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The Influence of Hydrologic Residence Time on Lake Carbon Cycling Dynamics Following Extreme Precipitation Events

Jacob A. Zwart,[1]* Stephen D. Sebestyen,[2] Christopher T. Solomon,[3] and Stuart E. Jones[1]

[1]Department of Biological Sciences, University of Notre Dame, 263 Galvin Life Sciences, Notre Dame, Indiana 46556-0396, USA; [2]United States Department of Agriculture Forest Service, Northern Research Station, Grand Rapids, Minnesota 55744, USA; [3]Cary Institute of Ecosystem Studies, Millbrook, New York 12545, USA

ABSTRACT

The frequency and magnitude of extreme events are expected to increase in the future, yet little is known about effects of such events on ecosystem structure and function. We examined how extreme precipitation events affect exports of terrestrial dissolved organic carbon (t-DOC) from watersheds to lakes as well as in-lake heterotrophy in three north-temperate lakes. Extreme precipitation events induced large influxes of t-DOC to our lakes, accounting for 45–58% of the seasonal t-DOC load. These large influxes of t-DOC influenced lake metabolism, resulting in lake net heterotrophy following 67% of the extreme precipitation events across all lakes. Hydrologic residence time (HRT) was negatively related to t-DOC load and heterotrophy; lakes with short HRT had higher t-DOC loads and greater net heterotrophy. The fraction of t-DOC mineralized within each lake following extreme precipitation events generally exhibited a positive relationship with lake HRT, similar to the previous studies of fractions mineralized at annual and supra-annual time scales. Event-associated turnover rate of t-DOC was higher than what is typically reported from laboratory studies and modeling exercises and was also negatively related to lake HRT. This study demonstrates that extreme precipitation events are ‘hot moments’ of carbon load, export, and turnover in lakes and that lake-specific characteristics (for example, HRT) interact with climatic patterns to set rates of important lake carbon fluxes.

Key words: lake heterotrophy; hydrology; lake metabolism; carbon cycling; hydrologic residence time; synchrony; extreme precipitation events.

INTRODUCTION

Extreme events have dramatic effects on ecosystem function. For example, wildfires can cause changes to vegetation structure and surface energy fluxes that last for many decades (Zedler and others 1983; Rocha and Shaver 2011), heat waves can cause drastic changes in terrestrial and aquatic biodiversity and changes in productivity (Garrabou and others 2009; Reichstein and others 2007; Wernberg

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Data and code for this manuscript have been archived at https://github.com/jzwart/PulseLags

**Corresponding author; e-mail:* jzwart@nd.edu

and others 2012), and spring crop freeze can cause substantial economic losses and reduce terrestrial carbon sequestration (Gu and others 2008). Clearly, extreme events play an integral role in shaping ecosystem structure and function. Given that many extreme events are predicted to increase in frequency with climate change (Huntington 2006; Rahmstorf and Coumou 2011; Coumou and Rahmstorf 2012), understanding their effects on ecosystems is essential to predict how ecosystems will function in the future and how ecosystem structure modulates their effects.

There is considerable conceptual, modeled, and observational evidence that extreme rainfall events have been increasing in frequency and intensity and are predicted to continue to increase under future climate scenarios (Meehl and others 2005; Tebaldi and others 2006; Min and others 2011; Westra and others 2014). Extreme rainfall events may impact lake ecosystem function; however, documentation of their impact on lake ecosystems is sparse. Increased annual precipitation will increase water, solute, and particulate fluxes from watersheds to lakes and reduce lake hydrologic residence time (HRT; lake volume divided by the sum of water losses). Additionally, increased frequency and intensity of short-duration extreme rainfall will disproportionately lead to runoff to lakes via subsurface storm flow or overland flow relative to groundwater recharge, thus changing watershed flow regimes (Sebestyen and others 2009).

Previous research has shown that precipitation regimes may be important for structuring lake ecosystem function, specifically lake carbon cycling. For example, Ojala and others (2011) show that large rain events can cause lakes to become heterotrophic and that these events can be responsible for a large portion of annual carbon dioxide (CO_2) and methane (CH_4) emissions from lakes to the atmosphere. Roehm and others (2009) showed that lake partial pressure of CO_2 (pCO_2) increased with increased annual precipitation. This increase in lake pCO_2 was driven by inorganic carbon loading and increased heterotrophy associated with increased organic matter loading. Notably, small lakes had larger interannual variability in lake pCO_2, indicating that they were more susceptible to variations in rainfall (Roehm and others 2009). In two southern Québec lakes, precipitation intensity influenced the relative importance of internal production versus external loading of CO_2 following storm events; however, there seemed to be an interacting effect of lake HRT (Vachon and del Giorgio 2014).

Lake hydrologic characteristics (for example, lake morphometry, HRT) may be a governing factor for lake carbon cycling dynamics following extreme precipitation events, especially if spatial patterns between HRT and various aspects of lake carbon cycling hold true temporally. Given that lake HRT is reduced following extreme precipitation events, spatial patterns indicate that the fate (for example, sedimentation, efflux, or export downstream) of watershed carbon influx should favor export downstream over retention as has been shown at annual and supra-annual timescales both empirically (del Giorgio and Peters 1994; Dillon and Molot 1997; Stets and others 2010) and through models (Hanson and others 2011; Brett and others 2012). Spatial patterns also suggest that the rate of lake ecosystem respiration should increase following extreme precipitation events, as Solomon and others (2013) have shown that watershed area to lake volume (WA:LV; a proxy for lake HRT and also terrestrial carbon loading) was positively correlated with background respiration (defined as respiration supported by recalcitrant allochthonous organic matter). Furthermore, HRT is negatively correlated to the turnover rate of organic carbon across all inland waters (Catalán and others 2016), and thus, extreme precipitation events may increase this rate through time via a reduction in lake HRT. These previous studies indicate that lake carbon cycling responses to extreme precipitation events may not only be substantial but also heterogeneous across the landscape, as terrestrial carbon fate and lake metabolism rates may be affected by lake hydrologic characteristics such as HRT. Understanding the influence of extreme precipitation events on lake carbon cycling requires high-frequency estimates of both watershed fluxes and lake metabolism. Though rare, coupled high-frequency estimates of watershed fluxes and lake metabolism reveal important dynamics of lake carbon cycling that are not evident by using simple steady-state approaches (for example, Vachon and del Giorgio 2014).

In this study, we focused on the influence of extreme precipitation events on daily terrestrially derived dissolved organic carbon (t-DOC) loading and daily lake metabolism in three lakes with HRTs varying over an order of magnitude. We chose to focus on extreme precipitation events because these events provided: (1) moments of natural perturbations to lake ecosystems, which allowed us to investigate how lake HRT impacts lake carbon cycling responses to the same extreme precipitation events; (2) time periods for which we could estimate excess t-DOC load (above the mean seasonal baseline) and excess metabolism (above or below the mean seasonal baseline), ultimately allowing us to compare the direct impact of a quantifiable t-DOC load to a quantifiable lake metabolic response; and (3) pertinent insight into potential impacts of expected increases in extreme precipitation events on lake carbon cycling. We expected that any individual extreme precipitation event would produce synchronous and significant increases in t-DOC loading among the lakes and induce or enhance lake heterotrophy in each lake. We expected the magnitude and variation in t-DOC flux and heterotrophy would be negatively related to lake HRT, indicating that lakes with shorter hydrologic residence times would be more responsive in terms of t-DOC flux and heterotrophic activity to temporal hydrologic changes (for example, extreme precipitation). Additionally, we hypothesized that the turnover rate of t-DOC would be negatively related to lake HRT as shorter residence time lakes would have a greater fraction of t-DOC turnover rate based on a relatively labile t-DOC source, and the fraction of t-DOC mineralized within the lake would be positively related to lake HRT.

METHODS

We used time series from three lakes with HRTs ranging from 36 to 727 days to examine the effects of extreme precipitation events on lake carbon cycling and the role of HRT in modifying these effects. We identify extreme precipitation events during these time series, estimate the excess t-DOC load and heterotrophy, as well as estimate t-DOC turnover rate and fraction t-DOC mineralized within each lake over each extreme precipitation event. We then explore whether HRT can explain the way that these lakes respond to extreme precipitation events.

Site Description

The three lakes are located at the University of Notre Dame Environmental Research Center (UNDERC; 46°13′N, 89°32′W) in Gogebic County, Michigan. Uplands surrounding all lakes are second-growth mixed hardwood forests. All lakes are within 7 km of each other and the precipitation gage used in this study was centrally located, with East Long (EL) being 2 km away, Morris (MO) 3.2 km away, and Crampton (CR) 4.3 km away from the precipitation gage. East Long is one of the basins of Long Lake, which was split into two basins with an impermeable curtain during the fall of 2012 to naturally increase dissolved organic carbon concentration in the EL basin for a separate whole-lake experiment as described by Zwart and others (2016). The EL time series used for this study was post-manipulation (2013–2014) and EL had reached a new equilibrium in terms of physiochemical parameters. Crampton and MO were studied during this same time period. The lakes differed in watershed area to lake volume (WA:LV), the fraction of the water budget that occurred as evaporation, and numbers of tributary streams flowing to each lake (Table 1). We delineated lake watersheds using a 1/3 arc second digital elevation model and the *Hydrology* tools under the *Spatial Analysis* toolbox from ArcGIS 10.1 (ESRI 2012).

Lake Physiochemical Sampling

To measure water chemistry in the lakes and streams for constituent flux estimates, we collected integrated water samples from the upper mixed layer at the deepest location of each lake and surface water samples from each inlet and outlet weekly to bi-weekly from May to August of 2013 and 2014. We measured DOC on the filtrate of lake water passing through pre-combusted (450°C for 4 hours) GF/F filters using a total organic carbon analyzer (TOC-V; Shimadzu Scientific Instruments). Total phosphorus (TP) was measured by colorimetric assay on a spectrophotometer (Spectronic Instruments, Inc., Genesys 5) after persulfate digestion of unfiltered water (Menzel and Corwin 1965).

Terrestrial-DOC Flux Estimates

We estimated daily t-DOC flux to each lake by estimating the water flux to each lake and multiplying by DOC concentration of each water source. To estimate the water inputs to each lake, we measured stream stage, precipitation amount, groundwater hydraulic heads, and saturated hydraulic conductivities of the groundwater aquifer. See supplementary materials for detailed information of t-DOC flux estimates. We report daily t-DOC inflow on a per lake volume basis with units of mg C (m^3 lake water)$^{-1}$.

We do not include particulate organic carbon (POC) in our analyses; therefore, our estimates of organic carbon loading following storm events are conservative. We simplified the organic carbon budget in our analyses because we have limited data on lake sedimentation rates and no data on areal deposition, which are two significant sources of POC fluxes for lakes. Inlet stream loading is another important POC flux for lakes; however, POC was less than 2% of total organic carbon in all inlet

Table 1. Lake Physiochemical Characteristics Including Watershed Area to Lake Area Ratio (WA:LA), Light Extinction Coefficient (k_D), Dissolved Organic Carbon Concentration (DOC), and Total Phosphorus Concentration (TP)

Lake	Lake volume (m^3)	Lake area (m^2)	Watershed area (m^2)	Max depth (m)	# of Inlets	# of Outlets	WA:LV	k_D (m^{-1})	DOC (mg C L^{-1})	TP (µg P L^{-1})
MO	142,000	59,000	1,122,000	7	3	1	7.90	4.52	18.9	34.3
EL	124,000	32,000	72,000	14	1	1	0.58	2.86	10.6	15.9
CR	1,303,000	259,000	320,000	16	0	1	0.25	0.89	4.8	11.1

streams. Therefore, we are confident that we are capturing a vast majority of organic carbon influx to our lakes despite only considering the dissolved fraction.

Lake Metabolism Estimates

To produce daily estimates of lake metabolism, we measured high-frequency (10 min interval) dissolved oxygen (DO) at a fixed depth in the epilimnion in each lake (YSI 6600 V2 Sonde, YSI Incorporated), temperature profiles using a fixed thermistor chain (Onset HOBO Pendants, Onset Computer Corporation), and meteorological parameters including wind speed, wind direction, air temperature, photosynthetically active radiation, relative humidity, and barometric pressure from a floating platform on West Long (adjacent basin to East Long; Onset HOBO met station, Onset Computer Corporation). All high-frequency data were adjusted for sensor drift at weekly to biweekly intervals. We estimated rates of gross primary production (GPP), respiration (R), and the sum of the two, termed net ecosystem production (NEP = GPP − R), by fitting a maximum-likelihood metabolism model to the high-frequency DO cycles and estimated uncertainties in daily metabolism rates using a bootstrapping routine (metabolism model with uncertainty described by Solomon and others 2013 and Zwart and others 2016). We report metabolism estimates in volumetric units (mg O_2 (L lake water)$^{-1}$ day^{-1}) and we use a 1:1 respiratory quotient of O_2:CO_2 to report metabolism estimates in units of mg C (m^3 lake water)$^{-1}$ for comparison to t-DOC flux.

The free water method can sometimes yield metabolism estimates with high uncertainty on a given day. This likely occurs because the metabolism model does not capture some processes of DO evolution, such as physical entrainment of O_2-rich or -depleted water, which can cause low signal-to-noise ratios (Rose and others 2014). Additionally, single-location estimates are not accurate representations of whole-lake metabolism at the daily scale due to spatial heterogeneity; however, averaging over multiple days for a single-sensor deployment is more representative of whole-lake metabolism (Van de Bogert and others 2012). Because we are interested in whole-lake responses to extreme precipitation events, we smoothed the metabolism estimates using a centered 9-day weighted moving average window with the inverse of the daily coefficient of variation as the weights, and the smoothed daily metabolism data were used in all subsequent analyses. An example of raw

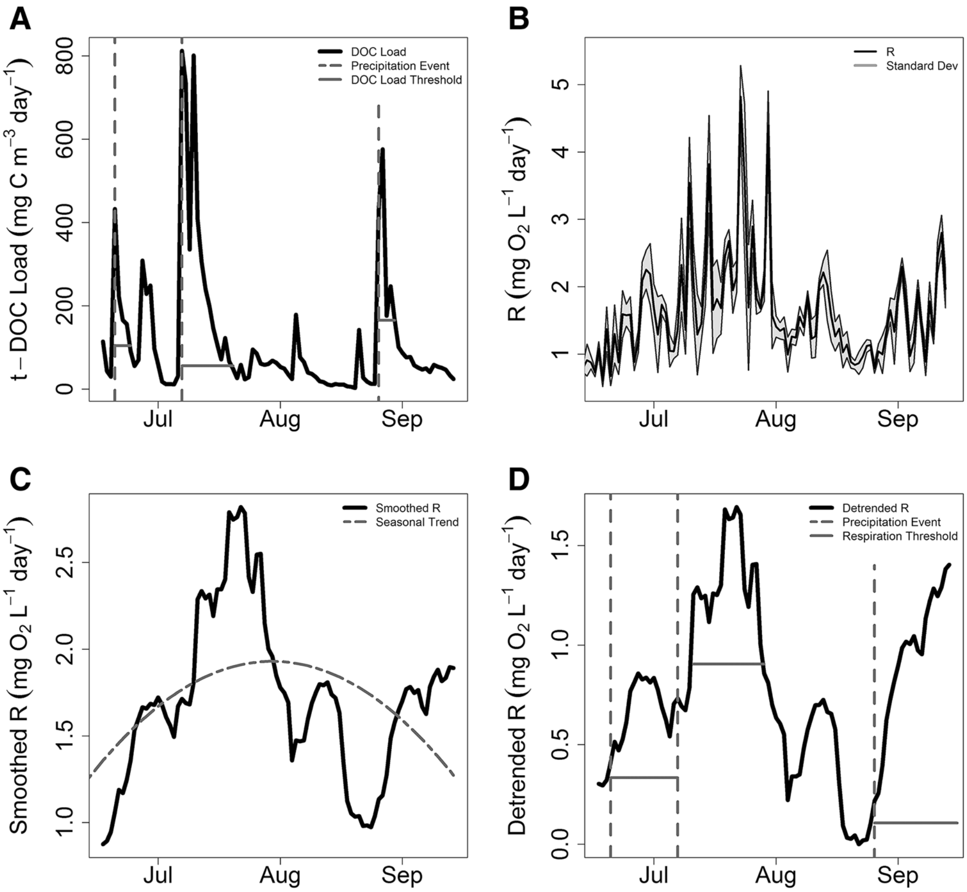


Figure 1. Example of work flow for detecting t-DOC pulse and the lake metabolic response. Data shown are from EL in 2013. (**A**) t-DOC load to EL with *vertical dashed gray lines* indicating the days for which extreme precipitation events occurred. The *horizontal solid gray lines* indicate the threshold which the t-DOC load must exceed before being considered a 'pulse.' (**B**) Lake ecosystem respiration (R) estimates with one standard deviation about the mean (indicated by the *shaded gray area*). (**C**) Seven-day moving average lake ecosystem R with the seasonal trend of R indicated by a quadratic *best fit line* (*dashed gray line*). (**D**) Detrended lake ecosystem R as the moving average R minus the R seasonal trend (quadratic fit in panel c) and standardized positive. The *vertical dashed gray lines* indicate the days for which extreme precipitation events occurred and the *horizontal solid gray lines* indicate the threshold which the detrended moving average R must exceed before being considered a 'response.'

metabolism and uncertainty estimates is shown in Figure 1B, and smoothed metabolism estimates used in the analyses are shown in Figure 1C.

Identification of Precipitation Events and Resulting t-DOC Loads and Metabolic Responses

We defined extreme precipitation events as any day in which the total precipitation exceeded the 95th percentile of daily precipitation over the time series (definition of 'extreme precipitation' similar to Tebaldi and others 2006). We identified nine extreme precipitation events over the time series. However, several of these events occurred in short succession (within 5 days of each other), in which case we used the earliest of the close-occurring events as the initial day of the extreme precipitation event, which reduced the number of events to six. We only use the earliest of the close-occurring events as the effects of the prior extreme precipitation event (for example, t-DOC load, metabolic responses) mask the effects from the later event when events are in such close succession. We used these extreme precipitation events as starting points from which to estimate duration (number of days) and magnitude (mass of carbon per lake volume) of event-derived t-DOC supply to the lake and lake metabolic response.

We estimated the duration and magnitude of t-DOC load and metabolic responses to precipitation events as follows. First, because metabolic responses to extreme precipitation events can be masked by the effects of seasonal trends in light and temperature, we seasonally detrended the smoothed daily metabolism estimates using the best-fit quadratic function (Figure 1C, D). Seasonal detrending did not affect the detection or duration of a t-DOC pulse, so t-DOC flux estimates were not detrended. Next, we set event- and flux-specific thresholds at two standard deviations above the mean t-DOC flux, GPP, and R for five days prior to each extreme precipitation event (Figure 1A, D). We defined the durations of the t-DOC pulse or metabolic response as the number of days for which the t-DOC flux, GPP, or R exceeded their respective event thresholds (Figure 1A, D). Terrestrial-DOC pulse and metabolic response durations were cut off at the beginning of the subsequent extreme precipitation event if the t-DOC pulse or metabolic response lasted that long. We estimated the magnitude of the t-DOC pulse and the GPP and R responses as the total t-DOC flux, GPP, and R exceeding the event threshold, summed across the duration of the event. We refer to these as the excess t-DOC flux, GPP, or R.

The duration of the NEP response following each extreme precipitation event was the number of days between the earliest and latest response date for GPP or R. The excess NEP per event was calculated as the excess GPP plus the excess R. Since our metabolic response detection for GPP and R used a deviation from the mean method, a lake that was always heterotrophic (negative NEP) could have had an extreme precipitation event that produced an autotrophic response and a lake that was always autotrophic (positive NEP) could have had an event that produced a heterotrophic response.

Hydrologic Residence Time, Fraction Mineralized, and t-DOC Turnover Estimates

Hydrologic residence time was calculated for each lake across the entire time series and also for each event. Hydrologic residence time was estimated as the lake volume divided by the sum of water losses (evaporation, outlet stream, and groundwater).

Fraction of t-DOC load mineralized within the lake was estimated for each event as the excess NEP (heterotrophic response) divided by the excess t-DOC load. Traditionally, fraction t-DOC mineralized is estimated as one minus the DOC outflow divided by the DOC inflow, and biological processing is not directly measured (for example, Dillon and Molot 1997). However, we coupled high-frequency t-DOC loads and in-lake metabolism along with examination of carbon cycling during extreme precipitation events that allow direct comparison of t-DOC loads and respiration.

We estimated the turnover rate of t-DOC by rearranging an equation used to estimate t-DOC retention from Brett and others (2012). Rearrangement gave us

$$\sigma = \frac{R \times \rho}{(1 - R)} \tag{1}$$

where σ is the turnover rate of t-DOC (units: day^{-1}); R is the fraction t-DOC mineralized estimated as the excess NEP divided by the excess t-DOC load; and ρ is the flushing rate for each event estimated as $\frac{1}{\text{HRT}_{\text{event}}}$ (units: day^{-1}). This method for estimating the turnover rate of t-DOC at the ecosystem scale utilizes measurements of biological processing (excess NEP) rather than inferring biological processing from the difference between inflowing and outflowing DOC. Furthermore, this method is useful in non-steady-state systems (for example, following extreme precipitation events) because it does not require an assumption that the change in storage of carbon within the ecosystem is zero.

Statistical Analysis

We were interested in the effects of extreme precipitation events on t-DOC flux and ecosystem metabolism and in the role of HRT in modifying these effects. We hypothesized that lakes would respond synchronously to precipitation events, and to test for this synchrony between lakes, we ran cross-correlation tests using the ccf function in the R *stats* package. We ran cross-correlation tests with a lag of zero between each lake on both the smoothed daily metabolism and daily t-DOC flux estimates.

We asked whether lake HRT plays a role in how these lakes responded to the extreme precipitation events. However, due to a low sample size (three lakes), we only compared mean and standard deviations of various metrics of interest across lakes. We note that, in comparing fraction t-DOC mineralized and t-DOC turnover to lake HRT, apparent spurious relationships could arise because hydrologic discharge is used in the denominator of HRT (lake volume divided by out flowing water) and fraction mineralized (heterotrophy divided by the product of t-DOC concentration and inflowing water), and subsequently fraction mineralized is used in the estimate of t-DOC turnover. We argue that these relationships are useful for understanding lake carbon cycling through time and across space and uphold criteria for legitimate relationships as described by Prairie and Bird (1989). Specifically, we argue that the physical constraints of hydrology on lake carbon cycling, and the potential utility of the relatively simple metric of HRT for scaling lake carbon cycles regionally legitimizes our examination of the relationships between HRT and these ecosystem-scale metrics of carbon processing. We used the R statistical package for all carbon budget calculations, lake metabolism model fitting, and subsequent analyses (R Core Team 2014). Data and code used in these analyses are available on GitHub at https://github.com/jzwart/PulseLags.

RESULTS

Seasonal Synchrony and Magnitude of t-DOC and Metabolic Fluxes

Groundwater contributed minimally to MO both in terms of water and carbon and contributed zero water and carbon in the lakes that seeped to groundwater, EL and CR (supplements and Table 2). The importance of precipitation to hydrologic inflows varied among the lakes, but contributed minimally to total t-DOC load across all lakes. Stream inflow contributed a majority of the hydrologic inflow for MO and a vast majority of the t-DOC load in both MO and EL, while shallow subsurface flow contributed a majority of water and carbon flux to CR, as it has no surface inflow.

Daily t-DOC loads and metabolic rates were significantly, positively correlated among lakes, showing that regardless of their hydrologic characteristics, these lakes respond synchronously to seasonal and daily drivers like climate and weather (Table 3). The magnitude of these important carbon fluxes, however, varied greatly across lakes with the highest carbon fluxes occurring in the shortest HRT lake and the lowest carbon fluxes occurring in the longest HRT lake (Table 4; Figures 2, 3, 4A).

We identified six extreme precipitation events across the time series that reflect episodic and drastic changes in lake hydrologic regimes. Terrestrial-DOC loads induced by these extreme precipitation events lasted 37% (MO), 25% (EL), and 10% (CR) of the time series' extent and contributed 58% (MO), 56% (EL), and 45% (CR) of the total t-DOC load over the time series.

Terrestrial-DOC and Metabolic Response to Extreme Precipitation Events

The mean and variance of the t-DOC load and heterotrophic responses across precipitation events declined with increasing lake HRT (Figure 4A; Table 4). On average, the excess t-DOC loads in

Table 2. Percent Contribution in Terms of Hydrologic Inflow and Terrestrial Dissolved Organic Carbon Inflow (t-DOC) to Each Lake from Groundwater, Precipitation, Inlet Streams, and Shallow Subsurface Flow

	Groundwater	Direct precipitation	Inlet stream	Shallow subsurface
% Hydrologic contribution				
MO	0.5	5.4	94.1	<0.1
EL	0.0	27.5	34.3	38.1
CR	0.0	46.5	0.0	53.4
% t-DOC contribution				
MO	0.3	0.7	99.0	<0.1
EL	0.0	2.5	71.6	25.9
CR	0.0	10.3	0.0	89.7

Table 3. Correlation Coefficient for Terrestrial Dissolved Organic Carbon Flux (t-DOC), Gross Primary Production (GPP), Respiration (R), and Net Ecosystem Production (NEP) Between Each Lake Combination

	t-DOC	R	GPP	NEP
EL & MO	0.84	0.53	0.50	0.57
EL & CR	0.89	0.40	0.41	0.53
MO & CR	0.63	0.51	0.45	0.74

All lakes were significantly correlated with each other for t-DOC flux and every metabolic metric.

Table 4. Mean Seasonal Rates of Terrestrial Dissolved Organic Carbon Flux (t-DOC), Gross Primary Production (GPP), Respiration (R), Net Ecosystem Production (NEP), and Hydrologic Residence Time (HRT) for Each Lake

	t-DOC (mg C m^{-3} day^{-1})	GPP (mg C m^{-3} day^{-1})	R (mg C m^{-3} day^{-1})	NEP (mg C m^{-3} day^{-1})	HRT (days)	t-DOC (mg C m^{-3} event^{-1})	Heterotrophy (mg C m^{-3} event^{-1})
MO	737.6	596.4	877.2	−280.8	36	9080 (6328)	2605 (2975)
EL	121.4	317.9	552.5	−234.6	296	1844 (1594)	936 (1392)
CR	22.4	96.8	119.4	−22.5	727	321 (272)	53 (293)

Units of t-DOC load and metabolism are in mg C (m^3 lake water)$^{-1}$ day^{-1}. Also reported are the mean and standard deviation (in parentheses) of excess terrestrial dissolved organic carbon (t-DOC) and excess NEP (heterotrophy) in response to extreme precipitation events, where the units are in mg C (m^3 lake water)$^{-1}$ event^{-1}.

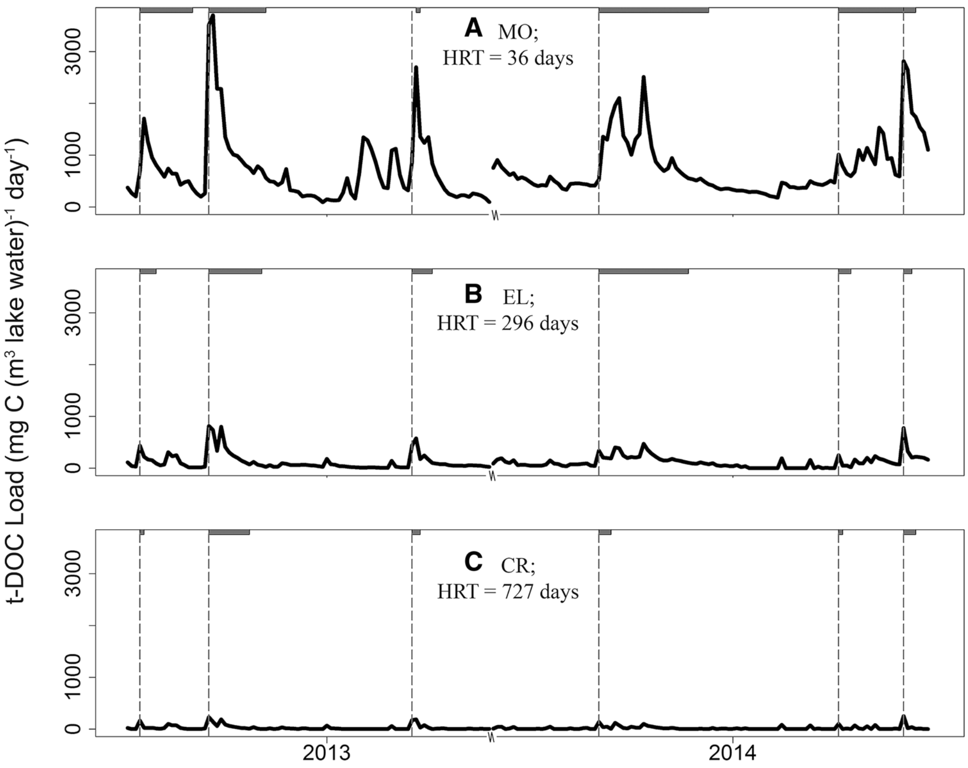


Figure 2. Time series of t-DOC load to (**A**) MO, (**B**) EL, and (**C**) CR. Extreme precipitation events are indicated by *vertical dashed gray lines* and the *horizontal gray bars* at the *top* of each panel indicate the duration of the t-DOC pulse. Two sampling seasons of data are shown, June 17 to September 14 for 2013 and June 1 to September 16 for 2014.

MO and EL were, respectively, 42 and 7 times greater than in CR, and MO had an excess t-DOC load 8 times greater than in EL. The magnitude of the heterotrophic response to precipitation events also varied among lakes, although this variation was smaller than the variation in t-DOC load. On average, the heterotrophic response in MO and EL was, respectively, 11 and 6 times greater than in CR, and MO had a heterotrophic response 3 times greater than in EL (Figure 4A; Table 4). The variance (expressed as standard deviation in Table 4) of t-DOC load and heterotrophy across the extreme precipitation events scales with the mean as the coefficient of variation (CV) for t-DOC load and heterotrophy were fairly consistent across lakes. The CV for t-DOC load was 0.70, 0.86, and 0.85 for MO, EL, and CR, respectively, and the CV for heterotrophy was 0.96, 0.67, and 0.80 for MO, EL, and CR, respectively.

Maximum metabolic rates in response to extreme precipitation events (maximum metabolic rate during response period minus event- and flux-specific threshold) were comparable to the maximum difference of the seasonal metabolic response (maximum minus minimum metabolic rate of the quadratic best-fit equation). On average, the R responses during events were 94, 99, and 43% of the maximum difference of the seasonal R response for MO, EL, and CR, respectively. And on average, the GPP responses during events were 33, 130, and

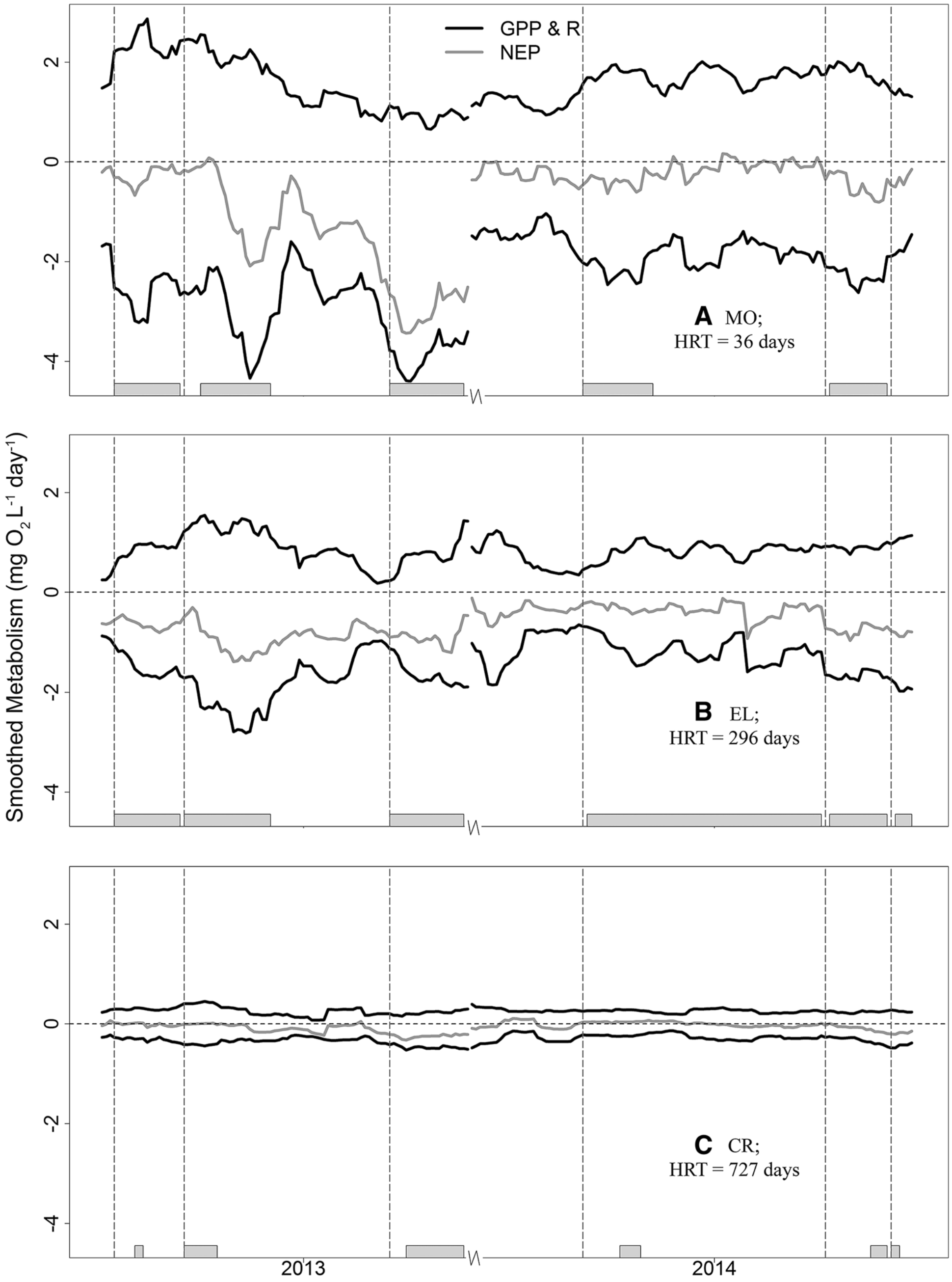


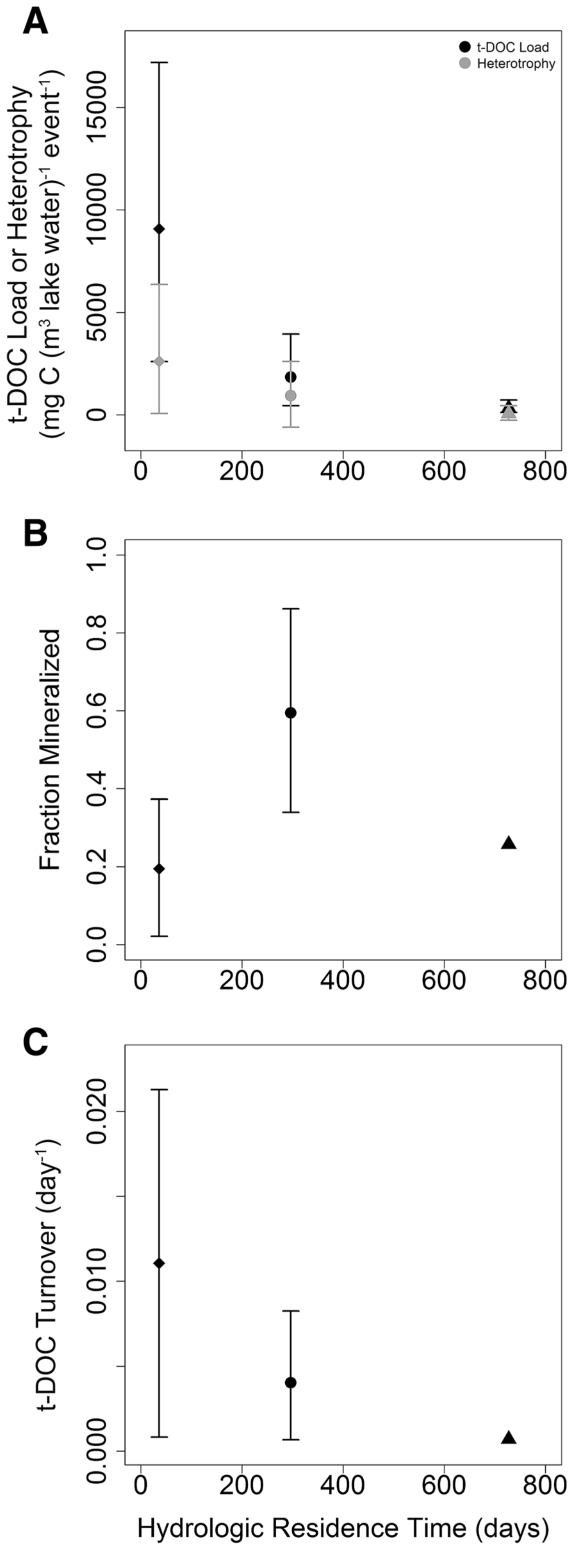
Figure 3. Smoothed metabolism data for (**A**) MO, (**B**) EL, and (**C**) CR. *Black lines* represent GPP (positive values) and ecosystem R (negative values). Net ecosystem production (NEP) is indicated by the *light gray line* and is the addition of GPP and R. Two sampling seasons of data are shown, June 17 to September 14 for 2013 and June 1 to September 16 for 2014. *Vertical gray dashed lines* indicated the extreme precipitation events and the *horizontal gray bars* at the *bottom* of each panel indicate the duration of the NEP response. The 6th and final extreme precipitation event did not elicit a response in MO, so there is *no gray bar* for this event.

54% of the maximum difference of the seasonal GPP response for MO, EL, and CR, respectively. This indicates that the magnitude of metabolic responses to extreme precipitation events was on par with the seasonal metabolic trends.

Fraction t-DOC Mineralized and Turnover Rate of t-DOC

Of the eighteen lake events, there were four for which the fraction of the excess t-DOC load that was mineralized exceeded one (for example, excess NEP was greater than excess t-DOC load), and five which produced autotrophic responses. For the other nine events for which the fraction mineralized was between zero and one (excess NEP was heterotrophic and less than excess t-DOC), on average MO had the lowest fraction mineralized (0.195), EL had the highest fraction mineralized (0.594), and CR was intermediate (0.258) (Figure 4B). The CR estimate was based on only one event.

For lake events that had a fraction mineralized between zero and one, we estimated a mean DOC



◀**Figure 4.** (**A**) Total excess t-DOC load (*black*) and excess lake heterotrophy (*gray*), (**B**) fraction mineralized of the t-DOC load, and (**C**) turnover rate of t-DOC plotted as a function of lake HRT. *Shapes* represent the mean rate or fraction mineralized for each lake (*MO* = diamonds, *EL* = circles, *CR* = triangles) with the 95th and 5th quantiles of the events. The fraction mineralized is calculated as the excess NEP divided by the excess t-DOC load. Not all events are included in panels b and c as some events induced autotrophy (n = 5) or had a fraction mineralized greater than one (n = 4).

turnover rate of 0.007 days^{-1} and a range from 0.0004 to 0.0214 days^{-1} across all lakes. There was over an order of magnitude difference in DOC turnover among lakes as the mean DOC turnover rate by lake was 0.0111, 0.0040, and 0.0007 days^{-1} for MO, EL, and CR, respectively (Figure 4C).

DISCUSSION

Terrestrial-DOC Load in Response to Extreme Precipitation Events

We observed patterns in t-DOC loads and lake heterotrophy that were consistent with strong effects of lake HRT at both the extreme precipitation event and seasonal scale. Terrestrial-DOC load was much higher in the shortest HRT lake at the seasonal scale (Figure 2), which echoes previous studies examining annual to supra-annual time scales of terrestrial carbon loading to lakes (del Giorgio and Peters 1994; Dillon and Molot 1997; Hanson and others 2011; Brett and others 2012). We show that this relationship is upheld for t-DOC load responses to extreme precipitation events (Figure 4A), indicating that predicted increases in the frequency and intensity of extreme precipitation events (Tebaldi and others 2006; Westra and others 2014) will heterogeneously affect t-DOC load to lakes subject to the same local precipitation events. Because the variance in t-DOC load in response to extreme precipitation events scales with the mean (for example, similar coefficient of variation across our lakes), our data suggest that lakes with shorter HRT are likely most susceptible to change in t-DOC loading in response to intensity of precipitation events. This patterning means that potential ‘hot spots’ during ‘hot moments’ (Vidon and others 2010) of t-DOC load could be identified if the relatively simple metric of lake HRT was known for lakes across a landscape.

These event-based t-DOC loads were a significant portion of the seasonal t-DOC flux, contributing 45–58% of seasonal t-DOC load to our lakes. Carpenter and others (2015) observed similar patterns with phosphorus (P) loads to a north-temperate lake, where on average 29 days per year accounted for 74% of annual P load. They showed that a three-part gamma distribution (for low, intermediate, and high P loads) best described the daily P loads to their north-temperate lake, and increases in high P load days (more draws from the third component of the three-part gamma distribution; for example, more extreme precipitation event days) greatly increased the P load to the lake. Similarly, increases in even just a few high t-DOC load days induced by extreme precipitation events could drive a large increase in the seasonal t-DOC load to lakes. Additionally, the shape of the daily t-DOC load distribution may be dependent on lake hydrologic characteristics such as HRT (Figure 2). However, daily t-DOC load distributions for many more lakes are needed to infer any general relationships between t-DOC load distributions and lake hydrologic characteristics, echoing the need for more complete lake organic carbon budgets (Hanson and others 2015), and we posit that there is tremendous value in having daily budgets.

Lake Heterotrophic Response to Extreme Precipitation Events

We show that these large fluxes of t-DOC to our lakes in response to extreme precipitation events induced responses in lake metabolism. Similar to t-DOC load, lake heterotrophic responses were the highest in the shortest HRT lake (Figure 4A). This pattern is supported conceptually since heterotrophy indicates respiration of allochthonous material and short HRT lakes had higher allochthonous flux following extreme precipitation events. Except for two instances, Vachon and del Giorgio (2014) observed inconclusive responses in lake metabolism to storm events in a study of two different lakes due to high day-to-day variability in metabolism estimates. The signal processing of metabolism data that we performed helped identify metabolic responses to t-DOC loading events that can be difficult to detect using noisy daily metabolism estimates. To the best of our knowledge, we are the first to demonstrate the link between t-DOC loading and metabolic responses empirically at such a short-time scale. Indeed, others have pointed to this pattern at longer time scales, such as the positive relationship between 'background respiration' and watershed area to lake volume (an indicator of allochthonous carbon flux; Solomon and others 2013). Lakes are typically sources of carbon to the atmosphere (Cole and others 1994), and our data suggest that the degree to which they are carbon emitters may be influenced by HRT.

Although the responses of both t-DOC load and heterotrophy following extreme precipitation events were negatively related to HRT, the range of t-DOC fluxes across lakes was much larger than for heterotrophic responses (Figure 2, 3, 4A; Table 4). This reduction in the range of carbon flux across lakes is due to the increased role of advection of t-DOC in short HRT lakes. Lakes with short HRT advect a majority of the t-DOC load downstream (del Giorgio and Peters 1994; Hanson and others 2011; Brett and others 2012), indicating that although short HRT lakes have high t-DOC load, much of the load is not in the lake long enough to be mineralized. This HRT-induced tradeoff between load and processing time dampens the potential effect of very large differences in t-DOC load on heterotrophic carbon fluxes in response to extreme precipitation events. This finding has important implications for scaling rates of heterotrophy and fate of t-DOC in lakes across a landscape, just as HRT at the landscape scale was important for predicting the character of organic carbon in Swedish lakes (Müller and others 2013). We suggest that classifying 'lake populations' based on the simple metric of lake HRT may be advantageous when scaling these important lake processes following the framework described by Winslow and others (2014).

Heterotrophic rates are dictated by both the amount of t-DOC transported to lakes as well as the turnover rate of t-DOC within the lake. Previously reported rates of t-DOC turnover varies greatly across lakes (<0.0001–0.0746 days^{-1}; Hanson and others 2011; Watras and others 2015; Catalán and others 2016), with factors such as water temperature, lability of t-DOC, and HRT influencing this rate. Estimated rates of t-DOC turnover in our lakes in response to extreme precipitation events spanned a large portion of the literature range (0.0004–0.0214 days^{-1}), although typically were at the high end of the literature values, and mean rates for our lakes varied over an order of magnitude (0.0007–0.0111 days^{-1}). The rate of t-DOC turnover following extreme precipitation events decreased with increasing lake HRT (Figure 4C), which is consistent with a large-scale analysis across aquatic systems (Catalán and others 2016). For the purpose of explaining the potential influence of HRT on the turnover rate of t-DOC, let us assume a labile fraction of t-DOC (evidence of a labile fraction from Berggren and others 2010; Guillemette and del Giogio 2011; Lapierre and del Giorgio 2014; Zwart and others 2016) that is constant and hold all other factors influencing t-DOC turnover rate constant (for example, water temperature). Lakes with short HRT will receive resupplies of the labile t-DOC fraction more regularly than lakes with long HRT, and thus a greater proportion of the whole-lake t-DOC turnover rate should be based on the relatively labile fraction of t-DOC. We do not have any data on t-DOC source lability across our lakes, so we cannot definitively say that lake HRT is driving the pattern we observed; however, this pattern is consistent with the spatial pattern reported by Catalán and others (2016) and corroborates the mechanism that 'fresher' t-DOC from more terrestrially influenced aquatic systems has higher lability (Lapierre and del Giorgio 2014). The relatively high t-DOC turnover compared to the previous literature could be due to the fact that we estimated t-DOC turnover during periods of shorter lake HRT (after extreme precipitation events); however, we do not have long-term estimates of t-DOC turnover using comparable methods. Indeed, Catalán and others (2016) showed that field studies had faster decay rates compared to bottle incubations for aquatic systems with short HRT (<1 year). They attributed this difference to fast decay processes that are not captured by bottle incubations, which become relatively more important in low HRT systems. When this concept is applied to a system through time, this means that extreme precipitation events, which induce high t-DOC loads, shorter HRT's, and higher t-DOC turnover rates, are 'hot moments' of t-DOC consumptions on the landscape.

Synchronous Lake Carbon Fluxes

Climatic patterns drive ecosystem processes across aquatic environments; however, ecosystem structure (for example, lake size, HRT) may modulate climatic effects on lake ecosystem processes. There is evidence of synchrony among lakes in a region for various lake parameters including DOC concentration and water color (Pace and Cole 2002), annual patterns of pCO_2 (Roehm and others 2009), and lake microbial and zooplankton population dynamics (Rusak and others 1999; Kent and others 2007; Rusak and others 2008). Our study adds to the lake synchrony literature as we are the first to show synchrony in lake heterotrophy and t-DOC loads, and this reiterates the importance of regional climatic and weather patterns in shaping in-lake processes. Despite the synchrony of these important carbon fluxes across our lakes, lake hydrologic characteristics (for example, HRT) interacted with regional weather patterns to set magnitude of these fluxes through time for a given lake (Figures 2, 3,4A). The recognition of the importance of lake-specific characteristics for dictating in-lake processes is increasing (for example, Vachon and del Giorgio 2014; Read and others 2015; Winslow and others 2015), and the regulatory nature of these lake-specific characteristics is fundamental to the hierarchal structure of landscape limnology (Soranno and others 2010). Our data demonstrate that lake HRT may be a fundamental lake-specific characteristic that influences the magnitude of lake t-DOC load and heterotrophy in response to temporal changes in regional weather patterns (for example, extreme precipitation events).

Metabolic Response Detection

Our ability to detect whole-lake metabolic responses to extreme precipitation events was robust to moving average window size as we detected ecosystem metabolic responses for 78–94% of precipitation events across all moving average window sizes investigated (moving average window sizes 1–11 days). Nine- and 11-day moving average window sizes had the highest metabolic detection rate, which were close to the 10-day moving average. Van de Bogert and others (2012) found appropriate for estimating whole-lake metabolic dynamics using single-sensor deployments. The weighted moving average subsumes both process and observation error along with spatial heterogeneity into the smoothed estimates, allowing for more accurate representation of ecosystem-scale metabolism (Van de Bogert and others 2012). Despite smoothing, there were still methodological difficulties in detecting this ecosystem response. For example, four lake events appeared to process more t-DOC than was loaded to the lake by the extreme precipitation event (fraction mineralized greater than one). Quantifying lake carbon flux responses to natural perturbations at short-time scales such as extreme precipitation events is challenging because preceding lake and catchment conditions can be important for how an ecosystem responds to such events, and the low signal-to-noise ratio in carbon fluxes of interest (for example, metabolism) can make detecting a response difficult. Despite such challenges, we are confident that we captured important patterns in lake carbon cycling, especially since our patterns with fraction mineralized and t-DOC load were similar to previous research using independent methods (for example, Curtis and Schindler 1997; Dillon and Molot 1997; Hanson and others 2011; Brett and others 2012).

CONCLUSION

We show that lake HRT strongly influenced t-DOC loading, lake heterotrophy, and the rate of t-DOC turnover following extreme precipitation events. The HRT-induced tradeoff between t-DOC load and processing time gave rise to the tradeoff between fraction t-DOC mineralized and heterotrophic rate. Clearly, HRT plays an integral role in determining lake carbon cycling dynamics. Furthermore, HRT may be a universal metric determining carbon processing rates and terrestrial carbon fates across all aquatic systems. For example, Hall and others (2016) show that, in general, heterotrophic respiration increases with increasing discharge in small- to medium-sized streams and rivers, and Caraco and Cole (2004) show that net heterotrophy generally increases with stream order from small streams (1–2 order) to large rivers (>8 order), thus reinforcing the trend that shorter HRT is related to higher rates of heterotrophy in aquatic systems. Hydrologic residence time is also negatively related to the turnover rate of organic carbon across all inland waters (Catalán and others 2016), and the HRT-induced tradeoff between organic carbon load and processing time seems to also dictate the fraction terrestrial organic carbon mineralized of streams and rivers as stream ecosystem efficiency (analogous to fraction mineralized in our study) increases in lower discharge systems (longer HRT) (Allen and Castillo 2007). We reiterate what many others have suggested, that the relatively simple metric of HRT is extremely useful for scaling aquatic ecosystem processes regionally or even globally at annual and supra-annual time scales (for example, Vollenwieder 1975; del Giorgio and Peters 1994; Curtis and Schindler 1997; Dillon and Molot 1997), and we also suggest that this metric is useful for scaling aquatic carbon processes within lakes through time.

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REFERENCES

Allen DJ, Castillo MM. 2007. Stream ecology: structure and function of running waters. Dordrecht: Springer. pp 313–14.

Berggren M, Ström L, Laudon H, Karlsson J, Jonsson A, Giesler R, Bergström AK, Jansson M. 2010. Lake secondary production fueled by rapid transfer of low molecular weight organic carbon from terrestrial sources to aquatic consumers. Ecol Lett 13:870–80.

Brett MT, Arhonditsis GB, Chandra S, Kainz MJ. 2012. Mass flux calculations show strong allochthonous support of freshwater zooplankton production is unlikely. PLoS ONE 7:e39508.

Caraco N, Cole J. 2004. When terrestrial organic matter is sent down the river: the importance of allochthonous carbon inputs to the metabolism of lakes and rivers. In: Polis GA, Power ME, Huxel GR, Eds. Food webs at the landscape level. Chicago: The University of Chicago Press. p 301–16.

Carpenter SR, Booth EG, Kucharik CJ, Lathrop RC. 2015. Extreme daily loads: role in annual phosphorus input to a north temperate lake. Aquat Sci 77:71–9.

Catalán N, Marcé R, Kothawala DN, Tranvik LJ. 2016. Organic carbon decomposition rates controlled by water retention time across inland waters. Nat Geosci 9:501–6.

Cole JJ, Caraco NF, Kling GW, Kratz TK. 1994. Carbon dioxide supersaturation in the surface waters of lakes. Science 265:1568–70.

Coumou D, Rahmstorf S. 2012. A decade of weather extremes. Nat Clim Change 2:491–6.

Curtis JP, Schindler DW. 1997. Hydrologic control of dissolved organic matter in low-order Precambrian shield lakes. Biogeochemistry 36:125–38.

del Giorgio PA, Peters RH. 1994. Patterns in planktonic P: R ratios in lakes: influence of lake trophy and dissolved organic carbon. Limnol Oceanogr 39:772–87.

Dillon PJ, Molot LA. 1997. Dissolved organic and inorganic carbon mass balances in Central Ontario lakes. Biogeochemistry 36:29–42.

ESRI (Environmental Systems Resource Institute). 2012. ArcMap 10.1. Redlands, CA: ESRI.

Garrabou J, Coma R, Bensoussan N, Bally M, Chevaldonné P, Cigliano M, Diaz D, Harmelin JG, Gambis MC, Kertsting DK, Ledoux JB, Lejeusne C, Linares C, Marschal C, Pérez T, Ribes M, Romano JC, Serrano E, Teixido N, Torrents O, Zabala M, Zuberer F, Cerrano C. 2009. Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. Global Change Biol 15:1090–103.

Gu L, Hanson PJ, Post WM, Kaiser DP, Yang B, Nemani R, Pallardy SG, Meyers T. 2008. The 2007 Eastern US spring freeze: increased cold damage in a warming world? BioScience 58:253–62.

Guillemette F, del Gigio PA. 2011. Reconstructing the various facets of dissolved organic carbon bioavailability in freshwater ecosystems. Limnol Oceanogr 56:734–48.

Hall RO, Tank JL, Baker MA, Rosi-Marshall EJ, Hotchkiss ER. 2016. Metabolism, gas exchange, and carbon spiraling in rivers. Ecosystems 19:73–86.

Hanson PC, Hamilton DP, Stanley EH, Preston N, Langman OC, Kara EL. 2011. Fate of allochthonous dissolved organic carbon in lakes: a quantitative approach. PLoS ONE 6:e21884.

Hanson PC, Pace ML, Carpenter SR, Cole JJ, Stanley EH. 2015. Integrating landscape carbon cycling: research needs for resolving organic carbon budgets of lakes. Ecosystems 18:363–75.

Huntington TG. 2006. Evidence for the intensification of the global water cycle: review and synthesis. J Hydrol 319:83–95.

Kent AD, Yannarell AC, Rusak JA, Triplett EW, McMahon KD. 2007. Synchrony in aquatic microbial community dynamics. Int Soc Microb Ecol 1:38–47.

Lapierre JF, del Giorgio PA. 2014. Partial coupling and differential regulation of biologically and photochemically labile dissolved organic carbon across boreal aquatic networks. Biogeosciences 11:5969–85.

Meehl GA, Arblaster JM, Tebaldi C. 2005. Understanding future patterns of increased precipitation intensity in climate model simulations. Geophys Res Lett 32:L18719.

Menzel DW, Corwin N. 1965. The measurement of total phosphorous in seawater based on the liberation of organically bound fractions by persulfate oxidation. Limnol Oceanogr 10:280–2.

Min SK, Zhang X, Zwiers FW, Hegerl GC. 2011. Human contribution to more-intense precipitation extremes. Nature 470:378–81.

Müller RA, Futter MN, Sobek S, Nisell J, Bishop K, Weyhenmeyer GA. 2013. Water renewal along the aquatic continuum offsets cumulative retention by lakes: implications for the character of organic carbon in boreal lakes. Aquat Sci 75:535–45.

Ojala A, Bellido JL, Tulonen T, Kankaala P, Huotari J. 2011. Carbon gas fluxes from a brown-water and a clear-water lake in the boreal zone during a summer with extreme rain events. Limnol Oceanogr 56:61–7.

Pace ML, Cole JJ. 2002. Synchronous variation of dissolved organic carbon and color in lakes. Limnol Oceanogr 47:333–42.

Prairie YT, Bird DF. 1989. Some misconceptions about the spurious correlation problem in the ecological literature. Oecologia 81:285–8.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from http://www.R-project.org/.

Rahmstorf S, Coumou D. 2011. Increase of extreme events in a warming world. Proc Natl Acad Sci 108:17905–9.

Read EK, Patil VP, Oliver SK, Hetherington AL, Brentrup JA, Zwart JA, Winters KM, Corman JR, Nodine ER, Woolway RI, Dugan HA, Jaimes A, Santoso AB, Hong GS, Winslow LA, Hanson PC, Weathers KC. 2015. The importance of lake-specific characteristics for water quality across the continental United States. Ecol Appl 25:943–55.

Reichstein M, Ciais P, Papale D, Valentini R, Running S, Viovy N, Cramer W, Granier A, Ogée J, Allard V, Auginet M, Bernhofer C, Buchmann N, Carrara A, Grünwald T, Heimann M, Heinesch B, Knohl A, Kutsch W, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Pilegaard K, Pumpanen J, Rambal S, Schaphoff S, Seufert G, Soussana JF, Sanz MJ, Vesala T, Zhao M. 2007. Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: a joint flux tower, remote sensing and modelling analysis. Global Change Biol 13:634–51.

Rocha AV, Shaver GR. 2011. Postfire energy exchange in arctic tundra: the importance and climatic implications of burn severity. Global Change Biol 17:2831–41.

Roehm CL, Prairie YT, Giorgio PA. 2009. The $p\mathrm{CO}_2$ dynamics in lakes in the boreal region of northern Québec, Canada. Global Biogeochem Cycles 23:GB3013.

Rose KC, Winslow LA, Read JS, Read EK, Solomon CT, Adrian R, Hanson PC. 2014. Improving the precision of lake ecosystem metabolism estimates by identifying predictors of model uncertainty. Limnol Oceanogr Methods 12:303–12.

Rusak JA, Yan ND, Somers KM, McQueen DJ. 1999. The temporal coherence of zooplankton population abundances in neighboring north-temperate lakes. Am Nat 153:46–58.

Rusak JA, Yan ND, Somers KM. 2008. Regional climatic drivers of synchronous zooplankton dynamics in north-temperate lakes. Can J Fish Aquat Sci 65:878–89.

Sebestyen SD, Boyer EW, Shanley JB. 2009. Responses of stream nitrate and DOC loadings to hydrological forcing and climate change in an upland forest of the northeastern United States. J Geophys Res 114:G02002.

Solomon CT, Bruesewitz DA, Richardson DC, Rose KC, Van de Bogert MC, Hanson PC, Kratz TK, Larget B, Adrian R, Babin BL, Chiu CY, Hamilton DP, Gaiser EE, Hendricks S, Istvánovics V, Laas A, O'Donnell DM, Pace ML, Ryder E, Staehr PA, Torgersen T, Vanni MJ, Weathers KC, Zhu G. 2013. Ecosystem respiration: drivers of daily variability and background respiration in lakes around the globe. Limnol Oceanogr 58:849–66.

Soranno PA, Cheruvelil KS, Webster KE, Bremigan MT, Wanger T, Stow CA. 2010. Using landscape limnology to classify freshwater ecosystems for multi-ecosystem management and conservation. BioScience 60:440–54.

Stets EG, Striegl RG, Aiken GR. 2010. Dissolved organic carbon export and internal cycling in small, headwater lakes. Global Biogeochem Cycles 24:GB4008.

Tebaldi C, Mayhoe K, Arblaster JM, Meehl GA. 2006. Going to the extremes: an intercomparison of model-simulated historical and future changes in extreme events. Clim Change 79:185–211.

Vollenwieder RA. 1975. Input-output models with special reference to the phosphorus loading concept in limnology. Schweiz Z für Hydrol 37:53–84.

Vachon D, del Giorgio PA. 2014. Whole-lake CO_2 dynamics in response to storm events in two morphologically different lakes. Ecosystems 17:1338–53.

Van de Bogert MC, Bade DL, Carpenter SR, Cole JJ, Pace ML, Hanson PC, Langman OC. 2012. Spatial heterogeneity strongly affects estimates of ecosystem metabolism in two north temperate lakes. Limnol Oceanogr 57:1689–700.

Vidon P, Allan C, Burns D, Buval TP, Gurwick N, Inamdar S, Lowrance R, Okay J, Scott D, Sebestyen S. 2010. Hot spots and hot moments in riparian zones: potential for improved water quality management. J Am Water Resour Assoc 46:278–98.

Watras CJ, Morrision KA, Crawford JT, McDonald CP, Oliver SK, Hanson PC. 2015. Diel cycles in the fluorescence of dissolved organic matter in dystrophic Wisconsin seepage lakes: implications for carbon turnover. Limnol Oceanogr 60:482–96.

Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettignies T, Bennett S, Rousseaux CS. 2012. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nat Clim Change 3:78–82.

Westra S, Fowler HJ, Evans JP, Alexander LV, Berg P, Johnson F, Kendon EJ, Lenderink G, Roberts NM. 2014. Future changes to the intensity and frequency of short-duration extreme rainfall. Rev Geophys 52:522–55.

Winslow LA, Read JS, Hanson PC, Stanley EH. 2014. Does lake size matter? Combining morphology and process modeling to examine the contribution of lake classes to population-scale processes. Inland Waters 5:7–14.

Winslow LA, Read JS, Hansen GJA, Hanson PC. 2015. Small lakes show muted climate change signal in deep-water temperatures. Geophys Res Lett 42:355–61.

Zedler PH, Gautier CR, McMaster GS. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California Chaparral and coastal scrub. Ecology 64:809–18.

Zwart JA, Craig N, Kelly PT, Sebestyen SD, Solomon CT, Weidel BC, Jones SE. 2016. Metabolic and physiochemical responses to a whole-lake experimental increase in dissolved organic carbon in a north-temperate lake. Limnol Oceanogr 61:723–34.