

NORTHWEST ENVIRONMENTAL ADVOCATES



December 20, 2022

Ben Rau
Washington State Department of Ecology
Water Quality Program, Watershed Planning Unit
P.O. Box 47600
Olympia, WA 98503

submitted via: <https://wq.ecology.commentinput.com/?id=Cipsj>

Re: Washington's Water Quality Management Plan to Control Nonpoint Sources of Pollution Draft for Public Review, Including Voluntary Clean Water Guidance for Agriculture Chapter 12 Riparian Areas & Surface Water Protection

Dear Ben:

This letter constitutes the comments of Northwest Environmental Advocates on the Washington Department of Ecology's 2022 319 Plan that includes four chapters of its agricultural best management practices ("BMPs").

Washington's Water Quality Management Plan to Control Nonpoint Sources of Pollution Draft for Public Review

Lack of comments on portions of the plan does not imply that NWEA agrees with the statements therein or the completeness of this document. We incorporate by reference the following two documents: (1) Letter from Nina Bell, NWEA, to Joelle Gore, National Oceanic and Atmospheric Administration ("NOAA"), Re: *Coastal Nonpoint Pollution Control Program: Intent to Find that Washington has Satisfied All Conditions of Approval Placed on its Coastal Nonpoint Pollution Control Program* (Sept. 14, 2020); (2) Letter from Nina Bell, NWEA, to Ben Rau, Ecology, Re: *Draft Washington's Water Quality Management Plan to Control Nonpoint Sources of Pollution* (June 5, 2015). These are documents that Ecology has in its possession and are therefore not attached. These previous comments continue to apply to Washington's nonpoint source program because, as the slight amount of editing of the 2022 219 Plan demonstrates, not much has changed.

Plan at 7-8: The draft Plan does not state that in describing how Ecology updated its Plan, Ecology included (or in some cases did not) the binding commitments made by Ecology in

Northwest Environmental Advocates v. U.S. Department of Commerce, Case No. C16-1866-JCC (Stipulated Order of Dismissal) (Jan. 8, 2021). For example, the red-lined addition on page 41 comes from this document.

Page 8: Lack of riparian protection is a source that contributes to nutrient pollution and dissolved oxygen depletion that should be included in Table 1.

Page 9: Table 2 is missing that mercury from atmospheric deposition enters waterways from agriculture and logging. *See, e.g.*, EPA/Oregon Department of Environmental Quality’s Willamette River basin Total Maximum Daily Load (“TMDL”) for mercury (demonstrating that these nonpoint sources are the majority source of mercury loadings to the Willamette).

Page 13b: Ecology states that “[t]he goal for this chapter is to develop guidelines for riparian management zones that, when implemented, will help restore and protect Washington State waters from agricultural pollution and facilitate the achievement of water quality standards.” However, the commitment by Ecology in *NWEA v. Commerce* for riparian area BMPs specifically is “to meet water quality standards to the extent possible.” “Facilitating the achievement” and designing practices to meet water quality standards is not the same thing. Not only does Ecology need to change its “goal” for the riparian chapter, it needs to conform its goal to its binding commitments.

Page 16: We appreciate Ecology’s addition of the *Lemire* case. Ecology should also include information on the number of enforcement actions it has taken since its last plan, evaluate and explain the reasons why it has and has not used enforcement as a tool to address nonpoint sources, and explain how it plans on using enforcement action in the years covered by the Plan. For example, enforcement is a key component of the Straight-to-Implementation (“STI”) alternative to TMDLs. If Ecology does not use enforcement, what effect will it have on the efficacy of the STI approach?

Page 16: Ecology states that it has enforcement authority with regard to logging. Has it ever used this authority?

Pages 17–18: Please inform the readers of how well the regulation of the dairy program has been working.

Pages 18–19: Please inform the readers of how well the on-site septic program has worked with regard to upgrading septic systems to control nitrogen pollution in Puget Sound. Does Ecology agree or disagree with NWEA’s assessment of this program set out in pages 67–73 of the above-referenced NWEA comments on the EPA/NOAA proposed CZARA approval, in particular its discussion of the Marine Recovery Areas?

Page 26: Please amend the list of items that the Clean Water Act supports with regard to nonpoint sources to include the requirements set out in the statute and discussed in the following pages, including not just “plans and programs” but also the identification of best management practices.

Page 31: Add in the recent history of Washington's CZARA approval, namely that EPA and NOAA held a public comment period on the proposed approval and the date of that proposal.

Pages 33–34: Ecology should include here under the Federal Farm Bill Programs (or elsewhere in the Plan) an explanation of how those programs do and do not meet the minimum BMPs that Ecology and its staff believe are necessary to meet water quality standards. Does Ecology believe that these conservation practices promoted by the federal agencies and their programs fully meet the need to control nonpoint source pollution to Washington waters?

Page 41: It is incorrect for Ecology to assert that “our TMDL approach . . . [d]esignates suites of BMPs for various land-use categories.” It may in the future but it has not done so to date.

Page 43: It is not enough for Ecology to state that “[i]f implementation [or TMDLs] stalls, for instance because of recalcitrant landowners, Ecology will utilize enforcement tools as necessary and appropriate.” The Plan should evaluate whether this statement is an accurate reflection of the way in which Ecology has conducted its nonpoint program in the recent past and explain how it will be the same or different in the future.

Page 44: The description of the STI process omits commitments made in the *NWEA v. Commerce* case, namely how it will conduct “watershed evaluations,” which is a term used to describe the STI process, in item nos. 2.a.i (“Washington shall . . . use the BMPs for . . . TMDL alternatives, including but not limited to Straight To Implementation projects, with nonpoint components” and 2.d.i–iv (“When pollution sources are identified and property operators are contacted, Washington shall discuss and recommend BMPs consistent with the agricultural BMP guidance”; “Washington shall track what BMPs are implemented at those sites”; “Washington shall provide training to its field staff on how to use the BMP guidance”; and “Washington shall develop outreach materials for each set of BMPs that can be used by field staff to assist in Washington’s communication and recommendation of BMPs.”). Note that on page 46 in the discussion of TMDL alternatives, Ecology has added the following language: “Ecology will discuss and recommend BMPs consistent with the Voluntary Clean Water Guidance for Agriculture when addressing agriculture sources.” This captures some but not all of the commitments that Ecology has made for TMDL alternatives.

Page 45: Ecology’s reference to the East Fork Lewis River Alternative Restoration Project is not consistent with its description of “Other Water Clean-up Projects in Advance of a TMDL.” Specifically, at 196 pages long, it hardly meets the description of such projects: “To reach that goal, like STIs, the focus is on doing, not planning.”

Page 46: See comments for page 44.

Page 49: Why is there only a reference to integrating with TMDLs instead of also STIs and other TMDL alternatives?

Pages 49–51: The description of the new tracking system is impressive. The Plan needs to describe how the tracking system will improve Washington’s poor record of achieving nonpoint

source controls. Tracking on its own does not help the designated uses of human health protection and aquatic life.

Page 54: Ecology correctly reflects its commitment to “use the Voluntary Clean Water Guidance when developing education and outreach materials related to agricultural sources” but it fails to state if and when it will “develop outreach materials for each set of BMPs that can be used by field staff to assist in Washington’s communication and recommendation of BMPs,” as it committed to do in *NWEA v. Commerce* item 2.3.iv.

Page 56: Noting typos: “The water quality program made changes to our nonpoint **fuunding** based on feedback”; “ There are no longer match **requirements** for our nonpoint source funding.”

Pages 55–56: The one thing that is most important to remedy environmental injustice is to actually implement nonpoint source controls to improve water quality, support healthy populations of fish and shellfish, and support the quality of fish and shellfish consumed by people. There is nothing in this section that makes that commitment. That suggests that Ecology believes the status quo is sufficient to address environmental injustice (as well as climate change, threatened and endangered species, and tribal treaty rights).

Pages 62–71, 110: Ecology needs to include the existing logging practices in this 319 Plan Update so that the plan meets statutory requirements and so that the practices are reviewed by EPA when it evaluates this Plan.

Pages 72–74, 111: Have there been any instances where Ecology has seen that since the Washington Department of Agriculture took over the regulation/oversight of Washington’s Dairy Nutrient Management program, water quality has deteriorated?

Pages 74–77, 111: Is Ecology aware of any instances when Marine Recovery Area (MRA) plans have been prepared if a local health jurisdiction identifies any areas where nitrogen has been identified as a contaminant of concern. *See* WAC 246-272A-0015 (1)(b)(ix). Why is this not discussed in the Plan?

Page 78: We understand that Ecology has not devoted sufficient time to updating this plan but it is peculiar in the extreme to assert three relevant 2016 goals and then to have made no determination of whether those goals were met.

Page 81: It is sad that Ecology can say nothing more about nitrogen reductions from nonpoint sources that will be needed to meet water quality standards in Puget Sound. You might at least note the very significant percentage of anthropogenic nitrogen that Ecology believes will be necessary to reduce from nonpoint sources.

Pages 84–85, 86–87, 88–90, 97–98: Sections on recovering wild fish, climate change, environmental justice, and Washington’s tribes could be improved by a more clear focus on the most important nonpoint source control action that can be taken: protecting and restoring riparian

areas. Ecology could reference its obligation to, for the agricultural BMPs, “establish necessary widths, and base riparian buffer plant composition guidance on mature vegetation communities composed of native species and consistent with ecological site potential, to meet water quality standards to the extent possible[.]” *See NWEA v. Commerce* item no. 2.1.iv. It should also describe how it will vastly increase its efforts to ensure that riparian areas are protected and replanted with sufficient vegetation to meet water quality standards. Business as usual is not adequate.

Pages 153–167: Because Ecology does not discuss the Clean Water Act section 319(h) annual work plans and annual reports in its Plan, it has not included the commitments made in *NWEA v. Commerce*, item nos. 2.e, f that pertain to these respectively. Please amend the Plan accordingly. As it stands, the only reference to these requirements is on page 166 (“Annual Section 319 project reports document accomplishments in aligning programs.”). This is not adequate.

Page 221: Please include an “Appendix I” with the current logging practices in order to meet the statutory requirements for a 319 plan.

Voluntary Clean Water Guidance for Agriculture Chapter 12 Riparian Areas & Surface Water Protection

These comments do not constitute a complete review of the document as due to its length and the timeframe for public comment, we were unable to conduct a full review.

Page 14c: In this chapter, Ecology establishes riparian buffer minimum requirements based on “riparian forest potential,” yet fails to include a definition of that phrase in the definition section. For example, at page 18b, Ecology states: “These default RMZ widths do not apply to streams without riparian forest potential; RMZ widths for these streams are primarily based on water quality protection.” In several places, such as page 24b, Ecology discusses what this means due to adjacent wetlands, but it is otherwise silent on how to address the issue. *See, e.g.*, page 36b. Instead, it uses the phrase “other streams without riparian forest potential (eastern WA).” *Id.* (emphasis added). Elsewhere, it refers to Eastern Washington waters “without riparian forest potential due to climate conditions.” *Id.* at 35b (emphasis added). On page 42b, the guidance states: “These default RMZ widths do not apply to streams without riparian forest potential; RMZ widths for these streams are primarily based on water quality protection and are presented later in the document (see pages 83-91).” Pages 83–91 include a summary of buffer size and its relationship to phosphorus removal/trapping and a portion of sediment in runoff. These pages do not cast any clarity on what the RMZ widths should be for streams that Ecology deems to be “without riparian forest potential,” a term that is never defined. (A word search does not identify alternative pages.) Tables 11–13, all of which pertain to eastern Washington streams “without forest potential due to climate conditions” include footnote 1, which reads: “See guidelines that precede tables for determining: when to include a filter strip and how to determine its width; when and how to modify zone widths; what vegetation should consist of in a given zone; and what activities should or should not occur in any given zone.” This footnote does not clarify when a stream fits into this approach and frankly refers to information that isn’t readily identified. It would be helpful in this regard for the guidance to be specific as to which

“guidelines that precede tables” Ecology refers. For example, does it mean the material on pages Pages 22b–24b: The guidance states: “A site potential (SP) plant community is composed of native vegetation species and has a plant density that would occur in a minimally managed condition on a site, e.g. a Douglas fir forest community, Black cottonwood forest community, Sandbar willow community, etc.” This requirement for use of native species is repeated elsewhere, e.g., page 23b: “Use current Level IV EPA ecoregions, NRCS Land Resource Area designations, and/or other resources to help determine appropriate native plant communities.” On page 24b, Ecology states:

It is not feasible to provide detailed species mixtures and plant density recommendations for all of the potential native riparian vegetation communities throughout the state. Suggestions on resources to consult for determining the appropriate native species mixtures and plant densities for a given site are provided in Ecology’s RMZ Implementation guidance.

This is plainly inconsistent with the commitments made by Ecology in *NWEA v. Commerce*, item no. 2.a.iv (emphasis added):

For the BMPs involving riparian areas, Washington shall establish necessary widths, and base riparian buffer plant composition guidance on mature vegetation communities composed of native species and consistent with ecological site potential, to meet water quality standards to the extent possible[.]

In addition, Ecology makes no effort to evaluate whether its recommended use of the “NRCS ecological site descriptions and/or an equivalent assessment of the potential natural vegetation community,” *see* draft Guidance at 15b, is sufficient to meet the goal of the BMPs. It merely assumes that they are sufficient, making a mockery of the science-based evaluation the agency has purportedly completed.

Pages 29b–31b: In a section titled “Western WA- Additional Buffer Configuration and Modification Recommendations” it is absolutely unclear what applies where Ecology, a landowner, or another agency determines that a stream lacks riparian forest potential.

Page 99b: The guidance states that “[t]he core zone of the RMZ should be vegetated with a native plant community consistent with the ecological site potential, as discussed later in this guidance.” *Id.* (emphasis added). But there is no discussion about “ecological site potential” later in the guidance other than page 126b that identifies site potential tree heights and suggests that where there are “no data” the area is “unsuitable for trees.” If the reference to what comes “later in the guidance” is to the entire guidance, that’s simply another way of Ecology’s saying nothing about what “ecological site potential” means.

Page 126b: Ecology defers to NRCS yet again in its description of “ecological site conditions are unsuitable for trees (e.g., arid sub-regions of the Columbia Plateau), or where current and expected future land use was judged by NRCS to never allow trees to become established (e.g., intensive agriculture).” There is no clarity as to whether Ecology is actually adopting the NRCS

conclusion about intensive agriculture (and other views) and no explanation by Ecology of why such streams would be excluded from meeting water quality standards.

However, to return to the central issue, which is what defines a stream “without riparian forest potential,” we want to make the following points. First, Ecology in its guidance and in some of its advisory committee meetings (where it referred to “natural riparian areas”), appears to take the position that in much of Eastern Washington there is no “riparian forest potential.” For example, in the guidance, Ecology states that “for western Washington in particular, the majority of agricultural lands adjacent to buffers were historically forested.” *Id.* at 111b. Second, Ecology is mistaken in this assumption and hinting that such potential does not exist and therefore drastically different guidelines apply—*compare* zones in “preferred option” and tables at 32b–34b with those on 35b–36b—because Ecology ignores the historic role played by beavers in retaining water in streams and creating the very conditions required for riparian forest potential.

Beavers, however, are not mentioned with regard to determining whether streams in Eastern Washington (or anywhere in the state) have “riparian forest potential.” A key issue is beaver occupancy, which was historically widespread. Beavers are the only efficient, cost-effective, and proven method of improving stream flow, hydrology, and habitat conditions in the highly damaged agricultural areas of Eastern Washington to support riparian forests in areas that have “climate conditions,” another phrase not defined by Ecology. But rather than look at the historic riparian forests that protected water quality and the key role beavers played in supporting those forests, Ecology uses the concept of “climate condition” as a get-out-of-jail card.

Instead, the whole of the guidance mentions beavers exactly once, at page 102b (“beaver ponds can have reach-scale effects upon stream temperatures, e.g. by influencing shading, water surface area, water velocity, etc.”) as compared to the literature review that includes, for example, a summary of Kozlowski *et al.*, Guidance at 235b, who are described as noting an “improvement in hydrology resulting from increased beaver dam occurrence.” Thereafter, the only references to beavers in the literature review are how they can cause damage to unprotected restoration seedlings. It’s as if Ecology intentionally put on blinders to an entire area of study in the field of restoration ecology.

Ecology needs to better understand that it incorrectly implies that eastern Washington has no riparian forest potential. We suggest that, to start, Ecology read the following, which we will not summarize here: (1) NMFS, *Oregon Beavers Engineer Better Fish Habitat, More Fish* (July 14, 2016) available at <https://www.fisheries.noaa.gov/feature-story/oregon-beavers-engineer-better-fish-habitat-more-fish>; (2) USDA, Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, *Using Beaver Dam Analogues for Fish and Wildlife Recovery on Public and Private Rangelands in Eastern Oregon* (July 2019); (3) Christian Dewey, *et al.*, *Beaver dams overshadow climate extremes in controlling riparian hydrology and water quality*, *Nature Communications* (2022) 13:6509; T.J. Beechie *et al.*, *Channel incision, evolution and potential recovery in the Walla Walla and Tucannon River basins, northwestern USA*, 33 *Earth Surf. Process. Landforms* 784-800 (2008); (5) Jeff Baldwin, *Institutional Obstacles to Beaver Recolonization and Potential Climate Change Adaptation in Oregon*, 79 *Yearbook of the Association of Pacific Coast Geographers* 93-114 (2017); (6) Rita K. McCreesh, *et al.*,

Reintroduced Beavers Rapidly Influence the Storage and Biogeochemistry of Sediments in Headwater Streams (Methow River, Washington) 93 Northwest Science 112-121 (2019); and (7) Nicholaas Bouwes, *et al.*, *Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (Oncorhynchus mykiss)*, Scientific Reports, 6:28581, DOI: 10.1038/srep28581 (2016). There is a great deal more literature on the historic role beavers played in maintaining riparian forests and how they can restore the streams that agricultural uses have destroyed.

Moreover, we urge Ecology to read these documents and then follow the science by including as agricultural BMPs the actions by landowners that will return beaver occupancy to streams, namely preventing: mechanical destruction of bank dens and tunnels by grazing cattle; destruction of banks' sedimentation and root structure needed for bank dens and refuge holes; stream dewatering below 2.5 feet; trapping or killing of established beavers, pregnant beavers, adult beavers caring for young under two years of age; and high velocity stream flows that blow out beaver dams—i.e., requiring the installation of beaver dam analogues (“BDAs”) for mitigation. The omission of beaver-related actions by landowners is a huge oversight by Ecology in its agricultural BMP guidance. This omission also renders the guidance inconsistent with the commitments made by Ecology in *NWEA v. Commerce*, item 2.a.iv (emphasis added):

For the BMPs involving riparian areas, Washington shall establish necessary widths, and base riparian buffer plant composition guidance on mature vegetation communities composed of native species and consistent with ecological site potential, to meet water quality standards to the extent possible[.]

Determining and achieving “ecological site potential” requires Ecology’s evaluation of and identifying the conditions for restoring beavers on the landscape.

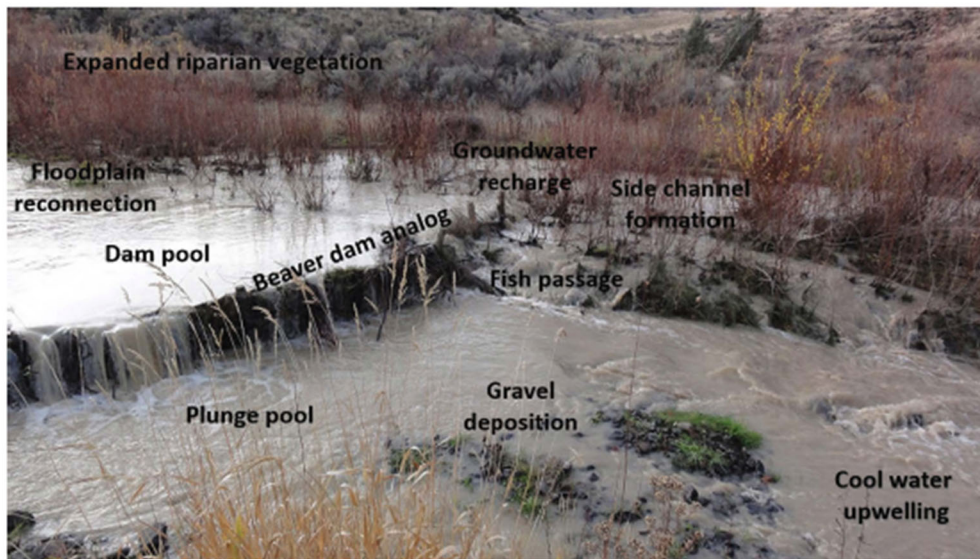


Figure 3. Example of a beaver dam analog (BDA) annotated with some of the expected responses.

(From Bouwes *et al.*)

Voluntary Clean Water Guidance for Agriculture Chapter 10 Livestock Management: Pasture & Rangeland Grazing

The comments on the riparian chapter apply to the pasture and rangeland grazing chapter, particularly with regard to incorporating the historic occupancy of beavers into both the analysis and the recommended BMPs.

Conclusion

As Narcissa Whitman described, prior to the virtual eradication of beavers by the early 1900s:

We descend a very steep hill in coming into Grande Ronde, at the foot of which is a beautiful cluster of pitch and spruce pine trees, but no white pine like that I have been accustomed to see at home. Grande Ronde is indeed a beautiful place. It is a circular plain, surrounded by lofty mountains, and has a beautiful stream coursing through it, skirted with quite large timber. The scenery while passing through it is quite delightful in some places. We nooned upon Grande Ronde river.

*The Letters and Journals of Narcissa
Whitman, August 28th, 1836*

Sincerely,



Nina Bell
Executive Director

Attachments:

NMFS, *Oregon Beavers Engineer Better Fish Habitat, More Fish* (July 14, 2016)
available at <https://www.fisheries.noaa.gov/feature-story/oregon-beavers-engineer-better-fish-habitat-more-fish>

USDA, Forest Service, Pacific Northwest Research Station, Forestry Sciences
Laboratory, *Using Beaver Dam Analogues for Fish and Wildlife Recovery on Public and
Private Rangelands in Eastern Oregon* (July 2019)

Christian Dewey, *et al.*, *Beaver dams overshadow climate extremes in controlling riparian hydrology and water quality*, *Nature Communications* (2022) 13:6509

T.J. Beechie *et al.*, *Channel incision, evolution and potential recovery in the Walla Walla and Tucannon River basins, northwestern USA*, 33 *Earth Surf. Process. Landforms* 784-800 (2008)

Jeff Baldwin, *Institutional Obstacles to Beaver Recolonization and Potential Climate Change Adaptation in Oregon*, 79 *Yearbook of the Association of Pacific Coast Geographers* 93-114 (2017)

Rita K. McCreesh, *et al.*, *Reintroduced Beavers Rapidly Influence the Storage and Biogeochemistry of Sediments in Headwater Streams (Methow River, Washington)* 93 *Northwest Science* 112-121 (2019)

Nicholaas Bouwes, *et al.*, *Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*)*, *Scientific Reports*, 6:28581, DOI: 10.1038/srep28581 (2016)

SCIENTIFIC REPORTS



OPEN

Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*)

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Nicolaas Bouwes^{1,2}, Nicholas Weber¹, Chris E. Jordan³, W. Carl Saunders^{1,2}, Ian A. Tattam⁴, Carol Volk⁵, Joseph M. Wheaton² & Michael M. Pollock³

Beaver have been referred to as ecosystem engineers because of the large impacts their dam building activities have on the landscape; however, the benefits they may provide to fluvial fish species has been debated. We conducted a watershed-scale experiment to test how increasing beaver dam and colony persistence in a highly degraded incised stream affects the freshwater production of steelhead (*Oncorhynchus mykiss*). Following the installation of beaver dam analogs (BDAs), we observed significant increases in the density, survival, and production of juvenile steelhead without impacting upstream and downstream migrations. The steelhead response occurred as the quantity and complexity of their habitat increased. This study is the first large-scale experiment to quantify the benefits of beavers and BDAs to a fish population and its habitat. Beaver mediated restoration may be a viable and efficient strategy to recover ecosystem function of previously incised streams and to increase the production of imperiled fish populations.

Beaver in Eurasia and North America were once abundant and ubiquitous¹. Their dense and barbed fur has great felting properties, and as early as the 1500s, intense trapping to provide pelts mainly for making hats occurred throughout Eurasia². By the early 1700s, beaver were nearly extirpated in Eurasia, and North America became the new source of pelts for international commerce. The exploration, settlement, and many territorial claims of North America by several European countries were driven mainly by the search for beaver-trapping opportunities².

When Lewis and Clark explored the Pacific Northwest in 1805, salmon and steelhead coexisted with beavers in very high densities^{1,3}. Fur trade in this region began around 1810, attracting pioneers to settle the area. When the British and United States jointly occupied the Oregon Territories (which included the Columbia River Basin), the Hudson Bay Company implemented their “scorched earth” or “fur desert” policy to eliminate all fur-bearing animals, in an attempt to discourage American settlement^{2,4}. As a result, beaver were nearly extirpated from the region by 1900. Around this time, a decrease in the great harvests of Pacific salmon and steelhead was first perceived. Anadromous salmon and steelhead populations have since declined precipitously in the Columbia River Basin, leading to their listing under the U.S. Endangered Species Act (ESA)^{5,6}. Agriculture, timber harvest, mining, grazing, urban development, and water storage and hydroelectric dam construction are commonly cited as the causes for salmonid habitat degradation and population declines⁷, with rare mention of the loss of beaver and their ability to alter aquatic ecosystems with their dam-building activities⁸.

Human activities, including the removal of beaver, have exacerbated the occurrence of stream channel incision, where a rapid down-cutting of the stream bed disconnects the channel from its floodplain^{8,9}. Channel incision is a ubiquitous environmental problem in the Columbia River Basin and throughout the world^{10–12}.

¹Eco Logical Research, Inc., PO BOX 706, Providence, Utah, 84332, USA. ²Watershed Sciences Department, Utah State University, 5210 Old Main Hill, Logan, Utah 84322, USA. ³Northwest Fisheries Science Center, 2725 Montlake Blvd E., Seattle, Washington 98112, USA. ⁴Oregon Department of Fish and Wildlife, Eastern Oregon University, 203 Badgley Hall, One University Boulevard, LaGrande, Oregon 97850, USA. ⁵South Fork Research, Inc. 44842 SE 145th Street, North Bend, Washington, 98045, USA. Correspondence and requests for materials should be addressed to N.B. (email: nbouwes@ecologicalresearch.net)

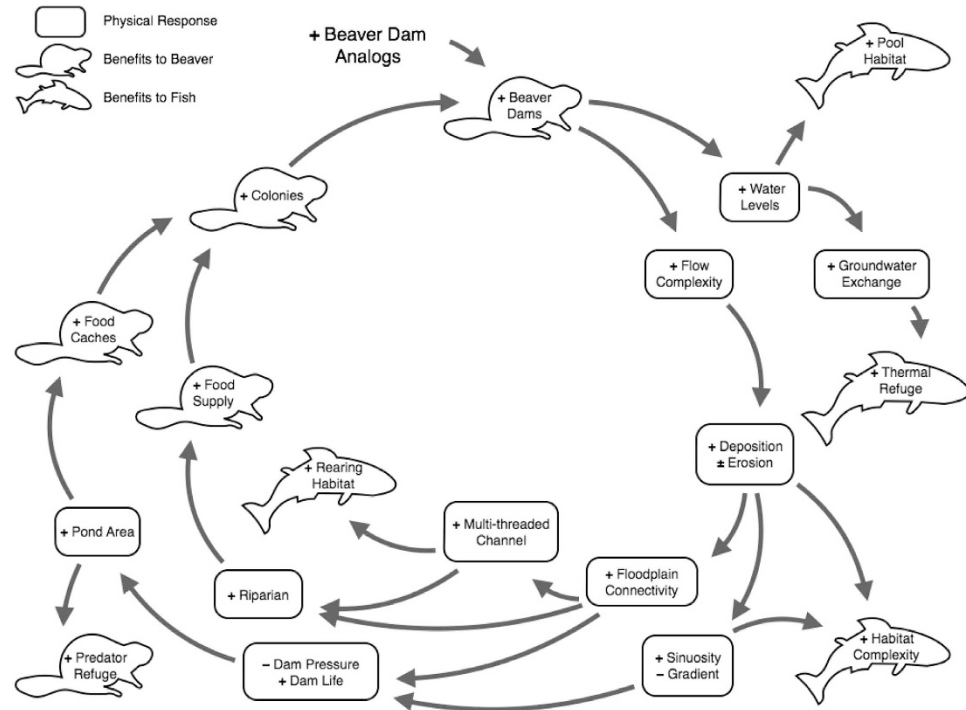


Figure 1. Expected changes following the installation of beaver dam analogs (BDAs). Beaver-made dams and BDAs slow and increase the surface height of water upstream of the dam. Beaver ponds above, and plunge pools below dams change the plane bed channel to a reach of complex geomorphic units providing resting and efficient foraging opportunities for juveniles. Deep pools allow for temperature stratification and greater hydraulic pressures forcing downwellings to displace cooler groundwater to upwell downstream, increasing thermal heterogeneity and refugia. Dams and associated overflow channels produce highly variable hydraulic conditions resulting in a greater diversity of sorted sediment deposits. Gravel bars form near the tail of the pond and just downstream from the scour below the dam, increasing spawning habitat for spawners and concealment substrates for juveniles. Complex depositional and erosional patterns cause an increase in channel aggradation, widening, and sinuosity and a decrease in overall gradient, also increasing habitat complexity. Frequent inundation of inset floodplains creates side channels, high-flow refugia and rearing habitat for young juveniles, and increasing recruitment of riparian vegetation. Flows onto the floodplain during high discharge dissipates stream power, and the likelihood of dam failure. The increase in pond complexes and riparian vegetation increases refugia for beavers, their food supply and caching locations, resulting in higher survival, and more persistent beaver colonies. Beaver will maintain dams and the associated geomorphic and hydraulic processes that create complex fish habitat.

Consequences of channel incision include a lowering of the water table, decreased base flows, warmer water temperatures, and reduced morphological complexity leading to a substantial loss of riparian plant biomass and diversity, and declines in fish populations and other aquatic organisms¹³. The succession of channel incision can be described by four phases: phase 1) rapid incision and disconnection of the floodplain, phase 2) widening of the incised trench, phase 3) building of inset floodplains and long-term aggradation, and phase 4) returning to a channel in dynamic equilibrium that is reconnected to its floodplain¹³. Incised channels can take centuries to millennia to fully recover to the dynamic equilibrium phase¹⁴. We hypothesized that beaver dams or simulated beaver dams that we construct (referred to as beaver dam analogs or BDAs) can greatly accelerate the incision recovery process¹⁴. We further hypothesized that advancing channel incision recovery would alter the hydrologic, thermal, geomorphic, and vegetation characteristics of stream reaches and their associated riparian habitats, which in turn would improve habitat conditions for steelhead (Fig. 1).

Ecosystem scale experiments have greatly improved our understanding of watershed processes and are a powerful method for evaluating and predicting responses to environmental change¹⁵. Such experiments generally involve large-scale perturbations simulating human impacts (e.g., logging, nutrient additions) and have led to changes in strategies to minimize environmental degradation^{16–18}. While insightful, these experiments are often costly and destructive, and do not necessarily address mechanisms of recovery processes. Implementing restoration as a watershed-scale experiment could greatly increase our understanding of ecosystem function, and our ability to achieve recovery goals while making better and more efficient use of the financial investments in mitigation¹⁹. We describe the results of a watershed-scale experiment designed to test whether constructing beaver dam analogs to encourage natural beaver dam development could aggrade a highly incised stream and improve habitat quantity and quality. Our focus here is to evaluate whether this manipulation resulted in an increase in juvenile steelhead density, growth, survival, and production.

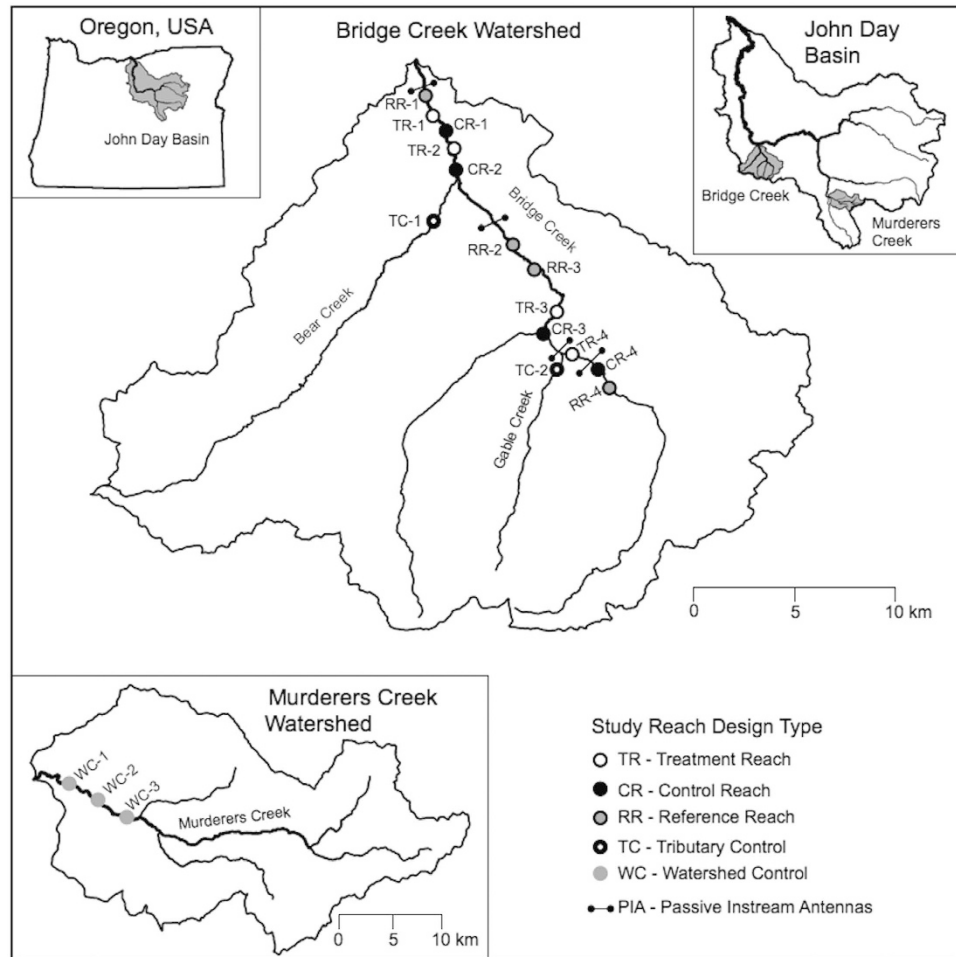


Figure 2. Map of the study areas. TR and CR dots represent treatment and control (similar to treatment reaches with beaver activity) study reach location. RR represent reference study reaches, which generally have minimal inset floodplains and minimal beaver influence. Reaches in tributaries to Bridge Creek (TC) and Murderers Creek (WC) served as additional controls. Passive Instream Antennas (PIAs) distributed throughout Bridge Creek detect Passive Integrated Transponder (PIT) tagged fish to determine viability and movement. Maps were created in ArcGIS version 10.1 (<http://desktop.arcgis.com/>) and Pixelmator version 3.4 (<http://www.pixelmator.com/mac/>).

Watershed-Scale Manipulation

Our experiment was conducted in the lower 32 km of Bridge Creek, a 710 km² watershed draining into the John Day River in north-central Oregon, USA. (Fig. 2). Steelhead are anadromous *Oncorhynchus mykiss* and are the targeted species for recovery in this watershed (hereafter referred to by their freshwater life stages as juveniles or spawners). Prior to the manipulation, steelhead habitat in Bridge Creek exhibited low complexity and poor quality. Most of the mainstem and lower tributary reaches of Bridge Creek were deeply incised, with riparian vegetation limited to a narrow band along the stream⁸. The stream morphology consisted of a plane-bed system with gradients from 0.5–3.0%, very poor pool habitat, and substrate dominated by coarse and embedded gravel and cobble. In addition, stream temperatures in the summer were warm for juveniles, with the lower portion of the study area approaching lethal thermal limits (~26 °C).

Previous research indicated that aggradation behind beaver dams in Bridge Creek can be rapid, and that connection to inset floodplains could be achieved within a decadal scale⁸. However, surveys of beaver dam distributions spanning the last 3 decades showed that dams within Bridge Creek are generally short lived²⁰. Due to the lack of large woody riparian vegetation, beaver dams in Bridge Creek were made with small-diameter materials (e.g., willow shoots). Consequently, dams consistently failed (e.g., 1–2 year lifespan) when subject to the typical annual flood in which all the flow energy was concentrated on the dams, as opposed to spreading out over a floodplain.

Our goal was to encourage beaver to build on stable structures (i.e., BDAs) that would increase dam life spans to facilitate channel aggradation, and eventually floodplain creation and reconnection¹⁴. BDAs were built by pounding wooden fence posts vertically into the channel bed and potential floodplain surfaces. Posts were spaced 0.3–0.5 m apart and at a height intended to mimic the crest elevation of an active beaver dam²¹. Willow branches were woven between the posts, and bed sediment was used to plug the base of structures. BDAs were designed

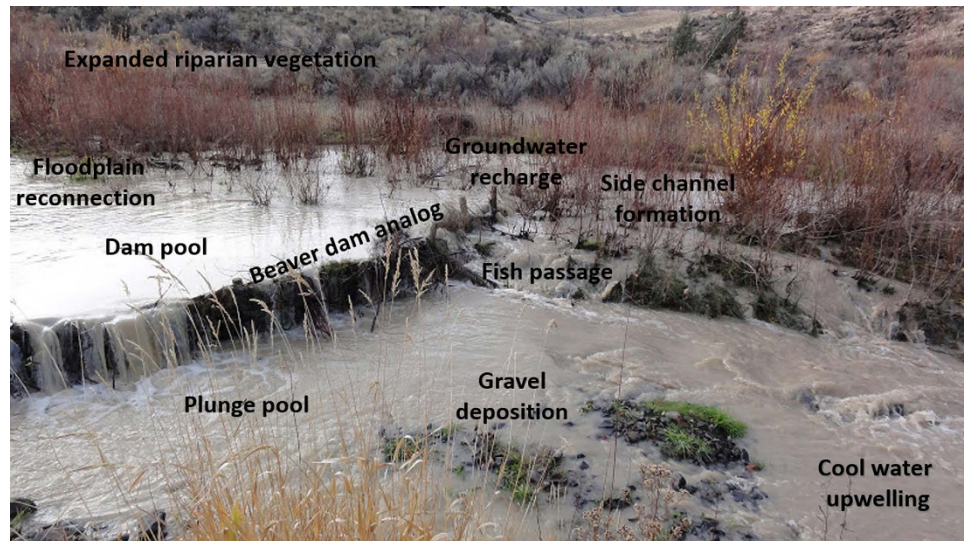


Figure 3. Example of a beaver dam analog (BDA) annotated with some of the expected responses.

to partially replicate many of the basic functions of a natural beaver dam (Fig. 3). The treatment design aimed to saturate four distinct reaches with BDAs, thereby providing resident beavers stable platforms that would encourage the establishment of stable multi-dam complexes to support persistent colonies (Fig. 1). This meant we added BDAs at the maximum frequency that beaver dams are found under natural conditions for a similar stream size and gradient¹. For most situations at the project site, water from a downstream structure is backed up to the base of the structure upstream during average discharge.

When BDAs were introduced we expected to effectively increase the number and longevity of functional natural and acting beaver dams that, in turn, would initiate a series of alterations that would ultimately restore processes that maintain a new stable state of floodplain reconnection¹⁴. Changes in both the quantity and quality of fish habitat accompanying this process were expected to elicit a fish population level response (Fig. 1).

The manipulation was implemented in a hierarchical²² experimental design where we established four of each treatment, control (both in the early phase 3 stage) and reference (in the early phase 2 stage with minimal beaver influence) reaches within Bridge Creek (Fig. 2). We also selected one control reach in each of two tributaries to Bridge Creek, and three reaches in a control watershed, Murderers Creek (Fig. 2). To assess localized habitat and steelhead responses we made comparisons between treatment, control, and reference reaches within Bridge Creek and its tributaries. To assess population level responses, we compared changes in juveniles in Bridge Creek (across all reach types) to Murderers Creek.

We monitored for three years pre-manipulation (2007–2009) and four years post-manipulation (2010–2013). We conducted an annual census of beaver dams and BDA locations and documented functionality. We monitored fish habitat attributes at sites within reaches once per year. Aerial imagery from 2005 and 2013 was also used to quantify changes in channel area and morphology. We monitored sites for juveniles, which were collected and tagged with Passive Integrated Transponder (PIT) tags each year in June, September, and January. In addition, we compared juvenile densities in impounded and unimpounded portions of three reaches in August and September of 2013 to evaluate their use of these different habitats. We also captured and PIT tagged spawners at a fish weir installed during their upstream migration in lower Bridge Creek (Fig. 2). Recapture of tagged fish provided information on density, growth, survival, and production, as well as the ability of spawners and juveniles to migrate throughout the study area. In general, we used intervention analyses to evaluate changes in habitat and fish responses pre- versus post-manipulation relative to controls²³ (see Methods for more details).

Results

Beaver Dam and BDA Abundance. Twenty years of beaver dam surveys in the study area prior to 2009 indicates dam-building activity was highly variable (\bar{x} = 40 dams counted per year, min = 9, max = 103, SD = 25; Fig. 4). After 2009, the year in which BDAs were first constructed, the total number of dams (natural beaver dams and BDAs) was on average four times more abundant than pre-manipulation (\bar{x} = 160, min = 122, max = 236, SD = 43; Fig. 4). In 2009, 76 BDAs were installed over 3.4 km of stream in the four treatment reaches. During 2010–2012, additional BDAs were built to replace those that failed during the first year and to continue the stream on the trajectory towards floodplain reconnection (e.g., added on top of BDAs buried by aggradation or to newly formed side channels). By 2012, 121 BDAs were functioning. Of the 236 total dams in Bridge Creek in 2013, nearly half (n = 115) were made by beavers. A total of 171 natural beaver dams and dams built on BDAs represents an 8-fold increase over the 2005–2008 pre-manipulation beaver dam average. The substantial increase in natural beaver dams occurred two years following the manipulation, primarily outside the treatment reaches (Fig. 4), suggesting the manipulation may have created a source of beavers for dispersal into unmanipulated areas. One control reach was subject to a high intensity flood event from an incoming tributary which greatly increased

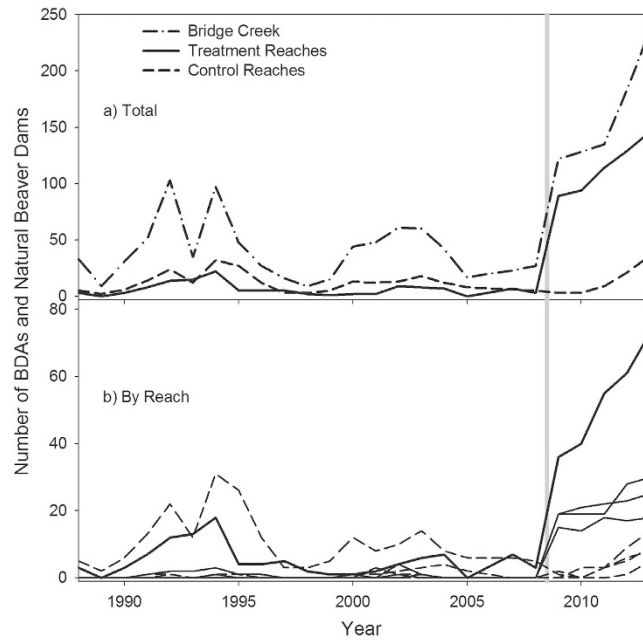


Figure 4. The number of dams (natural beaver dams and BDAs) through time. Upper panel represents the total number of dams for the Bridge Creek (dashed-dotted line), the sum of all treatment (solid line) and all control (dashed line) reaches. The lower panel is total number of dams for each of the four treatment (solid lines) and four control (dashed lines) reaches. Grey vertical line represents when BDAs were initially installed.

the number of new channels throughout the floodplain and was quickly occupied by beaver. With the exception of this reach, beaver dams in control reaches had a 10-fold higher failure rate than reinforced dams, similar to pre-manipulation conditions. No beaver dams were built in the four reference reaches during the study, however, occasionally dams were found in similarly incised channels elsewhere in Bridge Creek.

Habitat Response. Following the manipulation, habitat quantity and quality increased in treatment reaches and most control reaches with expanded beaver occupation relative to non-beaver-occupied reference reaches. BDAs and beaver dams both quickly raised the water, and created large upstream dam pools and downstream plunge pools. Relative to our reference reaches and Murderers Creek this resulted in a higher pool frequency (1.04 90% CI \pm 1.01 pools/100 m, $p = 0.09$ and 1.43 90% CI \pm 1.51 pools/100 m, $p = 0.11$, respectively; Supplementary Information Fig. 1) and deeper pools (0.10 90% CI \pm 0.054 m, $p = 0.02$ and 0.162 90% CI \pm 0.081 m, $p = 0.01$; respectively; Supplementary Information Fig. 2). Aggradation occurred rapidly, sometimes burying structures and channels, resulting in newly formed channels. From 2005 to 2013, inundation area of treatment reaches increased by 228%, considerably more than the control and reference reaches which increased 122% and 34%, respectively. New side channels were also formed as high flows were often forced onto inset floodplains. Area of side channels increased in treatment reaches by 1216%, but only by 479% in control reaches, with virtually no change in reference reaches.

Information from groundwater wells demonstrated a raising of the water table in a treatment reach relative to a control reach. Water levels below the land surface over the low-flow period averaged -2.527 90% CI \pm 0.052 m and -1.909 90% CI \pm 0.077 m in a control reach (CR-4) and treatment reach (TR-4), pre-manipulation, and -2.402 90% CI \pm 0.121 m and -1.531 90% CI \pm 0.169, respectively, post-manipulation. This equates to a 0.25 m ($p < 0.001$) increase in groundwater levels following the manipulation in our treatment reach relative to our control reach that also had some beaver activity post-manipulation.

Temperature loggers placed at the top and bottom of reaches indicated that temperature either dropped or remained constant as water traversed reaches with extensive beaver dams; whereas, temperatures increased in reaches without beaver dams. Maximum temperatures were on average 1.47°C (90% CI 1.34 to 1.72, $p < 0.001$) cooler in reaches that gained beaver dams after the manipulation (0 dams pre-manipulation to an average of 6.7 dams within 500 m upstream of the temperature loggers post-manipulation), than a reference reach that had no beaver dams within 500 m upstream over the study period.

For illustrative purposes regarding changes in channel planform, we compare water depth maps and longitudinal profiles of sites within the treatment reach (TR-4) and the closest upstream surveyed non-beaver-occupied reference reach (RR-4). Water depth maps and distributions depict greater variability in water depths, channel complexity, and an increase in the number of side channels in the treatment site (Fig. 5). Longitudinal profiles also emphasize differences in the variability of channel width and depths (Fig. 6a–d). We also compared day and night longitudinal temperature profiles for a site in TR-4 to a non-beaver-occupied site approximately 0.5 km upstream. During both day and night, the treatment site was cooler and contained considerably greater thermal heterogeneity (including cool refugia) than the unimpounded site which exhibited almost no longitudinal variability (Fig. 6e,f).

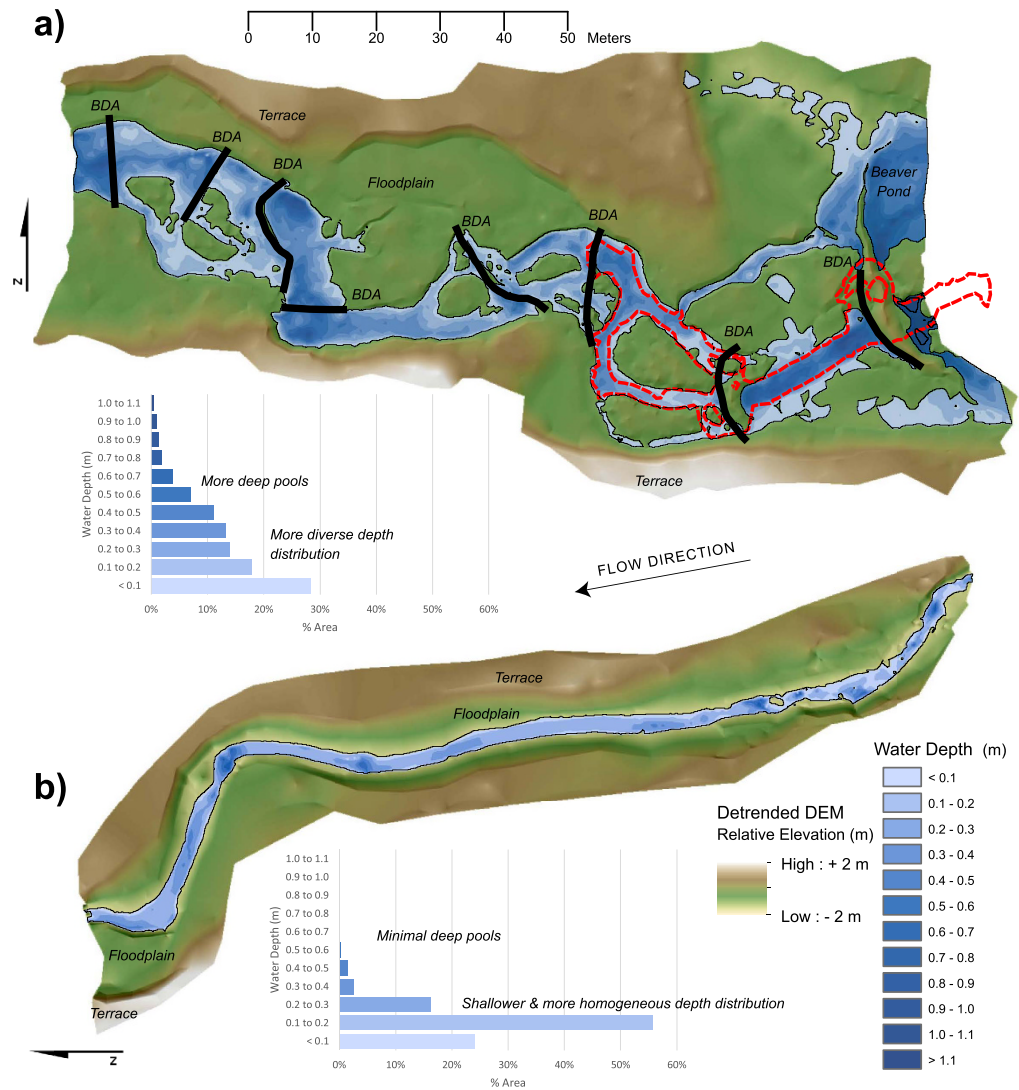


Figure 5. Water depth maps, relative topography and depth distributions for habitat sample site in treatment reach TR-4 (a) and a reference reach RR-4 (b). Digital elevation models (DEMs) were built from data collected from 2013 topographic surveys, with bottom elevations subtracted from water surface elevations to obtain water depths. Red outline in a) is the location of temperature survey information depicted in Fig. 6. Figure was created in ArcGIS 10.3 and Adobe Illustrator CS6.

Fish Population Response. We PIT tagged 35,867 juveniles from 2007 to 2013. When comparing a beaver pond to an adjacent upstream free-flowing site in three reaches on two dates, the linear and areal density of juveniles was on average 210 fish/100 m ($p = 0.007$) and 27 fish/100 m² ($p = 0.004$) greater in impounded than unimpounded reaches, suggesting a higher preference by juveniles for ponded areas. After the manipulation, fish density increased in Bridge Creek by 81 fish/100 m relative to our control watershed of Murderers Creek ($p = 0.01$; Fig. 7 and Supplementary Information Figs 3 and 4). In contrast, juvenile growth decreased after the manipulation by 6.1 grams per season in Bridge Creek relative to Murderers Creek ($p = 0.036$; Fig. 7 and Supplementary Information Fig. 5). Both Bridge and Murderers Creek exhibited density-dependent decreases in growth (growth = $-0.001 \cdot \text{density} + 0.215$, $R^2 = 0.59$, $p < 0.0001$; growth = $-0.001 \cdot \text{density} + 0.188$, $R^2 = 0.27$, $p = 0.02$, respectively). Following the manipulation, juvenile survival increased by 52% in Bridge Creek relative to Murderers Creek ($p = 0.004$; Fig. 7 and Supplementary Information Fig. 6). Production of juveniles, being the product of density, growth, and survival, is an informative quantitative indicator of population performance because it integrates multiple responses²⁴. Just four years after the manipulation, there was an increase of 175% in juvenile production in Bridge Creek, relative to Murderers Creek ($p = 0.06$; Fig. 7 and Supplementary Information Fig. 7).

Despite the dramatic increase in beaver dams and BDAs, we observed no changes in upstream spawner migration success based on detections of PIT-tagged spawners at upstream arrays. Prior to the manipulation 57%, 18%, and 17% (92% total) of tagged spawners were detected above PIAs 2 through 4, respectively (the spawner trap is located at PIA1). After the manipulation, we observed, on average, 49%, 31%, 14% (93.5% total) of the

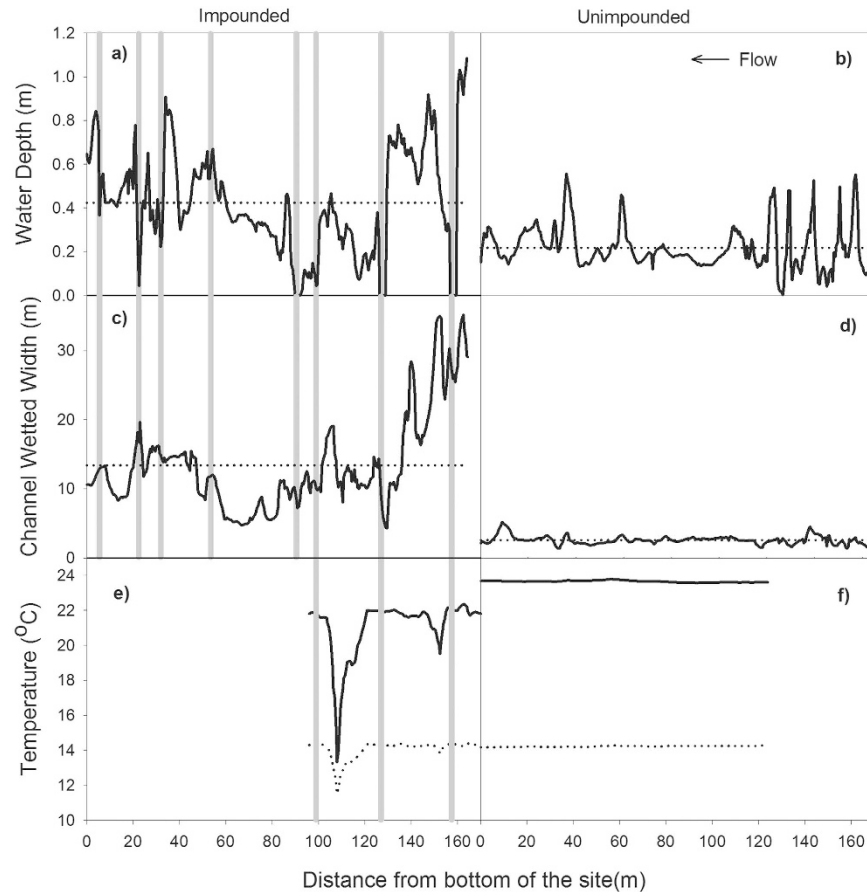


Figure 6. Longitudinal profile of stream characteristics. Water depth and channel width was determined from topographic survey information in 2013 in impounded TR-4 (panel a & c) and unimpounded RR-4 (panel b & d) sites, solid line is the metric value for each location, dotted line is the mean value for the reach. Longitudinal temperature profiles (panel e & f) were obtained from multiple temperature loggers in TR-4 (see Fig. 5) and an unimpounded reach just upstream (between TR-4 and CR-4). The solid line is maximum and dotted line is minimum temperatures. Grey vertical lines represent the locations of dams.

tagged spawners above these detection sites. Furthermore, several spawners were documented as having passed more than 200 dams and BDAs during their migrations. Likewise, more than 1000 PIT-tagged juveniles migrated downstream past the lower-most PIT tag array (PIA1) each year, the near expected amount given observed survival estimates and antenna efficiency. While upstream movement of juveniles is not common in Bridge Creek, we re-detected individuals in upstream reaches separated by more than 40 dams. Overall, mark-resight data indicate that neither beaver dams, nor BDAs, are barriers to spawner or juvenile movement.

Discussion

The addition of BDAs into Bridge Creek led to an immediate and rapid increase in the number of natural beaver dams, not only in our treatment areas but throughout much of Bridge Creek. Beavers build dams and dig canals to expand deep water to create refugia and to aid in the transport of the woody vegetation they harvest. We believe this increased activity throughout Bridge Creek was, in part, due to an increase in the population of beavers facilitated by BDAs. These structures provided stable places to build and expand natural beaver dam complexes that improved their habitat. Changes in the abundance of beavers are difficult to quantify because of their ability to quickly learn to avoid traps²⁵. Thus, we cannot state with certainty that the beaver population actually increased following the installation of BDAs. Whether their dam-building activities increased because of a demographic or behavioral response is somewhat immaterial, because the modification of the stream ecosystem, rather than the beavers themselves, likely caused the fish population response.

BDAs and beaver dams led to large changes in both fish and beaver habitat, and the steelhead population response largely followed our hypothesized pathways (Fig. 1). We found compelling evidence that beavers increased the quantity of juvenile habitat. We observed higher linear and areal densities of juveniles in impounded sections of stream relative to unimpounded sections. To demonstrate the potential for beavers to alter stream salmonid production, we believe linear density is the most indicative numeric response variable because dams increase the area of fish habitat per length of stream. Areal densities normalize across streams of different widths; thus a fish response might not be detected even if the population increased simply by increasing the width of the same length of stream (i.e. areal densities stayed the same or even decreased). Studies reporting the influence of

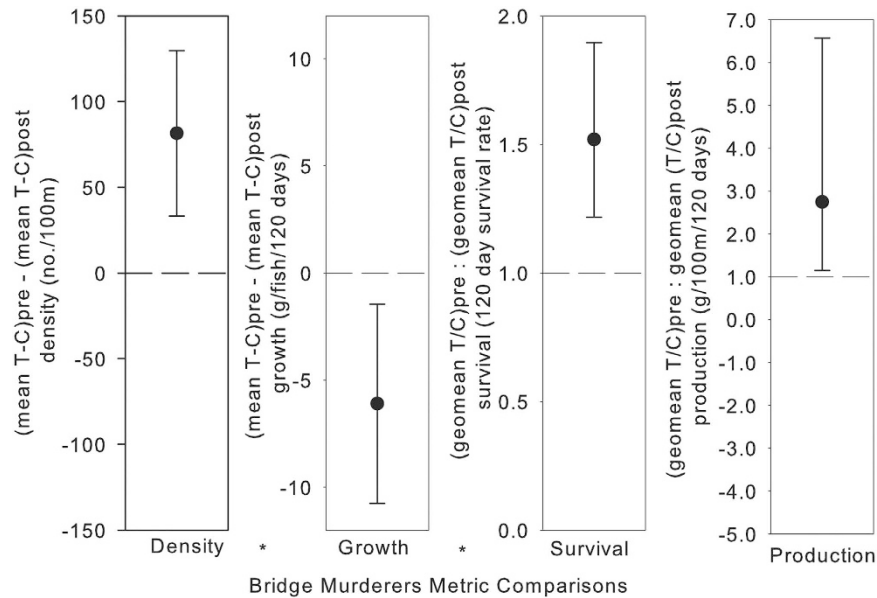


Figure 7. Summary of intervention analyses for juvenile steelhead responses. On every sampling occasion, the control (C) is subtracted (difference) or divided into (ratio) the treatment (T) value. Next, the average difference pre-manipulation is subtracted (difference) or divided into (ratio) the post-manipulation value. Confidence intervals (90%) not overlapping zero for difference and 1 for ratio indicates significance at $\alpha = 0.1$. Comparisons are made between Bridge Creek (treatment) and Murderers Creek (control), respectively. Results for difference in density and average growth, and ratio of survival and production (estimated as density* growth*survival) are displayed.

beaver ponds to produce more fish relative to other habitat types often use areal densities^{26,27}. An areal density response metric may under-represent the contribution this habitat type has to the population, because one mechanism by which beaver dams increase fish abundance is by increasing the quantity of fish habitat, as we observed.

Natural beaver dams and BDAs increased the area of juvenile habitat in the treatment reaches in Bridge Creek because these reaches were in the building of the inset floodplain phase (early phase 3) of the successional cycle of an incised channel. The combination of increasing the dam crest height up to the inset floodplain and channel aggradation behind the dam, allowed surface waters to spill out onto inset floodplains greatly increasing the habitat area. The benefits of creating more fish habitat would be diminished in an incised trench, because small increases in surface water area occurs as surface water elevation increases. This condition is representative of our reference reaches. However, beaver dams and BDAs likely increase the rate at which phase 2, or channel widening occurs, thus accelerating the channel incision recovery process to benefit fish populations¹⁴. In fact, we most commonly observe breaches on the ends of beaver dams or BDAs. Such breaches create an acceleration of a flow jet at the outside bank of the incision trench and increases the rate of widening and the sinuosity of the channel.

The increase in groundwater elevation surrounding beaver ponds likely results in increased flow throughout the summer as water is slowly released^{28,29}. We also found that water temperatures stayed the same or decreased throughout reaches with beaver ponds, and that diel fluctuation was dampened. Because dams slow water and often increase the area of solar input, a common assumption is that temperatures increase in impounded reaches³⁰. However, quantitative evidence supporting^{31,32} or refuting³³ this claim suggests that the complex interaction of solar input, and exchange with the hyporheic or groundwater call into question this simple generality²⁹. In Bridge Creek, increased residence time and the slowed release of potentially cooler water after the construction of BDAs also increases habitat quantity during times of very low discharge observed during hot summer conditions.

Increasing habitat complexity may also partially explain the observed increase in total juvenile abundance, survival and productivity. In sections with natural and simulated beaver dams, we observed higher variability in water depth, channel width, and temperature from dam-building activities, all indicators of increased habitat complexity. Increased habitat complexity provides fish a greater selection of locations at which to forage, rest, and avoid predation and high flow events, while reducing migration distances required to conduct these activities for multiple life-stages³⁴. Thus, we suspect that an increase in habitat complexity is partly responsible for the observed positive steelhead population responses.

This study provides further quantitative support to the proposal to reintroduce or expand beaver populations in their native range in North America and Eurasia to recover incised channels^{8,14,35}. However, the impacts of beaver reintroductions on fish populations, summarized in a recent review³⁰, have been debated. Of note is the paucity of rigorous empirical studies backing conclusions of both positive and negative impacts. Unfortunately, many approaches to managing beaver populations for fisheries enhancement are also based on assumptions or results from weak study designs. In fact, policies to remove beavers/beaver dams as a means to improve salmonid populations, still exist in some U.S. states³⁶. This does beg the question, how did both beavers and salmonids

coexist in far greater numbers than occurs today without human intervention? While we observed many of the commonly reported positive impacts (habitat complexity), many of the claims of negative impacts of beaver dams on fish (e.g., fish passage barriers, temperature increases) are not supported by our findings to date.

The factors contributing to variability in fish and habitat responses across systems deserves further inquiry and will only be illuminated as additional studies are pursued in widely varying systems. For example, one large scale study found evidence suggestive of an increase in brook trout production after the removal of 200 beaver dams maintained for over two decades, in a low gradient stream network in Wisconsin, USA.³⁷ In low-gradient systems with a reduced range of water velocities, beaver dams may not create the same heterogeneous environment as they do in relatively higher gradient systems like Bridge Creek. Multiple controlled experimental manipulations or comparative studies across a range of stream gradients would help establish whether salmonid and fish community responses to beaver-dominated systems are gradient dependent.

The use of BDAs to provide or enhance the benefits beavers have on stream ecosystems and salmonids could be a potential restoration strategy but requires additional rigorous assessments elsewhere. The use of BDAs as a restoration approach is certainly attractive from a cost perspective³⁸. In a stream like Bridge Creek, installation of a BDA takes three people approximately 1–4 hours to install, requires a hydraulic post driver and 20–40 wood posts, (at ca. US\$4 per post). The cost at a density of ~30 BDAs per km is less than \$11,000. In contrast, conventional restoration techniques to achieve such objectives often involve massive grading operations with heavy equipment and major revegetation efforts that are extremely expensive and uncertain. Not only was our manipulation large in scale, but we benefited from the help of beaver to maintain, and likely improve, structures until self-maintaining processes (e.g. floodplain connection) were restored.

More important than the feasibility is our demonstration that such a restoration strategy actually results in benefits to the target population. Billions of dollars are spent annually on stream restoration in the U.S. alone³⁹; however, very few studies have documented changes beyond localized increases in fish abundance following stream restoration⁴⁰. Far fewer demonstrate increases in responses associated with fitness (i.e., survival, growth, and production). The few studies that have detected positive population-level changes due to restoration were likely able to do so because they were conducted at large spatial and temporal scales (many km and 10+ years), included extensive monitoring, and maximized contrasts (e.g., before-after-control-intervention experimental designs)^{41,42}. Our ability to detect a fish response was, in part, due to the large signal created by adding BDAs to nearly 4 km of Bridge Creek, coupled with considerable localized changes caused by both BDAs and natural beaver dams. Although we tagged >35,000 juveniles, reach-level comparisons were difficult to make for responses requiring seasonal recaptures such as survival, growth, and production. We believe that large-scale experimental manipulations, rather than reach-level, opportunistic evaluations of small-scale habitat projects are necessary to increase our understanding of how fish respond to changes in their habitat or provide evidence of restoration benefits.

In order to improve our understanding of how organisms respond to their environment, ecosystem experiments that use restoration as a treatment and incorporate appropriate large-scale controls should be actively pursued. This approach is consistent with experimental and adaptive management and has recently been implemented to test the effects of stream restoration in several watersheds¹⁹. Effective implementation of this experimental restoration approach requires an investment in coordination, strong experimental designs, cost-effective yet extensive restoration strategies, and directed monitoring and research. However, the potential to implement more effective management and restoration actions while learning from such approaches readily justifies their cost.

Methods

Experimental and Survey Design. The manipulation was implemented in a hierarchical²² experimental design where we compared four treatment and four control reaches in the early phase 3 stage within Bridge Creek (Fig. 2). We identified four additional reference reaches with minimal beaver influence. To address effects at different scales, issues of potential non-independence, and to protect against loss of control site information (i.e., create redundancy), we selected one control reach in each of two tributaries to Bridge Creek, and three reaches in a control watershed, Murderers Creek (Fig. 2). All experimental reaches were between 500 and 2000 m in stream length.

We monitored for three years pre-manipulation (2007–2009) and four years post-manipulation (2010–2013). Sample sites (i.e. segments within reaches) were used to characterize reaches. We monitored sites once a year for fish habitat. Aerial imagery from 2005 and 2013 was also used to quantify changes in channel morphology. We monitored sites for juveniles, which were collected and tagged with 12 mm full duplex Passive Integrated Transponder (PIT) tags each year in June, September and January. A habitat preference study to compare densities of juveniles in impounded and unimpounded portions of three reaches was conducted in the fall of 2013. We captured spawners during their upstream migration at a fish weir located near the mouth of Bridge Creek (Fig. 2). All fish PIT tagged were weighed and measured, and spawner sex was determined. Recapture of tagged fish provided information on movement, density, growth, and survival. We estimated production as the product of these responses. In general, we used intervention analyses to evaluate changes in fish response following the manipulation relative to controls²³.

Beaver Dam Surveys. Beaver dam census surveys were enumerated throughout the study area on Bridge Creek in late December during each year from 1988 to 2013²⁰. During these surveys, beaver dams were recorded as being either intact (actively impounding water in pond to the maximum dam crest elevation), breached (partially impounding water) or blown out (not impounding water). When BDA structures were installed in 2009 they were surveyed in the same manner as natural beaver dams, and whether or not BDAs were being actively maintained by beavers was also recorded. These surveys were used to track the abundance and distribution of

natural dams and BDA structures being maintained by beaver throughout the control, treatment, and reference reaches of Bridge and Murderers Creek (Fig. 4).

Habitat Surveys. Fish habitat surveys were conducted in November of each year at a single site within each of the reach types, as well as on rotating basis (every other year) at supplementary sites. In total 48 sites within Bridge Creek and 3 sites in Murderers Creek were sampled. Sites were 160 m in length (approximately 20 bankfull widths) and were surveyed using the methods developed by the Columbia Habitat Monitoring Program⁴³. These surveys quantify a number of fish habitat attributes, and utilize survey-grade equipment to provide channel and floodplain topography and water surface extent and elevation. Topographic data were used to generate 10 cm resolution Digital Elevation Models (DEMs) of channel and water surface elevations that were differenced to create a third surface representing the water depths throughout each sub-site survey (Fig. 5). Longitudinal profiles of water depths and channel widths were extracted from water depth maps and wetted widths calculated at an interval of 0.5 m along the channel thalweg from the bottom to the top of the site (Fig. 6a–d).

Channel inundation area was calculated from high-resolution (15 cm) aerial imagery of Bridge Creek before and after the manipulation occurred and beaver dams proliferated. Aerial imagery was acquired on September 27, 2005 and a repeat acquisition was conducted on May 5, 2013 (Watershed Sciences, Corvallis, Oregon). Following acquisition, imagery was ortho-rectified and subject to rigorous quality assurance procedures to ensure spatial accuracy. Areas of inundation were extracted from the 2005 and 2013 aerial imagery by digitizing the extent of the wetted channel throughout each study site using ArcGIS.

Temperature loggers (Onset Tidbit V2, U22) were deployed at the top and bottom of all reaches, continuously recording temperature every 15 minutes. In addition, longitudinal stream temperature profiles were created from temperature monitoring in a portion of a site in a treatment and reference reach (Fig. 6e,f). Temperature loggers were fixed to the streambed for two weeks during the summer throughout the wetted channel at a density of approximately 0.04 m², and the location of each logger was surveyed using a Real Time Kinematic (RTK) GPS. Temperature information from each logger was used to construct digital temperature models depicting the spatial distribution of daily maximum and minimum temperature throughout the reach. The longitudinal profiles of stream temperatures presented in Fig. 6e,f, were created by extracting the maximum and minimum temperature on August 17, 2012 observed along the channel thalweg at an interval of 0.5 m from the bottom to the top of the surveyed reach.

Well fields were established adjacent to reaches TR-4 and CR-4 to compare groundwater elevational changes pre- and post-manipulation between a treatment and control reach. A line of 2 to 3 wells perpendicular to the channel extended back approximately 70 m on the terrace. Four and three lines of wells (lines were spaced 50–70 m apart parallel to the stream) produced 10 and 9 wells for the treatment and control reach, respectively. Groundwater elevation was obtained from wells drilled approximately 12 m deep and lined with 5 cm slotted PVC. In each well, water table elevation and groundwater temperature data were collected using HOBO Water Level Loggers (Onset Computer Corp., model U20-001-01) set to record data in one or two hour intervals over the duration of the study period.

Seasonal Juvenile Steelhead Surveys. Juvenile steelhead surveys were conducted in all reach types. Survey sites within these reaches ranged between 500–1000 m in stream length. On each juvenile steelhead survey occasion, two electrofishing passes were conducted, separated by a 24-hour period. During each pass juvenile steelhead were captured using a backpack electrofisher (SAMUS-725MP) and dip nets while fishing from the bottom to the top of the site. Captured salmonids ≥ 70 mm were anesthetized, measured (mm), weighed (g), and PIT tagged (Biomark HPT12, Boise, Idaho) in the abdominal cavity, then released back to their approximate capture location following recovery from the anesthetic. Methods of fish capture and handling were approved by the National Oceanic and Atmospheric Administration's Biological Opinion in accordance to their Federal Columbia River Power System Biological Opinion Letters of Determination 22-14-NWFSC100 and 23-14-NWFSC101 Scientific Research Permits.

Recapture information from each of the two electrofishing passes was used to estimate the population size of juvenile steelhead residing in each site during each seasonal sampling occasion using the Chapman equation⁴⁴. In some cases, low steelhead densities prevented recapture of tagged individuals, and an estimate of capture efficiency (no. marked fish/no. of recaptures) calculated for each site from previous sampling occasions was used to expand the number of fish captured during the first pass into an estimate of population size.

Although the Cormack-Jolly-Seber (CJS) model has traditionally been used to estimate survival rates for tagged fish in the Columbia River Basin, it does not account for emigration thus producing estimates of apparent rather than true survival. Additionally, CJS cannot accommodate continuously collected data, such as the resightings from passive instream antenna (PIAs) that constitute a large portion of our resight data. Therefore, we used the Barker model⁴⁵ that uses recapture and continuous “resight” information to simultaneously estimate rates of emigration, immigration, and survival to produce estimates of true survival⁴⁶.

We generated encounter histories for each individual PIT-tagged fish from active tagging, mobile antenna surveys, and continuous detections from PIA arrays. We used Akaike's Information Criterion corrected for small sample size (AICc)^{47,48} to determine the most parsimonious model for recapture/resight and movement parameters in the Barker model, while survival parameters were unconstrained (i.e., varied through time) in all models. Survival estimates and 95% credible intervals were computed using the Markov Chain Monte Carlo (MCMC) procedure in Program MARK^{48,49}. Seasonal survival rates were standardized to 120 days.

Juvenile steelhead growth rates were calculated by direct measurement of the change in weight of PIT-tagged individuals recaptured from one season to the next (reported as g/fish/120 d). Seasonal production (g/100 m/120 d) of juvenile steelhead was calculated for each site as the product of the beginning of season density, seasonal growth rate, and seasonal survival.

Analyses. We evaluated differences in pool frequency, residual pool depth, temperature, and groundwater elevation, as well as fish responses between treatments and controls using Before-After-Control-Impact paired (BACIP) design intervention analyses⁵⁰. These comparisons were made at the reach or watershed scale depending on the response. Controls in this sense are used as covariates where effects common to both treatment and control reaches (e.g. weather) are filtered from the treatment time series of information by subtracting the control value from the treatment value for all observations. The average of this difference pre-manipulation is compared to the average of the value post-manipulation using a t-test. An $\alpha = 0.10$ was used to create 90% confidence intervals. Intervals encompassing zero were taken to indicate a lack of significant pre- versus post-manipulation difference for each response variable (Fig. 7 and Supplementary Information Fig. 3). In the case of survival and production, a natural log transformation was necessary to meet assumptions of normality (evaluated by inspecting quantile to quantile plots of residuals), which is equivalent to using treatment:control ratios for each observation event in the time series and conducting a ratio t-test. If the 90% confidence intervals surrounding the ratio crosses 1 then a significant difference was not observed.

These types of intervention analyses can bias p-values if assumptions of additivity and serial independence are violated^{50,51}. To test the assumption of additivity, the presence of trends between the average versus the difference in paired treatment-control observations was evaluated for each response⁵⁰. To test for auto-correlation, the difference between a treatment-control pair at time t was compared to the difference at $t + 1$, for all observations⁵⁰. A significant positive correlation between t and $t + 1$ observations was taken as evidence for auto-correlation, suggesting that our p-values were negatively biased. In this case, we also noted whether a positive temporal trend in the difference between treatment-control pairs during the before period, as this violation of the additivity assumption is particularly egregious⁵².

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Author Contributions

N.B. performed analyses, N.B., N.W. and J.M.W. created figures and tables. All authors conceptualized the project, experimental and monitoring designs and contributed to the writing of the manuscript. C.E.J., M.M.P., W.C.S., I.A.T., C.V., J.M.W. reflect equal contributions to the manuscript.

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SCIENTIFIC REPORTS

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Corrigendum: Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*)

Nicolaas Bouwes, Nicholas Weber, Chris E. Jordan, W. Carl Saunders, Ian A. Tattam, Carol Volk, Joseph M. Wheaton & Michael M. Pollock

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This Article contains an error, where Supplementary Information Figure 6 is a duplicate of Supplementary Information Figure 7. The correct Supplementary Information Figure 6 appears below as Fig. 1.

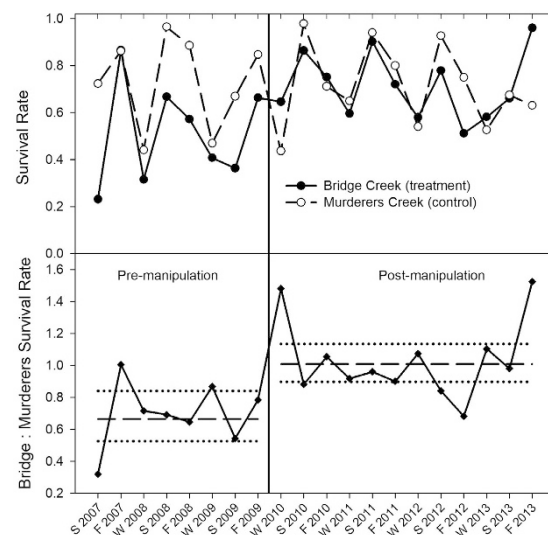



Figure 1.

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Reintroduced Beavers Rapidly Influence the Storage and Biogeochemistry of Sediments in Headwater Streams (Methow River, Washington)

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Reintroduced Beavers Rapidly Influence the Storage and Biogeochemistry of Sediments in Headwater Streams (Methow River, Washington)

Abstract

North American beavers (*Castor canadensis*) were targeted within North American headwater landscapes by European loggers and fur traders in the 19th century, reducing beaver populations to near extinction by 1900. The extirpation of beavers from river networks has had profound effects on riparian zones, including channel geomorphology, temperature regimes, sediment storage, channel-floodplain connectivity, carbon storage and nutrient dynamics. Consequently, reintroducing beavers has been provisionally implemented as a restoration approach within some watersheds. We characterized how reintroduced beavers influence the short-term dynamics of organic material accumulation within the sediments of 1st and 2nd order streams within the Methow River watershed of Washington State. In collaboration with the Methow Beaver Project, we identified four creeks where they had reintroduced beavers within the past five years, as well as a control non-beaver pond. At each site, we collected shallow sediment cores from upstream, downstream, and within beaver ponds, and then measured organic material via elemental analyses of sediment carbon (%C) and nitrogen (%N) content. We compared those samples to sediments accumulated in local pond areas not created by beaver activity. Our results show greater organic C and N content of sediments in beaver ponds than non-beaver ponds. C/N ratios indicate elevated accumulation of allochthonous organic material in beaver impoundment sediments that would otherwise not be integrated into headwater streams from the terrestrial landscape. These findings suggest that the reintroduction of beavers could be an effective means to promote restoration of whole ecosystem function.

Keywords: beaver reintroduction, river restoration, ecosystem functioning

Introduction

Freshwater systems are some of the most imperiled on the planet (Dudgeon et al. 2006, Abell et al. 2008). Restoring the functionality of these environments will require the persistence of essential species within them, and also the preservation of the biogeochemical heterogeneity that naturally occurs within river networks (Wohl et al. 2005, Palmer et al. 2014). Because beavers (*Castor ca-*

nadensis) are known to be significant ecosystem engineers, conservationists and wildlife managers have suggested that the reintroduction of beavers into watersheds that previously supported native beaver populations may benefit those environments at an ecosystem scale (reviewed in Rosell et al. 2005, Burchsted et al. 2010, Pollock et al. 2014). Particularly in river basins experiencing multiple landscape-scale anthropogenic stressors (i.e., agriculture, timber harvest, flow alteration, livestock grazing, fire, and climate change), beaver reintroductions could potentially mitigate the impacts of some human disturbances, buffering systems as they become increasingly modified (e.g., Pollock et al. 2007, Law et al. 2016, Puttock

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et al. 2017). However, little research has focused on the short-term (less than five years) effects that reintroduced beavers have on sediment biogeochemistry in low-order streams, particularly in montane areas of the western United States.

The effects of dam building by beavers on riparian geomorphology, ecology, and ecosystem function has been well documented; a recent literature review by Gibson and Olden (2014) identified several hundred papers published over the past century on these topics in both temperate and dryland ecosystems. Of particular relevance to our study are the sediment biogeochemical impacts of newly established dams in incised, low-order, mountain streams. Basic models can be used to predict how beaver dammed streams develop over time from the initial pond stage to complex riparian systems that include multithread channels and wetland networks (Pollock et al. 2014). Beaver wetlands and meadows often retain sediment, water, nutrients, and carbon in riparian areas that otherwise would not have substantial storage potential (Sutfin et al. 2016, Wegener et al. 2017). Carbon accumulation in headwater streams is often linked to organic-rich debris and sediments impounded behind beaver dam complexes, providing energy to bolster local riparian and aquatic ecosystem diversity and function (Naiman et al. 1994, Johnston 2014).

Within the field of restoration ecology over the past decade, native species reintroduction projects within aquatic ecosystems have become a more common tool used by wildlife managers and conservation organizations, often in tandem with habitat and flow restoration approaches (NOAA Fisheries 2011, US Fish and Wildlife Service 2017). However, species reintroductions often focus on reestablishing a single species' former abundance and distribution within a region, in step with the Endangered Species Act (ESA) guidelines (i.e., humpback chub [*Gila cypha*] in the American Southwest, US Fish and Wildlife Service 2010). While that approach is necessary for many species, modern conservation efforts have additionally concentrated on reestablishing ecosystem processes (i.e., system metabolism, organic matter decomposition, or secondary pro-

duction within rivers) within degraded environments, using strategic species reintroductions to promote self-sustaining positive outcomes for entire food webs (Marshall et al. 2014, Nummi and Holopainen 2014, Wohl et al. 2015, Law et al. 2016). Beavers are strong candidates for reintroduction because there were approximately 60–400 million beavers within North America prior to European colonization, and by 1900 the species was nearly extinct (Seton 1929, Jenkins and Busher 1979). Despite subsequent population increases in many watersheds in recent decades, opportunities to expand contemporary beaver populations' range and abundance to more closely reflect their historical influence on the landscape are numerous. Beaver bioengineering has the potential to be a useful watershed conservation tool, and the reintroduction of beavers may hasten the beneficial effects of their dam building.

Our aim was to understand the impact of reintroduced beavers on carbon storage in headwater stream segments, which would otherwise store little to no organic-rich sediments, within the first few years after their reintroduction. We used the organic carbon and nitrogen content of stream sediments, and measurements of water properties to characterize the biogeochemical influence of reintroduced beavers on four headwater streams within the Methow River watershed in Washington. Specifically, we explored to what extent recent beaver reintroduction has increased carbon retention in beaver-pond habitat. We also investigated the source (allochthonous vs. autochthonous) of organic material retained in habitats created by beavers. Our study sheds light on the utility of beaver reintroduction as a restoration tool to rapidly restore ecosystem function within complex, multi-use watersheds.

Methods

Study Area

The Methow Valley is a northwest-southeast trending river valley located in Okanogan County in Washington State (Figure 1). This valley lies just east of the North Cascades and west of the Columbia River. The major water body in the Methow Valley is the Methow River, which drains

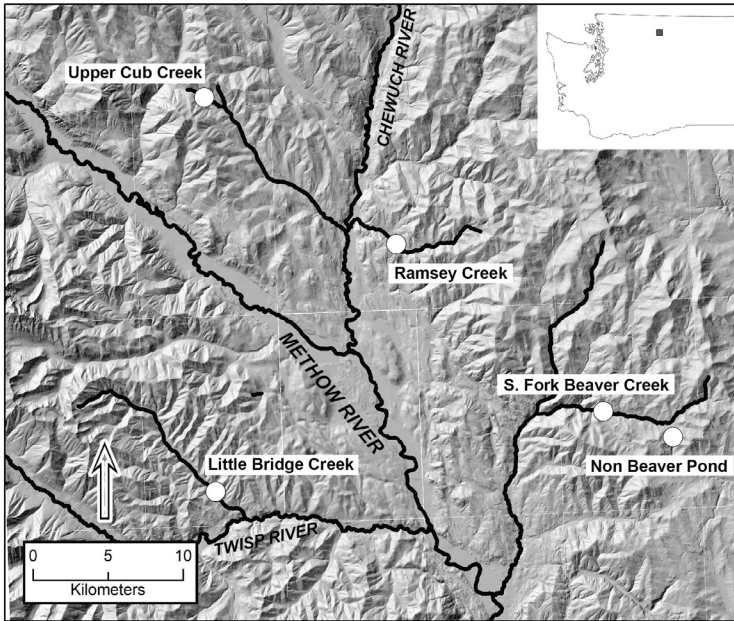


Figure 1. The Methow River watershed in north-central Washington State. Study locations are indicated by white circles. Beaver reintroduction sites are located on Little Bridge Creek, Ramsey Creek, South Fork Beaver Creek, and Upper Cub Creek. The non-beaver pond site is also included.

1,810 square miles from the North Cascades to the west (Konrad et al. 2003). Over 50% of the stream length within the Methow River watershed is comprised of first- and second-order streams. All our sampling locations are within such streams in the Okanogan-Wenatchee National Forest. Land use there is dominated by recreation, timber harvest, and livestock grazing (Woodruff 2015). This study area is also of interest because it contains steelhead and spring Chinook salmon, which are both listed as endangered under the ESA, as well as bull trout, which is listed as threatened. Consequently, restoring ecosystem processes throughout the watershed that promote dynamic and diverse food web structures is important to stakeholders, including US, state, and tribal governments.

Methow Beaver Project

Contemporary river-restoration practices typically characterize baseline stream conditions as continuous and free-flowing with the sporadic integration of woody debris (Burchsted et al. 2010). However, those river characteristics do not account

for the historical presence of large beaver populations throughout North America prior to European settlement. The Methow Beaver Project (Twisp, WA) integrates that understanding of the historic hydrologic landscape into the project's modern conservation approach, reintroducing beavers to low-order tributary creeks of the Methow River since 2008 (Woodruff 2015). The particular goals of the Methow Beaver Project are to improve the health of riparian ecosystems, provide instream habitat necessary for historic salmon runs, and examine the effects of beavers on regional aquifers and municipal water budgets in anticipation of climate change impacts throughout the Methow Valley (Woodruff 2015). The

project relocates "problem beavers" from downstream areas to upstream creeks; the number of relocations varies annually. For example, in 2014 the project released 38 beavers in 14 release events to 13 sites. The success of the Methow Beaver Project has been monitored by investigating patterns in ecosystem and watershed function. After the first seven years of reintroductions, the project reported positive effects on water storage and riparian ecosystem health from dam building activities (Woodruff 2015). However, the precise impact of these reintroductions on ecosystem processes like carbon flow within stream ecosystems is still poorly understood.

Study Design and Field Sampling

We identified four ponds (areas with water too deep to support emergent plants; Naiman et al. 1994) created by reintroduced beavers over the past two to five years in different stream segments, and one pond of a similar size that was not created by beaver activity. Sampling was conducted in June and July, 2016. We estimated that all ponds ranged

in area from approximately 79 to 531 meters². At each site, transects were laid out across the pond at its widest point, with the ends of the transects defined by the presence of emergent vegetation on the pond banks. This transect sampling approach was used to account for expected lateral heterogeneity of pond bottom sediment accumulation that might lead to areas of greater deposition in different parts of the ponds. Ten-centimeter (10-cm) sediment cores were then taken along each transect and spaced equidistantly, either one or two meters apart depending on the width of the pond. Sediment cores were extruded from the corer, placed into plastic bags, wet-weighed in the field, and individually frozen for transport. We measured water properties including temperature, pH, conductivity, and dissolved oxygen at each pond using a YSI probe (Yellow Springs Instruments, Yellow Springs, OH).

Upstream and downstream of each beaver pond (within 25 meters linear distance) we also collected water property data, and 10-cm sediment cores (hereafter referred to together as “stream” samples). These stream samples provided reference points to assess whether there was greater carbon content in the pond sediments relative to stream sediments above or below the impoundments. The stream sampling was not done along a channel-spanning transect as the pond sampling was. Instead, stream sediment cores were taken in slack water and point bar areas where deposition of suspended sediment would naturally occur in a headwater stream without the presence of an obstructing structure, like a beaver dam.

To investigate the sediment profile associated with partially submerged (wetland) areas immediately adjacent to a beaver pond, we excavated a pit at edge of the pond on the South Fork Beaver Creek site. Sediment samples were collected at 10-cm depth intervals from the pit sidewall to a depth of 30 cm. Below 30 cm the sediments were completely saturated. We measured bulk density, pH, %C, and %N in these samples. Wetland areas (versus pond or upland) were limited to narrow (few meter) sections adjacent to the ponds at the beaver pond sites.

Lab and Statistical Analyses

Sediment samples were oven- and then freeze-dried. After drying, each sample was weighed again in its entirety for weight percent water calculations. All samples were then sieved through a 2-mm sieve that separated leaf litter, pond vegetation, and other large organics from the sediment. The remaining sample material was homogenized in a ball mill, and 15 mg samples of sediment were weighed into tin boats for analysis of organic carbon and nitrogen content (weight percent). Samples were analyzed using a Costech Instruments 4010 Elemental Analyzer at the University of Puget Sound.

Statistical analyses of sediment %C and %N results were conducted using JMP (version 12.0, SAS Institute Inc.) software and R-Commander. We conducted Welch’s *t*-tests between mean pond and stream datasets. To investigate whether the amount (recorded by %C values) and source (interpreted from C/N ratios) of organic material differed among beaver ponds and the non-beaver site, we took two approaches. First, we used Welch’s *t*-tests to separately compare %C and C/N between all (pooled) beaver and non-beaver pond samples. We then used a multivariate test (MANOVA with post-hoc Pillai’s trace paired comparisons) to explore differences between %C and C/N among beaver ponds and the non-beaver site. A principle components analysis (PCA) helped assess the factors dominating the site-specific environmental variability between beaver ponds.

Results

Reintroduced beavers influenced the amount and source of organic material retained in the sediments of headwater streams in the Methow River watershed. When we compared the stream and beaver pond samples, we found significantly higher organic content (%C) in the pond sediments across all locations (Welch’s *t*-test; all locations $P < 0.001$; Figure 2). In fact, the mean %C in beaver pond samples from each site was at least 4X the stream mean %C. Furthermore, we found that mean %C was higher in ponds formed by reintroduced beaver impoundments than in a non-beaver pond within the same watershed (Table 1, Figure 3)

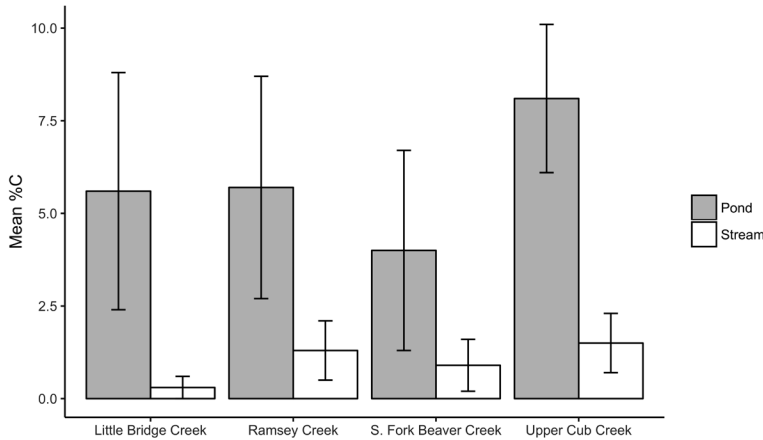


Figure 2. Paired pond and in-stream sediment %C comparisons were significant across all beaver reintroduction locations (Welch's *t*-test; $P < 0.001$).

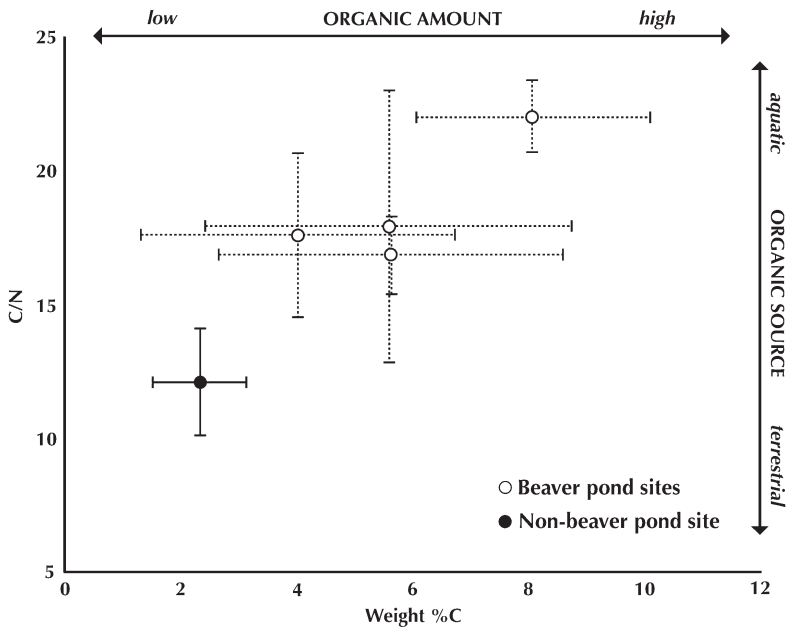


Figure 3. Mean and standard deviation for all %C and C/N ratios of pond sediment samples from each beaver reintroduction pond, and the non-beaver pond.

(Welch's *t*-test; $t = 6.437$, $df = 66.128$, $P < 0.0001$). %C was variable within each beaver pond, but the average across all beaver ponds was 2.2 times the mean %C of the non-beaver pond (5.3% versus 2.4%, respectively). The mean C/N ratios of

beaver pond samples were significantly higher than those for the non-beaver pond samples (Table 1, Figure 3) (Welch's *t*-test; $t = 8.491$, $df = 30.062$, $P < 0.0001$). All pond and stream %C, %N and C/N data are presented in Table S1 (available online).

The C/N ratios and %C values from each beaver pond and the non-beaver pond (Figure 3, Table 1) were significantly different (Whole Model; MANOVA – Pillai's Trace Test; approximate $F_{8,112} = 8.603$, $P < 0.0001$). To explore patterns among ponds, when each beaver pond was individually compared to the non-beaver pond using a post-hoc comparison, the mean %C and C/N were significantly higher in all beaver ponds ($P < 0.05$). Post-hoc multivariate pairwise comparisons of %C and C/N among beaver ponds ranged from non-significant to significant, emphasizing that every beaver pond is unique, both hydrologically and geochemically. When all beaver pond samples from all locations were combined, the difference in %C and C/N between the beaver ponds and the non-beaver pond was statistically significant (MANOVA – *F* Test; $F_{2,58} = 16.872$, $P < 0.0001$).

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C in the 0–10 cm sample to 3.3% C in the 10–20 cm sample (Table 2). In contrast, pH (overall) and bulk density increased with depth. Within beaver ponds, the PCA identified site-specific environmental variation in water parameters representing a range of temperature, pH, dissolved oxygen, and conductivity (PC1 representing 43% and PC2 representing 31% of variation; Figure 4; Table 3). The beaver and non-beaver ponds were all fairly dispersed in multivariate space indicating that each site was different in water parameter properties. In other words, reintroduced-beaver ponds were not consistently similar to each other when considering all the water parameter data simultaneously.

Discussion

The current literature on beaver ecology supports a robust understanding of how beaver dams influence the movement of sediment through watersheds (e.g., Pollock et al. 2014), and the storage of organic carbon in riparian sediments (e.g., Naiman et al. 1994). Sediment records from beaver meadows provide a long-term (decades to centuries) perspective on organic carbon storage (Wohl 2013), whereas samples of suspended stream sediments and sediments from active ponds reflect short-term dynamics (individual flood events to years) (Naiman et al. 1986, Wegener et al. 2017). The magnitude and quantification of the effect of beavers on carbon storage in sediments is generally reported as % organic carbon content, density of organic carbon, or as carbon per area, depending on the spatial and temporal scale of the study. Beaver meadows are particularly well-researched, and studies of beaver sediments have documented everything from local impacts on carbon reservoirs (e.g., the carbon density in beaver meadow soils was nearly two times that in adjacent forest soils after several decades of beaver presence in northern Minnesota [Johnston 2014]), to contributions to landscape scale carbon budgets (for example; active beaver meadow sediments account for

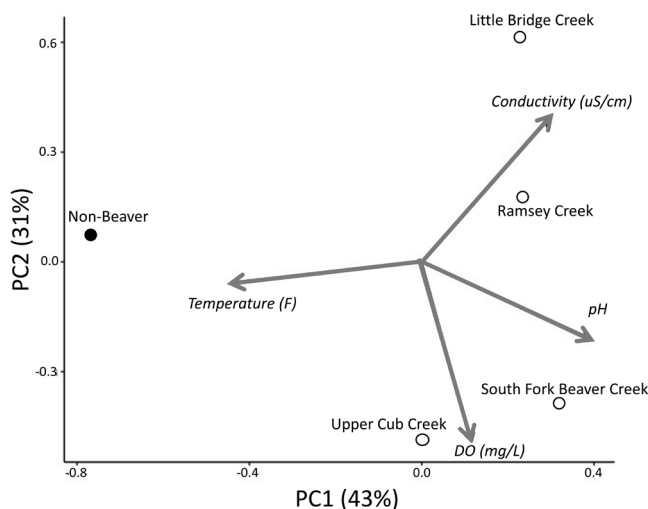


Figure 4. Principle component analysis (PCA) displaying the site-specific environmental variability of reintroduced beaver ponds and the non-beaver pond within the Methow River watershed. Environmental variation represents a range of temperature, pH, dissolved oxygen, conductivity, and pond size with PC1 representing 43% and PC2 representing 31% of variation.

nearly a quarter of total organic carbon storage in watersheds of the eastern Rockies [Wohl et al. 2012]). Even without beaver activity, floodplain and wetland sediments in forested riparian systems are substantial reservoirs of organic carbon, so persistent beaver activity enhances storage in a critical riparian area (Sutfin et al. 2016).

In Methow headwater stream sites the sampling and analysis of riparian sediments was constrained by both the recent timing of beaver reintroductions, and the geomorphic settings where reintroductions occurred. Specifically, since the beaver dams had only been active for two to five years—the sites were characterized by active or recently drained ponds, and very small areas of wetland immediately adjacent to the pond banks (no wetland or meadow networks). Additionally, most of the beaver reintroduction sites were in narrow steep-sided valleys with incised stream channels. We aimed to put our results into the context of the substantial literature on carbon storage in beaver sediments, but used caution because records from pond sediments in recently dammed streams may not be directly comparable

TABLE 1. Mean and standard deviation of %C, %N, and C/N ratio for pond samples from the four beaver creek sites, and the non-beaver pond site.

Site	Sample Size (<i>n</i>)	Pond Area (m ²)	%C Mean (SD)	%N Mean (SD)	C/N Mean (SD)
South Fork Beaver Creek	26	531	4.0 (2.7)	0.2 (0.2)	17.6 (3.1)
Little Bridge Creek	9	79	5.6 (3.2)	0.3 (0.2)	17.9 (5.1)
Ramsey Creek	12	113	5.7 (3.0)	0.3 (0.2)	16.8 (1.5)
Upper Cub Creek	10	314	8.1 (2.0)	0.4 (0.1)	22.0 (1.4)
Non-beaver pond	13	531	2.4 (0.8)	0.2 (0.1)	12.1 (2.0)

TABLE 2. South Fork Beaver Creek sediment pit sub-sample properties by depth. %C and %N decreased with depth, while in contrast, pH and bulk density generally increased with depth.

Depth	pH	Bulk Density	%C	%N
0–10	6.14	0.38 g/mL	20.03	0.77
10–20	6.09	1.09 g/mL	3.34	0.20
20–30	6.59	1.30 g/mL	1.61	0.14

to published records derived from wetlands and meadows systems with more complicated depositional and biogeochemical histories.

We found that beavers reintroduced into river segments of the Methow River watershed have had a significant impact on total carbon storage in sediments associated with the beaver impoundments. The Methow in-stream sediment samples (collected both up and down stream of the dam sites) are organic poor, with an average of approximately 1.0% C. The Methow beaver pond sediment average of 5.3% C falls within the range of 3% and 12% for relict, and active beaver meadows, respectively, in Rocky Mountain National Park (Wohl et al. 2012, Wohl 2013), and is comparable to the 6.25% C reported for active beaver ponds in Quebec (Naiman et al. 1986). The Methow pond %C values are much lower than the 23% C reported for pond sediments in Minnesota (Naiman et al. 1994), and generally lower than values reported for shallow (less than 10 cm) beaver meadow sediments from sites in Voyageurs National Park (Johnston 2014). Ultimately, sediment retention and carbon storage is system specific, and the absolute values may only be directly comparable in similar riparian settings in given region. Our

study suggests that while it may take decades before the full scope of abiotic and biotic impacts fully emerge, aquatic food webs may be substantially bolstered by increased carbon sequestration within only a few seasons of beaver reintroduction. This finding has restoration implications because little work has examined if impacts on sediment biogeochemistry are similar between transplanted beavers and beavers that independently choose dam locations. Our findings clearly suggest that transplanted beavers do substantially and rapidly influence carbon sequestration within their pond habitats on a similar scale to non-transplanted beavers (Naiman et al. 1986).

The higher average %C and C/N ratio in the beaver ponds compared to the non-beaver pond are likely from the active loading of terrestrial organic material by beavers into the ponds via feeding and dam building practices (Jenkins 1980, Naiman et al. 1986). Concurrently, variable mineralization conditions in response to altered oxidation-reduction reactions within the beaver ponds could be contributing to the higher %C values we observed (Naiman et al. 1994). Consistent with previous beaver studies, the reintroduced Methow beavers added organic carbon sources from the surrounding terrestrial environment into the aquatic food web, which otherwise, would not have been incorporated (e.g., France 2000). Across ecosystems, terrestrial plants tend to have much higher C/N ratios (generally greater than 10) than aquatic primary producers (generally less than 10) such as phytoplankton, macrophytes, algae and periphyton (reviewed in Finlay and Kendall 2007). In our system, the average C/N ratios of the organics that accumulated in the non-beaver and beaver ponds were 12.1 versus 18.2,

TABLE 3. Water property data for beaver and non-beaver pond sites.

Site	Dissolved Oxygen (DO) (mg L ⁻¹)	Temperature (°C)	pH	Conductivity (uS/cm)
Little Bridge Creek	4.82	11.4	7.52	708
S. Fork Beaver Creek	9.41	9.5	7.84	677
Upper Cub Creek	8.63	16.9	8.00	663
Ramsey Creek	6.85	10.6	7.57	693
Non-Beaver Pond	6.20	23.6	6.53	661

respectively. The non-beaver sediment organics were likely primarily derived from a mixture of aquatic materials, and terrestrial leaf litterfall. In contrast, the bioengineering and feeding activity of reintroduced beavers in the beaver ponds resulted in a higher amount of terrestrial organic material (i.e., wood, foliage, feces) being introduced and retained in headwater stream sediments. Based on observations by Kent Woodruff, the main tree and shrub species available to the reintroduced beavers are aspen (*Populus tremuloides* Michx.), willow (*Salix* spp.), alder (*Alnus* spp.), black cottonwood (*Populus trichocarpa* Torr. & A. Gray ex Hook), and red-osier dogwood (*Cornus sericea* L.), which together constitute over 70% of the deciduous trees found around our beaver pond sites.

Intriguingly, recruitment and retention of terrestrially-derived, organic carbon in riparian zones can produce both desired and undesired conservation outcomes on stream traits like alteration of riparian vegetation composition, stream temperature shifts, and native-fish-habitat modification (Rosell et al. 2005, Kemp et al. 2011). Nonetheless, the terrestrial carbon subsidies, in tandem with increased nutrient loads from runoff and beaver fecal matter, are known to augment algal production (Coleman and Dahm 1990), and aquatic invertebrate diversity (Naiman et al. 1988). For example, lentic invertebrates like oligochaetes, pycnopsods, and odonates are known to increase in abundance in soft bottom sediments within beaver ponds (McDowell and Naiman 1986, Hagglund and Sjöberg 1999). Such changes in stream community composition undoubtedly have bottom-up impacts on the structure and functioning of aquatic food webs (Malison et al. 2015).

Beavers facilitate the recruitment and storage of carbon in stream ecosystems in the form of terrestrial organic material because their dams increase the deposition of coarse wood and other debris. The sediment pit (0–30 cm depth) data from the South Fork Beaver Creek site (a site that would otherwise store little to no organic material), suggested that pond formation has influenced carbon accumulation in sediments adjacent to the ponds in the two years since beavers were reintroduced. (Table 2). Beaver-driven landscape modification adds habitat heterogeneity (i.e., lentic habitat) while also creating stepping-stone habitats for future wetland meadow formation (see successional model in Pollock et al. 2014). Presumably, even if the dams are not maintained within the landscape, legacy effects in terms of sediment and carbon accumulation could persist with wetland or meadow habitat for decades (Naiman et al. 1994, Burchsted et al. 2010).

Conclusions

This study adds to a growing body of literature suggesting that beavers can be used as an innovative tool for whole ecosystem restoration (Pollock et al. 2007, Gibson and Olden 2014, Petro et al. 2015, Law et al. 2017). More specifically, our findings suggest that a substantial increase in organic matter retention can occur within a few seasons, much faster than the well-established decadal timeline previously observed. Organic sediment retention in fluvial ecosystems is consequential because increased organic matter in beaver dam sediments provides energy to local pond, riparian and emergent wetland areas. Within our study region, the large-scale benefit of beaver reintroductions appears to have also increased

overbank flow thus contributing greater volumes of water to the valley's aquifers. Continued beaver reintroduction and its accompanying slackwater habitat creation, riparian area emergence, and carbon retention also improve salmon spawning and rearing habitat. The successful efforts of the Methow Beaver Project highlight the viability of reintroduced beavers as a conservation tool, and have resulted in a positive effect on ecosystem recovery via allochthonous carbon storage that will have lasting effects in the Methow Valley watershed. Our findings cautiously support the conclusion that whole ecosystem restoration may be augmented and accelerated by reintroducing beaver to areas of historically high abundance.

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Channel incision, evolution and potential recovery in the Walla Walla and Tucannon River basins, northwestern USA[†]

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Abstract

We evaluated controls on locations of channel incision, variation in channel evolution pathways and the time required to reconnect incised channels to their historical floodplains in the Walla Walla and Tucannon River basins, northwestern USA. Controls on incision locations are hierarchically nested. A first-order geological control defines locations of channels prone to incision, and a second-order control determines which of these channels are incised. Channels prone to incision are reaches with silt-dominated valley fills, which have sediment source areas dominated by loess deposits and channel slopes less than $0.1(\text{area})^{-0.45}$. Among channels prone to incision, channels below a second slope–area threshold ($\text{slope} = 0.15(\text{area})^{-0.8}$) did not incise. Once incised, channels follow two different evolution models. Small, deeply incised channels follow Model I, which is characterized by the absence of a significant widening phase following incision. Widening is limited by accumulation of bank failure deposits at the base of banks, which reduces lateral channel migration. Larger channels follow Model II, in which widening is followed by development of an inset floodplain and aggradation. In contrast to patterns observed elsewhere, we found the widest incised channels upstream of narrower reaches, which reflects a downstream decrease in bed load supply. Based on literature values of floodplain aggradation rates, we estimate recovery times for incised channels (the time required to reconnect to the historical floodplain) between 60 and 275 years. Restoration actions such as allowing modest beaver recolonization can decrease recovery time by 17–33 per cent. Published in 2007 by John Wiley & Sons, Ltd.

Keywords: channel incision; channel evolution; aggradation; stream restoration

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Introduction

Incised channels range from small rills and gullies to large, entrenched river channels (Harvey and Watson, 1986; Schumm, 1999). Gullying into unchanneled valleys or swales is commonly initiated when land use changes cause increased runoff or decreased vegetative cover (Montgomery, 1994; Prosser and Slade, 1994; Prosser and Soufi, 1998; Croke and Mockler, 2001), whereas stream channel entrenchment often results from base level lowering, climate or land use changes that increase stream flows, or loss of riparian vegetation (Balling and Wells, 1990; Booth, 1990; Magner and Steffen, 2000; Waters and Haynes, 2001; Croke and Mockler, 2001; Doyle *et al.*, 2003). In all of these cases, incision occurs when erosive forces of the stream overcome the strength of underlying materials (Harvey and Watson, 1986), often starting low in the drainage and progressing upvalley as a migrating vertical headcut (Leopold *et al.*, 1964). Both gullying and channel entrenchment are common throughout the world (Bravard *et al.*, 1997; Wasson *et al.*, 1998; Scott *et al.*, 2000), causing declines in both stream and riparian ecosystem functions (Shields *et al.*, 1995; Bravard *et al.*, 1997).

Although many studies have related the occurrence of incision to changes in climate or land use impacts (Cooke and Reeves, 1976; Schumm, 1999), few have sought to explain why some channels in a river basin are entrenched while others are not. Moreover, characteristics of entrenched channels (e.g. incision depth, cross-section shape) vary longitudinally as well as among tributaries (Patton and Schumm, 1975; Schumm *et al.*, 1984; Simon and Hupp, 1987; Thorne, 1999), and mechanisms underlying such patterns have received limited attention. In this paper our first aim is

to explain these patterns in a semi-arid river basin by identifying geological and fluvial controls on the occurrence and nature of channel entrenchment. Our approach to this problem relies on a hierarchical framework that first identifies which channels are prone to incision, and second identifies a slope–area incision threshold within the population of channels prone to incision. Channels that are prone to incision typically flow through silty valley fills, whereas channels in coarse-grained alluvium generally resist incision (Cooke and Reeves, 1976; Schumm, 1999). Therefore, we hypothesize that channel incision is limited to reaches in which the caliber of source sediment and low transport capacity caused accumulation of fine-grained valley fills. Among channels prone to incision, channels with greater flow strength are more likely to incise (Prosser and Abernethy, 1996; Montgomery, 1999), so we also hypothesize that – within the population of channels prone to incision – channels with steeper slope and larger drainage areas are more likely to be incised. Thus, we assess the degree to which channel slope, drainage area and the geology of sediment source areas are related to locations and depths of channel incision, and we identify both first- and second-order thresholds for channel incision.

Once incision begins, channels are commonly described as evolving through four stages: incision of a narrow channel, channel widening, development of an inset floodplain and aggradation (see, e.g., Schumm *et al.*, 1984; Simon and Hupp, 1987; Thorne, 1999). Region-specific channel evolution models vary in the number and details of these stages, but all encompass these four general phases. Incision typically occurs rapidly once it begins, but rates of subsequent widening and aggradation vary widely (Simon *et al.*, 1999; Elliott *et al.*, 1999). The length of each stage and the timing of transitions between stages are a function of bank height and material, erosive forces at the toe of the bank, the capacity of the stream to export failed materials and sediment retention mechanisms (Simon *et al.*, 1999; Elliott *et al.*, 1999). However, there has been little research describing variation in evolution pathways or rates, and little focus on restoration strategies that seek to aggrade channels to the level of their historical floodplains (Pollock *et al.*, 2007). Our second objective, therefore, is to describe basin-scale variation in channel evolution and potential recovery rates. Specifically, we show that published channel evolution models do not adequately describe the observed variation in channel form and evolution. Therefore, we propose a second evolution model to describe channels that do not fit traditional models, and show how channel size and incision depth determine which of two channel evolution models a reach is likely to follow. Finally, we estimate the time required for a channel to aggrade to the elevation of its former floodplain based on published aggradation rates, and examine the potential for decreasing recovery time through restoration actions.

Study Area

We selected a geologically simple study area comprised of two main lithologies, erosion resistant basalt (Mackin, 1961; Lasmanis, 1991) and fine-grained surficial deposits comprised of mainly of silt (Bretz, 1929) (Figure 1). These lithologies produce distinctly different size classes of sediments: mainly silt and finer sediments from the surficial deposits, and mainly gravel and coarser sediments from the basalts. The Walla Walla and Tucannon River basins have their headwaters in the Blue Mountains of southeastern Washington State, USA, which are comprised of Miocene Grande Ronde Basalt (Lasmanis, 1991). The middle and lower portions of the basins are dominated by loess hills and terraces of silt-dominated deposits of the Lake Missoula floods (Bretz, 1929). The glacial Lake Missoula repeatedly formed east of the Rocky Mountains between 15 300 and 12 700 years before present (ybp), when the continental ice sheet dammed what is today the Clark Fork River in northern Idaho (Pardee, 1910; Waitt, 1985). Each failure of the ice dam released a catastrophic flood through the Columbia basin (Bretz, 1923; Baker, 1978; Waitt, 1985), and left deep silt deposits in the backwater of flood flows near the mouth of the Walla Walla River (Bretz, 1923, 1925). Subsequent aeolian erosion of these deposits carried silts eastward to form the loess hills of the Palouse region (Busacca and McDonald, 1994), which cover the majority of the study area. Silt terraces in the lower Walla Walla River are remnants of the Lake Missoula flood deposits (Bretz, 1929).

The Walla Walla and Tucannon Rivers flow from the Blue Mountains into the Columbia and Snake Rivers (Figure 1). Peaks in the Blue Mountains typically exceed 1500 m in elevation, and the Palouse Hills to the west range in elevation from approximately 150 to 650 m. Mean annual precipitation ranges from less than 25 cm yr⁻¹ at low elevations in the western portion of the basin to more than 150 cm yr⁻¹ at higher elevations in the Blue Mountains (NRCS, 1998). Much of the winter precipitation falls as snow and melts later in the spring. Headwater channels in the study area are generally steep (slope > 0.10), and slopes of the major tributaries in narrow valleys of the Blue Mountains are typically 0.02–0.04. Our study focused on lower elevation streams with wide valley floors and channel slopes typically less than 0.02.

Natural upland vegetation is predominantly sage brush (*Artemisia* spp.) in the western lowlands, grasslands (*Agropyron* spp., *Festuca* spp.) in the Palouse hills and mixed grassland and ponderosa pine (*Pinus ponderosa*) forest in the Blue

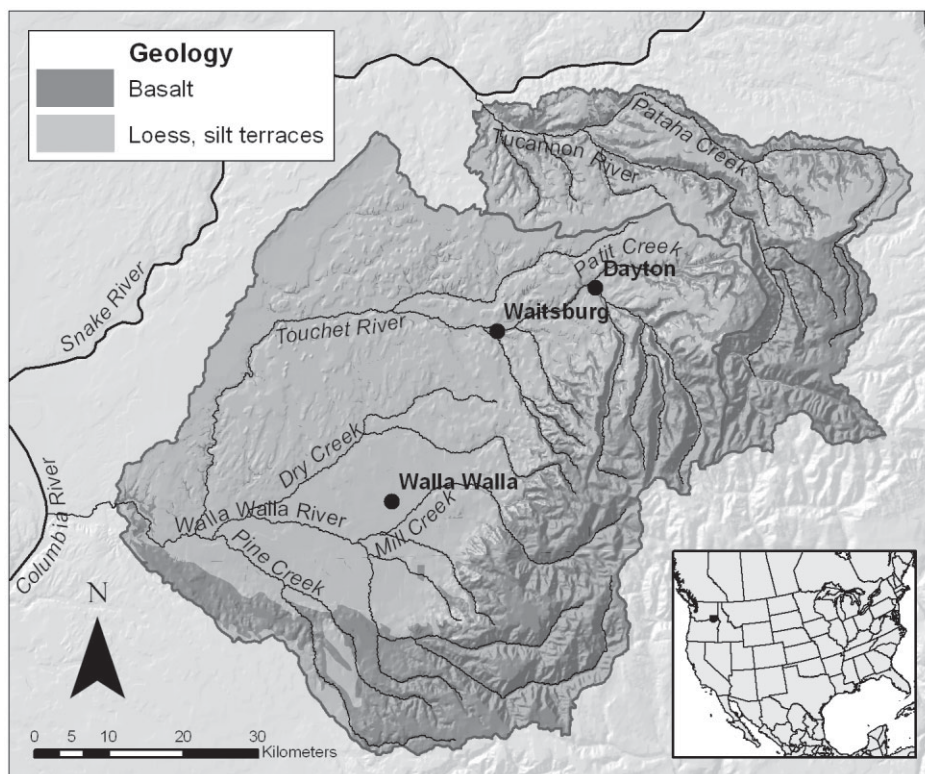


Figure 1. Study area locations and geologic map of the Walla Walla and Tucannon River basins in northwestern USA.

Mountains (Franklin and Dyrness, 1973). Natural riparian vegetation in the lower reaches is dominated by shrubs and small trees, including willow (*Salix* spp.) and red osier dogwood (*Cornus stolonifera*). Sedges (*Carex* spp.) are also common on inset floodplains in the lower reaches. Middle reaches are dominated by hardwood species including white alder (*Alnus rhombifolia*), black cottonwood (*Populus trichocarpa*) and quaking aspen (*Populus tremuloides*). The upper floodplain reaches are dominated by cottonwood, aspen and ponderosa pine.

The historical record indicates that channel incision in the Walla Walla and Tucannon River basins occurred later than 1863, as there was no mention of gullies or incised channels in prior surveys (General Land Office survey notes, 1860–1863). The presence and depth of channel incision varies among tributaries and reaches, with incised channels located predominantly in silt-dominated valley fills and non-incised channels in gravel or coarser valley fills (Figure 2). Erosion of loess soils has been substantial in the past century (Pimental *et al.*, 1995), with as much as 1 m of soil loss in some locations (Figure 3). Upland erosion rates estimated from sediment yields in the 1960s were 146 tonnes km⁻² yr⁻¹ in the Blue Mountains to over 1400 tonnes km⁻² yr⁻¹ in cultivated areas of the Palouse Hills (Mapes, 1969). Most sediment exported from the Walla Walla basin originated in the loess-dominated Dry Creek and Touchet River basins, with the highest sediment concentration (maximum 316 000 mg l⁻¹) recorded in Dry Creek (Mapes, 1969). Suspended load comprised 88–95 per cent of the total sediment load in the mountains, and 92–98 per cent of the load in the lowlands (Mapes, 1969). The suspended load was predominantly silt (60–75 per cent of the suspended load). Erosion control practices implemented since the 1970s are estimated to have reduced sediment yields by approximately 10 per cent from 1970s levels (Ebbert and Roe, 1998). Valley bottom soils are layered, silt-dominated deposits with bulk density of about 1.3 g cm⁻³ (Harris *et al.*, 1964).

Methods

In this study we first focused on determining why some relatively low-gradient (slope < 0.02 m m⁻¹) stream channels in the Walla Walla and Tucannon River basins had incised while others had not. We considered a channel to be incised ('entrenched' in the terminology of Schumm, 1999) when its former floodplain had become a terrace (Pickup and

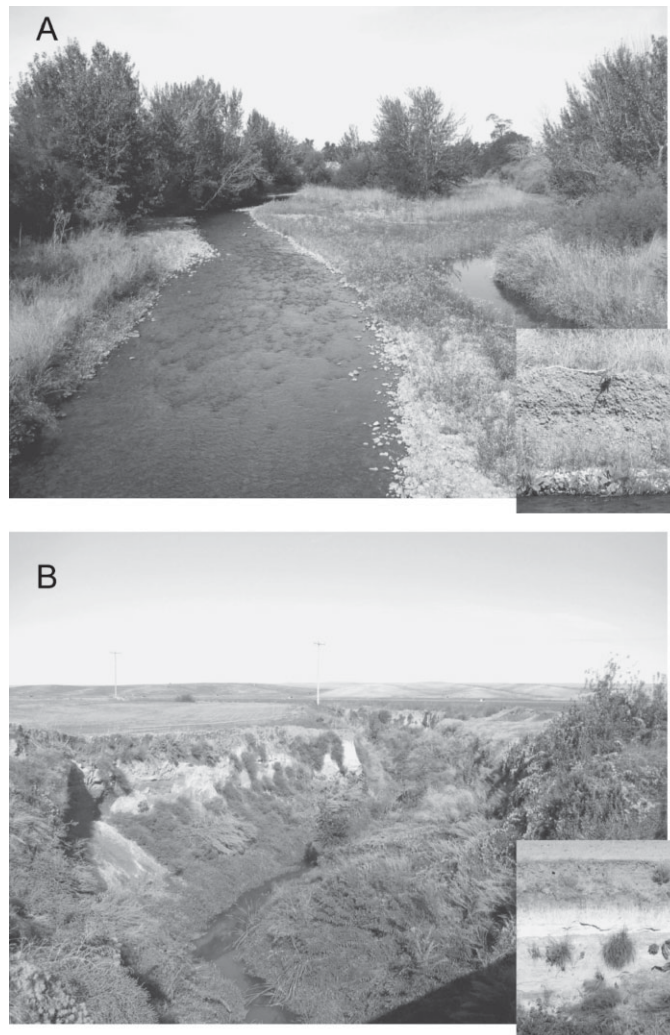


Figure 2. Typical incised and non-incised channels in the study area. (A) Non-incised channel with gravel floodplain (Walla Walla River). Active channel width is approximately 19 m; the inset shows a closer view of gravelly floodplain deposits. (B) Channel incised into cohesive silt deposits (Dry Creek). Active channel width is approximately 2.5 m, incision depth is ~7 m and the top width of the incised channel is ~24 m; the inset shows a closer view of silt-dominated terrace deposits (terrace height is ~5 m).

Warner, 1976), and we could identify a bankfull channel cross-section inset within a larger incised-channel cross-section (Montgomery and MacDonald, 2002). We defined the floodplain as the depositional surface adjacent to a stream that is flooded at least every few years (Dunne and Leopold, 1978), whereas a terrace is a former floodplain that is no longer inundated (Wolman and Leopold, 1957). Our second aim was to determine whether recovery pathways or rates vary among channels, and to explain the utility of using more than one channel evolution model in planning and implementing incised channel rehabilitation efforts. Finally, we estimated recovery time (the time required to refill the incised channel and reconnect it to its historical floodplain), and evaluated whether restoration actions can significantly decrease recovery time.

Channel mapping and measurement

We visited 63 sites in the two mainstem rivers and 10 of their tributaries, and measured key channel dimensions at 45 of these sites with a laser rangefinder (Impulse Laser 200 LR, Laser Technology). At the remaining 18 sites, we noted whether channels were incised or not to aid in mapping the extent of channel incision in the basin. We mapped the spatial extent of incision of 501 km of channel based on cross-section measurements and continuous visual surveys



Figure 3. Deflation of a loess soil surface by as much as 1 m around a cemetery at least 135 years old in the Dry Creek basin (cemetery established ca. 1869). The scarp at the lower right edge of the cemetery is approximately 1 m high, and the scarp near the post is approximately 50 cm high. Maximum erosion rate at this site over the past 135 years averages 0.07 cm yr^{-1} .

between cross-section locations. Where access was difficult and we could not conduct visual surveys between cross-sections (less than 10 per cent of the mapped channels), we inferred incision based on upstream and downstream conditions, and similarity of channel slope and valley floor width in the unobserved reach to slope and valley floor width of upstream and downstream reaches. Channel slopes and valley floor widths were measured from a 10 m resolution digital elevation model. At each of the 45 field sites we measured top width of the incised channel (width at the level of the historical floodplain) and incision depth (depth from historical floodplain to current channel bed) (Figure 4). Where bankfull channel dimensions could be reliably identified (39 of 45 sites), we also measured bankfull width (channel width at elevation of the inset floodplain) and bankfull depth (depth from inset floodplain to current channel bed). We classified the dominant bed, bank and terrace material as silt or finer ($<0.063 \text{ mm}$), sand ($0.063\text{--}2 \text{ mm}$), gravel ($2\text{--}64 \text{ mm}$), cobble ($64\text{--}256 \text{ mm}$) or boulder ($>256 \text{ mm}$), and described bank and floodplain vegetation. Site locations were recorded with a handheld global positioning system (GPS), and we later used a geographic information system (GIS) to calculate drainage area upstream of each site (A), the proportion of the drainage area mapped as basalt (B) and channel slope at the site (S) from a 10 m resolution digital elevation model.

Relating incision to drainage basin and channel characteristics

We examined the occurrence of channel incision in relation to drainage basin or channel characteristics in two ways. First, we assessed whether mean values of channel slope (S), drainage area (A) or percent basalt (B) differed

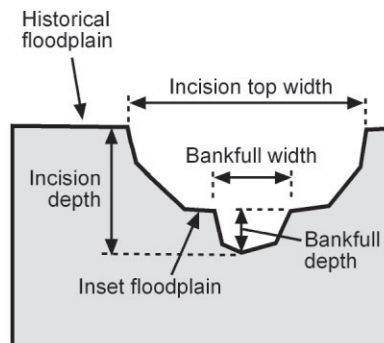


Figure 4. Schematic diagram of incised channel with inset floodplain and bankfull channel, illustrating measurements and terminology used in this paper.

significantly between incised and non-incised channels. Second, we identified slope–area domains of fine-grained and coarse-grained floodplains to document a potential threshold between the two (similar to slope–discharge thresholds in previous studies, Leopold and Wolman, 1957; Patton and Schumm, 1975; Church, 2002). We expected that channels with lower channel slope and smaller drainage areas would be more likely to accumulate fine sediments on their floodplains historically, and therefore were more likely locations for channel incision.

We examined whether incision depth was related to slope, discharge and percent basalt using regression analysis (Neter *et al.*, 1989). Incision depth was equivalent to depth of fine sediment accumulation, as incised channels cut through the entire fine sediment deposit until reaching a resistant layer (bedrock or paleo-river bed). We regressed sediment depth against individual variables, multiple variables and interaction terms among variables (Neter *et al.*, 1989). We hypothesized negative relationships between depth of accumulated sediment (d_{total}) and channel slope or percent basalt because lower slope reaches should retain more fine sediments and reaches with less of their drainage basin in basalt should have a higher supply of fine sediments (i.e., more of the total sediment load is from loess deposits). We also hypothesized a negative relationship between d_{total} and drainage area because reaches with smaller drainage areas have smaller discharge and should therefore aggrade more rapidly. Finally, we hypothesized that the relationship between d_{total} and the slope–area index (SA , channel slope multiplied by drainage area) would be negative because reaches with low stream power (a correlate of SA) should retain more fine sediment. Reaches with low percent basalt combined with either low channel slope or low stream power should have the deepest accumulations of fine sediment.

Results

We observed channel incision in over half of the stream length surveyed (259 km out of 501 km), with incision rarely occurring in the mountain valleys (Figure 5). Most channel incision was in the lower portions of rivers and tributaries, where only a small proportion of the drainage basin lithology was basalt (median percentage = 34 per cent basalt), and

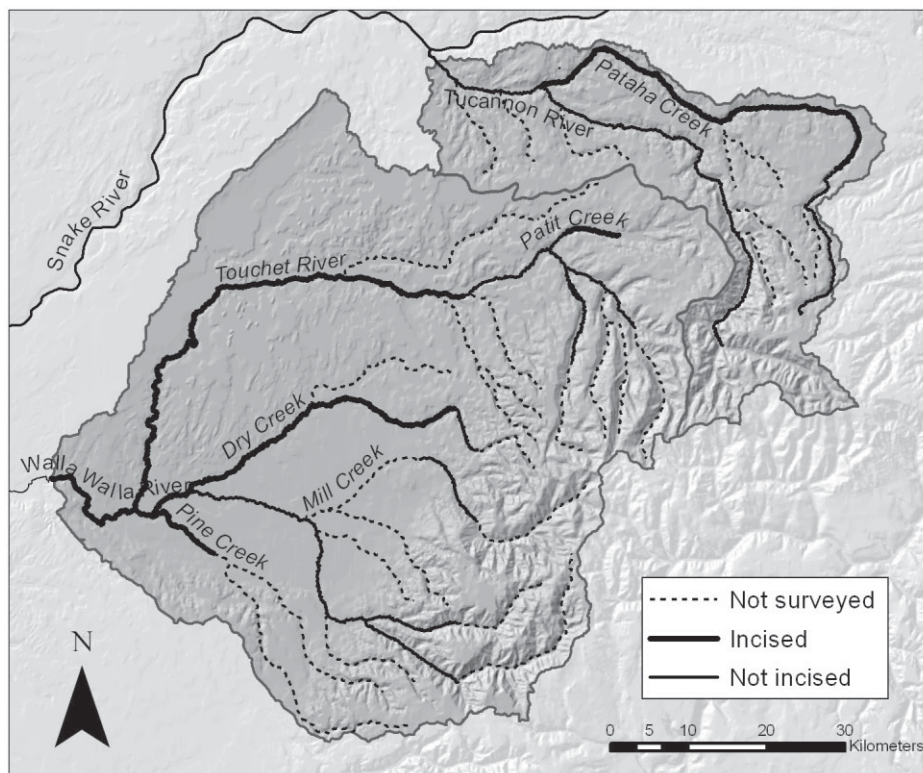


Figure 5. Location and extent of incised and non-incised channels in the Walla Walla and Tucannon River basins. Only the major tributaries were surveyed in this study.

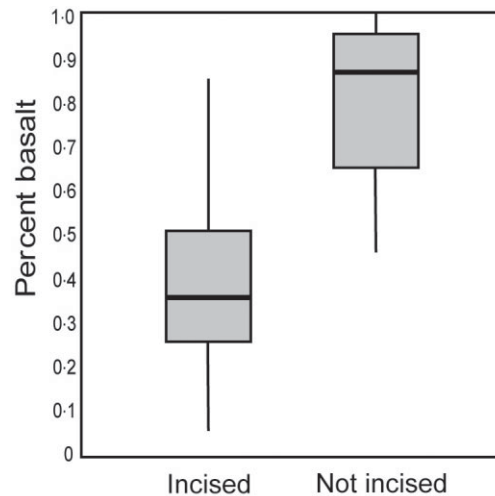


Figure 6. Proportion of drainage basin upstream of incised and non-incised cross-section sites mapped as basalt. Heavy line indicates median value, box indicates inter-quartile range and whiskers indicate range.

sediment source area was dominated by loess deposits. Drainage basins of almost all non-incised channels were dominated by basalt (median = 87 per cent basalt) (Figure 6).

Slope and drainage area clearly distinguished three groups of channels. Channels with slope steeper than about $0.1(A)^{-0.45}$ had floodplains of gravel and coarser particles, and none of these channels were entrenched (Figure 7). Channels with slope less than $0.1(A)^{-0.45}$ accumulated thick, valley-filling silt deposits prior to the late 1800s. Of these, only six reaches (on two streams) with slope less than $0.15(A)^{-0.8}$ were not entrenched, whereas the remaining channels had incised through relatively uniform silt-dominated deposits until reaching either bedrock or the gravel-cobble armor layer of a paleo-channel. We found no gravel or coarser deposits in the silt-dominated strata overlying the paleo-channel bed material, suggesting that channels were not armored with gravel or coarser material during the period of silt accumulation. However, 93 per cent (26/28) of entrenched channels have gravel or coarser beds today, indicating that present-day channels easily transport silt.

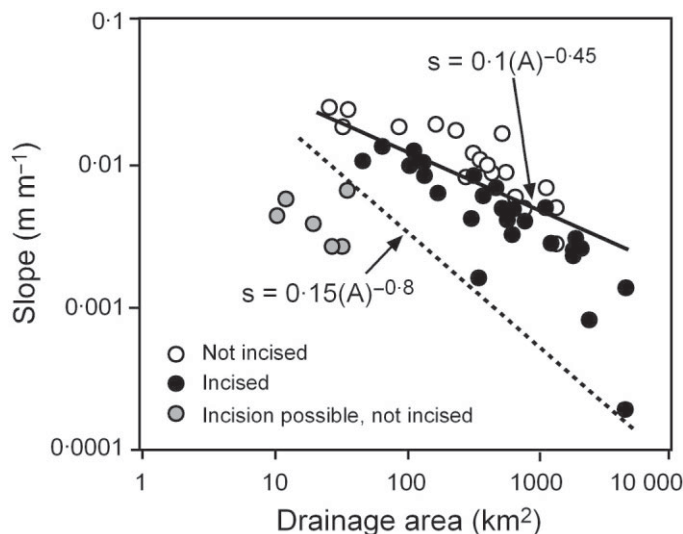


Figure 7. Drainage area and slope plot, illustrating that channels with slope exceeding $0.1(A)^{-0.45}$ are generally not incised, whereas incised channels tend to have slope less than $0.1(A)^{-0.45}$. Very small, low slope streams (gray filled circles) are prone to incision (i.e., they have slopes considerably less than $0.1(A)^{-0.45}$), but are not incised.

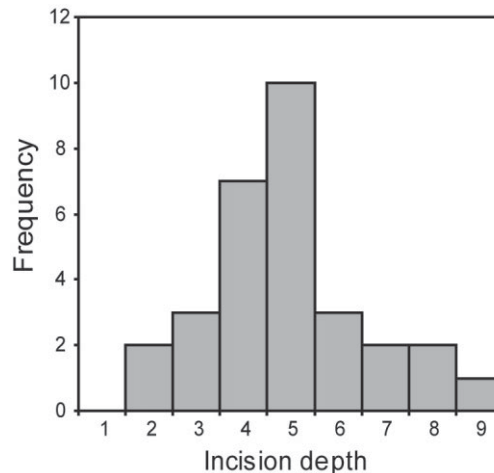


Figure 8. Histogram of incision depths measured at 30 locations in the Walla Walla and Tucannon River basins.

Channel incision depth ranged from 1.8 to 8.3 m, and more than 50 per cent of measured incision depths were between 4 and 6 m (Figure 8). Incision depth was negatively related to both slope ($P = 0.02$, $r^2 = 0.18$) and percentage of drainage basin in basalt ($P = 0.01$, $r^2 = 0.22$), but was more strongly related to the interaction term slope multiplied by percent basalt ($d_{\text{total}} = 0.93(SB)^{-0.21}$, $P = 0.0006$, $r^2 = 0.36$). This interaction term indicates that reaches with low slope and low percent basalt are most deeply incised, and also that incision depth decreases more rapidly with increasing channel slope where percent basalt is low. Incision depth was not significantly related to either drainage area or the slope–area index, either separately or in combination with other variables (i.e. where either variable was included in interaction terms or a multi-variable model).

Total cross-section areas of incised channels ranged from 18 to 327 m², and were on average about one order of magnitude larger than cross-section areas of non-incised channels (Figure 9(A)). Bankfull cross-section areas of incised channels were similar to those of non-incised channels on average, but were more variable (Figure 9(B)). Bankfull width–depth ratios of incised channels were consistently lower than those of non-incised channels (Figure 9(C)), and did not increase with increasing drainage area. By contrast, bankfull width–depth ratios of non-incised channels increased with increasing drainage area.

Channel form varied with drainage area and incision depth, but did not consistently follow idealized channel evolution models (Figure 10). Small channels that were deeply incised had sloped failure deposits buttressing the base of vertical silt banks, and apparently cannot widen and develop significant inset floodplains. These reaches had top width to incision depth ratios less than 6. The mainstem Walla Walla and Touchet Rivers are considerably wider, but the reaches with widest top width to incision depth ratios between 17 and 45) were upstream of reaches that have not yet widened and developed inset floodplains (width–depth ratios between 4 and 12).

Discussion

Our results highlight several new aspects of channel incision and evolution, each of which has important implications for understanding controls on locations of channel incision or for understanding rates and pathways of incised channel recovery. We examine these results and their implications in three parts. First, we discuss how regional patterns of relatively continuous channel entrenchment are controlled predominantly by geomorphic propensity for incision, rather than by the spatial pattern of land uses or channel modifications. To our knowledge, no prior studies have systematically examined a geological control on locations of channel entrenchment, although several studies have examined slope–discharge thresholds for discontinuous gullying (e.g. Patton and Schumm, 1975) or variation in land uses as a control on incision locations (e.g., Thorne, 1999). Second, we describe how rates and pathways of channel evolution vary as a function of channel size and incision depth, and propose a second channel evolution model for channels that do not evolve in a sequence consistent with traditional evolution models. The two models can be used to help identify where channel rehabilitation efforts are most likely to be successful (Shields *et al.*, 1998). Finally, we address the concept of ‘recovery time’ (Beechie *et al.*, 2000; Beechie, 2001), and estimate how long it may take for channels to reconnect to their historical floodplains both with and without restoration actions.

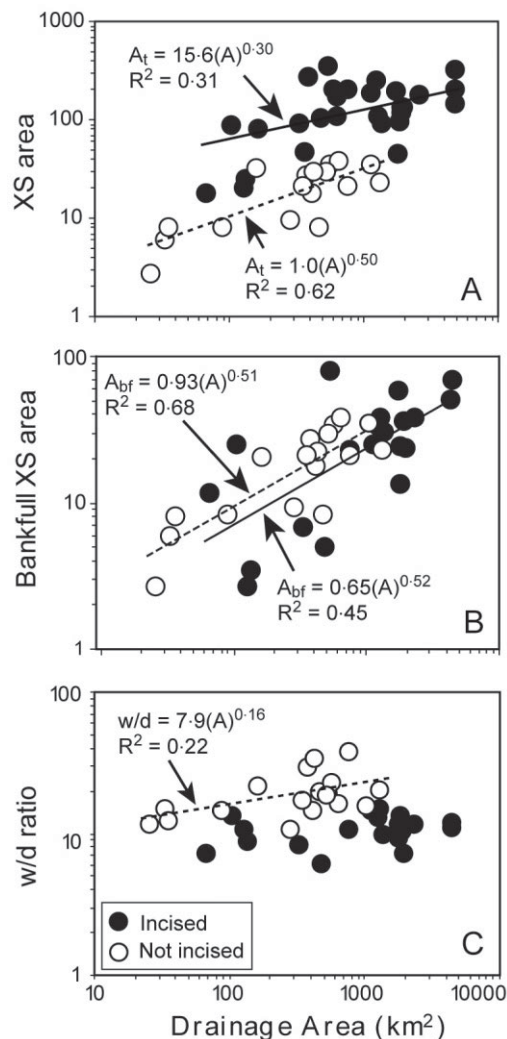


Figure 9. Channel dimensions of incised and non-incised channels: (A) incised channel cross-section area (for non-incised channels, bankfull channel cross-section areas are plotted), (B) bankfull cross-section areas and (C) width–depth ratio of the bankfull channel. Regression equations and R^2 values are shown for significant regressions ($p < 0.05$). Variables in equations are total cross-section area of incised channel (A_t), bankfull cross-section area (A_{bf}), width to depth ratio (w/d) and drainage area (A).

Hierarchical controls on channel incision locations and depth

We hypothesized that the spatial pattern of channel entrenchment in the Walla Walla and Tucannon River basins was largely controlled by location of silt-dominated valley fills, which in turn was determined by the availability of fine-grained source sediments and the capacity of reaches to retain fine sediment. Indeed, we found that reaches were prone to incision when their drainage basins were dominated by either loess or silt-dominated deposits of the Pleistocene Lake Missoula floods and had channel slopes less than $0.1(A)^{-0.45}$. We also observed that the smallest and lowest slope channels had not incised, indicating that some channels prone to incision did not have sufficient flow strength to initiate incision (i.e. those with slope less than $0.15(A)^{-0.8}$). These results are consistent with our hypotheses that incised channels are found only in silt-dominated-valley fills, that a supply of fine-grained sediment was prerequisite for deep accumulation of silts and that lower energy channels favoured retention of silt and finer sediments on the valley floor.

These results differ from previous studies in that (1) channels prone to incision are below a slope threshold for incision rather than above the threshold and (2) controls on channel incision locations are hierarchical. Previous studies of channel entrenchment and gullying into unchanneled valleys have shown that propensity for incision

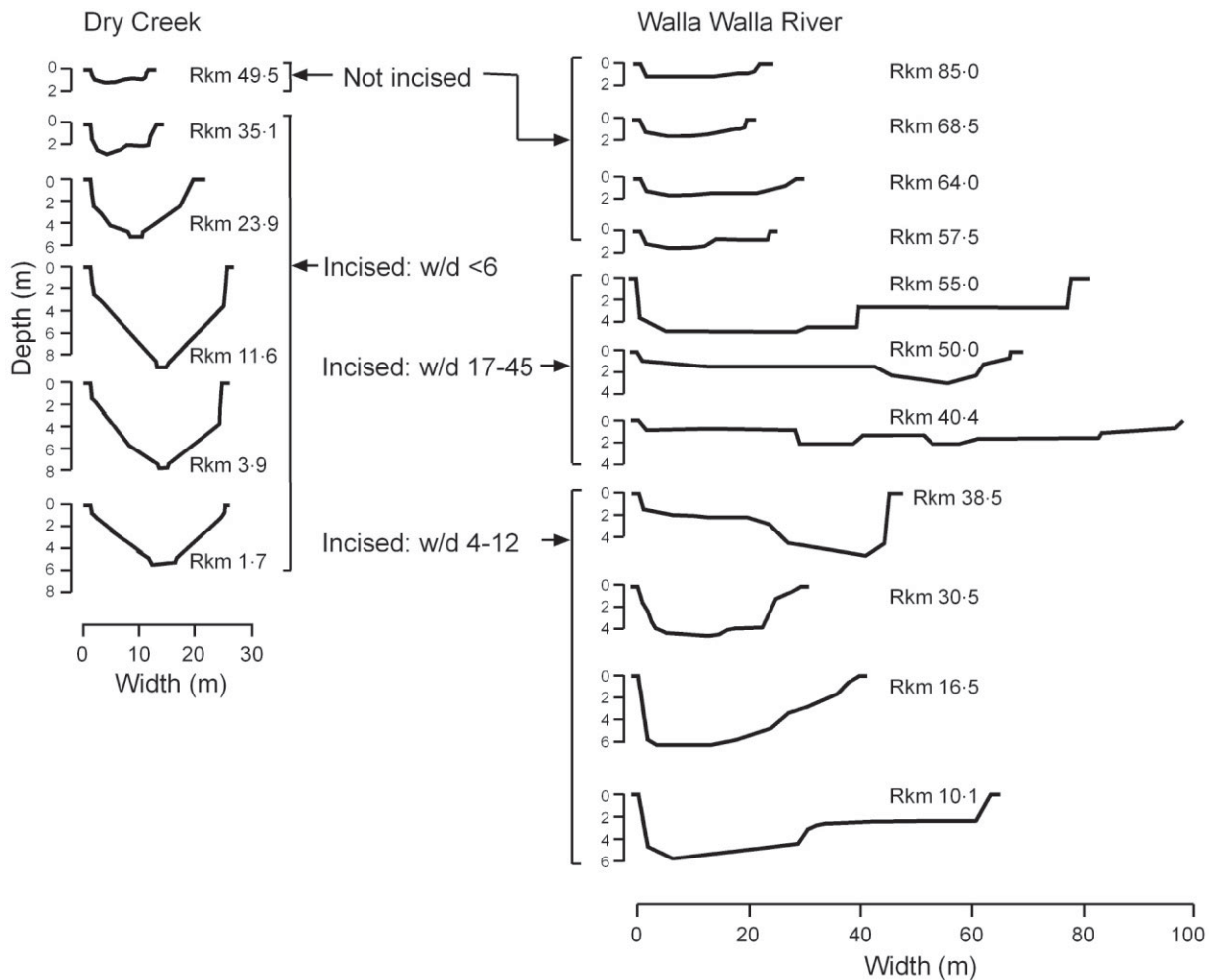


Figure 10. Cross-sections of Dry Creek and Walla Walla River indicate deviations from an idealized channel evolution model. Dry Creek cross-sections illustrate very low top width to incision depth ratios (w/d), apparently because small channels cannot export sediment delivered from failing banks and widening is limited. Walla Walla River cross-sections illustrate extreme widening and inset floodplain development in mid-basin, apparently because high gravel bed load supply from upstream reaches forces bank erosion and the large channel easily exports fine sediment from failing banks. Lower Walla Walla reaches have intermediate widening because bed load supply is low, bank erosion is relatively slow and the channel is large enough to export fine sediment from failing banks.

increases with increasing slope or drainage area (e.g. Patton and Schumm, 1975; Prosser and Abernethy, 1996; Montgomery, 1999), whereas we found the opposite. These results suggest differing mechanisms underlying incision thresholds, which in part reflect a lack of clarity regarding the hierarchical nature of controls on channel incision, and in part reflect fundamentally different physical controls on incision locations.

Controls on locations of channel entrenchment are hierarchical in that (1) some reaches are prone to incision whereas others are not (e.g., some of the network cannot be incised because there are no fine sediments through which the channel can erode) and (2) some reaches prone to incision may incise while others do not (e.g., some reaches with fine sediment accumulations will not incise because an incision threshold is not reached). Both types of threshold have been examined in previous studies, although the lack of a hierarchical framework for incision thresholds has made it difficult to ascertain which type of threshold each study addressed. The first-order control has been demonstrated by Patton and Schumm (1975), who noted that locations of oversteepened reaches were controlled by fine sediment accumulation at cross-valley alluvial fans, and that incision tended to occur on the steeper down-valley slope of the fan. Our result is similar in that fine sediment accumulation controlled incision location, but we found continuous incision in long low-slope reaches, which are controlled by relative supply of fine sediment and the ability of channels

to retain it. While both results reflect the first-order control of geologic propensity for incision, they differ in geomorphic setting and in processes that control incision locations. Among channels prone to incision, the second-order threshold is essentially one of flow strength. We found that, of the channels that were prone to incision, channels with steeper slope and greater drainage area were incised. This result is similar to those of other studies that have examined this second-order threshold (e.g., Prosser and Abernethy, 1996; Montgomery, 1999), indicating that not all channels prone to incision have sufficient flow strength to initiate incision.

Viewing channel incision thresholds in a hierarchical framework that asks (1) which channels are geologically prone to incision and (2) which of these channels actually incise helps achieve a more comprehensive explanation of patterns of channel incision within drainage basins. This hierarchy also puts previous studies into a broader conceptual context that helps explain relationships among seemingly contradictory results. Comparison of our results with those of other studies illustrates that the first-order geological control on locations prone to incision can produce differences in incision patterns (continuous or discontinuous), as well as differences in apparent incision thresholds (steep or low-slope channels). While these differences in geological controls at first appear contradictory, in both cases channels prone to incision flow through fine-grained valley fills. Hence, propensity for incision is indeed a function of valley fill texture (Cooke and Reeves, 1976; Schumm, 1999), but the spatial distribution of fine-grained valley fills varies with geologic and geomorphic setting (e.g., compare this study with Patton and Schumm, 1975). In examining the second-order control on channel incision, we found that, of channels prone to incision, our slope–area threshold parallels those of other studies. That is, ours and other studies have shown that the second-order control is a flow strength threshold, in which steeper channels are more likely to incise. While the specific slope and discharge values of second-order thresholds will vary among regions and basins, it is clear that this threshold reflects drivers of flow strength (slope and drainage area) (see, e.g., Prosser and Abernethy, 1996; Montgomery, 1999).

All of the incised channels had downcut to either bedrock or paleo-sediments coarse enough to prevent further incision. Because channels incised through the entire fine-grained alluvial fill, the depth of incision was roughly equivalent to the depth of silt deposits accumulated prior to incision. Depth of incision increased with decreasing channel slope and decreasing proportion of the drainage basin mapped as basalt, consistent with our hypotheses of negative relationships between incision depth and channel slope or per cent basalt. However, we did not find significant relationships between incision depth and drainage area or the slope–area index as we had expected, most likely because drainage area was negatively related to both channel slope and percent basalt. Thus, the expected increase in sediment retention at lower discharges was countered by the effects of steeper slope (reduced retention) and higher percent basalt (lower silt supply). Overall, the interaction of slope and percent basalt was the best predictor of incision depth, indicating that the deepest incision was in reaches with both a low channel slope and a sediment source area dominated by erodible, fine-grained materials (i.e. loess and Lake Missoula flood deposits). Thus, first-order geological controls on incision location (high silt loads and relatively low sediment transport capacity) also strongly influenced depths of incision.

Variation in channel evolution pathways

Cross-sections of incised channels in the study area indicate that channels follow at least two different evolutionary trajectories. Small, deeply incised channels tend to retain sediment from collapsed banks, apparently because they are too small to export sediment as rapidly as it is delivered (notably Dry and Pataha Creeks). Thus, these channels tend to resist widening, and develop a distinctive cross-section form with high vertical banks buttressed by failure deposits (Figure 10). These channels have bankfull widths roughly equal to or less than incision depth (Figure 11) and are likely to evolve slowly and begin aggrading prior to substantial widening. In other words, these channels follow an evolution model that differs from typical models in that there is no significant widening after incision (Figure 11). An alternative model for these channels (referred to here as Model I) includes (a) pre-incision, (b) degrading, (c) degrading and limited widening and (d) aggradation controlled by dense vegetation anchoring failure deposits at the base of the banks. While this model bears some similarity to the model for small and medium sized arroyos illustrated by Elliot *et al.* (1999), it differs in its lack of a distinct widening phase prior to the onset of aggradation.

In channels with bankfull width larger than incision depth, flow strength is sufficient to export fine-grained sediment entering the channel from bank failures (e.g. Touchet River and lower reaches of the Walla Walla River) and channels exhibit a characteristic widening phase after incision (Model II in Figure 11). Hence, Model II is described by (a) pre-incision, (b) degrading, (c) degrading and widening, (d) aggrading and widening and (e) quasi-equilibrium. Reaches following Model II in our study have widened to varying degrees, but the widest reaches tend to be upstream of narrower reaches – the opposite of patterns observed elsewhere (see, e.g., Schumm *et al.*, 1984; Elliott *et al.*, 1999). The upstream reaches have top width to incision depth ratios between 17 and 45, whereas the narrower downstream reaches have top width to incision depth ratios of 6–12. Nevertheless, both upstream and downstream reaches exhibit

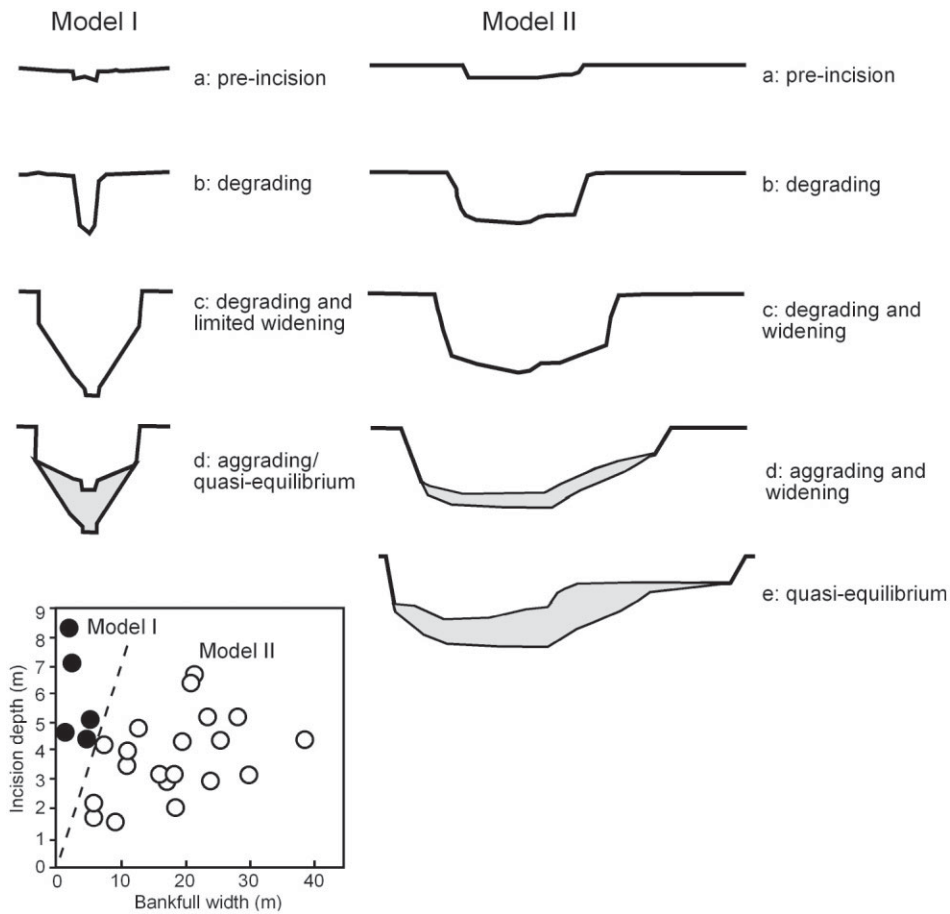


Figure 11. Alternative channel evolution models for entrenched channels in the Walla Walla and Tucannon River basins. Model I differs from published channel evolution models in its lack of a significant widening phase. Model II is similar to those of Simon and Hupp (1987) and Schumm *et al.* (1984). Model I applies to small, deeply incised channels (filled circles in graph, lower left), whereas Model II applies to larger channels (open circles).

a widening phase after incision, so we consider both to follow Model II, albeit at different rates. Both trajectories are similar to previous evolution models (see, e.g., Schumm *et al.*, 1984; Simon and Hupp, 1987), and differences between the two reaches resemble differences between channel evolution models for large and small arroyos (Elliott *et al.*, 1999).

A common explanation for differences in the degree of widening of incised channels is that channels incised into relatively cohesive materials tend to deepen more and widen less than channels incised into less cohesive materials (Schumm, 1999). However, all channels in our study have incised into similar silt-dominated fills. Hence, variation in valley fill texture does not explain variation in width–depth ratios of incised channels. Rather, this variation is largely explained by relative supply of non-cohesive bed load from upstream. The wide, upstream reaches have large gravel bars and relatively weak armoring of the bed, indicating a substantial supply of bed load from upstream (Dietrich *et al.*, 1989; Montgomery and MacDonald, 2002). In these reaches, the inset bankfull channel is formed in non-cohesive gravels, which favors a wide, shallow form and high lateral migration rates (Schumm, 1985; Thorne and Osman, 1988; Eaton *et al.*, 2004; Beechie *et al.*, 2006). Both factors force more rapid bank erosion and contribute to rapid widening of the incised channel. Bed load supply decreases in the downstream direction due to particle attrition and decreasing gravel sediment sources, so narrower downstream reaches exhibit none of the indicators of high bed load supply and have narrower width-to-depth ratios. These reaches still exhibit a widening phase, but widen more slowly than the upstream reaches. Hence, the downstream sequence from (1) non-incised channel to (2) wide incised channel to (3) narrow incised channel (see Figure 10) reflects a gradual transition from gravel-dominated to silt-dominated valley fills, which in turn reflects a decreasing supply of bed load to the channel.

Our identification of two channel evolution models implies that planning incised channel rehabilitation based on stage of evolution (Shields *et al.*, 1998; Watson *et al.*, 2002) should consider potential errors introduced by reliance on a single evolution model. Some planning approaches assert that stream rehabilitation should not begin until after a channel has reached the widened and aggrading stage (Stage D in our Model II), which helps to avoid failure of in-stream wood or boulder structures by undercutting or rapid widening (see, e.g., Shields *et al.*, 1998). This approach is based largely on traditional channel evolution models characterized by a distinct widening phase after incision, and on the assumption that widened channels have achieved a new equilibrium (Schumm *et al.*, 1984; Harvey and Watson, 1986; Bledsoe *et al.*, 2002; Brooks *et al.*, 2003). While this approach can be readily applied to our Model II channels, we also identified a second channel evolution pathway that does not include the commonly cited widening phase. Hence, application of this criterion in our study area would mean that channels evolving along the Model I pathway might never be targeted for rehabilitation because they appear to be at an early stage of evolution. In fact, incision and widening appear to have ceased in our Model I channels (i.e., they are at Stage C in Figure 11), and rehabilitation efforts may be no more likely to fail than rehabilitation structures installed in Model II channels that are at Stage D. Therefore, it is important to recognize which evolution model a channel follows and to adjust rehabilitation planning criteria accordingly.

Recovery time and potential restoration of incised channels

Efforts to rehabilitate incised channels have commonly focused on improving conditions within the incised channel (Shields *et al.*, 1995, 1998, 2004; Watson *et al.*, 2002), rather than considering reconnecting the channel to its historical floodplain. Perhaps because of this focus, there has been little effort towards estimating how long it will take for incised channels to aggrade to the level of their former floodplains (Elliot *et al.*, 1999), or how one might enhance sediment retention to achieve such an objective (Pollock *et al.*, 2007). Both are critical questions in planning stream rehabilitation efforts, as recovery time and restoration techniques both influence cost-effectiveness of restoration efforts (Beechie *et al.*, 1996). Here we examine recovery time of incised channels in the study area, focusing on how such calculations might influence restoration decisions.

The concept of recovery time is important in restoration planning, both for assessing feasibility of specific types of restoration effort and for setting appropriate expectations for restoration outcomes (Beechie *et al.*, 2000; Beechie, 2001). Recovery time can be generally defined as the time required to transition from a 'degraded' state to a state resembling a 'reference' condition. This reference condition is not necessarily static. Rather, it implies a state of natural geomorphological and ecological function similar to that expected when human impacts are absent (Beechie *et al.*, 1996). Here we estimate recovery time for incised channels, defining recovery time as the time required to reconnect incised channels to their historical floodplains.

Complete filling of entrenched channels and reconnection of the historical floodplain has historically occurred on timescales of hundreds to thousands of years (Elliott *et al.*, 1999), and published long-term aggradation rates (1000 years or more) are on the order of 10^{-2} cm yr⁻¹ (Table I). Such aggradation rates are too slow to aggrade most incised channels in our study area in less than 10 000 years. However, published aggradation rates measured over the last

Table I. Published long-term (>1000 years) and recent (<200 years) average aggradation rates of channels and floodplains

Location	Aggradation rate (cm yr ⁻¹)	Citation
<i>Long-term rates (>1000 years)</i>		
Cann River, Australia	0.01	Brooks <i>et al.</i> , 2003
Upper Mississippi Valley, USA	0.02	Knox, 1987
Bega River, Australia	0.08	Brooks and Brierly, 1997
<i>Short-term rates (<200 years)</i>		
Cache River, AR, USA	1.0	Kleiss, 1996
Bega River, Australia	1.3	Brooks and Brierly, 1997
Rio Puerco, NM, USA	1.6–5.2	Elliott <i>et al.</i> , 1999
River Garrone, France	0.5–2.5	Steiger <i>et al.</i> , 2000
Upper Mississippi Valley, USA	0.3–5.0	Knox, 1987
Coon Creek, WI, USA	0.5–15	Trimble, 1999
Bridge Creek, OR, USA	4–48*	Pollock <i>et al.</i> , 2007

* Rate of channel and floodplain aggradation upstream of beaver dams in incised channels.

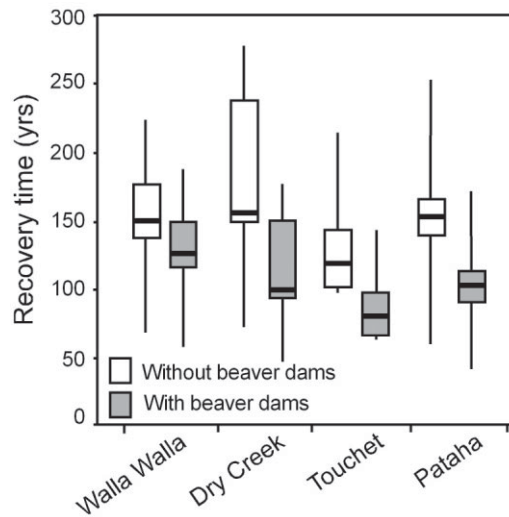


Figure 12. Box and whiskers plot of estimated recovery time (time required for the channel to aggrade to the level of its historical floodplain) for all sites in each of the four main river channels, both with and without restoring modest beaver populations. Heavy line indicates median value, box indicates inter-quartile range and whiskers indicate range. See text for explanation of recovery time calculations.

several decades are 10^{-1} – 10^1 cm yr^{-1} (Table I), one to three orders of magnitude higher than long-term aggradation rates. At these aggradation rates, channels may aggrade to their historical floodplains within decades to centuries (Elliott *et al.*, 1999). A simple assessment of which channels are likely to have relatively short recovery times (t_r) can be made assuming a modest aggradation rate based on literature values (Δd , in m yr^{-1}) and using a simple equation that relates incision depth (d_{total} , in m) to recovery time:

$$t_r = \frac{d_{\text{total}}}{\Delta d} \quad (1)$$

Assuming a relatively low aggradation rate in incised channels of the Walla Walla and Tucannon basins (~ 0.03 m yr^{-1}), recovery time could be as short as 40 years where incision is modest (< 2 m deep) or more than 200 years in deeper channels (> 7 m deep) (Figure 12). Such recovery periods are comparable to those of riparian forests and channel morphology in humid landscapes (Murphy and Koski, 1989; Beechie *et al.*, 2000), as well as to those of aggraded channels where sediment supply has significantly increased (Pitlick and Thorne, 1987; Harvey, 1987; Madej and Ozaki, 1996; Beechie, 2001). Hence, projected recovery times are within typical management time frames, suggesting that restoring entrenched channels may be a feasible restoration goal.

Recovery time of incised channels may be reduced by increasing retention of suspended sediment through restoration actions, or by simply allowing natural recovery processes to occur (Pollock *et al.*, 2007). For example, beaver recolonization and construction of beaver dams in the incised channel of Bridge Creek, OR, has led to local aggradation rates as high as 0.45 m yr^{-1} and average retention rates of approximately 0.10 m yr^{-1} (Pollock *et al.*, 2007). These rates are roughly one order of magnitude higher than most published aggradation rates. To illustrate the effects that restoring beaver populations could have on recovery time of incised channels in our study area, we estimated recovery time with and without beaver dams for each reach in the four largest incised channels. Using the relatively low aggradation rate of 0.03 m yr^{-1} as above, we estimated that recovery time without beaver dams ranges from 60 to 270 years across all sites (Figure 12). However, allowing even low densities of beaver dams (two dams per kilometer of stream on average, Pollock *et al.*, 2004) – each of which traps an average of 171 m^3 of sediment per year (Pollock *et al.*, 2007) – would decrease recovery time to 40–186 years (a decrease of 17–33 per cent).

These calculations are obviously oversimplified, and do not consider whether sufficient sediment is supplied to these channels to achieve the estimated aggradation rates. Estimates of annual storage volume required to sustain an aggradation rate of 0.03 m yr^{-1} (without beaver dams) ranged from $28\,500$ to $82\,400$ $\text{m}^3 \text{yr}^{-1}$ (Table II), and adding beaver-dam storage increases the range of estimates to $44\,900$ – $113\,900$ $\text{m}^3 \text{yr}^{-1}$. These values are a relatively small proportion of annual sediment yields, ranging from 3.0 per cent to 11.8 per cent of annual yield without beaver dams,

Table II. Annual storage volumes and percentages of annual sediment yield required to sustain an aggradation rate of 0.03 m yr^{-1} (without beaver dams), and the same aggradation rate plus beaver-dam storage of $171 \text{ m}^3 \text{ yr}^{-1}$ at a frequency of 2 dams km^{-1} . Sediment yields are based on mid-range values for each basin from Mapes (1969), with downward adjustments of 10 per cent to account for recent land use changes (Ebbert and Roe, 1998)

	Incised channel volume (m^3)	Annual sediment yield (m^3)	Annual storage without beaver dams (m^3) (per cent of annual yield)	Annual storage with beaver dams (m^3) (per cent of annual yield)
Walla Walla River	8 897 000	2 145 000	65 200 (3.0%)	78 600 (3.7%)
Dry Creek	5 559 000	633 000	28 500 (4.5%)	44 900 (7.1%)
Touchet River	11 262 000	1 519 000	82 400 (5.4%)	113 900 (7.5%)
Pataha Creek	6 765 000	320 000	37 600 (11.8%)	56 500 (17.7%)

and from 3.7 per cent to 17.7 per cent with beaver dams. These percentages are consistent with sediment retention rates measured elsewhere (14 per cent; Kleiss, 1996), indicating that our recovery time estimates are plausible given current sediment yields and typical aggradation rates. Hence, it appears reasonable to consider a restoration option that seeks to aggrade incised channels to the level of their historical floodplains, at least for channels with relatively shallow incision depths and high sediment yields.

Conclusions

Our study makes three novel contributions to the study of incised channels. First, we have shown that controls on the spatial pattern of incision in river basins are hierarchical, with a first-order geological control on location of channels prone to incision, and second-order control representing flow strength and the ability of channels to incise into cohesive materials. Channels prone to incision in our study area are below a slope–area threshold (in contrast to other studies, in which channels prone to incision are above a slope threshold), and channels prone to incision have incised only where they exceeded a second slope–area threshold. Second, we have shown that some incised channels do not follow the common channel evolution model characterized by a distinct widening phase after downcutting has ceased. These channels do not have sufficient flow strength to export sediments entering the channel from bank failures, which results in accumulation of failure deposits at the base of banks and prevention of channel widening. Thus, a second channel evolution model is required to adequately describe their recovery pathway, and this second model lacks a distinct widening phase. Recognition of which channel evolution model a particular reach is likely to follow is important in determining when a channel has reached an evolutionary stage at which rehabilitation efforts are appropriate. Finally, we apply the concept of ‘recovery time’ to incised channel restoration, illustrating that the time required to reconnect incised channels to their historical floodplains ranges from 60 to 270 years with modest sediment retention rates. Moreover, simple restoration actions such as allowing or encouraging recolonization by beaver can reduce recovery time by up to 33 per cent.

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Beaver dams overshadow climate extremes in controlling riparian hydrology and water quality

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Hydrologic extremes dominate chemical exports from riparian zones and dictate water quality in major river systems. Yet, changes in land use and ecosystem services alongside growing climate variability are altering hydrologic extremes and their coupled impacts on riverine water quality. In the western U.S., warming temperatures and intensified aridification are increasingly paired with the expanding range of the American beaver—and their dams, which transform hydrologic and biogeochemical cycles in riparian systems. Here, we show that beaver dams overshadow climatic hydrologic extremes in their effects on water residence time and oxygen and nitrogen fluxes in the riparian subsurface. In a mountainous watershed in Colorado, U.S.A., we find that the increase in riparian hydraulic gradients imposed by a beaver dam is 10.7–13.3 times greater than seasonal hydrologic extremes. The massive hydraulic gradient increases hyporheic nitrate removal by 44.2% relative to seasonal extremes alone. A drier, hotter climate in the western U.S. will further expand the range of beavers and magnify their impacts on watershed hydrology and biogeochemistry, illustrating that ecosystem feedbacks to climate change will alter water quality in river systems.

The exchange of water and solutes between river channels and the shallow subsurface (hyporheic exchange) exerts a predominant control on biogeochemical exports from mountain floodplains and is a primary determinant of riverine water quality. Hydrologic extremes, such as rapid snowmelt and severe rain events, alter water residence time and solute exchange rates across mountain hyporheic zones^{1–3}. As climate change reshapes temperature and precipitation regimes throughout mountain watersheds, shifts in the duration, magnitude, and timing of hydrologic extremes will drive coupled shifts in riparian fluxes of nutrients and contaminants, altering riverine water quality^{4–7}.

In the western U.S., warming temperatures and intensified aridification are occurring alongside the resurgence of the American beaver and, consequently, a proliferation of beaver dams. Ecosystem management practices have largely returned beaver populations to their

historical range^{8,9}, and in so doing have restored the ecosystem services that beavers provide, including increased water storage and residence times at the catchment scale¹⁰; increased hyporheic exchange of contaminants and nutrients^{11,12}; and reduced peak discharge^{13,14}. As temperatures warm and precipitation decreases throughout the western U.S., the range and density of beaver populations is expected to expand^{15,16}. Thus, not only will climatic factors directly impact riparian hydrologic and biogeochemical cycles by shifting the magnitude and timing of riparian hydrologic extremes; they will also compound the impacts of beaver dams on these cycles, driving potent a climate feedback in ecosystem services. However, the magnitude of the feedback is unknown. Continued expansion of beaver populations may drive hydrologic and biogeochemical changes in mountain river systems that rival the changes imposed by shifts in temperature and precipitation alone.

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In this study, we compare the effects of beaver dams and climatic hydrologic extremes on riparian fluxes of oxygen and nitrogen and their impacts on riverine water quality. Excess nitrate or ammonium, the predominant reactive nitrogen species in freshwater, is a persistent global threat to water quality^{17,18}. River headwaters are particularly effective at regulating downstream loading of reactive nitrogen, with hyporheic exchange playing a central role in determining exports of reactive nitrogen from mountain watersheds¹⁹. The hyporheic zone functions as a source or sink of reactive nitrogen depending on water residence time and nitrogen transformation rates within the shallow subsurface^{20–22}. Using field measurements and reactive transport modeling, we compared the hydrologic and biogeochemical impacts of beaver dams and climatic hydrologic extremes on hyporheic reactive nitrogen cycling in the headwaters of the Colorado River. We find that the hydraulic gradients imposed by beaver dams greatly exceed the gradients imposed by climate extremes, leading to shortened water residence times and increased oxygen and nitrogen fluxes across hyporheic zones. We reveal that beaver dams overshadow climatic hydrologic extremes in controlling the exports of reactive nitrogen from mountain riparian zones and, further, that management practices and ecosystem feedbacks to climate change can generate ecosystem services that overcome the detrimental effects of climate change.

Results and discussion

Seasonal and beaver-driven hydrologic extremes

Our study focuses on a meandering reach of the East River, a main tributary to the Colorado River, near Crested Butte, Colorado, USA. In 2018, historic low-water conditions occurred across the western U.S., foreshadowing the low-water extremes expected with continued warming and intensified aridification in the region^{23–25}. In contrast, 2019 was a moderately high-water year. Hydrologic conditions throughout the East River watershed reflected the regional trends in 2018 and 2019: between 1935 and 2021, peak discharge fell below the

2018 level only three times, reflecting the historic low-water conditions in that year, and exceeded the 2019 level 14 times (Supplementary Fig. 1). Over these two contrasting water years, we compared water levels and associated biogeochemical cycles in a riparian area bounded by the East River. We installed an array of pressure transducers throughout the riparian area, including in the river channel, to measure hourly water levels at the site across hydrologic transitions (Supplementary Fig. 2). We also installed a transect of piezometers aligned with the general direction of subsurface flow, from which we collected water samples one to three times a week between May and October in 2018 and 2019 (Supplementary Fig. 2).

In the summer of 2018, amid historic low-water conditions, a beaver dam was built in our study reach across the main channel of the East River (Supplementary Fig. 2), which allowed us to assess the effects of the dam on hydrologic and biogeochemical processes within the adjacent hyporheic zone. Construction of the dam began between July 26 and July 30, 2018, and continued until October 5, 2018, when the dam was destroyed. As construction of the dam proceeded, upstream water levels steeply increased, while downstream water levels did not, resulting in a large increase in the hydraulic gradient, i , across the riparian hyporheic zone (Fig. 1). Before the dam was destroyed, it imposed a maximum gradient of 0.017 m/m across adjacent hyporheic sediments and soils, an increase of 161.5% relative to the average gradient prior to construction of the dam. The maximum gradient imposed by the beaver dam dwarfed the maximum gradients imposed by snowmelt-driven hydrologic extremes in both 2018 (0.0073 m/m; 12.3% increase relative to pre-dam average) and 2019 (0.0061 m/m; 15.1% increase relative to the yearly average) (Fig. 1).

Redox zonation during hydrologic extremes

The beaver dam more than doubled the extent of the riparian aerobic zone relative to snowmelt-driven extremes. Pairing hydrologic observations with measurements of porewater pH, dissolved oxygen (DO),

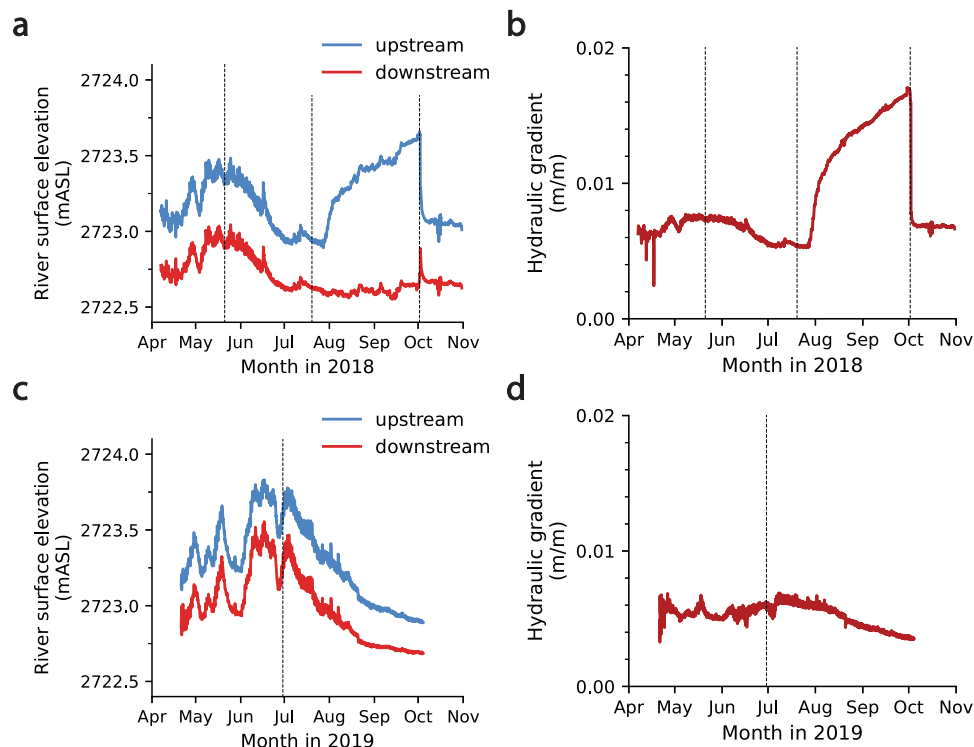


Fig. 1 | River surface elevations and hydraulic gradients. **a** Upstream (blue) and downstream (red) river surface elevations at the study site from April 7 through October 31, 2018. **b** The hydraulic gradient across the floodplain from April 7 through October 31, 2018. **c** River surface elevations from April 21 through October

2, 2019. **d** The hydraulic gradient across the floodplain from April 21 through October 2, 2019. Dashed black lines indicate dates for which profiles of dissolved oxygen (DO), nitrate (NO_3^-), and ammonium (NH_4^+) are shown in Fig. 2.

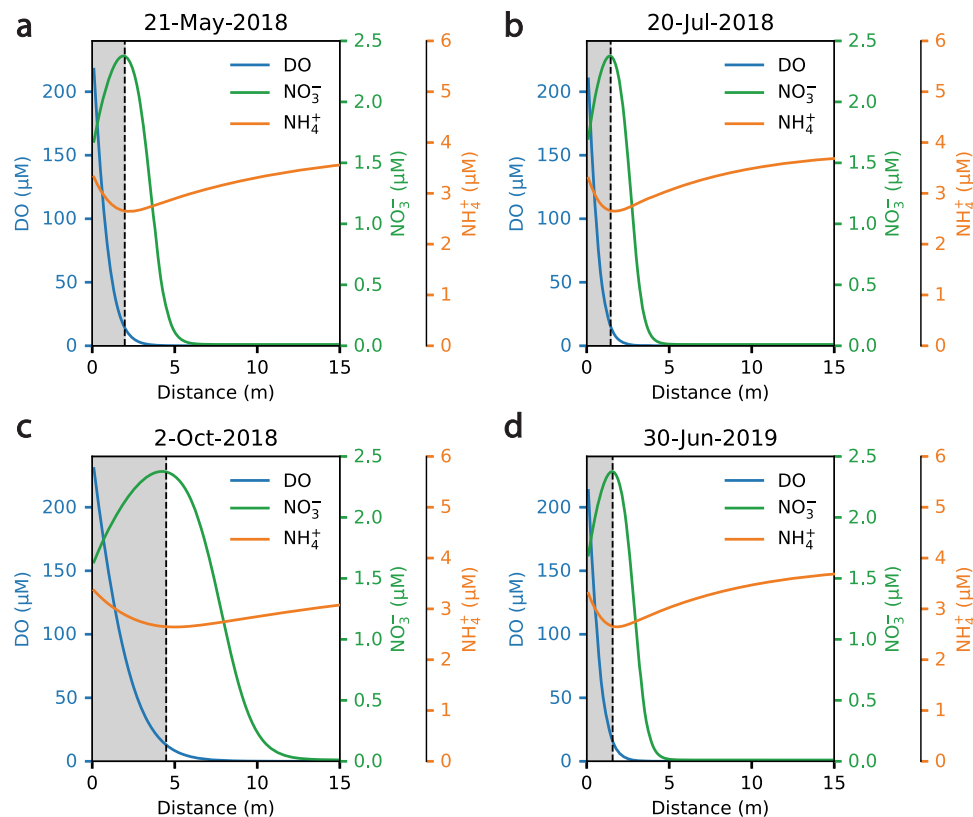


Fig. 2 | Flow path concentrations of dissolved oxygen and reactive nitrogen. Modeled concentration profiles of dissolved oxygen (DO, blue line), nitrate (NO_3^- , green line), and ammonium (NH_4^+ , orange line) along a riparian flow path at: **a** peak river discharge in 2018, a historically low water year; **b** baseflow conditions in 2018; **c** the maximum beaver dam water levels in 2018; and **d** peak discharge in 2019, a high-water year. Within each panel, gray shading indicates the extent of flow path over which DO concentrations are primarily determined by advection (i.e., where

the Damköhler number for DO, Da_{DO} , is less than 1). The dashed lines correspond to the point at which DO consumption overtakes advection as the primary determinant of DO concentration (i.e., where $\text{Da}_{\text{DO}} = 1$). The unshaded regions denote where DO consumption determines DO concentrations (i.e., where $\text{Da}_{\text{DO}} > 1$). Figure 1 indicates the water levels and hydraulic gradients corresponding to these concentration profiles. Model validation results are shown in Supplementary Figs. 13–15.

nitrate, ammonium, calcium, and dissolved carbon, we developed a reactive transport model to assess transient redox zonation across the monitored transect at our site. The biogeochemical reaction network contains rate formulations for aerobic microbial respiration, ammonification (mineralization), nitrification, denitrification, calcite precipitation and dissolution, and acetogenesis. Reaction parameters were constrained to values used in previously published studies and, where necessary, tuned to yield output consistent with our observations (sources and values of parameters are shown in Supplementary Tables 1–3). Details of the model formulation appear in the Methods section. We then employed a Damköhler analysis for DO (Da_{DO}) to delineate the aerobic and anaerobic zones along the flow path, defining the location on the flow path where $\text{Da}_{\text{DO}} = 1$ (i.e., where transport and reaction processes equally influence DO concentrations) as the transition from aerobic to anaerobic conditions. Beyond this location, microbial demand for DO outpaces its supply (via advection) and DO is rapidly depleted. At the maximum hydraulic gradient imposed by the beaver dam, the aerobic zone extends 4.37 m into the hyporheic zone (Fig. 2). In comparison, during the snowmelt-driven extremes, the aerobic zone extends only 1.92 m and 1.57 m in 2018 and 2019, respectively (Fig. 2). Extreme seasonal gradients only marginally increase advection along the flow path, whereas the beaver-driven gradient increases advection substantially, leading to increased supply of DO and a pronounced expansion of the riparian aerobic zone.

The expansion of the aerobic zone is paired with a narrowing of the denitrification zone. Within the expanded aerobic zone, nitrate concentrations increase due to mineralization of N-bearing soil organic matter (N-SOM) and nitrification^{20,21}. Simultaneously, the

presence of oxygen suppresses the use of nitrate as an electron acceptor, and the denitrification front is extended farther along the flow path²⁶. This is reflected in the DO, nitrate, and ammonium profiles along the representative flow path (Fig. 2 and Supplementary Figs. 3 and 4). Where DO concentrations are predominantly influenced by advection ($\text{Da} < 1$), nitrate concentrations increase, and ammonium concentrations decrease. Nitrate concentrations peak at the point along the flow path where DO consumption overtakes advection as the primary determinant of DO concentrations (i.e., where $\text{Da}_{\text{DO}} = 1$) (Fig. 2 and Supplementary Figs. 3 and 4). Immediately beyond this point, unutilized DO is rapidly depleted and denitrification becomes viable. Denitrification then predominates along the flow path until nitrate is consumed, and ammonium concentrations rebound due to ammonification of N-bearing soil organic matter²⁷.

The relative shifts in redox zonation between seasonal and beaver-driven hydrologic extremes is insensitive to parameterization of microbial mechanisms and remains proportional to shifts in the hydraulic gradient. We performed a set of Monte Carlo simulations (5000 realizations) in which we varied the rates of aerobic respiration and nitrification without changing other components of the model. Distributions for respiration and nitrification rates were derived from previously published studies^{2,28–31}, and realizations of the model were formulated by randomly sampling the distributions. For each realization, we determined the distance to the anaerobic zone (i.e., position of $\text{Da}_{\text{DO}} = 1$) at seasonal high-water and historic low-water conditions in 2018, as well as at the beaver-induced maximum gradient. Distributions of the distances to $\text{Da}_{\text{DO}} = 1$ for these conditions are shown in Supplementary Fig. 5. While the overall rate of oxygen consumption

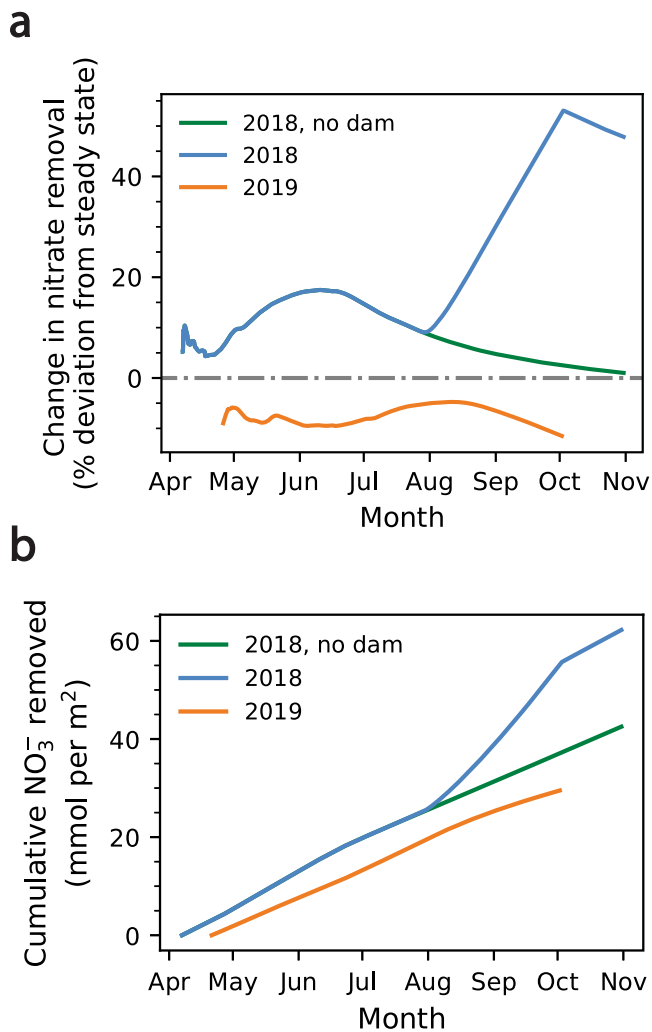


Fig. 3 | Comparison of nitrate removal across hydrologic conditions. **a** Change in nitrate removal, measured as percent deviation from steady-state hydrologic conditions, along a representative riparian flow path (58 m) under 2018 hydrologic conditions, with and without the beaver dam (blue and green lines, respectively), and 2019 hydrologic conditions (orange line). The mean of the initial hydraulic gradients in 2018 and 2019 was used to simulate steady-state conditions. **b** Cumulative nitrate removed in 2018 and 2019, expressed as mol NO₃⁻ removed per m² cross sectional discharge area.

affects the magnitude of the distance to $Da_{DO} = 1$, the relative impact of the beaver dam on this distance is unchanged for a given parameter set and is proportional to the relative shift in hydraulic gradient between the extremes.

Effects on transient fluxes and cumulative nitrate removal

As the transient hydrologic extremes shift advection and redox processes along the 58 m flow path at our study site, hyporheic fluxes of dissolved oxygen and nitrate are also altered. To determine the impacts of seasonal and beaver-driven hydrologic conditions on nitrate fluxes, we tracked hyporheic nitrate fluxes in 2018 and 2019 and compared them to nitrate fluxes under a steady-state hydrologic condition. In the steady-state simulation, the hydraulic gradient was set to the mean of the hydraulic gradients on the first days in 2018 and 2019 when the river channel was free of ice (April 7 and April 21, respectively). We also simulated and determined nitrate fluxes using water levels with the beaver dam hypothetically removed. We then quantified nitrate removal, defined as the difference in nitrate flux at

the upstream and downstream boundaries, along the flow path over the course of each hydrologic period.

Transient increases in advection also increase nitrate fluxes into the hyporheic zone. Because the flow path retains a region in which denitrification is viable—even at the maximum gradient imposed by the beaver dam—infusing nitrate is ultimately removed along the flow path, and an increase in nitrate influx is coupled with an eventual increase in nitrate removal. Nitrate removal generally follows the hydraulic gradient, but lags by 4–5 weeks (Figs. 1 and 3), reflecting that inflowing water must first travel across the aerobic zone, where denitrification is inhibited and, further, where mineralization and nitrification increase porewater nitrate concentrations. Thereafter, the flow reaches the denitrification front, at which point nitrate is reduced and removed from porewater. In 2018, as water levels decline from the snowmelt-driven peak in late May to baseflow conditions in mid-June, nitrate removal along the flow path increases 17.5% relative to steady state, reflecting the modest increase in gradient at seasonal high water and the associated increase in the flux of nitrate into the denitrification zone (Fig. 3). Following construction of the beaver dam and the associated increase in nitrate advection, nitrate removal increases to 53.1% of steady-state levels (Fig. 3). After the dam is destroyed, nitrate removal decreases slowly despite the rapid return to pre-dam hydrologic conditions, due to nitrate produced within the aerobic zone before the dam was destroyed (Fig. 3). In 2019, maximum nitrate removal, which occurs in August following the maximum hydraulic gradient in July, is 4.8% less than nitrate removal under the steady state condition, and 22.3% and 57.9% less than nitrate removal at, respectively, the snowmelt- and beaver-driven maxima of 2018 (Fig. 3).

Overall, the transient effects of the beaver dam increase cumulative nitrate removal by 44.2% relative to conditions without the dam. From April 7 and October 31, 2018, 0.062 mol NO₃⁻ are removed per m² of cross-sectional discharge area, whereas in the absence of the dam, only 0.043 mol NO₃⁻ are removed per m² (Fig. 3). Normalized to the duration of the observation period (207 d), this equates to an average of 3.0×10^{-4} and 2.1×10^{-4} mol NO₃⁻ removed per day per m² of cross-sectional area, with and without the dam, respectively. In contrast, between April 21 and October 6, 2019, a period of 168 days, 0.030 mol NO₃⁻ are removed per m² of cross-sectional area, an average of 1.8×10^{-4} mol NO₃⁻ per day per m² discharge area (Fig. 3).

Nitrate removal across the floodplain

As warming temperatures and intensifying aridification increase the range and density of beaver populations, the impacts of beaver dams on hyporheic nitrate fluxes will alter nitrate exports at the watershed scale. Already, beaver dams are common throughout the East River watershed. Using Google Earth imagery from October 2019, we identified 18 beaver dams within the 86 km² area of the watershed (Supplementary Figs. 6 and 7). This is likely an underestimation of the true number of dams constructed in 2019, as we only counted dams that were unambiguous in the satellite imagery. Given the prevalence of beaver dams in this watershed, their hydrologic and biogeochemical impacts are likely to affect nitrate fluxes regionally.

Yet, the impact of beaver dams on hyporheic nitrate fluxes depends on the lengths of affected flow paths, as path length is a primary determinant of hydraulic gradient. Thus, to assess the impacts of beaver dams on redox zonation and nitrate fluxes across the watershed, it is first necessary to determine the distribution of hyporheic flow path lengths. We determined an approximate distribution of flow path lengths within meandering regions of the East River floodplain using Google Earth™ satellite imagery (Supplementary Figs. 8 and 9; process of flow path selection described in detail in the Methods section). These regions are representative of average valley grade and river sinuosity across the meandering regions of the East River watershed, an assessment based on a digital elevation model

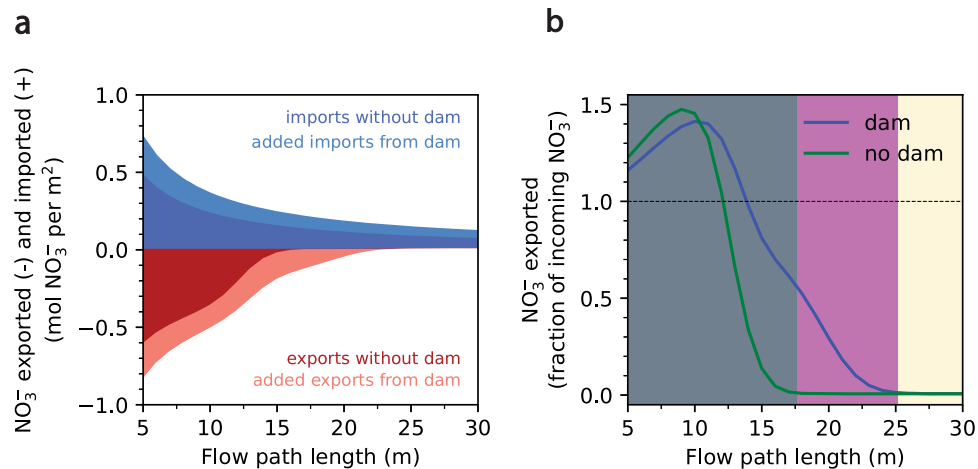


Fig. 4 | Effects of beaver dam on floodplain nitrate fluxes. a Total nitrate exported from flow paths between 5 and 30 m in length between April 7 and October 31, 2018, with and without the beaver dam. **b** Nitrate exported from these flow paths, expressed as a fraction of total nitrate imported over the same time period, with and without the beaver dam (blue and green lines, respectively). Flow

paths shaded in gray are those that export nitrate when the dam is not present. Flow paths shaded in magenta are those that export nitrate only in the presence of the beaver dam. Flow paths shaded in beige do not export nitrate under either condition.

of the East River watershed³². To evaluate the impact of path length on hyporheic nitrate fluxes and redox zonation, we created reactive transport models for each flow path between the minimum and maximum of the distribution (5 to 70 m) at 0.5 m increments. In each individual model, the reaction networks and boundary conditions (both hydrologic and geochemical) were identical to those used in the model of our site. We then simulated oxygen and reactive nitrogen transport across the range of flow paths and examined redox zonation at the seasonal and beaver-driven hydrologic extremes. During seasonal extremes, only flow paths shorter than 10.2 m, or approximately 3.6% of flow paths within the East River floodplain, are entirely aerobic and net nitrate exporters (Supplementary Fig. 8). In contrast, at the maximum beaver-driven gradient, flow paths up to 16.1 m in length (14.2% of flow paths) are entirely aerobic and export additional nitrate to the river (Supplementary Fig. 8). For flow paths longer than 16.1 m (85.8% of flow paths), the aerobic zone expands in response to the beaver dam; however, these flow paths remain net-denitrifying (although with a diminishing reach) during both the seasonal and beaver-driven hydrologic extremes (Supplementary Fig. 8).

Assuming beavers equally construct dams near long and short flow paths, most beaver dams predominantly affect flow paths that are net-denitrifying, even at the maximum beaver-driven gradient. However, beaver dams are often transient features within a watershed, and thus their impact on watershed-scale nitrate removal over the course of a hydrologic year is uncertain. To assess the impact of beaver dams on cumulative nitrate removal of potential hyporheic flow paths, we quantified total nitrate imported and exported for each flow path across the range of path lengths (5 to 70 m at 0.5 m increments) over the observed hydrologic conditions in 2018 (with the beaver dam) and the hypothetical hydrologic conditions in 2018 (without the beaver dam). Although the dam was present for only 68 of the 207 days within this period, its presence increases the total amount of nitrate imported into flow paths of all possible lengths, with the greatest increase occurring in short flow paths (Fig. 4). In contrast, the total amount of nitrate exported during this period depends on the flow path length. The beaver dam increases the range of net-nitrifying flow paths from 12.1 to 13.9 m, while the range of partial denitrifying paths (i.e., paths along which nitrate is not completely removed) increases from 17.6 to 25.1 m, reflecting that the dam converts flow paths in the latter range to partial exporters of nitrate (Fig. 4). Although denitrification occurs within these flow paths with the beaver dam, the shift in Da_{DO} toward transport dominance results in delayed denitrification and thus only

partial removal of porewater nitrate. Flow paths between 17.6 and 25.1 m comprise approximately 15.8% of all flow paths in the floodplain (Supplementary Fig. 8), and their conversion to partial exporters of nitrate increases the range of partial nitrate exporters by 42.6% (Fig. 4). Thus, the presence of the dam, albeit transient, increases the total amount of nitrate exported over the observation period from flow paths shorter than 25.1 m, which are either net-nitrifying (for flow paths up to 13.9 m in length), partial nitrate exporters with and without the dam (paths between 13.9 and 17.6 m), or converted from completely denitrifying to partial nitrate exporters (flow paths between 17.6 and 25.1 m) (Fig. 4). Finally, the dam increases total nitrate removal along flow paths longer than 25.1 m, which completely remove all imported nitrate regardless of whether the dam is present (Fig. 4). As the majority (66.8%) of flow paths in the watershed exceed 25.1 m and are therefore net-denitrifying (remove all porewater nitrate), an increase in the density of beaver dams is likely to drive a net increase in hyporheic nitrate removal at the watershed scale.

Finally, we find that the impacts of path length—and therefore hydraulic gradient—on the hyporheic nitrate mass balance greatly exceed the impacts of variability in the rates of microbially mediated reactions. Given potential ranges in the rates of denitrification and oxygen consumption, we assessed the sensitivity of the nitrate mass balance to (1) the denitrification rate, (2) the overall rate of DO consumption, and (3) the flow path length. We employed a Morris sensitivity analysis^{33,34} across the range of potential denitrification and oxygen consumption rates and three ranges of flow path lengths: 5 to 26 m; 26 to 48 m; and 49 to 70 m. Of the three parameters, path length most strongly affects the nitrate mass balance, indicating that the effects of hydraulic gradient overshadow the impacts of potential variability in reaction rates in determining the hyporheic nitrate balance (Supplementary Fig. 10). Thus, even allowing for variability and uncertainty in microbial reaction rates, beaver dams will increase nitrate removal across the watershed.

Due to the extreme hydrologic conditions that beaver dams impose, it is probable that beaver dams will overshadow future climate extremes in controlling exports of reactive N from mountain riparian zones. Growing beaver populations are likely to lead to greater hyporheic nitrate removal and reduced nitrate loading to downstream watersheds, potentially protecting freshwater quality. Our findings indicate that the impacts of beaver dams dwarf the direct hydrologic impacts of warming temperature and increased aridification, which decrease snowpack and peak discharge, on riparian water quality in

mountain watersheds. As future impacts of climate change on river hydrology and water quality are assessed, feedbacks from ecosystem changes, including those induced by management, need to be included.

Methods

Site description

Our field site is located within the East River watershed, near Crested Butte, Colorado, USA. The East River watershed is a mountainous, high-elevation system (2700–4100 mASL), in which hydrologic conditions are largely determined by seasonal snowmelt dynamics. Quaternary glacial soils occur throughout the watershed, underlain by Paleozoic and Mesozoic sedimentary rocks, including Cretaceous Mancos Shale, with intrusions of Tertiary laccoliths. The East River floodplains consist of 1–2 m of soil above 1–4 m of alluvium, which is underlain by bedrock. Water in the subsurface is hydrologically connected to the East River.

Collection of field samples and measurements

Field measurements and samples were collected from May through October in 2018 and 2019 at a single meander on the East River (Meander Z; Supplementary Fig. 2). Water table and river surface elevations were tracked with pressure transducers (HOBO Water Level Data Logger U20-001-01, Onset Computer Corporation). Three transects, each with three transducers, were installed within the floodplain to track subsurface hydrologic conditions (Supplementary Fig. 2). The transects were aligned with the average direction of subsurface flow. A single transducer was installed at the western edge of the site to determine lateral flow contributions from the hillside into the floodplain (Supplementary Fig. 2). The transducers were suspended on galvanized steel cables to depths of 1.5–1.7 m below ground surface within 2.0 m stilling wells (5.1 cm diameter; polyvinyl chloride (PVC); 1 mm screen slot). Two transducers were installed in the East River channel at two locations along the meander (Supplementary Fig. 2). The river transducers were suspended on galvanized steel cable in PVC well screens (1 mm slot), which were secured to fence posts driven 0.5 m into the riverbed. All transducers recorded hourly absolute pressure measurements. Absolute pressure was converted to hydrostatic pressure using barometric pressure measurements, which were recorded hourly by a transducer installed 1 m above ground surface at the site. A common datum was established at the site, and well casing elevations were measured relative to the datum using a survey-grade automatic level instrument. To convert recorded pressure to depth-to-water measurements, the distance from the top-of-casing to the water level was recorded at each transducer well one week after installation. This distance was measured twice annually to ensure transducer accuracy. Depth-to-water measurements were converted to water surface elevations.

Porewater and river water samples were collected from piezometers and the river channel using a peristaltic pump. A 2 L purge volume was collected and discarded from the piezometers prior to sampling. A multi-parameter probe was used to measure pH, electrical conductivity (EC, mS/m), and oxidation-reduction potential (ORP, mV) in the field. Dissolved oxygen (DO) was measured colorimetrically in the field on unfiltered water using the indigo carmine method (CHEMetrics, #K-7513, 1–15 ppm) or the Rhodazine D™ method (CHEMetrics, #K-7553, 0–1 ppm) and a portable spectrophotometer (CHEMetrics, Inc.). Filtered samples (0.45 mm PVDF syringe filter) were collected for quantification of anions (Cl⁻, SO₄²⁻, NO₃⁻), dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), ammonium (NH₄⁺), and metals. The filtered samples were shipped to the lab and stored at 4 °C prior to analyses. The 2018 porewater and river water data are published and publicly available³⁵, and the 2019 data will be published and available in the Watershed Function SFA, ESS-DIVE data repository.

Laboratory analyses of field samples

Elemental concentrations were measured by inductively coupled plasma mass spectrometry (ICP-MS; Perkins-Elmer Elan DRC II) after acidification and dilution with ultrapure 0.16 M nitric acid and addition of an internal standard. Anions (Cl⁻, SO₄²⁻, NO₃⁻) were measured by ion chromatography (IC; Dionex ICS 2100- IC, Thermo Scientific). Ammonium samples were acidified to pH 2 with 2 M HCl and analyzed by flow injection analysis using the colorimetric salicylate method (Lachat Instruments). Total dissolved carbon and organic carbon were measured on a Shimadzu TOC-V analyzer with a nondispersive infrared detector, and dissolved inorganic carbon was determined by the difference. Total dissolved carbon was measured by catalytically aided combustion at 680 °C, and DOC was measured as nonpurgeable organic carbon, for which samples were acidified with HCl and purged with N₂ (g) to remove inorganic carbon prior to analysis.

Reactive transport model development

A 1D reactive transport model was developed to represent the hydrologic and biogeochemical processes occurring along the hyporheic flow paths at the site. The model was developed using PFLOTRAN, an open-source reactive transport simulator code³⁶. For the base simulations, the model domain was based on the MZA transect, which is 58 m in length, and was composed of a structured grid consisting of 580 cells, corresponding to a uniform discretization of 0.1 m along the Y axis and 1 m in both the X and Z axes. In the variable flow length simulations, the Y axis length was varied between 5 and 70 m while the discretization was unchanged from the base simulations, resulting in grids ranging from 50 to 700 cells. The maximum timestep used in all simulations was 1 h.

PFLOTRAN was run in Richards mode, which solves the Richards Equation for variably saturated flow. All simulated flow paths were fully saturated. Average hydraulic conductivity of the floodplain alluvium was measured with a permeameter, for which five cores were collected with a slide hammer and translucent polycarbonate core sleeves from a trench wall perpendicular to the direction of flow. Prior to measurement, the cores were visually inspected to confirm uniform packing. They were then loaded directly into the permeameter. The average measured hydraulic conductivity values were converted to intrinsic permeability using the dynamic viscosity and specific weight of water. A permeability of 2.26×10^{-11} m² was used in the simulations. A porosity of 0.2 was used in the simulations and was based on the value determined by ref. 2 on similar soils from the same floodplain using pedotransfer functions.

We implemented a biogeochemical reaction network to simulate microbial and geochemical processes within the riparian zone. The reaction network consisted of aerobic microbial respiration; ammonification; nitrification; denitrification; calcite precipitation and dissolution; and acetogenesis. Dissolved organic carbon within the model was produced entirely through acetogenesis, which was simulated as the dissolution of a solid organic matter (SOM) phase to acetate, as in ref. 2. All DOC was represented as acetate. The rates of aerobic microbial respiration, denitrification, and nitrification were calculated using single Michaelis-Menten kinetic reactions applying the following general rate law:

$$R_S = \mu_{\max} \cdot X_{\text{im}} \cdot \frac{C_S}{K_S + C_S} \cdot \frac{C_{\text{TEA}}}{K_{\text{TEA}} + C_{\text{TEA}}} \cdot \frac{K_I}{K_I + C_I} \quad (1)$$

where μ_{\max} is the maximum reaction rate; X_{im} is the concentration of microbial biomass; C_S is the substrate concentration; C_{TEA} is the terminal electron acceptor concentration; C_I is the concentration of the inhibitor species; and K_S , K_{TEA} , and K_I are the half-saturation constants for the substrate, terminal electron acceptor, and inhibition species. Reaction stoichiometries and model parameters are shown in Supplementary Tables 1 and 2. Microbial biomass was fixed at 1×10^{-5}

mol-biomass / m³-bulk in all simulations. Biomass yield was set to zero, and no decay term was included. The maximum reaction rates for aerobic respiration, μ_{aer} and nitrification, μ_{nit} , were determined by fitting the model DO output to the observations while maintaining a $\mu_{\text{aer}} : \mu_{\text{nit}}$ ratio equal to the ratio of $\Delta G_{\text{aer}} : \Delta G_{\text{nit}}$ (Supplementary Table 2). This approach ensured that partitioning of $O_{2(\text{aq})}$ between the competing processes of aerobic respiration and nitrification was consistent with the relative energetics of these reactions²⁰, with aerobic respiration preferentially consuming $O_{2(\text{aq})}$. Calcite precipitation and dissolution were modeled as kinetic processes using transition state theory (TST) rate laws with the following form:

$$R_m = -A_m \cdot \left(k_n + (k_{\text{H}^+} \cdot a_{\text{H}^+}) + (k_{\text{HCO}_3^-} \cdot a_{\text{HCO}_3^-}) \right) \cdot \left(1 - \frac{Q}{k_{\text{eq}}} \right) \quad (2)$$

where k_n , k_{H^+} , and $k_{\text{HCO}_3^-}$ represent rate constants for neutral, acidic, and additional (j th) reaction mechanisms at 25 °C, respectively; a_{H^+} represents proton activity and $a_{\text{HCO}_3^-}$ represents bicarbonate activity; Q represents the ion activity product of the mineral phase; A_m represent the calcite surface area; and k_{eq} represents the calcite equilibrium constant. Dissolution of SOM was represented as an equilibrium process. Finally, ammonification was represented as the kinetically controlled dissolution of N-bearing SOM phase (N-SOM dissolution). Solid phase reaction stoichiometry and kinetic parameters are summarized in Supplementary Table 3.

Hydrostatic boundary conditions were imposed at the upstream and downstream boundaries of the model domain using observed upstream and downstream river elevations (Fig. 2). For simulations without the dam, a set of artificial river surface elevations was created by maintaining the difference between upstream and downstream water levels immediately prior to commencement of dam construction (Supplementary Fig. 11). Changes in upstream water levels over the period for which the dam was removed exactly mirror downstream water level changes, resulting in a steady gradient across the meander.

The average river water composition (Supplementary Table 4) was used as the geochemical boundary conditions at the upstream and downstream boundaries. Although the river water composition varied throughout the sampling period, we treated the composition as fixed because our modeling goal was not to exactly replicate the biogeochemical reactions occurring along the transect, but to develop a model that was representative of these processes more generally. For that purpose, using the average river water composition was appropriate.

The reactive transport model was validated against hydrologic and porewater observations from 2018 and 2019. The hydrologic component of the model produced output that was spatially and temporally consistent with observations across both years (Supplementary Fig. 12). Likewise, the reaction network yielded geochemical output that was spatially and temporally consistent with porewater observations (Supplementary Figs. 13–15).

Three sets of simulations were run: (1) base 2018 and 2019 simulations, in which the observed hydrologic conditions from 2018 and 2019 were applied as boundary conditions; (2) a 2018 no-dam simulation, in which the upstream hydrologic effects of the beaver were replaced with estimated 2018 upstream water elevations had the dam not been built; and (3) variable flow length simulations, in which the flow path length was varied between 5 to 70 m and the 2018 hydrologic conditions with and without the beaver dam were applied.

Damköhler calculations

Previous studies have demonstrated that net reactive N source or sink behavior of hyporheic zone flow paths is primarily a function of the transport timescale of water and the reaction timescale of DO consumption²⁰. This relationship reflects that elevated DO concentrations inhibit denitrification and promote nitrification while low

DO concentrations promote denitrification and inhibit nitrification. Thus, the extent to which a flow path will serve as a source or sink of reactive N will be predominantly controlled by the rates of DO supply and demand^{20,21}. The Damköhler number for DO, Da_{DO} , defined as the ratio of the water transport timescale and the DO reaction rate timescale, is therefore a strong indicator of the potential for the flow path to be either net-nitrifying or net-denitrifying. As in ref. 20, we define the Damköhler number for DO consumption as:

$$Da_{\text{DO}} = \frac{\tau}{V_{O_2}} \quad (3)$$

where V_{O_2} is the timescale of overall DO consumption, τ is the water residence time, and $\tau = \frac{L}{v}$ with L being the length of the flow path and v the mean advective velocity.

In our reaction network, DO is consumed by aerobic respiration and nitrification. The overall rate of DO consumption (mol- O_2 / s) can therefore be represented as the sum of the rates of these processes:

$$R_{O_2} = \left(\mu_{\text{aer}} \cdot X_{\text{aer}} \cdot \frac{[\text{DOC}]}{K_{\text{DOC}} + [\text{DOC}]} \cdot \frac{[O_{2(\text{aq})}]}{K_{O_2, \text{aer}} + [O_{2(\text{aq})}]} \right) + \left(\mu_{\text{nit}} \cdot X_{\text{nit}} \cdot \frac{[\text{NH}_{3(\text{aq})}]}{K_{\text{NH}_{3(\text{aq})}} + [\text{NH}_{3(\text{aq})}]} \cdot \frac{[O_{2(\text{aq})}]}{K_{O_2, \text{nit}} + [O_{2(\text{aq})}]} \right) \quad (4)$$

Along a given flow path of length L , the overall rate of DO consumption can be calculated at any point i along the flow path given the concentrations of DO, DOC, and $\text{NH}_3(\text{aq})$ at i . From the PFLOTRAN model output, we can obtain dissolved oxygen concentration, $[O_{2(\text{aq})}]$, dissolved organic carbon concentration, $[\text{DOC}]$, and ammonia concentration, $[\text{NH}_{3(\text{aq})}]$, at any point i along the flow path, and we thus can calculate the overall rate of oxygen consumption at i . The timescale of DO consumption at i is therefore determined as:

$$V_{O_2, i} = \frac{R_{O_2, i}}{m_{O_2, i}} \quad (5)$$

where $m_{O_2, i}$ is moles of O_2 at i . Given our model discretization of $1 \times 1 \times 0.1$ m and a porosity of 0.2, $m_{O_2, i}$ can be calculated as:

$$m_{O_2, i} = 0.1 \cdot 1 \cdot 0.2 \cdot 1000 \cdot [O_{2(\text{aq})}] \quad (6)$$

To calculate Da_{DO} , the transport timescale, τ , at i is needed, which can be calculated from the advective velocity, v , at i , which we obtain from the model output. If i is the distance from the upstream boundary, then

$$\tau = \frac{i}{v} \quad (7)$$

The Damköhler number for oxygen can therefore be calculated at any point i along a flow path as:

$$Da_{\text{DO}, i} = \left(\frac{i}{v} \right) / \left(\frac{R_{O_2, i}}{m_{O_2, i}} \right) \quad (8)$$

Using this formulation, we calculated Da_{DO} at each cell along the modeled flow paths. To assess whether the flow path was nitrifying or denitrifying, the Da_{DO} was evaluated at the last grid cell along the flow path.

Monte Carlo analysis of hyporheic redox zonation

The extent of the aerobic zone is determined by the overall rate of oxygen consumption and the rate of transport (advection) of dissolved oxygen. Thus, uncertainty in these parameters, and particularly the

rate of overall oxygen consumption, will affect uncertainty in the model output and predicted redox zonation. To assess uncertainty in redox zonation arising from uncertainty in the rate of overall oxygen consumption, we performed a set of Monte Carlo simulations (5000) in which we varied the rate constants, μ_{\max} , for aerobic respiration and nitrification—the two oxygen-consuming reactions in our reaction network. We determined possible ranges for these rate constants by examining published studies in which the rates were either measured or simulated. For aerobic respiration, this range was 1.30×10^{-4} to 2.01×10^{-3} ($\text{mol m}^3_{\text{bulk}} / (\text{L mol}_{\text{bio}} \text{ s})$), while for nitrification, the range was 4.68×10^{-5} to 7.26×10^{-4} ($\text{mol m}^3_{\text{bulk}} / (\text{L mol}_{\text{bio}} \text{ s})$). We intentionally considered a broad range of possible rate constants in order to examine the relative impacts of beaver dams and reactions rates on hyporheic redox zonation. As with the base simulation, within each Monte Carlo realization, the ratio of the aerobic respiration and nitrification rates was equal to the ratio $\Delta G_{\text{aer}} : \Delta G_{\text{nit}}$ to ensure partitioning of $\text{O}_{2(\text{aq})}$ between the competing reactions was consistent with the relative energetics of the reactions. All other model parameters were unchanged from the base simulation. Each realization was first spun up to steady state conditions over a period of 7000 h and then run over the 2018 hydrologic boundary conditions, as in the base simulation. For each model realization, we determined the distance to the point on the flow path where Da_{DO} was equal to 1, which is the location where transport and reaction processes equally influence DO concentrations, and which we define as the transition between aerobic and anaerobic zones. We then plotted the distributions of these distances at the three specified time points (Supplementary Fig. 5).

Determination of beaver dam prevalence

Beaver dams were identified visually in a GoogleTM Earth satellite image of the East River watershed taken in October 2019. Only clearly identifiable beaver dams were counted. We visited nine of the 18 locations identified in the imagery to confirm the presence of a beaver dam. The satellite images showing the locations of the dams are presented in Supplementary Fig. 6. Each individual dam is shown in Supplementary Fig. 7.

Determination of flow path length distribution

Flow path lengths were determined using the distance measuring tool in Google EarthTM. A flow path was defined as the shortest point across the riparian zone between upstream and nearest downstream riverbanks and were roughly aligned with the average valley grade. This method for determination of flow paths was based on and supported by empirical evidence from the field. Only flow paths between 5 and 70 m were considered. A histogram of measured flow path lengths is shown in Supplementary Fig. 8, and a map showing the measured flow paths is shown in Supplementary Fig. 9.

Morris sensitivity analysis of hyporheic nitrate mass balance

We employed a Morris sensitivity analysis to assess the sensitivity of the hyporheic nitrate mass balance to (1) the rate constant for denitrification, $\mu_{\max\text{-DEN}}$, (2) the rate of overall oxygen consumption, R_{DO} , and (3) flow path length, l . The analyses were performed using the SALib software package^{37,38}. The range of R_{DO} over which we examined the nitrate mass balance was the same range used in the Monte Carlo analysis described above, while the range of $\mu_{\max\text{-DEN}}$ (3.13×10^{-5} to 2.57×10^{-3} ($\text{mol m}^3_{\text{bulk}} / (\text{L mol}_{\text{bio}} \text{ s})$)) was determined from a literature analysis. We performed the sensitivity analysis over three ranges of flow path lengths: 5 to 26 m, 27 to 48 m, and 49 to 70 m. Results of the analyses are shown in Supplementary Fig. 10.

Data availability

The authors declare that the data supporting the findings of this study are available within the article and its Supplementary Information file.

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Author contributions

C.D., P.N., and S.F. conceived of and designed the study. C.D. developed and managed the field site, conducted sample collected, and performed in-field measurements. Field work was aided by P.F., P.N., and S.F. Laboratory analyses were performed by P.F. C.D. developed and implemented the PFLOTRAN model, with input from N.B. D.D. helped initiate PFLOTRAN and provided hydrologic expertise on East River. The manuscript was written by C.D. with N.B., P.N., and S.F.

Competing interests

The authors declare no competing interests.

Additional information

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