Phosphorus–chlorophyll relationship in temperate streams and its variation with stream catchment area[1]

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Abstract: Regression analysis of a data set compiled from the literature (n = 292) showed that summer mean chlorophyll concentration (Chl) among temperate streams bore a strong (R^2 = 0.67) curvilinear relationship with summer mean total phosphorus concentration (TP). The predicted slope of the TP–Chl relationship (Chl:TP) ranged between 0.22 at TP = 50 mg·m^{-3} and 0.08 at TP = 1030 mg·m^{-3}, the highest value of TP in our data set. A bivariate model indicated that stream catchment area had a significant effect on Chl at all levels of TP and predicted a 2.3-fold increase in Chl:TP as the stream catchment area increased from 100 to 100 000 km^2. We suggest that TP may provide a reliable basis for predicting Chl in small and large temperate streams worldwide.

Résumé : Le calcul de régression d'une série de données tirées de la littérature (n = 292) a montré que la concentration estivale moyenne de chlorophylle (Chl) dans les cours d'eau tempérés présentait une forte (R^2 = 0,67) relation curviligne avec la concentration estivale moyenne du phosphore total (PT). La pente prévue de la relation PT–Chl (Chl:PT) allait de 0,22 pour PT = 50 mg·m^{-3} à 0,08 pour PT = 1030 mg·m^{-3}, valeur la plus élevée de PT dans notre série de données. Un modèle à deux variables a indiqué que la superficie du bassin versant du cours d'eau avait un effet significatif sur Chl à toutes les concentrations de PT, et a prédit une augmentation d'un ordre de 2,3 du rapport Chl:PT si la superficie du bassin versant du cours augmentait de 100 à 100 000 km^2. Nous pensons que le phosphore total peut constituer une base fiable pour prédire la concentration de chlorophylle dans les cours d'eau petits et grands des régions tempérées du monde entier.

[Traduit par la Rédaction]

Introduction

A generally positive relationship between seasonal or annual mean chlorophyll (Chl) and total phosphorus concentration (TP) is well documented in temperate and subtropical lakes and reservoirs (Jones and Bachmann 1976; Canfield 1983; Hoyer and Jones 1983; Prepas and Trew 1983). Recent lake studies confirm that the TP–Chl relationship is curvilinear over broad ranges of TP values (Straskraba 1980, 1985; Prairie et al. 1989; Jones and Knowlton 1993) and that the slope or intercept of this relationship may vary systematically with some coregulatory factor, especially mean total nitrogen concentration (Smith 1982; Canfield 1983; McCauley et al. 1989) or the ratio of euphotic depth to mean depth (Verduin et al. 1978; Straskraba 1980). Such studies have increased understanding of the relationship between P supply and algal productivity in lentic ecosystems (Schindler 1978; Golterman and Kouwe 1980) and led to the development of predictive models for managing lake and reservoir water quality (Vollenweider and Kerekes 1980; Peters 1986; Walker 1986). Much less is known about the phosphorus–chlorophyll relationship in streams.

Previous studies indicate that Chl or other measures of mean sestonic algal abundance may indeed bear a positive relationship with TP or other measures of average P concentration in some streams (Nusch 1978; Jones et al. 1984; Shehata and Bader 1985; Soballe and Kimmel 1987; LaPerriere et al. 1989). In P-rich streams, however, average abundance of sestonic algae may not be correlated with average P or N concentration (Kilkus et al. 1975; Baker and Kromer-Baker 1979; Straskraba 1985; Bennet et al. 1986). Among these systems, mean sestonic algal abundance may vary instead with stream catchment area, mean depth, mean hydraulic flushing rate, or other physical factors (Kilkus et al. 1975; Baker and Kromer-Baker 1979; Bennet et al. 1986; Soballe and Kimmel 1987). Collectively, these studies suggest that the TP–Chl relationship in streams may, as in lakes, be curvilinear and that it likely varies systematically with some physical factor. To test this hypothesis, we analyzed the TP–Chl relationship for temperate streams on four continents (most in North America) and determined how this relationship varied with stream catchment area.

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Table 1. Summary statistics for summer (May–September) mean total phosphorus and chlorophyll concentrations and stream catchment area among temperate streams ($n = 292$).

Variable	Mean ± SE	Min.–Max.	Percentile 25%	Percentile 50%	Percentile 75%
Total P (mg P·m^{-3})	192±12	5–1030	48	100	263
Chlorophyll (mg·m^{-3})	27±1.8	0.4–170	4.9	17	35
Catchment area (km^2)	33 060 ± 3962	1 – 541 310	450	8130	42 000

Methods

Concurrent estimates of TP and Chl ($n = 292$) in 115 north temperate streams and 1 south temperate stream were compiled from 24 published or unpublished sources.[3] Most of the data set described North American streams ($n = 231$), especially tributaries of the Missouri or Lower Mississippi rivers ($n = 116$, Smart 1980; Smart et al. 1985; Soballe and Threlkeld *1985; Lohman 1988; Skadland 1992; Van Nieuwenhuyse* 1993), the Upper Mississippi River ($n = 65$, Soballe and Bachmann 1984; Metropolitan Council, Environmental Division 1976–1992; Greg Payne, Water Resources Division, U.S. Geological Survey, Mounds View, Minn., unpublished data), and Hudson Bay ($n = 49$, unpublished data from routine water quality monitoring program, available from Gary Dunn, Prairie Provinces Water Board, Room 201, 2050 Cornwall Street, Regina, SK S4P 2K5). Data for European streams ($n = 48$) included the Rhine River at Lobith, the Meuse River at Eijsden (unpublished data from routine water quality monitoring program, 1977–1993, available from RIZA (Dutch Governmental Institute on Inland Water Management and Waste Water Treatment), P.O. Box 10, 8200 AA Lelystad, The Netherlands), and the Ruhr River near Essen (Nusch 1978; Albrecht 1988). Also represented were the Nakdong River in Korea ($n = 2$, Choi and Park 1986), the Shatt Al-Arab River in Iraq ($n = 1$, Al-Saadi and Antoine 1981), and the Cox River in New South Wales, Australia ($n = 10$, Ferris and Tyler 1985). In all, 15 sites had ≥5 years of observations. Small streams sampled within a few kilometres of treated sewage outfalls (e.g., Wisniewski et al. 1985) were not included in our data set.

Each value of TP and Chl was calculated as the arithmetic mean of all samples collected at a single location during summer months (May–September), regardless of flow conditions. The sampling regime at all locations was periodic, with frequencies ranging from monthly ($n = 49$) to biweekly ($n = 191$) or weekly ($n = 52$). Total P concentration was measured using standard methods of chemical digestion and phosphate-P determination (e.g., Prepas and Rigler 1982). Chlorophyll concentrations were uncorrected for phaeophytin. Values of catchment area were taken directly from published sources ($n = 274$) or estimated by planimetry from scaled figures or maps.

All statistical analyses were conducted using $\log_{10}$-transformed values to help stabilize variance. Robust locally weighted sequential smoothing (LOWESS, Cleveland 1979) was used to provide an initial, model-free assessment of the form of the relationship between two variables (Prairie et al. 1989). Parameters used in all LOWESS analyses were $\delta = 0$, n – steps = 2, and $f = 0.5$. All interaction terms evaluated in multiple regression analyses were assumed to be multiplicative (McCauley et al. 1989). Antilogs of log Chl values calculated from regression models were corrected for transformation bias by multiplying the antilogs by e^c, where $c = 2.65 \cdot s^2$ and s = standard error of regression in $\log_{10}$ units (Ferguson 1986). Correlation coefficients were compared using Fisher's Z transformation and Student's t test (Zar 1974).

Results

Phosphorus concentration

The average total phosphorus concentration (TP) ranged between 5 and 1030 mg·m^{-3}, with a grand mean value of 192 mg·m^{-3} (Table 1). Most (65%) TP values, however, ranged between 50 and 500 mg·m^{-3}. Systems with TP < 50 mg·m^{-3} ($n = 79$) included some two dozen streams draining predominantly (>65% of land cover) forested catchments in south-central Missouri (e.g., Smart et al. 1985), the Cox River in Australia, and the Beaver, Battle, Carrot, Red Deer, and North and South Saskatchewan rivers in west-central Canada. Extremely fertile streams (TP > 500 mg·m^{-3}, $n = 38$) drained either densely populated catchments ($n = 28$), such as the Ruhr, Meuse, and Lower Rhine in northern Europe, or rural catchments where modern agriculture accounted for >80% of land cover ($n = 10$), such as the Minnesota, Grand, and Chariton rivers in the midwestern United States. Interannual variation in TP, as estimated by the coefficient of variation in mean TP among years at a site (CV_{TP}), ranged between 19 and 67% among sites for which ≥5 years of data were available. The median value of CV_{TP} was 35%.

Chlorophyll concentration

The average Chl ranged between 0.4 and 170 mg·m^{-3}, with a grand mean value of 27 mg·m^{-3} (Table 1). The lowest Chl value was in Clifty Creek, a 20-km^2 mostly (>90%) forested catchment in south-central Missouri (Lohman 1988). The highest value occurred in the Minnesota River at Jordan, a 42 000-km^2 agricultural catchment in southern Minnesota (Metropolitan Council, Environmental Services Division 1987; Payne 1994). Most (65%) Chl values, however, ranged between 5 and 65 mg·m^{-3}. At sites where ≥5 years of data were available, interannual variation in mean Chl (CV_{Chl}) ranged between 21 and 116%, with a median value of 45%.

Phosphorus–chlorophyll relationship

Analysis of the data using LOWESS suggested that the relationship between log TP and log Chl was slightly curvilinear, but not sigmoidal (Fig. 1). This observation was supported by

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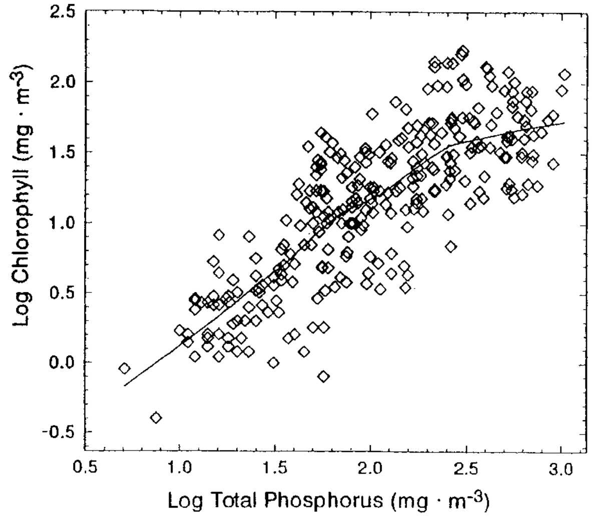
[3] Data may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Ottawa, ON K1A 0S2, Canada.

Fig. 1. Relationship between log total phosphorus and log chlorophyll concentrations among temperate streams. Each observation ($n = 292$) is the arithmetic mean of ≥5 samples collected periodically over a given summer (May–September). The trend line, estimated by robust locally weighted sequential smoothing (LOWESS), suggests a curvilinear relationship.



regression analysis. A quadratic model explained 3% more variance in log Chl than a simple linear model, whereas adding a third-order term had no effect on residual error ($t = -0.34$, $p = 0.73$). The TP–Chl relation in temperate streams could thus be approximated as

$$[1]\quad \text{Log Chl} = -1.65 + 1.99(\text{Log TP}) - 0.28(\text{Log TP})^2$$
$$(s = 0.32,\ R^2 = 0.67,\ F = 291,\ p < 0.001,\ n = 292)$$

This model (Fig. 2) indicated that the slope of the TP–Chl relationship (Chl:TP) decreased with increasing TP, attaining a maximum value of 0.22 at TP = 50 mg·m^{-3} and a minimum value of 0.08 at TP = 1030 mg·m^{-3}, the highest value of TP in our data set.

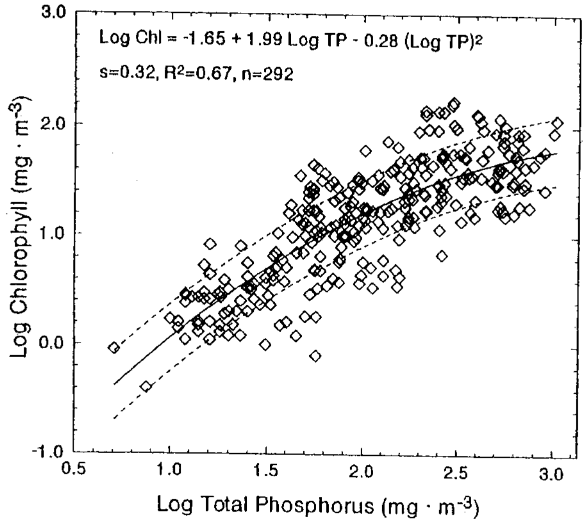
Effect of stream catchment area

Stream catchment area (A_c) ranged between 1 and 541 000 km^2 with a grand mean value of 33 060 km^2 (Table 1). The four largest catchments were the Shatt Al-Arab near Basrah (541 300 km^2), the Saskatchewan near The Pas, Manitoba (328 000 km^2), the Vistula at Warsaw (194 000 km^2), and the Rhine at Lobith (160 000 km^2). Sixty-five percent of observations, however, described streams with catchment areas ranging from 450 to 66 000 km^2.

There was a weak, but significant ($r = 0.44$, $p < 0.0001$) positive correlation between log A_c and log TP. An even stronger correlation ($r = 0.54$) was found between log A_c and log Chl (Fig. 3). Residual values calculated from eq. 1, when plotted as a function of log A_c (Fig. 4), indicated that eq. 1 overestimated log Chl in streams with small catchments while underestimating log Chl in large systems. These results suggested that stream catchment size might affect at least one of the three coefficients in the quadratic model.

This hypothesis was supported by multiple regression analysis. A series of regression models including log A_c and terms representing potential interaction effects with log TP or (log TP)^2 indicated that log A_c exerted a positive effect on the intercept of eq. 1 ($t = 8.14$, $p < 0.0001$), but had no effect on the coefficient of the linear or quadratic term ($t < 1.19$, $p > 0.11$). Consequently, the effect of stream catchment area on the TP–Chl relationship in streams could be approximated as

Fig. 2. Log–log relation between mean total phosphorus concentration and mean chlorophyll concentration among streams (eq. 1). Dashed curves approximate 65% confidence interval for individual predicted values.



$$[2]\quad \text{Log Chl} = -1.92 + 1.96(\text{Log TP}) - 0.30(\text{Log TP})^2 + 0.12(\text{Log } A_c)$$
$$(s = 0.29,\ R^2 = 0.73,\ F = 261,\ p < 0.0001,\ n = 292)$$

This model accounted for 18% of the variance in log Chl not explained by eq. 1 and indicated that the slope of the TP–Chl relationship at all levels of TP increased some 2.3-fold as A_c increased from 100 to 100 000 km^2 (Fig. 5).

Discussion

Our study confirms that there is a generally positive relationship between Chl and TP in temperate streams and that this relationship is curvilinear (Fig. 2). Moreover, the average precision (standard error of regression) of our stream model (0.32) falls well within the range of standard errors (0.23–0.53) associated with large-scale lake models (Jones and Bachmann 1976; Schindler 1978; Soballe and Kimmel 1987). Similarly, among-year variation in TP (19–67%) and Chl (21–116%) for systems with records for ≥5 years compares favorably with estimates of CV$_{\text{TP}}$ (2–80%) and CV$_{\text{Chl}}$ (0–400%) documented for lakes and reservoirs (e.g., Knowlton et al. 1984). These results support the view that lotic and lentic ecosystems respond similarly to P enrichment (Jones et al. 1984; Straskraba 1985) and that TP may provide a reliable basis for predicting the average abundance of sestonic algae in many temperate streams worldwide.

Specifically how increasing P concentration leads to increased Chl in streams remains unclear. Assuming, however, that Chl provides an index of mean annual productivity in aquatic ecosystems (Swanson and Bachmann 1976; Schindler

Fig. 3. Scatter plot and LOWESS trend line illustrating positive correlation between log stream catchment area and (*a*) log total phosphorus concentration or (*b*) log chlorophyll concentration. The correlation between area and chlorophyll concentration is stronger than between area and total phosphorus concentration (Fisher's $Z = 2.31$, $p = 0.02$).

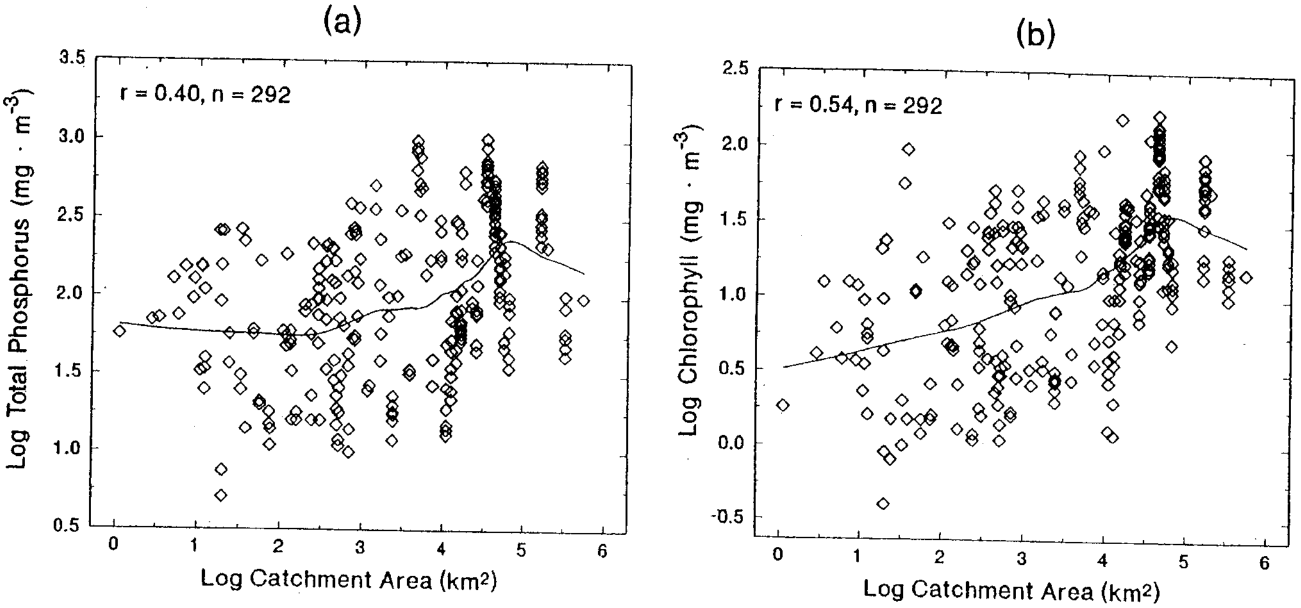


Fig. 4. Residual values of phosphorus–chlorophyll regression model for temperate streams (Fig. 2) plotted against log stream catchment area (A_c). The LOWESS trend line suggests that the univariate model (eq. 1) overestimates log Chl in catchments <7000 km^2 while underestimating log Chl in larger catchments.

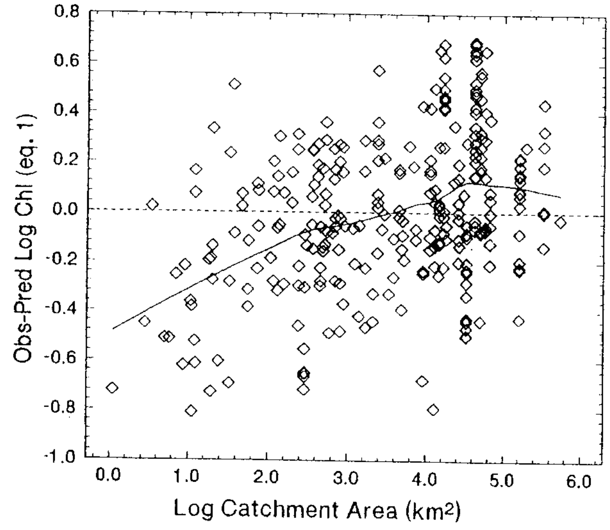
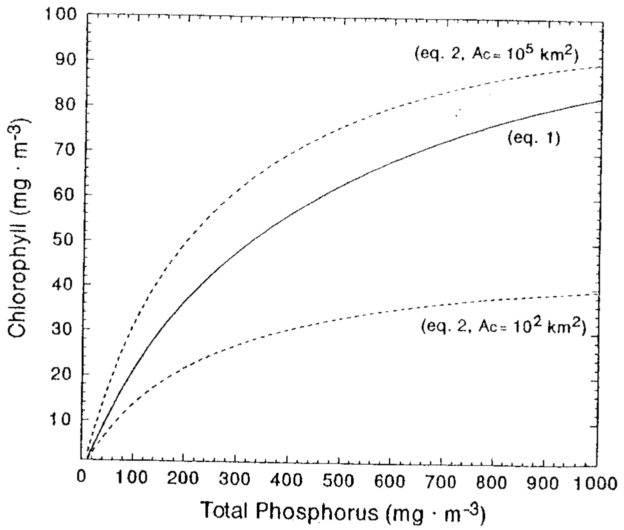


Fig. 5. Arithmetic-scale plot of the phosphorus–chlorophyll relationship in streams and its variation with stream catchment area (A_c). The solid curve shows the predicted relationship for streams regardless of A_c (eq. 1); the broken curves show the predicted relationship for streams of widely differing A_c (100 000 and 100 km^2). Values are corrected for transformation bias (see Methods).



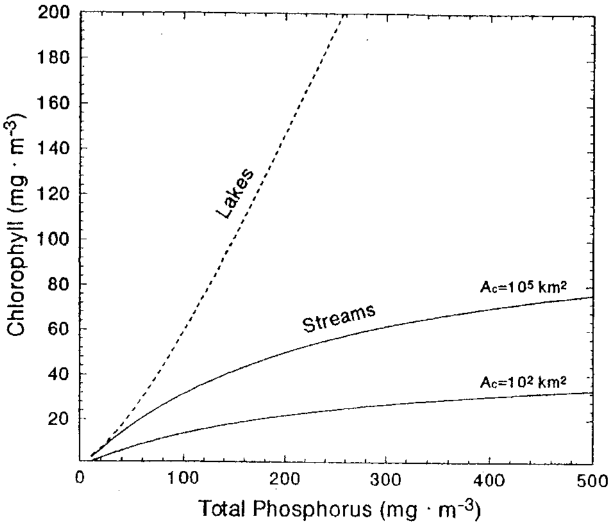
1978; Smith 1979; Golterman and Kouwe 1980), at least two general mechanisms may be postulated. First, P enrichment may stimulate algal growth directly in the water column, where Chl is measured. This mechanism presumably accounts for water blooms or other consequences of enhanced plankton productivity normally associated with P-rich lakes (Jones and Bachmann 1975; Kalff 1983; Ramberg 1988), but also well documented in streams, especially during dry-weather seasons when discharge is relatively low (Talling and Rzoska 1967; Kilkus et al. 1975; Lack et al. 1978; Nusch 1978; Meybeck et al. 1988; Cullen 1993). Alternatively, P enrichment may first stimulate algal growth on the streambed (Aizaki and Sakamoto 1988; Biggs and Close 1989; Lohman et al. 1992), leading to nuisance levels of benthic biomass under low flow conditions (Welch et al. 1988). This enhanced benthic productivity would likely also lead to increased abundance of sestonic algae because benthic algae are often sloughed into suspension as pseudoplankton under low flow conditions (Butcher 1932;

Blum 1956; Swanson and Bachmann 1976). Moreover, any benthic biomass not lost to sloughing, decomposition, or grazing under these comparatively benign hydraulic circumstances would be subject to severe scour and washout during subsequent high flow events (Dauta 1975; Swanson and Bachmann 1976; Tett et al. 1978; Jones et al. 1984; LaPerriere et al. 1989; Lohman et al. 1992). Thus, P enrichment may result in increased Chl regardless of whether the predominant mode of algal production in a particular stream is planktonic or benthic or some mixture of the two.

The positive effect of stream catchment area on Chl:TP (Fig. 4) suggests that physical factors may coregulate Chl at all levels of TP. Among the many factors known to vary predictably with stream catchment area (Dunne and Leopold 1978), mean hydraulic flushing rate (ρ) is perhaps the most important in determining sestonic algal abundance (Kilkus et al. 1975; Soballe and Kimmel 1987). The importance of ρ in coregulating Chl stems from its effect on the sestonic algal washout rate (Brook and Woodward 1956; Mann 1972; Sivko et al. 1972; Lack et al. 1978; Imhoff and Albrecht 1982; Soballe and Bachmann 1984; Soballe and Threlkeld 1985). In streams draining small catchments (≈100 km^2), ρ may average 1.0 d^{-1} or more, depending on the hydrologic region; whereas in a typical large system (≈100 000 km^2), ρ might drop to 0.1 d^{-1} or less (Talling and Rzoska 1967; Capblancq and Dauta 1978; Keup 1985; Ruyter van Steveninck et al. 1992; Van Nieuwenhuyse 1993). This 10-fold reduction in average flushing rate would substantially reduce the average washout rate imposed on sestonic biomass, given that the immersed weight of sestonic biomass (like all seston) is supported entirely by the water column (Eddy 1934; Ketchum 1954; Margalef 1960; Lack et al. 1978; Jones 1984). This reduced washout rate may help increase Chl directly, by allowing more time for algal photosynthesis, nutrient uptake, and cell reproduction to proceed in suspension (Talling and Rzoska 1967), or indirectly, by providing more time for dislodged benthic algae (pseudoplankton) to accumulate passively in the water column (Swanson and Bachmann 1976). Either way, Chl:TP may increase with stream catchment area in part because the average loss (washout) rate a stream imposes on sestonic algal biomass generally decreases with catchment size.

Our results also confirm previous studies (Burkholder-Crecco and Bachmann 1979; Jones et al. 1984; Soballe and Kimmel 1987) indicating that the average abundance of sestonic algae per unit TP is generally lower in streams than in lakes. According to our bivariate model for streams (eq. 2), long-term average Chl:TP near the mouth of a moderately fertile (TP = 100 mg·m^{-3}), 100 000-km^2 catchment would be 0.31. This value is about half of what would be predicted for a P-limited lake of comparable TP (McCauley et al. 1989). This disparity in Chl:TP between large streams and P-limited lakes is about the same as between small streams and large streams (Fig. 6). If the latter difference is indeed influenced by the differential loss (washout) rate of sestonic algae, then so may the former. According to this logic, Chl:TP may be lower in streams than in lakes in part because streams impose a more rapid average loss rate on sestonic algal biomass than lakes do. Low Chl:TP in lakes, however, is often associated with low nitrogen to phosphorus ratios (McCauley et al. 1989), low ratios of euphotic depth to mean depth (Verduin et al. 1978), or high concentrations of suspended solids (Jones and Knowlton 1993). Variation in Chl:TP among inland waters may thus owe more to factors influencing mean algal growth rate (Smith 1982) than to factors regulating mean algal loss rate.

Fig. 6. Comparison of the phosphorus–chlorophyll relationship in temperate streams and lakes. Solid curves show predicted Chl concentrations (eq. 2) in streams of widely differing catchment area (100 000 and 100 km^2). The broken curve depicts the trajectory of expected Chl concentration in P-limited lakes (i.e., total nitrogen to TP ratio = 25, Forsberg and Ryding 1980) and is calculated from McCauley et al.'s (1989) model on the basis of data compiled from the literature (n = 382, R^2 = 0.80, s = 0.23 assumed for bias correction).



In conclusion, our study indicates that there is a generally positive relationship between Chl and TP in temperate streams and that Chl:TP generally increases with stream catchment area. These findings suggest that TP may provide a reliable basis for predicting average abundance of sestonic algae in temperate streams great and small.

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