

BIOTIC AND PHYSICAL RESPONSES TO BIOMIMICRY STRUCTURES IN A ROCKY
MOUNTAIN INCISED STREAM

by

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of

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DEDICATION

This thesis is dedicated in loving memory to my grandmother Dolores Scanlan Reinert, the greatest person I ever had the pleasure of knowing.

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ABSTRACT

An increase in stream degradation resulting from land use change has motivated an increase in restoration efforts across the globe. Post-restoration monitoring is still lacking, however, and does not always incorporate biotic responses to changes in the physical template. Beaver mimicry structures (BMS) are becoming a popular tool to restore degraded streams throughout the American west, but relatively little is known about how these installations influence both biotic and abiotic factors, with consequences for ecosystem functioning. We monitored basal resource deposition and macroinvertebrate density, biomass, and production to quantify functional responses to BMS installations. We compared conditions at BMS sites to naturally occurring beaver dam and reference riffle sites in a low-gradient stream in southwest Montana. Thermal ranges were contracted, and daily maximum temperatures increased at BMS sites compared to reference riffle sites. Deposition of fine sediment and basal resources was similar at beaver and BMS sites, and both were higher than reference riffles. Densities and production of macroinvertebrates were higher at the BMS sites compared to reference sites and similar to beaver sites due to changes in physical habitat and basal resource availability, reflected by increases in production of shredders (beaver) and collector-gatherers (BMS). In this study site, changes to the physical template using BMS appear to have strong impacts on biotic functional responses, creating habitats similar to target conditions of natural beaver dams. Future research should consider the extent of degradation and temporal limitations of monitoring schemes to incorporate BMS into standard restoration practice. Functional response metrics provide an important and mechanistic approach to determine the efficacy of process-based stream restoration practices.

CHAPTER ONE

BIOTIC AND PHYSICAL RESPONSES TO BIOMIMICRY STRUCTURES IN A
ROCKY MOUNTAIN INCISED STREAM

Contribution of Authors and Co-Authors

Manuscript in Chapter 1

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Introduction

The number and scope of river restoration projects have increased, with billions of funding dollars allocated to rehabilitating degraded freshwater ecosystems (Bernhardt et al., 2005). Despite growing evidence that explicit consideration of biological responses improves restoration goals and outcomes (Trush, McBain, & Leopold, 2000), most projects still focus on changes to the physical template, such as channel stability, and do not quantify how biology interacts with the physical processes that are changed. Monitoring plans that assess biological outcomes are often lacking, and few restoration projects track their successes and failures due to limited funding (Bernhardt et al., 2005; Naiman et al., 2012). Projects are often completed with vague visions of what an ecologically functioning river should look like, and are likely to fall short of restoration goals (Palmer et al., 2005; Wohl, Lane, & Wilcox, 2015).

The assumption that biotic responses will parallel physical habitat improvements is under scrutiny and refining our understanding of restoration outcomes will require studies that directly link physical habitat conditions and ecological dynamics (Stewart et al., 2009). Recently, linkages between physical degradation, such as channel incision, and loss of ecosystem engineers have become a focal topic in restoration ecology. While channel incision, or lowered bed elevation, can occur naturally as climate changes (Cluer & Thorne, 2013), the accelerated rate of and ubiquity of channel incision in the western United States mostly stems from land use practices and the loss of plant and animal ecosystem engineers (Jones, Lawton, & Shachak, 1994; Pollock, Heim, & Werner, 2003). Perhaps the most recognized ecosystem engineer in streams is the North American beaver

(*Castor canadensis*), which is widely distributed throughout the continent and alters the hydrology, morphology, and ecology of streams ecosystems through dam building (Burchsted et al., 2010; Naiman et al., 1988). Over the last two centuries, extensive trapping and removal of beaver has occurred, decreasing their populations by an order of magnitude and eliminating their important effect on the landscape (Naiman et al., 1988; Pollock et al., 2003). As a result, stream incision is much more prevalent when these important biotic components are absent.

Because of declines in beaver population size and range, beaver mimicry structures (BMS) have gained popularity in recent years as a tool to address channel incision and stream degradation (Pollock et al., 2003). BMS are *in situ* structures designed to mimic the hydrologic and geomorphic effects of beavers on rivers and riparian corridors by raising water levels, modifying stream discharge, and increasing sediment deposition (Castro, Pollock, Jordan, Lewallen, & Woodruff, 2015; Pollock et al., 2014). Recent studies have shown BMS as an effective technique in reducing mean temperatures (Weber et al., 2017), increasing aquifer recharge (Bobst, 2019), and providing beneficial habitat for salmonids (Bouwes et al., 2018; Pollock et al., 2014). However, little is known about how the addition of BMS affects macroinvertebrate communities, ecosystem processes such as secondary production, and basal resources.

Because macroinvertebrates play an important role in regulating basal resources in streams and provide food for a large number of fish species, understanding how they respond to BMS will provide important and currently understudied ways in which restoration influences ecosystem function (Wallace et al., 1996). Metrics such as density,

biomass, and species richness may offer insight into ecological responses to changes in physical and chemical parameters but might not capture mechanisms that cause changes in stream processes (Frainer, Polvi, Jansson, & McKie, 2018). For example, in beaver-mediated reaches in southern Chile, species richness declined, but secondary production increased as a function of resource availability (Anderson & Rosemond, 2007).

Secondary production is a dynamic metric that incorporates individual-level growth, recruitment, and mortality and ecosystem-level processes like trophic interactions and energy fluxes over time (Benke, 1993; Dolbeth, Cusson, Sousa, Pardal, & Prairie, 2012). Monitoring macroinvertebrate biological responses through time after restoration with BMS may provide a more accurate predictor of success or failure by evaluating changes that may not be reflected in changes measured by species richness or biomass alone (Frainer et al., 2018; Herrick et al., 2006).

This study provides insight into how BMS affect multiple trophic levels in low gradient streams, and whether or not BMS achieve restoration goals that encompass both physical and biological function. We quantified the impacts of BMS installations on in-stream conditions in Montana, and how the modifications of temperature and sediment deposition affect particulate organic matter, biofilm standing biomass, and macroinvertebrate density, standing biomass, and production. We quantified the thermal regime, sediment deposition, summer secondary production of macroinvertebrates, and basal resource standing crop and deposition to address the following questions: (1) How do BMS alter physical and biological responses from a riffle state to a pooled state upstream of the BMS?; (2) How do functional responses of BMS compare to natural

beaver dams? Daily maximum temperatures and diel temperature ranges were predicted to increase due to decreased stream velocity and increased incoming solar radiation. We also predicted the deposition of fine sediments at BMS sites would be similar to fine sediment deposition found at natural beaver sites and higher than at reference riffle sites. We then expected these changes to the physical template to initiate biological responses. We predicted that densities, standing biomass, and production of macroinvertebrates at BMS sites would be similar to Beaver sites but different from Reference sites as a result of temperature and resource availability differences. Macroinvertebrate functional feeding groups (FFG) at BMS sites should be similar to Beaver sites, dominated by collector-gatherers and predators, compared to Reference sites that should have a more even distribution of filter-feeders, shredders, and scrapers. Together, our findings provide some of the first data to quantify process-based responses to restoration aiming to mimic the impacts of important ecosystem engineering animals.

Methods

Study Site

Long Creek is a 22 km long, third order tributary to the Red Rock River located in southwest Montana's Centennial Valley on the Nature Conservancy's Sandhill Preserve (Figure 1). Situated north of Idaho and west of Yellowstone National Park, the Centennial Valley is an east-west orienting valley that lies on the east side of the continental divide. The valley is roughly 48 miles long and encompasses 370,000 acres. The Long Creek drainage is located near the southern end of the Snowcrest Mountains and the southwest end of the Gravelly Mountains draining a total of 58.9 km². Long

Creek is classified as a riffle-pool and plane-bed stream, with slope of 0.25% and average annual precipitation of 43.82 cm. Vegetation throughout the valley ranges from Douglas fir, lodge pole pine, and aspen in the mountains, sagebrush in the foothills, to multiple species of willows throughout the riparian areas. The riparian corridor of Long Creek varies in vegetation composition throughout its length, primarily due to catchment geology and historical differences in land use. From the headwaters to the upstream third of the TNC property, willows are abundant on the stream banks. Grasses and sedges occupy the bottom third of the TNC property to the confluence with the Red Rock River. Extensive willow planting has occurred as part of ongoing restoration work on the lower half of Long Creek, with mixed outcomes of recruitment. For the restoration project studied here, the primary goals were to restore important physical attributes of the stream by reconnecting the channel to the floodplain during high flows, increasing the area of saturation during low flows, and restoring riparian and aquatic habitats.

Mimicry Structure Design and Installation

The BMS built on Long Creek during late August 2016 were “constructed” or “armored” riffles designed to produce hydrological patterns similar to traditional BMS that are intended to create local hydrologic and fluvial geomorphic features, such as pools, associated with beaver activity (Gillilan, 2015). The constructed riffles were also designed to specifically provide passage for one of the remaining populations of threatened adfluvial Arctic grayling that are endemic to the Upper Missouri Headwaters. During structure construction, excavators were used to transport materials from a nearby gravel pit and construct riffles consisting of 60% sand and silt, 20% gravel (<5 cm

diameter), and 20% cobbles (5-20 cm diameter). Banks were reinforced with donor sod when available. Nine total structures were installed over 1,544 m of stream (1 structure/257 m) (Gillilan, 2015).

To characterize the hydrologic regime, discharge measurements were taken on Long Creek twice per month at two different surface water stations throughout the TNC's parcel. Stream discharge measurements were taken within an eight-hour period of each other. Transects spanning the width of the stream were established, and twenty evenly spaced locations along the wetted width were measured for velocity and water depth. Velocity measurements were recorded using either a Hach FH950 or Marsh McBirney flow meter at 0.6 of the depth. Discharge was calculated by multiplying the area of the cross-section by the mean velocity of the water within that cross-section. Daily average discharge showed a mean difference of 0.95 cfs greater at the Reference (12.18 ± 0.47 cfs) than Mimic reach (11.22 ± 0.50 cfs). Measurement error associated with these discharge measurements suggests that ultimately, there were negligible differences in discharge between reaches.

Monitoring Locations

We established three treatments and a total of six monitoring sites throughout the Long Creek restoration project. The three treatments were (i) upstream of BMS (Mimic: $n = 2$), (ii) upstream of existing beaver dams (Beaver: $n = 2$), and (iii) reference riffles (Reference: $n=2$) located in a stream section directly upstream of both the mimicry structures and beaver dams. Mimic sites were riffles prior to the installation of BMS and the BMS created pools behind the structures where the riffles previously were located.

Because no pre-monitoring was conducted, reference riffles were established as a space-for-time substitution to compare changes that occurred as riffles became pools. Abiotic and biotic responses were measured at all sites throughout June-October 2018. Personnel and funding limitations restricted our sampling to a subset of all nine structures installed.

Physical and Environmental Characteristic Sampling

We measured sediment characteristics at each site by quantifying grain size and fine sediment deposition. Pebble counts were conducted in early July after the peak of the hydrograph and flows returned to wadeable levels. Riffles were walked in a zig-zag pattern, toe-to-heel, and a particle was picked up at each step. Each particle that was picked up was measured on the b-axis and placed behind the stride of the individual conducting the sample to avoid recording the same particle more than once. D_{50} was calculated using Wolman's method (Wolman 1954). Fine sediment was measured with a benthic core. A stovepipe (20 cm x 20 cm x 63 cm) was secured into the substrate of the stream, the benthic layer was agitated for thirty-seconds, and a syringe was used to collect 120 mL of fine sediment suspended within the core. Samples were frozen within 12 hours for storage. Once thawed, samples were passed through a pre-ashed GF/F 47mm filter and placed in a muffle furnace at 500 °C for 1.5 hours to measure the inorganic matter m^2 .

Water temperatures were recorded via Rugged TROLL 100 (In-Situ) pressure transducers hourly from September 2016 through November 2018. Transducers were placed within PVC stilling wells, attached to staff gauges in anchored positions near the stream bank. Transducers were sheltered from high flows and UV light (stilling well).

Temperature data was downloaded once a month during the ice-free season. Temperature was recorded at a single location within each of the Mimic and Reference reaches because funding constraints limited the number of loggers being deployed. Reference and Mimic reaches were selected to make comparisons as a result of the BMS installations. Although we do not have site-specific temperature data, we are still able to compare maximum and daily range in temperature between Mimic and Reference reaches.

Basal Resource Sampling

To sample biofilm biomass at each monitoring site, three cobbles of approximately 32 to 45 mm in diameter were randomly selected and scrubbed with a brush into a 63 μm sieve. The area scrubbed on each rock was delineated using a ruler and set to an area of 19.6 cm^2 . The scrubbed slurry was funneled into a WhirlPack and frozen within 12 hours. In the lab the slurry was thawed and the volume measured with a graduated cylinder. Each sample was passed through a pre-ashed GF/F 47mm filter and placed in a muffle furnace at 500 $^{\circ}\text{C}$ for 1.5 hours. Coefficients were used to scale from the sample area to reported response variables of ash-free dry mass (AFDM) or organic material m^{-2} . Distribution of sampled substrate was not uniform among sites and is representative of biofilm standing biomass on substrate greater than 32 mm in diameter.

Suspended fine particulate organic matter (FPOM) and suspended coarse particulate organic matter (CPOM) were sampled at each of the monitoring sites. Suspended CPOM was sampled by spanning a 1 m wide wire mesh (1 cm^2) screen across the upstream end of the riffle and recording water depth. The screen collected suspended CPOM for 30 minutes. Its contents were then collected carefully by hand and placed in a

WhirlPack and frozen within 12 hours. Suspended FPOM was sampled by placing a 1-mm mesh screen stacked over a 250- μm sieve in the stream perpendicular to the flow for three minutes. Water depth at the center of the screen placement was recorded, and the contents of the sieve were scraped into WhirlPacks and frozen within 12 hours. Each sample was emptied into a clean aluminum tin and dried at 55 °C for 24-48 hours until visually dry depending on the initial water content of the sample. Samples were weighed, then placed in a muffle furnace at 500°C for one hour, removed, and placed in a desiccation chamber to cool. Samples were then weighed again to obtain the ashed weight. The ashed weight of the sample was subtracted from dry weight of the sample to obtain the AFDM of the sample. Values were adjusted for area of the screen that was submerged in the water and are reported as AFDM m^{-2} .

Benthic CPOM was measured from Surber samples used for benthic macroinvertebrate sampling. A Surber sample was placed randomly three separate times at each sampling site, and the substrate was scrubbed and washed into a 243 μm mesh net. Sieves ($> 1\text{mm}$) were used to separate coarse from fine particulate matter ($< 1\text{mm}$), and a Folsom plankton splitter was used to subsample ($1/2$ - $1/32$) for at least 100 macroinvertebrate individuals. Once macroinvertebrates were picked from the samples, the organic and non-organic matter was dried in tins (55°C), weighed, and burned in a muffle furnace (500 °C). AFDM was determined by subtracting dried weight from the post-ash weight and multiplied by a correction coefficient to account for subsampling and obtain reported values of organic matter AFDM m^{-2} .

Benthic FPOM was measured using a benthic core comprised of a stovepipe (20 cm x 20 cm x 63 cm) secured into the substrate of the stream 1 meter from the left and right stream banks. The top 10 cm of the benthic layer was agitated for thirty-seconds. A syringe was used to collect 120 mL of the agitated fine sediment and organic matter within the core. Samples were frozen within 12-hours for storage. Samples were then thawed and passed through a pre-ashed GF/F 47mm filter and placed in a muffle furnace at 500 °C for 1.5 hours to measure the organic matter collected in the sample. The mass of the ashed sample was subtracted from the dried sample to obtain the organic matter AFDM m⁻².

Macroinvertebrate Sampling

Macroinvertebrates were collected at all sites using a Surber sampler with an area of 0.31m² and 243µm mesh netting. At each of the six sites, the Surber sampler was haphazardly placed three different times (n = 3) on the substrate by hand and held in place as the substrate was vigorously scrubbed. Any rocks with a diameter larger than roughly 40 mm were upturned, scrubbed, and their contents encouraged to swash into the mesh net. Samples were stored in 90% ethanol and stored at 4°C. These methods were used to sample on four separate dates over the course of the 2018 ice-free season on June 22nd, July 24th, August 24th, and September 22nd. This summer season was targeted for sampling in order to capture the time of year when the majority of in-stream production occurs, and secondary production was totaled across the range of sampling dates. Density and biomass were averaged across the sampling dates. We define the summer season by the 92-day interval between the first and last 2018 sampling efforts.

To quantify density and community composition by relative abundance of the macroinvertebrate community, each sample was divided into coarse (>1mm) and fine (<1mm) samples using nested sieves and processed in the laboratory by subsampling (1/2 to 1/32) with a Folsom plankton splitter (Wildlife Supply Company). We counted either at least 100 individuals by completing any subsample that was started, or the entire sample when less than 100 individuals were found. Macroinvertebrates were identified to Genus when possible (Merritt et al. 2008). Chironomidae were only identified as *Tanypodinae* or *NonTanypodinae*. Density (individuals m⁻²) was calculated by multiplying the number of individuals found per subsample by the fraction that was used for that sample and multiplied by a coefficient to correct for subsampling. Body length of individuals was measured to the nearest mm under a dissecting microscope at 60x magnification. Species richness was estimated as the total number of taxa m⁻². Biomass estimates (mg m⁻²) of each taxon were calculated using the length mass regression $M = aL^b$, where M = body mass, a = genus specific constant coefficient, b = genus specific constant coefficient, and L = body length that compares ash free dry mass (AFDM) via body length measurements (Benke et al., 1999). Additional sources were used for obtaining coefficients for biomass of gastropods (Stoffels, Karbe, & Paterson, 2003; Méthot et al., 2012). Community composition described by functional feeding groups were assigned to macroinvertebrates (i.e. scrapers, collector-gatherers, filter feeders, and predators) using descriptions from Merritt and Cummins (2008). Densities were used to conduct non-metric multi-dimensional scaling assessment of community structure.

Secondary Production Estimation

Summer secondary production (mg AFDM m⁻² summer⁻¹) was estimated using the instantaneous growth method (Gillespie and Benke 1979, Morin and Dumont 1994).

When cohorts of taxa were easily identifiable, changes in size-frequency distributions were used to calculate growth rates between sampling dates. Growth rates from cohorts were used to create an empirical model for the stream that predicts growth based on AFDM and temperature between sampling dates for non-identifiable cohorts:

$$g = 3.951 (\pm 0.194) - 0.1284 (\pm 0.0006167) \times (m) - 0.004599 (\pm 0.0006364) \times T$$

where g = instantaneous growth rate, m = AFDM of individuals (mg), and T = mean temperature (°C) between sampling intervals. Confidence intervals (CI) were calculated via bootstrapping through resampling with replacement 1,000 times for each taxon from size-specific abundance data (Benke and Huryn 2006). To estimate uncertainty of production estimates, bootstrapped biomass estimates were multiplied by size-specific growth equation (equation above) and by the number of days within the sampling interval and summed across the entire sampling period (June – September) and all taxa to estimate community summer secondary production. Medians and the 2.5% and 97.5% quantiles were calculated to estimate bootstrap 95% confidence intervals. Summer secondary production were estimated on a per square meter basis.

Statistical Analysis

Mixed effects models tested for differences across treatments for each response variable (sediment, CPOM, FPOM, Biofilm) to interpret variation in physical and biological responses to the installation of mimicry structures. Models were constructed with the fixed effect of treatment (Beaver, Mimic, Reference) and random effects of sampling date and habitat nested within site using the lme4 package in R (Bates, Maechler, Bolker, & Walker, 2015). Habitat was defined as being upstream of a dam (pool) or at a riffle site. Response variables were transformed when needed (log or $\log(x+1)$) in order to meet the assumption of normality. To compare response variables across treatments, analysis of variance (ANOVA) was used based on the mixed-effects models, with p-values ≤ 0.05 considered statistically significant. If the main effect was found to be statistically significant, a post-hoc comparison identified specific differences between treatments using the glht function from the multcomp package in R (Torsten, Bretz, & Westfall, 2008). Differences in water temperature ($^{\circ}\text{C}$) maxima and daily ranges were compared between Mimic and Reference sites using a Wilcoxon test, which accounted for data not being normally distributed.

Differences in mean macroinvertebrate density, biomass, and summer secondary production were assessed using 95% confidence intervals of bootstrapped values (Benke & Huryn, 2006). If confidence intervals did not overlap, differences were considered significant. We used forward stepwise assessment and p-values to choose the mixed effects model that best described secondary production between sampling intervals based

on environmental variables. Non-significant terms were removed until the most parsimonious model was identified.

Community structure of benthic macroinvertebrates among treatments was compared using non-metric multidimensional scaling (NMDS). PRIMER-E v7 (Clarke & Gorley, 2015; Kruskal, 1964; McCune, Grace, & Urban, 2002) was used to conduct NMDS with 100 restarts utilizing the satisfactory stress stopping value (0.010) from a 3-2 dimensional solution via Kruskal fit-scheme. Macroinvertebrate densities were square root transformed to reduce influence of higher density taxa. Bray-Curtis distance was used due to its ability to handle species abundance and measuring ecological distances based on count data. We tested for differences in benthic macroinvertebrate community assemblages based on densities among treatments, as well as pair-wise comparisons, using a permutational multivariate analysis of variance (PERMANOVA). The PERMANOVA used a type-III partial sum of squares with 9,999 restarts under a reduced model (Clarke & Gorley 2015). Homogeneity of dispersions between treatments was tested using a one-way PERMDISP from the PERMANOVA+ package in PRIMER v7 (Anderson, Gorley, & Clarke, 2008). PERMDISP allowed for us to test the validity of the PERMANOVA differences due to the multivariate position of samples rather than due to heterogeneous dispersion among treatments.

Results

Physical and Chemical

Beaver mimicry has substantial effects on physical and chemical characteristics of Long Creek (Table 1). Daily maximum temperatures were statistically higher in Mimic

sites compare to Reference sites (Wilcoxon; $v=201850$, $p = 0.026$), averaging $8.9\text{ }^{\circ}\text{C}$ for the Mimic and $8.7\text{ }^{\circ}\text{C}$ for the Reference. Diel temperature ranges were smaller within the Mimic sites compared to the Reference sites (Wilcoxon; $v = 234930$, $p < 0.001$; Figure 2). Fine sediment deposition varied among the three treatments (ANOVA; $F_{2,21} = 11.921$, $p = 0.021$; Figure 3a), with higher levels of fine sediment deposition at Beaver ($10,391 \pm 2,328\text{ mg m}^{-2}$) and Mimic sites ($20,438 \pm 3,105\text{ mg m}^{-2}$) compared to Reference sites ($846 \pm 150\text{ mg m}^{-2}$).

Basal Resources

Benthic CPOM was different among sites (ANOVA; $F_{2,21} = 5.3871$, $p = 0.007$) with Reference sites having the highest mean benthic CPOM ($155,00\text{ mg AFDM m}^{-2}$; Figure 3b), followed by Mimic ($71,300\text{ mg AFDM m}^{-2}$), and Beaver sites ($36,900\text{ mg AFDM m}^{-2}$). Post-hoc comparisons showed moderate statistical differences in benthic CPOM only between Beaver and Reference sites ($p = 0.07$). Suspended CPOM was also different among sites (ANOVA; $F_{2,21} = 14.794$, $p < 0.001$; Figure 3c). Reference sites had the highest suspended CPOM ($202 \pm 71\text{ g m}^{-2}$) followed by Mimic ($11 \pm 3\text{ mg AFDM m}^{-2}$), then Beaver sites ($10 \pm 2\text{ mg m}^{-2}$). Statistical differences of suspended CPOM were found between Beaver and Reference sites ($p = 0.001$) and Mimic and Reference sites ($p < 0.001$), but not between Beaver and Mimic sites ($p = 0.23$).

Benthic FPOM was statistically different among treatments (ANOVA; $F_{2,21} = 19.85$, $p < 0.001$; Figure 3d). There were significant differences between Beaver ($2,431 \pm 779\text{ mg AFDM m}^{-2}$) and Reference treatments ($242 \pm 76\text{ mg AFDM m}^{-2}$) ($p < 0.001$) and Mimic ($2,823 \pm 296\text{ mg AFDM m}^{-2}$) and Reference treatments ($p < 0.001$). Suspended

FPOM was moderately different among treatments (ANOVA; $F_{2,21} = 2.83$, $p = 0.06$; Figure 3e).

Biofilm standing crop differed among sites (ANOVA; $F_{2,21} = 19.85$, $p < 0.001$; Figure 3f), with differences between Mimic (3 ± 0.5 mg AFDM m^{-2}) and Reference sites (0.8 ± 0.2 mg AFDM m^{-2} ; $p < 0.001$) and between Beaver (4 ± 0.8 mg AFDM m^{-2}) and Reference sites ($p < 0.001$). There was no difference in biofilm standing crop between Beaver and Mimic sites ($p = 0.97$).

Macroinvertebrate Density, Biomass, and Production

Macroinvertebrate median densities were 20,756 ind m^{-2} (95% CI: 9,883-42,185) at Beaver sites, 6,959 ind m^{-2} (95% CI: 4,760-9,725) at Mimic sites, and 2,525 ind m^{-2} (95% CI: 1,636-3,743). Median biomass estimates were 2,449 mg AFDM m^{-2} (95% CI: 1,949-3,605) at Beaver sites, 1,701 mg m^{-2} (95% CI: 1,238-2,552) at Mimic sites, and 704 mg m^{-2} (95% CI: 129.58-1,712) at Reference sites (Figure 4b). Overlapping confidence intervals show no difference in median biomass estimates among treatments.

Community secondary production differed among our study sites (Figure 4c; Table A1). Median production at treatments were as follows: Beaver sites 3,919 mg AFDM m^{-2} summer⁻¹ (95% CI: 3,062-6,331), Mimicry sites 2,731 mg AFDM m^{-2} summer⁻¹ (95% CI: 2,155-3,932), and Reference sites 1,163 mg AFDM m^{-2} summer⁻¹ (95% CI: 256-2,596). Overlapping quantiles between Mimic and Reference sites, and Beaver and Mimic sites, suggest statistically similar values. Non-overlapping quantiles show a significant difference in summer production between Beaver and Reference sites. Production of collector-gatherers contributed almost half of the summer production at

Beaver sites (Figure 5), compared to a quarter of the summer production at Mimic and Reference sites. Increased shredder production was seen at Mimic sites (Figure 5).

To investigate potential drivers of secondary production, we explored linear relationships between basal resources and summer secondary production. Benthic CPOM was negatively related ($p = 0.051$, $R^2 = 0.60$; Figure 6b) and drifting CPOM was moderately negatively related ($p = 0.065$, $R^2 = 0.56$; Figure 6a) with summer secondary production. No statistical relationship was found between benthic FPOM ($p = 0.19$, $R^2 = 0.19$; Figure 6d) or drifting FPOM ($p = 0.311$, $R^2 = 0.21$; Figure 6c) and secondary production.

Macroinvertebrate Community Structure

The one-way PERMANOVA showed differences in community structure based on densities among treatments at the site level (Figure S1) ($F_{2,69} = 2.0229$, $p = 0.004$). Pairwise comparisons revealed differences in community composition between Beaver and Reference sites ($t = 1.6959$, $p = 0.002$), and between Mimic and Reference sites ($t=1.3758$, $p=0.032$). However, no difference in community structure was found between Beaver and Mimic sites ($t = 1.1419$, $p = 0.188$). Species richness did not differ among sites (PERMANOVA; $F_{2, 2.33} = 0.146$, $p = 0.872$). PERMDISP did not show an effect of dispersion among treatment sites (PERMANOVA; $F_{2,69} = 0.485$, $p = 0.638$); however, dispersion was slightly higher, although not significant, in Beaver sites (43.46 ± 1.58) than Mimicry sites (41.53 ± 1.23) or Reference sites (41.77 ± 1.69). This finding supports the conclusion that differences among communities resulted from the multivariate position of samples (a true treatment effect) and not from heterogeneous dispersions

among treatments (Anderson et al., 2008). Macroinvertebrate community structure (Figure S1) did reveal distinct communities between Beaver, Mimic, and Reference sites (NMDS; 2D stress = 0.22, analysis of similarity: Global R = 0.063, $p < 0.05$).

Discussion

Measurements of ecosystem processes could improve and refine goals and outcomes for stream restoration projects that are increasingly common across the world (Beechie, Pess, Roni, & Giannico, 2008); however, most restoration projects still rarely leverage ecosystem-level research approaches and measurements. In this study, we evaluated stream processes at BMS and compared them to unaltered reference riffles and naturally occurring beaver dams. We found that the installation of BMS altered physical characteristics and had consequences for resource availability, consumer density, biomass, and production patterns. Fine sediment deposition and organic matter transport and deposition were similar at Beaver and Mimic sites. Macroinvertebrate density in Mimic sites showed signs of becoming similar to Beaver sites, but Beaver sites had higher macroinvertebrate density compared to Mimic sites. Macroinvertebrate biomass was similar across all sites. Secondary production at Mimic sites was lower than Beaver sites, but higher than Reference sites. These increases in secondary production suggests that in the two years since the structures were installed, production of macroinvertebrates is becoming more similar to that in actual beaver dams, where water was relatively slow and warm, compared to riffles.

Our study had a unique opportunity to compare BMS to both reference riffles and to natural beaver dams. These comparisons among reference riffles, beaver dams, and

BMS are valuable because they allowed us to monitor changes from the reference riffle to the mimicry structure pools, and to compare the restoration effort to actual beaver dams, which loosely represent the hydrological goal of many BMS restoration projects focused on water storage. The beaver site versus mimic comparison is especially informative because beaver complexes are dynamic, and few studies have documented how biological responses at mimicry structures compare to natural beaver dams. For example, in 2018 the beaver sites on Long Creek experienced dam failure followed by a rebuilding stage. These dam failures are typical of naturally occurring beaver complexes (Levine & Meyer, 2014). Fine sediment deposition at Mimic sites was higher than at Beaver sites, likely due to the reinforced nature of the mimic structures that prevented failure from hydraulic stress in 2018 even given similar high snowmelt conditions that the beaver dams experienced that year (Gillilan, 2015; Pollock et al., 2014). This increase in sediment deposition is important to the aggradation phase of channel-evolution in incised streams (Pollock, Beechie, & Jordan, 2007; Pollock et al., 2014). Understanding how BMS installations compare to beaver dams that are considered the target conditions is important if BMS continue to be installed frequently.

Water temperature responded to the installation of the beaver mimicry structures. Diel temperature fluctuations were buffered at Mimicry sites compared to Reference sites, showing a more homogenous temperature regime. This finding supports those from previous studies that have shown reduction in daily maxima and temperature ranges due to increased groundwater-surface water connectivity (Bobst, 2019; Weber et al., 2017). The patterns of water temperature that we observed could have consequences for

metabolic rates of organisms (Brown, Gillooly, Allen, Savage, & West, 2004), community composition and size structure (Nelson et al., 2017a), and species distribution (Bouwes et al., 2016; Isaak, Wollrab, Horan, & Chandler, 2012; Nelson et al., 2017b). For example, the thermal range contraction we documented may benefit freshwater fishes such as salmonids that are expected to see constricted geographic ranges in the future due to their narrow thermal tolerances (Isaak, Young, Nagel, Horan, & Groce, 2015; Lohr, Byorth, Kaya, & Dwyer, 1996). However, future work is needed to address how both the range and the absolute temperatures resulting from beaver mimicry structures influences species of concern. Combined with a warming climate, the effects of beaver mimicry structures may have important implications for thermal regimes in northern Rocky Mountain streams (Nelson, Cross, Hansen, & Tabor, 2016).

We predicted that altered physical conditions by BMS would cascade to the river's biological composition and function. In fact, we found that secondary production estimates were higher within the beaver complex and the mimic sites than the reference riffles. The increases in secondary production measured in our study are congruent with patterns observed in one other study (Anderson & Rosemond, 2007). Increases in secondary production at Beaver and Mimic sites can be attributed to higher production of collector-gatherers and shredders, such as *Pteronarcella sp.*, *Baetis sp.*, and Chironomidae. We attribute the dominance of these particular groups to elevated fine sediment deposition and benthic FPOM, two factors that are positively related with the presence of these functional feeding groups (McDowell & Naiman, 1986; Wallace, Webster, & Meyer, 1995). Higher estimates of secondary production at Beaver and

Mimic sites likely resulted from differences in basal resource availability (Huryn & Wallace, 1987; Wallace et al., 1995), allochthonous inputs from riparian vegetation, (Albertson, Ouellet, & Daniels, 2018; Junker & Cross, 2014), and more stable thermal regimes (Benke, Arsdall, Gillespie, & Parrish, 1984; Tumbiolo, Downing, Nazionale, Vaccara, & Vallo, 1994). We have shown that changes to the physical template of former riffles turned pools upstream of BMS installation alter ecosystem functioning in a manner consistent with target conditions of naturally occurring beavers.

The initiation of a restoration project in a particular location often stems from the need to improve or reverse a degraded state or to improve conditions for a target species such as fish; however, it is difficult to define and assess the exact suite of parameters that will qualify as improved, which is a common issue in stream restoration (Bernhardt et al., 2005b). The biological goals of this restoration project, for example, were to improve in-stream conditions for Arctic grayling. Improvement could mean direct effects on fish such as thermally suitable habitat (Liknes & Gould, 1987; Lohr et al., 1996) or access to spawning tributaries (Cutting et al., 2018), but also indirect effects such as food resource availability (Cutting, Cross, Anderson, & Reese, 2016; Wipfli & Baxter, 2010).

Restoration projects often ignore non-target taxa, but these taxa are critical components of food webs that may support the species of concern (Lipsey, Child, Seddon, Armstrong, & Maloney, 2007; Naiman et al., 2012). Measuring static responses, such as macroinvertebrate density or biomass, do not always offer insight into changes occurring over time within a stream (Miller, Budy, & Schmidt, 2010), encouraging the use of dynamic, functional responses, such as secondary production, to provide a

comprehensive outlook on the effects of restoration practices (Dolbeth et al., 2012; Frainer et al., 2018). Our research has shown that beaver mimicry structures change the physical template of a stream and elicit biological responses similar to natural beaver dams, but may take more time to achieve conditions that match naturally occurring beaver sites due to land use, degree of degradation, and catchment geology (Boyd, Sacry, & Gillilan, 2018; Dobson, Bradshaw, & Baker, 1997).

Although we clearly demonstrate impacts of BMS on physical and biotic components of stream ecosystems, there are multiple elements of this study that present limitations. While a before-after-control-impact experimental design would be ideal, there was no pre-installation monitoring, which is a common reality in many studies. Thus, we had to use a space-for-time substitution to evaluate how BMS installations change streams. Although it would be best to have conducted this study on multiple rivers that were similar in geographic location and physical characteristics, funding restrictions and landowner permission limited the research to a single stream. Although we only have one stream, these patterns are still robust and offer strong insight to our original objectives and questions and could be applied and tested in other systems. Future research should consider how to involve multiple stakeholders, such as upstream or downstream landowners, in work like this (Gregory & Keeney, 1994; Lautz et al., 2019). Sampling was conducted during the summer months due to the physically harsh environment of this snowmelt-fed system during other times of the year, but future work might consider making measurements during other seasons. This additional temporal sampling could be important to capture winter production, which can show lower

production than other seasons (Junker & Cross, 2014). The physical form of the structures, armored riffles, used in this study is quite different from that of structures that are typically used for beaver mimicry restoration that are made of woven willow between wooden posts with mud and rock at the base of the dam (Castro et al., 2015). Differences in materials used for mimicry structures may produce changes to in-stream discharge and thermal regimes that alter resource pathways for consumers (Burchsted et al., 2010), and a comparison across structure types could be an area for future research. Despite these limitations, our findings clearly demonstrate the benefits of increased post-installation monitoring of BMS on understanding ecosystem functioning.

Incorporating biogeomorphic agents, a process-based sampling approach, and monitoring of functional response metrics is a major improvement in restoration design (Johnson et al., 2019). Our results show that BMS are able to mimic the physical responses of beavers and alter functional responses similarly to naturally occurring beaver activity, offering a low-budget strategy to restore channel incision in low-gradient streams throughout southwest Montana. However, given the degraded nature of the stream (altered flow and sediment regimes, decreased woody riparian vegetation, and loss of keystone species), expectations of a full recovery to pre-beaver extirpation conditions may need to be tempered by what is actually feasible. Ecosystem processes ultimately shape a river and are functions of biotic and abiotic interactions over time. Functional responses like secondary production allow a mechanistic approach to assessing whether rivers are able to recover from perturbations and stressors like droughts, scour, or floods, taking into account multiple trophic levels and resource availability and consumption due

to changes in physical processes, and should be used in future studies to assess viability of restoration work.

Table 1. Mean values for basal resources and fine sediment accumulation among treatment sites throughout the 2018 summer sampling season. All estimates are reported with standard errors.

Site	FPOM mg AFDM m ⁻²	Suspended FPOM mg AFDM m ⁻²	CPOM mg AFDM m ⁻²	Suspended CPOM mg AFDM m ⁻²	Biofilm mg AFDM m ⁻²	FS mg m ⁻²
Beaver	2,4312	142	36,933	10	4	10,392
(SEM)	(± 779)	(±51)	(±21,073)	(±2)	(± 0.1)	(±2,328)
Mimic	2,823	167	71,308	11.	3	20,437
(SEM)	(± 296)	(± 48)	(±23,375)	(±3)	(± 0.5)	(±3,105)
Ref	242	411	154,909	202	0.8	846
(SEM)	(± 76)	(±128)	(±46,983)	(±71)	(±0.2)	(±150)

AFDM, ash free dry mass; FPOM, fine particulate organic matter; CPOM, coarse particulate organic matter; FS, fine sediment; Ref, Reference.

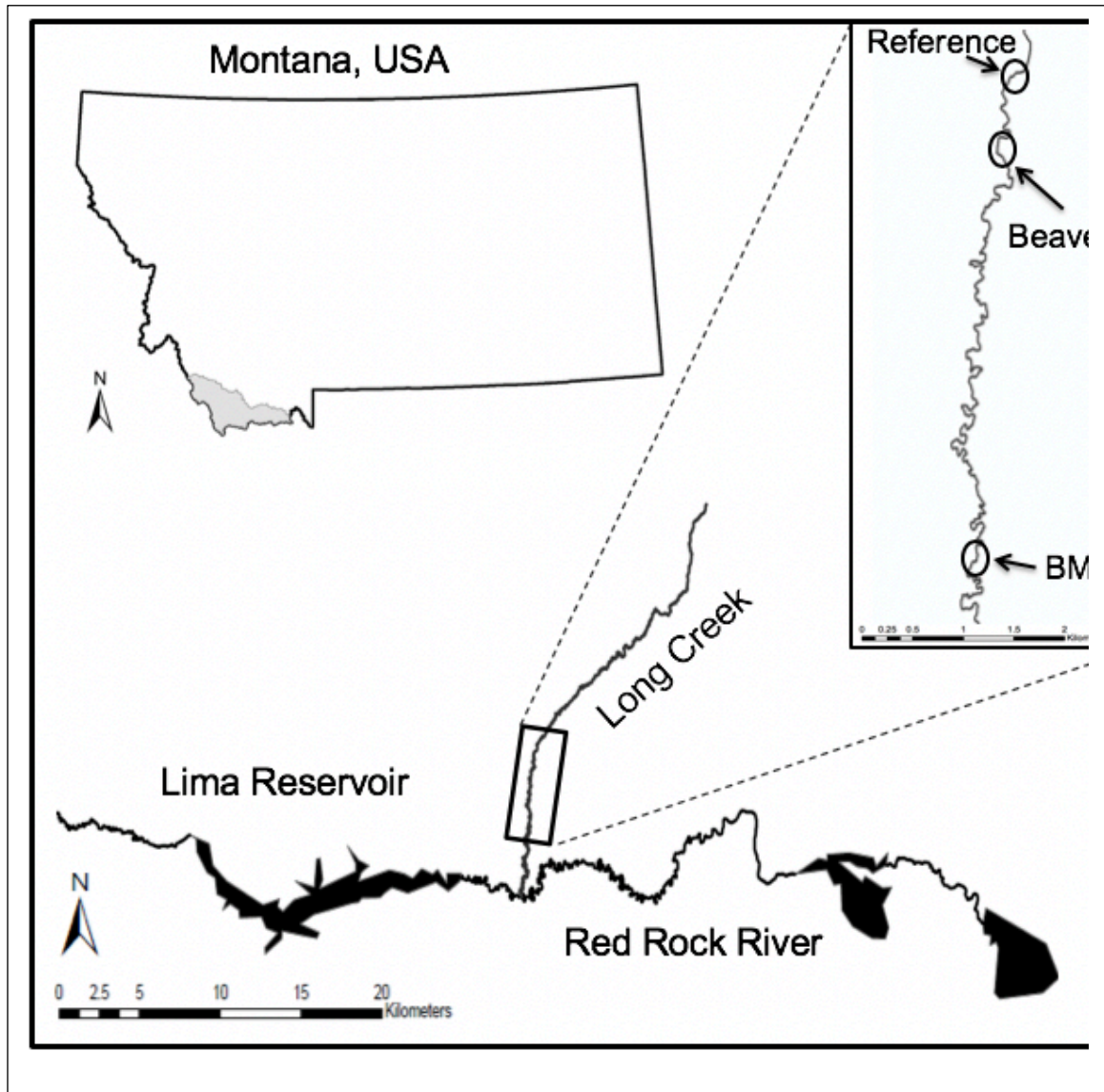


Figure 1. Map of the study area. Locations of beaver mimicy structure (BMS) treatment reaches within The Nature Conservancy’s parcel are located in the top right insert. Throughout the treatment reach a total of nine BMS were installed. Two structures in the middle of the treatment reach were monitored.

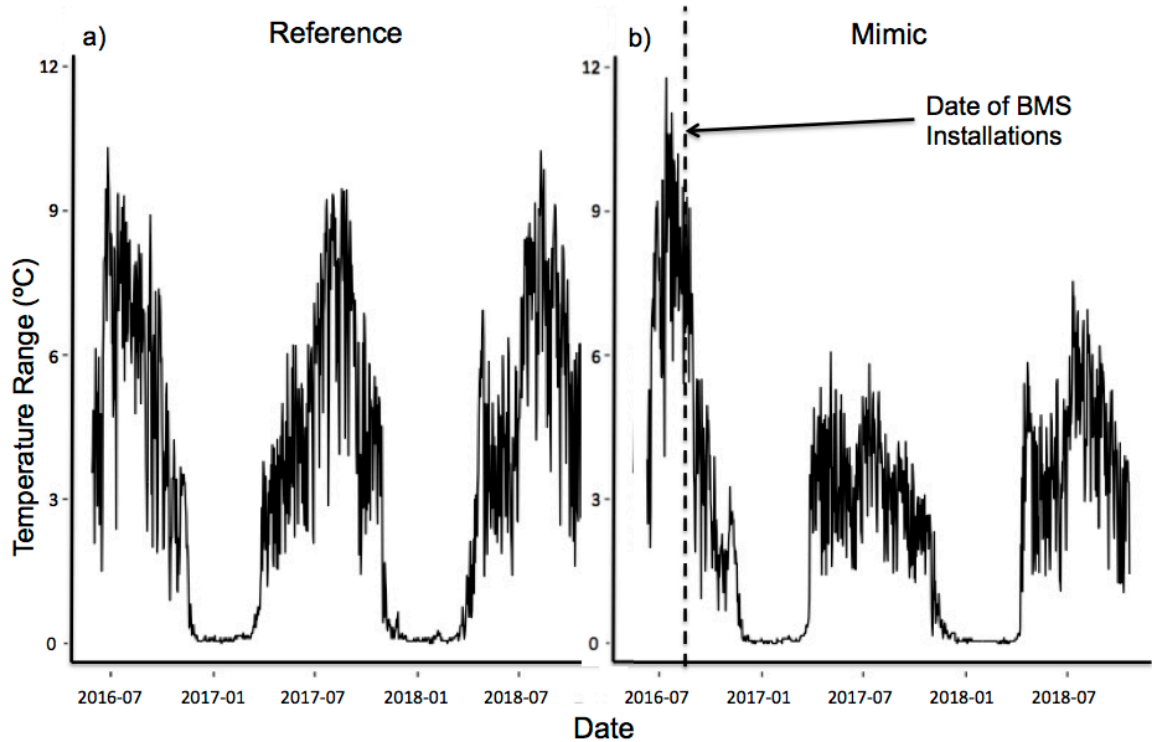


Figure 2. Diel temperature ranges (°C), estimated as daily maximum minus daily minimum, for Reference (**a**) and Mimic (**b**) sites across the duration of the study. Structures were installed in the reach with the Mimic sites in the fall of 2016. Following structure installation, the diel fluctuations in the 2017 and 2018 contract significantly in the Mimic site compared to the Reference site ($p < 0.001$).

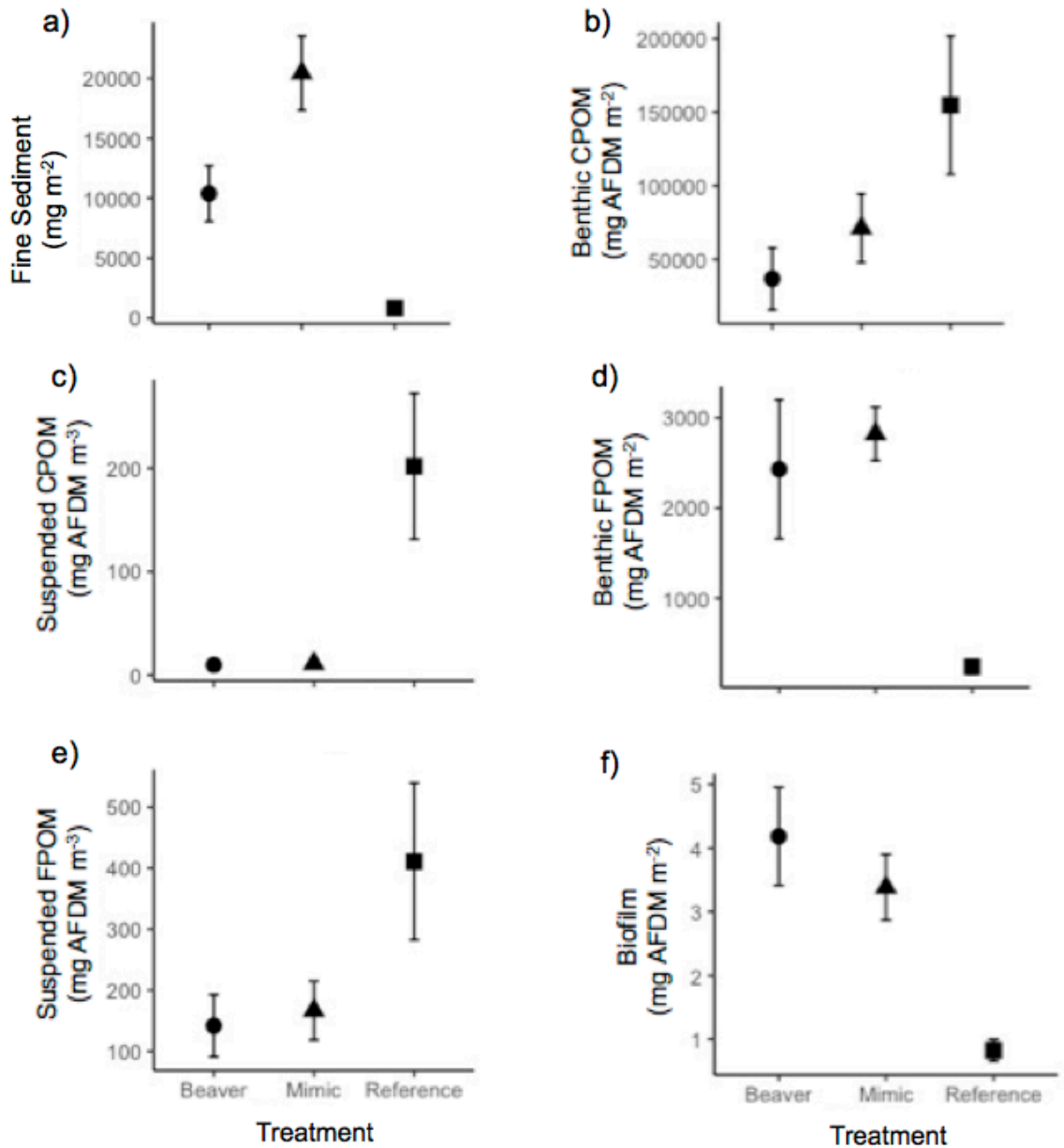


Figure 3. Benthic CPOM (a), drifting CPOM (b), benthic FPOM (c), drifting FPOM (d), biofilm standing crop (e), and fine sediment accrual (f) (mean \pm SEM) among Beaver (closed circle), Mimic (closed triangle), and Reference (closed square) treatments from June to August 2018. Error bars not visible are subsumed within the point.

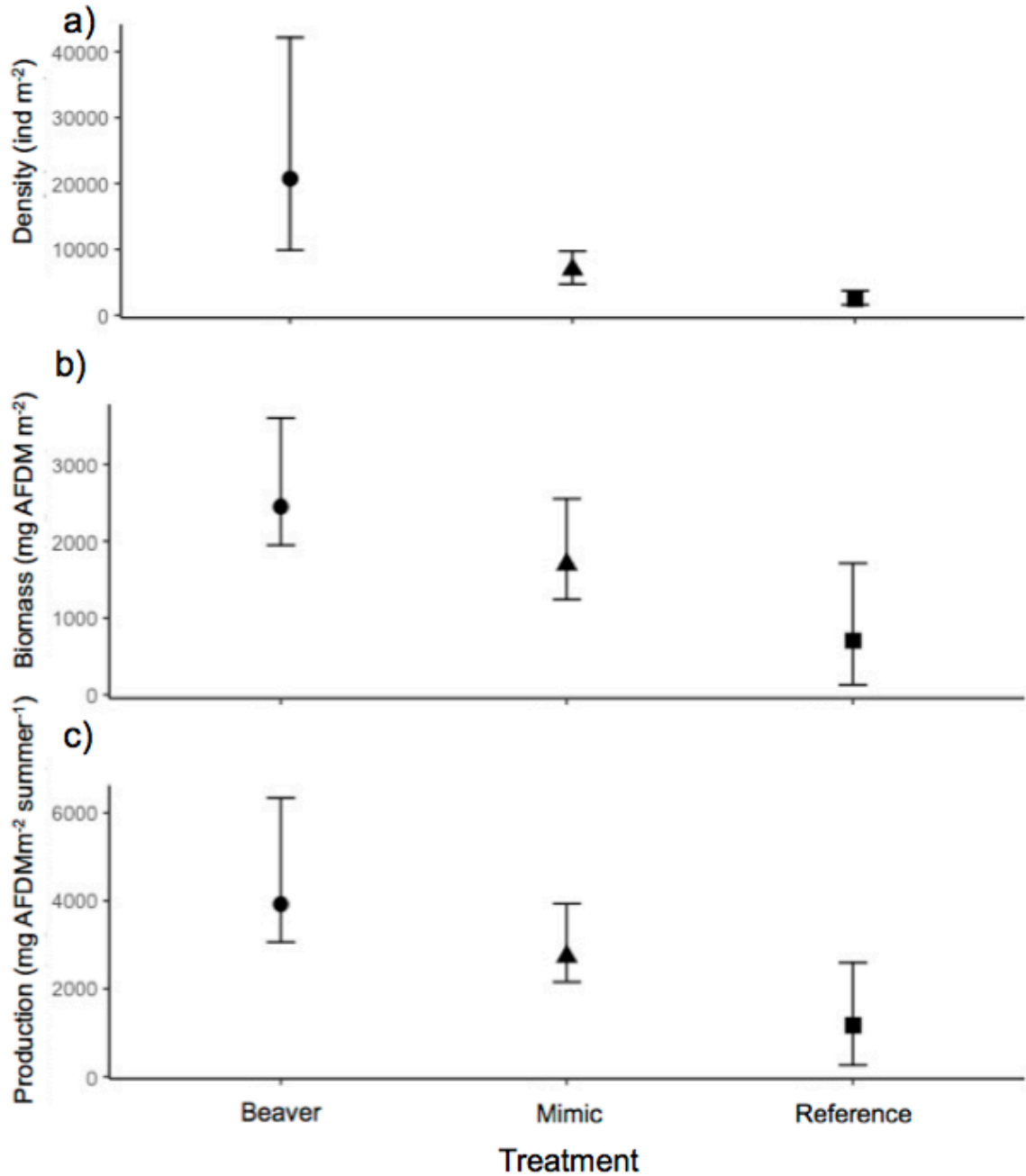


Figure 4. Macroinvertebrate densities (individuals m⁻²) (a), biomass (mg AFDM m⁻²) (b), and community secondary production (mg AFDM m⁻² summer⁻¹) (c) among Beaver (closed circle), Mimic (closed triangles) and Reference (closed squares) treatments for the 2018 summer season (bootstrapped median \pm 2.5% and 97.5% quantiles).

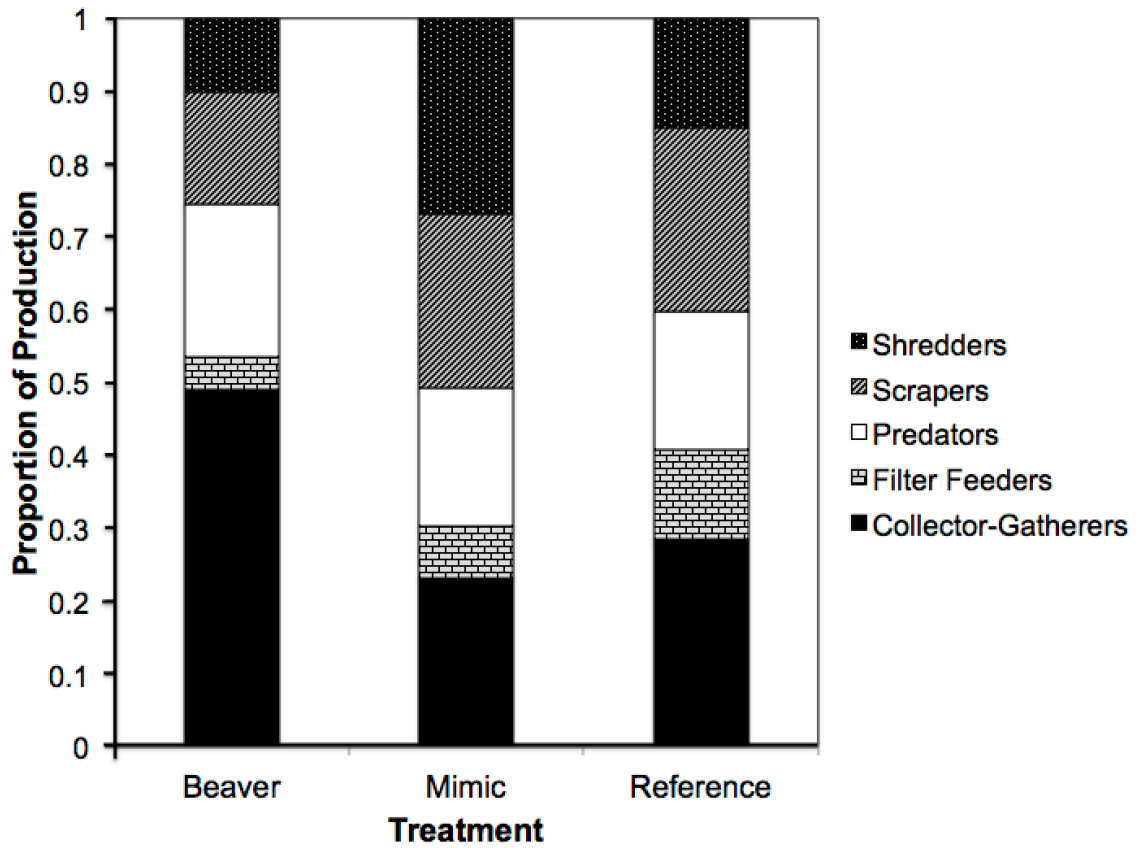


Figure 5. Mean proportion of functional feeding group (FFG) contribution to summer secondary production ($\text{mg m}^{-2} \text{summer}^{-1}$) across treatments.

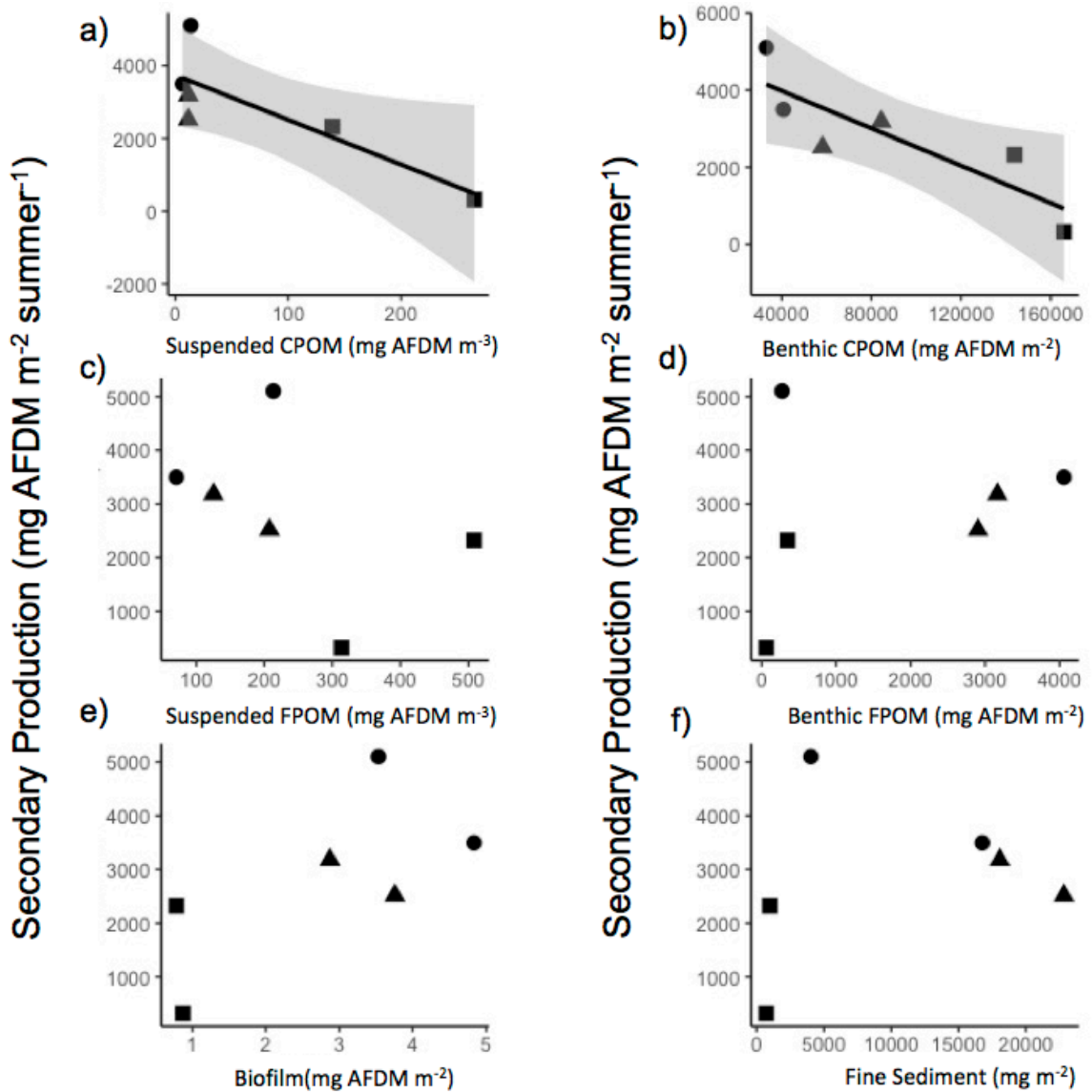


Figure 6. Relationships between secondary production (mg AFDM m⁻² summer⁻¹) and drifting CPOM (a), benthic CPOM (b), drifting FPOM (c), benthic FPOM (d), biofilm standing crop (e), and fine sediment accrual (f) and fine sediment among Beaver (closed circle), Mimic (closed triangles) and Reference (closed squares) sites. Regression lines and grey shading show significant relationships ($p < 0.1$) with confidence intervals.

REFERENCES CITED

- Albertson, L. K., Ouellet, V., & Daniels, M. D. (2018). Impacts of stream riparian buffer land use on water temperature and food availability for fish. *Journal of Freshwater Ecology*, 33(1), 195–210. <https://doi.org/10.1080/02705060.2017.1422558>
- Anderson, C. B., & Rosemond, A. D. (2007). Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. *Oecologia*, 154(1), 141–153. <https://doi.org/10.1007/s00442-007-0757-4>
- Anderson, M., Gorley, R. N., & Clarke, R. K. (2008). *Permanova+ for Primer: Guide to Software and Statistical Methods*.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using {lme4}. *Journal of Statistical Software*, 67(1), 1–48.
- Beechie, T., Pess, G., Roni, P., & Giannico, G. (2008). Setting River Restoration Priorities: A Review of Approaches and a General Protocol for Identifying and Prioritizing Actions. *North American Journal of Fisheries Management*, 28(3), 891–905. <https://doi.org/10.1577/m06-174.1>
- Benke, A. C. (1993). Concepts and patterns of invertebrate production in running waters.pdf. *Verh. Int. Veri. Limnol*, 25, 15–38.
- Benke, A. C., Arsdall, T. C. V., Gillespie, D. M., & Parrish, F. K. (1984). Invertebrate Productivity in a Subtropical Blackwater River : The Importance of Habitat and Life History. *Ecological Monographs*, 54(1), 25–63.
- Benke, A. C., & Huryn, A. D. (2006). Secondary production of macroinvertebrates. In *Methods in Stream Ecology* (pp. 691–710). Academic Press.
- Benke, A. C., Huryn, A. D., Smock, L. A., & Wallace, J. B. (1999). Length-Mass Relationships for Freshwater Macroinvertebrates in North America with Particular Reference to the Southeastern United States. *Journal of the North American Benthological Society*, 18(3), 308–343. <https://doi.org/10.2307/1468447>
- Bernhardt, E. S., Palmer, M. A., Allan, J. D., Alexander, G., Barnas, K., Brooks, S., ... Sudduth, E. (2005a). Synthesize U.S. River Restoration Efforts, 308(April), 636–638.
- Bernhardt, E. S., Palmer, M. A., Allan, J. D., Alexander, G., Barnas, K., Brooks, S., ... Sudduth, E. (2005b). Synthesize U.S. River Restoratio Efforts. *Science*, 308(April), 636–638.
- Bobst, A. (2019). *Using Beaver-Mimicry Restoration to enhance natural water storage in*

Missouri River headwater streams.

- Bouwes, N., Weber, N., Jordan, C. E., Saunders, W. C., Tattam, I. A., Volk, C., ... Pollock, M. M. (2016). Ecosystem experiment reveals benefits of natural and simulated beaver dams to a threatened population of steelhead (*Oncorhynchus mykiss*). *Scientific Reports*, 8(July), 1–12. <https://doi.org/10.1038/srep28581>
- Boyd, K., Sacry, A., & Gillilan, S. (2018). *Centennial Valley Riparian Potential Limiting Factors and Conceptual Restoration Alternatives: Long, Middle, and Hellroaring Creeks*. Bozeman.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a Metabolic Theory of Ecology. *Ecology*, 85(7), 1771–1789.
- Burchsted, D., Daniels, M., Thorson, R., & Vokoun, J. (2010). The River Discontinuum: Applying Beaver Modifications to Baseline Conditions for Restoration of Forested Headwaters. *BioScience*, 60(11), 908–922. <https://doi.org/10.1525/bio.2010.60.11.7>
- Castro, J., Pollock, M., Jordan, C., Lewallen, G., & Woodruff, K. (2015). The Beaver Restoration Guidebook. *Working with Beaver to Restore Streams, Wetlands, and Floodplains*, 1, 191. Retrieved from <http://www.fws.gov/oregonfwo/ToolsForLandowners/RiverScience/Beaver.asp%5Cnpapers2://publication/uuid/F5CC7199-5304-42F2-8C26-50AF48FC1A31>
- Clarke, K. R., & Gorley, R. N. (2015). Getting started with PRIMER v7. PRIMER-E: Plymouth, Plymouth Marine Laboratory.
- Cluer, B., & Thorne, C. (2013). A Stream Evolution Model Integrating Habitat and Ecosystem Benefits. *River Research and Applications*. <https://doi.org/10.1002/rra>
- Cutting, K. A., Cross, W. F., Anderson, M. L., & Reese, E. G. (2016). Seasonal change in trophic niche of adfluvial Arctic grayling (*Thymallus arcticus*) and coexisting fishes in a high-elevation lake system. *PLoS ONE*, 11(5), 1–19. <https://doi.org/10.1371/journal.pone.0156187>
- Cutting, K. A., Ferguson, J. M., Anderson, M. L., Cook, K., Davis, S. C., & Levine, R. (2018). Linking beaver dam affected flow dynamics to upstream passage of Arctic grayling. *Ecology and Evolution*, 8(24), 12905–12917. <https://doi.org/10.1002/ece3.4728>
- Dobson, A. P., Bradshaw, A. D., & Baker, A. J. M. (1997). Hopes for the future: Restoration ecology and conservation biology. *Science*, 277(5325), 515–522. <https://doi.org/10.1126/science.277.5325.515>

- Dolbeth, M., Cusson, M., Sousa, R., Pardal, M. A., & Prairie, Y. T. (2012). Secondary production as a tool for better understanding of aquatic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(7), 1230–1253.
<https://doi.org/10.1139/f2012-050>
- Frainer, A., Polvi, L. E., Jansson, R., & McKie, B. G. (2018). Enhanced ecosystem functioning following stream restoration: The roles of habitat heterogeneity and invertebrate species traits. *Journal of Applied Ecology*, *55*(1), 377–385.
<https://doi.org/10.1111/1365-2664.12932>
- Gillilan, S. (2015). PROJECT REPORT – LONG CREEK CONSTRUCTION, 1–15.
- Gregory, R., & Keeney, R. L. (1994). Creating policy alternatives using stakeholder values. *Management Science*, *40*(8), 1035–1038.
<https://doi.org/10.1287/mnsc.40.8.1035>
- Herrick, J. E., Schuman, G. E., & Rango, A. (2006). Monitoring ecological processes for restoration projects. *Journal for Nature Conservation*, *14*(3–4), 161–171.
<https://doi.org/10.1016/j.jnc.2006.05.001>
- Huryn, A. D., & Wallace, J. B. (1987). Local Geomorphology As a Determinant of. *America*, *68*(January), 1932–1942.
- Isaak, D. J., Wollrab, S., Horan, D., & Chandler, G. (2012). Climate change effects on stream and river temperatures across the northwest U.S. from 1980-2009 and implications for salmonid fishes. *Climatic Change*, *113*(2), 499–524.
<https://doi.org/10.1007/s10584-011-0326-z>
- Isaak, Daniel J., Young, M. K., Nagel, D. E., Horan, D. L., & Groce, M. C. (2015). The cold-water climate shield: Delineating refugia for preserving salmonid fishes through the 21st century. *Global Change Biology*, *21*(7), 2540–2553.
<https://doi.org/10.1111/gcb.12879>
- Johnson, M. F., Thorne, C. R., Castro, J. M., Kondolf, G. M., Mazzacano, C. S., Rood, S. B., & Westbrook, C. (2019). Biomic river restoration: A new focus for river management. *River Research and Applications*, (March), 1–10.
<https://doi.org/10.1002/rra.3529>
- Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as Ecosystem Engineers
Organisms as ecosystem engineers, *69*(3), 373–386.
- Junker, J. R., & Cross, W. F. (2014). Seasonality in the trophic basis of a temperate stream invertebrate assemblage: Importance of temperature and food quality. *Limnology and Oceanography*, *59*(2), 507–518.

<https://doi.org/10.4319/lo.2014.59.2.0507>

- Kruskal, J. B. (1964). Nonmetric multidimensional scaling: A numerical method. *Psychometrika*, 29(2), 115–129. <https://doi.org/10.1007/BF02289694>
- Lautz, L., Kelleher, C., Vidon, P., Coffman, J., Riginos, C., & Copeland, H. (2019). Restoring stream ecosystem function with beaver dam analogues: Let's not make the same mistake twice. *Hydrological Processes*, 33(1), 174–177. <https://doi.org/10.1002/hyp.13333>
- Levine, R., & Meyer, G. A. (2014). Beaver dams and channel sediment dynamics on Odell Creek, Centennial Valley, Montana, USA. *Geomorphology*, 205, 51–64. <https://doi.org/10.1016/j.geomorph.2013.04.035>
- Liknes, G. A., & Gould, W. R. (1987). The distribution, habitat and population characteristics of fluvial Arctic grayling (*Thymallus arcticus*) in Montana. *Northwest Science*, 61, 122–129.
- Lipsey, M. K., Child, M. F., Seddon, P. J., Armstrong, D. P., & Maloney, R. F. (2007). Combining the Fields of Reintroduction Biology and Restoration Ecology. *Ophthalmology*, 21(6), 2007. <https://doi.org/10.1111/j>
- Lohr, S. C., Byorth, P. A., Kaya, C. M., & Dwyer, W. P. (1996). High-Temperature Tolerances of Fluvial Arctic Grayling and Comparisons with Summer River Temperatures of the Big Hole River, Montana. *Transactions of the American Fisheries Society*, 125(6), 933–939. [https://doi.org/10.1577/1548-8659\(1996\)125<0933:httofa>2.3.co;2](https://doi.org/10.1577/1548-8659(1996)125<0933:httofa>2.3.co;2)
- McCune, B., Grace, J. B., & Urban, D. L. (2002). *Analysis of ecological communities* (Vol. 28). Glendened Beach, OR: MjM software design.
- McDowell, D. M., & Naiman, R. J. (1986). Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*). *Oecologia*, 68(4), 481–489. <https://doi.org/10.1007/BF00378759>
- Merritt, R. W., Cummins, K. W., & Berg, M. B. (2008). *An Introduction to the Aquatic Insects of North America* (4th ed.). Dubuque, IA: Kendall Hunt.
- Méhot, G., Hudon, C., Gagnon, P., Pinel-Alloul, B., Armellin, A., & Poirier, A.-M. T. (2012). Macroinvertebrate size–mass relationships: how specific should they be? *Freshwater Science*, 31(3), 750–764. <https://doi.org/10.1899/11-120.1>
- Miller, S. W., Budy, P., & Schmidt, J. C. (2010). Quantifying macroinvertebrate responses to in-stream habitat restoration: Applications of meta-analysis to river

- restoration. *Restoration Ecology*, 18(1), 8–19. <https://doi.org/10.1111/j.1526-100X.2009.00605.x>
- Naiman, R. J., Alldredge, J. R., Beauchamp, D. A., Bisson, P. A., Congleton, J., Henny, C. J., ... Wood, C. C. (2012). Developing a broader scientific foundation for river restoration: Columbia River food webs. *Proceedings of the National Academy of Sciences of the United States of America*, 109(52), 21201–21207. <https://doi.org/10.1073/pnas.1213408109>
- Naiman, R. J., Johnston, C. A., & Kelley, J. C. (1988). Alteration of North American Streams by Beaver. *BioScience*, 38(11), 753–762. <https://doi.org/10.2307/1310784>
- Nelson, D., Benstead, J. P., Huryn, A. D., Cross, W. F., Hood, J. M., Johnson, P. W., ... Ólafsson, J. S. (2017a). Experimental whole-stream warming alters community size structure. *Global Change Biology*, 23(7), 2618–2628. <https://doi.org/10.1111/gcb.13574>
- Nelson, D., Benstead, J. P., Huryn, A. D., Cross, W. F., Hood, J. M., Johnson, P. W., ... Ólafsson, J. S. (2017b). Shifts in community size structure drive temperature invariance of secondary production in a stream-warming experiment. *Ecology*, 98(7), 1797–1806. <https://doi.org/10.1002/ecy.1857>
- Nelson, R., Cross, M., Hansen, L., & Tabor, G. (2016). A three-step decision support framework for climate adaptation: selecting climate-informed conservation goals and strategies for native salmonids in the Northern U.S. Rockies, 20. Retrieved from <http://rmpf.weebly.com/cold-water-ecosystem-management-tool.html>
- Palmer, M. A., Bernhardt, E. S., Allan, J. D., Lake, P. S., Alexander, G., Brooks, S., ... Sudduth, E. (2005). Standards for ecologically successful river restoration. *Journal of Applied Ecology*, 42(2), 208–217. <https://doi.org/10.1111/j.1365-2664.2005.01004.x>
- Pollock, M., Heim, M., & Werner, D. (2003). Hydrologic and Geomorphic Effects of Beaver Dams and Their Influence on Fishes. *American Fisheries Society Symposium*, 37(October), 213–233. Retrieved from <http://www.afsbooks.org/x54037xm>
- Pollock, M. M., Beechie, T. J., & Jordan, C. E. (2007). Geomorphic changes upstream of beaver dams in Bridge Creek, an incised stream channel in the interior Columbia River basin, eastern Oregon. *Earth Surface Processes and Landforms*, 32(August 2007), 1174–1185. <https://doi.org/10.1002/esp>
- Pollock, M. M., Beechie, T. J., Wheaton, J. M., Jordan, C. E., Bouwes, N., Weber, N., & Volk, C. (2014). Using beaver dams to restore incised stream ecosystems.

BioScience, 64(4), 279–290. <https://doi.org/10.1093/biosci/biu036>

- Stewart, G. B., Bayliss, H. R., Showler, D. A., Sutherland, W. J., Pullin, A. S., Stewart, G. B., ... Pullin, A. S. (2009). Effectiveness of Engineered In-Stream Structure Mitigation Measures to Increase Salmonid Abundance : A Systematic Review. *Ecological Applications*, 19(4), 931–941. Retrieved from <https://www.jstor.org/stable/40346242>
- Stoffels, R. J., Karbe, S., & Paterson, R. A. (2003). Length-mass models for some common New Zealand littoral-benthic macroinvertebrates, with a note on within-taxon variability in parameter values among published models. *New Zealand Journal of Marine and Freshwater Research*, 37(2), 449–460. <https://doi.org/10.1080/00288330.2003.9517179>
- Torsten, H., Bretz, F., & Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, 50(3), 346–363.
- Trush, W. J., McBain, S. M., & Leopold, L. B. (2000). Attributes of an alluvial river and their relation to water policy and management. *Proceedings of the National Academy of Sciences of the United States of America*, 97(22), 11858–11863. <https://doi.org/10.1073/pnas.97.22.11858>
- Tumbiolo, M. L., Downing, J. A., Nazionale, C., Vaccara, V. L., & Vallo, M. (1994). An empirical model for the prediction of secondary production in marine benthic invertebrate populations. *Marine Ecology Progress Series*, 114(Fao 1993), 165–174.
- Wallace, J. B., Webster, J. R., & Meyer, J. L. (1995). Influence of log additions on physical and biotic characteristics of a mountain stream. *Canadian Journal of Fisheries and Aquatic Sciences*, 52(10), 2120–2137. <https://doi.org/10.1139/f95-805>
- Wallace, J. B., Webster, J. R., Meyer, J. L., Webster, J. R., ____, Strong, D. R., ... Nilsson, C. (1996). The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology*, 41(5322), 115–139. <https://doi.org/10.1146/annurev.en.41.010196.000555>
- Weber, N., Bouwes, N., Pollock, M. M., Volk, C., Wheaton, J. M., Wathen, G., ... Jordan, C. E. (2017). Alteration of stream temperature by natural and artificial beaver dams. *PLoS ONE*, 12(5). <https://doi.org/10.1371/journal.pone.0176313>
- Wipfli, M. S., & Baxter, C. V. (2010). Linking Ecosystems, Food Webs, and Fish Production: Subsidies in Salmonid Watersheds. *Fisheries*, 35(8), 373–387. <https://doi.org/10.1577/1548-8446-35.8.373>
- Wohl, E., Lane, S. N., & Wilcox, A. C. (2015). The science and practice of river

restoration. *Water Resource Research*, 51, 5974–5997.
<https://doi.org/10.1111/j.1752-1688.1969.tb04897.x>

APPENDIX A

MACROINVERTEBRATE COMMUNITY DATA

APPENDIX A

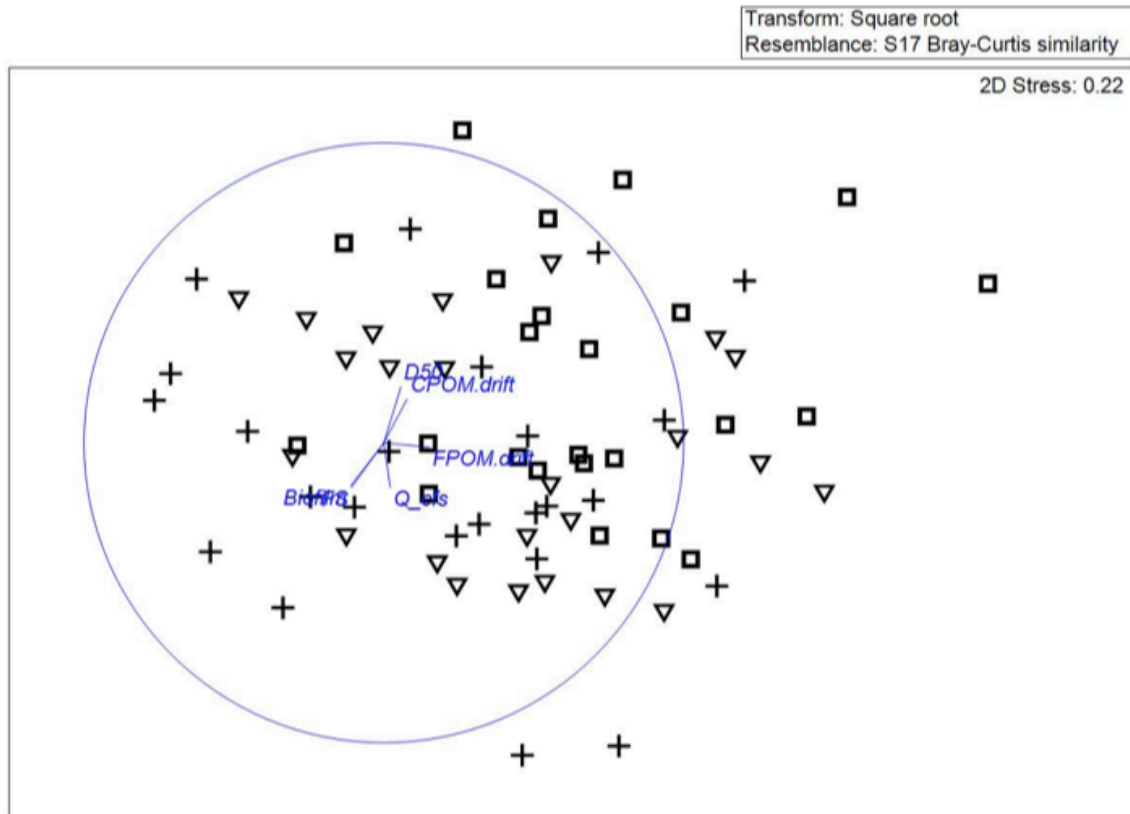


Figure A1. Non-metric multidimensional scaling (NMDS) ordination of macroinvertebrate densities and vectors of basal resources and environmental variables in Beaver (crosses), Mimic (inverted triangle), and reference (squares) sites. Each point is a sampling date at a specific site-type. Community structure showed significant overlap among treatment sites. NMDS-1 was positively loaded for CPOM, fine sediment, and biofilm, and negatively loaded for FPOM, D₅₀, discharge, drifting FPOM, and drifting CPOM. NMDS-2 was positively loaded for FPOM, fine sediment, biofilm, discharge, and drifting FPOM, and negatively loaded for CPOM, D₅₀, discharge, and drifting CPOM.

APPENDIX A

Table A1. Top five producing taxa by treatment by production (P; mg AFDM m⁻² summer⁻¹), standing biomass (B; mg AFDM m⁻²), and density (N; ind m⁻²). Shown are medians for taxa with 95% confidence intervals.

Beaver (Richness = 35)	P (mg AFDM m ⁻² summer ⁻¹)	B (mg AFDM m ⁻²)	N (ind m ⁻²)
<i>Baetis sp.</i>	466.94 (205.965 - 1,489.01)	245.19 (92.84 - 743.08)	1091.94 (864.70 – 4,362.97)
<i>Tipula sp.</i>	440.97 (0 - 993.03)	424.28 (0 - 922.08)	7.18 (0 - 21.53)
<i>Hygrotus sp.</i>	338.79 (338.79 - 567.38)	271.86 (271.86 - 461.58)	57.41 (57.41 - 86.11)
Chironomidae Non-Tanypodinae	294.72 (183.2471 - 477.55)	111.44 (70.25 - 178.06)	7,777.53 (4,329.31 – 19,078.44)
<i>Heterlimnius</i>	230.82 (113.88 - 349.53)	120.33 (60.76 - 191.13)	391.09 (248.77 - 588.43)
Mimic (Richness = 40)			
<i>Pteronarcella sp.</i>	327.44 (0 – 1,222.11)	279.75 (0 – 1,108.62)	17.94 (0 - 57.41)
<i>Helicopsyche sp.</i>	313.91 (107.14 - 706.98)	172.28 (65.64 - 385.30)	394.08 (182.99 - 864.70)
<i>Tipula sp.</i>	261.72 (92.57 - 545.48)	242.45 (72.04 - 528.03)	26.91 (17.94 - 43.06)

<i>Ceratopsyche sp.</i>	234.16 (64.63 - 415.53)	148.43 (39.70 - 259.53)	157.87 (32.29 - 287.04)
Chironomidae. Tanypodinae	189.37 (16.74 - 472.48)	91.14 (6.91 - 230.71)	593.81 (136.31 - 1269.04)
Reference (Richness = 42)			
<hr/> <i>Tipula sp.</i>	203.52 (60.66 - 203.52)	186.40 (41.07 - 186.40)	10.76 (10.76 - 10.76)
<i>Hydrobiidae sp.</i>	169.15 (54.79 - 351.04)	106.05 (31.10 - 224.20)	144.71 (65.18 - 243.38)
<i>Arctopsyche sp.</i>	101.90 (62.40 - 101.90)	92.32 (55.36 - 92.32)	7.18 (5.38 - 7.18)
<i>Lymnaeidae sp.</i>	87.79 (1.19 - 264.73)	77.75 (0.61 - 196.14)	26.91 (5.38 - 165.65)
<i>Limnephilus sp.</i>	84.65 (84.65 - 84.65)	70.74 (70.74 - 70.74)	3.59 (3.59 - 3.59)