Relative utility of foraminifera, diatoms and macrophytes as high resolution indicators of paleo-sea level in coastal British Columbia, Canada

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Abstract

A multiproxy analysis was carried out on diatom, foraminiferal and macrophyte assemblages across the saltmarsh at Zeballos, Vancouver Island, British Columbia. To determine which group, or combination of groups provided the most accurate elevational zonations, 36 stepwise multiple linear regressions (SMLR) were carried out using a variety of data transformations on an elevational training set. Adjusted R^2 values yielded statistically significant results in all analyses as follows: foraminifera (0.658–0.870); diatoms (0.888–0.974); macrophytes (0.671–0.844); foraminifera/diatoms (0.941–0.981); foraminifera/diatoms/macrophytes (0.958–0.993). The most realistic SMLR results were obtained when data transformations comprised of (ln) normalized fractional abundance data was carried out on species present in statistically significant numbers (NrfaEQ). Of the individual proxies assessed, diatoms yielded the most significant adjusted R^2 results, with the low marsh diatom *Achnanthes hauckiana* being one of the most important predictor variables (pv's). Amongst the foraminifera, the low marsh species *Miliammina fusca* and high marsh *Balticammina pseudomacrescens* were determined to be the most significant pv's. For macrophytes, the low marsh species *Carex lyngbyei*, the high marsh species *Juncus balticus*, Shannon–Wiener Diversity Index (SDI) and absence of plant cover on the tidal flat were the most important pv's. As SMLR analysis of all individual groups and combinations of groups yielded statistically significant results, the choice of proxies, or combinations of proxies that are suitable for paleo-sea level research is at the discretion of the researcher.
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1. Introduction

Changes in relative sea level can have a significant impact on marshes (Scott and Medioli, 1978; Scott and Medioli, 1980). These changes can be linked to a number of factors, including climate change (van de Plassche et al., 1998; van de Plassche, 2000), coseismic [land] movements (Guilbault et al., 1996; Shennan et al., 1996; Zong et al., 2003) and isostatic movements (Gehrels, 1999; Gehrels et al., 2002). The distribution of many intertidal organisms such as macrophytes, foraminifera, thecamoebians and diatoms are closely related to elevation and local tidal conditions (Patterson et al., 2000; Gehrels et al., 2001). If the indicative ranges (cf., van de Plassche, 1986) of these organisms are known with precision, then the presence of in situ fossil remains of the species preserved in intertidal sediments can be used to determine changes in marsh
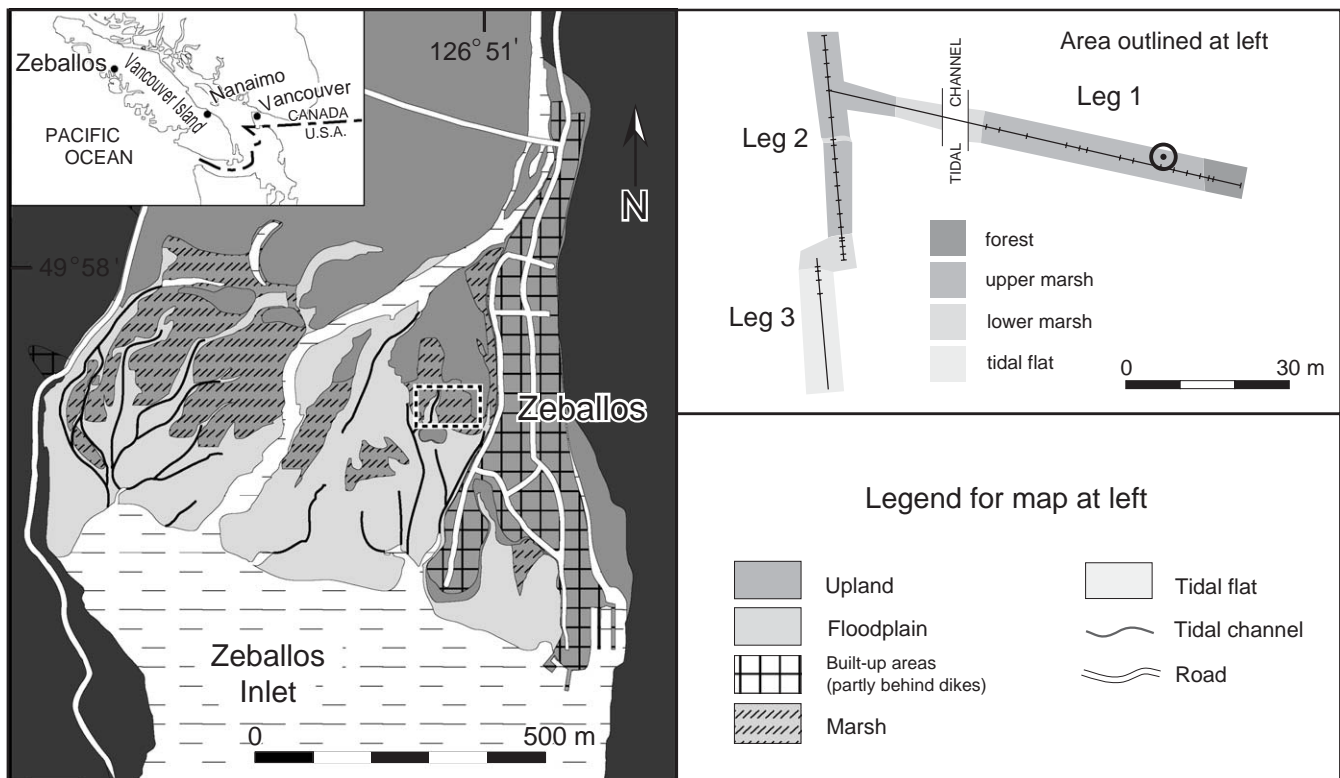
Fig. 1. Map of the Zeballos area (left) showing the location of the marsh transect and floodplain, marsh, tidal flat, and upland environments. Transect details are depicted on the right (modified after Patterson et al., 2000).

paleoelevation, whether caused by gradual sea-level change or abrupt changes related to earthquakes (Scott and Medioli, 1980; Varekamp et al., 1992).

Patterson et al. (2000) compared the vertical zonation of diatom, foraminifera, and macrophyte assemblages in a fjord-head marsh at Zeballos on the west coast of Vancouver Island, British Columbia, Canada (Fig. 1) to test whether all three groups of sea-level indicators could provide more accurate sea-level information than single indicators used in isolation. The purpose of that research was to integrate information on the vertical distribution of these three groups to see whether a higher resolution vertical zonation of the marsh could be obtained. An increase in elevational resolution is of considerable use to researchers as it permits recognition of even minor changes in relative sea level. A secondary goal was to permit sea-level change researchers, who generally only work with one type of marsh organism, to compare directly zonations obtained at different sites using different flora and fauna. This latter objective is particularly important as there have been relatively few research studies of this sort carried out (e.g. Patterson et al., 2000; Gehrels et al., 2001; Freund, et al., 2004).

Using Q-mode cluster analysis Patterson et al. (2000) determined that although diatom data alone produced the highest number of elevational zonations at Zeballos,

a composite analysis using foraminiferal, macrophyte and diatom data produced fewer misclassifications, resulting in more precise elevational determinations. Cluster analysis is a useful exploratory tool as it groups samples with similar species distribution together making it easy to visually assess the results (Fishbein and Patterson, 1993). However, as there is no statistical basis contained in most clustering models, there is little foundation for accepting one biofacies partitioning over another. Another drawback with most clustering algorithms is that the technique will generate clusters regardless of the existence of any true or significant structure, and will not always generate unique solutions (Hair et al., 1998). Although Patterson et al. (2000) utilized a clustering algorithm that emulated the results of a known but commercially unavailable clustering algorithm (Fishbein and Patterson, 1993), it was not possible to assess quantitatively the statistical validity of the elevation data for each group. Utilization of several statistically valid multiple linear regression techniques permit recognition of linear relations in data and automatically selects only those independent variables which influence the target variable the most (Patterson et al., 2004). The stepwise multiple linear regression (SMLR) algorithm is particularly useful for sea-level research as it can include categorical variables, in addition to numerical and logical variables, in the

regression analysis (Hair et al., 1998). The purpose of this paper is to:

(1) Statistically ascertain the validity of the results of Patterson et al. (2000) using SMLR, and to make the results of that study directly comparable with more recent research results elsewhere that also utilize the SMLR methodology.
(2) Assess which data transformations provide the most realistic SMLR results.
(3) Determine which foraminiferal, diatom and macrophyte species (i.e. predictor variables, pv's) have distributions that are most closely linked to elevation in the tidal marsh.

2. Methods

2.1. Field and laboratory

Seventy-six samples were collected for foraminiferal and diatom analyses at 38 stations along a single transect across the marsh at Zeballos on June 13, 1995 (Fig. 1, Fig. 2, Table 1). The foraminiferal samples were collected within the top 10 cm at each station. Previous research in the region has indicated that due to the taphonomic and infaunal habitat of these species this horizon is more directly comparable with the fossil record (Jonasson and Patterson, 1992; Ozarko et al., 1997). In addition, only dead populations of foraminifera were utilized in the subsequent analytical procedures as it has been demonstrated that dead populations more closely reflect the impact of taphonomic time averaging (Horton, 1999; Murray, 2000). As diatoms depend on photosynthesis for survival, these samples were collected from the top 5 mm of the marsh surface. A visual estimate of plant cover, expressed as a percentage, was also made at each station using a 1 m^2 quadrat grid subdivided into 100 cells. The relative elevations of each station were measured using a survey level. Absolute elevations were determined by tying observed high tide elevations in the marsh to recorded tidal elevations at the nearby Zeballos tide gauge. Detailed descriptions of the preparation techniques and analysis methodology utilized for the foraminifera, diatoms, and macrophytes is provided in Patterson et al. (2000). The data tables detailing the fractional abundance of statistically significant foraminiferal, diatom and macrophyte distribution across the Zeballos marsh that are used in this study are also found in Patterson et al. (2000).

2.2. Shannon–Wiener Diversity Index

The Shannon–Wiener Diversity Index (SDI) of Sageman and Bina (1997) is a useful tool for assessing the relative diversity of an environment (Patterson and Kumar, 2000). The SDI is defined as:

$$\text{SDI} = -\sum_{i=1}^{S} \left(\frac{X_i}{N_i}\right) \ln\left(\frac{X_i}{N_i}\right),$$

where X_i is the abundance of each taxon in a sample, N_i the total abundance of the sample, and S is equal to the species richness of the sample.

Previous research has shown a significant relationship between SDI and other environmental parameters (e.g. the distribution of arcellaceans in industrially contaminated lakes (Patterson and Kumar, 2000; Dalby, 2002)). We have therefore utilized SDI analysis as a proxy-value in SMLR, alongside taxonomic data (Fig. 3; Table 1).

2.3. Stepwise multiple linear regression

SMLR is considered to be one of the more robust multivariate analysis techniques available, because more constraints are placed on the data used and dangers of overfitting data are reduced (Hair et al., 1998). With this methodology, SMLR selects variables that have the best predictive correlation with the parameter being examined. SMLR then adds the next best predictor, and so on. The process continues for as long as results provide an increase in the combined explanatory power, or until the partial correlation coefficients become statistically insignificant (Hair et al., 1998).

The SMLR technique available in the software package SPSS 10 was utilized to identify and quantify covariant relationships between proxy and parametric variables (Tables 2–6). These variables included comparing the elevations of sample stations with various combinations of foraminfiera, diatoms, and macrophytes present in statistically significant populations, and the SDI. Any SMLR r^2 value obtained above a 0.5 threshold was considered to be statistically significant (Dalby, 2002).

2.4. Statistics

Tests for normality were conducted by examining the skewness (the measure of how off-centre the highest point of the distribution curve is) and kurtosis (the amplitude of the highest part of the distribution histogram) in the distribution of all data. Both skewness and kurtosis were corrected for by employing a natural logarithm (ln). While a perfect normal distribution is not a firm requirement in multiple regression analysis, it does facilitate obtaining more parsimonious regression results. The assumption of a linear relationship between proxies and parameters is also an important consideration as the multiple regression methodology employed assumes this to be the case (Hair et al., 1998; Jobsen, 1991).
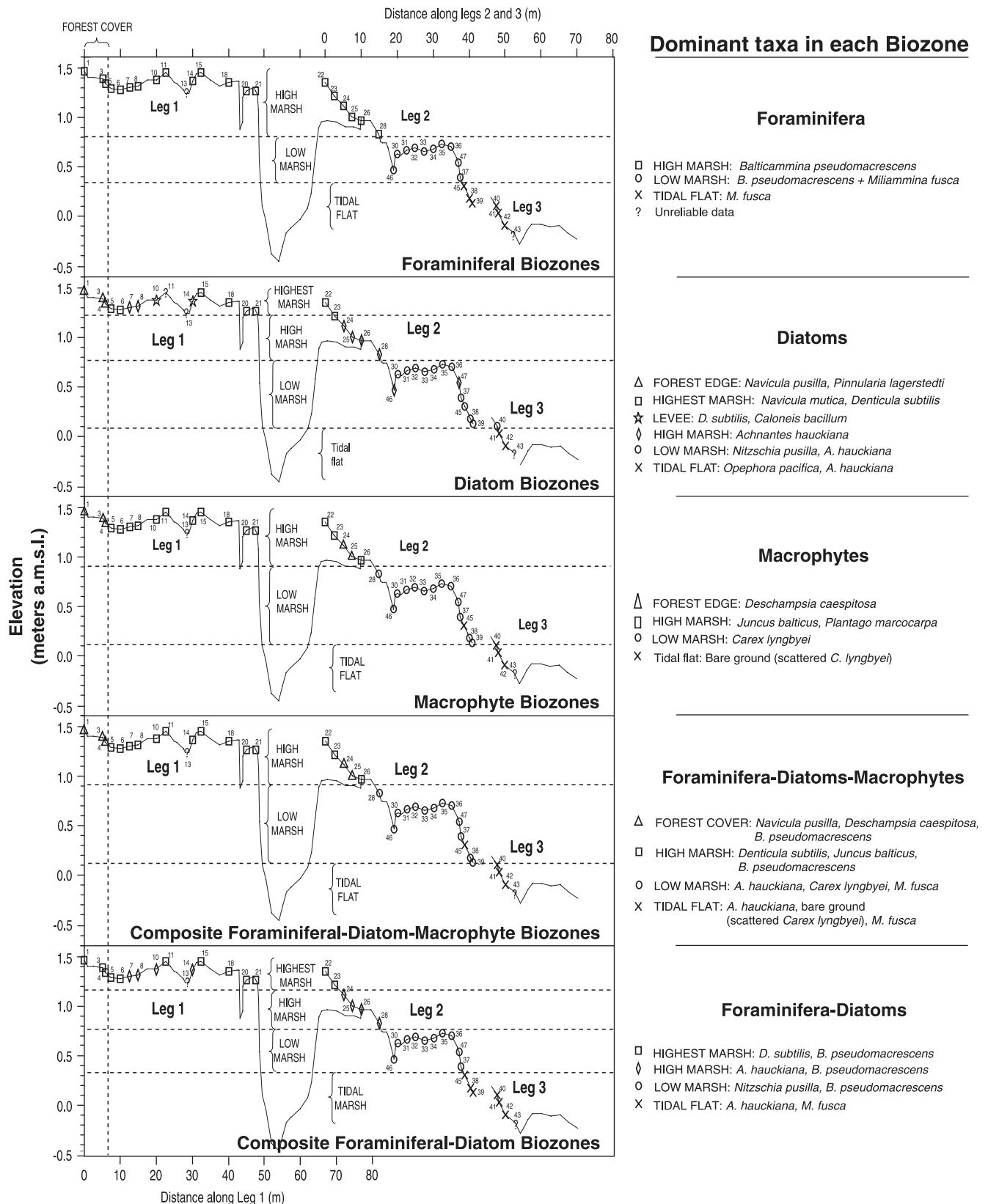
Fig. 2. Marsh transect profiles, showing the positions and elevations of sample stations and elevational zonations derived from Q-Mode cluster analysis of foraminifera, diatoms, macrophytes, as well as composite foraminiferer-diatom-macrophyte and composite foraminifer-diatom zonations. Dominant taxa in each marsh zone are listed. Redrafted after Patterson et al. (2000).

Table 1
Elevation (m above mean sea level) and SDI values for macrophytes, foraminifera and diatoms at each station

Sample	ZT1	ZT15	ZT11	ZT3	ZT10	ZT14	ZT22	ZT18	ZT5	ZT6	ZT21	ZT20	ZT13	ZT23	ZT24	ZT25	ZT26				ZT28	ZT35	ZT36	ZT32	ZT34	ZT31	ZT33	ZT30	ZT37	ZT38	ZT39	ZT40
Elevation	3.38	3.37	3.37	3.31	3.3	3.29	3.27	3.27	3.26	3.23	3.22	3.21	3.2	3.19	3.18	3.16	3.14	3.04	2.93	2.89	2.75	2.65	2.63	2.62	2.6	2.59	2.58	2.55	2.32	2.11	2.05	2.03
Macrophytes	0.80	1.29	1.41	0.33	1.43	0.71	1.31	1.29	0.98	1.49	1.10	1.75	1.12	1.01	1.40	1.22	1.67	1.44	1.45	1.25	0.63	0.80	0.50	0.60	0.85	0.98	0.97	0.87	0.50	0.50	0.61	0.10
Foraminifera	0.86	1.34	0.21	0.99	0.66	1.14	0.84	0.99	0.95	1.19	1.07	0.93	0.75	1.32	1.03	1.38	0.96	0.73	0.91	0.81	0.89	1.31	1.31	1.51	1.37	1.33	1.38	1.28	1.38	0.37	0.91	0.75
Diatoms	2.51	2.40	1.99	2.50	2.29	2.76	2.57	2.45	2.12	2.85	2.84	2.53	2.84	2.54	2.41	1.57	2.36	2.70	2.91	2.93	2.93	2.58	2.62	2.44	2.41	2.45	2.55	2.52	2.40	2.12	2.39	2.51

Stepwise linear regression was carried out on the foraminiferal, diatom and macrophyte data to relate them to environmental parameters. Both the measure of goodness of fit (R) and adjusted measure of goodness of fit ($R'2$) were generated. $R'2$ is a particularly useful parameter as it can encompass a large number of explanatory values, reducing the danger of data over-fitting (Jobsen, 1991). Any obtained $R'2$ SMLR values of <0.5 are considered statistically unreliable (Dalby, 2002).

Tests for multicollinearity amongst species in the various microfossil groups analyzed were performed and no collinear pairs were detected. All species pairs had moderate to high tolerance for each other, meaning low collinearity.

3. Results

A total of 36 SMLR analyses were carried out using various data permutations on the diatoms alone, foraminifera alone, macrophytes alone, diatom and foraminiferal data, and all data. The large number of SMLR analyses was in part the result of experimentation to determine whether data manipulation might influence the outcome of the floral and faunal analysis. These permutations included utilizing percent vs. raw floral and faunal counts, (ln) transformed vs. non-(ln) transformed data, and all variables vs. those taxa whose associated errors were lower than the actual abundance in at least 40% of the samples examined (Tables 2–6).

Statistically significant results were obtained for all analyses carried out on diatoms (0.888–0.974) (Table 2), foraminifera (0.658–0.870) (Table 3), macrophytes (0.671–0.844) (Table 4), foraminifera/diatoms (0.941–0.981) (Table 5), and foraminifera/diatoms/macrophytes (0.958–0.993) (Table 6).

The pv species derived from the diatom data was quite variable depending on the data transformation used (Table 2). Only *Navicula reichardtii* and *Opephora pacifica* were found to be present in all the analyses. *Achnanthes hauckiana* was another important driver, being present in seven analyses, while *Achnanthes groenlandica*, and *Melosira nummuloides* were determined to be important drivers in five different analyses.

The pv's found to drive the relationship for the foraminiferal data included *Miliammina fusca* ($>183\,\mu m$) in all eight data permutations, with *Balticammina pseudomacrescens* and *M. fusca* ($<183\,\mu m$) also found to be important in some analyses (Table 3).

In the combined diatom and foraminiferal SMLR analyses only one species, the diatom *O. pacifica*, was found to be a pv in all eight permutations (Table 4). The foraminifera *M. fusca* ($>183\,\mu m$) was important in seven data permutations. The only other species found to be important through many data permutations were
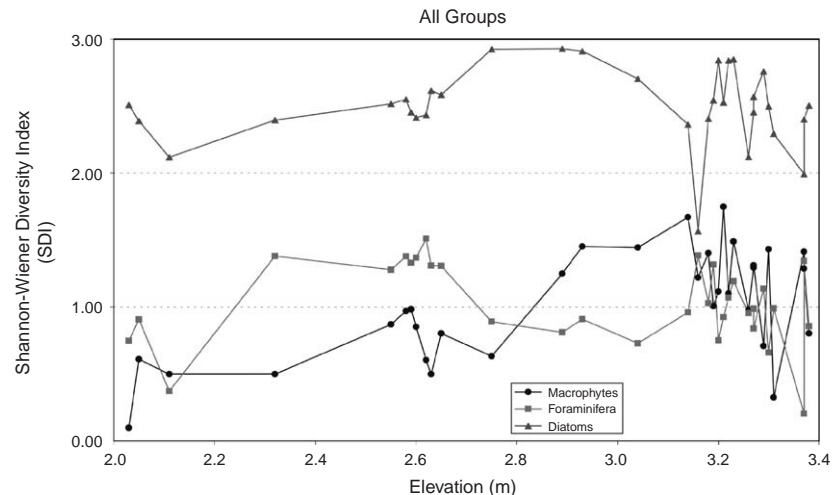
Fig. 3. Shannon–Wiener Diversity Index (SDI) values for diatom, foraminifera, and macrophytes at each station along the marsh at Zeballos.

the diatoms *A. hauckiana* and *Rhopalodia musculus*, present in six each.

For the macrophyte SMLR analyses, only the 'Tidal Flat' variable was found to be an important pv in all four permutations carried out, with *Carex lyngbyei* and *Juncus balticus* also being important in three transformations each.

For the combined foraminiferal, diatom and macrophyte dataset only the foraminifera *M. fusca* (>183 µm) and the macrophyte "Tidal Flat' were found to be important drivers in all SMLR permutations. No diatom species was found to be an important driver in all SMLR permutations although both *O. pacifica* and *A. hauckiana* were both found to be important drivers in six permutations.

4. Discussion

4.1. Importance of appropriate data transformation prior to SMLR

Although there were some exceptions, the species that were determined to be SMLR pv's were quite different depending on the data transformation methodology employed (Tables 2–6). Utilizing an appropriate data transformation technique is therefore an extremely important criterion. As discussed below we conclude that SMLR analysis using (ln) normalized fractional abundance data comprised only of species present in statistically significant numbers provides the most robust data transformation.

In the 36 SMLR analyses carried out for this study we utilized data that was both (ln) normalized (NRfaAL, NRfaEQ, NRrwAL, NRrwEQ) and (ln) unnormalized (UNfaAL, UNfaEQ, UNrwAL, UNrwEQ) (Tables 2–6). Both methodologies generated quite

different sets of species pv's, with unnormalized data generally yielding a larger number of pv's. To examine the degree of normality the datasets were analyzed for degree of skewness and kurtosis (Hair et al., 1998). Skewness is the measure of how off-center the highest point of the distribution curve is found to be, and is corrected by employing a natural logarithm (ln) function to the data (Dalby, 2002). Kurtosis is the amplitude of the highest part of the distributional histogram and is also corrected by utilizing the natural logarithm (Dalby, 2002). While a perfect normal distribution of data is not a prerequisite in SMLR analysis it does facilitate a more parsimonious regression result (Hair et al., 1998). The significant variation in pv's obtained when utilizing (ln) normalized and (ln) unnormalized data here indicates that skewness and kurtosis were significant factors for which a correction had to be applied (Tables 2–6).

Previous research has shown that statistically insignificant species should be removed from the dataset prior to carrying out multivariate analysis (Patterson and Fishbein, 1989; Fishbein and Patterson, 1993). The reason for this recommendation is that the presence of many rare species with statistically insignificant differences leads to a matrix with a high level of dimensionality that is overly influenced by taxa with unresolved fractional abundances. The numerous statistically insignificant species can overshadow the significant differences in the major species, leading to recognition of species groupings that have little in common. To test this hypothesis here, data was analyzed using datasets containing all taxa quantified (NRfaAL, NRrwAL, UNfaAL, UNrwAL) and another containing only those taxa whose associated standard errors were lower than the actual tallied abundances in at least 40% of the samples (NRfaEQ, NRrwEQ, UNfaEQ, UNrwEQ) (Tables 2–6). Overall results obtained are comparable (NRfaAL vs. NrfaEQ, etc.) and do not have as

Table 2
Stepwise linear regression analysis of diatom data results for the measure of goodness of fit (R) and adjusted goodness of fit ($R'2$) and associated error ($\pm$) using several data transformations (NR = (ln) normalized); UN = not (ln) normalized; fa = fractional abundance; rw = raw data counts; AL = all taxa analyzed; EQ = taxa whose associated errors were lower than the actual abundance in at least 40% of the samples examined)

ZEB diatoms	1. NRfaAL	2. NRfaEQ	3. NRrwAL	4. NRrwEQ	5. UNfaAL	6. UNfaEQ	7. UNrwAL	8. UNrwEQ
$R2$	0.971	0.949	0.974	0.945	0.955	0.936	0.934	0.888
$R'2$	0.960	0.936	0.963	0.930	0.942	0.924	0.916	0.870
$\pm$	0.1045	0.1323	0.0997	0.1379	0.1250	0.1440	0.1512	0.1877
Species	*Denticula subtilis*	*Denticula subtilis*	*Denticula subtilis*	*Denticula subtilis*	*Achnanthes hauckiana*	*Achnanthes hauckiana*	*Navicula reichardtii*	*Achnanthes hauckiana*
	Fragilaria pinnata	*Fragilaria pinnata*	*Fragilaria pinnata*	*Fragilaria pinnata*	*Opephora pacifica*	*Opephora pacifica*	*Achnanthes groenlandica*	*Navicula reichardtii*
	Nitzschia vitrea	*Navicula reichardtii*	*Nitzschia vitrea*	*Nitzschia pusilla*	*Synedra tabulata*	*Navicula reichardtii*	*Opephora pacifica*	*Achnanthes groenlandica*
	Achnanthes hauckiana	*Achnanthes groenlandica*	*Opephora pacifica*	*Navicula salinarum*	*Fragilaria construens*	*Achnanthes groenlandica*	*Melosira nummuloides*	*Opephora pacifica*
	Opephora pacifica	*Melosira nummuloides*	*Achnanthes hauckiana*	*Opephora pacifica*	*Navicula reichardtii*	*Melosira nummuloides*	*Synedra tabulata*	*Melosira nummuloides*
	Synedra tabulata	*Rhopalodia musculus*	*Navicula salinarum*	*Achnanthes deflexa* or *flexella*	*Achnanthes groenlandica*	*Rhopalodia musculus*	*Nitzschia levidensis*	
	Navicula salinarum	*Navicula salinarum*	*Synedra tabulata*	*Navicula reichardtii*	*Rhopalodia musculus*		*Denticula subtilis*	
	Navicula reichardtii	*Achnanthes deflexa* or *flexella*	*Navicula reichardtii*	*Rhopalodia musculus*	*Melosira nummuloides*		*Amphora coffaeformis*	
	Rhopalodia musculus	*Opephora pacifica*	*Navicula stankovicii*					
	Navicula stankovicii	*Achnanthes hauckiana*	*Rhopalodia musculus*					
			Fragilaria construens					

The diatom predictor variables (species) that were determined to drive the SMLR analysis results are listed under each data transformation.

Table 3
Stepwise linear regression analysis of foraminiferal data results for the measure of goodness of fit (R) and adjusted goodness of fit ($R'2$) and associated error ($\pm$) using several data transformations (NR = (ln) normalized); UN = not (ln) normalized; fa = fractional abundance; rw = raw data counts; AL = all taxa analyzed; EQ = taxa whose associated errors were lower than the actual abundance in at least 40% of the samples examined)

ZEBforams	1. NRfaAL	2. NRfaEQ	3. NRrwAL	4. NRrwEQ	5. UNfaAL	6. UNfaEQ	7. UNrwAL	8. UNrwEQ
$R2$	0.866	0.866	0.846	0.846	0.870	0.870	0.658	0.658
$R'2$	0.858	0.858	0.837	0.837	0.863	0.863	0.648	0.648
$\pm$	0.1963	0.1963	0.2101	0.2101	0.1930	0.1930	0.3090	0.3090
Species	*Miliammina fusca* (> 183 μm)	*Miliammina fusca* (> 183 μm)	*Miliammina fusca* (> 183 μm)	*Miliammina fusca* (> 183 μm)	*Miliammina fusca* (> 183 μm)	*Miliammina fusca* (> 183 μm)	*Miliammina fusca* (> 183 μm)	*Miliammina fusca* (> 183 μm)
	Jadammina macrescens	*Jadammina macrescens*	*Jadammina macrescens*	*Jadammina macrescens*	*Miliammina fusca* (< 183 μm)	*Miliammina fusca* (< 183 μm)		

The foraminiferal predictor variables (species) that were determined to drive the SMLR analysis results are listed under each data transformation.

Table 4
Stepwise linear regression analysis of macrophyte data results for the measure of goodness of fit (R) and adjusted goodness of fit ($R'2$) and associated error ($\pm$) using several data transformations (NR = (ln) normalized); UN = not (ln) normalized; fa = fractional abundance; rw = raw data counts; AL = all taxa analyzed; EQ = taxa whose associated errors were lower than the actual abundance in at least 40% of the samples examined)

ZEBmacro	1. Nrfa	1. NRfa + SDI	2. Unfa	2. UNfa + SDI
$R2$	0.778	0.826	0.671	0.844
$R'2$	0.735	0.804	0.642	0.830
$\pm$	0.2681	0.2304	0.3117	0.2148
Species	*Juncus balticus*	Shannon–Wiener Diversity Index (SDI)	Tidal Flat	Shannon–Wiener Diversity Index (SDI)
	Deschampsia cespitosa	Tidal Flat	*Carex lyngbyei*	Tidal Flat
	Tidal Flat	*Carex lyngbyei*	*Juncus balticus*	Carex lyngbyei
	Plantago macrocarpa	*Juncus balticus*		
	Potentilla pacifica			

The macrophyte predictor variables (species) that were determined to drive the SMLR analysis results are listed under each data transformation.

pronounced an impact on the final SMLR results as (ln) normalization. The major influence on SMLR results of not removing statistically insignificant species from the data matrix is that there is a slightly larger number of pv's identified (e.g. UNrwAL vs. UNrwEQ), the result of the higher level of data dimensionality.

The final data transformations utilized here included using both raw floral and faunal counts (NRrwAL, NRrwEQ, UNrwAL UNrwEQ) and data that had been converted to fractional abundances (NRfaAL, NRfaEQ, UNfaAL, UNfaEQ) (Tables 2–6). Fishbein and Patterson (1993) determined that fractional abundance (or percent) transformation of data prior to multivariate analysis is an ideal normalization methodology. The fractional abundance of a species in a sample is the number of specimens of each species divided by the total number of specimens. Thus the fractional abundances of the component species in a sample are not independent and always sum to one. The set of a sample's fractional abundances can therefore be used to visualize the coordinates of a point in a K-dimensional abundance space where each axis measures the fractional abundance of a single species. It is therefore easy to compare samples directly (e.g. those that are similar will have only small differences in their component species fractional abundances). Due to often-large variations in absolute abundances, direct comparison of raw species data will often generate spurious results (Fishbein and Patterson, 1993). Direct comparison of SMLR results obtained here utilizing fractional abundance and raw faunal counts revealed significant differences (e.g. UNfaAL vs. UNrwAL). Utilization of fractional abundance data as opposed to raw counts is as significant a factor as using (ln) normalized data in successful SMLR analysis.

4.2. Stepwise linear regression predictor variables

In addition to providing an assessment of the reliability of the data for assessing elevational change,

SMLR analysis also provides data on the species pv's that most influenced the outcome.

There are only a few cosmopolitan foraminiferal species able to survive in the harsh salt marsh ecotone (Scott and Medioli, 1978). For this group, the preferred (ln) normalized fractional abundance dataset that comprised only species present in statistically significant numbers (NRfaEQ) yielded *M. fusca* ($> 183\,\mu m$) and *B. pseudomacrescens* as the most important pv's in all SMLR analyses (Tables 3, 5 and 6).

Both *M. fusca* and *B. pseudomacrescens* have been widely reported from throughout the entire Cascadia region (e.g. Phleger, 1967; Williams, 1989; Patterson, 1990; Jennings and Nelson, 1992; Jonasson and Patterson, 1992; Guilbault et al., 1995, 1996; Nelson, et al., 1996; Scott et al., 1996; Ozarko et al., 1997; Hutchinson, et al., 1998; Patterson et al., 1999; Shennan et al., 1999; Williams, 1999). *B. pseudomacrescens* almost always dominates high marsh environments where it has a primarily infaunal habitat in coastal British Columbia (Ozarko et al., 1997; Patterson et al., 2000). *M. fusca* characterizes lower marsh environments where it is primarily epifaunal to slightly infaunal (Ozarko et al., 1997; Patterson et al., 2000). *M. fusca* was artificially broken into two size fractions and analyzed separately here according to the recommendation of Guilbault et al. (1995, 1996). They observed that $> 183\,\mu m$ *M. fusca* populations correlated well with elevation at various places along the British Columbia coast. In contrast juvenile ($< 183\,\mu m$) *M. fusca* populations did not correlate well when analyzed alone. A suggested reason for this observed distribution is that adverse conditions in the high marsh prevent *M. fusca* living there from reaching the adult stage. An alternative explanation is that some apparently juvenile specimens found at more hostile higher elevations are actually developmentally arrested adults (Guilbault and Patterson, 2000).

Previous linear correlation analysis of the distribution of marsh foraminifera from various sites on Vancouver Island corroborate the results obtained here

Table 5
Stepwise linear regression analysis of combined diatom/foraminiferal data results for the measure of goodness of fit (R) and adjusted goodness of fit ($R'2$) and associated error ($\pm$) using several data transformations (NR = (ln) normalized); UN = not (ln) normalized; fa = fractional abundance; rw = raw data counts; AL = all taxa analyzed; EQ = taxa whose associated errors were lower than the actual abundance in at least 40% of the samples examined)

ZEBf+d	1. NRfaAL	2. NRfaEQ	3. NRrwAL	4. NRrwEQ	5. UNfaAL	6. UNfaEQ	7. UNrwAL	8. UNrwEQ
R2	0.950	0.941	0.949	0.960	0.981	0.981	0.949	0.949
$R'2$	0.940	0.932	0.938	0.949	0.975	0.975	0.935	0.935
$\pm$	0.1274	0.1362	0.1303	0.1181	0.0826	0.0826	0.1332	0.1332
Species	*Miliammina fusca* (>183 μm) *Jadammina macrescens* *Opephora pacifica* *Achnanthes hauckiana* *Nitzschia hybrida* *Pinnularia subcapitata*	*Miliammina fusca* (>183 μm) *Jadammina macrescens* *Opephora pacifica* *Achnanthes hauckiana* *Pinnularia subcapitata*	*Miliammina fusca* (>183 μm) *Jadammina macrescens* *Opephora pacifica* *Achnanthes hauckiana* *Nitzschia hybrida* *Denticula subtilis* *Rhopalodia musculus*	*Jadammina macrescens* *Opephora pacifica* *Achnanthes hauckiana* *Rhopalodia musculus* *Denticula subtilis* *Nitzschia vitrea* *Navicula gregaria* *Synedra tabulata*	*Miliammina fusca* (>183 μm) *Achnanthes hauckiana* *Achnanthes groenlandica* *Opephora pacifica* *Synedra tabulata* *Rhopalodia musculus* *Navicula reichardtii* *Navicula cryptocephala*	*Miliammina fusca* (>183 μm) *Achnanthes hauckiana* *Achnanthes groenlandica* *Opephora pacifica* *Synedra tabulata* *Rhopalodia musculus* *Navicula reichardtii* *Navicula cryptocephala*	*Miliammina fusca* (>183 μm) *Achnanthes groenlandica* *Navicula reichardtii* *Rhopalodia musculus* *Synedra tabulata* *Opephora pacifica* *Navicula gregaria* *Nitzschia levidensis*	*Miliammina fusca* (>183 μm) *Achnanthes groenlandica* *Navicula reichardtii* *Rhopalodia musculus* *Synedra tabulata* *Opephora pacifica* *Navicula gregaria* *Nitzschia levidensis*

The diatom/foraminiferal predictor variables (species) that were determined to drive the SMLR analysis results are listed under each data transformation.

Table 6
Stepwise linear regression analysis of combined diatom/foraminiferal/macrophyte data results for the measure of goodness of fit (R) and adjusted goodness of fit ($R'2$) and associated error ($\pm$) using several data transformations (NR = (ln) normalized); UN = not (ln) normalized; fa = fractional abundance; rw = raw data counts; AL = all taxa analyzed; EQ = taxa whose associated errors were lower than the actual abundance in at least 40% of the samples examined)

ZEBall	1. NRfaAL	2. NRfaEQ	3. NRrwAL	4. NRrwEQ	5. UNfaAL	6. UNfaEQ	7. UNrwAL	8. UNrwEQ
R2	0.965	0.965	0.969	0.958	0.993	0.991	0.986	0.988
$R'2$	0.957	0.957	0.959	0.947	0.988	0.986	0.980	0.982
$\pm$	0.1080	0.1080	0.1058	0.1204	0.0568	0.0616	0.0742	0.0693
Species	*Miliammina fusca* (> 183 μm) *Jadammina macrescens* *Opephora pacifica* *Achnanthes hauckiana* Tidal Flat *Navicula peregrina* *Synedra tabulata*	*Miliammina fusca* (> 183 μm) *Jadammina macrescens* *Opephora pacifica* *Achnanthes hauckiana* Tidal Flat *Navicula peregrina* *Synedra tabulata*	*Miliammina fusca* (> 183 μm) *Jadammina macrescens* *Opephora pacifica* *Achnanthes hauckiana* *Nitzschia hybrida* *Denticula subtilis* *Juncus balticus* Tidal Flat *Synedra tabulata*	*Miliammina fusca* (> 183 μm) *Jadammina macrescens* *Opephora pacifica* *Achnanthes hauckiana* Tidal Flat *Synedra tabulata* *Potentilla pacifica* *Juncus balticus*	*Miliammina fusca* (> 183 μm) *Achnanthes hauckiana* *Opephora pacifica* *Synedra tabulata* *Miliammina fusca* (< 183 μm) *Rhopalodia musculus* *Potentilla pacifica* *Tidal Flat* *Navicula peregrina* *Juncus balticus* *Plantago macrocarpa* *Navicula reichardtii* *Navicula mutica* *Navicula stankovicii*	*Miliammina fusca* (> 183 μm) *Achnanthes hauckiana* *Opephora pacifica* *Synedra tabulata* *Miliammina fusca* (< 183 μm) *Rhopalodia musculus* *Potentilla pacifica* *Tidal Flat* *Navicula peregrina* *Juncus balticus* *Plantago macrocarpa* *Navicula reichardtii* *Navicula mutica*	*Miliammina fusca* (> 183 μm) *Navicula reichardtii* *Rhopalodia musculus* *Tidal Flat* *Denticula subtilis* *Synedra tabulata* *Trochammina salsa* *Pinnularia subcapitata* *Achnanthes lanceolata* *Navicula salinarum* *Navicula stankovicii*	*Miliammina fusca* (> 183 μm) *Navicula reichardtii* *Rhopalodia musculus* *Tidal Flat* *Denticula subtilis* *Synedra tabulata* *Trochammina salsa* *Pinnularia subcapitata* *Achnanthes lanceolata* *Navicula salinarum* *Haplophragmoides wilberti* *Nitzschia palea*

The diatom/foraminiferal/macrophyte predictor variables (species) that were determined to drive the SMLR analysis results are listed under each data transformation.

as Guilbault and Patterson (2001) demonstrated a strong negative correlation between elevation and *M. fusca* ($R = -0.93$; $R^2 = 0.86$) and a positive correlation between elevation and a grouping of several high marsh taxa including *B. pseudomacrescens* ($R = +0.92$; $R^2 = 0.85$).

The (NRfaEQ) result was somewhat more variable for the diatom SMLR analyses (Tables 2,5 and 6). Of the diatom taxa, two species, *O. pacifica* and *A. hauckiana,* were found to be important pv's in the analyses for the diatoms alone, as well as in those for the diatoms and foraminifera, and all three indicators combined. Several other species including *A. groenlandica* and *M. nummuloides,* were also important pv's.

O. pacifica is a polyhalobian diatom that has been reported in a wide range of littoral settings, including estuaries, tidal flats and the lower zones of saltmarshes (cf. Hendey, 1964; van der Werff and Huls, 1976; Tynni, 1986). These findings are consistent with the observed distribution of *O. pacifica* at the Zeballos site, where the species was most common in the low marsh and on the tidal flat. Here it ranged in abundance from 3% to 30% of the flora.

O. pacifica has been reported reasonably widely in salt marshes, but shows an erratic distribution, suggesting that factors other than elevation and tidal flooding influence its range. For example, Gehrels et al. (2001) reported *O. pacifica* in frequencies of up to 20% in low to mid marsh surface sediments in the Erme Estuary, south Devon, United Kingdom, yet the species was only present in low abundances ($<2\%$) or absent altogether in the equivalent zones of two other British marshes under investigation (Gehrels et al., 2001; Roe, unpublished data). Y. Zong (University of Durham, pers. comm., 1998) confirms that the species has a patchy distribution in salt marshes of the United Kingdom. The species is also notably absent from lists of key diatom species found in salt marsh sites in coastal Washington State (e.g., Hemphill-Haley, 1995; Atwater and Hemphill-Haley, 1997) and Oregon (Nelson and Kashima, 1993). It has nevertheless, been reported commonly in the fossil context in intertidal sediment cores from the coastal NE Pacific region. For example, *O. pacifica* achieved abundances of 15–25% in an intertidal sediment core from the lower Johns River, Alaska (Shennan et al., 1996). Here it occurred alongside significant frequencies of *Achnanthes delicatula,* a common epipsammic species. The species has also been reported in sand-dominated tsunamis deposits in Vancouver Island (Hutchinson et al., 1997). These findings may imply that substrate has an important control on its distribution.

Based on the uneven occurrence of *O. pacifica* in salt marsh sediments, its utility as a significant sea-level indicator or pv species may be somewhat limited in saltmarsh environments. It may also be significant that

O. pacifica is smaller than some of the other diatoms under consideration, with most specimens tending toward the lower end of the size range (8–60 μm) (cf. Hustedt, 1955). It is possible that the highly variable distribution observed at Zeballos may be related to selective winnowing or other taphonomic processes.

A. hauckiana is found throughout the marsh at Zeballos but is most abundant in the low marsh (Patterson et al., 2000). Linear correlation analysis determined that the distribution of the species is negatively correlated with elevation ($R = -0.77$; $R^2 = 0.59$), with abundance progressively declining towards higher elevations in the marsh (Patterson et al., 2000).

Other studies have determined that *A. hauckiana* is an epipsammic mesohalobian species that is most commonly found in low marsh environments (Campeau et al., 2000). This species is also very small (9–30 μm— van der Werff and Huls, 1976), and known to preferentially inhabit small depressions on the surface of sediment grains in areas with active currents (Campeau et al., 2000). The distribution of the species is therefore likely to be dominantly substrate controlled. This accords with its common distribution in marshes with a higher proportion of coarse silt such as in Willapa Bay, Washington (Hemphill-Haley, 1995) and the Fraser Delta, British Columbia (Hutchinson et al., 1998). The marsh and tidal flat at Zeballos is similar, and comprises silty material which extends from the tidal flat and into the low marsh. The sediments become progressively more organic rich in the high marsh. The distribution of *A. hauckiana* at Zeballos therefore mirrors local change in substrate across the marsh surface. As with *O. pacifica,* selective winnowing or concentration of these very small diatoms cannot also be over-ruled.

M. nummuloides was found throughout the marsh at Zeballos, peaking at frequencies of about 14% in the low marsh. This species is not widely reported in the literature. However, at Willapa Bay, Washington, Hemphill-Haley (1995) observed that *M. nummuloides* achieves greatest abundances in tidal flat and in tidal channel environments. The species is a sediment-associated chain-forming diatom that cannot withstand strong water turbulence (Hemphill-Haley, 1995). Hemphill-Haley also notes that although *M. nummuloides* tends to be quite abundant when alive, the large delicate frustules do not tend to preserve well in the sediments. Interestingly, she further notes that this species, like other epipelic diatoms, can sometimes be lifted up off the sediment surface and redeposited "up estuary" as a surface "film" (Hemphill-Haley, 1995). Thus whilst the SMLR indicates that *M. nummuloides* has a marsh distribution that can be correlated to elevation, its use as a pv must be treated with caution given that it is likely to be largely allochthanous in all but the low marsh and

tidal flat zones. It is potentially not appropriate to use a species that does not tend to preserve well as a key pv.

A. groenlandica is primarily found in the low marsh and tidal flat at Zeballos. In an examination of British diatoms, Hendey (1964) noted that this epilithic species forms "tightly adhering films upon rocks and other hard substrates". Although there were no appropriate hard substrates found in the tidal flat at Zeballos, the adjacent tidal flat was rocky, providing an ideal substrate for growth of the species. As was observed with *M. nummuloides*, *A. groenlandica* was probably transported into the marsh with the tides, becoming most abundant in the low marsh immediately adjacent to the source area. As with *M. nummuloides*, it might be inappropriate to use an allochthonous species as an elevation indicator in salt marshes.

The (NRfaEQ) results for the macrophytes indicated that the most important pv's were SDI, *C. lyngbyei*, *J. balticus*, and the absence of plant cover variable, 'Tidal Flat'. *C. lyngbyei* is the dominant low marsh species at Zeballos and through out coastal northwestern North America, particularly in areas where salinities are depressed (Hutchinson, 1988; Hutchinson et al., 1989). Patterson et al. (2000) found *C. lingbyei* to be strongly elevation controlled, having a high negative correlation with elevation ($R = -0.93$; $R^2 = 0.86$). *J. balticus* dominates the diverse high marsh plant community, where 12 of the 13 plant species recorded in the marsh survey were observed (Patterson et al., 2000). The emergence of SDI as an important predictor value is linked to the significant increase in macrophyte diversity in the high marsh zone (Table 1). The 'Tidal Flat' variable was an important elevation linked pv because the low-lying tidal flat areas were almost devoid of vegetation.

4.3. Utility of a multi-proxy approach to paleo-sea level research

A number of factors influence the selection of proxy indicator used in salt marsh-based sea-level research. The results presented here show that statistically significant outcomes are obtained for all individual proxies utilized in the SMLR study. The most accurate results were obtained using a combination of all three proxies though, which accords well with similar analyses carried out elsewhere (e.g. Gehrels et al., 2001).

There are factors that limit the utility of these groups under certain circumstances. These include (1) the elevation range, (2) the accuracy and spatical variability of the selected proxy, (3) preservation potential, (4) taphonomic effects, (5) ease of preparation, and (6) analytical methodology. For example, the enormous number of diatom species typically found in a salt marsh (138 here), complicated processing procedures, and a steep learning curve limit utilization of this group to

specialists only. In this region macrophyte material is often poorly preserved down-core, limiting the application of this proxy in most high-resolution sea-level studies.

Foraminifera, characterized by relatively few cosmopolitan and readily identifiable species in most temperate salt marshes, and samples that are easy to prepare for analysis, seems to provide the ideal tool for researchers seeking rapid characterization of the elevational history of a tidal marsh. There are difficulties associated with utilizing this group as well though. The differential geographic and environmentally influenced infaunal habitat of many foraminiferal species mean that this parameter has be to considered prior to application of any transfer functions to interpret core material.

5. Conclusions

(1) Data transformations comprised of (ln) normalized fractional abundance data using only species present in statistically significant numbers (NRfaEQ) is the most suitable away to prepare data for SMLR analysis.

(2) All proxy groups analyzed for SMLR analysis yielded statistically significant results. Of the individual proxies SMLR analysis of diatoms yielded the most significant adjusted $R'2$ (0.936—NrfaEQ transformation) value and a combined analysis of all proxies examined yielded the highest adjusted $R'2$ value over all (0.957—NrfaEQ transformation). A combination of diatoms and foraminifera yielded an adjusted $R'2$ value of 0.932 (NrfaEQ transformation), foraminifera alone gave an adjusted $R'2$ value of 0.858 (NrfaEQ transformation), while macrophytes had an adjusted $R'2$ value of 0.804 (NrfaEQ transformation).

(3) Several species amongst the various proxy groups utilized were determined to be important pv's in assessing elevations in the marsh. The low marsh diatom *A. hauckiana* was the most important diatom predictor pv, although several other species including *O pacifica*, *A. groenlandica*, and *M. nummuloides*, were also important elevational drivers. Amongst the foraminifera, the low marsh species *M. fusca* and high marsh species *B. pseudomacrescens* were determined to be the most significant pv's. For macrophytes, *C. lyngbyei*, *J. balticus*, SDI values, and absence of plant cover on the tidal flat were the most important pv's.

(4) SMLR analysis of all individual groups and combinations of groups yielded statistically significant results as all obtained values were above the statistically significant value of $R^2 = 0.5$. Thus the choice of proxies, or combinations of proxies that

are suitable for sea-level research is at the discretion of the researcher. For non-specialists seeking a rapid assessment of sea-level change in a salt marsh sediment sequence foraminifera are probably the best tool of the three examined here, as there are only a few readily identifiable cosmopolitan species and samples are easy to prepare for examination.

Acknowledgments

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