

# A comparison of the vertical zonation of diatom, foraminifera, and macrophyte assemblages in a coastal marsh: implications for greater paleo-sea level resolution

R.T. Patterson<sup>1</sup>, I. Hutchinson<sup>2</sup>, J.-P. Guilbault<sup>3</sup> and J.J. Clague<sup>4</sup>

<sup>1</sup>Ottawa-Carleton Geoscience Centre and Department of Earth Sciences, Carleton University, Ottawa, Ontario, K1S 5B6 Canada

<sup>2</sup>Department of Geography, Simon Fraser University, Burnaby, British Columbia, V5A 1S6 Canada

<sup>3</sup>BRAQ-Stratigraphie, 10555 rue Meilleur, Montréal, Québec, H3L 3K4 Canada

<sup>4</sup>Geological Survey of Canada, Suite 101, 605 Robson Street, Vancouver British Columbia, V6B 5J3 Canada, and Earth Sciences, Simon Fraser University, Burnaby, British Columbia, V5A 1S6 Canada

Email: tpatters@ccs.carleton.ca

**ABSTRACT:** Researchers generally use only one type of plant or animal to study a particular marsh. Consequently, it has been impossible to directly compare zonations obtained using different groups between sites. To facilitate such comparison, cluster analysis of foraminiferal, diatom, and macrophyte data collected in transects from a tidal marsh at Zeballos, northwestern Vancouver Island, British Columbia, was carried out. These analyses yielded three, six, and four mostly elevation-controlled assemblage zones, respectively. Physical parameters such as salinity and oxygen concentration affect the various taxa differently, resulting in significantly different assemblage boundaries between groups. A composite analysis of all groups yielded an assemblage zonation very similar to that obtained with the macrophytes alone. Although fewer assemblage zones were resolved with the composite analysis than with the diatom data alone, fewer sample misclassifications resulted in more precise elevation determinations. A second composite analysis using only foraminiferal and diatom data, which is more useful to paleo-sea level researchers, also gave four elevation controlled assemblage zones, although assemblage zone elevational boundaries differed slightly from those obtained with data from all groups. Our results will permit researchers working on diatoms, foraminifera or macrophytes to calibrate their zonations thus making it easier for workers in different fields to compare their results.

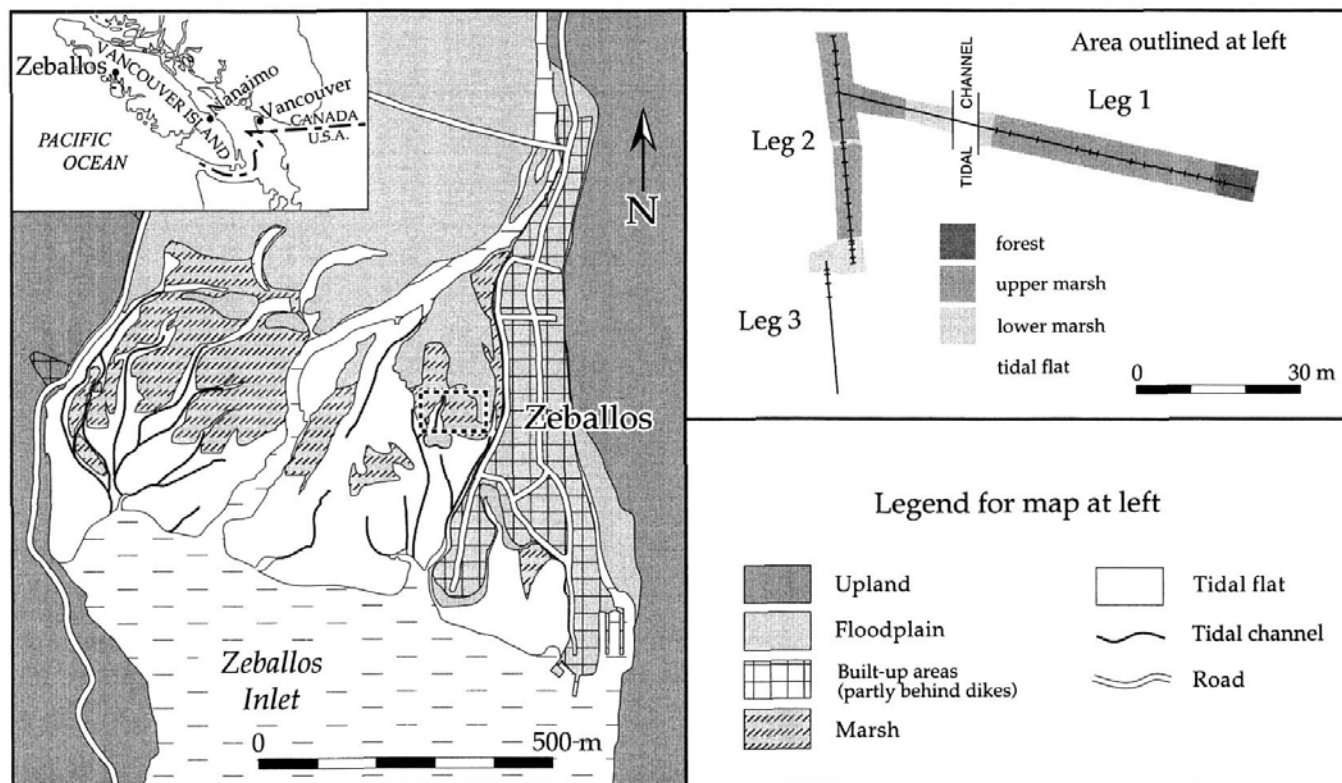
## INTRODUCTION

The distribution of coastal marsh and tidal flat communities is closely related to elevation and local tidal conditions. For this reason, these communities are commonly delimited by terms expressing their relative elevation: e.g. "Low Marsh, Middle Marsh, High Marsh". If the elevational ranges of the organisms constituting these communities are known with precision, the presence of *in situ* fossil remains of the species in intertidal sediments can be used to determine the former elevation of the site. A record of the changing elevation of the marsh through time can therefore be obtained by analyzing changes in the abundance of indicator species with depth in a sedimentary sequence.

This approach has been used to reconstruct recent sea-level change on many of the world's coasts. In the Pacific Northwest of North America, the impetus for using this approach has been the recognition that the coast overlies the Cascadia subduction zone, which generates great (moment magnitude 8+) earthquakes (Riddihough and Hyndman 1976; Mathewes and Clague 1994; Atwater et al. 1995; Atwater and Hemphill-Haley 1997). Abrupt subsidence during these earthquakes is recorded in estuarine settings by sharp changes in the lithology and biofacies of intertidal sediments (Friele and Hutchinson 1993). Analysis of fossil benthic foraminifera (Li 1992; Guilbault et al. 1995, 1996) and diatoms (Hemphill-Haley 1992, 1995a) di-

rectly above and below these boundaries has allowed estimates to be made at the magnitude of the coseismic subsidence. Attempts to improve the accuracy of these estimates, and to monitor sea-level changes between earthquakes, have focussed on multi-proxy approaches to the problem, combining distributional information, for instance, on vascular plants (pollen or plant macrofossils) and diatoms (Long and Shennan 1994; Nelson et al. 1996a, b; Shennan et al. 1996).

A major limitation in such studies is that information on the vertical zonation of these and other taxonomic groups in estuaries in the Pacific Northwest is relatively meagre. In this paper we address this deficiency by documenting the distribution of vascular plants, diatoms, and foraminifera in a fjord-head marsh at Zeballos on the west coast of Vancouver Island (text-figure 1). In addition, we assess the utility of determining relative elevation by integrating information on the vertical zonation of these three taxonomic groups. As species of these groups have very different elevation zonations, this approach should permit a higher resolution vertical subdivision of the marsh. The larger the number of modern assemblage zones one can recognize, the more precise will be the vertical resolution obtained from analogous fossil assemblage zones. If a multi-organism approach can provide a significant increase in resolution over the results obtained from single groups, it should be possible to recognize even minor changes in sea level in the past.



TEXT-FIGURE 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.

## METHODS

### Field and Laboratory

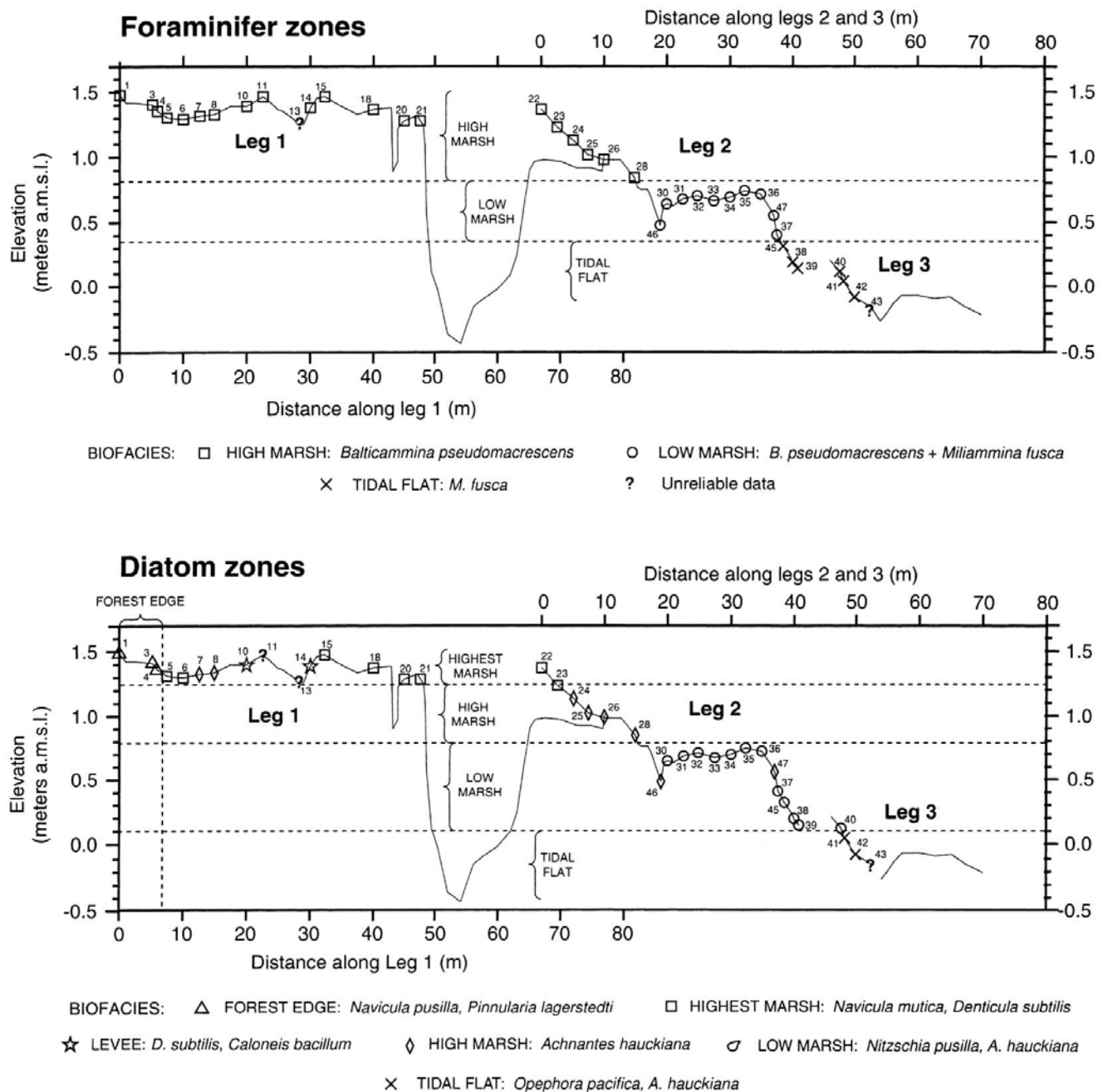
Seventy-six samples were collected for foraminiferal, arcellacean, and diatom analysis at 38 stations along three legs of a single transect across the marsh just west of the town of Zeballos on June 13, 1995 (text-fig. 1). In addition, a percent visual estimate of plant cover was made at each station using a 1 m<sup>2</sup> quadrat subdivided into 100 cells. The relative elevations of stations were measured with a surveying level and are accurate to within 1 cm. Absolute elevations were determined by tying observed high tide elevations in the marsh to recorded tidal elevations at the nearby Zeballos tide gauge. Fortunately, we surveyed the marsh at the time of the highest spring tide, a fact which allowed us to make a precise determination of the tidal submergence limit. The tide was actually found to be higher than the edge of the forest. Foraminifera were found living under the forest cover (compare text-figs. 1 and 2). This unusual situation is the result of the low salinity conditions (5-8‰) in the marsh, which is located at the mouth of a river and at the head of fjord.

A sample of the top 10 cm of sediment was collected at each of the 38 stations for foraminiferal and arcellacean analysis. Previous research in the region has indicated that samples of the top-most 10 cm of marsh sediments provide foraminiferal data that are more directly comparable with the fossil record than 0-1 cm samples, which are more typically collected and analyzed (Patterson et al. 1999). The thicker samples contain species that are absent or underrepresented in the 0-1cm samples (Jonasson

and Patterson 1992; Ozarko et al. 1997), and thus provide more detail on elevation-related variation in species habitat in the marsh. In addition, most taphonomic biasing that results from vertical tiering and related differential preservation of foraminifera occurs within 10cm of the marsh surface (Ozarko et al. 1997; Walker and Goldstein 1999).

Samples were stored in Ziploc plastic bags and treated in the field with isopropyl alcohol to prevent microbial decay of living protoplasm. In the laboratory, the sample was longitudinally split and approximately 10cm<sup>3</sup> of each sample were washed on a 63µm sieve.

Foraminifera-bearing samples were fixed for several hours in a solution of Rose Bengal stain and buffered formalin to differentiate live and dead foraminifera, these data were not utilized in this study. Patterson et al. (1999) and Scott and Medioli (1980) determined that it is not necessary to separate live and dead foraminiferal populations in most marsh studies because the precision of the results is not substantially improved. In cluster analyses carried out by Patterson et al. (1999), for example, the ordering of samples and shape of clusters differed for data sets of total foraminiferal vs. differentiated populations, but the placement of samples within assemblage zones at a common correlation coefficient was the same. After staining, the samples were washed in tap water and preserved in a 5% isopropyl alcohol solution. They were then washed through a 500µm screen to remove large plant debris that might inhibit counting. The residue was split using a wet splitter (Scott and Hermelin 1993) until a fraction of countable size was obtained.



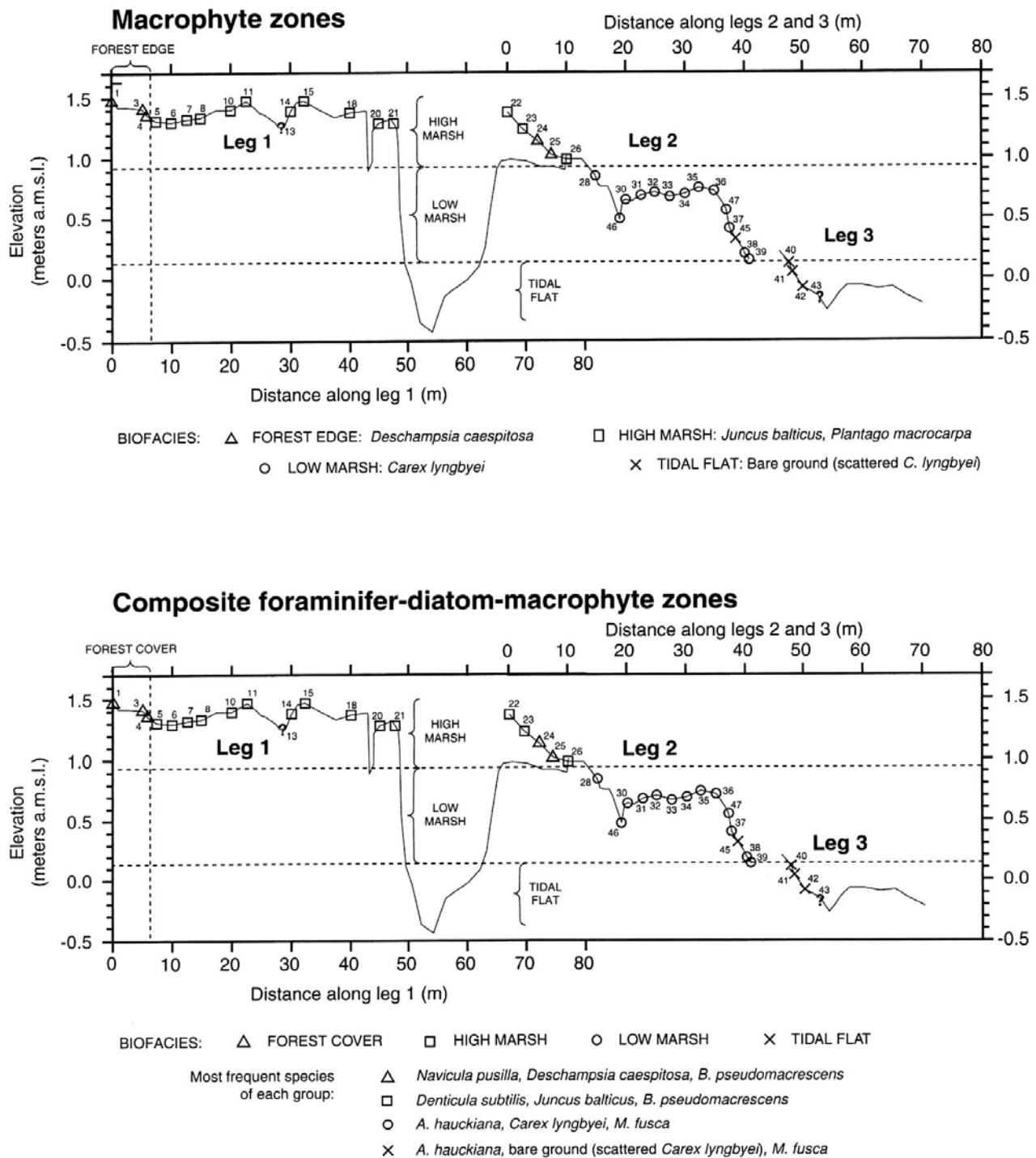
TEXT-FIGURE 2

Marsh transect profile, showing the positions and elevations of the foraminifera (top) and diatom (bottom) data. The prefix "ZT" has been omitted from the sample numbers.

Wet samples were examined under a binocular microscope, generally at around 40 X magnification. Arcellaceans, freshwater protists related to foraminifera and often common in high marsh samples, were enumerated along with the foraminifera. To simplify subsequent discussions, and as arcellaceans constitute only a minor component of the total fauna, both groups are lumped together as foraminifera.

One to two gram samples of surface soil from each site were brought back to the laboratory for diatom analysis. Organic matter in the samples was removed by H<sub>2</sub>O<sub>2</sub> digestion and the

remaining material dispersed in 250ml of distilled water. After repeated decanting and settling to remove fines and to bring the solution to a near-neutral pH, aliquots of suspended material were dried on glass slides and mounted in Hyrax. The diatom assemblage of each sample was determined at 1000 X by counting the first 200-300 specimens encountered in random parallel traverses. Taxonomic identifications were based on descriptions in Van Der Werff and Huls (1957-1974), Hendeby (1964), Patrick and Reimer (1966 1975), Rao and Lewin (1976), Foged (1981), Laws (1988), and Hemphill-Haley (1993).



TEXT-FIGURE 3 Marsh transect profile, showing the positions and elevations of the macrophyte (top) and composite foraminifer/diatom/macrophyte (bottom) data.

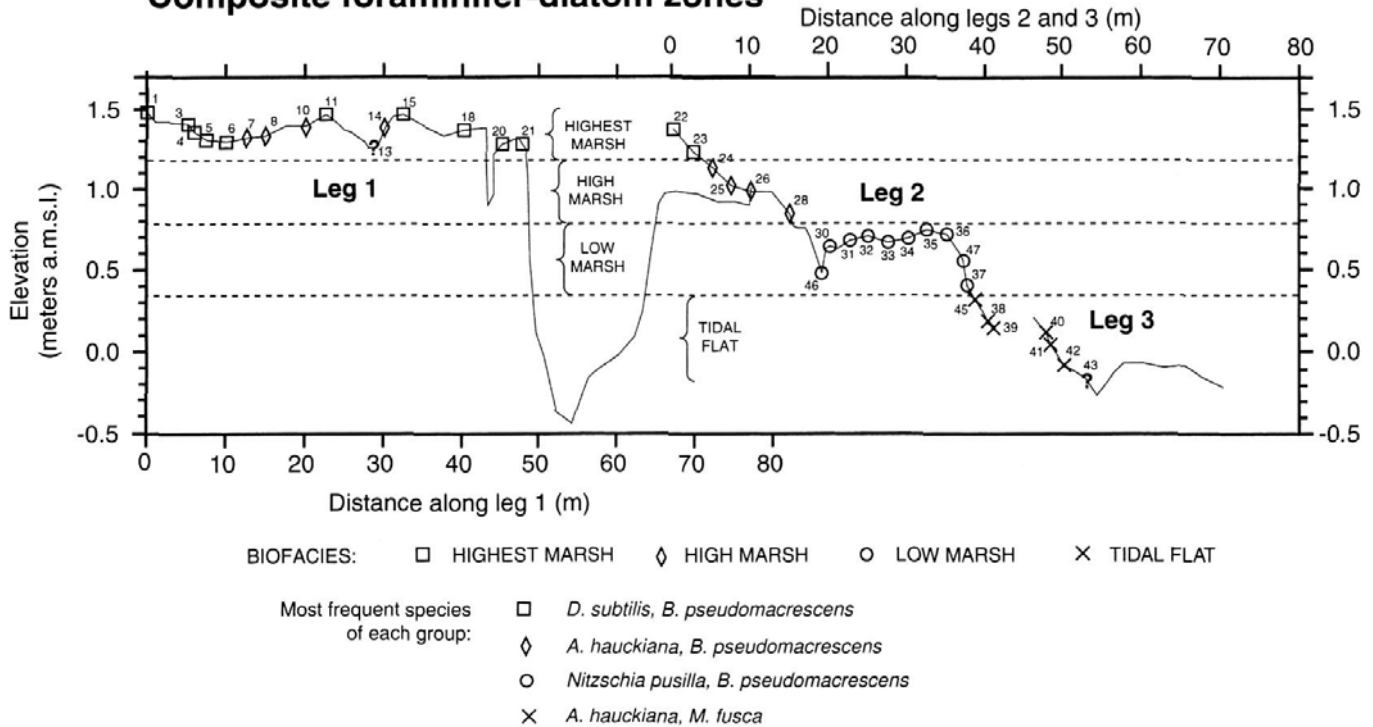
**Quantitative Analytical Procedures**

Foraminiferal (Appendix 1, Table 1), diatom (Appendix 2, Table 2), and macrophyte (Appendix 3, Table 3) data were converted into fractional abundances, and standard errors were calculated according to the formula proposed by Patterson and Fishbein (1989):

$$SX_i = [X_i(1 - X_i)/N]^{1/2}$$

where  $SX_i$  is the standard error;  $X_i$  is the estimated fractional abundance for each  $i = 1, 2, 3, \dots, I$  species, where  $I$  = the total number of species in the sample;  $i$  is each species; and  $N$  is the total number of specimens counted in a sample. When making  $N$  counts, the actual fractional abundance  $f_i$  lies between,

### Composite foraminifer-diatom zones



TEXT-FIGURE 4  
Marsh transect profile, showing the positions and elevations of the composite foraminifer/diatom data.

$$Xi - 1.96SXi \sim fi \sim Xi + 1.96SXi$$

95% of the time. Therefore, the 95% confidence interval on the estimated fractional abundances is  $Xi \pm 1.96SXi$ . The standard error for samples having no specimens of a particular species was calculated using the standard error equation ( $SXi$ ); see Mosteller et al. 1970):

$$SXi = 1 - (0.051/N)$$

All samples contained statistically significant numbers of foraminifera, diatoms, and macrophytes (Tables 1, 2, and 3; see Patterson and Fishbein 1989, for background on estimating statistical significance).

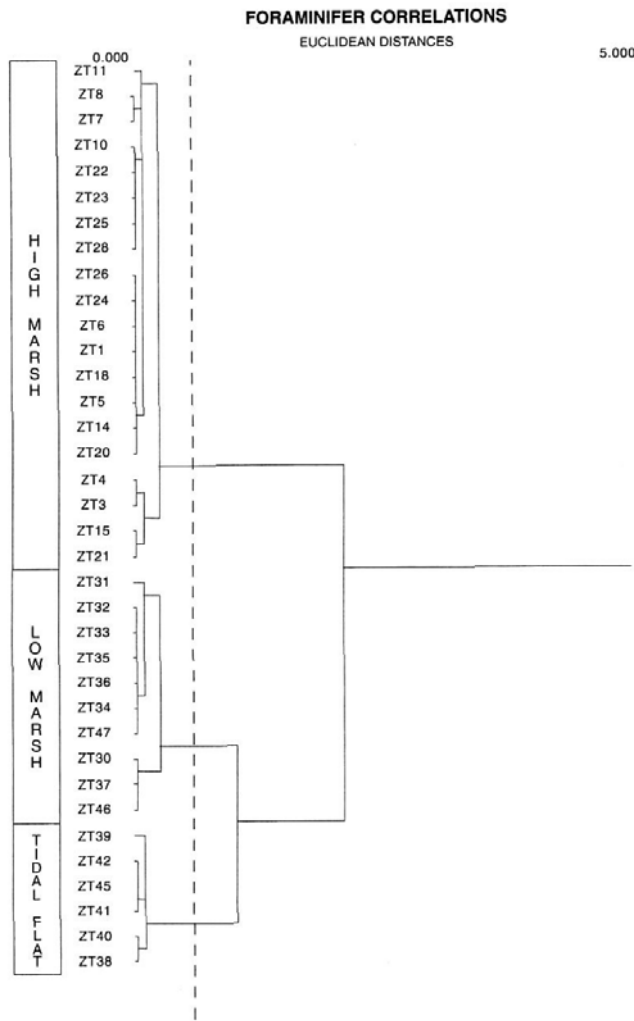
Q-mode cluster analysis was carried out on separate and combined foraminifer, diatom, and macrophyte data in order to group samples with similar species distributions. Samples grouped in this fashion are considered to be representative of a particular environment or biofacies. Due to their anomalous floral and faunal makeup, two samples were deleted from further cluster analysis. Samples ZT13 and ZT43, containing highly irregular diatom and foraminifer flora and faunas clustered anomalously (Table 1, 2). ZT13 at 1.26 m above mean sea level (amsl) was collected in a depression in the upper marsh almost completely filled with wood chips (text-figs. 2 and 3). This microenvironment, not encountered elsewhere along the transects, probably explains the unusual floral and faunal content. Sample ZT43 at -0.14m amsl, was also collected from a topographic depression in the marsh (text-figs. 2, 3, and 4); the foraminifer population is probably the result of tidal reworking.

Specimens of fifteen foraminifer and arcellacean species and "morphotypes" were observed in this study (Appendix 1), but only the nine species present in statistically significant numbers (Table 1) were used in the analysis. Statistically significant taxa were subjectively determined to be those with abundances equal to the standard error +1% at the 95% confidence level in at least one sample. In our analyses *Jadammina polystoma* Bartenstein and Brand, a morphotype of *J. macrescens* with a supplementary areal aperture, is included under the latter name. *Trochammina irregularis* Cushman and Brönniman, a morphotype of *T. salsa*, is lumped with that species.

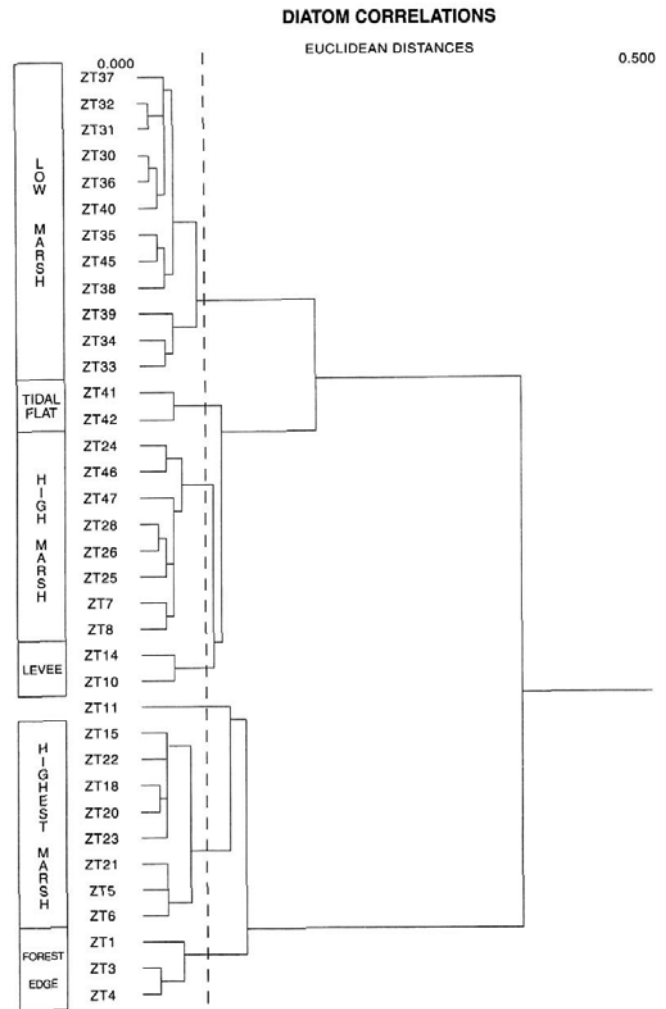
Specimens of 138 diatom species (Appendix 2) were observed but, as with the foraminifera, only the 40 species present in statistically significant numbers were used in the cluster analysis (Table 2).

Thirteen macrophyte taxa were observed along the transect (Appendix 3). Tabulation of macrophyte abundance data was based on the live plant cover of a gridded 100-mesh quadrat, a different methodology than employed for collecting microfossil data. However, as the data were calculated as percent relative abundance, the results are directly comparable with the micropaleontological results. Nine taxa were found to be present in statistically significant abundances (Table 3). An additional category, percent bare ground, was also included in the cluster analysis, as absence of plants in the marsh has ecological significance. Due to intergrowth of species in some cases percent coverage added up to more than 100% in some samples (e.g. ZT-7 where coverage equaled 112%).

Q-mode clustering of the reduced data sets was done on an Apple Macintosh computer using the SYSTAT v.5.2 statistical soft-



TEXT-FIGURE 5  
Q-mode cluster dendrogram of foraminiferal samples. Clusters of samples at Euclidean distances greater than a selected level (dashed vertical line) are considered to be assemblage zones.



TEXT-FIGURE 6  
Q-mode cluster dendrogram of diatom samples.

ware package and Ward's minimum variance method (Wilkinson 1992). The results of the cluster analyses were reported as Euclidean distances and arranged in hierarchical dendrograms (text-figs. 5, 6, 7, 8, and 9). The dendrograms were used to define sample associations or biofacies. This methodology simulates a statistically based Error-Weighted Maximum Likelihood (EWML) clustering method described by Fishbein and Patterson (1993).

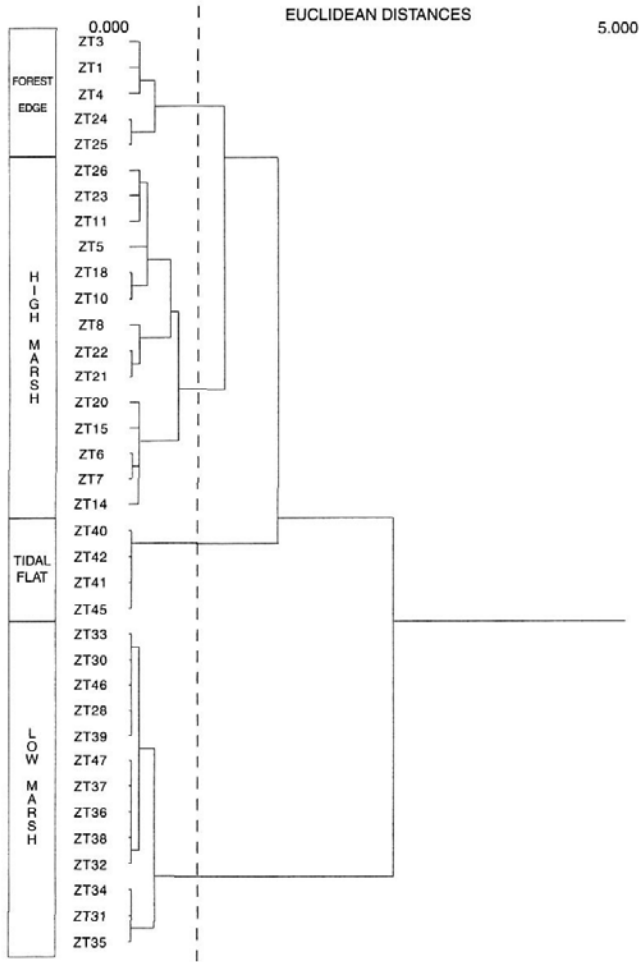
Separate cluster analyses were carried out on the foraminiferal (text-fig. 5), diatom (text-fig. 6), and macrophyte (text-fig. 7) data, and on combined foraminiferal/diatom/macrophyte (text-fig. 8) and foraminiferal/diatom (text-fig. 9) data sets. To facilitate comparison of the clusters, all dendrograms were interpreted using similar correlation coefficients of <1.0 (text-figs. 5, 6, 7, 8, and 9).

## RESULTS AND DISCUSSION

### Cluster Analysis of Foraminiferal Data

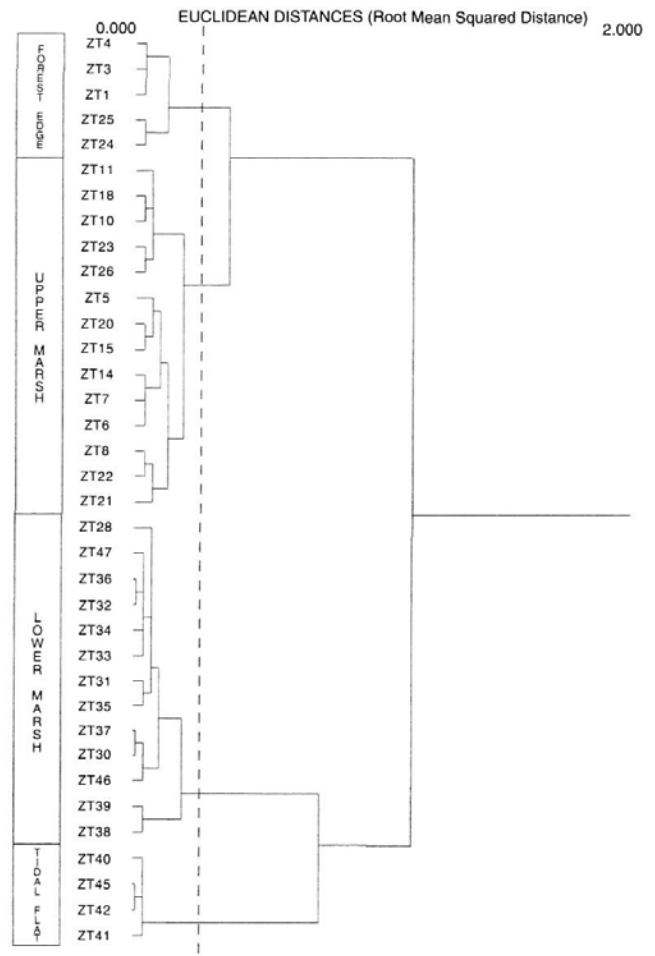
Cluster analysis of the foraminiferal data set yielded three foraminiferal assemblages at different elevations: High Marsh (0.8–1.5m amsl), Low Marsh (0.4–0.8m amsl), and Tidal Flat (-0.2–0.4m amsl) assemblages (text-figs. 2 and 5; Table 1). Marsh floras and faunas are often discussed in terms of "low" vs. "high" or "upper" marsh. This usage has become the norm in papers examining the distribution of foraminifera, diatoms, and macrophytes in marshes (e.g. Scott and Medioli 1978; Scott and Medioli 1980; Hutchinson 1982; Palmer and Abbott 1986; Williams 1989, 1999; Patterson 1990; Jennings and Nelson 1992; Hemphill-Haley 1995a; Hutchinson et al. 1995; Hutchinson et al., in press), both to informally denote position in the marsh and to demarcate absolute elevations. The boundary between

MACROPHYTE CORRELATIONS



TEXT-FIGURE 7  
Q-mode cluster dendrogram of macrophyte samples.

COMPOSITE ALL-ORGANISMS DISTANCE METRICS (4 CLUSTERS)



TEXT-FIGURE 8  
Q-mode cluster dendrogram for composite foraminifer, diatom and macrophyte data.

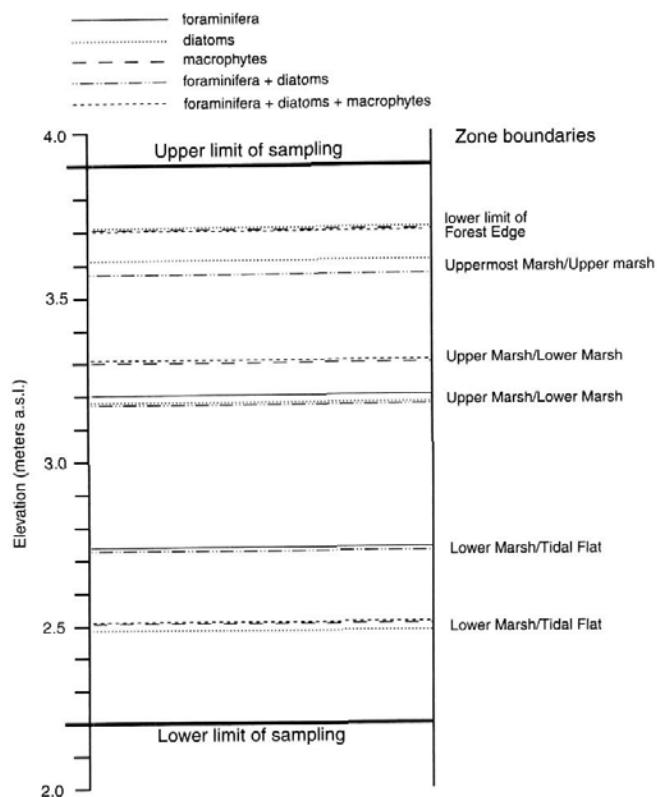
high and low marshes, however, changes locally depending on the tidal regime.

The High Marsh assemblage is dominated by *J. macrescens* and *B. pseudomacrescens*, the Low Marsh assemblage by *B. pseudomacrescens* and *M. fusca*, and the Tidal Flat assemblage by *M. fusca*. The extent and depth of infaunal foraminiferal occupation, even for individual species, changes from the low to the high marsh, and this has a major impact on the composition of the various assemblages found there. In addition, taphonomic processes such as dissolution and bioturbation also varies considerably in different areas of the marsh affecting assemblage structure. The marsh foraminiferal faunas at Zeballos and other sites on Vancouver Island (Guilbault et al. 1995, 1996; Ozarko et al. 1997) differ from those on the British Columbia mainland (Patterson 1990) in that no calcareous species are present. The absence of calcareous species at Zeballos may be related to lower pH values there. The excessive energy required to maintain calcium carbonate tests may exclude calcareous species from the Zeballos marsh and similar sites. It is noteworthy that by visual examination of the data alone it is possible to easily recognize a Low Marsh assemblage dominated by *M. fusca* all along the BC coast (Patterson 1990; Guilbault et al. 1995, 1996; Ozarko et al. 1997).

Cluster Analysis of Diatom Data

Cluster analysis yielded six mostly elevation-related diatom assemblages: Forest Edge (1.3–1.5m amsl); Levee (1.4m amsl); Highest Marsh (1.2–1.5m amsl); High Marsh (0.8–1.2m amsl); Low Marsh (0.1–0.8m amsl); and Tidal Flat (-0.2–0.1m amsl) assemblages (text-figs. 2, 6; table 2). It is important to note that the levee facies is not elevation-related and the elevation of the Forest Edge overlaps that of the Highest Marsh. None of these zones correspond to the foraminiferal assemblages, reflecting the different sets of environmental parameters that control the distribution of these species. Diatom species may have narrow or broad elevational ranges with maximum abundances centered at middle elevations or skewed towards the lower or upper marsh limits.

The Forest Edge assemblage is dominated by *Navicula pusilla* and *Pinnularia lagerstedti* while *Denticula subtilis*, *Navicula subtilis*, *Navicula cincta*, *Achnanthes hauckiana*, and *Navicula salinarum* dominate the Highest Marsh Assemblage. The Levee assemblage, found in samples ZT10 and ZT14, consists mainly of *Denticula subtilis* and *Caloneis bacillum*. The High Marsh



TEXT-FIGURE 9  
Summary of elevation boundaries resulting from the various cluster analyses.

assemblage is dominated by *Achnanthes hauckiana* and *Navicula salinarum*. *Navicula salinarum* reaches a peak in the transition zone between the Low and High marsh. The Low Marsh Assemblage is characterized by abundant *Nitzschia pusilla* and *Achnanthes hauckiana*. *Nitzschia pusilla* has a distribution centered in the low marsh, where it accounts for 30 to 40% of the total diatom assemblage. The Tidal Flat assemblage is dominated by *Opephora pacifica* and *Achnanthes hauckiana*. Species such as *Achnanthes hauckiana*, *Navicula cryptocephala*, and *Rhopalodia musculus* all have broad distributions and relatively constant abundances through the low marsh and intertidal flat. *Opephora pacifica* is a cosmopolitan species that commonly grows as epipsammon (i.e. attached to sand grains) on intertidal flats (Rao and Lewin 1976).

Sample ZT11 (1.5m amsl) clustered separately from all other samples. No such anomaly was observed in the foraminiferal data.

#### Cluster Analysis of Macrophyte Data

Four elevation-related macrophyte assemblages were delineated by cluster analysis. Forest Edge (1.3–1.5m amsl), High Marsh (0.9–1.3m amsl), Low Marsh (0.1–0.9m amsl), and Tidal Flat (-0.2–0.1m amsl) where very little vegetation was found (text-figs. 3 and 7; table 3). The Forest Edge assemblage has a ground cover dominated by *Deschampsia caespitosa* but also includes minor *Elymus mollis* and *Triglochin maritimum*. This zone corresponds well with the diatom assemblage of the same

name (Note that “forest” in this case denotes a cover of small trees and large bushes, rather than large trees). However, the macrophyte assemblage is present at slightly lower elevations (i.e. at ZT24 and ZT25) than the comparable diatom assemblage.

The High Marsh assemblage is dominated by *Juncus balticus*, *Plantago macrocarpa*, and *Carex lyngbyei*. The elevations spanned by this plant association correspond closely to those reported for the foraminiferal High Marsh assemblage. The High Marsh plant association is much more diverse than those of other zones in the marsh, including twelve of the thirteen species of vascular plants recorded in the survey.

There are two vegetation associations within the High Marsh: a *Juncus balticus*–*Plantago macrocarpa* phase, and a *Juncus*–*Carex lyngbyei* phase. Although the range of elevations occupied by these two phases is essentially the same, the mean elevation of the *Juncus*–*Carex* phase is slightly lower than that of the *Juncus*–*Plantago* phase. In addition, as 30% of the soil surface of the *Juncus*–*Carex* phase is unvegetated (compared to <5% bare soil for the *Juncus*–*Plantago* phase), this observation suggests that the micro-environments of these two associations are different. The *Juncus*–*Carex* phase appears to be characteristic of small hollows and shallow rills on the high marsh surface. Standing water may remain in these areas longer after tidal inundation. We speculate that they may consequently be more anoxic than neighbouring areas that support *Juncus*–*Plantago* phase.

The Low Marsh assemblage is characterized by abundant *Carex lyngbyei* and minor *Triglochin maritimum* and *Potentilla pacifica*. This assemblage zone has a similar elevational range to that of the Low Marsh diatom assemblage. The Tidal Flat assemblage is nearly lacking in macrophytes with the exception of some scattered clumps of *Carex lyngbyei*.

*Carex lyngbyei* is the dominant species in the low marsh of the Zeballos delta, as it is at other fjord-head deltas in British Columbia and southern Alaska, and at other estuaries in the Pacific Northwest with intermediate salinity levels (Hutchinson 1988; Hutchinson et al. 1989). In more saline estuaries in the Pacific Northwest, the low marsh community is dominated by *Salicornia virginica* and *Triglochin maritimum*, whereas in weakly brackish estuaries the dominant low marsh plants are *Scirpus* species (Jefferson 1975; MacDonald 1977; Hutchinson 1988; Nelson and Kashima 1993).

#### Cluster analysis of composite foraminiferal/diatom/macrophyte data

Cluster analysis of the composite foraminiferal-diatom-macrophyte data set discriminated four elevation-related assemblage zones (text-figs. 3, 8). The number of zones was the same as that obtained using the macrophytes but is less than that recognized using diatoms alone (text-figs. 2, 6). This result was surprising because in addition to the large number of variables in the analysis (58), there are considerable differences in the elevation limits of assemblages within the three groups (text-fig. 9). We therefore expected to find more zones. However, these factors combine to give maximum resolution, and result in highly accurate assemblage zones with very few sample misclassifications.

The boundaries of the composite Forest Edge assemblage (1.3–1.5m amsl), are coincident to the highest assemblage recognized by diatom cluster analysis and are near those obtained



for the highest elevation macrophyte assemblage. It is dominated by the foraminifer *Balticammina pseudomacrescens*, the grass *Deschampsia caespitosa* and the diatom *Navicula pusilla*. It also includes trees and bushes that were not included in the cluster analysis. The High Marsh Assemblage (0.9–1.3m amsl) is found in open marsh areas to the limit of the marsh. The foraminifer *Balticammina pseudomacrescens*, the macrophyte *Juncus balticus*, and the diatom *Denticula subtilis* are most abundant in this assemblage. The dominant species in the Low Marsh Assemblage (0.1–0.9m amsl) are the foraminifer *Miliammina fusca*, the macrophyte *Carex lyngbyei*, and the diatom *Achnanthes hauckiana*. The Tidal Flat Assemblage (-0.2–0.1m amsl) is almost devoid of vegetation, except for scattered *Carex lyngbyei*, but contains abundant *Miliammina fusca* as well as *Achnanthes hauckiana*.

**Cluster Analysis of Composite Foraminiferal/Diatom/Data**

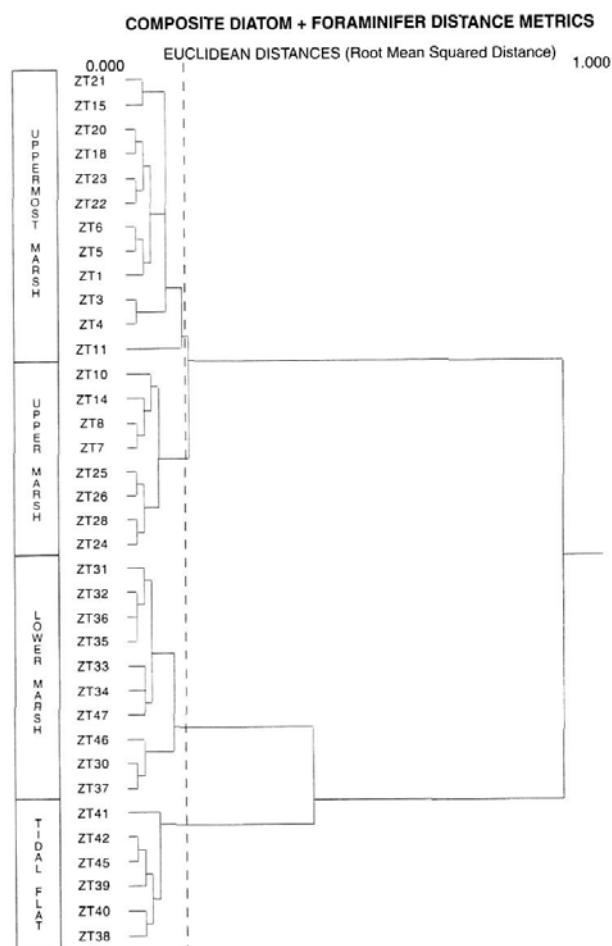
Macrophyte remains are commonly difficult to identify in buried marsh sediments. Thus the composite foraminiferal/diatom data set was analyzed to provide data more useful to researchers examining fossil and subfossil marsh sections. As with the foraminiferal/diatom/macrophyte data, cluster analysis identified four elevation-related assemblage zones (text-figs. 4, 10). The Highest Marsh assemblage (1.2-1.5m amsl) is dominated by *B. pseudomacrescens* and *D. subtilis*; the High Marsh Assemblage (0.8–1.2m) by *B. pseudomacrescens* and *A. hauckiana*; the Low Marsh Assemblage (0.3–0.8m) by *B. pseudomacrescens* and *Nitzschia pusilla*; and the Tidal Flat Assemblage (-0.2–0.3m) by *M. fusca* and *A. hauckiana*.

The most significant difference between the foraminiferal/diatom/macrophyte composite analysis and the foraminiferal/diatom composite analysis is that a distinct forest edge assemblage is not recognized in the latter, although the upper marsh was more finely divided. As discussed above, although more zones are provided by the diatom data alone, the elevational accuracy of the integrated foraminiferal/diatom data is greater due to fewer sample misclassifications (text-fig. 4). Thus, an integrated diatom/foraminiferal analysis of subsurface marsh sections should provide more accurate paleo-elevation data than could be obtained using either group alone. This approach is therefore recommended in studies where small coseismic land-level changes or sea-level changes need to be resolved.

**Correlation between the distribution of taxa and elevation**

The presence of faunal zones in the tidal marsh indicates that there is a strong correlation between elevation and the distribution of some tidal marsh species. Previous research on the distribution of marsh foraminifera in Vancouver Island marshes (Guilbault and Patterson (in press), for example, has shown a strong negative correlation between elevation and *Miliammina fusca* (R=0.93) and between elevation and the grouping *Balticammina pseudomacrescens*, *Jadammina macrescens*, and *Trochamminita salsa* (R=0.92).

Linear correlations carried out on the 58 species and morphotypes of foraminifera, diatoms, and macrophytes present in statistically significant numbers in this study (nearly 3600 possible combinations) indicate that some taxa, either individually or in small groups, can provide a solid base for statistical reconstruction (text-figs. 11, 12). *Miliammina fusca* and *Balticammina pseudomacrescens* correlate well with elevation, (R=0.94 and 0.89 respectively), and the correlation coefficient for the two between combined species (R=0.95) is the highest recorded for any pairing (text-fig. 11). Their high correlation

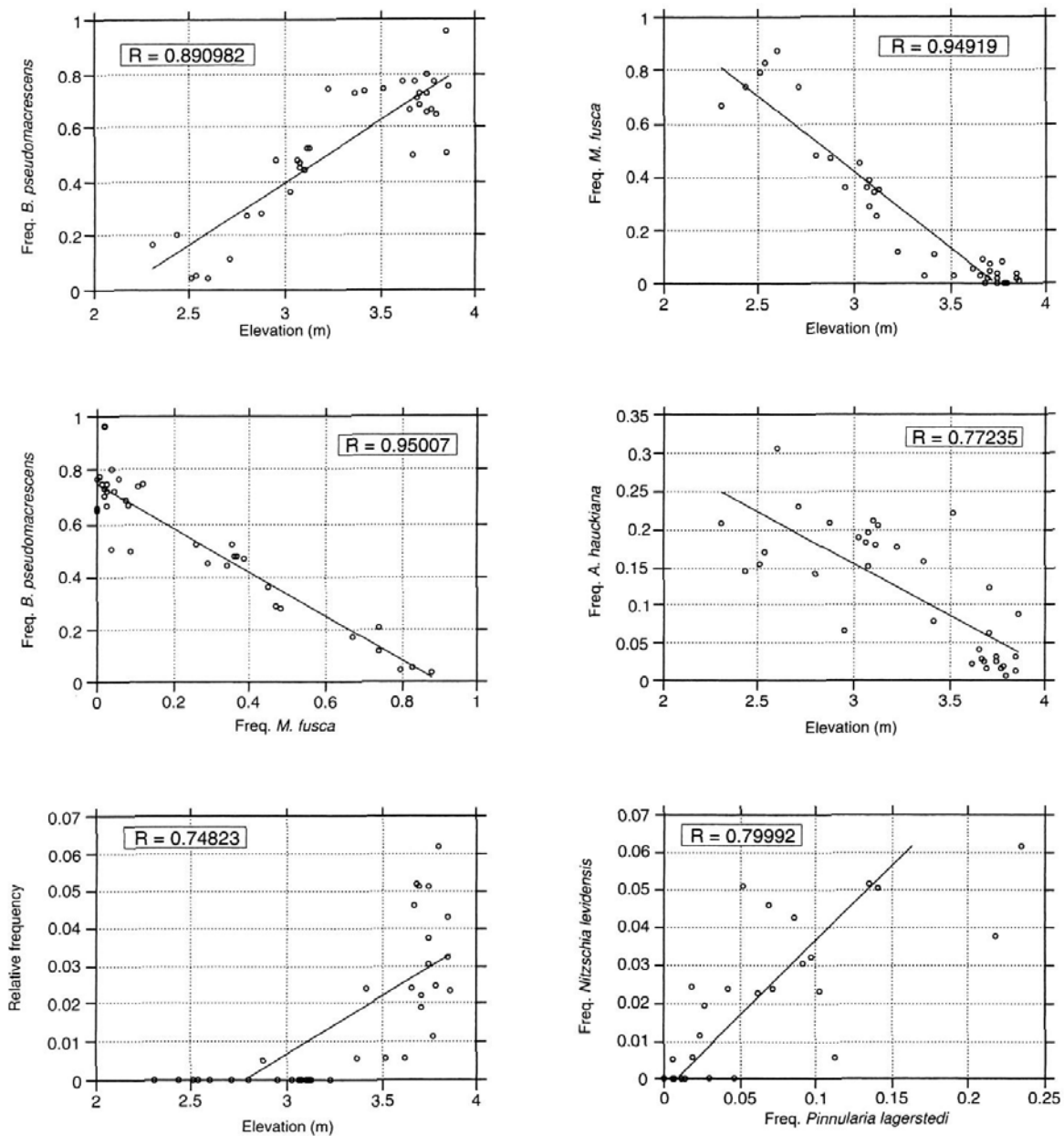


TEXT-FIGURE 10  
Q-mode cluster dendrogram of composite foraminifera and diatom data.

with elevation make these foraminifera particularly well suited for analysis utilizing linear correlation techniques.

The only macrophyte with such a high correlation (R=0.93) is *Carex lyngbyei* (text-fig. 12). Other macrophytes yield much lower correlation coefficients. Plants found abundantly only in the High marsh, for example, do not correlate well with elevation. In addition, *Deschampsia caespitosa* and *Plantago macrocarpa*, both locally common in the high marsh, plot as if they are mutually exclusive. This distribution may be the result of patchy colonization, resulting in a macrophyte distribution where one taxon or the other completely dominates a site.

Only three diatom species correlate well with elevation, *Fragilaria construens* (R=0.82), *Achnanthes hauckiana* (0.77) and *Nitzschia levidensis* (0.74) (text-fig. 11). The first two species are most abundant in the low marsh, whereas the third is common in the high marsh. *Fragilaria construens* and *A. hauckiana* both correlate well with *C. lyngbyei* (R=0.74 and 0.80, respectively) as does *M. fusca* (0.82) (text-fig. 12). Previous research has indicated that the distribution of foraminifera in tidal marshes, particularly *M. fusca*, is closely linked to dehydration (Scott and Medioli 1980). However, the distributional pattern displayed by the above-mentioned species could also be associated with salinity. De Rijk (1995) found that the distribution of *H. wilberti* is negatively correlated with salinity. If salin-



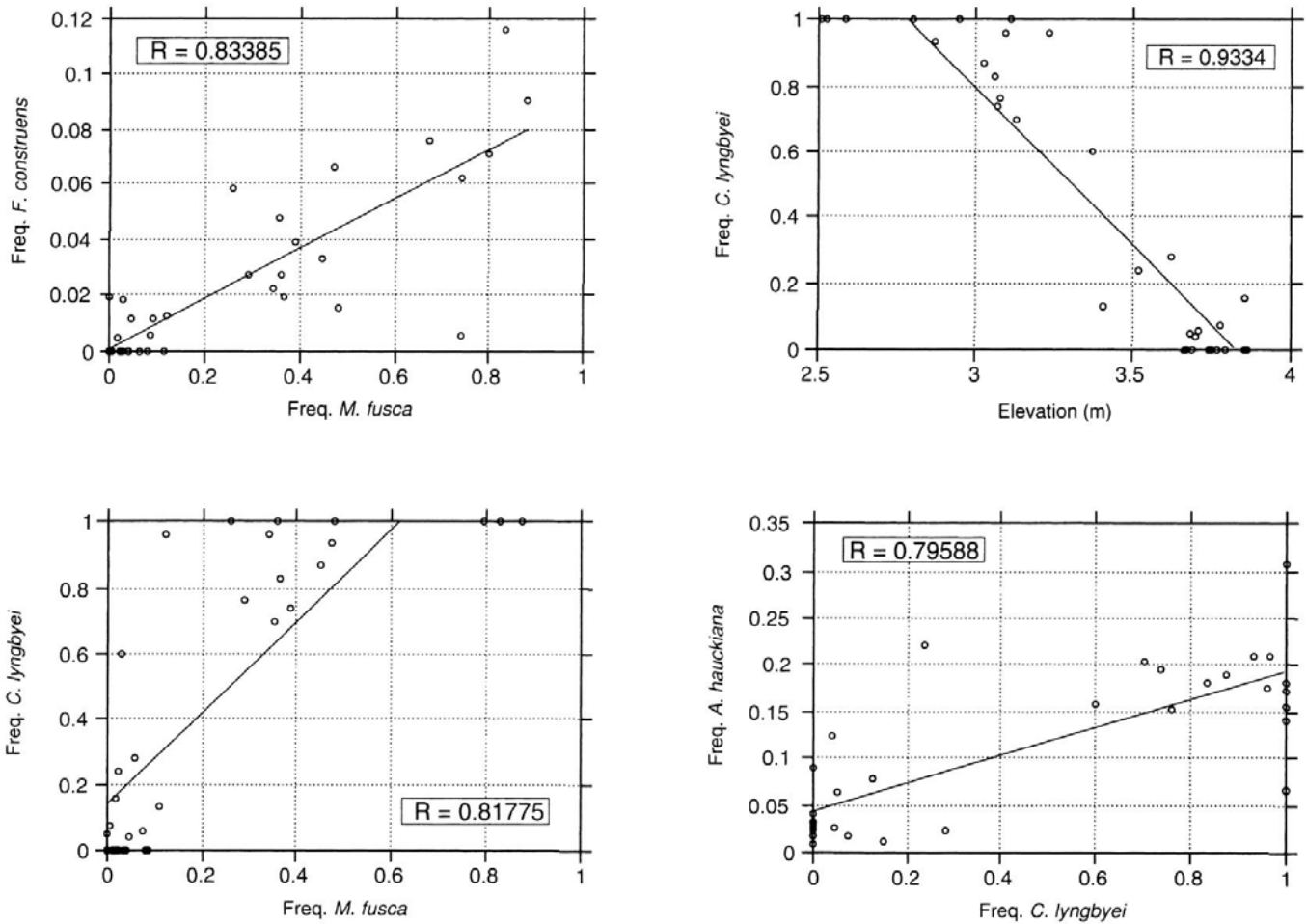
TEXT-FIGURE 11  
Linear correlation between various taxa, and between specific taxa and elevation.

ity controls the distribution of *C. lyngbyei*, *F. construens*, and *A. hauckiana*, a good correlation should be found between these species and *H. wilberti*. However, the correlation coefficient for the Zeballos data is less than 0.2, suggesting that salinity is not the major factor controlling the distribution of these species in the marsh. This is not surprising, given the low salinity all across the Zeballos marsh.

Linear correlation techniques are also useful in examining paleoecological relationships that are unrelated to elevation. For example, specimens of the foraminifer *Trochammina salsa*, especially the most irregularly shaped ones, are associated with unidentified plant debris at both Tofino (Guilbault et al. 1995) and Zeballos. This suggests that this species employs an epiphytic lifestyle in this area. However, statistical comparison

of *T. salsa* and the macrophytes indicates no relation between the distribution of this species and individual macrophytes. Only a marginally significant linear correlation (0.63), for example, was found between *T. salsa* and *Diploneis*.

Text-figure 13 compares the elevational ranges of foraminifera (Williams 1989; Patterson 1990; Jonasson and Patterson 1992; Jennings et al. 1992; Guilbault et al. 1996; Scott et al. 1996; Shennan et al. 1996; Williams 1999), diatoms (Nelson and Kashima 1993; Hemphill-Haley 1995b; Shennan et al. 1996; Hutchinson et al. 1998) and macrophytes (Scott et al. 1996; Shennan et al. 1996; Hutchinson et al. 1998) reported from previous studies along the northwestern coastline of North America with the results obtained at Zeballos. There is a reasonable correlation between the foraminiferal distribution found at dif-



TEXT-FIGURE 12  
Linear correlation between various taxa, and between specific taxa and elevation.

ferent sites, although factors such as local tidal range and salinity have an impact on the elevation of particular zones and accessory species found. The distribution of diatoms is quite variable from place to place. The lack of correlation in this case is due to the high diversity of diatom taxa endemic to marshes. These taxa tend to be much more stenotopic than the foraminifera characterizing the same marshes. Although it is much more difficult to directly correlate from one marsh to another using diatoms the particular set of species found in a particular marsh zone more precisely define local conditions. The macrophyte taxa also display considerable variability from marsh to marsh. Although, as with the diatoms, most of these species have very broad distributions local conditions have considerable influence over the species dominating particular marsh settings. Thus of the groups examined in this study it seems that foraminifera are probably the most reliable tool for routine correlation between marshes.

### CONCLUSIONS

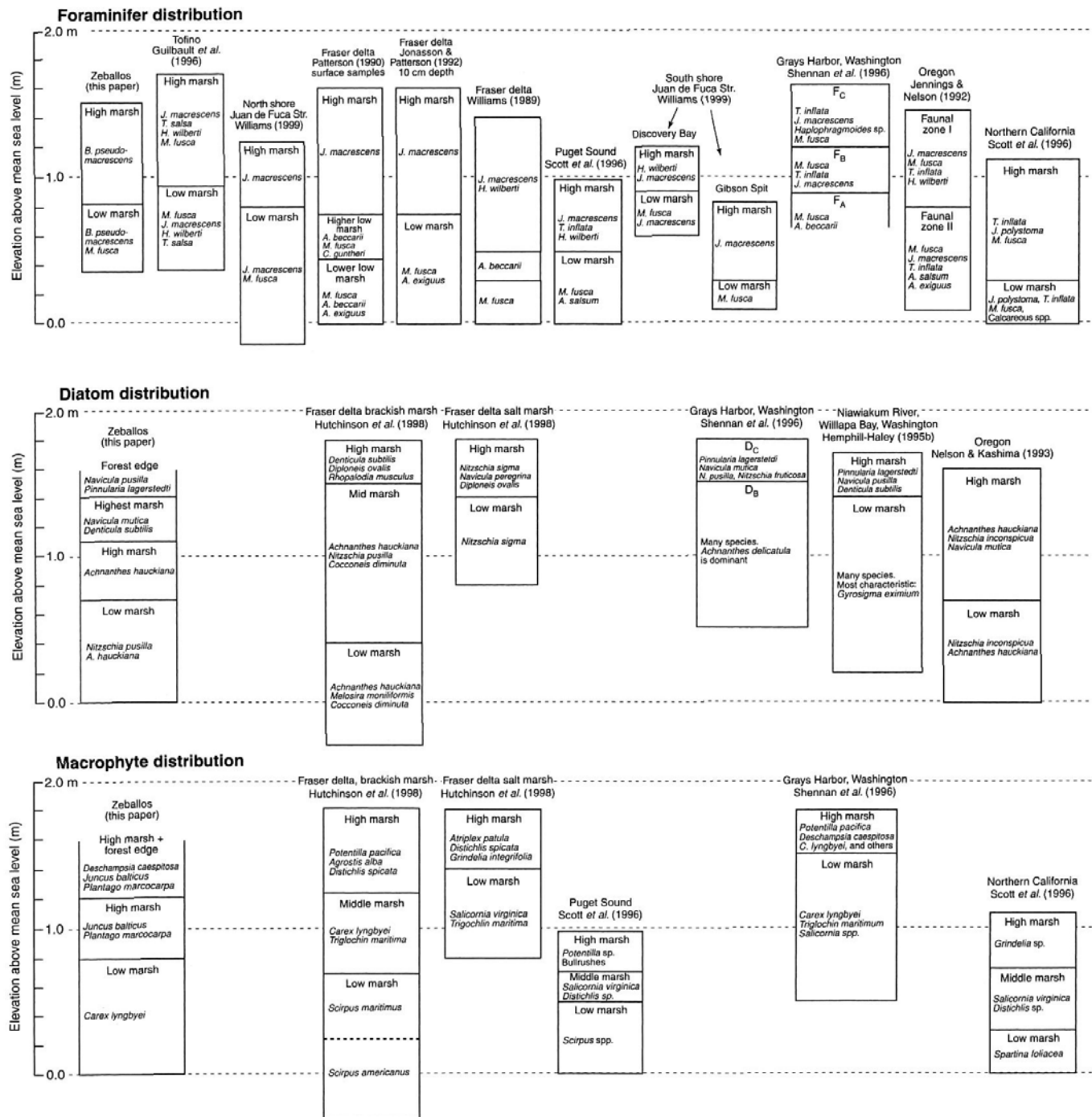
This study has provided, for the first time, direct comparisons of foraminiferal, diatom, and macrophyte assemblage zones across an intertidal marsh. As researchers generally use only one type of organism to characterize a marsh, it has previously

been impossible to compare zonations obtained using different groups between sites. This difficulty has been exacerbated by local variations in physical parameters such as salinity, and oxygen concentration which affect different organisms in different ways. The results presented in this paper will allow researchers, at least in a general way, to compare their results.

This study has also demonstrated that a much more accurate vertical zonation of the marsh community is possible when several groups are utilized simultaneously. When applied to fossil sections, this approach should allow even small paleo-sea-level changes to be recognized. This is important, for example, on the Pacific Northwest coast of North America, where coseismic elevational changes of a few tens of centimeters have occurred. This knowledge will greatly enhance our understanding of the seismic history of the region.

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TEXT-FIGURE 13 Distributions of foraminifera, diatoms and macrophytes as a function of elevation in tidal marshes of the northwestern coastline of North America.

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TABLE 1 Fractional abundances of statistically significant foraminifera and arcellacea in samples for the Zeballos marsh. Upper Marsh (UM), Lower Marsh (LM), Tidal Flat (TF).

Table with 37 columns (sites ZT-1 to ZT-37) and 25 rows (species and elevations). Rows include Assemblage, Total count, M. fusca (>183 um), M. fusca (<183 um), Bulminotina pseudomacrescens, Jadammina macrescens, Trochammina suba, Haplophragmoides wilberti, Psiculularium limatris, Centropages oculatus, and Arcella vulgaris.

TABLE 2 Fractional abundances of statistically significant diatoms in samples from the Zeballos marsh. Forest Cover (FC), Uppermost Marsh (UMM), Levee (L) Upper Marsh (UM), Lower Marsh (LM), Tidal Flat (TF).

Table with 37 columns (sites ZT-1 to ZT-37) and 30 rows (species and elevations). Rows include Achnanthes deflexa var flexella, Achnanthes greenlandica, Achnanthes haasiana, Achnanthes lanceolata, Achnanthes minutissima, Achnanthes puvilla, Amphora calyptiformis, Amphora ovalis, Caloneis bacillum, Denticula tabulifera, Diploneis pseudobacillifera, Fragilaria cuneirostris, Fragilaria pinnata, Fragilaria virescens, Frustulia vulgaris, Gyrodinium striatum/otoliqua, Melosira moniliformis, Melosira mammuloides, Navicula cincta, Navicula crumpeophthalma, Navicula greysii, Navicula mutata, Navicula peregrina, Navicula puvilla, Navicula radiosa, Navicula rehardii, Navicula salinarum, Navicula stankovicii, Nitiscula fasciculata, Nitiscula hybrida, Nitiscula leventidisi, Nitiscula palmata, Nitiscula pusilla, Nitiscula stygia, Nitiscula vitrea, Oporosira parvifera, Pinnularia ligustredii, Pinnularia sulcospina, Rhopalodia muculosus, and Synedra tabulata.

TABLE 3 Fractional abundances of statistically significant macrophytes in samples from the Zeballos marsh. Forest Cover (FC), Upper Marsh (UM), Lower Marsh (LM), Tidal Flat (TF).

Table with 37 columns (sites ZT-1 to ZT-37) and 25 rows (species and elevations). Rows include Achillea millefolium, Carex longyvei, Deschampsia caespitosa, Elymus albidus, Juncus balticus, Lathyrus japonicus, Plantago macrospora, Potamogeton nodosus, Triglochin maritima, and Bare ground.

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#### APPENDIX 1

Foraminiferal and Arcellacean taxa observed in Zeballos salt marsh.

##### Foraminifera

- Miliammina fusca* (Brady)  
*Jadammina macrescens* (Brady)  
*Balticammmina pseudomacrescens* Brönniman, Lutze and Whittaker  
*Trochamminita salsa* (Cushman and Brönniman)  
*Haplophragmoides wilberti* Andersen  
*Trochammina inflata* (Montagu)†  
*Reophax nana* Rhumbler†  
*Pseudothurammmina limnetis* (Scott and Medioli)

##### Arcellaceans

- Centropyxis aculeata* (Ehrenberg)  
*Centropyxis constricta* (Ehrenberg)†  
*Diffugia oblonga* (Ehrenberg)  
*Lagenodiffugia vas* (Leidy)  
*Arcella vulgaris* Ehrenberg  
*Lesquereusia spiralis* (Ehrenberg)  
 † Recorded in fossil (core) material only.

#### APPENDIX 2

Diatom taxa in the Zeballos marsh.

- Achnanthes brevipes*  
*Achnanthes conspicua*  
*Achnanthes deflexa or flexella*  
*Achnanthes groenlandica*  
*Achnanthes hauckiana*  
*Achnanthes lanceolata*  
*Achnanthes minutissima*  
*Achnanthes parvula*  
*Achnanthes wellsiae*  
*Actinocyclus normanii*  
*Amphipleura rutilans*  
*Amphiprora alata*  
*Amphora coffaeiformis*  
*Amphora granulata*  
*Amphora ovalis*  
*Amphora sp. (macilenta?)*  
*Anomoeneis serians*  
*Aulacoseira granulata*  
*Aulacoseira italica*  
*Bacillaria paxillifera*  
*Caloneis bacillum*  
*Caloneis brevis*  
*Caloneis westii*  
*Ceratoneis arcus*  
*Cocconeis diminuta*  
*Cocconeis fasciculata*  
*Cocconeis pellucida*  
*Cocconeis placentula*  
*Cocconeis scutellum*  
*Cocconeis vitrea*  
*Coscinodiscus spp*  
*Cyclotella meneghiniana*  
*Cyclotella stelligera*  
*Cymatosira belgica*  
*Cymbella affinis*  
*Cymbella aspera*  
*Cymbella caespitosa*  
*Cymbella cistula*  
*Cymbella hybrida*  
*Cymbella minuta/ventricosa*  
*Cymbella sinuata*  
*Cymbella turgida*  
*Denticula subtilis*  
*Diatoma vulgare*  
*Diatoma hiemale*  
*Diploneis crabro*  
*Diploneis didyma*  
*Diploneis interrupta*  
*Diploneis oblongella/ovalis*  
*Diploneis pseudo/subovalis*  
*Diploneis smithii*  
*Eunotia arcus*  
*Eunotia exigua*  
*Eunotia faba*  
*Eunotia monodon*  
*Eunotia perpusilla*  
*Eunotia praerupta*  
*Eunotia robusta*  
*Eunotia rostellata*  
*Fragilaria brevistriata*  
*Fragilaria capucina*  
*Fragilaria construens*  
*Fragilaria intermedia*  
*Fragilaria lapponica*  
*Fragilaria pinnata*  
*Fragilaria virescens*  
*Frustulia linkei*  
*Frustulia rhomboides*

*Frustulia vulgaris*  
*Gomphoneis eriense*  
*Gomphonema angustatum*  
*Gomphonema kamschaticum*  
*Gomphonema lanceolatum*  
*Gomphonema olivaceoides*  
*Gomphonema parvula*  
*Gomphonema truncatum*  
*Grammatophora oceanica*  
*Gyrosigma eximium/obliqua*  
*Hantzschia amphioxys*  
*Licmophora* spp.  
*Mastogloia elliptica*  
*Mastogloia exigua*  
*Melosira monoliformis*  
*Melosira nummuloides*  
*Meridion circulare*  
*Navicula abunda*  
*Navicula arvensis*  
*Navicula aurora*  
*Navicula bacillum*  
*Navicula cancellata*  
*Navicula cincta*  
*Navicula circumtexta*  
*Navicula contenta*  
*Navicula crucifera*  
*Navicula cryptocephala*  
*Navicula cryptolyra*  
*Navicula cryptonella*  
*Navicula digitoradiata*  
*Navicula disputans*  
*Navicula elegans*  
*Navicula flantica*  
*Navicula gelida*  
*Navicula graciloides*  
*Navicula granulata*  
*Navicula gregaria*  
*Navicula grevillei*  
*Navicula jaerenfeldti*  
*Navicula jamalinensis*  
*Navicula lanceolata*  
*Navicula litoricola*  
*Navicula lyra*  
*Navicula mutica*  
*Navicula normalis*  
*Navicula pelliculosa*  
*Navicula peregrina*  
*Navicula phyllepta*  
*Navicula praetexta*  
*Navicula pupula*  
*Navicula pusilla*  
*Navicula pygmaeae*  
*Navicula radiosa*  
*Navicula reichardtii*  
*Navicula rhombica*  
*Navicula rhyncocephala*  
*Navicula rostellata*  
*Navicula salinarum*  
*Navicula schoenfeldtii*  
*Navicula spicula*  
*Navicula stankovicii*  
*Navicula tripunctata*  
*Navicula viridula*  
*Navicula* sp. 1  
*Navicula* sp. 2 (Z-36a)  
*Navicula* sp. 3 (Z-36b)  
*Neidium lagodense*  
*Nitzschia bilobata*  
*Nitzschia commutata*  
*Nitzschia denticula*  
*Nitzschia fasciculata*

*Nitzschia gracilis*  
*Nitzschia hybrida*  
*Nitzschia lacuna*  
*Nitzschia lanceolata*  
*Nitzschia levidensis*  
*Nitzschia palea*  
*Nitzschia pseudohybrida*  
*Nitzschia pusilla*  
*Nitzschia sigma*  
*Nitzschia sinuata*  
*Nitzschia tryblionella*  
*Nitzschia vermicularis*  
*Nitzschia vitrea*  
*Odontella aurita*  
*Opephora pacifica*  
*Opephora marina*  
*Paralia sulcata*  
*Pinnularia abaujensis*  
*Pinnularia borealis*  
*Pinnularia intermedia*  
*Pinnularia lagerstedtii*  
*Pinnularia microstauron*  
*Pinnularia molaris*  
*Pinnularia parva*  
*Pinnularia subcapitata*  
*Rhabdonema arcuatum*  
*Rhizosolenia* spp.  
*Rhicosphaenia curvata*  
*Rhopalodia musculus*  
*Scoliopleura tumida*  
*Stauroneis amphioxys*  
*Stephanodiscus carconeis*  
*Stephanodiscus dubius*  
*Surirella crumena*  
*Surirella elegans*  
*Surirella ovata/brebissonii(?)*  
*Synedra acus*  
*Synedra fasciculata*  
*Synedra rumpens*  
*Synedra tabulata*  
*Synedra ulna*  
*Synedra vaucheriae*  
*Tabellaria fenestrata*  
*Tabellaria flocculosa*  
*Thalassionema nitzschiodes*  
*Thalassiosira decipiens*  
*Thalassiosira nodulolineata*  
*Trachyneis aspera*  
*Trachysphenia acuminata*  
*Trachysphenia australis*

#### APPENDIX 3

Macrophyte taxa in the Zeballos marsh.

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*Achillea millefolium* L.  
*Angelica lucida* L.  
*Carex lyngbyei* Hornem.  
*Daucus carota* L.  
*Deschampsia cespitosa* (L.) Beauv.  
*Elymus mollis* Trin.  
*Fragaria chiloensis* (L.) Duschene  
*Glaux maritima* L.  
*Juncus balticus* Willd.  
*Lathyrus japonicus* Willd.  
*Plantago macrocarpa* Cham & Schlect  
*Potentilla pacifica* Howell  
*Triglochin maritimum* L.