## Postprint

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Citation for the original published paper (version of record):

Müller, R., Futter, M., Sobek, S., Nisell, J., Bishop, K. et al. (2013)
Water renewal along the aquatic continuum offsets cumulative retention by lakes: implications for the character of organic carbon in boreal lakes.

Aquatic Sciences, 75(4): 535-545
http://dx.doi.org/10.1007/s00027-013-0298-3

Access to the published version may require subscription.
N.B. When citing this work, cite the original published paper.

Permanent link to this version:
http://urn.kb.se/resolve? urn=urn:nbn:se:uu:diva-208615

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# Water renewal along the aquatic continuum offsets cumulative 

 retention by lakes - implications for the character of organic carbon in boreal lakes


#### Abstract

The character of organic carbon (OC) in lake waters is strongly dependent on the time water has spent in the landscape as well as in the lake itself due to continuous biogeochemical OC transformation processes. A common view is that upstream lakes might prolong the water retention in the landscape, resulting in an altered OC character downstream. We calculated the number of lakes upstream for 24,742 Swedish lakes in seven river basins spanning from $56^{\circ}$ to $68^{\circ} \mathrm{N}$. For each of these lakes, we used a lake volume to discharge comparison on a landscape scale to account for upstream water retention by lakes ( $\mathrm{T}_{\mathrm{n} \text { tot }}$ ). We found a surprisingly weak relationship between the number of lakes upstream and $\mathrm{T}_{\mathrm{n}}$ tot. Accordingly, we found that the coloured fraction of organic carbon was not related to lake landscape position but significantly related to $\mathrm{T}_{\mathrm{n}}$ tot when we analysed lake water chemical data from 1,559 lakes in the studied river basins $\left(\mathrm{R}^{2}=\right.$ $0.21, \mathrm{p}<0.0001$ ). Thus, we conclude that water renewal along the aquatic continuum by lateral water inputs offsets cumulative retention by lakes. Based on our findings, we suggest integrating $\mathrm{T}_{\mathrm{n} \text { tot }}$ in studies that address lake landscape position in the boreal zone to better understand variations in the character of organic carbon across lake districts.


Keywords: lake, landscape, time, organic carbon, colour

## Introduction

The rate at which lake water is being renewed is crucial to time-dependent lake processes such as nutrient budgets (Vollenweider 1976; Hecky et al. 1993), carbon processing (Algesten et al. 2004; Battin et al. 2009) and lake water clarity (Schindler et al. 1996; Weyhenmeyer et al. 2012). During the last decade, more and more aquatic studies addressed a larger landscape, where it has been suggested that water may become older and the material in the water more processed the further down the water moves in the landscape (Egeberg et al. 1999; Steinberg 2003). This is certainly true for a single molecule travelling from headwaters via a series of lakes to the sea. However, lakes that are situated at low landscape positions not only receive water that has aged in lakes upstream but also from rainfall, groundwater and lateral tributary inflow. Thus, the age of water in lakes in the landscape is a result of complex runoff and mixing processes in the catchment (Lindström et al. 1997; Canham and Pace 2009).

Studies addressing lake landscape position indicate that the presence of upstream lakes affects downstream water quality at both the temporal (Goodman et al. 2011) and the spatial (Larson et al. 2007) scale. In situations where water follows specific lakechains from headwater lakes towards low landscape positions, material processing has been shown to occur (Soranno et al. 1999; Sadro et al. 2012). However, hydrological studies on drainage systems indicate that water residence time does not necessarily scale with catchment size, as observed for headwater systems (McGuire et al 2005; McDonnell et al. 2010) and along streams and rivers (Tokunaga 2003; Alexander et al. 2007). Alexander et al. (2007) demonstrated the important role of tributary streams for sustaining efficient water renewal throughout the entire drainage network of the northeastern United States. Martin and Soranno (2006) underpinned the relevance of such water renewal for lake-chains, as they identified stream connection as a major driver of variation in lake water chemistry and clarity across different landscape positions. The
efficiency of water renewal occurring in a larger drainage network is therefore fundamental to ecosystem functioning of lakes and reservoirs.

Lake volume and water discharge determine water retention by lakes, here referred to as lake water retention time and used synonymously with water renewal time (Schindler et al. 1992; Wetzel et al. 2001) and/or residence time (Monsen et al. 2002; Algesten et al. 2004). A simple measure of water retention time for single lake water bodies can be defined as the ratio between lake volume and mean discharge through the lake outflow $\left(\mathrm{T}_{\mathrm{n}}\right)$ and is frequently applied to indicate and compare general water exchange properties of lakes (Bolin and Rodhe 1973; Monsen et al. 2002). In the Experimental Lakes Area in Canada, comprising 58 small lakes with catchments of 0.1 to $8.4 \mathrm{~km}^{2}$ in size, Schindler et al. $(1992 ; 1996 ; 1997)$ have, for example, discussed OC concentrations, nutrients and water colour based on $\mathrm{T}_{\mathrm{n}}$. Based on empirical models, carbon sedimentation in lakes and reservoirs (Cole et al. 2007), carbon transport (Weyhenmeyer et al. 2012) and mineralization (Algesten et al. 2004) have found to be related to lake water retention times. Hence, the processing and transport of carbon in lakes is a function of time. However, estimates of water retention times are frequently applied and compared with limited knowledge of their actual distribution on a larger landscape, and the cumulative water retention by lakes remains largely unknown.

This study addresses water retention by lakes and its relevance for the character of OC. We used a dataset of 24,742 lakes $\left(>0.01 \mathrm{~km}^{2}\right)$ from seven river basins in Sweden, covering a $12^{\circ}$ latitudinal range. For each lake, we estimated two measures of water retention time. The first estimated measure $\left(\mathrm{T}_{\mathrm{n}}\right)$ corresponded to the mean water retention time for a single lake ( n ), as defined above. The second estimated measure ( $\mathrm{T}_{\mathrm{n}}$ tot ) included the sum of all lake volumes upstream of a lake (n), indicating a mean for the water retention by lakes on a landscape scale (Algesten et al. 2004). We hypothesized that lake landscape position is related to $\mathrm{T}_{\mathrm{n} \text { tot }}$ and also to the coloured fraction of OC. We further hypothesized that $\mathrm{T}_{\mathrm{n}}$ is strongly related to the coloured fraction of OC as
previously observed (Weyhenmeyer et al., 2012) but that the relationship becomes stronger when $T_{n}$ is replaced by $T_{n}$ tot. To test these hypotheses, we used lake morphometric and hydrological data, as well as lake water chemical data from the Swedish national lake monitoring program.

## Materials and Methods

## Datasets

Our lake dataset included 24,742 lakes larger than $0.01 \mathrm{~km}^{2}$ from seven river basins: (1) Lagan, (2) Mälaren, (3) Dalälven, (4) Ljungan, (5) Ångermanälven, (6) Umeälven and (7) Kalixälven (Fig. 1). The lakes represent approximately $25.9 \%$ of all lake water bodies ( $>0.01 \mathrm{~km}^{2}$ ) in the Swedish Lake Registry (ca. 95,700 lakes) as provided by the Swedish Meteorological and Hydrological Institute (SMHI). We chose the seven river basins (Table 1) according to the following criteria: (1) estimates of longterm (1961 to 1990) mean discharge were available for the entire basin, (2) volume estimates for large lakes and reservoirs were available, (3) the river basins were preferably large in size and (4) well distributed over Sweden. For each lake (n), we estimated its volume $\left(V_{n}\right)$, used the estimate of long-term mean discharge $\left(Q_{n}\right)$, counted the number of lakes $\left(>0.01 \mathrm{~km}^{2}\right)$ upstream, summed the lake volumes in the catchment including the volume of the lake ( n ) at hand $\left(\mathrm{V}_{\mathrm{n} \text { tot }}\right)$ and determined our two measures of water retention time $\left(\mathrm{T}_{\mathrm{n}}, \mathrm{T}_{\mathrm{n} \text { tot }}\right.$, see below).

Lake water chemistry data from the Swedish national lake monitoring program were made available by the Swedish University of Agricultural Sciences (SLU). We used water chemical data from lake water sampling campaigns run in the years 1995, 2000 and 2005 where a total of 1,559 lakes in the selected seven river basins were sampled. Some lakes were sampled several times, while others were sampled only once. We analysed the
dataset for each year separately and additionally calculated a long-term lake-specific median value. Sampled lakes were well distributed across the seven river basins (Fig. 1). Sampling was conducted geographically from north to south by a helicopter. Samples were taken at a depth of 0.5 m in the central part of each lake. Sampling periods stretched from September until November, when lake waters underwent autumn water column mixing and surface water samples become more representative of a lake's water chemistry (Göransson et al. 2004). Variables considered in this study were absorbance at 420 nm , measured on filtered $(0.45 \mu \mathrm{~m})$ samples in a 5 cm quartz cuvette ( $\mathrm{AbsF}_{420}$; reported with an analytical precision of $12 \%$ according to method SS-EN ISO 7887 v.1) and total organic carbon (TOC; reported with an analytical precision of $11 \%$ according to method SS-EN 1484 v.1). Absorbance data were converted to Napierian absorption coefficients $\mathrm{a}_{420}\left[\mathrm{~m}^{-1}\right]$, Eq. 1 :

$$
\begin{equation*}
a_{420}=\mathrm{AbsF}_{420} \times \ln (10) \times \mathrm{L}^{-1} \tag{1}
\end{equation*}
$$

where $\mathrm{AbsF}_{420}$ is the absorbance measured, $\ln (10)$ is the natural logarithm of 10 and L is the optical path-length [m], after Kirk (1994) and as recommended by Hu et al. (2002). TOC in Swedish lakes generally contains $97 \pm 5 \%$ dissolved organic carbon (DOC) (von Wachenfeldt and Tranvik 2008) and is therefore frequently used as a proxy for DOC. We calculated the ratio $\mathrm{a}_{420}\left[\mathrm{~m}^{-1}\right]$ over TOC $\left[\mathrm{mgL}^{-1}\right]$ which reflects specific absorbance at 420 nm and is thereby used as a measure of the character of OC (Wetzel 2001; Sulzberger and Durisch-Kaiser 2009).

## Lake volume estimates

Information on measured lake volumes for a total of 1,263 lakes was available from the Swedish Lake Registry (2009). Though these lakes represent only a minor fraction of the lake dataset by count ( $5.1 \%$ ), they include the majority of large lakes. To
estimate the lake volume of the remaining 23,479 lakes, we applied an existing empirically derived lake volume estimator after Sobek et al. (2011), Eq. 2 and Eq. 3:

$$
\begin{equation*}
\ln \left(\mathrm{V}_{\mathrm{n} \text { unt }}\right)=0.75+1.06 \times \ln (\mathrm{A})+0.056 \times \gamma_{\max 50} \tag{2}
\end{equation*}
$$ the lake water body (n). And

$$
\begin{equation*}
V_{n}=\exp \left(\ln \left(V_{n \text { unt }}\right)\right) \times \exp \left(0.5 \times s^{2}\right) \tag{3}
\end{equation*}
$$

where $\mathrm{V}_{\mathrm{n}}\left[\mathrm{Mm}^{3}\right]$ is the lake volume estimate corrected for log-transformation bias and $s^{2}$ the residual variance of the volume estimate. Eq. 2 explained $93 \%$ of the variability in lake volumes $\left(\mathrm{V}_{\mathrm{n}}\right)$. The model was calibrated with known lake volumes from the entire Swedish Lake Registry (6,943 lakes) and GIS derived morphological data $\left(\gamma_{\max 50}\right)$. The residual variance $\left(\mathrm{s}^{2}\right)$ used in Eq. 3 was 0.284 and was used to correct the volume estimates for log-transformation bias; for more detailed information on this model, we refer to Sobek et al. (2011). Published lake volumes were available for most large lakes in the selected seven river basins, but there were 49 lakes ( 10.04 to $60.69 \mathrm{~km}^{2}$ ) beyond the size range ( $>10 \mathrm{~km}^{2}$ ) used by Sobek et al. (2011), for which published lake volume estimates were not available. According to Sobek et al. (2011), extrapolation to lakes $>10 \mathrm{~km}^{2}$ was justified, and we therefore applied the volume estimator without further calibration. Sobek et al. (2011) noted that their volume estimates performed well as long as the lake count is kept high ( $\mathrm{n} \geq 15$ ). While the estimated volume of an individual lake had a considerable degree of uncertainty, the relative error of cumulative lake volumes was found to decrease during error propagation with the number of lakes by $\mathrm{n}^{(-0.5)}$, such that Eq. 2 is suitable to estimate lake volumes at a catchment or landscape scale. In our analyses, volume estimates were rounded to $10^{3} \mathrm{~m}^{3}$.

$$
\begin{equation*}
\mathrm{T}_{\mathrm{n}}=\mathrm{V}_{\mathrm{n}} \times \mathrm{Q}_{\mathrm{n}}^{-1} \tag{4}
\end{equation*}
$$

## Long-term (30 years) mean discharge

We used estimates of long-term mean discharge (Qn) [m3d-1] at the outflow of each lake (n), which were generated by the HBV (Hydrologiska Byråns Vattenbalansavdelning) runoff model (Lindström et al. 1997) for the Swedish reference period 1 January 1961 to 31 December 1990. Data were available from the SMHI as a raster data file with a resolution of $50 \times 50 \mathrm{~m}$. The input data to the HBV runoff model are observations of precipitation, air temperature and estimates of evapotranspiration. For more detailed information on the HBV runoff model, we refer to Lindström et al. (1997). We tested the accuracy of $\mathrm{Q}_{\mathrm{n}}$ estimates by calculating long-term mean runoff [ $\mathrm{mm} \mathrm{yr}^{-1}$ ] for each lake, as the ratio between long-term mean discharge and catchment area, which we compared to the published range of long-term mean runoff ( 140 to $1450 \mathrm{~mm} \mathrm{yr}^{-1}$ ) for the respective time period. There were 213 lakes, all comparably small in size ( $0.01-0.28$ $\mathrm{km}^{2}$ ) which lay outside the published runoff range and were excluded, reducing an original dataset of all available 26,264 lakes to a dataset of 26,051 lakes.

## Lake water retention time estimates

We used $Q_{n}$ and $V_{n}$ to estimate conventional water retention times $\left(T_{n}\right)$ for each
where $T_{n}[d], V_{n}\left[m^{3}\right]$ and $Q_{n}\left[\mathrm{~m}^{3} \mathrm{~d}^{-1}\right]$ are the water retention time, lake volume and long-term mean discharge estimates for a single lake (n). In addition, we estimated the second measure of water retention time, which has earlier been used to indicate a mean for the time water had been retained in lakes within the landscape (Algesten et al. 2004), Eq. 5:

$$
\begin{equation*}
\mathrm{T}_{\mathrm{n} \text { tot }}=\mathrm{V}_{\mathrm{n} \text { tot }} \times \mathrm{Q}_{\mathrm{n}}^{-1} \tag{5}
\end{equation*}
$$ own volume $\left(\mathrm{V}_{\mathrm{n}}\right)$ and the sum of the lake volumes upstream $\left(\mathrm{V}_{\mathrm{n} \text { upstr }}\right)$ including $\mathrm{V}_{\mathrm{n}}$, Eq. 6:

$$
\begin{equation*}
\mathrm{R}_{\mathrm{v}}=\frac{\mathrm{T}_{\mathrm{n}}}{\mathrm{~T}_{\mathrm{n} \text { tot }}}=\frac{\mathrm{V}_{\mathrm{n}}}{\mathrm{~V}_{\mathrm{n} \text { tot }}}=\frac{\mathrm{V}_{\mathrm{n}}}{\mathrm{~V}_{\mathrm{n} \text { upstr }}+\mathrm{V}_{\mathrm{n}}} \quad[\%] \tag{6}
\end{equation*}
$$

where $\mathrm{T}_{\mathrm{n} \text { tot }}[\mathrm{d}]$ is the lake volume to discharge comparison between the summed lake volumes in the catchment of a lake $(\mathrm{n})$, including the lake's own volume $\left(\mathrm{V}_{\mathrm{n} \text { tot }}\right)\left[\mathrm{m}^{3}\right]$, and the estimate of long-term mean discharge $\left(\mathrm{Q}_{\mathrm{n}}\right)\left[\mathrm{m}^{3} \mathrm{~d}^{-1}\right]$ read at the outflow of the lake (n). $T_{n}$ tot assumes that runoff from lakes upstream reaches lakes downstream. Evapotranspiration as well as groundwater are both considered in the water-balance of the HBV model used to estimate $\mathrm{Q}_{\mathrm{n}}$ (Lindström et al. 1997). The SMHI notes that evapotranspiration is effective in the southern part of Sweden, where more than $50 \%$ of the yearly precipitation may return back to the atmosphere. Replacement of runoff along flow and a weak connectivity amongst lakes may result in an overestimation of $\mathrm{T}_{\mathrm{n} \text { tot }}$ for lakes low in the landscape. We therefore applied $\mathrm{T}_{\mathrm{n} \text { tot }}(1)$ as a conservative measure of mean water retention by lakes on a landscape scale and (2) to observe how the ratio between cumulative lake volumes $\left(\mathrm{V}_{\mathrm{n} \text { tot }}\right)$ and long-term mean discharge $\left(\mathrm{Q}_{\mathrm{n}}\right)$ changes from headwater lakes towards lakes at low landscape positions (Fig. 2). Quantifying $\mathrm{T}_{\mathrm{n}}$ we identified water bodies $\left(>0.01 \mathrm{~km}^{2}\right)$ with theoretical water retention times of a few hours to days, implying that those water bodies rather resemble rivers than lakes. Excluding the lower 5 percentile, we limited our study to water bodies with a theoretical water retention time of 4 d and greater $\left(\mathrm{T}_{\mathrm{n}} \geq 4 \mathrm{~d}\right)$, leaving a final dataset of 24,742 lakes for analysis. However, we do test for the sensitivity of our results to this exclusion criterion (cut-off).

The ratio $\left(R_{v}\right)$ between $T_{n}$ and $T_{n}$ tot is equivalent to the ratio between the lake's

## Statistical analysis

We considered non-normality and heteroscedasticity (subgroups with unequal variability) in our data by using the non-parametrical Wilcoxon method when testing for differences between landscape positions. The strength of $T_{n}$ and $T_{n}$ tot as predictors for $\mathrm{a}_{420} / \mathrm{TOC}$ was tested by running a multiple regression model on log-transformed data. Statistical significance was assessed at $\mathrm{p}<0.05$. All statistical tests were carried out in JMP, version 9.0.2. (SAS Institute, Inc., 2010).

## Results and Discussion

## Lake water retention times in the landscape

We found that conventional water retention times $\left(\mathrm{T}_{\mathrm{n}}\right)$ for our dataset of 24,742 lakes ranged from 4 d to $10^{4} \mathrm{~d}$ with the upper and lower 2.5 percentiles ranging from 7 to $1,207 \mathrm{~d}$. The $\mathrm{T}_{\mathrm{n}}$ distribution had a positive skew (median $=120 \mathrm{~d}$, mean $=248 \mathrm{~d}$ ). The lower 2.5 percentile of the full $\mathrm{T}_{\mathrm{n}}$ distribution was dominated by small lakes ( $<0.1 \mathrm{~km}^{2}$ ) situated within the main stems of the seven river basins. The upper 2.5 percentile included headwater lakes where long-term mean water discharges were close to zero. Such low $\mathrm{Q}_{\mathrm{n}}$ for headwater lakes and the fact that $\mathrm{Q}_{\mathrm{n}}$ strongly increased with an increasing number of lakes upstream (Fig. 3b) explain why a non-parametric Wilcoxon test showed significantly higher $\mathrm{T}_{\mathrm{n}}$ values in the headwater group (median $\mathrm{T}_{\mathrm{n}}=178$ ) compared to the groups at low landscape positions (p<0.0001; Fig. 3c). Removing the cut-off for lakes with especially short water retention times $\left(T_{n}<4 d\right)$, the statistical significance of our results remained unchanged. Our findings suggest that the majority of lakes at low landscape positions experience increased water discharge, often resulting in a more efficient exchange of water, when compared to headwater lakes.

Accounting for water retention by upstream lakes using $\mathrm{T}_{\mathrm{n} \text { tot }}$ for our 24,742 lakes we found that $\mathrm{T}_{\mathrm{n} \text { tot }}$ ranged from 4 to $10^{5} \mathrm{~d}$ with the upper and lower 2.5 percentiles ranging from 15 to $1,288 \mathrm{~d}$. Like for $\mathrm{T}_{\mathrm{n}}$, the $\mathrm{T}_{\mathrm{n} \text { tot }}$ distribution had a positive skew (median $=178 \mathrm{~d}$, mean $=326 \mathrm{~d})$. In contrast to $\mathrm{T}_{\mathrm{n}}$ however, $\mathrm{T}_{\mathrm{n} \text { tot }}$ showed lower values in the headwater group compared to the groups at low landscape positions (non-parametric Wilcoxon test: p $<0.0001$; Fig. 3d). This pattern resulted from a strong increase in the summed lake volumes (Fig. 3a; $\mathrm{V}_{\mathrm{n} \text { tot }}$ ) with an increasing number of lakes upstream that exceeded the strong increase in discharge (Fig. $3 \mathrm{~b} ; \mathrm{Q}_{\mathrm{n}}$ ) with an increasing number of lakes upstream. Analysing each of the seven river basins separately, the significantly increased $\mathrm{T}_{\mathrm{n} \text { tot }}$ values at low landscape positions remained similar in six of the seven river basins (Lagan, Mälaren, Dalälven, Ljungan, Ångermanälven and Umeälven; Fig. 4). Removing the cut-off for lakes with especially short water retention times $\left(T_{n}<4 d\right)$, the statistical significance of our results remained unchanged.

We observed that more than $75 \%$ of the lakes at high landscape positions showed $\mathrm{T}_{\mathrm{n} \text { tot }}$ values $<365 \mathrm{~d}$, implying that the water in these lake-networks is exchanged within the course of one year (Fig. 4). In boreal Scandinavia, water retention times below one year are primarily driven by strong seasonal runoff events, mainly the yearly spring runoff after snowmelt but also strong rainfalls during summer (Lindström and Bergström 2004; Ågren et al. 2010). During runoff events, water retention times may drop to a fraction of their theoretical long-term means, with strong environmental effects for respective lake-ecosystems (Meili 1992; Ågren et al. 2010). Such seasonal variations are not explicitly considered in our approach but are included in the long-term (1961-1990) mean water discharge data. If processes in single lake ecosystems are studied, then high frequency water discharge measurements are needed. Not until then underlying mechanisms of water quality variations can be understood.

In headwater lakes (no lake $>0.01 \mathrm{~km}^{2}$ upstream) $\mathrm{T}_{\mathrm{n} \text { tot }}$ corresponds to $\mathrm{T}_{\mathrm{n}}$ by definition. Headwater lakes made up $62 \%$ of the lake count in our dataset. Thus, for the
majority of lakes, conventional water retention time $\left(\mathrm{T}_{\mathrm{n}}\right)$ is a suitable measure. Moving away from headwater systems, however, differences between $T_{n}$ and $T_{n}$ tot become obvious. The strongest discrepancies between $T_{n}$ and $T_{n \text { tot }}$, as expressed by the lowest $R_{v}$ values, are reached for lakes at low landscape positions. At these landscape positions, $\mathrm{R}_{\mathrm{v}}$ frequently showed values $<0.1$ (Fig. 5a), implying that $\mathrm{T}_{\mathrm{n} \text { tot }}$ was more than 10 times larger than $\mathrm{T}_{\mathrm{n}}$. At low landscape positions however, we also found some lakes that showed comparatively high $R_{v}$ values of $\geq 0.5$. High $R_{v}$ values are reached when the volume of a lake ( n ) is comparable to or larger than the summed lake volume upstream. This is the case for the majority of the 114 largest lakes ( $>10 \mathrm{~km}^{2}$ ) which collectively hold $74.5 \%$ of the total lake volume in our dataset (Table 2). Such large lakes are located at low landscape positions (circles, Fig. 5a). Consequently, the high $\mathrm{T}_{\mathrm{n} \text { tot }}$ values at low landscape positions are strongly affected by large lakes. These results and median $\mathrm{T}_{\mathrm{n} \text { tot }}$ values < 365 d for lakes upstream (see above) suggest that lakes across all landscape positions frequently receive water from lateral inputs, such as tributary or groundwater inflow and/or from precipitation. Such efficient water renewal needs to be considered by studies dealing with biochemical cycling on a landscape scale.

A comparison between the total lake volume in the seven river basins and longterm mean discharge has previously been assessed by Algesten et al. (2004) for Sweden's 21 river mouths. They found that water at the river mouths had been retained by lakes for periods between 0.5 and 13.5 years. Our own estimates at seven river mouths (Table 1) showed values between 0.4 and 3.5 years ( 156 to $1,265 \mathrm{~d}$, respectively) and were 14.5 to 70.3 \% lower than the values published earlier ( $\Delta \mathrm{T}$; Table 1 ). We interpret the deviating results to differences in the assessment of lake volumes. We used newly published information on lake volumes (see methods) that covered $89.2 \%$ of the volume held by the 114 large lakes mentioned above, as well as $73.3 \%$ of the entire lake volume in our dataset. Indeed, 26.7 \% of the total lake volume had to be estimated, but by comparing estimated lake volumes with published lake volumes (1,263 lakes), we received a slope
close to 1 and a non-significant intercept ( $\mathrm{p}>0.05$ ) indicating that our lake volume estimates are reliable.

The $T_{n}$ tot approach is based on the following two fundamental assumptions that need to be taken into consideration when $T_{n}$ tot is applied. (1) $T_{n}$ tot assumes that runoff from lakes upstream reaches lakes downstream. Replacement of the respective runoff along the aquatic continuum will result in an overestimation of $\mathrm{T}_{\mathrm{n} \text { tot }}$ for lakes at low landscape positions, suggesting that water renewal may be even more efficient than presented in this study. (2) $\mathrm{T}_{\mathrm{n} \text { tot }}$ assumes that a lake can be modelled as a well-mixed system, which neglects periods of stratification. Thus, $\mathrm{T}_{\mathrm{n} \text { tot }}$ indicates a long-term mean for water retention by lakes on a landscape scale and should not be confounded with more elaborate measurements of residence time (Bolin and Rodhe 1973) and age (Zimmerman 1988), which access the fate of solutes and particles travelling through a lake system (Monsen et al. 2002).

## Lake water retention times and the character of organic carbon

In accordance with previous results (Meili 1992; Schindler et al. 1992), we found that $\mathrm{T}_{\mathrm{n}}$ relates to the coloured fraction of OC in lakes, here defined as $\mathrm{a}_{420} / \mathrm{TOC}$. A relationship between $\mathrm{T}_{\mathrm{n}}$ and $\mathrm{a}_{420} / \mathrm{TOC}$ was significantly negative but had a low coefficient of determination (Fig. 6a; $\mathrm{R}^{2}=0.11, \mathrm{p}<0.0001$ ). It has been argued that a preferential colour loss along a $\mathrm{T}_{\mathrm{n}}$ gradient is primarily the result of solar radiation induced OC mineralization (Morris and Hargreaves 1997; Vähätalo and Wetzel 2004). Additionally, in-lake processes such as microbial degradation and flocculation with consequent sedimentation are known to result in a loss of the coloured fraction of OC (Tranvik 1998; von Wachenfeldt et al. 2008; Köhler et al. 2012). OC can also be produced in the lake, which usually is more transparent and labile than its terrestrial counterpart (Findlay and Sinsabaugh 2003; Steinberg 2003). Consequently, the presence of upstream lakes has an
effect on the OC character that is found downstream, both in terms of the amount and in the light-absorbing properties (Larson et al. 2007 and Sadro et al. 2012).

Since the conventional retention time estimator $T_{n}$ does not account for any water retention and carbon processing by upstream lakes, we expected an improvement in the relationship between lake water retention and $\mathrm{a}_{420} / \mathrm{TOC}$ when we replaced $\mathrm{T}_{\mathrm{n}}$ by $\mathrm{T}_{\mathrm{n} \text { tot }}$. Such an improvement was achieved for non-headwater lakes (911 lakes with $\mathrm{T}_{\mathrm{n}} \neq \mathrm{T}_{\mathrm{n} \text { tot }}$ ). First of all we were able to raise the coefficient of determination from 0.11 to 0.21 (Fig. $6 b)$, and secondly we found that $\mathrm{T}_{\mathrm{n} \text { tot }}$ was the stronger predictor for $\mathrm{a}_{420} /$ TOC when we ran a multiple regression model with both log-transformed $\mathrm{T}_{\mathrm{n}}$ and $\mathrm{T}_{\mathrm{n} \text { tot }}$ as explanatory variables $(t=-9.77, p<0.0001$ and $t=-1.97, p=0.0497$, respectively). The coefficient of determination became exceptionally high when we grouped our data and related median water retention times to median $\mathrm{a}_{420} /$ TOC values (Fig. 6a and 6b). An improved relation to the coloured fraction of OC by using $T_{n \text { tot }}$ instead of $T_{n}$ supports the concept that the character of OC in boreal lakes is related to the time OC has spent in lakes within the landscape.

Replacing $\mathrm{T}_{\mathrm{n} \text { tot }}$ by lake landscape position, we found a significant ( $\mathrm{p}<0.05$ ) decrease in $\mathrm{a}_{420}$ (Fig. 7a) and TOC (Fig. 7b) but not in $\mathrm{a}_{420} /$ TOC (Fig. 7c). These results suggest that there is either no preferential loss of the coloured fraction of OC across landscape positions or that highly coloured OC is supplied from lateral inflows at the same rate as it is lost by mineralization and sedimentation. Previous studies addressing lake landscape position suggested that changes in OC quantity and quality depend on hydrologic connectivity (Martin and Soranno et al. 2006) and lake-network structure (Soranno et al. 1999). Thus, measures of the character of OC, such as $\mathrm{a}_{420} /$ TOC, may increase or decrease when following a specific lake-chain. Moving from specific lakechains to a large scale across lake districts, as done in our study, increases variability and may obscure patterns that have been reported from within specific lake-chains (Sadro et al. 2012). Consequently studies that address changes within specific lake-chains, e.g. the
studies by Kratz et al. (1997) and Kling et al. (2000), differ from studies like ours that test differences across lake landscape positions based on data from numerous lake districts.

Seeing lakes from a large landscape perspective and assessing lakes beyond specific lake-districts become especially relevant in the carbon rich boreal zone, where river basins may hold several thousand lakes and the bulk lake area and volume is unevenly distributed (Table 2). As an integral part of the boreal landscape, lakes delay surface water runoff, giving time for carbon processing to occur, and thereby acting as regulators of carbon cycling (Cole et al. 2007; Tranvik et al. 2009). Seeing lakes from a landscape perspective may become increasingly relevant in the future, as lakes are monitored, modified and managed for such endeavours as hydropower generation (Barros et al. 2011) and multi-lake ecosystem management (Soranno et al. 2010).

## Conclusions

We conclude from our results that lake landscape position does not reflect well how long the water has travelled in a boreal landscape, limiting its use in explaining water retention time dependent processes. While $\mathrm{T}_{\mathrm{n}}$ is a useful tool to indicate lake water retention for single lake water bodies, we recommend using $\mathrm{T}_{\mathrm{n}}$ tot for large-scale approaches. Since we found a strong relationship between $\mathrm{T}_{\mathrm{n}}$ tot and the character of OC in the landscape for 1,559 lakes, we suggest that $\mathrm{T}_{\mathrm{n} \text { tot }}$ might also be a useful measure to explain variations of other nutrients in the landscape.

## Acknowledgments

Many thanks go to the Swedish Meteorological and Hydrological Institute (SMHI) for providing the hydrological and geomorphological base data used in this study, as well as to the Department of Aquatic Sciences and Assessment at the Swedish University of Agricultural Sciences (SLU) for providing data from thousands of lake water samples. We thank Dolly Kothawala and Blaize Denfeld, as well as three anonymous reviewers for constructive comments. Financial support was received from the Swedish Research Council (VR), the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS), and the Nordic Centre of Excellence "CRAICC -Cryosphere-atmosphere interactions in a changing arctic climate" supported by NordForsk. Martyn N. Futter was funded by the MISTRA Future Forests programme. This work developed as part of the project "The colour of water - interplay with climate, and effects on drinking water supply".

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Table 1 Dataset by river basins; area of river basin (size), highest point ( $\mathrm{z}_{\max }$ ), number of lakes larger than $0.01 \mathrm{~km}^{2}$ (lake count), summed lake volumes $\left(\mathrm{V}_{\mathrm{n}}\right.$ tot $)$, long-term (1961 to 1990) mean flow as discharge at the river mouth $\left(\mathrm{Q}_{\text {sea }}\right)$, and the ratio between $\mathrm{V}_{\mathrm{n} \text { tot }}$ and $\mathrm{Q}_{\text {sea }}\left(\mathrm{T}_{\text {sea }}\right)$. The percentage $\Delta \mathrm{T}$ presents the difference between $\mathrm{T}_{\text {sea }}$ and earlier estimates published by Algesten et al. (2004)

| ID | river basin | size <br> $\left[\mathrm{km}^{2}\right]$ | Z max <br> $[\mathrm{m}$ a.s.l. $]$ |  | lake count <br> $[-]$ | $\mathrm{V}_{\mathrm{n} \text { tot }}$ <br> $\left[\mathrm{Mm}^{3}\right]$ | $\mathrm{Q}_{\text {sea }}$ <br> $\left[\mathrm{m}^{3} \mathrm{~s}^{-1}\right]$ | $\mathrm{T}_{\text {sea }}$ <br> $[\mathrm{d}]$ | $\Delta \mathrm{T}$ <br> $[\%]$ |
| :--- | :--- | ---: | :--- | ---: | ---: | ---: | ---: | ---: | ---: |
| 1 | Lagan | 6,452 | 372 | 737 | 2,641 | 83 | 368 | - |  |
| 2 | Mälaren | 22,650 | 490 | 2,138 | 22,069 | 202 | 1,265 | - |  |
| 3 | Dalälven | 28,621 | 1,436 | 5,241 | 17,161 | 357 | 557 | $-51 \%$ |  |
| 4 | Ljungan | 12,851 | 1,577 | 2,187 | 5,340 | 150 | 412 | $-70 \%$ |  |
| 5 | Ångermanälv. | 31,079 | 1,564 | 5,450 | 29,502 | 520 | 657 | $-25 \%$ |  |
| 6 | Umeälven | 26,815 | 1,751 | 5,710 | 17,162 | 430 | 462 | $-37 \%$ |  |
| 7 | Kalixälven | 18,130 | 2,092 | 3,279 | 3,060 | 227 | 156 | $-15 \%$ |  |

Table 2 Lake count and volumes per lake size class A to E

| SMHI size classes $\left[\mathrm{km}^{2}\right]$ |  | lake count $[-, \%]$ |  | lake area $\left[\mathrm{km}^{2}, \%\right]$ |  | lake volume $\left[\mathrm{Mm}^{3}, \%\right]$ |  |
| :--- | ---: | ---: | ---: | :---: | ---: | :---: | ---: |
| E | $0.01-0.1$ | 18128 | $73.2 \%$ | 5,242 | $50.5 \%$ | 1,606 | $1.6 \%$ |
| D | $0.1-1$ | 5410 | $21.9 \%$ | 2,943 | $28.3 \%$ | 5,983 | $6.2 \%$ |
| C | $1-10$ | 1090 | $4.4 \%$ | 1,630 | $15.7 \%$ | 17,121 | $17.7 \%$ |
| A - B | $>10$ | 114 | $0.5 \%$ | 567 | $5.5 \%$ | 72,225 | $74.5 \%$ |
|  | Total | 24,742 | $100.0 \%$ | 10,382 | $100.0 \%$ | 96,935 | $100.0 \%$ |

Fig. 1 Geographic location of the seven river basins in our dataset; Lagan (1), Mälaren
(2), Dalälven (3), Ljungan (4), Ångermanälven (5), Umeälven (6), Kalixälven (7). Lakes sampled by the Swedish national lake monitoring program in 1995, 2000, 2005 marked (black dots)

Fig. 2 (a) An exemplary lake (n) with three lakes upstream. The lake volume to flow comparison $\mathrm{T}_{\mathrm{n}}$ tot is indifferent of the flow and lake distribution upstream of the lake ( n ) at hand. The summed lake volume $\left(\mathrm{V}_{\mathrm{n} \text { tot }}\right)$ includes the lake ( n ) at hand. (b) Following a lake series downstream, $T_{n}$ tot will decrease where flow as discharge $\left(\mathrm{Q}_{\mathrm{n}}\right)$ accumulates faster than the summed lake volume $\left(\mathrm{V}_{\mathrm{n} \text { tot }}\right)$ and conversely increase where $\mathrm{V}_{\mathrm{n}}$ tot accumulates faster than $\mathrm{Q}_{\mathrm{n}}$

Fig. 3 Distribution (median, $50 \%$ and $90 \%$ quantile ranges) of (a) summed lake volumes $\mathrm{V}_{\mathrm{n} \text { tot }}$ in the catchment of each lake, (b) long term (1961-1990) mean discharge $\left(\mathrm{Q}_{\mathrm{n}}\right)$ at the outflow of each lake, (c) water retention time $T_{n}$ for each lake. Asterisks indicate significance levels $\left(* \mathrm{p}<0.05,{ }^{* *} \mathrm{p}<0.001, * * * \mathrm{p}<0.0001\right)$ for a decrease in the median $\mathrm{T}_{\mathrm{n}}$ when compared to the headwater group (hg). Crosses mark medians for lakes sampled. (d) Water retention time $\mathrm{T}_{\mathrm{n} \text { tot }}$ where the increase in median $\mathrm{T}_{\mathrm{n} \text { tot }}$ from the headwater group towards the most downstream group is marked (dark-grey). Asterisks indicate significance levels ( $* \mathrm{p}<0.05$, ${ }^{* *} \mathrm{p}<0.001$, ${ }^{* * *} \mathrm{p}$ < 0.0001 ) for an increase in the median $\mathrm{T}_{\mathrm{n} \text { tot }}$ when compared to the headwater group (hg). Crosses mark medians for lakes sampled. For all figure parts lakes grouped by no, one, $2-5,6-10,11-$ 100 and $>100$ lakes $\left(>0.01 \mathrm{~km}^{2}\right)$ upstream

Fig. 4 Distribution (median, $50 \%$ and $90 \%$ quantile ranges) of $\mathrm{T}_{\mathrm{n} \text { tot }}$ in days for each river basin, with $\mathrm{T}_{\mathrm{n} \text { tot }}=365 \mathrm{~d}$ marked (dashed-line). Lakes grouped by no, one, $2-5,6-10,11-$ 100 and $>100$ lakes $\left(>0.01 \mathrm{~km}^{2}\right.$ ) upstream. Asterisks indicate significance levels $(* \mathrm{p}<0.05, * * \mathrm{p}$ $<0.001, * * * \mathrm{p}<0.0001$ ) for an increase in the median $\mathrm{T}_{\mathrm{n} \text { tot }}$ when compared to the headwater group (hg). For all figure parts lakes grouped by no, one, $2-5,6-10,11-100$ and $>100$ lakes ( $>0.01 \mathrm{~km}^{2}$ ) upstream

Fig. 5 (a) Distribution (median, $50 \%$ and $90 \%$ quantile ranges) for $T_{n}$ versus $\mathrm{T}_{\mathrm{n} \text { tot }}$ as ratio $R_{v}$. Lakes grouped by no, one, $2-5,6-10,11-100$ and $>100$ lakes $\left(>0.01 \mathrm{~km}^{2}\right)$ upstream
(b) Direct comparison between $T_{n}$ and $T_{n \text { tot }}$ for the entire dataset. For both figure parts $R_{v}=1.0$, 0.5 and 0.1 marked (dashed-line), and the 114 largest lakes ( $>10 \mathrm{~km}^{2}$ ) marked (circles)

Fig. 6 Relationship between (a) $\mathrm{T}_{\mathrm{n}}$ and $\mathrm{a}_{420} / \mathrm{TOC}$, (b) $\mathrm{T}_{\mathrm{n} \text { tot }}$ and $\mathrm{a}_{420} / \mathrm{TOC}$, respectively for 911 non-headwater lakes (grey dots) with the regression statistics (data) and the regression curve (curved line). Shown are also median values for grouped data (black circles) with standard deviations (black bars) and the regression statistics (median)

Fig. 7 Distribution (median, $50 \%$ and $90 \%$ quantile ranges) of $\mathrm{a}_{420}$, TOC and $\mathrm{a}_{420} /$ TOC for 1,559 lakes sampled. Asterisks indicate significance levels (* p < 0.05, ** $\mathrm{p}<0.001$, ${ }^{* * *} \mathrm{p}<$ 0.0001 ) for a decrease in $\mathrm{a}_{420}$, TOC and $\mathrm{a}_{420} /$ TOC when compared to the headwater group (hg). Changes in $\mathrm{a}_{420} /$ TOC across groups of different landscape positions were non-significant ( $\mathrm{p}>$ 0.05 ). Lakes grouped by no, one, $2-5,6-10,11-100$ and $>100$ lakes ( $>0.01 \mathrm{~km}^{2}$ ) upstream

## Fig. 1

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$20^{\circ} \mathrm{E}$


number of lakes $\left(>0.01 \mathrm{~km}^{2}\right)$ upstream

Fig. 3
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number of lakes $\left(>0.01 \mathrm{~km}^{2}\right)$ upstream

number of lakes (>0.01 km²) upstream

number of lakes $\left(>0.01 \mathrm{~km}^{2}\right)$ upstream

number of lakes (>0.01 km²) upstream

## Fig. 4

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number of lakes $\left(>0.01 \mathrm{~km}^{2}\right)$ upstream

Fig. 5


number of lakes (>0.01 km²) upstream

Fig. 6
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b


Fig. 7
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number of lakes (>0.01 km²) upstream

