SPECIAL ISSUE-LETTER

Pipes or chimneys? For carbon cycling in small boreal lakes, precipitation matters most

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Scientific Significance Statement

Aquatic fluxes of terrestrial dissolved organic carbon (DOC) and retention of DOC in lakes in boreal landscapes are impacted by global change. A shift in the role of lakes as processors of DOC and producers of atmospheric CO_2 is of interest to understanding the role of northern landscapes in the global carbon cycle. This study provides evidence that percentage of DOC retained in a boreal, humic lake catchment declines in years with high precipitation as a result of lower water residence times, while lateral DOC fluxes increase. The retained DOC is likely returned to the atmosphere as CO_2, suggesting that in a wetter climate, small northern lakes will, on balance, function more as pipes than chimneys.

Abstract

Are small lakes passive pipes transporting terrigenous organic carbon (dissolved organic carbon [DOC]), or chimneys for CO_2 release in the landscape? Using a unique combination of 30-yr measurements, sediment dating and modeling of a small humic lake and its catchment in southeast Norway, we calculated lateral DOC fluxes and in-lake retention. Concentrations and fluxes rose significantly, driven by declining sulfur deposition and increased precipitation. In-lake retention (% of inputs) declined because of higher discharge and lower residence times. DOC removal rates were not sensitive to residence time. Modeled in-lake DOC removal was driven primarily by microbial metabolism and, secondarily, by flocculation, suggesting that the likely fate of lake-retained DOC is CO_2 evasion to the atmosphere. Precipitation was the overriding landscape control on DOC fluxes and retention. In a wetter climate, small northern lakes will, on balance, function more as pipes than chimneys, with increasing lateral DOC fluxes but little change in CO_2 production.

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A significant fraction of the world's lakes are small and/or found in the boreal landscape (Verpoorter et al. 2014), which is one of the world's largest ecozones and contains over 20% of all soil carbon. Many boreal lakes are characterized by high inputs of terrigenous (catchment-derived, allochthonous) organic carbon and have low rates of primary productivity. Aquatic pathways form an integral part of the landscape through transport, processing, storage of terrestrial carbon, and release of greenhouse gases (Tranvik and Jansson 2002; Cole et al. 2007). In the soil-water continuum of northern landscapes, carbon cycling is sensitive to climate change (Catalán et al. 2016; de Wit et al. 2016*b*; Seddon et al. 2016) and atmospheric deposition (Monteith et al. 2007), and may add to climate warming through higher release of greenhouse gases (Campeau and Del Giorgio 2014) and lower terrestrial carbon sequestration (Oquist et al. 2014; de Wit et al. 2016*a*). In large parts of the northern hemisphere, changes in carbon cycling have been noted through the large increase of dissolved organic carbon (DOC) concentrations in surface waters (Monteith et al. 2007). Browning of surface waters has potential impacts on carbon storage and emissions of greenhouse gases (Tranvik et al. 2009) as well as ecological functioning of freshwaters, e.g., productivity (Finstad et al. 2014), mercury accumulation in aquatic foodwebs (French et al. 2014), oxythermal habitat for aquatic biota (Couture et al. 2015), and ecosystem services such as drinking water supply (Anderson et al. 2017). A better understanding of sensitivities and responses of carbon cycling in the catchment-lake aquatic continuum to environmental change is required to address a wide range of environmental challenges.

Quantitative accounting of aquatic organic carbon cycling in the carbon sink function of northern landscapes is complex because CO_2 effluxes from lakes originate both from catchment soils and in-lake production of CO_2. Especially in small, oligotrophic lakes with a large catchment to lake ratio, the imprint of terrestrial carbon on lakes is considerable (Prairie 2008; Roehm et al. 2009). Improved source attribution of surface water CO_2 dynamics to processing of terrigenous DOC (Jonsson et al. 2007) is valuable for understanding the role of surface waters in the carbon cycle.

Catchment DOC fluxes and concentrations as well as aquatic carbon storage are particularly sensitive to changes in precipitation, through changes in hydrological pathways, source mobilization of organic matter, and water residence times (Algesten et al. 2004; Raymond and Saiers 2010; Moody et al. 2013; Catalán et al. 2016). Other drivers include chemistry (Monteith et al. 2007), light (Cory et al. 2014), and temperature-driven respiration (Jonsson et al. 2001). Disentangling impacts of various drivers on carbon cycling has been shown to benefit from a combination of empirical and process-based approaches (Futter and de Wit 2008; Birkel et al. 2014; Couture et al. 2015). Combining process-based modeling with multi-decade series of empirical

lake input-outputs of DOC potentially allows for quantification of the fate of DOC and attribution of DOC removal to defined processes. Such time series are scarce, and to our knowledge, only one other long-term (> 10 yr) record of DOC fluxes boreal lake catchment, combined with process-based modeling, has been published (Holmberg et al. 2014).

Here, we present a unique time series of 30 yr of monitoring records (1986–2015), in combination with sediment dating and a process-based model to quantify a lake organic carbon (DOC) budget in a boreal catchment. We (1) quantify catchment DOC inputs, lake DOC export, and lake DOC retention, and (2) assess the relative importance of lake processing rates for DOC removal through application of a process-oriented model.

Methods

Study site

The Langtjern catchment (4.8 km^2; 510–750 m.a.s.l; 60.371 N, 9.727 E) is located in southeast Norway (Fig. 1) (de Wit et al. 2014; Couture et al. 2015).

Monitoring of water chemistry and hydrology started in 1972 under the national monitoring programme for effects of acid deposition. Land cover comprises 80% low- to unproductive Scots pine forest, and patches of Norway spruce, interspersed with peatlands (20%). The forest stands are mature or close to maturity, and the last small-scale forest harvest operations were conducted in the 1950s. The geology consists of till derived from felsic gneisses and granites, where thin mineral soils have developed. Deeper peaty soils are found at topographic depressions and close to streams. Mean annual temperature, precipitation, and discharge (1986–2015) are 2.5°C, 901 mm, and 650 mm.

The lake (0.23 km^2) is fed by two main inlet streams (LAE02, south; subcatchment area 1.8 km^2, LAE03, east, subcatchment area 0.8 km^2, Fig. 1) draining 60% of the catchment, and is ca. 1 km long and consists of three basins with a total volume of 5.6×10^5 m^3 and mean depth of 2 m, and has a mean residence time of 2.2 months. The lake is dimictic and establishes a thermocline in the summer at 1–3 m depth. Mean pH, total organic carbon (TOC), total P, and total N (2011-2015) are 5.0, 10.9 mg C L^{-1}, 4.9 μg P L^{-1}, and 268 μg N L^{-1}, respectively. Mean chlorophyll *a* is < 2 μg L^{-1}. The lake has shown a strong chemical recovery from acidification since the 1980s (Garmo et al. 2014).

Monitoring program

Discharge at the lake outlet has been monitored since 1973 by means of a V notch weir. Discharge in the LAE03 inlet is calculated based on a water balance for the lake (Supporting Information). Stream water grab samples for acid-base chemistry (major cations and anions, pH, alkalinity) are collected weekly (outlet) and weekly to monthly (inlets; LAE03 with the most complete time series), and have been analyzed for TOC since 1986. Details on sampling methods
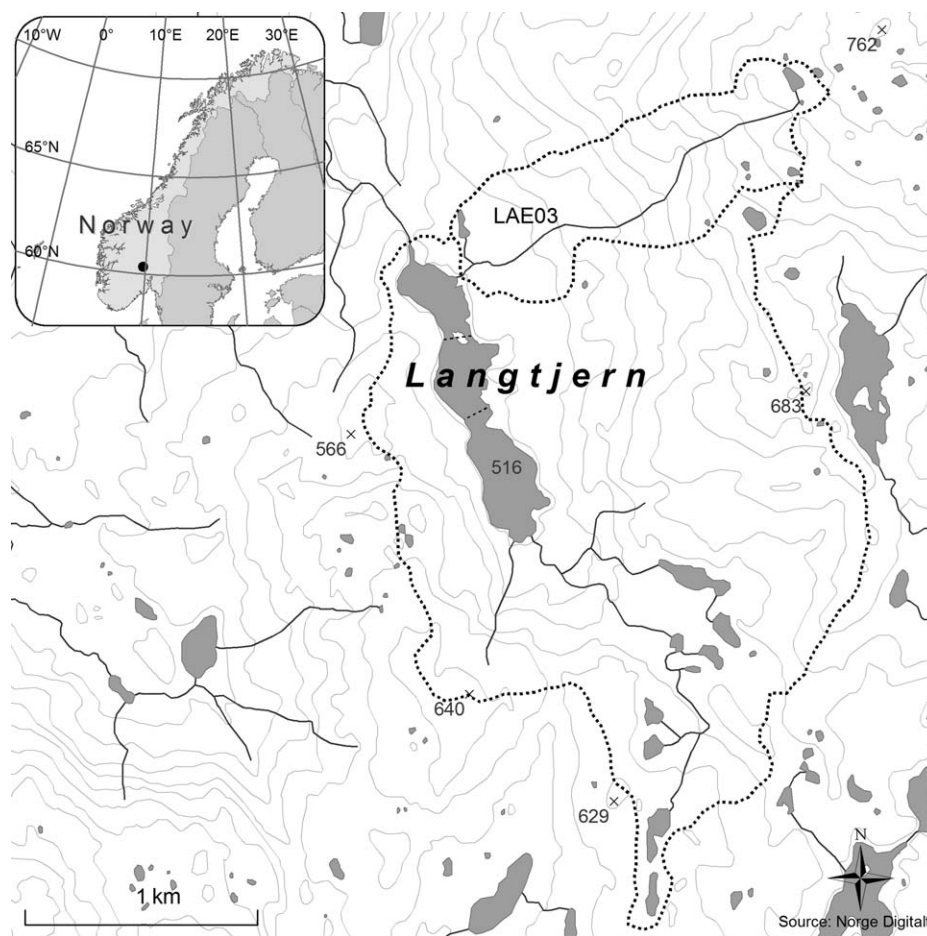
Fig. 1. The Langtjern lake catchment and its position in Norway. Subcatchment LAE03 to the east. The boarder between the three lake basins indicated by dotted line.

and chemical analysis are found in de Wit et al. (2014). DOC (filtered by 0.45 μm) is on average 94% of TOC which renders particulate OC (POC) as on average 6% of TOC (Supporting Information). We will henceforth refer to "DOC" instead of TOC.

Since June 2010, an on-site weather station has been recording air temperature, relative humidity, and wind direction and speed, while high-frequency sensors in a lake buoy monitor water temperature and dissolved oxygen, in the northern lake basin and data are transferred to NIVA daily (www.niva.no/langtjern).

Meteorological data

Time series of daily cloud cover, air temperature (°C), relative humidity (%), air pressure (kpa), wind speed (m s^{-1}), and precipitation (mm d^{-1}) were obtained from a nearby meteorological station as described in Couture et al. (2015). Air temperature and precipitation were adapted to local conditions using parallel weather records from the in situ weather station (Supporting Information).

Lake sediment

A sediment core was collected in April 2016 at the deepest point of the northern basin (9 m). Sediment mass and OC accumulation rates were determined by dating the samples using the ^{210}Pb approach, method which is a well-established method to assess the chronology of sedimentary deposits during the last 100–150 yr (Supporting Information).

Calculations

Element fluxes in inlet (LAE03) and outlet streams were calculated using measured daily discharge and estimated daily concentrations. Daily DOC concentration time series were either interpolated from measured concentrations through a cubic spline (data gap < 40 d) or were estimated using an empirical relationship between measured DOC and continuously monitored parameters (soil temperature) (Supporting Information). Daily concentrations of total P, nitrate, and ammonium were derived by interpolating observed data from LAE03 (data gap < 40 d) or using long-term monthly medians (data gap ≥ 40 d).

Table 1. Mean annual fluxes of water and DOC from the catchment to the lake, and at the lake outlet, and lake DOC retention, expressed on catchment area basis. Trends estimated using Sen-slope estimator and Mann-Kendal test. Significance levels: * $p<0.05$; ** $p<0.01$; *** $p<0.001$. n.s., not significant.

	Catchment to lake			Lake outlet			Lake retention	
	Discharge mm	Flux g C m^{-2}	Concentration mg C L^{-1}	Discharge mm	Flux g C m^{-2}	Concentration mg C L^{-1}	g C m^{-2}	% of inputs
Mean	627	7.3	11.9	669	6.7	10.4	0.6	8.4
Standard deviation	144	1.7	0.9	156	1.8	1.1	0.3	4.3
Slope	7.7	0.13	0.05	8.4	0.14	0.09	0.00	−0.3
Slope (% yr^{-1})	1.2	1.8	0.4	1.3	2.1	0.8	−0.4	—
P	*	***	**	*	***	***	n.s.	*

Daily DOC loads from the catchment to the lake were calculated by area-scaling the inlet discharge (LAE03 stream) and multiplying by the derived daily DOC time series. Parallel records of DOC in both inlet streams (1999, 2005 onward) showed strong correspondence in seasonality and absolute concentrations, which supports the area-scaling of LAE03 to the entire catchment. Daily DOC fluxes in the outlet were calculated by multiplying daily discharge with daily interpolated DOC. Lake DOC retention was calculated as the difference between annual catchment inputs and lake export, and was expressed as g C m^{-2} catchment yr^{-1}, or as % of the catchment DOC inputs. Water retention time (WRT, yr) was calculated as the ratio of lake volume (m^3) and annual inlet discharge (m^3 yr^{-1}).

The rate of DOC removal "k" (yr^{-1}) in the lake was calculated using annual mean DOC concentrations in inlet (DOC$_{in}$) and outlet (DOC$_{out}$) and WRT, using the equation provided in Catalán et al. (2016), i.e.,

$$k = -\frac{\ln\left(\frac{\text{DOC}_{out}}{\text{DOC}_{in}}\right)}{\text{WRT}}.$$

MyLake model

The lake model MyLake v. 2 is one-dimensional, general purpose lake model implemented as a MATLAB package and designed for the simulation of seasonal ice-formation, water column stability, daily heat distribution, P species dynamics, and phytoplankton abundance in lakes (Saloranta and Andersen 2007). The model has been used for simulating DOC dynamics in boreal lakes (Holmberg et al. 2014) and has recently been extended for coupled oxygen and carbon dynamics (Couture et al. 2015). State variables include POC (both autochthonous and allochthonous), DOC, and dissolved inorganic carbon (DIC). In addition to time series of weather inputs, the model requires daily inputs of inflow volumes (m^3 d^{-1}) and concentrations of DOC, dissolved oxygen, total P, nitrate, and ammonium, allocated to individual lake sub-basins. POC and DIC were not measured and are thus not provided as inputs. Formation of POC by algal growth was expected to be negligible because of nutrient and light limitation in this humic, oligotrophic lake.

We used MyLake to quantify in-lake DOC removal rates. Three key processes responsible for DOC processing represented in the model are: microbial metabolism, photomineralization, and flocculation-driven sedimentation. Metabolism and photo-mineralization both yield DIC, while flocculation yields POC. The sediment mass accumulation rate from the dated sediment core was used to constrain modeled flocculation rates. Parameter values were optimized using automated procedures derived from (Couture et al. 2015). Performance was evaluated using a calibration (1997–2001) and validation period (1991–1995), and for the entire time series. The two 6-yr time windows for calibration and validation were selected in the pre-2003 period because of higher water sampling frequency (i.e., weekly rather than monthly for the inlets). Daily DOC removal rates were calculated by integrating individual process rates over the entire water column. Further details on equations governing DOC processing and model calibration are given in the Supporting Information. Daily removal rates were summed to annual removal for each process. The mean annual total lake removal from MyLake was slightly lower than mean annual mass-balance based lake DOC retention. To correct for this in the lake carbon budget, each process removal rate was multiplied with the ratio of mass-balance based lake DOC retention to MyLake-based lake DOC retention.

Trend calculations and statistics

Trends and trend slopes were calculated using the Mann-Kendall test and the Sen's slope estimator (Helsel and Hirsch 1992). These methods are commonly used for quantification of trends in water chemistry time series (Monteith et al. 2007; Garmo et al. 2014; de Wit et al. 2016b). Details are given in Supporting Information.

Potential drivers of long-term change in mean annual DOC fluxes and concentrations were identified by testing for significant relationships between averaged annual streamwater sulfate concentrations, temperature, and summed
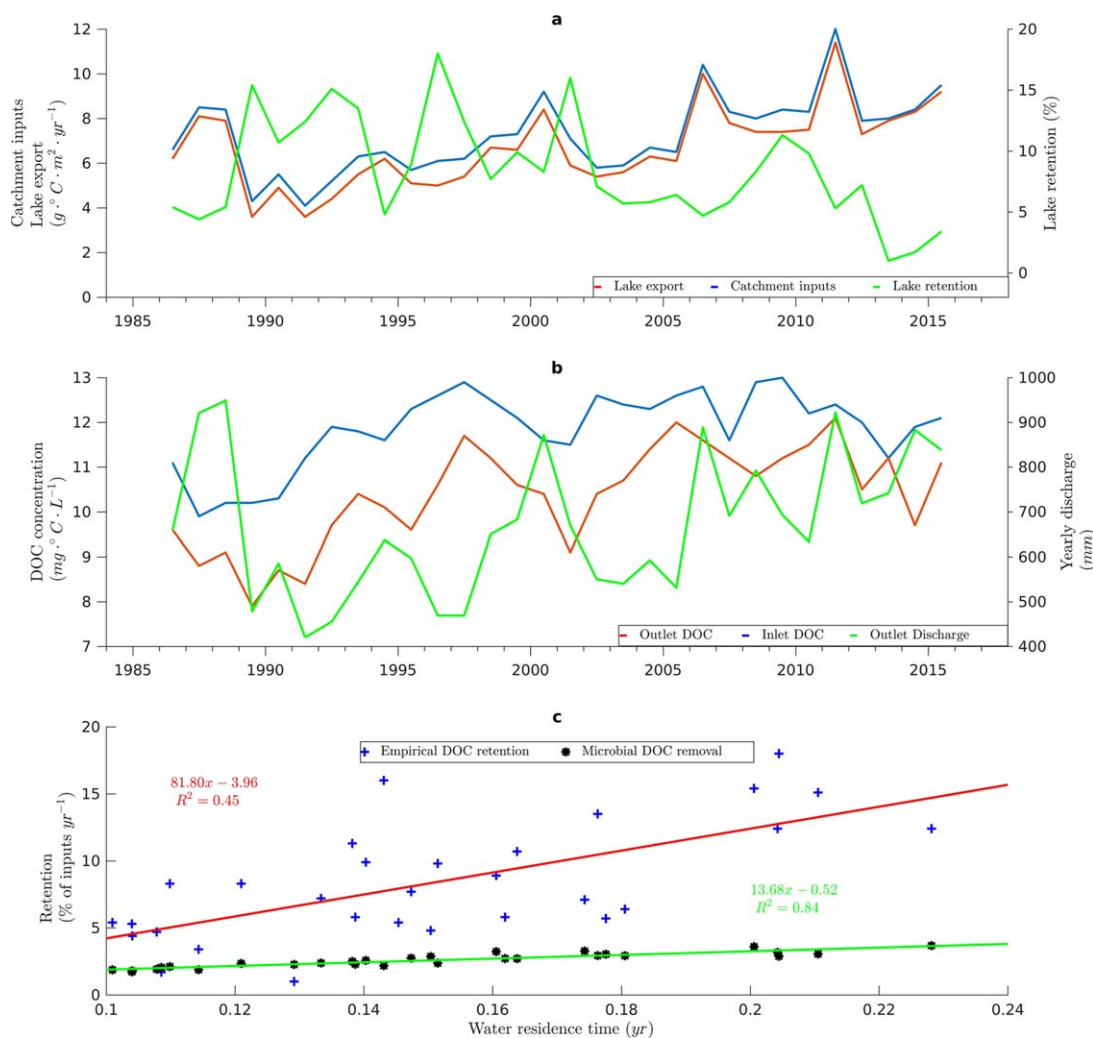
Fig. 2. Panel **a**, annual catchment DOC inputs to lake, lake DOC (left Y-axis), and lake carbon retention (calculated as difference between inputs and outputs) (right Y-axis) in g C m^{-2} catchment. Panel **b**, mean annual DOC concentrations in inlet (LAE03) and outlet (LAE01) in mg C L^{-1} (left Y-axis) and annual discharge of the outlet (mm) (right Y-axis). Panel **c**, annual lake DOC retention (empirical; calculated as difference between inputs and outputs) and modeled annual lake DOC removal by microbial metabolism (modeled), expressed in % of catchment inputs vs. water residence time (year). Linear regression lines added.

precipitation and discharge using forward selection multiple stepwise regression (SMR; 0.05 significance threshold). Dominant drivers of trends were assessed by testing for significance of the correlation between SMR model residuals and year.

Results

Fluxes, concentrations, and retention

DOC export from the lake outlet between 1986 and 2015 was on average 6.7 ± 1.8 g C m^{-2} catchment area yr^{-1} and increased significantly (Table 1; Fig. 2a).

Trends in inlet and outlet concentrations and fluxes were similar in direction and statistical strength. On average, lake DOC retention was 0.6 g C m^{-2} catchment yr^{-1} and did not

exhibit a temporal trend. However, percent lake DOC retention declined significantly. Interannual variation in DOC fluxes was larger than the long-term trend (Fig. 2b). Mean annual percent lake DOC retention was between 1% and 18% of the catchment-derived inputs to the lake, and was significantly ($p < 0.001$) positively related to water residence time (Fig. 2c).

Rates of lake DOC removal (yr^{-1}), estimated using annual lake DOC retention and WRT were on average 0.49 yr^{-1}. Annual rates of lake DOC removal (yr^{-1}) were on average 0.75 yr^{-1}, and did not correlate with WRT (Fig. 3).

Streamwater DOC concentrations and fluxes in both the inlet and outlet were all strongly related to year (Table 2), consistent with their positive trends (Table 1). The driver of upward DOC concentrations was identified as declining

Fig. 3. Lake DOC removal rates (yr^{-1}) vs. WRT (yr). Linear regression line added.

sulfate while precipitation added to explain interannual variation in the inlet. The upward trend in DOC fluxes related primarily to precipitation and secondly to sulfate. The significant decline in percent lake DOC retention could be explained by trends in annual discharge. Lake DOC retention in g C m^{-2} yr^{-1} was not significantly related to discharge.

Lake sedimentation

The estimated carbon sediment mass accumulation rate from the dated core was 12.2 g C m^{-2} lake yr^{-1}, which can be assumed to be the maximum sedimentation rate as the core was taken at the deepest point in the lake. This result was used to calibrate sediment accumulation rate of at the deepest point of the lake in the MyLake model.

Model-predicted lake carbon removal

MyLake reproduced outlet DOC concentration time-series well during the calibration and validation periods ($r^2 = 0.85$ for calibration period; 0.87 for validation period; 0.84 for 1986–2015) and root mean squared error of 1.14 mg C L^{-1} (calibration and validation periods) and 1.17 mg C L^{-1} (1986–2015). Correlation coefficients between measured and simulated daily and annual DOC export were 0.99. Modeled lake carbon removal was 0.4 g C m^{-2} catchment yr^{-1}, which is 25% lower than mass-balance estimated lake retention.

Table 2. Results of statistical analysis of catchment and lake carbon cycling at Langtjern. Linear regression between mean annual concentrations and summed fluxes, retention of DOC and year (*t*-ratio and *p* values). Linear regression models with variables (eligible: temperature, precipitation, SO$_4$, discharge) selected by forward stepwise selection, presented in sequence of selection (*t*-ratio, and *p* values for slope, R^2). Significance level of linear regression of model residuals (from one or two model variables) and year. Significance levels: * $p<0.05$; ** $p<0.01$; *** $p<0.001$; **** $p<0.0001$. n.s., not significant.

	Linear regression		Variables in linear regression models in order of selection (left to right)					Significance level of model residuals vs. year	
								Model variable	
	t-ratio year	*p*	*t*-ratio SO$_4$[†]	*p*	*t*-ratio Precip[‡]	*p*	R^2	SO$_4$[†]	
Inlet DOC concentrations	3.72	***	−5.28	****	−3.39	**	0.54	n.s.	—
Outlet DOC concentrations	4.91	****	−5.12	****	—	—	0.49	n.s.	—
			Precip[‡]		SO$_4$[†]			Precip[‡]	Precip[‡], SO$_4$[†]
Catchment inputs	3.81	***	3.65	**	−3.38	**	0.57	**	n.s.
Lake DOC export	3.9	***	3.75	***	−3.44	**	0.58	**	n.s.
	year		Discharge[§]					Discharge[§]	
DOC retention (g C m^{-2} yr^{-1})	—	n.s.	—	n.s.	—	—	—	n.s.	—
DOC retention (%)	−2.45	*	−4.45	****	—	—	—	n.s.	—

[†] Mean concentrations of streamwater SO$_4$.
[‡] Mean annual precipitation.
[§] Mean annual discharge.

Notwithstanding the excellent model fit of the DOC concentrations, annual modeled lake DOC export showed a small, (3.5%), but significant (pairwise comparison, $p < 0.0001$) underestimation of empirically estimated lake DOC export of 0.23 g C m^{-2} catchment area yr^{-1} (data not shown). Modeled daily DOC concentrations were slightly lower than measured values during high-flow situations (data not shown) when most export occurs, which likely explains the underestimation of in-lake retention. This underestimation is an artifact of the calibration procedure in which each concentration value was weighted equally, thereby down-weighting the influence of relatively rare high-flow events. The contribution of total annual lake carbon removal attributed to microbial metabolism, flocculation, and photo-mineralization (mean ± standard deviation) was 0.28 ± 0.06, 0.13 ± 0.01, and < 0.01, all in g C m^{-2} catchment yr^{-1}, respectively. The percentage of DOC inputs removed by microbial metabolism (Fig. 2C) increased significantly ($p < 0.0001$) with water residence time.

Lake carbon budget

The mean DOC budget for the lake (Fig. 4) shows that lake retention was small compared with catchment inputs and lake export. On average, 8% of all DOC entering the lake did not reach the outlet. Using the modeled removal rates, the relative contribution of microbial metabolism, flocculation, and photo-mineralization were calculated to be 68%, 32%, and $< 0.01\%$, respectively. In-lake removal rates (g C m^{-2} catchment area yr^{-1}) were calculated by multiplying these proportions with mass-balance based lake DOC retention estimates.

Discussion

A significant fraction of the worlds lakes is small and/or found in the boreal ecoregion (Verpoorter et al. 2014), where carbon budgets are highly sensitive to precipitation (Oquist et al. 2014). The degree to which surface waters process carbon (Cole et al. 2007) and whether lakes should be conceptualized as "passive pipes" transporting organic matter to the sea or active "landscape chimneys" emitting greenhouse gases to the atmosphere (Prairie 2008) is an important key to integration of terrestrial and aquatic carbon cycling.

Here, we demonstrate, using a combination of long-term monitoring records, sediment dating and modeling, that the proportion of terrestrially derived DOC retained in the lake of a boreal catchment is small (here, on average 8%) compared with catchment DOC inputs, and is strongly negatively dependent on precipitation. This is an important corroboration of the snapshot study presented by de Wit et al. (2016b) documenting precipitation controls on surface-water DOC fluxes in Nordic catchments. To our knowledge, Langtjern is one of very few multi-decadal records of annual lake DOC budgets except for Dillon and Molot (2005). Others have also found low DOC retention in small boreal catchments (i.e., 9%, Juutinen et al. 2013). The low fraction
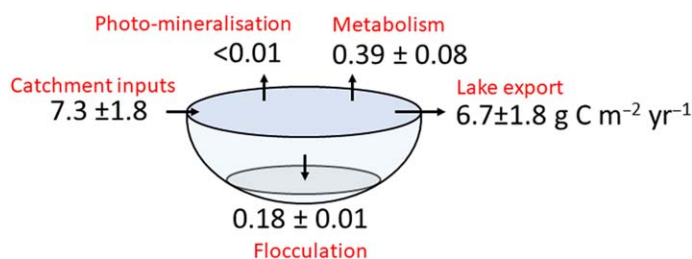
Fig. 4. Carbon budget of lake in g C m^{-2} catchment yr^{-1}. DOC inputs, DOC outputs, and lake DOC retention in annual mean ± standard deviations (1986–2015). Lake DOC retention (modeled) partitioned into three processes of carbon removal from water phase: (1) microbical metabolism, (2) flocculation, and (3) photo-mineralization.

of DOC retained is consistent with the low water residence times and low DOC removal in northern lakes with catchment to lake ratios over 6–10 (for Langtjern, this ratio is 21) (Engstrom 1987; Sobek et al. 2007).

The boreal catchment-lake continuum at Langtjern is a show-case of environmental change and its impact on catchment fluxes and lake cycling of DOC. The strong decline in sulfate concentrations, driven by reduced sulfate deposition, is typical for North American and European surface waters (Garmo et al. 2014). Here, we show that this decline not only impacts DOC concentrations, as shown many times previously (de Wit et al. 2007; Monteith et al. 2007) but also promotes catchment DOC export, suggesting that lateral DOC fluxes in the boreal landscape may currently be significantly higher than during the 1980s and 1990s, even without changes in precipitation. However, increasing precipitation is the dominant driver of increased lateral DOC fluxes at Langtjern, consistent with the mobilization effect of precipitation on DOC concentrations observed for Nordic surface waters (de Wit et al. 2016b). Similar effects of precipitation were also shown for catchment loadings of DIC (Roehm et al. 2009; Vachon and del Giorgio 2014), while positive relationships between precipitation and DOC fluxes have been reported elsewhere (e.g., Dillon and Molot 2005; Zwart et al. 2017). Increases in lateral DOC export from catchments to surface waters caused by higher rainfall could imply lower terrestrial carbon sequestration, if net primary productivity remains unaltered or even declines in wet years (Oquist et al. 2014).

The empirical mass balance provides evidence of long-term changes in lake DOC retention but is a black box with regard to the fate of terrestrially derived DOC. Using the process-based model MyLake, we suggest that microbial metabolism is the dominating process for in-lake DOC removal, while flocculation is secondary and photo-mineralization is negligible. These findings are consistent with who ascribed summer in-water losses of DOC in a humic lake 90% to biological activity and 10% photo-mineralization (Jonsson et al. 2001) as well as the simulations performed by Futter et al. (2008) for the carbon budget of a small humic lake and its catchment.

In our 30-yr time series, model optimization did not identify a significant impact of photo-mineralization on the fate of DOC in the entire water column, possibly in part because the lake is ice-covered for ca. 6 months. Measurements of photochemical DIC production as a function of depth in a humic lake by Groeneveld et al. (2016) suggest that photo-mineralization becomes negligible below 5 cm depth. Nevertheless, in shallow humic lakes, thermokarst and permafrost ponds in the arctic (Laurion and Mladenov 2013; Cory et al. 2014), photo-degradation of DOC to labile organics of smaller molecular weight was shown to be a dominant transformation process of DOC rendering DOC more labile. Our model results, suggesting that photo-mineralization did not play a substantial role for lake DOC removal at Langtjern, likely reflect that greater lake depth and lower water residence times allow that other processes than photo-mineralization become more dominant than for these arctic ponds.

The fate of retained DOC is thus primarily governed by microbial activity, turning DOC into CO_2, while sedimentation of flocculated DOC is second-important. The most likely fate of DOC removed by microbial activity is a return to the atmosphere via the intermittent state as DIC. The amount of carbon removed by flocculation is interpreted as the mean lake sedimentation rate, which was 31% of the maximum lake sediment rate estimated using the dated sediment core. The difference between mean and maximum sedimentation rates is recognized as driven by sediment focusing and usually presents a challenge for extrapolation of single-core information to the whole-lake (Engstrom and Rose 2013). Others have used sediment focusing corrections factors of 0.4–0.8 for upscaling of single core carbon accumulation to whole lakes (Buffam et al. 2011).

The landscape impact of increasing precipitation, promoting lateral DOC export but reducing percent in-lake DOC retention, primarily by microbial metabolism, implies that a lower proportion of the catchment DOC inputs will be converted to CO_2 under wetter conditions, associated with shorter WRTs. The annual lake DOC removal rate did not depend on WRT. This presents further support for our expectation of a lower conversion of DOC to CO_2 under increased precipitation.

The lack of relationship between DOC removal rates and WRT contrasts with the negative relationship between DOC decay rates and WRT demonstrated by Catalán et al. (2016). Our study suggests that lake carbon cycling under a wetting climate primarily results in a lower percent carbon retention, without a change in the decay rate. By contrast, Catalán et al. (2016) implied that lake DOC decay rates in boreal regions will increase under climate wetting. The basis for Catalán's projection of future lake DOC removal lies in the observed negative relationship between DOC decay rates and water residence time for a gradient of small headwaters to oceans. Catalán and coworkers explain the negative relation between decay rates and water residence time as the consequence of declining organic matter reactivity, expressed as fraction yr^{-1}, downstream along the aquatic continuum. In our case study, the process-based model describes the lower lake DOC removal without changing the lability of dissolved organic matter (DOM).

Catalán and coworkers use a space-for-time substitution to infer impacts of climate change, a method that assumes spatial variation is equivalent to temporal change (Pickett 1989). This assumption is challenged by our evidence from long-term monitoring records.

Space-for-time substitutions are frequently used as an approach to infer ecosystem responses to environmental change. Comparing insights on ecosystem responses from space-for-time substitutions and from temporal records is worthy of a far more extensive discussion than we can provide here. Clearly, long-term records of ecosystem monitoring are immensely valuable as ground truth data for assessing impacts of environmental change.

Our study suggests that in a wetter climate, small northern lakes will, on balance, function more as pipes than reactors, with increasing lateral DOC fluxes but little change in CO_2 production from microbial processing of terrestrial organic matter.

References

Algesten, G., S. Sobek, A. K. Bergstrom, A. Agren, L. J. Tranvik, and M. Jansson. 2004. Role of lakes for organic carbon cycling in the boreal zone. Glob. Chang. Biol. **10**: 141–147. doi:10.1111/j.1365-2486.2003.00721.x

Anderson, L. E., W. H. Krkosek, A. K. Stoddart, B. F. Trueman, and G. A. Gagnon. 2017. Lake recovery through reduced sulfate deposition: A new paradigm for drinking water treatment. Environ. Sci. Technol. **51**: 1414–1422. doi:10.1021/acs.est.6b04889

Birkel, C., C. Soulsby, and D. Tetzlaff. 2014. Integrating parsimonious models of hydrological connectivity and soil biogeochemistry to simulate stream DOC dynamics. J. Geophys. Res. Biogeosci. **119**: 1030–1047. doi:10.1002/2013JG002551

Buffam, I., M. G. Turner, A. R. Desai, P. C. Hanson, J. A. Rusak, N. R. Lottig, E. H. Stanley, and S. R. Carpenter. 2011. Integrating aquatic and terrestrial components to construct a complete carbon budget for a north temperate lake district. Glob. Chang. Biol. **17**: 1193–1211. doi:10.1111/j.1365-2486.2010.02313.x

Campeau, A., and P. A. del Giorgio. 2014. Patterns in CH_4 and CO_2 concentrations across boreal rivers: Major drivers and implications for fluvial greenhouse emissions under climate change scenarios. Glob. Chang. Biol. **20**: 1075–1088. doi:10.1111/gcb.12479

Catalán, N., R. Marce, D. N. Kothawala, and L. J. Tranvik. 2016. Organic carbon decomposition rates controlled by water retention time across inland waters. Nat. Geosci. **9**: 501–504. doi:10.1038/ngeo2720

Cole, J. J., and others. 2007. Plumbing the global carbon cycle: Integrating inland waters into the terrestrial carbon budget. Ecosystems **10**: 171–184. doi:10.1007/s10021-006-9013-8

Cory, R. M., C. P. Ward, B. C. Crump, and G. W. Kling. 2014. Sunlight controls water column processing of carbon in arctic fresh waters. Science **345**: 925–928. doi:10.1126/science.1253119

Couture, R.-M., H. A. de Wit, K. Tominaga, P. Kiuru, and I. Markelov. 2015. Oxygen dynamics in a boreal lake responds to long-term changes in climate, ice phenology, and DOC inputs. J. Geophys. Res. Biogeosci. **120**: 2441–2456. doi:10.1002/2015JG003065

de Wit, H. A., J. Mulder, A. Hindar, and L. Hole. 2007. Long-term increase in dissolved organic carbon in streamwaters in Norway is response to reduced acid deposition. Environ. Sci. Technol. **41**: 7706–7713. doi:10.1021/es070557f

de Wit, H. A., A. Granhus, M. Lindholm, M. J. Kainz, Y. Lin, H. F. V. Braaten, and J. Blaszczak. 2014. Forest harvest effects on mercury in streams and biota in Norwegian boreal catchments. For. Ecol. Manag. **324**: 52–63. doi:10.1016/j.foreco.2014.03.044

de Wit, H. A., J. L. J. Ledesma, and M. N. Futter. 2016*a*. Aquatic DOC export from subarctic Atlantic blanket bog in Norway is controlled by seasalt deposition, temperature and precipitation. Biogeochemistry **127**: 305–321. doi:10.1007/s10533-016-0182-z

de Wit, H. A., and others. 2016*b*. Current browning of surface waters will be further promoted by wetter climate. Environ. Sci. Technol. Lett. **3**: 430–435. doi:10.1021/acs.estlett.6b00396

Dillon, P. J., and L. A. Molot. 2005. Long-term trends in catchment export and lake retention of dissolved organic carbon, dissolved organic nitrogen, total iron, and total phosphorus: The Dorset, Ontario, study, 1978–1998. J. Geophys. Res. Biogeosci. **110**: G01002. doi:10.1029/2004JG000003

Engstrom, D. R. 1987. Influence of vegetation and hydrology on the humus budgets of Labrador lakes. Can. J. Fish. Aquat. Sci. **44**: 1306–1314. doi:10.1139/f87-154

Engstrom, D. R., and N. L. Rose. 2013. A whole-basin, mass-balance approach to paleolimnology. J. Paleolimnol. **49**: 333–347. doi:10.1007/s10933-012-9675-5

Finstad, A. G., I. P. Helland, O. Ugedal, T. Hesthagen, and D. O. Hessen. 2014. Unimodal response of fish yield to dissolved organic carbon. Ecol. Lett. **17**: 36–43. doi:10.1111/ele.12201

French, T. D., and others. 2014. Dissolved organic carbon thresholds affect mercury bioaccumulation in Arctic lakes. Environ. Sci. Technol. **48**: 3162–3168. doi:10.1021/es403849d

Futter, M. N., and H. A. de Wit. 2008. Testing seasonal and long-term controls of streamwater DOC using empirical and process-based models. Sci. Total Environ. **407**: 698–707. doi:10.1016/j.scitotenv.2008.10.002

Futter, M. N., M. Starr, M. Forsius, and M. Holmberg. 2008. Modelling the effects of climate on long-term patterns of dissolved organic carbon concentrations in the surface waters of a boreal catchment. Hydrol. Earth Syst. Sci. **12**: 437–447. doi:10.5194/hess-12-437-2008

Garmo, Ø. A., and others. 2014. Trends in surface water chemistry in acidified areas in Europe and North America from 1990 to 2008. Water Air Soil Pollut. **225**: 1880. doi:10.1007/s11270-014-1880-6

Groeneveld, M., L. Tranvik, S. Natchimuthu, and B. Koehler. 2016. Photochemical mineralisation in a boreal brown water lake: Considerable temporal variability and minor contribution to carbon dioxide production. Biogeosciences **13**: 3931–3943. doi:10.5194/bg-13-3931-2016

Helsel, D. R., and R. M. Hirsch. 1992. Statistical methods in water resources. Elsevier.

Holmberg, M., and others. 2014. Effects of changing climate on the hydrology of a boreal catchment and lake DOC - probabilistic assessment of a dynamic model chain. Boreal Environ. Res. **19**: 66–82. https://helda.helsinki.fi/handle/10138/228677

Jonsson, A., M. Meili, A. K. Bergstrom, and M. Jansson. 2001. Whole-lake mineralization of allochthonous and autochthonous organic carbon in a large humic lake (Ortrasket, N. Sweden). Limnol. Oceanogr. **46**: 1691–1700. doi:10.4319/lo.2001.46.7.1691

Jonsson, A., G. Algesten, A.-K. Bergström, K. Bishop, S. Sobek, L. J. Tranvik, and M. Jansson. 2007. Integrating aquatic carbon fluxes in a boreal catchment carbon budget. J. Hydrol. **334**: 141–150. doi:10.1016/j.jhydrol.2006.10.003

Juutinen, S., M. Väliranta, V. Kuutti, A. M. Laine, T. Virtanen, H. Seppä, J. Weckström, and E.-S. Tuittila. 2013. Short-term and long-term carbon dynamics in a northern peatland-stream-lake continuum: A catchment approach. J. Geophys. Res. Biogeosci. **118**: 171–183. doi:10.1002/jgrg.20028

Laurion, I., and N. Mladenov. 2013. Dissolved organic matter photolysis in Canadian arctic thaw ponds. Environ. Res. Lett. **8**: 12. doi:10.1088/1748-9326/8/3/035026

Monteith, D. T., and others. 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature **450**: 537–540. doi:10.1038/nature06316

Moody, C. S., F. Worrall, C. D. Evans, and T. G. Jones. 2013. The rate of loss of dissolved organic carbon (DOC) through a catchment. J. Hydrol. **492**: 139–150. doi:10.1016/j.jhydrol.2013.03.016

Oquist, M. G., and others. 2014. The full annual carbon balance of boreal forests is highly sensitive to precipitation. Environ. Sci. Technol. Lett. **1**: 315–319. doi:10.1021/ez500169j

Pickett, S. T. 1989. Space-for-time substitution as an alternative to long-term studies, p. 110–135. *In* G. E. Likens [ed.], Long-term studies in ecology: Approaches and alternatives. Springer-Verlag.

Prairie, Y. T. 2008. Carbocentric limnology: Looking back, looking forward. Can. J. Fish. Aquat. Sci. **65**: 543–548. doi:10.1139/f08-011

Raymond, P. A., and J. E. Saiers. 2010. Event controlled DOC export from forested watersheds. Biogeochemistry **100**: 197–209. doi:10.1007/s10533-010-9416-7

Roehm, C. L., Y. T. Prairie, and P. A. del Giorgio. 2009. The pCO$_2$ dynamics in lakes in the boreal region of northern Quebec, Canada. Global Biogeochem. Cycles **23**: GB3013. doi:10.1029/2008GB003297

Saloranta, T. M., and T. Andersen. 2007. MyLake - a multi-year lake simulation model code suitable for uncertainty and sensitivity analysis simulations. Ecol. Model. **207**: 45–60. doi:10.1016/j.ecolmodel.2007.03.018

Seddon, A. W. R., M. Macias-Fauria, P. R. Long, D. Benz, and K. J. Willis. 2016. Sensitivity of global terrestrial ecosystems to climate variability. Nature **531**: 229–232. doi:10.1038/nature16986

Sobek, S., L. J. Tranvik, Y. T. Prairie, P. Kortelainen, and J. J. Cole. 2007. Patterns and regulation of dissolved organic carbon: An analysis of 7,500 widely distributed lakes. Limnol. Oceanogr. **52**: 1208–1219. doi:10.4319/lo.2007.52.3.1208

Tranvik, L. J., and M. Jansson. 2002. Climate change - terrestrial export of organic carbon. Nature **415**: 861–862. doi:10.1038/415861b

Tranvik, L. J., and others. 2009. Lakes and reservoirs as regulators of carbon cycling and climate. Limnol. Oceanogr. **54**: 2298–2314. doi:10.4319/lo.2009.54.6_part_2.2298

Vachon, D., and P. A. del Giorgio. 2014. Whole-lake CO$_2$ dynamics in response to storm events in two morphologically different lakes. Ecosystems **17**: 1338–1353. doi:10.1007/s10021-014-9799-8

Verpoorter, C., T. Kutser, D. A. Seekell, and L. J. Tranvik. 2014. A global inventory of lakes based on high-resolution satellite imagery. Geophys. Res. Lett. **41**: 6396–6402. doi:10.1002/2014GL060641

Zwart, J. A., S. D. Sebestyen, C. T. Solomon, and S. E. Jones. 2017. The influence of hydrologic residence time on lake carbon cycling dynamics following extreme precipitation events. Ecosystems **20**: 1000–1014. doi:10.1007/s10021-016-0088-6