Journal of Foraminiferal Research, v. 50, no. 3, p. 266–278, July 2020

ENOUGH IS ENOUGH, OR MORE IS MORE? TESTING THE INFLUENCE OF FORAMINIFERAL COUNT SIZE ON RECONSTRUCTIONS OF PALEO-MARSH ELEVATION

Andrew C. Kemp[1,*], Alexander J. Wright[2], and Niamh Cahill[3]

ABSTRACT

Salt-marsh foraminifera are sea-level proxies used to quantitatively reconstruct Holocene paleo-marsh elevations (PME) and subsequently relative sea level (RSL). The reliability of these reconstructions is partly dependent upon counting enough foraminifera to accurately characterize assemblages, while counting fewer tests allows more samples to be processed. We test the influence of count size on PME reconstructions by repeatedly subsampling foraminiferal assemblages preserved in a core of salt-marsh peat (from Newfoundland, Canada) with unusually large counts (up to 1595). Application of a single, weighted-averaging transfer function developed from a regional-scale modern training set to these ecologically-plausible simulated assemblages generated PME reconstructions at count sizes of 10–700. Reconstructed PMEs stabilize at counts sizes greater than ~50 and counts exceeding ~250 tests show little return for the additional time invested. The absence of some rare taxa in low counts is unlikely to markedly influence results from weighted-averaging transfer functions. Subsampling of modern foraminifera indicates that cross-validated transfer function performance shows only modest improvement when more than ~40 foraminifera are counted. Studies seeking to understand multi-meter and millennial scale RSL trends should count more than ~50 tests. The precision sought by studies aiming to resolve decimeter- and decadal-scale RSL variability is best achieved with counts greater than ~75. In most studies seeking to reconstruct PME, effort is more productively allocated by counting relatively fewer foraminifera in more core samples than in counting large numbers of individuals. Target count sizes of 100–300 in existing studies are likely conservative and robust. Given the low diversity of salt-marsh foraminiferal assemblages, our results are likely applicable throughout and beyond northeastern North America.

INTRODUCTION

Reconstructions of Holocene relative sea level (RSL) are valuable (for example) in constraining and testing geophysical models of glacio-isostatic adjustment (e.g., Peltier, 1996; Engelhart et al., 2015); identifying large earthquakes that uplifted or submerged coasts (Nelson, 2013); quantifying the anomalous nature of recent global mean sea-level rise (e.g., Kopp et al., 2016); calibrating models that predict future changes (e.g., Bittermann et al., 2017); and interpreting coastal evolution (e.g., Mallinson et al., 2011). A primary source of Holocene RSL reconstructions is salt-marsh sediment preserved in the coastal stratigraphic record because the vertical distribution of salt marshes is intrinsically linked to tidal elevation (e.g., Redfield & Rubin, 1962; Bloom & Stuiver, 1963). Consequently, the remains of plants and microfossils that live within salt marshes are widely employed as proxies for sea level (e.g., Scott & Medioli, 1978; Donnelly, 2006; Horton & Edwards, 2006).

Salt-marsh foraminifera are used to reconstruct RSL through reasoning by analogy in which assemblages preserved in Holocene sediment are compared to their modern, observable counterparts to determine the tidal elevation of a former salt-marsh surface (termed paleo-marsh elevation; PME). Often, PME is quantitatively reconstructed using transfer functions, which are empirical equations derived from a modern training set (Sachs et al., 1977) that relate the abundance of foraminifera (or another group of microfossils such as diatoms or testate amoebae) to tidal elevation. In Holocene RSL reconstructions, the most commonly used transfer functions are weighted averaging (WA) and weighted averaging partial least squares (WA-PLS; Barlow et al., 2013; Kemp & Telford, 2015). Although these techniques represent populations using proportions (and are consequently blind to the underlying count size) there is a risk that foraminiferal assemblages are not adequately characterized (i.e., taxa proportions are inaccurate and/or rare species are incorrectly deemed absent) and the resulting PME is spurious. Therefore, the accuracy and precision of RSL reconstructions generated using transfer functions is partly dependent on counting enough tests to adequately characterize fossil assemblages that are typically low diversity. For example, in a regional-scale dataset of modern foraminifera comprised of 394 samples collected at 19 salt marshes between northern California and British Columbia, a total of 17 taxa were identified of which just five made up 94% of the ~125,000 counted individuals (previously published datasets compiled in Kemp et al., 2018a).

Due to the low diversity of foraminiferal assemblages in salt marshes it is common practice to target counts of 100–300 individuals per sample (e.g., Scott & Leckie, 1990; Horton & Edwards, 2006; Southall et al., 2006; Hawkes et al., 2010; Callard et al., 2011). However, in studies seeking to reconstruct RSL, researchers strive to achieve a practical balance between the number of individual foraminifera and the number of samples that can be counted in a project's timeframe. It remains unclear how many foraminifera should be counted in the specific case of applying widely-used transfer functions to assemblages of salt-marsh foraminifera to reconstruct PME and what the

---

[1] Department of Earth and Ocean Sciences, Tufts University, Medford, MA 02155, USA

[2] Department of Marine Biogeology, Faculty of Earth & Life Sciences, Vrije Universiteit Amsterdam, 1081 HV, Amsterdam, the Netherlands

[3] Department of Mathematics and Statistics, Maynooth University, Maynooth, Co. Kildare, Ireland

* Correspondence author. E-mail: andrew.kemp@tufts.edu

Downloaded from http://pubs.geoscienceworld.org/cushmanfoundation/jfr/article-pdf/50/3/266/5143690/i0096-1191-50-3-266.pdf
by Maynooth University user

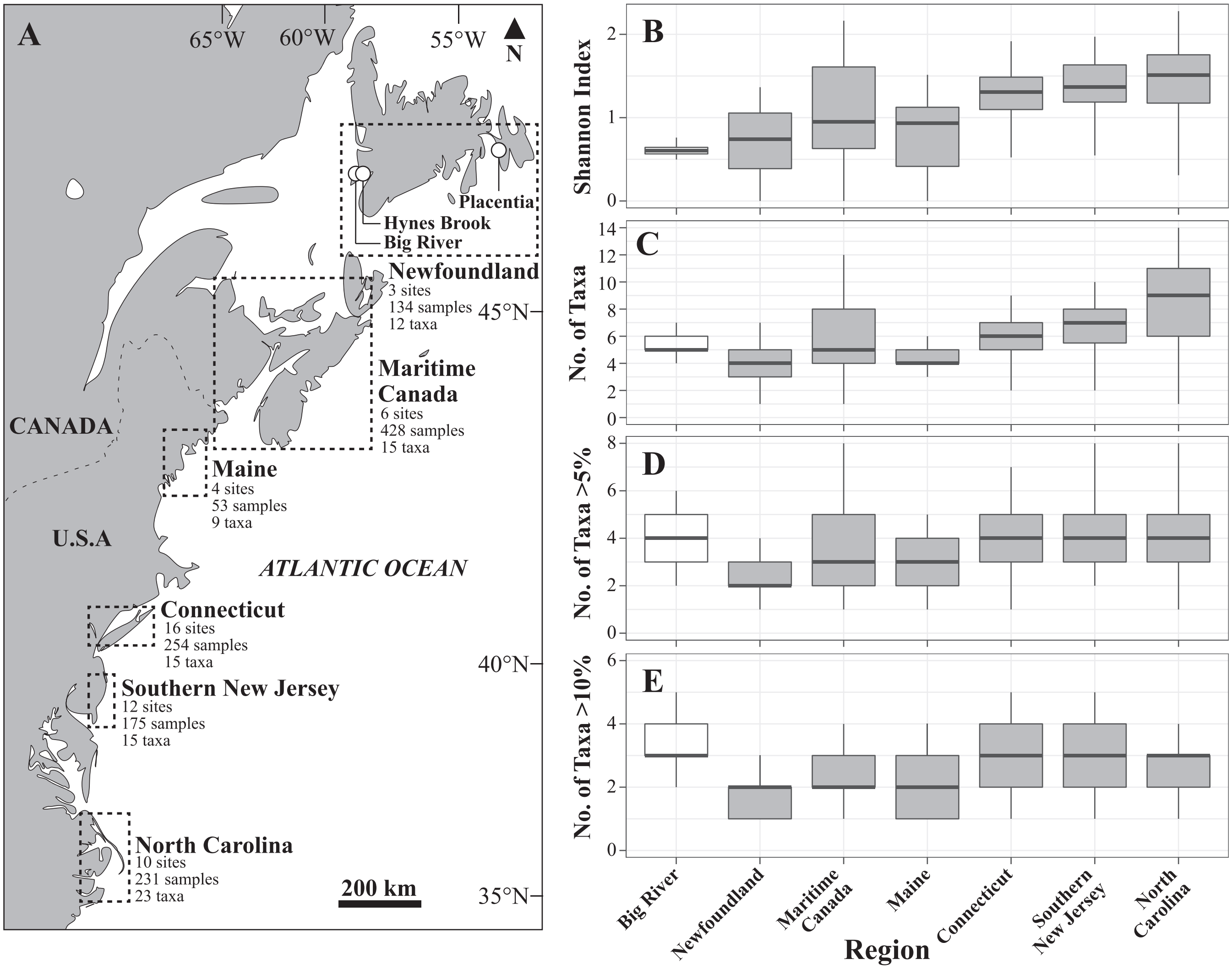


FIGURE 1. **(A)** Location of study site at Big River in eastern Newfoundland, Canada. The modern training set of salt-marsh foraminifera for Newfoundland consists of samples from multiple transects at Big River, Hynes Brook, and Placentia. The locations of five other regional-scale modern training sets are shown with summary data about the number of sites, samples, and taxa that comprise each dataset. Maritime Canada (Scott & Medioli, 1980; Scott et al., 1981; Patterson et al., 2004;); Maine (Gehrels, 1994); Connecticut (compiled from multiple studies in Kemp et al., 2015); Southern New Jersey (Kemp et al., 2013b); North Carolina (Kemp et al., 2009). **(B–E)** Diversity measured in individual samples across the six regional-scale modern training sets (grey) and in the Big River core (white) using (from top to bottom): the Shannon index, total number of taxa, taxa exceeding 5% of the assemblage, and taxa exceeding 10% of the assemblage. Diversity calculated after taxonomic standardization to support comparability among studies. Notably all calcareous species were combined as were all species of *Ammobaculites* and *Haplophragmoides*, while *Jadammina macrescens*/*Balticammina pseudomacrecens* and *Trochammina inflata*/*Siphotrochammina lobata* were combined. Box plots represent the median (solid horizontal line), 25th and 75th percentiles (hinges), and the largest value no further than 1.5 times the interquartile range from the hinge (approximately a 95% confidence interval for comparing medians; whiskers).

quantitative effect of counting fewer (or more) individuals may have on the resulting RSL record and why.

To provide insight into how count size influences the accuracy and precision of PME reconstructions generated using salt-marsh foraminifera-based transfer functions, we reanalyzed assemblages preserved in a core of salt-marsh sediment deposited during the past ~3000 years at Big River, Newfoundland (Fig. 1; Kemp et al., 2018b). This core is unusual because of the large number of foraminifera (average of 471, range from 4–1595) that were counted in individual samples. We repeatedly subsampled these empirical counts to generate ecologically-plausible fossil assemblages of variable size and then applied a single WA transfer function to each assemblage. We compared the resulting PME reconstructions across count sizes to infer the practical influence of count size on Holocene RSL reconstructions generated using salt-marsh foraminifera and WA transfer functions.

DATASETS

A modern training set that quantifies the relationship between salt-marsh foraminifera and tidal elevation in Newfoundland was previously generated from three sites (Big River, Hynes Brook, and Placentia; Fig. 1; Kemp

Downloaded from http://pubs.geoscienceworld.org/cushmanfoundation/jfr/article-pdf/50/3/266/5143690/i0096-1191-50-3-266.pdf
by Maynooth University user

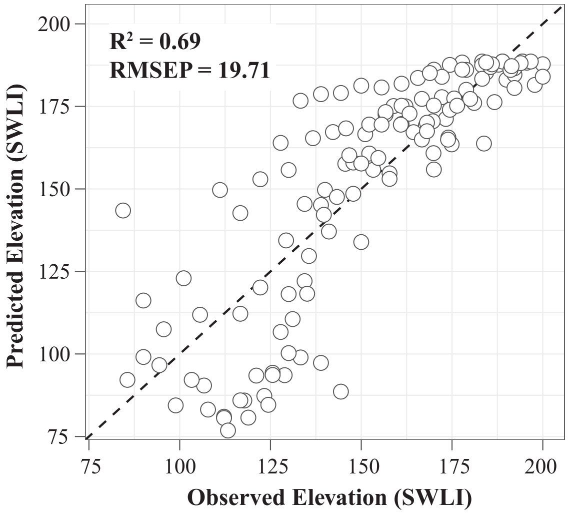


FIGURE 2. Performance of a transfer function (weighted averaging with classical deshrinking) under cross-validation (1000 bootstrapping cycles). The transfer function was empirically derived from a modern training set of 134 paired observations of foraminiferal assemblages in surface sediment and tidal elevation from three sites in Newfoundland. The dashed 1:1 line represents parity between observed and predicted elevations (expressed as a standardized water level index; SWLI, where a value of 100 is local mean tide level and 200 is the highest occurrence of foraminifera).

et al., 2017b; Wright et al., 2011). This dataset consists of 134 samples, in which 29,421 foraminifera from 12 taxa were identified. The five most abundant taxa (cumulatively 99.3% of counted individuals) were *Jadammina macrescens/Balticammina pseudomacrescens* (56%; these two species were combined to ensure taxonomic consistency among studies), *Miliammina fusca* (28%), *Tiphotrocha comprimata* (7%), *Trochammina inflata* (6%), and *Haplophragmoides* spp. (4%). Six taxa had relative abundances greater than 5% in at least one sample (those named above plus *Siphotrochammina lobata*). We retain *Jadammina macrescens* (as opposed to *Entzia macrescens*; Filipescu & Kaminski, 2008) because of its ubiquitous use in the literature pertaining to salt-marsh foraminifera and RSL. Since the samples in the modern training set were collected from sites with different tidal ranges, sample elevation is expressed as a standardized water level index (SWLI; e.g., Horton et al., 1999), where a value of 100 equates to local mean tide level and 200 is the highest occurrence of foraminifera at each site. This modern dataset provided the empirical observations necessary to build a transfer function (Fig. 2).

Core F25 from Big River, Newfoundland (Figs. 1 and 3) comprises ~3 m of salt-marsh peat within which are thin (<5 cm) and discontinuous lenses of fine-grained clastic material (Kemp et al., 2018b). Radiocarbon ages from 42 depths in the core coupled with recognition of pollution trends of known age in downcore elemental and isotopic profiles constrain the history of sediment accumulation and demonstrate that the core spans the past ~3000 years. Foraminifera were enumerated from 152, 1-cm-thick samples between the surface and a depth of 3.02 m (Fig. 3). These samples yielded 12 taxa with count sizes from 4–1595 individuals (mean of 471). Large count sizes indicate that the populations of foraminifera in core samples are likely accurately described (Lytle & Wahl, 2005). Although a count of any size from a subsample of sediment may be affected by random error, this influence is likely negligible because sample preparation (sieving, suspension in water, division using a wet splitter, resuspension, and pipetting) physically randomizes tests. Furthermore, samples with a thickness of 1 cm typically represent years to decades of sedimentation, which time averages assemblages to negate the influence of factors such as seasonality (e.g., Horton, 1999; Murray & Alve, 2000) and patchiness (e.g., Swallow, 2000; Kemp et al., 2011). Of the 71,552 counted individuals in core F25, *Jadammina macrescens/Balticammina pseudomacrescens* (57%), *Tiphotrocha comprimata* (15%), *Miliammina fusca* (14%), *Haplophragmoides* spp. (9%), and *Trochammina inflata* (4%) cumulatively made up 99% of identified specimens. There is a high degree of analogy between assemblages preserved in the Big River core and those in the modern training set (Kemp et al., 2018b).

METHODS

We developed a transfer function for reconstructing PME at Big River by using the 134 surface samples as a modern training set (Fig. 2). Input for the transfer function was the relative abundance of foraminifera expressed as proportions and elevation in SWLI units. The transfer function used WA because this specific numerical technique is widely used in studies seeking to reconstruct RSL (Barlow et al., 2013) and because extension of the model to include partial least squares (WA-PLS) offered little improvement in performance (e.g., Birks, 1995; Juggins & Birks, 2012). Reported results are for classical de-shrinking and were generated through cross validation (1000 bootstrapping cycles). This transfer function was subsequently applied to all fossil assemblages to reconstruct PME. Therefore, variability among reconstructions arises only from the composition of fossil assemblages and not from the specific transfer function used.

The transfer function was first applied to fossil assemblages characterized by all counted individuals to produce the "original" PME reconstruction. We then simulated ecologically-plausible assemblages of variable count size (*n*) by randomly drawing individual foraminifera from the original counts at each of the 152 sampled depths in the core. Drawing was done without replacement, meaning that an individual test could not be included twice in any randomly-generated assemblage and that the probability of any remaining test being drawn was updated after each draw (e.g., Quinlan & Smol, 2001). This approach approximates the physical randomization of tests during sample preparation and is more realistic than sampling with replacement, which allows an individual to be included more than once in a simulated assemblage (e.g., Heiri & Lotter, 2001; Lytle & Wahl, 2005; Payne & Mitchell, 2009). After drawing *n* individuals, taxon abundances were transformed into proportions and application of the WA transfer function generated a PME reconstruction with sample-specific (~1σ) uncertainty (units of SWLI) using 1000 bootstrapping cycles. This procedure was repeated 100 times to create a large dataset of PME reconstructions at count size *n*. We used several values for

Downloaded from http://pubs.geoscienceworld.org/cushmanfoundation/jfr/article-pdf/50/3/266/5143690/i0096-1191-50-3-266.pdf
by Maynooth University user

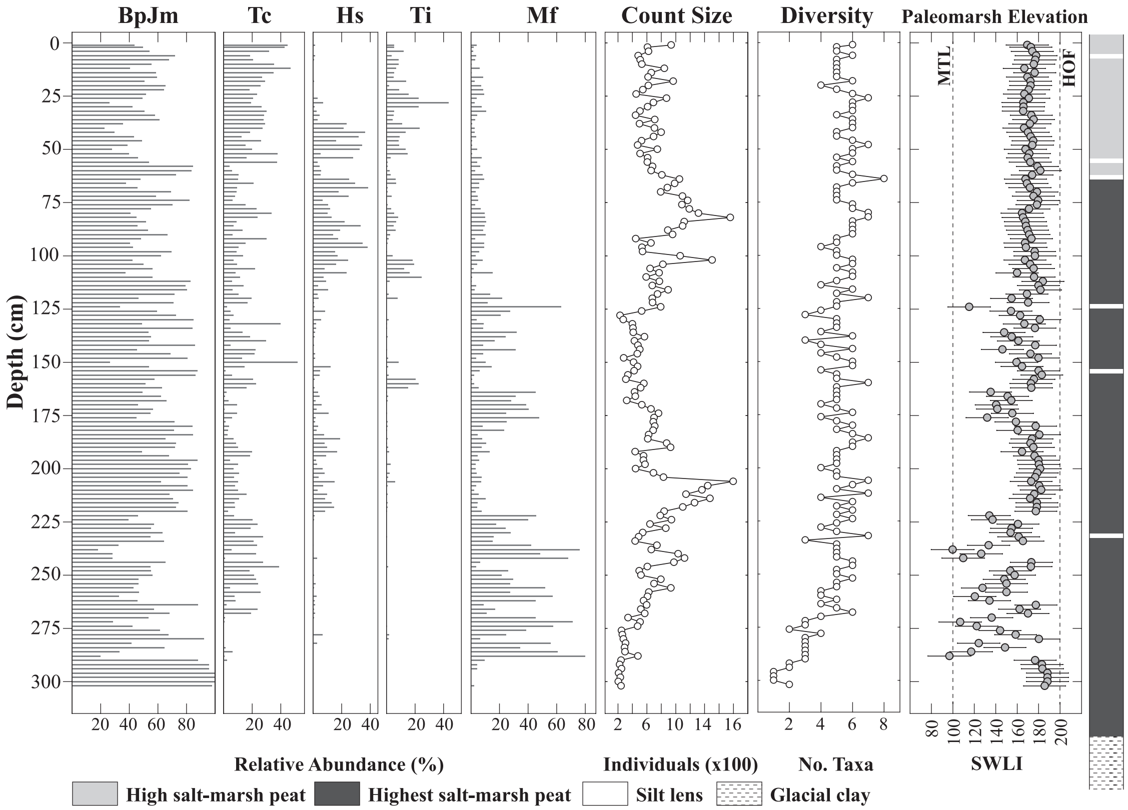


FIGURE 3. Foraminifera enumerated from 1-cm thick samples of sediment in core F25 from Big River, Newfoundland. Taxon abundance (cumulatively these taxa comprise 99% of counted individuals in the core) are shown as percentages for ease of comparison among samples, but count size is presented. BpJm = *Balticammina pseudomacrescens/Jadammina macrescens*; Tc = *Tiphotrocha comprimata*; Hs = *Haplophragmoides spp.*; Ti = *Trochammina inflata*; Mf = *Miliammina fusca*. Paleo-marsh elevation was reconstructed using a weighted averaging (WA) transfer function applied to full counts, where the relationship between foraminifera and tidal elevation was empirically determined from a regional-scale modern training set of 134 samples from Big River, Hynes Brook, and Placentia. SWLI = standardized water level index where a value of 100 corresponds to local mean tide level (MTL) and 200 is the highest occurrence of foraminifera (200). Modified from Kemp et al. (2018b).

n (10, 20, 30, 40, 50, 75, 100, 125, 150, 175, 200, 250, 300, 350, 400, 450, 500, 600, 700). If a core sample had original counts less than *n*, no assemblage was simulated and PME was not reconstructed. At each value of *n* and depth in the core we summarized the 100 PME reconstructions using the range (difference between the highest and lowest PME reconstructions) as a measure of variability. The proportion of PME values that fell within the uncertainty bounds of the original reconstruction and then within 10 cm was employed as a measure of accuracy. The 10-cm threshold approximates the likely scale of climate-driven sea-level variability during the past ~2000 years (e.g., Kopp et al., 2016) and is therefore illustrative of the precision sought by some Holocene RSL reconstructions. We plot these parameters against *n* to infer how count size influences reconstructions because a break in slope likely indicates diminishing return for additional foraminifera counted.

We calculated the number of taxa present in each randomly-generated assemblage and compared it to the corresponding number of taxa identified in the full counts. This comparison enabled us to estimate the probability that all taxa in each sample and at each count size were included in the simulated assemblage. From this data we estimated the odds (probability of having all taxa present divided by the probability of not having all taxa present) across all depths that a simulated assemblage with count size *n* would capture the presence of all taxa. To demonstrate how count size influences assemblage diversity, we calculated odds ratios among all possible pairs of count size.

Our approaches to examining how count size influences PME reconstructions and assemblage diversity implicitly assume that the original counts provide an accurate representation of the true proportions of taxa and that all taxa were captured by those counts. By extension we assume that the original PME reconstruction arising from the full counts is accurate. These assumptions are likely reasonable given the physical mixing of tests during sample preparation coupled with the large count sizes that make it unlikely that taxa were missed or their relative proportions materially misrepresented (Buzas, 1990; Fatela & Taborda, 2002; Lytle & Wahl, 2005). In addition to PME, reconstructing RSL using salt-marsh sediment requires the elevation and age of each core sample to be established (through leveling to tidal datums and dating/age-depth modeling, respectively), which is achieved independently of estimating PME from assemblages of foraminifera using a transfer function. Therefore, examining only PME reconstructions is appropriate for

Downloaded from http://pubs.geoscienceworld.org/cushmanfoundation/jfr/article-pdf/50/3/266/5143690/i0096-1191-50-3-266.pdf
by Maynooth University user

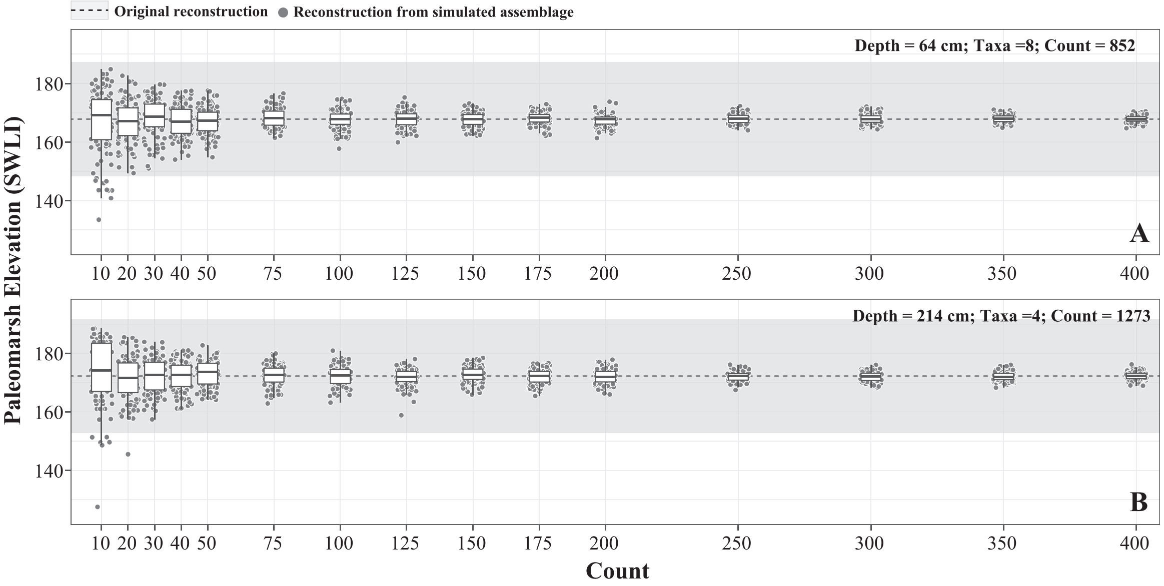


FIGURE 4. Two examples of paleo-marsh elevation (PME) reconstructions generated by simulating 100 assemblages of foraminifera at different counts sizes and applying the regional-scale weighted averaging transfer function (A is a sample from 64 cm in the Big River core where eight taxa were identified, and B is sample from 214 cm in which four taxa were present). The analysis was performed for count sizes up to 700 individuals, but results are shown only up to a count size of 400 for clarity of presentation. PME reconstructed using all counted individuals ("original") is represented by a horizontal dashed line and accompanying uncertainty envelope (~1σ; shaded). Box plots represent the median (solid horizontal line), 25th and 75th percentiles (hinges), and the largest value no further than 1.5 times the interquartile range from the hinge (approximately a 95% confidence interval for comparing medians; whiskers).

determining the effect of count size on Holocene RSL reconstructions.

RESULTS

Transfer Function Development and Application

The WA transfer function used to reconstruct PME from assemblages of foraminifera preserved in the Big River core was generated from a regional-scale modern training set. Performance of the model under cross-validation demonstrates that observed elevations (i.e., measured at the time of sample collection) are strongly correlated with those predicted by the transfer function ($R^2 = 0.69$; Fig. 2). The root mean square error of prediction (RMSEP; ~1σ) was ±19.71 SWLI, which at Big River equates to approximately ±0.16 m, or ±15% of great diurnal tidal range (mean lower low water to mean higher high water). Mean/maximum bias was 0.41/20.0 SWLI and model skill was 55.9. This performance is typical of transfer functions that relate salt-marsh foraminifera (or diatoms, testate amoebae) to tidal elevation across a wide geographic, geomorphic, and ecological range of study sites and regions (see, for example, table 3 of Barlow et al., 2013) and indicates that the model can accurately reconstruct PME.

We applied the WA transfer function to fossil assemblages in the Big River core (characterized using all counted individuals) to generate PME reconstructions with uncertainties (Fig. 3). Except for one sample, the midpoint of all PME reconstructions lay above mean tide level and below the highest occurrence of foraminifera. Samples with high abundances of *Miliammina fusca* returned reconstructed PME lower than ~150 SWLI. In contrast, samples with high relative abundances of *Jadammina macrescens/Balticammina pseudomacrescens*, *Haplophragmoides* spp., *Trochammina inflata*, and/or *Tiphotrocha comprimata* generated correspondingly high PME reconstructions. These results are ecologically plausible because they are consistent with the distribution of key taxa on modern salt marshes across and within a wide range of regions including Newfoundland (Kemp et al., 2017b), the Atlantic coast of North America (e.g., Scott & Medioli, 1978; Goldstein & Watkins, 1999; Edwards et al., 2004; Barnett et al., 2019), and beyond (e.g., Jennings & Nelson, 1992; Horton, et al., 2005; Strachan et al., 2015; Kemp, et al., 2017a). The mean uncertainty of PME reconstructions was ±19.5 SWLI (~1σ) with a standard deviation of 0.09 SWLI. Although the transfer function returns sample-specific errors, the low degree of variability among samples indicates that most uncertainty arises from quantifying the modern relationship between foraminifera and elevation in an empirical dataset rather than from applying the WA model to fossil assemblages (e.g., Juggins & Birks, 2012).

Paleo-marsh Elevation Reconstructions From Simulated Assemblages

We simulated 100 assemblages of foraminifera for each depth in the Big River core and for each count size of *n* individuals by randomly sampling the counted population. Application of the WA transfer function to each simulated assemblage generated a PME reconstruction. Figure 4 shows illustrative examples of this approach from two depths in the Big River core, chosen because they provide a contrast in diversity (eight and four taxa, respectively) and

Downloaded from http://pubs.geoscienceworld.org/cushmanfoundation/jfr/article-pdf/50/3/266/5143690/i0096-1191-50-3-266.pdf
by Maynooth University user

have large original counts (852 and 1273 individuals, respectively). The sample at 64 cm (Fig. 4A) yielded eight taxa of which five accounted for 98.4% of counted individuals. The original PME reconstruction for this sample was 167.85 ± 19.51 SWLI. When only ten foraminifera were randomly selected, PME reconstructions ranged from 133.5 to 184.9 SWLI and 10% of simulations lay outside the error bounds of the original reconstruction. Even a modest increase in count size caused a marked reduction in the range of reconstructed PME and improved convergence with the original reconstruction. When simulations comprised 20 or more individuals, all PME reconstructions fell within the uncertainty of the original reconstruction. With 75 or more individuals, 85% or more of simulations yielded a PME within 10 cm (±4.5 SWLI) of the original reconstruction. A similar pattern occurs for the lower-diversity (four taxa were present at abundances of 8.4–70.6%) sample at 214 cm (Fig. 4B).

At the 152 sampled depths in the Big River core, small count sizes result in a large range of reconstructed PME among the 100 simulations (Fig. 5A). For example, where an assemblage is ten foraminifera, the difference between the highest and lowest reconstructed PME for a single depth can exceed 100 SWLI, although for 95% of depths this range is less than 80 SWLI and the median range across all depths is 40 SWLI. In contrast, for foraminiferal assemblages consisting of 700 individuals, the range among simulations is small (less than ~5 SWLI for 95% of depths). The reduction in PME variability among simulations shows a break between counts of approximately 75 and 150 individuals, indicating that PME reconstructions stabilized and became insensitive to larger counts.

The percentage of simulations that generated a PME reconstruction within the uncertainty bounds of the original reconstruction (Fig. 5B) increases sharply with count size. For assemblages of ten individuals, 62–100% (median 96%, 5th percentile of 72%) of simulations at any single depth reproduced the original PME reconstruction within its uncertainty. When assemblages comprised 30 individuals, at least 93% of simulations at any single depth lay within the uncertainty range of the original reconstruction (median 100%, 5th percentile of 96%). This result suggests that a count size of ~30 individuals can generate a PME reconstruction that is unlikely to be statistically distinguishable from one based on a much larger population for most samples in the Big River core. However, the uncertainty threshold of ±19.71 SWLI is relatively broad and in studies seeking to reconstruct subtle changes in late Holocene RSL, this degree of variability may be larger than the paleoenvironmental signal being investigated. When the uncertainty threshold was narrowed to 10 cm (equivalent to ±4.5 SWLI), the general relationship between count size and the percentage of simulations that agreed with the original reconstruction remained, but the break in slope occurred at approximately 100–150 individuals rather than at ~30 (Fig. 5C).

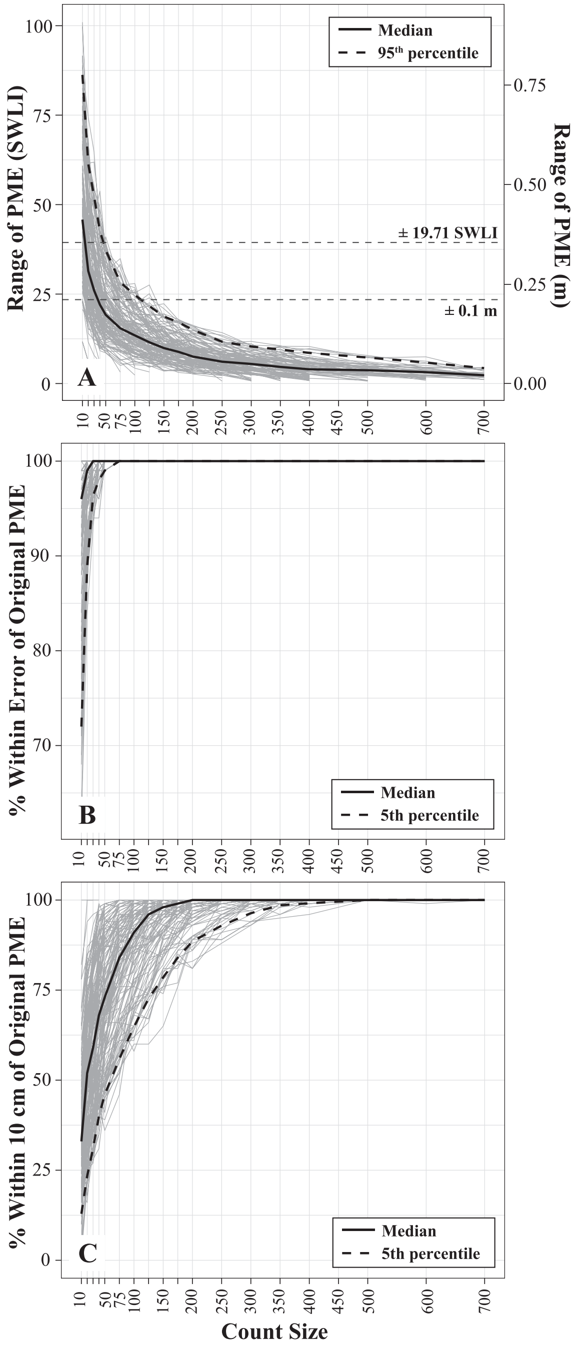
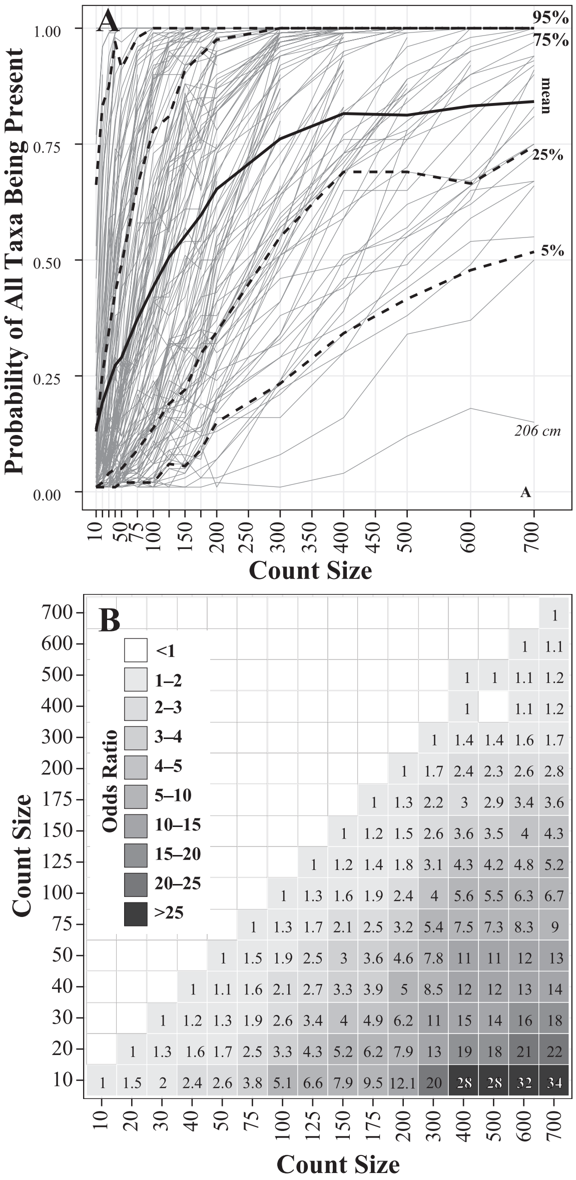


FIGURE 5. Influence of count size on reconstructions of paleomarsh elevation (PME) generated by applying the regional-scale weighted-averaging transfer function to simulated assemblages of foraminifera in the Big River core. Light grey lines represent results for individual depths in the core (total of 152 samples), while black lines are computed across all depths. **(A)** The absolute difference (in units of standardized water level index; SWLI) between the minimum and maximum PME reconstructions generated in 100 repeated simulations at each count size. Ranges converted to meters are applicable only to the Big River core and assume a constant tidal range through time. **(B)** Percentage of the 100 simulations at each count size where reconstructed PME lies within ±19.71 SWLI of the original reconstruction. At Big River this equates to an absolute elevation range of approximately ±0.17 m. **(C)** Percentage of the 100 simulations at each count size where reconstructed PME lies within ±10 cm of the original reconstruction. At Big River this equates to approximately ±4.5 SWLI.

ASSEMBLAGE DIVERSITY

The original counts of foraminifera in the Big River core yielded diversity for individual samples that ranged from one to eight taxa (Fig. 3; Shannon index less than 1.57), while simulated assemblages frequently included fewer taxa. The

Downloaded from http://pubs.geoscienceworld.org/cushmanfoundation/jfr/article-pdf/50/3/266/5143690/i0096-1191-50-3-266.pdf
by Maynooth University user



Count Size	10	20	30	40	50	75	100	125	150	175	200	300	400	500	600	700
700																1
600															1	1.1
500													1	1	1.1	1.2
400													1		1.1	1.2
300												1	1.4	1.4	1.6	1.7
200											1	1.7	2.4	2.3	2.6	2.8
175										1	1.3	2.2	3	2.9	3.4	3.6
150									1	1.2	1.5	2.6	3.6	3.5	4	4.3
125								1	1.2	1.4	1.8	3.1	4.3	4.2	4.8	5.2
100							1	1.3	1.6	1.9	2.4	4	5.6	5.5	6.3	6.7
75						1	1.3	1.7	2.1	2.5	3.2	5.4	7.5	7.3	8.3	9
50					1	1.5	1.9	2.5	3	3.6	4.6	7.8	11	11	12	13
40				1	1.1	1.6	2.1	2.7	3.3	3.9	5	8.5	12	12	13	14
30			1	1.2	1.3	1.9	2.6	3.4	4	4.9	6.2	11	15	14	16	18
20		1	1.3	1.6	1.7	2.5	3.3	4.3	5.2	6.2	7.9	13	19	18	21	22
10	1	1.5	2	2.4	2.6	3.8	5.1	6.6	7.9	9.5	12.1	20	28	28	32	34

FIGURE 6. **(A)** The probability of finding all taxa in a simulated assemblage, where the original full counts are assumed to be sufficiently large that they capture all taxa that were physically present in a sample. Presented values are the mean calculated across 100 simulations at each depth (thin grey lines). The sample from a depth of 206 cm is labeled because of its unusually low probability, which is discussed in the text. The solid black line is a mean calculated across all depths, and labeled dashed lines show percentiles of samples. **(B)** Relative odds of finding all taxa in a sample among all possible pairs of count sizes. Values (provided in individual cells with shading that corresponds to intervals; values greater than ten are rounded to the nearest whole number) are the odds ratio calculated across all depths and all simulations.

probability of finding all taxa in a simulated assemblage generally increases with count size (Fig. 6A). At a count size of 50 individuals, the mean probability (across all 152 sample depths) of including all taxa in a simulated assemblage is 0.29. This probability increases to 0.44 with a count size of 100 and to 0.65 at a count size of 200. Notably, even at very large count sizes there remains a high likelihood that some taxa are incorrectly assumed to be absent. For example, when 700 individuals are included in the simulated assemblage, the probability of capturing all species is 0.84 on average and approximately one quarter of samples yielded a probability of less than 0.75. In one case (sample at a depth of 206 cm; Fig. 6A), only 15 of the 100 simulated assemblages that included 700 foraminifera captured all species. A total of 1595 foraminifera were counted from this sample, including a single test of *Siphotrochammina lobata* and a single test of *Polysacammina ipohalina*. For comparison, there were 991 tests of *Jadammina macrescens/Balticammina pseudomacrescens*, 238 of *Haplohragmoides* spp., and 158 of *Tiphotrocha comprimata* (Fig. 3). It is therefore unsurprising that a count of 700 (which represents less than half of the counted individuals) would usually fail to capture all taxa. The stability of PME reconstructions at lower counts indicates that the absent taxa exert little influence on PME reconstructions generated using WA transfer functions.

The relationship between the count size and the probability of finding all taxa in a sample is expressed as an odds ratio among all possible pairs of count size (Fig. 6B). This ratio provides a convenient means to judge how much extra ecological information is (or is not) provided by counting more foraminifera, which is assumed to correspond linearly to time invested. If base counts are low, then there is a diminishing return for time invested. For example, counting 20/150/700 foraminifera increases the odds of finding all taxa by 1.5/7.9/34.1 times compared to a count size of ten, which corresponds to 2/15/70 times more time having to be invested. In contrast, when base counts are higher there is a more linear relationship between count size and the odds of finding all taxa. For example, compared to counting 50 tests, investing 50% more time to count 75 tests yields a corresponding 50% increase in the odds of finding all taxa. Likewise, investing 14 times more effort to count 700 foraminifera yields odds of finding all taxa that are 13 times better (Fig. 6B). This result indicates that counts lower than ~50 foraminifera likely produce unstable taxa proportions, while counts greater than ~50 begin to generate assemblages in which taxa proportions are similar to those in the full counts, except for the absence of some rare taxa.

DISCUSSION

APPLICABILITY TO OTHER REGIONS

The influence of count size on PME reconstructions is likely influenced by assemblage diversity, such that a higher/lower diversity assemblage could be more/less sensitive to count size. In the most extreme case, a true mono-specific assemblage would generate the same PME reconstruction regardless of count size. Diversity in modern assemblages of salt-marsh foraminifera is often greater at mid-latitudes than at high latitudes, where some regions have a bipartite division into low and high salt-marsh assemblages that are each characterized by a near-monospecific assemblage (e.g., Kemp et al., 2013a, 2017a). Since Newfoundland is a (relatively) high-latitude, low-diversity region, our results may not be applicable to higher-diversity regions.

Along the Atlantic coast of North America, there are several regional-scale datasets relating modern salt-marsh foraminifera to tidal elevation that were developed to reconstruct Holocene RSL (Fig. 1). Although it is difficult

Downloaded from http://pubs.geoscienceworld.org/cushmanfoundation/jfr/article-pdf/50/3/266/5143690/i0096-1191-50-3-266.pdf
by Maynooth University user

to control across datasets for factors such as the number and geomorphic type of sites, distribution of samples within a site, the preferred taxonomy of individual workers (e.g., lumpers versus splitters), and sample preparation protocols (e.g., sieve sizes), there are broad latitudinal trends in diversity (Fig. 1). Higher/lower latitude regions typically have lesser/greater diversity as measured using the Shannon index (Fig. 1B) or simply by the number of recorded taxa in the entire dataset (Fig. 1C), suggesting that our analysis may not be representative of, or applicable to, regions outside of maritime Canada and New England. However, PME reconstructions generated using WA transfer functions are inherently influenced more by abundant taxa than by rare taxa (weighting of taxa by their ecological tolerance rather than abundance is rarely used in PME reconstruction). Individual samples in modern training sets are typically dominated by few taxa even in regions with relatively high overall diversity (Wright et al., 2011). From North Carolina to Newfoundland there is little variability among regions in the number of taxa that make up at least 5% (Fig. 1D) /10% (Fig. 1E) of the assemblage. In this context, there are only minor spatial differences in the diversity of salt-marsh foraminiferal assemblages and therefore our results are likely applicable to other regions.

INFLUENCE OF MISSING TAXA

Some taxa are absent in simulated assemblages with low counts when they are known to be present from the original assemblage (Fig. 6A). Fatela & Taborda (2002) used the binomial distribution to estimate that a count of 100 individuals had a probability greater than 0.95/0.99 of including a species that comprised 3%/5% of the assemblage. Subsequently, they concluded that paleoenvironmental inferences based on species with an abundance greater than 5% are robust at count sizes of 100 or more. In contrast, Buzas (1990) discussed how other studies using the binomial distribution concluded that 300 specimens should be counted to accurately characterize the occurrence of taxa that make up ~10% of an assemblage (e.g., Patterson & Fishbein, 1989) and that this count size subsequently took on "an almost magical significance." This is perhaps why it is so common for studies seeking to reconstruct PME from salt-marsh foraminifera set a target of counting 300 specimens (e.g., Scott & Leckie, 1990; Jennings & Nelson, 1992; Culver et al., 1996; Javaux & Scott, 2003; Edwards et al., 2004; Callard et al., 2011). In a wide-ranging review of sampling benthic foraminifera, Schönfeld et al. (2012) adopted the convention of Patterson & Fishbein (1989) that 300 individuals should be counted, but noted explicitly that in lower-diversity, marginal-marine environments (salt marshes would meet this criterion) counts of 100 may be sufficient. The binomial distribution was also used to provide confidence intervals on proportional taxa abundances estimated at different count sizes, including specific applications to salt-marsh foraminifera (Wright et al., 2011; Edwards & Wright, 2015).

Since PME reconstructions generated using WA transfer functions are inherently driven by abundant rather than rare taxa, it is unlikely that the absence of some taxa in our simulated assemblages materially affected the corresponding estimates of PME. This is evidenced by stability in PME reconstructions being achieved at lower counts (~50; Fig. 5) than stability in the probability of finding all taxa, which remained less than ~0.85 for most samples even at a count size of 700 (Fig. 6A). Similar patterns were observed in studies that examined how count sizes of other microfossils influenced quantitative paleoenvironmental reconstructions generated using transfer functions. For example, Larocque (2001) showed that temperature reconstructions derived from chironomids stabilized at counts of 50, despite counts of 90 yielding four to seven more taxa per sample. Similarly, Payne & Mitchell (2009) used counts of testate amoebae in peatlands to reconstruct water table depth and recognized that most samples only have one taxon that makes up more than 25% individuals, and consequently, the number of taxa present in simulated assemblages plateaus at counts of ~50, but more than 150 individuals must be counted to record all taxa. Even with some taxa being absent, transfer functions produced stable reconstructions of water table depth with counts of 50–100 testate amoebae because they are insensitive to the abundance (and indeed absence) of rare taxa. Notably, the microfossil assemblages in these studies have a greater diversity (e.g., 48 taxa in the dataset used by Larocque, 2001) than assemblages of salt-marsh foraminifera and are therefore likely more sensitive to missing taxa. Studies of foraminifera in environments other than salt-marshes also recognized that fewer than 300 specimens could be counted to accurately characterize assemblages. For example, Culver (1988) sought to establish the zonation of benthic foraminifera in the Gulf of Mexico with respect to water depth and showed that analysis of species- and genera- (with and without rare genera) level assemblages yielded comparable results with the implication that rare taxa exerted little influence on paleoenvironmental reconstructions and that counts of 50–100 were reasonable (with the explicit caveat that even lower counts would likely be suitable for low-diversity assemblages of foraminifera on marshes). Likewise, Karlsen et al. (2000) showed that similar paleoenvironmental trends were produced from benthic foraminifera in the Chesapeake Bay at counts of 100 and 300. We conclude that the absence of rare taxa of salt-marsh foraminifera at low counts does not distort PME reconstructions generated by transfer functions. However, ecological studies, or those relying on qualitative analysis of indicator species to estimate PME using salt-marsh foraminifera, may need to count more than ~300 individuals to ensure that fewer than 5% of samples have missing taxa (Fig. 6A).

MODERN TRANSFER FUNCTION PERFORMANCE

The largest source of uncertainty in PME reconstructions is typically mis-specification in the WA model when it is developed from a modern training set that imperfectly captures biological variability (termed the S2 error; Juggins & Birks, 2012). Consequently, a large proportion of sample-specific uncertainties in PME reconstructions arises from the underlying WA transfer function rather than its application to fossil assemblages. Since one metric used to assess the influence of count size is the proportion of PME reconstructions that fall within the uncertainty range of the original reconstruction, we investigated how count size affects

Downloaded from http://pubs.geoscienceworld.org/cushmanfoundation/jfr/article-pdf/50/3/266/5143690/i0096-1191-50-3-266.pdf
by Maynooth University user

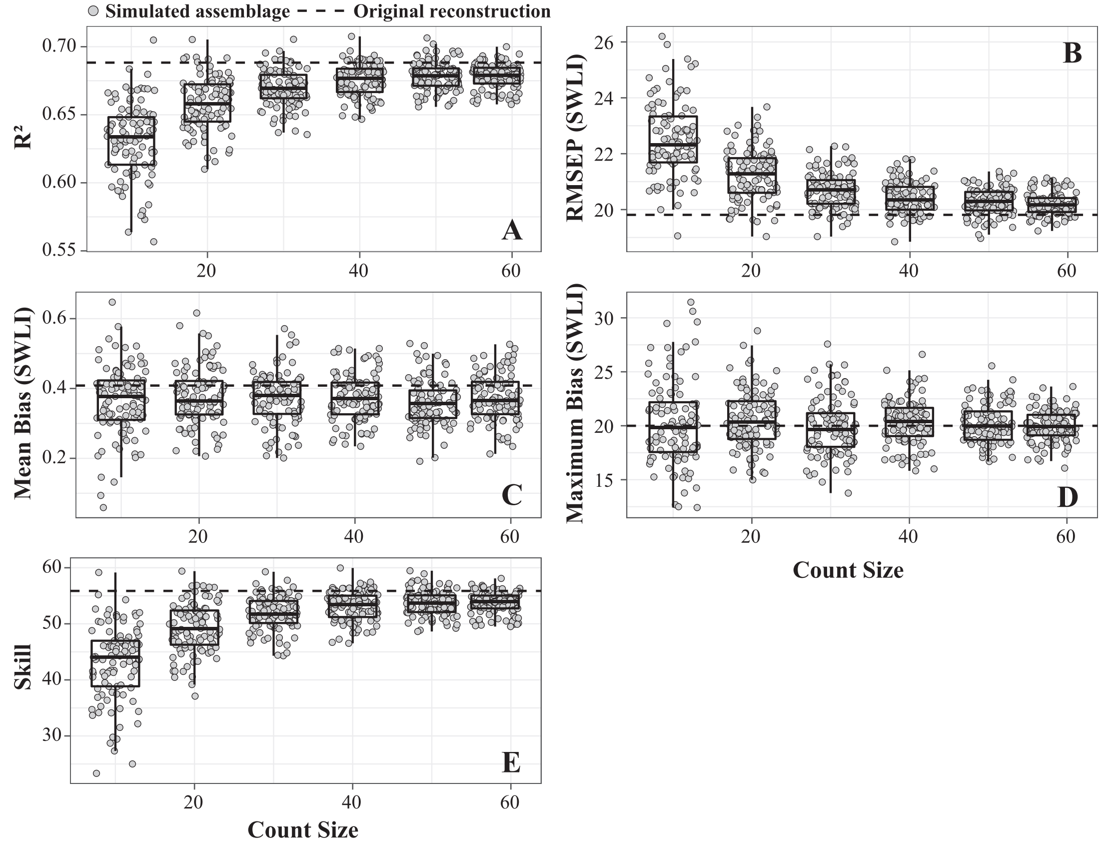


FIGURE 7. Effect of count size on transfer function performance as measured using cross-validated **(A)** R^2, **(B)** root mean square error of prediction (RMSEP, units of standardized water level index; SWLI), **(C)** mean bias, **(D)** maximum bias, and **(E)** model skill. Grey circles are results from 100 different weighted-averaging transfer functions generated at each count size by random subsampling of assemblages in the original modern training set. These simulations are summarized by the overlying box plots that represent the median (solid horizontal line), 25^{th} and 75^{th} percentiles (hinges), and the largest value no further than 1.5 times the interquartile range from the hinge (approximately a 95% confidence interval for comparing medians; whiskers). Performance of the original transfer function that used all available counts is shown for comparison (horizontal dashed lines).

transfer function performance by randomly subsampling assemblages in the modern training set (Fig. 7). A narrow range of *n* (10, 20, 30, 40, 50, 58) was tested because count sizes in the Newfoundland modern training set (mean of 220 individuals, range of 58–758) are typically lower than in core F25 from Big River. By limiting the count size to 58 (or fewer) foraminifera, we ensured that all transfer functions used the same modern samples and that variability in model performance arises solely from count size. At each value of *n*, 100 simulated assemblages were generated and used to construct a WA transfer function. Standard performance metrics (cross-validated R^2, RMSEP, mean/maximum bias, and skill) are used to compare models.

The cross-validated R^2 of the original WA transfer function was 0.69 with a RMSEP of ±19.71 SWLI (Fig. 2). This model had a mean/maximum bias of 0.41/20.0 SWLI and skill of 55.9. At count sizes of ten foraminifera, WA transfer functions performed less well than the original model, as evidenced by lower R^2 (average of 0.63 with a standard deviation of 0.03 across the 100 simulations) and skill (average of 43.0 with a standard deviation of 6.8), coupled with higher RMSEP (average of 22.77 SWLI with a standard deviation of 1.4 SWLI) and maximum bias (average of 20.2 SWLI with a standard deviation of 4.0 SWLI). There was little discernible difference in mean bias. Increasing the count size from ten to 30 individuals notably improved model performance across all metrics except mean bias, but count sizes greater than 40 showed only modest further improvement of R^2, RMSEP, maximum bias, and skill (Fig. 7). This trend indicates that the performance of WA transfer functions is only marginally improved by counting more than ~50 individual foraminifera, at least in low-diversity regions such as Newfoundland. This result supports decisions made in other studies to remove samples with counts of less than ~40 foraminifera from modern training sets prior to building transfer functions (e.g., Edwards et al., 2004; Southall et al., 2006; Barnett et al., 2016), but suggests that using a higher threshold may unnecessarily remove data (e.g., Haller et al., 2019). Even in microfossil groups with greater diversity than salt-marsh foraminifera in Newfoundland a similar correlation between transfer function and count size was demonstrated. In Payne & Mitchell (2009), transfer function performance stabilized at or before counts of ~50 in datasets of testate amoebae that included up to 18 different taxa (compared to 12 in the Newfoundland modern training set and Big River core) from contrasting peatlands in Alaska, Scotland, Greece, and Turkey. Similarly, Heiri & Lotter (2001) showed that the performance of transfer functions relating temperature to assemblages of chironomids stabilized at counts of ~50 individuals. We conclude

Downloaded from http://pubs.geoscienceworld.org/cushmanfoundation/jfr/article-pdf/50/3/266/5143690/i0096-1191-50-3-266.pdf
by Maynooth University user

that the uncertainty of PME reconstructions in the Big River core is unlikely to be reduced by counting more modern foraminifera and consequently that our assessment of the influence of count size, based on how many simulations lie within the uncertainty thresholds (Figs. 5B, C), is robust and likely not influenced by count sizes in the underlying modern training set. The stability of transfer function performance across several key metrics at counts over ~30 (Fig. 7) indicates that skilled models and accurate PME reconstructions can likely be generated using modern training sets in which assemblages are characterized by considerably lower counts than are usually targeted (e.g., Scott & Leckie, 1990; Horton & Edwards, 2006; Southall et al., 2006; Hawkes et al., 2010; Callard et al., 2011). A downward revision of target count size would enable more modern samples to be counted (e.g., Hayek & Buzas, 2010; Grand Pre et al., 2011), and this reallocation of effort may help to better capture natural variability within and among salt marshes, facilitate more detailed examination of replication (e.g., Buzas 1970; Buzas et al., 2002), and to expand the geographical, geomorphic, and ecological range of modern analogs that are available to interpret fossil assemblages against.

Implications for Holocene RSL Reconstructions

In the broadest sense, efforts to reconstruct Holocene RSL can be divided into two types based on the scale (vertical and chronological) of changes that are under investigation. Studies that aim to reconstruct (multi-) meter scale RSL trends often utilize discrete, radiocarbon-dated sea-level index points, and the uncertainty of PME reconstructions from WA transfer functions is small compared to the RSL signal (perhaps with the exception of regions with extremely large tidal ranges). These RSL changes can take place on centennial to millennial timescales along passive coastal margins dominated by glacio-isostatic adjustment (e.g., Horton & Edwards, 2006; Engelhart et al., 2011; Shennan et al., 2018), or be abrupt (minutes) in the case of co-seismic subsidence on active margins where great (M > 8) megathrust earthquakes occur (e.g., Nelson et al., 1996; Shennan & Hamilton, 2006; Briggs et al., 2014). In contrast, studies that aim to reconstruct centennial- and decimeter-scale RSL trends in the late Holocene (e.g., Gerlach et al., 2017; Barnett et al., 2019) often utilize a sequence of stratigraphically-ordered samples from a single core where the accumulation history is constrained by an age-depth model and uncertainty in PME reconstructions is relatively large compared to the underlying RSL signal. This is particularly true after detrending RSL reconstructions to remove the contribution from long-term subsidence, for example, in an attempt to isolate smaller, climate-driven signals. Consequently, these two types of study have different tolerances to the accuracy and precision of reconstructions and the influence of count size is partly dependent upon the resolution sought by investigations.

The precision of PME reconstructions is principally determined during construction of the WA transfer function using a modern training set and is relatively insensitive to count size (Fig. 7; Heiri & Lotter, 2001; Larocque, 2001; Payne & Mitchell, 2009). Therefore, count size in fossil samples influences accuracy rather than precision, and variability among PME reconstructions is an appropriate means to gauge how count sizes may influence proxy RSL records and their interpretation. With counts of ~30 foraminifera, more than 95% of PME reconstructions lie within the uncertainty of the original reconstruction and all reconstructions with a count size of ~75 meet this criterion (Fig. 5B). This result suggests that counting ~50 or more foraminifera is likely sufficient for generating sea-level index points because variability among PME reconstructions is low enough that RSL trends are unlikely to be misrepresented or wrongly interpreted. Similarly, efforts to reconstruct earthquake-induced subsidence (RSL rise) on the order of a meter that are typically associated with tidal-flat sediment overlying high salt-marsh peat (Hawkes et al., 2011; Engelhart et al., 2013; Milker et al., 2016) can likely generate accurate PME reconstructions using counts of ~50 foraminifera. Climate-driven sea-level trends during the late Holocene were on the order of tens of centimeters (e.g., Lambeck et al., 2004; Woodroffe et al., 2012; Kopp et al., 2016) and variability in PME reconstructions of similar magnitude are observed for single samples if count sizes are less than ~75. Variability of PME reconstructions for single samples at a low count size will usually yield correspondingly high variability among ordered samples in a core (Heiri & Lotter, 2001). There is a risk that this variability arising from low counts will be incorrectly interpreted as meaningful RSL changes. However, the likelihood of this misinterpretation is reduced by identifying RSL trends on the basis of coherent patterns in foraminiferal abundances and PME across multiple samples (Gehrels & Woodworth, 2012; Cahill et al., 2015), rather than by treating every change in PME from one sample to the next as a true RSL change. As such, smoothing of PME reconstructions downcore can often negate the influence of low count sizes in individual samples (Heiri & Lotter, 2001). This effect could be examined more formally and quantitatively by comparing RSL reconstructions developed from more/fewer samples in which fewer/more individual foraminifera were counted as a means to test how finite effort is best allocated between counting additional foraminifera or additional samples. We recommend that at least 75 foraminifera are counted in studies that aim to produce high-resolution and near-continuous RSL reconstructions and that a sample (or group of samples) with anomalous PME are revisited to increase count size as a means to determine if reconstructed trends are ecologically and physically robust or artifacts of count size (there is no reason why count sizes cannot vary greatly among samples). Alternatively, future studies could use our simulations to approximate the potential influence of count size given the number of salt-marsh foraminifera that were counted, or to estimate how many should be counted given a chosen tolerance for PME variability, missing taxa, or another count-dependent characteristic of PME reconstructions. In this context, counts of 100–300 salt-marsh foraminifera in studies of Holocene RSL history are conservative and the corresponding reconstructed RSL trends are unlikely to be artifacts of count size.

CONCLUSIONS

We investigated the influence of count size on reconstructions of PME (and subsequently RSL) generated by

Downloaded from http://pubs.geoscienceworld.org/cushmanfoundation/jfr/article-pdf/50/3/266/5143690/i0096-1191-50-3-266.pdf
by Maynooth University user

applying a WA transfer function to assemblages of foraminifera preserved in Holocene salt-marsh sediment. The WA transfer function was constructed from a regional-scale modern training set of salt-marsh foraminifera in Newfoundland, Canada and applied to ecologically-plausible assemblages of foraminifera generated by repeatedly subsampling counted populations (up to 1595 individuals, mean of 471) at 152 discrete depths in a sediment core that accumulated during the past ~3000 years. The count size of simulated assemblages ranged from 10–700 individuals. Our results indicate that PME reconstructions become insensitive to increasing count size when ~50 individuals are used to characterize the assemblage. At counts greater than ~30, approximately 93% of PME reconstructions from simulated assemblages lie within the uncertainty of the original PME reconstruction based on all available counts. However, when the threshold for similarity is lowered to 10 cm (similar to the resolution sought by studies of late Holocene RSL change) approximately 100–150 individuals must be counted. In simulated assemblages with lower counts, some rare taxa are erroneously deemed absent, but this has little effect on PME reconstructions generated using WA transfer functions because they are dominated by abundant taxa. Our results are similar to those reported for higher diversity groups of microfossils such as testate amoebae and chironomids and the low-diversity nature of individual samples of salt-marsh foraminifera likely means that our recommendations are applicable beyond Newfoundland. When reconstructing PME, we recommend allocating effort to counting relatively fewer foraminifera in more samples of core material rather than generating large counts from fewer core samples. We further tested the influence of count size on the cross-validated transfer function performance (R^2, RMSEP, mean/maximum bias, and skill) by simulating assemblages of different count sizes. These experiments show that the accuracy and precision of transfer functions developed from modern samples in which ~40 or more foraminifera were counted show little variability. Existing studies that typically targeted count sizes of 100–300 foraminifera in modern and fossil assemblages are conservative, and the resulting RSL reconstructions are unlikely to be artifacts of counting too few foraminifera.

ACKNOWLEDGMENTS

This work is a contribution to IGCP project 639 "Sea-level change from minutes to millennia" and PALSEA 3 (a PAGES / INQUA working group) and was supported by NSF awards OCE-1458921 and OCE-2002431. Foraminiferal data from Big River were collected as part of a series of projects including "Ocean-climate variability and sea level in the North Atlantic region since AD 0" funded by the Dutch National Research Program on Global air pollution and Climate Change, "Coastal Records" funded by Vrije Universiteit Amsterdam, and "Simulations, observations & palaeoclimatic data: climate variability over the last 500 years" funded by the European Union. We thank Marty Buzas, Steve Culver, Robin Edwards, Simon Engelhart, Andrea Hawkes, and Alan Nelson for their valuable input on an early version of this manuscript and an anonymous reviewer for their comments.

REFERENCES

Barlow, N. L. M., Shennan, I., Long, A. J., Gehrels, W. R., Saher, M. H., Woodroffe, S. A., and Hillier, C., 2013, Salt marshes as late Holocene tide gauges: Global and Planetary Change, v. 106, p. 90–110.

Barnett, R. L., Garneau, M., and Bernatchez, P., 2016, Salt-marsh sea-level indicators and transfer function development for the Magdalen Islands in the Gulf of St. Lawrence, Canada: Marine Micropaleontology, v. 122, p. 13–26.

Barnett, R. L., Bernatchez, P., Garneau, M., Brain, M. J., Charman, D. J., Stephenson, D. B., Haley, S., and Sanderson, N., 2019, Late Holocene sea-level changes in eastern Québec and potential drivers: Quaternary Science Reviews, v. 203, p. 151–169.

Birks, H. J. B., 1995, Quantitative palaeoenvironmental reconstructions, *in* Maddy, D., and Brew, J. S. (eds.), Statistical Modelling of Quaternary Science Data: Quaternary Research Association, Cambridge, U.K., p. 161–254.

Bittermann, K., Rahmstorf, S., Kopp, R. E., and Kemp, A. C., 2017, Global mean sea-level rise in a world agreed upon in Paris: Environmental Research Letters, v. 12, https://doi.org/10.1088/1748-9326/aa9def.

Bloom, A. L., and Stuiver, M., 1963, Submergence of the Connecticut coast: Science, v. 139, p. 332–334.

Briggs, R. W., Engelhart, S. E., Nelson, A. R., Dura, T., Kemp, A. C., Haeussler, P. J., Corbett, D. R., Angster, S. J., and Bradley, L.-A., 2014, Uplift and subsidence reveal a nonpersistent megathrust rupture boundary (Sitkinak Island, Alaska): Geophysical Research Letters, v. 41, p. 2289–2296.

Buzas, M. A., 1970, Spatial homogeneity: Statistical analyses of unispecies and multispecies populations of foraminifera: Ecology, v. 51, p. 874–879.

Buzas, M. A., 1990, Another look at confidence limits for species proportions: Journal of Paleontology, v. 64, p. 842–843.

Buzas, M. A., Hayek, L.-A. C., Reed, S. A., and Jett, J. A., 2002, Foraminiferal densities over five years in the Indian River Lagoon, Florida: A model of pulsating patches: Journal of Foraminiferal Research, v. 32, p. 68–92.

Cahill, N., Kemp, A. C., Horton, B. P., and Parnell, A. C., 2015, Modeling sea-level change using errors-in-variables intergrated Gaussian processes: Annals of Applied Statistics, v. 9, p. 547–571.

Callard, S. L., Gehrels, W. R., Morrison, B. V., and Grenfell, H. R., 2011, Suitability of salt-marsh foraminifera as proxy indicators of sea level in Tasmania: Marine Micropaleontology, v. 79, p. 121–131.

Culver, S. J., 1988, New foraminiferal depth zonation of the northwestern Gulf of Mexico: Palaios, v. 3, p. 69–85.

Culver, S. J., Woo, H. J., Oertel, G. F., and Buzas, M. A., 1996, Foraminifera of coastal depositional environments, Virginia, USA: Distribution and taphonomy: Palaios, v. 11, p. 459–486.

Donnelly, J. P., 2006, A revised late Holocene sea-level record for northern Massachusetts, USA: Journal of Coastal Research, v. 22, p. 1051–1061.

Edwards, R. J., and Wright, A. J., 2015, Foraminifera, *in* Shennan, I., Long, A. J., and Horton, B. P. (eds.), Handbook of Sea-Level Research: John Wiley & Sons, Chichester, p. 191–217.

Edwards, R. J., Wright, A. J., and van de Plassche, O., 2004, Surface distributions of salt-marsh foraminifera from Connecticut, USA: Modern analogues for high-resolution sea level studies: Marine Micropaleontology, v. 51, p. 1–21.

Engelhart, S. E., Horton, B. P., and Kemp, A. C., 2011, Holocene sea level changes along the United States' Atlantic Coast: Oceanography, v. 24, p. 70–79.

Engelhart, S. E., Horton, B. P., Nelson, A. R., Hawkes, A. D., Witter, R. C., Wang, K., Wang, P.-L., and Vane, C. H., 2013, Testing the use of microfossils to reconstruct great earthquakes at Cascadia: Geology, v. 41, p. 1067–1070.

Engelhart, S. E., Vacchi, M., Horton, B. P., Nelson, A. R., and Kopp, R. E., 2015, A sea-level database for the Pacific coast of central North America: Quaternary Science Reviews, v. 113, p. 78–92.

Fatela, F., and Taborda, R., 2002, Confidence limits of species proportions in microfossil assemblages: Marine Micropaleontology, v. 45, p. 169–174.

Downloaded from http://pubs.geoscienceworld.org/cushmanfoundation/jfr/article-pdf/50/3/266/5143690/i0096-1191-50-3-266.pdf
by Maynooth University user

Filipescu, S., and Kaminski, M. A., 2008, Re-discovering *Entzia*, an agglutinated foraminifer from the Transylvanian salt marshes: Eighth International Workshop on Agglutinated Foraminifera, Cluj-Napoca, Romania: Grzybowski Foundation Special Publication, v. 16, p. 29–35.

Gehrels, W. R., 1994, Determining relative sea-level change from salt-marsh foraminifera and plant zones on the coast of Maine, U.S.A: Journal of Coastal Research, v. 10, p. 990–1009.

Gehrels, W. R., and Woodworth, P. L., 2012, When did modern rates of sea-level rise start?: Global and Planetary Change, v. 100, p. 263–277.

Gerlach, M. J., Engelhart, S. E., Kemp, A. C., Moyer, R. P., Smoak, J. M., Bernhardt, C. E., and Cahill, N., 2017, Reconstructing Common Era relative sea-level change on the Gulf coast of Florida: Marine Geology, v. 390, p. 254–269.

Goldstein, S. T., and Watkins, G. T., 1999, Taphonomy of salt marsh foraminifera: an example from coastal Georgia: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 149, p. 103.

Grand Pre, C., Culver, S. J., Mallinson, D. J., Farrell, K. M., Corbett, D. R., Horton, B. P., Hillier, C., Riggs, S. R., Snyder, S. W., and Buzas, M. A., 2011, Rapid Holocene coastal change revealed by high-resolution micropaleontological analysis, Pamlico Sound, North Carolina, USA: Quaternary Research, v. 76, p. 319–334.

Haller, C., Smith, C. G., Hallock, P., Hine, A. C., Osterman, L. E., and McCloskey, T., 2019, Distribution of modern salt-marsh foraminifera from the eastern Mississippi Sound, U.S.A.: Journal of Foraminiferal Research, v. 49, p. 29–47.

Hawkes, A. D., Horton, B. P., Nelson, A. R., and Hill, D. F., 2010, The application of intertidal foraminifera to reconstruct coastal subsidence during the giant Cascadia earthquake of AD 1700 in Oregon, USA: Quaternary International, v. 221, p. 116–140.

Hawkes, A. D., Horton, B. P., Nelson, A. R., Vane, C. H., and Sawai, Y., 2011, Coastal subsidence in Oregon, USA, during the giant Cascadia earthquake of AD 1700: Quaternary Science Reviews, v. 30, p. 364–376.

Hayek, L.-A. C., and Buzas, M. A., 2010, Surveying Natural Populations: Quantitative Tools for Assessing Biodiversity: Columbia University Press, New York, 563 pp.

Heiri, O., and Lotter, A. F., 2001, Effect of low count sums on quantitative environmental reconstructions: An example using subfossil chironomids: Journal of Paleolimnology, v. 26, p. 343–350.

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

Horton, B. P., and Edwards, R. J., 2006, Quantifying Holocene sea-level change using intertidal foraminifera: Lessons from the British Isles: Cushman Foundation for Foraminiferal Research, Washington D.C., 97 p.

Horton, B. P., Edwards, R. J., and Lloyd, J. M., 1999, A foraminiferal-based transfer function: Implications for sea-level studies: Journal of Foraminiferal Research, v. 29, p. 117–129.

Horton, B. P., Whittaker, J. E., Thomson, K. H., Hardbattle, M. I. J., Kemp, A., Woodroffe, S. A., and Wright, M. R., 2005, The development of a modern foraminiferal data set for sea-level reconstructions, Wakatobi Marine National Park, Southeast Sulawesi, Indonesia: Journal of Foraminiferal Research, v. 35, p. 1–14.

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

Jennings, A. E., and Nelson, A. R., 1992, Foraminiferal assemblage zones in Oregon tidal marshes; Relation to marsh floral zones and sea level: Journal of Foraminiferal Research, v. 22, p. 13–29.

Juggins, S., and Birks, H. J. B., 2012, Quantiative environmental reconstructions from biological data, in Birks, H. J. B., et al. (eds.), Tracking Environmental Change Using Lake Sediments: Data Handling and Numerical Techniques: Springer, Dordrecht, The Netherlands, p. 431–494.

Karlsen, A. W., Cronin, T. M., Ishman, S. E., Willard, D. A., Kerhin, R., Holmes, C. W., and Marot, M., 2000, Historical trends in Chesapeake Bay dissolved oxygen based on benthic foraminifera from sediment cores: Estuaries, v. 23, p. 488–508.

Kemp, A. C., and Telford, R. J., 2015, Transfer Functions, *in* Shennan, I., Long, A. J., and Horton, B. P. (eds.), Handbook for Sea-Level Research: John Wiley & Sons, Chichester, p. 470–499.

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

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

Kemp, A. C., Engelhart, S. E., Culver, S. J., Nelson, A., Briggs, R. W., and Haeussler, P. J., 2013a, Modern salt-marsh and tidal-flat foraminifera from Sitkinak and Simeonof Islands, southwestern Alaska: Journal of Foraminiferal Research, v. 43, p. 88–98.

Kemp, A. C., Telford, R. J., Horton, B. P., Anisfeld, S. C., and Sommerfield, C. K., 2013b, Reconstructing Holocene sea-level using salt-marsh foraminifera and transfer functions: Lessons from New Jersey, USA: Journal of Quaternary Science, v. 28, p. 617–629.

Kemp, A. C., Hawkes, A. D., Donnelly, J. P., Vane, C. H., Horton, B. P., Hill, T. D., Anisfeld, S. C., Parnell, A. C., and Cahill, N., 2015, Relative sea-level change in Connecticut (USA) during the last 2200 years: Earth and Planetary Science Letters, v. 428, p. 217–229.

Kemp, A. C., Horton, B. P., Nikitina, D., Vane, C. H., Potapova, M., Weber-Bruya, E., Culver, S. J., Repkina, T., Hill, D. F., and Selezneva, E., 2017a, The distribution and utility of sea-level indicators in Eurasian sub-Arctic salt marshes (White Sea, Russia): Boreas, v. 46, p. 562–584.

Kemp, A. C., Wright, A. J., Barnett, R. L., Hawkes, A. D., Charman, D. J., Sameshima, C., King, A. N., Mooney, H. C., Edwards, R. L., and Horton, B. P., 2017b, Utility of salt-marsh foraminifera, testate amoebae and bulk-sediment δ^{13}C values as sea-level indicators in Newfoundland, Canada: Marine Micropaleontology, v. 130, p. 43–59.

Kemp, A. C., Cahill, N., Engelhart, S. E., Hawkes, A. D., and Wang, K., 2018a, Revising estimates of spatially variable subsidence during the A.D. 1700 Cascadia earthquake using a Bayesian foraminiferal transfer function: Bulletin of the Seismological Society of America, v. 108, p. 654–673.

Kemp, A. C., Wright, A. J., Edwards, R. J., Barnett, R. L., Brain, M. J., Cahill, N., Kopp, R. E., Horton, B. P., Charman, D. J., Hawkes, A. D., Hill, T. D., and van de Plassche, O., 2018b, Relative sea-level change in Newfoundland, Canada during the past ~3000 years: Quaternary Science Reviews, v. 201, p. 89–110.

Kopp, R. E., Kemp, A. C., Bitterman, K., Horton, B. P., Donnelly, J. P., Gehrels, W. R., Hay, C., Mitrovica, J. X., Morrow, E., and Rahmstorf, S., 2016, Temperature-driven global sea-level variability in the Common Era: Proceedings of the National Academy of Sciences, v. 113, p. E1434–E1441.

Lambeck, K., Anzidei, M., Antonioli, F., Benini, A., and Esposito, A., 2004, Sea level in Roman time in the Central Mediterranean and implications for recent change: Earth and Planetary Science Letters, v. 224, p. 563–575.

Larocque, I., 2001, How many chironomid head capsules are enough? A statistical approach to determine sample size for palaeoclimatic reconstructions: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 172, p. 133–142.

Lytle, D. E., and Wahl, E. R., 2005, Palaeoenvironmental reconstructions using the modern analogue technique: The effects of sample size and decision rules: The Holocene, v. 15, p. 554–566.

Mallinson, D. J., Smith, C. W., Mahan, S., Culver, S. J., and McDowell, K., 2011, Barrier island response to late Holocene climate events, North Carolina, USA: Quaternary Research, v. 76, p. 46–57.

Milker, Y., Nelson, A. R., Horton, B. P., Engelhart, S. E., Bradley, L.-A., and Witter, R. C., 2016, Differences in coastal subsidence in southern Oregon (USA) during at least six prehistoric megathrust earthquakes: Quaternary Science Reviews, v. 142, p. 143–163.

Murray, J. W., and Alve, E., 2000, Major aspects of foraminiferal variability (standing crop biomass) on a monthly scale in an intertidal zone: Journal of Foraminiferal Research, v. 30, p. 177–191.

Nelson, A. R., 2013, Tectonics and Relative Sea-Level Change, in Scott, A. E. (ed.), Encyclopedia of Quaternary Science (Second Edition): Elsevier, Amsterdam, p. 503–519.

Downloaded from http://pubs.geoscienceworld.org/cushmanfoundation/jfr/article-pdf/50/3/266/5143690/i0096-1191-50-3-266.pdf
by Maynooth University user

Nelson, A. R., Shennan, I., and Long, A. J., 1996, Identifying coseismic subsidence in tidal-wetland stratigraphic sequences at the Cascadia subduction zone of western North America: Journal of Geophysical Research, v. 101, p. 6115–6135.

Patterson, R. T., and Fishbein, E., 1989, Re-examination of the statistical methods used to determine the number of point counts needed for micropaleontological quantitative research: Journal of Paleontology, v. 63, p. 245–248.

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

Payne, R. J., and Mitchell, E. A., 2009, How many is enough? Determining optimal count totals for ecological and palaeoecological studies of testate amoebae: Journal of Paleolimnology, v. 42, p. 483–495.

Peltier, W. R., 1996, Global sea level rise and glacial isostatic adjustment: An analysis of data from the east coast of North America: Geophysical Research Letters, v. 23, p. GL00848.

Quinlan, R., and Smol, J. P., 2001, Setting minimum head capsule abundance and taxa deletion criteria in chironomid-based inference models: Journal of Paleolimnology, v. 26, p. 327–342.

Redfield, A. C., and Rubin, M., 1962, The age of salt marsh peat and its relation to recent changes in sea level at Barnstable, Massachusetts: Proceedings of the National Academy of Sciences of the United States of America, v. 48, p. 1728–1735.

Sachs, H. M., Webb, T., and Clark, D. R., 1977, Paleoecological transfer functions: Annual Review of Earth and Planetary Sciences, v. 5, p. 159–178.

Schönfeld, J., Alve, E., Geslin, E., Jorissen, F., Korsun, S., and Spezzaferri, S., 2012, The FOBIMO (FOraminiferal BIo-MOnitoring) initiative—Towards a standardised protocol for soft-bottom benthic foraminiferal monitoring studies: Marine Micropaleontology, v. 94, p. 1–13.

Scott, D. B., and Medioli, F. S., 1978, Vertical zonations of marsh foraminifera as accurate indicators of former sea levels: Nature, v. 272, p. 528–531.

Scott, D. B., and Medioli, F. S., 1980, Quantitative studies of Marsh Foraminiferal Distributions in Nova Scotia: Implications for Sea Level Studies: Cushman Foundation for Foraminiferal Research, 58 p.

Scott, D. B., Williamson, M. A., and Duffett, T. E., 1981, Marsh foraminifera of Prince Edward Island: Their recent distribution and application for former sea-level studies: Maritime Sediments and Atlantic Geology, v. 17, p. 98–129.

Scott, D. K., and Leckie, R. M., 1990, Foraminiferal zonation of Great Sippewissett salt marsh (Falmouth, Massachusetts): Journal of Foraminiferal Research, v. 20, p. 248–266.

Shennan, I., and Hamilton, S., 2006, Coseismic and pre-seismic subsidence associated with great earthquakes in Alaska: Quaternary Science Reviews, v. 25, p. 1–8.

Shennan, I., Bradley, S. L., and Edwards, R., 2018, Relative sea-level changes and crustal movements in Britain and Ireland since the Last Glacial Maximum: Quaternary Science Reviews, v. 188, p. 143–159.

Southall, K. E., Gehrels, W. R., and Hayward, B. W., 2006, Foraminifera in a New Zealand salt marsh and their suitability as sea-level indicators: Marine Micropaleontology, v. 60, p. 167–179.

Strachan, K. L., Hill, T. R., Finch, J. M., and Barnett, R. L., 2015, Vertical zonation of foraminifera assemblages in Galpins salt marsh, South Africa: Journal of Foraminiferal Research, v. 45, p. 29–41.

Swallow, J. E., 2000, Intra-annual variability and patchiness in living assemblages of salt-marsh foraminifera from Mill Rythe Creek, Chichester Harbour, England: Journal of Micropalaeontology, v. 19, p. 9–22.

Woodroffe, C. D., McGregor, H. V., Lambeck, K., Smithers, S. G., and Fink, D., 2012, Mid-Pacific microatolls record sea-level stability over the past 5000 yr: Geology, v. 40, p. 951–954.

Wright, A. J., Edwards, R. J., and van de Plassche, O., 2011, Reassessing transfer-function performance in sea-level reconstruction based on benthic salt-marsh foraminifera from the Atlantic coast of NE North America: Marine Micropaleontology, v. 81, p. 43–62.

Received 3 July 2019
Accepted 3 March 2020

2020 CELEBRATING 70 YEARS Cushman Foundation for Foraminiferal Research Inc

Downloaded from http://pubs.geoscienceworld.org/cushmanfoundation/jfr/article-pdf/50/3/266/5143690/i0096-1191-50-3-266.pdf
by Maynooth University user