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Patterns and Variation of Littoral Habitat Size Among Lakes

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Key Points:

- Littoral area is smaller in deeper lakes and those with lower light penetration. The relationship is modified by basin shape
- Scaling relationships can predict the relative size of littoral area for lakes with incomplete bathymetric information
- The littoral zone comprises 78% of Earth's total lake area

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract

The littoral zone varies in size among lakes from ~3% to 100% of lake surface area. In this paper, we derive a simple theoretical scaling relationship that explains this variation, and test this theory using bathymetric data across the size spectra of freshwater lakes (surface area = 0.01–82,103 km^2, maximum depth = 2–1,741 m). Littoral area primarily reflects the ratio of the maximum depth of photosynthesis to maximum lake depth. However, lakes that are similar in these characteristics can have different relative littoral areas because of variation in basin shape. Hypsometric (area-elevation) models that describe these patterns for individual lakes can be generalized among lakes to accurately predict the relative size of littoral habitat when there is incomplete bathymetric information. Collectively, our results provide simple rules for understanding patterns of littoral habitat size at the regional and global scales.

Plain Language Summary

Some lakes are comprised completely by littoral habitat while other have almost none, but the factors responsible for this variation are poorly described. We developed simple relationships to explain variation in the size of littoral habitats among lakes. The factors determining littoral habitat size were light penetration, maximum depth, and mean depth. We make several predictions based on these rules including that alpine lakes should have large littoral zones compared to lakes in forested, agricultural, and urban regions, and that lakes should generally have larger littoral zones than reservoirs. We also derive simple equations that accurately predict the relative size of littoral zones in lakes where bathymetric data are incomplete. Collectively, our results and predictions elucidate the connection between lake characteristics and the relative size of habitats within lakes, which provides enough information to understand patterns of littoral habitat size at the regional to global scale.

1. Introduction

The characteristics and dynamics of lake ecosystems strongly reflect the relative sizes of the littoral (the nearshore habitat where photosynthetically active radiation penetrates to the lake bottom in sufficient quantities to support photosynthesis) and pelagic zones (the rest of the lake; Lodge et al., 1988; Wetzel, 1990; Vander Zanden & Vadeboncoeur, 2020). However, predictive relationships for patterns of the relative size of these habitats across landscapes are not available, probably due to the paucity of bathymetric data relative to the global abundance of lakes (Hollister et al., 2011; Seekell, 2018; Wetzel, 1990). In particular, there is need to develop scaling relationships that relate habitat size to commonly measured lake characteristics (Cael et al., 2017; Seekell et al., 2013). Such relationships provide the simple rules used to generalize understanding of aquatic ecosystem patterns and processes at regional to global scales (Downing, 2009).

Among lakes, the littoral zone varies in size from nearly 0% to 100% of the total lake area. This variation is captured in a conceptual model created by Wetzel (1990), and popularized in his widely read text book, that depicts the relationship between the logarithm of lake abundance and the logarithm of the pelagic:littoral area ratio. However, this log-ratio formulation can neither accommodate lakes completely comprised by littoral area, which is relatively common for shallow lakes, nor does it explain why some similarly sized lakes are completely comprised by littoral area while others have almost none. An empirical analysis by Henson (1993) identified an inverse scaling relationship between relative littoral habitat size (littoral area/total surface area) and mean depth for lakes with mean depths greater than 4 m. However, about 85% of Earth's lakes have a mean depth less than 4 m, and this scaling relationship predicts that these lakes are comprised of >100% littoral area (Cael et al., 2017; Henson, 1993). Hence, this relationship is incorrect or incomplete. A third approach to studying patterns of relative littoral habitat variability is to use the shoreline development index (the ratio of shore length to the circumference of a circle with the same area as the lake) as a proxy based on the assumption that lakes with convoluted shorelines should have relatively large littoral zones (e.g., Dolson et al., 2009; Schindler & Scheuerell, 2002; Wetzel, 2001). However, this approach lacks theoretical support and empirical validations are inconsistent (Text S1 in Supporting Information S1). Hence, there is a clear need to develop new quantitative approaches for understanding variations in relative littoral habitat size (i.e., littoral surface area to total lake surface area ratio) among lakes.

In this study, we use hypsometric (area-elevation) analysis to predict how variations in lake characteristics affect relative littoral habitat size among lakes. We describe a simple and accurate relationship to predict relative littoral habitat area with incomplete bathymetric data. Finally, we test this relationship for lakes that encompass a wide range of surface areas (area = 0.01–82,103 km^2) and depths (maximum depth 2–1,741 m) using original and literature data. Collectively, our analyses provide simple rules for understanding patterns of relative littoral habitat availability at the regional and global scales, as well as clear mechanistic links between these patterns and geologic and water quality factors.

2. Theory

The littoral zone is the area between the shoreline and the compensation depth—the maximum depth of significant photosynthesis by rooted vascular plants and epilithic algae—which is generally operationalized as the depth where photosynthetically active radiation (400–700 nm) is 1% of surface irradiance (taxa-specific compensation depths vary around 1% this benchmark) (Kirk, 2011; Vander Zanden & Vadeboncoeur, 2020; Wetzel, 1990, 2001). Based on this definition, relative littoral area can be calculated deterministically (no free parameters) from measurements of vertical light extinction and mean and maximum depth, using hypsometric analysis (Strahler, 1952). Specifically,

$$\frac{A_L}{A_T} = \begin{cases} 1 & z_c \geq z_{\max}, \\ \left[\dfrac{z_c}{z_{\max}}\right]^{\zeta} & z_c < z_{\max}, \end{cases}$$

where A_L is littoral area (m^2), A_T is the total (pelagic + littoral) lake area (m^2), $z_{\max}$ is the maximum depth (m), and z_c is the compensation depth (m). The compensation depth is calculated $z_c = \log_e(100)/k$, where k is the vertical light attenuation coefficient for photosynthetically active radiation (m^{-1}). This specific formulation of the hypsometric equation states that lakes are completely comprised by littoral area if the compensation depth is greater than or equal to the maximum depth. When the compensation depth is less than the maximum depth, relative littoral area falls within the interval $0 < A_L/A_T < 1$, depending on the depth of light penetration relative to the maximum depth, and the dimensionless parameter ζ, which describes the relationship between relative depth and relative area for a vertical cross section through the center of the lake (Strahler, 1952). The basin is convex when $\zeta < 1$, indicating relatively large littoral zones, whereas the basin is concave when $\zeta > 1$, which describes bases with steeper nearshore areas and relatively small littoral zones (Strahler, 1952, Figure 1a). This distribution of lake area relative to depth is fully determined by the mean (z_{mean} m) to maximum depth ratio (D_R, dimensionless) if the basin shape approximates a quadric surface, for example, a hyperboloid ($D_R = 0.35$), paraboloid ($D_R = 0.5$), or ellipsoid ($D_R = 0.66$) (Carpenter, 1983). The mean to maximum depth ratio is related to the hypsometric exponent by

$$\zeta = \frac{D_R}{\left(1 - D_R\right)}.$$

This equation linearizes the relationship between shape and the mean to maximum depth ratio, and is accurate across the range of commonly observed mean to maximum depth ratios (Carpenter, 1983; Devlin et al., 2016; Lehman, 1975; Vadeboncoeur et al., 2008). Empirical deviations are due to a combination of measurement error and deviation from idealized quadric surfaces. It is possible to capture more complex area-depth relationships than those of idealized quadric surfaces, for example, by making the hypsometric equation a higher-order polynomial, although empirical deviations are typically minor and more complex models are not necessary for most lakes (Carpenter, 1983; Devlin et al., 2016; Harlin, 1978; Lehman, 1975; Likens, 1985).

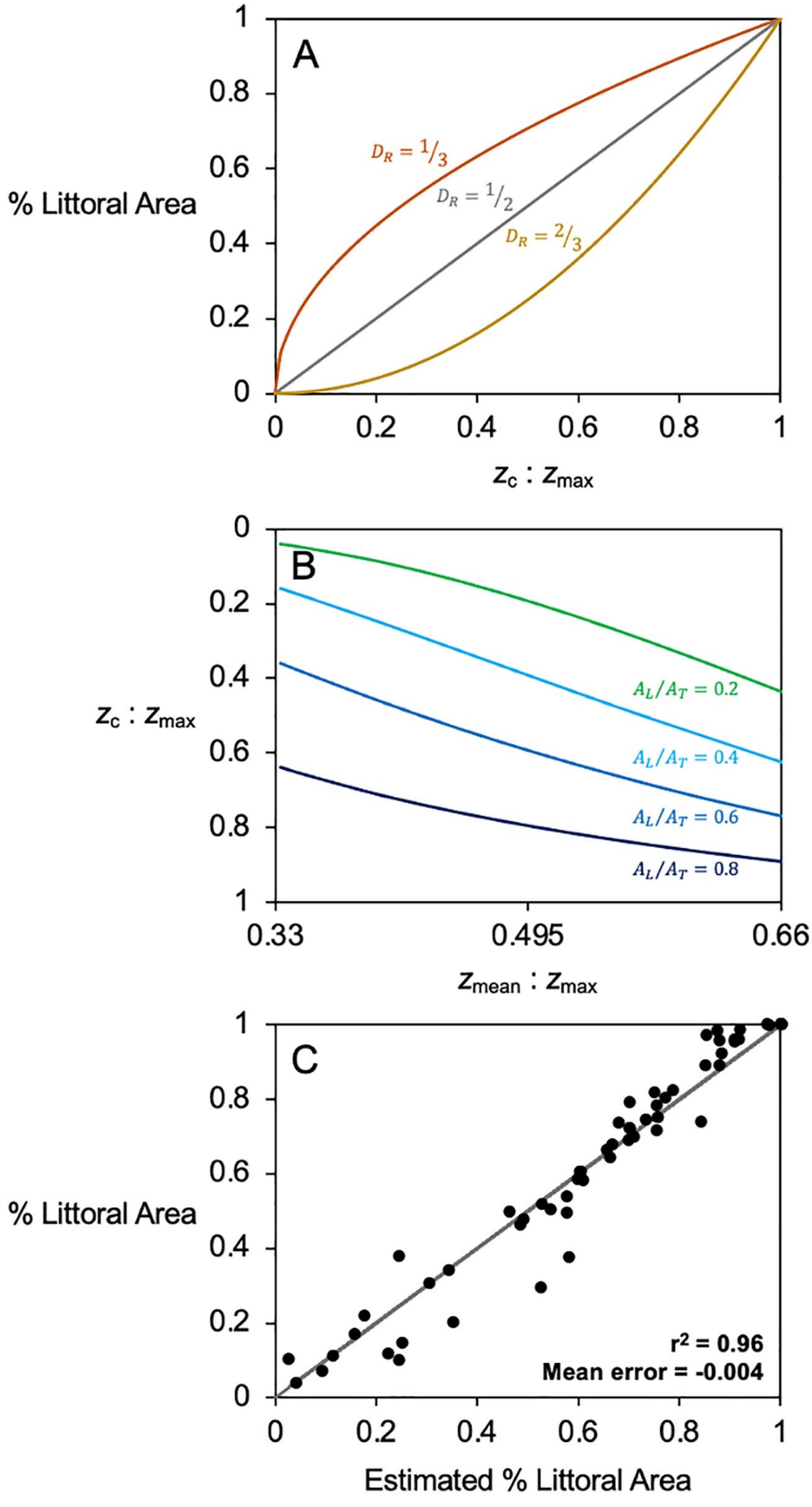

Figure 1. (a) Relative littoral area is greater for lakes with low mean to maximum depth ratios than lakes with high mean to maximum depth ratios when the compensation depth is less than the maximum depth. (b) For basins of similar shape, there is a higher proportion of littoral area in lakes with greater light penetration relative to the maximum depth (z_c:z_{max}). (c) Observed littoral area compared to estimated littoral area calculated from the hypsometric equation with no free parameters.

Table 1
Characteristics of Lakes Used in the Empirical Analysis Compared to the Typical Range for Lakes Based on Large Regional or Global Data Sets

Characteristic	Range in this study	Range in original data (Swedish lakes)	Typical range	Source for typical range
Surface area (km^2)	0.02–82,103	0.02–0.39	0.01–10	Cael and Seekell (2016) and Verpoorter et al. (2014)
Littoral area (%)	3–100	34–100	5–100	Henson (1993)
Maximum depth (m)	2.2–1,741	2.2–31.2	<20	Sobek et al. (2011) and Hollister et al. (2011)
Vertical light attenuation (m^{-1})	0.08–3.19	0.19–3.19	0.4–3.2	Seekell et al. (2018)
Mean: Max Depth (dimensionless)	0.19–0.62	0.19–0.51	1/3–2/3	Carpenter (1983)

Few of Earth's lakes have been depth-sounded, and for those that have been often only the mean or maximum depth is reported (Cael et al., 2017; Hollister et al., 2011; Oliver et al., 2016; Seekell, 2018). Maximum depth is most commonly reported, presumably because its measurement requires less mapping effort and planimetry compared to mean depth (planimetry is required to measure volume, mean depth is the volume divided by surface area). Relative littoral area of individual lakes can be predicted without mean depth if the distribution of mean to maximum depth ratios is sufficiently characterized. For example, the simplest way, but not the only way, to characterize this distribution is to assume that values within the range of depth ratios are equally likely (Table 1 and Text S2 in Supporting Information S1):

$$\bar{\zeta} = \frac{1}{D_{R\max} - D_{R\min}} \int_{D_{R\min}}^{D_{R\max}} \frac{D_R}{(1 - D_R)} dD_R,$$

which can be used in the hypsometric equation to calculate relative littoral area when mean depth is not known. For example, if lake depth ratios are between 1/3 and 2/3 are equally likely, the mean depth ratio is $\overline{D_R} = 0.5$ and the estimated exponent is $\zeta \approx 1.079$. An *R* function for calculating the hypsometric exponent is provided in Text S2 in Supporting Information S1.

In addition to the hypsometric exponent, the maximum depth can be estimated if the mean depth but not maximum depth is known. Maximum depth is estimated as the ratio of the mean depth and the average depth ratio (i.e., $\hat{z}_{\max} = {}^{z_{\text{mean}}}/_{\overline{D_R}}$). For example, when the mean depth ratio is $\overline{D_R} = 0.5$, estimated maximum depth is $\hat{z}_{\max} = {}^{z_{\text{mean}}}/_{0.5}$. Hence, when maximum depth is unknown the hypsometric equation is:

$$\frac{A_L}{A_T} = \begin{cases} 1 & z_c \geq \hat{z}_{\max}, \\ \left[\dfrac{z_c}{\hat{z}_{\max}}\right]^{\bar{\zeta}} & z_c < \hat{z}_{\max}, \end{cases}$$

These equations could also be written in terms of total surface area, assuming that the relationship between surface area and mean or maximum depth is sufficiently characterized (Text S3 in Supporting Information S1).

Collectively, these equations indicate that relative littoral area is primarily a function of the ratio of light penetration to maximum depth, which is moderated by the basin shape. This theory can be tested by regressing (without intercept) the logarithm of relative littoral area by the ratio of the compensation to maximum depths and testing if the coefficient is significantly different from the theoretically specified value (i.e., $\log_e\left(A_L/A_T\right) = \bar{\zeta} \times \log_e(z_c/z_{\max})$).

3. Empirical Analysis

3.1. Data

We took depth soundings of 54 Swedish lakes using an echo sounder with integrated global positioning system unit (Lowrance M52i; Klaus et al., 2021; Seekell et al., 2018). We digitized lake perimeters at the 1:10,000 scale from high-resolution satellite and aerial imagery, and calculated lake area from these outlines.

For each lake, we also took vertical depth profiles for photosynthetically active radiation (400–700 nm, in μ mol s^{-1} m^{-2}; PAR) using a spherical quantum sensor (LI-COR LI-193). We calculated the vertical light extinction coefficient from the slope of the linear regression of the logarithm of PAR versus measurement depth (Kirk, 2011). We calculated the compensation depth (1% light depth) for each lake as $\log_e(100)/k$ (Davies-Colley et al., 1993; Kirk, 2011). Finally, we calculated littoral area as the surface area between the shoreline and the position of the compensation depth contour. We complemented our original data with the literature data for 14 of Earth's deepest lakes which have been measured using methods that are directly comparable to our Swedish lakes (Vadeboncoeur et al., 2011). With this, our data set includes the largest and smallest of Earth's freshwater lakes in terms of surface area and maximum depth (Table 1). There are gaps in our coverage in terms of surface area, specifically mediums sized lakes, but not for the nondimensional parameters used to predict relative littoral area. Additionally, the diversity of lake formation processes is not completely represented. The Swedish lakes are of glacial origin while the literature lakes are primarily of tectonic origin.

3.2. Data Analysis

We first evaluated the basic patterns of relative littoral area across the typical range of variability of depth and light extinction (Table 1). We then calculated relative littoral area deterministically based on the hypsometric equation and our measurements of mean depth, maximum depth, and vertical light extinction, and compared these to our measured values. We regressed the logarithm of relative littoral area by the logarithm of compensation:maximum depth ratio to test the hypothesis that the regression coefficient should equal the mean hypsometric exponent of the lakes. Collectively, these analyses test the accuracy of the hypsometric model both with no free parameters and when an average description of lake morphometry is used instead of lake-specific values.

Our data were generally consistent with the assumption that lake depth ratios are uniformly distributed (Text S3 in Supporting Information S1), however, the range of depth ratios in our data set is shifted to lower levels (range = 0.19–0.62) compared to previous reports of typical values (D_R = 1/3 to 2/3) (e.g., Carpenter, 1983). Based on this range, we calculated our mean depth ratio as 0.41 and mean hypsometric exponent as 0.76 (Text S4 in Supporting Information S1). We used ordinary least squares regression to test if the fit values are significantly different from this theoretical value. We repeated this test using an estimated maximum depth from the mean depth and average depth ratio. These analyses represent tests of the adequacy of hypsometric scaling to predict relative littoral area when bathymetric information is incomplete.

Our analysis was conducted using R version 4.0.2 with the "boot" and "car" packages (Canty & Ripley, 2020; Fox & Weisberg, 2019; R Core Team, 2020). We report confidence intervals based on bootstrapping (n = 9,999 replications). We report r^2 values calculated as the squared correlation between the fit and observed values in the original units (as opposed to log-units). Measures of bias are also reported based on the original units.

4. Results

Basin shape has no impact on the size of the littoral area when the compensation depth equals or exceeds the maximum depth. Lakes comprised completely of littoral area are relatively common (19% of lakes in our data set), and are either shallow, have low light attenuation, or both. Low compensation to maximum depth ratios (<0.05) are uncommon because of the positive skew of depth and dissolved organic carbon distributions (Cael et al., 2017; Seekell et al., 2014; Sobek et al., 2007; Vesterinen et al., 2017). Lakes with high depth ratios must have substantially deeper light penetration to have the same littoral area as a lake with a lower depth ratio, and this pattern is particularly pronounced when the compensation to maximum depth ratio is low (Figure 1b). Within our data set, the compensation to maximum depth ratio is the primary factor controlling the relative size of the littoral zone (coefficient of variation = 0.93) with lake shape having a secondary effect (coefficient of variation = 0.25).

Deterministic calculation of littoral area based on the hypsometric equation is precise (r^2 = 0.96) and unbiased (mean error = −0.004) when evaluated among all lakes (Figure 1c). These results were unchanged (r^2 = 0.94, mean error = −0.005) when excluding lakes comprised completely by littoral area. This demon-

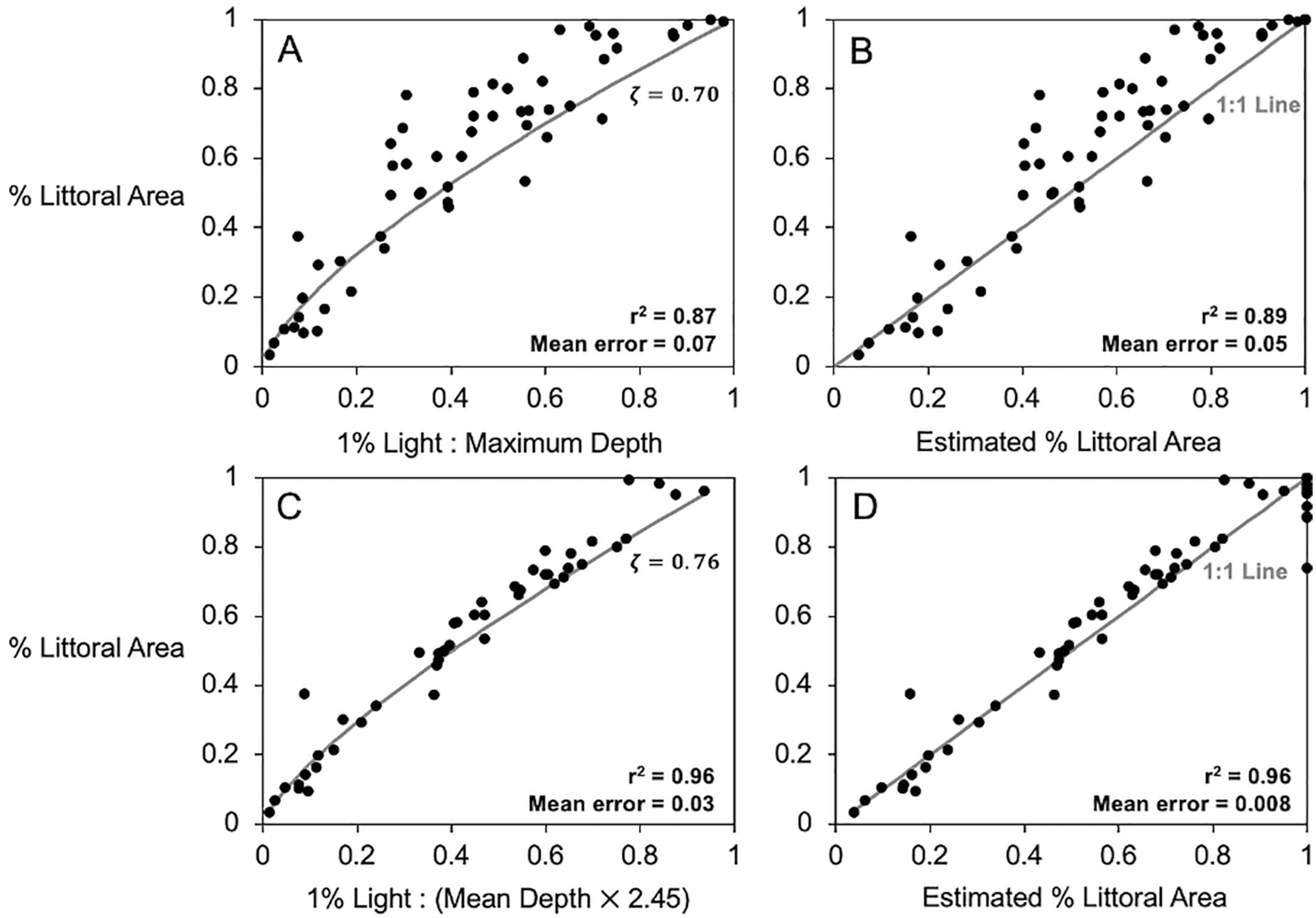

Figure 2. (a) The relationship between % littoral area and the ratio of the compensation depth (1% light depth) to maximum depth, when the hypsometric exponent is a free parameter. The figure only includes lakes used to fit the relationship (i.e., lakes with <100% littoral area). (b) Observed versus estimated relative littoral areas for all study lakes. (c) The relationship between % littoral area and the ratio of the one percent light depth to estimated maximum depth based on mean depth, when the hypsometric exponent is a free parameter. The figure only includes lakes used to fit the relationship (i.e., lakes with <100% littoral area). (d) Observed versus estimates relative littoral areas for all study lakes.

strates that the hypsometric equation for quadric surfaces is an adequate model for estimating relative littoral area in lakes across a wide range of depths, basin shapes, and vertical light attenuation coefficients.

When maximum depth is known, but mean depth is unknown, the hypsometric exponent calculated by regression ($\zeta = 0.70$, 95% CI = 0.62–0.76) was greater, but not significantly different from the mean of the observed values ($\zeta = 0.58$, 95% CI = 0.52–0.65) as indicated by overlapping 95% confidence intervals (Figure 2a). The fitted exponent is lower, but not significantly different than the theoretical $\zeta = 0.76$. The difference between the mean of the observed exponents and the theoretical exponent probably relates to errors associated with averaging discrete points of a nonlinear function. Among lakes scaling by the fit exponent (i.e., lakes where littoral area is <100% of total lake area), the fit is remarkably good ($r^2 = 0.87$), although biased—observed relative littoral areas were on average 0.07 greater than predicted values (i.e., lakes predicted to have 70% littoral area typically have 77% littoral area). The result is similar when all lakes are included in the analysis ($r^2 = 0.89$, mean error = 0.05) (Figure 2b). This demonstrates that relative littoral area can be predicted without lake-specific measurements of basin shape. In this formulation, relative littoral area can be predicted without measurements of mean depth.

When mean depth is known but the maximum depth was unknown, the hypsometric exponent calculated by regression ($\zeta = 0.76$, 95% CI = 0.70–0.81) was similar to the theoretical values ($\zeta = 0.76$) as indicated by the 95% confidence interval overlapping with this value (Figure 2c). Among lakes scaling by this exponent (i.e., lakes where littoral area is <100% of total lake area), predictions were precise ($r^2 = 0.96$), and less biased than when scaling relative littoral area by maximum depth (mean error = 0.03) (Figure 2d). The result is similar when all lakes are included in the analysis ($r^2 = 0.96$, mean error = 0.008). This demonstrates that relative littoral area can be accurately predicted when maximum depth is unknown.

5. Discussion

Scaling relationships provide simple rules for understanding hydrographic patterns at regional and global scales (Gardner et al., 2019; Seekell et al., 2021). Our study contributes to this understanding by identifying the key controlling factors of variation in littoral habitat size among lakes. Prior work has primarily focused on qualitative patterns (e.g., Carpenter, 1983; Vander Zanden & Vadeboncoeur, 2020), whereas our study provides a rigorous quantitative perspective and provides a model for prediction, even when complete bathymetric data are not available. Light penetration, maximum depth, and basin shape are the primary factors determining variation in the relative size of littoral habitat among lakes. Hence, our study implicitly integrates both the geomorphic factors that control basin shape and depth, and the water quality factors that control light penetration, and provides a clear opening for future studies seeking understanding the relationship between these factors and global scale patterns of habitat availability in lakes.

A particular merit of our study is our formulation of the hypsometric equation as an easily testable hypothesis. Specifically, we show that relative littoral area is a power-law function of the ratio of compensation to maximum depths. Additionally, by specifying specific power law exponents, we created a very challenging test for the admission of theoretical models compared to evaluating the power-law form alone. Our study provides both statistical support and a generative model for these patterns, a rare combination in the study of power-law patterns that comprises unusually strong evidence (Stumpf & Porter, 2012). In this sense, our study is a distinct advancement compared to previous studies that have sought to describe relative littoral area, including those that have employed variations of hypsometric equations (e.g., Casas-Ruiz et al., 2021; Vadeboncoeur et al., 2008).

The compensation depth to maximum depth ratio is the primary factor controlling the size of littoral area. The factors controlling compensation depth are phytoplankton biomass, the concentration of colored dissolved organic matter, and the concentration of nonpigmented particles (Davies-Colley et al., 1993; Kirk, 2011). Depth varies geographically among lakes at the lake-to-lake scale whereas light penetration, and the individual constituents controlling light penetration, primarily vary region-to-region (Lapierre et al., 2015, 2018; Seekell et al., 2014; Stephens et al., 2015). Hence, variations in relative littoral area among lakes in close proximity are primarily related to differences in maximum depth, whereas differences among regions relate to the concentrations of light absorbing constituents in the water. Hence, we predict that lakes in alpine regions characterized by clear waters (i.e., oligotrophic lakes) have greater relative littoral habitat sizes on average compared to lakes in agricultural and urban areas that are characterized by high concentrations of phytoplankton biomass (i.e., eutrophic lakes; Brezonik et al., 2019; Martínez-Arroyo & Jáuregui, 2000). Similarly, we predict that high-elevation alpine lakes, which are typically characterized by deep light penetration, have greater relative littoral sizes than forest lakes, which are often characterized by low light penetration due to high concentrations of colored dissolved organic carbon (Seekell et al., 2014). This pattern is visible within our Swedish data where boreal forest lakes had an average of 68% littoral area and lakes in the mountain regions had an average of 85% littoral area, despite the mountain lakes being deeper (average maximum depth = 9.5 versus 11.2 m, respectfully).

Lake ontogeny is generally characterized by reduced maximum depth at the centennial to millennial scale due to sedimentation (Lehman, 1975; Wetzel, 2001). Hence, littoral areas become relatively larger over the long term. For example, there has been a 42% increase in the littoral area of Mirror Lake (New Hampshire, USA) over the past 14,000 years due to changes in morphometry from sedimentation (Text S5 in Supporting Information S1). Decadal-scale changes in light penetration can mediate or amplify these ontogenetic changes. For example, acid rain increases light penetration and the relative size of littoral zones, whereas browning (long term increases in the concentration of colored dissolved organic matter) reduces the relative size of littoral zones by limiting light penetration. Such changes in light penetration have a stronger effect on the relative littoral area of lakes with high mean to maximum depth ratios than lakes with lower depth ratios.

Lake formation processes are thought to influence basin shape such that some geologic origins are associated with larger littoral areas than others (Carpenter, 1983). However, empirical patterns are poorly described and geologic processes are poorly integrated into scaling relationships (Seekell et al., 2021). Glacial processes are responsible for the formation of most of Earth's lakes and also the largest fraction of Earth's total lake area (Meybeck, 1995). These lakes typically have low mean to maximum depth ratios (D_R ~ 1/3), such that they are characterized by relatively large littoral zones (Carpenter, 1983; Text S6 in Supporting Information S1). Tectonic processes comprise the second most important source of lakes in terms of surface area, and are responsible for many of Earth's largest lakes and those with high societal value (Meybeck, 1995). Tectonic lakes have higher depth ratios (D_R ~ 3/7) than glacial lakes, indicating that they should, on average, have smaller relative littoral areas than glacial lakes. Data for other lake origins are scarce, as are data for specific processes within these broad categories. For example, tectonic uplift processes have higher depth ratios (relatively less littoral area) than graben lakes (D_R ~ 1/2 versus D_R ~ 2/5, respectively). This context enriches the understanding of hydrographical patterns that is engendered by scaling relationships because it integrates more detailed knowledge of geologic processes with the large-scale statistical relationships presented in our analysis (Seekell et al., 2021). Development of a more complete understanding of the link between pattern and process is a clear need both for understanding the relative sizes of habitats within lakes, and for understanding global scale patterns of lake characteristics more generally.

Many surface waters are of anthropogenic and not geologic origin. These reservoirs are subject to the same constraints in terms of factors determining the relative size of littoral and pelagic habitats, and our approach is equally applicable despite the anthropogenic origin. Reservoirs are built in diverse landscape contexts and as a broad group are not differentiated from natural lakes in terms of basin shape (mean to maximum depth ratio) (Rodgers, 2017). However, we predict that reservoirs typically have smaller relative littoral areas than lakes because reservoirs typically have significantly less light penetration due to higher concentrations of nitrogen and phosphorus that stimulate growth of light absorbing phytoplankton (Stephens et al., 2015).

Bathymetric surveys are expensive and therefore lakes with specific sizes, fish communities, recreational value, or water quality status tend to be overrepresented in bathymetric surveys, while other lake types are under-represented or unrepresented, for example fishless lakes or lakes that are difficult to access such as those in mountain regions (Håkanson & Karlsson, 1984; Hollister et al., 2011). We found evidence of uniform distribution over much of the range of depth ratios, but because of the biases that likely exist within bathymetric data sets we cannot say whether the patterns we observed are generalizable beyond the samples we analyzed. Our approach is still applicable if future mapping efforts reveal a different distribution of depth ratios. Specifically, the hypsometric exponent can simply be reestimated with a probability distribution that accounts for the unequal likelihood across the range of depth ratios (e.g., Rastetter et al., 1992).

Our analysis demonstrates that the hypsometric equation can be used to predict relative littoral area when bathymetric data are incomplete, specifically when either the mean or maximum depth are unknown. Hence, the hypsometric equation could be applied to global lake maps and databases of light penetration to estimate the global extent of littoral area. Based on our data, the hypsometric equation, and a Taylor expansion to estimate the expected compensation to maximum depth ratio from the average maximum and compensation depths, we estimate that 78% of the total global lake area is littoral habitat and 22% is pelagic habitat. This estimate is subject to substantial uncertainties regarding characterization of the statistical distributions of depth ratio and compensation depth. In particular, globally representative values of depth ratio and light penetration are needed to make such estimates with a high degree of confidence.

6. Conclusion

Our study describes basic rules for understanding patterns of littoral habitat size among lakes. Specifically, we show that maximum depth, mean depth, and vertical light attenuation control littoral habitat size, and that littoral area can still be predicted even if bathymetric data are incomplete. We provide geographic and temporal context for the factors affecting littoral area, which engenders predictions about patterns across space and time. A particular merit of our study is the definition of specific scaling exponents which provide a challenging criterion for the admission of theoretical models compared to evaluating the power-law form alone. Our analysis both advances basic understanding of the relative sizes of lake habitats and delineates and agenda for advancing future research on the topic.

Data Availability Statement

The original data and code used in this study are archived on Zenodo at www.doi.org/10.5281/zenodo.5259802 (doi: 10.5281/zenodo.5259802). The previously published data used in Texts S4, S6, and Table S1 in Supporting Information S1 are available their original sources, specifically Herdendorf (1982), Landers et al. (1988), Baker et al. (1990), Vázquez et al. (2004), and Alcocer et al. (2016). Table S2 in Supporting Information S1 contains data from Likens (1985). Table 1 contains exact values or representative values from distributions in Cael and Seekell (2016), Verpoorter et al. (2014), Henson (1993), Sobek et al. (2011), Hollister et al. (2011), Seekell et al. (2018), and Carpenter (1983).

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