Bias in the shoreline development index: Ecological implications illustrated with an analysis of littoral-pelagic habitat coupling

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Abstract

We reexamined the relationship between the shoreline development index and metrics of habitat coupling using a bias-corrected variant of the shoreline development index. Our findings suggest that previously reported correlations may be artifacts of scale-dependent bias in shoreline development index measurements. The results highlight the need for careful measurement when seeking to understand links between lake morphology and ecological processes.

Text

Lakes vary in shape from nearly perfect circles to the almost incomprehensively convoluted (Scheffers and Kelletat 2016; Seekell et al. 2022a). The shoreline development index – the ratio of shore length to the circumference of a circle with the lake's surface area – is widely used to quantify this variability so that it can be related to ecosystem function (e.g., Rawson et al. 1960; Gasith and Hasler 1976; Wetzel 2001; Dolson et al. 2009; McMeans et al. 2016; Stiling et al. 2023). For example, the shoreline development index has been identified as a key correlate of habitat coupling - when the dynamics of certain habitats are strongly influenced by adjacent, but ecologically distinct habitats, suggesting a link between lake morphology and ecosystem processes (e.g., Gasith and Hasler 1976; Schindler and Scheuerell 2002; Dolson et al. 2009;

McMeans et al. 2016). However, shore length is scale dependent such that measurements based on higher resolution maps are longer than those based on lower resolution maps (Hutchinson 1957; Kent and Wong 1982; Seekell et al. 2022a). A consequence of this is that the shoreline development index is biased so that it increases with surface area (Seekell et al. 2022a). Therefore, it cannot be used in comparative analyses of lakes with different surface areas, even when the shore lengths and surface areas are mapped at a common scale (Seekell et al. 2022a). Previously reported correlations between habitat coupling and the shoreline development index were based on comparative analyses of lakes with different surface areas, hence there is the possibility that these results do not represent ecologically meaningful connections to lake morphology but rather are the consequence of bias in the shoreline development index.

In this note, we correlate metrics of habitat coupling with a bias-corrected variant of the shoreline development index to test if the relationship between the shoreline development index and habitat coupling is ecologically meaningful. Correlation between metrics of habitat coupling and the bias-corrected variant is indicative of an ecologically meaningful relationship. In contrast, a correlation between metrics of habitat coupling and the traditional index, but not the bias-corrected variant, suggests a spurious relationship driven by scale-dependence induced bias in the shoreline development index.

We used metrics of habitat coupling previously reported by Dolson et al. (2009) for seven Ontario lakes (Table 1). Specifically, we examined trophic position and percentage of pelagic fish in the diet of lake trout (*Salvelinus namaycush*). The metrics were estimated by an isotopic mixing model applied carbon and nitrogen stable isotope analyses of several food web components. We selected this dataset for our analysis because lake trout are highly mobile predators that feed in both pelagic and littoral habitats, but are a cold-water species that can be thermally limited from foraging in large littoral zones, and because these data have been used in several previous analyses (Dolson et al. 2009; McMeans et al. 2016; Stiling et al. 2023). Dolson et al. (2009) hypothesized more reticulate lakes have larger and more complex littoral areas than more circular lakes, and that habitat coupling is weaker in in these lakes (Dolson et al. 2009; McMeans et al. 2016; Blanchfield et al. 2023). A positive correlation between the shoreline development index proportion of pelagic fish in the diet of lake trout should emerge due to difficulty in accessing littoral prey (Dolson et al. 2009). This should also be reflected in a positive correlation with trophic position because pelagic energy pathways are longer than littoral pathways (Dolson et al. 2009).

We measured the surface area (A, m^2) and shore length (L, m) of the study lakes using online maps from the Ontario Ministry of Natural Resources online mapping tools (http://www.ontario.ca/page/topographic-maps). Our measurements were made at the 1:72,223 map scale, which is one of the defaults in the application and which allows for digital measurement of the full range of lake sizes studied, consistent with best practices of measuring at a common scale (Seekell et al. 2022a). We used these measurements to calculate the shoreline development index:

$$D_L = \frac{L}{2\sqrt{\pi A}}$$

Next, we calculated the bias-corrected shoreline development index proposed by Seekell et al. (2022a):

$$D_{BC} = \frac{L}{2\sqrt{\pi} A^{(d/2)}}$$

d in this equation is the fractal dimension, which varies in the range $1 \leq d < 2$. The fractal dimension is a metric that characterizes the scale dependence of shorelines. We estimated lake specific fractal dimensions by measuring the shorelines at multiple map scales. We fit regressions of the logarithm of shore length by the logarithm of scale, and calculated the fractal dimensions as one minus the regression coefficient (Seuront 2010).

The rationale behind alternate formulation of the shoreline development index becomes clear when considering that shore length can be recast in terms of area based on the identity: $L = cA^{(d/2)}$, where c is a shape constant (Seekell et al. 2021a; Seekell et al. 2022b). Substituting this identity into the traditional shoreline development index formula and simplifying:

$$D_L = \frac{c}{2\sqrt{\pi}} \times A^{(d-1)/2}$$

When $d = 1$, D_L is the ratio of the shape constants c and $2\sqrt{\pi}$. However, when $d > 1$, the shoreline development index is also a function of area. In the bias-corrected variant, the exponent $d/2$ cancels area out of the numerator and denominator regardless of fractal dimension so that the index always only reflects the ratio of the shape constants:

$$D_{BC} = \frac{cA^{(d/2)}}{2\sqrt{\pi}A^{(d/2)}} = \frac{c}{2\sqrt{\pi}}$$

We use Bayes factors to evaluate the relative evidence for null (no positive relationship) and alternative hypotheses (positive relationship) (Wetzels and Wagenmakers 2012). We use this approach instead of null hypothesis testing (i.e. p-values) because Bayes factors evaluate relative evidence for the null and alternative hypotheses, something that is important for our interpretation of the correlation analysis, whereas null hypothesis testing only evaluates evidence for the alternative hypothesis. We report BF_{10}, which is the Bayes factor that indicates the weight of evidence for the alternative hypothesis relative to the null hypothesis. $BF_{10} = 1$ indicates that the hypotheses are equally likely, whereas $BF_{10} > 1$ indicates the alternative is more likely, and $BF_{10} < 1$ indicates the null hypothesis is more likely.

The range of fractal dimensions was 1.02-1.17 (median = 1.08), which indicate scale-dependence for all shorelines, and are consistent with the range and median of (range = 1.02-1.37, median = 1.10) of previously reported measurements for individual lake shorelines (Seekell et al. 2022a) (Figure 1). These fractal dimensions cause dramatic reductions in shoreline development index values when the bias-corrected metric is calculated. Specifically, the range of uncorrected values was 1.02-3.73 (mean = 2.58), whereas the range of bias-corrected values was 1.00-1.93 (mean = 1.29) (Table 1).

There is moderate evidence for the hypothesis that shoreline development index is inversely related to the metrics of habitat coupling, which is consistent with previous results based on these data (Dolson et al. 2009; McMeans et al. 2016). This means that there is less habitat coupling by lake trout in highly reticulate lakes compared to more circular lakes. Specifically, there was a positive correlation between shoreline development index and both lake trout trophic position ($r = 0.79$, $BF_{10} = 5.84$) and proportion of pelagic fish in diet ($r = 0.82$, $BF_{10} = 7.72$) (Figure 2). However, there is weak to moderate evidence of no positive relationship between bias-corrected shoreline development index and trophic position ($r = 0.15$, $BF_{10} = 0.59$) or proportion of pelagic fish in diet ($r = -0.37$, $BF_{10} = 0.29$). This contrasts with the previous results of Dolson et al. (2009) and McMeans et al. (2016) and suggests that the correlation between the shoreline development index and metrics of habitat coupling in those reports reflect bias in the shoreline development index rather than ecologically meaningful relationships.

Our statistical results were robust to a variety of priors. Additionally, we generated the same qualitative results when conducting our analysis with Kendall’s tau rank-based correlation coefficient, albeit with weaker correlations which is typical when comparing Pearson’s correlation coefficient to Kendall’s (Rupinski and Dunlap 1996). Specifically, there was a positive correlation between shoreline development index and both lake trout trophic position ($\tau = 0.52$, $BF_{10} = 2.67$) and proportion of pelagic fish in lake trout diet ($\tau = 0.62$, $BF_{10} = 4.27$), and weak evidence of no positive relationship between bias-corrected shoreline development index and trophic position ($\tau = -0.05$, $BF_{10} = 0.41$) and proportion of pelagic fish in diet ($\tau = -0.14$, $BF_{10} = 0.34$). Our statistical evidence for the null hypothesis is not overwhelming, but this is not surprising given the limited sample size. However, there are additional reasons to believe that the shoreline development index is not correlated with habitat coupling. Specifically, expected correlation is premised on the existence of a relationship between shoreline development index and the relative size of littoral habitats, but the empirical evidence for this is weak despite being widely stated in limnology textbooks (e.g., Wetzel 2001). Most lakes are small (< 1 km^2) and shallow (mean depth < 5 m, maximum depth < 10 m), with the entire lake comprising littoral habitat regardless of variation in shoreline development index (Seekell and Pace 2011; Verpoorter et al. 2014; Cael and Seekell 2016; Cael et al. 2017; Seekell et al. 2021b; Cael and Seekell 2022). Hence, shoreline development index and littoral area are often disconnected and correlations weak when examining large numbers of lakes (Seekell et al. 2021b).

The fractal dimension of a group of shorelines can be estimated by regressing the logarithm of the perimeters by the logarithm of surface areas. This is much faster than measuring fractal dimensions for individual lakes and facilitates estimation of fractal dimensions during syntheses of historical datasets when morphometrics but not original maps are available (Seekell et al. 2021a). However, these values are typically biased upwards compared to the average of shoreline fractal dimensions measured at the individual level and it is best practice to use individually measured fractal dimensions when bias correcting the shoreline development index, as we have done in our analysis (Matsushita et al. 1991; Seekell et al. 2022a). While conducting our analysis, we observed another reason to avoid using average shoreline development index values - the underlying selection of lakes may not be representative. For example, the fractal dimension calculated from the perimeter-area regression of the sample lakes in our study would be implausibly high, probably because the lakes were sampled uniformly across a wide range of shoreline development index values even though the underlying distribution of shoreline development index values is highly skewed, with most lakes having low index values compared to the overall range in values (Schiefer and Klinkenberg 2004; Verpoorter et al. 2014). This sampling strategy is common in comparative limnology and perimeter-area analysis cannot be used to adjust the shoreline development index in such studies.

Lake morphometry is so fundamental to aquatic sciences that it often seems trivial. Our analysis demonstrates that this is not the case and morphometry requires careful attention to detail to ensure that ecologically relevant relationships are correctly identified.

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Figure 1. Shore lengths measured at different map scales. The fractal dimension is one minus the regression coefficient when a linear regression is fit on log-log axes.

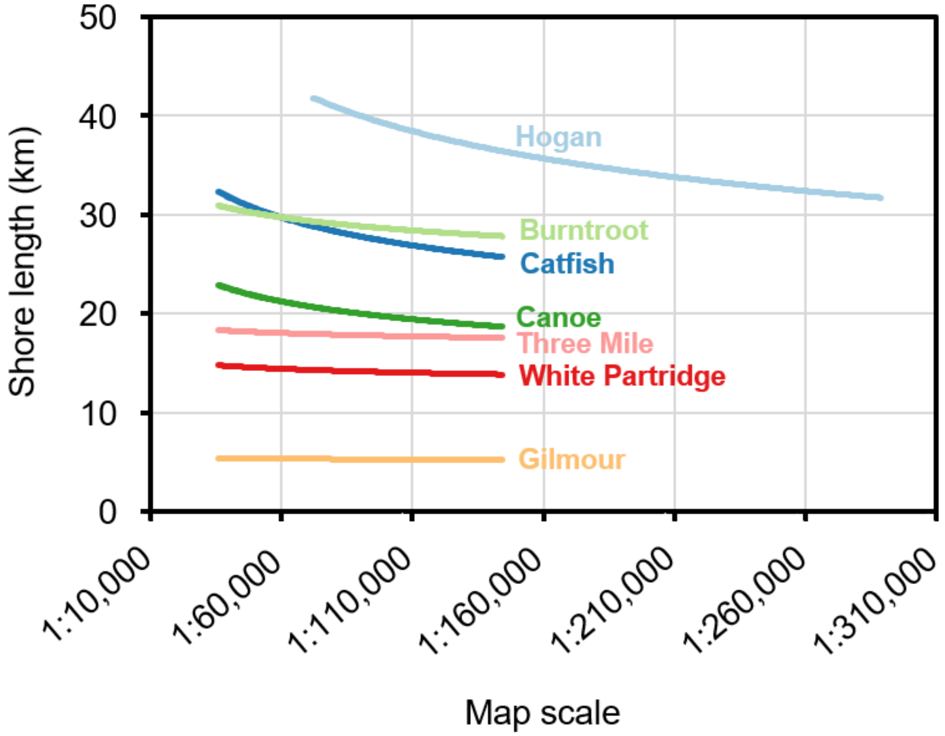

Figure 2. Correlations between habitat coupling metrics and shoreline development indices. The shoreline development index must be greater than or equal to one.

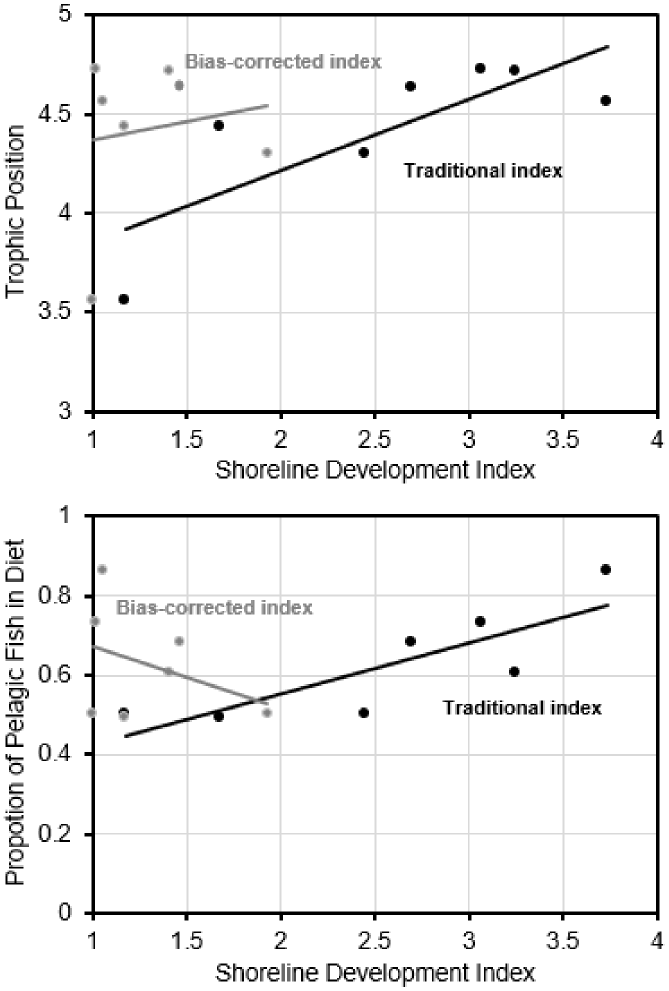

Table 1. Morphometric and food web data used in this analysis. Trophic position and pelagic fish in diet were reported by Dolson et al. (2009) and were estimated based on stable isotope analyses. Morphometric data are original to the present study.

Lake	Latitude	Longitude	Area (m^2)	Perimeter (m)	Fractal Dimension (*d*)	D_L	D_{BC}	Trophic Position	Pelagic Fish in Diet (%)
Gilmour	46.07°	-78.29°	1,626,185	5,297	1.02	1.17	1.00	3.56	51
Canoe	45.53°	-78.72°	3,691,778	20,905	1.15	3.07	1.02	4.73	73
Three Mile	45.98°	-78.9°	4,225,976	17,801	1.03	2.44	1.93	4.30	50
Catfish	45.92°	-78.55°	4,595,905	28,375	1.17	3.73	1.05	4.56	86
White Partridge	45.83°	-78.1°	5,748,242	14,270	1.05	1.68	1.17	4.44	49
Burntroot	45.85°	-78.67°	9,503,755	29,427	1.08	2.69	1.46	4.64	68
Hogan	45.87°	-78.5°	12,595,497	40,857	1.10	3.25	1.41	4.72	61