reproductive after a few years. Considering that gametes are produced, spawning takes place, and planulae develop under experimental conditions (Szmant, personal communication), it is unclear why this species has such low sexual recruitment. Possible explanations for this include high mortality of planulae before and shortly after settlement, and strict settlement-substrate requirements.

CONCLUSIONS

Benefits of Fragmentation

Several of the advantages commonly associated with asexual propagation of clonal organisms were documented in this study for *Acropora palmata* in the Florida Reef Tract (Table 5). Fragmentation followed by high survivorship of adult colonies and fragments resulted in an increase in cover and abundance of elkhorn coral. Even though many fragments were removed from their original settlement areas and carried away from the reef, those fragments that remained showed high survivorship and regrowth capabilities. Fragment survivorship was affected by location within the reef and bottom type, and survivorship was highest for those fragments placed on live elkhorn colonies. Similarly, those fragments that landed close to adult colonies on the reef had higher probability of remaining in the area. This clearly shows that the presence of adult colonies can increase the survivorship of asexual propagules.

The larger size of fragments compared to sexual recruits can provide these propagules with a competitive advantage over other benthic organisms (Williams, 1975). Fragments created by Hurricane Andrew and Tropical Storm Gordon in two Florida reefs were transported by waves and currents and deposited on back-reef areas where they piled up on top of each other and completely smothered colonies of other coral species that are commonly found there (e.g., *Porites astreoides*, *Siderastrea* spp.). Since elkhorn coral has been shown to be competitively inferior to other corals in the procurement of space under normal conditions (Lang, 1973), fragmentation and asexual recruitment can clearly increase the propagation capabilities of this species.

Fragmentation and asexual recruitment can also provide mechanisms for the creation of additional primary space and reef expansion (Highsmith, 1982). Patch reefs such as those found in the Florida Reef Tract are commonly surrounded by sand and seagrass beds that are not optimal habitats for coral recruitment (Jaap, 1984).