

Scaling the primary production of lakes

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Abstract: Kleiber’s $\frac{3}{4}$ -scaling Law for metabolism with mass is one of the most striking regularities in the biological sciences. We demonstrate that whole-lake primary production scales to the $\frac{3}{4}$ -power of lake volume, consistent with Kleiber’s Law but not explicable by analogy to theories developed for individual organisms. Instead, dimensional analysis offers a simple explanation. Because Earth’s topography is self-affine and whole-lake primary production scales isometrically with lake area after accounting for latitudinal gradients in temperature and insolation, sub-linear scaling for primary production by volume emerges; the $\frac{3}{4}$ scaling exponent derives from global-scale differences between vertical and horizontal scaling of topography. From these patterns we make novel inferences about lakes’ global annual productivity, photosynthetic efficiency, trophic structure, and role in the carbon cycle. More generally, our study suggests there are multiple paths to realizing $\frac{3}{4}$ -scaling of metabolism rather than a single unifying law, at least when comparing across levels of biological organization.

Significance Statement: Many phenomena scale to the $\frac{3}{4}$ -power with the size of biological systems, both for individual organisms and whole ecosystems. However, the mechanisms underlying this strikingly universal scaling law are unclear and contested, and may be different in different instances. Here we show that whole-lake productivity also scales to the $\frac{3}{4}$ -power with lake size (i.e. volume), but that this is a coincidental result of Earth’s topography being self-affine; after correcting for latitudinal differences in area and light, lakes’ productivity are proportional to their surface areas, which permits multiple inferences about global lake productivity and carbon cycling.

1 Introduction

2 Kleiber’s Law states that metabolism scales to the three-quarters power of mass [5, 25, 1]. Its per-
3 sistence across diverse species and ecosystems has fascinated successive generations of biologists and
4 motivated many attempts to provide a general explanation, which often require new ways of viewing
5 biological systems [5, 11, 25, 1]. Of particular interest in recent years have been observations that
6 this metabolic principle for individual organisms also holds for whole-ecosystem properties, such as
7 predator-prey ratios [9] or estuarine productivity [12], implying far greater generality and that in cer-
8 tain respects ecosystems self-organize to behave like superorganisms. However, the specificity of $\frac{3}{4}$
9 exponent is a challenging criterion for the admissibility of theoretical models, and the mathematical
10 and biological validity of many candidate models is contested [5]. Power-laws capture the essence
11 of complex systems and provide simple rules to understand them that are not strongly impacted by
12 higher-order effects. Hence, the failure to achieve a widely accepted explanation suggests that a key
13 feature of biological systems has yet to be described.

14 **Statement of the Main Results**

15 We observed three-quarters power scaling of whole-lake (benthic + pelagic) gross primary production
16 (GPP) by volume in a compilation of data from 73 lakes with seven orders of magnitude variation in
17 volume (60 m^3 - $2.822 \times 10^9 \text{ m}^3$)

$$\text{GPP} \propto \text{Volume}^{0.74 \pm 0.05}$$

18 Benthic primary production is rarely measured in lakes, despite comprising the majority of total
19 primary production in many systems [22, 17]. Our compilation contains nearly three times more lakes
20 than the next largest, allowing us the potential to describe novel patterns like this quarter-power
21 relationship (Figure 1a)[21, 17]. Collectively with a recent report of $\frac{3}{4}$ -power scaling of ecosystem-
22 scale primary production in estuaries [12], our observation suggests that the regularities that engender
23 Kleiber’s Law extend to higher levels of biological organization than organisms or communities [9].
24 However, explanations for Kleiber’s Law at the individual level are typically based on optimal resource
25 distribution networks [25, 5, 1, 12]. Analogous explanations for ecosystems are unclear, especially
26 for lakes where primary producers can be supplied significant nutrients from the sediments [13] and
27 especially because myriad factors influence aquatic primary productivity.

28 We also observed that lake primary production scales approximately isometrically with surface area
29 (Figure 1b). This relationship is perfectly isometric (i.e. $P \propto A^{1.00 \pm 0.04}$) when accounting for lat-
30 itudinal gradients in insolation and temperature, which affect the energy available and required for
31 photosynthesis, respectively (Materials and Methods, Figure 1c). This isometry suggests a simple ge-
32 ometric explanation for Kleiber’s Law in lakes, which in turn has implications for global scale patterns
33 of lake ecology. Specifically, Earth’s topography is well-characterized as a self-affine random fractal
34 [6, 3]. This means that topography scales differently in the horizontal and vertical directions. The
35 difference in vertical and horizontal scaling is characterized by the Hurst exponent H , which varies
36 between 0 and 1. Cael et al. [3] showed that a topography’s self-affinity imprints on the volume-area
37 scaling of lakes embedded on that topography, such that lake volume scales to lake area by

$$\text{Volume} \propto \text{Area}^{1+H/2}$$

38 The volume-area scaling exponent of 1.33 within our dataset (Figure 1d) is exactly consistent with re-

39 cent estimates of H for Earth's topography [6]. As we find that primary production scales isometrically
40 with area, it is therefore clear from volume area-scaling that primary production scales sub-linearly
41 with volume, with the $\frac{3}{4}$ exponent emerging based on the Hurst exponent. Hence we propose the
42 simple explanation that Kleiber's Law holds for lakes because lake GPP is isometric with lake area
43 and because of the self-affinity of Earth's topography.

44 Power-laws arise from scale-invariance, in this case because a single process - photosynthesis - is re-
45 sponsible for primary production across the full range of lake sizes [19]. Isometric scaling in particular
46 is indicative of solar insolation as the primary factors structuring variation in primary production
47 among lakes, even though photosynthesis depends on many factors such as light attenuation, which
48 varies by two orders of magnitude ($0.15\text{-}14\text{ m}^{-1}$) for the lakes in Figure 1. Specifically, the number of
49 photons reaching the lake should be proportional to area, whereas other factors constraining produc-
50 tivity are often considered proportional to shore length and would result in sub-linear scaling between
51 production and area; nutrient concentrations are one such example of this [7], though nutrient supply
52 is also influenced by other factors such as catchment size, hydrology, and land use. Consistent with this
53 reasoning, we did not find correlations between other variables that we investigated with the residuals
54 from our scaling relationships (nutrient concentrations, dissolved organic carbon concentration, or light
55 attenuation). Isometric scaling of lake primary production with surface area has been independently
56 reported for lakes in Denmark, providing some evidence that this key pattern is not specific to the lakes
57 we consider or an artefact of our data compilation or normalization procedure [18]. These patterns do
58 not minimize the role of nutrients or herbivory in shaping patterns of primary production, particularly
59 in lakes subject to eutrophication [16, 4]. Rather, our point is that in lakes, as in other systems [12],
60 the essence of global patterns of ecosystem primary production lies in the size of the system. It is
61 unlikely that a small hyper-eutrophic lake will fix more carbon than an ultra-oligotrophic lake many
62 orders of magnitude larger in size. The effects of nutrients and herbivory play out in significant ways
63 at different scales within the broader context of these scaling relationships.

64 Based on our scaling relationships, we estimate that global lake primary production is $520 (\pm 70)$ Tg
65 C y^{-1} , which indicates a constant areal light utilization efficiency (a.k.a. photosynthetic efficiency),
66 which we calculate is $0.044 (\pm 0.005)$ % when normalized to a mean annual air temperature of 0°C .
67 This is likely an underestimate of lakes' true photosynthetic efficiency because clear-sky insolation was
68 used, whereas meteorological conditions will tend to decrease the insolation reaching lake surfaces.
69 (Uncertainties are one standard error and are propagated from the bootstrap uncertainties in the

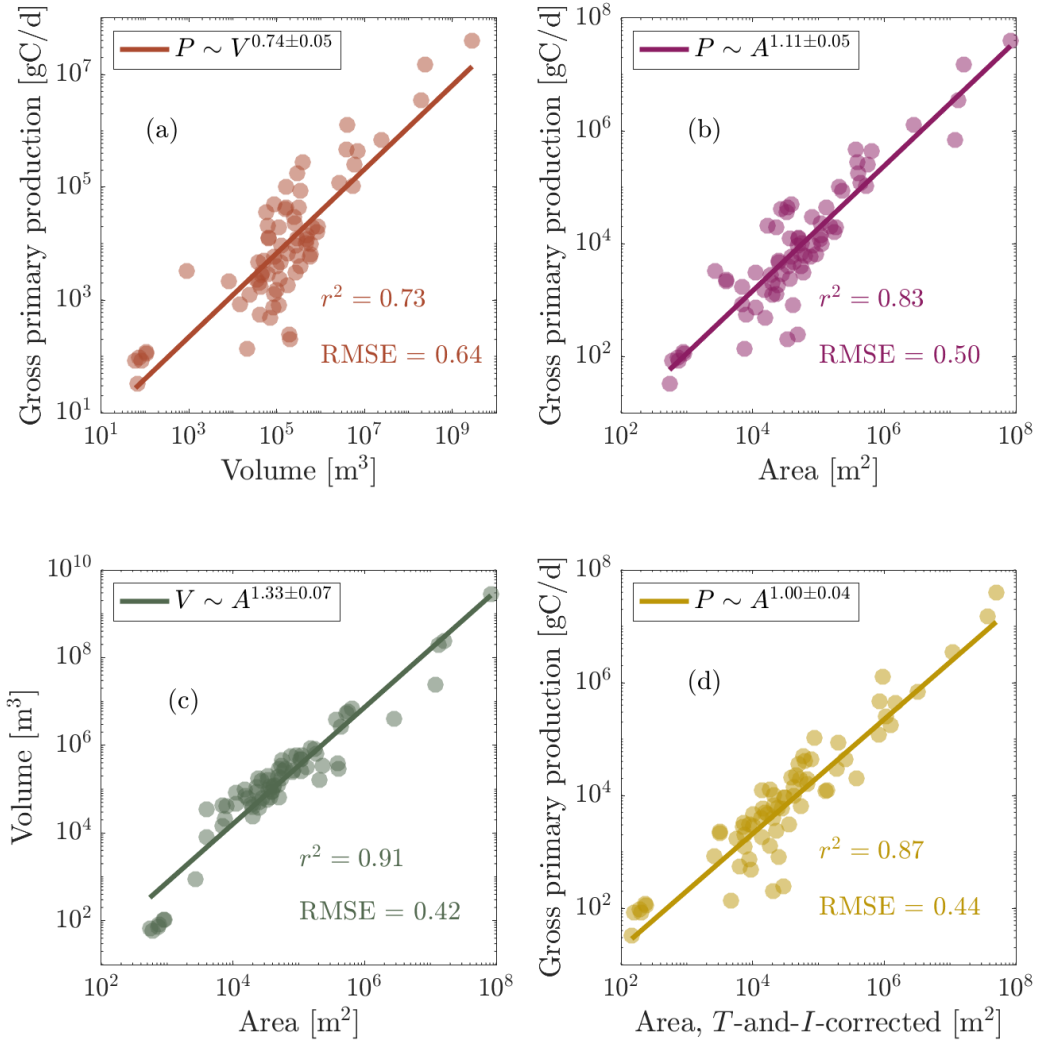


Figure 1: a) Lake volume (V) vs. whole-lake gross primary productivity (P), b) lake area (A) vs. whole-lake gross primary productivity, c) temperature (T)-and-light (I)-corrected area, and d) lake area vs. lake volume, for the data used in this study. See text for T -and- I -correction procedure. Exponents in each legend are the mean and standard deviation of the slopes of bootstrapped iterations of type I regression of the log-transformed variables; coefficient of variation (r^2) and root-mean-square-error (RMSE) are also those for the type I regression of the log-transformed variables, represented by the solid lines, in each case.

70 scaling coefficients; lake productivity and area measurements did not include uncertainties.) Direct
71 comparisons to other estimates of lake productivity or other components of the lake carbon cycle
72 are challenging in part because the global lake maps underlying these estimates vary substantially in
73 lake abundance and area [15, 10]. However, we are able to draw several general conclusions. First,
74 our estimate is not significantly different from two prior estimates of lake primary production each
75 made using different methodologies, after adjusting for difference in total lake area (ours relies on the
76 HydroLakes database (<https://www.hydrosheds.org/downloads>) and equates to 195 ± 26 gC/m²/y
77 versus 200 gC/m²/y [10] and 241 gC/m²/y [14]). This suggests that estimates of global lake primary
78 production are robust. Second, estimates of global lake respiration (~ 700 Tg y⁻¹) exceed our estimates
79 of primary production [14]. Hence, lakes are net heterotrophic at the global scale, a characteristic
80 that reflects the lateral transfer of organic material from land to the aquatic environment where it is
81 subsequently mineralized [14]. Finally, estimates of global net ecosystem exchange (-320 Tg y⁻¹) are
82 substantially less than net ecosystem production (-200 Tg y⁻¹) (negative values indicate the systems
83 are net sources of carbon dioxide to the atmosphere). This difference, which is about 38% of total lake
84 carbon dioxide evasion to the atmosphere, is caused by the lateral transfer of carbon from terrestrial
85 to aquatic environments, such as inorganic carbon created by weather which is transferred to lakes
86 through soil and groundwater where it evades to the atmosphere [15], though lateral transfers can also
87 include an organic carbon component and autotrophic production by aquatic plants can contribute
88 carbon to lakes that can be emitted after decomposition. This highlights the global role of lakes as both
89 reactors and chimneys for the transfer of carbon from terrestrial environment to the atmosphere, as
90 well as the broad insights allowed by scaling relationships of fundamental ecosystem characteristics
91 like primary production.

92 In contrast to our result for primary production, fish production scales sub-linearly with area [27].
93 These patterns are indicative of changes in trophic structure among lakes of different size, specifically
94 that small lakes have top-heavy biomass pyramids whereas large lakes have bottom heavy biomass
95 pyramids [9]. Because primary production scales isometrically with area, these patterns are the re-
96 sult of differences in energy pathways among lakes rather than differences in the magnitude of basal
97 production. Specifically, energetic pathways in near-shore benthic habitats are more efficient than
98 those in the open-water zone [24, 20]. Patterns of trophic structure reflect changes in energy pathways
99 associated with the sub-linear scaling of shore length with surface area. Hence, the factors that control
100 the relative abundance of small and large lakes on Earth's surface influence trophic patterns at broad

101 scales by constraining energy pathways.

102 Self-affine topography arises from the deformation caused by faulting, folding, and erosion [6]. The net
103 effect of these processes at the global scale, represented by the Hurst coefficient, is responsible for lake
104 production meeting the specificity of the $\frac{3}{4}$ scaling exponent. The Hurst coefficient varies significantly
105 among regions at smaller scales, and this observation suggests that Kleiber's Law likely only emerges at
106 scales large enough to sufficiently reflect the global topographic characteristics [6, 3]. Hence, Kleiber's
107 Law for lake production falls within the general class of emergent patterns, which arise at broad scales
108 from the accumulation of local patterns and are only becoming apparent for lakes in recent years as the
109 accumulation of ecological data in diverse regions has reached a critical point. Lakes are traditionally
110 studied individually or as a few systems in close proximity, but our study is illustrative of the diverse
111 and exciting emergent patterns that await global scale analysis of lake ecosystems.

112 In conclusion, Kleiber's Law for lakes is rooted in the interaction between the self-affinity of Earth's
113 topography and the isometric scaling of primary production with area. We have demonstrated that
114 this origin has far reaching implications for patterns of structure and function of lake ecosystems at
115 the global scale. Our explanation differs fundamentally from most explanations for Kleiber's Law in
116 organisms because it arises from the randomness that characterizes self-affine surfaces rather than
117 a mechanism rooted in principles of optimality, whether they be for nutrient distribution, heat
118 dispersion, or some other factor [5, 6]. Our explanation may be applicable to other ecosystems,
119 for example estuaries which have similar scaling patterns for productivity and similar volume-area
120 relationships [12]. However, we do not see a clear analogy to organisms. This suggests that there may
121 be multiple pathways to Kleiber's Law instead of a single unifying mechanism, at least when comparing
122 across levels of biological organization.

123 **Materials and Methods**

124 We compiled rates of whole-lake primary production from published sources. Primary production was
125 estimated using several methods, but all included habitat-specific measurements in the benthic and
126 pelagic zones. We used rates that are the daily average across the productive ice-free season. When
127 annual rates were provided, we converted them to productive season rates based on season lengths
128 stated in the original publication or based on graphs of seasonal patterns provided in the original
129 publication. We did not include estimates of macrophyte production, which is rarely reported [21].
130 We also did not include primary production estimated from free-water oxygen sensors because such

131 measurements typically do not capture benthic production [23]. We did not attempt to control for
132 differences in rates that might arise from methodological variation in the source data. Volume is an
133 appropriate analog for mass in our study because water density varies relatively little among lakes,
134 even those that are thermally stratified.

135 We used Type I regression of the log-transformed variables for our scaling analysis. Among the different
136 methods available to conduct allometric analysis, this is particularly appropriate for our analysis
137 because our data because the uncertainty in the independent variable in each case is negligible to that
138 of the dependent variable. We computed median estimates and uncertainties (standard errors) of the
139 scaling exponents by bootstrapping 10^6 times (ten 10^5 subsets agreed to three significant digits). We
140 used Kendall's tau when correlating other variables against the residuals of the area-production and
141 area-volume scaling relationships.

142 The energetics of photosynthesis are light and temperature-dependent [11, 2]. Both light and temper-
143 ature vary systematically with latitude and therefore we corrected for latitudinal differences among
144 lakes by adjusting lake area (A_{TI}) according to:

$$A_{TI} = \frac{A I(y) e^{-Ea/kT(y)}}{I(58.5^\circ\text{N}) e^{-Ea/k(273\text{K})}}$$

145 where $I(y)$ is the annual mean clear-sky insolation (W m^{-2}) at latitude y [8], Ea is the average
146 activation energy of photosynthesis (0.32 eV) [11], k is Boltzmann's constant (8.6×10^{-5} eV K^{-1}),
147 and $T(y)$ is annual mean surface temperature in Kelvin as a function of latitude [8]. We converted
148 latitude to temperature and light by fitting Fourier series to annual mean surface temperature and
149 insolation vs. latitude between $35\text{-}75^\circ\text{N}$, encompassing the latitudinal range of the lakes we considered;
150 we chose the Fourier series degree (1st and 2nd order, respectively) with the best adjusted r^2 , which
151 was $r^2 > 0.99$ in each case. This adjustment accounts for gradients in insolation and temperature by
152 normalizing to the latitude 58.5°N , which has a mean annual surface temperature of $\sim 0^\circ\text{C}$. Note that
153 this choice of temperature is arbitrary and does not affect our results. The advantage of introducing
154 this adjustment to area instead of primary production is that it preserves the ability to directly compare
155 r^2 and root square mean error (RMSE) values among the various scaling relationships in our study
156 (Figure 1). This approach is consistent with previous applications of adjustments for the impact of
157 variation in insolation and temperature on metabolic scaling [11, 2].

158 The production-volume scaling exponent was significantly greater than $2/3$ scaling (94.9% bootstrap

159 probability), which is a null hypothesis for volume-area relationships [5]. Latitude was correlated
160 ($p < 0.01$) with the residuals of the production-area relationship before but not after correcting for
161 latitudinal differences in mean annual air temperature and solar insolation. Other variables we in-
162 vestigated were not correlated with the residuals of these relationships (total nitrogen concentration,
163 dissolved organic carbon concentration, and the vertical light attenuation coefficient). Collectively,
164 these observations support the overall fit and interpretation of our scaling relationships.

165 We estimated global lake primary production based on our scaling relationships and lake areas included
166 in the World Wildlife Fund’s HydroLakes database (<https://www.hydrosheds.org/downloads>). We
167 calculated photosynthetic efficiency based on the one parameter model $P = \beta A_{TI}$ where β is propor-
168 tional to the photosynthetic efficiency at 0°C . We found that $\beta = 0.24 (\pm 0.03) \text{ g C m}^{-2} \text{ d}^{-1}$, which
169 results in a photosynthetic efficiency of $0.044 (\pm 0.005) \%$ from using the Gibbs free energy of 39,748
170 joules to convert a gram of CO_2 to glucose and comparing to $I(58.5^\circ\text{N})$. We computed length of ice-free
171 season by approximating its relationship with annual mean surface temperature in [26] by a Gaussian
172 function. Note that dividing the formula $P = \beta A_{TI}$ by A and substituting in the definition of A_{TI}
173 yields a formula for areal gross primary production (P/A , $\text{gC/m}^2/\text{d}$):

$$P/A = \frac{\beta I(y) e^{-Ea/kT(y)}}{I(58.5^\circ\text{N}) e^{-Ea/k(273\text{K})}}$$

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