

**Distribution of encrusting foraminifera at Cat Island,
Bahamas: Implications for foraminiferal assemblages in the geologic record**

by

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Encrusting foraminifera, paleoecology, carbonates,
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Abstract

Benthic foraminifera that are cemented by calcium carbonate or are otherwise firmly fixed to hard surfaces are commonly known as encrusting foraminifera. Very few studies focus on the use of encrusting foraminifera as paleoenvironmental indicators. However, their use as environmental indicators has many potential advantages over free foraminifera: they are sensitive to environmental factors such as light and water energy, and they are fixed in place, meaning they are more likely to stay in the original habitat. This means their tests remain in place after death, leaving a post-mortem history. Previous research on San Salvador, Bahamas, has established a potential model for the occurrence of encrusting foraminifera on small carbonate platforms. In this study, the encrusting foraminifera of neighboring Cat Island were studied and compared with those found at San Salvador.

Cobbles were collected by SCUBA at eight sites representing different environments from near-shore reefs to patch reefs and the platform-margin. Encrusting organisms were examined in 10-cm² quadrats by recording the number of individuals of each species and the area covered by each species. The difference between the various sites is readily apparent from both the overall density of encrusting organisms and the relative proportion of the different encrusting foraminiferan species. The near-shore localities are marked by high density assemblages dominated by well-preserved *Homotrema rubrum* and *Nubecularia*, with site-to-site variability as to which of the two

species is dominant. The patch-reef localities have a lower density of encrusting foraminifera as well as a greater proportion of *Planorbulina* in relation to *Homotrema rubrum*. The encrusting foraminifera at the patch-reef localities are also less well preserved. The shelf-edge locations are distinctive because of their even lower density of encrusting foraminifera and the dominance by *Gypsina plana*. Average size of species decreases offshore with the exception of *G. plana*, and quality of preservation also decreases from onshore to offshore. Most of this data is consistent with prior research on San Salvador, indicating possible trends of encrusting foraminifer occurrence. These trends could be used to perform paleoenvironmental analysis of ancient carbonate deposits.

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1. Introduction

Foraminifera are single-celled marine protists, dating back to the Cambrian Period, that play a major role in sedimentary geology. In most cases, they have a shell, or test, made up of sedimentary particles or of secreted calcium carbonate. There are two distinct groups: planktonic foraminifera, which reside in the water column, and benthic foraminifera, which live on the ocean bottom, either resting on the substrate (free foraminifera) or attached to structures on the ocean bed such as rock cobbles and corals (encrusting foraminifera). While both planktonic and benthic foraminifera are useful when performing biostratigraphic analysis, benthic foraminifera are also uniquely useful for paleoenvironmental analysis. Benthic foraminifera are extremely abundant and diverse, with their distribution patterns being determined by various environmental factors, including depth, salinity, and temperature (Armstrong and Brasier, 2005).

Interpretations of paleoenvironments derived from foraminifera require a firm understanding of how foraminiferal assemblages change with environmental factors. This is accomplished through the use of actualistic paleontological principles; that is, modern-day organisms and their lifestyles are studied in order to better understand ancient organisms. In this case, modern distribution patterns of foraminifera can be used to better understand the distribution of ancient foraminifera and potentially identify the paleoenvironments in which they lived.

Encrusting foraminifera are poorly known compared to their planktonic and free-living benthic counterparts. Very few studies focus on the use of encrusting foraminifera as paleoenvironmental indicators (Martindale, 1992; Bosellini and Papazzoni, 2003; Richardson-White and Walker, 2011; and Walker et al., 2011). However, the use of encrusting foraminifera as environmental indicators has many advantages. For example, by their very nature, encrusting foraminifera are fixed in place, making them difficult to transport and erode. In order to be transported, they either have to be broken off their substrates, or the entire substrate has to be transported with them. They also are extraordinarily sensitive environmentally, and they are diverse and abundant in their respective preferred environments.

In this study, the distribution of encrusting foraminifera at Cat Island, Bahamas, was investigated through analysis of clasts from locations selected along the onshore-to-offshore transition in order to (1) discover any patterns in distribution that might help to identify the environments present, to (2) compare these findings with previous research done on the surrounding islands in the Bahaman chain in order to find large-scale distribution patterns in the region, and to (3) establish criteria for identifying distance from shore and water depth in the geologic record using foraminifera distribution.

2. Previous Works

This section is organized into three parts reflecting the three most important areas of previous research: (1) the distribution of encrusting foraminifera, focusing on two key species, *Homotrema rubrum* and *Gypsina plana*, (2) the ecologic succession of encrusting foraminifera, and (3) the use of these encrusting foraminifera in paleoenvironmental analysis.

Distribution

Homotrema rubrum – *Homotrema rubrum* is the most widely recognized encrusting foraminiferan. Because of its distinctive red color and cosmopolitan distribution, it has been the subject of more research than any other encrusting species (Hickson, 1911; Hofker, 1927; MacKenzie et al. 1964; Rooney, 1970; Krautwig, 1998; Pillarczyk and Reinhardt, 2012; and Pillarczyk et al., 2014). However, different onshore-offshore distributions have been reported in the literature, as discussed below.

MacKenzie et al. (1964) researched *Homotrema rubrum* and its potential as an indicator of sediment transport off the coast of Bermuda. Using sediment samples collected from various locations on the Bermuda platform, they concluded that *Homotrema rubrum* originated in offshore outer-reef environments, with its presence in near-shore locations showing clear shoreward sediment transport. Other investigators (e.g., Gischler et al., 2003) also indicate that *Homotrema rubrum* reaches maximum abundance at platform-margins.

Choi and Ginsburg (1983) performed research on the distribution of encrusters, including *Homotrema rubrum*, in the Florida Reef Tract based on the analysis of cobbles.

They obtained samples of coral rubble from 21 different locations, representing different environments such as lagoon, lagoon-reef, marginal reef, and fore-reef. They chose large cobbles (averaging 20 to 30 cm in diameter) that would escape frequent movement during storm events, allowing for greater development of encrusters. Like the investigators before them, they found *Homotrema rubrum* to be more common on the platform-margin in deeper water than the near-shore environments in more shallow depths. In contrast, Tichenor and Lewis (2009) found that *Homotrema rubrum* dominated near-shore assemblages at San Salvador Island and was less common at the shelf edge.

In addition to distribution of species, *Homotrema rubrum* occurs in a number of forms (morphotypes; Fig. 1) and these may be limited by environmental variables. In a shape variation study, Elliot et al. (1996) found distinct morphotypes of *Homotrema rubrum* in Bermuda reefs. They collected 4002 specimens of *Homotrema rubrum* from various settings and found that these morphotypes varied with environmental conditions. For example, knobby and globose tests were dominant in restricted microenvironments, whereas hemispherical tests were most common on exposed reef substrates. However, this variance was only present on the small scale. Similar frequencies of the five morphotypes were found at all localities, indicating the variance of morphotypes is dependent on environmental conditions such as degree of illumination.

Gischler (1997) studied encrusters on the undersides of coral rubble collected from 10 sites in the Florida Reef Tract in order to see if a zonation existed in this area.

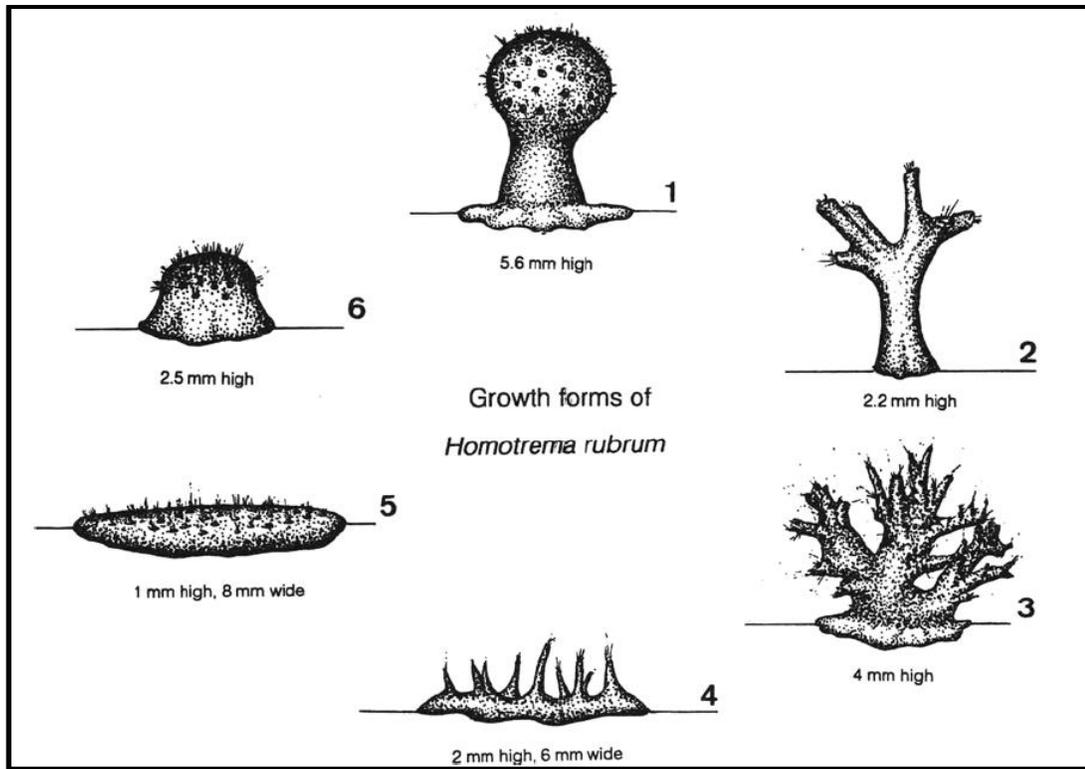


Figure 1- The morphotypes of *Homotrema rubrum* (Krautwig et al., 1998).

Among the encrusters studied was the seemingly ever-present *Homotrema rubrum*, while other foraminifera were not included in this study. Gischler compared the variance of several different types of encrusters between three reef types (Table 1). What is immediately noticeable is the high level of variance in *Homotrema* between the reef and the back reef, apparently caused by the high abundance of *Homotrema rubrum* on the reef proper. While encrusting foraminifera were not the main focus of Gischler's study, his results hint at the distribution zonation of *Homotrema*, which would be further explored in later studies.

Gypsina plana – Competing models of foraminiferal distribution have developed with the key difference revolving around the species known as *Gypsina plana*. While Martindale (1992) claims that *Gypsina plana* is found at all locations from near-shore reefs to offshore reefs, recent work by Tichenor and Lewis (2009, 2011) suggests that *Gypsina plana* is much more common in deep-water wall reefs and is typically not present at all in near-shore reef environments.

Martindale's (1992) study included not only encrusting foraminifera, but calcified epibionts in general, including crustose coralline algae, bryozoans, and serpulid worms. The field location was the island of Barbados in the southeast Caribbean Sea. Four hundred cobbles were obtained from various locations, representing each of the reef environments present (reef surfaces, cavity side ledges, roofs) and ranging from shore to 50-m depth offshore. The distribution of encrusting foraminifera was quantified by counting the number of occurrences/dm². The dominant encrusting foraminiferan on the illuminated surfaces was *Gypsina plana*, whereas shaded, shallow-water areas contained a more varied range of encrusting foraminifera that included *Homotrema rubrum* and

	Reef vs. fore reef	Reef vs. back reef	Back reef vs. fore reef
Crust. cor. algae	0.54	0.03*	0.06
Sponge	0.0005*	0.19	0.08
Bryozoan	0.00001*	0.0003*	0.41
Mollusk	0.45	0.04*	0.01*
Worm	0.05*	0.30	0.46
<i>Homotrema</i>	0.15	0.88	0.27
Total cover	0.0001*	0.34	0.008*
Individuals	0.39	0.83	0.43
Species	0.06	0.18	0.62
H'	0.006*	0.13	0.39
e	0.74	0.71	0.92
Success. stages	0.00001*	0.0002*	0.67

Table 1- Comparison in variance statistics between the different encruster varieties. Note the significant difference in *Homotrema* between the reef types (Gischler, 1997).

Carpenteria utricularis. A clear zonation, from onshore to offshore, of encrusting foraminifera was present (Fig. 2), allowing Martindale to make a preliminary analysis of nearby Pleistocene reefs in Barbados, showing that attached foraminifera, along with other encrusting organisms, could be used as a tool for paleoenvironmental analysis.

Tichenor and Lewis (2009, 2011) studied the distribution of encrusting foraminifera off San Salvador, Bahamas. Using SCUBA when necessary, they collected cobble samples along multiple transects from the shoreline to offshore. Samples were taken from sites representing distinct environments and reef types in the area, such as the near shore, the patch reef, and the deeper water platform-margin known as the “wall.” Samples from these locations were analyzed by counting individuals in 10-cm² quadrats and using digital imaging software (ImageJ) to measure the abundance of foraminifer species at each location. Three species of encrusting foraminifera were recognized as being the most common: *Homotrema rubrum*, *Planorbulina* spp., and *Gypsina plana*. The distribution of species at each location was then compiled into diagrams (Fig. 3).

Tichenor and Lewis (2009) found that *Homotrema rubrum* was most abundant in near-shore environments. *Planorbulina* tended to be present at a relatively stable level throughout the different transects, but was proportionately greatest in the mid-shelf patch reefs. *Gypsina plana* was only abundant in the deep water locations. This is interesting, because it conflicts with the previous study by Martindale in Barbados in 1992, where *Gypsina plana* was found to be present everywhere from near-shore to offshore. This discrepancy is one of the reasons that further study of foraminiferal assemblages in the Bahamas is necessary in order to explore which of the two models, if either, is a more accurate representation for the region.

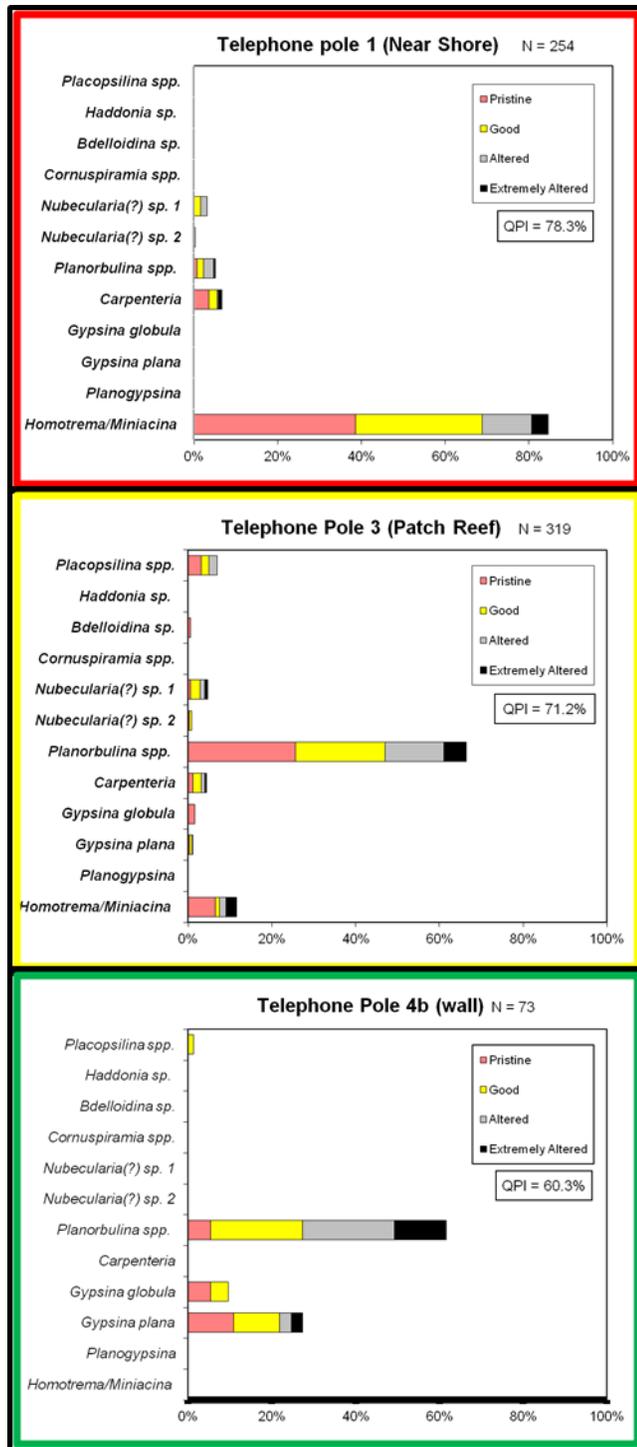


Figure 3- The relative abundance of common encrusting foraminifera along the “Telephone Pole Reef” transect off San Salvador, Bahamas. Note that *Gypsina plana* is much more common in the deep water location of the wall than it is at other sites. Data is based on counts of individuals and QPI is the Quality of Preservation Index, the percent of pristine and good categories (Tichenor and Lewis, 2009).

Ecologic Succession

A great deal of research involving encrusting organisms deals with ecologic succession, or the order in which the organisms appear on the substrate surface. Most of this research is not limited to foraminifera, but includes all encrusting organisms. The succession of encrusting organisms can be studied using (1) cobbles usually consisting of coral rubble, or (2) artificial panels or shells.

Choi (1984) worked to establish ecologic succession of encrusters in the Florida Reef Tract. Using the coral cobbles from the same 21 locations used in the aforementioned Choi and Ginsburg (1983) study, Choi analyzed the order in which the encrusters colonized these substrates and developed an overall model of succession (Fig. 4). He did this by sawing the cobbles vertically and making thin sections from the cut sides of the cobbles. Encrusting foraminifera, including *Homotrema rubrum*, were found to be among the earliest encrusters, usually the first to develop on the substrate.

Parsons (1993), while studying taphonomic attributes of mollusks as a predictor of carbonate depositional environments, touched upon the succession of encrusting foraminifera. Parsons did not find *Homotrema rubrum* in the first six months after initial substrate deposition. She did find *Planorbulina* very early on, however, as soon as one week after initial deposition. These results are matched by experimental research currently underway on San Salvador (Lewis et al., 2012). These studies show that *Planorbulina* occurs much earlier than *Homotrema rubrum*.

Richardson-White and Walker (2011) and Walker et al. (2011) present results from the nearby Lee Stocking Island in the Bahamas that established encrusting

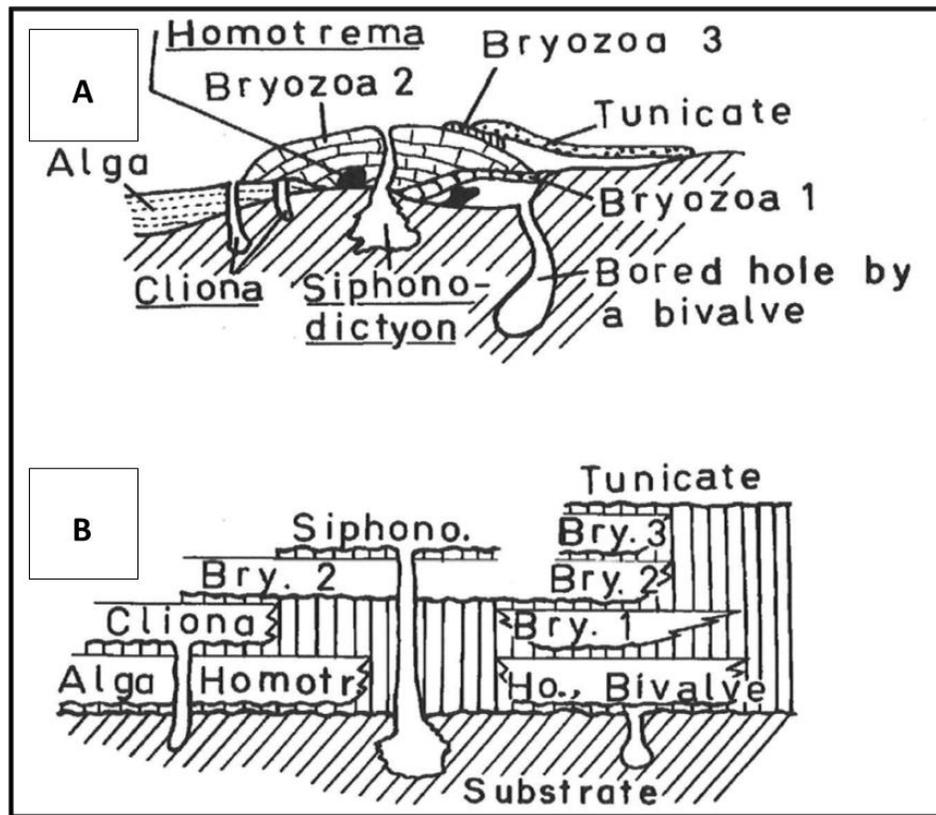


Figure 4- Diagram of encrusters on the underside of a cobble (A) and inferred sequence of colonization (B) (modified from Choi, 1984).

foraminiferal distribution, succession, and taphonomy along a bathymetric gradient. Uniquely, empty gastropod shells were used as substrates, placed inside mesh bags and tied to PVC arrays at six sites along a transect northeast of the island. The depths of the six locations were 15m, 30m, 70m, 183m, 226m, and 253m. It should be noted that the depth of the shelf (15m) and shelf-edge (30m) locations for this study differs from those of later studies (Tichenor and Lewis, 2009), where the depths are considerably lower. A submersible was used to place the bags and to retrieve them after two years. In regards to succession, encrusting foraminifera were found to be more competitive in marine encrusting communities than previously thought. Among the earliest colonizers of new substrate, encrusting foraminifera were found to consistently dominate the gastropod shell surface. After years, they were often found to have completely overgrown the shells. The researchers believed this pointed to the importance of encrusting foraminifera not only as early colonizers, but as contributors to carbonate environments as a whole.

Martin and Lewis (2015) used travertine tiles to test growth rates of attached foraminifera along an onshore-offshore transect in San Salvador, Bahamas. Three stations representing a single transect from onshore to offshore transition were selected. At each station, four concrete blocks were placed on the ocean floor. Eight 4x4 inch travertine tiles were attached to each concrete block, each in a different location on the block: two on the top, one on the ‘ceiling’ of each hole, one on a wall in each hole, and one on the ‘floor’ in each hole. Blocks were recovered at intervals of three months, six months, and one year. *Homotrema rubrum* was not found at any site within the first six months, but did show growth after one year. At the nearshore and patch-reef sites, *Planorbulina acervalis* was found in superior numbers after three months along with *Nubecularia*.

After six months however, *Planorbulina* was only dominant on the sunlit top portion of the blocks with *Acervulina inhaerens* dominating the more shaded regions. Encrusting organisms were scarce at the platform-margin, with *Gypsina plana* only being identified after one year. These findings suggest that *Planorbulina* and *Aervulina* are early settlers, while both *Homotrema rubrum* and *Gypsina plana* are late settlers.

Application to the Geologic Record

The role of encrusting foraminifera in the rock record has not been appreciated fully. Plaziat and Perrin (1992) presented findings demonstrating that an Eocene reef formation along the border between Spain and France, previously thought to have been formed by red algae, was actually formed by the acervulinid foraminiferan *Solenomeris*, a genus related to *Gypsina plana*. The formation is extremely large, 8 km in length, 2 km in width, and nearly 10 m thick. This is in stark contrast to modern-day encrusting foraminifera, which only operate on the mm-scale. Plaziat and Perrin argue that these huge foraminiferal reefs are actually very common in Eocene marine rock. Foraminiferal reefs are thought to have formed due to unusual bathymetry, light exposure, and oxygenation that favored foraminifera over coral. These foraminifera tended to prefer deeper water environments with lower oxygen levels and light exposure than did the coral of the time period.

Bosellini and Papazzoni (2003) conducted a study of an upper Eocene formation called the Nago Limestone located in Trentino, Italy. In this study, they sought to use foraminifera encrusting coral, to differentiate between facies in the Nago Limestone. In order to do this, the Nago Limestone was rigorously analyzed and split into 3 separate facies of a shallowing-upward parasequence. For each facies, the percentages of the

occurrences of the different foraminifera genera were compiled (Fig. 5). From the changes in foraminiferal distribution as the sequence shallowed upward, changes in bathymetry, light, and hydrodynamic energy were interpreted, signaling a clear shift in environment as time progressed. While this study dealt with ancient foraminifera, Bosellini and Papazzoni were able to analyze them because of knowledge of modern foraminifera and their preferred environments. For example, *Acervulina linearis* was closely related to the modern-day foraminiferan *Gypsina plana*, while *Miniacina* resembles modern-day *Homotrema rubrum*.

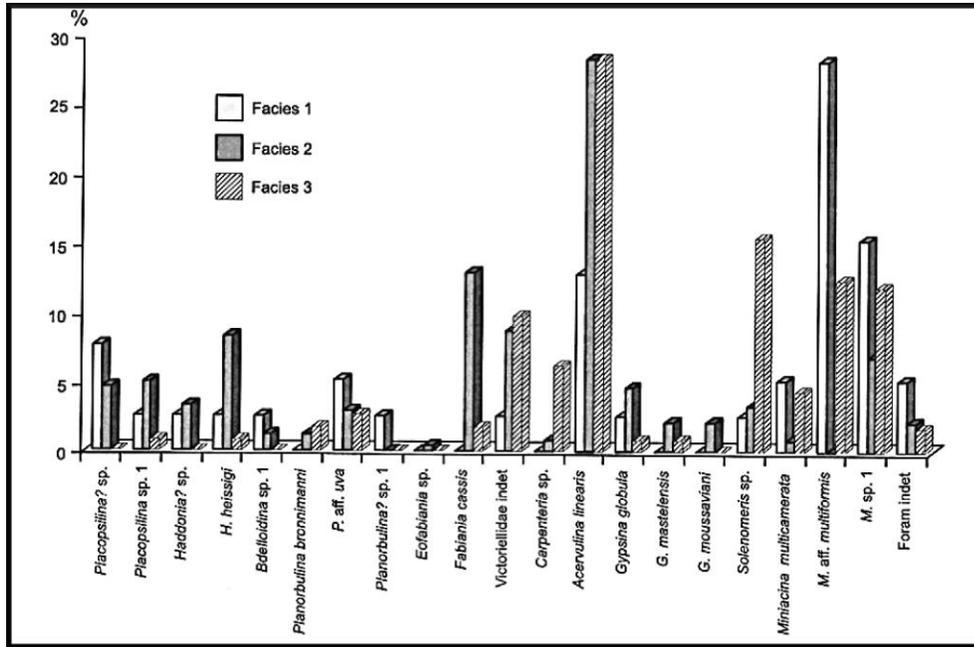


Figure 5- Relative abundance of encrusting foraminifera in the three facies of the Nago Limestone (Bosellini and Papazzoni, 2003). The three facies represent a shallowing upward sequence with Facies 1 on the bottom and Facies 3 on the top.

3. Methodology

Field Collection

Cobble specimens were collected during Spring Break, March 7-16, 2014, from a number of locations that best represent the different reef environments from nearshore to deeper water. Dr. Lewis, undergraduate assistant Kody Shellhouse, and I found lodging at the Bridge Inn, located near the center of the bay on the western side of Cat Island, and rented a car. From here, we were able to make contact with a local dive operation through the Greenwood Resort. The southern part of Cat Island featured many ideal access points for offshore locations. It is in this area that most of the sample locations were selected (Fig. 6).

Located off the southern coastline and named for a nearby warehouse, the Deep South Nearshore site is in a nearshore reef (fringing reef), and it is located approximately 50 meters from the shoreline. Small coral structures were scattered throughout the area with intermittent grass beds in water ranging from 5 to 8 feet in depth, averaging approximately 6 feet (2 m).

In the same area, a second site was found at approximately 200 meters from the shore. This reef was similar to the Deep South Nearshore, but because of the greater water depth here, we speculated that it could be a patch reef, and named it the Deep South Patch site. Water depth at this location averaged approximately 12 feet (4 m). Both of these locations featured waters with very low energy.

On the eastern side of the island, an extremely high-energy site is located in the northeasternmost part of the overall map area (Fig. 6). The site, called Ocean Dream

Nearshore because of a nearby resort of the same name, was 50 meters from the shore and averaged 6 feet (2 m) deep.



Figure 6- The study area, south end of Cat Island, Bahamas, showing sample sites (circles) and resort locations (arrows). Sites are abbreviated as such: ODN- Ocean Dream Nearshore, SB- Smith-s Bay, GP- Greenwood Patch, GW- Greenwood Wall, CH- Chi mney, ICH- Intermediate Chimney, DSP- Deep South Patch, DSN- Deep South Nearshore. See Figures 7-9 for detailed views and site names.



Figure 7- Close-up view of the northern part of the study area showing the Smith's Bay site on the left and the Ocean Dream Nearshore site on the right.



Figure 8- Close-up view of the eastern part of the study area showing the Greenwood Patch and Greenwood Wall sites indicated by circles, along with their namesake, Greenwood Resort indicated by an arrow.

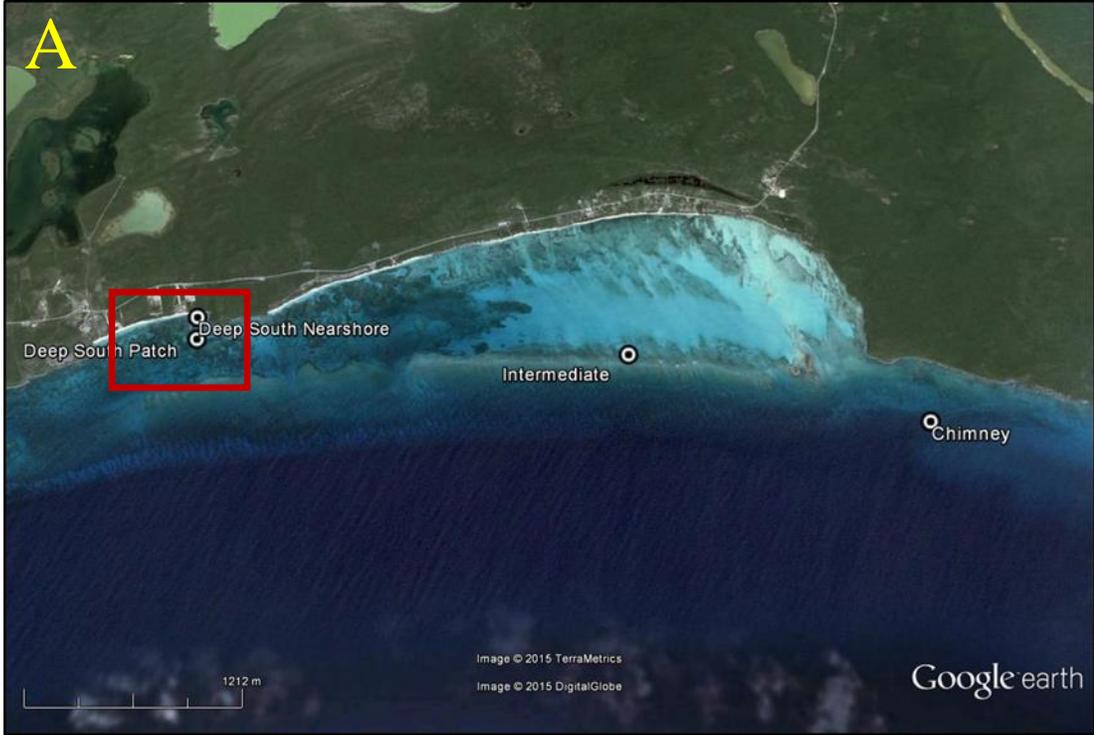


Figure 9- (A) Close-up view of the southern part of the study area showing the Deep South Nearshore, Deep South Patch, Intermediate Chimney, and Chimney sites, all indicated by circles. (B) Inset map of the Deep South Nearshore and Deep South Patch sites.

This site was constantly battered by intense wave action because of its place on the windward side of the island.

Also on this windward side, but further south, a second high-energy location was found and dubbed Greenwood Patch because of its proximity to another nearby resort of the same name. Roughly 120 meters (37 m) from shore and averaging 12 feet (3 m) deep, this site was also speculated to be a patch reef due to its deeper water.

One site was located on the western side of the island, named Smith's Bay Nearshore for a nearby marina of the same name. This location was notable for its low overall abundance of encrusting organisms, evident even in the field. It was also notable for being only 2 meters from shore and only roughly 3 feet (1 m) in depth.

Three additional sites were accessed from a boat. Two were located off the southern coast of Cat Island. One, called the Chimney due to a tunnel-like feature in the platform-margin reef, was located over 400 meters from shore and approximately 120 feet deep. This location was notable for being a true wall location with a sharply declined surface leading out into the deep sea. Another site in the same vicinity, but closer to the island and much shallower in depth at only 30 feet (9 m) in depth, was named the Intermediate Chimney. This site had rougher topography than the others, with many furrows and trenches throughout the reef structure. This spur and groove topography is typically found near platform-margins. The last of these three sites was named the Greenwood Wall, due to its proximity to the same resort that served as a namesake for the Greenwood Patch site. This site was a platform-margin, like the Chimney site, but had a much less steep decline in elevation and averaged approximately 90 feet (27 m) in depth.

These sites formed two transects: a southern transect consisting of the Deep South Nearshore, Deep South Patch, Intermediate Chimney, and Chimney sites, and an eastern transect consisting of the Ocean Dream Nearshore, Greenwood Patch, and Greenwood Wall sites. The Smith's Bay site was far from both transects and was the only site from the leeward side of the island, so it was kept separate from the other sites. The grouping of these transects allowed for easy side-by-side comparison of sites representing similar water depths and reef environments.

For all of the sites (Table 2), distance from shore was, when possible, calculated using the ruler function in Google Earth. In some cases, exact GPS coordinates for a site were impossible due to the inability to carry the GPS device when swimming some distance from shore. In those cases, a visual estimate was used. Water depth was measured using the SCUBA dive computer, initially in feet and later converted to meters.

Cobble samples were collected using a combination of SCUBA diving and free diving, either from the dive operator's boat or by swimming from shore. The size of the cobbles collected maintained an average of between 15 and 30 cm diameter, following Choi (1984). A total of six cobbles were taken from each site, and longitude and latitude were recorded using a Garmin marine GPS except at locations noted above. As samples were collected under water, they were placed in pre-labeled, numbered ziplock bags, and the number of the bag was written down on a dive slate by the diver, along with the general location and the depth of sample collection. At each location, general characteristics, including reef structure and relative amount of light, were noted in a log book. At the end of the week, all of the samples were carefully wrapped in packing

material (bubble wrap) and loaded into suitcases and crates for transport back to Auburn University.

Sample Preparation and Data Collection

In the laboratory, each cobble sample was thoroughly rinsed and washed using dish soap and brushes. First, a thorough brushing occurred with a large, heavily bristled brush. A second brushing followed with a toothbrush. Finally, a fine painter's brush was used with the aid of a microscope to clean off any other loose particles still clinging to the surface. This ensured that all free foraminifera such as *Sorites* or *Archaias* were removed with only encrusting foraminifera remaining. For the purposes of this study, encrusting foraminifera are defined as foraminifera that cement themselves to the substrate in a permanent or semi-permanent fashion. While it is still possible for certain encrusting foraminifera, such as *Planorbulina* to be removed from their cemented state, it takes a concerted effort to do so, and the washing process had no effect on these foraminifera.

In most cases, only lower surfaces of the cobbles were examined and photographed using a quadrat, or cardboard frame cut specifically to yield an area of 10 cm² (as in Tichenor and Lewis, 2009). In rare cases, in samples where overall encruster abundance was low, the tops of cobbles were also analyzed in order to reach the goal number of specimens. Multiple quadrats were analyzed on each cobble until a total of 200 encrusting organisms were found on each cobble, resulting in approximately 1200 encrusting organisms per site. The exceptions to this rule were the Smith's Bay samples, where occurrence was so low that a target number of 100 encrusting organisms per cobble was used instead. Encrusters other than foraminifera were identified in broad

categories such as polychaetes or bryozoans; foraminifera were identified to genus and species. The morphotype and taphonomic state of each foraminifer were also recorded. Live specimens were recognized by their intense color. Taphonomic condition of dead tests was ranked subjectively according to degree of alteration using the following categories, as in Buchan and Lewis (2009): pristine (in life condition), good (only mild damage), altered (noticeable damage including lack of delicate ornamentation), and extremely altered. An index known as the Quality of Preservation Index (QPI) was calculated for each site. The QPI is the percentage of all individuals that are ranked live, pristine, and good. In addition to counts of individuals, the surface area covered by each individual encrusting organism was measured using ImageJ software. Eventually the total counts and total area for species in each location were calculated, creating a series of distribution percentages.

Statistical Analysis

Both Q-mode and R-mode techniques of cluster analysis were used to group samples according to foraminiferal assemblages (Q-mode), and to recognize naturally co-occurring species (R-mode). Software used for this was PRIMER v5, with data transformed by the square root function and using the Bray-Curtis similarity coefficient and group average linking. This allowed for the use of both cluster analysis and multivariate dimensional scaling (MDS) plots.

Site Name	Site Type	Latitude	Longitude	Distance from Shore (m)	Water Depth (ft/m)
Ocean Dream Nearshore	Nearshore Reef	24.3526	75.4537	50*	6 (1.83)
Greenwood Patch	Patch Reef	24.1841	75.3021	120*	12 (3.66)
Greenwood Wall	Platform Margin	24.1726	75.2824	2231	90 (27.45)
Deep South Nearshore	Nearshore Reef	24.1503	75.4515	50*	6 (1.83)
Deep South Patch	Patch Reef	24.1494	75.3683	200*	12 (3.66)
Chimney Intermediate	Intermediate Zone	24.1429	75.3276	400	30 (9.15)
Chimney	Platform Margin	24.1423	75.3226	448	115 (30.75)
Smith's Bay Nearshore	Nearshore Reef	24.3485	75.4862	2	3 (0.915)
				* denotes a visual estimate	

Table 2- List of site locations, reef type, distance from shore, and water depth (see text for details).

4. Results

The eight sites are here divided into three groups: (1) an eastern transect consisting of the Ocean Dream Nearshore, Greenwood Patch, and Greenwood Wall sites; (2) a southern transect, consisting of the Deep South Nearshore, Deep South Patch, Intermediate, and Chimney locations; and (3) an outlier site, Smith's Bay. This allows for ease of presentation and comparison between similar sites.

Major Groups of Encrusting Organisms

Four major groups of encrusting organisms were found: foraminifera, coralline algae, polychaetes, and bryozoans. For assessment purposes, coralline algae were divided into taxa that form thin crusts and those that form tubes, and the tightly curled polychaete *Spirorbis* was recorded separately from other polychaetes. The resulting six categories are illustrated in Figure 10. The percentage of each taxonomic category present at each site was calculated and represented in two ways: by counts of individuals (shown in histograms) and by area covered (shown in pie charts). These data are presented in Table 3. In the eastern transect (Fig. 11), southern transect (Fig. 12), and outlier site (Fig. 13), a clear dominance of foraminifera can be seen in both count and area. The only site where there is an exception is the Smith's Bay location, which features a superior number of the polychaete *Spirorbis* in overall count. However, even here, the foraminifera remain dominant in area.

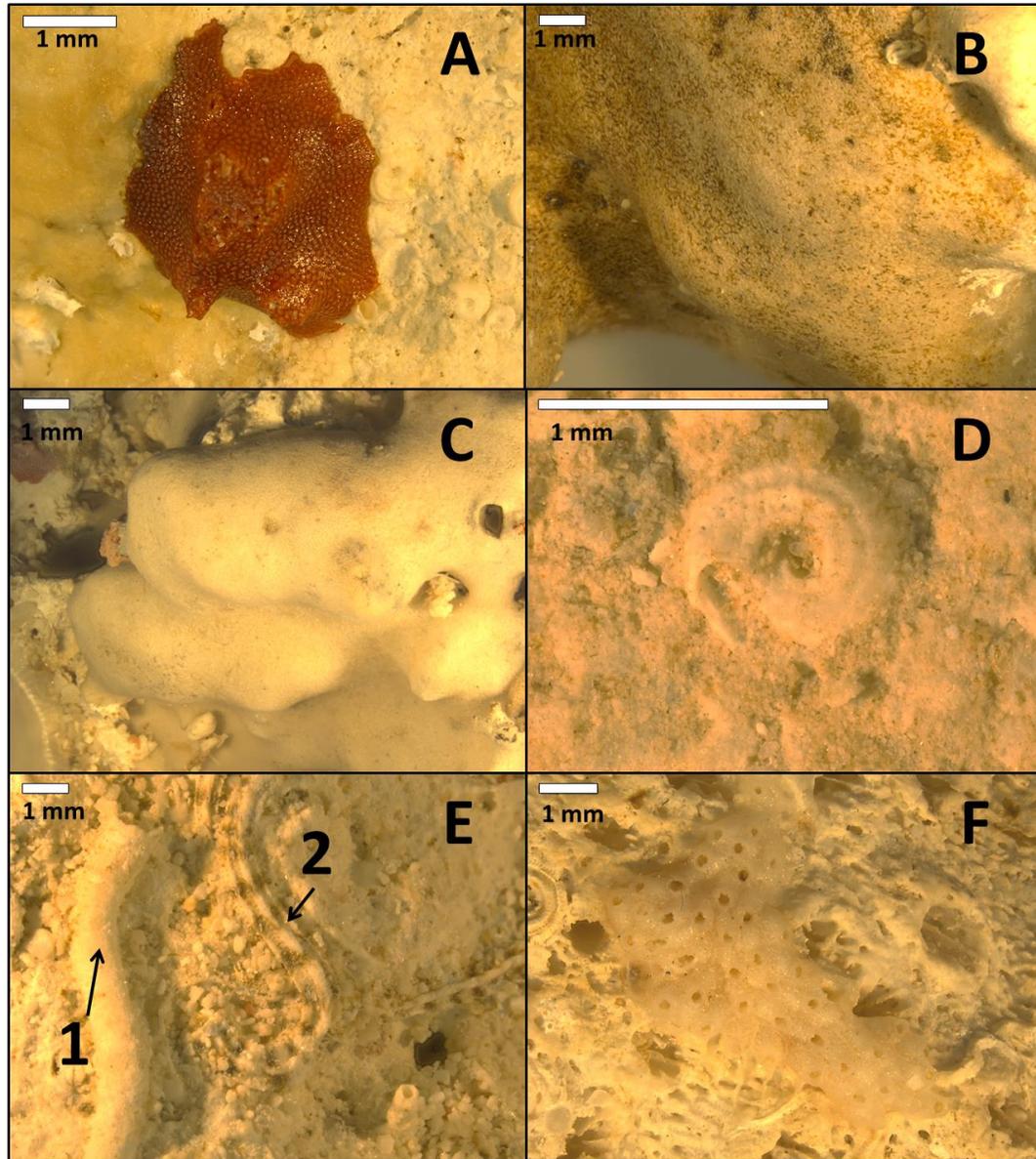


Figure 10- Representative photographs of each of the encrusting organism groups recorded: (A) Foraminifera (*Homotrema rubrum*), (B) Tubular Coralline Algae, (C) Crustose Coralline Algae, (D) *Spirorbis*, (E) Other polychaetes (1- Tubular polychaete, 2- Triangular polychaete), and (F) Bryozoa.

Ocean Dream Nearshore	Count (%)	Area (%)
Foraminifera	87.67	68.81
Tubular Coralline Algae	1.66	12.87
Crustose Coralline Algae	8.54	15.59
<i>Spirorbis</i>	0.16	0.03
Other Polychaetes	3.24	2.70
Bryozoans	0.00	0.00
Greenwood Patch	Count (%)	Area (%)
Foraminifera	76.45	78.69
Tubular Coralline Algae	0.00	0.00
Crustose Coralline Algae	2.40	8.48
<i>Spirorbis</i>	6.93	1.54
Other Polychaetes	14.22	11.29
Bryozoans	0.00	0.00
Greenwood Wall	Count (%)	Area (%)
Foraminifera	60.90	67.93
Tubular Coralline Algae	0.00	0.00
Crustose Coralline Algae	4.00	16.60
<i>Spirorbis</i>	0.49	0.01
Other Polychaetes	31.43	4.96
Bryozoans	3.18	10.49
Deep South Nearshore	Count (%)	Area (%)
Foraminifera	96.33	91.90
Tubular Coralline Algae	0.00	0.00
Crustose Coralline Algae	0.83	5.24
<i>Spirorbis</i>	0.00	0.00
Other Polychaetes	2.83	2.86
Bryozoans	0.00	0.00
Deep South Patch	Count (%)	Area (%)
Foraminifera	91.84	91.73
Tubular Coralline Algae	0.00	0.00
Crustose Coralline Algae	0.57	3.86
<i>Spirorbis</i>	0.00	0.00
Other Polychaetes	7.59	4.40
Bryozoans	0.00	0.00
Intermediate Chimney	Count (%)	Area (%)
Foraminifera	56.62	55.94
Tubular Coralline Algae	0.00	0.00
Crustose Coralline Algae	0.90	4.59
<i>Spirorbis</i>	0.00	0.00
Other Polychaetes	39.78	31.02
Bryozoans	2.70	8.46
Chimney	Count (%)	Area (%)
Foraminifera	63.26	71.66
Tubular Coralline Algae	0.00	0.00
Crustose Coralline Algae	1.39	5.75
<i>Spirorbis</i>	0.00	0.00
Other Polychaetes	34.21	18.18
Bryozoans	1.15	4.42
Smith's Bay Nearshore	Count (%)	Area (%)
Foraminifera	34.04	30.46
Tubular Coralline Algae	0.00	0.00
Crustose Coralline Algae	9.98	27.26
<i>Spirorbis</i>	44.93	13.27
Other Polychaetes	10.44	19.22
Bryozoans	0.61	9.79

Table 3- Percentages of encrusting groups counted for all eight sites.

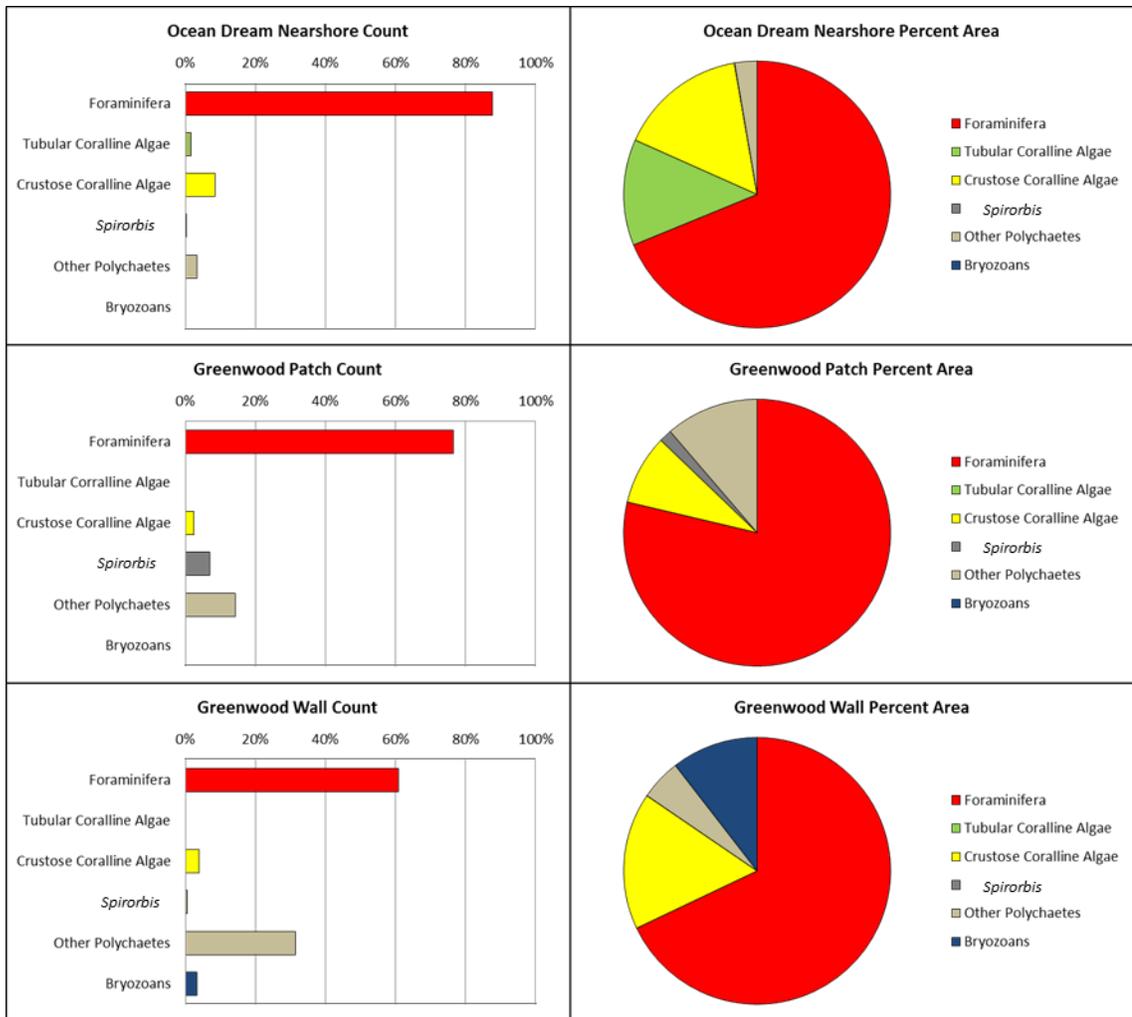


Figure 11- Major groups of encrusting organisms in the eastern transect. Histograms (left) show percentage based on counts of individuals. Pie diagrams (right) show percentage of all encrusters based on area covered. Note the overall dominance of foraminifera among encrusters by both count and area.

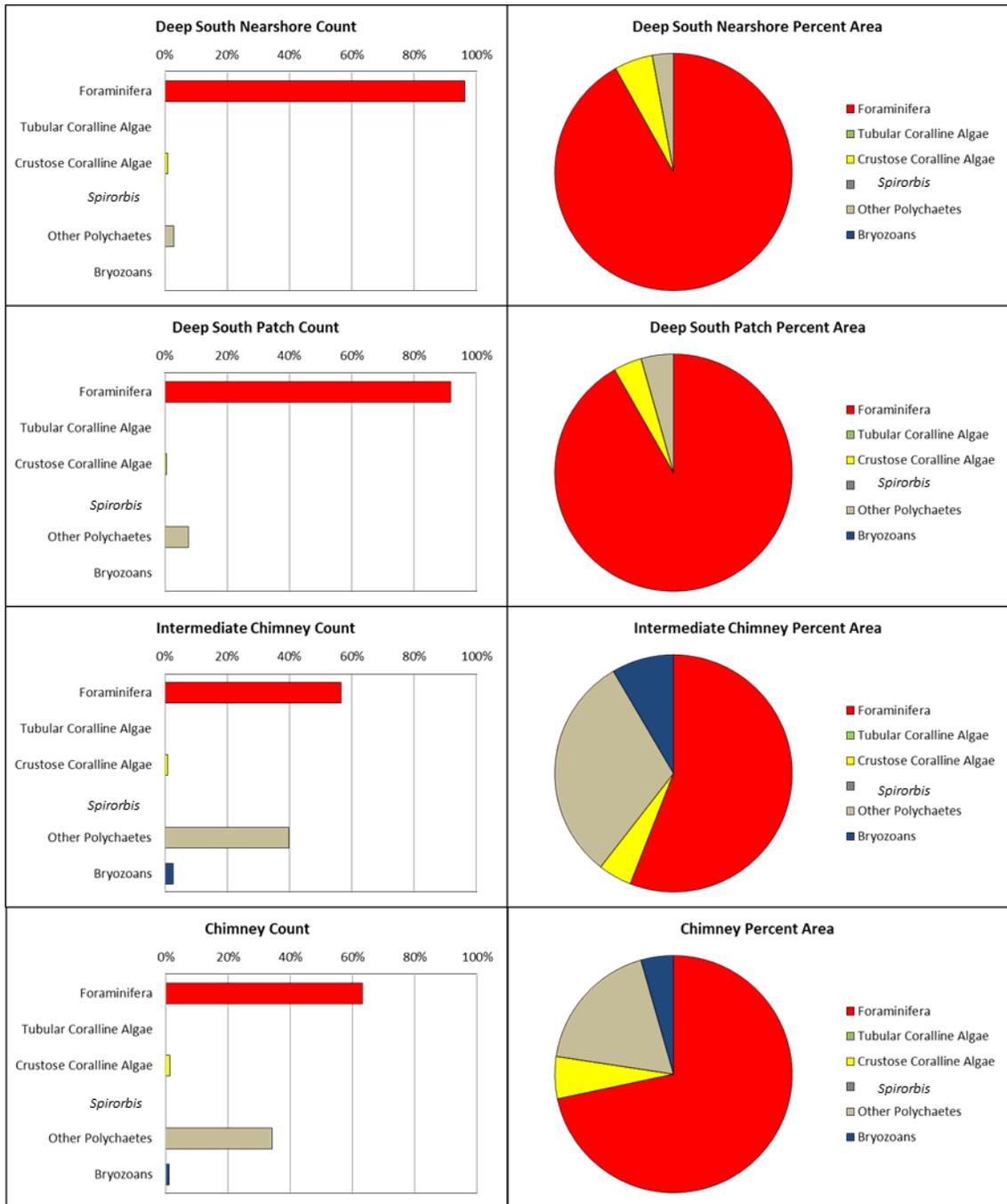


Figure 12- Major groups of encrusting organisms in the southern transect. Histograms (left) show percentage based on counts of individuals. Pie diagrams (right) show percentage of all encrusters based on area covered. Note the overall dominance of foraminifera among encrusters by both count and area.

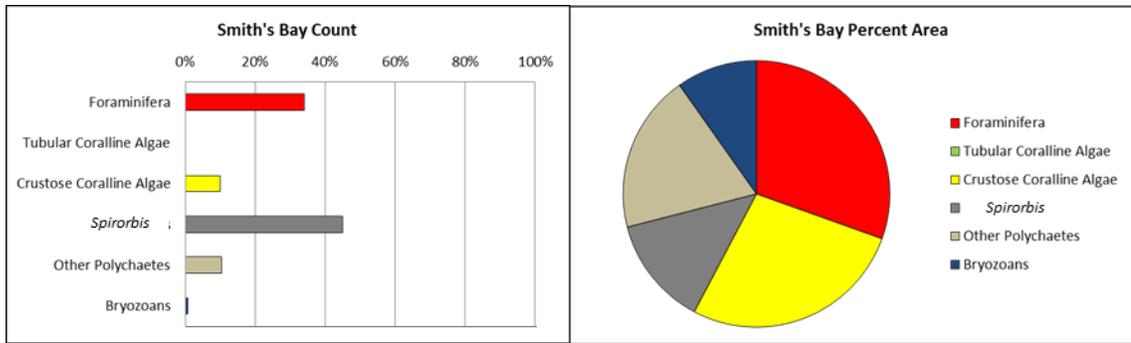


Figure 13- Major groups of encrusting organisms in the individual site, Smith's Bay. Histograms (left) show percentage based on counts of individuals. Pie diagrams (right) show percentage of all encrusters based on area covered. Note that Smith's Bay is the only location where foraminifera are not the overwhelming majority of encrusters by count, though they maintain dominance in area.

Foraminiferal Taxa

In sum, seven different taxa of foraminifera were observed in this study. There are two agglutinated taxa: *Placopsilina* and *Haddonina*; we have not yet attempted species-level identification of our few specimens of these genera. The only miliolid taxon identified was the genus *Nubecularia*. As in previous studies (Tichenor and Lewis, 2009; Martin and Lewis, 2015), we distinguish between a small radiate form and a large linear morphotype. *Nubecularia* proved to be the only non-rotaliine foraminifer to show up in substantial numbers. The vast majority of foraminifera identified were rotaliines: *Planorbulina* spp., *Carpenteria* sp., *Gypsina plana*, and *Homotrema rubrum*. We did not attempt to identify the *Planorbulina* to the species level, but they are most likely *P. acervalis*. All specimens show the distinctive clustered “bubble-like” appearance the genus is known for, but there was quite a bit of variation in color between different specimens, leading to our using a less specific identification. *Carpenteria* was also not identified to the species level, but all the specimens showed the distinct branching associated with the genus. *Gypsina plana* is often considered synonymous with *Acervulina inhaerens* and has a convoluted taxonomic history (Plaziat and Perrin, 1992). However, Perrin (1994) clarified the differences using thin-section and SEM analysis. *Acervulina inhaerens* was not seen in this study, but *Gypsina plana* was identified based upon its smoothly lobate perimeter. *Homotrema rubrum* is identified as the common red-colored foraminifer found at nearly every site, but there is no distinction made from *Miniacina*, because the two genera are very difficult to distinguish in adult form (Krautwig et al., 1998). Photographs of the different taxa recorded are provided in Figure 14.

The total count and total area for each individual taxonomic category of foraminifera was calculated for each cobble. The percentages of total count for each cobble are shown in Table 4, and the percentages of total area for each cobble are shown in Table 5. As before, the total counts are represented by a histogram, while the total areas are represented by pie charts.

In the eastern transect (Fig. 15), a clear progression can be seen from assemblages found in a nearshore reef (Ocean Dream Nearshore) to those in a patch reef (Greenwood Patch) and finally to platform-margin assemblages (Greenwood Wall). *Homotrema rubrum* is most prevalent in both count and area at the Ocean Dream Nearshore, while *Planorbulina spp.* is most prevalent in count and area at the Greenwood Patch. The platform-margin assemblage is dominated by *Homotrema rubrum* when measured by counts of individuals; however, in area, *Gypsina plana* is by far the most prevalent foraminifer.

In the southern transect (Fig. 16), a progression in assemblages is also apparent, although it is not as clear as in the eastern transect. At the Deep South Nearshore site, *Nubecularia* ranks first in total count, but *Homotrema rubrum* ranks first in area. The Deep South Patch is dominated by *Homotrema rubrum* in both count and area, but shows a substantial increase in *Planorbulina spp.* compared to the Deep South Nearshore. The Intermediate Chimney assemblage is dominated in counts by *Homotrema rubrum*, but shows nearly equal areas taken up by *Homotrema rubrum*, *Planorbulina spp.*, and *Gypsina plana*. Finally, *Planorbulina spp.* is most abundant in the Greenwood Wall assemblage. However, as in the Chimney site, this assemblage is clearly dominated by *Gypsina plana* with respect to area. From the initial data, the outlier site (Smith's Bay)

appears unique (Fig. 17). Smith's Bay is mostly made up of *Nubecularia sp.* in both count and area, with some substantial occurrence of *Planorbulina spp.*

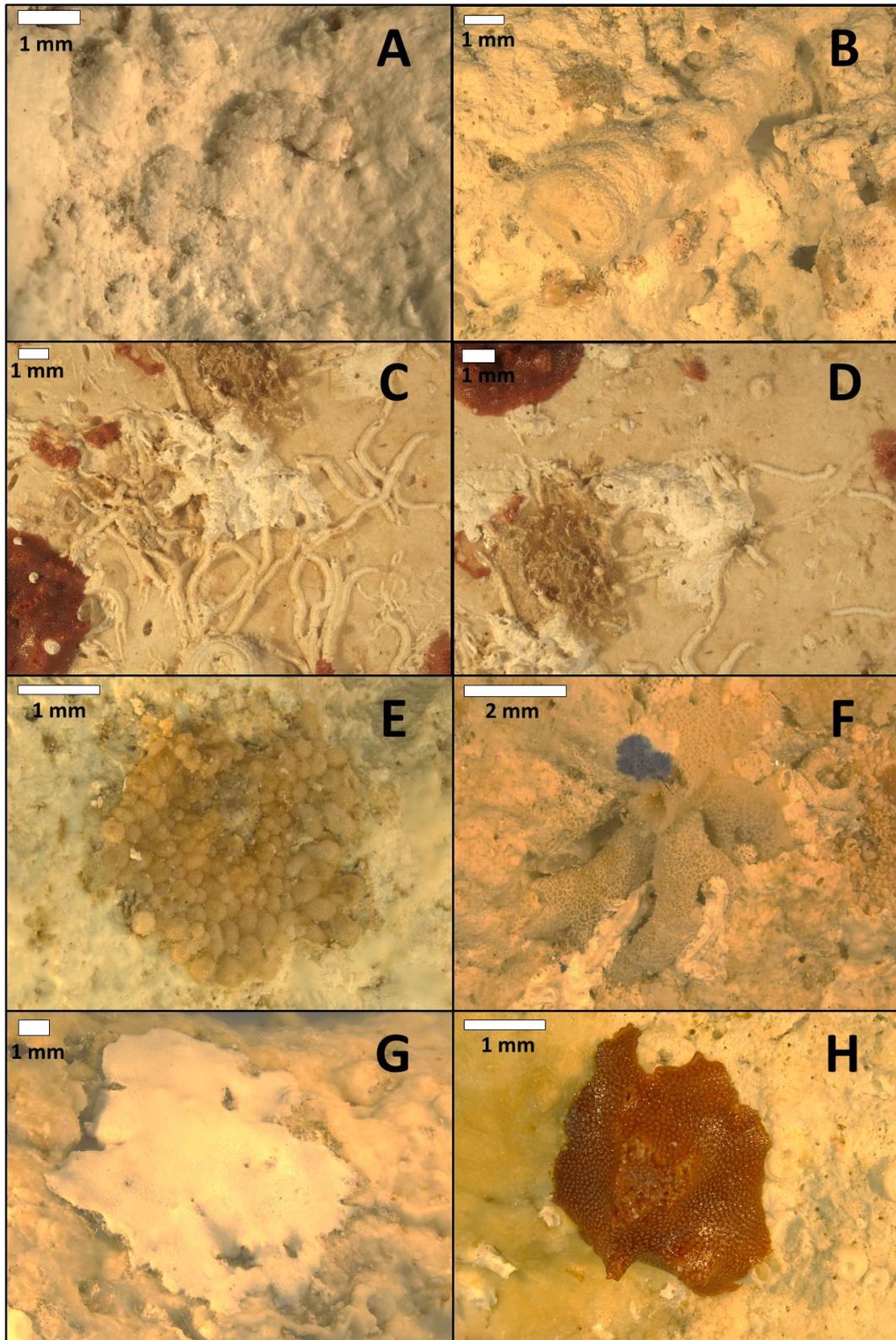


Figure 14- Representative photographs of each taxon of encrusting foraminifera recorded: (A) *Placopsilina* sp., (B) *Haddonina* sp., (C) *Nubecularia* (small/radiate), (D) *Nubecularia* (large/linear), (E) *Planorbulina* spp., (F) *Carpenteria* sp., (G) *Gypsina plana*, and (H) *Homotrema rubrum*.

Ocean Dream Nearshore (n=1109)	Sample 26 (n=206)	Sample 60 (n=153)	Sample 61 (n=196)	Sample 66 (n=197)	Sample 67 (n=210)	Sample 68 (n=150)
<i>Placopsilina</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Haddonia</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-small</i>	10.19	5.23	5.10	6.60	3.81	4.00
<i>Nubecularia-large</i>	1.46	1.31	7.65	4.57	1.43	2.00
<i>Planorbulina</i> spp.	20.39	22.22	40.82	42.13	12.38	15.33
<i>Carpenteria</i> sp.	0.00	0.00	0.00	0.51	0.48	0.00
<i>Gypsina plana</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Homotrema rubra</i>	67.96	71.24	46.43	46.19	81.90	78.67
Greenwood Patch (n=828)	Sample 84 (n=188)	Sample 87 (n=155)	Sample 89 (n=196)	Sample 90 (n=131)	Sample 94 (n=105)	Sample 100 (n=53)
<i>Placopsilina</i> sp.	0.00	0.00	1.53	0.76	0.00	0.00
<i>Haddonia</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-small</i>	0.53	7.10	5.10	4.58	1.90	0.00
<i>Nubecularia-large</i>	0.00	7.74	2.04	8.40	0.00	0.00
<i>Planorbulina</i> spp.	50.00	50.97	62.76	74.05	41.90	73.58
<i>Carpenteria</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Gypsina plana</i>	0.53	0.00	0.00	0.00	0.00	0.00
<i>Homotrema rubra</i>	48.94	34.19	28.57	12.21	56.19	26.42
Greenwood Wall (n=746)	Sample 30 (n=70)	Sample 32 (n=98)	Sample 35 (n=163)	Sample 37 (n=116)	Sample 40 (n=169)	Sample 46 (n=130)
<i>Placopsilina</i> sp.	0.00	0.00	1.23	0.00	0.59	0.00
<i>Haddonia</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-small</i>	4.29	1.02	1.84	0.00	4.14	0.00
<i>Nubecularia-large</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Planorbulina</i> spp.	8.57	51.02	29.45	16.38	37.28	20.00
<i>Carpenteria</i> sp.	1.43	0.00	0.00	0.00	0.00	0.00
<i>Gypsina plana</i>	21.43	12.24	11.04	10.34	6.51	0.77
<i>Homotrema rubra</i>	64.29	35.71	56.44	73.28	51.48	79.23
Deep South Nearshore (n=1156)	Sample 21 (n=193)	Sample 22 (n=200)	Sample 24 (n=199)	Sample 55 (n=197)	Sample 57 (n=177)	Sample 58 (n=196)
<i>Placopsilina</i> sp.	0.00	0.00	0.00	0.00	1.17	2.04
<i>Haddonia</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-small</i>	50.78	75.00	70.85	32.49	11.11	61.73
<i>Nubecularia-large</i>	15.03	0.00	3.52	7.11	0.00	3.06
<i>Planorbulina</i> spp.	1.55	1.00	2.01	4.57	11.70	9.18
<i>Carpenteria</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Gypsina plana</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Homotrema rubra</i>	32.64	24.00	23.62	55.84	76.02	23.98
Deep South Patch (n=1137)	Sample 88 (n=195)	Sample 20 (n=166)	Sample 25 (n=193)	Sample 27 (n=195)	Sample 29 (n=194)	Sample 64 (n=194)
<i>Placopsilina</i> sp.	2.05	3.61	0.52	0.00	1.03	1.03
<i>Haddonia</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-small</i>	8.21	6.63	0.00	3.59	26.80	7.73
<i>Nubecularia-large</i>	6.67	4.22	2.59	9.23	0.52	4.12
<i>Planorbulina</i> spp.	40.00	27.71	10.88	2.56	22.68	23.20
<i>Carpenteria</i> sp.	1.03	0.00	0.00	0.00	0.00	0.00
<i>Gypsina plana</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Homotrema rubra</i>	42.05	57.83	86.01	84.62	48.97	63.92
Intermediate Chimney (n=629)	Sample 2 (n=172)	Sample 7 (n=47)	Sample 10 (n=104)	Sample 11 (n=103)	Sample 16 (n=103)	Sample 18 (n=100)
<i>Placopsilina</i> sp.	0.58	0.00	0.00	0.00	0.00	0.00
<i>Haddonia</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-small</i>	0.00	0.00	0.00	28.16	0.00	0.00
<i>Nubecularia-large</i>	0.00	0.00	0.96	0.00	0.00	0.00
<i>Planorbulina</i> spp.	2.91	8.51	50.96	3.88	56.31	8.00
<i>Carpenteria</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Gypsina plana</i>	0.58	4.26	6.73	4.85	0.00	0.00
<i>Homotrema rubra</i>	95.93	87.23	41.35	63.11	43.69	92.00
Chimney (n=773)	Sample1 (n=122)	Sample 4A (n=108)	Sample 4B (n=133)	Sample 5 (n=128)	Sample 34 (n=163)	Sample 39 (n=119)
<i>Placopsilina</i> sp.	3.28	5.56	1.50	0.78	3.68	0.00
<i>Haddonia</i> sp.	0.00	0.00	0.00	1.56	0.00	0.00
<i>Nubecularia-small</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-large</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Planorbulina</i> spp.	54.10	34.26	87.97	89.84	85.89	18.49
<i>Carpenteria</i> sp.	0.00	0.00	0.00	0.78	0.00	0.00
<i>Gypsina plana</i>	1.64	1.85	4.51	3.91	7.36	0.84
<i>Homotrema rubra</i>	40.98	58.33	6.02	3.13	3.07	80.67
Smith's Bay Nearshore (n=225)	Sample 81 (n=5)	Sample 82 (n=65)	Sample 88 (n=105)	Sample 92 (n=48)	Sample 95 (n=0)	Sample 96 (n=1)
<i>Placopsilina</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Haddonia</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-small</i>	20.00	61.54	76.19	68.75	0.00	0.00
<i>Nubecularia-large</i>	20.00	12.31	10.48	10.42	0.00	0.00
<i>Planorbulina</i> spp.	60.00	26.15	13.33	20.83	0.00	0.00
<i>Carpenteria</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Gypsina plana</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Homotrema rubra</i>	0.00	0.00	0.00	0.00	0.00	100.00

Table 4- Percentage of foraminiferal taxa counted on each cobble sample for all eight locations. Total of all specimens (n) are a shown in parentheses.

Ocean Dream Nearshore (n=1109)	Sample 26 (n=206)	Sample 60 (n=153)	Sample 61 (n=196)	Sample 66 (n=197)	Sample 67 (n=210)	Sample 68 (n=150)
<i>Placopsilina</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Haddonia</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-small</i>	7.95	3.38	1.85	2.60	1.61	3.04
<i>Nubecularia-large</i>	4.29	1.91	8.04	9.97	2.53	4.38
<i>Planorbulina</i> spp.	19.81	18.41	25.11	64.62	11.91	17.89
<i>Carpenteria</i> sp.	0.00	0.00	0.00	0.77	0.42	0.00
<i>Gypsina plana</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Homotrema rubra</i>	67.96	76.30	65.00	22.03	83.54	74.69
Greenwood Patch (n=828)	Sample 84 (n=188)	Sample 87 (n=155)	Sample 89 (n=196)	Sample 90 (n=131)	Sample 94 (n=105)	Sample 100 (n=53)
<i>Placopsilina</i> sp.	0.00	0.00	1.37	0.60	0.00	0.00
<i>Haddonia</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-small</i>	0.28	3.02	2.35	1.88	0.65	0.00
<i>Nubecularia-large</i>	0.00	37.01	5.16	13.00	0.00	0.00
<i>Planorbulina</i> spp.	31.24	33.90	44.76	69.02	30.93	75.46
<i>Carpenteria</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Gypsina plana</i>	31.65	0.00	0.00	0.00	0.00	0.00
<i>Homotrema rubra</i>	36.84	26.06	46.35	15.51	68.42	24.54
Greenwood Wall (n=746)	Sample 30 (n=70)	Sample 32 (n=98)	Sample 35 (n=163)	Sample 37 (n=116)	Sample 40 (n=169)	Sample 46 (n=130)
<i>Placopsilina</i> sp.	0.00	0.00	0.30	0.00	0.15	0.00
<i>Haddonia</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-small</i>	0.34	0.01	0.15	0.00	0.71	0.00
<i>Nubecularia-large</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Planorbulina</i> spp.	0.37	2.03	6.29	6.15	7.43	6.53
<i>Carpenteria</i> sp.	0.22	0.00	0.00	0.00	0.00	0.00
<i>Gypsina plana</i>	96.14	96.72	82.61	87.23	79.18	65.23
<i>Homotrema rubra</i>	2.94	1.23	10.65	6.62	12.53	28.24
Deep South Nearshore (n=1156)	Sample 21 (n=193)	Sample 22 (n=200)	Sample 24 (n=199)	Sample 55 (n=197)	Sample 57 (n=177)	Sample 58 (n=196)
<i>Placopsilina</i> sp.	0.00	0.00	0.00	0.00	0.57	2.81
<i>Haddonia</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-small</i>	20.80	80.94	16.27	17.58	4.43	20.79
<i>Nubecularia-large</i>	26.04	0.00	12.95	19.67	0.00	14.36
<i>Planorbulina</i> spp.	5.47	3.35	6.40	12.38	13.11	29.05
<i>Carpenteria</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Gypsina plana</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Homotrema rubra</i>	47.69	15.71	64.38	50.37	81.76	32.99
Deep South Patch (n=1137)	Sample 88 (n=195)	Sample 20 (n=166)	Sample 25 (n=193)	Sample 27 (n=195)	Sample 29 (n=194)	Sample 64 (n=194)
<i>Placopsilina</i> sp.	0.55	4.02	0.16	0.00	0.28	0.28
<i>Haddonia</i> sp.	0.19	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-small</i>	4.25	1.71	0.00	1.38	12.25	1.02
<i>Nubecularia-large</i>	14.45	11.95	3.30	15.51	10.43	1.71
<i>Planorbulina</i> spp.	47.32	29.06	13.42	1.85	20.64	19.81
<i>Carpenteria</i> sp.	1.43	0.00	0.00	0.00	0.00	0.00
<i>Gypsina plana</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Homotrema rubra</i>	31.81	53.26	83.12	81.27	56.41	77.18
Intermediate Chimney (n=629)	Sample 2 (n=172)	Sample 7 (n=47)	Sample 10 (n=104)	Sample 11 (n=103)	Sample 16 (n=103)	Sample 18 (n=100)
<i>Placopsilina</i> sp.	0.27	0.00	0.00	0.00	0.00	0.00
<i>Haddonia</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-small</i>	0.00	0.00	0.00	5.80	0.00	0.00
<i>Nubecularia-large</i>	0.00	0.00	0.27	0.00	0.00	0.00
<i>Planorbulina</i> spp.	4.52	4.87	23.53	3.04	36.46	9.06
<i>Carpenteria</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Gypsina plana</i>	25.30	70.34	64.68	69.86	0.00	0.00
<i>Homotrema rubra</i>	69.92	24.80	11.51	21.30	63.54	90.94
Chimney (n=773)	Sample 1 (n=122)	Sample 4A (n=108)	Sample 4B (n=133)	Sample 5 (n=128)	Sample 34 (n=163)	Sample 39 (n=119)
<i>Placopsilina</i> sp.	1.82	0.79	0.37	0.28	0.53	0.00
<i>Haddonia</i> sp.	0.00	0.00	0.00	5.65	0.00	0.00
<i>Nubecularia-small</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-large</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Planorbulina</i> spp.	42.12	5.50	6.24	37.67	14.18	8.30
<i>Carpenteria</i> sp.	0.00	0.00	0.00	0.80	0.00	0.00
<i>Gypsina plana</i>	32.29	84.20	93.00	55.39	84.75	38.28
<i>Homotrema rubra</i>	23.77	9.50	0.39	0.21	0.54	53.42
Smith's Bay Nearshore (n=225)	Sample 81 (n=5)	Sample 82 (n=65)	Sample 88 (n=105)	Sample 92 (n=48)	Sample 95 (n=0)	Sample 96 (n=1)
<i>Placopsilina</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Haddonia</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia-small</i>	5.00	32.30	44.44	30.63	0.00	0.00
<i>Nubecularia-large</i>	42.70	31.59	39.15	54.32	0.00	0.00
<i>Planorbulina</i> spp.	52.30	36.11	16.41	15.05	0.00	0.00
<i>Carpenteria</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00
<i>Gypsina plana</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>Homotrema rubra</i>	0.00	0.00	0.00	0.00	0.00	100.00

Table 5- Percent area of foraminiferal taxa counted on each cobble sample for all eight locations. Total of all specimens (n) are shown in parentheses.

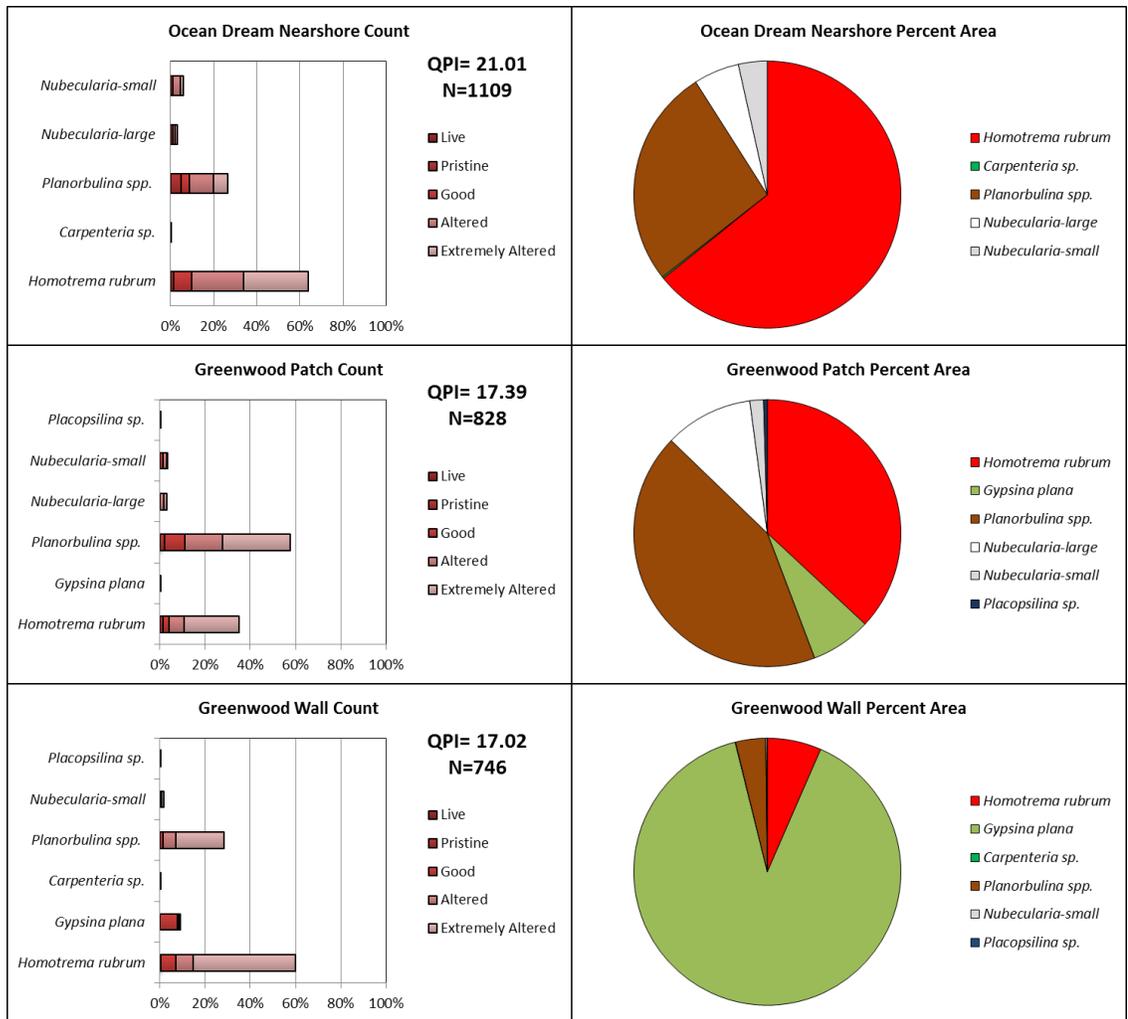


Figure 15- Principal taxa of foraminifera in the eastern transect. Histograms (left) show percentage based on counts of individuals. Pie diagrams (right) show percentage of foraminifera based on area covered. Note the clear dominance of *Homotrema rubrum* in the Ocean Dream Nearshore in contrast to *Planorbulina*'s dominance in the Greenwood Patch. Also note the clear dominance in area by *Gypsina plana* in the Greenwood Wall location.

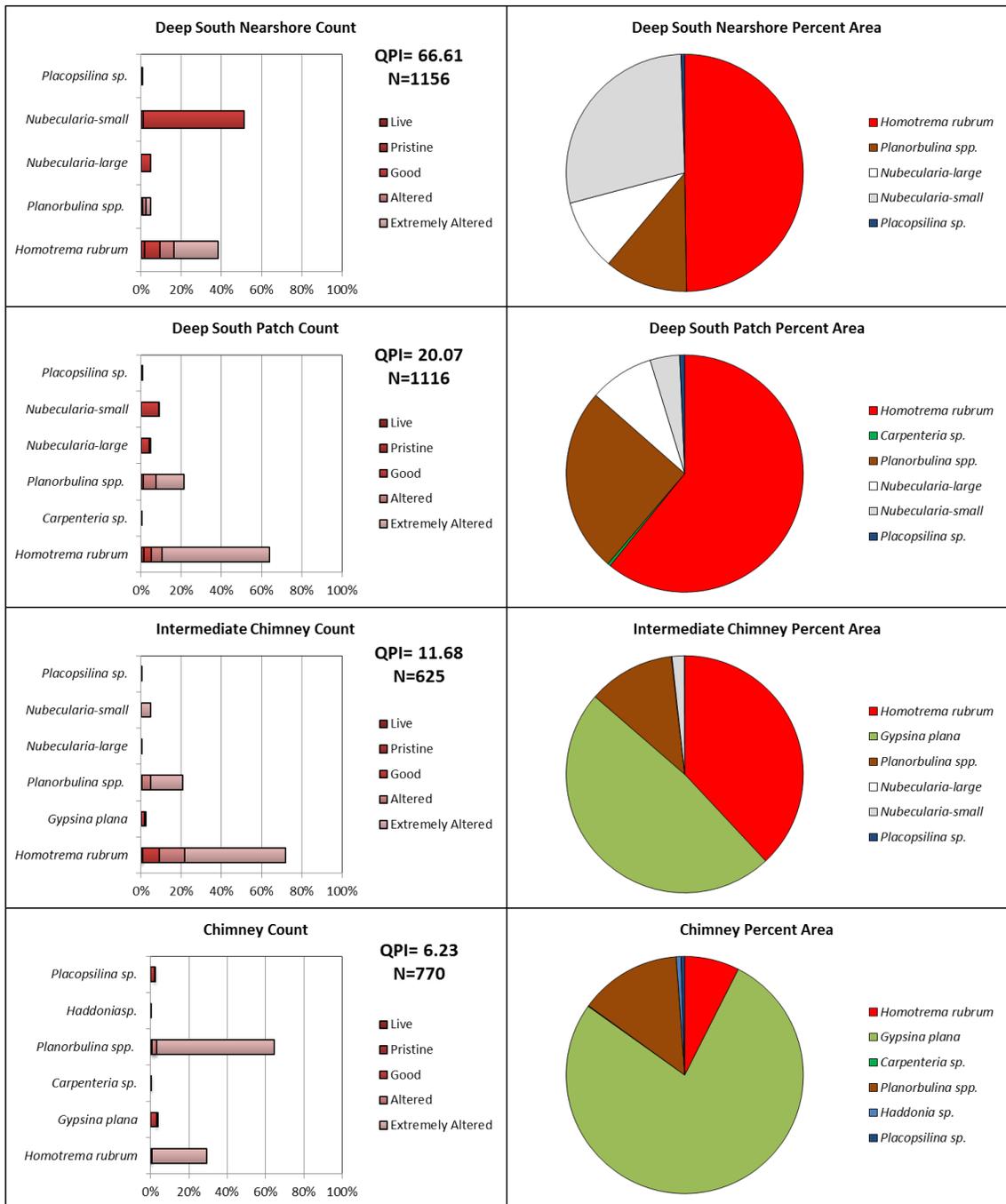


Figure 16- Principal taxa of foraminifera in the southern transect. Histograms (left) show percentage based on counts of individuals. Pie diagrams (right) show percentage of foraminifera based on area covered. Note the clear dominance of *Nubecularia* and *Homotrema rubrum* in both of the Deep South locations. Also note the clear dominance in area by *Gypsina plana* in the Chimney location.

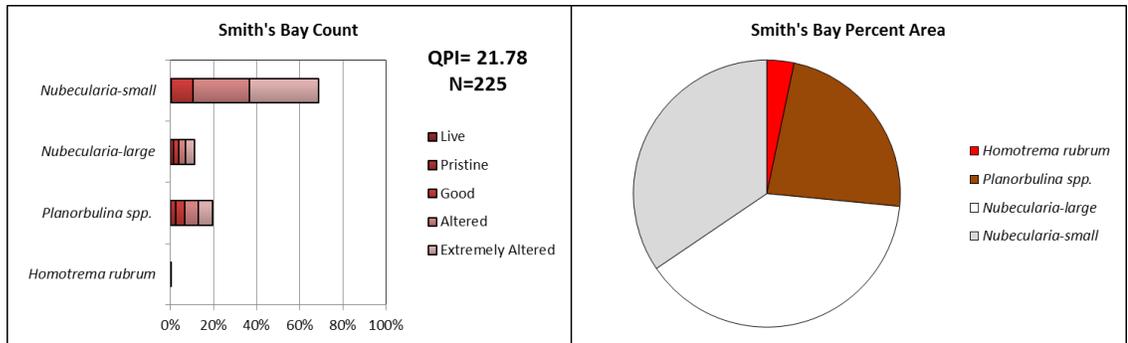


Figure 17- Principal taxa of foraminifera in the outlier site, Smith's Bay. Histograms (left) show percentage based on counts of individuals. Pie diagrams (right) show percentage of foraminifera based on area covered. Note the overwhelming dominance of *Nubecularia*.

Foraminiferal Morphotypes, Density, Size, and Preservation

The distribution of *Homotrema rubrum* morphotypes at each location is shown in Figure 18. The most common morphotype is multiple (M), almost to the exclusion of all others. The greatest diversity was seen at the nearshore sites, especially at the Ocean Dream Nearshore site. The overall density of foraminifera, calculated by dividing the total number of foraminifera per site by the number of quadrats analyzed, is illustrated in Figure 19. A clear decline in foraminiferal density can be seen from the nearshore sites to the offshore sites. The average size for each taxonomic category at each location is shown in Table 6. The two foraminifera found in abundance at each of the six sites that make up the two transects; *Homotrema rubrum* and *Planorbulina spp.*, are shown in Figure 20. A clear decrease in average size can be seen for both species in both transects from nearshore to offshore. Quality of preservation (QPI), shown in Figure 21, also shows a decline towards deeper water.

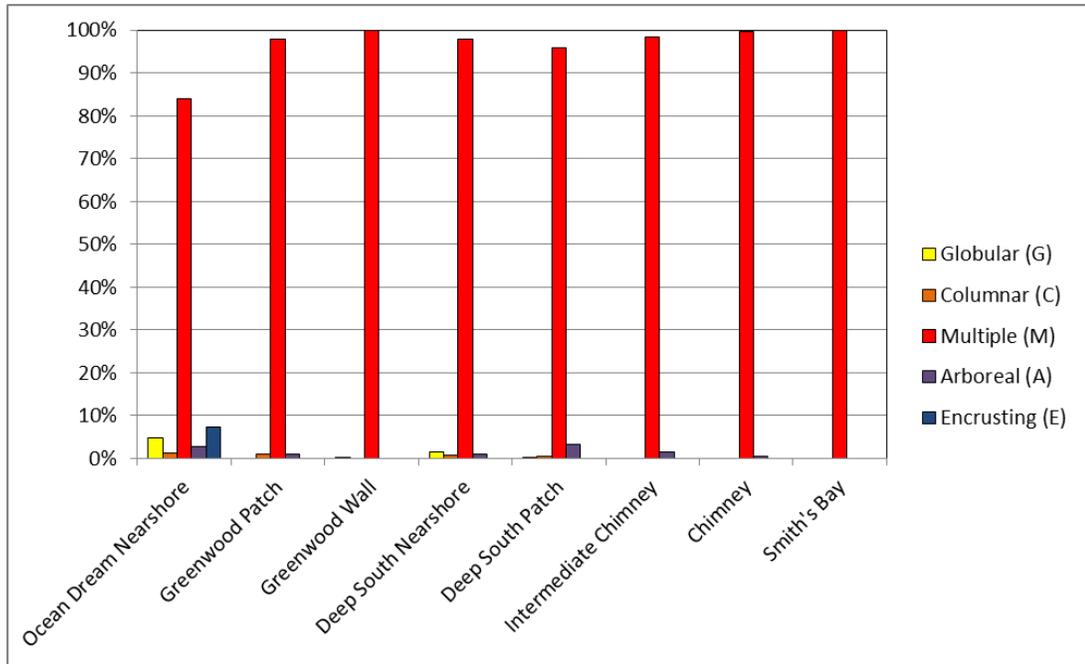


Figure 18- Distribution of the five morphotypes of *Homotrema rubrum* at each site.

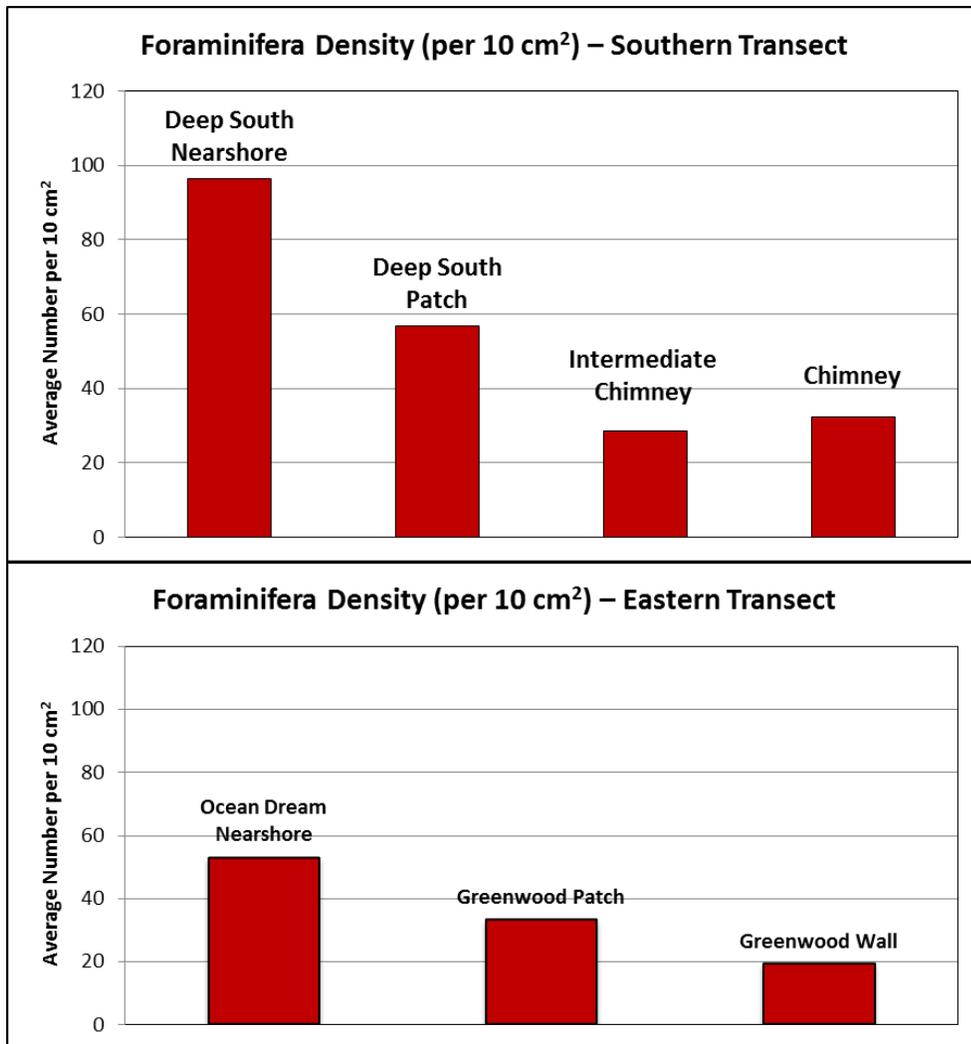


Figure 19- Density of foraminifera at each location in both transects, expressed as the mean number of foraminifera counted per 10 cm² quadrat. Both transects depict a steady decline in foraminifera density from nearshore toward the platform-margin.

	Ocean Dream Nearshore	Greenwood Patch	Greenwood Wall	Smith's Bay
<i>Placopsilina</i> sp.	NA	2.77	1.36	NA
<i>Haddonia</i> sp.	NA	NA	NA	NA
<i>Nubecularia-small</i>	2.02	1.35	0.90	1.10
<i>Nubecularia-large</i>	6.01	9.70	NA	7.71
<i>Planorbulina</i> spp.	3.41	2.21	1.41	2.61
<i>Carpenteria</i> sp.	7.76	NA	3.36	NA
<i>Gypsina plana</i>	NA	179.09	106.94	NA
<i>Homotrema rubrum</i>	3.45	3.12	1.20	16.27
	Deep South Nearshore	Deep South Patch	Intermediate Chimney	Chimney
<i>Placopsilina</i> sp.	2.26	1.26	1.01	1.10
<i>Haddonia</i> sp.	NA	NA	NA	12.74
<i>Nubecularia-small</i>	1.28	1.10	1.29	NA
<i>Nubecularia-large</i>	4.62	4.65	1.76	NA
<i>Planorbulina</i> spp.	5.36	2.91	1.99	1.13
<i>Carpenteria</i> sp.	NA	5.30	NA	3.60
<i>Gypsina plana</i>	NA	NA	71.60	111.80
<i>Homotrema rubrum</i>	2.96	2.30	1.87	1.34

Table 6- The mean size (mm) of each foraminiferal taxon at each location.

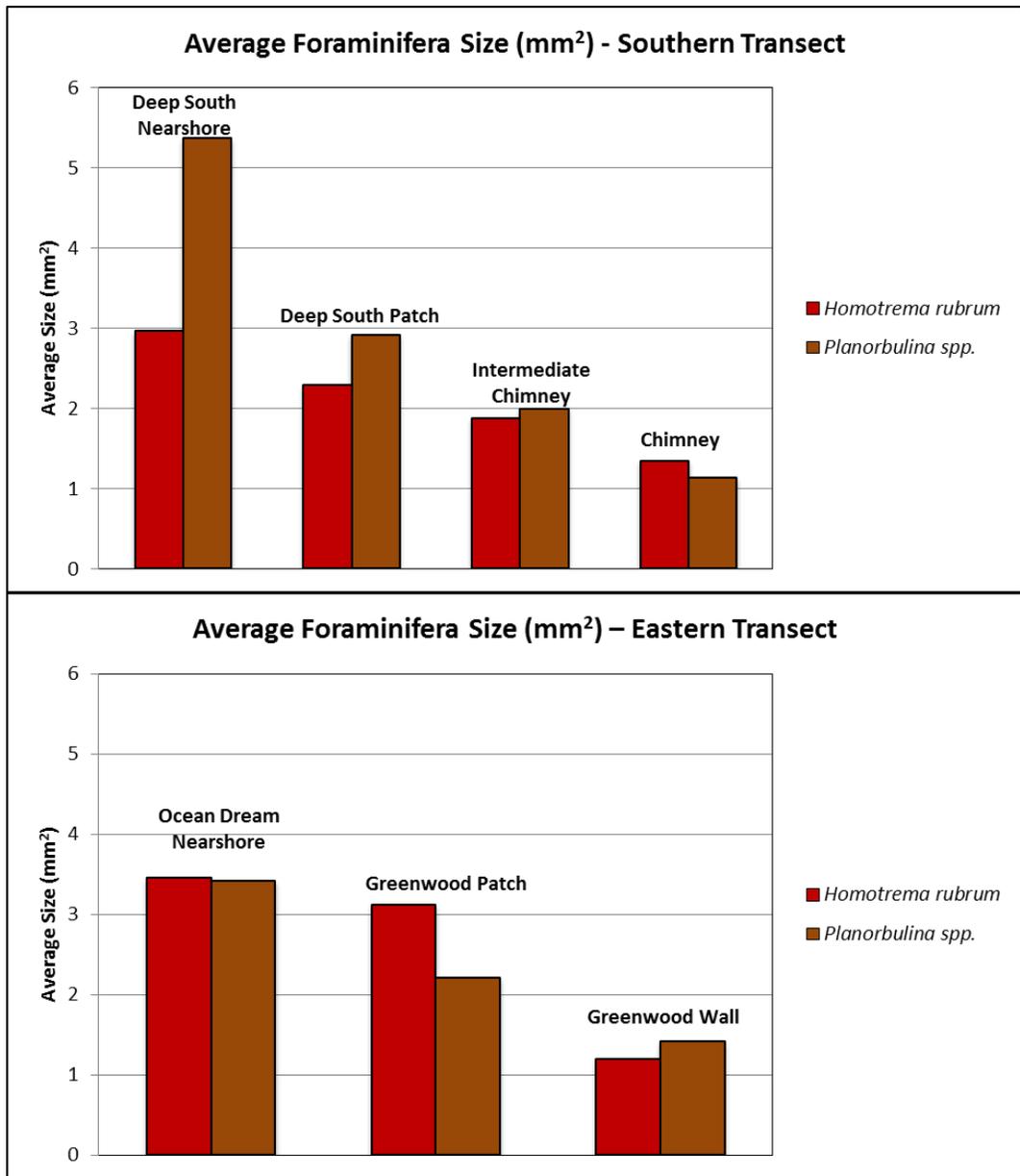


Figure 20- Bar graphs showing the average size of two key foraminifera species (*Homotrema rubrum* and *Planorbulina spp.*) at each location in both transects. These two species were measured because they were found at all locations. The size was measured in mm².

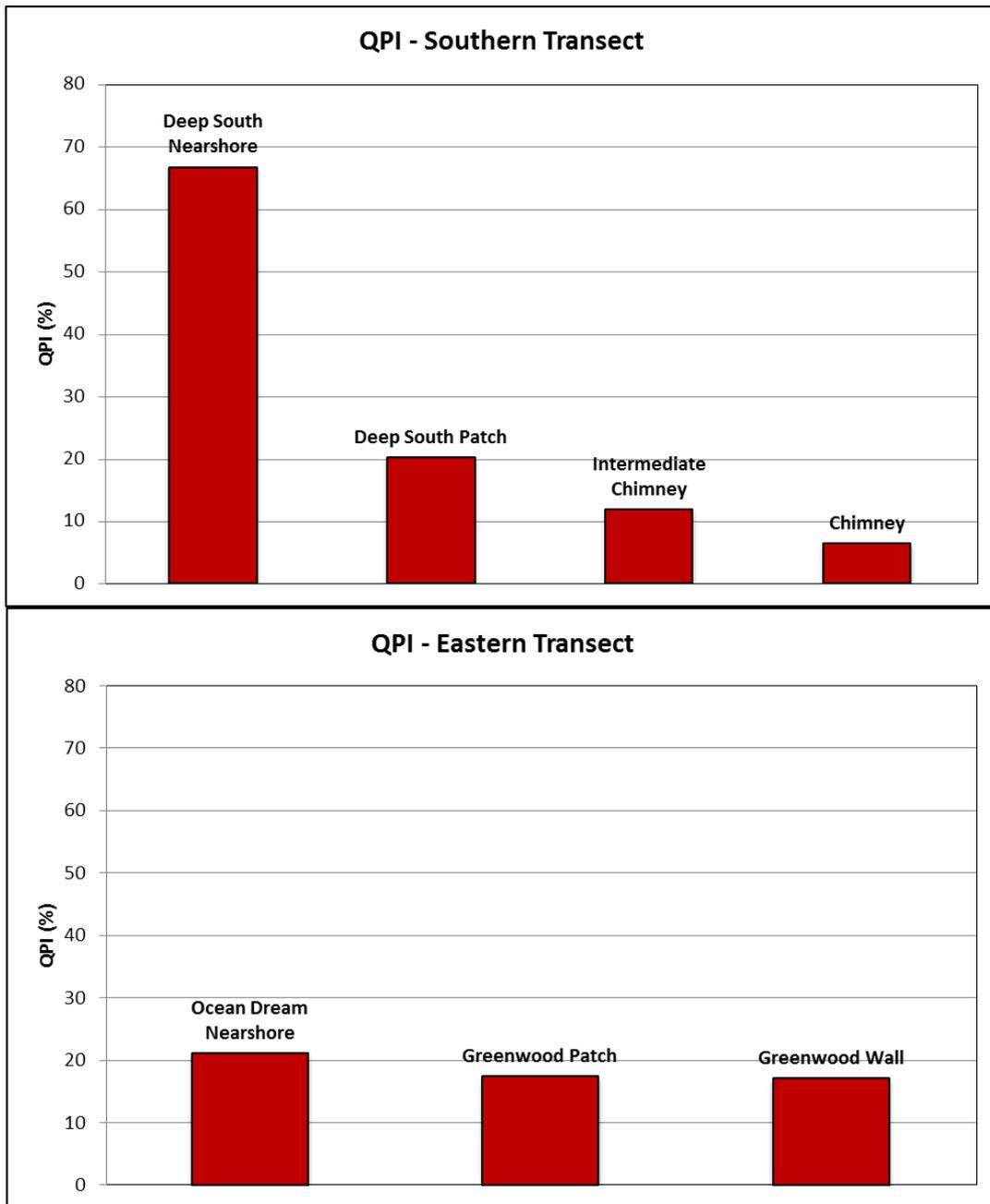


Figure 21- Bar graphs showing the Quality of Preservation Index (QPI) for both the Southern (top) and Eastern (bottom) transects.

Comparison of Key Species

Previous research (Tichenor and Lewis, 2009 and 2011) has shown that the three most important foraminiferal species when determining water depth and distance from shore are *Homotrema rubrum*, *Planorbulina spp.*, and *Gypsina plana*. Accordingly, the percentage of both count and area for just these three taxa were calculated for each and plotted on ternary diagrams, as previously practiced by Lewis et al. (2013) (Fig. 22). Both count and area plots show that nearshore sites trend toward the *Homotrema rubrum* pole. When area is taken into account, the platform-margin sites tend to trend toward *Gypsina plana*. In both count and area, the Greenwood Patch trends toward *Planorbulina spp.* However, the Deep South Patch trends toward *Homotrema rubrum*, albeit with still more *Planorbulina spp.* than the other nearshore sites. The Intermediate Chimney site trends toward *Homotrema rubrum* in count, while being relatively equal among all three species in area. The Smith's Bay site is nearly entirely *Planorbulina spp.*

The large numbers of *Nubecularia sp.* found at the nearshore sites indicates that it is a marker of shoreline deposits along with *Homotrema rubrum*. Consequently, a second pair of ternary diagrams was made with *Nubecularia sp.* added to *Homotrema rubrum* (Fig. 23). The results are largely the same; however, the Smith's Bay site plots nearer to the *Homotrema-Nubecularia* pole, more accurately representing its nearshore location.

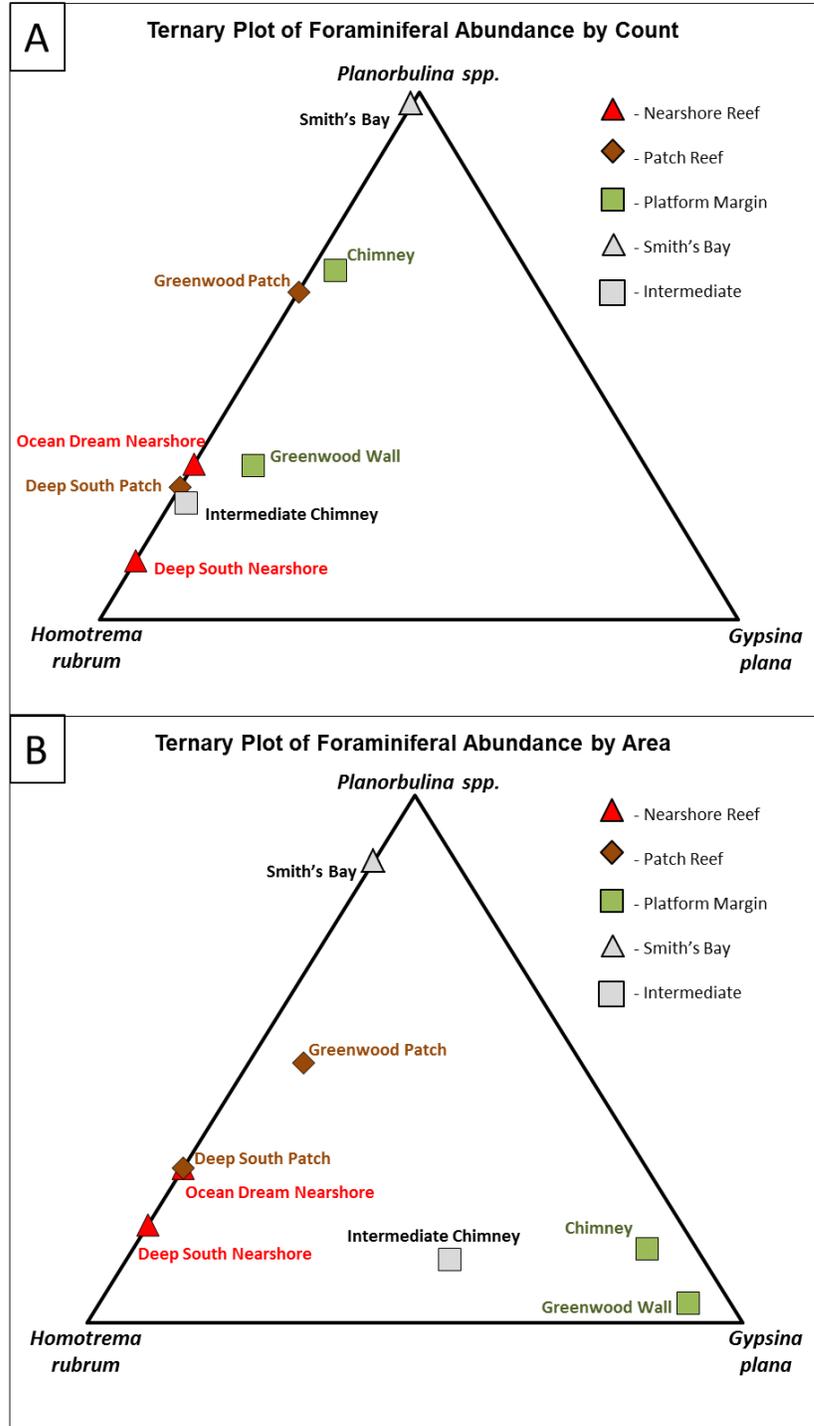


Figure 22- Relative abundance of the three dominant foraminiferal taxa, *Planorbulina spp.*, *Homotrema rubrum*, and *Gypsina plana*, as determined by counts of individuals (A) and by area covered (B) (as in Lewis et al., 2013).

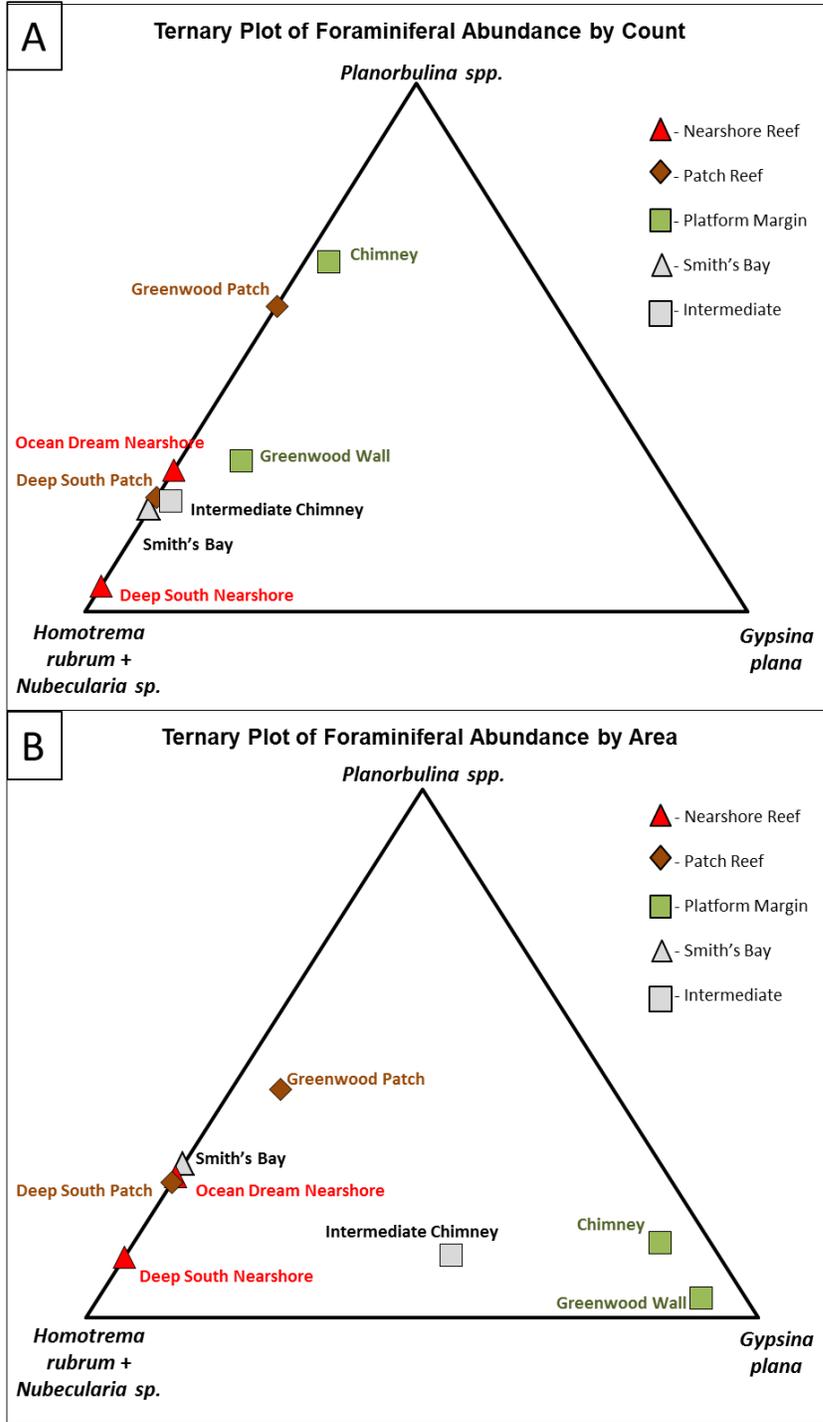


Figure 23- Relative abundance of the three dominant foraminiferal taxa, *Planorbulina spp.*, *Homotrema rubrum*, and *Gypsina plana*, as determined by counts of individuals (A) and by area covered (B) (as in Lewis et al., 2013). In contrast to Figure 22, these diagrams have been slightly altered so that *Homotrema rubrum* and *Nubecularia* have been added together. Notice the shift from the Smith's Bay location that occurs as a result of this change.

Similarity of Cobble Assemblages

The percentage of occurrence and the percentage of area for each taxonomic category for each cobble were compared by cluster analysis using programs in Primer IV. A Q-mode cluster diagram was produced comparing the similarity of each cobble as determined by its foraminiferal assemblage (Fig. 24). A non-metric multidimensional scaling (MDS) plot of counts was also created, showing similarity on a spatial plane (Fig. 25). While there are several outliers, both diagrams show a high degree of similarity between cobbles from the same site and reef type. A Q-mode cluster diagram and MDS plot of foraminiferal area also were created (Figs. 26, 27). The area cluster data shows an even more obvious similarity between cobbles from similar locations, with platform-margins in particular showing an extremely high degree of clustering.

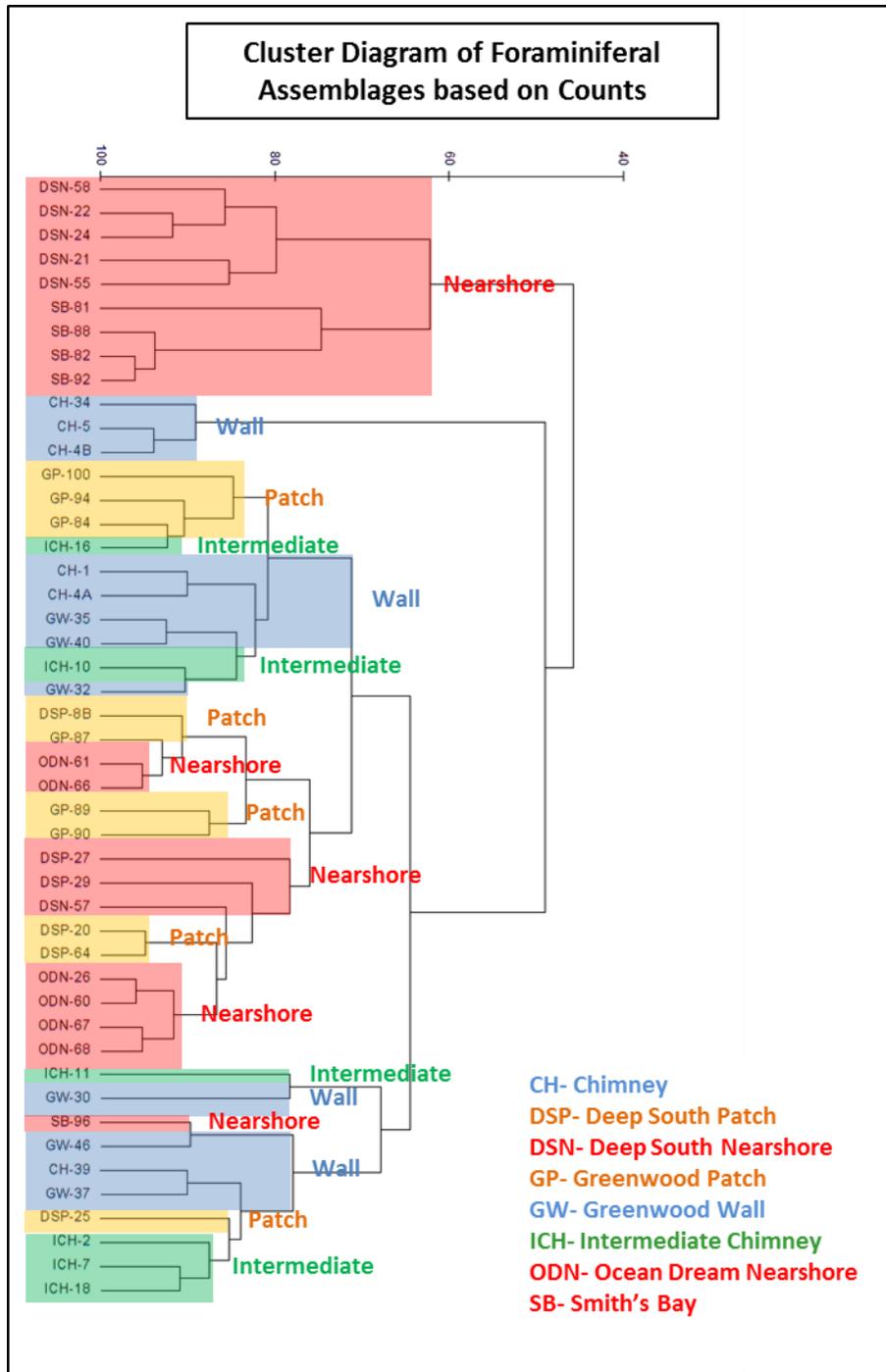


Figure 24- Q-mode cluster of all sites based on relative abundance as determined by counts of individuals (transformation: square root; similarity coefficient: Bray-Curtis; cluster group: group average). Cobble sample numbers are listed. Sites are represented by abbreviations (“DSN” for Deep South Nearshore, etc.). The axis along the top measures rate of similarity.

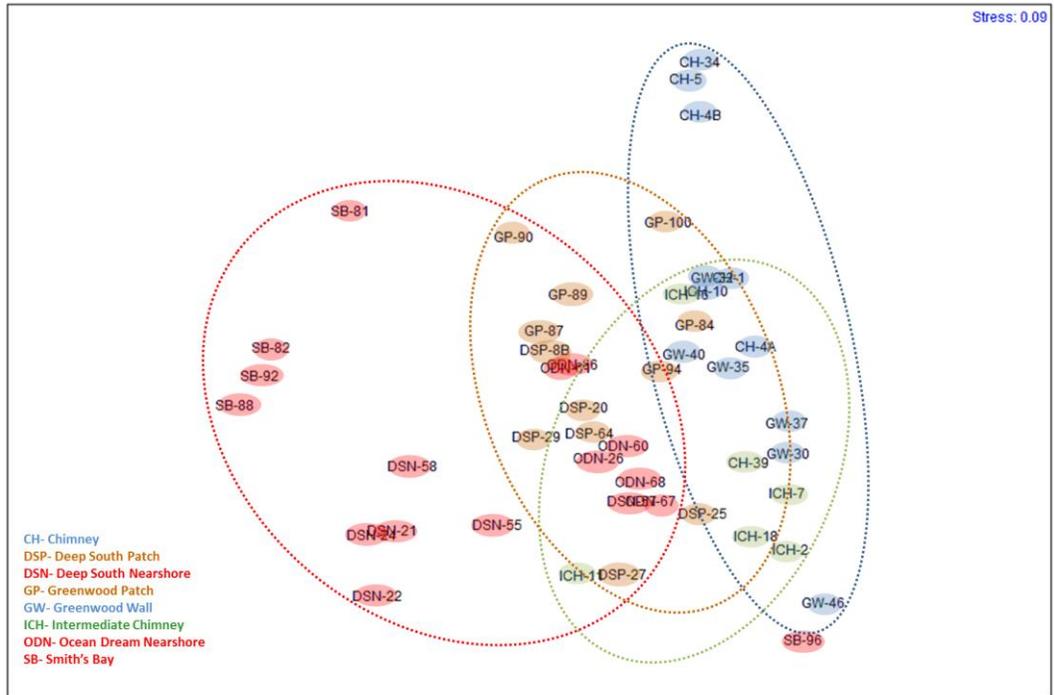


Figure 25- Multivariate dimensional scaling (MDS) plot illustrating the similarity of cobble samples based on their foraminiferal counts on a spatial plane. As in Figure 20, the cobble sample numbers are listed with abbreviations for each site. The dotted lines each represent a grouping of a different type of site (Red- Nearshore reef, Yellow- Patch reef, Green- Intermediate reef, Blue – Platform-margin). SB-96 is excluded from the nearshore cluster due to it being an outlier with only a single foraminifer counted.

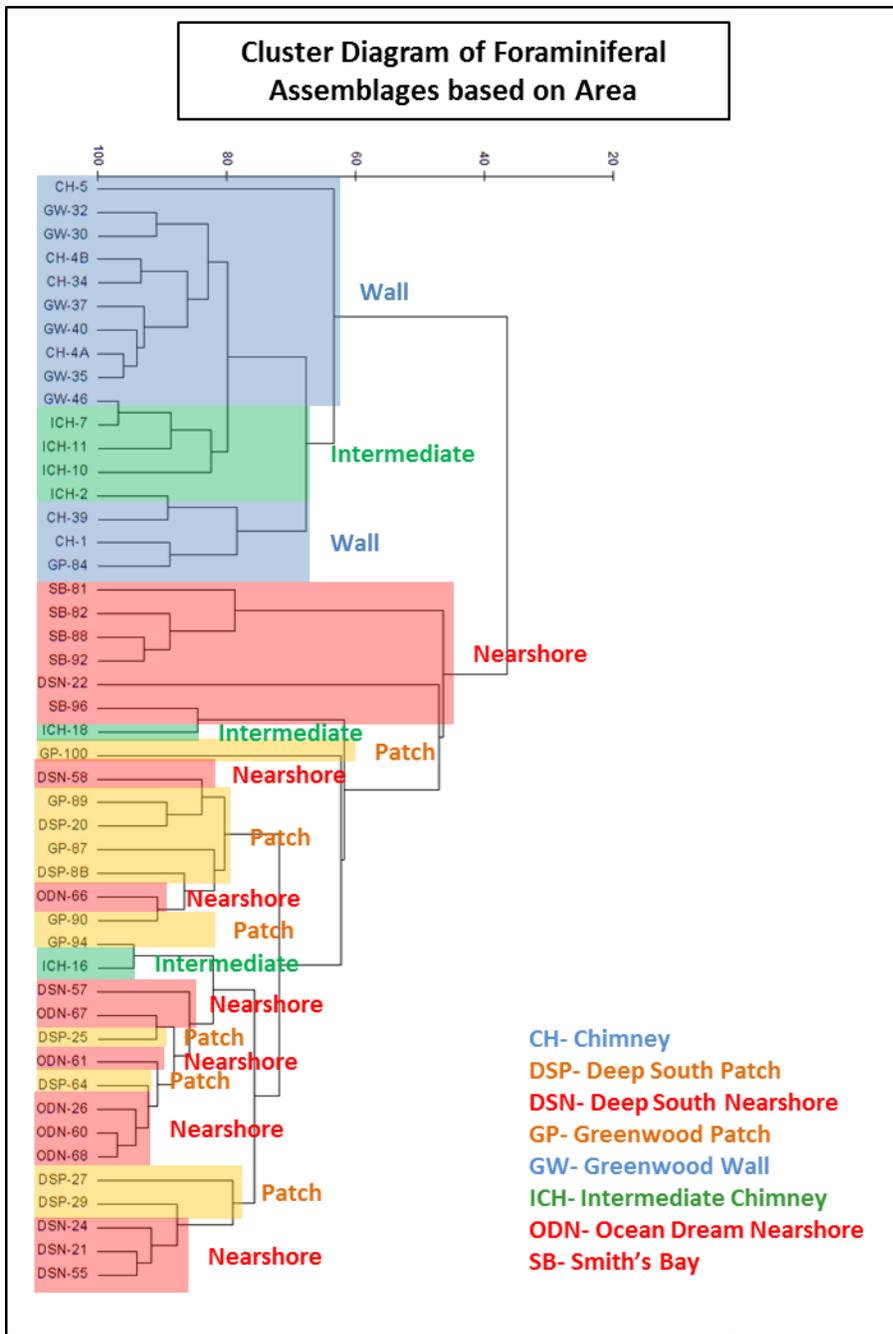


Figure 26- Q-mode cluster of all sites based on area of each species (transformation: square root; similarity coefficient: Bray-Curtis; cluster group: group average). Cobble sample numbers are listed. Sites are represented by abbreviations (“DSN” for Deep South Nearshore, etc.). The axis along the top measures rate of similarity.

5. Discussion

Foraminifera as Dominant Encrusters

Encrusting foraminifera at Cat Island were found to be the most dominant encruster in all reef environments. Nearshore reefs ranged from 80% to as high as 95% foraminifera by counts of individuals, patch reefs ranged from 70% to 85% foraminifera, while the platform-margins were approximately 60% to 65% foraminifera. The lone site that proved to be an exception regarding foraminiferal dominance was the Smith's Bay location, which is discussed below. The dominance of encrusting foraminifera over other organisms is unlike the findings of previous researchers, and the reason for the difference is not clear. It may be a matter of different procedures used, the specialty of investigators, or it may be that there are ecologic factors favoring foraminifera over other encrusters on Cat Island.

There is intense competition between encrusters for living space on substrates. The growth succession between the various encrusters depends largely on the growth rates and growth styles of individual species as well as the stability of the substrate; for example, if the substrate remains in one position for a long period of time, there would be an entirely different make-up of encrusters than if the substrate was routinely flipped or moved in some way (Taylor, 1990). It has been thought that foraminifera have difficulty competing with other encrusting organisms such as coralline algae due to their comparatively slower growth rates (Birkeland, 1977). This is especially the case on the upper surfaces of coral rubble because the top sides have more access to sunlight and therefore are prime locations for photosynthetic organisms such as crustose coralline and

filamentous algae. Thus, the nature of the surfaces examined is critical in comparing the results of one study to another.

Jackson and Winston (1982) studied encrusters attached to the undersides of foliaceous (ledge-shaped) living corals off Rio Bueno, Jamaica, at both 10 and 20 meters in depth. They found sponges, bryozoans, crustose algae, and other algae, but did not record any foraminifera. They found sponges to be more prevalent at 20 meters, while bryozoans were more prevalent at 10 meters. In this setting, there is open circulation of water on the shaded undersides of the sheet-like coral colonies.

However, many encruster studies (Choi and Ginsburg, 1983; Gischler and Ginsburg, 1996; Gischler, 1997; Mallela, 2007) deal with the undersides of coral rubble, as in my study. With less competition for space on the dark undersides of cobbles and with protection from predators in confined spaces, foraminifera thrive along with polychaetes, bryozoans, and other non-photosynthetic invertebrates. In some studies (e.g., Meesters et al., 1991, in which visual estimates were made underwater using 10 x 10 cm quadrats), only the most abundant and easily recognized species, *Homotrema rubrum*, is reported. Even when multiple encrusting foraminifera species were recognized and accounted for, they were found to be the most abundant encruster group only in certain reef environments, such as at the shelf margin (Choi and Ginsburg, 1983; Gischler, 1997) or on reef flats (Gischler and Ginsburg, 1996). Even these investigators do not include *Nubecularia* in their list of encrusting foraminifera, possibly because they do not recognize it because its agglutinated outer wall acts as camouflage. Another partial explanation for the predominance of foraminifera over other encrusters at Cat Island is shown most clearly at the Deep South sites. Here, rounded and cylindrical clasts are

coated with a thick mass of *Nubecularia*. It may be that these clasts are overturned frequently, allowing for the early colonizer *Nubecularia* to dominate once it has become established in the first few months.

Zonation Patterns of Foraminiferal Taxa

The distribution of encrusting foraminifera at Cat Island is very similar to that found on San Salvador (Tichenor and Lewis, 2011). In the general model laid out for San Salvador, *Homotrema rubrum* is dominant in low-diversity assemblages in nearshore localities, *Planorbulina spp.* is most abundant in diverse patch-reef assemblages, and abundant *Gypsina plana* characterizes platform-margin localities.

At both the Deep South and Ocean Dream Nearshore sites, *Homotrema rubrum* was the most dominant foraminifer present when assessed by area. Based on counts of individuals, *Homotrema rubrum* was most abundant at the Ocean Dream Nearshore, and *Nubecularia* was the most abundant at the Deep South Nearshore. At a third nearshore site, Smith's Bay, *Nubecularia* was most abundant by counts and by area. The relatively high abundance of *Nubecularia* at nearshore sites along with *Homotrema rubrum* is what led to the grouping of the two species as nearshore taxa on a ternary diagram (Fig. 23). In addition, the Q-mode cluster analysis and the MDS plot both show a high degree of similarity between the cobbles of Ocean Dream Nearshore and Deep South Nearshore sites when based on area.

The preponderance of *Homotrema rubrum* at nearshore sites is in contrast with earlier research on the species, with the exception of the distribution on San Salvador (Tichenor and Lewis, 2009, 2011). According to both MacKenzie et al. (1964) and Elliot et al. (1996), at Bermuda the species is most abundant offshore in outer reefs, and broken

pieces of the tests are transported shoreward. Pilarczyk and Reinhardt (2012) also report this pattern in the British Isles, making a case for the species as an indicator for sediment transport in washover fans. Pilarczyk et al. (2014) report similar results in Polynesia. However, the high abundance of *Homotrema rubrum* growing on nearshore cobbles at Cat Island, along with their relatively high quality of preservation when compared to those farther offshore, would seem to suggest the opposite.

The Smith's Bay site is very different from every other site; the total encruster occurrence is very low. The dominant foraminifer here is *Nubecularia*. Its presence is not unusual for a nearshore site, but the nearly complete lack of *Homotrema rubrum* is striking. This could be explained if the cobbles collected from Smith's Bay were relatively newly deposited, allowing only a short settlement time for encrusters. Prior research on San Salvador has shown that *Nubecularia* is one of the earliest foraminifera to settle, appearing within the first three months (Martin and Lewis, 2015), and *Homotrema rubrum* is not established until approximately one year, a finding of other researchers as well (Adey and Vassar, 1975; Parsons, 1993).

Another possibility is an unfavorable type of substrate. At all other locations sampled, nearly every cobble is a piece of coral rubble. However, at Smith's Bay, the cobbles were made up of oolitic limestone, perhaps indicating the presence of an unseen offshore oolitic shoal. Holocene oolitic eolianites are found near Alligator Point north of Smith's Bay; the source is thought to be oolitic sands on the leeward shelf of Cat Island (Myroie et al., 2006). Oolitic limestone is also known from Half Moon Cay (also known as Little San Salvador), which is located at the northwest extremity of the Cat Island shelf (Lewis, personal communication, January, 2015). In general, the west side of Cat Island,

the leeward side, seems to be sandier with fewer coral reefs than the east and south sides of the island. Because encrusting foraminifera accompany coral reefs, this may be the reason why the site is such an anomaly.

At the Greenwood Patch site, *Planorbulina spp.* was the most dominant in both abundance and area. This is in agreement with what was found at patch reefs in previous research from San Salvador (Tichenor and Lewis, 2009, 2011). The separate cobbles from the Greenwood Patch site showed a high degree of similarity to each other as shown by both cluster analysis and the MDS plot, especially when areas are compared. The Deep South Patch site was more unusual. Despite its water depth (approximately 12 feet), which would suggest an assemblage of foraminifera similar to that of the Greenwood Patch site, the Deep South assemblage instead shows a closer resemblance to the assemblages of the Deep South and Ocean Dream Nearshore sites based on the preponderance of *Homotrema rubrum* and *Nubecularia*. The best explanation for this is the configuration of the reef at Deep South Patch compared to the Greenwood Patch reef. At Greenwood Patch, there is a clear break between the nearshore reef and the patch reefs, with a sandy seafloor separating them. This probably allows for greater differentiation between the foraminiferal assemblages. In contrast, the Deep South Nearshore and Patch sites are very close to one another and are part of a nearly continuous reef, only broken up by scattered grass beds (Fig. 9). This probably led to less differentiation, and thus an assemblage resembling the nearshore sites, despite its greater water depth and its distance from shore.

Gypsina plana was found in abundance only at the platform-margin. While its numerical abundance was relatively low at both the Greenwood Wall and Chimney sites,

it was clearly dominant in area at these locations. Because of the extremely large size of individual members of the species, area provides a more accurate representation of the relative proportions of *Gypsina plana*. Along the southern transect (Fig. 9), the site designated as Intermediate Chimney lies on the outer shelf, in between the nearshore sites and the platform-margin site (Chimney). Its foraminiferal assemblage shows a composition expected for such a site based on the work of Tichenor and Lewis (2009, 2011). The site is dominated by *Homotrema rubrum* and *Planorbulina spp.*, just as in the many sites closer to shore and at shallower depths. However, *Gypsina plana* is present here, but not nearly as much as at the platform-margin sites. The assemblage appears to represent a true half-way point between nearshore and platform-margin assemblages.

Previous research on the distribution of encrusting foraminifera at platform-margins has shown conflicting results. As previously stated, Martindale (1992) found *G. plana* at all depths from the nearshore to the platform-margin. In contrast, Tichenor and Lewis (2009, 2011) found *G. plana* in abundance only at platform-margin locations. Martindale's research took place in Barbados. Here, the fringing reef extends nearly continuously from shore to the first barrier reef. As in the case of the Deep South patch reef discussed above, this may help to explain why *G. plana* has a wider range in Martindale's research than is seen in our research.

In addition to the dominant species present in the assemblages, there were many other patterns visible from onshore to offshore at Cat Island. Most apparent was the trend towards decreasing density of foraminifera from onshore to offshore. Mean foraminifer test size also showed a clear decline onshore to offshore (Table 6), coinciding with the drop in population density. The exception is *Gypsina plana*, which increased in size

offshore from the Intermediate Chimney site (71.60 mm) to the Chimney site (111.80 mm). The average size of *Gypsina plana* at the Greenwood Patch site (179.09 mm) was larger than at the Greenwood Wall (106.94 mm), but that is based on only a single large individual.

One last pattern apparent is the dramatic downward trend in quality of preservation from onshore to offshore. None of the sites had especially high QPI values. These overall low QPIs could be a byproduct of the persistent nature of encrusting foraminifera, with dead individuals remaining present long after death, combined with a low rate of addition of new tests. This could also explain the downward trend in preservation quality onshore to offshore. Much higher QPI values were found in previous research at San Salvador (Tichenor and Lewis, 2009, 2011). However, those previous studies also showed a decrease in preservation quality from onshore to offshore.

There is no notable pattern in the morphotypes of *Homotrema rubrum*. The vast majority of morphotypes counted were of the multiple variant, which accounted for as much as 100% of specimens at some locations (Fig. 18). This differs from the findings of Elliot et al. (1996), who found variation in morphotypes based on microenvironmental conditions. For example, they found knobby and globose tests to be more prominent in more protected habitats and the other morphotypes to be more abundant in locations reflecting changing environmental conditions. This was simply not the case at Cat Island. However, a very small trend toward a higher diversity of morphotypes (Multiple: 85%) can be seen as one gets closer to shore at Cat Island. This is most likely due to the nearshore cobbles being more irregular in shape, leading to more diverse growth environments for *Homotrema rubrum*. However, this small amount of variance still

differs greatly from previous research, where variation was much more apparent (Elliot, et al. 1996).

Controlling Environmental Factors

In order to explain the distinctive zonation seen in this study, it is important to explore the typical environmental controls on foraminifera. There are several different factors that control foraminiferal distribution: salinity, temperature, light intensity, nutrient level, and food availability (Hallock, 1986). Of these, salinity probably has the least relevance for Cat Island, as no restricted bays were sampled and none of the sites had any nearby freshwater input. The shallower reefs have more light and higher temperatures, while deeper reefs have less light and colder temperatures. However, light intensity and temperature variability usually must be more extreme to have a noticeable effect on zonation patterns of foraminifera (Murray, 2006). The variability in light and temperature present in the Cat Island sites would probably not be substantial enough to explain the zonation patterns.

In microhabitats of meiobenthos, or microorganisms living in ocean sediments, prior research has shown food to be the primary controlling factor (Shirayama, 1984; Jorissen et al., 1995). Recently, investigators have concluded that availability and type of food is a major controlling factor for benthic foraminifera as well (Murray, 2006). This seems to be a likely explanation for the zonation for encrusting foraminifera at Cat Island. Foraminifera in general utilize many different feeding strategies, from grazing to suspension feeding to predation and even parasitism. Most encrusting foraminifera, such as the ones in this study, are suspension feeders (Goldstein, 1999). Using tube-like extensions that elevate their apertures above the sediment into the water column, the

foraminifera are able to extend their pseudopodia into the water currents and capture food as it is carried by the current. This means that they are reliant on water currents to bring food to them. As a result, these foraminifera are often found in areas with relatively strong water currents (Goldstein, 1999). These foraminifera primarily feed upon bacteria and organic detritus (Richardson-White and Walker, 2011). Jackson and Winston (1982), in a study of encrusting organisms on the undersides of coral ledges at Jamaica, report that water flow and suspended food decrease with an increase in depth (see also Reiswig, 1971, 1972). This is to be expected at Cat Island as well because the preponderance of grass beds closer to shore, especially at the Deep South sites, would aid in generating the organic material used as a food source for foraminifera. This could also explain the larger sizes for foraminifera such as *Homotrema rubrum* nearer to shore at Cat Island. A greater food supply could lead to better nourishment, faster rates of growth, and perhaps longer lives.

The one foraminifer that does not conform to this pattern is *Gypsina plana*, as it almost exclusively exists at the platform-margin sites, and when it does occur closer to shore at the Intermediate Chimney sites, it is significantly smaller than specimens found at the platform-margin sites. Even though food availability decreases offshore, the size of this species increases. This could be explained by the presence of a symbiotic relationship, a mutually beneficial relationship between two types of organisms. Several foraminifer species have been found to have symbiotic relationships with algae (zooxanthellae), especially the larger foraminifer species (e.g., Haynes, 1965). As do reef-forming corals, the foraminifer provides the algae with living space plus access to light and in return the algal symbiont provides glucose, glycerol, amino acids, and

nutrients to the foraminifer by its process of photosynthesis (Leutenegger, 1984). This symbiosis would be of particular advantage in environments with scarce food such as at the platform-margins. In these high-stress environments, slightly less light and lower temperatures, along with less food, might lead to slower growth rates and longer lives, accompanied by maturation at larger sizes (Hallock, 1986).

Several investigators believe that *Gypsina plana* is one of these large symbiont-bearing foraminifera even though no direct observations have been made of the species' cell structure. Prager and Ginsburg (1989) assumed the presence of symbionts in *Gypsina vesicularis*, a closely related species found on Florida's outer shelf, because living individuals were colored ("greenish-tan") and lost color soon after collection. Walker et al. (2011) report that *G. plana* shows no preference for shaded versus sunlit surfaces and suggest symbionts could be present in *G. plana*. Martindale (1992) speculated that photosynthetic symbionts could explain the large test size and occurrence on exposed surfaces. Although Martindale (1992) and Walker et al. (2011) found no preference for shaded as opposed to sunlit upper surfaces, *G. plana* at Cat Island (and at San Salvador) are much more abundant on the undersides of cobbles. Even so, this could be explained by the reduced competition for space on undersides, along with the small amount of light available.

6. Conclusions

Foraminifera are the dominant encrusting organisms found on cobble undersides in the shallow waters surrounding Cat Island. The distribution of these cryptic encrusting foraminifera shows a clear zonation based on foraminiferal assemblages, and this closely resembles the findings of previous research on nearby San Salvador by Tichenor and Lewis (2009, 2011). Nearshore reef assemblages are dominated by *Homotrema rubrum* and *Nubecularia*. Patch reef locations are dominated for the most part by *Planorbulina* spp. with the exception of the Deep South Patch site, which resembles a nearshore location due to its continuous reef geography with the Deep South Nearshore site. Platform-margin locations are dominated in area by *Gypsina plana*. The Intermediate Chimney site shows a clear midway point between the nearshore and the platform-margin.

In addition, the density, average size, and preservation of foraminifera are linked with water depth and distance from shore. Larger populations, larger sizes of individuals, and higher quality of preservation closer to shore in shallow water give way to smaller populations, smaller sizes, and lower quality preservation farther from shore in deeper water.

The overall characteristics of modern encrusting foraminifer populations such as the one at Cat Island, from their species assemblages to their population density, average size, and preservation give us valuable information that might be applied to ancient foraminiferal assemblages as well. For decades, most foraminiferal paleoenvironmental research has revolved around free foraminifera, both planktonic and benthic. However, due to their dominance amongst encruster groups and their unique assemblages based

upon water depth, along with the advantages provided by their attached nature, it seems certain that encrusting foraminifera are indeed a viable and important potential tool in paleoenvironmental analyses.

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