

LETTER

Chlorophyll–total phosphorus relationships emerge from multiscale interactions from algae to catchments

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Scientific Significance Statement

Understanding controls of lake primary productivity is imperative to tackling issues related to water quality. A common way to assess lake water quality across broad spatial scales is the relationship between chlorophyll concentration and total phosphorus (TP). However, despite continuous refinement in our understanding of the chlorophyll–TP relationship, there is still uncertainty regarding the mechanisms underpinning the variation in chlorophyll at a given TP concentration. We used a process-model that primarily focuses on biogeochemical and physiological mechanisms to infer broad shifts in algal limitation status under the shape of the chlorophyll–TP relationship and these shifts in limitation are a product of interactions among landscape, ecosystem, and algal physiologic drivers. Our work provides integrative insights that place patterns of lake primary productivity in a more general framework.

Abstract

Chlorophyll and total phosphorus (TP) concentrations are key indicators of lake water quality and the relationship between them is a common tool for assessing lake trophic status. Despite the application of the chlorophyll–TP relationship in management settings, there is still an absence of a mechanistic understanding underlying its shape. We leveraged a process-based model that focuses primarily on biogeochemical and physiological mechanisms to develop a framework that reconciles interactions between multiscale drivers of the chlorophyll–TP relationship, such as hydrologic P loads, lake shape, and algal physiology. We found that combinations of lake shape and hydrologic P load induce broad shifts in algal limitation status that underly the shape of the chlorophyll–TP relationship. Furthermore, we highlight the importance of algal traits in controlling shifts in limitation. Our framework ties key landscape and ecosystem features to biological limitation and provides a synthetic and process-based understanding of the chlorophyll–TP relationship.

A common method of assessing patterns of lake primary productivity and determining nutrient reductions to achieve water quality goals is the chlorophyll *a*–TP relationship. Indeed, the ease by which chlorophyll and TP can be measured has made

the chlorophyll–TP relationship an attractive approach to monitor, compare, and predict the trophic status of lentic systems (Yuan and Pollard 2014). Past studies agree that the chlorophyll–TP relationship is non-linear and likely emerges from shifts in algal

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limitation status with increasing TP concentrations (Sakamoto 1966; Dillon and Rigler 1974a; McCauley et al. 1989; Chow-Fraser et al. 1994; Filstrup et al. 2014; Quinlan et al. 2020). However, global observations reveal that a wide range of chlorophyll concentrations can be found among lakes with the same TP concentration and uncertainty regarding the mechanisms underpinning chlorophyll-TP relationships remains (Dillon and Rigler 1974b; Smith 1982; Chow-Fraser et al. 1994; Filstrup et al. 2014; Quinlan et al. 2020).

Over the past 50 years, multiple approaches have shaped our understanding of chlorophyll-TP relationships and what regulates lake trophic status. Vollenweider (1975) used process-based phosphorus loading models to develop theory regarding the role of lake water residence time (WRT), phosphorus (P) loads, and depth in regulating lake TP concentrations and this model was subsequently extended to predict lake chlorophyll concentrations (Sakamoto 1966; Chapra and Tarapchak 1976; Jones and Bachmann 1976; Schindler et al. 1978). Recent large comparative analyses corroborate the early theoretical work, showing that land cover and other landscape variables influence chlorophyll and TP (Filstrup et al. 2014; Read et al. 2015; Filstrup and Downing 2017; Shuvo et al. 2021). Theory and comparative work also agree on the potential role of ecosystem-scale drivers, particularly mean depth, for TP concentrations and chlorophyll-TP relationships (Vollenweider 1975; Read et al. 2015; Quinlan et al. 2020). Finally, because algal limitation status and growth underpin chlorophyll dynamics in lakes, it is plausible for algal species composition and traits to modify the shape of chlorophyll-TP relationships (Smith 1982; Straskraba 1985; Reynolds 1992). However, a paucity of algal trait or physiology data across a large number of lakes coupled with the absence of algal physiological process from models has likely precluded empirical and theoretical assessment of these expectations.

To integrate past efforts to understand the chlorophyll-TP relationship, we have constructed a process-model that primarily focuses on biogeochemical and physiological mechanisms to explore the implications of interactions among regional land use and climate, lake morphometry, and algal physiology for lake trophic status. Our model highlights intuitive heuristics that link shifts in limitation status of algae to observed chlorophyll-TP patterns (Fig. 1). From our work, we infer broad shifts in limitation under the shape and variance around the chlorophyll-TP relationship and these shifts in limitation are a product of multiscale interactions among landscape, ecosystem, and algal physiologic drivers. Our work provides integrative insights that place patterns of lake primary productivity in a more general framework, which could aid in the management, prediction, and remediation of lentic ecosystems.

Methods

To explore multiscale drivers of the chlorophyll-TP relationship, we chose a relatively simple mathematical representation

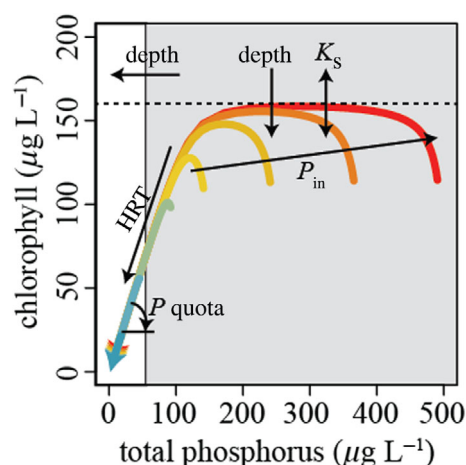


Fig. 1. A multiscale conceptual model for the relationship between chlorophyll and TP. Nonlinear chlorophyll-TP relationships are generated by interactions amongst landscape, ecosystem, and algal physiological characteristics. The concentration of phosphorus of the hydrologic loads (P_{in} ; line color) and lake WRT (increasing toward colored arrow heads) combine to dictate the expected TP concentration. Lake depth, and algal demand for light and P (K_s) determine when algae self-shading drives a shift from a P-limited state (white box) to a light-limited state (gray box) and maximum expected chlorophyll (horizontal dashed line). The TP concentration at which this shift occurs (white vs. gray box) is the inflection point where gains in chlorophyll as a function of TP begin to decelerate due to increased light limitation. Declining chlorophyll concentration at short WRT is driven by flushing of chlorophyll due to high hydrologic flows. The rate of increase in chlorophyll with increasing TP is determined by the C : P of algal biomass (P quota). The addition of nitrogen, micro-nutrient limitation, or elevated predation would drive a given lake's biomass to fall below the expected biomass depicted by the colored lines.

of a lake. The process model combined an algal physiological model (Huisman and Weissing 1994) and a lake ecosystem model similar to Vollenweider (1975). Model state variables included soluble reactive P, algal biomass, sediment phosphorus, and dissolved organic carbon (DOC), see Supporting Information Table S1 for a detailed description of model equations and parameters.

The abstract lake was cylindrical, defined by surface area and depth, and had a constant, instantaneously mixed volume. Hydrologic flows were via inlet and outlet streams and lake WRT was the quotient of lake volume and inlet discharge. Hydrologic P loads were a product of inlet discharge and P concentration. Internal P loading was modeled using the difference between the water column and sediment P concentrations. Static algal P : C and C : Chl quotas were used.

Algae can be limited by phosphorus, nitrogen, light, or herbivory. In the model, we focused on how catchment and lake variables and algal traits controlled algal growth via co-limitation by P and light. Because terrestrial DOC can influence light availability and grazing can impose top-down control on chlorophyll, we include these in our model (see Supporting Information Data S1; Beisner et al. 2003; Hall

et al. 2007; Jäger and Diehl 2014; Vasconcelos et al. 2016; Kelly et al. 2018). However, in order to focus on biogeochemical and physiological drivers of the chlorophyll-TP relationship we ignore terrestrial DOC ($C_{t=0} = C_{in} = 0$) and grazer ($g = 0$) effects for most of our model experiments.

Co-located observations of hydrologic P loads, lake morphometry, and chlorophyll and TP concentrations are not available for many lakes. Therefore, we could only calibrate our model using hydrologic P loads and lake TP concentrations (Brett and Benjamin 2008), see Supporting Information Data S1.

To make inference about the biogeochemical and physiological drivers of the chlorophyll-TP relationship, we conducted a set of systematic simulations with our calibrated model that explored gradients of P_{in} (20–500 $\mu\text{g P L}^{-1}$), WRT (10–10,000 d), and lake depth (2, 5, 10, and 20 m). We also considered algal physiologic drivers by altering algal quota (C_p ; 0.005, 0.015, 0.025 P : C) and the half-saturation constants for phosphorus (m_a ; 0.002, 0.003, 0.005 g P m^{-3}) and light (h_a ; 36, 80, 100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$). When exploring algal traits, lake depth was held constant at 10 m, but we varied P_{in} (20–500 $\mu\text{g P L}^{-1}$) and WRT (10–1e4 days).

After our systematic exploration of the sensitivity of the chlorophyll-TP relationship to multiscale drivers, we evaluated the ability of our model to recapitulate chlorophyll and TP concentrations for a large set of U.S. lakes (U.S. Environmental Protection Agency [EPA] 2016). Unfortunately, quantitative comparison of these data and our model is not possible because hydrologic and elemental loads (P_{in} and Q_{in}) are unavailable for these lakes. Instead, we asked whether our model could recreate the general shape of chlorophyll-TP observations in this large dataset. Given observed lake surface areas and depths for EPA NLA lakes sampled in 2012, we randomly assigned WRT and P_{in} concentrations to EPA NLA lakes using the observed distribution of WRT from EPA NLA lakes sampled in 2007 (Brooks et al. 2014) and the observed distribution of stream TP concentrations from the EPA's National Rivers and Stream Assessment (NRSA) conducted in 2013–2014 (U.S. EPA 2020; see Supporting Information Data S1 for details). After an initial comparison of our base model to EPA NLA chlorophyll-TP data, we tested whether including additional resource limitation and/or algal predators ($g > 0$) improved model qualitative performance. We imposed additional resource limitation via the effect of terrestrial DOC on light availability ($C_{in} > 0$, randomly assigned based on EPA NRSA data), but other work has considered nitrogen-limitation (Hall et al. 2007; Filstrup and Downing 2017). Because we do not have lake-specific WRT, P_{in} , C_{in} , and grazing rates, some simulations were run with unrealistic combinations of these drivers and generated extremely low equilibrium chlorophyll concentrations; these unrealistic lake scenarios were removed.

We ran all simulations using the lsoda algorithm implemented within the *ode* function in the R package *deSolve* (Soetaert et al. 2010). Simulations were run at daily timesteps

for 10,000 d by which time equilibrium was reached for all state variables based upon a daily percent change of less than 0.001%. We simulated our model using R version 4.1.0 (R Development Core Team 2021) and all code is available at GitHub (<https://github.com/MFEh2o/TPchloro>; Jones and Olson 2022).

Results and discussion

The goal of our modeling was to synthesize existing multiscale perspectives on biogeochemical and physiologic regulators of lake trophic status. Most past work focused on the average behavior of a large population of lakes through statistically inferred chlorophyll-TP relationships. We used a process-based simulation model that integrates landscape and ecosystem features with algal limitation and growth to extend these efforts and construct a systematic understanding of lake chlorophyll-TP relationships. Our model performed well following a two-step calibration process (Supporting Information Fig. S1) and revealed a set of useful heuristics that emerge from complex, multiscale interactions among landscape, ecosystem, and algal physiological characteristics (Fig. 1). We expect that a focus on quantitative translation of multiscale drivers to ecological process, such as algal limitation status and growth may improve opportunities for prediction of lake trophic status under future environmental change.

Shifts in limitation dictate the general shape of chlorophyll-TP relationships

Our model identifies shifting limitation status of algal growth as the proximate driver of nonlinear chlorophyll-TP relationships. Model simulations consistently reveal a linear response of chlorophyll to TP when TP concentrations are low and algal growth is strongly P-limited (Fig. 2). As P loads increase and lake TP concentrations increase, we see a shift from P-limitation to light limitation and a subsequent plateau of biomass concentrations beginning between 50 and 150 $\mu\text{g P L}^{-1}$ (Figs. 1, 2A). A shift from P to light limitation has been discussed in a number of past works but has been difficult to quantify and include in statistical assessment of chlorophyll-TP observations (Smith 1982; Straskraba 1985; Reynolds 1992; Filstrup and Downing 2017). While our model suggests light limitation from self-shading is sufficient to generate plateaus in chlorophyll with increasing TP, this does not preclude nitrogen limitation as a driver of nonlinear chlorophyll-TP relationships (McCauley et al. 1989; Filstrup and Downing 2017).

Interestingly, to reach the high end of observed TP concentrations with our model WRT becomes very short, causing hydrologic flushing to limit algae instead of P or light. This flushing of chlorophyll drives declines in chlorophyll with increasing TP for simulations with P_{in} greater than 100 $\mu\text{g P L}^{-1}$ (Fig. 2A). This decline in biomass even diminishes self-shading and light limitation at very short WRT (Fig. 2A). Streams are an extreme example of this dynamic where WRT

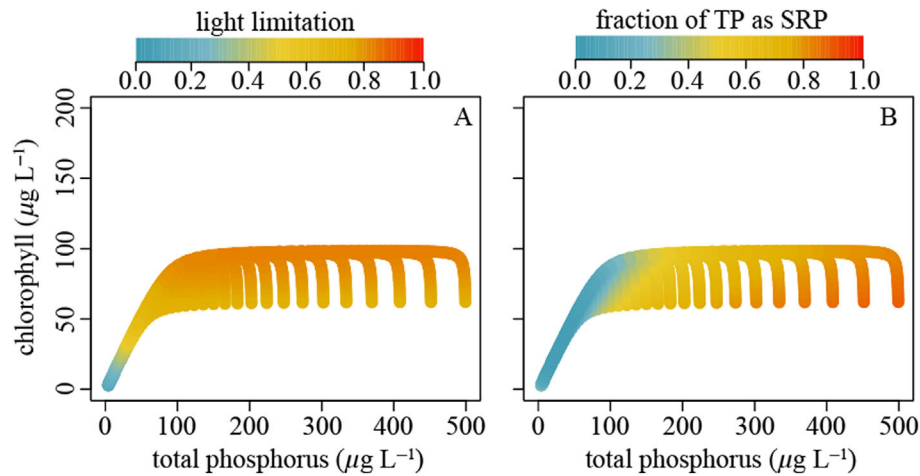


Fig. 2. Each panel depicts simulations (individual points) run at a depth of 10 m with continuous gradients of inlet phosphorus concentration (P_{in} , 20–500 $\mu\text{g P L}^{-1}$) and WRT (10–10,000 d). WRT decreases from left to right for a set of simulations with a given P_{in} . **(A)** Light limitation due to algal self-shading can drive nonlinear relationships between chlorophyll and TP. Declining chlorophyll and light limitation at short WRT are driven by flushing of chlorophyll due to high hydrologic flows. **(B)** The fraction of TP that is soluble reactive phosphorus (SRP) increases with shifts from P to light limitation.

is very short and algal biomass grows on surfaces (Vannote et al. 1980).

A secondary indicator of a shift to light or flushing limitation is the increased contribution of dissolved P to TP concentrations (Fig. 2B). Algal biomass is a large portion of TP under P-limited conditions because dissolved P entering the lake is rapidly sequestered by algae. However, dissolved P supply outpaces its demand under light or flushing limitation and dissolved P accumulates becoming an increasingly important contributor to TP concentrations. This is consistent with work that found dissolved P to dominate in highly flushed systems such as streams while algal P dominates in P-limited lakes (Champion and Currie 2000; Essington and Carpenter 2000).

A multitude of chlorophyll–TP relationships emerge from drivers interacting across scale

Our model extends past work to show that multiscale interactions among landscape, ecosystem, and algal physiological characteristics modify the expected non-linear shape of the chlorophyll–TP relationship. We used factorial simulations along gradients of P_{in} , WRT, lake depth, and algal traits to understand how these multiscale drivers interact to cause shifts in limitation status of algal growth and dictate the expected shape of the chlorophyll–TP relationship (Fig. 1).

Interactions between a lake’s catchment and morphometry are known to determine TP concentration, but they also dictate the expected chlorophyll at a given TP concentration via their effect on the limitation status of algae (Fig. 3). Catchment size, precipitation, and land use, dictate inlet discharge (Q_{in}) and P concentrations (P_{in}). In turn, Q_{in} interacts with lake volume to determine lake WRT. Regardless of whether P_{in} is low or high, long WRT lakes will have low TP concentrations because of low rates of P renewal and high loss of algal P

to lake sediments via sinking (Fig. 3A,B). Interestingly, these dynamics lead to a breakdown in the expected positive correlation between P_{in} and TP (Supporting Information Fig. S2, Schindler et al. 1978). Thus, long WRT lakes would be consistently nutrient-limited yielding low chlorophyll concentrations (Fig. 3B,D). In contrast, short WRT lakes can generate a variety of chlorophyll and TP concentrations primarily depending on P_{in} concentration (Fig. 3A,B). Algae in these lakes are less P-limited and reach higher chlorophyll concentrations (Fig. 3D). Although algal losses due to flushing can be high in short WRT lakes, this algal P is quickly replaced via hydrologic renewal of dissolved P. Catchment and lake morphometry also controlled the delivery of P to lake sediments and the magnitude of internal loading of P. Our model generated internal loading estimates ($0.42\text{--}103\text{ mg P m}^{-2}\text{ d}^{-1}$) were highest in simulations with high P_{in} and shallow depths and comparable to observations (Supporting Information Fig. S3; Søndergaard et al. 1999; Orihel et al. 2017). The complex balance between P fluxes mediated by WRT and morphometry will exacerbate or reduce P limitation at a given TP concentration and lead to changes in the expected shape of the chlorophyll–TP relationship (Figs. 2, 3).

The importance of WRT in regulating lake trophic status is one point where theory and comparative work seem to disagree. The role of WRT for phosphorus retention is central to past theoretical work (Vollenweider 1975; Brett and Benjamin 2008). In contrast, measures of WRT or proxies such as drainage ratio are rarely included in statistical models of chlorophyll, lake TP, or chlorophyll–TP relationships (Read et al. 2015; Quinlan et al. 2020). Difficulties in accurately estimating WRT for a large number of geographically distributed lakes could explain the absence of a WRT effect from these empirical studies. However, our model demonstrates that the

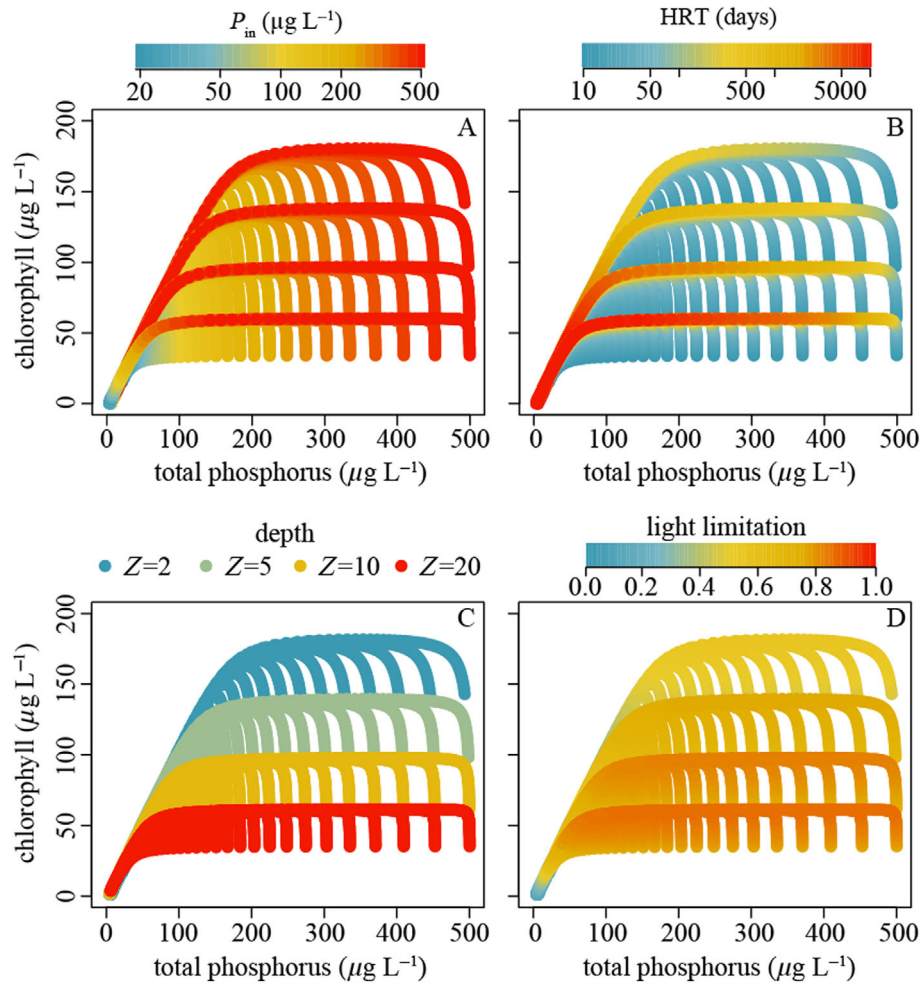


Fig. 3. Variation in inlet phosphorus concentration (P_{in}), lake WRT, and lake depth (Z) generate a wide diversity of predicted relationships between chlorophyll and TP concentration. All panels show the same set of simulations with systematically varied P_{in} , WRT, and Z , but simulations (individual points) are color coded by each forcing: (A) P_{in} (20–500 $\mu\text{g P L}^{-1}$), (B) WRT (10–1e4 d), and (C) Z (2, 5, 10, and 20 m). (D) Light limitation due to algal self-shading increases with increasing P_{in} , decreasing WRT, and increasing Z .

effect of WRT is strongly nonlinear (Fig. 3B) and interacts with other variables, like P_{in} , such that past comparative efforts may not have had the statistical power or model formulation capable of detecting the effect of WRT.

Although depth contributes to lake volume and thus, WRT, depth also has a modulating effect on lake chlorophyll-TP patterns via its influence on light availability. As lake depth increases, the maximum predicted chlorophyll decreases (Fig. 3C). This decrease in chlorophyll occurs because a deeper, completely mixed water column in our model magnifies self-shading effects. Lakes of greater depth also see onset of elevated light-limitation at a lower TP concentration (Fig. 3D). Our results corroborate past empirical and theoretical work highlighting the role of depth in regulating nutrient retention and chlorophyll-TP patterns (Vollenweider 1975; Reynolds 1992; Read et al. 2015; Quinlan et al. 2020). For example, in a global set of lakes, Quinlan et al. (2020) showed that lake

depth was significantly and negatively correlated with residuals from a chlorophyll-TP model fit.

Our model experiments support past calls for consideration of algal species or trait composition when considering chlorophyll-TP relationships (Smith 1982; Straskraba 1985; Reynolds 1992). We found that the phosphorus quota of algal cells influenced chlorophyll-TP relationships by shifting the initial slope (Fig. 4A). In reality and our model, algae C:P dictates the rate of increase in algal biomass (as chlorophyll or carbon) per increase in phosphorus availability (measured as TP). Adaptation to low P or light availability (half-saturation constants) alter the maximum attainable chlorophyll (Fig. 4B, C). Greater maximum predicted chlorophyll with a lower half-saturation constant for light is consistent with physiological and evolutionary studies of algae as it is common to see acclimation/adaptation of algae to low-light availability in turbid or stained waters (Dubinsky and Stambler 2009;

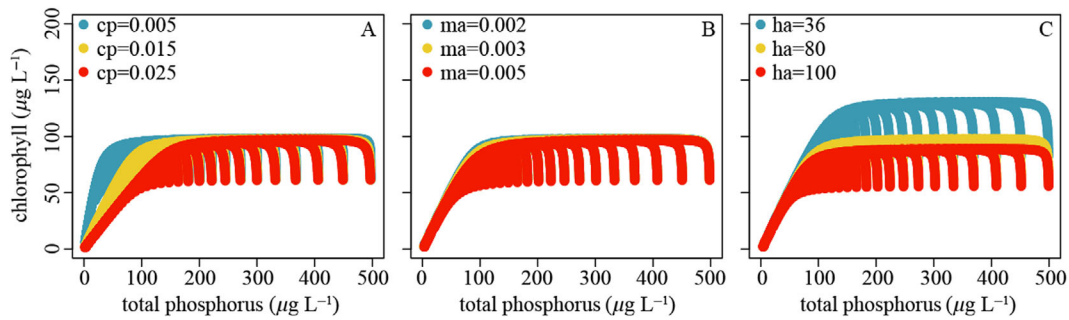


Fig. 4. Algal traits also influence relationships between chlorophyll and lake TP concentration. We inspected the influence of **(A)** algal quota (C_p) and the half-saturation constants for **(B)** nutrient (m_a) and **(C)** light (h_a). We used a lake depth of 10 m for all simulations, but varied P_{in} (20–500 $\mu\text{g P L}^{-1}$) and WRT (10–1e4 d). Each point is an individual simulation with a unique P_{in} –WRT combination and the points are color-coded by the parameterization of the respective algal trait.

Schwaderer et al. 2011). Although we did not consider varying cellular quota of chlorophyll, this too is known to respond plastically to nutrient and light availability (Riemann et al. 1989; Falkowski and LaRoche 1991).

Generality of our model and implications of model assumptions

Despite performing well, our calibrated model has a number of oversimplifications and assumptions that could be evaluated in the future (Fig. 5; Supporting Information Fig. S1). For example, our assumption of a fully mixed water column

and absence of chromophoric DOC likely amplified the effect of self-shading and light limitation. Previous empirical and modeling work show that DOC, lake surface area, and a stratified water-column strongly influence average light climate (Von Einem and Granéli 2010; Seekell et al. 2015; Kelly et al. 2018) in addition to geographic characteristics such as elevation, latitude, and seasonality (Dodds et al. 2019). Combinations of these drivers that reduce the average light climate, such as high DOC, large surface areas, low elevation, or high latitudes, would increase light limitation and reduce the maximum chlorophyll at a given TP, and the shift to light

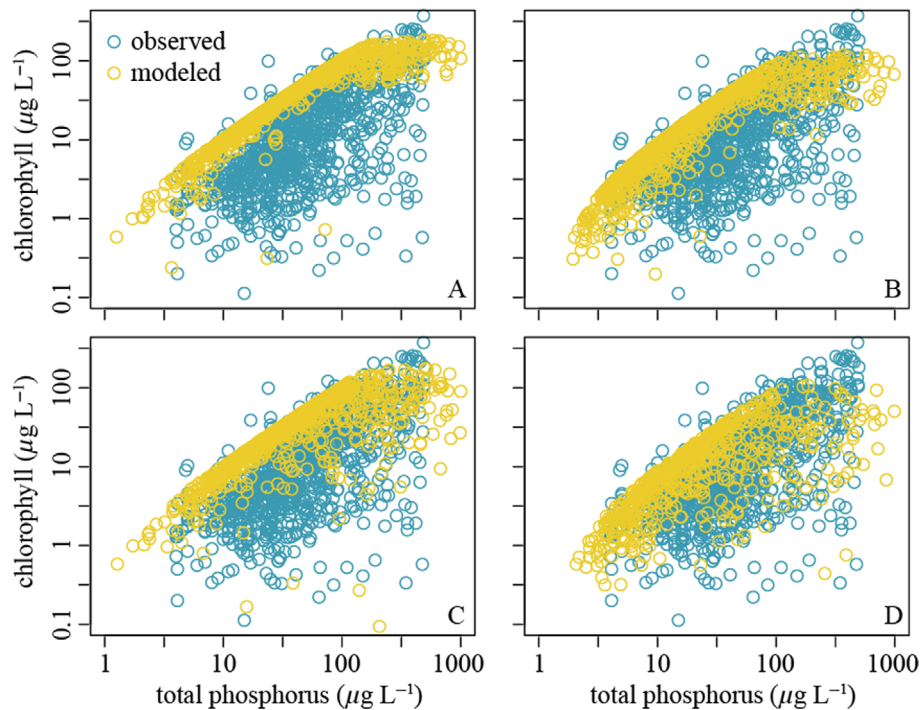


Fig. 5. Observed (EPA National Lake Assessment) and simulated chlorophyll–TP relationships parameterized using ~ 1000 lakes sampled in 2012. Simulations used observed lake surface area and depth, but random samples of discharge and inlet phosphorus concentration. **(A)** Our base simulation only included co-limited growth of algae by phosphorus and self-shading. Additional simulations added **(B)** herbivory, **(C)** terrestrial DOC, which competes with algae for light, or **(D)** both herbivory and terrestrial DOC.

limitation would occur at lower TP concentrations. Also, our formulation of algal sedimentation and internal P loading generated high rates of particulate matter sedimentation relative to past modeling and observations (Vollenweider 1975; Chapra and Tarapchak 1976; Burns and Rosa 1980; Brett and Benjamin 2008). Additional assessment of these model components would be important for understanding the influence of carbon and phosphorus sedimentation dynamics on algal P limitation via the permanent removal of P and contribution of internal loading of P to TP concentrations.

Our model experiments demonstrate algal traits drive the response of algal growth to environmental conditions and therefore chlorophyll-TP relationships (Tilman et al. 1982; Litchman and Klausmeier 2008; Zwart et al. 2015), but exploration of algal traits and community composition should be expanded. Future work could consider dynamic responses of algal traits, such as stoichiometry or carbon-to-chlorophyll ratio, to catchment and lake characteristics. Rather than using static, average algal traits, inclusion of dynamic traits may help to capture spatiotemporal variation in algal physiology and/or species composition. For example, algae may increase their chlorophyll content in response to low light availability or species with higher chlorophyll content may outcompete species with relatively low-chlorophyll content under nutrient-rich and light-limited conditions, which would increase the predicted maximum chlorophyll attained for a given TP under a light limited scenario.

The absence of other potential limiting mechanisms of algal growth in our model is a strong assumption, but relaxing this assumption provided useful inference in the context of the EPA's NLA data. In general, our base model was capable of capturing the relationship between chlorophyll and TP, and especially the upper bound of the chlorophyll-TP relationship observed in the EPA NLA data set (Fig. 5A). However, the model did not predict lakes with relatively low chlorophyll at a given TP concentration (Fig. 5A). After augmenting resource limitation via the effect of terrestrial DOC on light attenuation and/or herbivory, the model did a better job of capturing greater variance in chlorophyll at a given TP concentration (Fig. 5B–D). This variance in chlorophyll at a given TP may also be explained by other potential limitation mechanisms, such as nitrogen (N) or temperature that are not captured by our model. For example, low nitrogen concentration and temperature would increase algal growth limitation and lower chlorophyll at a given TP concentration. From this small model experiment, we suggest that our quantitative and conceptual model (Fig. 1) captures much of the possible variation in chlorophyll as a function of TP. However, future work could explore whether grazing, temperature, and nitrogen limitation differ in how they drive deviation from predicted chlorophyll-TP relationships. We would presume these additional limiting factors differ in their impact as grazers are subject to ecological feedbacks, temperature acts at relatively broad spatial scales, and nitrogen would be subject to similar hydrologic constraints as P.

Conclusions

For nearly 50 years, chlorophyll-TP relationships have been used, but questioned, for their ability to be predictive (Vollenweider 1975; Reynolds 1992). Poor predictive performance of existing chlorophyll-TP relationships likely stems from environmental stochasticity, observation error, and overly simplistic or phenomenological model structure. Many past surveys of lakes have created observations of chlorophyll and TP, and statistical models fit to those data. We argue these statistical models of chlorophyll and TP reflect the predominant depths, WRTs, P_{ins} , and algal quotas of lakes sampled, as well as the correlation structure among those variables. Our approach provides a process-driven conceptualization of chlorophyll-TP relationships and lake trophic status (Fig. 1) that can be tested through further modeling efforts, experimentation, and comparative work. To accurately predict the response of lentic ecosystems to environmental change, it is imperative that the effects of interactions among catchment, lake, and organismal drivers on algal limitation are accounted for.

References

- Beisner, B. E., C. L. Dent, and S. R. Carpenter. 2003. Variability of lakes on the landscape: Roles of phosphorus, food webs, and dissolved organic carbon. *Ecology* **84**: 1563–1575. doi:10.1890/0012-9658(2003)084[1563:VOLOTL]2.0.CO;2.
- Brett, M. T., and M. M. Benjamin. 2008. A review and reassessment of lake phosphorus retention and the nutrient loading concept. *Freshw. Biol.* **53**: 194–211. doi:10.1111/j.1365-2427.2007.01862.x
- Brooks, J. R., J. J. Gibson, S. Jean Birks, M. H. Weber, K. D. Rodecap, and J. L. Stoddard. 2014. Stable isotope estimates of evaporation: Inflow and water residence time for lakes across the United States as a tool for national lake water quality assessments. *Limnol. Oceanogr.* **59**: 2150–2165. doi:10.4319/lo.2014.59.6.2150
- Burns, N. M., and F. Rosa. 1980. In situ measurement of the settling velocity of organic carbon particles and 10 species of phytoplankton. *Limnol. Oceanogr.* **25**: 855–864. doi:10.4319/lo.1980.25.5.0855
- Champion, M., and D. J. Currie. 2000. Phosphorus-chlorophyll relationships in lakes, rivers and estuaries. *SIL Proc.* **1922-2010**: 1986–1989. doi:10.1080/03680770.1998.11901587
- Chapra, S. C., and S. J. Tarapchak. 1976. A chlorophyll a model and its relationship to phosphorus loading plots for lakes. *Water Resour. Res.* **12**: 1260–1264. doi:10.1029/WR012i006p01260
- Chow-Fraser, P., D. O. Trew, D. Findlay, and M. Stainton. 1994. A test of hypotheses to explain the sigmoidal relationship between total phosphorus and chlorophyll

- a concentrations in Canadian Lakes. *Can. J. Fish. Aquat. Sci.* **51**: 2052–2065. doi:[10.1139/f94-208](https://doi.org/10.1139/f94-208)
- Dillon, P. J., and F. H. Rigler. 1974a. The phosphorus–chlorophyll relationship in lakes. *Limnol. Oceanogr.* **19**: 767–773.
- Dillon, P. J., and F. H. Rigler. 1974b. A test of a simple nutrient budget model predicting the phosphorus concentration in lake water. *J. Fish. Res. Board Can.* **31**: 1771–1778. doi:[10.1139/f74-225](https://doi.org/10.1139/f74-225)
- Dodds, W. K., and others. 2019. The freshwater biome gradient framework: Predicting macroscale properties based on latitude, altitude, and precipitation. *Ecosphere* **10**: 1–33. doi:[10.1002/ecs2.2786](https://doi.org/10.1002/ecs2.2786)
- Dubinsky, Z., and N. Stambler. 2009. Photoacclimation processes in phytoplankton: Mechanisms, consequences, and applications. *Aquat. Microb. Ecol.* **56**: 163–176. doi:[10.3354/ame01345](https://doi.org/10.3354/ame01345)
- Essington, T. E., and S. R. Carpenter. 2000. Nutrient cycling in lakes and streams: Insights from a comparative analysis. *Ecosystems* **3**: 131–143. doi:[10.1007/s100210000015](https://doi.org/10.1007/s100210000015)
- Falkowski, P. G., and J. LaRoche. 1991. Acclimation to spectral irradiance in algae. *J. Phycol.* **27**: 8–14.
- Filstrup, C. T., and J. A. Downing. 2017. Relationship of chlorophyll to phosphorus and nitrogen in nutrient-rich lakes. *Inland Waters* **7**: 385–400. doi:[10.1080/20442041.2017.1375176](https://doi.org/10.1080/20442041.2017.1375176)
- Filstrup, C. T., T. Wagner, P. A. Soranno, E. H. Stanley, C. A. Stow, K. E. Webster, and J. A. Downing. 2014. Regional variability among nonlinear chlorophyll–phosphorus relationships in lakes. *Limnol. Oceanogr.* **59**: 1691–1703. doi:[10.4319/lo.2014.59.5.1691](https://doi.org/10.4319/lo.2014.59.5.1691)
- Hall, S. R., M. A. Leibold, D. A. Lytle, and V. H. Smith. 2007. Grazers, producer stoichiometry, and the light: Nutrient hypothesis revisited. *Ecology* **88**: 1142–1152.
- Huisman, J., and F. J. Weissing. 1994. Light-limited growth and competition for light in well-mixed model. *Ecology* **75**: 507–520.
- Jäger, C. G., and S. Diehl. 2014. Resource competition across habitat boundaries: Asymmetric interactions between benthic and pelagic producers. *Ecol. Monogr.* **84**: 287–302. doi:[10.1890/13-0613.1](https://doi.org/10.1890/13-0613.1)
- Jones, J. R., and R. W. Bachmann. 1976. Prediction of phosphorus and chlorophyll levels in lakes. *J. Water Pollut. Control Fed.* **48**: 2176–2182.
- Jones, S. E., and C. R. Olson. 2022. Aggregated chlorophyll–total phosphorus lake data, representative sampling of model forcings for water residence time and inlet concentrations of phosphorus and dissolved organic carbon, and Vollenweider lake data. *Zenodo*, [accessed 2022 March 29]. Available from <https://doi.org/10.5281/zenodo.6402458>.
- Kelly, P. T., C. T. Solomon, J. A. Zwart, and S. E. Jones. 2018. A framework for understanding variation in pelagic gross primary production of lake ecosystems. *Ecosystems* **21**: 1364–1376. doi:[10.1007/s10021-018-0226-4](https://doi.org/10.1007/s10021-018-0226-4)
- Litchman, E., and C. A. Klausmeier. 2008. Trait-based community ecology of phytoplankton. *Annu. Rev. Ecol. Evol. Syst.* **39**: 615–639. doi:[10.1146/annurev.ecolsys.39.110707.173549](https://doi.org/10.1146/annurev.ecolsys.39.110707.173549)
- McCauley, E., J. A. Downing, and S. Watson. 1989. Sigmoid relationships between nutrients and chlorophyll among lakes. *Can. J. Fish. Aquat. Sci.* **46**: 1171–1175.
- Orihel, D. M., H. M. Baulch, N. J. Casson, R. L. North, C. T. Parsons, D. C. M. Seckar, and J. J. Venkiteswaran. 2017. Internal phosphorus loading in Canadian fresh waters: A critical review and data analysis. *Can. J. Fish. Aquat. Sci.* **74**: 2005–2029. doi:[10.1139/cjfas-2016-0500](https://doi.org/10.1139/cjfas-2016-0500)
- Quinlan, R., and others. 2020. Relationships of total phosphorus and chlorophyll in lakes worldwide. *Limnol. Oceanogr.* **1–13**: 392–404. doi:[10.1002/lno.11611](https://doi.org/10.1002/lno.11611)
- R Core Team. 2021. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.R-project.org/>
- Read, E. K., and others. 2015. The importance of lake-specific characteristics for water quality across the continental United States. *Ecol. Appl.* **25**: 943–955. doi:[10.1890/14-0935.1](https://doi.org/10.1890/14-0935.1)
- Reynolds, C. S. 1992. *Eutrophication and the management of planktonic algae: What Vollenweider couldn't tell us*. p. 217. Freshwater Biological Association.
- Riemann, B., P. Simonsen, and L. Stensgaard. 1989. The carbon and chlorophyll content of phytoplankton from various nutrient regimes. *J. Plankton Res.* **11**: 1037–1045. doi:[10.1093/plankt/11.5.1037](https://doi.org/10.1093/plankt/11.5.1037)
- Sakamoto, M. 1966. Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. *Arch. Hydrobiol.* **62**: 1–28.
- Schindler, D. W., E. J. Fee, and T. Rusczyński. 1978. Phosphorous input and its consequences for phytoplankton standing crop and production in the experimental lakes area and in similar lakes. *J. Fish. Res. Board Can.* **35**: 190–196. doi:[10.1139/f78-031](https://doi.org/10.1139/f78-031)
- Schwaderer, A. S., K. Yoshiyama, P. De Tezanos Pinto, N. G. Swenson, C. A. Klausmeier, and E. Litchman. 2011. Eco-evolutionary differences in light utilization traits and distributions of freshwater phytoplankton. *Limnol. Oceanogr.* **56**: 589–598. doi:[10.4319/lo.2011.56.2.0589](https://doi.org/10.4319/lo.2011.56.2.0589)
- Seekell, D. A., J. F. Lapierre, J. Ask, A. K. Bergstrom, A. Deining, P. Rodriguez, and J. Karlsson. 2015. The influence of dissolved organic carbon on primary production in northern lakes. *Limnol. Oceanogr.* **60**: 1276–1285. doi:[10.1002/lno.10096](https://doi.org/10.1002/lno.10096)
- Shuvo, A., and others. 2021. Total phosphorus and climate are equally important predictors of water quality in lakes. *Aquat. Sci.* **83**: 1–11. doi:[10.1007/s00027-021-00776-w](https://doi.org/10.1007/s00027-021-00776-w)
- Smith, V. H. 1982. The nitrogen and phosphorus dependence of algal biomass in lakes: An empirical and theoretical

- analysis. *Limnol. Oceanogr.* **27**: 1101–1111. doi:[10.4319/lo.1982.27.6.1101](https://doi.org/10.4319/lo.1982.27.6.1101)
- Soetaert, K., T. Petzoldt, and R. W. Setzer. 2010. Solving differential equations in R: Package deSolve. *J. Stat. Softw.* **33**: 1–25. doi:[10.18637/jss.v033.i09](https://doi.org/10.18637/jss.v033.i09)
- Søndergaard, M., J. P. Jensen, and E. Jeppesen. 1999. Internal phosphorus loading in shallow Danish lakes. *Hydrobiologia* **408–409**: 145–152. doi:[10.1007/978-94-017-2986-4_15](https://doi.org/10.1007/978-94-017-2986-4_15)
- Straskraba, M. 1985. Lakes: Pollution and recovery, p. 79–90. *In Proceedings of the European Water Pollution Control Association*. Rome, ANDIS-Associazione nazionale di ingegneria sanitaria.
- Tilman, D., S. S. Kilham, and P. Kilham. 1982. Phytoplankton community ecology: The role of limiting nutrients. *Annu. Rev. Ecol. Syst.* **13**: 349–372. doi:[10.1146/annurev.es.13.110182.002025](https://doi.org/10.1146/annurev.es.13.110182.002025)
- U.S. Environmental Protection Agency. 2016. National aquatic resource surveys. National lake assessment 2012 (data and metadata files) [accessed 2022 March 29]. Available from <https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys>
- U.S. Environmental Protection Agency. 2020. National aquatic resource surveys. National rivers and streams assessment 2013–2014 (data and metadata files) [accessed 2022 March 29]. Available from <https://www.epa.gov/national-aquatic-resource-surveys/data-national-aquatic-resource-surveys>
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* **37**: 130–137.
- Vasconcelos, F. R., S. Diehl, P. Rodríguez, P. Hedström, J. Karlsson, and P. Byström. 2016. Asymmetrical competition between aquatic primary producers in a warmer and browner world. *Ecology* **97**: 2580–2592. doi:[10.1002/ecy.1487](https://doi.org/10.1002/ecy.1487)
- Vollenweider, R. A. 1975. Input–output models with special reference to the phosphorus loading concept in limnology. *Schweiz. Z. Hydrol.* **37**: 53–84. doi:[10.1016/S0723-2020\(11\)80108-6](https://doi.org/10.1016/S0723-2020(11)80108-6)
- Von Einem, J., and W. Granéli. 2010. Effects of fetch and dissolved organic carbon on epilimnion depth and light climate in small forest lakes in southern Sweden. *Limnol. Oceanogr.* **55**: 920–930. doi:[10.4319/lo.2009.55.2.0920](https://doi.org/10.4319/lo.2009.55.2.0920)
- Yuan, L. L., and A. I. Pollard. 2014. Classifying Lakes to improve precision of nutrient–chlorophyll relationships. *Freshw. Sci.* **33**: 1184–1194. doi:[10.1086/678465](https://doi.org/10.1086/678465)
- Zwart, J. A., C. T. Solomon, and S. E. Jones. 2015. Phytoplankton traits predict ecosystem function in a global set of lakes. *Ecology* **96**: 2257–2264. doi:[10.1890/14-2102.1](https://doi.org/10.1890/14-2102.1)

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