

Does Lake and Stream Connectivity Control Phosphorus Retention in Lakes?

Abstract

Lake water residence time and depth are known to be strong predictors of phosphorus (P) retention. However, there is substantial variation in P retention among lakes with the same depth and residence time. One potential explanatory factor for this remaining variation is that connectivity among lakes as well as connectivity between lakes and nearby streams influences either lake P trapping or the type of stream delivered P. Therefore, we examined the extent to which connectivity among lakes versus connectivity between lakes and streams contributes to differences in P retention among lakes. Specifically, we evaluated the effect of lake-based and stream-based connectivity metrics at multiple spatial extents on P retention using a hierarchical parameterization of the Vollenweider equation. We compared Vollenweider's k in lakes with high and low stream versus lake connectivity. We found that variation in k is more strongly associated with lake connectivity metrics compared to stream connectivity metrics. This result suggests that lake-associated processes, which likely control P trapping, play a larger role in determining P retention than stream-associated processes which may affect variation in the type of delivered P.

Introduction

Importance of nutrient predictions

A comprehensive understanding of P cycling at broad scales is necessary to predict nutrient concentrations among many different lake types and to better manage the risks of eutrophication from excess nutrient loading (Smith 2003). Such predictions can ultimately be used to implement management actions aimed at avoiding phenomena such as algal blooms and fish kills which can negatively affect human health and degrade ecosystem services (Carpenter 2005).

Importance of P retention

Although both nitrogen (N) and phosphorus loading contribute to eutrophication risk, studies on lake eutrophication commonly focus solely on phosphorus (P). This focus on P is a result of strong evidence that P rather than N is the primary limiting nutrient in lakes (Schindler 1977). Although later studies found that N and N:P ratios strongly control primary production in some lakes, P concentration is strongly correlated with phytoplankton primary production in most lakes (Downing et al. 2001, Elser et al. 2007). In the present study, we focus on P retention rather than P concentration because it is a unitless (%)

measure that can be compared among different lakes irrespective of their baseline nutrient concentrations or total nutrient inputs (Brett and Benjamin 2007). P retention is typically bounded at 0 in the case where all P inputs exit the lake via outflow or sedimentation and bounded at 1 in the case where all nutrient inputs are retained in the water column (Wetzel 2001).

Knowledge Gap

One of the primary challenges of predicting P retention is that lake nutrient concentrations are not simply a function of total inputs to the lake, but rather a function of complex interactions between lake characteristics and biogeochemical cycles. For example, lake phosphorus concentration is a function of biological response to phosphorus loading yet this response is not only a function of load but also depends on lake characteristics such as depth and biogeochemical cycling with iron (Sondergaard 2003, Wagner et al. 2011). Such interactions may obscure direct relationships between nutrient concentrations and total nutrient inputs and ultimately prevent accurate prediction of lake nutrient concentrations.

One way to account for the complex interactions between lake characteristics and biogeochemical cycles is to undertake detailed process-based study of each individual component that influences lake P processing. Specific components may include things like species specific-phytoplankton settling rates (Hamilton and Schadow 1997), POM speciation, or detailed representation of elemental cycling at the sediment-water interface (Amirbahman et al. 2013). Clearly, such detailed process-based study may not be feasible for hundreds of lakes at the regional scale and may be difficult to use for general understanding of variation in P retention among many different lake types.

Expectations/Hypothesis

An alternative approach for predicting lake nutrient concentrations is static mass-balance modelling using techniques such as the Vollenweider equations which typically predict P concentrations as a function of P loading and water residence time (Vollenweider 1975). Although such an approach cannot represent the complexity of potential interactions among lake characteristics and biogeochemical cycles, it offers the ability to evaluate relationships between P retention and lake characteristics among many lakes at the regional scale. In the present study, we extend the Vollenweider approach to explore the possibility that connectivity may explain some of the variation in P retention among lakes with the same depth and residence time. We expect that connectivity among lakes as well as connectivity between lakes and nearby streams may indicate differences in either watershed P trapping or the type of stream delivered P. Specifically, we tested the hypothesis that lake associated processes play a larger role in determining P retention than stream associated processes.

Methods

Dataset description

We used P retention and residence time data from the National Eutrophication Survey (USEPA 1975, Stachelek et al. 2018) for lakes located in 17 northeastern-most US states. Values in the dataset represent mean summer measurements spanning a period of 1972 to 1975. Lakes were excluded from analysis if they had a surface area of greater than 1000 km² or less than 0.1 km² and excluded if they had a depth of greater than 70 m. Lakes were also excluded if they lacked any upstream surface water connections or were located on the coast (e.g. had an ocean or inland sea in the upstream watershed). Overall, this left a dataset of approximately 130 lakes.

Empirical models

We modelled lake P retention using the Vollenweider equations (Vollenweider 1975) which relate P retention to water residence time. Although there are several variants of these equations, we limited our analysis to a specific 2-parameter form that has been shown to have good performance in multiple cross-sectional studies (Brett and Benjamin 2007, Cheng et al. 2010):

$$R_i = 1 - \frac{1}{1 + k\tau_i^x} \quad (1)$$

where R_i is the P retention in lake i , k and x are adjustable (fitted) parameter coefficients, and τ is water residence time in lake i . The value of k has been variously interpreted as either a bulk loss (decay) rate or as an approximation of sedimentation rate (Chapra 1997). We first used Eq. 1 to model the overall (non-hierarchical) relationship between P retention and water residence time for all lakes in the study dataset. Next, we explored hierarchical versions of Eq. 1 where k is modelled separately k_j as a function of a sub-population indicator g_i denoting membership in one of two groups (described below):

$$R_i = 1 - \frac{1}{1 + k_j\tau_i^x} \quad (2)$$

$$k_j = g_i \quad (3)$$

We assigned lake membership in each sub-population group based on several lake characteristics and connectivity metrics where the splitting criteria was determined from the results of conditional inference trees (Hothorn et al. 2006). The conditional inference tree (ctree) technique creates binary splits of the independent variables, which are recursively repeated, to find the split that maximizes

association with the dependent variable (Hothorn et al. 2006). In the present study, our dependent variable was P retention while our independent variable was a single lake characteristics or connectivity metric (Table 1). The advantage of the ctree technique over the more widely used classification-regression tree (CART) technique is that tree growth stopping rules are pre-specified. As a result, this avoids some of the subjectivity associated with post-hoc tree pruning.

We fit both non-hierarchical and hierarchical models in a Bayesian framework using the non-linear extension to the **brms** package to interface with the Stan statistical program (Burkner 2017, Stan Development Team 2017). In both models, we set an informative prior on k and x of $N(1.3, 0.1)$ and $N(0.45, 0.1)$ respectively. These priors were based on the confidence intervals presented in Brett and Benjamin (2007) and qualitatively matched those used by Cheng et al. (2010). We used the default settings of **brms** and **rstan** to generate posterior estimates using four chains of 4,000 iterations each with no thinning and random initial parameter values between -2 and 2.

Connectivity metrics

We calculated several connectivity metrics in order to fit our hierarchical versions of the Vollenweider equations (Eq. 2) and to ultimately determine the importance of stream and lake connectivity as they relate to P retention. Our stream connectivity metrics included average link length, stream order ratio, and the closest distance to an upstream lake. We focused on average link length and stream order ratio because they are approximations of stream network complexity (Rodriguez-Iturbe and Rinaldo 2001). For example, we consider low connectivity lakes to be those with highly complex stream networks characterized by a short average link length and a high stream order ratio. Our first step in calculating average link length was to dissolve stream network nodes that do not occur at a stream junction. Next, we divided the total stream length in the upstream watershed by the total number of stream reaches. We calculated (Strahler) stream order ratio by dividing the number of first-order streams in the upstream watershed of a given lake by the total number of higher order (> 1) streams (citation). Finally, we calculated closest distance to an upstream lake on a path-distance basis (as the fish swims) rather than on a straight-line basis (as the crow flies).

In addition to stream connectivity metrics, we calculated several lake connectivity metrics including total upstream lake area, number of upstream lakes, and presence/absence of an upstream lake. For the purposes of calculating lake connectivity metrics, we defined a lake as any waterbody with an area greater than 4 ha (0.04 km²). In terms of lake connectivity, we consider a low connectivity lake to be one with low total upstream lake area and few upstream lakes.

Finally, we fit hierarchical models on the basis of partitions of several non-connectivity lake characteristics including maximum depth, baseflow, and wetland

cover. This was intended as a check on the relative importance of connectivity effects relative to lake characteristics known to influence P retention such as maximum depth.

We calculated both lake and stream connectivity metrics at multiple scales (Figure 1). First, we calculated connectivity metrics at the scale of individual lake watersheds (iws scale). We defined an individual lake watershed as the area draining to a particular lake exclusive of any upstream areas that drain into a lake greater than or equal to 10 ha (0.1 km²). We also calculated connectivity metrics at the scale of entire upstream lake networks (nws scale). Network watersheds are defined as the area draining into any part the upstream network irrespective of the presence or absence of upstream lakes (Figure 1).

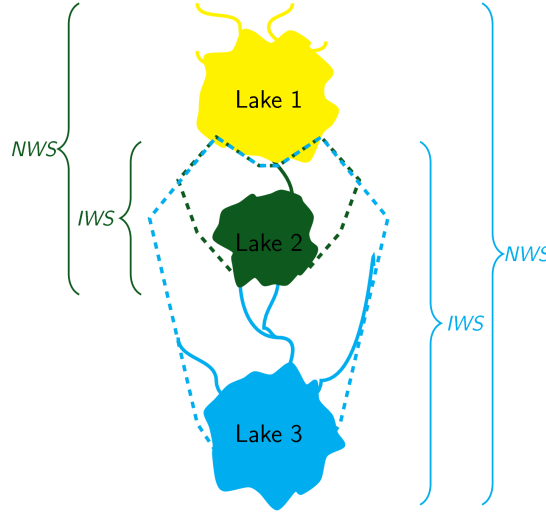


Figure 1: Diagram of the individual lake watershed and network watershed scales. In this example, the lake-watershed for lake 3 includes the lake-watershed of lake 2 because lake 2 is smaller than 10 ha.

We calculated all stream connectivity metrics using the **streamnet** and **nhdR** packages (Stachelek 2018a, Stachelek 2018b). The algorithms in the **streamnet** package use the **sf** R package (Pebesma 2018) as well as the **v.net** and **v.stream.order** modules (Jasiewicz and Metz 2011) included in GRASS GIS (GRASS Development Team 2017). We calculated lake connectivity metrics and non-connectivity lake characteristics using data from the LAGOSNE dataset (Soranno et al. 2017). Both lake and stream connectivity metrics were calculated using the National Hydrography Dataset (NHD) as a primary input. All processed data and code are available at [DOI].

Results

- The relationship between P retention and water residence time was well described by the Vollenweider equations.
- Connectivity played a larger role in determining P retention at the NWS scale than at the IWS scale.
- Longitudinal connectivity metrics were more important than lateral connectivity metrics at the NWS scale.
- Focal lake characteristics played a larger role in determining P retention at the IWS scale than connectivity metrics.
- Lake associated processes played a larger role in determining P retention than stream associated processes at the IWS scale.
- Lakes with both high lake connectivity and high stream connectivity were most often found in the northern portions of the study area.

Table 1: Table of partition splits generated with conditional inference trees. Refer to Figure 1 for scale definitions.

Abb	Scale	Metric	Split Value	Delta k
cd	nws	Closest lake distance	2776.81	0.27
ll	nws	Average Link Length	2237.34	0.19
lc	focal	Lake Connection	NA	0.17
la	nws	Upstream lake area	153.50	0.16
md	focal	Max Depth	19.81	0.15
ll	iws	Average Link Length	2177.08	0.14
sd	nws	Stream density	10.40	0.13
bf	iws	Baseflow	63.76	0.12
sr	iws	Stream order ratio	0.67	0.10
cd	iws	Closest lake distance	3773.61	0.05
sr	nws	Stream order ratio	0.47	0.05
sd	iws	Stream density	4.43	0.03
bf	nws	Baseflow	52.94	0.00

Discussion

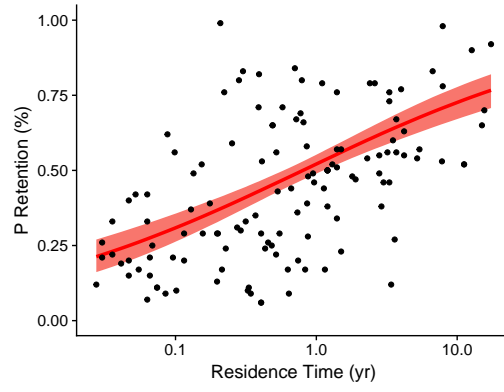


Figure 2: Population-level fit the Vollenweider P retention model where the dark circles are empirically measured values of P retention and residence time, while the light circles and vertical bars are posterior means and 95% credible intervals respectively.

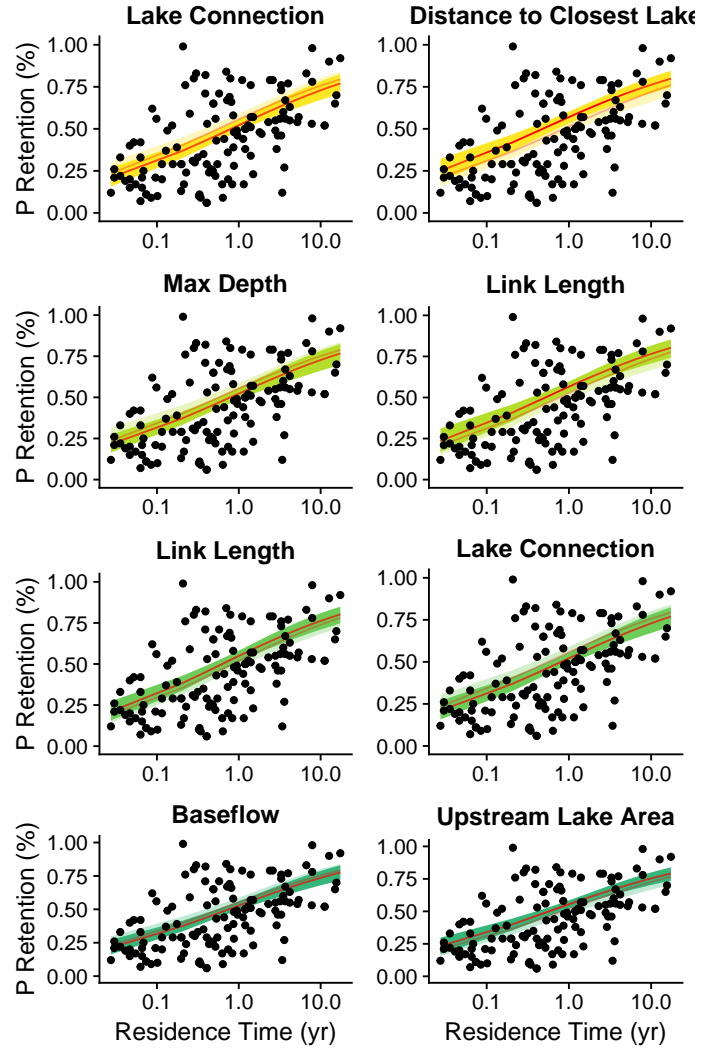


Figure 3: Partitioned (hierarchical) fits of the Vollenweider P retention model where the lines and shaded polygons represent the posterior mean and 95% credible interval respectively. Darker lines and polygons represent the left side of the partition which is usually smaller in magnitude.

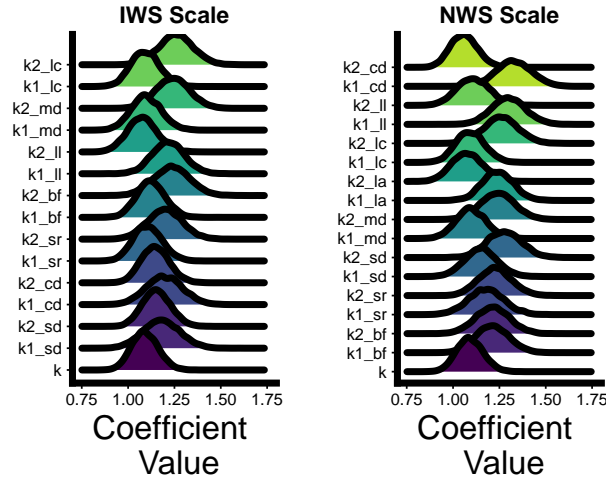


Figure 4: Comparisons of the posterior distribution of Vollenweider's k among lake sub-populations partitioned according to Table 1 where the subscript 1 denotes a subpopulation on the left side of the partition which is usually smaller in magnitude.

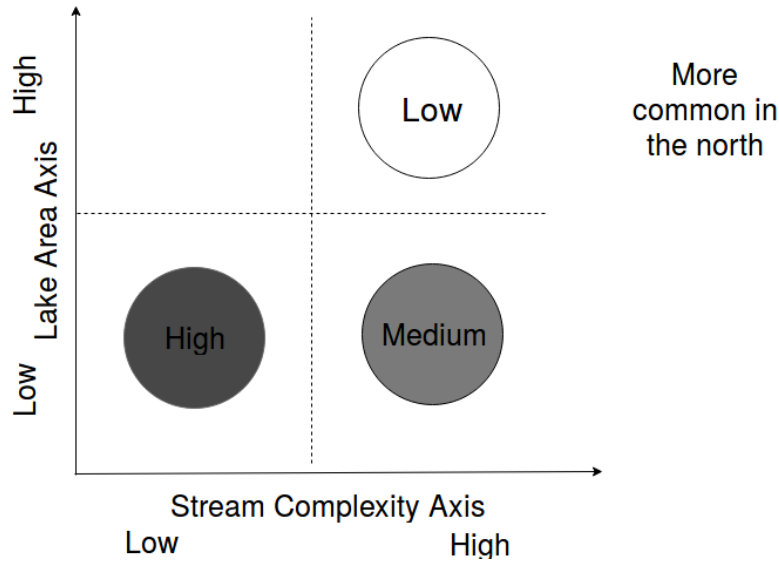


Figure 5: Conceptual diagram where the degree of shading indicates P retention. At the IWS scale lake connectivity metrics play a larger role than stream connectivity metrics in determining P retention. Lake connectivity metrics are also important at the NWS scale but metrics that reflect lake characteristics such as area become less important than lake characteristics that represent regional configuration such as closest distance to upstream lake.