Carbon is the currency of life. It plays a fundamental role in the flow and transformation of materials within and across all ecosystems. A substantial component of the carbon cycle in aquatic ecosystems are the transformations that occur through biological processing, i.e., metabolism. Although the range of aquatic ecosystems in which metabolism has been studied continues to grow, we lack a conceptual framework to connect such studies and to model carbon transformations across broader spatial scales. Here, we present a conceptual and quantitative model that simulates shifts in burial, export, and respiration of persistent and reactive organic carbon pools over water residence times of hours to decades along a continuum of lentic and lotic freshwaters. By integrating aquatic metabolism studies across a range of ecosystem types, we can provide greater mechanistic understanding of the controls of carbon fates within and across aquatic ecosystems.

Carbon plays a fundamental role in the flow and transformation of materials within and across all ecosystems. A substantial component of the carbon cycle in aquatic ecosystems are the transformations that occur through biological processing, i.e., metabolism. Although the range of aquatic ecosystems in which metabolism has been studied continues to grow, we lack a conceptual framework to connect such studies and to model carbon transformations across broader spatial scales. Here, we present a conceptual and quantitative model that simulates shifts in burial, export, and respiration of persistent and reactive organic carbon pools over water residence times of hours to decades along a continuum of lentic and lotic freshwaters. By integrating aquatic metabolism studies across a range of ecosystem types, we can provide greater mechanistic understanding of the controls of carbon fates within and across aquatic ecosystems.

Carbon is the currency of life. It plays a fundamental role in the flow and transformation of materials within and across all ecosystems. Key to carbon cycling in aquatic ecosystems is the anabolic and catabolic transformations that occur through biological processes, i.e., metabolism. Metabolism in aquatic ecosystems often represents a substantial component of carbon fluxes. Most aquatic metabolism studies remain within boundaries of bottles, stream reaches, reservoir basins, river corridors, and lake shores, often overlooking the inherently connected nature of inland water networks. Although the range of aquatic ecosystems in which metabolism studies have been conducted continues to grow, we still lack a conceptual framework with which to link such studies and to model carbon fluxes and processes across broader spatial scales.

Addressing aquatic carbon (C) cycling at broader spatial scales is possible using conceptual and analytical paradigms with the flexibility to cross ecosystem boundaries. However, process-based studies that include both lentic and lotic ecosystems or link ecosystem processes within aquatic networks are particularly rare. Thus, our understanding of dynamic spatial and temporal shifts in C sources and fate at the
ecosystem, watershed, continental, and global scales remains limited. Overcoming such limitations is necessary if we are to gain a broader, more synoptic understanding of the role of aquatic metabolism in multi-scale C cycling. Here, we present a conceptual framework for advancing our knowledge of aquatic metabolism across ecosystem gradients to better understand higher-level controls over metabolism and the ultimate fates of allochthonous and autochthonous C.

**Linking mechanism and flux: Metabolism in inland waters**

Continental-scale understanding of organic and inorganic C fluxes in aquatic ecosystems requires modeling approaches that cross freshwater ecosystem boundaries, but estimates are largely based on empirical measurements made at small spatial scales. In fact, our understanding of the prominence of inland waters in C cycling stems primarily from the many descriptive studies documenting the extent to which streams, rivers, and lakes tend to be supersaturated with CO2 relative the atmosphere (e.g., Cole et al. 1994; Raymond et al. 2013). While considerable research has focused on estimating C fluxes as a primary goal, a subset of studies integrated ecosystem metabolism with C budgets to identify the degree to which inland waters act as passive conduits of C from terrestrial ecosystems to the oceans and atmosphere vs. sites of active biological processing (Cole and Caraco 2001; Battin et al. 2009; Hotchkiss et al. 2015; Wilkinson et al. 2016).

Studies of widespread heterotrophy in freshwaters have highlighted the importance of C fluxes between ecosystems and the role of aquatic metabolism in transforming C at the catchment scale. A new era of metabolism research using process-based models, along with the advent of high-frequency observational data from sensor networks, ushered in the need to explain mechanisms underlying large gradients observed in the C balance of ecosystems. Quantifying ecosystem-scale respiration (R) and primary production (PP) and using the imbalance between PP and R provides insights into how the organic matter subsidies that inland waters receive from the landscape fuel metabolic heterotrophy (Odum 1956; Cole and Caraco 2001; Battin et al. 2009; Solomon et al. 2013). Through these approaches, we have been able to resolve differences in metabolic balance throughout the water column and different habitats within lake ecosystems (Lauster et al. 2006; Sadro et al. 2011; Van de Bogert et al. 2012), quantify die to annual trends in ecosystem metabolism (Roberts et al. 2007; Solomon et al. 2013; Hotchkiss and Hall 2014; Sadro et al. 2014), and identify controls over metabolism across broad gradients of ecosystems (Hanson et al. 2003; Hoellein et al. 2013). However, the boundaries between ecosystems have largely remained the boundaries of metabolism research, with the origin and fate of inputs to and exports from ecosystems uncategorized, and the effects of landscape-scale transformations of C on fluxes unexplored.

Here, we apply a general model of C metabolism (Hanson et al. 2014) across a simulated gradient of water residence times (WRTs) throughout lentic and lotic ecosystems to demonstrate how a more integrative approach clarifies differences in C transformations and fates among ecosystem types and can inform future cross-boundary ecosystem research. To better accommodate the heterogeneity of C sources and process rates among streams, lakes, reservoirs, and rivers, our simulations split the organic carbon (OC) pool into more persistent and reactive pools, reflecting distinct OC sources (e.g., allochthonous and autochthonous) that contribute to C fluxes. Our modeling approach is complementary to that of Duffy et al. (this issue), which explicitly links catchment and lake hydrology, and quantifies the transport and fate of OC by solving equations for an integrated lake-catchment system. Whereas they implemented their model for a single system and explored the influence of changing climate conditions on that system, our simulation assumes changes in hydrology and OC load across a diversity of freshwater ecosystem types, and solves OC budgets spanning broader hydrologic and C loading gradients. In this essay, we discuss the need to integrate metabolism studies across ecosystems by: (1) demonstrating how a simple, single-system multi-OC pool metabolism model can be applied to different ecosystem types, and (2) identifying knowledge gaps apparent from ecosystem-specific simulations to discuss future, cross-ecosystem research needs.

**Modeling aquatic carbon metabolism across lotic and lentic systems: Features common to all ecosystems can be used to predict OC fates**

Perhaps the largest challenge in creating a broadly relevant framework of C metabolism is applying a simple metabolic model across a range of aquatic ecosystems in ways that enable us to not only understand how ecosystems differentially process and control fates of C, but what such differences mean for quantifying C fluxes at broad spatial scales. Although there are numerous processes that affect both the creation and consumption of organic matter, in order to provide a generalizable simulation framework that easily scales through space and time (i.e., across categories of aquatic ecosystems), our model focuses on rates of PP and R. Our model divides OC into two admittedly simplistic categories based on differences in biological lability: more reactive OC and more persistent OC, here described as autochthonous OC fixed within each system, and allochthonous OC fixed outside the modeled system. In addition to metabolic rates, our model includes two other key processes related to OC flux: hydrologic transport and burial. Our conceptual model is illustrated in Fig. 1A.
This model is undeniably a generalization of the complex processes affecting linked organic and inorganic C fluxes in inland waters. We note that the term “inland waters” applies to a broad range of ecosystem types, each undoubtedly possessing unique issues relevant to OC cycling, but our thesis here is generalizability across systems. Our goal in updating and applying an established, generalized model is to highlight two areas critical to advancing metabolism studies in limnology: (1) how features common to all ecosystems enable us to simulate OC fates across a range of system-level controls; (2) how to prioritize future work on metabolism and C cycling, with the aim of understanding and quantifying network- and continental-scale C transformations and fluxes in linked aquatic ecosystems.

To explore metabolism over a range of inland aquatic ecosystems, we instantiated our conceptual model (Fig. 1A) as the equilibrium solution of a set of differential equations (Supporting Information), and then applied that model over gradients of WRT and with different reactivity rates of two OC pools. Each instance of the model represents a different ecosystem that falls along gradients in OC load and WRT. Gradients of WRT and pools with different OC lability were chosen because they are key controls over OC cycling and vary widely among aquatic ecosystems (Hanson et al. 2011; Catalán et al. 2016). While more recent studies quantifying links between variable WRT and terrestrial OC mineralization have focused on lakes (e.g., Evans et al. 2017; Vachon et al. 2017, Jones et al. this issue), we broaden this perspective to quantify how streams, rivers, reservoirs, and lakes differ in their capacity to transform different sources of OC. The results in Fig. 1 illustrate how behavior of thousands of simulations changes over these gradients. Although our model does not explicitly exclude reservoirs, their often complex morphometry and placement on higher order streams may complicate the generalization of C fates in

Fig. 1. Modeling the fates and proportions of organic matter fluxes across aquatic ecosystem types as a function of WRT. (A) A simple conceptual model for OC cycling in aquatic systems, whether the system represents a stream reach or lake. The two state variables, recalcitrant organic carbon (OCR) and labile organic carbon (OCL) are governed by a set of processes that include OC inflow, OC outflow, transformations through PP and respiration (R), and OC burial (B). PP and R consume and produce dissolved organic C (DIC), respectively. The total OC load is the sum of PP and inflow. Export (E) is the sum of the outflow flux of OCL and OCR. (B) Fate of total OC inputs (allochthony + autochthony) with uncertainty (dashed lines) reflecting a range of assumed OC lability. (C) The proportion of OC loads and fates derived from autochthony, with the remainder of each proportion derived from allochthonous OC. (D) Steady-state concentrations of OC as a function of both initial load (each individual line, ranging from 1 g OC m\(^{-3}\) to 60 g OC m\(^{-3}\)) and WRT. The shaded areas approximate the range of DOC concentrations found in a stream survey ($S$; Lottig et al. 2013) and a lake survey ($L$; Hanson et al. 2007) conducted in the Northern Highlands Lake District of northern Wisconsin. The blue line was estimated as the mean inflow concentration to lake ecosystems from Cardille et al. (2007).
**Table 1.** Gradients in metabolism from the extremes of small streams to large lakes and aquifers, and their respective roles in OC cycling over broader temporal and spatial scales, when viewed through the continuum lens of WRT (i.e., Fig. 1).

| Low WRT (e.g., small streams) | ↔ | High WRT (e.g., large lakes) |
|-------------------------------|---|-------------------------------|
| Metabolic behavior dominated by loads | Metabolic behavior dominated by trophic state |
| Events are a dominant time-scale feature | Integration of longer time periods is the dominant time-scale feature (long lags) |
| Allochthonous OC pool is relatively young | Allochthonous OC pool is relatively old |
| Mineralization of allochthonous OC $\geq$0.1 d$^{-1}$ | Mineralization of allochthonous OC $\sim$0.001 d$^{-1}$ |
| Particulate OC can be a dominant constituent of the transformed OC pool, because of high energy | Particulate OC rarely a dominant constituent of the transformed OC pool, because of low energy |
| Large gradient in biologically reactive solute concentrations (e.g., carbon, nutrients) at landscape scales | Smaller gradient in biologically reactive solute concentrations |
| Closely coupled with surrounding landscape | Loosely coupled with surrounding landscape |
| Allochthony is the dominant term in most metabolic budgets | Autochthony is the dominant term in metabolic budgets at decadal and longer time scales |

these ecosystems. Size plays an important role in determining where on this gradient of WRT a lake or reservoir will fall, with many small lakes resembling streams to a greater or lesser extent depending on seasonal hydrological variability. Fates of OC in our model are respiration as inorganic C (IC), burial, or export. Key assumptions about parameter values (e.g., morphometry, rates of net PP) determine where the dominance of one fate switches to another across ecosystem gradients. Across this large gradient of WRT simulations, model output is not very sensitive to changes in those parameters (Supporting Information Figs. S2, S3). While this model provides for easy scaling across a range of systems, from small, high-velocity streams to large, long WRT lakes, there are still many unknowns related to direct and indirect links between hydrology, OC sources, and network-scale relationships between our selected gradients and C fate (see further discussion in Supporting Information). Indeed, this model offers more questions than answers, but provides a framework within which to test controls on and patterns of C fluxes, metabolism, and fate.

Inferences from Fig. 1 shed light on how stream ecologists and lake ecologists historically viewed the world differently. Much of today’s ecosystem-specific research is still informed by those legacies; sampling methods, model choice, and even the framing of specific research questions are often rooted in the history of these sub-fields of limnology. Instead of forcing false dichotomies where there are no longer distinct boundaries, we begin with a simple conceptual model that has relevance to sub-disciplines, and can connect and understand what may initially appear as disparate views and approaches (Table 1). While the divide between lotic and lentic ecology has diminished over time, most studies still focus on a single aquatic ecosystem type, rarely integrating the heterogeneity of freshwater ecosystem types and residence times within networks of inland waters.

By applying a multi-pool OC cycling model at cross-ecosystem scales on the basis of WRT, we conceptually explore changes in the fate of OC across a range of simulated WRT from $< 1$ d (e.g., small streams) to decadal and longer time scales (e.g., aquifers and oceans) (Fig. 1B). A number of useful inferences emerge about the role of hydrology in governing C fluxes and fates across ecosystems. In this paradigm, streams look like pipes because of the dominance of export as a fate; however, imagine the view from a stream microbe: OC concentrations might be consistently extremely high ($\sim 60$ mgC L$^{-1}$), and therefore the respiration per unit area is higher than almost all lakes, an observation that may be obscured by simultaneous inputs of OC and rapid transport of metabolism substrates and products downstream. Even if respiration of OC exceeds 0.1 d$^{-1}$ in faster flowing systems, which is higher than most bioassay estimates but perhaps more in line with whole-ecosystem measurements of stream metabolism, it is still likely lower than export, which may exceed 1 d$^{-1}$. Consequently, the relative proportion of OC loads and fates derived from allochthonous and autochthonous OC shifts to more autochthony-dominated systems in the transition to longer WRT (Fig. 1C, Supporting Information Fig. S1). Indeed, large lakes look a lot like the open ocean (“century” in Fig. 1), in which much C burial is from phytoplankton. The implications of these shifts for the flow and fate of autochthonous and allochthonous OC through food webs remain an active area of research. Last, OC concentrations are highly variable in ecosystems with short WRT, while long WRT systems converge to low OC concentrations (Fig. 1D). Small lakes experience a wide range of WRT and will reflect upstream processes in similar ways as streams under certain hydrologic conditions. Our conceptual model accommodates this variation (Fig. 1D) as small lakes with short WRT have a less constrained distribution of OC concentrations than large lakes.
Future directions: Linked-ecosystem metabolism research in an era of rapid environmental change

One key gap in our understanding of C metabolism is the lack of process-based research that crosses ecosystem boundaries. How much organic matter must enter and be exported from headwaters to sustain downstream processes in larger streams, lakes, and rivers? What magnitude of within-network C inputs are we missing from budgets if we assume the majority of allochthonous C is loaded into headwaters only? By integrating estimates of inorganic and organic C fluxes and cycling within networks of connected ecosystems (Fig. 2), future research will better quantify the history of upstream inputs and processing, the consequences of upstream and within-site inputs for downstream ecosystems, and the network-scale contributions of aquatic metabolism to C budgets. An improved understanding of C metabolism across ecosystem types is critical to quantifying both the fluxes and the forms of terrestrial C inputs to inland waters, an area of high uncertainty in C budgets (Butman et al. 2016; Drake et al. 2017). Recent work revealed the significance of temporally dynamic WRT within stream networks for when and where dissolved OC is transported and processed (Raymond et al. 2016). Further, by intensively studying multiple sites within networks, we can identify areas functioning as “pipes” and “reactors” in dissolved organic matter budgets (e.g., Casas-Ruiz et al. 2017). Different freshwater networks may have unique emergent characteristics due to the heterogeneity and spatial order of terrestrial and aquatic ecosystems; this undoubtedly affects the loading, transport, and fate of C in ways that models based on simple continua of WRT alone cannot predict, especially during extreme flow events. Rarely have we integrated lentic and lotic ecosystems at temporal and spatial scales relevant to understanding whole-network fluxes and fate of all forms of C within the biosphere.

Integrated cross-ecosystem models will allow us to address a second critical knowledge gap: our limited capacity to predict how landscape-scale changes in meteorology, land use, and hydrology alter network-scale dynamics of C fluxes and fate. Despite considerable advances, our current ability to anticipate the consequences of changing WRT and C inputs on aquatic ecosystem processes at larger scales will remain crippled if we focus only on bioassay measurements and dissolved OC (DOC) decay without the broader context of organic and inorganic C fluxes and whole-ecosystem rates in linked streams, lakes, reservoirs, wetlands, and rivers. Shifts in climate, flow regimes, and land use are changing the magnitude and sources of C inputs into many freshwater ecosystems (Larsen et al. 2011; Butman et al. 2014; Mendonça et al. 2017; Wohl et al. 2017). The type of generalizable model we present here, while not a solution for all cross-ecosystem C research, can help us ask: How does WRT affect the fate of changing OC sources in aquatic ecosystems? To what extent will changes in stream, lake, and reservoir C concentrations reflect shifts in C inputs vs. internal processing? These questions motivate us to seek a more integrative and regional perspective on C cycling in aquatic ecosystems in the context of current and future environmental change. Linking the export and import fluxes of system-specific models may be further implemented to address how changing hydrologic regimes and the relative contributions of autochthonous and allochthonous C sources alter the delivery and fate of C at the scale of fluvial networks. Acknowledging the spatial and temporal heterogeneity of WRT and C inputs within networks presents an exciting challenge for future data collection and modeling efforts. We envision the application of simple models like the one presented here to test when and where our simulations of metabolism are wrong in order to identify critical areas for future research.

Conclusions

A research framework of carbon metabolism that crosses ecosystem boundaries to expand our knowledge of C metabolism allows for a more elegant integration of ecology and hydrology; direct comparisons of the importance of chemical residence time on what controls ecosystem and network-scale metabolism; and a better understanding of how changes in OC lability through integrated aquatic networks leads to observed differences among ecosystems. As long as we remain within our disciplinary and ecosystem boundaries, we will make limited progress on fundamental questions relevant to continental-scale C cycling.
References

Battin, T. J., L. A. Kaplan, S. Findlay, C. S. Hopkinson, E. Marti, A. I. Packman, J. D. Newbold, and F. Sabater. 2009. Biophysical controls on organic carbon fluxes in fluvial networks. Nat. Geosci. 2: 595–595. doi:10.1038/ngeo602

Butman, D., S. Stackpoole, E. Stets, C. P. McDonald, D. W. Clow, and R. G. Striegl. 2016. Aquatic carbon cycling in the conterminous United States and implications for terrestrial carbon accounting. Proc. Natl. Acad. Sci. USA 113: 58–63. doi:10.1073/pnas.1512651112

Butman, D. E., H. F. Wilson, R. T. Barnes, M. A. Xenopoulos, and P. A. Raymond. 2014. Increased mobilization of aged carbon to rivers by human disturbance. Nat. Geosci. 8: 112–116. doi:10.1038/ngeo2322

Cardille, J. A., S. R. Carpenter, M. T. Coe, J. A. Foley, P. C. Hanson, M. G. Turner, and J. A. Vano. 2007. Carbon and water cycling in lake-ridge landscape connections, lake hydrology, and biogeochemistry. J. Geophys. Res. Biogeosci. 112: 1–18. doi:10.1029/2006JG000200

Casas-Ruiz, J. P., and others. 2017. A tale of pipes and reactors: Controls on the in-stream dynamics of dissolved organic matter in rivers. Limnol. Oceanogr. 62: S85–S94. doi:10.1002/lno.10471

Catalán, N., R. Marcé, D. N. Kothawala, and L. J. Tranvik. 2016. Organic carbon decomposition rates controlled by water retention time across inland waters. Nat. Geosci. 9: 1–7. doi:10.1038/ngeo2720

Cole, J. J., N. F. Caraco, G. W. Kling, and T. K. Kratz. 1994. Carbon dioxide supersaturation in the surface waters of lakes. Science 265: 1568–1570. doi:10.1126/science.265.5178.1568

Cole, J. J., and N. F. Caraco. 2001. Carbon in catchments: Connecting terrestrial carbon losses with aquatic metabolism. Mar. Freshw. Res. 52: 101–110. doi:10.1046/j.1365-2419.2001.00884.x

Drake, T. W., P. A. Raymond, and R. G. M. Spencer. 2017. Terrestrial carbon inputs to inland waters: A current synthesis of estimates and uncertainty. Limnol. Oceanogr. Lett. 3: 132–142. doi:10.1002/lol2.10055

Duffy, C. J., H. A Dugan, and P. C. Hanson. 2018. The age of water and carbon in lake-catchments: A simple dynamical model. Limnol. Oceanogr. Lett. 3: 236–245. doi:10.1002/lol2.10070

Evans, C. D., M. N. Futter, F. Moldan, S. Valinii, Z. Frogbrook, and D. N. Kothawala. 2017. Variability in organic carbon reactivity across lake residence time and trophic gradients. Nat. Geosci. 10: 832–835. doi:10.1038/NGEO3051

Hanson, P. C., D. L. Bade, S. R. Carpenter, and T. K. Kratz. 2003. Lake metabolism: Relationships with dissolved organic carbon and phosphorus. Limnol. Oceanogr. 48: 1112–1119. doi:10.4319/lo.2003.48.3.1112

Hanson, P. C., S. R. Carpenter, J. A. Cardille, M. T. Coe, and L. A. Winslow. 2007. Small lakes dominate a random sample of regional lake characteristics. Freshw. Biol. 52: 814–822. doi:10.1111/j.1365-2427.2007.01730.x

Hanson, P. C., D. P. Hamilton, E. H. Stanley, N. Preston, O. C. Langman, and E. L. Kara. 2011. Fate of allochthonous dissolved organic carbon in lakes: A quantitative approach. PLoS One 6: e21884. doi:10.1371/journal.pone.0021884

Hanson, P. C., I. Buffam, J. A. Rusak, E. H. Stanley, and C. D. Watras. 2014. Quantifying lake allochthonous organic carbon budgets using a simple equilibrium model. Limnol. Oceanogr. 59: 167–181. doi:10.4319/lo.2014.59.01.0167

Hoellein, T. J., D. A. Brusewitz, and D. C. Richardson. 2013. Revisiting Odum (1956): A synthesis of aquatic ecosystem metabolism. Limnol. Oceanogr. 58: 2089–2100. doi:10.4319/lo.2013.58.6.2089

Hotchkiss, E. R., and R. O. J. Hall. 2014. High rates of daytime respiration in three streams: Use of δ18O2O and O2 to model diel ecosystem metabolism. Limnol. Oceanogr. 59: 798–810. doi:10.4319/lo.2014.59.3.0798

Hotchkiss, E. R., R. O. Hall, R. A. Sponseller, D. Butman, J. Klaminder, H. Laudon, M. Rosvall, and J. Karlsson. 2015. Sources of and processes controlling CO2 emissions change with the size of streams and rivers. Nat. Geosci. 8: 696–699. doi:10.1038/ngeo2507

Jones, S. E., J. A. Zwart, P. T. Kelly, and C. T. Solomon. Hydrologic setting constrains lake heterotrophy and terrestrial carbon fate. Limnol. Oceanogr. Lett. 3: 256–264. doi:10.1002/lol2.10054

Larsen, S., T. Andersen, and D. O. Hessen. 2011. Climate change predicted to cause severe increase of organic carbon in lakes. Glob. Chang. Biol. 17: 1186–1192. doi:10.1111/j.1365-2486.2010.02257.x

Lauster, G. H., P. C. Hanson, and T. K. Kratz. 2006. Gross primary production and respiration differences among littoral and pelagic habitats in northern Wisconsin lakes. Can. J. Fish. Aquat. Sci. 63: 1130–1141. doi:10.1139/f06-018

Lottig, N. R., I. Buffam, and E. H. Stanley. 2013. Comparisons of wetland and drainage lake influences on stream dissolved carbon concentrations and yields in a north temperate lake-rich region. Aquat. Sci. 75: 619–630. doi:10.1007/s00227-013-0305-8

Mendonça, R., R. A. Müller, D. Clow, C. Verpoorter, P. Raymond, L. J. Tranvik, and S. Sobek. 2017. Organic carbon burial in global lakes and reservoirs. Nat. Commun. 8: 1694. doi:10.1038/s41467-017-01789-6

Odum, H. 1956. Primary production in flowing waters. Limnol. Oceanogr. 1: 102–117. doi:10.4319/lo.1956.1.2.0102

Raymond, P. A., and others. 2013. Global carbon dioxide emissions from inland waters. Nature 503: 355–359. doi:10.1038/nature12760

Raymond, P. A., J. E. Saiers, and W. V. Sobczak. 2016. Hydrologic and biogeochemical controls on watershed dissolved organic matter transport: Pulse-shunt concept. Ecology 97: 5–16. doi:10.1890/14-1684.1
Roberts, B. J., P. J. Mulholland, and W. R. Hill. 2007. Multiple scales of temporal variability in ecosystem metabolism rates: Results from 2 years of continuous monitoring in a forested headwater stream. Ecosystems 10: 588–606. doi: 10.1007/s10021-007-9059-2

Sadro, S., J. M. Melack, and S. MacIntyre. 2011. Spatial and temporal variability in the ecosystem metabolism of a high-elevation lake: Integrating benthic and pelagic habitats. Ecosystems 14: 1123–1140. doi:10.1007/s10021-011-9471-5

Sadro, S., G. W. Holtgrieve, C. T. Solomon, and G. R. Koch. 2014. Widespread variability in overnight patterns of ecosystem respiration linked to gradients in dissolved organic matter, residence time, and productivity in a global set of lakes. Limnol. Oceanogr. 59: 1666–1678. doi:10.4319/lo.2014.59.5.1666

Solomon, C. T., and others. 2013. Ecosystem respiration: Drivers of daily variability and background respiration in lakes around the globe. Limnol. Oceanogr. 58: 849–866. doi:10.4319/lo.2013.58.3.0849

Vachon, D., Y. T. Prairie, F. Guillemette, and P. A. del Giorgio. 2017. Modeling allochthonous dissolved organic carbon mineralization under variable hydrologic regimes in boreal lakes. Ecosystems 20: 781–795. doi:10.1007/s10021-016-0057-0

Van de Bogert, M. C., D. L. Bade, S. R. Carpenter, J. J. Cole, M. L. Pace, P. C. Hanson, and O. C. Langman. 2012. Spatial heterogeneity strongly affects estimates of ecosystem metabolism in two north temperate lakes. Limnol. Oceanogr. 57: 1689–1700. doi:10.4319/lo.2012.57.6.1689

Wilkinson, G. M., C. D. Buelo, J. J. Cole, and M. L. Pace. 2016. Exogenously produced CO2 doubles the CO2 efflux from three north temperate lakes. Geophys. Res. Lett. 43: 1996–2003. doi:10.1002/2016GL067732

Wohl, E., R. O. Hall, K. B. Lininger, N. A. Sutfin, and D. M. Walters. 2017. Carbon dynamics of river corridors and the effects of human alterations. Ecol. Monogr. 87: 379–409. doi:10.1002/ecm.1261

Acknowledgments
We thank E. H. Stanley and P. A. del Giorgio for inviting us to collaborate on this carbon metabolism manuscript. We benefitted greatly from our cross-ecosystem discussions and encourage others to take a similar plunge into collaborations with colleagues from faster or more slowly flowing waters. We also thank three anonymous reviewers and editors, whose perspectives and comments improved our essay. P. C. H. was supported by the NTL LTER (NSF DEB-1440297).

Submitted 16 June 2017
Revised 06 December 2017; 29 January 2018
Accepted 04 March 2018