

Dynamic modeling of organic carbon fates in lake ecosystems

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ABSTRACT

Lakes are active processors of organic carbon (OC) and play important roles in landscape and global carbon cycling. Allochthonous OC loads from the landscape, along with autochthonous OC loads from primary production, are mineralized in lakes, buried in lake sediments, and exported via surface or groundwater outflows. Although these processes provide a basis for a conceptual understanding of lake OC budgets, few studies have integrated these fluxes under a dynamic modeling framework to examine their interactions and relative magnitudes. We developed a simple, dynamic mass balance model for OC, and applied the model to a set of five lakes. We examined the relative magnitudes of OC fluxes and found that long-term (> 10 year) lake OC dynamics were predominantly driven by allochthonous loads in four of the five lakes, underscoring the importance of terrestrially-derived OC in northern lake ecosystems. Our model highlighted seasonal patterns in lake OC budgets, with increasing water temperatures and lake productivity throughout the growing season corresponding to a transition from burial- to respiration-dominated OC fates. Ratios of respiration to burial, however, were also mediated by the source (autochthonous vs. allochthonous) of total OC loads. Autochthonous OC is more readily respired and may therefore proportionally reduce burial under a warming climate, but allochthonous OC may increase burial due to changes in precipitation. The ratios of autochthonous to allochthonous inputs and respiration to burial demonstrate the importance of dynamic models for examining both the seasonal and inter-annual roles of lakes in landscape and global carbon cycling, particularly in a global change context. Finally, we highlighted critical data needs, which include surface water DOC observations in paired tributary and lake systems, measurements of OC burial rates, groundwater input volume and DOC, and budgets of particulate OC.

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1. Introduction

Lakes are dynamic components of the landscape that actively process, store, and transport terrestrially derived organic carbon (OC) (Cole et al., 2007; Tranvik et al., 2009; Tanentzap et al., 2017), as well as emit inorganic carbon to the atmosphere (Arvola et al., 2002; Raymond et al., 2013; Weyhenmeyer et al., 2015), making them important in global carbon (C) cycling. Owing to few ecosystem-scale studies that fully balance OC budgets (Cole et al., 1989; Hanson et al., 2014, 2015), there remains a considerable knowledge gap in lake OC dynamics, and thus in fully understanding the role of lakes in the global C cycle. Global estimates of CO₂ emissions (i.e., evasion) from lakes and reservoirs are 0.32 Pg (petagrams) C yr⁻¹ (Raymond et al., 2013), whereas anywhere from 0.02–0.07 Pg C yr⁻¹ (Tranvik et al., 2009) to 0.06–0.25 Pg C yr⁻¹ are stored in sediments (Mendonça et al., 2017). These estimates, however, are highly uncertain, and models that dynamically account for major OC fluxes and storage terms in lakes and that explore uncertainties around those terms are needed to advance our understanding of lake OC cycling and their contribution to global C budgets (Hanson et al., 2015; Reed et al., 2018). Existing mass balance models are generally based on low spatio-temporal frequency data, confined to single lakes, and are often from boreal regions (Jonsson et al., 2001; Urban et al., 2005; Andersson and Sobek, 2006; Cremona et al., 2014). In a first step in overcoming some of these limitations, we developed and applied a dynamic mass balance model to examine the relative magnitudes of OC fluxes across a set of five lakes with whole-ecosystem OC budget data. Our goal was to build a simple OC model that could be applied in a range of lake ecosystems to capture seasonal and annual variation in OC concentrations.

1.1. Overview of concepts of key OC fluxes in lake ecosystems

For lakes, the term “mass balance” has been broadly used to quantify carbon or nutrient budgets as the combination of inputs, outputs, and changes to standing stocks in the water column and sediments (Pace and Lovett, 2013). Inputs to lake ecosystem OC budgets are the sum of allochthonous (externally derived) dissolved (DOC) and particulate OC (POC) inflows from surface and groundwater sources, atmospheric deposition via precipitation, dry deposits, and litterfall, and autochthonous (internally derived) DOC and POC (Kawasaki and Benner, 2006) and phytoplanktonic primary production. Outputs from the OC pool reflect mechanisms that mineralize (i.e., photo-oxidation and respiration) and export OC via surface and groundwater outflows. Here, for simplicity, all mineralization processes that convert OC to CO₂ are collectively modeled as respiration. The mass change in OC in the water column and lake sediments is considered as change in storage. Outputs and storage are the fates of OC loads, and their balances define the role of lakes in broader C cycling (Box 1, Fig. 1).

At the global scale, lakes are thought to be net sources of C to the atmosphere based on the mean CO₂ (Kortelainen et al., 2006; Tranvik et al., 2009; Raymond et al., 2013) and methane (Bastviken et al., 2011) concentrations at higher than atmospheric levels in lake surface waters. OC export is less frequently considered, but equally important, in terms of the quality and quantity of OC ultimately reaching the ocean via tributaries (Raymond and Bauer, 2001; Santoso et al., 2017). Because lakes store OC in sediments, they can also act as sinks in the global C cycle (Mulholland and Elwood, 1982; Dillon and Molot, 1997; Einsele

et al., 2001; Einola et al., 2011).

We synthesized existing knowledge of lake OC budgets into a model that integrates these important mechanisms, including both in-lake as well as external (i.e., watershed) processes (Fig. 1). Below we described these processes in three main categories of the dominant processes that influence long-term lake OC budgets: 1) allochthonous inputs, 2) autochthonous inputs, and 3) storage and export.

1.2. Allochthonous inputs

Allochthonous inputs include all externally derived OC, including terrestrial DOC and POC from surface and groundwater inflows, litterfall, and direct-fall precipitation (Box 1). Although surface water inflows regularly deliver DOC to lake ecosystems, the uncertainties around their sources and magnitudes are perhaps the most commonly overlooked aspect in OC budgets, largely owing to data limitations (Hanson et al., 2015; Duffy et al., 2018). Prior studies have included direct measurements of inflow stream concentrations of DOC when available (Schindler et al., 1997; Jonsson et al., 2001; Urban et al., 2005; Klump et al., 2009), but other approaches have included literature-derived input estimates (Striegl and Michmerhuizen, 1998), equations based on watershed area (Sobek et al., 2006), watershed-wetland area ratios (O'Connor et al., 2009), precipitation (Hanson et al., 2004; Staehr et al., 2010), or GIS-based estimates based on land cover and distance-weighted hydrological flow paths (Canham et al., 2004). In lakes without surface inflows, including closed-basin and seepage lakes, groundwater can be the dominant hydrological input (e.g., Gaiser et al., 2009) and can deliver DOC to lakes, especially in organic-rich soils (Schindler and Krabbenhoft, 1998). Empirical measurements of groundwater discharge and DOC concentration, however, are rare and difficult to estimate (Hanson et al., 2014). POC inputs from litterfall, and wet and dry atmospheric deposition are typically small and are generally estimated as a function of lake size and literature- or expert-based loading coefficients (Hanson et al., 2004).

1.3. Autochthonous inputs

Autochthonous DOC and POC originate within lakes through bacterial exudates and photosynthesis by primary producers. Since gross primary production (GPP) is difficult to measure at the ecosystem level, net primary production (NPP), considered the difference between GPP and autotrophic respiration, is measured instead (Pace and Lovett, 2013; Box 1). Approaches to estimate NPP include bottle incubations (Urban 2005, Yang et al., 2008) and high frequency measurements of dissolved oxygen or CO₂ concentrations (Cole et al., 2002; Staehr et al., 2010). Statistical relationships have also been developed to estimate NPP from lake temperature and total phosphorus (TP; Hanson et al., 2004), chlorophyll-a (chl-a; Jonsson et al., 2001; Ramlal et al., 2003), or static proportions of the overall OC pool (Åberg et al., 2004).

1.4. Storage and export

Long-term burial of POC in lake sediments is the mechanism by which lakes remove C from the global C cycle, and is therefore a critical component of our understanding of the fate of both allochthonous and autochthonous POC (Cole et al., 2002; Tranvik et al., 2009; Mendonça et al., 2017). POC burial in lakes is a product of in-lake POC

Box 1

Mass balance conceptual equations for organic carbon (OC) in lake ecosystems.

OCALLOCHTHONOUS: surface and groundwater inflows + litterfall + atmospheric deposition

OCAUTOCHTHONOUS: gross primary production - autotrophic respiration

Full budget: **OCALLOCHTHONOUS** + **OCAUTOCHTHONOUS** = respiration + burial + export + ΔOC (in water column)

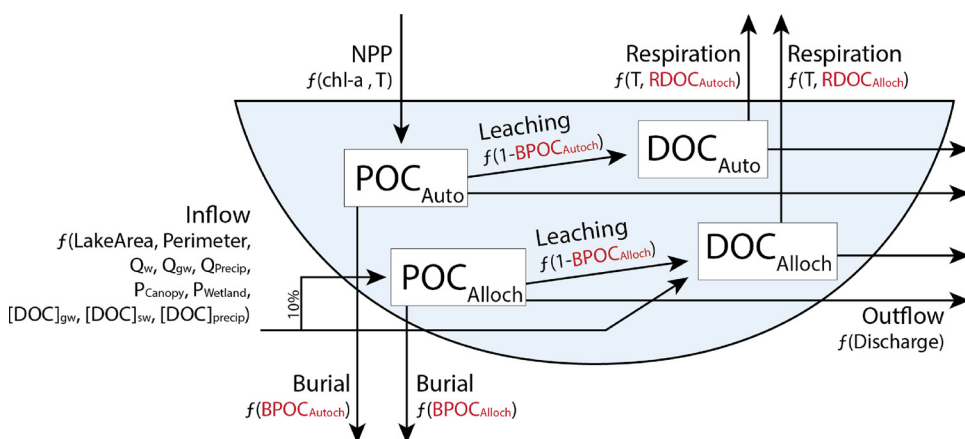


Fig. 1. Conceptual diagram of the organic carbon lake model depicting fluxes based on allochthonous (alloch; externally derived) and autochthonous (autoch; internally derived; NPP) inputs of organic carbon, long-term burial, leaching of particulate organic carbon (POC) to dissolved organic carbon (DOC), respiration of DOC to CO_2 , and export via outflow. Four parameters ($\text{RDOC}_{\text{Alloch}}$, $\text{RDOCA}_{\text{Alloch}}$, $\text{BPOC}_{\text{Autoch}}$, and $\text{BPOC}_{\text{Alloch}}$) were calibrated for each lake. Parameters and equations are defined in Tables 2 and 3.

concentrations, POC particle sizes and associated settling rates, sediment particle size and density that control resuspension, lake hydrodynamics that affect settling rates and resuspension, and benthic biogeochemistry (Downing et al., 2008; Xu et al., 2013). Methods for estimating sediment accumulation rates are diverse and commonly include functions based on lake area (Canham et al., 2004; Hanson et al. 2004), sediment cores (Yang et al., 2008; Klump et al., 2009; Heathcote and Downing, 2012), sediment traps (Jonsson et al., 2001; Ramlal et al., 2003), or bathymetry (Downing et al., 2008). A challenge associated with estimating accumulation rates is the reliance on point measurements to characterize sediment accumulation rates that can vary widely over both space and time. Allochthonous and autochthonous POC that is not buried is exported directly, mineralized, or leached in the form of DOC and exported via surface or groundwater (Cole et al., 1984). Exports represent allochthonous inputs to downstream aquatic ecosystems and therefore contribute to landscape C cycling (Kling et al., 2000).

1.5. Objective and research question

Our broad objectives were (1 to quantify long-term (i.e., > 10 year) dynamics and magnitudes of DOC fluxes through the development of a simple dynamic model, and (2 to use this model to reveal the dynamics of dominant drivers of OC fates (allochthonous vs. autochthonous load, and burial vs. respiration). We applied the model to five lakes that encompass contrasts in morphology, hydrology, and trophic state to understand the relative influence of these lake characteristics on OC cycling, and to address our overarching research question: What are the magnitudes and uncertainties in processes governing lake OC cycling and how do these change through time?

2. Methods

2.1. Study lakes and data sources

We modeled temporal dynamics of OC budgets for five lakes that span a range of limnological characteristics (e.g., hydrologic residence time, depth, trophic state; Table 1). Lakes were selected based on contrasting characteristics and availability of observational data. Required observational data included precipitation, hydrological inflow (discharge), inflow DOC concentration, and various in-lake measurements (surface water temperature, chl-*a* concentration, and Secchi depth). All lakes had a minimum of 10 years of limnological data used for model training and at least four years of in-lake DOC and DO measurements for model validation. See the appendix for detailed data descriptions and sources (Supplementary material). Our dataset included four oligotrophic lakes and one eutrophic lake. Lake areas ranged from 71.38 ha to 565,000 ha and mean depths ranged from 7 m to 27 m. Hydrologic residence times ranged from 0.8 years to 6.3 years.

In-lake mean annual DOC concentrations ranged from 3 g m^{-3} to 6 g m^{-3} . Watersheds are primarily forested for Harp Lake, Trout Lake, and Lake Vänern, whereas Toolik Lake is in a tundra-dominated watershed, and Monona is in an agricultural and heavily developed watershed.

2.2. General model approach

We developed a relatively simple, dynamic mass balance model (Fig. 1, Tables 2 and 3), that included four state variables representing OC (Table 3, Eqs. 1–4) and one representing dissolved oxygen (DO, Eq. 5). Literature-based and calibrated parameters for the equations are in Table 2. We used literature-based parameters for processes generally described in previous studies and when lake-specific information was unavailable, and to prevent overfitting of the model. Allochthonous DOC and POC (Eqs. 1–2) for the lakes were modeled separately from autochthonous DOC and POC (Eqs. 3–4). Model complexity was commensurate with the number of observational variables available. We operated the model on a daily time step for 10–13 years, based on data availability.

As all five lakes are drainage lakes with outlet streams, lake levels are relatively stable. From 1995 to 2017, Trout Lake varied < 0.5 m, and Lake Monona varied < 1 m (N. Lottig, personal communication). Lake Vänern varied < 1 m from 2003 to 2009 (Tongal and Berndtsson, 2014). Lake level, and therefore volume, was assumed static over the modeling period. Inflow discharge at a daily time step was available for all study lakes. DOC concentration of inflows was available at weekly or biweekly intervals. To model inflow DOC at a daily time step, we used the *loadflex* package in R to fit stream load models for each system (Appling et al., 2015). We first fit a regression model for each lake, which was then incorporated in a composite method, which uses model residuals from the regression model to adjust predictions based on observed data (Aulenbach, 2013; Kelly et al., 2018). After testing the nine available regression models, model 9 was used for all lakes, except Trout Lake where model 4 returned the best fit (see Kelly et al., 2018 for full regression model equations). When inflow DOC concentrations were not available for all tributaries, DOC was scaled to equal total inflow volume.

Observational data of in-lake chl-*a*, Secchi depth, and temperature were available weekly or bi-weekly and were linearly interpolated to a daily time step. Precipitation was assumed zero for missing dates; however, precipitation data gaps were rare. To account for the absence of winter data at Toolik, we set inflow DOC to 0 when the main inflow (Toolik Inlet) was frozen (Supplementary material). The model was written and executed in R version 3.3.2 (R Core Team, 2016). Model code and data are available here: <https://github.com/GLEON/SOS>.

Table 1
Lake characteristics.

Lake	Harp	Monona	Toolik	Trout	Vänern
Location	Ontario, Canada	Wisconsin, USA	Alaska, USA	Wisconsin, USA	Sweden
Lat, Long	45.38, -79.14	43.06, -89.36	68.63, -149.61	46.04, -89.69	58.87, 13.41
Data years	1991-2001	2003-2014	2001-2010	2004-2013	2001-2013
Lake area (ha)	71	1326	149	1610	565000
Perimeter (m)	4000	35200	8104	25900	2007000
z_{mean} (m)	12	8.3	7	14.6	27
RT (yr)	2.5	0.8	0.8	5.9	6.3
Trophic state	oligotrophic	eutrophic	oligotrophic	oligotrophic	oligotrophic
Secchi (m)	4.3	2.7	4.7	5.3	4.5
Chl- a ($\mu\text{g L}^{-1}$)	2.4	9.2	1.1	2.2	2.1
SW DOC (g m^{-3})	9.9	5.2	6.8	5.1	9.4
Lake DOC (g m^{-3})	4	6	5	3	4
P_{Canopy}	1.000	0.167	0.000	0.780	0.615
P_{Wetlands}	0.000	0.026	0.133	0.011	0.037
Burial rate ($\text{g m}^{-2} \text{yr}^{-1}$)	78	249	153	27	186
References	Yao et al. (2011)	NTL LTER	Kling et al. (2000)	Webster et al. (1996), NTL LTER	Kvarnäs (2001)

z_{mean} = mean depth, RT = hydrologic residence time, Secchi = Secchi depth, Chl- a = chlorophyll- a , SW DOC = inflow dissolved organic carbon, Lake DOC = in-lake DOC (mean water column). All values are means from all available model calibration data or were derived from cited references. NTL LTER = <https://lter.limnology.wisc.edu>. See Supplementary material for sources of burial rates.

2.3. Allochthonous DOC and POC

Changes in allochthonous DOC were modeled as a function of DOC load, deposition, leaching, mineralization, and export ($\text{DOC}_{\text{Alloch}}$, Eq. 1). Allochthonous DOC load was calculated as the sum of inflows (I_{DOC} , Eq. 1.1) from both surface ($I_{\text{DOC,SW}}$, Eq. 1.11) and groundwater ($I_{\text{DOC,GW}}$, Eq. 1.12), and deposition (DDOC , Eq. 1.2) from precipitation (D_{precip} , Eq. 1.21) and adjacent wetlands (D_{Wetland} , Eq. 1.22). Mass loads were calculated as the product of DOC concentrations and flows, except for D_{Wetland} , which was the product of the proportion of lake perimeter that is wetland (P_{Wetland}), a parameter representing a transfer coefficient ($\text{CDOC}_{\text{Wetland}}$) of DOC from the wetland to the lake, and lake perimeter (LakePerimeter). The third input (L_{Alloch} , Eq. 1.3) represented in-lake leaching of $\text{POC}_{\text{Alloch}}$ to $\text{DOC}_{\text{Alloch}}$ as the product of a first-order decay rate ($C_{L\text{Alloch}}$; $1 - \text{BPOC}_{\text{Alloch}}$) and the $\text{POC}_{\text{Alloch}}$ concentration. There were two fates of $\text{DOC}_{\text{Alloch}}$ (Eq. 1). The first was mineralization ($\text{MDOC}_{\text{Alloch}}$, Eq. 1.4), which was the product of a first-order decay rate ($\text{RDOC}_{\text{Alloch}}$), the $\text{DOC}_{\text{Alloch}}$ concentration, and a Q_{10} temperature adjustment using a standard Arrhenius equation. A temperature multiplier (θ) of 1.08 was used for all lakes, equating to a $Q_{10} \sim 2$ (Reynolds and Irish, 1997). The second was export downstream ($\text{EDOC}_{\text{Alloch}}$, Eq. 1.5), which was the product of $\text{DOC}_{\text{Alloch}}$ and outflow (Q_{outflow}).

Changes in allochthonous POC were modeled as a function of POC

load, deposition, leaching, burial, and export ($\text{POC}_{\text{Alloch}}$, Eq. 2). Allochthonous POC input (I_{POC} , Eq. 2.1) was modeled as a proportion of I_{DOC} ($\text{CPOC}_{\text{Factor}}$). Deposition (DPOC , Eq. 2.2) was the sum of canopy ($\text{DPOC}_{\text{Canopy}}$) and wetland ($\text{DPOC}_{\text{Wetland}}$) inputs, where $\text{DPOC}_{\text{Canopy}}$ (Eq. 2.21) was the product of the proportion of lake perimeter that is canopy (P_{Canopy}), a parameter representing a transfer coefficient ($\text{CPOC}_{\text{Aerial}}$) of POC from the canopy to the lake, and LakePerimeter. $\text{DPOC}_{\text{Wetland}}$ (Eq. 2.22) was assumed to scale with $\text{DDOC}_{\text{Wetland}}$ by the proportion $\text{CPOC}_{\text{Factor}}$. $\text{POC}_{\text{Alloch}}$ had a burial fate (B_{Alloch} , Eq. 2.3), calculated as the product of a burial coefficient ($\text{BPOC}_{\text{Alloch}}$) and $\text{POC}_{\text{Alloch}}$. As with $\text{DOC}_{\text{Alloch}}$, downstream export ($\text{EPOC}_{\text{Alloch}}$, Eq. 2.4) was included as the product of $\text{POC}_{\text{Alloch}}$ and outflow.

Daily precipitation (Q_{precip} , mm) was based on measurements from the weather station nearest to each lake. The concentration of DOC in precipitation was set to 2 g m^{-3} (Hanson et al., 2014). Time series of lake-specific groundwater inflow volume (m^3) and DOC concentration (g m^{-3}) were not available. We estimated the proportion of inflow as groundwater in our study lakes based on literature values when available, but assumed no groundwater in the absence of data (Supplementary material). Resulting estimated groundwater proportions were 0% for all lakes except Trout Lake, which we estimated at 19% (Hanson et al., 2014). Groundwater DOC concentration was assumed to be 10 g m^{-3} (Table 2: $\text{DOC}_{\text{GWConc}}$, Hanson et al., 2014). Shoreline-adjacent

Table 2
Lake model parameters (calibrated parameters italicized, $n = 4$).

Parameter	Description	Value	Units
$\text{DOC}_{\text{GWConc}}$	DOC concentration of groundwater	10	g m^{-3}
$\text{DOC}_{\text{PrecipConc}}$	DOC concentration of precipitation	2	g m^{-3}
$\text{CDOC}_{\text{Wetland}}$	Loading rate of POC from wetlands	1	$\text{g m-shoreline}^{-1} \text{d}^{-1}$
$C_{L\text{Alloch}}$	Proportion of allochthonous POC that is leached to DOC	$1 - \text{BPOC}_{\text{Alloch}}$	Unitless
$\text{RDOC}_{\text{Alloch}}$	Decomposition rate of allochthonous DOC in heterotrophic respiration	<i>Calibrated</i>	d^{-1}
θ	Temperature multiplier	1.08	Unitless
$\text{CPOC}_{\text{Factor}}$	Concentration of inflow POC relative to DOC	0.10	Unitless
$\text{CPOC}_{\text{Aerial}}$	Loading rate of aerial POC (i.e., leaf litter)	1	$\text{g m-shoreline}^{-1} \text{d}^{-1}$
$\text{BPOC}_{\text{Alloch}}$	Proportion of allochthonous POC buried in sediments	<i>Calibrated</i>	Unitless
$C_{L\text{Autoch}}$	Proportion of autochthonous POC that is leached to DOC	$1 - \text{BPOC}_{\text{Autoch}}$	Unitless
$\text{RDOC}_{\text{Autoch}}$	Decomposition rate of autochthonous DOC in heterotrophic respiration	<i>Calibrated</i>	d^{-1}
$\text{BPOC}_{\text{Autoch}}$	Proportion of autochthonous POC buried in sediments	<i>Calibrated</i>	Unitless
k	Gas flux coefficient	0.7	m d^{-1}
$R_{\text{Autotroph}}$	Proportion of GPP respired by autotrophs	0.8	Unitless

Table 3
Model equations.

No.	Equation
1	$DDOC_{Alloch}/dt = I_{DOC} + DDOC + L_{Alloch} - MDOC_{Alloch} - EDOC_{Alloch}$
2	$DPOC_{Alloch}/dt = I_{POC} + DPOC - L_{Alloch} - B_{Alloch} - EPOC_{Alloch}$
3	$DDOC_{Autoch}/dt = NPPDOC + L_{Autoch} - MDOC_{Autoch} - EDOC_{Autoch}$
4	$DPOC_{Autoch}/dt = NPPPOC - L_{Autoch} - B_{Autoch} - EPOC_{Autoch}$
5	$dDO/dt = NEPOC + F_{atm}$
Allochthonous DOC	
1.1	$I_{DOC} = I_{DOC,SW} + I_{DOC,GW}$
1.11	$I_{DOC,SW} = DOC_{SWconc} * Q_{SW}$
1.12	$I_{DOC,GW} = DOC_{GWconc} * Q_{GW}$
1.2	$DDOC = DDOC_{Precip} + DDOC_{Wetland}$
1.21	$DDOC_{Precip} = DOC_{PrecipConc} * Q_{Precip}$
1.22	$DDOC_{Wetland} = P_{Wetland} * CDOC_{Wetland} * LakePerimeter$
1.3	$L_{Alloch} = C_{L,Alloch} * POC_{Alloch}$
1.4	$MDOC_{Alloch} = RDOC_{Alloch} * DOC_{Alloch} * \theta^{(T - T_{Base})}$
1.5	$EDOC_{Alloch} = DOC_{Alloch} * Q_{Outflow}$
Allochthonous POC	
2.1	$I_{POC} = I_{DOC} * CPOCFactor$
2.2	$DPOC = DPOC_{Canopy} + DPOC_{Wetland}$
2.21	$DPOC_{Canopy} = P_{Canopy} * CPOCAerial * LakePerimeter$
2.22	$DPOC_{Wetland} = DDOC_{Wetland} * CPOCFactor$
2.3	$B_{Alloch} = BPOC_{Alloch} * POC_{Alloch}$
2.4	$EPOC_{Alloch} = POC_{Alloch} * Q_{Outflow}$
Autochthonous DOC	
3.1	$NPP_{Tot} = 10^{(1.18 + (0.92 * \log_{10}(chl-a * Z_{mix}) + (0.014 * T)) * (1 - R_{Autotroph}))}$
3.2	$NPPDOC = 0.2 * NPP_{Tot} * (chl-a * Z_{mix})^{-0.22} * (0.714)$
3.3	$L_{Autoch} = C_{L,Autoch} * POC_{Autoch}$
3.4	$MDOC_{Autoch} = RDOC_{Autoch} * DOC_{Autoch} * \theta^{(T - T_{Base})}$
3.5	$EDOC_{Autoch} = DOC_{Autoch} * Q_{Outflow}$
Autochthonous POC	
4.1	$NPPPOC = NPP_{Tot} - NPPDOC$
4.2	$B_{Autoch} = BPOC_{Autoch} * POC_{Autoch}$
4.3	$EPOC_{Autoch} = POC_{Autoch} * Q_{Outflow}$
DO	
5.1	$NEPOC = F_{atm} = NPP_{Tot} - R_{HTot}$
5.11	$NPP_{Tot} = NPPDOC + NPPPOC$
5.12	$R_{HTot} = MDOC_{Alloch} + MDOC_{Autoch}$
5.2	$F_{atm} = k * (DO - DO_{Sat}) * Z_{mix}^{-1}$

Abbreviations: I = Inflow, E = Export, D = Deposition, L = Leaching, M = mineralization, R = Respiration, B = Burial, $T_{Base} = 20^{\circ}C$.

wetlands and forests were estimated from publicly available spatial datasets (Supplementary material). We focused on wetlands adjacent to the shoreline because they contribute most of wetland-derived DOC to lakes not already captured in Eq. 1.1 (Hanson et al., 2014). To account for potential misalignment among spatial wetland and forest data and lake boundaries, we defined adjacency as within 30 m of lake boundaries.

2.4. Autochthonous DOC and POC

Our approach to modeling autochthonous inputs (Table 3, Eqs. 3–4) was generally similar to that of allochthonous inputs for leaching, mineralization, export, and burial (Eqs. 3.3–3.5, 4.2–4.3), but differed in the input terms: NPPDOC (Eq. 3.2) and NPPPOC (Eq. 4.1). Total autochthonous inputs (NPP_{TOT} , Eq. 3.1) were the product of GPP, which was modeled as a function of chl-a ($\mu g L^{-1}$), mixing depth (Z_{mix}) (set to half of photic depth; m), and surface water temperature (T , $^{\circ}C$) per Morin et al. (1999), and the proportion of GPP not respired by autotrophs ($1 - R_{Autotroph}$). The GPP function was calculated using observed temperature and chl-a data that ranged from 5 to 25 $^{\circ}C$ and 1–1000 $mg m^{-2}$, respectively, across all lakes. Since models of GPP are not well constrained at low temperatures, we set GPP to zero if surface water temperatures were $< 4^{\circ}C$. Chl-a concentrations were converted from volumetric to areal units by multiplying by photic depth, which was estimated from Secchi depth (m; Wetzel, 2001). The DOC fraction

of total NPP (NPPDOC) was calculated using the Pace and Prairie (2005) negative exponential equation (Eq. 3.2). The remainder of NPP_{TOT} was attributed to POC (NPPPOC, Eq. 4.1).

Water column dissolved oxygen (DO) was used to constrain net ecosystem production (NEPOC, Eq. 5.1), under the assumption that at short time scales and under pseudo-equilibrium conditions, atmospheric exchange (F_{atm}) approximated NEPOC. F_{atm} (Eq. 5.2) was calculated as a function of piston velocity (k), set to 0.7 $m d^{-1}$ (with no wind speed data, this is a conservative estimate), DO and DO saturation, and mixing depth (Z_{mix}). The saturation of DO (DO_{sat}) is temperature dependent and was determined using the Garcia-Benson method in the LakeMetabolizer R package (Winslow et al., 2016). Heterotrophic respiration (R_{HTot}) was calculated as a function of DOC_{Autoch} and DOC_{Alloch} concentration ($g m^{-3}$) in the photic zone, epilimnion temperature (assumed to be uniform through the photic zone), and two calibrated parameters: $RDOC_{Autoch}$ and $RDOC_{Alloch}$ (Tables 2 and 3, Eqs. 1.4, 3.4, 5.12) (see Model calibration and uncertainty analysis). We determined epilimnion temperature by averaging observed temperatures throughout the photic zone when data were available from multiple depths, but otherwise used surface temperature (Supplementary material).

2.5. Model calibration and uncertainty analysis

The collinearity of the four free parameters in the model (respiration: $RDOC_{Alloch}$, $RDOC_{Autoch}$, burial: $BPOC_{Alloch}$, and $BPOC_{Autoch}$; Table 2) was tested using the *collin* function in the R package FME (Soetaert and Petzoldt, 2010). In general, when the collinearity index is less than 20, linear independence is assumed (Brun et al., 2001; Omlin et al., 2001). Finding low collinearity, the four parameters were fit by minimizing the sum of the squared residuals of DOC and DO. DO residuals were weighted 0.25 that of DOC, and the total number of residuals was equally weighted between DO and DOC. The model was fit using a pseudo-random search algorithm in the FME package. Burial parameters were constrained in the model as a proportion between 0 (no burial of POC) and 1 (all POC is buried). $RDOC_{Alloch}$ was constrained between 0.0003 and 0.03 (d^{-1}) based on the range of OC decomposition rates for inland waters with residence times between 1–10 years presented in Catalán et al. (2016). $RDOC_{Autoch}$ was constrained between 0.003 and 0.3 (d^{-1}) (Hanson et al., 2004). Goodness of fit was evaluated with root mean square error (RMSE) and Nash-Sutcliffe efficiency (NSE) scores calculated for DOC and DO for each lake using the hydroGOF R package (Zambrano-Bigiarini, 2017). Goodness of fits were reported for DOC and DO because the model was fit to both simultaneously rather than individually. A sensitivity analysis of each parameter was conducted by allowing the parameter to vary at 100 different values within the set bounds while fixing the other three parameters at their calibrated values.

We estimated parameter means and uncertainties using a bootstrapping routine (per Dugan et al., 2017). Using the bootstrapped parameters, we calculated residual errors between observed and modeled DOC and DO. We created 100 pseudo-observational datasets by randomizing these residuals 100 times and adding each randomized residual set to the observed data. We then re-fit the parameters to the pseudo-observational datasets to provide 100 new parameter estimates. Finally, we recorded parameter distribution characteristics and assessed correlations among parameters within each lake.

3. Results

3.1. Model performance, parameter estimates, and sensitivity analysis

Modeled DOC and DO generally followed observed temporal patterns across years in each study lake (Fig. 2). The RMSE of the model fits for DOC and DO were below 0.6 $mg L^{-1}$ and 1.7 $mg L^{-1}$, respectively (Table 4). The NSE metric reveals if the modeled results are more

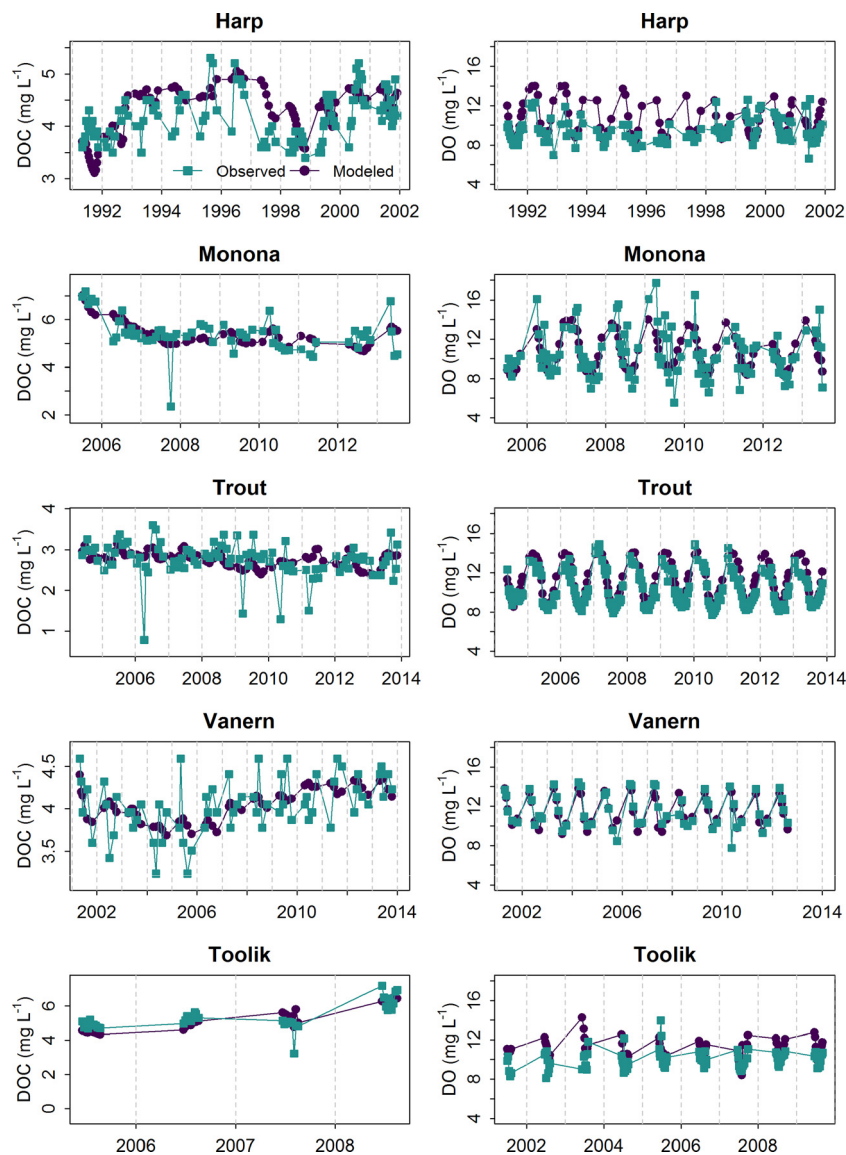


Fig. 2. Observed dissolved organic carbon (DOC) and dissolved oxygen (DO) concentrations in each lake (teal squares) compared to modeled concentrations (purple circles) for the same date. For some lakes, years differed between DOC and DO based on availability of observed data (Supplementary material). Toolik data are temporally clustered due to the short ice-free season (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

accurate ($NSE > 0$) than the long-term mean. NSE reveals strong model fits for Lake Monona and Vänern for both DOC and DO (Table 4). Trout Lake and Harp Lake had poor fits for DOC ($NSE < 0$), and Toolik and Harp Lake had poor fits for DO ($NSE < 0$). In these lakes, the model captured annual and seasonal DOC and DO dynamics, but did not consistently characterize the magnitude of short-term spikes in DOC (i.e., days to weeks; Fig. 2). Nonetheless, long-term model performance indicated the ability to account for lake variability in DOC and DO at

seasonal to inter-annual time scales.

Across all lakes, parameter estimates for the allochthonous components of the budget were generally more consistent and better constrained than those for autochthonous inputs (Table 4). Respiration of allochthonous DOC ($RDOC_{Alloch}$) ranged from about 0.0011–0.0025 d^{-1} among lakes and SEM values were about two orders of magnitude lower, indicating tightly constrained mean values. In contrast, respiration of autochthonous DOC ($RDOC_{Autoch}$) was higher and more

Table 4

Model goodness of fit and estimates of the parameter means (parentheses include standard error of the mean estimate, SEM). All parameters had a collinearity < 20 and were assumed independent. RMSE = root mean square error ($mg L^{-1}$), NSE = Nash-Sutcliffe Efficiency score.

Lake	RMSE (DOC)	NSE (DOC)	RMSE (DO)	NSE (DO)	$RDOC_{Alloch}$ (d^{-1})	$RDOC_{Autoch}$ (d^{-1})	$BPOC_{Alloch}$	$BPOC_{Autoch}$
Harp	0.55	-0.46	1.52	-0.64	0.0025 (2.1e-5)	0.0034 (9.4e-5)	1.0000 (4.2e-5)	0.8400 (2.2e-2)
Monona	0.61	0.31	1.74	0.45	0.0009 (9.3e-5)	0.1600 (1.3e-2)	0.4100 (3.2e-2)	0.6800 (3.5e-2)
Toolik	0.51	0.52	1.38	-1.42	0.0025 (3.2e-5)	0.0350 (5.6e-3)	1.0000 (1.4e-5)	0.0310 (1.7e-2)
Trout	0.47	-0.20	0.86	0.73	0.0014 (4.7e-5)	0.0320 (7.6e-3)	0.9300 (2.4e-2)	0.8700 (2.8e-2)
Vänern	0.28	0.23	1.01	0.65	0.0011 (5.1e-5)	0.4500 (8.0e-2)	0.9500 (1.8e-2)	0.5900 (4.7e-2)

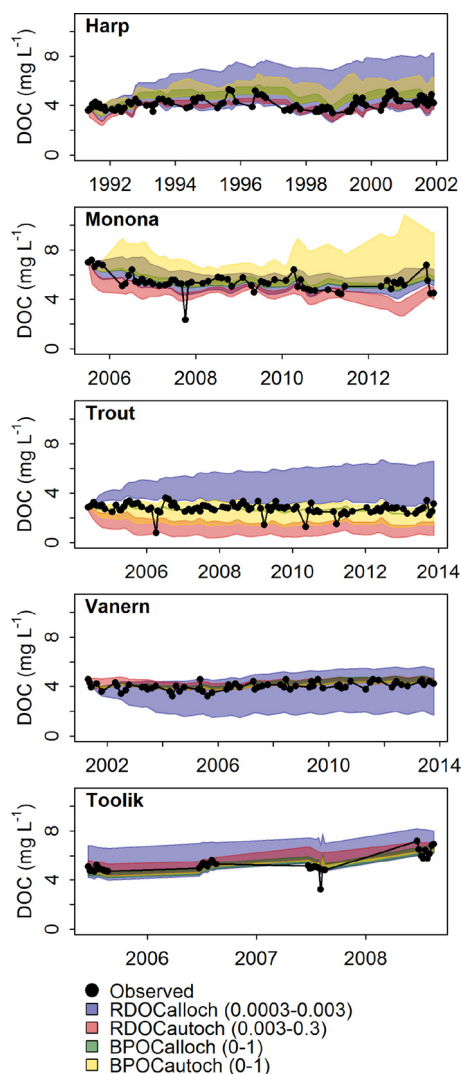


Fig. 3. Sensitivity of modeled dissolved organic carbon (DOC) concentrations to free parameters in the model. Each parameter was varied across a given range ($RDOC_{Alloch}$ 0.0003–0.003 d^{-1} , $RDOC_{Autoch}$ 0.003–0.3 d^{-1} , $BPOC_{Alloch}$ 0–1, $BPOC_{Autoch}$ 0–1) while the other three parameters remained fixed at their calibrated values. Shaded areas represent the range of modeled DOC concentrations as each parameter was varied. Black circles represent observed in-lake DOC concentrations.

variable than $RDOC_{Alloch}$ among lakes, ranging from about 0.0034–0.4500 d^{-1} . Burial rates for allochthonous inputs ($BPOC_{Alloch}$) were high, with values at or near the upper limit (1.0000 d^{-1}) for all lakes except Lake Monona. Burial of autochthonous inputs ($BPOC_{Autoch}$) was comparatively lower and more variable, ranging from approximately 0.0310–0.8700 d^{-1} . SEM values for burial tended to be about one order of magnitude smaller than corresponding parameter means across all lakes.

Modeled DOC ($mg L^{-1}$) was generally most sensitive to $RDOC_{Alloch}$, except for Lake Monona, for which modeled DOC was most sensitive to $BPOC_{Autoch}$ (Fig. 3). The other four lakes were minimally affected by changes in $BPOC_{Autoch}$ ($< 1 mg L^{-1}$ difference across the range of parameter values). Changes in $BPOC_{Alloch}$ had consistently small effects ($< 2 mg L^{-1}$) on modeled DOC across all lakes. Trout Lake, Harp Lake and Lake Vanern were the most sensitive to $RDOC_{Alloch}$, with modeled DOC ranging about 2–3 $mg L^{-1}$ across the range of parameter values, whereas Toolik Lake and Lake Monona were moderately sensitive (1–1.5 $mg L^{-1}$ differences) and Lake Vanern. Overall, parameter sensitivity was greatest for Harp Lake, Lake Monona, and Trout Lake, for

Table 5

Summary of modeled mean annual mass balances ($g m^{-2} yr^{-1}$), including allochthonous (Alloch) and autochthonous (Autoch) loads, respiration (Resp), burial, and export. Standard deviations (SD) of the annual means are in parentheses.

Lake	Alloch	Autoch	Total Load	Resp	Burial	Export
Annual means						
Harp	40.05 (10.85)	31.97 (8.01)	72.01 (11.53)	26.05 (3.01)	26.60 (5.38)	18.29 (4.76)
Monona	64.79 (24.30)	54.09 (17.98)	118.88 (21.77)	17.14 (0.97)	43.13 (12.89)	59.62 (20.06)
Toolik	76.06 (64.95)	11.27 (3.36)	87.33 (63.07)	24.60 (3.23)	5.71 (3.73)	55.68 (54.85)
Trout	15.65 (3.70)	28.05 (4.56)	43.69 (5.75)	33.04 (3.57)	7.46 (1.12)	3.96 (0.83)
Vänern	31.95 (5.61)	26.08 (4.60)	58.03 (5.61)	25.10 (1.87)	19.96 (3.10)	12.18 (2.47)
Proportion of total load						
Harp	0.55	0.44	1.00	0.36	0.37	0.25
Monona	0.54	0.46	1.00	0.14	0.36	0.50
Toolik	0.87	0.13	1.00	0.28	0.07	0.64
Trout	0.36	0.64	1.00	0.76	0.17	0.09
Vänern	0.55	0.45	1.00	0.43	0.34	0.21

which modeled DOC varied as much as 5–6 $mg L^{-1}$ across the range of parameter values (Fig. 3). Conversely, modeled DOC varied no more than 2 and 3 $mg L^{-1}$ for Toolik Lake and Lake Vanern, respectively.

3.2. Summary of fluxes and fates

With the exception of Trout Lake, OC loads were primarily driven by allochthonous inputs, underscoring the importance of terrestrially derived OC in overall lake budgets (Table 5, Fig. 4). Additionally, respiration exceeded burial in all lakes but Lake Monona. Trout Lake also had the smallest total annual OC load of the five lakes (43.69 $g m^{-2} yr^{-1}$), the lowest proportion of total load exported (0.09), and the largest proportional difference between respiration (0.76) and burial (0.17) among all lakes. Lake Monona had the largest total OC load (118.88 $g m^{-2} yr^{-1}$) among lakes, lowest proportion respired (0.14) and second-greatest proportion buried (0.36). Lake Monona was the only lake dominated by burial long-term; on average, burial rates were greater than twice respiration rates across modeled years. In contrast, proportions of burial (0.36) and respiration (0.37) in Harp Lake were approximately equal. Harp Lake also exhibited proportions of allochthonous (0.55) and autochthonous inputs (0.45) that were approximately similar in Lake Monona and Lake Vanern. Toolik Lake had the second largest (mean = 87.33 $g m^{-2} yr^{-1}$) but most variable (standard deviation; SD = 63.07 $g m^{-2} yr^{-1}$) total OC load and was the most driven by allochthonous inputs (0.87) among all lakes. This inter-annual variability in total OC load for Toolik Lake was driven by highly variable allochthonous inputs (SD = 64.95 $g m^{-2} yr^{-1}$), and also resulted in highly variable export (SD = 54.85 $g m^{-2} yr^{-1}$). Compared to other lakes, Toolik Lake on average demonstrated the lowest proportion buried (0.07) and greatest proportion exported (0.64).

3.3. Seasonal fates

Seasonal patterns in OC fluxes were consistent across entire respective time series for each lake, with autochthonous inputs and respiration increasing to a summer maximum (Fig. 4). As water temperatures increased during the growing season (e.g., May–Aug.), the balance between allochthonous and autochthonous inputs generally shifted toward autochthonous inputs due to increases in NPP, whereas the ratio between respiration and burial generally shifted towards respiration (Figs. 4 and 5). There was high seasonal variability in the

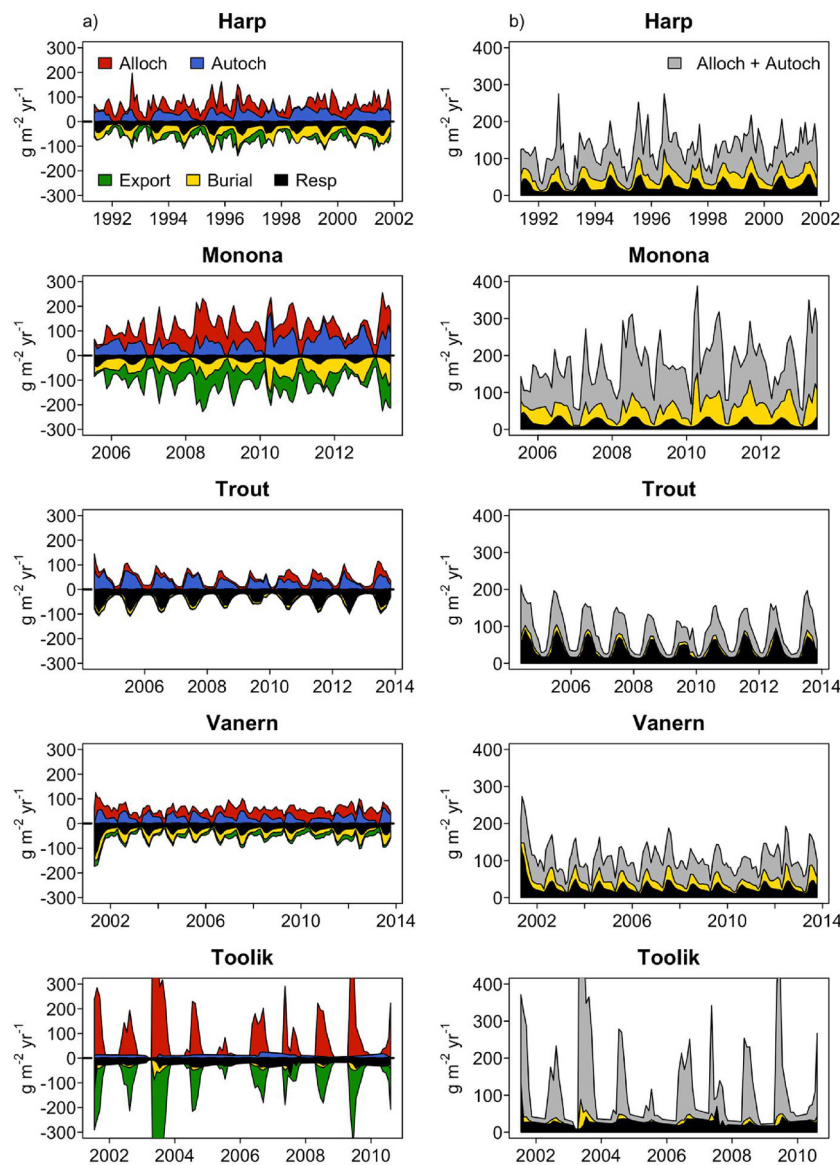


Fig. 4. Time series of organic carbon fluxes and fates. a) Colored areas represent magnitudes of input (allochthonous and autochthonous) and output fluxes (export, burial, and respiration). All lines are stacked to show cumulative magnitudes. b) Absolute values of burial, respiration, and input fluxes. Vertical axes for Toolik Lake plots were truncated to enable visualization of relatively lower fluxes. Maximum allochthonous inputs and export for Toolik Lake were 1378 and -868 $\text{g m}^{-2} \text{yr}^{-1}$, respectively (May 2003).

dominant fluxes in each lake (Fig. 5). Trout Lake remained dominated by respiration year-round, but respiration increased relative to burial as water temperatures warmed. Harp Lake and Lake Vänern were dominated by burial early in the growing season, but became dominated by respiration as temperatures warmed. Whereas respiration in Lake Monona exceeded burial late in the growing season, the lake remained dominated by burial when calculated on an annual basis (Table 5, Fig. 5). Toolik lake was dominated by respiration most of the year, and respiration increased as the ratio of autochthonous to allochthonous inputs increased. This distinct negative slope as the growing season progressed was unique to Toolik Lake, suggesting the importance of continued allochthonous inputs during summer months in the other lakes in addition to autochthonous inputs. Overall, these seasonal dynamics suggest that water temperatures are associated with changes in the balance between key OC fates (burial and respiration), but that such shifts are mediated by the balance between allochthonous and autochthonous inputs that vary across lake systems.

4. Discussion

4.1. Representing lake processes

Although our model is not exhaustive in accounting for all OC pathways and relies on empirically-derived equations, our results indicated that a relatively simple, dynamic model can recreate long-term trends in DOC and represent the set of key biogeochemical, trophic, and landscape processes that combine to determine the fate of OC in lake ecosystems. Further, the fluxes we modeled were within the range of other published studies for these lakes based on steady-state models. Using much of the same LTER data, Hanson et al. (2014) provided similar estimates for Trout of allochthonous inputs (Hanson: 15.92 $\text{g m}^{-2} \text{yr}^{-1}$, our model: 15.65 $\text{g m}^{-2} \text{yr}^{-1}$), burial (Hanson: 3.66 $\text{g m}^{-2} \text{yr}^{-1}$, our model: 7.46 $\text{g m}^{-2} \text{yr}^{-1}$), and export (Hanson: 4.95 $\text{g m}^{-2} \text{yr}^{-1}$, our model: 3.96 $\text{g m}^{-2} \text{yr}^{-1}$), but not for respiration (Hanson: 7.31 $\text{g m}^{-2} \text{yr}^{-1}$, our model: 33.04 $\text{g m}^{-2} \text{yr}^{-1}$), likely because Hanson et al. (2014) did not account for autochthonous inputs. Similar to our study, Whalen and Cornwell (1985) demonstrated that Toolik Lake was driven

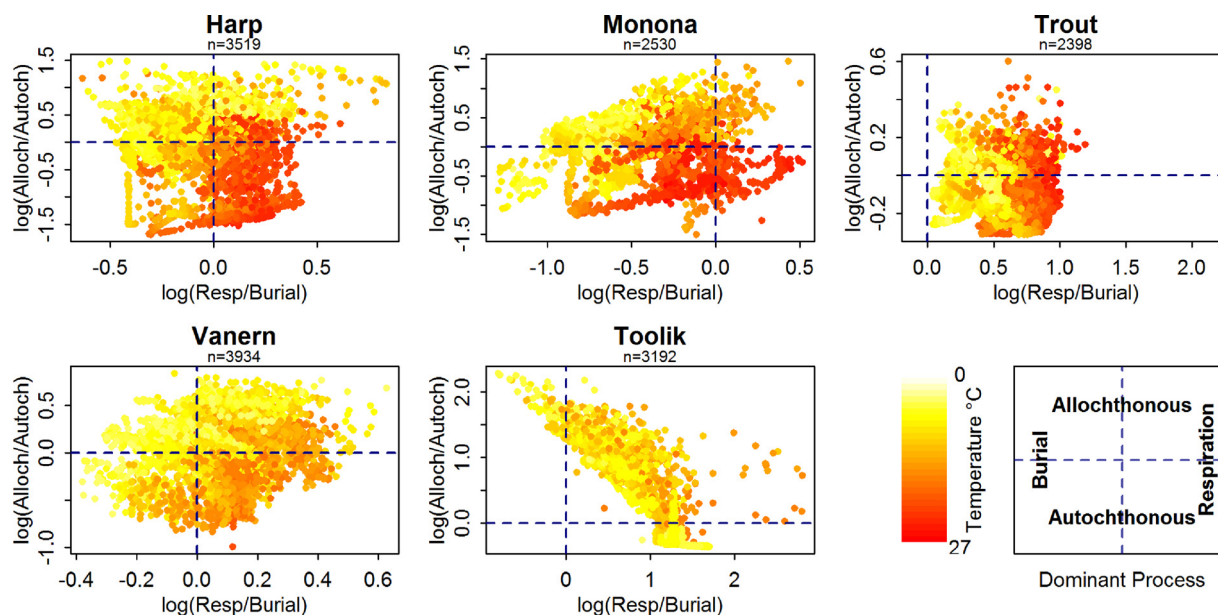


Fig. 5. Relationship between \log_{10} -transformed allochthonous/autochthonous inputs and respiration/burial ($\text{g m}^{-2} \text{yr}^{-1}$) of organic carbon, colored by epilimnion water temperature. The four quadrants in each figure represent the dominant processes in each lake (Vertical axis: dominant OC fate; horizontal axis: dominant OC input).

by high proportional allochthonous inputs (Whalen and Cornwall 0.91, our study: 0.87) relative to autochthonous inputs and low burial (Whalen and Cornwall: 0.02, our study: 0.07). Our proportion exported (0.64) contrasted somewhat with Whalen and Cornwall (0.82), but much of this excess export was respired (0.28) in our model. Dillon and Molot's (1997) proportional estimates for burial in Harp Lake were low compared to ours (Dillon and Molot: 0.01, our model: 26.60) and the magnitudes of allochthonous inputs were somewhat similar (Dillon and Molot: $28.9 \text{ g m}^{-2} \text{ yr}^{-1}$, our study: $40.05 \text{ g m}^{-2} \text{ yr}^{-1}$), but Dillon and Molot (1997) did not consider autochthonous inputs. Therefore, we are unable to compare total loads and differences in the proportion exported in Dillon and Molot (0.58) vs. our study (0.25), which may be explained by our inclusion of autochthonous inputs and respiration.

Differences in budget estimates may also be due to differences in study years (Dillon and Molot: 1981–1989, our study: 1991–2001). Although our results generally agreed with prior studies based on steady-state models, our estimated respiration rates were generally higher than those noted in the literature (Hanson et al., 2014; Dillon and Molot, 1997). We offer that dynamic models better represent these processes by accounting for seasonal changes in temperature and chl-*a* concentrations. Therefore, although steady-state models may be sufficient for recreating some key ecological processes, dynamic models are needed for determining the relative magnitudes of OC fates in lake ecosystems, given the importance of autochthonous inputs and respiration.

4.2. Key uncertainties in OC fates

Well-constrained estimates of OC burial in lakes remain a challenge to model. Although our estimates for burial parameters have relatively low uncertainties (Table 4), burial may be underestimated for these lakes. The sensitivity analysis revealed that modeled DOC generally varied $< 2 \text{ mg L}^{-1}$ as a function of $\text{BPOC}_{\text{Alloch}}$, which accounted for up to 50% of modeled DOC (except for Lake Monona, which was highly sensitive to $\text{BPOC}_{\text{Alloch}}$). A key consideration is that our model buried close to 100% of $\text{POC}_{\text{Alloch}}$ in all lakes except Lake Monona (Table 4: $\text{BPOC}_{\text{Alloch}}$); therefore, any increase in $\text{POC}_{\text{Alloch}}$ would be directly proportional to increases in burial. Owing to lack of observational data, we assumed $\text{POC}_{\text{Alloch}}$ was 10% of $\text{DOC}_{\text{Alloch}}$ ($\text{CPOC}_{\text{Factor}}$), but this may

be an underestimate, and does not account for potential seasonal variation in the DOC:POC ratio. Intense precipitation can increase POC concentration disproportionately to DOC concentration in streams (Jeong et al., 2012; Dhillon and Inamdar, 2013), which could temporarily increase $\text{POC}_{\text{Alloch}}$ and thus burial. Wet years increase $\text{DOC}_{\text{Alloch}}$ inputs to lakes at regional scales by increasing connectivity among waterbodies (Rose et al., 2017) and mobilizing DOC from soils (Tank et al., 2018), and probably also increase $\text{POC}_{\text{Alloch}}$; however, short-term spikes in POC are unlikely to have large effects on long-term OC budgets and ratios between POC and DOC. Although our burial estimates were somewhat uncertain due to underrepresentation of $\text{POC}_{\text{Alloch}}$ during precipitation events, burial would have to increase substantially over the course of the entire modeling period for burial to dominate over respiration, including three-fold or greater for Toolik Lake and Trout Lake (Table 5). Therefore, missing $\text{POC}_{\text{Alloch}}$ likely leads to underestimates of burial, but is unlikely to account for enough OC to affect long-term budgets and exceed the magnitudes of respiration in many lake ecosystems given the insensitivity of modeled DOC to $\text{BPOC}_{\text{Alloch}}$ across our five study lakes.

4.3. On-going research and data needs

Our work is an important advance in quantifying the fates of OC across aquatic ecosystems; however, we encountered constraints associated with current data availability. If requisite data were collected for a larger number of lakes spanning wider environmental gradients (e.g., climate, watershed conditions, trophic state, water residence times), contributions of lakes to landscape carbon cycles could be better estimated at broad spatial scales (Hotchkiss et al., 2018; Jones et al., 2018; Seekell et al., 2018). Although we designed our modeling framework to be flexible across different lake ecosystems, our study contained four north-temperate lakes and one arctic lake, all of which were deep and dimictic (summer and winter stratification and spring and autumn mixing of the water column). Literature-based parameters were obtained from previous research on these lake ecosystems and may not apply in all other lake ecosystems. Future work should include additional high-latitude, tropical, or shallow lakes to test the generalizability of our model across a more diverse set of lake ecosystems than those included in this study. Nonetheless, part of our intention for

including model data and code with this manuscript was so that future work can build off our model and make adjustments as more data across more diverse lake ecosystems become available.

During model development, we encountered a notable paucity of high-frequency measurements of inflow DOC concentration, of which broader collection would facilitate dynamic OC modeling in more lakes. Although collection of these data may be expensive and logistically challenging, the increasing availability of automated, high-frequency sensor equipment may alleviate long-term costs associated with sensor deployment and manual data retrieval. In addition, relatively little is currently known about POC budgets despite their key interactions with DOC (Einsle et al., 2001); we need more POC observational data for incorporation into dynamic models of OC, particularly in inflows for estimating POC_{Alloch} . Such studies would help constrain POC parameters and improve estimates of the fates of POC within overall OC budgets. Finally, data limitations required us to make simplifying assumptions about the volume of groundwater inputs and the lakes themselves. Although these are common assumptions in similar mass balance studies, the inability to account for groundwater may lead to underestimates of allochthonous inputs and may complicate comparisons across lakes, particularly isolated lakes. The one lake with non-zero estimated groundwater volume, however, was Trout Lake, for which modeled allochthonous inputs were lowest across lakes in this study. Nonetheless, a key implication of our study is the need for more observational data, particularly pertaining to surface water and groundwater volume and DOC concentrations, POC cycling, and burial rates.

Additionally, data limitations may explain poor NSE scores (< 0) for DOC for Harp Lake and Trout Lake, which indicate that modeled DOC was no more accurate than long-term DOC means (Table 4). For Harp Lake, modeled DOC was generally lower than observed DOC (Fig. 3), potentially due to artificially low DO measurements, which reduced NSE for DO for Harp Lake. Underestimated DO would lead to underestimated respiration, which would reduce autochthonous inputs. For Trout Lake, the model did not capture short-term spring-time dips in DOC (Fig. 3), which may potentially be explained by ice melt dynamics not represented in interpolated inflow DOC data. In addition, NSE was also poor for DO for Toolik Lake; modeled DO was consistently higher than observations (Fig. 3). This suggests overestimated autochthonous inputs and therefore underestimated allochthonous inputs, which may be attributed to undetected pulses in inflow DOC in surface water or groundwater. Additionally, food web dynamics (e.g., grazing) may also help explain large fluctuations in allochthonous inputs or poor NSE values. In general, whereas short-term spikes are unlikely to affect long-term OC fate estimates, consistent biases in observations may skew model outputs. Therefore, dynamic models such as ours can be used to identify important sources of uncertainty in overall OC budgets that can be targeted in future monitoring and research.

4.4. Lessons from a dynamic model: implications in a dynamic world

Prior to our study, it was known that lakes actively process, emit, and store globally significant amounts of C (Cole et al., 2007; Tranvik et al., 2009; Raymond et al., 2013). Our results demonstrate that a dynamic model can considerably advance knowledge on the role of lakes in landscape and ultimately global C cycling by highlighting dominant inputs and fates of OC in individual systems. Lakes more readily respire more autochthonous than allochthonous OC (Wetzel, 2001). In our study, our one lake dominated by autochthonous inputs (Trout Lake) exhibited the greatest respiration relative to burial (Table 5). Therefore, lakes as global C sources or sinks may depend both on the balances between 1) respiration and burial and 2) allochthonous and autochthonous inputs. The balance between respiration and burial can vary according to regional climate, and respiration is typically greater than burial in boreal lakes compared to those in higher latitudes (Anthony et al., 2014). This represents a potential negative feedback for

the global C cycle under a warming climate with poleward boreal advance and thawing of frozen, high-latitude lakes (Anthony et al., 2014).

Our model identified another important global change implication associated with warming water temperatures. Across all lakes in our study, warm surface temperatures were generally associated with a shift toward autochthonous relative to allochthonous inputs, as well as an increase in respiration relative to burial (Fig. 5). This likely is due to elevated NPP during summer growing seasons accompanied by relatively high respiration rates of autochthonous relative to allochthonous inputs (Table 4). Although the balance between respiration and burial appears to shift toward respiration with increases in temperature, it is also possible for burial to increase with temperature if temperature increases coincide with greater OC loads (e.g., warm-season precipitation events increasing POC_{Alloch} and consequently burial as a function of $BPOC_{Alloch}$). As such, our results suggest that processes favoring allochthonous inputs will generally have a greater effect on OC burial than processes that drive autochthonous inputs.

More broadly, however, lakes have generally become more productive under recent climate warming (Kraemer et al., 2016), which our study suggests favors autochthonous over allochthonous inputs and respiration over burial. Therefore, changes in both precipitation (including magnitude, timing, duration, and form) (de Wit et al., 2018) and air temperature have key implications for the fate of OC in lake ecosystems under a changing climate (Reed et al., 2018); however, effects of warming will vary according to the balance between allochthonous and autochthonous inputs, which is mediated by precipitation due to its effect on the origin of the total OC load. Although our model was not designed as a predictive tool, our findings illustrate the usefulness of a dynamic mass balance model for highlighting key global change processes and interactions that ultimately influence the role of lakes in global C cycling. Improved estimates of the contribution of lakes to global C budgets should account for the source and degradability of total OC loads and consequent effects on respiration and burial.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.ecolmodel.2018.08.009>.

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