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## RESEARCH ARTICLE

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## Controls on Lake Pelagic Primary Productivity: Formalizing the Nutrient-Color Paradigm



### Key Points:

- A mathematical formulation of the nutrient-color paradigm accurately captures spatial variability in lake primary production
- A data assimilation technique updated the lake process model parameters and improved model predictions
- This simple process model can be a useful tool for testing and predicting lake productivity responses to environmental change

### Supporting Information:

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

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**Abstract** Understanding controls on primary productivity is essential for describing ecosystems and their responses to environmental change. In lakes, pelagic gross primary productivity (GPP) is strongly controlled by inputs of nutrients and dissolved organic matter. Although past studies have developed process models of this nutrient-color paradigm (NCP), broad empirical tests of these models are scarce. We used data from 58 globally distributed, mostly temperate lakes to test such a model and improve understanding and prediction of the controls on lake primary production. The model includes three state variables—dissolved phosphorus, terrestrial dissolved organic carbon (DOC), and phytoplankton biomass—and generates realistic predictions for equilibrium rates of pelagic GPP. We calibrated our model using a Bayesian data assimilation technique on a subset of lakes where DOC and total phosphorus (TP) loads were known. We then asked how well the calibrated model performed with a larger set of lakes. Revised parameter estimates from the updated model aligned well with existing literature values. Observed GPP varied nonlinearly with both inflow DOC and TP concentrations in a manner consistent with increasing light limitation as DOC inputs increased and decreasing nutrient limitation as TP inputs increased. Furthermore, across these diverse lake ecosystems, model predictions of GPP were highly correlated with observed values derived from high-frequency sensor data. The GPP predictions using the updated parameters improved upon previous estimates, expanding the utility of a process model with simplified assumptions for water column mixing. Our analysis provides a model structure that may be broadly useful for understanding current and future patterns in lake primary production.

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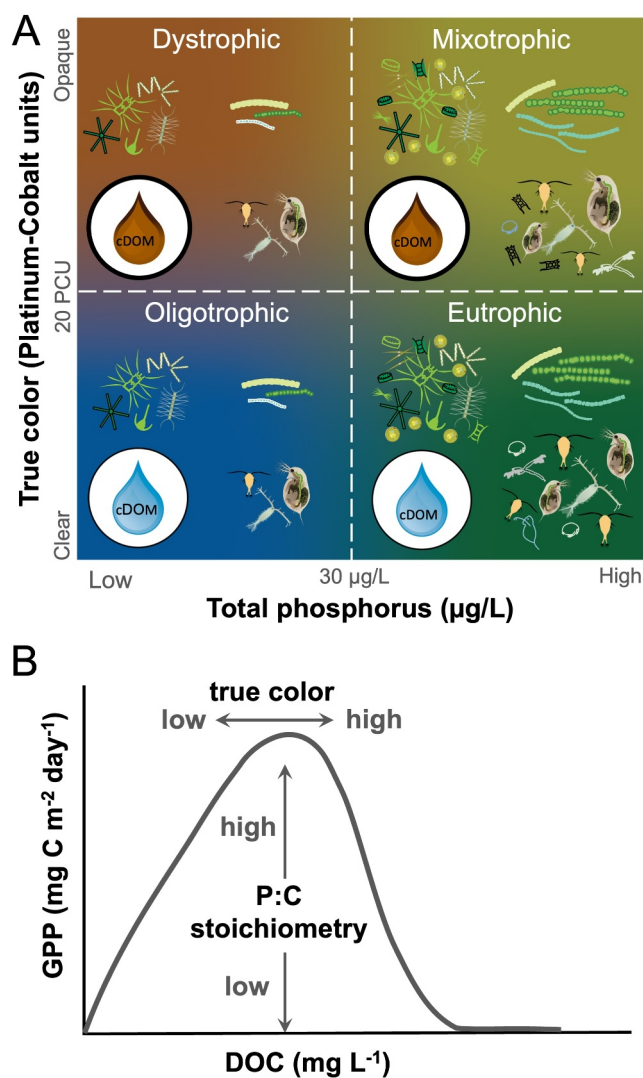
**Plain Language Summary** Understanding the controls on lake productivity is essential for predicting the response of lake ecosystems to global change. Recent advances in mathematical models have provided a conceptual framework for modeling lake pelagic productivity, but these models need to be tested and refined. In this study, we used data from 58 lakes around the world to develop and improve a mathematical model of the nutrient-color paradigm. We found that the updated model had better predictive power than previous models and accurately predicted primary production, mixed layer depth, and concentrations of nutrients in a diverse set of lakes. This improved model has the potential to be a valuable tool for understanding and predicting lake productivity in response to environmental changes.

## 1. Introduction

Primary production plays a central role in the ecology and biogeochemistry of ecosystems. Understanding the controls on primary production is, consequently, essential for understanding ecosystems and predicting their responses to global change. In lake ecosystems, one general conceptual model of the controls on pelagic gross primary productivity (GPP) is the nutrient-color paradigm (NCP; Williamson et al., 1999). This paradigm integrates two long-standing master variables in limnology by emphasizing the joint role of both nutrients and dissolved organic matter (DOM) in controlling pelagic GPP (Dillon & Rigler, 1974; Jones, 1992; Naumann, 1921; Thienemann, 1925; Vollenweider, 1968; Williamson et al., 1999). Specifically, the nutrient-color paradigm (NCP) focuses on how inputs of nutrients and DOM influence patterns of light and nutrient limitation of pelagic producers. Where lakes fall along axes of nutrient availability and colored DOM inputs are valuable for trophic state classifications, which are predictive of the various lake ecosystem characteristics such as biotic assemblages and lake productivity (Webster et al., 2008). Generally, clearer, more transparent waters are associated with lower nutrient levels (oligotrophic), whereas brown or green waters often indicate higher nutrient concentrations due to the presence of high organic material (dystrophic), algae (eutrophic), or both (mixotrophic; Figure 1). The NCP provides a unifying framework for contextualizing diverse patterns in limnology, such as the importance of nutrient management in controlling eutrophication and the importance of light limitation of food web productivity in humic systems (Karlsson et al., 2009; Maberly et al., 2020; Schindler, 1977).

Elements of this conceptual model have been formalized in a wide array of mathematical models of lake productivity (e.g., Jäger & Diehl, 2014; Jones et al., 2012; Kelly et al., 2018; Vadeboncoeur et al., 2008; Vasconcelos et al., 2018). Mathematical models of primary production like these are valuable for at least two reasons: they summarize explicitly what is known or hypothesized about the mechanisms that drive observed patterns, and they provide a tool for predicting responses of primary productivity to global change. In terrestrial ecosystems, for instance, models such as the Community Land Model are widely used to describe patterns in primary productivity across time and space (Lawrence et al., 2019), and there is a rich history in the terrestrial literature of model-data integration to update model formulation and parameterization (e.g., Caldararu et al., 2023; Keenan et al., 2012). Likewise, the oceanography community has a long history of building and refining ocean biogeochemistry models (Fennel et al., 2022), which are often coupled with larger earth system models (e.g., Community Earth System Model). As sufficient multisite, globally distributed data on lakes become easier to share and access via networks such as the Global Lake Ecological Observatory Network and other open science practices, limnologists are similarly poised to test and parameterize deterministic lake ecosystem models (Soares & Calijuri, 2021). The need for lake models is especially important as aquatic ecosystems are increasingly recognized as large components of earth's greenhouse gas budgets and for their potential as nature-based climate solutions.

In this study, we quantitatively test and parameterize the mathematical formalization of the NCP proposed by Kelly et al. (2018; Box 1). The mathematical formalization of the NCP introduced by Kelly et al. (2018) is a simple lake model that captures the effects of hydrologic residence time (HRT), input concentrations of dissolved organic carbon (DOC) and phosphorus, and lake surface area on the supply of co-limiting light and phosphorus for phytoplankton primary production (Figure 1b). This formulation of the NCP incorporates trade-offs between lake physical characteristics (e.g., light attenuation) and chemical properties (e.g., nutrient concentrations), which ultimately dictate biological processes (e.g., algal biomass and ultimately phytoplankton productivity). For example, hydrologic loading of carbon and nutrients will stimulate algal growth in lakes to a point, but in highly humic systems productivity will be limited by light availability (Houser, 2006; Kirk, 1994; Read & Rose, 2013).



**Figure 1.** Conceptual diagrams illustrating two different formulations of the nutrient-color paradigm (NCP). (a) In this version, lakes can be classified into four trophic states depending where they fall on an axis of phosphorus concentrations and true color. Figure modified from Meyer et al., 2023 and originally formulated in Williamson et al., 1999. (b) A mathematical formulation of the NCP originally introduced by Kelly et al. (2018). This model predicts that rates of primary production are a function of incoming C and P nutrient loads to a lake. The magnitude of peak gross primary production depends on the relative availability of P:C in the hydrologic inflows and the color of the dissolved organic matter (as dissolved organic carbon concentrations).

The process model assumes all primary production occurs in the surface mixed layer, the depth of which is determined by lake surface area and by the DOC concentration. The model includes three state variables—dissolved phosphorus, terrestrial DOC, and phytoplankton biomass—and generates realistic predictions for equilibrium rates of GPP.

Our approach is a process called data assimilation, which is widely used for understanding terrestrial primary production, respiration, and other Earth system processes. To optimize model parameterization, we used a Bayesian Markov chain Monte Carlo analysis to assimilate information from the model and the data (Peng et al., 2011; Williams et al., 2005). To that end, we used data from a set of 58 globally distributed lakes from the Global Lake Ecological Observatory Network with the goal of (a) understanding whether the model provides a useful and generalizable framework for describing variation in lake pelagic primary production, (b) highlighting potential improvements to the model, and (c) identifying the requisite data that might improve our ability to describe and predict primary production in lake ecosystems globally.

## 2. Methods

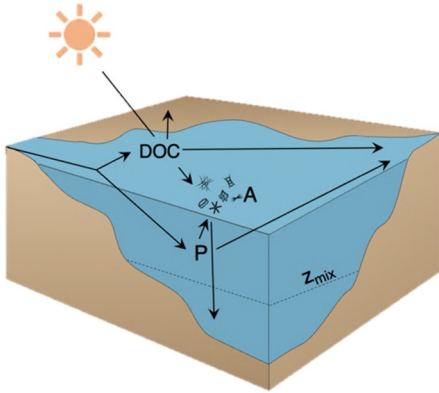
### 2.1. Overview

We assembled data on GPP, lake concentrations of total phosphorus (TP) and DOC, HRT, morphometry, and other characteristics for 58 lakes distributed across North America, Europe, Asia, and Oceania (Figure 2). The first stage of our analysis focused on a subset of 18 lakes for which data were available on stream inflow concentrations of TP and DOC (hereafter “calibration lakes”). We used these calibration lakes to parameterize the Kelly et al. (2018) model and quantify uncertainty in those parameters (Box 1, Table 1). In the second stage of our analysis, we used the parameterized model and observations of lake HRT, TP concentration, and DOC concentrations to predict surface mixed layer GPP, inflow TP concentrations ( $TP_{in}$ ), inflow DOC concentrations ( $DOC_{in}$ ), and mixed layer depth ( $z_{mix}$ ) in each of the 18 calibration lakes, which were chosen for their monitored lake inflows and the remaining 40 “validation lakes.” We compared these predictions to the observed values to understand model performance and identify biases or places for improvement all of which are outlined in detail below. All analyses were performed using R statistical software (version 4.2.1; R Development Core Team, 2022). All data produced in this analysis are published on Environmental Data Initiative (Oleksy et al., 2024).

### 2.2. Observed GPP Estimates

We estimated daily surface mixed layer GPP for 58 lakes by fitting a model to high-frequency dissolved oxygen (DO) data by maximum likelihood as described by Solomon et al. (2013) based on diel DO curves (hereafter “observed GPP”). We estimated mixed layer depth ( $z_{mix}$ ) as the shallowest depth at which the rate of density change exceeded  $0.075 \text{ kg m}^{-3} \text{ m}^{-1}$ , a value intermediate between the default in rLakeAnalyzer (Winslow et al., 2019,  $0.1 \text{ kg m}^{-3} \text{ m}^{-1}$ ) and Lamont et al. (2004,  $0.5 \text{ kg m}^{-3} \text{ m}^{-1}$ ). Then, we multiplied daily volumetric GPP estimates ( $\text{mg O}_2 \text{ L}^{-1} \text{ day}^{-1}$ ) by daily mixed layer depth (meters) and converted to units of C by assuming a 1:1 respiratory quotient; thus, GPP is reported in areal units of carbon ( $\text{mg C m}^2 \text{ day}^{-1}$ ). However, we recognize that a single respiratory quotient may lead to biases in GPP estimates (Trentman et al., 2023). Since the period over which DO was measured varied by lake, we trimmed the data sets to include only observations May 1 through October 1 in the northern hemisphere or November 1 through April 1 for the southern hemisphere (Figure

### Box 1 Model Description



**Overview:** The formalization of the nutrient-color paradigm introduced by Kelly et al. (2018) is a simple lake model that uses hydrologic residence time, input concentrations of terrestrial dissolved organic carbon and phosphorus, and lake surface area to produce estimates of pelagic phytoplankton primary production. The model assumes all primary production occurs in the surface mixed layer, the depth of which is determined by lake surface area and by the DOC concentration. The model includes three state variables—phosphate, terrestrial dissolved organic carbon, and phytoplankton biomass—and generates realistic predictions for equilibrium rates of primary production.

**Details:** The model developed by Kelly et al. (2018) focuses on estimating “equilibrium” or average GPP in a lake. The model includes a single, well-mixed population of phytoplankton ( $A$ ; Equation 2) residing in the lake epilimnion, and assumes that no primary production occurs below the thermocline. Losses from the phytoplankton pool include mortality ( $l_A$ ), sinking ( $v$ ),

and hydrologic outflow (which is assumed to be equal to inflow,  $Q_{in}$ ). Pelagic primary production ( $r$ ; Equation 3) has a theoretical maximum rate ( $p_A$ ) and is co-limited by the availability in the mixed layer of light (calculated from constant surface light  $I_0$ ,  $350 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ , and light at the bottom of the mixed layer  $I_{z_{mix}}$ ; Equation 8) and nutrients (dissolved phosphorus,  $P$ ) following Michaelis-Menten relationships with half-saturation constants  $h_A$  and  $m_A$ . The model includes a dynamic DOC pool ( $C$ ) and hydrologically linked inputs of DOC and biologically available phosphorus ( $C_{in}$ ,  $P_{in}$ ). Terrestrial DOC is gained and lost via stream flow ( $Q_{in}$ ) and is subject to first-order decay ( $d$ ; Equation 1). Phytoplankton experience the integrated light climate of the epilimnion and have access to an epilimnetic phosphorus pool ( $P$ ; Equation 4) derived from the watershed ( $P_{in}$ ). Phytoplankton have a fixed stoichiometry ( $c_A$ ), and  $P$  is partially recycled ( $q$ ) following mortality in the algal biomass pool ( $l_A$ ). The volume of the mixed layer ( $V_{mix}$ ) is estimated from  $z_{mix}$ , which is a function of lake  $C$  and lake surface area ( $S_A$ ; Equation 5). Light attenuation ( $k_D$ ) is calculated as the sum of the attenuations of DOC ( $k_{DOC}$ ) and phytoplankton ( $k_A$ ; Equation 6). Total  $P$  ( $TP$ ) is calculated as the sum of  $P$  in algal biomass ( $A$ ) and dissolved  $P$  (Equation 7). To solve the equations, we use the LSODA integration solver implemented within the *ode* function in the R package “deSolve” (Soetaert et al., 2010).

$$\frac{dC}{dt} = \frac{Q_{in}}{V_{mix}}(C_{in} - C) - Cd \quad (1)$$

$$\frac{dA}{dt} = A \left[ r - l_A - \frac{v}{z_{mix}} - \frac{Q_{in}}{V_{mix}} \right] \quad (2)$$

$$r = \frac{p_A}{k_D z_{mix}} \ln \left( \frac{h_A + I_0}{h_A + I_{z_{mix}}} \right) \left( \frac{P}{P + m_A} \right) \quad (3)$$

$$\frac{dP}{dt} = \frac{Q_{in}}{V_{mix}}(P_{in} - P) + qc_A l_A A - qrA \quad (4)$$

$$z_{mix} = 10^{\left( -0.515 * \log_{10} C + 0.115 * \log_{10} \left( 2\sqrt{\frac{S_A}{\pi} + 0.991} \right) \right)} \quad (5)$$

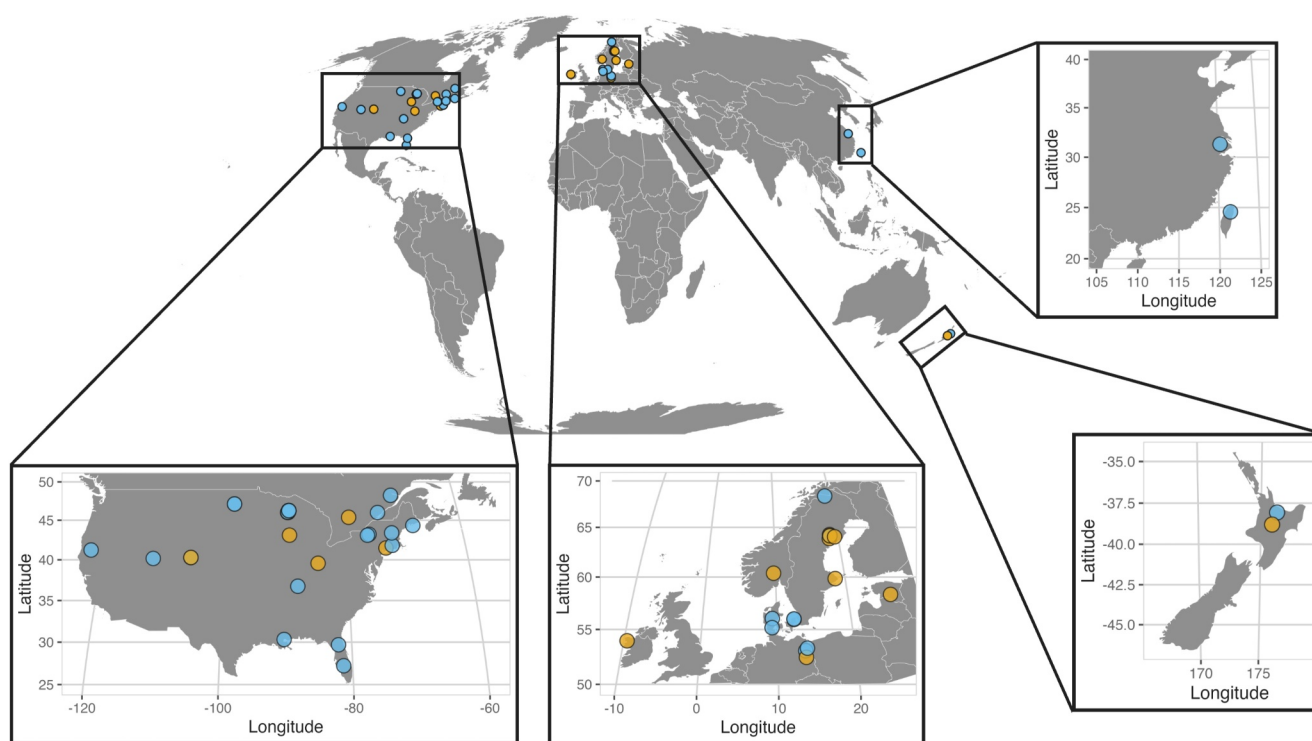
$$k_D = k_{DOC}C + k_A A \quad (6)$$

$$TP = qA + P \quad (7)$$

$$I_{z_{mix}} = I_0 * e^{-(k_D * z_{mix})} \quad (8)$$

Model scripts are available on <https://github.com/MFEh2o/loadsGPP>

S1 in Supporting Information S1). The model developed by Kelly et al. focuses on estimating “equilibrium” or steady-state GPP (e.g., the last simulation day). To test and parameterize that model, we compared the modeled output to the observed median GPP rates over that monitoring period. To examine empirical relationships between observed GPP and various chemical and morphometric characteristics of lakes, we fit several linear models



**Figure 2.** Global distribution of the 58 lakes included in this study. The “calibration” lakes are shaded in yellow and all others (“validation”) are in blue.

using the *glm* function in R. We used the gamma-distributed response family and logarithmic link function and report the Bonferroni adjusted p-values.

### 2.3. Model Calibration

We estimated the parameters of the model by fitting the model to the observed median summer GPP,  $z_{\text{mix}}$ , light attenuation ( $k_D$ ), and in-lake concentrations of TP, DOC, and phytoplankton biomass for the 18 calibration lakes. These observations were collected as part of this study, except for phytoplankton biomass, for which we took estimates for each lake from previously published studies (Table S1 in Supporting Information S1). We used lake-specific morphometry, HRT, stream discharge, and inflow TP and DOC concentrations to force the model (Kelly et al., 2018). We divided lake volume by HRT to calculate average daily inflow for each lake ( $\text{m}^3 \text{d}^{-1}$ ). To estimate DOC and TP concentrations in the inflow to each calibration lake, we calculated volume-weighted concentrations as the sum of the stream nutrient flux divided by the sum of the total discharge over the study period. Because the model generates predictions of change in biomass or net primary production (Box 1), we assumed that autotrophic respiration was 20% of GPP (Del Giorgio & Williams, 2005).

We fit the model using a Bayesian Markov chain Monte Carlo (MCMC) technique (Besag et al., 1995; Hararuk et al., 2018). We sampled from the posterior parameter distribution by proposing a set of parameters and accepting or rejecting it using the Metropolis criterion (Gelman et al., 2013). We used uniform proposal distributions for the first 30,000 iterations of the Markov chain and then calculated the parameter covariance matrix and switched the parameter proposal distribution to the multivariate normal for another 170,000 iterations, with the covariance matrix scaled by a factor of 1 for 30,000 iterations then by 0.2 for the next 40,000 iterations and 0.01 for the final 100,000 iterations (Xu et al., 2007). We initially used literature ranges as the bounds for the uniform proposal distributions (Table 1) but extended those ranges after initial runs showed that the posterior distributions of several parameters such as efficiency of phosphorus recycling from lost phytoplankton ( $q$ ), maximum algal production rate ( $p_A$ ), and half-saturation constant for light-limited phytoplankton ( $h_A$ ) ran up against the literature bounds. We ran four chains, each starting from a randomly chosen parameter set drawn from the uniform proposal distributions. Acceptance rates were around 27% for each chain. We discarded the first 100,000 iterations as a “burn-in” period and calculated mixing and convergence metrics ( $R_{\text{hat}}$  and effective sample size,  $N_{\text{eff}}$ ; Gelman

**Table 1**  
Parameter Definitions, Original Values, Values From the Literature and Their Sources As Well As the Optimization Values Used in This Study Following the Metropolis Algorithm Optimization

Parameter	Units	Definition	Original parameter	Updated parameter (95% CI)	Literature values	Literature sources
$k_{\text{DOC}}$	$\text{m}^2 \text{g C}^{-1}$	Light attenuation coefficient of dissolved organic carbon	0.42	0.117 (0.08–0.172)	0.16–0.22	Morris et al. (1995)
$k_A$	$\text{m}^2 \text{g C}^{-1}$	Light attenuation coefficient of phytoplankton	0.22	0.0009 (0.0004–0.0016)	0.0047–0.14	Morris et al. (1995)
$I_A$	$\text{day}^{-1}$	Loss rate of phytoplankton	0.1	0.33 (0.171–0.636)	0.028–1.067	Jassby and Goldman (1974); Lewis (1978); Tilzer (1984); Lehman and Sandgren (1985); Scavia and Fahnenstiel (1987); Garnier and Mourelatos (1991); Andersen (1997)
$p_A$	$\text{day}^{-1}$	Maximum production rate of photosynthesis	1	4.45 (0.615–26.2)	0–1.3	Visser et al. (1996); De Nobel et al. (1997); Huisman et al. (1999, 2002); Flynn and Raven (2017)
$h_A$	$\mu\text{mol photons m}^{-2} \text{s}^{-1}$	Half-saturation constant for light-limited production of phytoplankton	55	16.1(0.65–272)	18–53	Huisman et al. (1999); Litchman and Klausmeier (2001)
$m_A$	$\text{mg P m}^{-3}$	Half-saturation constant for nutrient-limited production of phytoplankton	2	2.08 (0.183–19.9)	0.15–5	Smith and Kalfif (1982); Auer et al. (1986); Huisman and Weissing (1995); Gurney and Nisbet (1998); Diehl (2002); Beston et al. (2018)
$d$	$\text{day}^{-1}$	Dissolved organic carbon mineralization rate	0.001	0.00118 (0.0005–0.002)	0.0001–0.05	Hanson et al. (2011); Evans et al. (2017)
$c_A$	$\text{mg P mg C}^{-1}$	Phosphorus to carbon quota of phytoplankton	0.015	0.0483 (0.0229–0.0729)	0.0005–0.043	Andersen (1997); Klausmeier et al. (2004)
$q$	Unitless	Efficiency of phosphorus recycling from lost phytoplankton	0.95	0.991 (0.977–0.997)	0.25–1	Thingstad and Sakshaug (1990)
$v$	$\text{m day}^{-1}$	Sinking rate of phytoplankton	0.1	0.000462 (0.00011–0.00418)	0–2.4	Reynolds (1984); Visser et al. (1996, 1997); Andersen (1997); Huisman et al. (2002)

Note. Values in parentheses refer to the 95% confidence intervals around the new parameter set.

et al., 2013) to assess performance of the algorithm. Following confirmation of algorithm performance, the chains were pooled, and the median value for each parameter was used as a point estimate for further simulations. From the pooled Metropolis parameter sets, 95% credible intervals were used to estimate our uncertainty in parameter estimates.

## 2.4. Model Validation

To test the predictive ability of our model, we used our calibrated parameter point estimates to simulate the model for the full 58 lake set (hereafter predicted GPP,  $\text{DOC}_{\text{in}}$ ,  $\text{TP}_{\text{in}}$ , and  $z_{\text{mix}}$ ). We compared observed median GPP values to steady-state model output. We sped up the approach to equilibrium conditions by setting initial conditions for simulations to observed phytoplankton biomass, DOC, and TP. We ran simulations for 2,000 time steps. The state variables and process rates from the final day of the simulation were used as steady state values.

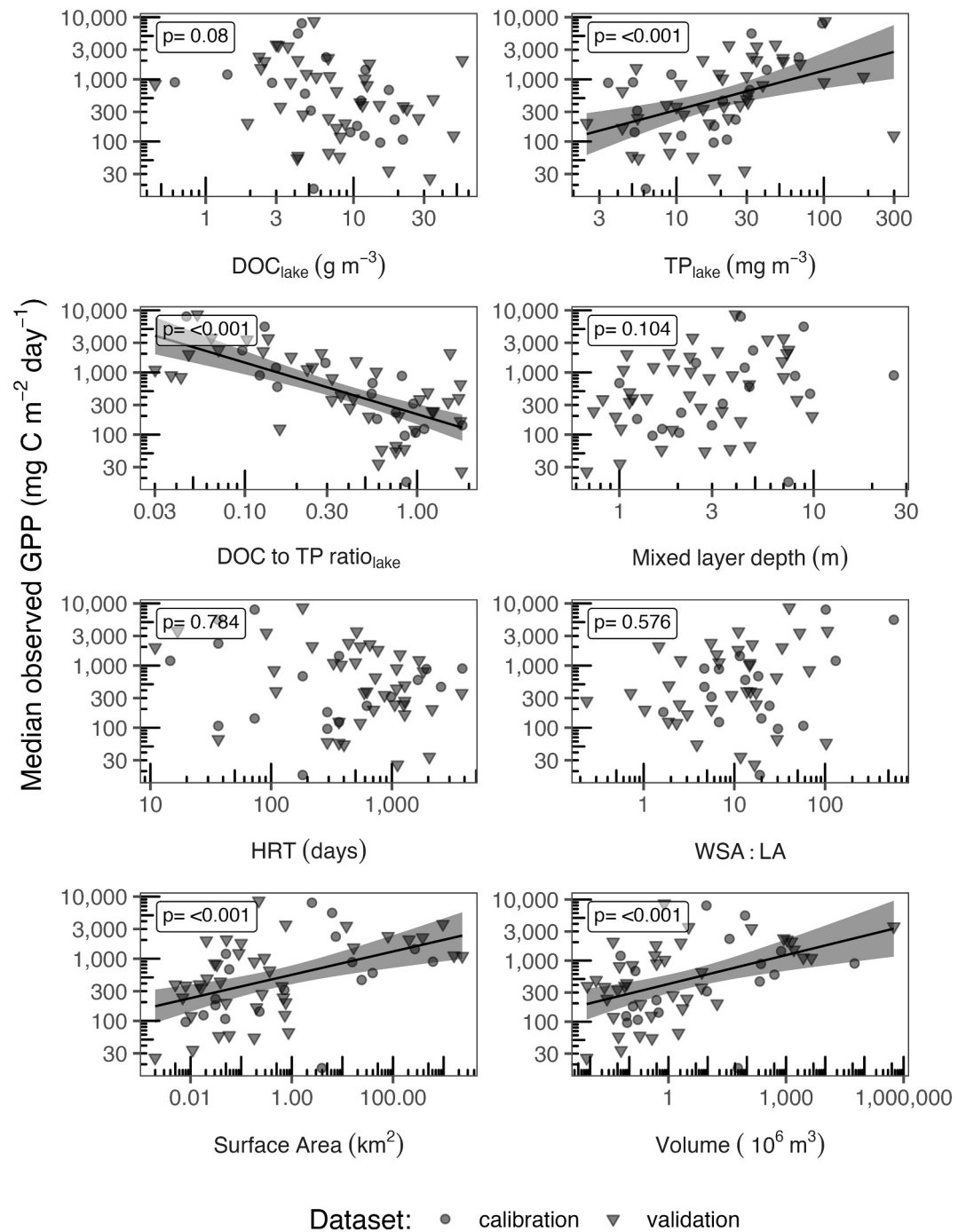
For most lakes (40 of 58), we lacked inflow concentrations of DOC and TP ( $\text{DOC}_{\text{in}}$  and  $\text{TP}_{\text{in}}$ ). Thus, to predict GPP for the validation lakes, we estimated  $\text{DOC}_{\text{in}}$  and  $\text{TP}_{\text{in}}$  for each lake by minimizing the sum of squared differences between predicted and observed in-lake concentrations of DOC and TP using the default Nelder-Mead algorithm in the *optim* function in R (Figure S2 in Supporting Information S1). The best performing  $\text{DOC}_{\text{in}}$  and  $\text{TP}_{\text{in}}$  were combined with lake morphometry and HRT as drivers of a model run; the volumetric equilibrium biomass production rate from each lake's model run is adjusted for autotrophic respiration (20% of GPP) and multiplied by modeled equilibrium mixed-layer depth (predicted  $z_{\text{mix}}$ ) to generate predicted GPP. Here, we use point estimates of parameters from our calibration data set, and we do not use observed GPP in the process of determining inflow DOC and TP concentrations. This allows us to generate predictions for GPP that are independent of the observed GPP values.

## 3. Results

The lakes included in our data set were diverse in size, shape, nutrient concentrations, and productivity (Figure S1, and Table S2 in Supporting Information S1). Most lakes were in the temperate biome ( $n = 44$ ), though six were subtropical and eight were boreal (Figure 2). Observed summer GPP varied over more than two orders of magnitude, from  $<20$  to  $>8,000$   $\text{mg C m}^{-2} \text{d}^{-1}$ . Lake morphometry as well as in-lake concentrations of nutrients and DOM were similarly variable (Figure 3). For instance, lake surface area ranged from 0.02 to  $>2,300$   $\text{km}^2$ , mean depth from 0.7 to 110 m, residence time from 0.03 to 10 years, DOC concentration from 0.4 to 54.4  $\text{mg L}^{-1}$  and TP from 2.4 to 298.5  $\mu\text{g L}^{-1}$  (Figure 3, Table S2 in Supporting Information S1). Several morphometric and chemical characteristics were correlated with rates of GPP; for instance, observed GPP was positively related to in-lake TP concentration and negatively related to the ratio of lake DOC:TP (Figure 3). Along a gradient of lake volume and surface area, GPP also generally increased.

Observed GPP varied nonlinearly with both inflow DOC and TP concentrations in a manner consistent with increasing light limitation as DOC inputs increased and decreasing nutrient limitation as TP inputs increased (Figure 4a). This relationship with GPP held for lake DOC and TP concentrations as well with lower overall concentrations of DOC and TP in lakes than inflows (Figure 4b, Figure S3 in Supporting Information S1). Generally, GPP was highest at relatively low  $\text{DOC}_{\text{in}}$  and intermediate-to-high  $\text{TP}_{\text{in}}$  and lowest at high  $\text{DOC}_{\text{in}}$  and high  $\text{DOC}_{\text{in}}:\text{TP}_{\text{in}}$  (Figure 4a, Figure S4 in Supporting Information S1).

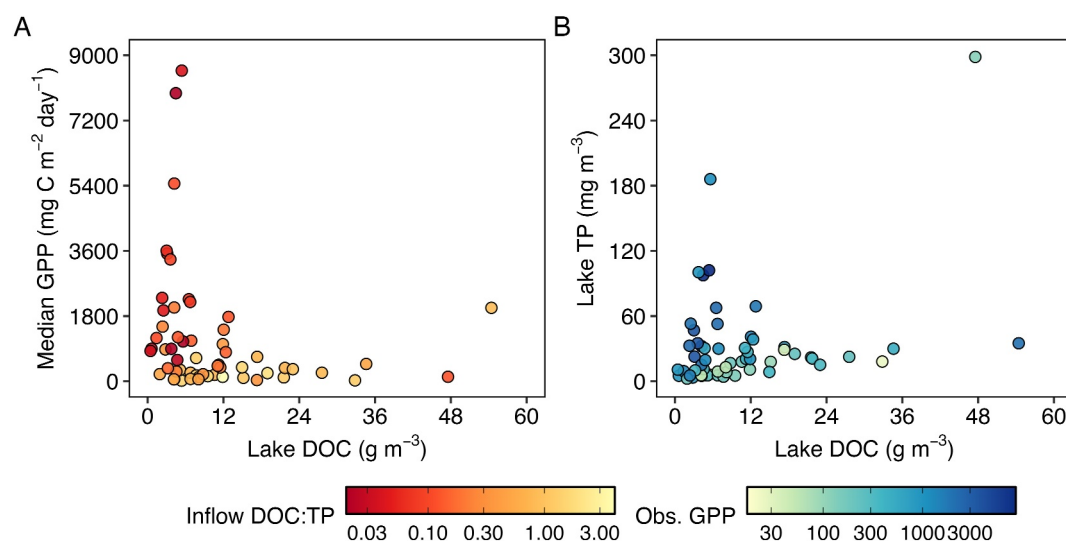
Model predictions of primary production, mixed layer depth, light attenuation, and in-lake concentrations of TP and DOC for the 18 calibration lakes achieved a good fit with observed values (adjusted  $R^2$  0.63–0.86). Predictions of GPP in the calibration lakes using the updated parameters (Table 1) were slightly biased (slope 0.5; 95% CI 0.41–0.92; Figure 5d); the underprediction of GPP was particularly notable for lakes with moderate to high observed GPP with very high  $\text{TP}_{\text{in}}$  (Figure S5 in Supporting Information S1). Predicted GPP had a symmetric mean absolute percent error (SMAPE) of 68% compared to observed GPP. Modeled to observed SMAPE was relatively small for in-lake concentrations of TP (39%) and DOC (39%) and for  $z_{\text{mix}}$  (33%; Figure 5). Intercepts and slopes for  $\text{DOC}_{\text{lake}}$ ,  $z_{\text{mix}}$ , and  $k_D$  were not different from 0 to 1, respectively (Figure S6 in Supporting Information S1). All parameters showed good performance in our MCMC run (Table S3 in Supporting Information S1). Overall, the predictions from the fitted model with updated parameters were much more precise and much less biased than those from the previous version of the model (Kelly et al., 2018), which used literature-derived point estimates of the parameters (Figure S7 in Supporting Information S1).



**Figure 3.** Empirical relationships between median gross primary production and a range of lake chemistry, hydrology, and morphometry variables for the 58 lakes in this study. Bonferroni-corrected p-values are printed on each plot and regression fits with 95% confidence intervals are shown for covariates with  $p < 0.05$ . Note  $\log_{10}$  scale on both axes. HRT = hydrologic residence time; WSA:LA = watershed area to lake area ratio.

Our calibrated model generated good predictions of mixed layer depth and pelagic GPP in the 40 validation lakes despite the need to estimate  $\text{DOC}_{\text{in}}$  and  $\text{TP}_{\text{in}}$  (Figures 5c and 5d). Predicted  $\text{TP}_{\text{lake}}$  and  $\text{DOC}_{\text{lake}}$  for the 40 validation lakes were identical to the observations by nature of the procedure that we used to estimate inflow concentrations for these lakes where observed  $\text{DOC}_{\text{in}}$  and  $\text{TP}_{\text{in}}$  were not available (Figures 5a and 5b). The accuracy of the GPP and  $z_{\text{mix}}$  predictions were similar for the full data set as for the calibration set with SMAPE of 72% and 34%, respectively (Figures 5c and 5d).





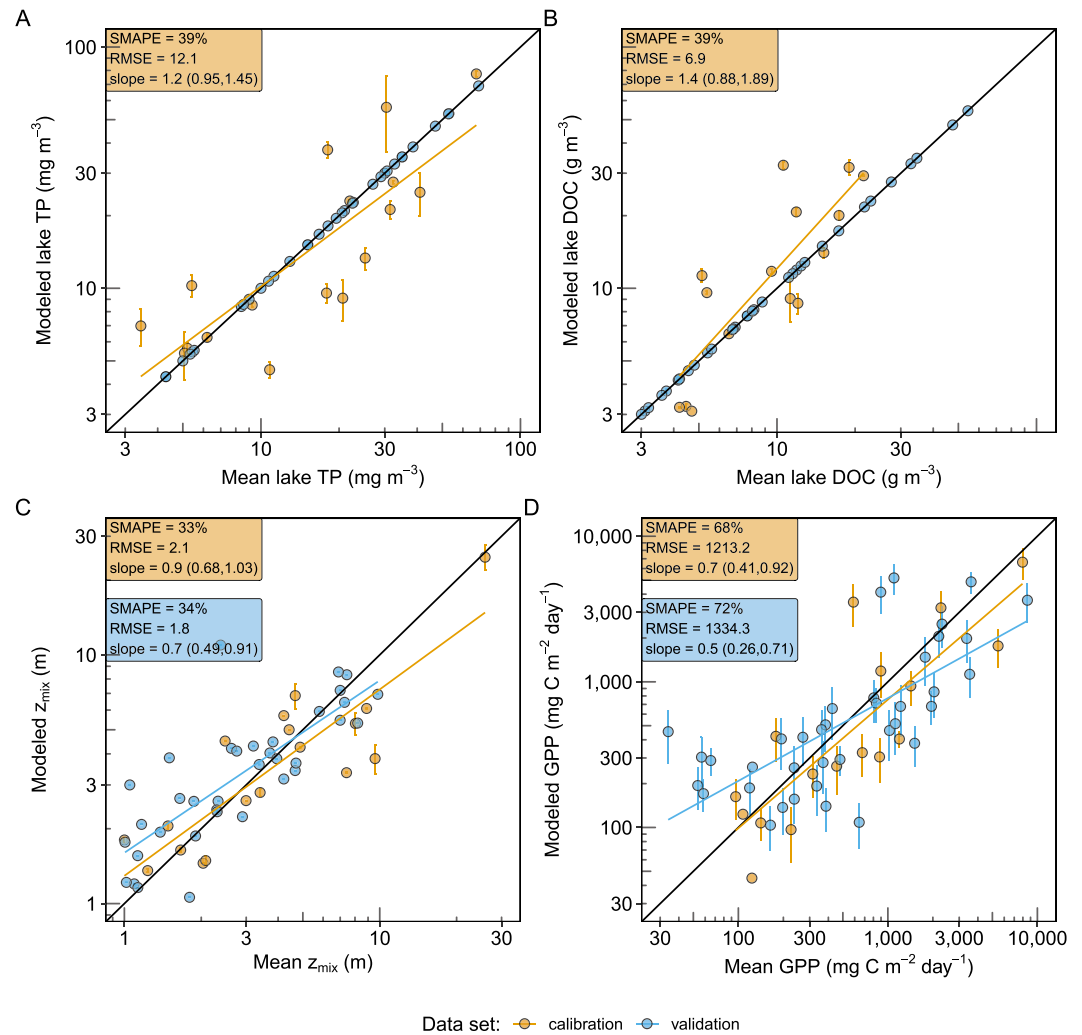
**Figure 4.** (a) Relationship between lake gross primary production (GPP) and lake dissolved organic carbon (DOC) as a function of DOC:TP of lake inflows and (b) Lake total phosphorus versus lake DOC as a function of GPP. Note  $\log_{10}$  scale on legends.

The updated parameter estimates were plausible relative to existing literature estimates of these parameters (Figure 6). For all 10 parameters, the 95% credible interval overlapped with, or was contained within, the range of values reported in the literature. Estimates of the DOC mineralization rates ( $d$ ), the light attenuation coefficient of phytoplankton ( $k_A$ ), efficiency of phosphorus recycling from lost phytoplankton ( $q$ ), and the sinking rate of phytoplankton ( $v$ ) parameters were close to the previously observed ranges suggested by literature reports (Figure 6). Credible intervals for the parameters were tightly constrained in some cases, such as  $d$ ,  $k_A$ ,  $k_{\text{DOC}}$ ,  $v$ ,  $q$ , and loss rate of phytoplankton ( $l_A$ ), but much broader in others.

#### 4. Discussion

The ability of the model to accurately predict pelagic GPP, with limited input data, across a tremendously diverse set of lakes in which GPP rates span orders of magnitude speaks to the utility of the NCP as an organizing principle (Naumann, 1921). The model captures some simple but fundamental mechanisms that govern phytoplankton productivity across lakes: specifically, how inputs from the watershed and lake morphology interactively influence the nutrient and light climate. Our calibrated and parsimonious model shows promise in addressing the long-standing challenge of accurately modeling pelagic GPP across spatial scales for the very least in temperate lake ecosystems. By testing and parameterizing this model, we advance the understanding of variation in pelagic production across a wide range of limnological characteristics. Although several recent observational and experimental studies have qualitatively evaluated this model (Bergström & Karlsson, 2019; Bogard et al., 2020; Isles et al., 2021; Olson et al., 2020; Puts et al., 2023; Senar et al., 2021), to our knowledge this work is the first to rigorously challenge the original model formulation and parameterization by confronting the model with observations from a diverse set of lakes from temperate, subtropical, and boreal biomes.

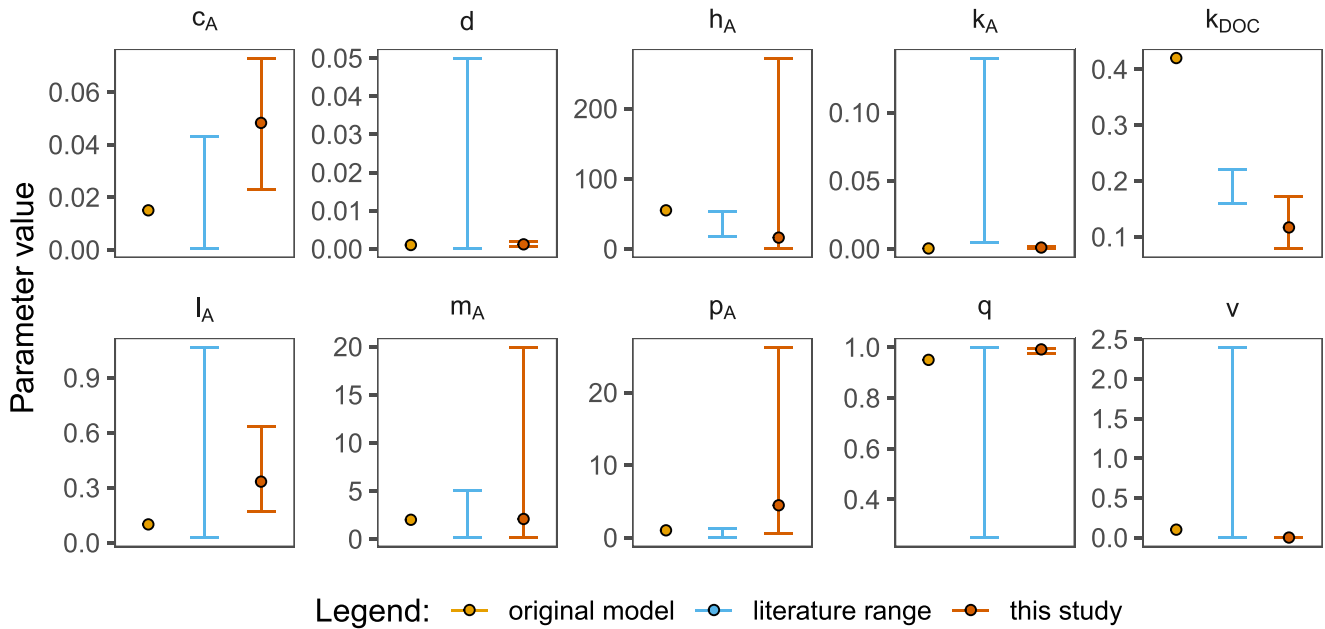
The calibrated model parameters mostly overlap with ranges reported in the literature, though in some cases the estimates were poorly constrained (Figure 6). For some of these parameters, the wide bounds likely arise because of substantial variation in the true value of that parameter among our study lakes;  $k_{\text{DOC}}$ , for instance, can be highly variable among lakes (Lapierre et al., 2013; Thottathil et al., 2018). In other cases, those wide bounds may indicate a lack of informative data for that parameter, equifinality issues in fitting a complex model, or the influence of processes that were not represented in the model structure (Table 1). Many of the more poorly constrained parameters are related to algal physiology (e.g.,  $p_A$ , the maximum production rate of photosynthesis and  $h_A$ , the half-saturation constant for light-limited production of phytoplankton), suggesting that physiological traits or other community-scale processes contribute to lake-to-lake variation (Edwards et al., 2013; Litchman, 2023; Zwart et al., 2015). There is a clear trade-off between generality, ease of use, and specificity in parameterization of any model. For future applications of this model, we have provided constrained intervals from which to pull



**Figure 5.** Predicted and observed values of lake total phosphorus, lake dissolved organic carbon, mixed layer depth ( $z_{\text{mix}}$ ), and gross primary production for the 18 “calibration” lakes (yellow) and 40 “validation” lakes (blue). Diagonal is the 1:1 line, and the yellow and blue lines are linear fits for each set of points. Summary statistics for the validation lakes, including the symmetric mean absolute percent error, the root mean squared error (RMSE), and the linear slope (and ranges of 95% confidence intervals) are shown in the blue box on panels C and (d). Error bars represent  $\pm 1$  standard deviation bars from the MCMC output. In panels A and B, modeled lakes fall exactly on the 1:1 line because of our procedure for estimating  $\text{TP}_{\text{in}}$  and  $\text{DOC}_{\text{in}}$  (see Methods *Model validation*). Note  $\log_{10}$  scale on both axes.

candidate parameter sets and identified parameters on which to focus further empirical and theoretical development (Table 1).

At least three priorities for model refinement are apparent from the systematic biases that we observed in some model predictions. First, the model's omission of internal P loading is a likely explanation for low GPP predictions in lakes receiving very high TP loads (Shatwell & Köhler, 2019; Welch & Cooke, 2005). Inclusion of internal P loading may more accurately capture internal recycling of P that is necessary to sustain such high rates of GPP in these eutrophic systems (Olson & Jones, 2022; Orihel et al., 2017). Second, in clear lakes where the euphotic zone extends below the mixed layer, we may be underestimating pelagic primary production (Leach et al., 2018). Further, benthic primary production can contribute substantially to whole-lake production in shallow and clear lakes (Seekell et al., 2015; Vadeboncoeur et al., 2003), thus improvements on the model should include these important contributors to whole-lake production. Lastly, the model may not capture the complete suite of mechanisms driving mixed-layer depth leading to an overprediction of  $z_{\text{mix}}$  in lakes with a shallow  $z_{\text{mix}}$  (Figure 5c). Currently,  $z_{\text{mix}}$  is a function of DOC concentration and surface area (Box 1; Perez-Fuentetaja



**Figure 6.** Parameter estimates from this study (maximum likelihood estimate and 95% credible interval) compared to the original values used by Kelly et al. (2018) and ranges observed in the literature (Table S1 in Supporting Information S1).  $c_A$  = phosphorus to carbon quota of phytoplankton;  $d$  = dissolved organic carbon (DOC) mineralization rate;  $h_A$  = half-saturation constant for light-limited production of phytoplankton,  $k_A$  = light attenuation coefficient of phytoplankton,  $k_{DOC}$  = light attenuation coefficient of DOC,  $l_A$  = loss rate of phytoplankton,  $m_A$  = half-saturation constant for nutrient-limited production of phytoplankton,  $p_A$  = maximum production rate of photosynthesis,  $q$  = efficiency of phosphorus recycling from lost phytoplankton,  $v$  = sinking rate of phytoplankton.

et al., 1999). However, inclusion of other important predictors including depth and chlorophyll *a* (Hanna, 1990; Osgood, 1988; Perez-Fuentetaja et al., 1999) or more complex representations of  $z_{mix}$  that incorporate wind stirring, convective overturn, and density-induced flows may improve estimates (Hipsey et al., 2019; Krishna et al., 2021). Future work could explore process-based formulations for modeling internal P loading and  $z_{mix}$  and balancing process inclusion and parsimony. Ultimately, integrating our model with a 1D physical model could improve model performance.

Additionally, the absence of a standard way of measuring and reporting water color or chromophoricity precluded our ability to properly pinpoint the role of variation in DOC chromophoricity in estimating GPP. However, inconsistent reporting in DOC composition makes it difficult to test this hypothesis or parameterize  $k_{DOC}$ . Some combinations of UV-Vis absorption and fluorescence spectra indicators such as DOC-specific absorbance at 254 nm, spectral slope ratio, fluorescence index, and others are reported in the literature (Jaffé et al., 2008; Sankar et al., 2020; Spencer et al., 2012). These measurements are representative of various DOM properties, including, but not restricted to, aromaticity, molecular weight, and source. Having simultaneously estimates of DOC, chlorophyll *a*, and  $k_D$  would allow us to better evaluate how much light the DOC is absorbing or not absorbing. Alternatively, in the absence of these measurements for all the lakes, we could improve  $k_{DOC}$  by developing components of the model that allow one to predict chromophoricity of DOC from lake state or other easily measured lake or lake-watershed characteristics.

Along with changes in model structure and parameterization, changes in the types of measurements limnologists make at their field sites may accelerate the process of learning from process-based models. Calls for full lake carbon and nutrient budgets have been made in other contexts; for example, making accurate predictions to climate-driven hydrologic changes (Hanson et al., 2015) or methane emissions (Beaulieu et al., 2019) will require nutrient load data. Recent work has demonstrated the power of empirical nutrient loads to predict lake metabolism (Corman et al., 2023). Nutrient loads are a key input to the model yet only 30% of the lakes had nutrient load measurements. Although 18 lakes were a sufficient sample size for this calibration, the broader application of this model relies on empirical estimates of lake nutrient loads. However, we acknowledge that standardizing nutrient budget estimates across lakes will be a challenge, particularly in hydrologically isolated lakes where inputs are largely diffuse (e.g., groundwater; Lewandowski et al., 2015).

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**5. Conclusion**

Models like the one that we considered here could be applied to understanding patterns and changes in lake ecosystems as they are improved and refined. Although terrestrial ecologists have a long history of model intercomparison projects (Fisher et al., 2014), analogous approaches in limnology have been largely limited to hydrodynamic modeling (e.g., LaKEMIP, ISIMIP). Our empirical test of this simple process model and data-driven calibration of its parameters will allow the limnological community to further test hypotheses and make predictions about lake GPP at broad spatial scales. For example, future applications include simulating potential environmental change impacts on lakes, such as how changes in precipitation or land use may alter GPP in lakes of different sizes and hydrologic settings. Ultimately, the process of iteratively developing, testing, and improving models is the key to moving our field toward better understanding and prediction of lake ecosystem function, allowing us to constrain the fate of C in lentic ecosystems globally.

**Data Availability Statement**

Raw data for this project were contributed by coauthors and compiled from publicly available data repositories by the National Ecological Observatory Network and the North Temperate Lakes Long-Term Ecological Research Program. All the daily metabolism estimates, high frequency sensor data (DO, surface, photosynthetically active radiation, and temperature), lake nutrients, lake nutrient loads, modeled output, and all appropriate metadata, including data provenance for previously published datasets, are available at Environmental Data Initiative via [10.6073/pasta/e27f31948f7bbf4a4af3bc323467e785](https://doi.org/10.6073/pasta/e27f31948f7bbf4a4af3bc323467e785).

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## Erratum

The originally published version of this article contained some errors. The Data Availability Statement should be changed to read as follows: “Raw data for this project were contributed by coauthors and compiled from publicly available data repositories by the National Ecological Observatory Network and the North Temperate Lakes Long-Term Ecological Research Program. All the daily metabolism estimates, high frequency sensor data (DO, surface, photosynthetically active radiation, and temperature), lake nutrients, lake nutrient loads, modeled output, and all appropriate metadata, including data provenance for previously published datasets, are available at Environmental Data Initiative via 10.6073/pasta/e27f31948f7bbf4a4af3bc323467e785.” In addition, the reference for Oleksy et al. (2023) should be changed to the following: Oleksy, I., C.T. Solomon, S.E. Jones, C. Olson, B.L. Bertolet, R. Adrian, et al. (2024). Metabolism dataset: one year of high-frequency temperature, dissolved oxygen, wind, photosynthetically active radiation observations and low-frequency nutrient data for 58 lakes in the Global Lake Ecological Observatory Network. ver 2. Environmental Data Initiative. <https://doi.org/10.6073/pasta/e27f31948f7bbf4a4af3bc323467e785>. The errors have been corrected, and this may be considered the authoritative version of record.