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APPLIED ISSUES

Efficacy of algal metrics for assessing nutrient and organic enrichment in flowing waters

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SUMMARY

1. Algal-community metrics were calculated for periphyton samples collected from 976 streams and rivers by the U.S. Geological Survey's National Water-Quality Assessment (NAWQA) Programme during 1993–2001 to evaluate national and regional relations with water chemistry and to compare whether algal-metric values differ significantly among undeveloped and developed land-use classifications.
2. Algal metrics with significant positive correlations with nutrient concentrations included indicators of trophic condition, organic enrichment, salinity, motility and taxa richness. The relative abundance of nitrogen-fixing algae was negatively correlated with nitrogen concentrations, and the abundance of diatom species associated with high dissolved oxygen concentrations was negatively correlated with both nitrogen and phosphorus concentrations. Median algal-metric values and nutrient concentrations were significantly lower at undeveloped sites than those draining agricultural or urban catchments.
3. Total algal biovolume did not differ significantly among major river catchments or land-use classifications, and was only weakly correlated with nitrate (positive) and suspended-sediment (negative) concentrations. Estimates of periphyton chlorophyll *a* indicated an oligotrophic–mesotrophic boundary of about 21 mg m^{-2} and a mesotrophic–eutrophic boundary of about 55 mg m^{-2} based on upper and lower quartiles of the biovolume data distribution.
4. Although algal species tolerance to nutrient and organic enrichment is well documented, additional taxonomic and autecological research on sensitive, endemic algal species would further enhance water-quality assessments.

Keywords: land use, metrics, National Water-Quality Assessment, nutrients, periphyton

Introduction

Nutrient and organic enrichment are major water-quality concerns in streams and rivers. According to the most recent U.S. Environmental Protection Agency (USEPA) inventory of the state of the Nation's waters, siltation, nutrients, bacteria and oxygen-depleting substances were among the top causes of water-quality impairment. Non-point source contamination from urban and agricultural land is the leading source of impairment in the U.S.A. (USEPA, 2002) as well as elsewhere. Excessive amounts of nutrients (nitrogen and phosphorus) in streams with relatively clear water can produce nuisance growths

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of periphyton (benthic algae) or algal seston (phytoplankton), particularly in exposed stream reaches with little riparian shading. Although algae are an important food resource for certain macroinvertebrates and fish (e.g. Lamberti, 1996), nuisance growths of algae can impair water quality and stream habitat by contributing large amounts of organic carbon to streams and rivers (autogenic organic enrichment). More fundamentally, nuisance algal growths in streams and rivers provide visible evidence of eutrophication and water-quality degradation to water-resource managers and the public.

Trophic-classification systems developed for lakes and reservoirs (e.g. Hutchinson, 1967; Carlson, 1977) have been based on nutrient concentrations, indicators of algal biomass (e.g. chlorophyll *a* or cell counts) and water clarity (e.g. Secchi depth transparency). Although these lake classification systems are used widely, proposals for similar trophic classification of streams and rivers, and procedures for establishing nutrient criteria in streams and rivers, have evolved only recently (e.g. Dodds, Jones & Welch, 1998; Biggs, 2000; Dodds & Welch, 2000). At present, guidance for establishing nutrient criteria for streams and rivers in the U.S.A. relies primarily on compiling historic data for nutrient concentrations, algal biomass and water clarity, and establishing nutrient and algal criteria based on frequency distributions (USEPA, 2000).

Assessments of algal-community structure can reveal that eutrophication problems exist or that water-quality conditions are favourable for such problems to develop. Many algal taxa can be identified reliably to species or variety (notably diatoms), and there is a 100-year history of understanding species relations with nutrient and organic enrichment for certain algal taxa (e.g. Kolkwitz & Marsson, 1908). Traditionally, algal indicators of eutrophication have been based on published accounts of species and water-quality relations, notably in extensive compilations of previous European and North American studies (e.g. Palmer, 1969; Lowe, 1974; VanLandingham, 1982; Bahls, 1993; van Dam, Mertens & Sinkeldam, 1994), as well as general taxonomic references that provide limited water-quality information (e.g. Hustedt, 1930; Prescott, 1962; Patrick & Reimer, 1966; Cholnoky, 1968).

Autecological attributes, the physiological requirements or tolerances of algal species, can be aggregated into metrics or autecological classes that indicate nutrient conditions, trophic status and indices of biotic integrity (IBI; McCormick & Cairns, 1994; Stevenson & Bahls, 1999; Stevenson & Smol, 2003). Diatom pollution and trophic indices were first developed in Europe (e.g. Lange-Bertalot, 1979; van Dam *et al*., 1994; Kelly & Whitton, 1995) and subsequently adapted for use in the U.S.A. (e.g. Bahls, 1993); however, there has been much greater application of diatom metrics and IBIs derived from diatom metrics in Europe than the U.S.A. Although these autecological classifications are categorical and qualitative, they have been used somewhat successfully in water-quality studies (Cuffney *et al*., 1997; Scudder & Stewart, 2001; Peterson & Porter, 2002; Coles *et al*., 2004) and periphyton IBIs (Hill *et al*., 2000; Fore & Grafe, 2002; Griffith *et al*., 2005) in the U.S.A.

The efficacy of these algal metrics, relative to their correspondence with nutrient and related water-quality variables and land-use characteristics, has not been demonstrated for streams and rivers throughout the U.S.A. For example, a trophic diatom index should be expected to correlate significantly with nutrient concentrations and (or) human sources of nutrient enrichment. Instead of calculating diatom IBIs developed and calibrated for European streams and rivers, we elected to examine responses of candidate algal attributes (e.g. trophic state, nitrogen metabolism, standing crop, salinity, pH, diversity, habitat, etc.) to provide understanding that would lead to developing components of regional algal IBIs for the continental U.S.A. We also included candidate metrics for soft (non-diatom) algae because of important functional attributes (e.g. nitrogen fixation by certain cyanobacteria; sestonic versus benthic algae) and the substantial biomass of soft algae found in many eutrophic streams that provides visible evidence of eutrophication to the public.

This study utilized a large national data set to address two study objectives: (i) to assess relations between published algal-autecological metrics and nutrient and suspended-sediment concentrations at large (national) and intermediate (regional) spatial scales and (ii) to determine whether differences in algal-metric values occur among undeveloped and developed land-use categories. We then compare the efficacy of algal and water chemistry approaches for assessing eutrophication and organic enrichment, and discuss implications for establishing nutrient and biological criteria for U.S.A. streams and rivers.

Methods

Study area and scope

This study includes results from periphyton samples collected throughout the continental United States by the U.S. Geological Survey's National Water-Quality Assessment (NAWQA) Programme during 1993–2001 (Gilliom, Alley & Gurtz, 1995). Although algal samples were collected in different years in various parts of the U.S.A., samples most commonly were collected during stable periods of low streamflow (Gurtz, 1994). More than 7000 algal samples have been collected from over 1500 streams and rivers since the full implementation of the NAWQA Programme in 1993 (Berkman & Porter, 2004). The spatial scope of this study focuses on 976 sites in the continental U.S.A. with algae and water chemistry data. For the purposes of this report, the continental United States was divided into eight contiguous areas based on water-resources regions (Fig. 1), a stratification approach that currently serves as a primary spatial framework for analysis of water-quality conditions and trends in

Region	Water-Resources Regions	Predominant ecoregions [1]	Climate [2]
Northeast (1)	New England and Mid-Atlantic basins	humid, warm continental (upland to coastal plain)	P>E
Southeast (2)	South Atlantic-Gulf and Tennessee basins	humid, subtropical (upland to coastal plains)	P>E
Midwest (3)	Upper Mississippi, Ohio, Great Lakes and Souris-Red-Rainy basins	humid, hot continental & prairie	P>E
Northern Plains (4)	Missouri River basin	dry temperate steppe (mountains) to humid prairie	--
Southern Plains (5)	Lower Mississippi, Arkansas-White-Red, and Texas-Gulf basins	humid, prairie to subtropical coastal plain	NCR
Southwest (6)	Rio Grande, Upper Colorado, Lower Colorado, and Great Basin	dry temperate steppe (mountains) to desert	P<E to P<< E
Northwest (7)	Pacific Northwest basins	dry temperate steppe (mountains) to humid marine	NCR
California (8)	California basins	mediterranean & dry steppe (mountains)	P<E

Fig. 1 Regions of the continental United States defined on the basis of water-resource regions (modified from Seaber *et al.*, 1987). P, average annual precipitation; E, average annual evaporation; NCR, no consistent relation; [1] from Bailey (1995); [2] from Winter & Woo (1990).

the NAWQA Programme and is consistent with an ongoing summary of nutrient conditions in U.S.A. streams and rivers (Mueller & Spahr, 2006).

Algal indicators

Periphyton samples were collected from submerged rocks or woody debris during seasonally low-streamflow conditions as described by Porter *et al.* (1993) and Moulton *et al.* (2002). Periphyton data are stored in NAWQA's Bio-TDB database and can be accessed from the NAWQA Data Warehouse at http://water.usgs.gov/nawqa/data. Algae (diatoms + soft algae) were identified to lowest possible taxon by the Academy of Natural Sciences, Patrick Center for Environmental Research (Charles, Knowles & Davis, 2002). About 600 algal cells were enumerated from each sample and results were tabulated as the abundance (cells cm^{-2}) and biovolume (μm^3 cm^{-2}) for each taxon. Biovolume was estimated by measuring the dimensions of 15 or more representative cells and calculating cell volume in accordance with the nearest geometric shape (Charles *et al.*, 2002). Taxa without distinct cell walls and certain colonial algae (e.g. cyanobacteria) were counted as operational units, generally 10 μm lengths or colonies. The relative abundance (% cell density) of each taxon was calculated for each sample. Taxon richness was reported as the number of taxa encountered during a count of about 600 algal cells (Charles *et al.*, 2002).

Indicators of periphyton standing crop such as total cell density (CELLDEN) and biovolume were calculated by summing results for all taxa in each sample. Total cell biovolume (BIOVOL) was converted to units of cm^3 m^{-2} by dividing by 10^8. Conversion of algal biovolume to algal biomass was based on a specific density of 1.0 g cm^{-3} (Leland & Porter, 2000; Leland, Brown & Mueller, 2001); thus, biovolume units of cm^3 m^{-2} are proportional to biomass units of g m^{-2}. The biomass conversions were used to estimate chlorophyll *a* values for samples based on previously established chlorophyll–biovolume relations (Porter, 2000). An autecological table of taxon-specific environmental requirements and tolerance was compiled based on published literature accounts (Porter, 2007).

Autecological characterization was based primarily on van Dam *et al.* (1994), Bahls (1993), Lange-Bertalot (1979), Lowe (1974) and Prescott (1962). Other references (e.g. Prescott, 1968; Palmer, 1969; Bold & Wynne, 1978; VanLandingham, 1982 and Wehr & Sheath, 2003) also were consulted for taxa not discussed by the primary references. More than 60 categories within 14 autecological attributes were evaluated relative to water chemistry, land use and hydrologic variables. Major groups of autecological attributes included indicators of nitrogen metabolism, trophic condition, organic enrichment, dissolved oxygen concentrations, physical conditions (pH, temperature and specific conductance) and habitat (Table 1). For each autecological attribute, the abundance of all characterized taxa was summed and divided by the total abundance of all taxa in the sample, thus low metric values indicate small percentages of the attribute (e.g. eutrophic diatoms) in the benthic-algal assemblage and a high metric value indicates that a large percentage of the assemblage was represented by taxa with the described attribute. Metric values (relative abundance) discussed here are relatively lower than if only characterized taxa (those with reported autecological information) had been used to calculate the metrics (cf. Stevenson & Smol, 2003) because published autecological information was not available for some species and identification was only possible to genus for other taxa.

Water chemistry indicators

Algal-metric values were compared with nutrient and suspended-sediment concentrations from water-quality samples collected on or near the same date of periphyton sampling. Water-quality samples generally were collected with a depth-integrating sampler at multiple vertical locations along a stream cross-section (Shelton, 1994). Samples for analyses of dissolved nutrients (ammonia, nitrite + nitrate and orthophosphate) were filtered (pore size = 0.45 μm) in the field within 2 h of sample collection. Filtered and unfiltered (total) nutrient samples were chilled to 4 °C and analysed by the USGS National Water-Quality Laboratory in Lakewood, Colorado. Dissolved nutrients were analysed according to methods published by Fishman (1993). Total Kjeldahl nitrogen was analysed as described by Patton & Truitt (1992). Total phosphorus (TP) concentrations were determined by a modified Kjeldahl procedure (Patton & Truitt, 2000) during 1993–98, and by a low-level persulphate digestion method (USEPA method 365.1; USEPA, 1993) after 1999. Suspended-sediment samples were

Table 1 Explanation of algal metrics with one or more significant correlations with nutrient and suspended-sediment concentrations

Algal metric	Definition	Attribute	Class	Source
CELLDEN	Cell density (total)	Standing crop	Cell density (cells/cm^2)	Various
BIOVOL	Biovolume (total)	Standing crop	Biovolume (cm^3/m^2)	Various
TAXARICH	Taxa richness	Diversity	Taxa richness	Various
SP_OL	Saprobity, oligo	Saprobity	Oligosaprobous diatoms	van Dam *et al.*, 1994
SP_BM	Saprobity, beta-meso	Saprobity	(β-mesosaprobous diatoms	van Dam *et al.*, 1994
SP_AM	Saprobity, alpha-meso	Saprobity	α-mesosaprobous diatoms	van Dam *et al.*, 1994
SP_AP	Saprobity, alpha-poly	Saprobity	α-meso-/polysaprobous diatoms	van Dam *et al.*, 1994
SP_PS	Saprobity, polysaprobous	Saprobity	Polysaprobous diatoms	van Dam *et al.*, 1994
ON_AL	Organic nitrogen, autotrophic, low	Nitrogen-uptake metabolism	Low nitrogen autotrophic diatoms	van Dam *et al.*, 1994
ON_AH	Organic nitrogen, autotrophic, high	Nitrogen-uptake metabolism	High nitrogen autotrophic diatoms	van Dam *et al.*, 1994
ON_NH	Organic nitrogen, nitrogen heterotrophic	Nitrogen-uptake metabolism	Nitrogen heterotrophic diatoms	van Dam *et al.*, 1994
NF_YS	Nitrogen fixer, yes	Nitrogen-fixing algae	Nitrogen fixer	Various
TR_O	Trophic, oligotrophic	Trophic state	Oligotrophic diatoms	van Dam *et al.*, 1994
TR_M	Trophic, mesotrophic	Trophic state	Mesotrophic diatoms	van Dam *et al.*, 1994
TR_E	Trophic, eutrophic	Trophic state	Eutrophic diatoms	van Dam *et al.*, 1994
ES_SF	Eutrophic soft algae	Trophic state	Eutrophic soft algae	Various
EUTROPHIC	Eutrophic algae	Trophic state	Eutrophic algae	Various
PC_MT	Pollution class, most tolerant	Pollution class	Most tolerant diatoms	Bahls, 1993
PC_LT	Pollution class, less tolerant	Pollution class	Less tolerant diatoms	Bahls, 1993
PC_SN	Pollution class, sensitive	Pollution class	Sensitive diatoms	Bahls, 1993
PT_VT	Pollution tolerance, very tolerant	Pollution tolerance	Very tolerant diatoms	Lange-Bertalot, 1979
PT_TA	Pollution tolerance, tolerant (A)	Pollution tolerance	Tolerant diatoms	Lange-Bertalot, 1979
PT_TB	Pollution tolerance, tolerant (B)	Pollution tolerance	Tolerant diatoms	Lange-Bertalot, 1979
PT_LA	Pollution tolerance, less tolerant (A)	Pollution tolerance	Less tolerant diatoms	Lange-Bertalot, 1979
PT_LB	Pollution tolerance, less tolerant (B)	Pollution tolerance	Less tolerant diatoms	Lange-Bertalot, 1979
SL_FR	Salinity, fresh	Salinity	Fresh water diatoms	van Dam *et al.*, 1994
SL_FB	Salinity, fresh-brackish	Salinity	Fresh-brackish water diatoms	van Dam *et al.*, 1994
SL_HB	Salinity, brackish	Salinity	Brackish water diatoms	van Dam *et al.*, 1994
BS_SE	Benthic/sestonic, sestonic	Habitat	Sestonic algae	Various
MT_YS	Motility, yes	Motility	Motile algae	Various
OT_AH	Oxygen tolerance, always high	Oxygen requirements	Continuously high (diatoms)	van Dam *et al.*, 1994
OT_FH	Oxygen tolerance, fairly high	Oxygen requirements	Fairly high (diatoms)	van Dam *et al.*, 1994
OT_MD	Oxygen tolerance, moderate	Oxygen requirements	Moderate (diatoms)	van Dam *et al.*, 1994
OT_LW	Oxygen tolerance, low	Oxygen requirements	Low (diatoms)	van Dam *et al.*, 1994
OT_VL	Oxygen tolerance, very low	Oxygen requirements	Very low (diatoms)	van Dam *et al.*, 1994

Key algal metrics selected for further analysis are in bold.

analysed at various USGS Water Science Centres as described by Guy (1969).

Land-cover classification

Land-cover information included a classification of sites into one of six categories based on percentages of major land-cover classes determined from National Land Cover Data digital maps, as revised by Nakagaki & Wolock (2005). Land cover upstream from sites in the 'agricultural' category generally was >50% agricultural and <5% urban, whereas land cover upstream from streams in the 'urban' category was >25% urban and <25% agricultural. Streams in the 'mixed' category contained substantial percentages of both agricultural and urban land cover.

Streams influenced by low-to-moderate percentages of either agricultural or urban land cover were classified partially developed ('partial'). Streams with <25% agricultural and <5% urban land cover were designated 'undeveloped'. Additional information about land-cover classification is reported by Nakagaki & Wolock (2005) and Mueller & Spahr (2006).

Although not strictly a land-cover classification, large rivers were separated for analysis because of presumed differences in water-quality processes and ecological function relative to wadeable streams (e.g Vannote *et al.*, 1980; Bott *et al.*, 1985; Allen, 1995). Because of considerable variation in large river hydrology across the U.S.A., the 'Large' classification was based on a combination of catchment area and long-term mean annual streamflow. Generally, large rivers were defined as those with a minimum catchment area of about 1500 km^2 and a mean annual discharge >85 $m^3 s^{-1}$. Rivers with mean annual discharge >56 $m^3 s^{-1}$ and catchments >5000 km^2, and those with mean annual discharge >14 $m^3 s^{-1}$ and catchments >25 000 km^2 also were included in the 'Large' classification.

Analysis of data

Spearman's rank correlation analysis was used to evaluate algal-metric relations with nutrient and suspended-sediment concentrations. Redundancy analysis (RDA; ter Braak & Smilauer, 1998) was used to investigate relations between the 35 algal metrics and water chemistry. Algal metrics were selected by evaluating the magnitude of RDA factor loadings, the strength of correlations with nutrient concentrations and relations with important algal processes (e.g. nitrogen fixation and heterotrophy). Differences in algal-metric scores and nutrient concentrations among land-use categories and major geographical regions were tested by Kruskal–Wallis analysis of variance (KW-ANOVA) on rank-transformed data (Conover & Iman, 1981). If a significant difference was determined by KW-ANOVA, differences between individual categories or regions were evaluated by applying Tukey's multiple-comparison test. SYSTAT (2004, version 11, SYSTAT Software, Inc., Richmond, CA, U.S.A.) or S-PLUS (MathSoft 1999) were used for data analyses and preparation of data figures. Map figures were prepared using geographical information software for qualitative interpretation of geographical distributions of algal metrics.

Results

National algal-metric relations with water chemistry

Thirty of the 35 algal metrics were significantly correlated with one or more forms of nutrients (Tables 1 & 2). Algal-metric correlation coefficients generally were larger for total than dissolved nutrient concentrations. Algal biovolume increased with nitrate concentrations, whereas both biovolume and cell density decreased with increases in suspended-sediment concentrations (Table 2). Taxon richness and the relative abundance of sestonic (tychoplanktonic) algae (BS_SE) increased significantly with suspended-sediment concentrations and all forms of nutrients except nitrate. The relative abundance of motile algae (MT_YS) also increased significantly with nutrient and suspended-sediment concentrations. Algal indicators of tolerance were positively correlated with all (or most) forms of nutrient and suspended-sediment concentrations, demonstrating the efficacy of the metrics for indicating nutrient and organic enrichment (Table 2). Based on the magnitude of correlation coefficients ($\rho > 0.5$), the best indicators of nutrient and sediment contamination were: (i) nitrogen heterotrophic diatoms (ON_NH); (ii) diatoms tolerant of low dissolved-oxygen concentrations (OT_LW); (iii) pollution-class most-tolerant diatoms (PC_MT) and (4) brackish-water (halobiontic) diatoms (SL_HB).

We hypothesized that 'sensitive' algal-metric values would be negatively correlated with nutrient and suspended-sediment concentrations. Algal metrics with significant, negative correlations with concentrations of most forms of nutrients (except ammonia) included low-nitrogen autotrophic diatoms (ON_AL) and diatoms found in streams with continuously-high dissolved oxygen concentrations (OT_AH) (Tables 1 & 2). The relative abundance of nitrogen fixers heterocytous cyanobacteria + diatoms (Rhopalodiaceae; NF_YS) was negatively correlated with nitrate and total nitrogen (TN) concentrations, whereas the abundance of sensitive diatoms (PC_SN) and 'less-tolerant' diatoms (PT_LB) was negatively correlated with phosphorus concentrations (Table 2). The only algal metric with a significant, negative correlation with suspended-sediment concentrations was OT_AH

Table 2 Spearman's rank correlations of algal metrics with nutrient and suspended-sediment concentrations

Algal metric (*n*)	NH_4 (975)	$NO_2 + NO_3$ (973)	TN (912)	TP (923)	PO_4 (974)	TSS (654)	PCTURB (976)	PCTAG (976)	PCTFOR (976)
CELLDEN						−0.190***			
BIOVOL		0.179***				−0.168*			
TAXARICH	0.195***		0.239***	**0.323*****	0.230***	**0.318*****		**0.360*****	−0.294***
SP_OL									
SP_BM		0.146**	0.144*				0.161***		
SP_AM	0.217***	**0.368*****	**0.487*****	**0.479*****	**0.421*****	**0.404*****	0.246***	**0.328*****	**−0.424*****
SP_AP	0.201***	**0.383*****	**0.499*****	**0.479*****	**0.420*****	**0.355*****	0.290***	**0.344*****	**−0.433*****
SP_PS		0.179***	**0.312*****	**0.358*****	0.266***	**0.357*****	0.151***	0.221***	**−0.324*****
ON_AL		−0.142**	−0.184***	−0.240***	−0.247***			−0.136*	0.200***
ON_AH		0.176***	0.198***				0.214***		
ON_NH	0.191***	**0.418*****	**0.547*****	**0.566*****	**0.502*****	**0.417*****	**0.315*****	**0.372*****	**−0.509*****
NF_YS		−0.242***	**−0.304*****				**−0.304*****	−0.153***	0.177***
TR_O									
TR_M									
TR_E		**0.386*****	**0.472*****	**0.423*****	**0.366*****	**0.330*****	0.266***	**0.303*****	**−0.424*****
ES_SF			0.170***	0.221***	0.163***			0.186***	−0.202***
EUTROPHIC		**0.325*****	**0.459*****	**0.442*****	**0.363*****	**0.351*****	0.241***	**0.309*****	**−0.446*****
PC_MT	0.192***	**0.395*****	**0.516*****	**0.503*****	**0.445*****	**0.373*****	**0.302*****	**0.334*****	**−0.445*****
PC_LT	0.160***	**0.364*****	**0.472*****	**0.434*****	**0.364*****	**0.403*****	0.248***	**0.318*****	**−0.428*****
PC_SN					−0.136*				
PT_VT	0.205***	**0.358*****	**0.447*****	**0.417*****	**0.381*****	**0.322*****	0.264***	0.267***	**−0.355*****
PT_TA	0.186***	**0.342*****	**0.418*****	**0.407*****	**0.406*****	0.276***	0.254***	0.228***	**−0.353*****
PT_TB	0.206***	0.217***	**0.344*****	**0.365*****	0.282***	**0.363*****	0.228***	0.245***	**−0.339*****
PT_LA		0.209***	0.190***				0.158***		−0.163***
PT_LB				−0.187***	−0.179***				
SL_FR									
SL_FB		0.265***	0.249***				0.217***		−0.154***
SL_HB	0.175***	**0.347*****	**0.514*****	**0.543*****	**0.445*****	**0.475*****	0.250***	**0.389*****	**−0.522*****
BS_SE	0.155***		0.257***	**0.335*****	0.234***	**0.306*****	0.146***	0.261***	−0.274***
MT_YS	0.199***	0.298***	**0.419*****	**0.411*****	**0.324*****	**0.433*****		**0.382*****	**−0.395*****
OT_AH		−0.158 ***	−0.247***	**−0.337*****	**−0.342*****	−0.204***		−0.289***	0.293***
OT_FH		**0.312*****	**0.397*****	0.294***	0.223***	0.277***	0.187***	0.284***	**−0.383*****
OT_MD	0.133*	**0.316*****	**0.395*****	**0.388*****	**0.358*****	0.242***	0.293***	0.194***	**−0.322*****
OT_LW	0.198***	**0.420*****	**0.531*****	**0.500*****	**0.439*****	**0.381*****	**0.312*****	**0.346*****	**−0.451*****
OT_VL		0.139*	**0.332*****	**0.442*****	**0.316*****	**0.378*****	0.155***	0.286***	**−0.391*****

NH_4, ammonia nitrogen; $NO_2 + NO_3$, nitrite + nitrate nitrogen; TN, total nitrogen; TP, total phosphorus; PO_4, orthophosphate; TSS, total suspended sediment; PCTURB, percentage of urban land cover; PCTAG, percentage of agricultural land cover; PCTFOR, percentage of forested land cover.

$^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

The numbers which are in bold are $\rho > 0.3$.

(Table 2). No significant correlations were found for other algal metrics that would indicate good water quality (SP_OL, TR_O and SL_FR). In all cases, the absolute magnitude of correlation coefficients was relatively lower for sensitive than tolerant algal metrics. Based on the strength of algal-metric correlations, the best overall indicator of good water-quality conditions (low nutrient and suspended-sediment concentrations) was OT_AH, whereas NF_YS was the best indicator of low nitrogen concentrations.

Redundancy analysis was used to investigate relations among significant algal metrics with similar information content, and to select six key algal indicators for further analysis. About 92% of the explained variance was associated with the first two RDA axes, with 86% of the variance accounted for by the first RDA axis ($\lambda_1 = 0.180$) (Fig. 2). Environmental variables with large (>0.5) loading factors on the first axis included TN and dissolved nitrite + nitrate ($NO_2 + NO_3$; hereafter, nitrate) concentrations and the percentage of agricultural (PCTAG, +) and

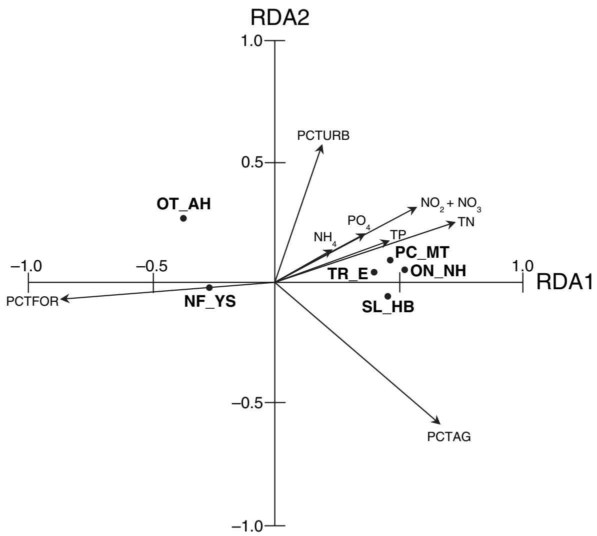

Fig. 2 Redundancy analysis (RDA) biplot of algal metrics selected for further analysis (refer to Table 1 for algal-metric definitions).

forested (PCTFOR, −) land cover. Variables with large factors on the second RDA axis ($\lambda_2 = 0.013$) included the percentage of urban land cover (PCTURB, + and PCTAG, −). Thus, nitrogen concentrations and a land-disturbance gradient (i.e. forest to agriculture) appear to account for most of the explained variance associated with algal-metric distributions, whereas differences in sources of nutrient enrichment (urban or agriculture) provide an additional 6% of explained variance.

Key algal metrics (Fig. 2, bold) were selected based on the magnitude of RDA factor loadings, the strength of correlations with nutrient and sediment concentrations, and relations with important algal processes. For example, the relative abundance of nitrogen-fixing algae (NF_YS) was hypothesized to increase when ambient concentrations of nitrogen were low because algal species in this autecological class are capable of fixing atmospheric nitrogen. We found no significant NF_YS correlations with phosphorus or suspended-sediment concentrations (Table 2), thus we conclude that NF_YS is an indicator of low nitrogen but variable phosphorus and sediment concentrations. OT_AH was selected as an indicator of good water quality because of species associations with well-oxygenated stream conditions.

Key algal-metric indicators of eutrophication selected for further analysis include two functional responses: tolerance to nutrient and organic enrichment (nitrogen-heterotrophic diatoms, ON_NH and most-tolerant diatoms, PC_MT; refer to Table 1) and tolerance to dissolved constituents, i.e. nutrients and major ions [eutrophic diatoms (TR_E) and halobiontic diatoms (SL_HB)]. The nitrogen-heterotrophic diatom metric was selected because of physiological requirements for organic forms of nitrogen (e.g. Tuchman, 1996), and PC_MT was chosen because more species are classified by this North American metric (Bahls, 1993) than by similar European tolerance metrics (e.g. Lange-Bertalot, 1979; van Dam *et al.*, 1994). Although halobiontic diatoms (SL_HB) is a metric designed to indicate salinity, chloride concentrations or specific conductance (Lowe, 1974; van Dam *et al.*, 1994), many studies have reported significant positive correlations of specific conductance with nutrient concentrations, particularly in relation to agricultural (Biggs, 1990a, 1995; Carpenter & Waite, 2000; Leland *et al.*, 2001) and urban (e.g. Leland & Porter, 2000; Potapova *et al.*, 2005) activities.

Regional algal-metric relations with water chemistry

With the exception of regions 2 (Southeast) and 3 (Midwest) (Fig. 1), regional algal-metric correlations with nutrient concentrations were similar to those observed nationally (Nat; Fig. 3). Correlation coefficients for TN concentrations with all key algal metrics except OT_AH were significantly larger in regions generally west of the Mississippi River (regions 4–8; hereafter, western) than in the eastern regions (regions 1–3; Mann–Whitney *U*-tests, $P < 0.05$). Similarly, correlations of TP concentrations with ON_NH and PC_MT were significantly larger in western than eastern regions. Algal-metric relations with nitrogen concentrations generally were poor in the Southeast and Midwest regions (Fig. 3). Correlations of TR_E with phosphorus concentrations also were poor in those primarily agricultural regions. Correlation coefficients for NF_YS generally were larger for concentrations of nitrogen than phosphorus, and correlations with nitrogen concentrations were significantly larger in the western than eastern regions. By contrast, correlation coefficients for OT_AH were larger for phosphorus than nitrogen concentrations. The regional distribution of algal-metric correlations with dissolved nutrients was similar to the pattern for total nutrient concentrations; however, correlation coefficients generally were lower for dissolved than total

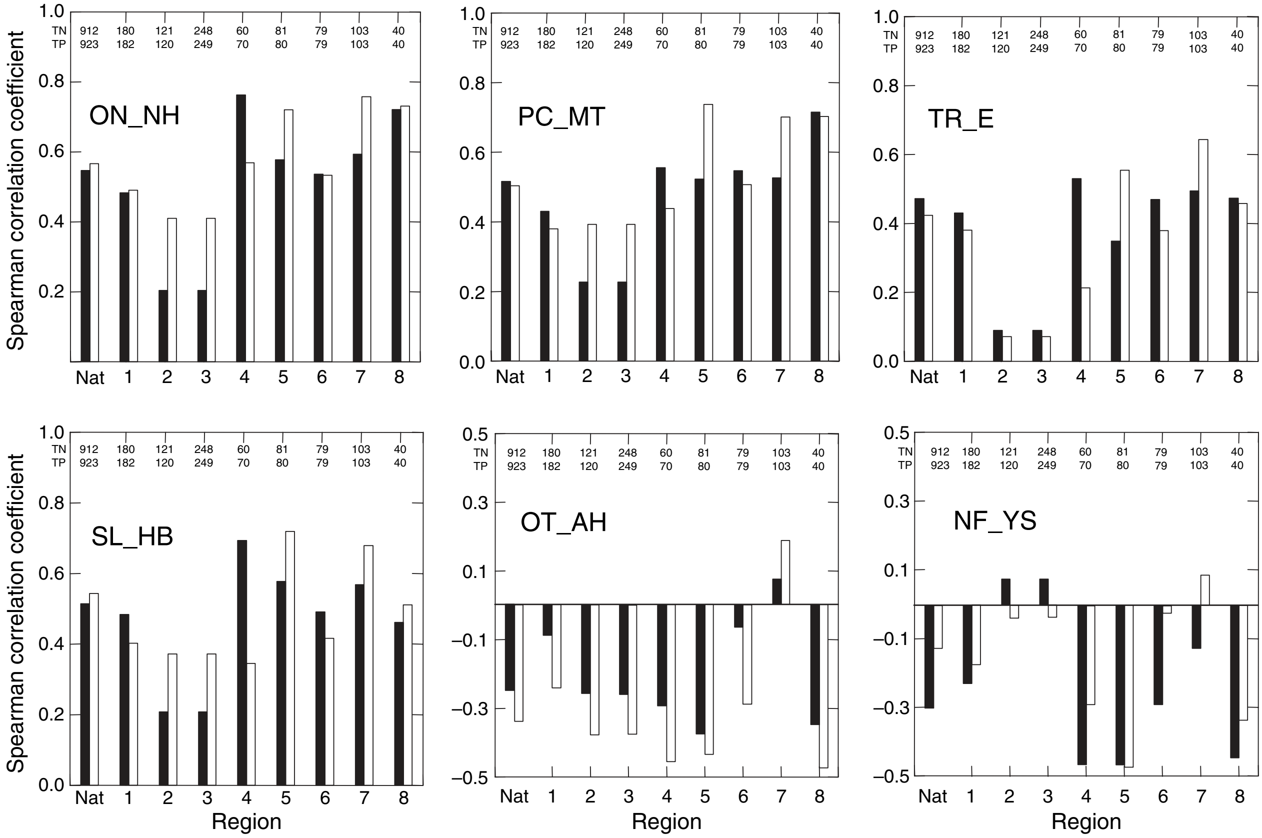

Fig. 3 Algal-metric correlations with total nitrogen (dark bars) and total phosphorus (light bars) concentrations. Refer to Fig. 1 for location of regions and Table 1 for explanation of algal metrics. Numbers of pairwise comparisons shown at top of graphs.

nutrient concentrations and, with the exception of NF_YS relations with nitrate, correlation coefficients did not differ, statistically, between eastern and western regions of the U.S.A.

Algal biovolume relations with water chemistry

Total algal biovolume ranged from <0.001 to 6329 cm^3 m^{-2} with median and mean values of 5.09 and 39.1 cm^3 m^{-2} respectively. Algal biovolume was significantly correlated with nitrate and suspended-sediment concentrations (Table 2); however, correlation coefficients were relatively weak ($\rho = 0.179$ and −0.168 respectively). No significant differences in median biovolume values were found among regional or land-cover classifications. Algal biovolume was positively correlated with one or more forms of nitrogen in regions 4, 7 and 8, and with phosphorus concentrations in region 7. Biovolume was negatively correlated with phosphorus and suspended-sediment concentrations in region 5 (Southern Plains).

Algal metric and nutrient relations with land-use classification

Overall, median values for algal indicators of nutrient and organic enrichment (ON_NH and PC_MT) were significantly larger at sites influenced by human development than undeveloped (Undev) or partially developed (Partial) sites; however, median PC_MT values in large rivers did not differ significantly from those at partially developed sites (Table 3). Median values and the ranges of metric distributions were similar for catchments draining agricultural (Ag) and urban land cover, combinations of those land uses (Mixed) and large rivers. Median values for algal indicators of dissolved nutrients (TR_E and SL_HB) were lowest at undeveloped sites. Although median values at partially developed sites did not differ significantly from urban sites, TR_E and SL_HB values were significantly higher at agricultural, mixed and large-river sites. Median values for sensitive algal indicators of low nitrogen (NF_YS) and phosphorus

Table 3 Regional relations of algal metrics and water chemistry concentrations with undeveloped and developed stream basins with five or more sites

Region	Land cover	Algal metrics								Nutrient concentrations						Sediment	
		n	ON_NH	PC_MT	TR_E	SL_HB	OT_AH	NF_YS	BIOVOL	*n*	NH_4	$NO_2 + NO_3$	TN	TP	PO_4	*n*	TSS
Region 1	Partial	51			+					44–51				+		23	
(Undev = 46)	Ag	42	+	+	+	+	+			24–42	+	+	+	+	+	21	+
	Urban	50	+	+	+	+				40–50	+	+	+	+	+	33	+
	Mixed	34		+	+	+	+			25–34	+	+	+	+	+	19	+
	Large	5		+			+			3–5		+	+	+		5	
Region 2	Partial	31				+				31		+	+			19	
(Undev = 30)	Ag	21					+			21			+			18	
	Urban	21						+		21		+	+			18	
	Mixed	11					+			10–11			+	+		5	
	Large	8				+	+			8						8	
Region 3	Partial	11			+	+	+			11			+			11	
(Undev = 12)	Ag	119	+	+	+		+			119		+	+	+	+	97	+
	Urban	20	+	+	+	+				20		+	+	+	+	8	+
	Mixed	56	+	+	+	+	+	+		56		+	+	+	+	14	+
	Large	31	+	+	+		+	+		30–31		+	+	+	+	28	+
Region 4	Partial	15								15						5	
(Undev = 24)	Ag	11								11						10	
	Large	17								17						12	
Region 5	Partial	19		+		+	+			19				+		19	
(Undev = 30)	Ag	16	+	+		+	+	+		15–16			+	+	+	15	+
	Mixed	8		+	+	+	+			8			+	+		6	
	Large	6		+		+				4–6			+	+	+	4	
Region 6	Partial	18		+	+	+				18			+	+		11	
(Undev = 46)	Urban	6	+	+						6	+	+	+	+		4	
	Large	5	+	+	+	+	+			5			+			5	+
Region 7	Partial	11								11		+	+	+		7	
(Undev = 45)	Ag	20	+	+	+	+			+	19–20	+	+	+		+	12	
	Urban	7								7	+		+	+	+	4	
	Mixed	9	+	+	+	+				9	+	+	+			4	
	Large	12								12		+	+			10	
Region 8	Urban	13	+	+		+		+		13	+	+	+	+	+	13	
(Undev = 15)	Large	5						+		5						5	

+, significant ($P < 0.05$) difference in median value relative to undeveloped sites (Kruskal–Wallis ANOVA; Tukey multiple-comparison test); refer to Methods section for explanation of land-cover classifications.

(OT_AH) concentrations were highest at undeveloped sites and lowest at mixed sites. Median NF_YS values were significantly lower at urban sites than undeveloped and partially developed sites, whereas median OT_AH values were lower at agricultural sites than undeveloped and partially developed sites. Values for large rivers were similar to those for small streams in partially developed catchments.

Overall median values for nutrient concentrations were significantly higher at sites influenced by human development (Table 3). Nutrient relations with land-use classifications generally were consistent with algal-metric results. Similar to ON_NH, median TN concentrations did not differ significantly among developed land-use categories; however, median values for partially developed and undeveloped sites were significantly lower than developed sites. For other forms of nutrients (nitrate, TP and orthophosphate), median values for partially developed and large-river sites were similar and generally lower than values for developed sites, similar to results for PC_MT. Comparison of algal-metric and nutrient values at large-river sites with those in other developed land-use classifications suggests that algal indicators of eutrophication may persist with increases in stream size, whereas dissolved-nutrient concentrations decrease longitudinally with increases in stream size (cf. Alexander, Smith & Schwarz, 2000).

Comparison of algal-metric values and nutrient concentrations in developed and undeveloped catchments

The efficacy of algal or nutrient indicators of eutrophication to contrast sites draining undeveloped and developed catchments varied among major river catchments and with land use. Among the 42 agricultural drainage catchments in region 1 (Table 3), median values for most algal metrics and all water chemistry constituents differed significantly (+) from those at the 46 undeveloped sites in this region. Overall, both algal and nutrient indicators were effective for contrasting undeveloped and developed catchments in this region. Similar results were noted for regions 3, 5 and 6. Neither algal nor nutrient values were able to contrast developed and undeveloped land-cover classifications in the Northern Plains (region 4). Nutrient concentrations appeared to be slightly better than algal metrics for comparing undeveloped and developed catchments in the Southeast (region 2) and along the west coast (regions 7 and 8; Table 3). Based on the number of significant differences between undeveloped and developed sites, the best overall eutrophication indicators for contrasting developed and undeveloped stream catchments were TN, TP, PC_MT and SL_HB.

With the exception of the Northern Plains, urban and agricultural sites were more reliably distinguished from undeveloped sites than partially developed or large river sites. Based on the percentage of possible significant differences (+) (Table 3), nutrient concentrations (80%) clearly were superior to algal metrics (42%) in urban settings, whereas the difference was less profound in agricultural settings (68% and 63% respectively). Algal indicators of tolerance (ON_NH, PC_MT, TR_E and SL_HB) generally were effective for contrasting undeveloped from urban and agricultural catchments. Relations were less certain (<33%) for partially developed sites, where human development may be increasing and an early signal of eutrophication might be important for water-resource managers.

Spatial distribution of eutrophic diatoms and algal biovolume

Sites with high eutrophic diatom (TR_E) values commonly were found throughout agricultural areas of the Northeast, Midwest, parts of the Northern Plains and Southwest, Northwest and California, as well as major urban areas of the U.S.A. (Fig. 4). Sites with low TR_E values were found in parts of the Southeast and Southern Plains regions, and in undeveloped, montane regions of the Western U.S.A. The distribution of algal biovolume (Fig. 5) generally was similar to TR_E, with high values in the Northeast, Midwest, agricultural areas of the western U.S.A. and in major urban areas. Low values were found in the Southeastern and Southern Plains regions, agricultural areas of the upper Midwest, Southwest region in western Colorado and along the upper Rio Grande, and undeveloped sites in forested regions of the western U.S.A.

Compared with the distribution of eutrophic diatoms, biovolume was not always a good indicator of trophic condition in streams with high water clarity and stable hydrologic conditions prior to sample collection, for example, those in portions of the

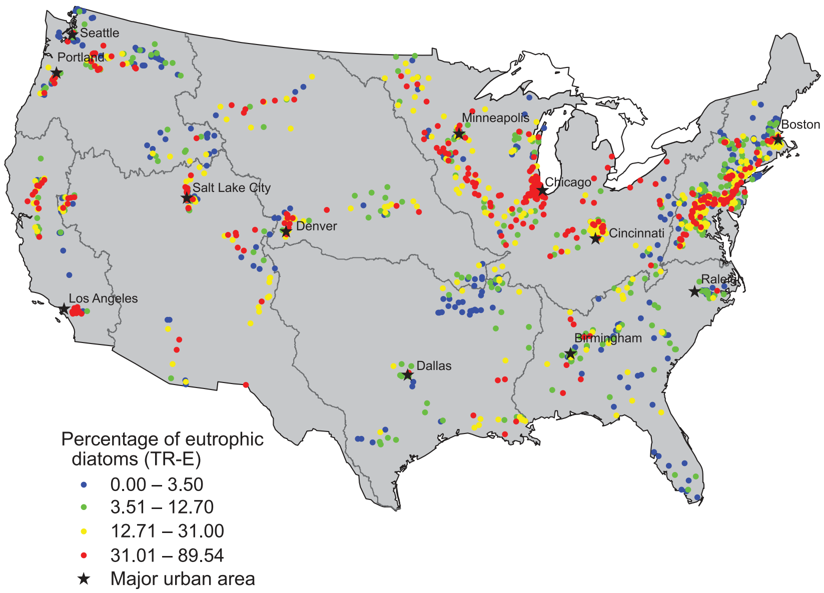

Fig. 4 Distribution of eutrophic diatoms in the continental United States.

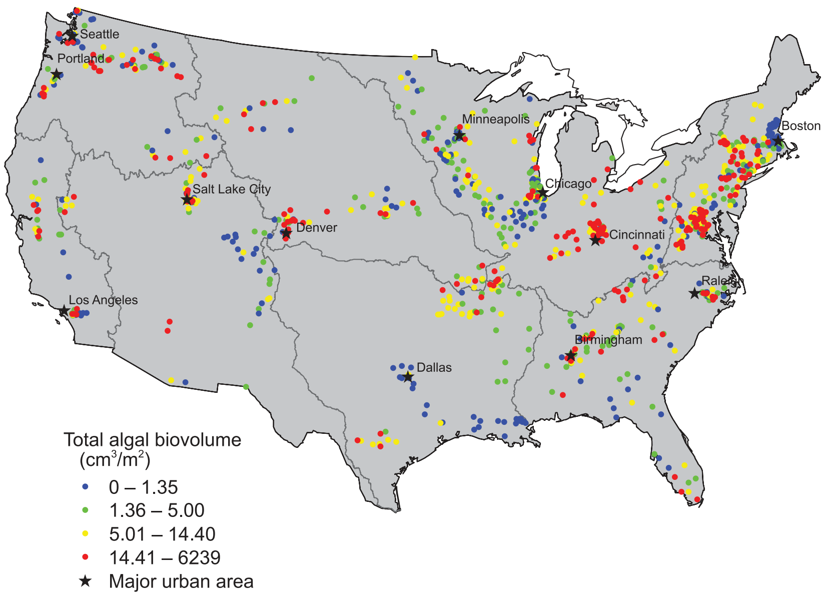

Fig. 5 Distribution of algal biovolume in the continental United States.

southern U.S.A. (regions 2 and 5) where algal biovolume was high, whereas the percentage of eutrophic diatoms was low (cf. Figs. 4 & 5). Similarly, turbid streams draining highly-disturbed, agricultural catchments in portions of the upper Midwest and western regions often contained low algal biovolume but high percentages of eutrophic diatoms. Thus, monitoring of algal-biomass indicators, alone, could result in incorrect conclusions concerning the trophic status of some streams and rivers.

Discussion

Algal-metric relations with water chemistry and land use

The algal metrics evaluated in this study were correlated with many of the water-quality conditions they are purported to indicate (e.g. nutrient concentrations, stream eutrophication). Many algal metrics were useful for contrasting stream trophic condition between undeveloped and developed drainage catchments in some, but not all, regions studied here. Relatively poor algal-metric correlations with nitrogen concentrations in the Midwest and Southeast regions could be related to extensive use of nitrogen fertilizers on agricultural fields or hydrologic factors (e.g. rainfall and runoff) that control nitrogen transport to streams. Because algae integrate water-quality conditions over time (e.g. Stevenson & Pan, 2000; Stevenson & Smol, 2003), periphyton-community structure may have been influenced by ambient nutrient concentrations during the period of algal colonization and growth more than by those during the time of algal sampling. For example, nitrate concentrations may have been relatively higher following rainfall and runoff events prior to the date of algal sampling in some streams or relatively lower in productive, eutrophic streams with substantial rates of algal uptake (e.g. Kalkhoff *et al*., 2000; Porter, 2001). Variance in nutrient concentrations associated with antecedent hydrologic or algal processes may partially account for low correlative relations between nutrient concentrations and algal-tolerance metrics in streams draining intensive agricultural catchments.

Differences in the efficacy of algal metrics to contrast developed from undeveloped sites among regions are not well understood. Although algal metrics and nutrient concentrations provided similar contrasts in most geographical regions, neither approach worked well in the Northern Plains region, despite good correspondence between algal metric and nutrient values. The operational definition of 'undeveloped' (<25% agriculture and <5% urban) may partially explain the poor performance of algal and nutrient indicators of eutrophication in this region. Whereas catchment percentages of agricultural and urban land cover are relatively modest, many of these land-use activities occur along perennial streams, particularly in the western, semi-arid parts of the region. Although the 'undeveloped' classification is not necessarily equivalent with 'near-pristine', it probably represents reference or best-attainable conditions within this region. Algal-metric and nutrient values were equally effective for separating undeveloped and developed catchments in the humid Northeast and Midwest regions; however, nutrient concentrations were superior to algal-tolerance metrics (ON_NH, PC_MT and TR_E) for indicating impaired water-quality in the southeast region and sensitive algal metrics (OT_AH and NF_YS) were the best indicators of good water-quality.

We suggest that algal metrics might be preferable, or at least complementary, to nutrient concentrations for assessing the trophic condition of streams draining partially developed catchments, where human development may be increasing, and for large rivers that integrate water-quality conditions in tributary streams that drain developed landscapes. Median nutrient concentrations often were lower in large rivers than in streams draining agricultural, urban or mixed land-use catchments, whereas median algal-metric values in large rivers generally were similar to those in streams draining other developed land-use categories. Although ambient nutrient concentrations in large rivers may have declined as a result of dilution from tributary or groundwater discharges, uptake by algal or macrophyte populations, denitrification or combinations of these factors, algal-metric indicators of eutrophication and tolerance to organic enrichment in large rivers remained at levels similar to tributary streams influenced by agricultural, urban or combinations of these land uses.

Algal biovolume relations with water chemistry and land use

Overall, algal biovolume was weakly correlated with nitrate and suspended-sediment concentrations. Biovolume relations with nitrogen were relatively stronger in the Northern Plains, Northwest and California regions where nitrogen-fixing algae were abundant, particularly at undeveloped sites. We hypothesize that nitrogen could be a limiting resource (or a prime determinant) for periphyton growth in relatively undeveloped, western regions of the U.S.A. This hypothesis is consistent with results presented by Grimm & Fisher (1986), Marks & Lowe (1993), Leland *et al*. (2001), Munn, Black & Gruber (2002) and Peterson & Porter (2002). Significant negative biovolume correlations with phosphorus and suspended sediment in the Southern Plains region may reflect light limitation due to water turbidity. Negative biovolume correlations with TP probably are related to strong association (e.g. adsorption) of phosphorus with suspended sediment. Biovolume frequently was high in urban areas throughout the U.S.A. (Fig. 5). Taylor *et al*. (2004) reported that benthic algal biomass (as chlorophyll *a*) increased with the percentage of urbanization and variables associated with urban density such as catchment imperviousness, drainage connection, TP concentrations and other factors.

Based on chlorophyll *a* relations with total algal biovolume reported by Porter (2000) for upper Midwest river systems, the biovolume boundary between the first and second quartiles of the data distribution is equivalent to a benthic chlorophyll *a* value of about 21 mg m^{-2}. Similarly, the boundary between the third and fourth quartiles of the distribution (14.47 cm^3 m^{-2}) is equivalent to a chlorophyll *a* value of about 55 mg m^{-2}. These chlorophyll estimates are relatively consistent with the oligotrophic–mesotrophic boundary (20 mg m^{-2}), but somewhat lower than the mesotrophic–eutrophic boundary (70 mg m^{-2}), for mean benthic chlorophyll in temperate streams reported by Dodds *et al.* (1998). Biggs (1996) reported median chlorophyll *a* values of 1.7 mg m^{-2} for New Zealand streams in undeveloped catchments, 21 mg m^{-2} for those in moderately developed catchments and 84 mg m^{-2} for enriched streams in catchments with highly developed agriculture or those underlain by nutrient-rich rocks.

Excessive phytoplankton biomass often is associated with nutrient enrichment of lakes and reservoirs (Jones & Bachman, 1976; Carlson, 1977), whereas the biomass of benthic algae in streams and rivers is related more to antecedent hydrologic stability, water clarity, light availability and the abundance of algal grazers than ambient nutrient concentrations (Rosemond, Mulholland & Elwood, 1993; Poff & Ward, 1995; Riseng, Wiley & Stevenson, 2004; Biggs, Nikora & Snelder, 2005). Benthic algal-nutrient processes most probably differ depending on whether algal communities are sparse and actively growing (nutrients stimulate algal growth; e.g. Stevenson *et al.*, 1991) or whether communities are dense and mature (algal uptake rates approach in-stream rates of nutrient transport; Newbold *et al.*, 1982; Mulholland, 1996). By the first process, biomass would be expected to increase with dissolved nutrient concentrations (positive correlation), whereas by the second process, nutrient concentrations would be expected to decrease with increases in algal biomass (negative correlation). Moreover, algal growth may become saturated at nutrient concentrations far less than those observed in many agricultural or urban streams (Bothwell, 1988, 1989; Biggs, 1990b; Horner *et al.*, 1990). Combinations of these processes, nationally and regionally, may partially account for the relatively poor correspondence between nutrient concentrations and benthic-algal biomass. Improved understanding of algal-nutrient relations in streams could be obtained by considering correlative or regression approaches that model algal biomass and community responses to nutrient concentrations, the frequency of flood disturbance (Biggs & Hickey, 1994; Biggs, 1995, 2000) and the abundance of algal grazers (Power, 1990; Steinman, 1996; Hillebrand, 2002).

Relevance to water-quality assessment

Assessment of algal species composition as an indication of water quality is a common element in many water-quality monitoring programmes such as NAWQA (Gilliom *et al.*, 1995) and the European WFD (European Commission, 2000). Accordingly, many attributes of algal species composition have been applied as autecological metrics or indicators of nutrient conditions, trophic status and biological integrity (Mills *et al.*, 1993; Pan *et al.*, 1996, 2004; Stevenson & Bahls, 1999; Hill *et al.*, 2000; Fore & Grafe, 2002; Griffith *et al.*, 2005; Wang, Stevenson & Metzmeier, 2005). Several published periphyton indices of biological integrity have included the same or similar algal metrics evaluated here and, whereas IBI relations with regional landscape characteristics (percentage of forest, mining or agriculture) or multivariate approaches appeared promising, specific relations with nutrient or suspended-sediment concentrations were relatively poor or not reported.

Diatoms have been the focus of most periphyton IBIs because they can be identified reliably to species and variety and relatively more autecological information is available for diatoms than other algal taxa (Stevenson & Pan, 2000). However, apart from taste-and-odour problems in water supplies associated with certain diatoms and recent emerging issues with *Didymosphenia geminata* (Lyngb.) M. Schmidt (Spaulding *et al.*, 2005), most problem or nuisance taxa traditionally have been associated with green algae, cyanobacteria or dinoflagellates. Considerable progress has been made with cyanobacterial taxonomy and autecology (Komarek, 2003; Komarek, Kling & Komarkova, 2003); however, more emphasis needs to be placed on the taxonomy and autecology of non-diatom algae, particularly the benthic Oscillatoriaceae and cyanobacteria capable of producing toxins (e.g.

Carmichael, 1994). Although most algal metrics evaluated in this report are based on diatoms, the most abundant nitrogen-fixing algae in the NF_YS metric were cyanobacteria (Rivulariaceae) rather than diatoms (Rhopalodiaceae).

A somewhat parallel effort in algal autecology based on paleolimnological research has employed weighted-average regression and calibration methods to quantify relations between species and various environmental variables including nutrients (Kelly & Whitton, 1995; Pan *et al.*, 1996; Leland & Porter, 2000; Winter & Duthie, 2000; Leland *et al.*, 2001; Munn *et al.*, 2002; Potapova *et al.*, 2004). Potapova & Charles (2007) developed lists of TN and TP indicator species from NAWQA data (similar to the data set used in this report) and classified species optima into low and high nutrient categories. The distribution of their high-nutrient metric among nutrient categories was similar to results from the 'eutraphentic' diatom metric (van Dam *et al.*, 1994); however, their low-nutrient metric clearly was superior to the European equivalent ('oligotraphentic' diatoms) for contrasting low, moderate and high nutrient stream categories (Potapova & Charles, 2007). There is nearly a 100-year history (e.g. Kolkwitz & Marsson, 1908) of understanding 'tolerant' algal-indicator species because they are found commonly at 'impacted' sites where many previous water-quality studies were focused. Although the tolerance metrics used in this study generally were successful for separating developed from undeveloped sites, improved understanding of the identity and autecology of 'sensitive' algal species, many of which appear to be undescribed (beyond genus) and probably endemic to North America (M. Potapova, pers. comm), should greatly enhance the use of periphyton communities as water-quality indicators.

Algal-tolerance metrics can indicate that eutrophication problems exist or that water-quality conditions are favourable for such problems to develop; however, the relation of those metrics with nuisance growths of filamentous green algae or blooms of eutrophic cyanobacteria (evidence of eutrophication to the public) will require some understanding of recent hydrologic disturbance (or days of accrual since the last scouring event (Biggs, 1995, 2000) plus potential influences from algal grazers that could maintain relatively low amounts of algal biomass while algal-tolerance metrics (and ambient nutrient concentrations) are indicating substantial nutrient and organic enrichment. The efficacy of evolving approaches for algal indices of stream condition may be dependent on innovative approaches for characterizing stream hydrology and grazer effects to place indicators of algal standing crop (e.g. chlorophyll *a*) in context with indicators of specific water chemistry conditions.

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