1 Variability of intertidal foraminiferal assemblages in a salt marsh, Oregon, USA

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Abstract

We studied 18 sampling stations along a transect to investigate the similarity between live (rose Bengal stained) foraminiferal populations and dead assemblages, their small-scale spatial variations and the distribution of infaunal foraminifera in a salt marsh (Toms Creek marsh) at the upper end of the South Slough arm of the Coos Bay estuary, Oregon, USA. We aimed to test to what extent taphonomic processes, small-scale variability and infaunal distribution influence the accuracy of sea-level reconstructions based on intertidal foraminifera. Cluster analyses have shown that dead assemblages occur in distinct zones with respect to elevation, a prerequisite for using foraminifera as sea-level indicators. Our nonparametric multivariate analysis of variance showed that small-scale spatial variability has only a small influence on live (rose Bengal stained) populations and dead assemblages. The dissimilarity was higher, however, between live (rose Bengal stained) populations in the middle marsh. We observed early diagenetic dissolution of calcareous tests in the dead assemblages. If comparable post-depositional processes and similar minor spatial variability also characterize fossil assemblages, then dead assemblage are the best modern analogues for paleoenvironmental reconstructions. The Toms Creek tidal flat and low marsh vascular plant zones are dominated by *Miliammina fusca*, the middle marsh is dominated by *Balticammina pseudomacrescens* and *Trochammina inflata*, and the high marsh and upland-marsh transition zone are dominated by *Trochamminita irregularis*. Analysis of infaunal foraminifera showed that most living specimens are found in the surface sediments and the majority of live (rose Bengal stained) infaunal specimens are restricted to the upper 10 cm, but living individuals are found to depths of 50 cm. The dominant infaunal specimens are similar to those in the corresponding surface samples and no species have been found living solely infaunally. The total numbers of infaunal foraminifera are small compared to the total numbers of dead specimens in the surface samples. This suggests that surface samples adequately represent the modern intertidal environment in Toms Creek.

1 Introduction

Intertidal foraminifera have been widely used as indicators of former sea levels, because they are often well preserved, easily identified and occur in high numbers, thus, providing a statistical basis for paleoenvironmental interpretation (e.g., Thomas and Varekamp, 1991; Varekamp et al., 1992; Gehrels, 1994; Nydick et al., 1995; Horton, 1999; Hayward et al., 1999; Edwards and Horton, 2000; Haslett et al., 2001; Horton and Edwards, 2006; Leorri et al., 2010). The utility of foraminifera as sea level indicators results from the strong correlation that intertidal assemblages have with elevation within the tidal frame (e.g., Scott and Medioli, 1978; Horton and Edwards, 2006). Along tectonically active coastlines such as Oregon's, this correlation with elevation is used to reconstruct former sea levels, from which coastal land-level changes during prehistoric great earthquakes on the plate-boundary thrust fault of the Cascadia subduction zone can be inferred (Fig. 1; e.g., Guilbault et al., 1995, 1996; Nelson et al., 2008; Hawkes et al., 2010; Hawkes et al., 2011; Engelhart et al., 2013a). In this paper, we address three potential problems with using foraminiferal assemblages as sea-level indicators at Cascadia.

Firstly, the use of intertidal foraminifera to reconstruct former sea levels requires a comprehensive understanding of modern assemblage distributions and their relationship to tidal environments (e.g., Phleger and Walton, 1950; Scott and Medioli, 1978; Patterson, 1990; Hayward et al., 1999, Gehrels, 2000; Horton and Edwards, 2006; Kemp et al., 2009). Much previous debate has focused on which type of assemblage—the live population, the dead assemblage or the total (live plus dead) assemblage—should be used to characterize modern environments and reconstruct prior sea levels. Many researchers state that total assemblages most accurately represent intertidal environments because they reflect temporal fluctuations (e.g., Scott and Medioli, 1980; Jennings et al., 1995; de Rijk, 1995). However, Murray (2000) notes that the use of total assemblages disregards taphonomic changes that affect live populations after their death. Many intertidal foraminiferal studies concentrate on agglutinated

1 foraminifera, because calcareous taxa are commonly not preserved (or not present) in low pH
2 salt-marsh environments. To investigate the extent of this effect, Culver and Horton (2005) and
3 Horton and Murray (2006, 2007) analyzed seasonal and post-depositional changes of
4 agglutinated and calcareous foraminiferal species from salt-marsh environments as well as
5 from tidal flat and sand flat environments along the U.S. Atlantic and U.K. coasts, respectively.
6 They concluded that if studies encompass the whole intertidal zone, the modern dead
7 assemblages are the most accurate analogues for fossil assemblages, because of the early
8 diagenetic dissolution of calcareous species.

9
10 Secondly, most sea-level reconstruction studies investigate modern surface foraminiferal
11 distributions along elevational transects across one or more intertidal zones (e.g., Horton and
12 Edwards, 2006). Transects are usually positioned perpendicular to the shore and extend from
13 tidal flats to freshwater-upland environments, but sampling along transects does not address
14 small-scale variability in foraminiferal distribution (Kemp et al., 2011). Such small-scale spatial
15 variability of foraminiferal distributions in intertidal environments has been reported both for
16 living populations (e.g., Buzas, 1968, 1970; Schafer, 1971; Swallow, 2000; Buzas et al., 2002)
17 and dead assemblages (Kemp et al., 2011) from different coastal regions. If foraminifera have
18 a patchy distribution in intertidal environments, then assemblages in samples along single
19 transects may be too variable to accurately describe the species-environment relationship and
20 so compromise the reliability of sea-level reconstructions.

21
22 Thirdly, most studies of the modern distribution of intertidal foraminifera have sampled surface
23 sediment (upper 1 to 2 cm) with the assumption that intertidal foraminifera are primarily
24 epifaunal (e.g., Scott and Medioli, 1980; Gehrels, 1994; de Rijk, 1995; Horton, 1999; Alve and
25 Murray, 2001; Horton and Edwards 2006; Kemp et al., 2009). Infaunal living foraminifera,
26 however, have been widely reported in North American and European salt marshes (e.g.,
27 Matera and Lee, 1972; Buzas, 1977; Steineck and Bergstein, 1979; Goldstein et al., 1995;
28 Goldstein and Watkins, 1998, 1999; Duchemin et al., 2005; Tobin et al., 2005; Berkeley et al.,

2007; Leorri and Martin, 2009). Preferentially infaunal species could change the composition of dead assemblages in subsurface sediments (Goldstein and Harben, 1993; Saffert and Thomas 1998; Patterson et al., 1999; Hippensteel et al., 2000; Culver and Horton, 2005). For example, the benthic foraminifer *Arenoparrella mexicana* is more abundant in subsurface than in surface samples in a Georgia salt marsh (Goldstein and Harben, 1993). Duchemin et al. (2005) also suggested that infaunal taxa need to be considered when analyzing the distribution of modern salt-marsh foraminifera. To include the effects of infaunal species, Ozarko et al. (1997) and Patterson et al. (1999) suggested the upper 10 cm of sediment as the most appropriate sampling depth for obtaining modern analogues for sea-level reconstructions. In contrast, Tobin et al. (2005) and Culver and Horton (2005) concluded that assemblages in the upper 1 cm of sediment provide good modern analogues for sea-level reconstruction.

The applicability of live populations, dead or total assemblages in sea-level reconstructions, the influence of patchiness in modern environments, and infaunal foraminiferal distribution have been little studied on the coasts of central western North America (e.g., Hawkes et al., 2010, 2011; Engelhart et al., 2013a). Here, we address these issues through the study of foraminiferal assemblages from a salt marsh in the South Slough arm of the Coos Bay estuary in southern Oregon (Fig. 1). We examine live and dead foraminiferal species on an elevational transect of 18 surface stations (St.) — each consisting of four replicate surface samples—to determine whether intertidal foraminifera show a vertical zonation with respect to the tidal frame, and to measure small-scale spatial variability in the distribution of surface foraminifera. At five stations we investigated the live infaunal distribution in 50-cm-long cores in order to determine how the distribution of infaunal foraminifera influences modern species distributions.

2 Study area

Toms Creek marsh is situated near the southern (upstream) end of the Winchester Creek Arm of the South Slough National Estuarine Research Reserve (NERR), a federally protected part

1 of the Coos Bay estuary (Fig. 1A, B). The marsh covers an area of 0.04 km² in a 20- to 100-
2 m-wide inlet between an old, eroded dike on its west-northwest side and a more recent dike
3 on its south side. The more recent dike separates the marsh that we studied from the main
4 Toms Creek marsh, whose stratigraphy was explored by Nelson et al. (1996; Fig. 1C).
5 Construction of dikes for logging and later pasturelands in this area began in the 1860s and
6 continued intermittently through the 1920s. Because the tide gate on the more recent southern
7 dike has eroded and was not maintained since the early 1950s, tides have had daily access to
8 Toms Creek marsh for at least 50 years (Nelson et al., 1996).

9
10 Tides in the Coos Bay estuary are semidiurnal and mesotidal. The observed mean diurnal
11 range (Mean Highest High Water (MHHW), 2.17 m NAVD88 to Mean Lowest Low Water
12 (MLLW), -0.149 m NAVD88) is 2.32 m, measured over the period from 1983 to 2001 at the
13 National Oceanic and Atmospheric Administration (NOAA) tide gauge station in Charleston,
14 ~7 km north of the study area (Fig. 1B; ID 9432780;
15 <http://tidesandcurrents.noaa.gov/index.shtml>).

16
17 The climate in the Coos Bay estuary is temperate (Peel et al., 2007). We sampled in early
18 October 2012. Seasonal temperatures, measured at the National Weather Service
19 Cooperative Observer (COOP) station in Coos Bay 8SW (Global Historical Climatology
20 Network (GHCND) ID: USW00004141), averaged 10.7°C for September to November 2012.
21 Mean seasonal precipitation for the same period is 175 mm.

22
23 Vascular plant species define the floral environments of Toms Creek marsh. The transect
24 across the marsh that we studied begins in a sparsely vegetated tidal flat (St. 1-4) with patchy
25 areas of algae (Fig. 1C). The lower edge of colonizing *Carex lyngbyei* is near St. 4 and this is
26 the only vascular plant species in the low marsh (St. 5-8). It provides complete cover at St. 7
27 and 8. *Deschampsia caespitosa* and *Distichlis spicata* are the two most prominent species in
28 the middle marsh (St. 9-13), with *Agrostis stolonifera* and *C. lyngbyei* as important secondary

species. Minor occurrences of *Triglochin maritima* are present at St. 9 and 13, with *Glaux maritima* and *Jaumea carnosa* at St. 13 near the gradual transition to high marsh. *Juncus balticus*, *C. lyngbyei* and *D. spicata*, are dominant in the high marsh (St. 14 and 15), with minor occurrences of *Potentilla pacifica*, *Argentina egedii*, *T. maritima* and *Aster subspicata*. In the marsh-upland transition zone (St. 16), *A. egedii*, *Carex obnupta*, *Oenanthе sarmentosa*, *Equisetum arvense* and *Lysitichitum americanus* are common, although *C. lyngbyei*, *J. balticus* and *P. pacifica* are the dominant species. At upland stations (St. 17, 18), we observed *C. lyngbyei*, *Lysitichitum americanus*, *Oenanthе sarmentosa*, *Picea sitchensis*, *Alnus ruba* and several species of ferns.

3 Methods

3.1 Sampling strategy

We sampled 18 stations, from tidal flat to upland, along a transect at Toms Creek marsh in early October 2012 (Table 1; Fig. 1C). Samples from the tidal flat and low marsh were collected at an ~10-cm vertical spacing, while samples from the middle marsh to the upland were collected at an ~20-cm vertical spacing, using a line-laser levelling system (reported errors for instrument of ± 3 mm). Station elevations were determined with a Real Time Kinematic-Global Positioning System (RTK-GPS) and/or total station with a precision of < 5 cm, and referenced to the North American vertical datum (NAVD88). Four replicate samples, each of approximately 10 cm³ volume (~10 cm² surface sample by 1 cm thick), were collected at each station in order to determine small-scale spatial variations in foraminiferal distribution. Distances between the replicate samples at the same station range from 6 to 50 cm (Table 1). A second set of samples (one per station) was taken for grain-size distribution and loss on ignition (LOI) analyses.

Five 32- to 50-cm-long cores (St. 2, 4, 7, 9, 15) were taken in order to analyze the infaunal foraminiferal distribution in the tidal flat (St. 2, 4), low (St. 7), middle (St. 9) and high (St. 15)

marshes (Table 1). Cores were collected using a 5-cm-diameter, half-cylinder Russian corer to minimize contamination by sediment from different depths. The cores were sliced into 1-cm-thick samples from 0 to 5 cm depth and into 2-cm-thick samples between 5 and 11 cm depth. Between 11 and 50 cm, 1-cm-thick samples were taken every 10 cm. Samples were stored in a buffered ethanol solution and refrigerated at 4°C prior to analysis.

3.2 Sediment analysis

Grain-size distribution of the surface samples was determined with a Laser Diffraction Particle Size Analyzer (Appendix A1). Prior to analysis, samples were treated with 20% hydrogen peroxide to oxidize the organic matter in the sediment before being measured. Particle-size interpretations were based on the Wentworth Phi Scale (Wentworth, 1922) and are reported as differential volume (the percentage of total volume that each size class occupies).

For loss on ignition (LOI; a proxy for percent organic matter) measurements, samples were wet sieved to remove the material larger than 2 mm, dried at 105°C for 24 hours, and heated in a muffle furnace at 550°C for 4 hours. LOI (%) was calculated by the difference in sample dry weight at 105°C and 550°C (Heiri et al., 2001; Appendix A1).

3.3 Foraminiferal analysis

All surface and core samples were stained with rose Bengal on the day of sampling. Staining with rose Bengal is a standard method to distinguish between live and dead specimens (Walton, 1952; Murray and Bowser, 2000). However, in some specimens dead cytoplasm may be stained due to slow cytoplasm degradation rates (Bernhard, 1988). Rose Bengal also may stain the inner organic lining of foraminiferal tests or bacteria and algae attached to or in foraminiferal tests (e.g., Bernhard, 1988; Bernhard et al., 2006). However, the method has given reasonable results for salt marsh foraminifera (Goldstein et al., 1995). To address these

1 issues, only tests having all chambers stained completely bright red (except for the last
2 chamber) were considered living at the time of collection (e.g., Murray and Alve, 2000; Horton
3 and Edwards, 2006).

4
5 For foraminiferal analysis, surface and core samples were wet sieved through 500 μm and 63
6 μm sieves. The greater than 500 μm fraction was examined for larger foraminifera before being
7 discarded. A wet-splitter (Scott and Hermelin, 1993) was used to split the fraction between 63
8 and 500 μm of the surface samples into eight equal parts, as described in Horton and Edwards
9 (2006). We used a settling time of 90 minutes and collected the overlying water in the wet
10 splitter to examine its foraminiferal residue. Where possible, we counted at least 200 dead and
11 100 living (rose Bengal stained) foraminiferal tests per sample. Minimal dead foraminiferal
12 specimens (32) and no living (rose Bengal stained) specimens were found in the samples from
13 the upland stations (St. 17, 18), and consequently these stations were excluded from the
14 analysis. All tests were counted wet to facilitate the detection of rose Bengal stained
15 foraminifera and to prevent drying of the organic residue (e.g., de Rijk, 1995). In the short
16 cores, living (rose Bengal stained) specimens from below the surface (0-1 cm) sediment layer
17 were defined as infaunal.

18
19 Foraminifera were identified following the taxonomic illustrations and descriptions in Horton
20 and Edwards (2006), Hawkes et al. (2010), and Wright et al. (2011) (Appendix A2). Juvenile
21 specimens of *Trochammina inflata*, *Jadammina macrescens* and *Balticammina*
22 *pseudomacrescens* that were difficult to distinguish from each other were assigned to juvenile
23 Trochamminids. Specimens of the genus *Ammobaculites* were combined into a single group,
24 because these species were often broken making it difficult to identify them to the species level
25 (Kemp et al., 2009). Due to the presence of inner organic linings of dead calcareous species
26 that are difficult to identify to species level, we assigned calcareous species (*Ammonia* sp. and
27 *Haynesina* sp.) to a single group (Edwards and Horton, 2000). All census counts can be found
28 in Tables A3 and A4 and foraminiferal illustrations in Plate 1.

3.4 Statistical analysis

We applied a hierarchical clustering method using relative abundance data to classify and consequently compare the live (rose Bengal stained) populations and dead foraminiferal assemblages. For this analysis, we selected the unweighted pair group average (UPGMA) algorithm to define groups on the basis of the mean distance between the foraminiferal assemblages in each group and used the Bray-Curtis similarity (Bray and Curtis, 1957) as the distance metric. In order to calculate the percentages of cluster replications, we applied a Monte Carlo test (1000 permutations).

We measured the Bray-Curtis similarity between the replicate samples by using both relative and absolute abundances to illustrate the small-scale spatial variability, where higher values (i.e., close to one) indicate a high similarity between the replicate samples. To further determine the small-scale spatial variability between the replicate samples and the influence of different tidal environments simultaneously, we numerically coded four categories (tidal flat, low marsh, middle marsh, high marsh to upland-marsh transition) and applied a two-way Non Parametric Multivariate ANalysis Of VAriance (NPMANOVA) approach (Anderson, 2001; 5000 permutations) with the Bray-Curtis similarity as the distance metric.

All statistical analyses were made with the PAST software package, version 2.15 (Hammer et al., 2001).

4 Results

4.1. Surface sediment characteristics

1 The intertidal zone of Toms Creek marsh (St. 1-15) is dominated by silty sediment (65-76%
2 silt) with lower percentages of clay (16-22%) and sand (1-18%; Figure A5). The upland-marsh
3 transition station (St. 16) and upland (St. 17, 18) are characterized by 46-51% sand and 43-
4 47% silt. Loss on ignition (LOI) is lowest in the tidal flat and low marsh (St. 1-8; 11-20%), higher
5 in the middle marsh (St. 9-13; 28-54%) and highest in upland (St. 17-18; 68-76%).

6 7 4.2 Distribution of live (rose Bengal stained) foraminifera in the surface samples

8
9 Fourteen different taxa were found in the live (rose Bengal stained) populations from the four
10 replicate samples at the 16 stations (64 samples). The populations are dominated by the
11 agglutinated species *Balticammina pseudomacrescens*, *Miliammina fusca*, *Trochammina*
12 *irregularis* and *Trochammina inflata* (Figs. 2, 3; Plate 1). We also observed *Ammobaculites*
13 spp., *Haplophragmoides manilaensis*, *Haplophragmoides wilberti*, *Jadammina macrescens*,
14 *Miliammina petila*, *Paratrochammina haynesi*, *Reophax moniliformis* and *Trochammina*
15 *ochracea* in low numbers (Plate 1). We also found calcareous species in the tidal flat and low
16 marsh sediments.

17
18 The tidal flat (St. 1-4) is dominated by *M. fusca* with a relative abundance between 42 and 95%
19 (Fig. 2). Calcareous species were also found in the tidal flat with a maximum relative
20 abundance of 53%. The low marsh (St. 5-8) is characterized by decreasing relative
21 abundances of *M. fusca* (88 to 9%) and calcareous species (12 to 0%). These species are
22 replaced by *B. pseudomacrescens* (2 to 66%) and *T. inflata* (0 to 30%). The middle marsh (St.
23 9-13) is dominated by *B. pseudomacrescens* (6 to 54%) and *T. inflata* (0 to 60%), with lower
24 relative abundances of *J. macrescens* (0 to 33%), *H. manilaensis* (0 to 30%) and *M. fusca* (0
25 to 26%). In the high marsh (St. 14-15), *T. irregularis* is the dominant species with a relative
26 abundance between 51 and 100%, while *B. pseudomacrescens* decreases along the transect
27 (12 to 0%). Living foraminifera were absent from the marsh-upland transition (St. 16).

1 The total number (per 10 cm³ sediment volume) of live (rose Bengal stained) foraminifera is
2 highest in the upper low marsh and in the middle marsh with up to 1855 specimens, and lowest
3 in the high marsh with up to 48 specimens. The absolute abundance of *M. fusca* (51 to 578
4 specimens) and calcareous species (0 to 215 specimens) is highest in tidal flat and low marsh
5 stations (St. 1-8) and then strongly decreases in the middle and high marsh (Fig. 3). The upper
6 part of the low marsh and the middle marsh are characterized by higher numbers of *T. inflata*
7 (0 to 876 specimen), *B. pseudomacrescens* (6 to 840 specimens) and *H. manilaensis* (0 to 130
8 specimens). At middle marsh St. 10, we found up to 26 specimens of *M. petila*. *Trochamminita*
9 *irregularis* occurs in the middle to high marsh with absolute abundances between 0 and 89
10 specimens.

11

12 4.3 Distribution of dead foraminifera in the surface samples

13

14 The dead assemblages were dominated by the same taxa as the live (rose Bengal stained)
15 populations at the same stations (*B. pseudomacrescens*, *M. fusca*, *T. inflata* and *T. irregularis*;
16 Figs. 2-5). However, there was a noticeable reduction in the relative and absolute abundance
17 of calcareous species (including their organic linings) (Figs. 2-5).

18

19 *M. fusca*, with a relative abundance between 41 and 79%, is the dominant species in the tidal
20 flat (St. 1-4; Fig. 4), with a lower relative abundance of *J. macrescens* (1 to 17%). In contrast
21 to the live (rose Bengal stained) populations, the relative abundances of calcareous species in
22 the tidal flat, including their organic linings are much lower (0 to 15%). *M. fusca* (36 to 88%)
23 and *B. pseudomacrescens* (5 to 51%) characterize the low marsh (St. 5-8). In the middle marsh
24 (St. 9-13), the dominant species are *B. pseudomacrescens* and *T. inflata* with relative
25 abundances of 1 to 74% and 0 to 53%, respectively. At these stations we also observed lower
26 relative abundances of *J. macrescens* (0 to 23%), *M. fusca* (2 to 26%) and *H. manilaensis* (0
27 to 20%). In the high marsh and upland transition (St. 14-16), *T. irregularis* is the dominant

species with a relative abundance between 50 and 95%. In addition, *B. pseudomacrescens* and *M. petila* were present with maximum abundances of 26 and 29%, respectively.

The total number (per 10 cm³ sediment volume) of dead foraminifera is higher than live (rose Bengal stained) foraminifera. The highest numbers of dead foraminifera are found in the upper low marsh and middle marsh (with up to 1855 specimens) with the lowest numbers in the high marsh and high marsh to upland transition (with up to 48 specimens). In the low marsh, we found lower numbers of calcareous species with 0 and 33 specimens, compared to the live (rose Bengal stained) assemblages with 0 to 215 specimens (Figs. 3 and 5). *Miliammina fusca* is present in the tidal flat (69 to 332 specimens), but has a higher absolute abundance in the low marsh dead assemblages (265 to 1514 specimens; Fig. 5) dead assemblages. The uppermost part of the low marsh and the middle marsh dead assemblages are characterized by higher numbers of *B. pseudomacrescens* (7 to 2070 specimens), *T. inflata* (0 to 1370 specimens), *J. macrescens* (0 to 696 specimens) and *H. manilaensis* (0 to 457 specimens). The high marsh and higher marsh to upland transition are characterized by higher numbers of *M. petila* (0 to 76 specimens) and *T. irregularis* (4 to 397 specimens).

4.4 Small-scale spatial variability of live (rose Bengal stained) and dead foraminiferal assemblages in the surface samples

The two-way NPMANOVA, which we applied to the relative and absolute abundances, shows that the live (rose Bengal stained) populations ($F = 0.5$ and $p = 0.6243$; $F = 0.4$ and $p = 0.9198$) and dead assemblages ($F = 0.7$ and $p = 0.6321$; $F = 0.3$ and $p = 0.9966$) have a non-significant intra-variability (at the 95% confidence level) between the replicate samples at each station. Although statistically non-significant, the Bray-Curtis similarity shows a higher variability between the replicate samples (i.e., in the middle marsh), and particularly when comparing absolute abundances (Fig. 6A-D). The comparison between the distance between replicates of each station and the median Bray-Curtis similarity for each station shows no significant

1 correlation between distance and variability, with $R = -0.24$ and -0.13 for the absolute live (rose
2 Bengal stained) and dead abundances, and $R = 0.12$ and 0.01 for the relative live (rose Bengal
3 stained) and dead abundances, respectively. (Fig. A6). This indicates that the observed small-
4 scale variability is not a function of the different distances between replicate samples.

5

6 The Bray-Curtis similarity between the relative abundances of live (rose Bengal stained)
7 populations in the replicate samples reveals that the tidal flat St. 2, the low marsh St. 7 and 8,
8 and, particularly the middle marsh St. 9-13, are characterized by a higher variability in species
9 composition than tidal flat St. 1, 3 and 4 or the high marsh St. 14 and 15. These similarities
10 vary between 0.34 and 0.95 (with medians between 0.40 and 0.82; Fig. 6A). The highest
11 variability is observed for St. 9 with values between 0.34 and 0.87 with a median of 0.40.

12

13 The Bray-Curtis similarity between the absolute abundances of live (rose Bengal stained)
14 populations indicates a higher variability between 0.46 and 0.80 (medians between 0.63 and
15 0.67) in the tidal flat (St. 1, 2) and between 0.36 and 0.91 (medians between 0.40 and 0.58) in
16 the uppermost low marsh and in the middle marsh stations (St. 8-13) compared to the upper
17 tidal flat (St. 3, 4) and lower low marsh stations (St. 4-7). It also has a high variability between
18 0.34 and 0.88 (medians between 0.63 and 0.75) in the high marsh stations (St. 14, 15; Fig. 6B)

19

20 The Bray-Curtis similarity between the relative and absolute abundances of dead assemblages
21 illustrates less variability than in the live (rose Bengal stained) populations (Fig. 6C, D). For
22 relative abundances, the median values of the dead assemblages vary from 0.62 to 0.93
23 compared to 0.40 to 0.97 for the live (rose Bengal stained) populations. Absolute abundances
24 vary from 0.46 to 0.85 for dead assemblages, compared to 0.40 to 0.83 for live (rose Bengal
25 stained) populations. The greatest variability in the relative and absolute abundances of dead
26 assemblages for all stations was found at St. 9 near the low end of the middle marsh, and at
27 St. 13, at the upper end of the middle marsh. At St 9 relative abundances have values between
28 0.49 and 0.86 (median of 0.67) and total abundances have values between 0.42 and 0.86

(median of 0.67), respectively. At St. 13 relative and total abundances vary between 0.41 and 0.81 (median 0.62) and between 0.28 and 0.80 (median of 0.46), respectively. The variability of the absolute abundances is high among the replicate stations of the tidal flat (St. 1, 2) with 0.34 and 0.86 (medians between 0.58 and 0.71), and the high marsh and the higher marsh to upland transition (St. 14-16) with 0.37 and 0.94 (medians between 0.64 and 0.74). In comparison, the variability of relative abundances at the same stations is lower with 0.58 and 0.94 (medians between 0.71 and 0.86; St. 1, 2) and 0.59 and 0.92 (medians between 0.77 and 0.81; St. 14-16), respectively.

4.5 Distribution of live (rose Bengal stained) and dead foraminifera in the surface samples

The two-way NPMANOVA revealed significant inter-variability (at the 95% confidence level) between tidal flat, low marsh, middle marsh and the high marsh to upland assemblages, for relative and absolute abundances of living (rose Bengal stained) specimens ($F = 31.1$ and $p = 0.0002$; $F = 34.2$ and $p = 0.0002$), and for the relative and absolute abundances of dead specimens ($F = 54.4$ and $p = 0.0002$; $F = 31.0$ and $p = 0.0002$). Cluster analyses of the live (rose Bengal stained) populations and dead assemblages of replicate samples also identified homogeneous groups (Fig. 7A, B).

The cophenetic correlation between the original and the dissimilarity matrix for the live (rose Bengal stained) populations is high with $R = 0.910$. The applied Monte Carlo test indicated three main clusters (Fig. 7A) with relative cluster replication of 48% for cluster Ia, 26% for cluster Ib and 58% for cluster II. The foraminiferal zonation defined by the cluster analysis differs slightly from the vascular plant zonation at Toms Creek marsh. Cluster Ia of the live (rose Bengal stained) populations consists of tidal flat (St. 1-4) and lower low marsh (St. 5, 6) stations with elevations between 1.02 and 1.80 m NAVD88 (Fig. 7C). This cluster is dominated by *M. fusca* (> 42% in all samples) and calcareous species (0-53%). Cluster Ib includes stations from the upper low marsh (St. 7, 8) and middle marsh (St. 9-12) with elevations

1 between 1.81 and 2.30 m NAVD88. This cluster is characterized by *B. pseudomacrescens* (6-
2 66%), *T. inflata* (1-60%) and *H. manilaensis* ($\leq 28\%$). Cluster II contains station 13 from the
3 middle marsh and the stations from high marsh (St. 14-15) with elevations between 2.55 and
4 2.62 m NAVD88. *Trochamminita irregularis* is the dominant species in this cluster ($> 52\%$ in all
5 samples).

6
7 The cophenetic correlation for the dead assemblages is comparable to those of the live (rose
8 Bengal stained) populations with $R = 0.912$. The applied Monte Carlo test showed three main
9 clusters (Fig. 7B). The relative cluster replication was lower for cluster Ia and Ib but higher for
10 cluster II compared to the live (rose Bengal stained) populations with 31% for cluster Ia, 16%
11 for cluster Ib, and 63% for cluster II. Again, the foraminiferal zonation defined by the cluster
12 analysis differs slightly from the zonation of vascular plants. Cluster Ia of the dead
13 assemblages consists of tidal flat stations (St. 1-4) and low marsh (St. 5-8) stations with
14 elevations between 1.02 and 2.01 m NAVD88 (Fig. 7C). In this cluster, *M. fusca* is the dominant
15 species with a relative abundance between 8 and 36%. Cluster Ib contains almost all middle
16 marsh stations (St. 9-12, 13B, C) with elevations between 2.16 and 2.42 m NAVD88. This
17 cluster is characterized by *B. pseudomacrescens* (14 to 74%), *T. inflata* (up to 53%) and *J.*
18 *macrescens* (up to 23%). Cluster II contains stations from the middle marsh (St. 13A, D) and
19 stations from the high marsh (St. 14-15) and upland transition (St. 16) with elevations between
20 2.55 and 2.65 m NAVD88. *Trochamminita irregularis* dominates this cluster, with a relative
21 abundance between 49 and 95%.

22 23 4.6 Surface and infaunal foraminiferal distribution in the short cores

24
25 We investigated the infaunal foraminiferal distribution in tidal flat (St. 2, 4), low (St. 7), middle
26 (St. 9) and high (St. 15) marsh environments (Appendix A4). We calculated the total numbers
27 of live (rose Bengal stained) specimens (per 10 cm³ sediment volume) and the relative
28 abundance of live (rose Bengal stained) specimens in each core (Fig. 8).

1
2 In the silty tidal flat cores (St. 2, 4), the total numbers of living (rose Bengal stained) foraminifera
3 in the surface samples (0-1 cm depth) is between 52 specimens (St. 2) and 118 specimens
4 (St. 4; Fig. 8). The living assemblage at the surface is dominated by *M fusca* with 43 specimens
5 at St. 2 and 89 specimens at station 4 with *Ammonia* spp. (18 specimens at St. 4) and *B.*
6 *pseudomacrescens* (6 specimens at St. 2). Highest total numbers of infaunal specimens is
7 observed between 1 and 4 cm depth (12 to 20 specimens) at St. 2, and at 1 to 2 cm depth (35
8 specimens) at St. 4. At both stations, the total numbers of living (rose Bengal stained)
9 specimens decrease from 9 to 1 specimens (St. 2) and 8 to 1 specimens (St. 4) between 4 cm
10 and 50 cm. The most abundant infaunal specimens in the tidal flat are *M. fusca* with maximum
11 total numbers of 15 specimens (St. 2) and 30 specimens (St. 4) between 1 and 2 cm, and with
12 decreasing numbers to a depth of 40 cm. Other infaunal specimens include *B.*
13 *pseudomacrescens*, found to a depth of 20 cm at St. 2 and to a depth of 10 cm at St. 4., and
14 *Ammonia* sp., found to a depth of 50 cm at St. 2 and to a depth of 4 cm at St. 4. The relative
15 abundance of living specimens is highest in the surface samples with 28% at St. 2 and 66% at
16 station 4. The abundance of infaunal specimens generally decreases with core depth. It varies
17 between 1 and 15% at St. 2 and between <1 and 14% at St. 4.

18
19 In the core from the low marsh (St. 7), peaty silt is found from 0 to 12 cm, which overlies silty
20 sediment (Fig. 8). The total number of live (rose Bengal stained) specimens in the 0-1 cm
21 surface sample is 365 specimens. The living assemblage in the surface sample is again
22 dominated by *M. fusca* (288 specimens), *B. pseudomacrescens* (42 specimens) and *Ammonia*
23 sp. (20 specimens). Higher numbers of living (rose Bengal stained) infaunal specimens (22 to
24 75 specimens) are observed between 1 and 20 cm with lower numbers (2 and 5 specimens)
25 between 30 and 40 cm. The most abundant species in the low marsh are *H. manilaensis* (0 to
26 49 specimens down to 40 cm depth), *B. pseudomacrescens* (0 to 40 specimens down to 30
27 cm depth), *Ammonia* spp. (5 to 18 specimens between 1 and 4 cm depth) and *M. fusca* (1 to
28 10 specimens down to 30 cm depth). The relative abundance of living specimens is highest in

1 the surface sample (33%). The abundance of living infaunal specimens ranges from 0 to 9%
2 with the exception of one sample at 6 cm depth where 17% of living foraminifera are found.

3
4 The core from the middle marsh (St. 9) consists of 13 cm of silty peat overlying a peaty silt
5 (Fig. 8). The total number of live (rose Bengal stained) specimens in the surface sample is 506
6 specimens and is dominated by *T. inflata* (200 specimens), *B. pseudomacrescens* (106
7 specimens) and *H. manilaensis* (82 specimens). The numbers of living (rose Bengal stained)
8 infaunal specimens range from 8 to 50 specimens from 1 to 10 cm depth, and from <1 to 9
9 specimens from 20 to 50 cm depth. The most important infaunal specimens are *H. manilaensis*
10 (<1 to 40 specimens down to 50 cm depth), *T. inflata* (0 to 17 specimens down to 20 cm depth)
11 and *B. pseudomacrescens* (0 to 8 specimens between 1 and 5 cm depth). The highest relative
12 abundance of live specimens is observed in the surface sample with 28%. The relative
13 abundance of live infaunal specimens ranges from 3 to 11% between 1 and 30 cm, and is <1%
14 below 30 cm.

15
16 The core from the high marsh (St. 15) consists of peat in the upper ~20 cm, peaty silt between
17 20 and 28 cm, and silty peat to 33 cm (Fig. 8). In the 0-1 cm surface sample, an almost
18 monospecific population of 15 specimens of *T. irregularis* was found. Higher numbers of live
19 (rose Bengal stained) infaunal specimens (24 to 32) are found between 1 and 4 cm. From 4 to
20 30 cm depth the number of live (rose Bengal stained) foraminifera ranges from 3 to 11
21 specimens. *Trochammina irregularis* is the only common species with 1 to 32 specimens at
22 depths deeper than 1 cm. In the deepest infaunal population at 30 cm, we observed living *H.*
23 *manilaensis* (3 specimens) and *H. wilberti* (1 specimen). We observed the highest relative
24 abundances of living specimens (16 to 22%) from 1 to 4 cm, whereas in the surface sample it
25 is 12%. Lower relative abundances of infaunal specimens (2 to 9%) are observed below 4 cm.

26 27 28 5 Discussion

5.1 Live (rose Bengal stained) populations versus dead foraminiferal assemblages

The production rates of live populations are variable, and the proportions, diversity and concentration of dead foraminiferal assemblages can be altered by cumulative post-depositional changes (e.g., Berkeley et al., 2007). Post-depositional changes vary among environments. In some environments the changes are insignificant, whilst in others assemblages may be strongly altered. At Toms Creek marsh, we found high numbers (per 10 cm³ sediment volume) of live (rose Bengal stained) and dead foraminifera in the low (average of 603 and 1366 specimens) and middle (average of 547 and 1747 specimens) marsh, compared to the tidal flat (260 and 278 specimens) and high marsh and higher marsh to upland transition (17 and 116 specimens). The higher numbers of specimens in the low and middle marsh may be explained by more stable environmental conditions compared to the tidal flat (due to two high tides a day), or in the high and higher marsh (due to brackish conditions or to drying of soils during dry seasons), resulting in greater environmental stress, or by differing environmental preferences by individual species. For example, species such as *J. macrescens* and *T. inflata* prefer higher amounts of organic matter than some other species (Armynot du Châtelet et al., 2009). Other studies have shown that some species have a preference for sandy substrates (*T. inflata*; Matera and Lee, 1972), or for clay substrates containing the mineral smectite (*M. fusca*; Armynot du Châtelet et al., 2008). In Toms Creek marsh, however, the intertidal area from tidal flat to high marsh is characterized by silty sediment with comparable amounts of clay and sand (Fig. A5). This implies that our species distributions vary as a result of environmental conditions other than substrate type. For example, some studies have suggested that *J. macrescens*, *H. manilaensis* and *B. pseudomacrescens* prefer more brackish conditions and that *H. wilberti* prefers higher salinities (Scott and Leckie, 1990; de Rijk, 1995; Edwards et al., 2004; Culver and Horton, 2005; Kemp et al., 2009).

1 On the tidal flat at Toms Creek marsh, we observed a maximum relative (absolute) abundance
2 of live (rose Bengal stained) calcareous species of 53% (215 specimens per 10 cm³ sediment
3 volume) compared to maximum relative (absolute) abundance of dead calcareous species,
4 including organic linings, of 15% (33 specimens per 10 cm³ sediment volume). This difference,
5 together with evidence of dissolution (white instead of transparent tests, presence of inner
6 organic linings), indicates that many calcareous tests were dissolved after burial. Early
7 diagenetic dissolution of calcareous tests has commonly been reported from intertidal
8 environments along North American Pacific coasts (e.g., Jonasson and Patterson, 1992;
9 Hawkes et al., 2010; Milker et al., 2015) and in other temperate and tropical regions (e.g.,
10 Murray and Alve, 1999; Wang and Chappell, 2001; Edwards and Horton, 2000; Horton and
11 Murray, 2006; Berkeley et al., 2009).

12

13 Dissolution has been related to a pH <~7, which results in an undersaturation of calcium
14 carbonate (Alve and Nagy, 1986; Reaves, 1986; Green et al., 1993; Le Cadre et al., 2003;
15 Berkeley et al., 2007). PH may decrease as a result of high amounts of metabolizable organic
16 matter, which cause an increase in the rate of microbial decay with precipitation of ferro-sulfite
17 minerals that are oxidized during times of reduced microbial activity (Reaves, 1986). If fossil
18 assemblages have been influenced by taphonomic alteration similar to that affecting modern
19 dead assemblages, then dead assemblages provide better modern analogues than total
20 assemblages (Horton, 1999; Murray, 2000; Horton and Murray, 2006, 2007). Sub-surface
21 (fossil) assemblages, as used in paleoenvironmental reconstructions, most accurately reflect
22 dead surface assemblages (e.g., Goldstein and Watkins, 1999; Patterson et al., 1999;
23 Hippensteel et al., 2002, Culver and Horton, 2005; Horton et al., 2005; Horton and Edwards,
24 2006; Horton and Murray, 2006). However, in this study, we didn't investigate the fossil dead
25 assemblages in the cores because we assume that these assemblages may not be
26 comparable to the modern assemblages due to different past and modern environmental
27 conditions in Toms Creek. But to minimize the effects of dissolution of calcareous tests on the
28 accuracy of sea-level reconstructions, the remaining dead calcareous species in an

assemblage are commonly grouped with organic linings as a single modern “species” (Edwards and Horton, 2000).

5.2 Patchiness of modern foraminifera

Small-scale spatial variations in foraminiferal assemblages have been documented in many studies (e.g., Buzas, 1968, 1970; Schafer, 1971; Swallow, 2000; Murray and Alve, 2000; Buzas et al., 2002; Morvan et al., 2006; Kemp et al., 2011). However, our NPMANOVA analyses indicate that small-scale variability is not significant in the distributional pattern of live (rose Bengal stained) and dead foraminifera in the intertidal zone at Toms Creek marsh. Lynts (1966) also observed a homogenous populations of modern foraminifera in the majority of shallow-water stations in Buttonwood Sound, Florida. Also in Florida, Buzas et al. (2002) found a nearly homogenous distribution of foraminifera in replicate samples collected within 1 m² in the Indian River Lagoon over a period of five years.

Despite the insignificance of spatial variability in assemblage composition throughout of the intertidal zone, we observed higher dissimilarities among live (rose Bengal stained) populations than among dead assemblages, particularly in the middle marsh (St. 9-12; Fig. 6A-D). Likewise, Buzas (1970) studied the distribution of live single-species and multi-species assemblages in the Rehoboth estuary, Delaware. Buzas (1970) found some variability in single-species assemblages, but nearly homogenous distributions of multi-species assemblages. Murray and Alve (2000) observed variability among three intertidal calcareous species (*Elphidium excavatum*, *Haynesina germanica*, *Ammonia beccarii* forma *tepida*) at two stations, each sampled within 1 m² over 27 months in the Hamble estuary, U.K. Kemp et al. (2011) studied the spatial distribution of six species (*M. fusca*, *T. inflata*, *Arenoparrella mexicana*, *Tiphotrocha comprimata*, *H. wilberti* and *J. macrescens*) of dead assemblages in a North Carolina marsh and attributed their patchy distributions in the middle marsh to variable environmental conditions. Alve and Murray (1999) reported a high abundance of living *J.*

1 *macrescens* at sites with decaying *Carex acuta* debris, which may indicate that this species
2 feeds on bacteria and decay products from rotting plants. At Toms Creek, the spatial
3 distribution of organic matter content (LOI) and vegetation is more variable in the middle marsh
4 than elsewhere along the transect (Fig. A5). Other studies (de Rijk, 1995; de Rijk and Troelstra,
5 1997; van der Molen, 1997) suggest that variability in the frequency and duration of inundation
6 within the middle marsh may influence the spatial distribution of foraminifera.

7 8 5.3 Vertical zonation of live (rose Bengal stained) and dead foraminifera

9
10 The successful use of intertidal foraminifera to reconstruct former sea levels requires a detailed
11 and accurate understanding of their modern vertical distributions with respect to the tidal frame
12 (Scott and Medioli, 1978). The vertical zonation of foraminifera result from changing
13 environmental conditions with respect to the tidal frame such as tidal inundation, salinity,
14 organic matter content or grain-size distribution (e.g., de Rijk, 1995; Horton and Edwards,
15 2006; Hawkes et al., 2010).

16
17 Both live (rose Bengal stained) populations and dead assemblages show distinct vertical
18 zonations at Toms Creek marsh (Fig. 7A, B), although live (rose Bengal stained) populations
19 and dead assemblages from the low marsh (St. 7, 8) cluster in different vertical zones (Fig.
20 7C). Because the dead assemblages provide better modern analogues for paleoenvironmental
21 reconstruction, we discuss the vertical zonation of dead assemblages in greater detail.

22
23 The vertical zonation of dead assemblages at Toms Creek is comparable to zonations within
24 other intertidal environments along North America's Pacific coast (e.g., Hunger, 1966; Williams,
25 1989, 1999; Jennings and Nelson, 1992; Guilbault et al., 1996; Nelson et al., 2008; Hawkes et
26 al., 2010; Engelhart et al., 2013a), but with notable site-specific differences. As elsewhere, the
27 dead foraminiferal assemblages of the tidal flat and low marsh (Cluster IIb, Fig. 7B) are
28 dominated by *M. fusca*, a species that has often been reported as an indicator species for

1 these environments (Williams, 1989, 1999; Jennings and Nelson, 1992; Hawkes et al., 2010;
2 Engelhart et al., 2013a; Milker et al., 2015). In the middle marsh, the dominant dead species
3 are *B. pseudomacrescens* and *T. inflata* (Cluster IIa, Fig. 7B). *Trochammina inflata* and *B.*
4 *pseudomacrescens*, as well as *J. macrescens*, have commonly been reported from middle
5 marsh environments (Guilbault et al., 1996; Jennings and Nelson, 1992; Nelson et al., 2008;
6 Hawkes et al., 2010; Engelhart et al., 2013a). The high marsh and upland transition at Toms
7 Creek is dominated by *T. irregularis* with lower percentages of *B. pseudomacrescens* and *M.*
8 *petila* (cluster I, Fig. 7B). *Trochammina irregularis* and *B. pseudomacrescens* have commonly
9 been observed as the dominant species in the high and highest marsh in North American
10 Pacific marshes (Hawkes et al., 2010; Engelhart et al., 2013a; Milker et al., 2015). *M. petila*,
11 however, has only been observed in the middle and high marshes of Siletz Bay (Engelhart et
12 al., 2013a). In contrast, *B. pseudomacrescens* is absent or has a low abundance in high marsh
13 and upland environments at marshes in northern Coos Bay, and in the Coquille River estuary,
14 17 km south of our study area (Jennings and Nelson, 1992; Hawkes et al., 2010).

15

16 5.4 The significance of infaunal foraminifera

17

18 Most investigators have assumed that intertidal foraminifera are primarily epifaunal, and for
19 this reason, in most studies of modern foraminiferal distribution the upper 1-2 cm of surface
20 sediment was sampled (e.g., Scott and Medioli, 1980; Gehrels, 1994; de Rijk, 1995; Horton
21 and Edwards 2006; Kemp et al., 2009). A number of studies, however, have found infaunal
22 foraminifera at depths as great as 80 cm in salt marshes and mangrove swamps (e.g., Matera
23 and Lee, 1972; Buzas, 1977; Steineck and Bergstein, 1979; Goldstein and Harben, 1993;
24 Goldstein et al., 1995; Ozarko et al., 1997; Goldstein and Watkins, 1998; Saffert and Thomas,
25 1998; Goldstein and Watkins, 1999; Patterson et al., 1999; Hippensteel et al., 2002; Culver
26 and Horton, 2005; Duchemin et al., 2005; Tobin et al., 2005; Berkeley et al., 2007; Leorri and
27 Martin, 2009; Culver et al., 2013). Patterson et al.'s (1999) study of total modern assemblages
28 in British Columbia found that foraminifera in samples from 0 to 10 cm depth better matched

1 the percentages in fossil assemblages owing to the inclusion of infaunal species that were
2 absent or underrepresented (*J. macrescens*, *B. pseudomacrescens* and *H. wilberti*) in the 0 to
3 1 cm surface samples. Use of such thick sampling intervals to characterize modern
4 environments relies on the assumption that environments have not changed over the time span
5 represented by 10 cm of sediment. In many tidal settings, such an assumption may not be
6 justified.

7
8 At Toms Creek marsh, the highest numbers of living specimens at the tidal flat, low and middle
9 marsh stations are found in the surface samples (Fig. 8), with relative abundance of the total
10 live epifaunal and infaunal population between 28% (St. 2, 9) and 66% (St. 4). However, at the
11 high marsh the maximum abundances of live specimens (16-22%) are found between 1 and 3
12 cm depth, compared to 12% in the surface sample. Collectively, the relative abundance of
13 living specimens is highest in the upper 10 cm (88 to 97%). Similarly, Horton (1999) and Horton
14 and Edwards (2006) illustrated that the intertidal foraminifera of Cowpen Marsh and Rusheen
15 Bay (Ireland), respectively, live primarily in the upper 1 cm. Alve and Murray (2001) also noted
16 that in the Hamble estuary, the majority of living foraminifera are restricted to the upper 0.25
17 cm of sediment. Our study is in accordance to other studies that reported infaunal habitats for
18 different species in salt marsh environments along the American and North European Atlantic
19 coasts (e.g., Matera and Lee, 1972; Buzas, 1977; Steineck and Bergstein, 1979; Goldstein
20 and Harben, 1993; Goldstein et al., 1995; Ozarko et al., 1997; Goldstein and Watkins, 1998;
21 Goldstein and Watkins, 1999; Saffert and Thomas, 1998; Hippensteel et al., 2002; Culver and
22 Horton, 2005; Duchemin et al., 2005; Tobin et al., 2005). These studies confirm that most live
23 species occur in the first centimeters of sediment but also show that live foraminifera can be
24 frequently found at deeper depths (Fig. 8).

25
26 Despite the considerable body of work on infaunal distributions, consensus on whether or not
27 many species are infaunal is lacking. At least in part, this is due to the fact that the infaunal
28 distributions of foraminifera are spatially and temporally variable, reflecting seasonal and local

1 changes in environmental conditions and differences in the extent and timing of bioturbation
2 (Buzas et al., 1993; de Stigter et al., 1998; Patterson et al., 2004; Culver and Horton, 2005;
3 Tobin et al., 2005; Horton and Edwards, 2006). For example, Alve and Murray (2001) and
4 Horton and Edwards (2006) concluded that the redox boundary is not the main limiting factor
5 in down-core abundance. Infaunal distributions of intertidal foraminifera may also be strongly
6 influenced by “oxygen oases” along plant roots and animal burrows that make it possible for
7 foraminifera to live infaunally (Steineck and Bergstein, 1979). Goldstein et al. (1995) concluded
8 that passive transport due to bioturbation may result in an apparent preference for infaunal
9 habitat as well. In contrast, Saffert and Thomas (1998) suggested that active migration of
10 foraminifera into the sediment may explain infaunal distributions and assumed that foraminifera
11 in salt marshes can migrate vertically with velocities as great as 10 mm/hour.

12

13 Possible errors in sea-level reconstructions caused by infaunal foraminifera are of particular
14 concern along the Pacific coast of central North America where such reconstructions are used
15 to infer the history of great earthquakes at the Cascadia subduction zone (e.g., Nelson et al.,
16 2008; Hawkes et al., 2010, 2011). For example, *M. fusca* is commonly the primary species in
17 the tidal flat and low marsh mud deposited in the days to decades following sudden coastal
18 subsidence during magnitude 8-9 earthquakes (e.g., Guilbault et al., 1996; Hawkes et al.,
19 2011; Engelhart et al., 2013a). In an experiment where modern high marsh sediment was
20 transplanted into the low marsh, Engelhart et al. (2013b) identified high abundances of *M.*
21 *fusca* in the transplanted high marsh sediment. Based on gradual downcore changes in
22 geochemistry that paralleled changes in the abundance of *M. fusca*, they concluded that the
23 abundance of *M. fusca* was caused by sediment mixing, not by infaunal migration of *M. fusca*.
24 This interpretation may be supported by our Toms Creek data, which show that percentages
25 of live *M. fusca* are $\leq 12\%$ in samples below 1 cm (compared to the total living population)
26 during the sampling time. Although our study lacks data about seasonal variability of infaunal
27 species, mixing may explain the high percentages of *M. fusca* found in the upper high marsh

transplant sample (64%) compared to the background level of 7% defined by Engelhart et al. (2013b).

We suggest, however, that the influence of infaunal species on the dead assemblage is minor. The numbers of infaunal specimens in the first ten cm of the cores are low compared to the total numbers of dead specimens in the corresponding surface samples. A ratio of 7318 (91%) dead surface to 703 (9%) live infaunal specimens is observed across all environments. Furthermore, we found all infaunal specimens present in the surface samples; that is, none of the species are solely infaunal. The most dominant infaunally observed species at each station has been also be found to be dominant in the dead surface assemblages. For example, *M. fusca*, *T. inflata*, *B. pseudomacrescens* and *T. irregularis* are the dominant species both in the live infaunal and dead surface assemblages,

6 Conclusions

(1) Dead foraminiferal assemblages at Toms Creek marsh are influenced by early diagenetic dissolution of calcareous tests. Dead assemblages provide better modern analogues than live (rose Bengal stained) or total assemblages for paleoenvironmental reconstructions, if similar post-depositional processes influence fossil assemblages.

(2) The live (rose Bengal stained) populations and dead assemblages at Toms Creek show non-insignificant small-scale spatial variability. The dissimilarity among live (rose Bengal stained) assemblages, particularly in the middle marsh, may result from variable environmental conditions, such as changes in vegetation or frequency and duration of tidal inundation.

(3) The live (rose Bengal stained) populations and dead assemblages at Toms Creek marsh show a distinct zonation with respect to elevation, but with differing elevational boundaries. The dead foraminiferal zonation is comparable to previously reported zonations for other

1 intertidal sites, but with notable site-specific differences. The tidal flat and low marsh at Toms
2 Creek marsh are dominated by *M. fusca*, the middle marsh is dominated by *B.*
3 *pseudomacrescens* and *T. inflata*, and the high marsh and upland transition zone are
4 dominated by *T. irregularis*.

5
6 (4) Live (rose Bengal stained) infaunal foraminifera are observed to 50 cm depth at Toms Creek
7 marsh, but highest numbers of living specimens are found in the first cm of sediment with the
8 exception of the high marsh where higher numbers of live specimens were found between 1
9 to 3 cm core depth.

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12
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3

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- 25
- 26

1 Appendices

2

3 Appendix A1: Grain-size and loss on ignition data for Toms Creek marsh stations.

4

5 Appendix A2: Taxonomic list of species mentioned in the text.

6

7 Appendix A3: Census counts of live (rose Bengal stained) and dead specimens for Toms Creek
8 marsh stations.

9

10 Appendix A4: Census counts of live (rose Bengal stained) and dead specimens in Russian
11 core samples from Toms Creek marsh.

12

13 Appendix A5: Grain-size distribution (percentages of sand, silt and clay), loss on ignition (LOI)
14 and elevation of the Toms Creek marsh (TM) stations, with tidal datums (MTL = mean tide
15 level; MHW = mean high water; MHHW = mean highest high water) adapted from the
16 Charleston tide gauge station (Fig. 1B).

17

18 Appendix A6: Distance between replicate samples versus median Bray-Curtis similarity
19 between the replicate samples from Russian cores. Given are the correlation coefficients
20 between the distance of the replicate samples and median Bray-Curtis similarities of the
21 absolute abundances of live and dead species (A) and relative abundances of live and dead
22 species (B).

23

24

1 Figure captions

2

3 Figure 1

4 Map of the North American Pacific coast showing major features of the Cascadia subduction
5 zone (A), the Coos Bay estuary with the study site in the South Slough National Estuarine
6 Research Reserve (NERR), and the tide gauge in Charleston (NOAA ID 9432780; B), and
7 station locations (surface samples and Russian cores; see Table 1) in Toms Creek marsh
8 along the Winchester Creek Arm of South Slough (C).

9

10 Figure 2

11 Relative abundances of the most abundant live (rose Bengal stained) foraminifera in the four
12 replicate samples (replicates A, B, C and D), taken from Toms Creek marsh, and sample
13 elevation profiles with tidal datums for MTL (mean tide level), MHW (mean high water) and
14 MHHW (mean highest high water).

15

16 Figure 3

17 Absolute abundances of the most abundant live (rose Bengal stained) foraminifera in the four
18 replicate samples (replicates A, B, C and D), taken from Toms Creek marsh, and sample
19 elevation profiles with the tidal datums for MTL (mean tide level), MHW (mean high water) and
20 MHHW (mean highest high water).

21

22 Figure 4

23 Relative abundances of the most abundant dead foraminifera in the four replicate samples
24 (replicates A, B, C and D), taken from Toms Creek marsh, and sample elevation profiles with
25 the tidal datums for MTL (mean tide level), MHW (mean high water) and MHHW (mean highest
26 high water).

27

28 Figure 5

Absolute abundances of the most abundant dead foraminifera in the four replicate samples (replicates A, B, C and D), taken from Toms Creek marsh, and sample elevation profiles with the tidal datums for MTL (mean tide level), MHW (mean high water) and MHHW (mean highest high water).

Figure 6

Box-Whisker plots of the Bray-Curtis similarities measured between the relative abundances of live (rose Bengal stained) (A) and dead (C) species and absolute abundances of live (B) and dead (D) species in the replicate samples. The boxes show the median and the 25th and 75th percentiles and the whiskers show the minimum and maximum values.

Figure 7

Dendrograms from the cluster analysis of live (rose Bengal stained) (A) and dead (B) foraminifera from Toms Creek marsh with percentages of cluster replications (1000 permutations), and the percentages of the most common live and dead species. Box whisker plots of the elevational range for clusters shown in A and B (C). The boxes show the median and the 25th and 75th percentiles and the whiskers show the minimum and maximum values.

Figure 8

Core lithologies, total and individual live (rose Bengal stained) foraminiferal numbers (per 10cm³ sediment volume), and total percentages of live (rose Bengal stained) specimens relative to the total live populations in each core taken from the tidal flat (St. 2, 4), low marsh (St. 7), middle marsh (St. 9) and high marsh (St. 15).

Plate 1

1 *Miliammina fusca*, side view, 2 *M. fusca*, side view, 3 *Miliammina petila*, side view, 4 *M. petila*, side view, 5 *Reophax moniliformis*, side view, 6 *Reophax* spp., side view, 7 *Ammobaculites dilatatus*, side view, 8 *Haplophragmoides manilaensis*, side view, 9 *H. manilaensis*, side view,

1 10 *Haplophragmoides wilberti*, side view, 11 *Trochamminita irregularis*, side view of lower
2 species part, 12 *Ammobaculites* spp., side view, 13 *Balticammina pseudomacrescens*, spiral
3 side, 14 *B. pseudomacrescens*, umbilical side, 15 *Paratrochammina haynesi*, spiral side, 16
4 *Trochammina inflata*, spiral side, 17 *T. inflata*, umbilical side, 18 *Trochammina ochracea*, spiral
5 side, 19 *T. ochracea*, umbilical side, 20 *Jadammina macrescens*, spiral side of a specimen
6 without secondary apertures, 21 *J. macrescens*, spiral side of a specimen with secondary
7 apertures, 22 *J. macrescens*, umbilical side, 23 *Haynesina* sp., side view, 24 *Haynesina* sp.,
8 apertural view, 25 *Ammonia* sp., spiral side, 26 *Ammonia* sp., umbilical side, 27 inner organic
9 lining of *Ammonia* spp., spiral side. Thick scale = 100 μm , thin scale = 20 μm .

10

11 Table captions

12

13 Table 1

14 Location (latitude, longitude), mean elevation (m NAVD88) of the sampled stations and mean
15 distance from one station to the next in Toms Creek marsh (TM). The asterisks mark stations
16 where Russian cores were collected.

17

18

Table 1

Station	Latitude	Longitude	Mean elevation (m NAVD88)	Distance between duplicate samples (cm)	Mean distance between stations (m)
1	43°16'48.55"N	124°19'05.50"W	1.02	50	0.00
2*	43°16'48.56"N	124°19'06.08"W	1.05	20	1.79
3	43°16'48.56"N	124°19'05.94"W	1.13	8	3.01
4*	43°16'48.56"N	124°19'05.90"W	1.23	7	1.00
5	43°16'48.59"N	124°19'05.86"W	1.42	12	1.30
6	43°16'48.59"N	124°19'05.68"W	1.60	6	4.04
7*	43°16'48.69"N	124°19'05.50"W	1.82	8	3.64
8	43°16'48.69"N	124°19'05.50"W	2.00	8	2.03
9*	43°16'49.12"N	124°19'05.29"W	2.15	10	14.06
10	43°16'49.71"N	124°19'04.68"W	2.10	22	29.49
11	43°16'50.07"N	124°19'04.25"W	2.24	20	15.73
12	43°16'50.33"N	124°19'03.99"W	2.31	20	10.78
13	43°16'50.46"N	124°19'03.63"W	2.42	15	9.32
14	43°16'50.60"N	124°19'03.33"W	2.60	10	9.11
15*	43°16'50.63"N	124°19'03.15"W	2.63	15	4.42
16	43°16'50.67"N	124°19'03.06"W	2.65	27	2.24
17	43°16'50.83"N	124°19'03.06"W	2.76	23	4.83
18	43°16'50.86"N	124°19'03.02"W	2.95	17	1.42

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6

Figure 7
A: Live populations

B: Dead assemblages

C: Elevational range of clusters

Figure 8