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GROWTH OF ATTACHED (ENCRUSTING) BENTHIC FORAMINIFERA ALONG AN ONSHORE-OFFSHORE TRANSECT, FERNANDEZ BAY, SAN SALVADOR, BAHAMAS: PRELIMINARY RESULTS

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ABSTRACT. Previous research has shown a distinct zonation of foraminifera attached to cobbles in the area of Telephone Pole Reef: *Homotrema rubrum* was very abundant and well preserved near the shore, *Planorbulina* dominated a diverse community at a mid-shelf site, and *Gypsina plana* covered much of the surface at the platform margin. Taphonomic conditions suggest different growth rates in these zones; in order to test this idea, we attached travertine tiles to concrete blocks and deployed them in March 2011 in the three areas. In addition, tiles varied in orientation and lighting conditions within the two openings in each block, described as roof, ceiling, wall, and floor. Four blocks were left at each site, ranging in water depths from 1-2 m near shore to 31 m on the wall at Vicki's Reef. Two of these blocks were recovered after three months and two after six months; in addition, previously deployed blocks provided one-year data from the near shore and platform margin. Tiles were retrieved and analyzed for encrusting growth by foraminifera and non-foraminifera encrusters such as crustose coralline algae.

Homotrema rubrum was not found at the near-shore site (or elsewhere) within the first six months; however, relatively large specimens were common on tiles from the one-year block deployed earlier. This is consistent with the findings of other researches. *Planorbulina acervalis* was the dominant species overall, occurring in the first three months along with *Acervulina inhaerens, Nubecularia* sp., and minor taxa. By six months, a clear difference was seen between *Planorbulina* on the sunlit tops of blocks and *Acervulina* on the inverted, shaded ceilings at the mid-shelf patch-reef site. Dominance of this species at the patch reef is consistent with the previous study of cobble communities.

In general, encrusters were found to be scarce on tiles at the platform margin; foraminifera were especially rare, and individuals were small. *Gypsina plana* was represented here by two small (~4 mm) specimens found after one year. Although more data are needed, this indicates late settlement for the species and does not rule out slow growth in the harsh conditions found at the wall. Our work is ongoing and will eventually include blocks deployed from other sites and for longer periods of time, in addition to results of calcium carbonate production rates by attached foraminifera.

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INTRODUCTION

Foraminifera are common marine protists, typically having a shell (test) made up of agglutinated grains or cemented calcium carbonate and with threadlike strands of cytoplasm extending beyond the test, known as reticulopods (Haynes, 1981; Lipps, 1993; Armstrong and Brasier, 2005). Most benthic species are mobile, using their reticulopods for locomotion and for temporary attachment to nearby vegetation as well as for feeding. Others, called attached or encrusting foraminifera, are firmly fixed to hard substrates such as shells and coral debris, either by means of a secreted, glue-like substance or by precipitation of calcium carbonate.

Whereas free species accumulate in the sea-floor sediment after death and are easily sampled at the sediment-water interface or by use of cores, sampling attached foraminifers requires recovering the substrate as well. A number of workers have sampled reef rubble, examining the attached foraminifers on the undersides of cobbles; for example, see Choi and Ginsburg (1983) in the Florida Keys, Meesters et al. (1991) at Curaçao and Bonaire, Martindale (1992) at Barbados, and Gischler and Ginsburg (1996) off Belize). Choi (1984) examined the sequence of settlement in the Florida Keys samples by sectioning the cobbles collected.

In the Bahamas, a similar approach was taken by Tichenor and Lewis (2009, 2011) on San Salvador. Cobbles were collected along transects through Telephone Pole Reef and off Rocky Point on the west side of the island, with additional samples taken at localities in Grahams Harbour and elsewhere. The goal of the study was to examine species distributions, including zonation from the shore to the platform-margin (wall), expected due to a gradient of conditions such as water depth, wave energy, and ambient light. Their data included percentages of total species present by numbers of individuals per area, taphonomic condition for each individual, and percent of area covered. As shown particularly well by the transect through Telephone Pole Reef, the assemblages did show a marked zonation: (1) *Homotrema rubrum* was very abundant and well preserved in near-shore sites, (2) *Planorbulina spp.* dominated a diverse community of attached species at a mid-shelf site, and (3) *Gypsina plana* was extensive at platform margin, with very large (up to 4-5 cm) tests covering much of the area on the underside of cobbles. The authors proposed that the different environmental conditions led to differences in growth rates. For example, repeated disturbance of cobbles near shore might cause re-colonization by *H. rubra*, and low availability of food in the deeper water at the platform edge might be reflected by slow growth in *G. plana*.

To test this hypothesis, Tichenor and Lewis deployed concrete blocks at various locations with travertine tiles attached, to be recovered at a later date to check for growth of attached foraminifera. In addition, a second set of experiments was initiated by Martin and Lewis to examine growth within the first year. Presented herein are the results to date of the second set of experiments along with some of the data from the first set. The results demonstrate taxonomic differences between year-one and year-two encrusters and suggest that both the near-shore setting and the platform margin are stressed environments in contrast to the more stable mid-lagoon.

PREVIOUS EXPERIMENTAL RESEARCH

Because of their sessile life style, growth rate studies of attached foraminifera can be assessed through settlement studies in which artificial panels or shells are deployed in the natural habitat and recovered at set intervals. The long history of settlement studies includes a few that are particularly relevant for the work described here.

Martindale (1992) refers to his use of concrete blocks left at various sites in Barbados for 3-18 months as part of a larger study, but no details of these experiments are given. Parsons (1993) used segments of conch (*Strombus gigas*) shells as experimental plates deployed on the sea floor at St. Croix and recovered at intervals of 7-24 weeks. Foraminifera identified were *Planorbulina* sp., *Gypsina* sp., *Homotrema rubrum*, and an unidentified agglutinated species.

Echols studied epibionts growing on crinoid ossicles fixed to panels at San Salvador (Lewis and Echols, 1994; Echols, 1995), some of which were foraminifera. Although foraminifera were not differentiated except for *Cornuspiramia*, she reported foramifera in the 1-, 2.5- and 3-month recoveries. Elliott et al. (1996) studied the distribution of *Homotrema rubrum* at Bermuda, including a five-year deployment of concrete blocks at a water depth of 9.5 m. Both Echols and Elliott used an array of panels similar to ours. Hall (1998) deployed whole, fresh conch (*Strombus gigas*) shells and fragments of shells used as panels at San Salvador and recovered them at intervals of 2 weeks, 1,5, and 12 months (Hall and Lewis, 1997). She compared these with natural (subfossil)

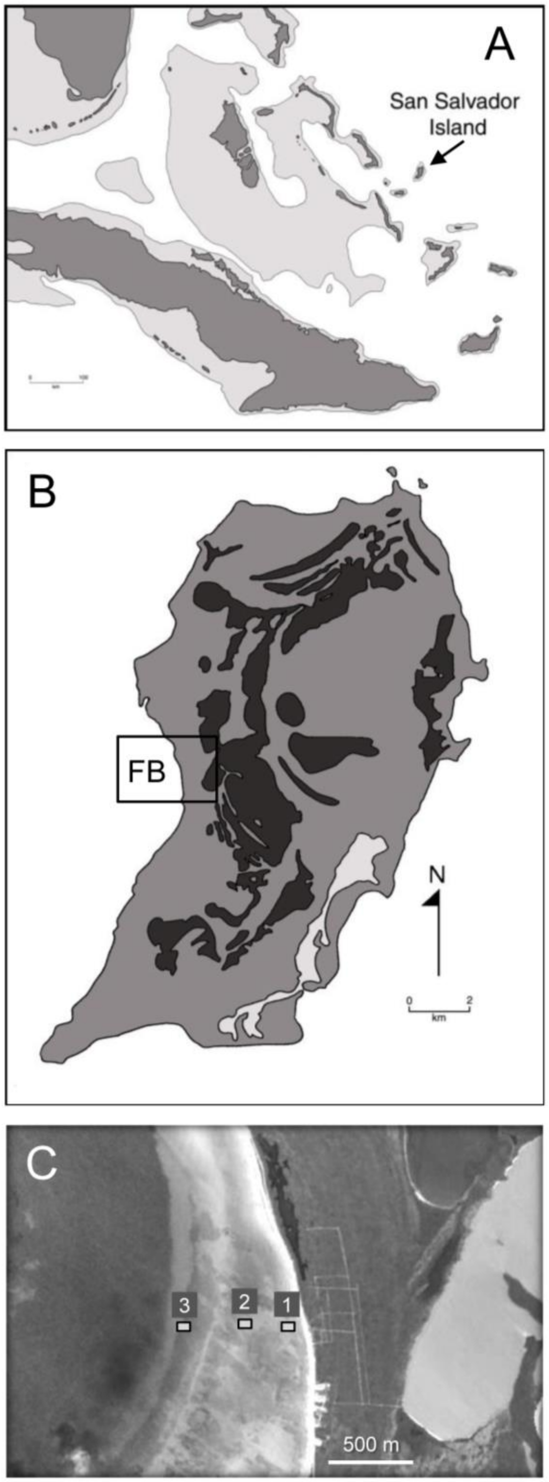

Figure 1. A. The island of San Salvador. B. Fernandez Bay (FB), the study area. C. The Telephone-Pole-Reef transect, showing the location of the three study sites.

conchs and recorded the attached foraminifera *Cornuspiramia*, *Planorbulina*, and *Homotrema rubrum.* Malella (2007) assessed fluvial effects along a gradient off north Jamaica using upright and inverted ceramic tiles, which were recovered after one year. Foraminifera included *Planorbulina* spp., *Carpenteria utricularis*, *Gypsina plana*, and *Homotrema rubrum*.

The SSETI project (Shelf and Slope Experimental Taphonomy Initiative) has provided some of the most detailed information to date on attached foraminifera in the West Indies, especially in recent papers dealing exclusively with foraminifera (Richardson-White and Walker, 2011; Walker et al., 2011). Experimental substrates (shells) were deployed in transects at Lee Stocking Island, Bahamas, in 1993 and 1994, with depths ranging from 15 meters to 270 meters. Shells were recovered at intervals of 1, 2, and 6 years. A total of 11 taxa of foraminifera were found firmly attached to the substrates; in addition to the taxa mentioned above, these included *Bdelloidina ?aggregata*, *Carpenteria balaniformis*, *Gypsina globularis*, and *Gypsina vesicularis.*

STUDY AREA AND METHODS

Field Work

This investigation took place in Fernandez Bay on the west side of San Salvador (Figure 1). In order to test the hypothesis of different rates of growth along a shore to shelf-edge transect, 4x4 inch travertine tiles were attached to concrete blocks by nylon fishing line and deployed in March 14-18, 2011. Eight tiles were attached to each block (Figure 2): two on the top of the block, one on the ‘ceiling’ of each hole, one on a wall in each hole, and one on the ‘floor’ of each hole. Four blocks were put on the seafloor at each of three stations along a transect through Telephone Poll Reef and ending at Vicki's Reef. Four were put in a near-shore location 55 meters from shore in 1-2 meters (4-5 feet) of water. Four were placed in 6 meters (19 feet) of water, and four were placed at the platform

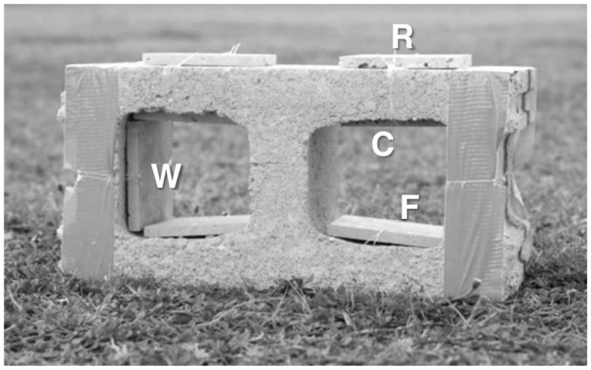

Figure 2. One of the concrete blocks used in the study showing 4x4-inch travertine tiles attached by fishing line to the roof (R), ceiling (C), wall (W), and floor (F) of the two openings.

wall (Vicki's Reef) in 27 meters and 31 meters (87 feet and 103 feet).

In June 2011, two blocks were recovered from each site along the transect, which provided three months of growth data. In addition, two blocks were recovered (by lift bag) from a deployment by Tichenor and Lewis in June 2010, yielding one-year tiles from 31 m. In September 2011, we collected the remaining two blocks at each site for the six-month recovery data. All blocks were photographed *in situ* prior to recovery, and again back at the Gerace Research Centre, where each tile was removed, rinsed with tap water, and photo-documented prior to packaging.

Laboratory Methods

Once at Auburn University, high-resolution photographs of each tile were taken: one of the entire tile, and one each of five 10-cm^2 quadrats per tile (the *center*, *top-left*, *top-right*, *bottom-left*, and *bottom-right*). The tiles were then soaked in water softener (Calgon®) and brushed with a soft brush to remove loose material. Foraminifera firmly attached to the tiles were identified and counted using a Nikon Stereo-200 m binocular microscope; free foraminifera (e.g., *Neoconorbina*) were not considered. Taxa identification was done with the aid of classical references (e.g., Bock et al., 1971; Loeblich and Tappan, 1988) and more recent literature (e.g, Perrin, 1994; Walker et al., 2011). Taphonomic states were recorded as in Buchan and Lewis (2009): live, pristine, good, altered, and very altered. Pristine tests were in the same state as those of live specimens, while good tests had some minor damage, particularly around the exterior of the test; altered had more extensive breakage and abrasion to test, and very altered tests showed a high degree of breakage and surface pitting (Figure 3). All encrusting organisms were identified, but, except for foraminifera, no attempt was made at identifying genera and species.

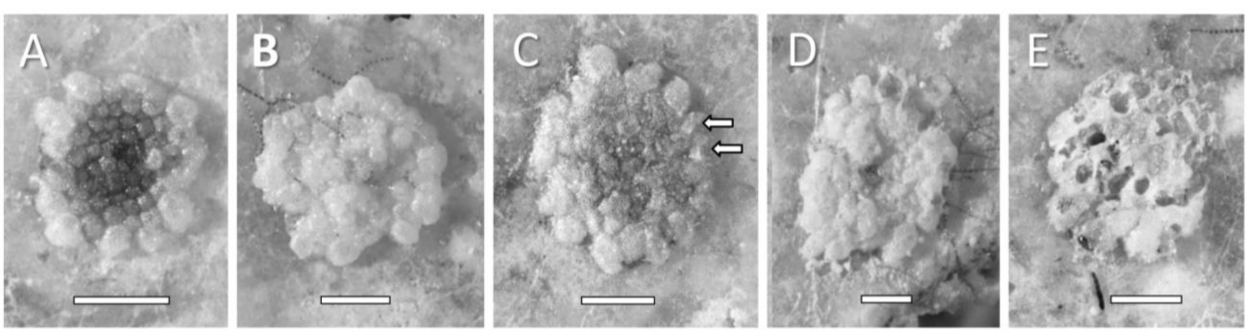

Figure 3. The taphonomic states as recorded in this study, illustrated by Planorbulina acervalis *from the patch reef at site 2 after three months. A. Live. B. Pristine. C. Good (note minor damage at arrows). D. Altered. E. Extremely altered. The scale shown in all figures is 0.5mm. Note that the full range of taphonomic conditions is shown in the first recovery, underscoring the early settlement of this taxon; see also Figure 6.*

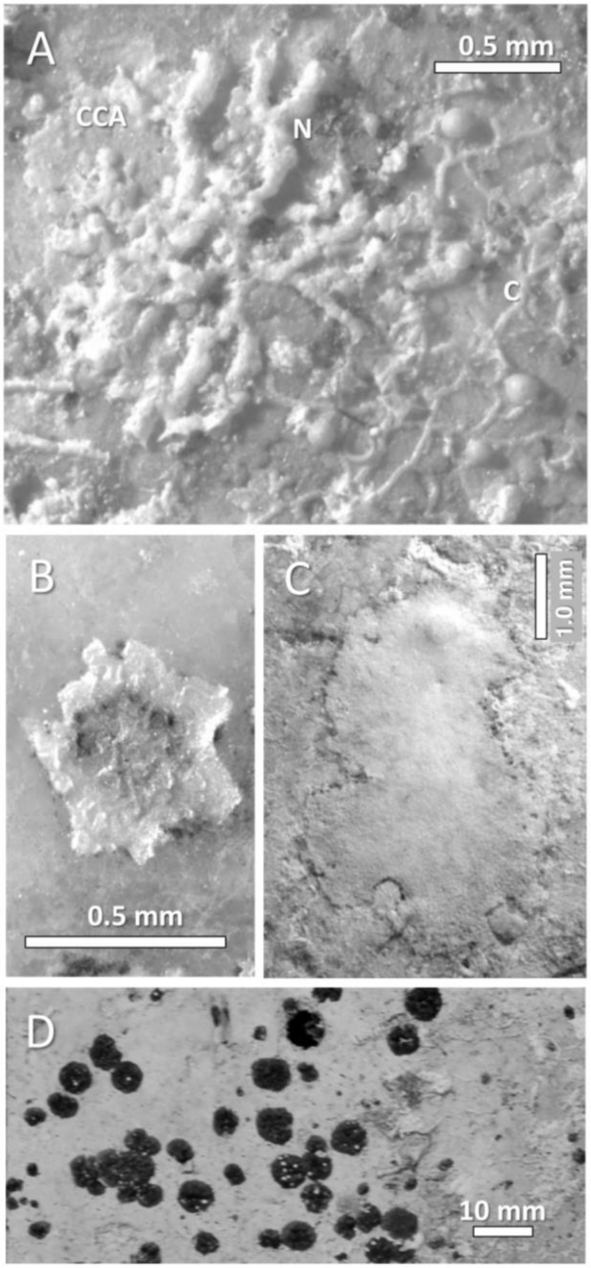

Figure 4. Select examples of attached foraminifera. A. Small Nubecularia sp. *(N) attached to a crustose coralline alga (CCA), with* Cornuspiramia ?antilarum *(C) at right, site 1, three months. B.* Acervulina inhaerens *showing characteristic star-like outline, site 1, three months. C.* Gypsina plana*, the largest of the three specimens found at site 3 after one year, found on a floor tile after one year. D.* Homotrema rubrum *found growing on a tile after one year, site 1, ceiling.*

RESULTS

Taxa Found

The only agglutinated taxon present is *Placopsilina*; we have not yet attempted species-level identification of our few specimens of this genus. As in the prior cobble study (Tichenor and Lewis, 2009, 2011), nubecularids play a minor but significant role. The presence and relative abundance of *Cornuspiramia c.f. C. antilarum* was noted, but is not included in the quantitative analysis in the present discussion because of the difficulties of analyzing its narrow, repeatedly branching test. A range of sizes are seen in what we identify as the genus *Nubecularia*. As in the previous cobble study, we distinguish between a small, radiate form (Figure 4A) and a large, linear morphotype. In addition, among the minor taxa and morphotypes not included in this report are several that may belong to this genus or closely related genera.

The remaining taxa are rotaliines, apparently the same species as those from related studies. We provisionally identify all of our *Planorbulina* as *P. acervalis*, although we recognize morphologic variation including color differences in our material. Although *Acervulina inhaerens* Schultz, 1854, and *Gypsina plana* Carter, 1877, have been considered as synonyms by some authors, and the history of their taxonomy is convoluted (see Plaziat and Perrin, 1992), Perrin (1994) clarifies the differences by thin-section and SEM analyses. In this study, we make the distinction between them and use *Acervulina inhaerens* for a form with a small test with an irregular radiate outline (Figure 4B) and *Gypsina plana* for the much larger tests with a smoothly lobate perimeter (see also Walker et al., 2011, who apparently do the same). We follow common usage of the term *Homotrema rubrum* for the common red-colored attached foraminifer found on the island, but we do not mean to imply a distinction from *Miniacina*, as the two are difficult to distinguish as adults (Krautwig et al., 1998).

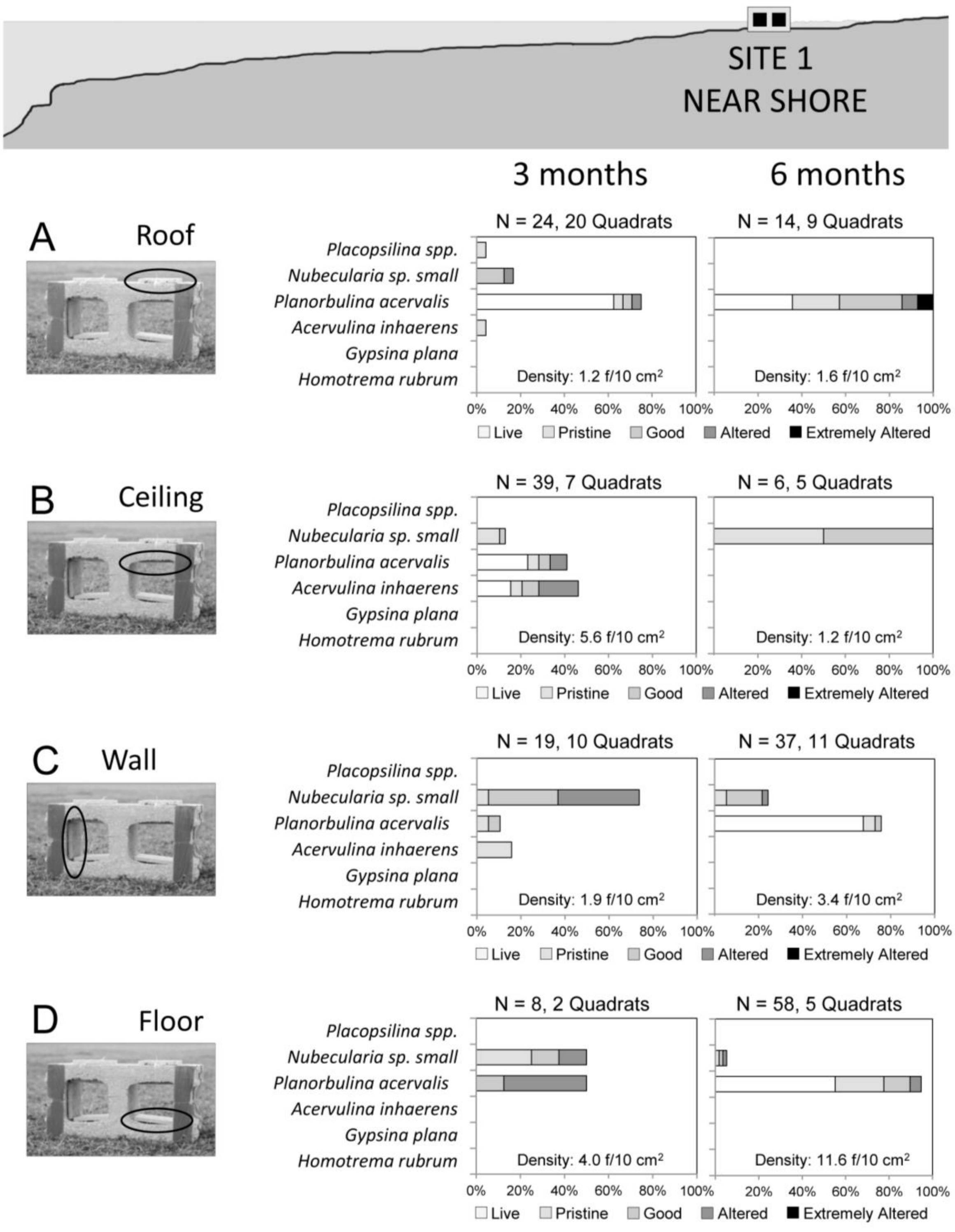

Figure 5. The results to date from the near-shore site after 3 months and 6 months. Relative abundance is shown as percent of individuals counted to date. Minor taxa and morphotypes are not included.

Site 1. Near Shore (Figure 5)

Condition of Implants. Although the four blocks were placed in natural depressions in March 2011 in order to protect them from heavy surf activity, some blocks were tilted, and one of the

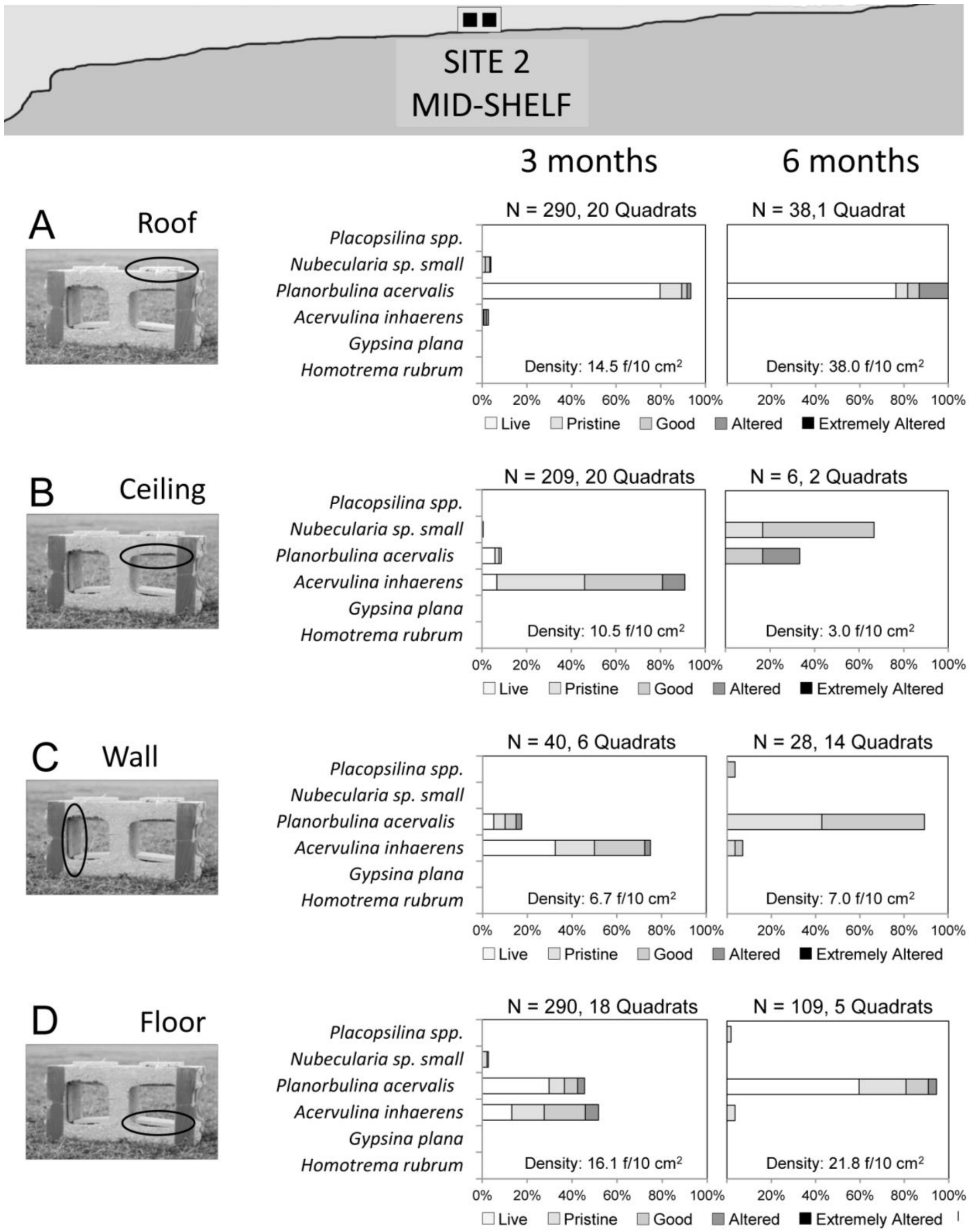

Figure 6. The results to date from site 2, a mid-shelf patch reef. Relative abundance is shown as the percent of individuals counted to date. Minor taxa and morphotypes are not included.

roof tiles was found in the sediment next to a block. The majority of tiles were covered with sediment, attributed to tidal energy and periodic storms, and required an unusual amount of cleaning. Each of the two blocks recovered in September 2011 had lost a roof tile; only one was recovered. One of the blocks was turned on its side. Sand cover on these tiles was significantly more abundant than in the three-month near-shore tiles, making it more difficult to prepare the tiles for study. In general, attached foraminifera are sparse on the near-shore tiles.

Roof. Roof tiles have the most crustose coralline algae (CCA) compared to the other tiles; serpulid worms are also common. The foraminiferal assemblage at three months is dominated by *Planorbulina*, most of which were live at the time of collection. In contrast, the assemblage studied to date has only one specimen of *Acervulina*. At six months, only *Planorbulina* occurse in the nine quadrats studied.

Ceiling. CCA are abundant but fewer than on roof tiles. The foraminifera found on the ceiling tiles at three months are dominated by *Acervulina* and *Planorbulina*, with *Acervulina* much more prevalent than on the roof tiles. *Nubecularia* is also present, and at six months, it is the only species found to date.

Wall. CCA are once again the dominant encruster on wall tiles, followed by relatively large serpulid worms, and small *Nubecularia*. A brown-colored sediment was found affixed to wall tiles in some quadrats that may have obscured other encrusters. By six months, large tests of *Planorbulina* occur along with small *Nubecularia*.

Floor. CCA are the most abundant encruster on floor tiles, followed by large *Planorbulina*, small *Nubecularia*, and serpulid worms. As in the wall tiles, large *Planorbulina* are particularly conspicuous after six months. *Cornuspiramia* was also common on floor tiles.

Site 2. Mid-Shelf Patch Reef (Figure 6)

Condition of Implants. Blocks deployed at the patch-reef location were partially covered by overhanging coral heads, allowing for part of the block to be in sun during the day, with the other part in the shade. These blocks were better protected from aggressive tidal currents and wave energy than were the near-shore blocks, and all were found in their original upright position; all tiles were found still attached to the blocks. On average, tiles from the mid-shelf were much cleaner than near-shore tiles; i.e., they were free from excessive sediment buildup. Overall, densities of attached foraminifera are relatively high at this site.

Roof. Roof tiles have considerably less CCA accumulation on patch-reef tiles compared to near-shore roof tiles. *Planorbulina* dominates assemblages, which include minor amounts of small *Nubecularia*.

Ceiling. Ceiling tiles were the most devoid of encrusting activity on all patch-reef tiles. In the three-month recovery, CCA are virtually non-existent in some quadrats, with serpulid worms becoming the dominant encruster. Bryozoans are also found in limited numbers. *Acervulina* is very common at three months, whereas *Planorbulina* is rare, the reverse of the roof assemblage (Fig. 4A). The six-month tiles lack *Acervulina*, but the data are very limited at present. Small *Nubecularia* were found along with serpulids and more CCA than in the three-month recovery.

Wall. CCA are more abundant on wall tiles than on ceiling and roof tiles at three months, while serpulid worms are less common than in ceiling-tile counterparts. *Planorbulina* is slightly more common on wall tiles than on ceiling tiles, but *Acervulina* dominates the assemblage (Fig. 4C). *Cornuspiramia* is also fairly abundant, but less common than *Planorbulina/Acervulina*. At six months, serpulid worms, CCA, and small-large *Planorbulina* are the major encrusters on wall tiles, followed by patches of *Cornuspiramia*. *Acervulina* is relatively rare.

Floor. CCA are the dominant encruster on floor tiles, which were found covered by a significant amount of sediment, particularly in the six-month recovery. *Planorbulina* and *Acervulina* occur in approximately equal amounts in the three-month sites, but *Acervulina* is nearly absent at six months, whereas *Planorbulina* are numerous and large.

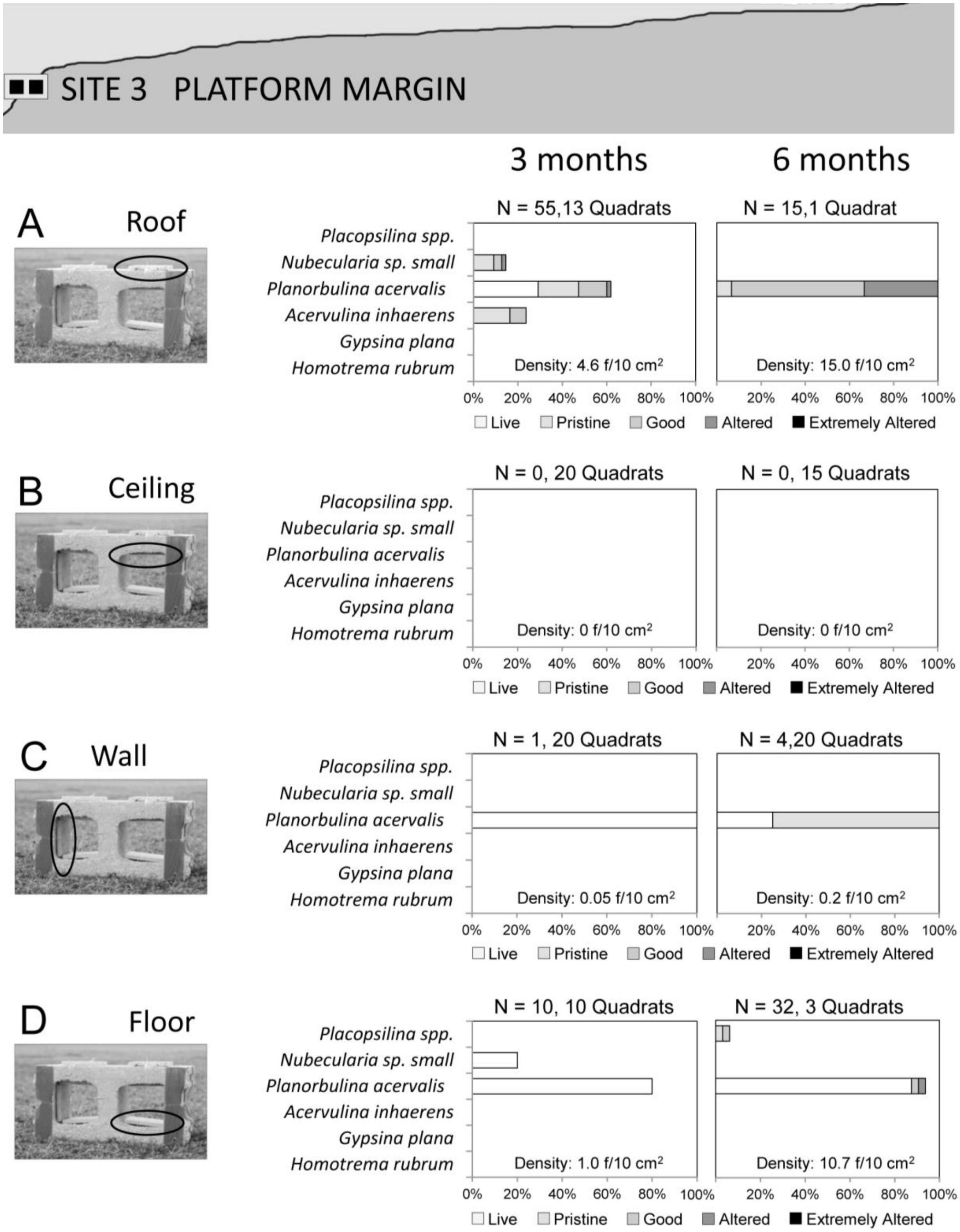

Figure 7. Results to date from the platform edge at Vicki's Reef after 3 months and 6 months. Relative abundance is shown as percent of individuals counted. Minor taxa and morphotypes are not included.

Site 3. Wall at Platform Margin (Figures 7-8)

Condition of Implants. Although blocks deployed prior to this study at the top of the wall (~12 m) were never recovered and were presumed to have been swept over the side by strong wave action, the blocks we placed in protected areas on wall ledges at depths of 27 and 31 m were found in an undisturbed condition, and all tiles remained in place. Data to date from tiles found on the 2 blocks recovered at three months and at six months are shown in Figure 7; data based on the two blocks in place for one year, which were deployed without roof tiles, are given in Figure 8. In general, encrusters are scarce on all wall tiles, and foraminifera are especially rare and individuals are small. Large serpulid worms and relatively large bryozoans are the most common encrusters on wall tiles in general, but their counts are significantly smaller than those on near-shore or patch-reef tiles.

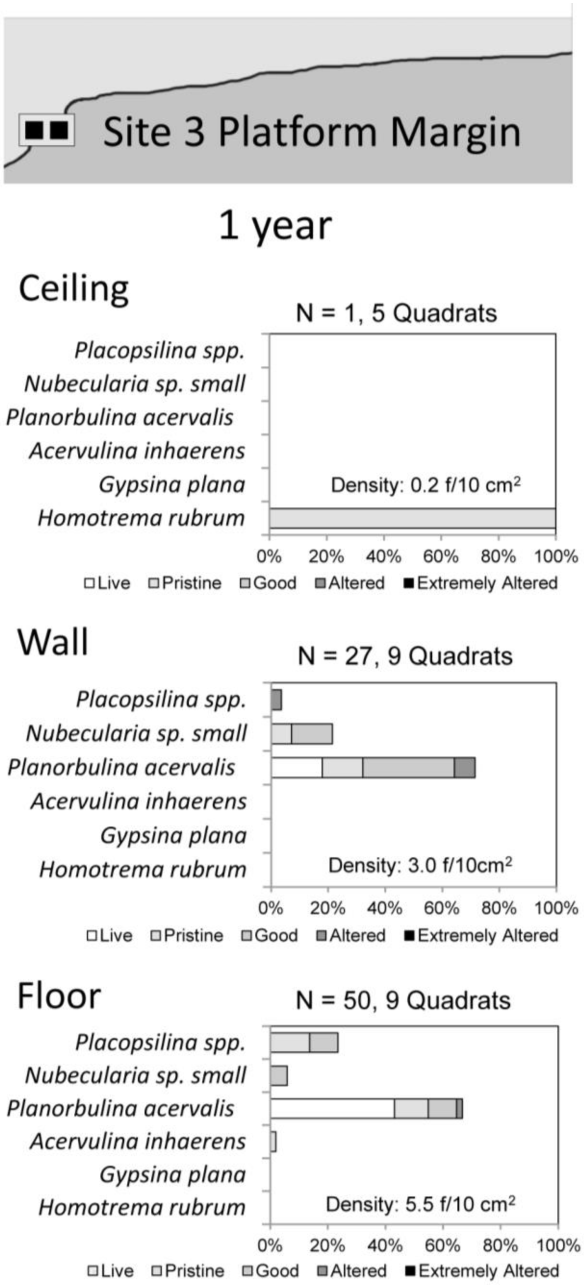

Figure 8. The results to date from the platform edge at Vicki's Reef after one year; water depth is 31 m. No roof tiles were attached in this earlier deployment. Relative abundance is shown as the percent of individuals counted to date. Minor taxa and morphotypes are not included.

Roof. Roof tiles showed the most biologic activity and were the only tiles to show CCA growth. Serpulid worms are notable on roof tiles. At three months, *Planorbulina* dominates an assemblage of foraminifera that includes *Acervulina* and small *Nubecularia*. Only *Planorbulina* is known to date from the six month recovery.

Ceiling and Wall. No foraminifera have been found on the ceiling tiles recovered after three months or after six months (Figure 7B) even though a total of 35 quadrats have been examined to date. Wall tiles are also essentially barren: only a few *Planorbulina* occur. After one year (Figure 8), the ceiling-tile data include one small (~1mm) ?*Homotrema*. One-year wall tiles have significantly higher foraminifera counts than those at three and six months, with *Planorbulina* continuing as the most common genus, followed by *Nubecularia* and *Placopsilina*. Two specimens of *Gypsina plana* occur outside the gridded area on a ceiling tile and another on a wall tile.

Floor. Small specimens of *Planorbulina* have been found on floor tiles after both three and six months, along with small *Nubecularia* at three months and *Placopsilina* after six months. In the one-year recovery, *Planorbulina* continues to be the most abundant, but specimens are relatively small. *Placopsilina* appears to be more common at this site than on the platform top (Figure 8). One specimen of *Gypsina plana* was found outside the gridded area (Figure 4).

DISCUSSION

The settlement experiments described here represent the first phase of our program, focusing on growth within the first year. Shallow-water encrusting foraminifera have received little detailed research attention within this time period (e.g., the SETTI experiments took place at water depths of 15 m and greater and recoveries began after one year). Consistent with the existing literature, our findings underscore that these early settlers were a low-diversity assemblage of opportunists: chiefly *Planorbulina*, *Acervulina*, *Cornuspiramia*, and small *Nubecularia*. The majority of foraminifera were found either alive or in pristine condition, which was expected considering the short deployment time of the tiles.

Our transect through Telephone Pole Reef consisted of one station in a mid-shelf patch reef (site 2); one in a near-shore, shallow-water location (site 1) that was stressed by tidal affects and surf; and the third at the platform edge (site 3), in conditions markedly different than those seen along the platform top. Starting with site 2 as the site with the largest dataset to date (Figure 6), the effects of tile orientations and different lighting conditions can be seen most clearly here. Most attached foraminifera are scarce on the sunlit roof tiles, where they have to compete for space with filamentous and crustose coralline algae. Only *Planorbula acervalis* thrives under these conditions, making up over 90% of the foraminiferal assemblage after three months. In contrast, *Acervulina inhaerens* flourishes on the shaded ceiling and wall tiles during the same time period, and the two taxa occur in approximately equal numbers on the floor tiles under mixed-lighting conditions. Curiously, *A. inhaerens* is rare at six months (at all sites) even though the number of specimens at site 2's floor (Figure 6D) is over 100. We speculate that the species is among the first wave of encrusters and is short lived; because it is not cemented to the substrate, it would fall off after death. We note that it absent or extremely rare at all sites after three months.

Our experiment shows limited support for the hypothesis that *H. rubrum* grows quickly in near-shore, high-energy conditions and that *G. plana* grows slowly under higher depth, stressed conditions at the platform margin. We have not found any *H. rubrum* to date on the three-month or six-month tiles from site 1 (June-September 2011). However, the taxon was found previously on a one-year recovery (June 2009-May 2010) from the same location. There are several possible explanations: (1) our blocks may have not been deployed at the correct disance from shore or not in the correct micro-enviroment, although this seems unlikely because we followed Tichenor's field notes closely; (2) *H. rubrum* settlement may depend on the season or even year-to-year variations (the species was observed by Lewis to be prolific on the beachrock in this area in 2003); and (3) *H. rubrum* may not be among the first foraminifera to encrust in this locality, but may appear here later than six months.

Although we suspect the second explanation has some merit, late settlement has also been reported by other researchers. Parsons (1993) found *Planorbulina* as early as one week after substrate deployment, whereas *Homotrema rubrum* did not occur after six months but was known from storm rubble dated at 2.5 years. Hall (1997) found *Planorbulina* after only one month in a reef environment and did not find *Homotrema rubrum* in implants deployed for up to one year but did find them on subfossils shells. Earlier, Adey and Vasser (1975) estimated a time period of one year for the appearance of *H. rubrum*. However, we note that late recruitment is not the same as slow growth. Specimens of *Homotrema rubrum* are common on our tiles from the previous one-year deployment at the near-shore zone and some are rich with full-sized (adult) individuals, as much as 6 mm in diameter (Figure 4D). Thus, it appears that they grew to this size within the six-month to one-year time interval. That is, late recruitment may be a modification to the Tichenor hypothesis rather than negating it: once the species finally gets started, it may grow fairly rapidly and dominate the near-shore foraminiferal assemblage.

We have found only four specimens of *Gypsina plana*, all at the deepest site on the platform margin (31m) and all after one year. All individuals lie outside the area assessed; therefore, they do not appear in the data above. In spite of close examination of 16 tiles, we found no examples of it earlier than one year. Nor did we find any specimens of it at sites 2 or 3. Thus, the limited dataset we have suggests selectivity with regard to location, and late recruitment at the optimal site. Unlike *Homotrema rubrum*, which was found at adult size after one year at site 1, the *G. plana* specimens are approximately one-tenth the size of adult tests, which commonly measure 30-40 mm in diameter. Although we have no data on rate of growth, the paucity of encrusters in general and diminutive size of foraminifera in particular at this site indicate that environmental conditions here were unfavorable. Thus, we infer that the species is slow to start and may grow slowly over a long life span as has been suggested for other large foraminifera (Hallock, 1985). Although somewhat conjectural, this is consistent with the understanding of other researchers about *Gypsina plana*'s life history (e.g., Walker et al., 2011).

Tiles deployed by Tichenor and Lewis in earlier years at Dump Reef and Gaulin's Reef were recovered, but have yet to be analyzed at the time of this article. Initial observations show that foraminferal assemblages include abundant *Homotrema* and large *Nubecularia*, as well as *Planorbulina* and will be as much as an order of magnitude greater in area covered than are the three- and six-month tiles at Telephone Poll Reef.

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REFERENCES

Adey, W.H., and Vassar, J.M., 1975, Colonization, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales): Phycologia, v. 14, p. 55-69.

Armstrong, H.A., and Brasier, M.D. 2005, Microfossils, 2nd Ed. Oxford, UK: Blackwell Publishing, 296 p.

Bock, W.D., Lynts, G.W., Smith, S., Wright, R., Hay, W.W., and Jones, J.I., 1971, A symposium of Recent South Florida foraminifera: Miami Geological Society, Memoir, 1, p. 245.

Buchan, O.C., and Lewis, R.D., 2009, Recent large benthic foraminifera as indicators of grassbed characteristics, San Salvador, Bahamas: The addition of taphonomy, *in* Demchuk, T.D., and Gary, A.C., eds, Geologic Problem Solving with Microfossils: SEPM Special Publication No. 93, p. 83-92.

Choi, D.R., and Ginsburg, R.N, 1983, Distribution of coelobites (cavity dwellers) in coral rubble across the Florida reef tract: Coral Reefs, v. 2, p. 165–172.

Choi, D.R., 1984, Ecological succession of reef cavity-dwellers (coelobites) in coral rubble: Bulletin of Marine Science, v. 35, p. 72-79.

Echols, C.S.d.E., 1995, Epibionts and Their Effects on the Taphonomy of Recent Crinoid Ossicles, Friday Harbor,Washington, and San Salvdor, Bahamas: Unpublished M.S. Thesis, Auburn University, 161 p.

Elliott, J.M., Logan, A., and Thomas, M.L.H., 1996, Morphotypes of the foraminiferan *Homotrema rubrum* (Lamarck): Distribution and relative abundance on reefs in Bermuda: Bulletin of Marine Science, v. 58, p. 261–276.

Gischler, E., and Ginsburg, R.N., 1996, Cavity dwellers (coelobites) under coral rubble in southern Belize barrier and atoll reefs: Bulletin of Marine Science, v. 58, p. 570–589.

Hall, J., 1998, Experimental Taphonomy and Neoichnology of *Strombus gigas* (Queen Conch) at San Salvador, Bahamas: A Comparison with the Fossil Record: Unpublished M.S. Thesis, Auburn University, 106 p.

Hall, J.K., and Lewis, R.D., 1997, Taphonomy and neoichnology of *Strombus gigas* (Queen Conch) at San Salvador island, Bahamas: Proceedings of the 8th Symposium on the Geology of the Bahamas and Other Carbonate Regions, May 30-June 3, 1996. Bahamian Field Station, San Salvador, Bahamas, p. 103-108.

Hallock, P., 1985, Why are larger foraminifera large?: Paleobiology, v. 11, p. 195-208.

Haynes, J.R., 1981, Foraminifera: London, Mac Millan Publication, Lmt., 433 p.

Krautwig, D.W.H., Hottinger, L., and Zankl, H., 1998, The lamellar-perforate, arborescent and coloured foraminifers *Miniacina*, *Homotrema*, and *Sporadotrema*: Facies, v. 38, p. 89-102.

Lewis, R.D., and Echols, C.M.H.M.S., 1994, Attachment studies on plastic panels and calcium-carbonate skeletal substrata in Fernandez Bay, San Salvador Island, Bahamas. Proceedings of the 26th Meeting of the Association of Marine Laboratories of the Caribbean, June 11-16, 1994: Bahamian Field Station Limited, p. 126-146.

Lipps, J.H., 1993, Fossil Prokaryotes and Protists: Boston, Blackwell Scientific Publications, Inc, 342 p.

Loeblich, A. J., and Tappan, H., 1988, Foraminiferal Genera and Their Classification. V.1-2: New York, Van Nostrand Teinhold Co., 1728 p.

Malella, J., 2007, Coral reef encruster communities and carbonate production in cryptic and exposed coral reef habitats along a gradient of terrestrial disturbance: Coral Reefs, v. 26, p. 775-785.

Martindale, W., 1992, Calcifed epibionts as palaeoecological tools: Examples from the recent and Pleistocene reefs of Barbados: Coral Reefs, v. 11, p. 167–177.

Meesters E., Knijn R., Willemsen P., Pennartz R., Roebers G., and Soest R.W.M., 1991, Sub-rubble communities of Curaçao and Bonaire coral reefs: Coral Reefs, v. 10, p. 189–197.

Murray, J.W., 1991, Ecology and Paleoecology of Benthic Foraminifera: New York, Pearson Education, 397 p.

Parsons, K.M., 1993, Taphonomic Attributes of Mollusks as Predictors of Environment of Deposition in Modern Carbonate Systems: Northeastern Caribbean: Unpublished Ph.D. dissertation, The University of Rochester, Rochester, N.Y., 418 p.

Perrin, C., 1994, Morphology of encrusting and free living acervulinid foraminifera: *Acervulina*, *Gypsina* and *Solenomeris*. Palaeontology 37, 425–458.

Plaziat, J., and Perrin, C., 1992, Multikilometer-sized reefs built by foraminifera *(Solenomeris)*from the early Eocene of the Pyrenean domain (S. France, N. Spain): Palaeoecologic relations with coral reefs: Palaeography, Palaeoclimatology, Palaeoecology, v. 96, p. 195-231.

Richardson-White, S. and Walker, S.E., 2011, Diversity, taphonomy and behavior of encrusting foraminifera on experimental shells deployed along a shelf-to-slope bathymetric gradient, Lee Stocking Island, Bahamas: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 312, p. 305–324.

Tichenor, H.R., and Lewis, R.D., 2009, Distribution of attached (encrusting) foraminifera across a carbonate platform, San Salvador Island, Bahamas: Preliminary results: Geological Society of America Abstracts with Programs, v. 41, p. 53.

Tichenor, H.R., and Lewis, R.D., 2011, Zonation of attached (encrusting) foraminifera across a small carbonate platform, based on species assemblages and area covered, San Salvador, Bahamas: Geological Society of America Abstracts with Programs, v. 43, p. 71.

Walker, S.E, Parsons-Hubbard, K., Richardson-White, S., Brett, C., and Powell, E., 2011, Alpha and beta diversity of encrusting foraminifera that recruit to long-term experiments along a carbonate platform-to-slope gradient: Paleoecological and paleoenvironmental implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 312, p. 325–349.