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INFLUENCE OF PATCHINESS ON MODERN SALT-MARSH FORAMINIFERA USED IN SEA-LEVEL STUDIES (NORTH CAROLINA, USA)

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ABSTRACT

We collected replicate samples at stations placed systematically along a transect at Oregon Inlet (North Carolina, USA) to investigate spatial homogeneity of dead assemblages of salt-marsh foraminifera. Analysis of variance (ANOVA) was used to investigate the differences in mean proportions for six species (*Miliammina fusca, Trochammina inflata, Arenoparrella mexicana, Tiphotrocha comprimata, Haplophragmoides wilberti and Jadammina macrescens*) selected because of their importance in distinguishing assemblages across salt marshes in the study region. As expected, ANOVA's on all species indicated significant differences among low-, middle-, and high-marsh zones defined by their flora. No significant differences were found between stations in the low- and high-marsh indicating homogeneity in these zones. In contrast, for all six species in the middle-marsh zone, significant outcomes for ANOVA, cluster analysis and post-hoc comparisons suggested that the middle-marsh should be divided into two zones. In addition, two species exhibited a patchy (inhomogeneous) distribution among all stations in the middle marsh. If confirmed by additional studies, our results indicate that sampling of modern salt-marshes to document the distribution of foraminifera for use in sea-level reconstructions should recognize the spatial variability associated with the middle-marsh floral zone.

INTRODUCTION

Foraminifera have been widely used as sea-level indicators on the basis of a quantifiable relationship between assemblage distributions and tidal elevations on modern salt marshes (e.g. Scott and Medioli, 1978; Gehrels, 1994; Horton and Edwards, 2006). A detailed understanding of the modern distribution of salt-marsh foraminifera is a necessary prerequisite for interpreting assemblage changes preserved in sedimentary archives (de Rijk, 1995). In studies focused upon reconstructing changes in sea level, this modern distribution has frequently been documented using transects across one or more salt marshes, which are positioned perpendicular to the shore and extend from shallow-subtidal to freshwater-upland environments (e.g. Scott and Medioli, 1978; Gehrels, 1994; Horton and others, 1999; Gehrels and others, 2001; Edwards and others, 2004; Southall and others, 2006; Kemp and others, 2009a; Hawkes and others, 2010). At stations positioned along each transect, the assemblage is typically described from a single sample of surface sediment usually 1 cm thick (Culver and Horton, 2005). This approach is appropriate for describing the distribution of foraminifera along a known environmental gradient despite the possible influence of spatial autocorrelation (Telford and Birks, 2005). Furthermore, it has implicit assumptions about the nature of foraminiferal populations including infaunal habitation (e.g. Goldstein and Harben, 1993; Ozarko and others, 1997; Goldstein and Watkins, 1998; Patterson and others, 1999; Horton and Murray, 2006; Leorri and Martin, 2009), seasonal and inter-annual variability (e.g. Buzas and others, 2002; Hippensteel and others, 2002; Horton and Murray, 2006; Berkeley and others, 2008; Martin and others, 2009) and small-scale (meter) spatial patterns, termed patchiness (Buzas, 1968; Swallow, 2000; Morvan and others, 2006). The latter is the focus of this paper.

At a sufficiently small spatial scale, it is reasonable to expect homogeneity of environmental conditions and that foraminifera will be randomly distributed as all spots are equally favorable (Buzas, 1968). This area of homogeneity for foraminifera has been considered to be on the order of 1–40 m^2 (Lynts, 1966; Buzas, 1969; Buzas, 1970; Swallow, 2000). Under such circumstances, any single sample from the area is equally as likely to be representative of the target population. In contrast, where this presumed random distribution does not exist, foraminifera may have an aggregated or patchy spatial distribution (Buzas, 1968). If salt-marsh foraminifera have a patchy distribution then single samples collected along transects may not adequately describe their modern distribution and compromise the reliability of any subsequent sea-level reconstruction. This concern may be particularly acute for studies seeking to produce high-resolution reconstructions concerned with decimeter-scale vertical variations in sea level (e.g. Gehrels and others, 2005; Gehrels and others, 2006; Gehrels and others, 2008; Leorri and others, 2008; Kemp and others, 2009b). Most investigations pertaining to the patchiness of foraminiferal assemblages have focused on ecological studies of living populations (Lynts, 1966; Buzas, 1968; Buzas, 1970; Schafer, 1971; Swallow, 2000; Buzas and others, 2002) and few have considered dead assemblages from salt-marsh environments (Swallow, 2000; Morvan and others, 2006), which are the most applicable for sea-level reconstructions (Gehrels, 2007).

In this study we investigate the influence of patchiness on dead assemblages of salt-marsh foraminifera at Oregon Inlet in North Carolina, USA. Replicate samples collected along a transect are used to test if single samples provide an appropriate modern analog for reconstructing former sea levels.

STUDY AREA

The Outer Banks of North Carolina on the Atlantic coast of the USA are an extensive chain of barrier islands

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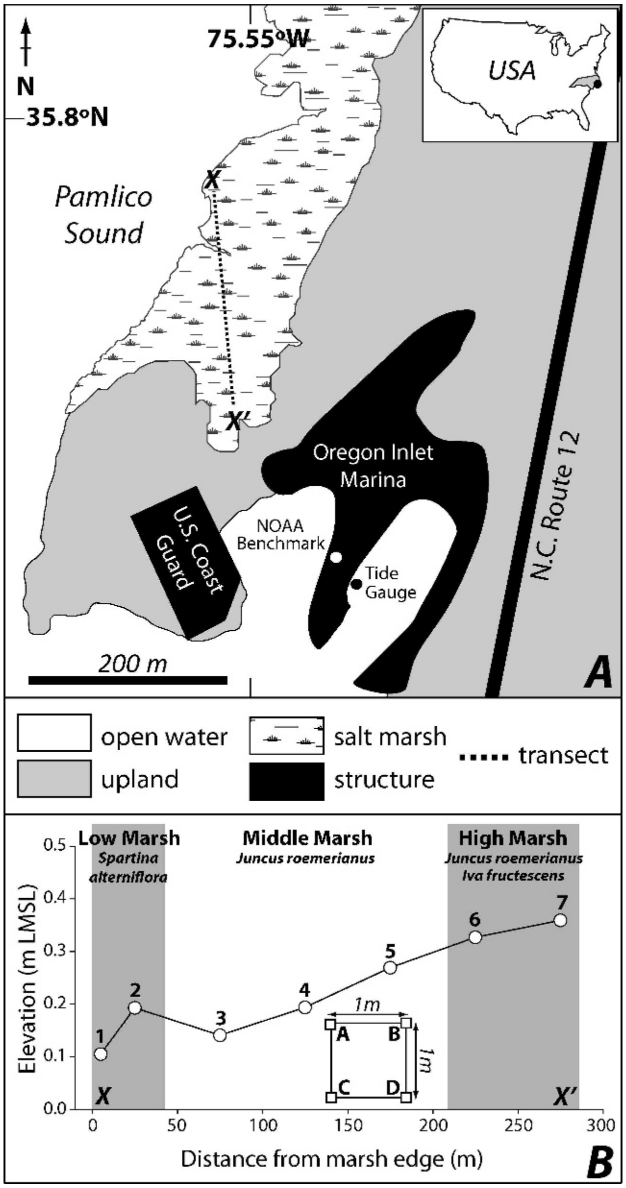

FIGURE 1. (A) Location of the Oregon Inlet study site in North Carolina, USA and the positioning of the transect (X to X′) across the salt marsh. (B) Elevation profile and positioning of sampling stations along the transect, LMSL = Local Mean Sea Level. Low marsh stations were situated in a floral zone of *Spartina alterniflora*, the middle marsh is vegetated by an expansive monospecific stand of *Juncus roemerianus* and the high marsh is characterized by *Juncus roemerianus* and *Iva fructescens*. Inset is a schematic representation of the replicate samples (A, B, C, D) collected from the four corners of a 1 m^2 quadrat at each of the seven sampling stations.

separated from the mainland by the Albemarle-Pamlico estuarine lagoon system. The study site is situated approximately 2 km north of Oregon Inlet, which is the only open inlet along the central and northern Outer Banks and allows exchange of marine waters between Pamlico Sound and the Atlantic Ocean (Fig. 1A). The site is a back-barrier salt marsh up to 300 m wide. Salinity in Pamlico Sound close to the study site varies from 26–30 ppt (Schwartz and Chestnut, 1973; Williams and others, 1973; Culver and Horton, 2005; Kemp and others, 2009a). Tidal range at the Oregon Inlet Marina tide-gauge (Fig. 1A) is 0.36 m (MLLW to MHHW).

TABLE 1. Classification of samples for use in Analysis of Variance. Four replicate samples (A, B, C, and D) were collected at each of seven sampling stations (1–7) along a transect. Salt-marsh environments were defined on the basis of vascular vegetation. LMSL = local mean sea level.

Sampling Station No.	Replicate	Elevation (m LMSL)	Salt-Marsh Floral Environment
1	A, B, C, D	0.10	Low
2	A, B, C, D	0.19	Low
3	A, B, C, D	0.14	Middle
4	A, B, C, D	0.19	Middle
5	A, B, C, D	0.27	Middle
6	A, B, C, D	0.33	High
7	A, B, C, D	0.35	High

Low-marsh floral settings at Oregon Inlet are vegetated by *Spartina alterniflora*, which is replaced inland by an extensive, monospecific middle marsh of *Juncus roemerianus*. High-marsh floral settings at the site are characterized by a mixed stand of *J. roemerianus* and *Iva fructescens* (Fig. 1B). The absence of a tidal-flat environment is common in this region, where most organic estuarine shorelines are undergoing active erosion (Riggs, 2001).

METHODS

SAMPLING REGIME

At the Oregon Inlet site we established a transect of seven sampling stations perpendicular to the shoreline from 0.10 m LMSL (Local Mean Sea Level) to 0.36 m LMSL. The sampling stations included low (stations 1 and 2), middle (stations 3–5) and high (stations 6 and 7) salt-marsh environments defined on the basis of vascular vegetation (Fig. 1, Table 1). The transect was in the immediate vicinity of those sampled by Culver and Horton (2005), Horton and Culver (2008) and Kemp and others (2009a). Sample elevations were established by leveling to a nearby geodetic benchmark and tide gauge at Oregon Inlet Marina (Fig. 1A). At each of the seven sampling stations we collected four replicate samples (termed A, B, C, and D) that represented the corners of a 1 m^2 quadrat (Fig. 1B). For hypothesis testing, environmental conditions were assumed to be the same for all stations (and replicates) within each of the salt-marsh floral zones, although it is acknowledged that variability may exist at this spatial scale, which is likely correlated with the elevational range of stations within each floral zone (Fig. 1B; Table 1). Sampling was undertaken in May 2007.

SAMPLE PREPARATION

For each replicate we collected a 10 cm^3 surface (1 cm thick) sediment sample. All samples were stored in buffered ethanol and stained using rose Bengal to allow recognition of individuals living at the time of collection (Walton, 1952; Murray and Bowser, 2000). Samples were sieved to isolate material in the 63–500 μm size range and divided into eight aliquots using a wet splitter (Scott and Hermelin, 1993). A minimum of 200 dead foraminifera were counted wet under a binocular microscope from a known fraction of the original sediment. In this paper we analyze the dead assemblages, as Culver and Horton (2005) concluded that they were the most appropriate analogs for sea-level reconstructions in North Carolina. Identifications of foraminifera were confirmed by comparison with type and figured specimens lodged at the Smithsonian Institution, Washington, D.C. and The Natural History Museum, London. Images of foraminifera from Oregon Inlet are included in Kemp and others (2009a). All species of *Ammobaculites* were combined into a generic group due to the difficulty of identifying broken individuals. Abundances reported in the text are an average ±1 standard deviation of the species' percentage abundance. Foraminiferal data are tabulated in the Appendix.

Statistical Analysis

We used Analysis of Variance (ANOVA) to investigate the distribution of six species of foraminifera, *Miliammina fusca* (Brady), *Trochammina inflata* (Montagu), *Arenoparrella mexicana* (Kornfeld), *Tiphotrocha comprimata* (Cushman and Brönnimann), *Haplophragmoides wilberti* (Andersen) and *Jadammina macrescens* (Brady), selected because of their importance in distinguishing assemblages across salt marshes in the study region (Kemp and others, 2009a). ANOVA is a technique for testing the significance of differences among means (Scheffe, 1959; Sokal and Rohlf, 2001). For this study we consider a <0.05 probability as significant.

We performed ANOVAs on one species at a time (unispecies analysis) following 2 arcsine square-root transformation of proportional abundance data (Owen, 1962). Transformation of the data was necessary to satisfy the assumptions of parametric statistical tests including ANOVA. Samples were classified (Table 1) on the basis of station number (1–7), replicate (A, B, C or D), and salt-marsh environment (high, middle, or low as defined by vascular vegetation). Classification of the samples enabled comparison of group means under any of the categories using ANOVA. In order to test hypotheses regarding patchiness of foraminifera, it was necessary to begin with an ecologically reasonable assumption about the area over which environmental variables and foraminifera may have a homogenous distribution (the null hypothesis). We assumed that the clear zonation of salt-marsh vegetation at Oregon Inlet is driven by the same factors that control the distribution of salt-marsh foraminifera (frequency and duration of inundation). Thus, there were two station means in the low-marsh floral zone (1A–D and 2A–D), three in the middle marsh (3A–D, 4A–D and 5A–D), and two in the high marsh (6A–D and 7A–D). Our initial assumption is independent of tidal range and does not contend that zones of salt-marsh vegetation and foraminifera should be vertically aligned (e.g. Gehrels, 1994).

Two hypotheses were tested using ANOVA. The first was the hypothesis that the six species of foraminifera had different mean abundances in low-, middle-, and high-marsh floral environments. The second hypothesis we tested was that there were significant differences between the mean abundance of the six species among stations from low-, middle-, and high-marsh floral environments. This hypothesis is the test of patchiness. We defined a patch as a station (or stations) significantly different from neighboring stations within the area of assumed homogeneity (salt-marsh floral zones). Homogeneity of samples was assumed if there was no significant difference (i.e. the probability of exceeding F was >0.05) among group mean abundances (Buzas, 1970) at the 95% confidence level (CL).

RESULTS

Distribution of Salt-marsh Foraminifera

A total of 16 species of foraminifera were identified in 28 samples collected at the Oregon Inlet site, of which nine had a maximum abundance >5% of the dead assemblage in at least one sample. The six species used in ANOVA (*M. fusca*, *Tr. inflata*, *A. mexicana*, *Ti. comprimata*, *H. wilberti*, and *J. macrescens*) represented 84–100% of the dead foraminifera enumerated in any single sample.

A narrow *S. alterniflora* low marsh is present at Oregon Inlet and was sampled at stations 1 and 2 (Fig. 1B). *M. fusca* (42±11.6%) was the dominant species in all eight replicate samples (Fig. 2). These samples were also characterized by *Tr. inflata* (25±11.9%), *Ti. comprimata* (14±8.4%), and *A. mexicana* (9±7%).

The middle marsh at Oregon Inlet is vegetated by a monospecific stand of *J. roemerianus* and was sampled at stations 3–5 (Fig. 1B). The most common foraminifera in these samples (Fig. 2) were *A. mexicana* (46%±15.9%), *Tr. inflata* (19%±10.4%), and *M. fusca* (16%±10.8%).

Sampling stations 6 and 7 were situated in the high-marsh floral environment (Fig. 1B) that was characterized by a mixed vegetation stand of *J. roemerianus* and *I. fructescens*. The dominant species of foraminifera in the eight samples (Fig. 2) were *H. wilberti* (58±9.0%) and *A. mexicana* (15±6.5%). *J. macrescens* (4.5±2.1%) was not a dominant species, but is associated with high-marsh floral environments at Oregon Inlet and has been widely recognized as an important high-marsh sea-level indicator (Scott and Medioli, 1978; Edwards and others, 2004).

Results of ANOVA demonstrated that the six species considered individually were significantly different in their mean abundance between low-, middle-, and high-marsh floral environments at the 95% CL (Table 2). Indeed, *M. fusca*, *A. mexicana*, *Ti. comprimata*, and *H. wilberti* displayed a significant difference among means at the >99% CL. This result supported the validity of our initial assumption of environmental homogeneity in salt-marsh floral zones.

Patchiness of Salt-Marsh Foraminifera

A series of 18 ANOVAs (6 species × 3 salt-marsh zones) were used to test the hypothesis that the mean abundance of six species of dead foraminifera was significantly different among stations situated in low-, middle-, and high-floral environments at Oregon Inlet (Table 3). We assumed homogeneity of environmental conditions within and between stations situated in the same floral zone. Therefore there were two low-marsh stations (1 and 2), three middle-marsh stations (3–5), and two high-marsh stations (6 and 7).

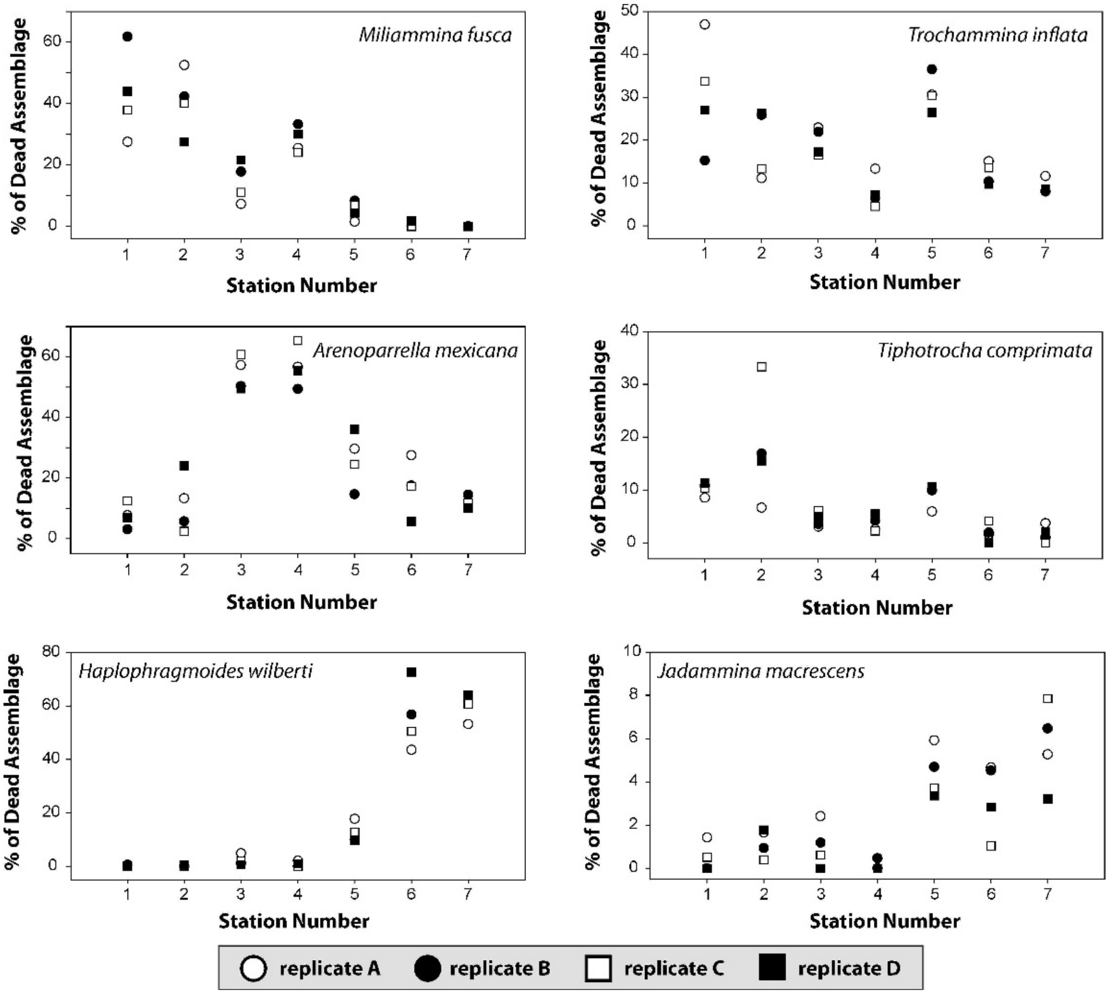

FIGURE 2. Distribution of the six species of salt-marsh foraminifera used for analysis along the Oregon Inlet transect. At each station four replicate samples (A, B, C and D) were collected representing the corners of a $1m^2$ quadrat. Results for each replicate sample (total 28) are presented as % of the dead assemblage.

Results of ANOVA for the low-marsh floral zone showed that none of the six species of foraminifera had significant differences among station means at the 95% CL (Table 3), indicating a lack of patchiness. For *M. fusca* (the dominant low-marsh taxon), the probability of exceeding F was 0.82. The species least likely to exceed F was *J. macrescens* (0.13). In contrast, there was a significant difference among station means for all six species in the middle-marsh floral zone at the 95% CL (Table 3); indeed, all were significant at the 99% CL. This suggests that middle-marsh foraminifera have a patchy distribution. The probability of exceeding F varied from 0.004 (*Ti. comprimata*) to <0.0001 (*Tr. inflata*). Unispecies ANOVA results for high-marsh floral settings showed that none of the six species had significantly different mean abundances among stations at the 95% CL (Table 3), indicating an absence of patchiness. For the high-marsh species *H. wilberti* and *J. macrescens*, the probabilities of exceeding F were 0.59 and 0.12, respectively. For other species the probability varied from 0.09 (*Tr. inflata*) to 0.90 (*Ti. comprimata*).

TABLE 2. One way Analysis of Variance results testing the significance of salt-marsh floral environment (high, middle or low) for the six species of foraminifera at Oregon Inlet. *Indicates that the species displayed a significant difference among group means at the 95% confidence level (probability <0.05), DF = degrees of freedom.

Species	DF	Sum of Squares	Mean Square	F ratio	Prob >F
Miliammina fusca	2, 26	7.49	3.75	52.96	<0.0001*
Trochammina inflata	2, 26	0.55	0.27	4.68	0.0187*
Arenoparrella mexicana	2, 26	4.50	2.25	30.07	<0.0001*
Tiphotrocha comprimata	2, 26	1.10	0.55	19.84	<0.0001*
Haplophragmoides wilberti	2, 26	13.18	6.59	137.91	<0.0001*
Jadammina macrescens	2, 26	0.31	0.15	7.00	0.0038*

TABLE 3. One way Analysis of Variance results testing the significance of patchiness within low, middle and high salt-marsh vegetation zones for the six species of foraminifera at Oregon Inlet. *Indicates that the species displayed a significant difference among group means at the 95% confidence level (probability <0.05), DF = degrees of freedom.

Marsh	Species	DF	Sum of Squares	Mean Square	F ratio	Prob >F
Low	*Miliammina fusca*	1, 6	0.00	0.00	0.06	0.82
	Trochammina inflata	1, 6	0.15	0.15	2.22	0.19
	Arenoparrella mexicana	1, 6	0.02	0.02	0.34	0.58
	Tiphotrocha comprimata	1, 6	0.08	0.08	1.88	0.22
	Haplophragmoides wilberti	1, 6	0.00	0.00	0.48	0.51
	Jadammina macrescens	1, 6	0.03	0.03	2.98	0.13
Middle	*Miliammina fusca*	2, 9	1.10	0.55	23.41	0.0003*
	Trochammina inflata	2, 9	0.77	0.39	35.32	<0.0001*
	Arenoparrella mexicana	2, 9	1.03	0.51	20.28	0.0005*
	Tiphotrocha comprimata	2, 9	0.13	0.06	10.81	0.004*
	Haplophragmoides wilberti	2, 9	0.77	0.39	23.93	0.0002*
	Jadammina macrescens	2, 9	0.31	0.15	18.64	0.0006*
High	*Miliammina fusca*	1, 6	0.01	0.01	1.00	0.36
	Trochammina inflata	1, 6	0.02	0.02	4.06	0.09
	Arenoparrella mexicana	1, 6	0.03	0.03	0.77	0.41
	Tiphotrocha comprimata	1, 6	0.00	0.00	0.02	0.90
	Haplophragmoides wilberti	1, 6	0.01	0.01	0.33	0.59
	Jadammina macrescens	1, 6	0.03	0.03	3.20	0.12

DISCUSSION

DISTRIBUTION AND PATCHINESS OF MODERN SALT-MARSH FORAMINIFERA

Results of ANOVA lead us to accept the hypothesis that dead foraminifera had significantly different mean abundances in low-, middle-, and high-marsh floral zones at Oregon Inlet (Table 2). The group means of the six species of foraminifera considered in unispecies ANOVA were shown to be different in the three salt-marsh floral zones with >95% confidence. This result supports the conclusion of studies that have recognized the vertical zonation of foraminifera in modern salt marshes (e.g. Scott and Medioli, 1978; Horton, 1999; Gehrels and others, 2001). Samples in the low-marsh floral zone were located at 0.10 m and 0.19 m LMSL, middle-marsh floral zone samples were between 0.14 m and 0.26 m LMSL, samples from the high-marsh floral zone were collected at 0.33 m and 0.36 m LMSL (Fig. 1B, Table 1). The zonation at Oregon Inlet further demonstrates that salt-marsh foraminifera form assemblages strongly associated with elevation in the tidal frame and that they can be used as sea-level indicators (e.g. Scott and Medioli, 1978; Edwards and others, 2004). The principal control on the distribution of salt-marsh foraminifera has been inferred to be the frequency and duration of inundation by marine water (e.g. Horton, 1999; Gehrels and others, 2001; Horton and Edwards, 2006).

We also used ANOVA results to reject the hypothesis that dead salt-marsh foraminifera in low- and high-marsh floral environments had a patchy distribution (Table 3). The assumed homogenous environmental conditions within these two zones likely produced a distribution of individuals lacking detectable spatial structure (Buzas, 1968). The small number of comparable studies support this conclusion. In a shallow subtidal environment (Rehoboth Bay, Delaware, USA), Buzas (1968) showed that in 12 of 15 cases, dead populations of foraminifera (including *Tr. inflata* and *J. macrescens*) had a non-patchy distribution. Similarly, a study from the Atlantic coast of France recognized that dead assemblages of foraminifera from intertidal environments were unlikely to have a patchy distribution, which was attributed to the time-averaging effect of dead assemblages (Morvan and others, 2006). In contrast, studies of living populations of foraminifera have frequently recognized patchiness (Buzas, 1968; Buzas, 1970; Schafer, 1971; Swallow, 2000; Buzas and others, 2002), which may be attributed to the clumping effect of reproductive blooms (Buzas, 1968; Boltovskoy and Wright, 1976; Swallow, 2000).

In the middle-marsh floral zone we were unable to reject the hypothesis that dead salt-marsh foraminifera had a patchy distribution (Table 3). Results of ANOVA showed that there was a significant difference among middle-marsh station means with 95% confidence for the six species considered. These results may be a product of either patchy distributions of foraminifera against a background of environmental homogeneity, or alternatively, distinct assemblages of foraminifera reflecting environmental variability within the middle-marsh floral zone.

Previous studies at Oregon Inlet have shown that there may be greater environmental variability in the middle-marsh floral zone than either the low or high marsh and suggest that the presumed environmental homogeneity in the middle-marsh floral zone may not be a valid assumption. Horton and Culver (2008) showed that organic content (loss on ignition) of sediments in the middle-marsh floral zone included both the lowest and highest values recorded along a transect. Additionally, they noted that the clay content and porewater salinity was more variable in the middle-marsh floral zone than it was in either the low- or high-marsh floral zones. In the Great Marshes of Massachusetts, studies of foraminifera (de Rijk, 1995; de Rijk and Troelstra, 1997) and tides (Van der Molen, 1997) suggested that the frequency and duration of inundation may be more variable in the middle-marsh zone than either high- or low-marsh environments. This variability and tidal distortion was influenced by vegetation, microtopography, and creeks (Van der Molen, 1997). Under such circumstances, it would

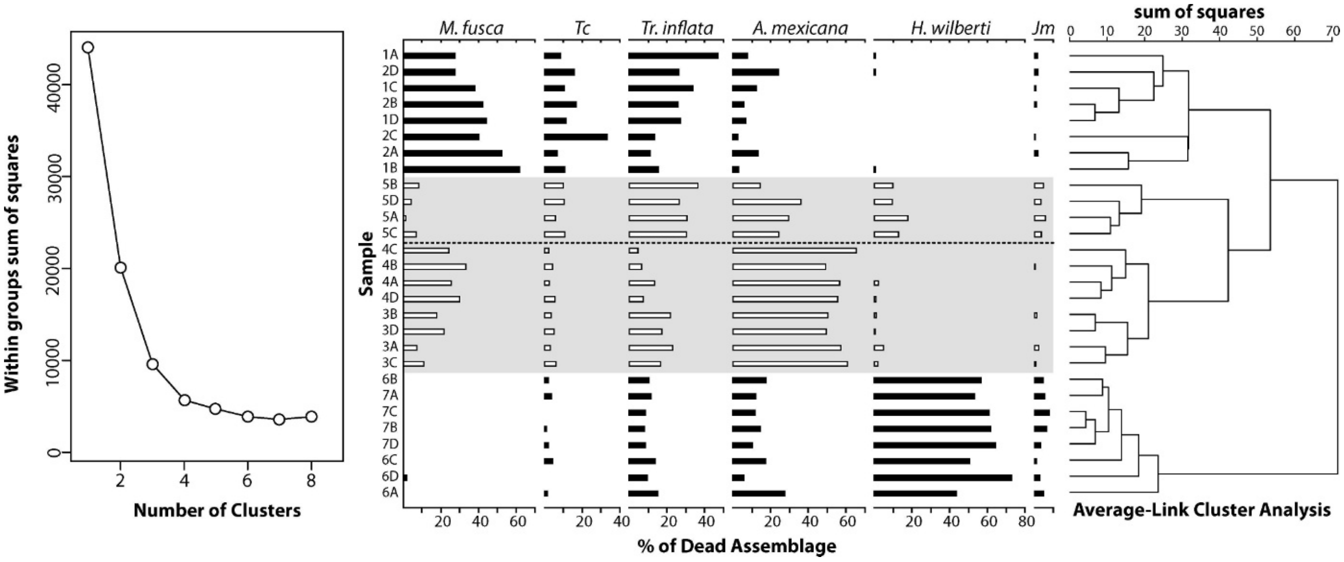

FIGURE 3. Cluster analysis of the 28 samples from Oregon Inlet. Average link was used because it minimized distortion of the data. Analysis was based on complete, dead assemblages although only the six species selected for unispecies ANOVA are presented. A broken stick plot (left) suggests that three or four groups were appropriate for distinguishing assemblages. Shading shows the division into three groups; a dashed horizontal line marks the separation of station five samples following the acceptance of a fourth group. *Jm* = *Jadammina macrescens*, *Tc* = *Tiphotrocha comprimata*.

be reasonable to expect the formation of foraminiferal assemblages reflecting varied environmental conditions within the middle-marsh floral zone. Environmental variability in the middle-marsh floral zone may also reflect the larger elevation (and horizontal) range it occupies in comparison to the low and high marsh.

We further explored the distribution of foraminifera and the apparent difference in patchiness among low-, middle-, and high-marsh floral environments using cluster analysis of all samples (Figure 3). Average-link, hierarchical agglomerative clustering was used to group samples after cophenetic correlation showed that this caused the least distortion to the data. This technique progressively joins samples (and groups of samples) having similar foraminiferal assemblages to form increasingly large groups using the average statistical distance between group members. A broken-stick plot was used to objectively determine that either three or four groups minimized dissimilarity among samples within each group and were therefore appropriate for describing foraminiferal assemblages (Fig. 3). The first split on the dendrogram separated the eight high-marsh samples (6A–D and 7A–D) from all others (Fig. 3), which reflected the abundance of *H. wilberti* that was 58±9% at stations six and seven compared to 3% ± 5% for the other stations (Figs. 2 and 3). A second split distinguished the eight low-marsh samples (1A–D and 2A–D) characterized by high abundances of *M. fusca* (41±11%) and relatively low amounts of *A. mexicana* (9.4±7.0%). This split also produced a third group consisting exclusively of the samples from the middle-marsh floral zone (Fig. 3). Recognition of a fourth group divided the middle-marsh into two groups where the samples from station five (A–D) are differentiated from those collected at stations three and four (Fig. 3). Samples 5A–D had increased *H. wilberti* (12.5±3.8%) and *Tr. inflata* (30.9±4.1%), while *A. mexicana* (26.2±9.1%) and *M. fusca* (5.3±3.0%) were less abundant in comparison to the other middle-marsh samples (Fig. 3). The grouping of samples by station confirmed that replicate (A, B, C, D) is unimportant in explaining the distribution of salt-marsh foraminifera. Results of ANOVA showed that all species had a p-value >0.92 when the significance of replicate was tested.

Acceptance of a fourth distinctive foraminiferal assemblage suggests that grouping of samples within the middle-marsh floral zone may not be adequate for describing the distribution of modern, dead foraminifera and supports our assertion that the assumption of environmental homogeneity within the middle-marsh floral zone may not be a valid one (Fig. 3). Cluster analysis implies that foraminifera in the middle-marsh floral zone can be divided into two distinct assemblages reflecting differing environmental conditions rather than having a patchy distribution against a background of environmental homogeneity.

To investigate the difference among the mean abundance of species at stations in the middle-marsh floral zone we used post-hoc Tukey's pairwise tests (Table 4). This method compared mean unispecies abundances at stations 3–5 in a pairwise fashion (3 vs. 4, 3 vs. 5, and 4 vs. 5). Where the reported p-value was <0.05, we considered the difference of species abundance between the paired stations to be significant. Where none of the pairs were significantly different, the species did not have a patchy distribution (or were all part of a single patch). If one of the station pairings was significantly different we inferred that the species formed two patches within the middle-marsh floral zone. For *Ti. comprimata*, *A. mexicana*, *H. wilberti*, and *J. macrescens*, the tests showed that two patches were present within the middle-marsh floral zone and, in each case, that station 5 was significantly different from stations 3 and 4 (Table 4). If all pairings were significantly different from one another, the species was considered to have formed three patches within the middle-marsh floral zone. This was the case for *M. fusca* and *Tr. inflata* (Table 4).

TABLE 4. Results of Tukey's pairwise tests for six species of foraminifera in the middle-marsh floral zone at Oregon Inlet. Species means among sampling stations 3, 4, and 5 are compared in a pairwise fashion. *Indicates that the species displayed a significant difference between paired station means at the 95% confidence level (probability <0.05).

Species	Stations		Difference	*p* - value
Miliammina fusca	3	4	−0.353	0.022*
	3	5	0.32	0.035*
	4	5	0.673	0.000*
Trochammina inflata	3	4	0.357	0.002*
	3	5	−0.262	0.016*
	4	5	−6.19	0.000*
Arenoparrella mexicana	3	4	−0.047	0.910
	3	5	0.594	0.001*
	4	5	0.641	0.001*
Tiphotrocha comprimata	3	4	0.043	0.720
	3	5	−0.194	0.015*
	4	5	−0.237	0.005*
Haplophragmoides wilberti	3	4	0.153	0.250
	3	5	−0.446	0.002*
	4	5	−0.599	0.000*
Jadammina macrescens	3	4	0.136	0.144
	3	5	−0.25	0.010*
	4	5	−0.386	0.001*

Further, we used post-hoc Scheffe's S-tests (Scheffe, 1959), to compare assemblages combined from stations 3 and 4 against those from station 5 (Table 5) in a pairwise fashion (3&4 vs. 5). For all six species the results of this test were significant and confirm that foraminifera from station 5 constituted a patch within the middle-marsh floral zone. This finding agrees with the results of cluster analysis (Fig. 3). These two types of additional tests indicate that it would be inappropriate to include samples from station 5 as part of a homogenous group with stations 3 and 4. When two assemblages of foraminifera are recognized in the middle-marsh floral zone, four of the six species (including the most abundant species, *A. mexicana*) did not have a patchy distribution. Post-hoc statistical tests and cluster analysis support the argument that the patch formed by samples from station 5 is likely a second and distinct assemblage of foraminifera reflecting unrecognized environmental variability within the middle-marsh floral zone. Although neither *M. fusca* nor *Tr. inflata* were dominant middle-marsh species, their distribution could not be completely explained by the presence of two assemblages, indicating that their distribution in the middle-marsh floral zone was patchy. Further investigation is needed to better understand their distribution.

Elsewhere on the mid-Atlantic coast of the USA, other studies have suggested that foraminiferal assemblages from the middle-marsh floral zone display greater variability within and between sites than either the low- or high-marsh floral zones. In North Carolina, Horton and Culver (2008) and Kemp and others (2009a) showed that the number and composition of middle-marsh zones varied throughout the region; at Oregon Inlet, however, neither documented the presence of a second middle-marsh assemblage. In Virginia, Spencer (2000) recognized a middle-marsh assemblage characterized by *Ti. comprimata* and *Tr. inflata*, but also a middle- to high-marsh transitional assemblage of *Ti. comprimata*, *Tr. inflata*, and *J. macrescens.* This was distinguished from a high-marsh zone of *J. macrescens* with *Trochamminita salsa.* In the Chesapeake Bay region, middle- and high-marsh environments were populated by variable proportions of *Ti. comprimata*, *A. mexicana*, *Tr. inflata*, *J. macrescens*, and *Ammoastuta inepta*, which were correlated with salinity gradients in the Chesapeake Bay system (Ellison and others, 1965; Ellison and Nichols, 1976). In Delaware, middle and high-marsh floral environments are associated with foraminiferal assemblages dominated by changing abundances of *A. mexicana*, *Tr. inflata*, and *J. macrescens* (Hippensteel and others, 2000; Hippensteel and others, 2002). Varied middle-marsh assemblages of foraminifera may represent transitional populations situated between low- and high-marsh environments occupied by species of foraminifera with narrow and specific ecological tolerances.

IMPLICATIONS FOR SEA-LEVEL RESEARCH

Sample stations were classified as being from low-, middle-, or high-marsh environments on the basis of vascular vegetation (Fig. 1b, Table 1). However, cluster analysis and post-hoc statistical tests showed that there were likely four distinctive assemblages of foraminifera (Fig. 3, Table 5). This suggests that foraminifera collected at regular intervals along transects may be useful in identifying additional salt-marsh environments that are not immediately apparent in visible physiographic or floral environments (Gehrels, 1994; Horton and others, 2003). For studies seeking to reconstruct sea level, recognition of additional assemblages of foraminifera has the potential to improve the accuracy and precision of reconstructions.

The use of foraminifera in reconstructing sea level is reliant upon a detailed understanding of their modern distribution on salt marshes, which is commonly described from samples collected along transects (Gehrels, 1994; Horton and Edwards, 2006). This approach assumes that

TABLE 5. Results of Scheffe's S-test for six species of foraminifera at Oregon Inlet. This test combined stations 3 and 4 and compared them to the assemblage from station 5. *Indicates that the species displayed a significant difference between means at the 95% confidence level (probability <0.05). DF = degree of freedom.

Species	DF	Sum of Squares	Mean Square	F ratio	*p* - value
Miliammina fusca	1, 9	0.658	0.658	29.134	0.000*
Trochammina inflata	1, 9	0.517	0.517	47.276	0.000*
Arenoparrella mexicana	1, 9	1.018	1.018	40.189	0.000*
Tiphotrocha comprimata	1, 9	0.124	0.124	21.090	0.001*
Haplophragmoides wilberti	1, 9	0.729	0.729	46.048	0.000*
Jadammina macrescens	1, 9	0.270	0.270	32.251	0.000*

foraminifera do not have a patchy distribution and that populations can be adequately defined by non-replicate samples collected along an environmental gradient. The Oregon Inlet data show that while replicate sampling captured variability in dead assemblages at stations with assumed environmental homogeneity (Fig. 2), foraminifera in low- and high-marsh floral zones were not patchy and could be reliably differentiated using single samples. In contrast, two distinct assemblages of foraminifera were recognized in the middle-marsh floral zone (stations 3&4 vs. 5), which likely reflected environmental variability rather than patchiness. However, *Tr. inflata* and *M. fusca* did have patchy distribution even under the revised assumptions about environmental homogeneity. Although neither was the dominant species in this floral environment (Figs. 2 and 3), both were an important part of the assemblage, implying that middle-marsh assemblages may be more susceptible to the influence of patchiness than either low or high-marsh populations. These results are from a single site and do not necessitate a change in the well-established sampling regimes used to describe the modern distribution of salt-marsh foraminifera. Rather they suggest that the distribution of samples along transects should anticipate greater spatial variability in the middle-marsh floral zone than in either the low- or high-marsh floral zones. More studies are necessary to test for the influence of patchiness in other regions and could be undertaken as a step in describing the modern distribution of foraminifera. These would provide the basis for understanding the influence of patchiness on sea-level reconstructions.

CONCLUSIONS

Sea-level reconstructions using salt-marsh foraminifera commonly rely upon modern distributions described from samples positioned along transects with the implicit assumption that dead foraminifera do not have a patchy distribution. We collected replicate surface samples along a transect at Oregon Inlet (North Carolina, USA), which included low-, middle-, and high-marsh floral zones to investigate the influence of patchiness using unispecies ANOVA for six species of foraminifera selected because of their importance in distinguishing assemblages. We demonstrated that each had a significantly different abundance in low-, middle-, and high-marsh floral zones with >95% confidence, supporting the concept of a vertical zonation of salt-marsh foraminifera which is the basis for their use in sea-level reconstruction. Within each of the floral zones we assumed environmental homogeneity and tested the influence of patchiness. There was no patchiness of any species in low- and high-marsh settings with 95% confidence. However, cluster analysis indicated that the assumption of environmental homogeneity throughout the middle-marsh floral zone may not be appropriate. Division of the middle-marsh floral zone into two assemblages of foraminifera (Scheffe's S-tests) showed that four of the six species of foraminifera did not have a patchy distribution. Two species had a patchy distribution in the middle-marsh floral zone, although neither was a dominant species. The spatial variability of foraminifera in middle-marsh floral settings should be considered when sampling modern salt marshes and interpreting downcore changes in assemblages. Further studies of the patchiness of dead salt-marsh foraminifera are necessary to support the adoption of new sampling schemes.

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APPENDIX. Relative abundance (%) of foraminiferal species in dead assemblages from Oregon Inlet, North Carolina. Four replicates (A–D) were collected at each sampling station (1–7). Values in each column total 100%.

Species	1A	1B	1C	1D	2A	2B	2C	2D	3A	3B	3C	3D	4A	4B	4C	4D	5A	5B	5C	5D	6A	6B	6C	6D	7A	7B	7C	7D
Jadammina macrescens	1.4	0.0	0.5	0.0	1.7	0.9	0.4	1.8	2.4	1.2	0.6	0.0	0.0	0.5	0.0	0.0	5.9	4.7	3.7	3.4	4.7	4.5	1.0	2.8	5.3	6.5	7.8	3.2
Haplophragmoides wilberti	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.4	4.8	1.2	1.8	0.6	2.0	0.0	0.0	0.9	17.7	9.9	12.8	9.6	43.5	56.8	50.5	72.7	53.2	61.7	60.8	64.2
Trochammina inflata	46.9	15.2	33.7	27.0	11.0	25.8	13.3	26.2	22.9	21.9	16.6	17.2	13.3	6.5	4.5	7.3	30.5	36.5	30.3	26.4	15.0	10.3	13.5	9.7	11.6	8.0	8.3	8.6
Tiphotrocha comprimata	8.5	10.8	10.4	11.3	6.6	16.9	33.3	15.6	3.0	3.6	6.1	5.0	2.6	4.1	2.3	5.5	5.9	9.9	10.6	10.6	1.6	1.9	4.2	0.0	3.7	1.0	0.0	2.1
Haplophragmoides manilaensis	0.5	0.0	0.0	0.0	0.6	0.0	0.0	0.4	0.6	0.6	0.6	0.6	0.0	0.0	0.8	0.0	3.0	5.2	5.3	3.8	5.2	7.1	6.3	4.0	11.1	6.5	5.9	8.6
Arenoparrella mexicana	7.6	2.9	12.4	6.9	13.3	5.6	2.4	24.0	57.2	50.3	60.7	49.4	56.6	49.3	65.4	55.5	29.6	14.6	24.5	36.1	27.5	17.4	17.2	5.7	12.1	14.4	11.8	10.2
Pseudothurammina limnetis	0.0	0.0	0.0	0.0	0.6	0.0	0.4	0.0	1.2	0.6	1.2	1.7	0.0	0.0	0.0	0.0	2.0	2.1	1.6	0.5	0.0	1.9	0.0	0.6	0.0	0.0	1.0	0.5
Miliammina petila	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.6	0.6	0.0	0.0	0.0	0.0	3.9	6.8	2.7	5.3	2.1	0.0	7.3	2.8	3.2	2.0	4.4	2.7
Miliammina fusca	27.5	61.8	37.8	44.0	52.5	42.3	40.2	27.6	7.2	17.8	11.0	21.7	25.5	33.2	24.1	30.0	1.5	8.3	6.9	4.3	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.0
Siphotrochammina lobata	0.0	0.5	1.6	0.6	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	1.6	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Reophax nana	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	1.4	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
Ammobaculites dilatatus	1.9	1.0	0.0	0.0	5.0	0.5	1.6	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ammotium salsum	5.2	6.4	3.6	10.1	7.7	7.5	6.0	3.6	0.0	1.8	0.6	3.3	0.0	5.1	3.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ammobaculites exiguus	0.0	1.0	0.0	0.0	0.0	0.0	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Ammonia parkinsonia	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eggerella advena	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0