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Dam tailwaters compound the effects of reservoirs on the longitudinal transport of organic carbon in an arid river

A. J. Ulseth[1,2,*] and R. O. Hall Jr.[2]

[1]Program in Ecology, University of Wyoming, Laramie, Wyoming, USA
[2]Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming, USA
[*]now at: École Polytechniqe Fédérale de Lausanne, Lausanne, Switzerland

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Correspondence to: A. J. Ulseth (amber.ulseth@gmail.com)

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Abstract

Reservoirs on rivers can disrupt organic carbon (OC) transport and transformation, but less is known how downstream river reaches directly below dams contribute to OC processing than reservoirs alone. We compared how reservoirs and their associated tailwaters affected OC quantity and quality by calculating particulate (P) OC and dissolved (D) OC fluxes, and measuring composition and bioavailability of DOC. We sampled the Yampa River near Maybell, Colorado, USA and the Green River above and below Fontenelle and Flaming Gorge reservoirs, and their respective tailwaters from early snowmelt to base flow hydrological conditions. In unregulated reaches (Yampa River, Green River above Fontenelle reservoir), DOC and POC concentrations increased with snowmelt discharge. POC and DOC concentrations also increased with stream discharge below Fontenelle reservoir, but there was no relationship between DOC and stream flow below Flaming Gorge reservoir. The annual load of POC was 3-fold lower below Fontenelle Reservoir and nearly 7-fold lower below Flaming Gorge reservoir, compared to their respective upstream sampling sites. DOC exported to downstream reaches from both reservoirs was less bioavailable, as measured with bioassays, than DOC upriver of the reservoirs. Lastly, tailwater reaches below the reservoirs generated OC, exporting 1.6–2.2 $g\,C\,m^{-2}\,d^{-1}$ of OC to downstream ecosystems. Changes in total fluxes from upstream to downstream of reservoirs and their tailwaters do not represent the simultaneous transformation and production of OC, which may lead to the underestimation of the quantity of OC mineralized, transformed, or retained in coupled river-reservoir-tailwater ecosystems.

1 Introduction

Unregulated streams and rivers compose a continuous ecosystem where a gradient of physical processes drive biological processes from headwaters to the river deltas (Vannote et al., 1980). Along this continuum, rivers receive terrestrial organic carbon

(OC) and export it to the ocean (Cole et al., 2007). The amount of OC that enters the oceans, however, is only a fraction of the estimated input from the terrestrial landscape (Aufdenkampe et al., 2011). A larger fraction of OC entering rivers and streams is believed to be stored and mineralized to CO_2 within these ecosystems (Cole et al., 2007; Battin et al., 2009; Aufdenkampe et al., 2011).

Flow regulation by damming has converted most rivers into a series of lotic and lentic reaches (Ward and Stanford, 1983; Benke, 1990), affecting OC cycling and transport (Ward and Stanford, 1983; Miller, 2012; Stackpoole et al., 2014). Reservoirs on rivers may trap particulate OC (POC) (Friedl and Wuest, 2002; Downing et al., 2008; Tranvik et al., 2009), and transform and produce dissolved OC (DOC) (Mash et al., 2004; Knoll et al., 2013). Increased water residence time (Vörösmarty et al., 1997; Sabo et al., 2010) allows for OC to be respired, incorporated into microbial production, or buried while production of autochthonous or microbial DOC increases (Mash et al., 2004; Knoll et al., 2013). Reservoirs may increase (Parks and Baker, 1997), decrease (Miller, 2012; Knoll et al., 2013), or not alter DOC concentrations to downstream ecosystems (Parks and Baker, 1997; Nadon et al., 2014). Prior work has shown DOC fluxes increased longitudinally in the upper basin of the Colorado River, but then decreased with the presence of large reservoirs in the lower basin (Miller, 2012; Stackpoole et al., 2014). Conversely DOC fluxes increased in the lower Missouri River despite the presence of large reservoirs (Stackpoole et al., 2014). Similarly, DOC composition did not change from upstream to downstream of reservoirs in boreal-forested rivers in northern Ontario where catchment characteristics had a stronger influence compared to the presence of impoundments (Nadon et al., 2014). These basin wide, large-scale studies have given insight into longitudinal OC fluxes in light of flow regulation by dams, but have not necessarily captured OC dynamics in the river reaches located directly downstream of dams.

Dams strongly affect the river reaches directly downstream from them, likely altering OC dynamics. These tailwater ecosystems physically and biologically differ from their upstream counterparts (Ward and Stanford, 1983). In tailwater reaches, sediment

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transport is lower and bed sediment is more stable than upstream of the reservoir (Schmidt and Wilcock, 2008). These highly altered physical processes confer increased primary production in tailwaters relative to the unaltered river (Davis et al., 2011). Such high production can increase transported POC and DOC (Webster et al., 1979; Perry and Perry, 1991; Lieberman and Burke, 1993; Benenati et al., 2001). Tailwater POC may consist of sloughed algae from production within the river reach (Webster et al., 1979; Perry and Perry, 1991). Algae in tailwaters may increase DOC concentration via exudation (Baines and Pace, 1991; Bertilsson and Jones, 2003). For example, autochthonous DOC flux was correlated with gross primary production in the tailwater of Glen Canyon Dam on the Colorado River and may equate to 7–91 % of gross primary production in the tailwater (Ulseth, 2012). Tailwater ecosystems produce algal OC, which is exported (Perry and Perry, 1991; Lieberman and Burke, 1993), transformed, buried, or consumed. These tailwater reaches can be found directly downstream of most, if not all, dams (Ward and Stanford, 1983); yet, coupled reservoir and tailwater OC fluxes are unclear within the context of riverine OC budgets.

We studied a series of reaches on the Green and Yampa Rivers located in the upper basin of the Colorado River, USA to quantify the role of hydrological regulation on OC quantity and quality. Within this objective, we asked the following questions: (1) How do OC concentration, fluxes, and DOC composition and bioavailability vary temporally in hydrologically regulated reaches compared to free-flowing rivers? (2) How does the bioavailability and composition of DOC vary longitudinally in a river altered by reservoir-tailwater ecosystems? We addressed these questions by quantifying POC and DOC concentration and DOC composition and bioavailability in regulated and unregulated river reaches in the upper Colorado River basin. We sampled from the onset of snowmelt, where we expected transport processes to dominate, and during base flow river conditions where we expected within ecosystem production to drive OC quality and transport.

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2 Methods

2.1 Study site

The Colorado River basin is heavily regulated (Nilsson et al., 2005) with 7 large impoundments (reservoirs with > 0.5 km^3 storage capacity) within its watershed, making it an opportune river basin to study DOC dynamics in regulated rivers. We selected sampling sites to capture OC processes of non-regulated reaches, above and below reservoirs, and also to capture tailwater OC dynamics. In total, we selected seven sites on the Green and Yampa Rivers located in the upper basin of the Colorado River (Fig. 1). Two sites served as unregulated reaches: the Green River above Fontenelle reservoir near La Barge, Wyoming and the Yampa River near Maybell, Colorado. To capture potential longitudinal changes in OC transport and DOC composition and quality, we continued our sampling downstream starting above Fontenelle reservoir. Fontenelle reservoir had a mean water capacity of 0.26 km^3 and a mean water residence time of 0.13 yr for 2011 (Table A1). We sampled below Fontenelle dam at two locations: directly below the dam (Fig. 1) and another site 39.6 km downriver to measure the OC dynamics in the tailwater (referred to as Fontenelle tailwater). Further downstream, we sampled above Flaming Gorge reservoir. During 2011, Flaming Gorge reservoir had a mean volume of 4.08 km^3 and a mean residence time of 1.61 yr (Table A1). We sampled at two locations below Flaming Gorge dam, immediately below the dam and 25.7 km further downriver to capture tailwater effects on OC dynamics (referred to as Flaming Gorge tailwater). Our sampling sites were located at US Geological Survey gaging stations, except for tailwater sites. For tailwater sites we assumed no change in discharge over these short distances from the dams.

We sampled from the onset of snowmelt to base flow in one year to compare processes during runoff and base flow in these snowmelt driven rivers. We sampled at the beginning of snowmelt in late April 2011 and continued into October of 2011 every 2–7 weeks for a total of 8 sampling periods. In 2011, the Yampa and Green Rivers had

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high-sustained flows into late July (Fig. 2). All sampling sites were accessible by car, and collection of samples took place over a two-day period for each round of sampling.

2.2 Sample collection

We collected samples to quantify DOC concentration, composition, and bioavailability as well as particulates for POC. We used acid-washed polyethylene Cubitainers to collect water from each sampling site. We immediately placed the collected water on ice, and filtered within 8 h of collection. We used a pre-rinsed Supor capsule filter (0.2 µm capsule filter; Pall SUPOR AcroPak 200) to filter approximately 4 L of water from each site for the bioassay experiments described below. From the remaining water, we collected samples for absorbance spectroscopy measurements and DOC concentration. The water samples were filtered into acid-washed, pre-combusted 40 mL amber glass vials. Four replicates were immediately acidified with 400 µL of 2N HCl for later DOC analysis, and four other replicates were used for spectral measurements. All DOC samples were kept cold and dark until analyses. We analyzed DOC samples on a Shimadzu TOC 5000A in Laramie, Wyoming. Individual samples were run a minimum of three times to estimate analytical precision. The coefficient of variation for replicate runs of the same sample was < 2 %.

2.3 DOC composition

We used spectrophotometric absorbance to evaluate DOC chemical composition. We used a scanning spectrophotometer to measure the absorbance of DOC from 200 to 600 nm on a Beckman DU spectrophotometer. We scanned the DOC samples using a 5 cm quartz cuvette and used deionized water as the blank. To characterize the structure of DOC, we used the absorbance measured at 254 nm, normalized by the DOC concentration to calculate specific ultraviolet absorption, otherwise referred to as $SUVA_{254}$ ($L\,mg\,C^{-1}\,m^{-1}$). $SUVA_{254}$ indicates the aromaticity of the C compounds and is positively correlated with double C bonds and molecular weight, with higher val-

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ues indicating more aromaticity of the DOC compounds (Chin et al., 1994; Weishaar et al., 2003). Additionally, we calculated the spectral slope ratio (S_R). S_R is the ratio of the spectral slopes ($S_{275–295} : S_{350–400}$) at wavelength regions of 275–295 and 350–400 (Helms et al., 2008). S_R is inversely correlated with DOC molecular weight and has been shown to shift in response to DOC photo alteration (Helms et al., 2008). By using $SUVA_{254}$ and S_R we expected higher $SUVA_{254}$ values and lower S_R values for more aromatic, higher molecular weight DOC, and lower $SUVA_{254}$, higher S_R for lower molecular weight DOC.

2.4 Bioassay experiments to estimate bioavailability of DOC

Bioassay experiments, where we measured the decline in DOC over time, represent the potential bioavailability of DOC to the microbial assemblage (del Giorgio and Davis, 2003). For each bioassay experiment, we added 1 L of 0.2 µm filtered river water to an acid-washed, pre-combusted glass jar. Then, we inoculated the filtered river water with 10 mL of 0.7 µm filtered water (pre-combusted glass fiber filter; Whatman GF/F). We inoculated deionized water with 10 mL of 0.7 µm filtered water as a control. We ran the bioassays in triplicate, with one control per site and date. We incubated all bioassay experiments in the dark throughout the experiment. We collected DOC samples from the bioassay jars every few days for 28 days and then preserved and analyzed as described above. The decline in DOC concentration over time was fit to a 1st order exponential decay model (del Giorgio and Pace, 2008) such that,

$$\ln DOC_{total} = \ln DOC_{initial} - kt \quad (1)$$

where $\ln DOC_{total}$ is the natural log transformed total DOC concentration ($mg\,L^{-1}$), $\ln DOC_{initial}$ is the natural log transformed initial concentration of DOC ($mg\,L^{-1}$), k is the decay rate (d^{-1}) and t is incubation time (d). We used the lm function (linear model) in R (R Development Core Team, 2012) to solve for k by regressing the natural log of DOC concentration by day.

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2.5 Particulate organic carbon

We filtered 0.2–5 L of river water, depending on the site and amount of sample visibly retained on the filter, through pre-combusted glass fiber filters to estimate POC (pre-combusted glass fiber filter; Whatman GF/F). Triplicate samples were dried at 60 °C, weighed for dry mass, and combusted at 500 °C. Following combustion, we re-wetted the filters to account for potential clay dehydration, re-dried, and weighed again. The ash free dry mass (AFDM, mg L^{-1}) of the particulate samples was calculated as the difference in the dry mass (mg) and combusted mass (mg) divided by the volume filtered (L). To estimate POC, we assumed that 45 % of the AFDM was OC (Whittaker and Likens, 1973).

2.6 Statistical analyses

To address longitudinal changes on OC transport, we compared the mean POC and DOC concentrations, $SUVA_{254}$, S_R, and bioavailability as k (d^{-1}) at each site along the Green River with the closest upstream site. We used a paired t test to evaluate if the mean OC concentrations, spectral data, and bioavailability statistically differed between sites in relation to upstream or downstream of Fontenelle or Flaming Gorge reservoirs and their respective tailwaters (Dalgaard, 2008). We used R (R Development Core Team, 2012) to conduct all statistical analyses.

2.7 Fluxes of DOC and POC

We calculated the daily fluxes and annual loads of DOC and POC for each sampling site. Daily fluxes of DOC and POC were calculated as:

$$\mathrm{Flux}_d = Q_d \times [\mathrm{OC}]_d \quad (2)$$

where Flux_d was the daily DOC or POC flux ($g\,d^{-1}$), Q_d ($m^3\,d^{-1}$) was the mean discharge of day d, and $[\mathrm{OC}]_d$ was the mean concentration ($g\,m^{-3}$) of either DOC or POC

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for day d. We developed a rating curve for each sampling site relating [OC] to Q using our 8 sampling points to estimate $[OC]_d$ for the 2011 calendar year where

$$\ln[OC] = \beta_0 + \beta_1 \ln Q + \beta_2 \ln Q^2 \quad (3)$$

[OC] is POC or DOC concentration, β_0, β_1, and β_2 are the model coefficients and Q is discharge ($m^3 s^{-1}$) (similar to Stackpoole et al., 2014). Equation (3) was parameterized for each sampling site (using lm function in R, R Development Core Team, 2012) to predict daily POC and DOC concentrations based on daily Q, except for sites located below Flaming Gorge dam and its respective tailwater where there was no statistical relationship between DOC concentration and Q (Table 1). For these sites, we used the mean of measured DOC concentrations for $[OC]_d$. We used linear regression (lm function in R, R Development Core Team, 2012) to compare predicted $Flux_d$ to observed $Flux_d$ to further quantify beyond model fit if Eq. (3) was appropriate for predicting $[OC]_d$ based on Q for the subsequent $Flux_d$ calculations. The estimated $Flux_d$ from predicting daily $[OC]_d$ from Eq. (3) (and using the mean DOC concentrations for sites located below Flaming Gorge dam) was similar to the $Flux_d$ estimates from measured $[OC]_d$ (Table 2), and therefore we were confident in extrapolating daily $Flux_d$ from predicted $[OC]_d$ and Q_d for the calendar year of 2011. These daily fluxes were then summed to estimate the 2011 annual loads for DOC and POC for each sampling site.

3 Results

3.1 Organic carbon concentrations and transport

Longitudinal OC concentrations, and the subsequent OC load for 2011 fluctuated in the presence of reservoir-tailwater ecosystems along the Green River (Table 3). POC concentrations were lower below both Fontenelle and Flaming Gorge dams compared to upstream of the reservoirs (Fig. 2). POC concentrations averaged 1.2 $mg L^{-1}$ above Fontenelle reservoir compared to 0.4 $mg L^{-1}$ below the dam (paired t test, $p = 0.002$).

Lower concentrations of POC directly below Fontenelle dam translated to an annual POC load that was nearly 3-fold lower compared to upstream of the reservoir (Table 3). POC concentrations (Fig. 2) and subsequent OC loads (Table 3) above Fontenelle reservoir also had the most temporal variability, similar to the Yampa River, compared to the other sampling sites along the Green River. POC concentrations above Flaming Gorge reservoir averaged 1.4 $mg\,L^{-1}$ compared to directly below Flaming Gorge dam, which averaged 0.2 $mg\,L^{-1}$ (paired t test, $p < 0.0001$). The annual POC load for 2011 was reduced nearly 7-fold directly below Flaming Gorge dam compared to upstream of the reservoir (Table 3).

Although POC loads were lower directly below both dams compared to above, POC concentrations increased within their tailwaters (Fig. 2). POC concentrations rebounded 2-fold at the Fontenelle tailwater site relative to directly below the dam (paired t test, $p < 0.0001$) and averaged 0.9 $mg\,L^{-1}$. Higher POC concentrations resulted in an annual POC load that was nearly 3-fold greater at the Fontenelle tailwater site compared to directly below the dam (Table 3). POC concentrations averaged 0.6 $mg\,L^{-1}$ at the Flaming Gorge tailwater site, which equated to a 3-fold increase in concentration (paired t tests, $p < 0.0001$) and an annual POC load for 2011 nearly 4-fold greater relative to directly below the dam (Table 3).

Variation in DOC concentrations and the annual load of DOC along the Green River was less pronounced than that for POC. Mean DOC concentrations did not vary above and below either reservoir during 2011 (paired t test, $p > 0.1$ for both reservoirs). However, snowmelt DOC concentrations above both reservoirs were greater than DOC concentrations directly below their respective dams, and vice versa during base flow conditions. Similar to the Yampa River, DOC concentrations peaked prior to peak discharge above Fontenelle reservoir, but peaked with discharge below the reservoir (Fig. 2). Although mean DOC concentrations did not differ, higher discharge below Flaming Gorge dam compared to upstream of the reservoir equated to a 1400 $Mg\,yr^{-1}$ increase in DOC annual load below the dam compared to above the reservoir (Table 3).

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Mean DOC concentrations increased from directly below both dams through their tailwater reaches, resulting in an increase of approximately 200–244 $Mg\,yr^{-1}$ of DOC. The DOC concentration directly below Fontenelle dam averaged 3.4 $mg\,L^{-1}$ compared to the tailwater sampling site, which averaged 3.5 $mg\,L^{-1}$ (paired t test, $p = 0.018$). This concentration increase in DOC equated to approximately a 200 Mg increase in the annual DOC load within the 39.6 km reach (Table 3). DOC concentration averaged 3.7 $mg\,L^{-1}$ at the Flaming Gorge tailwater sampling site compared to 3.6 $mg\,L^{-1}$ directly below Flaming Gorge dam (paired t test; $p < 0.0001$). The increase in DOC concentration between the two sampling sites equated to an annual load of 244 Mg of DOC within the 25.7 km Flaming Gorge tailwater reach (Table 3).

3.2 DOC bioavailability and composition

DOC bioavailability, as measured by the decay rate k (d^{-1}) of DOC, was lower directly downstream of both reservoirs than the bioavailability of the DOC upstream (Fig. 4, Table B1). Mean bioavailability above Fontenelle reservoir was 0.0036 d^{-1} compared to 0.0024 d^{-1} directly below the dam (paired t test, $p = 0.0005$). Average DOC bioavailability was 2-fold greater above (0.0030 d^{-1}) Flaming Gorge reservoir compared to directly below the dam (0.0014 d^{-1}, paired t test, $p = 0.0002$). Some seasonal variation in bioavailability was measured where k (d^{-1}) was higher during onset of snowmelt, but decreased and remained relatively constant through the remaining snowmelt and base flow conditions (Table B1).

Bioavailability was greater at the tailwater sites relative to sampling sites directly below their respective dams (Fig. 4, Table B1). Bioavailability of DOC significantly increased from directly below Fontenelle dam to the tailwater site downstream (0.0024 to 0.0030 d^{-1}; paired t test, $p = 0.04$). Although k (d^{-1}) increased from directly below Flaming Gorge reservoir to the tailwater site downstream, this difference was not statistically significant (0.0014 to 0.0018 d^{-1}; paired t test, $p = 0.09$).

The most pronounced changes in DOC composition, as measured by S_R and $SUVA_{254}$, was between the sampling sites upstream of Flaming Gorge reservoir and

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directly downstream of the dam. S_R increased, and $SUVA_{254}$ decreased from above Flaming Gorge reservoir to directly below its dam (Fig. 3). DOC composition directly below Flaming Gorge dam reflected less aromatic and smaller molecular weight DOC compared to more aromatic and larger molecular weight DOC above the reservoir (t test, $SUVA_{254}$: $p < 0.0001$, S_R: $p < 0.0001$). In comparison, $SUVA_{254}$ and S_R remained relatively unchanged above and below Fontenelle reservoir, although composition shifted at each site during the transition from snowmelt to base flow (Fig. 3).

DOC composition, based on $SUVA_{254}$ and S_R, varied little through the tailwater reaches. $SUVA_{254}$ decreased from directly below Fontenelle reservoir to the Fontenelle tailwater site, indicating less aromatic DOC (mean difference = 0.04 L mg C^{-1} m^{-1}, paired t test, $p < 0.0001$), but there was no statistically significant difference in S_R between these sites (paired t tests, $p = 0.1$). Flaming Gorge tailwater reach had no effect on $SUVA_{254}$ or S_R ($SUVA_{254}$: paired t test, $p = 0.27$, S_R: paired t tests, $p = 0.08$).

4 Discussion

Impoundments on rivers may disrupt longitudinal OC transport (Ward and Stanford, 1983; Miller, 2012; Stackpoole et al., 2014); however, the combination of reservoir-tailwater ecosystems on OC dynamics is less understood than the impact of reservoirs alone. By measuring OC concentrations and DOC composition and bioavailability, we found that longitudinal OC dynamics fluctuated in the presence of reservoir-tailwater ecosystems. POC concentrations and DOC bioavailability were reduced below both reservoirs compared to upstream reaches and OC was produced within the tailwaters. These combined effects of reservoirs and corresponding tailwater river reaches likely increased the impact on OC cycling compared to the presence of impoundments alone by magnifying the transformation of both POC and DOC.

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4.1 Temporal OC dynamics

Hydrological seasonality drove variation in POC and DOC concentrations in the upper Green and Yampa Rivers (Fig. 2). The hydrological flushing hypothesis posits that terrestrial carbon within the watershed accrues during low flows and is flushed into streams and rivers during the initial infiltration of melt water during the onset of snowmelt (Hornberger et al., 1994; Boyer et al., 1997). Therefore, our findings of peak OC concentrations preceding peak discharge were not surprising above Fontenelle reservoir and at the Yampa River sampling site. This pattern indicates the terrestrial supply of DOC is exhausted, resulting in hysteresis between DOC concentration and stream discharge (Hornberger et al., 1994; Finlay et al., 2006; Ågren et al., 2008). Peak concentrations of OC coincided with peak discharge below Fontenelle reservoir, which was likely driven by a combination of factors including dam operations and longer residence time of water in the reservoir relative to the river.

Riverine DOC sources, and therefore bioavailability and composition, can be seasonally dependent. The initial flushing of terrestrial OC from a watershed during early snowmelt can be more bioavailable than base flow DOC because shallow sub-surface runoff from the catchment can export stored terrestrial OC into aquatic ecosystems (Michaelson et al., 1998; Pacific et al., 2010; Pellerin et al., 2011). In contrast, DOC composition in semi-arid and arid rivers reflected autochthonous DOC during base flow conditions as opposed to high flows, due to the contribution of algal and microbial exudates from increased primary production (Westerhoff and Anning, 2000). High-sustained flows during spring and summer 2011 in the Yampa and Green Rivers (Fig. 2) likely decreased the onset and magnitude of primary production (Uehlinger, 2000), which could account for our findings of stable, as opposed to increasing, DOC bioavailability after peak snowmelt. Furthermore, increased $SUVA_{254}$ and S_R indicated that base flow DOC likely comprised more aromatic, but smaller molecular weight carbon molecules than snowmelt DOC, likely due to microbial or photo-transformation of DOC (Helms et al., 2008; Kraus et al., 2011; Miller, 2012) as opposed to production

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of labile DOC (Weishaar et al., 2003; Goodman et al., 2011). Transformation of DOC, rather than production of labile DOC from algal-exudation supports our DOC bioavailability findings.

4.2 Longitudinal DOC dynamics

Not only total water storage, but also the type of reservoir may alter DOC dynamics and longitudinal transport. The annual DOC loads ($Mg\,yr^{-1}$) above Fontenelle reservoir and directly below the dam were similar (Table 3). In comparison, the annual DOC load increased from upstream to downstream of Flaming Gorge reservoir, regardless of the hydrograph. These annual estimated DOC loads for the Green River were similar to the upper Colorado River with comparable drainage areas (Fig. 5, Miller, 2012; Stackpoole et al., 2014); yet, the increase in DOC annual load with drainage area was greater in the upper Colorado River (drainage area < 50 000 km^2) compared to the Green River (Fig. 5). The upper Colorado River had approximately 4.6 km^3 of reservoir storage dispersed among 464 dams within the upper reaches (drainage area < 46 300 km^2) (Miller, 2012). Similarly, the Green River directly downstream of Flaming Gorge dam has a drainage area of 39 083 km^2 and in 2011 the mean reservoir storage was approximately 4.3 km^3 (Table A1), but most of the storage was within Flaming Gorge reservoir. The difference in the relationship of DOC fluxes with watershed area between the upper Colorado River and Green River suggest reservoir type (i.e. many small vs. a few large reservoirs) and not just total water storage capacity of the basin may drive a decrease in OC loads in this semi-arid watershed.

Although we do not have the appropriate data to adequately budget OC for either of the reservoirs, residence time likely drove, at least in part, the longitudinal DOC concentration and flux patterns we observed in relation to the reservoirs. Increased residence time due to impounding a river reduces water velocity, which allows POC to settle and allows more time for the production and transformation of DOC (Mash et al., 2004; Kraus et al., 2011; Knoll et al., 2013). A similar shift in DOC concentration and timing of peak discharge occurred above and below natural lakes in snowmelt-dominated

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catchments because of residence time of the lakes (Goodman et al., 2011). The timing of reservoir filling and dam operations resulted in an arid reservoir (Westerhoff and Anning, 2000) and two temperate reservoirs (Knoll et al., 2013) to fluctuate between net source and net sink of DOC to downstream reaches. Also, seasonal shifts in reservoir primary production drove a reservoir in California to shift between a DOC source and sink (Kraus et al., 2011). A combination of residence time and autochthonous production within reservoirs may lead to production (Parks and Baker, 1997; Kraus et al., 2011) or loss of DOC (Kraus et al., 2011; Miller et al., 2012; Knoll et al., 2013) to downstream ecosystems, likely driven by magnitude of hydrological variation such as high vs. low flow years (Knoll et al., 2013).

DOC composition differed from upstream to downstream of both Fontenelle and Flaming Gorge reservoirs. All $SUVA_{254} < 3\,L\ mg\ C^{-1}\ m^{-1}$, which indicates that DOC across our sampling sites was of low aromatic content (Weishaar et al., 2003), similar to values found in the Colorado River (Miller, 2012). Despite this low range of values, DOC composition below Flaming Gorge dam was less aromatic (as indicated by $SUVA_{254}$) and reflected lower molecular weight OC (as indicated by S_R) compared to DOC composition upstream (Fig. 3). These small, but statistically significant, changes could be due to photodegradation (Brooks et al., 2007; Kraus et al., 2012; Cory et al., 2014) coupled with autochthonous production of DOC (Chin et al., 1994; Nguyen et al., 2002). A similar decreasing $SUVA_{254}$ pattern from upstream to downstream of reservoirs was reported below Lake Powell and Lake Mead in the lower Colorado River basin (Miller, 2012). In addition, DOC bioavailability was reduced below Flaming Gorge dam compared to upstream of the reservoir (Fig. 4). This pattern along with our absorbance data indicates that DOC exported from Flaming Gorge reservoir was likely a combination of transformed and microbially produced DOC. In comparison, DOC composition did not vary above and below Fontenelle reservoir based on $SUVA_{254}$ and S_R metrics. But, similar to Flaming Gorge reservoir, bioavailability of DOC was significantly lower below Fontenelle dam compared to above the reservoir (Fig. 4). Reduced bioavailability below the dam indicates that even with no observed spectral changes (i.e., $SUVA_{254}$ and

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S_R) above and below Fontenelle reservoir, DOC processing or transformation occurred within this reservoir ecosystem, but to a lesser extent than the larger Flaming Gorge reservoir.

POC concentrations were 10-fold lower downstream of Fontenelle and Flaming Gorge dams when compared to upstream of both reservoirs (Fig. 2), and subsequently resulted in a reduction of POC flux and annual load. This pattern is well established for large impoundments on rivers; impoundments allow for the settling of POC (Friedl and Wüest 2002; Downing et al., 2008; Tranvik et al., 2009). We did not measure within reservoir OC fate, but the fate of buried POC in reservoirs was likely a combination of preservation (Downing et al., 2008), mineralization to CO_2 (St. Louis et al., 2000; Knoll et al., 2013), and transformation to DOC (Meyer et al., 1998).

4.3 Tailwater organic carbon transport

Despite the low POC concentration emanating from Fontenelle and Flaming Gorge dams, POC concentrations increased to 40–74 % of above reservoir concentrations within the short tailwater reaches. There were no perennial tributaries in either tailwater; therefore the POC fluxes from the tailwater reaches were likely of autochthonous origin. Primary production likely drove this flux of POC from both tailwater reaches (Table 3). Tailwaters have high primary production (Webster et al., 1979; Davis et al., 2011) where algae and particulates are sloughed during discharge releases from the dam (Perry and Perry, 1991). The annual POC load from Fontenelle reservoir tailwater was similar to the annual POC load into the reservoir, indicating that an equivalent amount of the POC load reduced from above to below the reservoir was generated within the 39.6 km tailwater. Similarly, the Flaming Gorge tailwater generated about half the amount of POC that entered the reservoir (Table 3). We estimated POC area-specific fluxes from the tailwaters by dividing the difference in POC annual load ($g\,yr^{-1}$) by reach area (m^2) and 365 (d^{-1}). The POC daily flux from Fontenelle tailwater was 1.9 $g\,C\,m^{-2}\,d^{-1}$ and from Flaming Gorge tailwater 1.3 $g\,C\,m^{-2}\,d^{-1}$. Although we did not measure primary production in Flaming Gorge tailwater, primary production in

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Fontenelle tailwater can be has high as 8.1 $g\,C\,m^{-2}\,d^{-1}$ (Hall et al., 2015). Also, these POC area-specific flux estimates were within the upper 50th percentile of gross primary production measurements from 72 streams showing that primary production can support this high OC flux (Bernot et al., 2010). The POC flux likely consisted of current primary production and organic matter from primary production accrued throughout the year. Low discharge releases from Fontenelle and Flaming Gorge dams during the winter months combined, with the increased flows released from the dam during the onset of our sampling (Fig. 2), likely flushed the organic matter that had accrued within the tailwaters throughout the year (Parks and Baker, 1997; Brooks et al., 2007).

Fontenelle and Flaming Gorge tailwaters were likely a source of autochthonously produced DOC. The daily estimated flux of DOC from the tailwaters were 4 to 6-fold lower than POC fluxes, 0.3 $g\,C\,m^{-2}\,d^{-1}$ for both Fontenelle and Flaming Gorge tailwaters. Autochthonous DOC fluxes were similar from the tailwater segment directly below Lake Powell on the Colorado River (0.3–2.1 $g\,C\,m^{-2}\,d^{-1}$) and these fluxes were positively correlated with gross primary production (Ulseth, 2012). In addition, autochthonous DOC fluxes in the Grand Canyon reach of the Colorado River ranged from 0.09–0.39 $g\,C\,m^{-2}\,d^{-1}$ (Ulseth, 2012). Although estimated DOC fluxes were lower than POC fluxes, they were within the lower 50th percentile of primary production rates across 72 streams in North America (Bernot et al., 2010) indicating that autochthonous derived DOC flux, similar to POC flux, was potentially a substantial proportion of primary production (Hotchkiss and Hall, 2014) from these tailwater ecosystems. The DOC flux from tailwater algae had a minimal effect on total DOC composition, given our absorbance data. However, bioavailability was higher at the Fontenelle tailwater compared to directly below the dam, suggesting freshly produced, labile DOC. Increased total DOC bioavailability from the tailwater likely produced an export of labile DOC, potentially subsidizing the microbial food web in the downstream reaches.

The net effect of dams on the reduction of OC transport was essentially low (6–14 %), despite large changes in POC concentration and perhaps composition, as well as DOC composition. This finding affects how impoundments are viewed from an OC

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cycling perspective. The effect of impounding rivers on OC fluxes is potentially underestimated because total concentration based fluxes do not represent transformation processes in river-reservoir-tailwater ecosystems. Given that impoundments have increased the capacity of rivers to transform or store DOC and POC (Kraus et al., 2011; Miller, 2012), regulation of rivers in the Western United States has changed OC cycling in these ecosystems by altering the timing, magnitude, and composition of OC to downstream ecosystems (Miller, 2012; Stackpoole et al., 2014). The tailwater ecosystems contributed to the effect of reservoirs on OC transport in rivers by increasing the export of likely autochthonous OC downriver. Therefore, reservoirs regulate OC transport by reducing POC and altering the composition and bioavailability of DOC. The effect of impounding rivers on C cycling is larger than the reservoirs alone because of the additive impacts of tailwater reaches, which produce and then export a comparable amount of autochthonous OC than what is likely stored behind dams. To assess the effects in terms of regional carbon budgets, we need to consider not only reservoirs in regards to their capacity to transform terrestrial OC (Knoll et al., 2013), but also the additive effects of their tailwater ecosystems.

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Table 1. A regression model to estimate daily organic carbon concentrations [OC] from mean discharge (Q), $\ln[OC] = \beta_0 + \beta_1 \ln[Q] + \beta_2 \ln[Q]^2$, was fit for each sampling site in order to estimate annual [OC] loads. POC refers to particulate organic carbon and DOC is dissolved organic carbon. β_0, β_1, and β_2 are the model coefficients for each sampling site. P value and r^2 are selected corresponding model statistics at each site.

	POC					DOC				
Site	β_0	β_1	β_2	P value	r^2	β_0	β_1	β_2	P value	r^2
Above Fontenelle reservoir	−22.0	9.8	−1.0	0.02	0.79	−2.8	1.5	−0.1	0.01	0.82
Below Fontenelle dam	−14.6	5.5	−0.5	0.05	0.69	2.6	−1.0	0.1	0.00	0.96
Fontenelle tailwater	−6.9	2.1	−0.1	0.01	0.82	3.1	−1.2	0.2	0.00	0.94
Above Flaming Gorge reservoir	−25.3	10.9	−1.1	0.00	0.90	3.0	−1.1	0.2	0.00	0.95
Below Flaming Gorge dam*	−31.5	12.2	−1.2	0.05	0.70	NA	NA	NA	NA	NA
Flaming Gorge tailwater*	−41.5	16.3	−1.6	0.00	0.95	NA	NA	NA	NA	NA
Yampa River	−9.4	3.9	−0.3	0.00	0.95	−0.8	1.1	−0.1	0.02	0.79

* No statistical relationship between DOC concentration and Q, therefore mean measured DOC concentrations were used to estimate daily fluxes, and to calculate annual DOC load for 2011.

Table 2. Select model statistics from linear regression (lm in R, R Development Core Team, 2012) models to compare predicted organic carbon fluxes to observed particulate organic carbon (POC) and dissolved organic carbon (DOC) fluxes ($flux_d$, $Mg\,d^{-1}$) for each sampling site. Predicted organic carbon fluxes were calculated from estimated daily organic carbon (POC or DOC) concentrations ([OC]) and discharge (Q). Linear regression models were used to predict [OC] where $\ln[OC] = \beta_0 + \beta_1 \ln[Q] + \beta_2 \ln[Q]^2$, except for sites below Flaming Gorge dam where there was no statistical relationship between DOC and Q. Average measured DOC and discharge were used to estimate daily DOC fluxes for sites below Flaming Gorge dam. Observed OC fluxes were calculated multiplying the mean measured [OC] and corresponding mean daily Q.

	POC				DOC			
Site	intercept	slope	slope SE	r^2	intercept	slope	slope SE	r^2
Above Fontenelle reservoir	2.94	0.59	0.11	0.82	−1.19	1.04	0.04	0.99
Below Fontenelle dam	0.04	0.95	0.14	0.89	−0.21	1.01	0.01	1.00
Fontenelle tailwater	0.19	0.97	0.07	0.97	−0.28	1.01	0.02	1.00
Above Flaming Gorge reservoir	0.41	0.95	0.12	0.92	−0.27	1.01	0.01	1.00
Below Flaming Gorge dam	0.07	0.96	0.12	0.92	0.68	0.98	0.04	0.99
Flaming Gorge tailwater	0.29	0.96	0.08	0.96	0.41	0.99	0.04	0.99
Yampa River	22.69	0.70	0.16	0.76	2.45	0.97	0.06	0.97

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Table 3. Daily measured fluxes ($Flux_d$, $Mg\,d^{-1}$) and annual load ($Mg\,yr^{-1}$ for 2011) of dissolved organic carbon (DOC) and particulate organic carbon (POC) across sampling sites on the Green and Yampa Rivers.

	Above Fontenelle reservoir		Below Fontenelle dam		Fontenelle tailwater		Above Flaming Gorge reservoir		Below Flaming Gorge dam		Flaming Gorge tailwater		Yampa River	
Date	DOC	POC	DOC	POC	DOC	POC	DOC	POC	DOC	POC	DOC	POC	DOC	POC
30 Apr 2011	5.9	1.0	15.7	1.7	16.3	3.7	16.5	5.6	36.6	1.9	39.0	9.8	64.1	53.5
18 May 2011	26.9	23.8	24.6	5.3	24.0	10.8	17.3	15.1	36.6	2.6	41.4	8.6	161.7	231.4
1 Jun 2011	28.2	11.2	33.5	5.2	34.6	8.3	34.3	22.1	39.6	2.3	43.4	9.1	174.6	282.2
15 Jun 2011	84.5	49.4	65.8	9.7	67.1	18.2	54.9	23.1	74.5	2.6	74.2	16.3	163.6	140.7
30 Jun 2011	125.5	14.9	101.3	8.1	103.0	38.8	97.5	33.8	83.4	3.3	81.1	12.9	111.5	86.4
21 Aug 2011	5.9	0.9	12.1	0.5	12.3	1.3	11.1	2.3	23.1	0.9	22.8	2.3	8.9	1.3
11 Sep 2011	3.6	0.4	7.4	0.6	7.8	1.2	8.6	1.1	23.3	1.0	23.3	1.8	5.0	0.5
16 Oct 2011	3.1	0.2	7.7	0.4	8.0	0.7	7.8	0.8	19.0	0.3	18.7	0.7	4.0	0.2
Annual Load[a]	7604	2092	7641	715	7850	2106	8049	2341	9430[b]	350	9674[b]	1316	13 717	13 189

[a] A regression model to estimate daily organic carbon concentrations [OC] from mean discharge (Q), $\ln[Q] = \beta_0 + \beta_1 \ln[Q] + \beta_2 \ln[Q]^2$, was fit for each sampling site in order to estimate annual [OC] loads.
[b] No significant relationship between [OC] and Q, therefore annual loads were calculated by using the mean measured [OC] to estimate daily fluxes.

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Table A1. Fontenelle and Flaming Gorge reservoir volumes and residence time (R_t) for 2011. R_t was calculated by dividing reservoir volume (volume, m^3) by yearly outflow (Q_{out}, $m^3\,yr^{-1}$). Mean residence time was based on mean Q_{out} for 2011, including both base flow and snowmelt. Minimum residence time was based on Q_{out} during snowmelt period of discharge. Maximum residence time was based on base flow Q_{out} only.

Reservoir	Mean volume* (min, max) km^3	Mean R_t (min, max) yr^{-1}
Fontenelle	0.26 (0.12, 0.40)	0.13 (0.06, 0.30)
Flaming Gorge	4.08 (3.79, 4.43)	1.61 (0.86, 2.81)

* Volume data and Q_{out} for Fontenelle and Flaming Gorge reservoirs for 2011 were accessed from the Bureau of Reclamation Upper Colorado River Region Water Operations (http://www.usbr.gov/uc/crsp/GetSiteInfo).

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Table B1. Mean decay rates (k, d^{-1}) and mean percentage (%) loss of DOC over 28 day bioassay experiment. Mean percentage loss was calculated by dividing the difference in DOC concentration ($mg\,L^{-1}$) from day 0 to day 28 by the initial DOC concentration at day 0 and then multiplying by 100. 95 % confidence intervals were calculated for k d^{-1} and % loss of DOC from 3 replicate bioassay experiments for each site and each date.

Site	Date	Mean k (d^{-1}) (5, 95 % CI)	Mean % Loss DOC (28 d^{-1}) (5, 95 % CI)
Above Fontenelle reservoir	30 Apr 11	0.0056 (0.0051, 0.0063)	14.4 (12.7, 15.4)
Above Fontenelle reservoir	18 May 11	0.0024 (0.0017, 0.0029)	7.3 (4.5, 9.6)
Above Fontenelle reservoir	1 Jun 11	0.0029 (0.0023, 0.0037)	8.5 (6.8, 11.0)
Above Fontenelle reservoir	15 Jun 11	0.0036 (0.0031, 0.0042)	10.4 (7.8, 13.3)
Above Fontenelle reservoir	30 Jun 11	0.0031 (0.0029, 0.0032)	7.7 (7.2, 8.0)
Above Fontenelle reservoir	21 Aug 11	0.0044 (0.0040, 0.0050)	10.9 (10.4, 11.4)
Above Fontenelle reservoir	11 Sep 11	0.0025 (0.0020, 0.0029)	7.5 (5.8, 9.0)
Above Fontenelle reservoir	16 Oct 11	0.0043 (0.0037, 0.0050)	11.4 (9.3, 14.6)
Below Fontenelle dam	30 Apr 11	0.0036 (0.0032, 0.0040)	10.7 (9.7, 11.6)
Below Fontenelle dam	18 May 11	0.0038 (0.0034, 0.0043)	7.4 (7.3, 7.7)
Below Fontenelle dam	1 Jun 11	0.0021 (0.0016, 0.0027)	5.5 (3.8, 7.2)
Below Fontenelle dam	15 Jun 11	0.0020 (0.0014, 0.0024)	5.6 (4.1, 6.5)
Below Fontenelle dam	30 Jun 11	0.0020 (0.0017, 0.0023)	5.4 (4.4, 6.1)
Below Fontenelle dam	21 Aug 11	0.0019 (0.0014, 0.0023)	5.0 (4.7, 5.4)
Below Fontenelle dam	11 Sep 11	0.0020 (0.0013, 0.0028)	5.6 (3.2 7.9)
Below Fontenelle dam	16 Oct 11	0.0016 (0.0011, 0.0021)	4.8 (2.3, 6.9)
Fontenelle tailwater	30 Apr 11	0.0055 (0.0044, 0.0065)	16.6 (13.4, 19.5)
Fontenelle tailwater	18 May 11	0.0024 (0.0017, 0.0032)	5.6 (4.6, 7.0)
Fontenelle tailwater	1 Jun 11	0.0030 (0.0026, 0.0034)	9.0 (7.8, 11.0)
Fontenelle tailwater	15 Jun 11	0.0032 (0.0030, 0.0034)	9.2 (8.5, 9.6)
Fontenelle tailwater	30 Jun 11	0.0025 (0.0016, 0.0031)	6.4 (3.5, 8.2)
Fontenelle tailwater	21 Aug 11	0.0025 (0.0023, 0.0026)	4.4 (3.7, 5.1)
Fontenelle tailwater	11 Sep 11	0.0022 (0.0013, 0.0035)	6.2 (2.4, 10.6)
Fontenelle tailwater	16 Oct 11	0.0023 (0.0018, 0.0032)	6.1 (3.1, 9.1)
Above Flaming Gorge reservoir	30 Apr 11	0.0065 (0.0062, 0.0069)	17.4 (15.9, 18.9)
Above Flaming Gorge reservoir	18 May 11	0.0038 (0.0035, 0.0043)	10.9 (9.9, 11.7)
Above Flaming Gorge reservoir	1 Jun 11	0.0021 (0.0018, 0.0024)	5.0 (4.0, 5.7)
Above Flaming Gorge reservoir	15 Jun 11	0.0022 (0.0019, 0.0026)	5.2 (4.4, 5.8)
Above Flaming Gorge reservoir	30 Jun 11	0.0025 (0.0021, 0.0029)	7.9 (6.3, 8.8)
Above Flaming Gorge reservoir	21 Aug 11	0.0014 (0.0013, 0.0016)	2.7 (1.4, 3.7)
Above Flaming Gorge reservoir	11 Sep 11	0.0021 (0.0016, 0.0024)	4.8 (1.8, 7.2)
Above Flaming Gorge reservoir	16 Oct 11	0.0032 (0.0031, 0.0033)	7.9 (6.4, 8.9)

Table B1. Continued.

Site	Date	Mean k (d^{-1}) (5, 95 % CI)	Mean % Loss DOC ($28\,d^{-1}$) (5, 95 % CI)
Below Flaming Gorge dam	30 Apr 11	0.0010 (0.0002, 0.0015)	4.8 (1.8, 6.7)
Below Flaming Gorge dam	18 May 11	0.0009 (0.0007, 0.0011)	3.3 (2.8, 4.0)
Below Flaming Gorge dam	1 Jun 11	0.0011 (0.0008, 0.0014)	4.2 (2.5, 5.6)
Below Flaming Gorge dam	15 Jun 11	0.0008 (0.0005, 0.0010)	2.8 (1.4, 4.4)
Below Flaming Gorge dam	30 Jun 11	0.0028 (0.0014, 0.0043)	10.3 (5.2, 14.6)
Below Flaming Gorge dam	21 Aug 11	0.0026 (0.0021, 0.0033)	8.6 (7.9, 9.0)
Below Flaming Gorge dam	11 Sep 11	0.0011 (0.0009, 0.0014)	4.3 (3.0, 5.6)
Below Flaming Gorge dam	16 Oct 11	0.0011 (0.0009, 0.0013)	2.1 (1.2, 2.9)
Flaming Gorge tailwater	30 Apr 11	0.0019 (0.0012, 0.0029)	8.4 (6.5, 11.4)
Flaming Gorge tailwater	18 May 11	0.0025 (0.0020, 0.0030)	8.3 (7.2, 9.9)
Flaming Gorge tailwater	1 Jun 11	0.0021 (0.0017, 0.0023)	6.6, 9.1)
Flaming Gorge tailwater	15 Jun 11	0.0005 (0.0004, 0.0006)	2.1 (1.6, 2.6)
Flaming Gorge tailwater	30 Jun 11	0.0026 (0.0023, 0.0029)	8.5 (7.0, 10.2)
Flaming Gorge tailwater	21 Aug 11	0.0019 (0.0012, 0.0026)	4.5 (0.5, 8.0)
Flaming Gorge tailwater	11 Sep 11	0.0015 (0.0009, 0.0023)	2.5 (0.3, 4.6)
Flaming Gorge tailwater	16 Oct 11	0.0014 (0.0012, 0.0016)	3.0 (2.4, 4.0)
Yampa River	30 Apr 11	0.0043 (0.0042, 0.0045)	11.7 (11.5, 11.9)
Yampa River	18 May 11	0.0015 (0.0012, 0.0020)	2.8 (2.2, 3.5)
Yampa River	1 Jun 11	0.0013 (0.001, 0.0015)	3.5 (2.5, 4.6)
Yampa River	15 Jun 11	0.0017 (0.0011, 0.0023)	4.3 (1.9, 6.0)
Yampa River	30 Jun 11	0.0022 (0.0017, 0.0025)	6.2 (5.7, 6.8)
Yampa River	21 Aug 11	0.0035 (0.0021, 0.0044)	10.3 (6.9, 13.7)
Yampa River	11 Sep 11	0.0024 (0.0020, 0.0029)	7.0 (5.0, 9.2)
Yampa River	16 Oct 11	0.0025 (0.0024, 0.0026)	4.9 (3.5, 6.8)

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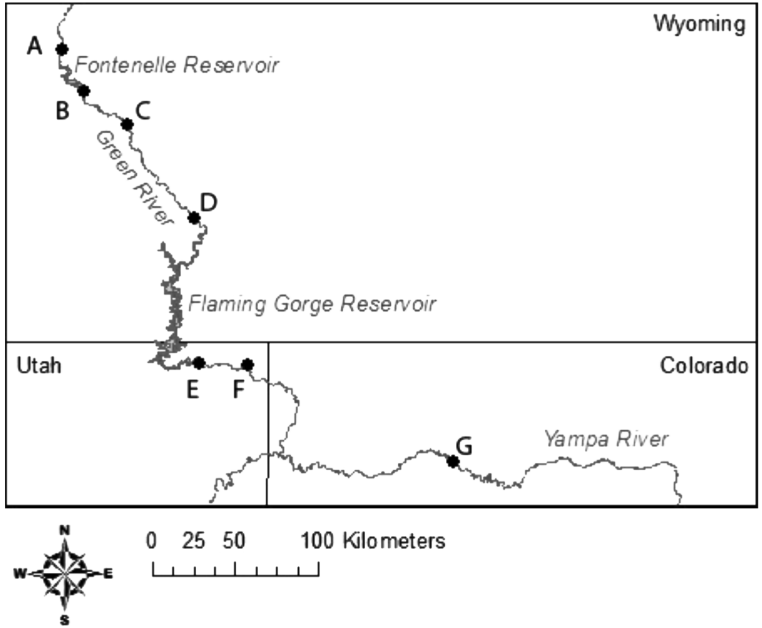

Figure 1. Map of Fontenelle and Flaming Gorge reservoirs located on the Green River in Wyoming and Utah and the Yampa River located in Colorado. The points along the rivers designate the locations from where we collected water from April–October 2011. Two sites located on unregulated river reaches: the Green River above Fontenelle reservoir (A) (USGS gaging station 09209400) and the Yampa River (G) (USGS gaging station 09251000). We also sampled directly below Fontenelle dam (B) (USGS gaging station 09211200) and 39.6 km down river for the Fontenelle tailwater (C). We sampled above Flaming Gorge reservoir (D) (USGS gaging station 09217000) and directly below Flaming Gorge dam (E) (USGS gaging station 09234500) and 25.7 km further downstream for Flaming Gorge tailwater (F).

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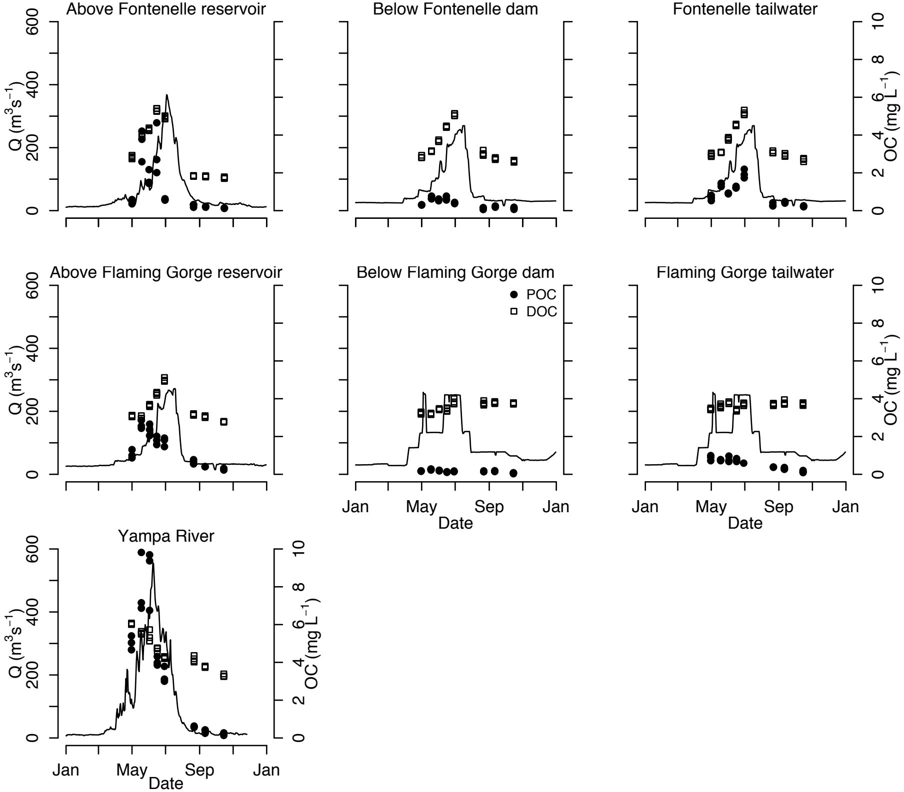

Figure 2. Discharge (line, Q m^3 s^{-1}) plotted for 2011 along with particulate organic carbon (POC, replicate samples plotted) and dissolved organic carbon (DOC, replicate samples plotted) concentrations from sampling sites located on the Green and Yampa Rivers.

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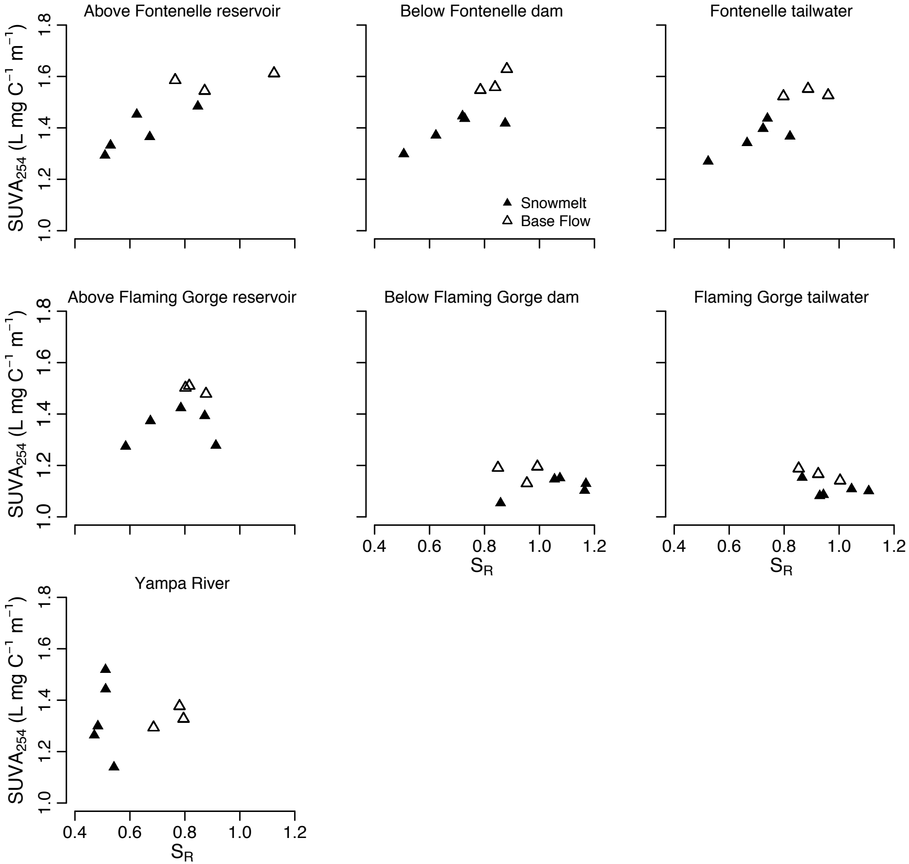

Figure 3. Mean specific ultraviolet absorbance at 254 nm ($SUVA_{254}$, $L\,mg\,C^{-1}\,m^{-1}$) plotted by the mean slope ratio (S_R) across sampling dates for each site during snowmelt and base flow conditions. Higher $SUVA_{254}$ and lower S_R indicate greater aromaticity and higher molecular weight DOC compared to lower $SUVA_{254}$ and higher S_R, which indicate lower aromaticity and lower molecular weight of DOC.

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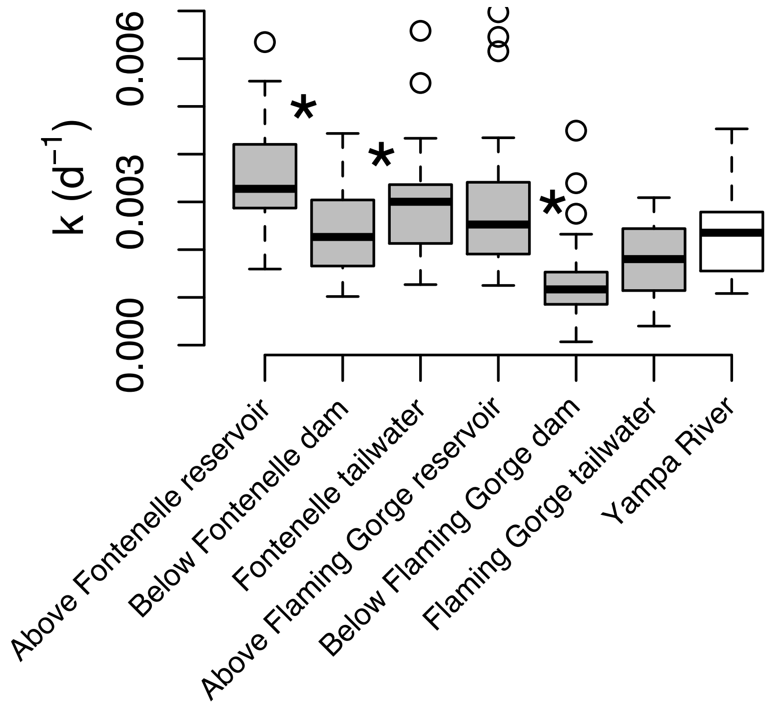

Figure 4. Dissolved organic carbon (DOC) bioavailability across all sampling sites as measured by the DOC decay rate per day (k, d^{-1}). The black line represents the median value of k (d^{-1}), the boxes are the upper and lower 25th and 75th percentile, the tails are the maximum and minimum values, and any points are outliers, which exceed 3/2 of the maximum or minimum values. The asterisk (*) designates significant differences (paired t test, $p < 0.05$) in bioavailability between sites.

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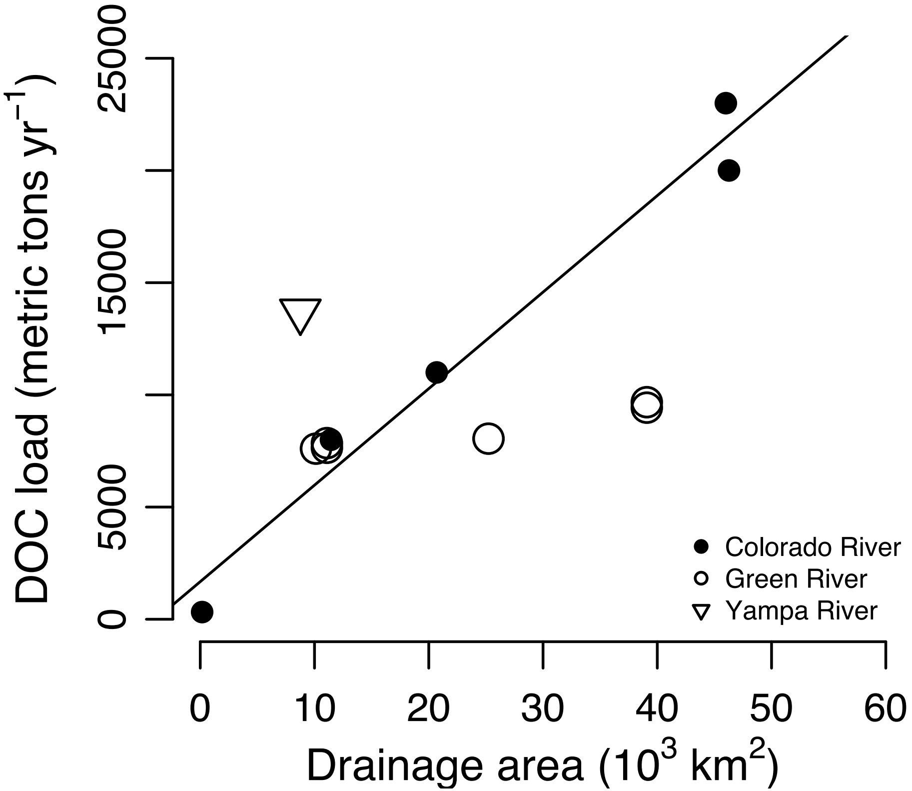

Figure 5. Annual DOC load ($Mg\,yr^{-1}$) plotted against drainage area (km^2) from the Green, Yampa, and upper reaches of the Colorado River ($< 50 \times 10^3\ km^2$, data from Stackpoole et al., 2014; Miller, 2012). Linear regression line was fitted through data from the upper Colorado River where DOC load ($Mg\,yr^{-1}$) $= 1675.7 + 430.1 \times km^2$, $P = 0.0001$, $r^2 = 0.98$)

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