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Chlorophyll Response to Nutrients and Non-algal Seston in Missouri Reservoirs and Oxbow Lakes

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Abstract

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When unaggregated summer chlorophyll data (Chl) from 184 Missouri reservoirs are plotted against total phosphorus (TP) a 'bow' in the distribution develops among a group of points with low Chl:TP ratios (averaging <0.05). Low Chl:TP is mostly associated with turbid, nutrient-rich inflows in reservoirs across the entire trophic range. Non-algal seston (NAS) is our best metric of these inflows and is a co-variable in Chl-TP regressions. This influence is most prominent in years of high runoff and is distinctly seasonal, being most prevalent in early summer prior to full stratification. In late summer, inflows typically enter as subsurface density currents, and nitrogen accounts for more variation in Chl-TP than NAS. Neither variable, however, greatly influences the long-term relation between Chl and TP, which is linear, relatively consistent, and matches the global pattern. In several oxbow lakes, high NAS caused by sediment resuspension is a chronic condition; it seems neither light nor flushing greatly influence Chl:TP in these shallow systems, and values approximate the statewide average. Temporal variation in Chl:TP is demonstrated by daily samples (n=1676) from a single reservoir, with average variability, that covers about 94% of the statewide Chl and about a third of the TP range. The Chl-TP pattern in over half of Missouri reservoirs deviates somewhat from predictions based on cross-system regression models. Nonetheless, for 97% of the study reservoirs, long-term Chl is within a factor of two above or below model predictions, and most are within ±25%. Such differences are modest when compared to the temporal variation measured in an intensively studied reservoir.

Key Words: Chlorophyll, phosphorus, turbidity, phytoplankton

The empirical link between chlorophyll and phosphorus (Chl-TP) is one of the most extensively studied general patterns in limnology. This strong association was first described by Deevey (1940) in Connecticut lakes and, using data from Japanese lakes, Sakamoto (1966) showed cross-system Chl:TP response was linear on a log-log scale; subsequently, it was presented in temperate lakes as a spring TP to summer Chl relation (Dillon and Rigler 1974) and as a summer Chl-TP relation (Jones and Bachmann 1976). Edmondson (1972) nicely demonstrated that the composite cross-system response also operated in an individual lake that underwent rapid changes in nutrient content, which is consistent with theory underlying the comparative approach (Peters 1986, Prairie and Marshall 1995). As such, the relation forms the basis for lake management techniques.

The synthesis by Smith (2003) details the global robustness of the Chl-TP relation, which has been demonstrated in lakes and reservoirs in most geographical regions of the world. Variation in the relation has been linked to nitrogen (Forsberg and Ryding 1980, Smith 1982, Canfield 1983, Jones *et al.* 1989, McCauley *et al.* 1989), seasonal climatic patterns (Jones *et al.* 2003), morphometry and/or stratification (Sakamoto 1966, Riley and Prepas 1985), grazing pressure by large bodied zooplankton (Shapiro 1980, Hansson 1992, Quirós 1990), and fish assemblage composition (Quirós 1990, 1995), among other factors. Assessments of sources of variation in the Chl-TP relation have provided insight about the timing and relative importance of chemical, physical and biological constraints on phytoplankton biomass in lakes.

In this paper we explore how nutrients and suspended sediment, measured as non-algal seston (NAS), influence algal biomass in Missouri reservoirs and oxbow lakes. Consistent with the nature of empirical evaluations, we will address these questions using a cross-system comparison with summer data, some year-round information, and data from an intensively studied impoundment, Lake Woodrail. Most lentic systems in the lower Midwest are artificial impoundments or shallow natural lakes formed by riverine processes. NAS is a physical factor in both lake-types (Jones and Knowlton 1993, Knowlton and Jones 1997). Reservoirs are constructed

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in the lower reach of erosional topography and have large watershed to volume ratios (Jones and Knowlton 1993, Jones *et al.* 2004). Erosional forces that formed the valley deliver sediment to these artificial lakes giving them short life spans relative to natural, glacial lakes. Previous studies show NAS depresses the yield of chlorophyll per unit of phosphorus as a result of poor light conditions (Jones and Novak 1981, Hoyer and Jones 1983, Jones and Knowlton 1993, Knowlton and Jones 2000). NAS is a regional source of variation in the Chl-TP relation addressed previously in a variety of systems and geographic regions (Canfield and Bachmann 1981, Ferris and Tyler 1985).

Database

Data for this assessment come from three principal sources. First, an ongoing summer inventory of Missouri reservoirs (n = 184) carried out between 1978 and 2003, and conducted annually since 1989, provides the basis for statewide characterization. In this effort reservoirs and oxbow lakes located within the major physiographic provinces of the state (Jones and Knowlton 1993) are sampled about every three weeks from mid-May to the third week in August (n = 3 or 4 samples per summer). Samples are seldom collected during the first week of July. Since 1989, annual summer collections have included 60 to 117 reservoirs, most sampled in at least eight summer seasons (median) with a range from 1 to 22 seasons. Second, data from the non-summer period come largely from a an unpublished inventory of 51 reservoirs sampled approximately every three weeks between February and December 1994 and from detailed studies of Mark Twain Lake (Knowlton and Jones 1995) and oxbow lakes in the Missouri River floodplain (Knowlton and Jones 1997). Third, Lake Woodrail, a 4-ha impoundment within the limits of Columbia, Missouri, was sampled daily between May 1992 and December 1996 (n = 1676).

In each study, water was collected from the surface layer at a central site, usually near the dam, and processed by standard methodology (Knowlton and Jones 1995). Starting in 1990, NAS was estimated as the sum of non-volatile suspended solids (Whatman 934AH filter) and the weight of fine particles in the filtrate. We used the procedure developed by Knowlton and Jones (2000) for Missouri waters to estimate filterable non-volatile solids from measurement of turbidity (NTU) of filtered samples. Organic particulate material was measured as the volatile fraction of total suspended solids. The data base includes 169 artificial impoundments, 12 oxbow lakes and 3 floodplain scour lakes. Floodplain lakes influenced by direct river input were excluded from the analysis. Because of the dominance of artificial lakes in the data set, the term reservoir is used as a collective term for all of the water bodies considered in the comparisons.

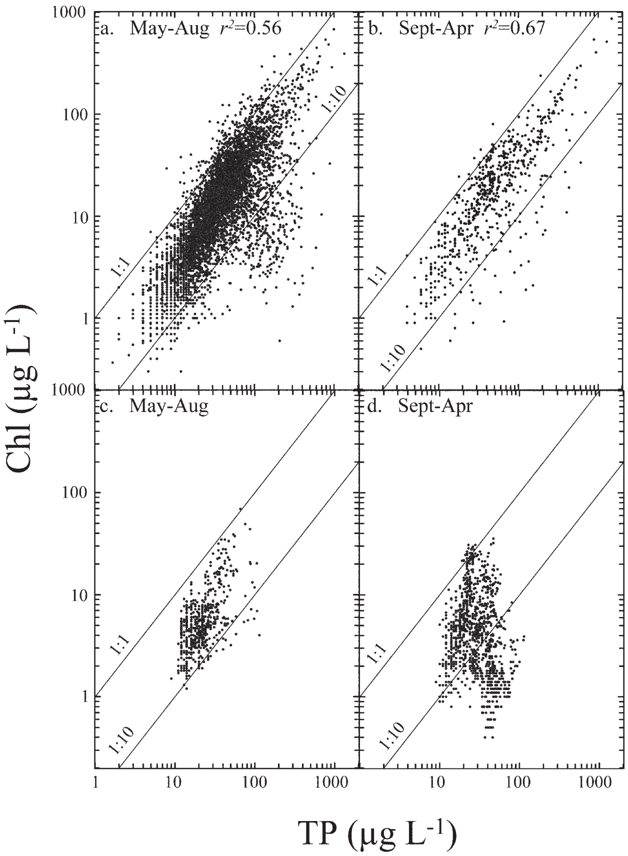

Figure 1.-Chlorophyll-total phosphorus plots of unaveraged data from Missouri reservoirs. (a) Statewide data set, May-August (n=5839). (b) Statewide data set, September-April (n=625). c) Lake Woodrail, May-August (n=597). (c) Lake Woodrail, September-April (n=1079). Reference lines show Chl:TP of 1.0 and 0.1.

Limnological data are used in standard correlation, regression, analysis of covariance and ANOVA tests (SAS 1991a, 1991b), with $P < 0.05$ unless otherwise stated. Effects of multicollinearity on regression results were assessed using procedures in PROC REG of SAS. Data were analyzed at the level of individual observations, seasonal means (samples from a given reservoir in a given summer averaged to the mean) and the long-term reservoir mean (seasonal means averaged over time). Unless otherwise stated, analyses were conducted with $\log_{10}$-transformed data. To assess time series trends during summer, data from individual reservoirs and years were normalized by dividing by their respective

Table 1.-Monthly geometric mean Chl:TP for Missouri reservoirs and Lake Woodrail. Means followed by the same lower case letters were not significantly different in the Duncan's new multiple range test ($p<0.05$).

Statewide Data (n=6464)		Lake Woodrail (n=1676)	
month	**Chl:TP**	**month**	**Chl:TP**
Aug	0.42a	Feb	0.29a
Oct	0.42a	June	0.26ab
Jan	0.41a	July	0.25ab
Sept	0.38a	May	0.24ab
Mar	0.36a	Mar	0.24abc
July	0.36a	Aug	0.22bc
Nov	0.34ab	Sept	0.22bc
Feb	0.32abc	Oct	0.19c
June	0.28bcd	Apr	0.12d
Apr	0.25cd	Jan	0.10d
May	0.25d	Dec	0.06e
Dec	0.25d	Nov	0.05e

Table 2.-Summary of lake-specific standard deviations ($\log_{10}$ data) of limnological variables during May-August. Statewide data include 184 reservoirs except NAS (n=179). Woodrail data include 597 observations.

	Statewide Data (n=184 reservoirs)[1]			Lake Woodrail
	mean	**median**	**range**	
Chl	0.286	0.269	0.089 - 0.668	0.277
TP	0.169	0.161	0.044 - 0.322	0.190
TN	0.124	0.117	0.036 - 0.384	0.112
NAS	0.282	0.265	0.104 - 0.781	--

[1] Five reservoirs lack NAS data.

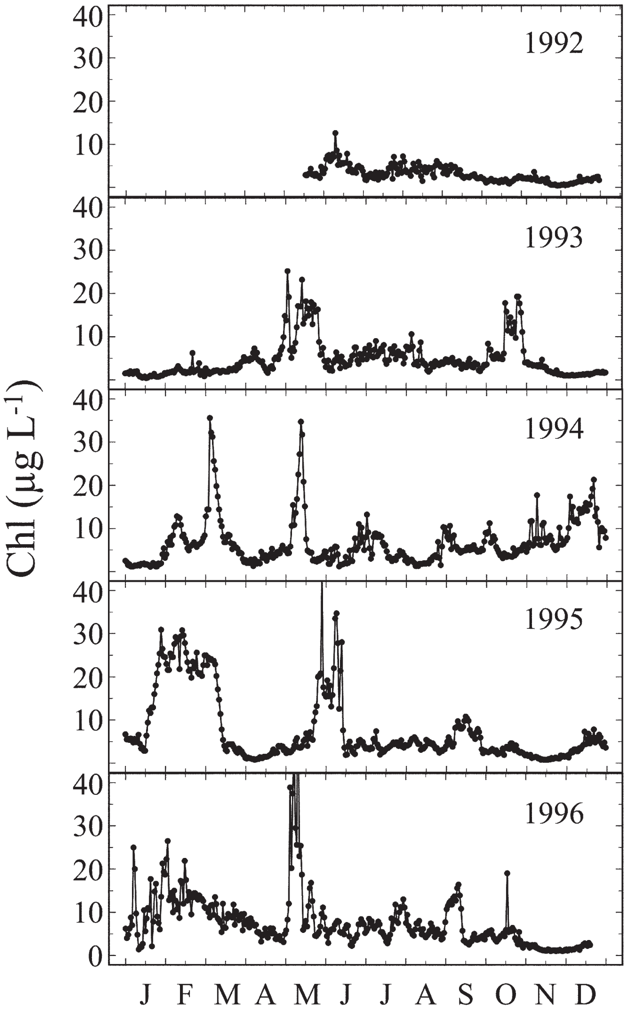

Figure 2.-Daily time series of chlorophyll from Lake Woodrail, Missouri. Off scale measurements not shown: 30 May 1995–43.8 μg L^{-1}, 8 May 1996–49.2 μg L^{-1}, 11 May 1996–69.2 μg L^{-1}.

seasonal means. Normalized data and day of the year were used in simple regression to detect trends, and slopes were estimated as mean percent change per month.

Results

Across the span of conditions in Missouri reservoirs, the fit between chlorophyll and phosphorus (Chl-TP), based on individual measurements from summer (Fig. 1a), show a 10-fold range of Chl:TP ratios. This degree of variation is evident in published data sets and seems inherent in the Chl-TP relation (Dillon and Rigler 1974, Jones and Bachmann 1976, Canfield 1983). Most Chl:TP ratios in Missouri (about 90%) range between 0.1 and 1.0. Ratios >1 comprise only 3% of summer observations and about 6% are <0.1. Limited data from non-summer (September-April, 625 observations from 65 reservoirs) show a similar Chl-TP pattern (Fig. 1b). Compared across time, mean Chl:TP peaks at ~ 0.4 in August, October and January and averages ~ 0.25 in April, May, and December (Table 1).

Lake Woodrail data from 1992-1996 showed the day-to-day variation of algal Chl in an individual reservoir (Fig 2). The phenology, magnitude and duration of Chl peaks varied among years. Chl peaks >12 μg L^{-1} (about double the mean and triple the median value) occurred each year in spring to early summer, only once was the fall overturn peak distinctive (1993), and wintertime peaks were usual (1994, 1995, 1996). Extended Chl minima often occurred in late autumn, and clear-water declines in Chl were evident in spring (1994, 1995). Chl concentration and variation were typically greater in early summer than late (Fig. 2). Overall, Chl varied from 0.4–69.2 μg L^{-1}, and this range encompasses 94% of Chl measurements statewide (Fig. 1). TP in Woodrail (9 to 114 µg L^{-1}) covered about a third of the statewide range (Fig. 1). In terms of measured variance during summer, Woodrail was about average for Missouri (Table 2). The standard deviation for log$_{10}$ Chl is 0.28 compared to a statewide mean of 0.29. For log$_{10}$TP, Woodrail had a standard deviation of 0.19 compared to a statewide mean of 0.17. Presumably, many Missouri reservoirs would show similar day-to-day variation in summer if sampled intensively. Summer Chl: TP (Fig. 1c) in Woodrail was rarely >1 (<1%) or < 0.1 (3%). Most Chl:TP values >1 in Woodrail occurred in January and February (Fig. 1d), and the largest monthly average was in February (Table 1). Unlike the statewide data, about one-third of non-summer samples from Woodrail had Chl: TP values <0.1 (Fig. 1d). Most low Chl:TP values occurred during fall holomixis (November and December) and spring, coincident with major inflow events or during a clear-water phase (Lampert 1978).

A prominent feature of the summer statewide data is a ‘bow’ of low Chl:TP points that fall below the central distribution, in the 100-500 µg L^{-1} range of TP (Fig 1a). Most samples within this zone have Chl:TP ratios <0.05 and are from reservoirs affected by flood events that produce turbid, nutrient-rich inflows with high levels of NAS. Comparison among years shows the ‘bow’ feature of the Missouri Chl-TP relation is more prominent in years with above-average rainfall and runoff than below (Fig. 3a and b, 1995 and 2000, respectively). Data from individual reservoirs show the condition is typically episodic rather than chronic. Most low Chl:TP observations are from the first collection in late-spring (Fig. 3c); Chl:TP ratios <0.1 account for 13% of the early samples but only 2% of late-July to mid-August samples (Fig 3d). On average, Chl:TP in Missouri reservoirs increases from 0.25 in May to 0.42 in August (Table 1).

This seasonal difference in Chl-TP is partly a product of stratification. In many Missouri reservoirs, inflows during peak summer stratification enter as subsurface density currents that have little effect on surface conditions (Knowlton and Jones 1995). Flood events are most influential when they occur before stratification is fully established when inflows directly influence the surface layer. For example, the Chl:TP ratio at the dam in Mark Twain Lake was 0.045 as a result of turbid inflows in March 1990, which mixed throughout the water column (Fig. 4), whereas a major inflow in July 1991 formed an interflow current (Fig. 4), leaving Chl:TP at 0.35 in the surface layer. Turbid inflows also punctuated the Woodrail series; nephalometric turbidity typically spiked in response to rainfall in spring and early summer, but much less so during full summer stratification when runoff formed an interflow below the surface (Fig 5). Thermal stratification, therefore, acts as a buffer mechanism blunting the effect of external turbid events.

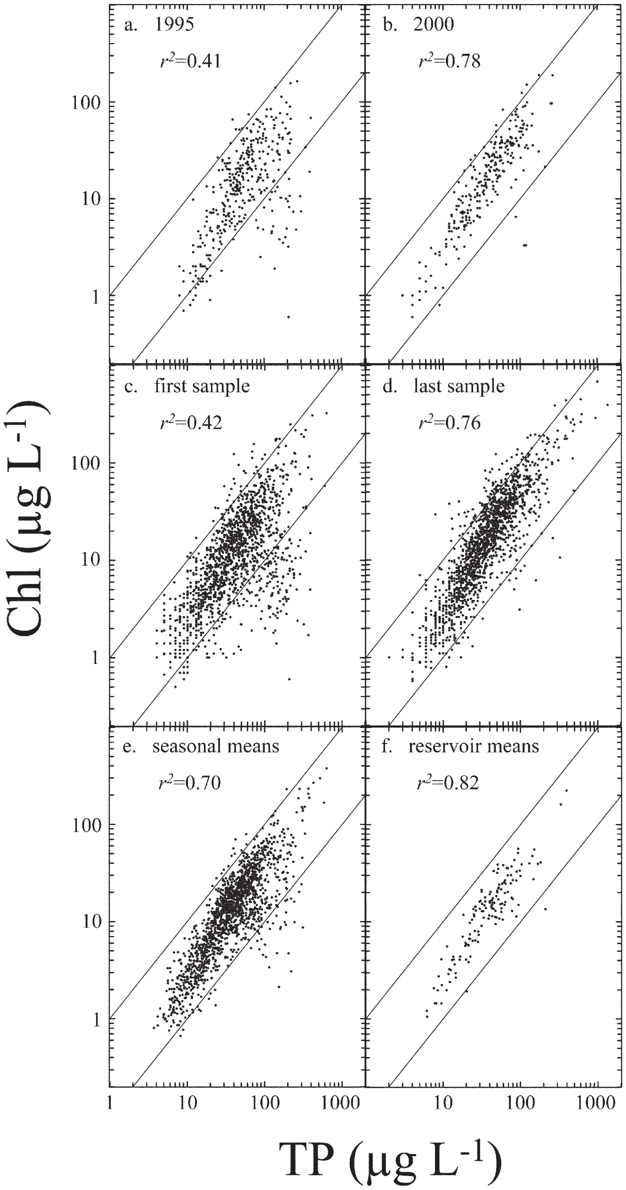

Figure 3.-Chlorophyll - total phosphorus plots of Missouri reservoir data. (a) May-August 1995 (*n*=371). (b) May-August 2000 (*n*=266). During April-August statewide rainfall averaged 72 cm in 1995 versus 49 cm in 2000; the statewide average (1976-2002) is 54 cm. (c) First sample collected from each reservoir during summer sampling (May-early June, *n*=1482). (d) Last sample collected from each reservoir during summer sampling (late July-mid August, *n*=1590). (e) Mean values from individual reservoirs and years (*n*=1545). (f) Grand means averaged by year, then by water body (*n*=143). Seasonal means are based on ≥3 observations per summer, reservoir means are based on ≥4 years of data. Reference lines show Chl:TP of 1.0 and 0.1. Fitted regressions for averaged data are: Seasonal means, $\log_{10}$ Chl = 1.02 x $\log_{10}$ TP – 0.52; grand means, $\log_{10}$ Chl = 1.09 x $\log_{10}$ TP – 0.63.

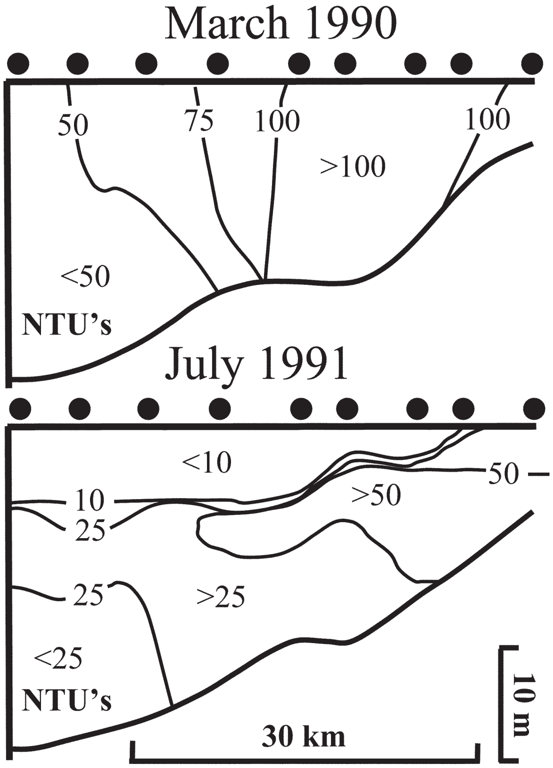

Figure 4.-Spatial distribution of nephalometric turbidity (NTU) in the mainstem and Middle Fork of Mark Twain Lake, Missouri, in March 1990 and July 1991 (Knowlton and Jones 1995). Black dots indicate sampling sites. The reservoir was thermally stratified in July.

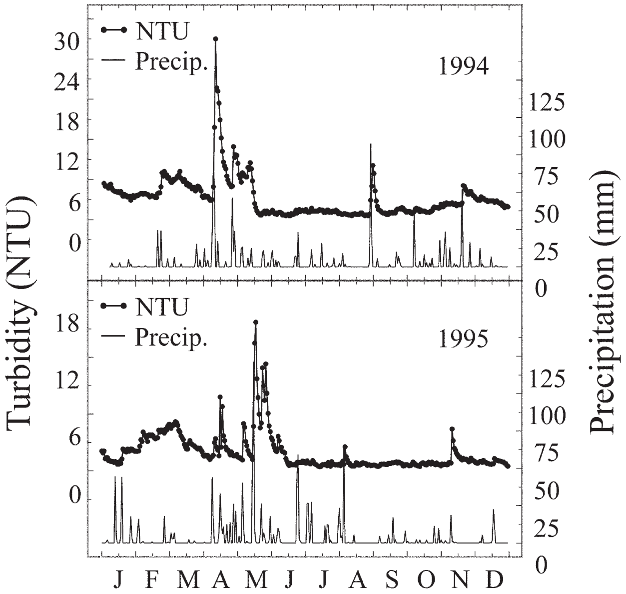

Figure 5.-Daily time series of nephalometric turbidity at Lake Woodrail, Missouri, and daily precipitation recorded at the Columbia Regional Airport 16 km southeast of the lake.

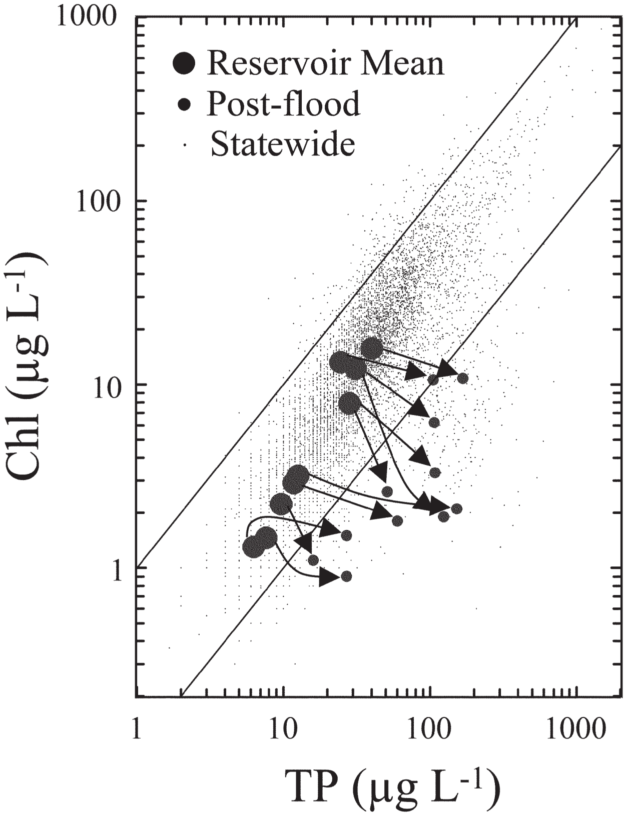

Figure 6.-Average chlorophyll and total phosphorus values for 9 Missouri reservoirs compared to individual Chl and TP values collected during a post-flood period in March-April 1994. Arrows connect average and individual observations from the same reservoir. Year-around, statewide Chl and TP data from Fig. 1a and 1b are shown in the background. Reference lines show Chl:TP of 1.0 and 0.1.

NAS, our best metric of mineral seston, includes both particulate and filtrate materials. Statewide, NAS has a median value of 4.4 mg L^{-1} (n=3622, range 0.2 to 606.1 mg L^{-1}). Small, filterable particles usually comprise a third or less of total NAS (median =32%), but in some reservoirs (*e.g.*, Mark Twain; Knowlton and Jones 1995) finely divided clay minerals make filterable turbidity the dominant fraction of NAS. About half the reservoirs in our data set have exhibited effects of turbid inflows at least once, but such events probably affect many others, resulting in spikes in nutrients and NAS and a reduction in Chl:TP. Effects of inflow events are brief in the Woodrail turbidity data (Fig. 5), suggesting the three-week intervals between sample collections in the large statewide effort missed some major inflow events. Also, following major inflow events in spring 1994 ephemeral reductions in Chl:TP occurred relative to the reservoir mean, even in oligotrophic reservoirs (Fig. 6). These data, and the Woodrail series (Fig. 5), suggest turbid inflows can be quantitatively important prior to the start of summer sampling.

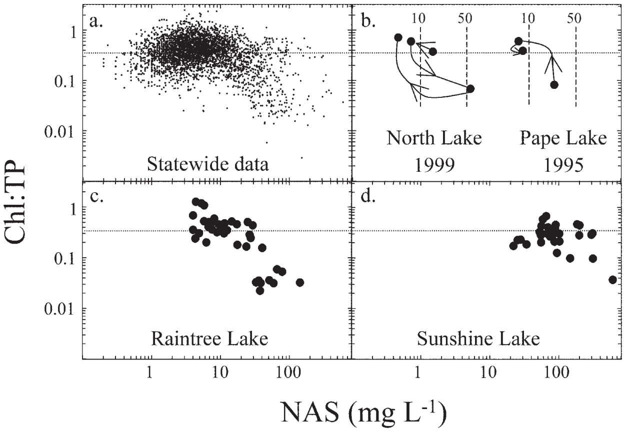

Figure 7.-Ratios of May-August Chl:TP versus NAS concentration. (a) Statewide data set. (b) North Lake 1999 and Pape Lake 1995. (c) Raintree Lake. (d) Sunshine Lake. The horizontal reference lines show the statewide median Chl:TP. In panel c, arrows indicate the sequence of the data and labeled vertical reference lines show the NAS scale.

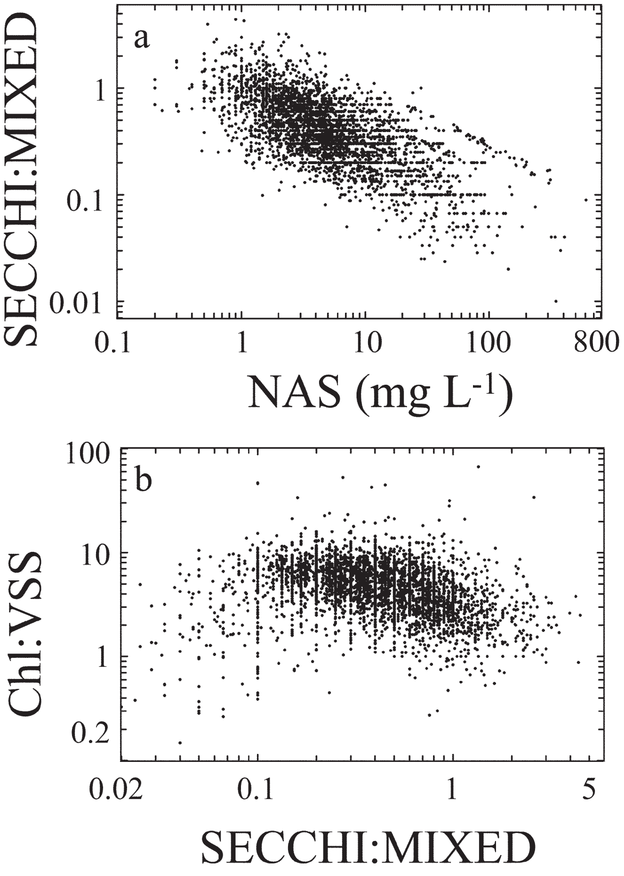

Figure 8.-Statewide, May-August data for: (a) the ratio of Secchi depth (m) to mixed depth (m) versus NAS concentration and (b) the ratio of Chl (µg L^{-1}) to VSS (mg L^{-1}) versus the ratio of Secchi depth to mixed depth. Three outlying observations in panel b are not shown.

Chl:TP ratios show a curvilinear pattern with NAS, tending to decline at values greater than 25 mg L^{-1} (Fig. 7a). Several factors contribute to this trend. High NAS is associated with poor light conditions, and statewide data show a greater than 10-fold decline in ratios of Secchi depth:mixed depth across the range of NAS (Fig. 8a). Light limitation associated with turbid inflow reduces biomass and depresses Chl:TP (Jones and Novak 1981, Knowlton and Jones 1996). High NAS is also associated with rapid flushing and is indicative of an elevated presence of sediment-bound, and potentially non-bioavailable, TP. Among summer samples, high NAS and reduced Chl:TP are most frequently observed in the first collection (*e.g.*, Pape Lake; Fig. 7b). Average NAS is twice as great in the first summer sample as in the last (7.3 vs. 3.6 mg L^{-1}). Low Chl:TP due to inflow is infrequent when stratification is fully developed (Fig. 3d) but occurs occasionally in shallow reservoirs (*e.g.*, North Lake; Fig. 7b). In a few reservoirs (*e.g.*, Raintree; Fig. 7c) frequent inflow events depress Chl:TP, resulting in a negative reservoir-specific Chl-TP relation. By contrast, in some shallow lakes – especially in shallow oxbow lakes – high NAS is a persistent, rather than episodic, feature. In lakes where NAS is consistently high, Chl:TP is usually not depressed because neither light nor flushing are particularly influential. Sunshine Lake represents this group, wherein Chl:TP approximates the statewide average despite NAS averaging 90 mg L^{-1} (Fig. 7d).

Statewide summer Chl:TP data show a systematic change across the tropic spectrum (Fig. 1). The ratio averaged 0.33 at TP <10 µg L^{-1} compared to 0.42 at higher TP, and McCauley *et al.* (1989) found the rate of change in Chl:TP accelerates across this TP range. The response of algal Chl content to light likely contributes to this pattern. Ratios of Chl to particulate organic material measured as VSS (Chl:VSS, µg L^{-1} to mg L^{-1}) decline with increasing light measured by ratios of Secchi depth to mixed depth (Fig. 8b). Phytoplankton are known to adapt to high light conditions by reducing their cellular Chl content (Reynolds 1984), and the reduced Chl:VSS ratio suggests this phenomenon occurs in the least fertile, most transparent Missouri reservoirs. As expected, Chl:VSS also is reduced at low ratios of Secchi:mixed depth because these conditions are associated with reduced light during turbidity events (Fig. 8b). Low Chl:VSS would also be affected by non-algal organic matter of allochthonous origin during inflows. The statewide pattern, therefore, between Chl:VSS and light within the water column is dome shaped, with reduced ratios at both ends of the continuum in response to light.

Among Missouri reservoirs, TP and TN are strongly correlated ($\log_{10}$ data, r=0.83, n=5214, Fig. 9). Ratios of TP and TN (by weight) are mostly between 5 and 40 (mean

Table 3.-Regression analyses for May-August Chl (µg L^{-1}) with slope estimates for total phosphorus (TP), total nitrogen (TN) and non-algal seston (NAS). All data in $\log_{10}$ units. Maximum collinearity condition index values were 4.5 for the statewide model and 2.1 for the Woodrail model (SAS 1991a).

	Statewide Data (*n*=3614)		Lake Woodrail (*n*=597)	
	Parameter Estimate	Partial r^2	Parameter Estimate	Partial r^2
TP (µg L^{-1})	1.081	0.598	0.612	0.372
TN (µg L^{-1})	0.519	0.018	0.749	0.056
NAS (mg L^{-1})	-0.406	0.064	--	--
Intercept	-1.789	--	-2.067	--
r^2	0.681	--	0.428	--
Standard Error	0.287	--	0.210	--

Table 4.-Regression analyses of May-August Chl (µg L^{-1}). All data in $\log_{10}$ units. "First sample" data were from May through early June, "last sample" data were from late July through late August. Maximum collinearity condition index value was 4.6 (SAS 1991a).

	First Sample (*n*=981)		Last Sample (*n*=1000)	
	Parameter Estimate	Partial r^2	Parameter Estimate	Partial r^2
TP (µg L^{-1})	1.120	0.409	0.955	0.793
TN (µg L^{-1})	0.363	0.011	0.676	0.025
NAS (mg L^{-1})	-0.524	0.100	-0.181	0.010
Intercept	-1.360	--	-2.102	--
r^2	0.520	--	0.828	--
Standard Error	0.331	--	0.218	--

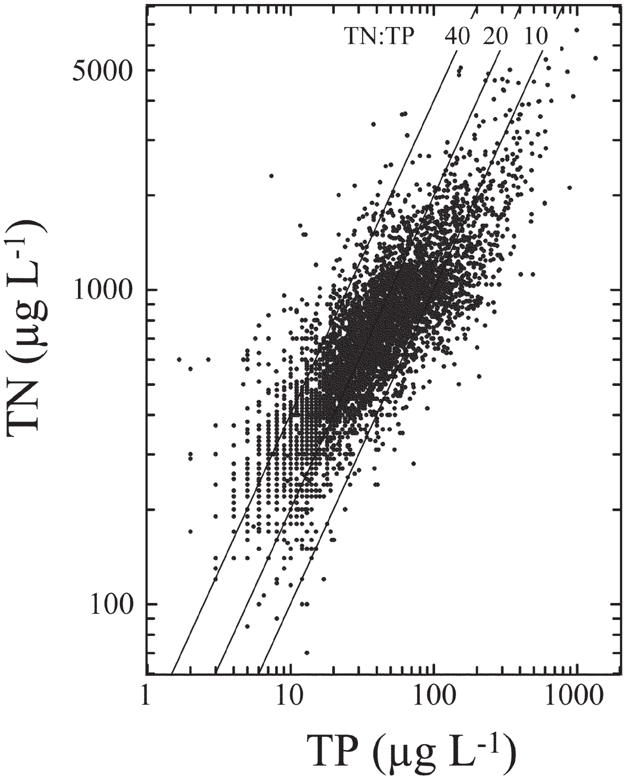

Figure 9.-Statewide, May-August TN versus TP. References lines show TN:TP (by weight) of 10, 20 and 40.

=21, median=18.5) and, consistent with the global pattern (Downing and McCauley 1992), decline with increasing concentrations. Some 56% of the observations have ratios <20, and 13% are <10. The pattern for Woodrail in summer was similar; these nutrients were correlated ($\log_{10}$ data, *r*=0.63, *n*=597) and 45% of the observations had TN:TP <20 but only 4% were <10.

Multicollinearity analysis suggests the correlation between TP and TN does not impede testing their independent effects on Chl in regressions (Table 3). Even though the simple correlation of Chl with TN is almost as strong as with TP (*r*=0.67 vs. 0.75 – summer data), in stepwise multiple regression, variation in TP accounts for 60% of Chl variation, while TN accounts for only an additional 1.8% (Table 3). For Woodrail summer data, TP explained 37% of Chl variation, with TN accounting for an additional 5.6%. In the statewide data, NAS is more consequential than TN, accounting for 6.4% of Chl variation in a model including TP and TN as co-independent variables (Table 3). NAS data are not available for Lake Woodrail.

During summer, nutrient and NAS values decline somewhat while Chl and transparency increase. Statewide, TP, TN and NAS decline at average rates of 7%, 8% and 27% per month, respectively, while Chl and Secchi depth increase by 8% and 7% per month. Woodrail showed similar trends, except that

Table 5.-Regression analyses for May-August Chl (µg L^{-1}) using data averaged by lake-season and then further averaged by lake. All data in $\log_{10}$ units. Seasonal means are based on ≥3 observations including all variables. Reservoir means are for lakes with ≥4 seasonal means. Maximum collinearity condition index values were 5.1 for the seasonal mean model and 6.0 for reservoir mean model (SAS 1991a).

	Seasonal Means (*n*=987)		**Reservoir Means (*n*=111)**	
	Parameter Estimate	**Partial r^2**	**Parameter Estimate**	**Partial r^2**
TP (µg L^{-1})	1.107	0.711	1.220	0.823
TN (µg L^{-1})	0.576	0.019	0.465	0.009
NAS (mg L^{-1})	-0.447	0.066	-0.459	0.048
Intercept	-1.967	--	-1.824	--
r^2	0.796	--	0.880	--
Standard Error	0.206	--	0.141	--

Chl usually decreased during summer. These patterns reflect a general shift from deep mixing, nutrient abundance and NAS turbidity in late spring to a condition in late-summer of established stratification, some nutrient-depletion, and algal dominance of the seston. Statewide Chl-TP relations reflect these seasonal trends (Fig. 3c and d, first vs. last collection). In a multiple regression based on just the first sample in late spring (mid-May to early June), TP accounts for only 41% of the variation in Chl, with TN and NAS accounting for an additional 1.1 and 10%, respectively (Table 4). Comparatively, in a model based on the last summer sample (late-July to mid-August), TP accounts for 79% of the variation in Chl with TN and NAS accounting for an additional 2.5 and 1%, respectively. This late summer Chl model shows the decreased influence of NAS and is a remarkably strong fit for unaveraged data, reflecting the strong TP-dependency of phytoplankton biomass during peak thermal stratification. Analysis of data from intermediate collections shows a decline in the importance of NAS and an increase in the role of TN.

Individual measurements of Chl and TP from Lake Woodrail, a reservoir with average summer variability (Table 2), showed extreme temporal variation (Fig 2). Aggregating individual observations from the Missouri reservoirs to seasonal or long-term means greatly reduces observed variation. As shown by Chl-TP plots in Fig. 3e, observations averaged to seasonal means (the typical practice in analyzing Chl-TP relations) are far less 'noisy' than the individual observations in Fig. 1a (r^2=0.56 vs. r^2=0.70). Averaging seasonal means to long-term reservoir means (Fig. 3f) further pulls the data closer to the overall central trend (r^2=0.82) and reduces variation in Chl:TP to about a 5-fold range, which is about half that of individual observations (Fig. 1a). Successive levels of averaging restrict Chl and TP values from each reservoir into an increasingly narrow Chl:TP range. Most turbidity events are episodic and infrequent, so aggregation reduces their influence. The Chl-TP pattern among reservoir means (Fig. 3f) shows little evidence of the 'bow' related to NAS that is prominent in less aggregated data sets (Figs. 1a and 3). In multiple regression, the relative role of NAS declines with aggregation (Table 5). With raw data, NAS accounted for 11% as much Chl variation as TP, whereas among reservoir means NAS accounts for only 6% as much Chl variation as TP. The importance of TN is also reduced among reservoir means (Table 5). Average Chl in Missouri reservoirs is a relatively consistent function of TP.

The Chl-TP pattern in many Missouri reservoirs deviates, on average, from predictions based on cross-system regression models. Analysis of residuals from the statewide multiple regression in Table 3 shows that 40% of the reservoirs have residuals significantly different from zero based on a two-tailed t-test. Thirty-seven reservoirs have significantly positive residuals with Chl averaging 144% of predicted, while 34 reservoirs had negative residuals with Chl averaging 56% of predictions. Also, in 54% of the reservoirs, residuals are significantly correlated with one or more independent variable (TP = 28%, TN = 24%, and NAS = 35%), indicating the statewide model does not universally apply. In total, residuals from >70% of the reservoirs were significantly non-zero or correlated with independent variables.

Data from Lake Woodrail also differed from the statewide pattern. Summer Chl:TP for Woodrail averaged less than the statewide data set (0.24 vs. 0.33, $p<0.0001$). Regression models of the effects of TP and TN on Chl (Table 3, NAS data are not available) also differ. The Woodrail data had a significantly lower intercept (-2.07 vs. -1.12) and significantly greater slope for TN (0.75 vs. 0.36) than the statewide version; however, regression coefficients for TP did not significantly differ (analysis of covariance – SAS 1991b). Collectively, these results suggest conditions specific to individual reservoirs account for part of the five-fold variation in Chl:TP that exists among long-term means in Missouri (Fig. 3f).

Discussion

Most Missouri reservoirs are either meso- or eutrophic (Jones and Knowlton 1993), with variation in nutrient levels largely determined by nonpoint source inputs from agricultural watersheds (Jones *et al.* 2004). A small number of oligo- and hypereutrophic water bodies occur within the state, each accounting for <10% of the total, but none have long-term TP means of <6 or > 400 µg L^{-1}. Given this range, the statewide Chl-TP relation fits within the central, most-linear part of the global distribution. Aggregated data (reservoir means, Fig. 3f) do not show the sigmoid shape seen in lake data with a broader nutrient ranges than Missouri (Forsberg and Ryding 1980, McCauley *et al.* 1989, Prairie *et al.* 1989). Coefficients for this Missouri Chl-TP relation are virtually identical to those reported for many temperate lakes (Vollenweider and Kerekes 1980, Riley and Prepas 1985, Quirós 1990, Jones *et al.* 2003). In this respect, the long-term average pattern between Chl and TP in Missouri matches the cross-sectional global response (Smith 2003).

Chl-TP models are usually based on summer data because it is considered the period of strong nutrient limitation. This assumption is probably most apt for high latitude lakes where winter light conditions are severe. Limited cross-sectional data for Missouri reservoirs show little indication of lower Chl:TP in the non-summer period (Figs. 1a and 1b). In the Lake Woodrail series, the non-summer period was conspicuous, not for consistently lower Chl:TP, but for variable Chl:TP covering a boarder range than summer (Figs. 1c and 1d). Presumably increased variation during the unstratified period is a common theme in this region (Knowlton and Jones 1995, Perkins and Jones 2000), with nutrients assuming a less dominant role and light, grazing, and inflows exerting a greater influence on biomass than in summer.

Residual uncertainty has repeatedly been the focus of inquiry in the Chl-TP relation since it was first introduced (Nicholls and Dillon 1978, Hoyer and Jones 1983). The large degree of unexplained variation in the relation is not surprising. The role played by TP and other nutrients in regulating phytoplankton is that of setting an upper limit (Kaiser *et al.* 1994), and various chemical, physical and biotic factors – including grazing and variation in pigment content within algal cells (Fig. 8b) – constrain algal biomass to levels below the maximum, resulting in wide variation in Chl-TP relations. Against this backdrop of inherent variability, the effects of secondary factors on biomass must be sizable to stand out as statistically significant. As such, most global multiple regression analyses show additional factors add little to the variability explained by TP alone (Prairie *et al.* 1989).

Analysis of Missouri reservoirs suggests accounting for turbid inflow, as measured by increased NAS levels, provides substantial improvement in Chl-TP regressions (Table 3). Turbid inflows, observed in about half the study reservoirs, are typically an episodic influence yielding an ephemeral reduction in Chl:TP ratios. Mechanisms contributing to this effect include poor light (Fig. 8a), rapid flushing, and high proportions of particulate, sediment-bound TP (Knowlton and Jones 2000). The influence is distinctly seasonal, being most prevalent in early summer prior to full stratification, when turbid inflows mix with the surface layer (Fig.3c). Because NAS, inflow events, and reduced Chl:TP are associated, NAS is a co-variable with TP in these analyses. Inflow events make the general response of Chl to TP seem asymptotic or curvilinear, which was the conclusion reached in an earlier assessment based on a much smaller data set (Jones and Knowlton 1993). In certain reservoirs, where maximum TP is consistently the result of turbid inflow (*e.g.*, Raintree; Fig. 7c), the system-specific Chl-TP pattern is genuinely curvilinear (Knowlton and Jones 1995), but there is little sign of this pattern in the overall, cross-system response (Figs. 1 and 3), and even less so when data are averaged.

In several shallow lakes, high NAS is not a post-flood phenomenon but a chronic condition caused by sediment resuspension by wind and benthivorous fish. Under these conditions, neither light nor flushing are particularly influential because Chl:TP ratios generally approximate the statewide average (Fig. 1a). Presumably the role of NAS differs in these two situations; therefore, NAS does not provide a precise or continuous quantification of its effect in the cross-system analysis. This caveat likely applies to the many other chemical, physical and biotic factors influencing algal biomass. At present, however, NAS is our best metric of the influence of turbid inflows on algal-nutrient patterns in these systems.

Other than inflow events, few conditions seem to consistently affect summer Chl-TP in Missouri reservoirs. The clear-water phase, observed in Lake Woodrail and a few other closely studied reservoirs, may be a factor in low Chl:TP ratios in spring (Table 1) but summer zooplankton in Missouri are dominated by small-bodied taxa (Canfield and Jones 1996), making prolonged biotic control of Chl by top-down processes in most reservoirs unlikely. Under relatively stable conditions in late summer, the influence of NAS on the Chl-TP relation is weak, whereas TN is a stronger co-variable during this period.

A regional feature in Missouri is low TN:TP ratios relative to other temperate zones (Jones and Knowlton 1993), and *in situ* experiments show nitrogen stimulates plankton growth in late summer in some reservoirs (Perkins and Jones 2000) but not others (Knowlton and Jones 1996). Often both nutrients are required to greatly increase algal biomass. The influence of TN on variation in Chl:TP in late summer is comparatively minor and may be tied to relative losses of these key nutrients from the surface layer during stratification and depletion of pools of available inorganic forms (Knowlton and Jones

2000). None of these analyses preclude N-limitation in some Missouri reservoirs, but the relatively small variation in long-term average Chl-TP (Fig. 3f) suggests that if N-limitation occurs it does not frequently depress biomass below expectations based on TP. Furthermore, the strong co-variation between TN and TP in Missouri reservoirs suggests it would be rare to find one of these nutrients in clear excess.

Regression models, based on statewide data, are space-for-time substitutions and are assumed to represent the response of individual reservoirs to changes in the independent variables. For management purposes, the comparative approach embodied in these models is used to predict conditions beyond the present range in a given water body, when system-specific models are not available. Calibrating system-specific models often requires the wide range of conditions found in lakes undergoing cultural eutrophication or renovation (Smith and Shapiro 1981). Few Missouri reservoirs show long-term changes in trophic state, but our data show individual reservoirs are highly variable and many cover an adequate range to provide a basis for extrapolation. At this point, however, data sets for most individual reservoirs are not sufficient for regression modeling of the effects of both nutrients and NAS on Chl. Few (<10%) of the reservoir data sets have more than 40 NAS observations. For most Missouri reservoirs, therefore, comparative analysis is the best tool for predicting changes in biomass.

Lack of system-specific models may not be a great disadvantage. Apart from observations affected by turbid inflows, Chl-TP in Missouri reservoirs is remarkably invariant and is our best approximation of the regional pattern. Among individual observations from late summer, when the influence of NAS is rare, TP accounts for 79% of the cross-system variation in Chl with a standard error of 0.218. The variability in this relation matches that found in global data sets with temporal variation dampened by aggregated to mean values (Jones *et al.* 1998). Uniform sampling during a narrow period of the annual cycle and uniform methods of measurement also contribute to the low degree of variation in this regional assessment (Nicholls and Dillon 1978). Lake management efforts usually focus on the long-term average condition of a lake. For 97% of the reservoirs in this study, long-term mean Chl values are within a factor of two above or below predictions from the reservoir mean model in Table 5, and most are within ±25%. Such differences are modest when compared to the >100-fold Chl range in Lake Woodrail, a reservoir with average variability (Table 2). Based on this comparison, the Missouri models show high precision relative to background variation in the data set and to lakes in general.

This regional analysis, based on data collected during the past 25 years, has identified sources of variation in the Chl-TP relation across the range of reservoir and oxbow lakes that occur in Missouri. Influences of NAS and TN contribute to seasonal variation, thereby providing insight about the timing and relative importance of factors regulating phytoplankton, but neither variable greatly influences the average relation between Chl and TP. When temporal variation is averaged out, the summer Chl-TP relation for Missouri is relatively invariant and matches that of other lake studies (Dillon and Rigler 1974, Jones and Bachmann 1976, OECD 1982, Canfield 1983, Jones *et al.* 2003). Much of the residual variation is likely due to lake-specific conditions. Additional factors will not likely explain much of the residual cross-system uncertainty, and the next step will focus on lake-specific differences in Chl-TP relations to better quantify controlling factors.

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