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Reconstructing sea-level change in the Falkland Islands (Islas Malvinas) using salt-marsh foraminifera, diatoms and testate amoebae

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Abstract

Proxy records of past sea-level change provide a means of extending sea-level histories from tide gauges into the pre-industrial period. This is especially valuable in the South Atlantic region where sea-level data are limited to only a few tide-gauge records. Multi-proxy approaches to sea-level reconstruction are relatively rare but have distinct benefits when groups of micro-organisms are sparse or under-represented in modern or fossil sediments. Here, we address this challenge by utilising surface foraminifera, testate amoebae and diatoms from a salt marsh at Swan Inlet, East Falkland. All three micro-organism groups occupied distinct vertical niches in the contemporary salt-marsh. We investigated the relative performance of each group of micro-organisms in providing a sea-level reconstruction using individual (group-specific) regression models and with a multi-proxy regression model that combined all three groups. Foraminifera alone were not a suitable proxy. Surveyed sample elevations were closely matched by estimated elevations using

Weighted-Average (WA) and Weighted-Average Partial-Least-Squares (WA- PLS) regressions. Relative sea-level reconstructions were derived by applying each model to microfossil assemblages recovered from a core (SI-2) from the same site. The combined transfer function yielded reconstructive precision (± 0.08 m) comparable to our best single-proxy transfer function (± 0.06 m) but only 17% of palaeo-samples were identified as having “close” or “good” analogues in the combined training data set. We highlight the benefit of a pragmatic approach to sea-level reconstructions whereby additional proxies should be employed if the use of only one proxy performs poorly across the width of the elevation gradient.

Keywords: South Atlantic; Sea Level Reconstruction; Transfer functions; Falkland Islands

1. Introduction

Proxy records of past sea-level change provide a means of extending sea-level histories from tide gauges into the pre-industrial period. Such proxy-based sea-level reconstructions make use of the micro-fauna that inhabit intertidal sediments as indicators of (palaeo)sea level. The most widely used microfossil proxy indicators are foraminifera (Scott et al., 1984; Gehrels, 1994; Gehrels et al., 1996, 2008, 2012; Kemp et al., 2013), diatoms (Hill et al., 2007; Szkornik et al., 2008; Woodroffe & Long, 2009; Barlow et al., 2014) and, to a lesser extent, testate amoebae (Charman et al., 1998, 2010; Barnett et al., 2015). These three groups of micro-organisms exhibit a consistent and quantifiable vertical zonation related to tidal influence in contemporary tidal marsh environments. Critical for the success of proxy reconstructions of sea-level change is that these micro-organisms are readily preserved in coastal sediments (Scott &

Medioli, 1978; Palmer & Abbot, 1986; Charman et al., 1998). In order to achieve robust microfossil-derived sea-level reconstructions, an understanding of the contemporary distributions of microfaunal assemblages in tidal marshes and quantification of their vertical relationship to sea level (termed the indicative meaning; IM) is required (van de Plassche, 1986; Shennan et al., 2015). These integrated assemblage-elevation data are collectively termed a 'training set'. Recent studies have used advanced statistical regression techniques to model the contemporary species-environment relationship of microfaunal assemblages to produce so-called transfer functions (see Telford and Kemp (2015) for a review). Transfer functions are equations that model the modern species-environment relationship which can be applied to generate quantitative environmental reconstructions based on fossil species data (Birks et al., 2010). The environmental variable of interest in sea-level studies is tidal marsh surface elevation. Transfer functions therefore permit quantitative reconstruction of the IM for microfossil samples providing estimates of palaeo-marsh surface elevation (PMSE). These PMSE estimates can then be converted to sea level by subtracting the transfer function-derived IM from the surveyed height of the fossil sample (e.g., Gehrels, 1999).

The purpose of this paper is to assess the suitability of foraminifera, testate amoebae and diatoms, both as stand-alone groups and collectively, to serve as sea-level proxies in the Southern Atlantic Ocean. The reconstructive precision of each individual proxy usually ranges from ±20cm to ±5cm, depending on the local tidal range (Zong & Horton, 1999; Gehrels, 2000; Charman *et al.*, 2010; Barlow et al., 2013). This study represents the first multi-proxy investigation of salt-marsh sea-level indicators in the Southern Hemisphere, an important region for understanding the global sea-level budget because of sparsity of tide-gauge data (Frederikse et al. 2018) as well as for detecting the contribution of Northern Hemisphere land-based ice melt to recent sea-

level change (Kopp et al. 2010; Gehrels et al. 2012). Furthermore, Holocene sea-level reconstructions from stable coastal areas in the South Atlantic Ocean are relatively rare. The thick sequences of salt-marsh sediments preserved in the Falkland Islands provide an opportunity to establish high-quality sea-level reconstructions spanning most of the Holocene.

Previous studies from the North Altantic region suggest that for any specific area the most accurate PMSE estimates may be achieved by combining foraminifera, diatoms and/or testate amoebae into a single transfer function (Gehrels et al., 2001; Kemp et al., 2009; Elliot, 2015). We test this by assessing the reconstructive ability of each group of micro-organisms in individual transfer functions compared with a multiproxy transfer function which combines all three groups.

2. Materials and methods

2.1 Study site and field sampling

Samples were collected from a salt marsh located on the banks of Swan Inlet (51°49'31S, 58°35'46W) in East Falkland, around 53 km southwest of the Falkland Islands' capital Stanley (Figure 1). At Swan Inlet a microtidal (mean tidal range: 0.7 m; spring tidal range: 1.1 m) salt marsh occupies the interface between the open estuary and freshwater valley-bottom marshes (Figure 1). This is the largest (~1.5 km^2) and best developed salt marsh in the Falkland Islands. There are four dominant vegetation zones at Swan Inlet. The uppermost marsh is dominated by *Cortaderia pilosa* (Falkland Island Whitegrass) which transitions to a *Festuca magellanica* (Fuegan

Fescue) dominated zone. At a break in slope, the mid-marsh zone is dominated by *Deschampsia antarctica* (Antarctic Hair-grass) and then a *Rostokovia magellanica* (Short or Brown Rush) dominated zone which marks the transition from salt marsh to mudflat. We established three surface sampling transects encompassing the range of vegetation zones (Figure 1). No nearby geodetic benchmark is available at Swan Inlet. Therefore, a benchmark was established at the edge of the salt marsh by planting a survey pin into the ground where the substrate was resistant to compaction(51°48'15.5 S, 58°35'41.7 W) from which relative elevations were measured. We refer to this benchmark as Swan Inlet Datum (SID). Using a differential Global Positioning System (dGPS) we determined that SID is 14.346 m above the reference WGS84 ellipsoid. Tidal datums (Table 1) were established by interpolation from Admiralty Tide Table data for Port Stanley. Differences in tidal magnitude between Port Stanley and Swan Inlet were established from measurements recorded with pressure transducers contemporaneously submerged for 1 week at both locations. A total of 49 surficial (0-1 cm) sediment samples were collected at ~4 cm elevational increments spanning the high and low marsh zones and into the tidal mudflat (Figure 2).

Table 1: Tidal datums at Swan Inlet relative to Swan Inlet Datum (m SID). MTL = mean tide level, MHHW = mean highest high water, MLLW = mean lowest low water, HAT = highest astronomical tide. HAT* was estimated from tidal predications (Admiralty Tide Tables, 2016) for Mare Harbour (Figure 1) based on the difference between HAT and MTL predictions.

MTL	MHHW	MLLW	HAT*
-1.89	-1.51	-2.09	-0.97

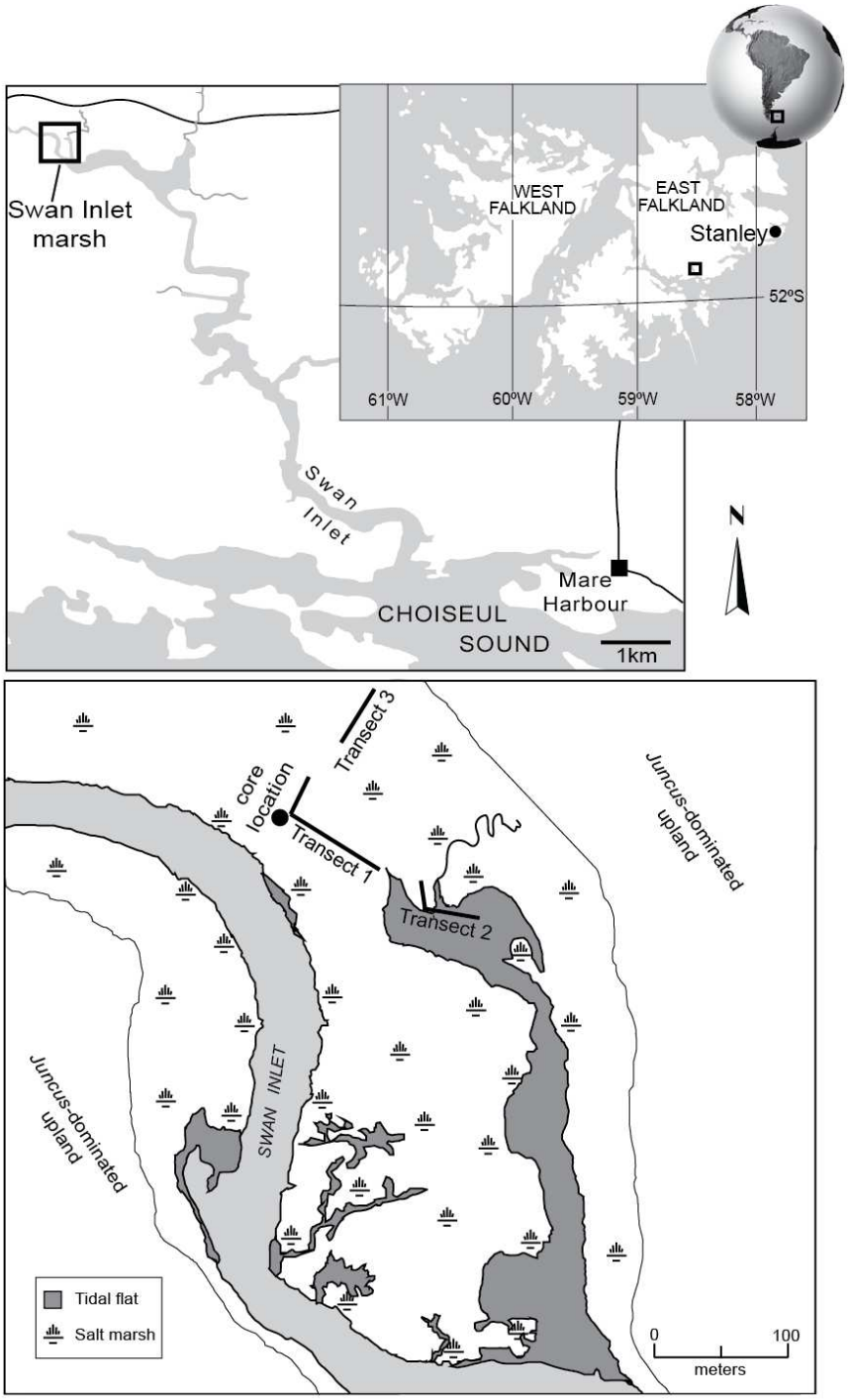

Figure 1: [top] Location of the Falkland Islands and the study site at Swan Inlet. [bottom] Schematic map of marsh sub-environments and surface transect locations.

2.2 Microfaunal analyses

Foraminifera samples were initially stained with rose Bengal in order to discriminate between individuals that were living or dead at the time of collection (Walton, 1952). Samples were processed and counted (minimum 150 individuals) following the standardised methods of Gehrels, Roe & Charman (2002). Our foraminiferal taxonomy follows Murray (2000) for common intertidal taxa and Cushman & Brönnimann (1948) for taxa specific to the Southern Hemisphere.

Testate amoebae were stained as above and samples were prepared following the standard methods employed in peatland studies (Charman et al., 2000). Studies of salt-marsh testate amoebae have experienced difficulties due low test concentrations and specimens being obscured by minerogenic particles. Charman et al. (2010) and Barnett et al. (2013) attempted to optimise the preparation procedure by using a mild alkali treatment and repeated micro-sieving. Our samples contained relatively high test concentrations and were low in minerogenic material. Therefore, we avoided the risk of damage to specimens by opting against a chemical pretreatment. Samples were counted until a minimum of 100 tests had been reached (cf. Payne and Mitchell, 2009). Specimens were identified under light microscopy (400x magnification) following the classification of Charman *et al.* (2000) with reference to salt-marsh specific taxa described in Charman *et al.*, (2002). In this study we only consider dead foraminiferal and testate amoebae assemblages on the premise that death assemblages represent an assembly of tests that are time-averaged and are therefore more likely to provide the closest analogues for the fossil assemblages employed in sea-level reconstruction (Horton, 1999).

Diatom preparation followed a slight modification of the standardised procedures outlined in Palmer and Abbott (1986) and Battarbee et al., (2001). Our only modification was to replace the centrifugation stage with successive manual decantations in the interest of reducing valve breakage (cf. Blanco, Alvarez & Cejudo, 2008). Diatoms were identified, where possible, to species and sub-species level under light microscopy (1000x magnification) primarily following the taxonomy of Krammer and Lange-Bertalot (1991a, 1991b, 1997a, 1997b). For each sample a minimum of 300 diatom valves were counted. It is assumed that the surficial (0-1cm) diatom assemblage encompasses several seasonal cycles, thus negating bias related to seasonal blooms in diatom species (Zong & Horton, 1999).

2.3 Data analyses

We applied a suite of statistical methods to model the contemporary species-environment relationship for each microorganism group and a combined dataset comprising all groups. Our initial assessment was to determine the species distribution along the environmental gradient (elevation) through detrended canonical correspondence analysis (DCCA; Birks,1995) performed in the program CANOCO for Windows version 4.5.6 (ter Braak, 1995). We employed constrained incremental sum-of-squares cluster analysis based on unweighted Euclidean distance (no data transformation) to determine the species vertical zonation across the marsh surface. Cluster analysis was performed using CONISS (Grimm, 1987) based on computations performed with the TILIA for Windows v. 1.7 program (Grimm, 1990). Before modelling our data for the development of transfer functions the assemblage data were subjected to screening in order to remove anomalous species data and thus improve accuracy in the reconstructive ability of the transfer function. The screening involved the use of raw species counts for all microorganism groups to calculate the fractional abundance

of each taxonomic unit (Patterson & Fishbein, 1989). Following Wright *et al.* (2011), the minimum fractional abundance (i.e. 5% is 0.05) was computed at the 95% confidence level using **eq. 1** (Fatela & Taborda, 2002):

Equation 1

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

p - minimum fractional abundance acceptable for a species

n – total number of individual specimens counted

f – specified confidence level

All species within a sample were deemed to have been sufficiently detected if fractional abundances exceeded this level. Species with fractional abundances below this level are determined to be insufficiently captured and are therefore omitted from the training sets for subsequent analysis. Our transfer functions were constructed based on regression analysis performed with the Rioja package in *R* (Juggins, 2015). We assess the predictive ability of each transfer function model using the bootstrapping cross-validation technique (10000 permutations; Birks, 1995) to calculate the root mean squared error of prediction (RMSEP, given in the same units as the environmental variable i.e. meters) and coefficient of determination (r^2_{boot}) following Barlow et al. (2013). There is no consensus approach for identifying outlier samples (Barlow et al. 2013), but here we employ a conservative approach (c.f. Juggins and Birks, 2012) defining outliers as samples with standardised residuals (under internal cross-validation (CV)) greater in absolute value than 2 (i.e. 5% of the expected distribution of observations).

3. Results and discussion

An overall vertical succession of testate amoebae, diatoms and foraminifera, from the highest sampled elevation (0.64 m SID) to the lowest mudflat (-1.94 m SID) elevations, is observed at Swan Inlet (Figure 2). Testate amoebae demonstrate a narrow vertical zonation but only occupy the highest elevations of the marsh, between MHHW and 0.3 m above HAT, in the zone dominated by *Cortaderia pilosa* and *Festuca magellanica*. For unknown reasons diatoms are scarce in the zone where testate amoebae are most abundant, but it is noted that their absence is constrained to elevations above HAT. Despite this, diatoms occupy the greatest elevation range, overlapping with the lowest zone of testate amoebae occurrence and the entire range of foraminiferal occurrence. Only four taxa of foraminifera were present.

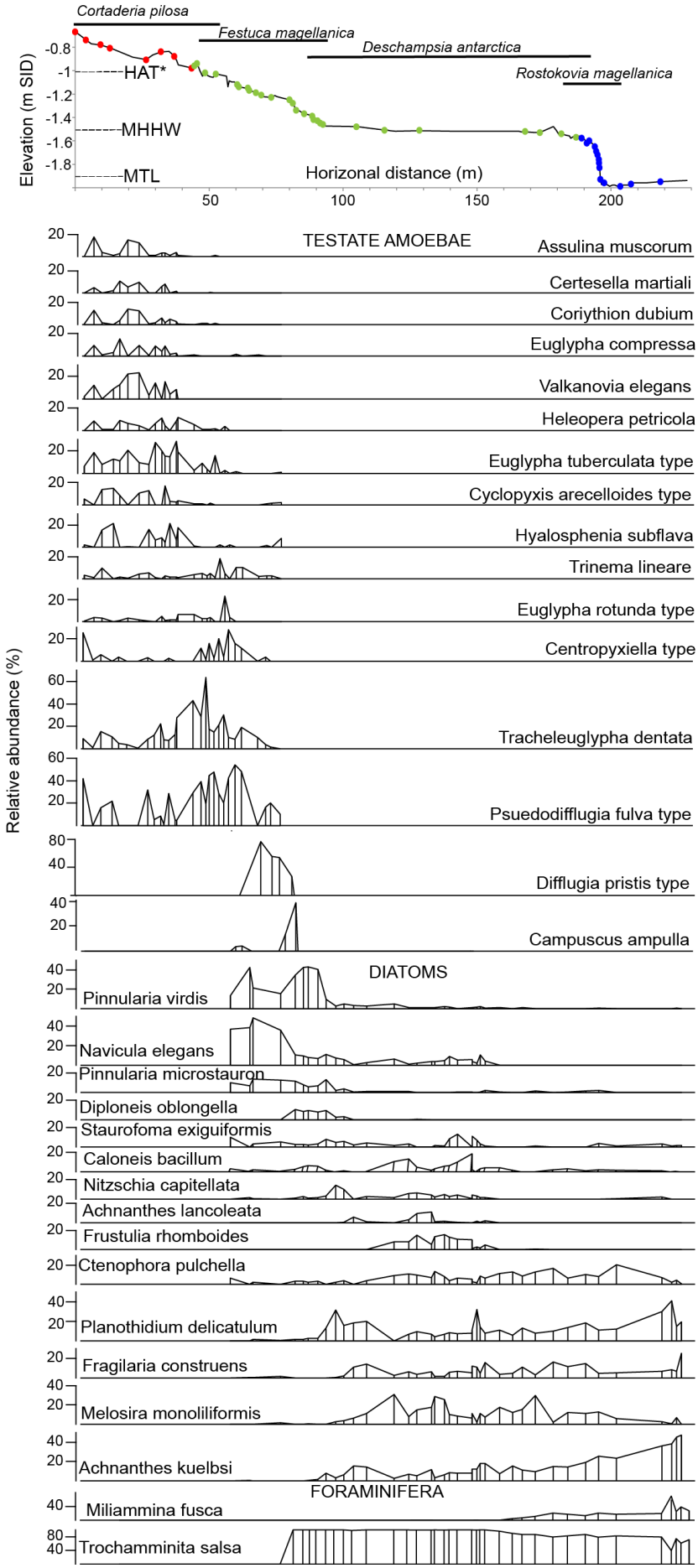
Cortaderia pilosa
Festuca magellanica
Deschampsia antarctica
Rostokovia magellanica
Elevation (m SID)
-0.8
-1
-1.2
-1.4
-1.6
-1.8
HAT*
MHHW
MTL
Horizonal distance (m)
50
100
150
200
TESTATE AMOEBAE
Assulina muscorum
Certesella martiali
Coriythion dubium
Euglypha compressa
Valkanovia elegans
Heleopera petricola
Euglypha tuberculata type
Cyclopyxis arecelloides type
Hyalosphenia subflava
Trinema lineare
Euglypha rotunda type
Centropyxiella type
Tracheleuglypha dentata
Psuedodifflugia fulva type
Difflugia pristis type
Campuscus ampulla
DIATOMS
Pinnularia virdis
Navicula elegans
Pinnularia microstauron
Diploneis oblongella
Staurofoma exiguiformis
Caloneis bacillum
Nitzschia capitellata
Achnanthes lancoleata
Frustulia rhomboides
Ctenophora pulchella
Planothidium delicatulum
Fragilaria construens
Melosira monoliliformis
Achnanthes kuelbsi
FORAMINIFERA
Miliammina fusca
Trochamminita salsa
Relative abundance (%)

Figure 2: Marsh surface topography with dominant vegetation and distributions of dominant microorganisms. Points on transect represent sampling locations from transect 1 (green), transect 2 (blue) and transect 3 (red).

3.1 Testate amoebae distributions

A total of 24 testate amoebae taxa were present in significant counts in 28 samples from -0.64 m SID to -1.4 m SID (0.76 m range). The distribution of the testate amoebae abundances is shown in Figure 3. Cluster analysis identified four major testate amoebae zones (TZ) within the species distributions. The uppermost high-marsh zones group into two clusters (*TZ-I* and *TZ-II*). These zones comprise the most diverse assemblages with 17 taxa having occurrences in these zones. The majority of samples (n=11) in *TZ-I* and *TZ-II* are from marsh levels above the limit of HAT. No taxa have a particular dominance within zones *TZ I* and *TZ II* with the assemblages being characterised by varying abundances of *Euglyphid* taxa (*Euglypha tuberculata* type*, Euglypha compressa* type*, Assulina muscorum, Valkanovia elegans*) and *Hyalosphenia subflava, Heleopera petricola, Cyclopyxis arcelloides* type*, Corythion dubium, Trinema complantanatum, Pseudodifflugia fulva* type *and Certesella martiali.* With the exception of *Pseudodifflugia fulva* type*,* which has not previously been reported in salt marshes, and *Certesella martiali* (Certes, 1888)*,* which is restricted to the southern hemisphere (Loeblich & Tappan, 1961; Meisterfeld & Mitchell, 2008) this an assemblage broadly similar to high marsh zones in the North Atlantic (Charman *et al.,* 1998; Gehrels *et al.,* 2001; Charman *et al.*, 2002, 2006; Gehrels *et al.,* 2006; Charman *et al.,* 2010; Barnett *et al.,* 2013, 2017). There is a general reduction in

species diversity toward lower elevations. The lowest elevations of testate amoebae occurrences group into two clusters (*TZ-III* and *TZ-IV*) is dominated by *Tracheleuglypha dentata* and *Pseudodifflugia fulva* type*,* which reach their peak abundances in these zones. The lowermost elevations (*TZ-IV*) are characterised by a dominance of *Difflugia pristis* type and *Cyphoderia ampulla* and *Pseudohyalosphenia* sp*.* (Barnett *et al.,* 2017) which have their distributions almost entirely within this zone. These lowermost taxa are also typically found in the lowest zone of testate amoebae occurrence in the North Atlantic (references above).

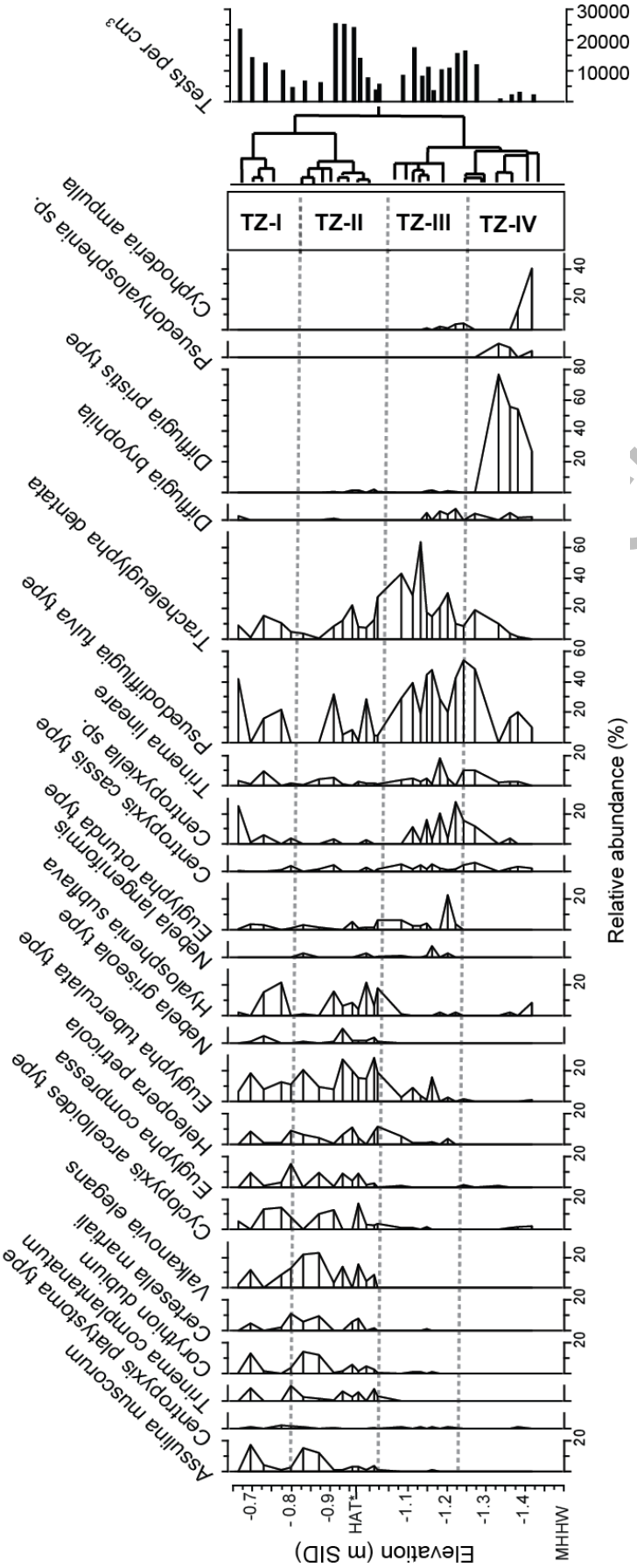
Tests per cm³
30000
20000
10000
TZ-I
TZ-II
TZ-III
TZ-IV
Cyphoderia ampulla
Pseudochlamydophrys sp.
Difflugia bryophila
Difflugia pristis type
Trachelleuglypha dentata
Pseudodifflugia fulva type
Trinema lineare
Centropyxiella sp.
Centropyxis cassis type
Centropyxis rotunda type
Nebela langeniformis
Nebela subflava
Hyalosphenia type
Nebela griseola type
Nebela tubercullata type
Euglypha petricola
Heleopera compressa
Euglypha arcelioides type
Cyclopyxis elegans
Valkanovia martiali
Centropyxis dubium
Corythion complanatum
Trinema type
Centropyxis platystoma type
Assulina muscorum
Relative abundance (%)
Elevation (m SLD)
-0.7
-0.8
-0.9
HAT
-1.1
-1.2
-1.3
-1.4
MHHW

Figure 3: Testate amoebae distributions and CONISS determined cluster zones.

3.2 Testate amoebae transfer functions

The testate amoebae were interpreted to be responding unimodally along the elevation gradient of the Swan Inlet marsh, i.e. they have an optimal occurrence and their abundance declines either side of the optimum (Shelford, 1931). This was demonstrated by the DCCA analysis (Table 1), which returned an axis 1 gradient length of 3.417 standard deviation units (SD). A full turnover of species along the environmental gradient is represented as 4 SD units. As a general rule-of-thumb, species are deemed to be responding unimodally if gradient lengths are >2 and transfer functions based upon unimodal regression models are most appropriate (ter Braak, 1986; Birks, 1995). Elevation is shown to be the dominant variable governing the testate amoebae distribution at Swan Inlet accounting for >59% of the species variance (Table 2). We only consider models based on weighted averaging (WA) and weighted averaging partial least squares (WAPLS) regression as these unimodal models are considered simple, robust and ecologically plausible (Birks, 1995; 2010) and are also widely used in sea-level studies (Barlow et al., 2013 and references within).

Table 2: Results of DCCA analysis on the testate amoebae training set. The canonical axis (Axis 1) represents the species response to elevation (gradient length measured in SD units) and the amount of assemblage variation explained by elevation. All other axes show the species response and amount assemblage variation related to other (unmeasured) environmental variables.

	Axis 1	Axis 2	Axis 3	Axis 4
Gradient Length	3.417	2.499	1.565	1.536
Proportion of variance	0.596	0.244	0.098	0.076

Number of samples	28
Number of taxa	24
Significance (p value)	0.002

Following data-screening, one taxon *Arcella discoides* (4 occurrences <3% relative abundance) was removed from the training set as this was deemed to be insufficiently detected (Eq. 1). We employ an iterative approach to identify the best transfer function from our testate amoebae training set. No outliers were identified in the initial set of transfer functions that were generated. Therefore, the testate amoebae training set comprising 28 samples and 23 taxa was used to produce the transfer function models. We recognise that this training set has a small sample size, as such results should be interpreted with caution. Despite the small sample size, because the upper and lower marsh limits of testate amoebae are established (i.e. the full gradient is sampled) we suggest this training set is potentially useful to sea-level studies in the Falkland Islands. Summary statistics for all models are presented in Table 3.

In this study we primarily use RMSEP and $R^2_{(boot)}$ as our metrics of transfer function performance (Birks, 1998; Barlow et al., 2013) and in each case seek to identify the 'minimal adequate model' (Birks, 1998). Based on these criteria, the best performing transfer function using all 28 samples was the tolerance downweighted WA model with inverse deshrinking (WATOL INV) as it demonstrated the most significant correlation between observed and predicted values ($R^2_{(boot)}$ 0.65 : Figure 4) and was capable of reconstructing marsh surface elevation to within 0.13m (RMSEP Table 3). We tested the ability of the transfer function to predict the elevation of a known reference by calibrating the elevation of the assemblage in the 0 cm sample (-1.03 m SID) of a core taken at Swan Inlet (Figure 1). The transfer function performed well in this assessment

returning a reconstructed elevation of -1.00 m SID which is within 0.03 m (under-prediction) of the surveyed elevation of the sample.

While the WATOL INV model performed the best, all the models (WA and WAPLS) exhibited a deflection in the linear spread of data at the upper end of the elevation range (Figure 4). The samples that contributed to this deflection were the four uppermost marsh surface samples from Transect 3 (Figure 2). These samples span an elevation range -0.75m to -0.64m relative to SID. This is 0.22 to 0.33m above the HAT (-0.97m; Table 1) and 0.76 to 0.87m above MHHW (-1.51m; Table 1). Two of those four samples have residual errors under internal cross validation that are >0.2m (half the standard deviation of the environmental gradient; Figure 4). All other samples within the WATOL INV model have prediction residuals within 0.2m of the observed elevation. We note that if less conservative outlier removal criteria are employed (e.g. Edwards, 2004) and the two samples whose residuals are greater than half the standard deviation of the environmental gradient are removed, then the RMSEP and $R^2_{(boot)}$ improve to 0.09 and 0.81 respectively (WA inverse deshrinking). Removal of all four samples yields substantial improvement in model performance in comparison with the use of all 28 samples (RMSEP = 0.07, $R^2_{(boot)}$ = 0.86 using WATOL INV; Table 4; Figure 5). Testate amoebae are widespread organisms in wetland environments and it is most likely that, at these high elevations above the HAT, their community assemblage may be more affected by other environmental factors such as precipitation-driven soil moisture content, changing salinity and pH value (Charman et al., 2002; Barnett et al., 2016). While we have no reason to omit these samples based on other criteria (e.g. unusual assemblages), the distance of the samples above HAT and the improvement in predictive performance from this intervention (Table 4; Figure

5) supports use of the model WATOL INV with the upper marsh samples removed (n=24) as our final testate amoebae transfer function.

Table 3: Summary performance statistics of weighted averaging (WA) and weighted averaging partial least squares (WAPLS) regression models applied to the testate amoebae training set using all 28 samples.

Model	RMSE	R^2	$R^2_{(boot)}$	RMSEP
WAPLS Component 1	0.12	0.69	0.60	0.14
WAPLS Component 2	0.10	0.76	0.60	0.15
WAPLS Component 3	0.10	0.79	0.60	0.18
WA (inverse deshrinking)	0.12	0.69	0.60	0.14
WA (classical deshrinking)	0.14	0.69	0.61	0.18
WA (tolerance downweighted, inverse deshrinking)	**0.11**	**0.73**	**0.65**	**0.13**
WA (tolerance downweighted, classical deshrinking)	0.13	0.73	0.66	0.15

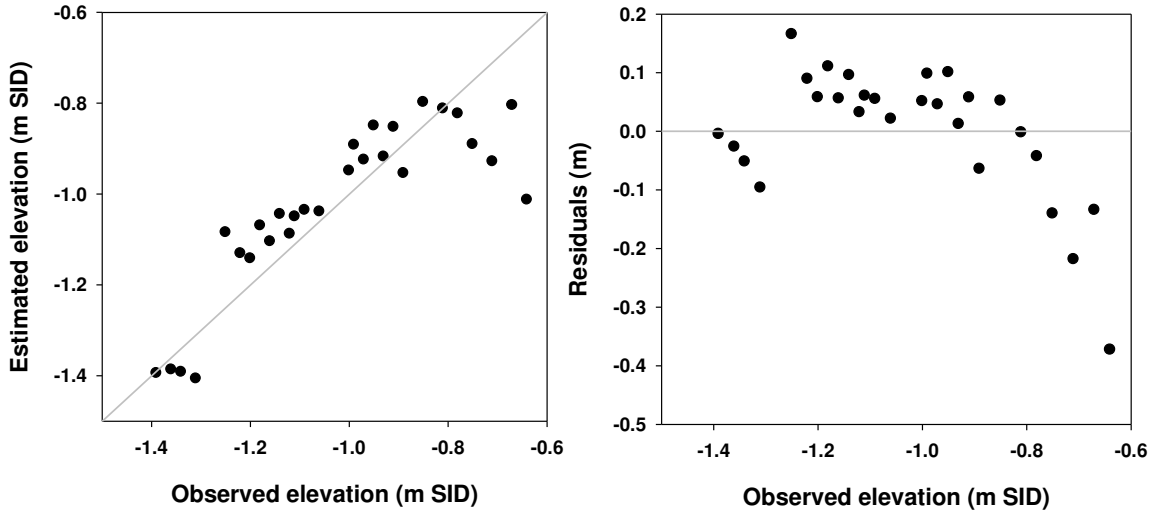

Figure 4: Scatterplots of observed vs predicted elevation (left) and observed elevation against prediction residuals (right) for the WA tol-inv testate amoebae transfer function using all 28 samples.

Table 4: Summary performance statistics of weighted averaging (WA) and weighted averaging partial least squares (WAPLS) regression models applied to the testate amoebae training set after removal of 4 upper marsh samples (n = 24)

Model	RMSE	R^2	$R^2_{(boot)}$	RMSEP
WAPLS Component 1	0.06	0.90	0.84	0.08
WAPLS Component 2	0.05	0.91	0.82	0.08
WAPLS Component 3	0.05	0.93	0.80	0.09
WA (inverse deshrinking)	0.06	0.90	0.83	0.08
WA (classical deshrinking)	0.06	0.90	0.84	0.08
WA (tolerance downweighted, inverse deshrinking)	**0.05**	**0.91**	**0.86**	**0.07**
WA (tolerance downweighted, classical deshrinking)	0.06	0.91	0.86	0.07

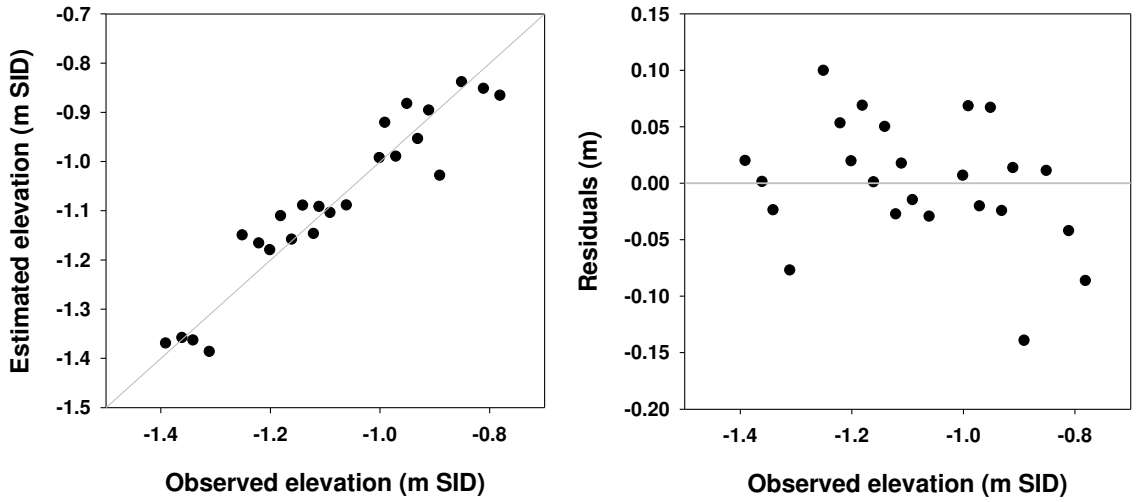

Figure 5. Scatterplots of observed vs predicted elevation (left) and observed elevation against prediction residuals (right) for the WA tol-inv testate amoebae transfer function after removal of 4 upper marsh samples (n = 24)

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3.3 Diatom distributions

Sufficient numbers of diatoms to meet the requirements of Eq. 1 were counted in 39 samples spanning an elevation range of 0.99 m, from -0.95 m SID on transect 2 down to our lowest sampled sub-environment (-1.96 m SID, transect 1). In total 60 taxa were identified in the 39 samples analysed. The results of the cluster analysis determined three distinct zones (Figure 6). The zone of the highest occurrence of diatoms (*SID I*) is dominated by the typically freshwater-brackish *Pinnularia* taxa and *Navicula elegans.* These taxa count for up to 90% of the total relative abundance of diatom assemblages within zone *SID I,* which is characterised by relatively low species diversity compared to other zones. The largest zone, in the middle marsh (*SID II)* from

1.80 – 1.30 m (CD), represents the most diverse and species rich diatom assemblages. All 32 of the dominant taxa occur in significant numbers (>2% relative abundance) in zone *SID II.* This zone is dominated by five taxa; *Ctenophora pulchella, Melosira monililiformis, Planothidium delicatulum, Fragilaria consrtruens* and *Achnanthes kuelbsii*, which fluctuate in relative abundance throughout but account for up to 85% of the total assemblages within this zone. There are also a number of non-dominant taxa that have their entire distribution within zone *SID II e.g. Frustulia rhomboides* and *Achnanthes lanceolata.* The low-marsh zone (*SID III)* is characterised by a decline in overall species diversity, although, the same five dominant taxa from zone *SID II* also dominate this zone. The brackish species *Planothidium delicatulum* and *Achnanthes kuelbsii* both reach their peak abundances toward the lower limit of this zone where tidal influence is greatest.

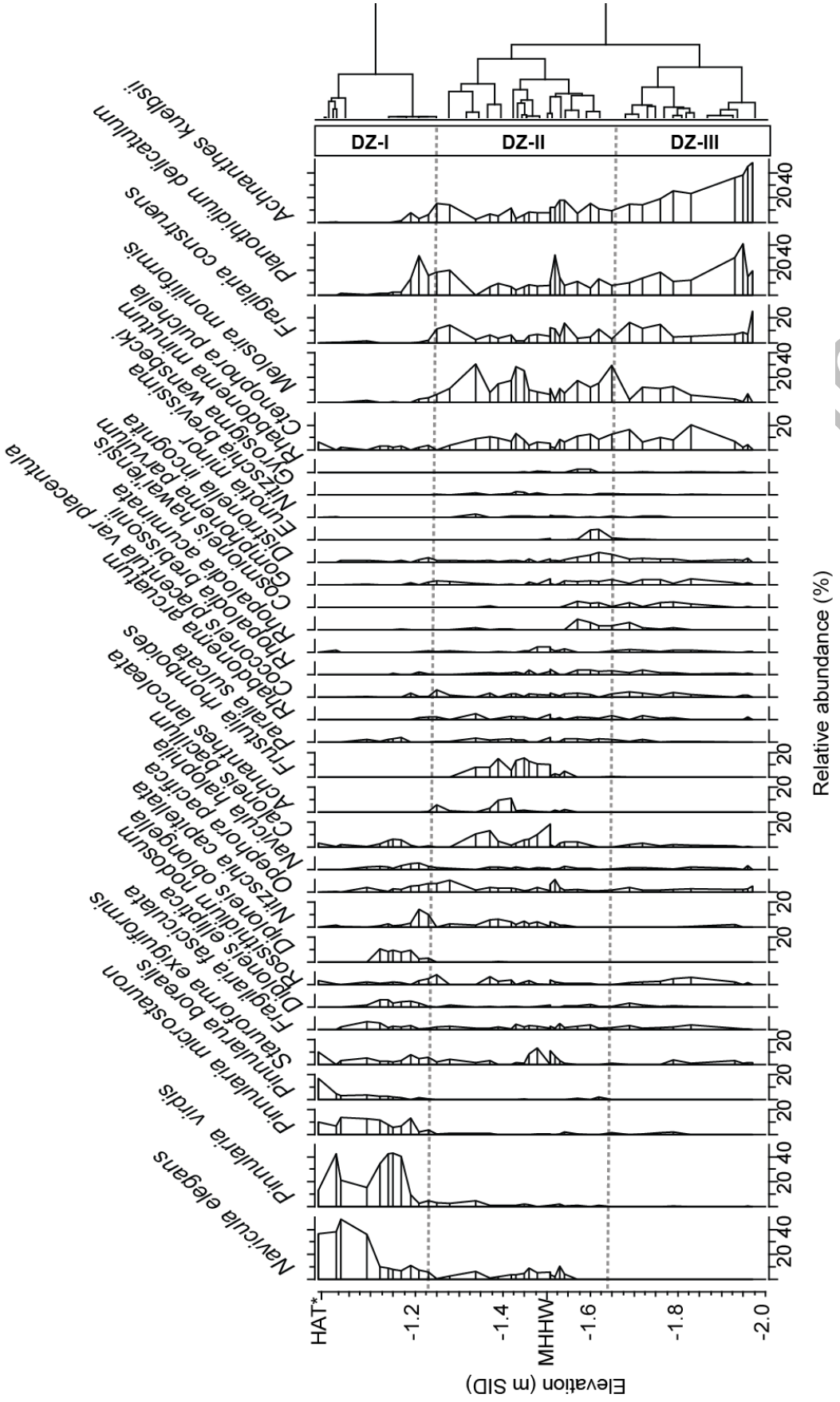

Figure 6: Dominant diatom distributions and CONISS cluster zones.

3.4 Diatom transfer function

After data screening and removal of insufficiently detected taxa following *Eq. 1*, a total of 32 taxa in 39 samples were used in subsequent gradient analysis and the transfer function development. The results of the DCCA (Table 5) indicate that the diatoms exhibit a unimodal response to elevation with a gradient length of 3.373 SD units. The canonical axis score for elevation (Axis 1, Table 5) demonstrates that elevation is the dominant environmental variable governing the diatom assemblage distributions, explaining 61.4% of the variance.

Table 5: Results of DCCA analysis on the diatom training set.

	Axis 1	Axis 2	Axis 3	Axis 4
Gradient Length	3.373	1.550	1.180	0.095
Proportion of variance	0.614	0.143	0.056	0.027

Number of samples	39
Number of taxa	32
Significance (p value)	0.002

In light of the DCCA we applied the same unimodal regression models as we used for the testate amoebae training set. Following the same method outlined earlier (Edwards et al. 2004), two outlier samples from transect 1 at -1.25 and -1.22m SID were removed from the training set. The removal of these two samples is further justified based on field observations related to the position on the salt-marsh from

which they were recovered. These samples were taken either side of a small creek which intersects the transect. Consequently, the diatom assemblages in these samples may be responding more strongly to local environmental variables associated with the creek (e.g. salinity or pH) than elevation, or could have been washed in through the creek, and are therefore anomalous of the species-elevation relationship governing diatom assemblages in the rest of the training set.

Our final diatom training set comprises 37 samples. The performance of the training set is statistically summarised Table 6. The WAPLS Component 3 model produces the most precise and appropriate transfer function for the diatom training set being capable of predicting marsh surface elevation to within 0.06m. The scatterplot of observed vs predicted values (Figure 7) produced by the WAPLS Component 3 model demonstrates the significance of this correlation ($R^2_{(boot)}$ 0.96). The choice of the component 3 model introduces greater statistical complexity than component 2 (Wright *et al.* 2011) but is justified on the basis of a >5% improvement in the RMSEP (Birks, 1998; Barlow et al., 2013; Table 2). By way of demonstration, the component 4 model yields no performance improvement in $R^2_{(boot)}$ and a worse performance in RMSEP (Table 6). The final test demonstrates the applicability of our diatom transfer function for sea-level studies in the Falkland Islands with the model (over)predicting the core top to within 0.025m which is more precise than the overall RMSEP for this model (± 0.06m).

Table 6: Summary performance statistics of weighted averaging (WA) and weighted averaging partial least squares (WAPLS) regression models applied to the diatom training set.

Model	RMSE	R^2	$R^{2\ (boot)}$	RMSEP	% change
WAPLS Component 1	0.10	0.87	0.84	0.12	0
WAPLS Component 2	0.06	0.96	0.94	0.07	37.82
WAPLS Component 3	**0.04**	**0.98**	**0.96**	**0.06**	**12.99**
WAPLS Component 4	0.04	0.98	0.96	0.07	-4.69
WA (inverse deshrinking)	0.10	0.87	0.84	0.12	
WA (classical deshrinking)	0.11	0.87	0.84	0.13	
WA (tolerance downweighted, inverse deshrinking)	0.09	0.90	0.86	0.10	
WA (tolerance downweighted, classical deshrinking)	0.10	0.90	0.86	0.10	

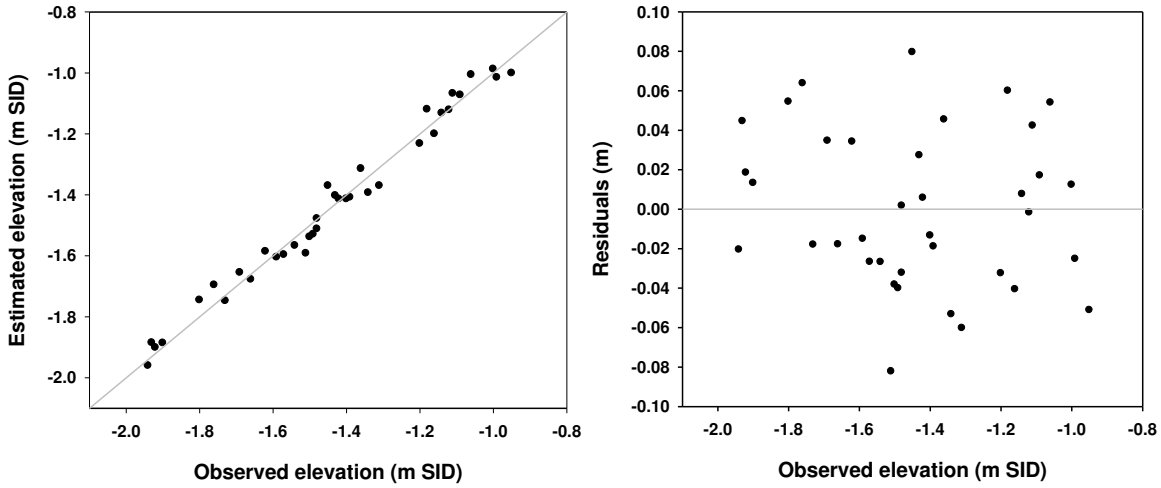

Figure 7: Scatterplot of observed vs predicted elevation (left) and observed elevation against prediction residuals (right) for the WAPLS Component 3 diatom transfer function

3.5 Foraminiferal assemblages

Foraminifera were present in significant abundance in 35 samples from the lowest mudflat environment up to upper salt marsh (Figure 2). Across the 35 samples only 4 taxa were present. The salt marsh is dominated by two species *Trochamminita salsa* and *Miliammina fusca*, with only isolated occurrences of *Trochammina inflata* and *Jadammina macrescens*. The low species diversity limits the dataset from being used on its own as a training set for constructing a reliable transfer function. However, there still remains a clear vertical zonation between these two dominant taxa. From -1.57 m SID to the upper limit of foraminiferal occurrence *Trochamminita salsa* accounts for virtually 100% of the sample assemblages and is a useful high marsh indicator as in other southern hemisphere salt marshes (Scott *et al.,* 1990; Jennings *et al.,* 1995; Scott *et al.,* 1996; Hayward *et al.,* 1996, 1999 ; Gehrels *et al*., 2008; Callard *et al.,* 2011). Below -1.57 m SID down to MSL the monospecific assemblage is broken by the occurrence of *Miliammina fusca*.

3.6 Combined testate amoebae, diatom and foraminifera transfer function

Based on the premise that a reconstruction is more likely to be accurate if multiple proxies show the same general trend it is generally believed that the application of multiple proxies in the same record leads to more robust reconstructions (Mitchell *et al.* 2013). We explored an alternative approach to using multiple independent proxy reconstructions by combining proxies (testate amoebae, diatoms and foraminifera) in

a single transfer function. This approach is pertinent for our study site as different proxies are more useful for different parts of the gradient (e.g. Gehrels *et al.* 2001) where there is no overlap between proxies such as at the upper limits of the environmental gradient (above -0.95 m SID) where only testate amoebae are present. Each proxy was effectively given equal weight in the training set, posing as true species-assemblage data along the environmental gradient. This was achieved by combining the individual relative abundances of testate amoebae, diatoms and foraminifera in each sample (so that the resulting total 'percentage' for each sample was 300%). Individual species are weighted by the regression model based on the number of occurrences and relative abundance (ter Braak & Looman, 1986). In combining the three proxies we extend the environmental gradient sampled to an elevation range of 1.18m.

The combined training set was subjected to DCCA. This confirmed that in combination the species still demonstrated a unimodal response to elevation with a gradient length of 3.632 (Axis 1: Table 7). For our combined transfer function, the initial model run returned with no significant outliers based on the same assessment criteria we used for the testate and diatom training sets. In this case we employed the full training set for the transfer function. Therefore, the final multiproxy transfer functions are built on regressions of 46 samples and 59 taxa. The performance of the unimodal regression models employed are statistically summarised in Table 8. Unlike the WAPLS models for testate amoebae and diatoms alone, each additional component of complexity brought some improvement in transfer function performance. However, we follow the general rule of thumb of Barlow *et al.*(2013) to apply no more than three components and only use the successive component if give it gives a reduction in prediction error (in cross-validation) of 5% or more of the RMSEP (Birks, 1998; Barlow *et al.,* 2013).

We therefore selected the WAPLS component 3 model as our final multiproxy transfer function model (RMSEP of 0.09m and $R^2_{(boot)}$ of 0.95 for the correlation between observed and predicted elevation; Figure 8). The combined transfer function ($R^2_{(boot)}$ 0.95) performs better than the testate amoebae-only transfer function ($R^2_{(boot)}$ 0.86). The combined and diatom-only transfer function have negligible difference in $R^2_{(boot)}$. The diatom-only TF, however, outperforms the combined TF in RMSEP (Combined = RMSEP 0.09m; Diatom-only = 0.06m). A summary table of all optima /species coefficients and their tolerances / standard errors for all iterations of the models is presented in Table 9.

Table 7: Results of DCCA analysis on the combined diatom, testate amoebae and foraminifera training set.

	Axis 1	Axis 2	Axis 3	Axis 4
Gradient Length	3.632	2.837	2.121	1.526
Proportion of variance	0.582	0.251	0.091	0.065

Number of samples	46
Number of taxa	59
Significance (p value)	0.002

Table 8: Summary performance statistics of weighted averaging (WA) and weighted averaging partial least squares (WAPLS) regression models applied to the combined data set.

Model	RMSE	R^2	R^2 (boot)	RMSEP	% change
WAPLS Component 1	0.12	0.88	0.86	0.13	0
WAPLS Component 2	0.08	0.95	0.92	0.09	26.04
WAPLS Component 3	**0.06**	**0.97**	**0.95**	**0.09**	**9.90**
WAPLS Component 4	0.04	0.99	0.95	0.09	2.26
WAPLS Component 5	0.03	0.99	0.96	0.08	4.37
WA (inverse deshrinking)	0.12	0.88	0.86	0.13	
WA (classical deshrinking)	0.13	0.88	0.86	0.14	
WA (tolerance downweighted, inverse deshrinking)	0.09	0.93	0.92	0.11	
WA (tolerance downweighted, classical deshrinking)	0.09	0.93	0.92	0.11	

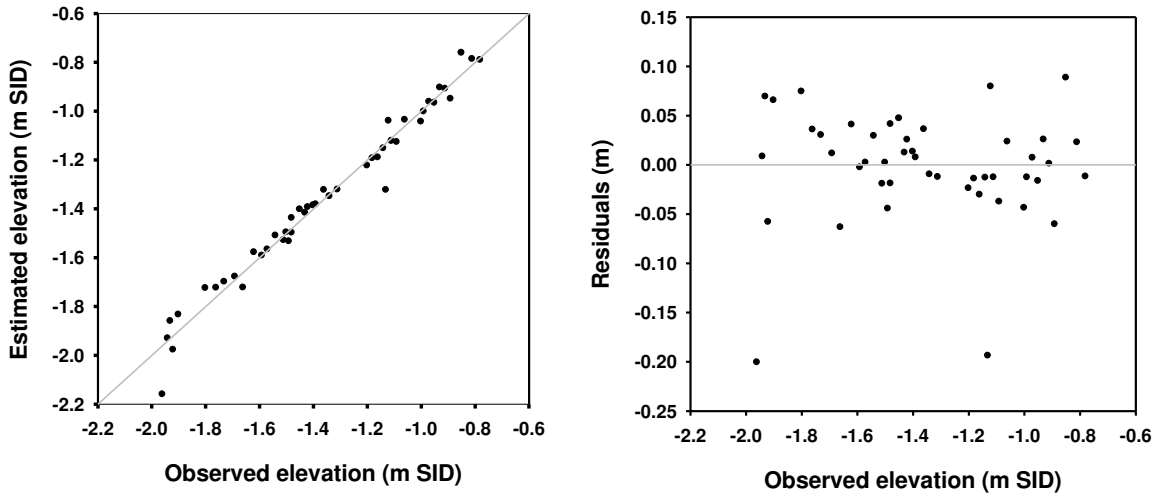

Figure 8: Scatterplot of observed vs predicted elevation (left) and observed elevation against prediction residuals (right) for the combined transfer function using WAPLS component 3.

Table 9: Summary table of all species optima /species coefficients and their tolerances / standard errors for all iterations of the models. Models selected are highlighted in bold.

	Single Proxy Transfer Function									Combined Transfer Function								
				Optima/ species coefficient estimates			Tolerance / error estimates						Species coefficient estimates			Standard Error estimates		
Testate Amoebae	Count	Max	N2		Optimum			Tolerance		Count	Max	N2	WAPLS C1	WAPLS C2	WAPLS C3	C1 SE	C2 SE	C3 SE
Cyphoderia ampulla	8	39.80	2.39		**-1.35**			**0.10**		7	39.80	2.10	-1.35	-1.20	**-1.33**	0.08	0.14	**0.21**
Psuedohyalosphenia sp.	3	8.76	2.76		**-1.34**			**0.04**		3	8.76	2.76	-1.32	-1.13	**-1.28**	0.04	0.13	**0.18**
Difflugia pristis type	13	76.64	3.96		**-1.33**			**0.08**		13	76.64	3.96	-1.30	-1.13	**-1.30**	0.05	0.09	**0.12**
Difflugia bryophila	10	7.19	7.57		**-1.22**			**0.11**		9	7.19	6.58	-1.13	-0.91	**-0.96**	0.06	0.11	**0.22**
Centropyxiella sp.	14	28.06	7.80		**-1.16**			**0.11**		12	28.06	5.89	-1.02	-0.77	**-0.69**	0.05	0.09	**0.18**
Difflugia pulex type	21	56.30	14.14		**-1.14**			**0.13**		19	47.71	12.75	-0.99	-0.86	**-0.97**	0.04	0.05	**0.07**
Trinema linere	21	18.27	10.75		**-1.12**			**0.15**		19	18.27	8.90	-0.95	-0.82	**-0.77**	0.05	0.06	**0.12**
Centropyxis cassis type	18	5.15	14.52		**-1.11**			**0.18**		16	4.59	12.95	-0.94	-0.87	**-0.91**	0.06	0.05	**0.11**
Tracheleuglypha dentata type	24	63.79	13.15		**-1.09**			**0.12**		22	63.79	11.74	-0.92	-0.84	**-0.89**	0.03	0.05	**0.07**
Euglypha rotunda type	15	23.08	5.73		**-1.07**			**0.13**		15	23.08	5.73	-0.93	-0.83	**-0.81**	0.06	0.08	**0.18**
Centropyxis platystoma type	11	1.82	9.99		**-1.06**			**0.22**		11	1.82	10.00	-0.91	-0.84	**-0.69**	0.10	0.08	**0.18**
Nebela langeniformis	8	7.34	4.25		**-1.06**			**0.14**		8	7.34	4.25	-0.90	-0.85	**-0.83**	0.07	0.08	**0.21**
Hylosphenia subflava	15	21.49	7.45		**-1.01**			**0.15**		13	21.49	7.23	-0.82	-0.97	**-1.20**	0.07	0.06	**0.13**
Euglypha tuberculata type	18	28.37	11.52		**-0.96**			**0.11**		17	28.37	11.44	-0.75	-0.94	**-0.95**	0.05	0.04	**0.06**
Heleopera petricola	16	11.62	10.12		**-0.95**			**0.13**		16	11.62	10.13	-0.75	-0.93	**-0.92**	0.05	0.05	**0.09**
Cyclopyxis arcelloides type	13	17.07	6.49		**-0.94**			**0.15**		13	17.07	6.49	-0.73	-0.90	**-0.90**	0.07	0.06	**0.11**
Nebela griseola type	8	9.74	3.78		**-0.93**			**0.05**		8	9.74	3.78	-0.71	-1.05	**-1.18**	0.07	0.08	**0.14**
Trinema complantanatum	9	10.00	6.19		**-0.90**			**0.09**		9	10.00	6.19	-0.66	-0.91	**-0.80**	0.08	0.08	**0.15**
Corythion dubium	13	14.40	5.86		**-0.88**			**0.09**		13	14.40	5.87	-0.64	-0.94	**-0.73**	0.07	0.06	**0.12**
Euglypha compressa	10	15.46	5.52		**-0.88**			**0.09**		9	15.46	5.38	-0.63	-0.93	**-0.74**	0.08	0.10	**0.17**
Valkanovia elegans	8	23.29	6.16		**-0.87**			**0.07**		8	23.29	6.16	-0.62	-0.94	**-0.71**	0.08	0.07	**0.07**
Assulina muscorum	11	15.20	4.75		**-0.87**			**0.09**		11	15.20	4.75	-0.62	-0.93	**-0.66**	0.07	0.06	**0.12**
Certesella martiali	7	10.91	5.18		**-0.87**			**0.09**		7	10.91	5.18	-0.61	-0.90	**-0.64**	0.08	0.09	**0.23**
Diatoms	Count	Max	N2	WAPLS C1	WAPLS C2	**WAPLS C3**	C1 SE	C2 SE	**C3 SE**									
Achnanthes kuelbsii	33	47.38	18.34	-1.88	-2.17	**-2.29**	0.07	0.06	**0.07**	33	47.38	18.34	-1.84	-2.15	**-2.43**	0.07	0.10	**0.12**
Achnanthes lancoleata	10	11.61	3.75	-1.34	-0.80	**-0.70**	0.05	0.14	**0.28**	10	11.61	3.75	-1.38	-1.24	**-1.37**	0.04	0.10	**0.17**
Caloneis bacillum	31	18.44	16.15	-1.34	-1.21	**-1.32**	0.05	0.07	**0.10**	31	18.44	16.15	-1.39	-1.27	**-1.32**	0.04	0.06	**0.09**
Cocconeis placentula	26	4.16	21.03	-1.64	-1.60	**-1.52**	0.06	0.10	**0.15**	26	4.16	21.04	-1.64	-1.68	**-1.71**	0.05	0.08	**0.12**
Cosmioneis hawaiiensis	13	8.15	6.56	-1.69	-1.59	**-1.39**	0.05	0.13	**0.16**	13	8.15	6.56	-1.68	-1.69	**-1.57**	0.05	0.12	**0.17**
Ctenophora pulchella	34	21.05	23.61	-1.60	-1.58	**-1.68**	0.05	0.08	**0.10**	34	21.05	23.61	-1.61	-1.64	**-1.71**	0.05	0.09	**0.13**
Diploneis elliptica	2	0.34	1.95	-0.97	-0.93	**-1.29**	0.28	0.21	**0.33**	2	0.34	1.94	-1.07	-1.01	**-1.06**	0.23	0.17	**0.19**
Diploneis oblengella	1	0.24	1.00	-1.41	-1.18	**-1.83**	0.00	0.00	**0.00**	1	0.24	1.00	-1.44	-1.15	**-0.86**	0.00	0.00	**0.00**
Distrionella incognita	27	4.94	16.33	-1.72	-1.81	**-1.89**	0.05	0.11	**0.14**	27	4.94	16.32	-1.71	-1.83	**-1.95**	0.04	0.09	**0.14**
Eunotia minor	34	7.95	21.15	-1.58	-1.52	**-1.43**	0.05	0.08	**0.11**	34	7.95	21.14	-1.59	-1.61	**-1.63**	0.04	0.07	**0.11**
Fragilaria construens	31	24.69	18.69	-1.77	-1.87	**-1.78**	0.07	0.10	**0.12**	31	24.69	18.69	-1.75	-1.92	**-2.03**	0.06	0.11	**0.13**
Fragilaria fasiculata	34	5.77	24.37	-1.37	-1.33	**-1.37**	0.06	0.07	**0.09**	34	5.77	24.36	-1.41	-1.34	**-1.34**	0.06	0.07	**0.10**
Frustulia rhomboides	15	16.59	9.81	-1.39	-1.06	**-1.30**	0.04	0.10	**0.09**	15	16.59	9.81	-1.43	-1.21	**-1.11**	0.03	0.11	**0.15**
Gomphonema parvulum	13	4.80	8.81	-1.82	-1.91	**-1.88**	0.06	0.15	**0.20**	13	4.80	8.81	-1.79	-1.97	**-2.08**	0.06	0.15	**0.27**
Gyrosigma wansbeckii	15	2.58	10.71	-1.50	-1.31	**-1.31**	0.07	0.13	**0.20**	15	2.58	10.72	-1.52	-1.41	**-1.32**	0.06	0.13	**0.17**
Melosira monoliliformis	30	32.66	17.96	-1.55	-1.38	**-1.48**	0.05	0.05	**0.05**	30	32.66	17.96	-1.56	-1.49	**-1.46**	0.04	0.09	**0.11**
Navicula elegans	24	50.68	11.05	-0.91	-0.90	**-0.90**	0.05	0.03	**0.05**	24	50.68	11.05	-1.02	-0.98	**-1.11**	0.06	0.04	**0.08**
Navicula halophila	28	5.75	19.17	-1.30	-1.14	**-0.98**	0.09	0.15	**0.23**	28	5.75	19.17	-1.35	-1.24	**-1.24**	0.08	0.13	**0.20**
Nitzschia brevissima	7	9.76	2.92	-1.69	-1.49	**-1.08**	0.04	0.13	**0.30**	7	9.76	2.92	-1.68	-1.65	**-1.45**	0.04	0.12	**0.21**
Nitzschia capitellata	24	20.13	10.71	-1.18	-0.69	**-0.29**	0.08	0.15	**0.16**	24	20.13	10.71	-1.25	-0.99	**-0.83**	0.05	0.10	**0.14**
Opephora pacifica	35	12.46	25.41	-1.37	-1.27	**-1.09**	0.06	0.08	**0.06**	35	12.46	25.41	-1.41	-1.34	**-1.31**	0.05	0.06	**0.09**
Paralia sulcata	23	4.35	16.96	-1.35	-1.23	**-1.29**	0.07	0.06	**0.10**	23	4.35	16.96	-1.39	-1.30	**-1.35**	0.06	0.08	**0.12**
Pinnularia borealis	13	15.70	5.48	-0.77	-0.93	**-0.86**	0.08	0.05	**0.10**	13	15.70	5.48	-0.90	-0.96	**-1.11**	0.08	0.06	**0.08**
Pinnularia microstauron	22	15.65	11.57	-0.90	-0.92	**-0.82**	0.04	0.07	**0.15**	22	15.65	11.57	-1.01	-0.92	**-0.99**	0.04	0.06	**0.09**
Pinnularia virdis	27	49.70	9.08	-0.82	-1.00	**-1.09**	0.05	0.04	**0.05**	27	49.70	9.07	-0.95	-0.90	**-1.05**	0.04	0.06	**0.10**
Planothidium delicatulum	34	41.14	21.09	-1.72	-1.81	**-1.71**	0.06	0.10	**0.10**	34	41.14	21.09	-1.70	-1.86	**-1.96**	0.07	0.11	**0.13**
Rhabdomena arcuatum	22	5.16	15.97	-1.54	-1.37	**-1.44**	0.06	0.11	**0.16**	22	5.16	15.98	-1.56	-1.49	**-1.47**	0.05	0.11	**0.16**
Rhabdomena minutum	8	2.44	3.87	-1.66	-1.50	**-1.36**	0.06	0.18	**0.44**	8	2.44	3.87	-1.65	-1.61	**-1.50**	0.05	0.13	**0.21**
Rhopalodia acuminata	21	4.17	13.86	-1.58	-1.52	**-1.50**	0.06	0.11	**0.20**	21	4.17	13.85	-1.59	-1.57	**-1.50**	0.05	0.11	**0.17**
Rhopalodia brebissonii	28	5.19	18.06	-1.57	-1.46	**-1.42**	0.04	0.08	**0.12**	28	5.19	18.07	-1.58	-1.57	**-1.57**	0.04	0.09	**0.13**
Rossithidium nodosum	29	6.49	20.32	-1.46	-1.38	**-1.32**	0.07	0.15	**0.22**	29	6.49	20.32	-1.49	-1.52	**-1.67**	0.06	0.10	**0.15**
Stauroforma exiguiformis	27	13.43	15.11	-1.27	-1.08	**-0.86**	0.07	0.12	**0.18**	27	13.43	15.11	-1.32	-1.17	**-1.08**	0.06	0.07	**0.10**
Forams																		
Trochamminita salsa										33	100.00	32.26	-1.53	-1.45	**-1.32**	0.04	0.05	**0.08**
Miliammina fusca										16	60.14	9.33	-2.07	-2.57	**-2.72**	0.09	0.10	**0.19**
Trochammina inflata										4	6.67	3.16	-1.68	-1.65	**-1.47**	0.04	0.13	**0.21**
Jadammina macrescens										4	1.38	3.37	-1.79	-1.99	**-2.24**	0.16	0.40	**0.64**

3.7 Implications for sea-level studies

In practice the value of a multi-proxy approach is a trade-off between the gained degrees of accuracy and precision required to answer the research questions versus the amount of time required to undertake the analyses. Our results show that diatoms were the most accurate and precise indicators of marsh surface elevation based on the assessment of $r^2_{(boot)}$ and RMSEP values as well as the scatterplot of observed vs predicted values. Diatoms are particularly useful as their distributions cover the greatest range of sub-environments at Swan Inlet. However, the scarcity of diatoms at the uppermost elevations hinders the recovery of the most accurate sea-level information; this is because the most accurate sea-level reconstructions are derived from cores collected in the uppermost reaches of the intertidal zone where accommodation space is created by sea-level rise (Allen, 1990). Charman et al. (2010) recommend that cores are taken within the main zone of testate amoebae occurrence in order to achieve the most accurate sea-level reconstructions.

Compared with foraminifera, analyses of diatoms and testate amoebae are considerably more time consuming (e.g. Gehrels et al., 2001). Although foraminifera from Swan Inlet are not suitable for developing a transfer function, the relatively quick and straightforward analysis they require, and their usefulness as indicators of mid-to-low marsh sub-environments, make it worthwhile to include them in addition to other (more precise) proxies. This raises the question: for which additional proxy (diatoms or testate amoebae) do we undertake microfossil analyses, in the interest of achieving the most accurate sea-level reconstructions, with the least investment of time?

Arguments can be made in support of conducting diatom or testate amoebae microfossil analyses. Testate amoebae analysis is the most time efficient of the two proxies and could potentially produce the most accurate reconstructions because their occurrences are entirely within the uppermost intertidal zone. On the other hand, the diatom transfer function is the most precise model. Furthermore, the diatom training set encompasses a greater environmental range, increasing the likelihood of providing analogues for the range of environments within the fossil samples. An alternative approach is to make an *a priori* decision by selecting a transfer function where the training set fits within the elevation range defined by the palaeoenvironments in the fossil core (e.g. Gehrels et al., 2006).

In spite of the statistical justifications for selecting an appropriate transfer function based on model performance under cross-validation, it is unrealistic to determine *a priori* which transfer function will perform best at predicting PMSE from microfossil assemblages. Although a single proxy transfer function (e.g. diatoms) may have the greatest precision in terms of RMSEP, it may not necessarily perform best on microfossil assemblages in terms of accuracy. This is in part because transfer function precision measured by RMSEP is an artefact of the length of the gradient sampled i.e. the maximum bias of the transfer function prediction is limited by the range of elevations sampled. With short gradients, the magnitude of error that is possible decreases, so lower RMSEPs are expected. Thus, RMSEP of the combined transfer function (0.09m) and the diatom transfer function (0.06m) being similar despite a 30% increase in the size of the gradient sampled gives confidence that the species-elevation relationship is robust and the RMSEP in this case being a reliable estimate of model predictive performance. The combined transfer function therefore has the

potential to produce the most accurate reconstruction because it reflects a greater range of sub-environments than either single transfer function with only a 0.03m reduction in precision. The accuracy of a transfer function, however, is largely dependent on the nature of the fossil data that are used for calibration. Transfer function reconstructions are most accurate when there are close analogues between the fossil assemblages and the contemporary assemblages in the training set. For 'local' training sets (composed of samples from a single site) such as those in this study, close analogues between the test set and removed subset used in model cross-validation are often inherent due to spatial autocorrelation (Telford and Birks, 2009). A reconstruction therefore requires strong similarities in species assemblages between the fossil and modern data to achieve accurate reconstructions of comparable precision to the RMSEP of the transfer function. Provided that there are species in common between the training set and the fossil calibration set a reconstruction will be generated, whether environmentally plausible or not. Although sample-specific errors are calculated by the transfer function for each reconstructed variable the precision gives little indication of the accuracy of the reconstructions.

It is therefore important to statistically evaluate the reliability of any reconstruction by performing some form of assessment of reconstructive accuracy (e.g. Juggins & Birks, 2012). One commonly used reconstruction diagnostic is to assess analogue quality using a modern analogue technique regression model (e.g. Barlow *et al.,* 2013). The modern analogue technique (MAT; (Birks, 1995; Jackson & Williams, 2004) produces minimum dissimilarly coefficients (minDC) for fossil samples which can be used to assess the reliability of reconstructed values (Watcham et al. 2013). A lack of modern analogue for fossil assemblages may be a caused by a number of factors, e.g.

unsampled sub-environments, taphonomic processes, environmental change and changes in species ecology (Barker et al., 1991; Jackson & Williams, 2004). It is impossible to know, without conducting the microfossil analyses, which microfossil group will exhibit the closest modern analogues. Previous studies have shown that 'regional' (composed of spatially-independent samples collected from a number of geographically proximate sites which have comparable climatic and oceanographic conditions) are less precise than local training sets, but often result in more accurate reconstructions because they include a wider range of possible analogues (Horton and Edwards, 2005; Kemp *et al.* 2009; Watcham *et al.,* 2013). Owing to the Falkland Islands' isolated location, and the presence of only one large accessible salt marsh, we were only able to collect a local training set. Nonetheless, the multiple proxies utilised in this study offer a potential alternative to using a regional training set to achieve better analogues, whilst also preserving the precision of a local training set. This is based on the assumption that combining samples with poor analogues for each individual proxy could yield closer analogues with the combined training set by increasing the range of available modern analogues i.e. spread in the fossil species data is better reflected by the range of contemporary sub-environments sampled. It may be that for some samples one microfossil group will demonstrate the closest analogue, whereas, in other samples another microfossil group may have the closest analogue. In cases where neither of the single-proxy transfer functions provide reliable reconstructions due to poor or no modern analogues then a multiproxy transfer function may offer improved analogue quality (Elliot, 2015).

3.8 Palaeo-reconstruction

In order to explore the issues raised above we assess the accuracy of PMSE reconstructions produced by each transfer function inferred from the same set of fossil assemblages. We utilise a MAT model as a diagnostic tool to assess the reliability of reconstructions. To generate our reconstructions, we calibrate our transfer functions on microfossil assemblages obtained from a short core (SI-2; 90 cm) sampled from Swan Inlet (Figure 9) and calculate PMSE estimates for each sample. This core documents an overall regressive sequence containing assemblages of testate amoebae, diatoms and foraminifera at the base of the sequence (70-90 cm) which are similar to those observed in the contemporary middle and low marsh environments. Above 70 cm foraminifera are mostly absent, and diatom and testate assemblages are similar to contemporary middle marsh assemblages. These transition toward high marsh assemblages up core. A short transgressive sequence between 40 and 50 cm is indicated by the presence of foraminifera and lack of testate amoebae.

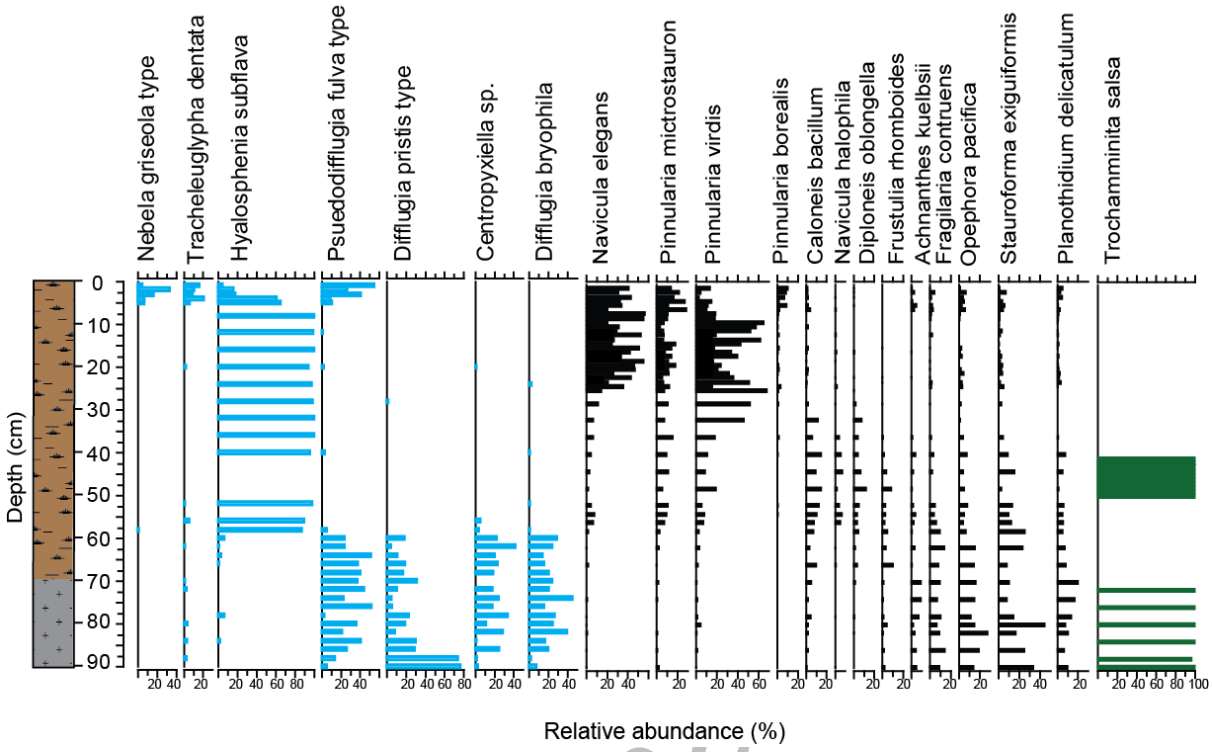

Figure 9: Summary diagram of dominant testate amoebae (blue) diatom (black) and foraminifera (green) taxa found in core SI-2 retrieved from Swan Inlet.

The PMSE estimates (relative to SID) for each reconstruction are presented in Figure 10 which shows each reconstruction individually along with a combined plot of the overlain 1-sigma uncertainties for each reconstruction. The general trends of all three reconstructions show a similar pattern although the sample by sample variations are quite different. This is evident in the grey shading in Figure 10 representing the minimum and maximum standard error values from all three of the models. The reconstructions are characterised by an up-core trend of increasing PMSE. In the upper part of the core (0-25 cm) the 1-sigma ranges of the testate and diatom reconstructions are overlapping for most samples which gives some confidence in the

reliability of those reconstructions throughout those depths. Generally, there is better agreement between these reconstructions towards the top of the core, although the greatest discrepancies occur between 25 cm and 40 cm where the PMSE estimates differ by up to 0.4m (Figure 10). In the testate amoebae record, this section of the core is dominated by a single taxon, *Hyalosphenia subflava*, which in the modern training samples represents relatively high marsh environments. The diatom stratigraphy through this section exhibits greater diversity and consequently provides a more detailed reconstruction of elevation changes. Between 40 and 50 cm the combined TF data are dominated by high-resolution foraminifera samples. These are also comprised 100% by a single taxon, *Trochamminita salsa*. Several diatom samples are also represented across this depth range and it is evident from the overlap in the 1 sigma errors for the diatom and combined TF models that, despite the limited precision through this depth interval, there remains agreement in two separate transfer functions for the elevation reconstructed. The combined transfer function exhibits less range of variability than the testate or diatom-only transfer functions. Towards the bottom of the core, below 60 cm the combined TF overestimates PMSE (compared with the two single-proxy transfer functions). Above 60 cm the opposite is observed. The noticeable accretion of the marsh throughout the record is therefore less well reconstructed in the combined TF. This may be an artefact of the use of a relatively complex component (3) of the WAPLS model, although the same component has been used for the diatom-only TF. The influence of particular taxa may also be more limited owing to the larger number of species present in the model and therefore their relative weighting. The combined transfer function also reconstructs a higher elevation value for the surface of the core in comparison with the testate amoebae transfer function. Only testate amoebae data exist for the 0 cm surface sample, so, essentially, two very different

values are being reconstructed based on identical core sample data. This surface sample is dominated (~40%) by *Tracheleuglypha dentata* type. In the testate-only TF this taxon has an optimum (species score) of -1.09m SID. In the combined TF it is -0.89m SID. The 20cm difference in the coefficient assigned to this taxon is the primary explanation for this disagreement between the models. We note that the surveyed height of the sample is -1.02 SID, slightly closer to the testate-only estimate.

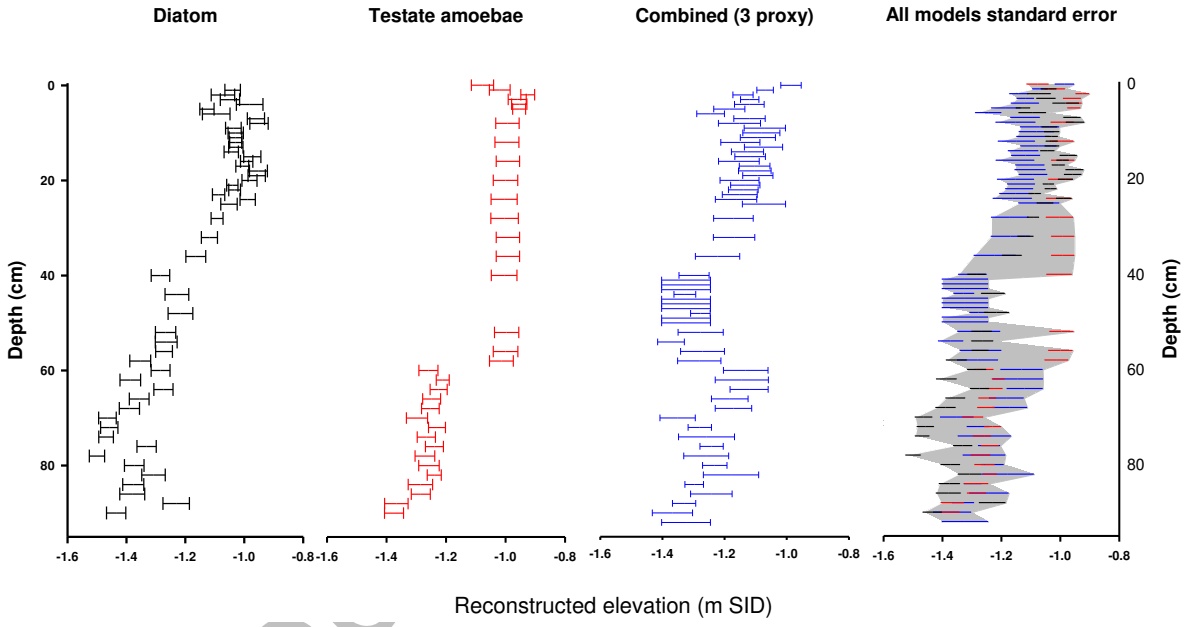

Figure 10: Reconstructed palaeo-marsh surface elevation (PMSE) of microfossil samples in core SI-2. The far right panel shows the aggregated range of 1-sigma uncertainties for all reconstructions (grey) and the 1-sigma uncertainties for diatom (black dash), testate amoebae (red dash) and combined testates+diatoms+forams (blue dash) transfer function reconstructions.

More broadly than this taxon alone, there are notable differences in the model optima (WA) or species coefficients (WAPLS) depending on whether those training data are in a single-proxy or multi-proxy training data set (Figure 11; Table 9). For the testate

amoebae, only 6 taxa (*Cyclopyxis arcelloidies, Heliopera petricola, Euglypha tuberculate, Diffugia pristis, Pseudohyalosphenia sp. and Cyphoderia ampulla*) have overlapping 1-sigma error ranges. For all but two of the other taxa, the combined TF species coefficients are at higher elevation than their testate-only equivalents. *Nebela griseola* and *Hyalosphenia subflava* are both modelled to have lower elevations in the combined transfer function. Conversely, comparison of the diatom-only transfer function with the combined model indicates generally lower species coefficients are given to the diatom-only TF. The differences in these model-assigned optima/coefficients demonstrates clearly the need for caution in their further use and interpretation and supports further analysis of the results through modern analogue testing.

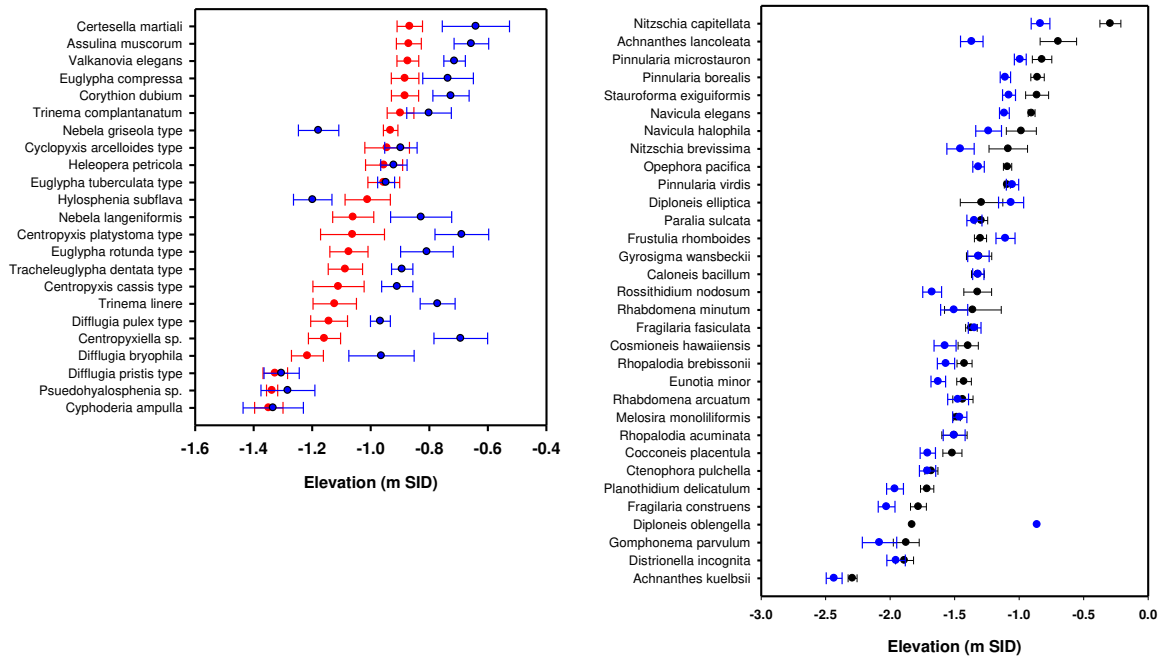

Figure 11: Comparison of modelled optima (WA) / species coefficients (WAPLS) and their tolerances (WA) or standard error estimates (WAPLS) from the testate-only (red) diatom-only (black) and combined (testate, diatom, foram) transfer functions.

The results of the analogue quality diagnostic assessment for each of our transfer function models are presented in Figure 12. This plots the minimum dissimilarity coefficient (minDC) for each fossil sample from its most similar modern assemblage using a squared chord distance dissimilarity metric (Overpeck *et al.,* 1985; Birks, 1995; Barlow et al., 2013). A minDC value of zero indicates an exact match with the assemblage composition of a modern sample. The higher the value, the less similar. We define the threshold between 'good', 'close' or 'poor' analogue quality following Watcham *et al.* (2013), with the 20th and 5th percentiles of the dissimilarity coefficients calculated between all modern samples as the cut-off for 'poor' and 'good' modern analogues respectively, with 'close' defined as any samples that fall between these thresholds (Figure 12).

Table 10: Percentage of close, good and poor analogues for each group of transfer function reconstructions.

	Analogue quality		
	Close (%)	Good (%)	Poor (%)
Diatom	4	37	58
Testate amoebae	3	50	47
Combined	15	2	83

Overall, the testate amoebae fossil samples were best represented by the modern assemblages (Table 10) with a smaller number of poor analogues (47%) compared with the diatoms (58%). In total 53% of the testate amoebae fossil samples were of close (3%) or good (50%) analogue quality. This compared with 41% of the diatom fossil samples having close (4%) or good (37%) analogues. For much of the upper part of the core, the diatom core samples have “good” modern analogues against which to train an elevation estimate. Below 36cm, the diatom samples are matched only by “poor” analogues. Conversely, the testate amoebae minDC values are generally poor for much of the upper part of the core (7 – 56 cm) and, instead, show greater analogue quality for the lower part of the core where all core samples below 60cm have an assemblage that is a “good” (n=13) or close (n=1) analogue of a modern surface training sample.

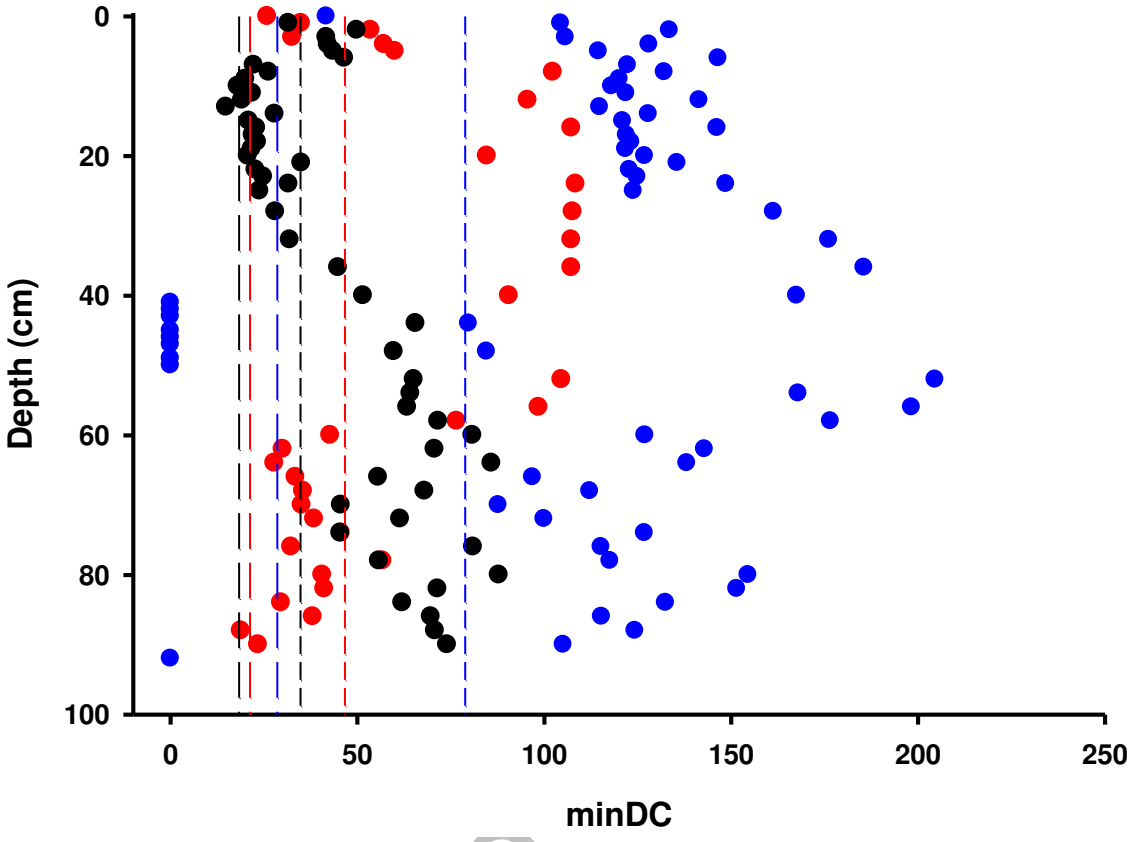

Figure 12: Minimum dissimilarity coefficients (min DC) based on squared chord distance from each fossil assemblage to the nearest modern analogue for the diatom (black), testate amoebae (red) and combined (blue) reconstructions. Long dashed lines mark the 5th percentile and short dashed lines mark the 20th percentile cut-offs for respective coloured series. Samples with min DC > the 20th percentile = "poor" analogues. Samples with min DC <20th but >5th percentile = "good" analogues and samples < 5th percentile = "close" analogues (Watcham et al, 2013).

Most of the poor-analogue situations for the testate amoebae fossil samples were between 5 and 50 cm depth, in the zone dominated by *Hyalosphenia subflava*. This is unsurprising as there are no such monospecific assemblages observed in the modern environment. In the contemporary testate amoebae distributions *Hyalosphenia subflava* is found in greatest abundance in association with mostly Euglyphid taxa

(*Euglypha, A. muscorum, C. dubium, Trinema, T. dentata, V. elegans*). These Euglyphid taxa all have idiosomic tests composed of delicate siliceous scales whereas *H. subflava* has a rigid, chitinoid test. This may, therefore, indicate a taphonomic contribution to the observed dissimilarity, where the more robust *H.subflava* is preferentially preserved. The taphonomy of testate amoebae in salt-marsh deposits is poorly understood (Roe *et al.,* 2002), but previous studies from upland and peatland environments indicate that tests comprised of idiosomic plates are most susceptible to decomposition (Lousier and Parkinson, 1981; Ruzicka, 1982; Tolonen, 1986; Swindles and Roe, 2007; Mitchell *et al.,* 2008). Conversely, previous studies suggest the tests of *Hyalosphenia* taxa are most resistant to decomposition (Ruzicka, 1982; Mitchell *et al.,* 2008). The improvement in analogue quality at depth may also be a consequence of taphonomy. Both testate and diatom community assemblages indicate lower PMSE through this deeper part of the core (Figure 8). The taxa observed in the core, and also in the comparable lower elevation surface samples, are typically composed of more robust testate with a lower proportion of those comprised of idiosomic plates (Figure 9).

The general reduction in analogue quality with depth for the diatom samples would be most likely to reflect a preservation issue if also supported by a general reduction in the diversity of species at greater depth. This is not the case. The numbers of species in fossil samples also observed in modern training samples remains similar across the core. It is possible, therefore, that the change in analogue quality with depth reflects a general change in the competitive relationship between species across the period covered by the core, possibly reflecting an unidentified influencing environmental variable.

Far from offering any improvement, the analogue quality is generally poor for the combined fossil assemblages. The analogue quality is strongly polarised between those samples where only foraminifera were observed and for which an identical assemblage exists in the modern training data and the remainder of the core samples. For those samples where *Trochamminita salsa* comprised 100% of the fossil record, we observed minDC values of 0. There is just one sample where a close analogue is observed. The remainder of fossil assemblages have poor analogues. The combined assemblages therefore tend to result in a reduction of analogue quality for samples which otherwise demonstrate a greater proportion of good/close analogues in either of the single-proxy datasets. Indeed, there was no depth in which the combination of proxies provided for an improved analogue in comparison with either of the single-proxy datasets. Rather, the only clear benefit was the provision of reconstruction estimates for those samples where neither diatoms nor testate amoebae were present, through the section of transgression in core SI-2 between 40 and 50 cm in depth. Because the transfer functions still reconstruct PMSEs for samples that lack good modern analogues we must therefore be cautious when interpreting these results. The uncertainty in these reconstructions is likely to be greater than the transfer function performance statistics (sample-specific RMSEPs) indicate as the bootstrapping technique used to calculate the uncertainty does not account for additional uncertainty caused by weak analogue situations. However, experiments with simulated data suggest that there is not a strong relationship between poor analogue samples (defined by the distance between fossil and modern assemblages) and increased reconstructive unreliability (Juggins and Birks, 2012). In fact, methods based on weighted averaging regressions have been shown to perform well under mild non-

analogue situations (ter Braak et al., 1993; ter Braak, 1995). Therefore, an examination of analogue quality should serve as a basic assessment of reconstruction reliability, highlighting any potential issues that may be explored using other diagnostics (Juggins and Birks 2012).

4. Conclusions

Salt-marsh microorganisms sampled at Swan Inlet in the Falkland Islands exhibit a quantifiable vertical distribution along the salt-marsh elevation gradient making them suitable sea-level indicators. As standalone proxies, only diatom and testate amoebae provide suitable training sets for transfer function development. Our transfer function performance statistics suggest that diatoms are the most precise sea-level indicators. Testate amoebae may be the most useful sea-level indicators as they occur in the uppermost intertidal sediments which provide the most accurate information for sea-level reconstructions. However, this study suggests that many of the taxa that comprise the uppermost salt-marsh testate amoebae assemblages may not be readily preserved, limiting their utility. We tested the applicability of a multiproxy approach to reconstructing sea level from Swan Inlet by combining foraminifera, diatoms and testate amoebae data into a single transfer function. The combined transfer function yielded reconstructive precision (RMSEP) comparable to (diatoms) or better than (testate) our single proxy transfer functions. However, the results of our analogue quality assessment demonstrate that, by combining multiple proxies into a single

transfer function, analogue quality is generally diminished. On the basis of these results we make the following recommendations to future studies that aim to produce robust proxy-derived sea-level reconstructions.

1. If the least amount of analytical time for the most precise sea-level reconstruction is required we recommend initially conducting either testate amoebae or diatom microfossil analysis.
2. We advocate a pragmatic approach whereby if the initial analysis of either fossil testate amoebae or diatoms yields samples with poor modern analogues then conduct microfossil analysis for the alternative group for these samples in an attempt to provide better analogues.
3. If the most robust and accurate sea-level reconstructions are required we recommend microfossil analyses for multiple proxies. If common trends between the independent proxies are observed the reconstruction is more likely to be accurate.
4. Reconstructions should be rigorously examined for reliability by employing a range of statistical 'reconstruction diagnostics' and the results of these assessments reported along with the reconstruction. If samples perform badly in the diagnostic assessment then we should be cautious when interpreting the reconstruction.

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