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Interactive comment on "Dam tailwaters compound the effects of reservoirs on the longitudinal transport of organic carbon in an arid river" *by* A. J. Ulseth and R. O. Hall Jr.

A. J. Ulseth and R. O. Hall Jr.

amber.ulseth@gmail.com

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Author comments in response to review:

We thank the two reviewers for their comments that have substantially improved our paper. Below we detail how we have changed the paper in light of the reviewers' comments and we provide the text of those changes as part of our response.

Anonymous Referee #1

Received and published: 6 May 2015

General Comments:

This is a well written manuscript that describes temporal and spatial patterns (above reservoirs, below reservoirs, and in reservoir tailwater reaches) in DOC and POC concentration, flux, composition, and bioavailability in an arid river of the Western US. The approach applied is technically sound and the results are placed in the context of existing literature. I expect that this manuscript will be of interest to scientists studying carbon cycling in large rivers.

Specific Comments:

1. Without first reading the manuscript, it is unclear what is meant by the last sentence of the abstract. While it is important to acknowledge the limitations of the work, I found this sentence to distract from the overall value of the work, and recommend that it be revised or removed from the abstract.

We deleted this particular sentence and replaced it with ‘Therefore, the effect of impounding rivers on C fluxes is greater than the impact of the reservoirs alone given the additive effect of tailwater reaches below dams, which may produce and export comparable amounts of likely autochthonous carbon to downstream reaches.’

2. Pg. 6087, line 6-8: In addition to stating that higher SR values indicate lower molecular weight DOC, I recommend stating that lower SUVA values indicate less aromatic DOC.

We changed the sentence to ‘By using SUVA254 and SR we expected higher SUVA254 values and lower SR values for more aromatic, higher molecular weight DOC, and lower SUVA254, higher SR for less aromatic and lower molecular weight DOC.’

3. Section 2.4: Further explanation of the bioassay experiments would be useful. For example, does using a 0.2 um filter remove microbes, whereas the 0.7 um allows microbes to pass through the filter?

To further explain the bioassay experiments, we included information regarding filter pore sizes in relation to microbe removal. Specifically we included this text: ‘We chose

0.7-μm filtered water as inoculum to exclude large particulates, but include bacteria that would likely not pass through the 0.2-μm filters.'

4. Section 2.7: It would be helpful to provide additional data to assess the accuracy of the flux models. For example, were normal probability plots and/or plots of model residuals vs. predicted values examined to assess the assumptions of normality of the distribution and the independence and homscedasticity of the residuals? See Helsel and Hirsch (2002; http://pubs.usgs.gov/twri/twri4a3/html/toc.html) for an excellent discussion of regression model diagnostics.

All of the models used to calculate the annual fluxes (Equation 3) were checked that they met model assumptions, including model diagnostics such as normal distribution of model residuals versus predicted variables. For example, we used the mean measured DOC concentrations for both sampling sites located below Flaming Gorge reservoir because there was not a linear or polynomial model that was appropriate for DOC concentration versus discharge. We included the following text in regards to model selection and fit: 'All linear models met the assumption of linear regression and given post-analyses diagnostics (Dalgaard 2008), the models were appropriate given the data.' Furthermore, we appreciate the reviewer's suggested publication by Helesl and Hirsch for further explanation of linear model diagnostics. We chose to site Dalgaard 2008 as we have the source for other statistical aspects presented in this manuscript.

5. Too much emphasis is sometimes placed on small differences in the amount or composition of OC, without incorporating uncertainty in model estimated values. For example, the changes in annual DOC loads of 200-244 Mg/yr from below the dams though the tailwater reaches are small relative to the total DOC loads. While there may be statistically significant differences, it is unclear if they are within the error associated with the regression models. Therefore, it would be helpful to report confidence intervals associated with the model-derived load estimates.

We agree and have calculated confidence intervals of the annual fluxes based on the error associated with the regression models for predicting daily OC concentrations from daily Q. Indeed, for some sites, the potential variability of our annual estimates is quite high, often higher for POC than DOC. This finding is not surprising given our relatively low number of samples (8 per site for the 2011) and the difficulty that can come with predicting OC concentrations from Q. We updated the methods, such that we now include a description of how we calculated the 95% confidence intervals for the annual load estimates. The text we included within the methods is as follows 'Furthermore, we estimated the potential variation of these annual loads for 2011. We used the 95% confidence interval of the predicted [OC]d from Eq. 3 to re-parameterize the equation in order to predict the 95% confidence interval for daily DOC and POC concentrations for each site. These predicted lower and upper bound [OC]d were then summed as described above to estimate the 2011 annual loads for both DOC and POC for each site. As for the sampling site below Flaming Gorge dam and its respective tailwater site, we used the lower and upper bound of the 95% confidence interval of the measured mean DOC concentration, as there was no linear relationship with DOC concentration and Q at these sites.'

We also updated the results, including Table 3. Because we updated the results where needed within the manuscript as opposed to adding a new paragraph or section here we summarize the results in light of the annual load estimates: The largest variability in the annual load estimates for both DOC and POC was the Yampa River sampling site and above and below Fontenelle dam. The 95% confidence intervals for the POC annual load estimates overlapped above, below and with the Fontenelle tailwater. As the changes in DOC concentration were not as pronounced as the longitudinal changes in POC, it was not a surprising finding that the 95% confidence intervals for the DOC annual fluxes overlapped above and below both reservoirs and their corresponding tailwater sampling sites.

Furthermore, given the high variability of our load estimates, we toned down the em-

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phasis on the differences in annual loads to reflect these results. We added the following text: ‘Recognizing the high variability of our annual load estimates, we compared the potential POC load to potential primary production within the reach.’. . . ‘Similar to POC annual loads, we recognize the high variability of the DOC annual loads, but also compared the potential daily flux of DOC to plausible primary production fluxes..’ We also included a the statement near the end of the discussion: . . .‘However, accurately quantifying annual fluxes of OC can be difficult, as illustrated by the potential variability of our annual load estimates (Table 3).’

Technical Corrections: 1. The first sentence of the abstract is not clear. A suggested revision is: “”. . .., but less is known about how river reaches directly below dams contribute to OC processing.”

We clarified the sentence by changing it to ‘Reservoirs on rivers can disrupt organic carbon (OC) transport and transformation, but less is known how river reaches directly below dams contribute to OC processing.’

2. Section 3.2: I recommend either switching figures 3 and 4 or the order in which the results presented in these figures are discussed. Currently, figure 4 is referenced in the text prior to referencing of figure 3.

The SR and SUVA plot is now Fig. 4 and the bioavailability plot is now Fig. 3.

3. Pg. 6091, line 28: change “was” to “were”

We changed ‘was’ to ‘were’.

4. Section 4.2: Given that both longitudinal patterns in DOC and POC are discussed, I recommend changing this heading title to “Longitudinal OC dynamics”.

We changed the heading as suggested by the reviewer to ‘Longitudinal OC dynamics’.

5. Pg. 6095, line 12: Change to: “All SUVA254 values were <. . .. . .”

We included ‘values were’ after All SUVA254, so the beginning of the sentence is now

‘All SUVA254 values were < 3 L mg C-1 m-1,. . .’

Anonymous Referee #2

Received and published: 25 May 2015

Review of Dam tailwaters compound the effects of reservoirs on the longitudinal transport of organic carbon in an arid river By Ulseth and Hall

This manuscript describes a study regarding carbon dynamics along a dam-impacted river with a focus on ascertaining the impact of dam tailwaters. The methods of the study are sound and the sampling scheme was well designed – temporally and spatially. The results are interesting as they clearly show the reduction in quantity and quality of organic carbon immediately downstream of the reservoirs compared to what entered them. The tailwaters were then locations set a few more kilometers downstream of the reservoir and in these locations there tended to be new carbon added to the systems, which the authors describe as an additive impact of the reservoir system on carbon dynamics. I believe that this point needs to be addressed more clearly (as described below) before the paper is ready for publication; however, I feel the data is of interest to the community and that upon minor revisions that this paper should be fully published.

General comments: A main discussion point that was not discussed but I believe should be in the paper is why the authors believe that the tailwater locations and their impact on carbon should be an additive effect of the impact of reservoirs without knowing what pre-dam conditions were like. It seems that the reservoirs do impact the flow of carbon, but further downstream the river begins to reset itself by adding more carbon. How do you know that this carbon would not have been added in this location had the reservoir not been upstream? I think this is a major issue with the interpretation of the data that needs to be addressed prior to publication.

Rivers below dams can ‘reset’ to above reservoir conditions, which is often attributed to tributary input of carbon (i.e. Serial Discontinuity Concept, Ward and Stanford 1983). However, this recovery distance can vary from hundreds of meters to hundreds of kilometers depending on dam type, river size, and number of tributaries downstream (Ward and Stanford 1983). For this particular study, we focused on tailwater reaches found directly downstream of dams. The distinction we attempted to make here was that input of carbon is likely from in-stream production due to increased primary production within these tailwater reaches, as opposed to input from tributaries. Tailwater reaches below dams often are more productive in regards to primary production compared to reaches upstream or reaches pre-dam in these arid rivers. For instance, Hall et al. (in revision) found gross primary production could be as high as 8.1 g C m-2 d-1 in the tailwaters of Fontenelle dam. These altered river reaches are more productive because dams alter the flow regime of tailwaters resulting in stable benthic substrate (Schmidt and Wilcock 2008), reduce sediment load and therefore increase light availability, and often have increase inorganic nutrients (Ward and Stanford 1983, Davis et al. 2011, Hall et al., in revision). Also, we selected tailwater reaches where there were no tributaries, therefore any increase or change in the carbon dynamics within these reaches we hypothesized to be attributed to in-stream carbon production.

We made this point clearer within the introduction that these tailwater reaches are different not only from upstream of the reservoir reaches, but also that these reaches are different than pre-dam reaches as well. The key difference we focused on within the introduction is the increased primary production because of the effects of damming the river. This increased primary production in the tailwater is essentially a shift in potential C source, which may affect OC composition and ultimately bioavailability. Specifically, we edited and added to the text so it now is: “Tailwater reaches can be found directly downstream of all dams (Ward and Stanford 1983); yet, coupled reservoir and tailwater OC fluxes are unclear within the context of riverine OC budgets. Within the scope of this research, we define tailwater reaches as the stream reach directly downstream of dams, which have no tributary input. These tailwater ecosystems physically and biologically differ from their upstream or pre-dam counterparts (Ward and Stanford

1983), which may affect DOC and POC dynamics. . . .” Specific comments:

1. P6082, L4-5- Something sounds strange here with the ‘processing than reservoirs alone’ – I guess you are trying to make the distinction between the effect of only reservoirs and tailwaters plus reservoirs but words are missing some- where.

We clarified the sentence by changing it to ‘Reservoirs on rivers can disrupt organic carbon (OC) transport and transformation, but less is known how river reaches directly below dams contribute to OC processing.’

2. P6082, L20 – I don’t think there is enough detail in the abstract for the reader to know how important ‘THE simultaneous transformation and production of OC’ is and how ‘upstream and downstream of reservoirs and their tailwaters do NOT represent’ this. I would reformulate this last sentence or divided into two to give more detail and make your point more clearly.

We deleted this particular sentence and replaced it with ‘Therefore, the effect of impounding rivers on C fluxes is greater than the impact of the reservoirs alone given the additive effect of tailwater reaches below dams, which may produce and export comparable amounts of likely autochthonous carbon to downstream reaches.’

3. P6083, L14 – ‘Reservoirs may increase, decrease, or not alter Doc concentrations. . .’ – I believe you should give a leading sentence prior to this stating how different studies have produced varying results when it comes to the impact reservoir may have on DOC concentrations. You actually go into detail of the refs in the following sentences so you could just replace that sentence with the more generalized one I suggested.

We changed sentence to ‘In regards to DOC concentration, various studies have found that 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).’ This revision incorporates the reviewer’s comments, but keeps the specific point of the sentence of the varying effect of reservoirs on DOC concentrations.

4. P6083, L25-26 – So you think that these other studies took a more large-scale approach, while yours is smaller scale? I don't see enough information from the description of those studies to tell that really. It seems that the Ontario did look at upstream and downstream of reservoirs. And you state that these studies don't capture OC dynamics in the river reaches below dams but then in the next paragraph you start discussing what is known about carbon dynamics in tailwaters.

We deleted 'basin wide, large-scale' from the sentence. While the studies mentioned in this paragraph studied longitudinal OC in relation to dams (i.e. Stackpoole et al. 2014, Miller 2012) and directly related to upstream and downstream of reservoirs for DOC composition (i.e. Nadon et al. 2014) – none of these studies specifically looked at the effect of the dam tailwaters.

Also, as we re-wrote parts of the introduction to address DOC bioavailability, we discuss the results from Nadon et al. 2014 in another section of the introduction.

We want to distinguish between reservoir effects on OC and tailwater effects. Therefore, the following paragraph describes how tailwater ecosystems are physically and biologically different than upstream of reservoirs or non-impounded river reaches. These processes may alter OC –cycling or parts of OC-cycling - but we do not know the effect of tailwaters in the context of riverine C budgets. We re-wrote and re-arranged the paragraph to better convey what was known and what was unknown about OC cycling in relation to tailwaters. 5. P6084, L2 – 'confer' doesn't seem needed here

We replaced the word 'confer' with 'result in' for clarification.

6. P6084, L14-15 – You may want to reformulate the introduction slightly so you start with this sentence so the reader knows where you are going with this study. It seems there has been quite a bit of work done on the subject, but perhaps only in pieces. You should really define what is unique about your study and describe that and then build

up to it with the rest of the introduction.

We made changes to the introduction to better emphasize what is unique about our study. In particular, we emphasized DOC bioavailability in conjunction with flux estimates above and below not only dams, but tailwater reaches as well, where basin-wide studies have not specifically looked at these unique stream reaches in the context of riverine OC-cycling. Key text that we added is as follows:

1. To highlight DOC bioavailability “This autochthonous DOC can be more bioavailable than terrestrial sources (del Giorgio and Davis 2003); therefore increasing autochthonous production within these ecosystems potentially increases the bioavailability of DOC, although there is little understanding of the bioavailability of DOC exported downstream of reservoirs. Compositional changes of DOC may or may not occur as well. For instance, 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). Therefore coupling DOC bioavailability and composition is needed to understand the transformative processes reservoirs can have on DOC and ultimately riverine C-cycling. . .

. . .These studies have given insight into longitudinal OC fluxes in light of flow regulation by dams, but an understanding of fluxes in combination with bioavailability and composition of DOC is less understood. Furthermore, these studies have not captured OC dynamics in the tailwaters of dams, which are the river reaches located directly downstream of all dams.”

2. To highlight tailwater ecosystems in the context riverine OC budgets, we moved the last sentence to the beginning of the paragraph as suggested by the reviewer where it now is:

‘Tailwater reaches can be found directly downstream of all dams (Ward and Stanford 1983); yet, coupled reservoir and tailwater OC fluxes are unclear within the context of riverine OC budgets. Within the scope of this research, we define tailwater reaches as the stream reach directly downstream of dams, which have no tributary input. These tailwater ecosystems physically and biologically differ from their upstream or pre-dam counterparts (Ward and Stanford 1983), which may affect DOC and POC dynamics. . .'

7. Introduction – You didn't really discuss bioavailability or auto- vs allochthonous carbon and the importance of such things in your introduction. This would help direct the reader as well. You are not only describing quantity of the carbon but also the quality.

We added text within the introduction to discuss autochthonous vs allochthonous DOC and the implications of the sources to overall DOC bioavailability. The text we included within the introduction is as follows: 'This autochthonous DOC can be more bioavailable than terrestrial sources (del Giorgio and Davis 2003); therefore increasing autochthonous production within these ecosystems potentially increases the bioavailability of DOC, although there is little understanding of the bioavailability of DOC exported downstream of reservoirs.

8. P6085, L14-21 – Use the labels A-G from Figure 1 in your text when describing sampling sites

We added the corresponding letters from Fig. 1 within the text site description.

9. Figures 2, 3 and 4 – also label the panels (Fig. 2, 3) and boxplots (Fig. 4) and Tables 1-3 with A-G accordingly (keep the long name too but adding the letters help a bit more)

We added the letters A-G, which correspond to the letter on the map, and kept the full names of each site for Fig. 2, 3, & 4 and Tables 1-3. We also included the text 'Letters A-G prior to the site names correspond to sites A-G in Fig. 1' to the appropriate figure and table legends.

10. Figure 3 and 4 should be switched – you discuss Figure 4 (bioavailability) before Figure 3 (Sr and SUVA)

The SR and SUVA plot is now Fig. 4 and the bioavailability plot is now Fig. 3.

11. P6092, L24 – ‘by magnifying the transformation of both POC and DOC, as will be discussed further.’ âĂŤ you need to either give the reasons for this now or say that you will discuss it now. This left the reader hanging.

As suggested by the reviewer, we included ‘We will discuss how. . .’ to the last sentence of the first paragraph of the discussion.

12. P6093, L11 – add ‘however’ in the sentence to contrast with previous finding

We included ‘In comparison’ at the beginning of the sentence to contrast with the finding below Fontenelle dam with the finding from above the reservoir.

13. P6093, L11-12 – maybe expand a bit your explanation here

We expanded the discussion point on timing of peak concentration and peak discharge below the reservoirs to include the following sentence: ‘In comparison, a similar finding of peak OC concentration with peak discharge was found below natural Alpine lakes in Idaho, USA, which was attributed to residence time of the lake (Goodman et al. 2011).’

14. P6094, L2 – do you know anything about production in the system?

At this time we do not have an estimate of in-stream primary production for the Yampa River and Green River above Fontenelle reservoir. However Hall et al. (in revision), have estimated that gross primary production in Fontenelle tailwater can be as high as 8.1 g C m-2 d-1, which we discuss in section 4.3.

15. P6094, L5 and L19 – Based on the last sentence of this paragraph, I believe you don’t mean ‘type’ of reservoir but rather ‘reservoir scheme’ – you state in the parentheses ‘many small vs few large’. . . and along those same lines, in the methods section you state that the Colorado River has 7 large dams and then here you may this distinction between many small and few large reservoir schemes. I am confused now. Please clarify somehow here and in the methods.

For clarification when describing the Colorado River basin, we removed '7 large impoundments' from the Study Site description. We further clarified by using 'reservoir size' and 'reservoir scheme' instead of 'reservoir type' to describe many small versus few large reservoirs within the first paragraph of the discussion under section 4.2.

16. P6094, L20 – delete 'and not just total water storage capacity of the basin'

We deleted 'and not just total water storage capacity of the basin' as suggested by the reviewer.

17. P6094, L22-23 – change the order of the sentence to start not with the negative: 'Residence time likely drove, at least in part, the longitudinal DOC concentration and flux patters we observed in relation to the reservoirs, although we do not have the appropriate data to adequately budget OC for either of the reservoirs.'

We rearranged the sentence it now reads: 'Residence time likely drove, at least in part, the longitudinal DOC concentration and flux patterns we observed in relation to the reservoirs, although we do not have the appropriate data to adequately budget OC for either of the reservoirs.'

18. P6095, L1-3 – where were these lakes and reservoirs? Be a bit more explicit with these examples.

Within this particular discussion section we use examples from the literature from natural Alpine lakes and several reservoirs to explain how residence time can shift DOC dynamics. We clarified and made the types of ecosystems clearer, including more site specific information. This section is now written as '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). Although not man-made reservoirs, residence time explained a similar shift in DOC concentration and timing of peak discharge above and below natural Alpine lakes in snowmelt-dominated catchments in Idaho, USA (Goodman et al.

2011). The timing of reservoir filling and dam operations resulted in an arid reservoir in Arizona, USA (Westerhoff and Anning 2000) and two temperate reservoirs located in Ohio, USA (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, USA to shift between a DOC source and sink (Kraus et al. 2011).'

19. P6095, L25 – do you mean 'autochthonous' instead of 'microbially produced' DOC?

Given the reduction in bioavailability of the DOC directly downstream of Flaming Gorge dam, along with lower SUVA254 and higher SR values compared to upstream of the reservoir, we conjecture that the DOC is likely transformed terrestrial and perhaps algal DOC along with microbially produced DOC. We shy away from using autochthonous (algal derived) given the low bioavailability, which if it was of algal origin, should be higher. Although technically speaking – microbially produced is also autochthonous. Because we have added information in the introduction on bioavailability and DOC sources, this portion of the discussion should be clearer now within the context of the manuscript.

20. P6096, L14 – delete 'of'

We clarified the sentence and changed 'of above reservoir concentrations' to 'of concentrations measured upstream of the reservoirs'.

21. P6097, L27-28 – how was this 6-14% calculated? Give a little bit more description here. And why are you determining the OC reduction as low? What are you basing that on?

We calculated the net effect of OC transport by Flaming Gorge and Fontenelle dam by simple mass balance of the annual fluxes (Table 3); (OCin – Cout)/OCin × 100.

We consider 6-14% reduction on total OC fluxes due to the two reservoirs to be relatively low when comparing the relatively large amount of POC trapped behind the reservoirs (66-85%) and the DOC transformation changes above and below the reservoirs.

We clarified the method for calculating the mass balance and why we consider 6-14% reduction on total OC fluxes to be low with the following text: ‘The net effect of dams on the reduction of OC (POC + DOC) transport was essentially low (6-14%, (Annual Load$_{in}$ – Annual Load$_{out}$)/Annual Load$_{in}$ × 100, Table 3), in comparison to the changes in POC concentration alone (66 – 85%) and likely POC and DOC composition.’

22. P6098, L1-3 – ‘The effect of impounding rivers on OC fluxes is potentially underestimated. . .’ Do you mean your study results or in general?

The comment could be conveyed to this study, we clarified this statement so the sentence is now: ‘We potentially underestimated the effect of impounding rivers on OC fluxes in the upper basin of the Colorado River because total concentration based fluxes do not represent transformation processes in river-reservoir-tailwater ecosystems.’

23. General – shouldn’t it be ‘impounded rivers’ instead of ‘impounding rivers’?

We used ‘Impounded rivers’ to describe the type of river and ‘impounding rivers’ was used when discussing or describing the action of altering the river by damming. We checked throughout the manuscript to make sure that this usage was consistent.

24. P6098, L7-12 – You say that that the tailwaters increased the export of autochthonous OC downstream and that this was an additive effect to the impact that reservoirs/dams have on carbon cycling in rivers, but how do you know that this additional autochthonous OC wouldn’t have been produced had there been no reservoir? The most obvious affect I see is that the reservoirs almost reset the carbon balance of the mainstream river by reducing flow of OC. Then it was restored in the tailwaters eventually, but that doesn’t mean that had the reservoir not been there that the same

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amount wouldn't have been added in that particular stretch of the river.

We addressed this comment within the general comments from this reviewer and have clarified where needed throughout the manuscript.

25. P6098, L1-16 - For this last paragraph to act more like a conclusion, I would suggest summarizing the specific main points of your study.

We shortened the last paragraph by putting more emphasis on summarizing our results within this study. The last paragraph is now as follows:

'The net effect of dams on the reduction of OC (POC + DOC) transport was essentially low (∼6-14%, (Annual Loadin – Annual Loadout)/Annual Loadin × 100, Table 3) given the high error associated with our flux estimates and in comparison to the changes in POC annual load alone (66 – 85%) and likely POC and DOC composition. This finding affects how impoundments are viewed from an OC cycling perspective. We potentially underestimated the effect of impounding rivers on OC fluxes in the upper basin of the Colorado River because total concentration based fluxes do not represent transformation processes in river-reservoir-tailwater ecosystems. The Fontenelle and Flaming Gorge tailwater ecosystems contributed to the effect of reservoirs on OC transport in the Green River by increasing the export of likely autochthonous OC downriver. Therefore, the reservoirs regulated OC transport by reducing POC and altering the composition and bioavailability of DOC. We suggest that 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. However, accurately quantifying annual fluxes of OC can be difficult, as illustrated by the potential variability of our annual load estimates (Table 3). 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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