ENVIRONMENTAL CONTROLS ON THE DISTRIBUTION OF MODERN BENTHIC FORAMINIFERA IN THE FLORIDA EVERGLADES AND THEIR USE AS PALEOENVIRONMENTAL INDICATORS

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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. Eight environmental variables, including average salinity, salinity range, pH, total phosphorus, temperature, and dissolved oxygen, and total organic carbon and total inorganic carbon measured on bulk sediments, as well as the elevation and 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 total organic carbon, followed by total inorganic carbon, distance from coastline, total phosphorus, and salinity. *Jadammina macrescens* and *Miliammina fusca* indicate lower salinities (<15 psu). Good indicators for higher salinities are *Haplophragmoides wilberti* (10–20 psu) and *Arenoparrella mexicana* (10–20 psu and 28–30 psu). *Ammonia* spp. prefer salinities >15 psu and *Elphidium* spp. >20 psu. *Ammonia tepida*, *Helenina anderseni*, *Trochammina inflata*, and *A. 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 coastal Everglades in South Florida. The purpose is to investigate the extent to which measured environmental factors (salinity, salinity range, 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 saltwater intrusion in the past. Kemp et al. (2011) and Milker et al. (2015) stressed the importance of collecting samples over a wide spatial area and from different habitats instead of along transects, which suggest a regular foraminiferal distribution. Verlaak et al. (2019) 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 (Murray, 1973).

One reason that salinity forms a limiting factor for foraminifera is that changes in salinity influence the water density and have osmotic effects (Murray, 1973). Pores in the tests of Rotaliina are diverse in shape, size, density, and accompanying structures, most likely a reflection of the different functions of pores. Besides osmoregulation, pores may also allow the exchange of gases or dissolved substances (Dubicka et al., 2015). Another reason salinity is a limiting factor for foraminiferal distribution is its relationship to calcium carbonate availability (Murray, 1973). The relative proportions of the suborders Miliolina, Textulariina, and Rotaliina are very useful for differentiating shallow-water environments (Murray, 1991) and very effective as indices for paleosalinity. The solubility of calcium carbonate is controlled by salinity, temperature, and carbon dioxide content so that calcium carbonate is more readily available in subtropical to tropical marine or hypersaline environments (Murray, 1973). Changes in salinity are controlled by river runoff, rain, evaporation, or mixing of water masses, in turn influencing the calcium ion concentration (Pytkowicz, 1969). Therefore, species with agglutinated tests and noncalcareous 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 continued sea-level rise over the last ~5000 years. With rising sea level, saltwater intrusion and inundation continue to progress in a landward direction (Price et al., 2010).

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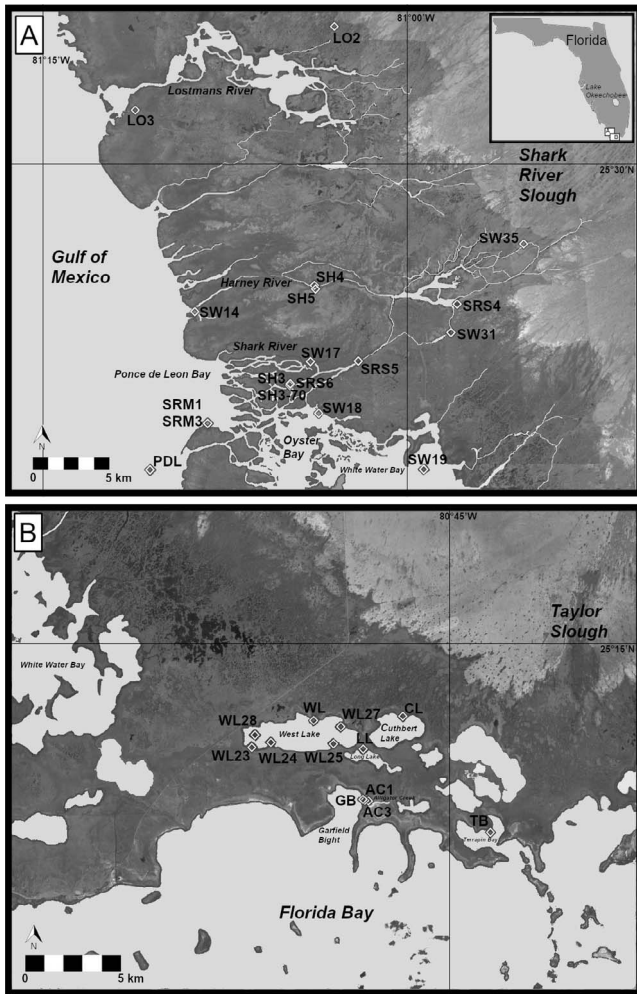* Correspondence author. E-mail: zverl001@fiu.edu

FIGURE 1. Map of study area and important water bodies for the southwestern Everglades, peninsular South Florida. A) The 18 sampling locations on western coast. B) The 12 sampling locations on southern coast. Darker gray land shows approximate location of mangroves and light gray areas are freshwater wetlands (adapted from Google Earth).

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 mainly calcareous to an agglutinated species composition.

TABLE 1. Taxonomic reference list with species abundance.

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
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
Nonionella atlantica Cushman, 1947	9
Rosalina candeiana d'Orbigny, 1839	12
Rosalina floridana (Cushman), 1922	5
Sagrina pulchella d'Orbigny, 1839	1
Trichohyalus aguayoi Bermudez, 1935	157
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 species per sample.

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	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**
Bolivina variabilis	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	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	1	0	0	2	0	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	1	1	0	0	2	0	0	0	0	0	0	0	2	0	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 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	5	0	0	0	**27**
Discorbis sp. 2	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**
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	26	0	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	9	0	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	8	0	0	5	1	6	63	13	2	7	15	6	12	0	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	1	3	0	1	17	0	4	2	3	0	6	7	0	0	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	5	5	0	0	2	0	0	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	1	0	0	0	3	0	1	0	0	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	6	0	16	21	13	5	12	0	0	0	**126**
Eponides sp.	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	1	0	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	1	0	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	2	0	2	0	42	1	66	48	28	10	0	2	0	34	19	2	0	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	5	0	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**
Trichohyalus aguayoi	0	0	0	0	0	0	80	1	0	2	7	11	0	30	0	0	2	1	0	0	0	0	0	0	0	2	21	0	0	0	**157**
Biloculinella eburnea	0	0	0	0	0	0	10	9	0	11	6	25	1	26	0	9	1	0	0	0	0	0	0	0	0	10	0	0	0	0	**108**
Cornuspira involvens	0	0	0	0	0	0	0	38	0	0	2	12	0	0	0	2	0	0	3	0	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	1	1	0	0	0	0	0	0	0	0	0	9	1	0	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	1	0	0	0	0	0	1	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	4	0	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	3	0	0	14	0	4	0	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	1	0	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	1	0	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	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**1**

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TABLE 2. Continued.

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
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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	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	1	0	1	0	0	3	0	0	0	0	0	0	0	3	0	3	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	1	0	0	0	0	0	0	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	0	1	21	8	2	0	0	0	0	0	0	7	0	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	0	0	5	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	74
Haplophragmoides sp.	0	0	0	0	0	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6
Jadammina macrescens	0	2	0	28	0	16	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	49
Miliammina fusca	3	40	4	0	0	4	0	8	0	3	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	64
Siphotrochammina lobata	0	0	0	0	0	0	0	0	0	3	0	0	3	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
Tiphotrocha comprimata	4	1	21	17	0	0	0	0	0	0	24	14	0	0	0	0	17	14	0	0	0	0	0	0	0	4	0	0	0	0	116
Trochammina inflata	0	0	143	23	0	56	0	0	0	0	4	4	153	0	2	0	22	14	0	0	0	0	0	0	0	0	0	0	0	0	500
Trochammina sp.	0	0	11	11	3	36	5	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	10	4	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	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	55
unidentified	0	2	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	2	2	0	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**

This study investigates: (1) how assemblage composition changes geographically across the Everglades, and which species contribute the most to these spatial differences; (2) whether salinity is the main controlling factor on the foraminiferal distribution and what the salinity preferences of the most characteristic species are; and (3) which other environmental factors play an important 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, 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, pH, total phosphorus, dissolved oxygen, or temperature measurements at the time of sampling. Instead, averages were calculated from long-term water quality data available from the South Florida Water Management District which includes a combination of data from multiple agencies and academic institutions (https://apps.sfwmd.gov/WAB/EnvironmentalMonitoring/index.html). Measurement of salinity, salinity range, pH, total phosphorus, dissolved oxygen, and temperature were compared to characteristics of 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 contained 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; these 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 representation of the taxa (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 much carbonate mud, which was very difficult to remove, even after thoroughly rinsing the sediment over nested screens because the mud clumped together upon air drying. Consequently, these samples were soaked overnight in paint thinner (adapted from USGS Varsol method), filtered to remove the paint thinner, and transferred to another beaker with water and one tablespoon of washing soda (as a buffer). This mixture was then cooked at a low simmer
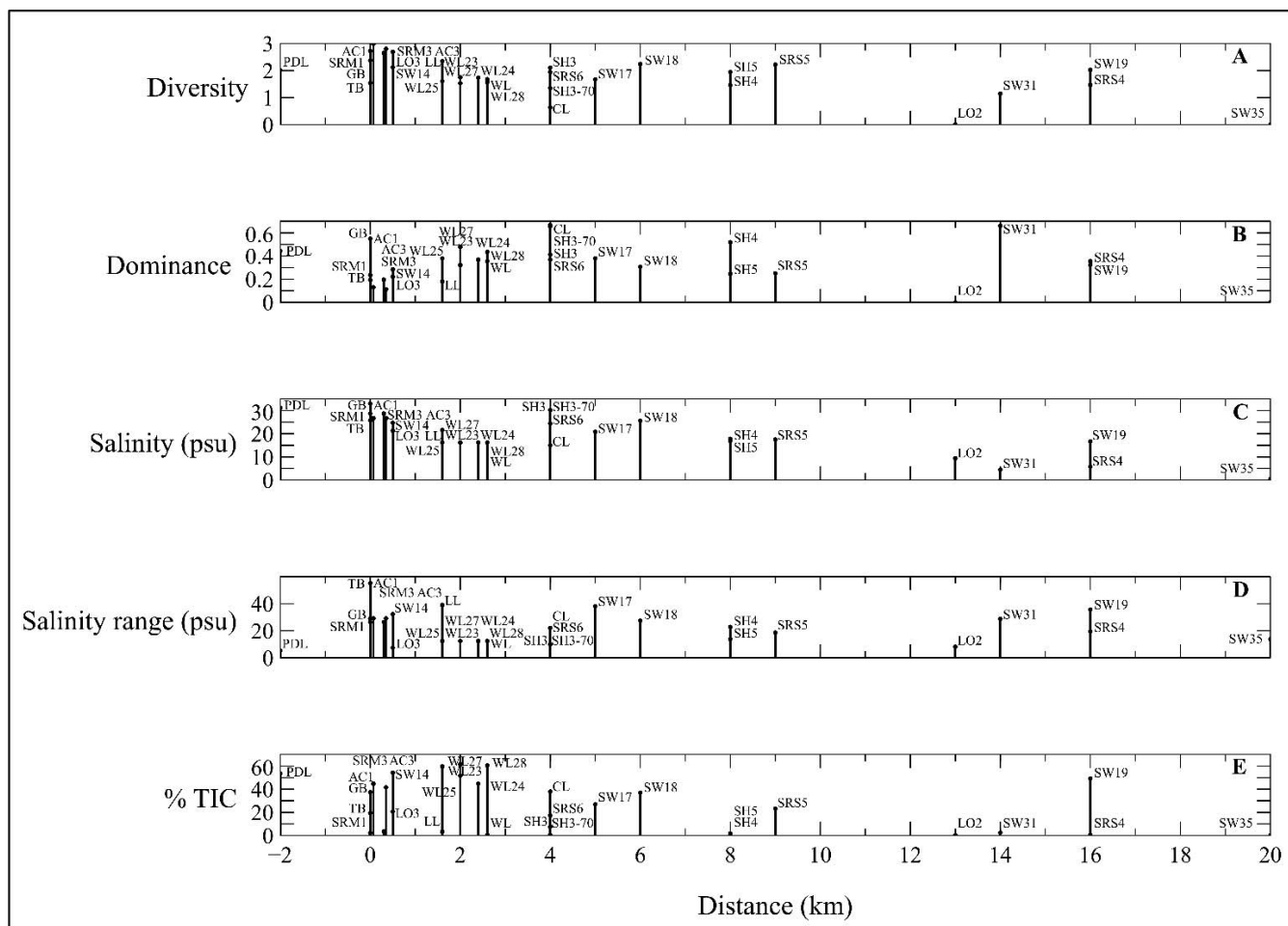
FIGURE 2. A) Shannon diversity index H', high values correspond to communities with many taxa; B) Berger Parker dominance index, represented by the relative abundance of the dominant species, C) Salinity (psu), D) Salinity range (psu); E) percentage of total inorganic carbon (TIC), with distance from coastline (km); F) percentage of total organic carbon (TOC); G) Elevation (m); and the relative abundance of the three wall types of H) Rotaliina, I) Miliolina, and J) Textulariina, with distance from coastline (km).

for about three hours, poured through a 63-μm sieve, rinsed thoroughly, and then transferred onto filter paper and air dried.

Literature on Gulf of Mexico and Caribbean marsh 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 were also 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 described for their sediment characteristics and then 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 two 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 two 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 percent-
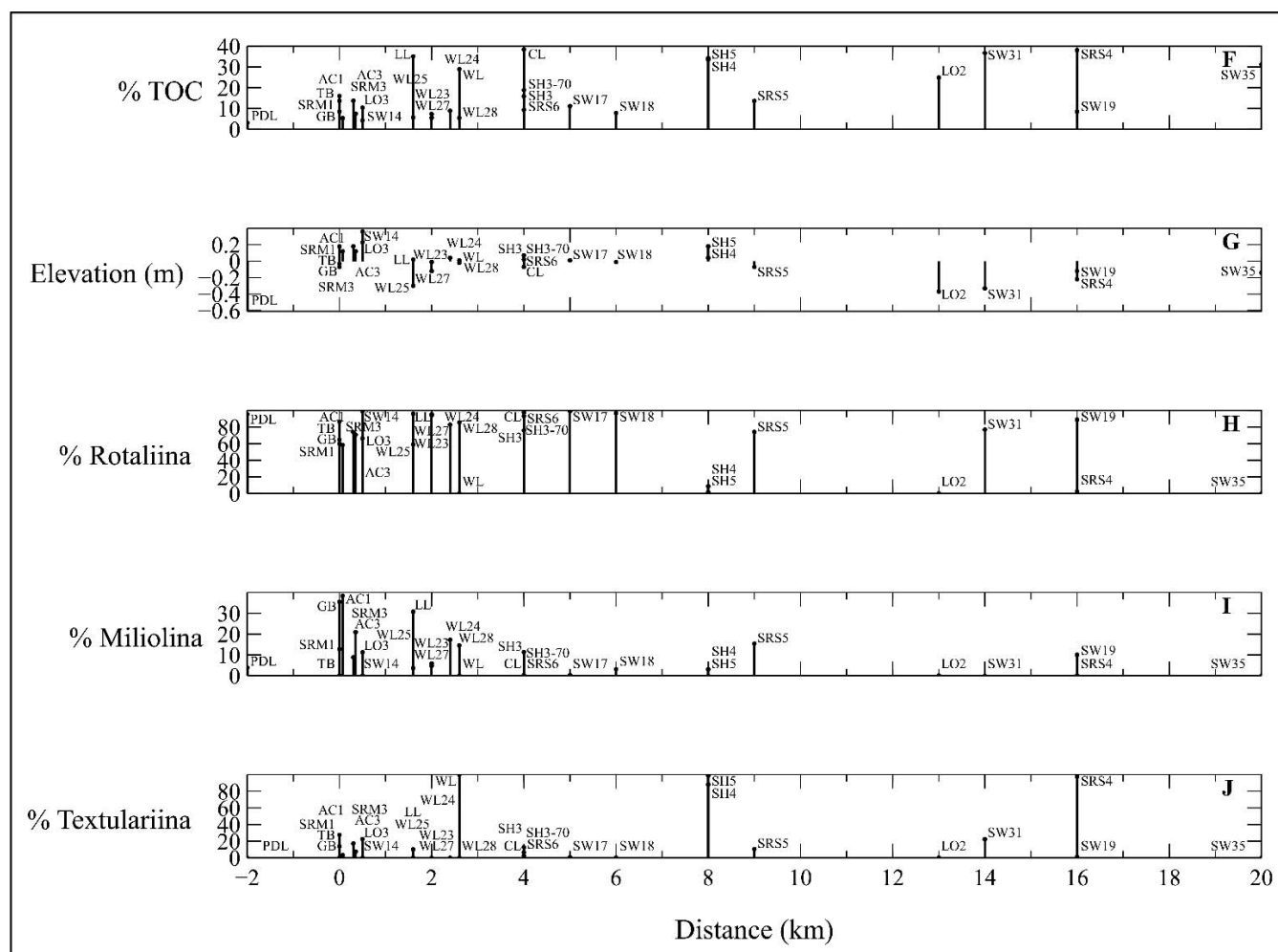
FIGURE 2. Continued

age of organic carbon by inserting each ceramic boat containing a sample into the furnace. 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 (%CaCO₃) by inserting each one 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 enabled distinction between agglutinated tests with organic cements and non-carbonate grains, and those with carbonate cements and/or carbonate grains.

QUANTITATIVE METHODS

Twenty-eight of the 30 samples contained foraminifera. 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 each sample (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). 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 were significantly different from each other (p<0.05).

TABLE 3. Significant correlations (p<0.05) between environmental variables (TOC = total organic carbon; TIC = total inorganic carbon; TP = total phosphorus; T = temperature; DO = dissolved oxygen), with correlation coefficients (r), coefficients of determination (r^2), and probabilities (p).

		Salinity	Salinity Range	pH	TOC	TIC	TP	T	DO	Elevation	Distance
Salinity	r	-	-	-	−0.42	-	-	0.52	-	-	−0.6
	r^2	-	-	-	0.17	-	-	0.27	-	-	0.36
	p	-	-	-	0.03	-	-	0.006	-	-	0.001
Salinity Range	r	-	-	0.4	-	-	0.42	-	-	-	-
	r^2	-	-	0.16	-	-	0.18	-	-	-	-
	p	-	-	0.04	-	-	0.03	-	-	-	-
pH	r	-	0.4	-	-	-	0.6	0.64	0.77	-	-
	r^2	-	0.16	-	-	-	0.35	0.41	0.59	-	-
	p	-	0.04	-	-	-	0.001	<0.001	<0.001	-	-
TOC	r	−0.42	-	-	-	−0.84	-	-	-	-	0.42
	r^2	0.17	-	-	-	0.71	-	-	-	-	0.18
	p	0.03	-	-	-	<0.001	-	-	-	-	0.03
TIC	r	-	-	-	−0.84	-	-	-	-	-	-
	r^2	-	-	-	0.71	-	-	-	-	-	-
	p	-	-	-	<0.001	-	-	-	-	-	-
TP	r	-	0.42	0.6	-	-	-	0.44	0.51	-	-
	r^2	-	0.18	0.35	-	-	-	0.19	0.26	-	-
	p	-	0.03	0.001	-	-	-	0.02	0.007	-	-
T	r	0.52	-	0.64	-	-	0.44	-	0.61	-	-
	r^2	0.27	-	0.41	-	-	0.19	-	0.37	-	-
	p	0.006	-	<0.001	-	-	0.02	-	<0.001	-	-
DO	r	-	-	0.77	-	-	0.51	0.61	-	-	-
	r^2	-	-	0.59	-	-	0.26	0.37	-	-	-
	p	-	-	<0.001	-	-	0.007	<0.001	-	-	-
Elevation	r	-	-	-	-	-	-	-	-	-	-
	r^2	-	-	-	-	-	-	-	-	-	-
	p	-	-	-	-	-	-	-	-	-	-
Distance	r	−0.6	-	-	0.42	-	-	-	-	-	-
	r^2	0.36	-	-	0.18	-	-	-	-	-	-
	p	<0.001	-	-	0.03	-	-	-	-	-	-

This test is based on comparing between-group with within-group distances and converting 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′),

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

with p_i as the relative proportion of each species (Shannon, 1948), accounting for 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 (d; Berger & Parker, 1970),

$$d = \frac{Nmax}{N}$$

where N is the total number of individuals and N_{max} is the number of individuals in the most abundant species (Hayek & Buzas, 2013). Percentages of foraminiferal wall type 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 its 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 (Jorissen, 1999).

To assess the extent to which the environmental variables influenced the foraminiferal distributions, we used non-metric multidimensional scaling and regression analysis. 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).

Multiple linear regression analysis evaluates whether one or more independent variables explain the variation of a dependent variable and how much they contribute to it (Hammer et al., 2001). For this study, relative abundances of individual species represent the dependent variable, and the ten (environmental) variables were selected as possibly contributing to the variation in species abundance. The analysis yields p-values for the individual explanatory variables and these were used to further refine the model by dropping variables that were not significant (p>0.05).

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, 2). Of the rare species (i.e., with a relative abundance <1% in any sediment sample), 36% were in Rotaliina, 21% in Textulariina, and 6% in Miliolina. 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*, reacted 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. From a peak near the coastline, diversity decreases landwards whereas species dominance (Berger-Parker index) increases (Figs. 2A, B). From the coastline inland, salinity decreases (Fig. 2C), and distance and salinity are negatively correlated (Table 3). The salinity range is high for most sites but is highest near the coastline (Fig. 2D). The total inorganic carbon (TIC) of the sediment decreases, and total organic carbon (TOC) content increases with distance from the coastline (Figs. 2E, F). In general, elevation ranges from less than 0.5 m below sea level to less than 0.5 m above sea level. Near the beach, 0–500 m inland, elevation is on average + 0.14 m and then progressively lowers from the coastline inland to an average elevation of - 0.06 m (Fig. 2G), unlike most regions studied for foraminiferal distributions relating to marsh elevations. Everglades sediments are biogenous carbonates with grain size ranging from mud to fine sand. Collected sediments consisted predominantly of partially decomposed plant matter or fragments of calcium carbonate shells and skeletal parts of bivalves, gastropods, corals, and benthic foraminifera.

The abundances of some species showed significant correlations with certain environmental variables. *Ammonia parkinsoniana* and *Elphidium excavatum* had negative correlations with sediment TOC content, and positive correlations with TIC content (Table 4). *Elphidium morenoi* had a positive correlation with TIC as well (Table 4). Abundances of the agglutinated species *Tiphotrocha comprimata* and *Trochammina inflata* were positively correlated with the TOC content of the sediment. The abundances of *Bisaccium imbricatum* and *Buccella hannai* were positively correlated with the total phosphorus content of the surface sediment (Table 4).

CLUSTER ANALYSIS AND FORAMINIFERAL ASSEMBLAGES

The Q-mode cluster analysis of foraminifera (Fig. 3) resulted in two major clusters of samples: predominantly agglutinated and predominantly calcareous assemblages. The agglutinated assemblages consisted of one group of samples (F), and the calcareous assemblages contained four groups of samples (A–D) and one outlier (site SW31; E). The ANOSIM significance test resulted in p-values less than 0.05 between associations A, B, C, D, and F, whereas the outlier, E (SW31), was not significantly related to any other association of samples (p>0.05; Table 5).

R-mode clustering of foraminifera revealed six species associations (clusters 1–4; Fig. 4). Two clusters of predominantly agglutinated species (assemblages 1 and 2) are separated from the other four predominantly calcareous assemblages (3–6). The SIMPER analysis (Table 6) identified 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*, *E. excavatum*, *T. inflata*, and *Arenoparrella mexicana*, in order of importance. The 30 taxa selected from the SIMPER results were used for simultaneous Q-mode and R-mode clustering (Fig. 5) in which five species assemblages were identified and 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, *Trichohyalus 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 *T. 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, while some show multiple abundance peaks. *Elphidium* species have a tolerance for salinities >16 psu, but a preference for salinities >20 psu (Figs. 6, 7). 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, 9). Most agglutinated taxa in this study have their maximum abundance at salinities <20 psu. However, *H. wilberti* occurs at salinities of 16–18 psu, and *A. mexicana* occurs

TABLE 4. Significant correlations (p<0.05) between environmental variables (TOC = total organic carbon; TIC = total inorganic carbon; TP = total phosphorus; T = temperature; DO = dissolved oxygen) and taxa, with correlation coefficients (r), coefficients of determination (r^2), and probabilities (p).

Variables			Salinity	Salinity Range	pH	TOC	TIC	TP	T	DO	Elevation	Distance
Taxa												
Ammonia parkinsoniana	r		-	-	− 0.41	− 0.67	0.77	-	-	-	− 0.44	-
	r^2		-	-	0.17	0.44	0.59	-	-	-	0.2	-
	p		-	-	0.03	<0.001	<0.001	-	-	-	0.02	-
Ammonia tepida	r		-	-	-	-	-	-	-	-	-	-
	r^2		-	-	-	-	-	-	-	-	-	-
	p		-	-	-	-	-	-	-	-	-	-
Bisaccium imbricatum	r		-	-	-	-	-	0.76	-	-	-	-
	r^2		-	-	-	-	-	0.58	-	-	-	-
	p		-	-	-	-	-	<0.001	-	-	-	-
Buccella hannai	r		-	-	-	-	-	0.86	-	-	-	-
	r^2		-	-	-	-	-	0.75	-	-	-	-
	p		-	-	-	-	-	<0.001	-	-	-	-
Elphidium excavatum	r		-	-	-	− 0.66	0.7	-	-	-	-	-
	r^2		-	-	-	0.44	0.5	-	-	-	-	-
	p		-	-	-	<0.001	<0.001	-	-	-	-	-
Elphidium discoidale	r		-	-	-	-	-	-	-	-	-	-
	r^2		-	-	-	-	-	-	-	-	-	-
	p		-	-	-	-	-	-	-	-	-	-
Elphidium galvestonense	r		-	0.61	-	-	-	-	-	-	-	-
	r^2		-	0.37	-	-	-	-	-	-	-	-
	p		-	<0.001	-	-	-	-	-	-	-	-
Elphidium koeboeense	r		-	-	-	-	-	-	-	-	-	0.41
	r^2		-	-	-	-	-	-	-	-	-	0.17
	p		-	-	-	-	-	-	-	-	-	0.03
Elphidium matagordanum	r		-	-	-	− 0.43	0.49	-	-	-	-	-
	r^2		-	-	-	0.18	0.24	-	-	-	-	-
	p		-	-	-	0.03	0.01	-	-	-	-	-
Elphidium mexicanum	r		-	-	-	− 0.42	0.42	-	-	-	-	-
	r^2		-	-	-	0.17	0.17	-	-	-	-	-
	p		-	-	-	0.03	0.03	-	-	-	-	-
Elphidium morenoi	r		-	-	-	− 0.61	0.74	-	-	-	-	-
	r^2		-	-	-	0.37	0.55	-	-	-	-	-
	p		-	-	-	<0.001	<0.001	-	-	-	-	-
Elphidium simplex	r		-	-	-	-	-	-	-	-	-	-
	r^2		-	-	-	-	-	-	-	-	-	-
	p		-	-	-	-	-	-	-	-	-	-
Haynesina depressula	r		-	-	-	-	-	-	-	-	-	-
	r^2		-	-	-	-	-	-	-	-	-	-
	p		-	-	-	-	-	-	-	-	-	-
Helenina anderseni	r		-	-	-	-	-	-	-	-	-	-
	r^2		-	-	-	-	-	-	-	-	-	-
	p		-	-	-	-	-	-	-	-	-	-
Trichohyalus aguayoi	r		-	-	-	-	-	0.42	-	-	-	-
	r^2		-	-	-	-	-	0.18	-	-	-	-
	p		-	-	-	-	-	0.03	-	-	-	-
Biloculinella eburnea	r		-	-	-	-	-	-	-	-	-	-
	r^2		-	-	-	-	-	-	-	-	-	-
	p		-	-	-	-	-	-	-	-	-	-
Cornuspira involvens	r		-	-	-	-	-	-	-	-	-	-
	r^2		-	-	-	-	-	-	-	-	-	-
	p		-	-	-	-	-	-	-	-	-	-
Miliolinella microstoma	r		-	-	-	-	-	-	-	-	-	-
	r^2		-	-	-	-	-	-	-	-	-	-
	p		-	-	-	-	-	-	-	-	-	-
Quinqueloculina bosciana	r		-	-	0.45	-	-	0.59	-	-	-	-
	r^2		-	-	0.2	-	-	0.34	-	-	-	-
	p		-	-	0.02	-	-	0.001	-	-	-	-
Quinqueloculina seminulum	r		-	-	-	-	0.45	-	− 0.42	-	-	-
	r^2		-	-	-	-	0.2	-	0.18	-	-	-
	p		-	-	-	-	0.02	-	0.03	-	-	-
Quinqueloculina sp.	r		-	-	-	-	-	0.43	-	-	-	-
	r^2		-	-	-	-	-	0.18	-	-	-	-
	p		-	-	-	-	-	0.03	-	-	-	-
Triloculina sp.	r		-	-	-	-	-	0.51	-	-	-	-
	r^2		-	-	-	-	-	0.26	-	-	-	-
	p		-	-	-	-	-	0.007	-	-	-	-

TABLE 4. Continued

Variables		Salinity	Salinity Range	pH	TOC	TIC	TP	T	DO	Elevation	Distance
Arenoparrella mexicana	r	-	-	-	-	−0.56	-	-	-	-	-
	r²	-	-	-	-	0.31	-	-	-	-	-
	p	-	-	-	-	0.002	-	-	-	-	-
Haplophragmoides wilberti	r	-	-	-	0.44	-	-	-	-	-	-
	r²	-	-	-	0.2	-	-	-	-	-	-
	p	-	-	-	0.02	-	-	-	-	-	-
Jadammina macrescens	r	−0.51	-	-	0.46	-	-	-	-	-	0.58
	r²	0.26	-	-	0.22	-	-	-	-	-	0.34
	p	0.007	-	-	0.01	-	-	-	-	-	0.001
Miliammina fusca	r	-	-	-	-	-	-	-	-	-	-
	r²	-	-	-	-	-	-	-	-	-	-
	p	-	-	-	-	-	-	-	-	-	-
Tiphotrocha comprimata	r	−0.46	-	-	0.65	−0.45	-	-	-	-	0.49
	r²	0.21	-	-	0.43	0.21	-	-	-	-	0.24
	p	0.02	-	-	<0.001	0.02	-	-	-	-	0.01
Trochammina inflata	r	-	-	-	0.63	−0.56	-	-	-	-	0.38
	r²	-	-	-	0.4	0.32	-	-	-	-	0.15
	p	-	-	-	<0.001	0.002	-	-	-	-	0.05
Trochammina sp.	r	-	-	-	0.45	-	-	-	-	-	-
	r²	-	-	-	0.2	-	-	-	-	-	-
	p	-	-	-	0.02	-	-	-	-	-	-
Trochamminita salsa	r	−0.41	-	-	0.43	-	-	-	-	-	-
	r²	0.17	-	-	0.18	-	-	-	-	-	-
	p	0.04	-	-	0.03	-	-	-	-	-	-

at salinities of 16–18 psu, as well as at higher salinities of 28–30 psu (Figs. 9, 10).

DISTRIBUTION OF ASSEMBLAGES AND ENVIRONMENTAL VARIABLES

Non-metric multi-dimensional scaling (Fig. 11) shows the ten environmental variables (Tables 7, 8) as vectors with lengths representing their relative influence on the distribution of the assemblages. The longest vectors are for TOC and TIC, followed (in order of length) by distance from the coastline, total phosphorus, salinity, elevation, pH, salinity range, temperature, and dissolved oxygen. The TIC, salinity, and salinity range vectors point in the same direction. The TOC vector points in a direction opposite to the inversely correlated TIC vector, as do the distance and elevation vectors. Salinity and distance from the coastline, as well as salinity and TOC, have a weak negative correlation (Table 3). Some of the other variables are also significantly correlated, including the positive correlations between pH and dissolved oxygen and between pH and temperature (Table 3). However, mainly TOC, TIC, and salinity show significantly higher correlations with the 30 species contributing >1% to the observed differences between sites (SIMPER results). Total phosphorus also showed a strong correlation with certain species (Table 4).

Multiple regression analysis on the 30 selected species indicates that the abundances of 23 taxa can be explained by the ten environmental variables included in this study (Table 9). Most species distributions are mainly controlled by TOC, TIC, TP, salinity, and associations between these variables. *Trochamminita salsa* is only controlled by salinity, while *J. macrescens* also shows a small dependency on temperature (Table 9). When performing regression analysis with only the samples from geographic area A (Fig. 1, Table 9), *J. macrescens* and *T. salsa* are only controlled by salinity, and the coefficients of determination increase substantially when compared to regression analysis including all the samples (area A and B; Fig. 1, Table 9).

DISCUSSION

ASSEMBLAGE CHARACTERISTICS

In this study of the southwestern Everglades, we recorded 82 species, which surpasses previous foraminiferal counts based in the Everglades 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 of Florida. A test with 10% HCl on the agglutinated taxa revealed that only *Ammobaculites dilatatus* and *Ammotium multiloculatum* 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 in the highly variable intertidal environment. Patchy, short-

TABLE 5. P-values of significance tests for groups A–F in Q-mode cluster analysis of Figure 3, analysis of similarities. A p-value <0.05 is in bold.

	A	B	C	D	E	F
A	0	**0.018**	**0.002**	0.096	0.238	**0.028**
B	**0.018**	0	**0.001**	**0.018**	0.165	**0.008**
C	**0.002**	**0.001**	0	**0.003**	0.076	**0.001**
D	0.096	**0.018**	**0.003**	0	0.248	**0.028**
E	0.238	0.165	0.076	0.248	0	0.195
F	**0.028**	**0.008**	**0.001**	**0.028**	0.195	0

TABLE 6. Average dissimilarity, percent contribution, cumulative contribution, and average abundance per sample association (A–F) of individual species produced with SIMPER analysis using Bray-Curtis dissimilarity index. Listed species have ≥1% contribution to general distribution pattern as illustrated by Q-mode cluster analysis (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	11.620	15.510	15.510	62.500	24.200	22.800	9.930	9.590	0.712
Ammonia parkinsoniana	9.244	12.340	27.850	10.200	10.000	30.800	10.000	1.110	0.680
Elphidium excavatum	6.564	8.762	36.610	1.950	6.870	12.700	3.240	66.000	0.000
Trochammina inflata	6.336	8.458	45.070	1.370	5.820	0.154	1.370	0.000	33.300
Arenoparrella mexicana	4.337	5.789	50.850	0.783	9.690	0.053	1.440	0.000	16.700
Haynesina depressula	2.840	3.791	54.640	12.300	3.920	2.730	3.810	0.740	0.085
Elphidium morenoi	2.777	3.707	58.350	0.000	1.450	8.340	2.390	0.000	0.000
Helenina anderseni	2.752	3.674	62.030	1.860	12.400	0.132	0.397	0.000	1.710
Quinqueloculina seminulum	2.650	3.537	65.560	0.000	0.920	6.280	8.260	0.000	0.000
Tiphotrocha comprimata	2.505	3.343	68.910	0.650	0.196	0.000	2.580	0.370	13.100
Jadammina macrescens	1.817	2.425	71.330	0.000	0.000	0.000	0.130	0.740	10.700
Trichohyalus aguayoi	1.757	2.345	73.680	0.197	1.090	0.084	12.200	0.000	0.000
Elphidium koeboeense	1.427	1.906	75.580	0.490	0.394	3.400	3.640	0.000	0.000
Biloculinella eburnea	1.387	1.852	77.430	0.097	3.060	0.000	6.940	0.000	0.085
Trochammina sp.	1.277	1.704	79.140	0.000	0.652	0.000	1.560	0.000	6.410
Haplophragmoides wilberti	1.137	1.518	80.660	0.000	0.070	0.000	0.200	0.000	6.700
Quinqueloculina sp.	0.995	1.329	81.980	0.000	0.232	1.420	4.340	0.000	0.000
Miliammina fusca	0.982	1.311	83.290	0.413	1.350	0.000	0.000	14.800	0.085
Buccella hannai	0.864	1.153	84.450	0.000	0.000	0.018	6.640	0.000	0.000
Trochamminita salsa	0.817	1.091	85.540	0.000	0.000	0.000	0.000	0.000	4.940
Elphidium galvestonense	0.815	1.089	86.630	2.070	0.826	1.380	0.993	0.000	0.000
Miliolinella microstoma	0.792	1.058	87.680	0.000	3.670	0.093	0.673	0.000	0.000
Elphidium discoidale	0.770	1.028	88.710	0.783	0.600	1.950	0.000	0.000	0.000
Elphidium matagordanum	0.612	0.817	89.530	0.000	0.434	1.560	1.160	0.000	0.000
Elphidium simplex	0.597	0.797	90.330	0.490	1.750	0.223	1.460	0.000	0.000
Elphidium mexicanum	0.518	0.691	91.020	0.000	0.282	1.310	0.940	0.000	0.000
Bisaccium imbricatum	0.507	0.677	91.700	0.000	0.706	0.000	3.010	0.000	0.000
Quinqueloculina bosciana	0.489	0.653	92.350	0.000	1.180	0.000	1.610	0.000	0.680
Triloculina sp.	0.474	0.633	92.980	0.000	0.000	0.373	2.830	0.000	0.000
Cornuspira involvens	0.388	0.518	93.500	0.000	1.870	0.087	0.000	0.000	0.000

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 (Figs. 2A, B, H–J). We also noted that taxa of the Rotaliina are equally abundant across all the intertidal environments, with the exceptions of where the organic carbon content is high and salinity drops below 18 psu. 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 previous Everglades foraminiferal studies of Benda & Puri (1962), Phleger (1965), Goldstein (1976), and Bock & Gebelein (1977).

The surface sediment samples collected from mangroves and sawgrass marshes were peaty and consisted predominantly of decomposed plant matter, yielding high TOC values. On the other hand, the sediments from bays and lake bottoms contained mostly calcium carbonate shells and

skeletal parts from bivalves, gastropods, corals, and benthic foraminifera, resulting in high TIC measurements.

Many Everglades species have also been 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, as most marshes are too acidic for the preservation of calcareous taxa, but in the Everglades, the limestone bedrock buffers sediment pH and prevents most dissolution (Verlaak et al., 2019). The most typical species with worldwide occurrences that are included in our study are: *A. parkinsoniana*, *A. tepida*, *T. 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 <20 psu. Even though no specific salinity values

TABLE 7. Average values of environmental variables (TOC = total organic carbon; TIC = total inorganic carbon; TP = total phosphorus; T = temperature; DO = dissolved oxygen) per sampling site. Total organic (TOC) and inorganic carbon (TIC) measured from collected sediment. Distance from coastline measured as straight line on a map. Other values obtained online from: https://apps.sfwmd.gov/WAB/EnvironmentalMonitoring/index.html.

Variable Unit	Salinity PSU	Salinity Range PSU	pH -	TOC %	TIC %	TP mg/l	T celsius	DO mg/l	Elevation m	Distance km
Site										
PDL	31.2	5.4	-	3.075	53.66	0.0122	26.1	6.2167	− 0.61	− 2
TB	25.7	55.2	8.3	15.96	19.45	0.057	26.8	5.656	− 0.03	0
SRM1	28.7	26.4	7.8	13.7	2.226	0.0202	25	4.7831	0.18	0
GB	33	28.9	-	8.495	37.39	-	26.8	-	− 0.07	0
AC1	26.7	29.2	7.7	5.311	44.71	0.1095	26.8	3.508	0.12	0.07
SRM3	28.7	26.4	7.8	13.72	3.586	0.0202	25	4.7831	0.18	0.3
AC3	26.7	29.2	7.7	7.534	41.5	0.1095	26.8	3.508	0.12	0.35
LO3	21.3	7.4	7.8	10.39	20.69	0.0223	20.6	5.2585	0.23	0.5
SW14	24.7	32.3	7.6	4.257	54.22	0.0323	25.1	4.187	0.36	0.5
WL25	16.2	12.4	-	5.724	59.59	-	-	-	− 0.3	1.6
LL	21.6	39	-	35.02	3.392	-	-	-	0.02	1.6
WL23	16.2	12.4	-	7.314	51.52	-	-	-	-0.01	2
WL27	16.2	12.4	-	5.536	61.44	-	-	-	− 0.12	2
WL24	16.2	12.4	-	8.882	44.77	-	-	-	0.04	2.4
WL	16.2	12.4	-	28.9	0.586	-	-	-	0.01	2.6
WL28	16.2	12.4	-	5.474	60.43	-	-	-	− 0.02	2.6
CL	15	22.1	-	38.38	0.5466	-	-	-	− 0.07	4
SRS6	24.4	10	7.4	9.355	37.93	-	25.7	-	0.02	4
SH3	30.2	9.9	-	15.87	17.35	-	22.8	-	0.07	4
SH3-70	30.2	9.9	-	18.87	7.471	-	22.8	-	0.07	4
SW17	20.8	38.1	-	11.14	26.97	-	25.9	-	0.01	5
SW18	25.6	27.5	7.8	7.848	36.99	0.0196	25.2	4.8445	− 0.01	6
SH4	17.8	22.8	7.4	33.48	0.5881	0.025	24.2	2.3251	0.04	8
SH5	16.9	13.8	-	34.15	1.758	-	21.6	-	0.18	8
SRS5	17.5	18.6	7.7	13.59	23.21	0.0162	26.052	3.2522	− 0.07	9
LO2	9.4	8.2	7.9	24.87	0.3857	-	23.9	5.6034	− 0.37	13
SW31	4.5	28.8	-	36.69	2.528	-	26.5	-	− 0.33	14
SRS4	5.8	19.5	7.8	38.07	0.7582	0.0138	25.1	4.152	− 0.22	16
SW19	16.7	35.7	7.9	8.553	49.25	0.0161	25.3	5.476	− 0.12	16
SW35	0.4	13.8	7.5	31.23	0.09408	0.0082	25.3	4.0642	− 0.14	20

are given, *T. salsa* is consistently recorded as having a low-salinity preference in mangroves, 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, USA (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, including smaller ranges from 1 to 4 psu, 6 to 9 psu, 18 to 20 psu, and 22 to 24 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 <20 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 1 and 4 psu, 6 and 9 psu, as well as 10 and 15 psu, we can only say that the species' salinity tolerance is <20 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 may occur in the higher marsh as well (e.g., Williams, 1994; Hayward et al., 1996).

TABLE 8. Sampling locations of surface sediments collected for foraminifera and water quality data. USGS = U.S. Geological Survey, SFWMD = South Florida Water Management District, LTER = Long-term Ecological Research project at FIU.

Sampling Site (sediment)	Latitude (N)	Longitude (W)	Water Quality Site	Latitude (N)	Longitude (W)	Collecting Agency
LO2	25° 35′ 35″	81° 2′ 29″	LO2	25° 35′ 35″	81° 2′ 29″	USGS
LO2	25° 35′ 35″	81° 2′ 29″	ENPWW	25° 35′ 15″	81° 2′ 37″	SFWMD
LO2	25° 35′ 35″	81° 2′ 29″	FLAB31	25° 34′ 3″	81° 4′ 17″	SFWMD
LO3	25° 32′ 21″	81° 11′ 3″	LO3	25° 32′ 21″	81° 11′ 3″	USGS
LO3	25° 32′ 21″	81° 11′ 3″	FLAB29	25° 33′ 16″	81° 11′ 1″	SFWMD
SH3	25° 21′ 51″	81° 4′ 42″	SH3	25° 21′ 51″	81° 4′ 42″	USGS
SH3-70	25° 21′ 49″	81° 4′ 42″	SH3	25° 21′ 51″	81° 4′ 42″	USGS
SH4	25° 25′ 25″	81° 3′ 38″	SH4	25° 25′ 25″	81° 3′ 38″	USGS
SH4	25° 25′ 25″	81° 3′ 38″	ENPHR	25° 25′ 28″	81° 03′ 36″	SFWMD
SH5	25° 25′ 17″	81° 3′ 35″	SH5	25° 25′ 17″	81° 3′ 35″	USGS
SW14	25° 25′	81° 8′	FLAB36	25° 24′ 42″	81° 8′ 29″	SFWMD
SW35	25° 27′	80° 55′	P-35	25° 27′ 41″	80° 51′ 53″	SFWMD
SW35	25° 27′	80° 55′	Site 22908295	25° 28′ 4″	80° 51′ 16″	SFWMD
SRM1	25° 20′ 34″	81° 7′ 57″	FLAB40	25° 20′ 59″	81° 7′ 28″	SFWMD
SRM3	25° 20′ 34″	81° 7′ 58″	FLAB40	25° 20′ 59″	81° 7′ 28″	SFWMD
PDL	25° 19′ 1″	81° 10′ 12″	SWS40	25° 15′ 37″	81° 15′ 36″	SFWMD
SW18	25° 21′	81° 4′	FLAB41	25° 19′ 52″	81° 4′ 22″	SFWMD
SW19	25° 19′	80° 60′	FLAB44	25° 19′ 55″	80° 59′ 1″	SFWMD
TB	25° 9′ 33″	80° 43′ 47″	ENPTB	25° 9′ 26″	80° 43′ 29″	SFWMD
TB	25° 9′ 33″	80° 43′ 47″	C111MC	25° 10′ 6″	80° 44′ 1″	SFWMD
GB	25° 11′	80° 48′	ENPGB	25° 10′ 2″	80° 48′ 5″	SFWMD
AC1	25° 11′	80° 48′	C111AC	25° 10′ 34″	80° 47′ 34″	SFWMD
AC3	25° 11′	80° 47′	C111AC	25° 10′ 34″	80° 47′ 34″	SFWMD
SRS4	25° 24′ 35″	80° 57′ 52″	SRS4	25° 24′ 35″	80° 57′ 52″	LTER
SW31	25° 24′	80° 58′	ENPTE	25° 24′ 36″	80° 57′ 50″	SFWMD
SRS4	25° 24′ 35″	80° 57′ 52″	FLAB38	25° 25′ 2″	80° 59′ 54″	SFWMD
SRS5	25° 22′ 37″	81° 1′ 56″	SRS5	25° 22′ 37″	81° 1′ 56″	LTER
SRS5	25° 22′ 37″	81° 1′ 56″	ENPGI	25° 22′ 41″	81° 1′ 46″	SFWMD
SRS5	25° 22′ 37″	81° 1′ 56″	FLAB39	25° 22′ 44″	81° 1′ 51″	SFWMD
SRS6	25° 21′ 53″	81° 4′ 41″	SRS6	25° 21′ 53″	81° 4′ 41″	LTER
SW17	25° 23′	81° 4′	ENPSR	25° 21′ 15″	81° 6′ 0″	SFWMD
SW17	25° 23′	81° 4′	SHARKRIVBG	25° 22′ 30″	81° 2′ 12″	SFWMD
WL	25° 13′	80° 49′	West Lake	25° 12′ 25″	80° 49′ 29″	LTER
WL23	25° 12′ 10″	80° 51′ 0.2″	West Lake	25° 12′ 25″	80° 49′ 29″	LTER
WL24	25° 12′ 17″	80° 50′ 25″	West Lake	25° 12′ 25″	80° 49′ 29″	LTER
WL25	25° 12′ 11″	80° 48′ 30″	West Lake	25° 12′ 25″	80° 49′ 29″	LTER
WL27	25° 12′ 39″	80° 48′ 15″	West Lake	25° 12′ 25″	80° 49′ 29″	LTER
WL28	25° 12′ 30″	80° 50′ 53″	West Lake	25° 12′ 25″	80° 49′ 29″	LTER
CL	25° 13′	80° 46′	Cuthbert Lake	25° 12′ 27″	80° 46′ 32″	LTER
LL	25° 12′	80° 48′	Long Lake	25° 11′ 47″	80° 47′ 37″	LTER

In the Everglades, as with *J. macrescens* (above), 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 a Massachussetts salt marsh (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 <20 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 British Columbia, Guilbault & Patterson (2000) described it as a low-salinity species. In New Zealand mangroves, it occurs at 3–20 psu (Hayward & 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*'s distribution clearly excludes salinities lower than 6 psu and may occur over a range as large as 10–20 psu. Therefore, this species is a good indicator for mangrove en-

vironments 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 at lower salinities (<20 psu), but *A. mexicana* also occurred at 28–30 psu. In other studies, both taxa are often dominant at low salinities (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). Kemp et al. (2009) found these taxa often associated with salinities around 20 psu. In the Everglades, both taxa can tolerate salinities <30 psu, and *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
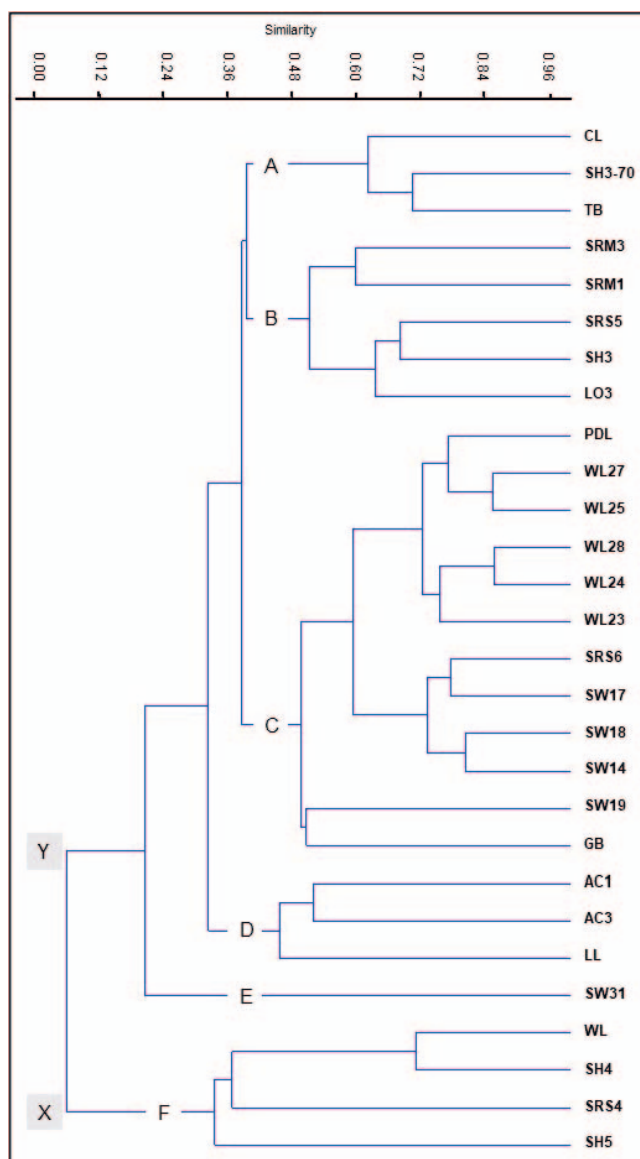
FIGURE 3. Q-mode cluster analysis of 28 surface samples of taxa with relative abundance >1% using unweighted pair group clustering with average linkage with the Bray-Curtis dissimilarity index. Cluster X = predominantly agglutinated assemblages. Cluster Y = predominantly calcareous assemblages. Clusters A–F mark the identified clusters of distinct assemblages, representing different habitats.

FIGURE 4. R-mode cluster analysis using unweighted pair group clustering with average linkage and Bray-Curtis dissimilarity index. Numbers 1 to 6 = distinct foraminiferal assemblages.

of *Ammonia* spp. >18 psu and *Elphidium* spp. >22 psu. For many other studies in salt marshes and 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). In the Everglades, *Ammonia* spp. indicate the higher salinities, of the order of >14 psu, that exist at the lower reaches of the intertidal environment. However, where they occur together with other species, (e.g., *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 in sediments containing between 3–11% TOC (Fig. 12). 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. 12). These species also occur over a wider range of salinity values, which suggests that TOC may be a more important limiting factor. For example, *A. mexicana* was observed at both 16–18 psu and 28–30 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 salinity seems to limit *T. inflata* in the Brazilian mangroves (Barbosa et al., 2005). *Ammonia tepida* apparently prefers sediments high in organic carbon for nutritional reasons (Debenay et al., 2002). Additionally,
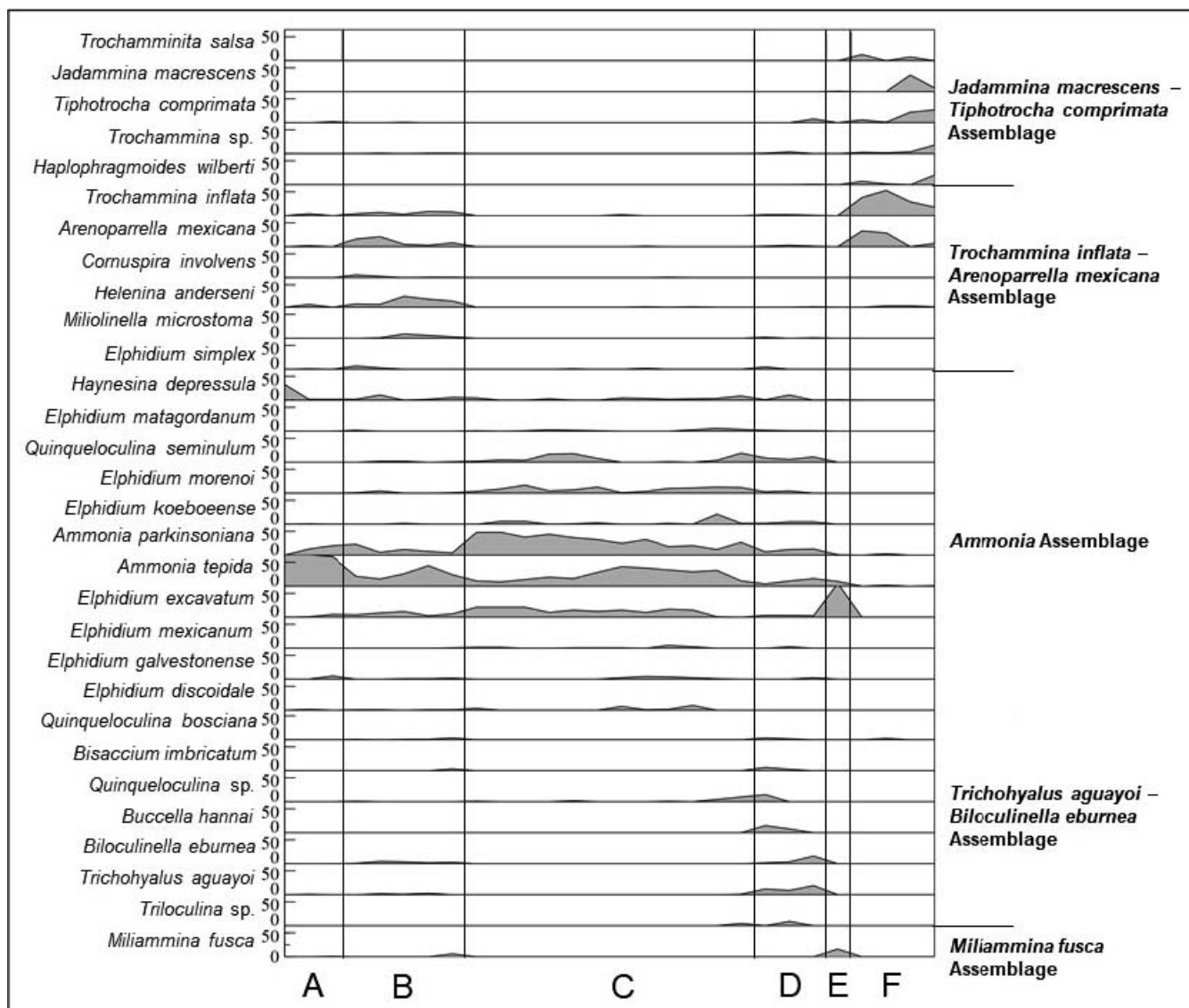
FIGURE 5.　Simultaneous Q- and R-mode clustering, showing the correlation between sample associations A–F and foraminiferal assemblages of the main contributing species, visualized with their relative abundance (%).

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 observed salinity gradient from the coastline inland (Chen & Twilley, 1999) is the combined result of seasonal rainfall and groundwater discharge, the porosity of the limestone bedrock, and tidal forces. The landward end of Everglades coastal mangroves 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. 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 marine influence along the coast (Price et al., 2006, 2010).

This Everglades study showed TOC, closely followed by TIC, to be the major controls on 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 and high
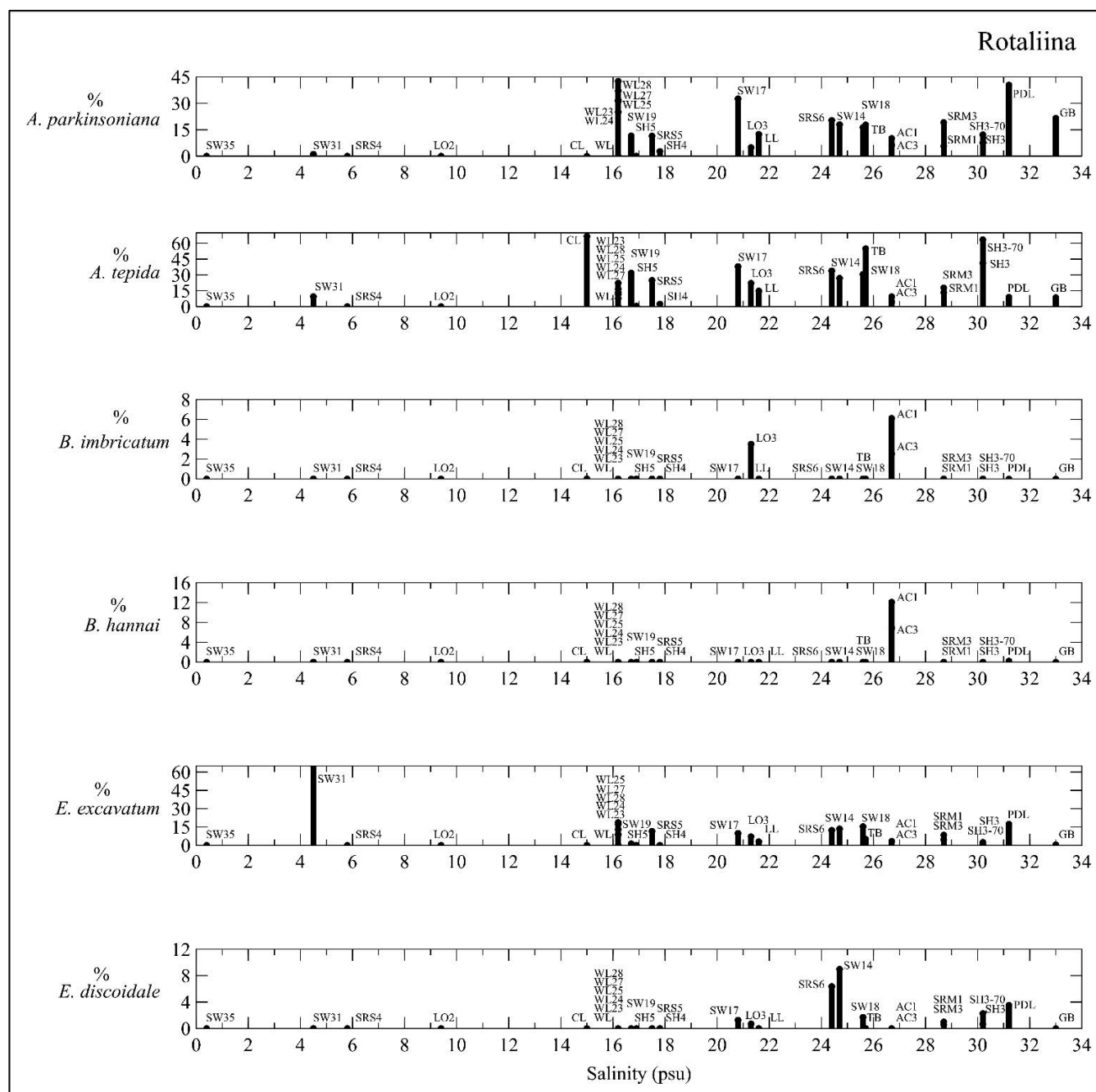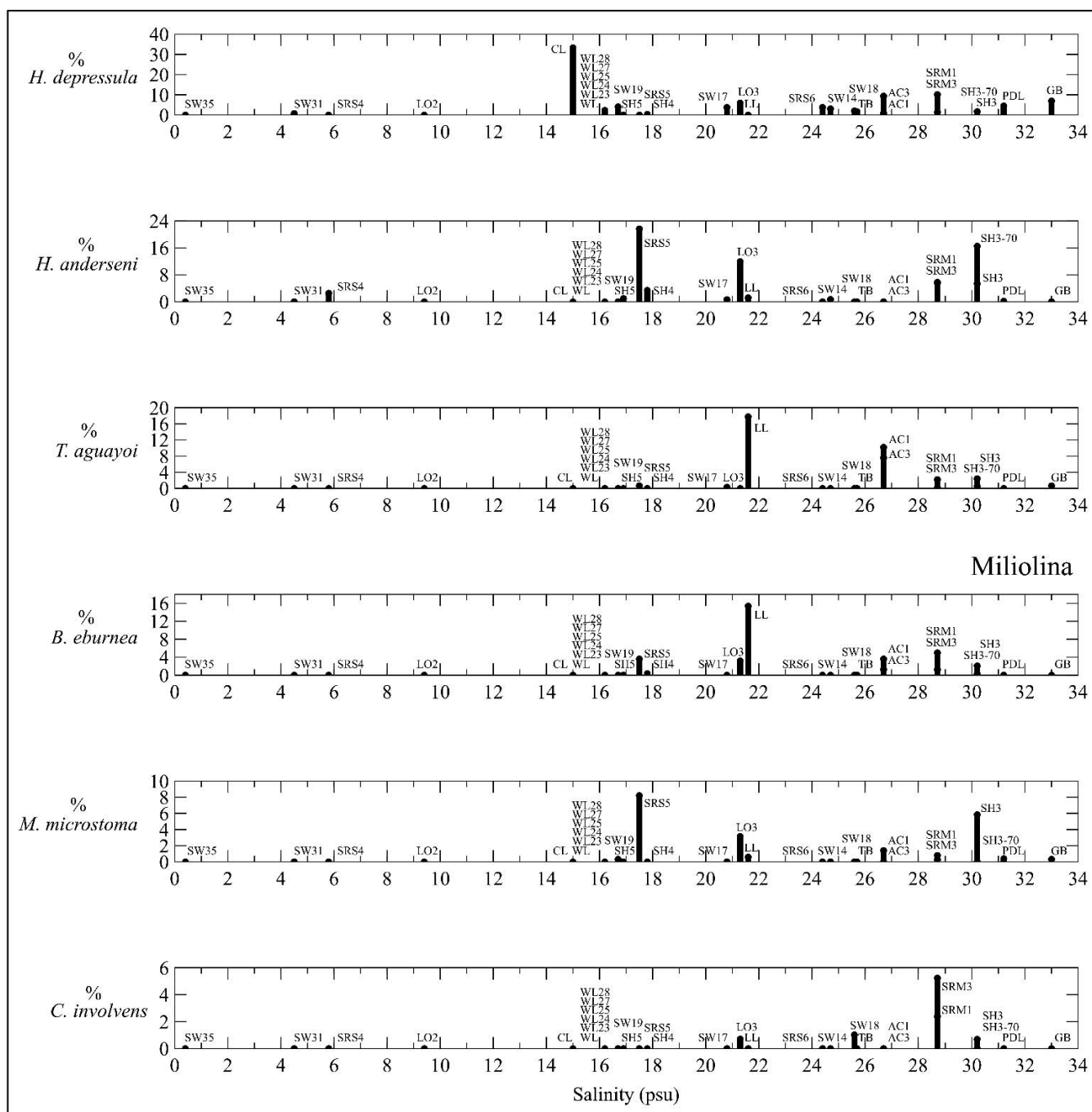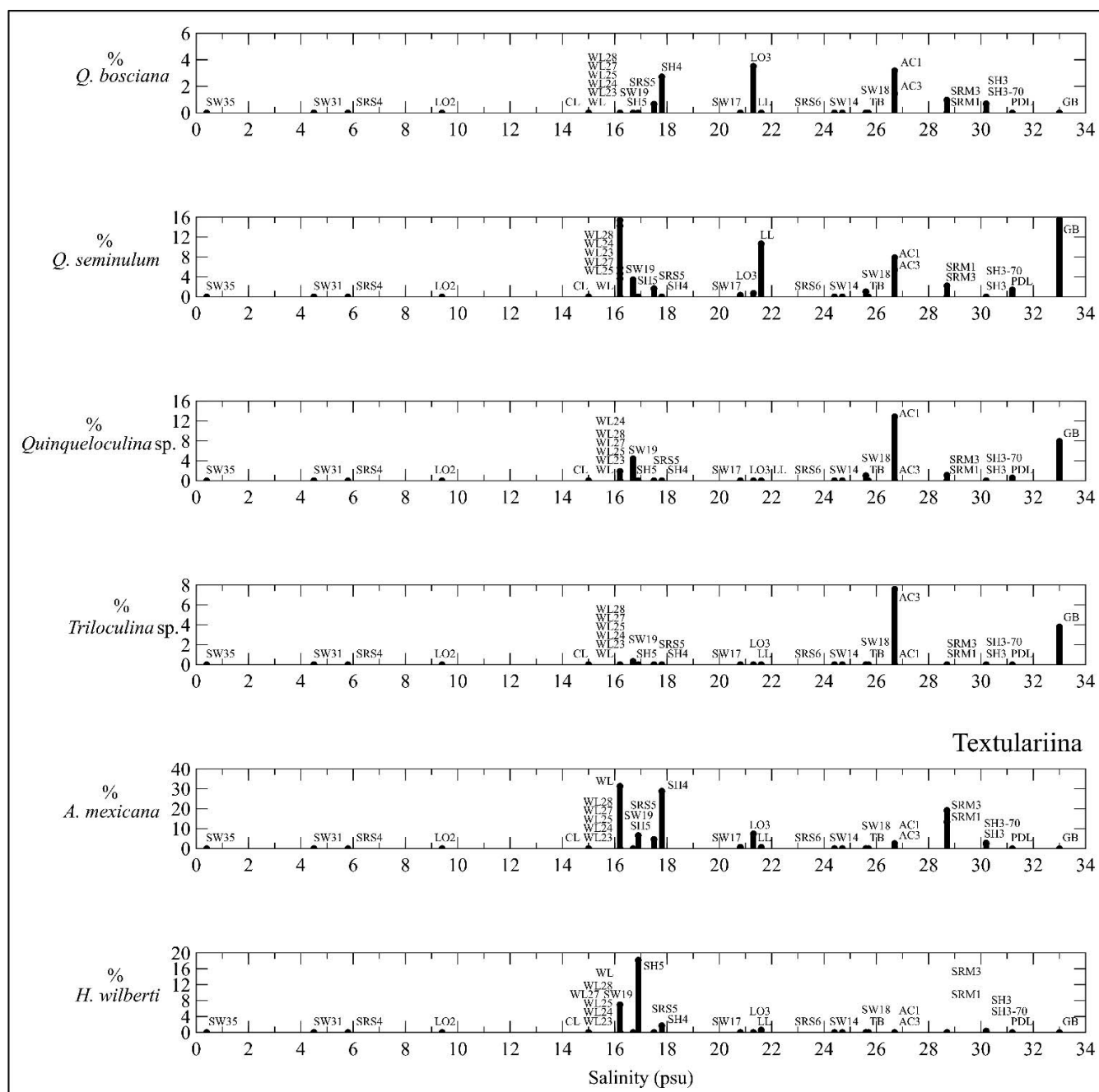
FIGURE 6.   Relative abundance of calcareous perforate taxa with at least 1% contribution to observed differences between habitats, with salinity (psu).

TOC from sites characterized by higher average salinities and medium to lower TOC values, resulting in the separation of distinct assemblages of either predominantly agglutinated or calcareous taxa, with agglutinated assemblages becoming more dominant in a landward direction. This disagrees 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 the most important control on the foraminiferal distributions. Linke & Lutze

(1993) suggest that, based on the results from foraminiferal microhabitat and behavioral studies, it is an adaptation to nutritional conditions rather than to physicochemical qualities of the environment that controls foraminiferal distribution.

OTHER ENVIRONMENTAL CONTROLS ON FORAMINIFERAL ASSEMBLAGES

Our non-metric multidimensional scaling (NMDS) results indicate that TOC and TIC are more important factors than
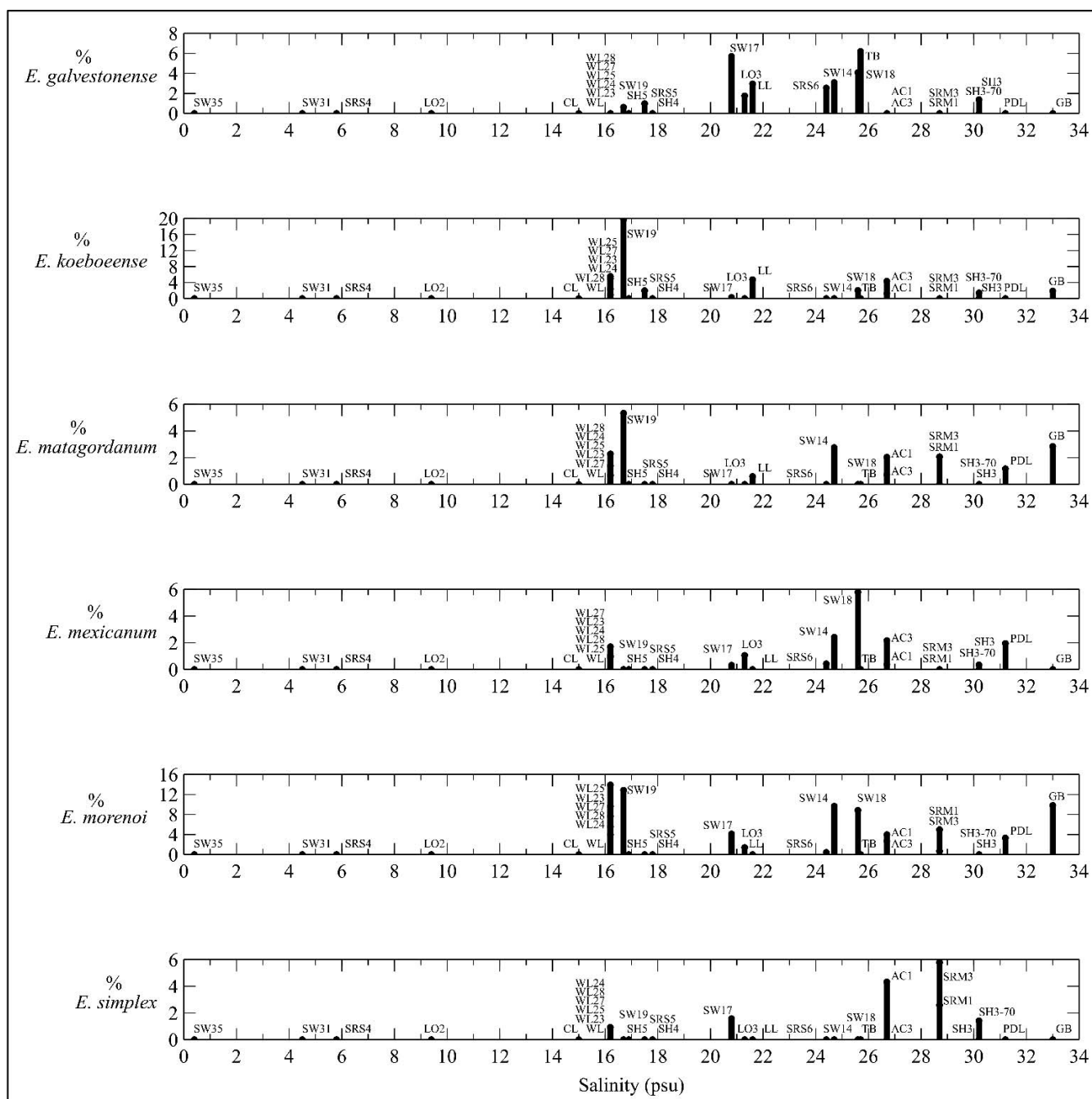
FIGURE 7.   Relative abundance of *Elphidium* species with at least 1% contribution to observed differences between habitats, with salinity (psu).

salinity (Fig. 11) in influencing the distribution of taxa. The vectors represent the direction and magnitude of the correlation coefficients between the environmental variables and the NMDS scores of the samples.

Salinity is an important control for *J. macrescens* and *T. salsa*, and for a few species it is one of multiple factors that determine their distribution (Table 9). Multiple regression revealed that some species, such as *Cornuspira involvens*, are only significantly correlated with salinity when analyzing geographic area "A" separately (Fig. 1; Table 9). Fur-

thermore, the abundances of *J. macrescens* and *T. salsa* are more strongly correlated with salinity when only considering geographic area A (Fig. 1) than when incorporating all the samples (areas A and B; Fig. 1; Table 9) in the regression analysis. Area A covers a salinity range (i.e., the difference between the lowest, 0.4 psu, and highest, 31.2 psu, salinity value) of 31 psu, from near freshwater to near normal marine salinities, while area B only covers a salinity range of 18 psu (i.e., the difference between the lowest, 15 psu, and highest, 33 psu, salinity value) with samples mainly collected

FIGURE 8. Relative abundance of calcareous perforate and imperforate taxa with at least 1% contribution to observed differences between habitats, with salinity (psu).

around lakes and thus covering less variability in salinity (Table 7) which could explain the differences in correlations of species distributions and salinity.

Salinity and TOC are negatively correlated (Table 3), thus low salinities are associated with high TOC and agglutinated assemblages. The sediments along the Shark River Slough have a generally higher percentage of organic matter than the sediments from Taylor Slough, and the organic matter content increases with distance from the coastline (Cham-

bers & Pederson, 2006). This study showed that the distance from the coastline and salinity are negatively correlated as well (Table 3) and that the foraminiferal assemblages follow the distance trends in salinity and TOC.

We also found a high positive correlation between *B. imbricatum* and *B. hannai*, and the total phosphorus content of the sediment (Table 4). In our NMDS analysis, the total phosphorus vector is longer, but close in length to the salinity vector. Multiple regression showed that also the abun-

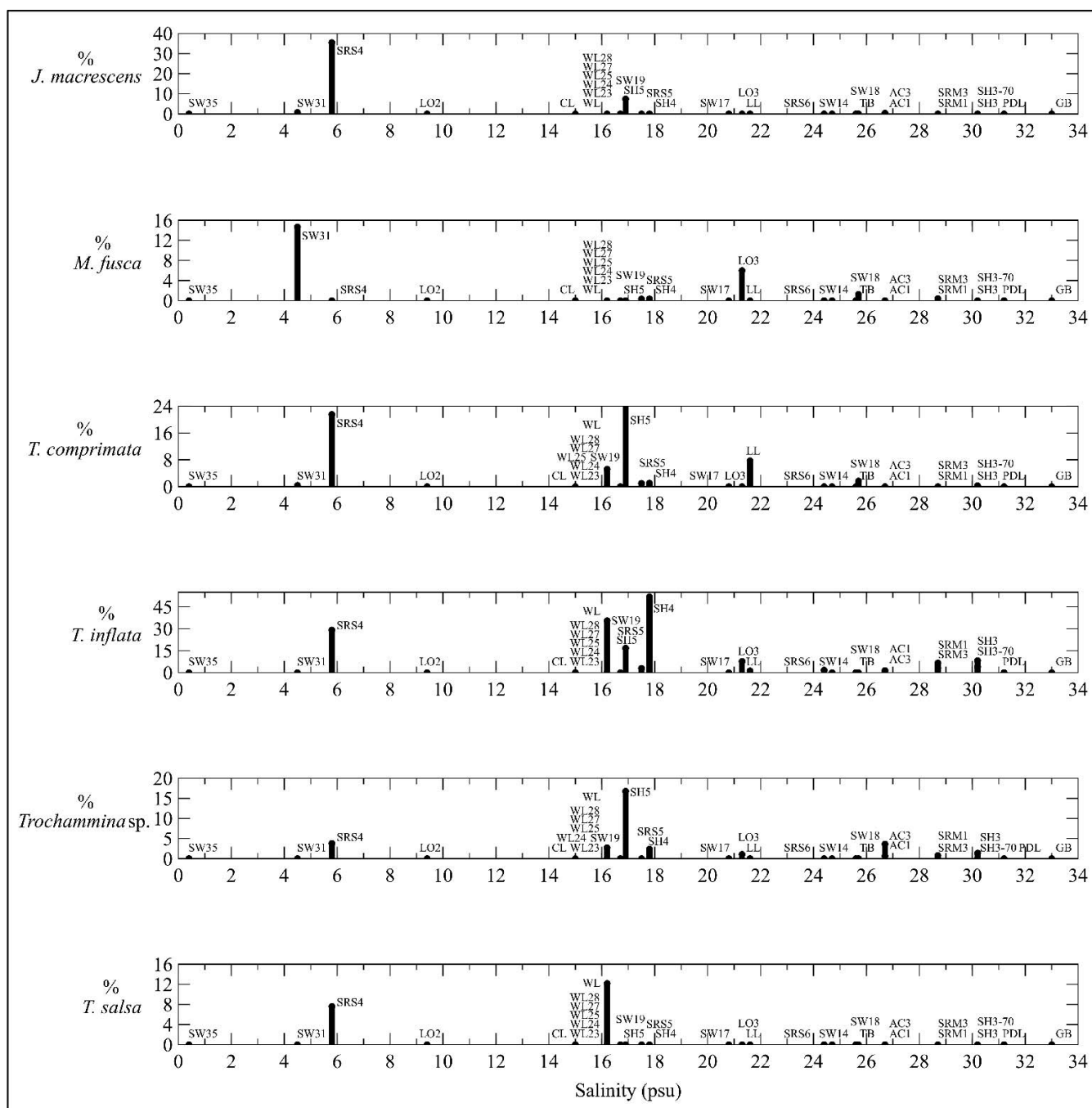FIGURE 9. Relative abundance of calcareous imperforate and agglutinated taxa with at least 1% contribution to observed differences between habitats, with salinity (psu).

dances of *T. aguayoi* and *Q. bosciana* are controlled by total phosphorus, however, this correlation is less strong or absent when only considering geographic area A (Fig. 1, Table 9). Therefore, we suspect it could be an additional factor controlling foraminiferal distributions.

TRANSPORTED SPECIMENS AND DATA OUTLIER

One obvious outlier 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).

As discussed below, either sediment or water containing *E. excavatum* tests might have been transported inland by tidal currents or a storm surge or *E. excavatum* individuals grew from a propagule bank, survived, and reproduced under very low salinity conditions.

Phleger (1970) observed that benthic foraminifera from marshes are regularly displaced from the habitat where they usually live. 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*

FIGURE 10. Relative abundance of agglutinated taxa with at least 1% contribution to observed differences between habitats, with salinity (psu).

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 but can be 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).

However, Everglades waters generally move with low energy, affected by weak tidal currents, so transport of foraminifera is probably minimal. The western coastline of

the Everglades, bordering the Gulf of Mexico, has semidiurnal 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
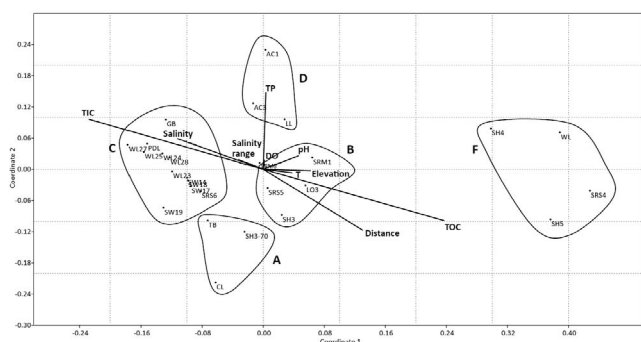
FIGURE 11. Two-dimensional ordination diagram of samples produced by NMDS using Bray-Curtis dissimilarity index. Lines originating from center are vectors representing direction and relative magnitude of correlation coefficients between each (environmental) variable and NMDS scores of samples. Encircled areas A–D and F refer to identified sample associations from Q-mode cluster analysis of Figure 3.

higher energy and speed to deposit storm layers far inland. For example, in 2005, Hurricane Wilma made landfall as a category 3 storm in the northwestern Everglades, producing water levels across the Shark River Estuary 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). The anomalously high abundance of *E. excavatum* at SW31 could have been caused by this storm.

Alternatively, through suspension in the water column, mainly dead 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. Alve (1995) defended 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 would be 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, although the frequency at which this occurs is unclear. 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. In their study on morphological and molecular characteristics of freshwater foraminifera, Siemensma et al. (2017), concluded that freshwater foraminifera only seem rare because of scarce recordings, though molecular data indicate a rich diversity. If the *E. excavatum* specimens were initially transported inland to site SW31, they might have survived to form a viable population.

Another possibility is that juveniles of *E. excavatum* were already present at site SW31 and were able to develop because local conditions became favorable. Goldstein & Alve (2011) demonstrated that very small juveniles, or propagules, of different species are typically present in 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 consisted mainly of *E. excavatum* (66%), *M. fusca* (15%), *A. tepida* (10%), and agglutinated species. Curiously, many species common at sites downstream of 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 ten measured environmental variables. We found eighty-two species belonging to 37 genera with 77% calcareous species, the majority of which belong to 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 TOC. 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 comprise combinations of *Helenina anderseni, Ammonia tepida, Haynesina depressula, Trochammina inflata,* and *Arenoparrella mexicana,* which all showed a preference for organic-rich sediments. Salinity and total phosphorus also played a role in spatial distribution. Salinity separates assemblages of purely agglutinated taxa from those consisting of a mix of agglutinated and calcareous taxa, and those that are purely calcareous assemblages. The lowest salinity preference of <15 psu was shown by *J. macrescens* and *M. fusca.* Other agglutinated taxa may occur at higher salinities; for example, *H. wilberti* occurred between 16–18 psu, as did *A. mexicana.* Of all agglutinated species, *A. mexicana* showed

TABLE 9. Multiple regression analysis results with 95% confidence of significant correlations (p<0.05) between environmental variables (explanatory variables; TOC = total organic carbon; TIC = total inorganic carbon; TP = total phosphorus; T = temperature; DO = dissolved oxygen) and individual taxa (dependent variable). Gray-colored table rows report results using the 15 samples from geographic area A (Fig. 1), and the other rows show results using data from all sampling locations (observations N = 27). Explanatory variables are listed with coefficients of determination (r^2) and probabilities (p), and inverse correlations are in bold. Regression statistics include multiple correlation coefficients (multiple r) and squared multiple correlation coefficients (multiple r^2). ANOVA significance tests for multiple regression list F statistic (F) and probabilities (p). Large F values indicate that null hypothesis (all regression coefficients are zero) can be rejected and p-values express chance of obtaining an F statistic of that value.

Taxa	Statistics	Salinity	Salinity Range	pH	TOC	TIC	TP	T	DO	Elevation	Distance	Regression Statistics		ANOVA	
Ammonia parkinsoniana	r^2	-	-	-	-	0.43	**0.02**	-	-	**0.24**	**0.23**	multiple r	0.96	F	20.74
	p	-	-	-	-	0.010	**0.017**	-	-	**<0.001**	**<0.001**	multiple r^2	0.92	p	<0.001
Ammonia parkinsoniana	r^2	-	-	-	-	0.59	**0.06**	-	-	-	0.14	multiple r	0.88	F	27.64
	p	-	-	-	-	<0.001	**<0.001**	-	-	-	0.011	multiple r^2	0.78	p	<0.001
Ammonia tepida	r^2	-	-	-	**0.23**	-	-	-	0.16	-	-	multiple r	0.77	F	8.78
	p	-	-	-	**0.004**	-	-	-	0.007	-	-	multiple r^2	0.59	p	0.004
Ammonia tepida	r^2	-	-	-	-	-	-	-	-	-	-	multiple r	-	F	-
	p	-	-	-	-	-	-	-	-	-	-	multiple r^2	-	p	-
Bisaccium imbricatum	r^2	-	-	0.04	**0.02**	-	-	0.39	-	0.06	0.06	multiple r	0.98	F	21.34
	p	-	-	0.040	**0.002**	-	-	<0.001	-	0.007	0.006	multiple r^2	0.96	p	<0.001
Bisaccium imbricatum	r^2	-	-	-	-	-	0.58	-	-	-	-	multiple r	0.82	F	25.5
	p	-	-	-	-	-	<0.001	-	-	-	-	multiple r^2	0.68	p	<0.001
Buccella hannai	r^2	-	-	**0.14**	0.10	0.19	-	-	0.14	**0.59**	0.14	multiple r	0.99	F	66.12
	p	-	-	**0.02**	0.003	0.002	-	-	0.004	**<0.001**	**<0.001**	multiple r^2	0.98	p	<0.001
Buccella hannai	r^2	-	**0.03**	-	-	-	0.75	-	**0.03**	-	-	multiple r	0.94	F	54.39
	p	-	**0.040**	-	-	-	<0.001	-	**<0.001**	-	-	multiple r^2	0.88	p	<0.001
Elphidium excavatum	r^2	-	-	-	-	0.50	-	0.27	-	-	0.30	multiple r	0.90	F	15.52
	p	-	-	-	-	0.009	-	0.028	-	-	0.003	multiple r^2	0.81	p	<0.001
Elphidium excavatum	r^2	-	-	-	**0.44**	-	0.03	-	-	-	-	multiple r	0.74	F	14.53
	p	-	-	-	**<0.001**	-	0.030	-	-	-	-	multiple r^2	0.55	p	<0.001
Elphidium discoidale	r^2	-	-	-	0.27	0.39	-	0.07	-	0.02	0.21	multiple r	0.94	F	10.71
	p	-	-	-	0.013	<0.001	-	0.008	-	0.003	0.028	multiple r^2	0.89	p	0.002
Elphidium discoidale	r^2	-	-	0.04	0.09	0.06	-	0.1	-	-	0.04	multiple r	0.73	F	3.69
	p	-	-	0.03	0.033	0.008	-	0.006	-	-	0.004	multiple r^2	0.53	p	0.012
Elphidium galvestonense	r^2	-	-	-	**0.22**	-	-	-	0.04	-	-	multiple r	0.75	F	4.84
	p	-	-	-	**0.004**	-	-	-	0.025	-	-	multiple r^2	0.57	p	0.022
Elphidium galvestonense	r^2	-	0.37	-	-	-	-	-	-	-	-	multiple r	0.61	F	14.45
	p	-	0.001	-	-	-	-	-	-	-	-	multiple r^2	0.37	p	0.001
Elphidium koeboeense	r^2	-	-	-	**0.04**	-	-	-	-	-	0.32	multiple r	0.83	F	13.06
	p	-	-	-	**0.003**	-	-	-	-	-	<0.001	multiple r^2	0.69	p	0.001
Elphidium koeboeense	r^2	0.03	0.05	-	-	0.14	-	**0.01**	-	-	0.17	multiple r	0.80	F	7.22
	p	0.012	0.022	-	-	0.001	-	**0.007**	-	-	<0.001	multiple r^2	0.63	p	<0.001
Elphidium matagordanum	r^2	-	-	-	-	0.29	-	-	-	-	-	multiple r	0.54	F	5.37
	p	-	-	-	-	0.037	-	-	-	-	-	multiple r^2	0.29	p	0.037
Elphidium matagordanum	r^2	-	-	-	-	0.24	-	-	-	-	-	multiple r	0.49	F	8.01
	p	-	-	-	-	0.009	-	-	-	-	-	multiple r^2	0.24	p	0.009
Elphidium mexicanum	r^2	-	-	-	-	0.28	-	-	-	-	-	multiple r	0.53	F	5.16
	p	-	-	-	-	0.041	-	-	-	-	-	multiple r^2	0.28	p	0.041

TABLE 9. Continued

Taxa	Statistics	Salinity	Salinity Range	pH	TOC	TIC	TP	T	DO	Elevation	Distance	Regression Statistics		ANOVA	
Elphidium mexicanum	r^2	-	-	-	-	0.17	-	-	-	-	-	multiple r	0.42	F	5.26
	p	-	-	-	-	0.030	-	-	-	-	-	multiple r^2	0.17	p	0.030
Elphidium morenoi	r^2	-	0.43	-	-	0.45	-	-	-	-	-	multiple r	0.88	F	21.09
	p	-	0.001	-	-	0.001	-	-	-	-	-	multiple r^2	0.78	p	<0.001
Elphidium morenoi	r^2	-	-	-	-	-	-	-	-	-	-	multiple r	-	F	-
	p	-	-	-	-	-	-	-	-	-	-	multiple r^2	-	p	-
Elphidium simplex	r^2	-	-	-	-	-	-	-	-	-	-	multiple r	-	F	-
	p	-	-	-	-	-	-	-	-	-	-	multiple r^2	-	p	-
Elphidium simplex	r^2	-	-	-	**0.02**	**0.04**	-	-	-	-	-	multiple r	0.58	F	6.17
	p	-	-	-	**0.003**	**0.002**	-	-	-	-	-	multiple r^2	0.34	p	0.007
Haynesina depressula	r^2	-	-	-	-	-	-	-	-	-	-	multiple r	-	F	-
	p	-	-	-	-	-	-	-	-	-	-	multiple r^2	-	p	-
Haynesina depressula	r^2	-	-	-	-	-	-	-	-	-	-	multiple r	-	F	-
	p	-	-	-	-	-	-	-	-	-	-	multiple r^2	-	p	-
Helenina anderseni	r^2	-	-	-	-	-	-	-	-	-	-	multiple r	-	F	-
	p	-	-	-	-	-	-	-	-	-	-	multiple r^2	-	p	-
Helenina anderseni	r^2	-	-	-	-	**0.10**	-	-	-	-	-	multiple r	0.50	F	4.10
	p	-	-	-	-	**0.009**	-	-	-	-	-	multiple r^2	0.25	p	0.029
Trichohyalus aguayoi	r^2	-	-	-	-	-	-	-	-	-	-	multiple r	-	F	-
	p	-	-	-	-	-	-	-	-	-	-	multiple r^2	-	p	-
Trichohyalus aguayoi	r^2	0.04	-	-	0.02	-	0.18	**0.01**	-	-	-	multiple r	0.68	F	4.62
	p	0.028	-	-	0.028	-	0.002	**0.014**	-	-	-	multiple r^2	0.46	p	0.007
Biloculinella eburnea	r^2	-	-	-	**0.01**	**0.11**	-	-	-	-	-	multiple r	0.70	F	5.72
	p	-	-	-	**0.011**	**0.006**	-	-	-	-	-	multiple r^2	0.49	p	0.018
Biloculinella eburnea	r^2	-	-	-	-	-	-	-	-	-	-	multiple r	-	F	-
	p	-	-	-	-	-	-	-	-	-	-	multiple r^2	-	p	-
Cornuspira involvens	r^2	0.14	-	-	-	**0.12**	-	-	0.10	-	-	multiple r	0.76	F	4.96
	p	0.024	-	-	-	**0.014**	-	-	0.029	-	-	multiple r^2	0.58	p	0.020
Cornuspira involvens	r^2	-	-	-	-	**0.09**	-	-	-	-	-	multiple r	0.67	F	9.57
	p	-	-	-	-	**<0.001**	-	-	-	-	-	multiple r^2	0.44	p	<0.001
Miliolinella microstoma	r^2	-	-	-	-	-	-	-	-	-	-	multiple r	-	F	-
	p	-	-	-	-	-	-	-	-	-	-	multiple r^2	-	p	-
Miliolinella microstoma	r^2	-	-	-	-	-	-	-	-	-	-	multiple r	-	F	-
	p	-	-	-	-	-	-	-	-	-	-	multiple r^2	-	p	-
Quinqueloculina bosciana	r^2	-	-	-	-	-	0.15	**0.27**	-	-	-	multiple r	0.71	F	5.98
	p	-	-	-	-	-	0.039	**0.014**	-	-	-	multiple r^2	0.50	p	0.016
Quinqueloculina bosciana	r^2	-	-	-	-	-	0.34	-	-	-	-	multiple r	0.67	F	9.69
	p	-	-	-	-	-	<0.001	-	-	-	-	multiple r^2	0.45	p	<0.001
Quinqueloculina seminulum	r^2	-	-	-	-	-	-	-	-	-	-	multiple r	-	F	-
	p	-	-	-	-	-	-	-	-	-	-	multiple r^2	-	p	-
Quinqueloculina seminulum	r^2	-	-	-	-	-	-	-	-	-	-	multiple r	-	F	-
	p	-	-	-	-	-	-	-	-	-	-	multiple r^2	-	p	-

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TABLE 9. Continued

| Taxa	Statistics	Salinity	Salinity Range	pH	TOC	TIC	TP	T	DO	Elevation	Distance	Regression Statistics		ANOVA	
***Quinqueloculina* sp.**	r²	0.01	-	-	-	-	-	-	0.19	-	0.18	multiple r	0.83	F	7.90
	p	0.010	-	-	-	-	-	-	0.008	-	0.002	multiple r²	0.68	p	0.004
Quinqueloculina sp.	r²	-	-	-	-	-	0.18	-	-	-	-	multiple r	0.43	F	5.64
	p	-	-	-	-	-	0.026	-	-	-	-	multiple r²	0.18	p	0.026
***Triloculina* sp.**	r²	-	-	-	-	-	-	-	-	-	0.30	multiple r	0.54	F	5.47
	p	-	-	-	-	-	-	-	-	-	0.036	multiple r²	0.30	p	0.036
Triloculina sp.	r²	-	-	-	-	-	0.26	-	-	-	-	multiple r	0.51	F	8.79
	p	-	-	-	-	-	0.007	-	-	-	-	multiple r²	0.26	p	0.007
Arenoparrella mexicana	r²	-	-	-	-	**0.38**	0.15	-	-	-	-	multiple r	0.78	F	9.40
	p	-	-	-	-	**0.003**	0.020	-	-	-	-	multiple r²	0.61	p	0.003
Arenoparrella mexicana	r²	-	-	-	-	**0.31**	-	-	-	-	-	multiple r	0.56	F	11.37
	p	-	-	-	-	**0.002**	-	-	-	-	-	multiple r²	0.31	p	0.002
Haplophragmoides wilberti	r²	-	-	-	-	-	-	-	-	-	-	multiple r	-	F	-
	p	-	-	-	-	-	-	-	-	-	-	multiple r²	-	p	-
Haplophragmoides wilberti	r²	**0.04**	-	**0.06**	-	-	-	-	-	0.04	-	multiple r	0.59	F	2.97
	p	**0.022**	-	**0.008**	-	-	-	-	-	0.033	-	multiple r²	0.35	p	0.042
Jadammina macrescens	r²	**0.51**	-	-	-	-	-	-	-	-	-	multiple r	0.71	F	13.37
	p	**0.003**	-	-	-	-	-	-	-	-	-	multiple r²	0.51	p	0.003
Jadammina macrescens	r²	**0.26**	-	-	-	-	-	0.02	-	-	-	multiple r	0.69	F	11.20
	p	**<0.001**	-	-	-	-	-	0.004	-	-	-	multiple r²	0.48	p	<0.001
Miliammina fusca	r²	-	-	0.05	**0.01**	-	-	**0.37**	-	**0.07**	**0.06**	multiple r	0.97	F	19.11
	p	-	-	0.031	**0.002**	-	-	**<0.001**	-	**0.008**	**0.007**	multiple r²	0.95	p	<0.001
Miliammina fusca	r²	-	-	-	-	-	-	-	-	-	-	multiple r	-	F	-
	p	-	-	-	-	-	-	-	-	-	-	multiple r²	-	p	-
Tiphotrocha comprimata	r²	-	-	-	0.59	0.20	**0.06**	-	0.04	-	-	multiple r	0.92	F	10.58
	p	-	-	-	<0.001	0.013	**0.007**	-	0.009	-	-	multiple r²	0.85	p	0.001
Tiphotrocha comprimata	r²	-	-	-	0.43	-	-	-	-	-	-	multiple r	0.65	F	18.52
	p	-	-	-	<0.001	-	-	-	-	-	-	multiple r²	0.43	p	<0.001
Trochammina inflata	r²	-	0.01	0.02	0.69	-	0.03	**0.05**	0.02	-	**0.14**	multiple r	0.98	F	22.59
	p	-	0.029	0.017	0.001	-	0.003	**0.011**	0.002	-	**0.020**	multiple r²	0.97	p	<0.001
Trochammina inflata	r²	-	**0.03**	0.02	0.40	-	-	-	-	-	-	multiple r	0.73	F	8.77
	p	-	**0.039**	0.045	<0.001	-	-	-	-	-	-	multiple r²	0.53	p	<0.001
***Trochammina* sp.**	r²	-	-	-	0.42	-	-	-	-	-	-	multiple r	0.65	F	9.59
	p	-	-	-	0.009	-	-	-	-	-	-	multiple r²	0.42	p	0.009
Trochammina sp.	r²	0.05	-	0.01	-	-	-	0.02	-	0.04	-	multiple r	0.63	F	3.63
	p	0.005	-	0.010	-	-	-	0.005	-	0.031	-	multiple r²	0.40	p	0.020
Trochamminita salsa	r²	**0.45**	-	-	-	-	-	-	-	-	-	multiple r	0.67	F	10.53
	p	**0.006**	-	-	-	-	-	-	-	-	-	multiple r²	0.45	p	0.006
Trochamminita salsa	r²	**0.17**	-	-	-	-	-	-	-	-	-	multiple r	0.41	F	4.95
	p	**0.035**	-	-	-	-	-	-	-	-	-	multiple r²	0.17	p	0.035
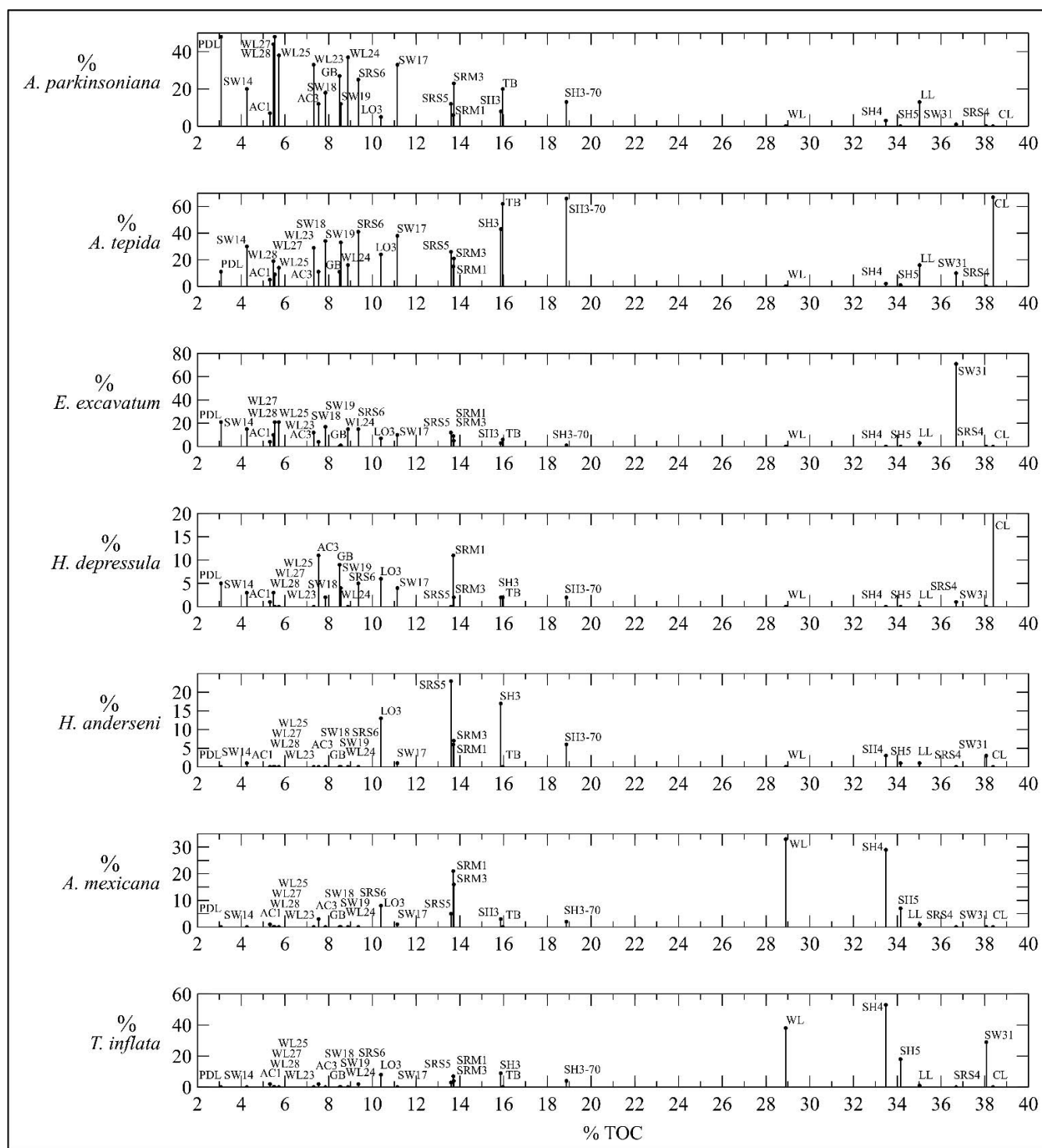
FIGURE 12.   Relative abundance of taxa common in organic-rich sediments, with percentage of total organic carbon (TOC) of sediment.

the highest salinity preference with a second, but lower abundance peak at 28–30 psu. *Ammonia tepida* and *A. parkinsoniana* occured abundantly over the widest range of salinities, above 15 psu. *Elphidium* spp. and other calcareous taxa prefer salinities above 20 psu. Additionally, total phosphorus may be a significant control on foraminiferal distribution, as

illustrated by the high positive correlations between *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 useful for predictions of coastal behavior and particularly important for monitoring environmental change in vulnerable ecosystems close to expanding coastal populations such as in the South Florida Everglades.

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REFERENCES

Alve, E., 1995, Benthic foraminiferal distribution and recolonization of formerly anoxic environments in Drammensfjord, southern Norway: Marine Micropaleontology, v. 25, p. 169–186.

Armstrong, H. A., and Brasier, M. D., 2005, Foraminifera, in Armstrong, H. A. and Brasier, M. D. (eds.), Microfossils (2nd edition): Blackwell Publishing Ltd, Singapore, p. 142–187.

Armynot du Chatelet, E., Recourt, P., Chopin, V., 2008, Mineralogy of agglutinated benthic foraminifera; implications for paleoenvironmental reconstructions: Bulletin de la Société Géologique de France, v. 179, p. 583–592.

Avnaim-Katav, S., Gehrels, W. R., Brown, L. N., Fard, E., and Mac-Donald, G. M., 2017, Distributions of salt-marsh foraminifera along the coast of SW California, USA: Implications for sea-level reconstructions: Marine Micropaleontology, v. 131, p. 25–43.

Barbosa, C. F., Scott, D. B., Seoane, J. C., and Turcq, B. J., 2005, Foraminiferal zonations as base lines for Quaternary sea-level fluctuations in south-southeast Brazilian mangroves and marshes: Journal of Foraminiferal Research, v. 35, p. 22–43.

Benda, W. K., and Puri, H. S., 1962, The distribution of foraminifera and ostracoda off the Gulf Coast of the Cape Romano area, Florida: Gulf Coast Association of Geological Societies, v. 12, p. 303–341.

Berger, W. H., and Parker, F. L., 1970, Diversity of planktonic foraminifera in deep-sea sediments: Science, v. 168, p. 1345–1347.

Berkeley, A., Perry, C. T., Smithers, S. G., and Horton, B. P., 2008, The spatial and vertical distribution of living (stained) benthic foraminifera from a tropical, intertidal environment, north Queensland, Australia: Marine Micropaleontology, v. 69, p. 240–261.

Bock, W., and Gebelein, C. D., 1977, Dynamics of Recent Carbonate Sedimentation and Ecology, Cape Sable, Florida: E. J. Brill, Leiden, The Netherlands, 120 p.

Boltovskoy, E., 1984, Foraminifera of mangrove swamps: Physis, Secciones A, v. 42, p. 1–9.

Boltovskoy, E., and Lena, H., 1971, The foraminifera (except family Allogromiidae) which dwell in fresh water: Journal of Foraminiferal Research, v. 1, p. 71–76.

Brady, G. S., and Robertson, D., 1870, The Ostracoda and Foraminifera of Tidal Rivers. With an analysis and descriptions of the Foraminifera by Brady, H. B.: Annals and Magazine of Natural History, v. 6, p. 1–33.

Bray, J. R., and Curtis, J. T., 1957, An ordination of the upland forest communities of southern Wisconsin: Ecological Monographs, v. 27, p. 325–349.

Briceño, H., Miller, G., and Davis, S. E., 2014, Relating freshwater flow with estuarine water quality in the Southern Everglades mangrove ecotone: Wetlands, v. 34, p. 101–111.

Buzas, M. A., Culver, S. J., and Isham, L. B., 1985, A comparison of fourteen elphidiid (Foraminiferida) taxa: Journal of Paleontology, v. 59, p. 1075–1090.

Buzas-Stephens, P., Pessagno, E. A., and Bowen, C. J., 2002, A review of species names for Ammonia and Elphidium, common foraminifera along the Texas Gulf Coast: The Texas Journal of Science, v. 54, p. 3–16.

Castañeda-Moya, E., Twilley, R. R., Rivera-Monroy, V. H., Zhang, K., Davis, S. E., and Ross, M., 2010, Sediment and nutrient deposition associated with Hurricane Wilma in mangroves of the Florida Coastal Everglades: Estuaries and Coasts, v. 33, p. 45–58.

Castañeda-Moya, E., Twilley, R. R., and Rivera-Monroy, V. H., 2013, Allocation of biomass and net primary productivity of mangrove forests along environmental gradients in the Florida Coastal Everglades, USA: Forest Ecology and Management, v. 307, p. 226–241.

Chambers, R. M., and Pederson, K. A., 2006, Variation in soil phosphorus, sulfur, and iron pools among south Florida wetlands: Hydrobiologia, v. 569, p. 63–70.

Chen, R., and Twilley, R. R., 1999, Patterns of mangrove forest structure and soil nutrient dynamics along the Shark River Estuary, Florida: Estuaries, v. 22, p. 955–970.

Cheng, J., Collins, L. S., and Holmes, C., 2012, Four thousand years of habitat change in Florida Bay, as indicated by benthic foraminifera: Journal of Foraminiferal Research, v. 42, p. 3–17.

Childers, D. L., Boyer, J. N., Davis, S. E., Madden, C. J., Rudnick, D. T., and Sklar, F. H., 2006, Relating precipitation and water management to nutrient concentrations in the oligotrophic "upside-down" estuaries of the Florida Everglades: Limnology and Oceanography, v. 51, p. 602–616.

Clarke, K. R., 1993, Non-parametric multivariate analyses of changes in community structure: Australian Journal of Ecology, v. 18, p. 117–143.

Culver, S. J., 1990, Benthic foraminifera of Puerto Rican mangrove-lagoon systems: Potential for paleoenvironmental interpretations: Palaios, v. 5, p. 34–51.

Culver, S. J., Mallinson, D. J., Corbett, D. R., Leorri, E., Rouf, A. A., Shazili, N. A. M., Yaacob, R., Whittaker, J. E., Buzas, M. A. and Parham, P. R., 2012, Distribution of foraminifera in the Setiu estuary and lagoon, Terengganu, Malaysia: Journal of Foraminiferal Research, v. 42, p. 109–133.

Culver, S. J., Leorri, E., Corbett, D. R., Mallinson, D. J., Shazili, N. A. M., Mohammad, M. N., Parham, P. R., and Yaacob, R., 2013, Infaunal mangrove swamp foraminifera in the Setiu wetland, Terengganu, Malaysia: Journal of Foraminiferal Research, v. 43, p. 262–279.

Debenay, J. P., and Guillou, J. J., 2002, Ecological transitions indicated by foraminiferal assemblages in paralic environments: Estuaries, v. 25, p. 1107–1120.

Debenay, J. P., Eichler, B. B., Duleba, W., Bonetti, C., and Eichler-Coelho, P., 1998, Water stratification in coastal lagoons: Its influence on foraminiferal assemblages in two Brazilian lagoons: Marine Micropaleontology, v. 35, p. 67–89.

Debenay, J. P., Guiral, D., and Parra, M., 2002, Ecological factors acting on the microfauna in mangrove swamps. The case of foraminiferal assemblages in French Guiana: Estuarine, Coastal and Shelf Science, v. 55, p. 509–533.

Debenay, J. P., Guiral, D., and Parra, M., 2004, Behaviour and taphonomic loss in foraminiferal assemblages of mangrove swamps of French Guiana: Marine Geology, v. 208, p. 295–314.

de Rijk, S., 1995, Salinity control on the distribution of salt marsh foraminifera (Great Marshes, Massachusetts): Journal of Foraminiferal Research, v. 25, p. 156–166.

de Rijk, S., and Troelstra, S. R., 1997, Salt marsh foraminifera from the Great Marshes, Massachusetts: Environmental controls: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 130, p. 81–112.

Dubicka, Z., Złotnik, M., and Borszcz, T., 2015, Test morphology as a function of behavioral strategies—Inferences from benthic foraminifera: Marine Micropaleontology, v. 116, p. 38–49.

Fatela, F., Moreno, J., Moreno, F., Araujo, M. F., Valente, T., Antunes, C., Taborda, R., Andrade, C., and Drago, T., 2009, Environmental constraints of foraminiferal assemblages distribution across a brackish tidal marsh (Caminha, NW Portugal): Marine Micropaleontology, v. 70, p. 70–88.

Goldstein, S. T., 1976, The distribution and ecology of benthic foraminifera in South Florida mangrove environment: Unpublished M.S. thesis, University of Florida, Gainesville, Florida, 111 p.

Goldstein, S. T., 1988, Foraminifera of relict salt marsh deposits, St. Catherines Island, Georgia: Taphonomic implications: Palaios, v. 3, p. 327–334.

Goldstein, S. T., and Alve, E., 2011, Experimental assembly of foraminiferal communities from coastal propagule banks: Marine Ecology Progress Series, v. 437, p. 1–11.

Gregory, M. R., 1973, Benthonic foraminifera from a mangrove swamp, Whangaparapara, Great Barrier Island: Tane, Auckland, v. 19, p. 193–203.

Guilbault, J. P., and Patterson, R. T., 2000, Correlation between marsh foraminiferal distribution and elevation in coastal British Columbia, Canada, in Hart, M. B., Kaminski, M. A., and Smart, C. W. (eds.), Proceedings of the Fifth International Workshop on Agglutinated Foraminifera: Grzybowski Foundation Special Publication 7, p. 117–125.

Hammer, Ø., Harper, D. A. T., and Ryan, P. D., 2001, PAST: Paleontological statistics software package for education and data analysis: Palaeontologia Electronica, v. 4, p. 1–9.

Hayek, L. A. C., and Buzas, M. A., 2013, On the proper and efficient use of diversity measures with individual field samples: Journal of Foraminiferal Research, v. 43, p. 305–313.

Hayward, B. W., and Hollis, C. J., 1994, Brackish foraminifera in New Zealand; a taxonomic and ecologic review: Micropaleontology, v. 40, p. 185–222.

Hayward, B. W., Grenfell, H., Cairns, G., and Smith, A., 1996, Environmental controls on benthic foraminiferal and thecamoebian associations in a New Zealand tidal inlet: Journal of Foraminiferal Research, v. 26, p. 150–171.

Horton, B. P., 1999, The distribution of contemporary intertidal foraminifera at Cowpen Marsh, Tees Estuary, UK: Implications for studies of Holocene sea-level changes: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 149, p. 127–149.

Horton, B. P., and Murray, J. W., 2007, The roles of elevation and salinity as primary controls on living foraminiferal distributions: Cowpen Marsh, Tees Estuary, UK: Marine Micropaleontology, v. 63, p. 169–186.

Horton, B. P., Larcombe, P., Woodroffe, S. A., Whittaker, J. E., Wright, M. R., and Wynn, C., 2003, Contemporary foraminiferal distributions of a mangrove environment, Great Barrier Reef coastline, Australia: Implications for sea-level reconstructions: Marine Geology, v. 198, p. 225–243.

Javaux, E. J., and Scott, D. B., 2003, Illustration of modern benthic foraminifera from Bermuda and remarks on distribution in other subtropical/tropical areas: Palaeontologia Electronica, v. 6, p. 1–29.

Jones, J. I., and Bock, W. D., 1971, A Symposium of Recent South Florida Foraminifera: Miami Geological Society, Miami, Florida, 245 p.

Jorissen, F. J., 1999, Benthic foraminiferal microhabitats below the sediment-water interface, in Sen Gupta, B. K. (ed.), Modern Foraminifera: Springer, Dordrecht, The Netherlands, p. 161–179.

Kemp, A. C., Horton, B. P., and Culver, S. J., 2009, Distribution of modern salt-marsh foraminifera in the Albemarle–Pamlico estuarine system of North Carolina, USA: Implications for sea-level research: Marine Micropaleontology, v. 72, p. 222–238.

Kemp, A. C., Buzas, M. A., Horton, B. P., and Culver, S. J., 2011, Influence of patchiness on modern salt-marsh foraminifera used in sea-level studies (North Carolina, USA): Journal of Foraminiferal Research, v. 41, p. 114–123.

Linke, P., and Lutze, G. F., 1993, Microhabitat preferences of benthic foraminifera—a static concept or a dynamic adaptation to optimize food acquisition?: Marine Micropaleontology, v. 20, p. 215–234.

Milker, Y., Horton, B. P., Nelson, A. R., Engelhart, S. E., and Witter, R. C., 2015, Variability of intertidal foraminiferal assemblages in a salt marsh, Oregon, USA: Marine Micropaleontology, v. 118, p. 1–16.

Miller, A. A., Scott, D. B., and Medioli, F. S., 1982, *Elphidium excavatum* (Terquem): Ecophenotypic versus subspecific variation: Journal of Foraminiferal Research, v. 12, p. 116–144.

Murray, J. W., 1973, Distribution and Ecology of Living Benthic Foraminiferids: Crane, Russak & Company, Inc., New York, 274 p.

Murray, J. W., Sturrock, S., and Weston, J., 1982, Suspended load transport of foraminiferal tests in a tide-and wave-swept sea: Journal of Foraminiferal Research, v. 12, p. 51–65.

Murray, J. W., 1991, Ecology and Palaeoecology of Benthic Foraminifera: Longman Scientific & Technical, New York, 397 p.

Parker, F. L., Phleger, F. B., and Peirson, J. F., 1953, Ecology of foraminifera from San Antonio Bay and environs, southwest Texas: Cushman Foundation for Foraminiferal Research, Special Publication No. 2, p. 1–67.

Parkinson, R. W., 1989, Decelerating Holocene sea-level rise and its influence on Southwest Florida coastal evolution; a transgressive/regressive stratigraphy: Journal of Sedimentary Research, v. 59, p. 960–972.

Parry, M. L., Canziani, O., Palutikof, J., Van der Linden, P., and Hanson, C., 2007, Climate Change 2007: Impacts, adaptation and vulnerability. Contribution of Working group II to the fourth assessment report of the IPCC: Cambridge University Press, Cambridge, UK, 982 p.

Patterson, R. T., 1990, Intertidal benthic foraminiferal biofacies on the Fraser River Delta, British Columbia: Modern distribution and paleoecological importance: Micropaleontology, v. 36, p. 229–244.

Patterson, R. T., Gehrels, W. R., Belknap, D. F., and Dalby, A. P., 2004, The distribution of salt marsh foraminifera at Little Dipper Harbour, New Brunswick, Canada: Implications for development of widely applicable transfer functions in sea-level research: Quaternary International, v. 120, p. 185–194.

Phleger, F. B., 1965, Living foraminifera from coastal marsh, southwestern Florida: Boletín de la Sociedad Geológica Mexicana, v. 28, p. 45–60.

Phleger, F. B., 1970, Foraminiferal populations and marine marsh processes: Limnology and Oceanography, v. 15, p. 522–534.

Price, R. M., Swart, P. K., and Fourqurean, J. W., 2006, Coastal groundwater discharge–an additional source of phosphorus for the oligotrophic wetlands of the Everglades: Hydrobiologia, v. 569, p. 23–36.

Price, R. M., Savabi, M. R., Jolicoeur, J. L., and Roy, S., 2010, Adsorption and desorption of phosphate on limestone in experiments simulating seawater intrusion: Applied Geochemistry, v. 25, p. 1085–1091.

Pytkowicz, R. M., 1969, Chemical solution of calcium carbonate in sea water: American Zoologist, v. 9, p. 673–679.

Saunders, J. B., 1957, Trochamminidae and certain Lituolidae (Foraminifera) from the recent brackish-water sediments of Trinidad, British West Indies: Smithsonian Miscellaneous Collections, v. 134, p. 1–20.

Saunders, J. B., 1958, Recent foraminifera of mangrove swamps and river estuaries and their fossil counterparts in Trinidad: Micropaleontology, v. 4, p. 79–92.

Scott, D. B., and Medioli, F. S., 1980, Living vs. total foraminiferal populations: Their relative usefulness in paleoecology: Journal of Paleontology, v. 54, p. 814–831.

Sen Gupta, B. K., 1999, Foraminifera in marginal marine environments, in Sen Gupta, B. K. (ed.), Modern Foraminifera: Springer, Dordrecht, The Netherlands, p. 141–159.

Sen Gupta, B. K., Smith, L. E., and Machain-Castillo, M. L., 2009, Foraminifera of the Gulf of Mexico, in Felder, D. L., and Camp, D. K. (eds.), Gulf of Mexico – Origins, Waters, and Biota: Volume 1, Biodiversity: Texas A&M University Press, College Station, Texas, p. 87–129.

Shannon, C. E., 1948, The mathematical theory of communication: Bell System Technical Journal, v. 27, p. 379–423.

Siemensma, F., Apothéloz-Perret-Gentil, L., Holzmann, M., Clauss, S., Völcker, E., and Pawlowski, J., 2017, Taxonomic revision of freshwater foraminifera with the description of two new agglutinated species and genera: European Journal of Protistology, v. 60, p. 28–44.

Spencer, R. S., 2000, Foraminiferal assemblages from a Virginia salt marsh, Phillips Creek, Virginia: Journal of Foraminiferal Research, v. 30, p. 143–155.

Verlaak, Z. R. F., Collins, L. S., and Hayek, C. L. A., 2019, Effects of Infaunal Foraminifera on Surface and Subsurface Assemblages in the Southwestern Everglades, USA: Baseline Study for Paleoenvironmental Analyses: SEPM Special Publication, No. 111, p. 3–14.

Wachnicka, A., Gaiser, E., Collins, L. S., Frankovich, T., and Boyer, J., 2010, Distribution of diatoms and development of diatom-based models for inferring salinity and nutrient concentrations in Florida Bay and adjacent coastal wetlands of South Florida (USA): Estuaries and Coasts, v. 33, p. 1080–1098.

Wang, P., and Chappell, J., 2001, Foraminifera as Holocene environmental indicators in the South Alligator River, northern Australia: Quaternary International, v. 83, p. 47–62.

Wantland, K. F., 1967, Recent benthonic foraminifera of the British Honduras shelf: Unpublished Ph.D. dissertation, Rice University, Houston, Texas, 300 p.

Warren, A. D., 1957, Foraminifera of the Buras-Scofield Bayou region, southeast Louisiana: Contributions from the Cushman Foundation for Foraminiferal Research, v. 8, p. 29–40.

Williams, H. F. L., 1994, Intertidal benthic foraminiferal biofacies on the central Gulf Coast of Texas: Modern distribution and application to sea level reconstruction: Micropaleontology, v. 40, p. 169–183.

Woodroffe, S. A., Horton, B. P., Larcombe, P., and Whittaker, J. E., 2005, Intertidal mangrove foraminifera from the central Great Barrier Reef shelf, Australia: Implications for sea-level reconstruction: Journal of Foraminiferal Research, v. 35, p. 259–270.

Zaninetti, L., 1977, La mangrove de Guaratiba et la baie de Sepetiba, état de Rio de Janeiro, Brésil: Foraminifères et écologie: Archives des Sciences, v. 30, p. 161–178.

Zaninetti, L., Brönnimann, P., Dias-Brito, D., Arai, M., Casaletti, P., Koutsoukos, E., and Silveira, S., 1979, Distribution écologique des foraminifères dans la mangrove d'Acupe, État de Bahia, Brésil: Note du Laboratoire de Paleontologie de l'Uniste de Geneve, v. 4, p. 1–17.