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Title: Source or sink? Integrating biogeochemical, trophic and landscape processes to model lake organic carbon budgets

Source or sink? Dominant processes in organic carbon cycling in lakes revealed by dynamic mechanistic modeling

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## **ABSTRACT**

Lakes are active processors of organic carbon (OC) and are thought to play important roles in landscape and global carbon cycles. Lakes integrate terrestrially derived OC from their surrounding watersheds, produce and consume OC during primary production and respiration, bury OC in lake bottom sediments and export OC via surface or groundwater outflows. Although these processes provide a basis for a conceptual understanding of lake OC budgets, few studies have integrated these various fluxes under a dynamic modeling framework to examine their interactions and relative magnitudes. We developed a flexible, dynamical mass balance model for OC rooted in our conceptual understanding of lake OC budgets and applied the model to 5 lakes that span a gradient of morphological characteristics. We examined the relative importance of OC fluxes and found that long-term lake OC dynamics were predominantly driven by allochthonous loads in 4 of the 5 lakes, underscoring the importance of terrestrially-derived OC in lake ecosystems. Burial, the main OC storage mechanism in lakes, represented a relatively small component of the total budget and was driven largely by autochthony. Respiration, the mechanism by which lakes export carbon to the atmosphere, ranged from 14.6-87.9% of total budgets. Given the relatively low rates of burial compared to respiration across lakes in 4 of the 5 lakes, we concluded that these lakes represented a net OC source. The exception was Lake Monona, Wisconsin, the most eutrophic lake in our dataset. Overall, we found that lakes generally transitioned seasonally from OC sinks to sources as water temperatures and lake productivity increased. Finally, we highlight critical research needs, which include the need for surface water DOC observations in paired river and lake settings, burial rates, and budgets of particulate OC. These data will help better constrain parameter estimates in future lake OC models and improve our understanding of landscape carbon cycling.

Key words: carbon cycle, limnology, mass balance, allochthony, autochthony, sedimentation, dissolved organic carbon, particulate organic carbon, LTER

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## **INTRODUCTION**

In this era of rapid environmental changes, understanding of the global carbon cycle is critically important for scientists, policymakers, and society as a whole. Whereas interests have largely focused on fossil fuel emissions, oceans, deforestation, and other land cover changes, we draw attention to the role of inland waters, particularly lakes, in the cycling of organic carbon (OC). Although it has been recognized that lakes actively process rather than simply transport terrestrially derived OC (Cole et al. 2007, Tranvik et al. 2009), as well as emit inorganic carbon to the atmosphere (Arvola et al. 2002, Weyhenmeyer et al., 2015, Raymond et al., 2013), efforts to model the internal processing of OC in lakes that adequately incorporate all critical OC fluxes (i.e., “mass balances”) through time are still relatively uncommon. Further, mass balances that have been published are generally confined to single lakes, and tend to be concentrated in boreal regions (e.g., Jonsson et al. 2001, Urban et al. 2005, Andersson and Sobek 2006, Cremona et al. 2014).

### *Overview of concepts of key OC fluxes in lake ecosystems*

The term “mass balance” has been broadly used to describe attempts to quantify nutrient budgets (not strictly OC) of a lake as the combination of inputs, internal processes and outputs. Inputs to lakes represent the sum of allochthonous (external derived) dissolved (DOC) and particulate OC (POC) inflows from surface or groundwater sources, precipitation and litterfall. Internal processes consist of autochthonous (in-lake) mechanisms that produce, consume and store OC (i.e., primary production, respiration, burial in sediments). Outputs comprise DOC and POC pools that exit a lake via surface or groundwater exports. Importantly, a lake does not function as simply a “source” or “sink” of OC. Lakes are carbon sinks (via burial), while at the same time acting as a source of carbon to the atmosphere (via respiration)..

described asclassifiedthe flux of across the air-water interface, and have not considered other carbon fluxes. Likewise, it has been recognized that lakes store OC in sediments, and therefore may act as important sinks in the global carbon cycle (Mulholland and Elwood 1982, Dillon and Molot 1997, Dean and Gorham 1998, Einsele et al. 2001, Kortelainen et al. 2004, Rantakari and Kortelainen 2005, Einola et al. 2011, Raymond et al. 2013). However, the magnitude of burial has not been adequately compared to other important fluxes in overall lake OC budgets (Hanson et al. 2015), precluding determination of net lake function in terms of OC. Here, we examine the dominant processes in lake OC cycling, and provide broad definitions of sources and sinks for lake OC to account for the interacting nature of fluxes (Box 1).

***Box 1. Mass balance conceptual equations for organic carbon in lake ecosystems***

*Allochthony:* surface and groundwater inflows + litterfall + atmospheric deposition

*Autochthony*: gross primary production - autotrophic respiration - heterotrophic respiration

*Pipe*:Export> Respiration + Burial

*Processor*: Export< Respiration + Burial

*Net Source*: Burial < Respiration

*Net Sink*: Burial > Respiration

*Full budget*: allochthony + autochthony = Respiration + Burial + Export+ ΔOC storage (in water column)

A limitation of many existing mass balance studies is oversimplification or inability to account for these key carbon fluxes that constitute the full budget. These fluxes interact with each other, underscoring the importance of including them together in a unified model framework. We synthesized existing knowledge of lake OC budgets into a conceptual model that integrates these important mechanisms, including both in-lake as well as external (i.e., watershed) processes. Below we described these mechanisms in three main categories 1) allochthony, 2) autochthony and 3) export.

### *Allochthony*

Allochthonous inputs include surface and groundwater inflows, litterfall and direct-fall precipitation. Although surface water inflows regularly deliver OC to lake ecosystems, the role of terrestrially derived OC from these inflows is perhaps the most commonly ignored set of processes in OC budgets, largely owing to data limitations (Hanson et al. 2015). These inflows originate from streams, wetlands and groundwater, each of which is affected by seasonal patterns of temperature and precipitation, as well as surrounding landscape composition. Prior studies have used direct measurements of inflow stream concentrations of OC when available (Schindler et al. 1997, Jonsson et al. 2001, Ramlal et al. 2003, Aberg et al. 2004, Urban et al. 2005, Klump et al. 2009, Xu et al. 2013, Cremona et al. 2014, Hanson et al. 2014), but other approaches have included use of literature-derived input estimates (Striegl et al. 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). Although groundwater delivers OC to lakes, especially when groundwater passes through organic-rich soils (Schindler and Krabennhoft 1998), groundwater volume and OC concentration data are rare and difficult to estimate (Hanson et al. 2014). In lakes without permanent tributaries, groundwater may be the dominant source of hydrological input (e.g., Gaiser et al. 2009). Inputs from litterfall, direct-fall precipitation and atmospheric deposition are generally small and have been estimated as a function of static load parameters and lake area (Hanson et al. 2004).

### *Autochthony*

Autochthonous OC is produced as a function of gross primary production (GPP) and autotrophic and heterotrophic respiration. These processes vary as a function of nutrient inputs and seasonal, ambient lake conditions. DOC supports a significant fraction of respiration in most lakes, affirming the importance of accounting for food web relationships and their effects on lake OC budgets (Cole et al. 2000). Similar to surface and groundwater inflows, GPP and respiration are commonly ignored in OC budgets owing to data limitations. Approaches previously employed to estimate GPP and respiration include measured dissolved oxygen (DO) (Cole et al. 2002, Staehr et al. 2010), total phosphorus (TP) (Hanson et al. 2004) or chlorophyll-A (ChlA) (Jonsson et al. 2001, Ramlal et al. 2003). Other methods include bottle incubation (Urban 2005, Yang et al. 2008) or static proportions of the overall OC pool (Aberg et al. 2004).

*Export*

Among the other fluxes in OC budgets, perhaps the most critical to source or sink dynamics is burial of both allochthonous and autochthonous OC. Burial is the storage of carbon in bottom sediments and is the main “sink” pathway for carbon in lakes (Cole et al. 2002, Tranvik et al. 2009). Permanent OC burial in lakes is a product of in-lake POC concentrations, POC particle sizes and associated settling rates, sediment particle size and density that affect resuspension, lake hydrodynamics that affect settling rates and resuspension and benthic biogeochemistry (citations to be added). The complexity associated with modeling each of these mechanisms cannot be well represented in a single-node model; uncertainties associated with each mechanism would likely yield questionable results. Methods for estimating sediment accumulation rates are diverse and have commonly included functions based on lake area, particularly for studies containing a large number of lakes (Canham et al. 2004, Hanson et al. 2004). Some studies have used historical accumulation rates measured from sediment cores (Yang et al. 2008, Klump et al. 2009, Xu et al. 2013), sediment traps (Jonsson et al. 2001, Ramlal et al. 2003), or estimates based on changing bathymetry (Downing 2008). A challenge associated with estimating accumulation rates is the reliance on sparsely distributed point measurements to characterize sediment accumulation rates that can vary dramatically over both space and time.

Quantities of allocthonous and autochthonous POC not buried are leached to DOC or exported (Cole et al. 1984). Exports may serve as allochthonous inputs to other aquatic ecosystems including lakes and therefore play an important role in landscape carbon cycling (Kling et al. 2000). A small amount of water relative to lake volume evaporates depending on seasonal weather conditions, but we did not account for this process. Finally, under anoxic conditions in the hypolimnion, buried sediments may undergo resuspension and release OC back into the water column (reference? This was from a Mindy comment).

### *Objective and research questions*

We integrated the various OC fluxes described above into a dynamical mass balance model applied over a heterogeneous set of 5 lakes. Our broad objective was to develop a flexible model that represented the magnitudes of key fluxes over time. We applied the model to ask the following questions:

1. What is the relative importance of mechanisms that drive lake OC budgets and lake function as net sources or sinks?
2. Under what conditions are lakes likely to be net sources or sinks of OC?

## **METHODS**

### *Study lakes and data sources*

We modeled OC budgets for 5 lakes that spanned a range of environmental conditions and limnological characteristics (e.g., hydrological residence time, depth) (Table 1). Lakes were selected primarily based on observational data availability. Lake Monona and Trout Lake (Wisconsin, USA), Lake Vanern (Sweden) and Harp Lake (Ontario, Canada) all are situated in north-temperate continental climates, whereas Toolik Lake (Alaska, USA), which sits 304 km north of the Arctic Circle, occurs in a subarctic climate based on Koppen classification (S1). Necessary observational data included daily precipitation, daily hydrological inflow (discharge), sub-annual inflow DOC concentration and sub-annual in-lake measurements (surface temperature, ChlA, and Secchi depth). Land cover datasets were used to calculate the proportion of lake shorelines occupied by forests and wetlands. All lakes had a minimum of 10 years of limnological data used for model training (Table 1) and at least 4 years of in-lake DOC and DO measurements for model validation. See supplemental material for detailed data descriptions (S2).

*General model approach*

Given our objective to represent the relative contributions of individual fluxes to whole-system OC dynamics, an overly complex modeling approach would considerably hinder our ability to apply the model across multiple lakes with limited observational data. We therefore specifically aimed to minimize the need for driving data and maintain generalizability across lake systems, using our conceptual framework as the foundation for the mass balance model. We operated the model on a daily time step. Lake volume was assumed static and inflow volume was assumed equal to outflow volume. Because daily observational data were not always available (i.e, weekly to bi-weekly for some lakes), we filled gaps using linear interpolations. We made an exception for precipitation: data gaps were filled as 0. To account for the absence of winter data at Toolik Lake, we set inflow DOC to 0 when the main inflow (Toolik Inlet) was frozen (S2). We summarized static and calibrated model parameters in Table 2. We developed the model using R version 3.3.2.

### *Allochthonous DOC and POC*

Allochthonous DOC load (DOCalloch) was calculated as a combined function of 1) stream load, 2) precipitation load, 3) wetland load and 4) groundwater load. POCalloch (5) is the sum of an aerial load based on canopy cover and 10% of DOCalloch.

1) Daily surface water inflow discharge (m3 s-1) was generally available for the main tributaries of all lakes. Inflow DOC concentration (DOC SW; g m-3) was calculated as a product of discharge volume and measured concentration (Table 3: Eq. 1a). This variable was one of the least frequently measured variables for our study lakes. When inflow DOC data were not available for all tributaries, DOC contributions for each tributary were estimated based on the proportion of total inflow volume and the assumption that inflow DOC concentration was the same in all tributaries.

2) DOC loads from precipitation were calculated as the product of lake surface area (m2) and daily precipitation (mm) measured at the weather station nearest to each lake (Table 3: Eq. 1b-c). The concentration of DOC in precipitation was set to 2 g m-3 (Hanson et al. 2014) (Table 2: DOC\_precip\_conc).

3) Contributions of OC from shoreline-adjacent wetlands were estimated using GIS and publicly available spatial datasets (S2). We focused on wetlands adjacent to the shoreline because they contribute the vast majority of wetland-derived OC to lakes; distant wetlands contribute negligible OC that is not transported via streams (Hanson et al. 2014). DOC contribution of wetlands was calculated by multiplying the proportion of lake shoreline covered by wetlands (Table 2: PropWetland) by lake perimeter (m), and then multiplying this value by a static parameter representing wetland DOC in g/m shoreline/day (Table 3: Eq. 1d).

4) Lake-specific groundwater inflow volume (m3) and DOC concentration (g m-3) were not available for any lake. The proportion of inflow resulting from groundwater in our study lakes ranged from (0-19%) (S1) and groundwater DOC concentration was assumed to be 10 g m-3 (Hanson et al. 2014) (Table 2: DOC\_GW). The contribution of groundwater to the allochthonous DOC load was therefore calculated as the product of DOC concentration and a percentage of total surface inflow (groundwater inflow rate) (Table 3: Eq. 1e).

5) We calculated the contribution of all adjacent forests, including coniferous, deciduous, and mixed stands (POC canopy), to the OC budget via litterfall by multiplying the proportion of lake shoreline covered by forests (Table 2: PropCanopy) by lake perimeter (m), and multiplying this value by an aerial POC rate of 1 g m shoreline-1 day-1 (Table 3: Eq. 1f) (Hanson et al. 2014).

### *Autochthonous DOC and POC: primary production*

Autochthonous OC production as GPP was modeled as a function of ChlA (ug L-1) or TP (ug L-1) (if ChlA was unavailable) and surface water temperature (°C) per Morin et al. (1999) (Table 3: Eq. 2a). This empirical statistical model was based on observational temperature and ChlA data that ranged from 5-25 °C and 1-1000 mg m2, respectively. Since this model does not predict GPP well for winter-temperatures, we set GPP to zero if surface water temperatures were < 4 oC. ChlA and TP concentrations were converted from volume to areal units by multiplying by photic depth, which was estimated from Secchi depth (m; Wetzel 1975). Autotrophic respiration (Table 2: R\_autotroph) was assumed to equal 80% of total GPP; therefore, net primary production (NPP) was set equal to 20% of GPP (Quay et al. 1986, Cole et al. 2002, Hanson et al. 2004) (Table 3: Eqs. 2b-2d). NPP was partitioned into DOCauto and POCauto fractions using the Pace and Prairie (2005) estimate that 40-70% (as a function of ChlA) of NPP is respired and therefore must be converted to DOC. The resulting rates of DOCauto and POCauto production were then applied to the whole-lake carbon balance by scaling with lake surface area (Table 3: Eqs. 2e-f).

Heterotrophic respiration was calculated as a function of DOCauto and DOCalloch concentration (g m-3) in the photic zone, epilimnion temperature and two free parameters: Respiration\_autoch and Respiration\_alloch (Table 2, Table 3: Eqs. 2g-h). Respiration\_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 Catalan et al. (2016). Since DOCauto is more autochthonous than DOCalloch in lakes (add some citations), Respiration\_autoch was constrained between 0.03 and 0.3 (d-1).

### *Burial of POC*

At each time step, a small proportion of POCauto and POCalloch was allowed to leave the lake via export, and the rest was either buried or leached to DOCauto based on the Burial\_autoch and Burial\_alloch parameters (Table 2, Table 3: Eqs. 3c-h). Given the uncertainty associated with estimating burial, burial parameters were treated as a free calibration parameter in the model and allowed to vary as a proportion between 0 (no burial of POC) and 1 (all POC is buried). This simple approach allowed burial to function as the expected feedback mechanism to high POC loads from inflows and/or primary production without the need for highly uncertain gross burial and resuspension estimates.

### *Model output and calibration*

All fluxes and loads of DOC and POC were tracked at the daily model time step. Net ecosystem production (NEP) was calculated as the difference between NPP and heterotrophic respiration (Table 3: Eq. 4a). Fatm (atmospheric flux rate) was calculated as k\*(DOconc - DOsat)/Zmix. The mix depth (Zmix) was set equal to half the photic depth (m) and k was set at 0.7 m d-1 (Table 3: Eq. 4b) The saturation of DO (DOsat) is temperature dependent and was determined using the Garcia-Benson method in the LakeMetabolizer R package (Winslow et al. 2016). NEP, Fatm and DO were used to calculate the change in DO in the surface water (Table 3: Eq. 4c).

The four free parameters in the model (Respiration\_autoch, Respiration\_alloch, Burial\_autoch and Burial\_alloch; Table 2) were fit by minimizing the sum of the squared residuals of DOC and DO modeled minus DOC and DO observed (equally weighted by number of observations). The model was fit using a pseudo-random search algorithm in the R package FME (Soetaert and Petzoldt 2010). Modeled DOC and DO were compared to corresponding observed concentrations using RMSE (root mean square error) and Nash-Sutcliffe efficiency scores for each lake to determine model goodness of fit. A sensitivity analysis of each parameter was conducted by allowing the parameter to vary within the set bounds (n=100) while fixing the other three parameters at their calibrated values.

*Bootstrapping*

We assessed parameter uncertainty using bootstrapping...

## **RESULTS**

### *Model performance, parameter estimates and sensitivity analysis*

Modeled DOC and DO generally mimicked observed temporal patterns across years and study lakes (Fig. 2). RMSE ranged 0.73-1.46 across lakes, demonstrating overall strong goodness of fit for both DOC and DO (Table 4). NSE values ranged 0.69-0.96, indicating that the model accounted for considerably more information than long-term means of DOC and DO. Although the model captured general upward and downward trends across years, as well as seasonal peaks and lows in DOC and DO, the model did not consistently characterize the magnitude of short-term spikes (i.e., days to weeks). Nonetheless, long-term model performance indicated the ability to account for lake variability in DOC and DO from seasonal to interannual time scales.

Burial\_alloch, which represented the daily proportion of allochthonous POC buried in sediments, was 1 (i.e., 1=100% burial, 0% leached to DOC) for all lakes (Table 2). Similarly, Burial\_autoch was near 1 for Monona, Vanern and Toolik; however, values were 0 for Harp and Trout, indicating nearly all autochthonous POC was leached to DOC in these two lakes. DOC respiration parameters were lower for allochthonous than autochthonous DOC across all lakes, indicating that respiration was largely driven by autochthony. Respiration\_alloch was largely similar across lakes, ranging 0.001-0.003, whereas Respiration\_autoch was more variable, ranging 0.015 (Trout) to 0.297 (Toolik).

The sensitivity analysis demonstrated that modeled DOC (mg L-1) was generally most sensitive to Respiration\_alloch, except for Monona, for which modeled DOC was most sensitive to Burial\_autoch (Fig. 3). The other 4 lakes were minimally affected by changes in this parameter (< 1 mg L-1 difference across the range of parameter values). Changes in Burial\_alloch had consistently minimal effects on modeled DOC across lakes. Harp and Monona were the only lakes with considerable sensitivity to Respiration\_autoch. Overall, parameter sensitivity was greatest for Vanern, Harp and Monona, for which modeled DOC varied as much as 5-6 mg L-1 across the range of parameter values. Conversely, modeled DOC varied no more than 2 and 3 mg L-1 for Toolik and Trout, respectively.

### *Summary of fluxes and fates*

The model tracked spring peaks and general seasonal declines in allochthony, as well as additional short-term spikes associated with precipitation events (Fig. 4). Trends in autochthony demonstrated annual peaks associated with summer water temperatures. Trajectories of burial, respiration and export followed similarly shaped trajectories within and across years. Some lakes showed variability in the magnitude of fluxes across years, demonstrating the ability of the model to account for interannual fluctuations. For example, overall trajectories were generally consistent over time for Trout and Vanern, whereas Harp, Monona and Toolik demonstrated more variability. In Harp, total budget variability was driven by trends in allochthony, autochthony and respiration, whereas burial and export were consistently smaller proportions of the budget. All fluxes were highly variable through time in Monona, except for consistently low respiration. Toolik demonstrated consistently low autochthony, respiration and burial; long-term variability in its total budget followed similarly shaped trajectories of allochthony and export.

On average across years, with the exception of Trout, lake OC budgets were predominantly driven by allochthonous OC, underscoring the importance of terrestrially derived OC in overall lake budgets (Table 5). Trout had the lowest allochthony (g m-2 yr -1)by nearly a factor of 3 or more, which translated into a relatively low allocthonous contribution (31.7%) to the overall budget compared to the other lakes (54.3 - 89.3%). Toolik was dominated by allochthony, accounting for 89.3% of its overall budget. Exports ranged from 9.5 (Trout) to 62.0% (Toolik) and were less than the sum of respiration and burial across all lakes except Toolik, indicating that these lakes actively processed OC (Box 1). Monona was a borderline processor, however, given that export basically equaled respiration plus sedimentation.

Respiration consistently exceeded burial in all lakes but Monona, indicating that these lakes were net sources of OC (Table 5, Box 1). Among the 5 lakes, respiration was lowest and burial was greatest for Monona by a factor of 2 or more for all lakes but Toolik (respiration). Burial accounted for 12.0% or less of total budgets for Harp, Toolik and Trout, indicating that burial was a relatively minor sink mechanism in these lakes. The burial rate for Vanern was closer to that of Monona than to the other three lakes, but was still close to half of its respiration rate. Monona was the only long-term net sink of OC due to its low rate of respiration relative to burial.

### *Seasonal fates*

As water temperatures increased during the growing season, the ratio between allochthony and autochthony generally shifted in favor of autochthony (due to increases in GPP), whereas the ratio between respiration and burial generally shifted towards respiration and therefore source status (Fig. 5). The four quadrants in Fig. 5 demonstrated seasonal variability in source or sink status for some lakes. Trout remained a source for the entire year, but became a greater source as the growing season progressed. Harp, Toolik and Vanern were sinks early in the growing season, but eventually became sources as temperatures warmed. Conversely, Monona remained a sink throughout most of the year and only became a source late in the growing season. Despite this late pulse in respiration, however, Monona remained a net sink on an annual basis (Table 5). Monona and Vanern also showed less of an increase in autochthony as the growing season progressed compared to other lakes, suggesting the importance of continued allochthonous inputs during summer months coinciding with increases in autochthony.

## **DISCUSSION**

### *Are lakes sources or sinks of organic carbon?*

Although prior studies have identified lakes as important OC sinks owing to burial in lake sediments, our study showed that burial can be a relatively small component of overall lake OC budgets. Many lakes, therefore, may actually be net OC sources due to the ratio between burial and respiration, which prior studies did not consider. Even with some uncertainty in burial parameters, the range of potential burial amounts essentially exists within the noise of the overall budget compared to other fluxes. Although lakes will continue to store carbon in lake sediments in the future, increases in water temperatures associated with climate warming could lead to increases in respiration and increase the net source capacity of lakes, particularly as lakes trend toward sources earlier in the growing season. Therefore, OC cycling has important implications for broader ecosystem responses to climate change.

Lakes as net sources of OC additionally have important implications for landscape cycling of OC. When respiration exceeds burial, this excess OC exits the lake and provides OC inputs to other landscape features such as streams or lakes. As such, warming-induced increases in respiration could increase exports to other aquatic systems across the landscape. Allochthonous loads already appear to be the dominant forcing of OC budgets in most lakes, so lakes may experience increases in both allochthony and autochthony under climate warming. Further, the turnover rate of autochthonous OC in lakes is faster than for allochthonous OC (based on respective respiration parameters). As such, increases in lake productivity could rapidly increase allochthonous inputs to other lakes.

### *Recreating important lake processes*

Our results indicated that a relatively simple, dynamical model can represent the set of key biogeochemical, trophic and landscape processes that combine to determine the fate of OC in lake ecosystems. Our model worked reasonably well for both eutrophic and oligotrophic lakes, temperate to subarctic climate zones, forested and agricultural watersheds and orders of magnitude differences in lake morphometry, which demonstrated the generalizable nature of our modeling approach. Further, the flux rates we produced 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 allochthony, burial and export, but not for respiration. Whalen and Cornwall (1985) modeled Toolik based on a different set of years from our study (1980-1981), but similarly demonstrated that the system contained high allochthony relative to autochthony, low burial and high export. Similar to Hanson et al. (2014), Dillon and Molot (1997)’s estimates for Harp of autochthony, burial and export, but not respiration (based on field data from 1981-1989), were comparable to our results. Although our results generally agreed with prior studies based on steady-state models, this was not true for autochthony and respiration. We offer that dynamical models better represent these processes by accounting for seasonal changes in temperature and ChlA concentrations. Therefore, although steady-state models may be sufficient for recreating some key ecological processes, dynamical models are needed for determining the net source or sink function of lakes, given the importance of autochthony and respiration.

### *On-going research needs and future implications*

Although we believe this work is an important advance in terms of understanding the fates of OC across aquatic ecosystems and landscapes, we also encountered constraints associated with current data availability. If necessary data were collected for a larger number of lakes spanning wider environmental gradients (e.g., climate, watershed conditions), contributions of lakes to landscape carbon cycles based on net lake function could be estimated at broad spatial scales. Particularly necessary are high-frequency measurements of inflow DOC concentration. These data were among the most infrequently collected among lakes we considered for this study, yet without them, examining whole-lake OC budgets is difficult. Our study generally used data collected at weekly or bi-weekly intervals; although data collection 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 (cite GLEON-esque example?). In addition, relatively little is currently known about POC budgets despite their key interactions with DOC (Einsele et al. 2001); we need more POC observational data for incorporation into dynamical models of OC. Such studies would help constrain POC parameters and improve estimates of the fates of POC within overall OC budgets. Finally, although burial is in many cases a relatively small OC flux in lake ecosystems, burial may be underestimated if large precipitation events are not included in meteorological observations and/or inflow volumes. Our model demonstrated responses to precipitation events when we had corresponding weather and inflow data, but we assumed no precipitation and linear changes in inflow volume (and DOC concentration) between observation points. Given the demonstrated importance of allochthony in lake OC budgets, the ability to characterize responses to large, infrequent precipitation events is therefore critical. Although future precipitation projections are variable within and across regions, wet years increase allochthonous DOC inputs to lakes at regional scales (Rose et al. 2016).

In conclusion, a key management implication of our study is the need for more observational data, particularly pertaining to surface water DOC concentrations, POC cycling and burial. Lake resource managers should be aware of the importance of allochthonous inputs derived from watershed sources in lake OC budgets; allochthony exceeded autochthony in 4 of the 5 lakes in this study. Allochthony not only strongly influences lake ecosystem productivity, but also may increase as connected lakes and streams receive relatively mobile autochthonous OC from upstream systems. Lakes become increasingly productive as water temperatures warm, which increases autochthony as well as the OC source capacity of lakes. As climates continue to warm, we would therefore expect lakes to become larger sources of OC over time.

## **ACKNOWLEDGMENTS**

This project was a product of the Global Lake Ecological Observatory Network (GLEON) Fellowship program supported by the US National Science Foundation’s Macrosystem Biology Program (Awards # EF1137353 and EF1137327). Logistical support was provided by the University of Wisconsin-Madison Center for Limnology, the Cary Institute for Ecosystem Studies, the University of Wisconsin Trout Lake Station, the Lake Sunapee Protective Association and Grace Hong of GLEON. Limnological data providers included the NSF Long-Term Ecological Research program (North Temperate Lakes DEB-1440297 and Arctic LTER), the Swedish Meteorological and Hydrological Institute, the Swedish University of Agricultural Sciences and the Dorset Environmental Science Centre. Additional details on data sources are included in supplementary material (S1). IMM, HAD, KJF, AMM, ZO, DR, FS and PCH acquired data, developed the model and performed data analyses. All authors participated in conceiving and developing the project and writing the paper.

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| **TABLES**  **Table 1. General lake characteristics** | | | |  | |  | |  | |  | |  | |  | | |  |  |  | |  |  |  |
| **Lake** | **Location** | **N lat,**  **W lon** | **Data years** | **zmean (m)** | **RT (yr)** | | **Trophic status** | | **Secchi (m)** | | **ChlA (µg L-1)** | | **SW DOC (g m-3)** | | **Lake DOC (g m-³)** | **References** | | | |
| Harp | Ontario, Canada | 45°38', 79°14' | 1991-2001 | 12 | 2.5 | | oligotrophic | | 4.47 | | 2.07 | | 9.35 | | 4 | Yao et al. 2011 | | | |
| Monona | Wisconsin, USA | 43°11', 89°42' | 2003-2014 | 8.3 | 0.8 | | eutrophic | | 3.03 | | 9.21 | | 5.09 | | 6 | North Temperature Lakes LTER | | | |
| Toolik | Alaska, USA | 68°63', 149°61' | 2001-2010 | 7 | 0.8 | | oligotrophic | | 4.53 | | 1.41 | | 7.72 | | 5 | Kling et al. 2000 | | | |
| Trout | Wisconsin, USA | 46°02', 89°40' | 2004-2013 | 14.6 | 5.9 | | oligotrophic | | 5.32 | | 2.23 | | 5.11 | | 3 | Webster et al. 1996, North Temperature Lakes LTER | | | |
| Vanern | Sweden | 59°06’, -13°62’ | 2001-2013 | 27 | 6.3 | | oligotrophic | | 4.47 | | 2.07 | | 9.35 | | 4 | Kvarnäs 2001 | | | |

**zmean** = mean depth, RT = hydrologic residence time, Secchi = Secchi depth, ChlA = chlorophyll-a, SW DOC = inflow dissolved organic carbon, Lake DOC = in-lake DOC. All values calculated from model calibration data or derived from cited references

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| --- | --- | --- | --- | --- | --- | --- | --- |
| **Table 2. Lake model parameters (free parameters italicized)** | | |  |  |  |  |  |
| **Parameter** | **Description** | **Harp** | | **Monona** | **Toolik** | **Trout** | **Vanern** |
| **General** |  |  | |  |  |  |  |
| Perimeter (m) | Lake perimeter | 4000 | | 35200 | 8104 | 25900 | 2007000 |
| Mean Depth (m) | Mean water depth | 12 | | 8.3 | 7 | 14.6 | 27 |
| Area (m²) | Lake surface area | 713800 | | 13260000 | 1.49E+06 | 16079000 | 5.65E+09 |
| Volume (m³) | Lake volume | 8320000 | | 1.10E+08 | 10566000 | 234753400 | 1.53E+11 |
| DOC\_init (g m-3) | Initial lake water DOC concentration | 3.70 | | 7.00 | 5.00 | 2.90 | 4.40 |
| POC\_init (g m-3) | Initial lake water POC concentration | 0.37 | | 0.10 | 0.50 | 0.29 | 0.40 |
| **Allochthony** |  |  | |  |  |  |  |
| PropCanopy | Proportion of shoreline with tree cover | 1.000 | | 0.167 | 0.000 | 0.780 | 0.615 |
| PropWetlands | Proportion of shoreline with wetlands | 0.000 | | 0.026 | 0.133 | 0.011 | 0.037 |
| WetlandLoad (g d-1) | Loading rate of POC from wetlands | 1 | | 1 | 1 | 1 | 1 |
| DOC\_gw (g m-3) | DOC concentration of groundwater | 10 | | 10 | 10 | 10 | 10 |
| PropGW | Proportion of lake inflow as groundwater | 0.00 | | 0.00 | 0.00 | 0.19 | 0.20 |
| DOC\_precip\_conc (g m-3) | DOC concentration of precipitation | 2 | | 2 | 2 | 2 | 2 |
| AerialLoad (g d-1) | Influx of aerial POC (i.e., leaflitter) | 1 | | 1 | 1 | 1 | 1 |
| **Autochthony** |  |  | |  |  |  |  |
| *Respiration\_alloch (d*-*1)* | *Decomposition rate of allochthonous DOC in heterotrophic respiration* | *0.002* | | *0.001* | *0.003* | *0.001* | *0.001* |
| *Respiration\_autoch (d-1)* | *Decomposition rate of autochthonous DOC in heterotrophic respiration* | *0.092* | | *0.003* | *0.297* | *0.015* | *0.069* |
| R\_autotroph | Proportion of GPP autotrophically respired | 0.8 | | 0.8 | 0.8 | 0.8 | 0.8 |
| **Burial** |  |  | |  |  |  |  |
| *Burial\_alloch* | *Proportion of allochthonous POC buried in sediments* | *1.000* | | *1.000* | *1.000* | *1.000* | *1.000* |
| *Burial\_autoch* | *Proportion of autochthonous POC buried in sediments* | *0.000* | | *1.000* | *0.968* | *0.000* | *1.000* |
| Observed\_MAR (g m² yr-1) |  | 78 | | 249 | 153 | 27 | 186 |
| **Other** |  |  | |  |  |  |  |
| POClc\_alloch | Proportion of allochthonous POC leached to | 0.000 | | 0.000 | 0.000 | 0.000 | 0.000 |
| POClc\_autoch | Proportion of autochthonous POC leached to | 1.000 | | 0.000 | 0.032 | 1.000 | 0.000 |

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| --- | --- | --- | --- | --- |
| **Table 3. Built model with equations** | | |  |  |
| **Allochthonous DOC and POC** | **Units** | **Reference** | | |
| 1a) DOC SW = surface water concentration \* surface water inflow rate \* 86400 | g d-1 | Hanson et al. 2014 | | |
| 1b) Daily precipitation = rainfall \* 0.001 \* Area | m3 d-1 | Hanson et al. 2014 | | |
| 1c) DOC precipitation = DOC\_precip \* Daily precipitation | g d-1 | Hanson et al. 2014 | | |
| 1d) DOC Wetland = PropWetland \* WetlandLoad \* Perimeter | g d-1 | Hanson et al. 2014 | | |
| 1e) DOC GW = groundwater concentration \* groundwater inflow rate \* 86400 | g d-1 | Hanson et al. 2014 | | |
| 1f) POC canopy = PropCanopy \* AerialLoad \* Perimeter | g d-1 | Hanson et al. 2014 | | |
| 1g) Inflow load DOC = DOC Wetland + DOC GW + DOC SW + DOC precipitation | g d-1 | Hanson et al. 2014 | | |
| 1h) Internal load POC = (DOC Wetland + DOC SW) \* 0.1 | g d-1 | Hanson et al. 2014 | | |
| 1i) Inflow load POC = POC Aerial + Internal load POC | g d-1 | Hanson et al. 2014 | | |
| 1j) POC Aerial = AerialLoad \* Perimeter | g m-1 d-1 | Hanson et al. 2014 | | |
| **Autochthonous DOC and POC: primary production** |  |  | | |
| 2a) GPP rate = 10^(1.18 + (0.92 \* log10(ChlA\* photic depth)) + (0.014 \* epilimnion temperature)) | mg m-2 d-1 | Morin et al. 1999 | | |
| 2b) GPP percent DOC = 71.4 \* (ChlA \* photic depth)^(-0.22) | % | Pace and Prairie 2005 | | |
| 2c) GPP DOC rate = GPP rate \* (GPP percent DOC/100) | mg m-2 d-1 |  | | |
| 2d) GPP POC rate = GPP rate \* (1-(GPP percent DOC/100)) | mg m-2 d-1 |  | | |
| 2e) NPP DOC\_autoch = GPP DOC\_autoch \* 0.2 \* Area / 1000 | g d-1 |  | | |
| 2f) NPP POC\_autoch = GPP POC\_autoch \* 0.2 \* Area / 1000 | g d-1 |  | | |
| 2g) Autochthonous Respiration = GPP DOC rate \* Respiration\_autoch(1.08^(epilimnion temp - 20)) | g m-3 |  | | |
| 2h) Allochthonous Respiration = GPP DOC rate \* Respiration\_alloch(1.08^(epilimnion temp - 20)) | g m-3 |  | | |
| **Burial** |  |  | | |
| 3a) MAR\_alloch = POC mass \* Burial\_alloch \* 365/Area | g m-2 yr-1 |  | | |
| 3b) MAR\_autoch = POC mass \* Burial\_autoch \* 365/Area | g m-2 yr-1 |  | | |
| 3c) POC Burial\_alloch = MAR\_alloch \* (1/365) \* Area | g d-1 |  | | |
| 3d) POC Burial\_autoch = MAR\_autoch \* (1/365) \* Area | g d-1 |  | | |
| 3e) POC\_alloch leached out = POC\_alloch concentration \* POClc\_alloch \* Volume | g d-1 |  | | |
| 3f) POC\_autoch leached out = POC\_autoch concentration \* POClc\_autoch \* Volume | g d-1 |  | | |
| 3g) DOC\_alloch leached in = POC\_alloch leached out | g d-1 |  | | |
| 3h) DOC\_autoch leached in = POC\_autoch leached out | g d-1 |  | | |
| **NEP and Oxygen Flux** |  |  | | |
| 4a) NEP (as O2) = (NPP - DOCrespired) \* 32/12 | g m-3 d-1 |  | | |
| 4b) Fatm = 0.7 \* (DOconc - DOsat)/Zmix | g m-3 d-1 |  | | |
| 4c) DO(t+1) = DOconc + NEP - Fatm | g m-3 d-1 |  | | |

MAR = mass accumulation rate, Fatm = atmospheric flux rate, Zmix = mixed depth (m)

**Table 4. Model goodness of fit**

|  |  |  |
| --- | --- | --- |
| **Lake** | **RMSE\*** | **NSE\*\*** |
| Harp | 1.22 | 0.86 |
| Monona | 1.46 | 0.70 |
| Toolik | 1.19 | 0.79 |
| Trout | 0.80 | 0.95 |
| Vanern | 0.73 | 0.96 |
| \* root mean square error (mg L-1) | | | |
| \*\* Nash-Sutcliffe efficiency | | | |

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Lake** | **Alloch** | **Autoch** | **Resp** | **Burial** | **Export** | **Total Load** |
| Harp | 39.227 | 32.973 | -49.362 | -5.240 | -16.722 | 72.200 |
| Monona | 64.279 | 53.989 | -17.297 | -43.586 | -59.071 | 118.268 |
| Toolik | 75.975 | 11.589 | -24.699 | -6.663 | -55.798 | 87.563 |
| Trout | 13.767 | 29.694 | -38.195 | -1.212 | -4.145 | 43.461 |
| Vanern | 40.947 | 26.868 | -35.341 | -20.541 | -12.473 | 67.815 |
|  |  |  |  |  |  |  |
| **Proportion of total load** | | |  |  |  |  |
| Harp | 0.543 | 0.457 | -0.684 | -0.073 | -0.232 |  |
| Monona | 0.543 | 0.457 | -0.146 | -0.369 | -0.499 |  |
| Toolik | 0.868 | 0.132 | -0.282 | -0.076 | -0.637 |  |
| Trout | 0.317 | 0.683 | -0.879 | -0.028 | -0.095 |  |
| Vanern | 0.604 | 0.396 | -0.521 | -0.303 | -0.184 |  |

**Table 5. Summary of mean mass balances (g m-2 yr-1)**

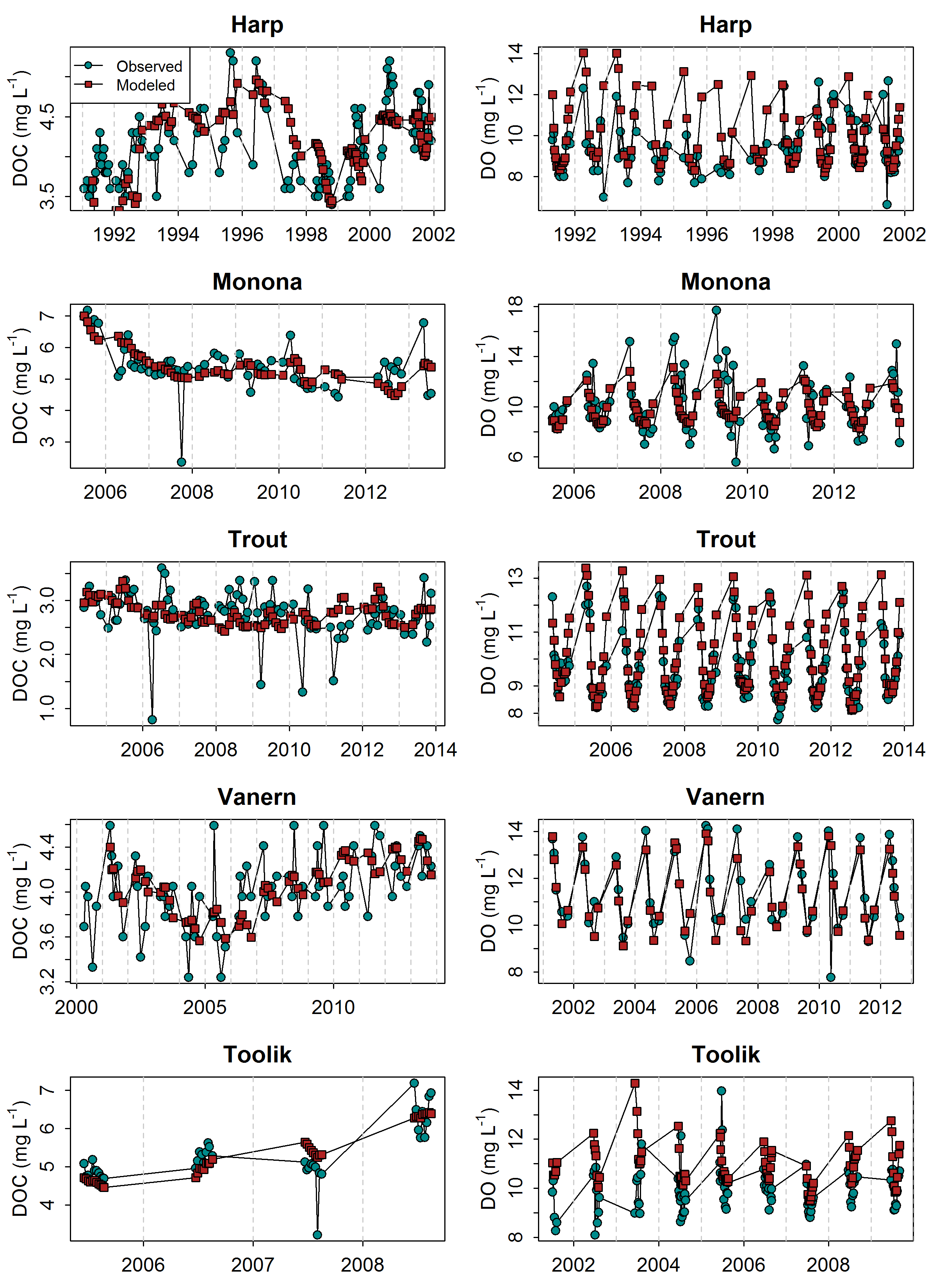
**FIGURE CAPTIONS**

**FIGURES**



**Fig. 1.**

Fig. 1. Conceptual diagram of the organic carbon lake model depicting fluxes based on allocthonous (inflow) and autochthonous (NPP) inputs of organic carbon, long-term burial, leaching of particulate organic carbon (POC) to dissolved organic carbon (DOC), respiration of DOC to CO2, and export via outflow. Four parameters (Respiration\_Auto, Respiration\_Alloch, Burial\_Auto, and Burial\_Alloch) are treated as free parameters and optimized for each individual lake.



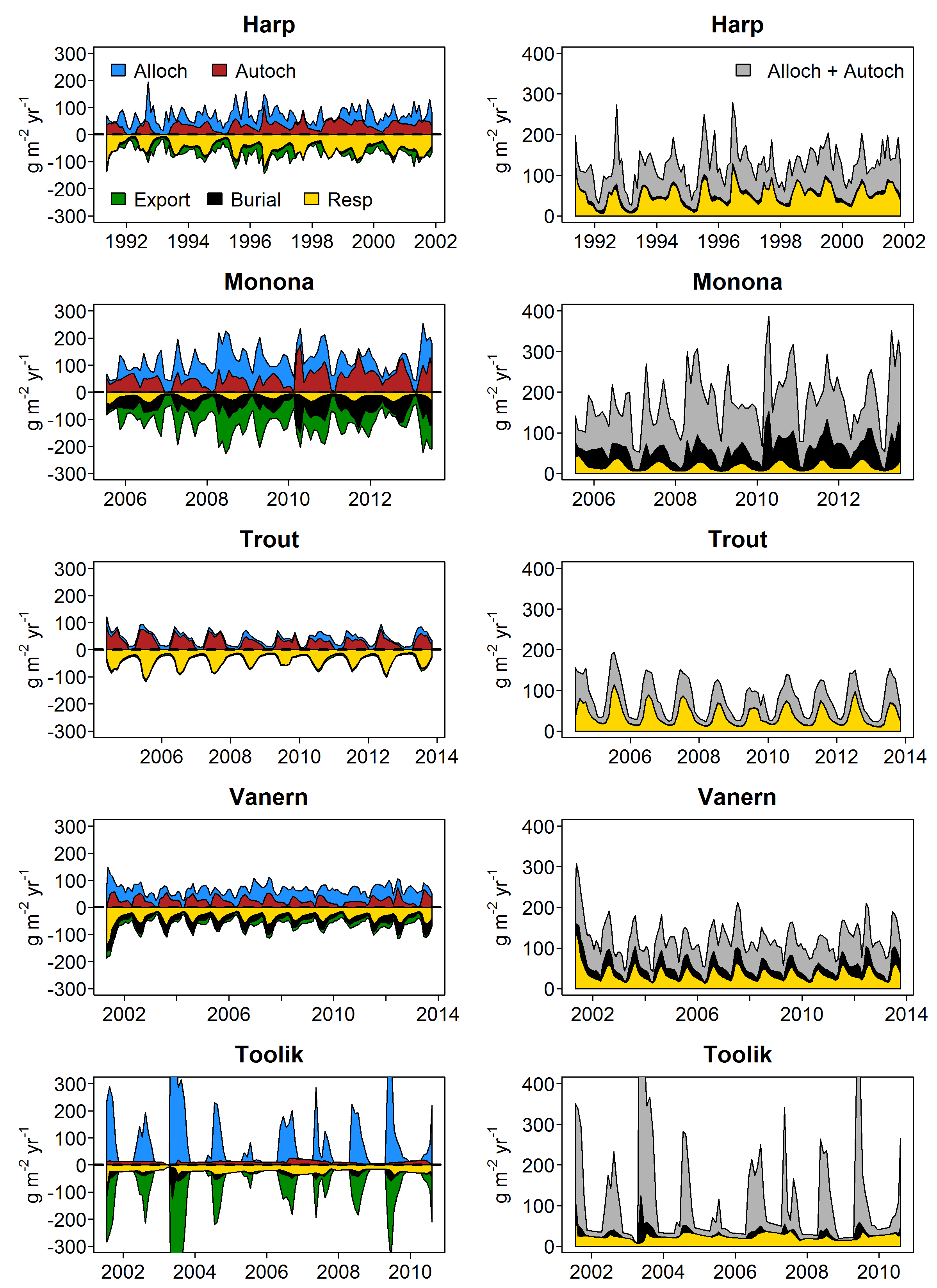
**Fig. 2.**

Fig. 2. Observed dissolved organic carbon (DOC) and dissolved oxygen concentrations in all lakes (blue circles) compared with modeled concentrations (red squares) on the same date.

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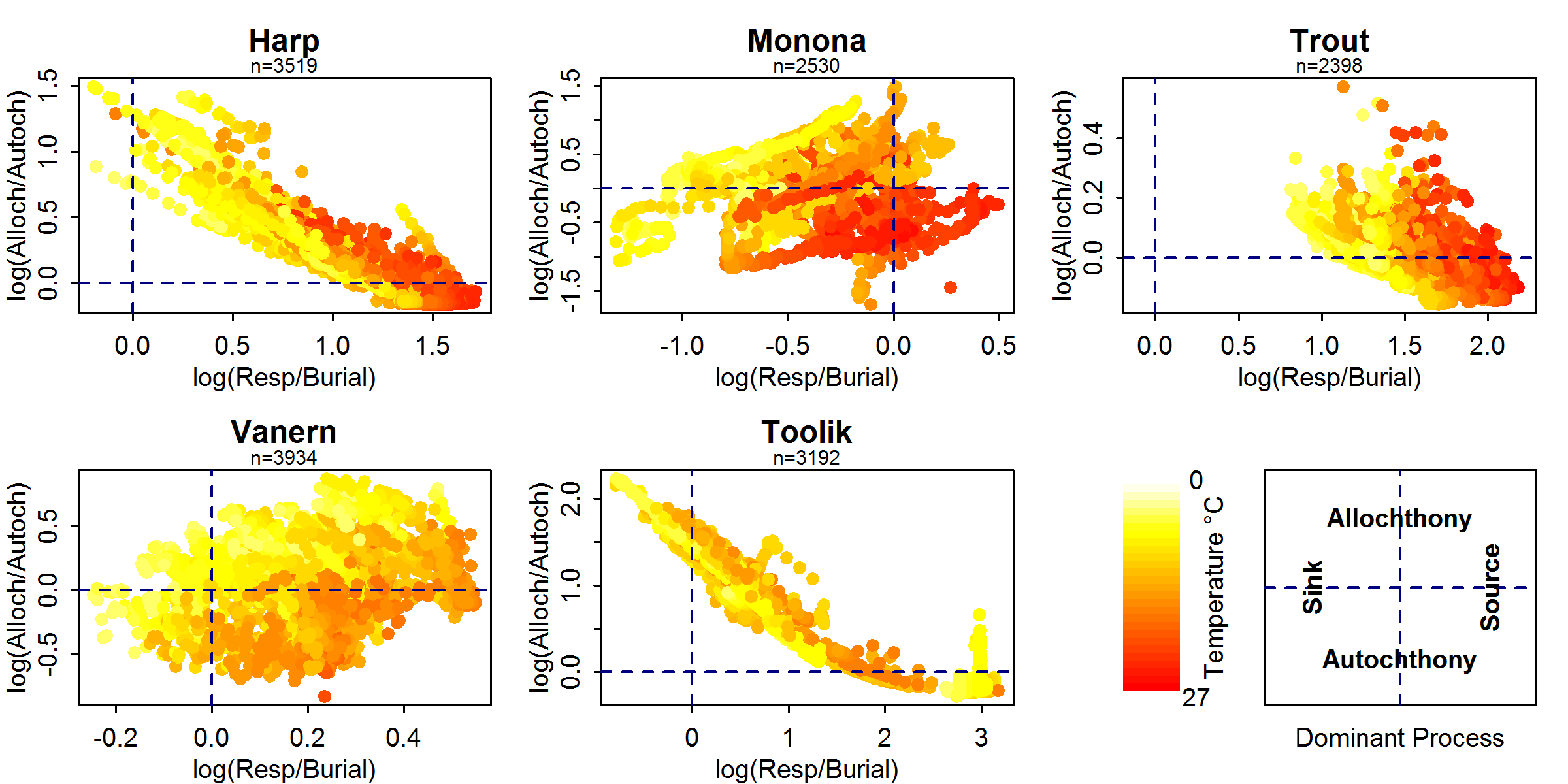
**Fig. 3.**

Fig. 3. Sensitivity of calibrated model parameters. Shaded areas represent the range of modeled DOC concentrations as a given parameter was varied across a specified range (see legend) while the three other parameters remained fixed at their calibrated value. Black circles represent the observed in-lake DOC concentrations.

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**Fig. 4.**

Fig. 4. Time series of organic carbon fluxes and fates. A) Colored areas represent relative magnitudes of input fluxes (allochthonous and autochthonous) and output fluxes (export, burial, and respiration). All lines are stacked to show cumulative magnitudes. b) Absolute values of export, burial and respiration. A lake is a net source when respiration exceeds burial.

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**Fig. 5.**

Fig. 5. Relationship between log-transformed (base 10) allochthony/autochthony and respiration/burial (g m-2 yr-1) of organic carbon. The four quadrants in each figure represent the dominant processes (either predominantly a source or sink, and either predominantly allochthonous driven or autochtonous driven) associated with each lake.

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