

**Distribution of encrusting foraminifera at Mayaguana, Bahamas: Determining assemblage composition and relationship of test size and density to food availability**

by

Eric Eubanks

A Thesis Submitted to the Graduate Faculty of  
Auburn University  
in Partial Fulfillment of the  
Requirements for the Degree of  
Master of Science

Auburn, Alabama  
August 4, 2018

Keywords: Encrusting foraminifera, paleoecology,  
meiofauna, actualistic paleontology

Copyright 2018 by Eric Eubanks

Approved by

Ronald D. Lewis, Chair, Associate Professor, Department of Geosciences  
Charles E. Savrda, Professor, Department of Geosciences  
Anthony G. Moss, Associate Professor, Department of Biological Sciences

## Abstract

Benthic foraminifera that are cemented by calcium carbonate or are otherwise firmly fixed to hard surfaces are known as encrusting or attached foraminifera. Relatively few actualistic studies focus on the use of encrusting foraminifera as paleoenvironmental indicators compared to the vast literature on free foraminifera. However, their sensitivity to environmental factors such as light and water energy and the fact that they are fixed in place and therefore are likely to remain in the original habitat after death makes encrusting foraminifera valuable in paleoecology. Previous research on San Salvador and Cat Island, Bahamas, has created models for the density and occurrence of these encrusting foraminifera on carbonate platforms. The data in this study, which focuses on nearby Mayaguana, are compared to those of the previous experiments done on San Salvador and Cat Island.

Cobbles were collected by both SCUBA and snorkeling at seven different sites that ranged from nearshore reefs to shoals to mid-shelf patch reefs and the platform margin. The sites vary considerably across localities regarding the size, density, and relative proportion of encrusting foraminifera. Nearshore localities contained considerable amounts of *Homotrema rubrum* and *Planorbulina*, with considerable site-to-site variability. Shoal environments not examined in previous Bahamian studies, were dominated by *Homotrema rubrum* in count and area, as was a bank barrier reef. Mid-shelf patch reefs were dominated by *Planorbulina* spp., whereas the platform margin was characterized by numerous large *Gypsina plana*. The size and density of foraminifera decreased from onshore to offshore, which compares well with prior

results from Cat Island. All five morphotypes of *Homotrema rubrum* were encountered at the shoals and bank barrier reef, although morphotype data gathered on *Planorbulina* spp. was inconclusive. Almost all data are consistent with previous research performed on San Salvador and Cat Island, which supports the model of encrusting foraminifera distribution developed by Tichenor and Lewis (2009).

Water samples were collected from beneath cobbles using a syringe and were buffered with a solution of 5% formalin. Three ml of each sample was analyzed using light microscopy to count and identify organisms within a certain area. Three water samples from two nearshore sites, the patch reef site, and the platform-margin site were studied. Microbes, pennate diatoms, and black “amorphous masses” were found at all sites, although they occurred in much greater abundance at the two sites located within the lagoon. There is very little relationship between the types or number of water taxa and water depth, density, or size of encrusting foraminifera at each locality, suggesting that food particles in water are just one of many variables that control the distribution of encrusting foraminifera.

Sediment samples were collected from beneath cobbles using a plastic container. A 5% solution of formalin was added to buffer the samples, which were stained with Rose Bengal and preserved in 190 proof ethanol. Three 1-ml subsamples were analyzed using light microscopy to count and identify stained organisms at each site. Two sediment samples were taken at all sites, except for *Goniolithon* Shoal, for a total of 39 ml of sediment analyzed. Nearshore sites varied significantly in their counts of meiofauna, which included foraminifera, crustaceans, nematodes, and annelids. A strong correlation was found between counts of meiofauna and encrusting foraminiferal size, density and assemblage composition, which suggests that more potential food particles in sediment influences the distribution of encrusting foraminifera.

## Acknowledgments

First, I would like to thank my thesis advisor, Dr. Ronald Lewis, whose near-infinite patience and invaluable guidance made this thesis possible. His effort, enthusiasm, and dry humor helped me to flourish at Auburn and made my experience a special and unforgettable one. I would also like to thank Dr. Anthony Moss for his immeasurable help with preserving and studying the water samples, which added a whole new dimension to my findings. I must also thank Dr. Charles Savrda for his tremendous editing prowess and for playing a huge part in my development as a sedimentary geologist. This research would not have been possible without funding from the Cushman Foundation for Foraminiferal Research. A special thanks also goes to Dr. Ashraf Uddin, who helped to keep me on track and who extended the offer for me to come to Auburn.

I would also like to thank all the friends I made here at Auburn. They were the best peers and colleagues I could have hoped for, and they provided the empathy, advice, and fun times to help me grow as a geologist and a person. I must also thank Shorty, the owner of the Baycaner Beach Resort in Mayaguana, for providing accommodations and organizing our excursions. Many thanks go to Jermain Deveaux, the boatman, who made it possible to explore the wall and bank barrier sites, and who also saved us from a tidal current. I would also like to recognize Will Bozeman, Anabelle Kline, and especially Travis Barefield, who did an excellent job of counting, measuring, and identifying the foraminifera on the cobbles. Recognition should also go to Skye

Walker and Sarah Stevens for the vital roles they played in identifying the organisms in the water and sediment samples, respectively.

Finally, I would like to extend my thanks to my friends and family for their constant support. I would like to thank Richardson Joyner and Nathan Ravenel for keeping me sane and always being there for me. I must also thank Christine and Kyle Letcher, who helped to guide my professional life and were always happy to see me. I would like to thank Brigid Fitzpatrick, whose love, devotion, and countless phone calls helped to ease stress, give me courage, and inspire me to persevere. Lastly, I am eternally grateful for my parents, Steve and Liz Eubanks, who supported me every step of the way and gave me the love and guidance I needed to succeed.

## Table of Contents

Abstract . . . . .	i
Acknowledgments . . . . .	iii
List of Tables . . . . .	vii
List of Figures. . . . .	viii
Introduction . . . . .	1
Previous Works . . . . .	3
<i>Homotrema rubrum</i> . . . . .	3
Assemblage Studies . . . . .	4
Controlling Factors . . . . .	8
Study Area and Methodology. . . . .	13
Study Area. . . . .	13
Site Descriptions . . . . .	13
Sample Collection . . . . .	20
Sample Preparation and Data Collection . . . . .	22
Results . . . . .	24
Foraminiferal Taxa. . . . .	24
Similarity of Cobble Assemblages. . . . .	37
Comparison of Key Species. . . . .	41

Foraminiferal Morphotypes, Size, and Density . . . . .	43
Biota in Water Samples. . . . .	47
Meiofauna in Sediment Samples. . . . .	51
Discussion. . . . .	55
Zonation Patterns of Foraminiferal Taxa . . . . .	55
Water and Sediment Samples . . . . .	62
Potential Food Sources in Water. . . . .	63
Potential Food Sources in Sediments. . . . .	64
Reflections . . . . .	68
Conclusions . . . . .	73
References . . . . .	77

## List of Tables

Table 1 – Site locations including reef type, latitude, longitude, distance from shore, and water depth. . . . .	14
Table 2 – The mean size of each foraminiferal taxon at the seven locations. . . . .	45
Table 3 – Total counts of organisms observed in the water samples. . . . .	48
Table 4 – Total counts of meiofauna contained within 6 ml of sediment. . . . .	52
Table 5 – Meiofaunal density, foraminiferal density, averaged <i>Homotrema</i> and <i>Planorbulina</i> sizes, and site depths. . . . .	52
Table 6 – Summary of results from encrusting foraminiferal counts, sizes, and densities with the amount of potential food particles in the water and in the sediment. Dominant taxa are bolded. Note the trend of <i>Homotrema rubrum</i> occurring with large foraminiferal sizes and high density of foraminifera and meiofauna. . . . .	69



## List of Figures

- Figure 1 – Morphotypes of *Homotrema rubrum* known in the Bahamas (1, 4, 5, and 6), Florida (2) and the Red Sea (3) (Krautwig et al., 1998). Morphotype 3 was not observed in this study . . . 6
- Figure 2 – A visualization of the Tichenor-Lewis model (after Tichenor and Lewis, 2009). . . . . 8
- Figure 3 – Data from Cat Island showing that both the density and size of encrusting foraminifera decrease with increasing depth (depth increases to the right in all figures) (Smith, 2015). . . . . 10
- Figure 4 – (A) The Bahamas, showing areas of previous study: San Salvador and Cat Island, as well as Mayaguana, the area of current study. (B) Northwestern corner of Mayaguana, Bahamas, including sample sites (white boxes), the resort location (white arrow), and island settlements (red circles). The sites are abbreviated like so: BBN – Betsy Bay Nearshore, PBN – Pirate’s Bay Nearshore, GS – *Goniolithon* Shoal, BS – Blackwood Shoal, PWPR – Pirate’s Well Patch Reef, BBR – Booby Cay Bank Barrier Reef, and NW – Northwestern Wall . . . . . 16
- Figure 5 – (A) Close-up view of the western side of the study area, showing the Betsy Bay Nearshore site and the Northwestern Wall site. (B) Close-up view of the southern part of the study area, displaying the Pirate’s Bay Nearshore, *Goniolithon* Shoal, and Pirate’s Well Patch Reef sites. . . . . 17
- Figure 6 – (A) Close-up view of the eastern side of the study area, showing the Blackwood Shoal site. (B) Close-up view of the northern side of the study area, showing the Booby Cay Bank Barrier Reef site. . . . . 18
- Figure 7 – Dr. Lewis inserting a plastic tube between the cobble and the substrate to get a water sample. . . . . 20
- Figure 8 – A Type 2 sample recovered from *Goniolithon* Shoal. Note how the tendrils of *Goniolithon* increase the surface area of the cobble and permit encrusting foraminifera to attach on several sides. . . . . 25
- Figure 9 – Representative photographs of each taxon of the encrusting foraminifera observed: (A) *Homotrema rubrum* (multiple), (B) *Planorbulina* spp. (brown), (C) *Nubecularia* sp., (D) *Carpenteria utricularis*, (E) *Gypsina plana*, (F) *Placopsilina* sp. Photograph A is from <http://www.aquaristics.ru/img/articles/foraminifera-homotrema-rubrum.jpg> . . . . . 27

Figure 10 – Betsy Bay Nearshore: Relative abundance of encrusting foraminifera on the undersides of cobbles based on counts of individuals. The quality of preservation index is derived from the percent of live, pristine, and good taphonomic states. . . . . 28

Figure 11 – Pirate’s Bay Nearshore: Relative abundance of encrusting foraminifera on the undersides of cobbles based on counts of individuals. The quality of preservation index is derived from the percent of live, pristine, and good taphonomic states. . . . . 29

Figure 12 – *Goniolithon* Shoal: Relative abundance of encrusting foraminifera on the undersides of cobbles based on counts of individuals. The quality of preservation index is derived from the percent of live, pristine, and good taphonomic states. “Type 2” signifies that the cobble is comprised entirely of *Goniolithon* . . . . . 30

Figure 13 – Blackwood Shoal: Relative abundance of encrusting foraminifera on the undersides of cobbles based on counts of individuals. The quality of preservation index is derived from the percent of live, pristine, and good taphonomic states. . . . . 31

Figure 14 – Pirate’s Well Patch Reef: Relative abundance of encrusting foraminifera on the undersides of cobbles based on counts of individuals. The quality of preservation index is derived from the percent of live, pristine, and good taphonomic states. . . . . 32

Figure 15 – Booby Cay Bank Barrier Reef: Relative abundance of encrusting foraminifera on the undersides of cobbles based on counts of individuals. The quality of preservation index is derived from the percent of live, pristine, and good taphonomic states. . . . . 33

Figure 16 – Northwestern Wall: Relative abundance of encrusting foraminifera on the undersides of cobbles based on counts of individuals. The quality of preservation index is derived from the percent of live, pristine, and good taphonomic states. . . . . 34

Figure 17 – Principal taxa of foraminifera. The bar graphs (left) show the relative abundance based on count. The pie charts (right) show the percentage of area that each taxa covered. QPI is based on the percentage of the live, pristine, and good categories. Note the dominance of *Homotrema rubrum* in the shoals in contrast to *Planorbulina*’s dominance at the nearshore sites. . . . . 35

Figure 18 – Principal taxa of foraminifera. The bar graphs (left) show the relative abundance based on count. The pie charts (right) show the percentage of area that each taxa covered. QPI is based on the percentage of the live, pristine, and good categories. Note the dominance of *Homotrema rubrum* at the bank barrier reef in contrast to *Planorbulina*’s dominance at Pirate’s Well Patch Reef. *Gypsina plana* displays a clear dominance at the Northwestern Wall location. . . . . 36

Figure 19 – Q-mode cluster of all sites based on relative abundance as determined by individual counts (transformation: square root; similarity coefficient: Bray-Curtis; cluster group: group average). Cobble and sites are represented through the notation “#-#” (“1-2” is site 1, cobble 2, etc.). The axis along the top measures rates of similarity. . . . . 38

Figure 20 – Q-mode cluster of all sites based on relative abundance as determined by foraminiferal areas (transformation: square root; similarity coefficient: Bray-Curtis; cluster group: group average). Cobble and sites are represented by the notation ‘#-#’ (“1-2 is site 1, cobble 2, etc.). The axis along the top measures rates of similarity. . . . . 39

Figure 21 – Non-metric multidimensional scaling (MDS) plot displaying the similarity of cobble based on their counts (A) and areas (B) on a spatial plane. The samples are denoted with the same notation as Figures 19 and 20. The dotted lines are groupings of each type of site (Red – nearshore, Blue – shoal, Brown – patch, Gray – bank barrier, Green – platform margin). . . . . 40

Figure 22 – Ternary diagrams of the relative abundance of the three dominant foraminifera, *Planorbulina* spp., *Homotrema rubrum*, and *Gypsina plana*, based on counts of individuals (A), and area covered (B) (as in Lewis et al., 2013; Smith, 2015). . . . . 41

Figure 23 – (A) Distribution of the five morphotypes of *Homotrema rubrum* at each site; depictions are from Krautwig et al., 1998 (B) Distribution of the two morphotypes of *Planorbulina* spp. at each site. . . . . 44

Figure 24 – Bar graph depicting the average size of the two most common foraminifera in this study: *Homotrema rubrum* and *Planorbulina* spp. These taxa were chosen because they represent over 95% of the individuals counts in this study and are found at all locations. Size is measured in mm<sup>2</sup>. . . . . 45

Figure 25 – Density of foraminifera, expressed as the mean number of foraminifera counted per 10 cm<sup>2</sup>. Note how density decreases as distance from shore increases. . . . . 46

Figure 26 – Representative photographs of the categories of potential food items in water samples: (A) 1 – Amorphous mass, 2 – Organic detritus littering the background, 3 – Pennate diatom. (B) Crab. (C) Harpacticoid copepod. (D) Unidentified microbe (circled) next to crystals of formalin. (E) Ostracod. (F) Foraminifer. . . . . 49

Figure 27 – Relationships between total potential food items in water samples and (A) foraminiferal density, (B) average *Homotrema rubrum* and *Planorbulina* spp. size, and (C) water depth. . . . . 50

Figure 28 – Representative photographs of the categories of meiofauna: (A) and (B) Harpacticoid copepod, (C) Polychaete, (D) Ostracod, (E) Roundworm, (F) Segmented nematode. . . . . 53

Figure 29 – Relationship between meiofauna density in sediments and (A) foraminiferal density, (B) average size of *Homotrema rubrum* and *Planorbulina* spp., and (C) water depth. . . . . 54

## 1. Introduction

Foraminifera are single-celled amoeboid marine protists whose geologic range extends back to the Cambrian Period; in addition to this long geologic range, they have significant paleoecological and paleoenvironmental relevance (Goldstein, 1999; Armstrong and Brasier, 2005). There are two main groups of foraminifera: planktonic and benthic. Planktonic foraminifera live in the water column above the ocean floor, whereas benthic foraminifera live on the ocean bottom and are either mobile or are attached to a hard substrate such as a coral reef or coral rubble (encrusting foraminifera). Encrusting foraminifera, the focus of this study, have distribution patterns that can be influenced by temperature, light level and salinity, nutritional conditions, and other variables (Linke, 1992; Linke and Lutze, 1993; Richardson-White and Walker, 2011; Smith, 2015). Because they are firmly attached to their substrate, they are less likely to be transported out of their habitat than free foraminifera are. This may provide for greater accuracy during analysis and modeling of environmental gradients.

Following James Hutton's concept that "the present is the key to the past" (Geikie, 1897), the factors affecting modern foraminiferal assemblage distribution may have influenced ancient foraminifera in the same way. In this vein, the distribution patterns of benthic foraminifera and their relationship to food availability can be used to draw connections and better understand the environments of ancient foraminifera in the Bahamas and elsewhere.

There is comparatively little literature that focuses on using encrusting foraminifera as paleoenvironmental indicators; however, researchers are starting to realize the unique value these organisms have in paleoenvironmental analysis. This study documents the species composition, diversity, abundance, and morphotypes of encrusting foraminiferal assemblages on cobble-sized

clasts in Mayaguana, Bahamas. The study also relates the food availability in the water and sediment to these variables.

## 2. Previous Research

This section has been divided into three parts to emphasize the most important aspects of the previous research: (1) publications on *Homotrema rubrum*, (2), studies of whole assemblages of attached foraminifera, and (3) investigations of factors controlling foraminiferal distribution.

### *Homotrema rubrum*

Of the encrusting foraminifera discussed in previous studies, *Homotrema rubrum* is by far the most widely recognized and researched; it has been the focus of studies ranging from sediment transport to taxonomy (MacKenzie et al. 1964; Rooney, 1970; Elliott et al., 1996; and Krautwig et al., 1998). Most investigators have concluded that it is most abundant in outer reefs, but Tichenor and Lewis (2009, 2011) found it to be abundant near shore as well. Many investigators have reported various intraspecific morphotypes beginning with Rooney (1970). Elliott et al. (1996) conducted a study in Bermuda based on these growth forms, and they were able to identify five distinct shapes: hemispherical, globose, knobby, encrusting, and columnar. Their study, which included 4,002 tests and covered various reef settings, concluded that knobby and globose tests were the predominant morphotype in lower-energy habitats, while hemispherical and encrusting tests were more typical of exposed, energetic environments. Although they were able to draw broad conclusions about the morphologies, they admitted that, like Rooney (1970), they were unable to recognize a definite correlation between morphotypes and any specific environment. Elliott et al. (1996) posited that there were a variety of factors, such as sedimentation rates, that controlled morphology, abundance, and distribution of *H.*

*rubrum* (Rooney, 1970). They also suggested that the test morphologies can be influenced by both ontogeny and the environment. For example, some *H. rubrum* may begin as encrusting juveniles, but may change into the globular shape as they reach sexual maturity. Other factors that affect *Homotrema rubrum*'s test morphology are wave and current action, light level, competition, predation and reproduction (Elliot et al., 1996).

Krautwig et al. (1998) encountered the globular, multiple, encrusting and columnar morphotypes of *Homotrema* in the Bahamas (morphotypes 1, 4, 5, and 6, shown in Fig. 1, above), along with the arboreal (morphotype 2, Fig. 2) growth form in Florida. All five morphologies of *H. rubrum* were found in a transect across Tennessee Reef in the Florida Keys by Phalen et al. (2016), who observed that the knobby, encrusting and hemispherical morphologies were most abundant. These different *Homotrema* growth forms were distinguished in the current study.

#### *Assemblage studies*

Choi and Ginsburg (1983) performed an analysis of encrusting organisms including *Homotrema rubrum* and foraminifera on the undersides of coral rubble in the Florida Reef Tract. They collected cobbles that were 20-40 cm in diameter from 21 different offshore locations, ranging from an in-shore lagoon setting to a fore-reef 40 m in depth. Like the investigators before them, they found *Homotrema rubrum* to be more common in platform-margin settings than in shallower nearshore environments. Gischler and Ginsburg (1996) examined the distribution of encrusting organisms living on the underside of cobbles along transects through the barrier reef off Belize and at Glovers Reef. They report the occurrence of 5 species of foraminifera, including *Homotrema rubrum*, *Planorbulina*, *Carpenteria*, and *Gypsina*) but only give data for *H. rubrum*, which were found to be most abundant near the reef crest and in the

shallow fore-reef. Gischler (1997) completed a study similar to Gischler and Ginsburg's (1996) that was based on sites in the middle keys and lower keys of the Florida Reef Tract. Reported foraminifera consisted only of *H. rubrum* and two unidentified taxa.



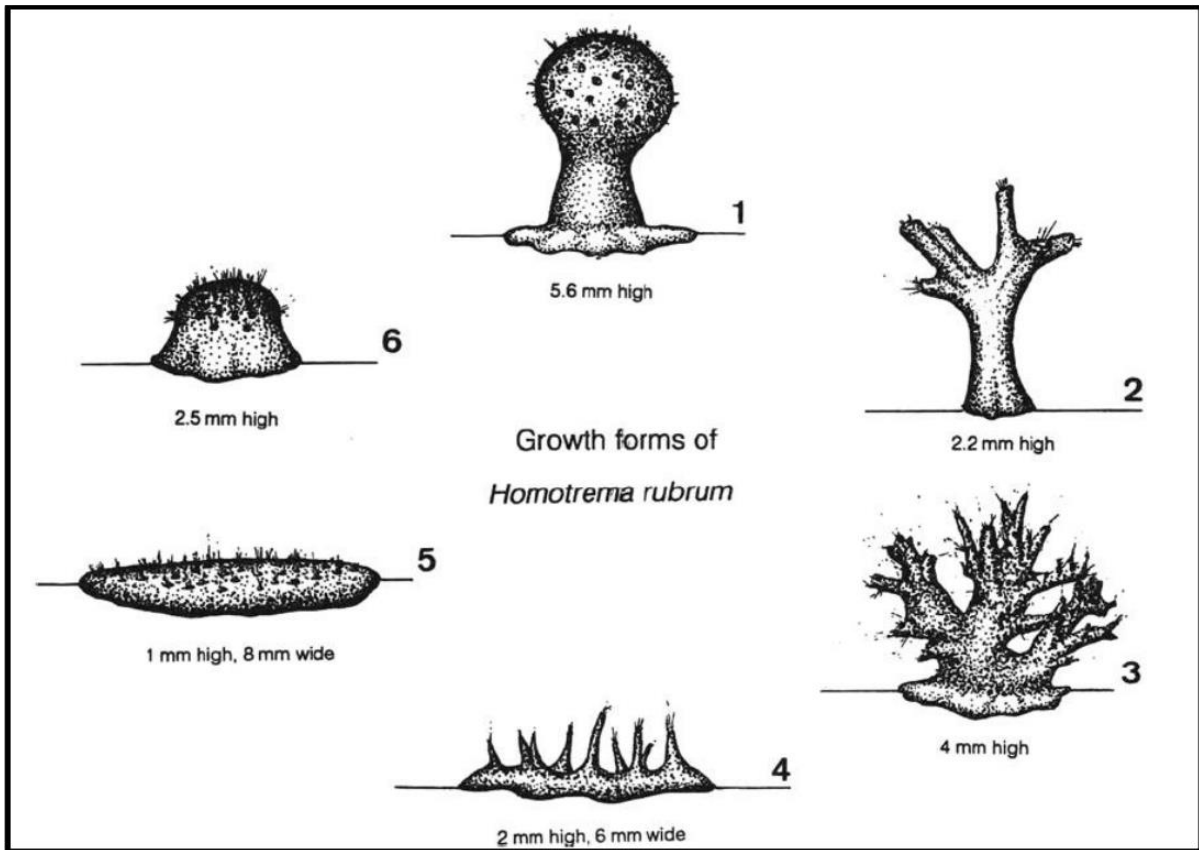


Figure 1 – The morphotypes of *Homotrema rubrum* (Krautwig et al., 1998). Morphotype 3 was not observed in this study.

Martindale's study (1992) involved collecting four hundred cobbles from various locations and reef environments around Barbados, in the Caribbean. This research documented *Carpenteria utricularis* and *Homotrema rubrum* in shallow (0-10 m) and mid-depth (10-30 m) habitats. In shallow, high-energy environments, these encrusting foraminifera had low-profile tests adhering closely to the substrate. Martindale noticed that *Homotrema rubrum*, in particular, exhibited a number of growth forms. In sheltered shallow-water environments, the tests sustained a "delicate branching morphology," and in cryptic shallow-water habitats, *Homotrema* had high-relief, globose tests. Globose-shaped tests were also observed in *C. utricularis* in cryptic habitats at mid-depth (10-30 m). Furthermore, Martindale (1992) found that *Gypsina plana* was present on the tops as well as the undersides of cobbles and was found at all water depths, which is contradictory to subsequent Bahamian studies (Tichenor and Lewis, 2009, 2011; Smith, 2015).

Tichenor and Lewis (2009, 2011) collected 15-25-cm clasts from reef transects at San Salvador, Bahamas. They developed a conceptual model of the zonation of encrusting foraminifera from nearshore to far-shore. This model can be described as follows: *H. rubrum* dominates nearshore assemblages; the mid-shore reefs are diverse, but are characterized primarily by *Planorbulina* spp., and deeper-water, far-shore reefs contain overwhelming amounts of *G. plana* (Fig. 2). They also added *Nubecularia* and *Haddonia* to the species list, taxa not recognized by previous investigators; small *Nubecularia* were found to be most abundant near shore, and *Haddonia* were reported in small numbers only at the platform-margin sites. Recent work suggests that this pattern is, to a large extent, resistant to hurricane impact (Lewis et al., 2016).

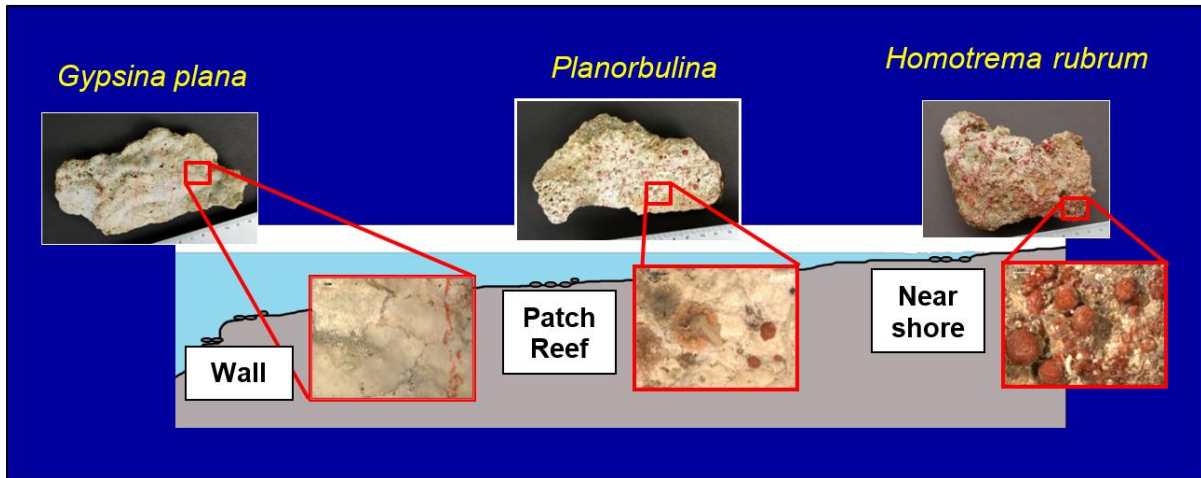


Figure 2 – A visualization of the Tichenor-Lewis model (after Tichenor and Lewis, 2009).

A similar study of foraminiferal zonation was undertaken by Smith (2015). He selected dozens of cobbles from nearshore to far-shore transects on Cat Island, Bahamas. His results, based on thousands of counts, supported the model proposed by Tichenor and Lewis (2009). In addition, Smith saw that the density of encrusting foraminifera (the number of foraminiferal test/cm<sup>2</sup>) decreased from nearshore to far-shore (Fig. 3). Furthermore, he noticed that the average size of *Planorbulina* spp. and *Homotrema rubrum*, the two most common foraminifera in his study, steadily decreased away from shore (Fig. 3). The current study took place on a third Bahamian island, Mayaguana, where the Tichenor-Lewis model was tested in order to support or challenge the previous observations of Tichenor and Lewis (2009, 2011) and Smith (2015) with regards to (1) assemblage composition, (2) density, and (3) test size.

#### *Controlling factors*

Some of the factors that control foraminiferal distribution are salinity, temperature, light intensity, nutrient level and food availability (Hallock, 1986; Linke, 1992; Linke and Lutze, 1993; Richardson-White and Walker, 2011). Salinity differences are thought to be irrelevant for the Bahamian islands of San Salvador, Cat Island, and Mayaguana, which have no freshwater input. Moreover, variations in temperature and light intensity should not be nearly enough to provide drastic changes in foraminiferal distribution patterns (Smith, 2015). Smith (2015) suggested decreasing food availability for the decrease in density and sizes of individuals.

This is supported by Reiswig's (1971, 1972) studies on particle feeding in sponge populations in Jamaica, where suspended food levels and water flow both decreased with increasing depth. *Gypsina plana* is an exception to the trend of decreasing size with increasing water depth. It thrives in the platform-margin environment, reaching sizes well over 100 mm<sup>2</sup>. Many researchers have hypothesized that *G. plana* harbors photosynthetic

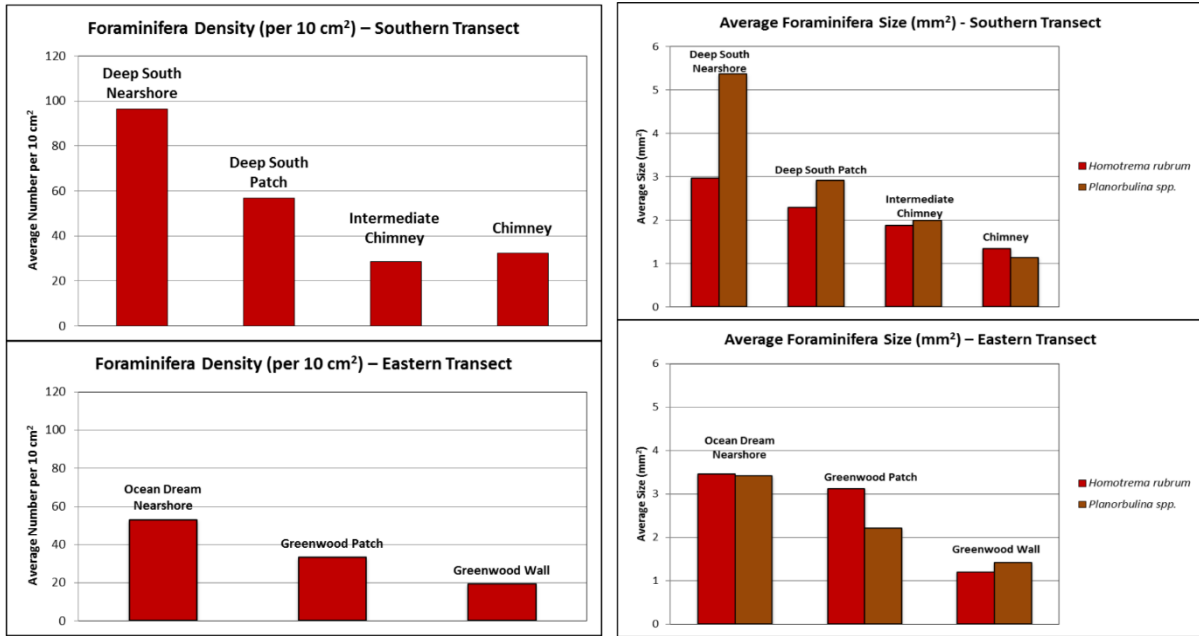


Figure 3 – Data from Cat Island showing that both the density and size of encrusting foraminifera decrease with increasing depth (depth increases to the right in all figures) (Smith, 2015).

symbionts, and that this may explain *G. plana*'s large test size (Prager and Ginsburg, 1989; Martindale, 1992; Walker et al., 2011; Smith, 2015). *G. plana* could also grow so large because of the reduced competition for substrate space out on the wall.

Food as a limiting resource for benthic foraminifera has not been examined in shallow-water carbonates, but has been studied in bathyal and abyssal communities. In these deeper settings, food availability can be a significant factor (Jorissen et al., 1995). Mackensen et al. (1985) conducted studies in the Norwegian-Greenland Sea, and concluded that the two main factors that control foraminiferal distribution are organic carbon flux and oxygen content, instead of specific physical or chemical water parameters. Duffield et al. (2014) tested potential food sources of bathyal benthic foraminifera, which included green algae, phytoplankton, and zooplankton, and found that certain species had varying responses to differing food inputs. Several of the foraminifera preferred to eat bacteria and detritus, and “may supplement their diet further with the arrival of phytoplankton” (Duffield et al., 2014). Others were found to be completely reliant on phytodetritus, and one species was even able to feed on dinoflagellates.

Most attached foraminifera, such as the ones in this study, are suspension feeders (Goldstein, 1999), meaning that they will extend their pseudopodia into the water column and capture food as the current carries it along, although *H. rubrum* has also been observed to engage in carnivory, consuming the nauplii of living brine shrimp in a laboratory setting (Phalen, 2015; Phalen et al., 2016). Consequently, many encrusting foraminifera should be found in areas with relatively strong currents, feeding on bacteria and organic detritus (Goldstein, 1999). Diatoms may also be a possible source of food (Duffield et al., 2014). In the current study, potential food items are assessed based on samples taken in the field to see if the amount and character of these

organisms is consistent with the distribution of encrusting foraminifera. No other study of this kind has yet been done.

### 3. Study Area and Methodology

#### *Study Area*

Mayaguana lies at the southeast end of the Bahamas, located at 22°22'27" N and 72°57'17" W (Fig. 4A, B). It measures 44 km (27 miles) across and is only sparsely populated: the island is 280 km<sup>2</sup> in area and has fewer than 300 inhabitants. This island was selected for research to test the extent of the model developed by Tichenor and Lewis (2009), which had been tested at San Salvador and nearby Cat Island (Fig. 4A). Most of our sites are in the bay known as Pirate's Well, on the northwestern edge of the island (Fig. 4B). Since Mayaguana has been virtually untouched by the scientific community, there is little background knowledge of the island. The only published work on the geology of the island is that done by Kindler et al. (2008), who explored the geology of the stratigraphic units visible on the eastern end of Mayaguana. No studies of the island's foraminifera are known.

#### *Site Descriptions*

All samples were collected over a week-long period from June 2-9, 2017. Dr. Lewis and I found suitable lodging at the Baycaner Beach Resort located in the northwestern part of the island near the settlement of Pirate's Well (Fig. 4B). Through this resort, we were able to rent SCUBA tanks, weights, and a truck, and to hire a boatman to ferry us to the distant sites. Conveniently, the resort was located on the lagoon that contained five of the seven diving / snorkeling sites that we explored. The eastern half of Mayaguana is pristine, untouched



**Table 1 – Site locations including reef type, latitude, longitude, distance from shore, and water depth.**

Site Name	Site Type	Latitude	Longitude	Distance from Shore (m)	Water Depth (ft/m)
Betsy Bay Nearshore	Nearshore	22° 26' 31.67"N	73° 7' 44.44"W	10	2.5 (.75)
Pirate's Bay Nearshore	Nearshore	22° 26' 45.46"N	73° 6' 44.73"W	3	1.7 (0.5)
<i>Goniolithon</i> Shoal	Shoal	22° 27' 2.82"N	73° 6' 48.02"W	254	6.5 (2)
Blackwood Shoal	Shoal	22° 26' 54.66"N	73° 4' 29.94"W	217	3.3 (1)
Pirate's Well Patch Reef	Patch	22° 26' 58.50"N	73° 6' 41.34"W	327	6.5 (2)
Booby Cay Bank Barrier Reef	Barrier	22° 28' 0.36"N	73° 6' 44.73"W	1829	5 (1.5)
Northwestern Wall	Platform Margin	22° 26' 38.34"N	73° 7' 53.70"W	257	72 (22)

wilderness which has a rocky coast, so SCUBA diving and snorkeling were limited to this lagoon and the western side of the island.

Samples were collected at seven different localities. Table 1 lists the sites in approximate order of increasing distance from shore and water depth. The exact site locations were measured on the boat before a dive, using a Garmin Marine GPS receiver unit. When the sites did not require a boat, GPS locations were obtained from the underwater camera. Water depths were recorded using a dive computer, and relative water energy was noted.

The first location that was selected for collection was the Pirate's Well Patch Reef (Fig. 5A), which was visible from shore. Starting from shore to the northwest of the resort, we swam out over 300 meters to the reef, which had an approximate water depth of just over 6.5 feet (2 m). Although the patch reef was not very big, the coral were large and healthy, consisting primarily of *Orbicella annularis*.

The second site is located just to the west, made noticeable by a line of breaking waves which turned out to be a ridge of *Goniolithon*. This location consists of a long, thin platform of *Goniolithon* covered in turtle grass, with very shallow water on top and a six-foot plunge on the lee side. This site is over 250 m from shore, but because it is a high-energy, oxygenated, and shallow, it was considered to be a shoal, earning it the name *Goniolithon* Shoal (Fig. 5B). This was a new type of locality not observed in any of the previous works by the Auburn team. We returned the next day with a boat and took our samples.

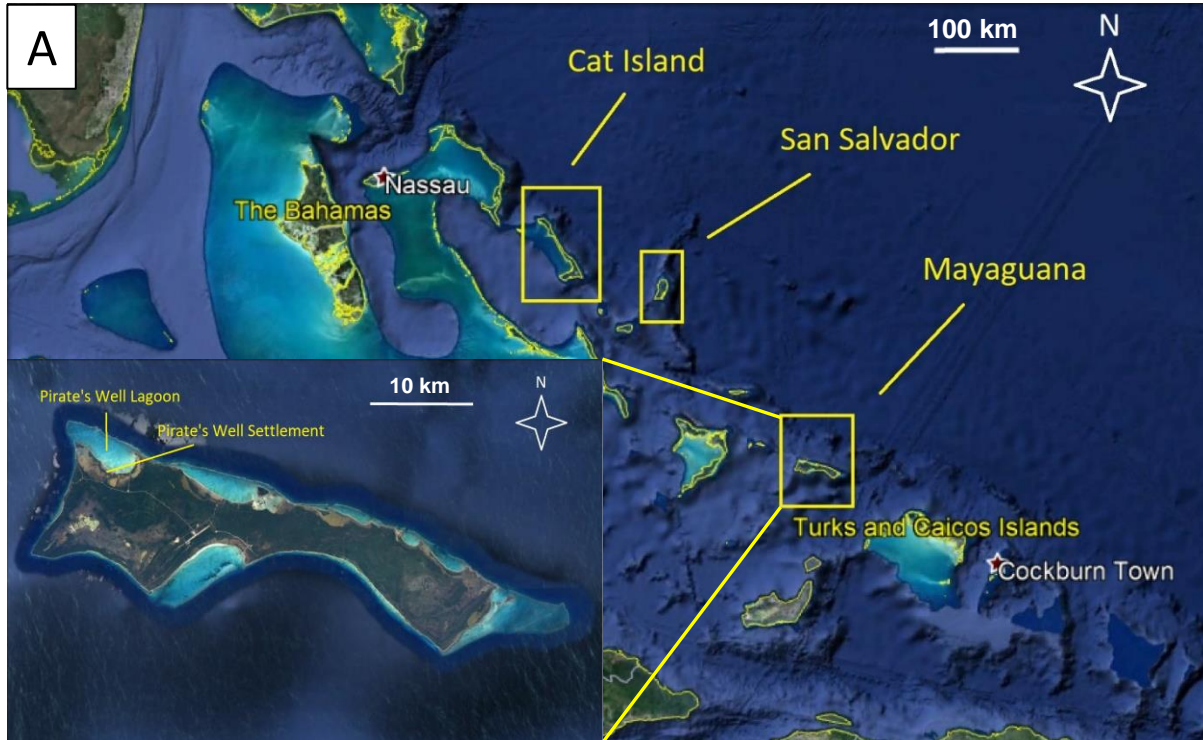
The Booby Cay Bank Barrier Reef site is located over 1800 m from shore at the edge of the lagoon (Fig. 6B), and samples were taken as close to the bank barrier reef as possible. While we were diving, Dr. Lewis noticed that he was being pulled out to sea by a mighty tidal current

and signaled for me to help; I grabbed his wrist and attempted to swim towards shore, to no avail. Our boatman, Jermain Deveaux, noticed our plight and immediately drove the boat over to us, dropping a pair of ropes and pulling us several hundred meters to safety. The water energy was high at this site, comparable to that of *Goniolithon* Shoal. The water depth was approximately 5 feet (1.5 m), and the reef contained *Acropora palmata* and *Millepora* spp.

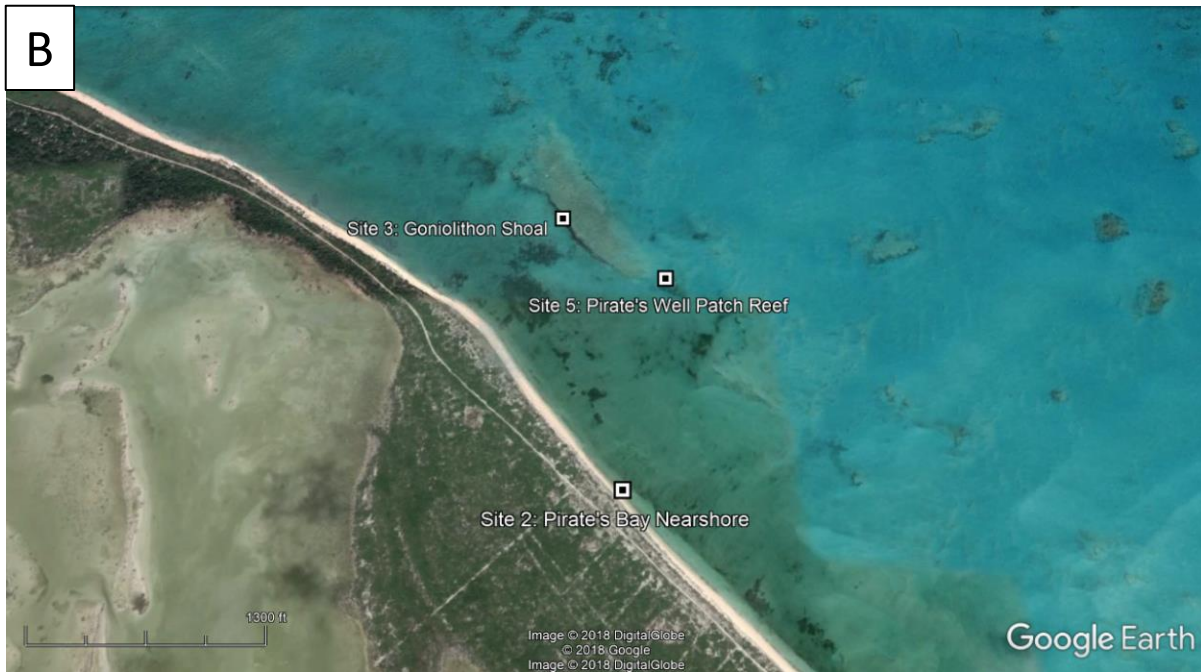
The fourth site, Betsy Bay Nearshore (Fig. 5A), is the first of two locations on the western side of the island. It was assessed from land using the rented truck. All cobbles were collected from this site by snorkeling, since the water depth is only 2.5 feet (0.75 m). The reef is ten meters from shore and its crashing waves made it a high energy site.

The boat was imperative for diving at the platform margin on the northwestern part of the island, which was the setting for our fifth site, Northwestern Wall (Fig. 5A). Diving down over 72 feet (22 m), the team collected cobble and water samples. Sediment sampling was not feasible at this particular location, since the cobbles were situated on a steep slope of pebble and cobble-sized reef rubble that contained no sand-sized sediment. This slope turned into a vertical wall that dropped off onto a sandy ledge that was located approximately 150 feet (46 m) down, but this was considered too deep to safely explore. Therefore, a second dive at a nearby site was required to obtain the sediment samples. At both locations, the water energy was very low and the reefs were pristine.

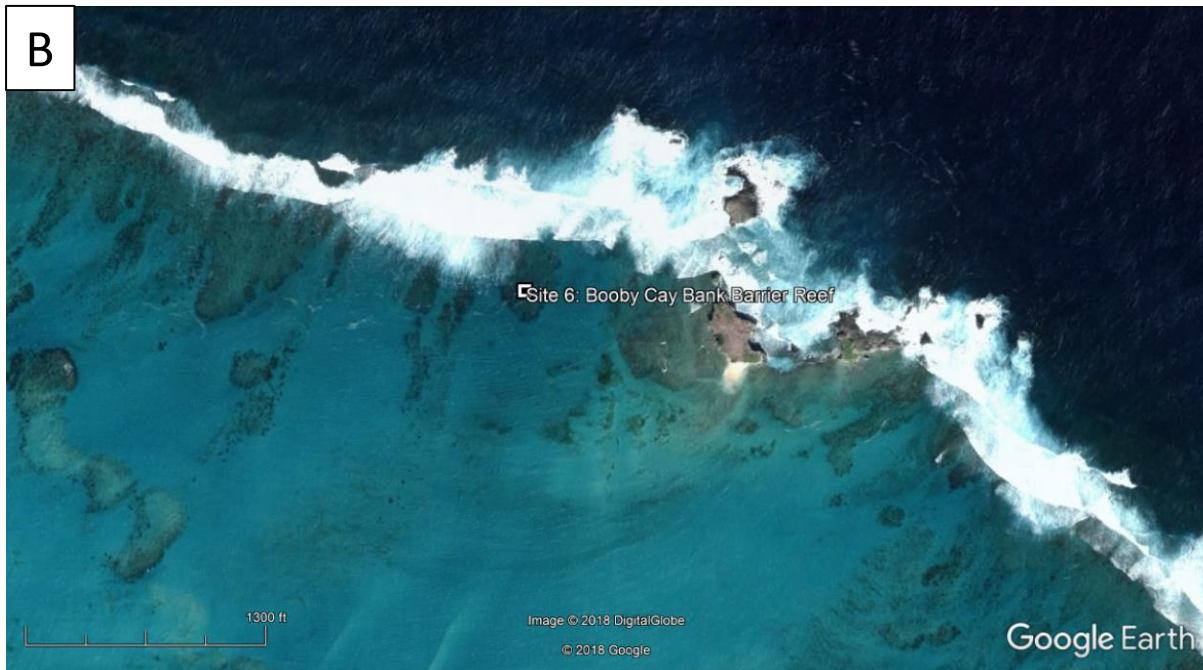
The last two sites were also accessed by boat. Pirate's Bay Nearshore (Fig. 5B) was explored first. It was located in the same general vicinity as Pirate's Well Patch Reef and *Goniolithon* Shoal; the boat was utilized here in preparation for the last site, Blackwood Shoal (Fig. 6B), which was located several km away close to a beach without any access roads. The nearshore site was only 3 meters from shore, at a depth of 1.5 feet (0.5 m). The reef itself was



**Figure 4 – (A) The Bahamas, showing areas of previous study: San Salvador and Cat Island, as well as Mayaguana, the area of the current study. (B) Northwestern corner of Mayaguana, Bahamas, including sample sites (white boxes), the resort location (white arrow), and island settlements (red circles). The sites are abbreviated like so: BBN – Betsy Bay Nearshore, PBN – Pirate’s Bay Nearshore, GS – *Goniolithon* Shoal, BS – Blackwood Shoal, PWPR – Pirate’s Well Patch Reef, BBR – Booby Cay Bank Barrier Reef, and NW – Northwestern Wall.**



**Figure 5 – (A) Close-up view of the western side of the study area, showing the Betsy Bay Nearshore site and the Northwestern Wall site. (B) Close-up view of the southern part of the study area, displaying the Pirate’s Bay Nearshore, *Goniolithon* Shoal, and Pirate’s Well Patch Reef sites.**



**Figure 6 – (A) Close-up view of the eastern side of the study area, showing the Blackwood Shoal site. (B) Close-up view of the northern side of the study area, showing the Booby Cay Bank Barrier Reef site.**

long and narrow, spanning nearly a dozen meters parallel to shore. Here, the water energy was high and the cobbles hosted growths of *Goniolithon*. Blackwood Shoal was another shallow, high-energy reef comprised of many scattered coral heads. Although the coral density was not very high, this reef was very spread out. The water was a meter deep and was located over 200 meters from shore.

### *Sample Collection*

Cobbles were located and photographed in place using a Nikon underwater camera. A range of cobble sizes were selected, with most between 15-25 cm in diameter, following the procedures of Choi (1984) and Smith (2015). Six to eight cobbles were chosen at each site. Prior to moving the selected cobble, a water sample was taken from the underside of the clast, where the encrusting foraminifera are located. This was done with a 20-ml syringe attached to a plastic tube inserted beneath the cobble, allowing a sample to be taken between the cobble and the substrate (Fig. 7). One water sample was gathered per cobble. Cobbles were then collected and placed in pre-labeled, numbered Ziploc bags. The bag number of the cobble and the syringe number were written down on a dive slate, along with water depth and relative water energy.

Immediately after removal, underlying sediment was scooped up and carefully poured into a numbered plastic container with a secure lid. Up to 60 ml of sediment was collected from beneath each cobble, although at some sites there was not enough sediment on the sea floor to fill the container up to this level. The number on the container was noted and recorded on the dive slate immediately after collection. To preserve the biologic materials collected, a stock solution of 10% buffered formalin was added to the water and sediment samples in the evening following their collection, yielding a solution of approximately 5% formalin.



**Figure 7 – Dr. Lewis inserting a plastic tube between the cobble and the substrate to get a water sample.**



### *Sample Preparation and Data Collection*

Cobbles were bubble-wrapped and transported back to the lab for analysis. Each cobble was cleaned with water and a stiff, coarsely-bristled brush and photographed using 10-cm<sup>2</sup> quadrats or 5-cm<sup>2</sup> quadrats if there was not enough space for a 10-cm<sup>2</sup> quadrat. A binocular microscope was used to count all encrusting foraminifera on the underside of each cobble until 200 foraminifera were included in the count, or until all of the surface was counted. This included listing the number of organisms, identifying taxa, determining the morphotype, and noting the quality of preservation for each encruster. Foraminifera were determined to have been live at the time of collection (as indicated by vivid coloration), dead but in pristine condition, good, altered, or very altered (Buchan and Lewis, 2009), and the Quality of Preservation Index (QPI), defined as the percent of live, pristine, and good specimens, was calculated for each cobble and for each site. In addition to counts, the area covered by each foraminifer was determined using an imaging software, ImageJ. This involved tracing the outline of each encruster, which allowed the size to be accurately measured and recorded. The foraminiferal density was determined by dividing number of foraminiferal tests per quadrat by the total area of the quadrat, and the percent of coverage is assessed by dividing the total area occupied by foraminifera by the quadrat area.

Water samples were taken to the laboratory and analyzed for biota using a Zeiss Axiovert 135 Inverted Fluorescence microscope. Three water samples were taken from each of four sites: the two nearshore localities, the patch reef, and the platform margin. A thin line was drawn across the diameter of the bottom of twelve 10x30-mm circular petri dishes using a fine-tip permanent marker. Samples were gently rolled along the countertop to homogenize the water. A 3-ml subsample was taken from the center of the water container and placed onto the petri dish,

which was just enough to coat the entirety of the dish. Data were collected by starting at one end of the line, taking an image, then moving the dish approximately 3 mm down the line and repeating the process until the line had been traversed. Approximately nine images were taken per sample at 5x magnification. If an unusual, well-preserved specimen was noticed along the transect, a 10x magnification picture of it was taken. Taxa from all images were identified at high taxonomic levels using standardized references and quantified as number of specimens per viewing area, as done by Reiswig (1972).

Sediment samples were prepared carefully before analysis. Rose Bengal was used to stain the living tissues of the meiofauna pink, making them much easier to identify. The staining solution was prepared by mixing 1 gram of Rose Bengal powder with 1 liter of 200 proof ethanol. The samples were carefully drained of seawater and the stain was added, soaking through the entirety of each sample. Samples were left in the stain solution for at least 48 hours before analysis. Each sample was then homogenized and sieved using a 1-mm screen. Two sediment samples from each site were selected for analysis. From each sample, three 1-ml subsamples were extracted with a spoon and were placed into a gridded dish 25 cm in diameter, for a total of 6 ml analyzed at each locality. *Goniolithon* Shoal was the only exception because sediment was gathered from beneath only one cobble. Sediment samples were treated as in published analyses of meiofauna; sample sizes were small and were spread out over the bottom of the observation dish (e.g., Somerfield and Warwick, 2013). A standard binocular microscope was used to separate meiofaunal elements at high taxonomic levels such as foraminifera, crustacea, roundworms (Nematoda), and polychaetes (Annelida), and counts of each category were made.

#### 4. Results

Unlike previous studies on San Salvador and Cat Island (Tichenor and Lewis, 2009; Martin and Lewis, 2015; Smith, 2015), no onshore-offshore transect was available in this study. This was partly due to the platform margin being inaccessible on the north side of the island, requiring us to sample it on the western side of the island, away from most of the other sites. Nonetheless, the variety of the sample localities does allow for discussion on the context of an onshore-offshore sequence. Shoals – offshore, shallow-water sites – have not been addressed in previous studies by our laboratory. Several of the cobbles collected at *Goniolithon* Shoal were distinct because they were composed entirely of the coralline algae *Goniolithon*. These samples were labeled as “Type 2” (Fig. 8), since their physical makeup provides a unique setting for foraminiferal growth in comparison to standard cobbles (“Type 1”), most of which are clasts of reef rubble with less surface area.

##### *Foraminiferal Taxa*

Overall, seven different foraminiferal taxa were identified in this study (Fig. 9). The only agglutinated taxon was *Placopsilina*, which was not identified to the species level. The only miliolid observed was *Nubecularia*, most of which were the small diameter, branching morphotype designated as “Small *Nubecularia*” in previous studies (Tichenor and Lewis, 2009, 2011, 2018). *Nubecularia* was the third most common of all the foraminifera and was the only non-rotaliine with significant counts. The rotaliines dominated the assemblages in both count and area. The taxa include *Homotrema rubrum*, *Carpenteria utricularis*, *Gypsina plana*, *Gypsina*



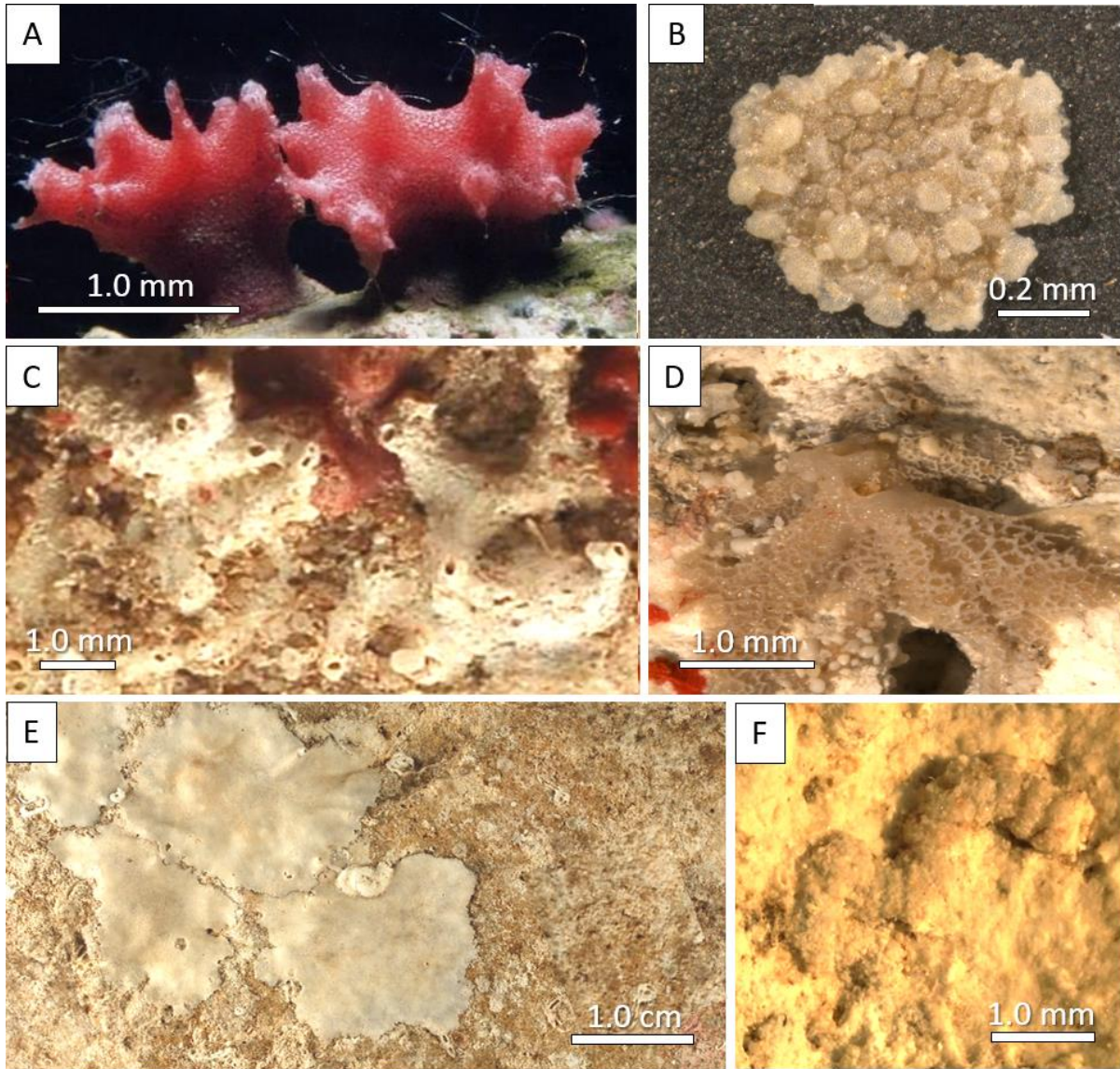
**Figure 8 – A Type 2 sample recovered from *Goniolithon* Shoal. Note how the tendrils of *Goniolithon* increase the surface area of the cobble and permit encrusting foraminifera to attach on several sides.**

*globula*, and *Planorbulina* spp. Aside from *Haddonina* sp., which was not found on Mayaguana, the taxa in this study are the same as those observed at San Salvador and at Cat Island.

*Planorbulina* was not identified to the species level, but it was most likely *P. acervalis* based on the “bubble-like” orb-shaped chambers that make up its test. We distinguished between brown and gray *Planorbulina*, which may or may not be different species, hence the genus-level classification. *Carpenteria* was identified as *C. utricularis*, as in several previous studies (e.g., Martindale, 1992; Tichenor and Lewis, 2011, 2018). *Gypsina plana* and *Homotrema rubrum* are important taxa and have been observed in many other studies (Martindale, 1992; Tichenor and Lewis, 2009, 2011, 2018; Richardson-White and Walker, 2011; Walker et al., 2011; Martin and Lewis, 2015; Smith, 2015). *Gypsina plana* is distinguishable because of its large, sheet-like appearance and “smoothly lobate perimeter” (Smith, 2015). *Gypsina globula* specimens are small and relatively rare.

Figures 10-16 show the count data for each taxonomic category of foraminifera on a cobble-by-cobble basis, including the state of preservation and calculated QPI. Graphs are arranged by similarity of the assemblages. In most cases, 4 or more of the 6-7 cobbles are quite similar. Figures 17 and 18 record the count and area data for each site (see also Appendix A and B). Bar graphs detail the count data, while the areas of individuals are expressed as pie charts.

Foraminiferal assemblages vary from nearshore to offshore sites. *Planorbulina* spp. dominates the assemblages at Pirate’s Bay Nearshore and Pirate’s Well Patch Reef. *Homotrema rubrum* recorded the largest total area at Betsy Bay Nearshore, *Goniolithon* Shoal and Blackwood Shoal. *Nubecularia* sp. was significant only at Betsy Bay Nearshore. *Planorbulina* spp. was by far the most abundant taxa by count at the Northwestern Wall platform margin, although the area was clearly dominated by *Gypsina plana*.



**Figure 9 – Representative photographs of each taxon of the encrusting foraminifera observed: (A) *Homotrema rubrum* (multiple), (B) *Planorbulina* spp. (brown), (C) *Nubecularia* sp., (D) *Carpenteria utricularis*, (E) *Gypsina plana*, (F) *Placopsilina* sp. Photograph A is from <http://www.aquaristics.ru/img/articles/foraminifera-homotrema-rubrum.jpg>.**

Site 1: Betsy Bay Nearshore

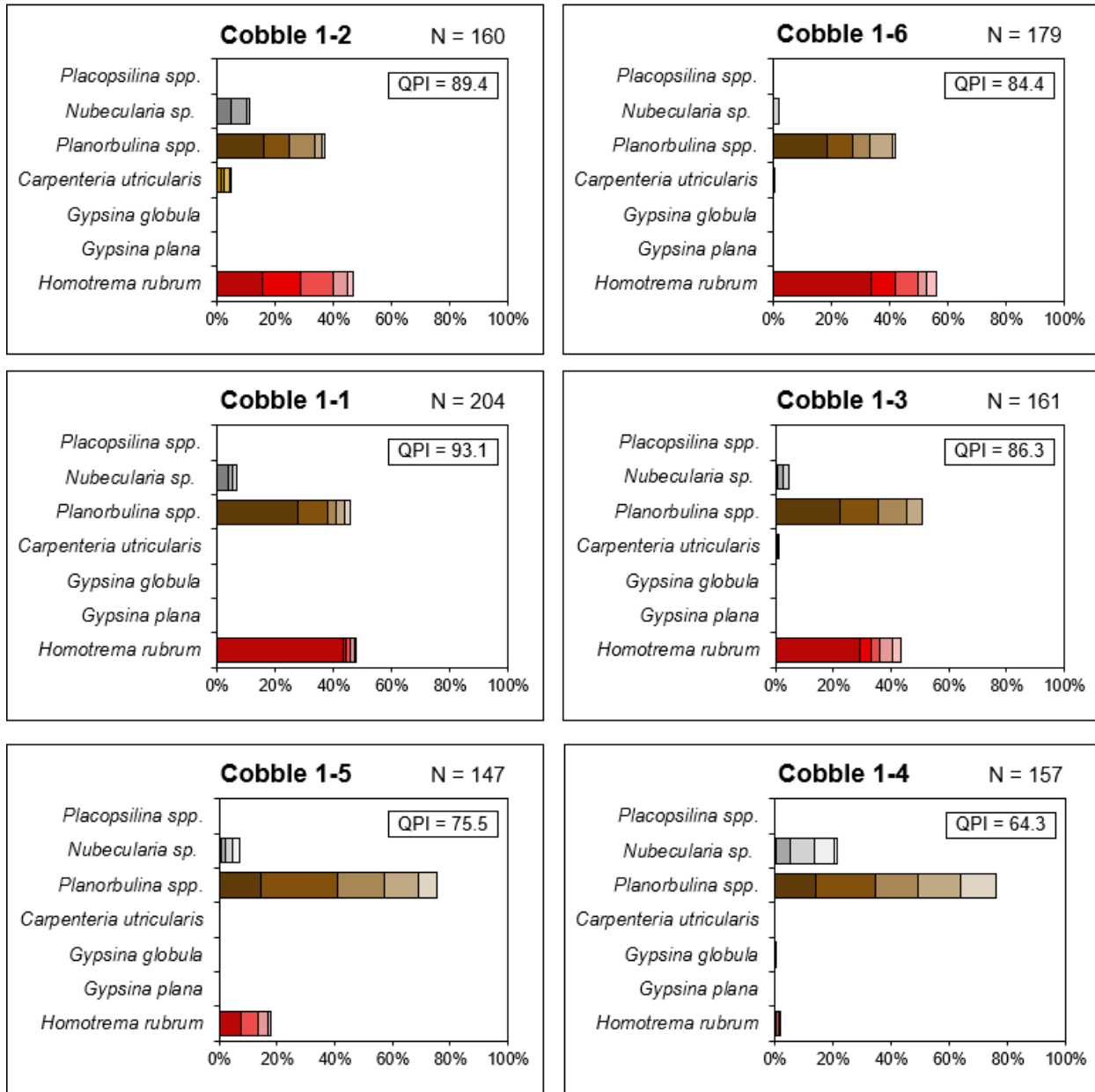


Figure 10 – Betsy Bay Nearshore: Relative abundance of encrusting foraminifera on the undersides of cobbles based on counts of individuals. The quality of preservation index is derived from the percent of live, pristine, and good taphonomic states.

Legend

- - Live
- - Pristine
- - Good
- - Altered
- - Extremely Altered

Site 2: Pirate's Bay Nearshore

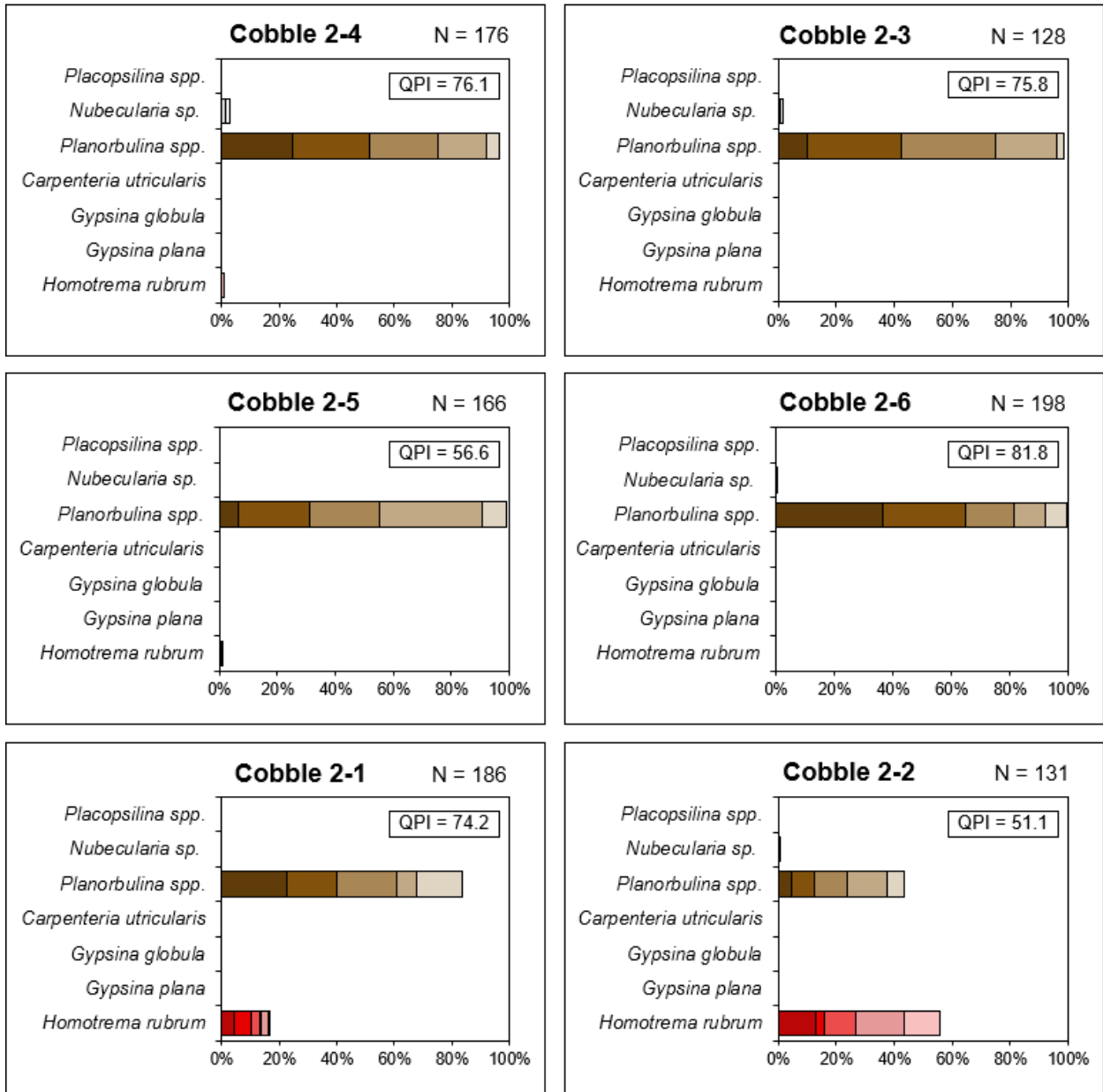


Figure 11 – Pirate's Bay Nearshore: Relative abundance of encrusting foraminifera on the undersides of cobbles based on counts of individuals. The quality of preservation index is derived from the percent of live, pristine, and good taphonomic states.

Legend

- - Live
- - Pristine
- - Good
- - Altered
- - Extremely Altered



Site 3: *Goniolithon* Shoal

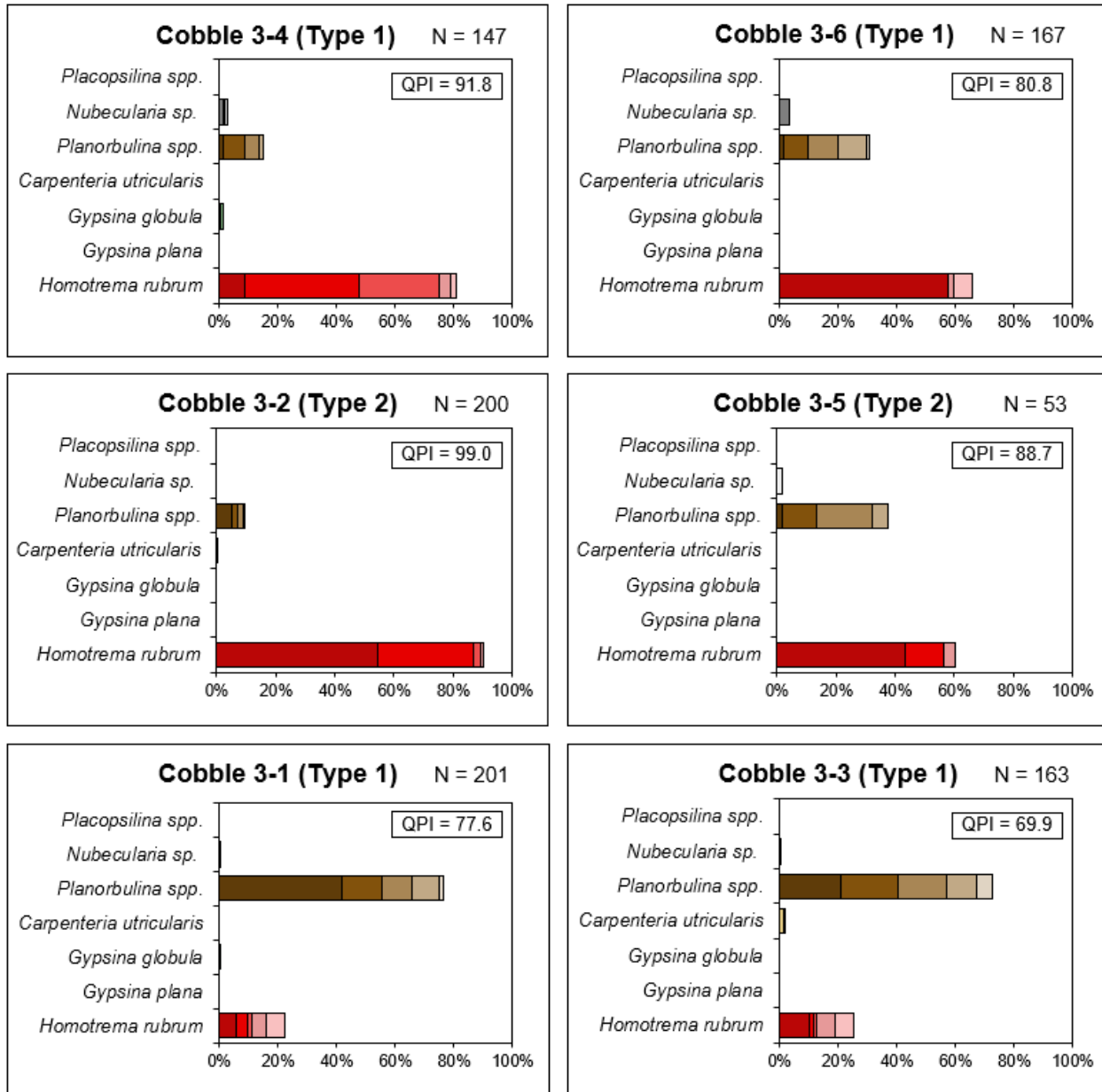


Figure 12 – *Goniolithon* Shoal: Relative abundance of encrusting foraminifera on the undersides of cobbles based on counts of individuals. The quality of preservation index is derived from the percent of live, pristine, and good taphonomic states. “Type 2” signifies that the cobble is comprised entirely of *Goniolithon*.

Legend

- - Live
- - Pristine
- - Good
- - Altered
- - Extremely Altered

Site 4: Blackwood Shoal

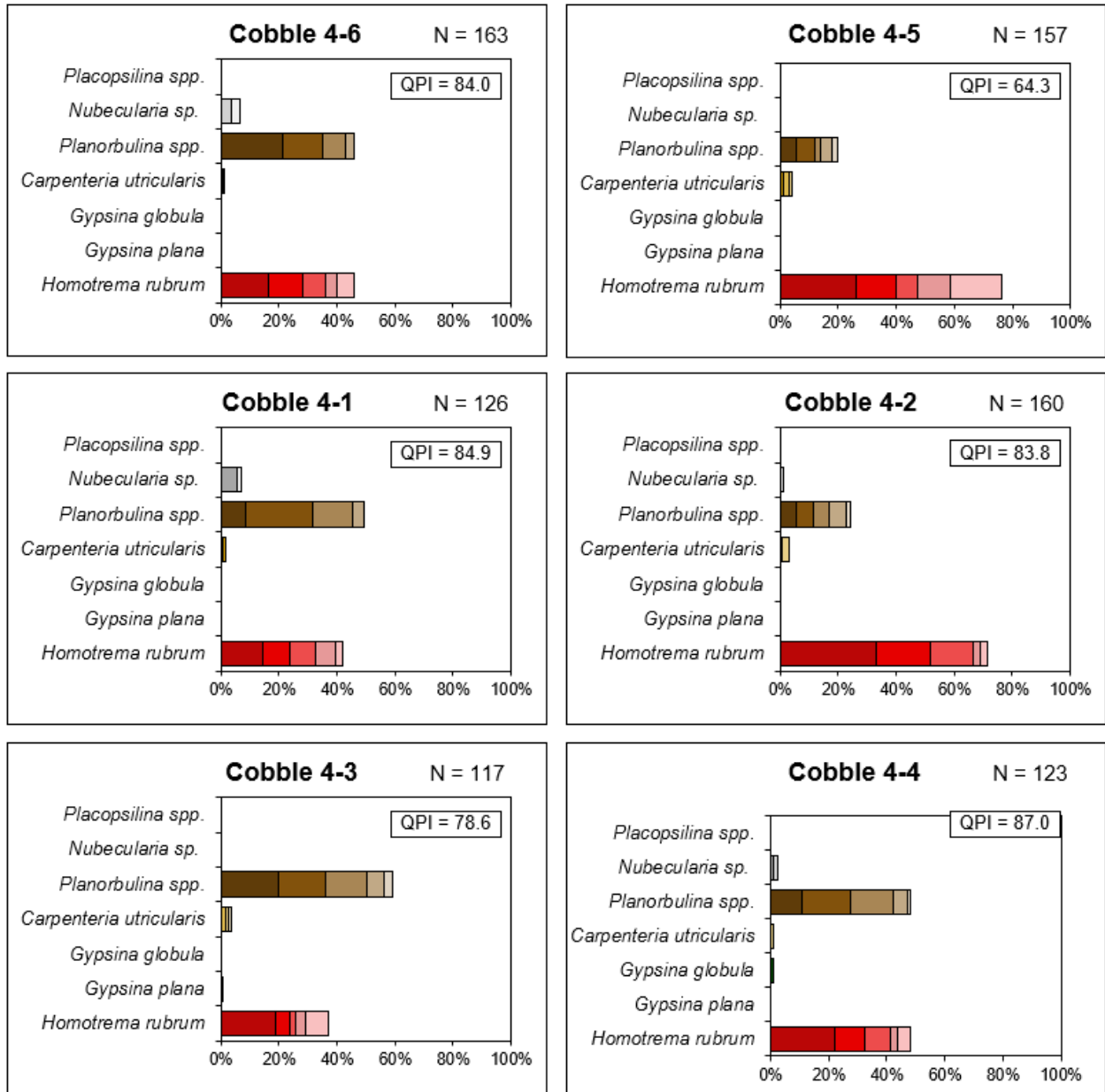
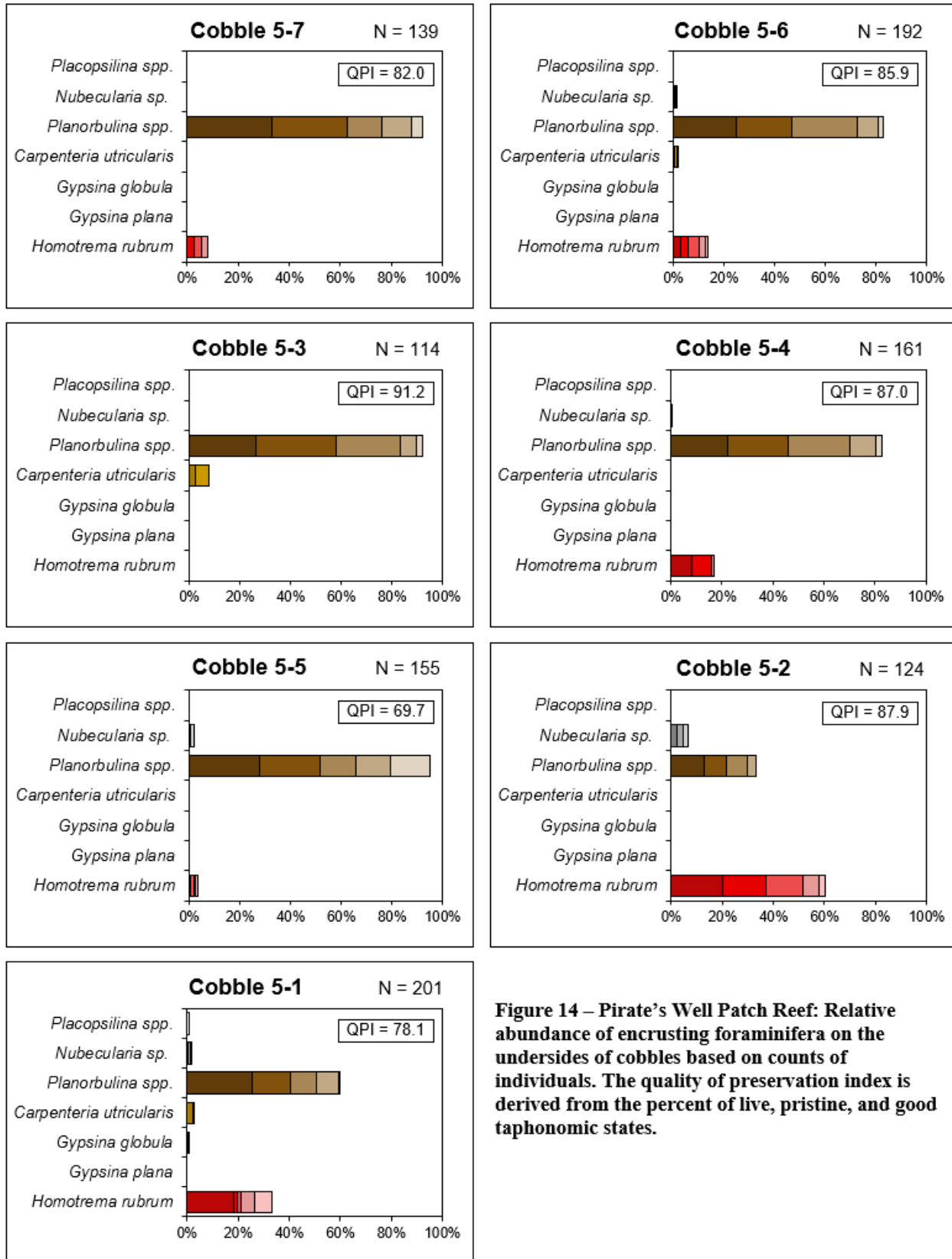


Figure 13 – Blackwood Shoal: Relative abundance of encrusting foraminifera on the undersides of cobbles based on counts of individuals. The quality of preservation index is derived from the percent of live, pristine, and good taphonomic states.

Legend

- Live
- Pristine
- Good
- Altered
- Extremely Altered

### Site 5: Pirate's Well Patch Reef



**Figure 14 – Pirate's Well Patch Reef: Relative abundance of encrusting foraminifera on the undersides of cobbles based on counts of individuals. The quality of preservation index is derived from the percent of live, pristine, and good taphonomic states.**

Site 6: Booby Cay Bank Barrier Reef

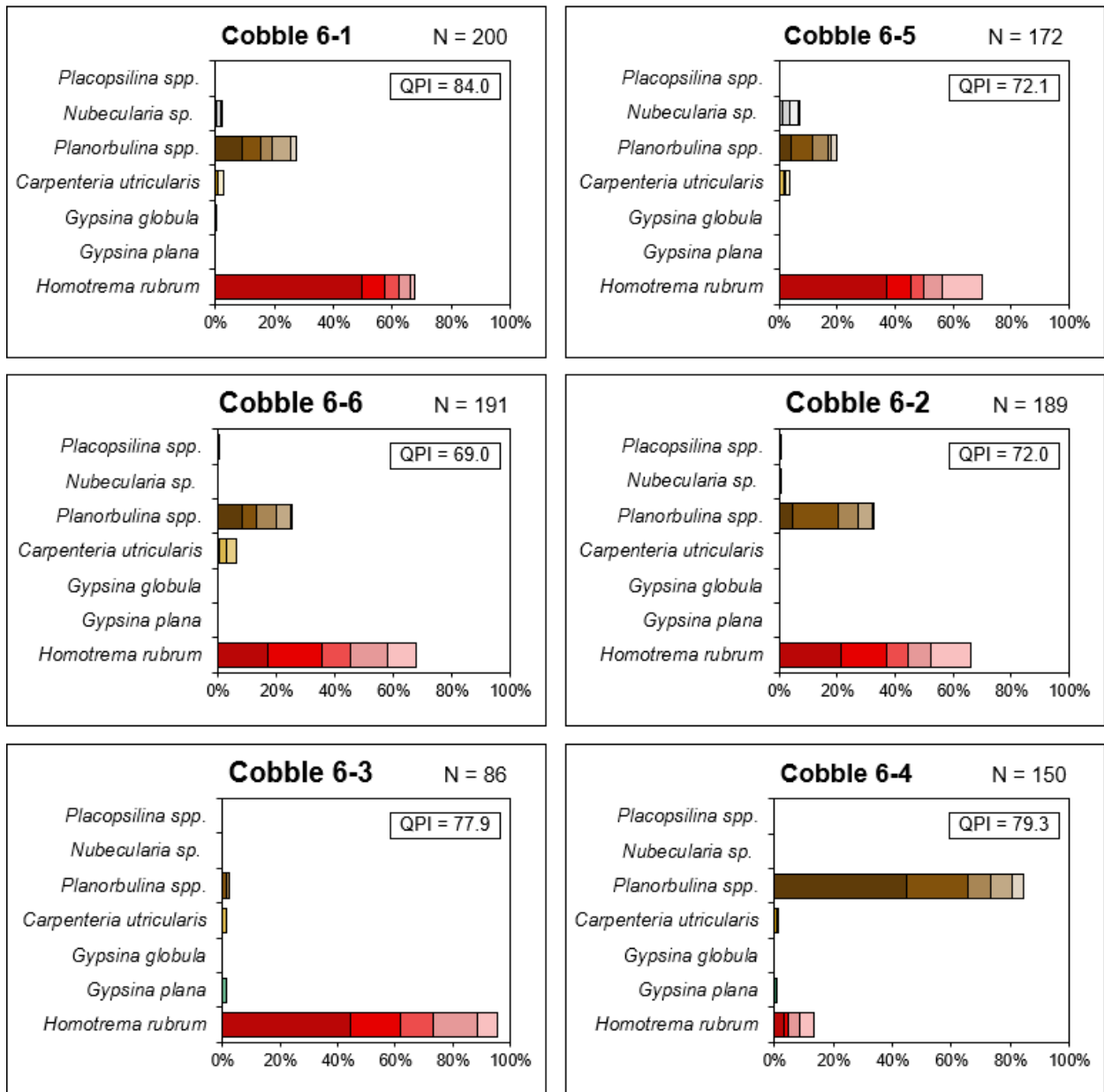
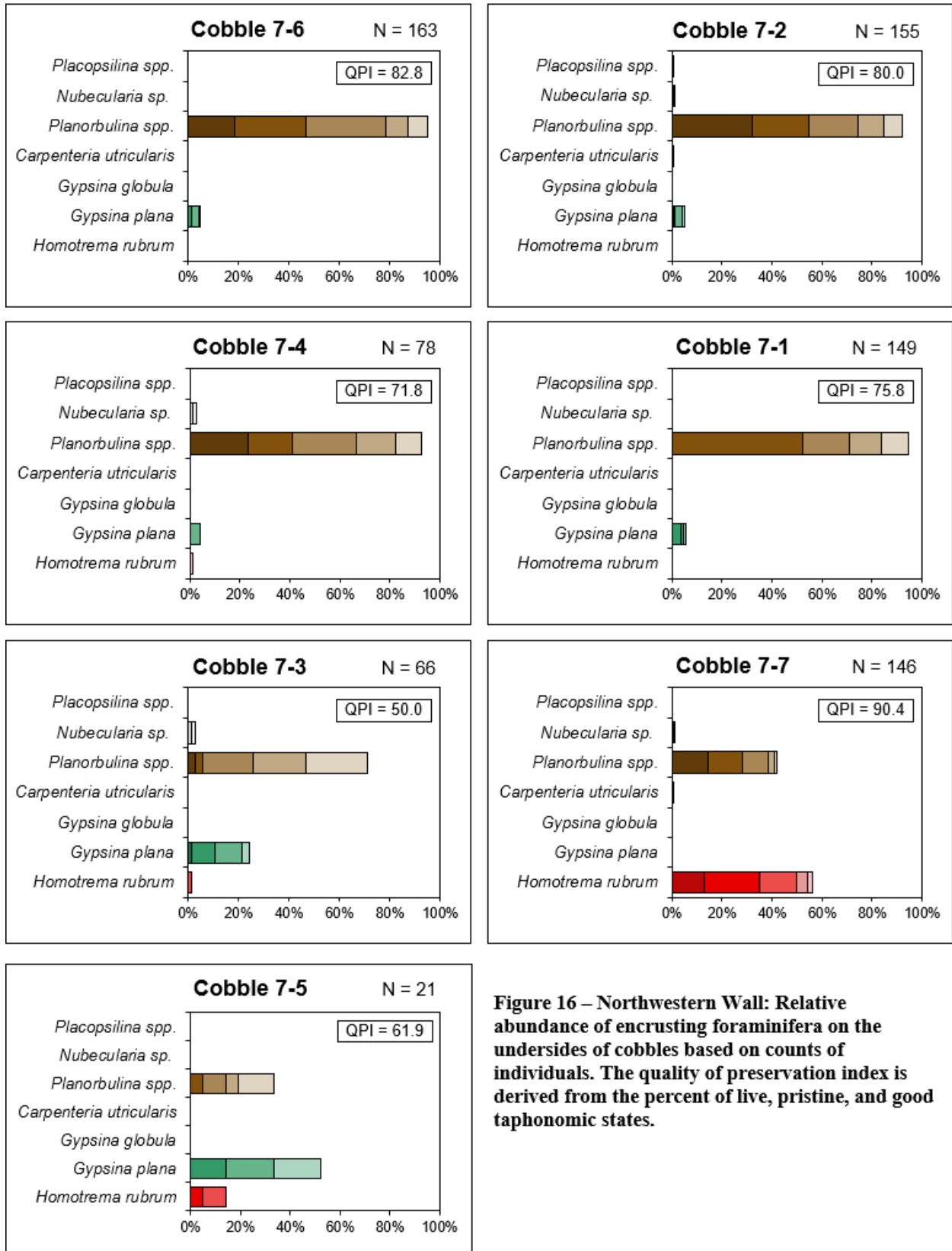


Figure 15 – Booby Cay Bank Barrier Reef: Relative abundance of encrusting foraminifera on the undersides of cobbles based on counts of individuals. The quality of preservation index is derived from the percent of live, pristine, and good taphonomic states.

Legend

- - Live
- - Pristine
- - Good
- - Altered
- - Extremely Altered

### Site 7: Northwestern Wall



**Figure 16 – Northwestern Wall: Relative abundance of encrusting foraminifera on the undersides of cobbles based on counts of individuals. The quality of preservation index is derived from the percent of live, pristine, and good taphonomic states.**

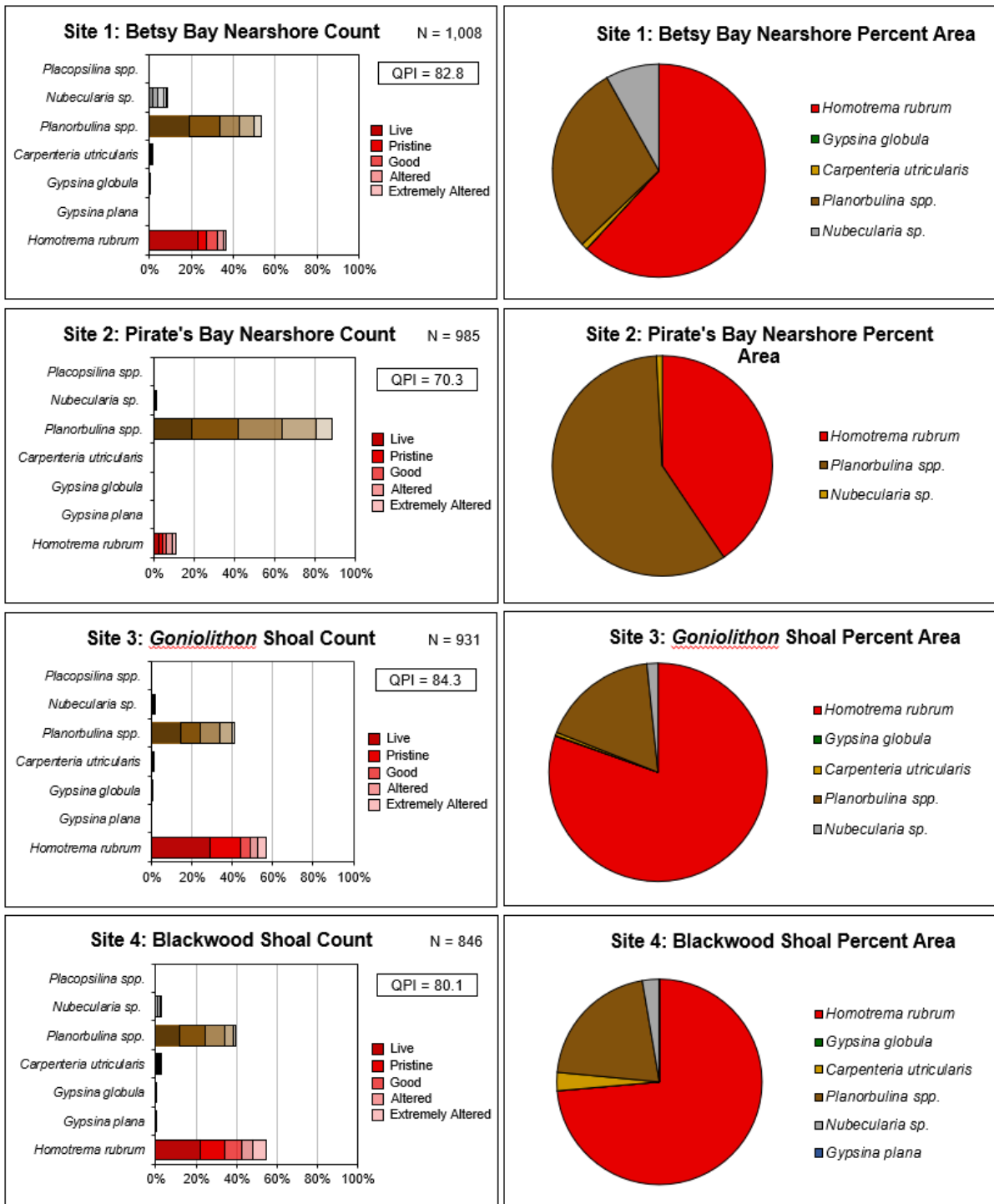
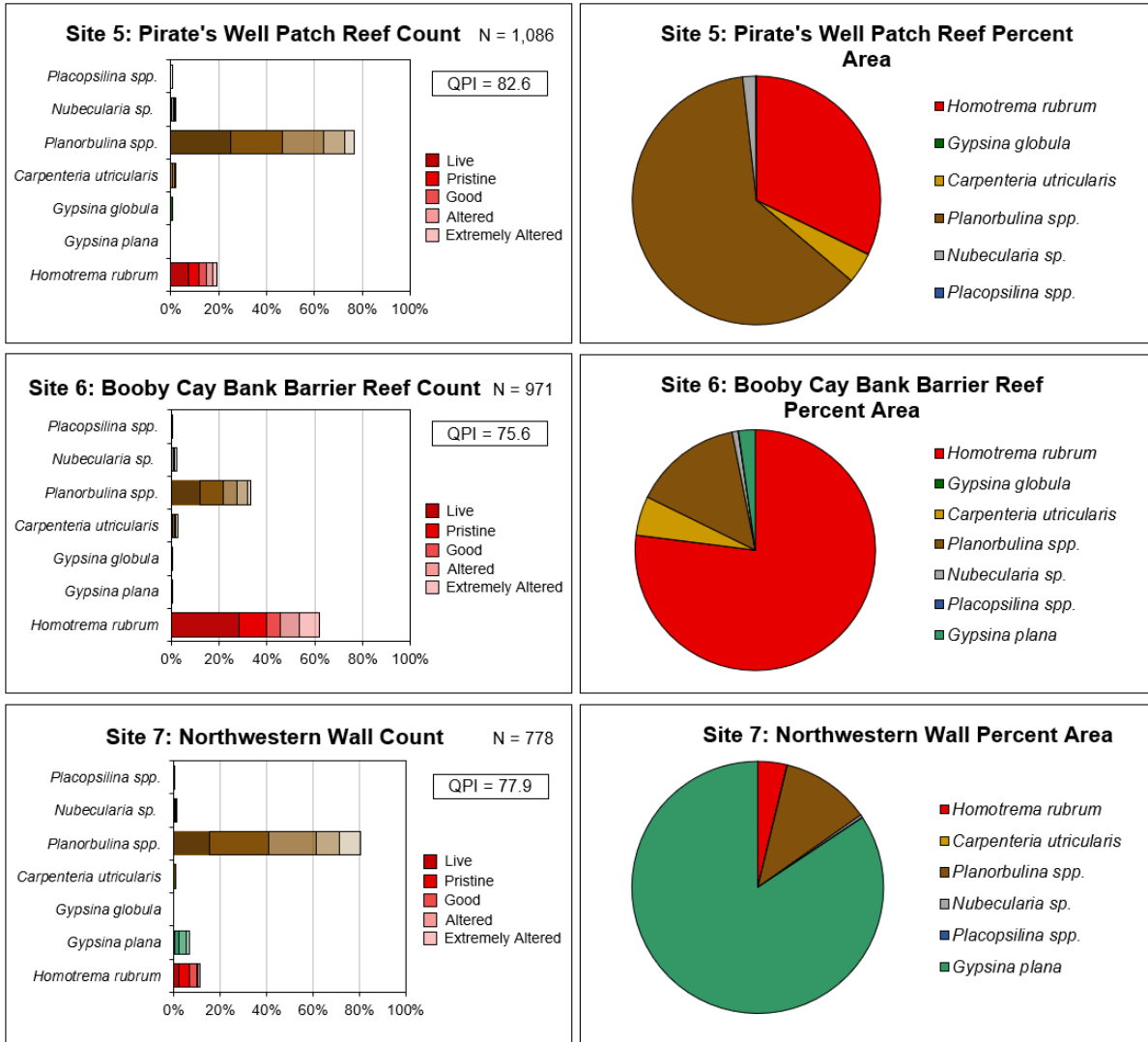


Figure 17 – Principal taxa of foraminifera. The bar graphs (left) show the relative abundance based on count. The pie charts (right) show the percentage of area that each taxa covered. QPI is based on the percentage of the live, pristine, and good categories. Note the dominance of *Homotrema rubrum* in the shoals in contrast to *Planorbulina*'s dominance at the nearshore sites.



**Figure 18 – Principal taxa of foraminifera. The bar graphs (left) show the relative abundance based on count. The pie charts (right) show the percentage of area that each taxa covered. QPI is based on the percentage of the live, pristine, and good categories. Note the dominance of *Homotrema rubrum* at the bank barrier reef in contrast to *Planorbulina*'s dominance at Pirate's Well Patch Reef. *Gypsina plana* displays a clear dominance at the Northwestern Wall location.**

### *Similarity of Cobble Assemblages*

Both the percentage of occurrence and percentage of area for each taxa of foraminifera were compared by cluster analysis using Primer V. A Q-mode cluster diagram, comparing the similarity of each cobble on the basis of its foraminiferal assemblage, as shown in Figure 19. A non-metric multidimensional scaling plot (MDS), which measured the similarity of the counts of foraminifera on a spatial plane, is shown in Figure 21A). The transformation was the square-root function, the similarity coefficient was Bray-Curtis, and the cluster group was a group average for the cluster diagrams. In both diagrams, there are sites that show high degrees of similarity, most notably the shoals. Others, such as the nearshore localities, showed moderate similarity. A Q-mode cluster diagram and an MDS plot were also created for foraminiferal areas (Figs. 20, 21B). These two figures display a higher degree of similarity than do count diagrams, especially the platform margin. However, the nearshore sites continue to show less clustering.



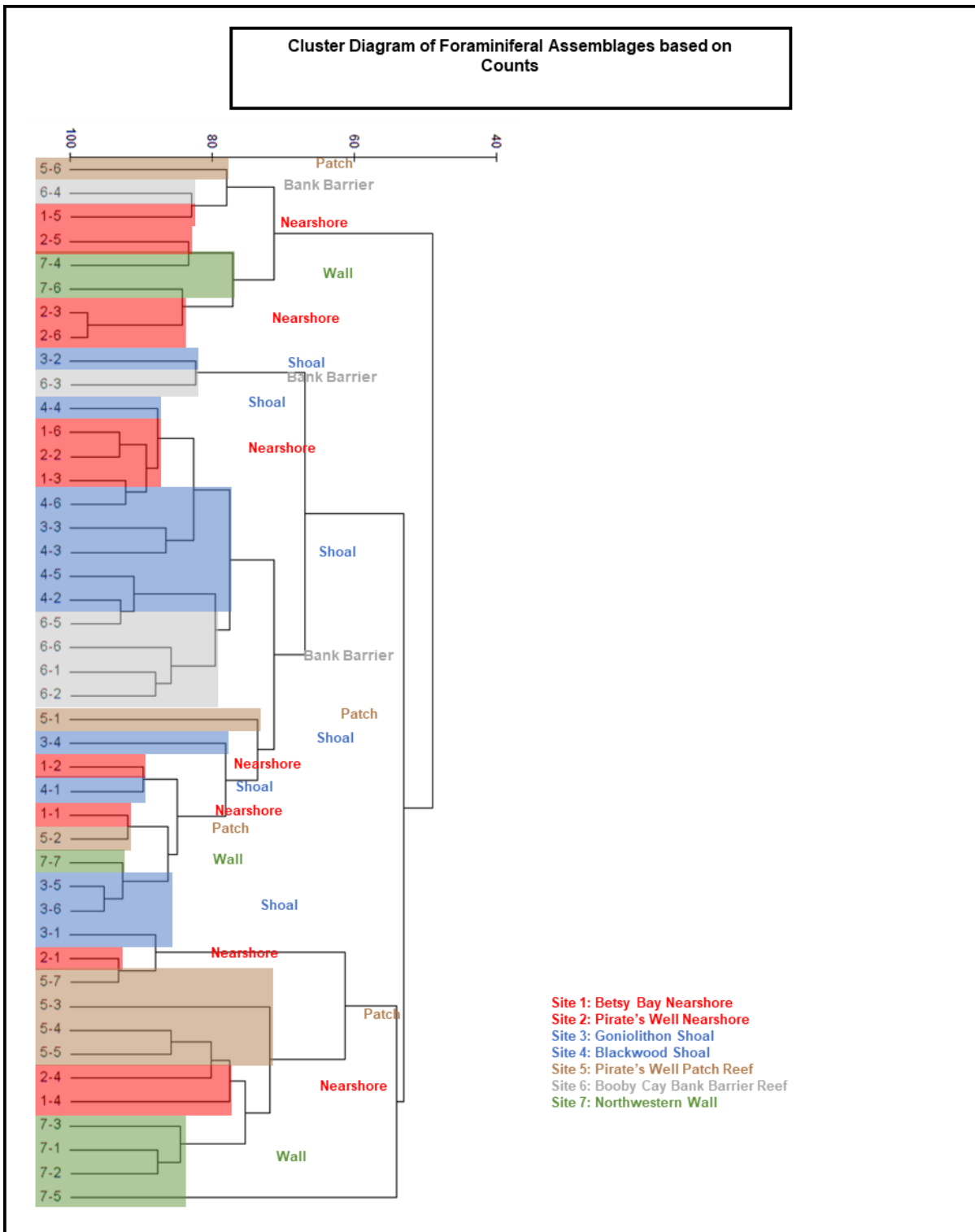


Figure 19 – Q-mode cluster of all sites based on relative abundance as determined by individual counts (transformation: square root; similarity coefficient: Bray-Curtis; cluster group: group average). Cobble and sites are represented through the notation “#-#” (“1-2” is site 1, cobble 2, etc.). The axis along the top measures rates of similarity.

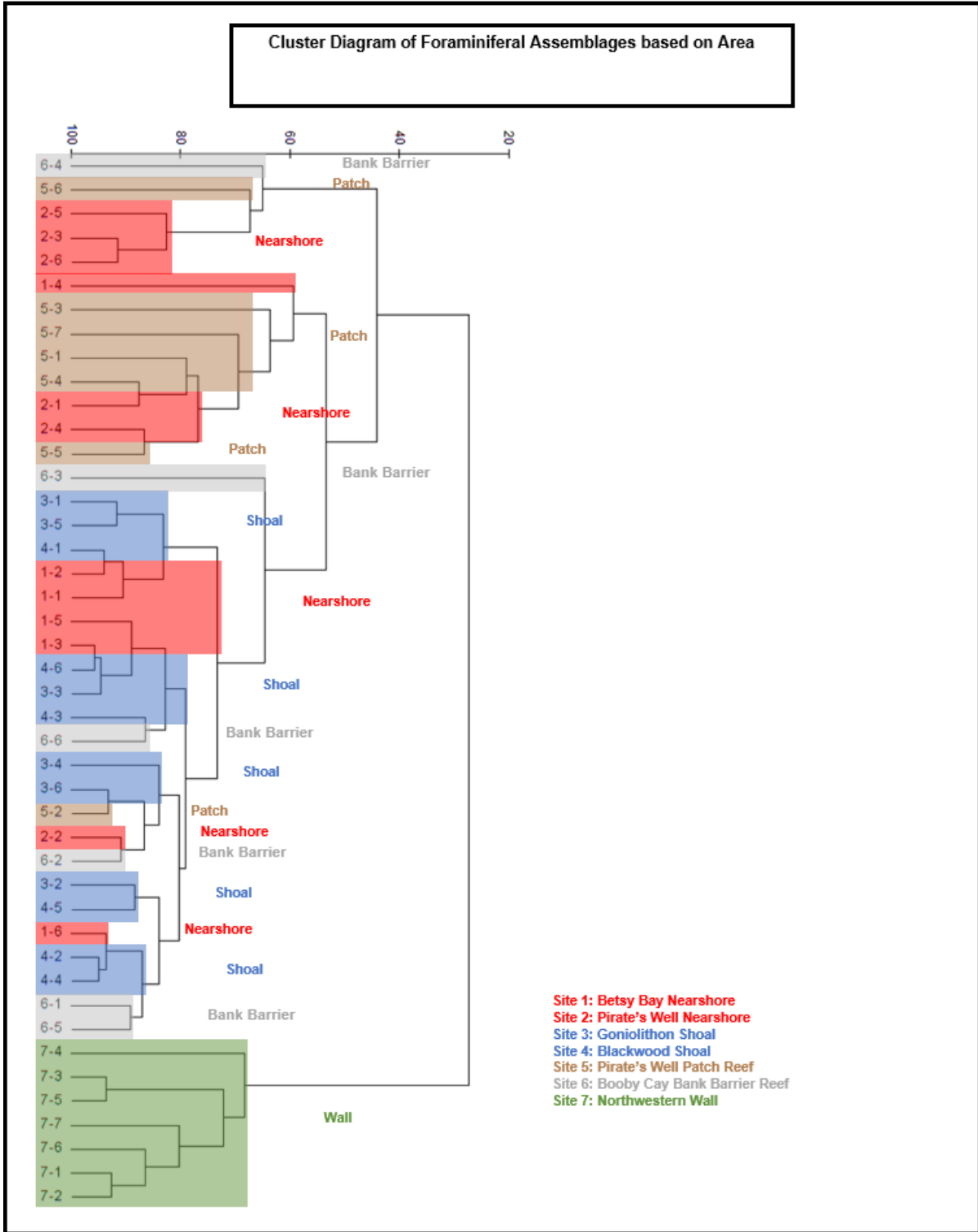


Figure 20 – Q-mode cluster of all sites based on relative abundance as determined by foraminiferal areas (transformation: square root; similarity coefficient: Bray-Curtis; cluster group: group average). Cobble and sites are represented by the notation ‘#-#’ (“1-2 is site 1, cobble 2, etc.). The axis along the top measures rates of similarity.

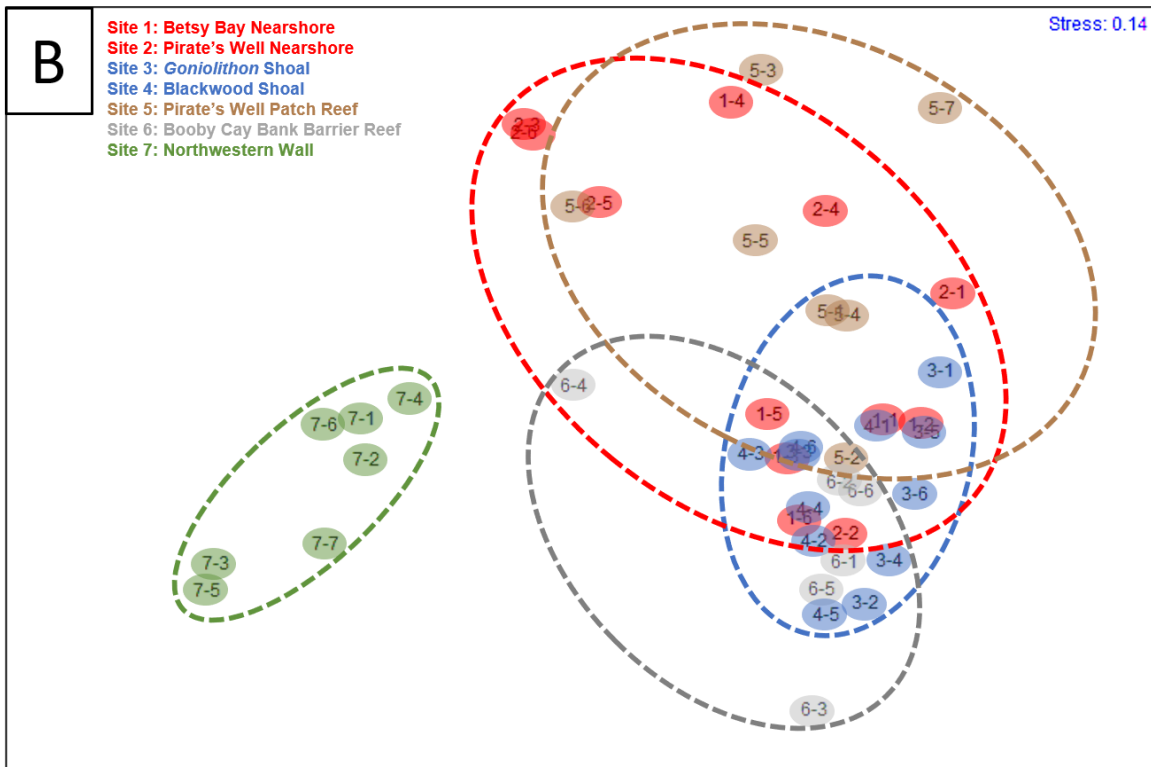
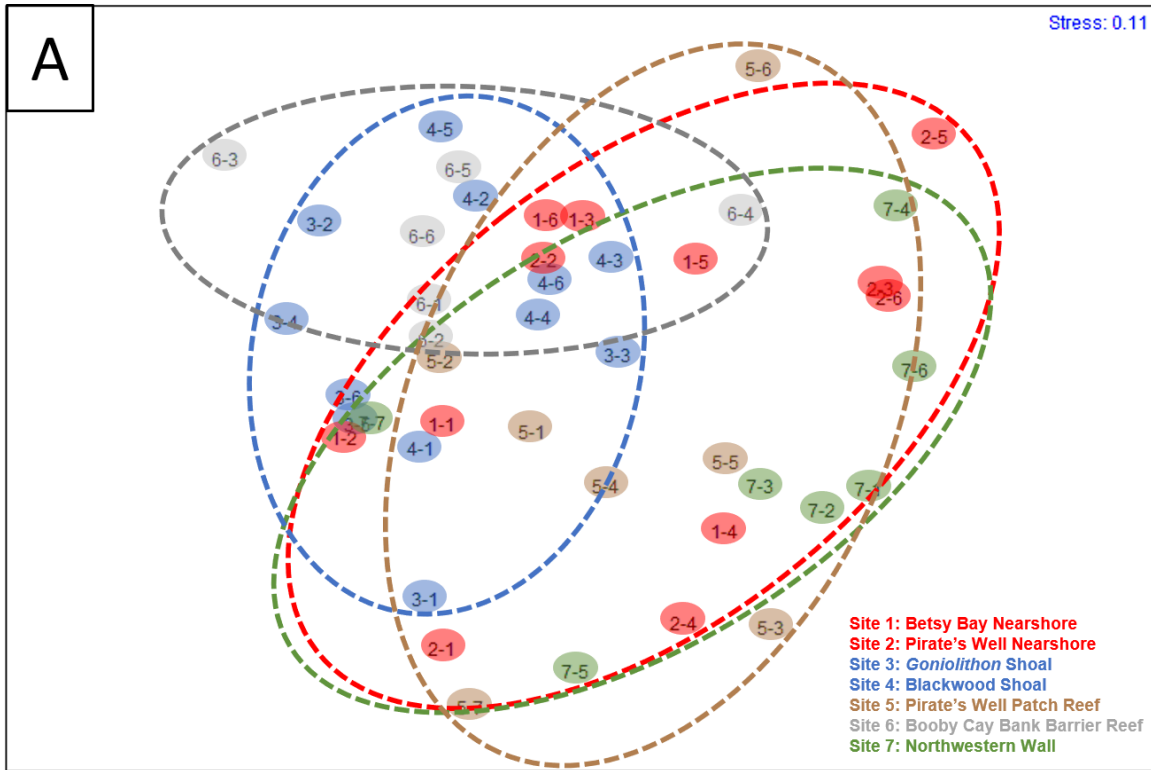


Figure 21 – Non-metric multidimensional scaling (MDS) plot displaying the similarity of cobble based on their counts (A) and areas (B) on a spatial plane. The samples are denoted with the same notation as Figures 19 and 20. The dotted lines are groupings of each type of site (Red – nearshore, Blue – shoal, Brown – patch, Gray – bank barrier, Green – platform margin).

### *Comparison of Key Species*

Previous research by Tichenor and Lewis (2009, 2011) and Smith (2015) demonstrated that *Homotrema rubrum*, *Planorbulina* spp. and *Gypsina plana* are the three most important foraminifera for determining distance from shore and water depth. Lewis et al. (2013) and Smith (2015) calculated the percentages of counts and areas for these three taxa, plotting them on ternary diagrams. Data from Mayaguana were plotted in a similar fashion (Fig. 22). These diagrams are modeled after Smith (2015) because they couple *Homotrema rubrum* with *Nubecularia* sp., another foraminifer that is found commonly at nearshore localities. The addition of *Nubecularia* made little difference due to the overwhelming count and area dominance of *Homotrema*, *Planorbulina*, and *Gypsina plana*.

The count and area of both shoals are very similar, and tend to plot towards the *Homotrema rubrum* pole, as did the bank barrier reef. The nearshore reefs trend closer to *Planorbulina* spp. for counts and *Homotrema* for area, varying noticeably between the two sites. The patch reef plots closer to *Planorbulina* for both count and area. The platform margin records significant counts of *Planorbulina*, and was the only site with extensive areal coverage by *Gypsina plana*.

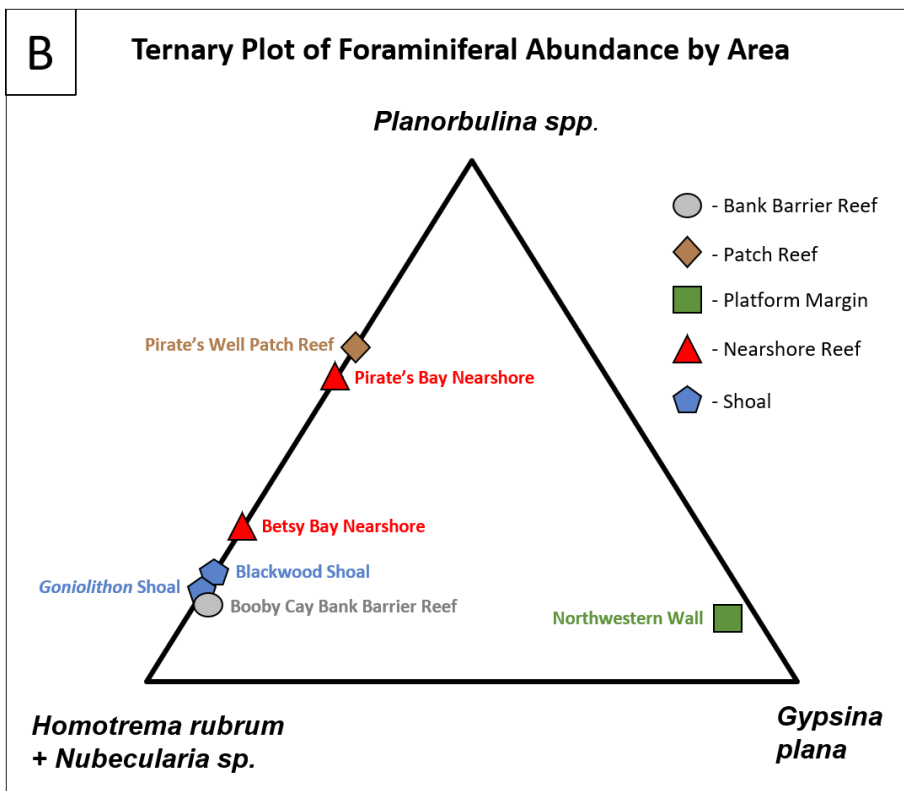
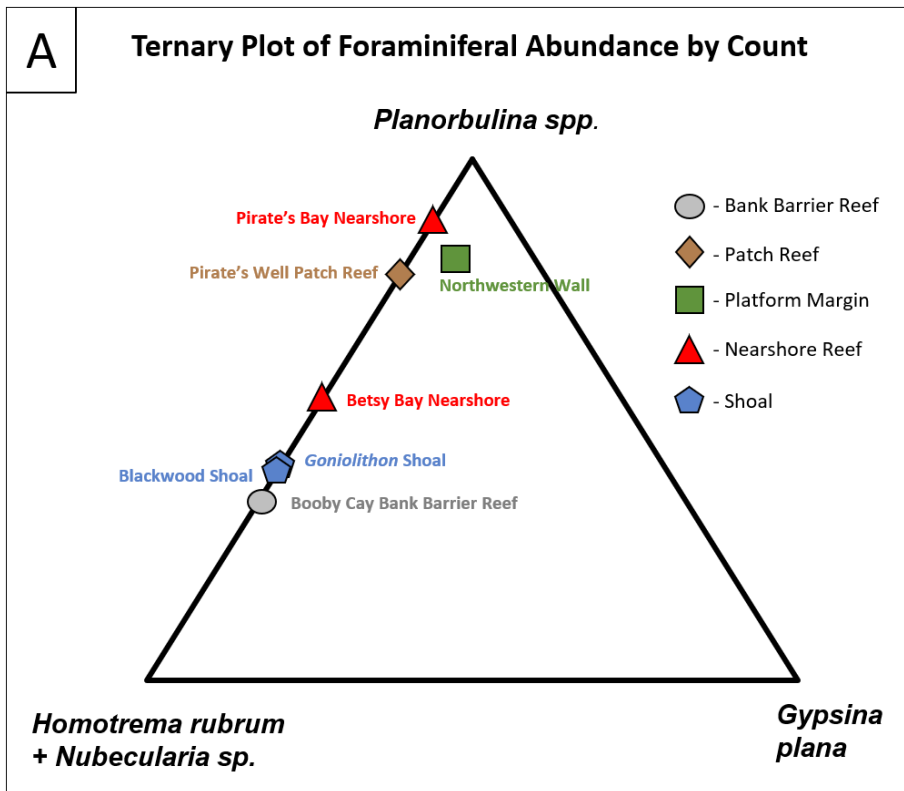
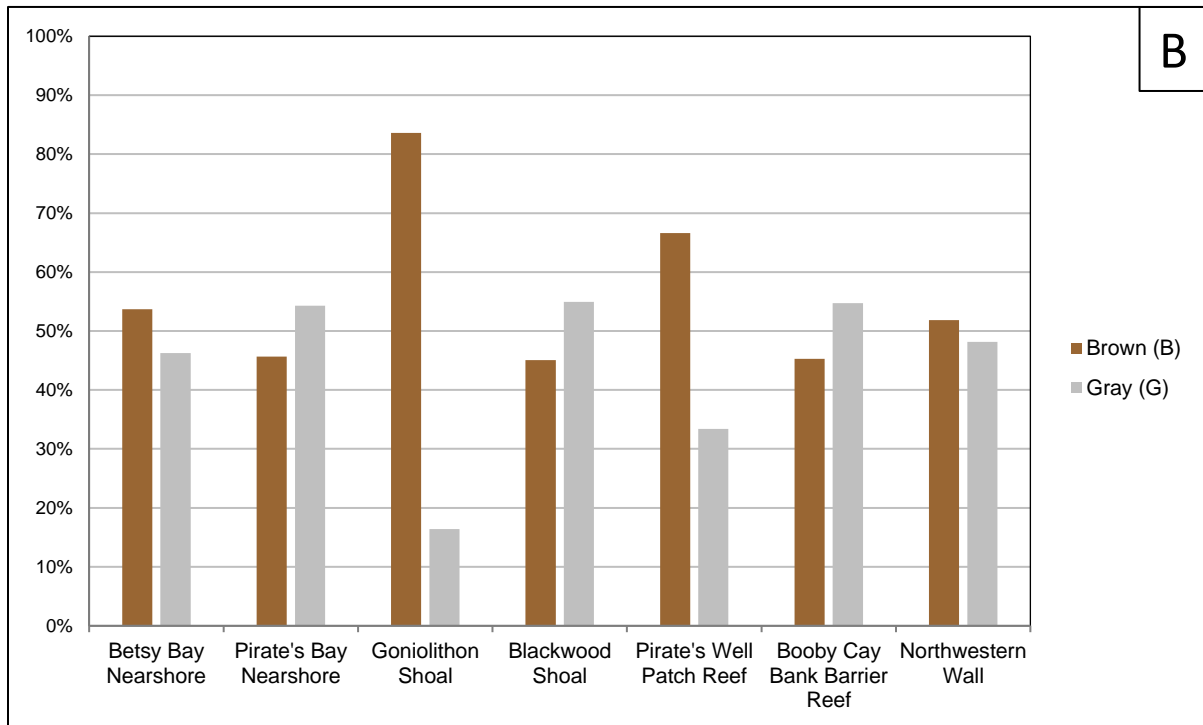
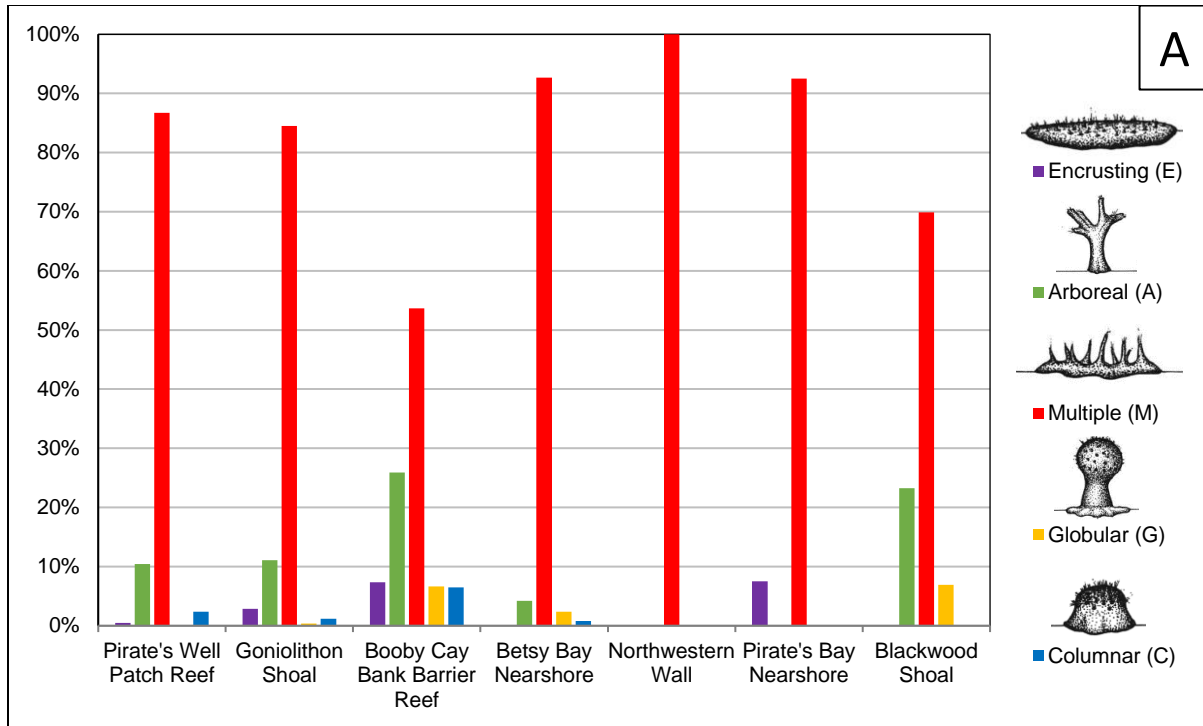


Figure 22 – Ternary diagrams of the relative abundance of the three dominant foraminifera, *Planorbulina* spp., *Homotrema rubrum*, and *Gypsina plana*, based on counts of individuals (A), and area covered (B) (as in Lewis et al., 2013; Smith, 2015).

### *Foraminiferal Morphotypes, Size, and Density*

The morphotypes of *Homotrema rubrum* and *Planorbulina* spp. are shown in Figure 23. The *Homotrema* morphotype known as “multiple” was by far the most common growth form across all sites. The bank barrier reef was the only site with all five morphotypes of *Homotrema*. The morphotypes of *Planorbulina* were very similar at most sites, although the brown morphotype was more abundant at the *Goniolithon* Shoal and the patch reef.

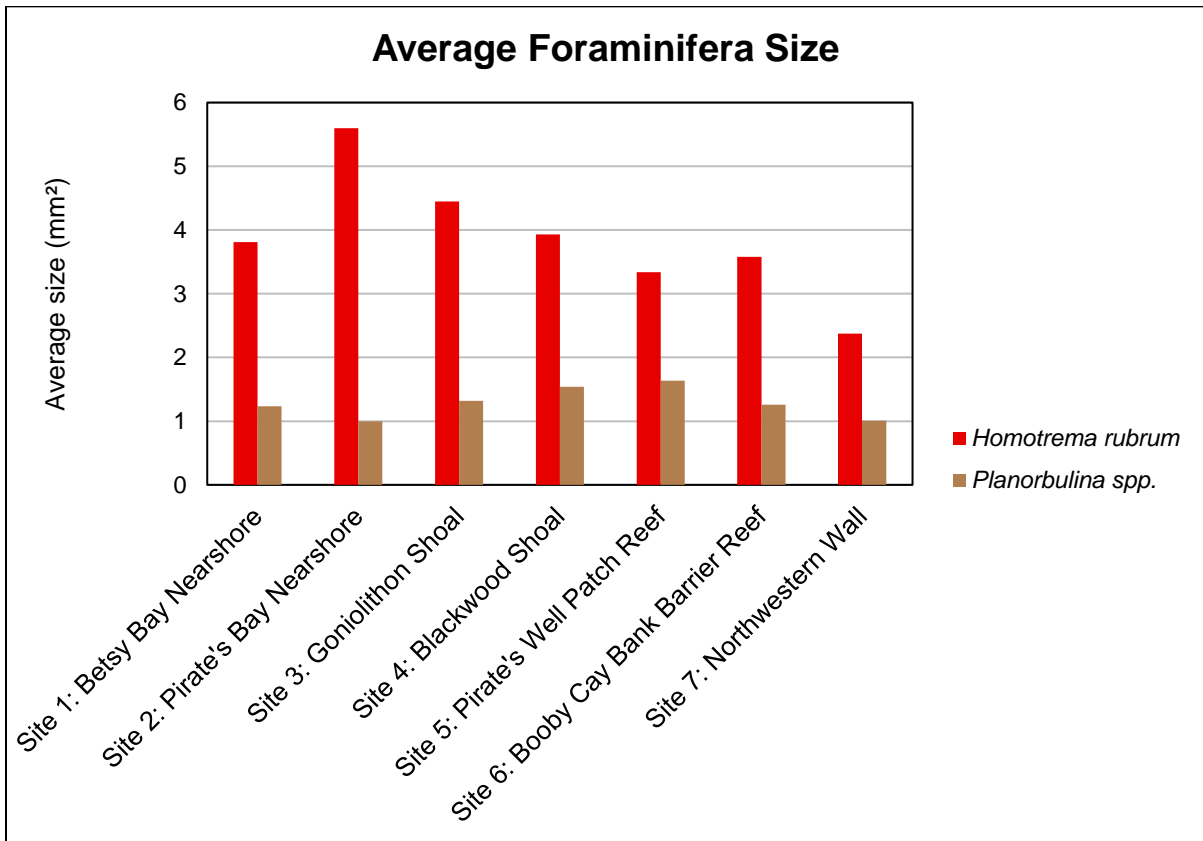
The sizes of foraminifera are listed in Table 2. Site-by-site size comparisons between *Homotrema rubrum* and *Planorbulina* spp. are displayed in Figure 24. *Homotrema* was larger than *Planorbulina* on average across all sites. There is also a clear decline in average size from nearshore to offshore. Foraminiferal density is displayed in Figure 25. There is a noticeable decline in density from nearshore to offshore.



**Figure 23 – (A) Distribution of the five morphotypes of *Homotrema rubrum* at each site; depictions are from Krautwig et al., 1998. (B) Distribution of the two morphotypes of *Planorbulina* spp. at each site.**

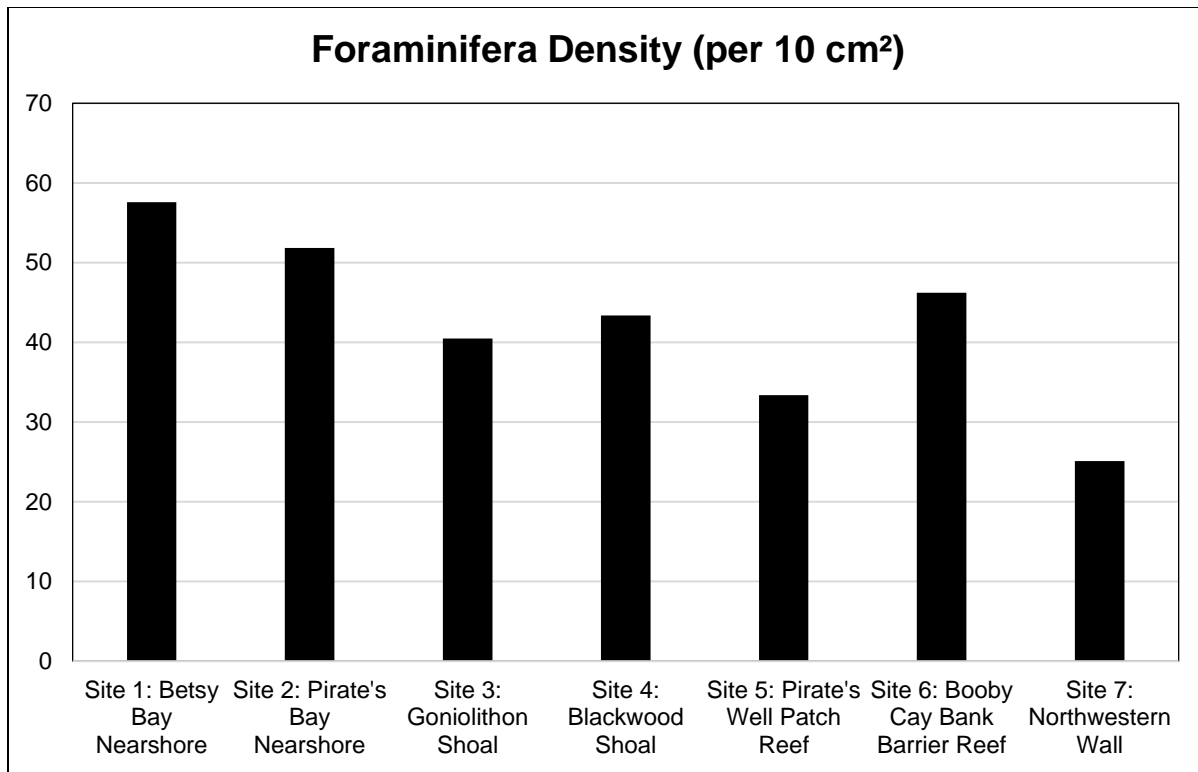
**Table 2 – Mean size of each foraminiferal taxon at the seven locations.**

	Site 1: Betsy Bay Nearshore	Site 2: Pirate's Bay Nearshore	Site 3: <i>Goniolithon</i> Shoal	Site 4: Blackwood Shoal
<i>Placopsilina</i> spp.	NA	NA	NA	NA
<i>Nubecularia</i> sp.	2.16	1.40	3.69	2.64
<i>Planorbulina</i> spp.	1.23	1.00	1.32	1.54
<i>Carpenteria utricularis</i>	2	NA	3.54	3.58
<i>Gypsina globula</i>	0.51	NA	0.87	0.12
<i>Gypsina plana</i>	NA	NA	NA	0.22
<i>Homotrema rubrum</i>	3.81	5.60	4.45	3.93
	Site 5: Pirate's Well Patch Reef	Site 6: Booby Cay Bank Barrier Reef	Site 7: Northwestern Wall	
<i>Placopsilina</i> spp.	0.33	0.76	2.08	
<i>Nubecularia</i> sp.	1.94	1.32	2.46	
<i>Planorbulina</i> spp.	1.63	1.26	1.01	
<i>Carpenteria utricularis</i>	6.25	5.89	0.69	
<i>Gypsina globula</i>	0.60	0.22	0.16	
<i>Gypsina plana</i>	NA	31.16	85.82	
<i>Homotrema rubrum</i>	3.34	3.58	2.37	



**Figure 24 – Bar graph depicting the average size of the two most common foraminifera in this study: *Homotrema rubrum* and *Planorbulina* spp. These taxa were chosen because they represent over 95% of the individuals counts in this study and are found at all locations. Size is measured in mm<sup>2</sup>.**





**Figure 25 – Density of foraminifera, expressed as the mean number of foraminifera counted per 10 cm<sup>2</sup>. Note how density decreases as distance from shore increases.**

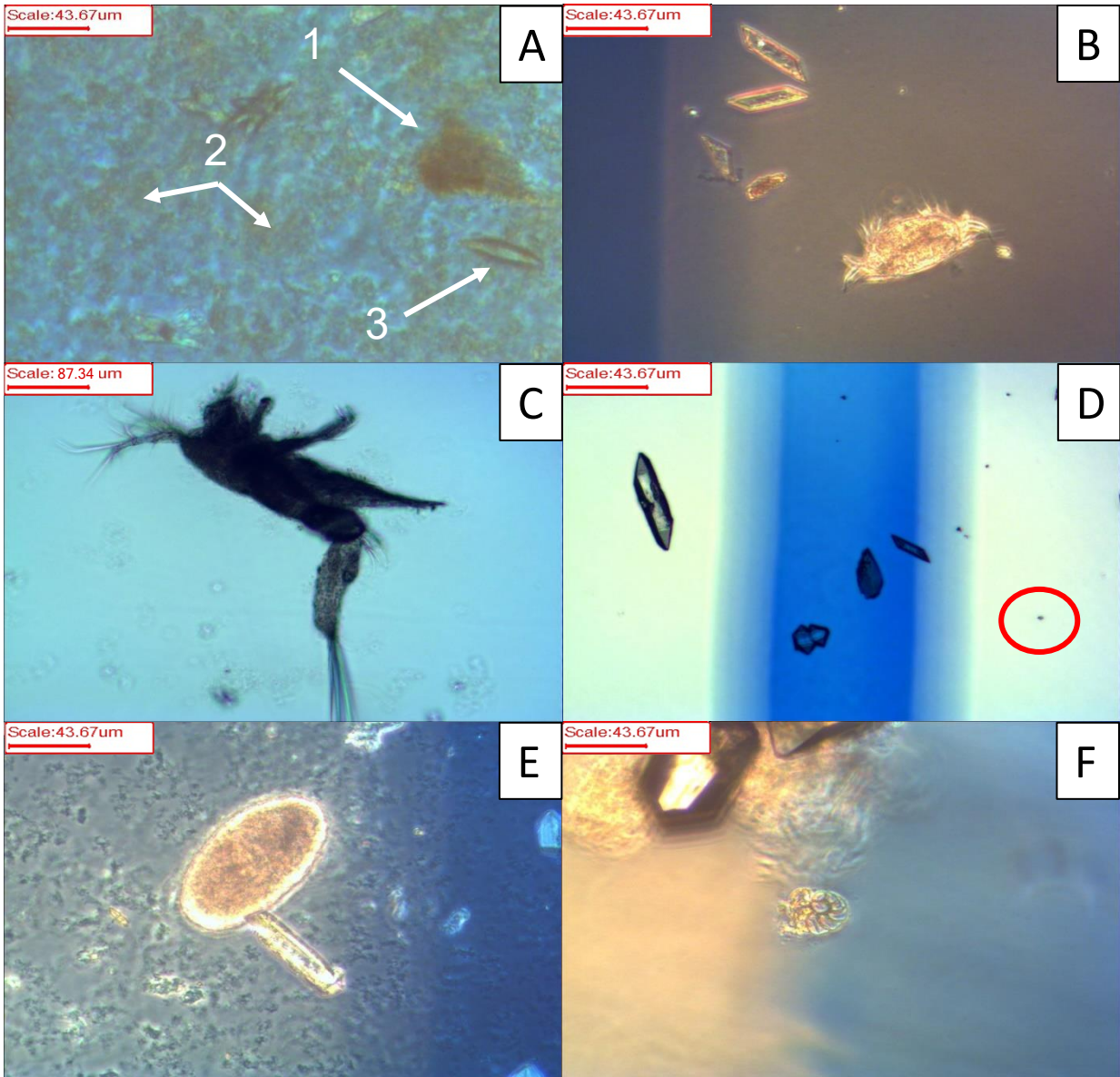
### *Biota in Water Samples*

Water samples were analyzed in order to gain insight to the type and amount of potential food particles contained within the water beneath the sampled cobbles. A large variety of microorganisms and organic material was observed in the water samples (Table 3). A category was created for common “amorphous masses”, which appear as dark agglomerations of organic material held together by translucent filaments (Fig. 26A). Broad taxonomic categories were established, such as crustacea, which included a crab, copepods and ostracods, unidentified microbes, and foraminifera (Fig. 26B-F). Dark specks in the petri dish were counted as possible bacteria, which comprised the microbe group (Fig. 26D). The Pirate’s Well Patch Reef site had the highest count of potential food particles, which included an abundance of pennate diatoms. All sites had microbe counts ranging in the hundreds. The lagoonal nearshore and patch reef sites (Pirate’s Bay Nearshore and Pirate’s Well Patch Reef) contain large numbers of amorphous masses.

Very little correlation is observed between counts of potential food items in water samples and the average size or density of foraminifera (Fig 27). The patch reef, which had by far the highest potential food item count, was intermediate in terms of size, foraminiferal density, and water depth in comparison to the nearshore reefs or the platform margin.

**Table 3 – Total counts of organisms observed in the water samples.**

	Site 1: Betsy Bay Nearshore	Site 2: Pirate's Bay Nearshore	Site 5: Pirate's Well Patch Reef	Site 7: Northwestern Wall
Organic detritus present?	No	Yes	Yes	No
Pennate diatoms	11	54	380	9
Radial diatoms	5	0	30	2
Foraminifera	0	0	1	1
Arthropods	2	0	3	1
Unidentified Microbes	319	555	516	410
Spines/spirochetes	0	5	1	0
Filaments	2	3	0	2
Amorphous mass	30	210	197	20
Organic sheaths	4	0	0	2
Unidentified	15	11	10	22
<b>Total</b>	<b>388</b>	<b>838</b>	<b>1138</b>	<b>469</b>



**Figure 26 – Representative photographs of the categories of potential food items in water samples: (A) 1 – Amorphous mass, 2 – Organic detritus littering the background, 3 – Pennate diatom. (B) Crab. (C) Harpacticoid copepod. (D) Microbe (circled) next to crystals of formalin. (E) Ostracod. (F) Foraminifer.**

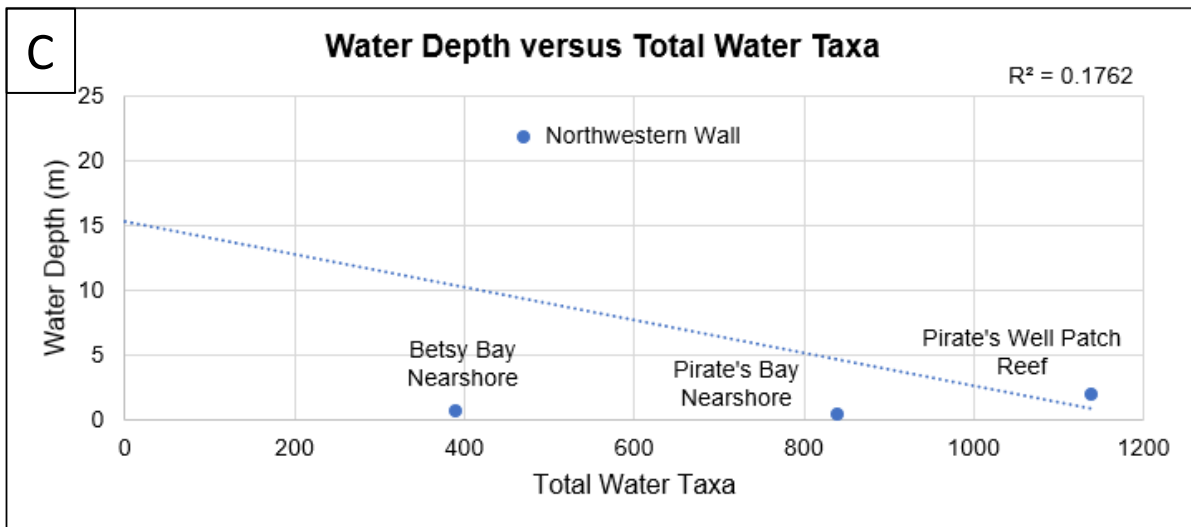
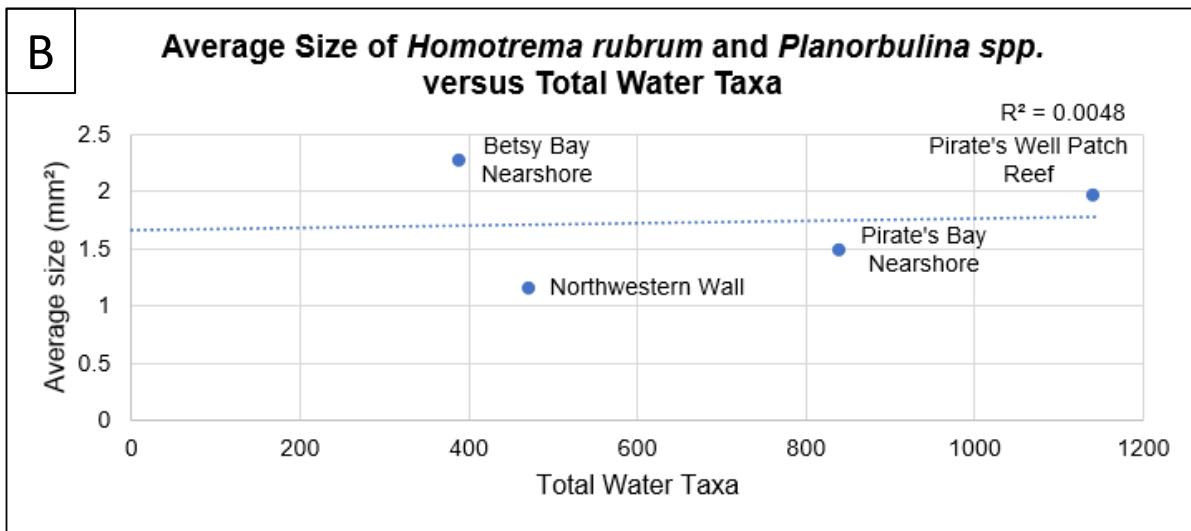
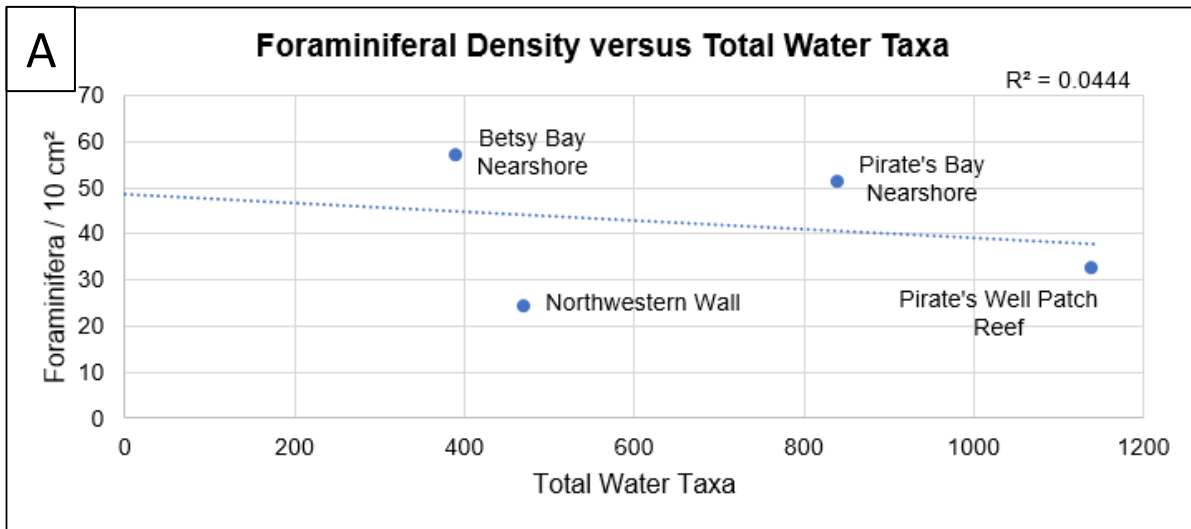


Figure 27 – Relationships between total potential food items in water samples and (A) foraminiferal density, (B) average *Homotrema rubrum* and *Planorbulina* spp. size, and (C) water depth.

### *Meiofauna in Sediment Samples*

Sediment samples were analyzed to get a better sense of the type and density of potential food particles present in nearshore, patch reef, bank barrier, and platform-margin settings. The meiofauna were categorized into broad taxonomic groups (Table 4) including foraminifera, annelids (most of which were polychaetes), crustacea, roundworms, and other, which included stained unidentified microorganisms (Fig. 28A-F). The crustacea observed included ostracods, copepods, and amphipods.

Localities with higher foraminiferal densities and a larger average size of foraminifera generally tend to have higher counts of meiofauna (Fig. 29A and B). The exception to this is Pirate's Bay Nearshore, which has high foraminiferal density but has relatively small foraminifera and a low meiofaunal density (Table 5). Meiofaunal density decreases with increasing water depth, with the highest numbers coming from Betsy Bay Nearshore and the smallest numbers coming from the platform margin (Fig. 29C, Tables 4 and 5).

**Table 4 – Total counts of meiofauna contained within 6 ml of sediment.**

		Foraminifera	Annelids	Crustaceans	Nematodes	Unknown	Total Meiofauna
<b>Site 1:</b>	Cobble 1-2	359	24	21	35	8	447
<b>Betsy Bay</b>	Cobble 1-3	183	4	10	6	6	209
<b>Nearshore</b>	Site 1 Total	542	28	31	41	14	<b>689</b>
<b>Site 2:</b>	Cobble 2-6	256	9	5	17	4	291
<b>Pirate's Bay</b>	Cobble 2-4	136	2	0	2	1	141
<b>Nearshore</b>	Site 2 Total	392	11	5	19	5	<b>432</b>
<b>Site 3:</b>	Cobble 3-5	144	23	54	23	6	250
<b>Goniolithon</b>							
<b>Shoal</b>	Site 3 Total	144	23	54	23	6	<b>250</b>
<b>Site 4:</b>	Cobble 4-1	382	2	10	6	4	404
<b>Blackwood</b>	Cobble 4-3	259	4	8	3	1	275
<b>Shoal</b>	Site 4 Total	641	6	18	9	5	<b>679</b>
<b>Site 5:</b>	Cobble 5-4	203	7	9	25	3	247
<b>Pirate's Well</b>	Cobble 5-2	100	1	8	25	7	141
<b>Patch Reef</b>	Site 5 Total	303	8	17	50	10	<b>388</b>
<b>Site 6: Booby</b>	Cobble 6-5	192	12	81	32	14	331
<b>Cay Bank</b>	Cobble 6-6	127	4	12	4	3	150
<b>Barrier Reef</b>	Site 6 Total	319	16	93	36	17	<b>481</b>
<b>Site 7:</b>	Cobble 7-5	32	4	16	10	9	71
<b>Northwestern</b>	Cobble 7-2	31	2	3	3	7	46
<b>Wall</b>	Site 7 Total	63	6	19	13	16	<b>117</b>

**Table 5 – Meiofaunal density, foraminiferal density, averaged *Homotrema* and *Planorbulina* sizes, and site depths.**

	Meiofauna/ml	Foraminifera/10 cm <sup>2</sup>	Averaged <i>Homotrema</i> and <i>Planorbulina</i> Sizes (mm <sup>2</sup> )	Average Site Depth (m)
Site 1: Betsy Bay Nearshore	114.83	57.6	2.28	0.75
Site 2: Pirate's Bay Nearshore	72	51.84	1.5	0.5
Site 3: <i>Goniolithon</i> Shoal	83.33	40.48	3.13	2
Site 4: Blackwood Shoal	113.17	43.38	2.93	1
Site 5: Pirate's Well Patch Reef	64.67	33.38	1.98	2
Site 6: Booby Cay Bank Barrier Reef	80.17	46.24	2.76	1.5
Site 7: Northwestern Wall	19.5	25.01	1.17	22



**Figure 28 – Representative photographs of the categories of meiofauna: (A) and (B) Harpacticoid copepod. (C) Polychaete. (D) Ostracod. (E) Roundworm. (F) Segmented nematode.**



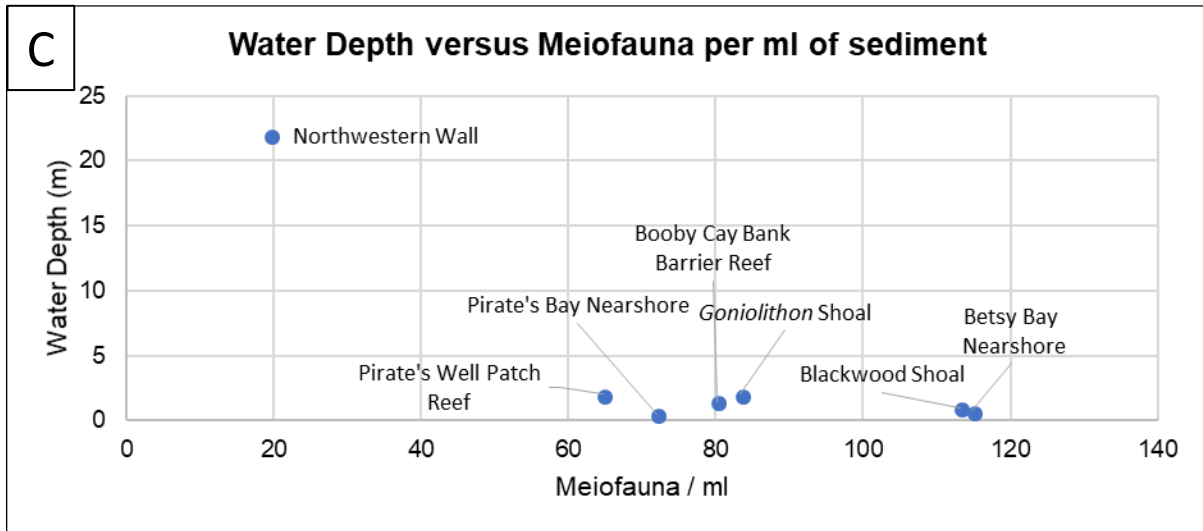
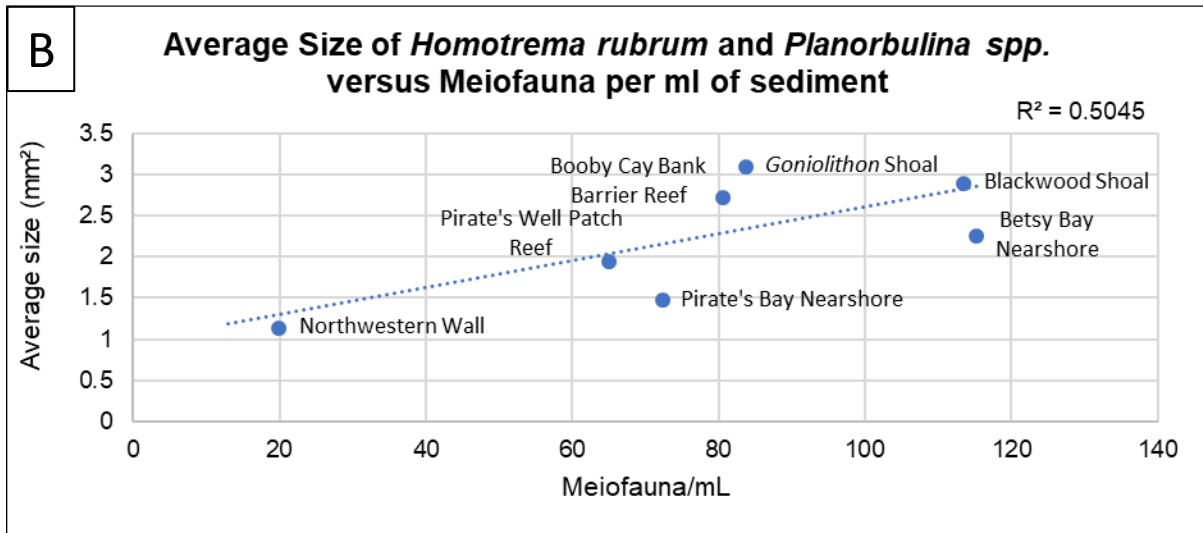
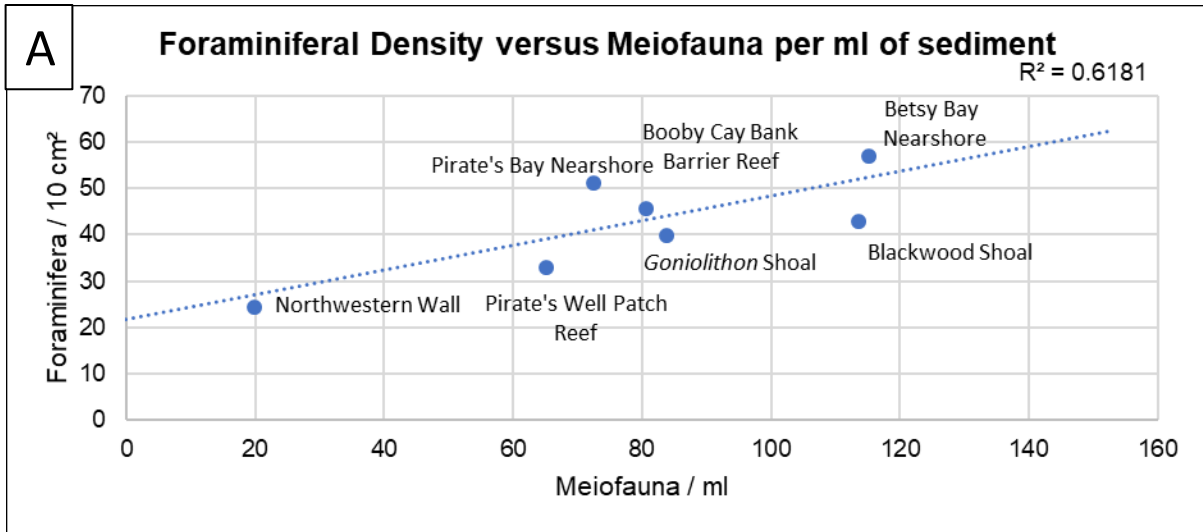


Figure 29 – Comparing average size of *Homotrema rubrum* and *Planorbulina* spp., foraminiferal density, and water depth with meiofauna per ml of sediment.

## 5. Discussion

### *Zonation Patterns of Foraminiferal Taxa*

The distribution of the encrusting foraminifera at Mayaguana closely resembles that of the assemblages at San Salvador (Tichenor and Lewis, 2011, 2018) and Cat Island (Smith, 2015). The primary objective of this study was to corroborate or challenge the model developed by Tichenor and Lewis (2009) at San Salvador, which was supported by Smith (2015): *Homotrema rubrum* characterizes high-energy nearshore habitats, *Planorbulina* spp. dominates diverse, mid-shelf patch reefs, and *Gypsina plana* is most prominent at platform-margin localities.

The two nearshore sites differed significantly in regards to *Homotrema rubrum* counts and area. Site 1, Betsy Bay Nearshore, had significant counts of this species along with areal dominance. *Planorbulina* spp. and *Homotrema* were nearly equal on most cobbles (Fig. 10), which is similar to results obtained at an exposed nearshore site on San Salvador (Tichenor and Lewis, 2018). *Nubecularia* sp. accounted for approximately ten percent of the counts and area for this site (Fig. 17). The abundances of *Homotrema* and *Nubecularia* are similar to those at Cat Island and one site at San Salvador, where *Nubecularia* was found at one site to be the most prominent taxon in terms of count and area (Smith, 2015; Tichenor and Lewis, 2018).

*Homotrema* was most abundant in count and area in the nearshore assemblages at Mayaguana, leading to its grouping with *Nubecularia* as nearshore taxa on the ternary diagram, emulating Smith (2015) (Fig. 22). *Planorbulina* spp. accounted for over fifty percent of counts at Betsy Bay Nearshore; however, because of its large sizes, *Homotrema* was more abundant in area (Fig. 17).

The other nearshore site, Pirate's Bay Nearshore, had few *Homotrema* and was instead dominated by *Planorbulina* spp. Although the average area of individual *Homotrema* was typical of nearshore sites, the overwhelming number of *Planorbulina* made it the most prominent taxon in terms of count and area, to the point that this nearshore site became reminiscent of a patch reef. This is reflected in the similarity of the bar graphs and pie charts of Pirate's Bay Nearshore and Pirate's Well Patch Reef, which compare the counts and areas of the sites (Fig. 17). In fact, *Homotrema rubrum* had a higher percentage of counts at the patch reef than this nearshore locality (Fig. 17).

Although the cobbles collected at the Pirate's Bay Nearshore site were approximately 300 meters away from the nearest patch reef or shoal, is it possible that these cobbles could have been transported inshore, which could result in a drastically different assemblage composition. One line of evidence that suggests this is the presence of *Goniolithon* along the edges of several cobbles from this site. A longshore current could have sent cobbles tumbling from Site 3, *Goniolithon* Shoal, through deeper water before arriving at this nearshore locality. Choi (1984) concluded that encrusting organisms were among the first organisms to colonize reef rubble within the Florida Reef Tract, citing *Homotrema rubrum* and *Planorbulina* spp. as among the first "pioneers". Martin and Lewis (2015) explored the growth rates of encrusting foraminifera at San Salvador, finding that *Nubecularia* and *Planorbulina* were among the first to colonize on new substrates; both appeared within three months, whereas *Homotrema* colonization occurred late, after approximately one year.

The reefs at Sites 3 and 4 were categorized as shoals because they were located over 200 meters offshore but in shallow water, to the point that the coral almost protruded from the ocean's surface. Site 3, *Goniolithon* Shoal, and Site 4, Blackwood Shoal, were strikingly alike in

some ways and differed in others. Site 3 was located on a ridge with an expanse of sandy seafloor between it and the shore, whereas Site 4 was a nearly continuous coral reef. Both sites were characterized by *Homotrema rubrum* as the primary encrusting organism based on counts and area covered (Figs. 12, 13, and 17). Their foraminiferal densities were also similar to each other, each of them containing fewer foraminifera per 10-cm<sup>2</sup> than nearshore sites, but more than the patch reef (Fig. 25). Also, the shoals plotted very close to each other on both ternary diagrams, displaying how similar their assemblages were in terms of foraminiferal counts and areas (Fig. 22). In addition, the Q-mode cluster diagrams and the MDS plots show a remarkable degree of similarity between the twelve cobbles collected from the shoals, especially in regards to area (Figs. 19, 20, 21).

*Goniolithon* Shoal recorded all five different morphotypes of *Homotrema rubrum*, as did the Bank Barrier Reef site (Fig. 23 A). Most *Homotrema* observed were of the multiple variant, which accounted for up to 100% of specimens at the platform margin. Smith (2015) also recorded morphotype data for *Homotrema*, and found all five morphotypes at one of the nearshore sites, using the same five growth forms as this study, bringing the total number of observed Bahamian environments containing all *Homotrema* morphotypes to three. The distribution of these morphotypes is related to several factors, but previous studies have struggled to pin down any single variable. Elliott et al. (1996) initially suggested that the growth forms of *Homotrema rubrum* in Bermuda are an adaptation to environmental conditions, and are influenced by several variables, including light level, sedimentation rates, and water action. This study also noted that newly-settled *Homotrema rubrum* would be the encrusting morphotype, and would grow into a hemispherical or columnar shape as they matured. But they, like Rooney (1970), could not correlate between *Homotrema* test morphology and any specific environment,

indicating that morphological variation may instead be affected by microenvironments, such as a protected vs. exposed substrates. Corliss and Chen (1988), noted that the morphologies of deep-water foraminifera from the Norwegian Sea were controlled by the amount of food particles in the water, while Richardson-White and Walker (2011) proposed that the presence of sponge spicules in the tests of *Homotrema rubrum* at Lee Stocking Island, Bahamas, may be related to predation and competition with other encrusting organisms. Like Smith, (2015) no distinguishable pattern was observed in the morphotypes of *Homotrema rubrum* at Mayaguana, although the presence of a high-energy environment was noted as a common trait between the shoals and the bank barrier reef. Lewis et al. (2015) reported that the globular morphotype was more common at the bank barrier reefs than at patch reefs, and was particularly abundant in restricted microenvironments.

*Planorbulina* spp. was also considered to have two morphotypes: brown and gray (Fig. 23 B). Most of the specimens in this study were of the brown morphotype, accounting for up to 80% of *Planorbulina* at *Goniolithon* Shoal (Fig. 23 B). Gray *Planorbulina* were slightly more abundant at three of the sites, but never reached 60% of counts at any one site. No studies have been performed specifically on *Planorbulina* spp. in the Bahamas, so knowledge of the factors that control growth forms is limited. It is possible that the gray *Planorbulina* is immature, and could change to the other morphotype over time. Brown or gray *Planorbulina* growth may be based on the amount of illumination or water circulation on the underside of the cobble. This microzonation on the underside of reef rubble was observed in the Florida Reef Tract by Choi and Ginsburg, (1983) who found that some areas of clasts were more likely to house encrusting foraminifera over other organisms. Another explanation is that there could be a natural color variation within the tests of *Planorbulina acervalis*, the species that most likely accounts for the

observed *Planorbulina* in this study, based on the orb-like appearance of the test. The morphotype data collected on *Planorbulina* at Mayaguana do not indicate any clear pattern, although it is the first documented study to collect any data on the color variations in *Planorbulina*.

*Planorbulina* spp. dominated both count and area data at Site 5, Pirate's Well Patch Reef (Figs. 14 and 18). Furthermore, this locality had a diverse assemblage of foraminifera, which matches the findings of the data collected at San Salvador (Tichenor and Lewis, 2009, 2011, 2018) and Cat Island (Smith, 2015). The *Planorbulina* at this site accounted for nearly 80% of the counts and 66% of the area of all encrusting organisms, and the average size of 1.63 mm<sup>2</sup> per specimen was the largest of all the sites studied (Fig. 18, Table 4). Most of the cobbles display a high degree of similarity between them in the cluster diagrams and MDS plots across both counts and area, except for two. One (Cobble 5-6) contained an overwhelming amount of gray *Planorbulina*, whereas the rest of the site was dominated by the brown morphotype. The other (Cobble 5-2) had a surprising number of large *Homotrema*, which skewed both the count and area. Perhaps this is not particularly unusual; at Cat Island, one of the patch reefs had several cobbles with assemblages reminiscent of a nearshore site (Smith, 2015).

At Site 6, Booby Cay Bank Barrier Reef, *Homotrema rubrum* made up over 60% of the counts and 75% of the area for encrusting foraminifera (Fig. 18). The diversity at this site was unparalleled: it had all morphotypes of *Homotrema* and was the only site to contain all seven taxa, including both morphotypes of *Planorbulina* (Fig. 23). This site is very similar to the bank barrier reef observed at San Salvador because of the remarkable diversity and the presence of *Gypsina plana* (Tichenor and Lewis, 2018). In addition, the foraminiferal densities observed at this bank barrier site are higher than all sites except for the nearshore localities, just like at San

Salvador. The MDS plots and cluster diagrams show that the cobbles have a high degree of similarity, especially in terms of count (Figs. 19, 20, and 21). The presence of *Gypsina plana* is the most likely reason that two of the cobbles are located next to the clustered platform margin entries (Figs. 19 and 20). The presence of a small amount of *G. plana* is another characteristic of bank barrier reefs studied at San Salvador and Cat Island (Lewis et al., 2015; Smith, 2015; Tichenor and Lewis, 2018).

*Gypsina plana* was found in abundance at Site 7, the Northwestern Wall. This falls in line with the findings from previous research at San Salvador (Tichenor and Lewis, 2009, 2011, 2018; Martin and Lewis, 2015) and Cat Island (Smith, 2015). This platform-margin site was the only one with significant counts and area of *Gypsina plana*, and, although *Planorbulina* was represented by many more individuals, *Gypsina* dominated the coverage on almost all cobbles (Fig. 18). Area is a much more accurate way to represent *Gypsina plana*, due to the incredible size of the species; several of these foraminifera from this site covered over 350 mm<sup>2</sup>, which is quite normal for the species. The unique presence of colossal *Gypsina plana* on the platform-margin cobbles causes them to be closely bunched together on the MDS plot and cluster diagrams when based on area in particular (Figs. 18, 19, and 20). The tremendous sizes of *Gypsina plana* also cause the Northwestern Wall to plot very differently on the area ternary diagram.

Widely different distributions of *Gypsina plana* have been reported in the West Indies. Martindale's (1992) work in Barbados found *G. plana* at all water depths from nearshore to the platform margin, which contrasts with previous work by Tichenor and Lewis (2009, 2011) and Smith (2015), who found significant *G. plana* only at the platform margin in the Bahamas. At Martindale's study site, the fringing reef extends almost continuously out to the first bank barrier

reef, as Smith (2015) pointed out, which may lead to less differentiation between foraminiferal assemblages on cobbles. This would give *G. plana* a wider geographic and water-depth range than in the Bahamas. Choi and Ginsburg (1983) did not find *G. plana* at the platform-margin on the Florida Reef Tract, while Gischler and Ginsburg (1996) reported that *G. plana* was observed at reef, but not fore-reef environments (Tichenor and Lewis, 2011). The SSETI (Shelf and Slope Experimental Taphonomy Initiative) research team deployed experimental substrates in deep water (15-270m) at Lee Stocking Island, Bahamas, and found that *Homotrema rubrum* and *Gypsina plana* were the most prevalent encrusting foraminifera at the 15-m site after six years (Walker et al., 2011).

*Gypsina plana* appears almost exclusively at the platform margin in greater sizes and abundances than any other locality, even though food availability decreases offshore (Reiswig, 1971, 1972). Just like at San Salvador and Cat Island, *G. plana* was found primarily on the underside of cobbles at Mayaguana; this, along with its increased areas, may be due to the lack of competition for space between the cobble and substrate (Tichenor and Lewis, 2009, 2011, 2018; Smith 2015). Another explanation for its expansive size could be a symbiotic relationship with another organism such as algae, whose photosynthetic cells would provide the foraminifer with nutrients in exchange for living space and access to sunlight, as discussed in Smith (2015). This could be particularly helpful because food is so scarce at the platform margin. However, these photosymbionts have not been observed directly in *G. plana* (Tichenor and Lewis, 2018). Prager and Ginsburg (1989) postulated the presence of these symbionts on *G. vesicularis*, a closely related species that was found on Florida's outer shelf, because the tests of living individuals were colored ("greenish-tan") and lost their coloration soon after collection. Martindale (1992) and Walker et al. (2011) both speculated the presence of symbionts on *G.*



*plana*, although neither found it to prefer sunlit vs. shaded surfaces. In contrast, Plaziat and Perrin (1992) doubted the presence of photosynthetic symbionts after analyzing the skeletal architecture and distribution of the closely related genus *Solenomeris*, from the Eocene of France.

There were other patterns present at Mayaguana besides the distribution of foraminiferal assemblages. Mean test size for most species decreased in general as distance from shore increased, although the largest average size of *Planorbulina* spp. were found at the mid-shelf patch reef (Fig. 24). An exception to this is *Gypsina plana*, which recorded the largest specimens at the platform-margin (Table 2). As water depth increases, there is a distinct trend of decreasing foraminiferal density (Fig. 25).

#### *Water and Sediment Samples*

Food availability has been shown to be a primary factor in benthic foraminiferal habitat preferences in deep water (Linke and Lutze, 1992; Jorissen, 1995). Although *Homotrema rubrum* has been observed to be a carnivore, many encrusting foraminifera are suspension feeders, including the ones in this study (Goldstein, 1999; Smith, 2015; Phalen et al., 2016). This involves the extension of pseudopodia away from the test to catch organisms suspended in the water column, which may be why these foraminifera are found in areas with relatively strong water currents (Goldstein, 1999). Since the encrusting foraminifera in this study grow primarily on the bottom of the cobbles, pseudopodia may also reach into the interstices of the sediment to encounter food particles. Linke and Lutze (1992) observed the deep-sea benthic foraminifer *Rupertina stabilis* using sponge spicules to help elevate its pseudopodial net away from the sediment surface and into the water column. They also observed that some foraminifers changed their feeding habits depending on environmental conditions, even switching from an epifaunal to

an infaunal mode. *Homotrema rubrum* is also known to employ sponge spicules to help catch prey (Elliott et al., 1996; Phalen et al., 2016). Living on the underside of cobbles, they could use spicules to reach down into the substrate. This study sought to explore the relationship between food availability and encrusting foraminiferal assemblages, including their composition, density and test size.

#### *Potential Food Sources in Water*

The presence of potential food particles in the water column is considered a controlling factor in the distribution of foraminifera (Hallock, 1986). Therefore, gathering water samples from beneath the cobbles, where the attached foraminifera would be feeding, may give more insight to the relationship of attached foraminifera and their food. Although Richardson-White and Walker (2011) report that these foraminifera feed mostly on organic detritus and bacteria, larger organisms such as copepods, ostracods, and foraminifera were also counted as potential food items for this study.

Diatoms, amorphous masses, and particularly prokaryotes accounted for the majority of organisms observed in the water samples (Table 3). Pirate's Bay Nearshore and Pirate's Well Patch Reef had significantly higher counts than Betsy Bay Nearshore or the Northwestern Wall and were the only sites to record significant particulate organic content, which appeared as a gray sludge (see Fig. 26 A). This detrital carbon could be due to the protective environment offered by the lagoon, which might slow the circulation of the ambient water and augment the concentration of particles contained within. The presence of grass beds, which were expansive and occurred only in the lagoon, could be another explanation for the heightened carbon content.

It appears that the amorphous masses are linked to the detrital carbon, which was only observed when these opaque black clusters numbered in the hundreds. The disarticulation of these amorphous clusters, which may be the remnants of unarmored organisms, could be the primary source of the particulate carbon. Distinguishing between the two was difficult because they appeared to be of the same material, although the clusters contained more translucent filaments that looked like decaying tissue, that bound them together. Distinctions between the two were made by noting the color differences and lack of shape of the detrital carbon.

The Betsy Bay Nearshore and Northwestern Wall sites, which were located on the western side of the island, recorded far fewer counts of nearly all organisms (Table 3). These localities were dominated by *Homotrema rubrum* and *Gypsina plana* as opposed to *Planorbulina* spp., which characterized Pirate's Bay Nearshore and Pirate's Well Patch Reef. This suggests that there may be a relationship between the amorphous masses and detrital carbon with dominant *Planorbulina* growth. There appears to be no relationship between the number of organisms in the water column and the average size of encrusting foraminifera ( $R^2=0.0048$ ) (Fig. 27). The amount of water taxa also had very little connection with the density of encrusting foraminifera ( $R^2=0.0444$ ) or water depth ( $R^2=0.1762$ ), due to the combination of low counts at both Betsy Bay Nearshore and the Northwestern Wall, which are polar opposites in terms of foraminiferal density and water depth. It was striking that these two sites have this lack of water taxa in common, especially since nearshore and platform-margin sites are dissimilar in terms of wave action, light-level, and foraminiferal distribution (Tichenor and Lewis, 2009, 2011, 2018; Smith, 2015).

#### *Potential Food Sources in Sediments*

Foraminifera constitute the majority of the meiofauna observed in sediments in the current study. The two nearshore sites, Betsy Bay Nearshore and Pirate's Bay Nearshore, posted high numbers of meiofauna, with Betsy Bay recording the highest count at 689 (Table 4 A). These two sites also recorded the second- and third-most foraminifera in the sediment: 575 for Betsy Bay, and 392 for Pirate's Bay, which is consistent with the high density of attached foraminifera seen at both sites. We counted foraminifera as potential food items because it is possible for encrusting foraminifera to ingest their cytoplasm by use of their extensive pseudopodia and phagocytosis (Goldstein, 1999). Similarly, foraminifera are known to eat other hard-shelled meiofauna, such as mollusks and small crustaceans (Armstrong and Brasier, 2005; Phalen, 2015; Phalen et al., 2016).

There appears to be a relationship between high counts of crustaceans and the abundance of *Homotrema rubrum*. Significant counts of crustaceans were recorded at Betsy Bay Nearshore, *Goniolithon* Shoal, Blackwood Shoal, and Booby Cay Bank Barrier Reef, which were all sites that were dominated by *Homotrema* in terms of both count and area (Table 4A, Figs. 17 and 18). These four sites had the highest meiofaunal densities from the study group, but the number of crustaceans was particularly notable. *Goniolithon* Shoal and Booby Cay Bank Barrier Reef produced remarkable numbers of crustaceans: 93 at Booby Cay Bank Barrier Reef and 54 at *Goniolithon* Shoal (in only 3 ml of sediment), which were the highest counts of any type of meiofauna at any site, excluding foraminifera (Table 4A). Sites with high counts of crustaceans are located in shallow water, have high foraminiferal densities, and exhibit largest average sizes of foraminifera, all traits that are generally associated with dominant *Homotrema* (Tichenor and Lewis, 2009, 2011, 2018; Smith, 2015). Crustaceans accounted for almost 22% of all meiofauna found at *Goniolithon* Shoal, the site that also recorded the largest average size of encrusting

foraminifera. It is possible that the prevalence of *Homotrema rubrum* is related to the high densities of meiofauna, although this foraminifer appears to prefer crustaceans. Phalen (2015) fed *Isochrysis galbana* (haptophyte), *Dunaliella sp* (algae), *Artemia sp.* (crustacean) and a mix of diatoms to *Homotrema rubrum* under laboratory conditions. The only food type that *Homotrema* was actively observed to ingest was the crustacean *Artemia sp.*, which was consumed by over 80% of specimens in the aquarium.

Pirate's Well Patch Reef contained 388 organisms composed primarily of foraminifera, although the sediment contained a significant amount of nematodes, more than any other site (Table 4). This patch reef's density of encrusting foraminifera, combined average sizes of *Homotrema rubrum* and *Planorbulina spp.*, and average site depths were all intermediate between those of Betsy Bay Nearshore and the Northwestern Wall (Table 1). Its density of 64.67 meiofauna/ml was also intermediate to that of Betsy Bay Nearshore (114.83/ml) and the Northwestern Wall (19.5/ml) (Table 5). This also highlights its similarity with Pirate's Bay Nearshore, which also recorded values of both foraminiferal density and average *Homotrema* and *Planorbulina* size that fell between Betsy Bay and the Northwestern Wall sites (Table 5). As previously noted, the assemblage composition of Pirate's Bay and Pirate's Well Patch Reef are strikingly alike, with *Planorbulina* dominating both count and area. The count and area data of the foraminifera seen at Pirate's Bay Nearshore are not necessarily abnormal for a nearshore locality, but its average foraminiferal size of 1.5 mm<sup>2</sup> and its density of 72 meiofauna/ml are both much lower than the other nearshore site, instead plotting much closer to the patch reef (Table 5). It is possible that the sediment obtained at this site could have come from the beach, which was only 3 meters away. Beach sand would most likely contain fewer marine meiofauna than a standard sediment sample, and the crashing waves may have pulled sand from the shore

and mixed it with the sediment at the reef, effectively diluting it and lowering the density of meiofauna.

The platform margin averaged 19.5 meiofauna/ml, which is far less than the densities for the nearshore and patch reef sites. Obtaining sediment at the wall was so difficult that it required a second dive to get satisfactory samples. Most of the collected cobbles were located on a steep slope that was composed of reef rubble, which made it difficult for the locality to accrue any sediment. Our study area differs from the normal “wall” site, which has vertical walls accompanied by sediment-rich ledges that form a stair-stepping pattern that gathers sediment better than a downward-sloping ramp. This could mean that the counts of meiofauna recorded in our sediment samples may not be representative of platform-margin cobbles as a whole. Also, one of the samples was taken as a proxy from a sandy area away from the slope, which may affect its validity. Regardless, the density of meiofauna decreases in general from nearshore to offshore, just like the size and density of encrusting foraminifera. The one foraminifer that does not conform to these patterns is *Gypsina plana*, which is at its largest and most prevalent at the platform-margin.

There is a correlation between the averaged sizes of *Homotrema rubrum* and *Planorbulina* spp. and the density of meiofauna ( $R^2=0.5045$ ), which may indicate a relationship between the size of attached foraminifera and the amount of food particles present in the sediment at Mayaguana (Fig. 29). *Homotrema* and *Planorbulina* were used to display changes in size because they constitute over 95% of the foraminifera counted in this study and are found in abundance at all sites. Total densities of encrusting foraminiferal had a stronger correlation with meiofaunal density ( $R^2=0.6181$ ). Meiofaunal density decreased significantly at the platform margin, which suggests that it decreases with increasing water depth. The presence of free

foraminifera in the sediment was the main contributor to these significant  $R^2$  values. The Pirate's Bay Nearshore had the second-highest meiofaunal density. However, if foraminifera were disregarded then it would have recorded the lowest density of all sites.

There were several aspects of the methodology that could be improved in general. Given the wave and current action, it was impossible to precisely scoop equal amounts of sediment from the top several centimeters of the seafloor and transfer it to the container. There were also variable amounts of sediment available per cobble, with some cobbles sitting directly on the bedrock or on other cobbles. This occurred at the platform margin, and required taking a proxy from a nearby location, which could have resulted in more, fewer, or different meiofauna. The results of this study are preliminary; future works should find a better method of standardizing samples and compensating for sites with little sediment.

### *Reflections*

The distribution of encrusting foraminifera at Mayaguana could be explained by the food availability in the sediment and water. There is a clear link between the density of meiofauna and both the size and density of the encrusting foraminifera found at each site: places with higher densities of meiofauna have more encrusting foraminifera, larger tests on average, and are dominated in count and area by *Homotrema rubrum*, as summarized in Table 6. Localities with fewer meiofauna, such as Pirate's Bay Nearshore, Pirate's Well Patch Reef, and Northwestern Wall, were characterized by *Planorbulina* spp. and fewer, smaller individuals. Although Pirate's Bay Nearshore had a high density of encrusting foraminifera and the largest average size of *Homotrema*, it was typified by numerous *Planorbulina* even smaller than the individuals found at the platform margin (Fig. 25, Table 5).

**Table 6 – Summary of the results from encrusting foraminiferal counts, sizes, and densities with the amount of potential food particles in the water and in the sediment. Dominant taxa are bolded. Note the trend of *Homotrema rubrum* occurring with large foraminiferal sizes and high density of foraminifera and meiofauna.**

Sites	Foraminiferal Count	Foraminiferal Area	Foraminiferal Density	Foraminiferal Size	Water Content	Meiofauna (Beside Foraminifera)	Meiofauna (Including Foraminifera)
Site 1: Betsy Bay Nearshore	<i>Planorbulina</i> , <i>Homotrema</i>	<i>Homotrema</i> , <i>Planorbulina</i>	<b>Highest</b>	Large	Low	<b>Nematodes,</b> <b>Crustaceans,</b> <b>Annelids</b>	High
Site 2: Pirate's Bay Nearshore	<i>Planorbulina</i>	<i>Planorbulina</i> , <i>Homotrema</i>	High	Moderate	<b>Organic detritus</b> <b>Amorphous mass</b>	<b>Nematodes</b>	Moderate
Site 3: <i>Goniolithon</i> Shoal	<i>Homotrema</i> , <i>Planorbulina</i>	<i>Homotrema</i>	High	<b>Largest</b>		<b>Crustaceans,</b> Nematodes, Annelids	High
Site 4: Blackwood Shoal	<i>Homotrema</i> , <i>Planorbulina</i>	<i>Homotrema</i>	High	Large		<b>Crustaceans</b> (moderate)	<b>Highest</b>
Site 5: Pirate's Well Patch Reef	<i>Planorbulina</i>	<i>Planorbulina</i> , <i>Homotrema</i>	Moderate	Moderate	<b>Organic detritus</b> <b>Amorphous mass</b> <b>Pennate Diatoms</b> <b>Radial Diatoms</b>	<b>Nematodes,</b> Crustaceans	Moderate
Site 6: Booby Cay Bank Barrier Reef	<i>Homotrema</i> , <i>Planorbulina</i>	<i>Homotrema</i>	High	Large		<b>Crustaceans,</b> Nematodes, Annelids	High
Site 7: Northwestern Wall	<i>Planorbulina</i>	<i>Gypsina</i> <i>plana</i> , <i>Planorbulina</i>	<b>Lowest</b>	<b>Smallest</b>	Low	<b>Crustaceans</b> (moderate)	<b>Lowest</b>



The water samples returned differing results from those found in the sediment data. The water samples from Pirate's Well Patch Reef, which had fewer and smaller encrusting foraminifera, contained abundant potential food particles. Meanwhile, water collected at Betsy Bay Nearshore had less food in comparison, even though the average size and density of its encrusting foraminifera were larger. I contend that ambient water is not as important of a factor as subsequent sediment in determining the food availability of encrusting foraminifera. The cobbles collected from each site were sitting on the ocean floor, and the only foraminifera that were counted were located on the undersides of the cobbles, facing down into the sediment. These individuals must be capable of surviving on the food in the sediment, since most of them will not regularly be exposed to water currents. The amount of food in the water appears to have little bearing on the size or density of the encrusting foraminifera in comparison to the density of the meiofauna found in the sediment.

Both the Betsy Bay Nearshore site and the platform margin had few food particles in the water, but had drastically different encrusting foraminifera assemblages (Figs. 17 and 18). This could be explained by the difference in the amount of sediment at both sites, with the nearshore site having plentiful sediment and the platform margin having very little. Since many of the cobbles at the wall were gathered from a slope, there was very little sediment per area touching each cobble. Therefore, foraminifera would acquire food primarily by suspension feeding from the nutrient-scarce water column. This would explain the lack of large tests seen out in deeper water and suggest that *Gypsina plana* is not reliant on meiofauna but relies on photosymbionts instead. Although *Goniolithon* Shoal had little sediment and a large density of meiofauna, the cobbles were sitting in turtle grass, which would provide nourishment for both encrusting foraminifera and meiofauna.

This was the first known study that attempted to quantify the number of potential food items for encrusting foraminifera in either the water column or sediment. The methods of collection and analysis were thorough, although some aspects could be altered for future work. The presence of the unrecognizable amorphous masses suggests that the 10% formalin solution by itself was not enough to fix the soft tissues of many microorganisms. Although fixing agents for light microscopy like osmium tetroxide could not have been transported or safely utilized in Mayaguana, a stronger solution of formalin or an immediate application of a fixing agent in the field may have been able to preserve more tissue and allow for more precise identification. Given the wave and current action, it was impossible to precisely scoop equal amounts of sediment from the top several centimeters of the seafloor and transfer it to the container. Future works should find a better method of standardizing samples and compensating for sites with little sediment. Another interesting concept would be to get close-up photographs of each cobble before and during collection to observe which parts on the undersides of each cobble were buried in sediment. This would allow researchers to draw more accurate conclusions about how the size, density, and composition of encrusting foraminiferal assemblages are affected by sediment, and whether or not this affects the microzonation on the underside of cobbles, as addressed by Choi and Ginsburg (1983).

Another improvement to this study would be to increase the number of different reef sites. For example, we sampled only one patch reef locality, which formed the basis for all of our mid-shelf assemblage data. Given how dissimilar Betsy Bay Nearshore and Pirate's Bay Nearshore are, another patch reef could have had very different results from Pirate's Well Patch Reef, which would have offered more insight into the distribution of encrusting foraminifera at Mayaguana. The Northwestern Wall and Booby Cay Bank Barrier Reef localities functioned as

proxy sites because it was not feasible to explore the bank barrier reef or a wall ledge directly. The bank barrier site had too strong of currents to safely sample the cobbles, and the best ledge to get platform-margin cobbles was at least 150 feet deep, and thus inaccessible. We had to collect samples from proxy sites instead: shoreward of the bank barrier reef, and on a steep slope above the platform-margin wall. Taking samples right at the bank barrier reef and at a wall ledge may have given more accurate results than our sites at Northwestern Wall and Booby Cay Bank Barrier Reef.

## 6. Conclusions

This study had two goals: (1) to describe the distribution of encrusting foraminifera at Mayaguana to see if that distribution matched what has been described at San Salvador and Cat Island, and (2) to assess the potential food items in water and sediment samples to see if food helps to explain the distribution of encrusting foraminifera. These findings, along with Smith (2015) at Cat Island, mark the third Bahamian island to corroborate the original distribution model that was developed at San Salvador by Tichenor and Lewis (2009, 2011, 2018). Nearshore sites are characterized by *Homotrema rubrum* with exception to Pirate's Bay Nearshore, which was dominated by *Planorbulina* spp., most likely due to the shoreward transportation of cobbles from *Goniolithon* Shoal. Pirate's Well Patch Reef was dominated in count and area by *Planorbulina*. *Homotrema* was the most prominent taxon in terms of count and area at the high-energy shoals and bank barrier reef. The platform-margin location was dominated in area by *Gypsina plana*.

Additionally, the density and average size of foraminifera are linked to distance from shore, water depth, and wave energy. Nearshore sites, which are shallow and high-energy, contain larger quantities and larger sizes of foraminifera. As the distance from shore and water depth increase, with exception to the bank barrier reef, both the size and quantity of foraminifera decrease.

The amount of potential food particles gathered from the water flowing beneath each cobble had little to no relationship with the size, density, or composition of encrusting

foraminifera. In contrast, the density of sediment meiofauna collected from beneath the cobbles was related to the size, density, and composition of encrusting foraminiferal assemblages. At sites with more meiofauna, the size and density of encrusting foraminifera were larger, and assemblages were characterized by abundant *Homotrema rubrum*. Sites with fewer meiofauna were dominated by *Planorbulina* spp. and had fewer counts and smaller average test sizes. Thus, the abundance and nature of the meiofauna seem to play an important role in determining the distribution of encrusting foraminifera.

APPENDIX A (COUNT)

<b>Betsy Bay Nearshore (n=1,008)</b>	<b>Cobble 1-1 (n=204)</b>	<b>Cobble 1-2 (n=160)</b>	<b>Cobble 1-3 (n=161)</b>	<b>Cobble 1-4 (n=157)</b>	<b>Cobble 1-5 (n=147)</b>	<b>Cobble 1-6 (n=179)</b>	
<i>Placopsilina</i> spp.	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Nubecularia</i> sp.	6.86	11.25	4.35	21.66	6.80	1.68	
<i>Planorbulina</i> (brown)	42.65	36.88	8.07	53.50	14.29	7.26	
<i>Planorbulina</i> (gray)	2.94	0.00	42.86	22.29	61.22	34.64	
<i>Carpenteria utricularis</i>	0.00	5.00	1.24	0.00	0.00	0.56	
<i>Gypsina globula</i>	0.00	0.00	0.00	0.64	0.00	0.00	
<i>Gypsina plana</i>	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Homotrema rubrum</i>	47.55	46.88	43.48	1.91	17.69	55.87	
<b>Pirate's Bay Nearshore (n=985)</b>	<b>Cobble 2-1 (n=186)</b>	<b>Cobble 2-2 (n=131)</b>	<b>Cobble 2-3 (n=128)</b>	<b>Cobble 2-4 (n=176)</b>	<b>Cobble 2-5 (n=166)</b>	<b>Cobble 2-6 (n=198)</b>	
<i>Placopsilina</i> spp.	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Nubecularia</i> sp.	0.00	0.76	1.56	2.84	0.00	0.51	
<i>Planorbulina</i> (brown)	83.33	12.98	18.75	88.07	2.41	20.20	
<i>Planorbulina</i> (gray)	0.00	30.54	79.69	8.52	96.39	79.29	
<i>Carpenteria utricularis</i>	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Gypsina globula</i>	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 rubrum</i>	16.67	55.73	0.00	0.57	1.20	0.00	
<b>Goniolithon Shoal (n=931)</b>	<b>Cobble 3-1 (n=201)</b>	<b>Cobble 3-2 (n=200)</b>	<b>Cobble 3-3 (n=162)</b>	<b>Cobble 3-4 (n=147)</b>	<b>Cobble 3-5 (n=53)</b>	<b>Cobble 3-6 (n=168)</b>	
<i>Placopsilina</i> spp.	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Nubecularia</i> sp.	0.50	0.00	0.62	2.72	1.89	3.57	
<i>Planorbulina</i> (brown)	76.62	8.00	37.04	14.97	38.46	30.95	
<i>Planorbulina</i> (gray)	0.00	1.50	35.80	0.00	0.00	0.00	
<i>Carpenteria utricularis</i>	0.00	0.50	1.85	0.00	0.00	0.00	
<i>Gypsina globula</i>	0.50	0.00	0.00	1.36	0.00	0.00	
<i>Gypsina plana</i>	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Homotrema rubrum</i>	22.39	80.00	24.69	80.95	60.38	65.48	
<b>Blackwood Shoal (n=846)</b>	<b>Cobble 4-1 (n=126)</b>	<b>Cobble 4-2 (n=160)</b>	<b>Cobble 4-3 (n=117)</b>	<b>Cobble 4-4 (n=123)</b>	<b>Cobble 4-5 (n=157)</b>	<b>Cobble 4-6 (n=163)</b>	
<i>Placopsilina</i> spp.	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Nubecularia</i> sp.	7.14	1.25	0.00	2.44	0.00	6.75	
<i>Planorbulina</i> (brown)	48.41	5.63	19.66	23.58	1.91	16.56	
<i>Planorbulina</i> (gray)	0.79	18.75	39.32	24.39	17.83	29.45	
<i>Carpenteria utricularis</i>	1.59	3.12	3.42	0.81	3.82	1.23	
<i>Gypsina globula</i>	0.00	0.00	0.00	0.81	0.00	0.00	
<i>Gypsina plana</i>	0.00	0.00	0.85	0.00	0.00	0.00	
<i>Homotrema rubrum</i>	42.06	71.25	36.75	47.97	76.43	46.01	
<b>Pirate's Well Patch Reef (n=1,085)</b>	<b>Cobble 5-1 (n=201)</b>	<b>Cobble 5-2 (n=124)</b>	<b>Cobble 5-3 (n=113)</b>	<b>Cobble 5-4 (n=163)</b>	<b>Cobble 5-5 (n=153)</b>	<b>Cobble 5-6 (n=192)</b>	<b>Cobble 5-7 (n=139)</b>
<i>Placopsilina</i> spp.	1.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia</i> sp.	1.99	6.45	0.00	0.61	1.31	1.56	0.00
<i>Planorbulina</i> (brown)	47.26	27.42	76.99	66.87	61.44	0.00	92.09
<i>Planorbulina</i> (gray)	12.44	5.65	15.04	15.95	33.99	82.81	0.00
<i>Carpenteria utricularis</i>	2.99	0.00	7.96	0.00	0.00	2.08	0.00
<i>Gypsina globula</i>	1.00	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	0.00
<i>Homotrema rubrum</i>	33.33	60.48	0.00	16.56	3.27	13.54	7.91
<b>Booby Cay Bank Barrier Reef (n=971)</b>	<b>Cobble 6-1 (n=200)</b>	<b>Cobble 6-2 (n=189)</b>	<b>Cobble 6-3 (n=86)</b>	<b>Cobble 6-4 (n=150)</b>	<b>Cobble 6-5 (n=172)</b>	<b>Cobble 6-6 (n=174)</b>	
<i>Placopsilina</i> spp.	0.00	0.53	0.00	0.00	0.00	0.57	
<i>Nubecularia</i> sp.	2.00	0.53	0.00	0.00	6.98	0.00	
<i>Planorbulina</i> (brown)	21.50	26.46	2.33	12.00	2.91	15.52	
<i>Planorbulina</i> (gray)	6.00	6.35	0.00	72.67	16.85	9.77	
<i>Carpenteria utricularis</i>	2.50	0.00	1.16	1.33	3.49	6.32	
<i>Gypsina globula</i>	0.50	0.00	0.00	0.00	0.00	0.00	
<i>Gypsina plana</i>	0.00	0.00	1.16	0.67	0.00	0.00	
<i>Homotrema rubrum</i>	67.50	66.14	95.35	13.33	69.77	67.82	
<b>Northwestern Wall (n=778)</b>	<b>Cobble 7-1 (n=149)</b>	<b>Cobble 7-2 (n=155)</b>	<b>Cobble 7-3 (n=66)</b>	<b>Cobble 7-4 (n=78)</b>	<b>Cobble 7-5 (n=21)</b>	<b>Cobble 7-6 (n=163)</b>	<b>Cobble 7-7 (n=146)</b>
<i>Placopsilina</i> spp.	0.00	0.65	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia</i> sp.	0.00	1.29	3.03	2.56	0.00	0.00	1.37
<i>Planorbulina</i> (brown)	54.36	62.58	48.48	5.13	28.57	27.61	41.78
<i>Planorbulina</i> (gray)	40.27	29.68	22.73	87.18	4.76	67.48	0.00
<i>Carpenteria utricularis</i>	0.00	0.65	0.00	0.00	0.00	0.00	0.68
<i>Gypsina globula</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Gypsina plana</i>	5.37	5.16	24.24	3.85	52.38	4.91	0.00
<i>Homotrema rubrum</i>	0.00	0.00	1.52	1.28	14.29	0.00	56.16

APPENDIX B (AREA)

<b>Betsy Bay Nearshore (n=1,008)</b>	<b>Cobble 1-1 (n=204)</b>	<b>Cobble 1-2 (n=160)</b>	<b>Cobble 1-3 (n=161)</b>	<b>Cobble 1-4 (n=157)</b>	<b>Cobble 1-5 (n=147)</b>	<b>Cobble 1-6 (n=179)</b>	
<i>Placopsilina</i> spp.	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Nubecularia</i> sp.	9.27	7.82	4.06	42.11	4.97	1.87	
<i>Planorbulina</i> (brown)	27.35	31.77	10.94	41.81	12.18	4.37	
<i>Planorbulina</i> (gray)	1.67	0.00	15.74	14.84	24.05	11.93	
<i>Carpenteria utricularis</i>	0.00	4.01	1.50	0.00	0.00	0.40	
<i>Gypsina globula</i>	0.00	0.00	0.00	0.39	0.00	0.00	
<i>Gypsina plana</i>	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Homotrema rubrum</i>	61.71	56.40	67.75	0.84	58.80	81.43	
<b>Pirate's Bay Nearshore (n=985)</b>	<b>Cobble 2-1 (n=186)</b>	<b>Cobble 2-2 (n=131)</b>	<b>Cobble 2-3 (n=128)</b>	<b>Cobble 2-4 (n=176)</b>	<b>Cobble 2-5 (n=166)</b>	<b>Cobble 2-6 (n=198)</b>	
<i>Placopsilina</i> spp.	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Nubecularia</i> sp.	0.00	0.63	2.55	2.29	0.00	0.33	
<i>Planorbulina</i> (brown)	64.52	7.23	8.74	81.22	8.10	16.16	
<i>Planorbulina</i> (gray)	0.00	3.19	88.70	7.31	82.42	83.51	
<i>Carpenteria utricularis</i>	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Gypsina globula</i>	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 rubrum</i>	35.49	88.94	0.00	9.18	9.48	0.00	
<b>Gonolithon Shoal (n=931)</b>	<b>Cobble 3-1 (n=201)</b>	<b>Cobble 3-2 (n=200)</b>	<b>Cobble 3-3 (n=162)</b>	<b>Cobble 3-4 (n=147)</b>	<b>Cobble 3-5 (n=53)</b>	<b>Cobble 3-6 (n=168)</b>	
<i>Placopsilina</i> spp.	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Nubecularia</i> sp.	0.43	0.00	0.65	1.40	0.91	4.62	
<i>Planorbulina</i> (brown)	47.40	2.91	15.59	6.40	34.69	17.19	
<i>Planorbulina</i> (gray)	0.00	0.94	13.75	0.00	0.00	0.00	
<i>Carpenteria utricularis</i>	0.00	1.07	1.62	0.00	0.00	0.00	
<i>Gypsina globula</i>	0.15	0.00	0.00	0.37	0.00	0.00	
<i>Gypsina plana</i>	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Homotrema rubrum</i>	52.02	95.08	68.38	91.83	64.42	78.18	
<b>Blackwood Shoal (n=846)</b>	<b>Cobble 4-1 (n=126)</b>	<b>Cobble 4-2 (n=160)</b>	<b>Cobble 4-3 (n=117)</b>	<b>Cobble 4-4 (n=123)</b>	<b>Cobble 4-5 (n=157)</b>	<b>Cobble 4-6 (n=163)</b>	
<i>Placopsilina</i> spp.	0.00	0.00	0.00	0.00	0.00	0.00	
<i>Nubecularia</i> sp.	7.13	0.93	0.00	1.93	0.00	3.79	
<i>Planorbulina</i> (brown)	31.06	3.80	11.69	6.98	0.35	15.73	
<i>Planorbulina</i> (gray)	1.59	8.32	20.96	8.58	6.23	11.97	
<i>Carpenteria utricularis</i>	2.01	2.27	10.22	1.83	1.98	2.20	
<i>Gypsina globula</i>	0.00	0.00	0.00	0.04	0.00	0.00	
<i>Gypsina plana</i>	0.00	0.00	0.09	0.00	0.00	0.00	
<i>Homotrema rubrum</i>	58.21	84.69	57.03	80.64	91.45	66.31	
<b>Pirate's Well Patch Reef (n=1,085)</b>	<b>Cobble 5-1 (n=201)</b>	<b>Cobble 5-2 (n=124)</b>	<b>Cobble 5-3 (n=113)</b>	<b>Cobble 5-4 (n=163)</b>	<b>Cobble 5-5 (n=153)</b>	<b>Cobble 5-6 (n=192)</b>	<b>Cobble 5-7 (n=139)</b>
<i>Placopsilina</i> spp.	0.26	0.00	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia</i> sp.	1.34	4.74	0.00	0.33	2.56	2.71	0.00
<i>Planorbulina</i> (brown)	45.46	17.70	77.15	57.71	57.48	0.00	95.13
<i>Planorbulina</i> (gray)	10.35	3.45	15.09	7.33	27.13	75.62	0.00
<i>Carpenteria utricularis</i>	7.79	0.00	7.76	0.00	0.00	5.85	0.00
<i>Gypsina globula</i>	0.14	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	0.00
<i>Homotrema rubrum</i>	34.66	74.12	0.00	34.63	12.83	15.83	4.87
<b>Booby Cay Bank Barrier Reef (n=971)</b>	<b>Cobble 6-1 (n=200)</b>	<b>Cobble 6-2 (n=189)</b>	<b>Cobble 6-3 (n=86)</b>	<b>Cobble 6-4 (n=150)</b>	<b>Cobble 6-5 (n=172)</b>	<b>Cobble 6-6 (n=174)</b>	
<i>Placopsilina</i> spp.	0.00	0.20	0.00	0.00	0.00	0.16	
<i>Nubecularia</i> sp.	1.29	0.31	0.00	0.00	2.49	0.00	
<i>Planorbulina</i> (brown)	4.86	14.99	0.14	8.29	0.67	18.00	
<i>Planorbulina</i> (gray)	1.87	4.81	0.00	51.27	5.07	3.33	
<i>Carpenteria utricularis</i>	6.78	0.00	1.33	1.33	10.08	9.08	
<i>Gypsina globula</i>	0.03	0.00	0.00	0.00	0.00	0.00	
<i>Gypsina plana</i>	0.00	0.00	4.32	15.83	0.00	0.00	
<i>Homotrema rubrum</i>	85.17	79.70	94.21	23.28	81.69	69.43	
<b>Northwestern Wall (n=778)</b>	<b>Cobble 7-1 (n=149)</b>	<b>Cobble 7-2 (n=155)</b>	<b>Cobble 7-3 (n=66)</b>	<b>Cobble 7-4 (n=78)</b>	<b>Cobble 7-5 (n=21)</b>	<b>Cobble 7-6 (n=163)</b>	<b>Cobble 7-7 (n=146)</b>
<i>Placopsilina</i> spp.	0.00	0.28	0.00	0.00	0.00	0.00	0.00
<i>Nubecularia</i> sp.	0.00	0.19	0.30	4.96	0.00	0.00	0.45
<i>Planorbulina</i> (brown)	18.14	18.46	0.85	2.12	0.86	5.23	22.01
<i>Planorbulina</i> (gray)	12.39	7.28	0.34	26.97	0.06	19.55	0.00
<i>Carpenteria utricularis</i>	0.00	0.10	0.00	0.00	0.00	0.00	0.25
<i>Gypsina globula</i>	0.00	0.00	0.00	0.00	0.00	0.03	0.00
<i>Gypsina plana</i>	69.47	73.68	98.50	61.67	98.74	75.19	77.29
<i>Homotrema rubrum</i>	0.00	0.00	0.00	4.28	0.34	0.00	0.00

## References Cited

- Armstrong, H.A., and Brasier, M.D., 2005, *Microfossils (Second Edition)*, Blackwell Publishing, Oxford, 304 pp.
- 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, R. D., 1984, Ecological succession of reef cavity-dwellers (coelobites) in coral rubble: *Bulletin of Marine Science*, v. 35, p. 72–79.
- Choi, R.D., and Ginsburg, R., 1983, Distribution of coelobites (cavity-dwellers) in coral rubble across the Florida Reef Tract: *Coral Reefs*, v. 2, p. 165-172.
- Corliss, B.H., and Chen, C., 1988, Morphotype patterns of Norwegian Sea deep-sea benthic foraminifera and ecological implications: *Geology*, v. 16, p. 716-719.
- Duffield, C. J., Edvardsen, B., Eikre, W., and Alve, E., 2014, Effects of different potential food sources on upper-bathyal foraminifera: an experiment with propagules: *Journal of Foraminiferal Research*, v. 44, p. 416-433.
- Elliott, J. M., Logan, A., and Thomas, M. L., 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.
- Geikie, Sir A., 1897, *The Founders of Geology: The Macmillan Company*, New York, v. 1, p. 167.
- Gischler, E., 1997, Cavity dwellers (coelobites) beneath coral rubble in the Florida Reef Tract: *Bulletin of Marine Science*, v. 61, p. 467-484.
- Gischler, E., and Ginsburg, R., 1996, Cavity dwellers (coelobites) under coral rubble in southern Belize barrier and atoll reefs: *Bulletin of Marine Science*, v. 58, p. 570-589.
- Goldstein, S. T., 1999, Foraminifera: A biological overview. *In* Sen Gupta, B. K. *Modern Foraminifera* 1st Ed: Kluwer Academic Publishers, Dordrecht, p. 37-56.
- Goldstein, B. J., and Pandolfi, J. M., 2003, Taphonomic alteration of reef coral: Effects of reef environment and coral growth form II: *The Florida Keys: PALAIOS*, v. 31, p. 495-509.
- Hallock, P., 1986, Larger foraminifera: A tool for paleoenvironmental analysis of Cenozoic carbonate depositional facies: *PALAIOS*, v. 1, p. 55-64.



- Jorissen, J. F., De Stigter, H. C., and Widmark, J. G. V., 1995, A conceptual model explaining benthic foraminiferal microhabitats: *Marine Micropaleontology*, v. 26, p. 3-15.
- Kindler, P., Godefroid, F., and Samankassou, E., 2008, Pre-Holocene island geology of the Caicos and Mayaguana (Bahamas) platforms: Similarities and differences: *Society for Sedimentary Geology*, v. 22, p. 211-213.
- Krautwig, D. W. H., Erlanger, L. H., Basel, H., and Zankl, M., 1998, The lamellar perforate, arborescent and coloured foraminifers *Miniacina*, *Homotrema* and *Sporadotrema*: *Facies*, v. 38, p. 89-102.
- Lewis, R. D., Tichenor, H.R., Turner, O.C., and Morgan, J.L., 2013, The use of taphonomic grade and biovolume data to supplement relative abundance: Benthic foraminifera from San Salvador, Bahamas: North American Micropaleontology Section (SEPM), Geologic Problem Solving with Microfossils III, The University of Houston, Houston, TX. Abstracts Volume with Program, p. 84-85.
- Lewis, R.D., Smith, C.W., Merrill, D., Tichenor, H.R., 2015, Comparison of encrusting foraminifera at bank barrier reefs and lagoonal patch reefs found at San Salvador and Cat Island, Bahamas: *Geological Society of America Abstracts with Programs*, v. 47 p. 347
- Lewis, R.D., Asher, S., Speetjens, S., and Sundbeck, S., 2016, Did Hurricane Joaquin alter the onshore-offshore zonation of encrusting foraminifera at San Salvador, Bahamas?: *Geological Society of America Abstracts with Programs*, v. 48, p. 7.
- Linke, P., 1992, Foraminifera to seasonally varying food input: *Marine Ecology Progress Series*, v. 81, p. 51-63.
- Linke, P., and Lutze, G. F., 1993, Microhabitat preferences of benthic foraminifera-a static concept or a dynamic adaptation to optimize food acquisition?: *Marine Micropaleontology*, v. 20, p. 215-234.
- Mackensen, A., Sejrup, H.P., and Jansen, E., 1985, The distribution of living benthic foraminifera on the continental slope and rise off southwest Norway: *Marine Micropaleontology*, v. 9, p. 275-306.
- Martin, L.D., and Lewis, R. D., 2015, Growth of attached (encrusting) benthic foraminifera along an offshore-onshore transect, Fernandez Bay, San Salvador, Bahamas: Preliminary results. Proceedings volume of the 16th Symposium on the Geology of the Bahamas and other Carbonate Regions. In press.
- Martindale, W., 1992, Calcified epibionts as palaeoecological tools: examples from the Recent and Pleistocene reefs of Barbados: *Coral Reefs*, v. 11, p. 167-177.
- Phalen, W. G., 2015, *Homotrema rubrum* (Lamarck): Distribution and biology of a potential reef bioindicator and underwater angler: Unpublished MSc Thesis, University of Georgia, 50 pp.
- Phalen, W. G., Bernhard, J. A., Bowser, S. S., and Goldstein, S.T., 2016, Distribution, abundance, and laboratory calcification of *Homotrema rubrum* from Tennessee Reef, Florida Keys, USA: *Journal of Foraminiferal Research*, v. 46, no. 4, p. 409-419.

- 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: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 96, p. 195-231.
- Prager, E.J., and Ginsburg, R.N., 1989, Carbonate nodule growth on Florida's outer shelf and its implications for fossil interpretations: *PALAIOS*, v. 4, p. 310-317.
- Reiswig, H.M., 1971, Particle feeding in natural population of three marine demosponges: *Biological Bulletin*, v. 141, p. 568-59.
- Reiswig, H.H., 1972, The spectrum of particulate organic matter of the shallow-bottom boundary waters of Jamaica: *Limnology and Oceanography*, v. 17, p. 341-348.
- 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.
- Rooney, W.S., 1970, A preliminary ecologic and environmental study of the sessile foraminifer *Homotrema rubrum* (Lamarck): Bermuda Biological Station Special Publication No 6., p. 7-18.
- Smith, C., 2015, Distribution of encrusting foraminifera at Cat Island, Bahamas: Implications for foraminiferal assemblages in the geologic record: Unpublished MSc Thesis, Auburn University. 74 pp.
- Somerfield, P., and Warwick, R., 2013, *Meiofauna Techniques: Methods for the study of Marine Benthos*, 4<sup>th</sup> Ed, p. 253-284.
- Tichenor, H. R., and Lewis, R. D., 2009, Assemblages of attached (encrusting) foraminifera across a small, carbonate platform, San Salvador, Bahamas: *Geological Society of America Abstracts with Programs*, v. 41, p. 105.
- 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.
- Tichenor, H.R., and Lewis, R.D., 2018, Distribution of encrusting foraminifer at San Salvador, Bahamas: A comparison by reef types and onshore-offshore zonation: *Journal of Foraminiferal Research*, v. 48, in press
- 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.