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THE EFFECTS OF HURRICANE JOAQUIN ON THE ONSHORE-OFFSHORE ZONATION OF ENCRUSTING FORAMINIFERA AT SAN SALVADOR, THE BAHAMAS

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ABSTRACT

Benthic foraminifera that are firmly attached to hard substrates (encrusting foraminifera) have been studied as part of the reef ecosystem and in actualistic studies to aid in paleoenvironmental reconstructions of shallow-water carbonates. A common research technique is to investigate their distribution by collecting cobble-sized pieces of reef rubble and other clasts from a range of environments. One benefit of focusing on encrusting foraminifera is that they are less likely to be transported out of their habitats than are free foraminifera. However, even large clasts can be transported great distances during high-energy storm events, an issue that has caused some concern for researchers.

The small Bahamian island of San Salvador provides a good test case to see if major storms alter the distributional patterns seen previously because its encrusting foraminifera are well known, and the island was impacted directly by Hurricane Joaquin, a Category 4 hurricane with sustained winds of 130 mph, which hit the island in early October 2015. We visited the island March 13-18, 2016 (5.5 months after the event). Cobbles were examined *in situ* and collected from 7 previously studied sites. Prior studies on San Salvador have shown that near-shore assemblages are dominated by well-preserved *Homotrema rubrum*; lagoonal patch reefs are varied but typically have prominent *Planorbulina*; bank barrier reefs are dominated by *Homotrema* but have some *Gypsina plana*; and shelf-margin assemblages are dominated by large *Gypsina plana*. Assemblages were compared before and after the storm based on 2008 and 2015 data, and individual cobbles were plotted on ternary diagrams showing the three principal taxa. Offshore sites, those from the middle of the lagoon to the shelf edge, showed no change. Nearshore sites displayed a small amount of possible shoreward transport and in-place disturbance (only one cobble was clearly upside down). Even cobbles with encrusting foraminifera found on land at French Bay did not seem to have been moved large distances based on the foraminiferal assemblages. Overall, the pattern of distribution observed previously was still intact.

INTRODUCTION

Benthic foraminifera that are cemented by calcium carbonate or are otherwise firmly fixed to hard surfaces are known as attached or encrusting foraminifera. Relatively few actualistic studies focus on the use of encrusting foraminifera as paleoenvironmental indicators compared to the vast literature on free-living foraminifera. However, because of their sensitivity to certain environmental variables that correlate with water depth and distance from shore on shallow-water carbonate platforms, these encrusting species are potentially useful in paleoecologic research.

Encrusting foraminifera have been studied *in situ* on the walls of underwater caves (e.g., Logan, 1981; Logan et al., 1984) and directly attached to coral heads in open water (e.g., Jackson and Winston, 1982; Martindale, 1992). In addition, settlement studies, in which artificial substrates are left on the seafloor for known periods of time, provide an important source of information on growth histories as well as distribution (e.g., White, 2002; Richardson-White and Walker, 2011; Walker et

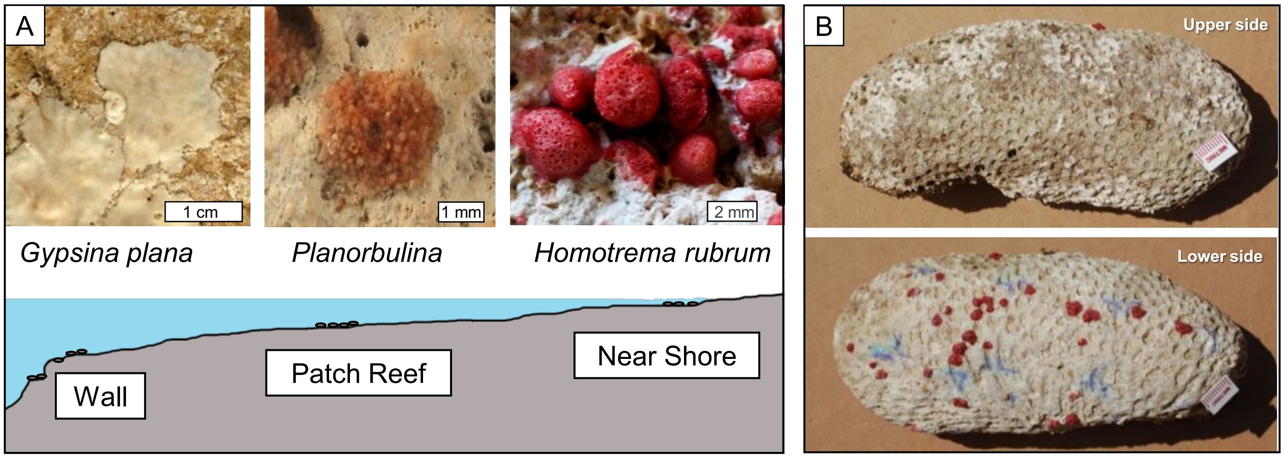

Figure 1. Distributional patterns of encrusting foraminifera. A) The "Tichenor-Lewis model" showing the typical distribution of encrusting foraminifera from shoreline to the wall at the platform margin, first seen at Fernandez Bay, San Salvador (after Tichenor and Lewis, 2009). B) The contrast between the top side of a cobble, bearing attached algae and Planorbulina, versus the underside, which is largely devoid of photosynthesizing organisms but includes the majority of encrusting foraminifera such as Homotrema rubrum, show here; cobble from Site 1, Telephone Pole Reef.

Site no.	Type	Location	Coordinates	Distance from shore	Water depth
1	Shoreline	Station 1 of Telephone-Pole Reef transect (rocky coastline: beachrock)	24° 02' 6.23" N 74° 31' 31.22" W	20 m	1 m
2	Mid-shelf patch reef	Snapshot Reef	24° 02' 14.7" N 74° 31' 55.3" W	275 m	5.2 m
3	Platform margin, ledge on wall	Narrow ledge on wall	24° 02' 13.2" N 74° 31' 55.3" W	582 m	27.1 m
4	Nearshore patch reef	Dump Reef	24° 07' 15.8" N 74° 28' 25.6" W	32–68 m	1–2 m
5	Bank Barrier Reef	Gaulins Reef	24° 08' 53.01" N 74° 28' 32.50" W	2,910 m N of island	3 m
6	Nearshore Reef	Near Salt Pond	24° 01' 24.2" N 74° 26' 59.35" W	20 m	1–1.5 m
7	Lagoonal Patch Reef	Near Salt Pond	24° 01' 20.1" N 74° 26' 56.1" W	135 m	4.5–6.0 m
8	French Bay	French Bay	23° 56' 54.5" N 74° 31' 16.7" W	N/A	N/A

Table 1: Sites studied. Location and water depth of localities visited in this study and in previous years; see Fig. 2.

al., 2011; Martin and Lewis, 2015). In the present study, we follow a method dating from the early 1980s, in which cobbles are recovered from the seafloor and taken back to the laboratory for study (Choi and Ginsburg, 1983; Meesters et al., 1991; Gischler and Ginsburg, 1996; Gischler, 1997).

These clasts have the advantage of making the foraminifera available for microscopic examination in the laboratory rather than trying to make identifications from underwater photographs or by direct observation in the field, and they are natural materials as opposed to artificial panels of some kind. Cobbles are available at reefs as part of the coral rubble at the base of coral heads and near shore as fragments of beachrock or lithified beach or dune facies. They can be taken from the island (with Bahamian government permission) with minimal damage to reefal ecosystems. The foraminiferal species are few in number and are distinctive (most are even "color coded"), allowing for easy data collection by student assistants.

Over the last decade, the senior author and students at Auburn University have studied the encrusting foraminifera at San Salvador (Tichenor and Lewis, 2009; 2011; 2018; Martin and Lewis, 2015) and other Bahamian outer islands (Smith, 2015; Smith and Lewis, 2016; Eubanks and Lewis, 2017; Eubanks, 2018) and have established the distributional pattern shown in Figure 1A: *Homotrema rubrum* dominates nearshore assemblages; lagoonal assemblages are diverse, but are characterized primarily by *Planorbulina* spp; and platform margin reefs have sparse, small foraminifera except for the very large tests of *Gypsina plana.* We refer to this as the Tichenor-Lewis model. Cobbles from bank barrier reefs, not shown in Figure 1A, are typically densely covered by *Homotrema* with some *Gypsina plana* and *Carpenteria.* In addition, *Nubecularia* can be common nearshore, *Carpenteria* is not, and *Haddonia* is restricted to the platform margin.

We have been asked, "Couldn't your cobbles have been transported from somewhere else?" We point out that cobbles are less likely to be transported out of their habitats than are free foraminifera, but of course transport is possible -- even boulders can be transported during high-energy events (e.g., Niemi, 2017). Storms are known to have an impact on subtidal encrusting communities in coastal settings by overturning clasts (Osman, 1977; Sousa, 1979; Wilson, 1987). A number of studies have assessed the impact of storms on coral reefs including sediment movement (e.g., Woodley et al., 1981; Hubbard et al., 1991; Hubbard, 1992), and Pleistocene coral rubble accumulations have been studied in order to recognize storm events based on encrusting organisms (e.g., Martindale, 1992; Perry, 2001).

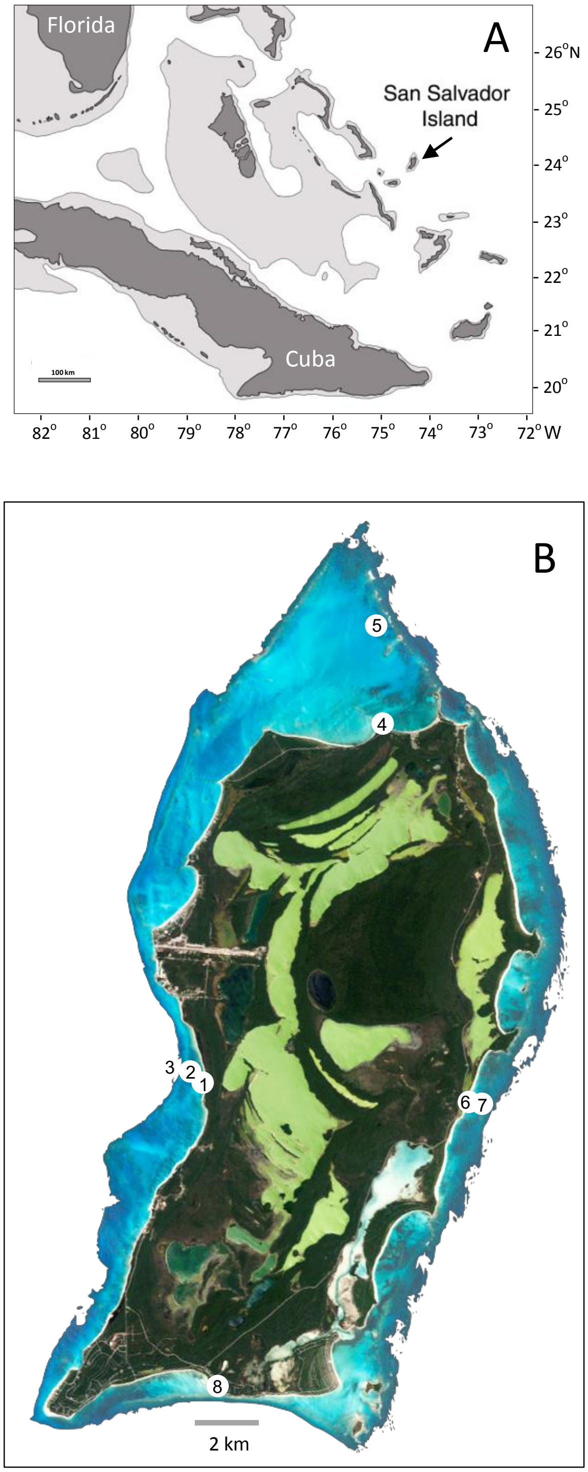

Figure 2. San Salvador island, showing the sites visited: A) Location of San Salvador. B) The sites visited in 2016: 1) Telephone Pole Reef nearshore, 2) Snapshot Reef, 3) Vicki's Reef, 4) Dump Reef, 5) Gaulins Reef, 6) Salt Pond nearshore, 7) Salt Pond patch reef, and 8) French Bay. See Table 1 for site data.

With regard to transport, individual foraminiferal tests have been shown to have moved back and forth between lagoons and forereef slopes (Chun et al., 1997). Specifically, pieces of the red-colored *Homotrema rubrum* have been used as an easily recognizable transport indicator in washover deposits (Pilarczyk and Reinhardt, 2012; Pilarczyk et al., 2014) and fully marine foraminifera, such as *Archaias,* found in lake cores on San Salvador are interpreted as indicators of hurricanes (e.g., Park, 2012).

San Salvador provides a particularly good test case for the question of whether the distribution of encrusting foraminifera found on cobbles can be taken at face value or whether storms move cobbles out of the habitat to such an extent that patterns are disturbed. The same sites have been sampled repeatedly over many years (with consistent results) prior to the direct impact of a major hurricane. In early October 2015, Hurricane Joaquin, a Category 4 hurricane with sustained winds of 130 mph, moved very slowly (5-6 mph) into the Bahamas from the northeast passing east of San Salvador, then turned north and hit Rum Cay before crossing San Salvador from southwest to northeast on October 2. With storm surge as high as 15 feet in some areas, it eroded cays and deposited sediment on the island itself. We visited the island in March 2016, ~ 5.5 months after the event.

RATIONALE

Attached organisms provide important clues to cobbles being overturned or transported out of the habitat. Photosynthetic organisms such as non-calcareous algae grow on the exposed, upper surface of cobbles and produce a green to brown color on the tops of cobbles, whereas the undersides are often lighter (Figure 1B). Most encrusting foraminifera are found on the underside, where competition for space is reduced. A notable exception is *Planorbulina*, which grows on the upper as well as the lower sides. Thus, overturned cobbles can be recognized as such.

Applying the Tichenor-Lewis model, encrusting foraminifera can be used to see if cobbles have been transported out of habitat. For example, cobbles transported from the platform margin (wall) shoreward will carry the large tests of *Gypsina plana* and *Haddonia* into shallower water where these tests are rarely found. Reef rubble transported oceanward from nearshore environments will have abundant *Homotrema rubrum* relative to *Planorbulina.*

Foraminifera grow quickly; some settle and grow to full size in a few months. Such is the case for *Planorbulina,* as has been shown by in-habitat experiments (e.g., Parsons, 1993; Martin and Lewis, 2015). However, the best-known species, *Homotrema rubrum,* does not appear until sometime between 6 months and one year, and *Gypsina plana* only shows up after one year on the wall site, and is less than 5 mm wide even then (Martin and Lewis, 2015). At approximately 5.5 months after the storm event, *Planorbulina* and *Nubecularia* may have grown on newly imported cobbles, but other taxa were most likely transported from their prior habitat.

METHODS

During a Spring Break field course on San Salvador, March 13-18, 2016, three undergraduate students participated in this post-storm study. Cobbles were examined *in situ*, and clasts were collected from the following, previously studied sites: Telephone Pole Reef, Dump Reef, and Salt Pond 1 (near-shore); Snapshot Reef and Salt Pond 2 (patch reefs); Gaulins Reef (bank barrier reef); and Vicki's Reef (platform margin). In addition to the six sites previously studied, one site showing obvious storm impact was examined (Figure 2; Table 1). Three of these sites, Snapshot Reef and Salt Pond nearshore and patch reef, had been sampled very recently (June 2015) and thus provide good "before" data. Other sites were sampled in 2008 and 2010. The condition of reefs was observed and photographed at each site, and cobbles were examined in situ prior to collection. In the laboratory at Auburn University, cobbles were washed and brushed to remove debris, encrusting foraminifera were identified using binocular microscopes, and their taphonomic states were assessed as was done previously (Buchan and Lewis, 2009; Lewis and Tichenor, 2018). The overall taphonomic state of each assemblage was described by the quality of preservation index (QPI), defined as the percent of all pristine and good specimens. Bar graphs were constructed to show the total assemblage for each site before and after the storm; ternary diagrams show the relative proportions of the three key taxa on a cobble-by-cobble basis.

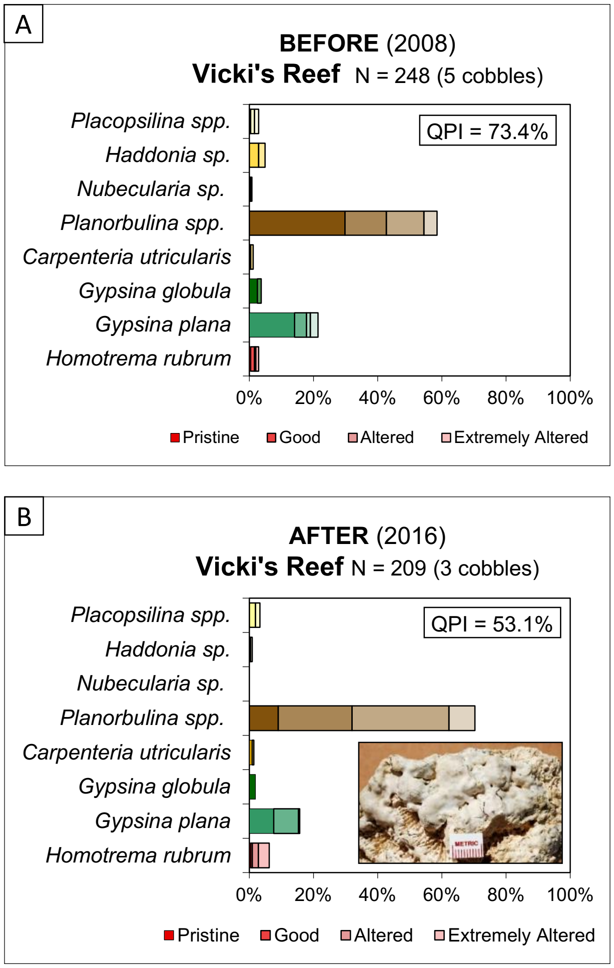

Figure 3: Foraminiferal assemblages before (A) and after (B) the storm at the "wall" off Fernandez Bay. Relative proportions are based on counts of individual tests; QPI stands for Quality of Preservation Index, the sum of all pristine and good individuals.

RESULTS

Offshore sites

Vicki's Reef (Site 3). This wall site, visited many times through the years by the senior author, showed no effects of storm damage. Samples were recovered from the platform-margin reef at a depth of 89 ft. (27.1 m). Cobbles were very eroded and heavily encrusted. The foraminiferal assemblages before and after the storm (Figure 3) were very similar: *Planorbulina* was most abundant based on counts of individuals, but *Gypsina plana* was second and, because of its large size, it accounts for most of the area covered by encrusters. *Haddonia*, an indicator of the wall habitat, was found on all three cobbles (and not on any of the other samples). The ternary diagram (Figure 4) shows a fairly tight grouping of all cobbles both before and after the storm.

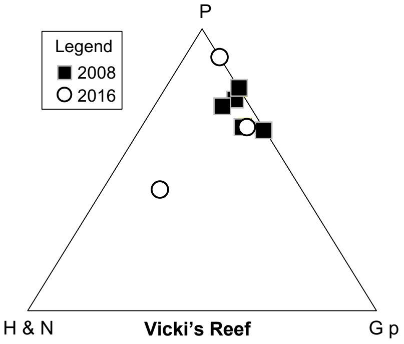

Figure 4: Figure 4. Ternary diagram for Vicki's reef showing the relative proportions of Homotrema rubrum plus Nubecularia sp. (H & N), Planorbulina (P), and Gypsina plana (G p) based on counts of individual tests. Individual cobbles before the storm are shown by black squares; cobbles recovered after the storm (this study) are shown by white circles.

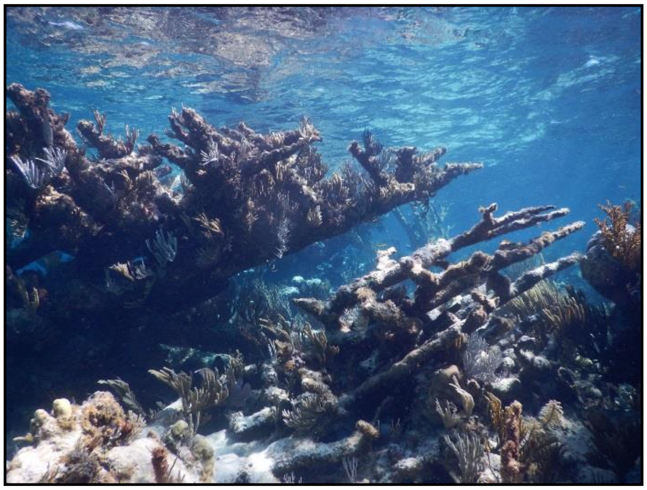

Figure 5. Erect Acropora palmata at Gaulins Reef, March 14, 2016.

Gaulins Reef (Site 5). Large, erect colonies of *Acropora palmata* near the spire known as "the seahorse" showed no signs of damage (Figure 5). Reef rubble was abundant, but no more than usual; in some places sand may have been deposited on the rubble. The cobbles were recognizable as flat pieces of *A. palmata* and other corals, densely encrusted by foraminifera. Assemblages before and after the storm (Figure 6) were dominated by *Homotrema rubrum* (including the globular morphotype) with *Carpenteria* second in abundance. *Planorbulina* was noticeably rare. The cobble-by-cobble analysis showed no outliers (Figure 7).

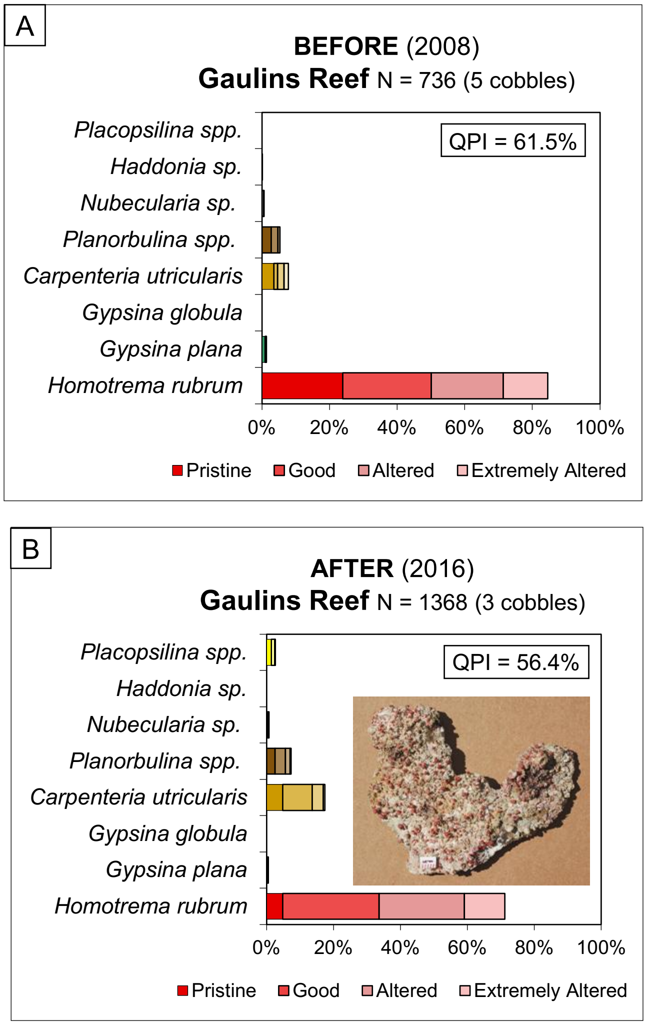

Figure 6. Foraminiferal assemblages before (A) and after (B) the storm at Gaulins Reef. Relative proportions are based on counts of individual tests; QPI stands for Quality of Preservation Index, the sum of all pristine and good individuals.

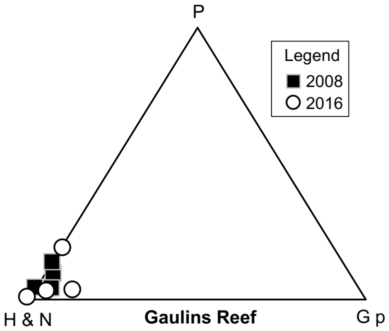

Figure 7. Ternary diagram showing the relative proportions of Homotrema rubrum plus Nubecularia sp. (H & N), Planorbulina (P), and Gypsina plana (G p) based on counts of individual tests. Individual cobbles before the storm are shown by black squares; cobbles recovered after the storm (this study) are shown by white circles.

Snapshot Reef (Site 2). This was one of the sites sampled in 2015 allowing for three collection times, and the assemblages are virtually identical over the eight-year time span (Figure 8). Numerous small tests of *Planorbulina* are dotted over otherwise relatively sparsely covered and somewhat abraded coral fragments. One cobble collected after the storm (Figure 9) plots at a distance from the others, but examination of this specimen shows it to be like all the others except for an unusually high number of *Homotrema rubrum.* Other elements of the assemblage, including minor amounts of small *G. plana,* and the rounded and abraded aspect of the cobble lead us to conclude that it was not transported from another habitat. A second patch reef (site 7), discussed below, was also much the same before and after the storm.

Nearshore sites

Telephone Pole Reef (Site 1). Nine cobbles were collected from ~1m water depth near the shoreline. Many of the cobbles showed evidence of overturning. This included the presence on all sides of yellow and brownish-gray staining, attached filamentous algae, and an abundance of *Planorbulina*, all of which indicate exposure to sunlight. In addition, even the largest cobbles had at least some *H. rubrum* on both upper and lower sides. We selected three cobbles for analysis which had a

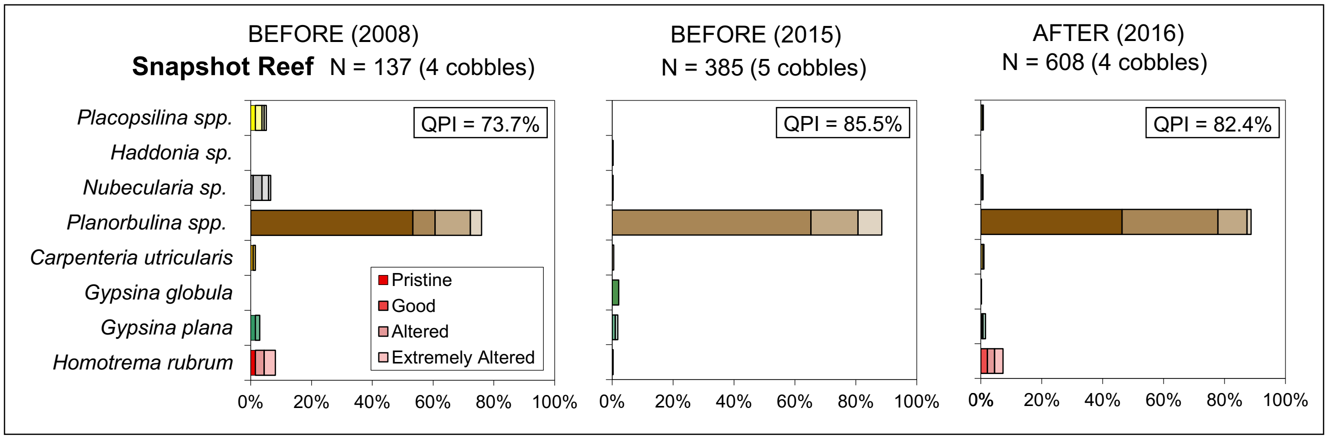

Figure 8. Foraminiferal assemblages from Snapshot Reef based on two recoveries before the storm, one in 2008 and another in June 2015, as well as the one after the storm. Note the consistency in assemblages throughout this time interval.

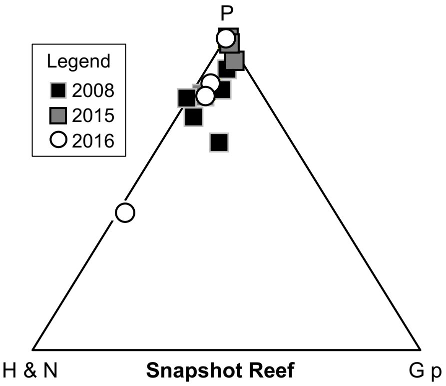

Figure 9. Ternary diagram showing the relative proportions of Homotrema rubrum plus Nubecularia sp. (H & N), Planorbulina (P), and Gypsina plana (G p) at Snapshot reef. Cobbles collected before the storm are shown by black and gray squares; cobbles recovered after the storm (this study) are shown by white circles. Note one outlier; see text for discussion.

relatively distinct lower side, which is in keeping with our standard protocol. Foraminiferal assemblages before and after the storm (Figure 10) were similar in that *H. rubrum* was first in abundance, however the post-storm data had proportionately more *Planorbulina*. Figure 11 shows the cobble that contributed most to this graph: the outlier plotting far from the other cobbles. Re-examination of

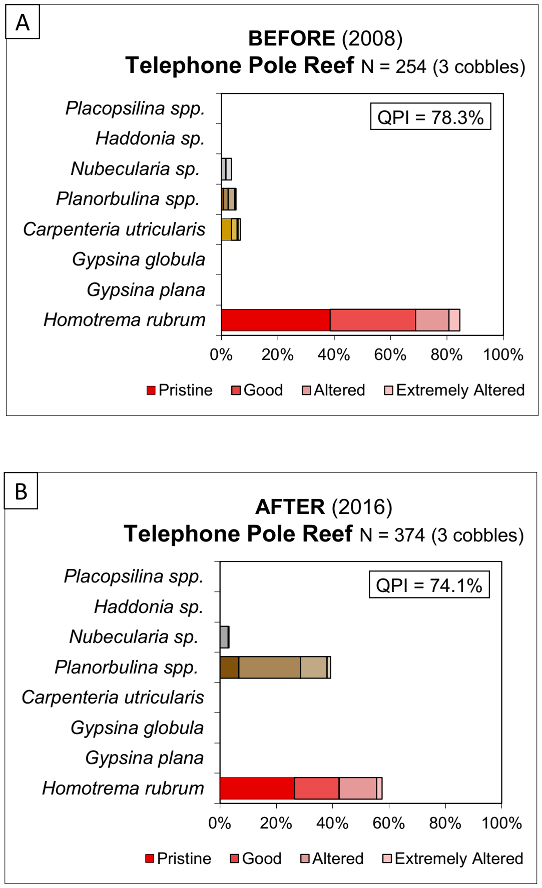

Figure 10. The foraminiferal assemblages before (A) and after (B) the storm near the shoreline at Telephone Pole Reef, Fernandez Bay. See text for a discussion of the increase in the relative amount of Planorbulina.

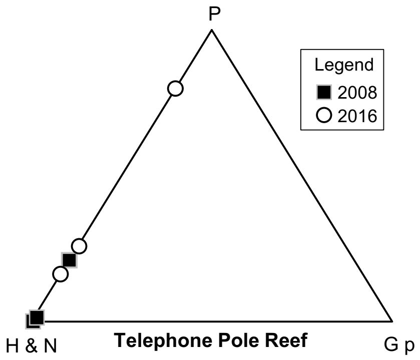

Figure 11. Ternary diagram for the Telephone Pole Reef site showing the relative proportions of Homotrema rubrum plus Nubecularia sp. (H & N), Planorbulina (P), and Gypsina plana (G p). Note one cobble with an unusually large proportion of Planorbulina suggesting possible transport from offshore.

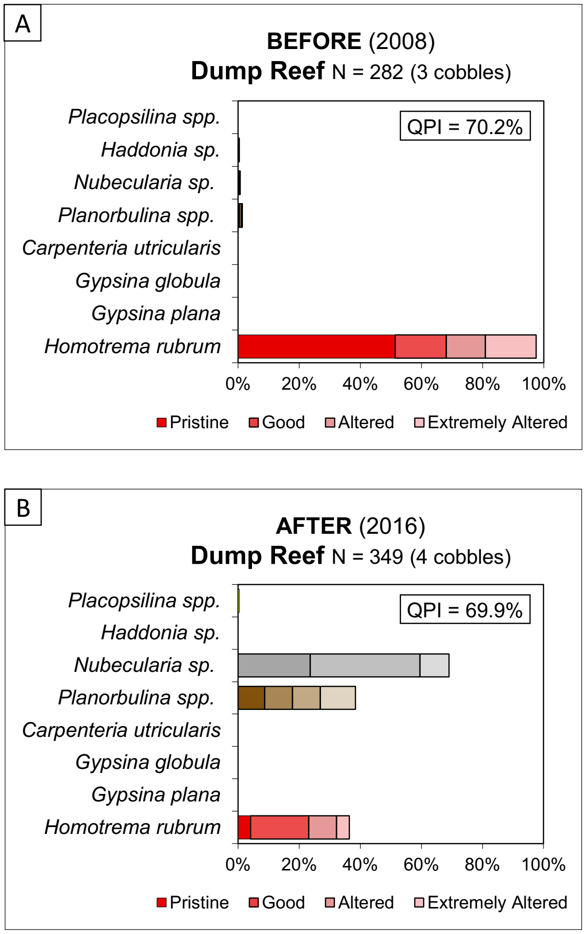

Figure 12. The foraminiferal assemblages before (A) and after (B) the storm at Dump Reef. Note the increase in Nubecularia in the 2016 dataset.

this cobble shows that the high number of *Planorbulina* cannot be explained by repeated overturning because it is the cobble we had chosen early on as an example of top versus bottom (Figure 1)! It could have been washed in from the lagoon, although the absence of minor taxa (e.g., *Carpenteria*) and the presence of *Nubecularia* do not support this interpretation.

Dump Reef (Site 4). This nearshore reef was sampled at its proximal (~32 m from shore) and distal (~68 m from shore) edges. Cobbles found in 2016 were more varied than those assessed in 2008 (Figure 12) with some having nothing but *H. rubrum*, and others with a significant amount of *Nubecularia* as well as *Planorbulina*. The relatively large proportion of *Planorbulina* found on cobbles at the distal edge (Figure 13) and the debris associated with them may indicate their having been washed ashore and piled up at the edge of the reef. On the proximal side of the reef a cobble was found in an upside-down orientation, as determined by the encrusting foraminifera on the top and algae on the bottom.

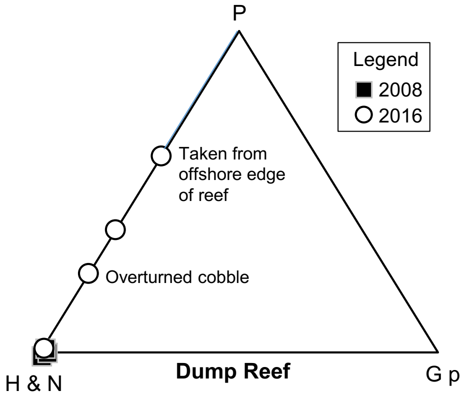

Figure 13. Ternary diagram showing the relative proportions of Homotrema rubrum plus Nubecularia sp. (H & N), Planorbulina (P), and Gypsina plana (G p) at Dump Reef. The three cobbles collected in 2008 had nearly 100% Homotrema, but those recovered in this study showed more variability, and one cobble was overturned.

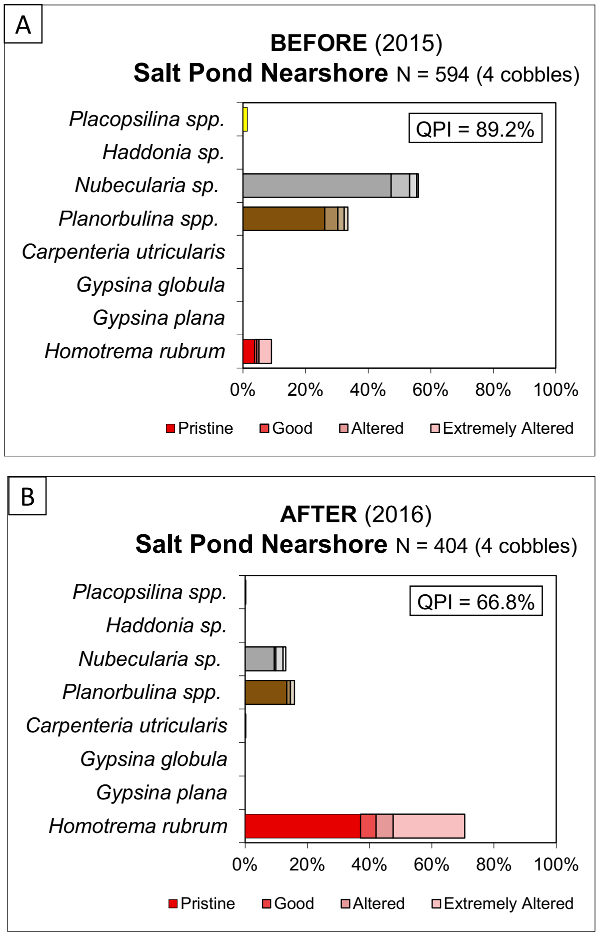

Figure 14. The foraminiferal assemblages before (A) and after (B) the storm near the shore at Salt Pond. See text for discussion.

Salt Pond (Site 6 and 7). Across the road from Salt Pond are two sites on the high-energy east side of the island. Both of these sites were found to be rich in *Nubecularia* sp. when first sampled in 2015; this was explained by the observation that this fast-growing species sometimes takes the place of *Homotrema rubrum* in nearshore settings, a phenomenon seen on Cat Island as well as San Salvador (Smith, 2015; Lewis and Tichenor, 2018). The 2016 re-sampling of the nearshore site (Figures 14 and 15) shows an assemblage more typical of nearshore environments: that is, *Homotrema rubrum* is much more abundant than any other taxon. One of these cobbles has a nodular surface resembling the patch reef cobbles sampled in 2015 suggesting shoreward transport.

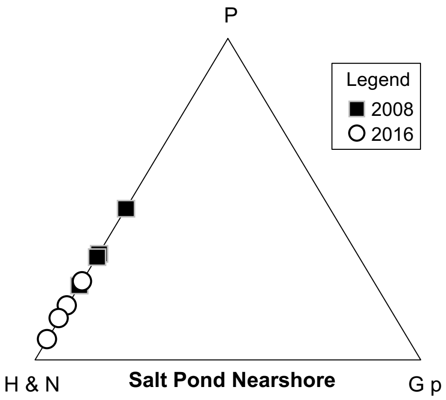

Figure 15. Ternary diagram for the Salt Pond nearshore site showing the relative proportions of Homotrema rubrum plus Nubecularia sp. (H & N), Planorbulina (P), and Gypsina plana (G p) based on counts of individual tests. Individual cobbles before the storm are shown by black squares; cobbles recovered after the storm (this study) are shown by white circles.

The patch reef (Site 7) sampled approximately 100 m offshore from Site 6 has nearly equal numbers of *H. rubrum*, *Nubecularia,* and *Planorbulina* both before and after the storm. The slight increase in *H. rubrum* between the two graphs (Figure 16) is consistent with the growth of this taxon shown at the nearshore site. As noted in 2015, *H. rubrum* tests were smaller at the patch reef than those at the nearshore site. Individual cobbles show a fairly wide variation in assemblage composition (Figure 17), which may be explained, in part, by differences in cobble size: the smaller cobbles may have been transported.

French Bay (Site 8). Samples were taken at the shoreline and in a nearby rubble field south of the road at the east end of French Bay (Figure 18). Both sets of cobbles were very well rounded, especially those taken at the water's edge, where foraminifera were only observable in protected pockets that had escaped abrasion. Both the assemblage from shore samples and the rubble-field assemblage were dominated by *Homotrema*, with significant amounts of *Planorbulina* as well (Figure 19).

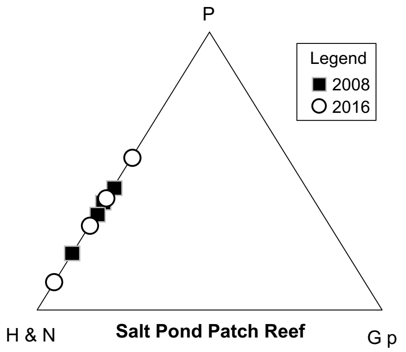

Figure 16. The foraminiferal assemblages before (A) and after (B) the storm at the patch reef off Salt Pond. Note the similarity in graphs; see text for discussion.

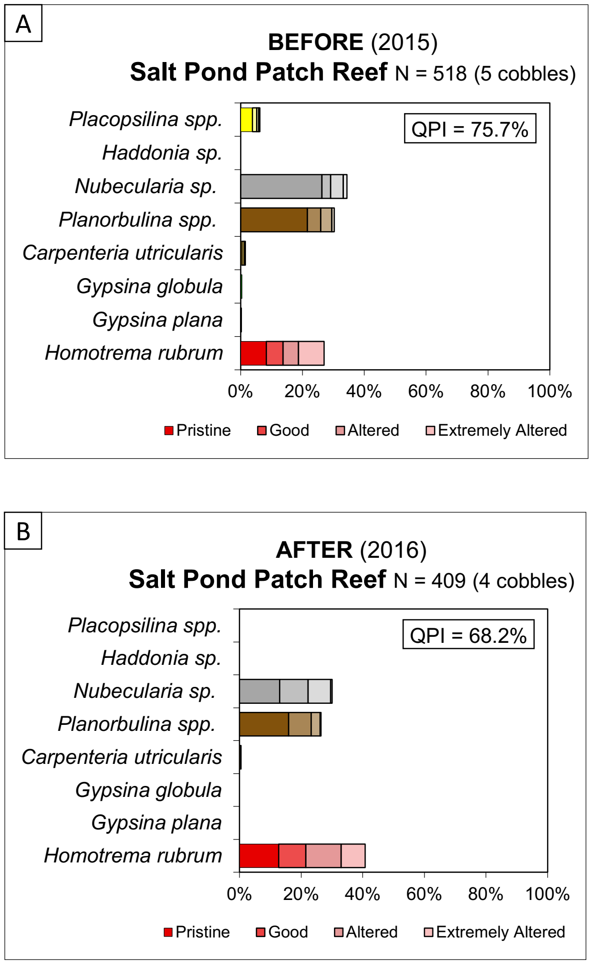

Figure 17. Ternary diagram for the Salt Pond patch reef showing the relative proportions of Homotrema rubrum plus Nubecularia sp. (H & N), Planorbulina (P), and Gypsina plana (G p) based on counts of individual tests. Individual cobbles before the storm are shown by black squares; cobbles recovered after the storm (this study) are shown by white circles.

French Bay was not included in earlier studies by the Auburn team, so no data is available from before the storm event. However, the large, low-profile morphotype of *Homotrema*, which is usually found near shore rather than in mid-shelf and outer reef environments, was common; and the *Homotrema*-dominated assemblage suggests a nearshore origin for these cobbles.

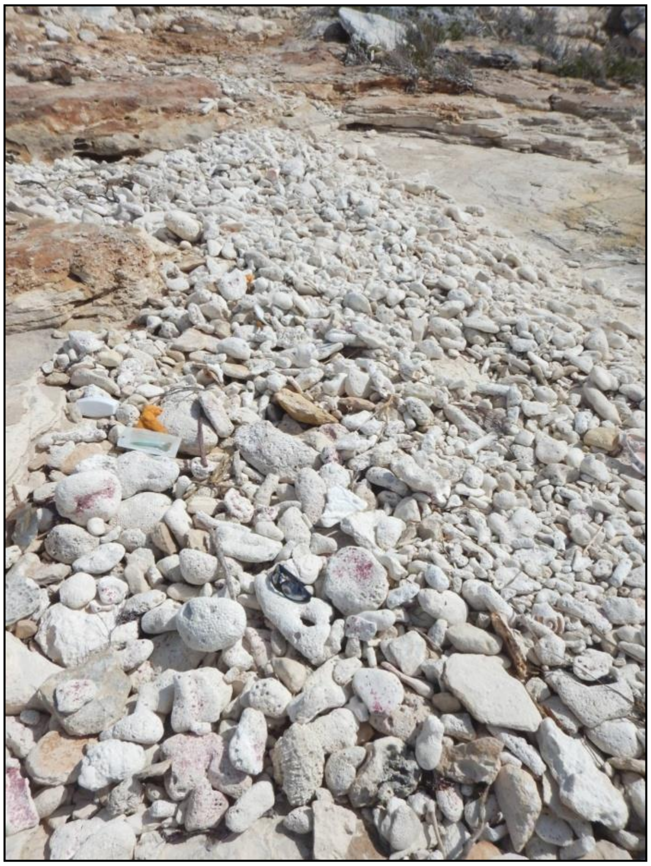

Figure 18. The rubble field south of the road at French Bay. Note sunglasses, lower middle, for scale. Samples were taken here and at the shoreline nearby.

DISCUSSION

Each of the offshore sites examined in this study have distinct assemblages of encrusting foraminifera. Vicki's Reef, like the other wall sites we have studied on Cat Island (Smith, 2015) and Mayaguana (Eubanks, 2017), is strikingly different from all other sites because of the abundance of large *Gypsina plana* tests in contrast to the small size of other taxa. None of these unique cobbles

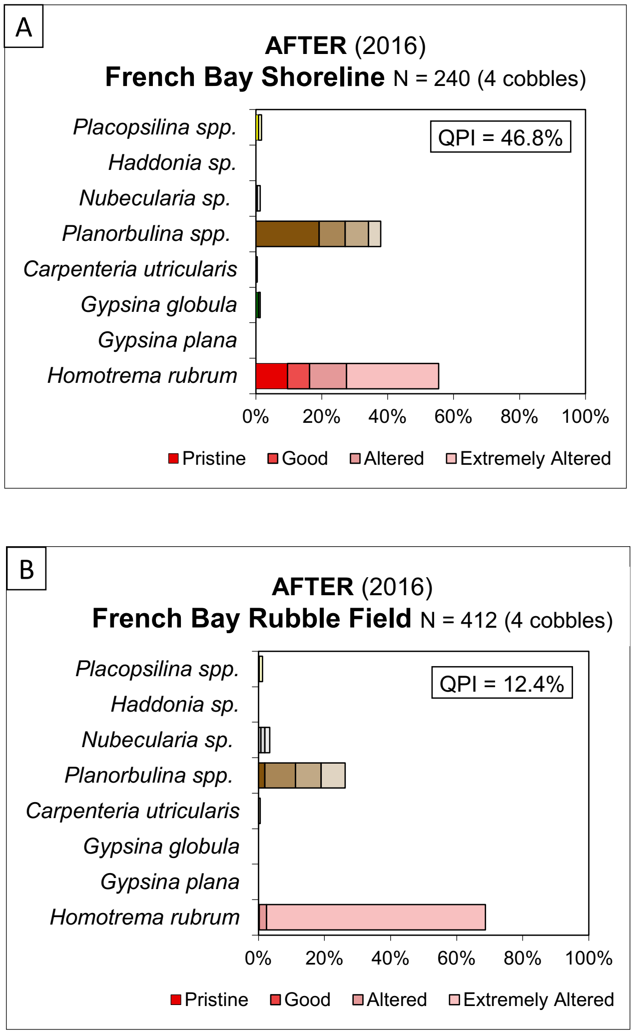

Figure 19. Foraminiferal assemblages found on cobbles recovered from the shoreline (A) and the rubble field (B). See text for discussion.

were found at other localities. The corals at Gaulins Reef seemed to have been undisturbed by Hurricane Joaquin, and the foraminiferal assemblages on coral rubble were very similar before and after the storm, with the same ranking of the top three taxa: *Homotrema* >> *Carpenteria* > *Planorbulina*. Even the relatively low QPI value, 61.5% vs 56.4%, was nearly the same after eight years. Consistency through the years was also shown at Snapshot Reef, a mid-shelf patch reef. The assemblages were overwhelmingly dominated by well-preserved *Planorbulina*. Even at the level of individual cobbles (Figure 9), three of the four cobbles plotted exactly as expected. The hurricane did not alter the pattern seem previously in these three offshore sites.

Nearshore and inner-lagoon samples are varied even in prolonged fair-weather intervals (Tichenor and Lewis, 2018), perhaps because of the effects of past storms. This is not surprising since *Planorbulina* grows on the tops of cobbles, and the relative amount of *Planorbulina* on the underside of cobbles increases with distance from shore. Therefore, either overturning or shoreward transport, or both, can increase the amount of *Planorbulina* relative to *Homotrema*. Even so, the observed effects of Hurricane Joaquin were minimal. As discussed above, one cobble at the Telephone Pole Reef site had an unusually high abundance of *Planorbulina*, suggesting that it may have been transported shoreward. On the north end of the island, the Dump Reef site showed possible evidence of the storm including the wide variation in *Homotrema*-*Planorbulina* ratios, with the highest amount of *Planorbulina* on the distalmost cobble, and one overturned cobble near shore.

The growth of *Nubecularia* at this site and at the Salt Pond sites complicates interpretation. This genus is not reported by other authors, but from our prior research (Martin and Lewis, 2015) we know it to grow within 3 months in nearshore settings; it seems to be a boom-and-bust opportunist, commonly found instead of/in addition to *Homotrema* in nearshore sites (e.g, Smith, 2015). *Nubecularia* was abundant in 2015 at the Salt Pond nearshore site but was replaced by *Homotrema* after the storm (Figure 14). Although more research needs to be done on the growth trajectories of these taxa, both graphs show assemblages indicative of a nearshore setting -- before and after the storm.

The extensive rubble field between the shore and the highway at French Bay on the south end of the island is clear evidence of the power of the hurricane. Sand also covered part of the road in this area. However, the encrusting foraminifera we examined do not indicate cobble transport for long distances. It is not clear if the cobbles in the rubble field came the shoreline area or further out in the bay, but the abundance and the morphology of the *Homotrema* indicate that the clasts were not moved very far.

CONCLUSIONS

Was the distribution of encrusting foraminifera shown in the Tichenor-Lewis model disturbed by the impact of a Category 4 hurricane? The answer is no. It may be that none of our sites suffered a direct hit; none of the reefs examined in this study showed effects of recent storm damage to the corals themselves. However, this may reflect the spotty nature of hurricane damage. The fact is that our sites were distributed around the circumference of the island and from the shore to the wall at the shelf edge. Bar graphs of foraminiferal assemblages from the three deeper water, offshore sites showed no effects of the storm. None of the distinctive cobbles from these sites were found in shallow-water, nearshore localities. Although nearshore sites showed possible transport of cobbles shoreward, none of them appeared to have originated further than the inner parts of the lagoon. The onshore-offshore zonation observed previously and even the site-to-site faunal compositions were not altered significantly by the direct impact of a Category 4 hurricane.

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