EFFECTS OF HURRICANES DAVID AND FREDERIC (1979) ON SHALLOW *ACROPORA PALMATA* REEF COMMUNITIES: ST. CROIX, U.S. VIRGIN ISLANDS

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ABSTRACT

Hurricanes David and Frederic caused substantial damage to shallow *Acropora palmata* reefs off St. Croix, U.S.V.I., in the fall of 1979. We labeled 100 storm-damaged *A. palmata* branches, both attached and detached, in each of two forereef areas off the north shore (Buck Island forereef and Tague Bay forereef). Eleven months after the storms, 66% of these branches at Buck Island and 35% at Tague Bay were still alive. The rest were dead and covered with algae. Many of the surviving branches had healed completely and had initiated new offshoot branches. Healing rates ranged from 0.01–0.05 cm/day and the average size of branches which healed was significantly smaller than branches which died.

In south shore areas where pre-hurricane data existed, the structural complexity of *A. palmata* stands was reduced by nearly one half by the storms, and some areas were virtually flattened. At north shore study sites, the mean number of fractured branches per m^2 decreased significantly with depth.

Broken stumps on upright colonies and fragments which fell to the base of the reef were colonized by over 30 species of algae and 61 species of sessile invertebrates, including three species of scleractinian corals (*Agaricia* sp., *Porites* sp., and *Favia* sp.).

The influence of hurricanes on coral reef community diversity (both evenness and species richness) is complex. Evenness can remain the same or decrease through fragmentation of *A. palmata* colonies as many fragments survive and start new colonies. However, destruction of rapidly growing branching corals can increase diversity by providing more light for slower-growing massive corals and by providing new substrate for the colonization of algae and invertebrates.

Biological and physical perturbations have dramatic effects on the diversity and organization of animal and plant communities (Paine, 1966; Dayton, 1971; Porter, 1972; Sammarco et al., 1974; Glynn, 1976). Hurricanes and tropical storms are significant perturbations which can affect coral reef communities through physical destruction of reef organisms (Glynn et al., 1964; Ball et al., 1967; Perkins and Enos, 1968; Shinn, 1976; Ogg and Koslow, 1978; Woodley et al., 1981), through increases in sedimentation and turbidity (Goreau, 1964; Banner, 1968), and through lowering of salinity and increasing of nutrient concentrations after heavy runoff (Goreau, 1964; Cooper, 1966; Banner, 1968; Johannes, 1972). Although turbid runoff following torrential rains can be devastating to coral reefs (Johannes, 1972), the direct physical effects from heavy swells and surge are often the most damaging (Stoddart, 1970).

The physical destruction of corals and other reef organisms can affect coral community structure in a variety of ways. The diversity (H'; Shannon and Weaver, 1949) of the system can change because of reduction in species richness with the elimination of certain species or because of shifts in relative abundances of organisms and concomitant changes in evenness (Pielou, 1966). The competitive interactions of coral reef organisms (Lang, 1973; Porter, 1974; Jackson and Buss, 1975; Buss and Jackson, 1979) can be altered through removal of the superior competitor or through alteration of the local environment. For example, destruction of a large branching colony could allow slower-growing head corals more light for growth (Wells, 1957; Lang, 1973). Destruction of branching species, such as *Acropora cervicornis* and *Acropora palmata*, will reduce the three-dimensional

Table 1. Characteristics of Hurricanes David and Frederic

	David	Frederic
Date	30 Aug 1979	4 Sept 1979
Distance and direction from St. Croix (km)	204 south	74 north
Wind velocity (km/h)	86	48–56 (gusts to 80)
Rainfall (mm)*	189	533
Wave height (m)	5.7	1.5–3.0

* Rainfall for David Aug. 30–Sept. 1 and for Frederic Sept. 3–Sept. 6.

structural complexity of the reef bottom and the amount of shelter for fish and other organisms. Fragmentation and overturning of corals will provide new surfaces for colonization by algae and invertebrates. Fragments often survive to start new coral colonies (Shinn, 1976; Highsmith et al., 1980).

Previous, largely observational, reports of storm damage to coral reefs show that the more fragile branching corals suffer the most damage (Glynn et al., 1964; Stoddart, 1974; Shinn, 1976; Woodley et al., 1981), but especially severe storms can remove all live coral from an area. For example, Stoddart (1974) stated that all live coral from British Honduras Reef was destroyed within 25 miles (40 km) of the path of Hurricane Hattie in 1961. Estimates of reef recovery after hurricanes range from a few years to several decades (Johannes, 1972). Recovery will be slower after especially severe storms and slower for coral communities comprised mostly of massive corals than for those dominated by faster-growing branching species (Shinn, 1976). A few authors refer to algae which colonize the new substrate (Stoddart, 1974; Ogg and Koslow, 1978) and to pioneer coral genera, such as *Agaricia, Porites,* and *Millepora* (Stoddart, 1974), but information on colonization after storms is sparse.

Between 30 August and 6 September 1979, Hurricanes David and Frederic swept by St. Croix, U.S. Virgin Islands, bringing winds up to 54 mph (86 kmh), estimated 19-ft (5.8-m) seas, and a total of over 28 km/h (722 mm) of rain, causing substantial damage to the reefs off the north and south shores of the island. Storm waves and surge shattered and overturned colonies of *Acropora palmata,* the dominant coral on St. Croix's shallow reefs, with the greatest damage sustained by the more exposed reefs off the south coast. Other hard corals received less damage, although colonies of *A. cervicornis* and the hydrozoan coral *Millepora complanata.* were fractured and several *Dendrogyra cylindrus* colonies toppled over.

The objectives of this study were to assess the storm damage to shallow St. Croix reefs, to document the recovery of *Acropora palmata,* to determine the colonization of organisms on freshly exposed coral skeletal surfaces, and to better understand the impact of storms on Caribbean reef community structure.

The Hurricanes

Hurricane David, the more intense of the two storms, passed 110 nautical miles (204 km) south of St. Croix on 30 August 1979, with winds gusting up to 54 mph (86 km/h) (Anon., 1980), rainfall of 7.5 in (189 mm), and estimated seas of up to 19 ft (5.8 m) (Table 1; Blanche, 1980). The rain diminished on 31 August with only a few scattered showers until 4 September when Hurricane Frederic passed about 74 km north of St. Croix in the early morning. Rain fell throughout the day and night, accompanied by sustained winds of 30–35 mph (48–56 km/h) gusting up to 40–50 mph (64–80 km/h) and seas of about 5–10 ft (1.5–3.0 m) (Table 1). A

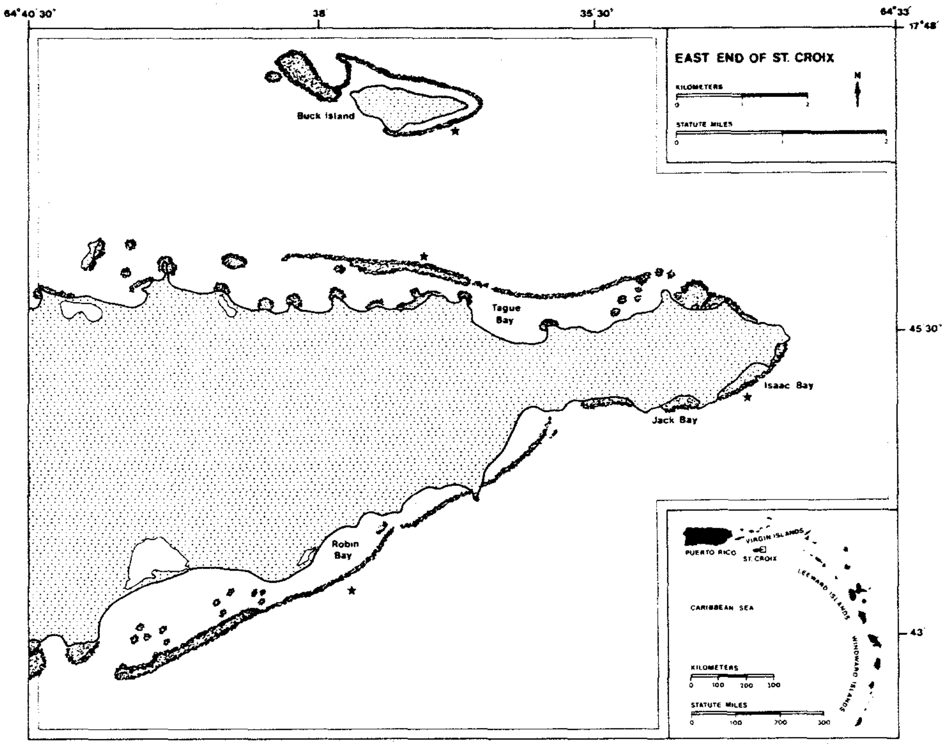


Figure 1. Location of study sites. Stars designate forereef study areas.

total of 28.4 in (722 mm) of rain fell between 29 August and 6 September (West Indies Laboratory rainfall records). By the afternoon of 4 September, brown, silt-laden water extended out towards Tague Bay Reef (Fig. 1). The following day, the sea was calmer and the winds had subsided. Brown water at that time extended out to the forereef. The turbid water cleared up within 2–3 days.

A National Disaster Survey Report (Anon., 1980) described David as a very severe and intense hurricane with record-breaking winds only in the immediate vicinity of the eye. Frederic was a less intense and less organized storm without a well-defined center. The main threat from David came from heavy seas and intense winds. The winds associated with Frederic were lighter but the heavy rainfall, up to 18 in (457 mm) in one 24-h period, caused extensive flooding. St. Croix is a low, dry island with no permanent rivers, and runoff was not as severe as it would have been for reefs near elevated land masses or major rivers. The destruction was from heavy swells and surge.

Study Sites

Because only minimal damage occurred in backreef areas, all our research focused on forereef areas. Most of our work took place on the forereefs of Buck Island and Tague Bay (Fig. 1). Robin and Isaac Bay reefs on the south shore (Fig. 1) were also observed, and quantitative data on storm damage were collected from Robin Bay.

The forereef site at Buck Island is on the southeastern side of the bank barrier reef described by Gladfelter et al. (1977) and faces south into Buck Island Channel (about 15 m deep) with a steep slope of about 50°. The reef crest is dominated by *Millepora complanata* in the shallowest water and by *Acropora palmata* at depths of 1–5 m.

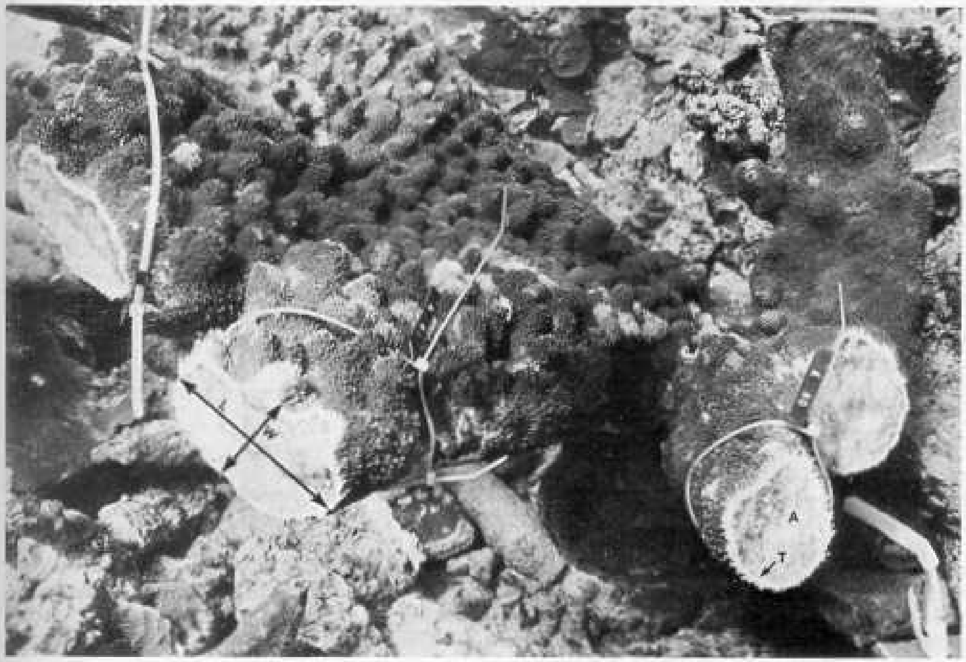


Figure 2. Storm-damaged branches of *A. palmata*. Note white peripheral band of exposed coral tissue and skeleton (T) surrounding algae (A) which have colonized fracture areas. Length (L) and width (W) dimensions used for approximate area calculations.

Tague Bay forereef faces north into Buck Island Channel with a slightly more gentle slope (30–40°). The reef crest is a mixture of *A. palmata* and *M. complanata* but again the region from 1–5-m depth is dominated by *A. palmata*.

Our Robin Bay study site on the south shore was seaward of a reef-crest dominated by *A. palmata* and east of an algal ridge comprised mostly of *Lithophyllum congestum* (Adey, 1975). Here the reef bottom is on a very gently sloping (about 5°) shelf about 3–5 m deep. Isaac Bay, near the extreme eastern tip of St. Croix, also has some algal ridge development. However, *A. palmata* dominates on the reef crest and seaward to depths of about 10 m (Adey, 1975).

METHODS

Quantification of Damage

To assess hurricane damage in these reef areas we used two approaches: (1) an analysis of *A. palmata* fragments within quadrats placed at different depths and (2) coral transects. Quadrat data provided information on size and number of fragments and total area of new substrate produced by shearing of *A. palmata* colonies. Coral transects documented relative abundances of different reef organisms and gave estimates of structural complexity.

The number of broken pieces of *A. palmata* in haphazardly placed m^2 quadrats was recorded at Robin Bay, Tague Bay, and Buck Island. Quadrats at Tague Bay and Buck Island were placed at depths from 2 to 20 feet (0.6–6.1 m). All measurements from Robin Bay forereef were from 12 feet (3.7 m). The dimensions of all fracture areas within each quadrat were calculated for Tague Bay. Because most fracture areas were elliptical, length and width measurements were used to calculate areas based on the area of an ellipse (A = length × width × 0.7854). The elliptical calculations of skeletal areas, though approximate, allowed in situ measurements and were sufficiently accurate to allow comparison of sheared areas from different depths. Total area of freshly exposed coral skeleton was calculated for each m^2 over the depth range of the forereef slopes at Buck Island and Tague Bay. The lengths of 72 broken *A. palmata* branches were measured at Tague Bay and 84 at Robin Bay.

Five 10-m coral transects were examined on the forereefs of Tague Bay and Robin Bay using a modification of methods used by Loya and Slobodkin (1971), Loya (1972), and Porter (1972). Adey

Table 2. Measurement and observation periods

Tague Bay Reef		Buck Island Reef	
Date	Weeks After Hurricanes	Date	Weeks After Hurricanes
9/25/79	3	10/17/79	6
10/12/79	6	10/31/79	9
10/26/79	8	11/21/79	12
11/10/79	10	12/12/79	15
11/26–12/2/79	12–13	01/23/80	21
01/25/80	21	03/13/80	28
03/13/80	28	05/9/80*	36
05/9/80*	36	07/15/80*	46
07/15/80*	46	07/23/80*	47
07/23/80*	47		

* Observations only.

et al. (1979) used this method in a 1978 study of Robin Bay, allowing a comparison between Robin Bay transects before and after the hurricanes. Unfortunately, there were no prior transect data for the Tague Bay reef.

Along each transect, a diver extended a 10-m line along the reef bottom. The diver then extended a chain below this line, carefully following the three-dimensional contours of the reef. The number of chain links which fell on living and dead coral or sand, and other reef components, were recorded. The ratio of the number of meters of chain to the number of meters of line gave an index of reef topography or structural complexity. A comparison of this index before and after the hurricanes allowed an evaluation of structural changes.

Recovery of *Acropora palmata*

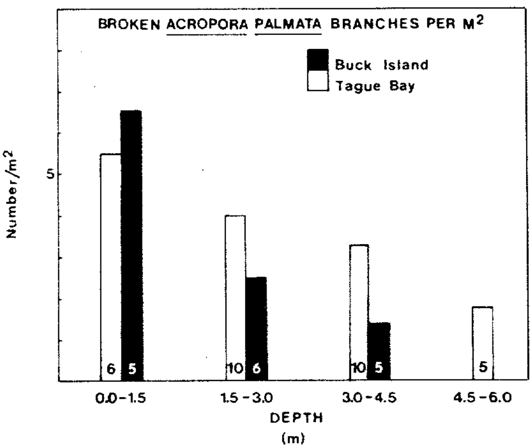
One week after the hurricanes, we observed *Acropora palmata* colonies at Tague Bay which were overturned and shattered. Algae were already growing on the skeletal areas exposed by fracturing except around the periphery of the fracture where there was a thin white band (ave. width = 0.4 cm) comprised of calcium carbonate interspersed with a network of living coral tissue (Fig. 2). Damaged branches recover when the peripheral coral encroaches upon the algae growing on the exposed skeleton, progressively reducing the area occupied by algae and finally fusing completely.

To study the recovery of *A. palmata* at both Tague Bay and Buck Island we secured numbered plastic electrical ties to 100 branches at depths of 5.5 m or less. We marked completely detached branches as well as stumps of branches which remained on parent colonies. All labeled branches had been sheared by storm waves or from impact with other broken branches. In a few cases, large colonies of *A. palmata* apparently broke at their bases and fell over, causing fracturing of distal branches.

Using SCUBA, we measured the length and width of the entire fracture area and the area covered

Table 3. Mean number of broken *Acropora palmata* branches and branch fracture areas at Tague Bay forereef, Buck Island forereef, and Robin Bay forereef

	Depth (m)	No. of Quadrats	No. of Branches	Broken Branches/m²		Fracture Area of each Branch (cm²)		Total Fracture Area (cm²/m²)
				$\bar{x}$	SD	$\bar{x}$	SD	
Tague Bay forereef	0.0–1.5	6	33	5.5	1.5	12.6	16.0	69.3
	1.5–3.0	10	40	4.0	2.6	27.5	21.9	110.0
	3.0–4.5	10	33	3.3	1.5	40.1	29.0	132.3
	4.5–6.0	5	9	1.8	1.3	32.8	26.5	59.0
Buck Island forereef	0.0–1.5	5	33	6.6	3.0			
	1.5–3.0	6	15	2.5	2.1			
	3.0–4.5	5	7	1.4	1.5			
Robin Bay forereef	3.7	10	59	5.9	2.7			



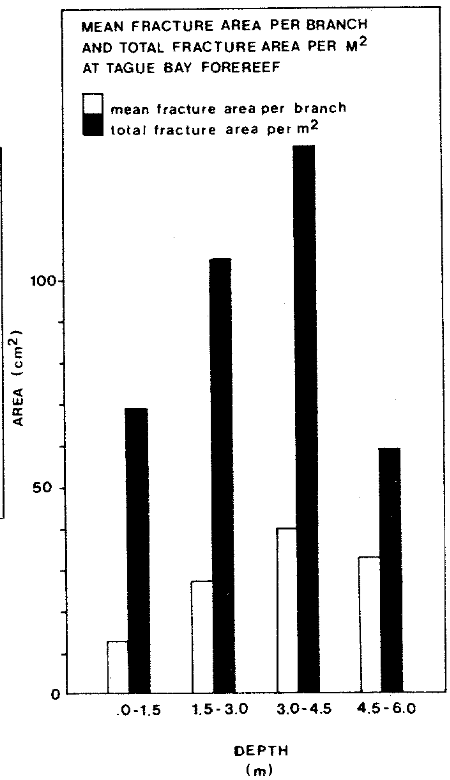


Figure 3. (Left) Mean number of fractured branches/m² at Tague Bay and Buck Island forereefs. Numbers within bars represent number of m² quadrats.

Figure 4. (Right) Mean fracture area per branch and total fracture area per m² at Tague Bay forereef.

by algae for each numbered branch with a flexible plastic ruler (estimated accuracy = ±1 mm). By measuring the algal area over time, we were able to determine if the coral was healing or if the algae were overgrowing the coral at the edges of the fracture areas. Measurement and observation periods appear in Table 2. The daily rate of coral or algal growth for each branch was calculated by averaging the difference between two sets of successive measurements.

Colonization of *Acropora palmata*

Both detached and attached branches of *A. palmata* were collected from Tague Bay forereef in September, October, November 1979 and January 1980 and from Buck Island forereef in November 1979 and January 1980. Branches were also collected from Robin Bay in October 1979 and February 1980. The algae colonizing the fracture areas were identified.

At Tague Bay, 25 detached, live fragments of *A. palmata* were labeled. Three of these branches were placed on top of intact *Acropora* colonies. The other branches were left on the reef bottom. After 13 months, eight of these branches were collected and all sessile invertebrates were identified as specifically as possible.

Results

Quantification of Damage

Destruction was greatest on the south shore reefs. Some south shore forereefs were virtually flattened, and piles of fresh coral rubble were everywhere. Buck Island and Tague Bay forereefs sustained heavy damage but the damage was patchy.

Table 4. Structural complexity and percent live coral for Robin Bay and Tague Bay forereef transects

Reef	Date	No. m	% Live *A. palmata*	% Live Other Coral Species	Structural Index
Robin Bay (before storms)	May 78	13	16	11	2.4
Robin Bay (after storms)	Nov 79	10	13	1	1.5
		10	16	8	1.3
		10	18	1	1.4
		10	18	1	1.4
		10	16	8	1.4
	Average =		16	4	1.4
Tague Bay	Nov 79	10	25	9	2.8
		10	16	17	2.7
		10	45	12	2.8
		10	21	8	3.2
		10	25	3	1.8
	Average =		26	10	2.7

At both Buck Island and Tague Bay, the mean number of fractured *A. palmata* branches/m^2 decreased with depth (Fig. 3, Table 3). The mean number of breaks/m^2 was significantly greater in the shallower water (0 to 1.5 m) at Buck Island and at Tague Bay (ANOVA, $P < 0.05$).

The mean total fracture area is the sum of the fracture areas of individual branches. The mean fracture area/m^2 was smallest near the surface (0–1.5 m) at Tague Bay and greatest between 3–4.5 m at Tague Bay forereef (Table 3, Fig. 4).

Measurement of the overall lengths of detached, living branches of *A. palmata* at Robin Bay and Tague Bay forereefs showed that the Robin Bay branches were significantly shorter than those in Tague Bay (ANOVA, $P < 0.05$). Mean length of Robin Bay branches was 28.8 ± 16.7 cm and Tague Bay branches 58.6 ± 28.7 cm.

As expected, the structural complexity of the Robin Bay reef decreased as a result of the hurricanes (Table 4). However, the percent of live *A. palmata* in November 1979 was the same as before the hurricanes because the broken branches were still alive. The percent of live coral of other species decreased slightly, but sample sizes were too small to evaluate the significance of this decrease. Although the data are limited, the similarity of the structural complexity indices for the five Robin Bay transects after the storms reflects the uniformity of the physical destruction on this reef, while the spatial indices for the Tague Bay transects reflect the patchiness of the damage there (Table 4). At Tague Bay, piles of fresh coral rubble were scattered among large colonies of *A. palmata* which escaped damage whereas at Robin Bay there were far fewer intact colonies, and rubble littered the bottom. The transect method is useful in assessing structural damage to coral reefs particularly when branching corals like *A. palmata*, which contribute substantially to the topographical relief of the reef, are abundant.

Recovery of *Acropora palmata*

Tague Bay corals grew faster during the first measurement period (4–6 weeks after the hurricanes) than during subsequent time intervals (ANOVA, $P < 0.05$), and these intital rates were greater than initial rates at Buck Island (7–9 weeks after the hurricanes). The branches healed at rates of 0.01 to 0.05 cm/day (Fig. 5).

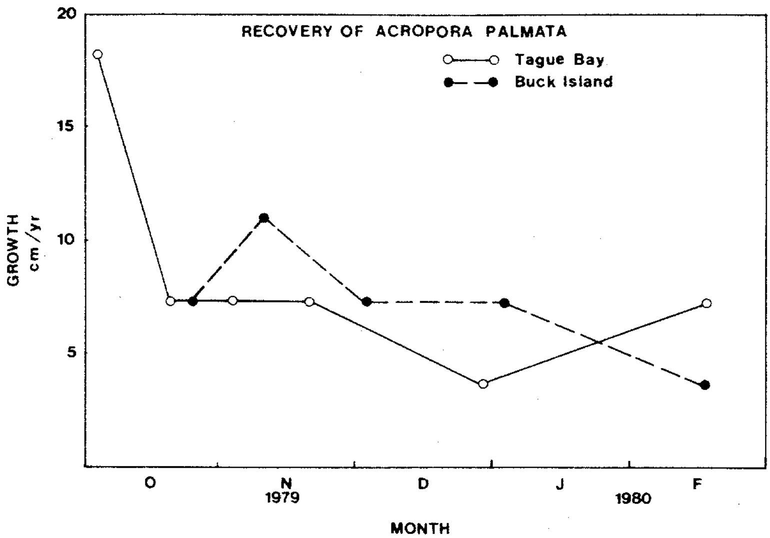


Figure 5. Growth rates of healing *A. palmata* branches at Buck Island and Tague Bay forereefs.

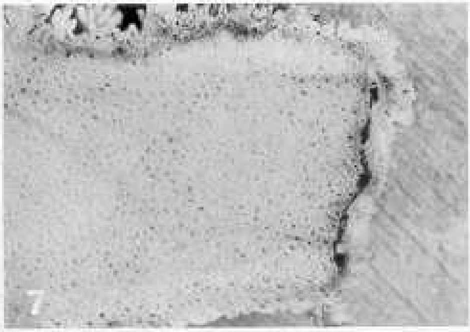
Figures 2 and 6 show the healing sequence for a branch of *Acropora palmata*. After fracturing, there is a thin white peripheral band of coral skeleton interspersed with a network of live coral tissue. Gradually, calcium carbonate is deposited and corallites form towards the center of the fracture area overtopping the algae. Eventually, the live coral merges and heals over the algae. Cutting of a longitudinal section of a completely healed branch of *A. palmata* revealed that the coral grows directly over the algae rather than displacing it along the growing edge. A remnant dark algal band remains directly under the new coral growth (Fig. 7).

In March 1980, almost 7 months after the hurricanes, small branches up to 2 cm long were growing from the completely healed fracture areas (Fig. 8) of two branches at Tague Bay and three at Buck Island. By July, many more branches had these new offshoots, and some damaged colonies showed lateral branching unassociated with fracture areas.

Small crabs (*Domecia* sp.) were found within the new offshoot branches on 1% of the marked Tague Bay branches and 6% of the Buck Island branches. These crabs were always associated with the new offshoot branches and were not found on dead or dying branches. Coral branches which did not heal became covered with algae. Threespot damselfish (*Eupomacentrus planifrons*) set up territories which included many of these algal-covered branches (Williams, 1980; Fig. 9).

The condition of storm-damaged branches 7 and 11 months after the hurricanes is summarized in Table 5. In March, only 3% of the labeled branches at Buck Island and 2% of those at Tague Bay had healed and had small offshoot branches (Fig. 8), whereas eleven months after the hurricanes, in July, 33% of the branches at Buck Island and 17% of the branches at Tague Bay exhibited this growth pattern. In March, 30% of the labeled branches at Buck Island and 43% of those at Tague Bay had died whereas 4 months later, 34% and 65% had died, respectively. Pooling the results for both study sites in July yields a 50/50 ratio of live to dead coral.

At both Buck Island and Tague Bay, branches which healed were smaller in cross-sectional area (averages = 12.7, 9.9 cm^2) than branches which died (aver-



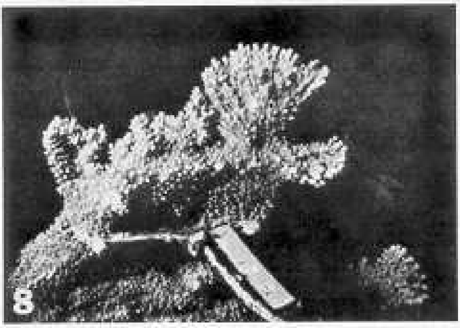


Figure 6. Healing of fractured *A. palmata* branch through growth of coral skeleton and tissue.

Figure 7. Residual algal band revealed after sectioning through completely healed *A. palmata* branch.

Figure 8. Offshoot branches arising from healed area on *A. palmata* branch.

Figure 9. Threespot damselfish near algal-covered *A. palmata* branch.

ages = 23.4, 31.5 cm) (ANOVA, $P < 0.05$). Larger branches did not just take longer to heal because of their size; they did not recover as effectively.

Growth rates during the time interval in which healing (fusion of coral over the algae) occurred were significantly higher than any other growth rates within fracture areas (ANOVA, $P < 0.05$). These rates are minimum growth rates because it was impossible to determine when fusion took place during the preceding interval.

Colonization of *Acropora palmata*

Over 20 species of red algae (Rhodophycophyta), 5 species of brown algae (Phaeophycophyta), 3 species of green algae (Chlorophycophyta), and 2 species

Table 5. Condition of damaged *A. palmata* branches 7 and 11 months after the hurricanes

	Total No. of Branches		% Healed Completely		% Healed With New Branches		% Healing		% Partly Healed Partly Dead		% Dead	
	Mar	Jul	Mar	Jul	Mar	Jul	Mar	Jul	Mar	Jul	Mar	Jul
Buck Island	86	88	31	22	3	33	35	5	—	6	30	34
Tague Bay	86	85	21	7	2	17	34	9	—	2	43	65
Average	—	—	26	15	3	25	35	7	—	4	37	50

Table 6. Algae growing on storm-damaged branches of *Acropora palmata* from Tague Bay forereef, Buck Island forereef, and Robin Bay forereef (S = September 1979; O = October 1979; N = November 1979; J = January 1980; F = February 1980)

	Tague Forereef	Buck Is. Forereef	Robin Forereef
Rhodophycophyta			
Acrochaetium sp.	S, N	N	
Liagora mucosa			O
Gelidium pusillum	N	N, J	F
Peyssonnelia sp.		J	
Jania		F	
Coelothrix irregularis	O		O
Antithamnion sp.	S, O		O
Griffithsia sp.			O
Spermothamnion sp.	O		
Ceramium sp.	O		O, F
Ceramium byssoideum	O	N	
Ceramium leptozonum	S		
Ceramium leutzelburgii			F
Ceramiella jolyi	O, N	J	O
Centroceras clavulatum	O	N, J	O
Taenioma nanum	S, O, N	N, J	O
Caloglossa leprieurii		J	
Polysiphonia sp.	O, N	N, J	O, F
Polysiphonia subtilissima	S		
Herposiphonia sp.	N	J	
Lophosiphonia cristata			O
Laurencia sp.			O
crustose corallines	S, O, N	N, J	O, F
Phaeophycophyta			
Giffordia sp.	O	J	
Giffordia duchassaigniana	S, O, N		
Giffordia rallsiae			O
Sphacelaria sp.	O		N, F
Sphacelaria nova-hollandiae		J	
Sphacelaria tribuloides		J	
Lobophora variegata		J	F
Chlorophycophyta			
Enteromorpha sp.	S, O	N	
Cladophora sp.	S, O, N	N	O
Derbesia sp.	S, O	J	
Cyanophycophyta			
Oscillatoria sp.	S, O	J	O
Calothrix sp.	S, N	J	

of bluegreen algae (Cyanophycophyta) colonized the storm-damaged branches of *A. palmata* from the Buck Island, Tague Bay, and Robin Bay forereefs (Table 6). One month after the storms, we observed a bloom of the red alga *Liagora mucosa*. Five months later, *Dictyopteris delicatula* grew abundantly in this area and *Liagora* was not observed. The most conspicuous algae from all three study areas were the filamentous reds, particularly *Polysiphonia* spp. and *Taenioma nanum*.

All but 3 of the 25 detached fragments of *A. palmata* from the Tague Bay forereef colonization study were dead 13 months after the storms. The 3 branches which had been placed on top of live *A. palmata* colonies had fused to the underlying coral tissue and skeleton.

Eight of the 25 labeled fragments were examined carefully 13 months after the storms for colonizing sessile invertebrates to a lower size limit of 1 mm. Taxa of sessile fauna ranged from 6 to 31 per side for any one coral fragment with a total of 61 taxa for all eight fragments (Table 7). Seven of the fragments had a higher number of taxa (including scleractinian corals) on the bottom sides than on the tops (ANOVA, $P < 0.05$). The bottom of fragment #5 (Table 7) had become embedded in sediment which prevented further colonization. The fauna which dominated these fragments were foraminifera, sponges, polychaetes, tunicates, and bryozoans with fewer hydroids, corals, and other cnidaria.

Agaricia sp. comprised 84% of the settled scleractinian colonies, *Porites* sp. 12%, and *Favia* sp. about 4%, similar to the findings of Bak and Engel (1979) in a shallow reef zone at Curaçao. The largest proportion of *Agaricia* sp. colonies (29%) were 2 mm in size and about 13% were only 1 mm across (Fig. 10). Assuming the growth rates for all settled coral colonies were approximately the same, the minimum linear growth rate for these juvenile corals would be about 1 mm per month but is likely two to three times that fast (Lewis et al., 1968; Bak, 1976).

Discussion

The destruction from Hurricanes David and Frederic was far more widespread and uniform on the south shore at Robin Bay and Isaac Bay reefs than at either Buck Island or Tague Bay reefs on the north shore. The south shore reefs were exposed to the more destructive forces of Hurricane David which passed south of St. Croix. The significantly shorter lengths of branches at Robin Bay is indicative of greater fracturing of *A. palmata* than on north shore reefs. Our coral transect data also suggest lower structural complexity at Robin Bay than at Tague Bay following the storms.

At Tague Bay, cross-sectional areas of the fractures tended to be smallest in shallow water because *A. palmata* branches broke off closer to their distal ends. In slightly deeper water, the branches tended to break near their bases where cross-sectional areas were larger. The number of broken branches per m^2 decreased with depth at both Tague Bay and Buck Island, but it would be incorrect to assume that the greatest overall damage occurred in the shallowest zones. Deeper branches which break at their bases leave larger surfaces for healing and for recolonization and indicate that more of the colony was lost than in the case of smaller more numerous branch fractures at the distal ends. Less overall damage (mean total fracture area in cm^2/m^2) in the shallowest zone at Tague Bay may reflect a buffering action of this zone by the deeper forereef corals which bore the brunt of the waves. The Buck Island forereef slope is steeper and narrower than the Tague Bay forereef slope. Destruction along the Tague Bay and Buck Island forereefs was patchy probably because some of the branches which broke in the deeper areas were transported into shallower water where they collided with other colonies.

With the exception of the initial recovery rates at Tague Bay (0.05 cm/day = 18 cm/yr), growth rates for Buck Island and Tague Bay ranging from 4 to 11 cm/yr were very similar to the linear growth rates reported by Gladfelter et al. (1978) for *Acropora palmata* colonies in the shallower forereef zone near our study site at Buck Island. Bak (1976) found a linear growth rate of about 8 cm/yr for *A. palmata* in Curaçao.

The faster initial growth rates were not observed at Buck Island possibly be-

Table 7. Area and number of invertebrate taxa colonizing the top and bottom coral fragments collected from Tague Bay forereef one year after the hurricanes

Fragment #	1	2	3	4	5	6	7	8	
Area of one side (cm^2)	183 top/bot	180 top/bot	152 top/bot	182 top/bot	108 top/bot	160 top/bot	212 top/bot	282 top/bot	Mean ± S.E.
Foraminifera	1/1	1/1	1/1	0/2	3/1	1/2	2/3	2/3	1.4 ± 0.9/1.8 ± 0.9
Porifera									
Demospongiae	6/7	2/3	1/3	4/4	0/1	1/5	0/6	1/4	1.9 ± 2.1/4.1 ± 1.9
Chordata									
Ascidiacea	1/4	2/2	0/2	0/2	1/1	2/8	0/6	2/3	1.0 ± 0.9/3.5 ± 2.4
Bryozoa									
Gymnolaemata	2/4	1/2	1/1	5/2	0/0	1/7	0/4	2/3	1.5 ± 1.6/2.9 ± 2.2
Annelida									
Polychaeta	3/4	4/4	2/4	5/4	3/3	2/5	2/5	3/4	3.0 ± 1.1/4.1 ± 0.6
Cnidaria									
Hydrozoa	0/2	0/0	1/2	0/1	1/0	0/1	0/2	1/2	0.4 ± 0.5/1.3 ± 0.9
Anthozoa	1/1	3/3	1/2	2/2	0/0	1/3	2/3	2/2	1.5 ± 0.9/2.0 ± 1.1
Mollusca									
Bivalvia	0/0	0/0	0/0	0/0	1/0	0/0	0/0	0/0	0.1 ± 0.4/0.0 ± 0.0
Total each side	14/23	13/15	7/15	16/17	9/6	8/31	6/29	13/21	10.8 ± 3.7/19.6 ± 8.2
Total both sides	33	19	16	28	13	33	30	24	24.5 ± 7.8
No. coral colonies	6/8	8/7	7/16	11/12	0/0	2/23	7/24	11/14	6.5 ± 3.9/13.0 ± 8.1
Coral density/m^2	327/437	444/383	460/1,053	604/660	0/0	125/1,438	330/1,132	390/426	335.0 ± 192.5/691.1 ± 476.8

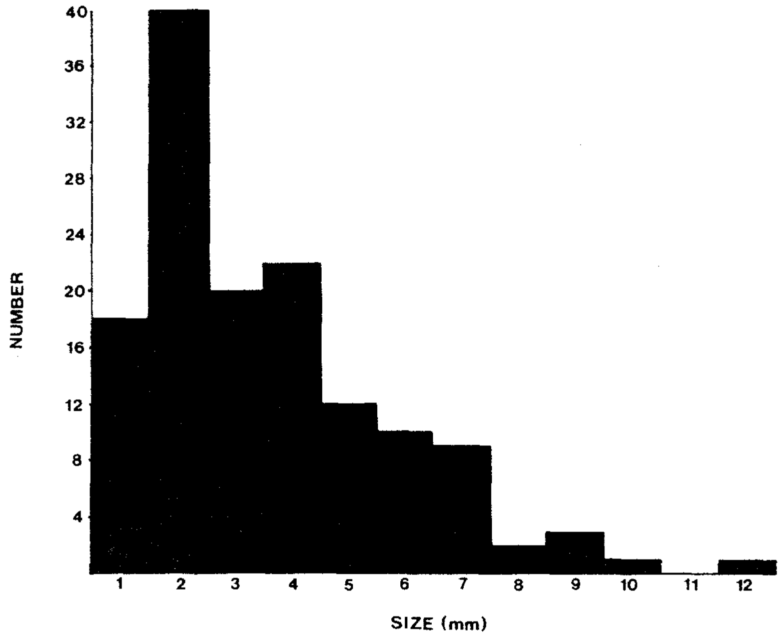


Figure 10. Size-frequency distribution of *Agaricia* colonies on *A. palmata* fragments 13 months after the hurricanes.

cause we did not begin measurements until three weeks later than at Tague Bay. Initially, coral healing may be faster because algal species are not well established yet. Possibly there is an edge effect in which coral tissue closer to the living periphery of the fracture area has a faster rate of growth.

Smaller branches tend to heal while larger branches tend to die. Larger cross-sectional areas are associated with the bases of branches while small areas correspond to branch tips. Goreau (1959) showed that calcification rates in a similar Pacific species, *Acropora conferta,* was highest near the branch tips and progressively decreased towards the base of the branch, suggesting that the slower growth or lack of growth of larger broken areas may simply reflect the slower growth rates associated with basal branch areas. Goreau (1959) found growth was 4–8 times faster at branch apices than in lateral and basal regions.

There has been considerable speculation about the influence of disturbance (either biological or physical) on ecosystem diversity. Paine (1966) stated that biological disturbance imposed by starfish predation maintained a high diversity of primary space occupiers in the temperate rocky intertidal zone. Lubchenco (1978) has shown that with very low disturbance levels (i.e., minimal or no grazing pressure by herbivores), or with high disturbance levels (i.e., intense grazing) the diversity of benthic algae is low. With intermediate disturbance, algal diversity is highest. In his discussion of diversity in rain forests and coral reefs, Connell (1978) applied these concepts to tropical systems. He noted that hurricane destruction of the reef crest and outer slopes at Heron Island (an intermediate disturbance) led to recolonization by several coral species and a higher diversity. Also, Grigg and Maragos (1974) found that the diversity of species colonizing lava flows in Hawaii was higher in more exposed areas.

The effects of hurricanes on coral reef diversity are complex and sometimes contradictory. Although disturbances of intermediate magnitude exert considerable control over species diversity in some areas (Connell, 1978), the pattern of high diversity following intermediate disturbance does not appear to apply to scleractinian coral diversity in the very shallow St. Croix reef zones dominated by *Acropora palmata*. These reef zones are disturbed the most by storms but have the lowest coral diversity. The highest coral diversity on St. Croix reefs occurs at moderate depths where no single species seems adapted to competitive exclusion of the others.

In the deepest reef zones, particularly the nearly vertical walls off the north shore of St. Croix, plate-forming corals, such as *Agaricia agaricites, Agaricia lamarcki,* and *Montastrea annularis,* dominate. The pattern is one of low coral diversity at the shallowest and deepest depths with high diversity at moderate depths. Only the most intense storms would significantly affect coral zones at great depths.

The dominance of *Acropora palmata* in shallow Caribbean waters is partly a function of its remarkable adaptations to physical stress. When overturned, colonies of *A. palmata* can reorient their growth, turning their branch tips towards the light. About 50% of all damaged branches from Buck Island and Tague Bay healed within one year of the hurricanes. Highsmith et al. (1980) found 46% survival of detached *A. palmata* branches after a hurricane on the Belize Barrier reef. Six months after Hurricane Edith devastated up to 100% of the *A. palmata* in some forereef areas in Puerto Rico, Glynn et al. (1964) observed several storm-damaged colonies which were flourishing. Not only did *A. palmata* branches at Buck Island and Tague Bay heal completely but new branches arose from the healed areas. In spite of the continuous surge in these shallow reef zones which rocks detached coral fragments back and forth, several fragments fused to the hard pavement and continued to live. Limited data from Robin Bay one month after the storms suggested no decrease in the amount of live *A. palmata* (although many of these live fragments undoubtedly died later). Fragmentation of *A. palmata* colonies can actually increase or maintain the dominance of this species by starting new colonies.

In contrast, moderate destruction of rapidly growing branching corals by major storms can increase reef community diversity primarily in two ways. The elimination of branching corals can result in an increase in the amount of light reaching the slower growing head corals. Wells (1957) and Lang (1973) note that ramose corals, because of their rapid growth rates, can displace corals with more massive growth forms. The structural complexity index for Robin Bay (the most affected region in our study) was reduced from 2.4 (pre hurricane condition) in May 1978 to 1.4 (post-hurricane condition) in November 1979 (Table 4).

In addition, the fragmentation of *A. palmata* branches provides new substrates for algae (Table 6) and invertebrates (Table 7). Over 30 algal species and 61 invertebrate taxa colonized storm-damaged fragments. Although we do not know what the small-scale diversity was prior to the hurricanes and not all colonizing organisms will survive to maturity, the storms did create a substantial amount of new substrate for colonization.

Hurricanes that make direct landfalls on St. Croix are infrequent but many pass through the Caribbean bringing swells and waves capable of fracturing *A. palmata* colonies. Between 1900 and 1977 there were 24 hurricanes which passed within 50 miles (80 km) of the Virgin Islands (U.S. Army, 1975). The most severe hurricanes occurred in 1916, 1924, 1928, and 1932 (Island Resources Foundation, 1977). These major storms and the more frequent minor storms which cause localized damage result in a mosaic of large, scattered *A. palmata* colonies interspersed with smaller ones on St. Croix's shallow reefs.

The type, intensity, and duration of a stress or disturbance influence the impact it will have on a coral reef and the subsequent rate of recovery. Lugo (1978) states that stresses, such as physical damage from hurricanes, which remove structure but do not drastically alter the primary productivity of the system may not have as much impact as a stress such as increased turbidity which reduces the ability of the system to photosynthesize and to replenish energy stores. Following a decrease in coral biomass as a result of physical forces, primary productivity would not necessarily decrease and in fact could increase because of the higher rates of productivity associated with algae colonizing the new substrate (Rogers and Salesky, 1981). Reefs are adapted to natural catastrophes but susceptible to "unnatural" stresses, such as excessive sedimentation from dredging, sewage, and oil pollution (Johannes, 1972).

In conclusion, Hurricanes David and Frederic did not alter the overall functioning of the St. Croix reefs although damage to branching forms in shallow water was substantial. Greatest impact was noted on south shore reefs where structural complexity was substantially reduced by Hurricane David. One year after the storms, about 50% of the experimental branches at Buck Island and Tague Bay had healed completely and many of these had initiated new growing tips. Some detached fragments fused to the substrate and are still alive. Others fell into the interstices of the reef and have been colonized by a myriad of algae and invertebrates.

Physical disturbance on the reefs of St. Croix by major storms can both increase and decrease coral reef community diversity. A decrease in diversity can occur because of the elimination of various coral species or because of initiation of new colonies of the already dominant species after dispersal of fragments. On the other hand, diversity can increase because head corals can survive after removal of overshadowing, branching species and because of the colonization of new substrates by a wide variety of reef organisms.

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