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Does lake size matter? Combining morphology and process modeling to examine the contribution of lake classes to population-scale processes

Luke A. Winslow,[1,2]* Jordan S. Read,[2] Paul C. Hanson,[1] and Emily H. Stanley[1]

1 University of Wisconsin-Madison, Center for Limnology, Madison, WI, USA
2 US Geological Survey, Center for Integrated Data Analytics, Middleton, WI, USA
** Corresponding author: lwinslow@usgs.gov*

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Abstract

With lake abundances in the thousands to millions, creating an intuitive understanding of the global distribution of morphology and processes in lakes is challenging. To improve researchers' understanding of large-scale lake processes, we developed a parsimonious mathematical model based on the Pareto distribution to describe the distribution of lake morphology (area, perimeter, and volume). While debate continues over which mathematical representation best fits any one distribution of lake morphometric characteristics, we recognize the need for a simple, flexible model to advance understanding of how the interaction between morphometry and function dictates scaling across large populations of lakes. These models make clear the relative contribution of individual lakes to the total amount of lake surface area, volume, and perimeter. They also highlight the critical thresholds at which total perimeter, area, and volume would be evenly distributed across lake-size classes having Pareto slopes of 0.63, 1.00, and 1.12, respectively. These morphological models can be used in combination with process models to create overarching "lake population" level models of process. To illustrate this potential, we combined the model of surface area distribution with a model of carbon mass accumulation rate. We found that even if smaller lakes contribute relatively less to total surface area than larger lakes, the increasing carbon accumulation rate with decreasing lake size is strong enough to bias the distribution of carbon mass accumulation toward smaller lakes. This analytical framework provides a relatively simple approach to upscaling morphology and process that can be easily generalized to other ecosystem processes.

Key words: lake morphology, macrosystem ecology, power-laws, small lakes, upscaling

Introduction

There is growing interest in better understanding the role of inland waters in carbon and nutrient cycles at broad scales (Bennett et al. 2001, Cole et al. 2007, Harrison et al. 2008, Tranvik et al. 2009). To develop science incorporating lakes into large-scale cycles, some have argued for increased efforts in the field of global limnology, defined as "quantifying and understanding the role of continental waters in the functioning of the biosphere" (Downing 2009). A key challenge for this rapidly evolving research arena is discovering and understanding regular patterns in process rates across aquatic ecosystems to facilitate upscaling.

An emergent lesson from global limnology is that lake size matters. Lakes with surface areas that differ by orders of magnitude (which we describe here as lakes in different "size classes") sometimes have substantially different area-normalized process rates. Gas exchange (Read et al. 2012) and organic carbon burial (Downing et al. 2008, Kastowski et al. 2011) are 2 examples of processes with rates predicted in part by lake size. Such processes with rates tied to lake area can be especially amenable for upscaling because, unlike variables that cannot be

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remotely sensed, the size and abundance are known with reasonable certainty for all but the smallest of lakes (McDonald et al. 2012).

Different processes likely have different scaling relationships, and these differences would lead to shifts in the balance among processes for different lake size classes. Such shifts in process balance with lake area have been hypothesized to occur where processes such as primary and secondary production (scaling with surface area) interact with the lateral import and export of materials (scaling with perimeter; Gasith and Hasler 1976, Vander Zanden and Gratton 2011). These differences in lake morphology distributions may have serious implications for how key processes in large-scale carbon cycling are distributed across lakes of different sizes.

To upscale process estimates, models linking lake process with lake size are often combined with empirical lake size–abundance distributions; however, information on the number of small lakes is often missing. These gaps may represent a substantial source of error because small waterbodies can have particularly high rates for some processes, such as carbon storage or efflux (Downing et al. 2008, Read et al. 2012). To fill in these gaps, lake size–abundance models based on the Pareto distribution have been used to extrapolate unobserved, small lake-size class abundances (e.g., Downing et al. 2008, Kastowski et al. 2011, Lewis 2011).

There are additional applications of lake size–abundance models beyond filling gaps in observation. Specifically, these models greatly simplify large and cumbersome datasets that contain information on many thousands (Lehner and Doll 2004) to millions (Downing et al. 2006) of lakes. When such a model approximates the full population to within a desired level of accuracy, the simplified mathematical form provides an easily manipulated representation, compared to a large empirical dataset, of the population and its key characteristics.

At the first level, the mathematical form of the model can be modified to describe the relative contribution of key morphological characteristics (lake area, perimeter, and volume) of different lake-size classes. These models describe the relative contribution of each lake-size class to total area, perimeter, and volume, and are referred to here as "morphology scaling relationships" (MSRs). These MSRs can provide a convenient and powerful mathematical representation of key components of the hydrosphere. MSRs may be combined directly with models of process to upscale process to the full population of lakes. This concept is similar to the use of large-scale, steady-state approximations of ocean dynamics to communicate key physical phenomenon in oceans (Brown et al. 1989). Such steady-state approximations are not directly used in modeling quantitative ocean process but are useful in communicating and understanding important phenomenon (e.g., Ekman transport and the Sverdrup balance). Similar simplified models for lakes may offer a new and unique opportunity for understanding the collective behavior of these aquatic ecosystems at continental and global scales.

We examined the applicability of the Pareto distribution as a simplified model of the lake size–abundance relationship within the continental United States to show how additional models can be derived from the lake size–abundance distribution to describe, with minimal error, the distribution of morphology, as perimeter and volume, across almost the entire size range of lakes to create MSRs. Finally, we used a published model of carbon mass accumulation rate to show how MSRs can be combined with models of process to create simple models describing process for the whole population of US lakes, although any large population of lakes could be used. We used these morphology and process models to answer the following questions. How do lake size and abundance combine to create MSRs of lake area, perimeter, and volume? What are the critical lake size–abundance distribution parameters that balance the contribution of small and large lakes to total estimates of global aquatic morphology? Finally, using carbon accumulation rate as an exemplar, we ask: Can we use the MSRs to quantify how strongly process must scale with lake size for the relative contribution of small versus large lakes to balance at the global scale?

Methods

Empirical relationships

For an empirical lake abundance, area, and perimeter dataset, we used the US Geological Survey's (USGS) National Hydrography Dataset (NHD; retrieved January 2013, http://nhd.usgs.gov). We used the data derived from high-resolution USGS topographical maps (1:24,000 scale; Simley and Carswell 2009) and excluded Alaska and Hawaii due to the differing resolution of data available. While the dataset covers all 48 continental US states, the Laurentian Great Lakes were not included in our analysis because their low number substantially reduces the applicability of population-level process simplifications and estimates. For all analyses and figure generation, we used the Mathworks Mapping Toolbox functionality (v2011a; http://mathworks.com). To avoid issues with missing or unobserved small lakes, only those with surface areas >0.01 km^2 (1 ha) were included here. For a more detailed methods and geographical visualization of the NHD data, see McDonald et al. 2012 and Winslow et al. 2014.

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Previous descriptions of lake size–abundance have used a Pareto distribution (Downing et al. 2006). The Pareto distribution:

$$pdf(A) = \alpha x_m^{\alpha} A^{-(\alpha+1)}, \tag{1}$$

is defined by 2 parameters, the scale parameter (x_m) and the shape parameter (α). Parameter x_m defines the minimum variable value of A, the values of the population of interest (in our case, A is lake area), and α is the exponent of the power law. To estimate α, we used the maximum likelihood estimator:

$$\hat{\alpha} = \frac{n}{\sum_{1}^{n} \ln \frac{X_i}{x_m}}, \tag{2}$$

where n is the number of observations; $\hat{\alpha}$ is the maximum likelihood estimate for the population's α; x_m is the minimum value from the population of interest; and X_i is the examined population variable, in this case, lake area (equation from Rytgaard 1990). Lastly, we used the NHD dataset to calculate a relationship between lake area and perimeter. The relationship was fitted using a nonlinear, least-squares exponential fit of area versus perimeter to estimate the exponential relationship parameters.

Extending the Pareto distribution

We used the Pareto probability density function (equation 1) to derive a number of functions to highlight the relative contribution of different lake-size classes to the global distribution of lake area, volume, and perimeter, as well as biogeochemical processes that scale with these morphological parameters. When used as a size–abundance model, the Pareto probability density function gives the fraction of total lakes at a given size class, which can be described roughly as:

$$pdf\,(A) \propto n\,(A), \tag{3}$$

where n is the number of lakes for a given lake area, A. The fraction of lakes in each size class multiplied by the area of that class ($n{*}A$) gives the relative total area contributed by that size class, analogous to weighting the probability density function by lake area. Because of its relative ease of observation, lake area is the most commonly used parameter for large-scale lacustrine biogeochemistry estimates. To derive an equation for the lake area–distribution across lake-size classes, we multiplied the size–abundance equation for the Pareto probability distribution by area and integrated:

$$A_{dens}\,(A) = \int \alpha x_m^{\alpha} A^{-(\alpha+1)\,*} A \; dA. \tag{4}$$

The result is an equation that describes the relative contribution to total lake area (A_{dens}) across different lake-size classes. Because we wanted to focus on the relative contributions of different lake-size classes and emphasize simplicity, we combined all constant terms into a single term, C:

$$A_{dens} = CA^{1-\alpha}. \tag{5}$$

For comparing process contribution of differently sized lakes, the absolute magnitude of the function is not important. Rather, how it scales across lake-size classes is the critical attribute.

The same methods were also applied to lake perimeter. This distribution is formulated from the observed relationship between lake abundance and surface area and requires a relationship between area and perimeter to be known. Given the lack of available data on this relationship in the literature, we assumed simply that a circle with a given area adequately represents lake perimeter and represents the lowest bound for perimeter of a given area. This relationship was derived from the equations of a circle:

$$P = 2(\pi A)^{½}, \tag{6}$$

where P is perimeter. To get the perimeter distribution across lake sizes, we combined the equation of a circle's perimeter (equation 6) with that of the Pareto distribution (equation 1) and again combined all constants into the term C, which after integrating became:

$$A_{dens}\,(A) = CA^{½-\alpha}, \tag{7}$$

where all constants were again subsumed into the C coefficient.

Lastly, while volume predicted from area alone results in relatively high uncertainty (±57% relative standard deviation of predicted vs. observed volume; Sobek et al. 2011), creating a similar model for volume is useful to contrast with area and perimeter distributions. To formulate the equation for volume distribution across lake sizes, we needed to substitute in a published relationship between area and volume into equation 5. Because we were unaware of any published relationships for US lakes, we used a relationship based on lakes in Sweden ($V \sim A^{1.12}$; Sobek et al. 2011), which substituting into equation 5 became:

$$V_{dens}\,(A) = CA^{1.12-\alpha}. \tag{8}$$

The derived MSRs for perimeter and volume were compared with observations by comparing the predicted fraction with the empirical distribution derived from the continental US NHD. The observations were summed into decadal lake-size bins (e.g., 1–10 km^2), and the model results and residuals were plotted for comparison.

We also used the Pareto distribution to show how lake processes scale across lake sizes. By combining equation 5 and a relationship of process rate with lake area (an area–rate relationship), we created a combined, overarching model with a simple form that estimates the relative contribution of each lake-size class to total process. Processes that have a power-function lake area–rate relationship are often represented in the literature as a log-transformed linear relationship and takes the form:

$$F = F_o A^{\beta}, \qquad (9)$$

where F is the process rate with units dependent on the process being described; F_o is a linear scaling parameter (i.e., the intercept); A is lake area; and β is the parameter that scales the process rate with lake area. When combined, this area–rate relationship (equation 9) and the MSR for area (equation 5) yielded a function that scales process across lake size:

$$F_{dens}(A) = CF^{\,1-\alpha+\beta}. \qquad (10)$$

We used carbon mass accumulation rate (CMAR) as an example of how equation 10 can be used with process rates reported in the literature. Existing work has found that organic carbon burial rates correlated with area, watershed slope, and percent cropland cover (Kastowski et al. 2011). The relationship was described by the equation:

$$\log(CMAR) = 1.00 - 0.217 * \log(lake\ area) + 0.194 * (slope) + 0.017 * (cropland\ \%), \qquad (11)$$

which shows that log-CMAR varied with log-lake area with a slope of −0.217. We used this β for CMAR and a published size–abundance slope (α = 0.92) in equation 10 to get the scaling equation:

$$CMAR = CA^{-0.177}, \qquad (12)$$

where C is a constant, A is lake area, and $CMAR$ is an index of the relative contribution of each lake-size class to overall carbon accumulation.

Results and discussion

The Pareto distribution and simple scaling laws can help us understand how lakes of different sizes contribute to the overall total of perimeter, area, and volume. For example, while it is unclear whether small lakes contribute more than large lakes to the total surface area globally (Downing et al. 2006, McDonald et al. 2012), using the Pareto distribution and some simple calculus we can illustrate how sensitive our inferences about total surface area are to our estimate of α. The distribution of lake surface area can be considered as a balance between decreasing area and increasing abundance with decreasing area. If lake abundance does not increase proportionally with decreasing area, then total surface area in each size class will increase (Fig. 1). Conversely, if the slope of lake abundance versus area is not steep enough, then total surface area in each size class will decrease, substantially altering our understanding of small versus large lake roles. Equation 5 illustrates this trade-off.

Critical lake size–abundance distribution parameters for area, perimeter, and volume

Our perspective on how the contribution of small versus large lakes depends on the value of α can be easily demonstrated using equation 5. The critical threshold for area is when α equals 1, resulting in an exponent of zero. An

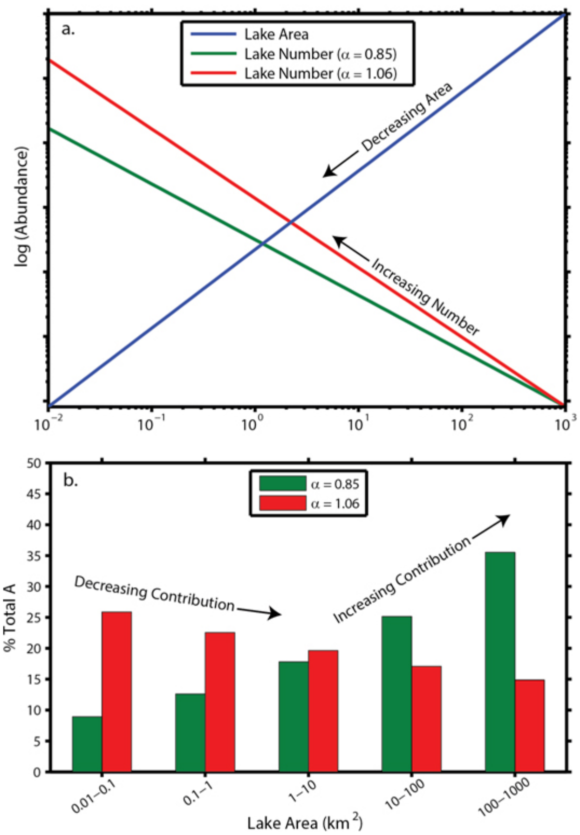

Fig. 1. Lake size and abundance trade-off. (a) The size–abundance distribution for 2 different published Pareto slope parameters, both showing increasing abundance with decreasing size. (b) The relative contribution of lake size categories to surface area (%Total A) for 2 different published Pareto slope parameters.

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exponent of zero makes the contribution by each size to total area unrelated to the surface area of the size class. Knowing this critical threshold helps explain the different results found by past studies in which the contribution of lake size classes to total lake surface area were examined. While some previous work calculated $\alpha = 1.06$ empirically from larger lakes of the globe (Downing et al. 2006), others found $\alpha = 0.85$ for a more complete size range of the continental US lake population (McDonald et al. 2012). Despite the 2 reported estimates of α being of seemingly similar magnitude, they fall on opposite sides of the critical α cutoff. If $\alpha < 1$, as reported by McDonald et al. (2012) and also found here ($\alpha = 0.92$; Fig. 2a), the exponent of area in equation 5 is positive, and larger lakes make an increasing contribution to the total surface area of lakes. If $\alpha > 1$, the exponent is negative, resulting in a decreasing contribution to global surface area of lakes with increasing area. The deviation from linearity in the large lakes likely represents the edge effects of the continent, where a large lake has a higher likelihood of intersecting the continental edge and therefore not forming a lake (Goodchild 1988).

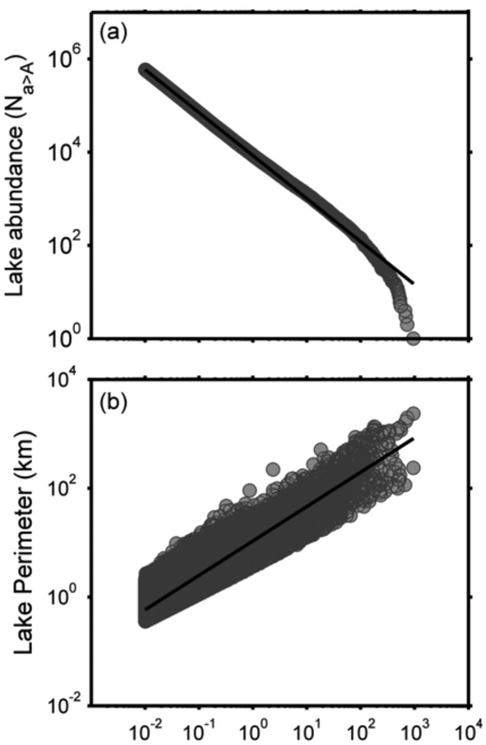

Fig. 2. Maximum likelihood size–abundance Pareto and lake area to perimeter fit. NHD lakes (a) size–abundance distribution with the maximum likelihood fit of the Pareto distribution and (b) power-law area to perimeter relationship. A nonlinear exponential fit is shown with slope 0.63, close to the theoretical relationship defined by the relationship between the area and perimeter of a circle (slope 0.5).

The perimeter MSR is described by equation 7, yielding a critical threshold for an even distribution of perimeter across all size classes of $\alpha = 0.5$ when lake shape is simplified to a circle. An $\alpha = 0.5$ would produce a zero exponent for the area term and thus a constant perimeter density across all size classes. In studies that have estimated values of α (Hamilton et al. 1992, Downing et al. 2006, Kastowski et al. 2011, McDonald et al. 2012) as well as here, α estimates are consistently >0.5, suggesting that the distribution of perimeter is skewed strongly toward small lakes. The contribution of any processes that scale proportionally to perimeter, such as particulate organic carbon) import (Gasith and Hasler 1976), would be skewed toward small rather than large lakes.

Using an empirical relationship between area and lake perimeter instead of a circular lake assumption can improve accuracy of the perimeter MSR. The nonlinear least-squares exponential fit of area versus perimeter for continental US lakes yielded a slope of 0.63 (Fig. 2b). This result suggests large lakes have, on average, higher perimeters relative to their areas than would be predicted if lakes had a constant geometrically scaled proportion of area to perimeter. Compared to a circular-lake assumption, steeper area to perimeter slope reduces the skew of perimeter toward small lakes, although the difference is not large enough to change the small-lake skew of perimeter. The US NHD lakes-based MSR of perimeter would be:

$$P_{dens}(A) = CA^{0.63-\alpha}. \tag{13}$$

Using the published model for Swedish lakes, the critical threshold for an even distribution of volume across all size classes would be $\alpha = 1.12$, higher than previous α estimates (Downing et al. 2006, McDonald et al. 2012). The α values reported for equation 8 for large collections of lakes are consistently <1.12, which demonstrates that volume is likely skewed strongly toward larger lakes. To improve our mathematical model for the contiguous US and beyond, future work examining area–volume relationships of other geographic regions is required.

For lake area and perimeter, the estimates made by the MSRs can be compared to a large-scale empirical lake distribution. Like any model, the desired accuracy is dependent on the scope and application. As in this case, when the geographic scope is large (continental US), even models that make predictions to within an order of magnitude may be useful. We compared the model results for contribution of each size class to area and perimeter with the empirical results (Fig. 3). For all size classes between 0.01 and 1000 km^2, the estimates of area were within 4% of the empirical values. For perimeter, all bins were within 7% of the empirical measurements. Caution should be taken when extrapolating these models to lakes

<0.01 km^2 because it is unclear if the power-law model accurately describes abundance below that size class (McDonald et al. 2012).

The distributions of area, perimeter, and volume strongly differ across size classes, and the understanding of how area is distributed is sensitive to the estimate of α (Fig. 4a–c). Given that different limnological processes may be more sensitive to different aspects of lake morphology, a varying α value affects not only estimates of absolute rates, but also the apparent balance between pelagic and perimeter processes. In a lake population with a large α, the median lake size is reduced, with the total area being fractured into many smaller lakes instead of a few larger lakes. With a smaller median lake size, the process balance would be skewed toward perimeter-dominated processes (e.g., terrestrial particulate organic carbon import and primary productivity; Gasith and Hasler 1976, Preston et al. 2008). Conversely, for small α values, the median lake size would be higher, resulting in a population of lakes more dominated by pelagic processes and autochthonous resources (Wilkinson et al. 2013).

Process across the lake size–abundance distribution

To examine how process is distributed across lakes of different sizes, we focused on the exponent of lake area, β. Care should be taken when fitting the β parameter; nonlinear fitting techniques, as opposed to log transformed linear regression which often distorts error, tend to be more robust and should be favored (Motulsky and Ransnas 1987).

The key result of equation 10 comes from the exponent of area, which indicates the direction of areal skew in the process (toward or away from large lakes). To reiterate the key point, a positive exponent would result in larger lakes making a larger relative contribution, a negative exponent would indicate that small lakes contribute more to the overall process magnitude, and an exponent at or very near zero would suggest no scaling with area and thus an equal contribution of all lake-size classes. Our maximum likelihood estimate of the lake size–abundance slope parameter was $\alpha = 0.92$. As we have shown, $\alpha < 1$ means smaller lakes contribute less to total surface area than larger lakes. Despite a lake area distribution skewed toward larger lakes, process rates do not need a strong negative relationship with lake size to overcome the skewed area distribution and to have an equal contribution

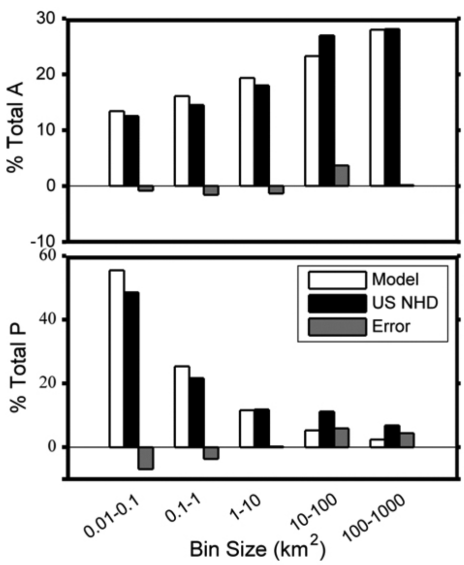

Fig. 3. Comparison of lake morphology model to empirical dataset. Comparison of the observed continental US dataset with the Pareto-based model. The difference between observed and modeled for any bin of area (A) and perimeter (P) did not exceed 4% and 7%, respectively.

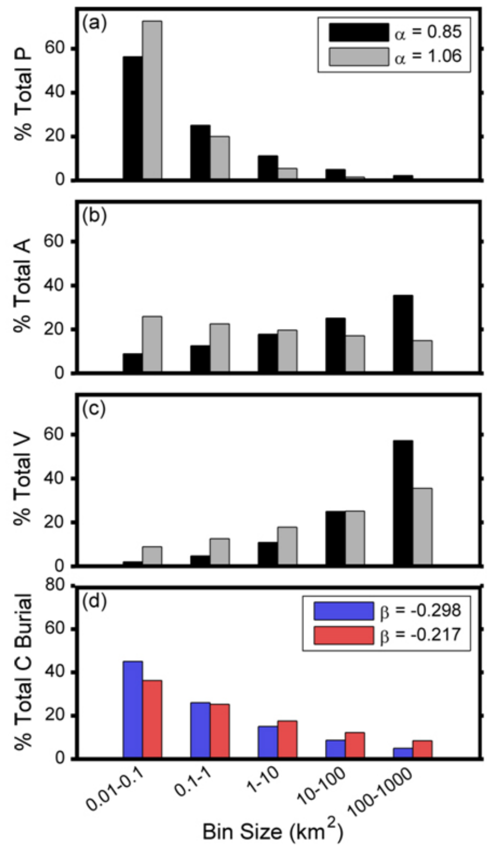

Fig. 4. Lake size-class contributions to total area, perimeter, volume, and carbon burial. Percent contribution of total for each lake size-class to total lake (a) area (A), (b) perimeter (P), and (c) volume (V) for the range of published α values (1.06: Downing et al. 2006; 0.85: McDonald et al. 2012). (d) Percent contribution to total carbon (C) burial for each lake size-class with $\alpha = 0.85$ and $\beta = -0.217$, estimated from European lakes (Kastowski et al. 2011). Black bars were calculated using $\beta = -0.298$ estimated from eutrophic lakes in Iowa, USA (Downing et al. 2008).

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across all lake sizes. For a given process to have an equal contribution across all lake sizes, the process scaling parameter (β) only needs to be –0.08, which would make the exponent of area zero (from equation 10: $1 - 0.92 + 0.08$). To put this finding into perspective, $\beta = -0.08$ would imply that the process rate in a 0.01 km^2 lake is ~2 times higher than in a 100 km^2 lake. If $\beta < -0.08$, small lakes would contribute a larger fraction to the overall process than larger lakes. If $\beta > -0.08$, large lakes would contribute a larger fraction.

A published example of such a process is the CMAR in European lakes (Kastowski et al. 2011). The scaling equation for CMAR (equation 12) has a negative area exponent, meaning that CMAR is skewed toward smaller lakes (Fig. 4d). Using a different reported relationship between lake area and carbon burial with $\beta = -0.298$ calculated from small eutrophic lakes in Iowa, USA (Downing et al. 2008), the distribution becomes even more strongly skewed toward smaller lakes (Fig. 4d). This skew suggests that despite being generally less studied than larger lakes (Downing 2010), the contribution of smaller lakes to global scale processes such as carbon storage may be disproportionately large. Unfortunately, carbon sedimentation in small lakes is highly variable, with commonly cited studies reporting maximum observed rates ranging over several orders of magnitude, from around 280 g m^{-2} yr^{-1} C (Mulholland and Elwood 1982) to as high as 10 000 g m^{-2} yr^{-1} C (Downing et al. 2008). The importance of small lakes, combined with high rate uncertainty and high abundance, will require novel research and ideas in the future to constrain large-scale carbon storage in small lakes.

This modeling framework represents a unique and simple approach to describe distributions of morphology and process across a population of lakes. While the quantification of morphology and process will always require detailed computational work using empirical data, this mathematical approach helps researchers form a more intuitive understanding of large populations of lakes while maintaining some quantitative aspects.

Conclusions

We presented a series of simple equations that highlighted the critical thresholds for the Pareto slope where morphological characteristics would be evenly distributed across lake-size classes. For area and perimeter, these values were 1 and 0.63 respectively. The volume relationship had the highest uncertainty, and when better estimates are available, the equation for volume should be updated. Despite this uncertainty, using the available published relationship for demonstrative purposes (Sobek et al. 2011) resulted in a critical Pareto slope threshold of 1.12 for volume. Given a Pareto slope parameter between 1.06 and 0.92, larger lakes likely contribute relatively less to total perimeter and more to total volume than smaller lakes. The skew of the area distribution was dependent on the Pareto slope parameter, although our estimate of 0.92 derived from a dataset spanning a large range of lake sizes suggests that smaller lakes contribute a decreasing fraction to total surface area. Despite the likely skew of surface area toward larger lakes, processes can offset the skew by having a process rate that increases with decreasing lake size, requiring a critical exponential slope with lake size of only −0.08 or less. The carbon mass accumulation process is one such example, with published exponential slopes from −0.217 to −0.298, which results in a skew of carbon accumulation contribution toward smaller lakes. These simple mathematical tools will help bring quantitative, global limnological thinking to a broader group of students and researchers.

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References

Bennett EM, Carpenter SR, Caraco NF. 2001. Human impact on erodable phosphorus and eutrophication: a global perspective. Bioscience. 51:227–234.

Brown E, Colling A, Park D, Phillips J, Rothery D, Wright J. 1989. Ocean Circulation. (Keynes M, editor.). Oxford (UK): Pergamon Press.

Cole JJ, Prairie YT, Caraco NF, McDowell WH, Tranvik LJ, Striegl RG, Duarte CM, Kortelainen P, Downing JA, Middelburg JJ, et al. 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. Ecosystems. 10:172–185.

Downing JA. 2009. Global limnology: up-scaling aquatic services and processes to planet Earth. Verh. Internat. Verein. Limnol. 30(8):1149–1166.

Downing JA. 2010. Emerging global role of small lakes and ponds: little things mean a lot. Limnetica. 1:9–24.

Downing JA, Cole JJ, Middelburg JJ, Striegl RG, Duarte CM, Kortelainen P, Prairie YT, Laube KA. 2008. Sediment organic carbon burial in agriculturally eutrophic impoundments over the last century. Global Biogeochem Cy. 22:1–10.

Downing JA, Prairie YT, Cole JJ, Duarte CM, Tranvik LJ, Striegl RG, McDowell WH, Kortelainen P, Caraco NF, Melack JM. 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnol Oceanogr. 51:2388–2397.

Gasith A, Hasler AD. 1976. Airborne litterfall as a source of organic matter in lakes. Limnol. Oceanogr. 21:253–258.

Goodchild MF. 1988. Lakes on fractal surfaces: a null hypothesis for lake-rich landscapes. Math Geol. 20:615–630.

Hamilton SSK, Melack JJM, Goodchild M, Lewis WM. 1992. Estimation of the fractal dimension of terrain from lake size distributions. In: Lowland Floodplain Rivers: Geomorphological Perspectives. p. 145–163.

Harrison JA, Maranger RJ, Alexander RB, Giblin AE, Jacinthe P-A, Mayorga E, Seitzinger SP, Sobota DJ, Wollheim WM. 2008. The regional and global significance of nitrogen removal in lakes and reservoirs. Biogeochemistry. 93:143–157.

Kastowski M, Hinderer M, Vecsei A. 2011. Long-term carbon burial in European lakes: analysis and estimate. Global Biogeochem Cy. 25:1–12.

Lehner B, Doll P. 2004. Development and validation of a global database of lakes, reservoirs and wetlands. J Hydrol. 296:1–22.

Lewis WM. 2011. Global primary production of lakes: 19th Baldi Memorial Lecture. Inland Waters. 1:1–28.

McDonald CP, Rover JA, Stets EG, Striegl RG. 2012. The regional abundance and size distribution of lakes and reservoirs in the United States and implications for estimates of global lake extent. Limnol Oceanogr. 57:1–12.

Motulsky H, Ransnas L. 1987. Fitting curves to data using nonlinear regression: a practical and nonmathematical review. FASEB J. 1:365–374.

Mulholland P, Elwood J. 1982. The role of lake and reservoir sediments as sinks in the perturbed global carbon cycle. Tellus. 34:490–499.

Preston ND, Carpenter SR, Cole JJ, Pace ML. 2008. Airborne carbon deposition on a remote forested lake. Aquat Sci. 70:213–224.

Read JS, Hamilton DP, Desai AR, Rose KC, MacIntyre S, Lenters JD, Smyth RL, Hanson PC, Cole JJ, Staehr PA, et al. 2012. Lake-size dependency of wind shear and convection as controls on gas exchange. Geophys Res Lett. 39:L09405.

Rytgaard M. 1990. Estimation in the Pareto distribution. Astin Bull. 20:201–216.

Simley J, Carswell J. 2009. The national map– hydrography: U.S. Geological Survey fact sheet 2009-3054.

Sobek S, Nisell J, Fölster J. 2011. Predicting the volume and depth of lakes from map-derived parameters. Inland Waters. 1:177–184.

Tranvik LJ, Downing JA, Cotner JB, Loiselle SA, Striegl RG, Ballatore TJ, Dillon P, Finlay K, Fortino K, Knoll LB, et al. 2009. Lakes and reservoirs as regulators of carbon cycling and climate. Limnol Oceanogr. 54:2298–2314.

Wilkinson GM, Carpenter SR, Cole JJ, Pace ML, Yang C. 2013. Terrestrial support of pelagic consumers: patterns and variability revealed by a multilake study. Freshwater Biol. 58:2037–2049.

Winslow LA, Read JS, Hanson PC, Stanley EH. 2014. Lake shoreline in the contiguous United States: quantity, distribution and sensitivity to observation resolution. Freshwater Biol. 59:213–223.

Vander Zanden J, Gratton C. 2011. Blowin' in the wind: reciprocal airborne carbon fluxes between lakes and land. Can J Fish Aquat Sci. 68:170–182.

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