Scaling relationships for whole-lake primary production

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Data Availability: The data and used to construct scaling relationships is in the Supplemental Materials, and the code is on Github (https://github.com/bbcael/lake_GPP).This data and code will be archived on Zenodo upon acceptance. The Hydrolakes data used in our up-scaling analysis is available online at: https://www.hydrosheds.org/

Abstract: Scaling relationships provide simple rules for understanding complex ecological patterns. We evaluated scaling relationships between whole-lake (benthic + pelagic) primary production and the surface areas and volumes of 73 lakes. Whole-lake primary production scales isometrically with surface area, after accounting for latitudinal gradients of temperature and insolation. Whole-lake primary production scales to the ¾-power of lake volume, a pattern analogous to Kleiber's Law for organismal metabolism except that its emergence is attributable to fractal characteristics of lake morphometry rather than optimal resource distribution networks. By applying our scaling relationships to a global lake database, we estimated that global lake primary production is 520 (±70) Tg C y^{-1}. We also apply the scaling relationships to make predictions about other global lake characteristics including trophic structure and carbon cycling.

Significance Statement:

Keywords: Primary production | Allometric scaling | Kleiber's Law | Lakes | Fractal

Introduction

Understanding the magnitude and patterns of primary production is a long-standing priority for aquatic scientists (e.g., Likens 1975; Lewis 2011; Staehr et al. 2012). However, global-scale estimates of lake primary production are scarce, highly variable, and often incomplete (Table S1). In particular, there considerable uncertainty relative to the contribution of benthic algae, which contribute 0-95% of total primary production, but are rarely measured (Vadeboncoeur and Steinman 2002; Vadeboncoeur et al. 2003; Seekell et al. 2015a). Scaling relationships capture the essence of complex patterns and provide simple rules for generalizing ecosystem characteristics at the global scale (Downing 2009; Seekell et al. 2021a). Hence, scaling relationships provide a means for integrating benthic primary production into the global-scale understanding of lakes, but to our knowledge such relationships are currently unavailable.

In this study, we evaluate scaling relationships between whole-lake (benthic + pelagic) primary production, lake surface area, and lake volume based on a compilation of previously published measurements. We then apply these relationships to global lake maps to estimate global lake primary production and to make predictions about other global lake characteristics including trophic structure and carbon cycling in a way that includes benthic primary production.

Methods

Primary Production Data

We compiled rates of whole-lake primary production from published sources (Supplementary Tables S2 and S3). Primary production was estimated using several methods, typically based on changes in isotopes or oxygen in chambers, but all included habitat-specific measurements in the benthic and pelagic zones. We did not include estimates of macrophyte production because they are rarely reported (Vadeboncoeur and Steinman 2002). We also did not include primary production measurements from free-water oxygen sensors because these measurements are often based on a single sensor placed in the upper mixed layer, and such deployments do not capture benthic production in stratified water columns (Van de Bogert et al. 2007; Staehr et al. 2010). We express primary production rates as daily averages for the productive ice-free season. When annual rates were provided in the original data sources, we converted them to daily rates either based on season lengths provided in the original publication (Supplementary Table S2).

Scaling Relationships

We evaluated scaling relationships by regressing primary production separately by surface area and volume, after log-transforming each variable. We used Type-1 regression, which is appropriate for our analysis because uncertainty in the independent variable (surface area, volume) in each case is negligible compared to that of the dependent variable (primary production) (Warton et al. 2006). We computed median estimates and uncertainties (standard errors) of the scaling exponents by bootstrapping 10^6 times, which is orders-of-magnitude more than needed to produce stable estimates (Andrews and Buchinsky 2001).

The energetics of photosynthesis are light and temperature-dependent (López-Urrutia et al. 2006; Cael et al. 2017a). Both light and temperature vary systematically with latitude and therefore we corrected for latitudinal differences among lakes by adjusting lake area (A_{TI}) according to:

$$1) \qquad A_{TI} = \frac{A\, I(y) e^{-Ea/kT(y)}}{I(58.5°N) e^{-Ea/(273k)}}$$

where $I(y)$ is the annual mean clear-sky insolation (W m^{-2}) at latitude y (Hartmann 2015), Ea is the average activation energy of photosynthesis (0.32 eV) (López-Urrutia et al. 2006), k is Boltzmann's constant (8.6×10^{-5} eV K^{-1}), and $T(y)$ is annual mean surface temperature in Kelvin as a function of latitude (Hartmann 2015). This correction is consistent with the methods of previous studies evaluating metabolic scaling at sites across a wide range of latitudes (López-Urrutia et al. 2006, Cael et al. 2017). The advantage of introducing the correction to independent variable instead of the dependent variable is that it preserves the ability to directly compare r^2 and root square mean error (RMSE) values among the various scaling relationships.

To apply the energetic correction, we converted latitude to temperature and light by fitting Fourier series to annual mean surface temperature and insolation versus latitude between 35-75°N, encompassing the latitudinal range of the lakes we considered; we chose the Fourier series degree (1st and 2nd order, respectively) with the best adjusted r^2, which was $r^2 > 0.99$ in each case. This adjustment accounts for gradients in insolation and temperature by normalizing to the latitude 58.5°N, which has a mean annual surface temperature of ~0°C. The specific temperature used for normalization does not affect our results.

Upscaling Analysis

We estimated global lake primary production by applying our primary production – lake area scaling relationship to the lakes included in the World Wildlife Fund's HydroLakes database (Lehner and Döll 2004; Downing 2009). This database contains 1.42×10^6 lakes covering 2.93×10^6 km^2, and has been widely applied in the analysis of global lake characteristics (e.g., Downing 2009; Cael et al. 2017b). We adapted the approach described by Weyhenmeyer et al. (2011) to estimate the ice-free season for these lakes, and propagated uncertainty in the equations through bootstrapping (Supplementary Text S1). We did not apply the scaling relation by volume to estimate global primary production because bathymetry is measured for relatively few of Earth's lakes, and hence the global datasets do not provide a basis for upscaling based on this parameter (Cael et al. 2017b; Seekell 2018).

Results

Our data compilation included measurements from 73 lakes of diverse morphometry and productivity (Table 1; Supplementary Table S3). Specifically, the range of lake size is thought to include >99% of Earth's lakes by both surface area and volume (Downing et al. 2006; Cael et al. 2017b; Seekell et al. 2021b). The range of vertical light attenuation, a parameter closely tied to benthic primary production, greatly exceeds the range of typical values on both the low and high ends of the range, as does the range of dissolved organic carbon concentrations (Ask et al. 2009; Seekell et al. 2014; Seekell et al. 2021b). Gross primary production varied between 33 g C d^{-1} in the smallest study lake, an Alaskan tundra pond (area = 546 m^2, mean depth = 0.12 m, volume = 67 m^3), to 4.03×10^7 g C d^{-1} in Lake Thingvallavatn, Iceland, which was the largest lake in our study by area (8.3×10^7 m^2), volume (2.82×10^9 m^3), and mean depth (34 m). Most lakes of the study lakes are located the United States (42%, n = 31), Sweden (30%, n = 22), or Finland (12%, n = 9), but we also included lakes from Canada (n = 5), Denmark (n = 3), Germany (n = 2), and Iceland (n = 1). This distribution is not representative of global distribution of lakes, but is generally representative of the distribution of published research on lake carbon cycling (Seekell et al. 2018).

Table 1. Characteristics of lakes included in the study. *k* is the vertical light (photosynthetically active radiation) attenuation coefficient and DOC is the concentration of dissolved organic carbon.

Characteristic	Minimum	Medium	Max
Area (m^2)	546	41,000	8.3×10^7
Volume (m^3)	60	153,900	2.82×10^9
Mean depth (m)	0.1	3.2	34
k (m^{-1})	0.148	0.8	13.64
DOC (mg L^{-1})	0.01	6.43	30
Gross Primary Production (g C d^{-1})	33	6,510	4.03×10^7

It is remarkable that despite substantial variation in lake characteristics, clear scaling patterns emerged during our analysis (Figure 1). Specifically, there is a strong ($r^2 = 0.83$), slightly super-linear relationship between gross primary production and surface area (Figure 1A). However, this relationship is stronger ($r^2 = 0.87$) and isometric (1:1 scaling) when surface area is corrected for latitudinal differences in temperature and insolation (Figure 1B). Primary production scales approximately to the ¾ power of lake volume ($r^2 = 0.73$). Based on the scaling relationships and global lake database, we estimate that global lake primary production is 520 (±70) Tg C y^{-1}.

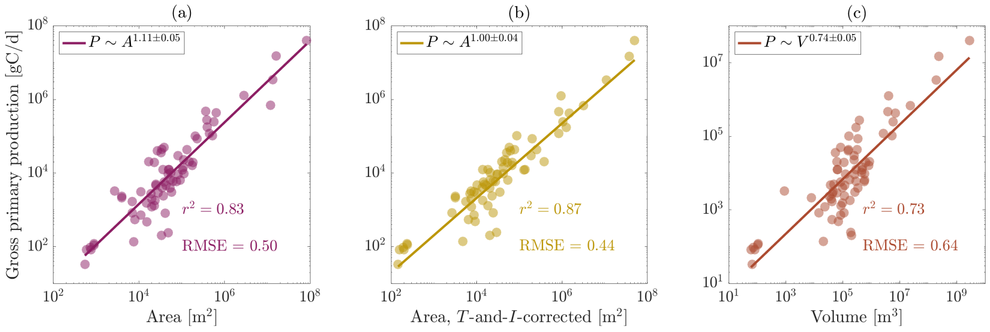

Figure 1. Scaling relationships for whole-lake (benthic + pelagic) primary production by A) surface area, B) surface area corrected for latitudinal differences in temperature and insolation, and C) volume.

Discussion

We identified clear scaling relationships for primary production by surface and volume. Power-law relationships imply scale-invariance (as opposed to scale-dependence) and in this case the power-laws emerge because a single process (photosynthesis) is responsible for primary production regardless of lake size. To our knowledge, we are reporting the first scaling relationships that include measurements of benthic primary production. Hence our interpretation of patterns implicitly includes the contributions of both pelagic and benthic primary producers.

Our global estimate of primary production is somewhat lower than some previous estimates both in terms of absolute magnitude (520 Tg C y^{-1}) and as an overall (total primary production / total lake area) areal rate (193 g C m^{-2} y^{-1}) (Table S1). However, the standard error for our estimate includes most previous estimates and in this sense our upscaling is consistent with previous analyses that have applied different methods. We can make several conclusions from these observations. First, overall areal rates of both primary and gross primary production are on the order of 10^2 g C m^{-2} y^{-1}. Second, both gross and net primary production are on the order of 10^{14} g C y^{-1}. Estimates based on extrapolating lake areas from a power-law distribution are somewhat higher, on the order of 10^{15} g C y^{-1}, but it has been repeatedly demonstrated that lakes do not conform to a power-lake size distribution such that these are probably overestimates (Seekell and Pace 2011; McDonald et al. 2012; Cael and Seekell 2016). The intercept of the scaling relationship used in our upscaling (0.24 +/- 0.03 g C m^{-2} d^{-1}) is proportional to the areal light utilization efficiency (photosynthetic efficiency), which is 0.044% (+/- 0.005) for our study. We are not familiar with any independent whole-ecosystem (benthic + pelagic) estimates of areal light utilization efficiency that we can use to validate this figure (published estimates are often only for phytoplankton), however equation 1 provides the means for normalizing to facilitate future comparison with our value.

The scaling relationships show that, in general, larger lakes fix more carbon than smaller lakes. This pattern does not minimize the role of nutrients and herbivory and shaping, particularly in lakes subject to eutrophication, which play out in significant ways at different scales. Rather, it reflects the massive variation in lake size and its foundational role in shaping patterns of global lake ecology. The isometric scaling of primary production by surface area is a particularly interesting pattern, because areal rates of ecological processes are often inversely correlated with lake area (e.g., Downing 2010). However, there is some prior evidence of isometric scaling for primary production by area. Specifically, Staehr et al. (2012) reported no significant correlation between the areal rate of gross primary production and surface area for Danish lakes. Because $P/a \propto a^{1-b}$, their absence of a significant correlation is equivalent to our result of isometric scaling in the equation $P \propto a^b$. We do not know of other reports for the correlation between areal rates of primary production and surface area, which is curious given the long history of investigation for rates of primary production. We suspect that this is a publication bias, correlations are not reported because they are not statistically significant, even though this lack of significance implies isometric scaling.

In contrast to our result of isomeric scaling of primary production by surface area, fish production has previously been reported to scale sub-linearly with surface area (e.g., Youngs and Heimbuch 1982; Downing 2010). The contrast in these patterns is indicative in changes in trophic structure among lakes of different size. Specifically, we predict that, when comparing lakes across the size spectrum, small lakes will typically have relatively top-heavy biomass pyramids whereas large lakes will have relatively bottom-heavy biomass pyramids (Hatton et al. 2015). These changes should be the result of differences in energy pathways among lakes of different size, rather than differences in the magnitude of primary production (ie. because isometric scaling indicates no change an areal rates of primary production). Specifically, energetic pathways in near-shore benthic habitats are more efficient than those in the open-water zone (Vander Zanden et al. 2006; Vadeboncoeur and Power 2017). Small lakes have relatively large littoral zones compared to large lakes, and hence differences in biomass pyramids probably result from the influence of lake morphometry on the relative sizes of littoral habitats and the consequent strength of littoral energy pathways (Seekell et al. 2021b). This observation is a potential bridge connecting broad-scale trophic patterns to the geologic factors controlling the relative abundances of small and large lakes.

Lakes function as both reactors and chimneys for carbon exchange between the terrestrial environment to the atmosphere (Cole et al. 2007). A previous estimate of global lake respiration (718 Tg C y^{-1}) by Pace and Prairie (2005) exceeds our estimate of primary production by approximately 200 Tg C y^{-1}. This difference implies that lakes are net heterotrophic at the global scale, an observation that highlights the role of lakes carbon reactors and reflects their location in landscape depressions where they are recipients of allochthonous organic material that is mineralized within the lake (Pace and Prairie 2005; Verheijen et al. 2022). Literature estimates of carbon dioxide exchange from lakes to the atmosphere (-320 Tg y^{-1}) exceed net ecosystem production (NEP = GPP – R, NEP = about -200 Tg C y^{-1})(Rayond et al. 2013). This observation implies that about 38% of carbon dioxide evaded to the atmosphere enters lakes as inorganic carbon, such as inorganic carbon creating by weather which is transfer laterally to lakes through soil and groundwater. These figures, while highly uncertain, are consistent with field studies (e.g., McDonald et al. 2013; Wilkinson et al. 2016; Verheijen et al. 2022) and highlight the magnitude and diversity of connections between terrestrial and lacustrine ecosystems.

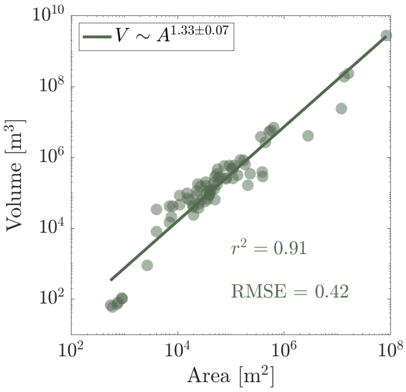

Figure 2. The scaling relationship between volume and surface area for the study lakes.

We found that primary production scales to the ¾ power of lake volume. This is remarkable because it is analogous to Kleiber's Law – that organismal metabolism scales to the ¾ power of mass – except at a higher level of biological organization (West et al. 1999; Banavar et al. 2010). Specifically, volume is analogous to mass because water density varies relatively little across the range of temperatures observed in lakes (Wetzel 2001). The emergence of Kleiber's law is generally attributed to optimal resource distribution networks (West et al. 1999; Banavar et al. 2010; Nidzieko et al. 2018). This explanation does not apply for lakes because it assumes a one-directional flow of nutrients, and internal nutrient loading from lake sediments, violates this assumption (Nürnberg 2009; Nidzieko et al. 2018). We instead attribute the emergence of Kleiber's Law for lake primary production to the fractal characteristics of lake morphometry (e.g., Seekell et al. 2013; Cael et al. 2017b; Seekell et al.

2021a). Specifically, the theoretical scaling of lake volume by surface area on a fractal surface is $v \propto a^{1+H/2}$, where v is volume, a is surface area, and H is the Hurst coefficient – a parameter that describes the difference in horizontal and vertical scaling (Cael et al., 2017b). This is equivalent to $a \propto v^{2/(H+2)}$, which predicts $P \propto v^{2/(H+2)}$ when substituted into the isometric relationship between primary production (P) and surface area (ie. $P \propto a^1$). Measurements of Earth's topography indicate that it is approximates a fractal surface with H=0.66 (Gagnon et aal. 2006), which by the preceeding equations predicts the relationship $P \propto v^{3/4}$. The volume-surface area scaling relationship for our study lakes ($v \propto a^{1.33}$, Figure 2) is completely consistent with this explanation based on fractal lake morphometry. While our explanation differs from the most common explanation for the emergence of Kleiber's law for organisms, they have a shared basis in the use of fractal theories to arrive at the ¾ power exponent.

Our analysis has several limitations. Because of variations in methodology, some primary production measurements are more representative of net primary production while others are more representative of gross primary production (Likens 1975). This is a long-standing challenge to synthesis in the aquatic sciences for which there remains no correction procedure (Likens 1975; Le Cren and Lowe-McConnell 1980; Vadeboncoeur and Steinman 2002; Seekell et al. 2015a; Nidzieko 2018). Hence while we express these values as gross primary production, there is some uncertainty to the extent that they fully capture this process. In our specific analysis, this uncertainty is minimized because our scaling analyses take place on log-scales – algal respiration is generally not sufficient to cause the order-of-magnitude differences needed to have a material impact on the patterns described by scaling relationships (Lewis 2011). Analyses based on free-water techniques may be able to overcome this limitation in the future should they be shown to accurately represent benthic production and are applied across a sufficiently large range of lake sizes. Another limitation is geographic bias in our underlying data. The relationships presented in our study would benefit from validation with measurements from regions less well represented in research on lake carbon cycling, in particular equatorial lakes which have the higher potential photosynthetic rates than the primarily northern lakes included in this study (Lewis 2011; Seekell et al. 2018). Finally, our explanation for Kleiber's Law for lake primary production is based on the Hurst coefficient H = 0.66. However, there is some uncertainty as to the generality of this value because it is rarely measured. Additionally, while lake volume scales by the ~ 1.33 power of surface area in many regions (e.g., Schiefer and Klinkenberg 2004; Cook and Quincey 2015; Sjöberg et al. 2022), deviations from this value have been reported in some regions (e.g., Cael et al. 2017b; Mosquera et al. 2017). We cannot resolve the extent to which such deviations are caused by limitations of theory versus limitations of sampling (e.g., related to sample size, sampling procedure, or how the study extent is defined). However, we can predict the scaling exponent for primary production by volume will be higher for lakes with in regions topography characterized by low Hurst coefficients (e.g. for H = 0.4, the expected scaling exponent is 0.83), and lower in regions characterized by high hurst coefficient (e.g., for H = 0.8, the expected scaling exponent is 0.71).

Conclusions

We developed scaling relationships that integrate benthic algae when seeking to generate simple rules about lakes lake ecology. We have made several testable observations and predictions based on these rules. First, we found isotropic scaling of whole-lake primary production by surface area, and ¾ power scaling by volume. We attribute the ¾ power scaling to the fractal nature of lake morphometry, and the equations used in our reasoning allow for straight forward empirical tests both in terms of functional form and parameter values. We also provide predictions that, overall, lakes are net heterotrophic and that their carbon dioxide exchange with the atmosphere is based on the mineralization of organic material and lateral transfer of inorganic carbon, in similar magnitudes (62% versus 38%, respectively). These aspects of lake carbon cycling are well studied at small scales, but to our knowledge this is the first global scale evaluation of these characteristics. In general, our study not only advances understanding of the patterns and magnitude of lake primary production at the global scale, it provides clear and testable hypotheses that can be used to advance global limnology, a discipline that has been largely descriptive to date.

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Supplemental Material

Text S1. Error in the global lake productivity is dominated by uncertainty in the intercept of the scaling relationship between productivity and light-and-temperature-correct area (0.24 +/- 0.03 g C m^{-2} d^{-1}). The global mean relationships between insolation and temperature versus latitude have negligible uncertainty, as do the latitude and surface area measurements of individual lakes, and the activation energy of photosynthesis and Boltzmann's constant are exact. The other source of uncertainty is from the number of ice-free days per year; to estimate uncertainty in this parameterization with temperature, we bootstrap resampled the observations from Weyhenmeyer et al. (2011) 10,000 times and fit a Gaussian function for ice-free days versus annual mean temperature to each bootstrap resampling. We then recalculated the productivity for each bootstrap resampling's associated parameter values for this parameterization. Including the resulting uncertainty does not change the overall uncertainty estimate within the significant digits we report; the value of 520 (±70) Tg C y^{-1} therefore reflects uncertainty in the intercept of the scaling relationship between productivity and light-and-temperature-correct area, with all other associated uncertainties being on the order of 1 Tg C y^{-1} or less.

Table S1. Estimates of global lake primary production

Estimate (Tg C y^{-1})	Lake Area (10^6 km^2)	Areal Rate (g C m^{-2} y^{-1})	Methods and Comments	Source
572	2	286	Product of total lake area and mean areal productivity. The origin of both figures is poorly documented. The estimate is presented as representing net primary production.	Likens 1973
363	2	181	Product of total lake area and mean areal productivity. The origin of both figures is poorly documents. The estimate is presented as representing net primary production.	Likens 1975
648	2.69	241	Based on a publish relationship between phosphorus concentration and planktonic production and assumptions about low contribution of benthic algae to production. The estimate is presented as representing gross primary production.	Pace and Prairie 2005
1510	4.2	360	Based on a simulation integrating the diverse factors constraining primary production. The estimate is presented as representing gross primary production and assumes that lakes conform to a power-law size distribution.	Lewis 2011
1050	3.1	339	Based on a simulation integrating the diverse factors constraining primary production. The estimate is presented as representing gross primary production and assumes that the distribution of small lakes deviates from a power-law.	Lewis 2011
1120	4.2	267	Based on a simulation integrating the diverse factors constraining primary production. The estimate is presented as representing net primary production and assumes that lakes conform to a power-law size distribution.	Lewis 2011
800	3.1	258	Based on a simulation integrating the diverse factors constraining primary production. The estimate is presented as representing net primary production and assumes that the distribution of small lakes deviates from a power-law.	Lewis 2011
520	2.69	193	Based on scaling relationships with various sources of uncertainty propagated. Represents	This Study

			a value between gross and net primary production.	

Table S2. Notes and sources for lake data

Lake	Comments
Tjabrak	Data from Ask et al. (2009), as reported in Seekell et al. (2015a)
Almberga	Data from Ask et al. (2009), as reported in Seekell et al. (2015a)
Vuorejaure	Data from Ask et al. (2009), as reported in Seekell et al. (2015a)
Ruozutjaure	Data from Ask et al. (2009), as reported in Seekell et al. (2015a)
Erkkijärvi	Data from Ask et al. (2009), as reported in Seekell et al. (2015a)
Estvåjärvi	Data from Ask et al. (2009), as reported in Seekell et al. (2015a)
Sourra	Data from Ask et al. (2009), as reported in Seekell et al. (2015a)
Knivsjön	Data from Ask et al. (2009), as reported in Seekell et al. (2015a)
Övre Björntjärn	Data from Ask et al. (2009), as reported in Seekell et al. (2015a)
Nedre Björntjärn	Data from Ask et al. (2009), as reported in Seekell et al. (2015a)
Lilla Björntjärn	Data from Ask et al. (2009), as reported in Seekell et al. (2015a)
Holmtjärn	Data from Ask et al. (2009), as reported in Seekell et al. (2015a)
Snotterjärn	Data from Ask et al. (2009), as reported in Seekell et al. (2015a)
Abborrtjärn	Data from Ask et al. (2009), as reported in Seekell et al. (2015a)
Rengårdstjärnen	Data from Ask et al. (2009), as reported in Seekell et al. (2015a)
Solbacka	Data from Seekell et al. (2015a), except for surface area which is original to this study and was measured for this study based on satellite imagery
A7	Data from Seekell et al. (2015a), except for surface area which is original to this study and was measured for this study based on satellite imagery
A9	Data from Seekell et al. (2015a), except for surface area which is original to this study and was measured for this study based on satellite imagery
AT3	Data from Seekell et al. (2015a)
AT4	Data from Seekell et al. (2015a)
GTH-99	Data from Northington et al. (2010) and Whalen et al. (2008)
NE-8	Data from Northington et al. (2010) and Whalen et al. (2008)
I-4	Data from Northington et al. (2010) and Whalen et al. (2008)
NE-12	Data from Northington et al. (2010) and Whalen et al. (2008)
GTH-112	Data from Northington et al. (2010) and Whalen et al. (2006)
GTH-114	Data from Northington et al. (2010) and Whalen et al. (2006)
I-8	Data from Northington et al. (2010) and Whalen et al. (2008)
GTH-100	Data from Northington et al. (2010) and Whalen et al. (2008)
Mekkojärvi	Data reported in Vesterinen et al. (2017), GPP digitized from a figure in this paper. Light extinction calcualted based on data in Vesterinen et al. (2017) and the equation for 1% light depth in Eloranta (1978)
Horkkajärvi	Data reported in Vesterinen et al. (2017), GPP digitized from a figure in this paper. Light extinction calcualted based on data in Vesterinen et al. (2017) and the equation for 1% light depth in Eloranta (1978)
Huhmari	Data reported in Vesterinen et al. (2017), GPP digitized from a figure in this paper. Light extinction calcualted based on data in Vesterinen et al. (2017) and the equation for 1% light depth in Eloranta (1978)

Möläkkä	Data reported in Vesterinen et al. (2017), GPP digitized from a figure in this paper. Light extinction calcualted based on data in Vesterinen et al. (2017) and the equation for 1% light depth in Eloranta (1978)
Nimetön	Data reported in Vesterinen et al. (2017), GPP digitized from a figure in this paper. Light extinction calcualted based on data in Vesterinen et al. (2017) and the equation for 1% light depth in Eloranta (1978)
Taavilammi	Data reported in Vesterinen et al. (2017), GPP digitized from a figure in this paper. Light extinction calcualted based on data in Vesterinen et al. (2017) and the equation for 1% light depth in Eloranta (1978)
Keskinen Rjajärvi	Data reported in Vesterinen et al. (2017), GPP digitized from a figure in this paper. Light extinction calcualted based on data in Vesterinen et al. (2017) and the equation for 1% light depth in Eloranta (1978)
Haukijärvi	Data reported in Vesterinen et al. (2017), GPP digitized from a figure in this paper. Light extinction calcualted based on data in Vesterinen et al. (2017) and the equation for 1% light depth in Eloranta (1978)
Tundra Pond J	GPP data from Stanley (1976). We assumed 78 day growing period per this paper. Surface areas for the ponds measured by planimeter from the maps in Stanley (1976). Volume was calculated based on the tuncated irregular cone method (Wetzel and Likens 2000) between 0 and 20 cm (no max depth given in paper).
Tundra Pond B	GPP data from Stanley (1976). We assumed 78 day growing period per this paper. Surface areas for the ponds measured by planimeter from the maps in Stanley (1976). Volume was calculated based on the tuncated irregular cone method (Wetzel and Likens 2000) between 0 and 20 cm (no max depth given in paper).
Tundra Pond C	GPP data from Stanley (1976). We assumed 78 day growing period per this paper. Surface areas for the ponds measured by planimeter from the maps in Stanley (1976). Volume was calculated based on the tuncated irregular cone method (Wetzel and Likens 2000) between 0 and 20 cm (no max depth given in paper).
Tundra Pond D	GPP data from Stanley (1976). We assumed 78 day growing period per this paper. Surface areas for the ponds measured by planimeter from the maps in Stanley (1976). Volume was calculated based on the tuncated irregular cone method (Wetzel and Likens 2000) between 0 and 20 cm (no max depth given in paper).
Tundra Pond E	GPP data from Stanley (1976). We assumed 78 day growing period per this paper. Surface areas for the ponds measured by planimeter from the maps in Stanley (1976). Volume was calculated based on the tuncated irregular cone method (Wetzel and Likens 2000) between 0 and 20 cm (no max depth given in paper).
Tundra Pond A	GPP data from Stanley (1976). We assumed 78 day growing period per this paper. Surface areas for the ponds measured by planimeter from the maps in Stanley (1976). Volume was calculated based on the tuncated irregular cone method (Wetzel and Likens 2000) between 0 and 20 cm (no max depth given in paper).
Ikroavik	Data from Stanley (1976). We assumed 78 day growing period per this paper.
Borax	Data from Wetzel (1964). Area and mean depth are the averages of the monthly values given in the paper.

Paul	GPP annual rates from Vadeboncoeur and Steinman (2002), converted to daily rates assuming five month growing season per their paper. DOC from Coloso et al. (2011). Light extinction coefficient calculated based on 1% light depth from Carpenter et al. (2001)
Peter	GPP annual rates from Vadeboncoeur and Steinman (2002), converted to daily rates assuming five month growing season per their paper. DOC from Coloso et al. (2011). Light extinction coefficient calculated based on 1% light depth from Carpenter et al. (2001)
West Long	Annual GPP rates from Vadeboncoeur and Steinman (2002), converted to daily rates assuming five month growing season per their paper. The vertical light attenuation coefficient was calculated based on 1% light depth from Carpenter et al. (2001) DOC is from Christensen et al. (1996)
East Long	Annual GPP rates from Vadeboncoeur and Steinman (2002), converted to daily rates assuming five month growing season per their paper. The vertical light attenuation coefficient was calculated based on 1% light depth from Carpenter et al. (2001) DOC is from Christensen et al. (1996)
Gollinsee	Data from Brothers et al. (2013). The annual rate was divided by 365 to get a daily rate, per the annualization procedure in their paper.
Schulzensee	Data from Brothers et al. (2013). The annual rate was divided by 365 to get a daily rate, per the annualization procedure in their paper.
Lake 18	Data from Ramal et al. (1994). The vertical light attenuation coefficient was calculated from secchi depth according to the equation in Davies-Colley et al. (1993)
Kalgaard	GPP from Søndergaard and Sand-Jensen (1978), converted from annual to daily rate by dividing by 213, the number of days between 1 April 1976 and 31 October 1976, which is the period used for the annualization in their study. Mean depth, surface area, and coordinates are from Søndergaard and Sand-Jensen (1979). The vertical light attenuation coefficient is from Sand-Jensen aand Søndergaard (1981); DOC is from Søndergaaard (1984)
Marion	Geographic coordinates, area, mean depth, and phytoplankton production are from Efford (1967). Phytoplankton production converted from annual to daily assuming 150 productive days per the 5 month productive season given in their paper. The vertical light attenuation coefficient is calculated from June depth profile of light transmission in Hargrave (1969). Annual epibenthic algal production taken from Hargrave (1969) and converted to daily rates based on 5 month growing season.
Mirror Lake	All data from Likens (1985). Phytoplankton production rates made daily based on a 227 day growing season, benthic production rates made daily based on a 200 day growing season. These season lengths were provided by the authors.
Lake 239	Area, mean depth and production data from Schindler et al. (1973). Annual phytoplankton production rates were made to daily rates assuming 188 day growing seaon, per their paper. The vertical light attenuation coefficient was calcualted as 1.7/Secchi disk depth, with the Secchi disk depth coming from Schindler (1971)

Lake 240	Area, mean depth and production data from Schindler et al. (1973). Annual phytoplankton production rates were made to daily rates assuming 188 day growing seaon, per their paper. The vertical light attenuation coefficient was calcualted as 1.7/Secchi disk depth, with the Secchi disk depth coming from Schindler (1971)
Char Lake	Data from Welch and Kalff (1974). Annual production data made daily assuming 107 productive days (June 15-Sept30) based on figures of light penetration into water. The vertical light attnuation coefficient is the mean of white light values reported in Schindler et al. (1974). DOC from Belzile et al. (2002)
Little Rock	Benthic GPP, area, mean depth, DOC, and vertical light attenuation coefficient from Devlin et al. (2015). Benthic GPP was digitized from the mean value in their Figure 2. Latitude and phytoplankton GPP are from Carpenter et al. (1991)
Crystal	Benthic GPP, area, mean depth, DOC, and vertical light attenuation coefficient from Devlin et al. (2015). Benthic GPP was digitized from the mean value in their Figure 2. Latitude and phytoplankton GPP are from Carpenter et al. (1991)
Sparkling	Benthic GPP, area, mean depth, DOC, and vertical light attenuation coefficient from Devlin et al. (2016). Benthic GPP was digitized from the mean value in their Figure 2. Latitude and phytoplankton GPP are from Carpenter et al. (1991)
Trout	Benthic GPP, area, mean depth, DOC, and vertical light attenuation coefficient from Devlin et al. (2016). Benthic GPP was digitized from the mean value in their Figure 2. Latitude and phytoplankton GPP are from Carpenter et al. (1991)
Pääjärvi	Data from Ilmavirta (1981), production converted from kJ to g C with conversion factor from Vadeboncoeur and Steinman (2002). Annual rate converted to daily rate assuming a four month growing season based on the seasonal figure provided by Ilmavirta. The vertical light attenuation coefficient wa back-calculated based on Pt-co color using the equation for 1% light depth for finnish lakes from Eloranta (1978)
Eckarfjärden	All data from Anderson and Brunberg (2006). Annual GPP rate converted to daily rate assuming a productive period of 213 days (1 April 2002 to 31 October 2002) per the seasonal diagram they provide (their Fig. 2). The vertical light attenuation coefficient was estimated from absorbance at 420nm based on the equation for Swedish lakes in Seekell et al. (2015b)
Thingvallavatn	Data from Jonsson (1992): Area, benthic GPP, benthic season length (May-October), vertical light attenuation coefficient (average of 1982 values). Jonasson et al. (1992) for mean depth, phytoplankton GPP and phytoplankton season length (-2 g C m^{-2} $month^{-1}$ for December through March to subtract winter production) Season is April-November)
Lawrence Lake	Data from Wetzel et al. (1972).
Lost Pond	Data from Cole and Fisher (1978) who used a mix of diel oxygen and incubation techniques. In this case the lake is extremely shallow (z_{mean} = 0.34m) and the O_2 is primarily reflecting the benthic processes, whereas the incubation captures the pelagic production. We calculated data rates based on a 112-day period based on the dates and % of annual production given in the paper for the most productive season. Used the

	volume and areas that coincided with this (these were lower than the max values quoted in the paper because of seasonal variation in size)
Stigsholm	Data from Liboriussen and Jeppesen (2003). Based on averages of the daily values given for Mar-Oct (when the seasonal charts show is the primary growing season) digitzed from figure.
Søbygård	Data from Liboriussen and Jeppesen (2003). Based on averages of the daily values given for Mar-Oct (when the seasonal charts show is the primary growing season) digitzed from figure.
Fog 2	Data from Daniels et al. (2015). Summer benthic GPP results given in the discussion transformed to daily rates assuming the 77 day summer (June 15-Aug31 is given in the paper). Epilimnion GPP given in the table is (0-3 m) is made areal and assumed to be a mean daily value. Vertical light attenuation coefficient is 1.7/Secchi disk depth.
Fog 4	Data from Daniels et al. (2015). Summer benthic GPP results given in the discussion transformed to daily rates assuming the 77 day summer (June 15-Aug31 is given in the paper). Epilimnion GPP given in the table is (0-3 m) is made areal and assumed to be a mean daily value. Vertical light attenuation coefficient is 1.7/Secchi disk depth.
E5 (pre-treatment)	Data from Daniels et al. (2015). Summer benthic GPP results given in the discussion transformed to daily rates assuming the 77 day summer (June 15-Aug31 is given in the paper). Epilimnion GPP given in the table is (0-3 m) is made areal and assumed to be a mean daily value. Vertical light attenuation coefficient is 1.7/Secchi disk depth.
E6 (pre-treatment)	Data from Daniels et al. (2015). Summer benthic GPP results given in the discussion transformed to daily rates assuming the 77 day summer (June 15-Aug31 is given in the paper). Epilimnion GPP given in the table is (0-3 m) is made areal and assumed to be a mean daily value. Vertical light attenuation coefficient is 1.7/Secchi disk depth.
Lake Stugsjön	Data from: Björk-Ramberg and Ånell (1985). Took the average of benthic algae PP + phyto PP for three years (benthic was mesaured for 4 years but phytoplankton for only 3). Did not include Hymenjaure because it was fertilized each year and there were no pretreatament values. Assumed 4 month ice free season per the paper and seasonal diagrams

Table S3. Study lake characteristics. Lake volume is $A \times z_{mean}$, after area is converted from hectares to m^2 (Cael et al. 2017b).

Lake	Lat.	Long.	Area (ha)	z_{mean} (m)	GPP (g C d^{-1})
Tjabrak	68.17	19.87	6.23	4.7	6043
Almberga	68.33	19.16	5.48	3.2	6631
Vuorejaure	68.19	19.61	4.28	2.8	4665
Ruozutjaure	68.20	19.57	3.5	2.8	3990
Erkkijärvi	67.66	21.51	10.99	2.3	23189
Estvåjärvi	67.60	20.90	2.47	1.5	4693
Sourra	68.28	19.10	17.42	4.7	16201
Knivsjön	68.29	19.11	10.85	4.5	14214
Övre Björntjärn	64.12	18.78	4.84	4	242
Nedre Björntjärn	64.12	18.78	3.37	6	202
Lilla Björntjärn	64.12	18.78	1.54	4.6	477

Holmtjärn	64.00	18.71	3.72	3.1	2381
Snotterjärn	63.92	18.86	2.48	2	4985
Abborrtjärn	64.11	18.70	5.82	4.6	3026
Rengårdstjärnen	63.69	19.24	4.86	2.6	9331
Solbacka	68.35	18.91	3.64	1.8	12485
A7	63.84	18.62	0.76	2.8	137
A9	64.26	19.76	4.1	2.7	820
AT3	64.48	19.43	9.3	6.4	6510
AT4	64.48	19.43	2.4	7.5	1824
GTH-99	68.50	-149.60	0.7	2.1	833
NE-8	68.65	-149.59	5	1.3	12550
I-4	68.58	-149.58	8.2	3.2	9266
NE-12	68.66	-149.62	7.5	7.6	5925
GTH-112	68.67	-149.25	2.8	2.2	2884
GTH-114	68.68	-149.23	3.9	2.2	5772
I-8	68.61	-149.58	18.3	3.5	19581
GTH-100	68.50	-149.60	5.4	6.4	3942
Mekkojärvi	61.23	25.14	0.4	2	2119
Horkkajärvi	61.21	25.16	1.1	7.7	725
Huhmari	61.19	25.13	1.1	4.2	3086
Möläkkä	61.18	25.21	0.7	6	1691
Nimetön	61.23	25.19	0.4	8.6	2323
Taavilammi	61.22	25.20	0.8	5.2	548
Keskinen Rjajärvi	---	---	1.5	6.6	1524
Haukijärvi	61.22	25.14	2.3	3.8	1292
Tundra Pond J	71.30	-156.70	0.0884	0.12	121
Tundra Pond B	71.30	-156.70	0.0901	0.12	111
Tundra Pond C	71.30	-156.70	0.0752	0.11	83
Tundra Pond D	71.30	-156.70	0.0595	0.10	82
Tundra Pond E	71.30	-156.70	0.0728	0.1	95
Tundra Pond A	71.30	-156.70	0.0546	0.12	33
Ikroavik	71.30	-156.70	1200	2	692308
Borax	38.98	-122.67	39.8	0.7	176500
Paul	46.25	-89.50	1.7	3.7	20513
Peter	46.25	-89.50	2.7	5.7	40860
West Long	46.24	-89.50	3.4	4.7	43973
East Long	46.24	-89.50	2.3	4.9	19320
Gollinsee	53.02	13.58	3.3	1.7	35622
Schulzensee	53.23	13.27	3.9	2.2	50540
Lake 18	69.51	-132.47	282.8	1.45	1273767
Kalgaard	56.02	9.46	10.5	4.6	12127
Marion	49.32	-122.55	13.33	2.4	43042
Mirror Lake	43.94	-71.69	15	5.75	20288
Lake 239	49.67	-93.72	56.1	10.5	248017
Lake 240	49.67	-93.72	44.1	6.1	119622
Char Lake	74.70	-94.83	52.6	10.2	103725
Little Rock	46.00	-89.70	8.1	3.1	29527
Crystal	46.00	-89.61	36.7	10.4	473474

Sparkling	46.01	-89.70	64	10.9	432243
Trout	46.04	-89.67	1607	14.6	15113514
Pääjärvi	61.07	25.08	1340	14.40	3431740
Lake Eckarfjärden	60.37	18.20	23	1.5	86480
Thingvallavatn	64.17	-21.17	8300	34	40251135
Lawrence Lake	42.44	-85.35	4.96	5.89	12366
Lost Pond	42.25	-72.50	0.27	0.34	3232
Stigsholm	55.98	9.49	20.70	0.80	101761
Søbygård	56.26	9.81	38.90	1.00	275957
Fog 2	68.62	-149.60	5.60	8.30	10321
Fog 4	68.62	-149.60	1.90	2.30	2789
E5 (pre-treatment)	68.62	-149.60	11.30	5.20	9718
E6 (pre-treatment)	68.62	-149.60	2.00	2.00	2000
Lake Stugsjön	68.45	18.45	2.00	1.20	1216

Supplemental Material References

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