# Storm-generated coral fragments - a viable source of transplants for reef rehabilitation

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## Abstract

Coral reefs throughout the world have been damaged by storms, diseases, coral predators, temperature anomalies, and human activities. During the past three decades, recovery has been limited and patchy. Although a damaged coral reef cannot be restored to its original condition, interest in reef restoration is increasing. In a pilot project in the Caribbean (U.S. Virgin Islands), storm-produced fragments of *Acropora palmata, A. cervicornis*, and *Porites porites* were collected from donor reefs and transplanted to nearby degraded reefs. Sixty coral fragments were attached to dead-coral substrate (usually *A. palmata* skeletons), at similar depths from which they had been collected (1 to 3.5 m), using nylon cable ties. Seventy-five intact colonies were designated as controls. Study colonies were assessed at 6-month intervals for 2 years (1999–2001) and annually thereafter (through 2004). One-fourth of the 135 colonies and fragments monitored were alive at the conclusion of the 5-year study. Survival of control and transplanted *A. cervicornis* and *P. porites* was very low (median survival 2.4 and 1.8 years, respectively), with no significant differences between transplant and control colonies. Site and depth did not contribute significantly to *A. palmata*-colony survival, but colony size and transplant/control status did. Probability of survival increased with colony size. Median survival for *A. palmata* was 1.3 years for transplant and 4.3 years for natural colonies when not controlled for size. *Acropora*

*palmata* was the only viable candidate for reef rehabilitation. Storm swells were the primary cause of mortality.

**Keywords:** *Acropora palmata*, acroporid, coral reef decline, coral reef rehabilitation, fragmentation, coral transplants

## 1. Introduction

William Beebe, clad in hardhat and heavy boots, crashed through thickets of *Acropora cervicornis* as he studied the shallow reefs of Haiti in the early 1900s (Beebe, 1937). Since that time, the undersea world has changed considerably, as have attitudes toward the marine environment and particularly coral reefs. The accelerating degradation of and damage to coral reefs worldwide continue to be widely reported in articles from the popular press to scientific literature (e.g., Gardner et al., 2003; Bellwood et al., 2004; Pandolfi et al., 2005). The list of proven and alleged causes is long and includes both natural events and human activities. The scale of damage runs from local to global, and the degree of degradation ranges from subtle signs to a seafloor scraped clean. Serial assaults from physical, biological, and/or socioeconomic factors further impede recovery of damaged reef systems (Birkeland, 2004).

The continuing decline of coral reefs has intensified interest in the restoration, rehabilitation, and repair of damaged reefs. Approaches vary from selection of sites for protection (Briggs, 2005) to development of conceptual principles to guide restoration (Yap, 2000; Epstein et al., 2003) to immediate action in the field. Repair of coral reefs began in response to severe damage from human activities: ship groundings (e.g., Davis, 1977; Hudson et al., 1989; Bruckner and Bruckner, 2001), thermal and sewage outfalls, dredging, blast fishing (Fox et al., 2005), coral mining (Clark and Edwards, 1994), and other localized destruction. Methods continue to be developed in response to the specifics of damage and the goals of intervention, from repair of small-scale damage to restoration of reefs (reviews by Jaap, 2000; Jaap et al., 2006): reattachment of displaced organisms;

stabilization and reattachment of large blocks of reef framework; removal of fine detrital material and rubble from pulverized corals and reef framework; transplantation of scleractinians and octocorals from nearby reefs to completely scoured seafloor; transplantation of rare corals from polluted to less impacted reefs (Plucer-Rosario and Randall, 1987); and, for severe damage, construction of rock piles as stable substrate (Fox et al., 2005) or rebuilding of reef framework using engineered structures (e.g., Hudson et al., 1989; Clark and Edwards, 1994).

Damaged coral reefs cannot be restored to their original state. True recovery of a damaged reef could take decades to centuries (Maragos, 1974), depending on the life histories of the reef-framework-building species (Potts et al., 1985) as well as physical, biological, and socioeconomic conditions at the site. Considerable controversy surrounds whether restoration should be attempted at all, particularly in response to mortality resulting from regional or global epizootics, temperature anomalies, predator outbreaks, powerful storms or chronic environmental stressors, and if so, what methods should be used (e.g., Jaap, 2000). Some critics argue that human intervention other than damage prevention is a waste of time and resources (e.g., Edwards and Clark, 1998), particularly when the root causes such as human-population pressures on marine and coastal resources are not addressed (Birkeland, 2004; Kaufman, 2006). Critics also point to the significant disparity that exists between the scale of restoration efforts (hundreds to thousands of square meters) and the scale of reef degradation (hundreds to thousands of square kilometers). These criticisms imply that local communities and reef managers should not act, even as key species become locally or regionally threatened and critical reef function shifts, but should wait until human pressures stabilize, marine and coastal resource use is sustainable, and

restoration efforts can be scaled up to thousands of square kilometers. Because those conditions may never be met, is it prudent and more realistic for local communities and reef managers to identify key species and simple methods that could be used to repair damage to or enhance reefs of economic, cultural, and ecological importance (Harriott and Fisk, 1988)? Over time, small-scale reef repair and enhancement activities could help slow reef declines, shifts in system function, and local loss of species (Maragos, 1974). Restoration of large areas or reefs damaged by chronic environmental impacts may not be reasonable or feasible, but damage repair or enhancement on a limited scale for specific outcomes could produce positive effects on multiple levels.

*Acropora palmata* and *A. cervicornis* are key reef-building species in the Caribbean (Goreau, 1959) and dominated Caribbean reefs until 90-95% of colonies were decimated by an epizootic of unknown origin in the late 1970s and early 1980s (e.g., Gladfelter, 1982; Aronson et al., 2002). The dramatic declines of *A. cervicornis* and *A. palmata* throughout the Caribbean region in the past 30 years seem to be the first significant interruption in dominance by these two species in the past 2 to 3 ka (Aronson et al., 2002; Shinn et al., 2003; Hubbard et al., 2005). Diseases, storms, human activities, and other factors continue to impede recovery of either species to early 1970s abundances (Knowlton et al., 1990; Hughes, 1994; Aronson and Precht, 2001a; Nagelkerken and Nagelkerken, 2004; *Acropora* Biological Review Team, 2005). In 2006, *A. palmata* and *A. cervicornis* became the first coral species listed as threatened under the U.S. Endangered Species Act.

In response to declines of scleractinian coral on Caribbean reefs and to losses of *A. palmata* and *A. cervicornis* in particular, a pilot coral-transplantation project was launched in Virgin Islands National Park (St. John, U.S. Virgin Islands; USVI). The primary research

objective was to evaluate the feasibility of using storm-produced coral fragments as the source of coral transplants to enhance degraded reefs. The working hypothesis was that survival rates do not differ between corals occurring naturally on the reef and transplanted coral fragments that were produced by storms. Transplantation of organisms is one of the most commonly used methods in coral reef rehabilitation (Maragos, 1974). Nonetheless, key questions remain regarding use of transplantation, even for small-scale damage repair and reef enhancement. 1) What is the source of transplants, or – is it appropriate to degrade one reef in order to repair or enhance another reef? 2) What will be the long-term survival of transplanted corals and other organisms? 3) Does the outcome justify the costs – environmental changes/losses from donor reefs, time or person days, and materials? Survival of unattached coral fragments is generally low (e.g., Rogers et al., 1982; Lirman and Fong, 1997; Lirman, 2000). Collection of unattached fragments from substrate or environmental conditions unfavorable to survival followed by transplantation to degraded or damaged reefs would be expected to: 1) maximize survival of fragments; 2) decrease damage to intact colonies from unattached corals; and 3) over time, increase spatial heterogeneity and abundance of key organisms on transplant-recipient reefs, thereby assisting reef recovery (Shinn, 1976; Sleeman et al., 2005; Linares et al., 2008). By using storm-generated coral fragments, one of the key concerns regarding transplantation is resolved since no reefs or colonies are damaged to obtain transplants. As an ancillary bonus, more fragments survive.

*Acropora palmata* (elkhorn coral), *A. cervicornis* (staghorn coral), and *Porites porites* (finger coral) were selected for the study because all three scleractinian species: 1) reproduce successfully via asexual fragmentation (Shinn, 1966; Highsmith, 1982; Potts et

al., 1985; Fong and Lirman, 1995); 2) grow rapidly compared to other stony corals (Goreau, 1959; Shinn, 1966; Gladfelter et al., 1978; Tunnicliffe, 1981); and 3) occur in sufficient numbers as fragments and intact colonies on USVI reefs. An equally important factor was the precipitous decline and lack of recovery of the important reef-builders, *A. palmata* and *A. cervicornis*. This study, built on decades of coral reef research, differs from previous work in that: 1) transplant survival was followed for 5 years - longer than most studies; 2) no coral colonies or donor reefs were damaged, because storm–generated coral fragments were transplanted; and 3) fragment sizes were naturally and not experimentally produced.

## 2. Materials and Methods

### *2.1 Transplantation*

This research was conducted from May 1999 to July 2004 on four reefs in Virgin Islands National Park (VINP; Fig. 1). One hundred thirty-five corals (60 transplanted fragments and 75 control colonies; Table 1) were tagged, photographed, measured, and qualitatively assessed at 6-month intervals from May 1999 to July 2001 and annually from July 2001 to July 2004. Two factors limited the final number of transplanted fragments (60): the scarcity of *A. cervicornis* and *P. porites* fragments (*A. palmata* was abundant); and the time required to monitor and measure transplants and control colonies. Storm-generated fragments of the three species of branching coral [elkhorn, staghorn (axial fragments only), and finger coral] were collected from shallow (1 – 3 m) sandy or bare substrate unfavorable

for survival due to abrasion and tumbling (e.g., Bowden-Kerby, 2001). Handled as little as possible, fragments were placed in buckets underwater, transported from the donor to transplant-recipient reef in covered buckets of seawater via boat, and transferred in buckets underwater, from the boat to the recipient reef. Inert nylon cable ties were used to attach each fragment to coral skeleton (Fig. 2A, B) in an orientation consistent with the growth strategy of each species (Soong and Chen, 2003), at a similar depth from which they had been collected. Dead, upright *A. palmata* skeletons were the preferred attachment substrate. They provided contoured surfaces to which fragments could be attached securely above abrasive sand and sediment, they withstood pounding by waves in shallow waters, and they indicated that the site had been suitable for coral growth. Maximum time between removal of a fragment from the donor reef and attachment to the recipient reef was 3 hours. Only one species was collected and transplanted per day. Initial attempts to clean dead-coral skeleton and attach fragments using epoxy were unsuccessful, messy, expensive, labor intensive, and time consuming. Donor sites were selected based on availability of at least 15 healthy unattached fragments of one species in an environment unfavorable for coral survival (e.g., on sand and in a surge zone). *Acropora palmata* fragments were plentiful (Grober-Dunsmore et al., 2006), particularly at certain times of the year, whereas healthy *A. cervicornis* and *P. porites* fragments were limited. Transplant-recipient reefs were chosen based on similarity to donor reefs (i.e., water quality, light regime, depth, water-residence time, community composition). Trunk Cay (Fig. 1; Table 1), offshore from a popular beach visited by 200,000 visitors annually (VINP unpublished data), was chosen as the primary transplant-recipient reef based on depth, presence of intact dead *A. palmata* skeletons for attaching fragments, and opportunity for public education. A second

transplant and control site (Whistling Cay; Fig. 1; Table 1) was selected because it provided greater protection from open-ocean swells and human activities, in addition to satisfying the same criteria (similar depth, water quality, presence of dead, intact *A. palmata*). To compare survival of transplanted fragments and intact coral colonies, an equal number of control colonies of each species was monitored. To control for environmental/site effects, control colonies were monitored on the reefs where fragments had been collected and where they were transplanted (Table 1). All donor and transplant-recipient reefs had similar and excellent water quality (pH, temperature regimes, salinity, nutrient concentrations, total suspended solids, transmissivity, and extinction coefficients) and water-residence times (Garrison and VINP unpublished data). Boat traffic was too hazardous for control-colony monitoring at Scott Beach, and coral abundance was too low at Trunk Cay. Control colonies were selected to be as similar to transplanted fragments as possible, based on size, depth, and exposure to ocean swells. Each transplant and control colony was identified by a numbered tag secured to the nearby reef.

Each colony was photographed and sketched, and live tissue on each branch and base was measured at each evaluation. Presence of bleaching, paling, tissue lesions (possible disease, predation, or physical damage), and predators (coral-eating snails, *Coralliophila* spp., and damselfishes, primarily *Stegastes planifrons*) were recorded. Measurement of *A. palmata* and *A. cervicornis* colony dimensions was challenging because of the energetic and dynamic nature of the shallow-reef environment and the highly variable nature of *A. cervicornis* and *A. palmata* growth. The morphology of a colony commonly changed dramatically owing to loss of part of the colony structure in

combination with growth of new branches. This rendered quantification of growth by consistent measurement of the colony structures impossible.

### *2.2 Data Analysis*

Coral colonies were considered dead and were removed from further inclusion in the dataset if: 1) the entire colony or fragment disappeared and could not be relocated (physical dislodgement), or 2) live tissue was not observed (100% tissue loss). To test for the effect of colony size on survival, the size of each coral fragment and control colony was estimated using the measurements of live coral tissue. The planar area ($cm^2$) of live *P. porites* tissue was derived from linear measures along the major (a) and minor (b) colony axes, as applied to the equation for the area of an ellipse ($A = \pi ab$). For *A. cervicornis* colonies, the sum of the linear measures (cm) of all live tissue was used (as in Knowlton et al., 1981). For *A. palmata*, the maximum linear dimension of live tissue (cm) was found to be the best metric. The increase (or decrease) in maximum linear dimension of *A. palmata* and of the sum of branch lengths in *A. cervicornis* was considered the most conservative estimate and the best indicator of growth (or tissue loss) in those species, on the basis of available data.

### *2.3 Survival-Model Specifications*

Differences in probability of survival were assessed using the generalized linear model module of Statistica 6.0 with a specified binomial distribution and a complementary log-log (Clog-log) link. Logistic regression procedures offer an alternative to ordinary least-

squares regression, since bivariate outcomes (e.g., survival or death) seldom meet statistical assumptions required for standard regression procedures (Peng et al., 2002). Additionally, the Clog-log link function is recommended when data are "interval-censored" (i.e., mortality occurs in continuous time, but events are observed at discrete intervals; Singer and Willett, 2003).

A primary, multivariate regression was run examining the main effects of species, location, transplant status, and depth on coral survivorship. Interaction effects of species with time (i.e., non-proportional, time-dependent effects) and transplant status were included by adding cross-product terms to the model. The effect of transplant status and the maximum linear size on coral-colony survival were examined in a separate logistic model, exclusively among *A. palmata* colonies. Low sample numbers over time precluded analysis of *A. cervicornis* and *P. porites*. To examine the effects of transplant status more closely over successive time periods, transplant effects were allowed to interact generally with each time period. Additionally, in an effort to provide some assurance that the effects of transplant status were not attributable to pre-existing size differences (Table 2), transplant - size interactions were included in an initial, preliminary model and were found not to contribute to significant improvements in model deviance (Wald $\boldsymbol{X^2} = 0.223$, $p = 0.637$). With this assurance of homogeneity among slopes, between transplant and control-colony probability response to size effects, the interaction term was then excluded and the model re-run with only main effects as recommended by Engqvist (2005). For all models, however, best-fit model parameters were chosen on the basis of significant improvements ($p < 0.05$) in deviance statistics relative to nested models. This method of model building is preferred over those based on asymptotic standard errors when sample sizes are relatively

small (Agresti, 1996). Statistical tests of the reduced model parameter estimates were assessed using Wald's chi-square statistics (Wald $X^2$). Standard errors supplied with survivorship graphs are Greenwood's approximations (Greenwood, 1926; Singer and Willett, 2003).

*2.4 Transplantation Costs*

Efforts to collect, transplant, and secure coral fragments to the reef were inexpensive despite three factors that increased the costs and time per transplant: this was a small-scale pilot project; boats and scuba were used (even when not essential); and multiple attachment methods were tested. Materials, boat and scuba, and scientist salary costs totaled US$1,250 or US$21 per transplant. Factoring out salary, transplantation costs decline to US$5 per transplant. Without boat and scuba expenses (only snorkeling from shore), cost plummets further to a fraction of US$1 per transplant for nylon cable ties. The time to collect, transport, and attach each fragment to a reef 1 - 5 km distant was 0.6 hr.

## 3. Results

*3.1 Colony Survival: Species, Transplant Status, and Size Effects*

One-fourth (34) of the 135 monitored coral colonies and fragments were alive at the end of the 5-year study. Of the 101 corals that did not survive, 58% had disappeared and 42% had died (Fig. 3). The main effects of transplant status, site, and depth did not significantly

contribute to overall differences in colony survival (overall model improvement); however, species effects and species/transplant interactions did contribute (Table 3).

Colony survival varied among species, with survival of *A. palmata* > *P. porites* > *A. cervicornis* (Fig. 4A). Survival of transplant and control colonies differed through time for *A. palmata* (Fig. 4B; Wald $\boldsymbol{X^2}$ = 8.32, p = 0.004) but not for *A. cervicornis* or *P. porites* (Table 3). Median survival was 2.4 years for *A. cervicornis,* 1.8 years for *P. porites,* and 1.3 and 4.3 years for *A. palmata* transplant and control colonies, respectively (Figs. 4A and B). The relative risk of colony death or physical dislocation diminished at a constant rate through time for both *A. palmata* and *P. porites* (Wald $\boldsymbol{X^2}$ = 4.79, p = 0.029). The relative risk of *A. cervicornis* mortality was initially indistinguishable from that of *P. porites* or *A. palmata* but increased at a constant rate through time (Wald $\boldsymbol{X^2}$ = 12.32, p < 0.001; Fig. 4A).

The initial log-mean live-tissue size of transplant-coral fragments differed from control corals across all species (Table 2). Tests for overall model fit indicated that the main effect of $\log_{10}$ maximum linear size and transplant status of *A. palmata* in Year 1 contributed significantly to reductions in model deviance (Table 4). However, Wald-based statistical tests indicated that control and transplant *A. palmata* colony survival also differed in Year 2 of the study (ß = 0.946, S.E. = 0.459, Wald $\boldsymbol{X^2}$ = 4.244, p = 0.039). The preferred reduced model (Table 4) estimated the probability of *A. palmata* transplant-colony dislocation or tissue loss in the first year of monitoring was 2.3-fold greater than that of control colonies (Wald $\boldsymbol{X^2}$ = 6.90, p = 0.009). Regardless of status as a transplant or control colony, however, for every 0.1 unit increase in log-maximum colony length, the probability

of mortality or dislocation in the following year decreased by 15% ($\beta$ = -1.60, 95% C.I. = -2.59, -0.61; Fig. 5), indicating that size was a factor in survival of *A. palmata* colonies.

### *3.2 Colony Growth*

After 5 years, most of the surviving coral colonies showed a net increase in size: 67% of fragments and 57% of control *A. palmata* colonies; the single surviving *A. cervicornis* (a control); and 75% of *P. porites* transplants. Colony mortality did not always follow loss of live tissue in the previous year(s). Some *A. palmata* colonies (fragments and controls) sustained repeated physical breakage and periodic loss of live tissue over most of the colony yet recovered and increased in size. Increases and losses in live tissue did not seem to follow any discernible pattern subsequent to damage or a period of growth.

Transplanted *A. palmata* fragments commonly overgrew nylon cable ties, and a few colonies grew along the uncut cable tie "tail," depositing skeleton. Two out of three *A. palmata* transplants initiated growth over cable ties in an average of 3.3 months [standard deviation (sd) = 2.4], and one-half of transplants completely overgrew the cable ties in 7.3 months (sd = 4.6). *Acropora cervicornis* and *P. porites* tissue was not observed to overgrow the cable ties, possibly an artifact of the small sample size combined with high mortality or the different growth strategies of these species. Some *A. palmata* colonies cemented to the substrate as early as 6 months after transplanting, yet others never cemented after 7 yrs. Only 20% of *A. cervicornis* and 13% of *P. porites* transplants cemented to the substrate during the study.

### *3.3 Agents of Mortality*

Physical dislodgement was the major cause of colony mortality over the 5-year study, accounting for: 58% of both transplanted fragment and control-colony mortality overall; 83% of *P. porites* loss; and, 50% of *A. palmata* and *A. cervicornis* mortality (Fig. 3). Dislodgement played an even greater role during the first 7 months of the study, causing 93% of both transplant and control-colony mortality, with only 7% attributed to a Category 5 hurricane. Greater survival of transplant than control *P. porites* and *A. cervicornis* colonies in the first 7 months was most likely a result of attachment (Fig. 3); all fragments were attached, whereas most control colonies were not.

Breakage of coral skeleton was commonly observed, usually in association with strong ocean swells. Incidence of breakage was greater in control (17%) than transplant (5%) colonies, presumably due to the larger size of most controls. The extent of breakage ranged from the loss of small branches to removal of a colony's entire vertical structure, leaving only the encrusting base. Some *A. palmata* colonies survived breakage multiple times, resulting in highly transformed colony structures. In a few colonies, serial breakage over 5 years produced a thicket of *A. palmata* clones. Direct damage to monitored colonies by snorkelers or divers was never observed during the study.

Disease-like lesions were observed on *A. palmata* and less often on *A. cervicornis*. Confirmation of disease requires culture or molecular techniques and was outside the scope of this study. However, the causative pathogen of acroporid serratiosis (*Serratia marcescens;* Patterson et al., 2002) was identified (culture-based techniques) from a single *A. palmata* colony on a study reef (Weil, 2004; Smith, G.W., personal communication).

Predators feeding on coral tissue were rarely observed on monitored colonies, but predation was inferred based on the pattern of tissue loss and the presence of the predators at the base of a colony. *Coralliophila* spp. were observed feeding on both *Acropora* species. Tissue loss on tips of *A. cervicornis* colonies appeared similar to that produced by *Hermodice carunculata* grazing, but no feeding was directly observed. Because observations in the final 3 years were at 12-month intervals, specific causes of mortality usually could not be determined.

## 4. Discussion

Healthy storm-generated coral fragments collected from environments unfavorable for survival and transplanted to degraded reefs survived and grew, with mixed results. Of the three species studied, only *A. palmata* was found to be a viable candidate for transplantation in the Virgin Islands. At the end of the 5-year study, one in five transplanted *A. palmata* fragments had survived and grown, in contrast to nearly 100% mortality of *A. cervicornis* and *P. porites* control and transplant colonies. Although the dramatic losses of these two species could be an artifact of small sample size, these findings are in agreement with research in the Caribbean region (e.g., Hughes, 1994; Aronson and Precht, 1997; Rogers, 1999; Aronson and Precht, 2001b), with one exception (Vargas-Ángel and Thomas, 2002; Vargas-Ángel et al., 2003). Despite being one of the major reef-building species on Caribbean reefs for thousands of years (e.g., Aronson and Precht, 1997; Pandolfi et al., 2005), *A. cervicornis* currently does not seem to be a good candidate for transplantation and will not be so until survival rates of natural colonies improve

significantly. The high mortality may be due to underlying environmental and/or intrinsic factors unfavorable to survival of these species. However, shallow coral reefs are highly dynamic systems with high turnover of coral colonies, and although individual colonies may not be long lived, the populations may persist over time (Jaap et al., 2006).

Survival of coral transplants varies by species, substrate type, environmental conditions (e.g., salinity, sedimentation, temperature, nutrients), experimental methods, orientation, site, duration of investigations, spatial arrangement (e.g., Yap et al., 1992; Rinkevich, 1995; Smith and Hughes, 1999; Nagelkerken et al., 2000; Rinkevich, 2000; Raymundo, 2001; Soong and Chen, 2003; Yap, 2004; Sleeman et al., 2005), and less clearly, initial size of transplant. Results from this study reinforce known findings: 1) transplant survival is directly dependent on size (e.g., Highsmith et al., 1980; Liddle and Kay, 1987; Smith and Hughes, 1999; Bowden-Kerby, 2001; Lindahl, 2003; this study Fig. 5, *A. palmata* only); 2) transplant survival varies among species; and 3) fragment/transplant mortality is greatest in the first year following disturbance (e.g., Knowlton et al., 1981; Clark and Edwards, 1995; Smith and Hughes, 1999; Lirman, 2000; Bowden-Kerby, 2001; this study, Fig. 3). Survival of coral fragments has been reported to be directly dependent on size in numerous studies (e.g., Highsmith et al., 1980; Smith and Hughes, 1999; Bowden-Kerby, 2001; Bruckner and Bruckner, 2001; Lindahl, 2003). However, others have found an inverse correlation (Rogers et al., 1982), no relation between survival and initial size (survival and growth were genet and not size dependent; Rinkevich, 2000), or mixed results (small fragments had the lowest rates of survival, but survival among larger fragments was not related to size; Bruno, 1998). Conventional wisdom holds that larger fragments have greater chances of survival because they have more resources to draw upon

for calcification and for coping with the physical stresses of abrasion, predation, disease, and transplantation. Conversely, the greater surface area of larger fragments makes them more vulnerable to displacement by water motion (Linares et al., 2008) and, possibly, to predation and disease (Grober-Dunsmore et al., 2006).

Survival of *A. cervicornis* transplants at 7 months in this study was similar to that reported by Bowden-Kerby (2001). Bruckner and Bruckner (2001) reported somewhat higher survival (57%) of *A. palmata* fragments 2 years after reattachment following a ship grounding at Mona Island, Puerto Rico. The difference in survival of reattached *A. palmata* fragments between Mona Island (Bruckner and Bruckner (2001) and this study may have been due in part to physical properties of attachment materials - nylon cable ties stretch more easily than stainless-steel wire. However, Bruckner and Bruckner (2001) reported higher survival of fragments secured with cable ties than with wire. Considering the overall low survival of the three species in this study, environmental conditions on the study reefs (even in a protected National Park) may not have been as conducive to coral survival and growth as in the oceanic waters of Mona Island.

The method selected here to affix fragments to substrate was simple, easy, fast, and inexpensive compared to other methods and can successfully be used by community volunteers with minimal training. Wire may have been more effective in securing fragments to dead coral in shallow water over time because wire stretches less than cable ties. However, wire has been reported to have severely abraded coral (e.g., *A. palmata* fragments at the *Fortuna Reefer* grounding site; Jaap, personal communication) and can produce more far-reaching and indirect effects. Iron, a major component of stainless-steel wire and a limiting micronutrient in the reef environment, can stimulate microbial growth

and may induce pathogenicity or virulence in normally benign microbes in the reef environment, triggering disease (Weinberg, 1996). Iron also stimulates growth of macroalgae (Bruckner and Bruckner, 2001) that in turn can physically abrade corals and secrete compounds that enhance microbial growth (Smith et al., 2006). Although inexpensive, simple, and widely available, monofilament line can damage coral tissue and can stretch over time, allowing the fragment to be dislodged. Cement and epoxy are commonly used attachment media but are more expensive, logistically complex, and require a clean substrate and, usually, trained divers using scuba.

Natural disturbances such as storms (Stoddart, 1962; Shinn, 1966; Rogers et al., 1982; Hughes, 1994), disease (Gladfelter, 1982; Harvell et al., 1999; Aronson and Precht, 2001a), and predation (Chesher, 1969; Knowlton et al., 1990) are well-known agents of mortality on coral reefs (Hughes and Connell, 1999). The primary cause of mortality in this study was the dislodgement of entire coral colonies by strong ocean swells (Fig. 3). No delayed mortality, such as that reported by Knowlton and colleagues (1981, 1990), was observed following passage of a Category 5 hurricane 5 months after this study began. A combination of transplant effect (for *A. palmata* only), size differences between transplants and control colonies, and serial damage from multiple winter storms may have obscured a delayed-mortality signal. Surprisingly, damage to colonies was not a predictor of colony mortality, as has been reported for branching colonies in the Pacific (Cumming, 2002). Some *A. palmata* colonies grew rapidly after being damaged repeatedly, while other colonies with little loss of tissue or skeleton died. Increase in colony size varied dramatically among individual transplants that survived for 5 years and was not related to site or environmental conditions. Although disease and predation are known to be

important drivers in shaping reef communities (e.g., Knowlton et al., 1990; Harvell et al., 1999; Aronson and Precht, 2001a), both appeared to play minor roles in the mortality of corals followed in this study. Similarly, direct damage from human activities (e.g., Woodland and Hooper, 1977; Liddle and Kay, 1987; Tilmant, 1987; Hawkins and Roberts, 1992; Rodgers and Cox, 2003; Epstein et al., 2005) was not observed to be a major factor. Extrinsic factors such as physical breakage from swells and intrinsic factors such as genetic differences in calcification (cementing to the substrate and skeletal growth) appeared to drive the survival and growth of individual *A. palmata* colonies. However, genetic/intrinsic effects, key factors in survival of colonies, were not controlled for in this study. Overall, the high mortality rates of control and transplant fragments of all three species point to underlying environmental and/or intrinsic conditions unfavorable to survival (Birkeland, 2004). As Hay and colleagues (2004) point out, subtle changes in the environment and organism interactions can shift conditions for coral survival from favorable to unfavorable.

## 5. Conclusions

This small-scale study sought to test the feasibility of using storm-generated coral fragments as transplants. Storm swells routinely produce an abundant supply of *A. palmata* fragments (Highsmith, 1982; Fong and Lirman, 1995; Grober-Dunsmore et al., 2006) and results from this 5-year study showed that storm-generated *A. palmata* fragments provide a viable source of coral for transplantation to degraded or damaged reefs. Fragment survival is maximized, and damage to intact colonies from loose corals is minimized for *A. palmata*, a key reef-building species listed as threatened. Conversely, the scarcity of fragments and

nearly 100% mortality of *A. cervicornis* and *P. porites* transplants and controls underscore that not all species are good candidates for transplantation of naturally produced fragments. The method investigated here was found to be simple, inexpensive, and easily conducted by community volunteers. This approach seems to be particularly suited for small-scale damage repair or reef enhancement conducted by reef managers and local communities in locations with limited resources. The approach is not suitable for scaling-up to address thousands of square meters or greater swaths of reef at the island or regional scale, or as the sole strategy for conserving threatened coral species.

To reiterate, damaged and degraded reefs cannot be restored or rehabilitated to their original condition. Until the basic processes driving declines on coral reefs worldwide are understood and forcing factors such as increasing human-population pressures on marine and coastal resources are addressed, the future does not look bright for coral reefs. However, there is a place for small-scale rehabilitation efforts. For little expense and using readily available materials, local communities can effectively, albeit modestly: 1) increase the live coral cover and spatial complexity of a reef without damaging other reefs; 2) minimize damage to intact corals by stabilizing loose fragments; 3) decrease incidence of reef damage from humans through community education; and, 4) contribute to the conservation of threatened species (in this case *A. palmata)*. Conducted at multiple locations throughout a region and sustained over time, these efforts become regional in scale and may buy time for threatened coral species and reefs.

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**Figure Captions**

Fig. 1 - Map of St. John, U.S. Virgin Islands, and study reefs: Donor reefs (H=Hawksnest Bay; L=Leinster Bay; S=Scott Beach) and transplant-recipient reefs (T=Trunk Cay; W=Whistling Cay).

Fig. 2 - Two transplanted *Acropora palmata* fragments of similar initial size at t=0 and t= 5 yrs: A. #127 at t=0; B. #124 at t=0; C. #127 at t=5 yrs; D. #124 at t= 5yrs. Fragments were attached to the dead-coral substrate using nylon cable ties (t = time).

Fig. 3 - Percent of colonies that survived, disappeared, or died for each coral species by transplant status over time.

Fig. 4 – (a) Proportion of *Acropora palmata* control colonies, and all *A. cervicornis* and *P. porites* colonies that survived with time, and (b) proportion of *A. palmata* control colonies and transplants that survived across time periods. Standard errors presented with proportion measurements are Greenwood's approximations.

Fig. 5 - Mean probability of mortality of *Acropora palmata* control-coral colonies across any given year with maximum linear size.

Table 1 - The numbers of monitored control colonies and transplanted fragments are shown for each species (*Acropora cervicornis, A. palmata,* and *Porites porites)* by site. Source reefs of transplanted fragments are indicated. Location of each transplant and donor reef site is given in latitude and longitude in degrees.

| Site<br>St. John, US Virgin Islands | Location latitude, longitude (degrees) | Coral species | # Control colonies monitored at site | # Fragments transplanted to site | Source of transplanted fragments |
|---|---|---|---|---|---|
| Trunk Cay | 18.353 N<br>64.763W | *A. cervicornis*<br>*A. palmata*<br>*P. porites* | | 15<br>15<br>15 | Scott Bay<br>Hawksnest Bay<br>Scott Beach |
| Hawksnest Bay | 18.347 N<br>64.780W | *A. palmata*<br>*P. porites* | 15<br>15 | | |
| Whistling Cay | 18.372 N<br>64.747W | *A. palmata* | 15 | 15 | Leinster Bay |
| Leinster Bay | 18.363 N<br>64.750W | *A. cervicornis*<br>*A. palmata* | 15<br>15 | | |
| Total colonies | | *A. cervicornis*<br>*A. palmata*<br>*P. porites*<br><br>All species | 15<br>45<br>15<br><br>75 | 15<br>30<br>15<br><br>60 | |

Table 2 - Mean transplant-fragment and control-colony size (in cm), and t-test results for mean $\log_{10}$ size differences are shown for *Acropora cervicornis*, *A. palmata,* and *Porites porites*. Individual colony sizes were taken from maximum linear field measurements (*Acropora cervicornis*, *A. palmata)* or estimated planar area (*P. porites*). SE = standard error, n = number, t = t-test result, and p = significance ($\alpha < 0.05$).

| Species | Initial control colony size | | | Initial transplant size | | | t-test Results | |
|---|---|---|---|---|---|---|---|---|
| | Mean | SE | n | Mean | SE | n | t | p |
| *Acropora cervicornis* | 71.6 cm | 11.7 | 15 | 30.7 cm | 2.7 | 15 | 3.5 | 0.002 |
| *A. palmata* | 25.4 cm | 1.9 | 45 | 17.9 cm | 1.7 | 30 | 2.8 | 0.006 |
| *Porites porites* | 249.3 $cm^2$ | 42.1 | 15 | 50.4 $cm^2$ | 8.5 | 15 | 5.8 | < 0.001 |

Table 3 - Reduced model, logistic regression results of the survival probability of 135 corals, monitored for five consecutive years. Logit parameter estimates ($\beta$) and standard errors, Wald's chi-square statistics (Wald $X^2$) and significance test results (p), and overall reduced-model fit are shown. The reduced model excludes those factors that did not significantly contribute to the values of the dependent variable (i.e., survival).

| **Effect** | **Level** | **$\beta$** | **SE $\beta$** | **Wald $X^2$** | **p** |
|---|---|---|---|---|---|
| Time | Linear | -0.210 | 0.096 | 4.79 | 0.029 |
| Species | *Acropora cervicornis* | -0.700 | 0.390 | 3.22 | 0.073 |
| | *A. palmata* | -0.810 | 0.292 | 7.70 | 0.006 |
| | *Porites porites* | -0.730 | 0.226 | 10.44 | 0.001 |
| Species × Time | *A. cervicornis* × time | 0.636 | 0.181 | 12.32 | < 0.001 |
| Species × Transplant | *A. palmata* × transplant | 0.840 | 0.291 | 8.32 | 0.004 |

| **Model Fit** | **-2*Log Likelihood** | **d.f.** | **p** |
|---|---|---|---|
| Reduced Model* | 420.71 | 393 | < 0.001 |

* Significance test results for the overall reduced model fit are relative to a constant time effects model (i.e., intercept only, base-line hazard does not vary across time periods; Deviance = 451.47, d.f. = 398).

Table 4 - Reduced-model, logistic regression parameter estimates of the probability of mortality of *Acropora palmata* based on $\log_{10}$ maximum linear colony size and transplant or control-colony status, at each time period. In the reduced model, Year 1 was the only period that showed a significant difference between control and transplant colony survival. However, Wald's chi square (Wald $X^2$) significance test results indicate control and transplant survival also differed in Year 2 (not shown). There was a significant difference in colony survival based on $\log_{10}$ maximum linear colony size.

| **Level** | ***ß*** | **SE *ß*** | **Wald $X^2$** | **p** |
|---|---|---|---|---|
| Intercept | 0.430 | 0.657 | 0.430 | 0.512 |
| Log Maximum. Size | -1.600 | 0.505 | 10.049 | **0.002** |
| Transplant Year 1 | 0.880 | 0.335 | 6.900 | 0.009 |
| Model Fit | -2*Log Likelihood | | d.f. | **p** |
| Reduced Model* | 219.96 | | 237 | **<0.001** |

* Significance test results for the overall reduced-model fit are relative to a constant time-effects model [i.e., intercept only, baseline hazard does not vary across time periods; Deviance = 239.30, degrees of freedom (d.f.) = 239].

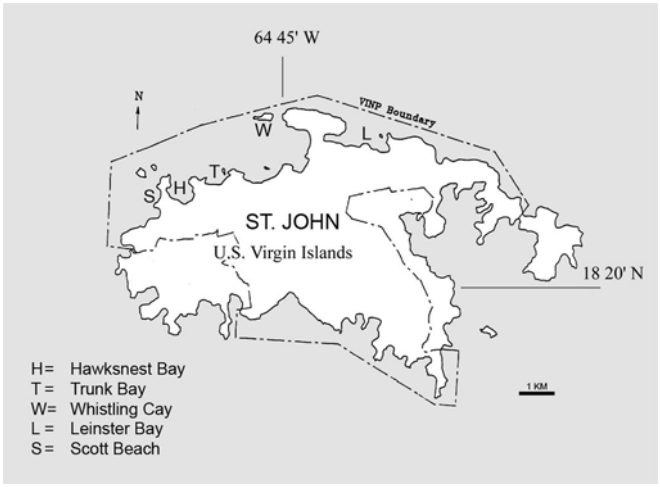
64 45' W
N
VINP Boundary
W
L
T
S
H
ST. JOHN
U.S. Virgin Islands
18 20' N
1 KM
H= Hawksnest Bay
T = Trunk Bay
W= Whistling Cay
L = Leinster Bay
S = Scott Beach

Figure 1


Figure 2

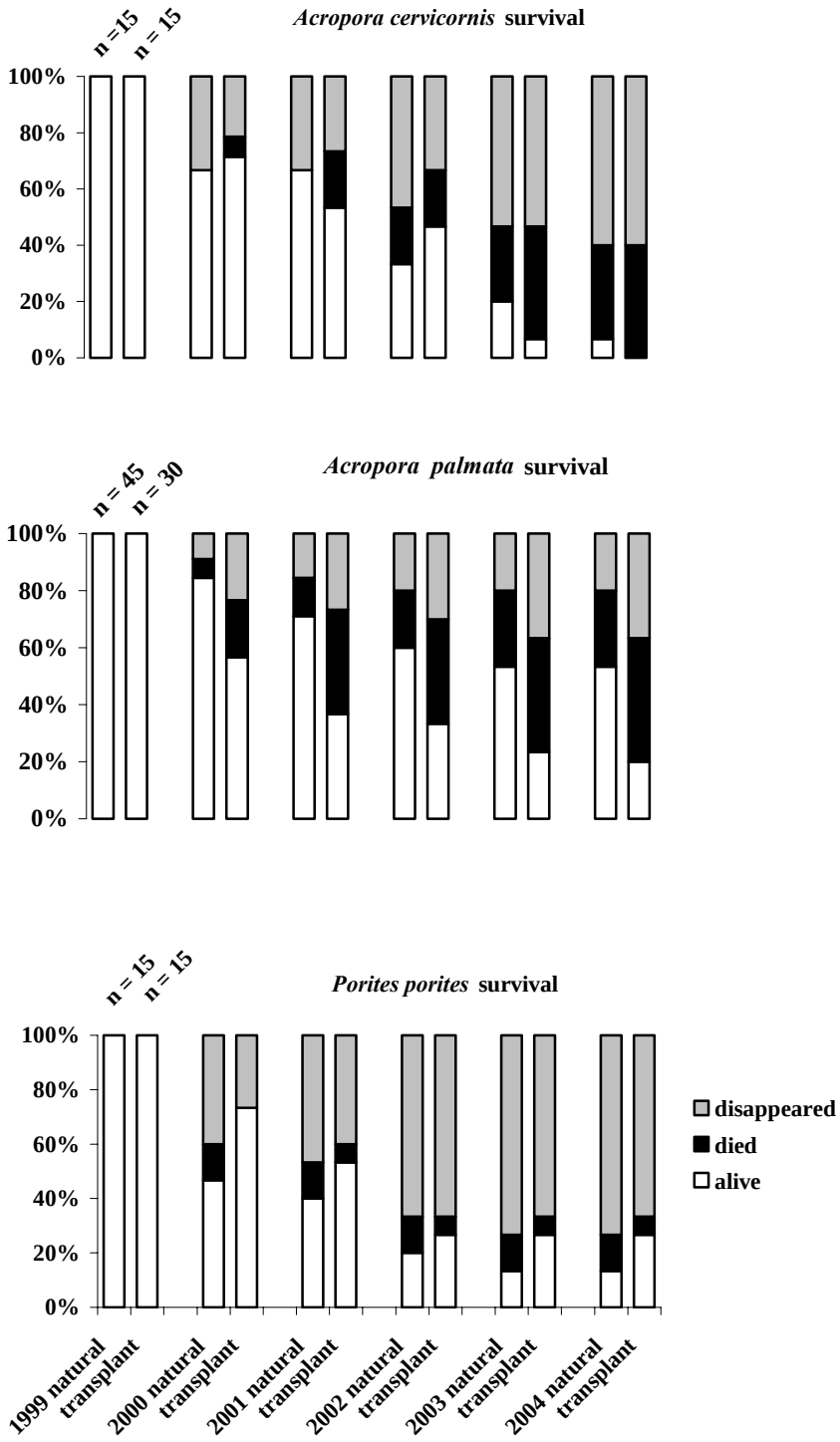
Acropora cervicornis survival
n = 15
n = 15
100%
80%
60%
40%
20%
0%
Acropora palmata survival
n = 45
n = 30
Porites porites survival
n = 15
n = 15
disappeared
died
alive
1999 natural transplant
2000 natural transplant
2001 natural transplant
2002 natural transplant
2003 natural transplant
2004 natural transplant

Figure 3

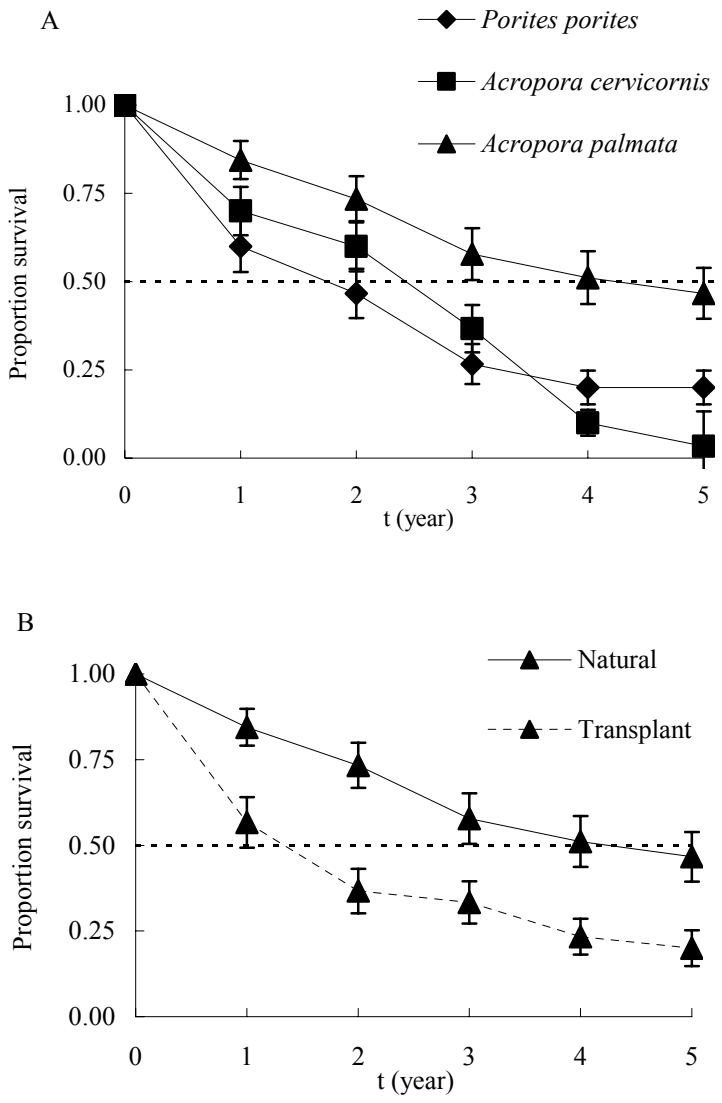
A
Porites porites
Acropora cervicornis
Acropora palmata
1.00
0.75
0.50
0.25
0.00
Proportion survival
0
1
2
3
4
5
t (year)
B
Natural
Transplant
1.00
0.75
0.50
0.25
0.00
Proportion survival
0
1
2
3
4
5
t (year)

Figure 4

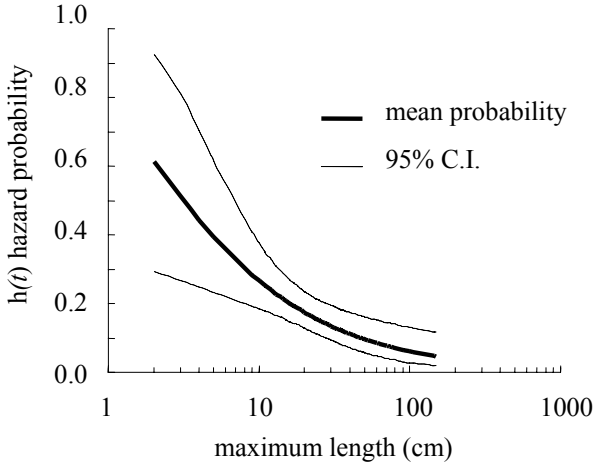
1.0
0.8
0.6
0.4
0.2
0.0
h(t) hazard probability
mean probability
95% C.I.
1
10
100
1000
maximum length (cm)

Figure 5