*Freshwater Biology* (2008) **53,** 1036–1054 doi:10.1111/j.1365-2427.2007.01951.x

APPLIED ISSUES

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

STEPHEN D. PORTER*, DAVID K. MUELLER*, NORMAN E. SPAHR*, MARK D. MUNN† AND NEIL M. DUBROVSKY‡

*Water Resources Discipline, U.S. Geological Survey, Denver, CO, U.S.A.

†Water Resources Discipline, U.S. Geological Survey, Tacoma, WA, U.S.A.

‡Water Resources Discipline, U.S. Geological Survey, Sacramento, CA, U.S.A.

## 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

Correspondence: Stephen D. Porter, Edwards Aquifer Research & Data Center, Texas State University, 248 Freeman Aquatic Building, San Marcos, TX 78666, U.S.A. E-mail: sp31@txstate.edu

 © 2007 Blackwell Publishing Ltd. No claim to original US government works

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.

© 2007 Blackwell Publishing Ltd. No claim to original US government works, 

## 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 ($\mu m^3$ $cm^{-2}$) 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

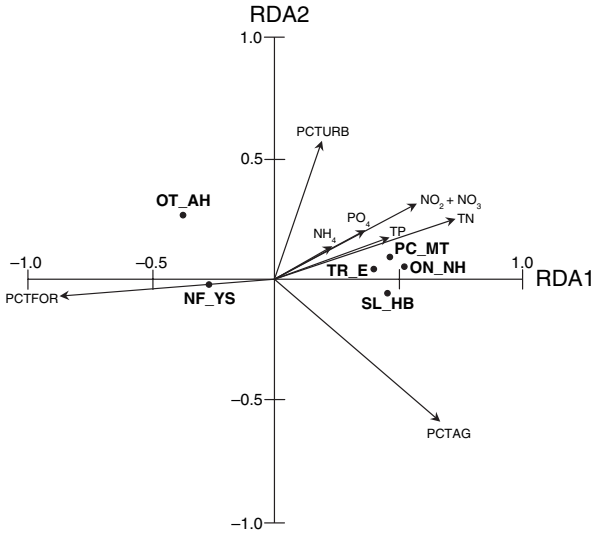


**Fig. 2** Redundancy analysis (RDA) biplot of algal metrics selected for further analysis (refer to Table 1 for algal-metric definitions).

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

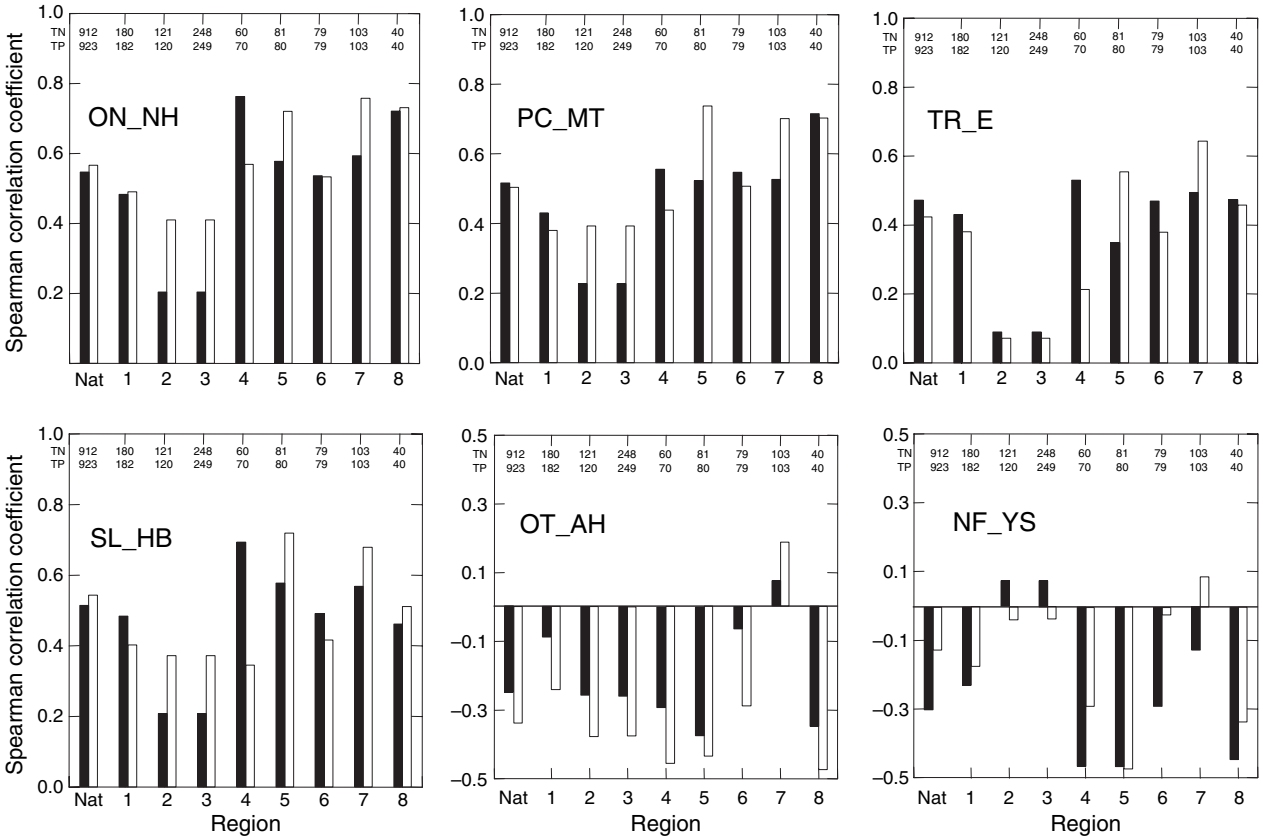


**Fig. 3** Algal-metric correlations with total nitrogen (dark bars) and total phosphorus (light bars) concentrations. Refer to Fig. 1 for location of regions and Table 1 for explanation of algal metrics. Numbers of pairwise comparisons shown at top of graphs.

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

| | | Algal metrics | | | | | | | | Nutrient concentrations | | | | | | Sediment | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Region | Land cover | *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.

© 2007 Blackwell Publishing Ltd. No claim to original US government works, 

(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

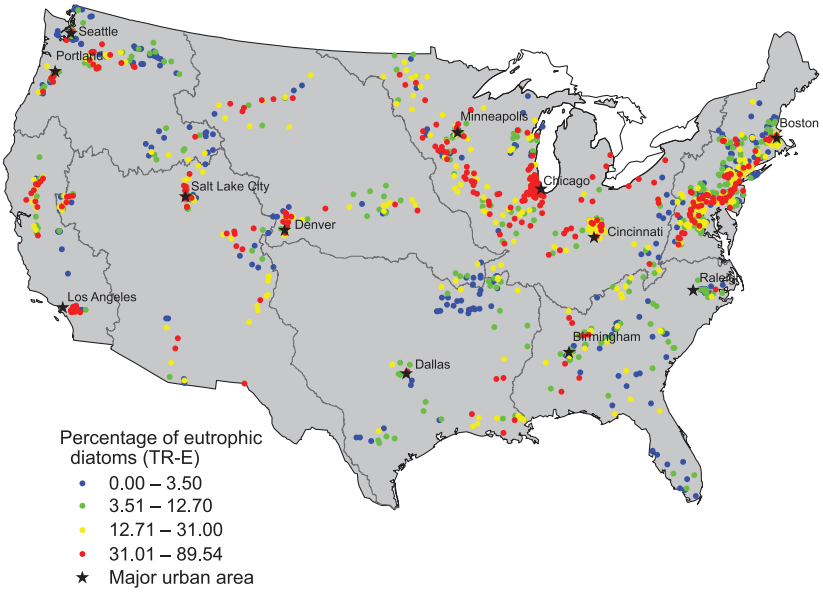


**Fig. 4** Distribution of eutrophic diatoms in the continental United States.

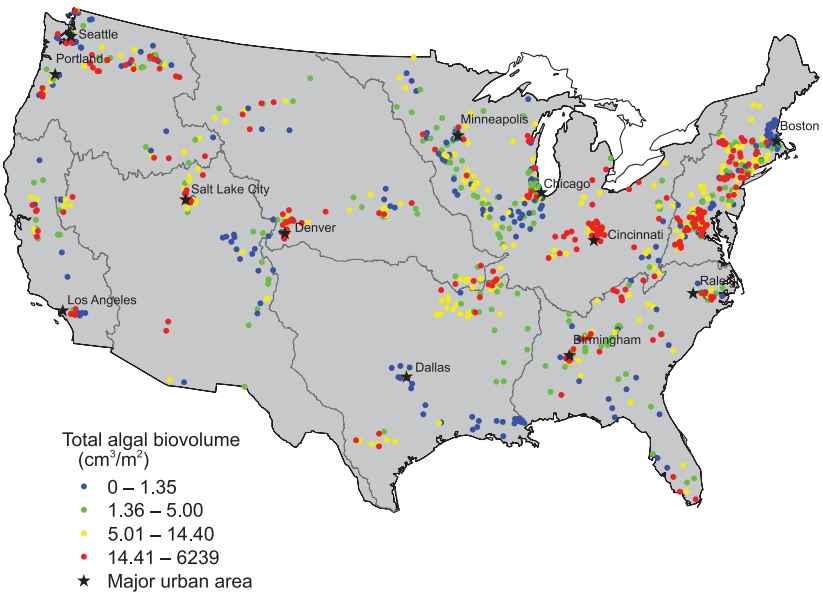


**Fig. 5** Distribution of algal biovolume in the continental United States.

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.

## Acknowledgments

This manuscript is a product of the USGS NAWQA National Synthesis effort. We thank Barbara Ruddy, USGS, Lakewood, Colorado for preparing the distribution maps used in this report and the many NAWQA ecologists and technicians who collected and processed the water quality and periphyton samples. We also thank Richard Johnson, Barbara Scudder, R. Jan Stevenson, Don Charles and two anonymous reviewers for their thoughtful review comments that significantly improved previous versions of this manuscript.

## References

Alexander R.B., Smith R.A. & Schwarz G.E. (2000) Effect of stream channel size on the delivery of nitrogen to the Gulf of Mexico. *Nature*, **403**, 758–761.

Allen J.D. (1995) *Stream Ecology. Structure and Function of Running Waters*. Chapman & Hall, London.

Bahls L.L. (1993) *Periphyton Bioassessment Methods for Montana Streams*. Water Quality Bureau, Department of Health and Environmental Services, Helena, MT.

Bailey R.G. (1995) *Description of the Ecoregions of the United States*. U.S. Department of Agriculture, Forest Service. Miscellaneous Publication 1391, Washington, DC, 108 pp.

Berkman J.A.H. & Porter S.D. (2004) An overview of algal monitoring and research in the U.S. Geological Survey's National Water Quality Assessment (NAWQA) Program. *Diatom*, **20**, 13–22.

Biggs B.J.F. (1990a) Periphyton communities and their environments in New Zealand Rivers. *New Zealand Journal of Marine and Freshwater Research*, **24**, 367–386.

Biggs B.J.F. (1990b) Use of relative specific growth rates of periphytic diatoms to assess enrichment of a stream. *New Zealand Journal of Marine and Freshwater Research*, **24**, 9–18.

Biggs B.J.F. (1995) The contribution of flood disturbance, catchment geology and land use to the habitat

template of periphyton in stream ecosystems. *Freshwater Biology*, **33**, 419–438.

Biggs B.J.F. (1996) Patterns in benthic algae in streams. In: *Algal Ecology – Freshwater Benthic Ecosystems* (Eds R.J. Stevenson, M.L. Bothwell & R.L. Lowe), pp. 31–56. Academic Press, San Diego, CA.

Biggs B.J.F. (2000) Eutrophication of streams and rivers: dissolved nutrient–chlorophyll relationships for benthic algae. *Journal of the North American Benthological Society*, **19**, 17–31.

Biggs B.J.F. & Hickey C.W. (1994) Periphyton responses to a hydraulic gradient in a regulated river in New Zealand. *Freshwater Biology*, **32**, 49–59.

Biggs B.J.F., Nikora V.I. & Snelder T.H. (2005) Linking scales of flow variability to lotic ecosystem structure and function. *River Research and Applications*, **21**, 283–298.

Bold H.C. & Wynne M.J. (1978) *Introduction to the Algae. Structure and Reproduction*. Prentice-Hall, Inc., Englewood Cliffs, NJ.

Bothwell M.L. (1988) Growth rate responses of lotic periphytic diatoms to experimental phosphorus enrichment: the influence of temperature and light. *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 261–270.

Bothwell M.L. (1989) Phosphorus-limited growth dynamics of lotic periphytic diatom communities: areal biomass and cellular growth rate responses. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1293–1301.

Bott T.L., Brock J.T., Dunn C.S., Naiman R.J., Ovink R.W. & Petersen R.C. (1985) Benthic community metabolism in four temperate stream systems: an inter-biome comparison and evaluation of the river continuum concept. *Hydrobiologia*, **123**, 3–45.

ter Braak C.J.F. & Smilauer P. (1998) *CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4)*. Microcomputer Power, Ithaca, NY.

Carlson R.E. (1977) A trophic state index for lakes. *Limnology and Oceanography*, **22**, 361–368.

Carmichael W.W. (1994) The toxins of cyanobacteria. *Scientific American*, **64**, 78–84.

Carpenter K.D. & Waite I.R. (2000) Relations of habitat-specific algal assemblages to land use and water chemistry in the Willamette Basin, Oregon. *Environmental Monitoring and Assessment*, **64**, 247–257.

Charles D.F., Knowles C. & Davis R.S. (Eds) (2002) *Protocols for the Analysis of Algal Samples Collected as Part of the U.S. Geological Survey National Water-Quality Assessment Program*. Patrick Center for Environmental Research Report No. 02-06. The Academy of Natural Sciences, Philadelphia, PA.

Cholnoky B.J. (1968) *Die Okologie der Diatomeen in Binnengewasser*. J. Cramer, Lehre.

Coles J.F., Cuffney T.F., McMahon G. & Beaulieu K.M. (2004) *The Effects of Urbanization on the Biological, Physical, and Chemical Characteristics of Coastal New England Streams*. Professional Paper 1696. U.S. Geological Survey, Reston, VA.

Conover W.J. & Iman W.J. (1981) Rank transformation as a bridge between parametric and nonparametric statistics. *The American Statistician*, **35**, 124–129.

Cuffney T.F., Meador M.R., Porter S.D. & Gurtz M.E. (1997) *Distribution of Fish, Benthic Invertebrate, and Algal Communities in Relation to Physical and Chemical Conditions, Yakima River Basin, Washington, 1990*. Water-Resources Investigations Report 96-4280, U.S. Geological Survey, Raleigh, NC.

van Dam H., Mertens A. & Sinkeldam J. (1994) A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. *Netherlands Journal of Aquatic Ecology*, **28**, 117–133.

Dodds W.K. & Welch E.B. (2000) Establishing nutrient criteria in streams. *Journal of the North American Benthological Society*, **19**, 186–196.

Dodds W.K., Jones J.R. & Welch E.B. (1998) Suggested classification of stream trophic state: distributions of temperate stream types by chlorophyll, total nitrogen, and phosphorus. *Water Resources*, **32**, 1455–1462.

European Commission (2000) *Directive of the European Parliament and of the Council 2000/60/EC* Establishing a Framework for Community Action in the Field of Water Policy. European Commission PE-CONS 3639/1/00 REV 1, Luxembourg.

Fishman M.J. (1993) *Methods of Analysis by the U.S. Geological Survey National Water Quality Laboratory – Determination of Inorganic and Organic Constituents in Water and Fluvial Sediments*. Open-File Report 93-125. U.S. Geological Survey, Denver, CO.

Fore L. & Grafe C. (2002) Using diatoms to assess the biological condition of large rivers in Idaho (USA). *Freshwater Biology*, **47**, 2015–2037.

Gilliom R.J., Alley W.M. & Gurtz M.E. (1995) *Design of the National Water-Quality Assessment Program: Occurrence and Distribution of Water-Quality Conditions*. Circular 1112. U.S. Geological Survey, Sacramento, CA.

Griffith M.B., Hill B.H., McCormick F.H., Kaufmann P.R., Herlihy A.T. & Selle A.R. (2005) Comparative applications of indices of biotic integrity based on periphyton, macroinvertebrates, and fish to southern Rocky Mountain streams. *Ecological Indicators*, **5**, 117–136.

Grimm N.B. & Fisher S.G. (1986) Nitrogen limitation in a Sonoran Desert stream. *Journal of the North American Benthological Society*, **5**, 2–15.

Gurtz M.E. (1994) Design of biological components of the National Water-Quality Assessment (NAWQA) Program. In: *Biological Monitoring of Aquatic Systems* (Eds S.L. Loeb & A. Spacie), pp. 323–354. Lewis Publishers, Ann Arbor, MI.

Guy H.P. (1969) *Laboratory Theory and Methods for Sediment Analysis*. Chapter C1, Book 5 in Techniques of Water-Resources Investigations. U.S. Geological Survey, Denver, CO.

Hill B.H., Herlihy A.T., Kaufmann P.R., Stevenson R.J., McCormick F.H. & Johnson C.B. (2000) Use of periphyton assemblage data as an index of biotic integrity. *Journal of the North American Benthological Society*, **19**, 50–67.

Hillebrand H. (2002) Top-down versus bottom-up control of autotrophic biomass – a meta-analysis on experiments with periphyton. *Journal of the North American Benthological Society*, **21**, 349–369.

Horner R.R., Welch E.B., Seeley M.R. & Jacoby J.M. (1990) Responses of periphyton to changes in current velocity, suspended sediment and phosphorus concentration. *Freshwater Biology*, **24**, 215–232.

Hustedt F. (1930) Bacillariophyta. In: *Die Susswasser-Flora Mitteleuropas* (Ed. A. Pascher). Gustav Fischer Verlag, Jena.

Hutchinson G.E. (1967) *A Treatise on Limnology, Volume II, Introduction to Lake Biology and the Limnoplankton*. John Wiley & Sons, Inc., New York, NY.

Jones J.R. & Bachman R.W. (1976) Prediction of phosphorus and chlorophyll levels in lakes. *Journal of the Water Pollution Control Federation*, **48**, 2176–2182.

Kalkhoff S.J., Barnes K.K., Becher K.D., Savoca M.E., Schnoebelen D.J., Sadorf E.M., Porter S.D. & Sullivan D.J. (2000) *Water Quality in the Eastern Iowa Basins, Iowa and Minnesota, 1996-98*. U.S. Geological Survey Circular 1210, Denver, CO.

Kelly M.G. & Whitton B.A. (1995) The Trophic Diatom Index: a new index for monitoring eutrophication in rivers. *Journal of Applied Phycology*, **7**, 433–444.

Kolkwitz R. & Marsson M. (1908) Okologie der pflanzlichen saprobien. *Berichte der Deutschen Botanischen Gesellschaft*, **26**, 505–519.

Komarek J. (2003) Coccoid and colonial cyanobacteria. In: *Freshwater Algae of North America. Ecology and Classification* (Eds J.D. Wehr & R.G. Sheath), pp. 59–116. Academic Press, San Diego, CA.

Komarek J., Kling H. & Komarkova J. (2003) Filamentous cyanobacteria. In: *Freshwater Algae of North America. Ecology and Classification* (Eds J.D. Wehr & R.G. Sheath), pp. 117–196. Academic Press, San Diego, CA.

Lamberti G.A. (1996) The niche of benthic food webs in freshwater ecosystems. In: *Algal Ecology, Freshwater Benthic Ecosystems* (Eds R.J. Stevenson, M.L. Bothwell & R.L. Lowe), pp. 553–564. Academic Press, Inc., San Diego, CA.

Lange-Bertalot H. (1979) Pollution tolerance of diatoms as a criterion for water quality estimation. *Nova Hedwigia*, **64**, 285–304.

Leland H.V. & Porter S.D. (2000) Distribution of benthic algae in the upper Illinois River basin in relation to geology and land use. *Freshwater Biology*, **44**, 270–301.

Leland H.V., Brown L.R. & Mueller D.K. (2001) Distribution of algae in the San Joaquin River, California, in relation to nutrient supply, salinity, and other environmental factors. *Freshwater Biology*, **46**, 1139–1167.

Lowe R.L. (1974) *Environmental Requirements and Pollution Tolerance of Freshwater Diatoms*. Publication EPA-670/4-74-005. Office of Research and Development, National Environmental Research Center, U.S. Environmental Protection Agency, Cincinnati, OH.

Marks J.C. & Lowe R.L. (1993) Interactive effects of nutrient availability and light levels on the periphyton composition of a large oligotrophic lake. *Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 1270–1278.

MathSoft (1999) *S-Plus 2000 Guide to Statistics*. Data Analysis Products Division, MathSoft, Inc., Seattle, WA.

McCormick P.V. & Cairns J. Jr (1994) Algae as indicators of environmental change. *Journal of Applied Phycology*, **6**, 509–526.

Mills M.R., Beck G., Brumley J., Call S.M., Grubbs J., Houp R., Metzmeier L. & Smathers K. (1993) *Methods for Assessing Biological Integrity of Surface Waters*. Division of Water, Kentucky Department for Environmental Protection, Frankfort, KY.

Moulton S.R., Kennen J.G., Goldstein R.M. & Hambrook J.A. (2002) *Revised Protocols for Sampling Algal, Invertebrate, and Fish Communities as Part of the National Water-Quality Assessment Program*. Open-File Report 02-150. U.S. Geological Survey, Reston, VA.

Mueller D.K. & Spahr N.E. (2006) *Nutrients in Streams and Rivers Across the Nation*. Scientific Investigations Report 2006-5107. U.S. Geological Survey, Denver, CO.

Mulholland P.J. (1996) Role in nutrient cycling in streams. In: *Algal Ecology. Freshwater Benthic Ecosystems* (Eds R.J. Stevenson, M.L. Bothwell & R.L. Lowe), pp. 609–639. Academic Press, Inc., San Diego, CA.

Munn M.D., Black R.W. & Gruber S.J. (2002) Response of benthic algae to environmental gradients in an

agriculturally dominated landscape. *Journal of the North American Benthological Society*, **21**, 221–237.

Nakagaki N. & Wolock D.M. (2005) *Estimation of Agricultural Pesticide use in Drainage Basins Using Land Cover map and County Pesticide Data*. Open-File Report 2005-1188, U.S. Geological Survey, Sacramento, CA.

Newbold J.D., O'Neill R.V., Elwood J.W. & Van Winkle W. (1982) Nutrient spiraling in streams: implications for nutrient limitation and invertebrate activity. *The American Naturalist*, **20**, 628–652.

Palmer C.M. (1969) A composite rating of algae tolerating organic pollution. *Journal of Phycology*, **5**, 78–82.

Pan Y., Stevenson R.J., Hill B.H., Herlihy A.T. & Collins G.B. (1996) Using diatoms as indicators of ecological conditions in lotic systems: a regional assessment. *Journal of the North American Benthological Society*, **15**, 481–495.

Pan Y., Herlihy A., Kaufmann P., Wigington J., van Sickle J. & Moser T. (2004) Linkages among land-use, water quality, physical habitat conditions and lotic diatom assemblages: a multi-spatial scale assessment. *Hydrobiologia*, **515**, 59–73.

Patrick R. & Reimer C.W. (1966) *The Diatoms of the United States*, **Vol. 1**. Academy of Natural Sciences of Philadelphia Monograph No. 1, Philadelphia, PA.

Patton C.J. & Truitt E.P. (1992) *Methods of Analysis by the U.S. Geological Survey National Water Quality Laboratory – Determination of Total Phosphorus by a Kjeldahl Digestion Method and an Automated Colorimetric Finish That Includes Dialysis*. Open-File Report 92-146, U.S. Geological Survey, Denver, CO.

Patton C.J. & Truitt E.P. (2000) *Methods of Analysis by the U.S. Geological Survey National Water Quality Laboratory – Determination of Ammonium Plus Organic Nitrogen by a Kjeldahl Digestion Method and an Automated Photometric Finish That Includes Digest Cleanup by gas Diffusion*. Open-File Report 00-170. U.S. Geological Survey, Denver, CO.

Peterson D.A. & Porter S.D. (2002) *Biological and Chemical Indicators of Eutrophication in the Yellowstone River and Major Tributaries During August 2000*. Proceedings of the 2002 National Monitoring Conference. National Water Quality Council, Madison, WI. Available at: http://wy.water.usgs.gov/YELL/nwqmc/nwqmc.pdf (last accessed on 30 August 2006).

Poff N.L. & Ward J.V. (1995) Herbivory under different flow regimes: a field experiment and test of a model with a benthic stream insect. *Oikos*, **71**, 179–188.

Porter S.D. (2000) Upper Midwest river systems – algal and nutrient conditions in streams and rivers in the upper Midwest region during seasonal low-flow conditions. Publication EPA-822-B-00-002. *Nutrient Criteria Technical Guidance Manual, Rivers and Streams*, pp. A-25–A-42. Office of Water, Office of Science and Technology, U.S. Environmental Protection Agency, Washington, D.C.

Porter S.D. (2001) *Influence of Natural Factors on the Quality of Midwestern Streams and Rivers*. U.S. Water-Resources Investigations Report 00-4288. U.S. Geological Survey, Denver, CO.

Porter S.D. (2007) *Algal Attributes. An Autecological Classification of Algal Taxa Collected by the USGS National Water-Quality Assessment (NAWQA) Program*. Data Series Report. U.S. Geological Survey, Denver, CO.

Porter S.D., Cuffney T.F., Gurtz M.E. & Meador M.R. (1993) *Methods for Collecting Algal Samples as Part of the National Water-Quality Assessment Program*. Open-File Report 93-409. U.S. Geological Survey, Raleigh, NC.

Potapova M. & Charles D.F. (2007) Diatom metrics for monitoring eutrophication in rivers of the United States. *Ecological Indicators*, **7**, 48–70.

Potapova M., Charles D.F., Ponader K.C. & Winter D.M. (2004) Quantifying species indicator values for trophic diatom indices: comparison of approaches. *Hydrobiologia*, **517**, 25–41.

Potapova M., Coles J.F., Giddings E.M.P. & Zappia H. (2005) A comparison of the influences of urbanization in contrasting environmental settings on stream benthic algal assemblages. In: *Effects of Urbanization on Stream Ecosystems* (Eds L.R. Brown, R.H. Gray, R.M. Hughes & M.R. Meador), pp. 333–359. American Fisheries Society, Bethesda, MD.

Power M.E. (1990) Effects of fish in river food webs. *Science*, **250**, 811–814.

Prescott G.W. (1962) *Algae of the Western Great Lakes Area*. W.C. Brown Publishers, Dubuque, IA.

Prescott G.W. (1968) *The Algae: A Review*. Houghton Mifflin Company, Boston, MA.

Riseng C.M., Wiley M.J. & Stevenson R.J. (2004) Hydrologic disturbance and nutrient effects on benthic community structure in Midwestern US streams: a covariance structure analysis. *Journal of the North American Benthological Society*, **23**, 309–326.

Rosemond A.D., Mulholland P.J. & Elwood J.W. (1993) Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology*, **74**, 1264–1280.

Scudder B.C. & Stewart J.S. (2001) *Benthic Algae of Benchmark Streams in Agricultural Areas of Eastern Wisconsin*. Water-Resources Investigations Report 96-4038-E. U.S. Geological Survey, Middleton, WI.

Seaber P.R., Kapinos F.P. & Knapp G.L. (1987) *Hydrologic Unit Maps*. Water-Supply Paper 2294. U.S. Geological Survey, Washington, DC.

Shelton L.R. (1994) *Field Guide for Collecting and Processing Stream-Water Samples for the National Water-Quality Assessment Program*. Open-File Report 94-455. U.S. Geological Survey, Sacramento, CA

Spaulding S.A., Hermann K., Steuven G. & Erickson J.W. (2005) *A Nuisance Diatom Species: Didymosphenia Germinata in Western Streams*. Available at: http://www.epa.gov/scienceforum/2005/pdfs/regionposter/spaulding_sarah.pdf (last accessed on 30 August 2006).

Steinman A.D. (1996) Effects of grazers on freshwater benthic algae. In: *Algal Ecology. Freshwater Benthic Ecosystems* (Eds R.J. Stevenson, M.L. Bothwell & R.L. Lowe), pp. 341–373. Academic Press, San Diego, CA.

Stevenson R.J. & Bahls L.L. (1999) Periphyton protocols. In: *Rapid Bioassessment Protocols for use in Streams and Wadeable Rivers: Periphyton, Benthic Macroinvertebrates, and Fish*, 2nd edn (Eds M.T. Barbour, J. Gerritsen, B.D. Snyder & J.B. Stribling), pp. 6-1–6-22. Publication EPA 841-B-99-002. Office of Water, U.S. Environmental Protection Agency, Washington, D.C.

Stevenson R.J. & Pan Y. (2000) Assessing environmental conditions in rivers and streams with diatoms. In: *The Diatoms. Applications for the Environmental and Earth Sciences* (Eds E.F. Stoermer & J.P. Smol), pp. 11–40. Cambridge University Press, Cambridge.

Stevenson R.J. & Smol J.P. (2003) Use of algae in environmental assessments. In: *Freshwater Algae of North America. Ecology and Classification* (Eds J.D. Wehr & R.G. Sheath), pp. 775–804. Academic Press, San Diego, CA.

Stevenson R.J., Peterson C.G., Kirschtel D.B, King C.C. & Tuchman N.C. (1991) Density-dependent growth, ecological strategies, and effects of nutrients and shading on benthic diatom succession in streams. *Journal of Phycology*, **27**, 59–69.

Taylor S.L., Roberts S.C., Walsh C.J. & Hatt B.E. (2004) Catchment urbanization and increased benthic algal biomass in streams: linking mechanisms to management. *Freshwater Biology*, **49**, 835–851.

Tuchman N.C. (1996) The role of heterotrophy in algae. In: *Algal Ecology. Freshwater Benthic Ecosystems* (Eds R.J. Stevenson, M.L. Bothwell & R.L. Lowe), pp. 299–319. Academic Press, Inc., San Diego, CA.

U.S. Environmental Protection Agency (1993) *Methods for the Determination of Inorganic Substances in Environmental Samples*. Publication EPA-600-R-93-100. Environmental Monitoring Systems Laboratory, U.S. Environmental Protection Agency, Cincinnati, OH.

U.S. Environmental Protection Agency (2000) *Nutrient Criteria Technical Guidance Manual. Rivers and Streams*. Publication EPA-822-B-00-002. Office of Water, U.S. Environmental Protection Agency, Washington, D.C.

U.S. Environmental Protection Agency (2002) *National Water-Quality Inventory – 2000 Report to Congress*. Publication EPA-841-R-02-001. Office of Water, U.S. Environmental Protection Agency, Washington, D.C. Available at: http://www.epa.gov/305b/2000report/ (last accessed on 30 August 2006).

VanLandingham S.L. (1982) *Guide to the Identification, Environmental Requirements and Pollution Tolerance of Freshwater Blue-Green Algae (Cyanophyta)*. Publication EPA-600/3-82-073. Office of Research and Development, Environmental Monitoring and Support Laboratory, U.S. Environmental Protection Agency, Cincinnati, OH.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130–137.

Wang Y., Stevenson R.J. & Metzmeier L. (2005) Development and evaluation of a diatom-based Index of Biotic Integrity for the Interior Plateau ecoregion, USA. *Journal of the North American Benthological Society*, **24**, 990–1008.

Wehr J.D. & Sheath R.G. (Eds) (2003) *Freshwater Algae of North America. Ecology and Classification*. Academic Press, San Diego, CA.

Winter J.G. & Duthie H.C. (2000) Epilithic diatoms as indicators of stream total N and total P concentration. *Journal of the North American Benthological Society*, **19**, 32–49.

Winter T.C. & Woo M.-K. (1990) Hydrology of lakes and wetlands. In: *Surface Water Hydrology* (Eds M.G. Wolman & H.C. Riggs), *The Geology of North America*, **Vol. 0–1**, pp. 159–187. Geological Society of America, Boulder, CO.

*(Manuscript accepted 10 December 2007)*