PRIMARY RESEARCH PAPER

Non-wadeable river bioassessment: spatial variation of benthic diatom assemblages in Pacific Northwest rivers, USA

Yangdong Pan · Robert M. Hughes ·
Alan T. Herlihy · Philip R. Kaufmann

Abstract Current bioassessment efforts are focused on small wadeable streams, at least partly because assessing ecological conditions in non-wadeable large rivers poses many additional challenges. In this study, we sampled 20 sites in each of seven large rivers in the Pacific Northwest, USA, to characterize variation of benthic diatom assemblages among and within rivers relative to environmental conditions. Analysis of similarity (ANOSIM) indicated that diatom assemblages were significantly different among all the seven rivers draining different ecoregions. Longitudinal patterns in diatom assemblages showed river-specific features. Bray–Curtis dissimilarity index values did not increase as a function of spatial distance among the sampled reaches within any river but the Malheur. Standardized Mantel r of association between assemblage similarity and spatial distance among sites ranged from a high of 0.69 (Malheur) to a low of 0.18 (Chehalis). In the Malheur River, % monoraphids, nitrogen-tolerant taxa, and beta-mesosaprobous taxa all decreased longitudinally while % motile taxa, especially *Nitzschia*, showed an opposite trend, reflecting a strong in-stream water quality gradient. Similar longitudinal trends in water quality were observed in other rivers but benthic diatom assemblages showed either weak response patterns or no patterns. Our study indicated that benthic diatom assemblages can clearly reflect among-river factors. The relationships between benthic diatom assemblages and water quality within each river may depend on the strength of the water quality gradients, interactive effects of water quality and habitat conditions, and diatom sampling design.

Y. Pan (✉)
Environmental Science and Management, Portland State University, Portland, OR 97207, USA
e-mail: pany@pdx.edu

R. M. Hughes
Amnis Opes Institute, Corvallis, OR 97333, USA

R. M. Hughes
Departmento de Biologia, Universidade Federal de Lavras, Lavras, MG 37200-000, Brasil

A. T. Herlihy
Department of Fisheries and Wildlife, Oregon State University, c/o US Environmental Protection Agency, Corvallis, OR 97333, USA

P. R. Kaufmann
US Environmental Protection Agency, 200 SW 35th Street, Corvallis, OR 97333, USA

Introduction

Assessing ecological conditions in non-wadeable rivers is challenging. Draining large areas of land with a variety of human disturbances, large rivers may be

affected concurrently by multiple anthropogenic activities (e.g., dams, channelization, timber harvest, agriculture, and urbanization). In addition, large rivers are managed for multiple human needs such as fisheries, flood control, and hydropower. Consequently, it is difficult to assess cause–effect relationships between the stressors and ecological conditions in rivers (Johnson et al., 1995). In non-wadeable rivers, benthic habitats suitable for algal growth may be restricted to shallow portions of rivers or river margins because increased river depth and turbidity limit benthic algal growth (Vannote et al., 1980). River littoral zone habitats have heterogeneous substrate and canopy cover, and exhibit great fluctuations in water depth, wave action, and light penetration. For instance, Hudon et al. (2000) concluded that site exposure, water depth, and transparency were the primary predictors for macrophytes in two Canadian rivers' littoral zones.

Few diatom-based bioassessment studies have been conducted in large rivers (but see Reavie et al., 2010; Sgro et al., 2010). Fore & Grafe (2002) developed a multimetric diatom index from a dataset collected from 23 Idaho rivers. Their index reflected human disturbance at both site and basin spatial extents. Several programs, aimed at assessing relationships between benthic diatoms and environmental conditions at the basin scale, do sample sites in headwaters, tributaries, and non-wadeable rivers (Leland et al., 2001). Lane et al. (2007) compared four methods for sampling algae in large rivers with an emphasis on sampling efficiency. However, there have been very few studies in which multiple sites within multiple large rivers have been sampled to assess spatial variability in benthic diatom assemblages. Consequently, the longitudinal or spatial variation of benthic diatoms in large river littoral zone habitats remains largely unknown. In this study, we assessed spatial variation of benthic diatom assemblages both among seven non-wadeable rivers and within each river in relation to environmental conditions. The rivers were selected across varying landscapes in the Pacific Northwest, USA and 20 sites in each river were sampled. We used systematic, transect-based sampling protocols developed by Peck et al. (in press) from wadeable stream protocols (Peck et al., 2006), in contrast to targeted sampling methods applied by others (e.g., Moulton et al., 2002). Weilhoefer & Pan (2007) reported that benthic diatom assemblages generated from targeted and transect sampling were similar for small wadeable streams, but not for non-wadeable river sites.

Methods

River sample sites

The Cascade Mountains divide the states of Oregon and Washington, USA, into two regions with contrasting climate and runoff characteristics (Jackson & Kimerling, 1993). The Willamette, Chehalis, and Umpqua rivers are located west of the Cascade Mountains with annual precipitation of 1–4 m (Fig. 1; Table 1). The mountain peaks of their headwaters can have 5–20 m snow caps. The John Day, Malheur, Okanogan, and Sprague rivers are on the arid east side of the Cascade Mountains with <0.5 m annual precipitation (Naiman & Bilby, 1998). The watershed areas ranged from 3,554 (Chehalis) to 28,912 km^2 (Willamette).

Twenty sites (length of each site = 50 × mean wetted channel widths) along each mainstem river were selected randomly from the U.S. River Reach File Version 3 (Stevens & Olsen, 2004) (Fig. 1). The sampled distance along each mainstem river ranged from 87 to 254 km. The study reach in these large rivers were substantially longer than those of the wadeable streams and may cover a variety of habitats. To characterize each study reach in a spatially balanced way, 11 cross-section transects (including a transect at the start and the end of each site) in each site were established by dividing the site into 10 equal length intervals. The river sites were sampled using 14-ft inflatable rafts with rowing frames attached. The use of inflatable rafts enables crews to access sample reaches inaccessible to most other boat types. Two rafts, each with a crew of two persons, sampled biota including benthic diatoms and characterized physio-chemical conditions, respectively (see the following sections). The sampling methods were described in detail by Peck et al. (in press).

Benthic diatoms

One benthic diatom sample was collected in the littoral zone at each of the 11 transects during the summers of 2006–2008. Benthic diatom samples were collected from alternating shorelines every two transects to reduce the effects of aspect and shading. At each transect, diatoms were collected from a 12 cm^2 area using a 1.5 cm long piece of 3.9-cm diameter PVC pipe as a template. For fine substrate, diatoms
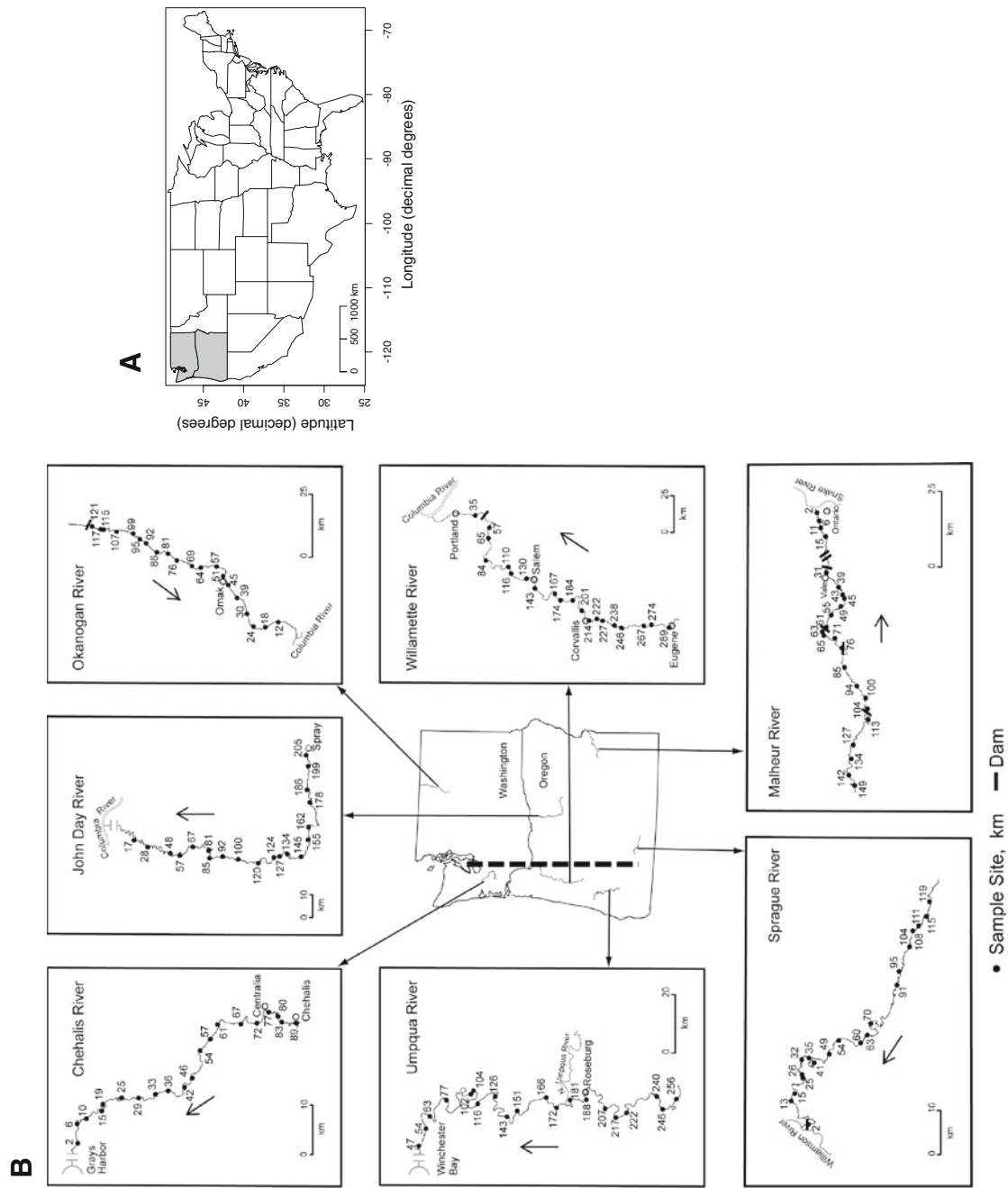
Fig. 1 **A** A map of the USA showing states of Oregon (OR) and Washington (WA), and **B** a map of OR and WA showing the locations of seven rivers and sampling sites in each river. The arrows indicate the direction of flow and the *black bars* across the rivers indicate the dams. The *vertical dash line* indicates the Cascade Mountains. The *site numbers* represent distances in km from the mouths

Table 1 Median and coefficient of variation (in parentheses) of selected environmental variables. W: west of the Cascade Mountains, E: east of the Cascade Mountains

Variable	Chehalis (W)	Umpqua (W)	Willamette (W)	John Day (E)	Malheur (E)	Okanogan (E)	Sprague (E)
Water quality							
Chloride (µeq/l)	174.45 (0.08)	109.02 (0.61)	82.22 (0.37)	39.07 (0.14)	142.72 (0.96)	99.43 (0.11)	34.83 (0.11)
Conductivity (µS/cm)	104 (0.05)	79 (0.38)	66.5 (0.15)	200 (0.09)	269.5 (0.81)	301 (0.1)	113 (0.07)
Maximum July PRISM air temperature (°C)	25.35 (0.02)	28.74 (0.03)	27.22 (0.01)	32.31 (0.04)	34.01 (0.01)	31.34 (0.02)	28.84 (0.02)
Sulfate (µeq/l)	70.58 (0.13)	44.66 (0.63)	87.44 (0.31)	112.27 (0.13)	371.95 (1.31)	732.97 (0.15)	14.99 (0.11)
Total nitrogen (µg/l)	550 (0.37)	160 (0.8)	355 (0.39)	215 (0.1)	465 (1.19)	160 (0.15)	250 (0.14)
Total Phosphorus (µg/l)	69.5 (0.23)	49 (0.68)	59 (0.28)	31 (0.12)	283.5 (0.24)	26 (0.26)	77.5 (0.18)
Turbidity (NTU)	0.97 (0.32)	0.48 (0.32)	1.62 (0.38)	0.55 (0.2)	16.8 (0.31)	0.89 (0.33)	2.55 (0.46)
Habitat							
% coarse dominant littoral substrate	31.82 (0.69)	18.18 (0.97)	45.45 (0.6)	59.09 (0.27)	54.55 (0.49)	27.27 (0.74)	0 (1.42)
% sand + fine dominant littoral substrate	27.27 (0.63)	18.18 (1.09)	36.36 (0.74)	13.64 (0.95)	27.27 (0.75)	54.55 (0.35)	59.09 (0.33)
Channel sinuosity (m/m)	1.26 (0.3)	1.17 (0.43)	1.27 (0.24)	1.5 (1.54)	1.21 (0.52)	1.13 (0.31)	1.44 (0.22)
Mean bank canopy density (%)	39.24 (0.36)	29.95 (0.43)	36.23 (0.32)	2.34 (0.86)	27.74 (0.37)	37.7 (0.37)	7.02 (0.96)
Mean littoral depth (m)	0.29 (0.44)	0.2 (0.76)	1.03 (0.22)	0.25 (0.27)	0.57 (0.43)	0.75 (0.27)	0.23 (0.35)
Mean width × thalweg depth (m^2)	76.97 (0.49)	152.61 (0.7)	291.49 (1.32)	66.37 (0.31)	19.53 (0.43)	100.92 (0.41)	34.78 (0.62)
Percent of reach with snags	57.69 (0.27)	20.1 (0.74)	47.5 (0.43)	0 (1.66)	2 (1.21)	39 (0.25)	3.91 (1.5)
Total riparian disturbance index values	1.42 (0.39)	1.43 (0.33)	1.73 (0.49)	0.89 (0.38)	1.28 (0.41)	2.21 (0.19)	1.35 (0.41)
Site elevation (m)	23.5 (0.6)	93.5 (0.64)	51 (0.59)	405 (0.26)	723 (0.1)	260.5 (0.05)	1305.5 (0.01)
Landscape							
Sampled watershed area (km^2)	3554.18	10490.76	28911.59	17819.92	8829.29	21115.41	4168.99
Sampled river distance (km)	86	208	256	190	123	110	108
% agriculture in 120 m buffer	9.69	7.63	20.85	1.46	4.62	4.97	3.88
% agriculture in Watershed	8.31	6.11	20.79	0.98	2.65	2.60	2.23
% urban in 120 m buffer	7.21	4.56	6.88	2.01	1.09	5.82	0.49
% urban in watershed	7.90	2.51	6.95	0.79	0.53	2.40	0.37
Population density in 120 m buffer (persons/km^2)	21	10	64	1	1	6	0
Population density in watershed (persons/km^2)	24	9	70	1	1	4	1
Road density in 120 m buffer (m/ha)	16.84	21.08	18.48	19.17	12.65	19.25	13.31
Road density in watershed (m/ha)	16.93	13.82	18.45	10.72	7.45	9.93	14.17

were aspirated into a 60 ml syringe and then placed into a container; in coarse substrate, diatoms were brushed off with a toothbrush and rinsed with river water into the same container. All samples ($n = 11$) were combined into one single diatom sample per site and preserved with 37% formalin.

Diatom valves were cleaned with concentrated nitric acid using the Microwave Accelerated Reaction System (Model MARS® 5, CEM Corporation). The digestion was done following a pre-programmed digestion scheme (temperature: 180°C, pressure: 350 PSI, ramp: 15 min, hold: 15 min). Digested diatoms were rinsed with distilled water repeatedly until the pH of the sample was approximately neutral. Cleaned valves were mounted in NAPHRAX® to make permanent slides for taxa identification and enumeration (Patrick & Reimer, 1966). A minimum of 600 valves were counted at $1,000\times$ magnification using an Olympus compound microscope with deferential interference contrast optics. Diatom taxonomy mainly followed Krammer & Lange-Bertalot (1986, 1988, 1991a, b) and Patrick & Reimer (1966, 1975).

Water quality

Conductivity and temperature were measured at each transect with a conductivity pen to assess within-site variation in water quality. At the downstream end of each site, a single 500-ml grab sample was collected to characterize water quality. The sample was sealed, and transported on ice to the laboratory for analysis. Anions were measured by ion chromatography. Total nitrogen (TN) and total phosphorus (TP) were estimated by persulfate oxidation and colorimetry. Detailed information on the analytical procedures used for each of the analyses can be found in US EPA (1987).

Physical habitat structure

Physical habitat was characterized in the thalweg and at each of 11 transects in the littoral zones. In-channel habitat characterizations of the main channel and its littoral areas were evaluated in a continuous longitudinal profile and in 11 20-m long plots extending 10 m from the river bank into the river and 10 m from the channel margin into the riparian zone. River habitat characterization included thalweg depth, bankfull width and depth, mean wetted width and depth, slope,

and surficial substrates. At each transect, the presence and the proximity of 11 categories of human activities in the riparian zone were also visually estimated (i.e., row crops, pasture, dams and revetments, buildings, pavement, roadways, pipes, landfill or trash, parks/lawns, logging operations, and mining activities). Proximity-weighted riparian disturbance indices were calculated by tallying the number of riparian transects at which particular types of disturbance was observed, weighting by their proximity to the river, and then averaged over all transects in the site (Kaufmann et al., 1999). Scores of disturbance indices ranged from 0 to 5 (low to high disturbance).

Data analysis

Variation of diatom assemblages within each river and among rivers were summarized using non-metric multidimensional scaling (NMDS), a multivariate ordination technique commonly used in ecological community analysis (Clarke, 1993). Diatom relative abundance was square-root transformed to dampen the impacts of dominant species on the ordination analysis. Bray–Curtis dissimilarity indices were calculated among the sites. NMDS projects each site into a species-defined ordination space with two or more dimensions based on their ranked dissimilarity. The goodness-of-fit for the NMDS projections was measured as a stress value which quantifies the deviation from a monotonic relationship between the distance among sites in the original Bray–Curtis dissimilarity matrix and the distance among sites in the ordination plot. The NMDS was run 20 times each with a random starting configuration. The final NMDS dimension was selected based on the lowest stress value among the best solutions. Both global and pair-wise analysis of similarity (ANOSIM) tests were performed to test if diatom assemblages were significantly different among the seven rivers. A Bonferroni correction for multiple tests was applied to the significance level when each pair-wise comparison was made. The NMDS axis scores were used to summarize diatom assemblages for each site and the relationships between the NMDS axis scores and environmental variables were assessed using Spearman Rank correlation coefficients (ρ).

Benthic diatom assemblages in each river were further characterized using indicator species analysis (Dufrêne & Legendre, 1997) and selected diatom

metrics (van Dam et al., 1994; Stevenson & Bahls, 1999). Indicator species were defined as the taxa with *P* values < 0.05. *P* values of indicator values for all taxa were determined using Monte Carlo permutation tests (1000 times).

We used regression trees (Brieman et al., 1984) to identify a set of environmental predictors that best explained diatom species/group distribution patterns. The tree-based model can automatically handle interactions between predictor variables and illustrate hierarchical relationships among predictor variables. A stopping point of the binary divisions was determined based on predictive errors generated from cross-validation analyses. This cross-validation procedure is similar to a leave-one-out jackknifing method.

The Mantel test (1967) was used to test if diatom assemblage similarity among sites was related to their spatial distances (river distance). We expected that sampled reaches close to each other would share more diatom species. The test was selected largely because of potential spatial dependence among the sites within each river. Bray–Curtis dissimilarity indices were calculated among the sites to summarize longitudinal variation of diatom assemblages within each river. Spatial distances among the sites were calculated based on river distance. The significance tests for the Mantel test statistics (standardized *r*) were performed with 1,000 permutations. All methods described above were performed using R software (R Development Core Team, 2007). Specifically, we used 'MASS' and 'vegan' packages for NMDS, ANOSIM and Mantel tests, 'rpart' for regression tree, and 'labdsv' package for indicator species analysis.

Results

### Variation in environmental characteristics and benthic diatom assemblages among rivers

The rivers situated west of the Cascade Mountains were generally low in median conductivity (Table 1). The Chehalis River had higher median nutrient concentration than the two other west side rivers. Median chloride concentration in the Chehalis River was highest among all seven rivers (Fig. 2). The rivers east of the Cascade Mountains were generally characterized by higher median conductivity and

maximum July PRISM (PRISM Climate Group, 2010) air temperature. Median turbidity in the Malheur River sites was 16.8 NTU, >5 times higher than the highest median turbidity of the other six rivers (Fig. 2; Table 1). The median total phosphorus concentration in the Malheur River was >9 times higher than those in the John Day River sites (Fig. 2).

Habitat structure along river banks and in littoral zones showed less clear patterns than water quality between the rivers separated by the Cascade Mountains (Table 1). Median bank riparian canopy cover was ~30% in the three rivers west of the Cascade Mountains. The sites in the John Day and Sprague rivers had much lower median canopy cover (2, 7%, respectively) but the sites in the Okanogan River had similar canopy cover (38%) as the rivers west of the Cascade Mountains. Median littoral zone depth varied from 1.03 m in the Willamette River to 0.20 m in the Umpqua River. Coarse substrates were common in the littoral zone in the John Day, Malheur, and Willamette rivers while % sand and fines as dominant substrates were relatively high (>50%) in the Okanogan and Sprague rivers.

Variation in benthic diatom assemblages among rivers was generally higher than that within rivers (Fig. 3). The NMDS site plot showed three clusters. The second NMDS axis separated the sites in the Chehalis and Willamette rivers, two western lowland rivers, from the three eastern rivers. The Umpqua River, situated within the east–west gradient in the diatom-based ordination space, was more similar to the eastern rivers. The Malheur River sites formed their own cluster separated from all other rivers along the first NMDS axis. ANOSIM tests showed that diatom assemblages were significantly different among all seven rivers ($R = 0.92$, $P < 0.001$), although not all sites were tightly clustered together in some rivers (e.g., the Umpqua River). The lowest ANOSIM R value (0.45, between the Willamette and Chehalis rivers) was still significantly different from random using a Bonferroni corrected α (0.002) for multiple comparison tests.

The diatom assemblages in both the Willamette and Chehalis rivers were dominated by two monoraphid diatom taxa, *Achnanthidium deflexum* (Reimer) Kingston and *Achnanthidium minutissimum* (Kützing) Czarnecki (Table 2). These two taxa were indicator species in the Chehalis River (Table 2). The indicator taxa in the Willamette River included two dominant
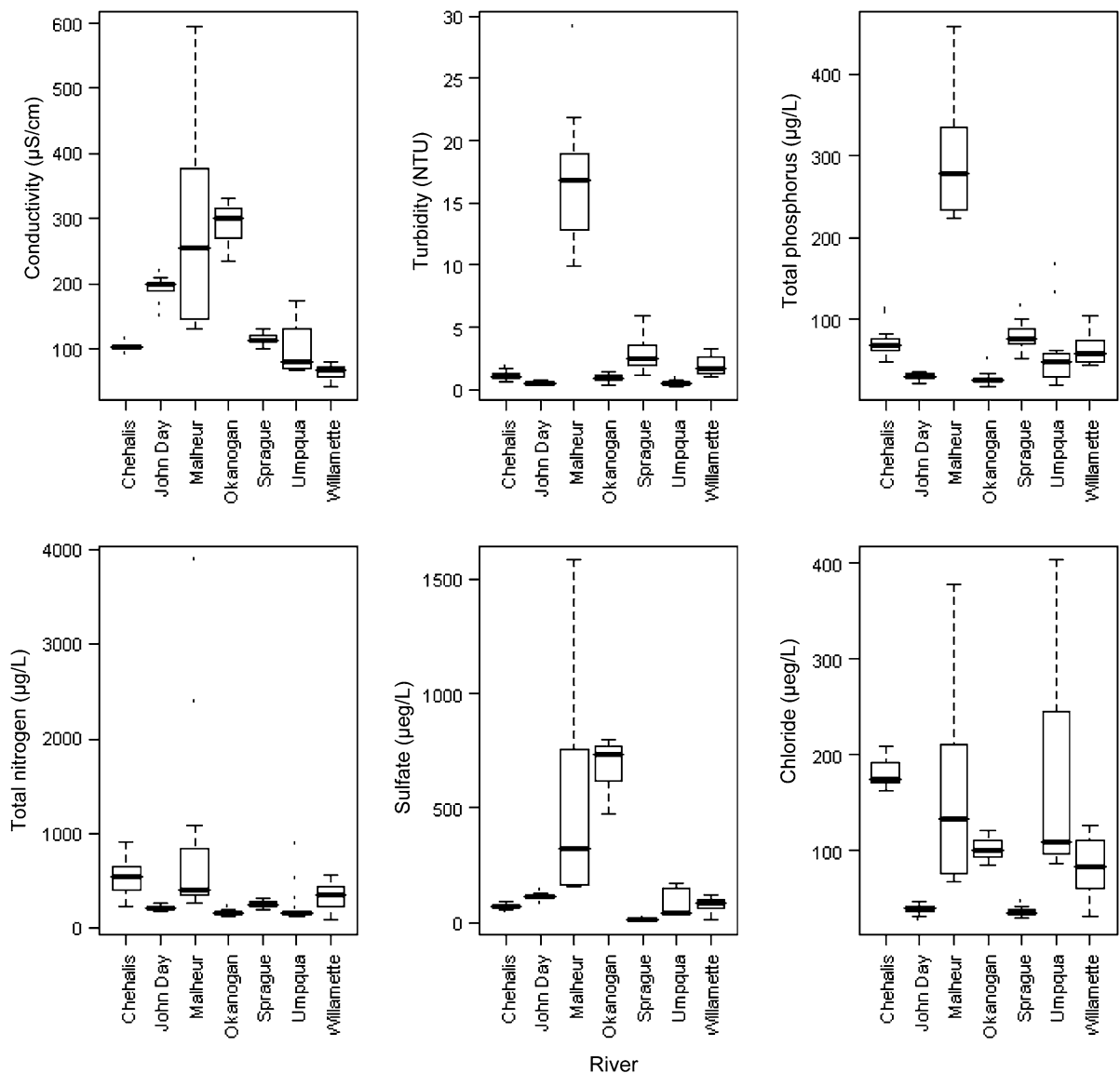
Fig. 2 Comparison of selected water quality variables among seven rivers

taxa (*Encyonema minutum* (Hilse.) Mann and *Nitzschia tropica* Hustedt) as well as 15 other taxa (Table 2). Several chain-forming small-size araphid Fragilariaceae taxa dominated the diatom assemblages in the rest of the rivers (Fig. 4).

This group of taxa reached a high abundance in the sites with low TN concentrations (Fig. 4a). Under low TN concentrations (<325 µg l^{-1}), substrate and conductivity further differentiated rivers based on relative abundances of the Fragilariaceae taxa (Fig. 4b). *Staurosira construens* var. *venter* (Ehrenberg)

Hamilton and *Pseudostaurosira brevistriata* (Grunow) Williams et Round were indicator species of the Okanogan River among other, less dominant, indicator taxa (Table 2). The diatom assemblages in the Sprague River were distinguished by several *Aulacoseira* species (Table 2). *Epithemia sorex* Kützing, a diatom species with N-fixing symbionts, was one of the dominant taxa in both the John Day and Umpqua rivers. In the John Day River, 11% of the diatom individuals were N-fixers (Table 3). The diatom assemblages in the Umpqua River were dominated
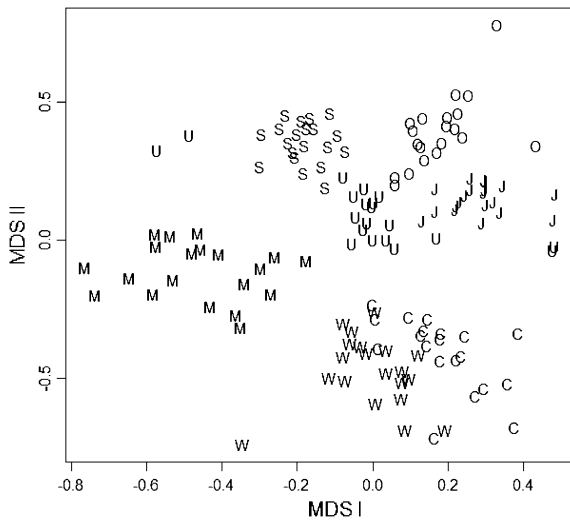
Fig. 3 An ordination plot of sites based on diatom assemblage dissimilarity showing all seven rivers and the sampled sites in each river (*C* Chehalis, *J* John Day, *M* Malheur, *O* Okanogan, *S* Sprague, *U* Umpqua, *W* Willamette)

by both small-size chain-forming Fragilariaceae species and *A. minutissimum.* Two out of the five dominant taxa in the Malheur River were *Nitzschia* taxa, and the majority of the indicator taxa were either *Nitzschia* or *Navicula* taxa. The diatom assemblages in the Malheur River on average had the highest relative abundance of taxa (54%) with high or moderate motility (*Nitzschia* and *Navicula* taxa) and the lowest relative abundance of pollution sensitive taxa (43%) among all the rivers (Table 3).

Overall, centric diatoms consisted of a low proportion of benthic diatom assemblages (Table 3). Percent of centric diatoms was 12 and 14% in the Malheur and Sprague rivers, respectively. For the rest of the rivers, the percentage was less than 5%.

Spatial variation in environmental characteristics and benthic diatom assemblages within rivers

Water quality showed relatively strong longitudinal trends within several rivers. Conductivity, chloride, sulfate, and nutrient concentrations all increased longitudinally downstream in the Malheur and Willamette rivers (Fig. 5, Table 4). At least one of these water quality variables showed a similar trend in the John Day, Okanogan, and Sprague rivers. The opposite trend for both chloride and TP was observed

in the Chehalis River. Turbidity decreased downstream in both the Sprague and Okanogan rivers. Longitudinal patterns were less evident for measured habitat condition variables. Both % coarse dominant littoral substrate and riparian disturbance decreased toward the river mouth in the Umpqua River.

Longitudinal patterns in benthic diatom assemblages varied among the rivers (Table 4). The NMDS axis II site scores, a surrogate of benthic diatom assemblages, were strongly correlated with the river distance to the mouth in both the Malheur and Okanogan rivers ($\rho > 0.8$). Proportion of pollution sensitive diatom taxa decreased longitudinally downriver in the John Day, Malheur, and Willamette rivers (Fig. 6). Bray–Curtis dissimilarity index values varied substantially with spatial distance among the sites, but did not increase as a function of spatial distance among the sites within each river except in the Malheur River (Fig. 7). Standardized Mantel r ranged from a high of 0.69 (Malheur) to a low of 0.18 (Chehalis). In the Malheur River, % of monoraphids, N-tolerant taxa, and β-mesosaprobous taxa all decreased longitudinally downriver. The diatom assemblages in the upriver sites were co-dominated by *Nitzschia, Navicula,* and two monoraphid taxa (*A. minutissimum* and *Cocconeis placentula* Ehrenberg.). *Nitzschia* in several downriver sites was approximately double that in upriver sites, with the site at km 50 the highest at 76% (Fig. 8D), whereas the relative abundance of the monoraphid taxa decreased to near zero in the downriver sites (Fig. 8A). The increase in *Nitzschia* relative abundance in the downriver sites was primarily contributed by *N. amphibia* Grunow (Fig. 8D).

Discussion

Spatial variation of benthic diatom assemblages among rivers

Benthic diatom assemblages in large rivers reflect coarse-scale factors such as climate, geology, and land-use. The assemblages, collected from 20 sites within each river, were significantly different among the seven rivers in the Pacific Northwest. The Cascade Mountains divide the Pacific Northwest into two regions with contrasting land-use, climate, and runoff characteristics. The Chehalis and Willamette rivers, two lowland western rivers, shared several dominant

Table 2 Dominant taxa (proportional abundances) and indicator taxa significant indicator values selected based on the within rivers

Taxa	Mean proportional abundance	Indicator value	*P* value
Chehalis River (W)			
Achnanthidium deflexum (Reimer) Kingston (M)	0.21	73.75	<0.001
Achnanthidium minutissimum (Kützing) Czarnecki (M)	0.16	30.41	<0.001
Cocconeis placentula Ehrenberg (M)	0.06		n.s.
Nitzschia inconspicua Grunow (B)	0.04		n.s.
Gomphonema minutum (Agardh) Agardh (B)	0.03	38.03	<0.001
Cyclotella atomus Hustedt ©	0.02	34.15	<0.001
Hippodonta capitata (Ehrenberg) Lange-Bertalot Metzelt in et Witkowski (B)	0.00	26.66	<0.001
Navicula gregaria Donkin (B)	0.01	48.09	<0.001
Nitzschia archibaldii Lange Bertalot (B)	0.01	15.90	0.039
Synedra acus Kützing (A)	0.01	30.50	0.001
Umpqua River (W)			
Pseudostaurosira brevistriata (Grunow) Williams et Round (A)	0.12		n.s.
Staurosira construens var. *venter* (Ehrenberg) Hamilton (A)	0.1		n.s.
Achnanthidium minutissimum (Kützing) Czarnecki (M)	0.07		n.s.
Nitzschia inconspicua Grunow (B)	0.05		n.s.
Nitzschia tropica Hustedt (B)	0.05		n.s.
Navicula minima Grunow (B)	0.04	35.35	0.001
Nitzschia fonticola Grunow (B)	0.04	35.65	<0.001
Caloneis bacillum (Grunow) Cleve (B)	0.03	61.68	<0.001
Cocconeis pediculus Ehrenberg (M)	0.02	29.89	<0.001
Navicula menisculus Schumann (B)	0.01	19.18	0.041
Willamette River (W)			
Achnanthidium minutissimum (Kützing) Czarnecki (M)	0.11		n.s.
Achnanthidium deflexum (Reimer) Kingston (M)	0.07		n.s.
Nitzschia inconspicua Grunow (B)	0.07		n.s.
Cocconeis placentula Ehrenberg (M)	0.05		n.s.
Encyonema minutum (Hilse) Mann (B)	0.05	47.55	<0.001
Nitzschia tropica Hustedt (B)	0.05	25.53	<0.001
Cymbella turgidula Grunow (B)	0.04	58.50	<0.001
Planothidium lanceolatum (Brébisson ex Kützing) Lange Bertalot (M)	0.04	25.91	0.007
Encyonema silesiacum (Bleisch) Mann (B)	0.02	32.86	0.002
Gomphonema kobayasii Kociolek et Kingston (B)	0.02	29.50	0.002
Luticola goeppertiana (Bleisch) Mann (B)	0.02	29.33	<0.001
Adlafia minuscula (Grunow) Lange Bertalot (B)	0.01	28.21	<0.001
Fragilaria capucina var. *capitellata* (Grunow) Lange Bertalot (A)	0.01	44.09	<0.001
Fragilaria vaucheriae (Kützing) Petersen (A)	0.01	23.73	0.005
Gomphoneis herculeana (Ehrenberg) Cleve (B)	0.01	28.31	<0.001
Gomphonema mexicanum Grunow ex Van Heurck (B)	0.01	33.49	<0.001
Gomphonema rhombicum Fricke (B)	0.01	23.61	0.003
Karayevia suchlandtii (Hustedt) Bukhtiyarova (M)	0.01	54.62	<0.001
John Day River (E)			
Gomphonema pumilum (Grunow) Reichardt et Lange Bertalot (B)	0.15	66.43	<0.001
Staurosira construens var. *venter* (Ehrenberg) Hamilton (A)	0.14		n.s.

Table 2 continued

| Taxa	Mean proportional abundance	Indicator value	*P* value
Epithemia sorex Kützing (B, N-fixer)	0.1	50.83	<0.001
Cocconeis placentula Ehrenberg (M)	0.08		n.s.
Diatoma moniliformis Kützing (A)	0.07	70.98	<0.001
Reimeria sinuata (Gregory) Kociolek et Stoermer (B)	0.04	32.69	<0.001
Cyclotella meneghiniana Kützing (C)	0.03	63.03	<0.001
Nitzschia palea (Kützing) Smith (B)	0.03	27.08	<0.001
Nitzschia acicularis (Kützing) Smith (B)	0.02	38.20	<0.001
Synedra ulna (Nitzsch) Ehrenberg (A)	0.02	25.42	<0.001
Cyclostephanos invisitatus (Hohn et Hellerman) Theriot Stoermer et Håkansson (C)	0.01	46.12	<0.001
Diatoma mesodon (Ehrenberg) Kützing (A)	0.01	32.50	<0.001
Gomphonema olivaceum (Lyngbye) Kützing (B)	0.01	20.99	0.034
Malheur River (E)			
Nitzschia inconspicua Grunow (B)	0.12	39.07	<0.001
Cocconeis placentula Ehrenberg (M)	0.09	21.60	0.012
Aulacoseira crassipunctata Krammer (C)	0.07	61.36	<0.001
Nitzschia amphibia Grunow (B)	0.06	36.68	0.003
Staurosira construens var. *venter* (Ehrenberg) Hamilton (A)	0.06		n.s.
Rhoicosphenia abbreviata (Agardh) Lange Bertalot (A)	0.05	24.64	0.001
Navicula subminuscula Manguin (B)	0.04	86.79	<0.001
Nitzschia dissipata (Kützing) Grunow (B)	0.04	27.23	0.002
Melosira varians Agardh (C)	0.03	25.87	0.008
Nitzschia capitellata Hustedt (B)	0.03	76.00	<0.001
Nitzschia gracilis Hantzsch ex Rabenhorst (B)	0.03	23.70	0.011
Nitzschia filiformis (Smith) Van Heurck (B)	0.02	60.91	<0.001
Gomphonema parvulum (Kützing) Kützing (B)	0.01	36.95	<0.001
Mayamaea atomus var. *permitis* (Hustedt) Lange Bertalot (B)	0.01	31.25	<0.001
Navicula erifuga Lange Bertalot (B)	0.01	63.99	<0.001
Okanogan River (E)			
Pseudostaurosira brevistriata (Grunow) Williams et Round (A)	0.14	34.73	<0.001
Achnanthidium minutissimum (Kützing) Czarnecki (M)	0.13		n.s.
Staurosira construens var. *venter* (Ehrenberg) Hamilton (A)	0.07		n.s.
Staurosira construens (Ehrenberg) Williams et Round (A)	0.05	63.23	<0.001
Cocconeis placentula Ehrenberg (M)	0.04		n.s.
Cymbella affinis Kützing (B)	0.02	46.16	<0.001
Encyonopsis microcephala (Grunow) Krammer (B)	0.02	94.59	<0.001
Navicula capitatoradiata Germain (B)	0.02	28.93	<0.001
Navicula cryptotenella Lange Bertalot ex Krammer et Lange Bertalot (B)	0.02	21.39	0.013
Discostella stelligera (Cleve et Grunow) Houk et Klee (C)	0.01	60.82	<0.001
Fragilaria crotonensis Kitton (A)	0.01	45.91	<0.001
Fragilaria tenera (Smith) Lange Bertalot (A)	0.01	66.06	<0.001
Navicula cryptocephala Kützing (B)	0.01	32.71	<0.001
Nitzschia linearis (Agardh ex Smith) Smith (B)	0.01	26.80	<0.001
Nitzschia sociabilis Hustedt (B)	0.01	15.76	0.036

Table 2 continued

Taxa	Mean proportional abundance	Indicator value	P value
Sellaphora pupula (Kützing) Meresckowsky (B)	0.01	29.05	<0.001
Synedra rumpens Kützing (A)	0.01	31.95	<0.001
Sprague River (E)			
Staurosira construens var. *venter* (Ehrenberg) Hamilton (A)	0.17	30.94	<0.001
Pseudostaurosira brevistriata (Grunow) Williams et Round (A)	0.11		n.s.
Cocconeis placentula Ehrenberg (M)	0.07		n.s.
Staurosirella pinnata (Ehrenberg) Williams et Round (A)	0.05	32.84	<0.001
Epithemia sorex Kützing (B, N-fixer)	0.04		n.s.
Aulacoseira ambigua (Grunow) Simonsen (C)	0.03	53.67	<0.001
Aulacoseira distans (Ehrenberg) Simonsen (C)	0.03	56.87	<0.001
Aulacoseira italica (Ehrenberg) Simonsen (C)	0.02	57.72	<0.001
Caloneis silicula (Ehrenberg) Cleve (B)	0.01	61.45	<0.001
Geissleria acceptata (Hustedt) Lange Bertalot et Metzeltin (B)	0.01	65.87	<0.001
Rhopalodia gibba (Ehrenberg) Müller (B, N-fixer)	0.01	31.75	<0.001
Staurosirella lapponica (Grunow) Williams et Round (A)	0.01	68.69	<0.001

W west of the Cascade Mountains, *E* east of the Cascade Mountains, *A* araphids, *M* monoraphids, *B* biraphids

diatom taxa (Table 2). *A. minutissimum* and *A. deflexum*, two pollution sensitive taxa, were common and abundant in wadeable Oregon coastal streams (Naymik et al., 2005; Weilhoefer & Pan, 2006; Gillett et al., 2009). Streams in the Pacific Northwest are characterized by low ionic strength, buffering capacity, and nutrient concentrations (Welch et al., 1998). It is interesting that low elevation rivers such as the Chehalis River shared these dominant taxa with the small streams despite the fact that water quality constituents such as solids and nutrients are expected to increase from high elevation to low elevation because of more time for contact between water and bedrock/soils and increased anthropogenic disturbance in the watershed (Welch et al., 1998).

In contrast, diatom assemblages in the rivers situated in more arid intermountain regions, were characterized by several small chain-forming Fragilariaceae taxa. Ecological preferences of these taxa are not clear. These taxa have been observed in high abundance (>80%) in a variety of habitats including mud, stones, and sand in a shallow English lake (Sayer, 2001) and a wide range of nutrient conditions (TP: 25–646 μg l^{-1}, Bennion et al., 1995). Lack of sensitivity to phosphorus and their high abundances often cause problems in developing numerical diatom-TP models (Bennion et al., 2001; Sayer, 2001).

However, the regression tree analysis suggested that variation in their relative abundances may be primarily associated with TN concentration in these Pacific Northwest rivers. Predicted mean relative abundance was high when TN < 325 μg l^{-1}. Nitrogen may likely be the limiting nutrient in the eastern rivers where volcanic rocks naturally contain phosphorus (Benke & Cushing, 2005). In the upper Deschutes River, adjacent to the John Day River in eastern Oregon, benthic diatom assemblages were almost a monoculture of a diatom species with an N-fixing symbiont (Y. Pan, personal observation). Abundant small chain-forming Fragilariaceae taxa in these rivers suggest that these taxa can tolerate low concentrations of nitrogen or can acquire nitrogen from their substrates such as sediments more effectively than other benthic taxa. The regression tree also indicated that under low TN conditions, habitat conditions became an important factor. Apparently, both light and substrates may also regulate the distribution of these taxa. The Fragilariaceae taxa were present in much lower abundance in the Malheur River, a river draining the high desert with volcanic rocks. But the Malheur River, especially the lower portion of the river, was higher in nutrients and turbidity. High abundances of diatom taxa with motility (i.e., *Nitzschia* and *Navicula* taxa) suggest high sedimentation and silty benthic habitats in rivers

a

b
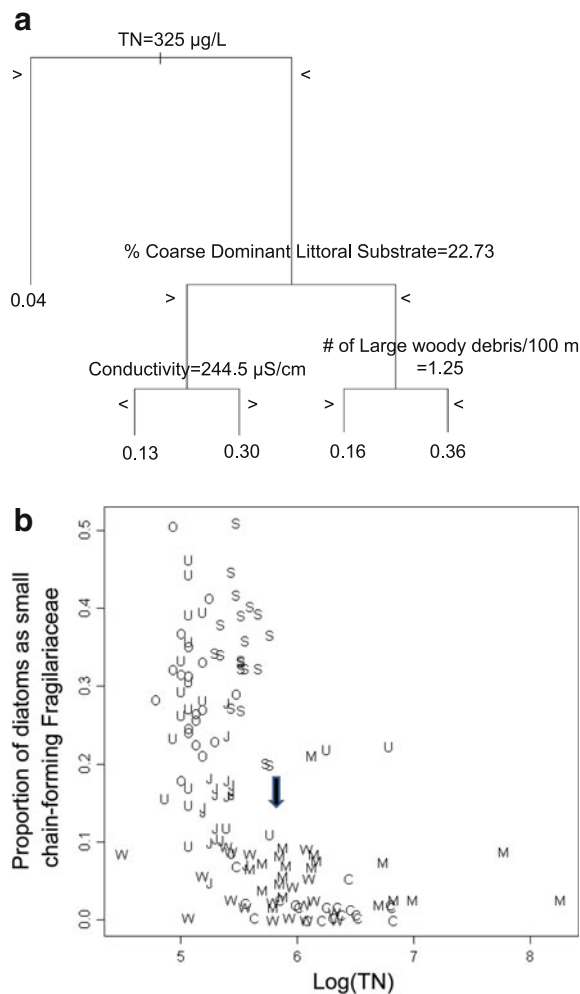
Fig. 4 Variation of small-size, chain-forming Flagilariaceae taxa in relation to environmental variables. **a** A regression tree showing the key environmental predictors, dividing points, and predicted mean proportion of the taxa group. **b** The relationship between proportion of the taxa group and log(TN) (*arrow* indicates the 325 μgTN/l cut-off as indicated by the regression tree in (**a**) and the abbreviation for each river is the same as Fig. 3)

(Dadoly & Michie, 2010). Sayer (2001) suggested that the Fragilariaceae taxa prefer shallow habitats with high light levels.

Spatial variation of benthic diatom assemblages within each river

Within-river variation in benthic diatom assemblages differed substantially among the seven rivers. Watershed land-use, especially irrigated agriculture

east of the Cascades Mountains, can substantially alter in-stream physical and chemical environments and subsequently biotic assemblages (Mebane et al., 2003). In the Malheur River, our data showed a strong longitudinal gradient of water quality including conductivity, chloride, TP, and TN between the most upstream and downstream sites we sampled (spanning a 123-km river distance). The in-stream water quality gradient may largely be associated with a strong longitudinal land-use disturbance gradient in the Malheur River watershed or with a natural gradient in soil nutrients. The upper portion of the Malheur River, situated in the Malheur National Forest, has been reserved as a Wild and Scenic River since 1988. The river is protected from development (e.g., dam) which can alter its natural character. The lower river, starting at river kilometer 110, however, has been extensively modified both in-stream (e.g., dams and reservoirs) and along the river (e.g., irrigation canals and dikes) for irrigated agriculture (Dadoly & Michie, 2010). High sediment and phosphorus loads have been attributed to eutrophic conditions in the Lower Malheur River, which is characterized by low dissolved oxygen and nuisance algal growth in summer (Dadoly & Michie, 2010). In our study, longitudinal changes in benthic diatom assemblages were mainly a result of increases in overall relative abundance of *Nitzschia*. Some *Nitzschia* taxa including *N. amphibia* are classified as nitrogen heterotrophs which demand organic forms of nitrogen such as amino acids and often dominate habitats with organic pollution (van Dam et al., 1994). Like most benthic diatoms with raphes, *Nitzschia* taxa possess the ability to move horizontally on substrate via gliding. Cohn (2001) reported that *Nitzschia* taxa were proficient at moving upward through the substrates in a lab experiment, probably due to their slender cell shapes, small cross-sectional area, and long raphe length to cell volume ratio. Light-stimulated vertical motility may help these *Nitzschia* taxa gain ecological advantage over other taxa in silty habitats in the Malheur River where median turbidity was >5 times higher than the highest median turbidity of the other six rivers. Longitudinal increases in this diatom group in the Malheur River are therefore likely to be indicative of both degraded water quality and habitat. LaVigne et al. (2008) reported analogous downstream patterns in fish assemblages with degradation at these same Malheur sites, where multimetric fish index scores declined from 53 to 0.5.

Table 3 Mean proportional abundances of selected diatom metrics for each river and metric definitions
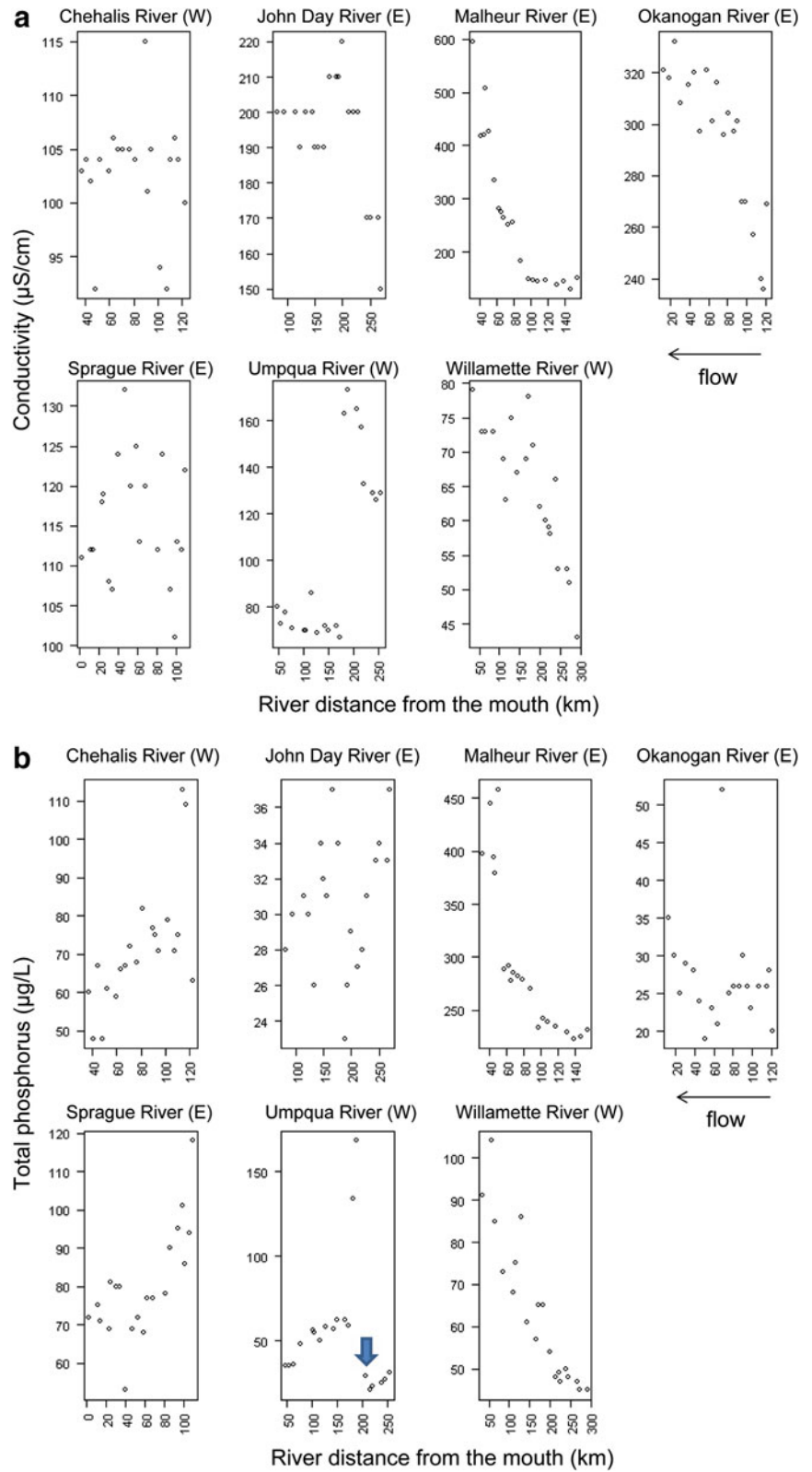
Metric	Chehalis (W)	Umpqua (W)	Willamette (W)	John Day (E)	Malheur (E)	Okanogan (E)	Sprague (E)
Araphid	0.06	0.30	0.08	0.26	0.09	0.38	0.37
Biraphid	0.43	0.54	0.61	0.55	0.67	0.39	0.36
Centric	0.05	0.01	0.03	0.04	0.12	0.04	0.14
Monoraphid	0.46	0.14	0.28	0.15	0.13	0.19	0.12
Pollution sensitive taxa	0.66	0.61	0.55	0.65	0.43	0.68	0.68
Fresh brackish taxa	0.79	0.81	0.70	0.80	0.62	0.85	0.80
N-tolerant autotrophic taxa	0.47	0.44	0.40	0.46	0.38	0.50	0.50
N-heterotrophic taxa	0.12	0.20	0.18	0.12	0.32	0.05	0.09
β-mesosaprobous taxa	0.38	0.51	0.36	0.54	0.36	0.54	0.54
α-mesosaprobous taxa	0.17	0.17	0.19	0.09	0.30	0.09	0.11
Eutraphentic taxa	0.30	0.38	0.33	0.36	0.56	0.22	0.32
Small Fragilariaceae	0.02	0.26	0.04	0.15	0.07	0.30	0.35
Navicula	0.09	0.13	0.11	0.07	0.15	0.13	0.07
Nitzschia	0.14	0.22	0.22	0.14	0.39	0.11	0.13
N-fixing taxa	0.00	0.06	0.00	0.11	0.00	0.01	0.05
Araphid	Morphological guild (no motility). Bilaterally symmetric diatom taxa with no raphes on both valves (e.g., *Meridion*)						
Biraphid	Morphological guild (with motility). Bilaterally symmetric diatom taxa with a raphe on both valves (e.g., *Navicula*)						
Centric	Morphological guild. Radially symmetric diatom taxa. Most of them are euplankton (e.g., *Cyclotella*)						
Monoraphid	Morphological guild (no motility). Bilaterally symmetric diatom taxa with a raphe only on one valve (e.g., *Achnanthedium*)						
Pollution sensitive taxa	Sensitive diatom taxa (Bahls 1993)						
Fresh brackish taxa	Salinity metric (van Dam et al. 1994)						
N-tolerant autotrophic taxa	Autotrophic diatoms tolerate high nitrogen levels (van Dam et al., 1994)						
N-heterotrophic taxa	Nitrogen heterotrophic diatoms (van Dam et al., 1994)						
β-mesosaprobous taxa	Saprobity metric (van Dam et al., 1994)						
α-mesosaprobous taxa	Saprobity metric (van Dam et al., 1994)						
Eutraphentic taxa	Eutrophic diatom taxa (van Dam et al., 1994)						
Small Fragilariaceae	Araphid, small-size and chain-forming Fragilariaceae taxa (e.g., *Staurosira*)						
Navicula	Biraphids with moderate or high mobility (Stevenson and Bahls 1999).						
	We used old *Navicula* concept which includes newly split genera such as *Hippodonta*, *Luticola*, *Adlafia*, etc.						
Nitzschia	Biraphids with moderate or high mobility (Stevenson and Bahls 1999)						
N-fixing taxa	Diatom taxa with nitrogen fixing symbiont (e.g., *Epithemia*)						

W west of the Cascade Mountains, *E* east of the Cascade Mountains

Similar longitudinal patterns in water quality were observed in other rivers (e.g., Willamette) but benthic diatom assemblages showed either weak response patterns or no patterns. Lack of longitudinal patterns in diatom assemblages is likely associated with less distinct water quality gradients than those that occur in the Malheur River and the complex interplay among spatially extensive factors (e.g., watershed land-use, climate, geology), local scale factors (e.g., habitat heterogeneity, confluence of tributaries, dams), and the issues with benthic diatom sampling in large rivers. Benthic diatoms in general respond to both

Fig. 5 Comparison of longitudinal variation of selected water quality variables among seven rivers. **a** Conductivity and **b** total phosphorus

Table 4 Spearman rank correlation coefficients between river distance from the mouth (km) and selected environmental variables and NMDS axis scores

Variable	Chehalis (W)	Umpqua (W)	Willamette (W)	John Day (E)	Malheur (E)	Okanogan (E)	Sprague (E)
Water quality							
Chloride (μeq/l)	0.85	0.49	−0.77	−0.68	−0.95	−0.74	−0.74
Conductivity (μS/cm)	0.03	0.55	−0.86	−0.33	−0.94	−0.88	0.09
Sulfate (μeq/l)	−0.11	0.65	−0.87	−0.42	−0.94	−0.93	−0.42
Total nitrogen (μg/l)	−0.45	0.29	−0.85	−0.3	−0.85	0.46	−0.56
Total phosphorus (μg/l)	0.72	−0.29	−0.95	0.28	−0.95	−0.22	0.66
Turbidity (NTU)	0.42	−0.22	−0.21	0.3	0.39	0.66	0.85
Habitat							
% coarse dominant littoral substrate	−0.17	0.81	0.45	−0.18	0.18	−0.03	−0.25
% sand + fine dominant littoral substrate	0.29	−0.44	−0.52	0.4	−0.37	0.07	0.09
Channel sinuosity (m/m)	0.45	−0.4	0.11	−0.49	−0.19	0.54	0.24
Mean bank canopy density (%)	−0.15	0.38	−0.11	0.46	−0.09	−0.35	−0.35
Mean littoral depth (m)	−0.05	−0.36	−0.17	0.29	0.6	−0.39	−0.3
Mean width*thalweg depth (m²)	−0.1	−0.85	−0.89	0.21	0.29	−0.39	−0.62
Percent of reach with snags	−0.02	0.15	−0.07	0.66	−0.03	−0.32	−0.18
Total riparian disturbance index values	−0.23	0.71	−0.19	0.49	−0.42	−0.49	0.07
Diatom assemblage							
NMDS axis I	0.18	−0.35	0.18	−0.62	−0.26	0.56	0.42
NMDS axis II	−0.58	−0.02	0.37	−0.12	0.9	0.82	−0.40
Araphids	0.23	−0.41	0.44	−0.7	−0.01	−0.38	0.17
Biraphids	0.43	0.13	−0.33	0.76	−0.28	−0.14	−0.59
Centric	−0.26	0.3	−0.32	−0.68	−0.31	0.32	0.51
Monoraphids	−0.15	0.1	0.24	0.25	0.85	0.58	−0.21
Pollution sensitive taxa	−0.23	−0.35	0.37	0.73	0.5	0.02	−0.09
Fresh brackish taxa	0.05	−0.34	−0.15	0.68	0.73	0.16	0.13
N-tolerant autotrophic taxa	−0.08	0.04	0.69	−0.22	0.82	0.46	0.06
N-heterotrophic taxa	0.38	0.21	−0.67	−0.77	−0.52	−0.14	0.28
β-mesosaprobous taxa	0.04	0.05	0.73	−0.31	0.81	0.47	−0.48
α-mesosaprobous taxa	0.13	0.42	−0.05	−0.29	−0.51	−0.2	0.36
Eutraphentic taxa	0.19	0.09	−0.66	−0.15	0.03	−0.7	0.11
Small Flagilariaceae	0.33	−0.49	0.39	−0.55	−0.02	−0.69	0.17
Navicula	0.12	0.11	−0.37	−0.3	0.18	−0.39	0.26
Nitzschia	0.41	0.12	0.37	−0.61	−0.56	−0.02	−0.35
N-fixing taxa	−0.15	−0.03	0.22	−0.22	0.54	−0.55	−0.74

A negative correlation coefficient values indicate that the values of the environmental variable increase downstream

chemical and physical habitat conditions (Biggs et al., 1998). In the littoral zones of the studied seven rivers, physical habitat conditions including canopy cover, depth, light penetration, and substrates vary locally among sites (Table 1; R. M. Hughes, personal observation). At a given depth within the site, substrate characteristics including organic matter varied substantially and macroinvertebrate density also showed high variability with no systematic patterns in the Fraser River (Rempel et al., 2000). Unlike macroinvertebrates, little is known about the distribution of benthic diatoms along the water depth gradient in large

Fig. 6 Longitudinal variation of proportion of pollution sensitive diatom taxa in each river
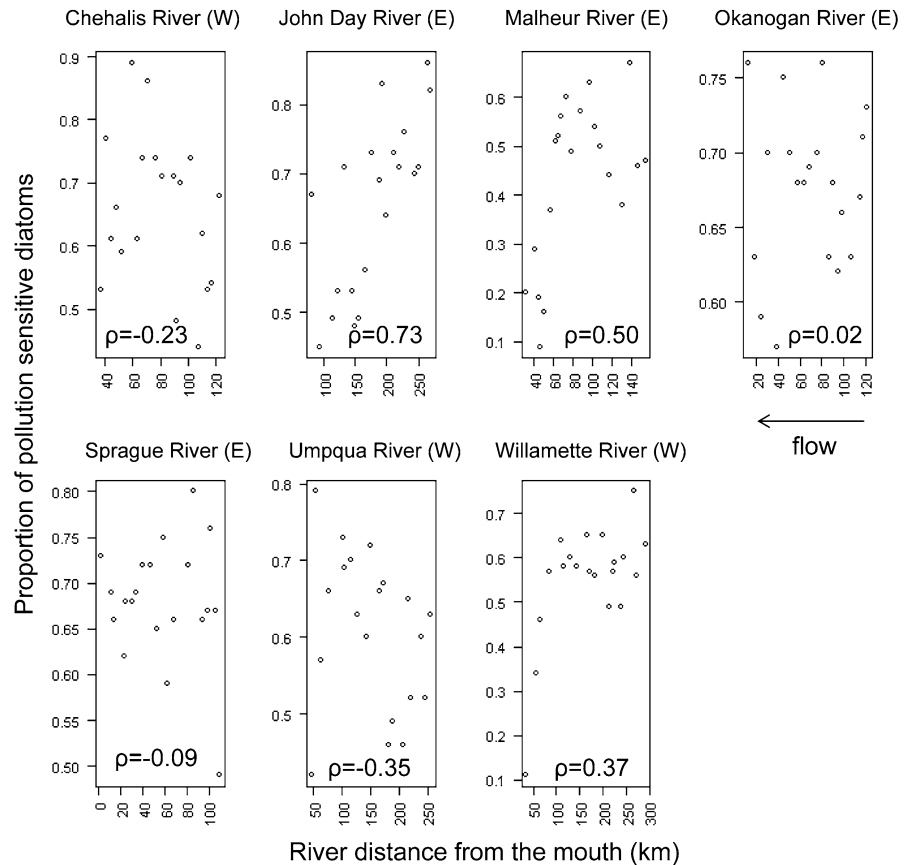
river littoral zones. However, the relationship between benthic diatoms and water depth has been investigated in lakes (Wolin & Duthie, 1999). For instance, Stevenson & Stoermer (1981) showed that benthic diatom biomass peaked in the mid-depth zone along the water depth gradient in Lake Michigan. In contrast, composition of benthic algal assemblages in rivers do not appear to exhibit systematic patterns, perhaps because they are related more to fluctuating depths and degrees of exposure both within and among sites. Burns & Walker (2000) examined the depth profile of periphyton assemblages at two littoral sites on the River Murray with contrasting water levels (impounded pool vs. tailwater). Algal biomass peaked in zones with maximum light and stable water levels. Further studies on assessing interactive effects of chemical and physical local habitat conditions on benthic diatoms in large river littoral zones are needed.

Conventional diatom sampling design, largely developed for wadeable streams, may not be effective to reflect longitudinal patterns of diatom assemblages

and their responses to environmental conditions within a large river, especially when the longitudinal water quality gradients are not very strong. Our study was constrained in several ways in terms of sampling design. First, both biotic and abiotic factors in large river mainstems, especially littoral zones, may be substantially affected by tributaries. This study was not specifically designed to assess the effects of tributaries on benthic diatoms. However, longitudinal variation of both environmental conditions and benthic diatoms in several rivers seems to suggest the importance of tributaries. The high nutrient concentrations were found in the sites near an urban center in the Umpqua River. Figure 5b suggests that the nutrient concentrations were decreased after the North Umpqua River, a large tributary draining the Cascades with more diluted water, joined the mainstem. A study specifically designed to assess the effects of stream network tributaries on water quality, habitat structure, and benthic diatoms could be informative.
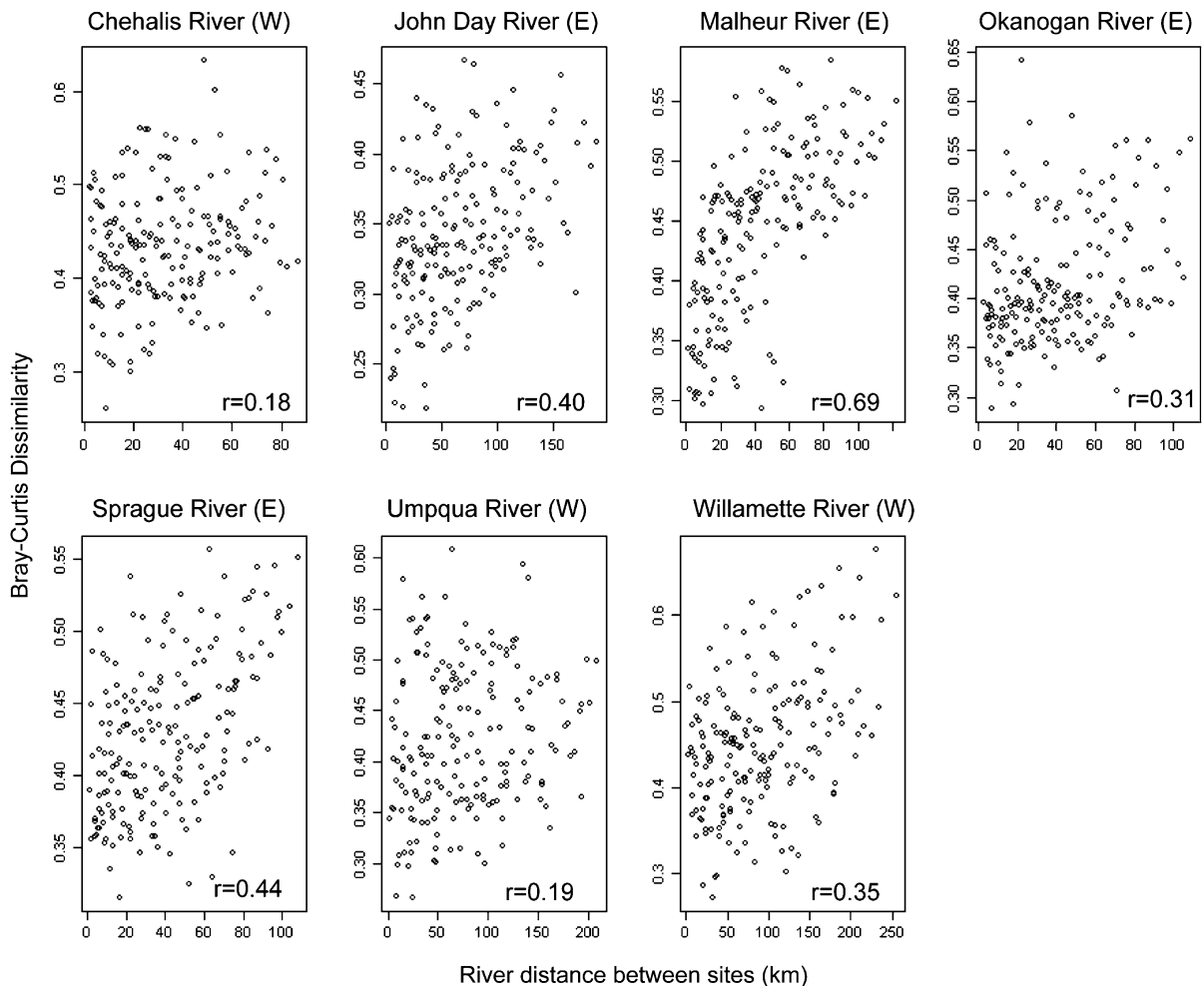
Fig. 7 Bray–Curtis dissimilarity of benthic diatom assemblages as a function of spatial distance between sampled sites in each river. *r* The Mantel standardized *r*

Second, spatial distribution of benthic diatoms in large river littoral zones has not been well characterized in our study or in general. Our study focused on site-scale bioassessment and a site in a large river littoral zone is difficult to define in an ecologically meaningful way. Reach length in wadeable streams and non-wadeable rivers has been defined based on fluvial geomorphology or hydrology (Moulton et al., 2002), or asymptotes of fish assemblage richness (Hughes et al., 2002; Hughes & Peck, 2008) or multimetric index scores (Hughes & Herlihy, 2007). Depending on the objectives of bioassessment, it is unclear if the same definition can be applied to benthic diatoms in large river littoral zones (Flotemersch et al., 2011). Lane et al. (2007) sampled littoral zones with a

site length of 1,000 m in four large rivers in the Ohio River basin using different sampling methods. The method of collecting diatom assemblages affected the strength of associations with water quality. Assemblages collected from five representative habitats in five locations within a site had much weaker correlations with water quality than those collected from all available micro-habitats in a reach. Leland et al. (2001) noted generally greater variability in benthic diatom assemblages in snag habitat than in depositional (sandy bottom) habitat in the San Joaquin River. Their study was conducted in three rivers and the results showed some river-specific features. With one composite sample from multiple locations within a site, one cannot determine the degree of within-site
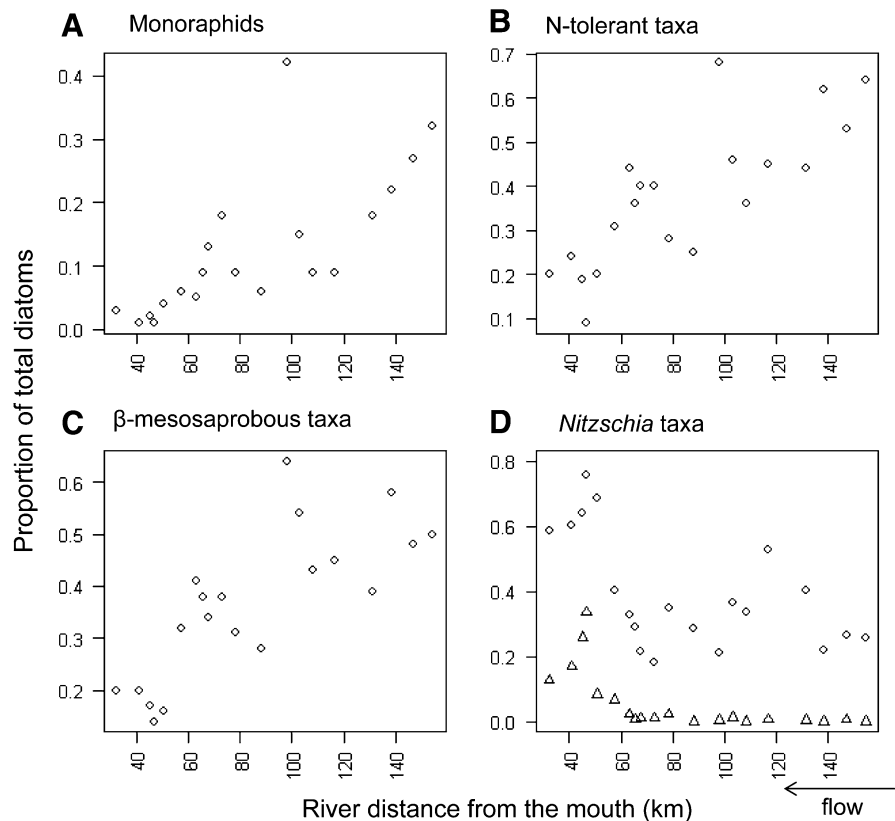
diatom assemblage variability in our study. A study aimed at both micro- and macro-habitat and diatom variability and how variability may change as a function of spatial extent could help determine the most appropriate definition of "site" and select the most appropriate sampling method for diatoms.

Finally, benthic diatom assemblages in large river littoral zones likely are a mixture of local resident taxa, washed-in benthic taxa from tributaries or upstream sites, and settling euplankton from the water column. Our data showed a large overlap in dominant taxa among the rivers, which suggests that some diatom taxa such as *A. minutissimum* and *C. placentula*, may be transported from headwaters. Stevenson & Pan (1999) suggested that such assemblages reflect environmental conditions over a large spatial extent (e.g., watershed or region). However, the diatom assemblage data including a mixture of resident and washed-in taxa are difficult to interpret when we do not know the origin of each component in an assemblage. The contribution of non-resident taxa to the assemblage may also vary from one location to another depending on environmental conditions such as hydrology and

hydraulics. In this study, overall contribution of centric diatom taxa, a group of diatom that are mainly euplankton associated with lentic systems (lakes/ reservoirs) or pools in large rivers, to benthic assemblages was relatively low (Table 3). Low contribution may be associated with relatively fast moving water and lack of major dams/reservoirs along the mainstem rivers. Discerning live from dead benthic diatoms in each assemblage may help identify resident from washed-in and dead benthic taxa in an assemblage (Gillett et al., 2009). Diatom analysis focusing on the live portion of the benthic assemblage may better elucidate the relationships between diatom assemblages and environmental conditions in large river littoral zones.

In summary, our results suggest that benthic diatoms in large river littoral zones provide valuable information on both among-river and among-site environmental conditions in large rivers. Benthic diatom assemblages can clearly reflect among-river factors. However, the relationships between benthic diatom assemblages and water quality within each river may depend on the strength of the water quality

gradients, interactive effects of water quality and habitat conditions, and diatom sampling design. Compared to wadeable streams, large river diatom-based assessment poses several additional challenges in both sampling design and data interpretation.

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