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# Relationships of total phosphorus and chlorophyll in lakes worldwide

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# Abstract

Lakes around the world are sensitive to water quality degradation and eutrophication through increases in primary production. Understanding the drivers of primary production has been a fundamental question in limnology since its early days. Here, we conducted a systematic review to develop a dataset of water chemistry and lake morphometry for 3874 lakes distributed across 47 countries around the world to answer: (1) What is the global relationship between chlorophyll a (Chl a) and total phosphorus (TP) in lakes? (2) Are there inflection points at which the TP-Chl a relationship is no longer linear? and (3) What explains the inflection points and nonlinearities in the TP-Chl a relationship? We found that a sigmoidal relationship between TP and Chl a explained 44% of the variation. We also found physical characteristics of the lake mediated the TP-Chl a relationship such as mean depth, Secchi depth, and elevation. The nonlinear segments of this relationship best described lakes located in very cold (mean annual temperature =  $-10^{\circ}$ C) and hot (> 25°C) climates, which also dominated the high and low ends of TP concentrations, respectively. A positive linear TP-Chl a relationship existed at intermediate concentrations of TP (0.004–0.23 mg L<sup>-1</sup>). A high degree of variability in Chl a exists between lakes at similar TP levels, highlighting the difficulty in simply decreasing nutrient inputs to manage eutrophication in lakes worldwide. Moreover, as global temperatures continue to rise, the Chl a-TP relationship in lakes located in very cold or warm temperate regions of the world may shift in response to these warmer temperatures.

Primary production is a foundation of aquatic ecosystem function, and understanding influences on phytoplankton biomass and growth is among the most fundamental questions in limnology. Resource limitation theory has been applied to identify the factors most limiting to phytoplankton growth and biomass (Redfield 1934; Elser et al. 2007), allowing empirical relationships to be developed and mechanisms to be explored (Gruber and Deutsch 2014; Yuan and Jones 2020). Phosphorus is widely considered to be the primary limiting factor of phytoplankton growth and chlorophyll concentration in lakes (Sterner 2008; Xu et al. 2010; Jin et al. 2020), and its relationship with chlorophyll (Fee 1979) allows total phosphorus (TP) to be used to determine lake trophic state. Thus, eutrophication is typically regulated by managing TP loading with the goal of improving water quality. However, this paradigm is being challenged for lakes undergoing both extreme eutrophication (Paerl et al. 2019) and oligotrophication (Huser et al. 2018), particularly under changing climates. Understanding the role of phosphorus is particularly important given current environmental change and declines in water quality associated with increases in eutrophication, algal blooms (Ho et al. 2019), and cyanotoxins (Paerl et al. 2019).

The controls of lake productivity have been explored by limnologists since the earliest days of the discipline (Birge and Juday 1922; Deevey 1940). Historically, empirical models of chlorophyll *a* (Chl *a*) were obtained from linear regression models with epilimnetic ice-free season TP as the predictor variable, with the relationship following a linear pattern in a log–log regression model (Dillon and Rigler 1974; Jones and Bachmann 1976; Nürnberg 1996; Havens and Nürnberg 2004). Linear relationships have been widely found in regional studies and at intermediate phosphorus concentrations (Deevey 1940; Dillon and Rigler 1974; Zou et al. 2020).

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Additional Supporting Information may be found in the online version of this article.

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However, as the range in phosphorus becomes greater, the relationship to Chl *a* becomes sigmoidal (McCauley et al. 1989; Chow-Fraser et al. 1994; Brown et al. 2000; Filstrup et al. 2014). At low concentrations of TP, lags (i.e., asymptotes) in Chl *a* values have been found in ultra-oligotrophic lakes, which is potentially due to large proportions of TP being biologically unavailable (Chow-Fraser et al. 1994; Kärcher et al. 2020). At high concentrations of TP, chlorophyll plateaus as limitation from other nutrients begins to occur when phosphorus availability is high (Søndergaard et al. 2017; Filstrup and Downing 2017). The strength of the TP–Chl *a* relationship also may vary with latitude, with weaker relationships in tropical lakes relative to temperate ones (Abell et al. 2012).

Variability in the TP-Chl *a* relationship is influenced by a variety of morphological and ecological factors. In addition to phosphorus, nitrogen is sometimes a limiting nutrient for algal growth in lakes (Guildford and Hecky 2000; Jones et al. 2008), and incorporating nitrogen into the TP-Chl a model better explains productivity (McCauley et al. 1989; Prairie et al. 1989; Søndergaard et al. 2017; Filstrup and Downing 2017). Other factors include lake depth and thermal regime. For example, shallow, polymictic lakes tend to have higher algal productivity compared to deep, stratified lakes of comparable trophic status (Riley and Prepas 1985; Havens and Nürnberg 2004). This is because of processes such as elevated nutrient levels due to sediment resuspension (Qin et al. 2020; Zhang et al. 2020) and shifts between alternative stable states (Beisner et al. 2003), which are more prevalent in shallow lakes. The TP-Chl a relationship is also mediated by zooplankton communities heavily grazing on algal populations (Fonseca Da Silva et al. 2019; Kunzmann et al. 2019; Pomati et al. 2020), high salinity levels limiting P bioavailability (Evans and Prepas 1997; McGowan et al. 2020), lower algal utilization of P in acidic conditions (Jansson et al. 1986; Gerson et al. 2016), variability in dissolved organic carbon (DOC) concentrations changing water clarity and algal productivity (Carpenter et al. 1998; Brothers et al. 2014), and landscape characteristics, such as pasture and wetlands (Wagner et al. 2011; Filstrup et al. 2014). The TP-Chl a relationship is thus complex and predicting patterns over time or space requires exploration of these co-occurring mechanisms.

Although a sigmoidal relationship between TP and Chl *a* would be predicted for lakes worldwide (McCauley et al. 1989; Abell et al. 2012), it is still unclear at which points the linear relationship breaks down for both high and low concentrations of TP and how climatic and lake morphological factors mediate the TP–Chl *a* relationship. We used a dataset of 3874 lakes distributed in 47 countries across a variety of lake typologies in diverse regions to determine the nature of the annually resolved TP–Chl *a* relationship at the global scale. In addition, we explored which variables influence the TP–Chl *a* relationship, taking into consideration landscape (elevation, watershed area) and lake morphometric characteristics (volume, depth, surface area, residence time) as well as water clarity (Secchi depth), nutrient limitation (total nitrogen [TN]), and air temperature. We addressed the following questions: (1) What is the global relationship between

Chl *a* and TP in lakes? (2) Are there inflection points at which the TP–Chl *a* relationship is no longer linear? and (3) What explains the inflection points and nonlinearities in the TP–Chl *a* relationship? Our analyses provide additional insights into the important variables that mediate the response of Chl *a* to TP at a global scale, providing information that could be helpful to policy-makers and resource managers. Our study provides a statistically rigorous assessment of the global Chl *a*–TP relationship by using annually resolved surveys and worldwide data across diverse lake typologies that have large ranges in Chl *a* and TP.

# Methods

# Data acquisition

We conducted a systematic literature review to acquire Chl a data from the primary literature. We screened 3322 publications in Web of Science between the years 2000 and 2018 using the search terms "chlorophyll" and "lake\*" and exhaustively searched online data repositories that contained lake Chl a and TP measurements on Dryad (https://datadryad.org/), KnB (https://knb.ecoinformatics.org/), and Google Dataset Search (https://toolbox.google.com/datasetsearch). The chemical and physical characteristics of lakes (e.g., surface area, shoreline length, pH) were expected to have a significant effect on both Chl a and TP concentrations. When possible, we extracted information that the authors reported about the chemical and physical characteristics of the lake including: Chl a, TP, TN, DOC, dissolved oxygen, pH, surface area, volume, maximum lake depth, mean lake depth, and Secchi depth. However, these data were reported inconsistently and, for some variables, were reported infrequently. To supplement the data reported by authors we extracted additional lake characteristics using the HydroLAKES database (https://www.hydrosheds.org/), such as maximum and mean lake depth, elevation, surface area, water residence time, length of shoreline, and area of watershed. HydroLAKES is a global database of lake characteristics that were measured using high-resolution mapping for lakes that are at least 10 ha in surface area (Messager et al. 2016). We acknowledge the unavoidable limitation of only acquiring morphometric characteristics for lakes that have HydroLAKES data in our dataset, however future studies incorporating all physical and chemical variables for lakes analyzed, regardless of the lakes surface area, would further increase our understanding of lake dynamics. All data are available in an open-access global chlorophyll and water quality database (Filazzola et al. in press).

In instances where the same lake was sampled in multiple locations, we took the median value of measured data for that lake. When a lake was sampled multiple times within the same year (e.g., monthly, weekly), we extracted data from the time when Chl *a* values were highest, assuming this represented the peak of the algal growing season. If a lake was sampled over multiple years, we selected data from the most recent year because it most closely resembles the current status of Quinlan et al.

that lake. Chl *a* and TP data consisted of either surface water samples or integrated water samples (Filazzola et al. in press). Chl *a* values of 0 mg L<sup>-1</sup> were excluded from the study owing to their disproportionate influence on the analyses (n = 93 lakes) and Chl *a* values of less than 0.0001 mg L<sup>-1</sup> (n = 7) were rounded to a value of 0.0001 mg L<sup>-1</sup> ( $= 0.1 \mu$ g L<sup>-1</sup>) as this is typically the analytical limit of Chl *a* detection using laboratory methods. The Laurentian Great Lakes were also excluded because of significant spatial heterogeneity in water quality due to their large size. For the purpose of this study, we reduced the data to a subset of lakes where both TP (mg L<sup>-1</sup>) and Chl *a* (mg L<sup>-1</sup>) were

measured. The final dataset used for all analyses had 3874 unique lakes distributed globally (Fig. 1).

While this dataset included samples collected with a variety of methodologies, we do not anticipate that the international multi-jurisdictional nature of the data will influence analyses, as Hanna and Peters (1991) showed that differences in protocol and sampling depth for TP and Chl *a* did not add variation to TP–Chl *a* response models. We did not differentiate between natural and artificial lakes as Canfield and Bachmann (1981) found that TP–Chl *a* relationships did not differ with lake type in a large-scale survey of 704 natural and artificial lakes.



**Fig 1.** Maps showing lake locations for which chlorophyll and water chemistry (particularly total phosphorus) were compiled in the world; inset figure: a close up of the midwestern and northeastern United States and southern central and eastern Canada. Lake Chl *a* concentrations are indicated on a log scale from 0.0001 to 1 mg  $L^{-1}$ .

**Table 1.** The relationship between select lake characteristics and the residuals of a linear TP–Chl a model. The number of lakes included in each comparison is reported. We also reported the model outputs from a linear fit between the lake characteristics and the residuals (*p*-value,  $R^2$  of model). Significance in these models indicates that the lake characteristic is contributing to a departure from linearity in the TP–Chl a relationship.

Lake characteristic	$\mathbf{Mean} \pm \mathbf{SE}$	Range	<i>n</i> -lakes	<i>p</i> -value	R <sup>2</sup>
Total nitrogen (mg $L^{-1}$ )	0.941 ± 0.025	0.013–9.70	1777	<0.001	0.036
Secchi (m)	$\textbf{2.58} \pm \textbf{0.08}$	0.01–61	1232	<0.001	0.050
Elevation (m a. s. l.)	$\textbf{303.4} \pm \textbf{6.5}$	-5.0 to 3392.0	2458	0.011	0.002
Lake volume (0.001 km <sup>3</sup> )	$\textbf{286.8} \pm \textbf{70.8}$	0.13–10 <sup>5</sup>	2458	0.052	0.001
Maximum depth (m)	$10.80\pm0.21$	0.50-122.0	2163	<0.001	0.015
Mean depth (m)	$6.68\pm0.20$	0.31-258.9	2782	<0.001	0.027
Lake surface area (km <sup>2</sup> )	$13.27\pm3.12$	0.0001-7833.0	3255	0.20	0.001
Area of watershed (km <sup>2</sup> )	$1234.6\pm246.2$	$0.10-4.6 \times 10^{5}$	2457	0.088	0.003
Water residence time (days)	$675.2 \pm 69.4$	$0.10 - 1.3 \times 10^{5}$	2453	0.36	0.001

#### Climate variables and zones

We categorized lakes based on broad climate zones including the tropics, Arctic-alpine, and temperate-arid. These categories were defined as follows: "tropics" were lakes located at latitudes between 23.6°S and 23.6°N, "Arctic-alpine" were lakes outside the tropics and with a mean air temperature in the hottest month less than 10°C (which approximately demarcates tree line in the northern hemisphere; D'Odorico et al. 2013), and "temperate-arid" were all remaining lakes. We grouped temperate and arid because potential evapotranspiration data were unavailable for most lakes, which did not permit for a reliable classification of lakes as "arid." The mean annual air temperature and temperature during the hottest month were extracted using the GPS coordinates of each lake



**Fig 2.** The relationship of TP (log transformed mg L<sup>-1</sup>) with Chl *a* concentrations (log transformed mg L<sup>-1</sup>). Solid line represents mean model fitted with GAM (panel A;  $R^2 = 0.44$ ; p < 0.001) and segmented regression (panel B;  $R^2 = 0.44$ ; p < 0.001). Breakpoints of segmented regression are -1.85 (0.0141 mg L<sup>-1</sup>) and -1.01 (0.0977 mg L<sup>-1</sup>). Dashed line represents the Redfield intercept where the mean model fit from Fig. 2 intercepts the molar ratio of TN: TP (TN: TP = 16: 1). Symbols correspond with the regional environment of each lake including Arctic and alpine (squares), temperate and arid (circles), and tropics (triangles) (n = 3874 lakes).

and datasets from the Climatic Research Unit (CRU) gridded Time Series (CRU TS v4; Harris et al. 2020). We extracted temperature variables for the same year that the chlorophyll variables were measured in the literature that was reviewed.

#### Data analyses

We used generalized additive models (GAMs) and segmented regression to model the TP-Chl a relationship. The GAM was fitted with log-transformed TP as the predictor variable and log-transformed Chl a as the response variable. GAMs allow nonlinear relationships to be fit between predictor and response variables using smooth functions (Wood 2017). We hypothesized a priori that a sigmoidal relationship (i.e., with a lower and upper asymptote in the model) may best explain the relationship between TP and Chl *a* as this relationship is expected to be weak both above the "Redfield intercept" (Supplementary S1), where TP is no longer limiting productivity and weak below a lower threshold where a large proportion of TP may be biologically unavailable. We compared the amount of variation explained by the  $3^{rd}$  order polynomial (k = 4) to a  $2^{nd}$  order polynomial (k = 3), and simple linear fits, using an ANOVA on the residual sum of squares from each model (function *anova*, package *stats*) to determine if more complex models had significantly (p < 0.05) improved model fit to observed values. We used a GAM (function gam, R package mgcv) fit to a Gaussian distribution, an identity link function, and a specified smoothing penalty k that approximates a  $3^{rd}$ order polynomial (i.e., k = 4). To identify specific inflection points where the relationship of TP and Chl a changes, we

conducted a segmented regression model (function *segmented*, package *segmented*) (Vito and Muggeo 2008) with TP as the predictor variable and Chl *a* as the response variable, and set the maximum number of breakpoints at two to approximate a sigmoidal response. Finally, we compared the amount of variation explained by the segmented regression and GAM using an ANOVA on the residual sum of squares.

We identified the threshold where average phosphorus concentration exceeded the Redfield ratio (i.e., a stoichiometric ratio of 16: 1 nitrogen to phosphorus), using the point along the TP gradient where the mean model fit between TN: TP and TP intercepted the Redfield ratio (-0.6438 [logTP] or 0.227 mg L<sup>-1</sup>; Supplementary S1). The fitted model value at the Redfield threshold (hereafter, Redfield intercept) was used to interpret subsequent TP and Chl *a* relationships as the point along the P gradient above which P is more likely no longer limiting algal primary productivity, with potential N-limitation or co-limitation with N due to nutrient stoichiometry (Supplementary S1 and S2).

To test if select lake characteristics such as morphometry and water clarity influenced the relationship between TP and Chl a, we fitted a log–log linear model with TP as the predictor variable and Chl a as the response variable. We then tested each of the lake characteristics acquired from the HydroLAKES dataset against the residuals from the linear model using a GAM approach. This analysis was used to identify any significant relationship between that lake characteristic gradient and linear model residuals, which may indicate that the lake characteristic influences the TP–Chl a relationship such that it



**Fig 3.** The distribution of mean annual temperatures (°C) associated with each lake and survey year separated by the TP–Chl *a* relationship identified from the segmented regression. Low TP lakes with a weak TP–Chl *a* relationship had on average lower mean annual temperatures with many observations below  $-5^{\circ}$ C. High TP lakes with no apparent TP–Chl *a* relationship had on average higher mean annual temperatures and included the only lakes with extremely warm (> 25°C) temperatures. Lakes with intermediate TP values that had a linear relationship with Chl *a* had a broad temperature values, but the majority were observed between  $-5^{\circ}$ C and  $25^{\circ}$ C.

deviates from a simple linear model. We compared each lake morphometric and chemistry variable in separate models against the residuals of the TP–Chl *a* relationship because there was inconsistent overlap in reporting of variables; a multivariate approach to include all of the nine variables we intended on testing would have resulted in only a small subset



**Fig 4.** Pattern of TP–Chl *a* model residuals along gradients of lake morphology, watershed characteristics, water clarity and total nitrogen. Residuals of the TP–Chl *a* model are from a linear log–log model. All variables are fitted to a linear model on the residuals. Model statistics can be found in Table 1.

of contiguous observations being usable (n < 30). Therefore, each single-variable model was fitted independently to maximize the number of lakes that could be included.

# Results

We obtained Chl *a* and TP concentrations for 3874 sites distributed across 47 countries and on every continent except Antarctica, but were most frequently found in North America (Fig. 1). Across all lakes, the mean  $\pm$  SE of Chl *a* concentrations was  $19.0 \pm 0.73 \ \mu g \ L^{-1}$  and the mean  $\pm$  SE of TP concentrations was  $62.3 \pm 2.35 \ \mu g \ L^{-1}$ . A subset of 1777 lakes also had measurements of TN and the mean  $\pm$  SE of TN concentrations was  $940.8 \pm 25.5 \ \mu g \ L^{-1}$  (Table 1).

A general additive model (GAM) with a sigmoidal relationship was the most parsimonious relationship between Chl *a* and TP explaining 44% of the variation ( $F_{3873} = 1009$ , p < 0.001; Fig. 2). A global simple linear model between TP and Chl *a* in freshwater lakes ( $F_{3872} = 2875$ , p < 0.001,  $R^2 = 0.426$ ) was significant, but both the GAM and segmented regression each explained significantly higher variation relative to the simple linear model (p < 0.001). The global linear model also had a higher AIC value (AIC = 4757.1) relative to the sigmoidal model (AIC = 4672.9). The model exhibited a positive linear relationship between TP and Chl a at intermediate concentrations of TP ( $0.004-0.23 \text{ mg L}^{-1}$ ). Nonlinearities appear below the inflection points of -2.4 logTP  $(0.004 \text{ mg L}^{-1})$  and above -0.64 logTP  $(0.229 \text{ mg L}^{-1})$ . It was these inflection points that contributed to the sigmoidal relationship being a better predictor relative to a linear model. Lakes above the Redfield intercept (TN: TP < 16) appeared to have no relationship between TP and Chl a (Pearson correlation TN:  $TP_{(<16)} \sim Chl a = 0.12$ ; Supplementary S1).

A segmented regression model identified breakpoint phosphorus values that significantly deviated from a simple linear relationship with Chl *a* at phosphorus values of  $-1.85 \log TP$  (0.014 mg L<sup>-1</sup>) and  $-1.01 \log TP$  (0.098 mg L<sup>-1</sup>) (Fig. 2B). The identified breakpoint at high TP values was considerably different from the Redfield intercept (breakpoint = 0.098 mg L<sup>-1</sup>) vs. ratio model threshold = 0.227 mg L<sup>-1</sup>). Both the GAM model and the segmented regression had nearly equivalent predictability in model fit when comparing differences in the residual sum of squares (p = 0.041) and explained variation (GAM  $R^2 = 0.439$ ; segmented regression  $R^2 = 0.439$ ); given the nearly identical explained variation we explored both model approaches.

Lakes from Arctic and alpine systems were a substantial portion of the observations found at low concentrations of TP below the inflection point of the sigmoidal relationship at 0.004 mg L<sup>-1</sup> (27 of 59 lakes). Conversely, tropical lakes in our dataset had high TP concentrations and had low Chl *a* relative to TP, and were predominantly above the TP inflection point of 0.23 mg L<sup>-1</sup>. This sigmoidal relationship was still present and significant when excluding these cold and warm

environments (Supplementary S3). In support of our climate zones, we found that mean annual air temperature (°C) separated the lakes into groups based on the TP–Chl *a* relationship (Fig. 3). Lakes in very cold regions (mean annual temperature <  $-5^{\circ}$ C) had a weak TP–Chl *a* relationship (Fig. 3). Lakes in hot regions (mean annual temperature >  $25^{\circ}$ C) also exhibited a weak TP–Chl *a* relationship (Fig. 3). Lakes found in temperate regions with moderate temperature ranges between  $-5^{\circ}$ C and  $25^{\circ}$ C were the lakes categorized as having a linear relationship between TP and Chl *a* (Fig. 3).

We compared the residuals of a simple linear model to morphometric and chemical gradients to determine which environmental gradients may influence the TP-Chl a relationship in a nonlinear fashion (Fig. 4). Results for TN and water clarity (as Secchi depth) indicated that they had a significant influence on the linearity of the TP-Chl a models and explained an additional 8.6% of the variation in the TP-Chl a relationship (Table 1; Fig. 4). The physical and watershed characteristics of lakes explained an additional 5.0% of the variation in the residuals of the TP-Chl a relationship. Maximum depth, mean depth, lake volume, shoreline length, and watershed area were significantly related to the TP-Chl a residuals (Table 1; Fig. 4). Water residence time and lake elevation did not have a significant relationship with residuals from the TP-Chl a model (Table 1; Fig. 4), suggesting that they did not add significant additional variation to the TP-Chl *a* relationship.

## Discussion

In this study, we tested a fundamental relationship between TP and Chl *a* using a global dataset of freshwater lakes. We found that a sigmoidal relationship between TP and Chl *a* holds for nearly 3900 lakes distributed around the world with diverse morphometric and water chemistry conditions. Our analysis revealed that linear relationships best represent the TP–Chl *a* relationship at intermediate concentrations of TP (0.014–0.098 mg L<sup>-1</sup>), but nonlinear relationships were evident at low and high TP concentrations. We found for the first time that the Chl *a*–TP relationship became weak at temperature extremes, where Arctic and alpine lakes tended to be at the low end of the sigmoidal relationship and tropical lakes were at the high end. The high degree of variation between lakes in the TP–Chl *a* relationship further highlights the challenge of managing freshwater systems for eutrophication.

#### Sigmoidal relationship between TP and Chl a

Using this extensive global dataset of TP and Chl *a*, we found that a sigmoidal relationship was the most parsimonious relationship explaining 44% of the variation in our global dataset of lakes. Multiple mechanisms have been suggested to explain this sigmoidal TP–Chl *a* relationship, including low phosphorus bioavailability in oligotrophic conditions (Chow-Fraser et al. 1994; Filstrup and Downing 2017), and nitrogen

limitation, or co-limitation, at high TP concentrations (Guildford and Hecky 2000; Xu et al. 2010; Bracken et al. 2015). Without detailed information on the composition of the TP data in our analyses, we were unable to test if low phosphorus bioavailability explained an asymptotic TP-Chl a relationship at low TP concentrations. We did note that many of the lakes with low phosphorus concentrations in our database tended to be in cold climates (e.g., Arctic and alpine), where nitrogen concentrations are also low and potentially co-limiting (average TN =  $0.382 \text{ mg L}^{-1}$  in Arctic and alpine lakes,  $0.944 \text{ mg L}^{-1}$  in arid and temperate lakes,  $2.270 \text{ mg L}^{-1}$  in tropical lakes; Supplementary S2). These unproductive lakes could have low nutrient concentrations from low nitrogen export in unvegetated watersheds in these regions (Wurtsbaugh et al. 1985; Morris and Lewis Jr 1988; Stuchlík et al. 2006), or due to lower rates of algal production at colder water temperatures (Butterwick et al. 2005) with a shorter icefree growing season (Whiteford et al. 2016). These findings support a recent study that alpine lakes have nonlinear patterns in Chl a and TP along an elevation gradient (Kärcher et al. 2020). At high TP concentrations representing hypereutrophic conditions, with high algal productivity and biomass, further TP increases may not result in further increases in Chl a concentrations because light limitations due to shading from dense algal blooms (Agusti et al. 1990; Brothers et al. 2014). Additionally, tropical lakes in monsoon zones may have lower Chl a yields per unit TP due to the much lower water residence time of these lakes during the rainy monsoon season (An and Park 2002). It is important to note that hypereutrophic conditions may still be phosphoruslimited when TN concentrations are also high, particularly in agricultural systems, where nutrients from runoff are rich in highly bioavailable nitrogen (e.g., fertilizers and manure) (Liu et al. 2020). Finally, at intermediate concentrations of TP and temperatures on a global scale, our findings demonstrate that the Chl a-TP relationship was best described as a positive linear relationship. Although influences of Chl a are dependent on numerous factors, such as climate processes (Rigosi al. 2014; Michalak 2016), community composition et (Kamarainen et al. 2008), nutrient concentrations (Bracken et al. 2015), and land use and land cover (Filstrup et al. 2014), our model identifies TP as the best predictor variable with average TP concentrations ranging between 0.004 and  $0.23 \text{ mg L}^{-1}$ . Therefore, identifying the cause of TP variation in lakes at intermediate levels may improve our ability to anticipate water quality conditions.

Our global sigmoidal relationship between TP and Chl *a* converges with the nutrient limitation paradigm based on the Redfield ratio. The upper breakpoint in the TP–Chl *a* model, using a GAM approach, was remarkably similar to the "Redfield intercept" (0.229 vs. 0.227 mg L<sup>-1</sup> TP, respectively), indicating that nitrogen limitation may be driving the asymptotic relationship at higher TP concentrations. Many of the tropical lakes in our dataset had low Chl *a* values relative

to TP concentrations, although nearly all had TP levels at hypereutrophic conditions (> 0.1 mg L<sup>-1</sup>), suggesting that there may be nitrogen limitation in these productive lakes possibly due to high rates of nitrogen loss via denitrification at warm water temperatures (Lewis 2002). We observed breakpoints similar to those of previous studies, with two asymptotes or breakpoints in the TP–Chl *a* relationship, the first occurring slightly above the transition from ultraoligotrophic to oligotrophic conditions (TP = 0.001) and the second occurring slightly below the transition from eutrophic to hypereutrophic conditions (TP = 0.1 mg L<sup>-1</sup>), which is consistent with trophic status classification gradients (Nürnberg 1996).

The choice of statistical model influences the calculation of breakpoints, making it difficult to compare breakpoints across studies. For example, McCauley et al. (1989) used a locally weighted robust sequential smoothing approach for 1041 measurements from 14 countries, while Chow-Fraser et al. (1994) used a "smoothing spline" to explain the sigmoidal relationship between TP and Chl a under different conditions across 119 Canadian lakes. Brown et al. (2000) used a third-order polynomial, similar to the GAM generated in this study, to model the TP-Chl a relationship in 316 Florida lakes. Filstrup et al. (2014) used locally weighted scatterplot smoothing (LOWESS) to examine the TP-Chl a relationship in 2105 lakes in six US states and generated numerous sigmoidal TP-Chl a models. Filstrup et al.'s (2014) sigmoidal TP-Chl a models had a lower asymptote at 0.01 mg  $L^{-1}$  TP, and several regional models with upper asymptotes at 0.1 mg  $L^{-1}$ TP. Using locally estimated scatterplot smoothing, Phillips et al. (2008) showed an upper asymptote of 0.1 mg  $L^{-1}$  TP in 1129 European lakes. Even within our own study's results the placement of asymptotes in the TP-Chl a relationship differed between the GAM and segmented regression models, indicating that choice of statistical methodology generates variability in the calculation of breakpoints and asymptotes. The location of the breakpoints was generally consistent with transitions between the trophic groups involving the oligotrophicmesotrophic boundary and the eutrophic-hypereutrophic boundary.

# Lake chemistry, morphometry, and temperature effects on TP–Chl *a* relationship

The relationship of lake nutrient concentrations with algal productivity is mediated by lake characteristics including its water chemistry, morphometry, and temperature. We interpreted both low and high TP lakes to be limited by nitrogen, although high TP lakes can also be light-limited. Water clarity explained an additional 5% of variation in the TP–Chl *a* relationship. We observed more negative residuals in clearer waters, indicating lower Chl *a* per unit TP. This may reflect that lakes with clearer water have less dense algal populations and conversely lakes with lower water transparency have denser concentrations of algae. However, it may also indicate that in clearer surface waters, pelagic phytoplankton may have

lower cell concentrations of chlorophyll because of higher light irradiance (Felip and Catalan 2000). Although previous studies have demonstrated that landscape-scale factors act as an important driver in determining Chl a concentrations (Riera et al. 2000; Martin and Soranno 2006; Zou et al. 2020), lake water residence time did not explain additional variation in the TP-Chl a relationship in our study. Lakes which have shorter water residence times, generally connected to a stream or river and undergo a "flushing effect," yield lower Chl a concentrations compared to isolated lakes having longer water residence times (Wagner et al. 2011; Filstrup et al. 2014; Zou et al. 2020). Further, landscape position and hydrological connectivity can also influence water quality (Riera et al. 2000; Quinlan et al. 2003; Martin and Soranno 2006). Our findings suggest that although the effects of land use practices and nutrient dynamics at different scales may influence in-lake processes, TP concentrations in our study lakes were characterized by other factors.

Lake morphometry explained additional variation in the TP-Chl a relationship. Deeper lakes (measured as either mean or maximum depth) had lower Chl *a* per unit TP relative to shallower lakes (Fig. 4). The dynamics of in-lake biogeochemical processes, including TP and TN enrichment and removal, depend on factors such as input, outflow, sedimentation, and denitrification that are related to depth-dependent processes (Qin et al. 2020). In shallow lakes, greater resuspension of sediments can both increase internal loading of TP and reduce nitrogen limitation (Holmroos et al. 2012; Blottière et al. 2017). In deeper lakes, thermal stratification allows residual phosphorus in non-metabolized particles to settle at the bottom of the lake and is associated with lower Chl *a* relative to polymictic lakes with equivalent TP concentrations (Riley and Prepas 1985; Qin et al. 2020). Lake surface area did not explain any substantive additional variation in the TP-Chl *a* relationship, highlighting that lakes of different sizes greater than 100 ha, but similar depth profiles, will respond similarly to changes in TP. These results contrast a dataset of several remote Canadian lakes, where Guildford et al. (1994) indicated that there was greater P-limitation in small lakes compared to larger lakes, possibly due to more stable thermoclines in small lakes resulting in greater nutrient retention. Ultimately, lake depth relative to lake surface area affects the degree of stratification, which is probably the more proximal factor influencing the TP–Chl *a* relationship.

There are additional intra-lake factors influencing TP–Chl *a* highlighted in previous literature that we were not able to explore in this study. For example, we were unable to test the effect of pH on the TP–Chl *a* relationship as our dataset had too few pH data points for a meaningful analysis on a global dataset. Lakes that are more acidic tend to be limited in their Chl *a* production because of decreased bioavailability of phosphorus (Vyhnálek and Kopáček 1994) and impairment of algal utilization of phosphorus (Jansson et al. 1986). While there were too few data points to examine the global relationship

between DOC concentrations and the TP-Chl a relationship, as higher DOC may inhibit algal productivity due to shading effects (Carpenter et al. 1998), we were able to examine the effect of water clarity via Secchi depth. In addition, extensive macrophyte cover in some shallower lakes can also reduce Chl a due to competition for nutrients with phytoplankton, reduction in sediment resuspension, and increased sedimentation of phytoplankton due to reduction in wave turbulence by macrophyte beds (Canfield Jr. et al. 1984; Zhu et al. 2015). We did not have information on dominant grazer communities in study lakes, as lakes whose zooplankton community is dominated by large herbivores have significantly lower Chl a yield compared to lakes with similar TP that were dominated by small herbivores (Mazumder and Havens 1998). We also did not have information on algal community composition in study lakes, as algal species differ in their Chl a: carbon ratio (i.e., amount of photosynthetic pigment per unit algal biomass)(Riemann et al. 1989). These various phenomena add variability to the TP-Chl a relationship, and comprise a portion of the unexplained variation that was not explained by TN, lake morphometry and water clarity.

We note a remarkable temperature pattern in our study where the TP-Chl a relationship in cold and hot lakes corresponded to the asymptotic portions of the sigmoidal global TP-Chl a model (i.e., where there was a weak or no relationship between TP and Chl a). The asymptotic pattern occurred for 54 of 65 lakes where the mean annual air temperature was colder than -5°C and 52 of 54 lakes located where MAT was warmer than 25°C. This suggests strong temperature controls in the TP-Chl a relationship at the extremes of annual temperature, overriding lake-specific characteristics such as lake chemistry, morphmetry, and concentrations of other potentially limiting nutrients. As all segments of the sigmoidal TP-Chl a model were well-represented within intermediate temperatures (-5°C and 25°C), this suggests that, in these climate regions, lake- and watershed-specific characteristics dominate over temperature controls on the TP-Chl a relationship. Temperature controls on the TP-Chl a relationship may have substantial implications on future Chl a concentrations in lakes located in Arctic and alpine regions and warm temperate regions that are expected to continue to warm into the future such that they will cross mean annual temperature thresholds of -5°C and 25°C.

# Management implications

Understanding the relationship between TP and Chl *a* is important for making decisions regarding the management of water quality in lakes. In particular, understanding the range of phosphorus levels where the TP–Chl *a* relationship is linear and where this breaks down is important for setting goals and expectations surrounding phosphorus management. For example, in lakes with extremely high TP (> 0.227 mg L<sup>-1</sup>), efforts to reduce TP will have little effect on Chl *a* levels until the phosphorus levels are reduced below the upper inflection point in the sigmoidal relationship (McCauley et al. 1989). In these cases, it may be more economical to reduce nitrogen, rather than undertake large reductions in P input (McCauley et al. 1989). Similarly, at low TP concentrations (< 0.001 mg L<sup>-1</sup>), micronutrients, nitrogen, and (cold) temperature may be better predictors of water quality. Therefore, an understanding of where a particular lake lies on the TP continuum can provide insight into the most efficient and effective management strategies.

Our study also demonstrated that several variables mediate the relationship between TP and Chl a. For example, deeper lakes tended to have lower Chl a than would be predicted based on the overall TP-Chl a relationship, while lakes with higher TN tended to have higher Chl *a* levels than predicted. Appreciating the contributions of variables other than TP to Chl *a* concentrations could be important to managers as they develop plans to improve water quality in systems with varying nitrogen loads and morphometry. We also found that the asymptotic segments of the TP-Chl a relationship strongly corresponded with temperature extremes in this dataset (very cold or hot regions of the world). TP management for algal blooms in temperate regions may have less efficacy in the future as temperatures warm to those equivalent to lakes with current mean annual temperatures greater than 25°C. Management of water quality via P-management will have to take into account future climate warming, where lakes in very cold regions will warm such that they switch to P-limitation, while lakes in warm temperate regions will switch to N-limitation or co-limitation as they warm to hot temperatures. Previous studies show that additional variables not considered in this study, such as land use and latitude, can also influence the relationship between TP and Chl a (Wagner et al. 2011; Abell et al. 2012; Filstrup et al. 2014). Taken together, this information suggests that models developed for use in management should be developed with these other characteristics in mind.

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# **Conflict of interest**

None declared.

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