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Quantifying lake allochthonous organic carbon budgets using a simple equilibrium model

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Abstract

We quantify the allochthonous organic carbon (OC) budgets for seven north temperate lakes, using diverse information about their land cover, hydrology, and limnological characteristics. We develop a simple equilibrium model within a Bayesian framework that exploits the differences among the lakes to estimate three key rates: aerial loading (A_{OC}) and wetland loading (W_{OC}) from adjacent ecosystems and whole-lake mineralization of OC (RDOC). Combined with observational data, these rates allow for estimates of the total OC loads, mineralization, and sedimentation within lakes and export to downstream ecosystems. A_{OC} was 1.15 g C m^{-1} (shoreline) d^{-1}, W_{OC} ranged from 0.72 to 3.00 g C m^{-1} (shoreline) d^{-1}, and RDOC, normalized to 20°C, ranged from 0.00083 to 0.0015 d^{-1}. Total loads ranged from about 5 to 55 g C m^{-2} yr^{-1}. Ecosystems immediately adjacent to lakes accounted for one-half or more of total OC loads for some lakes. Whether a lake processed and stored more allochthonous OC than it exported depended primarily on hydrologic residence time. Our equilibrium model provides a parsimonious approach to quantifying allochthonous OC budgets in lakes with relatively minimal baseline data.

Lakes have been identified as important sites of carbon cycling at local (Jonsson et al. 2001, 2003; Sobek et al. 2006) as well as regional (Christensen et al. 2007; Buffam et al. 2011) and continental and global (Cole et al. 2007; Tranvik et al. 2009) scales. Organic carbon (OC) storage in lakes is substantial, especially in northern latitudes where lake sediments, along with peat, can account for ~ 38% of total OC storage in the landscape (Buffam et al. 2011). Lakes also are mineralization sites for OC (Dillon and Molot 1997; Jonsson et al. 2001; Pace et al. 2004). The predominance of CO_2 supersaturation in lakes (Cole et al. 1994; Sobek et al. 2003; Roehm et al. 2009) has been attributed primarily to mineralization of OC in excess of primary production (Cole et al. 1994) and in some cases additionally to export of CO_2 from watersheds to lakes via groundwater or streams (Kling et al. 1991; Roehm et al. 2009). Furthermore, lakes are conduits and sources of OC for downstream freshwater and marine ecosystems (Weyhenmeyer et al. 2012). Understanding the roles that lakes play in the landscape and predicting how lakes might alter local- to global-scale carbon cycles requires that we account for the major pools and fluxes.

Although the pools of key constituents of the carbon budget are easily measured in some lakes, the fluxes tend to be more problematic. For example, large surveys of lake CO_2 concentration in lakes have indicated lakes as net sources of inorganic carbon to the atmosphere (Cole et al. 1994; Sobek et al. 2003; Roehm et al. 2009). Lake–atmosphere exchange of CO_2 can be measured and upscaled with some uncertainty or estimated from surface-water partial pressure, but this measurement of net CO_2 exchange does not translate in any simple way into within-lake process rates. Some fluxes, such as fluvial inputs and outputs, are easily measured. For example, a survey of Scandinavian streams quantifies an important component of lake dissolved organic carbon (DOC) budgets, providing insights into organic carbon (OC) half-life in broad terms (Weyhenmeyer et al. 2012). Other fluxes are more difficult to measure, such as aerial OC loads to lakes, groundwater fluxes, and contributions of OC by wetlands adjacent to lakes. The latter may be especially difficult in bog lakes, where easily identifiable flow paths between the lake and surrounding wetland do not exist. Finally, in-lake mineralization as an OC flux is difficult to quantify, and most studies have relied on laboratory experiments for this key ecosystem rate (Hanson et al. 2011).

An integrative approach to understanding the role of lakes in landscape C cycling that considers simultaneously major pools and fluxes of OC in lakes has two major challenges. For most lakes, we do not have good information on the actual loads because they are difficult to measure. We do not have well-constrained ecosystem-scale estimates of allochthonous OC mineralization and sedimentation rates. Unlocking these two components is key to quantifying C budgets and has broad implications for understanding lake trophic state (i.e., autotrophy vs. heterotrophy) and the roles that lakes play as storage and transformation sites of OC within the landscape. Fortunately, there are two factors that make the problem more tractable. The allochthonous OC budget may be represented by few processes, and we have useful albeit partial information about important fluxes.

Quantifying key rates and reducing their uncertainties at the ecosystem scale could benefit from simple lake carbon

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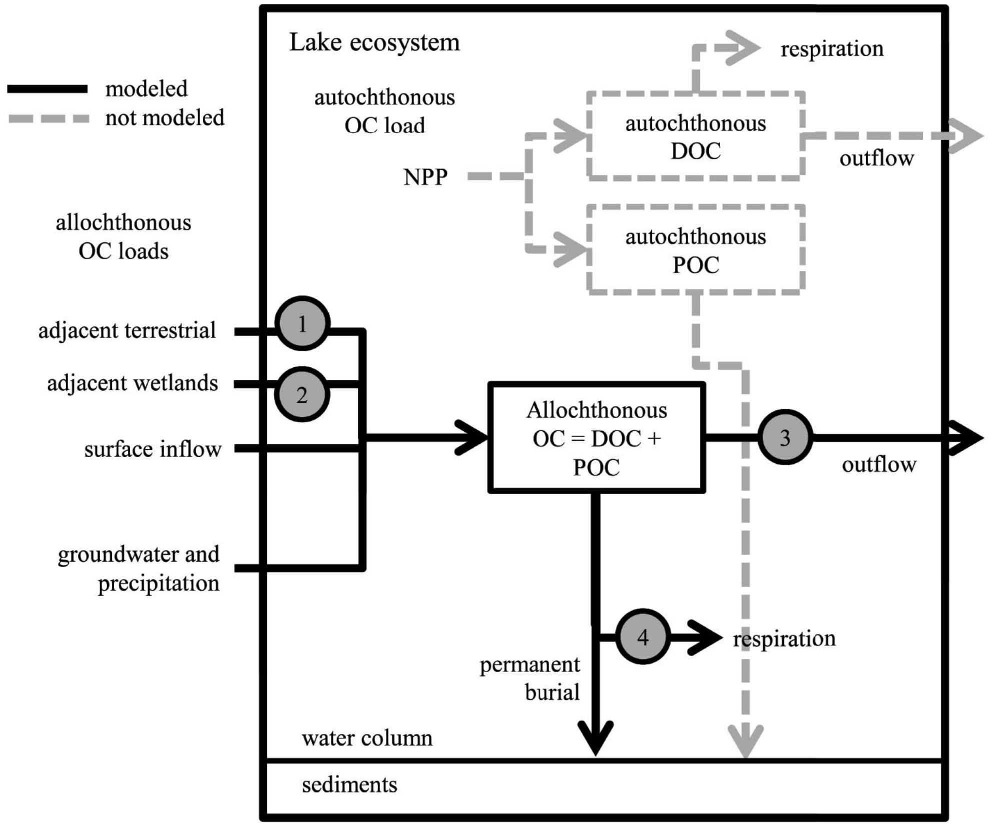

Stochastic components of the model (circles) influence key fluxes (*see* Eqs. in Table 3):

1. A_{OC}: Aireal loading rate (g m^{-1} (canopy shoreline) yr^{-1})
2. W_{OC}: Loading from adjacent wetlands (g m^{-1} (wetland shoreline) yr^{-1})
3. RT: Hydrologic residence time (yr)
4. RDOC: Respiration of DOC (yr^{-1})

Fig. 1. Ecosystem pools and fluxes of organic carbon in this study. Solid lines indicate allochthonous components of the model, and dashed lines are allochthonous and autochthonous components calculated from literature values or other data and included for comparison purposes. Model components that have a stochastic parameter are indicated in numbered circles. Even though respiration and burial are identified here, burial is simply assumed to be a fixed proportion of respiration.

cycling models, of which there are surprisingly few. Although many processes contribute to carbon cycling in lakes, the budget may be simplified at the annual time scale by considering only a few key components of the allochthonous portion (Hanson et al. 2011), that is, following OC, which is loaded to the lake from the watershed rather than produced in situ by primary production. In mass balance terms, we can state the dominant processes controlling lake allochthonous OC budgets as loads, within-lake transformations, within-lake storage, and export. In Fig. 1, we present a simplified allochthonous OC budget that includes pools (boxes) and fluxes (arrows) for a northern-latitude lake. There are but a few pathways by which most OC can enter the lake, and these include aerial from adjacent terrestrial systems (primarily as leaf litter and pollen), from adjacent wetlands, from precipitation and groundwater, and from surface water. These sources include DOC and particulate OC fractions, both of which contribute to the lake OC pool. There are three possible fates for this OC: export via hydrologic pathways, permanent burial in lake sediments, and mineralization to inorganic carbon. As noted above, there are observational data that would inform estimates of certain fluxes as well as literature values for certain process rates. The challenge is in combining the knowledge with observational data in a modeling framework that quantifies the central tendencies and uncertainties in the aforementioned OC terms to provide a parsimonious and generalizable model for allochthonous OC cycling in lakes.

In this study, we construct a simple mass balance model for allochthonous OC in lakes, validated with data from the North Temperate Lakes Long Term Ecological Observatory Network (NTL-LTER), to quantify key OC fluxes and their uncertainties. We embed the model in a Bayes-Net framework to combine observational data and existing ecological knowledge with more precisely

Table 1. Lakes and their characteristics. Column headers: perimeter (P); mean depth (Z); hydrologic residence time (RT); precipitation and all hydrologic inflow (Q_{In}), outflow (Q_{Out}), and evaporation (Evap); proportion of inflow as groundwater (GWP), stream-water (SWP), and precipitation (PP); temperature (T); dissolved organic carbon (DOC); total phosphorus (TP); mean annual organic carbon concentration in stream-water inflow (SW_{OC}); proportion of shoreline as canopy (PC) and proportion of shoreline as wetland (PW). T, DOC, and TP are hypsometrically weighted annual means. na = not applicable.

Name	Area (km^2)	P (km)	Z (m)	RT (yr)	Q_{In} (m yr^{-1})	Q_{Out} (m yr^{-1})	Evap (m yr^{-1})	GWP	SWP	PP	T (°C)	DOC (mg L^{-1})	TP (μg L^{-1})	SW_{OC} (mg L^{-1})	PC	PW
Allequash Lake* (AL)	1.12	5.9	3.2	0.73	4.38	3.67	0.70	0.31	0.55	0.14	10.5	3.5	15.7	3.14	0.61	0.48
Big Muskellunge (BM)	3.963	16.1	7.5	5.10	1.47	0.82	0.66	0.28	0.04	0.68	10.5	2.9	8.6	na	0.89	0.07
Crystal Bog (CB)	0.005	0.25	1.7	1.42	1.20	0.65	0.55	0.10	0.00	0.90	10.6	9.5	16.5	na	0.00	1.00
Crystal Lake (CR)	0.367	2.3	10.4	11.0	0.94	0.26	0.71	0.07	0.00	0.93	10.6	1.9	5.6	na	0.60	0
Sparkling Lake (SP)	0.640	4.3	10.9	8.88	1.23	0.61	0.64	0.05	0.19	0.76	10.6	3.3	7.2	na	0.95	0
Trout Bog (TB)	0.011	0.37	5.6	4.67	1.20	0.65	0.55	0.10	0.00	0.90	10.0	22.0	26.4	na	1.00	1.00
Trout Lake (TL)	16.08	25.9	14.6	5.28	2.77	1.96	0.81	0.19	0.46	0.35	9.8	2.9	6.9	5.8	0.76	0

* Allequash values represent the upstream basin only.

estimated ecosystem rates and fluxes. With this approach, we address four main questions: (1) What is the magnitude and source of the allochthonous OC load to lakes? (2) What are the mineralization rates of OC, and do they differ among lakes? (3) What are the implications for whole-lake OC budgets? (4) What do the results tell us about regional-scale C processing?

Methods

Our goals in this analysis are to estimate major components of the allochthonous OC budgets and their uncertainties for seven lakes that are part of the NTL-LTER program. Of particular interest is the value for ecosystem mineralization. Given that uncertainty can be high for many of the observations as well as for ecosystem rate estimates, we have chosen a Bayes-Net to sample distributions and estimate mean values as well as uncertainties for key fluxes and associated rates. Furthermore, we have some information from the literature about key rates, and that information can be combined with the observational data within the Bayes-Net framework to help inform the parameter estimates. It is important to note that the autochthonous parts of the budget are not modeled for sake of simplicity.

The lakes—The seven study lakes are part of the NTL-LTER program and are located in northern Wisconsin (Magnuson et al. 2006). A rich literature on these lakes, as well as contextual information and observational data, can be found at http://lter.limnology.wisc.edu. The seven lakes cover broad ranges in a number of characteristics relevant to carbon cycling (Table 1), including area, depth, hydrologic residence time, and carbon concentration. Two lakes, Allequash (AL) and Trout (TR), have substantial fluvial sources of OC. One lake, Crystal (CR), is hydrologically perched and includes only aerial inputs of OC. Two lake characteristics were determined from land cover data: the proportion of shoreline in canopy (PC) and in wetland (PW). Low values for PC are particularly noticeable in CR, which is surrounded by beach and Crystal Bog (CB), which is surrounded by relatively open peatland (Fig. 2). Trout Bog (TB) is another notable example, as it is surrounded by a forested peatland. For simplicity and naming consistency, we refer to TB and CB as "bog lakes." All data for these lakes were obtained from the NTL-LTER public database, except stream-water concentration of OC (SW_{OC}) and lake hydrologic budgets, which were provided by the U.S. Geological Survey (Hunt et al. 2013). Lake values for temperature (T), DOC, and total phosphorus (TP) in Table 1 are hypsometrically weighted mean annual values.

We have assumed that most of the observed lake DOC is of allochthonous origin (Wilkinson et al. 2013). Nonetheless, the time series for the nonbog lakes show a rapid summer increase (Fig. 3) coincident with increases and decreases in phytoplankton biomass, resulting in a 10–20% increase in bulk DOC during summer. In autumn, DOC decreases rapidly to its former baseline levels, such that the time series is near stationary at long time scales. We cannot account for this rapid rise and fall of DOC through load or

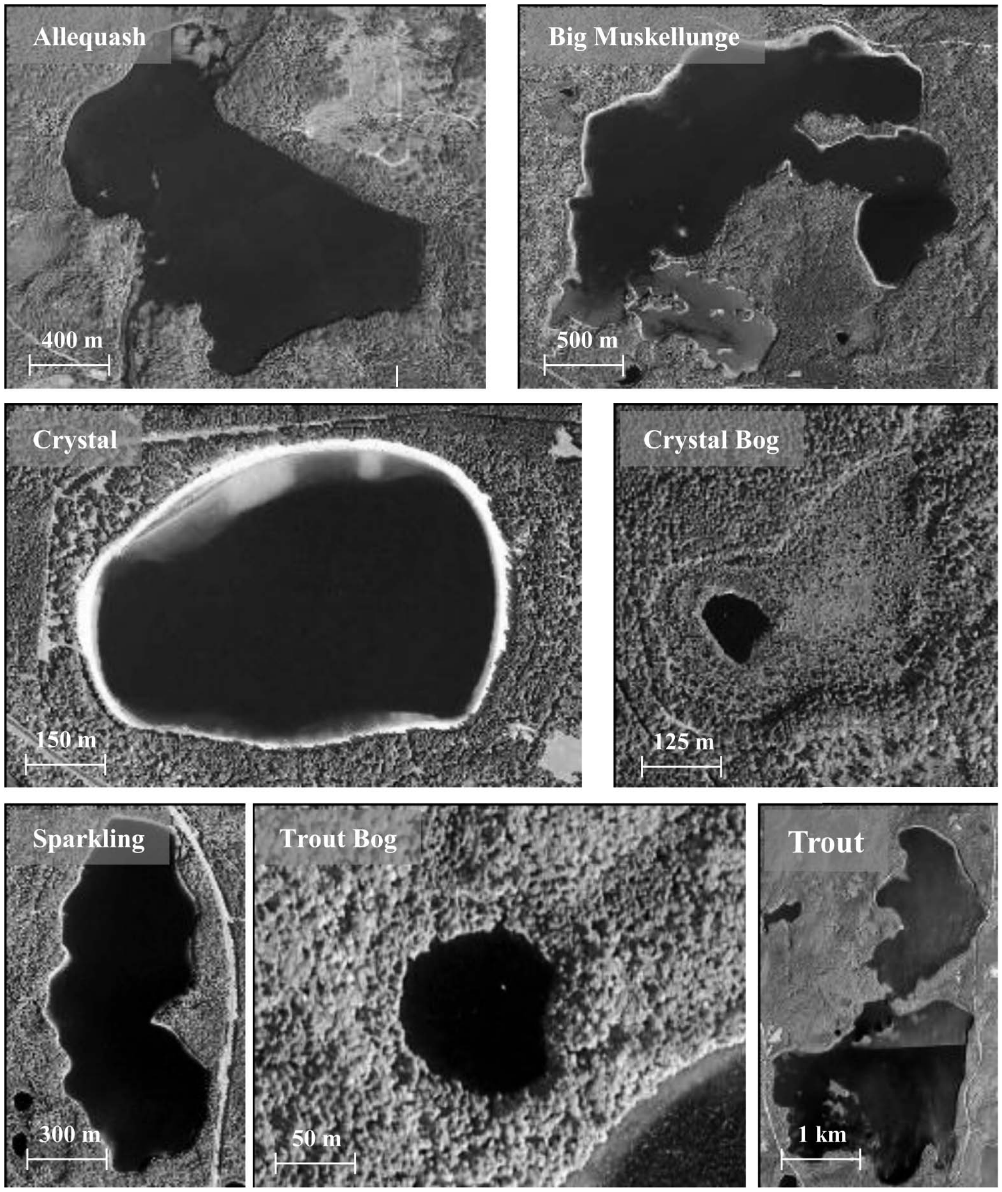

Fig. 2. Aerial view of the seven study lakes. Note the wide beach in Crystal Lake and the absence of nearshore canopy in Crystal Bog. (Images from Google Maps.)

export processes. Surface-water loading seems unlikely. Mean hydrologic residence time across lakes is 5.3 yr, and therefore, in the quarter in which lake DOC rises by about 20%, there is an exchange of only 5% of the water, only a small portion of which is surface water (Table 1). It also seems unlikely that leaf litter would account for the rapid rise for two reasons. The peak DOC is in summer, well after any spring pulse resulting from the previous autumn's leaf litter. There is a rapid decline in DOC in late summer to early autumn that mirrors the increase, yet this occurs as the water is cooling and temperature-dependent respiration is decreasing. In light of these arguments, we assume that the summer rise is of autochthonous origin. In Fig. 4, we show through linear regression that the mean annual DOC amplitude for each lake relates strongly to TP concentration ($R^2 = 0.94$; $p < 0.005$), with a y-intercept near zero, further supporting our assumption that the annual amplitude corresponds to primary productivity, or autochthonous DOC and not allochthonous DOC. For the bog lakes, the peak DOC occurs primarily during winter. For CB, which is shallow, this could be explained by cryoconcentration during ice cover. For TB, we have no good explanation. We removed the annual autochthonous component of the DOC signal as follows. A Fourier transform was fit to each lake independently, and the frequency representing the annual scale was removed. The result is a nearly stationary long-term signal with little pattern. For each lake, we calculated mean DOC of allochthonous origin (DOC_{alloch}) as the mean of the 20-yr time series after the annual signal was removed.

The hydrology for the lakes, including inflow, outflow, evaporation, and residence time, is given in Table 1. Values

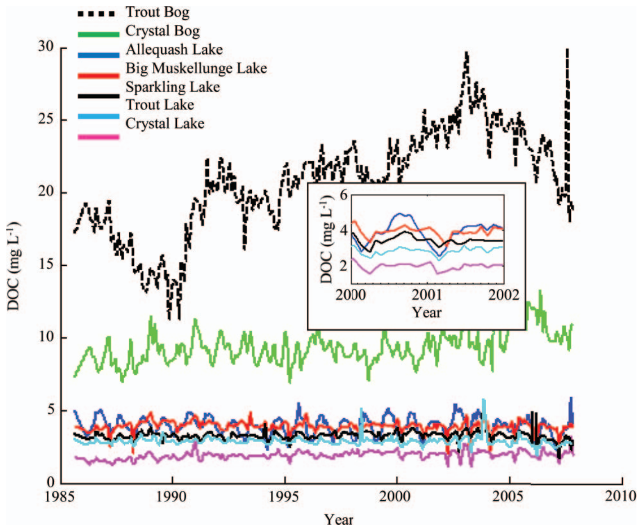

Fig. 3. Time series of DOC for each lake. Inset shows annual DOC peak occurs in months 6 and 7 for nonbog lakes. Lake name abbreviations as in Table 1.

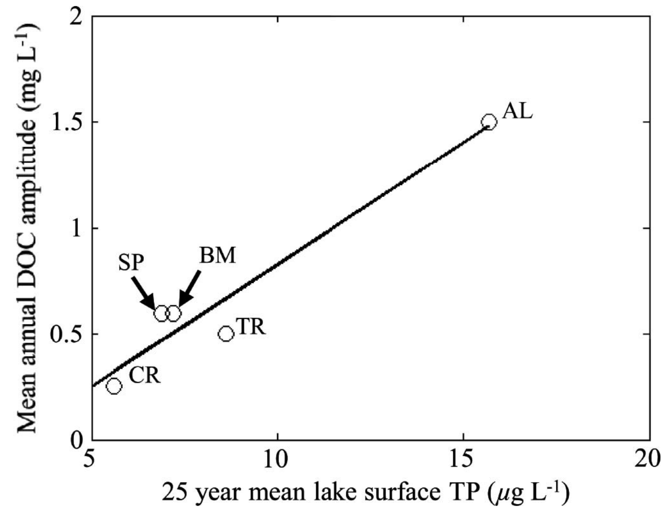

Fig. 4. Mean of the annual DOC amplitude for the five nonbog lakes vs. TP. Line is the fitted linear regression.

were provided by the U.S. Geological Survey (USGS; Hunt et al. 2013). DOC export is calculated as the product of the hydrologic outflow and the lake DOC concentration (Table 2, Eq. 4). Hydrologic outflow has been calculated by the USGS, taking into account evaporative losses (Table 1).

We do not have OC burial data for these lakes. Therefore, the sediment OC pool is not modeled explicitly. Rather, we assume the OC flux to the sediments to be proportional to the mineralization rate of DOC_{alloch}, and we elaborate on this assumption in the following section.

The model—The goal is to explain the differences among lakes in DOC_{alloch}, which is a single value for each lake representing the long-term mean concentration, with a relatively simple model. The model is the steady-state solution to a simple differential equation (Table 2, Eq. 1). The load to a lake is assumed to be a distribution with a mean value derived from the sum of aerial input ($Load_{Aireal}$) and wetland input ($Load_{Wetland}$) from the lake perimeter (P; Table 1), groundwater inflow ($Load_{GW}$) and precipitation (($Load_P$)), and stream-water inflow ($Load_{SW}$; (Table 2, Eq. 10). Precipitation concentrations of DOC are relatively low at approximately 2 mg C L^{-1} (Hanson et al. 2004). Our approach to modeling groundwater concentrations of DOC is articulated below. The mass load of carbon from $Load_P$ (Eq. 10e), $Load_{GW}$ (Eq. 10c). and $Load_{SW}$ (Eq. 10d) is the product of their respective concentrations and their inflow volumes (Table 1). The perimeter load is assumed to be the sum of three components, discriminated by the proportion of shoreline that is canopy and the proportion of shoreline that is wetland. The first two are the shoreline aerial loads (Eq. 10a), which include the product of the aerial loading factor (A_{OC}), the perimeter (P), and the proportion canopy (PC) plus a nominal load ($0.2 \times A_{OC}$) for shoreline without canopy ($1 - PC$; Preston et al. 2008). A_{OC} is discussed in more detail below. The third shoreline load is from adjacent wetlands (Eq. 10b). We have little information about the magnitude of this load, so we assume a mean value for W_{OC} of 1.0 g m^{-1}(shoreline) yr^{-1}, and the wetland load is the product of W_{OC}, P, and the proportion of shore as wetland (PW). Although we have assumed a mean value, we note that W_{OC} is a stochastic node in the model, with implications described in the next section. An important difference between A_{OC} and W_{OC} is that we assume one value of A_{OC} across lakes because the canopies around these lakes tend to be mixed deciduous and coniferous, with no large differences among lakes. In contrast, wetlands vary in their type among lakes. Furthermore, we have little information about the hydrologic transport of OC from adjacent wetlands to lakes. Therefore, we fit W_{OC} separately for each lake.

We have little information about the groundwater flux of OC into lakes. While deep groundwater wells in the area show low OC concentrations of about 2 g m^{-3}, there is reason to believe that groundwater accumulates additional OC as it passes through shallow soil horizons before reaching lakes (Christensen et al. 1996). Thus, we consider in our model a range of GW_{OC}, from 2 to 40 g m^{-3}. We determine the most likely concentration by evaluating uncertainties in posterior distributions for model parameters as well as goodness of fit between predicted and observed lake DOC concentrations (coefficient of determination, or R^2). Because uncertainty in environmental variables often scales with mean values, we use the coefficient of variation (CV = standard deviation [SD]/mean) in evaluating posterior distributions. We select the GW_{OC} that results in the lowest CVs and the highest R^2 for the model.

The literature for A_{OC} indicates a somewhat broad range. Some of these values are estimated indirectly, and implications of these calculations and assumed loading rates are addressed in the Discussion. Following are examples with units of g OC m^{-1}(shoreline) yr^{-1}: 299 in nearby Little Rock Lake, Wisconsin (Noll and Khalili 1990); 143 and 466 in Crampton Lake and Tuesday Lake, Michigan (Upper Peninsula), respectively (Carpenter et al.

Table 2. Model equations. Any constants in the following equations are referenced in the Methods section.

$dDOC_{alloch}/dt = Load - Respiration - Sedimentation - Export$

Under steady-state conditions, the lake dissolved organic carbon budget:
(1) $Load = Export + Mineralization + Sedimentation$
(2) $Mineralization = DOC_{alloch} \times RDOC$
(3) $Sedimentation = Mineralization \times 0.5$
(4) $Export = DOC_{alloch} \times OutDOC$
where
DOC_{alloch} is the long-term mean DOC mass minus the autochthonous fraction
RDOC (yr^{-1}) is mineralization of DOC_{alloch}
OutDOC (yr^{-1}) is hydrologic outflow factor
(5) RDOC (yr^{-1}, T)$= RDOC_{20} \times \theta^{(T-20)}$
(6) OutDOC (yr^{-1})$= Q_{Out}/Z$

Substitute Eqs. 2, 3, and 4 into Eq. 1:
(7) $Load = DOC_{alloch} \times OutDOC + DOC_{alloch} \times RDOC \times 1.5$
(8) $Load = DOC_{alloch} \times (OutDOC + RDOC \times 1.5)$
(9) $DOC_{alloch} = Load/(OutDOC + RDOC \times 1.5)$

Load equations:
(10) Load (g yr^{-1})$= Load_{Aerial} + Load_{Wetland} + Load_{GW} + Load_{SW} + Load_{P}$
(10a) $Load_{Aerial}$ (g yr^{-1})$= [PC \times A_{OC} \times perimeter] + [(1 - PC) \times 0.2 \times A_{OC} \times perimeter]$
where
PC is proportion of shore with canopy
A_{OC} is the aerial loading factor in g m^{-1} yr^{-1}
Perimeter is the lake perimeter in m
(10b) $Load_{Wetland}$ (g yr^{-1})$= [PW \times W_{OC} \times perimeter]$
where
PW is proportion of shore that is wetlands
W_{OC} is the adjacent wetland loading factor in g m^{-1} yr^{-1}
(10c) $Load_{GW}$ (g yr^{-1}): groundwater load$= GW_{OC} \times Q_{GW}$
where
GW_{OC} is the concentration of DOC in groundwater $= \sim 10$ g m^{-3}
Q_{GW} is the volume of water input per year (m^3 yr^{-1}) that is groundwater; partitioning of inflow according to proportions in Table 1.
(10d) $Load_{SW}$ (g yr^{-1}): stream-water load$= SW_{OC} \times Q_{SW}$
where
SW_{OC} is the concentration of DOC (g m^{-3}) in stream waters, which is lake specific
Q_{SW} is the volume of water input that is stream flow (m^3 yr^{-1})
(10e) $Load_{P}$ (g yr^{-1}): precipitation load$= P_{OC} \times Q_{P}$
where
P_{OC} is the concentration of DOC in precipitation $= \sim 2$ g m^{-3}
Q_{P} is the volume of water input per year (m^3 yr^{-1}) that is precipitation; partitioning of inflow according to proportions in Table 1

Stochastic parameters (nodes)
RT is hydrologic residence time per lake
Z is mean lake depth
W_{OC} is adjacent wetland loading rate per lake
A_{OC} is aerial loading rate (one factor for all lakes)
RDOC is respiration per lake

2005); 354 in Mirror Lake, New Hampshire (Likens 1985); and 320 in Lake Wingra, Wisconsin (Gasith and Hasler 1976). Based on these ranges, we estimated an annual airborne transfer of particulate organic carbon from forest to lakes of 143–466 g C m^{-1} shoreline (0.4–1.3 g C m^{-1} d^{-1}). We chose a mean A_{OC} of 1 g m^{-1} d^{-1} and describe further below how this estimate is used in the model.

Within-lake fluxes include mineralization and burial in sediments. We have little information on permanent burial rates of OC in lakes. A coarse estimate of the total fate of OC in lakes has been estimated to be two-thirds mineralization and one-third sedimentation (Tranvik et al. 2009). Therefore, we assume the sedimentation rate to be one-half that of the mineralization rate (Eq. 3). It is important to note that the design of the model and the data available do not allow for discrimination between mineralization and sedimentation. Rather, these are estimated as a combined output (Eqs. 2, 3), along with export (Eq. 4), to balance the loads (Eq. 7). Clearly, this partitioning has high uncertainty and will have some bearing on OC loads to the system. We address these implications in the discussion section. Mineralization, or "respiration," is the product of DOC_{alloch} and a mineralization rate (RDOC) that we estimate (Eq. 2). To allow for easier comparisons with the literature, we sometimes standardize the estimated RDOC to 20°C and report as $RDOC_{20}$ (Eq. 5). Because we are modeling steady-state conditions, temperature is not dynamic and thus has no effect on the estimation of that parameter. The literature

Table 3. Model parameters and stochastic nodes of the Bayesian framework. Stochastic nodes are assigned a prior distribution.

	Abbreviation	Units	Comments
Parameters			
Temperature scaling factor, theta	θ	Unitless	1.07 ~ Q10 of 2
Precipitation DOC concentration	P_{OC}	g C m^{-3}	Concentration of organic carbon in precipitation; assumed to be low at ~2 g C m^{-3}.
Inflow, non–surface-water DOC concentration	GW_{OC}	g C m^{-3}	Concentration of organic carbon in groundwater inflow; determined through model fitting to be ~10 g C m^{-3}.
Stochastic nodes			
DOC_{alloch} mineralization rate at 20°C	$RDOC_{20}$	d^{-1}	Typically ranges from 0.0007 to 0.005. We will use 0.001, with uniform variance of the prior. Parameter fit separately for each lake.
Aerial loading rate from the lake shoreline	A_{OC}	g C yr^{-1} m^{-1} canopy shoreline	Mean prior of 1.0 g m^{-1} yr^{-1}, with uniform variance. Middle of literature range and near equivalent to local lake study (0.82). One estimate of this parameter for all lakes.
Adjacent wetland loading rate	W_{OC}	g C yr^{-1} m^{-1} wetland shoreline	Mean prior of 1.0 g m^{-1} yr^{-1}, with uniform variance. Parameter fit separately for each lake.
Hydrologic residence time	RT	yr^{-1}	Mean in Table 2, with uniform variance prior.
Lake depth	Z	m	Mean and variance calculated from observed long-term data.

values for RDOC are summarized by Hanson et al. (2011) and range from about 0.0007 to 0.010 d^{-1}, based primarily on bottle experiments, but are thought to be close to 0.001 d^{-1}, based on ecosystem-scale calculations, which is the value we assumed as the mean.

We used a Bayesian framework to estimate parameter distributions and uncertainty in carbon fluxes. Some excellent examples in the literature can be found for modeling eutrophication (Borsuk et al. 2004), analysis of isotopes in lakes (Solomon et al. 2011), and many other ecological applications (Uusitalo 2007). A Bayesian approach allows for explicit formulation of uncertainty before the model is fit (i.e., prior distributions) as well as after the model is fit (i.e., posterior distributions). Prior knowledge, whether from data, the literature, or expert knowledge, can be included explicitly in the model description, along with assumptions about how informative that knowledge is. For example, we may not have direct measurements of ecosystem respiration for these lakes, but the literature provides some information about the possible range, even if we do not know the shape of the distribution. Lake depth, on the other hand, may be well described by a distribution of historical data. Clearly, the latter example is more informative than the former. Within the context of the model in this study (equations in Table 2), certain terms in the equation are assigned prior distributions and are called "stochastic nodes" (Fig. 1; Table 3). In the model-fitting process, stochastic node distributions are sampled and updated to posterior distributions, and uncertainty in key model terms, such as OC fluxes, are estimated. Thus, our uncertainties about model assumptions, for example, the values of stochastic nodes, are propagated into uncertainties in the values we wish to estimate, in this case the fluxes and fates of OC.

The stochastic nodes in the model were chosen because of high uncertainty in specific terms of the model (Table 3; Fig. 1). These nodes correspond to major terms of the model: total DOC_{alloch} in each lake, loads, respiration, and export. Export is a function of hydrology, which depends on residence time and lake volume. Hydrologic residence time (RT) was assumed to have a mean value per Table 1, with uninformed prior distribution of the variance. The mean and variance of lake depth were calculated from observed data, which affects total DOC mass, which is the product of the concentration and the lake volume. As described above, mineralization of DOC within the lake varies widely in the literature. RDOC is a stochastic node, and because of the high uncertainty in the mean, we assume a uniform prior distribution of the precision. We assumed a mean $RDOC_{20}$ of 0.001 d^{-1} (Hanson et al. 2011). Hydrologic inflow data and DOC concentrations are reasonably well constrained by observations, whereas aerial loads and loads from adjacent wetlands are not. Both the aerial shoreline loading factor (A_{OC}) and the adjacent wetland loading factor (W_{OC}) were given a mean value of 1.0 g m^{-1} yr^{-1} and uninformed prior variance.

We fit the model using WinBUGS software (Lunn et al. 2000), discarding the initial 1000 runs as burn-in. We thinned the remaining iterations and retained approximately 1000 samples from the posterior distributions of the parameters. From these distributions, we report the means and SDs. We assessed convergence by ensuring the scale reduction factor (Rhat) was < 1.1 (Gelman et al. 2004).

Results

There were large differences among the lakes in their surrounding landscapes and their physical and limnological characteristics. The two bog lakes, CB and TB, had the highest DOC_{alloch} and TP concentrations and were the smallest in area (Table 1). However, they differed in two important characteristics. CB was shallow with no surrounding canopy, while TB was relatively deep and surrounded by forest. The other extreme in size was TR, which was large in area and had the deepest mean depth and low DOC_{alloch} and TP. When viewed as a group (Fig. 5), the study lakes represent large gradients in multiple dimensions, three of which are shown: RT, proportion of the load that is aerial, and DOC_{alloch} concentration in mg m^{-2}. A lack of obvious correlation

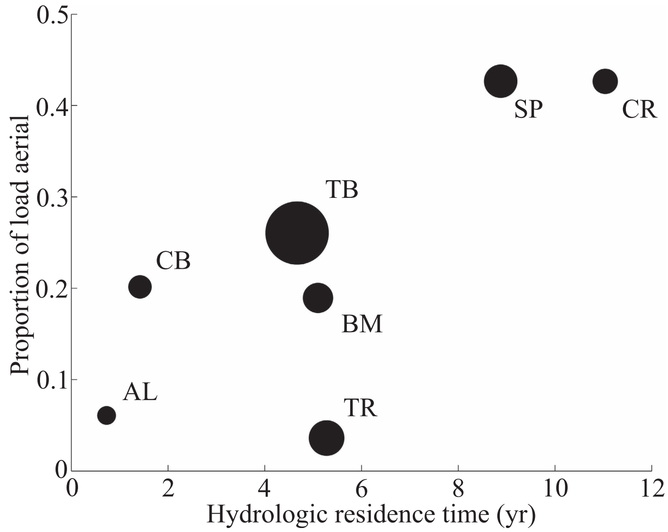

Fig. 5. Study lakes plotted across gradients of hydrologic residence time and proportion of load from aerial sources. The size of the dots represents magnitude of DOC concentration in g m^{-2} (Table 1, Z × DOC).

in these dimensions has advantages in fitting a model intended to reveal general characteristics across lake systems.

When the model was fit across a range of groundwater OC concentrations (GW_{OC}), predictable patterns in most fluxes and parameter occurred. In all cases but one, total load increased with increasing GW_{OC}, with increases ranging from 22% to 132%, reflecting the relative contribution of ground water in the hydrologic budgets (Table 1). CB had the least increase (from about 20 to 24 g m^{-2} yr^{-1}), and AL had the largest increase (from about 24 to 56 g m^{-2} yr^{-1}). TB was the only lake to decrease in total load (from about 55 to 50 g m^{-2} yr^{-1}). The decrease was an artifact of the model-fitting process, as parameters related to aerial (A_{OC}) and wetland loads (W_{OC}) fluctuated slightly across the range of GW_{OC}, suggesting modest correlation among the fitted parameters. Across all lakes, the average increase in load was 8.8 g m^{-2} yr^{-1}, with concomitant increases in outflow, mineralization, and sedimentation of 3.1, 3.8, and 1.9 g m^{-2} yr^{-1}, respectively.

To determine which GW_{OC} to use for subsequent analyses, we evaluated CVs of the stochastic nodes and R^2 of the regression between observed and predicted lake DOC concentrations. In all cases, other than the total load and A_{OC}, the CVs of the posterior distributions did not change noticeably with increasing GW_{OC}, suggesting that changes in uncertainties in the posterior distributions simply scale with mean values. However, the CV for the load increased slightly, and the CV for A_{OC} increased about 25%, as GW_{OC} increased beyond 10 g m^{-3}. Furthermore, R^2 remained nearly constant (~ 0.95) below GW_{OC} = 10 g C m^{-3} but decreased steadily as GW_{OC} increased beyond 10 g m^{-3} (e.g., at 20 g m^{-3}, $R^2 = 0.87$; at 30 g m^{-3}, $R^2 = 0.73$; and at 40 g m^{-3}, $R^2 = 0.65$). Because of the degrading model performance above GW_{OC} = 10 g m^{-3}, we chose that concentration for the remainder of the analyses.

Model results show marked differences among lakes in the origin and magnitude of their loads (Fig. 6; Table 4). Note that the fluxes are normalized to areal units. The moderately sized lakes, Big Muskellunge (BM), CR, and Sparkling (SP), had similar aerial loads of OC, ranging from about 5 to 9 g m^{-2} yr^{-1}. The largest lake, TR, had the lowest aerial load (~ 1 g m^{-2} yr^{-1}), and the two bog lakes, CB and TB, which were smallest in area, had the highest aerial loads (~ 4 and 15 g m^{-2} yr^{-1}, respectively). Lakes differed in groundwater OC load, with TB, CB, CR, and SP having only 1–2 g m^{-2} yr^{-1} and BM, AL, and TR having about 5–15 g m^{-2} yr^{-1}. All lakes had similar precipitation OC loads. Loads from adjacent wetlands for the nonbog lake, AL, were similar to the aerial loads at about 2 g m^{-2} yr^{-1}. Adjacent wetland were important for both bogs, with CB having a load of about 13 g m^{-2} yr^{-1} and TB having a load of about 36 g m^{-2} yr^{-1}. The three lakes with little or no surface inflow had low total loads, ranging from about 4–8 g m^{-2} yr^{-1}. AL and TR, which have substantial surface inflow, had total loads of about 24 and 16 g m^{-2} yr^{-1}, respectively, and the two bogs, CB and TB, had somewhat high loads at about 20 and 55 g m^{-2} yr^{-1}, respectively. The shoreline aerial loading factor, A_{OC}, was estimated across lakes and found to be 1.15 ± 0.47 (± standard error of the mean) g m^{-1} yr^{-1}, while the adjacent wetland loading factor, W_{OC}, had a mean across lakes of 1.96 g m^{-1} yr^{-1} (Table 4).

The fate of DOC_{alloch} was related closely to the hydrology of the lakes (Fig. 6). There are three possible fates: export, mineralization, and sedimentation. Not surprisingly, shorter residence time leads to higher export. When combined, mineralization and sedimentation as a percentage of total load was higher than export in BM (69%), CB (64%), CR (85%), SP (79%), TB (74%), and TR (69%). For AL, which has substantial surface inflow, the percentage of load as respiration and sedimentation was approximately 36%.

The mineralization rate, $RDOC_{20}$ (d^{-1}) was similar among lakes (Table 4; note mix of daily and annual units). The lowest rate, 0.00083 d^{-1}, was in SP, while the highest, 0.00152 d^{-1}, was in CB. The mean across lakes was 0.00108 d^{-1}. In other words, approximately 0.1% of the standing stock of DOC_{alloch} in a lake is mineralized each day when the temperature is 20°C. When adjusted to the annual mean T across lakes, which is approximately 10.4°C, the daily respiration (RDOC) across lakes is approximately 0.00056 d^{-1}, or approximately half the rate at 20°C (*see* Table 2, Eq. 5).

Steady-state lake DOC_{alloch} concentration was somewhat sensitive to temperature. When steady-state DOC_{alloch} was simulated across a 6°C range of water temperatures, DOC_{alloch} concentration changed inversely and near linearly with temperature, as expected. Within the range of observed mean temperatures across lakes (Fig. 7, vertical lines), DOC_{alloch} varied by as little as 0.3 g m^{-3} (CR) and as high as ~ 4 g m^{-3} (TB).

The sensitivity of the OC loads to key lake characteristics depends on the lake. In Fig. 8 we plot the modeled load (color gradient) required to maintain equilibrium across broad gradients of DOC_{alloch} (areal units) and chemical

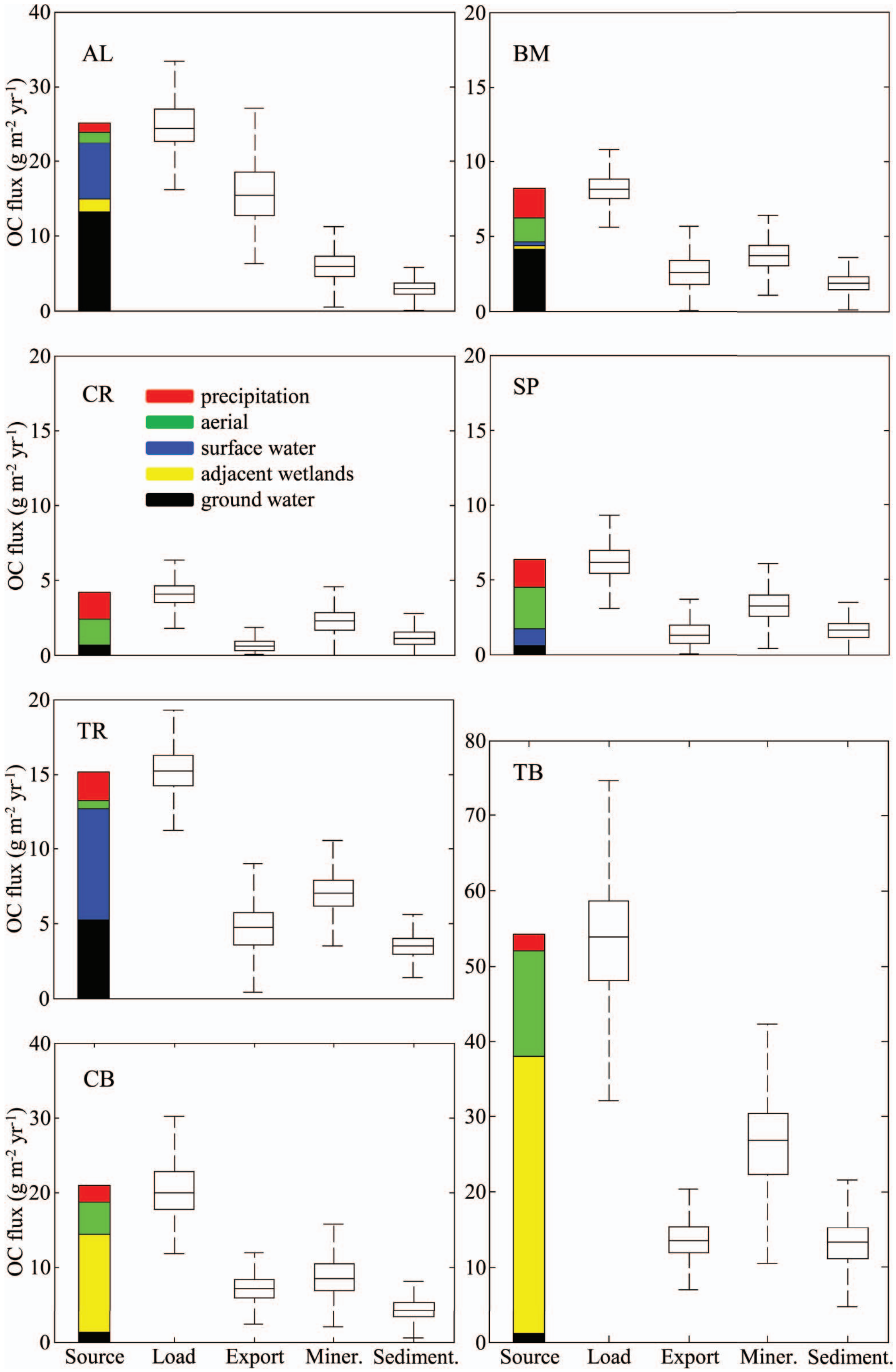

Fig. 6. Budgets for the lakes. The colored bars show the proportion of each source in the total load. In the box plots, the central mark is the median, the edges of the box are the 25th and 75th percentiles, and the whiskers extend to the most extreme data points not considered outliers. Note the different scale on the *y*-axis for AL, CB, and TB. miner. = mineralization, sedim. = sedimentation.

Table 4. Model results for two key rates and the overall fluxes. Unless otherwise specified, all values are means ± SD in g C m^{-2} (lake area) yr^{-1}. $RDOC_{20}$ units are 10^{-3} d^{-1}. Abbreviations per Table 3, except for $RDOC_{20}$, which is RDOC normalized to 20°C, and RT_{chem}, which is chemical residence time (Z/outflow).

	AL	BM	CB	CR	SP	TB	TR
Rates							
$RDOC_{20}$ ($\times 10^{-3}$ d^{-1})	1.46±0.54	0.87±0.44	1.52±0.48	0.98±0.48	0.83±0.46	0.93±0.39	1.00±0.44
W_{OC} (gC m^{-1} d^{-1})	1.85±1.06	2.26±1.38	0.72±0.21	na	na	3.00±0.91	na
A_{OC} (gC m^{-1} d^{-1})				1.15±0.47			
Fluxes (or C budget)							
Load	24.11±3.88	9.10±2.27	19.87±3.75	5.04±2.29	7.59±3.14	54.77±11.09	15.92±2.67
Export	15.32±3.86	2.83±1.22	7.07±1.79	0.77±0.88	1.60±0.97	13.98±2.57	4.95±1.62
Respiration	5.84±2.22	4.16±1.89	8.54±2.64	2.85±2.00	4.00±2.28	27.20±7.51	7.31±2.01
Sedimentation	2.94±1.43	2.09±1.20	4.27±1.60	1.43±1.29	2.00±1.43	13.60±3.84	3.66±1.40
Other stochastic variables							
RT (yr)	0.75±0.083	5.08±0.43	1.37±0.16	11.03±0.58	8.88±0.55	4.64±0.41	5.25±0.44
Z (m)	3.21±0.045	7.50±0.066	1.70±0.014	10.40±0.069	10.90±0.064	5.60±0.056	14.60±0.020

residence (RT_{chem} = Z/Q_{Out}; Table 1), which tends to be much longer than hydrologic residence time (RT) for most lakes (Table 4), as RT_{chem} does not include evaporation. We have chosen areal units to eliminate the depth dimension and RT_{chem} to eliminate differences among lakes in hydrologic partitioning. We have assumed a mean $RDOC_{20}$ of 0.001 d^{-1}, adjusted to a T of 10.4°C, in keeping with the results of this study (Table 4). Lakes in this study are plotted with open circles, and lakes from other studies have filled shapes with colors representing loads estimated in the respective studies. The filled colors allow us to compare loads between the studies and our expectations from the model at those coordinates. To interpret sensitivity, a lake's position on the *x*-axis can be changed by adjusting mean depth or DOC_{alloch} concentration and on the *y*-axis by adjusting mean depth or outflow volume. The sensitivity of loading to these changes can be assessed by viewing the color change at the new coordinates, which is the load required to maintain equilibrium DOC_{alloch} concentration. An interesting phenomenon occurs as either axis is approached. For lakes with low DOC_{alloch} concentration (~ 100 g C m^{-2} or less) and moderate residence times (~ 3 yr or greater), the load estimates are not especially sensitive to RT_{chem}. For lakes with short RT_{chem} (~ 1 yr or less) and moderate to high DOC_{alloch} concentration (~ 50 g C m^{-2} or more), the load estimates are not especially sensitive to DOC_{alloch} concentration. In short, if the lake is clear with $RT_{chem} > 3$ yr or stained with $RT_{chem} < 1$, then the loads are not very sensitive to assumptions of the model. Estimates of OC loads in other studies that are more empirical in nature are plotted as well (Dillon and Molot 1997; Kling et al. 2000; Jonsson et al. 2001). The symbol colors from these studies match reasonably well the color in the modeled lake space, corroborating our modeled load estimates.

Discussion

A challenge in quantifying lake carbon budgets is that most components of the allochthonous OC budget are difficult to observe directly in most ecosystems and have high uncertainties. In our simplified mass balance approach to the budget, in which loads are balanced by respiration, sedimentation, and export, we are able to constrain well the export term and have high confidence in a major component of the loads, the hydrologic inputs to the system. For lakes with substantial surface-water inflow, we have observations of OC from inflow. For all lakes, precipitation has low and consistent concentrations of organic carbon. The three major unknowns remaining are shoreline inputs (both aerial and wetland), groundwater inputs, and respiration and sedimentation. In most formulations of lake carbon cycling budgets that include inputs, outputs, and transformations, the load term cannot be separated analytically from in-lake processing terms (Hanson et al. 2011). Fortunately, we have information from the literature to support our prior assumptions about the distributions of these two budget components, and that is where we begin our discussion.

Aerial load, adjacent wetland load, and groundwater load—Adjacent habitats, such as shoreline forests or wetlands, appear to contribute in important ways to lake OC and may account for much of the differences in DOC_{alloch} concentrations among lakes. Previous surveys that have attempted to explain lake DOC by relatively coarse landscape characteristics have found that much of the variance across lakes remains unexplained (Gergel et al. 1999; Xenopoulos et al. 2003; Hanson et al. 2007). It is the landscape immediately adjacent to lakes that may account for some of the unexplained variance, and these are typically not easily identified in broad surveys that use low-resolution coverages (Creed et al. 2003). Previous modeling work of regional carbon cycling suggested that lakes receive most allochthonous OC from nearby sources (Cardille et al. 2007). Indeed, our results suggest that the origin for half the load extends only meters in lakes without substantial stream water inflow.

The aerial load was a substantial OC source to these lakes. In this study, it accounted for ~ 25–50% of the OC influx for lakes without substantial inflows (Fig. 6). This outcome was a result of the aerial loading rate (A_{OC}) being

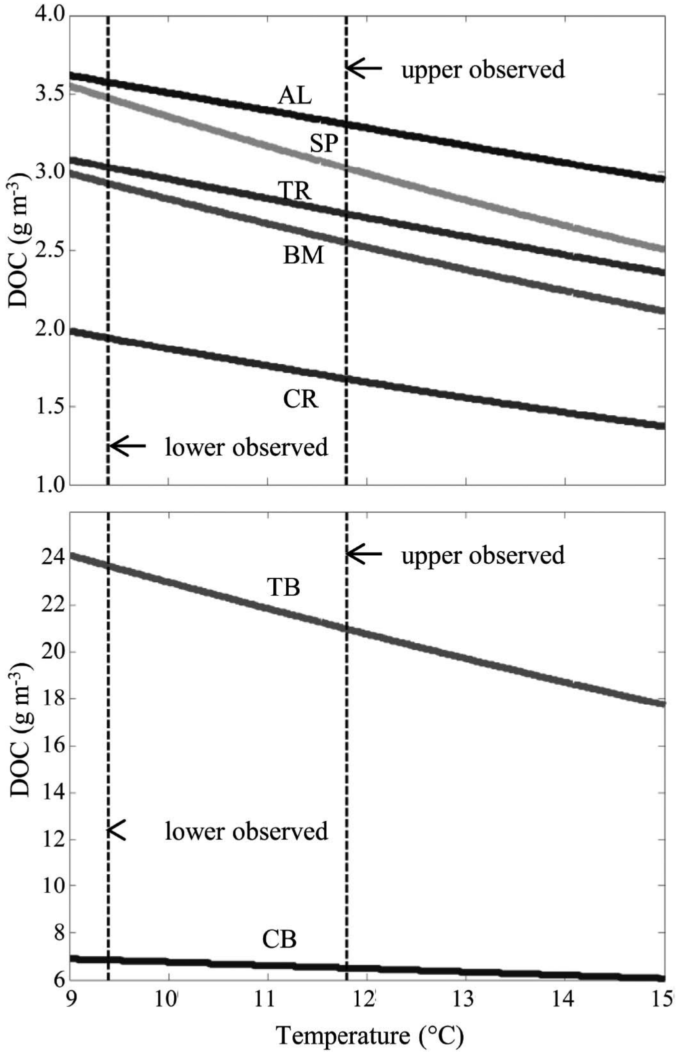

Fig. 7. Simulations of lake DOC steady state across simulated temperature gradients. Vertical dashed lines indicate the range of observed mean annual temperatures through time for lakes in this study.

estimated to be 1.15 ($\pm$ 0.47 SD) g m^{-1} d^{-1}. Unfortunately, airborne inputs of organic matter to lakes, such as leaf litter or pollen, are not often measured at our study site. However, several estimates exist for northern temperate lakes in forested landscapes. If we convert areal particulate load estimated by Carpenter et al. (2005) for experimental lakes in the region, we have an annual rate of 143–466 g C m^{-1} of shoreline. This is similar to the annual estimates for Mirror Lake, New Hampshire, of 354 g C m^{-1} yr^{-1} (Likens 1985) and for Lake Wingra (southern Wisconsin) of 320 g C m^{-1} shoreline yr^{-1} (Gasith and Hasler 1976), both of which include direct measurements of autumn leaf-fall inputs. There are more examples for airborne particulate flux from forest to streams. When these are converted from areal units (m^2) to shoreline units (m) in smaller streams, they might be considered to have approximately twice the shoreline loading as lakes because both stream shores may contribute to the same water surface. For example, Bear Brook, a 3-m-wide over-canopied headwater stream in New Hampshire, had about $\sim$ 416 g C m^{-1} shoreline yr^{-1} (Fisher and Likens 1973), and Fort River, a 14-m-wide fourth-order stream in Massachusetts, had $\sim$ 942 g C m^{-1} shoreline yr^{-1} (Fisher 1977). Based on these ranges, it seems reasonable that aerial loads from shoreline with canopy are at least 100 and perhaps as high as 500 g C yr^{-1} m^{-1} shoreline (0.27–1.37 g C d^{-1} m^{-1} shoreline). The mean value for A_{OC} is well within this range. We note that the shoreline input process in the model subsumes all aerial loading processes, including non–leaf-litter inputs, which for lakes in this region may approach 1 g m^{-2} yr^{-1} (Preston et al. 2008). The importance of the aerial OC flux to the whole lake budget underscores the point that the area adjacent to the lake is most relevant to OC loading and highlights the need for additional work on this potentially important carbon source.

Adjacent wetlands were an important source of OC for three of the lakes. We remind the reader that adjacent wetlands in these lakes have diffuse transport that cannot be easily quantified. Contributions of OC from wetlands elsewhere in the watershed are accounted by observational data from inflow streams. There were four lakes with adjacent wetlands, two of which (AL and BM) are nonbog lakes and two of which are bog lakes (CB and TB). BM has a relatively small proportion of shoreline in wetland ($\sim$ 7%), so wetland load turned out to be negligible at about 1% of the total load (Figs. 6, 7). AL has a high percentage of shoreline wetlands (48%). However, wetlands still contribute a small percentage of the total OC load ($\sim$ 10%) because of high stream-water and groundwater loads. The two bog lakes provide an interesting contrast. Both are surrounded by *Sphagnum*-dominated peatland up to 10 m thick (Buffam et al. 2010) yet have very different DOC concentrations as well as estimates of W_{OC}. CB input rate was estimated to be approximately one-fourth that of TB, which had a higher rate than the two nonbog lakes. One possible explanation for W_{OC} differences between the bog lakes is that interstitial water in the peatland surrounding CB has a lower DOC concentration than the water in the TB peatland. Peat pore-water sampling in three plots in each of these peatlands (Buffam et al. 2010) revealed differences in DOC concentration: 68 $\pm$ 23 mg L^{-1} for CB and 101 $\pm$ 35 mg L^{-1} for TB (I. Buffam unpubl.).

Groundwater load—The groundwater load of OC to lakes remains uncertain. Although we have no direct measurements for lakes in this study, a study on a nearby dark-stained seepage lake indicates GW_{OC} may be as high as 12–17 g m^{-3} (Christensen et al. 1996), which is substantially higher than the $\sim$ 2 g m^{-3} found in deep groundwater wells near our study lakes. What is the most likely concentration? In our study, model performance started to degrade when GW_{OC} was raised above 10 g m^{-3}, and at very high GW_{OC} concentrations (GW_{OC} = 40 g m^{-3}), the model fit poorly. However, this may be due in part to the model design. For example, we assumed the same GW_{OC} for each lake, yet each lake is likely different. Perhaps there are interactions at the lake–terrestrial interface (sloshing) that loads additional OC to lakes.

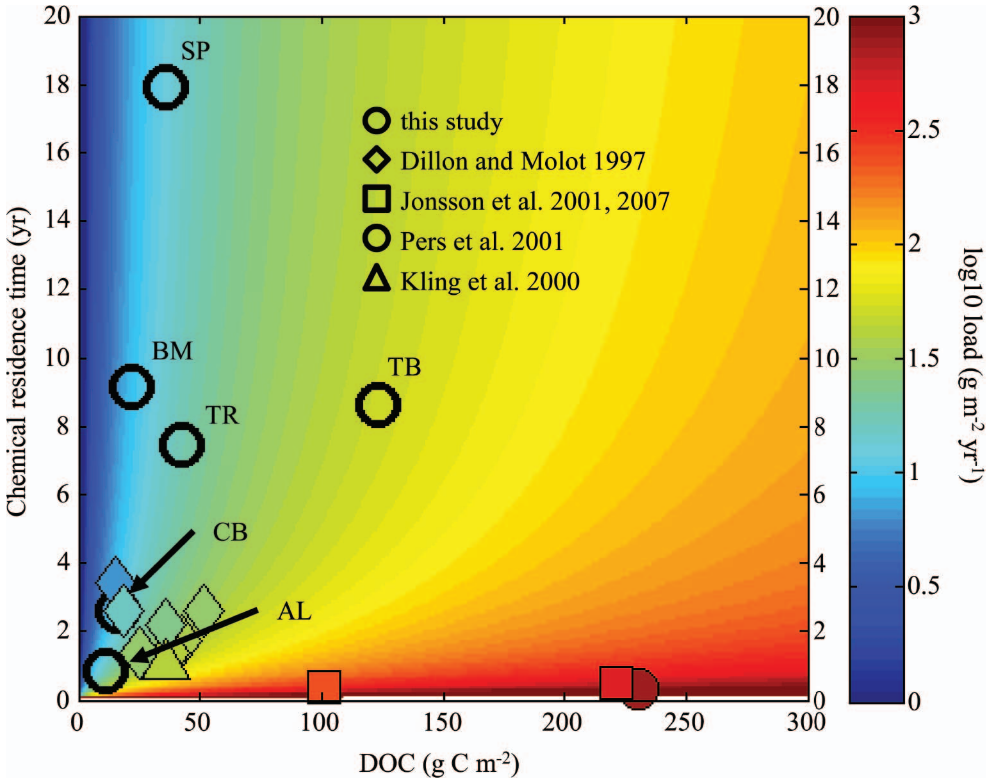

Fig. 8. Loads (z-axis) required to sustain equilibrium conditions for gradients of observed DOC (x-axis) and chemical residence time (y-axis) modeled in this study (circles) are plotted along with empirical results from the literature (filled shapes). Empirical results from the literature are colored according to load estimates from those studies. CR from this study, which has x, y, z of 14.45 g m^{-2}, 40.0 yr, and 4.34 g C m^{-2} yr^{-1}, respectively, is not shown to restrict the y-axis. For modeled results (circles), we have assumed $RDOC_{20}$ of 0.001 d^{-1} and mean annual T of 10.6°C.

Despite these possible mechanisms for additional load, our model did not demand an additional load to balance the budget. Again, this may be a model design issue. Had the system outputs (i.e., outflow, mineralization, and sedimentation) been higher, there would have been higher demand for loads. Raising the mineralization rate in particular, the output with highest uncertainty, could result in additional OC demand to balance the budget.

Mineralization and sedimentation—Mineralization rates of allochthonous OC are similar among lakes and are at the lower end of the range from the literature (Table 4). Daily mineralization rates (normalized to 20°C) ranged from 0.00083 to 0.0015 d^{-1}. These rates are at the lower end of the range (~ 0.0006–0.016 d^{-1}) summarized from the literature by Hanson et al. (2011), which vary nearly 20-fold depending on the methodology. Why are the rates similar among our lakes? (1) There are some similarities in the nature of the OC loads; for example, quality of OC in precipitation and groundwater probably does not vary much, and most aerial inputs are from mixed deciduous and coniferous sources. (2) Most allochthonous OC in lakes with moderate to long residence times, is highly recalcitrant, or would not remain present. Indeed, the two lakes with the shortest residence times, AL and CB, had the highest RDOC values. (3) Our estimates of respiration are made at the ecosystem scale, whereas many of the literature values are from laboratory experiments. Clearly, the low mineralization rates estimated in our study could have profound effects on estimated carbon budgets in studies that calculate the loads based in part on the demands of mineralization. We discuss those implications below.

How the mineralization rate scales with temperature is an important consideration when applying our results to warmer or colder regions. Lakes in this study have very similar mean annual temperatures (Table 1), so we could not address the temperature dependence of mineralization. Work on a diversity of biomes indicates high variability among systems and questions the sensitivity of respiration to temperature (Mahecha et al. 2010), although respiration in lake sediments has been found to be temperature sensitive (Gudasz et al. 2010). We are unaware of ecosystem-scale studies in lakes that cross sufficient temperature gradients to inform scaling coefficients. For terrestrial ecosystems, flux tower measurements of gas exchange indicate that, globally, Q_{10} is converging on about 1.41 (Mahecha et al. 2010). We assumed a θ of 1.07, which is nearly equivalent to a Q_{10} of 2. We report RDOC adjusted to 20°C (i.e., $RDOC_{20}$; Table 4), which is nearly 10°C greater than mean annual temperature for these lakes (Table 1). If instead we assume a Q_{10} of 1.41 (θ of ~ 1.04), then $RDOC_{20}$ is lowered from a cross-site mean of about

0.0010 d^{-1} to about 0.0007 d^{-1}. Although this does not alter the budget in these lakes because scaling to 20°C is for reporting purposes only, it does alter sensitivity analysis and application of these results to further studies. For example, DOC_{alloch} at steady state as a function of temperature (Fig. 7) would have a flatter slope. A better understanding of temperature scaling across lakes would be helpful in modeling C cycling in a broader range of ecosystems, but, as in terrestrial systems (Yuan et al. 2011), temperature effects will likely be confounded by other factors covarying across the temperature gradient.

Our assumption of a constant ratio between respiration and sedimentation (Tranvik et al. 2009) suggests that any uncertainty in the estimate of the free parameter for respiration (RDOC) also applies to sedimentation. The result is that sedimentation of allochthonous OC ranges from 1.4 to 14 g m^{-2} yr^{-1} and with SDs nearly as high. Although we do not have published rates of long-term OC burial for our lakes, our modeled rates are similar to those found by Ferland et al. (2012) for lakes at similar latitudes (3–5 g C m^{-2} yr^{-1}) but quite a bit lower than rates (22 g C m^{-2} yr^{-1}) for a more diverse set of lakes in Europe (Kastowski et al. 2011). It should be noted that cited work includes both allochthonous and autochthonous OC, whereas ours includes only the allochthonous fraction. Given the aforementioned total sedimentation rates from the literature, the allochthonous component in our study would be from 10% to 100% of the total sedimentation of OC, requiring autochthonous sources to supply from zero to about 20 g m^{-2} yr^{-1}. Higher certainty in OC burial rates, coupled with better information on OC sources, would be an important addition to lake OC budgets and would help constrain remaining flux estimates.

The carbon budgets and broader implications—Most studies that attempt to quantify the roles lakes play in C cycling at the landscape scale are empirical in nature or assume key rates. Classic work by Dillon and Molot (1997) sets the standard by observing inflows and outflows and calculating the differences. Others have assumed ecosystem mineralization rates, usually from bottle experiments (Reche et al. 2000; Jonsson et al. 2001; Pers et al. 2001); assumed the loads (Sobek et al. 2006); or upscaled from other work making such assumptions (Jonsson et al. 2007; Tranvik et al. 2009). There are very few studies that have published all the data necessary to estimate the loads. We have included a few of these in Fig. 8, even though we had to make some assumptions about RT and DOC concentrations in most cases, as studies tend not to provide outflow volumes, annual DOC concentration ranges, and mean depth as well as estimates of the OC loads from all reasonable sources. Based on the observed and modeled gradients, OC loads to lakes can range from a few to several hundred g C m^{-2} yr^{-1}. Making broad generalizations about the role lakes play in landscape OC cycling depends on the lake characteristics, including hydrology, observed lake concentration, and aforementioned adjacent ecosystems. There is space in Fig. 8 that we feel lakes are unlikely to occupy, which is roughly the upper right quadrant, because lakes with long residence times do not tend to have high DOC concentrations. Even a deep lake, such as Lake Superior, which has a mean depth of 147 m and wintertime DOC of about 1 g m^{-3} (Sterner 2011), has an areal DOC concentration of 147 g m^{-2}.

Are lakes in this study "hot spots" of carbon cycling in the landscape? Over millennial time scales, lakes store more organic carbon than forests in our region and are second in storage only to peat (Buffam et al. 2011). Contemporary estimates of net ecosystem exchange (NEE) of forests covering a broad range of growth stage (e.g., 40–350 g C m^{-2} yr^{-1}; Schimel et al. 2001; Curtis et al. 2002) are approximately 2–10 times total aquatic sedimentation on an areal basis, but much of that sedimentation may be autochthonous in origin. If we use only the allochthonous load to lakes and scale it to the ratio of land : lake surface in our study area, which is approximately 8 : 1 (Cardille et al. 2007), the overall mass flux of NEE is roughly 15–100 times that of allochthonous loads to lakes. Although observable rates indicate much lower mass flux in lakes than in terrestrial systems, OC buried in lake sediments remains there and accumulates substantially over long time scales. These results are similar to those of Buffam et al. (2011), who, in a regional-scale landscape analysis, estimated allochthonous OC inputs to lakes at 1/30th of forest NEE in the approximately 6400 km^2 region. A better metaphor for lakes may be "long-term cold storage" for OC.

A steady-state approach to modeling C cycling is appropriate for some lakes. For lakes in this study, there are three obvious components to long-term DOC signals: mean, annual cycle, and, in the case of TB, long-term trend (Fig. 3). The annual DOC dynamic appears to be closely related to generation and mineralization of autochthonous DOC (Fig. 4). Although not included as a process in our model, previous work suggests that autochthonous OC may lead to enhanced mineralization of the allochthonous OC (Guenet et al. 2010) and a commensurate underestimation of loads in our analyis. There may be transients in the loads, such as a springtime pulse of DOC, that are not accounted properly in the equilibrium model. Although we see no evidence in the annual dynamic of the time series for such a big load, it is worth some rough calculations, using AL as an exemplar, which is moderately sized and has substantial inflow. Mean DOC of AL is 11.2 g m^{-2}. If we assumed the aerial load (3 g m^{-2} yr^{-1}), which is probably dominated with leaf litter, to flow rapidly into the lake during spring snowmelt pulse, we would see a 27% increase in OC. A similar calculation for CR would yield an approximate 40% springtime increase in lake OC concentration. Alternatively, a springtime pulse may have substantial particulate OC, which may settle to the lake sediments and slowly leach a portion of its OC and thus not be apparent in the annual cycle of observed DOC. Although the sampling effort in these lakes does not allow us to discriminate between these possibilities, the DOC_{alloch} appears relatively stable, suggesting a more constant load.

The long-term trend in the two bog lakes may be related to changes in sulfate deposition (Hanson et al. 2006). There is a growing body of literature on DOC trends in aquatic ecosystems, and the often observed increase in DOC for northern surface waters during the past decades is generally attributed to decreased acid deposition (Monteith et al. 2007; Erlandsson et al. 2008), though other mechanisms may be at play as well (Freeman et al. 2004; Evans et al.

2005; Erlandsson et al. 2008). Our model does not address directly the acid base chemistry of lakes and their landscapes. Rather, these dynamics would be subsumed in the observational data from surface loads or unaccounted if changing loads were from adjacent wetlands. Future models targeting the time dynamics of lake DOC surely should address these kinds of depositional changes.

The outcomes of this work support a simple approach to modeling allochthonous OC cycling in most lakes, especially when scaling to broad regions. For example, temperature was surprisingly consistent among the lakes (Table 1), even though lakes varied by four orders of magnitude in volume. Respiration rates were surprisingly similar among lakes as well, and coefficients relevant to OC loads are reasonably well constrained. Although the conceptual model for OC cycling is simple, challenges remain in obtaining observational data necessary for quantifying the fluxes in a broader suite of lakes. Lake morphometry data exist but are often not digitized. Land cover data may not be of sufficient resolution for identifying adjacent ecosystems. Hydrology, especially for seepage lakes, can be difficult to quantify. The information on perimeter canopy and wetlands is tractable and either is already available or will likely be available soon with advances in remote sensing and GIS technologies. However, the importance of local hydrology, its variability among sites, and the difficulty of quantification make this a major challenge for the future and a crucial one for identifying key pressure points in aquatic and landscape C cycling.

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