

# Effects of eutrophication on maximum algal biomass in lake and river ecosystems

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## Abstract

To further clarify empirical relationships between maximum phytoplankton biomass per unit total phosphorus (TP) and the maximum:mean phytoplankton biomass ratio, predictive models were created from a meta-analysis of datasets from lakes worldwide. Peak concentrations of planktonic chlorophyll *a* were on average 2.6 times greater than the mean, with most maximum:mean chlorophyll *a* ratios falling within less than an order-of-magnitude band (from 1.2 to 6 times the mean value). Peak concentrations of planktonic algal biovolume in 22 Organisation for Economic Co-operation and Development (OECD) lakes were on average 3.3 times greater than the mean, with maximum:mean biovolume ratios ranging from 1.2 to 6.3. By contrast, the temporal dynamics of planktonic (suspended) algal biomass in Minnesota streams and rivers were far more constrained; peak concentrations of planktonic chlorophyll *a* were only on average 1.8 times greater than the mean, with maximum:mean chlorophyll *a* ratios ranging from 1.3 to 3.8. These data suggest regional differences in maximum chlorophyll *a* values may exist. Parallel analyses of periphyton biomass in streams and rivers showed far greater variability in the maximum:mean chlorophyll ratio for benthic algae. Peak concentrations of attached chlorophyll *a* were on average 4.3 times greater than the mean, with the observed maximum:mean chlorophyll *a* ratios exhibiting exceptionally high variability (ranging from 1.0 to 50 times the mean value), likely reflecting differences in the temporal dynamics of planktonic and benthic algal growth in freshwater ecosystems.

**Key words:** benthic algae, chlorophyll, eutrophication, extreme events, lakes, phytoplankton, rivers, water quality

## Introduction

Cultural eutrophication has degraded water quality in aquatic ecosystems distributed worldwide (Abell et al. 2012). Anthropogenic activities have dramatically increased global nitrogen and phosphorus exports from the landscape to rivers, lakes, and estuaries (Vitousek et al. 1997, Bennett et al. 2001, Graham and Smith 2004). Atmospheric loadings of both nitrogen and phosphorus to aquatic ecosystems have increased as well (Paerl 1997, Brunner and Bachhofen 1998), contributing to nutrient loading to surface waters (Elser et al. 2009).

Nuisance growth of algae is a visible effect of cultural eutrophication, with the growing seasonal mean of phytoplankton biomass directly responsive to nutrient enrichment (Smith 2003). Users and managers of

waterbodies, however, are not necessarily interested in average conditions. Lake user surveys report perceptions of aesthetic conditions in individual waterbodies are highly sensitive to temporal changes in chlorophyll (Chl-*a*; Smeltzer and Heiskary 1990, Hoyer et al. 2004). The frequency and the intensity of algal blooms are typically of greater interest than average biomass because the public responds to, and remembers, extreme water quality events (Jones et al. 1979). Bloom conditions often coincide with major water quality disruptions such as objectionable taste and odor events in drinking water (Cooke and Kennedy 2001, Smith et al. 2002), fish kills (Barica 1975), and acute toxic or poisoning events (Cooke and Kennedy 2001, Paerl and Otten 2013).

Similarly, cultural eutrophication degrades flowing waters. Nitrogen and phosphorus exported from catchments

enter stream and river channels and stimulate growth of both suspended algae (phytoplankton) and attached benthic algae. Nutrient-driven algal and cyanobacterial blooms in rivers can interfere with recreation, cause taste and odor problems, and elevate cyanotoxins (Aboal et al. 2005, Murdock and Dodds 2008, Oberholder and Ashton 2008).

Several approaches have been used to characterize peak algal conditions. Quantifying the frequency that algal biomass exceeds a set “threshold” value is one metric to describe nuisance conditions (Walmsley 1984, Walker 1985, Walker and Havens 1995, Bachmann et al. 2003, Jones et al. 2011). Others have delineated the upper boundary of Chl-*a* across the range of phosphorus concentrations found in study lakes to illustrate the extreme expression of algal biomass (Brown et al. 2000, Jones et al. 2011, Abell et al. 2012, Xu et al. 2015a).

This study furthers the characterization of extreme algal events by developing regression relationships between maximum and mean phytoplankton biomass in a global set of freshwater lake and river ecosystems. This work builds on the finding of strong relationships between mean and maximum Chl-*a* values in lakes (Stadelmann et al. 2001, Jones et al. 2008). Similarly, data from streams and rivers located worldwide were used to develop maximum:mean relationships for attached benthic algae.

## Methods

Investigator-reported data for total phosphorus (TP) concentrations ( $\mu\text{g L}^{-1}$ ) and phytoplankton biomass, estimated either as concentrations of Chl-*a* ( $\mu\text{g L}^{-1}$ ) or as algal fresh weight (biomass,  $\text{mg L}^{-1}$ ), came from published literature, open file reports, and personal data for 253 cases reported from freshwater lakes worldwide (Table 1). These author-reported data were variable in sampling intensity and frequency. Site-specific differences in sampling intensity could not be controlled. Mean and maximum Chl-*a* values were calculated for each system-year of data; thus, each data point in the figures relates to a different system and sampling year.

All pigment data were based on measurements of Chl-*a*, with the exception of data from Heiskary and Marcus (2001, 2003), who reported values for phaeophytin-uncorrected chlorophyll from sites in the Upper Mississippi River drainage system. Algal fresh weight data (Fricker 1980) were derived from investigator-reported inverted microscope counts, assuming a specific gravity of 1.0. A benthic Chl-*a* database was created by pooling data for 30 sites in 25 New Zealand streams and rivers (Biggs et al. 2001), 30 tributaries to the Etowah River in northern Georgia (USA), and the large global periphyton dataset compiled and analyzed by Dodds et al. (2002) and Dodds (2006).

**Table 1.** Sources of phytoplankton biomass data.

System	Reference
African lakes	Van Ginkel 2004
Irish lakes	McCarthy et al. 2000
Mississippi River	Heiskary and Markus 2001, 2003
New Zealand lakes	Duggan et al. 2001
OECD Nordic lakes	Ryding 1980
Subarctic Québec lakes	Smith unpubl.
Subalpine Italian lakes	Garibaldi et al. 2003
Temperate zone lakes	Marshall 1987

## Results

### Responses of mean and maximum phytoplankton biomass to total phosphorus

Strong power relationships were found between mean concentrations of TP and both mean and maximum values of phytoplankton Chl-*a* in lakes (Fig. 1a) and rivers (Fig. 1b) in this study. For lakes, the exponent for TP was  $>1$  for maximum Chl-*a* but  $<1$  for mean values. In contrast, the exponents for TP were essentially identical for maximum and mean phytoplankton Chl-*a* in rivers and streams (1.52 and 1.53, respectively), ecosystems more completely mixed but also more susceptible to disruption by extreme hydrological events.

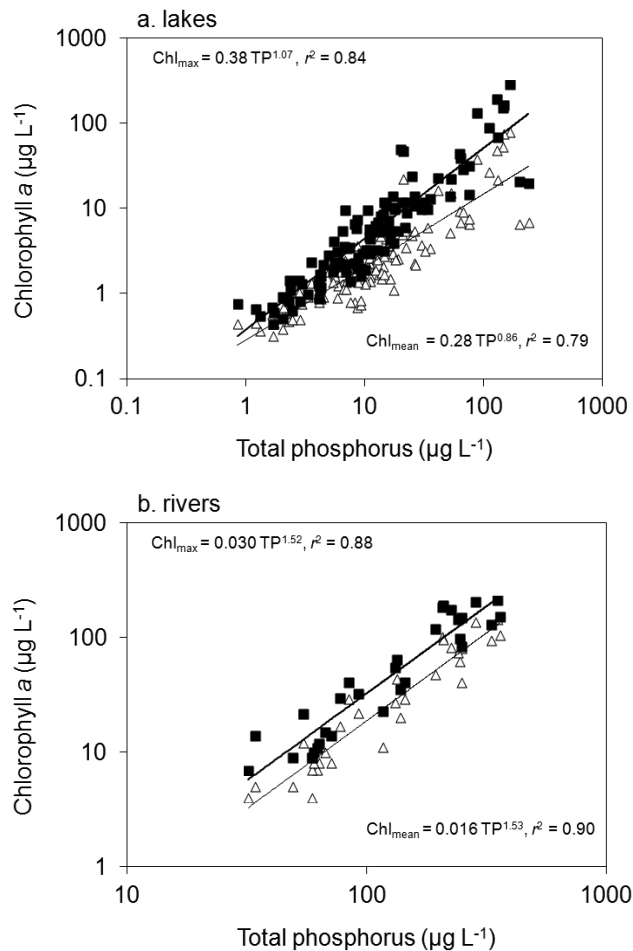
### Planktonic chlorophyll response patterns in lakes

When the maximum and mean Chl-*a* values in lakes were plotted (Fig. 2), more than 3 orders of magnitude of Chl-*a* concentrations fell within a relatively narrow band, with peak Chl-*a* concentrations ranging from 1.2 to 6 times the mean values. The average maximum:mean Chl-*a* ratio was 2.6:1 (SD = 1.17,  $n = 252$ ), and the overall relationship obeyed the power function:

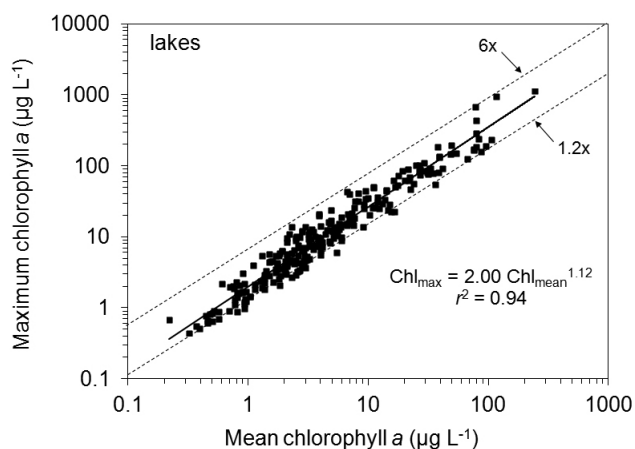
$$\text{Chl}_{\text{max}} = 2.00 \text{ Chl}_{\text{mean}}^{1.12}, r^2 = 0.94. \quad (1)$$

The exponent of equation 1 was  $>1$ , indicating the maximum:mean ratio increased with eutrophication.

The maximum:mean Chl-*a* ratio increased across the trophic state range (Fig. 3a). Maximum Chl-*a* in nutrient-poor lakes (TP  $<5 \mu\text{g L}^{-1}$ ) typically exhibited a maximum:mean ratio  $<2:1$ , with values  $>5.5:1$  among eutrophic lakes (TP = 25–70  $\mu\text{g L}^{-1}$ ), along with greater variation. Lakes with TP  $>100 \mu\text{g L}^{-1}$  had maximum:mean ratios peaking above 6:1.



**Fig. 1.** Relationships between mean total phosphorus (TP,  $\mu\text{g L}^{-1}$ ) and both mean (open triangles) and maximum (closed squares) concentrations of phytoplankton chlorophyll in (a) lakes and (b) rivers.

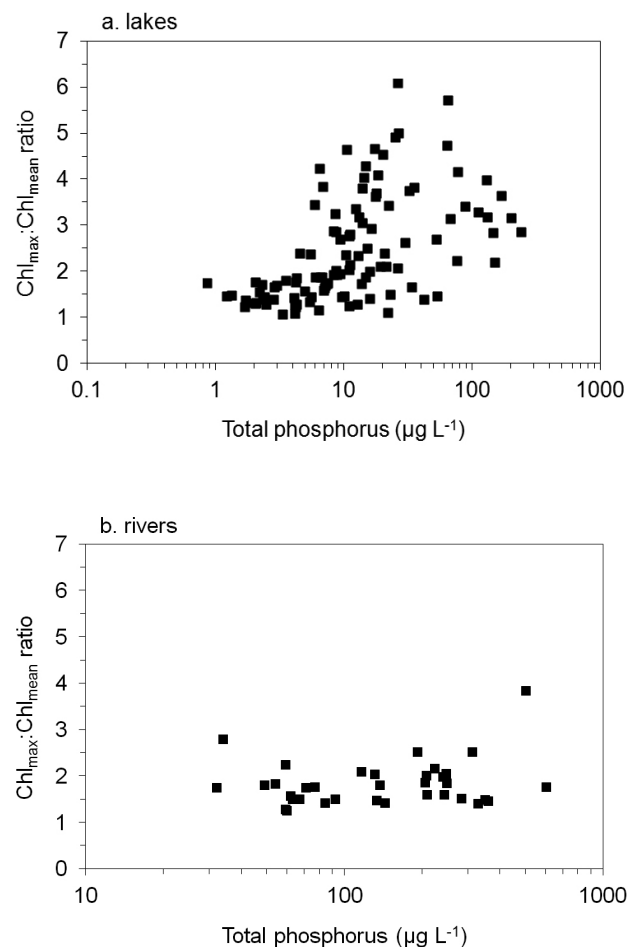


**Fig. 2.** Relationship between maximum and mean phytoplankton chlorophyll *a* concentrations in the lakes-only dataset.

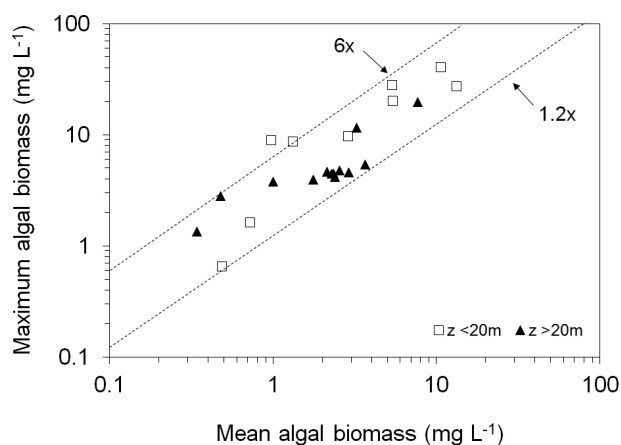
Parallel analyses of maximum and mean phytoplankton biovolume data from the Organisation for Economic Co-operation and Development (OECD) Alpine Lakes Programme (Fricker 1980) showed a similar power relationship. Unlike the Chl-*a* model for global lakes (equation 1), however, the exponent of equation 2 was slightly  $<1$  in this smaller and less geographically diverse dataset:

$$\text{Biomass}_{\text{max}} = 3.09 \text{ Biomass}_{\text{mean}}^{0.91}, r^2 = 0.75. \quad (2)$$

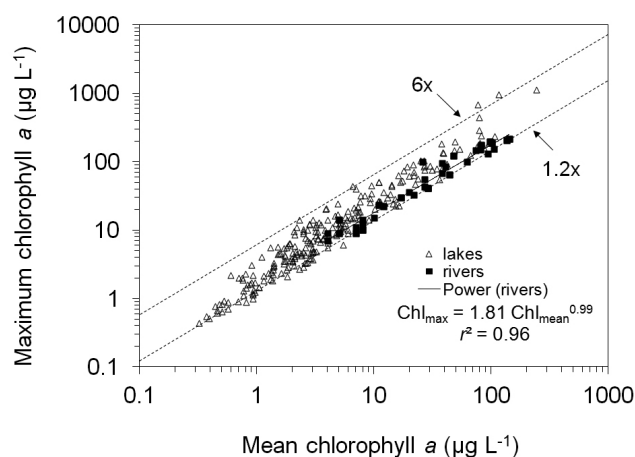
Peak algal biomass ( $\text{mg L}^{-1}$  fresh weight) in 22 OECD lakes was on average 3.3 times greater than the mean, and peak values fell within a band that ranged from  $\sim 1.2$  to 6 times the mean biomass values (Fig. 4). In contrast to earlier findings by Smith (1990), lake mean depth did not seem to influence maximum algal biomass.



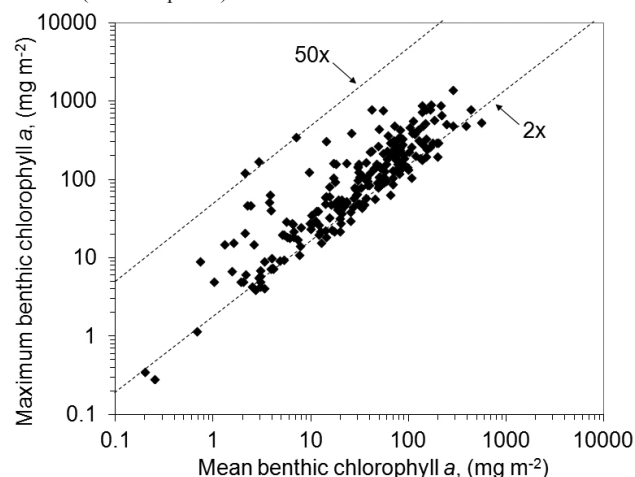
**Fig. 3.** Relationships between mean total phosphorus and the maximum:mean ratio (Chl<sub>max</sub>:Chl<sub>mean</sub>) for phytoplankton in (a) lakes and (b) rivers.



**Fig. 4.** Relationship between maximum and mean algal phytoplankton biovolume (biomass,  $\text{mg L}^{-1}$ ) in alpine OECD lakes with lake mean depths greater (closed squares) and less than (open squares) 20 m.



**Fig. 5.** Pooled relationship between maximum and mean chlorophyll concentrations for phytoplankton in lakes (open triangles) and streams (closed squares).



**Fig. 6.** Relationship between maximum and mean benthic chlorophyll  $a$  concentrations in the streams and rivers dataset.

## Planktonic chlorophyll response patterns in rivers

The planktonic Chl- $a$  response pattern in rivers was nearly indistinguishable from the maximum:mean response pattern in lake data. A plot of the pooled data (Fig. 5) shows that river values fell within the same relatively narrow band as lakes and obeyed the power relationship:

$$\text{Chl}_{\max} = 1.81 \text{ Chl}_{\text{mean}}^{0.99}, r^2 = 0.96. \quad (3)$$

The strong, near unity response in maximum:mean Chl- $a$  ratios in lakes and rivers is noteworthy given their physical, biological, and hydrological differences and suggests a general pattern for world surface waters.

The response of phytoplankton biomass to nutrient enrichment in streams and rivers in the Upper Mississippi River drainage, however, was much more constrained than in lakes. The average maximum:mean total Chl- $a$  ratio for the Minnesota streams and river phytoplankton dataset was 1.8, and only one value exceeded 3.0 (Fig. 3b). These limited data suggest the magnitude of the maximum:mean ratio will not increase with further nutrient enrichment (Fig. 3b).

## Benthic chlorophyll patterns in global rivers and streams

Maximum:mean benthic Chl- $a$  relationships were more variable than those found in lakes and rivers. Maximum and mean benthic Chl- $a$  ranged almost 4 orders of magnitude around the mean value, forming an exceptionally broad vertical band (Fig. 6) compared with lake and river phytoplankton (Fig. 2). Peak concentrations of benthic Chl- $a$  were on average 4.3 times greater than the mean ( $\text{SD} = 6.9$ ,  $n = 230$ ), ranging from 1 to ~50 times the mean. These results confirm and extend the analyses of Dodds et al. (1998).

## Discussion

Consistent with extensive eutrophication literature (OECD 1982, Brown et al. 2000, Champion and Currie 2000, Smith 2003, Jones et al. 2011, Abell et al. 2012), this study shows strong power relationships between mean water column concentrations of TP and phytoplankton biomass in geographically diverse lacustrine and fluvial systems (Fig. 1a and b). The exponents of these TP–algal biomass power relationships, however, were larger in rivers (~1.5) than in lakes (1.07 and 0.86 for maximum and mean Chl- $a$ , respectively). The mechanisms responsible for these apparent differences in algal biomass yield per unit TP are not clear and merit further research.

In particular, the effects of hydraulic residence time were not tested here. Rivers and streams typically exhibit far shorter hydraulic residence times than lakes, and hydrology may be extremely important in accounting for the responses of algal biomass dynamics to scouring and light-limiting nonalgal turbidity (Knowlton and Jones 2000). Moreover, theory related to the River Continuum Concept (Vannote et al. 1980) is relevant; as river size and order increase, nutrients, light, and longer residence time favor autochthonous productivity and greater yield of Chl-*a* per unit TP (Fig. 1b).

In the lake dataset presented here, Chl-TP relationship exponents were  $>1$  for maximum Chl-*a* and  $<1$  for mean Chl-*a*. This difference may result from an increasing tendency for algal biomass dynamics in eutrophic lakes to exhibit greater intraseasonal noise (see figure 3 in Smith 1990) or because phytoplankton communities in eutrophic systems are often dominated by bloom-forming species, which efficiently convert P to algal biomass. Alternatively, eutrophic lakes are generally shallow and more susceptible to wind-induced algal biomass resuspension into the water column from surface sediments. These testable hypotheses should be addressed in future research.

Although lake mean depth was initially found to affect maximum:mean phytoplankton biomass ratios Smith (1990), reanalysis of the OECD dataset does not support this conclusion. This preliminary conclusion was based on a visual inspection of untransformed data. A plot of these same data after logarithmic transformation (Fig. 4), however, showed no consistent effect of mean depth on the relationship between maximum and mean algal biovolume. Conclusions based on these OECD samples may only refer to alpine lakes or may be limited by the small sample size of the database. The complex relationship between maximum:mean algal biomass ratios and lake depth warrants study of geographically diverse lakes.

This analyses of maximum:mean biomass (Fig. 2–5) builds on and extends empirical quantitative relationships for peak algal biomass previously reported for lacustrine and fluvial ecosystems. Jones et al. (1979) initially proposed that the maximum summer Chl-*a* in north temperate lakes was a predictable multiple of the summer mean algal biomass:

$$\text{Chl}_{\max} = 1.7 \text{ Chl}_{\text{mean}} + 0.2, r^2 = 0.76. \quad (4)$$

Similarly, Havens (1994) reported a significant but higher variance relationship between maximum and mean algal biomass within a single lake ecosystem (Lake Okeechobee, Florida):

$$\text{Chl}_{\max} = 2.0 \text{ Chl}_{\text{mean}} + 0.3, r^2 = 0.43. \quad (5)$$

Recognizing the importance of log-transforming the data to help stabilize variance, Stadelmann et al. (2001) reported a strong log-linear relationship between mean and maximum Chl-*a* in 145 central Minnesota lakes:

$$\log \text{Chl}_{\text{mean}} = 0.91 \log \text{Chl}_{\max} - 0.20, r^2 = 0.91. \quad (6)$$

In a related study, Abell et al. (2012) analyzed data from 1316 lakes worldwide to explore nutrient–maximum algal biomass relationships using quantile regression methods and obtained the empirical model

$$\text{Chl-}a \approx_{\max(\text{TP})} = 0.87 \text{ TP} - 0.42, \quad (7)$$

where  $\text{Chl-}a \approx_{\max(\text{TP})}$  is a conditional Chl-*a* maximum.

Equations 4–6 suggest maximum observed phytoplankton biomass value should be at least twice the mean concentration measured in waterbodies monitored multiple times during the growing season. In this study, maximum Chl-*a* was on average 2.5 times the mean ( $n = 394$ ), similar to values equations 4–6 would predict. Jones et al. (2008), however, found that long-term single-system studies ( $>20$  years of record) will increase the likelihood of observing extreme value of maximum Chl-*a*, with intensive sampling maximums as high as 4-fold the mean Chl-*a* values commonly reported.

When the lake and river phytoplankton data compiled in this study were merged (Fig. 5), a strong and remarkably consistent relationship was observed between maximum and mean sestonic Chl-*a*. This finding supports the hypothesis (Lohman and Jones 1999, Smith 2005) that the responses of phytoplankton biomass to eutrophication tend to be relatively independent of ecosystem type, whether fluvial or lacustrine. Thus, although lakes and rivers are hydrologically and spatially complex and differ dramatically in terms of hydraulic residence time, light availability, and biotic structure, phytoplankton growth in each of these systems responded predictably to nutrient enrichment.

As emphasized by Boesch et al. (2001) and Smith (2005), the limnologically based eutrophication modeling framework developed for lakes provides policymakers and managers with credible and effective quantitative tools that can be used to manage algae-associated water quality problems worldwide. A recent meta-analysis showed that the rate of change in maximum Chl-*a* per unit change in TP was remarkably similar among temperate reservoirs (USA), subtropical lakes (USA), and for an international dataset (Jones et al. 2011). Given that relationships between nutrients and phytoplankton biomass seem weaker outside the temperate zone (Abell et al. 2012), however, and strongly influenced by latitude (e.g., 74% of variability in primary production; Håkanson and Boulion 2001), assessing the influence of geographical location on this general conclusion will be important.



Probabilistic approaches successfully used to create water quality protection tools for freshwater lakes and reservoirs (Heyman et al. 1984, Raschke 1994, Walker and Havens 1995, Bachmann et al. 2003, Heiskary and Wilson 2008, Jones et al. 2011) can also be applied to management of algae-related problems in streams and rivers. Important progress has been reported for fluvial ecosystems (Dodds et al. 1997, 1998, Smith and Tran 2010, Haggard and Scott 2011, Heiskary and Bouchard 2015), and an accelerated development of these statistical tools has been supported and strongly encouraged for future research (Xu et al. 2015b). Additionally, given the superior ability of high frequency, sensor-based technologies to accurately detect and measure growing season or annual Chl-*a* maxima, future long-term sensor-based research studies will only improve the quantification and understanding of maximum:mean Chl-*a* ratios. Although to date sensor technologies have predominantly been applied to lakes (Hamilton et al. 2014, Meinson et al. 2015), these techniques will also increase our understanding of algal biomass dynamics in lotic systems.

Results presented here amplify former publications by Dodds, Jones, and colleagues on the effects of eutrophication on flowing waters. As demonstrated by Van Nieuwenhuyse and Jones (1996) and by Dodds et al. (2002), regional Chl-TP models can be used to predict the concentrations of both phytoplankton and benthic algal biomass in temperate streams. Eutrophication science in fluvial ecosystems, however, has historically lagged behind that for lakes, and extensive additional research is needed (Dodds and Smith 2016). In particular, because nutrient enrichment strongly influences the growth and proliferation of attached algae in streams and rivers (Dodds et al. 1997, 1998, Stelzer and Lamberti 2001 and Dodds et al. 2006), additional research is needed to better quantify the effects of eutrophication on benthic algal biomass production and loss dynamics, especially in systems with complex relationships between flood frequency and maximum Chl-*a* (Lohman et al. 1992). Future couplings of appropriate nutrient loading and mass balance models for flowing waters, with the kinds of empirical models for maximum biomass presented here, will potentially contribute to the evolution of new quantitative frameworks for the management of eutrophication-related stream and river water quality.

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