HURRICANE HUGO'S IMPACT ON SALT RIVER SUBMARINE CANYON, ST. CROIX, U. S. VIRGIN ISLANDS

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ABSTRACT

This study examined the effects of Hurricane Hugo (1989) on the biota of Salt River Canyon, St. Croix. Although fish assemblages were not drastically altered, there were some changes in species composition after Hurricane Hugo. These differences were related primarily to changes in sedimentary distribution during the storm. An order of magnitude decline in the abundance of echinoderms was also apparently related to sediment movement. Videotaped transects showed a decline in coral cover after the storm at six depths between 8 and 33 m. The greatest effect on a coral species population occurred at greater depths, where the fragile, foliaceous *Agaricia lamarcki* experienced considerable damage from strong oscillatory flows during Hurricane Hugo. It appears that the observed, hurricane-induced changes in fish, coral, and echinoderm assemblages can be directly related to physical processes.

INTRODUCTION

Large-scale disturbances provide opportunities to observe community responses over a range of habitats at multiple sites. Despite their fortuitous nature and inherent statistical difficulties, the generalizations derived from 'natural experiments' can be more robust than conclusions based on smaller-scale field and laboratory experiments (Diamond, 1986). Hurricanes have aroused considerable interest among coral reef ecologists since Connell (1978) suggested their role in maintaining the diversity of sessile reef biotas. That role, and the importance of other natural and anthropogenic perturbations, remain controversial (Jackson, 1991). How important hurricanes are to the balance between corals and benthic macroalgae, how hurricanes interact with mass mortalities of the sea urchin *Diadema antillarum*, and how these processes will affect community dynamics over the next several decades are pivotal questions in the ecology of Caribbean coral reefs (Hughes, 1989; Knowlton, in press).

In 1980, Hurricane Allen devastated the reef at Discovery Bay, Jamaica (Woodley et al., 1981). Eight years later, Hurricane Gilbert reset fore reef communities there to the conditions that prevailed immediately after Allen. Long-term studies at Discovery Bay and nearby sites (Knowlton et al., 1990; Hughes et al., 1987; Liddell and Ohlhorst, 1987; Precht, in press) have enhanced our knowledge of hurricane effects. However, the pre-Allen ecology of these Jamaican reefs may have been atypical. Hurricanes pass close to the north coast of Jamaica more frequently than once per decade on average, but none had affected Jamaica for several decades preceding Hurricane Allen (Kjerfve et al., 1986). Moreover, Discovery Bay is heavily fished, a condition that, along with the *Diadema* dieoff, has contributed to post-hurricane alterations (Hughes et al. 1987). Studies elsewhere in the Caribbean have shown moderate to severe hurricane effects (Rogers et al., 1991; Mah and Stearn, 1986; Edmunds and Witman, 1991; Fenner, 1991).

Similar physical destruction was noted on some reefs in St. Croix, U.S. Virgin Islands following Hurricane Hugo, but, as with Hurricane Allen, the severity of the impact varied from place to place (Woodley et al., 1981; Hubbard et al., 1991). The submarine canyon at Salt River, St. Croix (Figure 1) experienced currents up to 5 $m \cdot sec^{-1}$ and wave heights of at least 3.5 m during Hurricane Hugo (Hubbard et al., 1991). Hard substrata were scoured by an enormous quantity of sediment that was transported down Salt River Canyon and off the shelf. Yet post-storm visual assessments suggested that fore reef damage at Salt River Canyon, as elsewhere along the north shore of the island, was less severe than at south-facing sites, which received greater wave energy (Hubbard et al., 1991). The fortuitous existence of pre-Hugo data on the composition of demersal fish, sessile benthic, and echinoderm assemblages provided an opportunity to examine hurricane effects at a site where the biota initially appeared not to have been radically altered by the storm.

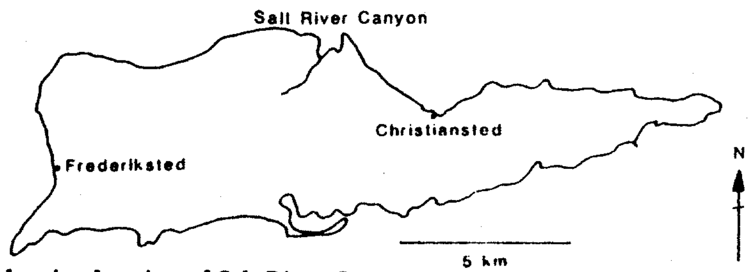

Figure 1. Map of St. Croix showing location of Salt River Canyon.

METHODS

Salt River Canyon

Hubbard (1989) described the geology of Salt River Canyon (64°45'N, 17°47'W). The sediment-covered Canyon floor runs roughly north-northwest from its shoreward boundary to its seaward opening on the north coast of St. Croix. The East Slope and the West Wall, which delimit Salt River Canyon, differ markedly in physical structure. Details of the Canyon environment are presented below as part of particular site descriptions (based on Hubbard (1989, 1992) and our own observations).

Fishes

Repeated counts of fish species were made on the East and West sides of Salt River Canyon before and after Hurricane Hugo. Both sites were at 15.2-18.3 m depth and ran horizontally for ≈50 m. Along the study site on the West Wall, the reef framework is steep--vertical in some places--and physically complex, with living and dead corals, buttresses, sand chutes, and many cavities and crevices. By contrast, the East Slope study area consists, over most of its length, of a gradually sloping limestone pavement, with lower coral cover and lower topographic complexity. The East Slope rises from the sand-covered Canyon floor at angles of 15-45°. At its seaward (northern) end, the East Slope site is covered in places by sediment flows, ending at the "Pinnacle Area", with foliose corals, high coral cover, and high physical complexity. Here the East Slope steepens and becomes similar to the West Wall in its microhabitat features. Before Hurricane Hugo, the study sites on both sides were in contact with the sandy floor of the Canyon over some portion of their length. However, large quantities of sediment were transported out of the Canyon during the hurricane, so that most of the West Wall site became separated from the sandy bottom by a 1-2 m vertical section of freshly exposed wall (Hubbard et al., 1991; Hubbard, 1992). Despite that net export, sediment was also imported from the shelf east of the Canyon, and some portions of the East Slope pavement were buried by sand.

Counts of fish species were made during 18-23 August 1989, one month before Hurricane Hugo, by four saturation divers working from NOAA's *Aquarius* undersea habitat. Fish species were counted by the same divers 38 days after the hurricane, during 26-30 October 1989, by three surface-based scuba divers. There were thus four sets of counts: (East and West Sides) X (Before and After Hugo). Ten counts of fish species were made on each side of the Canyon before the hurricane, and four counts were made on the West Wall and five counts on the East Slope after the hurricane. The counting method, described by Kaufman and Ebersole (1984), accumulates species over time until no new species are seen for 10 min.

Jaccard's Coefficient of Community (number of species shared/total number of species) was calculated for each pair of counts, and unweighted pair-group cluster analysis was performed on the matrix of similarity values. For further examination of how the hurricane affected species composition of the two fish assemblages, mean similarity for all possible pairwise combinations was calculated for four comparisons: East Before vs East After and West Before vs West After to determine which assemblage was affected more strongly by the hurricane, and East Before vs West Before and East After vs West After to determine whether the hurricane had reduced or enhanced the differences in species composition between the fish assemblages on the two sides of the Canyon. When all possible similarity values are computed, the same counts are included in several similarity values. To prevent problems of independence in statistical tests, subsets of similarity values with no counts in common were constructed by randomly drawing species counts from the four sets, without replacement.

Corals

Sebens and Johnson (1991) videotaped corals on the East Slope during an *Aquarius* saturation mission in August 1988, along six depth contours: 8, 12, 15, 21, 27, and 33 m, ± 1 m. One of us (RBA) videotaped those transects by surface-based scuba diving after Hurricane Hugo, in July 1990. The transects ran 100-150 m linear distance along the isobath.

The serendipitous nature of this study gave rise to a flaw in sampling design. Since the exact locations of the pre-hurricane transects were not marked, the post-hurricane transects could not be videotaped along identical tracks. Post-hurricane transects were situated within 2 m horizontal distance of the corresponding pre-hurricane transects. The only exception was at 15 m. At that depth, the post-hurricane transect covered a similar, adjacent area of reef. We therefore interpret our video results with caution, particularly the 15 m depth transects.

The transects were videotaped using a Sony V9 (8 mm) camcorder with video lights. A diver swam slowly above the reef along the depth contour, videotaping from a height of 30 cm above the reef surface. A 15 cm plastic ruler was attached to a metal rod that projected 30 cm forward from the camera housing. The ruler provided scale on the videotapes and standardized the distance from camera to reef substratum. This procedure produced clear stop-action frames that covered a width of 30-50 cm.

The videotapes were analyzed by playing them back on a monitor with ten random dots on a plastic screen overlay. The tapes were stopped blindly approximately every three seconds, and the identity of substratum occupants under each dot was recorded for that frame. Three seconds was long enough to assure that the tape had moved to a new, non-overlapping area of substratum. In this way, percent cover values for hard coral species (Scleractinia plus Milleporina) were calculated for hard substratum. Each transect was quantified by 1000-2000 random dots, of which half or fewer fell on living coral.

Echinoderms

One of us (RBA) censused echinoderms in a talus slope along the East Slope. The talus slope, which is shoreward (southeast) of the East Slope fish and video transect area described above, is composed of loose coral rubble covered with crustose coralline algae and algal turf. The echinoderms, which were almost exclusively ophiuroids, were sampled by swimming a randomly-determined number of fin kicks at 15 m depth, placing a 0.11 m^2 quadrat in the loose rubble habitat, turning over the cobbles, and identifying and counting the animals underneath. Ophiuroids down to a disk diameter of 5 mm were censused, and the ophiuroids and cobbles were placed back in their original positions. A pre-hurricane census (n=10 quadrats) was conducted in June 1989 during an *Aquarius* saturation mission. Eight post-hurricane censuses were conducted by surface-based scuba diving from November 1989 to September 1991 (n=25 in all cases).

RESULTS

Fishes

Before Hurricane Hugo, 129 fish species were counted in the Salt River Canyon study areas, and the two sides of the Canyon had roughly equal species richness (Table 1A). Asymptotic species accumulation curves (number of species *versus* time) indicate adequate sampling during the counts, and 79 of the 129 species were seen in at least half the censuses for one or both of the study sites. Species accumulation curves for counts after the hurricane are not qualitatively different from those for pre-hurricane counts. The variances in species richness are similar for all four sets of counts (Table 1A), obviating the need to test the homogeneity of variances. A two-way ANOVA, with Side and Hurricane as independent variables, shows that the hurricane had no effect on the average number of fish species per count in the Canyon as a whole (Table 1B). There is no statistically significant Before- vs After-hurricane difference in the number of species present on either side, although the average loss of more than six species per count on the West Wall, representing a reduction of nearly 10 %, is suspect at $p=0.065$. A significant Hurricane X Side interaction term in the ANOVA indicates that the loss of species on the West Wall does differ significantly from the gain on the East Slope (Table 1B).

Cluster analysis (Figure 2) indicates that differences between species counts are most strongly related to differences between Canyon sides, with the first branching of the dendrogram completely separating all East Slope counts from all West Wall counts. Later branchings indicate effects of the hurricane on species composition. The second major branching in the dendrogram separates all Before Hugo from After Hugo counts on the West Wall. Before and After counts on the East Slope also separate early in the dendrogram, but not as clearly, with one Before Hugo count clustering with the After Hugo group.

The earlier and more complete separation between Before and After Hugo counts on the West Wall suggests that the hurricane had more impact on species composition on the West Wall than on the East Slope. Direct comparison of Before and After similarity values for the two sides bears this out: the mean Coefficient of Community for the 50 possible East Slope Before vs After comparisons (0.605 ± 0.048 SD) is greater than that for the 40 possible Before vs After comparisons for the West Wall (0.529 ± 0.094 SD).

Table 1. Summary of fish data for Salt River Canyon. A. Mean number of fish species per count ± standard deviation, and (in parentheses) number of counts for East Slope and West Wall, Before and After Hurricane Hugo. B. ANOVA table with orthogonal contrasts for number of fish species per census.

A.	East Before	East After	West Before	West After
	62.7 ± 5.19 (10)	67.0 ± 5.96 (5)	62.9 ± 5.70 (10)	56.5 ± 5.45 (4)

B. Source of variation	df	SS	MS	F	p
Main Effects	3	73.845	36.923	1.172	0.326
Hurricane	1	72.188	72.188	2.292	0.143
Side	1	2.967	2.967	0.094	0.765
Hurricane X Side	1	172.862	172.862	5.488	0.027
Residual (Error)	25	787.500	31.500		
Total	28	1034.207			
A priori tests among means					
West Before vs After	1	117.029	117.029	3.715	0.065
East Before vs After	1	61.633	61.633	1.950	0.174

A two-tailed t-test of randomly-selected independent subsets (5 similarity values for East Slope, 4 similarity values for West Wall; no counts in common) indicates a significantly greater difference between Before and After counts on the West Wall than on the East Slope ($t_s = 2.412$, df=7, $p = 0.047$).

Comparing similarity values between counts indicates that Hurricane Hugo reduced the difference between sides in the species composition of fish assemblages. The mean Coefficient of Community for the 100 possible East vs West comparisons before the hurricane (0.524 ± 0.047 SD) is less than that for the 40 possible East vs West comparisons after the hurricane (0.575 ± 0.040 SD), but a t-test of randomly-selected independent subsets (no counts in common) falls just short of significance ($t_s = 2.106$, df=12, two-tailed $p = 0.067$), perhaps due to the small number of counts on the West Wall after the hurricane.

Examination of Before and After species lists for the two study sites reveals great changes in the occurrence of species associated with sandy substrata, while species associated with consolidated substrata exhibited only minor changes. These changes are associated with the most striking physical change in Salt River Canyon caused by Hurricane Hugo: sediment export and import, which raised the West Wall site from the sandy floor of the Canyon and increased the amount of sand substratum at the East Slope. The changes in species occurrence help account for the respective relative gains and losses in species richness on the East and West sides of the Canyon. However, they cannot account for the increased similarity between sides following the hurricane; rather, the sedimentary changes should have enhanced the differences between sides.

A second trend is a drastic post-hurricane decline of all cardinalfish (Apogonidae) on the West Wall. These nocturnal planktivores had been very common on the West Wall and relatively rare on the East Slope prior to Hurricane Hugo. It is not obvious why apogonids should have been so heavily reduced on the West Wall, but that reduction helps explain both the relative loss of species on the West Wall, and the slight reduction of differences between the East and West sides after Hurricane Hugo.

Corals

The video transects before and after Hurricane Hugo show substantial and significant declines in total coral cover at each depth: the 95 % confidence intervals about the before and after percent cover values do not overlap for any depth (Figure 3). For individual species, there were some changes after the hurricane, although few of these were dramatic.

At the shallowest depth, 8 m, coral species richness dropped from 14 before to 7 after Hurricane Hugo. The most common coral, *Montastrea cavernosa*, occupied 11.5 percent cover before but only 7.0 percent cover after. The second most common species was *Diploria strigosa*, at 8.8 percent cover before and 2.0 percent cover after. All but one of the other coral species declined in abundance. At 12 m depth, there were 14 species in the transect before the hurricane and 12 after. The same two species were the most abundant, with *M. cavernosa* at 7.3 percent cover before and 3.7 after, and *D. strigosa* at 2.9 percent cover before and 2.2 after. All but three of the other species declined.

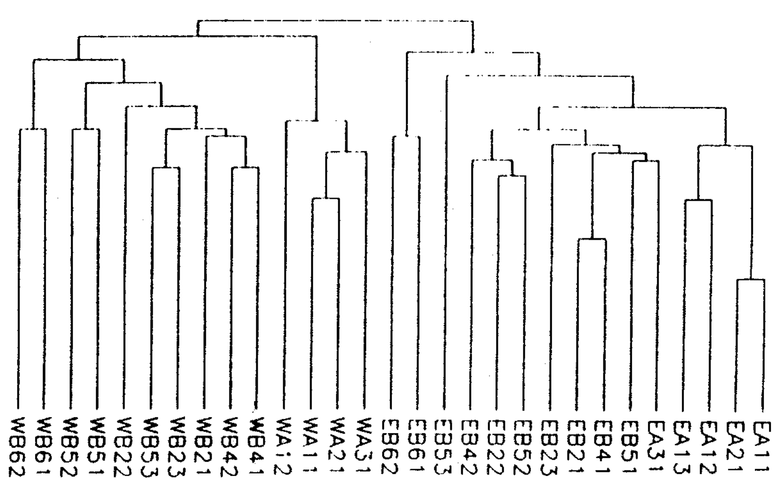

Figure 2. Dendrogram from cluster analysis of fish species counts. EB = East Slope before Hurricane Hugo, EA = East Slope after, WB = West Wall before, WA = West Wall after.

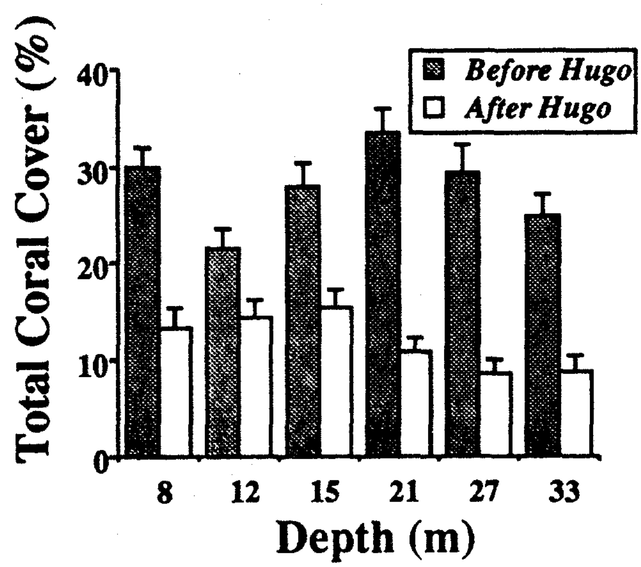

Figure 3. Percent cover of hard corals (Scleractinia plus Milleporina) before and after Hurricane Hugo. Error bars represent 95 % confidence intervals.

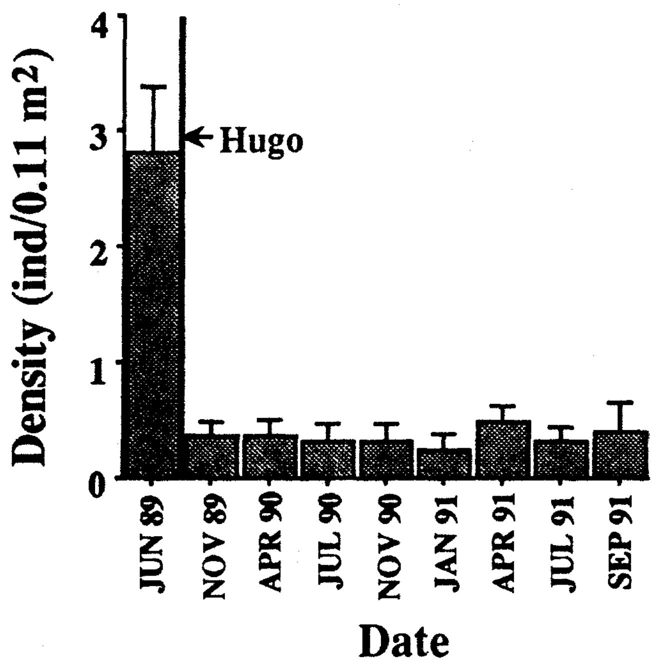

Figure 4. Ophiuroid abundance in the talus slope before and after Hurricane Hugo. Error bars represent standard errors.

At 15 m depth, all but one of the 14 species present before the hurricane declined. At 21 m depth, *Agaricia lamarcki* and *A. agaricites* were the most common corals. The former declined from 15.7 to 4.9 and the latter from 6.1 to 0.94 percent cover. *Montastrea annularis* decreased from 3.8 to 0.1 percent cover, and all other species either remained similar or declined after the storm. At 27 m depth, *A. lamarcki* was the only common coral prior to Hurricane Hugo, at 23.6 percent cover. This species declined to 7.1 percent cover after. The 7 other species present before the storm declined. At 34 m depth, *A. lamarcki* declined from 21.9 to 8.3 percent cover. Five other species declined, and *A. agaricites* increased from 0.1 to 0.4 percent cover.

Echinoderms

Echinoderms were the most abundant mobile benthic invertebrates under the rubble comprising the talus slope, and ophiuroids comprised 98 % of the 99 echinoderms counted. The remaining two individuals were regular echinoids, which appeared in post-hurricane censuses. Total ophiuroid density declined by approximately 90 % in Salt River Canyon after Hurricane Hugo (Figure 4), and ophiuroid populations did not recover during the two years of post-hurricane monitoring (ANOVA on log-transformed quadrat counts, $p < 0.0005$). Observations of sediment movement explain the ophiuroid decline on the East Slope. In the talus habitat, imported sediment filled in most of the interstices of the rubble, excluding the ophiuroids. Those holes and crevices remained filled for the two years over which the post-hurricane censuses were conducted.

DISCUSSION

At the three shallower depths along the East Slope, almost all coral species declined in percent cover after Hurricane Hugo, although none of the changes was of great magnitude. Because the post-hurricane transects were not in exactly the same positions as the pre-hurricane ones, differences were expected on that basis alone. However, the observed differences are large enough and the direction of change is consistent enough among coral species and depths to suggest a hurricane effect on the coral assemblage. The largest overall change occurred at 8 m depth, where species richness was halved and where the common species showed substantial reductions in percent cover. On the deeper reef, the one common species was severely affected. The large plating coral *Agaricia lamarcki* declined drastically at all depths below 15 m. The deep zones of the East Slope are normally exposed to very slow, unidirectional currents, on the order of ≤ 5 cm$\cdot$sec^{-1} (Sebens and Johnson, 1991), but they must have received strong oscillatory flows during the hurricane. It is likely that the large, fragile plates of *A. lamarcki* broke at that time.

Ophiuroids experienced an order of magnitude decline in abundance in the talus slope. Movement of sediment out of the talus slope presumably will permit ophiuroid immigration and recruitment. Likewise, many of the fish species most affected by the storm are closely associated with the sandy substratum that was so profoundly altered. The link between the observed changes in fish and ophiuroid assemblages and the impact of Hurricane Hugo on the physical environment reinforces earlier work on the importance of habitat structure (Kaufman and Ebersole, 1984; Moran and Reaka-Kudla, 1991).

Unlike Hurricane Allen's impacts in Jamaica, there is no evidence for great structural alteration or mass mortality of corals, with the exception of *Agaricia lamarcki*. Hughes and Jackson (1985) measured a maximum net recovery rate of 1 % growth in area per year for *A. lamarcki* in Jamaica. Applying this estimate to the drop in *A. lamarcki* cover observed in Salt River Canyon, complete regeneration of this population could take longer than 100 yr. Reversal of the hurricane-generated changes in fish assemblages are likely to depend on the reaccumulation of 2×10^6 kg of sediment in the Canyon and the redistribution of sediment away from the East Slope. Barring another major storm, the reaccumulation process could also take as long as 100 yr (Hubbard, 1992).

CONCLUSION

Hurricane Hugo caused changes in the fish, coral, and ophiuroid assemblages of Salt River Canyon. Despite the initial, qualitative impression that the storm had only minor effects on the biota, some large changes occurred. Those changes were attributable to sediment movement (fish and ophiuroids) and water movement (corals) during Hugo. We do not yet know how typical our results are of sites experiencing "non-catastrophic" levels of hurricane damage.

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