



Contemporary distributions of saltmarsh diatoms in the Seymour–Belize Inlet Complex, British Columbia, Canada: Implications for studies of sea-level change

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ABSTRACT

Surface diatom samples were collected from two saltmarshes in the Seymour–Belize Inlet Complex on the mainland coast of British Columbia to examine the controls on diatom distribution and provide training sets for regional studies of sea-level change. Cluster analysis and detrended correspondence analysis (DCA) were used to examine diatom distributions within and between the two marshes whilst canonical correspondence analysis (CCA) and partial canonical correspondence analysis (pCCA) were used to analyse species–environment relationships. The diatom assemblages were shown to be quite different between the two marshes, Waump and Wawwat'l. Q-mode cluster analysis separated the diatom assemblages from Waump into three zones corresponding to recognized vegetation zones; diatom zone C corresponds to the high marsh and is dominated by *Pinnularia obscura*, *Caloneis bacillum* and *Diploneis ovalis*, zone B spans the high- and mid marsh and is characterised by *Fragilaria exigua*, *Nitzschia palea* and *D. ovalis*, whilst zone A from the low marsh/tidal flat includes high frequencies of *Diploneis smithii*, *Ctenophora pulchella* and *F. exigua*. Three different diatom zones were recognised at Wawwat'l; two upper zones, E and F, corresponding to the mid-marsh which are dominated by mixed abundances of *N. palea* and *Fragilaria construens* var. *venter*, *Navicula peregrina* and *Navicula clementis* and zone D from the low marsh/tidal flat with increased frequencies of *F. exigua* and *Achnanthes delicatula*. At Waump, the major controls on diatom distribution were found to be elevation and to a lesser extent pH, whilst at Wawwat'l, the primary controls were grain size/organic content, conductivity and elevation. The results confirm that saltmarsh diatoms may have potential for future sea-level studies in this region. However, caution must be exercised as the significant difference in the diatom assemblages between the two marshes suggests that the diatoms are responding to a number of environmental variables on a local scale. Some of this variation may reflect highly seasonal changes in sedimentation and salinity resulting from the proximity of the marshes to adjacent streams which are subject to spring freshet. Local differences in elevation between the collected samples may also account for some of the assemblage variability. The results emphasize the great diversity and high sensitivity of intertidal diatom species to environmental controls.

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1. Introduction

Saltmarshes are important archives of sea-level change and provide a basis for comparing measured sea-level observations with those of the recent geological past. Sea-level reconstructions based in saltmarsh environments commonly rely on microfossil indicators. Amongst these, diatoms, foraminifera and testate amoebae are particularly useful for sea-level reconstruction (Scott and Medioli, 1978; Gehrels, 1994; Charman et al., 1998, 2002; Horton et al., 1999; Zong and Horton, 1999; Gehrels et al., 2001; Roe et al., 2002; Patterson et al., 2005). The vertical distributions of these organisms are closely

related to tidal levels, and they can therefore be used as precise sea-level indicators (Scott and Medioli, 1978; Gehrels, 2000; Gehrels et al., 2001). A number of recent studies have attempted to quantify the distributions of these indicators in modern saltmarsh environments to compare their utility in studies of relative sea-level (RSL) change. Gehrels et al. (2001) for example, compared the vertical distribution of diatoms, foraminifera and testate amoebae in three UK saltmarshes in relation to tidal flooding and elevation, whilst Patterson et al. (2005) investigated the distribution of diatoms, foraminifera and macrophyte species in a saltmarsh in western Vancouver Island, British Columbia against the same variables. The results of both studies showed that diatoms span the entire inter-tidal and supra-tidal area and are strongly correlated with flooding duration. In addition, diatoms are generally not subject to problems of in-faunal migration like

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foraminifera (Guilbault et al., 1995), and are generally well preserved in the fossil record, unlike testate amoebae which can show differential preservation (Roe et al., 2002).

A variety of environmental factors influence the distribution of inter-tidal diatoms, including nutrient supply, temperature, pH, salinity, substrate, vegetation, amount of irradiance, competition with other organisms, inter-tidal submergence and sub-aerial exposure (Whiting and McIntire, 1985; De Sève, 1993; Hemphill-Haley, 1995; Sawai, 2001). Differences in affinities for salinity, substrate and inter-tidal exposure make diatoms particularly suitable for reconstructing paleo-sea-level changes (Palmer and Abbott, 1986; Vos and de Wolf, 1988). Moreover, the recognition that certain taxa predomi-

nantly inhabit particular inter-tidal zones suggests that diatoms can be employed to identify small-scale RSL changes, by quantifying the vertical range of the assemblages associated with each zone (Nelson and Kashima, 1993; Hemphill-Haley, 1995).

The relationship between microfossils and the environmental gradients that control their distribution within saltmarshes, offers a vital link in determining the RSL history of coastal areas (Palmer and Abbott, 1986; Patterson et al., 2004; Sherrod, 1999; Gerdes et al., 2004). By quantifying the modern distribution of the microfossil indicators (for example, diatoms) relative to the target variable (for example, Mean Tide Level), the past distribution of the indicators can be used as a proxy for former RSL (cf. Zong and Horton, 1998, 1999;

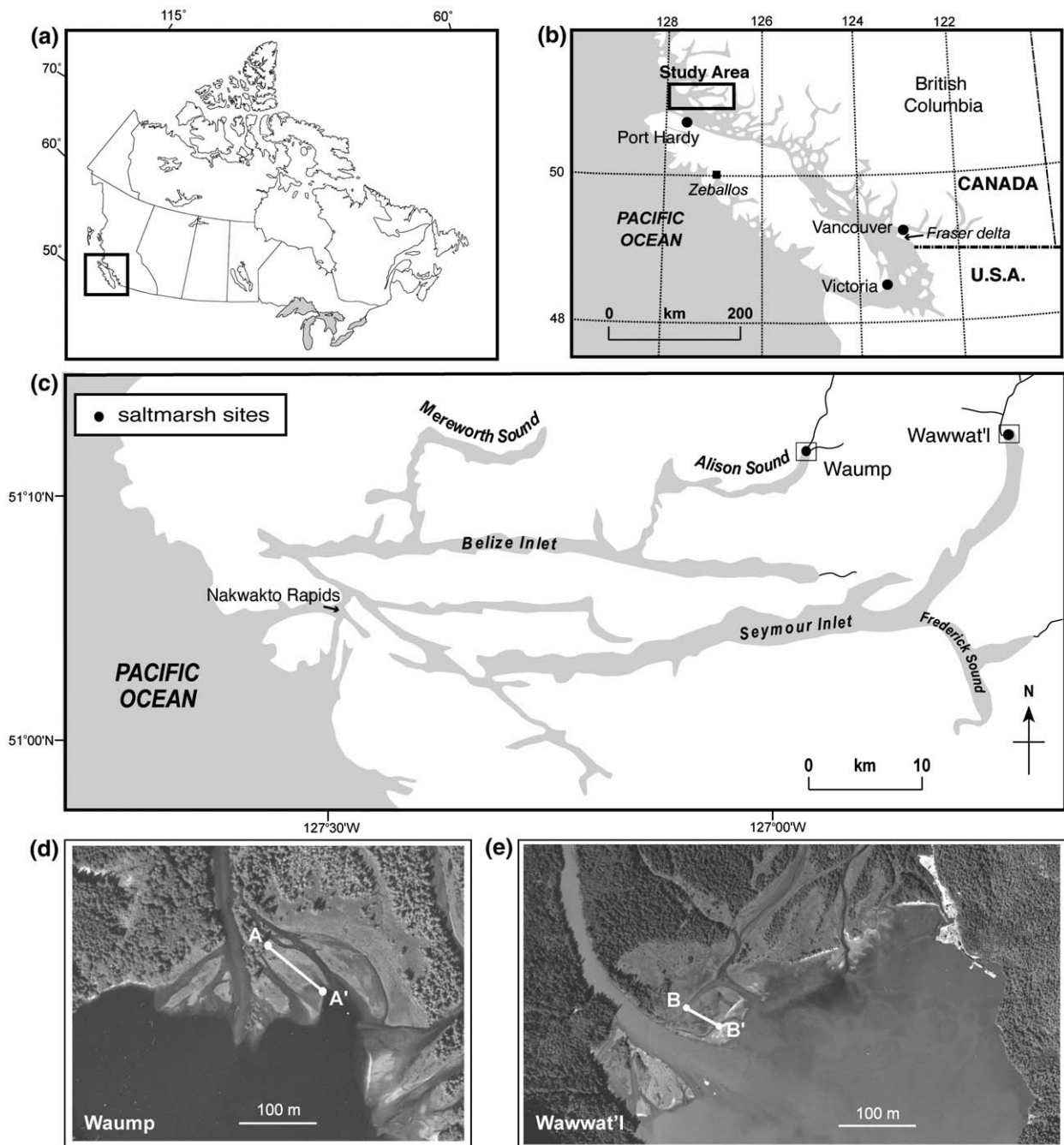


Fig. 1. Maps showing the location of the Waump and Wawwat'l marsh study areas and air photographs showing orientation of the transects. The saltmarsh at Waump is drained by the Waump Creek; the marsh at Wawwat'l by the Seymour River.

Horton et al., 1999; Plater et al., 2000; Gehrels et al., 2001; Patterson et al., 2005). These relationships can in turn be used to derive quantitative predictions of Holocene RSL change (e.g., Guilbault et al., 1995, 1996; Horton et al., 1999; Zong and Horton, 1999; Gehrels, 2000; Gehrels et al., 2001; Edwards et al., 2004; Szkornick et al., 2006).

This study has two main aims: i) to examine the controls on diatom distribution in two saltmarshes in the Seymour–Belize Inlet Complex (SBIC) of central mainland British Columbia (BC); and ii) to use this information to assess the suitability of the local saltmarshes for quantitative studies of relative sea-level change. The saltmarshes in this remote area remain hitherto uninvestigated, and there is a sparsity of Holocene RSL data in general for this region of central mainland BC (cf. Clague, 1983; Hetherington et al., 2004; Hetherington and Barrie, 2004; Doherty, 2005). Saltmarsh diatoms have nevertheless been utilised effectively in RSL studies elsewhere in British Columbia, for example, in the Fraser River delta area (Hutchinson et al., 1998) and in Zeballos, northwestern Vancouver Island, the closest site to the SBIC previously investigated (Fig. 1b). Diatoms have also been used extensively in the wider northwest Pacific region to identify RSL changes associated with co-seismic subsidence and/or tsunamis, for example, along the coast of Oregon (Hemphill-Haley, 1995, 1996), Washington (Shennan et al., 1996, 1998) and Alaska (Shennan et al., 1999, Zong et al., 2003; Hamilton and Shennan, 2005a,b). The acquisition of saltmarsh-derived RSL estimates for the SBIC region would provide important baseline data for examining recent RSL trends and for assessing the presence of any residual crustal (isostatic) or co-seismic movements within the region (cf. Clague, 1983).

2. Regional setting

The SBIC is located 40 km northeast of Vancouver Island on the mainland coast of British Columbia, Canada (Fig. 1). It is characterised by narrow, steep-sided fjords, which are densely forested and uninhabited. The surrounding hinterland to the east of the study area is characterised by mountainous terrain (locally over 2000 m) with a permanent snow cover. Small rivers drain into the head of the inlets, forming fjord-head deltas. Saltmarshes in this region are largely restricted to these fjord-head areas (Fig. 1). The two study sites, Waump and Wawwat'l saltmarshes, were chosen because they support well established saltmarsh vegetation and incorporate a range of sub-environments from mud-flat to high marsh. Waump saltmarsh extends across a small delta that is prograding into Alison Sound (51°11'15 N, 126°55'15 W) (Fig. 1c, d). It is influenced by discharges of freshwater from Waump Creek and smaller tributary streams. The tidal range at Alison Sound is 1.98 m (Canadian Hydrographic Service, 2002). Wawwat'l saltmarsh is located at the head of Seymour Inlet (51°11'36 N, 126°40'5 W) and lies 18 km east of Waump saltmarsh (Fig. 1c). It has again developed on a fjord-head delta and is influenced by freshwater discharge from the Seymour River. The surrounding terrain is steep sided and densely forested. The tidal range at adjacent Frederick Sound is 2.0 m (Canadian Hydrographic Service, 2002). A further two saltmarshes in the SBIC were considered for additional study, but the saltmarsh vegetation at these locations was of limited extent and the sites did not incorporate a full range of marsh sub-environments. Riveiros et al. (2007) examined

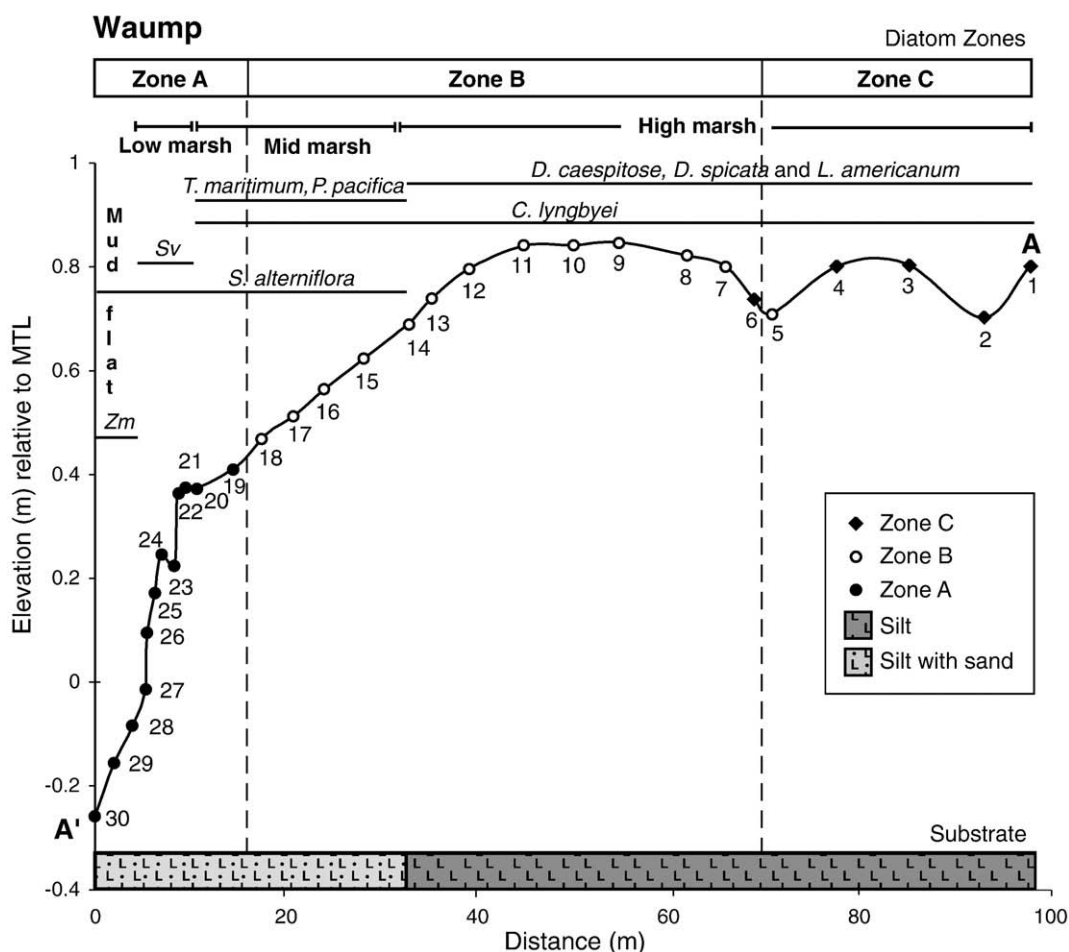


Fig. 2. Waump saltmarsh transect (elevation (m) relative to MTL) showing diatom zonations and their relationship to the associated vegetation zones. Zm=*Zostera marina*; Sv=*Salicornia virginica*.

foraminiferal and thecamoebian assemblages from Waump and Wawwat'l saltmarshes and the same samples are analysed for diatoms in this study.

3. Materials and methods

The saltmarshes in this remote region were investigated as part of a wider study aimed at examining the paleoclimate record of the fjord sediments of the SBIC in April and October 2002. The saltmarshes were sampled during low tide by shore parties from the CCGS *Vector*. Sampling transects were established which extended from the unvegetated tidal flats to the mid- and high marsh vegetation at the back of the marshes. The transect at Waump saltmarsh was 98 m in length and included four vegetation zones (Figs. 1 and 2). The mud-flat at this site ranges in elevation from -0.26 m to -0.09 m and the low marsh extends to $+0.37$ m above mean tide level (MTL). The mid-marsh ranges from $+0.37$ m to $+0.69$ m, while the high marsh extends to $+0.8$ m above MTL. *Salicornia virginica* and *Spartina alterniflora* feature on the pioneer marsh, while the low marsh is dominated by *Carex lyngbyei*. The mid-marsh is characterised by *S. alterniflora*, *C. lyngbyei*, *Triglochin maritimum* and *Potentilla pacifica*. In the high marsh, a diverse and highly mixed community of *Deschampsia caespitosa*, *Distichlis spicata*, *Lysichiton americanum* and *C. lyngbyei* are present. The adjacent upland beyond the high marsh includes a mixed tree and shrub community dominated by *Tsuga heterophylla*

(Western Hemlock), *Tsuga mertensiana* (Mountain hemlock) and *Gaultheria shallon* (Salal).

The transect at Wawwat'l saltmarsh extended from the mud-flat to the mid-marsh (68 m in length) and included three vegetation zones (Figs. 1 and 3). The high marsh at this locality could not be sampled due to the presence of a drainage channel which cuts through the back of the saltmarsh. The mud-flat extends from -0.31 m to -0.23 m below MTL, the low marsh ranges from -0.23 m to $+0.17$ m and the mid-marsh extends to $+0.38$ m above MTL. *Zostera marina* and *S. alterniflora* clumps occur on the mud-flats. There is a diverse community of vascular vegetation in the low marsh, mainly *S. alterniflora*, *C. lyngbyei*, *D. caespitosa* and *P. pacifica*. The mid-marsh is characterised by *T. maritimum*, *C. lyngbyei*, *D. caespitosa* and *P. pacifica* (Fig. 3).

The elevation of each surface sample was surveyed using a differential Leica 500 global positioning system (GPS), with reference to the elevation of the highest and lowest tide levels occurring on the days of fieldwork. The GPS readings of the tide levels were subsequently corrected to elevation in metres relative to MTL using the Canadian Hydrographic Service's (2002) predicted tide level data for Frederick Sound and Alison Sound for the days of sampling (Canadian Hydrographic Service, 2002). This was undertaken because, due to the remoteness of the region, there were no permanent survey markers (benchmarks) in the vicinity with known height relationships to local tidal datums. As an independent check to ensure that the

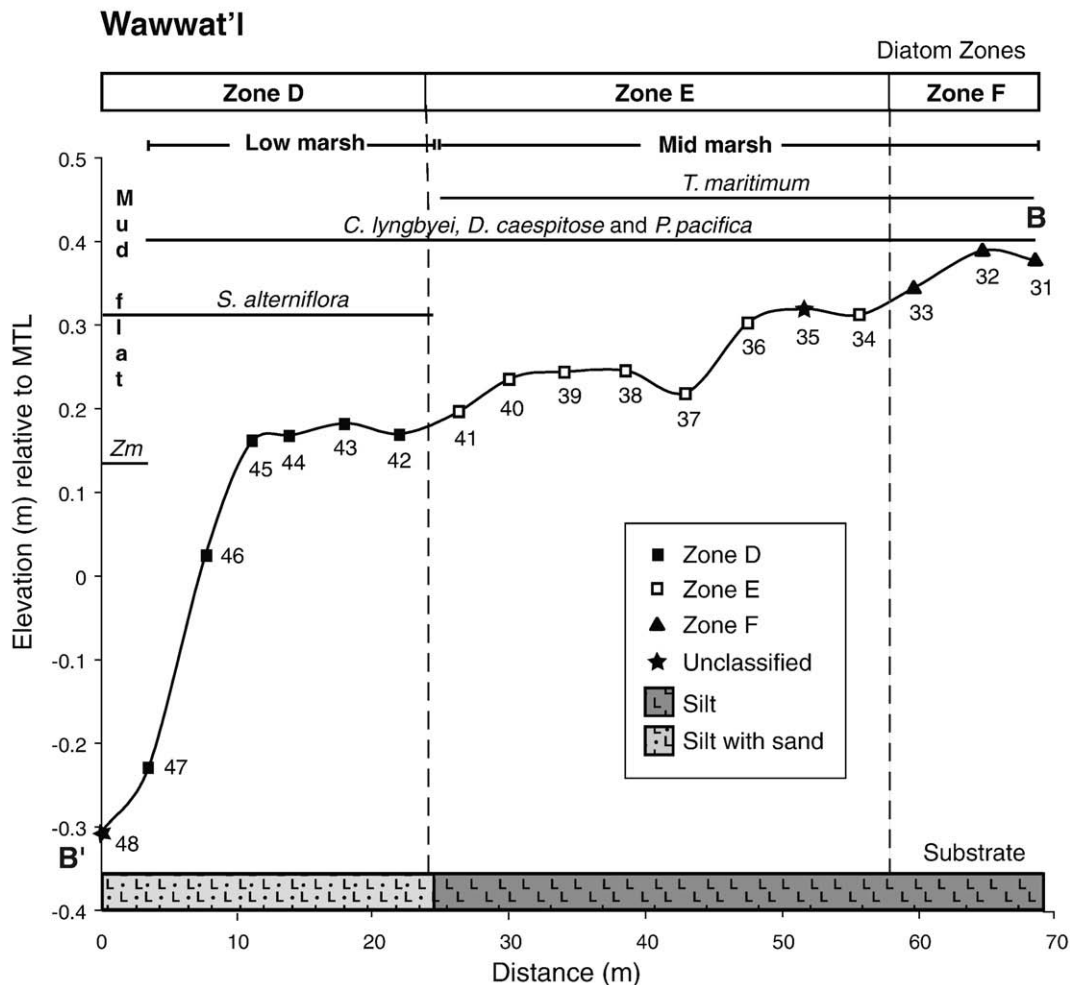


Fig. 3. Wawwat'l saltmarsh transect (elevation (m) relative to MTL) showing diatom zonations and their relationship to the associated vegetation zones. The dominant vegetation is shown (Zm = *Zostera marina*).

elevation calculations in relation to MTL were not distorted by meteorological conditions on the days of sampling, GPS measurements were also taken of local barnacle (*Cthamalus dalli*) elevations on rocky outcrops adjacent to the two saltmarshes (Doherty, 2005). This species of barnacle occupies a narrow vertical range near the Mean High Water Spring Tide (MHWST) mark (Stephenson and Stephenson, 1972; P. Lambert, Royal British Columbia Museum, pers. comm., 2005). Repeated measurements of the barnacle height distribution at different points around the inlets confirmed that the methodology for sample height calculation (in MTL) on the sampling days described above gave reasonable results. Total height errors associated with the height calculation methods described above are estimated to be no greater than a few centimeters, and any errors are likely to have been constant across the two marshes.

Diatom samples were collected from the surface of the two saltmarshes at regularly spaced (ca. 5 cm) vertical intervals and at key changes in the vegetation (cf. Zong and Horton, 1998, 1999). In total, 30 samples were collected from Waump saltmarsh and 18 from Wawwat'l. The samples were collected using a 6 cm diameter gouge which was pushed into the ground 10 cm at each sampling station to recover a mini-core. The top 1 cm of the mini-cores was later removed

in the laboratory for microfossil and environmental variable analyses. The upper 1 cm layer allows integrated samples of the diatom taxa to be examined that have accumulated over the previous few years, and avoids problems associated with seasonal blooms (cf. Admiraal et al., 1984). The samples were also used to determine the conductivity, pH, organic content, clay, silt and sand fraction of the sediment at each sampling point.

3.1. Diatom analysis

Preparation of the sediments for diatom analysis followed established techniques (cf. Battarbee et al., 2001). The diatoms were mounted in Naphrax and examined using light microscopy with a $\times 100$ oil immersion objective (magnification of $\times 1000$). At least 400 diatom valves were enumerated for most samples, although for a small number of samples where small quantities of fine sand was present in the residues a minimum of 300 valves were counted. Diatom frequencies were expressed as a percentage of total diatom valves (% TDV) counted in each sample (cf. Zong, 1997). Intact frustules were counted as two valves (cf. Hemphill-Haley, 1993) and fragments consisting of more than one half of a diatom valve were included in the

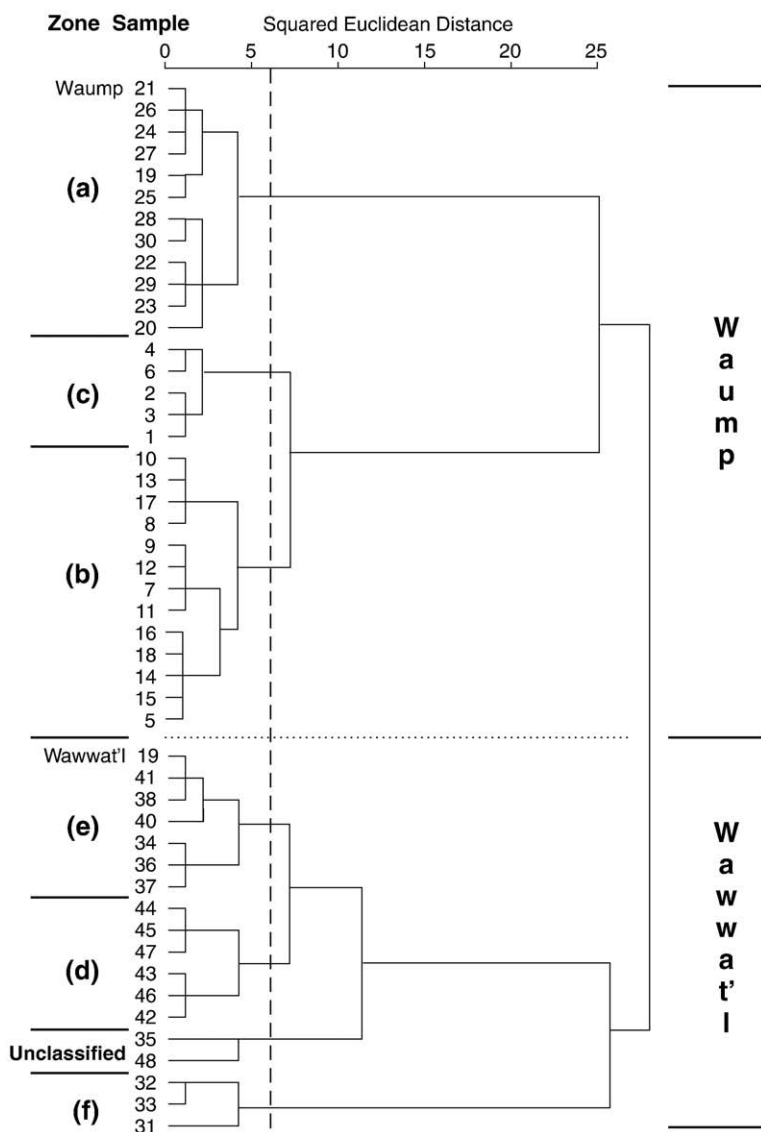


Fig. 4. Q-mode cluster diagram characterizing diatom populations quantified from samples collected on the Waump and Wawwat'l saltmarshes. The dashed line signifies the selected level of significance.

counts (Nelson and Kashima, 1993; Battarbee et al., 2001; Sawai, 2001). Diatom identifications were made with reference to a range of keys, including Cumming et al. (1995), Germain (1981), Hartley (1986), Krammer and Lange-Bertalot (1986, 1988, 1991a,b), Patrick and Reimer, (1966, 1975) and Van Der Werff and Huls (1976). The diatoms were classified according to the halobian system, which divides the diatom species into five categories of salt tolerance: polyhalobous (fully marine), mesohalobous (brackish-water), oligohalobous halophilous (salt-tolerant freshwater), oligohalobous indifferent (tolerate slightly saline water) and halophobous (exclusively freshwater, salt-intolerant) (cf. Corner and Haugane, 1993; Zong et al., 2003).

Seventy-seven species of diatoms were identified in the samples collected from the two marshes (Appendices 1–3). The relative fractional abundance (F_i) of each taxon for each sample was calculated as follows:

$$F_i = \frac{C_i}{N_i}$$

where C_i is the species counts and N_i is the total of all the species counts in that sample. Using this information, standard error (S_{xi})

associated with each taxon was calculated using the following formula:

$$S_{xi} = 1.96 \sqrt{\frac{F_i(1-F_i)}{N_i}}$$

If the calculated standard error was greater than the fractional abundance for a particular species in all samples then that species was not included in successive multivariate analyses (Patterson and Fishbein, 1989). Of the 77 diatom species recorded in the study, 67 were found in statistically significant numbers in at least one sample (Appendix A).

3.2. Environmental variables

The organic content of the sediment was calculated using the loss-on-ignition (LOI) technique. Samples were air-dried for 24 h at 45 °C and subsequent combustion at 550 °C for 4 h (cf. Zong, 1997). The organic matter content was calculated as a percentage of weight loss of the dried samples after combustion (Yu et al., 2003).

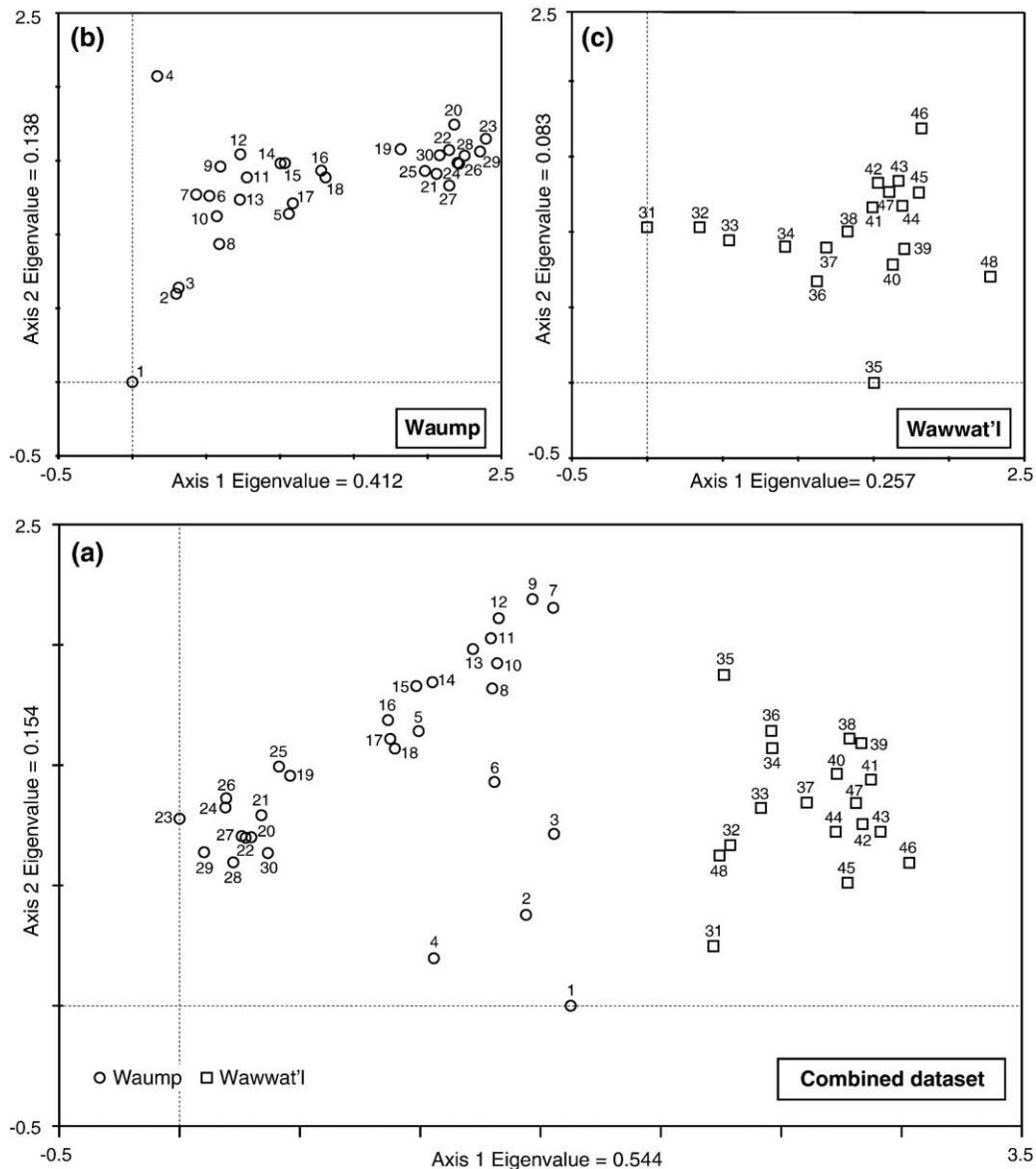


Fig. 5. Detrended correspondence analysis (DCA) results showing principal patterns of variation in the diatom populations for the combined dataset (a) and for the Waump (b) and Wawwat'l (c) saltmarshes.

The particle size of the saltmarsh surface samples was determined using a laser particle size analyser (GALAI CIS-100). 2–3 g of sediment was treated with 30% hydrogen peroxide to remove organic material. Mechanical dispersion by ultrasonic stirring was used to separate the sediment particles (Shi, 1995). Subsequently, approximately 1 g of sediment was introduced to a solution of filtered water with GALAI data collection set to the 99% confidence level (Nichol et al., 2003). The conductivity and pH of the samples were determined in the laboratory using conductivity and pH meters (Rowell, 1994). 5 cm³ of sediment was disaggregated with distilled water in a ratio of 1:2.5 until all the sediment was well mixed and in suspension (cf. Charman et al., 2002). The pH was measured using an Orion 410A pH meter, whilst conductivity readings were taken with a Hanna Instruments conductivity meter, keeping the suspension at a constant temperature of 20 °C.

3.3. Multivariate analysis

Statistical techniques were used to examine the diatom assemblage characteristics and to quantify the relationship between the diatom assemblages and the environmental variables within the two marshes. This approach has been extensively used in sea-level studies (Nelson and Kashima, 1993; Shennan et al., 1996; Hemphill-Haley, 1996; Zong, 1997; Zong and Horton, 1999; Szkornick et al., 2006). Q-mode cluster analysis was first used to group statistically similar populations using Ward's Minimum variance method, and recorded as squared-Euclidean distances (Fishbein and Patterson, 1993). Q-mode cluster analysis was carried out on the 67 species found in statistically significant populations in the 48 samples from the two marshes, and organized into a hierarchical diagram (Fig. 4). Q-mode cluster analysis was also performed separately on the samples from the two sites to examine intra-site diatom distribution patterns. Detrended correspondence analysis (DCA) was also carried out on the full dataset (77 species) and the two individual site datasets to explore the inter- and intra-site characteristics of the diatom populations (Fig. 5). As with cluster analysis, DCA does not include any environmental variables and is based exclusively on the species composition of each sample.

The relationship between diatom assemblages and environmental variables from the saltmarshes was explored using canonical correspondence analysis (CCA) and partial canonical correspondence analysis (pCCA). Analyses were undertaken using CANOCO (v. 3.12; Ter Braak, 1991). Prior to statistical analysis, species and environmental data were screened to identify and eliminate unusual or 'outlier' samples (Birks et al., 1990). No particularly unusual samples were identified, so the analyses were based on the entire dataset of 48 samples and 77 species. CCA uses a chi-square measure, which may give rare species a large influence on the ordination (Faith et al., 1987; Legendre and Legendre, 1998). However, CCA is applied here as the species dataset contains many null abundances and the chi-square distance should thus provide a good approximation for species with unimodal distributions along an environmental gradient (Ter Braak, 1985; Legendre and Gallagher, 2001). Rare species were down-weighted to reduce the effects of this problem in CCA (cf. Zong and Horton, 1999). The statistical significance of the CCA axes were determined using Monte Carlo permutation tests (with 499 permutations). A series of pCCA were used to determine the relative contributions of the environmental variables on assemblage composition (Borcard et al., 1992). Analyses were run for the two marshes individually and for the combined dataset (Table 1).

The numerous environmental factors which control diatom distribution in saltmarshes are often highly correlated (Anderson, 2000). For this reason, Pearson correlation analysis was used to determine the intercorrelations between the measured environmental variables (elevation, LOI, pH, conductivity, clay, silt and sand

Table 1

Canonical correspondence analysis (CCA) results for Waump, Wawwat'l and the combined datasets for the first four axes

Axes	1	2	3	4	Total inertia
Waump					
Eigenvalues	0.384	0.102	0.037	0.023	1.240
Species–environment correlations	0.968	0.738	0.642	0.681	
Cumulative percentage variance					
Of species data	30.9	39.1	42.1	44.0	
Of species–environment relation	66.8	84.5	90.9	95.0	
Sum of all eigenvalues					1.240
Sum of all canonical eigenvalues					0.574
Wawwat'l					
Eigenvalues	0.200	0.098	0.047	0.030	0.793
Species–environment correlations	0.911	0.868	0.686	0.752	
Cumulative percentage variance					
Of species data	25.3	37.7	43.6	47.4	
Of species–environment relation	49.6	74.0	85.6	93.0	
Sum of all eigenvalues					0.793
Sum of all canonical eigenvalues					0.404
Combined Waump and Wawwat'l					
Eigenvalues	0.339	0.266	0.054	0.030	1.861
Species–environment correlations	0.852	0.823	0.627	0.551	
Cumulative percentage variance					
Of species data	18.2	32.5	35.4	37.0	
Of species–environment relation	46.6	83.2	90.6	94.8	
Sum of all eigenvalues					1.861
Sum of all canonical eigenvalues					0.727

fraction) and hence provide some idea of the amount of redundancy in the environmental dataset (cf. Birks, 1995).

4. Results

4.1. Sediment analysis

The sediments from the Waump saltmarsh are generally composed of silts with some clay, and low levels of sand (Fig. 6). The clay fraction decreases from high marsh (18%) to low marsh (>3%). The organic content increases considerably from the pioneer marsh (9%) to the high marsh (72%), which coincides with the increasing coverage of vascular vegetation. The sediment pH increases from neutral at the high marsh (pH 6.8), to slightly more acidic (pH 5.5) at the low marsh as the frequency of tidal inundation increases. The conductivity is high at the seaward edge of the saltmarsh (ca. 500 µs), but generally decreases inland to ca. 200 µs.

The sediments across Wawwat'l saltmarsh are composed of silt with low levels of sand. The clay fraction fluctuates throughout the sampling transect (Fig. 7). The organic content within the sediments is low, despite the dense cover of vascular vegetation. The organic content is lowest (5–16%) in the mud-flat and low marsh zone, but reaches 18–31% in the mid-marsh. Hydrologically, the saltmarsh may be influenced episodically by discharges of freshwater from the Seymour River to the west of the sampling area (Fig. 1e). A small amount of freshwater also drains onto the back saltmarsh from the adjacent steep sided slopes. Freshwater inputs produce a wide range of salinities and pH values (Fig. 7).

4.2. Diatom zonation

Both the Q-mode cluster analysis (Fig. 4) and the DCA analysis results (Fig. 5) indicate that there is little statistical overlap of the diatom assemblages in the two marshes. The Q-mode cluster analysis results (Fig. 4) divide the diatoms into six assemblage zones; zones A, B, C for Waump (Figs. 2 and 8) and zones D, E, and F for Wawwat'l (Figs. 3 and 9). These Q-mode analysis cluster zones, which are shown for the combined dataset (Fig. 4), were found to be identical to the cluster zones defined by

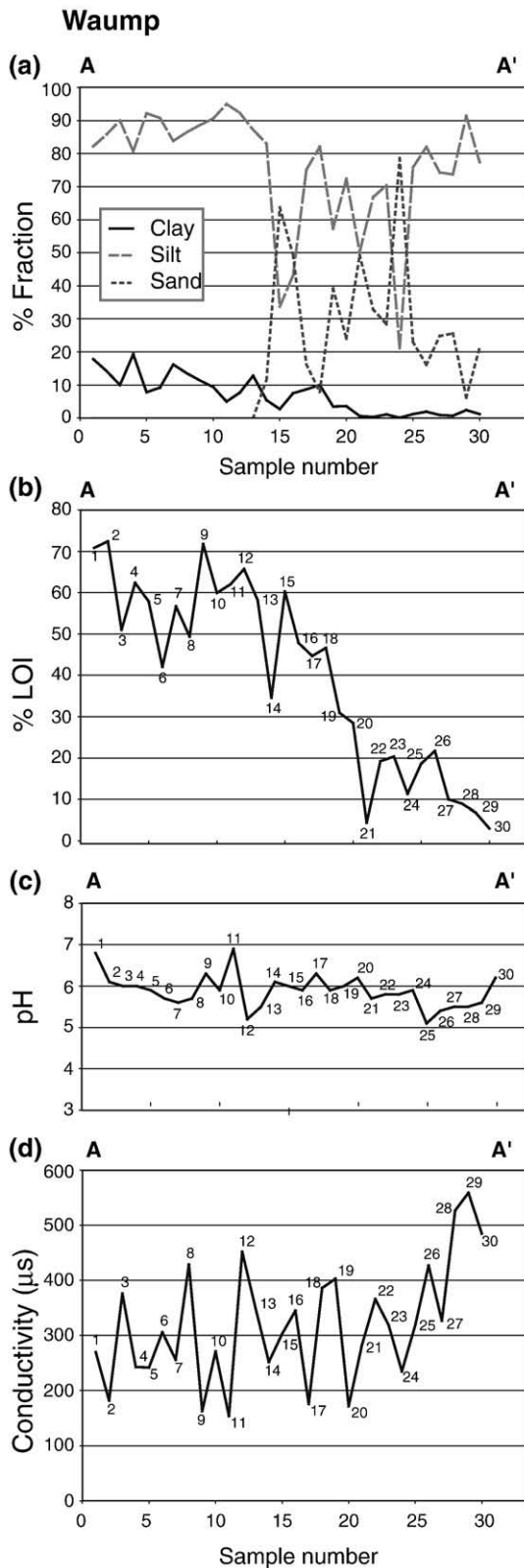


Fig. 6. Graphs showing a) the percentage clay, silt and sand fraction; b) the percentage LOI values; c) the pH; and d) the conductivity of the contemporary surface samples at Waump saltmarsh.

Q-mode mode cluster analysis for the two individual site datasets. For this reason the individual site plots are not presented here.

Zone A at Waump is recorded from the upper tidal flat and low marsh around the local Mean High Water Spring Tide (MHWST)

(−0.26 m to +0.45 m relative to MTL). The diatom assemblages are dominated by oligohalobous-indifferent species, with significant frequencies of *Fragilaria exigua* Grunow in Cleve & Möller 1878 (14–

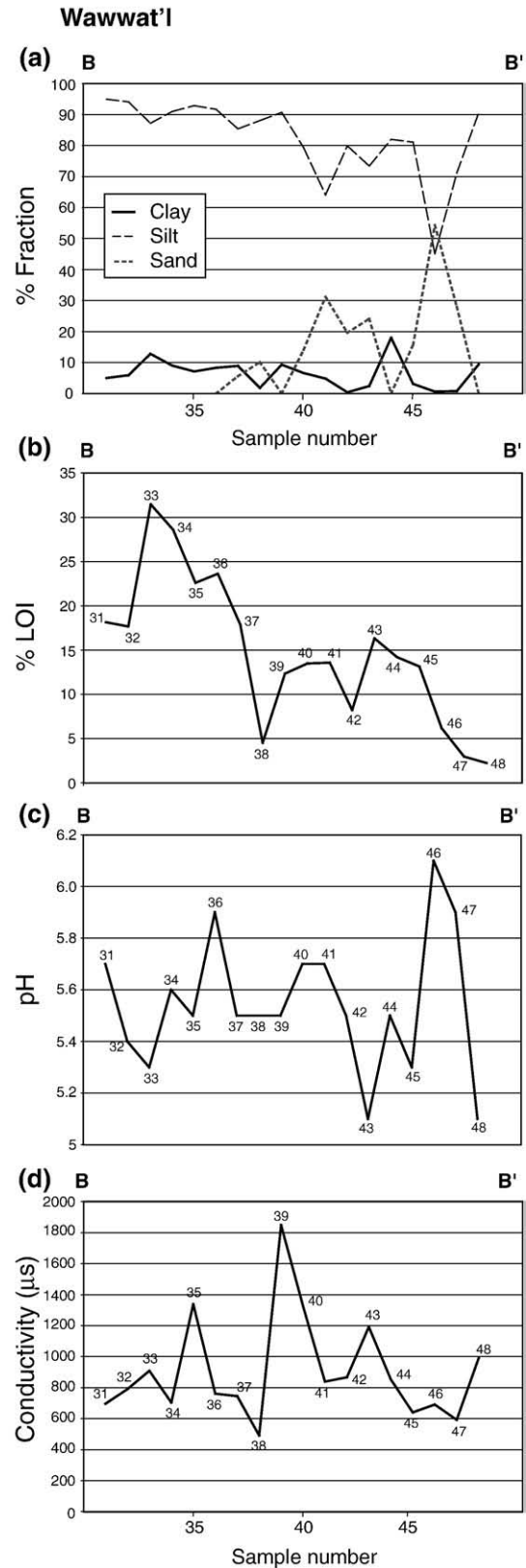
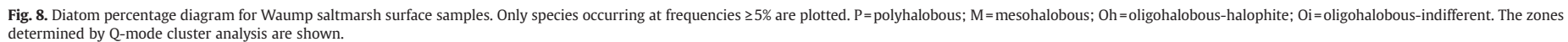


Fig. 7. Graphs showing a) the percentage clay, silt and sand fraction; b) the percentage LOI values; c) the pH; and d) the conductivity of the contemporary surface samples at Wawwat'l saltmarsh.



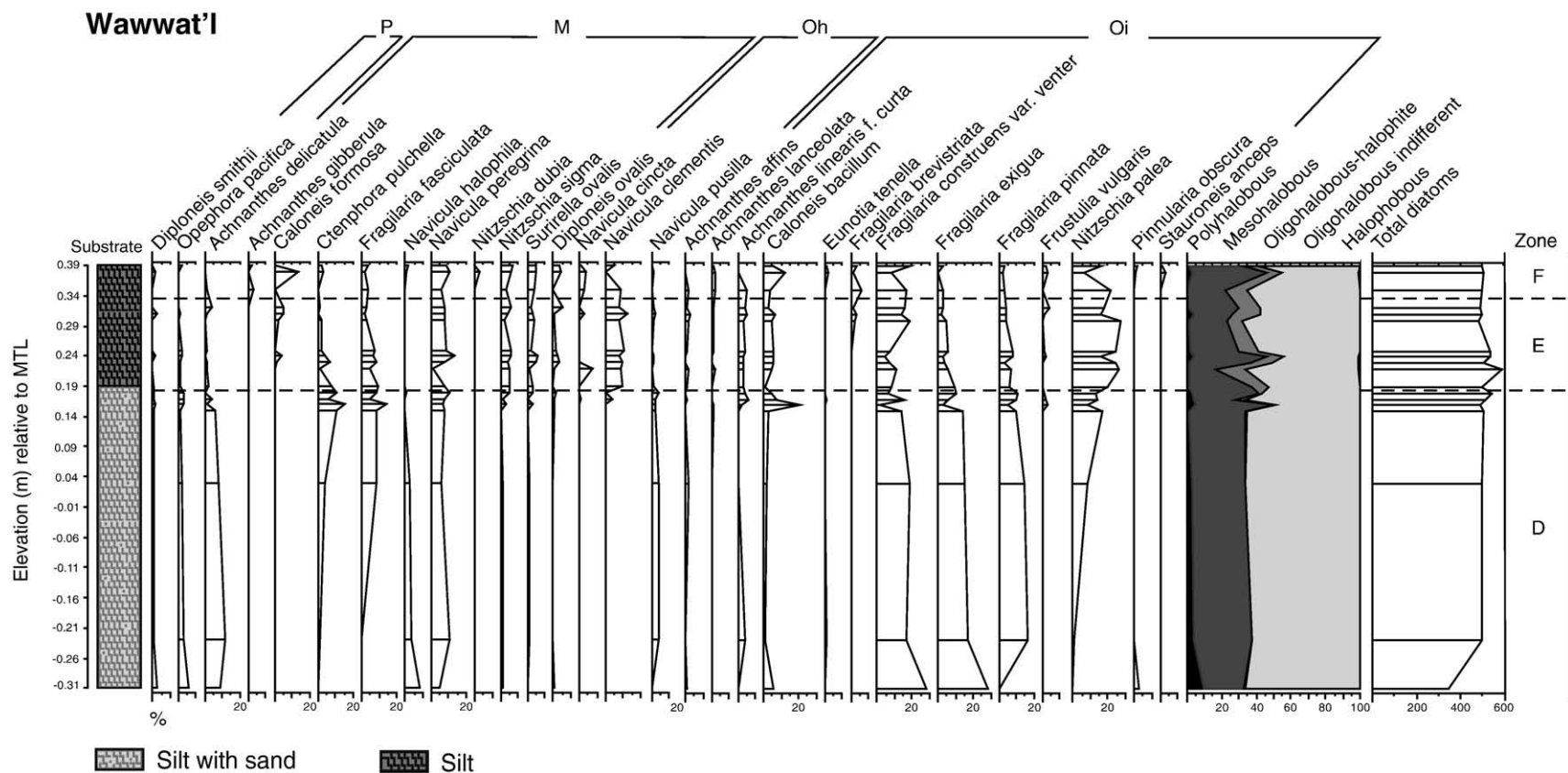


Fig. 9. Diatom percentage diagram for Wawwat'I saltmarsh surface samples. Only species occurring at frequencies $\geq 5\%$ are plotted. P=polyhalobous; M=mesohalobous; Oh=oligohalobous-halophite; Oi=oligohalobous-indifferent. The zones determined by Q-mode cluster analysis are shown.

30%) and the epipellic species *Caloneis bacillum* (Grunow) Cleve 1894 (7–22%), which is closely related to the silty tidal flat (Figs. 2 and 8). Polyhalobous species, dominated by the epipellic species *Diploneis smithii* (Brébisson ex W. Smith) Cleve 1894, generally decline throughout this zone. Mesohalobous species fluctuate between 4 and 27%, with significant frequencies of the epiphytic species *Ctenophora pulchella* (Ralfs ex Kützing) Williams & Round 1986.

Zone B is associated with the mid-marsh at Waump (+0.45 m to +0.84 m relative to MTL; Fig. 2) and is characterised by a pronounced increase in freshwater diatoms, particularly oligohalobous-indifferent species (51–76%; Fig. 8). These include high frequencies of *F. exigua* (23–54%) and the epipellic species *C. bacillum* (5–18%). Polyhalobous species fall to trace levels (ca. 1%). High frequencies of mesohalobous species, dominated by the epiphytic species *C. pulchella*, are recorded. Oligohalobous-halophite species, dominated by the aerophilous species *Diploneis ovalis* (Hilse in Rabenhorst) Cleve 1891, generally increase.

Zone C covers the high marsh at Waump (+0.71 m to +0.80 m relative to MTL; Fig. 2). It is characterised largely by oligohalobous-indifferent species (74–90%), and includes a decline in mesohalobous and polyhalobous species. The assemblages are dominated by *F. exigua*, *Nitzschia palea* (Kützing) W. Smith 1856, *Pinnularia obscura* Krasske 1932 and *C. bacillum* (Fig. 8). Oligohalobous-halophite species, dominated by *Diploneis ovalis*, increase, which is related to the increase in elevation and an associated decrease in the frequency of tidal inundation.

At Wawwat'l, Zone D is recorded from the upper tidal flat and low marsh (−0.31 m to +0.18 m relative to MTL; Fig. 3). The diatom assemblages are dominated by oligohalobous-indifferent species (52–67%), with significant frequencies of *Fragilaria construens* var. *venter* (Ehrenberg) Grunow 1881, *F. exigua*, *Fragilaria pinnata* Ehrenberg 1843, and *N. palea* (Fig. 9). There are moderate frequencies of mesohalobous species (23–45%), such as *Fragilaria fasciculata* (Agardh) Lange-Bertalot 1980, the epiphytic species *C. pulchella*, and the epipellic species *Navicula peregrina* (Ehrenberg) Kützing 1844.

Zone E is associated with the Wawwat'l mid-marsh (Fig. 3), recorded around the local MHWST (+0.18 m to +0.33 m relative to MTL) and is dominated by oligohalobous-indifferent species, such as *N. palea* and *F. construens* var. *venter* (Fig. 9). High frequencies of mesohalobous species (16–43%), with significant frequencies of *Caloneis formosa* (Gregory) Cleve 1894, and the epipellic species *N. peregrina* are recorded. Oligohalobous-halophite species generally increase.

Zone F is associated with samples from the upper part of the mid-marsh at Wawwat'l (+0.34 m to 0.39 m relative to MTL). It is characterized by a slight frequency increase in some oligohalobian species, including *C. bacillum*, *Fragilaria brevistriata* Grunow in Van Heurck 1885 and *Eunotia tenella* (Grunow) Hustedt in Schmidt 1913, and small increases in the frequencies of the mesohalobian species *C. formosa* and *Achnanthes gibberula* Grunow in Cleve & Grunow 1880. Other assemblage components are similar to the previous zone.

At Wawwat'l, two anomalous outlier samples, 35 and 48, were also identified based on the results of the Q-mode cluster analysis and subsequent visual analysis (Fig. 4). These were also confirmed to be anomalous based on the DCA results (Fig. 5c). The floras in these samples were probably transported, as a result of either seasonal flooding of the adjacent stream or wave action.

The DCA analyses for the individual sites (Fig. 5b and c) show similar clustering trends to those indicated by the Q-mode cluster analyses, particularly for Waump, where samples from diatom Zone A from the tidal flat and low marsh (samples numbers 19–30; Fig. 2) plot out in a separate cluster from those from Zone B from the mid to high marsh. For Wawwat'l the clustering is less distinctive, although the samples from the mid marsh (31–41) generally occur on the left side of the DCA plot whilst those from the low marsh (42–48) occur towards the right.

4.3. Canonical correspondence analysis

For the CCA analyses, the length of the environmental arrows represents their relative importance in explaining the variance in the diatom data and their orientation indicates their approximate correlations to ordination axes and other environmental variables (Weckstrom et al., 1997; Zong and Horton, 1999). Therefore, the longer arrows generally represent variables that have greater importance in

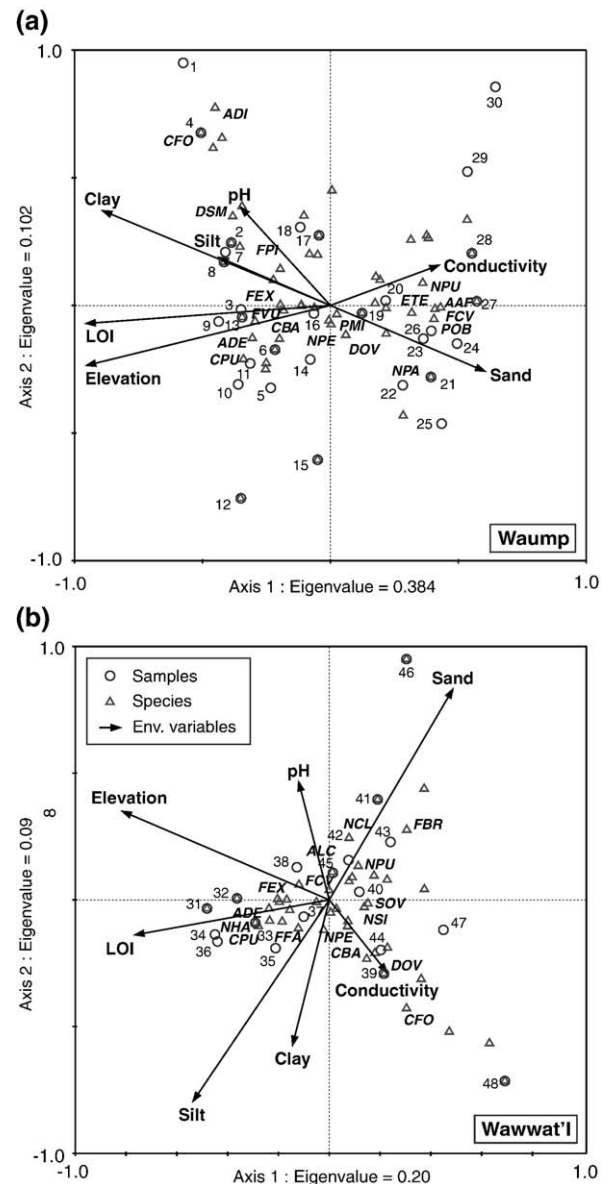


Fig. 10. CCA species-sample-environment tri-plots for the surface samples from Waump (a) and Wawwat'l (b) saltmarshes. The length of the arrows provides an indication of the strength of the correlation. The species names are indicated for species occurring at frequencies of $\geq 5\%$. *Achnanthes* affinis (AAF), *Achnanthes delicatula* (ADE), *Achnanthes linearis* f. *curta* H.L. Smith 1980 (ALC), *Aulacoseira distans* (ADI), *Caloneis bacillum* (CBA), *Caloneis formosa* (CFO), *Ctenophora pulchella* (CPU), *Diploneis ovalis* (DOV), *Diploneis smithii* (DSM), *Eunotia tenella* (ETE), *Fragilaria brevistriata* (FBR), *Fragilaria capucina* var. *vaucheriae* (Kützing) Lange-Bertalot 1980 (FCV), *Fragilaria exigua* (FEX), *Fragilaria fasciculata* (FFA), *Fragilaria pinnata* (FPI), *Frustulia vulgaris* (FVU), *Navicula clementis* (NCL), *Navicula halophila* (NHA), *Navicula peregrina* (NPE), *Nitzschia palea* (NPA), *Nitzschia pusilla* (NPU), *Nitzschia sigma* (Kützing) W. Smith 1853 (NSI), *Pinnularia microstaurum* (Ehrenberg) Cleve 1891 (PMI), *Pinnularia obscura* (POB), *Surirella ovalis* (SOV).

the dataset (cf. Ter Braak, 1986; Weckstrom et al., 1997). On species–sample–environment tri-plots, the taxa and samples are projected perpendicularly onto the environmental arrows, which approximate their weighted average optima along each environmental variable (Horton et al., 1999). As the Q-mode cluster results and the DCA analyses for the two marshes indicate that the associated diatom assemblages are quite distinct from each other, CCA was carried out on each marsh individually to better characterize the environmental variables influencing the assemblages at each site (Fig. 10). The CCA plot for the combined dataset (Fig. 11) allows the species–environment relationships to be considered for the dataset as a whole and

Table 2

Partial canonical correspondence analyses (pCCA) results for the Waump and Wawwat'l saltmarshes and for the combined dataset

	Waump		Wawwat'l		Combined	
	%	p<	%	p<	%	p<
Loss-on-ignition	3.66	0.752	7.18	0.592	5.64	0.120
pH	7.67	0.106	8.42	0.518	4.26	0.290
Clay	2.79	0.910	6.44	0.708	4.26	0.302
Sand and silt	4.88	0.436	19.31	0.018	5.23	0.144
Conductivity	4.01	0.742	13.86	0.150	19.39	0.002
Elevation	7.67	0.090	13.61	0.186	7.98	0.024
Intercorrelations	69.34	n/a	31.19	n/a	53.23	n/a

The results of the Monte Carlo permutation tests (p values) are shown. Silt and sand were combined in the analyses because the two variables showed a high degree of collinearity (Table 3).

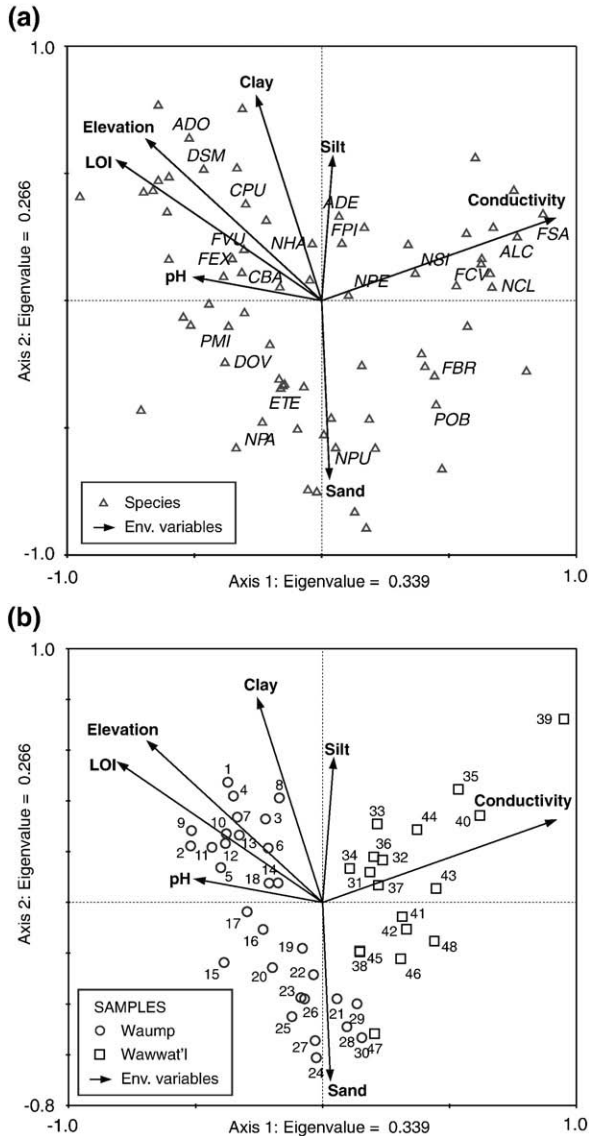


Fig. 11. CCA bi-plots for the combined dataset of surface samples from Waump and Wawwat'l marshes: (a) species–environment bi-plot; (b) sample–environment bi-plot. The length of the arrows provides an indication of the strength of the correlation. The species names are indicated for species occurring at frequencies of $\geq 5\%$. *Achnanthes affinis* (AAF), *Achnanthes delicatula* (ADE), *Achnanthes linearis f. curta* (ALC), *Aulacoseira distans* (ADI), *Caloneis bacillum* (CBA), *Caloneis formosa* (CFO), *Ctenophora pulchella* (CPU), *Diploneis ovalis* (DOV), *Diploneis smithii* (DSM), *Eunotia tenella* (ETE), *Fragilaria brevistriata* (FBR), *Fragilaria capucina* var. *vaucheriae* (FCV), *Fragilaria exigua* (FEX), *Fragilaria fasciculata* (FFA), *Fragilaria pinnata* (FPI), *Frustulia vulgaris* (FVU), *Navicula clementis* (NCL), *Navicula halophila* (NHA), *Navicula peregrina* (NPE), *Nitzschia palea* (NPA), *Nitzschia pusilla* (NPU), *Nitzschia sigma* (NSI), *Pinnularia microstauron* (PMI), *Pinnularia obscura* (POB), *Surirella ovalis* (SOV).

allows some preliminary observations to be made on the suitability of the combined dataset for local diatom-based RSL reconstructions.

4.3.1. Waump Marsh

For the Waump CCA result (Table 1), all canonical axes were significant at $p < 0.0020$. Axis 1 (eigenvalue=0.384) and Axis 2 (eigenvalue=0.102) together explained 39.1% of the variance in the species data and 84.5% of the species–environment relationship (Fig. 10a; Table 1). Conductivity and sand correlate with Axis 1, whilst elevation, loss-on-ignition clay and silt are negatively correlated. Samples from the lower part of the marsh and mudflat are strongly positively correlated with sand and conductivity. Species associated with these samples include *Diploneis ovalis*, *Navicula pusilla* (Kützing) Grunow 1862 emend. Lange-Bertalot 1976, *Achnanthes affinis* Grunow in Cleve & Grunow 1880, *E. tenella*, *P. obscura*, and *N. palea*, whilst species which are negatively correlated and associated with elevation and LOI include *Frustulia vulgaris* (Thwaites) De Toni 1891, *Achnanthes delicatula* (Kützing) Grunow in Cleve & Grunow 1880, *F. exigua* and *C. pluchella*. Species associated with silt and clay-dominated samples include *F. pinnata*, *C. formosa* and *Aulacoseira distans* (Ehrenberg) Simonsen 1979. It was calculated from the CCA that all of the environmental variables account for 46.3% of the explained variance in the Waump species data.

4.3.2. Wawwat'l Marsh

For the Wawwat'l CCA result (Table 1), the first canonical axis was significant at $p < 0.0080$ and the rest of the axes were significant at $p < 0.0140$. Axis 1 (eigenvalue=0.20) and Axis 2 (eigenvalue=0.098) together explain 37.7% of the variance in the species data and 74.0% of the species–environment relationship. Elevation, loss-on-ignition and silt are negatively correlated with Axis 1 and the other environmental variables correlate with both axes (Fig. 10b). A similar pattern is observed in the sample distributions, with lower marsh/tidal flat samples being positively correlated with conductivity and sand, and the higher marsh samples being negatively correlated with elevation, loss-on-ignition and more finely grained samples. Species correlating strongly with conductivity and sand include *C. formosa*, *D. ovalis*, *C. bacillum*, *F. brevistriata*, *Surirella ovalis* Brébisson 1838, *Nitzschia pusilla* and *Navicula clementis* Grunow 1882. Species correlating strongly with loss-on-ignition, elevation and the more finely grained samples include *Navicula halophila* (Grunow) Cleve 1894, *C. pluchella*, *A. delicatula* and *F. exigua*. It was calculated from the CCA that all of the environmental variables account for 50.9% of the explained variance in the Wawwat'l species data.

4.3.3. Combined dataset

For the combined Waump and Wawwat'l CCA result (Table 1), all canonical axes were significant at $p < 0.0020$. Axis 1 (eigenvalue=0.339) and Axis 2 (eigenvalue=0.266) together explained 32.5% of the variance in the species data and 83.2% of the species–

Table 3

Pearson correlation coefficients between environmental variables assessed in Waump and Wawwat'l marshes

		Elevation	LOI	pH	Conductivity	Clay	Silt	Sand
Elevation	Pearson correlation	1	0.892**	0.437**	-0.448**	0.566**	0.149	-0.281
	Sig. (2-tailed)		0.000	0.002	0.001	0.000	0.313	0.053
	N	48	48	48	48	48	48	48
LOI	Pearson correlation	0.892**	1	0.470**	-0.514**	0.636**	0.192	-0.337*
	Sig. (2-tailed)	0.000		0.001	0.000	0.000	0.191	0.019
	N	48	48	48	48	48	48	48
pH	Pearson correlation	0.437**	0.470**	1	-0.502**	0.151	-0.151	0.088
	Sig. (2-tailed)	0.002	0.001		0.000	0.304	0.306	0.554
	N	48	48	48	48	48	48	48
Conductivity	Pearson correlation	-0.448**	-0.514**	-0.502**	1	-0.024	0.210	-0.172
	Sig. (2-tailed)	0.001	0.000	0.000		0.873	0.153	0.242
	N	48	48	48	48	48	48	48
Clay	Pearson correlation	0.566**	0.636**	0.151	-0.024	1	0.431**	-0.640**
	Sig. (2-tailed)	0.000	0.000	0.304	0.873		0.002	0.000
	N	48	48	48	48	48	48	48
Silt	Pearson correlation	0.149	0.192	-0.151	0.210	0.431**	1	-0.969**
	Sig. (2-tailed)	0.313	0.191	0.306	0.153	0.002		0.000
	N	48	48	48	48	48	48	48
Sand	Pearson correlation	-0.281	-0.337*	0.088	-0.172	-0.640**	-0.969**	1
	Sig. (2-tailed)	0.053	0.019	0.554	0.242	0.000	0.000	
	N	48	48	48	48	48	48	48

** indicates that correlation is significant at the 0.01 level (2-tailed). * indicates that correlation is significant at the 0.05 level (2-tailed).

environment relationship (Fig. 11). Conductivity strongly correlates with Axis 1 as, to a lesser extent, do silt and fine sand. Clay, elevation, loss-on-ignition and fine sand are negatively correlated. As might be expected, there is a general similarity between the environmental variables and the distribution of species and samples to those shown in the individual CCA plots. For example, as in the plots for Waump and Wawwat'l (Fig. 10) samples from the low marsh correlate well with sand (Fig. 11). These samples are characterized by species such as *F. brevisstriata*, *N. pusilla* and *P. obscura*. In contrast to the results for the individual marsh sites, conductivity is the most important variable. However, some of the samples and the species associated with conductivity in the CCA analyses for the individual marshes are different to those associated with this variable in the combined CCA plot (Figs. 10 and 11). These inconsistent results in the combined dataset are likely to be an artifact of the significant difference in conductivity values measured between the two marshes (Figs. 6 and 7). It was calculated from the CCA that all of the environmental variables account for 39.1% of the explained variance in the combined dataset.

4.4. Partial canonical correspondence analysis

The partial canonical correspondence analysis (pCCA) quantifies the proportion of the variance that can be attributed to each of the measured environmental variables (Table 2) and provides confirmation that the factors influencing the distribution of the diatom assemblages in each marsh are quite variable. At Waump, elevation and pH both explain 7.67% of the variance, followed by grain size (4.88%) and conductivity (4.01%) (Table 2). At Wawwat'l, grain size (sand and silt) accounts for 19.31% and clay accounts for 6.44% of the variance, followed by conductivity (13.86%) and elevation (13.61%). For the combined dataset, conductivity explains 19.39%, elevation explains 7.98% of the variance. As noted above, the particularly high value attributed to conductivity in the combined dataset is again likely to be a product of the significant difference in the conductivity readings between the two sites (Figs. 6 and 7).

Pearson correlation analysis confirms that inter-correlations between measured variables are very strong (Table 3). For example, there is a strong correlation between loss-on-ignition and elevation (r value=0.892) and between elevation and conductivity (r = -0.448). This is an expected result in a saltmarsh environment, where the gradation from sandy sediments in the low marsh/tidal

flat to finer and more organic sediments in the mid and high marsh is the norm.

5. Discussion

5.1. Diatom distribution: patterns and controls

When considered as a whole, the surface diatom assemblages recorded in the two SIBC marshes show many similarities to those reported previously in other regional saltmarshes, particularly in relation to established vascular plant zones and other tidally-related controls, e.g., salinity and substrate (cf. Whiting and McIntire, 1983; Nelson and Kashima, 1993; Hutchinson et al., 1998). The high marsh assemblages described at Waump, for example, are dominated by oligohalobous indifferent species (e.g., *Pinnularia obscura*, *Caloneis bacillum*), aerophilous species such as *Diploneis ovalis*, and low levels of halophobous species. The associated vegetation, which includes *D. caespitose*, *D. spicata*, *L. americanum* and *C. lyngbyei*, is characteristic of the high marsh environment in this region (Hutchinson, 1982; Patterson, 1990; Hemphill-Haley, 1993; Nelson and Kashima, 1993). Similar oligohalobous diatom assemblages and plant community groupings have been reported in high marsh environments in the Fraser Delta, British Columbia (Hutchinson et al., 1998) and in southern Oregon (Nelson and Kashima, 1993).

The mid-marsh, recorded around the level of local MHWST, is associated with a wider range of diatom species than the high marsh, with mixed proportions of oligohalobous-indifferent (e.g., *Nitzschia palea*) and mesohalobian species (e.g., *Navicula peregrina*). Again, none of the species described are particularly remarkable in their distributions in the two SIBC marshes; the dominant species have all been reported previously in mid-marsh and mid- to high marsh settings in this region and elsewhere. The significant frequencies of *Fragilaria construens* at Wawwat'l saltmarsh are similar to those found at the landward section of Johns River, in south-west Washington (Shennan et al., 1996).

In common with other studies, the assemblages from the low marsh and tidal flats are dominated by increasing proportions of mesohalobian species, reflecting increased tidal flooding, and epipilic and epipsammic species reflecting substrate changes (cf. Whiting and McIntire, 1985; Hemphill-Haley, 1995; Shennan et al., 1996; Hutchinson et al., 1998). Elevated abundances of polyhalobian diatoms, e.g., *Opephora pacifica* (Grunow) Petit 1888, characterize the tidal flat samples.

Whilst the individual species distributions recorded in the two marshes are not particularly remarkable, the significant differences in assemblage composition between the two sites indicated by the Q-mode cluster analysis (Fig. 4) and the DCA analysis (Fig. 5a) are striking and require further explanation. These differences are particularly noteworthy given the similar depositional settings of the two marshes (both fjord-head marshes with drainage inputs from small rivers) and similar vegetation zones. The inlets where the marshes are located also have similar tidal ranges which differ only by a couple of centimetres (see Section 2) and samples were taken from overlapping elevations in the tidal frame. Several factors may account for the observed differences: i) environmental differences between the two sites (resulting in samples being collected from subtly different habitats); ii) seasonal and other sampling-related factors; and iii) taphonomic factors.

There is clear evidence to suggest that some of the differences in assemblage composition between Waump and Wawwat'l are related to variations in the measured environmental variables between the two sites. Most obvious amongst these are the differences in height recorded in the upper parts of the two sampling transects (the uppermost samples are ca. 45 cm different in height between the two marshes), and the associated absence in the dataset of any high marsh samples at Wawwat'l (Figs. 2 and 3). As stated above, samples could not be collected from the more elevated, landward part of the Wawwat'l marsh as access was hindered by a drainage channel. Logistical constraints prohibited further sampling of the high marsh elsewhere in this saltmarsh. If additional high marsh samples had been included from Wawwat'l, then the sample elevations would probably have been more similar between the two sites, possibly resulting in closer diatom assemblage clusterings. However, this does not explain why a significant proportion of the samples from the mid-to low saltmarsh zones and mudflat areas of the two marshes, which show overlapping heights, are so different. This indicates that other factors were operating.

The CCA and pCCA analyses provide some insights into the significance of other contributory factors. At Wawwat'l, the conductivity readings are notably higher than at Waump (Figs. 6 and 7) and the amount of variance explained by conductivity at Wawwat'l (13.86% $p < 0.150$) is considerably greater than at the latter site (4.01% $p < 0.742$) (Table 2). In general, the variable conductivity measurements (Figs. 6 and 7) suggest that the marshes are subject to considerable localised salinity variation, possibly driven by seepage as well as episodic fluctuations in river discharge. This is further suggested by the fluctuating, yet relatively high proportions of oligohalobous-indifferent diatom species (e.g., *Fragilaria exigua*) in the two low marsh/tidal flat assemblages zones (zone A at Waump and zone D at Wawwat'l) (Figs. 8 and 9), which indicate that freshwater throughputs are significant even in the most sea-ward areas of the saltmarshes. Moreover, the fact that 7.67% ($p < 0.106$) of the assemblage variance at Waump and 8.42% ($p < 0.518$) at Wawwat'l are explained by pH (Table 2), a variable which is closely inter-correlated with conductivity ($r = -0.502$; $p < 0.01$) (Table 3) and which would be expected to vary with freshwater inputs, further supports the idea that hydrological controls are important.

The CCA triplots and pCCA results also confirm that substrate and sediment organic content (LOI) have an impact on the assemblages. The low marsh and mud flat samples in particular were found to be strongly positively correlated with sand, as well as conductivity for both sites (Figs. 10 and 11). At Wawwat'l, sand and silt together explained 19.31% ($p < 0.018$) of the assemblage variance indicated by pCCA (Table 2). This result accords with the findings of Whiting and McIntire (1985) in Netarts Bay, Oregon who demonstrated that grain size is an important control on diatom distribution in estuarine and littoral areas, and noted that diatom floras associated with coarser substrates low in organic matter are often significantly different to those from vegetated tidal flats.

Some of the assemblage differences between the two marshes are also clearly a product of other abiotic variables and/or ecological factors that were not measured during the study. Subtle differences in habitat between the two sampling transects are certainly indicated by the varying abundances of some of the common species in the mid-marsh zone. The epiphytic species *C. pulchella*, for example, is more common at Waump than at Wawwat'l (Figs. 8 and 9). This species has been previously reported in association with surface macro-algae (Zong, 1997), which was noted sporadically at Waump but not measured in the field. The differing abundances of the dominant *Fragilaria* species between the two marshes, e.g., *Fragilaria exigua* and *Fragilaria construens* var *venter*, are also noteworthy. Little work has been undertaken to examine the controls on *Fragilaria* spp. in intertidal environments, although there is some evidence to suggest that nutrient availability may have an influence on some species (Lamontagne et al., 1986). Nutrient levels vary in turn with tidal dynamics (Lamontagne et al., 1986) and freshwater inputs (De Sève, 1993) and certainly both of these characteristics could have differed between the two sites, contributing to the observed assemblage differences. Fluctuations in temperature and irradiance also have an impact on tidal diatom communities (Admiraal and Peletier, 1980; Muylaert et al., 2000), although it is unlikely that these would have differed significantly between the two marshes.

In general, the rather mixed assemblages described from the mid-marsh zone are consistent with the findings of previous studies, which have reported diverse assemblages in these environments (e.g., Hutchinson et al., 1998; Hemphill-Haley, 1995; Patterson et al., 2000). Hutchinson et al. (1998) for example, found it difficult to distinguish between mid- and low marsh diatom assemblages in saltmarshes in the Fraser Delta of British Columbia. The mid-marsh zones are often transitional in character, being characterised by mixed salinities, varying degrees of intertidal exposure and variations in substrate. Together these would be expected to support a wide range of species.

A second set of factors which might explain some of the variation in the assemblages between the two sites relate to the method of sampling, including time of sampling and sample collection methods. For logistical reasons, the two saltmarshes were sampled at different times of year; Waump in April and Wawwat'l in October. These differences could have promoted differences in species abundances, with an inclusion of greater numbers of spring bloom diatoms in the Waump samples in relation to those from Wawwat'l. Diatom productivity is often enhanced in the spring and summer months in estuarine and intertidal areas as enhanced freshwater inputs introduce increased levels of nutrients into littoral waters, although different species respond differently to these changes (cf. De Sève, 1993; Sabbe, 1993). Temperature variations, irradiance, changes in photic depth and turbidity currents also vary seasonally and have an impact on diatom blooms (De Sève, 1993; Muylaert et al., 2000). Interestingly, the Waump samples yielded low (<2%) but persistent abundances of halophobe (freshwater, salt-intolerant) diatoms, unlike those from Wawwat'l, which might reflect recent input of spring freshet from the Waump Creek (Fig. 8). Since care was taken to ensure that the counts were based on the upper 1 cm of sediment – in line with many previous surface sampling studies (e.g., Gehrels et al., 2001; Zong et al., 2003; Hamilton and Shennan, 2005a; Szorknick et al., 2006) – and not the upper 1–2 mm which would have produced a more seasonal signal (cf. Hemphill-Haley, 1995), it seems unlikely that recent seasonal inputs would have had a significant impact on assemblage composition, and as such these inferences must be considered with caution. It is perhaps more likely that the 'averaged' signal obtained by analysing the top 1 cm layer of sediment could have biased the diatom counts towards assemblages that accumulated under slightly different hydrological, salinity or depositional regimes in the marshes in recent seasons/years. Again, these could have varied locally between the two sites, although no major differences were

noted in the vascular plant zones between the two marshes, which might have been the case if salinity/hydrological changes had persisted over a number of seasons. Further work is required to examine the effect of seasonal variations in river discharge on both diatom species distributions and clastic sediment inputs in these freshet-influenced, fjord-head marshes.

Finally, taphonomic processes may also account for some of the observed differences in assemblage composition between the two marshes. Intertidal diatom communities are well known to be subject to *post mortem* transportation associated with tidal movements, with the net effect that assemblages can include a significant allochthonous component (Vos and de Wolf, 1988, 1993; Hemphill-Haley, 1995; Sawai, 2001). In general, the allochthonous component increases with decreasing elevation in the intertidal zone as tidal influence increases (cf. Vos and de Wolf, 1988, 1993; Hemphill-Haley, 1995). As the sampling sets from the two SIBC saltmarshes include different proportions of high, mid- and low marsh samples, then the introduction of allochthonous diatoms from tidal mixing (and indeed from episodic freshwater pulses) may have differed between the two sites. Certainly some of the samples from the Wawwat'l saltmarsh (e.g., samples 48 and 35) seemed to display a number of assemblage differences to adjacent samples (Figs. 3 and 4) which might potentially have resulted from taphonomic factors. Several of the samples from both marshes also included significant levels of sand (Figs. 6 and 7) and as re-working has been observed to be greatest in association with clastic intertidal sediments (Vos and de Wolf, 1993), this may add tentative support to the idea that some degree of taphonomic mixing of diatom valves could have occurred. Overall though, it seems unlikely that tidal mixing and re-working could explain a significant amount of the assemblage variation between the two sites, particularly as the two marshes are similar in their tidal regimes. The other factors discussed above offer a more plausible explanation for the observed differences.

5.2. Suitability of the datasets for studies of relative sea-level change

For microfossil indicators to be used successfully in paleo-sea level studies, two criteria must be fulfilled: i) the indicators must show a known, and ideally a strong, quantifiable relationship to tidal elevation(s) in the modern environment; and ii) the fossil assemblages recovered from cores must be analogous to modern (surface) assemblages (cf. Zong and Horton, 1998, 1999; Horton et al., 1999; Gehrels et al., 2001; Patterson et al., 2005; Szkornick et al., 2006). The results of this study have shown that the surface diatom assemblages of the two SIBC saltmarshes display a zonation which is partly controlled by elevation, but is also influenced by other tidally-mediated controls, including conductivity, pH, substrate characteristics and LOI. This result is not atypical in a saltmarsh environment, given the known sensitivity of diatoms to a wide range of tidal and substrate-related parameters (cf. Vos and de Wolf, 1988, 1993; Zong and Horton, 1999). pCCA analysis demonstrates that out of seven variables measured, elevation explains 13.61% ($p < 0.186$) of the assemblage variance at Wawwat'l and 7.98% ($p < 0.09$) at Waump. However, at both sites other controls have a significant impact on diatom distribution. At Waump, for example, 7.67% ($p < 0.106$) of the assemblage variation is also explained by pH, whilst at Wawwat'l, sand and silt (at 19.31% $p < 0.018$) and conductivity (at 13.86% $p < 0.150$) have a greater influence on the diatom data than elevation.

For the combined pCCA dataset, elevation was found to be the second most important variable at 7.98% ($p < 0.024$) following conductivity (19% $p < 0.002$) in explaining assemblage variance (Table 2). However, the conductivity value was considered to be artificially high as it was determined to be a product of the conductivity readings having little overlap between the two sites.

We conclude that the saltmarsh diatom assemblages may have potential for quantitative reconstructions of RSL change in the SIBC

because i) elevation is a key control on assemblage distribution, particularly for the mid- and high marsh zones; ii) the other important controls, conductivity, substrate (particularly clay and LOI) and pH are strongly intercorrelated with elevation (Table 3); and iii) the indicative ranges of individual diatom species can be determined with relation to MTL for the two marshes, which could be used to derive quantitative MTL estimates based on fossil assemblages, providing the species are analogous to those in the modern environment (cf. Zong and Horton, 1999). The reconstructions should, however, proceed with caution, given that the measured controls have slightly different influences on the assemblages between the two sites and because CCA shows that a significant proportion of the total variance in the diatom data (53.7% for Waump, 49.1% for Wawwat'l and 60.9% for the combined dataset) is unexplained by the measured parameters (Table 1). This proportion is not, however, inconsistent with the findings of other modern saltmarsh diatom distribution studies which have measured a similar group of environmental variables (cf. Zong and Horton, 1999). With only 48 samples, the training set is also relatively small in comparison to some developed for intertidal diatoms in other regions. Zong and Horton (1999) for example, included 88 samples from six saltmarsh sites in a diatom-based training set for the UK. Interestingly, they also noted a certain degree of variation in diatom species composition between sites which they attributed to inter-site differences in freshwater inflow, tidal hydrology, sea-water salinity, substrate and ground-water acidity (Zong and Horton, 1999, p. 161). Given the remoteness and inaccessibility of the SIBC region and the associated difficulties of sample collection, the diatom dataset presented here nevertheless provides a useful foundation for interpreting fossil diatom datasets collected in the region (cf. Doherty, 2005).

Finally, it is interesting to note that the results of the surface diatom study compare well with the foraminiferal and thecamoebian analyses based on the same samples from the two marshes (Riveiros et al., 2007). This study also identified three surface assemblage zones based on unconstrained cluster analysis, the boundaries of which were similar to those identified by the diatoms (Riveiros et al., 2007 Fig. 5). CCA analysis of the foraminiferal dataset also demonstrated that Axis 1 is positively correlated with conductivity and negatively correlated with elevation, whilst the substrate variables (clay, silt and sand) were more closely correlated with Axis 2. The foraminiferal and thecamoebian assemblages were, however, more similar than the diatom assemblages, a reflection of the fact that foraminiferal marsh faunas are less diverse and appear to be less influenced by localised intertidal variables (cf. Patterson, 1990; Patterson et al., 2004; Riveiros et al., 2007). Further quantitative work is required to more fully compare the utility of the two groups of sea-level indicators in the two SIBC marsh environments (cf. Gehrels et al., 2001; Patterson et al., 2005).

6. Conclusions

This study set out to examine the controls on surface diatom distribution in two fjord-head saltmarshes in the Seymour–Belize Inlet Complex of central mainland British Columbia, with a view to assessing the utility of diatoms in regional studies of RSL change. Forty-eight surface sediment samples were collected from two marshes, Waump and Wawwat'l, and subject to diatom and environmental variable analysis (elevation, pH, conductivity, LOI, silt, clay and sand fraction). The diatom assemblages were found to be similar in their general distribution to those reported in previous regional saltmarsh studies, in that the assemblages become increasingly dominated by salt-tolerant and epipellic diatoms with decreasing tidal elevation. However, DCA analysis indicated that the assemblages are significantly different between the two sites. This result was confirmed by Q-mode cluster analysis which enabled the assemblages to be sub-divided into six distinct zones, three (zones A–C) from Waump and three (zones D–F) from Wawwat'l. The species–

environment relationships were investigated using CCA and pCCA which showed that the primary environmental controls influencing the assemblages are elevation (in relation to MTL) and pH at Waump, and conductivity, elevation and substrate (sand and silt) at Wawwat'l (Table 2). CCA shows that a significant proportion of the variance is also unexplained by the measured variables. We hypothesise that some of the observed variability in the diatom assemblages may reflect variations in river discharge or seepage between the two saltmarshes. This is not only indicated by the CCA analyses and the fluctuating conductivity and pH measurements between the two sites, but also by the varying abundances of some of the major oligohalobous diatom species (e.g., *Fragilaria exigua*) in the low marsh and tidal flat samples from both marshes. Such hydrological controls may also have affected the nutrient status or other physico-chemical properties of the collected marsh samples. The role of such episodic discharge events on both diatom distribution and clastic sediment inputs in this freshet influenced, fjord-head tidal marshes requires further examination. Differences in sample height between the two marshes may also have contributed to some of the assemblage variance. Other contributory factors, including taphonomic processes, were also evaluated but were considered to be of subsidiary importance to the measured and postulated environmental factors. In the light of the findings, we conclude that future diatom-based RSL reconstructions may be possible for the SIBC using the reported sampling (training) sets, although they should proceed with caution in recognition of the local differences in the key driving variables.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.marmicro.2008.12.001.

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