

Intertidal Diatoms from Willapa Bay, Washington: Application to Studies of Small-Scale Sea-Level Changes

Abstract

Sea-level reconstructions using estuarine diatoms are generally constrained by the absence of detailed ecological data regarding the distributions of modern intertidal species. As part of an on-going study to assess the biostratigraphic record of relative sea-level changes triggered by earthquakes in the Pacific Northwest, modern intertidal diatoms were collected in surface samples from northern Willapa Bay, Washington. Q-mode factor analysis was used to classify assemblages from tidal flats and banks, shallow subtidal channels, low and high marshes along two intertidal transects on the Niawiakum River, and in intertidal samples from the open bay. Autochthonous taxa dominated the assemblages, but in some cases probable allochthonous taxa scored relatively high in the factor analysis.

The results of the analysis suggests that diatoms can be used to identify three elevational zones relative to tidal level: (1) intertidal flats, channel banks, and shallow subtidal channels, below approximate mean lower high water (MLHW); (2) low marshes approximately between MLHW and mean higher high water (MHHW); and (3) high marshes approximately between MHHW and extreme high water (EHW). The marsh-upland transition, near FHW, coincides with the terminus of regular diatom productivity and is recognizable by the disappearance of high-marsh diatoms in soil deposits. Absolute elevations of the ecological zones are constrained by local tidal range. Because of the cosmopolitan distributions of many of the species observed in this study, these data are probably applicable to studies of Quaternary sea-level change and paleoseismicity throughout the coastal Pacific Northwest.

Introduction

The purpose of this study is to identify diatom taxa associated with vertically distributed estuarine deposits (i.e., high marshes, low marshes, tidal flats, sloughs, and banks) that can be used to reconstruct small-scale (< 3 m) paleo-sea-level changes related to paleoseismicity or eustatic processes in the Pacific Northwest. Transitions between marine and freshwater diatoms in coastal deposits are commonly used to identify major transgressions and regressions of Quaternary sea level (e.g., Palmer and Abbott, 1986; Eronen *et al.*, 1987), but the recognition of small-scale changes in paleo-sea-level must be based on more subtle changes in vertically distributed assemblages. Such studies are invariably hindered by the paucity of detailed data regarding the modern distributions of pertinent taxa (e.g., Eronen *et al.*, 1987).

Compelling stratigraphic evidence now suggests that some changes in relative sea-level in the Pacific Northwest during the Holocene may have resulted from large earthquakes, including a moment magnitude (M_w) > 8 event as recently as about 300 years ago (Atwater, 1987, 1992; Darienzo and Peterson, 1990; Atwater and Yamaguchi, 1991; Atwater *et al.*, 1991; Nelson, 1992; Clarke and Carver, 1992; Nelson and Personius, in press; Clague and Bobrowsky, 1994). Some of the paleo-earthquakes have been attributed to rupture

along the Cascadia subduction zone, the boundary between the Juan de Fuca plate and the over-riding North America plate (Figure 1), whereas others are believed to have been caused by displacements on shallow crustal faults (Nelson, 1992; Bucknam *et al.*, 1992; Nelson and Personius, in press). Coseismic land-level changes may result in sudden subsidence (e.g., Plafker, 1969; Atwater, 1987; 1992; Darienzo and Peterson, 1990; Nelson, 1992; Clarke and Carver, 1992) or uplift (Plafker, 1969; Bucknam *et al.*, 1992) of coastal and estuarine sites. The ecological consequences involve either a rapid rise or fall in relative sea level such that vegetated areas normally above the reach of tides are suddenly inundated, or conversely, normally intertidal surfaces are elevated out of the intertidal zone. Estimates of coseismic subsidence caused by the earthquake about 300 years ago range from about 0.5 m (Clarke and Carver, 1992; Darienzo and Peterson, 1990) to 2 m (Atwater, 1987; Atwater and Yamaguchi, 1991). This range in elevational change would be enough to quickly transform a lowland coastal meadow or forest into a tidal flat. Based on stratigraphic and biostratigraphic evidence in southwestern Washington, this process may have been repeated at least six times in about the last 3500 years (Atwater, 1988; Hemphill-Haley, unpub. data).

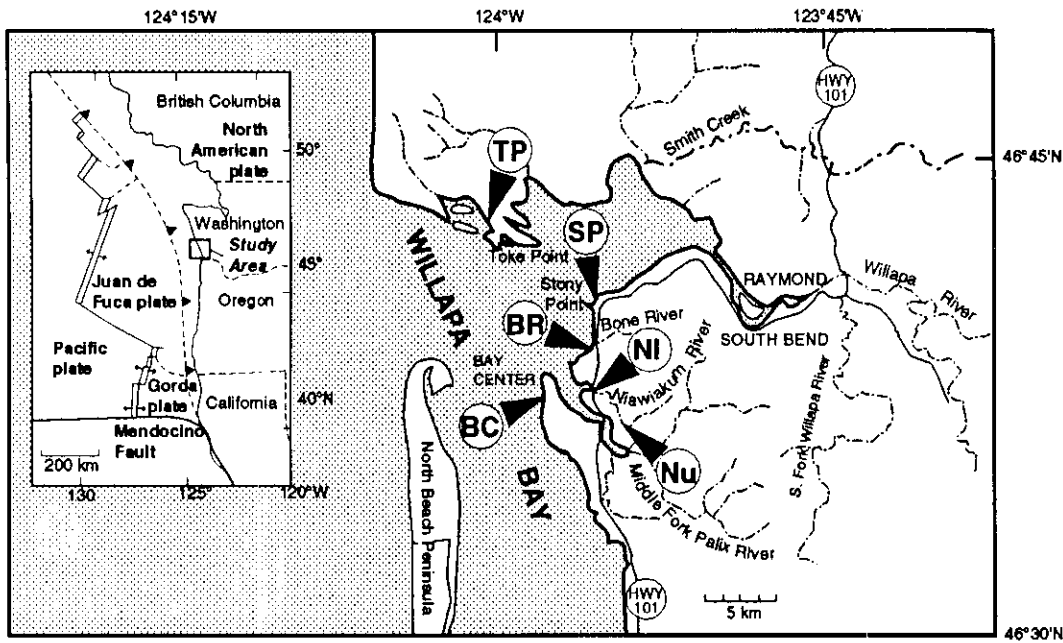


Figure 1. Willapa Bay, a mesotidal estuary in southwestern Washington. Sampling localities: BC—Bay Center tidal flat; BR—Bone River tidal flat; NI—transect NI, lower Niawiakum River; SP—Stony Point; Nu—transect Nu, upper Niawiakum River; TP—Toke Point.

Various kinds of coastal environments can be identified based on the classification of diatoms into ecological groups (Vos and de Wolf, 1988; 1993; Kosugi, 1988). In this paper, Q-mode factor analysis is used to cluster samples with similar diatom assemblages from the modern surfaces of tidal flats, intertidal river banks, shallow subtidal channels, low marshes, and high marshes in northern Willapa Bay, Washington (Figure 1). Upland samples, found to be barren of *in situ* diatoms, were excluded from the factor analysis.

Studies of modern estuarine diatoms have shown that many taxa are cosmopolitan (i.e., have a worldwide distribution) (McIntire and Moore, 1977; Tynni, 1986) and usually exhibit broader tolerances for salinity (Moore and McIntire, 1977; McIntire, 1978; Amspoker and McIntire, 1978; Admiraal, 1979) than for other factors such as exposure (Castenholz, 1963; Sullivan, 1978) and substrate (Amspoker and McIntire, 1978; Whiting, 1983; Whiting and McIntire, 1985; Kosugi, 1987). A series of ecological studies in Oregon documented the modern vertical distributions of attached or sediment-associated species in the lower part of the intertidal zone (Castenholz, 1963;

Riznyk and Phinney, 1972; Riznyk, 1973; Main and McIntire, 1974; Moore and McIntire, 1977; Amspoker and McIntire, 1978), but other than Nelson and Kashima (1993), differences in assemblages between tidal flats, marshes, and uplands have not been documented, and there are no such previous studies for coastal southwestern Washington.

Background

General Ecological Zonation Relative to Tidal Level

The mixed tides of the Pacific coast along southwestern Washington cause a fairly predictable three-tiered intertidal zonation, with lower intertidal flats, "low" marshes, and "high" marshes (Macdonald, 1977a; Macdonald and Barbour, 1977; Frey and Basan, 1985). The elevational ranges of these zones depends on the local tidal range, which varies both along the coast in the Pacific Northwest and within individual estuaries. In Willapa Bay, the tidal range between mean high water (MHW) and mean low water (MLW) ranges from 2.3 m near the mouth of the estuary to 3.4 m at its southernmost reaches (Major, 1989).

The initiation of low marsh vegetation in the Pacific Northwest is approximately equivalent to the elevation of mean lower high water (MLHW) (Macdonald and Barbour, 1977) and extends to approximately mean higher high water (MHHW), although vegetation is generally thicker between mean high water (MHW) and MHHW. Low marshes are commonly submerged once each tidal day (Frey and Basan, 1985) and thus support macrophytes capable of regular submergence. Sayce (1988) listed the dominant low-marsh macrophytes in Willapa Bay as *Salicornia virginica*, *Jaumea carnosa*, *Triglochin maritima*, and *Plantago maritima*. High marshes extend from MHHW to near extreme high water (EHW) (Macdonald and Barbour, 1977) and are submerged only during highest spring tides and storm surges. According to Frey and Basan (1985), high marshes are prone to desiccation because they "may remain continuously exposed for periods exceeding 10 days, between tidal inundations." Typical high-marsh macrophytes of Willapa Bay include *Distichlis spicata*, *Deschampsia caespitosa*, and *Agrostis alba*, with *Juncus balticus* and *Potentilla pacifica* at the highest levels (Sayce, 1988).

Tidal flats of the open estuary and channel banks of tidal rivers feeding the estuary extend downward from MLHW to approximately mean lower low water (MLLW). These flats and banks comprise a broad, mostly unvegetated region populated primarily by sediment-associated diatoms (Riznyk, 1973; Rao and Lewin, 1976; Amspoker and McIntire, 1978). *Zostera* spp. (eelgrass) beds may be present to provide a substrate for epiphytic diatoms, with *Z. marina* commonly found near MLLW and *Z. nana* found in the upper part of the zone, closer to MLHW. Shallow subtidal channels, as used in this study, refer to the river-channel floor less than 4 m below MLLW, which were sampled to determine whether this zone could be differentiated from the lower intertidal zone. As shown below, diatoms consist dominantly of allochthonous valves from the lower intertidal zone.

Methods

Sample collection

Results are based on diatom counts for 89 surface samples collected in 1990 in northern Willapa Bay (Figure 1). Samples BC-1, BC-2, and BC-3, from the Bay Center sand flat, were collected approxi-

mately 800, 500, and 200 m from shore, respectively. The flat is vegetated with sparse *Zostera nana* at the locations of samples BC-2 and BC-3. Samples BR-1 and BR-2 were collected from the unvegetated surface of a silty tidal flat north of the Bone River, approximately 150 and 300 m from shore. Samples were collected from the marsh and adjacent tidal flat at Stony Point: SP-1 and SP-2 are from the unvegetated flat; SP-3 is from the flat adjacent to a patch of *Triglochin maritima*; SP-4 is from a low marsh thickly vegetated with *Triglochin maritima* and *Salicornia virginica*; and SP-5 is from a high marsh in a thick stand of *Potentilla pacifica*, 3 m from the base of a Pleistocene terrace. Samples were collected from a marsh and tidal slough at Toke Point: TP-1 is from the floor of a sandy tidal slough covered with *Zostera marina* beds; TP-2 from a 1-m-diameter patch of *Triglochin maritima* at the marsh-to-flat transition; and TP-3 is from the low marsh thickly vegetated with *T. maritima* and *S. virginica*.

Samples from two intertidal transects along the Niawiakum River (N1 and Nu) were analyzed in addition to the intertidal samples from the open bay. Transect N1 extends from the channel floor to the transition from marsh to forested upland in the lower Niawiakum River valley (Figure 1, 2). The channel floor is approximately 3.5 m below MLLW, and the marsh-upland transition is estimated at 3.4 m above MLLW. Sampling station N1-1 is just below MLLW on a steep part of the channel bank thickly vegetated with *Zostera marina*. N1-2 is on an unvegetated area of the channel bank, and sparse *Z. nana* is growing at the level of sampling station N1-3. N1-4 is on a steep marsh scarp vegetated with *Salicornia virginica* and rare *Triglochin maritima*. N1-5, N1-6, and N1-7 are on a gently-sloping high marsh surface, and dominant macrophytes are *Distichlis spicata* and *Salicornia virginica* at N1-5, and *Deschampsia caespitosa* and *Potentilla pacifica* at N1-6 and N1-7. N1-8 is at the landward edge of the marsh, vegetated by *Carex obtusa* and *Achillea* sp.

Transect Nu extends from the channel floor to the highest part of a brackish marsh in the upper Niawiakum River valley (Figures 1, 3). The floor of the channel is graded to near MLLW, and the highest part of the marsh is estimated at 3.2 m above MLLW. Sampling station Nu-1 is on the unvegetated lower part of the channel bank. Nu-2 is just below the lower limit of vegetation. Nu-3 is on the steep marsh scarp vegetated with *Carex*

Transect NI - lower Niawiakum River

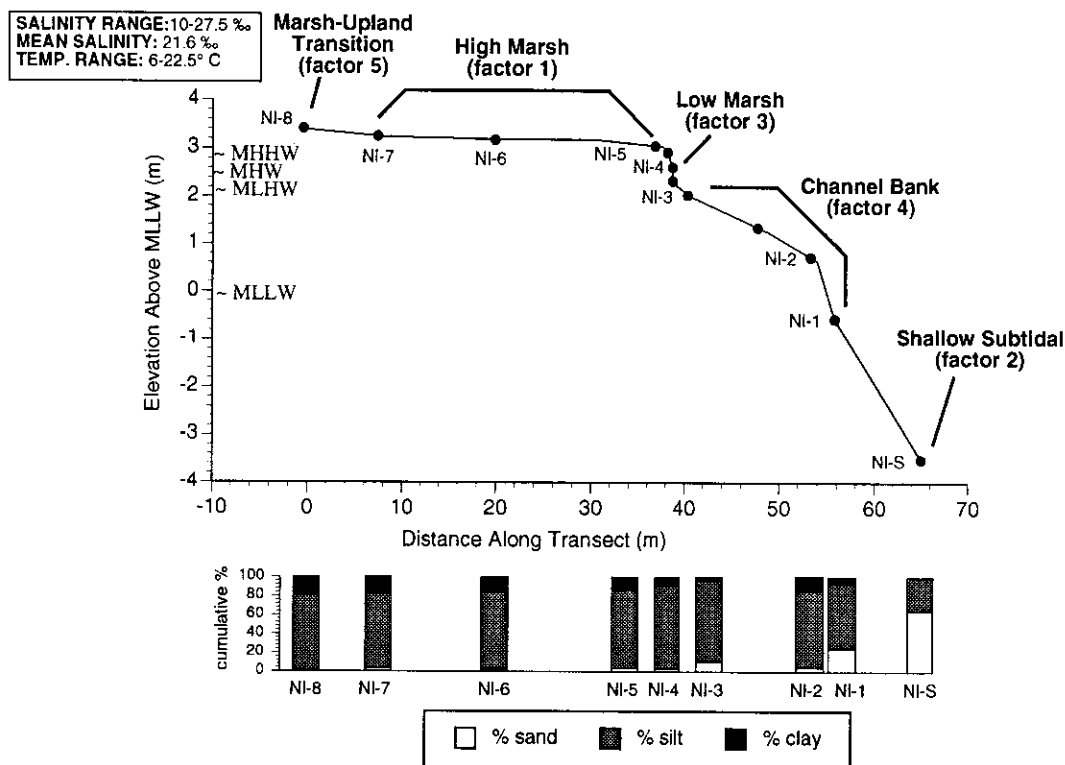


Figure 2. Profile along transect NI, on the lower Niawiakum River. Grain size, salinity, and temperature measurements are for 1990; estimated error for tidal datums is ± 0.10 m.

lyngbei and rare *Triglochin maritima*. Nu-4 is near MHHW, and dominant macrophytes are *Distichlis spicata* and *Deschampsia caespitosa*, with rare *C. lyngbei*. Nu-5, Nu-6, and Nu-7 are on the gently sloping marsh surface where the dominant macrophytes are *D. caespitosa* and *Potentilla pacifica*; Nu-8 is at the highest point on the marsh where the dominant macrophytes are *Juncus balticus* and *P. pacifica*.

Relative elevations along transects Nu and NI were measured with a self-leveling level, which is accurate to ± 1 cm for both horizontal and vertical distances. Tidal datums (Figures 2, 3) were estimated to be within ± 10 cm based on 6 observations of water levels at high and low tides during good weather, and comparison with tidal charts corrected for tidal variation in the estuary (Pacific County Planning Department, written comm., 1990). Diatom and grain-size samples were collected, and dominant macrophytes were

recorded, in April 1990 at eight sampling stations along each transect. Additional diatom samples were collected at the stations in July, September, and December 1990 to test for seasonal variation in diatom distributions. Preliminary analyses showed that relative abundances of species varied among samples collected during different times of the year, but distributions remained constant throughout the year. Therefore, the seasonal counts were combined for this report. Samples from the shallow subtidal channel of the Niawiakum River were collected by using a small dredge deployed from a canoe during low tide.

Diatom samples consisted of about 1 cm^3 of the uppermost 1-2 mm of surface sediment, scraped with a small spatula from and placed in buffered 2% formaldehyde in a glass vial. All modern intertidal surface samples collected in Willapa Bay contained abundant diatoms, some exceeding 5×10^5 cells/ cm^3 . Many of the most prolific species,

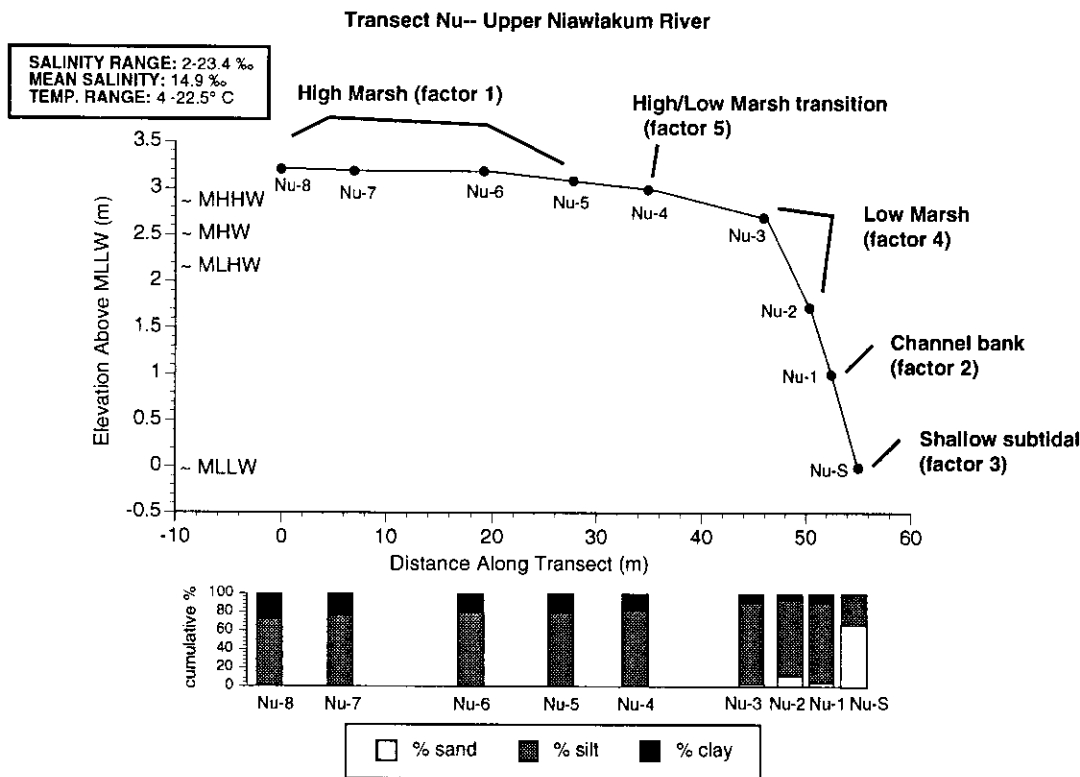


Figure 3. Profile along transect Nu on the upper Niawiakum River. Grain size, salinity, and temperature measurements are for 1990; estimated error for tidal datums is ± 0.10 m.

however, are delicate (e.g., small *Navicula* and *Achnanthes*) and have little chance of surviving in the fossil record. The disparity between the types of marine planktonic diatoms observed in productive surface waters (e.g., *Chaetoceros* spp., *Skeletonema* spp.) and taxa that actually survive dissolution and burial to become fossils (e.g., *Thalassionema* spp. and *Coscinodiscus* spp.) is well known. The same applies to benthic estuarine diatoms, such that many of the most prolific taxa make poor fossils (e.g., *Melosira* spp. and *Synedra* spp.), whereas some of the rarer diatoms in modern deposits (*Caloneis* spp., *Campylodiscus* spp.) may become, by virtue of their resilience to destruction, dependable fossils. Therefore, the factor analysis focused on the modern distributions of 84 diatom taxa that were also observed in Holocene fossil deposits around Willapa Bay (Hemphill-Haley, 1993a and unpub. data).

Macrophyte samples were also collected for qualitative assessment of epiphytic populations; references to an epiphytic life form for individual

species are based on these observations and the detailed analyses by Whiting (1983) and Main and McIntire (1974). Diatoms collected in the field (excluding Toke Point samples that dried out) were stained for evidence of intact cytoplasm with Fast Green FCF cytoplasm stain in buffered 2% formaldehyde, and mounted according to the Taft Syrup Mount (TSM) method (Taft, 1978; Stevenson, 1984). The refractive index of the TSM is sufficient for resolving the valve characteristics of most diatoms, although the fine structure of some delicate species (which are typically absent in fossil deposits) may not be resolvable. Stained samples can be rinsed, dried onto a cover slip, and mounted with Hyrax, which improves resolution of valve characteristics.

At least 400 diatom valves were counted at 625x along random vertical traverses near the middle of the cover slip, with magnifications increased to 1250x to examine smaller specimens (Hemphill-Haley, 1993a). Intact frustules were counted as two valves. For the factor analysis, total counts of

live plus empty frustules and single valves were used to allow for occurrences of both autochthonous and probable allochthonous diatoms, as would naturally occur in fossil assemblages. References to the relative abundances of diatoms are based on the percentage of each species relative to the total number of diatoms counted in each sample, normalized by dividing several dominant species (*Melosira moniliformis*, *M. nummuloides*, *Synedra fasciculata*, and *Paralia sulcata*) by an arbitrary factor of 10: very rare = < 2%; rare = 2-4.9%; frequent = 5-9.9%; common = 10-33%; abundant = > 33%.

Grain size analyses of Nu, NI, BC, and BR samples were completed with a Cimax Hydrophotometer and Rapid Settling Analyzer (RSA).¹ Calibration tests indicate that the hydrophotometer is precise to $\pm 3\%$ and the RSA to $\pm 5\%$ (Torresan, 1987). Sediment textures SP and TP samples were estimated in the field. Water temperature and salinity data along transects Nu and NI were collected from the adjacent channel near the surface at high tide using a YSI Model 33 S-C-T meter with reported accuracies of $\pm 0.5^\circ\text{C}$ and ± 0.5 ppm, respectively. Salinity data for the open bay were provided by the Washington Department of Fisheries Laboratory at Nahcotta. Data used for this study (diatom counts and taxonomy, grain-size results) are also available in U.S. Geological Survey Open-File Reports (Hemphill-Haley, 1993a, b).

Statistics

The program CABFAC was used to generate a Q-mode factor analysis (Klovan and Imbrie, 1971) to identify end-member groups of surface samples from three data sets: (1) transect NI; (2) transect Nu; and (3) the four sampling localities bordering the open bay. Variables for the factor analysis consist of 84 taxa observed in the modern samples that were likewise observed in fossil samples from Willapa Bay. Some varieties of species were included with the nominate forms where both were observed to commonly co-occur, including varieties of *Achnanthes brevipes*, *A. hauckiana*, *A. lanceolata*, *Frustulia vulgaris*, and *Navicula lyra*. The *Actinoptychus* spp. group includes *A. senarius* and *A. splendens*, and the *Odontella* spp. group includes

O. aurita and *O. obnuta*. Small forms of *Paralia sulcata* (less than 20 μm diameter) were counted separately from large forms because of evidence that valve size may be ecologically controlled (Roelofs, 1984) and observations that small forms are more widely distributed in lower-salinity areas of the estuary (Hemphill-Haley, 1993a).

The results of the factor analysis are based on the relative abundances of diatom taxa in each sample. Beginning with the raw census-data matrix [X] of n entities (i.e., samples) and m variables (i.e., taxa), value counts were transformed to the percentage of the range of total numbers for each variable, thereby giving as much weight to rare species with limited distributions as to common species that are particularly dominant in certain localities. The varimax rotation method was used to simplify the interpretation of factor loadings (i.e., the contributions of each sample to the factors). The varimax factor-loading and factor-score matrices provided by CABFAC list the contributions of each sample and each taxon to the factors, respectively. Taxa with the highest factor scores are indicative of the modern environment in which they are found either because of their restricted distribution or their particular abundance in that environment. The factor assemblages in this report include both autochthonous and suspected allochthonous species and show the influence of resuspension and mixing of diatom assemblages in the intertidal zone. For the analyses, the lowest number of factors explaining at least 75% of the variance was used. The sharp break from relatively high to low factor scores was used to separate important from extraneous taxa comprising each factor.

Results

Lower Niawiakum transect (NI)

Salinities ranged from 10‰ to 27.5‰ at transect NI, with a mean of 21.6‰ (Figure 2). A five-factor model (Figure 4) identified the marsh-upland transition (NI-8; Factor 5), high marsh (NI-5 to NI-7; Factor 1), low marsh (NI-4; Factor 3), channel bank (NI-1 to NI-3; Factor 4), and shallow channel (NI-S; Factor 2). Of the 84 species and groups considered in this study, 77 were observed along this transect, and 57 scored high in the factor analysis. The five-factor model explains 78% of the total variance, or 88% of the data (Table 1).

Marsh-upland transition—Factor 5 (Figure 4e). Important autochthonous diatoms include *Denticula*

¹Any use of trade, product, or firm names in this report is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Transect NI: Factor Scores

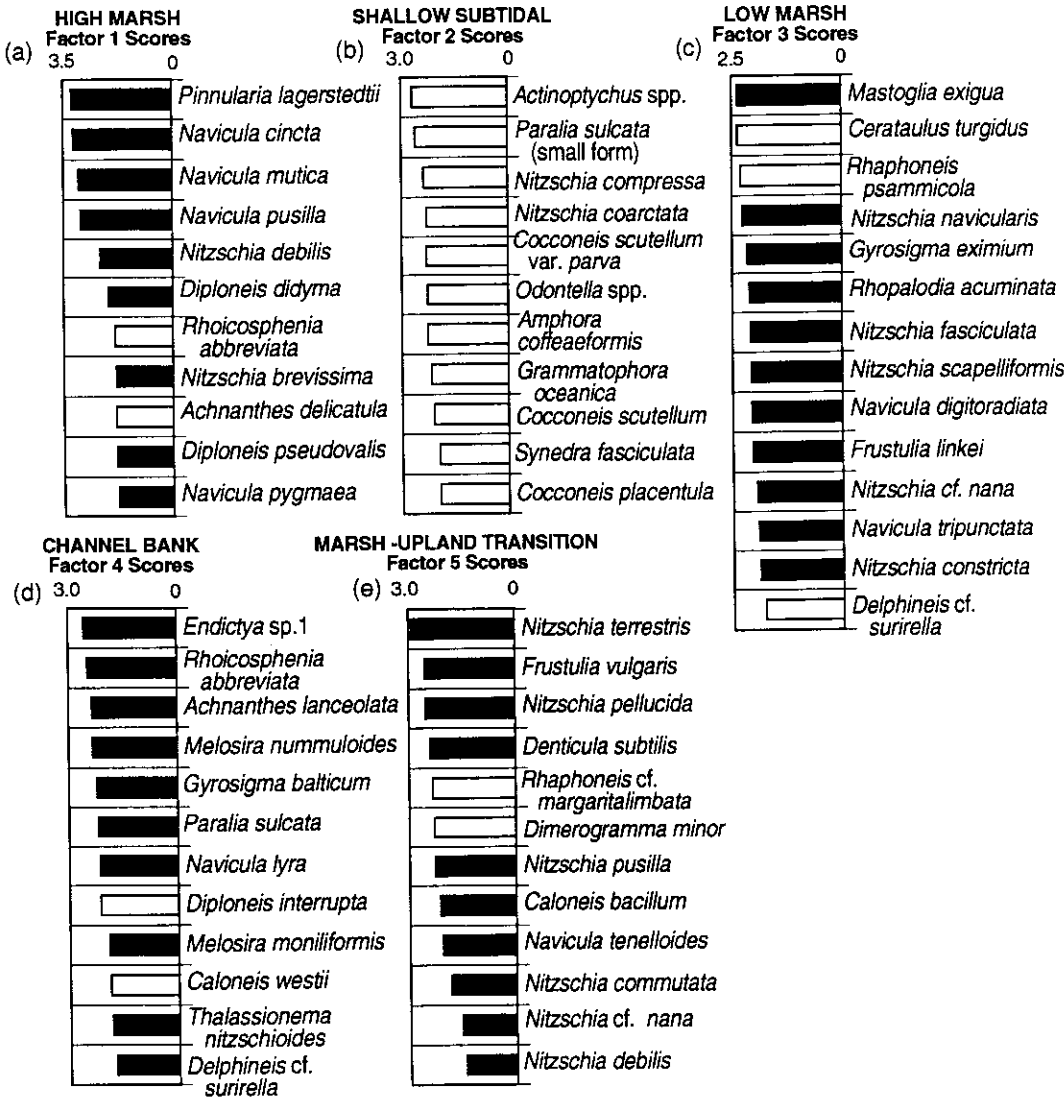


Figure 4. Factor scores along transect NI for autochthonous species (black bars) and suspected allochthonous species (white bars).

subtilis, *Nitzschia pusilla*, and *Navicula tenelloides*. *Nitzschia terrestris* was rare but scored high in the factor analysis because of its limited distribution. *Nitzschia commutata*, *Frustulia vulgaris*, *Caloneis bacillum*, *Nitzschia cf. nana*, and *Nitzschia debilis* are found in both low and high marshes. Allochthonous diatoms include very rare valves of *Raphoneis cf. margaritalimbata* and *Dimerogramma minor*.

High marsh—Factor 1 (Figure 4a). Autochthonous diatoms that can be used to define the high marsh include *Pinnularia lagerstedtii*, *Navicula pusilla*, and *Nitzschia brevissima*. *Navicula cincta*, *Navicula mutica*, *Diploneis pseudovalis*, *D. didyma*, and *N. debilis* are distributed in high and low marshes. Allochthonous diatoms include very rare valves of *Rhoicosphenia abbreviata* and *Achnanthes delicatula*. *Navicula pygmaea* is also very rare, and its significance is uncertain.

TABLE 1. Factor loadings for sampling stations along transect N on the lower Niawiakum River. Boldface numbers denote defining factors for each sampling station.

Station	communality	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Nl-S	0.884	0.077	0.925	0.021	-0.121	-0.086
Nl-1	0.669	-0.002	0.616	0.112	-0.515	-0.111
Nl-2	0.747	0.146	0.180	-0.025	-0.832	-0.029
Nl-3	0.529	0.094	0.457	0.258	-0.472	-0.148
Nl-4	0.781	0.155	0.090	0.860	-0.039	-0.086
Nl-5	0.769	0.658	-0.049	0.108	-0.291	-0.487
Nl-6	0.874	0.919	0.069	0.135	-0.081	0.000
Nl-7	0.804	0.820	0.046	0.090	-0.024	-0.347
Nl-8	0.925	0.278	0.181	0.080	-0.056	-0.897
	variance	23.186	16.963	9.61	14.344	13.477
	cumulative variance	23.186	40.148	49.759	64.103	77.58

Low marsh—Factor 3 (Figure 4c). Autochthonous diatoms that identify the low marsh include *Gyrosigma eximium* (common to abundant), *Nitzschia navicularis*, *Nitzschia scalpelliformis*, and *Frustulia linkei*. *Mastogloia exigua* may be primarily a low-marsh species, but it was also observed on the adjacent channel bank (Nl-3). It is frequent in low-marsh samples from Toke Point. *Rhopalodia acuminata*, *Navicula digitoradiata*, and *Nitzschia constricta* are found in both low marshes and adjacent flats, and *Nitzschia fasciculata* and *N. cf. nana* are found in low and high marshes. Allochthonous diatoms include very rare valves of *Cerataulus turgidus*, *Rhaphoneis psammicola*, and *Delphineis cf. surirella*.

Channel bank—Factor 4 (Figure 4d). Autochthonous channel-bank diatoms include *Melosira moniliformis*, *M. nummuloides*, and *Paralia sulcata*; *Gyrosigma balticum*, *Navicula lyra*, and *Endictya* sp. 1 (Hemphill-Haley, 1993b) are rare but scored high in the factor analysis because of their limited distribution. *R. abbreviata* and *Achnanthes lanceolata* are indicative of channel banks in less saline areas of northern Willapa Bay (Hemphill-Haley, 1993a), and may indicate periods of low-salinity runoff at this site. *Thalassionema nitzschioides* is a widely distributed marine neritic diatom (Cupp, 1943), but was also recorded by McIntire and Overton (1971) in attached lower intertidal samples in Yaquina estuary (Oregon). Allochthonous diatoms probably include rare valves of *Diploneis interrupta*, which was frequent in the transitional marsh at transect

Nu, and rare valves of *Caloneis westii*, which was frequent in the low marsh at Toke Point and Stony Point.

Shallow subtidal zone—Factor 2 (Figure 4b). By definition, all diatoms from the high-energy river channel are allochthonous (Vos and de Wolf, 1988). Species that scored high in the factor analysis consist of lower-intertidal epiphytes (*Grammatophora oceanica*, *Cocconeis scutellum*, *C. scutellum* var. *parva*, *Synedra fasciculata*), epipelton (*Nitzschia compressa*, *Nitzschia coarctata*, *Cocconeis placentula*), or tychoplanktonic diatoms (i.e., both benthic and planktonic—*Actinoptychus* spp., *P. sulcata* (small form), and *Odontella* spp.).

Upper Niawiakum transect (Nu)

Salinities ranged from 2‰ to 23.4‰ at transect Nu, with a mean of 14.9‰ (Figure 3). A five-factor model (Figure 5) identified the high marsh (Nu-5 to Nu-8; Factor 1), low-to-high transitional marsh (Nu-4; Factor 5), low marsh (Nu-2, Nu-3; Factor 4), channel bank (Nu-1; Factor 2) and channel floor (Nu-S; Factor 3) (Figure 2). Of the 84 species and groups considered in this study, 73 were observed along this transect, and 58 scored high in the factor analysis. The five-factor model explains 83% of the total variance, or 91% of the data (Table 2).

High marsh—Factor 1 (Figure 5a). Autochthonous diatoms indicative of the high marsh include *P. lagerstedtii*, *N. pusilla*, *D. subtilis*, *N. tenelloides*, *N. debilis*, and *Nitzschia pellucida*. *N. mutica*,

Transect Nu: Factor Scores

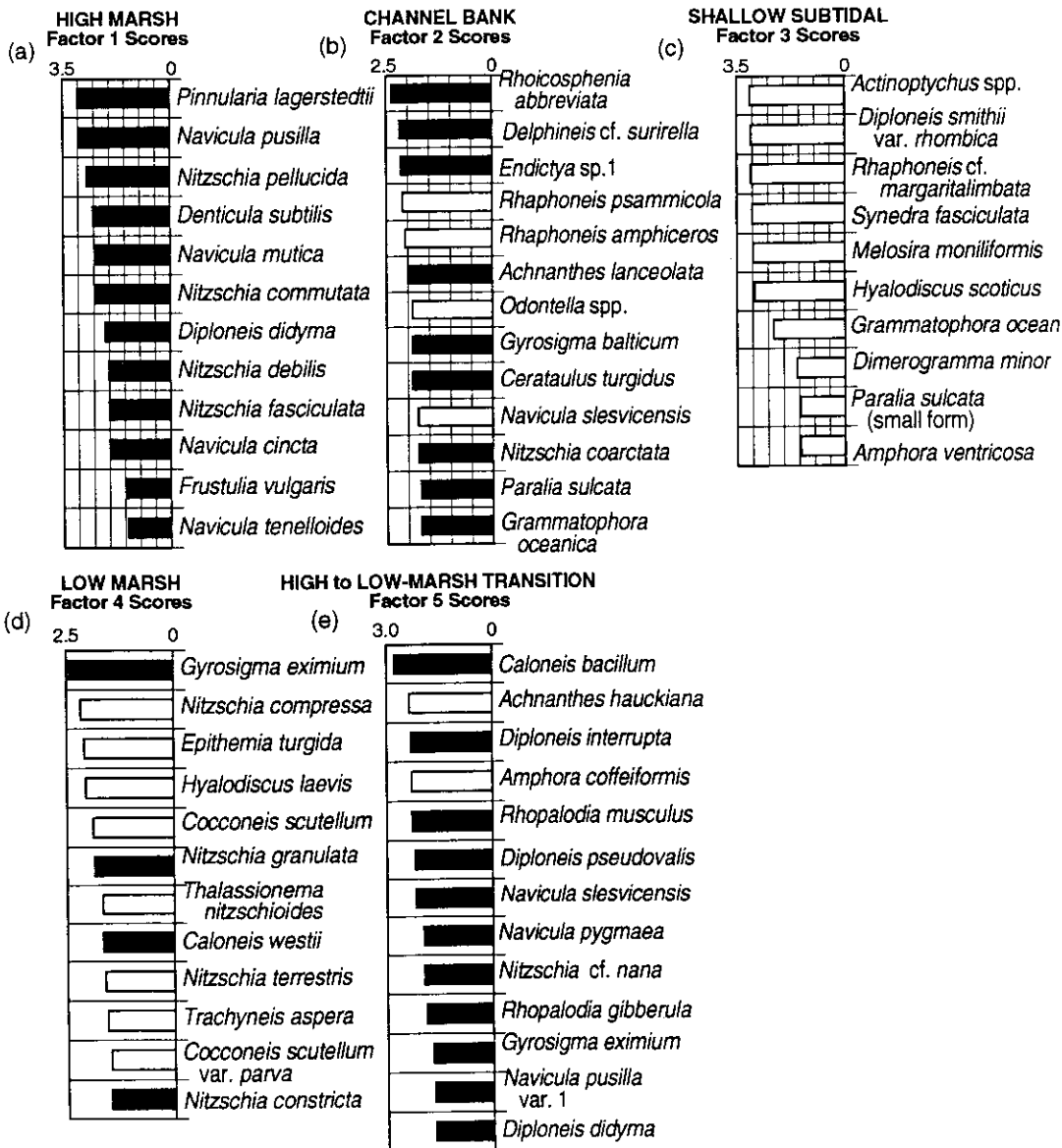


Figure 5. Factor scores along transect Nu for autochthonous species (black bars) and suspected allochthonous species (white bars).

N. cincta, *N. commutata*, *N. fasciculata*, *Diploneis didyma* and *Frustulia vulgaris* are distributed in high and low marshes.

Low-to-high transitional marsh—Factor 5 (Figure 5e). Sampling station Nu-4 is positioned near MHHW where it experiences substantially more tidal submergence than the high marsh stations and somewhat more emergence than stations lower on

the transect. Autochthonous diatoms include *C. bacillum* and *D. pseudovalis*, which were abundant at Nu-4 but also observed in high-marsh samples. *D. interrupta* totaled 3.4% of the assemblage at sampling station Nu-4, but was less than 1% in other marsh samples; *D. didyma*, *N. cf. nana*, and *Navicula pusilla* var. 1 are distributed in low and high marshes. *G. eximium* and *Rhopalodia*

TABLE 2. Factor loadings for sampling stations along transect Nu on the upper Niawiakum River. Boldface numbers denote defining factors for each sampling station.

Station	communality	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Nu-S	0.974	0.032	0.143	-0.970	-0.110	0.002
Nu-1	0.888	0.038	0.875	-0.196	-0.265	0.109
Nu-2	0.871	0.076	0.127	-0.204	-0.888	0.136
Nu-3	0.801	0.295	0.435	0.090	-0.714	0.087
Nu-4	0.922	0.312	0.186	0.013	-0.138	0.878
Nu-5	0.710	0.628	-0.145	-0.038	-0.198	0.504
Nu-6	0.740	0.751	-0.070	-0.043	-0.322	0.255
Nu-7	0.768	0.826	0.197	-0.090	-0.107	0.167
Nu-8	0.821	0.892	0.099	0.052	0.064	0.091
	variance	29.215	12.233	11.588	17.319	12.946
	cumulative variance	29.215	41.449	53.037	70.356	83.302

musculus were rare in these samples. Allochthonous diatoms include very rare valves of *Achnanthes hauckiana* and *Amphora coffeaeformis*.

Low marsh—Factor 4 (Figure 5d). Autochthonous species indicative of the low marsh include *G. eximium*, *Nitzschia granulata*, *C. westii*, and *N. constricta*. Allochthonous diatoms include very rare valves washed in from the adjacent muddy bank (*N. compressa*, *Epithemia turgida*, *Hyalodiscus laevis*, and *Trachyneis aspera*, *T. nitzschioides*) or high marsh (*N. terrestris*). Primarily empty frustules of *C. scutellum* and *C. scutellum* var. *parva* may also be allochthonous.

Channel bank—Factor 2 (Figure 5b). Autochthonous diatoms include *P. sulcata*, *G. oceanica*, *D. cf. surirella*, *N. coarctata*, *G. balticum*. Other possibly autochthonous, but very rare, diatoms include *Endictya* sp. 1, *C. turgidus*, *R. psammicola*, *R. amphiceros*, and *Odontella* spp. *R. abbreviata* and *A. lanceolata* are likewise distributed on the channel bank along transect N1. Allochthonous diatoms include very rare valves of *Navicula slesvicensis*, which is a high marsh species at Stony Point.

Shallow subtidal—Factor 3 (Figure 5c). All diatoms from the channel are considered to be allochthonous and include species distributed in lower-intertidal flats and *Zostera* beds. *Diploneis smithii* var. *rhombica* scored high in the factor analysis because of its limited distribution. No live cells were observed in Willapa Bay samples, but this species commonly occurs with *C. westii* in inter-

tidal marshes in the Copper River delta, Alaska (Hemphill-Haley, unpub. data).

Intertidal Samples Fringing the Open Bay

Salinity data for northern Willapa Bay, collected by the Washington Department of Fisheries Laboratory at Nahcotta, indicate typical ranges of 10-30‰, with occasional polyhalobous (>30‰) levels. An eight factor model (Figure 6) identified two sandy-tidal-flat assemblages (BC-1, BC-3; Factor 1; and BC-2; Factor 7), two silty-tidal-flat assemblages (SP-1 to SP-3; Factor 3; and samples BR-1, BR-2; Factor 4), a sandy-tidal-slough assemblage (TP-1; Factor 8), two *Triglochin* low-marsh assemblages (SP-4; Factor 6; and TP-2, TP-3; Factor 2), and a *Potentilla* high-marsh assemblage (SP-5; Factor 5). Of the 84 taxa considered for this study, 70 were observed in these samples, and 68 scored high in the factor analysis. The eight-factor model explains 81% of the variance, or 90% of the data (Table 3).

Sandy tidal flat 1—Factor 1 (Figure 6a): Indicative sandflat species include abundant valves of *C. scutellum* var. *parva* and *A. delicatula*. Other autochthonous species include *Trachysphenia australis*, *Cymatosira belgica*, *Navicula granulata*, *N. cancellata*, and *N. cryptolyra*. Allochthonous diatoms include very rare valves of *C. placentula*.

Sandy tidal flat 2—Factor 7 (Figure 6g): Sample BC-2 was separated from samples BC-1 and BC-3 in the factor analysis because of the high relative abundances of the autochthonous species *N. lyra*,

Open-Bay Samples: Factor Scores

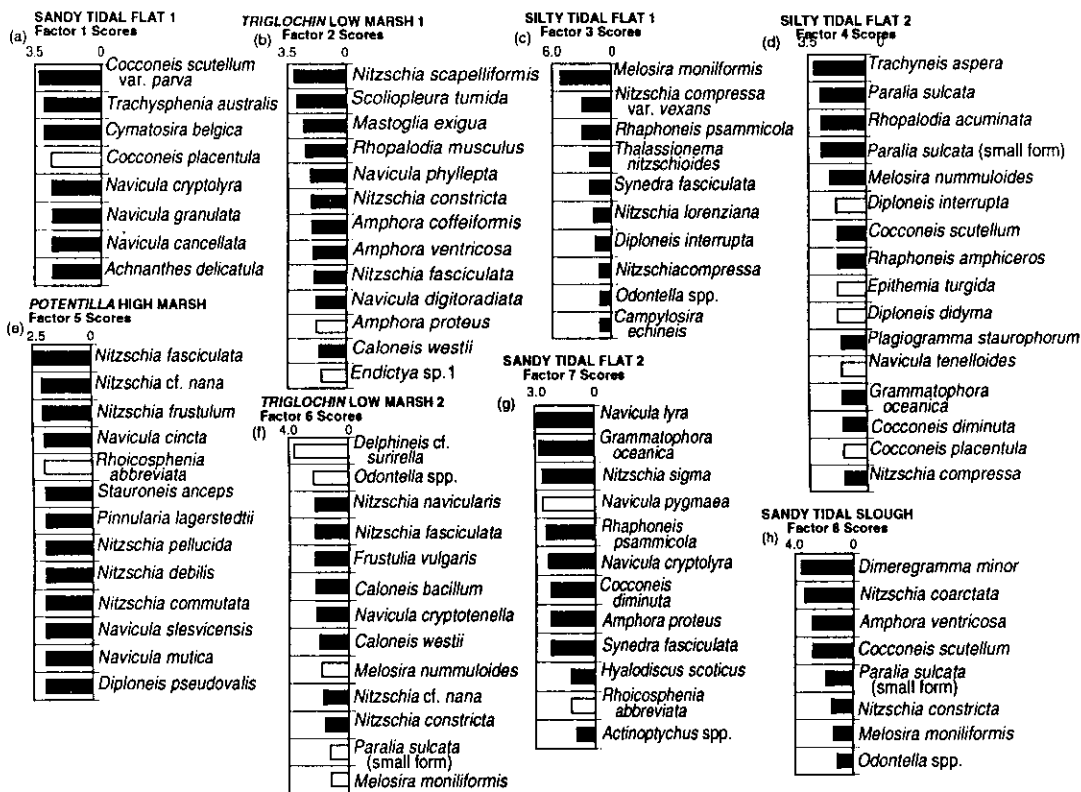


Figure 6. Factor scores of intertidal surface samples collected from the open bay for autochthonous species (by black bars) and suspected allochthonous species (white bars).

TABLE 3. Factor loadings for tidal flat and marsh samples collected from northern Willapa Bay. Boldface numbers denote defining factors for each sampling station.

Sample	communality	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Factor 8
SP-1	0.806	0.034	0.079	-0.832	0.050	-0.031	0.030	0.215	-0.237
SP-2	0.747	0.039	-0.146	-0.563	-0.153	-0.196	-0.505	-0.029	-0.300
SP-3	0.797	0.032	0.107	-0.833	-0.198	0.143	-0.060	0.027	0.160
SP-4	0.862	0.008	0.252	-0.026	-0.101	0.195	-0.865	0.029	0.025
SP-6	0.937	0.008	0.015	-0.039	-0.011	0.958	-0.104	0.026	-0.074
BR-1	0.775	0.022	-0.035	-0.097	-0.824	-0.061	-0.227	0.131	-0.116
BR-2	0.794	0.143	0.085	-0.064	-0.862	0.085	0.050	0.002	-0.096
BC-1	0.527	0.553	-0.022	0.017	-0.163	-0.044	-0.100	0.349	-0.245
BC-2	0.907	0.123	0.043	-0.182	-0.090	0.036	0.026	0.919	0.043
BC-3	0.896	0.941	0.046	-0.028	-0.046	0.014	0.045	0.007	0.066
TP-1	0.867	0.048	0.291	-0.109	-0.220	0.113	-0.023	-0.033	-0.840
TP-2	0.819	0.055	0.888	-0.064	0.052	-0.051	-0.018	0.127	-0.046
TP-3	0.814	0.029	0.840	-0.060	-0.108	0.078	-0.209	-0.075	-0.194
variance		9.51	13.021	13.643	12.285	8.091	8.695	8.129	7.784
cumulative variance		9.51	22.531	36.174	48.459	56.55	65.244	73.373	81.158

S. fasciculata, *G. oceanica*, and *Hyalodiscus scoticus*, and the restricted occurrence of *Amphora proteus*. *Cocconeis diminuta* and *N. cryptolyra* were observed attached to sand grains. *R. psammicola* was originally described by Riznyk (1973) from tidal flats in Yaquina Bay, Oregon. *Nitzschia sigma*, a cosmopolitan mesohalobous benthic diatom (Hendey, 1964), was very rare at this site. Allochthonous diatoms include very rare valves of *N. pygmaea* and *R. abbreviata*.

Silty tidal flat 1—Factor 3 (Figure 6c): Dominant autochthonous species include *M. moniliformis*, *S. fasciculata*, *Odontella* spp., *Nitzschia compressa* var. *vexans*, *R. psammicola*, *T. nitzschioides*, *Nitzschia lorenziana*, *N. compressa*, and *Campylodiscus echineis*. Allochthonous diatoms include very rare valves of *D. interrupta*.

Silty tidal flat 2—Factor 4 (Figure 6d): Autochthonous diatoms: *R. acuminata*, *G. oceanica*, and *C. scutellum*. Rare live cells of *Trachyneis aspera* and *Plagiogramma stauraphorum* may be autochthonous, which is consistent with tidal-flat distributions reported elsewhere (Hendey, 1964; Riznyk, 1973; Tynni, 1983). The highest relative percentages of *P. sulcata* (large form) were observed in these samples. Allochthonous diatoms include very rare valves of *D. interrupta*, *D. didyma*, *Epithemia turgida*, *N. tenelloides*, and *C. placentula*, possibly washed onto the tidal flat by the Bone River.

Sandy tidal slough—Factor 8 (Figure 6h): Autochthonous diatoms include species that favor a sandy substrate (*D. minor*, *N. coarctata*, *Amphora ventricosa*), are epiphytic on *Zostera* (*C. scutellum*, *M. moniliformis*), or are generally distributed on tidal flats (*N. constricta*, *Odontella* spp., *P. sulcata*).

Triglochin low marsh 1—Factor 2 (Figure 6b): Autochthonous diatoms include common valves of *M. exigua*, plus *Rhopalodia musculus*; *N. scalpelliformis*, *Navicula phyllepta*, *N. digitoradiata*, *C. westii*, and *Amphora coffeaformis*. *Scoliopleura tumida*, *A. ventricosa*, and *N. constricta* are rare but probably autochthonous. Allochthonous diatoms: very rare valves of *Amphora proteus* and *Endictya* sp. 1, which may have been washed in from the adjacent tidal slough.

Triglochin low marsh 2—Factor 6 (Figure 6f): Autochthonous species indicative of the low marsh include common cells of *C. westii*, *C. bacillum*, *N.*

constricta, *N. cf. nana*, and *Navicula cryptotenella*. Rare valves of *N. navicularis*, *N. fasciculata*, and *F. vulgaris* are probably also autochthonous. Allochthonous diatoms include very rare valves of *D. cf. surirella*, *Odontella* spp., *M. nummuloides*, *M. moniliformis*, and *P. sulcata* (small form).

Potentilla high marsh (Factor 5; Figure 6c): Autochthonous diatoms include common cells of *Navicula slesvicensis*, *N. mutica*, and *Stauroneis anceps*, and frequent cells of *P. lagerstedtii*, *N. commutata*, *N. pellucida*, and *N. cf. nana*. *N. cincta*, *N. debilis*, and *D. pseudovalis*, also observed in marsh samples from transects Nl and Nu, were rare at this locality. Allochthonous diatoms include very rare valves of *R. abbreviata*.

Discussion

The distributions of intertidal diatoms in southwestern Washington reflect the three-tiered intertidal zonation driven by differing amounts of tidal submergence, similar to the distributions of marsh macrophytes (Macdonald, 1977a, b; Frey and Basan, 1985; Sayce, 1988) and benthic foraminifers (Jennings and Nelson, 1992). The 84 taxa discussed in this report show variable affinities for different parts of the intertidal and shallow subtidal zone in northern Willapa Bay (Figure 7). Many species are distributed in more than one zone, whereas others are more restricted. The sampling interval in this study did not clearly differentiate the boundaries between intertidal zones, but as shown by Jennings and Nelson (1992) and Nelson and Kashima (1993), these boundaries may be transitional over several tens of centimeters. Although the factor analysis separated shallow-subtidal from lower-intertidal-channel-bank samples, the shallow-subtidal samples predominantly contain allochthonous diatoms from lower intertidal flats and channel banks, and thus it could be argued that lower-intertidal and shallow-subtidal fossil assemblages would be indistinguishable. There is some indication that deeper channels (>4 m deep) may be distinguishable from shallow subtidal channels in Willapa Bay by higher planktonic diatom/benthic diatom ratios (Hemphill-Haley, unpub. data), but this requires further investigation.

Overlapping salinities among the transects and open-bay localities allowed for similar diatom assemblages in ecological zones at different sites. This agrees with published observations of broad salinity ranges for many brackish species, with dramatic

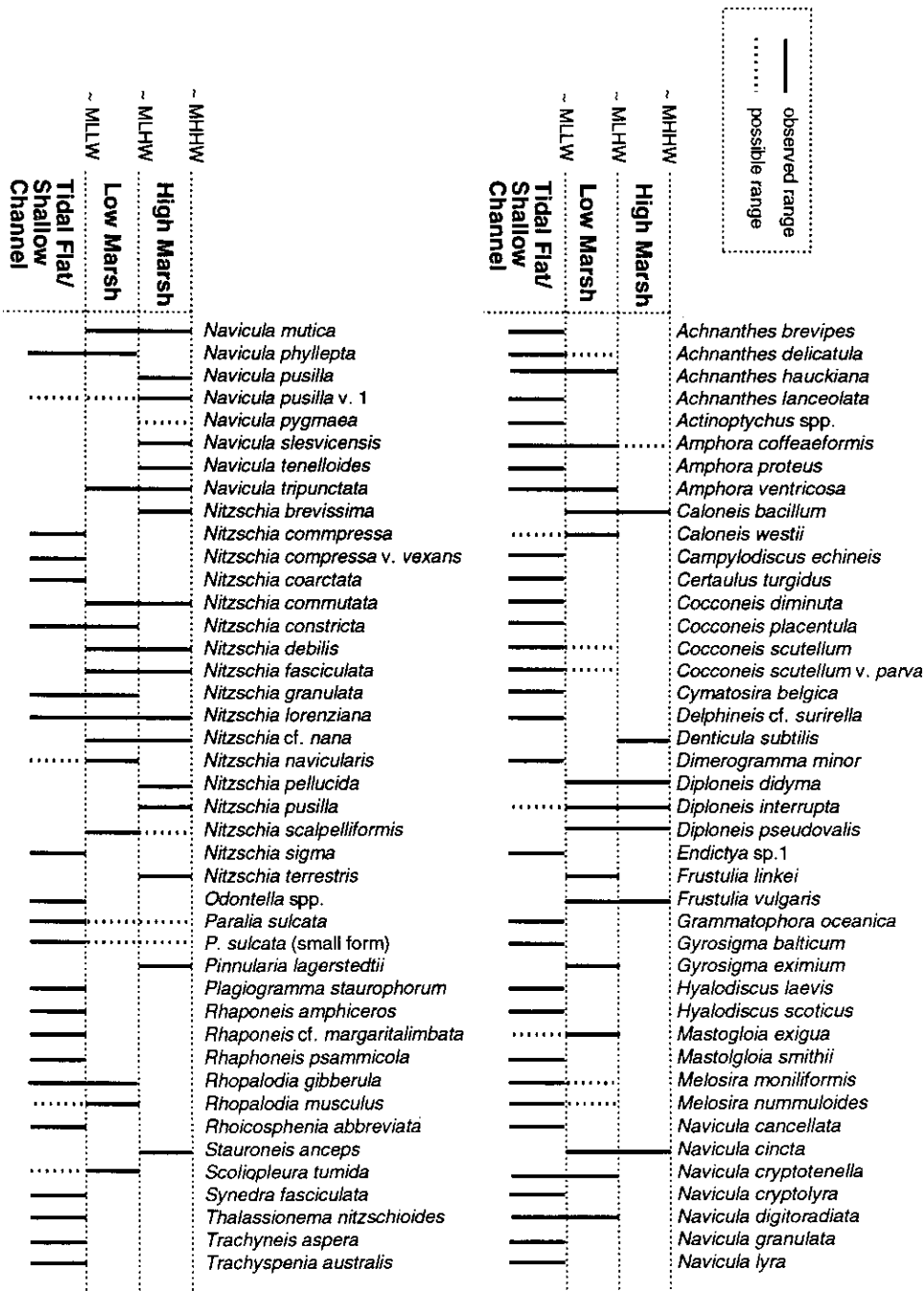


Figure 7. Intertidal ranges for 84 diatom species and groups from northern Willapa Bay. Solid lines, dominant range; dashed lines, possible range indicated by rare occurrences. Absolute elevations for the intertidal zones are not indicated because these elevations are constrained by local tidal range and vary with location in an estuary.

shifts in diatom populations (triggered by the osmotic capabilities of various taxa) occurring at salinities either below 5‰ or above 30‰ (Moore and McIntire, 1977; McIntire, 1978; Amspoker and McIntire, 1978; Vos and de Wolf, 1988; Hemphill-Haley, 1993a). However, lower average salinities at transect Nu, higher amounts of freshwater run-off from the Pleistocene terrace at Stony Point, and geomorphic differences between the low-marsh zones of the open bay and Niawiakum River may have contributed to some differences among diatom populations in this study. Muddy banks of the river and silty intertidal flats of the open bay were dominated by prolific species such as *Paralia sulcata*, *Melosira moniliformis*, *Synedra fasciculata*, and *Grammatophora oceanica*. The open bay sand flats, however, hosted assemblages that were distinct from the muddy epipelagic assemblages. Several species that are commonly observed in late Holocene deposits (particularly *Caloneis westii*, *Scoliopleura tumida*, *Navicula digitoradiata*, and *Campylodiscus echineis*; Hemphill-Haley, unpub. data) were either rare or absent in the steep low marsh zone along the river, but were frequent in the gently sloping, thickly vegetated, *Triglochin*-dominated low marshes of the open bay. Several small, sturdy species (e.g., *Pinnularia lagerstedtii*, *Navicula pusilla*, *N. mutica*, *Denticula subtilis*) appear to be reliable for identifying the high marsh, particularly *Deschampsia*-dominated high marshes.

The factor analysis identified a subzone at the marsh-upland transition because of the higher concentration of certain species (e.g., *D. subtilis*, *N. pusilla*) in that area. Regardless of whether a particular fossil assemblage can be recognized, the marsh-upland transition can be identified by the disappearance of diatoms in samples deposited above EHW. Unless standing water is present (which I observed only once during reconnaissance surveys in various areas of Willapa Bay), upland surfaces above the range of highest tides bordering estuarine marshes in southwestern Washington do not support diatom populations, including freshwater species (see also Nelson and Kashima, 1993). Therefore, the position of palco-EHW can be identified by the transition from peaty diatom-rich marsh deposits to upland peats barren of diatoms.

The amount of submergence or desiccation at different intertidal elevations is reflected in the physiology of the diatom species that inhabit differ-

ent intertidal zones and influences how well a fossil record is preserved. For example, the high-marsh diatoms observed in this study are dominated by small, solitary, heavily silicified species that are tolerant of large fluctuations in temperature, salinity, and periods of desiccation imposed by the higher elevation of the marsh environment (e.g., *D. subtilis*, *P. lagerstedtii*, *N. pusilla*). For example, the diurnally submerged bank and low marsh along transect N1 experienced average water temperatures that ranged from 20.5°C in July 1990 to 5.9°C in December 1990. In contrast, the high marsh was desiccated at air temperatures of 25.5°C in July 1990 and frozen in December 1990, yet abundant live diatoms were obtained in surface samples on both occasions, attesting to the resilience of the species observed there. Many of these species can be expected to fossilize well, in contrast to some low-marsh diatoms that undergo tidal submergence at least once per day and are more delicately silicified or live in gelatinous tubes (e.g., *G. eximium*, *N. scalpeliformis* (Williams, 1965)).

Substrate and sediment grain size are strong controlling factors in the distribution of benthic estuarine diatoms (e.g., McIntire and Moore, 1977; Amspoker and McIntire, 1978; Whiting, 1983; Whiting and McIntire, 1985; Kosugi, 1987). The propensity for organic carbon to accumulate in fine grained or poorly sorted silty sediment, as opposed to well-sorted sandy deposits, influences the distribution of intertidal diatoms. In general, diatoms are more abundant on silty tidal flats than on sandy tidal flats (Colijn and Dijkema, 1981; Laws, 1988) if they are not dominated by other organisms (Riznyk and Phinney, 1972). Therefore, finer grained paleoestuarine deposits can be expected to be more diatomaceous than sandy deposits, even excluding the effects of winnowing. In addition, diatoms are typically more abundant where certain macrophytes are present—either to trap fine-grained sediment or to act as substrate for epiphytes—than where they are absent (Round, 1971; Main and McIntire, 1974; McIntire and Moore, 1977). On the channel banks and tidal flats in Willapa Bay, epiphytes are prolific on *Zostera*, especially *M. moniliformis*, *M. nummuloides*, and *S. fasciculata*. However, these large, delicate species leave a poor fossil record. Although solitary species on silty flats (e.g., *Nitzschia acuminata*, *C. echineis*) are far less prolific than epiphytes on *Zostera*, they are much more likely to survive fossilization.

Transport and redeposition of diatom frustules in coastal areas cannot be ignored in biostratigraphic studies (e.g., Beyens and Denys, 1982; Vos and de Wolf, 1988; 1993). In this study, virtually all modern samples contained suspected allochthonous diatom valves, indicating what could be expected for fossil deposits. Spring high tides, particularly in association with storm surges, are capable of topping the highest marshes in Willapa Bay and scattering diatom frustules across upland surfaces. During typical weather conditions, many sediment-associated diatoms, especially such large chain-forming taxa as *Melosira* or *Paralia* that cannot withstand strong water turbulence, will readily be lifted into the plankton. Whiting (1983) likewise noted occurrences of benthic species in plankton samples.

With each rising tide, epipellic diatoms that fail to withdraw below the sediment surface may be lifted up and transported up estuary as a surface "film." Casual observation showed that most diatoms in the surface film are small, delicate epipellic species (e.g., *Navicula halophila* group; Hemphill-Haley, 1993b) that are not well represented in fossil deposits. Excluding the effects of localized differences in sediment texture causing patchy diatom distributions, this regular mixing and reseeded by tides results in a generally homogeneous lower intertidal zone (see Riznyk and Phinney, 1972; Riznyk, 1973; Amspoker and McIntire, 1978).

However, although diatom cells can be assumed to be redeposited on a regular basis in any estuary, observations of the modern Willapa Bay samples indicates that autochthonous benthic species typically far outnumber suspected allochthonous benthic species. Thus, this suggests that in most cases (assuming good preservation) it should be possible to reconstruct the depositional environment of a fossil deposit based on its autochthonous constituents. Sullivan (1975) noted that live allochthonous cells did not survive and reproduce in intertidal habitats for which they were physiologically unsuited, further suggesting that redistributed diatoms are unlikely to completely mask *in situ* assemblages associated with particular intertidal settings. Therefore, although allochthonous cells will almost certainly be present in a sample, it is reasonable to expect that the depositional setting of a fossil deposit may be inferred based on its autochthonous components.

Using the results of the factor analysis as an example of what can be expected in fossil deposits, allochthonous diatoms are present in most samples, with fewer allochthonous valves in high-marsh deposits and more frequent allochthonous valves in low-marsh and tidal-flat samples. Thus, because of the occurrences of allochthonous valves, low marshes and tidal flats and banks may be more difficult to recognize on the basis of diatom assemblages, unless autochthonous valves are dominant and/or better preserved (i.e., show evidence for being *in situ*).

Staining the diatom samples used for this study provided valuable insight into the distributions of modern estuarine species (see also Kosugi, 1987). Although acid cleaning removes organic material that may obscure the ornamentation of some valves, it prohibits the identification of cells that were live or recently deceased at the time of collection. Although epilithic or epiphytic samples can be assumed to be *in situ* (e.g., McIntire and Overton, 1971; Main and McIntire, 1974; Moore and McIntire, 1977), sediment-associated diatoms found on tidal flats and salt marshes may or may not be in place, and once a sample is cleaned it is impossible to discern whether or not a species was a living part of the assemblage (e.g., Riznyk, 1973; Tynni, 1986). Although identifying a live cell does not guarantee that it is autochthonous (as live cells of such easily transported species as *P. sulcata* were commonly observed), recognizing the extent of probable allochthonous input provides the kind of information necessary for improving paleoecological interpretations which ultimately must be based on co-occurrences of autochthonous and allochthonous taxa.

Conclusions

Diatoms were collected in surface sediment samples from tidal flats, intertidal channel banks, shallow subtidal channels, and low and high marshes in northern Willapa Bay, Washington. Diatom frustules were stained in order to identify possible allochthonous taxa in various ecologic settings. Q-mode factor analyses identified groups of intertidal samples composed of comparable diatom assemblages; although autochthonous species dominate, some allochthonous species also scored high in the factor analysis indicating the regular influence of reworking in the estuary and the prevalence of a mixed biocoenosis/thanatocoenosis in potential fossil deposits.

The results suggest that diatoms can be used to identify three environmental zones relative to tidal level: (1) tidal flats, channel banks, and shallow subtidal channels below MLHW; (2) low marshes between MLHW and MHHW; and (3) high marshes between MHHW and EHW. In some places, an additional zone may be recognizable on the basis of assemblages that thrive near EHW at the marsh-upland transition, but the position of paleo-EHW is also identifiable by the disappearance of diatoms in samples deposited above EHW. The absolute elevations of intertidal zones depend on the local tidal range, which varies within a large estuary such as Willapa Bay.

Because many of the species observed in this study have cosmopolitan distributions, these data are probably applicable to Quaternary estuarine paleoecological studies in other temperate areas of the world, as well as throughout the coastal Pacific Northwest.

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