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SMALL WATER BODIES

# Effects of beaver impoundments on dissolved organic matter quality and biodegradability in boreal riverine systems

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**Abstract** Beaver impoundments modify the structure of river reaches and lead to changes in ecosystem function and biogeochemical processes. Here, we assessed the changes in dissolved organic matter (DOM) quality and the biodegradation patterns in a set of beaver systems across Sweden. As the effect of beaver impoundments might be transient and local, we compared DOM quality and biodegradability of both pond and upstream sections of differentially aged beaver systems. Newly established dams shifted the sources and DOM biodegradability patterns. In particular, humic-like DOM, most likely leached from surrounding soils, characterized upstream sections of new beaver impoundments. In contrast, autochthonous and processed compounds, with both higher biodegradation rates and a broader spectrum of reactivities, differentiated DOM in ponds. DOM in recently established ponds seemed to be more humic and less processed compared to older ponds, but system idiosyncrasies determined by catchment particularities influenced this ageing effect.

**Keywords** Beaver · Ponds · Dissolved organic matter · Biodegradability

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## Introduction

Beavers were extirpated in the 19th century in many parts of Europe and North America. Reintroduction and protection measures during the 20th century have led to a dramatic recovery of the beaver population to its former natural ranges (Hartman, 2011; Halley et al., 2012). Only in Sweden, it has been estimated that there are currently more than 130,000 individuals of Eurasian Beavers (*Castor fibre*), bringing their global population over 1 million individuals (Rosell et al., 2005; Halley et al., 2012). Beavers convert streams into lentic systems by building dams and flooding the surrounding soils and terrestrial vegetation. These impoundments constitute major discontinuities in rivers and streams (Polvi & Wohl, 2012), and although they have been absent for over a century (Ward & Stanford, 1983; Polvi & Wohl, 2013), their presence in the landscape is increasing with the recovery of the beaver population (Rybczynski, 2007). The combined dam building, digging of burrows and channels as well as the beaver foraging strategy, all contribute to changes in hydrology, water chemistry, species diversity and community composition (Naiman et al., 1986; Rosell et al., 2005), along with increases in primary production and nutrient loads (Naiman et al., 1986; Margolis et al., 2001). Altogether, these apparent changes may indirectly affect key biogeochemical processes and ecosystem functioning. Furthermore, the impoundment of streams can create conditions that release toxic pollutants, previously bound to the soil organic matter, into the water column (Roy et al., 2009; Levanoni et al., 2015).

Regarding the effects of beaver dams on organic matter concentration in the water, previous studies found contradictory results, with increases (Naiman et al., 1986; Moore, 2003), decreases (Kothawala et al., 2006), and seasonal changes detected (Margolis et al., 2001). It is also unclear how carbon (C) processing is affected by beaver impoundments. Indeed, both enhanced retention (Naiman et al., 1988; Correll et al., 2000), increased export (Smith et al., 1991) and negligible changes in these C fluxes have been reported (Devito et al., 1986; Naiman et al., 1986), together with changes in dissolved organic matter (DOM) composition.

The changes in the DOM composition resulting from beaver dams are important in their own right with regards to ecosystem function. The compositional changes may also provide information about the processes that lead to the wide variation in observed effects on DOM concentration and pinpoint the mechanisms controlling DOM mineralization in beaver ponds. Previous studies have found that a high density of beaver impoundments can lead to a decrease of DOM molecular weight (Kothawala et al., 2006), as well as an increase in protein-like materials and DOM bioavailability (Lapierre & del Giorgio, 2014). However, most of these earlier studies in boreal systems considered beaver ponds as a type of wetland (Guillemette & del Giorgio, 2011; Lapierre et al., 2013), whereas beaver pond ecosystems are in many regards substantially different from boreal wetlands as the open water section confers high irradiance, longer water residence times and potential for sedimentation (Naiman et al., 1986). The dams cause dramatic changes in the stream hydrology and also affect the groundwater flows of the riverine system (Fuller & Peckarsky, 2011). Therefore, we expect different processes to affect DOM in a beaver pond compared to a typical boreal wetland.

Another feature of beaver impoundments that distinguish them from boreal wetlands is the influence of impoundment age on their biogeochemical role. A comparison can be made between beaver ponds and man-made, small scale reservoirs in order to understand the importance of dam ageing for C processing. The establishment of reservoirs modifies the carbon balance of the aquatic systems by enhancing both mineralization (Abril et al., 2005) and sedimentation (Mendonça et al., 2012). The enhanced carbon mineralization in recently created reservoirs has been attributed to the organic matter released from the flooded soils (Grimard & Jones, 1982), but this appears to be a transient effect (Weissenberger et al., 2010). Accordingly, DOM mineralization decreases with age of the reservoir, to stabilize after some years (Weissenberger et al., 2010).

If the same transient effect applies to beaver ponds, mineralization and DOM bioavailability should decrease with age of the impoundment. Accordingly, a significant effect of beaver impoundment age has been found to affect some biogeochemical functions such as mercury methylation (Roy et al., 2009; Levanoni et al., 2015). However, most studies dealing with DOM dynamics have focused on comparing features of catchments with and without beavers (Correll et al., 2000). Rarely has the age of the pond been taken into consideration.

In the present study, we hypothesize that signals of enhanced DOM processing should be found in the ponds compared to upstream sections of the rivers and also in old compared to newly created ponds. Accordingly, we determined changes in DOM quality and biodegradation patterns in a set of beaver ponds across Sweden.

## Materials and methods

### Study area and sampling

Water samples were collected from nine river systems distributed in a latitudinal gradient along the

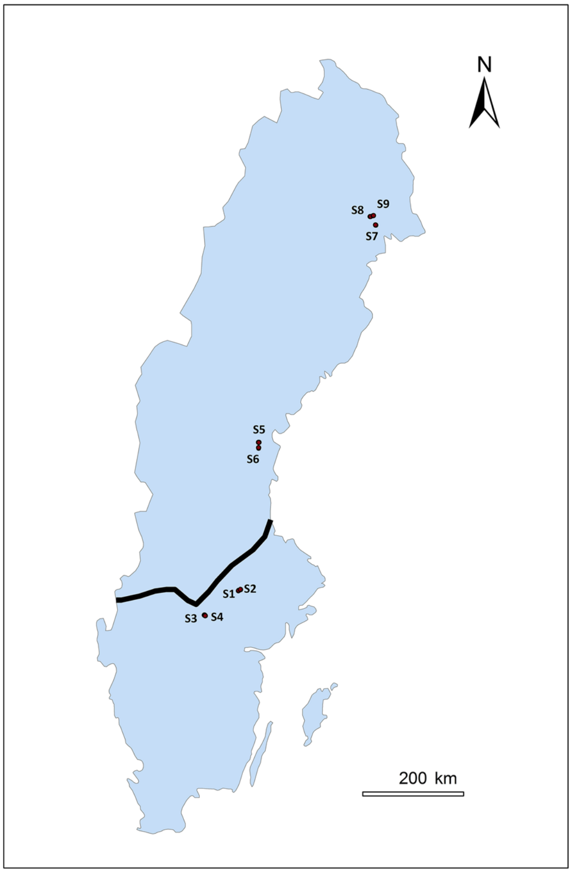


**Fig. 1** Map of the study sites (*filled circles*) in Sweden and in relation to the limes norrlandicus (*solid line*)

distribution range of beavers in Sweden. The samples were collected between late September and early October 2014 at locations distributed between the hemi-boreal and boreal vegetation zone (Fig. 1) in naturally acidic catchments mostly covered by coniferous forest. An overview of the location and characteristics of the different sites is given in Table 1. Aerial photography provided further insights into the study sites. The area of open water was determined based on changes in vegetation. The land uses in a 500 m buffer zone around each pond were also noted as a percentage of the total buffer area. The sites were classified by age group based on a real imagery analysis, field assessment and local knowledge. Based on Levanoni et al. (2015), systems with an estimated age under 10 years were considered as 'New' (S1, S2, S3, S4, S7 and S9), whereas sites colonized more than 10 years ago were considered as 'Old' (S5, S6 and S8). Because annual aerial photographs were not available, the age could only be estimated as a range, and therefore, its use as a continuous predictor had to be discarded (Table S1; Figure S1). More details on the age classification procedure are available in Levanoni et al. (2015).

In order to evaluate the impact of beaver impoundments on DOM processing in the fluvial system, we collected water samples in the open water section of the ponds, close to the dam, (referred to as "pond") and in the upstream running waters, at least 100 m before the inlet of the pond, (referred to as "upstream"). Triplicate water samples (0.5 m depth) for chemical characterization were collected in acid washed and pre-combusted glass bottles. Dissolved oxygen (DO), conductivity and temperature were measured both at the bottom and surface of each sampling site (WTW Conductometer LF 191). A water subsample from each site was used to measure pH in the laboratory (PW20 Philips).

## Chemical characterization of water and sediment samples

From unfiltered surface water, a subsample of 200 ml was filtered through 0.7 μm pre-combusted GF/F filters (Whatman). The filters were placed in polypropylene falcon tubes and frozen until Chl-a analysis according to Jespersen and Christoffersen (1987). From the GF/F filtrate, 80 ml were saved in two 40 ml pre-combusted glass vials and kept at 4°C for DOC concentration analysis and optical characterization. The DOC content from the water column was measured by high-temperature catalytic oxidation (Shimadzu-TOC-L) (Benner & Strom, 1993). Another subsample of unfiltered surface water (50 ml) was kept in a polypropylene falcon tube and stored at 4°C for analysis for reactive phosphorus according to Murphy and Riley (1962). Water samples were filtered within 24 h after the sampling. All water chemistry analyses were completed within no more than one week after sampling.

## DOM characterization

For optical characterization of DOM, the absorbance spectra (200–800 nm) were measured with a Lambda 40 spectrophotometer (Perkin-Elmer, Waltham, USA).

**Table 1** Location, morphometrics, physico-chemical characteristics (dissolved oxygen, conductivity, pH and temperature) and major land uses for the 9 beaver impoundments (*P* pond, *U* upstream section)

| Site | | Coordinates | | Area* (Ha) | $z^1$ (m) | Land use | | Physico–chemical properties | | | | Age |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Other (%) | Forest (%) | DO (%) | $C$ µS cm$^{-1}$ | pH | $T$ (°C) | |
| S1 | P | 59°42′31″ | 16°5′35″ | 2.9 | 0.9 | A (47) | 53 | 31 | 84 | 5.6 | – | N |
| | U | 59°42′18″ | 16°5′56″ | | – | | | 87 | 53 | 5.6 | 7.4 | |
| S2 | P | 59°41′18″ | 16°1′53″ | 1.7 | 0.7 | Ur (1) | 99 | 67 | 71 | 5.7 | – | N |
| | U | 59°40′57″ | 16°1′19″ | | – | | | 81 | 49 | 5.6 | – | |
| S3 | P | 59°14′52″ | 14°50′25″ | 0.9 | 0.6 | A (52) | 48 | 85 | 71 | 6.2 | – | N |
| | U | 59°14′49″ | 14°50′7″ | | 0.15 | | | 96 | 70 | 6.4 | 9.3 | |
| S4 | P | 59°14′11″ | 14°52′6″ | 0.3 | 0.5 | Ur (2) | 98 | 91 | 82 | 6.3 | 8.7 | N |
| | U | 59°14′11″ | 14°51′58″ | | 0.2 | | | 97 | 88 | 6.4 | 9.3 | |
| S5 | P | 62°19′5″ | 16°49′45″ | 2 | 0.8 | Cc (1) | 99 | 95 | 37 | 6.4 | 5.7 | O |
| | U | 62°18′55″ | 16°48′36″ | | 0.15 | | | 96 | 33 | 6.4 | 9 | |
| S6 | P | 62°13′12″ | 16°48′38″ | 1.7 | 0.4 | – | 100 | 98 | 33 | 6.5 | 7.3 | O |
| | U | 62°12′58″ | 16°48′50″ | | 0.1 | | | 96 | 32 | 6.5 | 7.5 | |
| S7 | P | 66°3′18″ | 22°5′18″ | 1.6 | 0.8 | Cc (40) | 60 | 88 | 21 | 6 | 5.7 | N |
| | U | 66°3′40″ | 22°5′2″ | | 0.15 | | | 98 | 19 | 6.1 | 6 | |
| S8 | P | 66°12′54″ | 21°53′9″ | 3.9 | 0.7 | – | 100 | 68 | 20 | 6 | 5.5 | O |
| | U | 66°12′47″ | 21°54′21″ | | 0.5 | | | 96 | 26 | 6.2 | 5.9 | |
| S9 | P | 66°13′37″ | 22°1′37″ | 0.3 | 0.4 | W (14) | 86 | 48 | 30 | 5.5 | 4.2 | N |
| | U | 66°13′41″ | 22°2′3″ | | 0.15 | | | 84 | 29 | 5.7 | 5 | |

Land uses are classified as following: *A* agricultural land, *Ur* Urban areas, *Cc* clear-cutting areas, *W* wetlands. The age (*N* new, *O* old) of the beaver impoundment was previously described by Levanoni et al. (2015). See details in Table S1 for age ranges

* Pond impoundment size determined by aerial photography

The samples were measured in a 1 cm quartz cuvette and Milli-Q water was used as a blank. All the specific absorbance wavelengths, ratios and slopes used to characterize DOM properties have been detailed elsewhere (Catalán et al., 2013). Briefly, the slopes (S) of the absorbance spectra at wavelength ranges of 275–295 and 350–400 nm were obtained by nonlinear fitting of the exponential curve $a_\lambda = a_{\lambda 0}\, e^{S(\lambda 0-\lambda)}$ (Stedmon et al., 2000), where $a_\lambda$ is the absorbance coefficient at wavelength $\lambda$ and $a_{\lambda 0}$ at a reference wavelength $\lambda_0$. SUVA was calculated according to Weishaar et al. (2003) and reported as L mg C$^{-1}$ m$^{-1}$.

Fluorescence excitation—emission matrices (EEM) were obtained with a fluorescence spectrophotometer (SPEX Fluoromax-4, Horiba Jobin–Yvon). Excitation wavelengths ranged from 250 to 445 nm at intervals of 5 nm, and the emission wavelengths from 300 to 600 nm at increments of 4 nm. A Milli-Q blank was run the same day and subtracted from each sample to eliminate Raman scattering. The area underneath the water Raman scan was calculated and used to normalize all sample intensities. Correction factors supplied by the manufacturer were used to correct for instrument-specific biases. Spectra were corrected for the inner filter effect using the absorbance-based approach (McKnight et al., 2001; Kothawala et al., 2013). Both corrections were applied using the FDOM correct toolbox for MATLAB (Mathworks, Natick, MA, USA) following Murphy et al. (2010). Due to the low number of samples, it was impossible to fit a PARAFAC model (Murphy et al., 2013). Therefore, we selected different wavelengths found in the literature to be related with different chemical properties of DOM. Accordingly, we used peaks (C, A, T, B and M) (Coble, 1996; Parlanti et al., 2000; Fellman et al., 2010). We also calculated the total fluorescence by summing the intensity across the entire EEM, with the peaks evaluated both as raw signal, reported in Raman Units (R.U.), and standardized to the total fluorescence for the respective sample. We also calculated several indices derived from the EEMs, including the freshness or biological index (BIX) according to Parlanti et al. (2000) and the humification index (HIX, described in Ohno, 2002 ; Huguet et al., 2009).

## DOM biodegradation dynamics

Biodegradable DOM (BDOM) was determined in dark incubations (Amon & Benner, 1996; Guillemette & del Giorgio, 2011). Water from the ponds and upstream sections from four systems classified as New (i.e. S1, S2, S7 and S9) were filtered through pre-combusted GF/C filters (Whatman) and distributed into 40 ml muffled glass vials. Each vial was filled to the brim, closed to avoid air bubbles and incubated in the dark at 20°C. For each site, triplicate vials were sacrificed for analyses at time zero and after 1, 2, 4, 7, 14, 21, 28, 35, 42 and 57 days. Incubated samples were filtered through 0.2 µm membrane filters and acidified with 10 µl of 10% v/v HCl. The reported total biodegradable DOM (BDOM) was the difference between the final and the initial DOC of the samples.

DOM degradation kinetics was studied by applying a reactivity continuum model following a similar approach as in Koehler et al. (2012). We modelled the relative DOC concentration ($DOC_t/DOC_0$) over time as

$$\frac{DOC_t}{DOC_0} = \left(\frac{\alpha}{\alpha + t}\right)^v,$$

where the parameter $\alpha$ controls the lifetime of the most reactive compounds (Arndt et al., 2013) and $v$ determines the shape of the distribution at a decay coefficient close to 0, interpreted as the relative abundance of the most recalcitrant compounds (Koehler et al., 2012). Therefore, high $v$ and low $\alpha$ values indicate dominance of labile compounds in the DOM, while low $v$ and high $\alpha$ values indicate a dominance of refractory compounds (Arndt et al., 2013). The decay coefficients ($k$) over the incubation time are calculated as $v/\alpha + t$ (Koehler et al., 2012). In order to test the reactivity continuum (RC) model assumption, we fitted the data also to a linear regression using a single-pool exponential model and calculated the Akaike weights of the three models, following the procedure described in Koehler and Tranvik (2015). The RC model did not converge in one of the 8 series, neither did the linear or the exponential models. This time series (site 7 pond) showed an unclear DOM loss pattern and no model was finally fitted for this time series. Model parameters were estimated using the nonlinear regression package in R 3.2.1 (R core team, 2015).

## Data analyses

Distributional properties of the data and transformations required to meet assumptions of normality were checked prior to the analysis of the data. Linear mixed effects models were applied to test for significant differences in the DOM descriptors between Age groups (New vs. Old systems), Section (upstream vs. pond of each system) and the interaction of both factors. The different sites were included in the models as a random effect. Significance of the fixed effects was evaluated using analysis of variance (Crawley, 2009). Multiple post hoc Tukey comparisons on the models were carried on using the *glht* function in package *multcomp* for R.

Non-metric dimensional scaling (NMDS, Manhattan) was used to ordinate the samples according to their DOM properties (Sr, SUVA, BIX, HIX, FI and Fluorescence peaks in R.U.). A permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) was performed over the same dataset used in the NMDS to analyse the influence of Age and Section on the ensemble of DOM properties, with Site as a grouping factor. A second NMDS shows DOM properties ordered by site to check for site-specific characteristics. A secondary matrix comprising the land uses in the buffer area around each pond was fitted to this second NMDS as linear vectors. The environmental correlation was generated with the *envfit* function, the NMDS with the *metaNMDS* function and the PERMANOVA with the *adonis* function, all of them available in the *vegan* package for R (Oksanen et al., 2015).

Estimation of the RC-modelled parameters was conducted using nonlinear mixed effects models. All data analyses were performed in R version 3.1.2 (R Core team, 2015).

## Results

### Characteristics of beaver impoundments

Characteristics and DOM descriptors of the different sites are given in Tables 1 and 2. We compared the differences on DOM descriptors between the upstream and the pond sections of beaver systems and between recently established (New: S1, S2, S3, S4, S7 and S9) and aged dams (Old: S5, S6 and S8). We did not observe significant differences in pH values between upstream and pond sections. A decrease in DO ($O_2$%) was detected from the upstream to the pond sections especially in systems 1, 2 and 9. Low chlorophyll (Chl-a) concentrations were measured in the studied systems (ranging from 0.5 to 2.8 μg $l^{-1}$) and significant increases were found in the ponds compared to the upstream sections in New sites (Tables 2, 3). DOM concentrations were significantly affected by the interaction between Age and Section of the ponds (Table 3); however, they did not vary significantly between the upstream and the pond sections of each age category (Fig. 2a). A strong variability was observed between systems, with both increases and decreases in DOM between upstream and pond sections (Table 2).

### Impact of beaver impoundments on DOM descriptors

The NMDS based on spectroscopic DOM descriptors clearly separated the samples according to age group and within the New systems according to section (Fig. 3a). The first axis of the NMDS represented a gradient from strong humic character to samples with increased protein-like fluorescence properties. Within New systems, upstream samples are located towards the upper left corner of the NMDS with respect to the pond samples. Therefore, upstream samples presented higher humification index and humic-like peak C fluorescence compared to samples from the ponds (Table 2), while the later had higher protein-like fluorescence and SUVA values (Figs. 2b, c, S1). Differences in spectroscopic DOM descriptors between upstream and pond sections were only observed in New sites (Fig. 3a; Table 3).

Regarding differences between age groups, New systems showed higher SUVA and HIX values, indicative of aromatic and humic materials, while the Old ones clustered at the opposite extreme of that axis. Accordingly, significantly higher values were found for all the fluorescence peaks (R.U.) and the total fluorescence in New compared to Old ponds (Table S1). Moreover, also when expressed in relative fluorescence, significant differences between Age groups were found for humic-like peak A and protein-like peak T (Table 3). The EEMs of the Old sites show more prominent protein-like fluorescence than the EEMs of the new ponds (Fig. S2) and significantly higher values of the A:C ratio (Fig. 2d).

The PERMANOVA analysis indicated significant differences between Age groups (5.6%, $F = 3.28$, $P = 0.0001$), Section (7%, $F = 4.12$, $P = 0.0001$) and the interaction of these factors (2.8%, $F = 1.67$, $P = 0.0007$). However, the variance explained by these factors was low (16%) as the quality of DOM is very strongly dependent on each site. Accordingly, the NMDS based on spectroscopic DOM descriptors also separated the samples by site, signalling the relevance of local factors on determining the quality of DOM (Fig. 3b). The land uses significantly correlated ($P < 0.01$) with the NMDS are shown as arrows over the diagram. Although system S7 was classified as New, it clustered with Old systems and appears related to clear-cutting. In agreement with this, the A:C ratio and other descriptors of DOM quality uncovered significant differences between Old and New ponds when system S7 was excluded from the analysis.

### Biodegradability of DOM in new beaver impoundments

The biodegradability patterns of DOM were studied exclusively in New beaver systems (New: S1, S2, S3, S4, S7 and S9) as we expected higher differences between sections for this age category. The total BDOM as percentage of the initial DOM was significantly higher in ponds compared to upstream samples (Table 3). The results of the RC model reveal a faster loss of the most reactive DOM types (parameter $\alpha$) in upstream compared to pond samples ($P < 0.001$; Table 4). The $v$ parameter (i.e. relative preponderance of the more refractory compounds) showed the corresponding opposite pattern, with higher values in ponds than in upstream DOM samples ($P < 0.001$, Table 4). In contrast, the initial apparent decay coefficients did not show any systematic variation between upstream and ponds DOM (Table 4). This

**Table 2** Mean and standard deviation values of Chla, DOC, biodegradable DOC (BDOC) and spectroscopic descriptors, specific UV absorbance (SUVA), biological index (BIX), humification index (HIX), peaks A, C and B, ratio of the peaks A and C (A:C) and total fluorescence (TF) in raman units in the studied beaver impoundments at the pond (P) and upstream (U) sections

| Site | | Chla ($\mu g\ l^{-1}$) | DOC ($mg\ l^{-1}$) | SUVA ($l\ mg^{-1}\ m^{-1}$) | BDOC (%) | BIX | HIX | Peak A | Peak C | A:C | Peak B | TF (R. U.) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *New* | | | | | | | | | | | | |
| S1 | P | 2.8 ± 0.3 | 23.6 ± 0.2 | 5.8 ± 0.5 | 15.5 ± 0.7 | 0.518 ± 0.004 | 12.2 ± 0.8 | 6.62 ± 0.22 | 2.84 ± 0.07 | 2.33 ± 0.04 | 0.56 ± 0.11 | 4703 ± 145 |
| | U | 0.6 ± 0.5 | 24.4 ± 1 | 4 ± 0.2 | 14.2 ± 2 | 0.557 ± 0.005 | 12.3 ± 0.1 | 4.18 ± 0.09 | 2.05 ± 0.02 | 2.04 ± 0.04 | 0.29 ± 0.06 | 3150 ± 38 |
| S2 | P | 2.8 ± 0.5 | 15.2 ± 0.7 | 5.6 ± 0.2 | 20.3 ± 2.8 | 0.55 ± 0.0002 | 9.5 ± 0.5 | 4.55 ± 0.03 | 1.962 ± 0.007 | 2.32 ± 0.02 | 0.45 ± 0.02 | 3250 ± 12 |
| | U | 0.9 ± 0.5 | 14 ± 0.4 | 3.6 ± 0.2 | 8.5 ± 2.3 | 0.551 ± 0.004 | 12.7 ± 0.1 | 2.32 ± 0.02 | 1.065 ± 0.003 | 2.18 ± 0.02 | 0.16 ± 0.02 | 1657 ± 8 |
| S3 | P | 0.8 ± 0.01 | 8.6 ± 0.3 | 4 ± 0.1 | 9.3 ± 2.4 | 0.529 ± 0.016 | 12.9 ± 0.5 | 1.54 ± 0.02 | 0.647 ± 0.003 | 2.38 ± 0.02 | 0.14 ± 0.03 | 1027 ± 6 |
| | U | 0.6 ± 0.2 | 8.4 ± 0.03 | 4.04 ± 0.01 | 9.7 ± 1.2 | 0.519 ± 0.005 | 13.8 ± 0.2 | 1.53 ± 0.01 | 0.64 ± 0.004 | 2.385 ± 0.004 | 0.111 ± 0.007 | 1021 ± 8 |
| S4 | P | 0.8 ± 0.2 | 10.1 ± 1.2 | 4.3 ± 0.6 | 7.5 ± 2.9 | 0.518 ± 0.005 | 13.5 ± 0.1 | 1.88 ± 0.03 | 0.81 ± 0.016 | 2.32 ± 0.03 | 0.172 ± 0.003 | 1297 ± 19 |
| | U | 0.6 ± 0.5 | 9.4 ± 1.3 | 3.6 ± 0.5 | 11.2 ± 3.2 | 0.532 ± 0.007 | 14.2 ± 0.3 | 1.65 ± 0.01 | 0.695 ± 0.005 | 2.37 ± 0.02 | 0.121 ± 0.009 | 1101 ± 9 |
| S7 | P | 0.9 ± 0.2 | 6 ± 0.4 | 2.7 ± 0.2 | 12.8 ± 2.7 | 0.608 ± 0.052 | 6.4 ± 1.7 | 0.65 ± 0.09 | 0.27 ± 0.025 | 2.4 ± 0.12 | 0.107 ± 0.01 | 449 ± 43 |
| | U | 0.8 ± 0.4 | 6 ± 1 | 2.4 ± 0.4 | 8 ± 3 | 0.581 ± 0.002 | 7.9 ± 0.3 | 0.63 ± 0.02 | 0.245 ± 0.007 | 2.58 ± 0.04 | 0.093 ± 0.008 | 411 ± 11 |
| S9 | P | 2.1 ± 0.7 | 12.6 ± 0.6 | 4.5 ± 0.5 | 24.5 ± 6.8 | 0.457 ± 0.005 | 11.0 ± 1.1 | 1.69 ± 0.08 | 0.734 ± 0.028 | 2.3 ± 0.02 | 0.252 ± 0.004 | 1127 ± 46 |
| | U | 1.3 ± 0.7 | 12.4 ± 0.8 | 3.9 ± 0.3 | 9.3 ± 0.8 | 0.47 ± 0.01 | 14.5 ± 0.4 | 1.77 ± 0.02 | 0.801 ± 0.017 | 2.2 ± 0.02 | 0.211 ± 0.007 | 1239 ± 23 |
| *Old* | | | | | | | | | | | | |
| S5 | P | 0.9 ± 0.2 | 5.9 ± 0.4 | 3.25 ± 0.07 | 7.5 ± 1.3 | 0.561 ± 0.015 | 9.1 ± 1.1 | 0.89 ± 0.06 | 0.37 ± 0.017 | 2.41 ± 0.04 | 0.111 ± 0.012 | 601 ± 29 |
| | U | 1.5 ± 0.7 | 6.4 ± 0.4 | 3.2 ± 0.2 | 7.3 ± 1.5 | 0.558 ± 0.005 | 9.4 ± 0.3 | 0.94 ± 0.01 | 0.364 ± 0.004 | 2.57 ± 0.01 | 0.106 ± 0.006 | 594 ± 7 |
| S6 | P | 0.5 ± 0.4 | 7.7 ± 0.2 | 4.2 ± 0.1 | 12.5 ± 0.8 | 0.518 ± 0.013 | 11.4 ± 1.3 | 1.34 ± 0.04 | 0.56 ± 0.013 | 2.39 ± 0.02 | 0.114 ± 0.019 | 889 ± 21 |
| | U | 0.9 ± 0.2 | 8.6 ± 0.4 | 4.6 ± 0.2 | 12.5 ± 1.8 | 0.517 ± 0.002 | 11.5 ± 0.3 | 1.65 ± 0.01 | 0.672 ± 0.005 | 2.45 ± 0.03 | 0.134 ± 0.015 | 1087 ± 12 |
| S8 | P | 1.3 ± 0.6 | 8.6 ± 0.3 | 3.8 ± 0.1 | nd | 0.546 ± 0.035 | 9.5 ± 0.9 | 1.2 ± 0.03 | 0.471 ± 0.006 | 2.54 ± 0.04 | 0.15 ± 0.02 | 769 ± 14 |
| | U | 2.1 ± 0.7 | 8.9 ± 0.08 | 3.76 ± 0.03 | nd | 0.542 ± 0.004 | 10.7 ± 0.6 | 1.27 ± 0.03 | 0.489 ± 0.001 | 2.6 ± 0.05 | 0.136 ± 0.008 | 803 ± 10 |

**Table 3** *P* values from the ANOVA on the linear mixed effects models testing the effects of factors age (new vs. old), section (upstream vs. pond) and their interaction on Chl-a, DOC, BDOC and DOM descriptors derived from absorbance and fluorescence measurements

| | Chla | DOC | BDOC | $SUVA_{254}$ | Total fluo | BIX | HIX | A:C | Peak C | Peak A | Peak T | Peak B |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Age | 0.859 | 0.245 | 0.425 | 0.672 | 0.274 | 0.741 | 0.361 | **0.043** | 0.397 | **0.029** | 0.159 | 0.707 |
| Section | 0.029 | 0.889 | **0.013** | **<0.001** | **0.003** | 0.478 | **<0.001** | 0.982 | 0.050 | 0.242 | **<0.001** | **<0.001** |
| Age × section | **<0.001** | **0.042** | 0.170 | **<0.001** | **<0.001** | 0.429 | **0.044** | **0.003** | **0.009** | **0.018** | 0.083 | **0.027** |

Significant *P* values ($P < 0.05$) are printed in bold. Site was included as a random effect in all cases

The units of each variable are as follows: Chla (μg $l^{-1}$), DOC (mg $l^{-1}$), $SUVA_{254}$ (l $mg^{-1}$ $m^{-1}$), Sr (unitless) BDOC (%), total fluo (R.U.), BIX, HIX and A:C are unitless and fluorescence peaks are reported as percentage of the total fluorescence. A440 and BIX were transformed by ln ($x$), Peak T by ($x^{-2}$) and % BDOC was arcsin square-root transformed

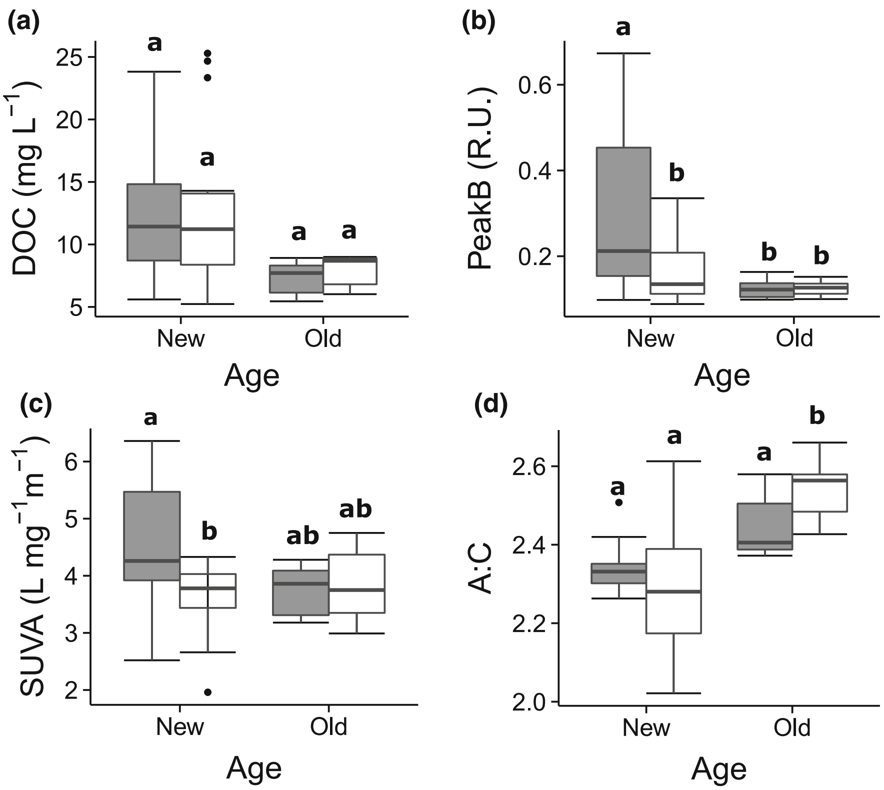


**Fig. 2** Relative percentage of change between pond (*grey*) and upstream (*white*) at each group age. Data are given in Tukey boxplots. Significant differences between groups ($P < 0.05$, post hoc tests) are marked with different *letters*

parameterization translated into $k$ declining less pronouncedly over time in the pond than in the upstream in all the New sites (Fig. 4a). The probability distributions of initial reactivity show different patterns for upstream and pond sites (Fig. 4b). Both in the ponds and in the upstream sites, around 5% of the initial DOC was likely to decay at rates of 0.05 $d^{-1}$ or faster (Fig. 4b). However, in upstream sites reactivity decreased very fast and almost 90% of the initial DOC had decay rates of 0.002 $d^{-1}$ or slower, while in the pond sites, this slowly reacting pool only made up 68% of the DOC.

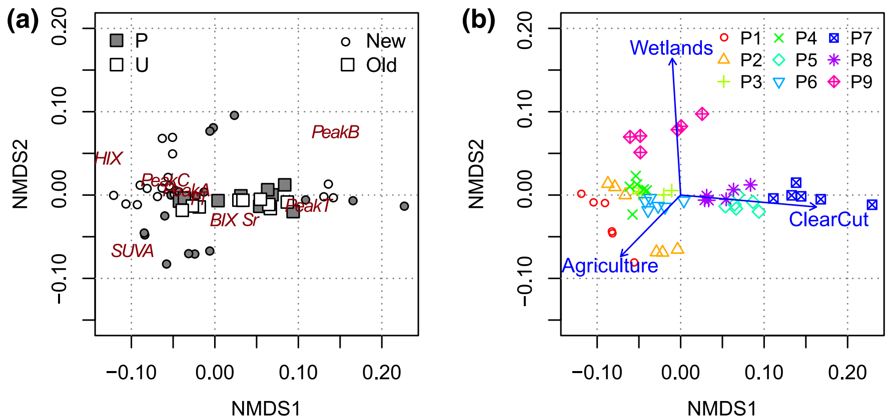


**Fig. 3** Two-dimensional NMDS ordination of all the samples based on DOM descriptors. In **a** it is represented the ordination of the optical descriptors; samples ordinated by age (*circles*: old; *squares*: new) and section (*grey*: pond; empty: upstream). In **b** the *arrows* are the land uses (agriculture, clear-cutting and wetland) significantly related ($P < 0.01$) with the ordination; samples ordinated by site

## Discussion

### When the stream becomes a pond

Colonization of a stream stretch by beavers and the construction of a dam will lead to a local transformation of the stream into a lentic system. In order to determine the changes in DOM linked to this process, we compared the differences of DOM descriptors between the upstream and the pond sections of beaver systems. We predicted higher differences of DOM variables between upstream and pond for the youngest beaver dams (New: S1, S2, S3, S4, S7 and S9), as mobilization of biologically available DOM was expected to be substantial only for a limited time after damming. Accordingly, differences in the DOM descriptors between upstream and pond were only found for New sites (Fig. 3a). Therefore, in this section, we will focus primarily on the New sites.

Taking into account our results on DOM concentrations and those reported in the literature (Naiman et al., 1986; Moore, 2003; Kothawala et al., 2006), it cannot be concluded whether beaver impoundments increase or decrease DOM concentrations of a river system. This inconsistency is likely due to counteracting processes happening in the water column, as increased photodegradation and sedimentation rates that will diminish DOC concentrations, or leaching from inundated soils that will increase them.

While we did not observe significant differences in concentration, the changes observed in spectroscopic DOM descriptors provided information on the processes affecting the DOM. Upstream DOM presented higher humification index values compared to samples from the ponds (Table 2; Fig. 3a). In contrast, we observed a significant increase between upstream and pond in fluorescence peak B, related to the presence of protein-like materials (Fig. 2b). Protein-like fluorescence is linked to unprocessed materials (Lapierre & del Giorgio, 2014), enhanced microbial activity or autochthonous production (Fellman et al., 2010). In the studied sites, this is probably derived from an increased autotrophic planktonic community (e.g. significantly higher Chla levels; Tables 2, 3) and longer water residence time in the pond compared to the upstream. In contrast with this, pond samples had significantly higher values of $SUVA_{254}$ (Fig. 2c), an indicator of aromaticity (Weishaar et al., 2003). This increase could be related to the release of terrigenous DOM from recently inundated soils (Mladenov et al., 2005) and the decomposition of wood in the bottom of the ponds. These processes might affect particularly systems 1 and 2 with especially high SUVA values (Table 2), which could lead to the apparent discrepancy between this descriptor and HIX when comparing pond and upstream values. Moreover, DO ($O_2$%) decreased from the upstream to the pond, especially in systems 1, 2 and 9 (Table 1), portraying the relevance

**Table 4** Parameters of the reactivity continuum model applied to the DOC degradation of pond (P) and upstream (U) samples of systems classified as new

| | System 1 | | System 2 | | System 7 | | System 9 | |
|---|---|---|---|---|---|---|---|---|
| | *P* | U | *P* | U | *P* | U | *P* | U |
| $\alpha$ (*d*)[a] | 10.36 ± 1.55 | 5.16 ± 1.67 | 7.53 ± 1.53 | 3.22 ± 2.69 | n.a | 3.88 ± 0.65 | 9.28 ± 2.02 | 10.09 ± 1.66 |
| $v$[b] | 0.085 ± 0.007 | 0.062 ± 0.008 | 0.102 ± 0.008 | 0.027 ± 0.007 | n.a | 0.027 ± 0.005 | 0.135 ± 0.007 | 0.0489 ± 0.008 |
| $k$ ($d^{-1}$)[c] | 0.0082 ± 0.0051 | 0.0119 ± 0.0047 | 0.0136 ± 0.0053 | 0.0084 ± 0.0026 | n.a | 0.0069 ± 0.0007 | 0.0145 ± 0.0035 | 0.0049 ± 0.0046 |

[a] Apparent age of the most reactive compounds

[b] Unitless, relative preponderance of the most persistent compounds

[c] Initial apparent decay coefficient

of organic matter transformation processes at the bottom of the ponds. Indeed, the quality and transformation processes of DOM will be modulated by the site particularities, which include factors such as land use (Fig. 3b). However, even taking into account this variability, differences between upstream and pond are apparent in New sites (Fig. 3).

The significant higher BDOM obtained in ponds compared to upstream samples (Table 3) suggests that beaver ponds are important sites for carbon processing. The difference in the DOM decay coefficients and probability distributions of initial reactivity observed for upstream and pond sites (Fig. 4) confirms the impact of beaver impoundments on the reactivity of DOM in boreal riverine systems. Results from the RC model reveal that upstream samples present a pool of compounds that disappear very quickly and a large pool of slowly degrading compounds. Within 2 months, at the end of the incubation, pond samples still present higher decay coefficients than upstream sites, explaining the higher percentage of biodegradable DOC in pond samples. As this has been attributed to samples differing in their spectrum of reactivities (Koehler & Tranvik, 2015), we conclude that upstream samples present a predominant pool of compounds that disappear very quickly and determine the decay pattern. This can be linked to the presence of biodegradable macromolecules derived from terrestrial systems, as indicated by a more prominent peak C than in pond sites (Kothawala et al., 2012). Similar results have been found elsewhere (Catalán et al., 2013; Lapierre et al., 2013) suggesting a pool of easily degradable and fresh material in rivers' DOM, despite their predominantly terrestrial origin. In the case of pond sites, the broader spectrum of DOM reactivity types signals a variable origin of the material. Beaver ponds receive the terrestrial DOM from the upstream sections, but the recently inundated soils constitute a second temporary source of organic matter that can shift both the fluorescence and absorbance patterns of the organic matter (Mladenov et al., 2005). A third source of DOM originates from autochthonous production and secondary organic matter processing (Weissenberger et al., 2012). In support of this, water from beaver dams had significantly higher representation of the protein-like peaks and a decrease in longer-wavelength fluorescent DOM (Fig. S2).

Finally, regarding the Old systems, the results of the optical DOM properties confirmed our initial hypothesis

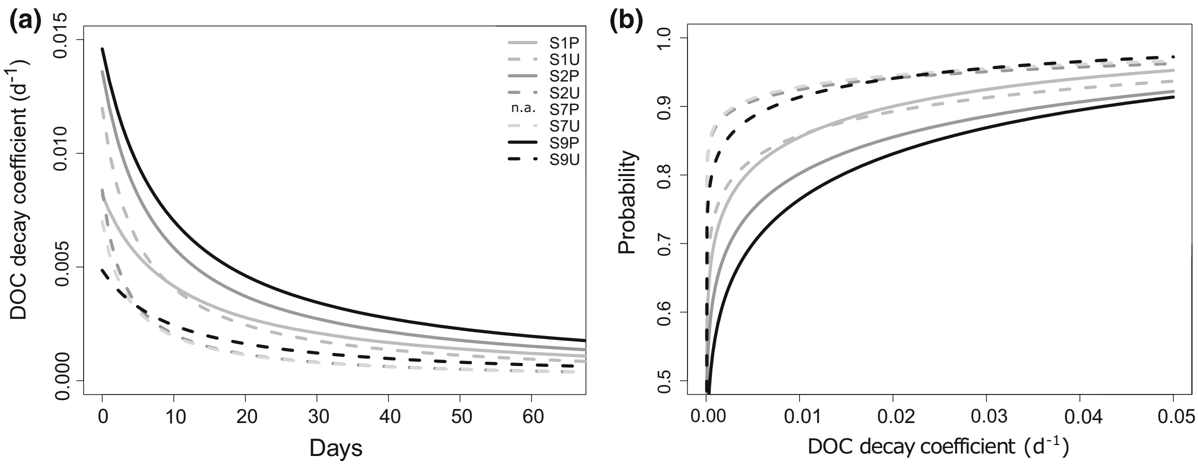


**Fig. 4** Apparent decay coefficients for DOM during incubation (**a**) and cumulative distribution function (**b**) of the pond (*continuous lines*) and upstream (*dashed lines*) of the sites classified as new

that the main remobilization of DOM due to damming is substantial only for a limited period after impoundment, most likely of less than 10 years (Table S1; Levanoni et al., 2015). Moreover, this absence of differences between upstream and pond indicates a potential effect of the damming at the whole river system level as beaver ponds can have extensive effects on land cover or groundwater flow patterns (Fuller & Peckarsky, 2011).

In summary, the damming process or the transformation of a stream into a lentic system due to beaver impoundments, shifts the sources and DOM biodegradability patterns. The range of compounds transported from upstream systems, released from soils or internally produced, increased the spectrum of reactivity of DOM and ultimately enhanced its biodegradation.

## When the pond grows old

The high variability in DOM concentration found between the different rivers, even within the same age group suggest that catchment- or landscape-specific differences might prevail in defining DOM concentrations compared to impoundment effects. In contrast to DOM concentration, spectroscopic DOM descriptors clearly separated the samples according to age group (Fig. 3a), confirming the impact of beaver dams on river dynamics. In the NMDS, pond samples grouped according to beaver system (Fig. 3b) further indicating that the idiosyncrasies of each system (e.g. catchment features) are key factors determining DOM characteristics. Therefore, although ageing is an important factor defining DOM properties in beaver ponds, the deviating results for site S7 clearly show that DOM quality can be indicative of an old pond even if it was recently built or recolonized.

New ponds had higher fluorescence peaks (R.U.) and total fluorescence than Old ponds (Table S1). Although, this can be partially explained by the higher concentrations of DOM in the New systems compared to the Old ones, the relative contribution of the individual peaks to the total fluorescence (%) also changes between age groups (Table 3). Indeed, peak A, expressed in relative fluorescence, is more prominent compared with peak C (Table 3; Fig. S2). The peak C has previously been related to DOM of large size and humic character (Fellman et al., 2010; Kellerman et al., 2015) and is sensitive to both photodegradation (Moran et al., 2000) and biodegradation processes (Kothawala et al., 2012). In both cases, peak C has been described to be lost preferentially with regard to peak A, and therefore, increases in the ratio A:C indicate enhanced DOM degradation processes (Fig. 2d; Kothawala et al., 2012). Comparing our observations to earlier work, DOM in the New ponds seems to be less processed (Kothawala et al., 2012; Catalán et al., 2013) and more humic in nature than DOM in the Old ponds. Accordingly, the A:C ratio (Fig. 3d) and other descriptors of DOM quality uncovered significant differences between Old and New ponds when system S7 was excluded from the analysis. The fact that the DOM of the new pond S7 presented a signature of a typically old beaver pond system demonstrate that the age of the dam is not the only feature controlling the DOM quality. The land use around this site is very influenced by clear-cutting, which might result in lower organic carbon inputs from vegetation and increased exposure to solar radiation, processes affecting older ponds (Fig. S1). The land use, together with other particularities of system S7 compared with the others (e.g. low nutrients and a sandy substrate; Table 1; Levanoni et al., 2015) have a stronger effect on DOM composition than ageing. Indeed, ageing effects are modulated by system idiosyncrasy, calling for further studies that include beaver impoundments covering different hydrological, geological and landscape features.

## Conclusions

Changes in DOM spectroscopic properties and biodegradability in beaver ponds are complex and depend both on the ageing and specific features of the beaver systems.

The damming (i.e. upstream vs. pond) and ageing (i.e. New vs. Old systems) processes have analogous effects on DOM quality. Hence, when the beaver pond age reaches the last stages of the succession towards a lentic system, initial differences in DOM quality between upstream and pond sites dissipate. Beaver impoundments, at least temporarily, provide a boost of terrigenous organic matter from the inundated surrounding soils and a more extended DOM input from enhanced autochthonous production. This leads to a diversification in the reactivity of the organic matter and in essence a rewiring of the carbon cycle in the boreal landscape with effects that may also extend to pollutant turnover and transport, food web structure and biodiversity patterns. The constitution of a lentic system modified DOM sources and processing permanently, with a main pulse occurring immediately after damming. The identification of these transient effects is of major significance to assess the impacts of the increasing beaver population over the biogeochemical function of freshwater ecosystems.

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