LIMNOLOGY AND OCEANOGRAPHY
Letters

Open Access
Limnology and Oceanography Letters 00, 2017, 00–00

doi: 10.1002/lol2.10054

SPECIAL ISSUE-LETTER

Hydrologic setting constrains lake heterotrophy and terrestrial carbon fate

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Scientific Significance Statement

Lakes are heterogeneous in their size and hydrology, and we expect this has implications for lake-mediated decomposition of terrestrial carbon. Existing efforts to model broad-scale lake carbon cycling ignore inter-lake heterogeneity. Our simple decomposition model demonstrates strong effects of lake size and hydrology for terrestrial carbon decomposition and provides an opportunity for process-based scaling of lake carbon cycling.

Abstract

Current efforts to scale lake processes rely heavily on empirical observations and do not consider inter-lake heterogeneity that is likely to regulate terrestrial dissolved organic carbon (tDOC) decomposition in lakes. We created a simple, analytical model of tDOC decomposition in lakes that highlights the role of lake size and catchment hydrologic export. Our model predicts a hydrologically mediated tradeoff between the instantaneous rate of tDOC decomposition and the fraction of the tDOC load that is decomposed within a lake. We also predict that variation in the importance of evaporation as a hydrologic export generates meaningful variation in tDOC decomposition at a given hydrologic residence time. These patterns of tDOC decomposition that emerge from lakes' hydrologic settings suggest that past attempts to scale lake carbon biogeochemistry may be biased. Our model provides context for empirical studies of lake carbon cycling and enables informed scaling of lake carbon biogeochemistry.

Because lakes and reservoirs integrate the terrestrial landscape around them, they serve as globally important biogeochemical hotspots, elemental storage basins, and greenhouse gas vents (Cole et al. 2007; Tranvik et al. 2009; McDonald et al. 2013). Although lakes are important for global carbon cycling, efforts to scale lake carbon cycling remain simplistic and ignore important inter-lake heterogeneity in morphometry, hydrology, and catchment land cover. This may in part result from a traditional focus of lake ecologists on in-lake processes *OR* pattern across lake regions, rather than on

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Author Contribution Statement: SEJ and JAZ designed the study. SEJ led model development with significant input from JAZ, PTK, and CTS. SEJ drafted the manuscript with input and edits from JAZ, PTK, and CTS.

Data Availability Statement: Our model code is open source and available at https://github.com/MFEh2o/ratesVfates. Contextual data from the U.S. Environmental Protection Agency's (EPA) National Lakes Assessment (U.S. EPA 2010; McDonald et al. 2013; Brooks et al. 2014; Read et al. 2015) and the North Temperate Lakes Long Term Ecological Research site (Hanson et al. 2007) are publicly available from those entities and our Github repository.

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

This article is part of the Special Issue: Carbon cycling in inland waters
Edited by: Emily Stanley and Paul del Giorgio

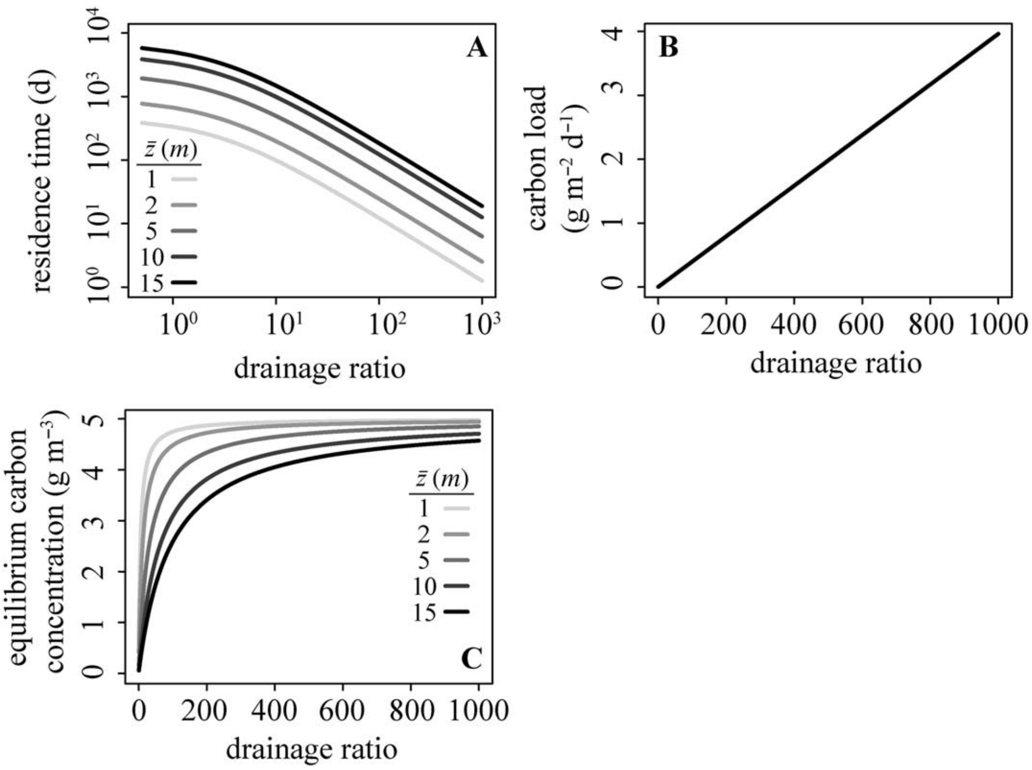

Fig. 1. (**A**) Residence time of model lake basins depends on the drainage ratio (catchment : lake area; *x*-axis) and lake mean depth ($\bar{z}$). Note the log$_{10}$-log$_{10}$ axes. (**B**) The daily carbon load per m^2 of lake area increases linearly with drainage ratio. Because we use areal load, mean depth has no effect on this relationship. (**C**) Equilibrium terrestrial dissolved organic carbon (tDOC) concentration in the lake is also related to drainage ratio. Note that the tDOC concentration in hydrologic loads (C_{in}) for these simulations was 5 g C m^{-3}, and therefore lake concentrations cannot exceed this level.

process *AND* pattern across scales. In order to generate quantitative predictions of carbon transport or fate, we must develop a process-based framework that leverages detailed understanding of within-lake dynamics (Berggren et al. 2010; Logue et al. 2015) and accounts for geospatial context of lakes to generate emergent patterns observed by landscape limnologists (Rasmussen et al. 1989; Soranno et al. 2015).

Lake size and catchment size, precipitation, and evapotranspiration (hydrologic setting) are important aspects of lake geospatial context that likely influence lake carbon cycling across scales. Hydrologic setting, along with catchment land cover, control the amount of terrestrial carbon supplied to a lake and interact with lake size to determine how long it undergoes decomposition, making them strong regulators of lake carbon biogeochemical rates (Canham et al. 2004; Brett et al. 2012). Fortunately, these characteristics, or at least useful proxies for them, can be quantified using widely available geospatial datasets. For example, the ratio of catchment area to lake area (i.e., the drainage ratio) is an appealing and widely used proxy for thinking about lake hydrologic loads, hydrologic residence time, and elemental loads (del Giorgio and Peters 1993; Algesten et al. 2004; Seekell et al. 2014).

We developed a simple analytical model to explore the influence of lake size and hydrologic setting on lake carbon biogeochemical processes. We use it to ask how drainage ratio and lake volume interact to dictate hydrologic properties of lakes and their contribution to decomposition of terrestrial dissolved organic carbon (tDOC). We also compare the importance of hydrologic setting to that of the quantity and quality of tDOC exported to lakes. Our goal is to provide context for empirical studies of lake carbon cycling and highlight additional paths for refinement of regional- to global-scale estimates of lake carbon cycling.

Methods

Given that the goal of our modeling was to investigate how lake volume and drainage ratio could be used to constrain predictions of lake hydrology and terrestrial carbon decomposition, we chose very simple representations of both lake physics and biology. Our model lake was cylindrical, mixed, and defined by its area and mean depth. Surrounding the lake was a catchment described by its area and the average concentration of tDOC in the surface runoff from the catchment to the lake. The model lake residence time was dictated by the catchment area, mean annual precipitation, catchment evapotranspiration, lake evaporation, and lake volume. The only model state variables were the mass of labile and recalcitrant tDOC, which originated from catchment inputs and were subject to first-order decay.

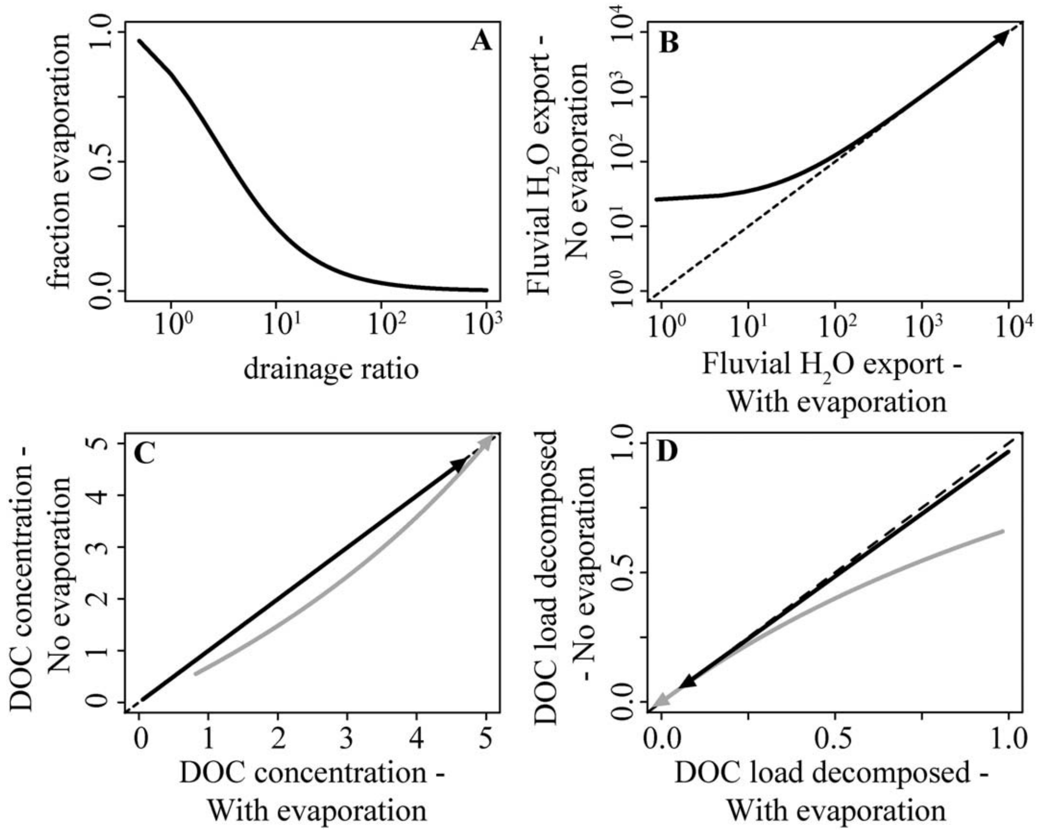

Fig. 2. (**A**) Drainage ratio (catchment : lake area; *x*-axis) influences the proportion of hydrologic loss that is due to evaporation. This proportion varies from nearly 100% at the lowest drainage ratio to < 1% at the highest drainage ratio. (**B**, **C**, **D**) Plots of model simulations with and without evaporation (dashed line is 1 : 1) included in the hydrologic budget show that the importance of evaporation depends on both lake mean depth (gray line = 1 m; black line = 15 m) and drainage ratio (increasing in direction of arrowhead). This is the case for (**B**) fluvial export of water (m^3 d^{-1}), although no effect of mean depth is observed here (lines are on top of each other); (**C**) equilibrium terrestrial dissolved organic carbon (tDOC) concentration (g C m^{-3}), note that the tDOC concentration in hydrologic loads (C_{in}) for these simulations was 5 g C m^{-3}, and therefore lake concentrations cannot exceed this level; and (**D**) the fraction of tDOC load that is decomposed.

Because we were interested in the long-term, average behavior of systems, we investigated model behavior at equilibrium using analytical solutions. Therefore comparison of our results to observations are likely most useful at average annual or longer time scales. We systematically investigated the responses of hydrologic residence time, the fraction of hydrologic loss via evaporation, tDOC concentrations, and tDOC decomposition to interacting influences of drainage ratio and mean depth. We considered a range of drainage ratios and lake mean depths consistent with those observed in the United States Environmental Protection Agency's National Lakes Assessment (U.S. EPA 2010). Therefore, our results reflect a diverse suite of lake types found across the U.S. and can be compared to empirical observations (McDonald et al. 2013; Brooks et al. 2014). We also systematically varied concentration and quality of tDOC in catchment exports to compare their effects to that of hydrologic setting. See Supporting Information Material for a full description of the model and its parameterization.

Results and discussion

Our model makes several intuitive predictions about the effect of drainage ratio on water and carbon budgets (Fig. 1; *see* also Algesten et al. 2004; Brett et al. 2012). Drainage ratio is related positively to hydrologic load and negatively to residence time. Mean depth also influences residence time and equilibrium tDOC concentration (multiple lines in Fig. 1), but cannot impact the areal tDOC load. Drainage ratio and mean depth are non-linearly related to tDOC concentration owing to the effect of drainage ratio on catchment load, mean depth's effect on dilution of the load by lake volume, and their combined effect on hydrologic residence time, which dictates the extent of tDOC decomposition.

The role of evaporation

One difference between our model and other simple lake biogeochemistry models is our explicit inclusion of evaporation. Evaporation can approach 100% of hydrologic exports in shallow, low drainage ratio lakes (Fig. 2A). Available empirical water budgets support this result (Stets et al. 2010).

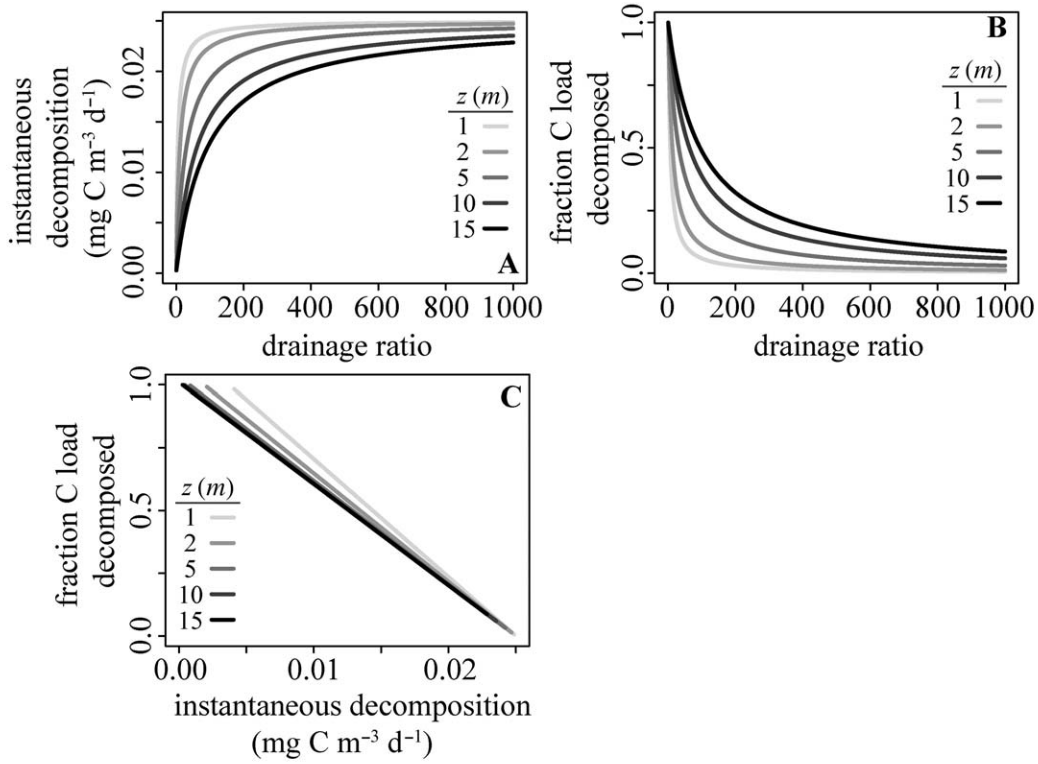

Fig. 3. (**A**) Instantaneous rates of decomposition increase non-linearly with drainage ratio and decrease with mean depth. (**B**) In contrast, the fraction of terrestrial dissolved organic carbon (tDOC) entering the lake that is decomposed declines non-linearly with drainage ratio (catchment : lake area) and increases with mean depth. (**C**) The opposing responses of these processes generate a trade off between the rate of decomposition and fraction of tDOC load that is decomposed. The slope of this negative relationship is steeper in lakes with shallower mean.

Because evaporation is an areal process, the volume of water evaporated (and thus the volume of hydrologic import available for export given our constant volume assumption) depends on surface area but not on mean depth or volume (Fig. 2B). Nonetheless, depth and volume strongly affect residence time (Fig. 1A).

Evaporation also concentrates lake tDOC, which influences lake carbon dynamics, especially in shallow lakes. In a lake with a mean depth of 1 m evaporation can increase equilibrium tDOC concentration by up to 33%, but this effect is much smaller in deeper lakes (Fig. 2C). Qualitatively similar effects of evaporation on tDOC concentrations have been observed elsewhere (Curtis and Adams 1995; Hanson et al. 2014). Evaporative concentration of tDOC is reduced in deeper lakes by a much larger total mass of tDOC and a longer residence time, which increases the importance of decomposition for determining equilibrium tDOC concentration. Evaporative concentration can be important for shallow lakes, but at intermediate drainage ratios. In shallow lakes with high drainage ratios, fluvial inputs overwhelm the effects of evaporation, and the long residence time of shallow lakes with low drainage ratios makes decomposition the dominant processes determining equilibrium tDOC concentrations (Fig. 2C).

Evaporation-driven decoupling of water and carbon residence time means that models that fail to account for evaporation can severely underestimate tDOC decomposition (Fig. 2D). For instance, a shallow lake with a low drainage ratio processes almost twice as much of its carbon load when evaporation is included in the water budget. The magnitude of this effect is reduced with greater lake depth and drainage ratio. Because we model tDOC decomposition as a first-order process, the concentrating effect of evaporation also enhances the instantaneous rate of decomposition, and we see similar dependencies on lake depth and drainage ratio.

A rate vs. fate tradeoff

Variation in hydrologic setting (drainage ratio and therefore residence time) of lakes also generates an interesting, negative relationship between the instantaneous rate of decomposition (g C m^{-3} d^{-1}) and the fraction of tDOC load that is decomposed by the receiving lake (Fig. 3). Instantaneous decomposition increases with drainage ratio (Fig. 3A) because high drainage ratio lakes have higher equilibrium tDOC concentrations (Fig. 1C) and tDOC decomposition is thought to be a first-order process. Conversely, the fraction of tDOC load decomposed decreases with drainage ratio (Fig. 3B) because high drainage ratio lakes have shorter residence times (Fig. 1A) and the majority of their carbon load is exported downstream. These two relationships generate a negative linear relationship between instantaneous rates of decomposition and the fraction of tDOC load that is decomposed for a given lake, with a slope dependent on lake depth (Fig. 3C). To our knowledge, this hydrology-mediated negative correlation between rates of tDOC decomposition and fate of tDOC load has not been explicitly described elsewhere, but it has important implications for scaling lake carbon cycling.

Although not a biophysical tradeoff, this negative correlation in two quantities describing tDOC decomposition does present a "tradeoff" in how we conceptualize lake carbon biogeochemistry. For example, one might describe low-drainage-ratio lakes as important for tDOC decomposition because they decompose nearly all of the tDOC they receive, but instantaneous rates of decomposition are much higher in high-drainage-ratio lakes. As a result, this rate vs. fate tradeoff creates challenges for scaling lake carbon biogeochemistry. Currently, the tDOC decomposition and CO_2 emission rates used in constructing regional and global carbon budgets tend to be biased toward large lakes that also have large drainage ratios (Cole et al. 2007; Wagner et al. 2008). Given the rate vs. fate tradeoff, these budgets may simultaneously overestimate CO_2 emissions (due to high instantaneous decomposition rates of large drainage-ratio lakes) and underestimate the fraction of tDOC inputs processed by inland waters (due to biased sampling against small-drainage ratio lakes that retain much of their carbon load). A more explicit treatment of lake hydrologic setting and acknowledgement of the rate vs. fate tradeoff in our conceptualization of lake carbon cycling would provide improved estimates of both loads to lakes and the extent of tDOC decomposition in lakes. The use of process-based models for scaling of lake biogeochemistry to broad scales would also allow the field to make inference about how broad-scale carbon cycling by lakes has and will change in response to climate change.

DOC decomposition as an emergent property

Our model predicts that a wide range of ecosystem-level decomposition rates of terrestrial carbon can emerge from the interactions between drainage ratio, mean depth, and evaporation, even for lakes that share identical climate, watershed land cover (here treated as tDOC concentration in fluvial export), and tDOC decay kinetics (Fig. 4). Previous work has identified the expectation for a saturating relationship between residence time and fraction of tDOC load decomposed, which is generated by first-order decay kinetics and the chemostat-like behavior of high drainage ratio lakes (Algesten et al. 2004; Hanson et al. 2011; Brett et al. 2012; Vachon et al. 2017). However, evaporation and its effect on chemical residence time of terrestrial tDOC alters this relationship between residence time and fraction of tDOC load decomposed.

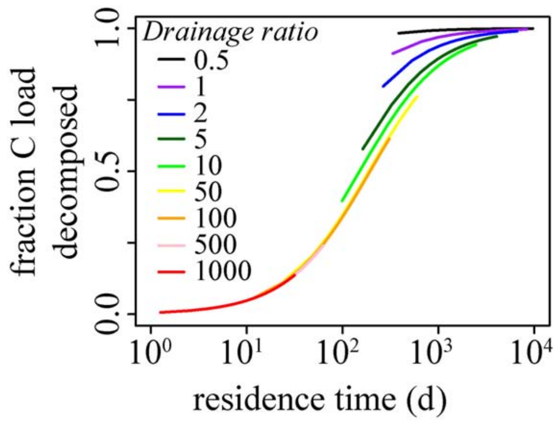

Fig. 4. Variation in drainage ratio (colored lines) and mean depth (increasing from left to right for each line) drive variation in residence time (*x*-axis) and the importance of evaporation as a hydrologic loss, which drive heterogeneity in the fraction of terrestrial dissolved organic carbon supplied to the lake that is decomposed.

In lakes with relatively large drainage ratios (> 100), fluvial processes dominate the hydrologic budget and the fraction of tDOC load that is decomposed increases linearly with residence time. However, in lakes with drainage ratios < 100, evaporation begins to contribute meaningfully to the hydrologic budget, which causes tDOC residence time to exceed hydrologic residence time. This generates much higher fractions of tDOC load decomposed than expected based on residence time in a purely fluvial system (Fig. 4). These relationships also hold, but in the opposite direction, for instantaneous decomposition rates given the negative, linear relationship between fraction of tDOC load that is decomposed and instantaneous decomposition rates (Fig. 3C).

The role of DOC quantity and quality

A tremendous amount of empirical work has investigated the quantity and quality of tDOC exported from catchments to surface waters (Canham et al. 2004; Freeman et al. 2004; Sebestyen et al. 2009; Kellerman et al. 2014; Kothawala et al. 2015; Mostovaya et al. 2016). Clearly the quantity of tDOC supplied to a lake has diverse and strong implications (Jones 1992; Solomon et al. 2015). At times tDOC quality has also been identified as a regulator of ecosystem-scale carbon cycling/decomposition. Given the past attention paid to the effects of quantity and quality on lake carbon decomposition, we explored the relative importance and any potential interactions between the quantity/quality of catchment tDOC and lake hydrologic setting.

More tDOC in hydrologic loads increases equilibrium lake tDOC concentrations and decomposition rates. However, hydrologic setting and mean depth determine the sensitivity of lake equilibrium tDOC concentrations and decomposition rates to carbon concentration of hydrologic loads (Fig. 5A,B).

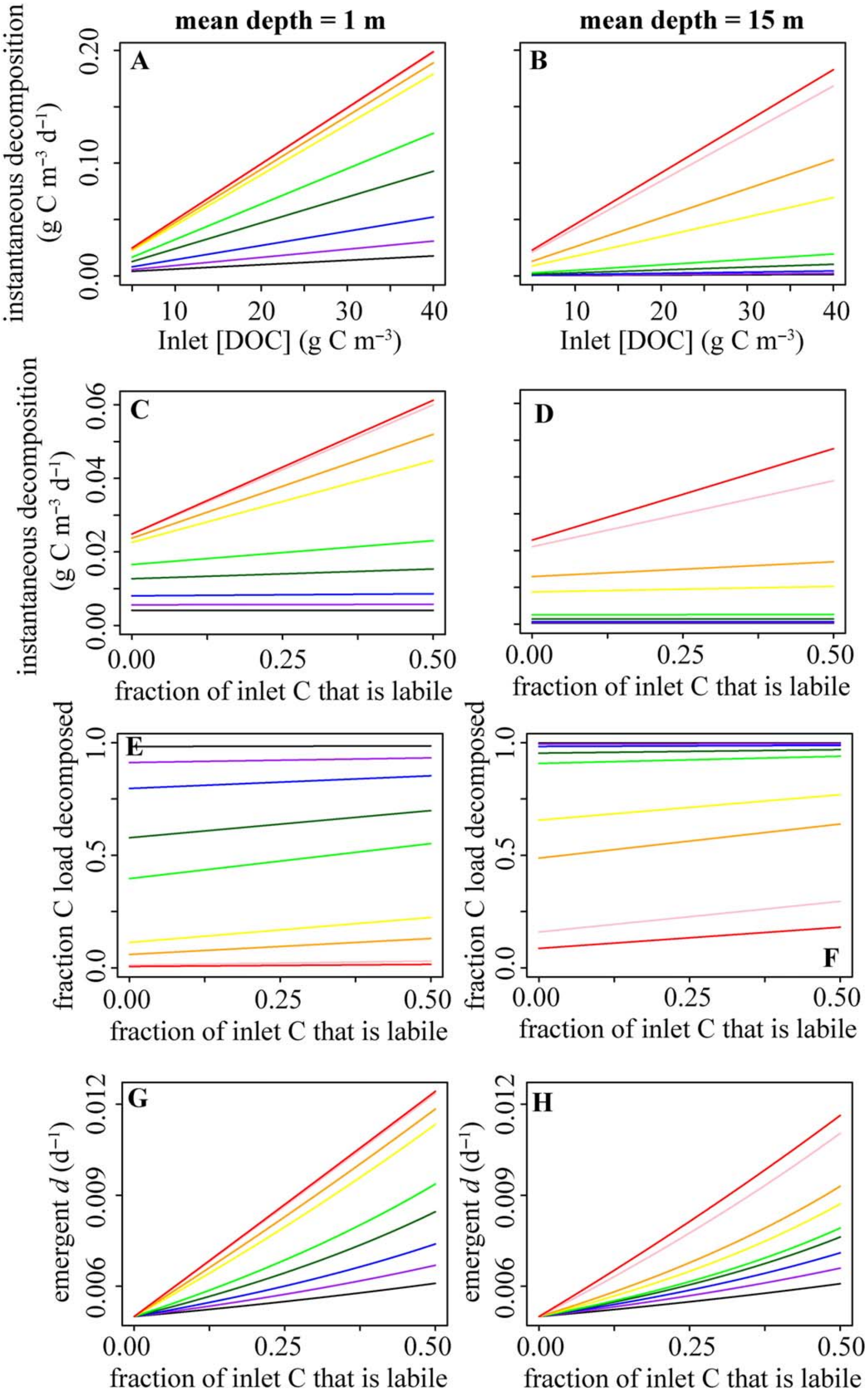

Fig. 5. Both terrestrial dissolved organic carbon (tDOC) concentration in hydrologic loads (**A, B**) and tDOC quality (**C–H**) interact with hydrologic setting to alter tDOC decomposition dynamics. The impacts of tDOC concentration and quality are more pronounced in shallow lakes (left column) compared to deep lakes (right column) and in lakes with higher drainage ratios (warmer colored lines). Color coding of lines is the same as in Fig. 4.

Small drainage ratio, deep lakes are quite insensitive to changes in the incoming tDOC concentration because they receive a relatively small tDOC input per volume of lake and decompose a large fraction of their loads given their long tDOC residence times. On the other hand, shallow, large drainage ratio lakes are more sensitive. In contrast to decomposition rates, the fraction of tDOC load that is decomposed is insensitive to changes in incoming tDOC concentration because this quantity is expressed relative to the carbon load and tDOC decay kinetics in the model are not sensitive to tDOC concentrations (first order).

The quality of tDOC also influences equilibrium tDOC concentration, volumetric respiration rates, and the fraction of tDOC load that is respired (Fig. 5C–H). Interestingly, the effect of a labile fraction of tDOC load on these characteristics is modified by drainage ratio and mean depth via their effect on lake residence time. Lakes with the shortest residence time (shallow, high drainage ratio lakes) had the largest increase in volumetric respiration when a labile tDOC fraction was added (Fig. 5C,D), but tDOC lability had little impact on respiration rates in lakes with residence times greater than $\sim$ 6 months (deeper, low drainage ratio lakes). In short residence time systems, constant renewal of the labile carbon pool generates a higher emergent instantaneous decomposition rate (Fig. 5G,H). In contrast, the carbon residence time in lakes with smaller drainage ratios is long enough that much of the labile carbon, and even the recalcitrant carbon, is degraded prior to hydrologic export. The long carbon residence time yields a much lower emergent decomposition rate and much lower sensitivity to variation in the quality of tDOC exported from the catchment. This effect of drainage ratio on emergent rates of decomposition of a heterogeneous tDOC pool (low and high quality pools) and the relationship between drainage ratio and evaporation combine to make the fraction of tDOC load decomposed most sensitive to tDOC quality in lakes with an intermediate drainage ratio (Fig. 5E,F). Having said that, in general tDOC quality had a fairly small effect on the fraction of tDOC load decomposed when compared to the influence of hydrologic setting.

Clearly hydrology and tDOC quality interact to determine tDOC decomposition in lakes (Berggren et al. 2010; Hanson et al. 2011; Vachon et al. 2017; Zwart et al. 2017), but our model suggests the role of resource quality may be over emphasized. Both Vachon et al. (2017; their Fig. 6) and Hanson et al. (2011; their Fig. 9) highlight that heterogeneous decomposition constants can explain observed decomposition in short and long hydrologic residence time lakes. In contrast, predictions from our model (Figs. 4, 5) suggest that heterogeneous carbon decomposition kinetics or reactivities can emerge with little or no heterogeneity in loaded carbon quality. Although previous studies acknowledge the potentially important role of hydrology, they still may overemphasize the importance of inter-lake or inter-catchment variation in tDOC quality by misattributing variation in lake tDOC decomposition driven by evaporation to tDOC quality of catchment exports.

Extending insights to real lakes

The patterns generated by our analytical model are hypotheses to be tested. Previously compiled data supports some of the simplest hydrologic predictions generated by our model (Fig. 1; Brett et al. 2012). Further work is required to evaluate whether our more interesting biogeochemical predictions play out in reality. Certainly if the chemical composition of terrestrial carbon, species composition of microbial communities, or disturbance history of lakes are major drivers of lake carbon biogeochemistry we would expect empirical results to deviate strongly from our model output. However, the physical constraints set by a lake's hydrologic setting may dictate biogeochemical boundaries within which carbon chemistry and microbial communities can alter lake-mediated decomposition of tDOC.

Our model predicts interesting interactions between lake hydrologic setting and carbon biogeochemistry. Many of the effects of hydrologic setting on carbon biogeochemistry are strongest when the drainage ratio is less than 50, residence time is greater than 100 d, and evaporation is a meaningful hydrologic export (> 50%). Is this merely an interesting theoretical case or do a meaningful number of lakes exist in this hydrologic setting? Based upon the 2007 EPA National Lakes Assessment, nearly half of U.S. lakes fall in this theoretically complex hydrologic setting, and this proportion may be higher in some regions (Supporting Information Table S2). We may expect regional climate to alter the critical drainage ratio for generating strong effects on carbon biogeochemistry, but expect the residence time and importance of evaporation to hold across regions.

Our model's simplicity allowed us to identify hydrologic controls on tDOC decomposition in lakes, but we have also ignored potentially important physical, chemical, and biological features, such as density stratification. We also made strong assumptions to homogenize spatial and temporal behavior of our model lake catchment. Given the minimal inclusion of limnological process, our model may be useful as a "null model." In this role, our model identifies what can be explained by basic catchment processes and lake size, and deviations of observations from our model predictions are likely due to more complex physical, chemical, or biological processes or significant spatiotemporal heterogeneity (Kothawala et al. 2015; Vachon and del Giorgio 2014; Logue et al. 2015; Zwart et al. 2017). For example, our use of mean daily loads of water and tDOC obscures significant temporal heterogeneity in water and tDOC delivery, which may amplify some of our predicted effects of hydrologic setting on tDOC decomposition (Vachon and del Giorgio 2014; Zwart et al. 2017).

Simple process models like ours would also be useful in scaling lake processes to regional and global scales. Clearly, based upon our results, catchment and lake hydrology can play a central role in regulating decomposition of terrestrial carbon in lakes. Therefore, to generate hydrologically informed estimates of broad-scale lake carbon biogeochemistry, we must integrate simple process models that include some hydrologic detail with geospatial datasets or scaling relationships that provide hydrologic and chemical forcings. Our model, or a version that includes some additional physiochemical detail, likely captures the necessary level of process detail. Also, availability of the necessary geospatial datasets is increasing rapidly. These resources place limnologists in an outstanding position to soon provide spatially explicit, dynamic predictions of lake biogeochemistry that can inform the next generation of earth system models.

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Acknowledgments

This project benefited from National Science Foundation support under award DEB-1552343 to SEJ. JAZ was supported by the National Science Foundation Graduate Research Fellowship award DGE-1313583.

Submitted 19 April 2017
Revised 27 July 2017
Accepted 25 September 2017