

Effect of Hurricane Hugo on molluscan skeletal distributions, Salt River Bay, St. Croix, U.S. Virgin Islands

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ABSTRACT

Just prior to the passage of Hurricane Hugo over St. Croix, U.S. Virgin Islands, 35 molluscan skeletal samples were collected at 30 m intervals along a sampling transect in Salt River Bay, on the north-central coast. Three months after the hurricane, the transect was resampled to permit direct assessment of storm effects on skeletal distributions. Results indicate that spatial zonation of molluscan accumulations, associated with environmental transitions along the transect, was maintained in the wake of the hurricane. However, limited transport was diagnosed by comparing the compositions of prestorm and poststorm samples from the deepest, mud-rich subenvironment on the transect. In aggregate, the species richness of samples from the southern half of this zone increased from 16 to 40, and the abundance of species that were not among the characteristic molluscs of this subenvironment increased from 11% to 26%. These storm effects could probably not have been recognized, and attributed directly to Hugo, had there been no prestorm samples with which to compare directly the poststorm samples.

INTRODUCTION

For paleontologists concerned with the fidelity of the marine fossil record, the question of skeletal transport during storms has become a central concern. Specifically, to what degree do storms alter spatial distributions of accumulating skeletal material on the sea floor? Some studies suggest that storm-induced skeletal transport can be substantial (e.g., Westrop, 1986). However, in habitats not subjected to storm-generated unidirectional currents, but where storm energy is nevertheless sufficient to produce tempestites, lateral transport of skeletal material may be limited (see Kreisa, 1981; Aigner, 1985).

To assess their effects on skeletal distributional patterns, it would obviously be desirable to measure directly the transport that storms in the present induce. For the purposes of a different (though related) study, we collected a suite of molluscan skeletal samples along a transect on the bottom of Salt River Bay, St. Croix, Virgin Islands, during September 1989, immediately prior to the passage of Hurricane Hugo over the island. Thus, we had a unique opportunity to determine the effects of this major storm on skeletal distributions by resampling the transect after its passage; this was accomplished three months later, in December.

Here we present our initial comparison of pre- and post-Hugo skeletal distribution data from Salt River Bay. Although spatial patterns in these data associated with environmental zonation on the transect were not disrupted greatly by the hurricane, a storm overprint could never-

theless be distinguished. The nature of this overprint has implications for the recognition of storm transport among assemblages preserved in the fossil record.

HUGO'S PASSAGE OVER THE STUDY AREA

On the night of September 17–18, 1990, Hurricane Hugo passed directly over St. Croix (Fig. 1, right inset). As it moved northwestward, the eye of the storm traversed St. Croix's west end after making initial landfall on the south-central coast of the island. Salt River Bay, on the north-central coast (Fig. 1), was under the northern part of the hurricane's eye wall (zone of maximum winds) during initial landfall. The bay was beneath the northeastern, and later the southeastern, quadrant of the eye wall for several hours as Hugo continued northwestward away from St. Croix. Maximum sustained winds exceeded 220 km/h; gusts were as high as 250 km/h (meteorological information discussed herein was summarized in *Storm Data*, a monthly publication of the National Climate

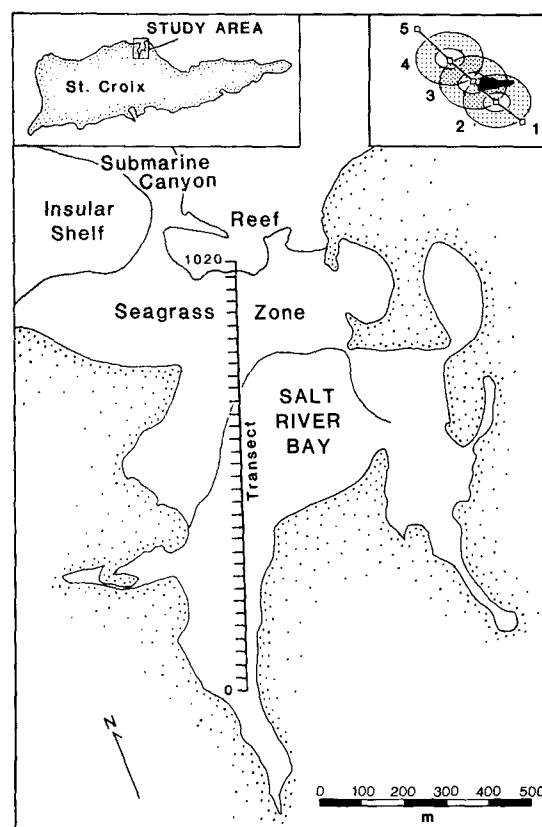


Figure 1. Study area showing location of transect line (see text for further description). Right inset: Passage of Hurricane Hugo over St. Croix. Rings outline successive positions of eye wall (illustrated eye-wall diameter is minimum estimate); eye was roughly elliptical as Hugo traversed island. Eye locations 1 (at 2253 Atlantic Standard Time [AST] on 9/17/89), 2 (0105 AST on 9/18/89), and 5 (0805 AST on 9/18/89) are based on reconnaissance data provided by National Hurricane Center. Locations 3 (0305 AST on 9/18/89) and 4 (0505 AST on 9/18/89) are based on interpolation between locations 2 and 5.

Data Center; supplementary data were acquired from the National Hurricane Center).

Because of the shape of the embayment and its location relative to Hugo's path, the direction and intensity of storm wave and current activity in the study area are difficult to quantify. Of the potential storm effects listed by Hine (1977), the most relevant in this instance is the possibility of a current generated by the return flow of water piled up by storm surge (1–2 m during Hugo) at the back of the bay. A return current would be strongest in the vicinity of the reef cut at the northern end of the bay, which serves as the principal focal point for water and debris that exit the bay and enter the adjacent submarine canyon to the north (Hubbard, 1989; Fig. 1). Because the northern part of the sampling transect was relatively close to this opening, there may have been considerable current activity in this area. However, its effects were probably baffled to some degree by seagrass, which was abundant in this transect zone (see below). Following the hurricane, there were no overt signs of wholesale sediment removal, in notable contrast to the adjacent submarine canyon, which clearly served as a return flow focal point for water that piled against the insular coastline (Hubbard et al., 1991).

TRANSECT AND SAMPLING METHODOLOGY

A 1020 m sampling transect, trending N20°E, was established in Salt River Bay during late August 1989; it extended from the back of the bay's western arm to the reef at the northern boundary (Figs. 1 and 2); 35 sample stations were fixed at 30 m lateral intervals (in all figures and text discussion the station number represents its distance, in metres, from the southern

end of the transect). A traverse from south to north revealed five distinct benthic zones based on prestorm vegetation and sediment data (Fig. 2; see also Gerhard, 1978). (1) In the back bay (stations 0–60) there was sparse (<500 blades/m²) to absent coverage by the wide-bladed seagrass *Thalassia*; the calcareous macroalga *Halimeda* was more abundant here than in other zones (average of ~50 plants/m²). The back bay was subject to reduced salinity (possibly <30‰) during periods of heavy rainfall (Hubbard, 1989). (2) The muck pit (stations 90–630) was the deepest part of the transect; sediment mean grain size was considerably finer than other zones (Fig. 2B). Mud fractions exceeded 90%, and no attached vegetation was apparent. (3) The south seagrass bed (stations 660–870) included a southern subzone characterized by the leafy macroalga *Caulerpa* (leaf densities of *C. prolifera* exceeded 1000/m² at station 690); the northern subzone was carpeted by *Thalassia* and the narrower-bladed seagrass *Syringodium* (densities of *Thalassia* exceeded 1500 blades/m² at some stations). (4) In the north seagrass bed—near reef (stations 900–990), coral rubble was prevalent; *Thalassia* was replaced by *Syringodium* and the wispy-bladed seagrass *Halodule* as the predominant floral elements (densities of *Syringodium* and *Halodule* both exceeded 2000 blades/m² at stations 960 and 990); blowouts were common throughout this zone, both before and after the storm. (5) The reef (station 1020) was the fifth benthic zone.

Prestorm and poststorm sampling of molluscan skeletal material at each station involved the sinking of a 29-cm-diameter metal cylinder into the substrate. The contents were airlifted by means of a suction dredge with an attached 5 mm mesh bag to depths of as much as 50 cm below the sediment-water interface (technique

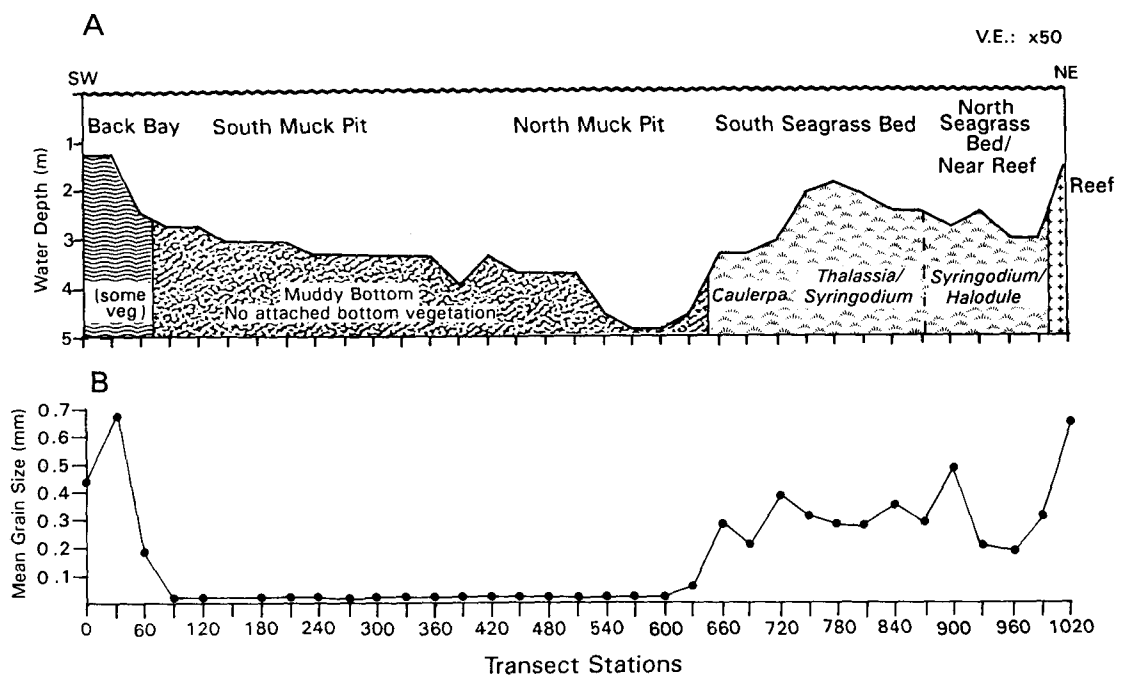
similar to that of Miller, 1988). The molluscan contents of the bag were evaluated subsequently by identifying all species and tabulating their relative abundances (only specimens containing an apex or umbo were counted). For bivalves, abundances of left and right valves were determined separately for each species; relative abundances were tabulated as the *larger* of the two numbers.

Two marker buoys, located along the middle one-third of the transect prior to Hugo, remained in place during the storm and were still present the following December, permitting us to confidently reestablish the transect for post-storm sampling. While we thus remained generally faithful to the prestorm transect, we believe that we veered slightly to the west of the original line (~20 m) by the time the southern end of the transect was reached.

RESULTS AND DISCUSSION

The 35 prestorm samples contained a total of 5245 molluscan individuals belonging to 101 species; a Q-mode cluster analysis of these data is presented in Figure 3A. Most notable on the dendrogram is the degree to which samples sorted with respect to their geographic positions along the transect. Cluster 1 contained samples 0 through 60, from the back bay, plus an additional sample from the opposite end of the muck pit. Samples from the southern and northern halves of the muck pit were included in clusters 2A and 2B (Fig. 3), respectively. Cluster 3 contained samples from the south seagrass bed, whereas samples from the north seagrass bed were grouped in cluster 4. There were two outliers: sample 1020, from the back reef, and sample 630, which is geographically transitional between the muck pit and the south seagrass bed.

Figure 2. Environmental attributes of sampling transect. A: Depth profile, with environmental zones depicted, based on transitions in benthic vegetation (see text). B: Graph of mean grain sizes of sediment samples (no data for station 150). There appears to be close association between mean grain size, depth, and vegetation in study area.



The most abundant molluscan species among the samples contained in each Q-mode cluster and available information on their life habits are summarized in Table 1. These data indicate considerable spatial fidelity among accumulated skeletal debris with respect to environmental patterns and transitions along the transect. Thus, most individuals were apparently not subject to postmortem transport beyond the boundaries of the subenvironments in which they lived.

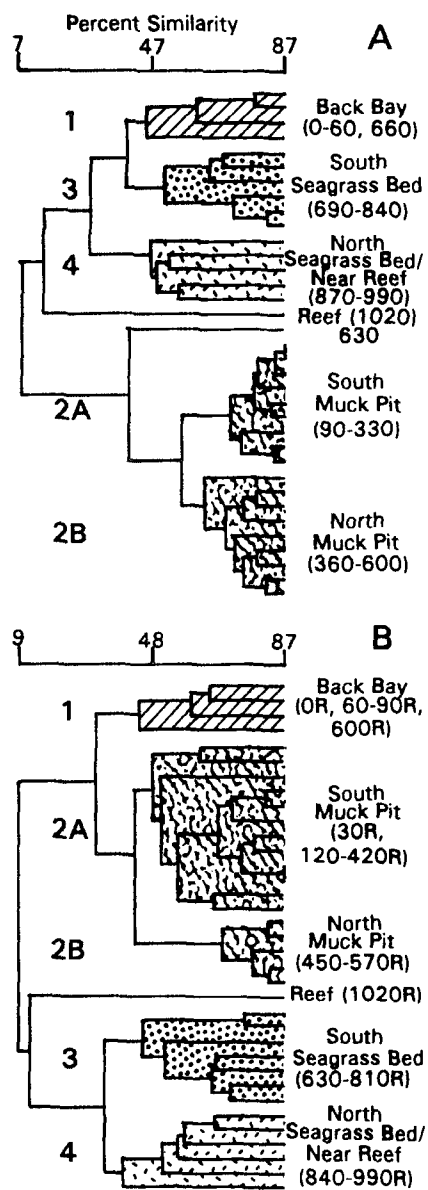


Figure 3. Q-mode cluster analyses of pre-storm and poststorm molluscan skeletal data (unweighted pair-group method with arithmetic averaging; percent transformation of samples; quantified Dice similarity coefficient). **A:** Pre-storm; cophenetic correlation coefficient = 0.94. **B:** Poststorm; cophenetic correlation coefficient = 0.87. Large numbers to left of dendrograms designate cluster numbers discussed in text; numbers in parentheses to right of dendrograms designate sample numbers represented by individual branches in each cluster (R refers to poststorm sample).

A Q-mode cluster analysis of the 35 post-storm samples, which contained 4766 individuals belonging to 96 species, is presented in Figure 3B (in figures and text discussion, "R" after the sample number designates a poststorm sample). Although there was minor shifting of samples among clusters, as well as some rearrangement of the clusters themselves, these differences between the pre-storm and poststorm dendrograms may be artifacts of the clustering methodology (ordinations of these same data, not presented here, bear this out). In general, poststorm dendrogram structure is comparable to that of the pre-storm structure. Most important, the poststorm dendrogram demonstrates that environmental zonation among molluscan skeletal material was essentially retained in the wake of Hugo, indicating that there was no wholesale lateral mixing of skeletal material within the study area.

TABLE 1. AVERAGE ABUNDANCES OF THE SIX MOST ABUNDANT SPECIES AMONG SAMPLES COMPRISING EACH PRESTORM Q-MODE CLUSTER

Species	Abundance (%)	Habitat*
Cluster 1		
<i>Chione cancellata</i>	23	Vb
<i>Anomalocardia brasiliana</i>	12	Vb, Eu
<i>Gouldia cerina</i>	11	Vb
<i>Codakia costata</i>	7	Th, Sd
<i>Tellina versicolor</i>	6	n.d.
<i>Diplodonta punctata</i>	5	Sd
Total	64	
Cluster 2A		
<i>Tagelus divisus</i>	30	Md, Th
<i>Tellina versicolor</i>	17	n.d.
<i>Tellina angulosa</i>	15	Md
<i>Macoma tenta</i>	12	Md
<i>Diplodonta semiaspera</i>	11	Vb
<i>Laevicardium pictum</i>	2	n.d.
Total	87	
Cluster 2B		
<i>Diplodonta semiaspera</i>	35	Vb
<i>Macoma tenta</i>	24	Md
<i>Tagelus divisus</i>	14	Md, Th
<i>Tellina versicolor</i>	11	n.d.
<i>Tellina angulosa</i>	9	Md
<i>Laevicardium pictum</i>	4	n.d.
Total	97	
Cluster 3		
<i>Gouldia cerina</i>	14	Vb
<i>Trachycardium muricatum</i>	12	Se
<i>Codakia costata</i>	11	Th, Sd
<i>Chione cancellata</i>	9	Vb
<i>Turbo castanea</i>	6	Epi
<i>Columbella mercatoria</i>	6	Epi
Total	58	
Cluster 4		
<i>Codakia costata</i>	19	Th, Sd
<i>Codakia orbicularis</i>	11	Se
<i>Columbella mercatoria</i>	10	Epi
<i>Bulla striata</i>	8	Ss
<i>Modulus carchedonius</i>	4	Epi
<i>Gouldia cerina</i>	4	Vb
Total	56	

*Vb = variable bottom, Eu = euryhaline water, Th = *Thalassia*, Sd = sandy (bare bottom), n.d. = not determined, Md = muddy (bare bottom), Se = seagrass, Epi = epifaunal on seagrass and other solid substrates, Ss = surface sediment. Sources for habitat information include Stanley (1970, 1981), Narchi (1972), Jackson (1973), Robertson (1975), Holm (1978), Hamilton and Winter (1984), and our own observations.

However, differences among the pre-storm and poststorm samples are evident through comparison of the muck-pit clusters in the two dendrograms (Fig. 3, A and B). On the pre-storm dendrogram, samples from the muck pit divided evenly into southern and northern components (clusters 2A and 2B), each containing nine samples, because of substantial transitions in the average abundance percentages of several molluscan species that were most common throughout this benthic zone (Table 1). In contrast, the post-storm muck-pit samples did not show this equitable division. Moreover, a perusal of similarity levels exhibited by the dendrogram branches suggested that the general level of similarity among poststorm muck-pit samples was less than that of the pre-storm samples. This was confirmed with detrended correspondence analysis (an ordination technique) for direct comparison of pre-storm and poststorm samples from the southern half of the muck pit (to be conservative, station 90 was not included because it was a "boundary" sample between the back bay and the muck pit). A perspective plot illustrates the positions of these samples on the first three ordination axes (Fig. 4); poststorm samples grouped separately from and were more diffusely distributed than corresponding pre-storm samples.

Such contrasts indicated that the poststorm samples from the south muck pit were compositionally different and more variable than their pre-storm counterparts. The data presented in Table 2 provide an explanation for these differences and suggest that they were direct consequences of Hurricane Hugo. Samples 120-330 from the south muck pit were pooled and compared with the corresponding poststorm aggregate. The poststorm aggregate was enriched with individuals belonging to species other than those consistently among the six most abundant in the south muck pit. The abundance percentages of these "other" species increased from 11% to 26% in the poststorm aggregate, and species richness

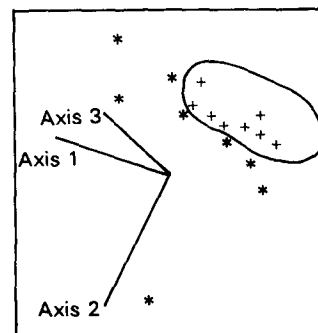


Figure 4. Perspective plot of scores on axes 1, 2, and 3 for pre-storm (crosses) and poststorm (stars) samples from south half of muck pit (station 90 excluded), as determined with detrended correspondence analysis. Axes are sketched on plot as visual aids; their respective eigenvalues were 0.822, 0.188, and 0.099.

increased from 16 to 40. In effect, this diluted a fauna lower in diversity and more spatially homogeneous, thereby reducing similarities among samples and generating the pattern shown in Figure 4.

The sample size of the poststorm aggregate was 597 individuals, whereas that of the prestorm aggregate was 438, suggesting that the increased species richness and apparent dilution of the poststorm aggregate might have been artifacts of increased sample size. However, rarefaction analysis demonstrated that this was not the case. Sanders's (1968) method and a modified version proposed by Hurlbert (1971; see also Raup, 1975) were both utilized to estimate what the species richness of the poststorm aggregate would have been had it been composed of just 438 individuals. In both instances, the calculated species richness for the rarefied sample was 37, still more than twice that of the prestorm aggregate.

Natural history and abundance data in Table 1 indicate that several of the most abundant species in the muck pit were specialized for life in those unique circumstances. In contrast, few, if any, of the other molluscan species found in the study area were indigenous to the muck pit; among prestorm samples, the six most abundant species composed 87% of total abundance in the south muck pit and 97% in the north muck pit. Furthermore, several of the "other" species in both the prestorm and poststorm aggregates were more abundant in other subenvironments (Table 2).

Thus, within the study area, Hurricane Hugo was apparently responsible for the movement of a limited amount of molluscan skeletal debris from other subenvironments into the south muck pit, although there was no wholesale movement of material. These findings suggest that, in ancient storm-deposited strata, the possibility of storm-generated overprints on spatial distributions cannot be discounted, even where

there is close correspondence between biotic and (apparent) paleoenvironmental zonation. However, because of the continued spatial fidelity exhibited by Salt River skeletal material in the wake of Hugo, it is reasonable to ask whether these subtle, but potentially important, storm effects can possibly be diagnosed for the geologic past, given that there are no prestorm samples available to compare directly to storm-deposited fossil assemblages.

One potential solution involves the use of a comparative taphonomic approach. First introduced by Brett and Baird (1986), comparative taphonomy has gained favor among paleobiologists as a means of delineating paleoenvironments on the basis of measured differences in the taphonomic conditions of contained fossil material. Parsons (1990; and unpublished) demonstrated that mollusc shells in various zones in Salt River Bay carried the signatures of the environments in which they lived and died. For example, because of differences in bottom conditions, shells from the south and north seagrass beds were routinely more abraded and encrusted than those from the muck pit. Thus, in the muck pit, exotic skeletal elements might be distinguished from indigenous material on a taphonomic basis alone; a test of this hypothesis is being conducted. This is not to suggest that the storm itself imparted a particular taphonomic signature on transported skeletal material. Indeed, Davies et al. (1989) demonstrated that specific storm signatures may be unlikely. Rather, storm-transported skeletal material would be expected to carry the taphonomic signature of the environment in which it resided previously. In the fossil record, storm exotics might be distinguished on the basis of taphonomic signature(s) unique from those of (more abundant) indigenous elements.

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TABLE 2. COMPARISON OF PRESTORM AND POSTSTORM AGGREGATE FAUNAL COMPOSITION FOR STATIONS 120-330

Species	Abundance (% of total)	
	Prestorm	Poststorm
<i>Tagelus divisus</i>	30	24
<i>Tellina versicolor</i>	18	15
<i>Tellina angulosa</i>	16	8
<i>Macoma tenta</i>	12	13
<i>Diplodonta semiaspera</i>	10	9
<i>Laevicardium pictum</i>	3	5
Other species	11	26
Aggregate species richness:	Prestorm--16	Poststorm--40

Note: Abundant species from other zones (Table 1) that were present in south muck pit aggregate: prestorm--*Codakia costata*, *Chione cancellata*, *Bulla striata*; poststorm--*Diplodonta punctata*, *Codakia costata*, *Trachycardium muricatum*, *Anomalocardia brasiliana*, *Gouldia cerina*, *Chione cancellata*, *Modulus carchedonius*, *Bulla striata*.