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Influence of beaver mimicry restoration on habitat availability for fishes, including Arctic grayling (*Thymallus arcticus*)

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Abstract

Beaver dam mimicry is an emergent conservation practice. We evaluated the influence of constructed riffles, a unique type of beaver mimicry aimed to store water and allow fish passage, on habitat for fishes in one control reach and one manipulated reach with mimicry structures added. The beaver mimicry reach had deeper pool habitats and deeper and wider riffle habitats compared to an unmanipulated control reach. Dissolved oxygen was similar among reaches, averaging 8.7 ± 0.2 and 8.9 mg/L in the beaver mimicry and control reaches, respectively. Sediment size was also similar among reaches, with a D_{50} of 8.1 and 10.6 mm in the beaver mimicry and control reaches, respectively. The beaver mimicry reach had little to no overhanging bank vegetation or riparian vegetation shade cover, while the control had 38% of its bank covered by canopy and 56% overhung by vegetation. These riparian characteristics result from a legacy of livestock grazing and lack of consistent vegetation planting during restoration. Longnose dace (*Rhinichthys cataractae*) and white sucker (*Catostomus commersonii*) dominated in the beaver mimicry reach, together comprising 70% of the fish assemblage post-structure installation. Arctic grayling (*Thymallus arcticus*) was not found in the beaver mimicry reach but was present in the control, albeit in small numbers of only 3% of the assemblage post-structure installation. These results highlight the need to consider both in-stream and riparian habitat features for fishes, as well as timescales of both hydrological and ecological outcomes in restoration design.

KEYWORDS

aquatic-terrestrial linkage, community assemblage, ecohydrology, geomorphology, monitoring, salmonid

1 | INTRODUCTION

Natural freshwater habitats have been fundamentally altered by human activities in most parts of the world (Kuehne et al., 2020; Lovelock, 2009). To counteract freshwater degradation, restoration science and practice aims to improve habitats that have experienced anthropogenic-driven change (Palmer et al., 2010; Wohl et al., 2015). Although impressive strides have been made in the past decade to improve restoration design (Bennett et al., 2016), many restoration practices are still costly, and their long-term success is unknown (Bernhardt et al., 2005; Palmer et al., 2010). Many agencies and researchers are now employing new approaches that are less invasive, intentionally reinvigorate ecosystem processes and explicitly consider ecological and hydrological outcomes in project goals (Atkinson et al., 2018; Beechie et al., 2010; Palmer, 2009; Pasternack, 2020; Palmer & Bernhardt, 2006).

Installation of in-stream structures that mimic natural beaver dams has been championed as a potential low-cost, non-invasive river restoration practice (Burchsted et al., 2010; Pollock et al., 2015; Johnson et al., 2020). Beaver dams fundamentally alter water temperature, water table levels, geomorphology, in-stream fauna and riparian flora (Ecke et al., 2017; Majerova et al., 2015; Naiman et al., 1988; Pollock et al., 2007; Weber et al., 2017). Installation of beaver mimicry structures (BMS) or beaver dam analogues (BDA) has been successful in many cases (Law et al., 2016; Norman, 2020). However, project success appears to be site-specific and may not always accomplish what it is intended to at every location (Pilliod et al., 2018). Several underlying features of the ecosystem may govern whether restoration goals are met (Pasternack, 2020; Nash et al., 2021). These include geology, stream gradient, sediment supply and transport regime, presence of nearby beaver populations, hydrology, level of previous degradation and type of structure used to mimic the beaver activity. Many projects aim to increase water storage, but the influence of a change to the timing or amount of water storage on populations and communities of aquatic organisms is less well incorporated into restoration design (Beechie et al., 2010; Trush et al., 2000). Monitoring and consideration of timescales required to achieve biological goals is often lacking, leading to unknown interim and long-term recovery trajectories (Hamilton, 2012). Despite its growing use, there are still many scientific questions remaining as to how beaver mimicry restoration affects biodiversity and ecosystem processes.

The motivation behind many restoration projects in the United States is often to increase target fish populations that are sensitive to human-induced alterations to geomorphology, hydrology and water chemistry (He et al., 2019; García-Vega et al., 2020; Strayer & Dudgeon, 2010). Threats to fish populations include altered discharge magnitude and timing, altered sediment supply and transport, altered thermal dynamics, toxic pollution, competition from introduced species, overharvest and decreased connectivity (Hall et al., 2011a; Lynch et al., 2016; Poesch et al., 2016). A common restoration tactic is to restore in-stream habitat, such as gravel for spawning, to specifically improve conditions for target fish species or fish life-stages (Bernhardt et al., 2005; Kondolf & Wolman, 1993). However, outcomes of restoration activity are rarely monitored pre- or post-restoration or for long-term ecological responses (Downs et al., 2011; Pilliod et al., 2018). Additionally, riparian interfaces can control habitat, food sources, water temperature, bank stabilization and fine sediment erosion that are all especially important for juvenile fish life-stages, yet are often left out of restoration design (Albertson et al., 2013; Naiman & Décamps, 1997; Wipfli & Baxter, 2010). Because of the tight connection between changes in hydrology and geomorphology due to restoration and the subsequent condition of fish habitat, a comprehensive evaluation of restoration projects that includes post-installation monitoring of fish habitat could help improve our understanding of whether multifaceted restoration goals are met.

The upper Missouri River headwaters in Southwestern Montana host one of the last remaining natural populations of adfluvial Arctic grayling (*Thymallus arcticus*). Natural resource agencies and conservation organizations in southwestern Montana's Centennial Valley have taken critical steps toward preserving and restoring habitat for this fish of concern. Limiting factors identified in the Centennial Valley include water diversion, loss of floodplain connection, lack of deciduous woody riparian vegetation and reduced beaver distribution and abundance (Boyd et al., 2018). State and federal fish and wildlife agencies, conservation non-governmental organizations (NGOs) and private landowners are implementing measures across the Centennial Valley to increase stream flows, improve riparian vegetation, reduce fragmentation and eliminate entrainment in irrigation diversions to restore Arctic grayling populations. Restoring natural processes of streams, including naturalized flow regimes, sediment transport, channel evolution (e.g., migration, avulsion, and pool scour) and presence of beaver is considered the most effective approach to creating the habitats and connectivity that Arctic grayling require over a broad scale. However, this broad systems approach may fail to deliver site-specific life-history requirements on time-scales necessary to preserve vulnerable populations.

Beaver dams were a driver of channel dynamics, willow establishment and flow regimes in upper Missouri streams prior to their basin-wide reduction in the late 1800′s (Levine & Meyer, 2014, 2019). Their influence on fishes is well documented, yet quite variable and context specific. Many fish species benefit from beaver activity (Collen & Gibson, 2000; Johnson-Bice et al., 2018), and beaver can create suitable habitat for particular life stages of salmonids such as juveniles (Bouwes et al., 2016). By raising groundwater levels and increasing stream recharge from shallow aquifers, beaver may mitigate anticipated drought and climate change effects in Montana and across the West (Boyd et al., 2018; Cross et al., 2012), which could be especially helpful to keep rivers cool for cold-water species such as salmonids However, beaver activity can also be detrimental to native fishes by inducing changes to flow and thermal conditions (e.g. habitat such as warm, deep pools) and food sources, as well as by supporting competitively superior invasive species (Gibson et al., 2015). Beaver dams may limit access to habitat and restrict movement (Malison et al., 2016; Virbickas et al., 2015). As such, the ability of beaver mimicry restoration to effectively restore stream function and provide suitable habitat over acceptable timescales for Arctic grayling in southwestern Montana is relatively unknown.

In this study, we documented fish habitat 2 years after a restoration project that used beaver mimicry restoration. We compared a reach with BMS to an upstream control reach that was unmanipulated. We measured habitat characteristics that were selected to specifically align with habitat requirements for Arctic grayling because this species has high conservation need (Lamothe & Magee, 2004; Liknes & Gould, 1987). Other fishes may also be influenced by these same characteristics. We hypothesized that a reach with BMS would have similar physical habitat conditions to the control and that habitat conditions would generally be suitable for Arctic grayling. Because of underlying differences in riparian vegetation cover in the two reaches pre-restoration,

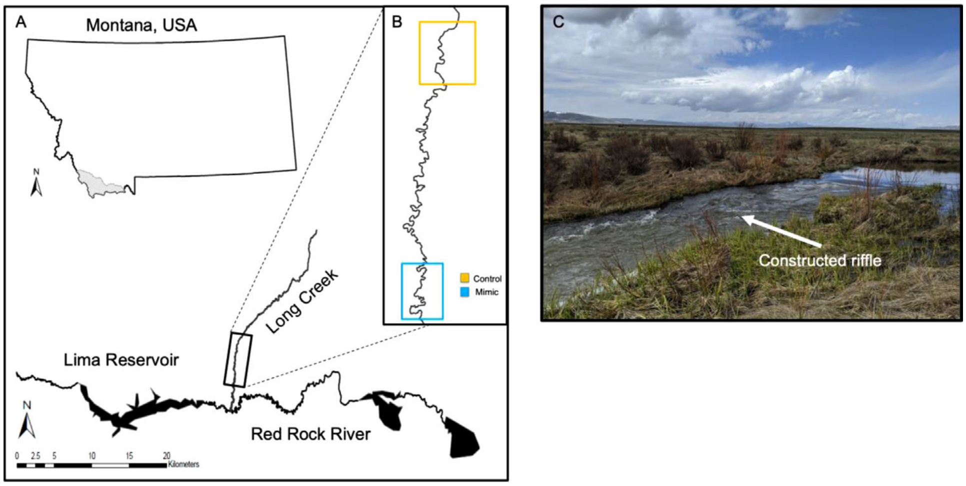

FIGURE 1 (a) Study location in southwestern Montana. (b) Responses in a reach with beaver mimicry structures (BMS; blue) were compared to an upstream, unmanipulated control reach (orange) that did not receive the restoration. (c) The beaver mimicry structures used in this restoration effort were constructed riffles intended to pool up water immediately upstream and to allow fish passage

combined with decades of livestock grazing in both reaches (Boyd et al., 2018), we predicted that riparian and in-stream vegetation characteristics would be different in the BMS reach compared to the control. Our study provides insight into restoration intended to not only influence hydrology but also fishes of concern in the Northwest Rocky Mountains.

2 | METHODS

This study was conducted in Long Creek (lat 44.68830, long -112.10170) in southwestern Montana's Centennial Valley (Figure 1), which sits at elevations between 2130 m at the valley floor to 3050 m in the mountains. Vegetation throughout the valley is Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*) and quaking aspen (*Populus tremuloides*) in the mountains, sagebrush steppe in the foothill flats, mesic grasslands and wetlands in the valley bottom and riparian areas with multiple species of willows along streams. The riparian corridor of Long Creek varies in vegetation composition throughout its length, primarily due to catchment geology and historical differences in land use. The study section of Long Creek was historically grazed by livestock until 2009, when it was acquired by The Nature Conservancy (TNC). In an effort to restore natural processes, reconnect floodplain access in an incised reach and promote healthy instream and riparian habitat, TNC installed nine BMS in August 2016. The in-stream dam structures selected for this project were constructed riffles. Although not as widely used as willow weave BDA (Pollock et al., 2015), the constructed riffle design was chosen over a traditional willow weave BDA to achieve water storage in a similar fashion but to also create (1) more stable, yet deformable, structures that could raise the streambed elevation > 0.3 m, (2) lower annual maintenance and (3) allow fish passage. The decision centred around concern over passage of Arctic grayling populations as well as limited long-term funding for continued maintenance. The constructed riffle consists of a wedge of sediment composed of 60% sand and silt, 20% gravel (<50 mm diameter) to raise the bed elevation of the stream, capped with less mobile cobbles (50–200 mm diameter), and lined with sod mats along banks. Structures were shaped to provide fish passage by integrating a defined low-flow thalweg. While the structures were intended to persist with minimal maintenance, they were designed to be deformed over the long term by natural channel forming processes on the scale of 10s to 100s of years. Nine structures were installed over 1.5 km of stream. Some natural beaver colonies were present upstream of the structures, although beaver activity in the project area on Long Creek was minimal in 2016 when the structures were installed (Boyd et al., 2018; Gillilan, 2016). Some willows have been planted in this reach, but survival, growth and success have been limited due to incised channel conditions. Due to the stable nature of the constructed riffle design and the importance of processes such as dam breaching for successful willow recruitment, we posit that this restoration technique may minimize opportunity for new willows to establish (Cooper et al., 2006). However, elevating the local water table was expected to benefit willows that were already established or planted.

Fish species and relative abundance were determined using electrofishing surveys in summers of 2010, 2011, 2012 and 2018. Electrofishing was conducted in a segment of Long Creek chosen by Montana Fish, Wildlife & Parks (MT FWP) for fish monitoring prior to developing the plan and installation for BMS. This segment included what became the BMS reach after structures were installed in 2016, as well as an unmanipulated control reach located approximately 4 km upstream, so we were able to delineate fish sampled from each of the two reaches pre- and post-installation. Fish were sampled using a mobile anode tote-barge and custom rectifying unit in a single-downstream pass. All sampled fish were netted, identified to species and released.

The control reach was used as a reference condition, however there were differences in reaches that existed prior to the restoration. For fish species data, we had pre- and post-installation data. However,

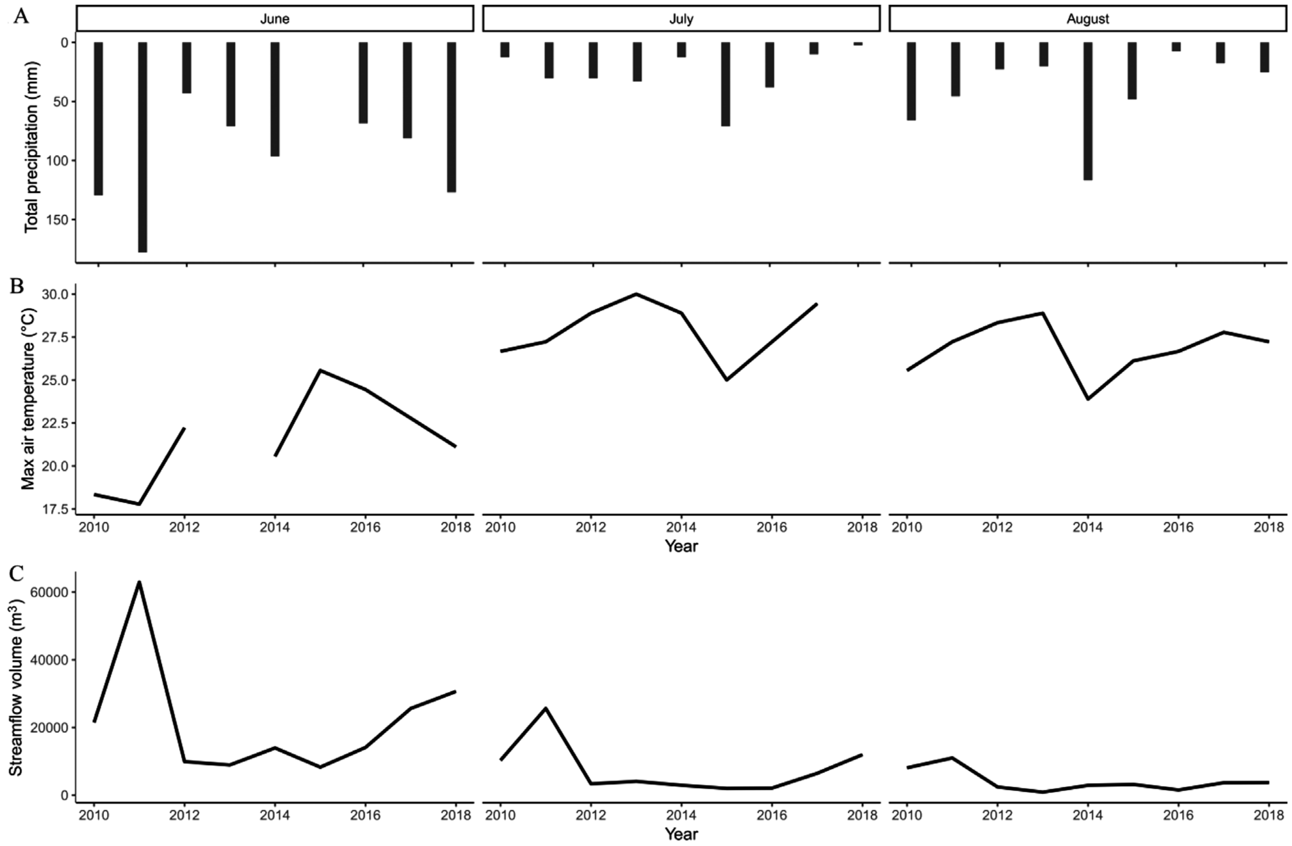

FIGURE 2 (a) Precipitation, (b) air temperature and (c) stream flow volume measured near the study site in Lima, MT by the USDA for three summer months. Pre-BMS includes years 2010–2016 and post-BMS includes years 2017–2018. Patterns in precipitation, air temperature and stream flow volume are not drastically different pre- and post-BMS installation, suggesting that measurements we report for our study in 2018 were collected under weather conditions that are generally representative of this area

for habitat characteristics we only had post-installation data. We therefore used a space-for-time substitution in this study to draw conclusions about the influence of BMS on current habitat conditions, an approach that was necessary in the absence of pre-restoration monitoring (Pretty et al. 2003). Although we recognize the clear limitations associated with using this approach and acknowledge that pre-data would be ideal to have, space-for-time substitutions are extremely common and provide important insight into current differences among compared reaches when a before-after-control-impact (BACI) design simply is not feasible due to constraints imposed by timing of project initiation, funding or communication among restoration groups and researchers (Albertson et al., 2011; Bennett et al., 2016; Pickett 1989; Stewart-Oaten et al., 1986). The control reach contained evidence of natural beaver dams, although they were classified as abandoned in 2016 and failed (breeched) in 2018 (Gillilan, 2016; Reinert personal field observation). The control reach also had more riparian vegetation prior to the 2016 restoration due to historical differences in grazing, as well as minor natural differences in channel morphology, substrate and slope resulting from position within the watershed.

We evaluated the maximum air temperature (°C), total precipitation (mm) and stream flow volume (m^3) for the years 2010–2018, which encompassed the range of dates when fish data were available. Data were collected from the USDA Natural Resources Conservation Service National Weather and Climate Centre for a location (Lima, MT) near the study site. Conditions were generally similar among years. An exception is 2014, which was cooler and wetter than the rest of the series, and June 2011 flow volume and precipitation, which was higher than other years (Figure 2). Given these patterns, we concluded that differences in these abiotic conditions between 2010 and 2018 were not likely major drivers of changes to the fish assemblages through time and that comparison between reaches was an effective way to evaluate how installation of BMS influences current habitat for Arctic grayling and other fishes.

We employed two types of habitat surveys that took place on 26 and 27 July, 2018 in Long Creek that aligned with the electrofishing reaches. First, we used transects to make detailed measurements of physical, chemical and vegetation characteristics at BMS. Using transects oriented perpendicular to the direction of water flow, we quantified characteristics directly upstream of BMS ($n = 7$) and compared them to riffles in the control reach ($n = 7$). Second, we surveyed geomorphic characteristics of all riffles and all pools in each of the two reaches. We measured response variables specifically known to influence Arctic grayling, which is a species of concern in MT and is experiencing reduced population sizes throughout much of its historical range (Lamothe & Magee, 2004; Liknes & Gould, 1987). At the transect sites, we measured dissolved oxygen (mg/L, YSI Pro Plus multimeter, Yellow Springs, Ohio), velocity (m/s, Hach FH950 at a single location positioned at 0.6 of the depth), channel bankfull width (m), channel wetted edge (m), sediment size (mm) and instream and riparian vegetation cover (%). Pebble counts were conducted by randomly selecting 100 pebbles from the stream bed at each transect and measuring the B-axis (Wolman, 1954). The 10th, 50th and 90th percentiles of the grain size distribution from the pebble count were estimated using Gradistat (Blott & Pye, 2001). Discharge was calculated by multiplying the area of the cross-section by the mean velocity of the water within that cross-section (Hauer & Lamberti, 2017) using velocity and water depth measured at twenty evenly spaced locations along the wetted width of each transect. Canopy cover proportion was estimated using a spherical densiometer held flat at 1.0 m above the water surface and 1.0 m from both the left and right stream bank. In-stream vegetation was measured as the proportion of 40 locations evenly spaced along a transect spanning the wetted width of each site that contained a positive macrophyte presence as identified by one consistent observer. Overhanging vegetation was estimated as a proportion of a bank Section 2 m in length on each of the left and right banks of the end points of each transect.

We surveyed geomorphic characteristics of all riffles and pools in both reaches. We counted each pool and riffle and measured their length (m), width (m) and thalweg depth (m). Pool or riffle categorization was assigned based on visual assessment of surface flow characteristics and water depth (Jowett 1993). Although this approach is rough, one consistent observer made every classification to ensure that habitats across reaches could be compared. To estimate glide (also commonly termed 'run') habitat (neither riffle nor pool), the sum of all lengths of measured pools and riffles was subtracted from total reach length. To calculate how much of a reaches' length might move gravel-sized sediment (riffles), we used the mean riffle length in each reach multiplied by the number of riffles surveyed in each reach and divided by total length. This calculation provided an estimate of the percentage of each reaches' length that was riffle. We used the same method to calculate how much of a reaches' length might store fine sediment (pools). Riffle to pool ratio was estimated for each reach using counts of each habitat category and dividing the number of riffles by the number of pools. Density of riffle or pool habitat was calculated by dividing the number of each habitat feature counted by total reach length. Water temperature was recorded hourly (Rugged TROLL 100, In-Situ) at one location in each reach and is reported as the proportion of hours in July 2018 when temperatures met or exceeded 17°C to align with data reported in Liknes & Gould (1987).

Student's *t*-tests were used to compare responses between BMS and control transects. To compare the BMS and control reach survey characteristics, student's *t*-tests were used. Responses were log or square root transformed as appropriate when they did not meet the assumptions of normality as estimated by a Shapiro–Wilks test. All analyses were conducted in R version 3.6.3. We qualitatively evaluate our findings in relationship to a prior study (Liknes & Gould 1987) where high relative abundance of Arctic grayling was observed in 'Section 1' of the Big Hole River, approximately 225 kilometres from the Long Creek site.

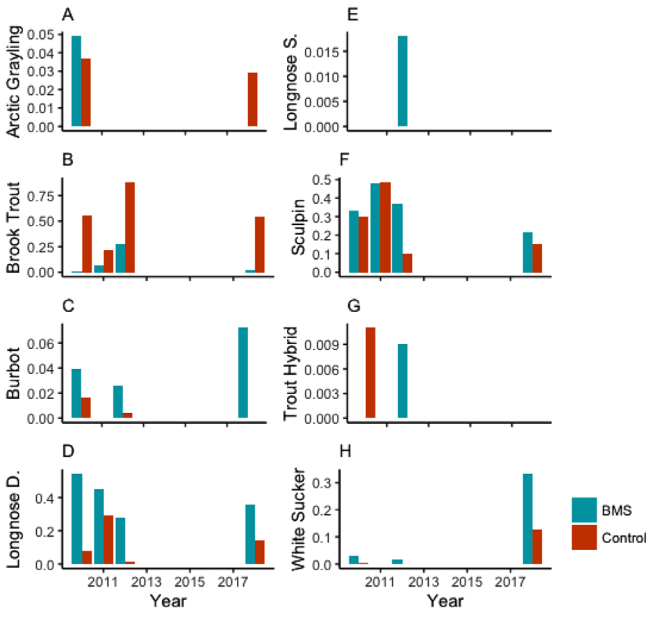

FIGURE 3 Proportion of fish species surveyed in BMS and control reaches across years (2010, 2011, 2012 and 2018) when sampling was conducted. BMS were installed in 2016. Missing values in sampled years are true zeros. Arrangement of panels is alphabetical order

3 | RESULTS

Fish assemblages differed between the BMS and control reaches (Figure 3; Table 1). In all years prior to BMS installation, Arctic grayling showed identical presence/absence responses in the two reaches. They were either present in both (2008) or absent in both (2010, 2011). However, in 2018 after BMS installation, they showed divergent responses. Arctic grayling were only present in the control reach in 2018. Brook trout (*Salvelinus fontinalis*) dominated the control reach but were minimal in the BMS reach, and this pattern was consistent through time. Hybrid cutthroat (*Oncorhynchus clarkii*) trout were not present in 2018 in any reach although they had been sporadically documented in low proportions in prior years. Proportion of burbot (*Lota lota*) and white sucker (*Catostomus commersonii*) was higher in 2018 in the BMS reach compared to the control and to any previous year. The proportion of Longnose dace (*Rhinichthys cataractae*) and Rocky Mountain sculpin (*Cottus bondi*) was higher in the BMS reach than the control and was lower in 2018 than in previous years for both species.

Our comparison of areas immediately upstream of installed BMS with control riffles revealed similarities and differences, suggesting that some current habitat characteristics associated with BMS may be suitable for Arctic grayling and other cold-water fishes, while other characteristics may not. Dissolved oxygen and discharge were similar between BMS and control reaches (Figure 4; Table 2). Canopy cover and overhanging vegetation were significantly lower in the BMS than the control reaches, as was the case prior to restoration, but in-stream

TABLE 1 Proportions of fish species observed in BMS and Control reaches across years when sampling took place. Arrangement is in alphabetical order

	BMS				Control			
Species	2010	2011	2012	2018	2010	2011	2012	2018
Arctic grayling	0.049	0	0	0	0.037	0	0	0.029
Brook trout	0.010	0.072	0.281	0.024	0.550	0.219	0.882	0.548
Burbot	0.039	0	0.026	0.072	0.016	0	0.004	0
Longnose dace	0.543	0.452	0.281	0.357	0.079	0.295	0.011	0.144
Longnose sucker	0	0	0.018	0	0	0	0	0
Sculpin	0.330	0.476	0.368	0.214	0.302	0.486	0.103	0.154
Trout hybrid	0	0	0.009	0	0.011	0	0	0
White sucker	0.029	0	0.017	0.333	0.005	0	0	0.125

TABLE 2 Responses measured along transects for each reach ($n = 7$). Significant differences marked in bold

Response	BMS mean (±SE)	Control mean (±SE)	t value	P
Dissolved oxygen (mg/L)	8.68 (0.23)	8.90 (0.16)	−0.799	0.442
Discharge (cfs)	2.03 (0.17)	2.16 (0.16)	−0.575	0.576
Wetted width (m)	3.78 (0.25)	3.42 (0.19)	0.831	0.424
Bankfull width (m)	7.04 (2.27)	5.31 (1.04)	0.683	0.513
D_{10} (mm)	2.13 (0.03)	2.16 (0.05)	−0.476	0.645
D_{50} (mm)	8.09 (4.95)	10.63 (4.36)	−0.604	0.556
D_{90} (mm)	71.26 (16.53)	52.77 (19.94)	1.63	0.149
Canopy cover (prop.)	0 (0)	0.38 (0.10)	−5.02	**0.002**
Overhanging vegetation (prop.)	0.01 (0.01)	0.56 (0.06)	−12.5	<**0.001**
In-stream vegetation (prop.)	0.43 (0.06)	0.48 (0.09)	−0.422	0.681

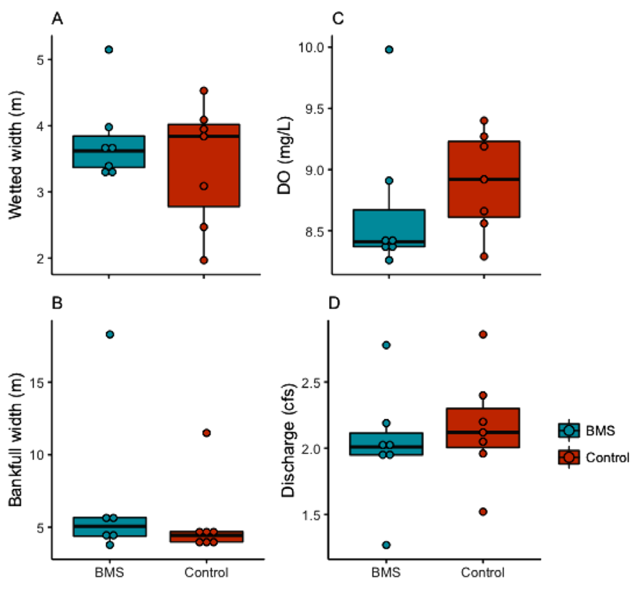

FIGURE 4 Physical characteristics measured on July 26 or 27, 2018 along seven riffle transects within either the BMS or control reach. (a) channel wetted width, (b) bankfull width, (c) dissolved oxygen and (d) discharge. Boxes show 25th and 75th percentiles. Thick black line shows median. Data points are jittered for display purposes

vegetation was similar (Figure 5a–c; Table 2). Sediment size was similar between reaches (Figure 5d–f).

There were 13 riffles and 23 pools in the BMS reach and nine riffles and 21 pools in the control reach. Riffles were wider and the thalweg of both riffles and pools was deeper in the BMS reach compared to the control (Figure 6; Table 3). Pools were longer, more variable in length, and deeper in the BMS reach compared to the control, although depth was the only statistically different comparison (Table 3). The BMS reach also had more glide habitat and a higher riffle:pool ratio than the control (Table 4). Density of habitat features, defined as pools or riffles, was half as much in the BMS reach compared to the control (Table 4).

We qualitatively compared habitat characteristics observed in the BMS reach, where Arctic grayling were absent, and the control reach, where Arctic grayling were present, to those in a prior study that identified habitat characteristics supporting high relative abundance of Arctic grayling ('Section 1 in Liknes & Gould 1987). Compared to Section 1, riffle and pool width were narrower, discharge was much lower, and thalweg depth was similar in the BMS reach (Table 5). The proportion of sediment categorized as fine-grained was high in both the BMS and control reaches compared to Section 1. Additionally, pool:riffle ratios were much higher in the BMS and control reaches compared to those measured in Section 1.

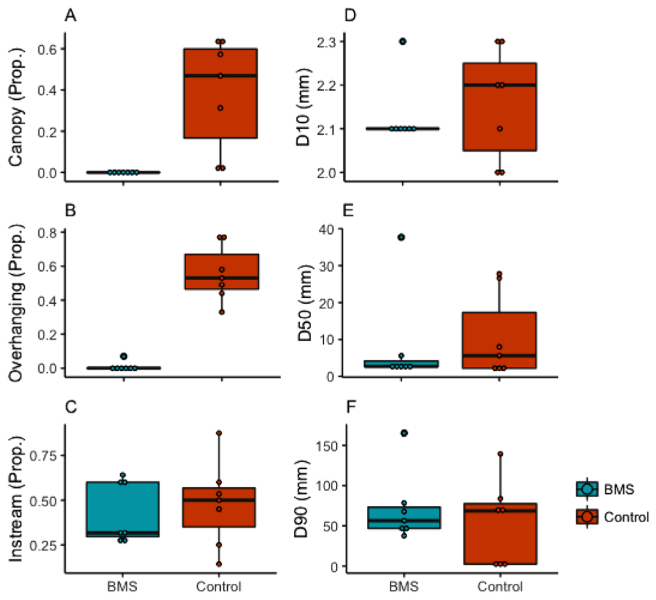

FIGURE 5 Characteristics of (a) canopy cover, (b) overhanging vegetation, and (c) instream vegetation along the transects at BMS or control riffles. The (d) 10th, (e) 50th and (f) 90th percentiles of sediment size distributions along the transects near BMS and control riffles. Boxes show 25th and 75th percentiles. Thick black line shows median. Data points are jittered for display purposes

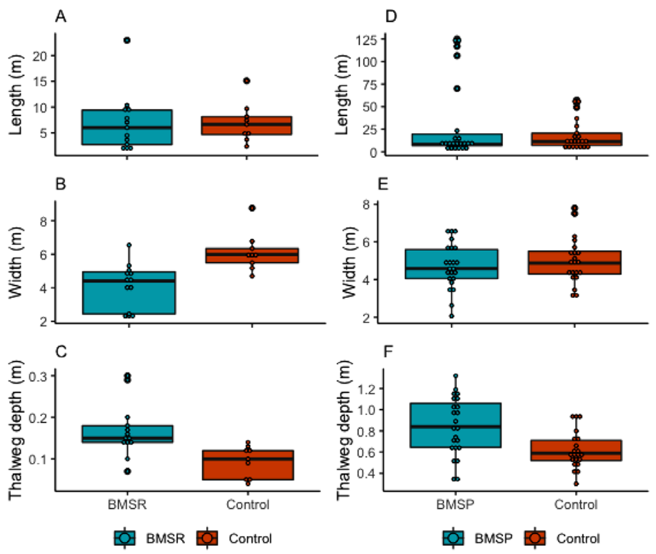

FIGURE 6 Geomorphic characteristics in riffles (panels a–c; denoted 'R') and pools (panels d–f; denoted 'P') across BMS or control reaches. Boxes show 25th and 75th percentiles. Thick black line shows median. Data points are jittered for display purposes

4 | DISCUSSION

BMSs, including small dams that create pooled water, are increasingly used to improve water storage capacity in areas facing growing water demand and reduced supply. An integrated understanding of the changes these dam-like structures make to in-stream and riparian organisms, food webs and hydrology is needed (Burchsted & Daniels, 2014; Majerova et al., 2015; Pollock et al., 2007). We found that a reach with BMS supported fish species and contained habitat characteristics that varied from an unmanipulated control reach. Arctic grayling were found in the upstream, unmanipulated control reach but were not present in the BMS reach. Brook trout dominated the control but were in very low relative abundance in the BMS reach. The BMS reach was dominated by longnose dace and white suckers. In the BMS reach, riffles were narrower and deeper, while pools were deeper than those in an unmanipulated control reach. Riparian vegetation was also substantially different. BMS had almost no canopy cover or overhanging vegetation compared to the control. This difference existed before restoration due to historical grazing and channel morphology differences but that had not converged to the control condition within the time frame of this study 2 years post-BMS installation. Dissolved oxygen and in-stream vegetation conditions were similar between BMS and control reaches. These findings suggest that restoration using BMSs may create conditions in the short-term that are unsuitable for some salmonids such as Arctic grayling and Brook trout that are sensitive to fine sediment, lack of riparian vegetation and warm water temperature. Our findings highlight the need for continued long-term evaluation of biological responses to restoration efforts and a clear a priori understanding of the timescale required to achieve desired end state, especially when a species of concern may reach drastically small populations before the long-term development of suitable habitat (Schmutz et al., 2016; Wilson et al., 2011). Many fish populations are declining, and restoration that does not include components of their habitat may miss an opportunity to meet multiple goals or may meet some goals (water storage) at the expense of others (suitable habitat for cold-water fisheries).

Cold-water fish species such as salmonids that are disproportionately impacted by climate change and increasing river temperatures (Crisp 2008; Elliott & Elliott, 2010; Isaak et al., 2015; Schindler et al., 2008; Wenger et al., 2011) are often the targets of river restoration efforts (Mohseni et al., 2003; Sinnatamby et al., 2020). However, differences in geomorphic and hydrologic requirements for various fish species and life-stages make it imperative to evaluate and understand how restoration affects habitat characteristics. We found that BMS provided habitats that support a variety of fish species typical of montane valley streams (MFWP 2019), including burbot, longnose dace, sculpin and white suckers. Brook trout were much more abundant in the BMS reach in 2012 than in 2018, and Arctic Grayling were observed in low abundance in the BMS reach in 2010 but not present at all in 2018. The assemblage of fish in the BMS reach suggests that the habitat was generally more suitable for species that are tolerant of fine sediment and warm water. In contrast, the control reach was dominated by Brook trout and did contain Arctic grayling, albeit in small numbers, which are both cold-water species.

Other responses that will be important to evaluate in future studies include movement, behaviour and feeding. The design of the structures for this restoration project was specifically selected to allow passage, a common limitation observed for fishes near natural beaver dams. Passage over even small barriers can be challenging for fishes,

TABLE 3 Survey of all riffles and all pools in each reach in July 2018. BMS riffle $n = 13$; Control riffle $n = 9$; BMS pool $n = 23$; Control pool $n = 21$. Significant differences marked in bold

	Riffle				Pool			
Response	BMS mean (±SE)	Control mean (±SE)	*t* value	*p*	BMS mean (±SE)	Control mean (±SE)	*t* value	*p*
Length (m)	6.94 (1.58)	6.99 (1.27)	−0.515	0.613	30.4 (9.00)	18.7 (3.63)	0.024	0.981
Width (m)	4.07 (0.380)	6.12 (0.390)	−3.78	**0.001**	4.70 (0.250)	5.00 (0.270)	−0.796	0.431
Thalweg depth (m)	0.169 (0.018)	0.093 (0.013)	3.41	**0.003**	0.841 (0.057)	0.617 (0.038)	3.26	**0.002**

TABLE 4 Geomorphic conditions measured in the two reaches in the survey in July 2018

Reache	Total length (m)	Estimated glide length (m)	% length riffle	% length pool	Pool:riffle ratio	Density of riffles (No./m)	Density of pools (No./m)
BMS	986	197	9.2	70.9	7.7	0.01	0.02
Control	599	144	10.5	65.6	6.2	0.02	0.04

TABLE 5 Habitat characteristics observed in BMS and control reaches in this study compared to habitat characteristics observed in a prior study. The location from Liknes and Gould was reported to have high relative abundance of Arctic grayling ('Section 1' from Liknes & Gould 1987)

Response	BMS	Control	Section 1 from Liknes and Gould 1987
Riffle width (m)	4.07	6.12	10.83
Pool width (m)	4.7	5.0	8.95
Thalweg depth (m)	0.505	0.355	0.547
Pool-riffle ratio	7.70	6.20	1.51
Discharge (cfs)	2.03	2.16	24.01
Bottom materials (%)			
Boulders (>260 mm)	0	0	0.9
Rubble (260–64 mm)	9.6	10.3	41.5
Gravel (63–20 mm)	29.1	15.9	42.8
Fines (<20 mm)	61.3	73.9	14.8
July hours over 17°C (%)	57	43	60

especially during low-flow periods when water temperature is warm, which is an important consideration when using constructed riffles (Cutting et al., 2018; Virbickas et al., 2015). Although we cannot evaluate passage explicitly with our dataset, use of the BMS reach by salmonids was minimal, suggesting that increased salmonid survival and production observed in other systems may be site- or structure-type specific (Bouwes et al., 2016). The BMS reach had riffles and pools that were narrower and a pool:riffle ratio that was higher than in a prior study documenting the factors positively associated with high densities of Arctic grayling (Liknes & Gould, 1987), suggesting availability, type or spacing of riffle habitat needs further evaluation (Munir & Westbrook, 2021). Habitat complexity achieved by other types of small dam structures, such a willow weave dams, may be fundamentally different from that achieved by constructed riffles, and these differences may be further compounded by differences in underlying geology or historical land use (Bouwes et al., 2016). Fish may also respond positively to beaver mimicry because of the addition of woody material involved with building the dams, so constructed riffles comprised primarily of rock and sand may not achieve those same outcomes (Raymond et al., 2019; Roni & Quinn, 2001; Sweka & Hartman, 2006). Future work is needed to identify how BMS influences fish upstream and downstream passage success and frequency of use across days, seasons, species and life-stages.

Along with evaluating the aquatic environment, assessment of riparian cover associated with suitable conditions for salmonids provides insight into whether the restoration effort is currently capable of supporting fish species of concern (O'Briain et al., 2020; Opperman & Merenlender, 2004). We documented that the BMS reach was highly exposed, with little to no riparian cover, suggesting that conditions for willow establishment have not yet been met. This finding is consistent with the legacy of long-term grazing on this property. We posit that soil and water saturation conditions that support colonization and growth of riparian vegetation species such as willow may not be suitable or may take longer than 2 years to develop (Levine & Meyer, 2019). In addition, the constructed riffles were not designed to be breached over the short term, and dam breaching and failure is a mechanism necessary for willow establishment. Research indicates that establishment of willow and cottonwood within a 15-month time frame is increased substantially when planted in deep holes that provide water table access and provided protection by plastic covers (Hall et al., 2011b), a technique that may be necessary to use for future restoration efforts that aim for increased riparian cover. Groundwater discharge changes due to BMS may also play a role in regulating in-stream temperatures and deserves further exploration (Bobst, 2019; Weber et al., 2017). Additionally, changes to channel geomorphology resulting from BMS may substantially influence water temperature. Water temperature can be controlled by geomorphologic features such as the percent of channel that is pool habitat, the presence of undercut bank, groundwater resurgences, which are sometimes even more important than the shade cover (Hawkins et al., 1997; Ouellet et al., 2017; Tate et al., 2007; Wawrzyniak et al., 2016; Woltemade, 2017). Many restoration projects do not have funds or time to plant riparian vegetation, despite the crucial role it plays in creating shade and cooler water refuges, providing food, modifying erosion and increasing hydrological connectivity (Dick et al., 2017; Naiman & Décamps, 1997; Schlosser & Karr, 1981). The continuation of minimal riparian vegetation cover after the large-scale in-channel restoration highlights the need for future projects to consider monitoring time scales and factors linking in-stream processes to riparian recovery.

Beaver dams and beaver mimicry structures likely influence other taxa besides fish and could promote changes to food web dynamics and ecosystem processes. Previous research suggests that beaver activity increases invertebrate diversity and secondary production and can change community structure (Hood & Larson, 2014; Law et al., 2016; Reinert et al., 2022). Beaver ponds can increase habitat for amphibians but may require current occupation by beavers to achieve these documented positive effects (Dalbeck et al., 2014; Zero & Murphy, 2016). The immediate habitat around BMS may be more relevant to less mobile species such as invertebrates and periphyton because they cannot as easily or quickly move to avoid undesirable locations. Future work might consider the number, spacing and type of structure to determine how BMS will alter lower trophic levels (Munir & Westbrook, 2021) and ultimately influence food availability for fish (Reinert et al., 2022).

Despite evidence from our study that BMS create habitats that are relatively unsuitable for salmonids, we acknowledge that our research approach has several limitations. Because we only identified presence/absence of fishes on a single date, we can only draw conclusions about general suitability rather than mechanistic influences of BMS on density, movement, physiology, reproduction and survival. Because Arctic grayling spawn in downstream areas or other tributaries in this system and were observed in the upstream control reach but not in the BMS reach, we conclude that they must spend effort to move through the BMS reach. We did not characterize how quickly or easily they were able to do so (Gander et al., 2019). Because young-of-the-year Arctic grayling were not sampled in the survey, we cannot evaluate whether this particular life stage responds to the BMS. Future research would need to verify this possibility given that juvenile Arctic grayling and other salmonids have been shown to benefit from removal of beaver dam structures (Foote et al., 2020; Wuttig, 2000). Because our study took place within 2 years of BMS installation, we captured the short-term influence of this restoration effort on habitat for biota. Although we are unable to capture the full potential for riparian vegetation or instream fauna to colonize over the long-term, the time scale over which we did measure is crucial for understanding the persistence of a highly vulnerable Arctic grayling population. Given the low numbers of Arctic grayling that currently exist in Montana, they may be extirpated in a time frame much shorter than is needed to establish vegetation cover and restore key geomorphological processes. Although this work needs to be upscaled to know how changes at the reach scale will influence fish at the watershed scale, we hope these findings motivate future monitoring and integrative research and support long-term monitoring programs.

5 | CONCLUSION

Management challenges include meeting multiple goals that may be synergistic or antagonistic. Increasing late-season summer water availability is almost always a goal when installing beaver mimicry structures, especially in the arid Rocky Mountain West where climate change and agricultural water use exceeds supply (Chambers & Pellant, 2008; Chambers & Wisdom, 2009). However, a long history of research demonstrates how in-stream structures change water velocity and the timing and magnitude of floods in ways that very likely, and often negatively, influence biota (Poff et al., 1997, Pretty et al. 2003; Statzner et al., 1988). Yet, little research to date has linked a short- or long-term ecological response to the hydrologic changes associated with this increasingly common restoration approach (Palmer & Bernhardt 2006). A next step is for managers and stakeholders to understand, prioritize and perhaps place financial value on both the hydrologic and ecological outcomes of installing BMS and, most importantly, the timescales required to attain them (Kuehne et al., 2020). Indeed, studying BMS with an integrated perspective can link the different biological, geomorphological and hydrological components to address their full restoration potential as tool to improve flow regimes, riparian vegetation and instream habitat conditions for threatened fishes.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Valerie Ouellet: Data curation; Formal analysis; Writing – original draft; Writing – review & editing. J. Holden Reinert: Conceptualization; Data curation; Investigation; Methodology; Writing – original draft; Writing – review & editing. Nathan Korb: Project administration; Writing – original draft; Writing – review & editing. Matthew Jaeger: Methodology; Project administration; Writing – original draft; Writing – review & editing

ETHICS STATEMENT

Ethical and legal approval was obtained from Montana Fish, Wildlife, & Parks prior to the start of the study and followed their sampling and animal handling policies.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be made openly available in https://doi.org/10.5061/dryad.47d7wm3fq.

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