MODERN POLLEN AND VEGETATION RELATIONSHIPS IN BAY OF FUNDY SALT MARSHES

by

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ABSTRACT

This study examines modern relationships among salt marsh plant species and their pollen in three salt marshes located on the northwest coast of the Bay of Fundy, New Brunswick. Linear regression analysis of pollen in 35 surface sediment samples and vegetation cover on small (<15 m) and broad (>15 m) scales show that, with the exception of Poaceae and Cheno Am, pollen corresponds well with fine-scale patterns of salt marsh vegetation. Scatter diagrams of paired pollen and cover data illustrate that cover of *Triglochin* is over-represented by its pollen, *Glaux* is under-represented, and Poaceae, Cheno Am, and *Plantago* are inconsistent. Tidal mixing and differential inputs from local, regional, and extra-regional sources with elevation limit the establishment of plant-pollen relationships for Cheno Am and Poaceae but not for other taxa. Comparison of 35 modern analogs from five vegetation zones using squared chord distance show that zones are distinct such that the marsh-terrestrial interface can be tracked with the greatest degree of certainty in a salt marsh paleo-ecological record and other marsh zones can be tracked when a conservative threshold of dissimilarity is used.

RÉSUMÉ

Cette etude examine les relations modernes existant entre les espèces floristiques de marais salant et leurs pollens dans trois marais salants situés sur la côte Nord-Est de la Baie de Fundy, au Nouveau Brunswick. Les resultats des régressions lineaires entre la composition du pollen de 35 échantillons de surface et la composition floristique à petite (<15m) et grande (>15m) échelles démontrent, à l'exception de Poaceae et Cheno Am, l'abondance de pollen correspondent bien à la composition floristique à petite échelle. Les graphiques de l'abondance de pollen en fonction de la composition floristique démontre que *Triglochin* est sur-representé par rapport à son pollen, *Glaux* est sous-representé et Poaceae, Cheno Am, et *Plantago* sont inconsistents. L'action des marées ainsi que la contribution différentielle des sources de pollen locales, régionales et extra-régionales en fonction de l'élévation du marais limite l'établissement de relations plantes-pollens de Cheno Am et Poaceae, sans toutefois limiter l'établissement de telles relations pour d'autres espèces de marais salants. La comparison avec 35 analogues moderns représentés par cinq différentes zones de végétation en utilisant la méthode du 'squared chord distance' démontre que les differentes zones ont une signature palynologique distinctes de sorte que l'interface marais-terrestre peut être identifiée avec un grand degree de certitude pour les données paleo-écologiques de marais salants. Les autres zones de marais peuvent également être identifiées si des des critères de dissimilarité plus conservateurs sont utilisés.

ACKNOWLEDGEMENTS

The threads of this thesis were woven by many, with whom completion eventually became reality and I wish to express my deepest gratitude to Gail Chmura for her dedication, insight, and support, Vera Pospelova for her steadfast encouragement, Nigel Roulet for his constructive feedback, and NSERC, FCAR, The Centre for Climate and Global Change Research, and the Huntsman Marine Science Centre for their financial and/or technical support. Many thanks also go to the greatest field assistants on the planet, Leslie Underwood and Michelle Hollis.

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DEDICATION

I would like to dedicate the effort and energy that have been invested in this three-year process to John, Wendy, and Andrew Beecher for their love, faith, encouragement and support, Julie Wavrunek for everything wonderful that a big sister is, and Joe Wavrunek for lending a compassionate ear. I would also like to include Dan Sweeney for his unwavering belief in me and choice to grow with me through this endeavor and Naomi, Steve, and Carly Sweeney for sharing their home and hearts and showing me that obstacles are only challenges that take a bit more perseverance to overcome.

"The world is round and the place which may seem like the end may also be only the beginning."

~Ivy Baker Priest

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INTRODUCTION

Importance of paleo-ecological studies

Paleo-ecological research is based on the premise that relationships between environmental variables and modern ecosystems can be extended to past ecosystems and their environment. "Palynology, the analysis of pollen and spores, has been at the heart of environmental reconstruction for over three-quarters of a century" and has been used in a variety of systems to examine ecosystem dynamics, investigate climate change, and explore processes related to climate change over various spatial and temporal scales (MacDonald and Edwards, 1991). For example, pollen assemblages ('spectra') have provided evidence for invasion and expansion of tree populations in southern Ontario over the last 10,000 yr (Fuller, 1997), periods of drier climate over the last 3,000 yr in the southern Pennines (Tallis, 1997), and tidal salt marsh development and sea level rise in Long Island over the last 500 yr (Clark, 1986).

Identification of modern analogs allows paleo-ecologists to reconstruct past vegetation and climate from pollen data and analysts have developed two vegetation reconstruction methods using the modern vegetation-pollen relationship (Davis, 1963; Wright, 1967). The species-level approach involves deriving pollen-vegetation conversion factors (*R*-values) based upon quantitative descriptions of modern vegetation around modern pollen sampling sites (Davis, 1963; Wright, 1967). The community-level approach involves comparing unknown pollen spectra with a range of modern spectra from known vegetation to identify a modern analog for the fossil vegetation (Birks, 1976).

Modern analog identification is limited by biases that are inherent in pollen data and those resulting from choices made during data selection and analysis (Davis, 1963; Webb et al., 1978). Pollen spectra are inherently biased representations of vegetation because pollen production varies between species, particular pollen types are not preserved in sediments, and processes that transport, deposit, and mix sediments (e.g., erosion, bioturbation, flooding) can alter the composition of the pollen spectra, termed 'taphonomy'. Additional biases are the result of misidentification or destruction of pollen grains, inaccurate determination of modern vegetation assemblage and modern pollen rain, heterogeneous distribution of species on the landscape, vegetation that does not contribute pollen to sediments, and variation over time of factors that influence pollen production, sedimentation, and preservation (Davis, 1963). It follows that modern analogs are easier to define for ecosystems with species diversity and composition that can be represented in a pollen assemblage from a sampling location with simple taphonomy and minimal additional bias. Many paleo-ecological studies have focused on reconstructing forest ecosystems because tree pollen is abundant and easily transported, many pollen types are preserved in sediments, most types can be identified to the genus or species level, modern vegetation data is available and widespread, and many lakes, examples of sampling locations with simple taphonomy, are located in forested regions.

The quantitative nature of pollen data allows paleo-ecologists to address the accuracy and precision in using pollen spectra to represent and reconstruct vegetation using a species- or community-based approach. Investigators have demonstrated the influence of sources of error that affect the nature of tree-pollen relationships to derive correction coefficients and argued that additional modern analogs of forests need to be identified that represent a range of spatial scales

(e.g., Heide and Bradshaw, 1982; Bradshaw and Webb, 1985). Overpeck et al. (1985) used a community-based approach and numerically compared modern pollen spectra from four forest types to identify modern analogs and determine the degree of certainty in identifying a modern analog based upon the dissimilarity coefficient used. Identification of modern analogs is important because it can justify the use of calibration coefficients of environmental variables (e.g., temperature and precipitation) based on pollen and vegetation data from the region containing the modern analog (Overpeck, et al., 1985). Identification and use of modern analogs in quantitatively reconstructing terrestrial ecosystems has paved the way for the application of paleo-ecological calibration techniques and modern analogs in wetlands (Rich, 1995; Bunting et al., 1998; Willard et al., 2001; O'Neal et al., in press), but pollen from coastal salt marsh vegetation in more northern locations has yet to be calibrated and modern analogs have yet to be identified.

Paleo-ecological approaches to determine error and calibrate pollen assemblages

Species-level approach: plant-pollen relationships

Quantitative paleo-ecological reconstructions require examination of the relationship between pollen and the vegetation that produces it and consideration of sources of error that introduce bias to the relationship in order to develop correction coefficients that are used to interpret paleo-ecological data. Davis (1963) examined plant-pollen relationships by comparing tree pollen percentages (of a total arboreal sum) with vegetation surveys, developing '*R*-values' or ratios of pollen percentage to species abundance. The *R*-values indicate whether plant species abundances are over-, under-, or equitably-represented by their pollen taxa. Thus *R*-values are

the basis for correction factors, but additional biases must be examined to determine the error involved in using this species-based reconstruction approach.

Using pollen from surface samples and modern vegetation surveys (Wright, 1967), variability of plant-pollen relationships can be determined over various spatial scales using study areas of different sizes or depositional environments (Webb et al., 1978). Tree pollen assemblages from lake sediments tend to represent vegetation patterns at the formation scale (Bradshaw and Webb, 1985; Jackson, 1991) whereas pollen spectra from moss or soil samples in forests record vegetation variation at the stand scale (Webb et al., 1978). Studies have succeeded in using pollen from lakes and moss polsters to determine tree-pollen relationships on the stand to formation scale (e.g., Heide and Bradshaw, 1982). However, determining error in tree pollen data from wetland environments or that results from small-scale heterogeneity in vegetation is more problematic (Bunting et al., 1998; Jackson and Kearsley, 1998; Mulder and Janssen, 1999).

Webb et al. (1978) discussed how choices in data collection and analysis influence the vegetation pattern portrayed in the paleo-ecological record. They used species-pollen relationships derived from three sets of modern pollen and tree-inventory data to examine how study location and size, pollen types, depositional environment, number of analysts involved in data collection, and degree of smoothing resulting from combining data or pollen types (i.e., 'noise') control the evidence or scale of vegetation pattern represented by the pollen data (i.e., 'signal'). Numerical analyses using principal components analysis (PCA) and Pearson product-moment correlation coefficients provided empirical evidence for the degree to which each choice in data selection affected the 'signal-to-noise' ratio as represented by comparisons of distributions for selected

pollen types or principal components between the different data sets. These results showed that all choices influence the vegetation pattern represented in pollen data but study area size, pollen types examined, and the amount of smoothing have the greatest influence.

Parsons and Prentice (1981) used statistical approaches (cluster and principal components analyses) and mathematical models to quantify the error and refine the estimation of *R*-values. This provided a methodological foundation for investigating the plant-pollen relationship based upon a linear model that includes an intercept attributable to long-distance pollen transport. Surface samples and vegetation data from southeastern Canada were used to illustrate how individual and average *R*-values for oak pollen are too high due to long-distance transport of oak pollen and subsequently how linear models adequately represented oak percentages at each sampling site when long-distance transport was considered. The methods presented in their study represent a turning point in determining error in paleo-ecological reconstruction methods based upon plant-pollen relationships, however the authors acknowledged that vegetation heterogeneity and differential pollen transport remain limitations to reconstruction precision.

Paleo-ecologists recognize that pollen data for any given taxa is a compilation of contributions from close and distant sources and the influence of particular sources depends upon the scale of vegetation pattern represented by the pollen data. Heide and Bradshaw (1982) addressed the influence of study area size by examining tree-pollen relationships for 20 pollen types from moss polster data and used regression analysis to calculate correction coefficients that were then compared to those derived from lake sediments. The authors noted differences in the pollen-tree relationship between moss polsters and lakes with all taxa more equitably represented by moss polster data. Regression analyses supported the hypothesis that pollen productivity is the major

influence on relationships from moss polster data while pollen dispersion is the major influence for lake data. The study showed that paleo-ecological studies must carefully consider the depositional environment since estimates of tree percentage from similar fossil-pollen percentages of a particular tree species will vary depending upon the type of basin from which the pollen was derived. Results presented by Bradshaw and Webb (1985) supported these findings and described how the relative size of the pollen-source area varied between seven major tree species (*Acer*, *Betula*, *Fagus*, *Pinus*, *Quercus*, *Tsuga*, and *Ulmus*) based upon the regression analysis of their plant-pollen relationships from moderate-sized lakes. These studies emphasized the sensitivity of tree-pollen relationships to the scale at which pollen assemblages represent vegetation patterns and subsequent studies have examined tree-pollen relationships and the effects of differences in pollen dispersibility, pollen production, and vegetation heterogeneity on the vegetation pattern 'sensed' by pollen data (e.g., Sugita, 1994; Jackson and Wong, 1994; Jackson and Kearsley, 1998). For example, Jackson (1991) compared modern tree pollen percentages in the Adirondak Mountains with lake elevation using scatter plots and correlation and regression analysis. The author concluded that pollen dispersal explains the obvious vegetation patterns with increased smoothing.

Tree-pollen relationships have been the primary focus of paleo-ecological reconstructions, but plant-pollen relationships have been determined in other environments. Janssen (1984) examined the distribution of pollen types as a function of peatland vegetation and discussed the pattern in pollen in relation to 'local,' 'extra-local,' 'regional,' and 'extra-regional' pollen sources. Local deposition is reflected by high and irregular percentages of pollen types from sources within 20 m of a sample site whereas extra-local pollen is deposited from sources within

a few hundred meters from the sample site and pollen proportions are slightly higher than regional percentages. Regional pollen sources occur within the formation but are beyond several hundred meters from the sample site and accumulate in 'specific proportions' whereas extra-regional pollen is transported from an area beyond the scale of the vegetation formation (several thousand meters).

Janssen (1984) collected pollen and spores from moss polsters in different peatland vegetation and made comparisons to vegetation patterns in the peatland and the Midwestern United States. The pollen data corresponded well with peatland and regional upland vegetation patterns and the nature of dispersal patterns of all pollen types at that site were explained with respect to pollen source area. Delineation of pollen source area permitted spatial differentiation of vegetation around the site and improved the precision of paleo-ecological reconstruction at that site and other plant communities in the region. Mulder and Janssen (1999) utilized modern plant-pollen relationships from moss polsters along a transect from *Betula-Quercus* forest to heathlands to quantify contributions from local and regional sources and were able to make similar contributions to reconstructions using pollen from Dutch heathlands.

Bunting et al. (1998) used pollen and spore assemblages from 11 deciduous swamp communities to assess the influence of wetland pollen sources on the representation of upland communities. She found that although all wetland communities adequately recorded the diversity of the surrounding upland, the proportion of pollen influx from upland sources varies as a function of wetland community. She concluded that reconstructions using wetland data are unreliable

without a "detailed understanding of the local wetland community, its dynamics over time, and its effects on the upland signal."

Tidal ecosystems present a more difficult environment in which to examine plant-pollen relationships. Clark and Patterson (1985) discussed the contribution of local and regional pollen sources and the influence of tides on pollen deposition in surface samples across an elevation gradient in a tidal salt marsh. The palynological record of upland vegetation from salt marsh sediments was compared with those from a nearby lake to illustrate changes in upland vegetation on watershed (local) and regional scales. A similar exercise for pollen sources of tidal salt marsh vegetation is more problematic. Clark (1986) noted that paleo-ecological records from salt marshes commonly show high percentages for Poaceae, Cyperaceae, and Cheno Am, all of which have marsh and terrestrial sources therefore local inputs are over-represented and obscure regional inputs. In addition, pollen dispersal and sedimentation characteristics of tidal marshes are unknown. It is the latter difficulty that limits modern analog identification in salt marshes and hinders the determination of plant-pollen relationships. Although the surface transect Clark and Patterson (1985) studied provided modern analog data for the range of depositional environments in their salt marsh study area, they did not quantify salt marsh plant-pollen relationships because surface samples were not replicated within community types.

Community-level approach: modern analogs

Identification of modern analogs allows paleo-ecologists to reconstruct past vegetation over various spatial scales. The precision and accuracy with which a modern analog 'matches' an unknown fossil pollen assemblage can be determined by applying multidimensional scaling

methods to modern pollen spectra. Some studies have used principal components analysis (Birks, 1977), cluster analysis (Birks et al., 1975; Bunting et al., 1998; Willard et al., 2001; O'Neal et al., in press), and dissimilarity coefficients (Overpeck et al., 1985). These techniques allow paleo-ecologists to determine the degree of similarity between pollen spectra such that sources of error and degree of certainty in using the modern analog approach to paleo-ecological reconstruction are addressed.

Prentice (1980) reviewed the underlying theory and method of multidimensional scaling techniques within the context of their use as paleo-ecological research tools, including principal components analysis (PCA), principal co-ordinates analysis (PCO), and canonical variates analysis (CVA). He established the guidelines for choosing a particular method, emphasizing method assumptions and choice of dissimilarity coefficient (in PCA and PCO). These techniques have been used to examine affinity between pollen spectra of forests in eastern North America (Overpeck et al., 1985), glacier foreland vegetation (Birks, 1977; Caseldine and Pardoe, 1994), a coniferous swamp (Bunting et al., 1998), and wetland sub-environments (Willard et al., 2001) to consider the limitations of their modern analogs.

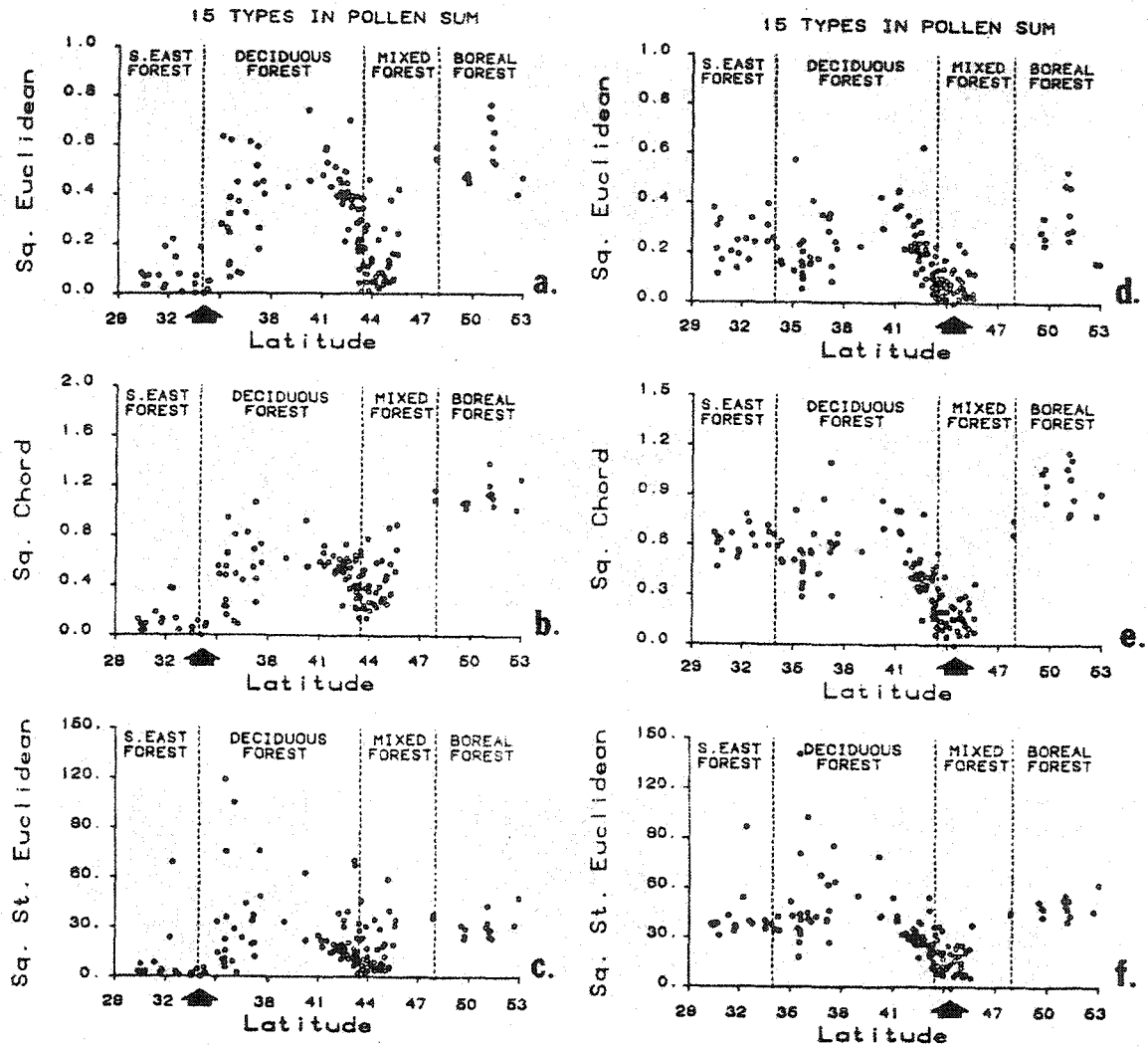
The level of detail possible in a paleo-ecological reconstruction depends upon the limitations of modern analogs in 'sensing' a vegetation community, separating it from other vegetation types, and how many modern analogs have been identified. Paleo-ecologists interested in environments that existed during glacial and inter-glacial periods often find pollen spectra for which no modern analog exists and studies have compared modern spectra to fill in these 'gaps' and identify 'blind spots' in paleo-records. Birks (1977) described four vegetation types in an

area near the Klutlan Glacier in the Yukon Territory, Canada and used CVA and PCA to compare pollen spectra and explain patterns of similarity or dissimilarity. Birks (1977) concluded that the variability of pollen percentages from two vegetation types (*Picea glauca* forests and *Betula glandulosa* shrub-tundra) was such that their modern spectra were not distinct, as opposed to the distinct pollen spectra from *Dryas integrifolia* tundra and *Populus balsamifera* forests. High percentages of pollen types representing characteristic species and the presence of 'indicator' species contributed to the distinction. This study is an example of an effort to identify modern analogs of communities for which no modern analog has been identified to provide additional detail for paleo-data. Caseldine and Pardoe (1994) continued the search for modern analogs of glacier forelands using detrended correspondence analysis with modern pollen spectra from four vegetation groups representing two scales of vegetation patterns in southern Norway. Comparisons suggested that modern analog matching with fossil samples could be improved by sampling over smaller spatial scales using similar media, but direct analogs could not be identified.

The precision and accuracy of modern analogs also depends upon the comparison used to determine similarity between pollen spectra. Overpeck et al. (1985) compared the responsiveness of eight dissimilarity coefficients of three types (unweighted, equal-weight, and signal-to-noise) in recognizing four different modern forest types. Dissimilarity coefficients are statistical measures of the "degree of analogy" between a pair of multivariate samples, taking a maximum value for spectra that are entirely different and a minimum when they are identical (Legendre and Legendre, 1983; Figure 1). They are preferred over other statistics that display

affinity (e.g., PCA) between multivariate samples because they provide direct measurements of the "degree of analogy" (Overpeck et al., 1985).

Figure 1. Figure 2 reproduced from Overpeck et al. (1985). Scatter diagrams of latitude versus three dissimilarity measures between a modern pollen sample (marked by the large arrow) and all of the other modern pollen samples along a north-south transect.



Overpeck et al. (1985) demonstrated that pollen from the four forest types were distinct but increasingly dissimilar with increasing geographical distance. They concluded that squared chord distance is the most reliable signal-to-noise coefficient in sensing the differences between pollen spectra at the formation scale and discriminates well among spectra at the scale of the forest type. The comparison of modern spectra allowed determination of critical values for each dissimilarity coefficient to determine the level of confidence in a 'match' between a modern analog and fossil spectra. Overpeck et al. (1985) defined two critical values ('V1' and 'V2') for comparing spectra from different forest types. They are related to the certainty that a sample represents a particular forest type. If the match's coefficient value is below the lower critical value (V1) then the sample is most likely from the same formation, if it is between the two critical values the certainty is less, and if it exceeds both thresholds, it is unlikely that a fossil spectra would be from the same vegetation formation.

In contrast to the findings of Bunting et al. (1998), some wetland communities produce distinct pollen assemblages while others are more difficult to separate (Bunting et al., 1998). This is because floristic diversity of distinct wetland vegetation cannot always be detected palynologically due to poor pollen preservation (e.g., Cupresseaceae or *Populus*) or under-representation of characteristic taxa (e.g., *Acer rubrum*). Bunting et al. (1998) noted that surrounding vegetation and habitat can influence the palynologically distinct elements such that spectra that are difficult to separate from one location are distinct in another and stressed the importance of regional studies in developing modern analogs of wetland ecosystems. Rich (1995) also noted an 'invisibility' problem in his study of 17 fossil pollen-bearing marine samples due to the absence of characteristic taxa used to separate Pliocene from Pleistocene

deposits in the southeastern United States and 'uniformity' of pollen flora due to pollen sorting by wind, currents, and waves. However, he reported a distinct assemblage with taphonomic significance could be used to define the depositional environment and confidently interpret the marine paleo-environment in his study area.

Modern analogs of wetlands have been identified using numerical comparisons of pollen in surface samples and demonstrate the potential for quantitative reconstruction of wetlands. Willard et al. (2001) examined modern pollen spectra of eight sub-environments from the Florida Everglades and found them palynologically distinct. They analyzed 170 modern spectra from sawgrass marshes, cattail marshes, sloughs with floating aquatics, wet prairies, brackish marshes, tree islands, cypress swamps, and mangrove forests and modern analogs were identified using squared chord distance in cluster analysis. Comparison of modern and fossil spectra helped identify hydrologic changes over the last 200 yr. Similarly, O'Neal et al. (in press) used cluster analysis of surface pollen from the Florida Everglades and found that clusters strongly corresponded to five main physiographic provinces of the area. These pollen zones provided the objective basis to interpret two paleo-ecological sedimentary sequences.

Meyerson (1972) noted that identification of modern analogs using fossil strata of salt marsh vegetation is difficult because changes in environmental conditions (salinity, sediment deposition) that influence vegetation patterns vary across the marsh and over time. Similarly, Clark and Patterson (1985) noted the individualistic and varied response of salt marsh plants to factors that influence their distribution. Clark (1986) argued that 'salt marsh vegetation reconstruction is not possible due to the individualistic response of salt marsh plants to factors

that influence their distribution across the marsh landscape and over a historical context, the factors and degree of influence vary such that edaphic and historical factors cannot be separated.' These studies and the complex taphonomy of tidal salt marshes have deterred quantitative salt marsh reconstruction pursuits and examination of plant-pollen relationships. Many salt marsh plants have pollen that is preserved in sediments and can be identified to the family and often genus level. It is this detectable diversity that allowed Clark (1986) to follow historical changes in salt marsh vegetation, however description of salt marsh modern analogs using empirical comparisons has not been published.

The focus of this study is the investigation of the relationship between salt marsh plants and their pollen. The species-pollen relationship and modern analog approaches are used in three Bay of Fundy marshes to define salt marsh modern analogs and examine the limitations of paleo-ecological reconstructions of salt marsh vegetation. The concept of pollen source area is of primary importance (Jacobson and Bradshaw, 1981) and has been discussed in several paleo-reconstruction and modern analog studies to elucidate the geography of the plants that contribute pollen to surface sediments (Heide and Bradshaw, 1982; Janssen, 1984; Bradshaw and Webb, 1985; Clark and Patterson, 1985; Sugita, 1994; Bunting et al., 1998; Mulder and Janssen, 1999). In this study, wetland pollen types are the primary focus and the pollen types that represent the salt marsh vegetation come from that marsh and may be transported by wind or tides from other marshes. However, these same pollen types may also come from nearby terrestrial environments. Tides play an important role in pollen transportation and redistribution within and between salt marshes via pollen deposition from 'regional' and 'extra-regional' sources and redistribution of 'local' pollen in surface sediments.

Relative contributions of local, regional, and extra-regional sources to pollen spectra are defined following Janssen's (1973) terminology. Local pollen is derived from vegetation within 15 m of the sample site, regional pollen originates from salt marsh vegetation within several hundred meters and includes pollen from plants in other salt marshes, and extra-regional pollen is transported to the marsh from terrestrial vegetation hundreds or thousands of meters from a sample site and includes pollen types that originate from plants other than salt marsh plants. Relationships between salt marsh plants and their pollen are examined and relative influences of local, regional, and extra-regional pollen sources are discussed. These results are used to interpret comparisons of modern pollen spectra from salt marsh vegetation assemblages ('zones') and address limitations of salt marsh vegetation reconstruction.

STUDY AREA

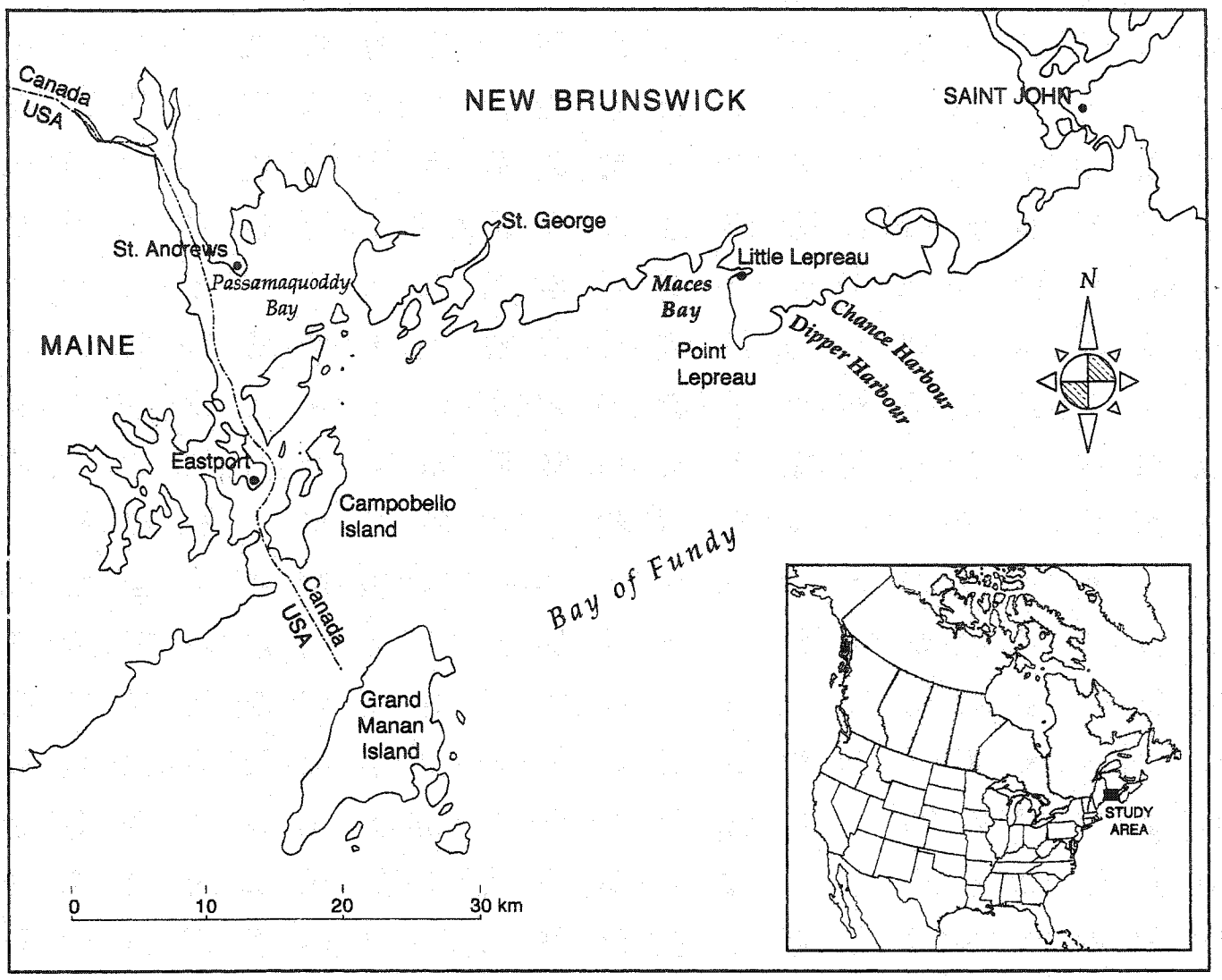
The three salt marsh study areas are on Point Lepreau, on the New Brunswick coast of the Bay of Fundy. At Point Lepreau, the tidal range varies from 6 m to an extreme tide of 8 m. Dipper Harbour is located on the east coast of Point Lepreau, 28 km southwest of Saint John (Figure 2). Chance Harbour is 7 km northeast of Dipper Harbour and the salt marsh is situated behind a cobble barrier. Little Lepreau marsh is located behind a cobble barrier on the west coast of the Point Lepreau peninsula at the head of Maces Bay. The upland regions surrounding Dipper Harbour and Chance Harbour are characterized by steep slopes and vegetated by mixed coniferous-deciduous forest. The topography surrounding Little Lepreau has lower relief than the other two marshes but surrounding vegetation is similar.

Dipper Harbour, Chance Harbour, and Little Lepreau salt marshes each have a meandering 'tidal creek' that dissects the marsh (Figure 2) and the marsh surface is perched more than a meter above the creek bottom. Dipper Harbour and Chance Harbour have tidal creeks that empty completely between flooding events and reveal this 'perched marsh platform' feature as the marsh edge or 'cliff face' is exposed at low tide. This is not evident at Little Lepreau because the talweg is almost 6 m above the average low tide elevation on the seaward side of the barrier and the tidal creek does not drain between flooding events. Small, shallow ponds are present at all three sites (Figure 2). Some ponds persist throughout the growing season while others exist ephemerally between flooding events and *Ruppia* is often present in the former.

The vegetation observed at Dipper Harbour, Chance Harbour, and Little Lepreau salt marshes is characterized by a mosaic of vegetation existing within larger scale transitions between dominant vegetation along an elevation gradient that is typical of other Bay of Fundy salt marshes (Figure 3; Ganong, 1903; Chmura et al., 1997) and those further south (Jacobson and Jacobson, 1989; Bertness and Hacker, 1994). This can be explained by differences in plant morphology and physiology as they relate to physical stresses caused by flooding frequency (salinity and submergence) (Bertness and Ellison, 1987) and is typically referred to as a 'belting' pattern (Warren and Niering, 1993). *Spartina alterniflora* and *Spartina patens* dominate lower and higher elevations, respectively with *Plantago maritima* dominating intermediate elevations. *S. alterniflora* typically dominates in monospecific stands and other species are present in *S. patens* zones, but usually contribute less than 5% cover (Figure 3). *Juncus gerardi* replaces *S. patens* at higher elevations that give way to *Juncus balticus* at the uppermost elevations. At this high elevation, cover of other salt marsh plants increases but constitutes <15% cover (although *S.*

patens can contribute up to 40% cover in *J. gerardi*-dominated vegetation). Other salt marsh plants include *Salicornia europeae*, *Spergularia canadensis*, *Suaeda*, *Glaux maritima*, *Potentilla anserina*, *Triglochin maritima*, *Limonium nashii*, *Ligusticum scothicum*, *Atriplex*, *Carex*, and *Scirpus*. Small-scale patches (<15 m) of vegetation are evident at all three locations and Little Lepreau salt marsh is exceptionally patchy along intermediate to high elevations and micro-topography of the marsh surface is variable in comparison to Dipper Harbour and Chance Harbour.

Figure 2. Location of Dipper Harbour, Chance Harbour, and Little Lepreau salt marshes, Bay of Fundy, New Brunswick, Canada.



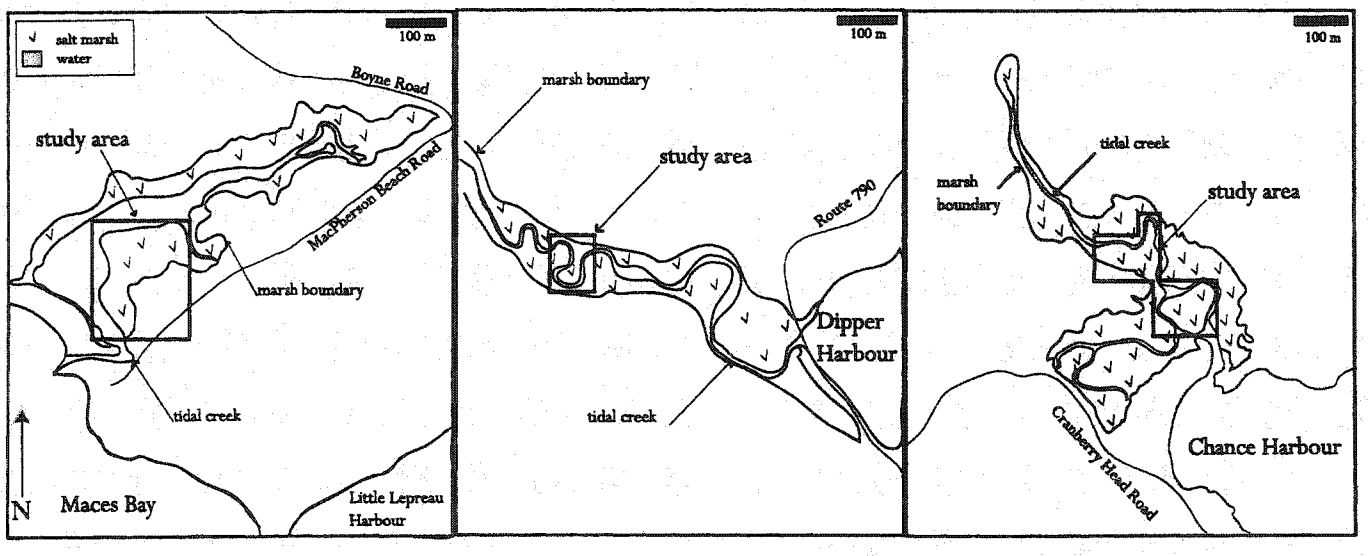
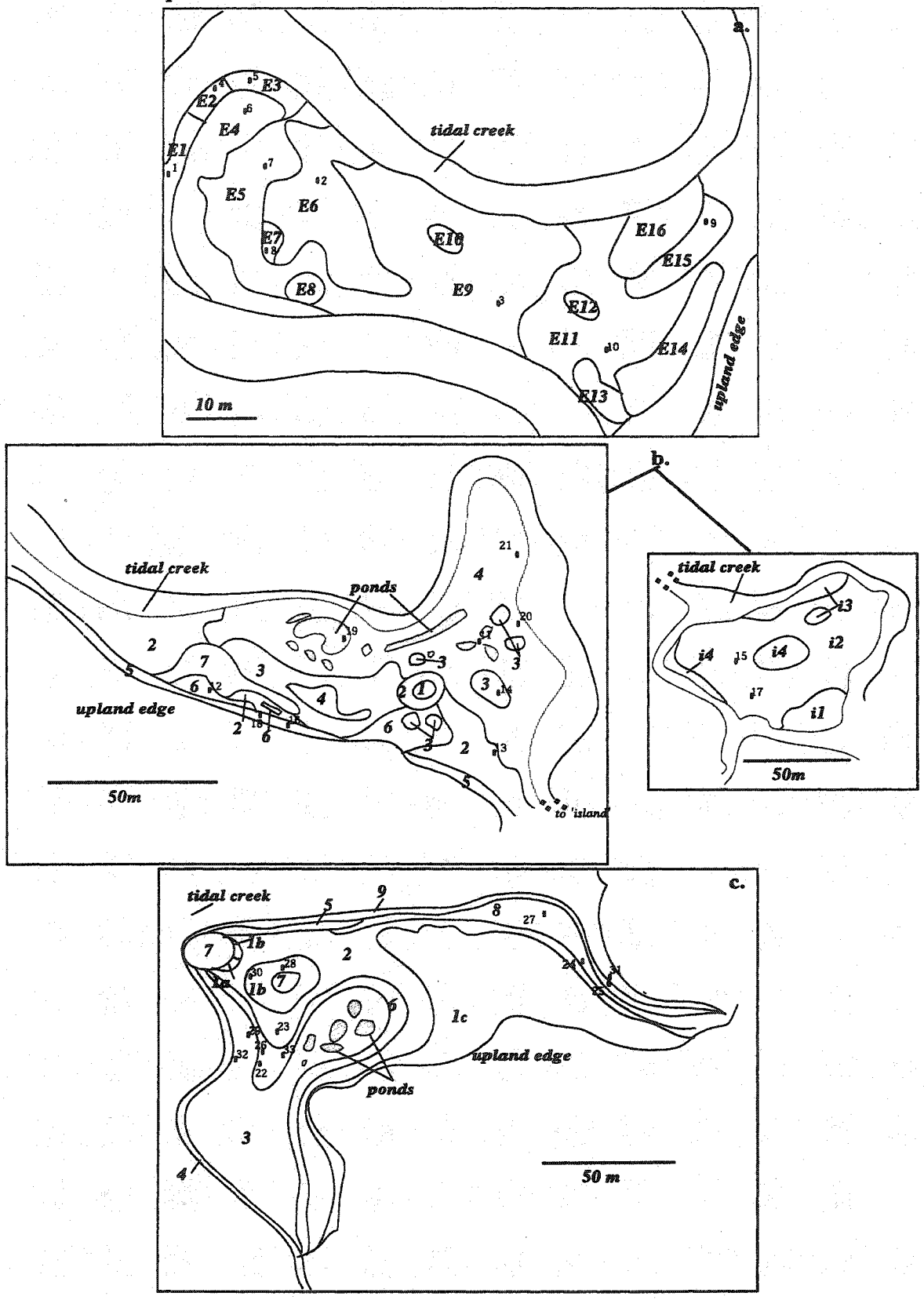


Figure 3. Vegetation zones and sampling locations in (a.) Dipper Harbour, (b.) Chance Harbour, and (c.) Little Lepreau salt marhses, Bay of Fundy, New Brunswick, Canada. See Table 1 for code descriptions.



METHODS

Field sampling

Dipper Harbour broad-scale vegetation units were identified, mapped, and elevation surveyed as part of an earlier study (Chmura et al., 1997) (Figure 3a, Table 1). In July 2000, vegetation units of sample areas were mapped at Chance Harbour and Little Lepreau salt marshes using low altitude aerial photographs (1:10,000) as a base. The smallest mapping unit was 10 m. Percent cover of each species was recorded and represents each species contribution to total vegetation, disregarding un-vegetated portions (i.e., excludes bare ground). Species with trace amounts were assigned 0.1% cover therefore total percent cover for some units exceeded 100%.

Sample areas are hydrologically isolated from other sections of the marsh, bounded on the seaward side by the tidal creek channels and on the landward side by terrestrial vegetation. Vegetation units are located within general vegetation zones that exist as a function of differences in flooding frequency across an elevation gradient from low marsh (dominated by *Spartina alterniflora*) to high marsh (dominated by *Spartina patens*). Similar units are evident in sample areas at all three study sites. Most plant-pollen relationship studies utilize sampling locations based upon the degree to which they reflect the 'average' vegetation cover (Heide and Bradshaw, 1982; Bradshaw and Webb, 1985; Clark, 1986; Bunting et al., 1998; Willard et al., 2001). In this study, sampling locations or 'patches' within sampling areas at Chance Harbour and Little Lepreau salt marsh were chosen to maximize the cover of vegetation representing a particular wetland pollen type to focus on the influence of small-scale (<15 m) heterogeneity on salt marsh plant-pollen relationships.

Table 1. Bay of Fundy salt marsh surface samples (see text for explanation of 'ID-2'). Unit ID refers to the broad vegetation unit surrounding the surface sample, shown in Figure 3. Elevations are relative to the average *S. alterniflora* lower limit at each marsh. The vegetation zone codes are: *S. alterniflora* (SA), *P. maritima* (PM), *S. patens* (SP), Cyperaceae (C), *J. gerardi* (JG), and *J. balticus* (JB).

Study area	Sample ID	Sample ID-2	Sample name	Unit ID	Zone	Sampling plot dimensions (m)	Relative elevation (m)
Dipper Harbour	1	140	DHE1	E1	SA	--	0.58
	2	415	DHE6	E6	SP	--	1.43
	3	215	DHE9	E9	PM	--	1.43
	4	210	DHE2	E2	PM	--	0.98
	5	220	DHE3	E3	PM	--	1.13
	6	155	DHE4	E4	SA	--	1.03
	7	225	DHE5	E5	PM	--	1.33
	8	230	DHE7	E7	PM	--	1.28
	9	345	DHE15	E15	C	--	1.63
	10	420	DHE11	E11	SP	--	1.43
Chance Harbour	11	235	Cheno Am	4	PM	0.2 (diameter)	1.10
	12	355	Cyperaceae	6	C	12 x 7	1.80
	13	365	*Glaux*	2	JG	1.0 (diameter)	2.21
	14	275	Poaceae	3	SP	14.5 x 9	1.57
	15	240	*Limonium*	i2	PM	3 x 4	0.83
	16	640	*Ligusticum*	5	JB	1.0 (diameter)	2.61
	17	245	*Plantago*	i2	PM	2.5 (diameter)	0.35
	18	645	*Potentilla*	5	JB	1.5 (diameter)	2.34
	19	250	*Ruppia*	4	PM	--	1.10
	20	255	*Spergularia*	4	PM	0.2 (diameter)	1.10
	21	260	*Triglochin*	4	PM	0.5 (diameter)	0.98
Little Lepreau	22	340	Cheno Am	6	SP	3 x 4	1.10
	23	545	Cyperaceae	2	JG	6 x 7	1.44
	24	555	*Glaux*	8	JG	1.0 (diameter)	1.28
	25	160	Poaceae	4	SA	--	1.12
	26	435	Poaceae	6	SP	10 x 12	0.99
	27	560	*Limonium*	8	JG	4 x 6	1.34
	28	655	*Ligusticum*	1	JB	14 x 8.5	2.52
	29	265	*Plantago*	3	PM	5.0 (diameter)	1.02
	30	660	*Potentilla*	1	JB	3 x 1	2.08
	31	165	*Ruppia*	4	SA	pond	0.99
	32	370	*Spergularia*	3	PM	1 x 3	1.43
	33	285	*Triglochin*	2	JG	3 x 4	1.30
Dipper Harbour	34	440	B core (1.2cm)	C1	SP	--	1.97
	35	445	A core (1.4cm)	B3	SP	--	1.60

In the summer of 1994, ten surface samples from ten different vegetation units were taken from a sample area at Dipper Harbour salt marsh (Figure 3a). The top 10 millimeters of sediment were collected for pollen analysis. Two additional samples from Dipper Harbour used in this study were retrieved from the upper portions of two cores (A and B) extracted in 1996 by Clegg (1999). The corrected mid-depths of the 6 mm-thick samples used were 1.4 cm and 1.2 cm for A and B cores, respectively. Based upon the accumulation rates determined by ^{137}Cs-dating on the B core, the temporal resolution of these samples is approximately 3.6 yr with mid-depths corresponding to ~1988 and 1989, respectively (Clegg, 1999). Assuming that the vegetation units in which the cores were taken had not changed during the decade prior to extraction, it is reasonable to use these two samples as additional surface samples. These units were located in sample areas not shown in Figure 3.

A total of 23 surface samples, each representing maximum local cover of salt marsh taxa corresponding to a single wetland pollen type, were collected from Chance Harbour and Little Lepreau salt marshes. A sample from the top centimeter of sediment was removed and the area of the small-scale vegetation measured. *Ruppia* samples were retrieved by collecting the surface ~5 mm of pond mud from underneath the plant. At Little Lepreau, an additional surface sample was taken from the adjacent assemblage, a few cm from the perimeter of the *Ruppia* pond. Considering the sediment sampling method and given the historical accumulation rates of these sites (Chmura et al., 2001), the pollen contained in surface samples integrate vegetation assemblages over 2.8 yr at Dipper Harbour (1991-1994), 5.3 yr at Chance Harbour (1995-2000), and 6.7 yr at Little Lepreau (1993-2000).

Elevation of each sample area at Chance Harbour and Little Lepreau was measured using standard survey techniques. A minimum of four measurements was taken for each sampling plot, including the center. The lower elevation limit of *S. alterniflora* and upper limit of *Juncus balticus* were surveyed over the extent of the sampling areas. Within each marsh, elevations are expressed relative to the average lower elevation of the *S. alterniflora* zone. Average relative elevations for vegetation units were calculated using the relative elevations of all patches in that unit and zone averages included all units with the same dominant vegetation among all three marshes (Figure 4).

Pollen processing and analysis

Surface samples were sub-sampled for pollen extraction and concentration. Processing steps followed the methods described by Moore et al. (1991) including HCl, KOH, glacial acetic acid, acetolysis, and hot HF. A known concentration of *Lycopodium* spores was added in the HCl step to allow calculation of pollen concentrations. All samples were washed through a 40 □m sieve, retained on a 10 □m sieve, stained with safranin, and pollen aliquots mounted in glycerin jelly. Pollen was counted with a 630x magnification oil immersion lens and identified with the use of published keys (McAndrews et al., 1973; Moore et al., 1991) and a reference collection held at the McGill Paleoenvironmental Research lab. A minimum of 300 wetland grains was counted for each sample with the exception of four samples with low wetland pollen concentrations (Appendix 1). The entire slide was counted to ensure that potential differential sorting of grains on the slide did not affect calculated pollen proportions and rare pollen types (if present on the slide) important for assemblage recognition would be identified. Pollen diagrams were generated using Psimpoll 2.30 plotting software (Bennett, 1997).

Source vegetation for wetland pollen types identified in surface samples was determined (Table 2). The wetland sum includes eighteen pollen taxa and was determined on the basis of regional and extra-regional wetland types. The percent of wetland taxa is expressed as a proportion of the total pollen count, including arboreal as well as herbaceous taxa. Grains that could not be identified because diagnostic features were hidden or were corroded, folded, or torn were included in the total count as 'hidden' and 'indeterminate', respectively.

Dipper Harbour wetland pollen was counted by Helmer (1994). Her wetland pollen sums ranged from 20 to 329 grains with five wetland sums <100 and four <300. Total grains counted ranged from 410 to 641 grains with a mean of 482 grains. I mounted additional slides for 9 of the 10 samples in an effort to bring wetland pollen sums closer to 300 grains and increase probability of more statistically appropriate representations of pollen proportions (Rull, 1987). Combined 1994 and 2001 wetland sums ranged from 93 to 351 (mean, 235). Six of the ten samples exceeded 300 wetland grains, with total pollen sums ranging from 465 to 2490 grains (mean, 845). This two-fold increase in mean total pollen counted is assumed to diminish the identification inconsistencies and subsequent variations in pollen assemblages resulting from using counts that are cumulative between two different analysts. The two 'core' Dipper Harbour samples counted Clegg (1999) and were left with wetland counts of 51 and 115.

Figure 4. Elevation (m) for salt marsh vegetation assemblages relative to the average lower limit of *S. alterniflora* measured at Dipper Harbour, Chance Harbour, and Little Lepreau salt marshes. 'Small-scale' refers to the relative elevation calculated from a series of measurements taken around the sampling locations representing similar small-scale vegetation characteristics and were not measured at Dipper Harbour. 'Broad-scale' refers to the average elevations of samples retrieved in the same vegetation unit in each marsh. Dashed lines delimit general vegetation zones, solid lines represent relative elevation ranges of zones and include all three study sites.

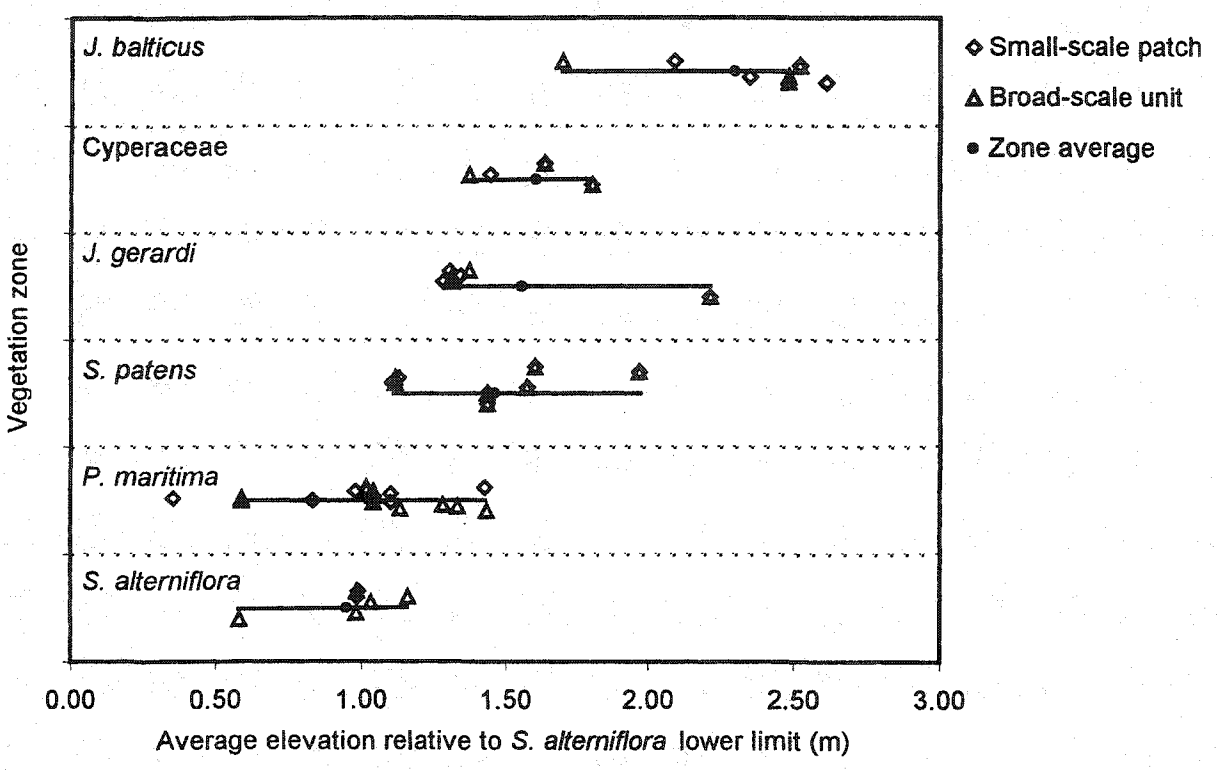


Table 2. Pollen types identified in surface sediment samples and source vegetation in Dipper Harbour (DH), Chance Harbour (CH), and Little Lepreau (LL) salt marshes, Bay of Fundy, New Brunswick.

Wetland pollen type	Source vegetation	Family
Chenopodiaceae Amaranthaceae ('Cheno Am')	*Atriplex* *Salicornia* sp. *Suaeda*	Chenopodiaceae
Cyperaceae	*Carex* sp. *Scirpus* sp.	Cyperaceae
Glaux	*G. maritima*	Primulaceae
Ligusticum	*Ligusticum scothicum*	Apiaceae
Limonium	*Limonium nashii*	Plumbaginaceae
Plantago	*Plantago maritima*	Plantaginaceae
Poaceae	*Spartina alterniflora* *Spartina patens* (and other grasses)	Poaceae
Potentilla	*Potentilla anserina*	Rosaceae
Potamogeton type	*Triglochin maritima*	Juncaginaceae
Ruppia	*Ruppia maritima*	Zosteraceae
Spergula type	*Spergularia canadensis*	Caryophyllaceae

Data analyses

Percent cover was plotted against percent total wetland pollen for each diagnostic pollen type, using local and broad scale observations. Regression was performed using Systat 8.0 on both spatial scales to assess which scale of vegetation cover is a better predictor of pollen proportion. Scatter plots of pollen against small-scale and broad-scale cover include a line representing a 1:1 relationship. Points above this line are interpreted as under-representation of plant cover by percent pollen and below, over-representation. Data points representing *Ruppia* samples used cover values of the vegetation unit adjacent to the sampling location. Positive y-intercepts of regressions for plant-pollen relationships over small and broad scales are interpreted as relative pollen contributions from regional and extra-regional sources, respectively.

Dissimilarity coefficients are statistical measures invoked to compare multivariate data arrays, taking a maximum value when the arrays are completely different and a value of zero when identical. Squared chord distance is a dissimilarity coefficient that is commonly used with biological data and is suitable for data sets containing abundance values (Legendre and Legendre, 1983). Biological data, particularly abundance data, is characterized by the dominance of a few species and presence of many others with small values. It follows that pair-wise comparisons between all multivariate arrays in a species abundance data set are characterized by many 'double zeros' that indicate absence of species identification or lack of information. A dissimilarity coefficient considers the state 'zero' as having the same comparative value as every other variable (Legendre and Legendre, 1983) therefore a double zero is interpreted as a similarity. In the case of species abundance, the absence of a species at two sampling stations cannot be interpreted as an indication of similarity because its absence

could be the result of a niche replacement by another species, associated with dispersion patterns, or may have resulted from different physiological or ecological constraints (Legendre and Legendre, 1983). Squared chord distance is a modified Euclidean distance that is not influenced by double zeros, therefore is suitable for modern analog studies incorporating abundance data (e.g., Overpeck et al., 1985).

Squared chord distance was calculated for all pairs of samples using the equation given by Overpeck et al. (1985):

$$d_{ij} = \sum_k \left(p_{ik}^{1/2} - p_{jk}^{1/2} \right)^2$$

where d_{ij} is the dissimilarity coefficient value between two wetland pollen spectra i and j and p_{ik} is the proportion ($0.0 \leq p_{ik} \leq 1.0$) of wetland pollen type k in wetland pollen spectrum i; hence the minimum value a squared chord distance coefficient can take is zero (spectra are identical) and the maximum is 2.0 (spectra are dissimilar).

Samples were organized into six groups on the basis of their elevation assemblage (Figure 4), named for the dominant plant: *S. alterniflora* (100's), *P. maritima* (200's), *S. patens* (400's), *J. gerardi* (500's), *J. balticus* (600's), and transition to high marsh (HM) (300's) which includes samples that were located near an ecotone (samples 9, 12, 13, 22, and 32). Therefore, all groups reflect the nature of the broad scale (>15 m) vegetation surrounding the sampling locations (Table 1). Samples that were collected from isolated vegetation units 10-15 m in diameter (samples 14 and 33) were grouped according their location within a larger vegetation unit (Table 1, Figure 3). Dissimilarity coefficients were plotted on the basis of these groupings and critical values were determined in a manner similar to that described in Overpeck et al. (1985).

RESULTS & DISCUSSION

Vegetation

Dipper Harbour vegetation units had the lowest species diversity compared with Chance Harbour and Little Lepreau (Tables 3-5). At least 13 different plant species representing 8 families were observed and 16 vegetation units identified in the Dipper Harbour sampling area (Figure 3). Nine units are dominated by *S. patens* with others by *S. alterniflora*, *P. maritima*, Cyperaceae, *J. gerardi*, or *J. balticus* (Table 3). Fifteen plant families were represented by at least 20 species in 11 units and 22 species in nine units identified in sampling areas at Chance Harbour and Little Lepreau, respectively (Tables 4-5, Figure 3). (N.B. Little Lepreau vegetation unit 1 was divided into three sub-assemblages (a, b, and c) to reflect proportional differences in *Atriplex* and to note additional species (*Triglochin maritima*, *J. balticus*, and *Suaeda*) observed between July and September 2000).

At Dipper Harbour, the highest species diversity was recorded in *Plantago* and *S. patens* zones, but vegetation units above *S. patens* were not recorded. With the exception of *Spergularia canadensis*, all species were observed in more than one general vegetation zone. At Chance Harbour and Little Lepreau, the highest species diversity was at the highest elevations and the pattern with elevation is similar for all three marshes. For the same zones, species diversity was higher in Chance Harbour and Little Lepreau than Dipper Harbour. With the exception of the highest elevations, elevation ranges of zones overlap among all marshes: *S. alterniflora* ranged from 0.58-1.03 m, *P. maritima* from 0.63-1.43 m, *S. patens* from 1.11-1.68 m, and *Juncus* spp. above 1.31 m (Tables 3-5, Figure 4). Regardless of overlap between successive zones, a general

increase in average relative elevation is obvious (*S. alterniflora* followed by *P. maritima*, *S. patens*, *J. gerardi*, Cyperaceae, and *J. balticus*).

Tables 1, 6 and 7 summarize the small-scale (<15 m diameter) vegetation and elevation data collected for 11 sampling locations at Chance Harbour and 12 at Little Lepreau salt marshes. As samples 19 and 31 were retrieved from ponds and sample 25 was near the pond margin; small-scale cover data was not collected for these samples. Small-scale surveys in *Plantago* zones at Chance Harbour generally had the lowest diversity, averaging two less species per sampling location than in other vegetation zones. However, six samples were located in *Plantago* zones hence other zones had less sampling replication. Sampling was more equitable among vegetation zones at Little Lepreau and species diversity was similar in all samples. Most species are present in more than one vegetation zone and the main difference in vegetation composition between samples from *Plantago* zones and those above intermediate elevations is the presence of *S. alterniflora*.

Table 3. Total cover (%) of broad vegetation units identified in Dipper Harbour salt marsh, New Brunswick. Zones indicate the dominant vegetation: *S. alterniflora* (SA), *Plantago maritima* (PM), *S. patens* (SP), Cyperaceae (C), *Juncus* sp. (J). Unit ID's correspond to broad vegetation surrounding surface samples as shown in Figure 3.

	Vegetation zone and unit ID															
	SA		PM				SP							C	J	
	E1	E4	E2	E3	E9	E5	E8	E7	E6	E10	E11	E12	E14	E15	E13	E16
Relative elevation (m)	0.58	1.03	0.98	1.13	1.43	1.33	1.28	1.28	1.43	1.58	1.43	1.58	1.68	1.63	1.58	1.43
Spartina alterniflora	70	100	30		6	16	1		1							
Plantago maritima			64	92	87	65	40	50	5	32						
Spartina patens						6	60	50	90	64	90	67	56		40	
Juncus gerardi											6				55	85
Triglochin maritima					6	5							43	5		
Salicornia europeae				1		1				1	1	33				
Glaux maritima						5			1					11	5	10
Spergularia canadensis									1							
Limonium nashii	1		1	6	1	1	1		1	1						
Suaeda sp.	29		5			1			1	1	1					
Atriplex sp.				1					1	1	1					
Carex sp.														84		
Scirpus sp.											1		1			5
Total cover	100	100	100	100	100	100	102	100	101	100	100	100	100	100	100	100
Total number of taxa	3	1	4	4	4	8	4	2	8	6	6	2	3	3	3	3

Table 4. Total cover (%) of broad vegetation units identified in Chance Harbour salt marsh, New Brunswick. Zones indicate the dominant vegetation: *S. alterniflora* (SA), *Plantago maritima* (PM), *S. patens* (SP), Cyperaceae (C), and *Juncus* sp. (J). 'Upland' (U) refers to a unit dominated by terrestrial grasses. Unit ID's correspond to broad vegetation surrounding surface samples as shown in Figure 3. See text for details regarding units without elevation data.

	Vegetation zone and unit ID										
	SA	PM		SP				C	J		U
	i3	4	i2	3	7	i1	i4	6	2	5	1
Relative elevation (m)	--	1.10	0.63	1.61	--	--	--	1.84	2.25	2.52	--
Spartina alterniflora	52.5	30	7.5	10	1	23.4	2		1		
Plantago maritima		40	65	5		10	10		2	2	15
Spartina patens		0.1		70	90	23.3	35			2.5	
Juncus gerardi								5	80	15	
Juncus balticus								5		55	
Triglochin maritima		20	10	5	3		10	15		10	
Salicornia europeae	0.1	1	5	0.1		0.1					
Glaux maritima		2		10	5		0.1	2	15	1	4
Spergularia canadensis		1	0.1							1	
Achillea											0.1
Aster sp.										1	
Atriplex sp.				0.1						1	5
Ligusticum scothicum											0.1
Limonium nashii		2	0.1	0.1		0.1	0.1				0.1
Potentilla anserina								2	1	5	1
Solidago										0.1	
Suaeda sp.	0.1	1	5			20	8				5
Cyperaceae					1			70		0.1	
other grasses	47.5	3	7.5			23.3	35	1	1	2.5	70
Total cover	100.2	100.1	100.2	100.3	100	100.2	100.2	100	100	95.1	100.3
Total number of taxa	4	10	8	8	5	7	8	7	6	13	9

Table 5. Total cover (%) of broad vegetation units identified in Little Lepreau salt marsh, New Brunswick. Zones indicate dominant vegetation: *S. alterniflora* (SA), *Plantago maritima* (PM), *S. patens* (SP), Cyperaceae (C), *Juncus* sp. (J), Upland (U). Unit ID's correspond to broad vegetation surrounding surface samples as shown in Figure 3. Taxa present in trace amounts were assigned values of 0.1. See text for details regarding units without elevation data.

	Vegetation zone and unit ID										
	SA		PM		SP	J					
	4	9	3	5	6	1a	1b	1c	2	7	8
Relative elevation (m)	0.99	--	1.22	--	1.11		2.30		1.37	--	1.31
Spartina alterniflora	70	45	5	2.5	1				0.1		
Plantago maritima	15	30	50	10	2				1		2.5
Spartina patens			5		50				10		
Juncus gerardi								5	60		37.5
Juncus balticus						5	48	42.5	2	30	
Triglochin maritima		15			5			1	1		5
Salicornia europeae	10	3.3	15	60	2				0.1		
Glaux maritima		3.4		2.5	0.1		0.1		15		37.5
Spergularia canadensis			5		0.1						
Achillea						1	1				
Aster sp.						3	1	1		3	
Empetrum							0.1	0.1		2	
Ligusticum scothicum						10	5	0.1		35	
Limonium nashii		0.1	0.1								5
Potentilla anserina		0.1		0.1	0.1	1	1	2	1		0.1
Rubus						0.1					
Suaeda sp.	5	3.3	15	15	10			1	0.1		
Atriplex sp.						75	2		4		2.5
Cyperaceae				5					1		0.1
other grasses			5	5	30	5	42	47.5	5	30	10
Total cover	100	100	100.1	100.1	100.3	100.2	100.2	100.2	100.3	100	100.2
Total number of taxa	4	8	8	8	10	8	9	9	13	5	9

Table 6. Total cover (%) of local vegetation assemblages in Chance Harbour salt marsh, New Brunswick. Surface sample ID's correspond to those in Figure 3 and are grouped by the zone they were collected in: *S. alterniflora* (SA), *Plantago maritima* (PM), *S. patens* (SP), Cyperaceae (C), *J. gerardi* (JG), and *J. balticus* (JB). See text for details regarding the lack of values for sample 19.

	Surface sample ID and corresponding vegetation zone										
	PM						SP	C	JG	JB	
	11	15	17	19	20	21	14	12	13	16	18
Relative elevation (m)	1.10	0.83	0.35		1.10	0.98	1.57	1.80	2.21	2.61	2.34
Spartina alterniflora	25	2.5	12		15	1					
Plantago maritima	15	40	79		25	15	5.5				
Spartina patens							77.7		7.5	20	5
Juncus gerardi								15	25		
Juncus balticus								15		15	30
Triglochin maritima			9			80	5.5	3	5		5
Salicornia europeae	50	5			25	1					
Glaux maritima		10				3	11.2	27	50		10
Spergularia canadensis	5	0.1			35					60	
Achillea										5	5
Ligusticum scothicum											
Limonium nashii		40									
Potentilla anserina								5	5		40
Suaeda sp.	5										
Atriplex sp.							0.1				
Cyperaceae								33			
other grasses		2.5						2	7.5		5
Total cover	100	100.1	100		100	100	100	100	100	100	100
Total number of taxa	5	7	3		4	5	5	7	6	4	7

Table 7. Total cover (%) of local vegetation assemblages from which surface samples were collected in Little Lepreau salt marsh, New Brunswick. Surface sample ID's correspond to those given in Figure 3 and are grouped by the zone they were collected in: *S. alterniflora* (SA), *P. maritima* (PM), *S. patens* (SP), Cyperaceae (C), *J. gerardi* (JG), and *J. balticus* (JB). See text for details regarding lack of values for samples 25 and 31.

	Surface sample ID and corresponding vegetation zone											
	SA		PM		SP		JG				JB	
	25	31	29	32	22	26	23	24	27	33	28	30
Relative elevation (m)			1.02	1.43	1.10	0.99	1.44	1.28	1.34	1.30	2.52	2.08
Spartina alterniflora				25								
Plantago maritima			60	25	0.1				2.5	0.1	0.1	
Spartina patens			3		20	74.4	2			5		
Juncus gerardi							35	10	30			
Juncus balticus											25	20
Triglochin maritima						7.4	5			80		0.1
Salicornia europeae			1	5	30	3	2			1		
Glaux maritima			30	30	20	0.1	15	90	30	5		
Spergularia canadensis				10								
Ligusticum scothicum											55	0.1
Limonium nashii									25			
Potentilla anserina			1			0.1	2		10	1		60
Suaeda sp.			5	5	30	15	2			3		
Atriplex sp.							2					
Cyperaceae							35					
other grasses									2.5	5	20	20
Total cover			100	100	100.1	100	100	100	100	100.1	100.1	100.2
Total number of species			6	6	5	6	9	2	6	8	4	5

Pollen spectra

Local and regional source vegetation was determined for all wetland pollen types identified in surface samples from Dipper Harbour, Chance Harbour, and Little Lepreau (Table 2) to determine which pollen types are indicators of salt marsh vegetation zones. Some indicator species do not contribute to wetland pollen spectra, for example, *Juncus gerardi* and *Juncus balticus* dominate the uppermost elevations but *Juncus* pollen is not preserved in chemical processing for pollen concentration. However, *Ligusticum scothicum* is consistently observed in pollen spectra from *Juncus*-dominated vegetation and rarely observed in those from lower elevations. Hence, *L. scothicum* could be considered diagnostic of vegetation at higher elevations. The variability of salt marsh vegetation is such that sources for many pollen types exist in most zones (Figure 5), but some types indicate proximity to particular marsh features, for example, *Ruppia* pollen is only found in samples from vegetation at elevations with shallow ponds, suggesting that its presence in pollen spectra indicates proximity to ponds.

The wetland pollen spectra of samples from each vegetation zone have higher pollen diversity than is observed in source vegetation (Figure 5). Eighteen wetland pollen types were identified among the 35 samples considered in this study (Table 8; Appendix 1), and eleven of these types have salt marsh sources (Table 2). A minimum of six and maximum of 16 wetland pollen types were identified per sample with an average of 10 types per sample. Samples collected in *Plantago* zones had the greatest variability in number of wetland pollen types (7-16) and *Juncus gerardi* zones had the least (8-11). The percent wetland of total pollen ranged from 11% to 60% with wetland and total counts ranging from 93-657 and 415-2791 grains, respectively.

Figure 5. Percent wetland pollen in surface samples from vegetation zones in Dipper Harbour, Chance Harbour, and Little Lepreau, Bay of Fundy, NB.

ANALYST: C.B. Beecher

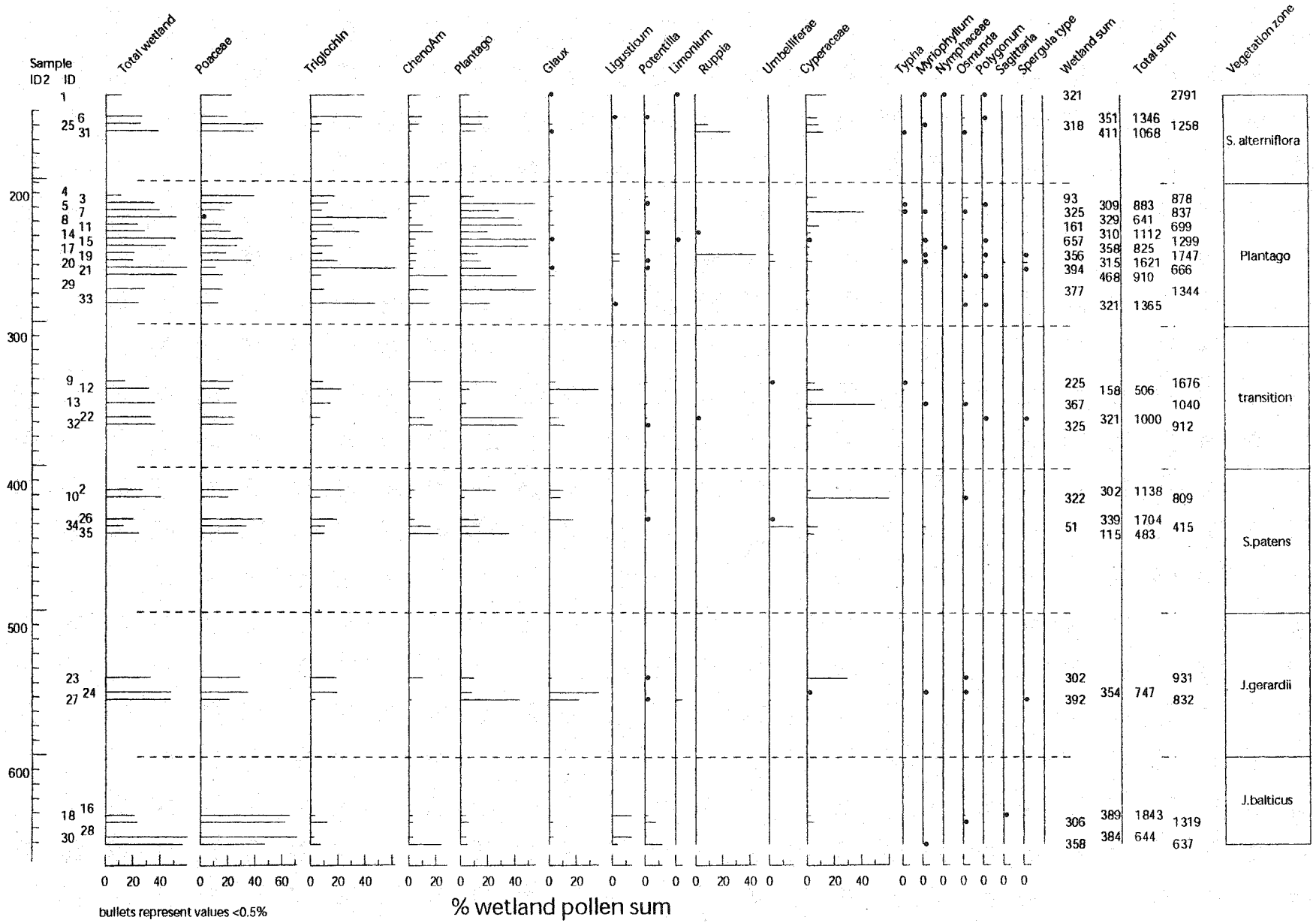


Table 8. Summary of wetland pollen (%) in surface sediment samples collected from units with the same dominant vegetation (broad scale) in three Bay of Fundy salt marshes. The range is followed by the average in parentheses.

	Dominant vegetation (broad scale)					
Pollen type	*Spartina alterniflora* n=4	*Plantago maritima* n=12	*Spartina patens* n=7	*Cyperaceae* n=2	*Juncus gerardi* n=5	*Juncus balticus* n=4
Cheno Am	2.4-15.1 (8.8)	1.2-28.4 (8.7)	9.9-24.4 (12.3)	0.8, 1.3	0.6-14.6 (7.7)	2.9-24.0 (8.3)
Cyperaceae	7.5-15.0 (10.4)	0.2-42.2 (5.7)	0.6-60.2 (12.1)	12.0, 49.9	0.3-29.5 (7.2)	0.0-4.9 (1.9)
Glaux	0.0-3.2 (1.3)	0.0-11.1 (2.1)	0.0-17.4 (5.9)	3.3, 36.1	1.6-36.4 (13.8)	0.0-3.4 (1.7)
Ligusticum	0.0-0.3 (0.1)	0.0-5.4 (0.9)	--	0.0, 0.6	0.0-0.3 (0.1)	0.0-14.3 (8.1)
Limonium	0.0-0.3 (0.1)	0.0-0.5 (0.0)	--	--	0.0-4.8 (1.0)	--
Plantago	6.9-20.8 (12.8)	12.6-55.3 (35.6)	2.8-55.2 (24.6)	3.8, 6.3	8.5-45.8 (25.8)	3.9-5.9 (4.7)
Poaceae	19.7-45.6 (33.1)	0.3-36.5 (19.9)	15.6-45.1 (27.3)	20.3, 26.2	12.1-34.5 (24.1)	47.2-71.1 (61.5)
Potentilla	0.0-2.2 (0.8)	0.0-3.8 (0.6)	0.0-2.6 (0.8)	0.0, 1.4	0.0-1.2 (0.5)	1.0-12.3 (5.9)
Sagittaria	0.0-0.6 (0.2)	0.0-1.9 (0.2)	--	--	--	0.0-0.3 (0.1)
Spergula type	0.0-1.1 (0.4)	0.0-3.2 (0.4)	0.0-1.0 (0.2)	--	0.0-0.3 (0.1)	0.0-1.0 (0.4)
Triglochin	6.1-40.2 (21.6)	1.8-62.2 (20.4)	6.8-24.5 (12.6)	14.2, 22.2	3.3-47.0 (18.9)	2.9-12.1 (6.4)
Myriophyllum	0.0-0.6 (0.4)	0.0-0.6 (0.1)	0.0-2.0 (0.6)	0.0, 0.3	0.0-0.7 (0.2)	0.0-0.8 (0.3)
Nymphaceae	0.0-0.3 (0.1)	0.0-0.3 (0.0)	--	--	--	--
Osmunda	0.2-4.3 (1.9)	0.0-1.3 (0.4)	0.0-1.3 (0.5)	0.0, 0.3	0.0-1.0 (0.4)	0.0-1.5 (0.5)
Polygonum	0.0-0.3 (0.3)	0.0-1.6 (0.3)	--	--	0.0-0.3 (0.1)	0.0-0.7 (0.2)
Ruppia	0.0-9.7 (7.3)	0.0-44.7 (3.8)	0.0-1.3 (0.4)	--	0.0-0.3 (0.1)	--
Typha	0.0-1.1 (0.3)	0.0-0.6 (0.1)	0.0-0.4 (0.1)	0.0, 1.3	--	0.0-0.5 (0.1)
Umbelliferae	--	0.0-4.1 (0.6)	0.0-17.6 (2.6)	--	0.0-0.8 (0.2)	--
% Wetland	**11-26 (22)**	**19-59 (38)**	**12-40 (23)**	**31, 35**	**24-47 (37)**	**21-60 (40)**
Wetland sum	**93-351 (299)**	**161-657 (359)**	**51-377 (247)**	**158, 367**	**302-392 (338)**	**306-389 (359)**
Pollen types	**10-14 (11)**	**7-16 (10)**	**6-12 (8)**	**8, 9**	**8-11 (10)**	**7-13 (9)**
Total sum	**878-2791 (1468)**	**641-1747 (1012)**	**415-1704 (1081)**	**506, 1040**	**747-1365 (975)**	**637-1843(1110)**
Pollen types	**32-47 (39)**	**18-45 (33)**	**26-48 (36)**	**26, 30**	**25-33 (30)**	**22-44 (31)**

In general, Poaceae and *Triglochin* pollen dominate wetland pollen spectra from most vegetation zones (Figure 5). The exception is spectra from *Plantago* zones that are dominated by *Plantago* and *Triglochin* pollen. Wetland pollen spectra from *J. balticus*-dominated vegetation have the highest proportion Poaceae pollen (62-71%) and others typically have <46%.

Vegetation-pollen relationships

Linear regressions show that plant-pollen relationships are stronger over small-scales (<15 m) than broad scales because, in the latter, cover is averaged over a larger area (Table 9). The exceptions are Poaceae and Cheno Am, which do not have significant plant-pollen relationships on either scale (Figure 6, Table 9). Scatter diagrams show that cover of *Triglochin* is over-represented by its pollen, *Glaux* is under-represented, and Poaceae, Cheno Am, and *Plantago* are inconsistent (Figure 6). In most vegetation zones, cover of Cyperaceae, *Limonium*, *Ligusticum*, *Potentilla*, or *Spergularia* is in trace amounts and percent pollen representing these species is too low to detect trends in representation in scatter plots.

Differences in pollen production may explain regression results and the inconsistent relationship between Poaceae cover and pollen (Table 9, Figure 6). Poaceae pollen in salt marsh sediments is derived from local, regional, and extra-regional sources that represent different species including *Spartina* grasses (primarily local and regional sources) and 'terrestrial' grasses (extra-regional sources). Poaceae cover is consistently under-represented by Poaceae pollen in *Spartina alterniflora* zones (i.e., >45% Poaceae cover) and generally over-represented in all other zones (Figure 6). It is suspected that *S. alterniflora* produces little pollen (Clark, 1986), a possible explanation for this relationship.

Local, regional, and extra-regional sources

With the exception of Poaceae and Cheno Am, regression results suggest that changes in pollen percentages reflect similar changes in source vegetation (Table 9). The relative contributions of regional and extra-regional sources can be separated using the y-intercepts of plant-pollen relationships over small and broad scales that represent regional and extra-regional influences, respectively. For broad and small scales, the y-intercepts for *Ligusticum*, *Limonium*, *Potentilla*, and *Spergularia* are close to zero. This suggests that local sources are the principle sources of *Ligusticum*, *Limonium*, *Potentilla*, and *Spergularia* pollen and contributions from regional and extra-regional sources are minimal (Table 9). All other pollen types receive inputs from regional and extra-regional sources but the relative contribution varies among taxa.

When local sources are the primary contributors to pollen spectra, pollen proportions are highly variable (Janssen, 1984). The high variability in percent *Triglochin* pollen suggests that local sources contribute *Triglochin* pollen to a vegetation zone on broad and small scales (Figure 6). Isolated 'rosettes' of *Triglochin* are found across the marsh surface (≤0.5 m-diameter) and are several cm higher than nearby sediments (Khan and Ungar, 1999). This patchy distribution across many elevations and high pollen production provide ample amounts of local *Triglochin* pollen for tidal mixing along and across elevations and may explain the high y-intercepts and lack of relationship between broad scale *Triglochin* cover and *Triglochin* pollen. Regional *Triglochin* pollen amplifies local *Triglochin* pollen resulting in consistent over-representation of small-scale *Triglochin* cover (Table 9, Figure 6). *Glaux maritima* produces less pollen than wind-pollinated plants and *Glaux* pollen consistently under-represents plant cover (Figure 6). Pollen deposition is assumed to be close to the plant, resulting in a 'patchy' pollen distribution

and is supported by stronger relationships between small-scale *Glaux* cover and *Glaux* pollen and low y-intercepts (Table 9).

Plantago has a larger y-intercept for smaller-scale cover than larger-scale (Table 9). This illustrates that regional sources contribute substantially more *Plantago* pollen than extra-regional sources (Table 9). Cheno Am and Poaceae do not have significant relationships between plant cover and pollen and the y-intercepts are large, suggesting that regional and extra-regional pollen sources contribute substantially more pollen than local sources and may limit establishment of their plant-pollen relationships (Figure 6, Table 9).

Table 9. The plant-pollen relationship for wetland pollen types representing salt marsh plants observed in Bay of Fundy salt marshes. Those based on small-scale plant cover do not include surface samples from Dipper Harbour (N=21) and those based on broad scale cover include all 35 samples from Dipper Harbour, Chance Harbour, and Little Lepreau salt marshes.

	Broad scale			Local scale		
	R^2	p	y-int	R^2	p	y-int
Cheno Am	-	ns	-	-	ns	-
Cyperaceae	0.13	0.034	7.61	0.88	0.000	2.40
Glaux	0.41	0.000	2.35	0.58	0.000	0.84
Ligusticum	0.40	0.000	0.63	0.89	0.006	0.51
Limonium	0.23	0.004	0.06	0.33	0.000	0.06
Plantago	0.30	0.001	15.49	0.31	0.009	17.91
Poaceae	-	ns	-	-	ns	-
Potentilla	0.23	0.004	0.79	0.87	0.000	0.75
Spergularia	-	ns	-	0.84	0.000	0.16
Triglochin	-	ns	-	0.71	0.000	10.19

Figure 6. Pollen proportion in surface samples retrieved from Little Lepreau and Chance Harbour marshes as a function of vegetation percent cover given on two spatial scales. The solid line represents x=y, dotted (local scale), and dashed (broad scale).

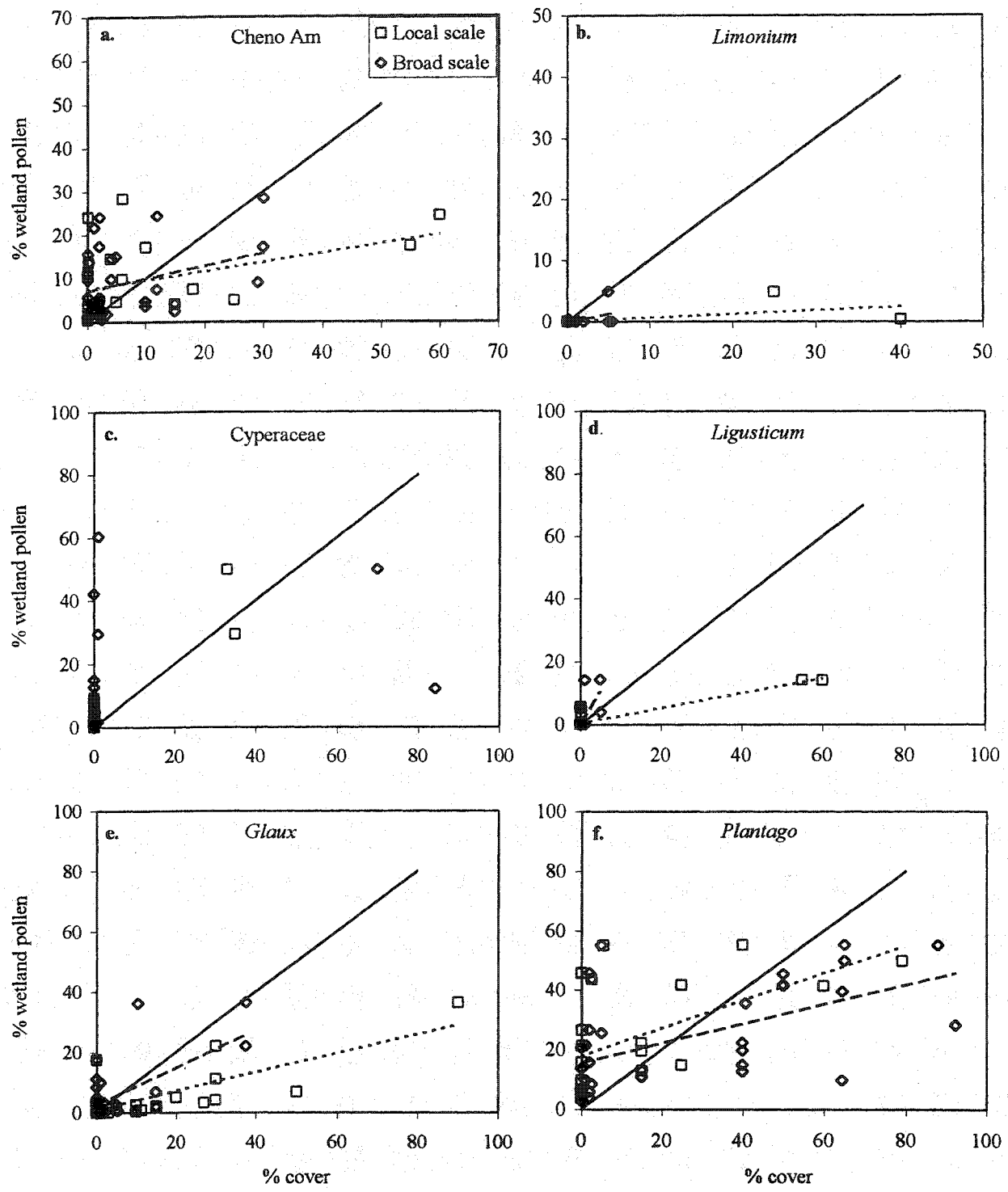
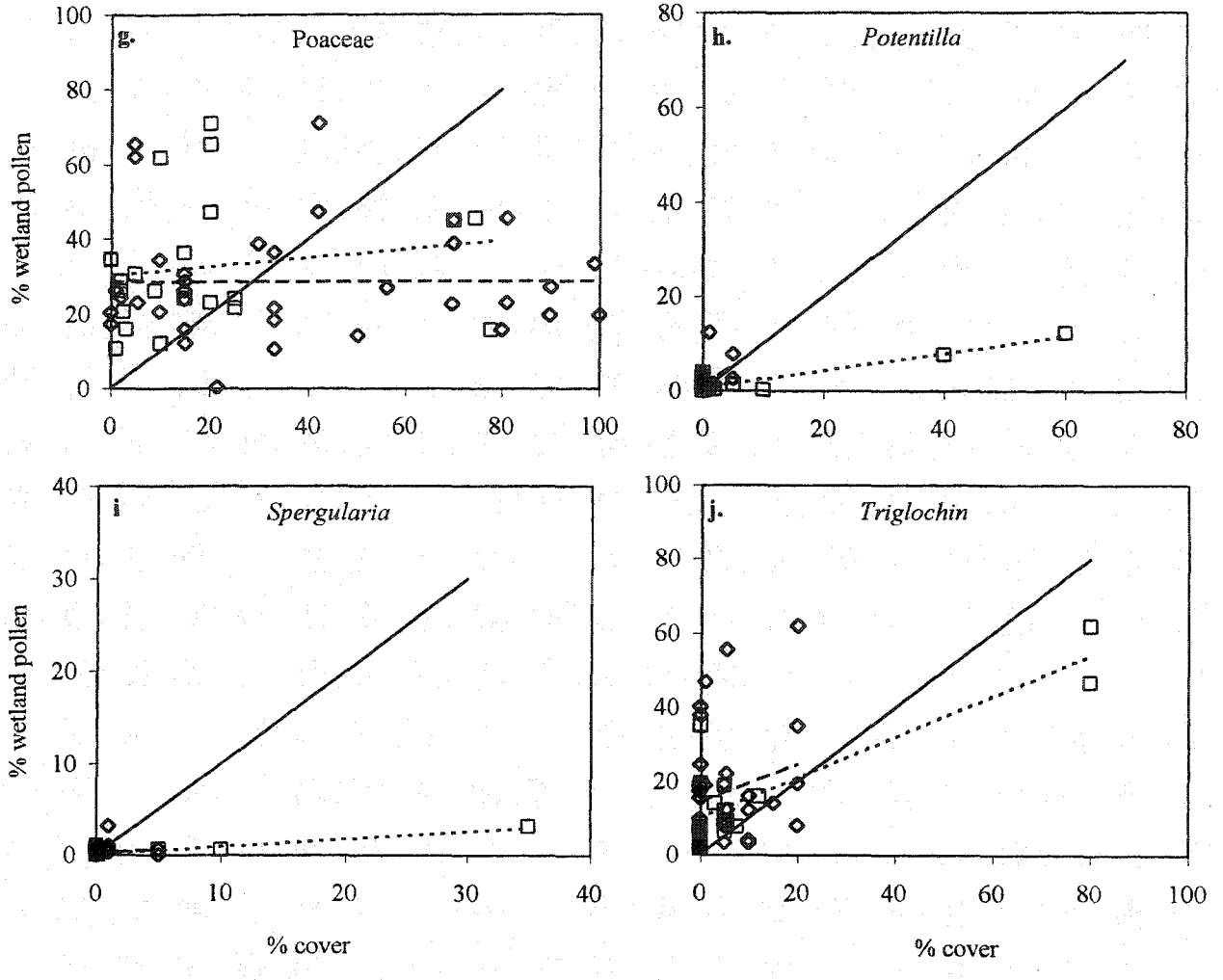


Figure 6 (cont.).



Small and broad scale *Plantago* cover is as low as 0% in zones below *Juncus*. Variability in *Plantago* pollen in these zones suggests that influence of regional sources on pollen spectra is most important at intermediate elevations, less at lower elevations, and minimal at the highest elevations (Table 9, Figure 6). *Plantago* pollen is strongly related to small and broad cover and y-intercepts are large, suggesting that the plant-pollen relationship is equally influenced by local and regional deposition (Table 9). Local scale *Plantago* cover is <20% in zones above *J. gerardi* and >25% below, with consistent over- and under-representation of *Plantago* cover by *Plantago* pollen, respectively (Table 6). This suggests that the influence of regional deposition on the relationship between *Plantago* cover and pollen varies predictably as a function of flooding frequency and tidal mixing does not hinder the establishment of this plant-pollen relationship. In contrast, inputs from regional sources of *Triglochin* pollen result in over-representation of *Triglochin* cover at the most frequently flooded elevations such that *Triglochin* pollen does not have a significant relationship with broad scale cover (Table 9, Figure 6). *Triglochin* and *Plantago* plant-pollen relationships and variability of percent pollen in spectra of samples from the same small and broad scale cover suggest the influence of regional sources is greatest in pollen spectra from vegetation zones below *J. gerardi* and less at higher elevations (Figure 6).

The relative influence of extra-regional pollen sources on pollen spectra and plant-pollen relationships is illustrated by comparing pollen spectra between vegetation zones. Pollen from extra-regional sources are brought to the marsh surface via upland drainage, tidal flooding, and airborne deposition and can amplify the percent pollen of marsh species with the same pollen type (e.g., Cyperaceae, Cheno Am and Poaceae), or increase pollen diversity by contributing distinct pollen types that are not represented by marsh taxa (e.g., *Osmunda*, *Myriophyllum*, and

Nymphaceae). Pollen spectra from zones at the intermediate and highest elevations (i.e., *J. balticus* and *Plantago* zones) have more pollen types with exclusively extra-regional sources than spectra from other zones. This suggests that extra-regional inputs are greatest at these elevations and the influence of extra-regional sources on the plant-pollen relationships of Poaceae, Cyperaceae, and Cheno Am is most important here.

Differences in the relative influence of extra-regional sources at study areas may explain the regression results and inconsistent relationship between Cheno Am cover and pollen (Figure 6, Table 9). The Cheno Am scatter plot suggests that the relative inputs of Cheno Am pollen from extra-regional sources differs between the three study sites and limits establishment of the Cheno Am plant-pollen relationship (Figure 6). Broad and small-scale vegetation with <10% Cheno Am cover is over-represented by Cheno Am pollen and >10% cover is under-represented (Figure 6). The former corresponds to spectra from all Chance Harbour and Dipper Harbour salt marsh zones and the latter to spectra from Little Lepreau, suggesting extra-regional sources have a greater influence on spectra at Dipper Harbour and Chance Harbour than at Little Lepreau.

Pollen spectra dissimilarity

Dissimilarity results suggest that on the basis of single comparisons of modern pollen spectra, *S. alterniflora*, *Plantago maritima*, *S. patens*, transition, *J. gerardi*, and *J. balticus* zones can be considered distinct (Figures 6-9). However, with the exception of *J. balticus* samples, a single sample does not have the same affinity to all samples from the same vegetation zone. The critical threshold value, 0.10, is similar to 'V1' in Overpeck et al. (1985) and represents the maximum value below which 'matches' are consistently within the same vegetation.

Spartina alterniflora zone (samples 1, 6, 25, and 31)

S. alterniflora zones can be separated from all other salt marsh zones on the basis of their wetland pollen spectra. All four pollen samples from *S. alterniflora* have at least one comparison with $d_{ij} \leq 0.10$, not including the self-comparison (Figure 7A). Three of the four spectra match each other ($d_{ij} \leq 0.10$) and the 'matches' for the fourth sample include spectra of vegetation zones adjacent to *S. alterniflora*. Remaining comparisons ($d_{ij} \geq 0.10$) suggest that *S. alterniflora* zones are only distinct when conservative threshold criteria are used (i.e., threshold of 0.10).

Spartina patens zone (samples 2, 10, and 26)

The distinction of wetland pollen spectra from *S. patens* zones is also promising (Figure 7B). Two of three spectra have at least one comparison with $d_{ij} \leq 0.10$, not including the self-comparison and the smallest coefficient for all spectra represents *S. patens* vegetation or a zone adjacent to the pollen sample site (Figure 7B). Similar to the scatter diagrams for *S. alterniflora* analogs, comparisons above the critical threshold suggest that *S. patens* zones are only distinct when conservative threshold criteria are used.

Plantago maritima zone (samples 3, 4, 5, 7, 8, 11, 14, 15, 17, 19, 20, 21, 29, and 33)

For more than 50% of *Plantago* samples, the dissimilarity results suggest that these spectra could be used to identify *Plantago* zones in a fossil sedimentary sequence when conservative threshold criteria are used (Figure 8). In all cases, the minimum coefficient represents a sample from

either the same zone in a different marsh or a different zone in another marsh that is the same as the zone adjacent to the sampling location (Figures 2, 7).

Transition to high marsh (samples 9, 12, 13, 22, and 32)

The results for transition samples suggest that this group is distinct from other vegetation zones on the basis of its wetland pollen spectra (Figure 9). Four of five 'transition' pollen spectra have a high degree of affinity for each other with at least one comparison meeting the threshold criteria and the lowest consistently representing either another transition sample or a zone adjacent to the sampling site (Figures 2, 8). Comparisons that do not meet threshold criteria suggest that these analogs are distinct only when a conservative critical value is used. Although transition sample 9 does not have comparisons that meet threshold criteria, all samples from *S. patens* and *J. gerardi* zones have lower coefficients than those from other zones (with the exception of samples 34 and 35). This suggests that this sample could be used to identify *S. patens* and *J. gerardi* zones with a less conservative critical value.

Juncus gerardi (samples 23, 24, and 27)

Samples from *J. gerardi* cannot be separated from other vegetation on the basis of their wetland pollen based on critical threshold criteria (Figure 10A). Only two comparisons meet threshold criteria among the three samples. All samples have a greater affinity to spectra from *S. patens* and transition zones than to each other more-so than spectra of other zones (Figure 10A).

J. balticus zones (samples 16, 28, 18, and 30)

In contrast to samples from all other zones, most *J. balticus* samples have the strongest affinity for each other (Figure 10B). Comparisons with samples from other zones consistently have higher coefficients, suggesting that a higher critical threshold could be used for *J. balticus* analogs. Thus, *J. balticus* vegetation could be tracked with the highest degree of certainty if a less-conservative dissimilarity threshold is used.

Figure 7. Squared chord distance coefficients between a sample (shaded symbol) retrieved in *S. alterniflora* (A) and *S. patens* (B) zones (d_{ij}=0) and all other samples from three Bay of Fundy salt marshes. Dashed lines delimit vegetation zones. The horizontal axis is coded to correspond to the vegetation zone the sample was collected in: 100-199 *S. alterniflora*, 200-299 *Plantago*, 300-399 transition (see text for explanation), 400-499 *S. patens*, 500-599 *J. gerardi*, 600-699 *J. balticus*.

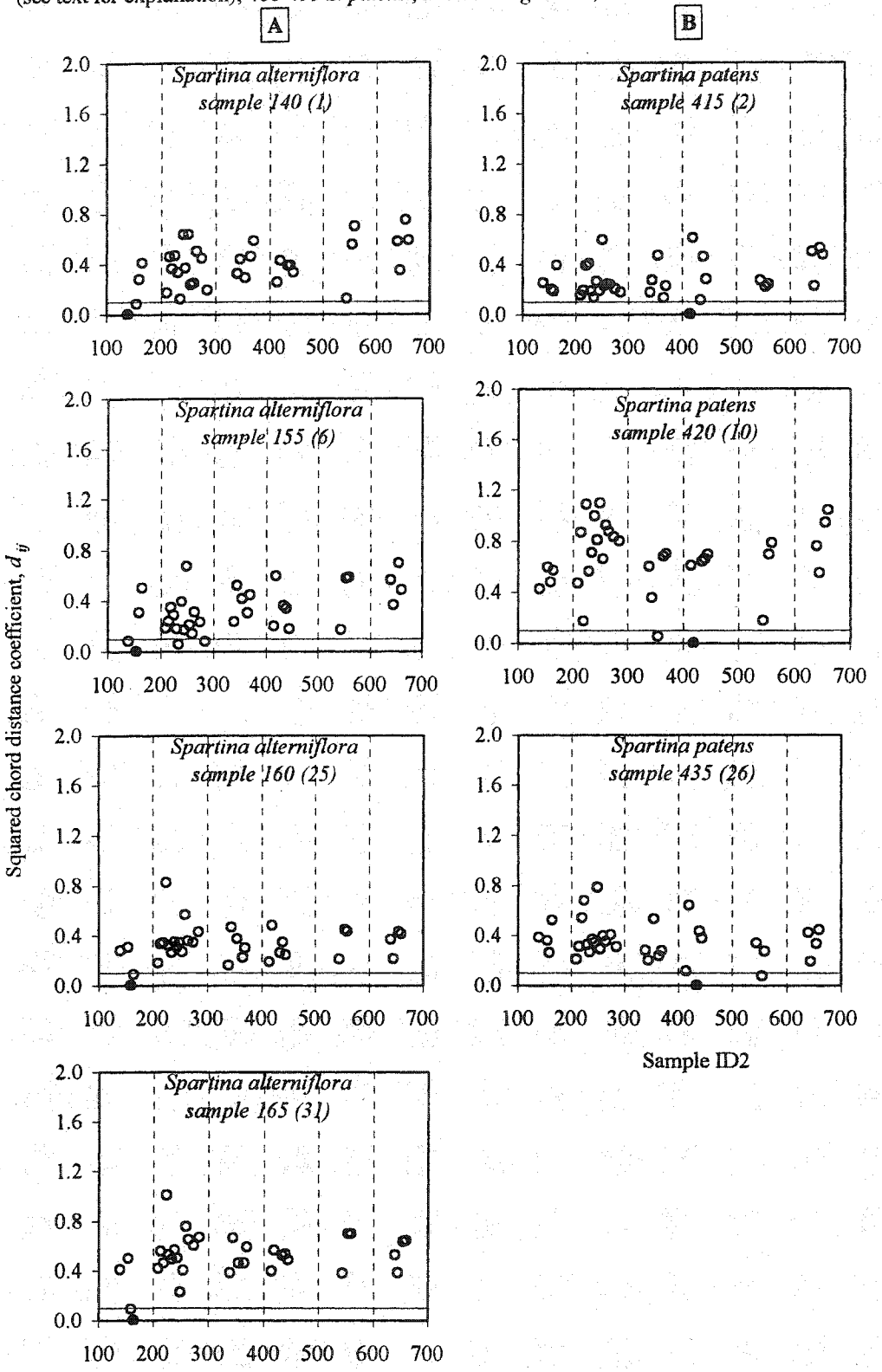


Figure 8. Squared chord distance coefficients between a sample (shaded symbol) retrieved in *Plantago maritima* zones (d_{ij}=0) and all other samples in three Bay of Fundy salt marshes. Dashed lines delimit vegetation zones. The horizontal axis is coded to correspond to the vegetation zone: 100-199 *S. alterniflora*, 200-299 *Plantago*, 300-399 transition (see text for explanation), 400-499 *S. patens*, 500-599 *J. gerardi*, 600-699 *J. balticus*.

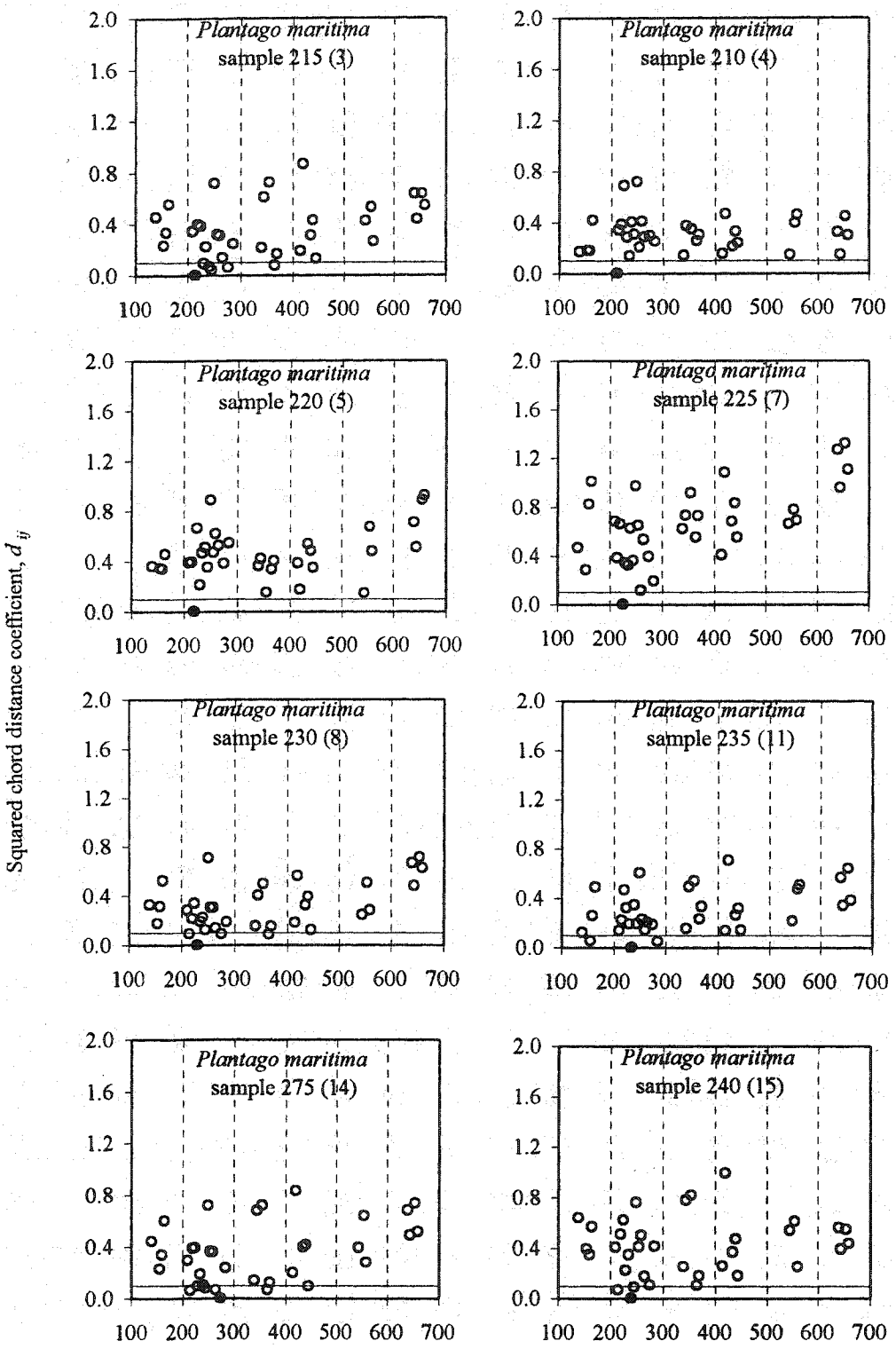


Figure 8 (cont.)

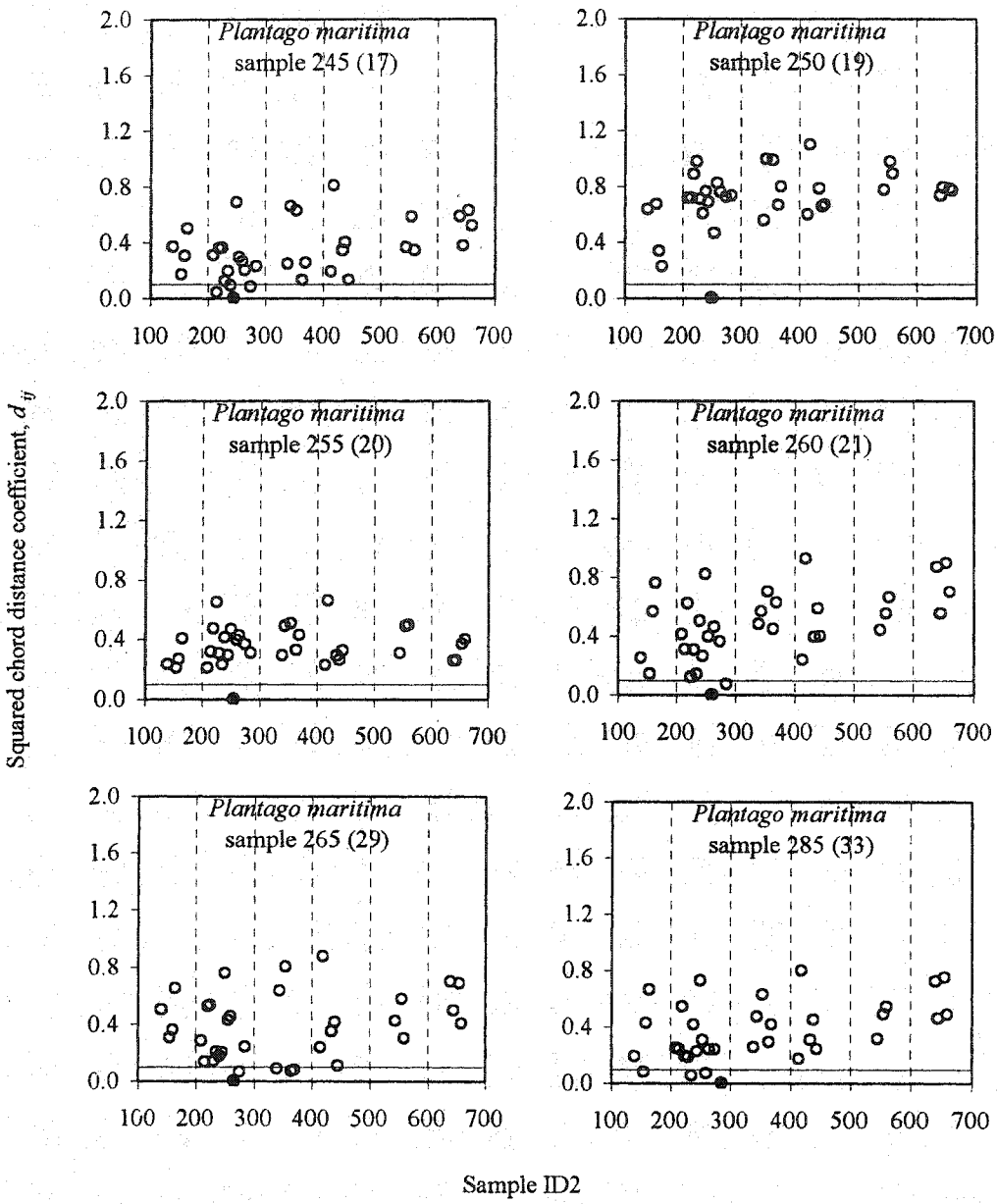


Figure 9. Squared chord distance coefficients between a sample (shaded symbol) retrieved in transition zones (see text for explanation) (d_{ij}=0) and all other samples for lower Bay of Fundy salt marshes. Dashed lines delimit vegetation zones. The horizontal axis is coded to correspond to the vegetation zone: 100-199 *S. alterniflora*, 200-299 *Plantago*, 300-399 transition (see text for explanation), 400-499 *S. patens*, 500-599 *J. gerardi*, 600-699 *J. balticus*.

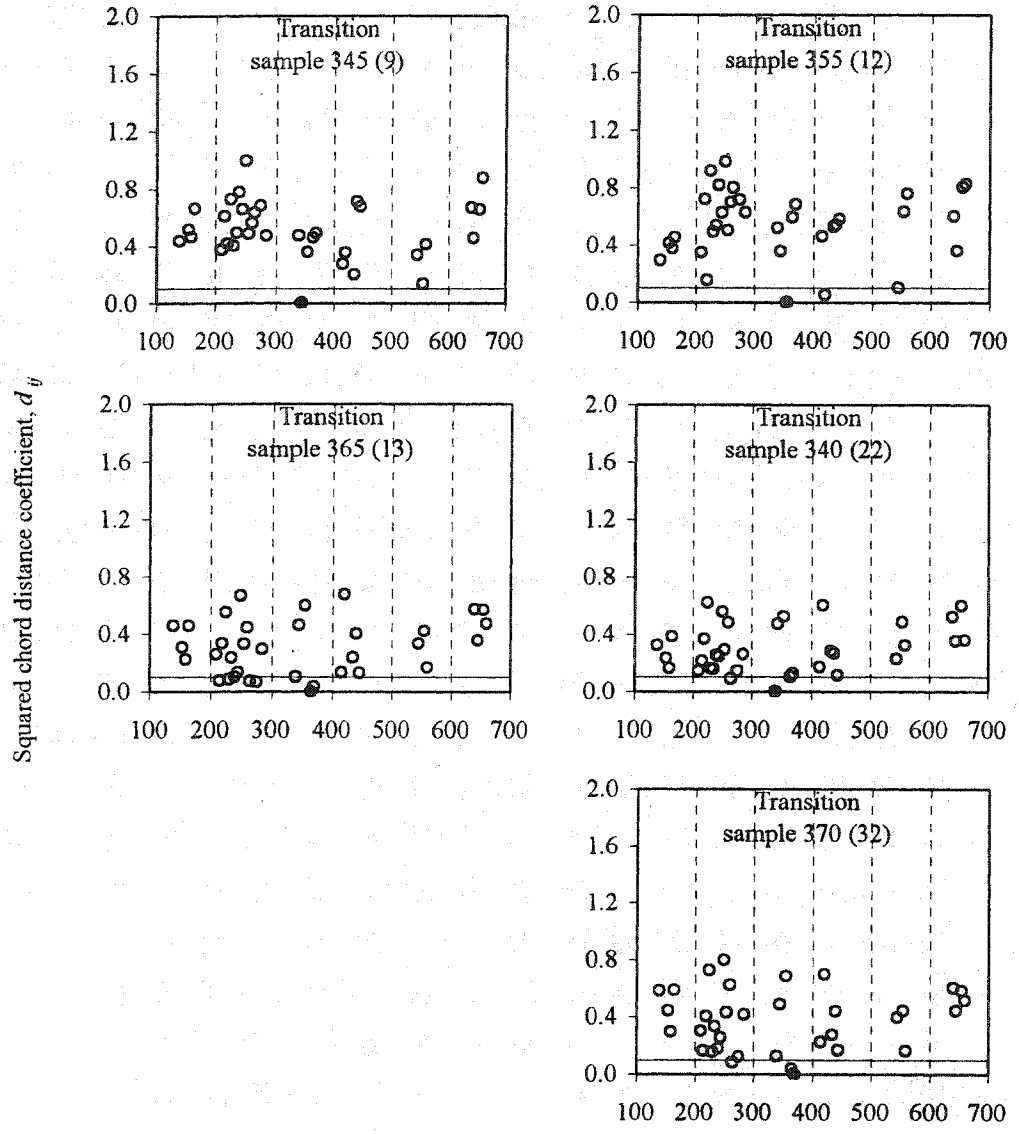
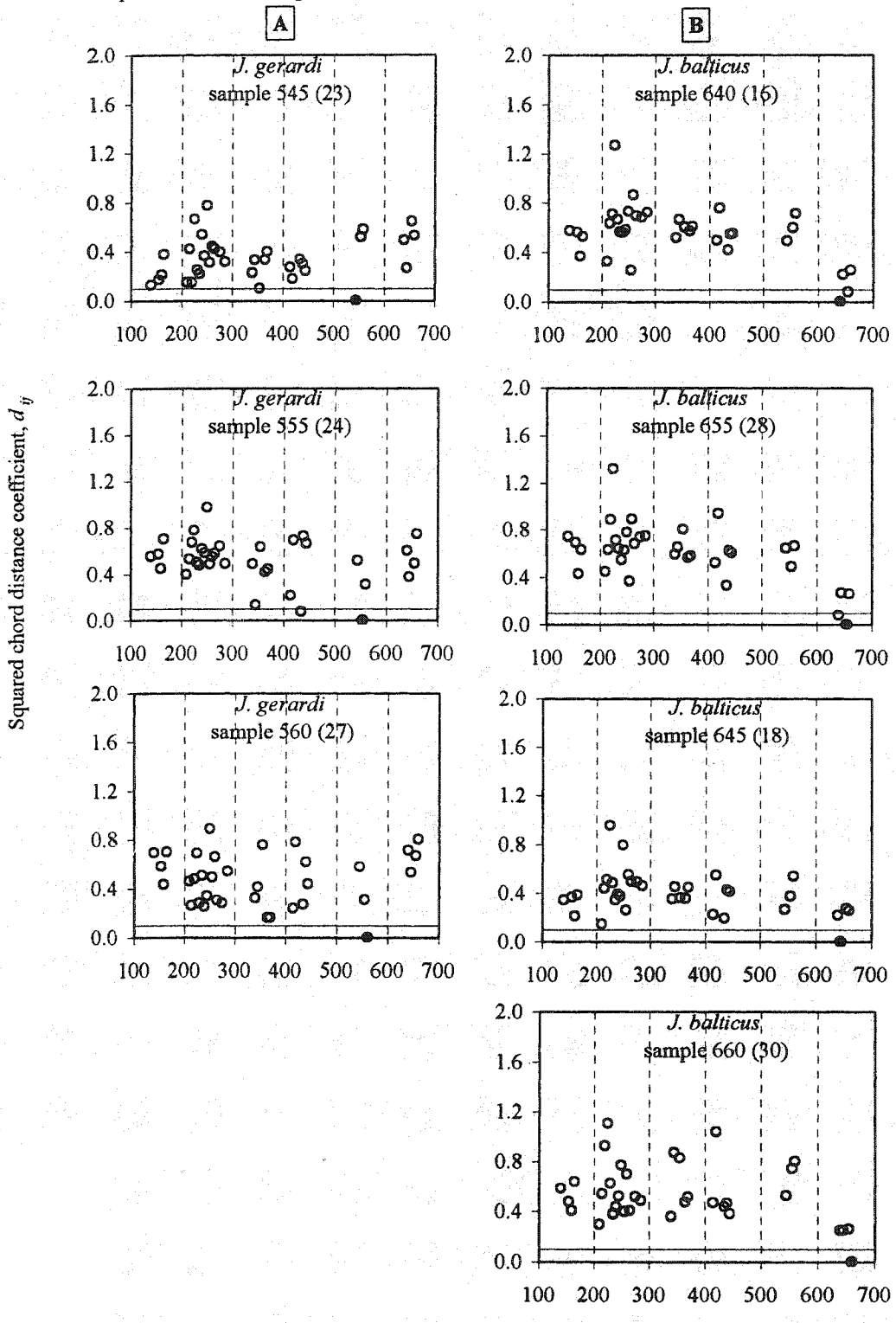


Figure 10. Squared chord distance coefficients between a sample (shaded symbol) retrieved in *Juncus gerardi* (A) and *Juncus balticus* (B) zones (d_{ij}=0) and all other samples for lower Bay of Fundy salt marshes. Dashed lines delimit vegetation zones. The horizontal axis is coded to correspond to the vegetation zone: 100-199 *S. alterniflora*, 200-299 *Plantago*, 300-399 transition (see text for explanation), 400-499 *S. patens*, 500-599 *J. gerardi*, 600-699 *J. balticus*.



Plant-pollen relationships in Bay of Fundy salt marshes

The nature of modern plant-pollen relationships has been examined in various ecosystems to establish modern analogs for the reconstruction of past vegetation (e.g., Clark and Patterson, 1985; Bradshaw and Webb, 1985; Bunting et al., 1998). Many of these studies suggest that the level of detail with which vegetation can be reconstructed depends upon the scale of vegetation represented by the modern analog and some have addressed sources of error and problems associated with plant-pollen relationships in wetland environments (e.g., Clark and Patterson, 1985). Clark and Patterson (1985) have suggested that in salt marshes, over-representation of local inputs, 'patchy' vegetation, and tidal redistribution of pollen limit establishment of salt marsh plant-pollen relationships and complicate the separation of local and regional influences.

In contrast to Clark and Patterson's conclusions, variability in vegetation and tidal mixing do not limit the establishment of most salt marsh plant-pollen relationships or hinder determination of the influence of regional sources in marsh zones. This study has illustrated that differences in local, regional, and extra-regional sources can be revealed because of replication that is not present in Clark and Patterson's study. In concordance with Janssen's findings, local scale results from this study suggest that, with the exception of Cheno Am and Poaceae, pollen proportions reflect source vegetation.

Additionally, these results support differential influences from non-local sources with elevation. The influence of regional pollen is greatest below the *S. patens* zone and decreases with elevation. It appears that pollen assemblages at intermediate elevations receive more inputs from regional and extra-regional sources (freshwater, tidal, and aerial) than other elevations but the

local signal still dominates. Freshwater and tidal components have the greatest influence at the highest and lowest elevations, respectively with lesser influences across subsequently lower and higher elevations. The greater influence of extra-regional pollen sources at lower and intermediate elevations indicates that tides are the primary source of extra-regional pollen to assemblages below the *J. gerardi* zone. This is shown by the frequency and diversity of pollen types that are exclusively extra-regional (e.g., *Osmunda*, *Myriophyllum*, or *Nymphaceae*) in wetland pollen spectra of *S. alterniflora* and *P. maritima* zones compared with higher elevations (Figure 5).

Extra-regional pollen contributions are assumed to be tidal at the lowest elevations, freshwater at the highest elevations, and both at intermediate elevations thus have the greatest influence on pollen assemblages at intermediate elevations where pollen proportions of Cyperaceae, Poaceae, and Cheno Am are amplified by all three extra-regional sources. Due to the greater surface run-off, salt marshes surrounded by high relief may receive larger proportions of extra-regional wetland pollen at the highest elevations than those with lower relief. This could explain the under-representation of Cheno Am at intermediate and high elevations at Little Lepreau, where surrounding relief is low, and over-representation at Dipper Harbour and Chance Harbour.

Salt marsh modern analogs: implications for paleoecological reconstructions

Limitations to wetland reconstruction have been addressed in salt marsh (Clark, 1986), coniferous swamp (Bunting, 1998), and coastal sub-environments (Willard, 2001). Wetland communities can be separated on the basis of their pollen spectra (Willard et al., 2001; O'Neal et al., in press), yet the floristic diversity of some wetland communities may not be reflected by

their pollen spectra (Bunting et al., 1998). This is because some key 'indicator' species are not preserved or are under-represented (Rich, 1995; Bunting et al., 1998). Clark (1986) added that modern analogs cannot be used for reconstruction of past salt marsh environments because these plants organize themselves individualistically along spatial gradients.

The results of this study illustrate that salt marsh reconstruction is possible despite small-scale heterogeneity because of the influence of regional sources of *Plantago* pollen and extra-regional sources that are not represented by salt marsh vegetation. *Plantago* dominance at intermediate elevations is characteristic of northern salt marshes (Chmura et al., 1997) and the results of this study suggest that local and regional sources of *Plantago* pollen help to distinguish vegetation zones on the basis of their pollen spectra. *Juncus*-dominated elevations can be detected despite absence of *Juncus* pollen because other taxa found only at the highest elevations compensate for the palynological 'invisibility' of *Juncus gerardi* and *Juncus balticus* vegetation. Other zones are distinct because of differential influences of regional and extra-regional sources. Therefore, identification of modern analogs for northern salt marshes is possible given that vegetation zones can be detected due to the tidal redistribution and deposition of a palynologically distinct component, unique to northern salt marsh systems, and the concentration of fringe taxa at the uppermost elevations.

The pollen spectra illustrate that plant diversity in all marsh zones cannot be detected palynologically even when vegetation zones are distinct (e.g., *Juncus* sp.), but dissimilarity results show that modern analogs of all vegetation zones are distinct. This suggests that spectral separation of vegetation zones is not driven by differences in species diversity. The evaluation

of pollen sources suggests that extra-regional inputs and changes in percent *Plantago* pollen as a function of elevation are the basis upon which spectra are separated. Comparison of all pollen for vegetation below *J. balticus* suggest that salt marsh reconstruction is possible with a high degree of certainty only when conservative threshold criteria are used (critical value=0.10) and it is likely they represent patches of vegetation.

As marsh pollen spectra are the product of multiple years of deposition, they will integrate shifts in plant zones. Comparisons that exceed threshold criteria for all vegetation zones below *J. balticus* suggest that, to some degree, these spectra integrate vegetation across elevations below the *J. balticus* zone. For example, *J. balticus* sample 18, collected near a *Plantago* zone (Figure 3), has a dissimilarity coefficient that possibly reflects a shift from *Plantago*- to *J. balticus*-dominated vegetation (Figure 10B). Such changes could be verified only by a vegetation survey at least three years prior to surface pollen sampling and such monitoring was beyond the scope of this study.

Dissimilarity results show that *J. balticus* modern analogs are distinct with a less conservative threshold value (critical value>0.10). This suggests that these spectra are most-influenced by extra-regional and local pollen sources whereas spectra from other zones are dominated by influences of tidal mixing of local and regional sources. Tidal mixing and subsequent differential over- and under-representation of characteristic salt marsh taxa limits the degree of certainty in 'matches' and suggests the need for conservative threshold criteria.

Intermediate and high elevations can be separated using dissimilarity results when wetland pollen spectra of *Plantago* and *J. gerardi* zones are considered. *Juncus gerardi* and *Plantago*

zones have the highest proportion of wetland pollen, however *Plantago* zones have the highest wetland pollen diversity and *J. gerardi* zones have the lowest. These observations can be used within the context of a core to verify whether a fossil assemblage 'matching' a *J. gerardi* or *Plantago* analog reflects an intermediate or high elevation. Hence, distinct and detectable *Plantago* distribution and the influence of extra-regional sources with elevation facilitate the separation between intermediate and high elevations thereby setting these marshes apart from those in more southern locations.

CONCLUSIONS

Salt marshes have high sources of error relative to palynological studies in other environments. Tidal mixing and vegetation heterogeneity complicate the examination of plant-pollen relationships and the identification of modern analogs. This study demonstrates the success and limitations of palynological studies.

The investigation of plant-pollen relationships illustrates how contributions from local, regional, and extra-regional sources to wetland pollen spectra vary across the marsh surface in a predictable manner as a function of flooding frequency. The surface samples in this study show that there is considerable variability (i.e., local signal dominates) and relative contributions of regional and extra-regional pollen sources vary as a function of elevation, hence vegetation zone, resulting in differential over- and under-representation of most salt marsh plants along an elevation gradient. With the exception of Poaceae and Cheno Am, this does not limit the establishment of plant-pollen relationships. With respect to modern analogs, heterogeneity within a zone means that all samples do not look alike and cannot be consistently separated from

other vegetation zones, however, most have a greater affinity to at least one other sample from the same zone than another zone.

Contrary to past salt marsh studies, this research has demonstrated that in these northern salt marshes, wetland pollen spectra reflect vegetation zones. Dissimilarity results suggest that the proportion of *Plantago* pollen and the differential contribution of extra-regional sources with elevation are such that most vegetation zones can be separated on the basis of their pollen spectra and these zones can be tracked with a high degree of certainty using conservative threshold criteria (coefficient <0.10). The uppermost vegetation can be tracked with the most certainty, thus paleo-ecological reconstructions of marsh environments can track the marsh-terrestrial interface throughout a core. Regression results show that these reconstructions reflect fine-scale vegetation patterns (i.e., patches) and suggest that these patches have meaning in the context of the marsh ecosystem. The modern analogs identified in this study encourage the identification of additional analogs that together will provide a foundation for quantitative salt marsh reconstruction in northern salt marshes and further the understanding of these dynamic coastal ecosystems.

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Appendix 1. Pollen counts and sample identification information for 33 surface samples (and 2 core samples from Dipper Harbour) collected from Dipper Harbour, Chance Harbour, and Little Lepreau salt marshes, Bay of Fundy, New Brunswick, Canada.

Sample ID	Sample assemblage code	Lab ID	Location	Sample name	Zone ID	Zone description	*Cheno-Am*	*Cyperaceae*	*Glaux*	*Poaceae*	*Limonium*	*Ligusticum scothicum*	*Myriophyllum*	*Nymphaceae*	*Osmunda*	*Plantago*	*Polygonum*	*Potentilla*	*Ruppia*	*Sagittaria*	*Spergula type*	*Triglochin*	*Typha*	*Umbelliferae*	*Abies*	*Acer*	*Alnus*	*Ambrosia*	*Artemisia*	*Betula*	*Carya*	*Caryophyllaceae*
1	140	545	DH		E1	*S. alterniflora*	29	48	1	73	1	0	1	1	7	22	1	0	3	2	3	129	0	0	21	12	99	8	1	308	1	4
2	415	546	DH		E6	*S.patens*	13	8	30	82	0	0	0	0	3	77	0	8	4	0	3	74	0	0	34	8	19	10	0	71	0	0
3	215	547	DH		E9	*Plantago*	18	3	3	71	0	0	0	0	0	171	1	1	0	2	0	38	1	0	8	1	21	3	0	80	0	0
4	210	581	DH		E2	E2	14	7	3	36	0	0	0	0	4	9	0	2	0	0	1	16	1	0	13	4	30	4	0	176	0	0
5	220	582	DH		E3	E3	4	137	8	56	0	0	1	0	1	92	0	0	0	0	0	25	1	0	13	6	33	3	0	58	0	1
6	155	583	DH		E4	*S. alterniflora*	34	28	0	69	0	1	2	0	7	73	1	1	0	2	0	133	0	0	43	5	45	4	0	189	0	2
7	225	584	DH		E5	*Plantago*	6	4	2	1	0	0	0	0	3	130	0	0	0	0	0	183	0	0	8	4	16	1	0	57	0	0
8	230	585	DH		E7	*Plantago*	16	15	6	23	0	1	0	0	0	73	1	0	0	0	0	25	1	0	8	4	16	0	1	38	1	0
9	345	590	DH		E15	E15	2	19	57	32	0	1	0	0	0	10	0	0	0	0	0	35	2	0	8	3	24	1	0	78	0	0
10	420	594	DH		E11	Core site (*S. patens*)	6	194	27	63	0	0	0	0	1	9	0	0	0	0	0	22	0	0	15	4	23	4	0	78	0	0
11	235	1398	CH	*Cheno Am*	*4*	*Plantago/ S.alterniflora*	54	8	2	67	0	0	2	0	3	61	0	1	1	0	2	109	0	0	5	10	36	6	0	205	2	3
12	355	1402	CH	*Cyperaceae*	*6*	Cyperaceae/ *Triglochin*	3	183	12	96	0	0	1	0	1	14	0	5	0	0	0	52	0	0	4	9	11	5	1	93	3	2
13	365	1403	CH	*Glaux*	*2*	*J. gerardii*	36	11	22	78	0	0	0	0	0	147	1	4	1	0	1	20	0	0	1	6	40	1	0	152	4	0
14	275	1394	CH	*S. patens*	*3*	*S. patens*	52	9	3	59	0	0	0	0	4	208	0	4	0	0	2	36	0	0	8	11	31	2	0	107	0	0
15	240	1393	CH	*Limonium*	*i2*	*Plantago*	31	1	3	202	3	0	1	0	0	363	1	25	0	0	0	27	0	0	7	4	26	3	0	144	1	0
16	640	1396	CH	*Ligusticum scothicum*	*5*	*J. balticus*	12	10	3	255	0	55	3	0	6	15	0	10	0	1	4	13	2	0	23	10	65	32	1	207	0	1
17	245	1401	CH	*Plantago*	*i2*	*Plantago*	13	8	0	94	0	0	0	1	2	179	2	2	0	0	0	57	0	0	2	3	22	1	0	67	1	0
18	645	1395	CH	*Potentilla*	*5*	*J. balticus*	9	15	8	190	0	0	0	0	1	18	2	24	0	0	2	37	0	0	17	12	24	10	3	121	2	0
19	250	1400	CH	*Ruppia*	*4*	*Plantago/ S.alterniflora*	20	5	0	65	0	18	1	0	2	45	1	0	159	0	1	29	0	10	4	5	73	5	0	249	1	1
20	255	1397	CH	*Spergularia*	*4*	*Plantago/ S.alterniflora*	16	13	3	115	0	17	1	0	4	47	5	1	2	6	10	61	1	13	35	3	99	1	1	367	1	0
21	260	1399	CH	*Triglochin*	*4*	*Plantago/ S.alterniflora*	13	3	1	42	0	0	0	0	0	88	0	1	0	0	1	245	0	0	1	1	9	0	1	46	1	0
22	280	1414	LL	*Cheno Am*	*6*	*S. patens*	55	13	11	52	0	0	3	0	3	60	0	4	3	0	0	19	1	1	9	3	65	3	0	407	2	0
23	545	1409	LL	*Carex*	*2*	*J. gerardii*	30	89	6	87	0	0	2	0	1	29	0	1	0	0	0	57	0	0	10	6	40	3	1	211	0	0
24	555	1406	LL	*Glaux*	*8*	*J. gerardii/ Glaux*	2	1	129	122	0	0	1	0	1	30	0	0	0	0	0	68	0	0	3	6	6	3	0	97	0	0
25	160	1407	LL	*S. alterniflora*	*4*	*S. alterniflora*	24	29	8	145	0	0	1	0	3	50	0	2	31	0	0	25	0	0	10	7	52	11	0	204	1	1
26	435	1404	LL	*S. patens*	*6*	*S. patens*	14	2	59	153	0	0	0	0	0	44	0	1	0	0	0	65	0	1	6	6	39	2	0	167	1	3
27	560	1405	LL	*Limonium*	*8*	*J. gerardii/ Glaux*	8	5	86	81	19	0	0	0	4	171	0	1	0	0	1	13	0	3	6	5	22	4	0	80	0	1
28	655	1412	LL	*Ligusticum scothicum*	*1*	*J. balticus*	12	0	13	273	0	55	0	0	0	16	0	4	0	0	0	11	0	0	4	0	6	1	1	52	0	0
29	265	1413	LL	*Plantago*	*3*	*Plantago*	133	4	19	74	0	0	0	0	1	194	1	7	0	0	0	35	0	0	3	2	35	1	1	108	0	0
30	660	1411	LL	*Potentilla*	*1*	*J. balticus*	86	0	0	169	0	14	1	0	0	18	0	44	0	0	0	26	0	0	0	2	8	5	0	38	0	0
31	165	1415	LL	*Ruppia*	*4**	*S. alterniflora*	10	52	2	160	0	0	3	0	1	44	4	3	106	0	0	25	1	0	2	4	45	6	0	165	1	1
32	370	1408	LL	*Spergularia*	*3*	*Plantago*	56	10	36	78	0	0	0	0	0	136	0	1	0	0	2	6	0	0	8	3	36	1	1	136	0	0
33	285	1410	LL	*Triglochin*	*2*	*J. gerardii*	47	5	5	39	0	1	0	0	1	69	1	2	0	0	0	151	0	0	140	0	9	2	1	88	1	0
34	440	719	DH	Bs core; 1.2 cm	C1	*S. patens*	8	4	0	17	0	0	1	0	0	7	0	0	0	0	0	5	0	9	2	3	19	4	0	74	0	0
35	445	748	DH	A core; 1.4 cm	B3	*S. patens*	25	6	0	31	0	0	1	0	0	41	0	0	0	0	0	11	0	0	8	2	6	6	0	42	0	2

App. 1 (cont). Pollen counts and sample identification information for 33 surface samples (and 2 core samples from Dipper Harbour) collected from Dipper Harbour, Chance Harbour, and Little Lepreau salt marshes, Bay of Fundy, New Brunswick, Canada.

Sample ID	Sample assemblage code	*Celtis*	*Compositae-liguliflorae*	*Compositae-tubuliflorae*	*Corylus*	*Daphne*	*Ericaceae*	*Fagus*	*Fraxinus*	*Ilex*	*Juglans*	*Larix*	*Lycopodium*	*Morus/ Urtica*	*Myricaceae*	*Nyssa*	*Ostrya/ Carpinus*	*Picea*	*Pinus*	*Pinus strobus*	*Polypodium*	*Quercus*	*Ranunculus type*	*Rhinanthus*	*Rosaceae*	*Rubus*	*Rumex*	*Salix*	*Sorbus*	*Sphagnum*	*TCT*	*Tsuga*	*Ulmus*	*monolete-psilate*	*trilete*	*Monotropa*	*Equisetum*	*Agosera*	*Colchicum autumnale*	*Primula*	*Rhus*	*Sambucus*	*Stellaria*	*Thuja*
1	140	0	2	10	38	0	2	7	4	0	0	1	36	0	22	1	3	1260	212	22	4	7	12	0	1	0	6	3	0	24	46	64	0	83	18	0	4	0	1	0	0	0	0	0
2	415	0	0	2	22	0	0	0	6	0	0	0	34	0	1	0	0	384	95	3	1	9	5	0	3	0	0	0	0	7	18	23	0	17	12	0	0	2	0	0	0	0	0	3
3	215	0	0	3	30	0	0	3	7	0	0	0	12	1	1	1	1	184	104	4	0	14	2	3	0	0	0	0	0	2	5	13	2	13	8	0	0	1	0	0	0	0	1	0
4	210	0	1	7	9	0	0	5	7	0	0	2	12	0	6	0	1	296	56	0	0	7	5	0	0	0	1	0	0	6	3	64	0	18	10	0	0	0	0	0	0	0	0	0
5	220	0	0	6	1	0	0	4	2	0	0	0	18	0	1	0	0	198	87	1	4	4	1	0	0	0	0	0	0	3	7	24	0	11	3	0	1	0	0	0	3	0	0	0
6	155	0	1	9	20	0	3	1	8	0	0	0	11	0	7	0	3	346	114	4	0	7	9	1	0	0	3	0	0	7	5	37	0	20	6	0	1	0	0	0	2	0	0	0
7	225	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	102	73	0	0	4	0	0	0	0	0	0	0	0	0	28	0	7	3	0	0	0	0	0	0	0	0	0
8	230	0	0	3	2	0	0	2	2	0	0	3	4	0	3	0	1	269	94	0	1	6	3	0	0	0	0	0	1	0	5	12	0	20	4	0	0	0	0	0	0	0	0	0
9	345	0	0	2	3	0	0	0	12	0	0	0	5	1	0	0	0	106	29	0	0	1	0	0	0	0	0	0	1	0	2	11	0	10	3	0	0	0	0	0	15	0	0	4
10	420	0	0	3	0	0	0	0	2	0	0	0	7	0	2	0	0	162	70	0	0	6	1	0	0	0	0	1	0	0	17	13	1	7	2	0	0	0	0	0	9	0	0	12
11	235	0	0	3	2	0	1	0	6	0	0	0	5	0	1	0	1	366	40	0	0	11	2	0	3	0	4	0	2	2	2	12	1	10	1	0	1	0	0	0	0	0	0	0
12	355	0	0	3	0	0	1	2	2	0	0	0	3	0	0	0	0	358	57	1	0	18	0	0	0	0	1	0	0	9	0	4	2	5	2	0	0	0	0	0	0	0	0	0
13	365	0	0	5	0	0	2	0	0	0	0	0	3	1	1	0	0	276	51	4	0	7	1	0	0	0	0	0	0	16	1	11	0	10	1	0	1	0	0	0	0	0	0	0
14	275	0	0	2	2	0	0	1	4	0	0	4	3	0	0	0	0	497	90	9	0	24	1	0	0	0	2	0	0	2	19	7	1	10	5	1	2	0	0	0	0	0	0	0
15	240	0	0	3	0	1	1	1	1	0	0	1	1	0	1	2	0	273	45	0	0	14	7	0	0	0	13	0	6	5	1	3	0	6	2	0	0	0	0	0	0	0	0	0
16	640	0	1	10	15	0	25	0	2	2	2	0	2	0	16	0	0	656	107	11	0	19	6	0	2	0	5	1	1	22	2	14	1	7	9	0	2	0	0	0	0	0	0	0
17	245	0	0	0	0	0	0	2	0	1	0	0	2	0	0	0	0	178	48	3	0	10	2	0	0	0	0	0	0	4	27	3	0	4	1	0	0	0	0	0	0	0	0	0
18	645	0	0	5	3	0	3	0	3	0	0	0	9	0	0	0	0	520	62	11	2	20	3	0	0	0	2	0	0	31	2	14	2	12	0	1	1	0	0	0	0	0	0	0
19	250	0	1	5	1	1	2	6	5	1	1	0	12	0	1	0	0	708	86	0	1	35	6	0	0	0	3	2	0	17	28	19	2	15	7	0	0	0	0	0	0	0	0	0
20	255	0	0	4	1	0	1	6	5	0	1	3	4	0	0	1	2	432	88	87	0	1	11	0	0	0	7	0	0	2	33	24	2	14	2	0	1	0	0	0	0	0	0	0
21	260	0	0	2	1	0	0	1	1	0	0	0	1	0	2	0	0	138	15	2	0	5	0	0	0	0	2	1	0	2	0	2	1	0	2	0	0	0	0	0	0	0	0	0
22	280	0	0	6	1	0	1	6	2	1	1	1	13	0	0	1	2	615	86	10	2	9	9	0	0	0	5	0	35	1	24	25	1	28	0	0	1	0	0	1	0	0	0	0
23	545	0	0	4	2	0	2	6	1	0	1	0	2	0	2	0	1	227	37	0	0	5	6	0	0	0	2	0	1	2	4	4	0	4	2	0	0	0	0	0	0	0	0	0
24	555	0	0	0	0	0	1	0	3	0	0	0	1	0	0	0	0	169	25	1	0	5	0	0	0	0	1	0	3	2	0	4	2	1	0	0	0	0	0	0	0	0	0	0
25	160	0	0	7	5	0	7	1	2	1	0	7	11	0	2	0	1	308	83	3	1	13	0	0	0	0	2	0	43	3	11	10	2	20	5	0	0	0	0	0	0	0	0	0
26	435	0	1	9	1	1	0	8	0	1	4	0	5	0	0	0	0	764	169	5	0	7	3	0	0	1	10	2	13	0	8	7	2	9	3	0	0	0	0	0	0	2	0	0
27	560	0	0	2	2	0	4	1	1	0	0	0	0	0	0	0	0	151	34	0	0	9	0	0	0	0	4	1	4	2	1	7	0	0	1	0	0	0	0	0	0	0	1	0
28	655	0	1	1	0	0	3	1	0	0	0	0	0	0	0	0	1	96	44	2	0	3	0	0	0	0	0	0	0	0	0	4	0	0	1	0	0	0	0	0	0	0	0	0
29	265	0	2	0	3	0	3	1	3	0	2	0	2	0	1	0	0	140	30	0	0	6	0	0	0	0	0	0	7	1	0	1	0	12	0	0	0	0	0	0	0	0	0	0
30	660	0	0	2	0	0	0	0	2	0	0	0	1	0	0	0	1	130	35	1	0	5	0	0	0	0	1	0	0	2	0	1	1	2	0	0	0	0	0	0	0	0	0	0
31	165	0	0	9	0	1	6	3	1	1	2	0	13	0	3	1	2	210	38	0	1	7	3	0	0	0	2	1	49	0	7	6	0	19	1	0	0	0	0	0	0	0	0	0
32	370	0	0	6	4	0	2	1	4	0	1	0	5	0	0	0	0	199	57	0	0	7	3	0	0	0	2	0	7	0	18	6	1	11	0	0	0	0	0	0	0	0	0	0
33	285	0	0	3	0	0	1	3	0	0	0	0	1	0	0	0	0	606	105	1	0	0	0	0	0	0	1	0	1	0	2	1	1	1	0	0	0	0	0	0	0	0	0	0
34	440	0	0	8	0	0	0	3	0	1	0	0	0	3	0	0	0	96	71	1	0	7	0	0	0	0	0	5	0	0	0	15	1	4	6	0	0	0	0	0	0	0	0	0
35	445	0	0	1	0	0	0	1	2	0	0	0	0	2	4	0	0	145	56	2	0	5	0	0	0	0	1	2	0	0	0	16	2	13	11	0	0	0	0	0	0	1	0	0

App. 1 (cont). Pollen counts and sample identification information for 33 surface samples (and 2 core samples from Dipper Harbour) collected from Dipper Harbour, Chance Harbour, and Little Lepreau salt marshes, Bay of Fundy, New Brunswick, Canada.

Sample ID	Sample assemblage code	*Tilia*	*Vitis*	*Indeterminate triporate*	*Indeterminate*	*unknown*	*hidden*	*TOTAL MARSH*	*TOTAL SUM*	*MARKER GRAINS*	*Operculodinium*	*Spiniferites sp.*	*unknown dinoflagellate cysts*	*total dinoflagellate cysts*	*forams (>3)*	*colony of freshwater algae*	*Botryococcus*	*Halodinium*	*Pediastrum*	*Cymatosphera*	*stomate*	*unknown palynomorphs:*	*(dark) inaperturate spheroidal*	*inaperturate spheroidal echin*	*other*
1	140	0	0	14	92	2	15	321	2791	582	383	84	1	468	60	0	0	7	1	4	0	0	0	3	0
2	415	0	1	1	32	8	2	302	1138	372	15	4	0	19	163	0	0	11	0	0	0	0	0	0	0
3	215	0	0	0	38	4	3	309	883	180	11	0	0	11	71	0	0	1	0	0	0	0	0	0	0
4	210	0	0	4	25	6	5	93	878	168	37	4	1	42	12	0	0	2	0	2	11	0	0	0	0
5	220	0	0	4	10	3	4	325	837	169	9	0	0	9	30	0	1	28	0	0	0	0	0	0	0
6	155	0	0	20	54	4	8	351	1346	289	125	21	1	147	56	1	0	0	0	0	0	0	0	2	0
7	225	0	0	0	3	2	0	329	641	77	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	230	1	0	1	22	4	8	161	699	205	19	6	0	25	35	0	1	2	0	0	1	0	0	0	0
9	345	0	0	0	17	11	0	158	506	184	2	0	0	2	7	0	0	0	0	0	0	0	0	0	0
10	420	0	0	2	31	8	7	322	809	155	4	1	0	5	24	0	0	15	0	0	0	0	0	0	0
11	235	0	0	5	45	5	3	310	1112	370	81	24	0	105	32	1	2	0	0	0	0	1	0	1	0
12	355	0	0	0	57	0	20	367	1040	151	18	5	0	23	19	0	1	0	0	0	4	0	0	0	0
13	365	0	0	0	50	0	34	321	1000	147	5	5	0	10	28	1	6	9	1	0	1	2	0	2	0
14	275	0	0	7	103	2	10	377	1344	247	94	10	0	104	46	0	2	0	0	3	1	0	0	0	0
15	240	0	0	4	55	2	9	657	1299	215	82	26	0	108	54	0	3	0	0	1	0	23	23	0	0
16	640	0	0	25	120	0	30	389	1843	316	7	0	0	4	51	0	2	0	0	1	12	387	387	0	1
17	245	0	0	1	80	0	5	358	825	121	81	14	0	95	53	0	0	0	2	1	0	1	0	1	0
18	645	0	0	16	71	0	31	306	1319	210	7	1	0	8	25	0	1	0	1	0	11	5	5	0	1
19	250	0	0	3	72	5	8	356	1747	466	141	31	0	172	6	1	0	1	0	2	0	4	0	3	1
20	255	0	0	2	46	1	18	315	1621	1122	54	8	0	62	108	0	1	0	0	0	0	0	0	0	0
21	260	0	0	1	31	0	3	394	666	91	49	12	0	61	12	0	4	0	0	1	3	4	0	4	0
22	280	0	0	1	56	3	15	225	1676	743	12	3	0	15	17	1	3	14	0	1	0	0	0	0	0
23	545	0	0	1	26	4	13	302	931	164	2	1	0	3	4	0	117	3	1	0	0	0	0	0	0
24	555	0	0	0	38	0	22	354	747	83	2	0	0	2	54	0	3	16	0	0	0	6	0	0	0
25	160	0	0	2	85	0	19	318	1258	379	10	2	0	12	9	12	44	4	1	0	1	0	0	0	0
26	435	0	0	3	83	1	19	339	1704	213	57	10	1	68	35	2	37	6	0	0	2	21	0	0	0
27	560	0	0	0	65	1	31	392	832	128	3	0	0	3	45	1	2	7	1	0	0	0	0	0	0
28	655	0	0	0	30	0	9	384	644	88	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
29	265	0	0	3	68	0	7	468	910	141	4	3	0	7	21	0	4	1	0	1	0	1	0	0	0
30	660	0	0	0	34	0	8	358	637	92	0	1	0	1	27	0	2	3	1	0	0	7	0	0	0
31	165	0	0	0	38	1	8	411	1068	377	13	1	0	14	6	8	5	5	0	1	0	0	0	0	0
32	370	0	0	0	60	1	7	325	912	205	1	2	0	3	46	0	11	4	1	0	0	0	0	0	0
33	285	0	0	1	50	1	24	321	1365	112	1	0	0	1	87	1	1	17	0	0	0	0	0	0	0
34	440	0	0	0	38	3	0	51	415	89	0	0	0	0	0	0	34	0	0	0	0	0	0	0	0
35	445	1	0	0	37	0	0	115	483	118	0	0	0	0	0	0	40	0	0	0	0	0	0	0	0