Citation:

Buzas-Stephens, P., M. A. Buzas, J. D. Price, and C. H. Courtney. 2018. Benthic superheroes: Living Foraminifera from Three Bays in the Mission-Aransas National Estuarine Research Reserve, USA. Estuaries and Coasts 41: 2368-2377. https://doi.org/10.1007/s12237-018-0425-4

Benthic Superheroes: Living Foraminifera from Three Bays in the Mission-Aransas National Estuarine Research Reserve, USA

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Acknowledgements

The authors wish to thank Joan Bernhard for her invaluable comments; Frank Ernst, for captaining the boats and helping with sampling; and Brent Elliott and Tiffany Humberson for their help with sampling. We are also grateful to editors and reviewers who helped strengthen and clarify the paper. This work was supported in part by Midwestern State University Faculty Grants.

The final publication is available at

https://link.springer.com/article/10.1007/s12237-018-0425-4

ABSTRACT

Studies of living foraminiferal assemblages provide much information about their roles in present environments and a perspective on interpreting the past. Along modern coasts, benthic Foraminifera act as ecological indicators in their responses to different natural and anthropogenic conditions such as food availability, oxygen concentrations, salinity, and trace metal concentrations. A detailed survey of foraminiferal populations was undertaken in the Mission-Aransas National Estuarine Research Reserve, Texas, close to the time of its establishment in 2006. The purpose was to gauge the overall status of populations and provide baseline data for future comparison. The arid south Texas Gulf Coast is a variable and often harsh environment where biota are subject to multiple anthropogenic stressors. Despite these rigors, living Foraminifera were prolific in the Reserve. This paper discusses the results from Mesquite (July 2008), Copano (May 2006), and Mission Bays (June 2006). Populations were robust in each bay, with *Ammonia parkinsoniana, Ammotium salsum,* and *Elphidium excavatum* being most abundant. Highest numbers corresponded mainly to areas of greater circulation. In Mission Bay,

elemental analysis of shells, prompted by the presence of sulfur grains in sediments and by yellow tests, detected elevated levels of barium, strontium, and iron. Most sediment samples were black and sulfidic, and ubiquitous framboidal pyrite in sediment and shells suggests that forams were frequently subject to low-oxygen conditions. Abundant living numbers, tolerance of low-oxygen conditions, and the ability to cycle trace metals emphasize the resilience of Foraminifera in taxing environments and their integral position as lower trophic level members.

Key Words

benthic Foraminifera; pyrite; Texas coast; trace metals; low-oxygen

INTRODUCTION

In shallow coastal settings, such as bays and lagoons, living benthic Foraminifera are often subject to varying natural conditions as well as potential anthropogenic inputs. Sometimes the combination of these factors provides a natural laboratory for studying the response of forams to relatively severe environments, such as on the south Texas coast (Buzas-Stephens and Buzas 2005; Buzas-Stephens et al. 2011) where ranges in temperature and precipitation are extreme. Average winter minimums are 8.3–8.9˚C and summer maximums are 33.3–35.6 ˚C, and gross annual evaporation exceeds precipitation by a factor of about 1.7 (Evans et al. 2012). Since Foraminifera are basic to the food web and often form a great deal of the sediment

biomass, populations can be used as indicators of the health of an ecosystem as a whole (Culver and Buzas 1995).

When the Mission-Aransas National Estuarine Research Reserve (NERR) (Fig. 1) was first established along the south Texas coast in 2006, foraminiferal populations were sampled in order to obtain baseline information for future comparison. The present study reports on sampling in Mesquite, Copano, and Mission Bays- primary, secondary and tertiary bays

in the Reserve. Understanding the characteristics of living forams may also

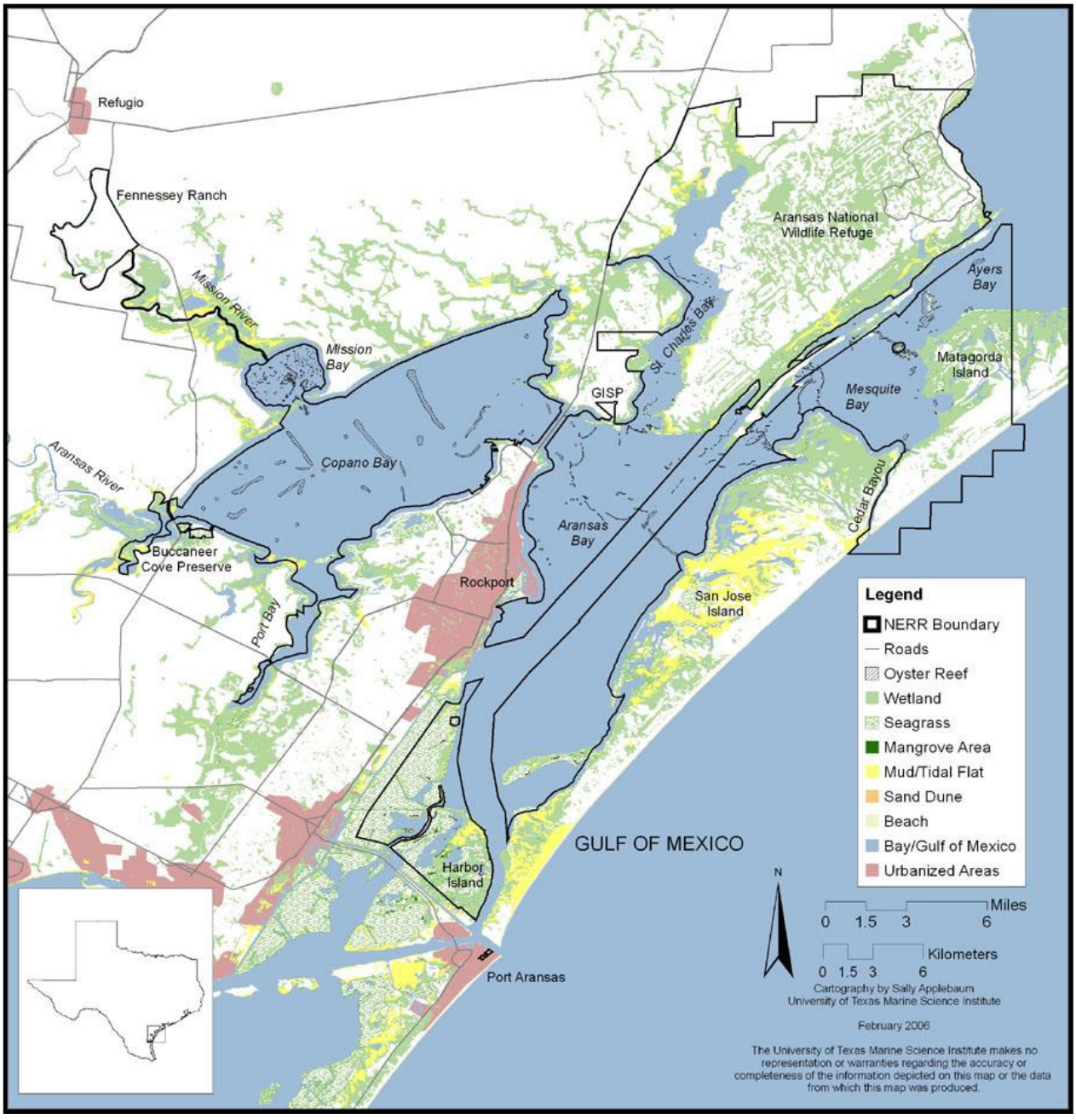

Fig. 1. Mission-Aransas National Estuarine Research Reserve, Texas. Living Foraminifera sampled at 4 stations each bay: Mesquite, Copano, and Mission (subsumed under one triangle).

contribute to better definition of past climate processes and depositional settings (Leorri and Cearreta 2004; Leorri et al. 2006; Billeaud et al. 2009; Buzas-Stephens et al. 2014).

Located on the south Texas coast, the Mission-Aransas NERR (Fig. 1) is named for the Mission and Aransas Rivers that flow into Mission and Copano Bays respectively. The reserve covers about 185,708 acres and contains bays, wetlands, and terrestrial environments. It is administered by the University of Texas in cooperation with state and local agencies. A mandatory site profile (Evans et al. 2012) provides much information on habitats, water quality, climate, and other aspects of the Mission-Aransas NERR. Stations were set up to monitor real-time water quality variables and nutrients in east and west Copano Bay, and in Mesquite Bay, which is considered a pristine site (Evans et al. 2012). Some additional physical and biological characteristics of these bays, such as the geochemistry of sediments, are reported in Submerged Lands of Texas (White et al. 1983), a coastal study by the Bureau of Economic Geology.

Circulation patterns in the bays are mainly the result of wind direction, which is primarily from the north in the winter and the southeast in the summer (White et al. 1983). Freshwater inflow is low, with a combined daily mean into Mission and Copano Bays of about 28 $m^3 s^{-1}$ (Poag 2015). Even with such limited inflow, the Mission/Aransas drainage was one of two out of seven evaluated systems with inflow sufficient to sustain healthy bays. The drainage area is not heavily populated and there are no dams on the Mission

or Aransas Rivers, which are not used for water supplies. The U.S. Geological Survey has gauging stations along each river, and various state and local organizations monitor inflow to constrain amounts required for sustained economic and recreational use (Evans et al. 2012).

The bays in the Mission-Aransas NERR are shallow, often < 3m deep, and salinities can fluctuate rapidly depending on rainfall and temperature. During periods of heavier rainfall salinities are as low as 3, while during droughts they can be > 50. Excess nutrients from increased run-off and/or anthropogenic sources sometimes lead to low dissolved oxygen content in the bays. Due to contamination from point and non-point sources, Copano and Mission Bays do not support oyster harvest, and tidal segments along the Aransas and Mission Rivers are not suitable for "contact recreational pursuits" (Evans et al. 2012).

The Mission-Aransas NERR, as with much of the Texas Gulf Coast, also has plentiful oil and gas resources, with drilling onshore and offshore. Exploration and production in what are now the reserve lands date to 1910 (online Texas Almanac: http://texasalmanac.com/frontpage), and are ongoing in San Patricio and Refugio Counties. Abnormally high levels of barium in Copano Bay (1400–2700 ppm) and Mission Bay (1160 ppm) reported by White et al. (1983) are attributed to the barium sulfate in drilling muds. High levels of zinc (92 ppm), lead (24 ppm), and copper (16–19 ppm) recorded in Copano Bay are likely from a variety of industries (White et al. 1983).

Foraminiferal distributions (living, dead, and/or total assemblages) reported from Texas bays to date are summarized in Poag's 2015 *Benthic Foraminifera of the Gulf of Mexico* and described in terms of predominant generic facies. In the Mission-Aransas NERR (Fig. 1), Copano Bay has the *Ammonia* facies, which is also prevalent in eastern Mesquite Bay, though the western part has the *Ammonia-Elphidium* group (Poag 2015). While dead foraminiferal assemblages were documented in many of the Mission-Aransas NERR bays, living forams were studied only from Aransas and Mesquite Bays (Parker et al. 1953; Phleger 1956). The current authors are the first to study Foraminifera at all in Mission Bay, and are also the first to report on living numbers in Copano Bay.

Aside from distributions, previous research on the Texas coast has also focused on foraminiferal response to different environmental variables (Parker et al. 1953; Poag 1981, 2015; Williams 1995; Buzas-Stephens et al. 2003, 2011, 2014; Buzas-Stephens and Buzas 2005). One of the most notable responses is to salinity (Parker et al. 1953; Poag 1981, 2015; Williams 1995; Buzas-Stephens et al. 2011). While the calcareous taxa discussed above (*Ammonia* spp. and *Elphidium* spp.) are predominant in the bays, agglutinated Foraminifera (with shells made of cemented particles) usually dominate at lower salinities such as in marshes (Phleger 1960; Poag 2015) or during periods of high precipitation and inflow (Williams 1995; Buzas-Stephens et al. 2011). A change from a calcareous to an agglutinated population in response to increased inflow can take place in a matter of months (Buzas-

Stephens et al. 2011), although such changes would not necessarily be evident in the sedimentary record unless they were sustained over a number of years.

Inflow into estuaries also influences densities of living Foraminifera and the overall health of the population. Since nutrients in Texas bays are supplied mainly by rivers (Whitledge and Stockwell 1995; Mannino and Montagna 1997), foraminiferal densities are often higher closer to river mouths where more food is available (Phleger 1956; Buzas-Stephens et al. 2011). A study in Nueces Bay showed that at low to moderate inflow, densities were higher at the south shore where the Nueces River enters. Subject to elevated trace metals, the living forams also had high incidences (3–17% of the population) of dissolution, and framboidal pyrite was common. However, when inflow into Nueces Bay was high, densities were high throughout the bay and dissolution was negligible (Buzas-Stephens et al. 2011).

METHODS

Four replicate 3.2 cm-diameter cores (ranging 10-30 cm deep) were taken at each of four stations in Copano (May 2006), Mission (June 2006), and Mesquite (July 2008) Bays. The stations were selected along transects extending from river mouth to bay mouth, in the case of Copano and Mission Bays, and from the north to south entrances in Mesquite Bay (Fig. 1). In each core, the top 2 cm of sediment were stained with rose Bengal in ethanol,

a protein-specific stain to identify living or recently living organisms (Walton 1952; Murray and Bowser 2000). Sediments were then immediately iced in a cooler in order to minimize reactions that could destroy shell material. Salinity, dissolved oxygen content, and pH were measured with a Hydrolab® in Mesquite and Copano Bays, and in Mission Bay salinity was taken with a hydrometer when the Hydrolab® malfunctioned. All measurements were taken midway in the water column.

Once back at the lab, the replicate samples were frozen until use, and then 10 mL of sediment from the top 2 cm were washed over a 63-µm sieve. This size sieve opening seems to capture nearly all specimen sizes including juveniles. Samples were dried and all stained individuals were counted under a thin film of water and Kodak® Photo-Flo in a 100-square counting tray. As data from each bay were tabulated, statistical analyses were performed using versions of SYSTAT. Analysis of variance (ANOVA) with Tukey's pairwise post hoc tests were used to compare mean densities of the nine most abundant species in each bay, and then the three localities were compared with multiple discriminant analysis. Original counts in each 10 mL sediment sample were transformed to $\ln(x + 1)$, where x is the count.

When yellow sediment grains and yellow shells were found while counting forams from Mission Bay, shells were analyzed by laser-induced breakdown spectrometry (LIBS) (Harmon et al. 2006; McMillan et al. 2007). LIBS targets a UV laser at a small area (70-µm) from which material is ejected and forms a plasma; a spectrometer records peak fluorescent

intensities for near IR-visible, near-UV wavelengths. Trial and error revealed that the optimal fluence was 1000 J cm^{-2}. The technique requires averaged multiple shots. A beam was applied to a shell until the material was completely gone. Because most shells were obliterated on the first shot, only two specimens withstood multiple shots, one living (*Quinqueloculina seminula*) and one dead (*Ammonia parkinsoniana*). The stained (living) specimen had dark spots in the protoplasm, which were also observed in other individuals. The dead specimen took ten shots with the laser before disintegrating, while the stained specimen took only four. A sample shell (*Ammonia parkinsoniana*, from Nueces Bay) and the glue used to hold specimens were also run for comparison. The intensities for each recorded wavelength were averaged for all shots and then normalized to the strongest nitrogen peak, N 749.79 (atmospheric component in the plasma common to all samples).

RESULTS AND DISCUSSION

Physical Conditions and Populations in Bays

The most common living foram sampled in the Mission-Aransas Reserve bays was *Ammonia parkinsoniana*, which was most abundant at each station but one (Station 1, northern Mesquite Bay), making up 34–86% of the population. Depending on the bay, following *A. parkinsoniana* in abundance were *Ammotium salsum, Elphidium excavatum,* and *Quinqueloculina wiesneri* (Online Resource 1; https://doi.org/10.1007/s12237-018-0425-4).

These same genera and/or species are typical of coastal environments worldwide, and assemblages have been demonstrated to differentiate less saline nearshore environments (agglutinated-dominant) from more saline offshore environments (calcareous-dominant) (e.g., Debenay and Guillou 2002; Benito et al. 2016).

Mesquite Bay

Water depths were 1.4–1.7 m at the four stations (Fig. 1), and salinities were ~ 34 at Stations 1, 3, and 4 and 37 at Station 2. Dissolved oxygen (6.4–6.8 mg L^{-1}) and pH (7.95–8.0) were similar among stations, providing a suite of relatively consistent variables along the transect (Table 1).

Total population densities (individual counts, 10 mL) were higher at the northern stations (average station 1 = 471, standard deviation, SD, = 106.17; average station 2 = 570, SD = 145.07) compared to the southern stations (average station 3 = 307, SD = 15.64; average station 4 = 301, SD = 120.10)

	MESQUITE BAY				**COPANO BAY**				**MISSION BAY**			
Station	***depth m***	***salinity ppt***	***pH***	***D.O. mg/L***	***depth m***	***salinity ppt***	***pH***	***D.O. mg/L***	***depth m***	***salinity ppt***	***pH***	***D.O. mg/L***
1	**1.3**	**34.6**	**7.98**	**6.42**	**1.78**	**21**	**7.86**	**6.4**	**0.74**	**11**	**7.9**	**N/A**
2	**1.48**	**37**	**7.95**	**6.4**	**2.37**	**31**	**7.8**	**7.5**	**0.89**	**24**	**7.95**	**N/A**
3	**1.63**	**34**	**7.98**	**6.75**	**2.07**	**32**	**7.86**	**7.7**	**0.89**	**26.5**	**7.98**	**N/A**
4	**1.48**	**34.3**	**8**	**6.8**	**2.37**	**34**	**7.82**	**7.4**	**0.68**	**27**	**7.9**	**N/A**

Table 1. Physical variables each station measured with a Hydrolab®. Dissolved oxygen (D.O.) not applicable in Mission Bay due to equipment malfunction.

(Table 2), most likely due to greater circulation and hence food availability at the north end of the bay (Phleger 1956; Buzas-Stephens et al. 2011). Although Phleger's (1956) living data are not directly comparable to these, as he took one 10-mL sample per station versus four here, he also found a higher number of living individuals at the northern two stations (n = 71 and n = 113) compared to the southern two (n = 36 and n = 97). The notable discrepancies in living densities between Phelger's (1956) data and those here are somewhat attributable to sampling technique, but environmental conditions such as inflow (Phleger 1956; Buzas-Stephens et al. 2011) or increased nutrient content could also be factors.

In terms of richness, the highest species richness documented for this study was at the south station (#4), which had 10 species compared to 7 species at stations 1-3. With Cedar Bayou providing access to the Gulf of Mexico at the south end of Mesquite Bay, influx of Gulf taxa is possible

	MESQUITE BAY			**COPANO BAY**			**MISSION BAY**		
Station	***ave living***	***SD***	***species #***	***ave living***	***SD***	***species #***	***ave living***	***SD***	***species #***
1	**471**	**106.17**	**7**	**1323**	**689.66**	**11**	**152**	**46.73**	**12**
2	**570**	**145.07**	**6**	**1873**	**962.18**	**10**	**476**	**325.52**	**12**
3	**307**	**15.64**	**7**	**1257**	**672.45**	**11**	**442**	**215.37**	**12**
4	**301**	**120.10**	**10**	**1025**	**333.41**	**12**	**912**	**365.47**	**14**

Table 2. Average living density (individual counts), standard deviation (SD), and number of living species, 10 mL. Four stations each bay, four replicate cores per station.

(Parker et al. 1953) but does not seem to be the case as it was mainly a nearshore form, *Palmerinella palmerae*, which was unique to station 4. Phleger (1956) found 16 living species compared to 10 in our study, though some of the difference was caused by misidentifications and changes in taxonomic nomenclature. Both studies list seven living genera and although some of the less common ones are not the same, *Ammonia parkinsoniana*, a taxon that tolerates a wide range of oxygen levels and salinities, was the most common foraminifer at every station (except for Station 1, Mesquite Bay; this study) . Thus foraminiferal populations appear to have been relatively stable in Mesquite Bay for at least the past 50 years.

Analysis of variance among the four stations showed significant differences in the mean densities of 5 taxa: *Elphidium gunteri, Quinqueloculina wiesneri, Q. seminula, Ammotium salsum,* and *Trochammina inflata.* However, the only north-south trend as noted by contrasts was for *Ammotium salsum* (Table 3). This species was much more abundant at the northern stations (station 1, average 216; station 2, average 200), away from Gulf influence, versus the southern stations (station 3, 82 average; station 4, 42 average) (Online Resource 1; https://doi.org/10.1007/s12237-018-0425-4). These data illustrate the utility of *A. salsum* for discriminating nearshore (lower salinity) versus offshore environments (Debenay and Guillou 2002). As mentioned previously, due to the absence of pollutants, Mesquite Bay is used as a pristine standard for comparison with other bays in the Mission-Aransas Reserve (Evans et al.

2012). While test dissolution in living individuals is quite common in many Texas bays, very little dissolution was noted in Mesquite Bay during counting. Occurrence of pyrite, which is generally widespread in these shallow bays and indicative of low oxygen and/or heavy metals (Buzas-Stephens and Buzas 2005; Buzas-Stephens et al. 2011), was also minimal in sediments and foraminiferal tests.

Table 3. One-way ANOVA's for differences between mean densities at four stations in Mesquite Bay. Original counts per 10 mL of sediment transformed to ln(x+1) where x is count. Each station has four replicates so $N = 16$. $p(F) < .05$ is significant; NS = not significant. Contrasts show station density from high to low.

Species	**p(F)**	**contrasts**
Ammonia parkinsoniana	0.163	NS
A. tepida	0.426	NS
Elphidium gunteri	0.012	2 = 3 = 4 > 1
E. excavatum	0.090	NS
Haynesina germanica	0.006	3 > 1 = 2 = 3
Quinqueloculina seminula	0.001	2 = 4 > 1 = 3
Q. wiesneri	0.026	1 = 2 = 4 > 3
Triloculina oblonga	0.169	NS
Ammotium salsum	0.000	1 = 2 > 3 > 4

Copano Bay

In Copano Bay (Fig. 1) the water depth was 1.8–2.6 m at each of the four stations and salinities were 38–41, with the lowest salinity at Station 1 near

the mouth of the Aransas River. The dissolved oxygen (7.4–7.8 mg L^{-1}) and pH (7.7–7.85) values were also similar at all stations (Table 1).

Population numbers (stained individuals) were quite high, averaging 1323 individuals at station 1 (SD = 689.66), 1873 at station 2 (SD = 962.18), 1257 at station 3 (SD = 672.45) and 1025 at station 4 (SD = 333.41). The densities at each station in Copano Bay were generally 2-3 times higher than they were in Mission and Mesquite Bays, and can likely be attributed to the size of the bay and to higher levels of nutrients entering through the Aransas River at the east end. Although they were not counted, stained allogromiid Foraminifera (agglutinated monothalamids) were also very common.

Analysis of variance showed significant differences in mean densities of three species at the four stations, *Haynesina germanica*, *Q. wiesneri*, and *A. salsum.* The data readily show that *A. salsum* was much more abundant near the mouth of the Aransas River (Station 1, mean density = 582; Stations 2, 3, and 5, mean densities 61, 54, and 47, respectively; (Online Resource 1; https://doi.org/10.1007/s12237-018-0425-4), and contrasts confirm this observation (Table 4). Again, the presence of *A. salsum* distinguishes inner versus outer bay sediments.

Many of the samples in Copano Bay contained abundant framboidal pyrite. Framboids were distributed throughout the surface sediment, associated with decaying organics, in dead foraminiferal shells, and in a few live Foraminifera. Often the pyrite was accompanied by test

decalcification/dissolution in the living individuals. Incidence of pyrite is discussed below.

Table 4. One-way ANOVA's for differences between mean densities at four stations in Copano Bay. Original counts per 10 mL of sediment transformed to ln(x+1) where x is count. Each station has four replicates so $N = 16$. $p(F) < .05$ is significant; NS = not significant. Contrasts show station density from high to low.

Species	**p(F)**	**contrasts**
Ammonia parkinsoniana	0.228	NS
A. tepida	0.489	NS
Elphidium gunteri	0.207	NS
Elphidium excavatum	0.506	NS
Haynesina germanica	0.006	3 > 1 = 2 = 4
Quinqueloculina seminula	0.700	NS
Q. wiesneri	0.003	4 = 2 > 3 = 1
Triloculina oblonga	0.169	NS
Ammotium salsum	0.001	1 > 2 = 3 = 4

Mission Bay

Mission Bay was quite shallow, 0.7-0.9 m at each station (Fig. 1). Though dissolved oxygen was not measured due to equipment malfunction, salinity was 11 at the mouth of the Mission River and 27 at the bay mouth (Table 1).

Population density showed a definite increase toward the mouth of the bay, with an average of 152 living individuals (SD = 46.73) at Station 1 (river mouth), 476 (SD = 325.52) at Station 2, 442 (SD = 215.37) at Station 3, and 912 (SD = 365.47) at Station 4 (bay mouth; Table 2). Clearly forams in this bay were thriving at the higher salinities near the Mission Bay mouth. In this

case salinity appeared to be a major abundance-controlling factor in addition to food. Not surprisingly, statistical analysis showed all species but two to be significantly different among the stations (Table 5) since most Foraminifera were more abundant at Station 4.

Table 5. One-way ANOVA's for differences in mean densities between 4 stations in Mission Bay. Original counts per 10 mL of sediment transformed to ln(x+1) where x is count. Each station has 4 replicates so $N = 16$. $p(F) < .05$ is significant; NS = not significant. Contrasts show station density from high to low.

Species	**p(F)**	**contrasts**
Ammonia parkinsoniana	0.017	4 >2 = 3 >1
A. tepida	0.261	NS
Elphidium gunteri	0.002	4 > 1 = 2 = 3
E. excavatum	0.003	4 > 2 = 3 > 1
Haynesina germanica	0.067	NS
Quinqueloculina seminula	0.025	4 > 1 = 2 = 3
Q. wiesneri	0.001	4 > 1 = 2 = 3
Triloculina oblonga	0.083	NS
Ammotium salsum	0.000	4 = 3 > 1 = 2

Many samples in this bay also contained abundant pyrite and had living individuals with partially decalcified/dissolved shells. Additionally, bright-yellow particles, presumably elemental sulfur, and yellow foraminiferal shells were evident. Discussions on pyrite and analysis of shells with laser induced breakdown spectrometry (LIBS) are found below.

Statistical Comparison Among Bays

Analysis of variance (ANOVA) comparing average densities of the nine most common species showed that the only species that was not significantly different among the three bays was *Ammotium salsum*. Contrasts revealed that the main trend was the increase in miliolids (*Quinqueloculina seminula* and *Q. wiesneri*) in Mesquite Bay (Table 6), which is a primary bay and thus has a closer connection to the Gulf than Copano (a secondary bay) and Mission (a tertiary bay). *Quinqueloculina* spp. have been noted for their ability to distinguish higher salinity and more open-water (offshore) environments (Buzas-Stephens et al. 2014; Buzas et al. 2017) and thus along with *A. salsum*, which prefers lower salinities nearshore, may be useful for documenting climate or sea-level change.

Table 6. One-way ANOVA's for difference in mean density of species among the three bays: 1 = Mission; 2 = Copano; 3 = Mesquite. Original counts in 10 mL transformed to ln(x+1) where x is count. Contrasts show station density from high to low.

Species	**p(F)**	**contrasts**
Ammonia parkinsoniana	0.000	2 > 1 = 3
A.tepida	0.000	1 > 2 > 3
Elphidium gunteri	0.041	2 > 1 = 3
E. excavatum	0.000	1 = 2 > 3
Haynesina germanica	0.000	2 > 1 > 3
Quinqueloculina seminula	0.000	3 > 1 = 2
Q. wiesneri	0.000	3 > 1 = 2
Triloculina oblonga	0.000	1 = 2 > 3
Ammotium salsum	0.445	NS

Multiple discriminant analysis established that Mission and Copano Bays are most similar to each other in terms of mean living species densities, a result which is likely due to proximity. The first eigenvalue (first canonical variate = CV1) shows this similarity and separates Mission and Copano Bays from Mesquite Bay (Table 7). As noted with the ANOVA above, the preponderance of *Quinqueloculina* spp. in Mesquite Bay distinguishes this bay from the others.

Table 7. Canonical scores of group means for discriminant analysis of Mission, Copano, and Mesquite Bays on ln (x+1) where x is density of 9 species. First eigenvalue (CV1) accounted for 86% of variability and second for 14%.

Bay	CV1	CV2
Mission	2.669	-1.874
Copano	2.685	1.870
Mesquite	-5.534	0.004

Laser Induced Breakdown Spectrometry: Mission Bay

When counting Foraminifera in Mission Bay, many bright-yellow sediment grains and yellow foraminiferal tests were encountered, prompting a preliminary elemental analysis of shells. Laser induced breakdown spectrometry (LIBS) recorded barium, strontium, and iron peaks in both the living (stained *Quinqueloculina seminula*) and dead (*Ammonia parkinsoniana*) tests from this bay. Peaks were stronger from the dead specimen since it withstood ten shots before disintegrating versus four shots

for the live specimen. A sample test of *Ammonia parkinsoniana* from Nueces Bay and the glue holding the shells were run for comparison (Fig. 2). Presence of elevated barium in tests from Mission Bay is not surprising since White et al. (1983) detected high levels (1160 ppm) of barium that were attributed to the barium sulfate in drilling muds. Barium levels (70 ppm) in Nueces Bay were not elevated (White et al. 1983), and barium peaks were not as pronounced in the shell analyzed from this bay (Fig. 2). Whether or not the barium found in foraminiferal tests from Mission Bay is from older or newer drilling, or from other sources, is unknown. Drilling muds may also contain strontianite ($SrCO_3$) which naturally occurs with barite (White et al. 1983), and the LIBS did pick up strontium peaks. Sulfur, presumably coloring the shells yellow, does not emit readily detectable peaks even at high concentrations and was not detected here.

The LIBS analysis also showed peaks in iron (Fig. 2), which could be substituting for calcium or be present as a sulfide. In Copano Bay, where there are excess levels of barium, lead, and zinc (White et al. 1983), it is likely that Foraminifera are incorporating all of these trace metals into their shells (Madkour and Ali 2009; Rumulo et al. 2009; Cherchi et al. 2012), though mass spectrometry would be required for verification.

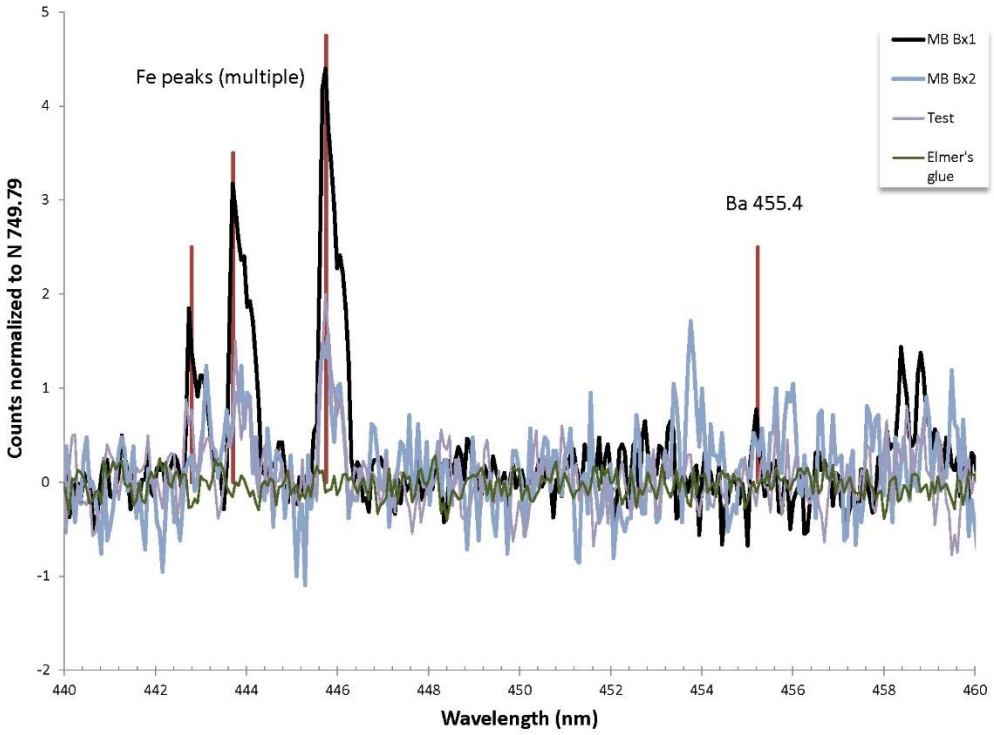

Fig. 2 Laser induced breakdown spectrometry on specimens from Mission Bay and Nueces Bay. Results are averages normalized to a nitrogen peak. MB Bx1= Mission Bay, *Ammonia parkinsoniana* (dead); MB Bx2= Mission Bay, *Quinqueloculina seminula* (living); Test= Nueces Bay, *Ammonia parkinsoniana* (dead). On horizontal axis: wavelength, nm; vertical axis: counts normalized to N 749.79.

Incidence of Framboidal Pyrite

The presence of pyrite in ancient and modern sediments has long been associated with low-oxygen conditions (Berner 1970; Blatt et al. 1972). While the exact chemical pathways leading to the formation of low temperature (<100˚C) pyrite are complex and not completely resolved (Konhauser 2007), elemental sulfur reduces an iron monosulfide mineral in the final step (Berner 1970). Crystallization of pyrite in marine environments

is limited by amounts of decomposing organics, sulfate ions, and reactive iron minerals (Berner 1970). When oxygen is present, organics are usually the limiting variable, but with low-oxygen it is iron minerals that are more likely to be limiting (Berner 1984).

Framboidal pyrite, in which pyrite crystals aggregate to form raspberry-like clusters, is a very common crystal habit and is the main form pyrite takes in the Mission-Aransas Reserve bays (Fig. 3). Growth of framboids can occur abiotically (Berner 1970; Butler and Rickard 2000) as well as biotically (Berner 1970; Folk 2005; MacLean et al. 2008; Bottrell et al. 2009). When framboids crystallize through the action of sulfate-reducing bacteria, stable isotope analysis shows the lower $\delta^{34}S$ signatures characteristic of organic activity (Bottrell et al. 2009).

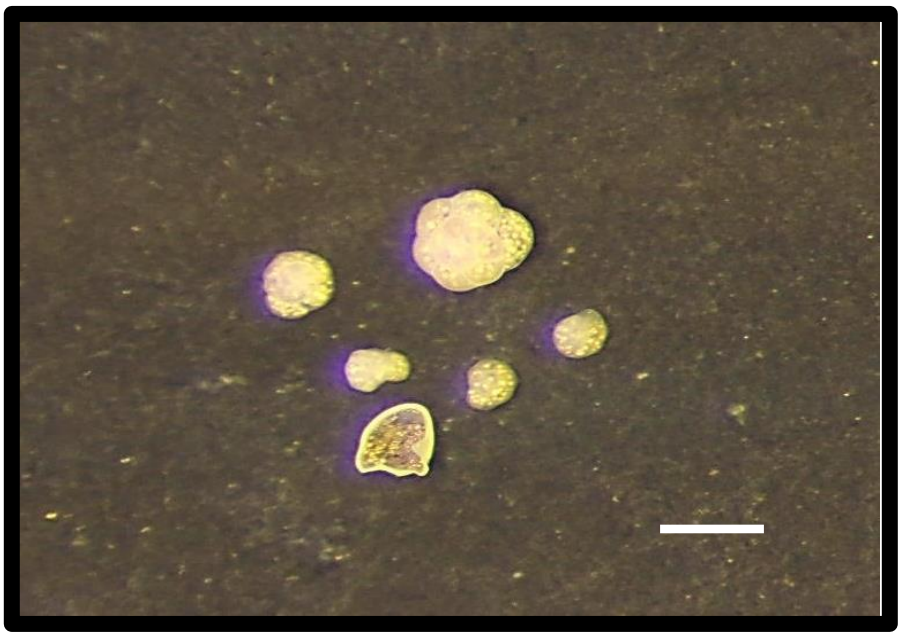

Fig. 3. Framboidal pyrite inside dead *Ammonia* spp. and *Elphidium* spp. tests from Copano and Mission Bays. Scale bar = 250 μm.

Abundant framboids were found inside of foram tests and throughout muddy and sandy sediments of Copano and Mission Bays. There were far fewer framboids in the less impacted Mesquite Bay. Sediment samples in all bays were usually dark grey to black, and smelled of hydrogen sulfide and/or methane. In Foraminifera, most of the framboid-filled tests were in dead individuals but there were also many occurrences inside living species, mainly *A. parkinsoniana* and sometimes *Elphidium* spp. or *Quinqueloculina seminula.* Had the ubiquity of the framboids been known, a more quantitative approach would have been taken. However, to give an example of "abundant" framboids, a sample from Copano Bay had 47 counts of framboidal pyrite in one small area (1.5 cm x 0.8 cm) of a counting tray. Twenty-two of the 47 were in dead foraminiferal tests, and the rest were disseminated in the sediment.

With the high living foraminiferal densities in Mission and Copano Bays occurring in conjunction with abundant framboidal pyrite, obviously forams can flourish in low-oxygen, sulfidic sediments. Are some of these shallow-water benthic Foraminifera acting as facultative anaerobes, using sulfate-reducing and/or sulfide-oxidizing bacteria as part of a pathway that also produces pyrite? The LIBS showed iron peaks in the shell, though it is unknown how the iron is bonded.

Many authors have suggested or shown that Foraminifera can be facultative anaerobes, employing alternate metabolic processes that enable

their survival in harsh places (Sen Gupta and Machain-Castillo 1993; Bernhard and Sen Gupta 1999; Wladyslaw et al. 2011; Koho and Piña-Ochoa 2012). In deep sea, sulfidic sediments, *Virgulinella fragilis* was found to sequester chloroplasts and bacterial endobionts in what appears to be a multiple symbiosis (Bernhard 2003). *Ammonia beccarii*, a shallow-water taxon similar to *A. parkinsoniana* (the most common species in the present study), has likewise been demonstrated to take up living bacteria (Langezaal et al. 2005). Some species of Foraminifera store nitrate and use it to respire anaerobically, although neither *A. beccarii* nor *A. tepida* does (*A. parkinsoniana* has not been tested) (Koho and Piña-Ochoa 2012). The anaerobic pathways Foraminifera operate for survival in severe environments are just beginning to be understood (Koho and Piña-Ochoa 2012). Further research will be required to determine if shallow-water Foraminifera in low-oxygen, sulfidic conditions are involved with framboidal pyrite formation.

It is noteworthy that the bays with elevated levels of trace metals (Copano, Mission, and Nueces [Buzas-Stephens and Buzas 2005]) also had abundant pyrite and shell dissolution, while Mesquite Bay, designated as the pristine standard, had neither. Trace metals are able to substitute for Fe in pyrite (Sugawara et al. 2013), and may hasten redox reactions. Pyrite in tests and sediments has been documented to occur in conjunction with various types of pollution (Yanko et al. 1999), which the observations in this paper support. In nearby Nueces Bay, which also had high trace metals (Zn), test dissolution and framboidal pyrite were also common. However, since parts of

Nueces Bay often suffered from poor mixing (and hence food), numbers of living individuals could be very low (40–135 average) (Buzas-Stephens and Buzas 2005). In contrast, bays in the Mission-Aransas Reserve had thriving populations (Table 2; (Online Resource 1; https://doi.org/10.1007/s12237-018-0425-4). Clearly, given enough food, Foraminifera are able to proliferate when subject to non-toxic levels of trace metals (whatever these may be) and low-oxygen conditions accompanying pyrite formation.

CONCLUSIONS

Although subject to extremes in temperature and precipitation, low-oxygen in sediments, and elevated trace metals, foraminiferal populations were thriving along the south Texas Gulf Coast in the Mission-Aransas National Estuarine Research Reserve. *Ammonia parkinsoniana* was the most common species in each of the three bays studied, followed by *Elphidium* sp., *Ammotium salsum*, and *Quinqueloculina wiesneri.* In Copano and Mission Bays, which had high trace metals, there was often copious framboidal pyrite in tests and sediments, along with some shell dissolution. Still, benthic foraminiferal populations were flourishing in these low-oxygen, sulfidic environments. Abundance of pyrite may be related to elevated trace metals since Mesquite Bay, which is relatively pristine, had much less pyrite and tests did not show dissolution. In Mission Bay, elevated barium, likely from the barium sulfate of drilling muds, was detected in foraminiferal tests. Thus trace metals are biotically available and being cycled by Foraminifera. Foraminifera are adaptive organisms, proliferating in environmental conditions that many

organisms would find taxing. This persistence is important for the food web, and such resilience is probably a factor in species longevity, which is five to ten times greater in Foraminifera than in other taxa (Buzas and Culver 1984).

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