Nitrogen and phosphorus relationships to benthic algal biomass in temperate streams

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Abstract: Knowledge of factors limiting benthic algal (periphyton) biomass is central to understanding energy flow in stream ecosystems and stream eutrophication. We used several data sets to determine how water column nutrients and nonnutrient factors are linked to periphytic biomass and if the ecoregion concept is applicable to nutrient–periphyton relationships. Literature values for seasonal means of biomass of periphyton, nutrient concentrations, and other stream characteristics were collected for almost 300 sampling periods from temperate streams. Data for benthic chlorophyll and nutrient concentrations from a subset of 620 stations in the United States National Stream Water-Quality Monitoring Networks were also analyzed. The greatest portion of variance in models for the mean and maximum biomass of benthic stream algae (about 40%) was explained by concentrations of total N and P. Breakpoint regression and a two-dimensional Kolmogorov–Smirnov statistical technique established significant breakpoints of about 30 µg total P·L^{-1} and 40 µg total N·L^{-1}, above which mean chlorophyll values were substantially higher. Ecoregion effects on nutrient–chlorophyll relationships were weak. Ecoregion effects were cross-correlated with anthropogenic effects such as percent urban and cropland area in the watershed and population density. Thus, caution is necessary to separate anthropogenic effects from natural variation at the ecoregion level.

Résumé : La connaissance des facteurs qui limitent la biomasse des algues benthiques (périphyton) est essentielle à la compréhension de l'eutrophisation des cours d'eau et du passage de l'énergie dans les écosystèmes d'eau courante. L'utilisation de plusieurs séries de données nous a servi à déterminer comment les nutriments et d'autres facteurs non-nutritionnels de la colonne d'eau sont reliés à la biomasse des algues et de voir si le concept d'écorégion peut s'appliquer aux relations nutriments–périphyton. Des données de la littérature ont été colligées, représentant presque 300 périodes de récolte sur des cours d'eau tempérés et traitant de biomasse moyenne saisonnière de périphyton, de concentrations de nutriments et d'autres caractéristiques. Nous avons aussi pu analyser des mesures de concentrations de chlorophylle benthique et de nutriments provenant d'un sous-ensemble de 620 stations du United States National Stream Water-Quality Monitoring Networks. Dans les modèles décrivant les biomasses moyennes et maximales des algues benthiques en eau courante, la plus grande partie de la variance (environ 40 %) s'explique par les concentrations totales de N et de P. Des méthodes de régression avec points de rupture et des techniques statistiques bidimensionnelles de Kolmogorov–Smirnov ont permis d'identifier des points de rupture significatifs à environ 30 µg·L^{-1} P total et 40 µg·L^{-1} N total, au dessus desquels les concentrations sont considérablement plus élevées. Les effets de l'écorégion sur les relations nutriments–chlorophylle sont faibles. Les effets de l'écorégion sont en corrélation croisée avec les effets anthropiques, tels que le pourcentage de terres agricoles ou de surfaces urbanisées dans le bassin versant et la densité de la population. Il faut donc prendre soin de distinguer les effets anthropiques de la variation naturelle à l'échelle de l'écorégion.

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Introduction

Nitrogen and phosphorus are often the primary limiting nutrients for aquatic algal production because they are frequently in short supply relative to cellular growth requirements. Accrual of algal biomass, and thus overall ecosystem productivity, may be controlled by the type and intensity of nutrient limitation. Understanding links between nutrient concentration and algal biomass is also important in efforts to manage eutrophication in streams (Smith et al. 1999; Biggs 2000; Dodds and Welch 2000) and in efforts to delineate stream trophic state (Dodds et al. 1998).

Nutrient enrichment typically stimulates periphyton growth in flowing waters (e.g., Blum 1956). For example, nutrient enrichment bioassays in a variety of streams have demonstrated that benthic algal biomass can be stimulated by the addition of N, P, or both nutrients (Francouer 2001). Thus, we know that nutrients can stimulate growth when

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added in excess and that N or P can be in short supply. However, nutrient limitation assays do not provide the predictive relationships between nutrient concentrations and algal biomass that we need to manage eutrophication in streams over broad geographic regions or to understand ecosystem-level relationships between nutrient loading and biomass of algal primary producers.

Empirical regression models that link algal biomass and water column nutrients have been used with great success worldwide in the eutrophication management of freshwater lakes and reservoirs (Cooke et al. 1993; Smith 1998; Smith et al. 1999). Attempts to derive similar relationships for nutrients and periphyton biomass in streams are less advanced and have been primarily regional in nature (e.g., Lohman et al. 1992; Biggs 2000). Generally, relationships between nutrients and chlorophyll are weaker in streams than in lakes, and this may explain why such models are not as highly developed for streams. The development of equivalent eutrophication models for streams is a pressing need, however, because these quantitative relationships can provide an objective framework for stream water quality management and because they can also be extended to predict key ecosystem properties that are important to the structure and function of lotic food webs.

Several important questions remain about the relationship between nutrient availability and periphyton biomass in streams. These questions include which nutrient(s) are limiting and how much of the observed variation in algal biomass can be explained by nutrient availability. In addition, it is still unclear whether distinct ecoregions (Omernik 1977) alter these nutrient–periphyton relationships. It is not clear if ecoregions based on terrestrial vegetation and land use have any influence on nutrient loading and nutrient–periphyton relationships in spite of the fact that regulatory agencies (e.g., U.S. Environmental Protection Agency) are attempting to set ecoregion-specific nutrient criteria.

Our approach to creating general models to predict benthic chlorophyll in streams was to construct a large database derived from a wide variety of temperate zone streams and then to use this database to quantify the relationships between key environmental variables and periphyton biomass. The aims of our study were to clarify links between water column nutrient concentrations and periphyton biomass and to identify other nonnutrient factors that may influence this relationship. We compared data taken from several different sources to expand the geographic coverage of our modeling efforts and to evaluate potential biases in our data collection.

Methods

We compiled data from the literature on periphyton biomass, nutrient concentrations, and abiotic variables from almost 300 distinct sites located in more than 200 rivers in North America and New Zealand (hereafter referred to as the "literature data set"). A detailed description of a major portion of this literature data set and its sources has been published elsewhere (Dodds et al. 1997). Additional literature data were added from a Spanish river (four seasons, Romaní and Sabater 1999), an Australian stream (one season, Mosisch et al. 1999), 12 streams from Quebec (Bourassa and Cattaneo 1998), a river in British Columbia

(two sites, two seasons, Dubé et al. 1997), nine Quebec streams (Cattaneo et al. 1997), eight Oklahoma streams (Toetz et al. 1999), two groups of sites on the St. Lawrence River (Vis et al. 1998), and 13 streams in Ontario and Quebec (Chétlat et al. 1999).

Annual mean values were used in our analyses when possible (except for maximum chlorophyll concentrations); otherwise, seasonal means (at least 2 months) were used. Arithmetic means were used when available, but occasionally, only geometric means were reported by the original investigators. The entire data set for mean chlorophyll included 362 values composed of 110 values from the central United States, 68 from New Zealand, 82 from the northwestern United States and southwestern Canada, 77 from the northeastern United States and southeastern Canada, seven from the southeastern United States, five from alpine or Alaskan sites, 11 from Europe, and one each from Australia and the southwestern United States. A wide range of river sizes was included in the data set, ranging from large rivers such as navigation pools in the upper Mississippi and the St. Lawrence River to small first- or second-order streams, although more small streams were included than large rivers.

Where values were reported, we entered total P (TP), dissolved inorganic N (DIN), soluble reactive P (SRP), total N (TN), temperature, latitude, substrate type (natural or artificial), stream gradient, mean discharge, maximum discharge, minimum discharge, stream width, and stream order in the literature data set.

Three other data sets were also constructed to use for these analyses. Additional data for stream periphyton and nutrients were obtained from the United States Geological Survey National Stream Water-Quality Monitoring Networks (Alexander et al. 1996) (hereafter referred to as the "USGS data set"). Two subsets of stream data were derived from the original USGS data set. The first subset initially contained all dates for all sampling stations that contained no missing values for chlorophyll (determined spectrophotometrically), TN, or TP. This trimmed database was further refined to include only stations having more than four values for chlorophyll, resulting in a working USGS subset containing 2870 chlorophyll measurements from 314 stations. Values were taken from these stations for percent cropland, farmland, forest, pasture, range, and urban area in the watershed. Values were also retained for ammonium, conductivity, dissolved oxygen, drainage area, instantaneous discharge, latitude, nitrate, human population in the watershed (as of 1990), SRP, temperature, and turbidity.

Mean chlorophyll values from each site in the USGS data set were coupled with ecoregions derived from maps produced by the National Health and Environmental Effects Research Laboratory of the United States Environmental Protection Agency for levels I, II, and III (Omernik 1987; Commission for Environmental Cooperation 1997). The ecoregion at the sampling point was used. Three subsets of data (one for each ecoregion level) were created for analysis by ecoregion; only ecoregions at each level were considered with 10 or more sampling stations within the ecoregion. Potential errors associated with watershed boundaries that cross ecoregions are explored in the discussion.

A second USGS data subset that contained values for both TN and TP was also created. This data set was used to eval-

uate distribution of TN and TP values. The means for each station with more than 10 values were obtained, resulting in mean TN and TP values from 658 stations (means calculated from a total of 84 934 sampling events). All data from all years for each single station were averaged to lower the amount of variance and allow comparison with the other literature values.

A lake data set containing values for growing season mean TN, TP, and chlorophyll *a* concentrations for 300 lakes as derived from table 1 in Smith (1982) was used to compare stream chlorophyll–nutrient relationships with those derived from lakes.

Both nonparametric and parametric methods were used to explore the relative importance of chemical and physical factors that regulate stream periphyton biomass. An initial screening for significant relationships among the candidate variables was made with Kendall's τ-b multiple comparison correlation procedure. This nonparametric method accounts for unequal and nonnormal distributions based on the number of concordant and discordant pairs of observations and uses a correction for tied pairs. Correlations were determined for all factors associated with chlorophyll in the literature and USGS data sets.

Predictive empirical models were then constructed using multiple regression analysis. When multiple regressions were used to develop statistical relationships between TN, TP, and chlorophyll, only those cases in the data sets that simultaneously contained values of both TN and TP were used in the analysis. For both nonparametric and parametric comparisons between artificial versus natural substrates using the literature data set, the substrate type was coded as a dummy variable in which the substrate was coded as 0 for artificial substrates and 1 for natural substrates.

Different subsets of the literature and USGS data sets were also used for the regression analyses. In most cases, not all values were present for all potential independent variables along with chlorophyll. For example, DIN and SRP values were not always available when chlorophyll *a*, TN, and TP were because not all sites had all types of data. Few chlorophyll values in the literature data set had all of the variables (i.e., TP, DIN, SRP, TN, temperature, latitude, substrate type (natural or artificial), stream gradient, mean discharge) present. The more variables that we included, the smaller the complete data set. Thus, we could not construct more complex predictive regression models (e.g., stepwise regression, path analysis) using multiple variables. Therefore, we only report regression models using TN, TP, DIN, or SRP to predict chlorophyll. Analysis of variance (ANOVA) was used to assess potential influences of ecoregions within the USGS data set. If the overall ANOVA gave a significant result, then pairwise comparisons were made with Fisher's least significant difference method.

Analysis for breakpoints in the chlorophyll–TN and chlorophyll–TP data were conducted on the literature data set using two techniques. Breakpoint regression is a nonlinear regression procedure that uses quasi-Newton search methods to find two linear relationships that describe the highest proportion of the variance and was analyzed with Statistica software (StatSoft, Tulsa, Okla.). Two-dimensional Kolmogorv–Smironov tests were used to test for breaks in variance in bivariate data (Garvey et al. 1998).

Table 1. Significant nonparametric correlations among mean chlorophyll (chl), maximum chlorophyll, TN, TP, DIN, SRP, stream gradient, latitude, water temperature, substrate type (natural or artificial), and maximum discharge for the literature data set (Kendall's τ-b procedure).

Factor 1	Factor 2	r	p	N
Mean chl	Max. chl	0.67	<0.0001	186
	TP	0.32	<0.0001	259
	Gradient	–0.32	0.001	49
	DIN	0.28	<0.0001	233
	SRP	0.23	<0.0001	200
	TN	0.20	<0.0001	209
	Temperature	0.18	0.01	91
	Latitude	–0.17	0.00005	267
	Substrate type	0.15	0.0001	300
	TN:TP	–0.11	0.05	148
Max. chl	Mean chl	0.67	<0.0001	186
	TN	0.32	<0.0001	109
	Gradient	–0.29	0.004	46
	DIN	0.21	0.00003	181
	TP	0.20	0.003	145
	DIN:SRP	0.20	0.005	93
	Latitude	–0.20	0.002	149
	TN:TP	–0.18	0.008	104
	Substrate type	0.16	0.02	170
	Max. discharge	–0.16	0.03	77

Note: TN, total nitrogen; TP, total phosphorus; DIN, dissolved inorganic nitrogen; SRP, soluble reactive phosphorus; max. maximum.

Results

Correlation analyses

Analyses of the literature data set (Table 1) revealed that benthic chlorophyll was significantly correlated with water column nutrients. Both mean and maximum concentrations of benthic chlorophyll were positively correlated with TN and TP concentrations. Mean and maximum concentrations of benthic chlorophyll were more weakly correlated with total DIN concentrations relative to TN and TP concentrations, and SRP was significantly correlated only with maximum benthic chlorophyll.

Of the nonnutrient factors in the literature data set that could be related to benthic chlorophyll, stream gradient appeared to be most important, with lower chlorophyll concentrations occurring in steeper gradient systems. High water temperatures and lower latitudes were also correlated with higher mean benthic chlorophyll levels, although more weakly than with nutrient concentrations. Both mean and maximum chlorophyll were positively correlated with the dummy variable for substrate in the literature data, indicating that benthic chlorophyll values were typically higher on natural than on artificial substrates.

Correlation analyses of the USGS data set (Table 2) confirmed the results obtained from the literature data. TN and TP were positively correlated, temperature was positively correlated, and latitude was negatively correlated with benthic chlorophyll concentrations. Three indicators of human impacts that were not available in the literature data set

Table 2. Significant correlations among mean chlorophyll, TN, TP, ammonium, nitrate, latitude, temperature, mean discharge, and human influence variables for the USGS data set.

Factor	r	p	N
Nitrate	0.29	<0.0001	256
TN	0.25	<0.0001	314
Latitude	–0.18	<0.0001	314
TP	0.17	<0.0001	314
Temperature	0.17	<0.0001	314
% urban	0.17	<0.0001	314
Ammonium	0.16	0.002	233
% cropland	0.12	0.001	314
Dissolved oxygen	–0.11	0.002	302
Drainage area	0.11	0.002	314
Conductivity	0.11	0.002	314
% pasture	0.10	0.01	314
Discharge	0.09	0.02	307

Note: Nonsignificant correlations were found for percent forest, percent rangeland, turbidity, suspended solids, and SRP (Kendall's τ-b procedure). TN, total nitrogen; TP, total phosphorus.

but were in the USGS data set (percentage of watershed in urban, cropland, and pasture) were also positively correlated with benthic chlorophyll.

Comparative analyses of nutrient limitation status in streams and lacustrine ecosystems

Nitrogen to P ratios are commonly used as empirical criteria for the assessment of nutrient limitation status in aquatic ecosystems, so we used three data sets to compare the relative frequencies of potential N and P limitation in stream versus lacustrine ecosystems (Fig. 1). The range of TN:TP ratios in the literature data set was somewhat greater than that in the much larger USGS data set, and the literature data set also contained lower TN:TP values than did either the lake or the USGS data set. The mean TN:TP values were 14.2, 17.6, and 22.4 by mass for the USGS, literature, and lake data sets, respectively. These three statistical distributions also differed significantly from each other ($p < 0.001$, Kolmogorov–Smirnov test).

Testing factors that may influence chlorophyll yield per unit nutrient

Mean chlorophyll levels were divided by water column TN to provide an index of chlorophyll yield per unit nutrient. The resulting ratio was subjected to nonparametric correlation analyses using both the literature and the USGS data sets (Table 3). There was a significant positive effect of TP in both data sets, indicating that the chlorophyll yield per unit N is greater when TP is greater. In the USGS data set, there was also a trend towards a higher yield of benthic chlorophyll per unit N at higher water temperatures, lower latitudes, larger drainage basin areas, and higher percentage of watershed in cropland.

The chlorophyll yield per unit water column N was also tested by ecoregion (Table 4). Ecoregion level III had the only significant effects of ecoregion on chlorophyll:TN. This was driven primarily by high chlorophyll yield in the

Fig. 1. TN:TP (total nitrogen : total phosphorus) mass ratios for (a) streams in the USGS stream data set, (b) streams in the literature stream data set, and (c) north-temperate lakes (data from Smith 1982). The distributions of TN:TP were significantly different from each other ($p < 0.001$) using the nonparametric Kolmogorov–Smirnov analysis to test for differences in mean values as well as skew (Press et al. 1986).
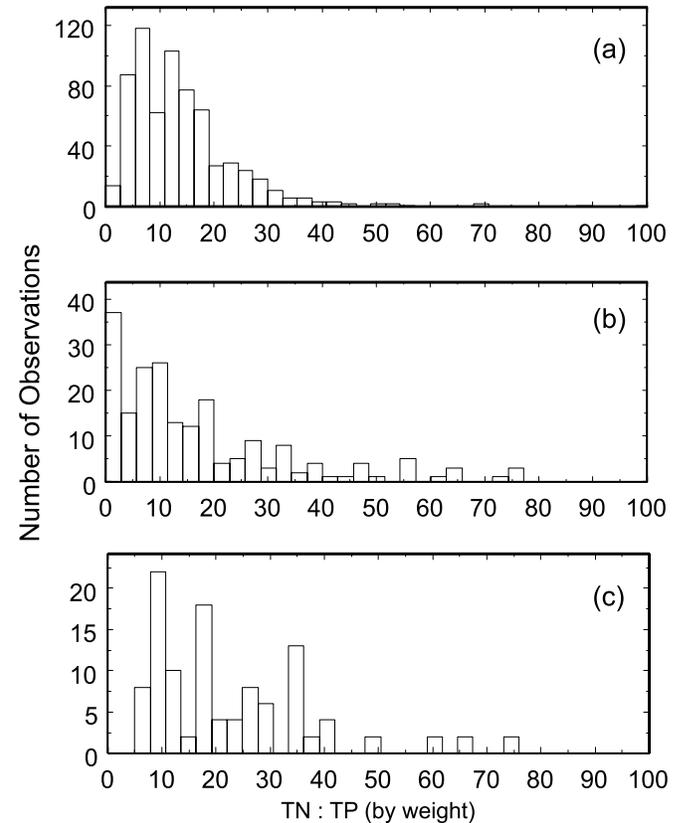

Table 3. Significant correlations of environmental factors with the chlorophyll:TN for the literature and USGS data sets (Kendall's τ-b procedure).

Factor	r	p	N
Literature data set			
TN:TP	–0.53	<0.000001	201
TP	0.37	<0.000001	201
Max. chlorophyll	0.34	0.002	109
Order	–0.20	0.01	136
USGS data set			
Population	0.29	<0.000001	314
Latitude	–0.25	0.000005	314
% urban	0.24	0.00002	314
Temperature	0.24	0.00002	314
TP	0.18	0.001	314
Drainage area	0.16	0.004	314
Dissolved oxygen	–0.15	0.009	302
% cropland	0.14	0.01	314
Conductivity	0.12	0.03	314

Note: TN, total nitrogen; TP, total phosphorus.

Table 4. Results of analysis of variance (ANOVA) of TN, TP, chlorophyll, and chlorophyll:TN from USGS data by ecoregion.

| Independent variable	Dependent variable	N	F	p
Ecoregion level I	TN	6	3.98	0.0017
	TP	6	1.65	0.1457
	Chlorophyll	6	5.51	0.0001
	Chlorophyll:TN	6	1.00	0.4173
Ecoregion level II	TN	16	3.82	<0.0001
	TP	16	0.81	0.6684
	Chlorophyll	16	2.78	0.0005
	Chlorophyll:TN	16	1.20	0.2756
Ecoregion level III	TN	7	6.97	0.0000
	TP	7	1.53	0.1773
	Chlorophyll	7	3.73	0.0025
	Chlorophyll:TN	7	3.01	0.0113

Note: TN, total nitrogen; TP, total phosphorus.

Southern Coastal Plain (most of Florida and some Gulf and Atlantic low coastal areas to the north and west of Florida). Very high N values were found in the Central U.S. Plains classified in ecoregion level II, an ecoregion that encompasses most of Illinois, Indiana, and western Ohio (data not shown). At ecoregion level I, there were low TN values in forested regions and the highest TN values in the Mediterranean California ecoregion.

Regression analyses

Multiple regression analysis was used to develop quantitative relationships between benthic chlorophyll and water column nutrients using data separately from both the literature and the USGS data sets (Table 5). For mean and maximum chlorophyll concentrations in the literature data set, mean stream water TN and TP concentrations described 40 and 31% of the total variance, respectively. However, an interaction between TN and TP in the literature data set is evident (Fig. 2), which indicates that low TN:TP values typically result in a lower yield of chlorophyll at any single value of TP relative to higher stream water TN:TP values. Comparable regression models for the USGS data set were similar in structure but were typically weaker; for example, TN and TP together only described 12% of the variance in mean chlorophyll. Although the relationships between chlorophyll and water column nutrients were more variable in the USGS data set than in the literature data set (Table 5; Fig. 2), a TN–TP interaction was still evident in the USGS data set (Fig. 2). In all regression analyses, TP explained more variance in benthic chlorophyll concentrations than did SRP. Similarly, DIN explained far less variance in chlorophyll than did TN.

Analysis of the chlorophyll–TN and chlorophyll–TP relationships by two statistical methods revealed significant breakpoints with agreement between the two methods except in the case of maximum chlorophyll as a function of TP (Table 6). In general, breakpoints were higher when considering maximum chlorophyll–nutrient relationships as compared with mean chlorophyll–nutrient relationships and higher for chlorophyll–TN than for chlorophyll–TP relationships. The breakpoints provide evidence for a saturation effect of nutrients on periphyton biomass accrual.

Fig. 2. Relationships between total phosphorus and mean benthic chlorophyll a as a function of the TN:TP mass ratio in stream water for the (a) literature data set and (b) USGS data set. Lowess curve fitting was used to fit points in this plot to illustrate how chlorophyll yield varies with TN:TP. Circles and dotted lines are for points with TN:TP less than 15 by mass, and triangles and solid lines represent points with TN:TP greater than 15.
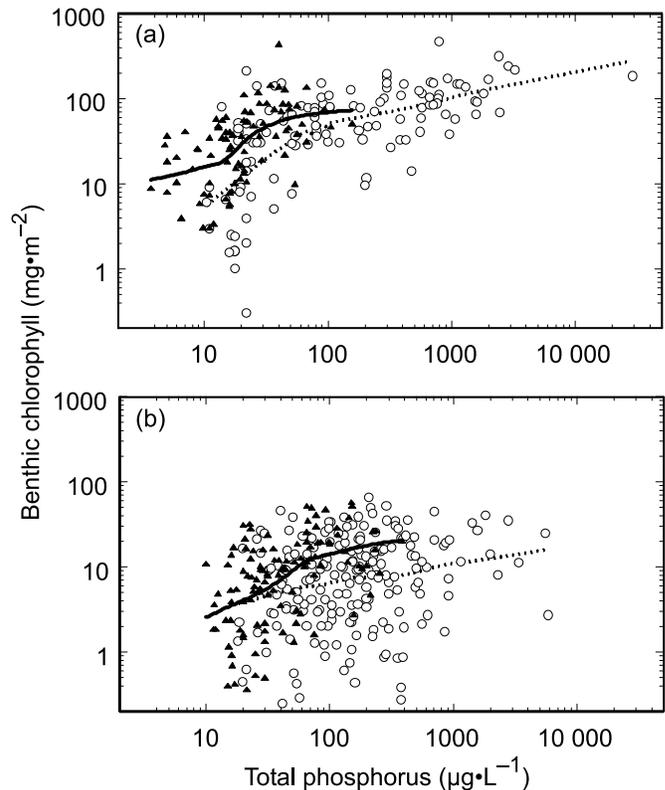
Discussion

Nitrogen and P limitation

Although the occurrence of N limitation in streams is inconsistent with the early view that P is generally the primary limiting factor in inland freshwaters, experimental nutrient enrichment bioassays have confirmed N limitation in a variety of different stream ecosystems (Francouer 2001; also see relevant citations in Smith et al. 1999). The data reveal a significant N–P interaction in streams and suggest that it is necessary to consider both N and P as potentially limiting nutrients for periphyton biomass accrual in lotic ecosystems.

The hyperbolic relationship between TN or TP and chlorophyll reported in an earlier, more limited version of the literature data set (Dodds et al. 1997) could be interpreted as an indication of lack of nutrient limitation at high water column nutrient concentrations. This saturation effect was not evident in the literature or the USGS data set using the statistical method employed by Dodds et al. (1997) to assess a saturation effect (a test for significance of the squared term of the second-order polynomial). However, the two statistical techniques used in this paper are more appropriate for determining if breakpoints occur in data, and they did

Table 5. Regression models for mean and maximum benthic chlorophyll in streams using the literature and the USGS data sets as a function of TN, TP, DIN, and SRP.

Dependent variable	Intercept	Independent variable 1	Independent variable 2	N	Adjusted r^2 or R^2
Literature data set					
log(mean chl)	1.101***	log(TN) 0.182**		209	0.05
log(mean chl)	0.847***	log(TP) 0.364***		259	0.20
log(mean chl)	0.155	log(TN) 0.236***	log(TP) 0.443***	200	0.40
log(mean chl)	0.676***	log(DIN) 0.367***		233	0.19
log(mean chl)	0.981***	log(SRP) 0.368***		200	0.13
log(mean chl)	0.298	log(DIN) 0.388***	log(SRP)	141	0.27
log(max. chl)	0.653*	log(TN) 0.546***		109	0.24
log(max. chl)	1.391***	log(TP) 0.339***		145	0.11
log(max. chl)	0.714*	log(TN) 0.372*	log(TP) 0.223*	103	0.31
log(max. chl)	1.385***	log(DIN) 0.263***		181	0.09
log(max. chl)	1.721***	log(SRP) 0.115		97	0.01
USGS data set					
log(mean chl)	–0.804***	log(TN) 0.544***		314	0.12
log(mean chl)	0.374***	log(TP) 0.241***		314	0.05
log(mean chl)	–0.923***	log(TN) 0.632***	log(TP) –0.074	313	0.12
log(mean chl)	–0.130	log(DIN) 0.388***		230	0.16
log(mean chl)	0.729***	log(SRP) 0.103		49	0.01
log(mean chl)	–0.409	log(DIN) 0.576***	log(SRP) –0.091	41	0.18

Note: Mean and maximum stream chlorophyll (mean chl and max. chl, respectively) in mg·m^{-2}; total phosphorus (TP), total nitrogen (TN), dissolved inorganic nitrogen (DIN), and soluble reactive phosphorus (SRP) in mg·m^{-3}. Significance levels for regression coefficients: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Table 6. Analysis of breakpoints from regression and two-dimensional Kolmogorov–Smirnov (2DKS) in TP, TN, and mean and maximum chlorophyll relationships using the literature data set.

Dependent variable	Independent variable	Breakpoint from regression (µg·L^{-1})	Breakpoint from 2DKS
log(mean chl)	log(TP)	31	29
log(mean chl)	log(TN)	36	41
log(max. chl)	log(TP)	100	27
log(max. chl)	log(TN)	147	145

Note: Mean and maximum chlorophyll, mean chl and max. chl, respectively; total phosphorus (TP), total nitrogen (TN). $p < 0.0002$ for all 2DKS determinations.

indicate saturation breakpoints in the literature data set. Hyperbolic relationships have been documented for TP and phytoplankton in lakes (McCauley et al. 1989; Prairie et al. 1989) and for TP and seston in rivers and streams (Van Nieuwenhuyse and Jones 1996). Such saturation may be an important effect; nutrient control strategies should take into account the possibility that it is less likely that there will be a decrease in benthic algal biomass unless water column nutrients are lowered below some threshold value.

We suggest that a pattern of colimitation will become evident as has been broadly observed in lakes (Elser et al. 1990) when more flowing waters are tested for nutrient deficiency and that a shifting balance between N and P limitation of algal growth will be observed along strong N:P supply gradients (Smith 1982). This pattern of nutrient colimitation in lakes has been explained by the presence of nonequilibrium conditions and mixed phytoplankton species assemblages (Dodds et al. 1989); these two conditions are major characteristics of stream periphyton communities.

We also found nutrient data for streams that may indicate a greater degree of N limitation than lakes where nutrient data were available. The water column TN:TP values were lower in both the stream literature and the USGS stream data sets than in Smith's (1982) lake data set. A similar pattern documenting lower particulate N:P in stream seston than in lacustrine phytoplankton has been reported for the Experimental Lakes Area of Canada (Hecky et al. 1993).

Variance in nutrients and benthic chlorophyll

Nonequilibrium conditions are clearly important in lotic systems, and we conclude that this environmental noise results in a markedly higher statistical variance in algal–nutrient relationships in temperate streams than is observed for lakes. For example, our best regressions using TN and TP to estimate benthic chlorophyll had R^2 values of 40%, whereas models to estimate planktonic chlorophyll in lakes using TN and TP published by Smith (1982) had R^2 values ranging from 69 to 76%, and regressions between TP and chlorophyll on regional lake

data sets commonly yield R^2 values greater than 90% (Cooke et al. 1993).

There also may be lower variance in relationships between water column nutrients and suspended (sestonic) chlorophyll in rivers than we observed for benthic chlorophyll in streams. Data analyses published for suspended chlorophyll in streams demonstrate that the relationship between TP and suspended algal biomass yields higher R^2 values, about 70% (Van Nieuwenhuyse and Jones 1996), than the similar comparison with our benthic chlorophyll data. This progressive decoupling of nutrients from chlorophyll from lake phytoplankton to river seston to benthic river algae could be in part because suspended P must be high when suspended chlorophyll is high because algal cells contain both chlorophyll and P. River seston is probably more likely to contain suspended nonliving particles that contain N and P from the benthos than many lakes because streams have greater turbulent energy.

Data for chlorophyll–nutrient relationships from the USGS data set were even more variable than those from the literature data set. This is consistent with our earlier attempts to synthesize literature data. We needed at least several points within each season to minimize variance in the data, and most data points in the literature data set are composed of several points per season. The USGS chlorophyll data are not taken frequently enough in most cases to provide seasonal averages (i.e., only four times over a year) and thus probably encompass more variation.

A number of factors may account for the large proportion of across-system variance that remains unexplained in our relationships. The hydrological parameters that we used were crude, but better data were not available for a wide variety of systems. Hydraulic disturbance and flow can be important determinants of periphyton biomass. Considerably more variance was accounted for in two detailed studies of benthic stream chlorophyll (Lohman et al. 1992; Biggs 1995) where hydrological and land use parameters were more closely monitored, locale was more restricted, and procedures remained consistent within studies. Lohman et al. (1992) were able to explain between 47 and 60% of the variance in periphyton with TN and TP models for Ozark streams (Missouri, U.S.A.), respectively, and were also able to relate the length of time since the last flood to periphyton biomass. Similarly, Biggs (1995) analyzed 16 New Zealand stream sites and was able to explain 89% of the variance with a model that considered flood frequency, land use, and geology. These studies show that regional relationships likely will provide a greater degree of predictive ability. We sacrifice predictive power for generality by including more studies done with a variety of procedures in a wider range of habitat types.

In the literature data set, there was more benthic chlorophyll on natural than on artificial substrates. However, multiple regression analysis demonstrated that including substrate type only improved R^2 by 1% (data not shown). Artificial versus natural substrates have been previously shown to alter estimates of benthic chlorophyll (Cattaneo and Amireault 1992). This could be an important observation because many scientists use artificial substrates to assess algal biomass in natural streams, although our regression analysis suggests that the effect is minor.

Light availability can also influence algal biomass in streams, and nutrient limitation can be influenced by light (Triska et al. 1983). Two possible variables related to light in this study were turbidity and suspended solids data from the USGS data set, and neither of these parameters was correlated with benthic chlorophyll or with chlorophyll:TN. However, it is likely that researchers are biased against measurement of algal biomass in highly shaded, deep, or highly turbid streams, so our data cannot be used to rule out differences in light regime increasing variance in nutrient – benthic chlorophyll relationships. The higher chlorophyll at low latitudes could be related to greater light.

Grazing was not considered, and interactions may exist among parameters that we could not assess in this study. For example, hydrodynamic scouring can interact with grazing by invertebrates to create an extremely variable habitat for periphyton, and these factors and others may influence biomass simultaneously. The interaction between limitation by grazers and nutrients was not assessed here, but such relationships are expected to increase observed variance in the chlorophyll–nutrient relationships and should receive attention in future studies.

Relevance of our data analysis to eutrophication problems in streams

Regardless of the existence of factors that decouple relationships between algal biomass and nutrients, eutrophication of lotic systems is an important issue. Benthic chlorophyll from 100 to 150 mg·m^{-2} has been considered excessive (Welch et al. 1988). In the literature data set, 22% of the mean benthic chlorophyll and 56% of the maximum chlorophyll values exceeded 100 mg·m^{-2} (Fig. 3). Even if it is only possible to explain a limited amount of variance in benthic algal biomass using water column nutrients, most other factors (e.g., light, flooding, grazing) cannot be controlled, leaving management of nutrient loading as the most likely method to control excessive algal biomass in streams.

Methods of applying equations such as those in this study to controlling eutrophication in streams have been published elsewhere (Dodds et al. 1997) using an earlier subset of the literature data set. Adding values from other systems altered the regression equations, substantially in some cases. For example, TN alone was less able to explain variance when the new data were added. This change in regression equations, combined with the variance in the relationships between nutrients and chlorophyll, indicates that care should be taken in using any specific set of published equations for management decisions.

The USGS data set was much more variable and contained no chlorophyll values that were in excess of 100 mg·m^{-2}. There may be a number of reasons why the USGS data set had lower chlorophyll than the literature data set, including different methods, sampling turbid rivers, sampling deeper waters, and more winter (low light) samples collected. Because our experience suggests that at least some of the waters sampled should have mean chlorophyll values in excess of 100 mg·m^{-2}, and the USGS data set was more variable, we are more confident in models constructed from the literature data set. However, the USGS data set correlations followed those obtained from the literature data set, so

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Fig. 3. Cumulative frequency distributions for (*a*) mean and (*b*) maximum benthic chlorophyll from the literature data set.
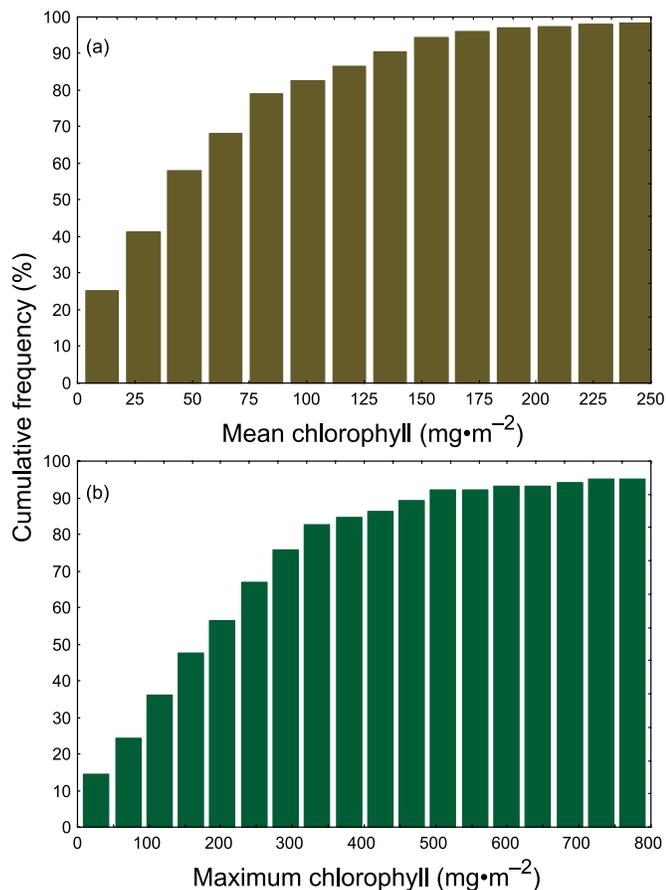
the overall trends resulting from the USGS data set (e.g., the ecoregion analysis) seem reliable.

The literature data set included breakpoints that may provide important guidance. They suggest that there is little probability of low benthic algal chlorophyll above the breakpoint value for TN or TP. If TN or TP is below the breakpoint, there is more likely to be low chlorophyll (but not in all cases). Probably the most prudent method for establishing nutrient criteria to control benthic chlorophyll is to use regression equations (best from the regions of interest, alternatively those published here for the literature data set), keep in mind a potential breakpoint effect, and also use a reference site approach wherever reasonably pristine sites are available to employ as a baseline.

Ecoregions and benthic chlorophyll–nutrient relationships

The concept of ecoregions has been considered for setting nutrient criteria. Ecoregions had little discernable influence on chlorophyll yield related to TP in European lakes (Seip et al. 2000). Pan et al. (1999) demonstrated a possible ecoregion effect using periphyton samples taken in the mid-Atlantic region of the United States. TP was correlated weakly, but significantly, with algal biomass expressed as chlorophyll but not TN across the entire region. However, subregions varied, with N, P, or neither correlating signifi-

cantly with algal biomass. This suggests a potential existence of chlorophyll–nutrient ecoregions.

We did see an ecoregion effect on chlorophyll yield (chlorophyll:TN) but only in the Southern Coastal Region. This ecoregion effect is consistent with correlation analysis that demonstrated that low-latitude (high-light) and high-temperature sampling stations had higher chlorophyll. The Southern Coastal Region was the furthest southern ecoregion that had sufficient data (10 or more sampling stations) to be analyzed by ANOVA. However, this difference in chlorophyll yield only occurred at one ecoregion level. This is in spite of the fact that TN and chlorophyll values varied significantly with ecoregion.

Our data do not rule out an ecoregion approach. For example, correlation analyses suggest that stream gradient, temperature, and latitude may have altered benthic chlorophyll. There are reasonable physical explanations for these correlations; growth rates are greater with higher temperature, light and temperature are higher at lower latitudes, and higher gradient systems may have more intense floods that remove algal biomass. However, high-gradient systems may be less likely to receive nutrient pollution, and high temperatures may be associated with lowland streams with greater anthropogenic input. In addition, anthropogenic effects that we were able to test (e.g., percent urban and cropland watershed area) were all correlated with increased chlorophyll. This suggests that any attempts to establish ecoregions should clearly identify and separate anthropogenic effects from basic ecological characteristics.

The ecoregion approach is difficult to apply to large watersheds. This is because watersheds can span several ecoregions (Omernik and Bailey 1997). However, chlorophyll yield could be more specific to local effects such as light, grazers, and flood history. Consideration of ecoregions may assist in water quality management (Griffith et al. 1999), but a more detailed approach is necessary than that taken here.

Better data are required to establish the validity of the ecoregion approach with regard to benthic chlorophyll–nutrient relationships. This would mean establishing pristine reference streams within each ecoregion and then using those systems as a baseline to compare within and between ecoregions. Currently, it would not be prudent to assume that ecoregion-specific stream eutrophication models will be useful in management of nutrient pollution, particularly because chlorophyll:TN did not vary over most of the United States according to our analysis.

We can draw several important conclusions from this data analysis: (*i*) nutrient availability (bottom-up control) can explain about 40% of the variation in autotrophic biomass in a wide variety of temperate streams, (*ii*) both N and P should be considered as potential limiting nutrients, (*iii*) the exact regression coefficients depend on the data set being considered; extending the scale of the observations may require more data (collected with carefully controlled methods) than are currently available and a geographic approach similar to that of Omernik (1977) may improve results, (*iv*) there are breakpoints such that when TN and TP in the water column exceed certain levels, low benthic chlorophyll values are unlikely, (*v*) there may be some basis for natural ecoregions with regard to chlorophyll–nutrient relationships, but these

may be difficult to separate from human-instigated land use changes, and (*vi*) nonequilibrium conditions and multiple limiting factors are more likely to predominate in streams than in lakes and lead to inherently high variability of primary producer biomass.

Acknowledgments

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