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Eutrophication and trophic state in rivers and streams

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Abstract

Many natural streams are net heterotrophic, so I propose that trophic state be divided into autotrophic and heterotrophic state. This division allows consideration of the in¯uence of external carbon sources as well as nutrients such as nitrogen and phosphorus. Empirical results suggest that phosphorus and nitrogen are the most important nutrients regulating autotrophic state in ¯owing waters and that benthic algal biomass is positively correlated to gross primary production in streams. Reference (minimally in¯uenced by human activities) nutrient concentrations and correlations of nutrients with algal biomass are used to characterize reference distributions of stream autotrophic state. Only when reference nutrient concentrations are in the upper one third of those expected in the United States, is maximum benthic chlorophyll projected to exceed 100 mg m^{22} (a concentration commonly used to indicate nuisance levels) . 30% of the time. Average reference nutrient concentrations lead to sestonic chlorophyll concentrations above those considered typical of eutrophic lakes (. 8 mg m^{23}) less than half the time. Preliminary analysis suggests that autotrophic state is variable in small pristine streams because it is in¯uenced by canopy cover (light), but heterotrophic state is less variable because it can be based on allochthonous or autochthonous production. Nitrogen and phosphorus enrichment can in¯uence both heterotrophic and autotrophic state, and these effects could cascade to animal communities. Stoichiometry should be considered because carbon, nitrogen, and phosphorus are all involved in trophic state. The proposed de®nition of trophic state offers a starting conceptual framework for such considerations.

The evolution of concepts regarding enrichment in streams

In its course from the source to the sea, the progressive eutrophication of a river water by drainage from cultivated and inhabited districts is an almost inevitable natural process.
ÐButcher 1947

Although current concerns about stream eutrophication mainly focus on nitrogen (N) and phosphorus (P) enrichment (e.g., Smith 2003), early water quality and nutrient enrichment studies in lotic systems focused on carbon (C) enrichment from untreated sewage. Excessive loading of biochemical oxygen demand (BOD) made rivers completely anoxic downstream of sewage treatment plants. Hynes (1960) considered the physical, biological, and chemical effects of sewage loading to create a general conceptual model on the basis of the research of Butcher (1946) and others. The conceptual model of Hynes in part considered the in¯uence of increased organic C on dissolved oxygen (O_2) and subsequently on hypoxia- and anoxia-sensitive animals. He noted that most animals immediately downstream from a sewage outfall disappear under anoxic conditions and that, as O_2 enters the stream via aeration, high densities of pollution-tolerant fauna could be found. Eventually, as the in¯uence of the sewage diminished downstream, Hynes predicted a return to the clean water animal communities found upstream of the sewage outfall.

Enrichment by N and P were also considered in the Hynes model. He noted a substantial increase in ammonium, phosphate, and nitrate immediately downstream from the sewage outfall that diminished farther downstream. In the anoxic zone, the prevalence of cyanobacteria (*Oscillatoria* and *Phormidium*) and *Euglena,* and further downstream substantial biomass of *Cladophora,* were predicted. A decade later, Hynes (1970) speci®cally noted that nutrient enrichment could occur in rivers and streams as a direct result of human alteration of land use (in addition to sewage input). He described the amounts of increase in fertilizer use and made preliminary calculations of how much fertilizer might reach rivers and streams. At that time, however, Hynes documented a paucity of studies on the effects of nutrient enrichment alone but predicted that planktonic algae in large rivers would be stimulated.

There has been conceptual progress related to de®ning trophic state and characterizing lotic eutrophication on several fronts in the last three decades. Omernik (1977) proposed that various regions are expected to have distinct baseline amounts of nutrients related to geology, topography, and land uses. He described areas of the United States that would be expected to have relatively greater concentrations of nutrients in streams, and he de®ned the concept of nutrient ecoregions. The idea that a reference baseline trophic level occurs naturally in a region forms the basis of many current efforts to regulate stream nutrients. Over the last three decades, numerous research programs were designed to link nutrient enrichment to increases in autotrophic biomass in rivers and streams by methods that included the ``clay pot'' nutrient±diffusing substrata experiments, experimental

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stream channel enrichment experiments, whole-stream enrichments, and a de®nition of nuisance amounts of algae (Welch et al. 1988).

At a more fundamental level, there have been few attempts to de®ne the trophic state of lotic ecosystems and provide a comprehensive de®nition of eutrophication applicable to rivers and streams. Thus, I initially attempt to provide such a de®nition, and under this framework, I describe how prior research can be viewed given my de®nition.

De®ning trophic state and eutrophication in streams

The de®nition of tropic state I develop here is designed to include both autotrophic and heterotrophic components; thus, there is a ``heterotrophic state'' and an ``autotrophic state'' of a stream or river. Heterotrophic state can be de®ned as the metabolic activity of the stream (typically measured as average O_2 demand [respiration, R] during dark periods and scaled to 24 h). Autotrophic state is the gross primary production (GPP) during lighted periods (typically measured as production and scaled to 24 h). The delineation of heterotrophic and autotrophic state in ¯owing waters was pioneered by Odum (1956). I propose that eutrophication in lotic habitats be de®ned as an increase in a nutritive factor or factors that leads to greater whole-system heterotrophic or autotrophic metabolism.

Heterotrophic state and autotrophic state are not mutually exclusive; a system with substantial autotrophic activity will likely have high heterotrophic activity and certainly have high respiration. This link between autotrophy and respiration can lead to a positive correlation between respiration and GPP (Fig. 1). But, a system with more heterotrophic activity does not necessarily have more autotrophic activity (e.g., the condition obtained with high BOD loading). Thus, GPP:R can indicate the balance between heterotrophic and autotrophic state. Considering both autotrophic and heterotrophic components accounts for enrichment by organic C in addition to N and P, and accounts for the observation that lotic food webs can be based on consumption of autotrophic or heterotrophic organisms.

My proposed de®nition of lotic trophic state is based on total heterotrophic and autotrophic production and in¯u-enced by emerging research on lakes. Although production of lakes has often been linked to planktonic biomass (usually expressed as chlorophyll concentrations), lakes can be net heterotrophic and highly in¯uenced by terrestrial C inputs (e.g., Cole et al. 1994). Thus, solely emphasizing autotrophic biomass might not accurately describe trophic structure in lentic ecosystems. Rivers and streams are likely to be more dominated by heterotrophic processes than lakes given their stronger linkage to terrestrial systems as a source of organic C and the greater likelihood that light is intercepted. In small streams, the riparian canopy often shades the stream bottom, turbidity greatly attenuates light in many large, well-mixed rivers, and in some streams (blackwater streams), dissolved organic C colors the water and retards primary production. In many rivers and streams, much allochthonous organic matter enters seasonally and through storm water runoff. The net production of most streams is negative (i.e., GPP:R ,

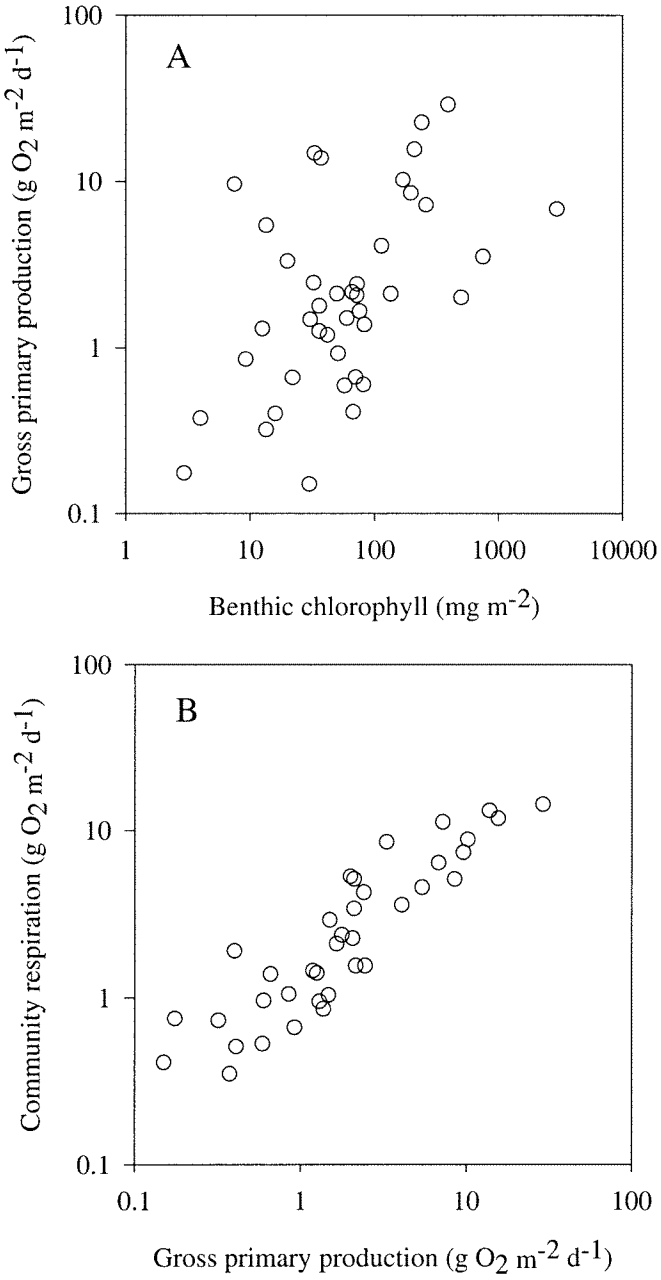

Fig. 1. (A) Relationships between benthic chlorophyll and gross primary production and (B) between gross primary production and community respiration. Data are taken from literature compiled by Bott et al. (1985); ranges were reported for values at one site, and the mean of the minimum and maximum is plotted. The relationship in (A) is signi®cant by linear regression (p , 0.05, r^2 5 0.24) and in (B) (p , 0.05, r^2 5 0.80).

1), even in open-canopy, shallow, clear-water streams (Mulholland et al. 2001). Thus, any de®nition of eutrophication in streams should consider heterotrophic activity.

Autotrophic activity can also be important in rivers and streams. Some streams with open canopies are net autotrophic (Mulholland et al. 2001). Phytoplankton production can supply a signi®cant portion of the productivity in medium to large rivers that are not highly turbid and do not com-

pletely mix because they have zones with limited water replacement (e.g., Thorp et al. 1998; Wehr and Descy 1998). Thus, allochthonous and autochthonous sources of C both should be considered, as well as inorganic and organic forms of nutrients such as N and P, when de®ning trophic status of lotic ecosystems.

Historically, trophic state in lakes was de®ned on the basis of clear delineation between anoxic hypolimnia and oxygenated waters (i.e., the difference between a mesotrophic and a eutrophic lake) and subsequent increases in the prevalence of cyanobacterial blooms, eutrophication- resistant animals, decreased water clarity, and taste and odor problems. Foremost, biogeochemical processes favor increased internal loading of P, leading to a positive feedback that stabilizes the eutrophic state with an anoxic hypolimnion (Dodds 2002). Such clear delineation of eutrophic conditions does not occur in shallow lakes, wetlands, and lotic systems for a variety of reasons.

Rivers and streams are relatively shallow and have considerably greater rates of atmospheric exchange compared with lentic systems, except under very low ¯ow conditions when they become similar to small, shallow lentic systems. Thus, it is dif®cult for biota to consume all the O_2 in the water column without substantial inputs of BOD and adequate nutrients to support very rapid rates of heterotrophic activity. Anoxia is rare in the water column of natural rivers and streams, even in forested streams under deciduous canopies immediately after leaf fall. In most lotic systems, internal loading of P and N tends to be dominated by remineralization, groundwater inputs, and erosion. Subsequently, alternative methods are required for describing trophic distributions in lotic ecosystems.

An approach that uses statistical distribution of benthic chlorophyll and water column nutrients was proposed to classify trophic state in streams given a lack of breakpoints (Dodds et al. 1998). Trophic categories by statistical distributions signify the probabilities of each trophic state. However, Dodds et al. (1998) used distributions from data sets that included affected sites; thus, the proposed categories do not represent natural trophic distributions. Many regions of developed countries completely lack such reference sites. However, a broad de®nition of stream trophic state requires consideration of the historical condition of streams before substantial modi®cation that might in¯uence heterotrophic or autotrophic state.

Which nutrients might be expected to control trophic state in lotic systems?

Before I propose trophic categories, it is important to justify which nutrients need to be considered to classify trophic state (i.e., if respiration and production are the response variables, what are the driver variables?). The most in¯uential limnologist in modern times, G. E. Hutchinson (1957), stated ``Phosphorus is in many ways the element most important to the ecologist, since it is more likely to be de®cient, and therefore to limit the biological productivity of any region of the earth's surface, than are the other major biological elements.'' This has led to the view that ``Excessive concentrations of P is [sic] the most common cause of eutrophication in freshwater lakes, reservoirs, streams, and in the headwaters of estuarine systems'' (Correll 1999). These assertions are not based on speci®c experimental and empirical observations of lotic ecosystems. How well do the data support the statement that P is the primary agent of autotrophic eutrophication in rivers and streams?

One of the common methods for assessing nutrient limitation of benthic algae in ¯owing waters is measuring chlorophyll accumulation on nutrient-diffusing substrata (e.g., Pringle et al. 1986; Winterbourn 1990). Francoeur (2001) performed a meta-analysis of 237 nutrient enrichment studies in temperate streams and found that 16.5% indicated an N response, 18.1% indicated a P response, 23.2% required N and P be added together for a response, 5% had N or P inhibition, and 43% had no response to N or P.

Tank and Dodds (2003) tested for autotrophic nutrient limitation across 10 North American streams with the use of silica (glass ®ber ®lters) or wood (thin layers of wood veneer) substrata in nutrient-diffusing agar devices. Algae responded differently to nutrients, depending on the substrata on which they were growing, and there was no primary positive response of algae to P enrichment alone at any site. No response to nutrient enrichment was a common result of these experiments, but N or N and P stimulated algal biomass at unshaded sites. The lack of nutrient response was closely linked to sites with limited light and a large amount of canopy cover. Tank and Dodds (2003) also presented a literature review that closely mirrored that of Francoeur (2001) in the percent responses to N and N 1 P treatments.

Few nutrient-releasing substrata experiments have tested for nutrient responses other than N and P. Chessman et al. (1992) tested for trace nutrient concentrations in eight streams during two seasons in Australia. They found no evidence for trace nutrients (Ca, Mg, K, S, Fe, Mn, Co Cu, Zn, thiamine, biotin, or B_{12}) stimulating algal growth in any stream during any season. The most common response was to N addition alone, with secondary P limitation occurring frequently.

Whole-stream fertilization experiments are rarely conducted under natural conditions, but Stockner and Shortreed (1978) used streamside enrichment troughs in British Columbia and demonstrated a strong P enrichment effect on algal biomass, with a secondary N enrichment effect. Enrichment of the Nechako River in British Columbia indicated N limitation (Perrin and Richardson 1997). Enrichment of a tundra river with P for four consecutive summers ®rst stimulated algal biomass and productivity and eventually stimulated ®sh production (Peterson et al. 1993).

An alternative, empirical approach for determining the response of algal biomass to nutrients is to establish the statistical relationship between in-stream nutrients and algal biomass. This approach was applied across Missouri streams of varied nutrient enrichment, and positive relationships between water column total N and benthic chlorophyll were found, with a similar relationship between total P and mean benthic chlorophyll (Lohman et al. 1992). Nutrient-enriched sites in this study had more rapid chlorophyll accrual after a scouring ¯ood than nutrient-poor sites. Lohman et al. (1992) speculated that N was more important in these

Table 1. Some studies of ¯owing waters reporting nitrogen and phosphorus enhancement of heterotrophic activities.

Location	Response variables	Response	Reference
Shaded New Zealand stream	^{14}C glucose incorporation, endocellulase activity	N and P stimulated endocellulase activity, but not glucose uptake	Tank and Winterbourn 1996
Small Appalachian streams	Microbial respiration, fungal biomass, extracellular enzyme activity	N and P colimitation	Tank and Webster 1998
Laboratory with stream assemblages	Leaf degradation by bacteria and fungi	N and P stimulated degradation	Gulis and Suberkropp 2002
10 North American streams	Fungal biomass (ergosterol)	2 streams, no effect; 2, P effect; 4, N stimulation; 2, P stimulation	Tank and Dodds 2003
Laboratory experiment	Leaf mass loss	Both N and P effects found	Bärlocher and Corkum 2003
Coastal wetland soil	Bacterial activity	P stimulated bacteria, whereas N stimulated macrophytes	Sundareshwar et al. 2003
Laboratory experiments on plankton from blackwater streams of North Carolina	Bacterial counts	Both N and P stimulated bacteria	Mallin et al. 2004
Carolina streams	Fungal biomass (ergosterol)	High N- and P-sites had greater ergosterol accumulation	Padgett et al. 2000

streams than P. Similar relationships were subsequently established for 13 rivers in southern Ontario (Châtelat et al. 1999).

A cross-system analysis of temperate streams established that total N and total P in the water column were signi®cantly related to benthic algal biomass (Dodds et al. 1997). This relationship is relevant to trophic state because production is positively correlated with algal biomass (Fig. 1). Subsequent analysis of an expanded data set suggested that mean and maximum algal biomass were signi®cantly correlated with total N and, to a lesser extent, with total P in the water column and that the best predictive model for algal biomass included both N and P. This analysis also suggested that in excess of a threshold value of total N and total P, there are no increases in mean benthic chlorophyll, thus indicating that nutrient limitation is overcome when water column nutrient concentrations are great enough (Dodds et al. 2002).

Positive correlations also exist between planktonic chlorophyll and water column nutrients in lotic systems. An analysis of suspended chlorophyll in temperate rivers and streams showed a positive relationship between water column total P and suspended chlorophyll (Van Nieuwenhuyse and Jones 1996), with an apparent decrease in planktonic chlorophyll yield per unit P when total P was in excess of approximately 300 mg m^{23}. These authors did not consider total N, so the relative importance of N and P could not be assessed from their data. However, Basu and Pick (1996) studied 31 Canadian Shield rivers and found positive correlations of sestonic chlorophyll with total N in addition to total P, but did not demonstrate any decrease in chlorophyll yield at high nutrient concentrations.

Nutrient enrichment experiments on heterotrophic activity are less numerous. However, the existing laboratory and ®eld experiments suggest that nutrients can limit heterotrophic activity (N, P, or both can be important, Table 1). A survey of stream metabolism across eight streams from various North American biomes indicated that soluble reactive P concentrations were positively correlated with both GPP and respiration (Mulholland et al. 2001).

The forms that N and P are in might not be extremely important determinants of heterotrophic or autotrophic state. Algae can use organic N as a primary N source (Antia et al. 1991). In addition, heterotrophic bacteria can be strong competitors for dissolved inorganic nutrients as well as nutrients in dissolved organic compounds (Dodds 2002).

Both N and P (in organic and inorganic forms) could be important determinants of autotrophic and heterotrophic activity in rivers and streams. This is borne out by manipulative experimental approaches and empirical analyses. There is little experimental support for minor nutrients stimulating heterotrophic or autotrophic microbial activity. As discussed in the introductory section, it is clear that C additions will have a strong in¯uence on system heterotrophic activity (O_2 consumption). It is probably unwise to assume a priori that P is the limiting nutrient of the autotrophic state in any particular stream.

Determining boundaries of trophic state

Data presented in the previous section suggest that water column N and P should be considered when characterizing the autotrophic state of rivers and streams and perhaps when determining heterotrophic state. The relative trophic state should be based on the frequency distribution of relatively pristine lotic waters because anthropogenic inputs change over time, as will trophic boundaries. Whereas Dodds et al. (1998) considered total N, total P, and benthic chlorophyll across a wide variety of streams, they did not account for streams that are naturally heterotrophic and did not attempt to use only reference streams to create an expected distribution in the absence of anthropogenic effects.

Reference nutrient data can be used to establish rough limits on the autotrophic state of streams with regard to nutrients; I present one possible approach. Reference nutrient

Table 2. Lower one-third and upper one-third of the distribution of stream total N and total P pooled across 14 ecoregions according to reference values determined for each individual ecoregion by Smith et al. (2003), 13 ecoregions for total P, and 12 ecoregions for total N from Dodds and Oakes (2004) and the relationship of the boundary numbers from Smith et al. (2003) data to cumulative frequency distribution of benthic chlorophyll (Chl) as a function of total N or total P (Fig. 1) expressed as the percentage of benthic chlorophyll mean or maximum values exceeding 100 mg m^{22} when nutrient values were less than the boundary value. For example, when seasonal mean of total N was , 714 mg m^{23}, then 10% of the streams had mean benthic chlorophyll values exceeding 100 mg m^{22} and 29% had maximum values exceeding that amount.

		Concentration (mg m^{23})		Cases exceeding 100 mg m^{22} (%)	
Nutrient	Autotrophic state boundary	Smith et al. 2003	Dodds and Oakes 2004	Mean Chl	Maximum Chl
Total N	Lower one-third	285	370	7	27
	Upper one-third	714	659	10	29
Total P	Lower one-third	29	23	5	17
	Upper one-third	71	48	13	25

concentrations from modeling, including a correction for atmospheric N deposition, have been proposed for 14 nutrient ecoregions across the United States (Smith et al. 2003). I ranked the median values (one for each ecoregion), and the distribution was divided into the lower, middle, and upper one third (oligotrophic, mesotrophic, and eutrophic, respectively, following limnological convention) of the reference nutrient values (Table 2). The distribution of reference nutrient values roughly agreed with those provided by Dodds and Oakes (2004), who corrected for anthropogenic in¯uences (as represented by human population density and land use characteristics) on stream nutrient concentrations with analysis of covariance across the same ecoregions (Table 2).

There is a positive correlation between autotrophic activity and benthic chlorophyll concentrations in rivers and streams (Fig. 1). Therefore, I initially base autotrophic boundaries on standing stocks of algal biomass, as is the convention in lakes. To accomplish this, the reference nutrient values from Smith et al. 2003 are applied to observed frequency distributions of seasonal mean and maximum benthic chlorophyll, plotted against water column nutrients (Fig. 2). These frequency distributions are used to calculate the probability that a stream will have a given amount of chlorophyll at a speci®c level of nutrients (Table 2). Relationships derived from those developed by Dodds et al. (2002, corrected for errors Dodds made when entering data from Lohman) also can be used to calculate expected mean and maximum values for benthic chlorophyll on the basis of the nutrient boundaries presented in Table 2 (Table 3).

Benthic chlorophyll values . 100 mg m^{22} previously have been considered a nuisance (Welch et al. 1988). This analysis suggests that a mean value of 100 mg m^{22} of chlorophyll is attained in , 7% of oligotrophic streams and in 10±13% of eutrophic systems. The regression analyses also suggest that oligotrophic systems should exhibit maximum benthic chlorophyll values . 100 mg m^{22} only 27% of the time. Other approaches are possible (e.g., Dodds et al. 1998), but the method presented in this paper considers the dynamic nature of chlorophyll in streams and is reference based.

A similar approach to determining reference trophic state can be taken with regard to planktonic chlorophyll in rivers and streams. A large data set (n 5 292) of lotic planktonic chlorophyll and water column total P was assembled for temperate rivers and streams, and associated regression equations can be used to link nutrients and phytoplankton biomass (Van Nieuwenhuyse and Jones 1996). A smaller data set from 31 rivers in southern Ontario and western Quebec related total N (mg m^{23}) and total P to planktonic chlorophyll (mg m^{23}; Basu and Pick 1996). This paper presented a regression equation for total P, but regression of their raw data yielded the following relationship.

$$\log_{10}(\text{planktonic chlorophyll}) \quad 5 \quad 2 1.247 \quad 1 \quad 0.676 \log_{10}(\text{total N}) \qquad r^2 \quad 5 \quad 0.65$$

The distribution of reference values from Smith et al. (2003) can then be used to calculate autotrophic categories from these equations (Table 4). These data agree roughly with both the Van Nieuwenhuyse and Jones (1996) and the Basu and Pick (1996) equations for total P, but the total N boundaries derived from the Basu and Pick chlorophyll±total N relationship were substantially lower than those derived for total P from the same data set. The data suggest that planktonic chlorophyll only exceeds values considered typical of eutrophic lakes (8 mg m^{23}; Dodds 2002) when nutrients are abundant relative to the reference condition. The data also are consistent with the idea that the amount of planktonic chlorophyll per unit total N or total P is less in lotic waters than in lentic waters (Sùballe and Kimmel 1987).

More limited data are available for whole-stream estimates of autotrophic and heterotrophic state, but some idea of the ranges expected for the trophic states can be gleaned from analysis of the results of a cross-system study (Mulholland et al. 2001). Although this study and an additional data point (P. Mulholland pers. comm.) only covers nine streams, it has three important characteristics. First, all the measurements were done the same way at each site with methods likely to give the best results (two-station diel O_2 method, corrected for groundwater in¯uences). Second, all the sites studied but one were relatively pristine small streams, so the data can be used to determine trophic boundaries mostly in the absence of human effects. Third, the streams were located in a variety of biomes, including one desert, one prairie, one tropical, one arid montane, one mesic montane, and four temperate deciduous biomes (Mulholland et al. 2001). Whole-stream autotrophic state varied over 150-fold in this data set (very high rates of GPP were associated with the lighted desert stream), with the central one third of the distribution falling between 0.4 and 1.8 g O_2 m^{22} d^{21} (Table 5). Heterotrophic state was considerably less variable, ranging about 10-fold with the central one third of the distribution falling between 6.7 and 8.3 g O_2 m^{22} d^{21} (Table 5).

Bott et al. (1985) reviewed studies of ; 70 streams with

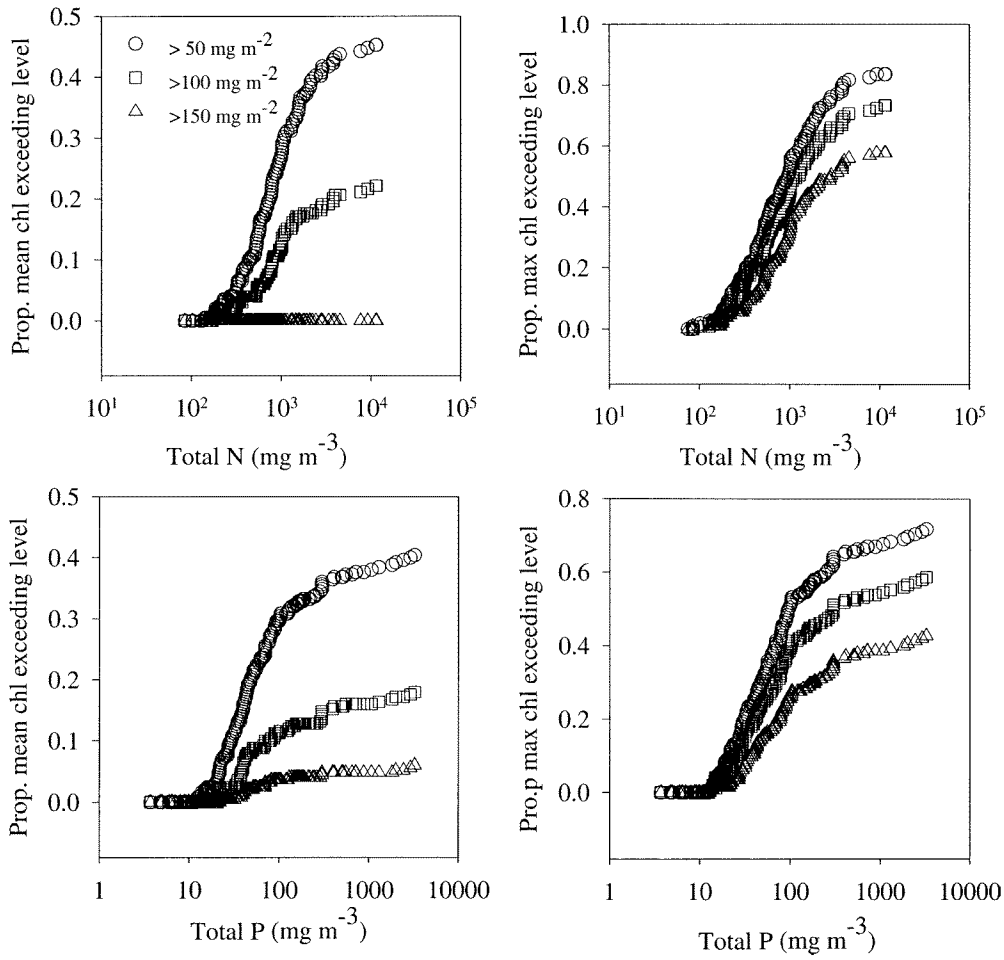

Fig. 2. Relationships between seasonal mean water column nutrients (total N and total P) and proportion of instances in which seasonal mean and maximum chlorophyll exceed 50, 100, or 150 mg m^{23}. Data are from literature sources compiled in Dodds et al. (2002), mostly for shallow rivers and streams. This compilation previously had incorrect values for data reported by Lohman et al. (1992). Those values now match the original source. *n* 5 250 for total P and *n* 5 199 for total N.

maximum rates of 48 and 50 g O_2 m^{22} d^{21} for GPP and respiration, respectively. These rates were from streams with human effects and were several-fold higher than the maximum from more pristine streams. This indicates that both autotrophic state and heterotrophic state can be in¯uenced by eutrophication. Maximum rates of GPP are probably limited by light under nutrient-replete conditions, whereas respiration is probably limited by O_2 aeration rate in streams with high loading of biochemical oxygen demand.

I speculate that light limits autotrophic state of streams (interception by the canopy), but not heterotrophic state, because although light is intercepted by riparian vegetation, it

Table 3. Corrected regression equations for data presented in Dodds et al. (2002) and expected autotrophic state mean and maximum benthic chlorophyll (Chl) values calculated from nutrient concentrations in Table 1 with these equations. Equations are of the form $\log_{10}$(mg chlorophyll m^{22}) 5 Intercept 1 B1 $\log_{10}$(mg m^{23} total N or total P) 1 B2 [$\log_{10}$(mg m^{23} total N or total P)]^2.

Relationship	Intercept	B_1	B_2	R^2	Expected chlorophyll (mg m^2) Lower Ä	Upper Ä
Mean Chl versus total N	22.638	2.460	20.320	0.401	30	60
Maximum Chl versus total N	0.438	0.613		0.295	88	154
Mean Chl versus total P	20.608	1.486	20.255	0.402	36	65
Maximum Chl versus total P	0.216	1.680	20.297	0.371	109	204

Table 4. Autotrophic state boundaries for suspended chlorophyll in temperate rivers and streams as calculated from the reference nutrient concentrations from Smith et al. (2003) and regression equations based on Van Nieuwenhuyse and Jones (1996) and Basu and Pick (1996).

Nutrient	Autotrophic state boundary	Nutrient conc. (mg m^{-3})	Planktonic chlorophyll (mg m^{-3}) Van Nieuwenhuyse and Jones (1996)	Basu and Pick (1996)
Total N	Lower one-third	285		2.4
	Upper one-third	714		4.5
Total P	Lower one-third	29	4.6	6.4
	Upper one-third	71	11.9	12.3

Table 5. Distribution of whole-stream metabolism rates from nine small, relatively pristine streams (data from Mullholland et al. [2001] plus one point from Ball Creek, North Carolina [Mulholland pers. comm.]). Respiration rates are corrected for groundwater input.

Distribution	Metabolism (g O_2 m^{-2} d^{-1}) Gross primary production	Respiration	Net primary production
Upper one-third	1.8	8.3	−4.2
Lower one-third	0.4	6.7	−6.7
Minimum	0.06	2.4	−29
Maximum	15	29	6.7

does not substantially influence rates of C input. I predict that the amount of C fixed by the riparian canopy that enters the streams to fuel heterotrophic activity is approximately equal to what would enter by autochthonous production in a lighted stream without canopy cover.

Small streams in forested biomes are shaded, have substantial amounts of organic C input from nearby riparian areas fueling heterotrophic activity, and have minimal autotrophic production (except in deciduous seasonal forests in which light can penetrate the canopy when leaves are not present). Prairie, tundra, or desert streams have limited riparian canopy and substantial autotrophic production fueling heterotrophic activity. An independent measure of total metabolic activity, N uptake rates, also varied little across the range of biomes studied by Mulholland et al. (2001), supporting the concept of relatively constant heterotrophic activity in small pristine streams (Webster et al. 2003). Heterotrophic state might be more variable in rivers; canopy has less of an influence, and turbidity could substantially interfere with riverine C production.

Although the approach taken here might provide useful in setting boundaries for autotrophic and heterotrophic state, more comprehensive measurements of stream metabolism are required. Until such comprehensive measurements are made, the values for boundaries presented here should be used with caution. In addition, whole-river metabolism rates are difficult to measure, and data are difficult to come by for such rivers. Very few large rivers remain in temperate regions that are relatively weakly influenced by humans, so it might not be possible to set definitive autotrophic and heterotrophic state boundaries for larger lotic systems in some regions.

Although determining trophic boundaries could be useful in describing fundamental ecosystem processes, changes in trophic state must be linked to other aspects of stream ecosystems for such boundaries to be relevant. Furthermore, it is important to explore how stream eutrophication is propagated through the food web to influence biotic integrity and community structure.

Effects of eutrophication

Producers—Stevenson and Pan (1999) reviewed the uses of diatoms for assessing environmental conditions in rivers and streams. They traced the use of species compositions of algae to infer amount of pollution to work by Kolkwitz and Marsson in the early 1900s, with substantial contributions by Ruth Patrick in the 1940s and 1950s (as cited by Stevenson and Pan 1999). Studies that use algal assemblages as indicators of the extent of pollution rely on the concept that predictable species shifts occur with set amounts of enrichment (e.g., Kelly 2002). Detailed work has been carried out relating nutrients to diatom and other algal assemblages in several places, mostly in temperate, developed countries.

The green alga *Cladophora* has often been associated with eutrophication events (Hynes 1960) and is ubiquitous in nutrient-rich flowing waters (Dodds and Gudder 1992). Large streamers of *Cladophora* develop under nutrient-rich conditions. These streamers potentially lead to low O_2 events at night, alter the community structure, snag fish lures, slow water flow in canals, and clog industrial and domestic water intakes (Dodds and Gudder 1992).

One of the problems with predicting eutrophication effects in streams is that variability caused by flooding can influence autotrophic state. At one extreme, algal biomass might not accrue with ample light and nutrients if floods always scour biomass. On the other end of the spectrum, attached algae might be able to attain impressive biomass in nutrient-poor water because periphyton can use the small amounts of nutrients that continuously flow by. Biggs (2000) developed a comprehensive model linking hydrologic regime and nutrients to accrual of algal biomass. This model was developed with a database from New Zealand rivers and streams across a wide range of land use practices and hydrologic patterns. Regressions considering only dissolved inorganic nutrients could predict algal biomass with r^2 values of approximately 30%. Consideration of the time of accrual (time since the last scouring flood) increased r^2 values to about 70%. The work of Biggs (2000) supports the proposition that eutrophication effects will be stronger under stable flow regimes.

The effects of eutrophication on macrophytes in flowing waters have been poorly studied, and the effects of nutrient reductions on macrophyte biomass are difficult to predict (Chambers et al. 1999). Biomass of macrophytes declined in the Bow River (Alberta) in response to nutrient control (particularly N) from municipal wastewater sources (Sosiak 2002). Sewage effluent led to substantially greater macrophyte biomass in the Saskatchewan River (Saskatchewan),

and this was correlated with somewhat decreased dissolved O_2 concentration (Chambers and Prepas 1994).

In some rivers and streams with reduced water replacement times, phytoplankton blooms can become problematic, with cyanobacterial blooms more likely in excess-nutrient conditions (Smith 2003). Shorter water turnover time (hydraulic residence time) leads to a decreased amount of suspended chlorophyll per unit concentration of P (Sùballe and Kimmel 1987). Problems occur with phytoplankton blooms in European and other rivers around the world (Wehr and Descy 1998). In the Murray Darling river system in South Australia, water withdrawals reduce ¯ow to a near standstill in the river, and excess amounts of nutrients, strati®cation, and warm temperature stimulate algal blooms (Maier et al. 2001). These blooms are commonly dominated by the hepatotoxic *Microcystis*. Other slow-¯owing rivers in the world suffer a similar fate, particularly those with limited quantities of light-intercepting ®ne sediments.

Microbial heterotrophs Ð Although enrichment experiments have documented that rates of microbial heterotrophic processing of organic materials can be stimulated by nutrients (as previously discussed), less is known about in¯uences on the heterotrophic microbial community. If the primary source of organic C to a stream or river is leaf material, N and P need to be obtained from the water column, and nutrient enrichment will increase C utilization rates. One study documented that nutrient enrichment causes shifts in fungal taxa associated with decomposing leaf litter (Gulis and Suberkropp 2002). Presumably, some bacteria that decompose organic matter are better competitors for organic nutrients than others, leading to shifts in community structure in response to nutrient enrichment. Future studies are likely to document this effect, given the recent expansion of molecular techniques. Clear increases in the rates of heterotrophic microbial biogeochemical cycling (denitri®cation) related to nutrient enrichment by agricultural practices have been demonstrated (Kemp and Dodds 2002).

Food web effects Ð Effects of C and, particularly, N and P loading on animals in streams are less clear. The effects of C on the animal community are obvious, with greater rates of organic C loading leading to dominance by pollution-tolerant invertebrates (such as *Tubifex, Limnodrilus, Chironomus*), decreases in diversity, and increases in raw abundance (Hynes 1960). With the advent of BOD treatment in sewage and industrial ef¯uents in developed nations, less attention has been paid to the effects of BOD loading.

Enrichment effects related to N and P are less well established. Macroinvertebrate assemblage structure has been correlated statistically with P concentration (Miltner and Rankin 1998). Nutrient enrichment can cause increases in invertebrate abundance and alters assemblage structure (Bourassa and Cattaneo 1998). The clearest study to date on the importance of sustained nutrient loading to the food web occurred on the Lawrence River downstream of Montreal, Quebec. This study used the distinctive isotopic signal of ^{15}N to establish that nutrients from the sewage outfall signi®cantly enriched macroinvertebrates and production of both macroinvertebrates and ®shes (deBruyn et al. 2003). The sewage was treated for BOD, but stimulated secondary production over ®vefold in spite of the small amount of N and P that entered the food web in the sewage plume 10 km down from the sewage outfall.

Control of cultural eutrophication Ð Given the de®nition of the trophic state proposed, and the potential effects of autotrophic and heterotrophic eutrophication, what considerations are important in controlling eutrophication? Mechanistic methods are only beginning to be established for linking in-stream nutrient concentrations to watershed activities. Empirical methods have prevailed (e.g., Dodds et al. 1997) until recently. Modeling efforts are beginning to re®ne nutrient concentration and loading estimates for rivers, but there still is some dif®culty in linking models created for small streams with larger river systems (e.g., Alexander et al. 2002). Ultimately, linking land use practices, including both point and nonpoint sources of nutrients, to instream nutrient concentrations will be necessary to control cultural eutrophication that in¯uences autotrophic state, and potentially in¯uences heterotrophic state.

Nutrient control is, on one level, simple. Agricultural practices, atmospheric loading, and human sewage outfall increase inorganic and organic nutrients in rivers and streams. Technology is available to decrease that input (but nonpoint sources of nutrients such as atmospheric deposition and runoff from cropland remain dif®cult to control). Best management practices of cropland include riparian buffer strips, cropland terracing, and the use of only the necessary amounts of fertilizer. Ef¯uent from human sewage and livestock-handling facilities can be treated with existing tertiary treatment methods (e.g., denitri®cation facilities, P precipitation) to reduce N and P loads to lotic waters. The effective reduction of BOD into the waters of most developed countries exempli®es the technical ability of water treatment engineers and managers to remove potentially harmful pollutants at acceptable costs. The challenge now is to determine what lengths are necessary to control point and nonpoint source pollution, and to what degree the bene®ts of nutrient control justify the costs. Determining the reference trophic state provides a starting point for cost±bene®t and feasibility analyses of eutrophication control schemes.

Nutrient cycles do not occur in isolation, and colimitation of algal and heterotrophic activity is commonly seen in bioassays (Tank and Dodds 2003). We are only beginning to understand the implications of the effects of humans on the stoichiometry of nutrient loading (Turner 2002). Stoichiometric changes could alter algal assemblages and relative rates of material ¯ux (e.g., Woodruff et al. 1999). Changes in stoichiometry could then cascade to higher trophic levels (Frost et al. 2002).

Given the broad de®nition of eutrophication presented herein, organic C enrichment should be considered, as well as anthropogenic processes causing shifts in the relative heterotrophic and autotrophic states. For example, increased BOD from sewage has de®nite in¯uences on stream heterotrophic state. In addition, shifts in riparian vegetation, such as loss of riparian forests, might increase the autotrophic state and decrease the heterotrophic state. In systems such as tallgrass prairies, historically dominated by little riparian

vegetation, increases in riparian vegetation could alter the fundamental ecosystem and community structure (Dodds et al. 2004). Finally, organic C enrichment might interact with N and P enrichment. The highest rates of C consumption and the greatest biomass of heterotrophic organisms are expected when loading of N, P, and C are simultaneously high.

Water retention times might alter nutrient stoichiometry and heterotrophic and autotrophic states by in¯uencing deposition and nutrient processing rates. Small and large impoundments that were not historically present are now a ubiquitous feature on many river networks. Such impoundments could also alter the balance between heterotrophic and autotrophic states because many recalcitrant C-rich particulate organic materials can settle in the reservoir, and plankton with relatively low values of C:N and C:P could dominate reservoir tail waters (Whiles and Dodds 2002).

Humans will affect ever more river miles with hydrologic modi®cation, alter the inputs of organic C and its form to lotic waters through alteration of riparian vegetation and input of BOD in sewage from humans and livestock. Increased fertilizer to grow the crops necessary to feed an expanding human population and increases in industrial livestock operations resulting in vast production of animal waste will cause further eutrophication of already affected rivers and streams. These effects will continue to spread into the few relatively pristine watersheds that remain on earth, altering water quality and in¯uencing the biotic integrity of these waters. Understanding the full implications of these effects will require further knowledge of the native trophic state of streams as a baseline. More complete comprehension of how nutrient interactions in¯uence trophic state, and determination of trophic states of medium to large rivers will improve the scienti®c basis for managing eutrophication of lotic waters.

References

ALEXANDER, R. B., P. J. JOHNES, E. W. BOYER, AND R. A. SMITH. 2002. A comparison of models for estimating the riverine export of nitrogen from large watersheds. Biogeochemistry **57/58:** 295±339.

ANTIA, N. J., P. J. HARRISON, AND L. OLIVEIRA. 1991. The role of dissolved organic nitrogen in phytoplankton nutrition, cell biology and ecology. Phycologia **30:** 1±89.

BÄRLOCHER, F., AND M. CORKUM. 2003. Nutrient enrichment overwhelms effects in leaf decomposition by stream fungi. Oikos **101:** 247±252.

BASU, B. K., AND F. R. PICK. 1996. Factors regulating phytoplankton and zooplankton biomass in temperate rivers. Limnol. Oceanogr. **41:** 1572±1577.

BIGGS, B. J. F. 2000. Eutrophication of streams and rivers: dissolved nutrient-chlorophyll relationships for benthic algae. J. N. Am. Benthol. Soc. **19:** 17±31.

BOTT, T. L., J. T. BROCK, C. S. DUNN, R. J. NAIMAN, R. W. OVINK, AND R. C. PETERSEN. 1985. Benthic community metabolism in four temperate stream systems: an inter-biome comparison and evaluation of the river continuum concept. Hydrobiolgia **123:** 3±45.

BOURASSA, N., AND A. CATTANEO. 1998. Control of periphyton biomass in Laurentian streams (Québec). J. N. Am. Benthol. Soc. **17:** 420±429.

BUTCHER, R. W. 1946. The biological detection of pollution. Institute of Sewage.

———. 1947. Studies in the ecology of rivers: VII. The algae of organically enriched waters. J. Ecol. **35:** 186±191.

CHAMBERS, P. A., R. E. DEWREEDE, E. A. IRLANDI, AND H. VANDEMEULEN. 1999. Management issues in aquatic macrophyte ecology: a Canadian perspective. Can. J. Bot. **77:** 471±487.

———, AND E. E. PREPAS. 1994. Nutrient dynamics in riverbeds: the impact of sewage ef¯uent and aquatic macrophytes. Water Res. **28:** 453±464.

CHESSMAN, B. C., P. E. HUTTON, AND J. M. BURCH. 1992. Limiting nutrients for periphyton growth in sub-alpine, forest, agricultural and urban streams. Freshw. Biol. **28:** 349±361.

CHÂTELAT, J., F. R. PICK, A. MORIN, AND P. B. HAMILTON. 1999. Periphyton biomass and community composition in rivers of different nutrient status. Can. J. Fish. Aquat. Sci. **56:** 560±569.

COLE, J. J., N. F. CARACO, G. W. KLING, AND T. K. KRATZ. 1994. Carbon dioxide supersaturation in the surface waters of lakes. Science **265:** 1568±1570.

CORRELL, D. L. 1999. Phosphorus: a rate limiting nutrient in surface waters. Poultry Sci. **78:** 674±682.

DEBRUYN, A. M. H., D. J. MARCOGLIESE, AND J. B. RASMUSSEN. 2003. The role of sewage in a large river food web. Can. J. Fish. Aquat. Sci. **60:** 1332±1344.

DODDS, W. K. 2002. Freshwater ecology: concepts and environmental applications. Academic Press.

———, K. GIDO, M. WHILES, K. FRITZ, AND W. MATHEWS. 2004. Life on the edge: ecology of Great Plains prairie streams. Bioscience **53:** 207±218.

———, AND D. A. GUDDER. 1992. The ecology of *Cladophora*. J. Phycol. **28:** 415±427.

———, J. R. JONES, AND E. B. WELCH. 1998. Suggested classi®cation of stream trophic state: distributions of temperate stream types by chlorophyll, total nitrogen, and phosphorus. Water Res. **32:** 1455±1462.

———, AND R. M. OAKES. 2004. A technique for establishing reference nutrient concentrations across watersheds impacted by humans. Limnol. Oceanogr. Methods **2:** 333±341.

———, V. H. SMITH, AND K. LOHMAN. 2002. Nitrogen and phosphorus relationships to benthic algal biomass in temperate streams. Can. J. Fish. Aquat. Sci. **59:** 865±874.

———, V. H. SMITH, AND B. ZANDER. 1997. Developing nutrient targets to control benthic chlorophyll levels in streams: a case study of the Clark Fork River. Water Res. **31:** 1738±1750.

FRANCOEUR, S. N. 2001. Meta-analysis of lotic nutrient amendment experiments: detecting and quantifying subtle responses. J. N. Am. Benthol. Soc. **20:** 358±368.

FROST, P. C., R. S. STELZER, G. A. LAMBERTI, AND J. J. ELSER. 2002. Ecological stoichiometry of trophic interactions in the benthos: understanding the role of C:N:P ratios in lentic and lotic habitats. J. N. Am. Benthol. Soc. **21:** 515±528.

GULIS, V., AND K. SUBERKROPP. 2002 Effect of inorganic nutrients on relative contributions of fungi and bacteria to carbon ¯ow from submerged decomposing leaf litter. Microb. Ecol. **45:** 11±19.

HUTCHINSON, G. E. 1957. A treatise on limnology. Geography, physics and chemistry. V. 1. Wiley.

HYNES, H. B. N. 1960. The biology of polluted waters. Liverpool Univ. Press.

———. 1970. The ecology of running waters. Univ. of Toronto Press.

KELLY, M. G. 2002. Role of benthic diatoms in the implementation of the urban wastewater treatment directive in the River Wear, north-east England. J. Appl. Phycol. **14:** 9±18.

KEMP, M. J., AND W. K. DODDS. 2002. Comparisons of nitri®cation

and denitri®cation in pristine and agriculturally in¯uenced streams. Ecol. Appl. **12:** 998±1009.

LOHMAN, K., J. R. JONES, AND B. D. PERKINS. 1992. Effects of nutrient enrichment and ¯ood frequency on periphyton biomass in northern Ozark streams. Can. J. Fish. Aquat. Sci. **49:** 1198±1205.

MAIER, H. R., M. D. BURCH, AND M. BORMANS. 2001. Flow management strategies to control blooms of the cyanobacterium, *Anabaena circinalis,* in the River Murray at Morgan, South Australia. Reg. Riv. Res. Manage. **17:** 637±650.

MALLIN, M. A., M. R. MCIVER, S. H. ENSIGN, AND L. B. CAHOON. 2004. Photosynthetic and heterotrophic impacts of nutrient loading to blackwater streams. Ecol. Appl. **14:** 823±838.

MILTNER, R. J., AND E. T. RANKIN. 1998. Primary nutrients and the biotic integrity of rivers and streams. Freshw. Biol. **40:** 145±158.

MULHOLLAND, P. J., AND OTHERS. 2001. Inter-biome comparison of factors controlling stream metabolism. Freshw. Biol. **46:** 1503±1517.

ODUM, H. T. 1956. Primary production in ¯owing waters. Limnol. Oceanogr. **1:** 102±117.

OMERNIK, J. M. 1977. Nonpoint source-stream nutrient level relationships: a nationwide study. EPA-600/3-77-105. U.S. Environmental Protection Agency.

PADGETT, D. E., M. A. MALLIN, AND L. B. CAHOON. 2000. Evaluating the use of ergosterol as a bioindicator for assessing water quality. Environ. Monit. Assess. **65:** 547±558.

PERRIN, C. J. AND J. S. RICHARDSON. 1997. N and P limitation of benthos abundance in the Nechako River, British Columbia. Can. J. Fish. Aquat. Sci. **54:** 2574±2583.

PETERSON, B. J., AND OTHERS. 1993. Biological responses of a tundra river to fertilization. Ecology **74:** 653±672.

PRINGLE, C. M., P. PAAB, P. D. VAUX, AND C. R. GOLDMAN. 1986. In situ nutrient assays of periphyton growth in a lowland Costa Rican stream. Hydrobiologia **134:** 207±213.

SMITH, R. A., R. B. ALEXANDER, AND G. E. SCHWARZ. 2003. Natural background concentrations of nutrients in streams and rivers of the conterminous United States. Environ. Sci. Technol. **37:** 2039±3047.

SMITH, V. H. 2003. Eutrophication of freshwater and coastal marine ecosystems. A global problem. Environ. Sci. Pollut. Res. **10:** 126±139.

SÙBALLE, D. M., AND B. L. KIMMEL. 1987. A large-scale comparison of factors in¯uencing phytoplankton abundance in rivers, lakes, and impoundments. Ecology **68:** 1943±1954.

SOSIAK, A. 2002. Long-term response of periphyton and macrophytes to reduced municipal nutrient loading to the Bow River (Alberta, Canada). Can. J. Fish. Aquat. Sci. **59:** 987±1001.

STEVENSON, J., AND Y. PAN. 1999. Assessing environmental conditions in rivers and streams with diatoms, p. 11±40. *In* E. F. Stoermer and J. P. Smol [eds.], The diatoms: applications for the environmental and earth sciences. Cambridge Univ. Press.

STOCKNER, J. G., AND K. R. S. SHORTREED. 1978. Enhancement of autotrophic production by nutrient addition in a coastal rainforest stream on Vancouver Island. J. Fish. Res. Board Can. **35:** 28±34.

SUNDARESHWAR, P. V., J. T. MORRIS, E. K. KOEPFLER, AND B. FORWALT. 2003. Phosphorus limitation of coastal ecosystem processes. Science **299:** 563±565.

TANK, J. L. AND W. K. DODDS. 2003. Nutrient limitation of epilithic and epixylic bio®lms in 10 North American streams. Freshw. Biol. **48:** 1031±1049.

———, AND J. R. WEBSTER. 1998. Interaction of substrate and nutrient availability on wood bio®lm processes in streams. Ecology **79:** 2168±2179.

———, AND M. J. WINTERBOURN. 1996. Microbial activity and invertebrate colonisation of wood in a New Zealand forest stream. N. Z. J. Mar. Freshw. Res. **30:** 271±280.

THORP, J. H., M. D. DELONG, K. S. GREENWOOD, AND A. F. CASPER. 1998. Isotopic analysis of three food web theories in constricted and ¯oodplain regions of large river. Oecologia **117:** 551±563.

TURNER, R. E. 2002. Element ratios and aquatic food webs. Estuaries **25:** 694±703.

VAN NIEUWENHUYSE, E. E., AND J. R. JONES. 1996. Phosphorus-chlorophyll relationship in temperate streams and its variation with stream catchment area. Can. J. Fish. Aquat. Sci. **53:** 99±105.

WEBSTER, J. R., AND OTHERS. 2003. Factors affecting ammonium uptake in streamsÐan inter-biome perspective. Freshw. Biol. **48:** 1329±1352.

WEHR, J. D., AND J.-P. DESCY. 1998. Use of phytoplankton in large river management. J. Phycol. **34:** 741±749.

WELCH, E. B., J. M. JACOBY, R. R. HORNER, AND M. R. SEELEY. 1988. Nuisance biomass levels of periphytic algae in streams. Hydrobiologia **157:** 161±168.

WHILES, M. R., AND W. K. DODDS. 2002. Relationships between stream size, suspended particles, and ®lter-feeding macroinvertebrates in a Great Plains drainage network. J. Environ. Qual. **31:** 1589±1600.

WINTERBOURN, M. J. 1990. Interactions among nutrients, algae, and invertebrates in a New Zealand mountain stream. Freshw. Biol. **23:** 463±474.

WOODRUFF, S. L., W. A. HOUSE, M. E. CALLOW, AND B. S. C. LEADBEATER. 1999. The effects of a developing bio®lm on chemical changes across the sediment±water interface in a freshwater environment. Int. Rev. Hydrobiol. **84:** 509±532.

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