

A Framework for Understanding Variation in Pelagic Gross Primary Production of Lake Ecosystems

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ABSTRACT

Light and nutrient availability are key physiological constraints for primary production. Widespread environmental changes are causing variability in loads of terrestrial dissolved organic carbon (DOC) and nutrients from watersheds to lakes, contributing to simultaneous changes in both light and nutrient supply. Experimental evidence highlights the potential for these watershed loads to create complex and context-dependent responses of within-lake primary production; however, the field lacks a predictive model to investigate these responses. We embedded a well-established physiological model of phytoplankton growth within an ecosystem model of nutrient and DOC supply to assess how simultaneous changes in DOC and nutrient loads could impact pelagic primary production in lakes. The model generated a unimodal relationship between GPP and DOC concentration when loads of DOC and nutrients were tightly correlated across space or time. In this unimodal relationship, the magnitude of the peak GPP was primarily determined by the DOC-to-nutrient ratio of the load, and the location of

the peak along the DOC axis was primarily determined by lake area. Greater nutrient supply relative to DOC load contributed to greater productivity, and larger lake area increased light limitation for primary producers at a given DOC concentration, owing to the positive relationship between lake area and epilimnion depth. When loads of DOC and nutrients were not tightly correlated in space or time, the model generated a wedge-shaped pattern between GPP and DOC, consistent with spatial surveys from a global set of lakes. Our model is thus capable of unifying the diversity of empirically observed spatial and temporal responses of lake productivity to DOC and mineral nutrient supply presented in the literature, and provides qualitative predictions for how lake pelagic primary productivity may respond to widespread environmental changes.

Key words: gross primary production; dissolved organic carbon; nutrient loads; phytoplankton; ecosystem model; light limitation.

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INTRODUCTION

Models predicting ecosystem productivity are important to understanding global fluxes and storage of carbon and other elements, and are key to predicting ecosystem responses to widespread environmental changes (Dillon and Rigler 1974; Vitousek and Reiners 1975; Sato and others 2007).

In general, these models leverage a physiological framework in which ecosystem processes are governed by specific environmental constraints, like atmospheric CO₂ concentration, temperature, and the availability of light and nutrients. Assessing the role of these constraints in regulating ecosystem productivity under significant environmental change is vital to forecasting how biogeochemical cycling is likely to change in the future.

The main regulators of lake primary productivity—water column light and nutrient availability—have undergone significant change and are likely to continue to change into the future due to anthropogenic activity. For example, there has been a marked increase in terrestrially derived dissolved organic carbon (DOC) loading from watersheds to lakes in the northern hemisphere (Monteith and others 2007). The chromophoric, light absorbing properties of terrestrial DOC change the vertical distribution of light and heat through the water column, with greater concentrations of DOC increasing the rate of light extinction, and reducing the depth of the mixed surface layer (Kirk 1994; Morris and others 1995; Williamson and others 1996; Houser 2006; Read and Rose 2013). The combined impacts on light extinction and mixed-layer depth are important for controlling light availability for pelagic primary producers, as they regulate the habitat depth for phytoplankton, as well as the light available at a given depth (Kunz and Diehl 2003). Additionally, nutrient concentrations in lakes have undergone significant changes due to anthropogenic activity (Arbuckle and Downing 2001; Raïke and others 2003; Abell and others 2011). Increases in fertilizer applications have led to increased delivery of both nitrogen and phosphorus to lakes, particularly in watersheds dominated by agricultural land use (Carpenter and others 1998; Cooke and Prepas 1998; Fraterrigo and Downing 2008; Abell and others 2011). In some north temperate or boreal systems, most of the nutrient load may be directly coupled to DOC load (Dillon and Molot 1997), and therefore, increases in nutrient loads may be a function of DOC-associated nutrients (Lennon and Pfaff 2005). Regardless of origin (anthropogenic or DOC-associated), these increases in nutrient supply can decrease nutrient limitation for phytoplankton, thereby increasing primary productivity.

Ongoing, concurrent changes in terrestrial DOC and nutrient loads simultaneously influence light and nutrient limitation in lakes and potentially create unexpected and context-dependent responses in primary production. Cross-lake surveys have highlighted the potential for a wedge-shaped

negative relationship between areal gross primary production (GPP) and lake DOC concentration, with variable GPP at low DOC but always low GPP at high DOC (Karlsson and others 2009; Solomon and others 2013). These spatial surveys suggest strong control of GPP by DOC via its effects on light availability. In contrast, Zwart and others (2016) observed an unexpected increase in GPP following a whole-lake experimental increase in DOC concentration. They attributed this result to two mechanisms: a DOC-induced reduction in mixed-layer depth which offset the effect of DOC-induced light extinction on the average light availability for epilimnetic phytoplankton and an increase in phosphorus load concurrent with the increase in DOC inputs. Seekell and others (2015) further highlighted the potential for concurrent increases in both DOC and nutrient concentration to increase GPP, as they observed a unimodal relationship between lake DOC and whole-lake primary production. This unimodal relationship was hypothesized to be due to a shift from nutrient limitation to strong light limitation as lake DOC concentration increased. Additionally, Finstad and others (2014) observed unimodal relationships between lake DOC concentration and fish catch per unit effort, which may be due to a similar unimodal pattern in resource flow up the food web.

Light climate as influenced by the chromophoricity of DOC and lake size may also be essential factors in determining the response of primary production to changes in watershed loads. The chromophoricity of DOC may be variable due to bleaching and microbial processing (Tranvik and others 2009; Hanson and others 2011), ultimately impacting the degree of light attenuation by DOC and light climate in the mixed layer. In addition, physical processes that vary in importance with lake size may have a significant impact on mixed-layer depth and ultimately lead to systematic patterns between lake size and light climate. In particular, as lake size increases, wind-driven mixing becomes increasingly important to turbulence in the lake surface waters (Imberger and Parker 1985; Mazumder and Taylor 1994) contributing to greater mixed-layer depths in large lakes relative to smaller lakes at a given light extinction (Fee and others 1996). This increases the mean depth occupied by phytoplankton circulating within the mixed surface layer and thus decreases the mean light availability that they experience. Light limitation may therefore be stronger in large lakes than small lakes given the same light attenuation (Diehl 2002; Diehl and others 2002).

Despite a general understanding of how DOC and nutrient loads impact lake productivity, there is not yet a model that captures the complex interacting chemical and physical effects of nutrient and DOC load and lake area on lake pelagic primary productivity. A process-based model may provide important context for how concurrent changes in DOC and nutrient load interact with lake morphological characteristics to regulate pelagic primary production. Additionally, process-based models may unify the varying relationships between pelagic primary production and DOC concentration found in the literature, which have included wedge-shaped and unimodal relationships between lake DOC concentration and lake GPP (Hanson and others 2003; Ask and others 2009; Solomon and others 2013; Seekell and others 2015; Zwart and others 2016). We use an algal physiological model embedded within a lake ecosystem model to explore how concurrent changes in DOC and nutrient load (or DOC:nutrient load stoichiometry) impact lake GPP. We predict that light and nutrient limitation will lead to a unimodal response of lake GPP as DOC loads (and correlated nutrient loads) increase. We also predict that the relationship between load stoichiometry and lake GPP response will be a function of light climate, with the location of GPP along a DOC axis due to variable chromophoricity of DOC and a greater increase in light limitation per unit DOC increase in large lakes than in small ones (Figure 1). Results from our model provide important insights into the complex and context-dependent responses of lake productivity to changes in loads from the watershed, and reveal a process-based understanding of how lake primary production will respond to future widespread environmental changes.

METHODS

Model Overview

We used a well-established algal physiological model (Huisman and Weissing 1994) embedded within a lake ecosystem model to explore the impact of DOC and nutrient loads on lake pelagic primary productivity. For simplicity, we assumed that phosphorus was the limiting nutrient for pelagic phytoplankton (Schindler 1977; but see Sterner 2008), and therefore only modeled loads and cycling of bioavailable phosphorus within the lake. We assumed that phytoplankton growth was restricted to the mixed surface layer, and therefore modeled dynamics in the mixed layer of a consistently stratified lake. The hydrology of the lake was

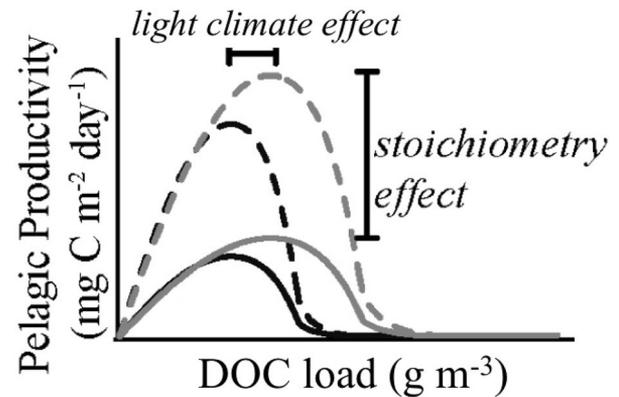


Figure 1. Hypotheses regarding the response of lake pelagic GPP to changes in DOC load [g inflowing DOC (m^{-3})] for a lake with a given residence time. We expect a unimodal relationship between GPP and DOC loads as loads of DOC and phosphorus increase at a constant C:P stoichiometry. Lake transition from nutrient limitation under low DOC and phosphorus loads to light limitation as DOC load increases past a threshold. We predict that the height of the maximum in GPP is primarily a function of the load carbon-to-phosphorus stoichiometry (stoichiometry effect, *solid vs. dashed lines*), as lower C:P loads will more rapidly increase phosphorus availability for a given increase in DOC load. We predict that the location of the light limitation threshold on the DOC axis is primarily related to light availability and lake size (light climate effect). Larger lakes will be more light-limited, as they retain deeper mixed layers due to wind-driven mixing compared to smaller lakes at the same DOC concentration. Therefore, we predict the light limitation threshold to be at a lower DOC concentration in larger lakes. Additionally, variable chromophoricity of DOC may increase or decrease the DOC concentration of the maximum in GPP as chromophoricity impacts the strength of light extinction by DOC, and ultimately the light climate for phytoplankton.

controlled by hydrologic inflow and outflow to/from the mixed layer, ignoring evaporation and precipitation for simplicity. We describe the model in the following sections and summarize parameter values and units in Table 1.

Algal Biomass and Primary Production

Growth of pelagic algal biomass (A) was modeled as a function of productivity in the mixed surface layer (r ; Eq. 2) limited by light and nutrients and loss of algae, which included mortality (l ; Anderson 1997), sinking (v ; Berger and others 2006), and loss from the outflow (which has discharge equal to the inflow, Q_{in}):

$$\frac{dA}{dt} = rA - lA - \frac{v}{z_{\text{mix}}}A - \frac{Q_{\text{in}}}{V_{\text{epi}}}A \quad (1)$$

V_{epi} represents the volume of the mixed surface layer, which is the product of mixed-layer depth (z_{mix} ; see Eq. 7) and lake surface area (S_A).

Our model describes pelagic primary production as a function of light and nutrient limitation of phytoplankton, and these are influenced by concentrations of DOC and phosphorus. We formulated mixed-layer integrated primary productivity similar to Jäger and Diehl (2014) and Huisman and Weissing (1994), with co-limitation by light and phosphorus modeled multiplicatively:

$$r = \frac{p_A}{k_D * z_{\text{mix}}} * \ln\left(\frac{h + I_0}{h + I_{z_{\text{mix}}}}\right) * \frac{P}{P + m} \quad (2)$$

where k_D is light attenuation (see Eq. 6), and the maximum gross primary production rate of phytoplankton (p_A) is reduced by light (light at the surface— I_0 and light at the bottom of the mixed layer— $I_{z_{\text{mix}}}$; see Eq. 8) and dissolved phosphorus availability (P) and their respective half-saturation constants (h and m). We assume that all inflowing and lake dissolved phosphorus (P) is accessible to phytoplankton (that is, bioavailable). Equilibrium areal lake GPP estimates were the product of equilibrium phytoplankton growth rate, phytoplankton volumetric density, and mixed-layer depth (rAz_{mix}).

Lake Hydrologic and Biogeochemical Characteristics

We modeled DOC and dissolved phosphorus as concentrations in the mixed surface layer of the lake. DOC concentration in the mixed layer (C) was modeled as a function of hydrologic inputs and losses from mineralization (d) and outflow:

$$\frac{dC}{dt} = \frac{Q_{\text{in}}}{V_{\text{epi}}} (C_{\text{in}} - C) - dC \quad (3)$$

where C_{in} is the concentration of DOC in the inflowing water. For mixed-layer phosphorus concentration (P), sources of bioavailable phosphorus inputs included external supply from inflow and recycling from dead phytoplankton. Losses of phosphorus from the water included uptake by phytoplankton within the mixed layer and direct outflow:

$$\frac{dP}{dt} = \frac{Q_{\text{in}}}{V_{\text{epi}}} (P_{\text{in}} - P) + qIAe - qrA \quad (4)$$

where P_{in} is inlet dissolved phosphorus concentration, q is algal phosphorus quota, r is phytoplankton production rate (see Eq. 2), and e is recycling efficiency of phosphorus from dead phytoplankton. Volume of the mixed layer (V_{epi}) is variable as mixed-layer depth (z_{mix}) is a function of DOC concentration (C) and lake size (S_A ; see Eq. 7). One

Table 1. Parameter Description and Values Used for GPP Model

Parameter	Description	Value	Units
A	Algal biomass concentration in mixed layer	–	mg C m ⁻³
P	Phosphorus concentration in mixed layer	–	mg P m ⁻³
C	DOC concentration in mixed layer	–	g C m ⁻³
l	Loss rate of phytoplankton	0.1	day ⁻¹
v	Sinking rate of phytoplankton	0.1	m day ⁻¹
Q_{in}	Inflow discharge	Variable	m ⁻³ day ⁻¹
V_{epi}	Epilimnetic volume	Variable	m ³
C_{in}	DOC load concentration	Variable	g C m ⁻³
P_{in}	Dissolved phosphorus load concentration	Variable	mg P m ⁻³
q	Phosphorus to carbon quota of phytoplankton	0.015	mg P mg C ⁻¹
e	Efficiency of phosphorus recycling from lost phytoplankton	0.95	unitless
S_A	Lake surface area	0.01, 0.1, 1, 10	km ²
d	DOC mineralization rate	0.001	day ⁻¹
p_A	Maximum production rate of phytoplankton	1	day ⁻¹
I_0	Incoming light	600	μmol photons m ⁻² s ⁻¹
h	Half-saturation constant for light-limited production of phytoplankton	55	μmol photons m ⁻² s ⁻¹
m	Half-saturation constant for nutrient-limited production of phytoplankton	2	mg P m ⁻³
k_A	Light attenuation coefficient of pelagic phytoplankton	0.00022	m ² mg C ⁻¹
k_C	Light attenuation coefficient of DOC	0.00042	m ² mg C ⁻¹

quantity of interest in our examination of model dynamics is the ratio of DOC to P loaded to the lake, which we calculate on a mass:mass, g C (g P)⁻¹, basis from C_{in} and P_{in} and refer to as the C:P stoichiometry of the load.

For comparison with empirical observations, we calculated in-lake total phosphorus concentration (TP) as the sum of phosphorus in algal biomass and dissolved, bioavailable phosphorus:

$$TP = qA + P \quad (5)$$

Light Availability

We modeled light availability (photosynthetically active radiation) and light limitation for phytoplankton as a function of both light attenuation (k_D) and mixed-layer depth (z_{mix}) to give light availability at the bottom of the mixed layer ($I_{z_{mix}}$). Light attenuation (k_D) was calculated based on an adaptation from a statistical model from Morris and others (1995) and was the sum of the attenuations due to DOC (k_C), algal biomass (k_A):

$$k_D = k_C C + k_A A \quad (6)$$

While light attenuation per unit of DOC can be variable across lakes and season (Molot and Dillon 1997), we used a single, representative value of k_C for simplicity.

To model mixed-layer depth, we considered both DOC concentration and lake surface area (S_A). Larger lakes, in general, are subject to greater wind-driven mixing (depending on lake orientation, landscape features, and morphology) and therefore have deeper mixed-layer depths at a given DOC concentration (C) (Fee and others 1996). Accordingly, we modeled mixed-layer depth (Pérez-Fuentetaja and others 1999) as follows:

$$z_{mix} = 10^{(-0.515 * \log_{10}(C) + 0.115 * \log_{10}(2\sqrt{\frac{S_A}{\pi}} + 0.991))} \quad (7)$$

We used light availability at the bottom of the mixed layer ($I_{z_{mix}}$, similar to Thrane and others 2014) as a way to summarize the response of light availability to changing DOC and P loads:

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

Light attenuation (k_D), mixed-layer depth (z_{mix}), and light at the bottom of the mixed layer ($I_{z_{mix}}$) were dynamic parameters in the model and varied with changing dissolved organic carbon concentration (C) and phytoplankton density (A).

Model Experiments

We conducted four separate simulation experiments with the model to explore equilibrium behavior of our model across DOC and phosphorus loads, and lake size gradients. These experiments included visualizing the response of GPP across wide gradients of DOC supply, phosphorus supply, and lake size; exploring the response of GPP as DOC and phosphorus loads changed at several constant C:P stoichiometries; exploring how lake size interacted with changes in DOC and phosphorus loads to affect GPP; and exploring GPP response to uncorrelated variability in DOC and phosphorus loads (that is, variable C:P stoichiometries). For all simulations, we set inflow discharge at a rate that generated a residence time of 1 year for a completely mixed lake. Because discharge was constant for a given lake size, we manipulated DOC and phosphorus loads by changing inflow concentrations (C_{in} and P_{in}). We present model results primarily as a function of these inflow concentrations, but also in relation to equilibrium lake DOC concentrations to facilitate comparison with empirical studies, for which it has been much more common to report lake DOC concentration than details about the loads to the lake.

Experiment 1

First, we wanted to visualize how varying DOC and phosphorus loads independently impacted lake primary productivity, light availability, and mixed-layer depth across a range of lake sizes. We explored GPP across a grid of DOC inflow concentrations that varied from 1 to 40 g C m⁻³, and bioavailable phosphorus inflow concentrations from 0.005 to 0.150 g P m⁻³. We ran simulations for these loads for lakes that varied in area from 0.01 to 10 km².

Experiment 2

Second, we were interested in how the magnitude of GPP varied as loads of DOC and phosphorus changed in a correlated way (that is, constant C:P load stoichiometry). To observe these effects, we ran scenarios in which we increased inflow DOC concentration from 1 to 30 g C m⁻³, and simultaneously varied bioavailable phosphorus inflow concentrations at a C-to-P mass ratio of 0.2, 0.6, and 1.2. We ran these simulations for a lake size of 0.1 km² and at a residence time of 1 year.

Experiment 3

Third, we were interested in how lake size modulates the effects of correlated increases in DOC and phosphorus loads on GPP. To observe these effects, we ran scenarios in which we increased inflow DOC concentration from 1 to 30 g C m⁻³ and simultaneously increased the bioavailable phosphorus load at a C-to-P mass ratio of 0.6, for lakes of 0.01, 0.1, 1, and 10 km².

Experiment 4

Fourth, we explored the patterns in GPP that emerged across a set of lakes which varied widely in the C-to-P ratios of their loads and surface areas. Our intention here was to mimic the process of sampling a set of lakes across a landscape, exploring the response of lake GPP to non-correlated changes in DOC and bioavailable phosphorus loads and variable lake areas. To parameterize the model, we used data from a set of 25 lakes that varied in lake area, residence time, DOC, and total phosphorus concentrations (Solomon and others 2013). We used data from each lake on the mean residence time and in-lake DOC and phosphorus concentrations to calibrate inflow discharge rate (Q_{in}), and DOC and phosphorus inflow concentrations. We systematically adjusted DOC and bioavailable phosphorus concentration in the inflow for each lake until modeled and observed lake concentrations of DOC and total phosphorus approximately matched (modeled vs. observed DOC $r = 0.99$; phosphorus $r = 0.99$), and visualized resulting GPP as a function of DOC concentration for all lakes.

The previous literature has used in-lake DOC concentration as a predictor of lake GPP (Hanson and others 2003; Ask and others 2009). Although in-lake DOC concentration is an emergent property of our model, we are using these simulations to demonstrate the potential for loads to drive variability in GPP, as well as reproduce patterns between lake DOC concentration and GPP that have been observed in the literature. Therefore, we visualize *Experiment 1* across inflow DOC and phosphorus concentrations [g C m⁻³ or g P L⁻³] to observe how lake GPP varies across DOC and phosphorus supply, and *Experiments 2–4* across axes of lake DOC concentration for a more general application of the model for comparisons to patterns observed in the literature.

We ran all simulations to equilibrium using the LSODA integration solver implemented within the *ode* function in the R package *deSolve*. We ran all simulations at daily timesteps for 1500 days, which assured that all simulations reached equilibrium

DOC, phosphorus, and GPP. Our model was built and all simulations and analyses were performed using the R statistical software (R Core Team 2015). The model, data, and analysis scripts are available at <https://github.com/MFEh2o/loadsGPP>.

RESULTS

Model Simulations

Experiment 1

Our model produced nonlinear and interacting responses between lake GPP and inflowing DOC and P concentrations that were modulated by lake area (Figure 2). We observed a nonlinear decline in GPP with an increase in inflow DOC concentration, and a nonlinear increase in GPP with an increase in inflow phosphorus concentration (Figure 2). This qualitative pattern was constant across lake areas, but GPP declined at a lower inflowing DOC concentration in larger lakes.

Light availability was mainly a function of DOC inflow concentration, lake area, and resulting algal biomass (Figure 3). Light extinction was influenced both by lake area and inflow DOC concentration, increasing linearly with greater inflow DOC concentration with a marginally shallower slope in larger lakes (Figure 4a). Mixed-layer depth was a function of inflow DOC concentration, and modulated by lake area, with a more rapid decrease in mixed-layer depth per unit increase in inflow DOC concentration in smaller lakes. This relationship resulted in mixed-layer depths approximately 15% deeper at a given inflow DOC concentration for every order of magnitude increase in lake size (Figure 4b). These relationships contributed to a unimodal pattern in equilibrium algal biomass with increasing inflow DOC concentration, with the location and magnitude of maximum algal biomass a function of lake area. Specifically, smaller lakes had greater maximum algal biomass at a higher inflow DOC concentration compared to larger lakes (Figure 4c). Inflowing DOC concentrations were positively related to equilibrium in-lake DOC concentration, and also modulated by lake size, with a marginally steeper slope in smaller lakes (Figure 4d).

Experiment 2

Our model produced a unimodal response of GPP as loads of DOC and phosphorus increased at a constant C:P stoichiometry. Gross primary production increased rapidly with lake DOC concentration at low DOC concentrations, reached a peak at low

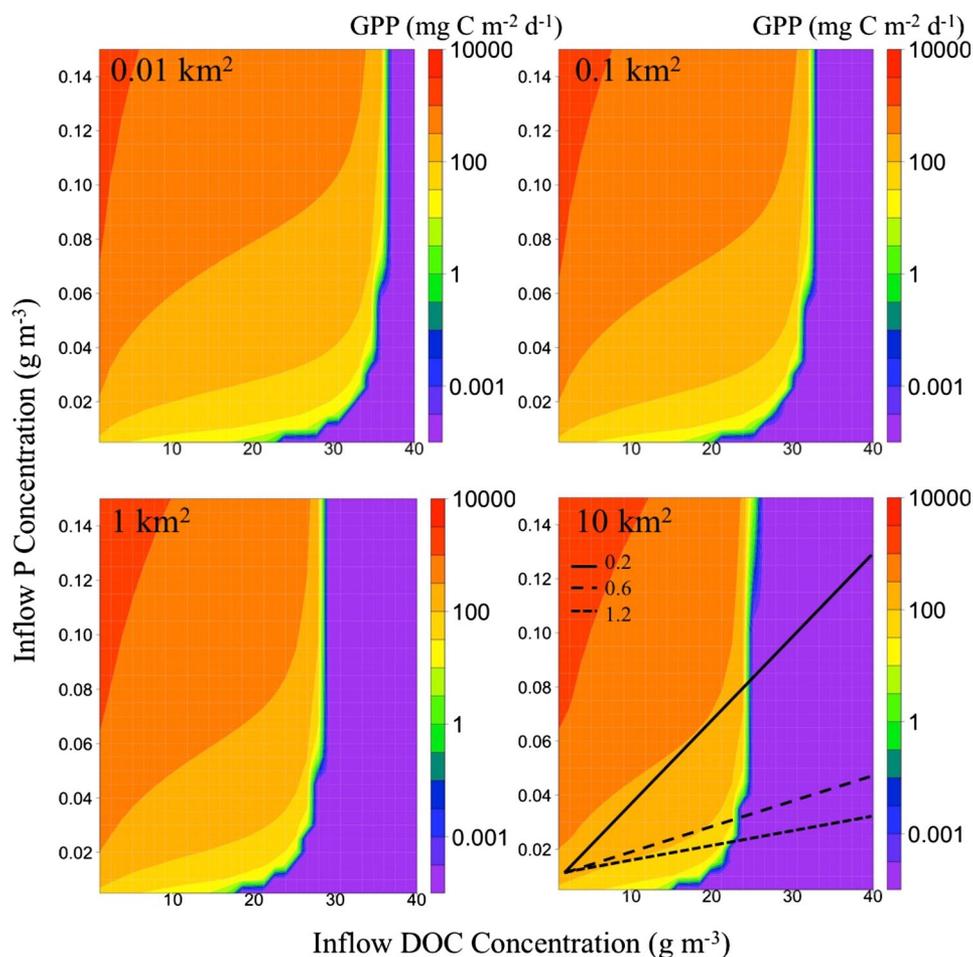


Figure 2. Result of model simulations from model *Experiment 1*. Contour plots of areal gross primary production [$\text{mg C} (\text{m}^2 \text{ lake area})^{-1} \text{ day}^{-1}$] as a function of both dissolved organic carbon and phosphorus load inflow concentration [g C or $\text{g P} (\text{m}^{-3})$], for lake sizes from 0.01 to 10 km^2 (separate panels). Lines represent loads at DOC-to-P mass ratios of 0.2 , 0.6 , and 1.2 , which were used in *Experiments 2* and *3*.

to intermediate DOC concentrations, and decreased at higher lake DOC concentrations (Figure 5a). The height of the GPP maximum and its location along the DOC axis were a function of the DOC-to-phosphorus load ratio. Simulations with lower DOC-to-phosphorus load ratios had greater maximum GPP and greater GPP across the DOC gradient. For example, the maximum in predicted GPP was between 8 and 11 times greater (varying by lake size) in the low DOC:P load scenario compared to the high DOC:P scenario (Figure 5a).

Experiment 3

The location of the GPP maximum (that is, the lake DOC concentration at which it occurred) was related to lake size (Figure 5b). For example, with all else held equal the DOC concentration at which

maximum GPP occurred was 10 mg L^{-1} in a 10 km^2 lake but 15 mg L^{-1} in a 0.01 km^2 lake. The DOC-to-P ratio of the load had a smaller effect on the location of the GPP maximum than lake size. This difference in location of maximum GPP was due to deeper mixed-layer depths at a given lake DOC concentration in large lakes compared to small lakes.

Experiment 4

We observed a wedge-shaped relationship between GPP and lake DOC concentration when we considered a set of lakes in which the C:P stoichiometry of the loads varied widely (coefficient of correlation between estimated C_{in} and $P_{\text{in}} = 0.4$). This pattern was characterized by variable GPP at low lake DOC

concentration, but exclusively low GPP at higher DOC concentrations (Figure 5c), and was similar to the empirically observed pattern between lake GPP and in-lake DOC concentrations (Figure 5d).

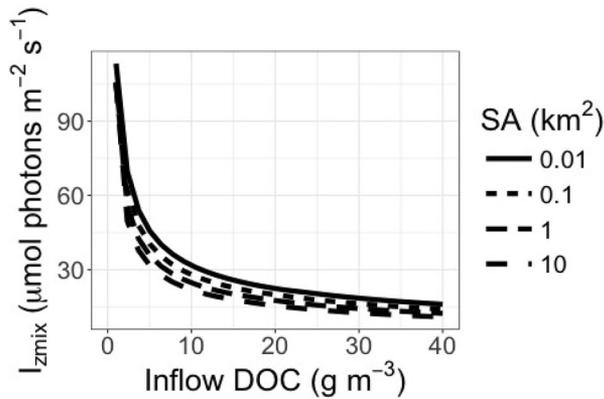


Figure 3. Relationship between inflow DOC concentration [g C (m⁻³)] and light at the bottom of the mixed layer ($I_{z_{mix}}$; see Eq. 8) from the model output. Line type corresponds to lakes of different surface areas. The relationship between DOC load and $I_{z_{mix}}$ was the same across all DOC-to-phosphorus load ratios considered in the simulations.

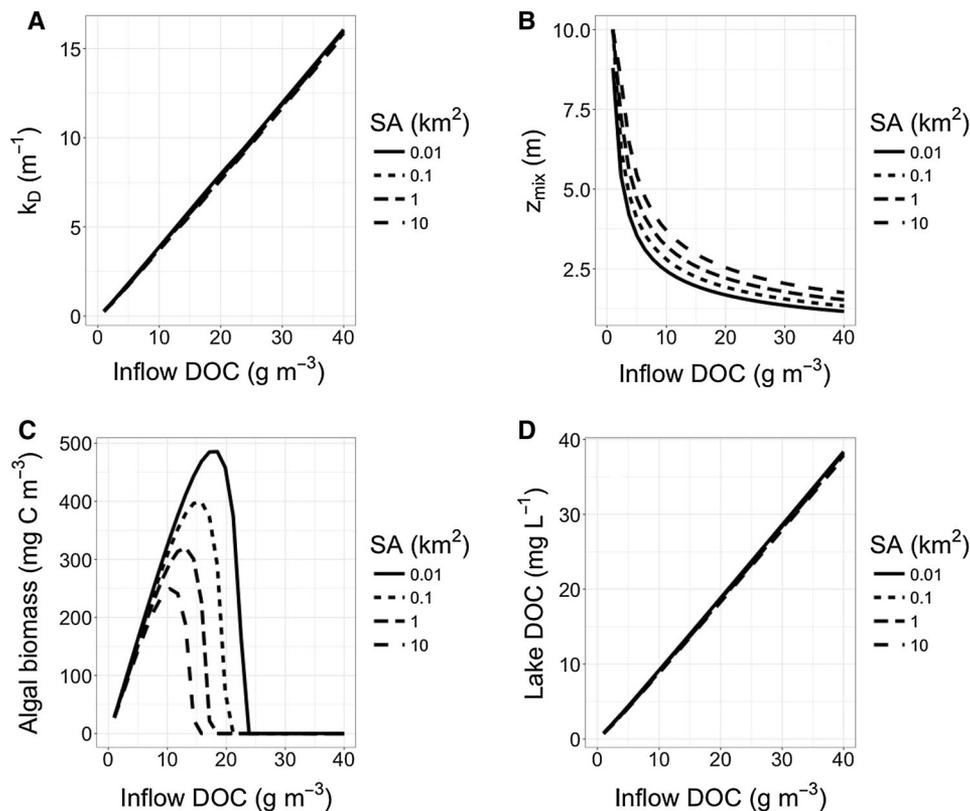


Figure 4. Model output of the relationship between inflow DOC concentration [g C (m⁻³)] and (A) light extinction (k_D), (B) mixed-layer depth (z_{mix}), (C) equilibrium biomass of algae (A), and (D) equilibrium in-lake DOC concentration (C). The combination of patterns in panels a and b generate the relationship depicted in Figure 3 between DOC load and $I_{z_{mix}}$.

DISCUSSION

Our model results identify nonlinear effects of DOC and nutrient loads on pelagic lake productivity due to light and nutrient limitation, with these effects further modulated by lake area. We also provide a process-based context that can explain the role of light and nutrient limitation in regulating lake GPP (Seekell and others 2015) and previously unexpected responses of lake productivity to increases in DOC concentration (Zwart and others 2016). The ability of our model to recreate observations of patterns between pelagic GPP and DOC concentration from the literature suggests the potential for simple physiological process models to qualitatively predict how lake primary production may vary under future changes to DOC and nutrient loads.

Response of GPP to Changes in Loads at a Constant $C:P$ Stoichiometry

Our model provides realistic qualitative expectations for pelagic (or mixed surface layer) GPP resulting from complex interactions of correlated changes in DOC and nutrient loads. Seekell and

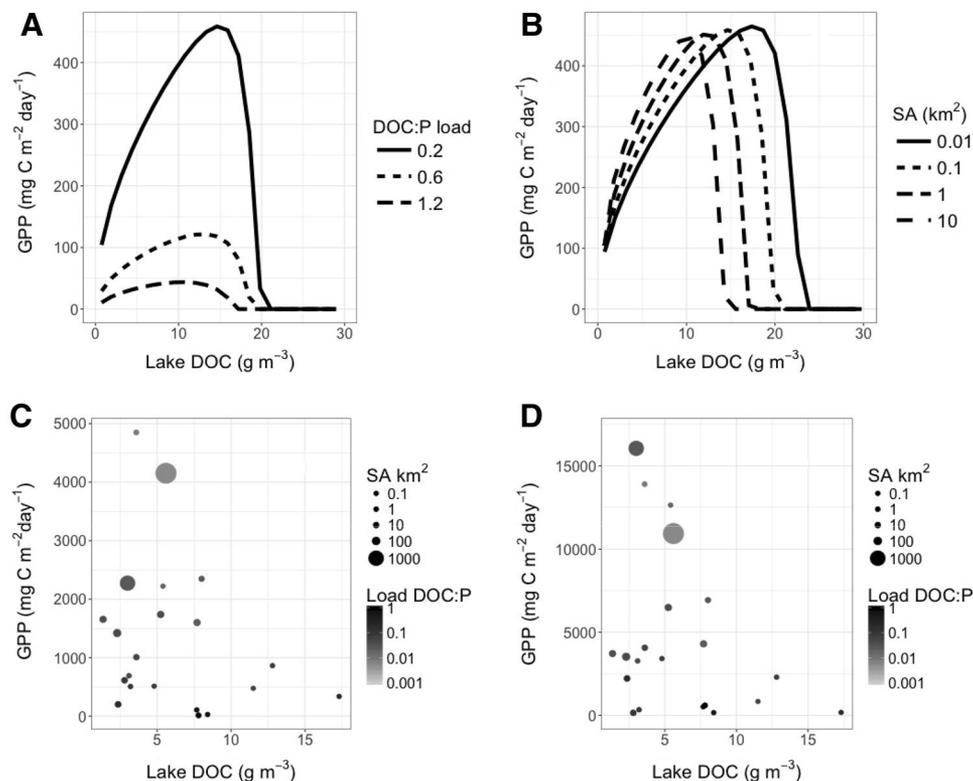


Figure 5. Output of model simulations for *Experiments 2–4*. (**A**) *Experiment 2*. Trajectories of GPP along a lake DOC concentration axis as DOC and P loads increase at constant DOC-to-P ratios. Line type corresponds to different DOC-to-P mass ratios. Lake surface area was 0.1 km². (**B**) *Experiment 3*. Trajectories of GPP along a DOC axis with a correlated increase in DOC-to-phosphorus load ratios. Line type corresponds to different lake surface areas. DOC-to-phosphorus load mass ratio was held at 0.2. (**C**) *Experiment 4*. GPP in a suite of 25 lakes (Solomon and others 2013) with uncorrelated DOC-to-phosphorus loads. Point color corresponds to different estimated (see “Methods”) load DOC-to-P mass ratios, and point type corresponds to varying lake surface areas. (**D**) Measured GPP from the 25 lakes modeled in (**C**). Point color corresponds to different load DOC-to-P mass ratios, and point type corresponds to varying lake surface areas. Load DOC-to-P mass ratios across lakes ranged between 0.005 and 1, with a median of 0.05. A majority of lakes had load DOC-to-P mass ratios below 0.2.

others (2015) provided statistical evidence for a unimodal relationship between lake DOC and GPP as a result of a transition between nutrient and light limitation, as both lake DOC concentration and lake nutrient concentration increased among their study lakes. Although Seekell and others (2015) suggested that regional differences in the DOC-to-nutrient load ratio contributed to this pattern, other studies have observed potentially unimodal patterns within the same geographic region (Ask and others 2009). Our model suggests that these patterns can be explained by a trade-off between nutrient and light limitation as DOC and phosphorus loads increase at a constant C:P stoichiometry. Our modeling results are similar to those from models developed by Diehl (2002; see also Berger and others 2006; Jäger and Diehl 2014) that demonstrate the potential for unimodal patterns along gradients of background attenuation or

mixed-layer depth due to trade-offs between light and nutrient availability.

The magnitude of the unimodal peak in GPP in our model was a function of the DOC-to-phosphorus load ratio. Because of the nutrient and light limitation trade-offs described above, greater nutrient availability relative to light-limiting DOC loads may result in higher productivity at a given DOC concentration. These results accurately reflect the potential for significantly increased primary production under scenarios of anthropogenic eutrophication of lakes, as increased nutrient application in the watershed contributes to significantly lower DOC-to-nutrient ratios in the loads.

Additionally, the DOC load at which light becomes more limiting than nutrients is a function of lake area. Our model produced greater light limitation in large lakes than in small ones at a given DOC supply concentration, because large lakes had

deeper mixed layers. In small lakes, convective mixing is typically the strongest source of turbulence in the mixed surface layer and elevated DOC decreases mixed-layer depth since vertical structure of heat is driven by solar radiation and molecular diffusion of heat (Read and others 2012). The reduction in mixed-layer depth may compensate for increases in light attenuation by chromophoric DOC, thereby increasing, or at least holding constant, the average light availability for phytoplankton in the epilimnion (Zwart and others 2016). This agrees with empirical results from cross-system surveys that have observed strong relationships between light limitation of primary production and mixed-layer depth, after accounting for water clarity or DOC concentration (Kunz and Diehl 2003; von Einem and Granéli 2010). The mechanistic understanding of these context dependencies is important both in providing explanations for past experimental and survey results, as well as predicting the response of lakes to changes in DOC and nutrient loads.

Response of Lake GPP to Loads of Variable $C:P$ Stoichiometry

Our model predicts that GPP is unimodally related to DOC load given fixed lake size and DOC-to-phosphorus load ratio (Figure 5a), yet empirical data on GPP in lakes spanning DOC concentration gradients may not show this clear unimodal relationship (Hanson and others 2003; Solomon and others 2013; Figure 5d). We suspect that the lack of unimodal responses in these and other studies reflects variability in the load stoichiometry and size of the sampled lakes. Although the mechanisms of physiological constraints on GPP are likely similar across lakes in a region, our comparisons of constant and variable watershed load stoichiometry highlight the potential for variation at regional scales in DOC and phosphorus load and lake size to mask the expected unimodal pattern (Figure 5a–c). This contrast may also have implications for a lake that is experiencing a temporal change in watershed DOC and nutrient loads, as the DOC-to-phosphorus load stoichiometry will influence the likely trajectory of lake productivity in response to recovery from acid precipitation (Monteith and others 2007) or changes in watershed management strategies. For example, if a lake maintains a constant DOC-to-phosphorus load stoichiometry, we expect a unimodal pattern in productivity (Figure 5a) in response to changing DOC concentration; however, if load stoichiometry is variable, we may expect an increase, a decline, or no change in

lake GPP that more closely resembles the patterns from uncorrelated loads (Figure 5c).

Our Model and Reality

Our model results suggest a position of the maximum in GPP at approximately $6\text{--}15\text{ mg L}^{-1}$ in-lake DOC concentration. This estimate for the position of maximum in GPP is in line with other estimates from spatial surveys (Figure 5A; $4\text{--}7\text{ mg L}^{-1}$ in Seekell and others 2015, and approximately $10\text{--}15\text{ mg L}^{-1}$ in Hanson and others 2003) and a temporal experimental DOC increase to a lake ($> 11\text{ mg L}^{-1}$; Zwart and others 2016), but suggests maximum in GPP may be variable across different lakes or regions. For example, the main source of water loss within the experimental lake in Zwart and others (2016) was evaporation, and as such, the hydrologic and chemical residence times were decoupled, a process not accounted for in our model. The increased chemical residence times compared to hydrologic residence times may reduce chromophoricity of DOC through bleaching (Curtis and Schindler 1997; Tranvik and others 2009; Hanson and others 2011), thereby contributing to light limitation at a higher lake DOC concentration threshold. Accounting for this difference in light attenuating properties of the in-lake DOC in our model (increasing or decreasing k_c) shifts the maximum in GPP to lower or higher DOC concentrations. Variability in phytoplankton sinking velocities may also play an important role in regulating the location of the maximum in GPP. Faster sinking velocities of phytoplankton lead to a greater reduction in primary production with an increase in DOC concentration, as phytoplankton losses increase with a decline in mixed-layer depth (caused by increased lake DOC concentration). The increased loss of phytoplankton at a lower DOC concentration would shift the light limitation threshold to a lower DOC concentration as a result. Variability in this parameter may therefore alter the location of the maximum in GPP due to different lake hydrologic characteristics or algal species with different sinking rates.

Our model predicts near-zero GPP at high DOC concentrations ($> \sim 17\text{ mg L}^{-1}$ for a 1 km^2 lake). This prediction seems unrealistically extreme; large lakes with high DOC concentrations are rare, and estimates of GPP from such lakes are even rarer, but intuitively we expect measurable (albeit low) GPP under those conditions. One possible explanation for this failure of our model is its lack of community or individual phytoplankton adaptation toward increased light use efficiency in

reduced light climates. In environments with less light availability, species sorting may preferentially select for phytoplankton communities comprised of species with greater light use efficiency, and increase rates of GPP per unit of available light (Edwards and others 2013). Taxa-specific light use efficiency has been demonstrated to be important when predicting GPP based on community data (Zwart and others 2015), and the addition of phytoplankton trait flexibility in our model may improve our model's estimate of GPP at higher DOC concentrations.

The simplicity of our model and the assumption that phytoplankton, and therefore GPP, is constrained to the mixed surface layer preclude the possibility for the formation of areas of high GPP below the thermocline. In clear, stratified lakes, high chlorophyll concentrations have been observed below the thermocline where light is still available for photosynthesis (Fee 1976). These bands of high chlorophyll may represent areas of high primary productivity, due to adequate light availability and high nutrient concentrations constrained in the hypolimnion (Fee 1976). Although the bulk of GPP is generally located within the epilimnion in most lakes, deeper waters can contribute significantly to pelagic GPP in lakes where the euphotic zone (1% light depth) extends beyond the mixed layer (Obrador and others 2014; Giling and others 2017). In our simulations, 1% light depth was only significantly (that is, > 1 m) deeper than z_{mix} in the lowest DOC and phosphorus load lakes. This suggests a bulk of the GPP is constrained in the epilimnion across our simulations.

CONCLUSIONS

One of the primary goals in ecology is to gain a better understanding of process behind patterns observed in nature, and to be predictive about the future responses of an ecosystem to environmental change (Houlahan and others 2017). Different patterns have been observed in responses of GPP to changes in carbon and nutrient loads, suggesting the need for a better understanding of how lakes respond to environmental changes if we intend to meet this challenge. Although statistical models are useful in predicting ecosystem responses based on correlations, these relationships between function and environmental variables may be region-specific or miss important non-linearities generated by interacting physical, chemical, and biological processes. In contrast, process models have the promise to be more portable than regionally specific models (Rastetter and others 2003; Zwart and

others 2015), especially given potential differences between ecosystem responses inferred from spatial comparisons and projections through time (Kratz and others 2003). Using basic algal physiology, and an understanding of the environmental constraints set within the physical context of lakes, we provide the ability to understand qualitative patterns between pelagic primary production under varying DOC and nutrient loads. This framework is an important next step in gaining a mechanistic insight into how lake biogeochemical cycling will respond to a changing environment.

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