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# Can Florida's Springs Coast provide a Potential Refuge for Calcifying Organisms? Evidence from Benthic Foraminifera

Kyle E. Amergian University of South Florida

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# Can Florida's Springs Coast provide a Potential Refuge for Calcifying Organisms? Evidence

from Benthic Foraminifera

by

Kyle E. Amergian

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science College of Marine Science University of South Florida

Major Professor: Pamela Hallock Muller, Ph.D. Susan Bell, Ph.D. Kendra Daly, Ph.D.

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Keywords: Distribution, Miliolida, refugia, bioindicator, *Archaias angulatus*

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# DEDICATION

To my grandfather, Richard Amergian, who always believed in me, and my love for the microscopic world. Without his encouragement and support this would not have been possible.

#### ACKNOWLEDGMENTS

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## ABSTRACT

Florida's Springs Coast, located in the northeast Gulf of Mexico, includes an extensive system of salt marshes that discharge millions of liters of fresh water into coastal waters daily. The chemical properties of the spring waters include high alkalinity and high calcium concentrations due to the Paleogene limestone lithology of this region of Florida. Benthic foraminifers, which are recognized as ecologically important bioindicators, occur abundantly on the shallow shelf off the Springs Coast. Based on the prevalence of the benthic foraminifer *Archaias angulatus* in the seagrass beds along this shallow shelf, a previous study proposed that the Springs Coast provides favorable conditions for such "subtropical" calcifying organisms, despite existing literature indicating that salinities and winter temperatures are suboptimal for such species. Thus, a motivation for my study was to provide insight into the hypothesis that, during times of ocean acidification, limestone lithofacies may provide suitable water chemistry and physical habitat to provide refuges for calcifying organisms.

Selected environmental parameters and sediments from 41 sites at depths  $\leq 8$  m were sampled in September 2013, during routine seagrass monitoring by researchers from the Florida Fish and Wildlife Research Institute. The 152 benthic foraminiferal species identified included 71 porcelaneous, 67 hyaline, and 14 agglutinated species. Overall, 74% of the specimens identified were porcelaneous and most of the remainder were hyaline; agglutinates composed <1% of those counted. Species dominance in samples revealed an apparent distribution reversal compared to previous reports from Gulf of Mexico coastal habitats. Smaller miliolids, notably

*Quinqueloculina* spp., dominated in samples from most of the inshore brackish sites. In contrast, at the more offshore sites characterized by normal marine salinities, hyaline taxa such as *Haynesina* spp. were much more abundant. We postulate that these unusual distributions are associated with the calcium and carbonate chemistry of the brackish waters. The salinity threshold for small miliolids appeared to be lowered by the carbonate saturation state  $(Ω)$ .

Although 152 species were identified, only 13 species accounted for 56% of the specimens counted. The high diversity coupled with low abundances of most species may indicate the influence of foraminiferal propagule dispersal. The seasonal range of environmental conditions and the diversity of habitats available within the seagrass may allow a diverse array of propagules to recruit and grow at suitable times during the year, while not necessarily establishing sustained populations.

# INTRODUCTION

### **Florida's Springs Coast**

In seagrass meadows along Florida's Spring Coast, the common Caribbean foraminiferal species, *Archaias angulatus* (Fichtel and Moll), was observed in abundance by Dr. Paul Carlson of the Seagrass Integrated Mapping and Monitoring Program (SIMM) of Florida Fish and Wildlife Conservation Commission's Research Institute (Jones et al., 2016). The observation of a thriving population of this subtropical/tropical soritid species, which hosts chlorophyte endosymbionts, came as a surprise because both the winter temperatures and reduced salinities were below the environmental limits previously published for this species (e.g., Martin, 1986; Hallock & Peebles, 1993; Weinmann et al., 2013). Observations of *Ar. angulatus* in an unusual area prompted the collection of sediment samples during a FWRI survey of the seagrass habitat along the Springs Coast during the late summer of 2013.

Florida's Springs Coast is a unique coastal system of salt marshes spanning approximately one degree of latitude (28˚–29˚N) along Florida's west coast. Many springs discharge directly into coastal waters or into rivers that collectively discharge millions of liters of fresh water into coastal waters every day. The lithology in this region of Florida is dominated by Paleogene limestone that extends offshore, with a limited cover of quartz sand and shell debris (e.g., Beckwith, 2016, and references therein). The chemical properties of the spring water include elevated alkalinity and calcium concentrations (Beckwith et al., 2019).

## **Foraminifera as Bioindicators**

Benthic protists of the Phylum Foraminifera occur abundantly worldwide, living in estuaries, marshes, and other shallow shelf systems similar to Florida's Springs Coast, as well as in most other marine environments and even in some freshwater and moist terrestrial habitats. Though foraminifers lacking shells are being increasingly identified using molecular genetics (Pawlowski et al., 2003), most research has focused on shelled forms, because of the preservation potential of the shells, also commonly called "tests" (e.g., Sen Gupta, 1999; Murray, 2006).

Environmental parameters such as food availability, pH, alkalinity, dissolved oxygen, salinity, temperature, and substrate variability influence the abundance and diversity of foraminiferal assemblages. Benthic foraminifers fill specific niches and have relatively short lifespans, which allow them to quickly respond to environmental change, making them useful in differentiating between long-term changes and episodic events (e.g., Hallock et al., 2003; Carnahan et al., 2009). Additionally, foraminifers are widely distributed, diverse, and typically well preserved in the sediment record. Sampling of foraminifers is relatively easy and inexpensive due to their small size and high abundance, and collection has both low environmental impact and cost (e.g., Schafer, 2000; Hallock et al., 2003). As a consequence, benthic foraminifers are becoming more widely utilized as ecologically important bioindicators (e.g., Hallock, 2012, and references therein; Schönfeld et al., 2012, and references therein).

#### **Foraminiferal Functional Groups**

Several studies have used the concept of functional or morphological groups in ecological studies of benthic foraminiferal assemblages. Perhaps the most common categorization is

infaunal versus epifaunal (e.g., Bandy, 1954; Jorissen, 1999; Murray, 2006, and references therein). Large changes in pore-water chemistries can take place within the sediment-water interface and within sediments immediately below the interface. This is particularly characteristic of fine-grained sediments, because coarse-grained sediments allow for a deeper penetration of water motion and oxygen. However, in shallow-water environments similar to the Springs Coast, living Foraminifera are found in considerable sediment depths without noticeable compositional changes with depth (Jorrissen, 1999).

Murray (e.g., 1973, 2006) refers to foraminifers as morphospecies that are primarily defined by wall structure, chamber and test shape, and the positions of apertures, and therefore used ternary diagrams to distinguish habitats, plotting wall structure (agglutinated, porcelaneous and hyaline) as the three reference points. Agglutinated taxa are commonly prevalent in shallow waters with low carbonate saturations such as most brackish environments, while miliolid taxa tend to be prevalent in highly carbonate-saturated waters that are common in warm, normalmarine to hypersaline conditions.

Langer (1993) categorized four epiphytic morphotypes, including attached, temporarily motile, suspension-feeding motile, and grazing-motile. Other authors, especially those working in the Mediterranean where seagrasses are prolific, have adopted or modified Langer's (1993) epiphytic morphotypes (e.g., Mateu-Vicens et al., 2014). Mateu-Vicens et al. (2014) further separated attached morphotypes into two categories: encrusting and sessile.

Hallock et al. (2003) defined three benthic-foraminiferal functional groups that occur in lower-latitude, warm coastal waters: algal-symbiont-bearing, stress-tolerant, and other smaller taxa, which includes most smaller miliolids, some smaller rotaliids, and some agglutinates. Each functional group has an optimal range of environmental parameters in which the foraminifers can

thrive. Large, symbiont-bearing foraminifers, like *Ar. angulatus*, prefer warm-water environments with normal marine salinity and low nutrients. Stress-tolerant taxa can thrive in marginal environments defined by having high variability in environmental parameters such as temperature, salinity, food supply, dissolved oxygen, pH and alkalinity. *Ammonia* is a welldocumented eurytopic genus found in coastal and estuarine environments; Poag (2015) considered this the dominant genus in inshore-coastal waters around the Gulf of Mexico. Agglutinated species also are common among low salinity environments (e.g., Poag, 2015, and references therein). Most smaller miliolids and smaller rotaliids thrive where food supplies are adequate but not in sufficient excess to deplete oxygen concentrations at the sediment-water interface (Hallock et al., 2003). Miliolids typically thrive in normal to hypersaline waters (e.g., Murray, 2006), because their calcification mechanism requires relatively high carbonatesaturation states (Bentov & Erez, 2006; de Nooijer et al., 2009).

# **Previous Work in the Gulf of Mexico**

Research on foraminiferal assemblages of the Gulf of Mexico has a long history, summarized in three major compendia (Culver and Buzas, 1981; Poag, 1981, 2015). Remarkably, in reviewing 77 publications recognizing 295 species, Culver & Buzas (1981) showed only one sample site just north of my study area (Parker, 1954, 28°49' N, 83°40' W), as well as four samples along an east–west transect off Tarpon Springs (Bandy, 1956; 28°08' N, 82°57'–28°09' N, 83°41'W) near the southern boundary of the watershed classified as the Springs Coast by the Southwest Florida Water Management District (see Beckwith, 2016, fig. 16).

Some coastal areas around the Gulf of Mexico, with salinities ranging from brackish to hypersaline, and coastal temperatures reaching 38˚C, have been classified by Murray (2006) as

marginal-marine environments. Three genera, *Quinqueloculina, Triloculina,* and *Elphidium,* are among the dominant genera in coastal and shelf habitats throughout the Gulf of Mexico. Murray (2006) plotted species diversities with site salinities, based upon numerous studies from the Gulf of Mexico (p. 109, fig. 4.16), which showed sites classified as normal marine to have higher diversities than brackish sites. The ternary plot of foraminiferal shell type for the Gulf of Mexico from Murray (2006, fig. 4.19) shows brackish sites to be dominated by agglutinated foraminifers, while normal marine sites have a more even distribution of species with porcelaneous and hyaline walls. Murray (2006) concluded that, in general, "brackish subtidal environments have assemblages with a mixture of agglutinated and hyaline walls."

Poag (2015) provides an extensive review and summary of benthic foraminiferal distributions showing predominant genera of facies and biofacies in the Gulf of Mexico. *Ammonia* is mapped as the dominant genus along the coastal area of the west Florida shelf, extending approximately 40 km offshore in the Springs Coast area. Past 40 km offshore in this area, miliolids are mapped as the dominant biofacies. Poag (2015) illustrates this common distribution pattern throughout the Gulf of Mexico, with stess-tolerant foraminifers such as *Ammonia* and *Elphidium* dominating coastal areas.

# **Motivation for this Research**

Earth's geological record shows numerous natural events and changes related to carbon cycling and global climate change throughout the past 300 million years (e.g., Honisch et al., 2012). Processes such as ocean acidification have been studied using paleoenvironmental indicators, including foraminifers. The assemblages and shell geochemistries of these organisms

have been used to create models to predict the influences of modern-day ocean acidification, global climate change, and the Earth's response to future changes (Whiteside & Grice, 2016).

At several intervals in Earth's history, mass extinction events have been recorded, typically characterized by a hiatus in preservation of calcium carbonate shells and skeletons (e.g., Coccioni & Luciani, 2004; Dameron et al., 2017). An interesting paleontological phenomenon has often been observed following mass extinctions; the "Lazarus phenomenon" refers to observations of fossil species that disappear from the fossil record, but reappear, often millions of years later (e.g., Flessa & Jablonski, 1983; BouDagher-Fadel & Price, 2009). Apparently, when ocean acidification events have occurred, the shells of many species disappeared from the fossil record. However, many species, especially of foraminifers, can live in environments where there is very little preservation potential (Engel et al., 2015). When the ocean waters reequilibrate so that shells can be preserved, some species reappear in the fossil record. For example, Uthicke et al. (2013) predicted that ongoing ocean acidification will result in the extinction of all foraminifers that produce calcium-carbonate shells by 2100. In contrast, Engel et al. (2015), Knorr et al. (2015) and others have suggested that many carbonate-producing foraminifers will survive in areas where temperatures and chemical properties allow them to live, even though their shells will dissolve after the death of the individual protists.

Among the foraminifers, members of the Order Miliolida are assumed to be most vulnerable to ocean acidification because they produce shells of 10–15 mol% Mg-calcite, which are more soluble than shells containing lower concentrations of Mg (Knorr et al., 2015). As a consequence, the Miliolida tend to be most abundant in normal to slightly elevated salinities (Murray, 2006) and many can thrive at salinities >40 (e.g., Amao et al., 2018). Miliolids also decline in abundance with decreasing temperatures (Waters & Hallock, 2017). Temperature and

salinity both influence carbonate saturation of the water and, therefore, the calcification and survival of miliolid foraminifers (Crevison & Hallock, 2007).

Algal symbiont-bearing miliolids, such as *Ar. angulatus*, are typically abundant in carbonate sediments of the Caribbean and western tropical Atlantic (Hallock et al., 1986; Martin, 1986; Langer & Hottinger, 2000). Within the Gulf of Mexico, Poag (2015, p. 86) reported their distribution as being "especially notable in Florida Bay, and on West Florida and Campeche shelves." *Archaias angulatus* has been characterized as a stenohaline species that prefers normal salinity, well oxygenated waters, are often associated with high-energy reefs (Martin, 1986), and can withstand winter temperatures as low as 14˚C (Hallock & Peebles, 1993).

The occurrence of *Ar. angulatus* in higher latitudes and lower salinity environments than considered typical has sparked the question: might the chemical properties of the freshwater from Florida springs provide environmental conditions that allow subtropical/tropical taxa to thrive in this region? If so, can this occurrence provide insight into how and where calcareous taxa have survived during past ocean acidification events and where they may continue to live as ocean acidification increases over the next century or more? To explore this question further, my thesis research will document the distribution of total foraminiferal assemblages as they relate to the unique environmental setting and microhabitats off Florida's Springs Coast.

## MATERIALS AND METHODS

## **Sample Collection and Laboratory Analyses**

Surface-sediment samples were collected in September 2013 along Florida's Springs Coast by Dr. Paul Carlson and other members of the seagrass-habitat team of the Florida Fish and Wildlife Conservation Commission's Research Institute. Surface-sediment samples from 41 sites throughout the Springs Coast were used for this research (Fig. 1). The northernmost sample was taken approximately 8 km north of Homosassa Springs; the southernmost sample was taken approximately 13 km north of Anclote Key. Samples were sealed in 118-ml widemouth containers and frozen. Location and environmental data, which were collected at the same time as the sediment samples, are provided in Appendix A.

Standard sieving procedures were performed for all 41 samples to determine grain-size fractions (e.g., Carnahan et al., 2009). Frozen samples were removed from the freezer to partially thaw for approximately one hour to subdivide the sample without disturbing grain distributions. Then  $1/8$ <sup>th</sup> of the sample was rinsed briefly in deionized (DI) water to remove salts and placed on a pre-weighed, consumer-grade coffee filter within a fume hood to dry overnight. Once dried, the subsample was weighed, recording the weight of the sample and filter. The dry subsample was placed in DI water in a 50-ml beaker and sonicated for five minutes using a Fisher Scientific® Ultrasonic Cleaner. Once disaggregated, the subsample was washed over a 63 μm-mesh sieve to remove mud. Again, the subsample was placed into a pre-weighed filter and dried overnight.

Once dry, the sample was weighed to determine the sand fraction. The difference between the first and second dry weight was recorded as part of the mud fraction.

Grain-size distribution for each sample was determined using a standard set of 10 cmdiameter sieves (2 mm, 1 mm, 0.5 mm, 0.25 mm, 0.125 mm, 0.063 mm) and the pan that collects the finest sediments <0.063 mm (Folk, 1980). Each sieve and pan were weighed. Each subsample was placed into the tower of sieves and set on a shaker for 10 minutes at medium setting. Each sieve was reweighed with the sediment, and the weight percent for each range of grain size was calculated, including the original mud removed prior to dry sieving.

All 41 samples also were assessed for total foraminiferal assemblages. A second  $1/8<sup>th</sup>$ portion of the sediment from each sample site was isolated, washed over a 63 μm mesh sieve with DI water, dried, and weighed. From this subsample, increments of sediment of approximately 0.2 g were weighed, examined using a stereo-zoom microscope, and all foraminiferal specimens were removed. This process was repeated until a minimum of 200 foraminiferal specimens were collected for each site. For each sample site, the foraminiferal specimens were identified to species level, then glued onto a micropaleontology slide with approximately 1–6 individuals per grid.

# **Data Analyses**

This study used the Shannon Diversity Index (H), Fisher's alpha (*a*), and inverse Simpson's [1/(1-D)] to assess the diversity of the foraminiferal assemblages (e.g., Hayek and Buzas, 1997). Buzas & Gibson's (1969) evenness measure (*eH/S*) was used to describe how evenly the species were distributed within the assemblage identified for each sample. Evenness



**Figure 1**. Sampling sites along Florida's Spring Coast. The site numbers are written above each point. Predominant terrestrial sediments are also noted.

values range from zero to one, with a value of zero representing a site containing a single taxon, and a value of one representing an evenly distributed assemblage. Shannon Diversity Index,

Fisher's alpha, Simpson's diversity, and evenness were calculated using PAST3 (Hammer et al., 2001). Qualitative data (species identification) and quantitative (total assemblage, foraminiferal-shell density per gram of sediment, absolute and relative abundance of species) analyses of the assemblages were performed.

I also assessed assemblage distributions using functional groups that included a blend of the Murray (2006) ternary approach and the Hallock et al. (2003) sensitivity/stress-tolerance approach. This resulted in five categories: taxa known to host algal endosymbionts (e.g., *Ar. angulatus*), taxa recognized as "stress tolerant" (e.g., *Ammonia*), and other members of the three groups used by Murray (2006), smaller rotaliids, miliolids and agglutinates that were not specifically known to be stress tolerant.

Test degradation (dissolution and breakage) of *Archaias angulatus* was analyzed using a light microscope for 12 sites containing ten or more *Ar. angulatus* specimens. Specimens that were alive during the time of sample collection [indicated by green coloration (Fig. 4)] were excluded in this analysis. For each site, ten specimens were randomly selected and classified according to the stage criteria of Cottey & Hallock (1988, table 1). For the four sites with abundances of 30 or more *Archaias* specimens (sites 159, 120, 140, and 180), the random selection and classification of ten individuals was repeated three times. After a dissolution and breakage stage was assigned to each specimen, the relative abundance of each stage was determined for the 12 sites.

## **Multivariate Analyses**

Multivariate analyses were performed using MATLAB\_R2017a. A square-root transformation was applied to all relative-abundance data prior to analyses to meet the assumption of normality. Cluster analyses and non-metric multidimensional scaling (nMDS) plots were constructed for foraminiferal assemblages (R-mode) and sites (Q-mode) using the Bray-Curtis similarity index. This index is widely used for multivariate analyses of assemblage data (Clarke et al. 2006). An agglomerative, hierarchal, and unweighted pair-group method with arithmetic mean (UPGMA) was used for all cluster analyses reported in this thesis.

A nMDS plot is a dimension reduction and ordination technique that constructs a configuration of sites or variables. For each plot, a stress value, ranging from 0–1, indicates the "badness of fit." A stress value from 0–0.05 is considered to be excellent, 0.05–0.1 is good, 0.1– 0.2 is considered useful, and a stress value of 0.2–0.3 indicates a poor 2-dimensional representation. Both the cluster analyses and nMDS plots were made using the Fathom Toolbox for Matlab (Jones, 2012).

Distance-based redundancy analyses (db-RDA) were performed to determine the variability of relative foraminiferal abundance that is explained by the environmental factors that included percent grain-size distribution and percent seagrass cover. The  $R<sup>2</sup>$  value represents the amount of variability explained by the environment. A p-value  $\leq 0.05$  indicates a significant multivariate relationship between the response and predictor variables. Canonical axes I and II represent the amount of variability being explained by the X and Y axes, respectively. The vector headings represent the direction of underlying gradient increase.

Multivariate analyses were performed on both species and generic level data for comparability of this research to previously published work. Additionally, functional groups

were used for some db-RDA's. Relative abundance data were used for all analyses unless otherwise noted. The primary environmental data used in this study included abiotic measurements from the bottom-water (temperature, pH, salinity, and dissolved oxygen), sediment grain-size data, and percent coverage from seagrass.

## RESULTS

### **Environmental Parameters**

The depths of sampling sites ranged from 1.10–8.05 m, excluding Site 47 for which depth was not recorded. Site 177 was both deepest and furthest from shore. The shallowest location, Site 48, was the closest site to shore. All but four sites had clear visibility throughout the entire water column. Water clarity data were not recorded for Site 47. Site 180 was the most turbid.

Bottom-water temperature, salinity, pH, and dissolved-oxygen data were collected at all 41 sites. Bottom-water temperatures ranged from 26.7˚C–30.7˚C. The highest temperatures were observed at the southernmost stations, and the lowest temperatures were observed at the northernmost stations. Bottom-water salinity ranged from  $22.5-34.6$ . Sites with salinity  $\leq 30$ were considered brackish. Sites with salinities of 30–36 were considered normal marine. The lowest salinities were observed at sites closest to shore. Bottom-water pH ranged from 8.09–8.46 for all sites. Bottom-water dissolved oxygen saturations ranged from 75–127%. Seagrass was present at all sites, ranging from 5–100% cover.

# *Grain size*

The sediment samples in this study were heavily dominated by sand across a range of grain sizes [very coarse to very fine as described by Folk (1980)]. A grain-size distribution map is provided in Figure 2 as well as a grain-size summary in Table 1. Sand accounted for an average of 83% of all sediment samples (n=41). Fine sand was the most abundant grain size

(average 38%). The average contribution of gravel  $(> 2 \text{ mm})$  was 5% of all sediment sampled, and the average for mud  $(< 0.063$  mm) was 12%. Samples with the highest percent of fine sand were dominated by quartz sand, while samples with coarser grain sizes were dominated by shell debris.

Of the 41 sites sampled, 32 had median grain  $\Phi$  sizes of three (Table 1), which is classified by Folk (1980) as fine sand. All of these sites had >34% fine sand. Site 85 had the highest percentage of fine sand (85%). Six of the sites (93, 147, 153, 67, 120, and 180) had median Φ size of two (medium sand). The most medium sand was observed at sites between near shore and offshore stations. Site 159 had a median  $\Phi$  size of one (coarse sand) and was dominated by granule gravel (31%). Site 135 had a median Φ size of four (very fine sand). Site 95 had a median grain Φ size of less than four (mud), as made up 50% of the sampled sediment. Very fine sand and silt were more common at sites near shore.

## **Benthic Foraminiferal Distribution**

In 41 surface samples analyzed, 152 species of foraminifers were identified. These species belong to 5 orders, 36 families, and 62 genera. Of these species, 71 are calcareousporcelaneous, including seven species of symbiont-bearing miliolids. Another 67 of the species are calcareous-hyaline, and 14 are agglutinated. The most abundant species across all samples was *Quinqueloculina seminula* (8.5% overall abundance). *Haynesina germanica* dominated at 14 sites, ranging from 9–23%. *Quinqueloculina seminula* dominated six sites (9–24%). *Archaias angulatus* dominated five sites (10–47%): abundance was directly related to grain size (Fig. 3). *Ammonia tepida* dominated four sites (8–30%). *Triloculina bermudezi* dominated three sites, with 11–17% abundance at those sites. *Quinqueloculina impressa* dominated two sites (9% and

13%) as did *Q. laevigata* (6% and 11%). *Ammonia parkinsoniana, Cibicides kullenbergi, Elphidium discoidale, Flintinoides labiosa,* and *Pseudotriloculina linneiana* each dominated one site (18%, 19%, 9%, 15%, and 20% respectively).

The 13 most abundant species (each making up  $\geq$ 2% total relative abundance) across the entire study area are (in descending order) *Q. seminula, H. germanica, Ar. angulatus, T. bermudezi, Q. laevigata, Q. poeyana, Q. bosciana, E. discoidale, Am. tepida, F. labiosa, Q. impressa, Am. parkinsoniana,* and *H. depressula* (Figs. 4, 5)*.* These 13 species made up 56% of the total 9004 specimens counted.

# *Functional groups*

Smaller miliolids were the dominant functional group, making up an average of 58% of total biota. Collectively the samples consisted of an average of 6% algal symbiont-bearing taxa, 28% stress-tolerant taxa, 8% smaller rotaliids, and <1% agglutinated taxa. The most common symbiont-bearing taxon was *Ar.angulatus* (5% overall abundance). *Haynesina germanica* was the most common stress-tolerant taxon (8% overall abundance). *Cibicides kullenbergi* was the most common smaller rotaliid taxon (2% overall abundance). *Quinqueloculina seminula* was the most common species of the smaller miliolids (9% relative abundance). The relative abundance of small miliolids was inversely related to salinity (Fig. 6). The brackish sites (inshore) were heavily dominated by smaller miliolids, while the normal marine sites had a more even distribution of stress-tolerant and smaller-miliolid taxa (Fig. 7).



Figure 2. Sediment grain-size distribution for all sites (n=41); the primary terrestrial sediment types along the Springs Coast of Florida are also shown.

|             | <b>Sample</b> |                         |         |              |           |                |             | >0.063         | < 0.063 |
|-------------|---------------|-------------------------|---------|--------------|-----------|----------------|-------------|----------------|---------|
| <b>Site</b> | wt $(g)$      | <b>Median</b>           | $>2$ mm | $>1$ mm      | $>0.5$ mm | $>0.25$ mm     | $>0.125$ mm | mm             | mm      |
|             |               | $\Phi$                  | $-1$    | $\mathbf{0}$ | 1         | $\overline{2}$ | 3           | $\overline{4}$ | >4      |
| 34          | 7.41          | 3                       | 7%      | 9%           | 9%        | 6%             | 34%         | 18%            | 17%     |
| 40          | 9.11          | $\overline{\mathbf{3}}$ | 5%      | 7%           | 5%        | 5%             | 50%         | 16%            | 11%     |
| 46          | 7.35          | $\overline{\mathbf{3}}$ | 4%      | $2\%$        | 2%        | 4%             | 40%         | 24%            | 24%     |
| 52          | 10.59         | $\overline{\mathbf{3}}$ | $0\%$   | 0%           | 0%        | $1\%$          | 74%         | 21%            | 4%      |
| 59          | 8.06          | 3                       | 4%      | 2%           | 3%        | 5%             | 52%         | 25%            | $8\%$   |
| 88          | 13.72         | $\overline{3}$          | 7%      | 12%          | 12%       | $9\%$          | 37%         | 20%            | 4%      |
| 94          | 4.47          | $\overline{\mathbf{3}}$ | 3%      | $7\%$        | 20%       | 20%            | 39%         | $6\%$          | $5\%$   |
| 100         | 6.45          | $\overline{3}$          | 3%      | 5%           | 14%       | 22%            | 32%         | 11%            | 12%     |
| 106         | 7.28          | 3                       | 4%      | 6%           | 12%       | 16%            | 31%         | 20%            | 12%     |
| 81          | 6.88          | 3                       | $5\%$   | 14%          | 16%       | 11%            | 35%         | 11%            | $8\%$   |
| 93          | 4.12          | $\overline{2}$          | 5%      | $8\%$        | 19%       | 19%            | 21%         | 12%            | 16%     |
| 135         | 9.75          | $\overline{4}$          | 3%      | 4%           | 4%        | 5%             | 25%         | 45%            | 13%     |
| 141         | 4.38          | $\overline{\mathbf{3}}$ | 11%     | 3%           | 6%        | 16%            | 24%         | 16%            | 24%     |
| 147         | 3.26          | $\overline{c}$          | 4%      | 7%           | 26%       | 28%            | 16%         | 7%             | 13%     |
| 159         | 3.76          | $\mathbf{1}$            | 31%     | 12%          | 22%       | 15%            | 7%          | 3%             | $9\%$   |
| 165         | 7.40          | 3                       | 6%      | $3\%$        | 6%        | 13%            | 43%         | 18%            | 10%     |
| 177         | 19.44         | $\overline{\mathbf{3}}$ | $1\%$   | 2%           | 5%        | 7%             | 52%         | 27%            | $7\%$   |
| 140         | 4.42          | $\overline{\mathbf{3}}$ | 2%      | 5%           | 16%       | 18%            | 32%         | 15%            | 11%     |
| 153         | 5.72          | $\overline{2}$          | $3\%$   | $8\%$        | 20%       | 21%            | 21%         | 15%            | 11%     |
| 166         | 6.77          | 3                       | $1\%$   | 2%           | $5\%$     | 13%            | 33%         | 24%            | 21%     |
| 178         | 11.23         | 3                       | $3\%$   | $3\%$        | $8\%$     | 17%            | 42%         | 19%            | $7\%$   |
| 61          | 6.19          | 3                       | 6%      | 16%          | 10%       | 7%             | 38%         | 17%            | $6\%$   |
| 67          | 9.80          | $\overline{c}$          | 4%      | 11%          | 19%       | 19%            | 35%         | 7%             | 5%      |
| 73          | 13.34         | $\overline{3}$          | 5%      | 4%           | 7%        | 10%            | 48%         | 17%            | 10%     |
| 85          | 14.82         | 3                       | $0\%$   | $0\%$        | $0\%$     | $1\%$          | 86%         | 9%             | $3\%$   |
| 114         | 5.45          | $\overline{\mathbf{3}}$ | $11\%$  | 11%          | 11%       | 7%             | 36%         | 13%            | 11%     |
| 120         | 7.68          | $\overline{2}$          | 3%      | $9\%$        | 28%       | 24%            | 23%         | 6%             | $7\%$   |
| 128         | 3.87          | $\overline{\mathbf{3}}$ | $1\%$   | $7\%$        | 15%       | 14%            | 27%         | 11%            | 25%     |
| 132         | 6.91          | $\overline{3}$          | $1\%$   | 3%           | 9%        | 16%            | 26%         | 21%            | 24%     |
| 95          | 11.79         | >4                      | $0\%$   | $0\%$        | $1\%$     | 2%             | 32%         | 13%            | 50%     |
| 113         | 7.47          | $\overline{\mathbf{3}}$ | 4%      | 5%           | $8\%$     | 14%            | 41%         | 15%            | 13%     |
| 41          | 16.03         | $\mathfrak{Z}$          | 7%      | 13%          | 10%       | 7%             | 44%         | 15%            | 3%      |
| 47          | 16.50         | 3                       | 7%      | 13%          | 10%       | 7%             | 43%         | 14%            | 6%      |
| 48          | 19.46         | $\overline{\mathbf{3}}$ | $0\%$   | $1\%$        | $2\%$     | 4%             | 66%         | 23%            | 4%      |
| 54          | 7.45          | 3                       | 12%     | 16%          | 9%        | 5%             | 39%         | 13%            | 6%      |
| 66          | 6.37          | 3                       | 3%      | 4%           | $5\%$     | $7\%$          | 42%         | 27%            | 11%     |
| 72          | 12.25         | 3                       | $0\%$   | $1\%$        | $2\%$     | $4\%$          | 68%         | 21%            | $4\%$   |
| 174         | 3.38          | 3                       | 10%     | 4%           | 6%        | 12%            | 27%         | 17%            | 23%     |
| 180         | 8.78          | $\overline{c}$          | 6%      | $9\%$        | 29%       | 26%            | 16%         | 7%             | 7%      |
| 204         | 4.38          | 3                       | $1\%$   | 3%           | 3%        | 4%             | 49%         | 30%            | 10%     |
| 205         | 10.76         | $\mathfrak{Z}$          | $2\%$   | 3%           | 9%        | 18%            | 40%         | 21%            | $5\%$   |

**Table 1**. Grain-size summary and median Φ for all sites (n=41).



**Figure 3**. Raw abundance of *Archaias angulatus* plotted against the percent of medium/coarse grain-size sediments at each site (n=41). Sediment with a  $\Phi$  of -1–2 are considered medium/coarse.  $R^2 = 0.42$ ; p < 0.0001



**Figure 4.** Images of *Archaias angulatus*, the third most abundant foraminifer in the Springs Coast. The green coloration of the specimen on the left is due to preserved color of the chlorophyll symbionts within the test, indicating that the specimen was alive when collected. Scale  $bar = 500 \mu m$ .



**Figure 5.** Electron micrographs of the species from Florida's Springs Coast with a total relative abundance of ≥ 2% in descending order, excluding *Archaias angluatus*. **1** *Quinqueloculina seminula,* lateral view; **2** *Haynesina germanica,* lateral view; **3** *Triloculina bermudezi*, lateral view, 3b view opposite of 3a; **4** *Quinqueloculina laevigata*, lateral view, 4b view opposite of 4a; **5** *Quinqueloculina poeyana*, lateral view, 5b view opposite 5a; **6** *Quinqueloculina bosciana*, lateral view; **7** *Elphidium discoidale*, lateral view; **8** *Ammonia tepida*, spiral view, 8b umbilical view; **9** *Flintinoides labiosa,* lateral view, 9b view opposite 9a with aperture visible; **10** *Quinqueloculina impressa,* lateral view, 10b view opposite 10a; **11** *Ammonia parkinsoniana,* spiral view, 11b umbilical view; **12** *Haynesina depressula,* lateral view. Scale bars = 100 μm.



**Figure 6.** Raw abundance of small miliolids plotted against salinity for all sites (n=41). Note that each axis starts at 20, and  $\sim$ 200 specimens were counted in each sample.  $R^2$  = 0.32; p = 0.0001

# *Species richness and diversity*

A minimum of 200 individuals were picked for all samples (n=41). In two cases (sites 40 and 205), only 199 individuals were identified because some specimens were too degraded to identify to species.

Species richness (S) varied from 30–58 species per site (Table 2). Site 54 had the lowest species richness. Site 205 had the highest at 58, followed by Site 204 with 57; these two sites are the northernmost sites and furthest offshore. The average species richness across all sites was 41 [standard deviation  $(sd) = 7.5$ ].

The density of foraminiferal tests per gram of sediment across all sites varied over more than an order of magnitude, from 110–1455 specimens/g (Table 2). Sites 174 and 88 had the highest density of tests (1455 and 1315specimens/g respectively). Site 85 had the lowest density (110 specimens/g) and Site 52 had the second lowest with 125 specimens/g; sediment at both sites was primarily fine quartz sand.

At Site 205, the northernmost offshore station, the highest Shannon's diversity index (H = 3.78) and the highest Fisher's alpha (*a =* 27.5) were recorded. Site 159 had the lowest H value (2.52) and site 48 had the lowest *a* value (8.3). Across all sites, the average H = 3.15, and  $a =$ 15.5. Evenness values varied from 0.29–0.76. The site with the highest H also had the highest evenness (Site 205) and the site with the lowest H had the lowest evenness (Site 159). The dominance of *Ar. angulatus,* which made up 47% of the specimen counted at Site 159, resulted in the low evenness value. Site 72 had the second lowest evenness value (0.42) as *Am. tepida* made up 30% of the specimens at this station. Overall, normal marine salinity sites had higher diversities than brackish sites (Fig. 8).

# *Foraminiferal shell type*

The total foraminiferal specimens counted at all sites combined was 9004. Of that total count, porcelaneous specimens made up 74% and hyaline specimens made up 26%; with agglutinated specimens making up <1%. Both porcelaneous and hyaline taxa were present at all sites. Agglutinated taxa were present at 21 of the 41 sites. Site 66 had the most agglutinated specimens (10), which made up 5% of the sample, followed by Site 106, which had 9 agglutinated specimens making up 4% of the sample. Site 41 had the greatest number of porcelaneous foraminifers (273), which made up 96% of the sample. All of the nearshore sites except Site 135 were dominated by porcelaneous taxa. Sites 135 and 166 had the most hyaline specimens present, at 71% and 68% respectively.



Figure 7. Functional group distribution for all sites (n=41) and the primary terrestrial sediment types along the Springs Coast of Florida.

A clear delineation can be seen between normal marine salinity sites and brackish sites (Fig. 9). Brackish sites were dominated by porcelaneous taxa while normal marine sites had a more even distributions of porcelaneous and hyaline taxa. Site 135 is an outlier, as it was dominated by hyaline species *Haynesina germanica* (19% relative abundance), *Elphidium* spp. and *Cribroelphidium* spp.



**Figure 8.** Shannon diversity index (H) and Fisher's alpha (*a*) plotted for all sites (n=41, p < 0.0001)



Figure 9. Ternary plot of foraminiferal shell type for all sites (n=41).



**Table 2**. Number of individuals, number of taxa, density per 1 g of sediment, and diversity indices for total foraminiferal assemblages at all sites (n=41) along Florida's Springs Coast.

*Note*: Asterisks represent sites with brackish salinity.

## **Test Surface Degradation of** *Archaias angulatus*

*Archaias angulatus* tests are white with a smooth appearance. The surface of the test is covered with shallow pseudopores. Internally, the tests are divided into rectangular chamberlets and, as the lateral chamber wall is removed, the chamberlets become visible (Cottey & Hallock, 1988). This is a common feature seen with both test dissolution and breakage (Fig. 10).

A total of 200 *Archaias* tests were analyzed for test dissolution and breakage (Fig. 11). Four sites (159, 120, 140, and 180) had relatively abundant *Archaias* (>30 individuals), for which 30 specimens per site were analyzed. For each of the remaining eight sites, 10 individuals were analyzed. Across all sites (Fig. 12), 70 individuals (35%) exhibited minimal dissolution (Stage 1), 50 (25%) were in Stage 2, 16 (8%) in Stage 3, 14 (7%) in Stage 4, and 50 (25%) in Stage 5. The highest percentage of tests in Stage 1 dissolution (70%) was found at Site 81, while sites 153 and 177 had the lowest (10%). Sites 177 and 67 had the highest percentages of tests with Stage 5 dissolution (both 50%). Across all sites, tests in dissolution stages 3 and 4 accounted for 7% each of the total.

Test breakage of *Archaias* was determined by the extent of the outer test edge that was broken (Cottey & Hallock, 1988). Across all sites (Fig.13), 64 tests (32%) were near pristine (Stage 1), and 60 tests (30%) were in Stage 2. The fewest broken tests were found at Site 81, with 60% Stage 1 tests. Stage 5 breakage was found in 15% of the specimens assessed. Similar to the dissolution stages analyzed, tests at breakage stages 3 and 4 were the least common, making up 12% and 11%, respectively.

No relationship was found between *Archaias* test dissolution or breakage and grain sizes. A negative relationship between *Archaias* tests at Stage 5 of dissolution and pH was noted (Appendix C). Sites with a lower pH had higher percentages of Stage 5 dissolved tests.
#### **Multivariate Analyses**

#### *Species level analyses*

The 13 foraminiferal species each with total abundances  $\geq$ 2% for all sites were separated into three natural groups and three individual species using a SIMPROF cluster analysis (Fig. 14). In the dissimilarity profile analysis, a pi value of 5.93 was calculated. The pi value was analyzed for significance using a p-value of 0.001, implying that there is multivariate structure within this data set. *Ammonia tepida* and *Am. Parkinsoniana* formed one group, as they are similar stress-tolerant taxa. *Archaias angulatus*, *H. depressula*, a stress-tolerant species, and *Q. impressa* each exhibited distributions distinct from other species. *Triloculina bermudezi* and *Flintinoides labiosa* formed a group. Both species are small miliolids and *F. labiosa* was previously named *Triloculina labiosa* (d'Orbigny, 1839). The remaining species grouped together, with the other *Quinqueloculina* spp. Clustering strongly at <25% dissimilarities in their distributions. The stress-tolerant species, *H. germanica* and *E. discoidale,* more loosely clustered with the *Quinqueloculina* spp.

Based on the cluster analysis (Fig. 14), a nMDS was performed (Fig. 15). The stress value of this nMDS was 0.078, indicating a good 2-dimensional representation of the data. *Archaias angulatus*, which was the only large, symbiont-bearing species that occurred in sufficient abundance to include in the analyses, plotted well away from the other taxa. The two *Ammonia* species formed their own cluster. Interestingly, *Elphidium discoidale* grouped with the smaller miliolids.



**Figure 10.** *Archaias angulatus* tests from Site 159 illustrating the five stages of test dissolution and breakage described by Cottey & Hallock (1988). Images taken with Dino-Lite Digital Microscope. Scale bar = 500 μm.



**Figure 11**. Results of taphonomic analysis of *Archaias angulatus* test from 12 sites. The colored legend depicts the five stages of dissolution and breakage. Stage criteria are illustrated in Figure 13.

The db-RDA plot (Fig. 16) has a p-value of 0.001, indicating a significant effect of the environmental parameters on the abundance and composition of the foraminiferal assemblages. An  $\mathbb{R}^2$  value of 0.32 indicated that 32% of the variability is explained by these environmental parameters. *Ammonia tepida* and *Am. Parkinsoniana* show a positive relationship with temperature. *Archaias angulatus* negatively correlates with temperature and seagrass coverage.

#### *Genus-level analyses*

As previously stated, all foraminiferal multivariate analyses were also performed at genus level. A SIMPROF analysis of the relative abundance data indicated three natural groups, with most of the genera plotting independently of others (Fig. 17). A pi value of 4.92 was calculated, indicating significant multivariate structure (p= 0.001). *Quinqueloculina* taxa were most



**Figure 12.** Distribution map of *Archaias angulatus* tests in dissolution stages 1–5 described by Cottey & Hallock (1988). The site numbers are above each pie chart. Arrows denote the four sites from which 30 tests were analyzed.



**Figure 13.** Distribution map of *Archaias angulatus* tests in breakage stages 1–5 described by Cottey & Hallock (1988). The site numbers are above each pie chart. Arrows denote the four sites from which 30 tests were analyzed.

Dissimilar to other taxa, as the most abundant genus within the Springs Coast, making up 39% of the total identified. Five other genera, including *Cibicides, Pseudotriloculina, Ammonia, Archaias,* and *Cribroelphidium*, also did not group with other genera. Similar to the species level SIMPROF (Fig. 14), *Haynesina* and *Elphidium* clustered closely, with *Triloculina* associated with <25% dissimilarity.

A nMDS analysis was performed based on the genus level SIMPROF (Appendix B). With a stress level of 0.153, plot is considered a useful 2-dimensional representation of the data. However, the only distinct grouping from this analysis was *Elphidium* and *Haynesina*.

The output of the distance-based redundancy analysis (db-RDA) provided an F-statistic of 4.69 with a p-value of 0.001 (Fig. 18), therefore there is a significant effect of environmental characteristics on the abundance and composition of foraminiferal genera present. An  $\mathbb{R}^2$  value of 0.40 indicates that 40% of the variability is explained by the environmental data. Canonical axes I and II account for about 35% of the total variation. The sites with *Archaias, Cibicides, Bolivina, Rosalina,* and *Haynesina* taxa showed an inverse relationship with temperature and seagrass coverage. *Ammonia* and *Elphidium* taxa were associated with sites having higher seagrass coverage. The pH levels appeared to influence distributions of *Flinitinoides, Quinqueloculina,* and *Triloculina* taxa. *Flinitinoides* and *Triloculina* have an inverse relationship with salinity and a positive relationship with dissolved oxygen. Variation among the sites is primarily driven by salinity, temperature, and pH. A notable inverse relationship is seen between salinity and pH.

The db-RDA of genus-level abundance data and sediment grain-size distribution produced an F-statistic of 4.03, with a p-value of 0.001, revealing a significant effect of sediment texture on the abundance and composition of foraminiferal assemblages (Fig. 19). An  $\mathbb{R}^2$  value of

0.46 indicated that nearly half of the variability is explained by the grain-size distribution. *Ammonia* spp. Are characterized by sites with a high percentage of very fine sands (0.063 mm < X ≤ 0.125 mm). Sites dominated by *Archaias* are characterized by medium to coarse sand-sized grains  $> 0.25$  mm.

#### *Analyses of sites*

To determine which sites exhibited the most similar foraminiferal assemblages, a SIMPROF cluster analysis was performed using the species-level relative abundance data (Fig. 20). In this analysis, 12 natural groups were identified. The pi value was 21.7, giving a p-value of 0.001. For this cluster analysis, a dissimilarity cutoff was set at 0.475 illustrated by the red dashed line, indicating five major groups (A, B, C, D, and E). The results for all 41 sites are graphically represented in an nMDS plot (Fig. 21) with a stress value of 0.19. The groups are represented by different colored text. All but one of the brackish sites (Site 135) clustered into group D.



**Figure 14.** Cluster analysis (R mode) of the species making up  $\geq 2\%$  of total specimens identified.

Group A consisted of one sample, Site 159, which had the highest relative abundance of *Ar. angulatus* (47%). Group B also consisted of one sample, Site 205, which had the highest diversity. Group C consisted of five samples predominately from the southwestern region of the Springs Coast. This group was characterized by having a relatively even distribution of small miliolids and stress-tolerant taxa. Group D consisted of 19 sites, including all but one of the brackish sites (Site 135). This group was characterized by low salinity and a high relative abundance of small miliolids (73%). Group E consisted of 15 sites with normal marine salinity. This group had relatively even distributions of small miliolids and stress-tolerant taxa, and the greatest abundance of agglutinated taxa.

The db-RDA in Figure 20 has a p-value of 0.001, indicating a significant effect of the environmental parameters on the foraminiferal functional group abundance and composition. The environmental data explains 33% of the variability.



**Figure 15**. nMDS plot (R mode) of species making up ≥2% of all specimens identified. The colors represent the functional group of each species: green = Symbiont bearing; red = Stress tolerant; blue = Smaller miliolids.



Figure 16. db-RDA of the species making up ≥2% total relative abundance and environmental parameters (temperature, pH, salinity, dissolved oxygen, and percent seagrass coverage).



**Figure 17.** Cluster analysis (R mode) of the genera making up  $\geq$ 2% of total relative abundance.



**Figure 18**. db-RDA analysis of all Springs Coast sites using the abundance data of genera with a total abundance ≥2%. The environmental parameters used are temperature, pH, salinity, dissolved oxygen, and percent seagrass cover.



**Figure 19.** The db-RDA analysis of all Springs Coast sites comparing the abundance of genera with a total abundance ≥2% with grain-size data.



**Figure 20**. SIMPROF Cluster analysis (Q mode) of all sites. An asterisk next to the site name represents a brackish site. Those without asterisks have normal marine salinity. The red dashed line represents the dissimilarity cutoff.

**Table 3**. Statistics (median and range) for each group of sites (defined in Fig. 21): abundance (specimens per g), measures of diversity (Species richness, Fisher index, Shannon Index, and Evenness), grain-size data, and seagrass coverage data.



*Note*: For median Φ calculations 5 was substituted for > 4 to calculate overall median.



**Figure 21**. An nMDS plot of sites (Q-mode) created using all relative abundance data. The colors represent groups created by a SIMPROF cluster analysis (Fig. 20). The groups are represented by different colored text. Group A is illustrated by green text, Group B is in red text, Group C is in blue text, Group D is in black text, and Group E is in purple text All sites with an asterisk are brackish (salinity <30) and sites without an asterisk are normal marine (salinity 30– 36).



**Figure 22**. The db-RDA of the Springs Coast foraminiferal functional group data and environmental data (temperature, salinity, pH, dissolved oxygen, percent seagrass coverage).

#### DISCUSSION

The Seagrass Integrated Mapping and Monitoring Program (SIMM) of Florida Fish and Wildlife Conservation Commission's Research Institute was developed to protect and manage seagrasses in Florida. The Big Bend and Springs Coast region monitored by SIMM makes up 25% of the seagrass acreage in Florida state waters (Yarbro & Carlson, 2016). Seagrass beds are an extremely valuable natural resource and marine habitat. Seagrasses provide numerous important ecological services, such as nutrient cycling, carbon sequestration, stabilizing sediments, and maintaining coastal diversity (Orth et al., 2006; Yarbro & Carlson, 2016). In recent years seagrass coverage has been in decline. Yarbro & Carlson stated that light limitation was the primary cause of seagrass decline in many locations in Florida during the  $20<sup>th</sup>$  century.

During a seagrass mapping and monitoring survey (Jones et al., 2016), Dr. Paul Carlson observed an abundance of live *Archaias angulatus* on seagrass blades, which prompted collection of the sediment samples used in this study. The Springs Coast has a stable trend in seagrass coverage, making up 379,100 acres (153,416 hectares) as of 2007 (Yarbro & Carlson, 2016). Seagrass coverage is an important variable in consideration of shell-producing organisms as it may buffer changes in ocean chemistry and ecological impacts of ocean acidification (Garrard et al., 2014). In a study by Garrarg et al. (2014) seagrass density increased in response to a lower pH, as did the number of shell-forming organisms. This finding provides evidence to suggest that highly productive, nearshore habitats, similar to that of the Springs Coast, may provide refuge to its associated calcifying organisms from ocean acidification.

#### **Benthic Foraminiferal Distribution**

The original motivation for this study, focused on the distributions of benthic foraminiferal tests in sediments of the Spring Coast area of the inner West Florida Shelf, was observations by seagrass researchers of live, large *Archaias angulatus* attached to seagrass blades (Fig. 23). This species hosts chlorophyte endosymbionts and is a dominant foraminiferal taxon in carbonate-rich environments in subtropical and tropical waters of the western Atlantic and Caribbean. The thesis research by Beckwith (2016, published in part in Beckwith et al., 2019) explored some of the physical and chemical characteristics of the coastal waters and the freshwaters that are discharged into the coastal waters, including seasonal temperatures and salinities, as well as  $Ca^{2+}$  concentrations ( $[Ca^{2+}]$ ) and alkalinities. Beckwith hypothesized that the elevated  $[Ca^{2+}]$  and alkalinities in the freshwaters might allow this species, which produces a porcelaneous, hi-Mg-calcite test (Toler & Hallock, 2001), to thrive in cooler, lower salinity environments than what was previously reported for this species (e.g., Hallock et al., 1986; Martin et al., 1986; Murray, 2006 and references therein). Beckwith (2016) further hypothesized that waters with elevated  $\lceil Ca^{2+} \rceil$  and alkalinities might provide refuges for calcareous organisms during times of ocean acidification. My study was motivated by the Beckwith findings, and while *Ar. angulatus* distributions were important, my work focused on the total assemblage of foraminiferal taxa in this area, to determine if other taxa might also reflect the unusual water chemistry.

Indeed, the distributions of the tests of benthic foraminiferal taxa in the Springs Coast samples are surprising in the context of previously published work on coastal foraminiferal assemblages around the Gulf of Mexico, which has been summarized in detail by Murray (2006)



**Figure 23.** *Archaias angulatus* attached to a seagrass blade. Photo provided by Dr. Paul Carlson.

and Poag (2015). In my samples, the nearshore, brackish sites are dominated by smaller miliolids rather than stress-tolerant foraminifers, specifically *Ammonia,* as depicted by Poag (2015). Previously published data indicate that miliolids tend to prefer normal to elevated salinities (Murray, 2006), while stress-tolerant species like *Ammonia* are eurytopic. The spring-fed freshwater entering the coastal waters are high alkalinity and highly saturated with respect to calcium carbonate (Beckwith et al., 2019), which may account for this atypical distribution. Miliolids are more vulnerable to lower alkalinity than rotaliids due to differences in their calcification mechanisms (Bentov & Erez, 2006; de Nooijer et al., 2009). The hi-Mg-calcite tests produced by miliolids are more susceptible to dissolution when calcite saturation declines, which it typically does under lower temperature and reduced salinity. However, the high alkalinity and saturation state in the Springs Coast waters reported by Beckwith (2016) may be the dominant abiotic factor controlling miliolid distributions, rather than salinity and temperature. Evidence in support of this interpretation includes the positive correlation of smaller miliolids with increasing pH and dissolved oxygen, and negative correlation with salinity (Fig. 22). While I did not have alkalinity data from my sample sites, only pH and salinity, the significant correlation between

higher pH and abundance of smaller miliolids supports the hypothesis that increased alkalinity is a major factor regarding the foraminiferal distribution in the Springs Coast, including the prominent occurrence of *Ar. angulatus*.

Two additional parameters that apparently influence the distributions of foraminiferal tests in the Springs Coast sediments are seagrass cover and sediment texture, which themselves negatively co-vary. Seagrasses and associated macroalgae and filamentous algae are important habitat for benthic foraminifers. This relationship is demonstrated by the positive relationships of foraminiferal-test abundance and diversity with seagrass cover (Appendix Fig. B3). Seagrass and algal cover also baffle water motion, allowing finer sediments, including small foraminiferal tests, to accumulate. The opposite effect was seen in the abundance of *Ar. angulatus* at Site 159, which was characterized by very coarse sediment (> 2 mm). Most of the *Archaias* specimens found at this site were dead at the time of collection, as indicated by lack of residual green color from their chlorophyte symbionts. This observation was not surprising for two reasons. First, the larger *Archaias* tests will be concentrated where finer sediments have been winnowed out. At the same time, seagrass and associated algae provide optimum habitat for *Archaias* (e.g., Fujita & Hallock, 1999). Thus, the abundance of *Archaias* tests in individual samples increases with sediment sorting that can occur where there is limited seagrass cover.

The majority of the sites clustered into either a nearshore group (D in Fig. 21) or an offshore group (E). Group D included 19 sites with relatively low salinities, including 13 brackish sites. These sites were dominated by small miliolids, with *Quinqueloculina* as the most abundant genus, followed by *Triloculina*. These sites were also characterized by fine sediments and had the highest foraminiferal densities, but not the highest diversities (Table 3).

As a whole, the Group E sites had relatively high diversity indices, relatively similar percentages of smaller miliolids and rotaliids, high percent seagrass coverage, and were mud-rich (Table 3). This group included 15 sites, all of which had normal marine salinities except Site 135, closest to the mouth of the Homosassa River, which had a salinity of 22.5. Unlike the other brackish sites in the Springs Coast, this site was dominated by stress-tolerant species *Haynesina germanica* and *Elphidium discoidale*. Armynot du Châtelet et al. (2004) suggested that *H. germanica* may be a bio-indicator of pollutants. An influx in such contaminants via the Homosassa River could be an explanatory factor for this foraminiferal assemblage. More likely, *H. germanica* is inversely correlated with dissolved oxygen concentrations, and Site 135 had one of the lowest oxygen concentrations of the sites included in this study.

The SIMPROF cluster analyses identified two additional small groups. Group B was represented only at Site 205, which was characterized by high diversity, despite having the lowest density of foraminifers (Table 3). Of the 58 different species found at Site 205, 44 of them had a raw abundance of less than 5, and 17 species occurred only once. Group C consisted of five samples predominately from the southwestern region of the Springs Coast. This group was characterized by having a relatively even distribution of small miliolids and stress-tolerant taxa. The dominant genera were *Quinqueloculina* and *Ammonia.* This group had intermediate species richness, diversity indices, and percent mud composition (Table 3).

Foraminiferal assemblages within the Springs Coast of Florida have not previously been well documented. In a study by Parker (1954), the distribution of foraminifers in the northeastern Gulf of Mexico included one transect extending offshore from Cedar Key (Parker, 1954, fig. 1). Sites along her transect had a salinity of 36, indicating there was not a strong influence from the freshwater input of the springs. Her site closest to shore (depth  $= 12$  m) was dominated by

foraminifers of the family Miliolidae (42%). All of my sample sites were well inshore of the 12 m isobath; the deepest site (177) was 8.05 m and was where the highest salinity was recorded (34.6). Although the most inshore sites in my study were dominated by miliolids, the salinity differences between the sample areas do not allow for a conclusive comparison. The second most abundant family of foraminifers found by Parker (1954) was Peneroplidae (16%). In contrast, I recorded four peneroplid species, none of which exceeded 2% of the assemblage. The family Peneroplidae includes algal symbiont-bearing foraminifers, but does not include *Ar. angulatus*. Foraminifers belonging to these two families had relatively high abundances extending offshore to sites with a depth of approximately 60 m. Parker (1954) also noted an abundance of *Ammonia beccarii* at the inner end of the transect, similar to the findings of Poag (1981) and the dominance of stress-tolerant rotaliids in the more offshore sites sampled for my study. Poag (1981) documented *Ammonia* as the dominant biofacies extending 30 km off shore, and then a transition to miliolids for about 20 km. In the southern half of the Springs Coast area, Poag (1981) illustrates *Archaias* as a dominant biofacies approximately 20 km offshore.

Bandy (1956) also documented foraminifers in the northeastern Gulf of Mexico, including a transect south of the Springs Coast, extending offshore from Tarpon springs (Bandy, 1956, fig. 25). In contrast to the findings of my study, Bandy (1956) documented hyaline species dominating brackish bay areas, with *Ammonia* [previously named *Streblus* (Fischer de Waldheim, 1817)] being most abundant at the mouth of rivers. In the Springs Coast, high abundances of *Ammonia* were found in the more offshore sites while *Haynesina* was the dominant inshore stress-tolerant genus. *Archaias angulatus* was found abundantly off Tarpon Springs in a depth range of 5–32 m and Bandy (1954) noted that where *Archaias* was present, *Ammonia* was found in very low abundances or was absent. I also observed this inverse

relationship; *Ammonia* specimens were absent in the three sites with the highest abundance of *Archaias* (Sites 159, 180, and 120), and Figures 17 and 18 show *Ammonia* and *Archaias* plotting opposite of each other.

#### *Species richness and diversity*

Murray (2006, p. 109, fig. 4.16) plotted the Shannon diversity index (H) and Fisher's alpha (*a*) index for the Gulf of Mexico for sites with brackish, normal-marine, and hypersaline salinities. The highest diversities were found in normal-marine environments, with a maximum H value of 3.0 and Fisher's alpha of about 14.0. The maximum H value documented for a brackish site was 1.5. Consistent with Murray's synthesis, the Springs Coast sites with near normal marine salinity had the highest diversity. However, the H values and *a* values in the Springs Coast are higher than what was documented by Murray for both the normal marine salinity and brackish sites. The H values of brackish sites in the Spring Coast had a maximum of 3.45 (Site 94) and a minimum of 2.79 (Site 61). Murray stated that "regardless of salinity all marshes and mangals have low diversity" and that "estuaries and lagoons also have low diversity." Salinity is having an effect on foraminiferal diversity in the Spring Coast, as seen in Figure 8, but this marsh/estuarine environment does not have a low diversity of foraminifers.

The unusually high diversity in the Springs Coast, coupled with sites having low species repetition, suggests an influence of foraminiferal propagule dispersion. Alve & Goldstein (2002, 2003) have suggested that passive transport of propagules may be an efficient means of dispersal in many shallow-water species. Some species of shallow subtidal foraminifers can be passively transported to environments with favorable conditions and grow after surviving in a cryptic state

for months (Alves & Goldstein, 2009). The smallest and lightest propagules have the highest potential for passive dispersion.

Alve & Goldstein (2009) documented small rotaliid and agglutinated genera that are dispersed through propagule transportation, three of which were found in low abundances among the Springs Coast sites. These genera include *Textularia, Bolivina,* and *Planorbulina.* More abundant genera found in the Springs Coast, such as *Haynesina* and *Ammonia,* have also been documented utilizing propagule dispersion (Alve & Goldstein, 2002, 2003; Weinmann & Goldstein, 2017). Weinmann & Goldstein (2017) experimentally demonstrated that propagules of foraminiferal species with normal-marine salinity requirements are transported by tidal currents deep into marsh habitats where their recruitment is prevented by low-salinity conditions. They proposed that, with rising sea level, the propagules of species from normal salinity environments will be able to recruit as salinities rise within the flooding marsh habitats.

Weinmann & Goldstein (2017) also concluded that propagule dispersal is a major mode of transport in shallow-water environments. Based on their documentation of propagule dispersal, combined with the high diversity of rare taxa found in my samples, I suspect that propagule dispersal is influencing the foraminiferal assemblages within the Springs Coast. This environmental setting, with its range of salinities and relatively strong seasonality in temperature, rainfall and wind direction, may allow the recruitment of propagules from around the Gulf of Mexico, but not provide sufficient persistence of suitable environmental conditions to allow many of the species to establish viable populations. To further assess this hypothesis, the <32 µm-sized fraction of sediments from the Springs Coast should be tested for foraminiferal recruitment using the "propagule methods" proposed by Alve & Goldstein (2009).

#### **Test Surface Degradation of** *Archaias angulatus*

*Archaias angulatus* is often found in abundantly in warm-water carbonate sediments where seagrass is present (Martin, 1986; Martin & Wright, 1988; Buchan & Lewis, 2009). This robust foraminifer is relatively resistant to destruction. In my study *Ar. angulatus* was the third most abundant foraminiferal species and was found in varying stages of dissolution and breakage. However, tests in pristine condition were the most common. Buchan & Lewis (2009) found that sites with high vegetation density had a higher quality of preservation. Across all Springs Coast sites for which *Archaias* taphonomy was analyzed, Site 81 was the only site with 100% seagrass coverage. This site also had the highest percent of pristine *Archaias* tests in both dissolution and breakage taphonomy analyses. Buchan & Lewis (2009) suggested that sites with sparse vegetation cover allow foraminifer tests to be broken and abraded over time. In my study, sites with seagrass coverage ranging from 15–60% had the highest percent of Stage 5 broken tests. It is important to note that all *Archaias* tests used in this analysis were dead at the time of collection and were therefore subject to sorting and differential preservation, and may not accurately represent the living populations on vegetation (Martin & Wright, 1988).

The majority of *Archaias* tests in the Springs Coast were in excellent condition, however the data do exhibit bimodality. Stage 1 and 2 tests (pristine/near pristine) accounted for 62% of the *Archaias* tests for both dissolution and breakage. Stage 5 degradation was also common, accounting for 25% of Stage 5 dissolution and 15% of Stage 5 breakage. Tests in stages 3 and 4 degradation were less common. The high percentage of tests in excellent conditions may be associated with the high carbonate saturation state, while the elevated presence of Stage 5 tests may be a consequence of low sedimentation rates along the West Florida shelf. In this study area, carbonate sediments are predominantly heterozoan carbonates, with low accumulation rates of

centimeters per 1,000 years (Beck, 2010). The abundance of Stage 5 tests may represent specimens that have been in the sediment for years or decades.

The causes of dissolution and breakage of *Ar. angulatus* in the Springs Coast are unclear. Sediment grain size did not have a significant effect on *Archaias* test degradation. To further investigate the cause of test degradation, it would be useful to determine the percent quartz and calcium carbonate of the sediment at each site. A higher percentage of quartz sand is abrasive to the tests, which could induce breakage and abrasion that could mimic dissolution.

The data presented in this research shows that sediment sorting has a significant effect on the abundance of *Ar. angulatus* tests. The environmental energy required to sort the sediment in the Springs Coast region may influence the breakage and dissolution of the tests analyzed, as high-energy environments have been linked to increased abrasion and breakage by previous studies (Cottey & Hallock, 1988; Martin & Wright, 1988).

The influence of the high alkalinity, high carbonate-saturation state  $(\Omega)$  spring water in the Springs Coast area (Beckwith et al., 2019) is likely limiting dissolution rates of *Ar. angulatus*. Collecting Ω data from all sites in this study could provide insight into the dissolution and breakage rates, as well as the abundance of *Archaias* at specific sites. Beckwith et al. (2019) hypothesized that there is a calcification "sweet spot" within the Springs Coast, referring to an ideal calcification environment. Comparing *Archaias* taphonomy within and outside the "sweet spot" could provide information about the influence of  $\Omega$  on test dissolution and breakage, and on calcifying organisms as a whole.

#### **CONCLUSIONS**

- 1. In 41 sediment samples from seagrass beds in the Florida Springs Coast, 152 species were identified; *Quinqueloculina seminula* and *Haynesina germanica* were the dominant species.
- 2. Diversities of benthic foraminiferal assemblages in the Springs Coast sediments were higher than previously reported for coastal waters of the Gulf of Mexico.
- 3. The unusually high number of species, coupled with relatively few individuals representing more than 90% of the specimens identified, suggest that a continuous influx of foraminiferal propagules can produce recruits that do not establish viable populations.
- 4. The inshore sites, most of which were influenced by brackish salinities, were dominated by small miliolids. These sites also were characterized by fine sediments and had the highest foraminiferal densities, but not the highest diversities.
- 5. The more offshore sites, characterized by normal-marine salinities, high seagrass coverage, and mud-rich sediments, had relatively high densities and diversities with relatively similar percentages of smaller miliolids and rotaliids.
- 6. The significant positive correlation between pH and abundance of smaller miliolids supports the hypothesis that increased alkalinity is a major factor regarding the foraminiferal distribution in the Springs Coast, including the prominent occurrence of *Ar. angulatus*.

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APPENDICES

### APPENDIX A: ENVIRONMENTAL DATA FOR EACH SITE

# **Table A1:** Environmental data for each site, collected by SIMM.



# **Table Table A1 (Continued)**



*Note*: A Secchi disk reading of 999 indicates the water column was clear to the bottom.





**Figure B1:** Relative abundance of *Archaias* in Stage 5 dissolution plotted against pH. R<sup>2</sup> = 0.1442.



**Figure B2:** Absolute foraminiferal abundances plotted against the percent of fine sand (Φ=3) for all sites (n=41).  $R^2 = 0.19$ .



**Figure B3:** Foraminiferal density plotted against seagrass coverage ( $R^2 = 0.02$ ).



**Figure B4:** Fine sediment/mud (0.125 mm  $\leq$  X  $\leq$  0.063) and medium/coarse sediment (X  $\geq$  0.25 mm) plotted against seagrass coverage.



**Figure B5:** nMDS plot of the genera making up ≥2% of total relative abundance.



**Figure B6:** Distance-based redundancy analysis of all Springs Coast sites using the abundance data of genera with a total abundance  $\geq 2\%$  and grain size distribution.  $R^2 = 0.44$ ,  $p = 0.001$ .

### APPENDIX C: LIST OF ALL SPECIES, GENERA, FAMILIES, AND ORDERS PRESENT IN THE SPRINGS COAST SAMPLES

# **Table C1:** List of all species, genera, families, and orders present in the Springs Coast samples.



#### **Table C1 (Continued)**

*Cibicides rugosus Monalysidium Cibicides corpulentus Neopateoris Cibicidoides pachyderma Pseudotriloculina Cibicidoides robertsoniana Pyrgo Cibicidoides umbonata Quinqueloculina Cibicidoides wuellerstorfi Siphonaperta Cymbaloporetta atlantica Spiroloculina Discorbis aguayoi Triloculina Discorbis mira Vertebrasigmoilina Discorbis rosea Wiesnerella Discorbis vilardeboanus Clavulina Epistominella vitrea Cribrostomoides Eponides repandus Eratidus Eponides turgidus Haplophragmoides Eubuliminella morgani Paratrochammina Fursenkoina compressa Trochammina Fursenkoina mexicana Spirotextularia Fursenkoina pontoni Textularia Fursenkoina punctata Tritaxis Globocassidulina parva Ammodiscus Hanzawaia concentrica Lobatula* sp. *Neoconorbina terquemi Palmerinella palmerae Paracassidulina minuta Planoglabratella opercularis Planorbulina mediterranensis Rosalina* sp. *Rosalina bahamaensis Rosalina floridensis Rosalina subaraucana Uvigerina laevis Valvulineria araucana Affinetrina planciana Articularia sagra Articulina antillarum Articulina mucronata Articulina pacifica Cornuspira involvens Cycloforina sidebottomi Flintinoides labiosa Miliammina fusca Miliolinella circularis Miliolinella fichteliana Miliolinella suborbicularis Miliolinella subrotunda Monalysidium politum*
#### **Table C1 (Continued)**

*Neopateoris* sp. *Pseudotriloculina granulocostata Pseudotriloculina linneiana Pseudotriloculina rotunda Pseudotriloculina subgranulata Pyrgo elongata Pyrgo sarsi Pyrgo subsphaerica Pyrgo williamsoni Quinqueloculina agglutinans Quinqueloculina bassensis Quinqueloculina bicarinata Quinqueloculina bicostata Quinqueloculina bosciana Quinqueloculina candeiana Quinqueloculina carinata Quinqueloculina collumnosa Quinqueloculina compta Quinqueloculina crassa Quinqueloculina impressa Quinqueloculina laevigata Quinqueloculina lamarckiana Quinqueloculina linneiana Quinqueloculina parkeri Quinqueloculina poeyana Quinqueloculina seminula Quinqueloculina* sp. *Quinqueloculina striata Quinqueloculina subpoeyana Quinqueloculina tenagos Quinqueloculina tipswordi Quinqueloculina triangularis Quinqueloculina vulgaris Siphonaperta distorqueata Spiroloculina antillarum Spiroloculina attenuata Spiroloculina soldanii Triloculina affinis Triloculina bermudezi Triloculina elongata Triloculina fiterrei Triloculina inflata Triloculina oblonga Triloculina rotunda Triloculina* sp. *Triloculina tricarinata Triloculina trigonula*

#### **Table C1 (Continued)**

*Triloculina variolata Vertebrasigmoilina mexicana Wiesnerella auriculata Clavulina* sp*. Cribrostomoides* sp*. Eratidus foliaceus Haplophragmoides wilberti Paratrochammina challengeri Trochammina squamata Spirotextularia floridana Textularia* sp. *Textularia agglutinans Textularia candeiana Tritaxis fusca Ammodiscus tenuis*

#### APPENDIX D: LIST OF ALL SPECIES FOUND IN THE SPRINGS COAST, THE SPECIES AUTHOR, AND THE YEAR IT WAS NAMED

**Table D1:** List of all species found in the Springs Coast, the species author, and the year it was named.



# **Table D1 (Continued)**



# **Table D1 (Continued)**



# **Table D1 (Continued)**



#### APPENDIX E: RAW ABUNDANCE DATA FOR ALL SITES



# **Table E1**: Raw abundance data for sites 34, 40, 46, 52, 59, 88, 94, 100, and 106





# **Table E1 (Continued)**



# **Table E1 (Continued)**



| <b>Species</b>              | <b>SC135</b>     | <b>SC141</b>     | <b>SC147</b>             | <b>SC159</b>     | <b>SC165</b>     | <b>SC177</b>             | <b>SC61</b>      | <b>SC67</b>      | <b>SC73</b>      |
|-----------------------------|------------------|------------------|--------------------------|------------------|------------------|--------------------------|------------------|------------------|------------------|
| Affinetrina planciana       | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$         | $\theta$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Ammodiscus tenuis           | $\mathbf{0}$     | $\mathbf{0}$     | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Ammonia beccarii            | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{1}$             | $\boldsymbol{0}$ | $\mathbf{1}$     | 9                |
| Ammonia parkinsoniana       | 14               | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | 6                | 8                        | $\boldsymbol{0}$ | $\mathbf{1}$     | 12               |
| Ammonia takanabensis        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Ammonia tepida              | 11               | $\mathbf{0}$     | $\mathbf{0}$             | $\mathbf{0}$     | $\overline{c}$   | 21                       | $\mathbf{0}$     | $\mathbf{1}$     | 14               |
| Archaias angulatus          | $\boldsymbol{0}$ | $\boldsymbol{0}$ | 13                       | 101              | $\overline{c}$   | 14                       | 1                | 21               | 1                |
| Articularia sagra           | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Articulina antillarum       | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Articulina mucronata        | $\mathbf{0}$     | $\mathbf{0}$     | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Articulina pacifica         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{1}$             | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\overline{c}$           | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Bigenerina irregularis      | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\mathbf{1}$     | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Bigenerina sp.              | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\mathbf{1}$     |
| Bolivina alata              | $\mathbf{0}$     | $\mathbf{0}$     | $\mathbf{0}$             | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Bolivina albatrossi         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Bolivina barbata            | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Bolivina lanceolata         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Bolivina lowmani            | $\mathbf{0}$     | $\mathbf{0}$     | $\mathbf{1}$             | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | 1                |
| Bolivina ordinaria          | $\mathbf{1}$     | $\mathbf{1}$     | $\boldsymbol{0}$         | $\mathbf{1}$     | $\overline{c}$   | $\mathbf{1}$             | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\overline{3}$   |
| Bolivina striatula          | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\mathbf{1}$     | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| <b>Bolivina</b> translucens | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{1}$             | $\overline{2}$   | 3                | 5                        | $\mathbf{0}$     | $\mathbf{1}$     | $\overline{3}$   |
| Bolivinita quadrilatera     | $\mathbf{0}$     | $\mathbf{0}$     | $\mathbf{0}$             | $\overline{0}$   | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\mathbf{0}$     | $\boldsymbol{0}$ |
| Broeckina orbitolitoides    | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\mathbf{1}$     | $\boldsymbol{0}$         | $\mathbf{0}$     | 9                | 1                |
| Bulimina marginata          | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Buliminella elegantissima   | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cibicides io                | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\overline{c}$           | 5                | 14               | 5                        | $\mathbf{1}$     | $\boldsymbol{0}$ | 1                |
| Cibicides kullenbergi       | $\overline{2}$   | $\overline{2}$   | 15                       | 12               | 38               | $\overline{\mathcal{A}}$ | $\boldsymbol{0}$ | $\mathbf{1}$     | $\sqrt{2}$       |
| Cibicides mayori            | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cibicides mollis            | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cibicides rugosus           | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cibicides corpulentus       | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{1}$             | $\sqrt{2}$       | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cibicidoides pachyderma     | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{1}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cibicidoides robertsoniana  | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | 6                | $\mathbf{1}$             | $\boldsymbol{0}$ | $\overline{c}$   | $\boldsymbol{0}$ |
| Cibicidoides umbonata       | $\boldsymbol{0}$ | $\boldsymbol{0}$ | 1                        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cibicidoides wuellerstorfi  | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\overline{\mathcal{A}}$ | 7                | 3                | 2                        | $\mathbf{0}$     | $\overline{0}$   | $\boldsymbol{0}$ |
| Clavulina sp.               | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cornuspira involvens        | $\mathbf{1}$     | $\boldsymbol{0}$ | 1                        | $\overline{4}$   | 1                | $\boldsymbol{0}$         | $\mathbf{0}$     | $\overline{c}$   | 6                |
| Cribroelphidium excavatum   | $\overline{3}$   | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cribroelphidium incertum    | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cribroelphidium poeyanum    | 24               | $\sqrt{2}$       | $\overline{c}$           | $\boldsymbol{0}$ | $\boldsymbol{0}$ | 5                        | 1                | $\boldsymbol{0}$ | 5                |
| Cribrostomoides sp.         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cycloforina sidebottomi     | $\boldsymbol{0}$ | $\mathbf{1}$     | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\mathbf{1}$     | $\boldsymbol{0}$ |
| Cyclorbiculina compressa    | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{1}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cymbaloporetta atlantica    | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf 1$              | $\mathbf{1}$     | $\boldsymbol{0}$ | $\mathbf{1}$             | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |

**Table E2**: Raw abundance data for sites 135, 141, 147, 159, 165, 177, 61, 67, and 73.

# **Table E2 (Continued)**



# **Table E2 (Continued)**





#### **Table E2 (Continued)**

| <b>Species</b>              | <b>SC85</b>      | <b>SC114</b>     | <b>SC120</b>     | <b>SC128</b>             | <b>SC132</b>            | <b>SC81</b>      | <b>SC93</b>      | <b>SC95</b>      | <b>SC113</b>     |
|-----------------------------|------------------|------------------|------------------|--------------------------|-------------------------|------------------|------------------|------------------|------------------|
| Affinetrina planciana       | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | 2                | $\theta$         |
| Ammodiscus tenuis           | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{0}$            | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ |
| Ammonia beccarii            | $\overline{2}$   | $\overline{0}$   | $\mathbf{0}$     | $\overline{0}$           | $\boldsymbol{0}$        | $\boldsymbol{0}$ | 3                | $\overline{0}$   | $\boldsymbol{0}$ |
| Ammonia parkinsoniana       | 6                | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | 1                | 1                |
| Ammonia takanabensis        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Ammonia tepida              | 6                | $\mathbf{0}$     | $\mathbf{0}$     | $\boldsymbol{0}$         | $\overline{\mathbf{3}}$ | $\mathbf{1}$     | $\boldsymbol{0}$ | $\mathbf{0}$     | $\mathbf{1}$     |
| Archaias angulatus          | $\mathbf{0}$     | $\overline{7}$   | 61               | $\overline{\mathbf{3}}$  | $\mathbf{1}$            | 10               | 5                | $\mathbf{0}$     | $\boldsymbol{0}$ |
| Articularia sagra           | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Articulina antillarum       | $\mathbf{0}$     | $\mathbf{0}$     | $\mathbf{0}$     | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Articulina mucronata        | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ |
| Articulina pacifica         | $\mathbf{0}$     | $\mathbf{0}$     | 5                | $\mathbf{1}$             | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Bigenerina irregularis      | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Bigenerina sp.              | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Bolivina alata              | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ |
| Bolivina albatrossi         | $\mathbf{0}$     | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Bolivina barbata            | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Bolivina lanceolata         | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\mathbf{1}$            | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Bolivina lowmani            | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\overline{2}$          | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\overline{2}$   |
| Bolivina ordinaria          | $\mathbf{1}$     | $\mathbf{0}$     | $\mathbf{0}$     | $\boldsymbol{0}$         | $\overline{\mathbf{3}}$ | $\boldsymbol{0}$ | 6                | $\mathbf{1}$     | 5                |
| Bolivina striatula          | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{0}$     |
| <b>Bolivina</b> translucens | $\boldsymbol{0}$ | $\mathbf{0}$     | $\overline{2}$   | $\boldsymbol{0}$         | $\overline{4}$          | $\boldsymbol{0}$ | $\overline{2}$   | $\boldsymbol{0}$ | $\overline{7}$   |
| Bolivinita quadrilatera     | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ |
| Broeckina orbitolitoides    | $\mathbf{0}$     | $\overline{7}$   | $\mathbf{1}$     | 11                       | $\boldsymbol{0}$        | 5                | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ |
| Bulimina marginata          | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Buliminella elegantissima   | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cibicides io                | $\mathbf{1}$     | $\mathbf{0}$     | $\mathbf{0}$     | $\boldsymbol{0}$         | $\overline{\mathbf{3}}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ |
| Cibicides kullenbergi       | $\mathbf{0}$     | $\mathbf{0}$     | $\mathbf{0}$     | $\overline{\mathcal{L}}$ | $\overline{2}$          | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ |
| Cibicides mayori            | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cibicides mollis            | $\boldsymbol{0}$ | $\mathbf{0}$     | $\mathbf{0}$     | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cibicides rugosus           | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$ |
| Cibicides corpulentus       | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cibicidoides pachyderma     | $\mathbf{0}$     | $\overline{0}$   | $\boldsymbol{0}$ | $\overline{0}$           | $\boldsymbol{0}$        | $\overline{0}$   | $\overline{0}$   | $\boldsymbol{0}$ | $\theta$         |
| Cibicidoides robertsoniana  | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\overline{2}$          | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cibicidoides umbonata       | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{0}$     | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cibicidoides wuellerstorfi  | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{1}$             | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Clavulina sp.               | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | 1                       | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cornuspira involvens        | $\boldsymbol{0}$ | 1                | 1                | $\boldsymbol{0}$         | 5                       | $\mathbf{1}$     | 5                | $\boldsymbol{0}$ | 3                |
| Cribroelphidium excavatum   | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cribroelphidium incertum    | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cribroelphidium poeyanum    | $\overline{4}$   | 1                | $\boldsymbol{0}$ | $\overline{2}$           | $\overline{2}$          | $\overline{2}$   | 1                | 6                | 4                |
| Cribrostomoides sp.         | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$         | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |
| Cycloforina sidebottomi     | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\mathbf{1}$             | $\boldsymbol{0}$        | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ | $\boldsymbol{0}$ |

**Table E3:** Raw abundance data for sites 85, 114, 120, 128, 132, 81, 93, 95, and 113.

*Cyclorbiculina compressa* 0 0 0 0 0 0 0 0 0

# **Table E3 (Continued)**



# **Table E3 (Continued)**











#### **Table E4 (Continued)**



#### **Table E4 (Continued)**



# **Table E4 (Continued)**







#### **Table E5 (Continued)**



#### **Table E5 (Continued)**



# **Table E5 (Continued)**

