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Relationships between environmental variables and benthic diatom assemblages in California Central Valley streams (USA)

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Abstract

This study examines distributional patterns of benthic diatom assemblages in relation to environmental characteristics in streams and rivers in the California Central Valley ecoregion. Benthic diatoms, water quality, and physical habitat conditions were characterized from 53 randomly selected sites. The stream sites were characterized by low mid-channel canopy cover and high channel substrate embeddedness. The waters at these sites were enriched with minerals and turbidity varied from 1.3 to 185.0 NTU with an average of 13.5 NTU. A total of 249 diatom taxa were identified. Average taxa richness was 41 with a range of 7–76. The assemblages were dominated by *Staurosira construens* (11%), *Epithemia sorex* (8%), *Cocconeis placentula* (7%), and *Nitzschia amphibia* (6%). Multivariate analyses (cluster analysis, classification tree analysis, and canonical correspondence analysis) all showed that benthic diatom assemblages were mainly affected by channel morphology, in-stream habitat, and riparian conditions. The 1st CCA axis negatively correlated with mean wetted channel width ($r = -0.66$) and thalweg depth ($r = -0.65$) (Table 4). The 2nd axis correlated with % coarse substrates ($r = 0.60$). Our results suggest that benthic diatoms can be used for assessing physical habitat alterations in streams.

Introduction

Anthropogenic activities such as damming and diverting waters for irrigation of agricultural land, urban water use, and flood control have substantially altered lotic environments worldwide, especially physical habitat conditions (Mount, 1995). The intensities of these activities and their effects on the lotic ecosystems are most noticeable in semi-arid and arid regions with increasing agricultural and urban development such as in California Central Valley ecoregion. Benthic diatoms have been an integral part of both national and state stream assessment programs (Kroeger et al., 1999; Stevenson & Bahls, 1999). Using diatoms as indicators of water quality has a long history. Researchers have shown that changes in diatom assemblages are often associated with eutrophication, acidification, heavy metal contamination, and pesticides (see review by Stevenson & Pan, 1999). Assessment of physical habitat conditions with diatoms, however, has received less attention.

Several conceptual models have suggested that physical habitat conditions may closely associate with benthic diatom assemblage structure in streams (Biggs, 1996; Stevenson, 1997; Biggs et al., 1998). In their habitat matrix model, Biggs et al. (1998) extended the CSR model developed by Grime (1977) for terrestrial plants to benthic algae. In a given stream site with open canopy, diatom assemblages may be largely predicted by habitat stability and resource supply. Empirical studies have shown the close association between diatom life strategies/composition and habitats. For instance, diatom assemblages in habitats with excessive and periodic fine sediment deposition are often dominated by the species with relatively high motility (e.g., *Gyrosigma*, *Surirella*, *Nitzschia*) while epipsammon, diatoms attached on unstable sandy substrates, often consists of small adnate species such as *Achnanthidium minutissimum* (Miller et al., 1987). Recently, several diatom metrics (e.g., % *Achnanthes*/*Achnanthidium*, % biraphids) have been suggested as potential indicators of stream physical habitat conditions (Stevenson & Bahls, 1999). Kutka & Richards (1996) reported that % bank erosion and overall riparian conditions correlated well with these diatom metrics in a Minnesota agricultural basin.

The main objective of this study was to identify distributional patterns of benthic diatom assemblages in relation to physical habitat conditions and other environmental variables in California Central Valley ecoregion. A better understanding of changes in benthic diatom assemblages in relation to environmental characteristics will eventually enhance development of numerical criteria for physical, chemical, and biological attributes in the region and state.

Materials and methods

Study area and design

The Central Valley ecoregion is surrounded by the Coast Ranges on the west and the Sierra Nevada foothills on the east. The ecoregion covers two major drainage basins, the Sacramento River in the north, and San Joaquin River in the south. The climate ranges from semiarid in the north to arid in the south. Streams in the ecoregion have been significantly modified by human activities, including damming and diverting waters for irrigation of agricultural land, urban water use, and flood control (Saiki, 1984; Mount, 1995). Due to these extensive modifications, sampled "streams" in this study include ditches, drains, natural streams and rivers, and isolated water-bodies which do not connect to any downstream channels. Natural streams on the eastern and central portion of the valley have narrow riparian habitat with agriculture and levee construction next to the streams, and constructed conveyances (ditches) as having little to no habitat. In some water districts, constructed conveyance habitat is lined with concrete or sprayed with herbicides to control vegetation. Streams on the western side of the valley are predominantly ephemeral or intermittent. Land use on the western side of the valley is predominantly rangeland with a few valley oak.

Sampling sites were selected using a tessellation stratified design, described by Stevens & Olsen (1999) and Stevens (1997), to represent the two main populations of interest: natural streams and man-made waterways (Hall et al., 2000). The stream population in the region was estimated based on digitized versions of the USGS 1:100,000 scale topographic maps. A study reach (40× mean wetted channel width), ranging from 150 to 500 m, was sampled around each of the selected sample sites. Eleven cross-section transects were set up in each study reach by dividing the reach into 10 equal length intervals (includes transects at the start and end of each reach). Periphyton, water quality, and physical habitat conditions were characterized from 53 unique sites during the baseflow from early August to late September in 1994 and 1995.

Sampling and sample analysis

Periphyton samples were collected from each of the 9 transects (excludes transects at the start and end of each reach) and combined into either a depositional (pool/glide) or erosional habitat (riffle/run) composite sample. Transects with no visible water movement were defined as depositional habitat, those with visible water movement were considered erosional habitat. At each transect, periphyton were collected from a 12 cm^2 area of stream bed using a 1.5 cm long piece of 3.9 cm diameter PVC pipe as a template. For fine substrate, periphyton were suctioned into a 60 ml syringe; in coarser substrate, periphyton were scraped off using a toothbrush and rinsed with distill water. The end result was one composite periphyton sample for erosional habitats and one for depositional habitats for each stream site. Depositional samples were collected at only few sites and thus this study was based on erosional samples. Samples were processed for chl *a*, ash-free dry mass, and species composition. The subsample of the preserved periphyton suspension (final concentration of 4% formalin) was acid-cleaned and mounted in NAPHRAX® to enumerate diatom species (Patrick & Reimer, 1966). A minimum of 500 diatom valves was counted at 1000× magnification unless the sample was silty with sparse cells. Sites with less than 250 valve counts were excluded from the analysis. Patrick & Reimer (1966, 1975) and Krammer & Lange-Bertalot (1986; 1988; 1991a, b) were used as primary references for diatom taxonomy. Diatom taxa mobility classification follows Stevenson & Bahls (1999).

A 4-l sample of water was collected at a flowing portion near the middle of each stream. Within 48–72 h of collection, water samples were split into aliquots and preserved for different assays (see Table 1). The aliquots for dissolved metals were filtered (0.45 μm pore size) and preserved with concentrated HNO_3. The aliquots for nutrient analysis were preserved with concentrated H_2SO_4. Base cations and metals were determined by ICP spectrophotometry. Anions were measured by ion chromatography. Nutrients were determined with a flow-injection analyzer. Detailed information on the analytical procedures used for each of the analyses can be found in USEPA (1987).

Vegetative cover over the stream was measured at each of the 11 cross section transects using a convex spherical densiometer. At each transect, epifaunal substrate (e.g., grain size, embeddedness) and presence and proximity of 11 categories of human activities (i.e., row crops, pasture, dams and revetments, buildings, pavement, roadways, pipes, landfill or trash, parks/lawns, logging operations, and mining activities) were estimated (Kaufmann & Robison, 1998). Proximity-weighted riparian disturbance indices were calculated by tallying the number of riparian stations at which a particular type of disturbance was observed, weighting by its proximity to the stream, and then averaging over all stations on the reach (Kaufmann & Robison, 1998). Stream habitat characterization included thalweg, mean wetted width, mean reach cross-section, width/depth, slope, residual pool area, and surficial channel substrates. Field methods and metric calculation, respectively, are described in more detail by Kaufmann & Robison (1998) and Kaufmann et al. (1999).

Table 1. Summary of selected environmental and biotic variables

Variables	Median	Minimum	Maximum
Aluminum ($\mu g\ l^{-1}$)	116	48	297
Boron ($\mu g\ l^{-1}$)	76	6	4300
Calcium ($mg\ l^{-1}$)	20.65	1.77	90.1
Iron ($\mu g\ l^{-1}$)	56	6	810
Magnesium ($mg\ l^{-1}$)	6.33	0.359	60.4
Manganese ($\mu g\ l^{-1}$)	4	BD	649
Potassium ($mg\ l^{-1}$)	1.565	0.612	25
Selenium ($\mu g\ l^{-1}$)	0.8	0.7	5.0
Sodium ($mg\ l^{-1}$)	14.65	1.57	242.00
Chloride ($mg\ l^{-1}$)	8.00	0.66	365.00
Sulfate ($mg\ l^{-1}$)	5.70	0.59	468.00
Nitrate ($mg\ l^{-1}$)	0.08	0.01	22.00
Ammonia ($mg\ l^{-1}$)	0.10	0.10	1.50
TP ($\mu g\ l^{-1}$)	100	29	3600
Turbidity (NTU)	13.5	1.3	185.0
Chl-a ($\mu g\ cm^{-2}$)	0.22	BD	4.37
AFDM ($mg\ cm^{-2}$)	0.84	0.05	23.60
Mean bank angle (degree)	42	15	95
Mean bankside canopy cover (%)	82	0	100
Mean mid-channel canopy cover (%)	9	0	100
Mean embeddedness (%)	100	0	100
% filamentous algae cover	0.05	0.00	0.88
Total riparian disturbance	3.42	0.00	6.38
Non-ag. riparian disturbance	2.70	0.00	5.67
Agriculture riparian disturbance	0.71	0.00	1.50
Log_{10} erodible substrate diameter	0.75	−1.86	1.73
Log_{10} relative bed stability	−2.41	−3.94	4.13
Mean thalweg depth (cm)	82.61	5.00	334.88
Mean wetted stream width (m)	5.85	0.29	59.57

BD: below detection.

Data analysis

We used two approaches to examine the relationships between diatom assemblages and environmental variables in the region. In a region where landscapes have been substantially modified by human activities, it is often difficult or expensive to adequately characterize environmental variation. On the other hand, benthic diatom assemblages may integrate both temporal and spatial variation of environmental conditions. With well-developed sampling and analytical protocols (Stevenson & Balhs, 1999), we can characterize benthic diatom assemblages much better than the environmental variables especially human-related disturbance.

The first approach was an indirect analysis of relationships between diatom species composition and environmental factors. We characterized diatom distributional patterns using clustering methods. Two-way indicator species analysis (TWINSPAN), a divisive cluster method, uses a 'top-down' approach. The division starts with the entire data set based on 'global' differences in the data set and successively divides it into smaller groups (Hill et al., 1975). A flexible, unweighted pair-group method (UPGMA) clustering method, an agglomerative hierarchical method, uses a 'bottom-up' approach, which starts with individual sites and repeatedly combines them into larger groups. Rare taxa, defined as $<1\%$ relative abundance with <3 sites occurrences, were excluded from the analyses. The UPGMA was performed using the Bray–Curtis distance with a β-value of -0.25.

To better characterize each diatom-based cluster group, we performed an indicator species analysis. This analysis identifies a set of indicator species affiliated with each stream site group (Dufrene & Legendre, 1997). Statistical significance of each species indicator value was tested using a Monte Carlo permutation test (999 permutations, $p<0.05$). TWINSPAN, UPGMA, and indicator species analysis were performed using PC-ORD v.4 statistics software (McCune & Mefford, 1999).

A classification tree analysis was used to identify a set of environmental predictors, which can best discriminate diatom-based groups. The method is an attractive alternative to linear and additive regression methods. This binary recursive partitioning method selects a set of hierarchically organized environmental variables that reveals relative importance of each selected variable and their interactions with relation to response variables (Clark & Pregibon, 1993). The classification tree analysis was performed using S-plus statistics software (MathSoft, 2000). For all analyses, continuous environmental variables, except pH, were log-transformed. Proportional environmental variables were double transformed with square root and then arcsine.

The second approach is a direct analysis on the relationship between diatom assemblages and environmental variables. Canonical correspondence analysis (CCA) focuses on the portion of the diatom assemblages that co-varies with measured environmental variables (ter Braak, 1986). Water quality variables and physical habitat variables were selected using a forward-selection option. The importance of these variables in relation to diatom assemblages was tested using a Monte Carlo permutation test (999 permutations, $p<0.05$). CCA was performed using CANOCO v.4 statistics software (ter Braak & Smilauer, 1998).

Results

Environmental conditions

Sampled stream sites varied considerably in stream types, physical habitat conditions, and water quality (Table 1). Approximately 58% of the sites were in the San Joaquin River Basin. A large proportion of the sites (66%) were ditches and drains. Only 28% of sites were regular, natural streams. Of these natural sites, stream sizes ranged from 1st to 8th order. Mean wetted stream width varied from 0.29 m to 59.57 m, and mean thalweg depth ranged from 0.05 to 3.35 m.

The study stream sites were characterized by low mid-channel canopy cover and high channel substrate embeddedness. Where present, vegetative ground cover consisted of grasses, forbs and bramble, mid-story consisted predominantly of shrub willow, and the upper-story/canopy consisted of cottonwoods and some eucalyptus trees. In the man-made conveyances the larger mean substrate grain size is attributed to the presence of hardpan, a hard caliche layer below valley floor sediments. Channel substrate and composition for ditches and drains is predominantly fine sand and silty-clay with only 15% of sites having a substrate of coarse sand and gravel. In natural streams, 86% had a substrate composed of coarse sand and larger material. Median % fine substrates (< 0.08 mm) and % embeddedness were 95 and 100%, respectively.

Stream waters were overall mineral enriched. The median Ca^{2+} concentrations were 20.65 mg l^{-1} with a maximum value of 90.10 mg l^{-1}. The median Na^{+} concentrations were 14.65 mg l^{-1} with a maximum value of 242.00 mg l^{-1}. Turbidity varied from 1.3 to 185.0 NTU with a median value of 13.5 NTU. Total phosphorus concentrations varied from 29 to 3600 μg l^{-1} with a median value of 100 μg l^{-1}.

Diatom-based stream site classification

A total of 249 diatom taxa were identified. Average taxa richness was 41 with a range of 7–76. On average, the assemblages were dominated by taxa in 2 genera, *Nitzschia* (23%) and *Navicula* (18%). *Staurosira construens* Ehr. (11%), *Epithemia sorex* Kütz. (8%), *Cocconeis placentula* Ehr. (7%), and *Nitzschia amphibia* Grun. (6%) were the most common species. Most of taxa occurred in < 3 sites with < 1% relative abundance. After deleting these 'rare' taxa, 65 taxa were used for data analyses. The assemblages were characterized by a relatively high abundance of motile diatom taxa. Average relative abundances of diatom taxa with high mobility (e.g., *Nitzschia*) or medium mobility (e.g., *Navicula*) were 25 and 35%, respectively. (Fig. 1).

The UPGMA divided 53 sites into four groups based on visual examination of the dendrogram (Fig. 2). Indicator species analysis showed that each group was characterized by different sets of indicator taxa with maximum relative abundance and frequency (Table 2). Group A was characterized by *Amphora veneta* Kütz. and *Nitzschia amphibia*. A total of 11 indicator species including *Navicula cryptotenella* Lange-Bert., *Cymbella silesiaca* Bleisch, and *Achnanthidium minutissimum* (Kütz.) Czarnecki had significant indicator values for Group B. Group C was characterized by a centric diatom (*Cyclotella meneghiniana* Kütz.) and a chain-forming biraphid (*Diadesmis confervacea* Kütz.) and other two taxa. Group D was characterized by two araphids (*Staurosira construens, Synedra parasitica* (W. Sm.) Hust.) and one monoraphid (*Cocconeis placentula*).

For the comparison, the TWINSPAN also produced four groups. Group A was characterized by *Aulacoseira granulata* (Ehr.) Simonsen, *Epithemia turgida* (Ehr.) Kütz., and *Staurosira construens. Nitszchia constricta* (Kütz.) Ralfs was the only significant indicator taxon for Group B. Group C was characterized by *Amphora pediculus* (Kütz.) Grun., *Diatoma vulgare* Bory, *Rhoicosphenia abbreviate* (Agardh) Lange-Bert., *Nitszchia inconspicua* Grun. and three *Navicula* taxa. Group D was characterized by *Planothidium lanceolatum* (Bréb. ex Kütz.) Lange-Bert., *Cymbella silesiaca*, and other four taxa.

The correspondence between the stream groups classified using the UPGMA and TWINSPAN was poor (Table 3). For example, 19 sites in UPGMA Group B were split equally between the TWINSPAN group C and D. The UPGMA groups corresponded poorly to the Sacramento and San Joaquin drainage basins and 'streams'

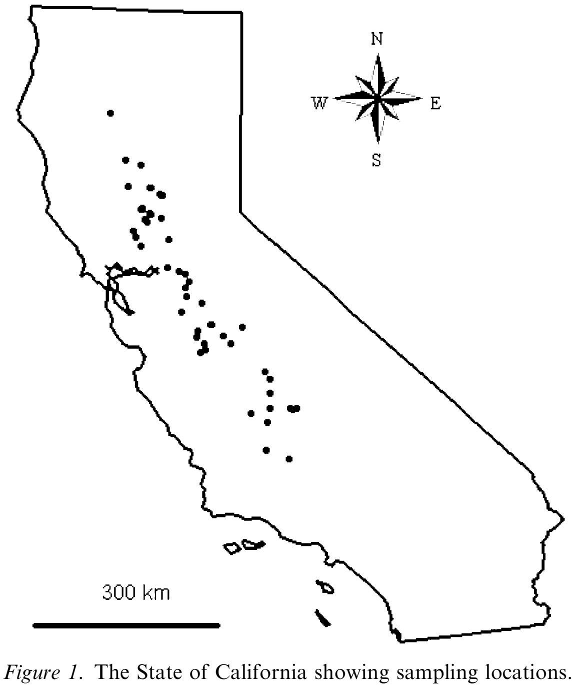


Figure 1. The State of California showing sampling locations.

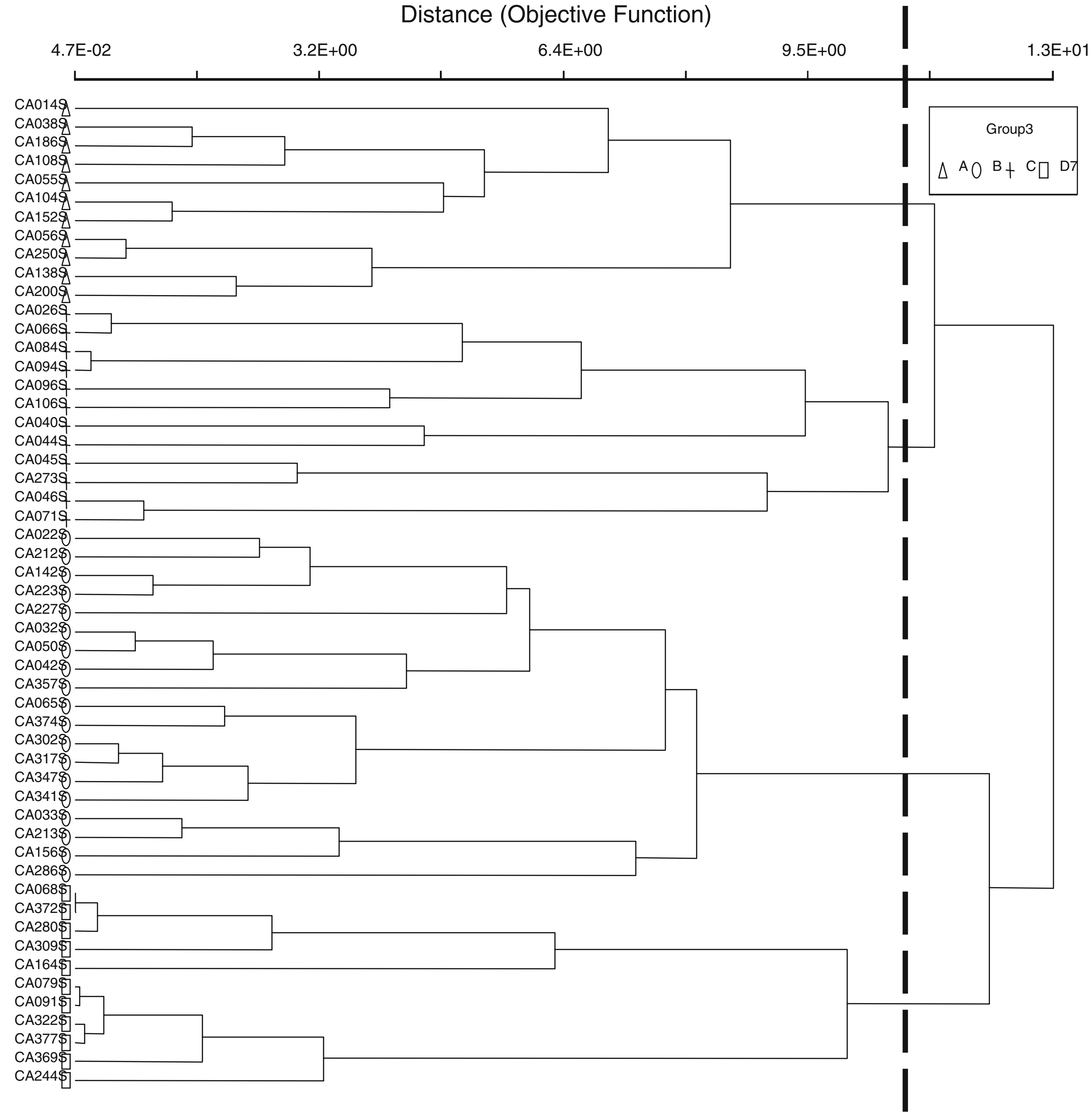


Figure 2. Dendrogram of diatom-based stream site classification using the UPGMA method. The dashed line is the cutting line for defining 4 diatom-based stream site groups.

types (i.e., natural stream, man-made conveyances). The TWINSPAN groups showed a much better correspondence to the drainage basins (Table 3). All three sites in Group A and all sites in Group D except one were located in the San Joaquin River Basin. Most of the sites in Group C were in the Sacramento River Basin.

The classification tree analysis showed that hierarchically organized physical habitat variables might be important in relation to the variability among diatom-based groups (Fig. 3). Channel morphology (mean bankfull width), in-stream habitat (relative stream bed stability) and riparian conditions (riparian disturbance index) were

Table 2. Summary of indicator species analysis showing indicator taxa, relative abundance, relative frequency, and indicator value for each diatom-based stream group classified using the UPGMA method

Taxa	Relative abundance				Relative frequency				Indicator value			
	Group				Group				Group			
	A	B	C	D	A	B	C	D	A	B	C	D
Amphora veneta Kütz.	77	7	8	9	73	37	50	36	**56**	2	4	3
Nitzschia amphibia Grun.	66	8	13	14	100	74	83	73	**66**	6	11	10
Planothidium lanceolatum (Bréb. ex Kütz.) Lange-Bert.	5	56	20	19	36	89	83	73	2	**50**	17	14
Achnanthidium minutissimum (Kütz.) Czarnecki	12	70	3	15	45	89	42	55	5	**62**	1	8
Caloneis bacillum (Grun.) Cl.	23	55	13	9	45	79	42	27	10	**43**	5	3
Cymbella silesiaca Bleisch	4	67	7	22	27	95	42	64	1	**64**	3	14
C. sinuata Greg.	12	68	0	21	18	63	0	27	2	**43**	0	6
Diatoma vulgare Bory	3	89	5	4	9	63	8	9	0	**56**	0	0
Fragilaria capucina Desm.	20	56	19	6	18	74	42	36	4	**41**	8	2
Navicula cryptotenella Lange-Bert.	15	73	2	10	45	95	8	36	7	**69**	0	3
N. viridula (Kütz.) Kütz. emend. V. H.	9	64	13	14	27	63	42	27	2	**40**	5	4
Nitzschia dissipata (Kütz.) Grun.	13	73	5	9	45	79	33	27	6	**58**	2	2
Rhoicosphenia abbreviate (Agardh) Lange-Bert.	15	57	3	24	55	79	33	64	8	**45**	1	16
Cyclotella meneghiniana Kütz.	8	10	76	6	55	84	92	64	4	9	**70**	4
Diadesmis confervacea Kütz.	6	5	90	0	18	47	58	0	1	2	**52**	0
Nitzschia calida Grun.	29	7	64	0	45	21	67	0	13	2	**43**	0
Rhopalodia gibberula (Ehr.) O. Müll.	13	2	83	2	18	16	50	9	2	0	**41**	0
Cocconeis placentula Ehr.	6	30	3	61	55	100	58	91	3	30	2	**56**
Staurosira construens Ehr.	3	7	8	83	36	84	58	91	1	6	5	**75**
Synedra parasitica (W. Sm.) Hust.	6	6	1	88	9	26	8	55	1	1	0	**48**

The bold numbers are significant indicator values ($p < 0.05$, Monte Carlo permutation test).

Table 3. Correspondence among diatom-based stream groups, drainage basins, and "stream" types

	TWINSPAN group				Drainage basin		"Stream" type		
	A	B	C	D	Sacramento	San Joaquin	Ditch/drain	Natural	Isolated
UGPMA group									
A (11)	0	8	2	1	7	4	10	0	1
B (19)	0	1	9	9	9	10	15	4	0
C (12)	0	8	2	2	5	7	6	5	1
D (11)	3	1	0	7	2	9	4	6	1
TWINSPAN group									
A (3)					0	3	2	1	0
B (18)					11	7	11	6	1
C (13)					11	2	9	3	1
D (19)					1	18	13	5	1

The numbers in the parenthesis are the total number of sampled sites for each group. The numbers in the table show the distribution of the sites among different categories of each classification.

identified as important variables to discriminate among the diatom-based groups classified using the UPGMA (Fig. 3). For the TWINSPAN groups, riparian conditions (mean bankside canopy cover) channel morphology (mean bankfull width, mean thalweg depth) and in-stream habitat conditions (erodible substrate diameters) were identified.

Relative importance of water quality and physical habitat conditions on diatom assemblages

CCA with a forward selection option identified channel morphology (mean wetted stream width, mean thalweg depth, mean bank angle), in-stream habitat (% coarse substrates), riparian conditions (non-agricultural riparian disturbance index), and cations (manganese) as important in relation to diatom assemblages (Monte Carlo permutation test, $p < 0.05$) (Fig. 4). These variables explained a total of 21% variance in diatom species data set. The 1st CCA axis negatively correlated with mean wetted channel width ($r = -0.66$) and thalweg depth ($r = -0.65$) (Table 4). The 2nd axis correlated with % coarse substrates ($r = 0.60$). Bivariate correlation analysis showed that % *Cymbella* significantly correlated with mean bank angle ($r = 0.51$, $p = 0.0001$, $n = 53$). Percent of *Navicula* increased with mean wetted width ($r = 0.40$, $p = 0.03$, $n = 53$).

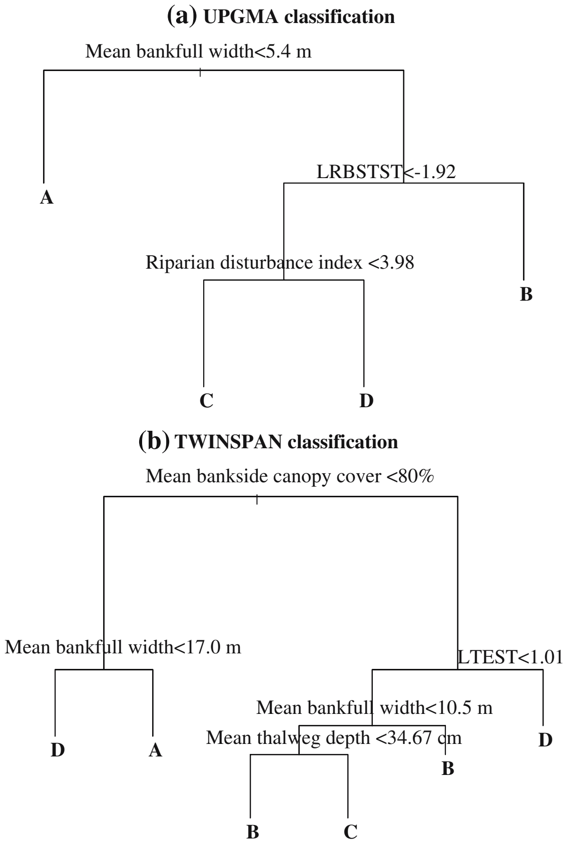


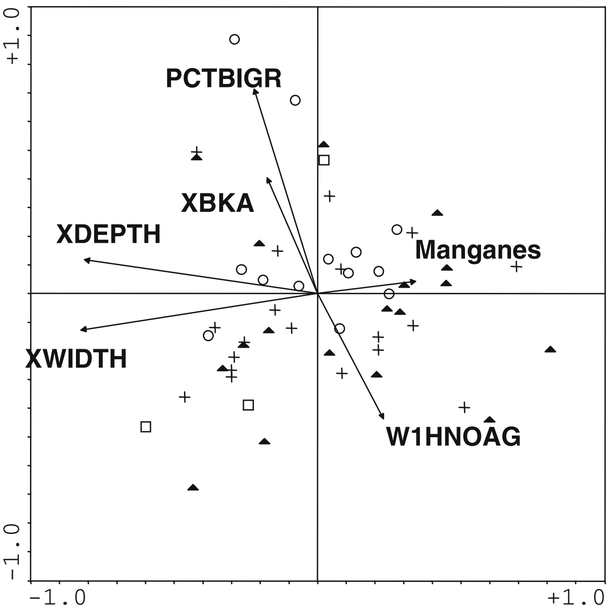
Figure 3. Classification tree analysis showing hierarchically organized physical habitat variables which were important in relation to the variability among diatom-based groups. LRBSTST: $\log_{10}$ relative bed stability, LTEST: $\log_{10}$ erodible substrate diameters.

Discussion

Our analyses showed that stream diatom assemblages in the Central Valley ecoregion were mainly associated with physical habitat conditions. The classification tree analysis indicated that the variability among the diatom-based stream groups could be best accounted for by the variables associated with riparian conditions, in-stream habitat, and channel morphology. Canonical correspondence analysis indicated that variables associated with these same physical habitat categories could explain the largest amount of the variability in the diatom data set. It is not surprising that physical habitat conditions accounted for most of the variability in the diatom assemblages. Streams in this ecoregion have been extensively modified by human activities including intensive agriculture and urbanization (Mount, 1995). Most of these activities involve direct or indirect alteration of natural flow regimes and channel morphology in streams and rivers.

Our results were consistent with several studies conducted in the region. As part of the same Regional Environmental Monitoring and Assessment Program (REMAP), Griffith et al. (2003) found that channel morphology and substrates were the major environmental variables related to aquatic macroinvertebrates. In a separate study, Brown & May (2000) reported that stream-size gradient associated with combined agricultural and urban land use in the basin was the major environmental gradient related to macroinvertebrates found on large woody debris. In contrast, Leland et al. (2001) reported that algae in the San Joaquin

(a) CCA ordination site plot showing the TWINSPAN groups



(b) CCA ordination site plot showing the UPGMA groups

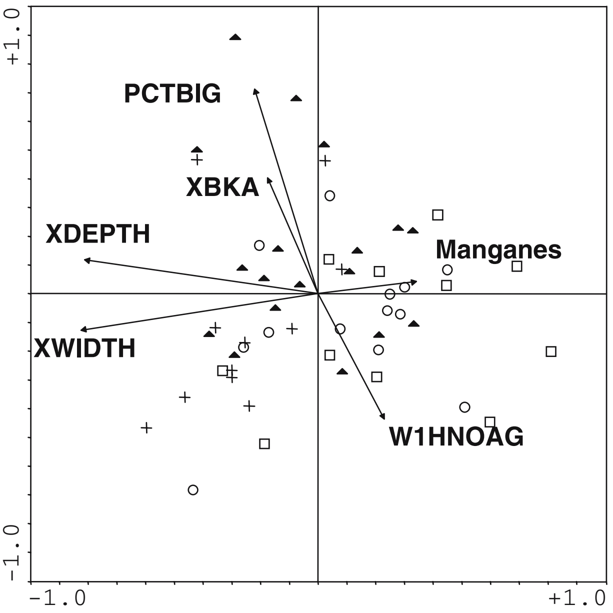


Figure 4. Ordination site plot of canonical correspondence analysis showing environmental variables identified by a forward selection method. PCTBIGR: % of coarse substrates (>16 mm), W1HNOAG: mean Non-agricultural riparian disturbance index, XWIDTH: mean wetted stream width, XDEPTH: mean thalweg depth, XBKA: mean bank angle (degrees).

River and its major tributaries were strongly associated with salinity and nutrients. The difference in patterns observed between Leland et al. and those found in our study may derive from different sampling designs. Their sampling sites, mainly located along the main stem of the San

Table 4. Correlation coefficients between selected environmental variables and the 1st two CCA axes

Variables	CCA ordination	
	I	II
% streams as coarse substrates	−0.18	0.60
Manganese	0.28	0.04
Mean bank angle (degree)	−0.14	0.34
Mean wetted stream width	−0.66	−0.11
Mean thalweg depth	−0.65	0.10
Non-agricultural riparian disturbance	0.18	−0.37
% variance of species data explained	5.3	4.9

Joaquin River, reflect large river habitat conditions while most of our sampling sites were 1st-order ditches and drains with only a few large river sites. In addition, their study included several sites in the Sierra Nevada foothills, which produces stronger gradients of salinity and nutrients in their data set.

Because stream types and physical habitat conditions varied so much among our sites, it was expected that diatom-based classification would yield several discrete stream groups that might correspond to the major environmental characteristics. Two classification methods (UPGMA and TWINSPAN) commonly used in ecology and bioassessment yielded substantially different memberships for each group (Table 3). Neither diatom-based stream classification corresponded well with stream types, indicating that within-stream-type variability of environmental variables in relation to diatom assemblages may be high. The TWINSPAN groups corresponded better with the drainage basin than the UPGMA groups. Two basins are different in natural environmental settings. For example, the San Joaquin is more xeric than the Sacramento River with higher soil salinity and erodibility. The TWINSPAN method based on the 'top-down' approach seems to capture basin-related variability among stream sites better than the UPGMA method.

Indicator species analysis identified sets of indicator taxa for each diatom-based stream groups. However, interpretation of these indicator taxa in relation to the environmental variables identified by the classification tree method is difficult. For example, a total of 11 indicator taxa were identified for the UPGMA-Group B (Table 2). Most of these taxa have been classified as either non-motile (e.g., *Staurosira*) or stalked taxa (e.g., *Achnanthidium*, *Cymbella*, *Rhoicosphenia*). The classification tree model indicated that these sites may have larger channel sizes and higher in-stream bed stability (Fig. 3). However, non-motile taxa (*Staurosira* and *Cocconeis*) were also indicative for Group D that was characterized by relatively lower in-stream bed stability. The difficulty in relating indicator taxa to a particular set of environmental variables may partly be due to the complex interactions among environmental variables related to diatoms, and possible mismatches between diatoms and measured environmental variables across both spatial and temporal scales. For example, in this study samples were collected from 9 different locations in each 150–450 m long study reach and combined as one sample. This mixture of the samples from the multiple sampling locations, each possibly with different substrates and microhabitats, may decrease our ability to infer ecological processes which may be responsible for location-specific diatom assemblages, and consequently lower diatom sample response sensitivity. The composite samples, aiming at assessing overall reach-scale conditions, may reflect only strong and coarse-scale environmental conditions.

Poor association between diatom assemblages and water chemistry may reflect overall impaired water quality in this region. Despite the high variability of nutrients among sites, overall nutrient concentrations may be high enough for diatom growth. Bothwell (1989) suggested that areal periphyton biomass, dominated by diatoms, may peak around 28 μg PO_4^{3-}-P l^{-1} based on three long-term artificial stream enrichment studies. Recently, use of soluble reactive phosphorus concentrations to indicate nutrient status in stream field studies has been questioned (Dodds, 2003). Dodds recommended that total phosphorus (TP) may be a better indicator of nutrient limitation in surface water studies. Unlike lentic systems, the relationship between TP and lotic trophic conditions has not been adequately quantified. Dodds et al. (1998) suggested that streams may be classified as oligotrophic if $TP < 29$ μg l^{-1}. In this study, the median concentration of TP was 100 μg l^{-1} with a range from 29 μg l^{-1} to 3600 μg l^{-1}. The relationship between nutrients and lotic diatom assemblages in this ecoregion may be further confounded by applications of herbicides in streams or near-riparian areas. Herbicides have been used to control excessive algal growth in some streams, especially constructed conveyance habitats.

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