INFAUNAL MARSH FORAMINIFERA FROM THE OUTER BANKS, NORTH CAROLINA, U.S.A.

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ABSTRACT

The distribution and abundance patterns of live (rose Bengal stained) and dead, shallow infaunal (0–1 cm depth) and deep infaunal (>1 cm depth) benthic foraminifera have been documented at three locations representing different salinity settings on the fringing marshes along the Pamlico Sound and Currituck Sound coasts of North Carolina's Outer Banks. Two cores taken at each site represent the lower and higher marsh.

Twenty-two taxa were recorded as live. Of these, eight taxa were found only at shallow infaunal depths; the other 14 taxa occur at deep infaunal depths in one or more cores. Only *Jadammina macrescens* and *Tiphotrocha comprimata* were recorded as living in all six cores. The distributions of the other taxa were restricted by combinations of the criteria of infaunal depth, salinity regime and location on the marsh.

The tests of infaunal foraminifera were generally more likely to be preserved in the lower marsh than the higher marsh at low- and intermediate-salinity sites. The opposite pattern was evident at the high-salinity site but this may be due to the low numbers of deep infaunal specimens recovered. *Arenoparrella mexicana*, *Haplophragmoides wilberti*, *Jadammina macrescens* and *Trochammina inflata* are the most resistant taxa, whereas *Miliammina fusca* is the species whose tests are most likely to be lost to post-mortem degradation. In five of six cores, foraminiferal assemblages and populations do not differ significantly with depth which suggests that the foraminifera of the 0–1 cm depth interval provide an adequate model upon which paleoenvironmental (including former sea level) reconstructions can be based.

INTRODUCTION

Salt marsh foraminifera are known to live infaunally (see Goldstein and others, 1995, for a brief summary). They have been recorded "live" (i.e., rose Bengal stained) as deep as 60 cm in marsh sediments from Delaware, although they were particularly abundant in the top 20 cm of sediment (Hippensteel and others, 2000). Goldstein and Harben (1993) and Goldstein and others (1995) reported living foraminifera at 30 cm depth in Georgia marshes, probably as the result of bioturbation; most living foraminifera were in the top 5 cm of marsh sediment (Goldstein and others, 1995; Goldstein and Watkins, 1998). Ozarko and others (1997) and Patterson and others (1999) found abundant live foraminifera in the top 10 cm of sediment of cores from British Columbia, whereas Akers (1971) found stained foraminifera down to 30–35 cm below the marsh surface at Beaufort, North Carolina. The deepest records of living marsh foraminifera were noted by Saffert and Thomas (1998) at 50 cm in New England and at 60 cm by Hippensteel and others (2000) in Delaware salt marshes. In contrast, studies on the Atlantic coast of northwestern Europe have documented live infaunal marsh foraminifera mainly in the top 3 cm of sediment (Horton, 1997; Horton and Edwards, in press a). Clearly, the depth at which marsh foraminifera live in the sediment varies considerably from location to location (and, probably, from time to time), presumably due to local environmental conditions and chance bioturbation.

Abundance and distribution patterns of infaunal marsh foraminifera are of importance because marsh foraminiferal zonations, constructed from surficial (0–1 cm) samples, have been utilized widely for the past 25 years in sea level reconstructions (e.g., Scott and Medioli, 1978, 1986; Horton, 1999; Horton and others, 1999a, b, 2000, 2003; Edwards and Horton, 2000; Scott and others, 2001; Gehrels, 2002; Horton and Edwards, 2003, in press; Edwards and others, 2004). If infaunal foraminiferal populations are different taxonomically from those in surficial samples, or if infaunal populations are taxonomically similar to surficial ones but infaunal abundances are considerable or variable across the intertidal zone, then the reconstruction of former sea levels based upon foraminiferal assemblages can be a more complex endeavor. For example, if a sample taken at 10 cm depth in a salt marsh peat core contains a mixture of fossil *Miliammina fusca* (that lived when the sample of peat in which they occur was accumulating at the surface of a marsh) and *Jadammina macrescens* (that is living infaunally at 10 cm depth), then the sample (if the mixed nature of the assemblage is not recognized) could be interpreted as representing a high-low marsh transition (*M. fusca* is generally agreed to indicate a low marsh and *J. macrescens* a high marsh; see, for example, Scott and Medioli, 1978). The correct interpretation would be low marsh because the sample contains two temporally distinct groups of specimens that should not be treated as coeval. Further, as pointed out by Goldstein and Harben (1993), foraminifera that live infaunally may become numerically "enriched" through time compared to species that are primarily epifaunal. Paleoenvironmental interpretations will likely be affected by such enrichment.

Thus, it would behoove us to document more fully the infaunal distribution of salt marsh foraminifera in a variety of environmental settings and geographic locations, so that we can more fully understand what we are reconstructing when making sea level interpretations from the foraminifera contained in ancient marsh peat. The many previous studies of marsh foraminifera, commencing with Scott and Medioli (1978), deal with marsh foraminiferal zonations at locations characterized by astronomic tides of various amplitudes. In

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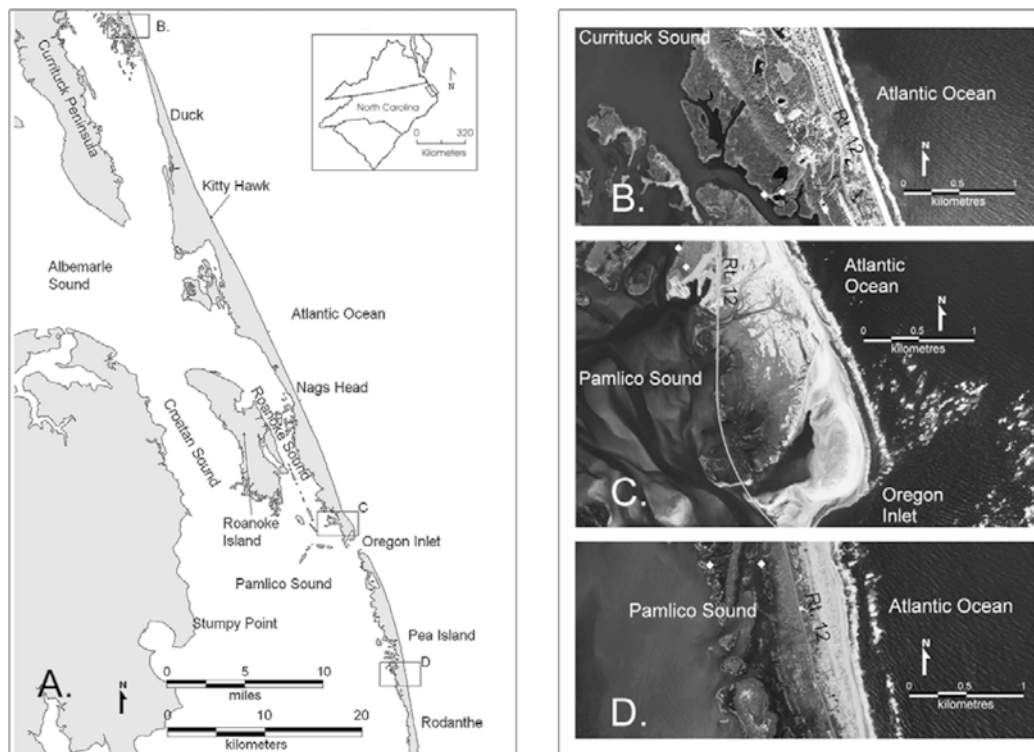
FIGURE 1.   A, Northern Outer Banks of North Carolina showing location of field sites on the Currituck barrier island (B), at Oregon Inlet (C) and Pea Island National Wildlife Refuge (D). B, Location (white diamonds) on the Currituck barrier island of short cores CUR02PC05 adjacent to Currituck Sound in the low marsh and CUR02PC06 in the high marsh. C, Location (white diamonds) at Oregon Inlet of short cores OR03PC03 adjacent to Pamlico Sound in the low marsh and OR02PC04 in the high marsh. D, Location (white diamonds) on Pea Island of short cores PI02PC02 adjacent to Pamlico Sound in the low marsh and PI02PC01 in the high marsh.

this study, we present data on infaunal foraminifera from three marshes characterized by minor (less than 0.35 m) diurnal tidal fluctuations, but significant, and highly variable, wind tides up to more than 3 m (during hurricanes) in amplitude (Riggs, 2002). The three marshes are located on the west side of North Carolina's Outer Banks (Fig. 1) and have different salinity regimes due to their varying distances from a major barrier island inlet. The surficial (0–1 cm) distributions of marsh foraminifera in transects across these three marshes are provided in Horton and Culver (in press).

MATERIALS AND METHODS

The marshes are located on the north side of Oregon Inlet at Pea Island, 14 km to the south of Oregon Inlet, and on the Currituck barrier island, 56 km north of Oregon Inlet (Fig. 1). Salinity varies greatly from season to season and from year to year on the sound side of the Outer Banks, but the sites were selected to cover the range from near normal seawater salinity at Oregon Inlet to very low brackish salinity on Currituck barrier island. At the time of sample collection (August, 2002), the salinity of Pamlico Sound at the Oregon Inlet site was 31. At the Pea Island site, the salinity of Pamlico Sound was 29 (somewhat higher than normal; Williams and others, 1973). At the Currituck barrier island site, the salinity of Currituck Sound was 6. Salinity of the marsh surface at any site can vary from fresh to hypersaline, depending on the recent history of inundation, rainfall and evaporation. Two short push cores were taken near the ends of shore-normal transects at each of the three

sites within the low and high marsh environments. Compaction of the sediment during sampling was negligible. CUR02PC5, CUR02PC6, PI02PC1, PI02PC2 and OR02PC04 were taken in August 2002. OR03PC3 was taken 12 months later. The cores, taken by hammering a 7.8 cm diameter plastic tube into the surface of the marsh, were capped and later the same day extruded; the top 10 cm were cut into 1 cm slices. The outside of each slice was removed to preclude any contamination via up- or down-core smearing. A 20-cc sample was cut from the remainder of the slice and transferred to a plastic bottle containing a mixture of buffered alcohol and the protein-specific stain rose Bengal (Walton, 1952; Murray and Bowser, 2000). On return to the laboratory, the samples were washed over a nest of 63- to 710-micron sieves to remove clay, silt and large plant material. The remaining sample was split into manageable aliquots using a wet splitter (Scott and Hermelin, 1993). A one-eighth fraction was spread evenly under water in a gridded plastic petri dish and, except when foraminifera were extremely rare, 100–300 specimens were picked from a known fraction of the split. (When foraminifera were rare, one-half to an entire split was picked; when abundant, one or more squares to be picked were selected using a random numbers table.) Specimens were picked wet to prevent adherence to plant material and to enhance the ability to recognize "live" rose Bengal-stained foraminifera. Only brightly stained specimens were enumerated as live. Specimens with patchy or pale pink stain were counted as unstained and, therefore, dead at time of collection (see Bern-

hard, 1988, 1992; Goldstein and others, 1995, for a discussion of recognition of ''live'' foraminifera).

RESULTS

Living infaunal benthic foraminifera were found in all six cores. However, the number of live foraminifera, the depth at which they were found living, and the species that were found to be living infaunally varied considerably from location to location and from core to core. Raw numbers of live foraminifera are given in Tables 1–6 and plotted as percents of the total assemblage in Figures 2–7. When numbers are very small, percentage data can be visually misleading; thus, the raw counts of live individuals are also plotted in Figure 8.

OREGON INLET

Core OR03PC03 (High-Salinity Site, Low Marsh)

Core OR03PC03 (35° 47′ 57.75″N, 75° 33′ 01.32″W) was taken 1 m from Pamlico Sound in a short *Spartina alterniflora* fringing, low-marsh environment. The pore-water salinity in the top 1 cm of sediment was 17.7 ppt at time of sampling. Extensively rooted muddy sand characterized the entire core. The proportion of quartz sand increased down core and a few quartz gravel particles occurred from 3–5 cm in depth (Fig. 2).

Live foraminifera were found down to 4 cm (Fig. 2A) but were most abundant in the 0–1 cm interval, where they comprised 18% of the total assemblage (Fig. 2A, Table 1). The living population in the 0–1 cm interval was dominated by *Ammotium salsum* and *Arenoparrella mexicana* (Fig. 2A, Table 1). Few living specimens were found in the 1–2 cm interval, but the population at this depth was dominated by *Haplophragmoides wilberti* (Figs. 2A, 8; Table 1). A few living specimens of this and other taxa were recovered from the 2–3 and 3–4 cm intervals.

Dead assemblages from the surface to the 4–5 cm interval were dominated by *Miliammina fusca* and *Ammotium* cf. *A. salsum* (Fig. 2B), with a few other rare species (Table 1). Dead specimens were much more abundant than live ones throughout the core (Fig. 2A, B).

Core OR02PC04 (High-Salinity Site, High Marsh)

Core OR02PC04 (35° 47′ 52.09″N, 75° 32′ 58.77″W) was taken 130 m from Pamlico Sound in a high marsh environment dominated by dense *Juncus roemerianus.* The 0–1 cm interval pore-water salinity at time of sampling was 9.4 ppt. The top centimeter of core was composed of loose plant material in a muddy sand (Fig. 3). Plant material formed a peat turf from 1–5 cm. Below that, to the base of the core, loose plant material occurred in a quartz sand with occasional quartz granules. The top 2 cm of the core contained abundant short cylindrical clay aggregates (possibly fecal pellets of fiddler crabs).

Live foraminifera were found down to 10 cm although they were rare at this depth (Fig. 3A). Most live foraminifera were found in the 0–1 and 1–2 cm intervals where they comprise 35% and 33%, respectively, of the total assemblage (Fig. 3, Table 2). Several species were abundant in the top centimeter of the core (*Trochammina inflata, Hap-*

lophragmoides wilberti, Arenoparrella mexicana, Tiphotrocha comprimata, Miliammina petila and *Haplophragmoides bonplandi*; Fig. 3A). With the exception of *T. comprimata* and *H. bonplandi,* which were restricted to 0–1 and 0–2 cm depths, respectively, this population essentially characterized the entire depth of the sediment where live foraminifera occurred (Fig. 3A). A few live infaunal specimens of several species, in particular *Siphotrochammina lobata* and *Jadammina macrescens,* also occurred. The peaks of infaunal relative abundance of *T. inflata* at 2–3 cm and *H. wilberti* at 9–10 cm are artifactual, resulting from the very low number of live foraminifera recovered from those depths (Figs. 3A, 8; Table 2).

Dead assemblages throughout the entire 10 cm of core were dominated by *Trochammina inflata* and *Haplophragmoides wilberti,* with the latter species increasing in proportion in the lower 5 cm of the core (Fig. 3B). Several other taxa were present in generally consistent relative abundances down core (*Arenoparrella mexicana, Miliammina petila, Siphotrochammina lobata, Trochammina* sp.), whereas *Haplophragmoides bonplandi* was restricted to the top 6 cm of the core (Fig. 3B, Table 2).

PEA ISLAND

Core PI02PC02 (Intermediate-Salinity Site, Low Marsh)

Core PI02PC02 (35° 39′ 22.67″N, 75° 29′ 07.75″W) was taken 50 cm from Pamlico Sound in a fringing low marsh environment consisting of short *Spartina alterniflora.* The 0–1 cm interval pore-water salinity at time of sampling was 30 ppt. The core was composed of marsh peat turf from 0–9 cm with minor amounts of quartz sand that increased down-core. At 9 cm depth, the peat rested with a relatively sharp contact on rooted fine quartz sand with abundant heavy minerals (Fig. 4A).

Live foraminifera occurred throughout the core, but were very rare in the lower 2 cm of peat and in the underlying sand (Figs. 4A, 8; Table 3). Live foraminifera were most abundant in the 0–1 cm interval where they comprised 54% of the total assemblage (Table 3). The proportion of live foraminifera gradually decreased down core. The 0–1 cm interval was dominated by living *Trochammina inflata* and *Arenoparrella mexicana* with common *Tiphotrocha comprimata, Jadammina macrescens, Siphotrochammina lobata* and *Haplophragmoides wilberti.* The composition of populations stayed essentially the same down to the 3–4 cm interval, although absolute numbers of live specimens declined (Figs. 4A, 8; Table 3). With the exception of a few specimens at 6–7 cm, living *Trochammina inflata* were absent from the core below 4 cm. Live specimens of *A. mexicana* increased in proportion from 4–5 cm down to the base of the peat at 9 cm. *Tiphotrocha comprimata* also occurred live for the entire thickness of the peat, as did *J. macrescens,* although occurrences of the latter species were more sporadic towards the bottom of the peat (Figs. 4A, 8). Live specimens of several other taxa, notably *S. lobata, H. bonplandi* and *H. wilberti* occurred sporadically down core (Fig. 4A). The apparent peak abundance of *J. macrescens* at 9–10 cm resulted from the recovery of only one live specimen (Figs. 4A, 8).

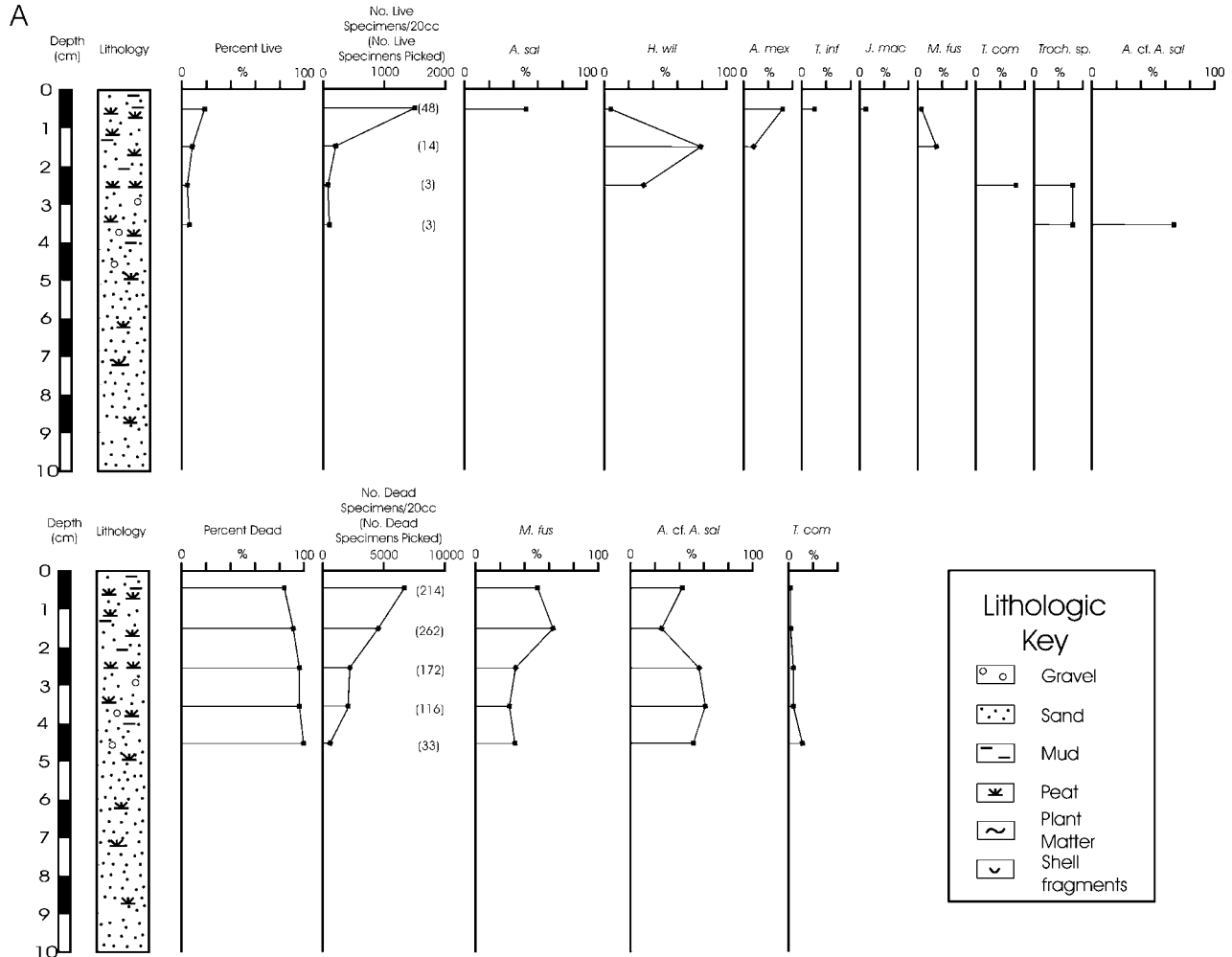Dead specimens increased in absolute abundance down

FIGURE 2. A, Relative abundance of all taxa comprising the live population in core OR03PC03 in the low marsh adjacent to high salinity Pamlico Sound at Oregon Inlet. Note that peaks may result from recovery of low numbers of live specimens (see text and Fig. 8). B, Relative abundance of all taxa comprising 5 percent or more of the dead assemblage in one or more samples in core OR03PC03. Key to abbreviations of names given in Appendix B.

core for the entire thickness of the peat with the exception of the 7–8 cm interval, where very few foraminifera per unit volume occurred (Fig. 4B). Over 12,000 specimens per 20 cc occurred in the immediately overlying 1-cm interval. Dead assemblages were generally consistent in composition throughout the peat with the exception of *Jadammina macrescens,* which increased in proportion in the lower 4 cm of the peat (5–9 cm) at the expense of *Tiphotrocha comprimata* (Fig. 4B). *Arenoparrella mexicana* also exhibited an increase in proportion at the 8–9 cm interval (the base of the peat). Dead specimens of *Ammotium* cf. *A. salsum* and *Miliammina fusca* were generally restricted to the upper 5 cm of peat, whereas *Trochammina* sp. (composed of unidentifiable, usually juvenile trochamminids) was restricted to the lower half of the peat (4–9 cm; Fig. 4B, Table 3).

Core PI02PC01 (Intermediate-Salinity Site, High Marsh)

Core PI02PC01 (35° 39′ 22.49″N, 75° 28′ 49.90″W) was taken 250 m from Pamlico Sound in dense *Juncus roemarianus* high marsh with patches of *Spartina patens.* The 0–1 cm interval pore-water salinity at time of collection was 36.5 ppt. The top 9 cm of core was composed of marsh turf with minor quartz sand; the proportion of sand increased in the lower 2 cm (7–9 cm) of the peat where a few quartz granules and molluscan shell fragments also occurred. The peat rested with relatively sharp contact on a fine, heavy-mineral-rich sand containing a few grains of quartz gravel, a few molluscan shell fragments and roots from the overlying peat (Fig. 5).

Live foraminifera were abundant in the top 6 cm of peat and became rare in the lower 3 cm. No live foraminifera were recovered from the underlying sand (Fig. 5A). Although the abundance of live foraminifera decreased towards the bottom of the peat, the proportion of live foraminifera remained generally constant throughout the entire thickness of the peat (Figs, 5A, 8; Table 4). There was a subsurface peak of live foraminifera at 2–3 cm, where the highest number of live foraminifera per 20 cc in this study (2600) was recorded (Fig. 5A, Table 4). However, the composition of the live population at this depth did not differ significantly from the immediately overlying and underlying intervals. The top 4 cm of peat were characterized by a

TABLE 1. Oregon Inlet, Core OR03PC03 (high salinity, low marsh). Numbers of living and dead foraminifera. Key to abbreviations of names given in Appendix B.

Sample depth (cm)	Live, Dead, Total	A. sal	A. mex	T. inf	J. mac	M. fus	H. wil	A. cf. sal	T. com	H. bon	M. pet	S. lob	Troch. sp	Reo. sp	A. sub	A. exig	T. rot	R. nan	indet.	Total	%	No. Species
0–1	L	24	14	5	2	1	2													48	18.3	6
	D		3	4		109		92	3	1	1	1								214	81.7	8
	T	24	17	9	2	110	2	92	3	1	1	1								262	100	11
1–2	L		1			2	11													14	5.1	3
	D	24	1	2		170	6	66	2				5	5	3	1	1			262	94.9	11
	T	24	2	2		172	17	66	2				5	5	3	1	1			276	100	12
2–3	L						1		1				1							3	1.7	3
	D					55	1	98	6				1	3	5		1	2		172	98.3	9
	T					55	2	98	7				2	3	5		1	2		175	100	9
3–4	L							2					1							3	2.5	2
	D		1			31	4	73	3				1						4	116	97.5	6
	T		1			31	4	75	3				1						4	119	100	7
4–5	L																			0	0	0
	D					10		17	4				1	1						33	100	5
	T					10		17	4				1	1						33	100	5

population dominated by *Tiphotrocha comprimata, Trochammina inflata, Jadammina macrescens, Arenoparrella mexicana* and *Siphotrochammina lobata* (Fig. 5A). *Arenoparrella mexicana* did not occur live below 4 cm and *T. comprimata* decreased in proportion down to the 7–8 cm interval. In strong contrast, living specimens of *J. macrescens* increased in proportion down core and dominated populations from 3–9 cm (Fig. 5A). A few living specimens of the calcareous benthic foraminifer *Helenina anderseni* occurred in the top 6 cm of the core. No dead specimens of this taxon were found, presumably because the calcareous tests were dissolved after death in the acidic marsh environment.

The dead assemblages in PI02PC01 showed very similar patterns to the live populations (Fig. 5A, B). The number of dead specimens per 20 cc generally decreased down core from 4 cm to 10 cm. The taxonomic composition of the dead assemblage closely paralleled that of the live populations and similar down-core patterns were also evident for most taxa. *Jadammina macrescens* increased in proportion down core, whereas *Tiphotrocha comprimata* and *Trochammina inflata* decreased in proportion down-core (Fig. 5B). In contrast to the live populations, dead specimens of *Miliammina fusca* increased in proportion in the lower few centimeters of peat (Fig. 5B, Table 4).

CURRITUCK SOUND

Core CUR02PC05 (Low-Salinity Site, Low Marsh)

Core CUR02PC05 (36° 15′ 30.32″N, 75° 47′ 43.99″W) was taken from a muddy, detrital peat surface between patches of *Juncus roemerianus* within the low marsh that fringed Currituck Sound. The 0–1 cm interval pore-water salinity at time of collection was 7.0 ppt. The core was composed of muddy detrital peat with minor amounts of quartz sand down to 5 cm. From this depth to the base of the core, loose peat turf occured with the muddy detrital peat).

Live foraminifera occurred in generally low numbers down to 7 cm with the exception of a subsurface peak at 3–4 cm (Fig. 6A, Table 5). The proportion of live foraminifera increased slightly in this interval but proportions were generally low for the entire thickness of core in which live foraminifera occurred (Fig. 6A). The upper 4 cm of core was characterized by a population dominated by *Ammobaculites subcatenulatus, Miliammina fusca, Ammotium salsum* and *Jadammina macrescens*. From 4–7 cm, *J. macrescens* and, to a lesser degree, *T. comprimata*, increased in proportion (although absolute numbers were very low) and *M. fusca* and *A. salsum* did not occur. The apparent subsurface peak in living *Haplophragmoides bonplandi* is an artifact of the very low number of live foraminifera recovered from 5–7 cm (Figs. 6A, 8; Table 5).

The number of dead foraminifera per 20 cc generally decreased down-core from the surface to 8 cm with the exception of a peak at 3–4 cm, which coincided with the peak in numbers of live foraminifera at this depth (Fig, 6A, B). Down-core patterns of dead assemblages (Fig. 6B) generally matched those of live foraminifera (Fig. 6A). Assemblages were dominated by *Jadammina macrescens, Ammobaculites subcatenulatus, Miliammina fusca* and *Ammotium sal-*
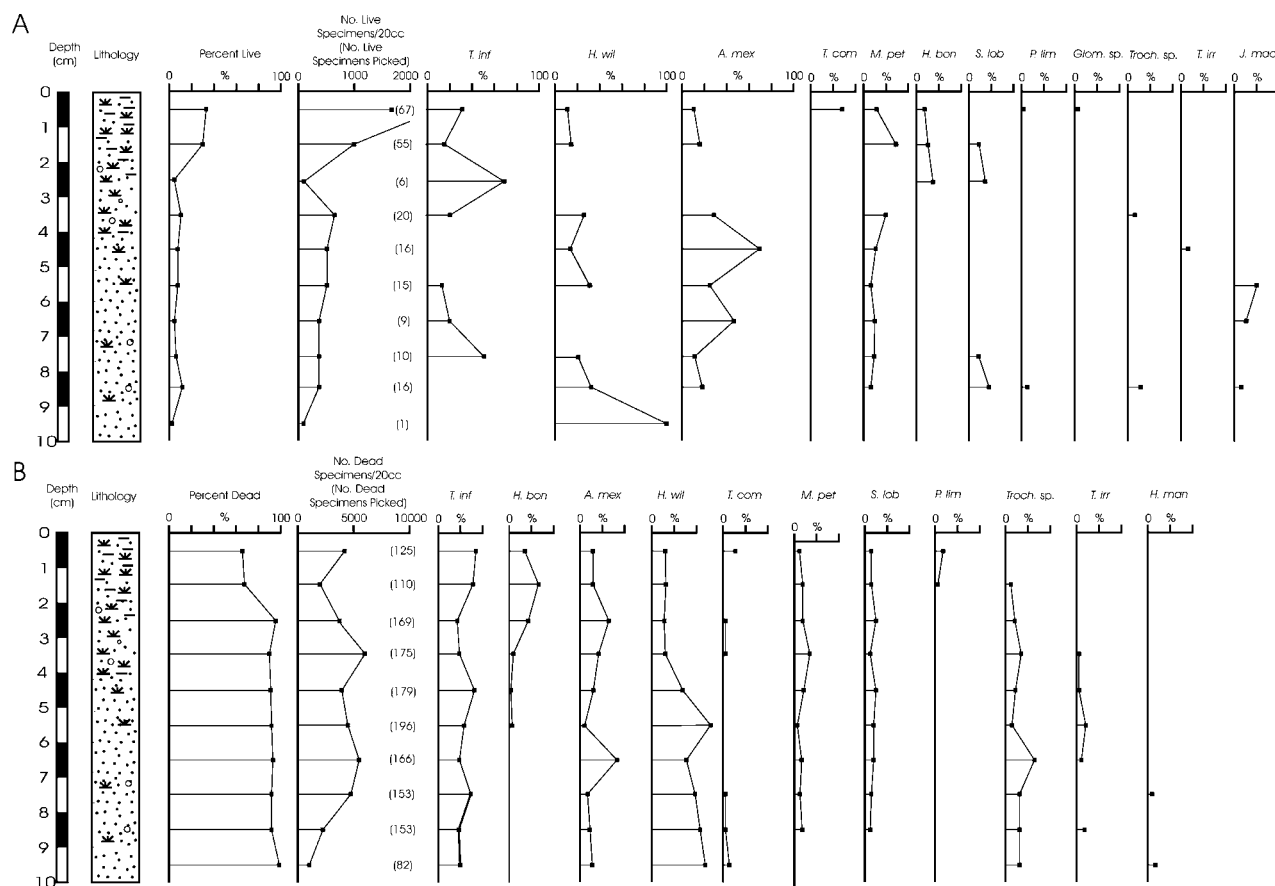
FIGURE 3.   A, Relative abundance of all taxa comprising the live population in core OR02PC04 in the high marsh near Oregon Inlet (high salinity). Note that peaks may result from recovery of low numbers of live specimens (see text and Fig. 8). B, Relative abundance of all taxa comprising 5 percent or more of the dead assemblage in one or more samples in core OR02PC04. Key to abbreviations of names given in Appendix B.

sum. Jadammina macrescens increased slightly in proportion down core and *A. subcatenulatus* and *M. fusca* essentially disappeared below 5 cm. Several additional dead taxa were quite common throughout the entire interval within which live foraminifera occurred, most notably *Trochamminita irregularis, Haplophragmoides bonplandi,* and *Trochammina* sp.; these taxa increased slightly in proportion from 5–8 cm (Fig. 6B, Table 5).

Core CUR02PC06 (Low-Salinity Site, High Marsh)

Core CUR02PC06 (36° 15′ 30.87″N, 75° 47′ 37.37″W) was taken 100 m from Currituck Sound in a dense, mixed *Juncus roemerianus* and *Spartina cynusoroides* high marsh environment. The 0–1 cm interval pore-water salinity at time of sampling was 9.0 ppt. The core was composed of muddy detrital peat with a few quartz sand grains down to 2 cm where loose peat turf began to appear. The peat turf became quite dense from 6–10 cm and quartz sand also increased slightly in abundance in the lower half of the core (Fig. 7A).

Live foraminifera were abundant in the top 2 cm of core CUR02PC06 but decreased rapidly in absolute abundance down core, paralleling the down-core decrease in the proportion of live foraminifera (Figs. 7A, 8; Table 6). The living population in the entire interval of core where live fo-

raminifera occurred was dominated by *Jadammina macrescens.* Living specimens of *Tiphotrocha comprimata* were quite abundant from 0–2 cm (Fig. 7A).

Numbers of dead specimens per unit volume (20 cc) were uniformly low from 0–9 cm (Fig. 7B). The dead assemblage, like the living population, was dominated by *Jadammina macrescens. Miliammina petila* was the only other taxon that occurred with any significant abundance in the dead assemblage (Fig. 7B, Table 6).

DISCUSSION

DISTRIBUTION PATTERNS OF LIVE FORAMINIFERA

The surfaces of salt marshes are not hard, and so truly epifaunal species most likely do not inhabit this environment. The corollary of this observation is that all marsh foraminiferal taxa are infaunal. Species dwelling in the 0–1 cm interval were termed shallow infaunal by Buzas and others (1993) who called taxa dwelling at >1 cm, deep infaunal; this scheme is followed here.

Figure 9 summarizes the infaunal depth ranges of all taxa recorded live in the six Outer Banks salt marsh cores (Figs. 2–7). Fourteen of 22 taxa occur in one or more cores as deep infaunal species. Of these, four taxa (*Ammoastuta inepta, Ammobaculites crassus, Ammobaculites* sp. and

TABLE 2. Oregon Inlet, Core OR02PC04 (high salinity, high marsh). Numbers of living and dead foraminifera. Key to abbreviations of names given in Appendix B.

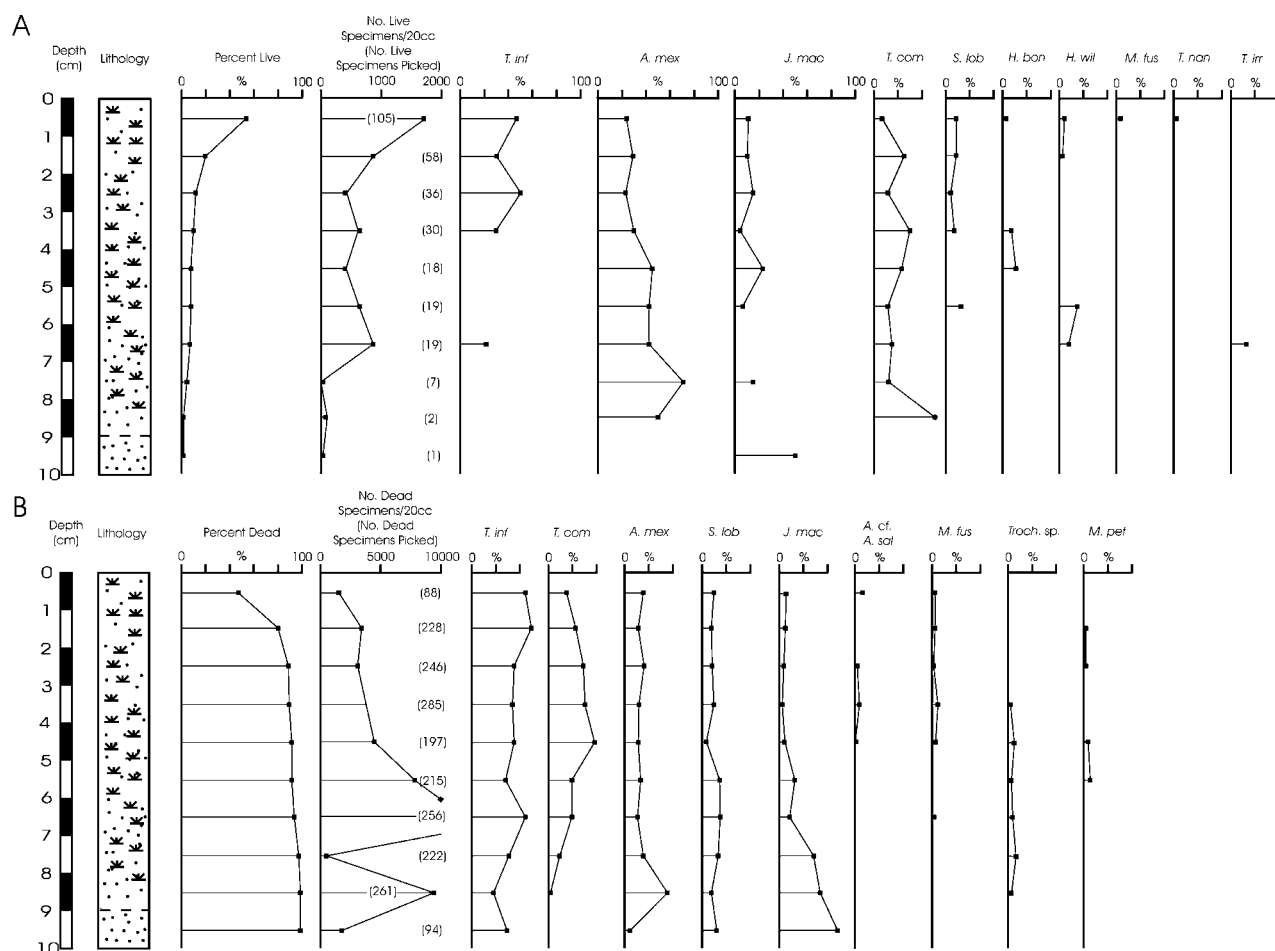| Sample depth (cm)	Live, Dead, Total	T. com	T. inf	M. pet	A. mex	H. wil	H. bon	P. lim	Glom. sp	J. mac	S. lob	Troch. sp	T. och	T. irr	P. ipo	M. fus	H. man	Haplo. sp	indet.	Total	%	No. Species	Aliquot Picked
0–1	L	17	18	9	7	9	4	1	2											67	34.9	8	
	D	12	44	5	15	16	20	6		2	5									125	65.1	9	
	T	29	62	14	22	25	24	7	2	2	5									192	100	10	1/36
1–2	L		9	15	9	13	5				4									55	33.3	6	
	D		36	9	13	11	27	1			4	3	2						4	110	66.7	10	
	T		45	24	22	24	32	1			8	3	2						4	165	100	10	1/16
2–3	L		4				1				1									6	3.4	3	
	D	2	31	14	42	20	30		2	1	15	12								169	96.6	10	
	T	2	35	14	42	20	31		2	1	16	12								175	100	10	1/24
3–4	L		4	4	6	5						1								20	10.3	5	
	D	1	34	26	29	23	5		5	6	14	28		1					3	175	89.7	12	
	T	1	38	30	35	28	5		5	6	14	29		1					3	195	100	12	1/32
4–5	L			2	11	2								1						16	8.2	4	
	D		59	16	22	49	1			2	16	12		2						179	91.8	9	
	T		59	18	33	51	1			2	16	12		3						195	100	9	1/24
5–6	L		2	1	4	5				3										15	7.1	5	
	D		46	3	6	101	4				13	7		13	2	1				196	92.9	10	
	T		48	4	10	106	4			3	13	7		13	2	1				211	100	11	1/24
6–7	L		2	1	4					1				1						9	5.1	5	
	D		31	11	6	56				4	11	42		5						166	94.9	8	
	T		33	12	10	56				5	11	42		6						175	100	8	1/32
7–8	L		5	1	1	2					1									10	6.1	5	
	D	2	44	7	7	60					6	20			4		3			153	93.9	9	
	T	2	49	8	8	62					7	20			4		3			163	100	9	1/32
8–9	L			1	3	5		1		1	3	2								16	9.5	7	
	D	2	27	9	13	68				2	4	20		7				1		153	90.5	9	
	T	2	27	10	16	73		1		3	7	22		7				1		163	100	11	1/16
9–10	L					1														1	1.2	1	
	D	3	16		9	39						11					4			82	98.8	6	
	T	3	16		9	40						11					4			83	100	6	1/16

FIGURE 4. A, Relative abundance of all taxa comprising the live population in core PI02PC02 in the low marsh adjacent to intermediate salinity Pamlico Sound on Pea Island. Note that peaks may result from recovery of low numbers of live specimens (see text and Fig. 8). B, Relative abundance of all taxa comprising 5 percent or more of the dead assemblage in one or more samples in core PI02PC02. Key to abbreviations of names given in Appendix B.

Ammotium cf. *A. salsum*) are restricted to deep infaunal habitats (Fig. 9). Six taxa are only found in the lower part of the marsh adjacent to the sound; *Ammotium salsum* and *Ammotium* cf. *A. salsum* are at Oregon Inlet (high salinity); *Trochammina nana* is at Pea Island (intermediate salinity); and *Ammoastuta inepta, Ammobaculites crassus, Ammobaculite*s sp. and *Ammotium salsum* are found at Currituck (low salinity, Fig. 9). Four taxa are only found in the upper part of the marsh: *Glomospira* sp. at Oregon Inlet, *Ammobaculites* sp. and *Helenina anderseni* at Pea Island, and *Haplophragmoides manilaensis* at Currituck (Fig. 9). Only two taxa, *Glomospira* sp. and *Trochammina* sp., are restricted to the marsh adjacent to high-salinity water (Oregon Inlet). Three taxa, *Ammobaculites* sp., *Helenina anderseni* and *Trochammina nana,* are restricted to the marsh adjacent to intermediate-salinity water (Pea Island). Four taxa are restricted to the marsh adjacent to low-salinity water of Currituck Sound: *Ammoastuta inepta, Ammobaculites crassus, Ammobaculites subcatenulatus* and *Haplophragmoides manilaensis* (Fig. 9). Three taxa, *Arenoparrella mexicana, Haplophragmoides wilberti* and *Siphotrochammina lobata,* are restricted to the high- and intermediate-salinity marshes.

No species are restricted to low- and intermediate-salinity marshes (Fig. 9).

The restricted distributions are summarized in Table 7. Unfortunately, many of these taxa cannot be used reliably as indicators of the environments to which they are restricted. These are taxa that are always rare (arbitrarily defined in this instance as never comprising >5% of a population within a sample). This rarity means that these taxa are more likely to have a restricted distribution as a result of their lower probability of being found.

The only taxa that, theoretically, can be used reliably as indicators of a particular environment in this data set are as follows (Table 7). *Trochammina* sp. is indicative of deep infaunal, high-salinity habitats, but it is composed mainly of juvenile specimens that may represent more than one species. *Trochamminita irregularis* has a generally (four of five records) deep infaunal habitat. *Ammobaculites subcatenulatus* is restricted to low-salinity, lower marsh environments. *Ammotium salsum* is found only in lower marsh environments. Three species, *Arenoparrella mexicana, Haplophragmoides wilberti* and *Siphotrochammina lobata,* are only found in the marshes adjacent to intermediate- (Pea

TABLE 3.   Pea Island, PI02PCO2 (intermediate salinity, low marsh). Numbers of living and dead foraminifera. Key to abbreviations of names given in Appendix B.

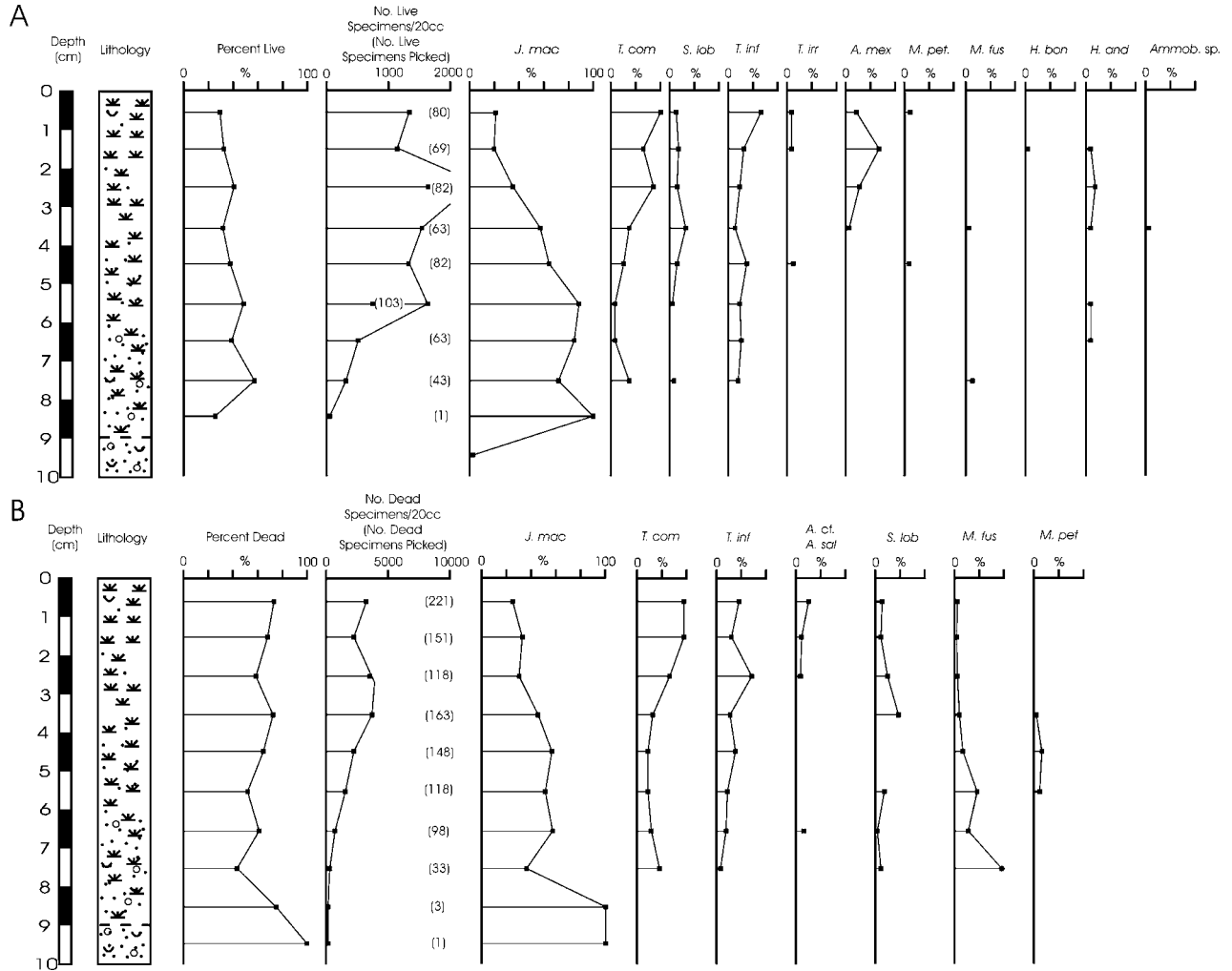| Sample depth (cm)	Live, Dead, Total	T. inf	A. mex	T. com	J. mac	M. fus	T. nan	S. lob	H. wil	H. bon	A. cf. sal	A. sal	Glom. sp	M. pet	T. ear	Troch. sp	Reo. sp	P. ipo	T. irr	Total	%	No. Species	Aliquot Picked
0–1	L	48	24	6	11	3	1	7	3	2										105	54.4	9	
	D	37	13	15	4	3		8	2		4	1	1							88	45.6	10	
	T	85	37	21	15	6	1	15	5	2	4	1	1							193	100	12	1/16
1–2	L	18	16	14	5			4	1											58	20.3	6	
	D	109	25	51	10	6		15		9				3						228	79.7	8	
	T	127	41	55	15	6		19	1	9				3						286	100	9	1/16
2–3	L	18	8	4	5			1												36	12.8	5	
	D	88	42	67	8	4		20		11	3			2	1					246	87.2	10	
	T	106	50	71	13	4		21		11	3			2	1					282	100	10	1/12
3–4	L	9	9	9	1					2										30	9.5	5	
	D	100	35	79	5	14		27		10	8					6	1			285	90.5	10	
	T	109	44	88	6	14		27		12	8					6	1			315	100	10	1/24
4–5	L		8	4	4					2										18	8.4	4	
	D	70	22	76	5	1		6		5	2					9		1		197	91.6	10	
	T	70	30	80	9	1		6		7	2					9		1		215	100	10	1/24
5–6	L		8	2	1			1	3					4						19	8.1	6	
	D	61	29	42	28			28	5					11		5		2	4	215	91.9	10	
	T	61	37	44	29			29	8					15		5		2	4	234	100	10	1/36
6–7	L	4	8	3				1	1										2	19	6.9	6	
	D	107	26	52	19	2	1	35						1		8			5	256	93.1	10	
	T	111	34	55	19	2	1	36	1					1		8			7	275	100	11	1/48
7–8	L		5	1	1															7	30.1	3	
	D	69	34	18	63			27	1							8		2		222	69.9	8	
	T	69	39	19	64			27	1							8		2		229	100	8	5/12
8–9	L		1	1																2	0.8	2	
	D	49	95	2	89			19								4		3		261	99.2	7	
	T	49	96	3	89			19								4		3		263	100	7	1/36
9–10	L				1															1	1.1	1	
	D	28	4		47			10	1									4		94	98.9	5	
	T	28	4		48			10	1									4		95	100	5	1/16

FIGURE 5. A, Relative abundance of all taxa comprising the live population in core PI02PC01 in the high marsh on Pea Island (intermediate salinity). Note that peaks may result from recovery of low numbers of live specimens (see text and Fig. 8). B, Relative abundance of all taxa comprising 5 percent or more of the dead assemblage in one or more samples in core PI02PC01. Key to abbreviations of names given in Appendix B.

Island) and high-salinity (Oregon Inlet) water. Only two species, *Jadammina macrescens* and *Tiphotrocha comprimata*, are found living in all six cores (Fig. 9).

TAPHONOMIC INFERENCES

Comparisons of distributions of live and dead tests of a taxon allow taphonomic inferences to be made. In core OR03PC03, the number of live foraminifera per 20cc of sediment decreases rapidly down core from the 0–1 cm interval (Fig. 2A). This pattern is paralleled by the down-core decrease in dead specimens. Only 500 specimens occur in 20 cc of sediment at 4–5 cm depth, down from 6800 per 20 cc at 0–1 cm. This suggests that, in the environment immediately adjacent to the high-salinity Pamlico Sound, foraminifera are poorly preserved in the subsurface.

Foraminiferal tests are more likely to be preserved in the subsurface in the higher marsh environment at Oregon Inlet. Although the extrapolated numbers of live foraminifera decrease down core from over 2000 per 20 cc in the 0–1 cm interval to almost zero in the 9–10 cm interval (Fig. 3A),

dead foraminifera occur in generally high numbers down to 7–8 cm and are still relatively abundant (1500 specimens per 20 cc) at 9–10 cm (Fig. 3B).

The preservation potential of infaunal foraminifera tests at the Pea Island site immediately adjacent to intermediate-salinity waters of Pamlico Sound (PI02PC02) is good. Numbers of live foraminifera per 20 cc decrease down core to the 7–8 cm interval (Fig. 4A). In comparison, with the exception of the 7–8 cm interval, numbers of dead specimens per 20 cc increase significantly down core to the 8–9 cm interval. The number of dead specimens decreases precipitously from 8–9 to 9–10 cm at the relatively sharp contact between sandy peat and rooted sand (Fig. 4B).

Infaunal foraminifera are less likely to be preserved after death in the higher marsh site at Pea Island (PI 02PC01). Numbers of live foraminifera per 20 cc decrease down core from a peak at 2–3 cm down to the sandy peat to rooted gravelly sand contact at 9 cm (Fig. 5A). Dead specimens similarly decrease in numbers per 20 cc down core throughout the entire thickness of the peat (Fig. 5B), suggesting that tests are being destroyed through time rather than in-

TABLE 4.　Pea Island, PI02PC01 (intermediate salinity, high marsh). Numbers of living and dead foraminifera. Key to abbreviations of names given in Appendix B.

Sample depth (cm)	Live, Dead, Total	T. com	T. inf	J. mac	A. mex	T. irr	S. lob	A. cf. sal	M. fus	Glom. sp	M. pet	H. bon	H. and	P. ipo	Ammob. sp.	T. compa	Troch sp.	indet.	Total	%	No. Species	Aliquot Picked
0–1	L	32	20	17	6	2	3												80	26.6	6	
	D	84	41	52	8		11	19	5	1									221	73.4	8	
	T	116	61	69	14	2	14	19	5	1									301	100	9	1/16
1–2	L	18	9	14	17	2	4				2	1	2						69	31.4	9	
	D	57	20	49	6	4	6	6	2			1							151	68.6	9	
	T	75	29	63	23	6	10	6	2		2	2	2						220	100	11	1/16
2–3	L	29	7	28	9		4		2										82	41.0	6	
	D	30	34	33	2		12	4	2					1					118	59.0	8	
	T	59	41	61	11		16	4	2				5	1					200	100	8	1/32
3–4	L	10	4	36	1	1	9		1		1		1		1				63	27.9	8	
	D	21	20	75	4	1	31		6		1				1	2	1		163	72.1	11	
	T	31	24	111	5		32		7		1		1		2	2	1		226	100	12	1/24
4–5	L	8	12	53		3	4				2								82	35.7	6	
	D	12	24	84		1			11	3	9				2			3	148	64.3	9	
	T	20	36	137		4	4		11	3	11		1		2	1		3	230	100	12	1/16
5–6	L	3	6	91			1						2						103	48.6	5	
	D	9	11	61			7		23		5				2				118	53.4	7	
	T	12	17	152			8		23		5		2		2				221	100	8	1/16
6–7	L	2	7	53			1												63	39.1	4	
	D	11	8	57	2		1	5	13				1					1	98	60.9	8	
	T	13	15	110	2		2	5	13									1	161	100	8	1/8
7–8	L	7	2	31					2										43	56.6	5	
	D	6	1	12					13										33	43.4	5	
	T	13	3	43					15										76	100	5	1/8
8–9	L			1															1	25.0	1	
	D			3															3	75.0	1	
	T			4															4	100	1	1/8
9–10	L																		0	0	0	
	D			1															1	100	1	
	T			1															1	100	1	1/8

TABLE 5. Currituck barrier island, Core CUR02PC05 (low salinity, low marsh). Numbers of living and dead foraminifera. Key to abbreviations of names given in Appendix B.

| Sample depth (cm)	Live, Dead, Total	A. sub	J. mac	M. fus	A. sal	H. bon	M. pet	A. inep	T. irr	T. com	A. mex	P. lim	T. inf	Troch. sp.	A. cras	H. man	P. ipo	H. will	Glom. sp	indet.	Ammob. sp	Total	%	No. Species	Aliquot Picked
0–1	L	7	6	5	4	3	2															27	11.7	6	
	D	25	71	26	22	8	15	7	7	3	3	3	8	5								203	88.3	13	
	T	32	77	31	26	11	17	7	7	3	3	3	8	5								230	100	13	1/16
1–2	L	5	1	2	1		1		1							1						12	4.8	7	
	D	46	55	40	23	9	19	15	6	6	1	2	1	4		10	2					239	95.2	15	
	T	51	56	42	24	9	20	15	7	6	1	2	1	4		11	2					251	100	15	1/8
2–3	L	7		5	5			2					1									20	6.9	5	
	D	72	56	45	34	4	13	10	12		1	4		8	5	5		1				270	93.1	14	
	T	79	56	50	39	4	13	12	12		1	4	1	8	5	5		1				290	100	15	1/16
3–4	L	18	8	6	8		2					1		1								44	13.5	7	
	D	82	54	42	27	9	25	10	3	5	1	3	1	9	2	4		1	1	1		280	86.5	18	
	T	100	62	48	35	9	27	10	3	5	1	4	1	10	2	4		1	1	1		324	100	18	1/8
4–5	L	8	4					1	1	1					1					4		20	9.2	7	
	D	53	54	24	10	10	9	1	5	5		5	4	4	4	5		1		4		198	90.8	16	
	T	61	58	24	10	10	9	2	6	6		5	4	4	5	5		1		8		218	100	16	1/8
5–6	L		2			3																5	2.4	2	
	D	10	115	4	6	17	4	3	31	1				10				2				203	97.6	11	
	T	10	117	4	6	20	4	3	31	1				10				2				208	100	11	1/8
6–7	L		5			1																6	2.5	2	
	D		93		3	22	9		54					28		13	3	3		2	3	233	97.6	11	
	T		98		3	23	9		54					28		13	3	3		2	3	239	100	11	1/8
7–8	L																					0	0	0	
	D		72	1	2	38	16		57	3				21		20		4		8		242	100	11	
	T		72	1	2	38	16		57	3				21		20		4		8		242	100	11	1/8

FIGURE 6. A, Relative abundance of all taxa comprising the live population in core CUR02PC05 in the low marsh on Currituck barrier island adjacent to low salinity Currituck Sound. Note that peaks may result from recovery of low numbers of live specimens (see text and Fig. 8). B, Relative abundance of all taxa comprising 5 percent or more of the dead assemblage in one or more samples in core CUR02PC05. Key to abbreviations of names given in Appendix B.

creasing by the addition of new, deep infaunal specimens. This is the only site in this study where the calcareous marsh species *Helenina anderseni* was recorded. It occurred live from 0–6 cm but no dead tests were found. Clearly, tests of this species are dissolved in the low-pH marsh environment soon after death.

Live infaunal foraminifera show a peak in numbers per 20 cc at 3–4 cm in the lower marsh core at the low-salinity Currituck site (CUR02PC05; Fig. 6A). The curve for numbers of live foraminifera per 20 cc down core parallels that for dead foraminifera; a similar peak occurs at 3–4 cm (Fig. 6A.B). Numbers of live and dead foraminifera per 20 cc both decrease down core from this peak. Live foraminifera are found from 5–7 cm in very low numbers and none were found immediately beneath this depth. Dead foraminifera per 20 cc are still quite abundant at this depth (> 2000 per 20 cc) and do not decrease significantly in numbers down core from 5–8 cm. Thus, although some tests are lost down core, their preservation potential at this site is quite high.

At the higher marsh site (CUR02PC06), numbers of dead foraminifera per 20 cc are quite consistently low from 0–9 cm (the limit of this study, Fig. 7B). In comparison, live foraminifera are very abundant in the top 2 cm of the core and then decrease in numbers quite rapidly down core (Fig. 7A). This suggests that tests of foraminifera are destroyed in considerable numbers soon after death. *Jadammina ma-*

crescens dominates both the live population and the dead assemblage, but *Tiphotrocha comprimata,* which is quite abundant in the live population from 0–2 cm, is not found in the dead assemblage in the entire core (Fig. 7B, Table 6). Thus, this species suffers selective, rapid (and complete) loss of tests very soon after death at this site.

Observations made during the picking process suggest that several common taxa were particularly resistant to postmortem disintegration of tests, in particular, *Arenoparrella mexicana, Haplophragmoides wilberti, Jadammina macrescens* and *Trochammina inflata,* all taxa with generally fine agglutinated particles. Other taxa exhibited partial breakage, particularly of the uniserial part of the test from the planispiral portion in species of *Ammobaculites* and *Ammotium.* Especially delicate species that often broke during the picking process were *Ammoastuta inepta, Ammotium salsum, Pseudothurammina limnetis, Polysaccammina ipohalina* and *Trochamminita irregularis. Miliammina fusca,* however, was the single taxon that was most likely to break and disintegrate during picking.

COMPARISON WITH OTHER INFAUNAL STUDIES IN ATLANTIC COAST MARSHES

Buzas (1965) showed that shallow marine foraminifera in Long Island Sound could live infaunally as well as epifaun-
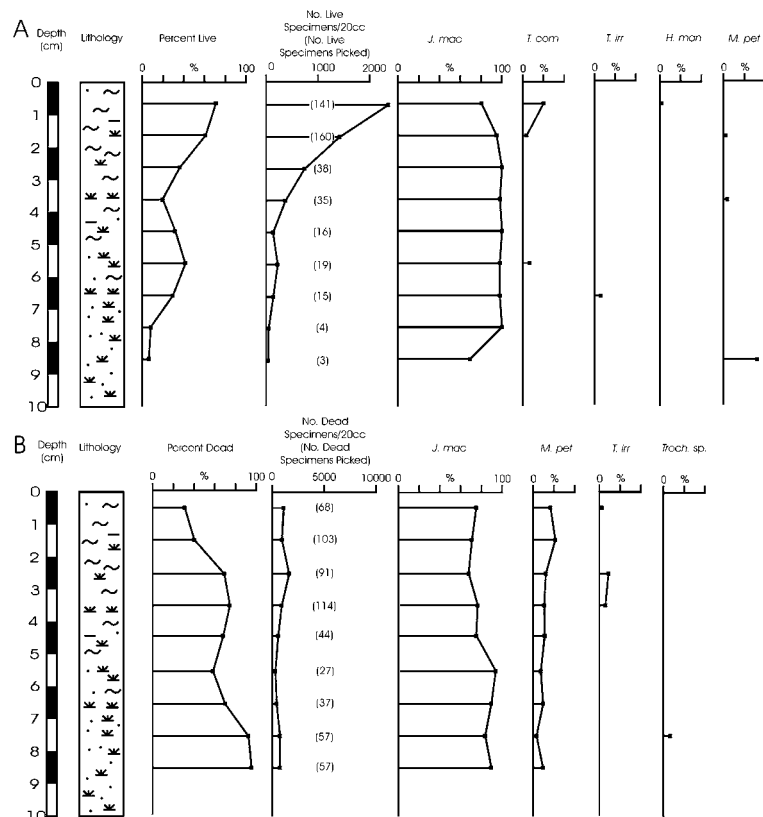
FIGURE 7. A, Relative adundance of all taxa comprising the live population in core CUR02PC06 in the high marsh on the Currituck (low salinity) barrier island. Note that peaks may result from recovery of low numbers of live specimens (see text and Fig. 8). B, Relative abundance of all taxa comprising 5 percent or more of the dead assemblage in one or more samples in core CUR02PC06. Key to abbreviations of names given in Appendix B.

ally. Several years later, living infaunal marsh foraminifera were first documented along the North American Atlantic coast by Akers (1971), who found *Ammonia beccarii, Arenoparrella mexicana, Miliammina fusca, Tiphotrocha comprimata* and *Trochammina laevigata* living at various depths down to 40 cm in a Beaufort, North Carolina marsh. Further living infaunal records of several agglutinated (*Miliammina fusca, Trochammina inflata, Tiphotrocha comprimata, Ammotum salsum, Ammobaculites exiguus, Ammomarginulina fluvialis*) and calcareous (*Ammonia beccarii, Elphidium* spp.) taxa down to 10 cm depth at Larchmont Harbor, New York (Steineck and Bergstein, 1979) indicated the variety of taxa that can dwell in infaunal marsh habitats. The calcareous taxa *Ammonia* spp. and *Elphidium* spp., which have been recorded as inhabiting a wide variety of intertidal and shallow subtidal environments (Culver and Buzas, 1980; Woo and others, 1997), were not recorded in the current study. Only the calcareous marsh species (Scott and Medioli, 1980a) *Helenina anderseni* was recorded living infaunally at PI02PC01 (Fig. 9, Table 7). (Note that the infaunal agglutinated and calcareous taxa recorded by Matera and Lee (1972) at a Long Island, New York salt marsh were collected from mudflats rather than a vegetated marsh.)

Goldstein and Harben (1993), Goldstein and others (1995) and Goldstein and Watkins (1998, 1999) investigated the infaunal distribution and taphonomy of foraminifera in the mesotidal marshes of Sapelo Island and St. Catherines Island, Georgia. Samples were taken at 0–1, 3–5, 8–10, 13–

15 and 28–30 cm intervals below the marsh surface at Sapelo Island (Goldstein and Harben, 1993). *Arenoparrella mexicana* and *Haplophragmoides wilberti* were found living down to 30 cm depth. Several taxa, *Ammonia beccarii, Miliammina fusca* and *Trochammina inflata,* were found living down to 15 cm, but the majority were determined to be predominantly surface dwellers (i.e., living in the 0–1 cm interval; Goldstein and Harben, 1993). Although the North Carolina cores in this study exhibit considerably shallower records of living infaunal foraminifera than the Georgia cores of Goldstein and Harben (1993), *Arenoparrella mexicana* and *Haplophragmoides wilberti* were also found living in deep infaunal habitats, but not exclusively so (Fig. 9). In the North Carolina material, several other taxa, most notably *Jadammina macrescens,* were recorded living at deep infaunal depths (1–10 cm, Fig. 9). Goldstein and Harben (1993) similarly noted that *Miliammina fusca, Ammotium salsum* and *Ammobaculites dilatatus* (this latter binomen was not used in the current study) were less likely than other taxa to be preserved in the subsurface after death.

Goldstein and others (1995) undertook a similar study on St. Catherines Island, Georgia, taking samples at 0–1, 1–3, 3–5, 9–11, 19–21 and 29–31 cm intervals. They found that most of the commonly occurring living species could be characterized as epibenthic to intermediate infaunal (0–10 cm). A few taxa, in particular *Arenoparrella mexicana* and *Haplophragmoides wilberti*, were found living in significant numbers as deep as 30 cm below the marsh surface
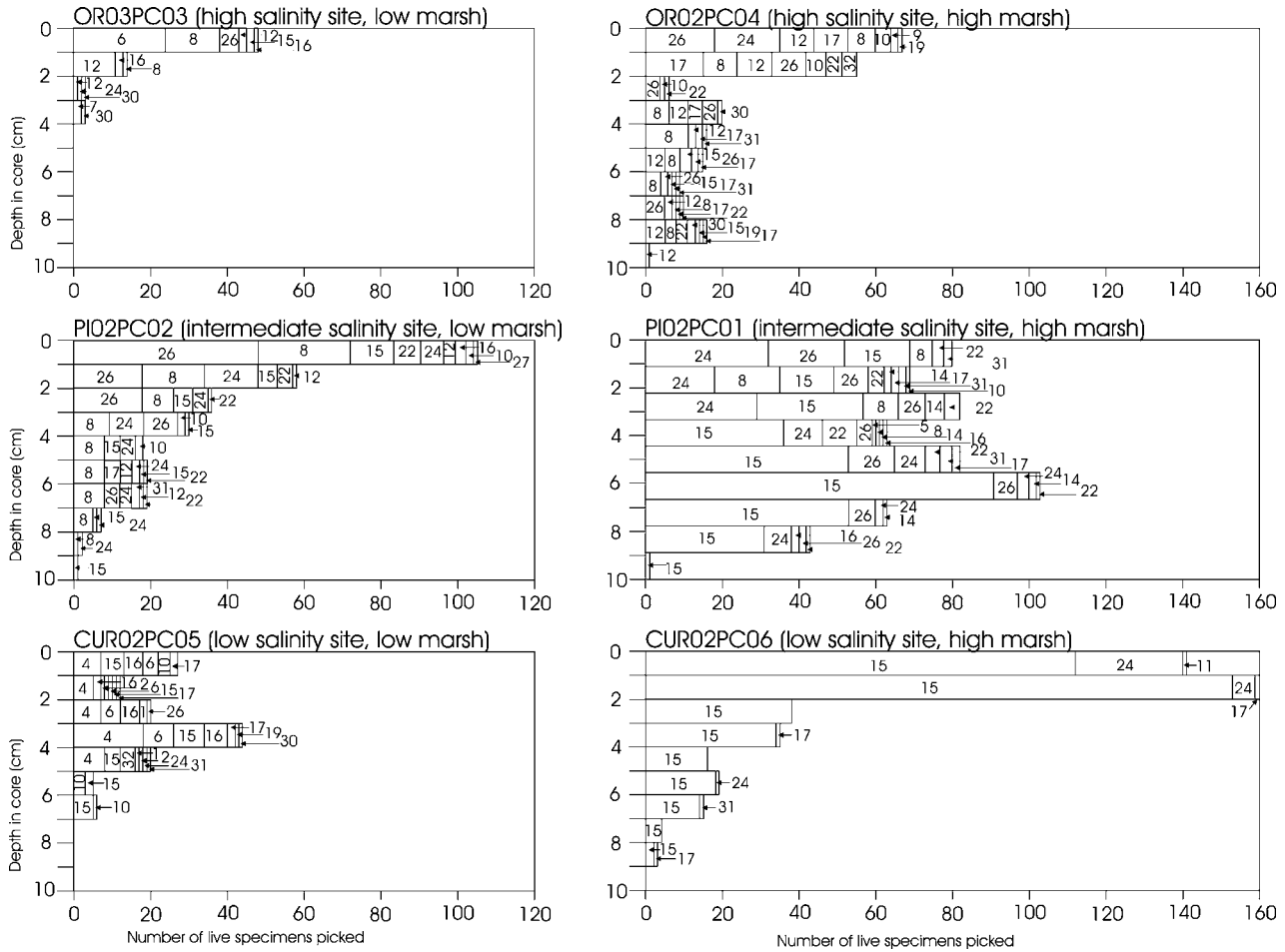
FIGURE 8. Raw counts of live foraminifera plotted with depth in each of six cores. 1, *Ammoastuta inepta*; 2, *Ammobaculites crassus*; 4, *A. subcatenulatus*; 5, *Ammobaculites* sp.; 6, *Ammotium salsum*; 7, *Ammotium* cf. *A. salsum*; 8, *Arenoparrella mexicana*; 9, *Glomospira* sp.; 10, *Haplophragmoides bonplandi*; 11, *H. manilaensis*; 12, *H. wilberti*; 14, *Helenina anderseni*; 15, *Jadammina macrescens*; 16, *Miliammina fusca*; 17, *M. petila*; 19, *Pseudothurammina limnetis*; 22, *Siphotrochammina lobata*; 24, *Tiphotrocha comprimata*; 26, *Trochammina inflata*; 27, *T. nana*; 30, *Trochammina* sp.; 31, *Trochamminita irregularis*; 32, indeterminate agglutinated.

(Goldstein and others, 1995). These results are generally consistent with the infaunal distributions from North Carolina marshes (Fig. 9) although, as for Sapelo Island, live foraminifera were found much deeper at St. Catherines Island. Seven calcareous species were found living at St. Catherines Island, in strong contrast to North Carolina marshes where only *Helenina anderseni* was found living (Fig. 9). The taxa that were less likely to be preserved after death (Goldstein and others, 1995) were the same as those on Sapelo Island, again consistent with the results of this study. Goldstein and Watkins (1998, 1999) reiterated that *Miliammina fusca, Ammotium* spp. and *Pseudothurammina limnetis* were less likely to be preserved than other agglutinated taxa as a result of bacterial degradation of the cements holding agglutinated particles together. They also described ''half tests'' of *Miliammina fusca, Arenoparrella mexicana* and *Trochammina* spp. and attributed this to metazoan predation, possibly by fiddler crabs (Goldstein and Watkins, 1999). Similar half-tests were observed in the North Carolina marsh material, and fiddler crabs are abundant in this region. However, breakage of tests can also oc-

cur during processing and so predation may not be the cause of this mode of preservation.

Collins (1996), in his study of infaunal marsh foraminifera from three South Carolina marshes, found live foraminifera in short cores to a depth of 20 cm. In low marsh cores, most live foraminifera occurred in the upper 5 cm, whereas in a middle marsh core, living foraminiferal densities were highest between 7 and 14 cm (Collins, 1996). This result contrasts with the current study where no significant abundance peaks of live foraminifera were discerned. The taxa Collins (1996) found living in the subsurface were generally the same as in this study (*Miliammina fusca, Trochammina inflata, Jadammina macrescens, Ammotium salsum, Arenoparrella mexicana* and *Tiphotrocha comprimata*). Also similar to the current study, deep infaunal living populations were generally taxonomically similar to shallow infaunal (0–1 cm) populations. Collins (1996) noted that marsh foraminifera from South Carolina were poorly preserved in the subsurface. He attributed this to metazoan bioturbation and bacterial breakdown of agglutinated tests. As noted above, bacterial degradation is also

TABLE 6. Currituck barrier island, Core CUR02PC06 (low salinity, high marsh). Numbers of living and dead foraminifera. Key to abbreviations of names given in Appendix B.

Sample depth (cm)	Live, Dead, Total	J. mac	T. com	H. man	M. pet	A. inep	T. inf	T. irr	Ammob. sp	M. fus	P. lim	H. bon	P. ipo	Troch. sp.	indet.	Total	%	No. Species	Aliquot Picked
0–1	L	112	28	1												141	67.5	3	
	D	51			11	3	1	1	1							68	32.5	6	
	T	163	28	1	11	3	1	1	1							209	100	8	1/8
1–2	L	153	6		1											160	60.1	3	
	D	73			22	4				4						103	39.9	4	
	T	226	6		23	4				4						263	100	5	1/24
2–3	L	38														38	29.5	1	
	D	61			11	2		8		1	3	2	1		2	91	70.5	9	
	T	99			11	2		8		1	3	2	1		2	129	100	9	1/24
3–4	L	34			1											35	23.6	2	
	D	89			16	1	1	6		1						114	76.5	6	
	T	123			17	1	1	6		1						149	100	6	1/24
4–5	L	16														16	32.0	1	
	D	38			5								1			44	68.0	3	
	T	54			5								1			50	100	3	1/36
5–6	L	18	1													19	41.3	2	
	D	25			2											27	58.7	2	
	T	38	1		2											46	100	3	1/24
6–7	L	14							1							15	28.8	2	
	D	34			3											37	71.2	2	
	T	48			3			1								52	100	3	1/12
7–8	L	4														4	6.6	1	
	D	51			2									4		57	93.4	3	
	T	55			2									4		61	100	3	1/8
8–9	L	2			1											3	5.0	2	
	D	52			5											57	95.0	2	
	T	54			6											60	100	2	1/8
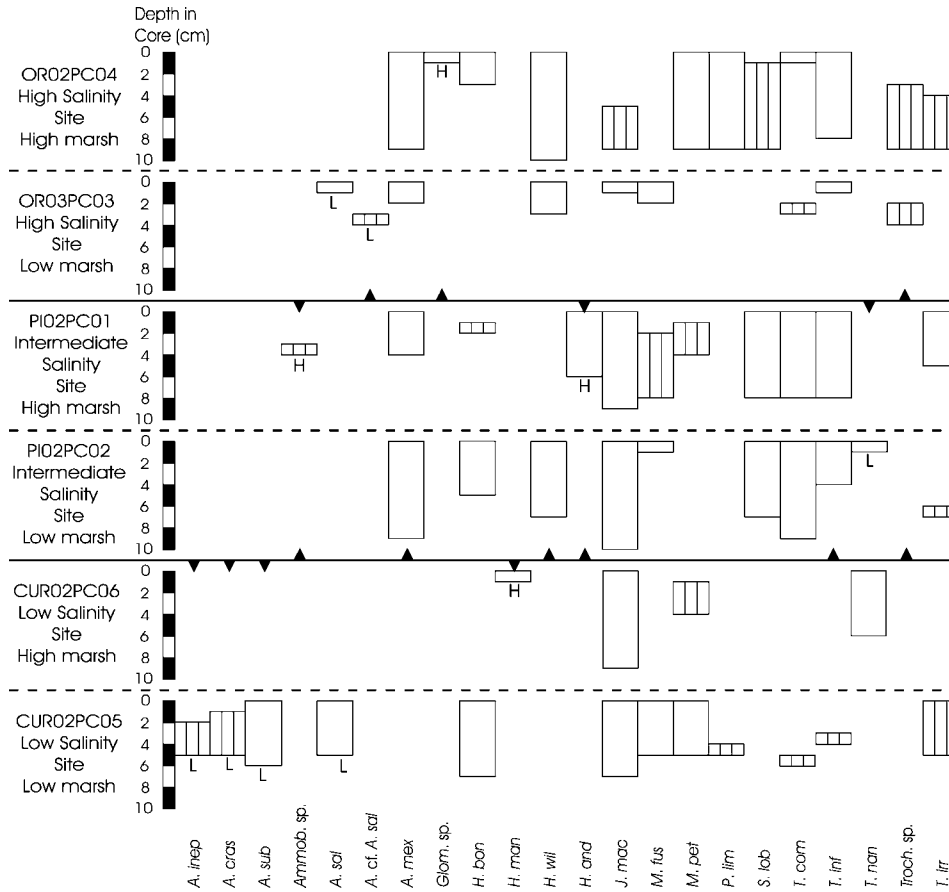
FIGURE 9.   Depth ranges (cm) of all live taxa recorded in six Outer Banks salt marsh cores. Vertical bars, deep infaunal only records; L, records of taxa only found in low marsh; H, records of taxa only found in high marsh. Key to abbreviations of names given in Appendix B.

TABLE 7.   Lists of live taxa with restricted distributions. *indicates taxa that are always rare (never >5% of a population) (i.e., unreliable indicators because more likely to have a restricted distribution due to lower probability of being found). Note that taxa may be listed more than once.

Infaunal only	Deep infaunal (4 of 5 records)	Shallow infaunal only
Ammoastuta inepta	*Trochamminita irregularis*	*Glomospira* sp.
Ammobaculites crassus		*Haplophragmoides manilaensis*
Ammobaculites sp.		*Trochammina nana*
Ammotium cf. *A. salsum*		
Trochammina sp.		

Low salinity site only	Intermediate salinity site only	High salinity site only
Ammoastuta inepta	*Ammobaculites* sp.	*Ammotium* cf. *A. salsum*
Ammobaculites crassus	*Helenina anderseni*	*Glomospira* sp.
Ammobaculites subcatenulatus	*Trochammina nana*	Trochammina sp.
Haplophragmoides manilaensis		

Low to intermediate salinity sites	Intermediate to high salinity sites	
	Arenoparrella mexicana	
	Haplophragmoides wilberti	
	Siphotrochammina lobata	

Low marsh only	High marsh only	
Ammoastuta inepta	*Ammobaculites* sp.	
Ammobaculites crassus	*Glomospira* sp.	
Ammobaculites subcatenulatus	*Haplophragmoides manilaensis*	
Ammotium salsum	*Helenina anderseni*	
Ammotium cf. *A. salsum*		
Trochammina nana		

probably a common process in North Carolina marshes. Collins (1996) contrasted this poor preservation of marsh foraminifera with the generally good preservation of marsh foraminifera in the subsurface in the more northerly locations of Maine (Gehrels, 1994) and Nova Scotia (Scott and others, 1995a), where bioturbation is less extensive.

Saffert and Thomas (1998) documented the live infaunal population in two northern marshes, in Connecticut and Massachusetts. They sliced short cores into 2–5 cm segments, but also sampled the 0–1 cm interval of the immediately adjacent marsh. As in the current study, the majority of live specimens were found in the 0–1 cm and 2–5 cm intervals, although a significant number were also found down to 15 cm. Saffert and Thomas (1998), however, did find specimens living as deep as 50 cm, much deeper than in the current study, where live specimens were restricted to the top 10 cm (or shallower) of sediment (although this was the result of a major change in lithology at 10 cm in two cores and the lack of samples from much deeper depths). Saffert and Thomas (1998) argued that deep infaunal populations are probably related to bioturbation by metazoa. Where bioturbation was present (low and middle marsh) live specimens were found at depth. In the high marsh, which is not bioturbated by metazoa, live specimens were not found deeper than 25 cm (although this would be a very deep record in North Carolina cores). *Trochammina inflata* was consistently found living at depth, although it was most abundant in the 0–1 cm interval. *Miliammina fusca* and *Ammotium salsum* were consistently found living at shallow infaunal depths (Saffert and Thomas, 1998). Thus, the abundance of living infaunal specimens varied with species, probably (according to Saffert and Thomas, 1998) as a result of differential survival rates after specimens were introduced to deeper infaunal habitats by metazoan bioturbation. These results are not inconsistent with those of the current study (see, for example, patterns of infaunal occurrences for *T. inflata, M. fusca* and *A. salsum* in Fig. 9, Table 7). However, it is not clear from the North Carolina data if this is due to differential survival or differential preservation or, indeed, both.

Hippensteel and others (2000, 2002) reported on a seasonal study of infaunal marsh foraminifera. They sampled three sites in coastal Delaware every three months over three years. Only the five most abundant species, *Jadammina macrescens, Trochammina inflata, Arenoparrella mexicana, Miliammina fusca* and *Pseudothurammina limnetis*, were counted at low-, intermediate- and high-marsh sites in 0–1, 1–3, 3–5, 10, 20, 30, 40, 50, and 60 cm intervals. Live foraminifera were found as deep as 60 cm but were concentrated in the upper 20 cm (Hippensteel and others, 2000, 2002). *Jadammina macrescens, T. inflata* and *A. mexicana* were widely distributed throughout the cores and seasons, but were particularly abundant in the high marsh. *Miliammina fusca* and *P. limnetis,* in contrast, had more patchy distributions (Hippensteel and others, 2000, 2002). *Jadammina macrescens* is more likely to dominate the living populations at higher marsh sites in North Carolina (Figs. 2A, 3A, 4A, 5A, 6A, 7A), but *T. inflata* and *A. mexicana* are dominant species in the higher marsh only at Oregon Inlet (high salinity). At Pea Island (intermediate salinity), they are more dominant in the low marsh, whereas

at Currituck (low salinity), *A. mexicana* does not occur live and *T. inflata* is rare (Figs. 2A, 3A, 4A, 5A, 6A, 7A).

Tobin and others (2005) analyzed seasonal infaunal data from Chezzetook Inlet, Nova Scotia, and North Inlet, South Carolina, and replotted data from Nanaimo, British Columbia (Ozarko and others, 1997). They were particularly interested in investigating the effect of living infaunal populations on the relative percentages of species in the total assemblage (living plus dead). They concluded that neither living infaunal populations nor taphonomic processes significantly affect the total assemblage down core at all three sites. That same conclusion can generally be drawn from a comparison of live and dead plots in Figures 2–7, with the exception of variable, taxon-specific loss of tests down core. The live population closely resembles the dead assemblage in terms of taxonomic composition in all cores except OR03PC03 (high-salinity, low marsh), where the patterns are unclear due to the presence of very low numbers of specimens.

Infaunal studies from the Atlantic marshes of northwestern Europe are rare. Horton (1999) studied the intertidal foraminifera of Cowpen Marsh, Tees Estuary, UK. He identified ten living foraminiferal species from the three environments (high marsh, low marsh and tidal flat). Three agglutinated species (*Jadammina macrescens, Miliammina fusca* and *Trochammina inflata*) and two calcareous species (*Elphidium williamsoni* and *Haynesina germanica*) dominated the living assemblage. The highest number of living foraminifera for each of these five species was observed in the surface sample (0 to 1 cm depth), which indicates that these taxa are primarily shallow infaunal. The surface sample contained 75.2% of all living foraminifera. However, 24.8% were found below the surface sample, 7.6% below 3 cm, and only 1.2% below 6 cm. Small, living populations of *Brizalina inflata* and *Cibicides lobatulus* were found at depths of 9 and 11 cm. This deep infaunal occurrence of living foraminifera may be due to an 'oxygen oasis' within which living foraminifera may cluster (Goldstein and Harben, 1993) or to bioturbation, whereby living foraminifera bypass the surface through biogenic transport or by falling into tubes or burrows (Green and others, 1993).

Horton and Edwards (in press a) investigated the salt-marsh and tidal flat environments of Rusheen Bay, Ireland. They concluded that the intertidal foraminifera of Rusheen Bay live primarily in shallow infaunal habitats. The silt substrate of the high, middle and low marsh environments prevents significant penetration and, thus, deep infaunal foraminifera do not occur. Using a Sediment Profile Imagery Camera, Horton and Edwards (in press a) showed that these marsh environments have a 3-cm-deep oxygenated layer of sediment in which the foraminifera live. In contrast, the tidal flat environment of Rusheen Bay, which has a sandier substrate, contains a deeper oxygenated layer (5cm) and better aerated sediment (Kitazato, 1994), and subsequently, a greater percentage of infaunal foraminifera.

IMPLICATIONS FOR SEA LEVEL RECONSTRUCTION

Following the work of Phleger (1965, 1970), who suggested that salt marsh foraminifera might be distributed in zones related to height above mean sea level, Scott (1976)

and Scott and Medioli (1978, 1980a) demonstrated such a relationship. They pointed out that this zonation could be used to relocate former sea levels to an accuracy of ± 5 cm. Since that time, many studies around the world have repeatedly shown a marsh foraminiferal zonation that can be used for sea level studies (e.g., Scott and Medioli, 1986; Patterson, 1990; Thomas and Varekamp, 1991; Van de Plaasche, 1991; Gehrels, 1994, 2000; Williams, 1994, Scott and others, 1990, 1995a, b, c, 2001; Hayward and others, 1999; Horton, 1999; Horton and others, 1999a, b, 2000, 2003; Edwards and Horton, 2000; Horton and Edwards, 2003, in press b; Edwards and others, 2002).

Scott and Medioli (1978, 1980a, and succeeding works) defined marsh foraminiferal zonations using the 0–1 cm interval of marsh sediments. More recently, Ozarko and others (1997), Patterson and others (1999) and Goldstein and Watkins (1999), noting significant infaunal populations and taphonomic loss of particular taxa, suggested that foraminifera of the 0–10 cm interval rather than the 0–1 cm interval should be used as the baseline data for paleoenvironmental studies. However, Patterson and others (2004) demonstrated that whether the 0–1 or 0–10 cm intervals should be used is dependent on geographic location. Thus, the pattern of infaunal foraminiferal distributions should be discerned for each location before a sampling scheme is chosen.

The results from the current study suggest that the 0–1 cm interval represents the deeper infaunal populations and assemblages quite well in 5 of 6 cores. The exception is core OR03PC03 taken from the low marsh immediately adjacent to high-salinity waters of Pamlico Sound at Oregon Inlet. At this site, live foraminifera penetrate only 4 cm into the substrate even though the marsh is bioturbated. The vast majority of live specimens are located in the 0–1 cm interval. Thus, it is not surprising that the deeper infaunal populations, containing just a few specimens per unit volume (Fig. 2A), are dominated by different taxa than the 0–1 cm interval. Because live specimens are so low in number, they would not significantly affect the composition of the dead assemblage if added to them to form a total assemblage. In essence, the dead assemblage *is* the total assemblage (Buzas, 1965).

In the other five cores, the live populations are generally similar to the dead assemblages through the entire depth interval in which live foraminifera occur (Figs. 3–7). Further, the live population or dead assemblage in the 0–1 cm interval is very similar to the populations and assemblages at all depths (Figs. 3–7) even though some taxa (*Miliammina fusca* in particular) are preferentially affected by bacterial degradation of the cement that holds their tests together.

Thus, in the North Carolina marshes located on the Outer Banks and fringing Pamlico and Currituck Sounds, live populations and dead assemblages in the 0–1 cm interval are generally representative of the deeper infaunal foraminifera population and assemblages and can be used as the basis for paleoenvironmental reconstructions, including those of former sea levels. Whether live populations, dead assemblages or total assemblages should be used (see alternative viewpoints from Scott and Medioli, 1980b and Murray, 2000) is, in our opinion, somewhat moot. The results from

this study suggest that an unstained 0–1 cm sample will provide a model assemblage that can be used to interpret fossil assemblages. In most cases live foraminifera are so outnumbered by dead specimens that the dead assemblage is essentially indistinguishable from the total assemblage (Buzas, 1965). What is also clear from this study is that danger lies in using contemporary assemblages from a particular salinity regime as a model to interpret fossil assemblages from a different salinity regime. The differences between the foraminifera at the three sites in this study (Figs. 2–9, Tables 1–7) suggest that errors in interpretation caused by this potential problem would be more significant than those caused by the presence or absence of deep infaunal foraminifera, or by differential taphonomic loss of specimens of particular taxa.

Would the results and conclusions of this study be different if seasonal data had been available rather than one-time data? The results of many previous seasonal studies (e.g., Bradshaw, 1957, 1961; Phleger and Lankford, 1957; Boltovskoy, 1964; Buzas, 1965; Brooks, 1967; Lutze, 1968; Boltovskoy and Lena, 1969; Wefer, 1976; Murray, 1983; Basson and Murray, 1995; Murray and Alve, 2000) suggest that reproduction often takes place throughout the year and patterns and levels of density for particular taxa vary from year to year. This is confirmed by the longest running seasonal study of shallow water benthic foraminifera, in the Indian River, Florida (Buzas, 1978; Buzas and Hayek, 2000; Buzas and others, 2002). Conclusions drawn from a single sampling period are likely, therefore, to be as representative as seasonal samples taken over several years. Further, it is simply not logistically feasible to sample over many seasons in each study at every locality.

SUMMARY AND CONCLUSIONS

Twenty-two taxa of benthic foraminifera have been recorded live in six cores from three different salinity settings in back-barrier marshes of North Carolina's Outer Banks. Of these, eight taxa are found only in the shallow infaunal depth interval (0–1 cm) and 14 occur in one or more cores as deep infaunal (>1 cm depth) species. Only two species, *Jadammina macrescens* and *Tiphotrocha comprimata,* were recorded live in all six cores. The other 20 taxa exhibit restricted distributions in ten categories related to different combinations of salinity regime, physical location on the marsh, and depth of infaunal habitat.

The pattern of preservation potential of infaunal foraminifera is not consistent. At Pea Island (intermediate salinity) and Currituck (low salinity), foraminifera are more likely to be preserved in the lower marsh than in the higher marsh. In contrast, the (high salinity) Oregon Inlet locality exhibits the opposite pattern. *Arenoparrella mexicana, Haplophragmoides wilberti, Jadammina macrescens* and *Trochammina inflata* are the taxa most resistant to post-mortem breakage and/or disintegration. *Ammobaculites* and *Ammotium* tend to exhibit breakage. *Miliammina fusca* is the species most susceptible to test disintegration, probably as a result of bacterial degradation of the test cement.

Comparison of the results of this study with those from other marshes along the North American Atlantic coast indicate that infaunal foraminifera in North Carolina marshes,

in general, do not live as deep as in other marshes. In part, this is due to down-core lithologic (i.e., environmental) change and, perhaps, to the possibility that patchy occurrences of rare live foraminifera deeper than 10 cm were not noted as a result of the sampling scheme. It is clear, however, that live foraminifera are concentrated in the upper few centimeters of core and, in all cases, numbers of live foraminifera decrease to zero by 10 cm depth. In contrast to several previous studies, only one calcareous species, *Helenina anderseni,* is found living in North Carolina's salt marshes (although other calcareous taxa have been found in the muddy deposits of small intra-marsh ponds on Pea Island).

The results of this study indicate that the population/assemblage of foraminifera found in the 0–1 cm interval represents well the deeper infaunal populations/assemblages. This suggests that, in this geographic location, the foraminifera of the 0–1 cm interval can serve as the model upon which older marsh deposits can be related to past sea level change.

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APPENDIX A

Original references to the taxa identified to the specific level. * indicates taxa found living.

*Ammoastuta inepta (Cushman and McCulloch) = *Ammobaculites ineptus* Cushman and McCulloch. 1939, p. 89, pl. 7, fig. 6.

*Ammobaculites crassus Warren = *Ammobaculites crassus* Warren, 1957, p. 32, pl. 3, figs. 5–7.

Ammobaculites exiguus Cushman and Bronnimann *Ammobaculites exiguus* Cushman and Bronnimann, 1948b, p. 38, pl. 7, figs. 7–8.

*Ammobaculites subcatenulatus Warren *Ammobaculites subcatenulatus* Warren, 1957, p. 32, pl. 3, figs. 11–13.

*Ammotium salsum (Cushman and Bronnimann) *Ammobaculites salsus* Cushman and Bronnimann, 1948a, p. 16, pl. 3, figs. 7–9.

*Arenoparrella mexicana (Kornfeld) *Trochammina inflata* (Montagu) var. *mexicana* Kornfeld, 1931, p. 86, pl. 13, fig. 5.

*Haplophragmoides bonplandi Todd and Bronnimann *Haplophragmoides bonplandi* Todd and Bronnimann, 1957, p. 23, pl. 2, fig. 2.

*Haplophragmoides manilaensis Andersen *Haplophragmoides manilaensis* Andersen, 1953, p. 22, pl. 4, figs. 8a,b.

*Haplophragmoides wilberti Andersen *Haplophragmoides wilberti* Andersen, 1953, p. 21, pl. 4, fig. 7.

*Helenina anderseni (Warren) *Pseudoeponides anderseni* Warren, 1957, p. 39, pl. 4, figs. 12–15.

*Jadammina macrescens (Brady) *Trochammina inflata* (Montagu) var. *macrescens* Brady, in Brady and Robertson, 1870, p. 47, pl. 11, figs. 5a–c.

*Miliammina fusca (Brady) *Quinqueloculina fusca* Brady, in Brady and Robertson, 1870, p. 47, pl. 11, figs. 2–3.

*Miliammina petila Saunders *Miliammina petila* Saunders, 1958, p. 88, pl. 1, fig. 15.

Polysaccammina ipohalina Scott *Polysaccammina ipohalina* Scott, 1976, p. 318, pl. 2, figs. 1–4, text figs. 4a-c.

*Pseudothurammina limnetis (Scott and Medioli) *Thurammina* (?) *limnetis* Scott and Medioli, 1980a, p. 43, 44, pl. 1., figs. 1–3.

Reophax nana Rhumbler *Reophax nana* Rhumbler, 1911, p. 182, pl. 8, figs. 6–12.

*Siphotrochammina lobata Saunders *Siphotrochammina lobata* Saunders, 1957, p. 3, pl. 9, figs. 1,2.

Textularia earlandi Parker Parker, 1952, p. 458. Parker and Athearn, 1959, p. 340, p. 50, fig. 7.

*Tiphotrocha comprimata (Cushman and Bronnimann) *Trochammina comprimata* Cushman and Bronnimann, 1948b, p. 41, pl. 8, figs. 1–3.

Trochammina compacta Parker *Trochammina compacta* Parker, 1952, p. 458, p. 2, figs. 13–15.

*Trochammina inflata (Montagu) *Nautilus inflatus* Montagu, 1808, p. 81, pl. 18, fig. 3.

*Trochammina nana (Brady) *Haplophragmium nanum* Brady, 1881, p. 50.

Trochammina ochracea (Williamson) *Rotalina ochracea* Williamson, 1858, p. 55, pl. 4, fig. 112.

Trochammina rotaliformis Wright *Trochammina rotaliformis* Wright in Heron-Allen and Earland, 1911, p. 309, pl. 13, figs. 11,12.

*Trochamminita irregularis Cushman and Bronnimann *Trochamminita irregularis* Cushman and Bronnimann, 1948a, p. 17, pl. 4, figs. 1–3.

APPENDIX B

Abbreviations for names used in Tables 1–6 and Figures 2–7.

A. inep	=	*Ammoastuta inepta*
A. cras	=	*Ammobaculites crassus*
A. exig	=	*Ammobaculites exiguus*
A. sub	=	*Ammobaculites subcatenulatus*
Ammob. sp.	=	*Ammobaculites* sp.
A. sal	=	*Ammotium salsum*
A. cf. *A. sal*	=	*Ammotium* cf. *A. salsum*
A. mex	=	*Arenoparrella mexicana*
Glom. sp.	=	*Glomospira* sp.
H. bon	=	*Haplophragmoides bonplandi*
H. man	=	*Haplophragmoides manilaensis*
H. wil	=	*Haplophragmoides wilberti*
Haplo. sp.	=	*Haplophragmoides* sp.
H. and	=	*Helenina anderseni*
J. mac	=	*Jadammina macrescens*
M. fus	=	*Miliammina fusca*
M. pet	=	*Miliammina petila*
P. ipo	=	*Polysaccammina ipohalina*
P. lim	=	*Pseudothurammina limnetis*

R. nan   = *Reophax nana*
Reo. sp.   = *Reophax* sp.
S. lob   = *Siphotrochammina lobata*
T. ear   = *Textularia earlandi*
T. com   = *Tiphotrocha comprimata*
T. comp   = *Trochammina compacta*

T. inf   = *Trochammina inflata*
T. nan   = *Trochammina nana*
T. och   = *Trochammina ochracea*
T. rot   = *Trochammina rotaliformis*
Troch. sp. = *Trochammina* sp.
T. irr   = *Trochamminita irregularis*
Indet.   = indeterminate agglutinated