

DIATOM-BASED BIOASSESSMENT IN WETLANDS: HOW MANY SAMPLES DO WE NEED TO CHARACTERIZE THE DIATOM ASSEMBLAGE IN A WETLAND ADEQUATELY?

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Abstract: Diatom-based bioassessment in wetlands requires quantitative characterization of spatial and temporal variability of the diatom assemblages within each wetland. The purpose of this study was to examine surface-sediment diatom distributional patterns in a wetland to determine how best to sample these systems to capture spatial variability in the assemblage. Diatoms and environmental conditions were characterized from 29 sampling points within a wetland in the floodplain of the Columbia River, Oregon, USA. A total of 159 diatom taxa were identified in the surface-sediment samples. Species richness was high at each sampling point (median: 42, range: 23–57), and relative abundances of common taxa varied between 15 and 39% throughout the wetland. Assemblages contained taxa with both benthic (e.g., *Staurosira construens*, *Nitzschia palea*, *Fragilaria capucina*, *Achnantheidium minutissimum*) and planktonic (e.g., *Aulacoseira granulata* and *Tabellaria* spp.) preferences. Non-metric multidimensional scaling (NMDS) techniques detected differences in the low marsh and upper marsh sediment diatom assemblages. Geostatistical analysis showed spatial autocorrelation of the diatom assemblage in the wetland, measured as semivariance and Moran's I. A simulation procedure indicated that changes in diatom species richness stabilized after approximately five samples were composited. Our results suggest that the wetland surface sediment diatom assemblage is heterogeneous and that hydrologic gradients may be an important structuring force. Diatom-based bioassessment has the potential to be a useful tool in assessing wetland environmental conditions; however, the shallow nature and complex hydrology of these systems require careful sampling design to adequately characterize the diatom assemblage.

Key Words: diatoms, bioassessment, nonmetric multidimensional scaling (NMDS), geostatistics, Oregon Columbia River Floodplain

INTRODUCTION

The utility of algae in the environmental assessment of aquatic habitats, particularly lakes and streams, has been well-documented (Dixit and Smol 1994, Stevenson and Pan 1999). Algal assemblages are sensitive to the impacts of human activities on aquatic habitats, including acidification, eutrophication, sedimentation, and pesticide and heavy metal pollution. For example, calcareous algal mats, native algal assemblages in the Everglades, diminished with increases in agricultural runoff (McCormick and O'Dell 1996, Pan et al. 2000). Changes in diatom assemblages have been related quantitatively to water quality variables, including conductivity, along a human disturbance gradient in western Kentucky wetlands (Pan and Stevenson 1996). Because algae are often a major primary producer in wetlands (see review by Goldsborough and Robinson 1996), changes in algal assemblages in

response to anthropogenic factors may reflect the impacts of these factors on overall wetland conditions. Several researchers have proposed conceptual models for changes in algal assemblages with relation to environmental conditions in wetlands (Goldsborough and Robinson 1996) and protocols for algal-based wetland bioassessment (Stevenson and Bahls 1999).

However, the extension of algal-based bioassessment from streams and lakes to wetlands is met with several challenges. Wilcox et al. (2002) cautioned against the use of biological indicators in hydrologically variable wetlands due to the influence of water-level history in shaping biologic assemblages. The surface-sediment diatom assemblage is often used in paleolimnological studies because it is thought to integrate diatoms from different habitats over the last several years (Dixit et al. 1992, Fritz et al. 1999). However, spatial heterogeneity has been demonstrated for the diatom assemblage deposited

in the surface sediment of lakes of different morphologies and depths (Bradbury and Winter 1976, Earle et al. 1988, Anderson 1990). Spatial heterogeneity might be an even more important issue in wetlands as uneven topography and water depths influence the habitat structure available for algal colonization. Both algal biomass and assemblage structure in wetlands have been related to water depth (Shalles and Shure 1989, Robinson et al. 1997a, b) and resulting vegetation composition (Pip and Robinson 1984, Cattaneo et al. 1998). In paleolimnological studies, surface-sediment diatom samples are typically taken from the deepest area since it is assumed that sediments and diatoms from all lake habitats are deposited here (Dixit et al. 1992). The spatial and temporal complexity of the wetland environment might preclude sediments and diatoms from all habitats from being deposited in one location and, therefore, from there being one ideal location to collect samples for algal-based wetland bioassessment. Multiple sampling locations that capture heterogeneity might be necessary to characterize the wetland algal assemblage adequately.

For successful algal-based bioassessment in wetlands, the patterns and amount of heterogeneity in the algal assemblage within a wetland must be quantified, and subsequently, a sampling method that accurately characterizes the algal assemblage must be developed. The main objectives of this study were to (1) explore spatial variability in surface-sediment diatom assemblages with a wetland and (2) determine how many surface-sediment samples are needed to characterize the wetland diatom assemblage for bioassessment adequately. By exploring spatial patterns in wetland diatom assemblages, we will be able to provide guidance on the best sampling protocol to use for diatom-based wetland bioassessment.

MATERIALS AND METHODS

Study Site and Study Design

Rooster Rock wetland (45.542 N, 122.247 W) is located in the northwestern foothills of the Western Cascade ecoregion of North America (Level III Ecoregion, Omernik and Gallant 1986; Figure 1). The Western Cascades ecoregion extends from the Columbia River Gorge in the north to the Klamath Mountains in the south and between the heavily populated and extensive agricultural lands in the Willamette Valley to the west and the dry ponderosa pine forests of the Eastern Cascades ecoregion to the east. This ecoregion is underlain by volcanic basaltic

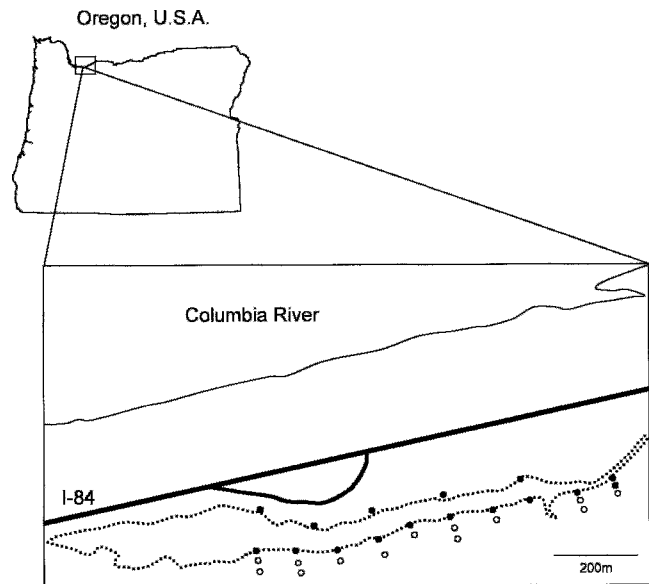


Figure 1. Map of Rooster Rock wetland, Columbia River Basin, Oregon, USA with locations of surface-sediment sampling points. Closed circles are low marsh sites and open circles are upper marsh sites.

rock formed during the Cenozoic Era, with steep ridges in the west and broad valleys in the east. The area has a moist, temperate climate, with seasonal precipitation patterns. The heaviest precipitation falls as rain and snow from October through March. Spring snow-melt is an important source of water to most streams/wetlands in the region. The natural vegetation of the area is conifer forest, predominantly western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco.), and western red cedar (*Thuja plicata* Donn.).

Rooster Rock wetland has several features that make it ideal for the study of spatial complexity of wetland algae. It is relatively large (1100 m × 150 m) and one of the relatively undisturbed wetlands in the area (J. Maser, personal communication). In addition, its complex hydrology results in zonation of vegetation and variable water chemistry. It can be broadly classified as a riverine-impounded wetland according to the modified hydrogeomorphic classification system of Brinson (Adamus 2001). The wetland is fed continuously at its eastern end by a small stream. It is impounded at its northwestern end by Interstate 84, producing a large pond area with relatively deep (<2 m in summer), slow-moving water. Occasional hydrologic exchanges with the Columbia River occur at its far western edge through a small culvert, primarily in the wet season. A steep rock face borders the southwestern edge of the wetland, and snowmelt produces several water-

falls during the spring months. These interacting factors result in two hydrologic gradients within the wetland: (1) a lateral gradient, running approximately north-south, of decreasing inundation from the low marsh habitat to the high marsh habitat and (2) a longitudinal gradient (approximately east-west) of increasing open water area from the inflow to the impoundment. At the time of sampling, water depth varied between 6 and 59 cm throughout the wetland (median = 23 cm) and was greater in the low marsh and near the impoundment. In addition to these spatial hydrologic gradients, water levels change temporally, attributable to strong seasonal patterns of precipitation in the Pacific Northwest. Water levels can be 1–2 m higher in the winter and spring months. This cycle of flooding and drawdown results in isolated patches with standing water in the summer that become connected during flooding in the winter months.

Macrophyte distribution reflects the complex hydrology. The low marsh areas were dominated by smaller emergent macrophytes, including *Sagittaria latifolia* Willd., *Eleocharis palustris* (L.) R & S, and *Juncus* spp., while the upper marsh was dominated by larger species *Phalaris arundinacea* L. and *Scirpus validus* Vahl. The invasive reed canary grass (*P. arundinacea*) was more abundant near the impounded end. Sampling points tended to have greater water depths and less vegetation cover in the low marsh and closer to the impounded end.

To ensure comparable sampling efforts along both lateral and longitudinal hydrologic gradients, 35 sampling points were selected on an aerial photograph. Sixteen sampling points were selected within the low marsh. The low marsh was defined as the area along the water's edge with abundant emergent macrophytes. Nineteen sampling points were selected within the upper marsh. The upper marsh was defined as the area between the low marsh and the wetland-upland ecotone. Due to the proximity of the interstate, only low marsh samples were collected on the north side of the wetland. Of the original 35 sampling locations selected in the laboratory, samples were collected from the 29 locations with standing water (low marsh $n = 16$, upper marsh $n = 13$; Figure 1).

Field Sampling

Geographic coordinates of each sampling location were measured with a Garmin Etrex Vista GPS (datum: WGS 1984). At each sampling point, within a one-week period in August 2002, specific conductance, dissolved oxygen, and temperature were measured at mid-depth in the water column with a Hydrolab DS5 multiprobe. Water pH was

measured using an Orion Model 210A meter. Water samples were collected at mid-depth for nutrient analysis. Two water samples were taken at each sampling point, one filtered on site (47 mm Millipore® type HA filters, 0.45 μm pore size), the other left unfiltered and stored on ice until returned to the laboratory for nutrient analysis. Water depth at the center of each plot was measured using a meter stick.

Twenty-nine surface-sediment samples were collected during the same time period as water quality samples. Water depth was less than 59 cm throughout the wetland, so samples were collected by wading. A 6.5-cm clear PVC tube (inside diameter) was used to collect an approximately 10-cm long sediment core. Flocculent material was allowed to settle, and the top 2 cm of the core were extruded. Sediment samples were stored in whirl-pak bags, placed on ice, and frozen upon returning to the lab until preparation for diatom analysis.

Laboratory Analyses

Water samples were analyzed for nitrate and nitrite by the cadmium reduction method (Clesceri et al. 1998). Ammonium nitrogen was measured by the phenol-hypochlorite method (Wetzel and Likens 1991). Total nitrogen was measured by alkaline persulfate digestion followed by cadmium reduction (Ameel et al. 1993). Soluble reactive phosphorus (SRP) was measured by the ascorbic acid method (Wetzel and Likens 1991). Total phosphorus was measured by the alkaline persulfate digestion method followed by the ascorbic acid method (Ameel et al. 1993).

Surface sediment samples were allowed to thaw for 12 hours. When samples were thawed, whirlpaks were kneaded for 5 minutes to homogenize the sediment samples. Approximately 5–10 ml of homogenized sediment were prepared for diatom identification. Samples were digested using concentrated sulfuric acid and potassium dichromate for between 12 and 24 hours. Samples were rinsed repeatedly with deionized water until the pH was approximately neutral and mounted on slides with Naphrax® high resolution mounting medium. Transects were scanned until at least 500 diatom valves were identified and enumerated to the species level using a Nikon Eclipse E600 microscope at 1000 \times magnification. The primary references for diatom taxonomy were Krammer and Lange-Bertalot (1986, 1988, 1991a,b, 2000) and Patrick and Reimer (1966, 1975). Diatom autecological indices were calculated for each site based on the ecological indicator values of Van Dam et al. (1994) and Kelly and Whitton (1995).

Table 1. Environmental variables (median and range) for the entire wetland and sites grouped by lateral and longitudinal marsh position.

	Entire Wetland	Lateral Position		Longitudinal Position	
		low marsh	upper marsh	inflow	impoundment
water depth (cm)	23 (6–59)	28 (9–59)	22 (6–30)	19 (6–39)	27 (7–59)
water temperature (°C)	16.5 (15.0–20.7)	16.3 (15.0–20.7)	16.6 (16.1–19.8)	16.2 (15.0–16.6)	16.9 (15.7–20.7)
pH	6.6 (6.2–7.0)	6.6 (6.3–7.0)	6.5 (6.2–6.8)	6.6 (6.3–6.6)	6.6 (6.2–7.0)
Dissolved oxygen (mg/L)	7.4 (5.6–9.5)	7.7 (6.7–9.5)	6.7 (5.6–8.8)	7.7 (5.9–8.7)	7.2 (5.6–9.5)
Conductivity (mS/cm)	0.05 (0.00–0.07)	0.05 (0.00–0.05)	0.05 (0.00–0.07)	0.05 (0.00–0.06)	0.05 (0.00–0.07)
Total nitrogen (µg/L)	31 (2–219)	27 (2–89)	34 (4–219)	22 (4–182)	38 (2–219)
Total phosphorus (µg/L)	30 (9–87)	25 (10–80)	31 (9–87)	23 (9–80)	30 (14–87)

Data Analysis

Diatom Assemblage Analysis. Diatom assemblage data were represented as proportion of total species at each sampling point (relative abundance). In an effort to reduce the influence of “rare” species in the dataset, only species occurring with greater than 1% relative abundance or present at three or more sampling points were included in the data analysis ($n = 50$). Relative abundances were $\log(x+1)$ transformed to down weight dominant taxa.

To examine spatial patterns in diatom assemblages, sampling points were ordered based on diatom assemblages using non-metric multidimensional scaling techniques (NMDS). The NMDS were performed using PC-ORD v. 4.14 (Bray-Curtis distance measure, 40 real runs, and 400 maximum iterations, McCune and Mefford 1999). The Monte-Carlo permutation procedure was used to evaluate if the axes extracted by NMDS were stronger than would be expected by chance alone (PC-ORD, 50 randomized runs).

Geostatistical Analysis. Spatial variability in the distribution of diatom assemblage (represented by NMDS axis scores), and dominant species were modeled using semi-variance and autocorrelation (Moran’s I) (Legendre and Fortin 1989, Passy 2001). Semi-variance describes the variance between data points separated by a specified distance (“lag”). Distance between sampling points ranged between 0 and 880 m (mean distance = 310 m). Omnidirectional semi-variograms were estimated with the geostatistical software package GS+ (Gamma Design Software) for the entire length of the wetland (890 m). Spatial autocorrelation can vary with both direction and distance. However, unidirectional variograms (anisotropic models) could not be calculated because of the small number of points sampled in the north-south direction. Moran’s I statistic was calculated as the measure of spatial autocorrelation. Moran’s I has values between -1

and 1 depending on the direction and degree of autocorrelation (Sokal and Oden 1978).

Sampling Effort Simulation. The effects of increasing sampling efforts on the characterization of the surface-sediment diatom assemblage were evaluated using a simulation procedure. A similar procedure has been used for assessing effects of counting and sampling efforts for macroinvertebrate-based stream assessment (Cao et al. 2002). To evaluate the effect of collecting increasing numbers of samples (sampling effort) and compositing them prior to counting while holding the counting effort constant at 500 individuals on the diatom assemblage (i.e., species richness), we generated samples of different composite amounts by (1) pooling all diatom counts from the 29 sampling points serving as a ‘population,’ (2) generating a composite sample by randomly drawing a fixed number of individuals for different composite samples ten times (1, 2, 3...29), and (3) for each of the composite sample, randomly drawing 500 individuals (without replacement) from the simulated assemblages 99 times. Mean and standard deviation of diatom richness were calculated for each composite sample to examine the influence of sampling effort on diatom assemblage.

RESULTS

Water depths showed spatial patterns, tending to be higher in the low marsh and near the impoundment (Table 1). Water quality variables showed no clear spatial patterns (Table 1). Water-column pH was neutral to slightly acidic (median 6.6, range 6.2–7.0). Nitrogen and phosphorus levels were variable throughout the wetland, with no clear pattern relating to spatial position or water depth. Total nitrogen and total phosphorus concentrations were low overall compared to many Oregon wetlands (Weilhoefer, unpublished data).

Sediment diatom species assemblages varied between the 29 sampling plots. A total of 159

Table 2. Relative abundance of dominant diatom taxa and diatom metrics (median and range) for the entire wetland and sites grouped by lateral and longitudinal marsh position.

	Entire Wetland	Lateral Position		Longitudinal Position	
		low marsh	upper marsh	inflow	impoundment
Diatoms:					
<i>Staurosira construens</i>	24 (2–39)	29 (9–39)	15 (2–34)	21 (2–34)	29 (3–39)
<i>Fragilaria capusina</i>	11 (1–40)	13 (6–40)	7(1–24)	10 (3–24)	11 (1–40)
<i>Nitzschia palea</i>	10 (4–31)	10 (7–18)	10 (4–31)	10 (4–18)	10 (6–31)
<i>Achnanthydium minutissimum</i>	6 (2–17)	7 (2–17)	5 (2–14)	9 (5–17)	4 (2–8)
<i>Melosira varians</i>	2 (0–45)	2 (1–19)	5 (0–45)	2 (0–18)	1 (0–45)
<i>Fragilaria-Staurosira-Staurosirella</i> taxa	35 (11–58)	46 (25–58)	26 (11–52)	31 (25–55)	45 (11–58)
Metrics:					
Species richness	42 (23–57)	42 (36–57)	41 (23–53)	43 (35–57)	41 (23–50)
Planktonic taxa (%)	5 (1–50)	6 (2–21)	3 (1–50)	5 (2–50)	5 (1–25)
Periphytic taxa (%)	92 (46–97)	92 (79–97)	92 (46–97)	93 (46–97)	91 (75–97)
Trophic Diatom Index	2.8 (2.3–3.7)	2.8 (2.5–3.7)	2.8 (2.3–3.5)	2.8 (2.3–3.5)	2.8 (2.5–3.7)
Circumneutral taxa (%): pH ~ 7	37 (10–60)	35 (10–54)	40 (12–60)	36 (10–54)	37 (12–60)
Alkaliphilous taxa (%): pH > 7	56 (29–87)	56 (34–87)	51 (29–82)	54 (34–87)	56 (29–82)
N–autotrophic I taxa (%)	36 (4–48)	32 (4–48)	36 (15–47)	28 (9–47)	36 (4–48)
Continuously high O ₂ levels (%)	41 (8–56)	38 (8–56)	42 (19–55)	36 (22–56)	44 (8–54)

diatom taxa were identified in the wetland. Diatom species richness ranged between 23 and 57 species per plot (median = 42; Table 2). The surface sediment assemblages contained both benthic and planktonic species and were dominated by benthic forms (median = 92%). Over 37% of the total diatoms counted were from the chain-forming *Fragilaria-Staurosira-Staurosirella* taxa. *Staurosira construens* Ehrenb. was the most abundant species throughout the wetland (median relative abundance = 24%, range 2–39%; Table 2). *Achnanthydium minutissimum* (Kütz.) Czarn. was present in all surface sediment samples (median relative abundance = 6%, range 2–17%). Assemblages were dominated by taxa preferring alkaline (median = 56%; Table 2) and circumneutral (median = 37%) waters. Most taxa were nitrogen-autotrophs, preferring high levels of oxygen and being tolerant to moderate levels of nutrients and pollution (Trophic Diatom Index value median = 2.8). Overall siltation index was low (median = 29%), but there were some plots with large abundances of siltation tolerant species.

The relative abundance of some taxa varied by more than 40% between the sampling points. For example, the relative abundance of *Fragilaria capusina* Desm. was 1% at a sampling point located in the upper marsh near the impoundment and 40% at a sampling point in the lower marsh near the impoundment. The relative abundance of *S. construens* was 2% at a sampling point in the upper

marsh near the inflow and 39% at a sampling point in the lower marsh near the impoundment. Relative abundance of the five most common species varied between 15 and 39% throughout the wetland. *Aulacoseira granulata* (Ehrenb.) Simonsen, the most common planktonic species, was the most variable species, varying by 49%. *Fragilaria-Staurosira-Staurosirella* taxa tended to be more abundant in the low marsh (Table 2). *Achnanthydium minutissimum* tended to be more abundant at sampling points closer to the inflow. Diatom species richness was heterogeneous but did not display strong spatial patterns (Table 2). Overall, diatom assemblages were more similar within the low marsh than within the upper marsh. Average Bray-Curtis similarity was greater between sampling points in the low marsh (mean = 69%, range = 50–85%) than sites within the upper marsh (mean = 49%, range = 18–70%). Average Bray-Curtis similarity was greater between sites closer to the inflow (mean = 63%, range = 36–83%) than those closer to the impoundment (mean = 57%, range = 18–85%). Diatom autecological metrics did not show spatial patterns (Table 2).

Ordination detected patterns in sediment diatom assemblages related to spatial hydrologic gradients, with low marsh assemblages appearing to be distinct from those in the upper marsh. Spatial patterns in the assemblage were less distinct between plots near the inflow and those near the impoundment. A three-dimensional solution was obtained for the NMDS that explained 93% of the variance in the

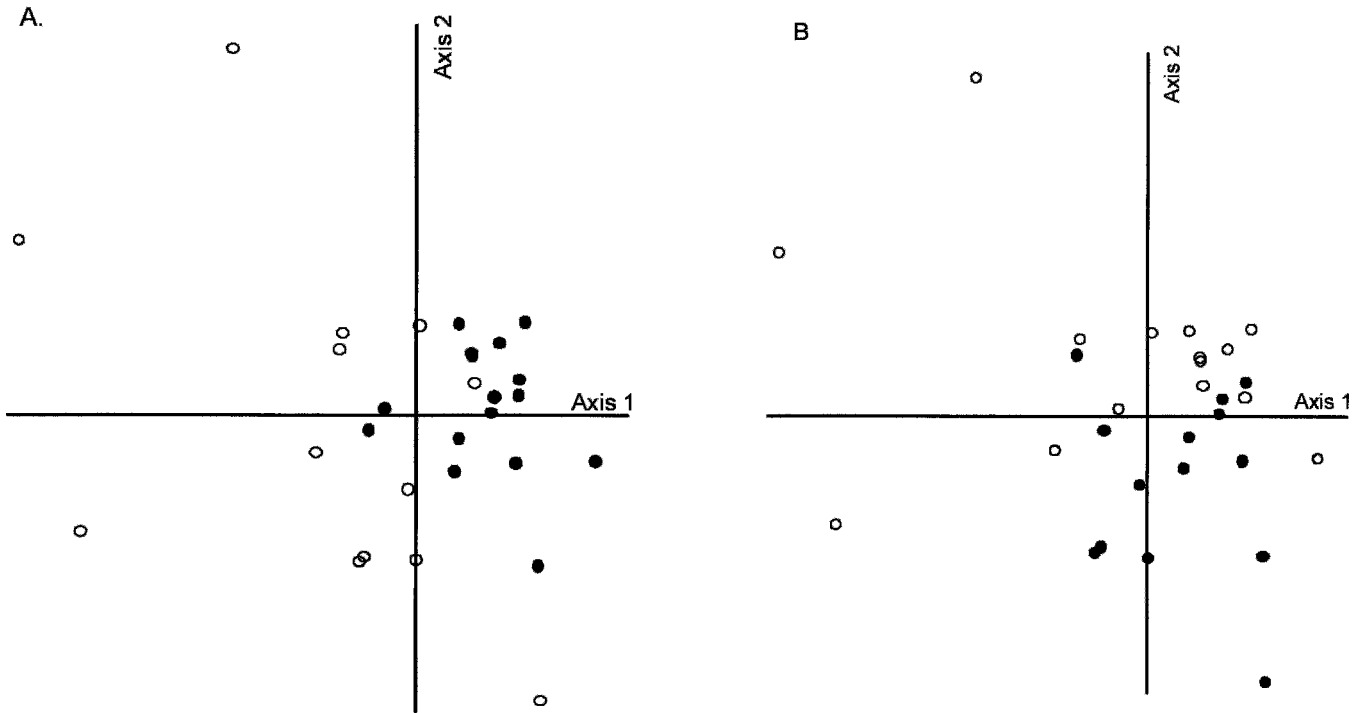


Figure 2. Non-metric multidimensional scaling ordination plot based on diatom species assemblages (sites in species space). A. Lateral marsh position: closed circles indicate low marsh sites and open circles indicate upper marsh sites. B. Longitudinal marsh position: closed circles indicate sites closer to the inflow and open circles indicate sites closer to the impoundment.

diatom distance matrix (Figure 2). Seventy-nine percent of the variance was partitioned between the 1st ($r^2 = 0.56$) and 2nd axis ($r^2 = 0.23$). The axes explained significantly more variance than would be expected by chance based on Monte Carlo permutation tests ($p = 0.03$). Axis 1 was driven primarily by the relative abundance of *F. capucina* ($r = 0.67$) and *M. varians* ($r = -0.74$). Axis 2 was driven primarily by the relative abundance of *S. construens* ($r = 0.61$) and *A. minutissimum* ($r = -0.64$). Lateral marsh position separated along the 1st axis, with sites in the low marsh being positively correlated with the first axis (Figure 2a). Longitudinal marsh position was not clearly separated along the ordination axes (Figure 2b).

Patterns of spatial autocorrelation, measured as semi-variance and Moran's I, differed between dominant diatom species and entire assemblage (NMDS axis scores). NMDS1 (Figure 3c) displayed a trend of linearly increasing semi-variance for distances up to 300 m. For distances greater than 325 m, there was no clear pattern in spatial correlation. In contrast, the NMDS2 and relative abundance of *A. minutissimum* displayed strong spatial patterns along the entire length of the wetland. For NMDS2, semi-variance increased almost linearly for distances greater than 150 m

(Figure 3a). Moran's I calculated for NMDS2 was noisy but displayed an overall trend of positive spatial autocorrelation for distances up to approximately 330 m and negative spatial autocorrelation for greater distances (Figure 3d). For *A. minutissimum*, semi-variance increased for all distances (Figure 3b). Moran's I calculated for *A. minutissimum* was noisy, but displayed an overall trend of negative spatial autocorrelation for distances greater than 570 m (Figure 3e). The relative abundance of *S. construens*, *F. capucina*, and *Nitzschia palea* (Kütz.) W. Sm. did not display spatial dependence.

Simulation results showed that species richness increased as a function of sampling effort until the simulation of collecting and compositing of five samples (richness = 54, Figure 4). Simulating the compositing of additional samples did not increase richness. Variability of richness among the 99 replicates tends to stabilize after five samples are composited.

DISCUSSION

Common approaches for diatom-based bioassessment include inference models that define species optima and tolerances to environmental variables (Pan and Stevenson 1996, Winter and Duthie 2000,

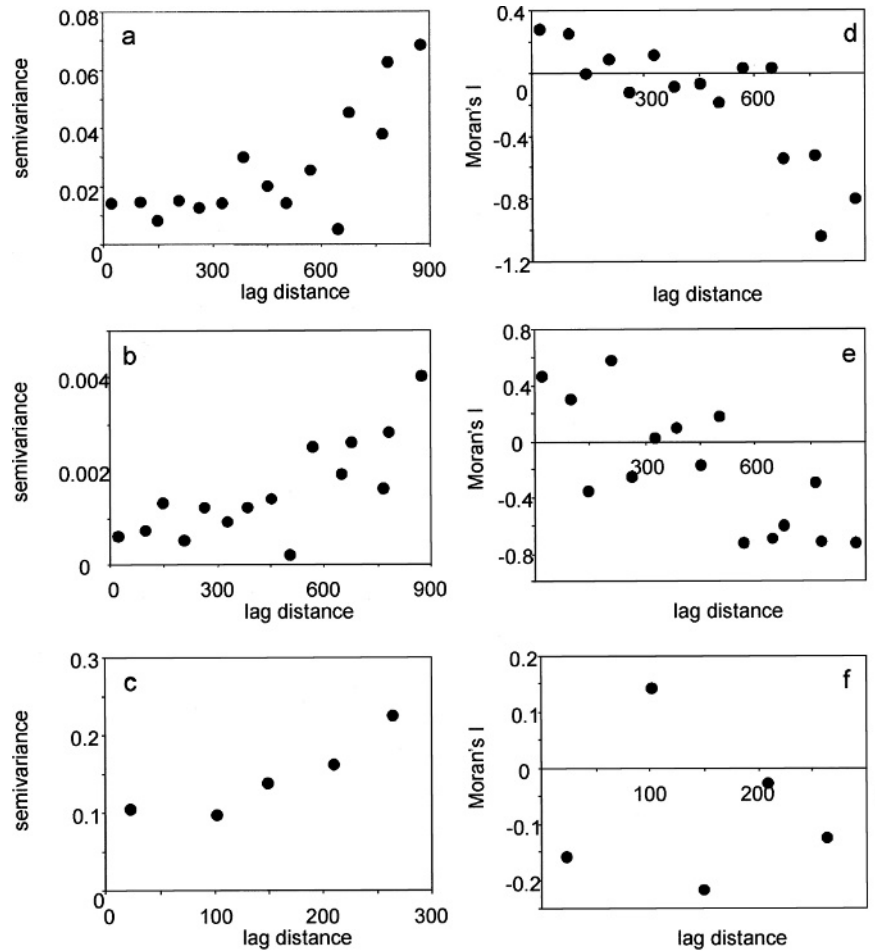


Figure 3. Semivariograms (a. NMDS2 axis scores; b. *A. minutissimum* relative abundance; c. NMDS1 axis scores) and correlograms (d. NMDS2 axis scores; e. *A. minutissimum* relative abundance; f. NMDS1 axis scores) calculated in GS+.

Potapova et al. 2004) and metrics based on ecological preferences of common taxa (Stevenson and Bahls 1999). Both approaches require that the

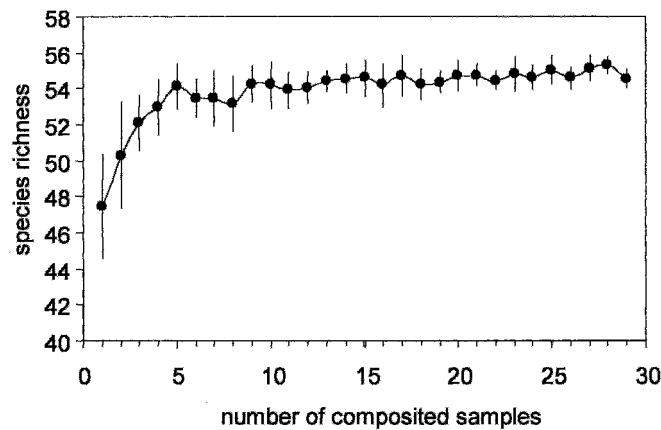


Figure 4. Effect of counting effort on diatom species richness for Rooster Rock surface-sediment diatom assemblages (mean and standard deviation of 99 replicates).

diatom assemblage be accurately characterized prior to inferring environmental conditions. Multiple lines of evidence explored in this study demonstrate that the wetland surface-sediment diatom assemblages display spatial heterogeneity and are complex, integrating species from benthic, epiphytic, and planktonic habitats. All sampling points contained both benthic and planktonic taxa, and the proportion of each type varied throughout the wetland (median % benthic = 92%, range 46–97%). The most abundant taxa included both benthic (e.g., *A. minutissimum*, *F. capucina*, *N. palea*) and planktonic species (e.g., *A. granulata*, *Tabellaria* spp.). *Staur-osira construens*, the most common taxon in the wetland, is characterized as tycho planktonic with a benthic preference (Kienel and Kumke 2002). Tycho planktonic *Fragilaria-Staurosira-Staurosirella* taxa are often very abundant in shallow systems, with relative abundances of 80% being reported in surface sediments (Brugam et al. 1998). Several studies have reported a mixture of diatoms from multiple habitats deposited in the surface sediments

that relates to water depth (Earle et al. 1988, Anderson 1990). Moos et al. (2005) found that the ratio of benthic to planktonic taxa in the surface sediments varied with water depth, with a shift to dominance by benthic taxa at depths less than 8 m. In contrast, Wolfe (1996) found that the relative abundance of benthic taxa varied up to 30% in the surface sediments but was not related to water depth. Relative abundances of the five most common taxa were variable throughout Rooster Rock wetland, with differences ranging between 15 and 39%, on the order reported for similar studies. *Stephanodiscus hantzschii*, the dominant planktonic species, varied by over 30% between surface sediment samples (Anderson 1990). *Fragilaria acidobiontica* relative abundance ranged between 7 and 41% in the surface sediments due to the varying importance of littoral and planktonic species (Charles et al. 1991).

Environmental forces, driven by the complex hydrology of Rooster Rock, may be responsible for the spatial heterogeneity of the surface-sediment diatom assemblage. The low marsh has more seasonally stable conditions, potentially driving the greater similarity of surface sediment samples within this area. Water depth changes gradually from the low marsh to the upper marsh, resulting in a lateral gradient of distinct vegetation zones. Surface sediment assemblages were related more to lateral location than longitudinal position. Vegetation influences the type of algae present by acting as a substrate for colonization, changing the light environment and by mediating the available nutrients. Pip and Robinson (1984) found that the frequency of *Fragilaria* taxa varied by more than 35% on different wetland macrophytes. Eminson and Moss (1980) found that the influence of plant host type on the periphyton assemblage was most important in infertile lakes. Rooster Rock has low levels of nutrients compared to other Oregon wetlands (Weilhoefer, unpublished data), so differences in vegetation composition between the low marsh and upper marsh might contribute to the spatial heterogeneity of the surface sediment diatom assemblage. The interaction of hydrology and vegetation may also result in differential sediment mixing and re-suspension throughout the wetland, and subsequently, spatial heterogeneity of surface sediment diatom assemblages. Wind mixing of sediments has been shown to be heterogeneous in shallow lakes, with only a small proportion of the lakebed being subjected to mixing at any point in time (Carper and Bachmann 1984). Wind mixing of sediments is lower in vegetated areas (Dieter 1990, Fennessy et al. 1994). In Rooster Rock, relative abundance of dense clumping grasses, such as

Phalaris arundinacea, was higher in the upper marsh, potentially resulting in reduced sediment re-suspension compared to the low marsh.

In dynamic ecosystems, such as wetlands, successful diatom-based models must be able to separate the variability caused by natural factors from that due to anthropogenic factors. Wilcox et al. (2002) reported that their multimetric models developed in Great Lake shoreline wetlands may not be valid unless the models were calibrated against temporal hydrologic variability. Dominant algal assemblages in a freshwater wetlands often experience seasonal cycles as conceptualized by Goldsborough and Robinson (1996). However, the surface sediment contained siliceous remains of benthic, epiphytic, and planktonic diatom species, indicating that it integrates species growing in different wetland habitats over time and might be the ideal collection substrate for diatom-based bioassessment. Inference models based on these sediment diatom assemblages may be more robust than models developed based on a one-time sampling of diatom assemblages. However, spatial heterogeneity of surface sediment diatom assemblages within a wetland may affect the accuracy and precision of diatom-based inference models that require adequately estimated species richness and their abundances. Our results suggest that we need to collect at least five composite samples to characterize the diatom assemblage in the Rooster Rock wetland adequately. The actual number of composite samples in each wetland may vary according to the wetland's size and hydrologic and habitat complexity. Further study is needed to focus on the cost-benefit between sampling efforts and bioassessment goals.

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LITERATURE CITED

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