LIMNOLOGY AND OCEANOGRAPHY
Letters

ASLO
Open Access

Limnology and Oceanography Letters 3, 2018, 49–56

doi: 10.1002/lol2.10078

SPECIAL ISSUE-ESSAY

A geography of lake carbon cycling

David A. Seekell,[1,2] *Jean-François Lapierre*,[3,4]* *Kendra Spence Cheruvelil*[5,6]

[1]Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden; [2]Climate Impacts Research Centre, Umeå University, Umeå, Sweden; [3]Département de sciences biologiques, Université de Montréal, Montreal, Quebec, Canada; [4]Groupe de Recherche Interuniversitaire en Limnologie et en Environnement Aquatique (GRIL); [5]Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan; [6]Lyman Briggs College, Michigan State University, East Lansing, Michigan

Scientific Significance Statement

Carbon cycling in lakes is highly variable among lakes within regions, and across regions and continents, but the underlying causes of this variation among lakes and regions are not well understood. In this essay, we propose two main mechanisms that operate at the regional scale and contribute to broad-scale interlake variation in carbon cycling. This essay sets the foundation for a geographic understanding of lake carbon cycling, which facilitates developing testable hypotheses to improve estimates of the role of inland waters in global elemental cycles.

Lake carbon cycling is influenced by external factors controlling the transfer of mass (e.g. carbon, nutrient) and energy (e.g. light, heat) on lake processes (e.g. primary production, respiration, greenhouse gases emissions), either directly or through the terrestrial landscape (Leavitt et al. 2009; Lapierre et al. 2015). Although these transfers of mass and energy should affect all lakes similarly, studies of lake carbon cycling conducted in regions with contrasting climate, land cover, and land use suggest that how strongly limnological first principles are expressed, and their relative importance to ecosystem functions, vary geographically. This fact may be due to the mismatch in spatial scales that characterize the geographic factors behind these contrasting patterns (e.g. climate, land use/land cover) as compared to that of individual lake ecosystems (100's–1000's km^2 vs < 1 km^2; Lapierre et al. 2015; Cael and Seekell 2016). Historically, broad-scale studies of lake carbon cycling exceeded the logistic abilities of individual lab groups and were outside the mandate of most governmental lake monitoring programs. However, publicly accessible geographic and limnological data originating from individual studies and from data synthesis efforts are increasingly available for broad extents across wide environmental gradients to develop understanding of the geographic patterns in lake carbon cycling (e.g., Soranno et al. 2017).

Landscape- and global-scale limnology have received increased attention in recent years. For example, landscape

*Correspondence: jean-francois.lapierre.1@umontreal.ca

Author Contribution Statement: DAS and JFL are co-leads of this paper; they developed the conceptual framework and wrote large sections of the essay. KSC contributed ideas, feedback, and text throughout the manuscript development, writing, and revising process. All authors read and approved the paper.

Data Availability Statement: Data are available at the following repositories or tables in published articles: https://figshare.com/articles/Latitudinal_gradients_in_phosphorus_and_vegetation_biomass_for_Sweden_and_Denmark/5614588, https://figshare.com/articles/Institutions_studying_lake_carbon_cycling/5612968, http://doi.org/10.7927/H40Z715X, http://doi.org/10.1029/2006JD007377, http://doi.org/10.7927/H4NP22DQ, and Imhoff and Bounoua 2006.

This article is an invited paper to the Special Issue: Carbon cycling in inland waters
Edited by: Emily Stanley and Paul del Giorgio

limnology has quantified and explained variation in ecosystem states and lake responses to multi-scaled pressures (e.g. Soranno et al. 2010) and global-scale limnology has developed global rate estimates for carbon exchange between surface waters and the atmosphere that can be compared with other aspects of global elemental cycles (Downing 2009). Less well-known are the fundamental limnological patterns at an intermediate, regional scale, where non-linear and threshold relationships between lake processes and their in-lake and landscape drivers often emerge and have major implications for broad-scale understanding of lake carbon cycling. Moreover, the mechanisms responsible for the presence of geographically varying relationships in aquatic ecosystems remain unknown. Therefore, we argue that such geographically varying relationships could have profound implications for broad scale understanding of lake carbon cycling, and that these implications have seldom been explored.

In this essay, we propose a geographic framework for studying lake carbon cycling that can connect within-ecosystem carbon processes with their broader-scaled drivers, including climate, land cover, and human activities. We present two regional-scale mechanisms related to thresholds that we hypothesize can give rise to geographically varying relationships between lake carbon cycling and its drivers, which can account for the often contrasting results from the literature. Finally, we present a way to conceptualize and delineate testable, hypothetical regions of lake carbon cycling that could account for the above contrasting relationships and help to synthesize studies of carbon in widely different regions.

The role of geographic context in lake carbon cycling

There are many variables driving the processes involved in lake carbon cycling, but a few of them play a central role. Along with phosphorus concentration and lake size, dissolved organic carbon (DOC) concentration is commonly used to compare, predict, and generalize patterns of lake carbon cycling (Williamson et al. 1999; Prairie 2008). DOC is the largest carbon pool in the water column and it strongly influences diverse physical, chemical, and biological characteristics (Prairie 2008). In particular, DOC is colored and has a primary role in limiting light (Carpenter et al. 1998; Williamson et al. 1999). DOC also binds with nutrients and lakes with higher DOC concentrations typically have higher total phosphorus and nitrogen concentrations (e.g. Seekell et al. 2015*a*). However, these relationships vary geographically, which affects lake functioning. For example, DOC may not co-vary with nutrients in more impacted regions (Lapierre and del Giorgio, 2012), and both positive and negative effects of DOC on whole-lake primary production have been reported in regions with contrasting land cover (Seekell et al. 2015*a*). Therefore, even the most basic relationships between carbon, nutrients, and lake ecosystem processes may show unexpected patterns depending on where the study was conducted. We argue that these conflicting results may be due to regional-scale differences in geographic context, which drives broad-scale heterogeneity in patterns of lake carbon cycling.

Landscape limnology sets the context for resolving conflicting findings among studies conducted in different areas of the globe. This subdiscipline of limnology has formalized the importance of the regional scale (e.g., Cheruvelil et al. 2013) and the concept of cross-scale interactions (which occur when the drivers interact across spatial scales or study regions (Soranno et al. 2014) for improved understanding of aquatic ecosystems. However, the examples that have been so far have not included carbon, nor have they described how geographic context may alter fundamental ecosystem functions. We propose two regional-scaled mechanisms that can lead to such geographic variation in lake carbon cycling. First, different regions may have a DOC frequency distribution that fall on either side of a threshold relationship between DOC and an aquatic process (Fig. 1a). In this context we define threshold as a point across which there is a change in the direction of a relationship or a fundamental shift in ecosystem function in response to a driver. For example, a threshold may be observed as a ratio shifting from above to below 1 or as a net rate shifting from a positive to a negative value (e.g. P : R ratio or net ecosystem production; blue line on Fig. 1), or as a unimodal relationship whereby the direction of a trend shifts with changing DOC concentration (red line in Fig. 1). Second, threshold relationships may occur when geographic gradients intersect and alter the balance between production, delivery, and processing of carbon and nutrients to and within lakes. This phenomenon may be particularly relevant when natural and human gradients intersect (Fig. 1b). Within our geographic framework of lake carbon cycling, we discuss examples based on relationships of key lake processes with DOC and nutrients, and argue that these ideas may be applicable for other limnological patterns and processes.

Mechanism 1: Threshold relationships explained by regional heterogeneity in dissolved organic carbon concentrations

Lakes often have nonlinear relationships with drivers that create thresholds or breakpoints in ecosystem patterns or processes along an environmental gradient (Dodds et al. 2010). For example, a study found that temperate lakes on the Canadian Shield were typically autotrophic (Carignan et al. 2000), whereas another study found that temperate lakes in southern Quebec were typically heterotrophic (del Giorgio and Peters 1994). However, when the lakes from these two studies were placed along a common DOC gradient, Prairie et al. (2002) observed a threshold DOC

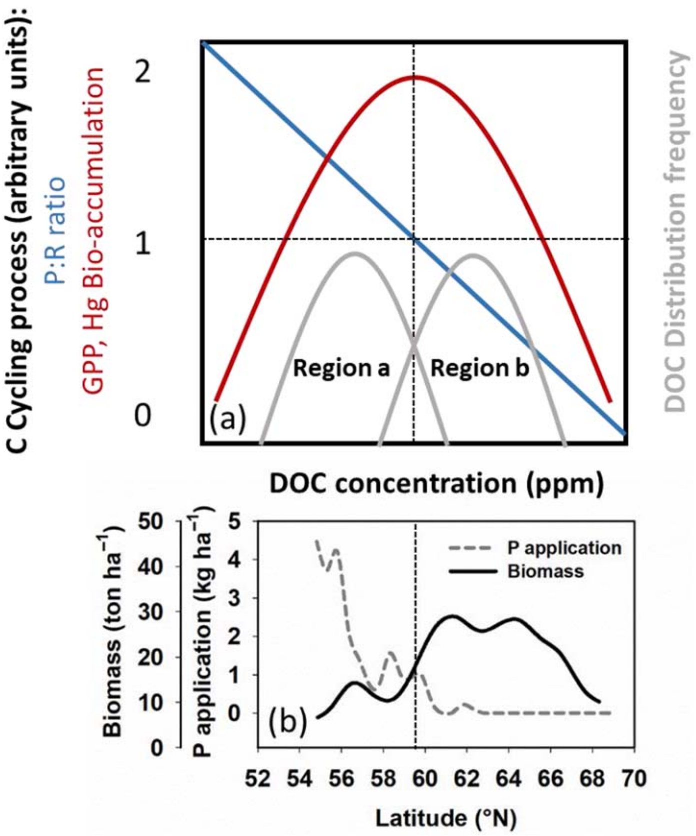

Fig. 1. Conceptual diagram of how cross-regional thresholds in lake C cycling may emerge. (**a**) Certain lake processes (e.g., photosynthesis to respiration (P : R) ratios) decrease linearly, while some others (e.g., whole lake gross primary production [GPP], or mercury bio-accumulation [Hg Bio-accumulation]) exhibit a bell shaped relationship along a common DOC gradient. However, because lakes in regions a and b have different DOC distributions, threshold relationships emerge across regions and studies conducted in either region a or region b come to very different conclusions about the relationship between DOC and lake processes. (**b**) There are strong latitudinal gradients in phosphorus fertilizer and manure application (dotted gray) and aboveground vegetation biomass (solid black) for Sweden and Denmark. An intersection between human and natural gradients can lead to cross-regional contrasts in energy and mass transfer to lakes and explain the presence of thresholds in lake C cycling. Data were averaged within latitudinal bands for the extent of Sweden and Denmark and plotted as splines to emphasize the overall patterns. Data sources are Cheruvelil et al. 2017*b*, Potter et al. 2010, and Reusch and Hibbs 2008.

concentration for the production to respiration (P : R) ratio that represents a transition from autotrophy to heterotrophy. Autotrophy was prevalent on the Canadian Shield because most lakes there fell below the DOC threshold. In contrast, lakes in southern Quebec exhibited heterotrophy because most lakes in that region were above the DOC threshold. Because DOC is a primary controlling variable for the P : R ratio, geographic structure in DOC between regions created regional-scale patterns in lake metabolic status.

Much has been said about how measured concentrations or fluxes of different forms of carbon in and from lakes vary in different regions of the globe, but exploration is needed for geographically varying driver-response relationships for lake carbon cycling (e.g. Seekell et al. 2014; Lapierre et al. 2017). This type of patterning is common in geographic ecology (e.g., Rodríguez et al. 2008) and can explain apparently conflicting patterns of lake carbon cycling. For example, measured rates of whole-lake primary production are similar in sub-arctic and boreal Sweden, but correlations between whole-lake primary production and key variables like nutrient concentrations are different between these two regions. In fact, there is a positive correlation between primary production and nutrient concentrations in the sub-arctic and a negative correlation in boreal Sweden (e.g. Seekell et al. 2015*a*,*b*). In sub-arctic Sweden where DOC concentrations are low, primary production increases with nutrient concentration because lakes are nutrient limited and suffer little of the DOC-driven light penalty. However, in the boreal zone where DOC concentrations are typically above a threshold, there is a negative correlation between primary production and DOC because lakes are light limited and light extinction increases at a higher rate than do nutrient concentrations. Similarly, a positive relationship between DOC and mercury bio-accumulation in Canada's Western Arctic thaw lakes was observed at concentrations < 8.5 mgL^{-1}, whereas a negative relationship was observed in a nearby region's lakes that did not originate from thawing where DOC > 8.5 mgL^{-1}; the same threshold relationship has been observed between mercury photo-demethylation rates and DOC across different Arctic and temperate regions (French et al. 2014; Girard et al. 2016). In all examples, the within-region distributions of DOC concentrations fell on either side of the threshold observed between DOC and an aquatic process (see Fig. 1a). Therefore, when the data are combined, the threshold results in a unimodal relationship across regions (Fig. 1a). This fact suggests that the effect of the geographically widespread increases in DOC on lake processes could differ dramatically among regions.

Mechanism 2: Threshold relationships explained by regional variation in energy and mass transfer to lakes

Geographic variation in energy and mass transfer to lakes may result in different coupling of DOC, nutrients, light, and primary production among regions, likely in response to sharp shifts in terrestrial biomass and in fertilizer use. For example, the northern Sweden threshold in nutrient and light limitation across a DOC gradient depends on the regionally changing coupling of light and nutrients that is mediated by DOC (Seekell et al. 2015*b*). In boreal Sweden, whole-lake primary production decreases across nutrient gradients because they are tightly bound to DOC, and the negative effect of increased light attenuation on benthic primary producers at high nutrient concentrations offsets the positive effect of the higher nutrient concentrations on pelagic primary productions (Seekell et al. 2015*a*). In contrast, only a weak relationship was found between nutrients and DOC in temperate Denmark (Staehr et al. 2012), indicating weak nutrient-light coupling by DOC, and in this region there is a positive relationship between nutrients and whole-lake GPP. Similar to what was observed in Sub-Arctic Sweden (Seekell et al. 2015*a*), GPP was stimulated when natural DOC content (and the co-occurring nutrients) was experimentally increased in a pristine North Temperate lake (Zwart et al. 2016). However, a negative relationship between DOC and GPP was observed in the same lake when nutrients were added to simulate the effects of eutrophication (Carpenter et al. 1998). It is not clear if shift in GPP vs. DOC relationship between Sweden and Denmark is due to natural or anthropogenic causes, but we note that there is substantially more phosphorus fertilizer application and manure production in temperate Sweden and Denmark (latitude $< 60°N$) than there is in boreal Sweden ($> 60°N$, Fig. 1b). These agricultural practices are a potential source of nutrients that may decouple nutrient availability and light attenuation from DOC. In temperate Denmark, increased phytoplankton production across total phosphorus gradients offsets losses of benthic primary production due to light attenuation (Vadeboncoeur et al. 2003), resulting in a positive primary production-total phosphorus relationship that contrasts with the pattern seen in boreal lakes.

Other aspects of lake carbon cycling also appear to follow threshold relationships along environmental and geographic gradients. For example, CO_2 supersaturation is not tightly correlated with carbonate weathering in soft waters, but CO_2 supersaturation is strongly correlated with alkalinity in hard waters that exceed 1 mequiv L^{-1} (Marcé et al. 2015). Because alkalinity is related to geological characteristics that vary at the regional scale (Cheruvelil et al. 2013; Marcé et al. 2015), regional-scale patterns of alkalinity may explain why biological pathways dominate CO_2 supersaturation in some regions, whereas geological/hydrological pathways dominate CO_2 supersaturation in other regions. Along the same line, pCO_2 tends to be positively correlated with DOC in mostly pristine boreal lakes, but this relationship is either negative or nonexistent in more disturbed U.S.A. lakes where the natural balance between the terrestrial loadings of carbon and nutrients has been altered (Lapierre and del Giorgio 2012; Lapierre et al. 2017). In the presence of abundant, human-derived nutrients, the effect of DOC as a substrate for degradation is overwhelmed by the nutrient effect on primary production, resulting in no relationship, or even a negative relationship between DOC and pCO_2. These examples demonstrate ways that regional variation in the magnitude and coupling of energy and matter inputs can provide a mechanism for heterogeneous relationships in various aspects of lake carbon cycling that emerge at broad scales.

Creating regions of lake carbon cycling from natural and human gradients

The concept of ecological regions has a long history in biogeography and is used globally for research, management, and conservation (e.g., Christian 1958; Klijn et al. 1995; McMahon et al. 2004; Abell et al. 2008; Cheruvelil et al. 2017*a*). This concept is also important for a geographic understanding of lake carbon cycling. The exact gradients that contribute to the formation of regions across which geographically varying relationships can occur in terms of lake carbon cycling have yet to be determined, but the above examples suggest that both natural and anthropogenic factors play a central role. On one hand, natural gradients of mean annual air temperature are strongly related to terrestrial DOC production and export to lakes (Lapierre et al. 2015). On the other hand, anthropogenic gradients of cultural eutrophication due to agricultural and urban land uses can transition lakes across thresholds, for example from being net sources of atmospheric CO_2 to being net sinks of atmospheric CO_2 (e.g., Pacheco et al. 2013), or change the strength of coupling between energy and matter inputs. Moreover, the geographic extents of these types of factors have changed through time, which means that regional boundaries could be dynamic.

As an effort to promote research related to a geography of lake carbon cycling, we have developed a global map of potential lake carbon cycling "regions" (Fig. 2). In Fig. 1, we illustrated how the intersection of natural (e.g. terrestrial above-ground vegetation biomass) and human (e.g. fertilizer use) gradients at the regional scale can match threshold relationships involved in lake carbon cycling. In Fig. 2, we extend this idea to illustrate how regions may emerge from the intersection of natural and human gradients at the global scale. These regions were not created with quantitative regionalization techniques; rather, we overlaid three relevant factors to show that region boundaries emerge organically because of the intersection of natural and anthropogenic gradients. We included terrestrial net primary production because it is a good integrator of climate (temperature and precipitation), topography, and geology, and we included fertilizer use (phosphorus) and human population density because they represent distinct pathways through which human activity may affect lake carbon cycling via nutrient inputs (Peierls et al. 1991). Based on this exploration, we suggest that (1) much knowledge on lake carbon cycling originates from regions with relatively homogenous geographic contexts and (2) studies conducted in geographic areas with contrasting natural land cover and human land uses are likely to find novel, nonlinear relationships emerging across regions.

Our search of ISI Web of Science for studies in the field of "ecology" and "limnology" containing the words lake, carbon, and cycling over the last 15 yr found that a large

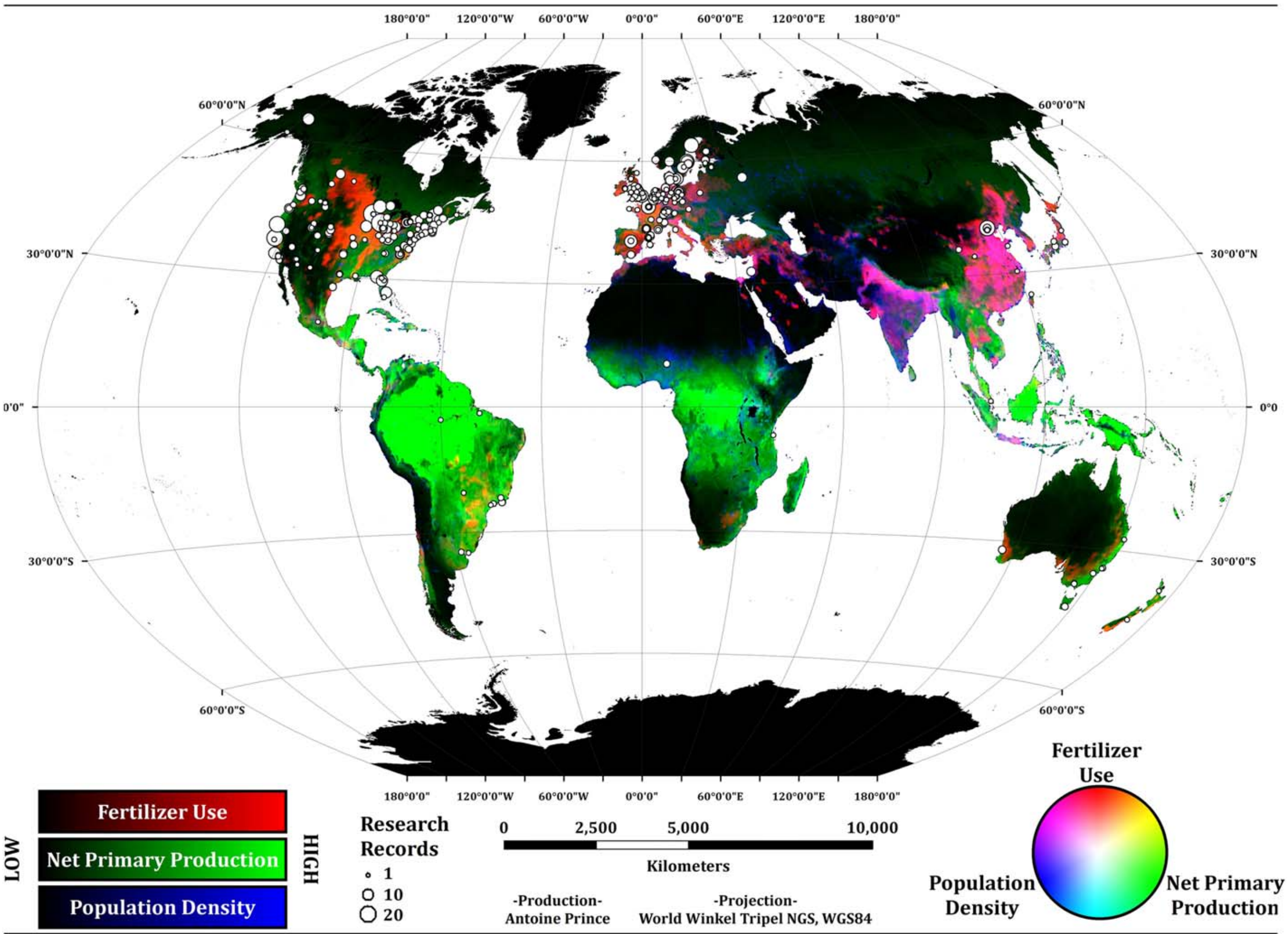

Fig. 2. Demonstration of how regions can emerge at the intersections of human and natural gradients. Gradients were created by overlaying human population density (2015), net primary productivity (1995), and phosphorus fertilizer application (1994–2001) using a red, green, blue additive color scheme (see map key). White circles represent institutions where studies of lake carbon cycling have been conducted over the last 15 yr, based on web of science records, with larger diameter circles indicating a larger number of records ("lake" and "carbon" and "cycle" terms in the "limnology" and "ecology" categories). Institution data sources are Cheruvelil et al. 2017*c* and GIS layers used to create the map are from Imhoff et al. 2004, Imhoff and Bounoua 2006, Potter et al. 2010, 2011, and Center for International Earth Science Information Network (CIESIN) 2016.

proportion of the knowledge in the field comes from studies within only a few administrative areas (e.g. U.S.A., Canada, Nordic countries, Western Europe, Fig. 2). In particular, research has been conducted primarily in temperate and boreal areas that have very low terrestrial NPP, fertilizer use, and human population density (black portions of Fig. 2), or temperate to sub-tropical areas with high fertilizer use (red portions of Fig. 2). Nevertheless, contrasting relationships of lake carbon cycling have been found even within these narrow geographic gradients (compared to global gradients), and we suggest that further, unexpected patterns are likely to emerge if more studies are conducted in lakes from tropical regions with high NPP but low population density and fertilizer use (green portions of Fig. 2), or combined high population density and fertilizer use (pink portions of Fig. 2).

The bias in the geographic context in which most studies of lake carbon cycling are conducted may limit generalization and extrapolation to understudied regions. For example, we hypothesize that the relationships derived from northern, more pristine landscapes (e.g. DOC vs. pCO_2 or vs. GPP relationships) will poorly explain lake carbon cycling in regions with high human impacts (red to blue spectrum of Fig. 2), where plankton and gas dynamics will be more tightly linked with nutrient and oxygen concentrations than with DOC concentrations and light penetration. A shift from lakes being mainly sources to sinks of carbon may be expected in such conditions (see Pacheco et al. 2013). Methane may also become a dominant gas involved in lake carbon budgets (especially in terms of warming potential) that are beyond a threshold of human influence, particularly in hotter and more productive regions, because methane is more sensitive than CO_2 to nutrients and temperature at the ecosystem-level (DelSontro et al. 2016). An important point to consider is whether all lakes within a "similar" environmental context would behave the same or not. For example, would lakes in Greenland, North Africa and Central Australia with low NPP, population density and fertilizer use (i.e. black regions on Fig. 2) have similar relationships between carbon cycling processes and their drivers? Based on the arguments presented here we would suggest that indeed the relationships would be qualitatively similar (relatively speaking, but see Prairie et al. 2002) if Fig. 2 represented definite regions for lake carbon cycling. This figure, however, probably depicts an incomplete portrait of the geographic gradients that drive spatially varying relationships in lake C cycling. For example, even regions with similar climate may have considerable differences in terms of light intensity and photoperiod due to latitude differences, different regions with similar geographic context may have contrasting lake morphometry that would lead to differential response of lake processes to comparable loadings of carbon and nutrients, and different farming and wastewater treatment practices may cause contrasting nutrient loadings to the receiving aquatic ecosystems for a similar fertilizer use and population density. Nevertheless, we hope that future studies will identify the main geographic gradients underlying the broad scale geographic patterns in lake carbon cycling and understand where- and why- these relationships are similar and different.

Conclusion

A more complete understanding of lake carbon cycling will have to go beyond tweaking the parameters of linear, global relationships. We are not suggesting that empirical relationships involved in lake carbon cycling are simply different depending on where a study is conducted. Rather, we argue that there are specific conditions under which different ecological and biogeochemical pathways are predominantly expressed, hence that it is by understanding how the changing geographic context drives the relative expression of different limnological first principles across human and natural gradients that major advances will be made. Therefore, we advocate for a need to greatly increase the diversity of lakes and regions that we study. In particular, studies of lakes from more productive and human-impacted regions will enhance understanding of lake carbon cycling and prediction of the response of lakes to various aspects of global change. The geography of lake carbon cycling constitutes a fertile area for the development of novel testable hypotheses that will further the evolution of the field of limnology.

References

Abell, R., and others. 2008. Freshwater ecoregions of the world: A new map of biogeographic units for freshwater biodiversity conservation. BioScience **58**: 403. doi:10.1641/B580507

Cael, B. B., and D. A. Seekell. 2016. The size-distribution of Earth's lakes. Sci. Rep. **6**: 29633. doi:10.1038/srep29633

Carignan, R., D. Planas, and C. Vis. 2000. Planktonic production and respiration in oligotrophic Shield lakes. Limnol. Oceanogr. **45**: 189–199. doi:10.4319/lo.2000.45.1.0189

Carpenter, S. R., J. J. Cole, J. F. Kitchell, and M. L. Pace. 1998. Impact of dissolved organic carbon, phosphorus, and grazing on phytoplankton biomass and production in experimental lakes. Limnol. Oceanogr. **43**: 73–80. doi:10.4319/lo.1998.43.1.0073

Center for International Earth Science Information Network - CIESIN - Columbia University. 2016. Gridded Population of the World, Version 4 (GPWv4): Population Density. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). doi:10.7927/H4NP22DQ

Cheruvelil, K. S., P. A. Soranno, K. E. Webster, and M. T. Bremigan. 2013. Multi-scaled drivers of ecosystem state: Quantifying the importance of the regional spatial scale. Ecol. Appl. **23**: 1603–1618. doi:10.1890/12-1872.1

Cheruvelil, K. S., and others. 2017*a*. Creating multithemed ecological regions for macroscale ecology: Testing a flexible, repeatable, and accessible clustering method. Ecol. Evol. **7**: 3046–3058. doi:10.1002/ece3.2884

Cheruvelil, K. S., J.-F. Lapierre, and D. Seekell. 2017*b*. Latitudinal gradients in phosphorus and vegetation biomass for Sweden and Denmark. doi:10.6084/m9.figshare.5614588.

Cheruvelil, K. S., J.-F. Lapierre, and D. Seekell. 2017*c*. Institutions studying lake carbon cycling. doi:10.6084/m9.figshare.5612968.

Christian, C. S. 1958. The concept of land units and land systems. Proceedings of the Ninth Pacific Science Congress. V. **20**, p. 74–81.

del Giorgio, P. A., and R. H. Peters. 1994. Patterns in planktonic P-R ratios in lakes - influence of lake trophy and dissolved organic carbon. Limnol. Oceanogr. **39**: 772–787. doi:10.4319/lo.1994.39.4.0772

DelSontro, T., L. Boutet, A. St-Pierre, P. A. del Giorgio, and Y. T. Prairie. 2016. Methane ebullition and diffusion from northern ponds and lakes regulated by the interaction between temperature and system productivity. Limnol. Oceanogr. **61**: S62–S77. doi:10.1002/lno.10335

Dodds, W. K., W. H. Clements, K. Gido, R. H. Hilderbrand, and R. S. King. 2010. Thresholds, breakpoints, and nonlinearity in freshwaters as related to management. J. North Am. Benthol. Soc. **29**: 988–997. doi:10.1899/09-148.1

Downing, J. A. 2009. Global limnology: Up-scaling aquatic services and processes to planet Earth. Verh. Int. Verein. Limnol. **30**: 1149–1166. doi:10.1080/03680770.2009.11923903

French, T. D., and others. 2014. Dissolved organic carbon thresholds affect mercury bioaccumulation in Arctic lakes. Environ. Sci. Technol. **48**: 3162–3168. doi:10.1021/es403849d

Girard, C., M. Leclerc, and M. Amyot. 2016. Photodemethylation of methylmercury in Eastern Canadian Arctic thaw pond and lake ecosystems. Environ. Sci. Technol. **50**: 3511–3520. doi:10.1021/acs.est.5b04921

Imhoff, M. L., L. Bounoua, T. Ricketts, C. Loucks, R. Harriss, and W. T. Lawrence. 2004. HANPP Collection: Global Patterns in Net Primary Productivity (NPP). Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). doi:10.7927/H40Z715X

Imhoff, M. L., and L. Bounoua. 2006. Exploring global patterns of net primary production carbon supply and demand using satellite observations and statistical data. J. Geophys. Res. **111**: D22S12. doi:10.1029/2006JD007377

Klijn, F., R. W. de Waal, and J. H. Oude Voshaar. 1995. Ecoregions and ecodistricts: Ecological regionalizations for the Netherlands' environmental policy. Environ. Manage. **19**: 797–813. doi:10.1007/BF02471933

Lapierre, J. F., and P. A. del Giorgio. 2012. Geographical and environmental drivers of regional differences in the lake pCO2 versus DOC relationship across northern landscapes. J. Geophys. Res. **117**: 1–10. doi:10.1029/2012JG001945

Lapierre, J.-F., D. A. Seekell, and P. A. del Giorgio. 2015. Climate and landscape influence on indicators of lake carbon cycling through spatial patterns in dissolved organic carbon. Glob. Chang. Biol. **21**: 4425–4435. doi:10.1111/gcb.13031

Lapierre, J.-F., D. A. Seekell, C. T. Filstrup, S. M. Collins, C. E. Fergus, P. A. Soranno, and K. S. Cheruvelil. 2017. Continental-scale variation in controls of summer CO2 in United States lakes. J. Geophys. Res. **122**: 875–885. doi:10.1002/2016JG003525

Leavitt, P. R., and others. 2009. Paleolimnological evidence of the effects on lakes of energy and mass transfer from climate and humans. **54**: 2330–2348. doi:10.4319/lo.2009.54.6_part_2.2330

Marcé, R., B. Obrador, J.-A. Morguí, J. Lluís Riera, P. López, and J. Armengol. 2015. Carbonate weathering as a driver of CO2 supersaturation in lakes. Nat. Geosci. **8**: 107–111. doi:10.1038/ngeo2341

McMahon, G., E. B. Wiken, and D. A. Gauthier. 2004. Toward a scientifically rigorous basis for developing mapped ecological regions. Environ. Manage. **34**: S111–S124. doi:10.1007/s00267-004-0170-2

Pacheco, F. S., F. Roland, and J. A. Downing. 2013. Eutrophication reverses whole-lake carbon budgets. Inl. Waters **4**: 41–48. doi:10.5268/iw-4.1.614

Peierls, B. L., N. F. Caraco, M. L. Pace, and J. J. Cole. 1991. Human influence on river nitrogen. Nature **350**: 386–387. doi:10.1038/350386b0

Potter, P., N. Ramankutty, E. M. Bennett, and S. D. Donner. 2010. Characterizing the spatial patterns of global fertilizer application and manure production. Earth Interact. **14**: 1–22. doi:10.1175/2009EI288.1

Potter, P., N. Ramankutty, E. M. Bennett, and S. D. Donner. 2011. Global Fertilizer and Manure, Version 1: Phosphorus Fertilizer Application. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). doi:10.7927/H4FQ9TJR

Prairie, Y. T. 2008. Carbocentric limnology: Looking back, looking forward. Can. J. Fish. Aquat. Sci. **65**: 543–548. doi:10.1139/f08-011

Prairie, Y. T., D. F. Bird, and J. J. Cole. 2002. The summer metabolic balance in the epilimnion of southeastern Quebec lakes. Limnol. Oceanogr. **47**: 316–321. doi:10.4319/lo.2002.47.1.0316

Ruesch, A., and H. K. Gibbs. 2008. New IPCC Tier-1 Global Biomass Carbon Map for the Year 2000. Carbon Dioxide Information Analysis Center. Oak Ridge National Laboratory, Oak Ridge, Tennessee, [accessed 2017 May 5]. Available from http://cdiac.ess-dive.lbl.gov.

Rodríguez, M. Á., M. Á. Olalla-Tárraga, and B. A. Hawkins. 2008. Bergmann's rule and the geography of mammal body size in the Western Hemisphere. Glob. Ecol. Biogeogr. **17**: 274–283. doi:10.1111/j.1466-8238.2007.00363.x

Seekell, D. A., J. F. Lapierre, M. Pace, C. Gudasz, S. Sobek, and L. Tranvik. 2014. Regional-scale variation of dissolved organic carbon concentrations in Swedish lakes. Limnol. Oceanogr. **59**: 1612–1620. doi:10.4319/lo.2014.59.5.1612

Seekell, D. A., J.-F. Lapierre, J. Ask, A.-K. Bergström, A. Deininger, P. Rodríguez, and J. Karlsson. 2015*a*. The influence of dissolved organic carbon on primary production in northern lakes. Limnol. Oceanogr. **60**: 1276–1285. doi:10.1002/lno.10096

Seekell, D. A., J. Lapierre, and J. Karlsson. 2015*b*. Trade-offs between light and nutrient availability across gradients of dissolved organic carbon concentration in Swedish lakes: Implications for patterns in primary production. Can. J. Fish. Aquat. Sci. **72**: 1663–1671. doi:10.1139/cjfas-2015-0187

Soranno, P. A., K. S. Cheruvelil, K. E. Webster, M. T. Bremigan, T. Wagner, and C. A. Stow. 2010. Using landscape limnology to classify freshwater ecosystems for multi-ecosystem management and conservation. BioScience **60**: 440–454. doi:10.1525/bio.2010.60.6.8

Soranno, P. A., K. S. Cheruvelil, E. G. Bissell and others. 2014. Cross-scale interactions: quantifying multi-scaled cause–effect relationships in macrosystems. Front. Ecol. Environ. **12**: 65–73. doi:10.1890/120366

Soranno, P., and others. 2017. LAGOS-NE: A multi-scaled geospatial and temporal database of lake ecological context and water quality for thousands of U.S. lakes. Gigascience **6**:1–22. doi:10.1093/gigascience/gix101.

Staehr, P. A., L. Baastrup-Spohr, K. Sand-Jensen, and C. Stedmon. 2012. Lake metabolism scales with lake morphometry and catchment conditions. Aquat. Sci. **74**: 155–169. doi:10.1007/s00027-011-0207-6

Vadeboncoeur, Y., E. Jeppesen, M. J. Vander Zanden, H.-H. Schierup, K. Christoffersen, and D. M. Lodge. 2003. From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. Limnol. Oceanogr. **48**: 1408–1418. doi:10.4319/lo.2003.48.4.1408

Williamson, C. E., D. P. Morris, M. L. Pace, and O. G. Olson. 1999. Dissolved organic carbon and nutrients as regulators of lake ecosystems: Resurrection of a more integrated paradigm. Limnol. Oceanogr. **44**: 795–803. doi:10.4319/lo.1999.44.3_part_2.0795

Zwart, J. A., N. Craig, P. T. Kelly, S. D. Sebestyen, C. T. Solomon, B. C. Weidel, and S. E. Jones. 2016. Metabolic and physiochemical responses to a whole-lake experimental increase in dissolved organic carbon in a north-temperate lake. Limnol. Oceanogr. **61**: 723–734. doi:10.1002/lno.10248

Acknowledgments

We thank A. Prince for producing Fig. 2 and N. F. St-Gelais for help with analyses. R. Maranger, P. Soranno (as EIC), the Associate Editor and three anonymous reviewers have provided valuable feedback. This paper is based on research supported by the Knut and Alice Wallenberg Foundation, Université de Montréal, the National Science and Engineering Research of Canada, the Groupe de Recherche Interuniversitaire en Limnologie et en Environnement Aquatique (GRIL), and the U.S. National Science Foundation (EF-1065786 and EF-1638679).

Submitted 28 June 2017
Revised 17 November 2017; 07 February 2018
Accepted 04 March 2018