ADVANCING EARTH AND SPACE SCIENCES

JGR Biogeosciences

RESEARCH ARTICLE

10.1029/2024JG008140

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

Isabella A. Oleksy[1,2], Christopher T. Solomon[2], Stuart E. Jones[3], Carly Olson[4], Brittni L. Bertolet[5], Rita Adrian[6], Sheel Bansal[7], Jill S. Baron[8], Soren Brothers[9,10], Sudeep Chandra[11], Hsiu-Mei Chou[12], William Colom-Montero[13], Joshua Culpepper[11,14], Elvira de Eyto[15], Matthew J. Farragher[16], Sabine Hilt[6], Kristen T. Holeck[17], Garabet Kazanjian[18], Marcus Klaus[19], Jennifer Klug[20], Jan Köhler[6], Alo Laas[21], Erik Lundin[22], Alice H. Parkes[23], Kevin C. Rose[24], Lars G. Rustam[17], James Rusak[25,26], Facundo Scordo[11,27,28], Michael J. Vanni[29], Piet Verburg[30], and Gesa A. Weyhenmeyer[31]

[1]Institute for Arctic and Alpine Research, Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO, USA, [2]Cary Institute of Ecosystem Studies, Millbrook, NY, USA, [3]Department of Biological Sciences, University of Notre Dame, Notre Dame, IN, USA, [4]University of Nebraska-Lincoln, School of Natural Resources, Lincoln, NE, USA, [5]Department of Ecology and Evolutionary Biology, University of California Irvine, Irvine, CA, USA, [6]Department of Community and Ecosystem Ecology, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany, [7]U.S. Geological Survey, Northern Prairie Wildlife Research Center, Jamestown, ND, USA, [8]U.S. Geological Survey, Fort Collins Science Center, Fort Collins, CO, USA, [9]Department of Natural History, Royal Ontario Museum, Toronto, ON, Canada, [10]Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada, [11]Global Water Center, Biology Department, University of Nevada Reno, Reno, NV, USA, [12]National Center for High-performance Computing, Hsinchu City, Taiwan, [13]Erken Laboratory, Department of Ecology and Genetics, EBC, Uppsala University, Uppsala, Sweden, [14]Department of Biology, York University, North York, ON, Canada, [15]Fisheries Ecosystems Advisory Services, Marine Institute, Newport, Ireland, [16]University of Maine, School of Biology and Ecology, Climate Change Institute, Orono, ME, USA, [17]Department of Natural Resources and the Environment, Cornell University, Ithaca, NY, USA, [18]Acopian Center for the Environment, American University of Armenia, Yerevan, Armenia, [19]Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden, [20]Biology Department, Fairfield University, Fairfield, CT, USA, [21]Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Tartu, Estonia, [22]Abisko Scientific Research Station, Swedish Polar Research Secretariate, Luleå, Sweden, [23]Université du Québec à Montréal, Sciences Biologiques, Montreal, QC, Canada, [24]Department of Biological Sciences, Rensselaer Polytechnic Institute, Troy, NY, USA, [25]Department of Biology, Queen's University, Kingston, ON, Canada, [26]Dorset Environmental Science Centre, Ontario Ministry of the Environment, Toronto, ON, Canada, [27]Instituto Argentino de Oceanografía, Universidad Nacional del Sur (UNS)-CONICET, Bahía Blanca, Argentina, [28]Departamento de Geografía y Turismo, Universidad Nacional del Sur, Buenos Aires, Argentina, [29]Department of Biology, Miami University, Oxford, OH, USA, [30]School of Geography, Environment and Earth Sciences, Victoria University of Wellington, Wellington, New Zealand, [31]Ecology and Genetics/Limnology, Uppsala University, Uppsala, Sweden

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.

Correspondence to:

I. A. Oleksy,
Isabella.Oleksy@colorado.edu

Citation:

Oleksy, I. A., Solomon, C. T., Jones, S. E., Olson, C., Bertolet, B. L., Adrian, R., et al. (2024). Controls on lake pelagic primary productivity: Formalizing the nutrient-color paradigm. *Journal of Geophysical Research: Biogeosciences*, *129*, e2024JG008140. https://doi.org/10.1029/2024JG008140

Received 25 MAR 2024
Accepted 13 NOV 2024

Author Contributions:

Conceptualization: Christopher T. Solomon, Stuart E. Jones
Data curation: Isabella A. Oleksy, Carly Olson, Brittni L. Bertolet, Rita Adrian, Sheel Bansal, Jill S. Baron, Soren Brothers, Sudeep Chandra, Hsiu-Mei Chou, William Colom-Montero, Joshua Culpepper, Elvira de Eyto, Matthew J. Farragher, Sabine Hilt, Kristen T. Holeck, Garabet Kazanjian, Marcus Klaus, Jennifer Klug, Jan Köhler, Alo Laas, Erik Lundin, Alice H. Parkes, Kevin C. Rose, Lars G. Rustam, James Rusak, Facundo Scordo, Michael J. Vanni, Piet Verburg, Gesa A. Weyhenmeyer
Formal analysis: Isabella A. Oleksy
Funding acquisition: Christopher T. Solomon, Stuart E. Jones
Investigation: Isabella A. Oleksy
Methodology: Christopher T. Solomon, Stuart E. Jones

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.

Project administration: Isabella A. Oleksy
Software: Isabella A. Oleksy, Christopher T. Solomon, Stuart E. Jones
Supervision: Christopher T. Solomon
Validation: Stuart E. Jones, Carly Olson, Brittni L. Bertolet
Visualization: Isabella A. Oleksy
Writing – original draft: Isabella A. Oleksy, Christopher T. Solomon, Stuart E. Jones, Carly Olson, Brittni L. Bertolet
Writing – review & editing: Isabella A. Oleksy, Christopher T. Solomon, Stuart E. Jones, Carly Olson, Brittni L. Bertolet, Rita Adrian, Sheel Bansal, Jill S. Baron, Soren Brothers, Sudeep Chandra, Hsiu-Mei Chou, William Colom-Montero, Joshua Culpepper, Elvira de Eyto, Matthew J. Farragher, Sabine Hilt, Kristen T. Holeck, Garabet Kazanjian, Marcus Klaus, Jennifer Klug, Jan Köhler, Alo Laas, Erik Lundin, Alice H. Parkes, Kevin C. Rose, Lars G. Rustam, James Rusak, Facundo Scordo, Michael J. Vanni, Piet Verburg, Gesa A. Weyhenmeyer

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).

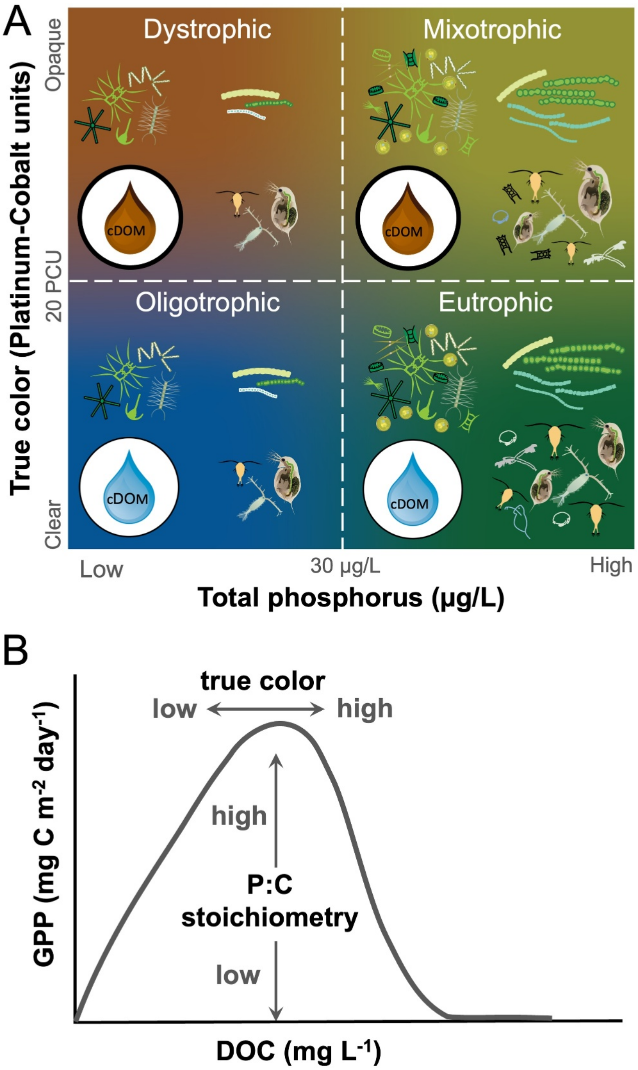


Figure 1. Conceptual diagrams illustrating two different formulations of the nutrient-color paradigm (NCP). (a) In this version, lakes can be classified into four trophic states depending where they fall on an axis of phosphorus concentrations and true color. Figure modified from Meyer et al., 2023 and originally formulated in Williamson et al., 1999. (b) A mathematical formulation of the NCP originally introduced by Kelly et al. (2018). This model predictions 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

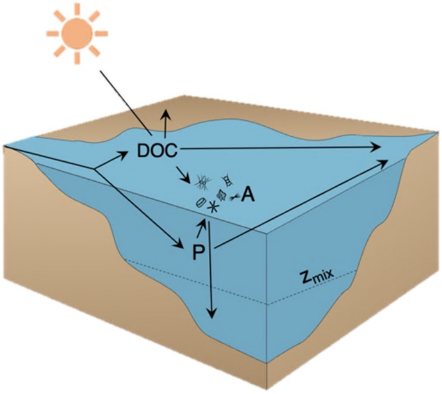
2.1. Overview

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., 2023).

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 kg m^{-3} m^{-1}, a value intermediate between the default in rLakeAnalyzer (Winslow et al., 2019, 0.1 kg m^{-3} m^{-1}) and Lamont et al. (2004, 0.5 kg m^{-3} m^{-1}). Then, we multiplied daily volumetric GPP estimates (mg O_2 L^{-1} 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 (mg C m^2 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 μmol photons m^{-2} s^{-1}, and light at the bottom of the mixed layer $I_{z\text{mix}}$; 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).

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

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

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

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

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

$$k_D = k_{\text{DOC}} C + k_A A \tag{6}$$

$$TP = qA + P \tag{7}$$

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

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

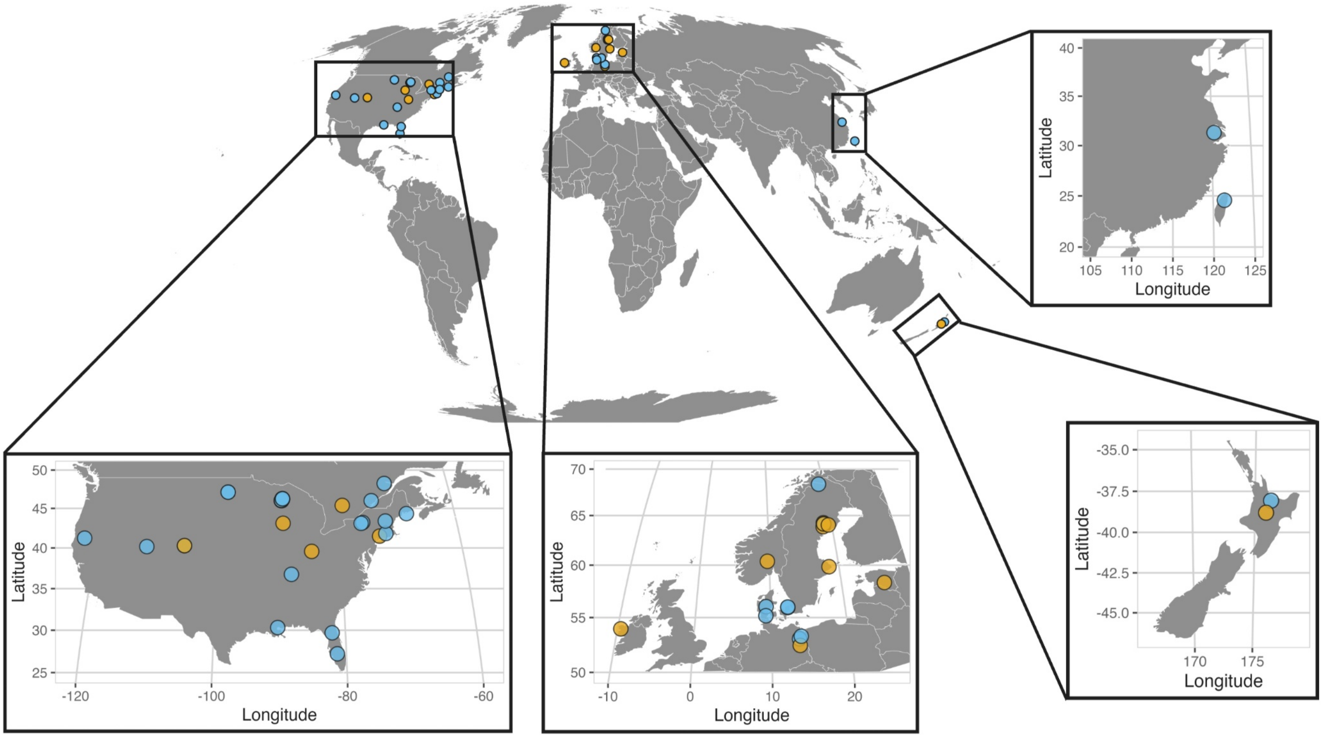


Figure 2. Global distribution of the 58 lakes included in this study. The "calibration" lakes are shaded in yellow and all others ("validation") are in blue.

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_{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_{hat} and effective sample size, N_{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_{DOC}	m^2 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	m^2 g C^{-1}	Light attenuation coefficient of phytoplankton	0.22	0.0009 (0.0004–0.0016)	0.0047–0.14	Morris et al. (1995)
l_A	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	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	μmol photons m^{-2} 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	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 Kalff (1982); Auer et al. (1986); Huisman and Weissing (1995); Gurney and Nisbet (1998); Diehl (2002); Bestion et al. (2018)
d	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	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	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, DOC_{in}, TP_{in}, and z_{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 (DOC_{in} and TP_{in}). Thus, to predict GPP for the validation lakes, we estimated DOC_{in} and TP_{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 DOC_{in} and TP_{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_{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 mg C m^{-2} 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 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 mg L^{-1} and TP from 2.4 to 298.5 μg 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 DOC_{in} and intermediate-to-high TP_{in} and lowest at high DOC_{in} and high DOC_{in}:TP_{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 TP_{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_{mix} (33%; Figure 5). Intercepts and slopes for DOC_{lake}, z_{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).

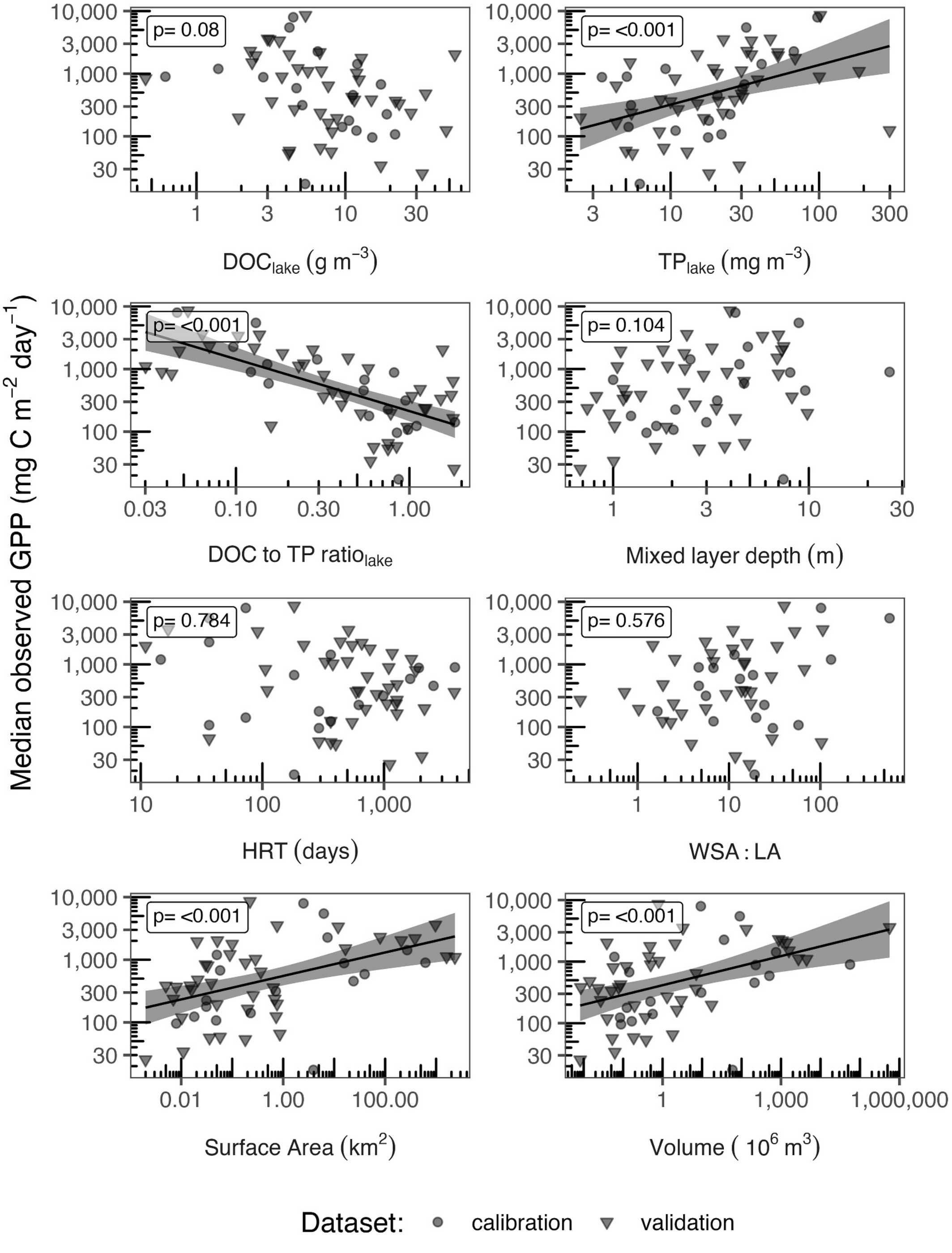


Figure 3. Empirical relationships between median gross primary production and a range of lake chemistry, hydrology, and morphometry variables for the 58 lakes in this study. Bonferroni-corrected p-values are printed on each plot and regression fits with 95% confidence intervals are shown for covariates 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 DOC_{in} and TP_{in} (Figures 5c and 5d). Predicted TP_{lake} and DOC_{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 DOC_{in} and TP_{in} were not available (Figures 5a and 5b). The

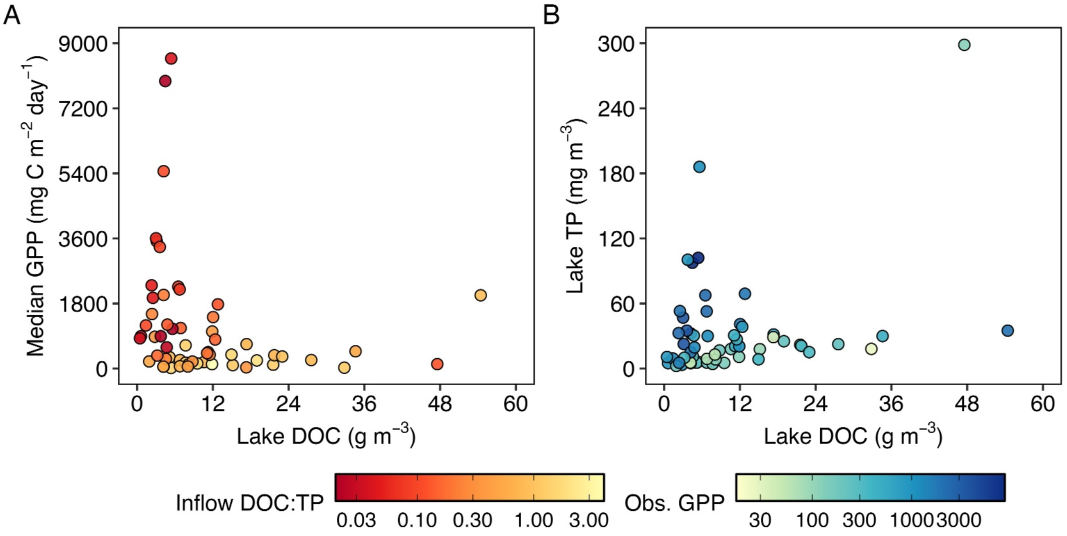


Figure 4. (a) Relationship between lake gross primary production (GPP) and lake dissolved organic carbon (DOC) as a function of DOC:TP of lake inflows and (b) Lake total phosphorus versus lake DOC as a function of GPP. Note $\log_{10}$ scale on legends.

accuracy of the GPP and z_{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).

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_{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_{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

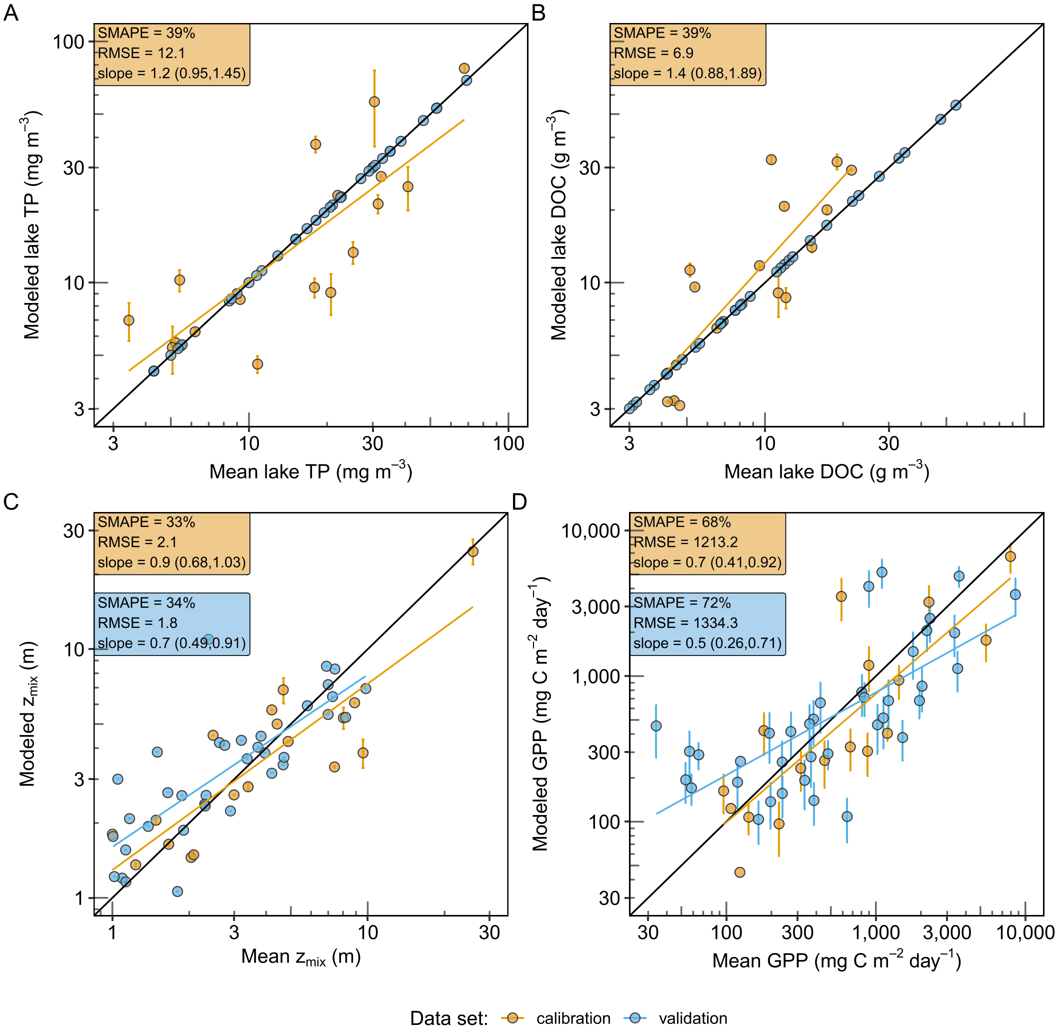


Figure 5. Predicted and observed values of lake total phosphorus, lake dissolved organic carbon, mixed layer depth (z_{mix}), and gross primary production for the 18 "calibration" lakes (yellow) and 40 "validation" lakes (blue). Diagonal is the 1:1 line, and the yellow and blue lines are linear fits 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 ±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 TP_{in} and DOC_{in} (see Methods *Model validation*). Note $\log_{10}$ scale on both axes.

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 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

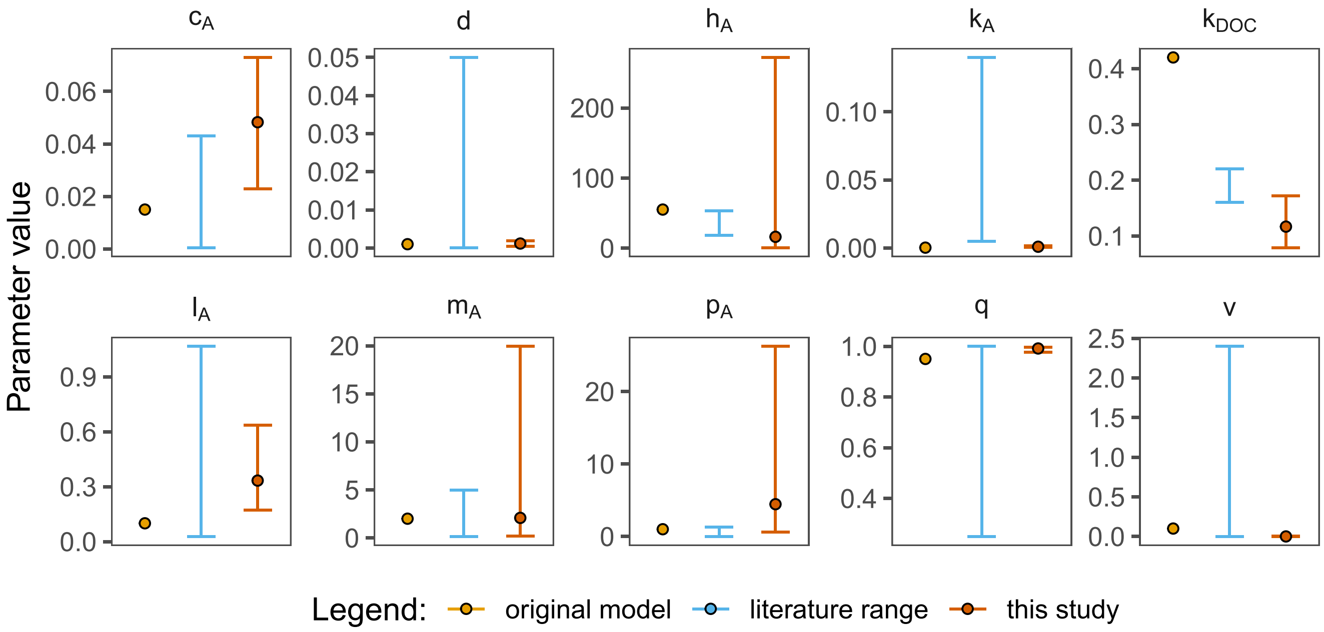


Figure 6. Parameter estimates from this study (maximum likelihood estimate and 95% credible interval) compared to the original values used by Kelly et al. (2018) and ranges observed in the literature (Table S1 in Supporting Information S1). c_A = phosphorus to carbon quota of phytoplankton; d = dissolved 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.

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_{mix} in lakes with a shallow $\mathrm{z}_{\mathrm{mix}}$ (Figure 5c). Currently, z_{mix} is a function of DOC concentration and surface area (Box 1; Perez-Fuentetaja 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 $\mathrm{z}_{\mathrm{mix}}$ 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).

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

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 used in the study are available at Environmental Data Initiative via 10.6073/pasta/d041ff3adf09ebf3f4d947f52fdd2c73.

References

Anderson, T. (1997). *Pelagic nutrient cycles: Herbivores as sources and sinks*. Springer-Verlag.Visser et al.

Auer, M. T., Kieser, M. S., & Canale, R. P. (1986). Identification of critical nutrient levels through field verification of models for phosphorus and phytoplankton growth. *Canadian Journal of Fisheries and Aquatic Sciences*, *43*(2), 379–388. https://doi.org/10.1139/f86-048

Bansal, S., Johnson, O. F., Meier, J. A., & Tangen, B. A. (2021). *Dissolved oxygen concentrations, light penetration, and temperature along the water-depth profile of wetlands P1 and P8 of the Cottonwood Lake Study area in North Dakota, USA, 2019*. U.S. Geological Survey data release. https://doi.org/10.5066/P9Q0OMYS

Beaulieu, J. J., DelSontro, T., & Downing, J. A. (2019). Eutrophication will increase methane emissions from lakes and impoundments during the 21st century. *Nature Communications*, *10*(1), 1375. https://doi.org/10.1038/s41467-019-09100-5

Bergström, A. K., & Karlsson, J. (2019). Light and nutrient control phytoplankton biomass responses to global change in northern lakes. *Global Change Biology*, *25*(6), 2021–2029. https://doi.org/10.1111/gcb.14623

Besag, J., Green, P., Higdon, D., & Mengersen, K. (1995). Bayesian computation and stochastic systems. *Statistical Science*, *10*(1), 3–41. https://doi.org/10.1214/ss/1177010123

Bestion, E., Schaum, C. E., & Yvon-Durocher, G. (2018). Nutrient limitation constrains thermal tolerance in freshwater phytoplankton. *Limnology and Oceanography Letters*, *3*(6), 436–443. https://doi.org/10.1002/lol2.10096

Bogard, M. J., St-Gelais, N. F., Vachon, D., & Giorgio, P. A. (2020). Patterns of spring/summer open-water metabolism across boreal lakes. *Ecosystems*, *23*(8), 1581–1597. https://doi.org/10.1007/s10021-020-00487-7

Caldararu, S., Rolo, V., Stocker, B. D., Gimeno, T. E., & Nair, R. (2023). Ideas and perspectives: Beyond model evaluation–combining experiments and models to advance terrestrial ecosystem science. *Biogeosciences Discussions*, *20*(17), 1–22. https://doi.org/10.5194/bg-20-3637-2023

Corman, J. R., Zwart, J. A., Klug, J., Bruesewitz, D. A., de Eyto, E., Klaus, M., et al. (2023). Response of lake metabolism to catchment inputs inferred using high-frequency lake and stream data from across the northern hemisphere. *Limnology & Oceanography*, *68*(12), 2617–2631. https://doi.org/10.1002/lno.12449

Del Giorgio, P. & Williams, P. (Eds.) (2005)., *Respiration in aquatic ecosystems*. OUP Oxford.

De Nobel, W. T., Huisman, J., Snoep, J. L., & Mur, L. R. (1997). Competition for phosphorus between the nitrogen-fixing cyanobacteria *Anabaena* and *Aphanizomenon*. *FEMS Microbiology Ecology*, *24*(3), 259–267. https://doi.org/10.1016/s0168-6496(97)00067-6

Diehl, S. (2002). Phytoplankton, light, and nutrients in a gradient of mixing depths: Theory. *Ecology*, *83*(2), 386–398. https://doi.org/10.1890/0012-9658(2002)083[0386:plania]2.0.co;2

Dillon, P. J., & Rigler, F. H. (1974). The phosphorus-chlorophyll relationship in lakes. *Limnology & Oceanography*, *19*(5), 767–773. https://doi.org/10.4319/lo.1974.19.5.0767

Edwards, K. F., Litchman, E., & Klausmeier, C. A. (2013). Functional traits explain phytoplankton responses to environmental gradients across lakes of the United States. *Ecology*, *94*(7), 1626–1635. https://doi.org/10.1890/12-1459.1

Evans, C. D., Futter, M. N., Moldan, F., Valinia, S., Frogbrook, Z., & Kothawala, D. N. (2017). Variability in organic carbon reactivity across lake residence time and trophic gradients. *Nature Geoscience*, *10*(11), 832–835. https://doi.org/10.1038/ngeo3051

Fennel, K., Mattern, J. P., Doney, S. C., Bopp, L., Moore, A. M., Wang, B., & Yu, L. (2022). Ocean biogeochemical modelling. *Nature Reviews Methods Primers*, *2*(1), 76. https://doi.org/10.1038/s43586-022-00154-2

Fisher, J. B., Huntzinger, D. N., Schwalm, C. R., & Sitch, S. (2014). Modeling the terrestrial biosphere. *Annual Review of Environment and Resources*, *39*(1), 91–123. https://doi.org/10.1146/annurev-environ-012913-093456

Acknowledgments

We thank the Global Lake Ecological Observatory Network for facilitating the formation of this working group. IAO was supported by the US National Science Foundation awards DEB-1754363, DEB-1754561, EPS-2019528, and OIA-2019528. RA was funded through the "LimnoSCenES" project (AD 91 CE/22-1) supported by BiodivERsA and the Belmont Forum. S. Bansal was funded through U.S. Geological Survey, Ecosystems Mission Area, Land Change Science Research and Development Program; U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research, Grant DE-SC0023084. JSB was funded through USGS Climate R&D program. BLB was funded through US National Science Foundation Postdoctoral Research Fellowship in Biology under Grant 2109350. S. Brothers was funded through Utah Division of Water Quality. WCM was funded through Swedish Infrastructure for Ecosystem Science. MJF was funded through Friends of Acadia Jordan Pond Buoy Grant. KTH was funded through New York State Department of Environmental Conservation (New York Federal Aid in Sport Fish Restoration Project F-63-R); Cornell University Brown Endowment. JC and FS were supported by the University of Nevada Reno's College of Science and Global Water Center. GK was funded through The LandScales project of the Wissenschaftsgemeinschaft Leibniz. AL was supported by the Estonian Research Council Grants PRG1167 and PRG709. AHP was supported by Natural Sciences and Engineering Research Council of Canada CRD 543873-19. KCR was supported by US National Science Foundation awards 2048031 and 1754265. JAR was supported by Natural Science and Engineering Council of Canada Discovery Grant (RGPIN/05199-2018). MJV was funded by US National Science Foundation Grant DEB-0743192. PV was funded by New Zealand's Ministry of Business, Innovation & Employment Grant C01X2205. GAW received financially support from the Swedish Research Council (VR Grant 2020-03222 and FORMAS Grant 2020-01091). GAW was funded by the Swedish Infrastructure for Ecosystem Science (SITES) for provisioning of data from Lake Erken. SITES receives funding through the Swedish Research Council under the Grant 2017-00635. Data collected by the U.S. Geological Survey can be found at Bansal et al. (2021). We further acknowledge the following people and organizations in making this global synthesis possible either via data collection or helpful conversations early in the collaboration: Patrick Kelly, Jacob Zwart, Daniel Langenhaun, Thomas Hintze, Jasmine Saros, David C. Richardson, Tanner Williamson, Keli Goodman, Steve Sadro, John Harrison, Silke Langenhaun, Jan

Karlsson, William Gawley, Scott Daly, the field staff of the Marine Institute in the Burrishoole catchment, New York Department of Environmental Conservation, Castle Lake Environmental Research and Education Program, Loch Vale Watershed Ecological Monitoring and Research Program, and Swedish Infrastructure for Ecosystem Science (SITES; under the Grant 2017-00635 via the Swedish Research Council). We thank several anonymous reviews and Robert Ladwig for their helpful critiques in the development of this manuscript.

Flynn, K. J., & Raven, J. A. (2017). What is the limit for photoautotrophic plankton growth rates? *Journal of Plankton Research*, *39*(1), 13–22. https://doi.org/10.1093/plankt/fbw067

Garnier, J., & Mourelatos, S. (1991). Contribution of grazing in phytoplankton overall losses in a shallow French lake. *Freshwater Biology*, *25*(3), 515–523. https://doi.org/10.1111/j.1365-2427.1991.tb01394.x

Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2013). *Bayesian data analysis*. CRC press.

Gurney, W., & Nisbet, R. M. (1998). *Ecological dynamics*. Oxford University Press.

Hanna, M. (1990). Evaluation of models predicting mixing depth. *Canadian Journal of Fisheries and Aquatic Sciences*, *47*(5), 940–947. https://doi.org/10.1139/f90-108

Hanson, P. C., Hamilton, D. P., Stanley, E. H., Preston, N., Langman, O. C., & Kara, E. L. (2011). Fate of allochthonous dissolved organic carbon in lakes: A quantitative approach. *PLoS One*, *6*(7), e21884. https://doi.org/10.1371/journal.pone.0021884

Hanson, P. C., Pace, M. L., Carpenter, S. R., Cole, J. J., & Stanley, E. H. (2015). Integrating landscape carbon cycling: Research needs for resolving organic carbon budgets of lakes. *Ecosystems*, *18*(3), 363–375. https://doi.org/10.1007/s10021-014-9826-9

Hararuk, O., Zwart, J. A., Jones, S. E., Prairie, Y., & Solomon, C. T. (2018). Model-data fusion to test hypothesized drivers of lake carbon cycling reveals importance of physical controls. *Journal of Geophysical Research: Biogeosciences*, *123*(3), 1130–1142. https://doi.org/10.1002/2017jg004084

Hipsey, M. R., Bruce, L. C., Boon, C., Busch, B., Carey, C. C., Hamilton, D. P., et al. (2019). A general lake model (GLM 3.0) for linking with high-frequency sensor data from the Global Lake Ecological observatory network (GLEON). *Geoscientific Model Development*, *12*(1), 473–523. https://doi.org/10.5194/gmd-12-473-2019

Houser, J. N. (2006). Water color affects the stratification, surface temperature, heat content, and mean epilimnetic irradiance of small lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *63*(11), 2447–2455. https://doi.org/10.1139/f06-131

Huisman, J., Arrayás, M., Ebert, U., & Sommeijer, B. (2002). How do sinking phytoplankton species manage to persist? *The American Naturalist*, *159*(3), 245–254. https://doi.org/10.1086/338511

Huisman, J., Jonker, R. R., Zonneveld, C., & Weissing, F. J. (1999). Competition for light between phytoplankton species: Experimental tests of mechanistic theory. *Ecology*, *80*(1), 211–222. https://doi.org/10.1890/0012-9658(1999)080[0211:cflbps]2.0.co;2

Huisman, J., & Weissing, F. J. (1995). Competition for nutrients and light in a mixed water column: A theoretical analysis. *The American Naturalist*, *146*(4), 536–564. https://doi.org/10.1086/285814

Isles, P. D. F., Creed, I. F., Jonsson, A., & Bergström, A. K. (2021). Trade-offs between light and nutrient availability across gradients of dissolved organic carbon lead to spatially and temporally variable responses of lake phytoplankton biomass to browning. *Ecosystems*, *24*(8), 1837–1852. https://doi.org/10.1007/s10021-021-00619-7

Jaffé, R., McKnight, D., Maie, N., Cory, R., McDowell, W. H., & Campbell, J. L. (2008). Spatial and temporal variations in DOM composition in ecosystems: The importance of long-term monitoring of optical properties: Variations in DOM composition in ecosystems. *Journal of Geophysical Research*, *113*(G4). https://doi.org/10.1029/2008JG000683

Jäger, C. G., & Diehl, S. (2014). Resource competition across habitat boundaries: Asymmetric interactions between benthic and pelagic producers. *Ecological Monographs*, *84*(2), 287–302. https://doi.org/10.1890/13-0613.1

Jassby, A. D., & Goldman, C. R. (1974). Loss rates from a lake phytoplankton community 1. *Limnology & Oceanography*, *19*(4), 618–627. https://doi.org/10.4319/lo.1974.19.4.0618

Jones, R. I. (1992). The influence of humic substances on lacustrine planktonic food-chains. *Hydrobiologia*, *229*(1), 73–91. https://doi.org/10.1007/bf00006992

Jones, S. E., Solomon, C. T., & Weidel, B. C. (2012). Subsidy or subtraction: How do terrestrial inputs influence consumer production in lakes? *Freshwater Reviews*, *5*(1), 37–49. https://doi.org/10.1608/FRJ-5.1.475

Karlsson, J., Bystrom, P., Ask, J., Ask, P., Persson, L., & Jansson, M. (2009). Light limitation of nutrient-poor lake ecosystems. *Nature*, *460*(7254), 506–509. https://doi.org/10.1038/nature08179

Keenan, T. F., Davidson, E., Moffat, A. M., Munger, W., & Richardson, A. D. (2012). Using model-data fusion to interpret past trends, and quantify uncertainties in future projections, of terrestrial ecosystem carbon cycling. *Global Change Biology*, *18*(8), 2555–2569. https://doi.org/10.1111/j.1365-2486.2012.02684.x

Kelly, P. T., Solomon, C. T., Zwart, J. A., & Jones, S. E. (2018). A framework for understanding variation in pelagic gross primary production of lake ecosystems. *Ecosystems*, *21*(7), 1364–1376. https://doi.org/10.1007/s10021-018-0226-4

Kirk, J. (1994). Light and photosynthesis (2nd ed.).

Klausmeier, C. A., Litchman, E., & Levin, S. A. (2004). Phytoplankton growth and stoichiometry under multiple nutrient limitation. *Limnology & Oceanography*, *49*(4part2), 1463–1470. https://doi.org/10.4319/lo.2004.49.4_part_2.1463

Krishna, S., Ulloa, H. N., Kerimoglu, O., Minaudo, C., Anneville, O., & Wüest, A. (2021). Model-based data analysis of the effect of winter mixing on primary production in a lake under reoligotrophication. *Ecological Modelling*, *440*, 109401. https://doi.org/10.1016/j.ecolmodel.2020.109401

Lamont, G., Laval, B., Pawlowicz, R., Pieters, R., & Lawrence, G. A. (2004). Physical mechanisms leading to upwelling of anoxic bottom water in Nitinat Lake. In *17th ASCE engineering mechanisms conference*. University of Delaware.

Lapierre, J. F., Guillemette, F., Berggren, M., & del Giorgio, P. A. (2013). Increases in terrestrially derived carbon stimulate organic carbon processing and CO2 emissions in boreal aquatic ecosystems. *Nature Communications*, *4*(1), 2972. https://doi.org/10.1038/ncomms3972

Lawrence, D. M., Fisher, R. A., Koven, C. D., Oleson, K. W., Swenson, S. C., Bonan, G., et al. (2019). The community land model version 5: Description of new features, benchmarking, and impact of forcing uncertainty. *Journal of Advances in Modeling Earth Systems*, *11*(12), 4245–4287. https://doi.org/10.1029/2018MS001583

Leach, T. H., Beisner, B. E., Carey, C. C., Pernica, P., Rose, K. C., Huot, Y., et al. (2018). Patterns and drivers of deep chlorophyll maxima structure in 100 lakes: The relative importance of light and thermal stratification. *Limnology & Oceanography*, *63*(2), 628–646. https://doi.org/10.1002/lno.10656

Lehman, J. T., & Sandgren, C. D. (1985). Species-specific rates of growth and grazing loss among freshwater algae 1. *Limnology & Oceanography*, *30*(1), 34–46. https://doi.org/10.4319/lo.1985.30.1.0034

Lewandowski, J., Meinikmann, K., Nützmann, G., & Rosenberry, D. O. (2015). Groundwater – The disregarded component in lake water and nutrient budgets. Part 2: Effects of groundwater on nutrients. *Hydrological Processes*, *29*(13), 2922–2955. https://doi.org/10.1002/hyp.10384

Lewis Jr, W. M. (1978). Dynamics and succession of the phytoplankton in a tropical lake: Lake Lanao, Philippines. *Journal of Ecology*, *66*(3), 849–880. https://doi.org/10.2307/2259300

Litchman, E. (2023). Understanding and predicting harmful algal blooms in a changing climate: A trait-based framework. *Limnology and Oceanography Letters*, *8*(2), 229–246. https://doi.org/10.1002/lol2.10294

Litchman, E., & Klausmeier, C. A. (2001). Competition of phytoplankton under fluctuating light. *The American Naturalist*, *157*(2), 170–187. https://doi.org/10.1086/318628

Maberly, S. C., Pitt, J.-A., Davies, P. S., & Carvalho, L. (2020). Nitrogen and phosphorus limitation and the management of small productive lakes. *Inland Waters*, *10*(2), 159–172. https://doi.org/10.1080/20442041.2020.1714384

Meyer, M. F., Topp, S. N., King, T. V., Ladwig, R., Pilla, R. M., Dugan, H. A., et al. (2023). *National-scale, remotely sensed lake trophic state (LTS-US) 1984-2020 ver 1*. Environmental Data Initiative. https://doi.org/10.6073/pasta/212a3172ac36e8dc6e1862f9c2522fa4

Morris, D. P., Zagarese, H., Williamson, C. E., Balseiro, E. G., Hargreaves, B. R., Modenutti, B., et al. (1995). The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnology & Oceanography*, *40*(8), 1381–1391. https://doi.org/10.4319/lo.1995.40.8.1381

Naumann, E. (1921). *Einige Grundlinien der Regionalen Limnologie—Lund* (p. 17). Lunds Universitets, Arsskript NI.

Oleksy, I., Solomon, C. T., Jones, S. E., Olson, C., Bertolet, B. L., Adrian, R., et al. (2023). *One year of high-frequency temperature, dissolved oxygen, wind, photosynthetically active radiation observations and low-frequency nutrient data for 58 lakes in the Global Ecological Observatory Network ver 1*. Environmental Data Initiative. https://doi.org/10.6073/pasta/d041ff3adf09ebf3f4d947f52fdd2c73

Olson, C. R., & Jones, S. E. (2022). Chlorophyll–total phosphorus relationships emerge from multiscale interactions from algae to catchments. *Limnology and Oceanography Letters*, *7*(6), 483–491. https://doi.org/10.1002/lol2.10281

Olson, C. R., Solomon, C. T., & Jones, S. E. (2020). Shifting limitation of primary production: Experimental support for a new model in lake ecosystems. *Ecology Letters*, *23*(12), 1800–1808. https://doi.org/10.1111/ele.13606

Orihel, D. M., Baulch, H. M., Casson, N. J., North, R. L., Parsons, C. T., Seckar, D. C., & Venkiteswaran, J. J. (2017). Internal phosphorus loading in Canadian fresh waters: A critical review and data analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(12), 2005–2029. https://doi.org/10.1139/cjfas-2016-0500

Osgood, R. A. (1988). Lake mixis and internal phosphorus dynamics. *Archiv für Hydrobiologie*, *113*(4), 629–638. https://doi.org/10.1127/archiv-hydrobiol/113/1988/629

Peng, C., Guiot, J., Wu, H., Jiang, H., & Luo, Y. (2011). Integrating models with data in ecology and palaeoecology: Advances towards a model–data fusion approach. *Ecology Letters*, *14*(5), 522–536. https://doi.org/10.1111/j.1461-0248.2011.01603.x

Perez-Fuentetaja, A., Dillon, P. J., Yan, N. D., & McQueen, D. J. (1999). *Significance of dissolved organic carbon in the prediction of thermocline depth in small Canadian shield lakes*.

Puts, I. C., Ask, J., Deininger, A., Jonsson, A., Karlsson, J., & Bergström, A. (2023). Browning affects pelagic productivity in northern lakes by surface water warming and carbon fertilization. *Global Change Biology*, *29*(2), 375–390. https://doi.org/10.1111/gcb.16469

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Read, J. S., & Rose, K. C. (2013). Physical responses of small temperate lakes to variation in dissolved organic carbon concentrations. *Limnology & Oceanography*, *58*(3), 921–931. https://doi.org/10.4319/lo.2013.58.3.0921

Reynolds, C. S. (1984). *The ecology of freshwater phytoplankton* (Vol. 384). Cambridge University Press.

Sankar, M. S., Dash, P., Lu, Y., Mercer, A. E., Turnage, G., Shoemaker, C. M., et al. (2020). Land use and land cover control on the spatial variation of dissolved organic matter across 41 lakes in Mississippi, USA. *Hydrobiologia*, *847*(4), 1159–1176. https://doi.org/10.1007/s10750-019-04174-0

Scavia, D., & Fahnenstiel, G. L. (1987). Dynamics of lakelake Michigan phytoplankton: Mechanisms controlling epilimnetic communities. *Journal of Great Lakes Research*, *13*(2), 103–120. https://doi.org/10.1016/s0380-1330(87)71635-9

Schindler, D. W. (1977). Evolution of phosphorus limitation in lakes. *Science*, *195*(4275), 260–262. https://doi.org/10.1126/science.195.4275.260

Seekell, D. A., Lapierre, J. F., Ask, J., Bergström, A. K., Deininger, A., Rodríguez, P., & Karlsson, J. (2015). The influence of dissolved organic carbon on primary production in northern lakes. *Limnology & Oceanography*, *60*(4), 1276–1285. https://doi.org/10.1002/lno.10096

Senar, O. E., Creed, I. F., & Trick, C. G. (2021). Lake browning may fuel phytoplankton biomass and trigger shifts in phytoplankton communities in temperate lakes. *Aquatic Sciences*, *83*(2), 21. https://doi.org/10.1007/s00027-021-00780-0

Shatwell, T., & Köhler, J. (2019). Decreased nitrogen loading controls summer cyanobacterial blooms without promoting nitrogen-fixing taxa: Long-term response of a shallow lake. *Limnology & Oceanography*, *64*(S1), S166–S178. https://doi.org/10.1002/lno.11002

Smith, R. E., & Kalff, J. (1982). Size-dependent phosphorus uptake kinetics and cell quota in phytoplankton 1. *Journal of Phycology*, *18*(2), 275–284. https://doi.org/10.1111/j.1529-8817.1982.tb03184.x

Soares, L. M. V., & Calijuri, M. C. (2021). Deterministic modelling of freshwater lakes and reservoirs: Current trends and recent progress. *Environmental Modelling and Software*, *144*, 105143. https://doi.org/10.1016/j.envsoft.2021.105143

Soetaert, K., Petzoldt, T., & Setzer, R. W. (2010). Solving differential equations in R: Package deSolve. *Journal of Statistical Software*, *33*(9), 1–25. https://doi.org/10.18637/jss.v033.i09

Solomon, C. T., Bruesewitz, D. a., Richardson, D. C., Rose, K. C., Van de Bogert, M. C., Hanson, P. C., et al. (2013). Ecosystem respiration: Drivers of daily variability and background respiration in lakes around the globe. *Limnology & Oceanography*, *58*(3), 849–866. https://doi.org/10.4319/lo.2013.58.3.0849

Spencer, R. G. M., Butler, K. D., & Aiken, G. R. (2012). Dissolved organic carbon and chromophoric dissolved organic matter properties of rivers in the USA: Dissolved organic matter in U.S. Rivers. *Journal of Geophysical Research*, *117*(G3). https://doi.org/10.1029/2011JG001928

Thienemann, A. (1925). *Die Binnengewässer Mitteleuropas: eine limnologische Einführung*. E. Schweizerbart.

Thingstad, T. F., & Sakshaug, E. (1990). Control of phytoplankton growth in nutrient recycling ecosystems. Theory and terminology. *Marine Ecology Progress Series*, *63*, 261–272. https://doi.org/10.3354/meps063261

Thottathil, S. D., Reis, P. C. J., del Giorgio, P. A., & Prairie, Y. T. (2018). The extent and regulation of summer methane oxidation in northern lakes. *Journal of Geophysical Research: Biogeosciences*, *123*(10), 3216–3230. https://doi.org/10.1029/2018JG004464

Tilzer, M. M. (1984). Estimation of phytoplankton loss rates from daily photosynthetic rates and observed biomass changes in Lake Constance. *Journal of Plankton Research*, *6*(2), 309–324. https://doi.org/10.1093/plankt/6.2.309

Trentman, M. T., Jr Hall, R. O., & Valett, H. M. (2023). Exploring the mismatch between the theory and application of photosynthetic quotients in aquatic ecosystems. *Limnology and Oceanography Letters*, *8*(4), 565–579. https://doi.org/10.1002/lol2.10326

Vadeboncoeur, Y., Jeppesen, E., Zanden, M. J. V., Schierup, H. H., Christoffersen, K., & Lodge, D. M. (2003). From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. *Limnology & Oceanography*, *48*(4), 1408–1418. https://doi.org/10.4319/lo.2003.48.4.1408

Vadeboncoeur, Y., Peterson, G., Vander Zanden, M. J., & Kalff, J. (2008). Benthic algal production across lake size gradients: Interactions among morphometry, nutrients, and light. *Ecology*, *89*(9), 2542–2552. https://doi.org/10.1890/07-1058.1

Vasconcelos, F. R., Diehl, S., Rodríguez, P., Karlsson, J., & Byström, P. (2018). Effects of terrestrial organic matter on aquatic primary production as mediated by pelagic–benthic resource fluxes. *Ecosystems*, *21*(6), 1255–1268. https://doi.org/10.1007/s10021-017-0217-x

Visser, P., Ibelings, B. A. S., Van Der Veer, B., Koedood, J. A. N., & Mur, R. (1996). Artificial mixing prevents nuisance blooms of the cyanobacterium Microcystis in Lake Nieuwe Meer, The Netherlands. *Freshwater Biology*, *36*(2), 435–450. https://doi.org/10.1046/j.1365-2427.1996.00093.x

Visser, P. M., Passarge, J., & Mur, L. R. (1997). Modelling vertical migration of the cyanobacterium Microcystis. *Hydrobiologia*, *349*, 99–109.

Vollenweider, R. A. (1968). *Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication*. (p. 192).

Webster, K. E., Soranno, P. A., Cheruvelil, K. S., Bremigan, M. T., Downing, J. A., Vaux, P. D., et al. (2008). An empirical evaluation of the nutrient-color paradigm for lakes. *Limnology & Oceanography*, *53*(3), 1137–1148. https://doi.org/10.4319/lo.2008.53.3.1137

Welch, E. B., & Cooke, G. D. (2005). Internal phosphorus loading in shallow lakes: Importance and control. *Lake and Reservoir Management*, *21*(2), 209–217. https://doi.org/10.1080/07438140509354430

Williams, M., Schwarz, P. A., Law, B. E., Irvine, J., & Kurpius, M. R. (2005). An improved analysis of forest carbon dynamics using data assimilation. *Global Change Biology*, *11*(1), 89–105. https://doi.org/10.1111/j.1365-2486.2004.00891.x

Williamson, C. E., Morris, D. P., Pace, M. L., & Olson, A. G. (1999). Dissolved organic carbon and nutrients as regulators of lake ecosystems: Resurrection of a more integrated paradigm. *Limnology & Oceanography*, *44*(3part2), 795–803. https://doi.org/10.4319/lo.1999.44.3_part_2.0795

Winslow, L., Read, J., Woolway, R., Brentrup, J., Leach, T., Zwart, J., et al. (2019). Package 'rLakeAnalyzer. *Lake Phys Tools*, *6*(9).

Xu, P., Liu, Y., Shen, Y., & Fukuda, Y. (2007). Estimability analysis of variance and covariance components. *Journal of Geodesy*, *81*(9), 593–602. https://doi.org/10.1007/s00190-006-0122-0

Zwart, J. A., Solomon, C. T., & Jones, S. E. (2015). Phytoplankton traits predict ecosystem function in a global set of lakes. *Ecology*, *96*(8), 2257–2264. https://doi.org/10.1890/14-2102.1

References From the Supporting Information

Arst, H., Noges, T., Noges, P., & Paavel, B. (2008b). Relations of phytoplankton in situ primary production, chlorophyll concentration and underwater irradiance in turbid lakes. *European Large Lakes Ecosystem changes and their ecological and socioeconomic impacts*, 169–176.

de Wit, H. A., Couture, R. M., Jackson-Blake, L., Futter, M. N., Valinia, S., Austnes, K., et al. (2018). Pipes or chimneys? For carbon cycling in small boreal lakes, precipitation matters most. *Limnology and Oceanography Letters*, *3*(3), 275–284. https://doi.org/10.1002/lol2.10077

Deininger, A., Jonsson, A., Karlsson, J., & Bergström, A.-K. (2019). Pelagic food webs of humic lakes show low short-term response to forest harvesting. *Ecological Applications*, *29*(1), e01813. https://doi.org/10.1002/eap.1813

Hamilton, D. P., O'Brien, K. R., Burford, M. A., Brookes, J. D., & McBride, C. G. (2010). Phosphorus sources and demand in deep, warm monomictic lakes. *Aquatic Sciences*, *72*(3), 295–307. https://doi.org/10.1007/s00027-010-0131-1

Kamarainen, A. M., Penczykowski, R. M., Van de Bogert, M. C., Hanson, P. C., & Carpenter, S. R. (2009). Phosphorus sources and demand during summer in a eutrophic lake. *Aquatic Sciences*, *71*(2), 214–227. https://doi.org/10.1007/s00027-009-9165-7

Lafrancois, B. M., Nydick, K. R., Johnson, B. M., & Baron, J. S. (2004). Cumulative effects of nutrients and pH on the plankton of two mountain lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *61*(7), 1153–1165. https://doi.org/10.1139/f04-053

Molot, L. A., & Dillon, P. (1991). Nitrogen/phosphorus ratios and the prediction of chlorophyll in phosphorus-limited lakes in central Ontario. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*(1), 140–145. https://doi.org/10.1139/f91-019

Peterson, G. D., Beard, T. D., Beisner, B. E., Bennett, E. M., Carpenter, S. R., Cumming, G. S., et al. (2003). Assessing future ecosystem services: A case study of the northern highlands lake district, Wisconsin. *Conservation Ecology*, *7*(3), art1. https://doi.org/10.5751/es-00557-070301

Poste, A. E., Veiteberg Braaten, H. F., de Wit, H. A., Sørensen, K., & Larssen, T. (2015). Effects of photodemethylation on the methylmercury budget of boreal Norwegian lakes. *Environmental Toxicology and Chemistry*, *34*(6), 1213–1223. https://doi.org/10.1002/etc.2923

Rusak, J. A., Tanentzap, A. J., Klug, J. L., Rose, K. C., Hendricks, S. P., Jennings, E., et al. (2018). Wind and trophic status explain within and among-lake variability of algal biomass. *Limnology and Oceanography Letters*, *3*(6), 409–418. https://doi.org/10.1002/lol2.10093

Shatwell, T., Adrian, R., & Kirillin, G. (2016). Planktonic events may cause polymictic-dimictic regime shifts in temperate lakes. *Scientific Reports*, *6*(1), 24361. https://doi.org/10.1038/srep24361

Solomon, C., Jones, S., Weidel, B. C., Bertolet, B., Bishop, C., Coloso, J., et al. (2022). *MFE database: Data from ecosystem ecology research by Jones, Solomon, and collaborators on the ecology and biogeochemistry of lakes and lake organisms in the Upper Midwest*. https://doi.org/10.25390/caryinstitute.7438598.v6

Sparber, K., Dalton, C., de Eyto, E., Jennings, E., Lenihan, D., & Cassina, F. (2015). Contrasting pelagic plankton in temperate Irish lakes: The relative contribution of heterotrophic, mixotrophic, and autotrophic components, and the effects of extreme rainfall events. *Inland Waters*, *5*(3), 295–310. https://doi.org/10.5268/iw-5.3.828

Vadeboncoeur, Y., Devlin, S. P., McIntyre, P. B., & Vander Zanden, M. J. (2014). Is there light after depth? Distribution of periphyton chlorophyll and productivity in lake littoral zones. *Freshwater Science*, *33*(2), 524–536. https://doi.org/10.1086/676315