Chlorophyll maxima and chlorophyll: Total phosphorus ratios in Missouri reservoirs

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NOTE

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Abstract

Reducing the magnitude and frequency of peak algal biomass is a common goal of lake management. To better quantify such conditions in Missouri reservoirs, an upper boundary delineating maximum algal chlorophyll (Chl_{max}) across the range of total phosphorus (TP) was developed using summer monitoring data (n = 8839) and compared with 2 other Missouri datasets (n = 8188 and 5151). Typically, other factors constrain Chl below the maximum, and most samples contained a fraction of Chl_{max}. Near maximum conditions (Chl_{nm}) were provisionally defined as 70% of Chl_{max}; individual reservoirs differ in their history of supporting Chl_{nm} measurements (from 0 to 43% of samples) irrespective of nutrient status or the duration of summer monitoring. There was a rapid increase in the yield of Chl_{max} per unit TP across the oligo–mesotrophic range, while within the eutrophic range Chl_{max} varied with changes in TP in a near-unity response. This general pattern was similar for Chl_{nm} and provides a basis for predicting how high Chl levels would change with nutrient management. Values of Chl_{max} in Missouri reservoirs are lower than lakes in Florida and larger than values in an international dataset, but the rate of change in Chl across the TP range is quite similar among these datasets, suggesting this pattern applies to different lake types.

Key words: algal biomass, chlorophyll, maximum chlorophyll, Missouri reservoirs

Lake management efforts often focus on reducing the magnitude and frequency of peak algal biomass to prevent extreme conditions considered most objectionable (Walker 1985, Bachmann et al. 2003). In this analysis we determined both maximum chlorophyll (Chl_{max}) values and Chl to total phosphorus ratios (Chl:TP) in association with the upper boundary of the Chl–TP distribution in large datasets from Missouri reservoirs and compared our findings with Florida lakes (Brown et al. 2000) and an international data set (Pridmore and McBride 1984). This approach treats the cross-system pattern as the potential Chl maximum at a given TP value rather than the standard approach of accounting for variation around the center of the response, as described by best-fit regression (Jones and Knowlton 2005, Jones et al. 2008). Others have considered the Chl–TP relation from the viewpoint of the upper boundary, and our analysis contributes to this line of inquiry (Hosper 1980, Smith and Shapiro 1981, Pridmore and McBride 1984, White 1989, Kaiser et al. 1994, Brown et al. 2000, Lewis 2011).

Thomson et al. (1996) promoted estimating the upper edge of data distributions where a variable, such as TP, acts as a limiting factor for a response variable, such as Chl, to better understand and quantify spatial structure in cross-system comparisons in ecology. Evaluating response variables relative to a potential maximum is consistent with the ecological concept of limiting factors described by the phosphorus limitation paradigm and implicit in the Chl–TP relationship (Kaiser et al. 1994, Smith 2003, Sterner 2008). Variation in Chl–TP is attributed to the bioavailability of nutrient pools, nitrogen supplies relative to TP, composition of the phytoplankton community, climate, hydrology, stratification patterns, grazing pressure, and light availability, as determined by color and/or mineral particulates. Regardless of other influences, most variation in Chl is related to TP in lakes.

Maximum expression of algal biomass has been addressed based on Chl–TP ratios by White (1989) who considers potential phytoplankton biomass relative to the nutrient content of the sample. This approach differs from viewing algal blooms as a response to nutrient pulses from internal or external sources and does not imply that Chl_{max} is necessarily associated with harmful or nuisance conditions (Smayda 1997, Carstensen et al. 2007). Alternatively, high Chl events have been characterized by quantifying the frequency that observed Chl exceeds specific threshold values in individual lakes (Walmsley 1984, Walker 1985, Walker and Havens 1995, Bachmann et al. 2003).

Using individual Chl–TP pairs from Missouri reservoirs during summer, we fitted a reference line to delineate the upper boundary of Chl (uncorrected for pheophytin, n = 8839, 0.2–447 μg/L, median 13.5 μg/L) across the range of TP (2–831 μg/L, median 36 μg/L; Fig 1a). The data were binned based on the distribution of $\log_{10}$TP values (n = 38 bins, each with <6% of the total observations). Within each bin, Chl–TP pairs were ranked to identify Chl_{max} within the given nutrient range; obvious outliers were excluded. A line was fitted to the Chl_{max} values using stepwise regression with $\log_{10}$TP and $\log_{10}$TP^3 ($R^2 = 0.98$, $p < 0.01$) to describe the upper edge of the distribution of the data; $\log_{10}$TP^2 and higher-order terms for $\log_{10}$TP were not significant:

$$\log_{10} Chl_{max} = -0.61 + 1.62(\log_{10} TP)$$
$$-0.059(\log_{10} TP^3). \tag{1}$$

The boundary is not distinct (Fig. 1a), and variation around the upper edge is inherent in distributions of this type (Kaiser et al. 1994). For this dataset, 1.4% (n = 129) of observed chlorophyll values (Chl_{obs}) were greater than Chl_{max} (Chl_{obs}:Chl_{max} >1); in more than half of this group Chl_{obs} was larger than Chl_{max} by <20%. In 8 samples Chl_{obs} was more than double Chl_{max}, and one was more than 4 times the
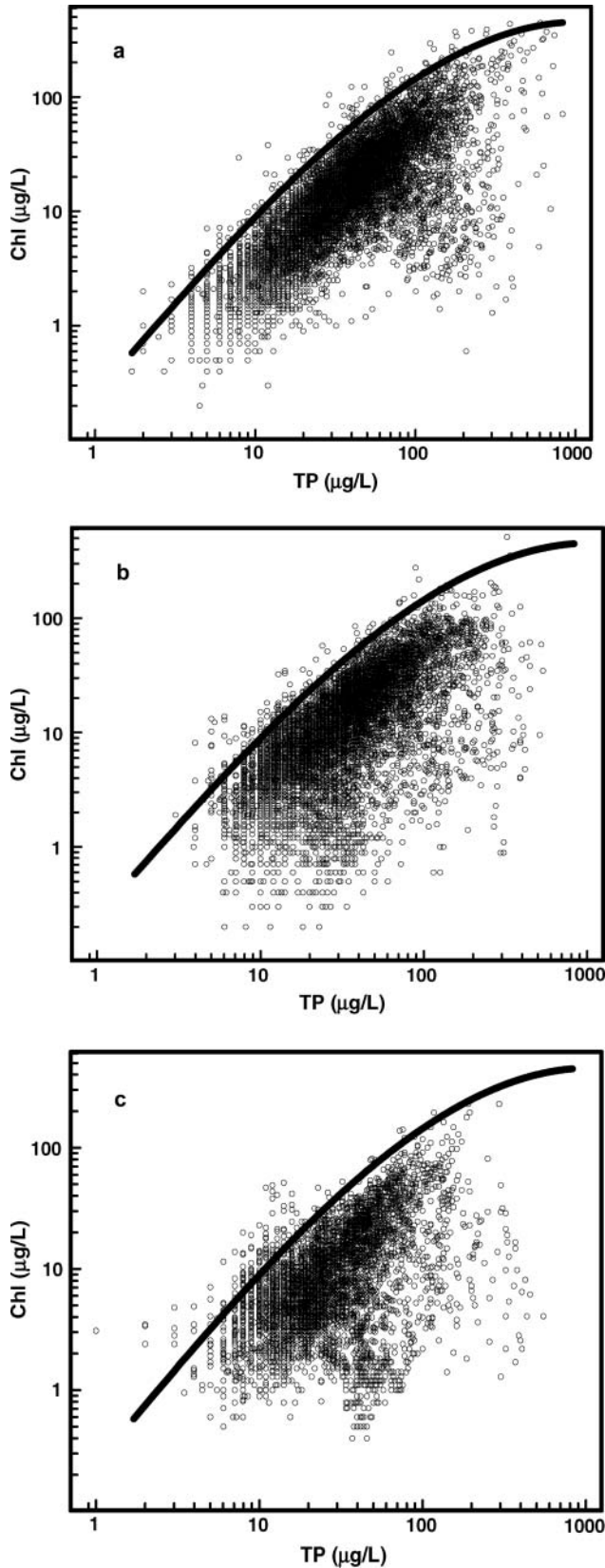
empirical limit. Review of the analytical records provided no basis to remove these samples; they likely represent rare, extreme conditions in the monitoring record. A similar presentation by Brown et al. (2000) shows a small number of observations quite distant from the edge of the data envelope, and our largest values fit within their distribution.

Most samples contained a fraction of Chl_{max}; the median ratio of $Chl_{obs}:Chl_{max}$ was 0.31 (Fig. 1a, interquartile range 0.22–0.44, mean 0.35). This ratio was >0.8–1 in only 2.4% of the observations, and an additional 2.7% of the values had ratios >0.7<0.8. This distribution suggests values near Chl_{max} are infrequent in routine summer monitoring data. Noteworthy, Chl_{max} values and $Chl_{max}:TP$ ratios are at least 3 times larger than the conventional limits used to categorize reservoir trophic state in Missouri reservoirs (Jones et al. 2008; Table 1). This comparison further illustrates that Chl_{max} values represent extreme conditions associated with a given nutrient value.

The empirical Chl_{max} described by equation 1 also applies to other datasets from Missouri reservoirs. It envelops the upper boundary of data collected by citizen volunteers (n = 8188, TP 3–539 μg/L, median 31 μg/L; Fig 1b); some 1.6% of Chl_{obs} were larger than Chl_{max} and most come from Table Rock Lake, an impoundment with low mineral turbidity with large Chl:TP ratios (Thorpe and Obrecht 2008). The Chl_{max} boundary (equation 1) also envelops an aggregated dataset that includes daily collections from several reservoirs during summer and numerous nonsummer samples (n = 5151, TP 2–543 μg/L, median 25 μg/L; Fig. 1c). Some 2.6% of Chl_{obs} was larger than Chl_{max}; most were from Table Rock Lake or collected during fall destratification, a period of high Chl:TP ratios (Jones and Knowlton 2005). The median ratio $Chl_{obs}:Chl_{max}$ of 0.27 was, however, somewhat lower than the other datasets (Fig. 1), in part because this dataset includes midwinter collections when low Chl:TP ratios are common (Jones and Knowlton 2005). Together, these comparisons suggest the equation for Chl_{max} broadly applies to Missouri reservoirs.

The Chl_{max} response for Florida lakes by Brown et al. (2000) is about twice the value for the Missouri Chl–TP pattern

← **Figure 1.-**Chlorophyll (Chl) and total phosphorus (TP) from Missouri reservoirs and oxbow lakes during summer (panel a, n = 8839; Jones et al. 2008). The upper boundary on Chl in all 3 panels was described by equation 1 from the text: $\log_{10}Chl_{max} = -0.61 + 1.62(\log_{10}TP) - 0.059(\log_{10}TP^3)$. This upper boundary was also plotted with data from Missouri reservoirs collected by citizen volunteers (panel b, n = 8188) after TP data were increased by 2 μg/L to account for loss during storage (Obrecht et al. 1998) and data from Missouri reservoirs collected from reservoirs sampled daily during summer and seasons other than summer (panel c, n = 5151).

Table 1.-Trophic state criteria for Missouri reservoirs (Jones et al. 2008) with the corresponding Chl:TP ratios for conditions at the upper boundary. Maximum and near-maximum chlorophyll (see text) and corresponding Chl:TP ratios are shown for the upper TP value in each trophic state category.

Trophic State	Upper Limit of Trophic State			CHL (μg/L) at		CHL:TP ratio at	
	TP (μg/L)	CHL (μg/L)	CHL:TP	Max	Near Max	Max	Near Max
Oligotrophic	10	3	0.30	9	6	0.90	0.62
Mesotrophic	25	9	0.36	31	22	1.25	0.86
Eutrophic	100	40	0.40	145	100	1.45	1.00

(Fig. 2a). This discrepancy likely reflects differences in climate and lake type between the 2 regions; Brown et al. (2000) previously concluded some Florida lakes have larger Chl:TP ratios than northern lakes. Suppression of Chl yields

Figure 2.-Plot of maximum chlorophyll (Chl_{max}) against total phosphorus (TP) calculated using a nonlinear (upper line, panel a) equation for Florida lakes by Brown et al. (2000) and equation 1 from the text for Missouri reservoirs and for international lakes (Pridmore and McBride 1984). Data from panel a were replotted in panel b to show the rate of change in Chl_{max} [$= (Chl_{max})_{TP} - (Chl_{max})_{TP-1}] / (Chl_{max})_{TP}$] across much of the observed TP range in the dataset.

by mineral turbidity could also reduce Chl_{max} in some Missouri reservoirs (Jones and Knowlton 2005). In contrast, values of Chl_{max} estimated for an international suite of lakes (Pridmore and McBride 1984) averaged about 60% of Chl_{max} in Missouri (Fig. 2a). Longer collection records for the Florida and Missouri datasets would increase the likelihood of sampling high Chl events, thereby contributing to larger Chl_{max} values (Brown et al. 2000, Jones et al. 2008). Regardless, these comparisons suggest regional differences in Chl_{max}.
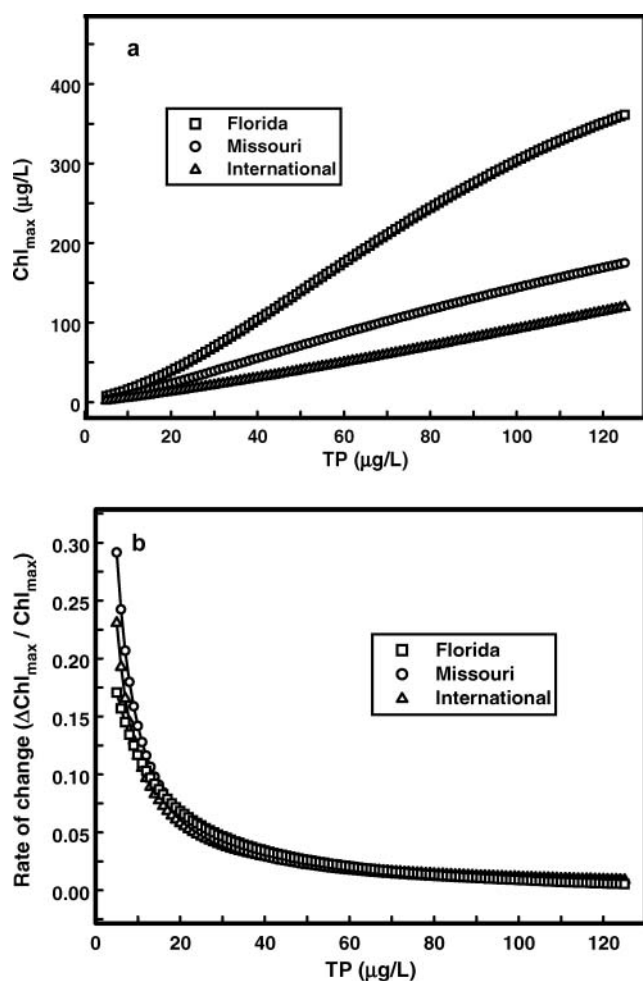
As a preliminary approach to identify near-maximum algal biomass in Missouri reservoirs and to broaden the scope of the comparative analysis beyond Chl_{max}, we calculated the upper 95% confidence limit on mean Chl within each of the $\log_{10}TP$ bins used to generate equation 1 (mean + 1.64*Standard Deviation). The cross-system pattern matched 70% of Chl_{max} and serves as a provisional limit for identifying near-maximum Chl (Chl_{nm}) in these reservoirs. These data include samples within approximately 5% of Chl_{max} and those located above the upper boundary (Fig. 1a). Values of Chl_{nm} and Chl_{obs}:TP ratios are more than double the conventional limits used to categorize reservoir trophic state boundaries (Table 1).

Phytoplankton taxonomic composition varies with lake trophic state, and the cellular Chl content differs within and among species (Watson et al. 1992, 1997); both factors may influence Chl_{nm} in Missouri reservoirs. Taxonomic data from July 2003 (63 reservoirs; Jones et al. 2008) showed that 6% of the samples exceeded Chl_{nm} criteria, as did 1 of 15 reservoirs in August 2004; these samples were from eutrophic reservoirs dominated by either *Anabaena* or *Aphanizomenon* (87–98% of total biovolume). These limited data indicate Chl_{nm} can be exceeded when the phytoplankton community is dominated by large cyanobacteria. Additional taxonomic information is needed to determine the algal community dominating other Chl_{nm} events, particularly in oligotrophic and mesotrophic reservoirs.

Conditions that favor Chl_{nm} in individual reservoirs may be short-lived. Daily collections from Little Dixie Lake during summer 2004 (n = 108; Fig. 3) show 9% of samples exceeded the Chl_{nm} threshold during a single event in late
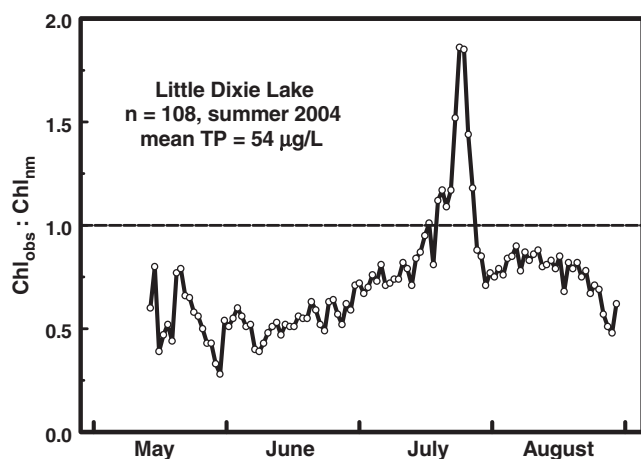
Figure 3.-Ratio of observed chlorphyll to near-maximum chlorophyll (Chl_{obs}:Chl_{nm}) in daily collections from Little Dixie Lake during summer 2004. Values above the horizontal line indicate samples where Chl_{obs} exceeded Chl_{nm}.

July. This ephemeral peak was consistent with a bloom event wherein Chl deviates from the normal seasonal cycle for a short period of time (Hutchinson 1967, Carstensen et al. 2007). These events would not always be captured in routine summer monitoring (Knowlton and Jones 2000, Jones et al. 2008) and suggest that Chl_{max} and Chl_{nm} are best assessed using large datasets.

Among the most intensively sampled reservoirs in our dataset (n = 113, 33–151 summer samples, median 53), two-thirds of samples exceeding Chl_{nm} were collected during July and August, consistent with an earlier finding that Chl increases in late summer (Jones and Knowlton 2005). Individual reservoirs in this group differ in their history to support Chl_{nm}; 23% never expressed Chl_{nm}, 37% supported Chl_{nm} in 0.1–5% of samples, and 40% supported Chl_{nm} in $\geq$5–43% of samples. Interestingly, neither mean TP (6–180 μg/L, median = 39 μg/L) nor the number of samples collected from an individual reservoir showed a significant correlation with Chl_{nm} ($p > 0.05$). These outcomes suggest frequency of Chl_{nm} is not a simple function of nutrient status or the duration of monitoring as represented in our summer inventory.

Lake managers have addressed undesirable algal abundance as the frequency that Chl_{obs} exceeds nuisance levels (Walmsley 1984, Walker 1985, Walker and Havens 1995, Bachmann et al. 2003). The frequency of high Chl levels is known to increase with trophic state, with large values common in enriched lakes. We followed this convention and calculated the frequency of Chl values of $\geq$10, $\geq$20, $\geq$30, $\geq$40, and $\geq$50 μg/L from intensively sampled reservoirs in the dataset (n = 113; Fig. 4) and found similarities with lakes in other regions and previous findings for Missouri reservoirs (Jones et al. 2008). In general, the frequency of Chl $\geq$10 μg/L increased sharply among reservoirs with mean TP $\geq$20 μg/L but was uncommon in reservoirs with lower mean TP (Fig. 4).

Another feature of this analysis is that within each trophic state category an increase in Chl_{obs} represents a progressively larger ratio of Chl_{obs}:Chl_{nm} and therefore is less frequently observed in the data distribution (Fig. 4; Table 2). For example, among mesotrophic reservoirs, a Chl value of $\geq$10 μg/L equates to nearly two-thirds of Chl_{nm}, while 40 μg/L Chl closely matches Chl_{nm}, and 50 μg/L Chl exceeds the Chl_{nm} criteria (Table 2). This general pattern holds for Chl values across all trophic states (Table 2). Conversely, for any given Chl value, the ratio of Chl_{obs}:Chl_{nm} declines with trophic state (Table 2). To illustrate, $\geq$10 μg/L Chl closely matches Chl_{nm} in oligotrophic reservoirs, and equates to nearly two-thirds, half, and one-third of Chl_{nm} in mesotrophic, eutrophic, and hypereutrophic systems, respectively (Table 2). The magnitude of these high Chl events in individual reservoirs (Fig. 4) is masked by aggregation in the presentation of the Chl–TP relationship as seasonal or long-term mean values (Jones et al. 1998, Jones and Knowlton 2005). These extreme values are the basis for estimating Chl_{max} in summer monitoring data (Fig. 1).

Table 2.-Trophic state criteria for Missouri reservoirs based on TP (Jones et al. 2008) with the mean ratio of observed average chlorophyll:near-maximum chlorophyll (Chl_{obs}:Chl_{nm}) in Chl_{obs} samples of $\geq$10, $\geq$20, $\geq$30, $\geq$40, and $\geq$50 μg/L from intensively sampled reservoirs in the dataset (n = 113). The eutrophic category was divided at 50 μg TP/L to better illustrate the cross-system pattern in Chl_{obs}:Chl_{nm}.

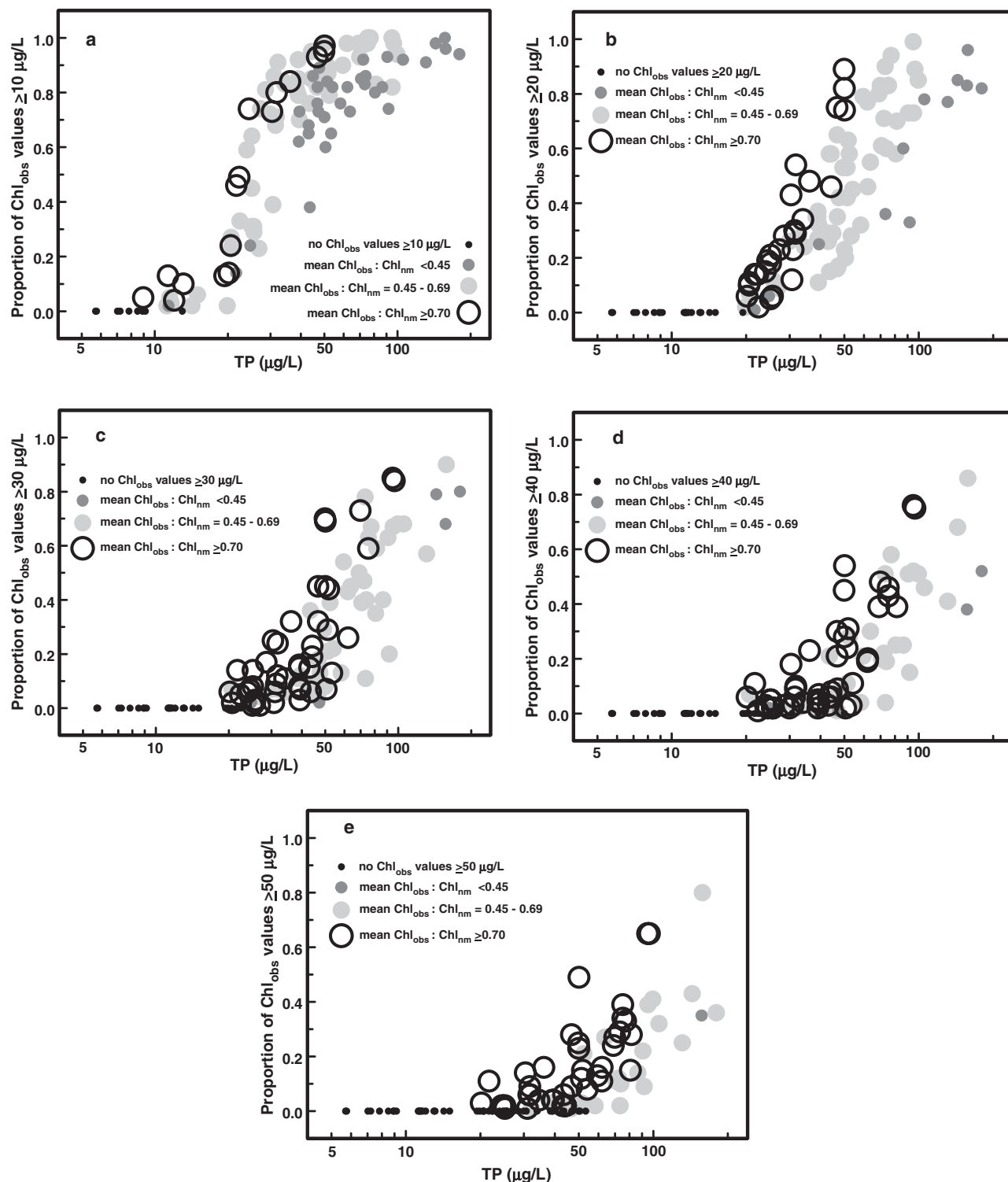| Trophic State	# Lakes	TP (μg/L) Criteria	Chl_{obs} : Chl_{nm} values when Chl_{obs}				
			$\geq$10 μg/L	$\geq$20 μg/L	$\geq$30 μg/L	$\geq$40 μg/L	$\geq$50 μg/L
Oligotrophic	9	<10	0.97	—	—	—	—
Mesotrophic	22	$\geq$10–<25	0.63	0.79	0.96	1.04	1.60
Lower Eutrophic	45	$\geq$25–>50	0.53	0.67	0.77	0.83	0.92
Upper Eutrophic	31	$\geq$50–<100	0.46	0.55	0.63	0.70	0.75
Hypereutrophic	6	>100	0.34	0.38	0.42	0.48	0.53

Figure 4.-The proportion of observed chlorophyll (Chl_{obs}) values that exceed 10, 20, 30, 40 and 50 μg/L (panels a–e, respectively) plotted against the mean $\log_{10}TP$ value from intensively sampled reservoirs in the dataset (n = 113). The mean ratio of Chl_{obs} to near-maximum chlorophyll (Chl_{nm}) was calculated for each reservoir using Chl values that exceeded the cutpoint for the respective panels. Mean Chl_{obs}:Chl_{nm} ratios were divided into 4 categories and are represented in the panels by unique symbols to show the cross-system pattern.

The ratio of Chl_{max}:TP forms a dome-shaped distribution across the range of Chl_{obs}:TP values in the dataset when both are plotted against trophic state (as $\log_{10}TP$; Fig. 5a). This pattern clearly shows a rapid increase in the yield of Chl_{max} per unit TP across the oligo- and mesotrophic ranges, followed by high ratios throughout the eutrophic range and subsequent decline among the most fertile samples. Overall, ratios of Chl_{max}:TP increase sharply from $\sim$0.6 at 5 μg TP/L to unity at 13 μg TP/L, and the ratio increases to 1.25 at the upper boundary of the mesotrophic conditions (25 μg TP/L). Across this range, the increase in Chl_{max}, from 3.2 to 31.2 μg/L, was double the 5-fold increase in TP. Between 25 and 30 μg TP/L, the increase in Chl_{max} was just slightly larger than the proportional increase in TP. Near the center of the data distribution, Chl_{max}:TP forms a broad dome. Ratios were 1.4 at 44 and 125 μg TP/L with a peak ratio of 1.46 at 74 μg TP/L. As a consequence, Chl_{max} closely tracks changes in TP in a near-unity response within the eutrophic range. For example, halving TP from 100 to 50 μg TP/L corresponds with halving Chl_{max} (from 144 to 71 μg/L). The decline in Chl_{max}:TP among the most fertile samples (>125 μg TP/L, 8% of the total; Fig. 5a) is largely a function of light limitation and available supplies of dissolved P in turbid samples (Knowlton and Jones 2000, Jones and Knowlton 2005, Jones et al. 2008).

The pattern seen in Chl_{max}:TP ratios also holds for the 90th, 70th, and 50th percentile values in the TP bins used to generate equation 1 (Fig. 5b, values >125 μg TP/L not shown). Within each category, Chl:TP shows a statistically significant increase with TP across oligotrophic to near-eutrophic range (r $\geq$ 0.93, n = 17, TP = 5–38 μg/L), with a nonsignificant, near-flat response between 40 and 125 μg TP/L. Collectively, these patterns illustrate how high Chl levels in Missouri reservoirs would respond to changes in TP (Fig. 5a and b).

Among samples in the 30th, 25th, and 20th percentiles in the various TP bins (Fig. 5c), the initial significant increase in Chl_{obs}:TP with TP (r $\geq$ 0.93, n = 17, TP = 5–38 μg/L) was followed by a significant decline in Chl_{obs}:TP (r $\geq$ -0.94, n = 10). This pattern indicates the yield of Chl per unit of TP is not asymptotic across all samples within the eutrophic range. For example, halving TP from 80 to 40 μg TP/L only results in a 20–35% reduction in Chl within the 20th to 30th percentiles within the cross-system pattern (Fig. 5c). This analysis suggests the response to phosphorus reduction would differ between the upper and lower half of the Chl–TP data distribution (Fig. 5).

Overall, this analysis proposes Chl_{max} and Chl_{nm} metrics for Missouri reservoirs that characterize peak algal biomass and serves as a basis to quantify controlling factors, assess seasonal patterns, and compare with lakes in other regions. The upper boundary on the cross-system Chl–TP pattern (Fig.
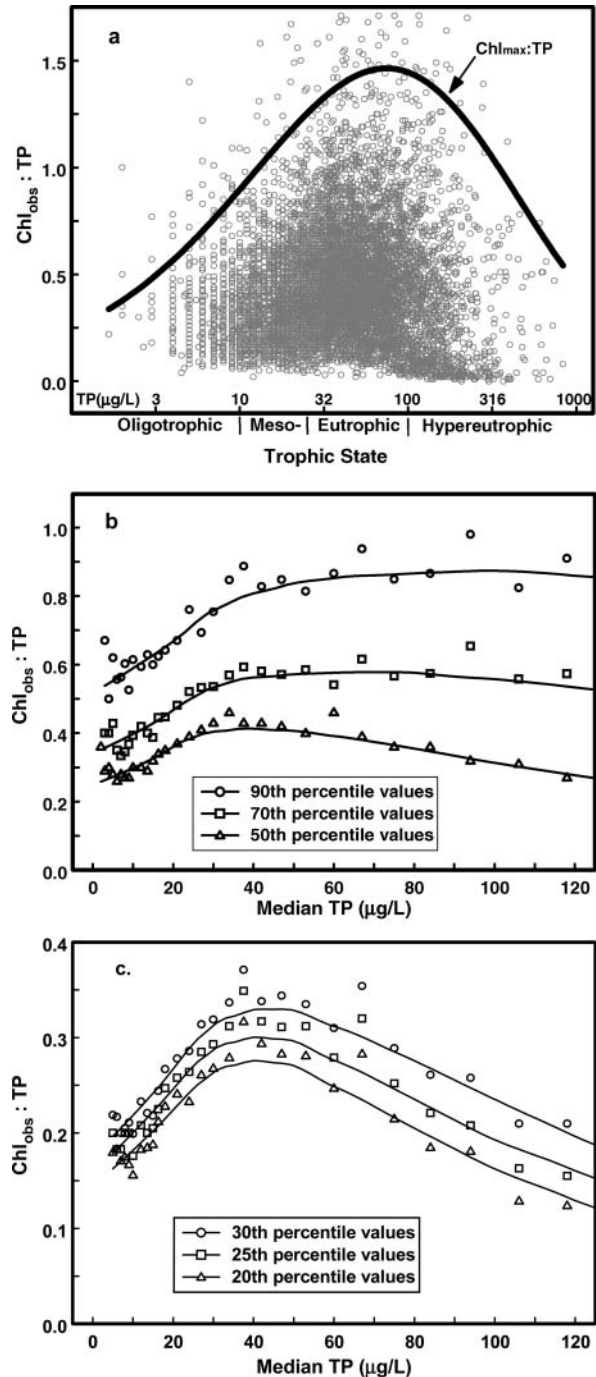

Figure 5.-Chlorophyll (Chl_{obs}) and total phosphorus (TP) data from Figure 1a were replotted in panel a as the Chl_{obs}:TP ratio against $\log_{10}TP$ with trophic state boundaries for TP (Jones et al. 2008) shown on the x-axis. The ratio of maximum chlorophyll (Chl_{max}) to TP (as calculated from equation 1 divided by the observed TP) forms a dome across the data distribution. Samples with the most extreme Chl_{obs}:TP ratios were not included. In panel b, Chl_{obs}:TP ratios for the 90th, 70th, and 50th percentile values in the TP bins used to generate equation 1 (see text) were plotted against the corresponding median TP value for each bin. In panel c, Chl_{obs}:TP ratios for the 30th, 25th, and 20th percentile values in the TP bins were plotted against the corresponding median TP value.

1) represents the general distribution in which other factors constrain responses below the maximum. Conditions of Chl_{max} and Chl_{nm} represent near-potential algal biomass for a given TP concentration (Fig. 4; Table 2) and were generally rare in summer monitoring data (Fig. 1). An important outcome is that history and frequency of high Chl events differ among individual reservoirs and suggest system-specific constraint of Chl by biotic and abiotic factors. A detailed analysis of factors that determine the degree to which Chl_{obs} is less than Chl_{max} or Chl_{nm} in individual reservoirs is beyond the scope of this note but remains a research question.

The distribution of Chl_{max}:TP ratios across the TP range has management implications. The sharp increase across the least fertile samples and the near-asymptote across the eutrophic range (Fig. 5) provide a framework for interpreting how phosphorus control will reduce Chl. Interestingly, when expressing this relationship as the rate of change in Chl per unit TP, the pattern is quite similar for Missouri reservoirs, Florida lakes, and a selection of international lakes (Fig. 2b), despite large differences in actual Chl_{max} values among the datasets (Fig. 2a). This pattern also holds for average Chl values predicted using the least squares regression based on long-term reservoir means (Jones et al. 2008, data not shown). The clear inference is that the rate of change in Chl across observed TP values applies to a broad range of lake types and is consistent with the early finding that the slope coefficient of the Chl–TP relationship differs with TP and is nonlinear (Straskraba 1980, Watson et al. 1992, Brown et al. 2000). The transition between rapid change in Chl_{max}:TP and gradually declining rate of change is near the conventional boundary between meostrophic and eutrophic conditions (30 μg TP/L; Nürnberg 1996; Fig. 2b).

Control of algal biomass and associated nuisance conditions is an objective of most lake management efforts (Bachmann et al. 2003), and this analysis furthers our understanding of these issues in Missouri reservoirs.

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