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Reassessing transfer-function performance in sea-level reconstruction based on benthic salt-marsh foraminifera from the Atlantic Coast of NE North America

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ABSTRACT

The need to increase the number and distribution of sea-level records spanning the last few hundred years has led to particular interest in developing high-precision, geologically based sea-level reconstructions that capture decimetre and multi-decadal scale changes. Transfer functions for tide level are statistical tools that quantify the vertical relationship between inter-tidal microfossils and elevation within the tidal frame and their use in sea-level reconstruction is growing in popularity. Whilst a range of sampling strategies, dataset qualities and underlying statistical models have been used in transfer-function development, all variants share the common requirement of accurately extracting precise species-elevation relationships from surface data, and reliably applying these to fossil assemblages to infer past conditions.

We present surface foraminiferal data from six transects sampled at three sites spanning a large latitudinal range extending from Newfoundland (Canada) to North Carolina (USA). These data demonstrate that significant spatial differences exist within the high-marsh foraminiferal assemblages commonly used to reconstruct past relative sea-level (RSL). We standardise these data to account for inter-site differences in tidal range using several variants of the standardised water level index (SWLI) of Horton et al. (1999b) and show that the best performance is achieved by using the highest occurrence of foraminifera as the upper tidal datum level.

The standardised surface foraminiferal data are used to develop a suite of foraminiferal transfer functions for tide level which are then applied to fossil assemblages from two sediment cores to reconstruct palaeomarsh-surface elevation. We highlight the manner in which species-elevation relationships are extracted and modified during transfer-function development, and the impacts that choices in dataset composition and transfer-function type have on the resulting reconstructions. Our results graphically illustrate the importance of these choices and the impacts of temporal and spatial variability in foraminiferal distributions, none of which are adequately represented or discernible from the standard summary statistics of performance that commonly accompany transfer-function reconstructions.

We conclude that a more explicit treatment of the transfer-function development process is required to support the growing body of precise RSL reconstructions that are now appearing in the literature. To that end, we make the following four recommendations for a framework to assist in transfer-function development that will allow better record inter-comparison and minimise the potential for producing precise but ultimately inaccurate reconstructions: 1) sampling for surface data should focus on capturing complete species response curves rather than simply compiling modern analogues for fossil material; 2) The similarity between the surface assemblages used to produce transfer functions and the fossil assemblages to which they are applied, should be better quantified using range of statistical approaches, and must accompany any reconstruction; 3) where modern analogues are lacking in local surface assemblages, data from additional sites should be added, with selection based on fulfilling the requirements of the previous two recommendations. The manner in which individual species optima are combined to produce a composite optimum, and the extent to which this

provides a reasonable representation of the surface data should also be documented; 4) the application of WA PLS component 2 (and higher) cannot be justified solely on the grounds of increased performance measures (e.g. r^2_{jack} and RMSEP), and if applied, the pattern of optima updates should be used to highlight species that may distort reconstructions.
KEYWORDS

1. INTRODUCTION

Following the pioneering work of Scott and Medioli (1978, 1980a), the Atlantic coast of NE North America has become a locus for studies investigating the spatial distribution and ecological niche preferences of modern benthic salt-marsh foraminifera. Whilst the distribution of salt-marsh foraminifera is influenced by a range of environmental variables such as salinity, pH and grain size, numerous studies have demonstrated that assemblages are vertically zoned with respect to tide level, reflecting the strong environmental gradients that exist across inter-tidal environments (e.g. Scott et al., 1981; Gehrels, 1994b; Edwards et al., 2004a; b; Kemp et al., 2009b). Sample elevation, as a surrogate for hydroperiod and associated co-variables, is strongly correlated with foraminiferal content, permitting statistically significant relationships between elevation and species distribution to be developed (e.g. Horton et al. 1999a). When applied to fossil assemblages preserved in salt-marsh sediments, these species-elevation relationships can be used to precisely reconstruct past relative sea-level (RSL), often with quoted vertical error terms of a decimetre or less (e.g. Gehrels, 2000; Edwards et al., 2004b; Gehrels et al., 2005; Kemp et al., 2009c). This level of precision, which is much greater than most other geologically-based sea-level indicators, means that reconstructions based on salt-marsh foraminifera can be meaningfully compared with instrumental (tide gauge) records (Edwards, 2007). Several studies have demonstrated good agreement between foraminifera-based reconstructions and local tide-gauge records, and have gone on to explore the timing, magnitude and spatial patterns of recent accelerations in the rate of RSL rise (e.g. Gehrels et al., 2006a, 2008; Leorri et al., 2008a; Kemp et al., 2009c).

Whilst the quality of these kinds of reconstruction hinges on the accurate distillation of species-elevation relationships derived from surveys of modern salt-marsh foraminifera, there is currently no consensus regarding the appropriate spatial composition of these modern datasets, with approaches ranging from site specific (e.g. Gehrels et al., 2006a) to regional in scope (e.g. Horton and Edwards, 2006). Choices made during transfer-function development are often difficult to determine from the published literature, despite the fact that dataset composition can have profound effects on the resulting reconstructions (e.g. Horton & Edwards, 2006; Woodroffe, 2009a). Often the implicit justification for the choice of a particular combination of modern data is that it produces transfer functions that perform well in terms of a range of summary statistical measures. However, these performance measures of potential precision do not readily translate into confidence of reconstruction accuracy. Comparing recent reconstructions with instrumental data can provide some indication of accuracy, but becomes equivocal with increasing record length due to the greater potential for changes in environmental conditions at a site. In the absence of more definitive measures of accuracy, it is clearly desirable to establish a framework for transfer-function development that minimises the potential for producing precise but ultimately inaccurate reconstructions.

In this paper, we propose a framework for transfer-function development that seeks to minimise the potential for erroneous reconstructions by focussing on the manner in which species-elevation relationships are extracted from modern surface distributions of salt-marsh foraminifera. Integral to this is the wider issue of dataset composition (e.g. sampling strategy and number of sites) and the influence that it has on transfer functions for tide level.

We illustrate this process by first presenting surface foraminiferal distributions from three sites distributed along the Atlantic coast of NE North America. These data are then used to explore the influence that dataset composition has on transfer functions for tide level. In this analysis, we pay explicit attention to the manner in which elevation information is extracted from the foraminiferal data, how specific distribution-elevation relationships are modified during transfer-function development, and the extent to which this process is (not) reflected in summary performance statistics. We then illustrate the significance of these results by producing a suite of reconstructions from fossil assemblages recovered from two salt-marsh sediment cores. We conclude with a set of recommendations for transfer-function development which, whilst focussed on salt-marsh foraminifera, will also be applicable to other microfossil groups used in sea-level reconstruction.

2. METHODOLOGY

2.1 Site selection

Marshes investigated in this study span a large latitudinal range along the Atlantic coast of NE North America (Figure 1), encompassing an area with an extensive history of research into the relationships between modern foraminiferal distributions and RSL (e.g. Prince Edward Island, Nova Scotia and New Brunswick in Canada (Scott and Medioli, 1980a; Scott et al., 1981; Smith et al., 1984; Patterson et al., 2004); and Maine, Massachusetts, Connecticut, Virginia and North Carolina in the USA (Scott and Leckie, 1990; Gehrels, 1994b; de Rijk, 1995a, b; de Rijk and Troelstra, 1997; Gehrels and van de Plassche, 1999; Spencer, 2000; Edwards et al., 2004a; Horton and Culver, 2008; Kemp et al., 2009b)). Between 1999 and 2005 (Table 1), we sampled two transects within each of three study sites: Hynes Brook marsh (Newfoundland, Canada), Pattagansett River marsh (Connecticut, USA), and Elizabeth River marsh (North Carolina, USA). These salt-marsh systems are representative of the kinds of sites that have typically been used to produce records of RSL change.

Developed in an incised valley (Brookes et al., 1985), lower "Hynes Brook" (local name) is the smallest of all three marshes (approx. 0.04 km^2), semi-enclosed by a barrier beach/spit formation at its entrance and fed by a small brook which together prevent the full expression of low waters (Figure 2a). The site exhibits a clear zonation of upper, high and low-marsh vegetation which includes *Iris versicolor*, *Scirpus* spp., *Spartina patens*, *Distichlis spicata*, *Plantago maritima*, *Triglochin maritima*, *Spartina alterniflora* short (e.g. Brookes et al., 1985). Monthly average air temperatures reach ~16°C in summer and are below freezing from December to March (Canadian Climate Normals for 1971-2000, station Stephenville A, http://climate.weatheroffice.gc.ca).

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This dataset from the lower Pattagansett estuary is part of a larger study conducted in Connecticut and previously published in Edwards et al. (2004a; b). The sampled marsh area of Pattagansett River is located at the mouth of the river estuary (South Beach), where it is protected by a barrier beach/spit formation (Figure 2b). It is part of a larger, patchy and less enclosed system (approx. 0.7 km^2) which was, as much of Connecticut and the surrounding states, subject to extensive ditching for mosquito control during the Great Depression in the 1940s (Roza, 1995). The present upper, high and low-marsh vegetation zonation is typical of southern New England tidal marshes and includes *Iva frutescens*, *Juncus gerardii*, *Spartina patens*, *Distichlis spicata*, *Spartina alterniflora* short/tall (e.g. Orson et al., 1987). Monthly average air temperatures reach ~22°C in summer and are below freezing in January (US Climate Normals for 1971-2000, station Groton, http://hurricane.ncdc.noaa.gov).

Elizabeth River is the largest of all three sites, forming part of an estuary system (approx. 23.6 km^2) located adjacent to the mouth of the Cape Fear River (Figure 2c). This area is dissected by the Atlantic Intracoastal Waterway (AIWW), which was constructed through this part of North Carolina between 1930 and 1936 (Parkman, 1983). The upper, high and low-marsh vegetation zonation is characterised by *Borrichia frutescens, Limonium carolinianum*, *Distichlis spicata*, *Juncus roemerianus, Spartina alterniflora* short/tall (e.g. Adams, 1963), with the latter two species widely dominating. Monthly average air temperatures reach ~26°C in summer and do not fall below freezing in winter (US Climate Normals for 1971-2000, station Southport, http://hurricane.ncdc.noaa.gov).

2.2 Foraminiferal Sampling

Samples of the upper centimetre of sediment were recovered at regularly spaced vertical intervals of 5 ± 1 cm along transects spanning the full range of available vegetated salt-marsh sub-environments (Figure 2). At each site, local tidal data were collected and all foraminiferal samples were then surveyed to produce sample elevations relative to the tidal frame. These data are subsequently normalised to permit inter-site comparison as detailed in Section 2.3.

Sediments were preserved in a solution of ethanol buffered by sodium bicarbonate with Rose Bengal added to distinguish specimens that were live at the time of collection (Walton, 1952; Murray and Bowser, 2000). In the laboratory, samples were washed through 0.5 mm and 0.063 mm sieves and counted wet under a binocular microscope following the methods of Scott & Medioli (1980).

We employ the death assemblage recovered from the topmost centimetre of sediment since this represents the most appropriate analogue for material that is subsequently found in the fossil record (e.g. Horton, 1999; Horton et al., 1999a; Murray, 2000; Horton and Edwards, 2003; Edwards et al., 2004a; b; Gehrels et al., 2006a; Horton and Edwards, 2006; Horton and Culver, 2008; Leorri et al., 2008a; Kemp et al., 2009b). The surface foraminiferal data comprises a total of 141 samples (Table 1)

with counts of individual species expressed as their percentage relative abundances per sample (unidentified species are excluded in the summation).

The sub-surface material used to illustrate transfer-function application (Section 4) was collected from the study sites at Pattagansett (Figure 2b) and Elizabeth River (Figure 2c). Continuous cores of salt-marsh sediment were removed with a gouge auger and divided into 1cm thick intervals in the laboratory. A hole-punch was used to remove samples with a consistent volume to be prepared and analysed for foraminiferal analysis as outlined above, omitting the use of Rose Bengal

Studies of North American salt-marsh foraminifera have employed a range of taxonomic approaches which introduces additional complications when trying to compare their results. Whilst the data presented in this paper come from a large geographical range, we have been careful to employ a consistent taxonomic approach to facilitate inter-site and regional comparison. Our taxonomy, which is outlined in Appendix A, broadly follows that of de Rijk (1995a; b), de Rijk and Troelstra (1997) and Gehrels and van de Plassche (1999).

2.3 Tidal datum calculation and normalisation

Local tidal parameters (predominantly measured by on-site logging) are compared with established tide-gauge stations to produce representative long-term values for mean tide level (MTL), mean high water (MHW) and mean higher high water (MHHW) as outlined in Table 2.

When combining datasets from multiple sites it is necessary to normalise elevation data to account for differences in tidal range. We employ the frequently used standardised water level index (SWLI) approach (after Horton et al., 1999b), such that sample elevation (*Elev*), is expressed relative to selected lower (*lowTD*) and upper (*uppTD*) local tidal datum-levels, e.g. MTL and MHHW respectively (Equation 1). This approach has the added advantage of removing systematic errors arising from any inter-site uncertainties in absolute datum level such as can arise when converting between national levelling systems. A variety of upper and lower datum-levels have been employed in previous studies, and we compare the performance of several SWLI variants in Section 3.1.

Equation 1

$$SWLI = \left\{ \left(\frac{Elev - lowTD}{uppTD - lowTD} \right) \times 100 \right\} + 100$$

2.4 Data analysis

We employ a range of standard cluster and ordination methods to describe and explore our data (e.g. Birks, 1986; 1992 in Horton and Edwards, 2006; Horton et al., 2005; Woodroffe et al., 2005). Unconstrained cluster analysis (incremental sum of squares, Euclidean distance, un-weighted, with no data transformation or standardisation) is performed using the program CONISS in Tilia version 2.0.b.4 (Grimm, 1991) with Tilia Graph version 2.0.2 (Grimm, 2004). We use this agglomerative,

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hierarchical technique to classify samples into more-or-less homogeneous faunal zones (Grimm, 1987).

Ordination is achieved using two variants of correspondence analysis in the program CANOCO version 4.5 (ter Braak and Šmilauer, 2003). We use detrended correspondence analysis (detrending by segments, no data transformation) to provide further information on sample associations and assist in the allocation of boundaries between cluster groups. We use detrended canonical correspondence analysis (DCCA) to quantify the extent to which foraminiferal assemblages change with elevation. This 'species turnover' (referred to as gradient length) is measured by DCCA axis 1, with gradient lengths of two or more indicating species are collectively responding in a unimodal fashion to elevation (ter Braak and Juggins, 1993; ter Braak et al., 1993; Birks in Maddy and Brew, 1995; Birks, 1998). This information is used in selecting whether unimodal or linear-based transfer functions are appropriate, and we develop transfer functions in Section 4 using the program C^2 version 1.5 (Juggins, 2007).

Prior to statistical analysis, dataset quality was assessed qualitatively (e.g. *a priori* on grounds such as evidence of human disturbance at sampling locations (Edwards et al., 2004b)), and quantitatively (e.g. based upon species percentage abundances and sample total counts (Patterson and Fishbein, 1989; Fatella and Taborda, 2002)). Of the 141 surface samples collected, 125 contain foraminifera of which 9 are removed on the basis of low counts (Table 1). The remaining 116 sample death assemblage dataset (average of 266 individuals per sample) is used to illustrate species distributions (Section 3; Figure 3) before being subject to screening according to Equation 2 proposed by Fatela and Taborda (2002, pp. 170).

Equation 2

$$p = 1 - f(0.05)^{1/n}$$

It follows from Equation 2, that the total number of individual specimens counted in a sample (n) is used to compute the minimum fractional abundance (i.e. 10% is 0.1) acceptable for a species (P) given the specified confidence level (i.e. 95% confidence level f (0.05)). All species identified in that sample must have fractional abundances which exceed this level to be considered as having been sufficiently detected: those with contributions below this level are removed from the sample. This method removes no additional samples but screens out the low abundance agglutinated *Allogromia* spp., which is recorded in transect ER1 at Elizabeth River marsh (Figure 3c).

3. SURFACE FORAMINIFERAL DISTRIBUTIONS

The foraminiferal distributions recorded at each site are summarised in Figure 3. The use of a consistent taxonomic framework makes it possible to examine reliably inter-site differences in the occurrence of some key species (see Appendix A). In each transect there is a clear bi-partite division

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between a low-marsh assemblage characterised by the cosmopolitan species *Miliammina fusca* and a high-marsh assemblage of more variable composition (see Appendix B, Figure B1 for site-specific cluster analysis and ordination).

At Hynes Brook (Figure 3a), the high-marsh fauna can be sub-divided into upper and lower assemblages, with *Balticammina pseudomacrescens* and *Jadammina macrescens* co-dominating samples above MHHW, and a more mixed assemblage also including *Miliammina fusca*, *Tiphotrocha comprimata* and *Haplophragmoides* spp. extending between MHHW and MHW. *Miliammina fusca* dominates the low-marsh assemblage below MHW.

At Pattagansett River (Figure 3b), *Jadammina macrescens* and *Trochammina inflata* co-dominate the samples above MHHW, with an almost monospecific assemblage of *Jadammina macrescens* in the uppermost samples of transect PR1. Once again, *Trochammina comprimata* is relatively abundant in the interval between MHW and MHHW, where it contributes to a mixed assemblage that also includes *Siphotrochammina lobata*. In the low marsh below MHW, *Miliammina fusca* is joined by *Arenoparella mexicana* and *Ammobaculites dilatatus*.

At Elizabeth River (Figure 3c), *Haplophragmoides* spp. make a significantly greater contribution to the high-marsh fauna than at other sites, with *Jadammina macrescens* notably lower in relative abundance. The assemblage is co-dominated by *Trochammina inflata* and *Siphotrochammina lobata*, with *Trochammina comprimata* spanning a broader zone extending from above MHHW to well below MHW. Whilst *Miliammina fusca* dominates the lowest marsh fauna, *Ammobaculites dilatatus* and *Ammoastuta inepta* are co-dominant in places, particularly in transect ER1.

These distributions are collectively summarised using a combination of cluster analysis and detrended correspondence analysis (DCA, Table 4) to classify samples into more-or-less homogenous faunal zones. The analysis is performed on the combined (116 sample) dataset and distinguishes a single low-marsh cluster containing samples from all sites, and three distinct, site-specific high-marsh clusters (Figure 4). The single low-marsh grouping most likely reflects the universal presence and dominance of *Miliammina fusca*. In contrast, the high marsh at Hynes Brook is principally distinctive for its abundance of *Balticammina pseudomacrescens*; Pattagansett River for its co-dominance of *Jadammina macrescens* and *Trochammina inflata*; and Elizabeth River for the low abundance of *Jadammina macrescens* and co-dominance of *Haplophragmoides* spp., *Trochammina inflata* and *Siphotrochammina lobata*.

3.1 Normalising the Vertical Distribution of Foraminifera

To interpret the vertical distribution of foraminiferal species it is necessary to normalise the elevation data to account for inter-site differences in tidal range (Section 2.3). It should be noted that sample elevation (normalised or otherwise) is not an ecological parameter. Instead, it is a linear approximation of inundation frequency, which is widely recognized as predominantly influencing species distributions (e.g. Scott and Medioli, 1980a; Horton et al., 1999a; Horton and Edwards, 2005)

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along with other variables such as salinity (e.g. de Rijk 1995a, b; de Rijk and Troelstra, 1997; Hayward et al., 2004b; Kemp et al., 2009b). Due to the non-linear relationship between elevation and inundation, the SWLI variant employed influences the vertical alignment of samples from different sites, and ultimately the calculated environmental gradient lengths. This issue is discussed by Woodroffe and Long (2010) in the context of diatom-based sea-level reconstruction in Greenland.

We evaluate the use of three different upper tidal datum levels by conducting repeated DCCA along consecutive segments of the environmental gradient (Figure 5, Table 3). This analysis highlights the elevations at which peaks in faunal turnover (i.e. changes in foraminiferal assemblage) occur. All three variants show a strong peak in turnover centred on the middle of the environmental gradient, reflecting the clear transition between high marsh and low-marsh assemblages that is evident from the foraminiferal distributions in Figure 3, and the cluster and DCA analyses (Figure 4). However, for the MHW and MHHW variants, a second, spurious peak in turnover is produced; primarily as a result of poor vertical alignment of the upper-marsh samples (Figure 5a, b). This poor alignment reflects the fact that the non-linearity between elevation and tidal inundation is most pronounced in the highest marsh environment toward the upper limit of marine influence. This effect is compounded when extrapolating to samples above the height of the upper reference datum used.

One way to circumvent this problem is to use the well-established ecological relationship between the highest occurrence of foraminifera (HOF) and the upper limit of marine influence (e.g. Scott and Medioli, 1978; Scott and Medioli, 1980a; Scott et al., 1981; Gehrels, 2000). Using HOF has the advantage of avoiding site-specific differences in the quality of tidal data and should be accurate to within ~10 cm given the high vertical sampling resolution applied (5 ±1 cm) to well above the upper-marsh limit. It also removes the need to extrapolate beyond the limits of the reference tidal datum-levels used, and means that alignment of the uppermost samples is inherently improved. The success of this approach is evident in Figure 5c, as the alignment of the upper samples removes spurious species turnover in the upper marsh, whilst sharpening and increasing the peak in turnover in the middle of the environmental gradient. This latter effect, which arises as a consequence of bringing the high to low-marsh transitions recorded at each site into alignment, is not inherent in the selection of HOF, but provides further support for its effectiveness in describing the real assemblage structure apparent in the dataset.

3.2 Regional Patterns in Surface Foraminiferal Assemblages

In contrast to other studies which have tended to emphasise the similarity of high-marsh assemblages and the diversity of those in the lower intertidal zone (e.g. Scott & Medioli, 1980a; Edwards et al., 2004b), the combined dataset presented here shows that when sampling over the typical range of elevations used for sea-level reconstruction, the character of the high-marsh fauna is extremely variable (Figures 3 & 4).

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The classic mono-specific *Trochammina macrescens* assemblage (faunal zone 1a of Scott and Medioli, 1980a) is clearly present in Hynes Brook (providing *Balticammina pseudomacrescens* is grouped together with *Jadammina macrescens*). This highest faunal zone exists as a few mono-specific *Jadammina macrescens* samples in Pattagansett River, but is totally absent from Elizabeth River where it is replaced by a combination of species including *Haplophragmoides* spp., *Trochammina inflata* and *Siphotrochammina lobata*.

Comparison of our data with those studies in which it is possible to extract information on *Balticammina pseudomacrescens*, suggests that this species is spatially restricted. For example it has been identified in abundance in Maine (Gehrels and van de Plassche, 1999) and Massachusetts (de Rijk, 1995a; b; de Rijk and Troelstra, 1997), the latter where it is identified as *Trochammina macrescens* type A in de Rijk (1995a). It is also likely present as part of the interspecific gradational series *Trochammina macrescens* (variant *macrescens*) identified in Prince Edward Island (Scott et al., 1981) and Nova Scotia (Scott and Medioli, 1980a; Smith et al., 1984). Its apparent absence from modern assemblages in Connecticut has been observed in previous studies (i.e. Gehrels and van de Plassche, 1999; Edwards et al., 2004a) and is striking given its large relative abundance in neighbouring Massachusetts. This absence continues in our site in Elizabeth River, and is consistent with its apparent absence in the adjacent Albemarle-Pamlico estuarine system (Horton and Culver, 2008; Kemp et al., 2009b). Significantly however, this apparent modern distribution is not always reflected in the fossil record, with *Balticammina pseudomacrescens* being reported in Menunketesuck River marsh, Connecticut, from core MRM32, where it appears below ~222 cm core depth (Gehrels and van de Plassche, 1999). Similar fossil occurrences are evident in core material at another site in Pattagansett River, where relative abundances can reach over 20% of the assemblage (Edwards, unpubl. data).

The patterns associated with *Jadammina macrescens* are less clear in that whilst it has a limited presence in our North Carolina site and at a neighbouring marsh in Virginia (Spencer, 2000), it is found in large numbers in the high marsh of two other sites in North Carolina (Currituck Barrier Island, Horton and Culver, 2008; Sand Point, Kemp et al., 2009b). Both these areas are noted for their lower salinity, whilst in other, more saline parts of the Albemarle-Pamlico estuarine system, *Jadammina macrescens* is rare. It seems unlikely that salinity is a significant influencing factor however, given that this species is found in large numbers in sites with a wide range of salinities (e.g. Murray, 1991 p.58). For example de Rijk and Troelstra (1995a) report a strong positive correlation between *Jadammina macrescens* (identified as *Trochammina macrescens* type B) and salinity in the Great Marshes at Barnstable (Massachusetts, USA). If consistent discrimination is possible, a revised sub-division on the basis of supplementary apertures (i.e. forma polystoma versus forma macrescens of Scott & Medioli, 1980a) may bring greater clarity to this issue.

Similar local variability is evident in the distribution of the other principal high-marsh species encountered at our sites. *Trochammina inflata* is absent at Hynes Brook, but is present at sites in

neighbouring Prince Edward Island (Scott et al., 1981); Nova Scotia (Scott and Medioli, 1980a; Smith et al., 1984) and Maine (Gehrels, 1994a; b). *Siphotrochammina lobata* is highly abundant in Elizabeth River transect ER1, but is only found in low abundance within the adjacent Albemarle-Pamlico estuarine system (Kemp et al., 2009b). Finally, whilst *Haplophragmoides* spp. are only minor contributors to the assemblage at Pattagansett River, they have been found in high abundance in both Massachusetts (de Rijk, 1995b) and Connecticut (Gehrels and van de Plassche, 1999; Edwards et al., 2004a).

Although we have focussed attention on the diversity of the upper-marsh assemblages, it would be wrong to imply that the low-marsh fauna, whilst dominated by *Miliammina fusca*, are completely uniform. In Pattagansett and Elizabeth River, *Miliammina fusca* is found in association with *Ammobaculites dilatatus*. Similar assemblages are reported (with *A. dilatatus* as „*Ammotium salsum'*) in Wallace Basin and Chezzetcook, Nova Scotia, (Scott and Medioli, 1980a), Machiasport and Gouldsboro, Maine (Gehrels, 1994a; b), the Great Marshes, Massachusetts (de Rijk and Troelstra, 1997) and as „*Ammobaculites* spp.' in the Albemarle-Pamlico estuarine system, North Carolina (Kemp et al., 2009b).

In our data the highest relative abundances of *Arenoparella mexicana* are found at Elizabeth River, with no occurrences recorded in Hynes Brook. There is notable intra-site variability at Pattagansett and Elizabeth River, although the discrepancies at the latter could reflect differences in sampling range between transects. Although *Arenoparella mexicana* is well represented in samples from Massachusetts (de Rijk, 1995b), it is only reported in low relative abundances on Prince Edward Island (Scott et al., 1981) and in Maine (Gehrels, 1994a; b).

In summary, the fauna characterising the high- (and low-) marsh assemblages along the Atlantic coast of NE North America show substantial spatial variability which, in the absence of more detailed, site-specific data concerning a range of environmental variables (e.g. salinity, substrate etc), cannot be examined further. In addition, sub-surface assemblages do not always mirror the modern distributions recorded at a study site. The significance of these features for transfer function-based RSL reconstructions will now be considered.

4. FORAMINIFERAL TRANSFER FUNCTIONS FOR TIDE LEVEL

The spatial variability evident in the high-marsh assemblages presented in Section 3.2 strongly cautions against attempts to use vertical zonations established at one site to interpret sequences recovered from another (i.e. de Rijk and Troelstra, 1997). However, it is also clear that where species distribution has varied through time, such as is the case with *Balticammina pseudomacrescens* in the marshes of Connecticut, a local modern dataset will not be sufficient to interpret the fossil assemblages encountered in core material. These issues are at the heart of the debate concerning whether local or regional modern datasets are most appropriate for the reconstruction of past sea

levels (e.g. Horton et al., 1999a; Allen and Haslett, 2002; Horton and Edwards, 2005; 2006; Leorri et al., 2010).

In order to explore the issue of dataset compilation and its significance for transfer function-based RSL reconstruction, we develop and compare a series of transfer functions for elevation (SWLI) based on the foraminiferal data presented in Figure 3. To ensure that all transfer functions are directly comparable we restrict our dataset to the shortest SWLI range sampled (i.e. the Pattagansett River site which spans an environmental gradient from 200 – 120 SWLI). This range captures the transition from high to low-marsh fauna, and in all instances results in a gradient length close to or above 2 standard deviations (Table 3). This means that sufficient turnover in species composition has occurred in all cases for unimodal species response models and weighted averaging-based (WA) transfer functions to be applied.

The decision as to which transfer function will ultimately be used to calibrate fossil samples and predict the elevations at which they formed, is frequently based upon cross-validated (i.e. jack-knifed or bootstrapped) summary measures of performance such as root mean square error of prediction (RMSEP), average and maximum bias, and correlation coefficient (R^2). The performance of a range of jack-knifed ($_{jack}$) transfer-function variants is presented in Table 5, indicating that all available WA-based transfer-function methods for all datasets perform well. High R^2_{jack} values (0.73 to 0.95) indicate strong relationships between observed and predicted sample elevations, whilst low RMSEP values suggest precise reconstructions are possible, with vertical error terms typically 0.10 m or less.

4.1 Representing species optima and tolerance

The WA transfer functions distil and express the elevation preferences of each species in terms of species optima („preferred' elevation) and tolerance (range of elevations encountered). Species optima are calculated from the abundance weighted average of the SWLI values of all samples in which each species occurs (ter Braak and Barendregt 1986; ter Braak and van Dam, 1989) whilst the tolerance is the abundance weighted standard deviation (e.g. Oksanen et al., 1988; Birks et al., 1990).

Figure 6a presents species optima (and tolerances) derived from simple weighted averaging of data from individual sites and for the combined dataset from all sites. For ease of comparison, species are arranged according to the vertical ordering of their optima in the combined dataset (for which the tolerances are also shown). Of the 18 species represented in the combined dataset, only 15 have at least three effective occurrences (using Hills N2). Of these, 6 are present at all three sites and so we focus the following discussion on these „cosmopolitan' species *Jadammina macrescens*, *Haplophragmoides* spp., *Siphotrochammina lobata*, *Trochammina inflata*, *Tiphotrocha comprimata* and *Miliammina fusca*.

Separation of high and low-marsh species optima reflects the bipartite division in fauna, and this is most clearly visible in the Elizabeth River and combined datasets. The tendency for species optima

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to cluster within the high or low marsh contributes to the low values of species turnover recorded within all datasets for these two sub-environments (Figure 5). This clustering is partly attributable to „edge-effects' where truncation of the species response curves occurs at the limits of the environmental gradient, promoting under-prediction of the highest marsh optima and over-prediction of the lowest marsh optima (Mohler, 1983 in Birks, 1995).

The greatest inter-site consistency is apparent in the optima for *Miliammina fusca* and *Trochammina comprimata* with the result that their optima in the combined dataset provide an accurate summary of species distribution. The high-marsh taxa of *Jadammina macrescens, Trochammina inflata* and *Haplophragmoides* spp., exhibit a greater spread in their optima. In the case of *Jadammina macrescens*, the divergence is principally due to the samples from Elizabeth River although on balance, the optimum in the combined dataset is still a good approximation of the overall distribution pattern. Similarly, the combined optima for *Trochammina inflata* and *Haplophragmoides* spp. are reasonable reflections of the general characteristics of their distributions, although the accuracy is weakest for samples from Hynes Brook. The distribution of the final cosmopolitan species, *Siphotrochammina lobata*, shows the greatest inter-site variability, primarily due to the Elizabeth River data.

In summary, optima for the cosmopolitan species produced by the combined dataset can reasonably be applied to all sites with the exception of that for *Siphotrochammina lobata* which is only applicable to two out of the three marshes.

4.2 Updating species optima

Transfer functions based on WA predict sample elevation on the basis of foraminiferal content by taking the weighted average of the various optima of all species contained within that sample. Because this is an „average of an average' it causes compression in the vertical range of predicted sample elevations, necessitating a „deshrinking' correction to be applied. The precise nature of this correction varies between WA variants, but its effect is to produce updated species optima (technically termed „species coefficients'). This is illustrated in Figure 6b for weighted averaging partial least squares (WA-PLS) component 1, equal to simple WA with inverse deshrinking, where it is evident as a small increase in the spread of species optima in the high-marsh fauna (e.g. *Siphotrochammina lobata*), and a clear lowering of optima in the low-marsh species. Significantly, the ecological ordering of the updated species optima remains unchanged and the general patterns between datasets are largely unaffected.

This form of deshrinking fails to completely correct for the truncation of upper-marsh species response curves, (upper-marsh sample elevations are consistently under predicted), whilst the lack of turnover in species optima within the high marsh sub-environment results in over prediction for samples around the transition from low to high-marsh fauna. In an attempt to improve transfer-function performance and reduce these systematic failures, alternative variants can be used. In

common with many other studies, Table 5 indicates that the greatest improvement is obtained by using further components of WA-PLS. WA-PLS components 2 (and higher) exploit structure in the residuals to further update these optima and ultimately better predict dataset sample elevations (ter Braak, 1995a). This improvement in summary performance statistics has made it the favoured approach in many microfossil-based transfer functions for tide level (e.g. Edwards et al., 2004a; Szkornik et al., 2006; Horton et al., 2007; Leorri et al., 2008a; Kemp et al., 2009b; Woodroffe, 2009a).

Here, we limit the number of WA-PLS components to two, as this is both sufficient for the purposes of illustration, and conforms to the principle of parsimony which recommends using the „minimum adequate model' (Crawley, 1993 in Birks, 1998). The updated species optima are plotted in Figure 6c and reveals that the improvement in performance is achieved by substantially shifting many of the species optima such that some are moved to well beyond the boundary of the sampled marsh environment. Every update is unique not only to each dataset, but also to each species depending on whether they were predominantly found in samples that were over or under predicted. Consequently, inter-site differences in distributions are amplified with the result that species optima derived from the various datasets exhibit increasingly large vertical spreads.

For example, whilst the optimum for *Jadammina macrescens* derived from the combined dataset is in good agreement with those derived from Hynes Brook and Pattagansett River, these values diverge significantly from the optimum for the Elizabeth River dataset. This large divergence is due to the fact that *Jadammina macrescens* is restricted to the uppermost samples in Elizabeth River, which inevitably experience under-prediction due to the „edge effect'. Consequently, the optimum is updated to improve prediction by dramatically raising it and resulting in a significant departure from the values associated with the other sites. Similar effects can be seen in the optima updates for *Haplophragmoides* spp., *Trochammina inflata* and *Siphotrochammina lobata*.

In summary, whilst the additional updates of species optima associated with WA-PLS component 2 improve predictions and summary statistics, the species- / site-specific nature of these updates means that optima derived from the composite dataset show increased divergence from some of the locally-derived values.

4.3 Illustrating the significance of species optima updates

To illustrate the effects of the optima updates described in the previous section, we use transfer functions developed from three different datasets to reconstruct palaeomarsh-surface elevation changes from fossil foraminifera contained within two salt-marsh cores. The fossil data and associated reconstructions, with fossil sample-specific bootstrap cross-validated eSEP errors (estimated standard error of prediction) are presented in Figure 7 and summarised in Table 6. The reconstructions for each core are generated from the combined surface dataset (shown in grey with eSEP errors) and plotted alongside the reconstruction produced by the local dataset from the core site alone (black line, eSEP errors omitted for clarity). In both cases, reconstructions are produced

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using WA-PLS component 1 (equivalent to simple WA with inverse deshrinking), and WA-PLS component 2 (incorporating the additional optima updates described in the preceding section and illustrated in Figure 6c). On the basis of summary statistics alone, all transfer-function variants can be said to perform well, with high correlation coefficients (R^2_{jack}) and small vertical error terms (RMSEP), with WA-PLS component 2 out-performing simple WA (Table 5). Additionally, we present the results of the Modern Analogue Technique (MAT) which is used to quantify the similarity between surface and fossil foraminiferal samples.

The MAT results indicate the fossil material from Connecticut is very similar to samples found in both the local and the combined surface datasets (Figure 7a). The reconstructions produced by the local and regional transfer functions show good (within eSEP error) agreement based on both component 1 and component 2 WA-PLS (Table 6). There is a slight tendency for the local dataset to produce larger palaeomarsh-surface elevation changes than appear in the combined dataset, and this tendency is amplified in the reconstructions associated with WA-PLS component 2. Inspection of Figure 6c reveals that this is primarily due to the way in which the optima for *T. comprimata* and *S. lobata* are updated.

In contrast to Connecticut, the fossil material from North Carolina shows much greater dissimilarity with the surface dataset (Figure 7b). The local surface dataset from Elizabeth River is particularly poorly suited for interpreting the fossil record since none of its samples provide good modern analogues for the sub-surface assemblages. The combined dataset performs much better with only two fossil samples having poor matches, suggesting that the conditions experienced at Elizabeth River in the past can be inferred from modern environments at other locations.

However, whilst the relative performance of the local versus combined datasets differs hugely in terms of MAT, the similarity of reconstructed palaeomarsh-surface elevation for WA-PLS component 1 is striking. In fact, all of the locally-derived reconstructions are identical (within eSEP error) to those of the combined dataset reflecting the close correspondence of species optima apparent in Figure 6b. This situation is radically different if WA-PLS component 2 is used to produce the reconstructions. The offset between reconstructions increases substantially with differences greater than error for a significant portion of the upper part of the core (Table 6, ER-A60 9-22 cm core depth). In this instance, the local reconstructions are clearly in error since they produce palaeomarsh-surface elevation estimates above the height of the highest occurrence of foraminifera. Again, inspection of Figure 6c reveals the cause of these erroneous reconstructions: in this instance it is the dramatic update of the optimum for *Jadammina macrescens* in the Elizabeth River dataset which was highlighted in Section 4.2.

5. DISCUSSION

The surface data presented in Section 3 reiterate the well established relationship between inter-tidal foraminiferal distributions and tide levels, and support the fact that these can be used to develop

foraminiferal transfer-functions capable of producing precise relative sea-level reconstructions. Whilst all the datasets show a clear bipartite division between high and low-marsh fauna, the composition of these assemblage zones varies between sites. Although variability in low inter-tidal contexts is widely acknowledged, heterogeneity within high-marsh environments is less frequently discussed, perhaps due to the reduced diversity of the assemblages encountered. Whilst taxonomic inconsistencies often obscure the details, the literature demonstrates that high-marsh variability is not a unique feature of the datasets presented here. For example, in one of the few regional-scale surveys of inter-tidal foraminifera, Horton & Edwards (2006) present surface distributions from fifteen sites in Britain and Ireland. Although not explicitly commented upon, the British and Irish data exhibit significant spatial variability in the composition of high-marsh assemblage zones, comparable to the surface distributions presented in this paper.

Spatial variability complicates the compilation of composite datasets from multiple sites and it is therefore logical to begin by using local, site-specific distributions in transfer-function development. A single site approach has the additional advantages of reduced logistical complexities and time spent in the field, coupled with a tendency for the magnitude of the vertical error term (RMSEP) to be reduced, thereby permitted more precise reconstructions (RMSEP or eSEP) to be developed (e.g. Table 5). This latter point is of particular significance since the increase in popularity of the transfer-function approach is driven by the need to produce "high resolution" sea-level records with small, but quantified vertical error terms.

The site-specific approach works well providing the modern, local conditions are sufficiently diverse to accurately represent the species-environment relationships exhibited in the fossil data upon which reconstructions are based. However, as the data presented here and in other publications show, there are many instances in which local surface distributions do not provide reliable modern analogues for sub-surface assemblages. In such situations additional analogues from other sites need to be incorporated into the surface dataset, although this tends to reduce transfer-function precision (see RMSEP in Table 5; and Horton & Edwards, 2005). This phenomenon is an expression of the spatial variability noted above, since contrasting species-elevation characteristics at individual sites are combined into a single averaged multi-site value that may (or may not) effectively represent their distribution (Figure 6). Together, these factors result in an inevitable tension between fulfilling the requirements for reconstruction precision (small RMSEP or eSEP) and accuracy (stable, robust species-elevation representation).

In an attempt to address the issue of reduced precision, it is natural to turn to higher components of WA-PLS since the manner in which species optima are updated improves performance in situations where the inter-site differences in secondary variables distort species-elevation relationships. However, these updates, which can be large and unsystematic, are dataset specific (Figure 6c), and this specificity means that reconstructions become increasingly sensitive to dataset composition. The result is that even comparatively modest differences between modern and fossil assemblages can

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result in substantial vertical error in the reconstructed elevation (Figure 7b). This effect is most pronounced when species with large optima updates make significant contributions to the fossil assemblage (e.g. *Jadammina macrescens* in the local dataset of Elizabeth River marsh: Figure 6c and 7b). Consequently, the drive to produce high-precision reconstructions has a tendency to inherently build-in hyper-sensitivity to assemblage composition, increasing the potential for significant (greater than error) inaccuracies.

Three things follow from these simple observations. Firstly, demonstrating the similarity between surface and fossil assemblages is at least as important as presenting summary statistics indicating good transfer-function performance, and this becomes increasingly critical when developing transfer functions based on higher components of WA-PLS. However, whilst the sea-level literature now abounds with WA-PLS based transfer functions accompanied by summary statistics such as R^2 and RMSEP, the treatment of similarity is much more variable and in some cases is lacking altogether. Whilst MAT is a useful starting point, there is currently no consensus on precisely how a „good analogue' should be defined, and even apparently good analogues can produce spurious reconstructions (see discussion in Woodroffe, 2009a). Future work should address this issue in a more comprehensive manner, utilising complementary approaches to MAT, such as cluster analysis and other ordination techniques.

Secondly, much more explicit consideration should be given to species optima and the manner in which they are updated during transfer-function development. For example, there is a particular need to examine the manner in which species optima from individual sites are combined to produce a composite optimum for that species as illustrated in Figure 6. In some instances, combining species data from multiple sites effectively produces an average response curve with a wider tolerance which arguably results in less precise but more robust reconstructions: this is the case for many of the cosmopolitan species present in our NE North American dataset. In contrast where the niche of a taxon varies between sites (e.g. *Siphotrochammina lobata* in our data), the composite regional dataset produces an updated optimum that is significantly different from that found at some contributing sites. Consequently, reconstructions based on the composite dataset may be considerably in error when applied to fossil assemblages that reflect these site-specific conditions. Significantly, this error is not detectable from the summary transfer-function statistics (see Table 5), nor from the kind of modern analogue test used by Horton & Edwards (2005; 2006), since the expanded dataset will contain matching assemblages even though their ecological meaning has been distorted.

It is important to note at this point that the species optima of the lower marsh fauna are influenced by the vertical range of sampling which is the reason why we limit inter-site comparison to samples from a common SWLI range (200-120). If we include data from the lower, longer transects, the optimum of any species whose range extends below a SWLI of 120 will be correspondingly lower. For this reason, it is important that surface sampling extends beyond the range of sub-environments that are

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encountered in the fossil record. This requires a re-assessment of the way in which surface datasets are collected, replacing the focus on simply compiling analogous environments with an alternative strategy that places greater emphasis on capturing complete species response curves.

Thirdly, whilst there is an understandable desire to apply the most precise transfer-function variant, in instances where reliable modern analogues are equivocal, the use of higher components of WA-PLS is not advisable. In some instances, simple WA (or WA-PLS component 1) can still produce realistic reconstructions even in the absence of modern analogues (e.g. Figure 7b). Consequently, simple WA reconstructions should be used as a baseline for comparison with other transfer-function variants.

6. CONCLUSIONS & RECOMMENDATIONS

Microfossil-based transfer functions for tide level can produce precise relative sea-level reconstructions and will undoubtedly continue to play a central role in research seeking to better quantify climate-sea level relationships and the significance of recently recorded sea-level change (e.g. Gehrels et al., 2005; 2006a; 2008; Leorri et al., 2008a; Kemp et al., 2009c; 2011). Whilst great emphasis is placed upon their quantitative nature, transfer-function development incorporates a series of choices regarding dataset composition and statistical approach that have profound impacts on the resulting reconstructions but are not adequately reflected in summary statistical measures of performance.

In this paper we have highlighted the subtle but significant effects of temporal and spatial variability in foraminiferal assemblages and the ways in which species optima can be distorted during dataset compilation and transfer-function development. We also note the critical importance of ascertaining the similarity between the assemblages used to produce transfer functions and those to which they are applied, particularly when dealing with higher components of WA-PLS which is often the method of choice for RSL reconstruction. Despite their importance, these elements are often given little or no explicit consideration in the literature, leaving the reader with the impossible task of trying to gauge reconstruction quality on the basis of some limited statistical measures.

The proliferation of transfer function-based studies provides much needed improvements in spatial coverage and record replication, but inherently necessitates comparison between salt-marsh systems with contrasting assemblage characteristics. Whilst time-consuming, complex and data intensive, many salt-marsh sediments will require bespoke transfer functions that are explicitly tailored to the foraminiferal assemblages they contain. The inevitable diversity of the resulting transfer functions and the datasets used to produce them, demands that transfer-function development and performance is more explicitly demonstrated than is often the case in the current literature. To assist in this process, we outline a simple framework for transfer-function development and make some recommendations regarding the kinds of information that should be included in publications and supplementary material. Whilst aimed at foraminiferal transfer functions for tide level, many of the points will be of relevance to other microfossil groups.

These recommendations are:

1) The collection of surface data for use in transfer function-based reconstructions should focus on capturing complete species response curves rather than simply compiling modern analogues for fossil material. Sampling should be directed to delimiting species tolerances rather than just covering their optimal elevations. For example, low marsh to mudflat environments are often considered less reliable sources of sea-level information and are generally avoided in the fossil record. However, their inclusion in surface datasets is useful where it better delimits the distributions of higher elevation taxa, thereby improving the stability of their species optima and the reliability of the resulting reconstructions.

2) The assemblage composition of fossil and surface foraminifera should be compared using a range of statistical approaches to quantify similarity (e.g. MAT, cluster and ordination analyses). These indicators of similarity must accompany any reconstruction. Providing local datasets are sufficiently large and contain good analogues for fossil material, transfer functions based on site-specific data can be developed and applied.

3) Where modern analogues are lacking in local surface assemblages, data from additional sites should be added. The selection of which additional site or sites are included should, in the first instance, be based on the joint criteria of providing modern analogues and capturing species responses as outlined above. It should then consider explicitly the manner in which individual species optima are combined to produce a composite optimum, and the extent to which this provides a reasonable representation of the surface data.

4) The application of WA-PLS component 2 (and higher) cannot be justified solely on the grounds of increased performance as represented by standard summary statistical measures (e.g. R^2_{jack} and RMSEP). If higher components are to be used, demonstrating the comparability of surface and fossil data becomes critical, as does explicitly documenting the manner in which species optima are updated (e.g. Figure 6). The pattern of optima updates should be used to highlight species that may distort reconstructions, and the precautionary principle applied when dealing with any numerically significant species exhibiting a significantly updated optimum.

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FIGURE CAPTIONS

FIGURE 1: a-c) Location maps for marshes studied and 1-5) tide-gauge records used.

FIGURE 2: a-c) Maps for marshes studied including location of fossil cores in b) Pattagansett River marsh and c) Elizabeth River marsh, i-iv) sampled transect locations, elevations relative to North American Datum of 1983 (NAD83) or National Geodetic Vertical Datum of 1929 (NGVD29) and vegetation descriptions. No vertical profile is available for transect PR2 from Pattagansett River.

FIGURE 3: a-c) Individual species distributions per transect (death unscreened assemblage) versus sample elevation, including total number of death specimens (death COUNT) and percentage of live specimens (% LIVE) counted per sample.

FIGURE 4: C1-C4) Division of samples between groups (death screened assemblage), having applied a) cluster and b) DCA ordination (detrended correspondence analysis). Indicated are the high (Hm) or low (Lm) mash sub-environment affiliation and dominant site (HB, PR, ER) for each group. Single high-marsh sample (*HB0-1*) from HB found in the PR high-marsh cluster C4 is indicated in the DCA by (1), as is the minor over lap between PR and ER high-marsh cluster groups (2).

FIGURE 5: DCCA scores represent the length of detrended canonical correspondence analysis (DCCA) axis 1 in units of standard deviation, performed on individual 30 SWLI unit sections in consecutive steps of 5 SWLI for the entire vertical range captured in each marsh. a-c) Impact of SWLI variant on the vertical alignment of samples in the combined dataset (death screened assemblage) and resulting DCCA scores when amalgamating data from sites with different tidal characteristics. a) MTL-MHW; b) MTL-MHHW; c) MTL-HOF; cluster groups as in Figure 4. Peaks in DCCA scores (Turnover) coincide with the transition between high and low-marsh clusters and in the case of a) and b) due to misalignment of the upper samples (false turnover). Similar results are obtained for moving windows with widths of 50 and 60 SWLI units.

FIGURE 6: a-c) Comparison of the progressive update to individual species optima for local (individual marsh) and combined dataset (death screened assemblage limited to 200-120 SWLI). when moving from simple weighted averaging (WA) to more complex weighted averaging partial least squares (WA-PLS).

FIGURE 7: a-b) Fossil foraminiferal assemblage data from cores located proximal to the modern surface transects in a) Pattagansett River marsh Connecticut and b) Elizabeth River marsh N. Carolina (species abbreviations as in Figure 4). Results of modern analogue technique analysis (MAT, chord distance dissimilarity coefficient) where each fossil sample is considered to have a good, close or poor modern analogue within the combined or local datasets if it's calculated „distance' is ≤10th, between 10th-20th and >20th percentiles respectively. Reconstructed palaeomarsh-surface heights within the tidal frame are expressed in MTL-HOF SWLI units for both WA-PLS components 1 and 2 transfer functions for the combined dataset, ± fossil sample specific bootstrap eSEP errors (estimated standard error of prediction) and local dataset, for which eSEP errors are excluded to maintain clarity in the figure.

Fig. 1

Newfoundland: Hynes Brook marsh

transects HB0, HB2

Connecticut: Pattagansett River marsh

transects PR1, PR2

transects ER1, ER2

N. Carolina: El... River marsh

Key to abbreviations:

Sc.	*Scirpus spp.*	*Sp.*	*Spartina patens*
If.	*Iva frutescens*	*Ds.*	*Distichlis spicata*
Jr.	*J. roemerianus*	*Sa.*	*Spartina alterniflora*
+Jr.	Grasses & *J. roem.*	*Sa(s).*	*S. alter.* (stunted)

MTL mean tide level
MHW mean high water
MHHW mean higher high water
AIWW: Atlantic Intracoastal Waterway

beach | salt marsh / sample transect | salt marsh / core site | upland / trees & shrubs | upland / chenier dune | upland / granitic outcrop

Fig. 2

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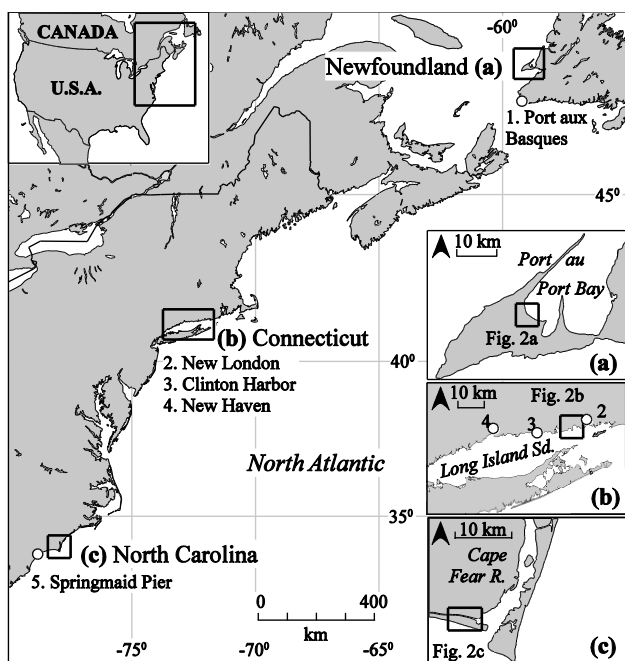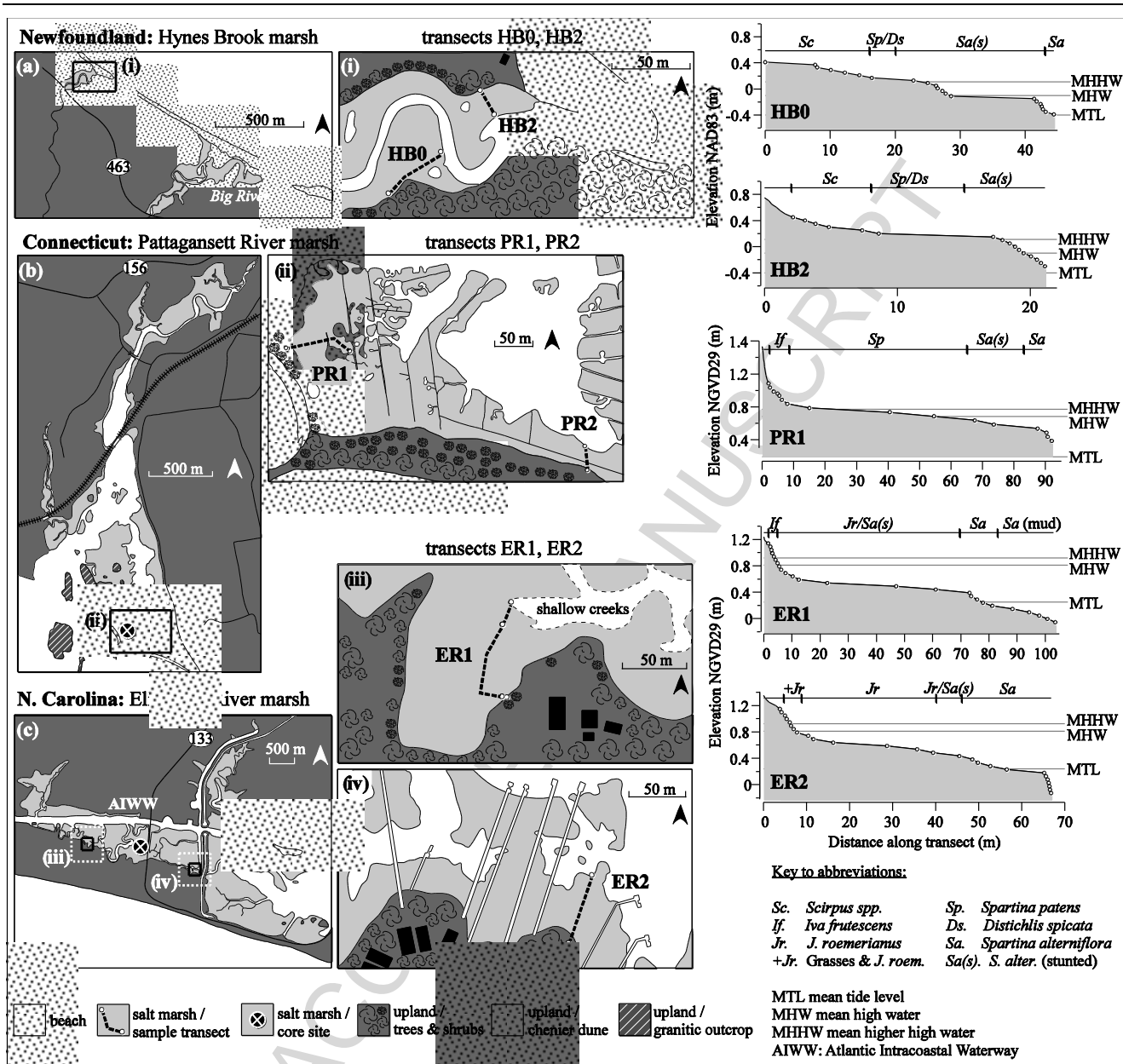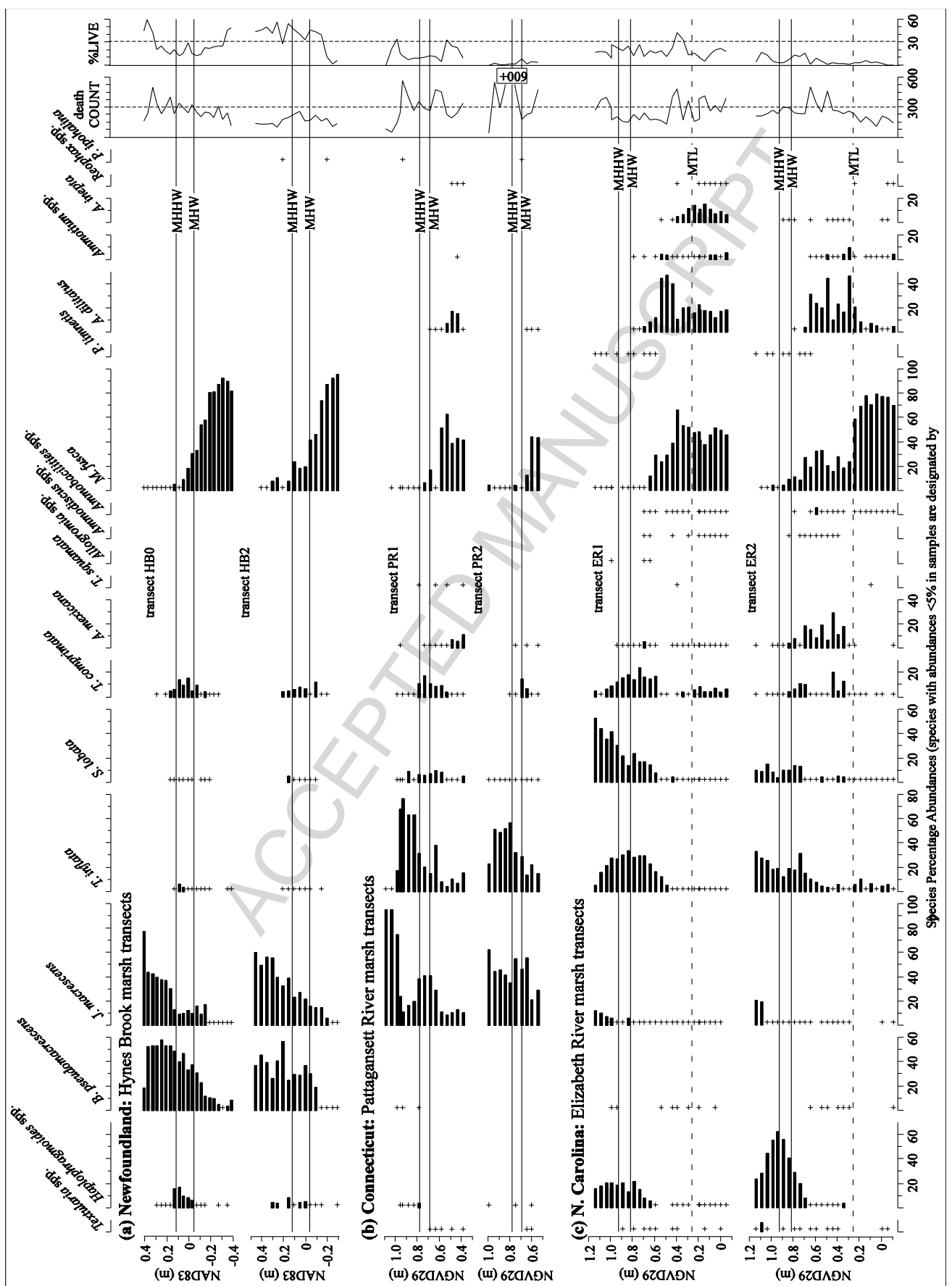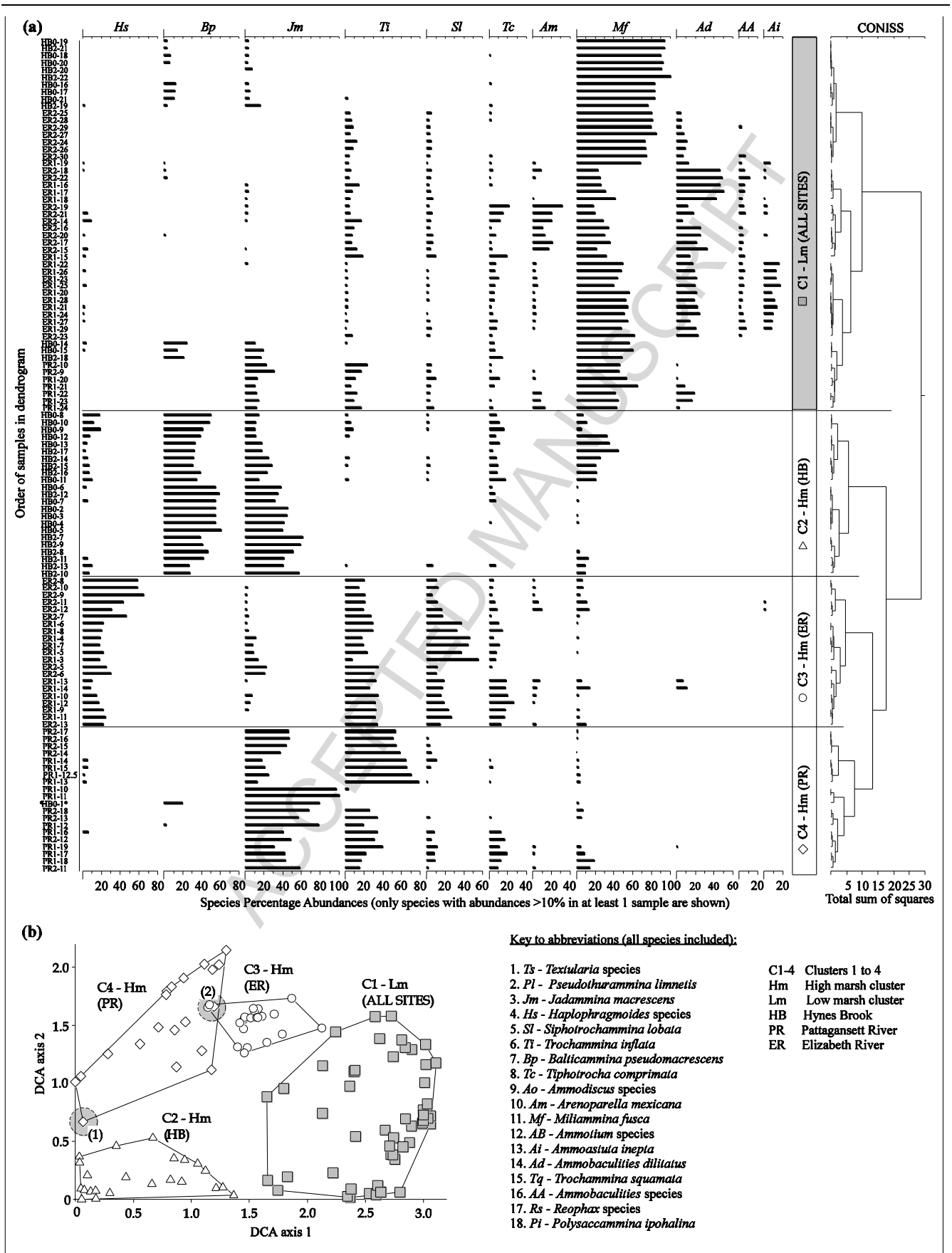Fig. 3

Fig. 4

Fig. 5

Fig. 6

Fig. 7

TABLE 1: Sampling data

Transect	Year	No. T	No. F	No. S	Notes
HB0	1999	21	21	21	Lm
HB2	2001	22	17	16	HOF / Lm
PR1	2001	25	16	16	HOF / Lm
PR2	1999	14	14	10	HOF
ER1-1	2000	17	17	17	Lm
ER1-2	2002	12	11	10	HOF / LM
ER2	2005	30	29	26	HOF / LM

Hynes Brook (HB), Pattagansett River (PR), Elizabeth River (ER) samples 7-23 (ER1-1); samples 1-6 and 24-29 (ER1-2), total number of samples 141 (No. T), 125 with foraminifera and (No. F) 116 after screening 116 (No. S). Highest occurrence of foraminifera captured (HOF), low marsh reached (Lm) or extensively sampled (LM), former codes applied in Edwards et al. (2004a; b) PAT1 (PR1) and PAT2 (PR2). All surface samples were collected during spring or summer fieldtrips, specifically April/May (ER1-1, ER1-2, ER2); June/July (HB0, HB2, PR1, PR2).

TABLE 2: Tidal datums

NEWFOUNDLAND	HOF	MHHW	MHW	MTL	Dist	Notes
Hynes Brook	0.45	0.13	-0.01	-0.40	-	Measured 13 Jul. to 10 Nov. 2001 in Big River marsh (NAD83), MTL the elevation of 50% flood duration.
Port aux Basques	-	1.71	1.64	1.19	-	13 Jul. to 10 Nov. 2001 tide gauge hourly data (CD).
Port aux Basques	-	1.69	1.60	1.16	-	1983-2001 tide gauge hourly data (CD).
*Hynes Brook	0.45	0.11	-0.05	-0.43	-	1983-2001 using vertical offsets (NAD83).
CONNECTICUT						
New Haven	-	1.35	1.26	0.31	69	14 Jun. to 31 Aug. 2002 tide gauge high-low water data
Clinton	-	1.06	0.97	0.28	38	(NGVD29) used to establish linear ‚elevation-distance'
New London	-	0.71	0.62	0.24	0	relationship.
New London	-	0.66	0.57	0.18	0	1983-2001 tide gauge high-low water data (NGVD29).
*Pattagansett River	1.09	0.77	0.68	0.19	12	1983-2001 using linear relationship (NGVD29)
N. CAROLINA						
Elizabeth River	1.14	0.78	0.70	0.13	-	Measured 15 Mar. to 6 May 2001 (NGVD29), MTL the elevation of 50% flood duration.
Springmaid Pier	-	0.90	0.80	0.05	-	15 Mar. to 6 May 2001 tide gauge high-low water data (NGVD29).
Springmaid Pier	-	1.05	0.93	0.16	-	1983-2001 tide gauge high-low water data (NGVD29)
*Elizabeth River	1.14	0.93	0.83	0.24	-	1983-2001 using vertical offsets (NGVD29)

* Final calculation in meters for each marsh investigated for the 1983-2001 National Oceanic and Atmospheric Administration, National Tidal Datum Epoch. Abbreviations include highest occurrence of foraminifera (HOF), mean higher high water (MHHW), mean high water (MHW), mean tide level (MTL), distance from New London tide gauge in kilometres (Dist) North American Datum of 1983 (NAD83), Chart Datum (CD), National Geodetic Vertical Datum of 1929 (NGVD29).

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TABLE 3: DCCA ordinations

SWLI variant	Combined	HB	PR	ER
	Full length			
MTL-MHW	3.5	2.2	1.9	3.0
MTL-MHHW	3.2	2.1	1.9	3.0
MTL-HOF	3.0	2.1	1.9	3.0
% variance	23.4%	60.9%	37.1%	40.1%
	200-120 SWLI limited			
MTL-HOF	2.1	1.9	1.9	2.5
% variance	19.0%	56.2%	37.1%	41.5%

Detrended canonical correspondence analysis (DCCA) axes 1 gradient length results in standard

deviation units for SWLI variants for local (HB, PR, ER) datasets, and when combined for both the full

length and 200-120 SWLI limited datasets (death screened assemblages). The percentage of

species variance explained (% variance) is included for the MTL-HOF variation only and is significant

in each instance (significance tested using 499 unrestricted permutations, reduced model, all P values

reported at 0.002). For other abbreviations see Tables 1 and 2.

TABLE 4: DCA ordination

Axes	1	2	3	4	Total inertia
Eigenvalues	0.630	0.310	0.171	0.105	2.241
species-environment correlations:	3.109	2.146	1.988	2.201	-
Cumulative % variance					
-of species data:	28.1	41.9	49.5	54.2	-
Sum of all eigenvalues:	-	-	-		2.241

Detrended correspondence analysis (DCA) using the full length combined dataset and MTL-HOF

SWLI variant (death screened assemblages, detrending by segments, no data transformation).

TABLE 5: Transfer functions

Parameter	200-120 SWLI limited				Full length		
	Combined	HB	PR	ER	Combined	HB	ER
WA - classical deshrinking							
r^2_{jack}	0.78	0.89	0.74	0.82	0.83	0.91	0.86
RMSEP	11.9	8.15	12.5	11.1	16.0	8.6	16.5
RMSEP [m]	-	[0.07m]	[0.11m]	[0.10m]	-	[0.08m]	[0.15m]
Averge bias$_{jack}$	0.27	0.25	0.90	0.29	0.20	0.19	0.02
Maximum bias$_{jack}$	13.4	11.9	21.4	18.1	28.6	11.2	21.8
WA - classical deshrinking with species tolerance downweighting							
r^2_{jack}	0.80	0.92	0.76	0.82	0.83	0.92	0.85
RMSEP	11.4	6.6	11.3	11.1	16.2	7.8	16.9
RMSEP [m]	-	[0.06m]	[0.10m]	[0.10m]	-	[0.07m]	[0.15m]
Averge bias$_{jack}$	0.31	0.25	0.83	0.43	0.07	0.19	-0.08
Maximum bias$_{jack}$	12.6	9.5	27.9	19.7	25.84	9.02	23.5
WA – inverse deshrinking with species tolerence downweighting							
r^2_{jack}	0.79	0.92	0.76	0.82	0.83	0.92	0.85
RMSEP	10.5	6.5	10.6	10.3	15.0	7.7	15.9
RMSEP [m]	-	[0.06m]	[0.09m]	[0.09m]	-	[0.07m]	[0.14m]
Averge bias$_{jack}$	0.20	0.22	0.54	0.23	0.60	0.17	0.002
Maximum bias$_{jack}$	16.8	11.3	18.6	18.0	34.3	11.3	27.3
WA-PLS C1 – partial least squares component 1 (same as WA with inverse deshrinking)							
r^2_{jack}	0.78	0.89	0.73	0.82	0.83	0.91	0.86
RMSEP	10.8	7.8	11.2	10.4	14.8	8.3	15.6
RMSEP [m]	-	[0.07m]	[0.10m]	[0.09m]	-	[0.07m]	[0.14m]
Averge bias$_{jack}$	0.17	0.19	0.61	0.14	0.18	0.14	0.08
Maximum bias$_{jack}$	17.7	14.3	19.1	16.5	36.4	13.9	27.4
WA-PLS C2 – partial least squares component 2							
r^2_{jack}	0.84	0.94	0.95	0.91	0.85	0.95	0.90
RMSEP	9.2	5.6	6.2	7.3	14.0	6.2	12.8
RMSEP [m]	-	[0.05m]	[0.06m]	[0.06m]	-	[0.05m]	[0.11m]
Averge bias$_{jack}$	0.009	0.25	0.21	-0.01	0.12	0.21	0.04
Maximum bias$_{jack}$	11.7	7.2	8.7	8.4	34.3	8.7	18.2

Summary performance statistics resulting from observed versus transfer function predicted sample elevations using local (HB, PR, ER) datasets, and when combined for both the full length and 200-120 SWLI limited datasets. Transfer functions are all weighted averaging-based (WA) and jack-knife cross-validated ($_{jack}$). Statistical measures are reported in SWLI units including correlation coefficient (r^2_{jack}) with the root mean square of the errors of prediction (RMSEP) additionally back converted to standard units of measure in meters [m].

TABLE 6: Fossil reconstruction

Transfer function	Core	Reconstructed SWLI: local minus combined (avrg. ±stdev.)	Combined SWLI: bootstrap error (avrg. ±stdev.)	Local SWLI: bootstrap error (avrg. ±stdev.)
WA-PLS C1	PX	-2.9 ±1.8	11.2 ±0.1	11.5 ±0.1
WA-PLS C2	PX	-5.3 ±4.2	9.7 ±0.2	10.6 ±0.3
WA-PLS C1	ER-A60	5.3 ±2.4	11.7 ±1.0	11.5 ±0.8
WA-PLS C2	ER-A60	7.7 ±16.4	10.6 ±1.7	10.8 ±2.5
WA-PLS C1	ER-A60 (9-22cm)	7.1 ±2.4	11.2 ±0.1	11.3 ±0.4
WA-PLS C2	ER-A60 (9-22cm)	26.0 ±11.0	9.6 ±0.1	11.8 ±2.3

Bootstrap cross-validated, weighted averaging partial least squares components 1 and 2 (WA-PLS C1, C2) transfer-function reconstructed palaeomarsh-surface heights in SWLI units. Summarised as average (avrg.) and standard deviation (stdev.), having applied and compared the local and combined training sets for the Pattagansett River (PX) and Elizabeth River (ER-A60) fossil records respectively.

Highlights

- High and low-marsh foraminifera assemblages are unique to each site investigated
- Sample elevations are best normalised using the highest occurrence of foraminifera
- Illustrating species (updated) optima simplifies reconstruction interpretation
- It is vital to establish the similarity between modern and fossil assemblages
- Transfer-functions with improved precision are not necessarily more accurate.

Fig. A1

1) *Balticammina pseudomacrescens* — 1a (NF), 1b (NF), 1c (NF), 1d (NC)
2) *Arenoparrella mexicana* — 2a (CT), 2b (CT), 2c (CT)
3) *Textularia* spp. — 3a (CT), 3b (NC)
4) *Eggerella advena* (NF)
5) *Jadammina macrescens* — 5a (NF), 5b (NF), 5c (NF), 5d (CT), 5e (CT), 5f (NC), 5g (NC), 5h (NC)
6) *Reophax* spp. — 6a (NC), 6b (NC)
7) *Haplophragmoides* spp. — 7a (NF), 7b (NF), 7c (CT), 7d (CT), 7e (NC), 7f (NC), 7g (NC), 7h (NC)
8) *Pseudothurammina limnetis* — 8a (NC), 8b (CT), 8c (NC), 8d (NC)
9) *Trochammina inflata* — 9a (NF), 9b (NF), 9c (NF), 9d (CT), 9e (CT)
10) *Siphotrochammina lobata* — 10a (NF), 10b (NF), 10c (CT), 10d (CT)

Fig. A2

1) *Tiphotrocha comprimata*
1a (NC) 1b (NF) 1c (CT) 1d (CT) 1e (NC) 1f (NC) 1g (NC) 1h (NC) 1i (NC)

2) *Miliammina fusca*
2a (NF) 2b (NF) 2c (CT) 2d (CT) 2e (NC) 2f (NC) 2g (NC) 2h (NC) 2i (NC) 2j (NC)

3) *Ammoastuta inepta*
3a (NC) 3b (NC) 3c (NC) 3d (NC)

4) *Ammobaculites spp.*
4a (NC) 4b (NC) 4c (NC) 4d (NC) 4e (NC) 4f (NC) 4g (NC) 4h (NC)

5) *Polysaccammina ipohalina* (NF)

6) *Ammodiscus spp.*
6a (NC) 6b (NC) 6c (NC)

7) *Ammobaculites dilatatus*
7a (NC) 7b (NC) 7c (NC) 7d (NC) 7e (NC) 7f (NC) 7g (NC)

8) *Ammotium spp.*
8a (NC) 8b (NC) 8c (NC) 8d (NC) 8e (NC)

Fig. B1

Newfoundland:
Hynes Brook
transects HB0, HB2

Connecticut:
Pattagansett River
transects PR1, PR2

N. Carolina
Elizabeth River
transects ER1, ER2