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Benthic Foraminiferal Assemblages from Marshes and Mangroves in the Everglades (South Florida, USA) and Their Application as Proxies for Habitat Shifts due to Sea Level Rise

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BENTHIC FORAMINIFERAL ASSEMBLAGES FROM MARSHES AND MANGROVES IN THE EVERGLADES (SOUTH FLORIDA, USA) AND THEIR APPLICATION AS PROXIES FOR HABITAT SHIFTS DUE TO SEA LEVEL RISE

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Zoë Rosina Francesca Verlaak

2019

To: Dean Michael R. Heithaus
College of Arts, Sciences and Education

This dissertation, written by Zoë Rosina Francesca Verlaak, and entitled Benthic Foraminiferal Assemblages from Marshes and Mangroves in the Everglades (South Florida, USA) and Their Application as Proxies for Habitat Shifts due to Sea Level Rise , having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

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Vice President for Research and Economic Development
and Dean of the University Graduate School

Florida International University, 2019

DEDICATION

I dedicate this dissertation to my husband, Robert Blatt. I travelled this long road with him by my side and he never hesitated to lend a hand, whether it was in the lab or while beating mosquitos during field work in the Everglades. He has always expressed the genuine interest in my research and future aspirations I needed to propel myself forward.

ABSTRACT OF THE DISSERTATION

BENTHIC FORAMINIFERAL ASSEMBLAGES FROM MARSHES AND MANGROVES IN THE EVERGLADES (SOUTH FLORIDA, USA) AND THEIR APPLICATION AS PROXIES FOR HABITAT SHIFTS DUE TO SEA LEVEL RISE

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This study examined benthic foraminifera from marsh and mangrove habitats along the coasts of the Everglades in South Florida for their use as proxies for salinity, and applied the results to assess the nature and rates of past changes due to sea level rise over the last ~3400 years. Research on modern foraminiferal assemblages from the Everglades are scarce, and this is the first foraminiferal based paleoenvironmental study for the region.

The study of living assemblages examined the extent to which infaunal foraminifera bias modern and fossil assemblages. The goal was to investigate which sediment interval should be used as a modern analog for paleoenvironmental studies in this area. As most benthic foraminifera live in the surface 1 cm of sediment, most

research is based on the upper 1–2 cm of sediments. The living depths deepened in a landward direction, possibly due to the landward increase in the oxygenation of subsurface sediments. However, subsurface production is negligible, and we can safely use foraminifera from the upper 2 cm as a modern analog.

In the modern foraminiferal distribution, diversity decreases, dominance increases, and agglutinated taxa increase from the coastline inland. The most important factor controlling foraminiferal distribution is salinity, followed by total organic carbon and total inorganic carbon. Benthic foraminifera from the Everglades are excellent salinity proxies and can be used to determine the history of habitat change in this region.

The study of fossil and subfossil assemblages found that environments changed over time from upper mangrove, to lower mangrove, and finally the marine-influenced habitat of the study site today. The shifts in foraminiferal assemblages over time are related to an increase in salinity with sea level rise. They also accelerated toward the present by AD 1950. These research results can be used to predict future shifts in coastal habitats, of importance to South Florida's growing coastal population and the Everglades ecosystem.

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Chapter 1

Introduction

Significance of Study

This study examined benthic foraminifera from marsh and mangrove environments along the coasts of the Everglades in South Florida (Fig. 1) for their use as salinity proxies and applied the results to assess past trends in habitat change due to sea level rise over the last ~3400 years for this region. Research on modern foraminiferal assemblages from the Everglades is scarce and consists only of the studies by Benda and Puri (1962), Phleger (1965), Goldstein (1976), and Bock and Gebelein (1977), and this is its first foraminiferal based paleoenvironmental study. Microfossil-based quantitative paleoenvironmental reconstructions allow a precise reconstruction of former sea levels (Woodroffe et al., 2005), of interest to the many researchers investigating past, present, and future impacts of sea level change on South Florida's coasts. Worldwide, the responses of these forested wetlands to sea level rise have not received the same scientific attention as the salt marsh coasts of North America and Northwestern Europe (Woodroffe et al., 2005; Parry et al., 2007; Culver et al., 2013), even though mangrove forests comprise 70% of the tropical and subtropical coasts (Culver et al., 2013).

Geologic History of the Everglades

The Florida peninsula is the emerged part of a larger continental extension of the North American Plate called the Florida Platform or Floridan plateau (Vaughan, 1910), and South Florida is situated on its southeastern corner. The plateau is composed of igneous, sedimentary, and volcanic rocks from Precambrian to Jurassic Age (Arthur, 1988), and tilts westwards so that only its eastern half is raised above sea level. The western edge of the Floridan Plateau extends over 100 km off the coast into the Gulf of Mexico, whereas its eastern edge is only a few km off Florida's Atlantic coastline (Parker et al., 1955).

Mid-Jurassic to Holocene sedimentary strata deposited unconformably upon the bedrock (Scott et al., 2001), increasing in thickness from over 1200 m in North-Central Florida to more than 4500 m in South Florida (Parker et al., 1955). During the Pleistocene, the Okeechobee Basin formed in which later the Everglades developed (Parker et al., 1955). The sediments that make up the Okeechobee Basin consist of undifferentiated Upper Oligocene to Pliocene strata belonging to the Hawthorn Group (Scott, 1988) and Tamiami Formation (Mansfield, 1939). The impermeable clayey sands, silty clays, and clays of the Hawthorn Group form the confining unit of the Surficial Aquifer System. The fossiliferous sands and sandy fossiliferous limestone of the Tamiami Formation range from permeable, where they make part of the Biscayne Aquifer, to impermeable, where they form a confining unit to the Surficial Aquifer System (Scott et al., 2001).

The youngest sediments of the Okeechobee Basin floor previously formed the Pliocene sea bottom (Parker and Cooke, 1944). In southern Florida the Pliocene sediments are dominantly fossiliferous, siliciclastic strata, and carbonates form a more important component in southwestern Florida (Scott et al, 2001). During the glacial stage at the beginning of the Pleistocene, the basin floor underwent erosion and dissolution followed by the deposition of the first sedimentary layers of the Fort Thompson Formation (Parker and Cooke, 1944). The highly permeable sedimentary strata of the Fort Thompson Formation (Cooke, 1945) consist of alternating fresh water, marine and brackish water deposits, reflecting the subsequent glacial and interglacial stages of the Pleistocene (Parker et al, 1955).

During the Sangamon Interglacial interval, the modern-day, higher elevation landscape features bordering the Okeechobee Basin were formed (Parker et al, 1955). The oolite facies of the Miami Limestone (Sanford, 1909) formed an extensive bar, the northeast-southwest oriented Atlantic Coastal Ridge. Coquina sands of the Anastasia Formation accumulated north of this ridge, south of it a coral reef (Key Largo Limestone) developed (Parker et al., 1955), and west of it, in the Okeechobee depression, the bryozoan facies of the Miami Limestone formed, covering most of what is now the Everglades (Neal et al., 2008). The Fort Thompson Formation and the Miami Limestone form the most important units of the Biscayne Aquifer of the Surficial Aquifer System (Scott et al., 2001). After a last erosional phase during the Wisconsin Glacial interval, sea level rose again as the Laurentide Ice Sheet retreated (Parker et al., 1955). The change to a subtropical climate increased the amount of rainfall, and peats started to develop as

early as 5000 years ago (Gleason and Stone, 1994), eventually forming the Everglades as we know it today.

South Florida's Mangrove Ecosystem

Spanning most of South Florida, the Everglades are a large tropical-subtropical wetland bordered to the west by the Gulf of Mexico and to the south by Florida Bay. Sheet flow from Lake Okeechobee through the Everglades discharges westwards through the Shark River Slough into the Shark River Estuary, then into the Gulf of Mexico and southwards through the Taylor Slough into Florida Bay (Fig. 1). With dense mangrove forests extending over 80 km along the southwestern coastline of South Florida, it is one of the most extensive mangrove wetlands in the world (Castañeda-Moya et al., 2013).

Mangroves function as sediment accumulation sites, trapping fine sediments and peats underneath their root system in concert with sea level rise (Morris et al., 2002; McKee et al., 2007; Parry et al., 2007; Alongi, 2008; Kirwan et al., 2010). In the past 50 years, mangroves in the Florida Everglades have migrated landward into adjacent wetland communities, indicating that sea level rises faster than the mangroves can respond by vertical accretion (Ross et al., 2000). Mangrove ecosystems are also important nursery grounds and breeding sites for birds, mammals, fish crustaceans, shellfish, and reptiles, some of which are commercially important (McKee et al., 2007; Alongi, 2008). Additionally, mangroves act as a filter for nutrients and contaminants (Alongi, 2008; McKee et al., 2007; Nicholls et al., 1999), minimizing their input into more sensitive habitats bordering the mangrove ecosystem, such as seagrass beds and

coral reefs (McKee et al., 2007). Furthermore, they form a natural protection from floods and storm waves, tidal bores, tsunamis and hurricanes (Nicholls et al., 1999, McKee et al., 2007; Alongi, 2008). The growing awareness of the different societal and physical impacts of sea level rise resulting from anthropogenic warming of the atmosphere and oceans on coastal areas has increased interest in past sea level change and its effects on coastal regions, such as the increase in saltwater intrusion (Leorri and Martin, 2009).

In this dissertation, Chapter 2 "Effects of Infaunal Foraminifera on Surface and Subsurface Assemblages in the Southwestern Everglades, USA: Baseline Study for Paleoenvironmental Analyses" (Verlaak et al., 2018) discusses the effects of infaunal foraminifera on the composition of surface and subsurface assemblages, and the preservation of foraminiferal tests. Next, Chapter 3 "Environmental Controls on the Distribution of Modern Benthic Foraminifera in the Florida Everglades for their use as Paleoenvironmental Indicators" identifies the main environmental controls on the distribution of modern foraminiferal assemblages. Chapter 4 "History of Paleoenvironmental Changes in the Southwestern Everglades using Foraminiferal Assemblages" examines changes in benthic foraminiferal assemblages, shifts in the environment, and changes in the rate of habitat change due to sea level rise over the past ~3400 years, as well as taphonomy. Finally, Chapter 5 "Conclusions" presents general conclusions of the chapters 2–4.

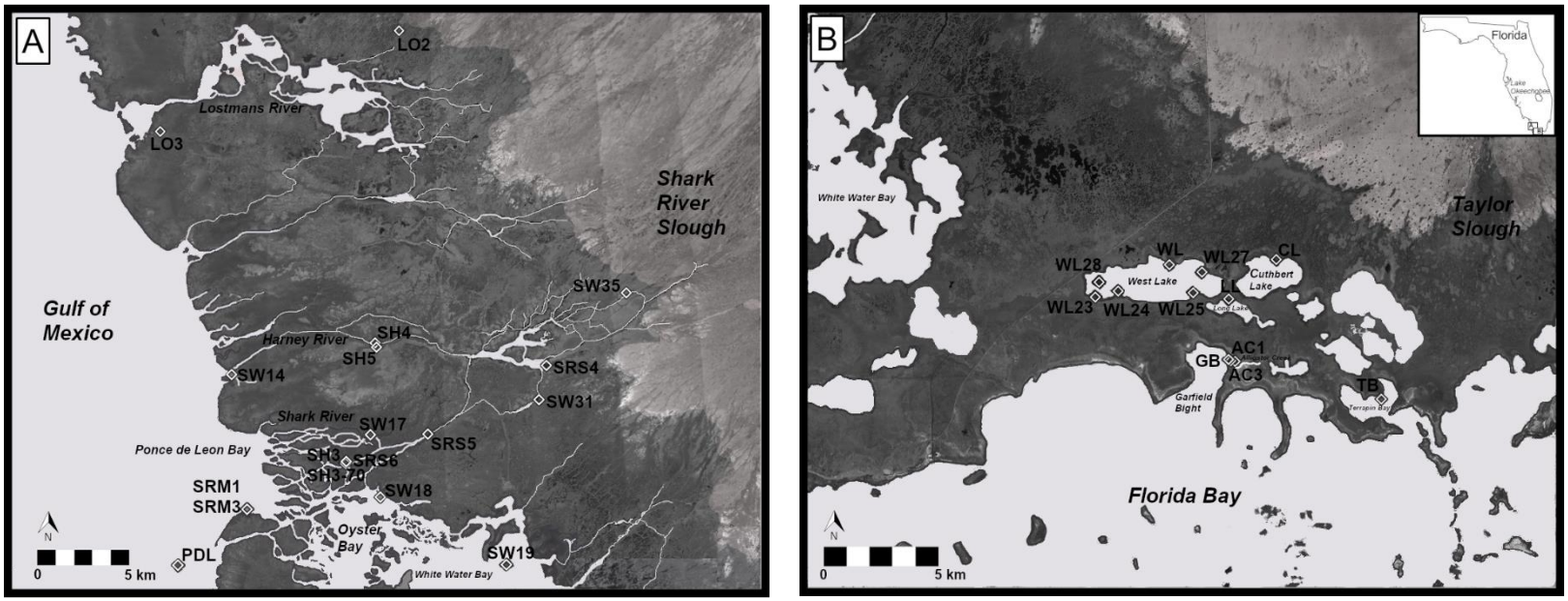

Figure 1 – Map of the study area and important water bodies for the southwestern Everglades. A) The 18 sampling locations on the western coast, sampled (0–2 cm) to study modern assemblages. At sites SRS4, SRS5, and SRS6, 30-cm-long cores were also taken to study living assemblages. Additionally, at site SRS6, a 445-cm-long core was retrieved by Yao and Liu (2017), from which this study used a 262-cm-long section to examine fossil assemblages; B) The 12 sampling locations on the southern coast, sampled (0–2 cm) to study modern assemblages. At site GB, a 13-cm-long core was also collected to study living assemblages. The coastal zone colored in different shades of darker gray shows the approximate location of mangroves. The upland, light gray area is freshwater wetland. Figure is adapted from Google Earth.

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Chapter 2

Effects of Infaunal Foraminifera on Surface and Subsurface Assemblages in the Southwestern Everglades, USA: Baseline Study for Paleoenvironmental Analyses

ABSTRACT

This study investigated the extent to which deep-dwelling, infaunal foraminifera bias modern and fossil distributions in the subtropical mangroves of the Everglades (southwest Florida), and which sediment interval should be used as a modern analog for paleoenvironmental studies in this area. Typically, these studies are based on modern analogs from the upper 1 to 2 cm of sediments, as most benthic foraminifera live in the surface 1 cm, but in tropical mangrove environments, deep-dwelling infaunal foraminifera may be more common. The vertical distributions of live assemblages in cores from a mudflat and three mangrove sites were investigated. To examine the preservation potential of dead tests, distributions of wall types and inner test linings were recorded.

The living depths of benthic foraminifera showed a landward deepening from 1 to 3 cm in mudflats and low mangroves and from 7 to 10 cm in middle and high mangroves, possibly due to a landward increase in oxygenation of the subsurface sediments. Modern assemblages from the top 2 cm included species common in the deep infauna and contained, on average, 36% of the total standing crop. Additions to total assemblages at greater depths by subsurface production were negligible. Thus, the upper 2 cm of the sediment column would be sufficient as a modern analog for paleoenvironmental studies in the southwestern Everglades. Preservation of dead tests is influenced by a landward increase in the degradation of agglutinated taxa through oxidation/bacterial breakdown of organic cements. Fortuitously, calcareous taxa preserve well in the carbonate-buffered sediments of the Everglades.

INTRODUCTION

Intertidal benthic foraminifera have closely defined ecological tolerances and narrow intertidal zones of land elevation, and they have, therefore, been widely used as the basis for studies of past environments and sea levels (Scott and Medioli 1978; Horton et al. 2003; Woodroffe et al. 2005; Berkeley et al. 2006, 2007; Goldstein and Alve 2011). Paleoenvironments based on fossil assemblages are inferred from their similarity to modern distributions at the sediment surface. In intertidal zones, foraminifera use much deeper infaunal habitats than in any other marine environment, partly because the presence of vegetation with deep root systems allows oxygen to reach greater depths. Also, in marine environments, bioturbation creates a homogenized upper layer, whereas in intertidal environments, it increases subsurface heterogeneity, creating microenvironments of oxygen and redistribution of food particles (Goldstein and Harben 1993, Goldstein et al. 1995, Jorissen 1999). This study investigated the extent to which foraminifera living at depth in mangrove sediments can bias both modern and fossil distributions in the Everglades, southwestern Florida.

The Everglades are a large, tropical–subtropical wetland spanning most of south Florida, bordered to the west by the Gulf of Mexico and to the south by Florida Bay. Sheet flow from Lake Okeechobee through the Everglades discharges southwards through Taylor Slough into Florida Bay and westwards through the Shark River Slough into the Shark River Estuary and then the Gulf of Mexico. With dense mangrove forests extending about 80 km along the southwestern coast of Florida, the Everglades is one of the most extensive mangrove zones in the world (Castañeda-Moya et al. 2013). Mangrove environments characterize 70% of tropical to subtropical coastlines (Debenay et al. 2002), but they have received little attention compared to temperate salt marshes (Berkeley et al. 2008, Culver et al. 2013), and only a few studies have focused on their foraminiferal infauna.

The majority of benthic foraminifera commonly live in the surface 1 cm of the sediment column (Van der Zwaan et al. 1999), so paleoenvironmental and sea-level studies are typically based on modern analogs from the upper 1 to 2 cm of sediments (Culver et al. 2013). Infaunal contributions to assemblages at greater depths than the surface sediment, however, are not included when defining the modern assemblage in this way (Berkeley et al. 2006). The results from the two existing studies on infauna in tropical mangrove environments implied that deep-dwelling foraminifera may be more common in the tropics, and, therefore, the surface sediment interval (0–2 cm) may be insufficient as a modern analog (Berkeley et al. 2008, Culver et al. 2013). For example, the maximum depth to which live specimens have been found is 30 cm for Georgia salt marshes (Goldstein 1988, Goldstein and Harben 1993, Goldstein et al. 1995, Goldstein and Watkins 1999) and 50 to 80 cm for tropical mangroves in Australia and Malaysia (Berkeley et al. 2008, Culver et al. 2013), although maximum abundances are within the upper 10 to 16 cm (Goldstein et al. 1995, Berkeley et al. 2008, Culver et al. 2013). In contrast, in temperate New England, Canadian, and Oregon salt marshes, maximum abundances are within the upper 3 to 5 cm (Saffert and Thomas 1998, Tobin et al. 2005, Milker et al. 2015). The occurrence of deep infaunal foraminifera is mainly a problem when they occur in large numbers, and an additional problem when they are also taxonomically different from the surface taxa. As a result, the complete species composition or the correct relative abundances of species of the modern assemblage may not be known (Goldstein and Watkins 1999, Culver and Horton 2005, Berkeley et al. 2006, Culver et al. 2013). Additionally, once they die, these living specimens will directly contribute to the subsurface assemblages and thus change the residual assemblages in the fossil record.

Another potential problem with tropical–subtropical microfossil studies is dissolution of calcareous taxa (Culver et al. 2013). In mangrove swamps, dissolution is caused by the organic acids generated by decaying plant matter and affects mainly calcareous tests. However, because of the

underlying limestone bedrock of the Everglades, the sediment composition is mainly calcium carbonate in the form of fine mud and shelly material, creating a carbonate buffered environment that allows for an exceptional preservation of calcareous taxa (Phleger 1965). On the contrary, agglutinated taxa degrade through oxidation of their organic cements (Hoge 1994; Goldstein et al. 1995; Berkeley et al. 2007, 2009; Culver et al. 2013).

To provide baseline data for future determinations of Everglades paleoenvironments over the last few thousand years, the present study investigated three aspects of the vertical distribution patterns of living assemblages and their influence on surface to subsurface assemblages in subtropical mangroves: (1) the sediment depths occupied by living foraminifera from the coastline inland; (2) the extent of the influence of deep-dwelling foraminifera on the composition of surface and subsurface total assemblages; and (3) possible geographic patterns of dissolution revealed by foraminiferal wall type and inner test linings. To address these questions, we counted the number of live individuals, test linings, and dead tests down to a maximum depth of 30 cm of sediment, and we categorized the latter by wall type. For sites at higher (inland) vs. lower (coastal) elevations, we interpreted the results by comparing microhabitat preference; i.e., the depth interval at which the maximum abundance of live individuals occurred (Jorissen 1999). Furthermore, the down-core counts of dead and live + dead tests were compared, as well as the taxonomic composition of the live assemblage between the surface 0 to 2 cm and the subsurface sediments. These results were then used to address the question of whether the surface 0 to 2 cm interval is accurate for use as a modern analog for the Everglades mangrove swamps in southwestern Florida.

METHODS

Field Methods

The four study sites were situated within Everglades National Park along the Shark River and at Garfield Bight, along the southwestern and southern coastlines of the Everglades, respectively (Fig. 1). Three 30-cm-long surface cores were collected using a 5-cm-diameter Russian corer from three sites along the Shark River (west coast). The decision to limit sampling to 30 cm depth followed information from previous studies of infaunal marsh foraminifera, which showed that substantial live contributions decrease below 10 cm (e.g., Goldstein 1988, Ozarko et al. 1997, Saffert and Thomas 1998, Patterson et al. 1999). The Russian corer, also called a D-section or McAuley corer, has a semicylindrical barrel with a sharpened edge, and a pointed end. Once the device has been inserted into the sediment, the barrel is rotated around a stationary blade, enclosing a half cylinder of sediment. A Russian corer is commonly used for paleoecological studies in salt marshes, and it is suitable for the fine-grained, peaty sediments that characterize these environments. It is easy to operate, offers the possibility to collect samples below the water level, minimizes contamination and compaction by overlying sediments, and allows for immediate sectioning of the core in the field (Bricker-Urso et al. 1989). Additionally, we took the opportunity to add a sample from another study at Garfield Bight on the southern edge of the Everglades, where a 13-cm-long core was collected with a 3.7-cm-diameter plastic syringe.

Salinities in the Everglades fluctuate greatly, but, on average, the four sampling locations have values, 35 psu. At the time of sampling, the Garfield Bight site was hypersaline (51 psu), with an average salinity of 34 psu. The average salinity range for the three Shark River locations is 8 to 26 psu, although, at the time of sampling, the salinity range was greater (4–32 psu).

The Garfield Bight mudflats core was collected in May 2015 and transported to the laboratory on ice, where it was sampled every 1 cm and preserved in an 85% buffered alcohol solution. The sediments were tan colored and muddy, and a larger proportion of very fine grains was observed than at the other sites. The soil surface was covered with several centimeters of dry/decaying seagrasses that were removed before sampling the core.

Along Shark River, the low-elevation mangrove site SRS6 was sampled in July 2015. Beneath a few centimeters of leaf litter, the sediment was tan to dark brown with some faint laminations or layers. The sediment was firm below the top 8 cm and mainly consisted of finer grain sizes such as silts and fine sands, and some peat. Fine roots were present throughout the core with some thicker roots within the upper 20 cm. The core was sampled in the field every 1 cm down to 10 cm, and then 1 cm samples were taken at the following intervals: 12 to 13 cm, 15 to 16 cm, 18 to 19 cm, 23 to 24 cm, and 29 to 30 cm. The samples were stored in an 85% buffered alcohol solution and transported back to the laboratory on ice to preserve any protoplasm of individuals alive at the time of sampling, and to maintain stable pH conditions to avoid degradation of tests.

The Shark River high-elevation mangrove site SRS4 was also sampled in July 2015. Below a few centimeters of leaf litter, the sediment consisted mainly of very loose peat, especially in the upper 15 cm. The upper half of the core's sediment was black, and the lower half changed gradually to dark brown. Fine roots were dominant, with some thicker roots throughout the core.

The Shark River's middle-elevation mangrove site SRS5 was sampled in June 2016. This site was sampled a year later than the other locations because we wanted to cover more sites than were available to sample in the previous year. Beneath the sparse leaf litter, the sediment consisted mainly of a dark brown to black, loose peat that was especially uncompacted in the

upper 5 cm. Fine roots were conspicuous throughout the core, with some plant leaves at several intervals.

Laboratory Methods

Each sample was stained overnight with Rose Bengal (modified from Walton 1952), a nonvital dye frequently used to differentiate between cytoplasm-containing (‘‘live’’) and empty tests. The stain is adsorbed onto proteins, the main cytoplasmic components, turning the cytoplasm bright pink. Whereas Bernhard (2000) pointed out that foraminiferal cytoplasm may react with Rose Bengal months after an individual’s death, Berkeley et al. (2008) and Culver et al. (2013) showed that in tropical mangrove environments, dead cytoplasm should degrade within days. A study of a New Zealand salt marsh demonstrated that the nonvital Rose Bengal method performed as well as the vital CellTracker™ Green method (Culver et al. 2013).

In this study, individuals with fully stained, bright pink, nongranular, continuous content in chambers were considered live at the time of collection. After staining overnight, the samples were rinsed over nested screens of 2.80 mm (to separate out nonforaminiferal larger grains and organic particles) and 63 µm (to remove finer silts and clays) and split into subsamples using a wet splitter (Scott and Hermelin 1993). Stained individuals were wet picked under a thin water layer to better see the staining (Buzas-Stephens and Buzas 2005, Culver and Horton 2005) and sorted onto slides for identification, while dead individuals were counted according to wall type. Foraminiferal inner test linings were evident in the sediments of most sites but did not stain, and so they were not counted as ‘‘live’’ specimens. A simple test with 10% HCl was performed on some agglutinated foraminifera to observe their reaction to low pH.

To address the questions on microhabitat preference, and vertical distribution and composition of the live assemblages, we plotted the total live counts (Fig. 2) and counts per species

with depth in the core (Fig. 3). To address the question of dissolution, relative proportions of dead individuals of the three wall types (Rotaliina, Miliolina, Textulariina) were plotted for each site (Fig. 4). To visualize how substantial the influence of deep-dwelling individuals was on total assemblages, we also plotted the counts of live + dead tests and dead tests with depth in the core (Fig. 5).

RESULTS

Garfield Bight, Mudflats

The total count of live tests was 25, consisting of 13 calcareous taxa. The maximum depth at which live individuals were found, indicating the tolerance of species, was 13 cm (bottom of core, Fig. 2A). The greatest abundance of live individuals, indicating microhabitat preference, fell within the upper 1 cm of the sediment column, where 60% of the total standing crop was found (Fig. 2A). In this sediment interval, the most common species (48%) were *Ammonia tepida* and *Ammonia parkinsoniana* (Fig. 3A).

The dead assemblages at the mudflat site were dominated by calcareous foraminifera, with more than twice as many Miliolina as Rotaliina (Fig. 4A). The dead calcareous tests remained relatively constant throughout the core. The sum of live + dead individuals was very close to the count of dead tests with depth in the core (Fig. 5A).

Shark River Slough, Low Mangroves

At site SRS6, the total count of live specimens was 17. Five taxa were found, and most of the individuals were calcareous. The maximum observed living depth was 24 cm, while the maximum

abundance of the living assemblage was concentrated in the upper 3 cm, which contained 65% of the total standing crop (Fig. 2B). *Ammonia tepida* was the single most common species in the surface as well as subsurface microhabitats, with its highest abundance at the surface 1 cm of sediment (Fig. 3B).

The dead assemblages at the low mangroves site were dominated by calcareous taxa, mostly Rotaliina (Fig. 4B). The total count of mainly rotallinid-shaped foraminiferal linings was 142, the majority of which occurred within the bottom 7 cm of the core (Fig. 4B). The correlation between foraminiferal linings and Rotaliina tests was high and negative ($r = 0.91$; $r^2 = 0.83$) for the 5 to 30 cm interval, and it was low for agglutinated taxa. The sum of live + dead individuals was very close to the count of dead tests with depth in the core (Fig. 5B).

Shark River Slough, Middle Mangroves

At site SRS5, the total count of live specimens was only nine (Fig. 2C), of which most were calcareous foraminifera belonging to three taxa. The maximum living depth was 30 cm (bottom of core). The 0 to 10 cm interval contained the maximum abundance of the living assemblage (67% of the total standing crop) and exhibited a single large subsurface maximum at 10 cm (Fig. 2C). *Ammonia tepida* was the single most common species in the surface as well as subsurface habitats, with its highest abundance at 9 to 13 cm (Fig. 3C).

The taxa of the dead assemblages were predominantly calcareous. However, the dead calcareous tests decreased sharply below 5 cm. Agglutinated taxa dominated the dead assemblage at greater depths, while calcareous taxa dominated the dead assemblage in the surface 5 cm (Fig. 4C). In total, 197 mainly rotallinid-shaped foraminiferal linings were counted, with relatively high abundance at 5 cm (Fig. 4C). The downcore abundance patterns of foraminiferal linings and

Textulariina were negatively correlated over most of the core ($r = 0.97$ and $r^2 = 0.94$ at 9 to 30 cm), although within the upper 9 cm of the core, a high negative correlation ($r = 0.94$; $r^2 = 0.89$) was found between foraminiferal linings and Rotaliina. The sum of live + dead individuals was very close to the count of dead tests with depth in the core (Fig. 5C).

Shark River Slough, High Mangroves

At site SRS4, the total count of live specimens was 112, of which more than 80% were calcareous, and nine different taxa were identified. The maximum living depth was 19 cm. The living assemblage reached its maximum abundance within the upper 7 cm, with surface and subsurface maxima at 0 to 2 cm and 7 cm, respectively, and the upper 7 cm contained 76% of the total standing crop (Fig. 2D). Species common at the surface and also found in the subsurface microhabitats were *Helenina anderseni*, *Anomalinoides* (?) sp., and *Trochammina inflata* (Fig. 3D). Their maxima were found at 4 to 8 cm, 7 to 9 cm, and 0 to 4 cm, respectively.

Agglutinated foraminifera were the dominant wall type for the dead assemblages in this core. Dead calcareous tests decreased down core below 3 cm, while the number of agglutinated tests remained dominant (Fig. 4D). In total, 477 mainly rotallinid-shaped foraminiferal linings were counted, and their amounts increased with depth in the core (Fig. 4D). The down-core abundance patterns of foraminiferal linings and Textulariina showed an inverse relationship, and their correlation was negative and high over the length of the core ($r = 0.86$; $r^2 = 0.74$), with a very high negative correlation ($r = 0.97$; $r^2 = 0.95$) over the 4 to 30 cm interval. No such relationship existed with the calcareous tests. The number of tests for the total assemblage (live + dead) and dead assemblage with depth in the core revealed overlapping patterns over most of the length of the core (Fig. 5D).

For three of the sites, the ratio of live tests to live + dead tests over the whole length of each core was, on average, 0.01. For the high mangroves site, the average ratio was 0.1. At this site, the lowest total number of dead tests was also recorded, which explains the higher ratio.

DISCUSSION

Live Assemblages

Living infaunal assemblages in marshes and wetlands are spatially and temporally variable, reflecting, for example, seasonal and local changes in physical conditions, or differences in lithology, the extent of bioturbation, or vegetation cover (Saffert and Thomas 1998, Patterson et al. 2004, Culver and Horton 2005, Tobin et al. 2005, Berkeley et al. 2008, Leorri and Martin 2009, Milker et al. 2015). In contrast to other subtropical, intertidal settings in North America, the Everglades (Chen and Twilley 1999) are mainly vegetated by the mixed mangrove species *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove), *Laguncularia racemosa* (white mangrove), and *Conocarpus erecta* (buttonwood), and the sedge *Cladium jamaicense* (sawgrass).

Even for marshes in the same climatic zone, microhabitat preferences of infaunal foraminifera cannot be generalized (Patterson et al. 2004), and regardless of many studies worldwide on infaunal distributions, a consensus on the vertical distributions and abundances of infaunal species is lacking (Milker et al. 2015). This has inspired discussion of the contributions of deep-dwelling individuals to total assemblages and the need to investigate their influence in order to correctly define modern analogs (Goldstein and Watkins 1999, Culver and Horton 2005, Berkeley et al. 2006, Culver et al. 2013).

In this study, lower counts of live individuals (9–25) were observed for the lower elevation sites as compared to the upper mangrove site further inland (112). These observations agree with foraminiferal studies of temperate salt marshes (Leorri and Martin 2009) as well as tropical mangrove swamp settings (Berkeley et al. 2008, Culver et al. 2013). In the Everglades, while agglutinated taxa prefer shallower sediment depths (0–4 cm), more than half of the calcareous taxa were found below 5 cm depth in the high mangroves site, whereas in the middle and low mangroves, small numbers of calcareous taxa occupied greater sediment depths, and agglutinated taxa became more rare. Overall, at all four sites, most of the live species were calcareous. Three calcareous species, *Ammonia tepida*, *Anomalinoides*? sp., and *Helenina anderseni*, were found infaunally in relatively high counts, and the last two were only common in the high mangroves.

In the salt marshes of Georgia (Goldstein 1988, Goldstein and Harben 1993, Goldstein et al. 1995, Goldstein and Watkins 1999) and North Carolina (Culver and Horton 2005), only one calcareous species occurred infaunally, *Ammonia beccarii* in Georgia and *Helenina anderseni* in North Carolina. In New England marshes (Saffert and Thomas 1998) and mangrove swamps in Malaysia (Culver et al. 2013), no calcareous taxa were found to live infaunally. However, Berkeley et al. (2008) found several living, calcareous, infaunal taxa in Australian mangrove swamps, most commonly *H. anderseni* (upper mangroves), and *Ammonia aoteana*, *Rosalina* spp., *Ammonia pustulosa*, *Elphidium oceanicum*, *Triloculina oblonga*, and *Shackoinella globosa* (lower mangroves).

Subsurface patterns of live foraminifera are often partially explained as the result of differences in oxygenation, caused by differences in the depth of plant root growth and other bioturbation processes (Goldstein and Harben 1993, Goldstein et al. 1995, Saffert and Thomas 1998, Culver and Horton 2005, Berkeley et al. 2008, Leorri and Martin 2009). Despite the decrease with depth in resources such as oxygen, bacteria, and organic matter, many species of foraminifera can

live at greater depths within the sediment. Oxygen is not a limiting factor, but the combination of anoxia and hydrogen sulfide is lethal to all foraminifera, and the depth at which this combination occurs will form their lowermost boundary (Jorissen et al. 1995, Van der Zwaan et al. 1999). Through bioturbation, living foraminifera may also reach subsurface sediments by passive transport (Goldstein et al. 1995, Saffert and Thomas 1998, Hayward et al. 2014), perhaps explaining some extensive, deep infaunal occurrences. In subtidal zones, the constant mixing of sediments by macrobenthos generates a more homogeneous layer. However, in the intertidal zone, bioturbation creates a patchy subsurface environment that may offer suitable microhabitats for foraminifera (Goldstein et al. 1995), for example, by creating oxic pockets or by redistributing food particles (Goldstein and Harben 1993, Jorissen 1999).

Influence of Infauna on Total Assemblages

For this study, surface cores were only collected during the summer season, because even though variability from season to season and between species is apparent, data collected by Buzas et al. (2002) in the Indian River Lagoon (south Florida), which is latitudinally and geographically near our sites, show that the summer season usually has larger densities of living, reproducing taxa, and many studies mention temperature as an important factor in controlling reproduction (Murray and Alve 2000, Hippensteel et al. 2002). Even though many field studies show maximum densities during specific seasons, reproduction is commonly continuous throughout the year (Buzas et al. 2002) but slower during colder months (Murray and Alve 2000). The collection of samples in the season during which the highest abundances of live individuals are recorded was also followed by Duchemin et al. (2005).

In the current study, the overall low ratios (0.01 and 0.1) of live tests to live + dead tests over the whole length of each core illustrate that the counts of live individuals were very low and will

obviously not have a large impact on the total assemblage. Furthermore, the downcore distribution of the total count (live + dead individuals) did not exceed the counts of dead individuals by much, demonstrating that infaunal live production did not exert a substantial influence on subsurface assemblages, so that the dead assemblage and total assemblage were essentially the same. A similar conclusion was reached by Culver and Horton (2005). In the Everglades, as with studies in Georgia by Goldstein and Harben (1993) and Goldstein et al. (1995), British Columbia, Canada, by Ozarko et al. (1997), New England by Saffert and Thomas (1998), North Carolina by Culver and Horton (2005), and Oregon by Milker et al. (2015), none of the taxa was found exclusively in subsurface habitats, and the upper 2 cm of the sediment column contained, on average, 36% of the total standing crop. Studies in other areas have also confirmed that surface samples sufficiently represent the modern assemblage, such as for Chezzetcook Inlet, Canada (Tobin et al. 2005), and Coos Bay, Oregon (Milker et al. 2015). For our high mangroves site, the contribution of live individuals was at least twice as large in the surface 2 cm as for any other depth. At the other sites, the down-core live contribution was negligible, because the live specimens were very low in number. We agree with Culver et al. (2013) that as long as all abundant taxa occur both in shallow and deep subsurface habitats, the 0 to 2 cm interval is sufficient as a modern analog, although their 0 to 2 cm interval contained, on average, only 7% of the total standing crop. Using larger intervals is not necessary because: (1) total assemblages (live + dead) instead of live assemblages will be used as modern analogs because they incorporate the temporal and spatial variations characterizing live assemblages (Scott and Medioli 1980), and (2) the Everglades have slow sedimentation rates (2.5 mm/yr to 3.6 mm/yr [Smoak et al. 2013]; 0.9–2.5 mm/yr [Koch et al. 2015]), so a 2-cm interval represents about 6 to 22 years of sediment accumulation.

Studies of other marshes have indicated that a thicker surface sample should be used for modern analogs. In Georgia salt marsh studies (Goldstein 1988, Goldstein and Watkins 1999), *Arenoparrella mexicana* showed a contribution to subsurface assemblages by infaunal individuals,

so a 0 to 10 cm modern analog was recommended. For the temperate marsh studies by Ozarko et al. (1997) and Patterson et al. (1999) in British Columbia, Canada, and that by Saffert and Thomas (1998) in New England, it was necessary to use a 10-cm modern analog. Leorri and Martin (2009) concluded that the modern analog for the Delaware marshes should be the upper 5 cm of the sediment column. Recommendations to use the thicker sampling intervals to characterize the modern assemblage assume that environments have not changed over the time span represented by that sediment interval, which may not be justified for many intertidal settings (Milker et al. 2015). For the Everglades, our short cores may not have recorded shifting habitats; cores dated by Yao et al. (2015) and Yao and Liu (2017) included a ^{14}C date of 0 to 280 cal yr B.P. for the upper 56 cm of sediment, which was 24 to 84 cm above the last environmental change. Thus, we can safely assume that our 2 cm modern analog only represents the current habitat.

Variability in Microhabitat Preferences

Our observation that microhabitat preferences are deeper for individuals living at the higher, more inland elevations (7–10 cm deep) than for individuals living at the lower elevations (1–3 cm deep) is in line with observations by Berkeley et al. (2008) for Australian mangroves. They found average living depths of ~10 cm for the upper mangroves and ~5 cm for the lower mangroves and mudflats. Additionally, for the Delaware marshes, Leorri and Martin (2009) found peak concentrations at 1 to 10 cm, 1 to 5 cm, and 3 to 5 cm, for the high, intermediate, and low marshes, respectively. The study of Ozarko et al. (1997) for British Columbian salt marshes revealed that in the high marsh, 95% of the standing crop was found at 0 to 24 cm, while in the low marsh, it was at 0 to 12 cm. On the other hand, an opposite trend was found in New England marshes, with high abundances at 0 to 2.5 cm and 2.5 to 5 cm for the high marsh and lower marsh, respectively (Saffert

and Thomas 1998), although the differences in depths were much less than in the studies cited above.

In the upper mangroves of the Everglades, results show that several common subsurface taxa have specific microhabitat preferences. *Trochammina inflata* occupies a shallow subsurface habitat (0–4 cm), similar to the findings by Goldstein and Harben (1993), Goldstein et al. (1995), and Hayward et al. (2014). In the Everglades, the habitat preference of single species differs among sites; e.g., *Ammonia tepida* had a shallower preference in the mudflats and low mangroves (0–1 cm), but a deeper preference in the middle mangroves (9–13 cm). Similarly, Goldstein et al. (1995) found that infaunal distributional patterns varied for all taxa between marsh habitats.

During the present study, we observed that: (1) live foraminifera occur over a deeper interval in sediments with higher amounts of peat, as at the middle and high mangroves sites (compare Fig. 2C, D with Fig. 2A, mudflats); and (2) live individuals are absent in the surface sediment where the soil is covered with sparse leaf litter (middle mangroves site; see Fig. 2C). A deeper microhabitat preference at higher elevations may result from a deepening of the redox interface in a landward direction (Berkeley et al. 2008, Leorri and Martin 2009). Everglades mangroves increase their belowground biomass landward in the form of fine roots (Castañeda-Moya et al. 2013). Leorri and Martin (2009) related higher root densities to greater oxygenation of the subsurface sediments, although lithology (Buzas 1977, Culver and Horton 2005), vertical fluid motion, and differences in vegetation (Saffert and Thomas 1998) can also explain infaunal microhabitats in intertidal environments.

Preservation

Geographic changes in the abundance of linings suggest an inland increase in dissolution/degradation; from the low mangroves toward the high mangroves sites, there is a large

increase in the total number of foraminiferal inner test linings and a sharp decrease in the total number of dead tests. In general, most foraminiferal species have inner test linings, with some exceptions (Lipps 1973); thus, the observed linings could have originated from calcareous as well as agglutinated foraminifera. The higher ratio of live to dead specimens for the high mangroves site could also reflect an increase in taphonomic loss (Hayward et al. 2015). In the low mangroves, the high negative correlation ($r = 0.91$; $r^2 = 0.83$) between Rotaliina and inner test linings over 5 to 30 cm suggests dissolution and taphonomic loss of calcareous tests by low pH. For the middle mangroves, dissolution of calcareous taxa is restricted to the upper 9 cm ($r = 0.94$; $r^2 = 0.89$ for Rotaliina and inner test linings), but in the lower part of the core, the negative correlation between Textulariina and inner test linings ($r = 0.97$; $r^2 = 0.94$) suggests the degradation and taphonomic loss of agglutinated taxa. For the high mangroves, degradation of agglutinated taxa occurs over the complete length of the core ($r = 0.86$; $r^2 = 0.74$).

In the subtropics and tropics, seasonal fluctuations in evaporation and freshwater input from rivers or rainfall are greater (Culver and Horton 2005, Cesbron et al. 2016), causing large differences in salinity, pH, and carbonate content, for example. Additionally, seasonal fluctuations in pH, and associated dissolution of calcareous tests, become more severe further inland (Debenay et al. 2002). Agglutinated taxa typically become more abundant in a landward direction with decreasing salinity (Goldstein 1976). Thus, for our study, the low total count of dead tests and the increase in linings at the more inland sites imply that mainly agglutinated tests seem to be affected by degradation through oxidation, but most likely not low pH. The preservation of agglutinated taxa is determined by the type of their cement, which can be wholly organic or biomineralized (Loeblich and Tappan 1989, Roberts and Murray 1995, Bertram and Cowen 1998), and also by the microstructure of their organic cement (Bender and Hemleben 1988). Oxidation (Hoge 1994; Goldstein et al. 1995; Berkeley et al. 2007, 2009; Culver et al. 2013) and bacterial degradation affect agglutinated tests with organic cements (Goldstein and Watkins 1999; Berkeley et al. 2007, 2009). The typical salt

marsh species *Trochammina inflata*, *Miliammina fusca*, and *Jadammina macrescens* have an organic cement (Bender and Hemleben 1988, Armynot du Chatelet et al. 2008), and from the lack of reaction to 10% HCl by agglutinated taxa from our high mangroves site, we conclude that our intertidal, agglutinated species also have organic cements.

Degradation is enhanced by sediment oxygenation, which can be increased by burrows made, for example, by crustaceans (Goldstein et al. 1995, Leorri and Martin 2009, Culver et al. 2013). During low tide, numerous crab burrows were visible at our mangrove sites, so bioturbation in the Everglades may be similar to the salt marshes of Georgia (Goldstein et al. 1995) and the mangroves of Malaysia (Culver et al. 2013). Reworking of sediments by bioturbators can also increase dissolution rates of calcareous tests, because increased bioturbation prevents alkalinity accumulation (Debenay et al. 2004). However, in the case of a carbonate-buffered system like the Everglades, preservation of calcareous foraminifera is enhanced (Phleger 1965, Berkeley et al. 2007).

Oxygenation of the sediment is also associated with extensive plant root systems transferring oxygen into the sediment (Goldstein et al. 1995, Berkeley et al. 2009, Culver et al. 2013). The cores retrieved along the Shark River revealed a dense to very dense network of mainly very fine plant roots, and at some sites, thicker roots were also present. The landward increase in the belowground biomass in the form of fine roots (Castañeda-Moya et al. 2013) can potentially increase the oxygenation of the sediment, creating a deeper redox front (Leorri and Martin 2009), which increases the vertical area in which agglutinated dead tests can be affected by degradation through oxidation (Hoge 1994).

CONCLUSIONS

We investigated living depths of infaunal foraminifera of the southwestern Everglades. In total, for all four sites, 27 live taxa were found, of which 20 were calcareous. Overall, more than

80% of the live specimens in surface and subsurface habitats belonged to calcareous taxa, of which the most common were *Helenina anderseni*, *Anomalinoides* (?) sp., and *Ammonia tepida*. Live agglutinated taxa were mainly found in the more inland, lower salinity sites, where total (dead + live tests) assemblages consisted of more dead agglutinated taxa. Where they occurred, agglutinated taxa showed a shallower habitat preference (e.g., *Trochammina inflata* at 0–4 cm) than calcareous taxa (e.g., *H. anderseni* at 4–8 cm). The upper mangroves site had much higher total counts of live specimens (112) than the other three sites (9–25). In a landward direction, the microhabitat preference deepened from 1 to 3 cm (mudflats and low mangroves) to 7 to 10 cm (middle and high mangroves). A possible explanation is that a landward increase in fine root density leads to greater oxygenation of subsurface sediments.

We also examined the influence of deeper-dwelling individuals on total assemblages. The common taxa found in infaunal habitats also occurred in the surface sediment. Downcore, counts of live + dead tests and dead tests were basically indistinguishable because live production was very low throughout the cores, so that the influence of the deeper infauna on subsurface assemblages was negligible. Additionally, the 0 to 2 cm interval contained, on average, 36% of the total standing crop. Therefore, (1) the composition of the total assemblage in the 0 to 2 cm interval, representing the modern assemblage, adequately represents the entire live assemblage, which includes deep-dwelling species; and (2) the total assemblage at greater depths, which is that preserved for paleoenvironmental analyses, will not be altered meaningfully by the minor subsurface production. Thus, the upper 2 cm interval of the sediment column is sufficient as a modern analog for paleoenvironmental studies in the southwestern Everglades.

Last, we studied the preservation of dead tests. The calcium carbonate-rich sediments of the Everglades create a carbonate-buffered environment in which calcareous taxa are preserved exceptionally well. Although the presence of test linings indicates that some dissolution takes place, the results suggest that the main factor influencing preservation is the degradation of

agglutinated taxa through oxidation/bacterial breakdown of organic cements. The landward increase in oxygenation of the sediment may create a deeper redox front that increases the vertical extent to which agglutinated dead tests can be affected by oxidation.

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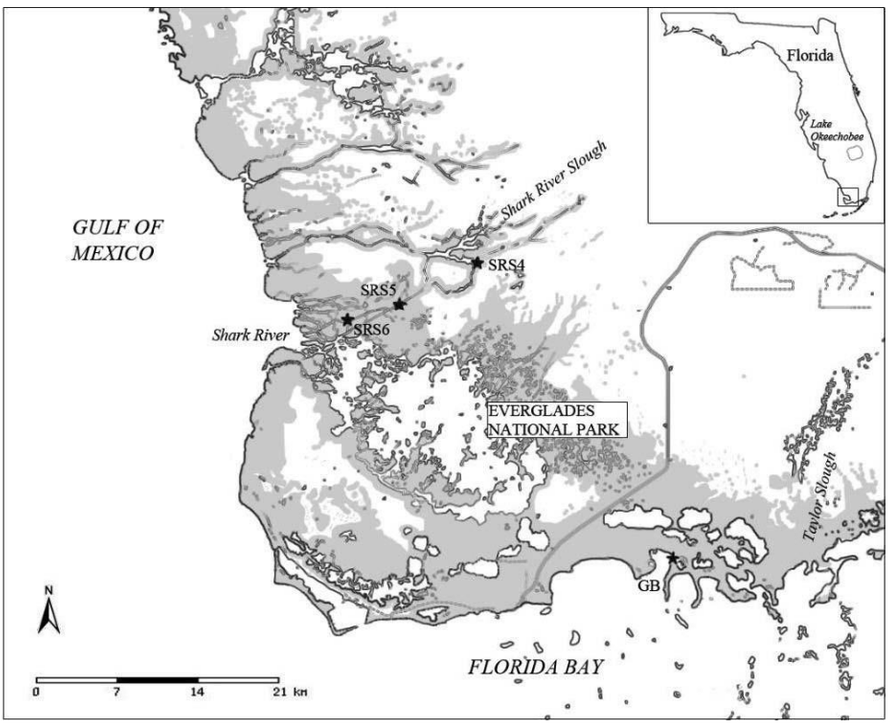

FIG. 1.—Map of the study area showing the sampling locations SRS4, SRS5, and SRS6 along the Shark River and Shark River Slough, and location GB at Garfield Bight. The coastal zone shaded in gray shows the approximate location of mangroves. On this map, the double line represents State Highway 9336, and the dashed lines are park trails. Figure is adapted from Google Maps and South Florida Water Management District (1995) land-use map.

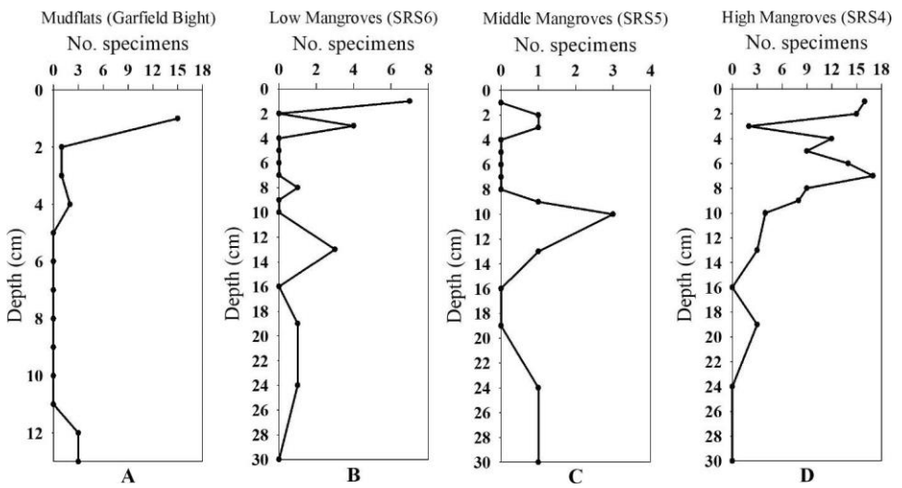

FIG. 2.—Live counts with depth in core for sites: A) mudflats (Garfield Bight); B) low mangroves (SRS6); C) middle mangroves (SRS5); and D) high mangroves (SRS4).

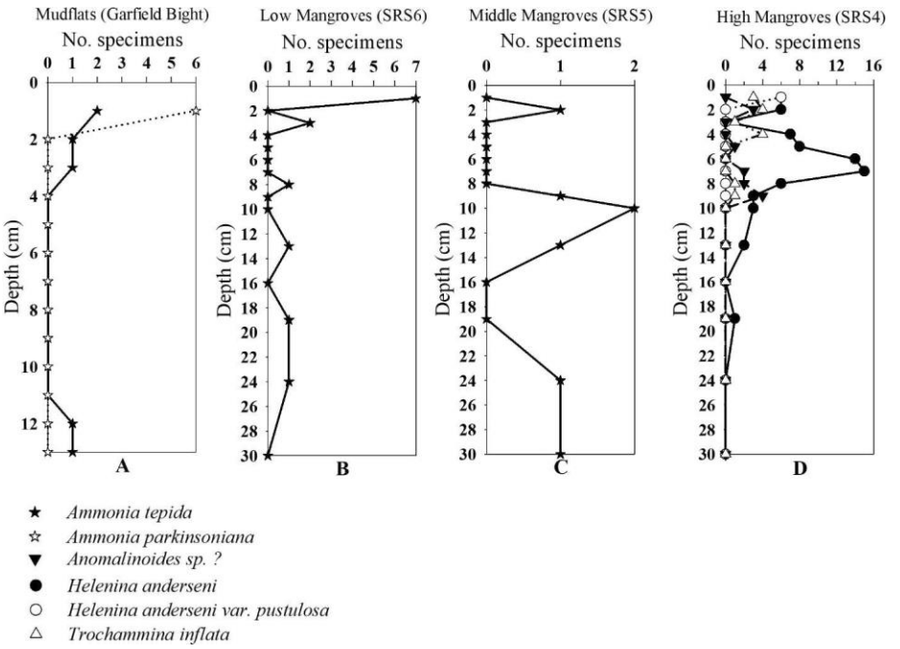

FIG. 3.—Counts of live species with depth in core for sites: A) mudflats (Garfield Bight); B) low mangroves (SRS6); C) middle mangroves (SRS5); and D) high mangroves (SRS4).

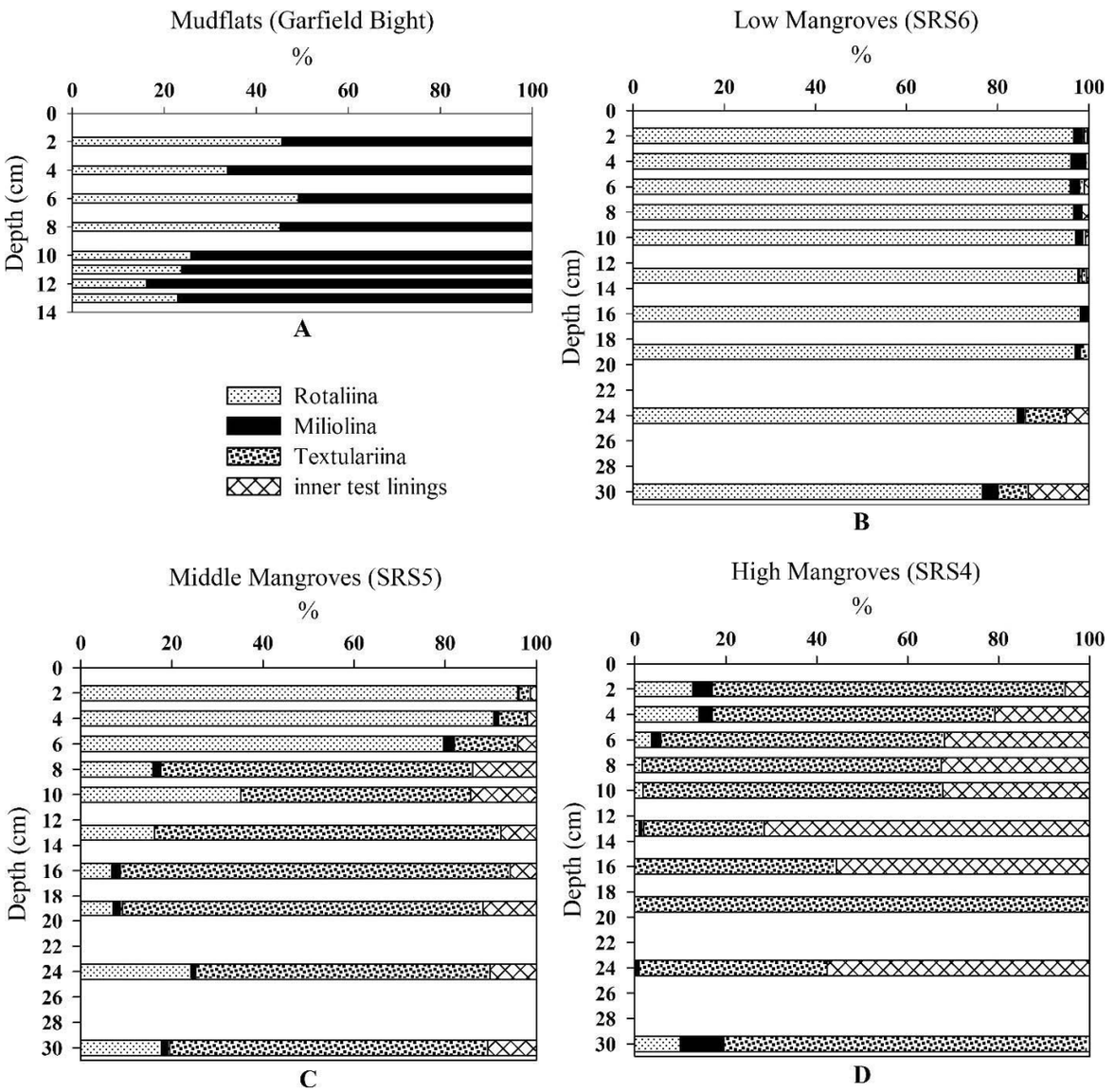

FIG. 4.—Relative abundance of the three wall types of Rotaliina, Miliolina, and Textulariina, and foraminiferal inner test linings for the dead assemblages with depth in core for sites: A) mudflats (Garfield Bight); B) low mangroves (SRS6); C) middle mangroves (SRS5); and D) high mangroves (SRS4). Two-centimeter-thick samples were analyzed down to 10 cm, and then 1-cm-thick samples were analyzed down to 13 cm (A), and down to 30 cm (B–D).

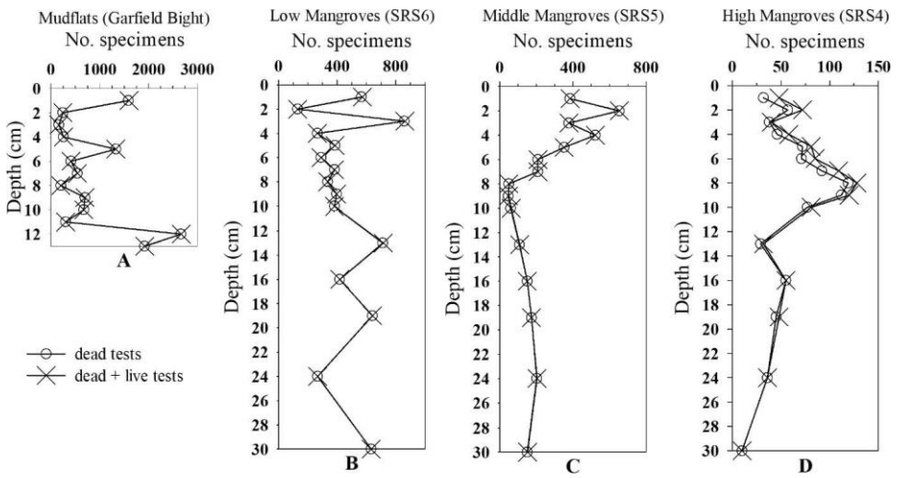

FIG. 5.—Counts of dead tests and dead + live tests with depth in core for sites: A) mudflats (Garfield Bight); B) low mangroves (SRS6); C) middle mangroves (SRS5); and D) high mangroves (SRS4).

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APPENDIX

Table 1— Counts of the three wall types (Rotaliina, Miliolina, and Textulariina), inner test linings, and stained "live" individuals with depth in core for the Mudflats (Garfield Bight), Low Mangroves (SRS6), Middle Mangroves (SRS5), and High Mangroves (SRS4) sites.

	Mudflats, Garfield Bight					Low Mangroves, SRS6					Middle Mangroves, SRS5					High Mangroves, SRS4				
depth (cm)	**Rotaliina**	**Miliolina**	**Textulariina**	**linings**	**live**	**Rotaliina**	**Miliolina**	**Textulariina**	**linings**	**live**	**Rotaliina**	**Miliolina**	**Textulariina**	**linings**	**live**	**Rotaliina**	**Miliolina**	**Textulariina**	**linings**	**live**
0-1	721	865	3	0	15	548	14	5	2	7	377	2	6	5	0	10	4	18	3	16
1-2	115	128	0	0	1	129	2	0	0	0	632	2	20	8	1	2	0	55	2	15
2-3	55	108	0	0	1	830	27	3	0	4	347	5	26	8	1	10	2	26	1	2
3-4	87	169	0	1	2	252	9	5	0	0	487	4	32	10	0	5	1	40	21	12
4-5	717	611	2	0	0	374	8	4	0	0	317	8	28	8	0	3	1	68	12	9
5-6	139	271	0	0	0	282	6	3	7	0	150	6	53	16	0	5	3	63	55	14
6-7	286	255	0	0	0	377	6	0	5	0	38	5	166	32	0	3	0	89	53	17
7-8	52	155	0	0	0	329	7	0	6	1	10	0	40	10	0	2	0	117	49	9
8-9	155	544	0	0	0	386	7	4	0	0	19	0	28	11	1	3	0	109	10	8
9-10	200	474	0	0	0	377	6	0	6	0	25	0	35	7	3	2	0	75	80	4
10-11	72	230	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11-12	431	2236	0	0	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12-13	441	1480	1	0	3	700	6	7	4	3	19	0	89	9	1	1	1	27	73	3
15-16	-	-	-	-	-	412	7	0	1	0	11	3	137	9	0	0	0	55	69	0
18-19	-	-	-	-	-	623	7	12	0	1	14	4	156	23	0	0	0	45	0	3
23-24	-	-	-	-	-	237	5	25	14	1	55	2	146	23	1	0	1	35	49	0
29-30	-	-	-	-	-	561	25	48	97	0	30	3	118	18	1	1	1	8	0	0
Total	**3471**	**7526**	**6**	**1**	**25**	**6417**	**142**	**116**	**142**	**17**	**2531**	**44**	**1080**	**197**	**9**	**47**	**14**	**830**	**477**	**112**

Table 2— Counts of individual species for the stained "live" individuals with depth in core for the Mudflats (Garfield Bight), Low Mangroves (SRS6), Middle Mangroves (SRS5), and High Mangroves (SRS4)

	Mudflats													**Low Mangroves**					**Middle Mangroves**			**High Mangroves**								
	calcareous													**calcareous**			**aggl.**		**calcareous**		**aggl.**	**calcareous**				**agglutinated**				
Species / **Depth (cm)**	*Ammonia parkinsoniana*	*Ammonia tepida*	*Elphidium morenoi*	*Cribroelphidium poeyanum*	*Cribroelphidium incertum*	*Rosalina candeiana*	*Rosalina sp.*	*Quinqueloculina bicostata*	*Quinqueloculina poeyana*	*Miliolinella californica*	*Triloculina fiterrei*	*Triloculina rotunda*	*Heterillina cribrostoma*	*Ammonia tepida*	*Bolivina striatula*	*Bolivina paula*	*Textularia agglutinans*	*Trochammina inflata*	*Ammonia tepida*	*Quinqueloculina seminulum*	*unknown*	*Helenina anderseni*	*Helenina anderseni var. pustulosa*	*Quinqueloculina bosciana*	*Anomalinoides sp.*	*Haplophragmoides columbiensis*	*Haplophragmoides manilaensis*	*Trochammina inflata*	*Miliammina fusca*	*Siphotrochammina lobata*
0-1	6	2	2	1	0	0	0	2	0	1	1	0	0	7	0	0	0	0	0	0	0	6	6	0	0	1	0	3	0	0
1-2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	6	0	2	3	0	0	4	0	0
2-3	0	1	0	0	0	0	0	0	0	0	0	0	0	2	1	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0
3-4	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	4	1	0
4-5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	1	0	0	0	0	0
5-6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0
6-7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	0	0	2	0	0	0	0	0
7-8	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	6	0	0	2	0	0	1	0	0
8-9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3	0	0	4	0	0	1	0	0
9-10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	3	0	0	0	0	0	0	0	1
10-11	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11-12	0	1	0	0	0	1	0	0	0	0	0	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12-13	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	1	0	0	2	0	0	0	0	0	0	1	0
15-16	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18-19	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0
23-24	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
29-30	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Total	**6**	**6**	**2**	**1**	**1**	**1**	**1**	**2**	**1**	**1**	**1**	**1**	**1**	**13**	**1**	**1**	**1**	**1**	**7**	**1**	**1**	**71**	**6**	**3**	**12**	**1**	**2**	**14**	**2**	**1**

Chapter 3

Environmental Controls on the Distribution of Modern Benthic Foraminifera in the Florida Everglades for Their Use as Paleoenvironmental Indicators

ABSTRACT

This study examined the environmental factors that control the distribution of modern foraminiferal assemblages in the Everglades in order to provide baseline data for a paleoenvironmental study. Total assemblages from the surface 2 cm of 30 sites across the marsh and mangrove environments of southwest Florida were investigated. Seven environmental variables, including average salinity, pH, total phosphorus, temperature, and dissolved oxygen, and total organic carbon and total inorganic carbon measured on bulk sediments, as well as the distance from the coastline were determined for each of the 30 sampling locations.

In total, 82 species were identified, the majority of which were calcareous. Diversity decreases, dominance increases, and agglutinated taxa increase from the coastline inland. Rotaliina are equally abundant across the intertidal environment, whereas Miliolina are common near the coast and in lagoons or inland lakes. The most important factor controlling foraminiferal distribution is salinity, followed by total organic carbon and total inorganic carbon. *Jadammina macrescens*, *Tiphotrocha comprimata, Trochammina inflata, Trochamminita salsa,* and *Miliammina fusca* indicate lower salinities (<18 psu). Good indicators for higher salinities are *Haplophragmoides wilberti* (16–18 psu) and *Arenoparrella mexicana* (16–18 psu and 28–30 psu). *Ammonia*

spp. prefer salinities >15 psu and *Elphidium* spp. >20 psu. *Ammonia tepida*, *Helenina anderseni*, *Trochammina inflata*, and *Arenoparrella mexicana* prefer organic-rich sediments. Thus, the benthic foraminifera from Everglades sediments are excellent salinity proxies and can be used to determine the history of habitat change in this area, as well as to assess past trends in the rate of sea level rise.

INTRODUCTION

This study examines changes in assemblage composition of modern benthic foraminifera from marshes and mangroves along the coast of the Everglades in South Florida. The purpose is to investigate which environmental factors (salinity, pH, total organic carbon, total inorganic carbon, total phosphorus, temperature, dissolved oxygen) control the distribution of foraminiferal assemblages and to assess their use as proxies for salinity in the past.

Kemp et al. (2011) and Milker et al. (2015) stress the importance of collecting samples over a wide spatial area and from different habitats instead of along transects, which suggest a regular foraminiferal distribution. Most benthic foraminifera commonly live in the surface 1 cm of the sediment column (Van der Zwaan et al., 1999). Verlaak et al. (2018) demonstrated that the upper 2 cm of sediment sufficiently represents the modern assemblage to be used as an analog for paleoenvironmental studies in the southwestern Everglades.

Salinity is known to be one of the important controlling factors on foraminiferal distribution (e.g., Murray, 1973; Hayward & Hollis, 1994; Cheng et al., 2012; Culver et

al., 2012). However, foraminiferal abundances and assemblage composition may change under the influence of many possible factors, including nutrition (e.g., labile organic matter), dissolved oxygen, pH, sediment grain size, temperature, duration of subaerial exposure, and the amount of vegetation cover (Armynot du Chatelet et al., 2008). Benda & Puri (1962) remarked that the distribution patterns of foraminiferal assemblages in the northwestern Everglades seem to be controlled by a combination of ecologic factors rather than a single factor.

Most foraminifera are adapted to normal marine salinities between 32 and 37 psu (Armstrong & Brasier, 2005), and only tolerate small changes (Murray, 1973). As a result, normal salinities are characterized by the highest-diversity assemblages, although some species can tolerate larger fluctuations in salinity and are adapted to marginal marine environments in low-diversity assemblages. Most of the species living in hyposaline conditions (≤32 psu) are restricted to this environment, while species living in hypersaline environments (>37 psu) could also live under normal marine conditions (Murray, 1973).

One reason that salinity forms a limiting factor for foraminifera is that changes in salinity influence the water density and osmotic effects (Murray, 1973). The imperforate tests of the suborders Miliolina and Textulariina are better than the perforate tests of Rotaliina at protecting the endoplasm of the cell from stressful osmotic gradients caused by salinity fluctuations (Armstrong & Brasier, 2005). Relative proportions of these suborders are very useful for differentiating shallow-water environments (Murray, 1991), and very effective as indices for paleosalinity. Another reason salinity is a limiting factor for wall type distribution is its relationship to calcium carbonate availability. The

solubility of calcium carbonate is controlled by salinity but also by temperature and carbon dioxide content so that calcium carbonate is more readily available in subtropical to tropical marine or hypersaline environments. Therefore, species with agglutinated tests and non-calcareous cements will dominate where calcium carbonate availability is low, as in hyposaline environments (Murray, 1973).

At any given location across the intertidal environment, the salinity and the degree of inundation change over time due to continuing sea level rise over the last ~5000 years. With rising sea level, salt water intrusion and inundation continue to progress in a landward direction (Price et al., 2010). The responses of mangrove wetlands to sea level rise have not received the same scientific attention as salt marsh coasts in North America and Northwestern Europe, even though mangrove forests comprise 70% of tropical and subtropical coasts (Woodroffe et al., 2005; Parry et al., 2007; Culver et al., 2013). From the only previous foraminiferal studies of South Florida's coastal mangrove-influenced environments (Benda & Puri, 1962; Phleger, 1965; Goldstein, 1976; Bock & Gebelein, 1977), two important conclusions can be made: (1) A larger number of calcareous species than expected for most marsh environments is attributed to the sediment composition, which is mainly calcium carbonate in the form of fine mud and shelly material (Phleger, 1965). The calcium carbonate neutralizes the organic acids resulting from decaying plant matter, allowing the preservation of calcareous forms. (2) In a landward direction, diversity decreases, and foraminiferal assemblages change from a mainly calcareous to an agglutinated species composition.

This study investigates: (1) how assemblage composition changes geographically across the Everglades, and which species contribute the most to these spatial differences,

(2) what the salinity preferences of the most characteristic species are, (3) whether salinity is the main controlling factor on foraminiferal distributions, and (4) what other environmental factors play a role in their spatial distribution.

METHODS

Field Methods

Sediment samples were collected at 30 study sites across the southwestern part of Everglades National Park (Fig. 1). The main water bodies within which or along which sampling took place were Shark River, Harney River, Lostmans River, Ponce de Leon Bay, Oyster Bay, White Water Bay, West Lake, Long Lake, Cuthbert Lake, Alligator Creek, Terrapin Bay, and Garfield Bight. The samples were collected from the upper 2 cm of sediment using a putty knife.

The water quality of the coastal Everglades, indicated by factors such as salinity and nutrient content, fluctuate seasonally with rainfall (Childers et al., 2006; Briceño et al., 2014); therefore, we did not make single salinity measurements at the time of sampling. Instead, averages were calculated based on long-term water quality data (https://apps.sfwmd.gov/WAB/EnvironmentalMonitoring/index.html), a combination of data from multiple agencies and academic institutions. Salinity, pH, total phosphorus, dissolved oxygen, and temperature were compared to the foraminiferal assemblages.

Laboratory Methods

Each sediment sample was rinsed over nested screens of 2.80 mm to remove larger sediment particles or organic matter, and 63 µm to remove silts and clay-sized grains. The residue, which contains the benthic foraminifera (adults and most juveniles), was then transferred onto filter paper, air-dried overnight, and split into subsamples containing up to ~300-400 individuals, which were picked and sorted onto slides for identification. The number of species in an assemblage is related to the number of individuals collected, but above ~400 individuals, larger sample sizes do not significantly improve accuracy (Murray,1973, 1991). In agreement with the conclusions of Scott & Medioli (1980), this study used total assemblages.

West Lake samples WL23, WL24, WL25, WL27, and WL28, as well as Alligator Creek samples AC1 and AC3, contained a lot of carbonate mud, which was very difficult to remove, even after thoroughly rinsing the sediment over nested screens, and the mud would clump together upon air drying the sediment. Consequently, these samples were soaked overnight in paint thinner (adapted from USGS Varsol method), afterwards transferred onto filter paper to remove the paint thinner and moved into another beaker which was filled for about ¾ with water and one tablespoon of washing soda. This mixture was then cooked at a low simmer for about 3 hours on a hotplate. Next, the sediment was poured through a 63 µm sieve and rinsed thoroughly, then transferred onto filter paper and air dried.

Literature on Gulf of Mexico and Caribbean benthic foraminifera that aided the taxonomic identifications were by Parker et al. (1953), Saunders (1957, 1958), Warren

(1957), Wantland (1967), Jones & Bock (1971), Miller et al. (1982), Buzas et al. (1985), Debenay et al. (1998), Buzas-Stephens et al. (2002), Javaux & Scott (2003), Berkeley et al. (2008), and Sen Gupta et al. (2009). Specimens of this study were compared to primary and secondary types in the Cushman Collection of Foraminifera at the Smithsonian Institution, National Museum of Natural History, Washington, D.C.

Total inorganic carbon and total organic carbon content were measured from the collected sediment samples. Prior to performing carbon measurements, all dried sediment samples were ground to a very fine powder. The ceramic boats for holding sediment samples and carbon standards were cleaned by soaking them in 10% HCl for 2 hours to remove any inorganic residues from prior use, then rinsed in deionized water until neutral pH was reached, and oven-dried overnight at 70˚C. The following day, the boats were heated at 560˚C for 2 hours to remove any organic residues.

Next, eleven ceramic trays were filled with increasing amounts, between 0.05 and 0.10 g, of an EDTA standard with a known organic carbon content of 41%, and another eleven trays were filled with increasing amounts, between 0.05 and 0.40 g, of a carbonate standard with a known inorganic carbon content of 100%. Afterwards, 30 ceramic boats were filled with ~0.25 g of each of the 30 powdered sediment samples. The carbon analyses were performed using a LECO CR-412 furnace in the carbon laboratory, Department of Earth and Environment, Florida International University. The carbon analyzer uses an infrared cell to measure the CO_2 produced by combustion of the powdered sediment samples.

Each tray with the EDTA standard was heated in a furnace at 800˚C to obtain calibration. Afterwards, the exact initial weights of the powdered sediment samples

(~0.25 g) were entered in the computer connected to the carbon analyzer and the samples were analyzed for their total percentage of organic carbon by inserting the ceramic boats containing the samples into the furnace one at a time. Subsequently, the oven temperature was raised to 1400˚C and the carbon analyzer was calibrated using the trays with the carbonate standard. The same sediment samples, used to obtain the organic carbon content, were then used to analyze their total inorganic carbon content (%$CaCO_3$) by inserting them one at a time into the furnace. The values for the sample weights were the same as initially entered (~0.25 g), before measuring the total organic carbon content of the sediments. Therefore, for each sample, both the %TIC and %TOC represent the fraction of the total initial weights of the samples.

We also performed a simple test using 10% HCl on one specimen of each agglutinated species recorded in this study. The reaction to acidic conditions would allow us to distinguish between agglutinated tests with organic cements and non-carbonate grains, and those with carbonate cements and/or carbonate grains.

Quantitative Methods

From a total of 82 identified species, 60 taxa with a relative abundance of at least 1% in at least one sample, herein considered the common taxa, were selected for statistical analyses. Eliminating the rarest taxa reduces “noise” in the data analyses, although some rare species themselves can be used as environmental indicators. For all analyses that require the selection of a distance measure, we used the Bray-Curtis dissimilarity index

$$2w/(a+b)$$

where w is the sum of the lesser value for species that are in common between two samples, and a and b are each the sum of the quantitative measures in one sample and the other sample, respectively (Bray & Curtis, 1957). This algorithm is commonly used when identifying associations of samples (e.g., Culver, 1990; Hayward et al., 1996; Wachnicka et al., 2010).

Two of the 30 samples were barren of foraminifera, so were omitted from the statistical analyses. All analyses and diversity measures discussed below were completed using the open-source PAST (PAleontological STatistics) software package, version 2.17c (Hammer et al., 2001).

To identify sites that were most similar in their species composition, we performed unweighted pair-group, Q-mode cluster analysis. One-way ANOSIM or analysis of similarities (Clarke, 1993) was used to assess whether the identified clusters are significantly different from each other ($p < 0.05$). This test is based on comparing between-group with within-group distances and converts these distances to ranks.

We also performed R-mode clustering of the common taxa to visualize species associations. Next, an overall multi-group SIMPER (similarity percentage) analysis indicated the percentage-contribution of each species to the dissimilarity between the groups (Clarke, 1993). The most important contributing species (at least 1% contribution) were selected for a simultaneous Q-mode and R-mode cluster analysis to show the correlation between sample associations and species associations. Within each association, the dominant species were identified by calculating the average abundance of each (modified after Hayward et al., 1996).

In order to quantify taxonomic diversity, we used the Shannon diversity index

$$H' = - \sum p_i \ln (p_i)$$

with p_i the relative proportion of each species (Shannon, 1948), taking into account both the number of individuals as well as the number of taxa. A value of zero corresponds to an assemblage of a single taxon, and higher values result from assemblages with many taxa consisting of few individuals. Dominance, which measures the spread of the individuals across species, was calculated with the Berger-Parker Index (Berger & Parker, 1970)

$$d = N_{max} / N$$

with N the total number of individuals and N_{max} the number of individuals in the most abundant species (Hayek & Buzas, 2013). The species contributing the most to the observed differences between groups of samples, wall type percentage, and diversity and dominance indices were plotted against distance from the coastline, to examine the geographic changes in foraminiferal assemblages.

The salinity preference of each species was investigated by plotting species abundance against salinity. If total assemblages accumulated over several seasons and years, as is typical, then they represent average abundances of species at a specific location, and preference can be defined as the salinity range at which the species exhibits its maximum abundance (cfr. Jorissen, 1999).

To assess the extent to which the environmental variables influenced the foraminiferal distributions, we used principal component analysis and non-metric multidimensional scaling. Principal component analysis of the foraminiferal assemblages reduces the dataset by calculating hypothetical variables (principal components) that

explain the maximum amount of variance and can be hypothesized as correlated with underlying (environmental) variables (Hammer et al., 2001). Therefore, the most important environmental variables can be identified as those most strongly associated with the first principal component, which explains most of the variance of the dataset.

Non-metric multidimensional scaling plotted samples and environmental variables in a two-dimensional space. Variables are plotted as vectors with different lengths originating from the origin. The vector with the longest relative length influences the distribution of the assemblages most strongly (Hammer et al., 2001; Wachnicka et al., 2010).

RESULTS

Assemblage Characteristics

In total, 77% of the 82 identified species were calcareous, with 46 species belonging to the suborder Rotaliina, 17 to the Miliolina, and 19 to the Textulariina (Tables 1 and 2). Rare species in the Rotaliina included 36% (i.e., with a relative abundance <1% in any sediment sample), the Miliolina 6%, and the Textulariina 21%. The selection of the 60 common species used in the statistical analyses consisted of 29 belonging to the Rotaliina, 16 to the Miliolina, and 15 to the Textulariina. None of the agglutinated taxa, except for *Ammobaculites dilatatus* and *Ammotium multiloculatum*, react to 10% HCl.

The sampling sites cover the full hyposaline range (0.5–32 psu), over which taxonomic diversity (Shannon diversity index) is generally low. After a peak near the coastline, diversity decreases landwards, whereas species dominance (Berger Parker index) increases (Fig. 2A, B). From the coastline inland, salinity decreases (Fig. 2C), and distance and salinity are negatively correlated (Table 3). The total inorganic carbon (TIC) of the sediment decreases and total organic carbon (TOC) content increases with distance from the coastline (Fig. 2D, E).

The abundance of some species shows correlations with certain environmental variables. *Ammonia parkinsoniana* has a weak negative correlation with the TOC content of the sediment, but a high positive correlation with the TIC content (Table 4). *Elphidium morenoi* has a positive correlation (Table 4) with TIC as well. Three species are positively correlated with the total phosphorus content of the surface sediment: *Elphidium bartletti*, *Bisaccium imbricatum*, and *Buccella hannai* (Table 4).

Cluster Analysis and Foraminiferal Assemblages

The Q-mode cluster analysis of foraminifera (Fig. 3) resulted in two major clusters of samples: dominantly agglutinated assemblages and dominantly calcareous assemblages. The agglutinated assemblages consist of one group of samples (association F), and the calcareous assemblages contain four groups of samples (association A-D) and one outlier (site SW31; association E). The ANOSIM significance test resulted in p-values lower than 0.05 between associations A, B, C, D, and F, whereas between E (SW31) and any other association of samples the p-value was higher than 0.05 (Table 5).

R-mode clustering of foraminifera revealed six species associations (Fig. 4, clusters 1–4). Two clusters of predominantly agglutinated species (assemblages 1 and 2) are separated from the other four predominantly calcareous assemblages (3-6). The main contributing species obtained through the SIMPER analysis (Table 6) resulted in 30 species contributing at least 1% to the observed differences between the associations produced by the Q-mode cluster analysis. Fifty percent of the contributions come from *Ammonia tepida, A. parkinsoniana, Elphidium excavatum, Trochammina inflata*, and *Arenoparrella mexicana*, in order of importance. The 30 taxa resulting from the SIMPER analysis were used for simultaneous Q-mode and R-mode clustering (Fig. 5), in which five species assemblages are named after the two most dominant taxa (based on the average relative abundance): the *Jadammina macrescens–Tiphotrocha comprimata* assemblage, *Trochammina inflata–Arenoparrella mexicana* assemblage, *Ammonia* assemblage, *Discorbis aguayoi–Biloculinella eburnea* assemblage, and *Miliammina fusca* assemblage.

Comparing the five foraminiferal assemblages, named above, to cluster associations A through F (Fig. 5) produces the following observations: Association F consists of the *J. macrescens–T. comprimata* assemblage and the agglutinated component of the *T. inflata–A. mexicana* assemblage. Association B contains the *T. inflata–A. mexicana* assemblage with a high abundance of *A. tepida*, whereas association A replaces the agglutinated species and *Helenina anderseni* with *Haynesina depressula*. Association C consists of the *Ammonia* assemblage, and association D consists of the *D. aguayoi–B. eburnea* assemblage. Association E includes only site SW31 and consists of the *M. fusca* assemblage with a high abundance of *E. excavatum*.

Species Distribution and Salinity

Of the 30 species that contribute at least 1% to the observed differences between sites in the SIMPER analysis, some such as *A. tepida* and *A. parkinsoniana* occur over a wide range of salinities, 15 – 33 psu, whereas most other species' salinity ranges are more restricted (Figs. 6–10). Most of the 30 species occur within a range of salinities, whereas others show multiple abundance peaks. *Elphidium* species have a tolerance for salinities >16 psu, but a preference for salinities >20 psu (Figs. 6–8). This is also the case for most taxa in the suborder Miliolina, which prefer salinities above 20 psu, though have a tolerance for salinities >16 psu (Figs. 8 and 9). Most agglutinated taxa in this study have their maximum abundance at salinities <18 psu. However, *H. wilberti* occurs at salinities of 16–18 psu, and *A. mexicana* occurs at salinities of 16–18 psu, as well as at higher salinities of 28–30 psu (Figs. 9 and 10).

Distribution of Assemblages and Environmental Variables

The principal component (PC) analysis of foraminiferal taxa from sediment samples (Fig. 11; Table 7) was performed without site SW31, the outlier in the cluster analysis due to unusually large numbers of *E. excavatum*. Including the outlier produced a total variance for the first two PCs of 61%, whereas without it the first two PCs explain 67% of the variance in the dataset. Along PC1 (accounting for 39% of the variance) cluster association F is separated from associations A, B, C and D. For PC1, calcareous

taxa have positive loadings, in contrast to agglutinated taxa with negative loadings. PC2 (28% of the variance) separates associations A, B and F from associations C and D. Positive loadings along PC2 coincide with calcareous species, of which *A. parkinsoniana* has the strongest loading, whereas other relatively high loadings are linked with *E. excavatum, E. morenoi*, and *Quinqueloculina seminulum*. The negative loadings correspond to agglutinated species such as *T. inflata*, *A. mexicana*, and *J. macrescens*; however, also some calcareous taxa, of which *A. tepida* has the strongest loading, but other important negative loadings on PC2 are associated with *H. depressula* and *H. anderseni* (Table 7).

Non-metric multi-dimensional scaling (Fig. 12) shows the eight environmental variables (Tables 8, 9) as vectors with different lengths, representing their relative influence on the distribution of the assemblages and orientation in two dimensions. The longest vectors are for TOC and TIC, followed (in order of length) by distance from the coastline, salinity, total phosphorus, pH, temperature, and dissolved oxygen. The TIC vector and salinity vector point in the same direction. The TOC vector points in a direction opposite to the TIC vector, as does the distance vector. Total organic carbon and TIC have a high negative correlation. Salinity and distance from the coastline have a weak negative correlation (Table 3). The total phosphorus, pH, temperature, and dissolved oxygen vectors are not, or very weakly, correlated, except for pH and dissolved oxygen which have a high positive correlation (Table 3), so these will not be further discussed, although total phosphorus showed correlation with certain species.

DISCUSSION

Assemblage Characteristics

In this study of the southwestern Everglades, we recorded 82 species, which surpasses previous foraminiferal counts based in the Everglades. Previously, the largest diversities were published by Benda & Puri (1962), who recorded 41 species from northwestern Everglades mangroves and lagoons, and by Goldstein (1976), who counted 60 species from a Biscayne Bay site on the southeastern coast. A test with 10% HCl on the agglutinated taxa recorded in this study, revealed that only *Ammobaculites dilatatus* and *Ammotium multiloculatum* react to acidic conditions, indicating that they secrete calcareous cements and/or that they use carbonate particles to build their tests. The choice to use total assemblages follows from the fact that, in contrast to the living assemblage, the total assemblage does not change significantly from season to season, even for the highly variable intertidal environment. Patchy, short-term fluctuations in living assemblages are incorporated into the total assemblage, making it a more accurate indicator of overall environmental conditions (Scott & Medioli, 1980).

Our study observed that the number of agglutinated taxa increases in a landward direction to the most interior sites, where they make up low-diversity assemblages characterized by higher dominance, while calcareous taxa dominate in more coastal locations in high-diversity assemblages of low dominance (Fig. 2A, B, F–H). We also noted that taxa of the Rotaliina are equally abundant across all the intertidal environments, with some exceptions where the organic carbon content is high and

salinity drops below 18 psu, as fewer Rotaliina are adapted to low salinity (Armstrong & Brasier, 2005). More variation is shown by members of the Miliolina, which reach their highest relative abundances near the coast but are also abundant in inland lagoons or marine-influenced lakes. Additionally, some agglutinated taxa occur closer to the coast where the sediments are richer in organic carbon, such as at river mouths. These general patterns agree with findings of the prior Everglades foraminiferal studies of Benda & Puri (1962), Phleger (1965), Goldstein (1976), and Bock & Gebelein (1977).

In the Everglades, many of the species are the same as the ones recorded in other salt marshes and mangroves worldwide (overviews by Phleger, 1970; Boltovskoy, 1984; Sen Gupta, 1999; Debenay & Guillou, 2002; Javaux & Scott, 2003). Most of these recorded taxa are agglutinated species, as most marshes are too acidic for the preservation of calcareous taxa. The most typical species with worldwide occurrences that are included in our study are *A. parkinsoniana*, *A. tepida*, *D. aguayoi*, *H. anderseni*, *Ammotium salsum*, *A. mexicana*, *Haplophragmoides* spp., *J. macrescens*, *M. fusca*, *T. comprimata* and *T. inflata*, as well as *Ammobaculites* spp., *Siphotrochammina lobata*, *Trochamminita irregularis*, and *T. salsa*, typically reported in mangroves. Some of these species, for example, *M. fusca* and *T. inflata*, cannot be considered endemic to salt marshes or mangrove swamps because they are also known to occur outside of these environments (Boltovskoy, 1984).

Salinity Preferences of Taxa

In our study, high relative abundances of *T. salsa*, *J. macrescens*, *T. inflata*, *T. comprimata*, and *M. fusca* occur at salinities <18 psu. Even though no specific salinity values are given, *T. salsa* is consistently recorded as having a low-salinity preference in mangroves, for example, as recorded by Saunders (1958), Hayward & Hollis (1994), and Sen Gupta (1999). Also, in salt marshes of New Zealand (Hayward et al., 1996) and Virginia (Spencer, 2000), *T. salsa* is common in low-salinity or uppermost tidal environments. Some researchers (e.g., Guilbault & Patterson, 2000) consider *T. irregularis* as a morphotype of *T. salsa* and group these two species together, although the small difference between them becomes clear from Saunders' (1957) description of specimens from Trinidad: the test shape of *T. irregularis* changes between the juvenile and adult stage from planispiral to very irregular, whereas adult tests of *T. salsa* can have a slight tendency to irregularity. Saunders (1957, 1958) remarks that in the mangroves of Trinidad, *T. irregularis* has a much more restricted distribution than *T. salsa*. This corresponds to our observations in the Everglades, where *T. irregularis* was present only at one low-salinity site, where it occurred together with *T. salsa*. In other studies, *T. irregularis* was observed to occur at low salinity or in the uppermost marsh (e.g., Debenay et al., 2002, 2004; Milker et al., 2015). Salinities between 10 and 15 psu were not covered by the locations sampled across the Everglades. Therefore, we cannot say conclusively whether *T. salsa* has a bimodal distribution (i.e. at <6 psu and 16–18 psu) or exhibits it maximum abundance over the full range of <18 psu.

Jadammina macrescens is common at lower salinities and in the uppermost reaches of salt marshes (Goldstein, 1988; Hayward et al., 1996; Sen Gupta, 1999; Spencer, 2000) as well as mangroves (Debenay & Guillou, 2002; Barbosa et al., 2005; Woodroffe et al., 2005). As in our study of the Everglades, Kemp et al. (2009), in their study of a North Carolina salt marsh, found *J. macrescens* at salinities <6 psu. In some marshes it has been recorded at higher salinities, for example, above 20 psu in a Massachussetts salt marsh (de Rijk & Troelstra, 1997). In the Everglades, as we do not have species abundance information for salinities between 10 and 15 psu, we can only say that the species' salinity tolerance is <18 psu, but its salinity preference may be for a larger range than <6 psu.

Miliammina fusca is commonly associated with low salinities or the landward edge of the intertidal mangrove zone (Wang & Chappell, 2001; Debenay et al., 2002, 2004; Barbosa et al., 2005; Woodroffe et al., 2005; Culver et al., 2012), but in salt marshes it seems to occur more often at lower elevations (Patterson, 1990; Horton, 1999; Sen Gupta, 1999; Guilbault & Patterson, 2000; Patterson et al., 2004; Fatela et al., 2009; Milker et al., 2015). It is not unlikely for it to occur in the higher marsh as well (e.g., Williams, 1994; Hayward et al., 1996). For the Everglades, the same comment can be made as above, as the exact range of salinity preference may be larger.

Tiphotrocha comprimata is a typical high-salt-marsh species (Sen Gupta, 1999). Saunders (1958) and Spencer (2000) encountered it in the lower part of the high marsh. In the Massachussetts salt marsh studied by de Rijk & Troelstra (1997), it prefers higher elevations where salinity exceeds 20 psu. In this study, *T. comprimata* could have a salinity preference for as large a range as <18 psu.

In the Everglades, we found *Haplophragmoides wilberti* at salinities of 16–18 psu. Worldwide, this species occurs at a wide range of salinities. In the British Columbia study by Guilbault & Patterson (2000) it is described as a low-salinity species. In the New Zealand mangroves, it occurs at 3–20 psu (Hayward and Hollis, 1994). In a North Carolina salt marsh, it was associated with salinities of 19–36 psu (Kemp et al., 2009). In Trinidad this species ranges from the lower part of the high mangroves to the coast (Saunders, 1958). In this study, *H. wilberti* clearly excludes salinities lower than 6 psu, it prefers higher salinities than the species discussed above, and may occur over a range as large as 10–18 psu. Therefore, this species is a good indicator for mangrove environments further away from the very low salinity (<6 psu) ecotone between the freshwater and upper mangroves habitat, at slightly higher salinities.

In our study, *T. inflata* and *A. mexicana* occurred both at lower salinities (<18 psu), whereas *A. mexicana* also occurred at 28–30 psu. In other studies, both taxa are often dominant at low salinity (e.g., Williams, 1994; Hayward et al., 1996; Wang & Chappell, 2001), but are not uncommon over a wider range of elevations and salinities (de Rijk, 1995; Spencer, 2000; Woodroffe et al., 2005; Horton & Murray, 2007; Kemp et al., 2009). However, according to Kemp et al. (2009) these taxa are often associated with salinities around 20 psu. For the Everglades, *A. mexicana* is the only agglutinated species that prefers salinities as high as 28–30 psu, making it a good salinity indicator for that range.

For this study, *A. tepida* and *A. parkinsoniana* are both very abundant over the intertidal environment and cover a wide range of salinities (>15 psu and >16 psu, respectively). Other calcareous taxa, such as *Elphidium* spp. and other members of the

Rotaliina and Miliolina, occur mostly at salinities >20 psu. Murray (1991) states salinity preferences of *Ammonia* spp. >18 psu and *Elphidium* spp. >22 psu. For many other studies in salt marshes as well as mangroves, calcareous species increase in abundance towards the coast and higher salinities (Gregory, 1973; Culver, 1990; Hayward & Hollis, 1994; Williams, 1994; Hayward et al., 1996; Horton, 1999; Debenay et al., 2002, 2004; Horton et al., 2003; Woodroffe et al., 2005; Horton & Murray, 2007; Avnaim-Katav et al., 2017). For the Everglades, *Ammonia* spp. indicate salinities that exist at the lower reaches of the intertidal environment. However, where they occur together with other species, for example, *Elphidium* spp., more specific salinity values can be inferred.

Organic Carbon Preferences of Taxa

High relative abundances of *A. parkinsoniana,* a species that showed a significant negative correlation with TOC (Table 4), are observed between 3–11% TOC (Fig. 13). Using this as a reference point, *H. anderseni*, *A. tepida*, *T. inflata,* and *A. mexicana*, which occur together in some assemblages, showed a preference for TOC values >11% (Fig. 13). All of these species also occur over a wider range of salinity values, which may show that salinity is not particularly limiting, but TOC may be. For example, *A. mexicana* was observed at both 16–18 psu and ~28 psu, but it always occurred at sites with a higher organic carbon content.

Helenina anderseni and *A. tepida* are common at both low and high salinities (Sen Gupta, 1999, Debenay & Guillou, 2002; Debenay et al., 2002). *Trochammina inflata* and *A. mexicana* are also not uncommon over a wide range of salinities (Horton & Murray,

2007; Kemp et al., 2009), and de Rijk (1995) concluded that their distribution is not controlled by salinity, although in the Brazilian mangroves salinity seems to be a limiting factor for *T. inflata* (Barbosa et al., 2005). *Ammonia tepida* apparently prefers sediments high in organic carbon for nutritional reasons (Debenay et al., 2002). Additionally, *A. mexicana* and *T. inflata* are often associated with high organic matter content (Debenay & Guillou, 2002; Avnaim-Katav et al., 2017). Hayward & Hollis (1994) observed that *H. anderseni* usually occurs together with *T. inflata*. These findings agree with our results, from which we infer that *H. anderseni*, *A. tepida*, *T. inflata,* and *A. mexicana* all show a preference for organic-rich sediments.

Environmental Controls on Total Assemblages

The landward end of the coastal mangroves of the Everglades receives southwestward- and southward-flowing surface freshwater through the Shark River Slough and Taylor Slough, respectively (Fig. 1). The seaward end of the coastal mangroves is influenced by waters of the Gulf of Mexico and Florida Bay. The observed salinity gradient from the coastline inland is the combined result of seasonal rainfall and groundwater discharge, the porosity of the limestone bedrock, and tidal forces. During the wet season (May–October), the freshwater surface flow increases, which reduces brackish groundwater discharge to near zero. When the amount of freshwater supply is large enough it recharges the groundwater reservoir. During the dry season (November–April), the reduced freshwater flow allows the brackish groundwater to discharge into and mix with surface waters. A very flat topography and a porous carbonate aquifer,

together with tidal forces and sea level rise, enable saltwater intrusion and increase the marine influence along the coast (Price et al., 2006, 2010). The net effect is a decrease in salinity from the coastline inland (Chen & Twilley, 1999).

This study based in the Everglades showed salinity to be the major control on the foraminiferal distribution. Cluster analysis identified significantly distinct clusters ($p<0.05$; Table 5) of foraminiferal assemblages and separated more inland sampling sites with low salinity from sites with higher average salinities and resulted in the separation of distinct assemblages of either predominantly agglutinated or calcareous taxa, with agglutinated assemblages becoming more dominant in a landward direction. This agrees with the studies of mangrove swamps by Saunders (1958), Zaninetti et al. (1977, 1979); Hayward & Hollis (1994); Wang & Chappell (2001); Debenay et al. (2002, 2004), and Culver et al. (2012), and of salt marshes by Patterson (1990) and Fatela et al. (2009), where salinity was also considered the most important control on the foraminiferal distributions.

Other Environmental Controls on Foraminiferal Assemblages

In the Everglades, besides salinity, other variables that change greatly from the coastline inland are TIC, TOC, and total phosphorus. In the PCA, PC1 is most strongly associated with salinity and PC2 corresponds mostly to TIC and TOC, based on the PC loadings for different taxa along the PC axes (Fig. 11, Table 7).

With non-metric multidimensional scaling (NMDS), TIC and TOC are interpreted as more important than salinity (Fig. 12), because the environmental variables are not

included in the ordination. They are plotted as vectors with different lengths and directions originating from the origin of the two-dimensional space. The vectors represent the direction and magnitude of the correlation coefficients between the environmental variables and the NMDS scores of the samples. When performing PCA with environmental variables, excluding taxa, the results show that TIC and TOC can be related to PC1 and salinity to PC3; this order of importance agrees with the order of vector lengths for these variables produced through non-metric multidimensional scaling.

In the PCA, the negative values along the PC1 axis were associated with agglutinated taxa and positive values with calcareous taxa (Table 7). This differentiation of wall types along PC1 axis supports its correlation with salinity. For the PC2 axis, the positive end was associated with *A. parkinsoniana*, whereas negative values were associated with *A. tepida, T. inflata*, *A. mexicana, H. anderseni,* and *H. depressula* (Table 7). The connection between PC2 and TIC and TOC is supported by the following observations: (1) there is a high positive correlation (Table 4) between TIC and *A. parkinsoniana*. (2) *Ammonia tepida* often exhibited the poorest test preservation with a clear indication of dissolution, most likely the result of its thinner test wall, while *A. parkinsoniana* was much better preserved. The wall thickness of foraminifera generally decreases with a decreasing carbonate ion concentration of the water (de Nooijer et al., 2009), and thus lower TIC. (3) *Ammonia tepida*, *T. inflata*, *A. mexicana*, and *H. anderseni* prefer organic-rich sediments (Fig. 13).

This study also found a high positive correlation between the taxa *E. bartletti*, *B. imbricatum*, and *B. hannai*, and the total phosphorus content of the sediment (Table 4). In the PCA, all three species also have high positive loadings along the third principal

component axis (8% of the variance; Table 7). Other species in assemblages containing *E. bartletti*, *B. imbricatum*, and *B. hannai* are also associated with positive values along PC3. In non-metric multidimensional scaling, the total phosphorus vector is shorter, but close in length to the salinity vector. We suspect total phosphorus could be an additional factor, after salinity, TIC, and TOC, in controlling foraminiferal distributions.

Transported Specimens

One obvious outlier occurred in the distribution of foraminifera is an unusually high relative abundance of *E. excavatum* at site SW31 ~14 km inland at a salinity <6 psu (Fig. 6). This species would not be expected to live, survive, and reproduce under these conditions because taxa with perforated tests would not be able to protect the endoplasm of the cell from stressful osmotic gradients caused by salinity fluctuations (Armstrong & Brasier, 2005), which are more severe at the landward end of the mangroves (Debenay et al., 2002). There are several possible explanations, as discussed below: (1) Sediment or (2) water containing *E. excavatum* tests was transported inland by tidal currents or a storm surge; or (3) *E. excavatum* individuals grew from a propagule bank, survived, and reproduced under very low-salinity conditions.

Benthic foraminifera from marshes are regularly displaced from the habitat where they usually live into adjacent ones. The abundance of the transported species can be a function of the amount and persistence of runoff (Phleger, 1970). In a Texas salt marsh, *M. fusca* was transported into more coastal habitats by freshwater runoff, and *A. tepida* was found further upstream than usual because of the infiltration of bay water into the

marsh (Williams, 1994). In most cases, postmortem transport is negligible and a potential source of strong bias in more high-energy environments where strong waves and tidal currents can transport a substantial number of foraminiferal tests (Debenay & Guillou, 2002).

The Everglades generally have a low-energy movement of water, affected by weak tidal currents, so transport of foraminifera is expected to be minimal. The western coastline of the Everglades, bordering the Gulf of Mexico, has semi-diurnal tides with a tidal range of 1.1 m (microtidal), whereas the southern coastline, bordering Florida Bay, is non-tidal and mainly influenced by precipitation, runoff, and wind (Parkinson, 1989). About 18 km inland from the west coast, the main influence comes from runoff, and (minor) tidal effects are mainly observed during the dry season (Castañeda-Moya et al., 2010, 2013). However, tropical storms and hurricanes that have hit South Florida once every three years on average produce water flows of much higher energy and speed to deposit storm layers far inland. For example, in 2005, Hurricane Wilma (category 3), made landfall in the northwestern Everglades, producing the highest wind speeds just above the Shark River Slough (Fig. 1A). Water levels across the Shark River Estuary were elevated above the sediment surface up to 4 m at the mouth and up to 0.5 m ~18 km inland near site SW31, depositing shelf sediments as storm layers with decreasing thickness to 10 km inland (Castañeda-Moya et al., 2010).

Through suspension in the water column, mainly dead rather than living benthic foraminifera can be transported separately from the sediments in which they are found (Murray et al., 1982). Wang & Chappell (2001), in their study of a macrotidal estuary, observed the suspension and upriver postmortem transport of tests, resulting in size-

sorted dead assemblages with allochthonous tests. However, Alve (1995), defends suspension and lateral transport as the most plausible dispersal mechanism, arguing that the 76-µm sieve used by Murray et al. (1982) may not have recorded smaller live specimens, and that the larger, stronger pseudopodia of adults can anchor better to the substrate. Consequently, dead tests and juvenile live specimens are more prone to be swept up from the sediment surface and transported along with a current (Alve, 1995).

Foraminifera are also capable of living in fresh water. Brady & Robertson (1870) observed foraminifera living at much lower salinities than expected in an Irish freshwater lake. Boltovskoy & Lena (1971) reviewed non-Allogromiidae species that survive in freshwater, including the common brackish water *M. fusca*, *A. parkinsoniana*, *E. excavatum*, and *H. wilberti*. They considered them to be surviving invaders of the freshwater milieu, but do not state whether these species are able to reproduce there.

Another possibility is that individuals of *E. excavatum* were already present at site SW31 and were able to develop because conditions were favorable. Goldstein & Alve (2011) proved that very small juveniles, or "propagules," of different species are present in all fine-grained sediments of intertidal environments, termed propagule banks. Under varying conditions, different assemblages may grow from the same propagule bank.

In this study, the assemblage at site SW31 consists mainly of *E. excavatum* (66%), *M. fusca* (15%), *A. tepida* (10%), and agglutinated species. Curiously, many species common at sites downstream to site SW31 do not occur at that site. For example, the assemblage at nearest site SRS4 consists of 97% agglutinated species, and at the second nearest site, SRS5, 90% are calcareous with *E. excavatum* comprising only 11%. If either postmortem transport or suspension followed by lateral transport resulted in the

assemblage composition at SW31, the prediction would be a larger variety of species, and more species from downstream sites. Thus, the propagule mechanism seems most probable in explaining this data outlier.

CONCLUSIONS

Modern foraminiferal assemblages from the southwestern Everglades were assessed for their use as proxies of salinity. We analyzed the spatial changes in assemblage composition across different habitats and distances from the coast and analyzed species' relationships to seven measured environmental variables. Eighty-two species belonged to 37 genera, and 77% are calcareous species, the majority of which are Rotaliina. Fifteen of the species are typically found in many mangrove swamps and salt marshes worldwide. The assemblages furthest inland consist mainly of agglutinated taxa, while towards the coast abundances of calcareous taxa generally increase and abundances of agglutinated taxa decrease. Rotaliina are equally abundant across the intertidal environment, while members of the Miliolina show peak abundances near the coast, inland lagoons and lakes. Landward, foraminiferal diversity decreases, and assemblages show higher species dominance, a reflection of more extreme physical conditions for foraminifera.

The main controlling factor on the foraminiferal distributions was salinity, which decreases landwards. It separates assemblages of purely agglutinated taxa from those consisting of a mix of agglutinated and calcareous taxa, and purely calcareous assemblages. The lowest salinity preference, <18 psu, is shown by *Jadammina*

macrescens, *Tiphotrocha comprimata*, *Trochammina inflata*, *Trochamminita salsa*, and *Miliammina fusca*. Other agglutinated taxa may occur at higher salinities; for example, *Haplophragmoides wilberti* occurred between 16 – 18 psu, as does *Arenoparrella mexicana*. Of all agglutinated species, *A. mexicana* showed the highest salinity tolerance with a second, but lower abundance peak at 28–30 psu. *Ammonia tepida* and *Ammonia parkinsoniana* occur abundantly over the widest range of salinities, above 15 psu. *Elphidium* spp. and other calcareous taxa prefer salinities above 20 psu.

Other environmental factors also played a role in the spatial distribution. The total organic and total inorganic carbon content of the sediment (TOC and TIC, respectively) are controls that are secondary to salinity. In a landward direction, TIC content decreases whereas TOC content increases. High TOC values are associated with agglutinated taxa such as those that occur predominantly at the landward end of the intertidal zone. High TOC values also occur closer to the coastline in other habitats such as river mouths, where assemblages are combinations of *Helenina anderseni*, *A. tepida*, *Haynesina depressula*, *T. inflata*, and *A. mexicana*, which all showed a preference for organic-rich sediments. Additionally, total phosphorus may be a tertiary control on the foraminiferal distribution, as illustrated by the high positive correlations between *Elphidium bartletti*, *Bisaccium imbricatum*, and *Buccella hannai* and the total phosphorus content of the sediment.

We explain the unusually high abundance of *Elphidium excavatum* at one inland site where the salinity is <6 psu by its recorded ability to survive in freshwater. Thus, during a period of favorable conditions this species may have grown from a propagule bank and reproduced.

The benthic foraminifera from the Everglades prove to be excellent proxies for salinity, and we successfully identified species that can be used as salinity indicators. This study provides baseline data for a paleoenvironmental study in this region, assessing past trends in the rate of habitat changes with sea level rise. The low-lying microtidal coasts of South Florida are highly sensitive to saltwater intrusion and inundation resulting from rising sea level. Paleoenvironmental studies are very useful when making predictions of coastal behavior, of importance to South Florida's growing coastal population and the Everglades ecosystem.

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Table 1 – Taxonomic reference list with total count of each species across the study area.

Taxa	Total Count
Rotaliina	
*Ammonia parkinsoniana (*d'Orbigny), 1839	1463
*Ammonia tepida (*Cushman), 1926	1681
Bisaccium imbricatum Andersen, 1951	65
Bolivina lowmani Phleger and Parker, 1951	5
Bolivina paula Cushman and Cahill, 1932	13
Bolivina striatula Cushman, 1922	48
Bolivina subspinescens Cushman, 1922	1
Bolivina torqueata Cushman and McCulloch, 1942	2
Bolivina variabilis (Williamson), 1958	18
Bolivinella pacifica (Cushman and McCulloch), 1942	7
Bolivinita rhomboidalis (Millett), 1899	1
Buccella hannai (Phleger and Parker), 1951	115
Buliminella elegantissima (d'Orbigny), 1839	12
Cancris oblongus (Williamson), 1958	2
Cassidulina minuta Cushman, 1933	3
Cribroelphidium poeyanum (Petri), 1954	2
Discorbis aguayoi Bermudez, 1935	157
Elphidium advenum (Cushman), 1922	1
Elphidium bartletti Cushman, 1933	19
Elphidium excavatum (Reuss), 1863	787
Elphidium discoidale (d'Orbigny), 1839	89
Elphidium galvestonense Kornfeld, 1931	79
Elphidium gunteri Cole, 1931	10
Elphidium koeboeense Leroy, 1939	154
Elphidium macellum (Fichtel and Moll), 1798	17
Elphidium matagordanum (Kornfeld), 1931	89
Elphidium mexicanum Kornfeld, 1931	58
Elphidium morenoi Bermudez, 1935	337
Elphidium simplex Cushman, 1933	101
Elphidium translucens Natland, 1938	46
Haynesina depressula (Walker and Jacob), 1798	232
Haynesina germanica (Ehrenberg), 1840	24
Helenina anderseni (Warren), 1957	258
Hopkinsina pacifica Cushman, 1933	1

Table 1 – (continued)

Taxa	Total Count
Nonionella atlantica Cushman, 1947	9
Rosalina candeiana d'Orbigny, 1839	12
Rosalina floridana (Cushman), 1922	5
Sagrina pulchella d'Orbigny, 1839	1
Miliolina	
Biloculinella eburnea (d'Orbigny), 1839	108
Cornuspira involvens (Reuss), 1850	57
Massilina protea Parker, 1953	49
Miliolinella circularis (Bornemann), 1855	1
Miliolinella microstoma Warren, 1957	73
Quinqueloculina bosciana d'Orbigny, 1839	58
Quinqueloculina lamarckiana d'Orbigny, 1839	3
Quinqueloculina poeyana d'Orbigny, 1839	36
Quinqueloculina seminulum (Linnaeus), 1758	306
Sigmoilopsis schlumbergeri (Silvestri), 1904	5
Triloculina bermudezi Acosta, 1940	15
Triloculina oblonga (Montagu), 1803	19
Triloculina planciana d'Orbigny, 1839	11
Triloculinella dilatata (d'Orbigny), 1839	6
Triloculinella obliquinodus Riccio, 1950	4
Textulariina	
Ammobaculites exiguus Cushman and Bronnimann, 1948	1
Ammobaculites dilatatus Cushman and Bronnimann, 1948	16
Ammotium multiloculatum Warren, 1957	1
Ammotium palustre Warren, 1957	17
Ammotium salsum (Cushman and Bronnimann), 1948	12
Arenoparrella mexicana (Kornfeld), 1931	486
Haplophragmoides manilaensis Andersen, 1952	22
Haplophragmoides wilberti Andersen, 1953	74
Jadammina macrescens (Brady), 1870	49
Miliammina fusca (Brady), 1870	64
Siphotrochammina lobata Saunders, 1957	10
Tiphotrocha comprimata (Cushman and Bronnimann), 1948	116
Trochammina inflata (Montagu), 1808	500
Trochamminita irregularis (Cushman and Bronnimann), Em. Saunders, 1957	8
Trochamminita salsa (Cushman and Bronnimann), Em. Saunders, 1957	55
Total	**8106**

Table 2 – Counts of individual species and total number of specimens per species and per sampling site.

Taxa/ Sites	TB	SW31	WL	SRS4	CL	SH5	AC1	SRM3	PDL	SRS5	SH3	SRM1	SH4	WL28	LL	SRS6	LO3	SH3-70	SW17	SW18	SW19	WL27	WL24	WL23	WL25	GB	AC3	SW14	LO2	SW35	Total
Ammonia parkinsoniana	43	3	0	0	0	0	49	139	207	35	22	29	8	130	21	48	14	43	103	48	37	100	67	73	96	68	28	52	0	0	**1463**
Ammonia tepida	133	26	0	0	2	1	34	129	46	76	120	67	7	58	25	80	63	224	120	90	102	18	29	65	35	27	26	78	0	0	**1681**
Ammonia spp. (juvenile or incomplete)	0	0	0	0	0	0	5	9	15	0	0	0	0	28	1	15	0	11	0	0	3	20	33	48	26	14	23	0	0	0	**251**
Bisaccium imbricatum	0	0	0	0	0	0	48	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	7	0	0	0	**65**
Bolivina lowmani	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**5**
Bolivina paula	0	0	0	0	0	0	0	1	2	0	0	1	0	0	0	3	1	2	0	1	0	0	0	0	0	0	0	2	0	0	**13**
Bolivina striatula	1	0	0	0	0	0	1	6	6	0	1	7	0	0	0	6	2	0	0	11	0	0	0	0	0	2	0	5	0	0	**48**
Bolivina subspinescens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Bolivina variabilis	0	0	0	0	0	0	0	5	4	0	1	6	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	**18**
Bolivina torqueata	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**2**
Bolivina sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Bolivina sp. 2	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**3**
Bolivinella pacifica	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	**7**
Bolivinita rhomboidalis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Buccella hannai	0	0	0	0	0	0	95	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	0	0	0	**115**
Buliminella elegantissima	0	0	0	0	0	0	0	2	4	0	0	0	0	0	0	1	1	0	0	2	0	0	0	0	0	0	0	2	0	0	**12**
Cancris oblongus	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**2**
Cassidulina minuta	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**3**
Cribroelphidium poeyanum	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**2**
Discorbis aguayoi	0	0	0	0	0	0	80	1	0	2	7	11	0	0	30	0	0	2	1	0	0	0	0	0	0	2	21	0	0	0	**157**
Discorbis sp.	0	0	0	0	0	0	0	6	2	0	0	5	0	0	0	9	0	0	0	0	0	0	0	0	0	0	0	5	0	0	**27**
Discorbis sp. 2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Elphidium advenum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Elphidium bartletti	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**19**
Elphidium excavatum	12	179	0	0	0	0	24	33	89	35	7	42	0	30	5	29	20	3	31	45	4	44	28	26	52	1	9	39	0	0	**787**
Elphidium discoidale	0	0	0	0	0	0	0	4	18	0	2	5	0	0	0	15	2	8	4	5	0	0	0	0	0	0	0	26	0	0	**89**
Elphidium galvestonense	15	0	0	0	0	0	0	0	0	3	4	0	0	0	5	6	5	0	18	12	2	0	0	0	0	0	0	9	0	0	**79**
Elphidium gunteri	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	3	0	1	0	3	0	0	0	0	0	0	**10**
Elphidium koeboeense	0	0	0	0	0	0	10	0	0	6	0	0	0	0	8	0	0	5	1	6	63	13	2	7	15	6	12	0	0	0	**154**
Elphidium macellum	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**17**
Elphidium matagordanum	0	0	0	0	0	0	16	15	6	0	0	0	0	8	1	0	0	0	0	0	17	0	3	2	2	9	2	8	0	0	**89**
Elphidium mexicanum	0	0	0	0	0	0	3	0	10	0	1	0	0	0	0	1	3	0	1	17	0	4	2	3	0	0	6	7	0	0	**58**
Elphidium morenoi	0	0	0	0	0	0	21	5	17	0	0	25	0	14	0	1	4	0	13	26	41	18	12	28	42	31	11	28	0	0	**337**
Elphidium simplex	0	0	0	0	0	0	34	42	0	0	0	13	0	0	0	0	0	5	5	0	0	0	2	0	0	0	0	0	0	0	**101**
Elphidium translucens	0	0	0	0	0	0	0	41	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0	1	0	0	0	0	**46**
Elphidium spp. (juvenile or incomplete)	0	0	0	0	0	0	0	3	22	0	0	4	0	24	0	0	0	0	0	0	0	6	0	16	21	13	5	12	0	0	**126**
Eponides sp.	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	1	0	0	**7**
Eponides sp.2	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**5**
Fursenkoina sp.	0	0	0	0	0	0	0	0	1	0	0	3	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	**7**
Haynesina depressula	4	2	0	0	1	0	7	10	23	0	5	51	1	8	0	9	17	6	12	6	13	0	0	0	0	22	26	9	0	0	**232**
Haynesina germanica	0	0	0	0	0	0	2	0	1	0	0	0	0	0	1	0	10	0	1	0	1	0	0	0	0	8	0	0	0	0	**24**
Helenina anderseni	0	0	0	2	0	2	0	42	1	66	48	28	10	0	2	0	34	19	2	0	0	0	0	0	0	0	0	2	0	0	**258**
Hopkinsina pacifica	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Nonionella atlantica	0	0	0	0	0	0	0	2	1	0	1	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	**9**
Rosalina candeiana	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**12**
Rosalina floridana	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**5**
Rosalina spp.	0	0	0	0	0	0	0	0	5	2	0	0	0	0	1	4	0	0	0	0	0	0	0	0	1	0	0	1	0	0	**14**
Sagrina pulchella	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Biloculinella eburnea	0	0	0	0	0	0	10	9	0	11	6	25	1	0	26	0	9	1	0	0	0	0	0	0	0	0	10	0	0	0	**108**
Cornuspira involvens	0	0	0	0	0	0	0	38	0	0	2	12	0	0	0	0	2	0	0	3	0	0	0	0	0	0	0	0	0	0	**57**
Massilina protea	0	0	0	0	0	0	27	0	4	4	2	0	0	0	1	0	0	0	0	0	1	0	0	0	0	9	1	0	0	0	**49**
Miliolinella circularis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Miliolinella microstoma	0	0	0	0	0	0	11	2	2	25	17	4	0	0	1	0	9	0	0	0	1	0	0	0	1	0	0	0	0	0	**73**
Quinqueloculina bosciana	0	0	0	0	0	0	25	7	0	2	2	0	8	0	0	0	10	0	0	0	0	0	0	0	0	0	4	0	0	0	**58**
Quinqueloculina lamarckiana	0	0	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**3**
Quinqueloculina poeyana	0	0	0	0	0	0	24	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	**36**
Quinqueloculina seminulum	0	0	0	0	0	0	62	0	7	5	0	11	0	50	18	0	2	0	1	3	11	11	33	17	11	49	15	0	0	0	**306**
Quinqueloculina sp.	0	0	0	0	0	0	101	8	3	0	0	0	0	0	0	0	0	0	0	3	14	0	4	0	0	25	0	0	0	0	**158**
Quinqueloculina sp. 2	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	**11**
Triloculina bermudezi	0	0	0	0	0	0	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**15**
Triloculina oblonga	0	0	0	0	0	0	12	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	**19**
Triloculina planciana	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	**11**
Triloculina sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	12	21	0	0	0	**34**
Triloculinella dilatata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	**6**
Triloculinella obliquinodus	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**4**
Ammobaculites exiguus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Ammobaculites dilatatus	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**16**
Ammobaculites sp. 2	4	12	0	0	0	0	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**19**
Ammotium multiloculatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	**1**
Ammotium palustre	1	0	5	0	0	0	0	0	0	5	0	0	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	**17**
Ammotium salsum	5	6	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**12**
Ammotium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Arenoparrella mexicana	0	0	126	0	0	14	7	97	0	14	8	96	85	0	1	0	21	8	2	0	0	0	0	0	0	0	7	0	0	0	**486**
Haplophragmoides manilaensis	0	0	8	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**22**
Haplophragmoides wilberti	0	0	28	0	0	39	0	0	0	0	1	0	5	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**74**
Haplophragmoides sp.	0	0	0	0	0	0	0	3	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**6**
Jadammina macrescens	0	2	0	28	0	16	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**49**
Miliammina fusca	3	40	0	0	0	0	0	0	0	1	0	2	1	0	0	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	**64**
Siphotrochammina lobata	0	0	4	0	0	4	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**10**
Tiphotrocha comprimata	4	1	21	17	0	53	0	0	0	3	0	0	3	0	13	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	**116**
Trochammina inflata	0	0	143	23	0	36	10	23	0	9	24	33	153	0	2	4	22	14	0	0	0	0	0	0	0	0	4	0	0	0	**500**
Trochammina sp.	0	0	11	3	0	36	5	0	0	0	4	4	7	0	0	0	3	0	0	0	0	0	0	0	0	0	10	0	0	0	**83**
Trochamminita irregularis	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**8**
Trochamminita salsa	0	0	49	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**55**
unidentified	0	2	0	0	0	0	0	2	3	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	2	3	0	0	**14**
Total	**242**	**273**	**403**	**79**	**3**	**215**	**786**	**726**	**512**	**305**	**287**	**499**	**295**	**351**	**169**	**236**	**285**	**353**	**316**	**294**	**315**	**235**	**215**	**291**	**302**	**316**	**276**	**290**	**0**	**0**	**8869**

Table 3 – Significant correlations ($p < 0.05$) between the environmental variables. Showing correlation coefficients (r), coefficients of determination (r^2), and probabilities (p).

		Distance	Salinity	TOC	TP	pH	T
Salinity	r	-0.67	-	-0.51	-	-	-
	r^2	0.45	-	0.3	-	-	-
	p	0.00009	-	0.006	-	-	-
TIC	r	-	-	-0.84	-	-	-
	r^2	-	-	0.71	-	-	-
	p	-	-	0.00000002	-	-	-
pH	r	-	-	-	0.6	-	-
	r^2	-	-	-	0.36	-	-
	p	-	-	-	0.0007	-	-
T	r	-	-	-	-	0.6	-
	r^2	-	-	-	-	0.36	-
	p	-	-	-	-	0.0007	-
DO	r	-	-	-	0.52	0.77	0.57
	r^2	-	-	-	0.27	0.6	0.33
	p	-	-	-	0.005	0.000001	0.002
Distance	r	-	-	0.5	-	-	-
	r^2	-	-	0.25	-	-	-
	p	-	-	0.007	-	-	-

Table 4 – Significant correlations ($p < 0.05$) between the environmental variables and taxa. Showing correlation coefficients (r), coefficients of determination (r^2), and probabilities (p).

Variables	**Distance**			**TOC**			**TIC**			**TP**		
Taxa	**r**	**r^2**	**p**	**r**	**r^2**	**p**	**r**	**r^2**	**p**	**r**	**r^2**	**p**
A. parkinsoniana	-	-	-	-0.69	0.48	0.00004	0.76	0.58	0.000002	-	-	-
B. imbricatum	-	-	-	-	-	-	-	-	-	0.75	0.56	0.000004
B. hannai	-	-	-	-	-	-	-	-	-	0.85	0.73	0.000000008
E. bartletti	-	-	-	-	-	-	-	-	-	0.71	0.5	0.00002
E. morenoi	-	-	-	-0.63	0.39	0.0004	0.74	0.54	0.000008	-	-	-
R. candeiana	-	-	-	-	-	-	-	-	-	0.62	0.38	0.0005
Q. bosciana	-	-	-	-	-	-	-	-	-	0.57	0.33	0.001
***Quinqueloculina* sp. 2**	-	-	-	-	-	-	-	-	-	0.53	0.3	0.003
T. bermudezi	-	-	-	-	-	-	-	-	-	0.62	0.38	0.0005
T. planciana	-	-	-	-	-	-	-	-	-	0.57	0.33	0.001
***Triloculina* sp.**	-	-	-	-	-	-	-	-	-	0.51	0.26	0.006
T. obliquinodus	-	-	-	-	-	-				0.62	0.38	0.0005
A. mexicana	-	-	-	-	-	-	-0.52	0.27	0.005	-	-	-
J. macrescens	0.52	0.34	0.001	-	-	-	-	-	-	-	-	-
T. comprimata	-	-	-	0.59	0.35	0.0009	-	-	-	-	-	-
T. inflata	-	-	-	0.56	0.31	0.002	-0.53	0.28	0.004	-	-	-

Table 5 – P-values of the significance test for the groups in the Q-mode cluster (Fig. 3), using ANOSIM or analysis of similarities, $p < 0.05$ are shown in bold face. The letters correspond to the labels in Fig. 3.

	A	B	C	D	E	F
A	0	**0.0183**	**0.0021**	0.0955	0.238	**0.0279**
B	**0.0183**	0	**0.0005**	**0.0177**	0.1647	**0.0076**
C	**0.0021**	**0.0005**	0	**0.0027**	0.0762	**0.0009**
D	0.0955	**0.0177**	**0.0027**	0	0.2475	**0.0278**
E	0.238	0.1647	0.0762	0.2475	0	0.1948
F	**0.0279**	**0.0076**	**0.0009**	**0.0278**	0.1948	0

Table 6 – The average dissimilarity, percent contribution, cumulative contribution, and average abundance per sample association (A-F) of individual species produced with SIMPER analysis using the Bray-Curtis dissimilarity index. The listed species have ≥ 1% contribution to the general distribution pattern as illustrated by the Q-mode clustering (associations A-F, see Fig. 3).

Taxa	Average Dissimilarity	% Contribution	Cumulative %	Average Abundance					
				Association A	Association B	Association C	Association D	Association E	Association F
Ammonia tepida	11.62	15.51	15.51	62.5	24.2	22.8	9.93	9.59	0.712
Ammonia parkinsoniana	9.244	12.34	27.85	10.2	10	30.8	10	1.11	0.68
Elphidium excavatum	6.564	8.762	36.61	1.95	6.87	12.7	3.24	66	0
Trochammina inflata	6.336	8.458	45.07	1.37	5.82	0.154	1.37	0	33.3
Arenoparrella mexicana	4.337	5.789	50.85	0.783	9.69	0.0525	1.44	0	16.7
Haynesina depressula	2.84	3.791	54.64	12.3	3.92	2.73	3.81	0.74	0.085
Elphidium morenoi	2.777	3.707	58.35	0	1.45	8.34	2.39	0	0
Helenina anderseni	2.752	3.674	62.03	1.86	12.4	0.132	0.397	0	1.71
Quinqueloculina seminulum	2.65	3.537	65.56	0	0.92	6.28	8.26	0	0
Tiphotrocha comprimata	2.505	3.343	68.91	0.65	0.196	0	2.58	0.37	13.1
Jadammina macrescens	1.817	2.425	71.33	0	0	0	0.13	0.74	10.7
Discorbis aguayoi	1.757	2.345	73.68	0.197	1.09	0.0842	12.2	0	0
Elphidium koeboeense	1.427	1.906	75.58	0.49	0.394	3.4	3.64	0	0
Biloculinella eburnea	1.387	1.852	77.43	0.0967	3.06	0	6.94	0	0.085
Trochammina sp.	1.277	1.704	79.14	0	0.652	0	1.56	0	6.41
Haplophragmoides wilberti	1.137	1.518	80.66	0	0.07	0	0.2	0	6.7
Quinqueloculina sp.	0.9954	1.329	81.98	0	0.232	1.42	4.34	0	0
Miliammina fusca	0.9821	1.311	83.29	0.413	1.35	0	0	14.8	0.085
Buccella hannai	0.8636	1.153	84.45	0	0	0.0183	6.64	0	0
Trochamminita salsa	0.8172	1.091	85.54	0	0	0	0	0	4.94
Elphidium galvestonense	0.8154	1.089	86.63	2.07	0.826	1.38	0.993	0	0
Miliolinella microstoma	0.7923	1.058	87.68	0	3.67	0.0925	0.673	0	0
Elphidium discoidale	0.7704	1.028	88.71	0.783	0.6	1.95	0	0	0
Elphidium matagordanum	0.6123	0.8173	89.53	0	0.434	1.56	1.16	0	0
Elphidium simplex	0.597	0.797	90.33	0.49	1.75	0.223	1.46	0	0
Elphidium mexicanum	0.5179	0.6913	91.02	0	0.282	1.31	0.94	0	0
Bisaccium imbricatum	0.5068	0.6766	91.7	0	0.706	0	3.01	0	0
Quinqueloculina bosciana	0.4893	0.6532	92.35	0	1.18	0	1.61	0	0.68
Triloculina sp.	0.4743	0.6332	92.98	0	0	0.373	2.83	0	0
Cornuspira involvens	0.3879	0.5178	93.5	0	1.87	0.0867	0	0	0

Table 7 – The eigenvalue, % variance, and PC loadings of individual taxa for the first three principal component axes (PC1, PC2, and PC3) from the principal component analysis.

Principal Components	**PC1**	**PC2**	**PC3**
Eigenvalue	477.092	338.093	99.7033
% Variance	39.437	27.947	8.2417
Taxa			
Rotaliina			
Ammonia parkinsoniana	0.3433	0.6535	-0.3757
Ammonia tepida	0.6841	-0.5938	-0.2105
Bisaccium imbricatum	-0.01028	0.0004732	0.0596
Bolivinella pacifica	0.0008519	0.000002433	-0.001112
Bolivina paula	0.004073	-0.001604	-0.005324
Bolivina striatula	0.008622	0.001208	-0.007692
Bolivina variabilis	0.0002251	0.0013	-0.005722
Buccella hannai	-0.0182	0.01142	0.1259
Discorbis aguayoi	-0.02376	0.006485	0.2226
Discorbis sp.	0.006143	-0.0003609	-0.01088
Elphidium bartletti	-0.002838	0.001632	0.01866
Elphidium excavatum	0.1312	0.2602	-0.1838
Elphidium discoidale	0.02846	0.001108	-0.03435
Elphidium galvestonense	0.03293	-0.01887	-0.008184
Elphidium gunteri	0.003264	0.003323	-0.003747
Elphidium koeboeense	0.02775	0.03525	0.09697
Elphidium macellum	-0.0006472	0.0004572	-0.005258
Elphidium matagordanum	0.009128	0.0239	0.03535
Elphidium mexicanum	0.0119	0.01871	0.000879
Elphidium morenoi	0.06522	0.1541	0.02296
Elphidium simplex	-0.002542	0.0005795	0.008143
Elphidium translucens	0.000321	0.003433	-0.01291
Eponides sp.	-0.00009615	-0.0004842	-0.0009542
Haynesina depressula	0.09259	-0.1544	0.1084
Haynesina germanica	-0.001698	0.001215	0.01708
Helenina anderseni	-0.01081	-0.1002	-0.05144
Nonionella atlantica	0.001962	-0.0002358	-0.001257
Rosalina candeiana	-0.001735	0.0009923	0.01113
Rosalina spp.	0.003519	0.003978	-0.002831

Table 7 – (continued)

Principal Components	PC1	PC2	PC3
Eigenvalue	477.092	338.093	99.7033
% Variance	39.437	27.947	8.2417
Taxa			
Miliolina			
Biloculinella eburnea	-0.01714	-0.009232	0.1129
Cornuspira involvens	-0.002932	-0.003223	-0.01386
Massilina protea	-0.003497	0.008077	0.04118
Miliolinella microstoma	0.0008596	-0.02199	0.01013
Quinqueloculina bosciana	-0.0168	-0.007783	0.002131
Quinqueloculina poeyana	-0.004587	0.006993	0.03407
Quinqueloculina seminulum	0.02685	0.1799	0.1605
Quinqueloculina sp.	-0.009734	0.02828	0.136
Quinqueloculina sp. 2	-0.002526	-0.00001908	0.009207
Sigmoilopsis schlumbergeri	0.0007863	-0.0008619	0.005821
Spiroloculina sp. 2	0.0009058	-0.003432	-0.001116
Triloculina bermudezi	-0.002161	0.001236	0.01386
Triloculina oblonga	-0.003598	0.002222	0.03501
Triloculina planciana	-0.001498	0.001433	0.01065
Triloculina sp.	-0.005498	0.01006	0.06007
Triloculinella dilatata	-0.0003196	0.003606	0.008256
Textulariina			
Ammobaculites dilatatus	0.01419	-0.01442	-0.00921
Ammobaculites sp. 2	0.003073	-0.003832	-0.00291
Ammotium palustre	-0.006913	-0.005703	-0.01579
Ammotium salsum	0.004386	-0.004469	-0.00317
Arenoparrella mexicana	-0.2738	-0.1172	-0.4822
Haplophragmoides manilaensis	-0.02645	-0.006223	0.02205
Haplophragmoides wilberti	-0.08579	-0.0221	0.03886
Jadammina macrescens	-0.1416	-0.03276	0.2375
Miliammina fusca	-0.001907	-0.01138	-0.003802
Siphotrochammina lobata	-0.01185	-0.003243	-0.003207
Tiphotrocha comprimata	-0.1672	-0.04264	0.2508
Trochammina inflata	-0.4843	-0.1992	-0.5042
Trochammina sp.	-0.08494	-0.02313	0.09224
Trochamminita irregularis	-0.007479	-0.002297	-0.01258
Trochamminita salsa	-0.07129	-0.02014	-0.03508

Table 8 – Average values of the environmental variables per sampling site. Total organic (TOC) and inorganic carbon (TIC) were measured from the collected sediment samples. Distance from the coastline was measured on a map of the sampling sites. Other values were obtained from https://apps.sfwmd.gov/WAB/EnvironmentalMonitoring/ index.html

Variable	Salinity	pH	TOC	TIC	TP	T	DO	Distance
Unit	PSU	-	%	%	mg/l	celsius	mg/l	km
Site								
PDL	31.2	-	3.075	53.66	0.0122	26.1	6.2167	-2
TB	25.7	8.3	15.96	19.45	0.057	26.8	5.656	0
SRM1	28.7	7.8	13.7	2.226	0.0202	25	4.7831	0
GB	33	-	8.495	37.39	-	26.8	-	0
AC1	26.7	7.7	5.311	44.71	0.1095	26.8	3.508	0.07
SRM3	28.7	7.8	13.72	3.586	0.0202	25	4.7831	0.3
AC3	26.7	7.7	7.534	41.5	0.1095	26.8	3.508	0.35
LO3	21.3	7.8	10.39	20.69	0.0223	20.6	5.2585	0.5
SW14	24.7	7.6	4.257	54.22	0.0323	25.1	4.187	0.5
WL25	16.2	-	5.724	59.59	-	-	-	1.6
LL	21.6	-	35.02	3.392	-	-	-	1.6
WL23	16.2	-	7.314	51.52	-	-	-	2
WL27	16.2	-	5.536	61.44	-	-	-	2
WL24	16.2	-	8.882	44.77	-	-	-	2.4
WL	16.2	-	28.9	0.586	-	-	-	2.6
WL28	16.2	-	5.474	60.43	-	-	-	2.6
CL	15	-	38.38	0.5466	-	-	-	4
SRS6	24.4	7.4	9.355	37.93	-	25.7	-	4
SH3	30.2	-	15.87	17.35	-	22.8	-	4
SH3-70	30.2	-	18.87	7.471	-	22.8	-	4
SW17	20.8	-	11.14	26.97	-	25.9	-	5
SW18	25.6	7.8	7.848	36.99	0.0196	25.2	4.8445	6
SH4	17.8	7.4	33.48	0.5881	0.025	24.2	2.3251	8
SH5	16.9	-	34.15	1.758	-	21.6	-	8
SRS5	17.5	7.7	13.59	23.21	0.0162	26.052	3.2522	9
LO2	9.4	7.9	24.87	0.3857	-	23.9	5.6034	13
SW31	4.5	-	36.69	2.528	-	26.5	-	14
SRS4	5.8	7.8	38.07	0.7582	0.0138	25.1	4.152	16
SW19	16.7	7.9	8.553	49.25	0.0161	25.3	5.476	16
SW35	0.4	7.5	31.23	0.09408	0.0082	25.3	4.0642	20

Table 9 – Sampling locations (latitude, longitude) of the surface sediments for this study and the corresponding locations (latitude, longitude) and collecting agencies from where water quality data (salinity, pH, total phosphorus, temperature, and dissolved oxygen) was obtained.

Sampling Site (sediment)	Latitude (N)	Longitude (W)	Water Quality Site	Latitude (N)	Longitude (W)	Collecting Agency
LO2	25° 35' 35.412''	81° 2' 29.4''	LO2	25° 35' 35.412''	81° 2' 29.4''	USGS
LO2	25° 35' 35.412''	81° 2' 29.4''	ENPWW	25° 35'15"	81° 02'37"	SFWMD
LO2	25° 35' 35.412''	81° 2' 29.4''	FLAB31	25° 34'03"	81° 04'17"	SFWMD
LO3	25° 32' 21.192''	81° 11' 3.408''	LO3	25° 32' 21.192''	81° 11' 3.408''	USGS
LO3	25° 32' 21.192''	81° 11' 3.408''	FLAB29	25° 33'16"	81° 11'01"	SFWMD
SH3	25° 21' 50.688''	81° 4' 42.492''	SH3	25° 21' 50.688''	81° 4' 42.492''	USGS
SH3-70	25° 21' 49.2''	81° 4' 41.5''	SH3	25° 21' 50.688''	81° 4' 42.492''	USGS
SH4	25° 25' 24.6''	81° 3' 37.584''	SH4	25° 25' 24.6''	81° 3' 37.584''	USGS
SH4	25° 25' 24.6''	81° 3' 37.584''	ENPHR	25° 25'28"	81° 03'36"	SFWMD
SH5	25° 25' 16.788''	81° 3' 34.884''	SH5	25° 25' 16.788''	81° 3' 34.884''	USGS
SW14	25° 24.560'	81° 08.487'	FLAB36	25° 24'42"	81° 08'29"	SFWMD
SW35	25° 26.757'	80° 54.977'	P-35	25°27'41"	80°51'53"	SFWMD
SW35	25° 26.757'	80° 54.977'	Site 22908295	25°28'04"	80°51'16"	SFWMD
SRM1	25°20'34.0"	81°07'57.4"	FLAB40	25˚20'59"	81˚07'28"	SFWMD
SRM3	25°20'33.9"	81°07'57.7"	FLAB40	25˚20'59"	81˚07'28"	SFWMD
PDL	25°19'01.3"	81°10'12.4"	SWS40	25˚15'37"	81˚15'36"	SFWMD
SW18	25° 20.815'	81° 03.573'	FLAB41	25˚19'52"	81˚04'22"	SFWMD
SW19	25° 18.787'	80° 59.530'	FLAB44	25˚19'55"	80˚59'01"	SFWMD
TB	25°9'32.6"	80°43'47.3"	ENPTB	25˚09'26"	80˚43'29"	SFWMD
TB	25°9'32.6"	80°43'47.3"	C111MC	25˚10'06"	80˚44'01"	SFWMD
GB	25°10.6'	80°47.657'	ENPGB	25˚10'02"	80˚48'05"	SFWMD
AC1	25°10.571’	80°47.603'	C111AC	25˚10'34"	80˚47'34"	SFWMD
AC3	25°10.551’	80°47.493’	C111AC	25˚10'34"	80˚47'34"	SFWMD
SRS4	25° 24' 35.1511''	80° 57' 51.5167''	SRS4	25° 24' 35.1511''	80° 57' 51.5167''	LTER
SW31	25° 23.559'	80° 58.173'	ENPTE	25° 24'36"	80° 57'50"	SFWMD
SRS4	25° 24' 35.1511''	80° 57' 51.5167''	FLAB38	25°25'02"	80°59'54"	SFWMD
SRS5	25° 22' 37.2814''	81° 1' 56.4499''	SRS5	25° 22' 37.2814''	81° 1' 56.4499''	LTER
SRS5	25° 22' 37.2814''	81° 1' 56.4499''	ENPGI	25°22'41"	81°01'46"	SFWMD
SRS5	25° 22' 37.2814''	81° 1' 56.4499''	FLAB39	25°22'44"	81°01'51"	SFWMD
SRS6	25° 21' 52.6676''	81° 4' 40.6063''	SRS6	25° 21' 52.6676''	81° 4' 40.6063''	LTER
SW17	25° 22.648'N	81° 03.855'	ENPSR	25°21'15"	81°06'00"	SFWMD
SW17	25° 22.648'	81° 03.855'	SHARKRIVBG	25°22'30"	81°02'12"	SFWMD
WL	25°12.846'N	80°49.075'	West Lake	25°12'24.5"	80°49'29.0"	LTER
WL23	25° 12' 9.9282"	80° 51' 0.1908"	West Lake	25°12'24.5"	80°49'29.0"	LTER
WL24	25° 12' 17.0208''	80° 50' 24.7344''	West Lake	25°12'24.5"	80°49'29.0"	LTER
WL25	25° 12' 10.5264''	80° 48' 29.664''	West Lake	25°12'24.5"	80°49'29.0"	LTER
WL27	25° 12' 38.6676''	80° 48' 14.8644''	West Lake	25°12'24.5"	80°49'29.0"	LTER
WL28	25° 12' 30.402''	80° 50' 53.4516''	West Lake	25°12'24.5"	80°49'29.0"	LTER
CL	25°12.868'N	80°46.334'	Cuthbert Lake	25°12'26.7"	80°46'31.7"	LTER
LL	25°12'	80°47.59'	Long Lake	25°11'47.3"	80°47'36.8"	LTER

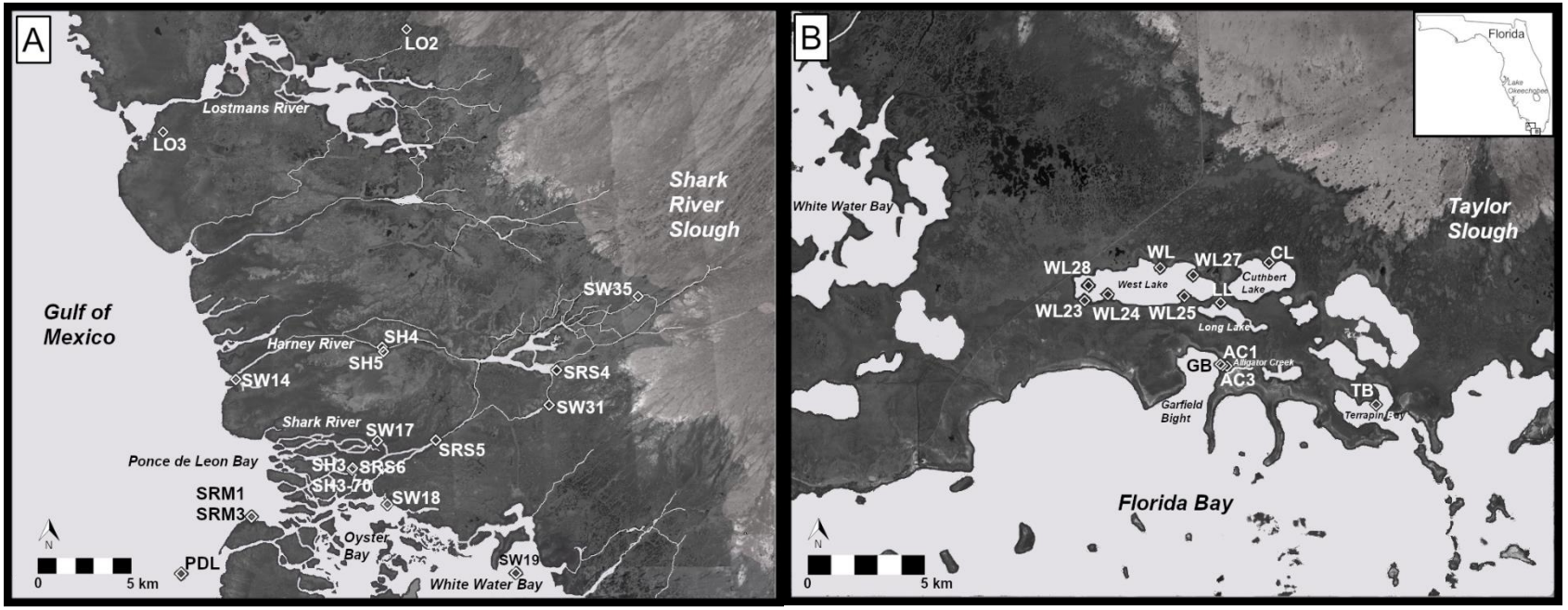

Figure 1 – Map of the study area and important water bodies for the southwestern Everglades. A) The 18 sampling locations on the western coast; B) The 12 sampling locations on the southern coast. The coastal zone in darker gray shows the approximate location of mangroves. The upland, light gray area is freshwater wetland. Figure is adapted from Google Earth.

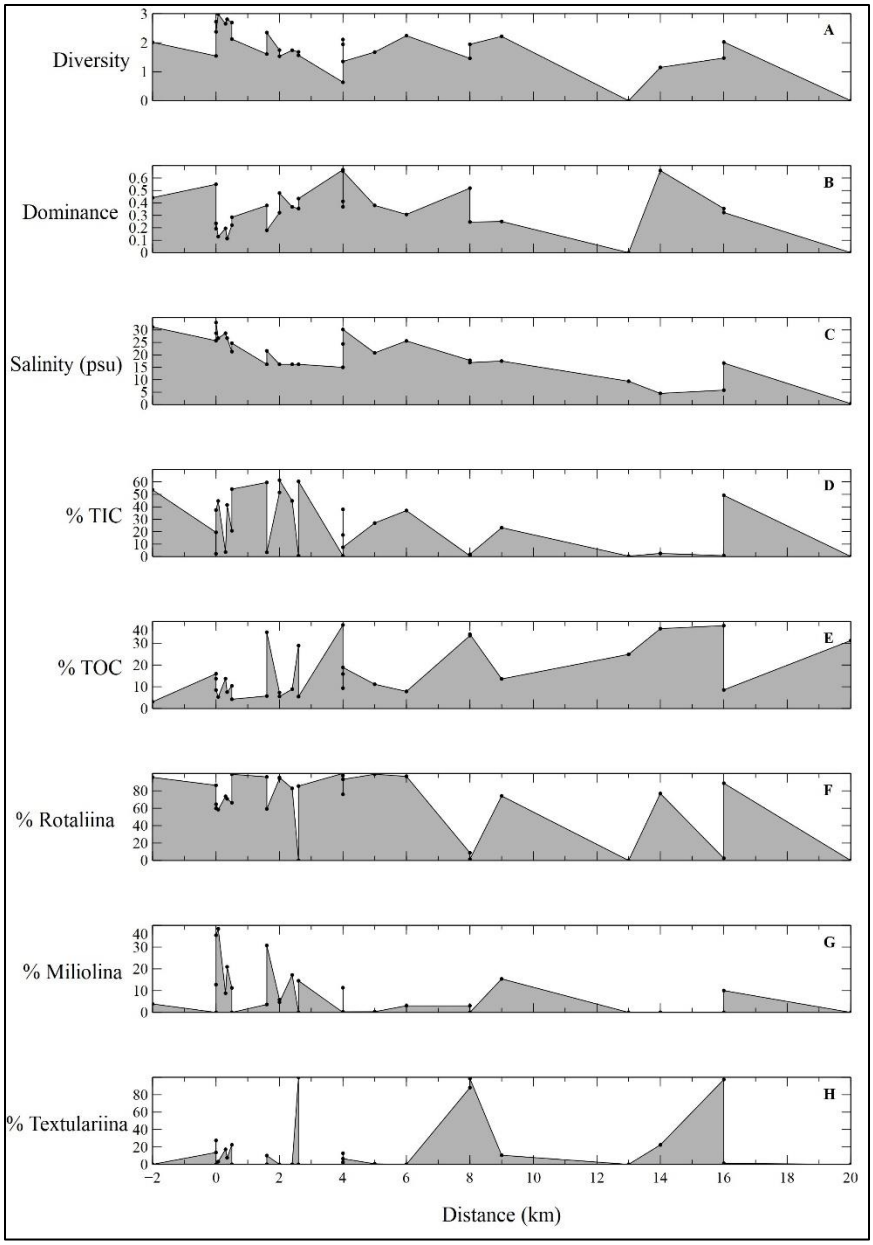

Figure 2 – A) Shannon diversity index H′, high values correspond to communities with many taxa; B) Berger Parker dominance index, represented by the relative abundance of the dominant species; C) Salinity (psu); D) percentage of total inorganic carbon (TIC); E) percentage of total organic carbon (TOC); and the relative abundance of the three wall types of F) Rotaliina, G) Miliolina, and H) Textulariina, with distance from the coastline (km).

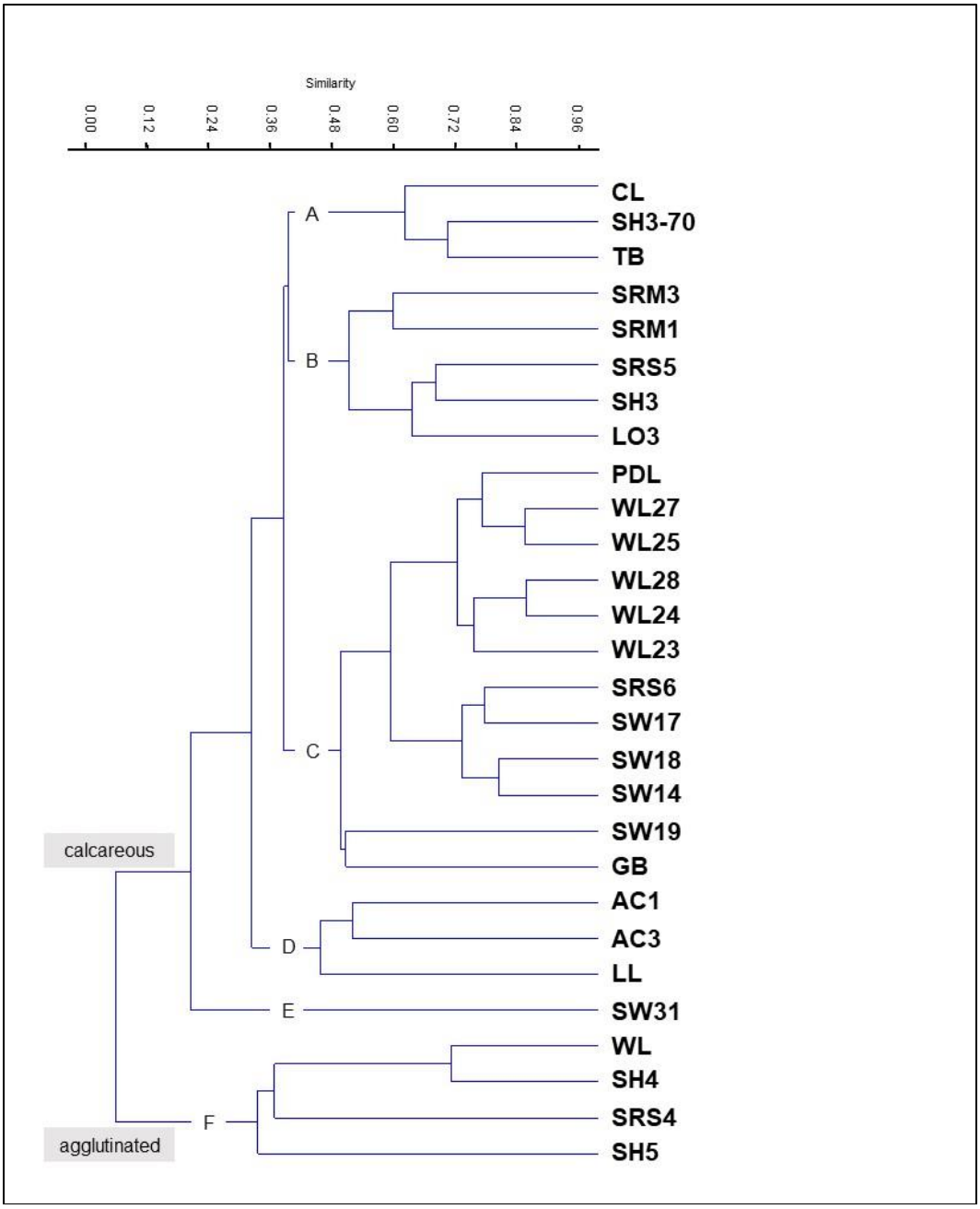

Figure 3 – Q-mode cluster analysis of 28 surface samples and taxa with a relative abundance >1% using unweighted pair group clustering with average linkage, Bray-Curtis dissimilarity index. The letters, A-F, mark the identified clusters of distinct assemblages, representing different habitats.

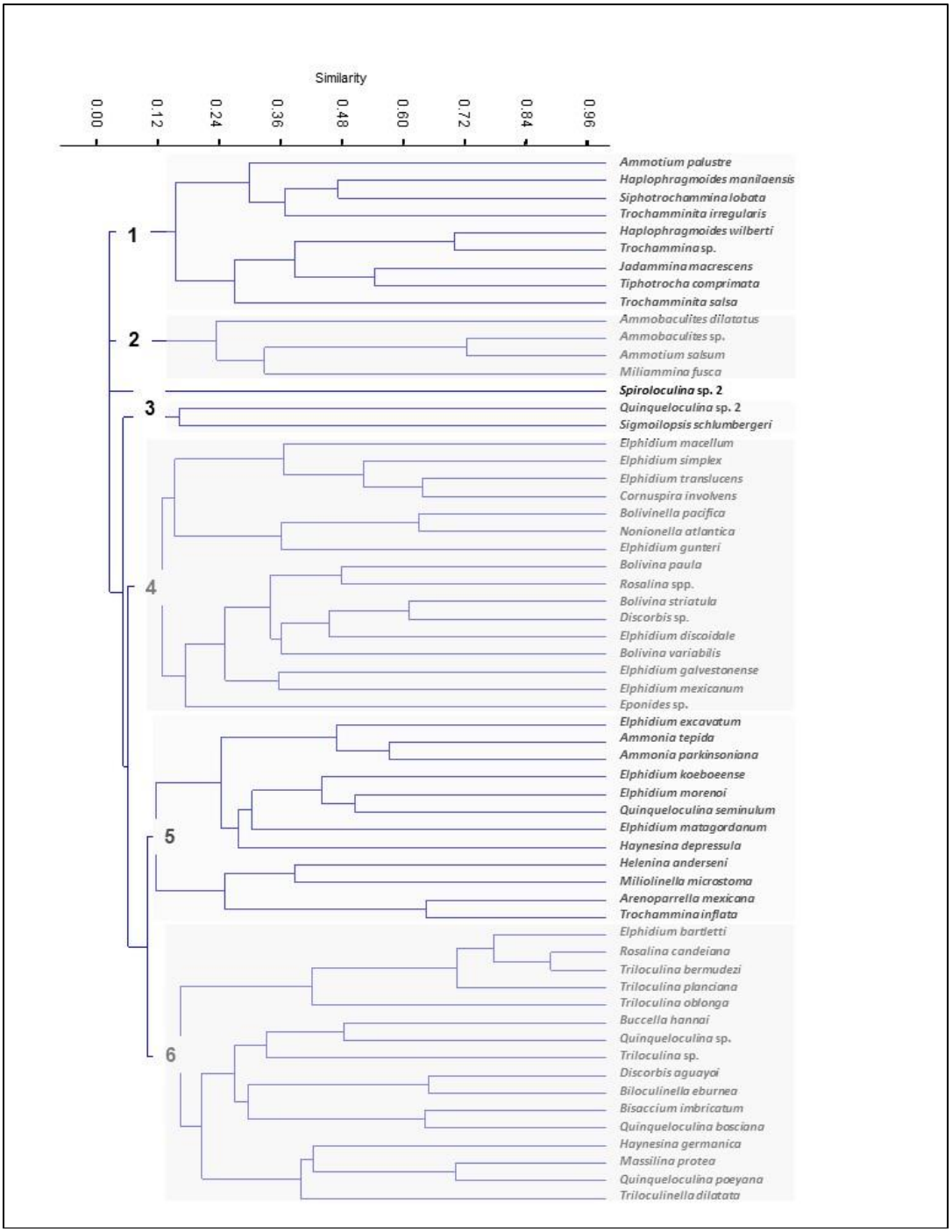

Figure 4 – R-mode cluster dendrogram for all identified species using unweighted pair group clustering with average linkage and Bray-Curtis dissimilarity index. Clusters 1 to 6 discussed in text.

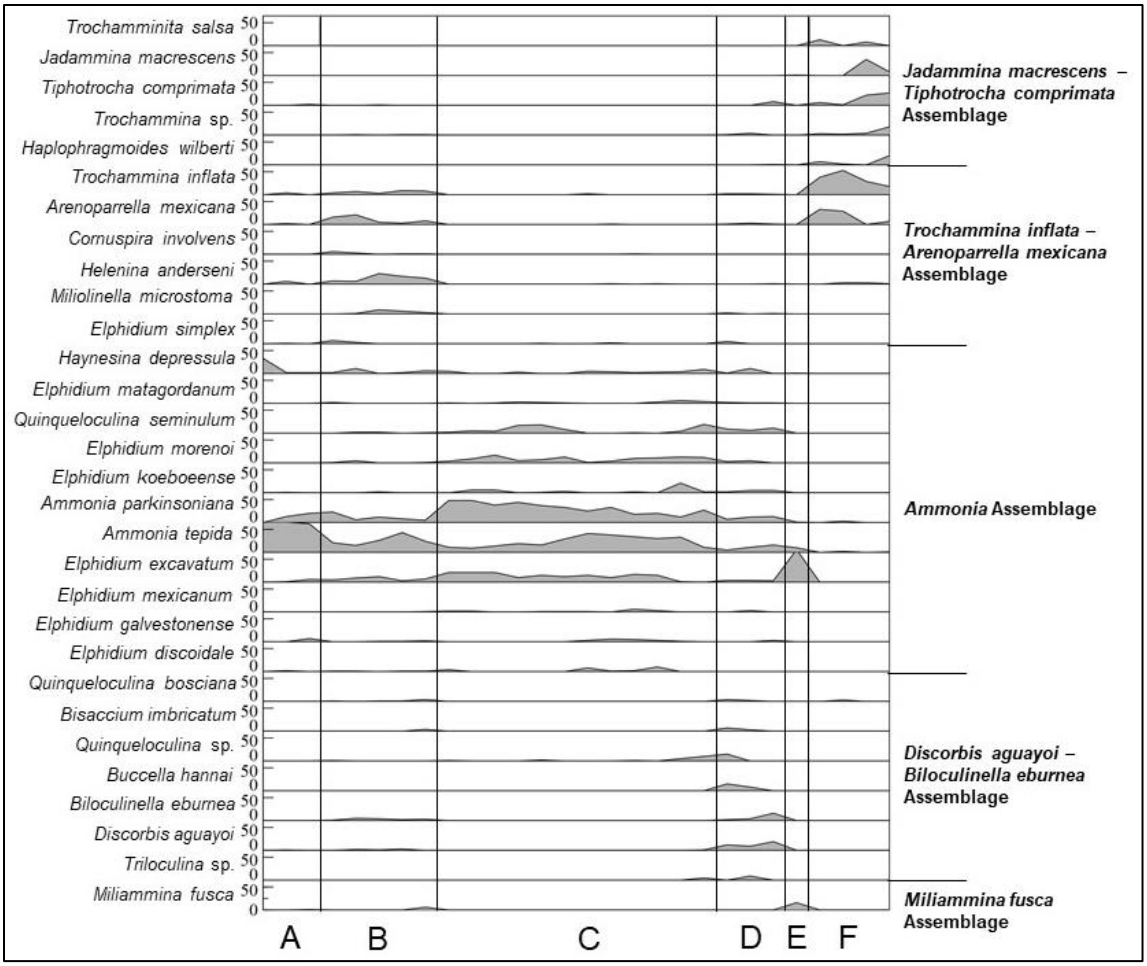

Figure 5 – Simultaneous Q- and R-mode clustering, showing the correspondence between the sample associations A-F and the foraminiferal assemblages from the SIMPER analysis that identifies the most contributing species, visualized with their relative abundance (%).

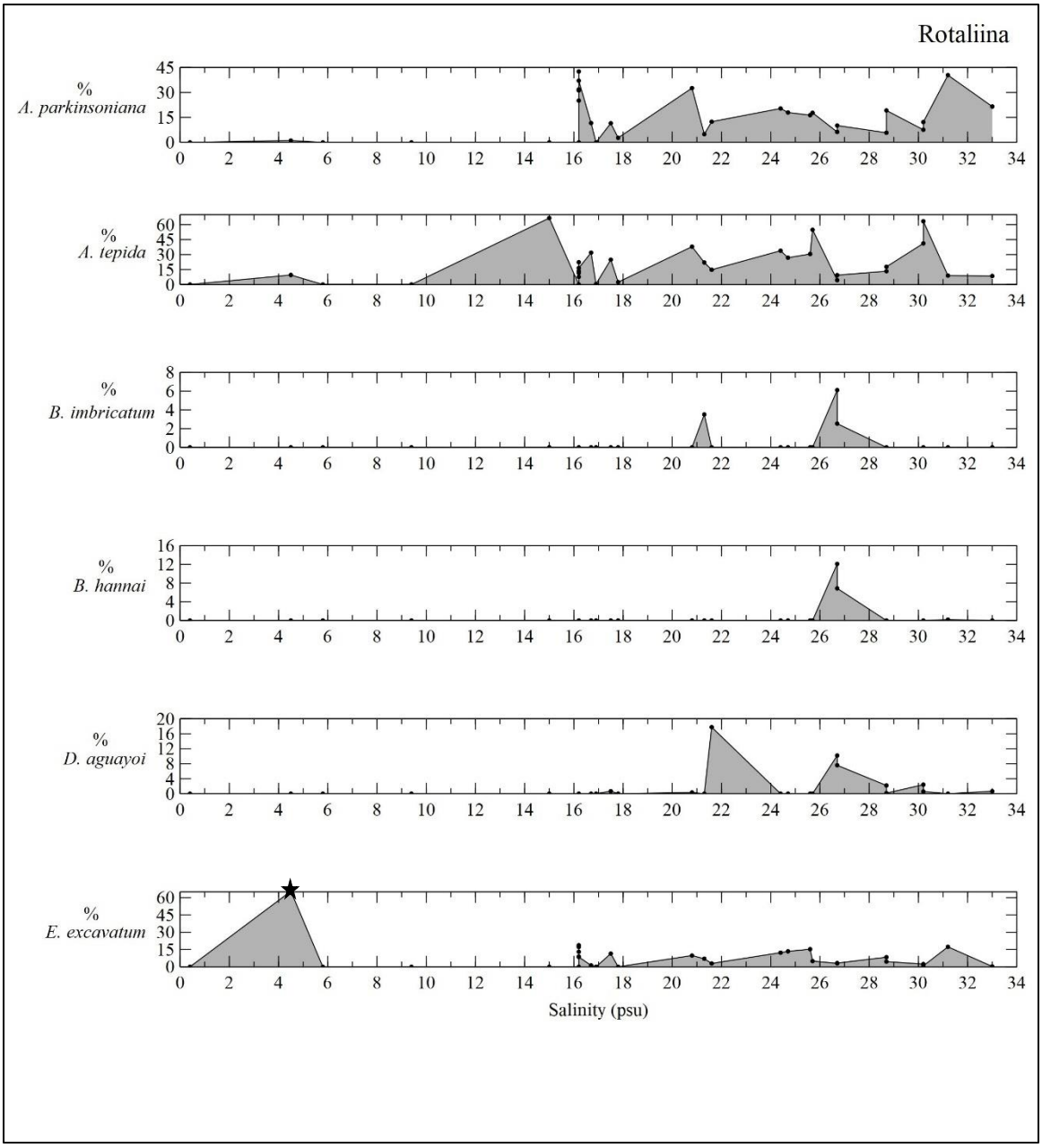

Figure 6 – The relative abundance of some calcareous perforate taxa, which have at least a 1% contribution to the observed differences between habitats, compared with salinity (psu). The black star indicates an outlier.

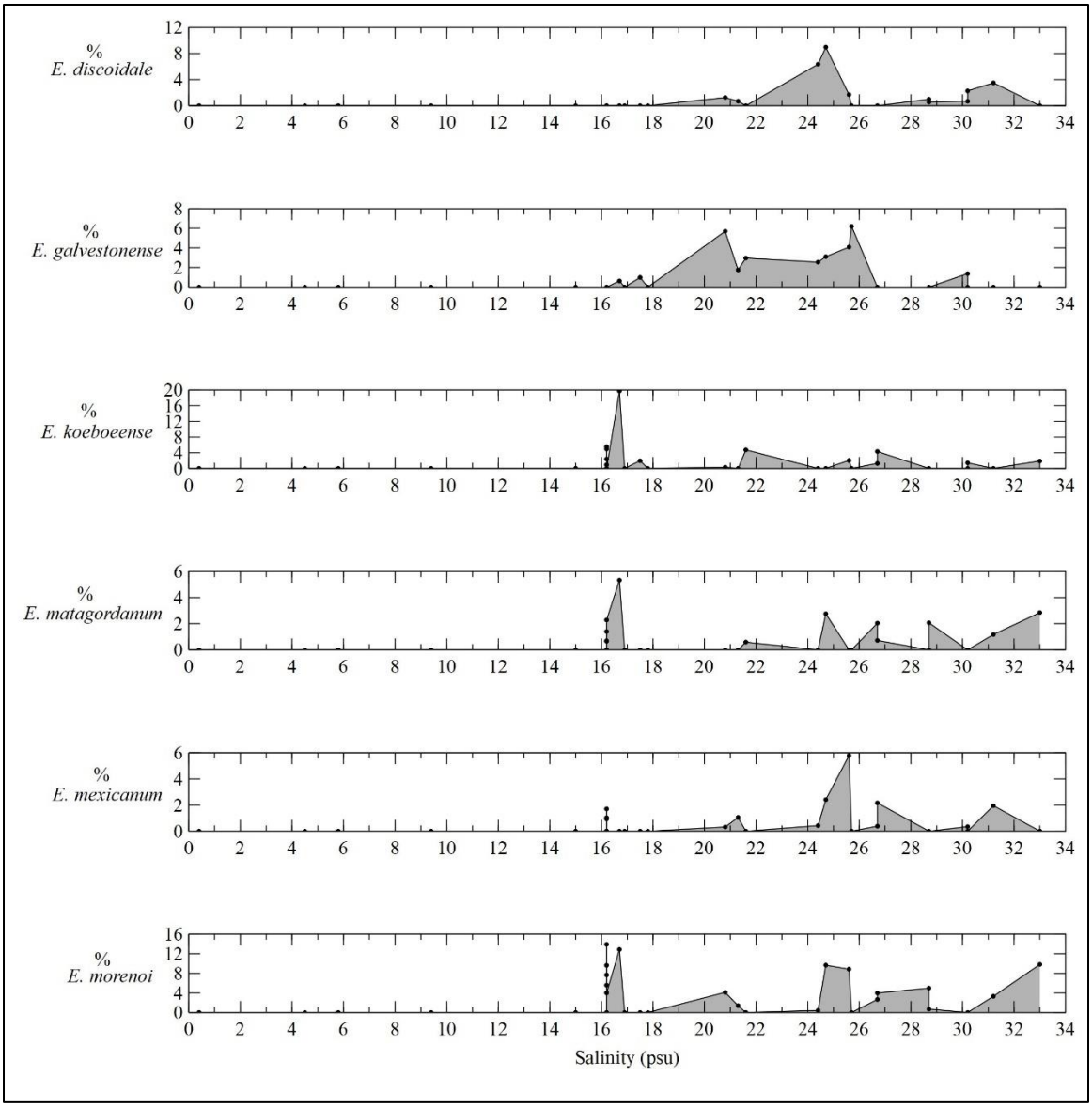

Figure 7 – The relative abundance of some *Elphidium* species, which have at least a 1% contribution to the observed differences between habitats, compared with salinity (psu).

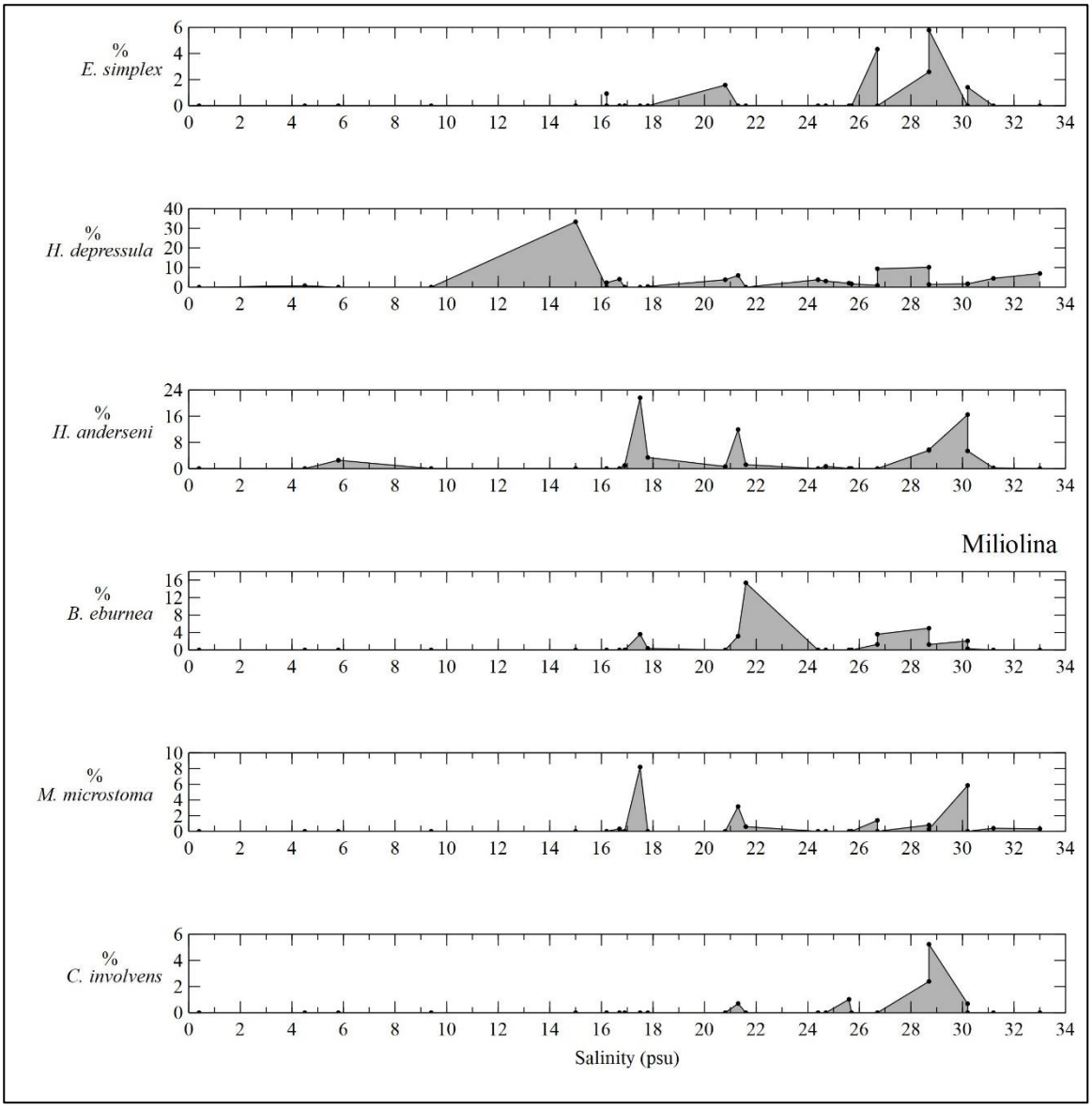

Figure 8 – The relative abundance of some calcareous perforate and imperforate taxa, which have at least a 1% contribution to the observed differences between habitats, compared with salinity (psu).

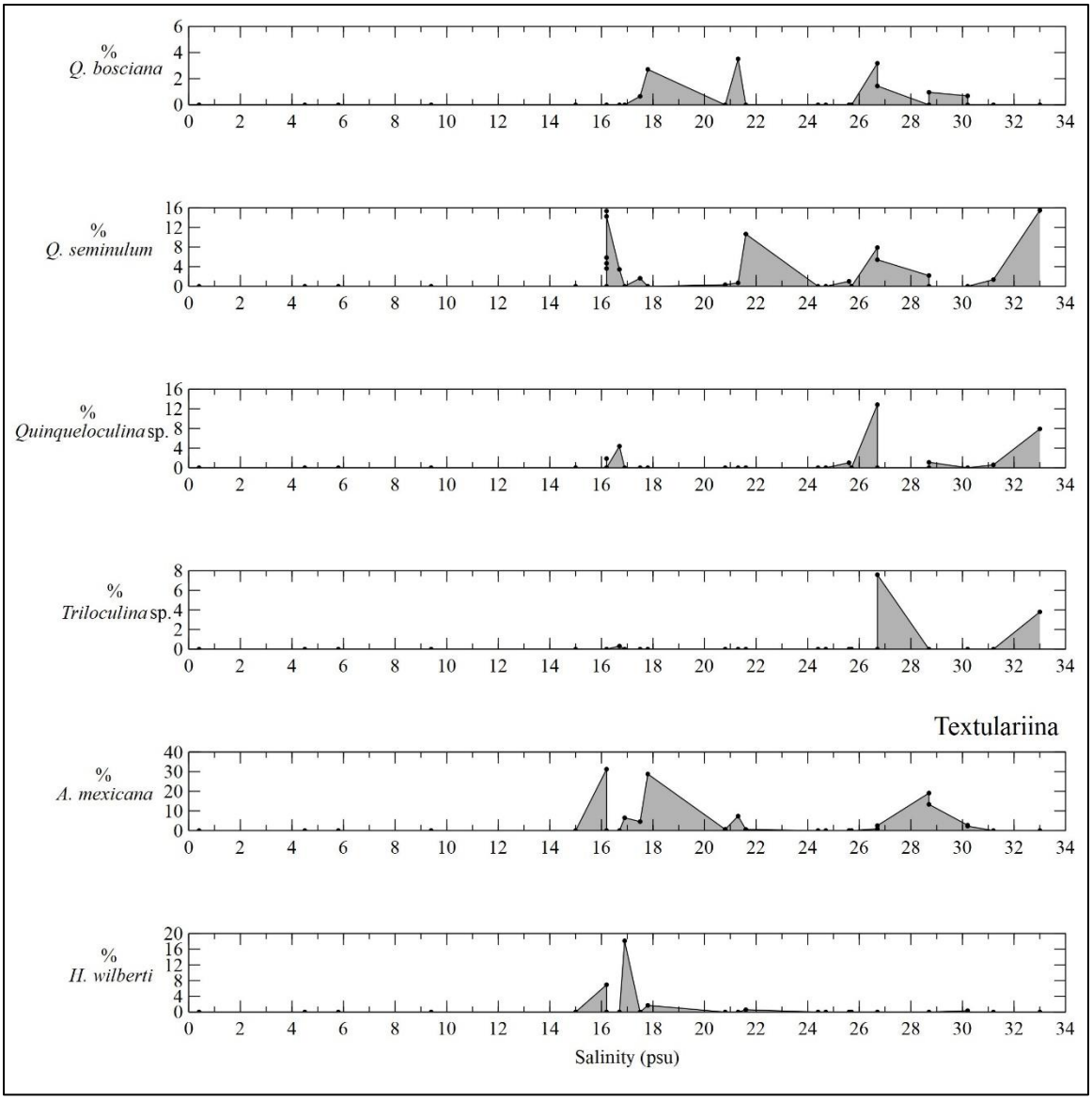

Figure 9 – The relative abundance of some calcareous imperforate taxa and agglutinated taxa, which have at least a 1% contribution to the observed differences between habitats, compared with salinity (psu).

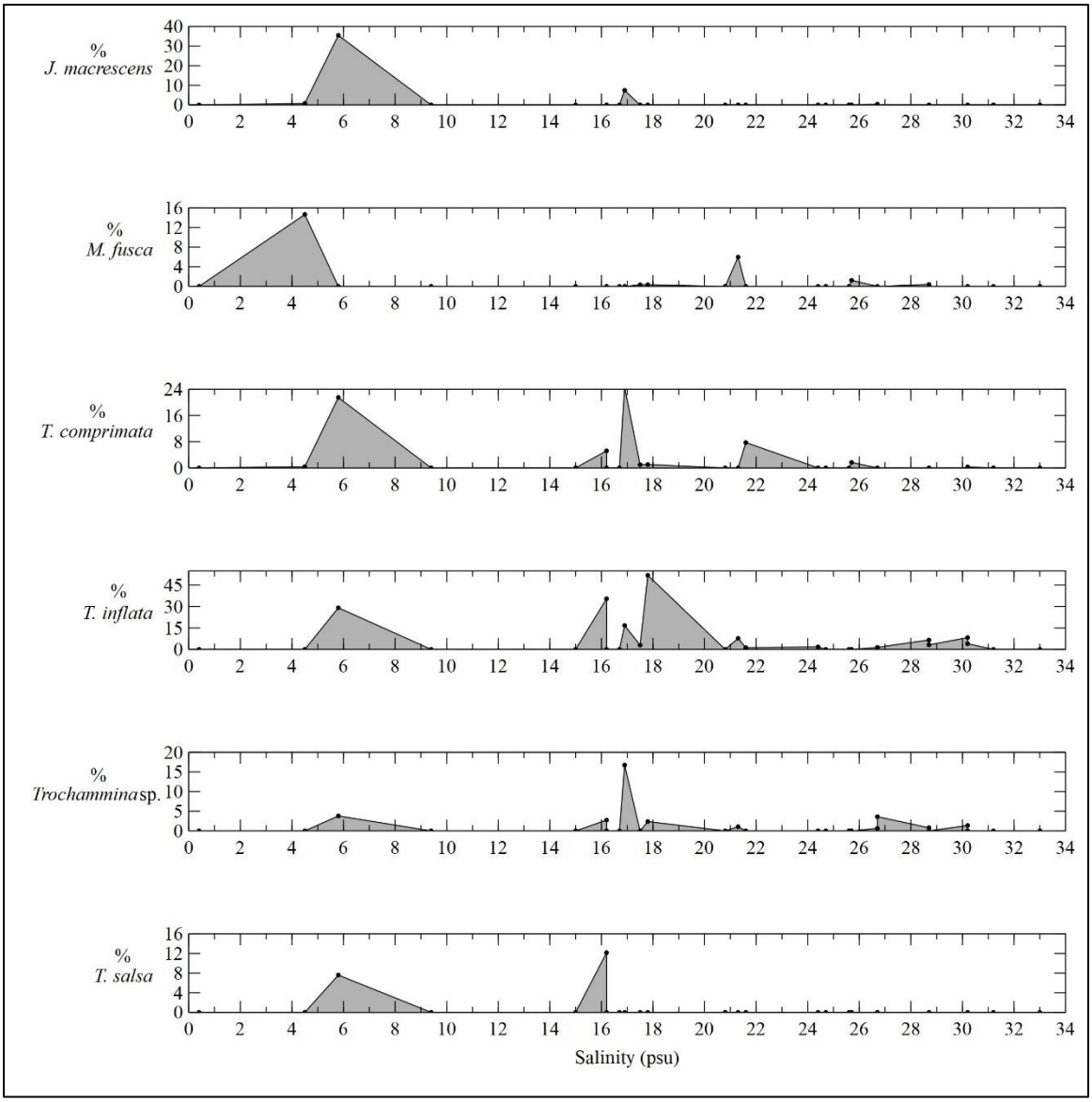

Figure 10 – The relative abundance of some agglutinated taxa, which have at least a 1% contribution to the observed differences between habitats, compared with salinity (psu).

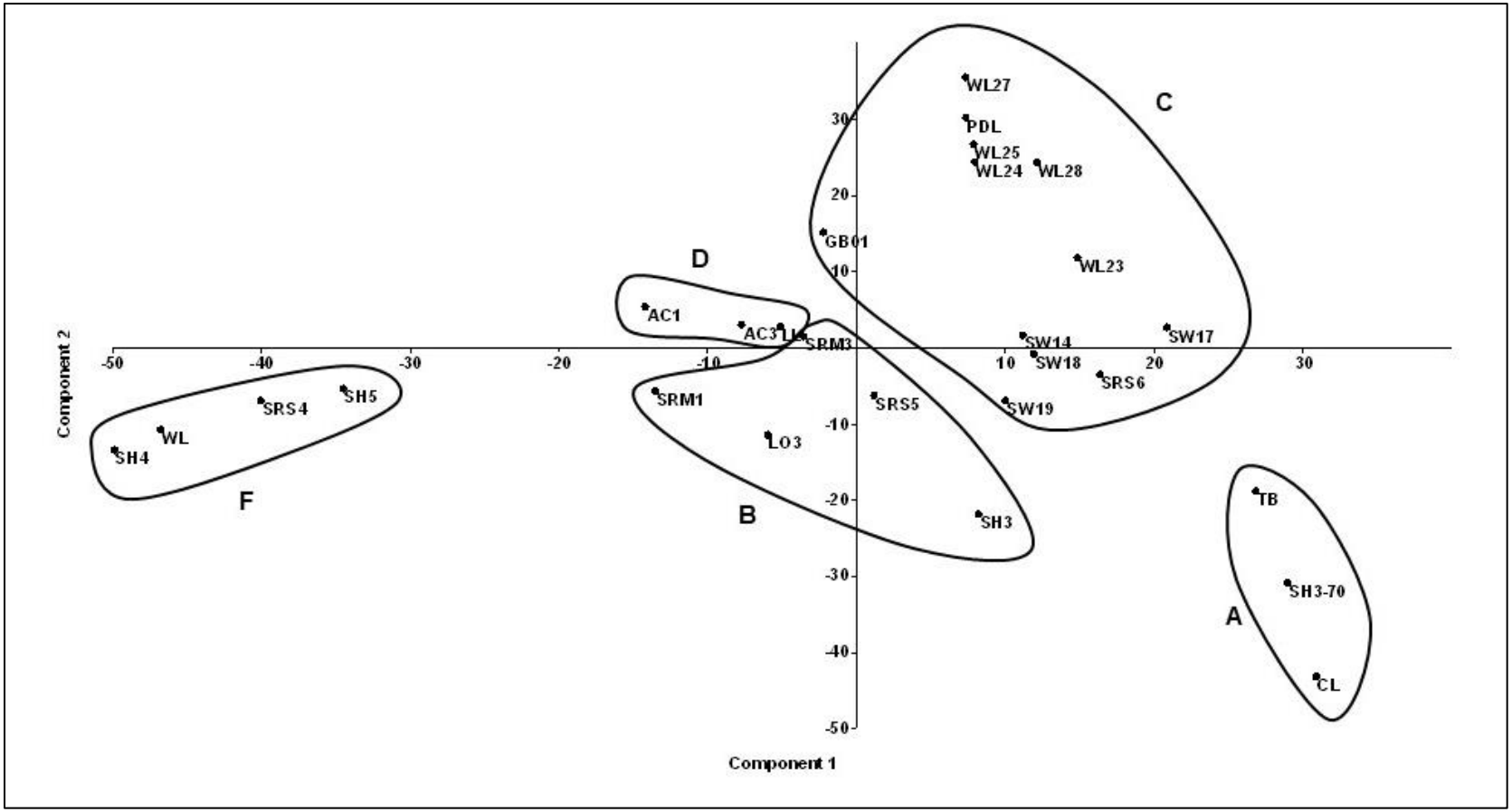

Figure 11 – Principal component analysis of foraminiferal assemblages from 27 sites (excluding site SW31). Principal Component 1 explains 39% of the variance and Component 2 accounts for 28% of the variance. The encircled samples labelled with letters A-D, and F refer to the sample associations identified from the Q-mode cluster (see Fig. 3).

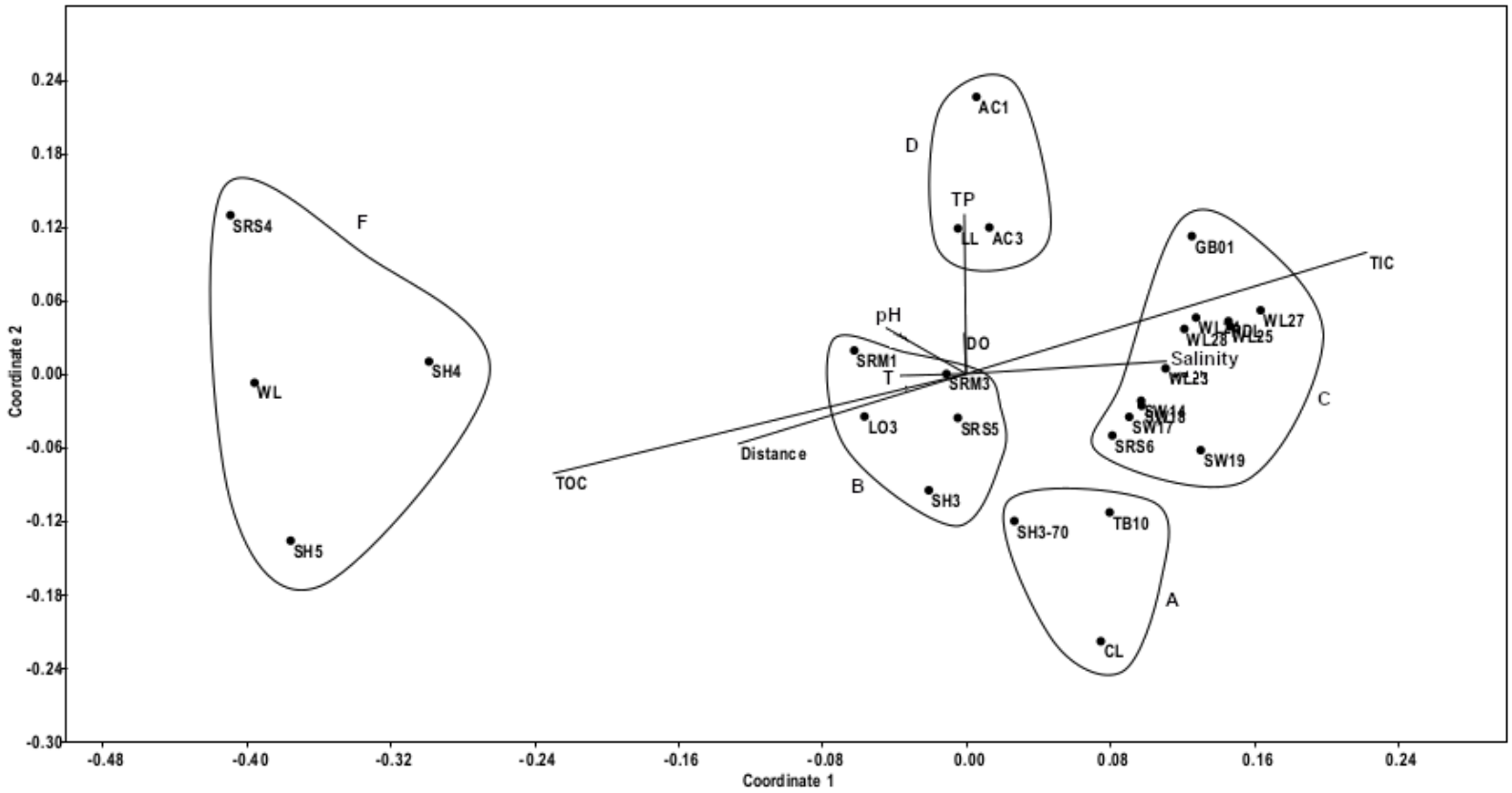

Figure 12 – Two-dimensional ordination diagram of samples produced by non-metric multidimensional scaling (NMDS), using the Bray-Curtis dissimilarity index. The lines originating from the center are vectors representing the direction and relative magnitude of the correlation coefficients between each environmental variable and the NMDS scores of the samples. The encircled areas labelled with letters A-D, and F refer to the identified sample associations from the Q-mode cluster (see Fig. 3).

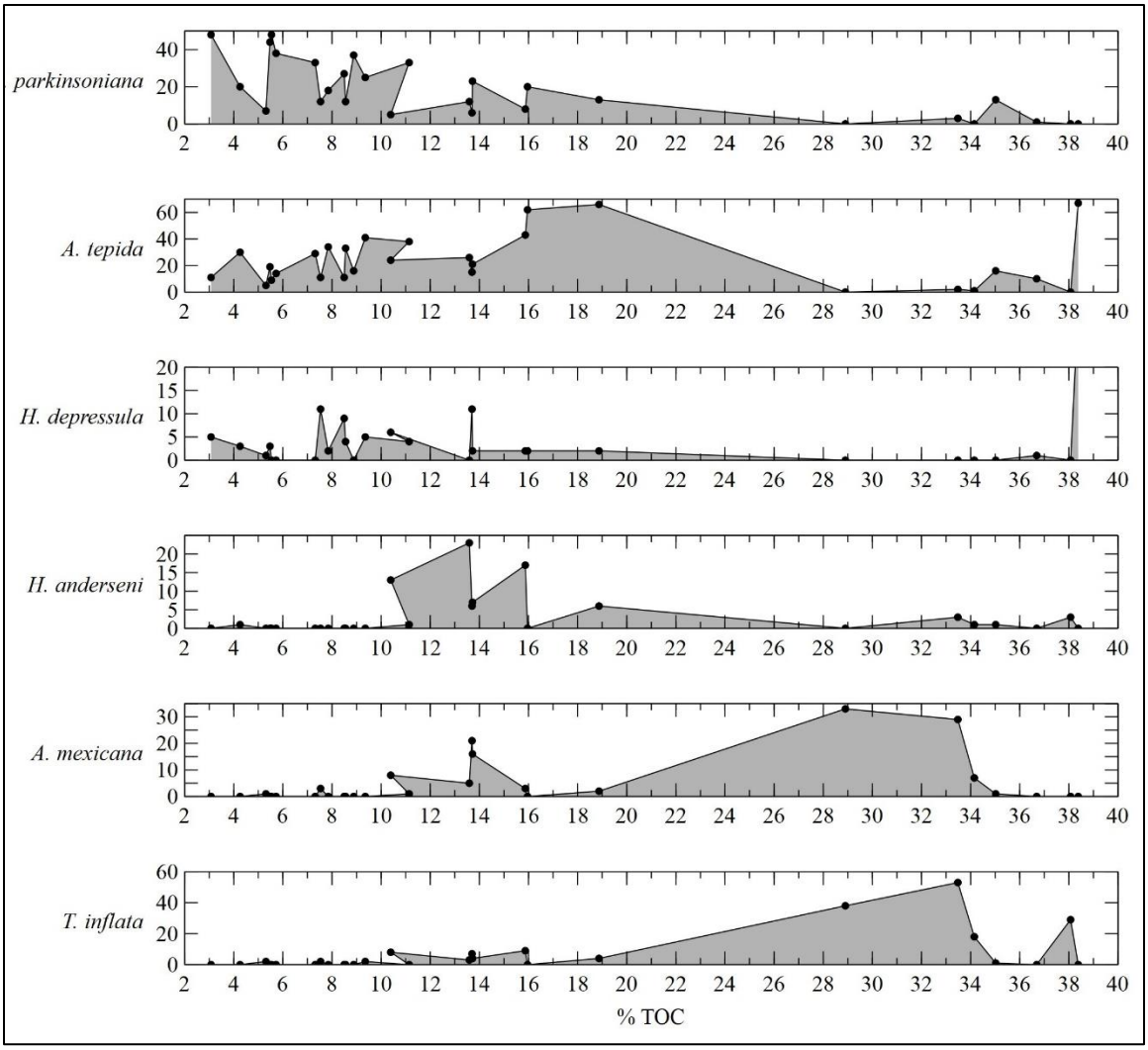

Figure 13 – The relative abundance of some taxa common in organic-rich sediments with the percentage of total organic carbon (TOC) of the sediment

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Chapter 4

History of Paleoenvironmental Changes in the Southwestern Everglades using Foraminiferal Assemblages

ABSTRACT

The history of paleoenvironmental change in Florida's Everglades over the past ~3400 years was interpreted from foraminiferal assemblages preserved in a sediment core and based on the ecology of extant foraminifera in the region. The low-lying, microtidal coasts of southwest Florida are fringed by marsh and mangrove habitats. As this region is underlain by a highly porous aquifer, it is highly sensitive to inundation and saltwater intrusion. This study is the first to provide a foraminiferal based paleoenvironmental study for this region, and only a few studies of modern foraminiferal assemblages of South Florida exist. Worldwide, mangrove forests have received less scientific attention than salt marshes, even though they comprise 70% of the world's tropical and subtropical coasts.

Twenty-seven samples were analyzed from a 262-cm-long section of a sediment core which was retrieved about 4 km inland along the Shark River, and was radiocarbon dated. In total, 51 species were identified, the majority of which were calcareous. Using constrained cluster analysis, an upper mangrove, lower mangrove, and coastal, marine-influenced habitat were recognized. Two transitional environments, one between the bottom of the core section and the upper mangroves, and one between the lower mangroves and the coastal habitat, were identified. The shifts in foraminiferal

assemblages over time are related to an increase in salinity caused by transgression with rising sea level. The rate of habitat change accelerated from <0.005 changes/yr to >0.03 changes/yr by AD 1950, which is consistent with studies of local sea level.

INTRODUCTION

This study examined temporal changes in benthic foraminiferal assemblages and habitat change over the past ~3400 years for the southwestern coastal Everglades. South Florida's low-lying coasts are fringed by marsh and mangrove environments, and subject to a microtidal regime. Additionally, the region is underlain by a highly porous aquifer, making the area sensitive to inundation (Parry et al., 2007; Alongi, 2008; Price et al., 2010) and saltwater intrusion (Price et al., 2006, 2010) that are resulting from a transgression caused by rising global sea level (Price et al., 2006, 2010; Alongi, 2008).

The first major human influences on South Florida's coastal areas date back to the early 1900s. The first onset of saltwater intrusion, for example, resulted from lowering of the groundwater levels in the Biscayne Aquifer, southeastern coastal Florida, due to the construction of levees and canals in the 1920s and 1930s in order to drain surface water from Lake Okeechobee and the Everglades to the Atlantic Ocean and Gulf of Mexico (Price et al., 2006; Saha et al., 2011, Wachnicka et al., 2013). Between 2000 and 2010, the highest increase in the coastal population for Florida happened in South Florida (Florida Coastal Management Program, 2010). Further coastal population growth and associated coastal utilization throughout the 21st century is expected and will result in a coastal squeeze, restricting the landward migration of coastal ecosystems as sea level

rises (Parry et al., 2007; Wachnicka et al., 2010). Paleoenvironmental studies are useful as baseline data for making predictions of coastal behavior (Parry et al., 2007). These studies unravel environmental changes through time, and determine if this happens gradually, suddenly, or at a constant rate, trends which can then be extrapolated to the future (Parry et al., 2007).

Previous foraminiferal marsh studies in South Florida's coastal mangrove settings are few (Benda and Puri, 1962; Phleger, 1965; Goldstein, 1976; Bock and Gebelein, 1977), and this is the first foraminiferal based paleoenvironmental study for the Everglades. Even though mangrove forests comprise 70% of the world's tropical and subtropical coasts, the responses of mangrove wetlands to sea level rise have not received the same scientific attention as salt marsh coasts in North America and Northwestern Europe (Berkeley et al., 2008; Culver et al., 2013).

The Everglades' geology is a clear advantage for paleoenvironmental studies in South Florida. Because of the underlying limestone bedrock, the sediment composition is mainly calcium carbonate in the form of fine mud and shelly material, creating a carbonate-buffered environment that allows for exceptional preservation of calcareous taxa (Phleger, 1965). For potential sea level reconstructions in this region, the microtidal regime, tectonic stability, and relatively minor isostatic effects of glacial rebound (Hawkes et al., 2016) are also a benefit. As the vertical error calculation for sea level reconstruction (Shennan and Horton, 2002) includes the mean tidal range, Culver et al. (2013) concluded that this should consequently result in a small error for their study of a mangrove wetland with a small tidal range. Furthermore, Florida is located along a passive margin where Holocene relative sea level changes are mainly driven by eustatic

and isostatic processes. The region between Georgia and Florida is located on the edge of the collapsing peripheral forebulge of the former Laurentide Ice Sheet, so uplift is on the order of 0.45 mm/yr (Hawkes et al., 2016).

For this study of Everglades foraminifera, we investigated: (1) the times during which assemblage shifts occurred, (2) the rate at which observed changes occurred, (3) changes in assemblage composition through time and its paleoenvironmental significance for shifts in habitat, and (4) the potential effects of selective preservation of specimens, which could affect interpretations of paleoenvironmental change.

METHODS

Field Methods

The study site (SRS6) is located on a river bank about 4 km inland from the mouth of the Shark River, Everglades National Park (Fig. 1). We used a part of the 445-cm-long sediment core obtained and radiocarbon dated by Yao and Liu (2017). The core was collected using a 5-cm-in-diameter Russian corer, also called a D-section corer or McAuley corer, a commonly used tool to sample the fine-grained, peaty sediments that characterize salt marshes or mangrove swamps (Bricker-Urso et al., 1989, Verlaak et al. 2018). Yao and Liu (2017) sectioned the brackish to marine part of the core, from which we received 27 5-cm-thick samples (0 – 262 cm). These intervals lie between the sediment sections they used for their pollen study on this core.

Chronology

Four samples consisting of leaf fragments and organic silt were selected from the 0–262 cm section of the core at 114 cm, 200 cm, 232 cm, and 303 cm depth by Yao and Liu (2017) and sent to the NOSAMS Laboratory at Woods Hole Oceanographic Institution and Beta Analytic Inc. for AMS ^{14}C measurements. All ^{14}C dates were calibrated by Yao and Liu (2017) using the CALIB 7.0 program (Stuiver et al., 2010) and reported as calibrated years before present (cal yr BP).

To estimate the ages corresponding to our stratigraphic horizons at which assemblage shifts occurred, we interpolated between the four known 2σ age ranges (cal yr BP) for the 0–262 cm section of the core (Table 1), assuming a linear relationship to calculate the ages of these sediment horizons. As the two uppermost stratigraphic horizons of interest are younger than or equal to AD 1950 (0 cal yrs BP), we used the known sediment accumulation rate of 3.6 mm/yr from a location less than 100 m from site SRS6 (Smoak et al., 2013) to find the corresponding age. After obtaining the dates for each of these depths, we then calculated the time span between them.

Laboratory Methods

The 27 sediment samples were rinsed over nested screens of 2.80 mm to remove larger sediment particles or organic matter and 63 μm to remove finer silts and clays. The residue, which contains benthic foraminifera and other sand- to gravel-sized particles, was then transferred onto filter paper, air-dried overnight, and split with a sediment

microsplitter into subsamples containing approximately 300-400 individuals. The number of species in an assemblage is related to the number of individuals collected, but above ~400 individuals, larger sample sizes do not significantly improve accuracy (Murray,1973, 1991). Below 132 cm, fewer than 300 tests were preserved in the samples; thus, we scanned through all the available sediment for each of the samples from this depth to the bottom of the core section. The foraminiferal tests were removed under a binocular microscope and sorted onto slides for identification. The taxonomy was aided by the same literature on the Gulf of Mexico and Caribbean as was used to identify modern foraminiferal assemblages (Chapter 3), as well as by comparison to the identified modern species (Verlaak et al., 2018).

We also performed a simple test using 10% HCl on one specimen of each agglutinated species recorded in this study. The reaction of acidic conditions would allow us to distinguish between agglutinated tests with organic cements and non-carbonate grains, and those with carbonate cements and/or carbonate grains.

Quantitative Methods

To determine when major shifts in the assemblage composition occurred, we performed constrained, paired-group cluster analysis, using the Bray-Curtis dissimilarity index. This index quantifies dissimilarity using the equation

$$2w/(a+b)$$

where, assuming one is comparing more than two sets of samples, w is the sum of the lesser value for species that are in common between two samples, compared to the value

of w for other pairs of samples, and a and b are each the sum of the quantitative measures in one sample and the other sample, respectively (Bray and Curtis, 1957). Constrained cluster analysis maintains the chronological order of the samples and only compares samples or groups of samples that are stratigraphically adjacent to each other, so the obtained clusters represent distinct, chronologically arranged groups of foraminiferal assemblages (Hammer et al., 2001). One-way ANOSIM or analysis of similarities (Clarke, 1993) was used to assess whether the identified clusters are significantly different from each other ($p < 0.05$). This test is based on comparing between-group with within-group distances and converts these distances to ranks.

To analyze changes in diversity, dominance, wall type, and species composition over time, we plotted Shannon diversity, Berger-Parker dominance, the percentage of wall types, and common taxa, respectively, against their depth-in-core. To quantify taxonomic diversity, we used the Shannon diversity index H′ (Shannon, 1948), which is calculated as

$$H' = - \sum p_i \ln (p_i)$$

with p_i the relative proportion of each species. This diversity index takes into account both the number of individuals as well as the number of taxa because diversity generally increases as more taxa are counted. A value of zero corresponds to an assemblage of a single taxon, while higher values result from assemblages with many taxa consisting of few individuals each (Hayek and Buzas, 2013).

We used the Berger-Parker Index d (Berger and Parker, 1970) to quantify dominance, calculated as

$$d = N_{max} / N$$

with N the total number of individuals in a washed sediment sample and N_{max} the number of individuals of the most abundant species (Hayek and Buzas, 2013). Cluster analysis and the calculation of diversity measures were completed using the open-source PAST (PAleontological STatistics) software package, version 2.17c (Hammer et al., 2001).

Possible preservational effects on specimen counts were investigated by analyzing and comparing the downcore abundance patterns of the taxa common in this core. Well-preserved taxa usually exhibit a constant or increasing relative abundance with depth (Goldstein and Watkins, 1999).

RESULTS

Downcore Assemblage Characteristics

Our study recorded 51 species (Table 2) in the studied section of core, of which 26 are calcareous perforate taxa (Rotaliina), 2 are calcareous imperforate (Miliolina), and 23 are agglutinated (Textulariina). Eighty-four percent of the taxa found in the core were also found in the modern assemblages. The upper 10 cm of the core consists of more than 95% calcareous taxa, dropping to 20% between 10 and 21 cm (Fig. 2). Below 21 cm, the dominant wall type is agglutinated, making up at least 98% of the assemblage, except for the 252-cm depth where only 14% are Textulariina. Shannon diversity increases as Berger Parker dominance decreases in the upper 21 cm of the core. Below 21 cm in depth, the core shows a lower diversity and higher dominance, and both fluctuate more below 120 cm in depth (Fig. 2).

Cluster Analysis

The cluster analysis resulted in clusters A, B, C, D, and E, and samples 21, 212, 252, and 262 of distinct foraminiferal assemblages (Fig. 3). Samples 5 and 10 (cluster A), comprising mainly of calcareous taxa, are most dissimilar from the rest of the core samples, which dominantly consist of agglutinated assemblages. Sample 21 and 252 are assemblages with a mixture of agglutinated and calcareous taxa. From the bottom of the core to the top, the largest change or dissimilarity occurs between sample 252 and cluster E. Smaller dissimilarities, in order of importance, can be observed between cluster B and sample 21, between sample 21 and cluster A, and between clusters C and B. Dissimilarities of the same order can be noted between cluster E and sample 212, sample 212 and cluster D, and clusters D and C. Including the bottom of the core section, there are five stratigraphic horizons where major assemblage shifts occurred: 252 cm, 242 cm, 152 cm, 21 cm, and 10 cm. The analysis of similarities (ANOSIM; Table 3) resulted in p-values less than 0.05 between each of the groups or samples of distinct foraminiferal assemblages, except for between cluster A and sample 21, between cluster A and samples 252 and 262, and between sample 21 and the other clusters ($p>0.05$).

Vertical Species Distributions

The relative abundance of some common taxa with depth in the core (Fig. 4) shows that *Arenoparrella mexicana* and *Trochammina inflata* are generally abundant

throughout the lower 252 cm of the core, mostly exceeding 20% in abundance. Between 262 cm (bottom of core section) and 242 cm, assemblages consist only of *A. mexicana*, *Haynesina depressula*, and *Miliolinella microstoma*. Between 242 cm and 152 cm, the common taxa are *Haplophragmoides manilaensis*, *Haplophragmoides wilberti*, *Jadammina macrescens*, *Tiphotrocha comprimata*, and *Trochamminita salsa*. The interval between 152 cm and 21 cm is characterized by a low (4%) but constant abundance of *Miliammina fusca*, a consistently high abundance of 75 % for *A. mexicana*, an increase in abundance of *Textularia earlandi*, and the decrease in abundance of *T. comprimata*. The upper half of this interval also shows a high abundance of *H. wilberti*, but it is only about half of the abundance in the prior interval. From 21 cm to 10 cm depth, *T. earlandi* has its peak abundance and *T. inflata* still is about as abundant as below, whereas *A. mexicana* shows a reduced abundance. Furthermore, a peak in the relative abundance of *Helenina anderseni* can be observed. Lastly, the upper 10 cm consists mainly of calcareous taxa, dominated by *Ammonia* spp. (2 species) and *Elphidium* spp (8 species).

DISCUSSION

Temporal Changes in Assemblage Structure

Below 21 cm depth, foraminiferal assemblages are predominantly agglutinated, with a low diversity and high dominance. In the upper 21 cm of the core, assemblages consist primarily of calcareous taxa that increase in diversity and decrease in dominance

towards the top of the core. Fluctuations in diversity and dominance occur below 132 cm depth. Over the sediment interval between 262 cm and 132 cm, each sample contained less than 300 specimens, even though all the sediments were examined. Additionally, where diversity fluctuates, it always shows lower values than the average diversity across the 262- to 21-cm interval, possibly because of specimen loss or fewer specimens originally. The same can be said about dominance.

Modern foraminiferal distributions (Chapter 3) demonstrate that low-diversity, high-dominance agglutinated assemblages are typical for stressed, low-salinity (<6 psu) habitats at the landward end of intertidal environments, whereas high-diversity, low-dominance calcareous assemblages mainly exist in near-coastal, higher salinity habitats, which agrees with previous studies of the region (Benda and Puri, 1962; Goldstein, 1976; Bock and Gebelein, 1977) and of other mangrove swamps (Culver, 1990; Hayward and Hollis, 1994; Woodroffe et al., 2005) and salt marshes (Hayward et al., 1996; Lei et al., 2017). The results indicate that over time, salinity increased, as expected from studies documenting sea level rise (Kemp et al., 2014; Hawkes et al., 2016; Gerlach et al., 2017) and a brackish environment was replaced by near-marine conditions.

Timing of Assemblage Change

For the Everglades core, changes in assemblage composition accelerated as the present was approached (Table 1; Fig. 5) and are substantially faster since AD 1950. The rate of habitat change was <0.005 changes/yr prior to AD 1950, after which it accelerated to >0.03 changes/yr. This corresponds well to the timing of an accelerated rate of sea

level rise recorded by tide gauges in Bermuda, northeastern Florida, and Key West, as well as along the Gulf coast in Naples, Fort Meyers, and St. Petersburg (Ellison, 1993; Kemp et al., 2014; Hawkes et al., 2016; and Gerlach et al., 2017). For our study, shifts in foraminiferal assemblages can be related to environmental change (section below) and follow local sea level trends.

Sea level studies of Florida based on foraminiferal assemblages and other proxies from salt marsh sediments (Kemp et al., 2014; Hawkes et al., 2016; Gerlach et al., 2017), as well as studies based on changes in sedimentary facies (Goodbred et al., 1998), and a study of Bermuda mangrove peats (Ellison, 1993), determine that the rate of sea level rise was generally low, with some fluctuations, over the past 8000 years. Hawkes et al. (2016) discovered that climatic wet and dry cycles contributed to fluctuations in the rate of sea level rise in northeastern Florida, for example, from 0.35 mm/yr between ~4600 and ~2800 cal yrs BP to 1.17 mm/yr between ~2800 and ~2300 cal yrs BP. We may have recorded these fluctuations in the Everglades core as minor changes in the foraminiferal assemblages (between clusters C, D, E, and sample 212 in Fig. 3), but these identified variations in the rate of sea level rise did not cause detectable, major habitat changes on the southwestern Florida coast. Gerlach et al. (2017) and Goodbred (1998) identified a slowing rate of sea level rise between ~2300 and ~2000 cal yrs BP, after which it remained at a rate of near zero, with a possible short-lived increase, until AD 1500 (~450 cal yrs BP). For a similar time period, between ~2600 cal yrs BP and ~100 cal yrs BP (or AD 1850), Kemp et al. (2014) also calculated a low rate (0.41 mm/yr) and attributed this to glacio-isostatic adjustments.

According to Gerlach et al. (2017) sea level rise started accelerating as early as AD 1500, and the rate of sea level rise reached 1.5 mm/yr in AD 1850 (Kemp et al, 2014), and 2.05 mm/yr in AD 1897 (Hawkes et al., 2016). A tide gauge record from Bermuda reported a rate of 2.8 mm/yr since AD 1932 (Ellison, 1993).

Paleoenvironmental Changes Through Time

Coring site SRS6 is located 4 km from the coastline in a high-stature, dense, mixed mangrove forest (Chen and Twilley, 1999). The site is marine influenced with an average salinity of 24 psu (Chapter 3). The modern foraminiferal assemblages are characterized by high diversity and low dominance and consist primarily of calcareous taxa dominated by the genera *Ammonia* and *Elphidium* (Chapter 3).

Transitional Interval 1

In the lowermost part of the studied core section, 262 to 242 cm (~3449 to ~3244 cal yrs BP; Table 1; Fig. 5), the calcareous species *M. microstoma* and *H. depressula* and agglutinated species *A. mexicana* occur. As the ecotone between the mangroves and the freshwater environment is typified by drastic differences in salinity (Debenay et al., 2002), we expect that foraminiferal species with a tolerance for such changes would live here. *M. microstoma*, *H. depressula*, and *A. mexicana* are most abundant in places with low salinity (15-18 psu) as well as high salinity (28-30 psu, Chapter 3). In addition, miliolids and agglutinated taxa are known to survive in both hypersaline as hyposaline

environments (Bender and Hemleben, 1988; Armstrong and Brasier, 2005), and Boltovskoy and Lena (1971) found that even some perforate calcareous taxa can survive under freshwater conditions. Our modern assemblages showed that it is not uncommon to find such mixed assemblages at the landward edge of the mangrove zone; however, agglutinated species usually dominate. A significance test (Table 3) found significant ($p<0.05$) differences between this interval and the mangrove environments above. Therefore, we interpret this interval as a period of transition from a freshwater to a brackish water environment, during which site SRS6 was located close to the landward edge of the upper mangroves, and where salinity fluctuated between <18 psu and >28 psu, based on the low- as well as high-salinity preference of the three species involved.

Yao and Liu (2017) determined with pollen that prior to 3800 cal yrs BP (below our studied 262-cm depth) this area was a freshwater marsh mainly vegetated by herbaceous taxa (e.g. Amaranthaceae) with some grasses (e.g. Poaceae), aquatic plants (e.g. *Sagittaria*), and conifers (e.g. *Pinus*). Our transitional interval corresponds to a period during which grasses and herbaceous plants were still very abundant, while the numbers of *Rhizophora* pollen increased. These early red mangroves were scrub-size, and occasionally accompanied by *Avicennia* or black mangrove, *Laguncularia* or white mangrove, and *Conocarpus* or buttonwood (Yao and Liu, 2017).

Upper Mangrove Environment

The 242- to 152-cm interval (~3244 to ~1288 cal yrs BP) is characterized by fully agglutinated assemblages, and based on modern assemblages (Chapter 3), it represents

the upper mangrove zone, characterized by salinities on the order of <18 psu. The most characteristic species, considering their relative abundance and their prevalence within this stratigraphic interval, are *H. manilaensis*, *H. wilberti*, *J. macrescens*, *T. comprimata*, and *T. salsa*. Most of these taxa showed a low salinity preference (<18 psu), whereas *H. wilberti* preferred higher salinities (16–18 psu) in the modern study (Chapter 3). In the modern-day Everglades, assemblages consisting of these species occur at sites with low stature mangroves or sawgrass. The pollen study (Yao and Liu, 2017) indicates that grasses and herbaceous taxa were in decline, while Rhizophora, and other mangrove species increased their abundance over the time represented by this sediment interval. Clusters C, D, sample 212, and cluster E were all interpreted as Upper Mangroves, as a significance test (Table 4) resulted in p-values higher than 0.05 between these groups.

Lower Mangrove Environment

The section between 152 and 21 cm (~1288 cal yrs BP to AD 1950) also comprises agglutinated assemblages. We interpret this interval as the lower mangrove zone, characterized by salinities of >16 psu. This is based on the decrease in relative abundance of *T. comprimata* (low salinity species, <18 psu) and the increase in abundance of *T. earlandi*. We did not find any specimens of *T. earlandi* in our modern Everglades assemblages, but this species is known to occur at the seaward end of estuaries (Hayward and Hollis, 1994; Barbosa et al., 2005) or in hypersaline marshes (Phleger, 1967). Additionally, we observed a very high abundance of *A. mexicana*, which showed a preference for salinities above 16 psu (Chapter 3). The Everglades pollen

record (Yao and Liu, 2017) shows an increase in *Rhizophora* (red mangrove) and *Avicennia*, and a decrease in *Conocarpus*, indicating increased tidal influence and proximity to the coast (Urrego et al., 2010).

Transitional Interval 2

Between 21 and 10 cm (corresponding to AD 1950–1982; Table 1; Fig. 5) another transitional interval within which environmental conditions changed from brackish to marine-influenced, is characterized by salinities between 17 and 20 psu, based on the modern study (Chapter 3). Within this stratigraphic segment, *T. earlandi* reaches its highest abundance, *T. inflata* is still present with high relative abundance, and *H. anderseni* makes its first appearance. In our modern study, *T. inflata* and *H. anderseni* occurred at salinities <18 psu and >17 psu, respectively. All these species are common at high salinities at the seaward end of estuaries (Murray, 1971; Hayward and Hollis, 1994). The transitional interval is mainly characterized by the high dominance of *Rhizophora*, while other mangrove species are also present in relatively high numbers (Yao and Liu, 2017). The significance test (Table 3) shows that sample 21 is not significantly different from the other clusters of samples, but when grouped with cluster B (Lower Mangroves) it is significantly ($p<0.05$) different from cluster A (Coastal Environment).

Coastal Environment

The upper 10 cm of the environment represented in the core (AD 1982 to Present) compares very well to the modern day with salinities >20 psu and predominantly calcareous taxa, mainly *Ammonia* spp. and *Elphidium* spp. (Fig. 4). Most *Elphidium* spp. in the modern study (Chapter 3) preferred salinities >20 psu.

In the pollen study by Yao and Liu (2017), the upper 10 cm of the core was interpreted as a storm deposit from Hurricane Wilma, which hit the west coast of the Everglades in AD 2005. However, even though storm deposits near the coastline reached a thickness of about 10 cm, they rapidly decreased in thickness in a landward direction. Consequently, storm deposits here were less than 3 cm thick (Castañeda-Moya et al., 2010). As this is smaller than our sampling resolution of 5 cm, we unfortunately cannot detect foraminiferal assemblage shifts, if present, within this layer.

Core samples 5 and 10 consist of plant particles (twigs, pieces of bark, etc.) and a sand-sized fraction of mainly carbonate components, such as grains and rounded shell and coral fragments, as well as a minor amount of sponge spicules and quartz grains or crystals. Grain size analysis on sample 5 (0–5 cm) shows that most of the sand-sized carbonate fraction of the sediment is between 63 and 125 µm, about 56% of the total weight of the sediment. The remainder of the sediment, between 125 µm and 2 mm, consists of plant fragments or nodules of plant material with carbonate traces. For sample 10 (0–10 cm) about 57% of the sediment, about half of which is plant fragments, has a grain size between 63 and 355 µm and contains most of the carbonate fraction. Below 10 cm depth no carbonates occur, and the sediment consist primarily of plant fragments,

though up to 21 cm depth some coral fragments occur, whereas quartz grains or crystals are common up to 82 cm depth. Similar to foraminiferal assemblages from the top 10 cm of the studied core section, assemblages from modern sites SRS6, SH3, and SH3-70 (Fig. 1), at the same distance from the coast along the Shark River as core site SRS6, consist of > 87% calcareous taxa.

The 0–10 cm interval is significantly distinct ($p<0.05$) in its foraminiferal assemblages from the intervals interpreted as mangrove habitat. Q-mode cluster analysis compiling modern and core samples (Fig. 6) results in the separation of agglutinated assemblages, which include all the core samples except for samples 5 and 10, and calcareous assemblages, which include core samples 5 and 10. Sample 5 is most similar to near-coastal sites SRS6, SW14, SW17, and SW18, whereas sample 10 is most similar to site SW19. It is plausible that the 0–10 cm in the studied core section contains storm deposits, but these may have been mixed over time with the local peats at site SRS6, explaining the discrepancy between the measured storm layer of less than 3 cm thick (Castañeda-Moya et al., 2010) and the observed carbonate-rich sediment within the upper 10 cm of the studied core section.

Preservation

This study shows that the downcore patterns of species abundance are the result of environmental changes rather than selective preservation because the downcore decrease in the abundance of calcareous taxa and *T. earlandi* cannot be related to dissolution or degradation of their tests. In this study, *A. mexicana* and *T. inflata* have a

constant relative abundance throughout most of the core. Other species, such as *J. macrescens, T. comprimata*, and *T. salsa*, show a downcore increase in abundance. Both downcore patterns indicate that these species are well-preserved (Goldstein and Watkins, 1999). Another explanation for downcore enrichment of dead tests would be the presence of infaunal populations, introducing new tests which tend to be better preserved (Goldstein and Watkins, 1999); however, a prior study of infaunal foraminifera confirmed that in the Everglades, the addition of live tests to total assemblages at greater depths is negligible (Verlaak et al., 2018; Chapter 2).

For this study, between 21 and 152 cm depth, *T. earlandi* exhibits a decrease in relative abundance, which might imply that this species is affected by degradation. However, Bender and Hemleben (1988) concluded in their study of the microstructure of the cementing material in agglutinated taxa, that the single-strand cement of *M. fusca*, and the fibrous meshwork cement of *T. earlandi* and *T. inflata*, are more resistant against test disaggregation than the foam-like cement structure of *J. macrescens*. In our study, *T. inflata* has a high and constant relative abundance over the same sediment interval as *T. earlandi*. As Bender and Hemleben (1988) state that *T. inflata* and *T. earlandi* should be equally resistant to degradation, we conclude that the downcore decrease in abundance of *T. earlandi* is not due to selective preservation, but rather, the species' response to changing environmental conditions.

Similarly, the downcore decrease in the abundance of calcareous taxa is not due to dissolution caused by a low pH. *Helenina anderseni,* which was poorly preserved in a North Carolina salt marsh (Culver and Horton, 2005) and Malaysian mangroves (Culver et al., 2013), maintains a constant relative abundance up to 21 cm depth in our study.

Some miliolids, also prone to dissolution, occur up to 31 cm in depth. Additionally, *A. tepida* and *A. parkinsoniana* show the same downcore abundance pattern, even though many of the *A. tepida* specimens we observed had thinner tests than the *A. parkinsoniana* specimens, and were more corroded, indicating preferential dissolution. The exceptional preservation of calcareous taxa in the Everglades is because of the underlying limestone bedrock and calcium carbonate sediments, resulting in a carbonate-buffered environment (Phleger, 1965). Additionally, a test with 10% HCl on the modern and fossil agglutinated species recorded in this Everglades study, revealed that most agglutinated taxa do not react to acidic conditions (Chapter 3), indicating that they do not secrete calcareous cements or use carbonate particles to build their tests. Two species, found only in modern-day samples, did react: *Ammobaculites dilatatus* and *Ammotium multiloculatum*.

Below 132 cm depth, we consistently retrieved less than 300 specimens from the sediment samples (Table 1). This could be because of specimen loss or because there were fewer specimens to begin with in a less favorable environmental setting. However, as we observed broken tests at several intervals throughout the core, and we did not notice this becoming more severe below 132 cm depth, the second explanation is favored.

Preservation of calcareous taxa is controlled by wall structure, thickness, and architecture, but most importantly by the chemical composition of their test, and mainly influenced by dissolution through low pH (Murray and Wright, 1970; Peebles and Lewis, 1991; Berkeley et al., 2009). Pores, such as those present in the Rotaliina, are preferential sites of dissolution because they increase the permeability of the test and the surface area exposed to dissolution processes under acidic conditions (Berkeley et al., 2009). The inner wall layer of Miliolina consists of loosely packed, randomly oriented calcite

crystallites in an organic matrix. When the outer wall layer is stripped away this exposes the inner layer, which is a larger surface area that can be affected by dissolution. Additionally, the organic matter within this inner wall layer is prone to bacterial degradation or oxidation (Murray and Wright, 1970; Peebles and Lewis, 1991). Younger, thinner test chambers are less calcified and have higher concentrations of organic matter; hence, they are more susceptible to dissolution than older, thicker test chambers (Berkeley et al., 2009). The Rotaliina are made up of low-magnesium calcite, which is more stable than the high-magnesium calcite of the Miliolina (Peebles and Lewis, 1991).

Preservation of agglutinated taxa is mainly affected by oxidation and bacterial degradation of their organic constituents (Goldstein and Watkins, 1999; Berkeley et al., 2007, 2009). The response of agglutinated tests to degradation is determined by the type of cement, which can be wholly organic or biomineralized (Loeblich and Tappan, 1989; Roberts and Murray, 1995; Bertram and Cowen, 1998), and by the microstructure of their organic cement (Bender and Hemleben, 1988).

CONCLUSIONS

Changes in benthic foraminiferal assemblages and habitats over the past ~3400 years were investigated for the Everglades. We identified 51 species of which 23 are agglutinated. Eighty-four percent of the taxa were also found in the modern assemblages (Chapter 3). Calcareous taxa quickly reach 97% abundance from 21 cm depth in the core to the top. Below 21 cm, diversity is low and dominance is high, characteristic of assemblages at the landward end of intertidal environments, whereas above 21 cm

diversity increases and dominance decreases. High-diversity, low-dominance assemblages are typical of coastal habitats, because of less extreme physical conditions for foraminifera.

We examined the timing of changes in assemblage composition, and if these transitions happened gradually at a constant rate. We found that the major shifts occurred at ~3449 cal yrs BP, ~3244 cal yrs BP, ~1288 cal yrs BP, AD 1950, and AD 1982. The time span between these changes decreases towards the present, pointing to an accelerating trend after AD 1950. The rate of habitat change was <0.005 changes/yr prior to AD 1950, after which it accelerated to >0.03 changes/yr.

The history of paleoenvironmental changes revealed three different habitats and two transitional environments: (1) Transitional Interval 1, between ~3449 and ~3244 cal yrs BP. This interval reflects the transition of our study site from a freshwater to brackish water environment, with salinities fluctuating between <18 psu and >28 psu. Assemblages were characterized by a mix of agglutinated and calcareous taxa: *M. microstoma, H. depressula,* and *A. mexicana*. These are species that can tolerate changes in salinity, such as are present in the ecotone between mangroves and freshwater habitats.

(2) The Upper Mangroves Environment, from ~3244 to ~1288 cal yrs BP, consists of agglutinated assemblages that point to salinities <18 psu. The taxa found here are typical of lower salinity habitats: *Haplophragmoides* spp., *J. macrescens*, *T. comprimata*, and *T. salsa*.

(3) The Lower Mangroves Environment, between ~1288 cal yrs BP and AD 1950, is characterized by agglutinated assemblages that indicate salinities between >16 psu.

Over this time interval *T. comprimata* decreases in abundance, whereas *T. earlandi* increases. The latter species is common at the seaward end of estuaries.

(4) Transitional interval 2, from AD 1950 to AD 1982, marks the transformation from a brackish environment to a habitat closer to the coast and reflects salinities between 17 and 20 psu. This interval is characterized by a peak in *T. earlandi*, *H. anderseni* (which appears for the first time), and *T. inflata* (which disappears after this time period).

(5) The modern-day Coastal Environment, with salinities >20 psu, appears at AD 1982, and assemblages are dominated by *Ammonia* spp. and *Elphidium* spp, distinctive of environments with such salinity values. The pollen study (Yao and Liu, 2017) identified a brackish marsh vegetated with grasses, herbs, and shrub mangroves between ~3400 cal yrs BP and ~1100 cal yrs BP (i.e., the upper mangrove habitat for this study), and a mixed mangrove forest from ~1100 cal yrs BP to Present (i.e., the lower mangrove and coastal habitat in this study).

Finally, the observed downcore patterns of species abundance are the result of environmental change rather than selective preservation. Though, some minor loss of tests over time is possible.

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Table 1 – Conventional and calibrated ^{14}C ages (Yao and Liu, 2017) and depths at which they were determined (shaded rows). Minimum, maximum, and/or average age for sediment depths analyzed in this study were calculated by using sediment accumulation rates (Smoak et al., 2013), or linear interpolation using the known ^{14}C ages (Yao and Liu, 2017). Right two columns show average time span for each stratigraphic interval. "Transitional Interval 1" at 242–262 cm and "Transitional Interval 2" at 10–21 cm indicated in bold face, defined by their mixed (calcareous and agglutinated) assemblage composition and dissimilarity from stratigraphically adjacent clusters of assemblages.

Depth (cm)	Conventional C14 Age (yrs BP*)	2-σ Calibrated Range (cal yrs BP*)	Age Calculation						Stratigraphic Interval (cm)	Average Time Span (yrs)
			Min	Max	Average	Method		Unit		
10	-	-	-	-	1982	3.6 mm/yr	accumulation rate	AD	0 to 10	28
21	-	-	-	-	1950	3.6 mm/yr	accumulation rate	AD	**10 to 21**	32
114	500 ± 25	510-540								
152	-	-	1240	1335	1288	y=0.0521x+87.418 y=0.0478x+88.2	Linear interpolation, known ^{14}C dates	cal yrs BP*	21 to 152	1288
200	2260 ± 20	2160-2340								
232	2970 ± 90	2920-3360								
242	-	-	3041	3446	3244	y=0.0835x-11.906 y=0.1164x-159.08	Linear interpolation, known ^{14}C dates	cal yrs BP*	152 to 242	1956
262	-	-	3280	3618	3449	y=0.0835x-11.906 y=0.1164x-159.08	Linear interpolation, known ^{14}C dates	cal yrs BP*	**242 to 262**	205
303	3570 ± 25	3770-3970								

*BP = before present; "present" = January 1, 1950

Table 2 – Counts of individual species with depth in core, as well as the total number of specimens (N) and the number of species per sample of total assemblages (S).

	Calcareous Taxa																														Agglutinated Taxa																							
Depth (cm)	***Ammonia parkinsoniana***	***Ammonia tepida***	***Ammonia* spp.**	***Bolivina paula***	***Bolivina striatula***	***Bolivina variabilis***	***Bolivinita rhomboidalis***	***Bolivina* sp.**	***Bulimina* sp.**	***Buliminella elegantissima***	***Cancris oblongus***	***Discorbis aguayoi***	***Discorbis* sp.**	***Elphidium excavatum***	***Elphidium discoidale***	***Elphidium galvestonense***	***Elphidium koeboeense***	***Elphidium matagordanum***	***Elphidium mexicanum***	***Elphidium morenoi***	***Elphidium simplex***	***Elphidium* spp.**	***Eponides* sp.2**	***Fursenkoina* sp.**	***Haynesina depressula***	***Helenina anderseni***	***Nonionella atlantica***	***Rosalina* sp.**	***Cornuspira involvens***	***Miliolinella microstoma***	***Acupeina triperforata***	***Ammobaculites exiguus***	***Ammotium multiloculatum***	***Ammotium palustre***	***Ammotium subdirectum***	***Arenoparella mexicana***	***Haplophragmoides manilaensis***	***Haplophragmoides subinvolutum***	***Haplophragmoides wilberti***	***Haplophragmoides* sp.**	***Jadammina macrescens***	***Miliammina fusca***	***Siphotrochammina lobata***	***Textularia earlandi***	***Tiphotrocha comprimata***	***Trochammina inflata***	***Trochammina* sp.**	***Trochammina* sp.2**	***Trochamminita irregularis***	***Trochamminita salsa***	***Valvulina oviedoiana***	***Warrenita palustris***	**N**	**S**
5	266	160	15	18	18	16	5	0	0	6	16	1	27	116	46	10	0	16	16	66	8	25	3	2	35	43	6	1	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	950	26
10	96	57	5	2	12	0	0	2	1	0	0	4	5	4	0	1	48	6	0	51	1	0	0	2	11	5	3	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	7	0	0	0	2	0	0	329	22
21	12	14	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	8	0	0	0	0	0	10	0	0	1	2	0	0	0	0	3	85	0	0	5	0	0	2	0	12	2	86	0	0	3	0	0	0	247	16
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1	0	0	0	107	0	0	2	6	0	1	0	3	1	46	2	0	0	0	0	0	172	10
42	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	4	0	0	0	0	411	0	1	25	4	0	7	0	3	5	172	8	0	4	4	0	2	652	15
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	157	0	0	11	2	0	2	0	0	2	73	4	0	0	0	1	0	255	10
62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	205	0	0	30	4	1	10	0	2	2	87	3	0	3	0	0	1	350	13
72	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	175	0	0	16	3	2	13	1	0	8	31	0	1	0	0	0	1	251	10
82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	227	0	0	13	1	0	10	5	3	8	51	0	0	0	0	0	0	318	8
92	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	164	0	0	19	2	0	9	0	3	17	34	2	0	0	0	0	0	251	9
102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	124	1	0	8	2	0	4	0	1	16	38	2	0	0	0	0	0	196	9
112	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	324	0	0	0	6	14	19	0	0	35	95	7	0	0	1	0	0	501	8
122	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	360	0	0	6	4	4	7	0	0	17	85	0	0	0	0	0	0	483	7
132	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	155	0	0	0	0	11	11	0	1	19	97	0	0	0	4	0	0	298	7
142	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	65	0	0	2	0	0	7	0	0	27	53	0	0	0	1	0	0	155	6
152	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	72	0	0	1	0	5	4	0	0	15	33	1	0	0	1	0	0	131	7
162	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34	3	0	2	0	19	1	0	0	40	33	0	0	0	0	0	0	132	7
172	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	3	1	2	0	22	0	0	0	13	11	0	0	0	1	0	0	65	8
182	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	11	0	0	0	13	11	0	0	0	5	0	0	43	5
192	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	11	4
202	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	3	0	0	0	0	0	0	16	0	0	0	0	0	0	35	3
212	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	4	0	7	3	0	0	5	8	0	0	0	1	0	0	29	7
222	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	23	1	0	7	0	4	0	0	0	9	9	1	0	0	0	0	0	54	7
232	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0	0	0	0	2	0	0	0	1	9	0	0	0	0	0	0	36	4
242	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	66	0	0	0	0	0	3	0	0	2	37	6	0	0	4	0	0	118	6
252	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	4	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	3
262	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1

Table 3 – P-values of the significance test for the groups in the constrained cluster analysis (Fig. 3), using ANOSIM or analysis of similarities, $p < 0.05$ are shown in bold face. The letters and numbers correspond to the labels in Fig. 3.

	A	21	B	C-E	252-262
A	0	0.3359	**0.0094**	**0.0187**	0.3379
21	0.3359	0	0.073	0.3035	1
B	**0.0094**	0.073	0	**0.0001**	**0.0082**
C-E	**0.0187**	0.3035	**0.0001**	0	**0.0173**
252-262	0.3379	1	**0.0082**	**0.0173**	0

Table 4 – The P-values of the significance test for clusters C, D, sample 212, and cluster E in the constrained cluster analysis (Fig. 3), using ANOSIM or analysis of similarities, show that the differences between these clusters are not significant ($p>0.05$).

	C	D	212	E
C	0	0.1031	0.2461	0.1018
D	0.1031	0	0.3345	1
212	0.2461	0.3345	0	0.2454
E	0.1018	1	0.2454	0

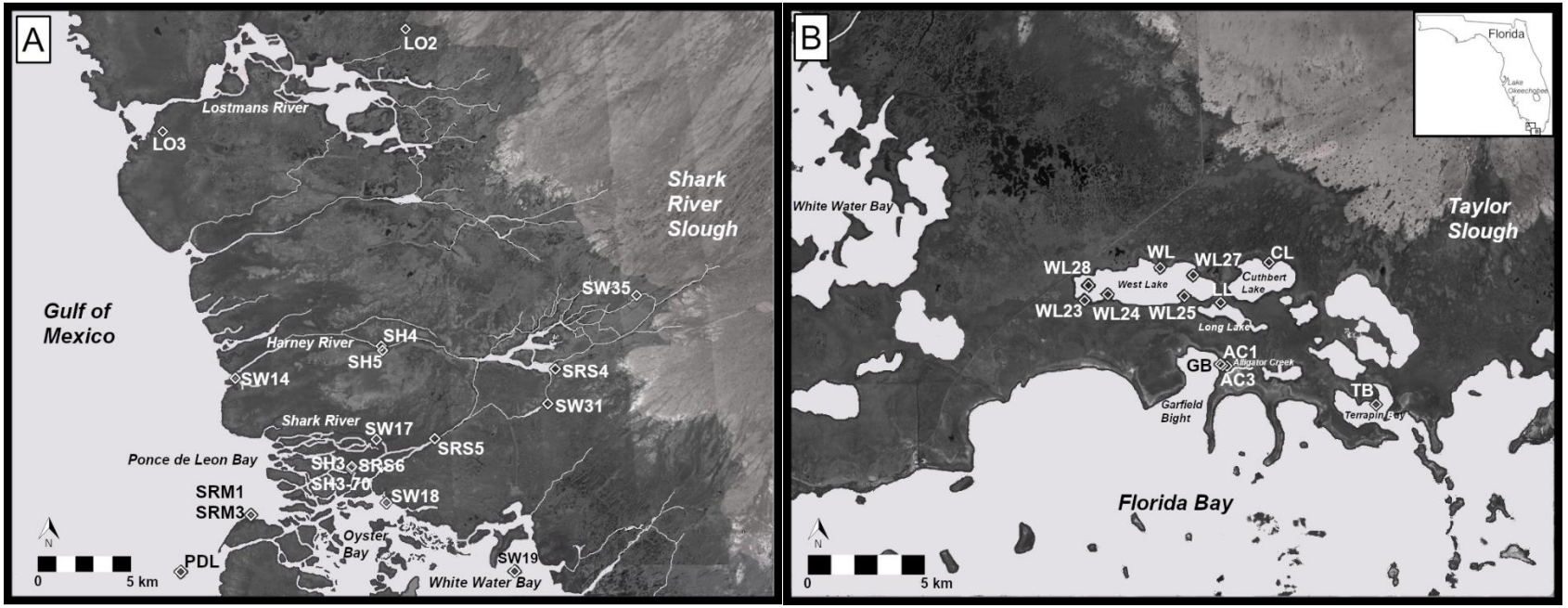

Figure 1 – Map showing the locations where modern surface samples were taken (includes site SRS6), and the coring location at site SRS6 along the Shark River. The coastal zone in darker gray shows the approximate location of mangroves. The light gray area to the northeast is freshwater wetland. Figure adapted from Google Earth.

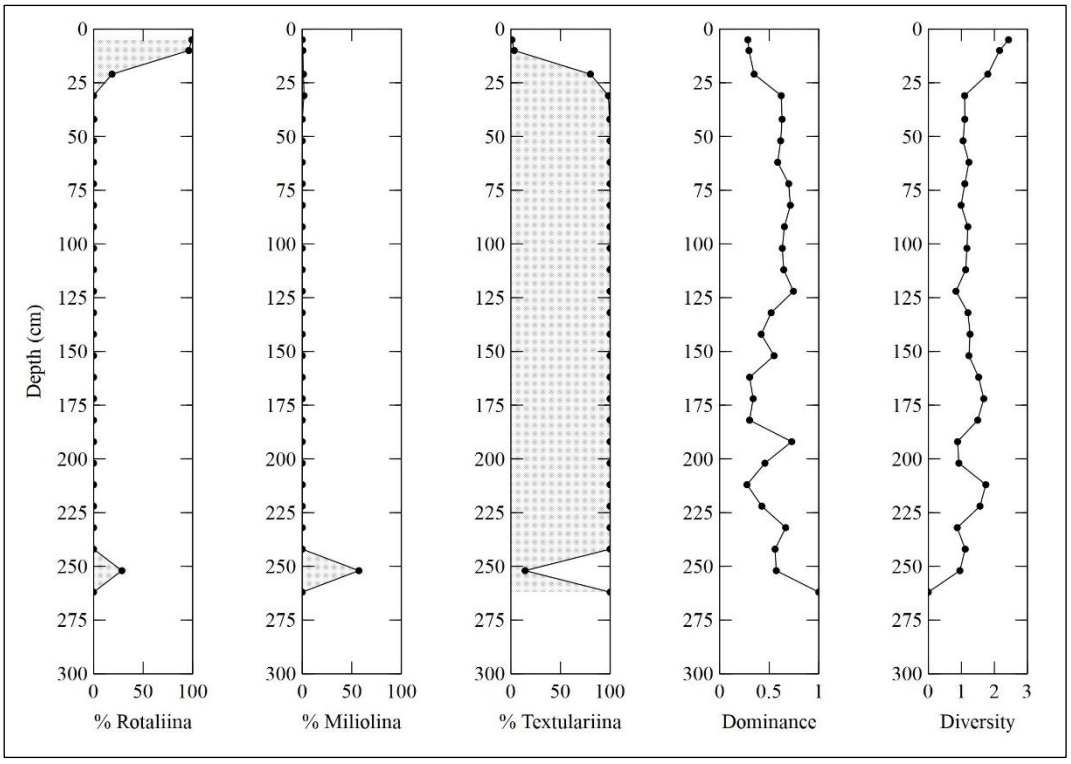

Figure 2 – Relative abundance downcore of the three wall types of Rotaliina, Miliolina, and Textulariina, compared to Berger-Parker dominance and Shannon diversity.

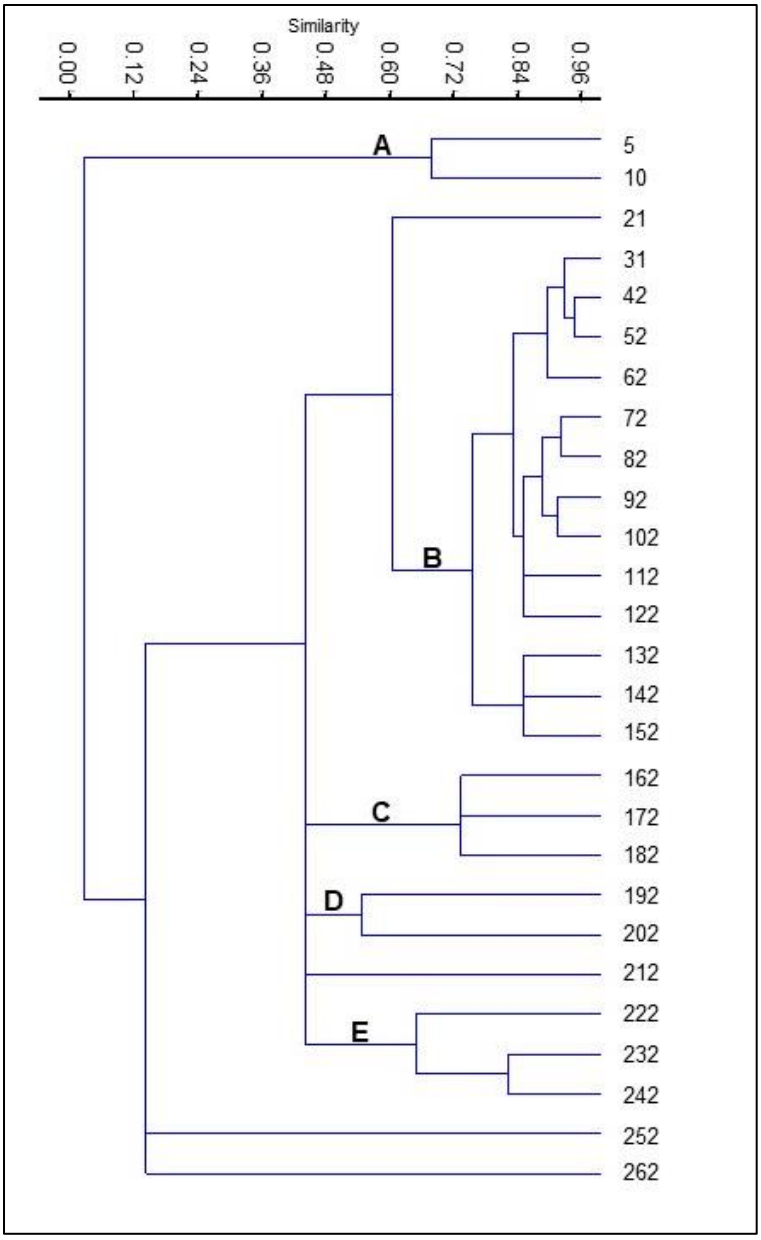

Figure 3 – Constrained cluster analysis of 27 samples of foraminifera using the unweighted paired group with average linking algorithm and the Bray Curtis dissimilarity index. Samples are numbered by depth-in-core (cm), right column. Clusters A, B, C, D, and E are associations consisting of more than one sample.

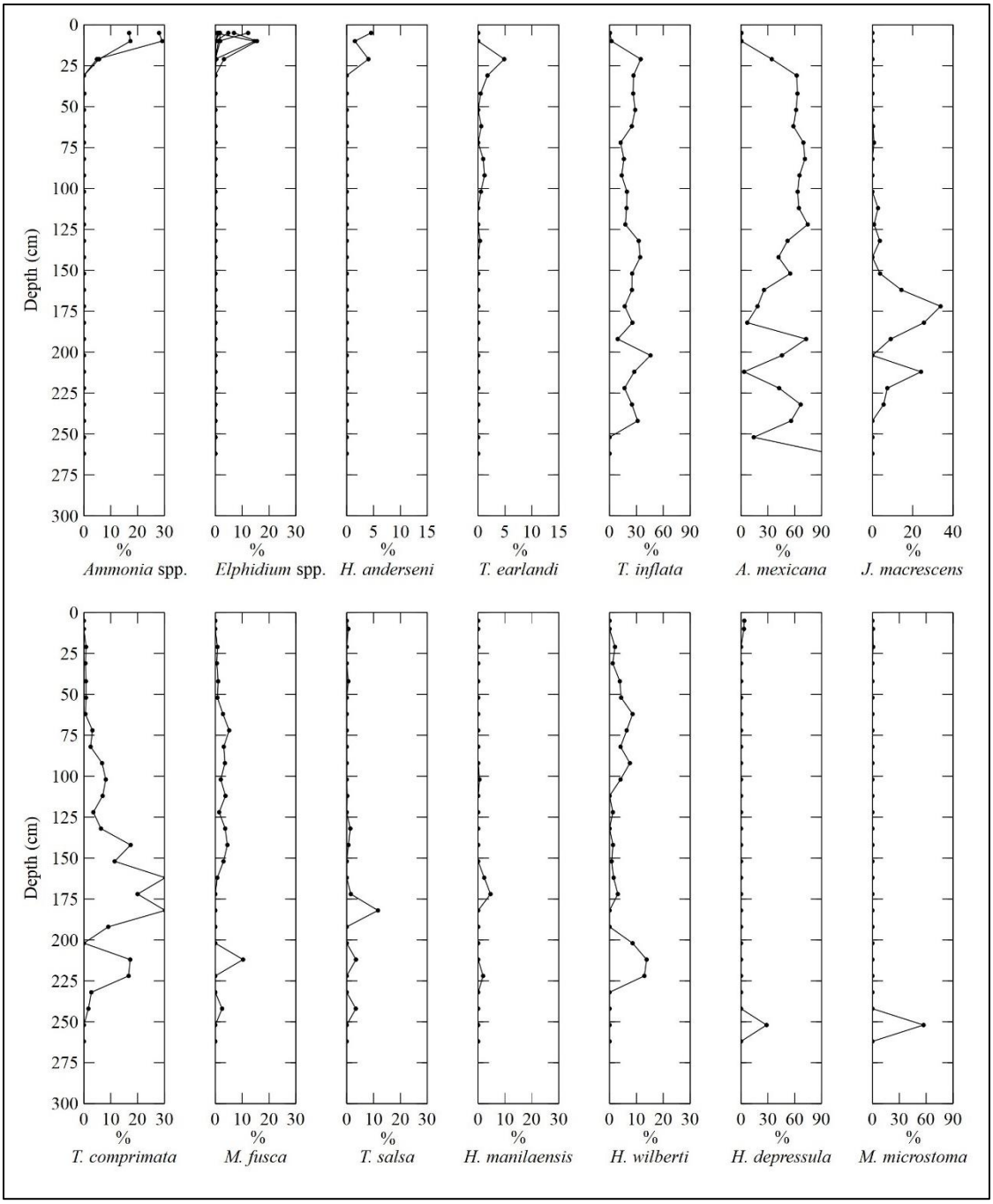

Figure 4 – Relative abundance of the most common taxa (>4% in at least one sample) with depth in core.

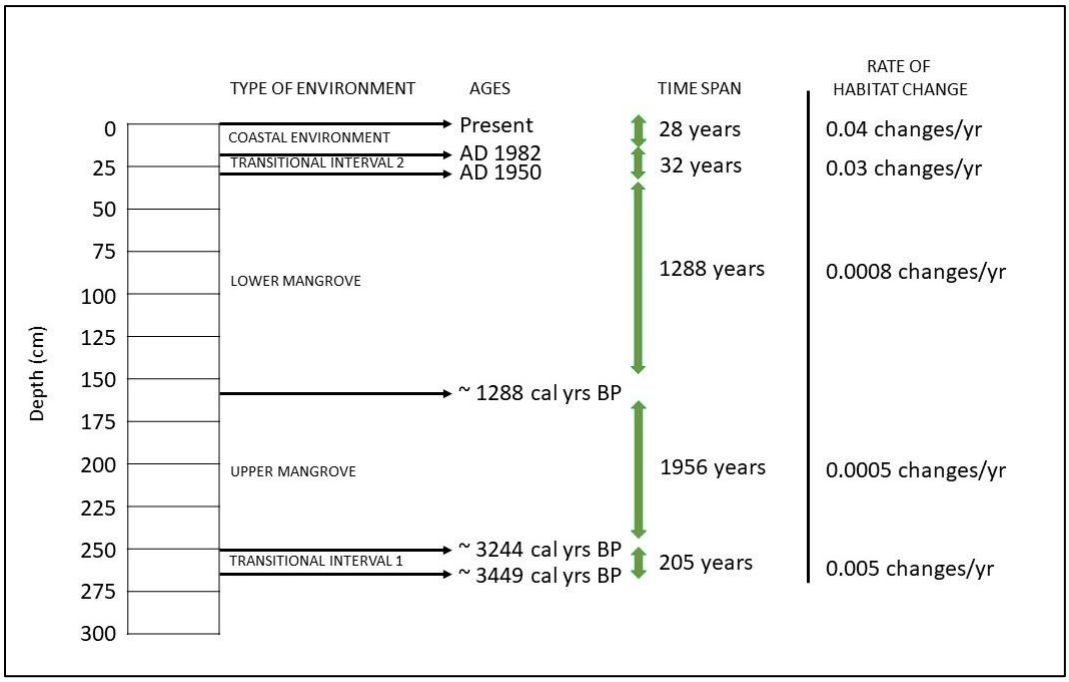

Figure 5 – Overview of the changes in the type of environment as indicated by foraminiferal assemblages throughout the studied core section, as well as the ages, time spans, and rates of habitat change.

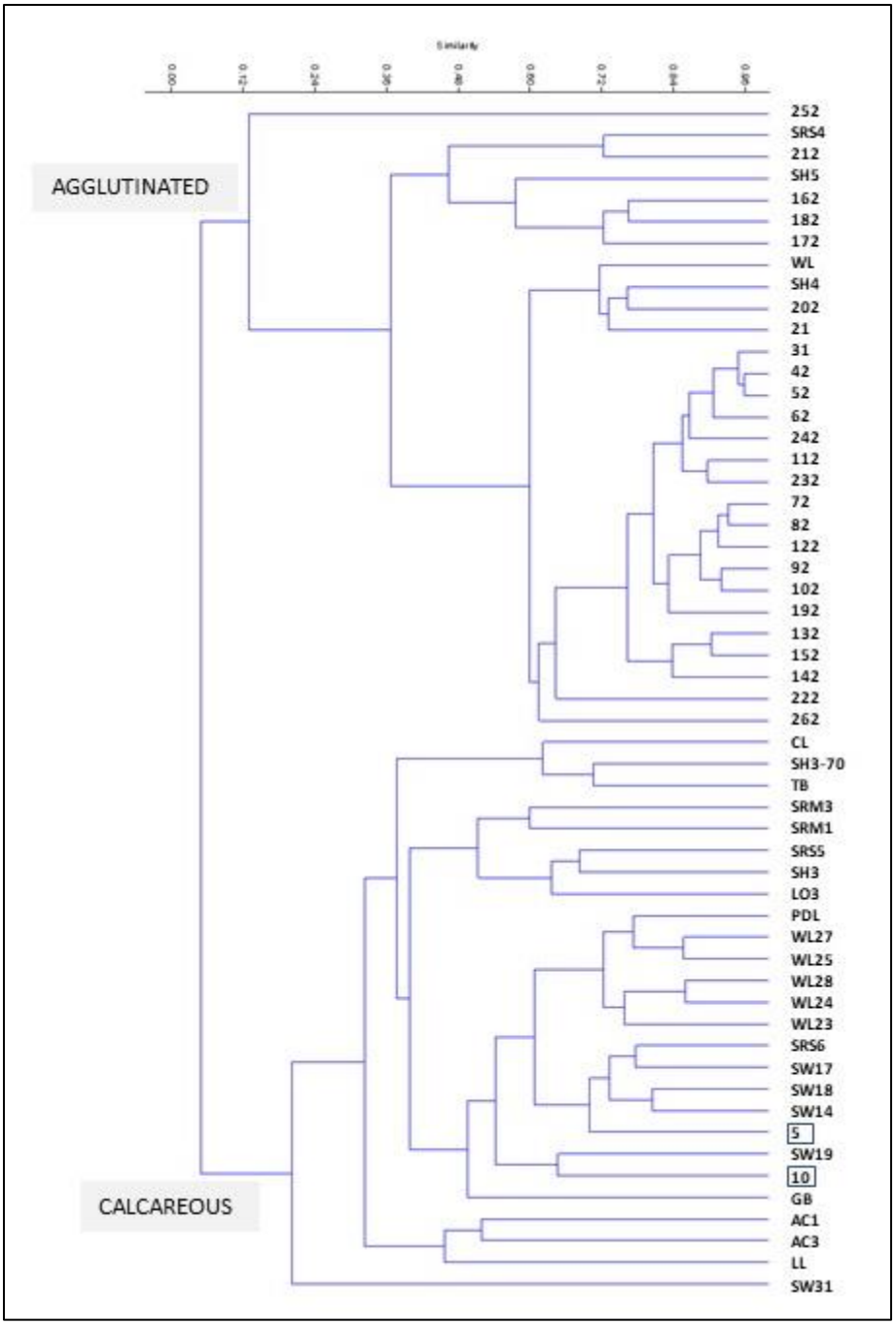

Figure 6 – Q-mode cluster analysis of 28 modern surface samples and 27 core samples using unweighted pair group clustering with average linkage, Bray-Curtis dissimilarity index. The core samples 5 and 10 are circled with a rectangle.

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Chapter 5

Conclusions

Purpose of Study

I investigated live and total foraminiferal assemblages from surface samples, as well as fossil and subfossil assemblages from core samples from Everglades National Park, southwest Florida. The goal was to assess the use of benthic foraminifera from this area to track habitat change and trends in the rate of sea level rise for the past ~3400 years.

The first part of the study (Chapter 2) was mainly concerned with the living depth of infaunal foraminifera to examine the extent of their influence and potential bias on both surface and subsurface assemblages, and, consequently, which vertical sediment interval can be used as a modern analog. The second part (Chapter 3) investigated the environmental controls on the foraminiferal distribution of species across the southwestern Everglades, to examine their usefulness as salinity proxies and assess their relationship to other measured environmental variables. Lastly, Chapter 4 applied the obtained baseline data from modern assemblages to a paleoenvironmental study of a sediment core that recorded Everglades history over the past ~3400 years.

Effects of Foraminiferal Infauna on Subsurface Assemblages

This chapter was published by Verlaak et al. (2018). In total, for all four sites investigated, 27 taxa were identified, mainly calcareous species. Where they occurred,

agglutinated taxa had a shallower habitat preference than calcareous taxa. The highest numbers of live individuals were collected in the upper mangrove site. In a landward direction, the microhabitat preference deepened from 1–3 cm (mudflats and low mangroves) to 7–10 cm (middle- and high mangroves). I attributed this to the landward increase in fine root density leading to greater oxygenation of subsurface sediments.

Live production is very low throughout the cores, so that the influence of the deeper infauna on subsurface assemblages is negligible. Additionally, the 0–2 cm interval contains, on average, 36% of the total standing crop. Therefore: (1) the composition of total assemblages in the 0–2 cm interval, i.e., the modern assemblages, adequately represented the entire live assemblage that includes deep-dwelling species; and (2) total assemblages at greater depths, i.e., those used for paleoenvironmental analyses, will not be altered meaningfully by the minor subsurface production. Thus, the upper 2 cm of the sediment column is sufficient as a modern analog for paleoenvironmental studies in the southwestern Everglades.

Degradation through oxidation/bacterial breakdown of the organic cements of agglutinated taxa increased in a landward direction. Calcareous taxa preserved exceptionally well in the carbonate buffered sediments of the Everglades.

Modern Foraminiferal Distributions

For the 28 sites studied, we identified 82 species, of which 77% were calcareous. Fifteen of the reported species are typically found in many mangrove swamps and salt marshes worldwide. The assemblages furthest inland consisted mainly of agglutinated

taxa, while towards the coast abundances of calcareous taxa generally increased and abundances of agglutinated taxa decreased. Rotaliina are equally abundant across the intertidal environment, while members of the Miliolina show peak abundances near the coast, inland lagoons and lakes. Landward, foraminiferal diversity decreased, and assemblages show higher species dominance.

The main controlling factor on the foraminiferal distributions was salinity, which decreased landwards. It separates assemblages of purely agglutinated taxa from those consisting of a mix of agglutinated and calcareous taxa, and purely calcareous assemblages. I also successfully identified species that can be used as salinity indicators. The total organic and total inorganic carbon content of the sediment (TOC and TIC, respectively) are secondary controls. In a landward direction, TIC content decreased while TOC content increased. High TOC values are associated with agglutinated taxa, such as occur predominantly at the landward end of the intertidal zone. High TOC values also occur closer to the coastline in other habitats such as river mouths, where assemblages are combinations of *H. anderseni*, *A. tepida*, *H. depressula*, *T. inflata*, and *A. mexicana*. Consequently, the benthic foraminifera from the Everglades proved to be excellent proxies for salinity, and this study provided the necessary baseline data for the paleoenvironmental study and assessing past trends in the rate of sea level rise (Chapter 4).

History of Paleoenvironmental Changes

Over the full length of the studied core, we identified 51 species, of which 23 are agglutinated. Eighty-four percent of all the identified taxa were found in the modern assemblages. Calcareous taxa quickly reach 97% abundance from 21 cm depth in the core to the top. Below 21 cm depth, diversity is low and dominance is high, characteristic of assemblages at the landward end of intertidal environments, whereas above 21 cm diversity increased and dominance decreased. High-diversity, low-dominance assemblages are typical of coastal habitats, because of the less extreme physical conditions for foraminifera. The downcore patterns of species abundance reflect the species' responses to environmental changes over time because the downcore decrease in the abundance of calcareous taxa and *T. earlandi* cannot be related to dissolution or degradation of their tests.

I found that over the past ~3400 years, assemblage shifts occurred at ~3449 cal yrs BP, ~3244 cal yrs BP, ~1288 cal yrs BP, AD 1950, and AD 1982. We recognized three different habitats and two transitional environments: (1) a transitional habitat from fully freshwater to a brackish environment at the bottom of the studied interval of the core, followed by (2) upper mangroves, (3) lower mangroves, (4) a transition from lower mangroves to a marine influenced environment, and lastly, (5) the modern-day, coastal habitat. The time span between these changes decreased towards the present, pointing to an accelerating trend from <0.005 changes/yr prior to AD 1950 to >0.03 changes/yr after AD 1950, and this study predicts that in the future habitats will continue to change at least at that same rate.

For the Everglades, this study added valuable information on the living depths of foraminiferal infauna, highlighting the unique Everglades advantage of excellent calcite preservation, as well as a full examination of the environmental controls on modern distributions in a tropical/subtropical coastal setting. It is the first foraminiferal study of paleoenvironments for this region, and the results can be used to predict shifts in coastal habitats, of importance to South Florida's growing coastal population and the Everglades ecosystem.

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PUBLICATIONS AND PRESENTATIONS

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