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ARTICLE

Freshwater Ecology

Influence of biomimicry structures on ecosystem function in a Rocky Mountain incised stream

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Abstract

Rising levels of stream degradation have motivated a boom in restoration projects across the globe. However, postrestoration monitoring is still frequently lacking and does not always incorporate biotic responses to changes in the physical template. Beaver mimicry structures (BMSs) 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 resources, organic and inorganic material standing stocks, and macroinvertebrate density, biomass, and production to quantify functional responses to BMS installation. 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 were higher, in the BMS treatment compared to the reference riffle treatment. Fine sediment standing stock and basal resources were similar in Beaver and BMS treatments, and both treatments were higher than reference riffles. All treatments differed in macroinvertebrate density, which was highest in the Beaver treatment, followed by Mimic and then Reference treatment. Biomass and secondary production were higher in Beaver and BMS treatments compared to the Reference treatment, but only Beaver and Reference treatments differed significantly, likely due to differences in physical habitat and basal resource availability. Consequently, production of collector–gatherers in the BMS treatment and shredders in the Beaver treatment was higher than in reference riffles. Changes to local hydrology and sediment dynamics resulting from BMS influence biotic functional responses like organic material standing stock and secondary production, creating habitat and ecosystem function distinct from riffles and similar to target conditions of natural beaver dams. To continue to improve BMS as a standard restoration practice, future research could consider the extent of degradation, increasing temporal scale of monitoring. Alterations to aquatic–terrestrial subsidies and impacts to fishes.

KEYWORDS
beaver dam analog, beaver mimicry, macroinvertebrate, restoration, secondary production

INTRODUCTION

Restoration of degraded ecosystems has gained incredible traction in the past several decades (Clewell & Aronson, 2013). The number and scope of river restoration projects in particular is extensive, with billions of funding dollars allocated to rehabilitating degraded freshwater ecosystems (Bernhardt et al., 2005; Wohl et al., 2015). Despite growing evidence that explicit consideration of biological responses improves restoration goals and outcomes (Trush et al., 2000), most projects still focus on changes to the physical template and do not quantify how biology interacts with the physical processes that are changed (Sudduth et al., 2011). 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; Louhi et al., 2011; Naiman et al., 2012). Projects are often undertaken and completed with vague visions of what an ecologically functioning reference system is, a lack of sufficient monitoring protocols, consideration of societal needs, and are likely to fall short of restoration goals as a result (Abelson et al., 2020; Palmer et al., 2005; Wohl et al., 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 with 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 river restoration ecology (Law et al., 2016). While channel incision, or lowered bed elevation, can occur naturally as climate changes (Cluer & Thorne, 2013), the accelerated rate 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 et al., 1994; Pollock et al., 2003). Perhaps the most recognized ecosystem engineer in streams is the North American beaver (*Castor canadensis*), which is widely distributed throughout the continent (Naiman et al., 1988). Dam building by beavers impounds water, aggrades stream beds, buffers stream temperatures, and creates diverse aquatic and terrestrial habitats; these changes can alter resource availability for macroinvertebrates that then extends to higher trophic levels and across ecosystem boundaries (Burchsted et al., 2010; McCaffery & Eby, 2016). Over the last two centuries, extensive trapping and removal of beaver have 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 (BMSs) have gained popularity in recent years as a tool to address channel incision and stream degradation (Pollock et al., 2003). BMSs 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 standing stock (Castro et al., 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 salmonid populations (Bouwes et al., 2016; Pollock et al., 2014). However, less is known about how the physical processes associated with the addition of BMS translate to effects on biological communities and ecosystem processes, such as the storage of organic matter and energy flow through ecosystems (Rubin et al., 2017; Wallace et al., 1996).

Aquatic macroinvertebrates represent an important nexus of energy flux between basal resources such as particulate organic matter and higher trophic levels such as fish (Wallace et al., 1996). Quantifying energy flux by estimating the formation of biomass through time (i.e., secondary production) of macroinvertebrates connects aspects of individual growth, reproduction, recruitment, and mortality to ecosystem processes (Dolbeth et al., 2012). Basal resource availability (allochthonous detritus and algal food sources) has been shown to drive patterns in secondary production and alter community structure of macroinvertebrates in aquatic ecosystems (Cross et al., 2003; Minshall, 1967). Basal resource availability can fluctuate due to variation in flow and temperature (Junker & Cross, 2014), catchment geology (Huryn & Wallace, 1987), riparian habitat (Wipfli & Baxter, 2010), and restoration (Entrekin et al., 2009). 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 et al., 2018). For example, beaver-mediated reaches in southern Chile showed species richness decline but secondary production increase as a result of altered resource availability when beavers were present (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 and may improve our understanding of restoration outcomes (Benke, 1993; Dolbeth et al., 2012). Monitoring macroinvertebrate production after restoration with BMS may provide a more accurate predictor of success or failure by documenting changes that are not reflected in species richness or biomass measurements alone (Frainer et al., 2018; Herrick et al., 2006).

This study provides insight into how BMSs affect basal resources and secondary production in low-gradient streams and whether or not BMS can achieve restoration goals that encompass both physical and biological function. We monitored the impacts of BMS installations on in-stream and riparian conditions, and evaluated how modifications to temperature and sediment affect particulate organic matter, biofilm standing crop, and macroinvertebrate density, standing biomass, and secondary production. We quantified the thermal regime, fine sediment standing stock, daily secondary production of macroinvertebrates, and basal resource standing crop to address the following questions: (1) How do BMS alter physical and biological responses? and (2) How do functional responses of BMS compare to natural beaver dams? Daily maximum temperatures and diel temperature ranges were predicted to be higher due to lower stream velocity and higher incoming solar radiation. We also predicted the standing stock of fine sediment at BMS sites would be similar to fine sediment standing stock found at natural beaver sites and higher than at reference riffle sites. We 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 riffle sites as a result of temperature and resource availability differences. Macroinvertebrate functional feeding groups (FFGs) at BMS sites should be similar to beaver sites, dominated by collector–gatherers and predators, compared to reference riffle 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 that mimics 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 (TNC) 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 77 km long and encompasses $1500\ \text{km}^2$. 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 $58.9\ \text{km}^2$ and averaging 43.82 cm of annual precipitation. Long Creek is classified as a riffle-pool and plane-bed stream with slope of 0.25%. 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 (*Salix boothi*, *Salix drummondiana*, and *Salix exigua*) 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. For the restoration project studied here, the primary goals were to restore 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 (Boyd et al., 2018).

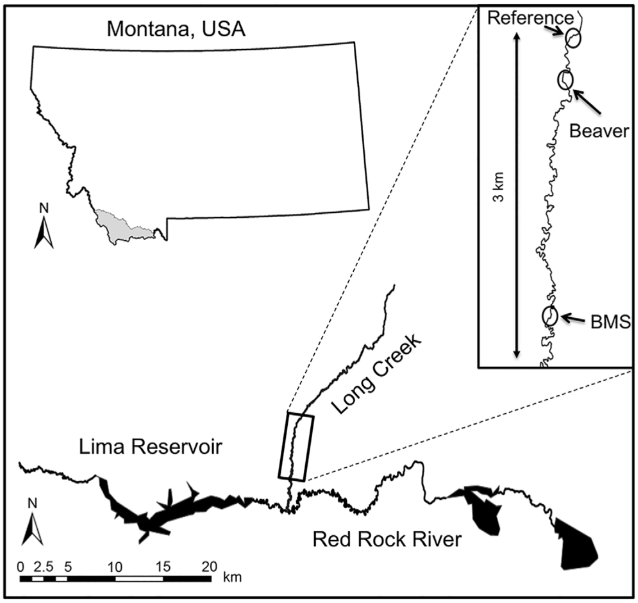

FIGURE 1 Map of the study area. Locations of the beaver mimicry structure (BMS), Beaver, and Reference riffle treatment reaches within The Nature Conservancy's parcel are located in the top right inset. Throughout the BMS reach, a total of nine BMSs were installed. Two structures in the middle of the reach were monitored for this study

Mimicry structure design and installation

The BMSs built on Long Creek during late August 2016 were "constructed" or "armored" riffles (hereafter, constructed 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 (Figure 2). The constructed riffles were also designed to specifically provide passage for one of the remaining populations of threatened adfluvial Arctic grayling (*Thymallus arcticus*) 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 1544 m of stream (1 structure/257 m).

To characterize the hydrologic regime, discharge measurements were taken on Long Creek twice per month at two different surface water stations throughout the TNC parcel. Transects spanning the width of the stream were established, and 20 evenly spaced locations along the wetted width were measured for velocity and water depth. Velocity measurements were recorded using either a Hach FH950 or a Marsh McBirney flow meter at 60% 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 0.03 $m^3 s^{-1}$ greater at the reference riffle sites (0.35 ± 0.01 $m^3 s^{-1}$) than the BMS sites (0.32 ± 0.0 $m^3 s^{-1}$). Note, these surface water stations were part of a partner project and conducted at an alternative spatial scale than for most measurements described below.

Monitoring locations

We established three treatments and a total of six monitoring sites throughout the Long Creek restoration project. The three treatments were (1) upstream of BMS (hereafter Mimic: $n = 2$), (2) upstream of existing beaver dams (hereafter, Beaver: $n = 2$), and (3) reference riffles (hereafter, Reference: $n = 2$). The reference riffles were located in a stream section directly upstream of both the mimic and beaver dam sections. Because no premonitoring was conducted, reference riffles were established as a space-for-time substitution to compare changes that occurred as the mimics affected the physical habitat. Abiotic and biotic responses were measured at all sites throughout June–October 2018.

Physical characteristic sampling

We measured sediment characteristics at each site by quantifying grain size and fine sediment standing stock. Pebble counts were conducted in early July after the peak of the hydrograph and flows returned to wadable 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

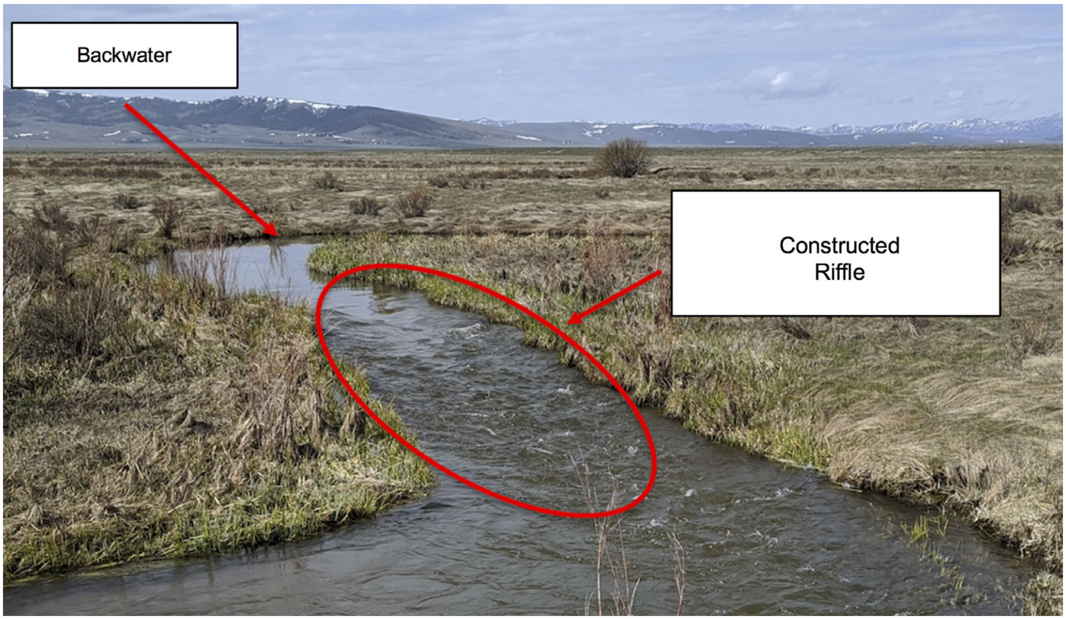

FIGURE 2 An example of a beaver mimicry structure (BMS) installed on Long Creek using a constructed riffle style. The BMS is highlighted by the oval, and the structure created a backwater behind it, which is the location where sampling was conducted

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 stovepipe core (20 × 20 × 63 cm) secured into the substrate of the stream, the benthic layer was agitated for 30 s, and a syringe was used to collect 120 ml of fine sediment suspended within the core. Samples were frozen within 12 h for storage. Once thawed, samples were passed through a pre-ashed GF/F 47-mm filter (pore size = 0.45 μm), dried for 24 h at 60°C, weighed, placed in a muffle furnace at 500°C for 1.5 h, and reweighed, to calculate the inorganic matter and, lastly scaled to a per square meter basis (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 were downloaded once a month during the ice-free season. Temperature was recorded at a single location within each of the Mimic and Reference reaches. 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 32–45 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 h. 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 47-mm filter, dried for 24 h at 60°C, weighed, placed in a muffle furnace at 500°C for 1.5 h, and reweighed to obtain the ash-free weight. The ash-free weight of the sample was subtracted from dry weight of the sample to obtain the ash-free dry mass (AFDM) of the sample. Coefficients were used to scale from the sample area to 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 mesh size) screen across the upstream end of the riffle and recording water depth. The screen collected suspended CPOM for 30 min. Its contents were then collected carefully by hand and placed in a Whirl-Pak and frozen within 12 h. 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 3 min. Water depth at the center of the screen placement was recorded, and the contents of the sieve were scraped into Whirl-Paks and frozen within 12 h. Each sample was emptied into a clean aluminum tin and dried at 55°C for 24–48 h 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 1 h, removed, and placed in a desiccation chamber to cool. Values were adjusted for area of the screen that was submerged in the water and are reported as AFDM per square meter.

Benthic CPOM was measured from Surber samples used for benthic macroinvertebrate sampling (see below). Once macroinvertebrates were picked from the samples, the organic and nonorganic 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 per square meter.

Benthic FPOM was measured using a benthic core comprised of a stovepipe (20 × 20 × 63 cm) secured into the substrate of the stream 1 m from the left and right stream banks. The top 10 cm of the benthic layer was agitated for 30 s. A syringe was used to collect 120 ml of the agitated fine sediment and organic matter within the core. Samples were frozen within 12 h for storage. Samples were then thawed and passed through a pre-ashed GF/F 47-mm filter and placed in a muffle furnace at 500°C for 1.5 h 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 per square meter.

Macroinvertebrate sampling

Macroinvertebrates were collected at all sites using a Surber sampler with an area of 0.31 m^2 and 243-μm 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 22 June, 24 July, 24 August, and 22 September. The summer season was targeted for sampling in order to capture the time of year when the majority of in-stream production likely occurs. Secondary production was summed across the 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 (>1 mm) and fine (<1 mm) 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 non-*Tanypodinae*. Density (individuals per square meter) was calculated by multiplying the number of individuals found per subsample by the fraction that was used for that sample and by a coefficient to correct for subsampling. Body length of individuals was measured to the nearest 1 mm under a dissecting microscope at ×60 magnification. Species richness was estimated as the total number of taxa. Biomass estimates (in milligrams AFDM per square meter) of each taxon were calculated using the following length mass regression:

$$M = aL^b,$$

where M is the body mass, a is the genus-specific constant coefficient, b is the genus-specific constant coefficient, and L is the body length that converts body length measurements to AFDM (Benke et al., 1999). Additional sources were used for obtaining coefficients for biomass of gastropods (Méthot et al., 2012; Stoffels et al., 2003). Macroinvertebrates were assigned into functional feeding groups (FFGs; scrapers, collector–gatherers, filter feeders, and predators) using descriptions from Merritt et al. (2008).

Secondary production estimation

Daily secondary production (in milligrams AFDM per square meter per summer) was estimated using the instantaneous growth method (Gillespie & Benke, 1979; Morin & Dumont, 1994). When cohorts of taxa were easily identifiable, changes in size–frequency distributions were used to calculate growth rates between the sampling dates. Growth rates from cohorts were used to create an empirical model for the stream that predicts growth based on body size (AFDM) and temperature between sampling dates for nonidentifiable cohorts:

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

where g is the instantaneous growth rate, m is the AFDM of individuals (in milligrams), and T is the mean temperature (in degrees Celsius) between sampling intervals. This model integrates information across multiple taxa and feeding guilds ($r^2 = 0.12$) and allowed us to incorporate environmental and biological information (temperature and body size) known to influence organism metabolism and growth rates (Brown et al., 2004). Importantly, this approach allows us to connect differences in biological structure to differences in ecological function among sites. To estimate secondary production, bootstrapped biomass (in milligrams AFDM per square meter) estimates were multiplied by the size-specific growth equation above and by the number of days within the sampling interval. Community daily secondary production was calculated by summing across the entire sampling period (June–September) and all taxa, then dividing by the number of days throughout the sampling period. Confidence intervals (CIs) were calculated via bootstrapping through resampling with replacement 1000 times for each taxon from size-specific abundance data (Benke & Huryn, 2006). Medians and the 2.5% and 97.5% quantiles were calculated to estimate bootstrap 95% CIs.

Statistical analysis

Mixed-effects models tested for differences across treatments for each response variable (i.e., 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, and Reference) and random effects of sampling date and habitat nested within site using the “lme4” package in R (Bates et al., 2015; R Development Core Team, 2020). Habitat was defined as being upstream of a dam (pool) or at a riffle site. Response variables were transformed when needed (natural log or natural log$[x + 1]$) in order to better meet the assumptions of normality and heteroscedasticity. 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 et al., 2008). Differences in water temperature (in degrees Celsius) 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 secondary production were assessed using 95% CIs of bootstrapped values (Benke & Huryn, 2006). If CIs did not overlap, differences were considered statistically 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. Nonsignificant terms were removed until the most parsimonious model was identified.

Community structure of benthic macroinvertebrates among treatments was compared to nonmetric multidimensional scales (NMDS) using the *metaMDS* function from the R package "Vegan" (Oksanen et al., 2020). Macroinvertebrate densities were square root transformed to reduce the influence of high-density taxa, and Bray–Curtis index was used to calculate distance due to its ability to handle species abundances based on count data. Two convergent two-dimensional solutions were fit using a minimum of 1000 random restarts. We tested for differences in benthic macroinvertebrate community assemblages based on densities among treatments, as well as pairwise comparisons among treatments, using a permutational multivariate analysis of variance (PERMANOVA) performed with the *adonis* function in "Vegan" package. We further tested for homogeneity of dispersion among treatments using the *betadisper*

TABLE 1 Mean values (with SE in parentheses) for basal resources and fine sediment accumulation among treatments throughout the 2018 summer sampling season

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 (SEM)	2431 (±779)	142 (±51)	36,933 (±21,073)	10 (±2)	4 (±0.1)	10,392 (±2328)
Mimic (SEM)	2823 (±296)	167 (±48)	71,308 (±23,375)	11 (±3)	3 (±0.5)	20,437 (±3105)
Ref (SEM)	242 (±76)	411 (±128)	154,909 (±46,983)	202 (±71)	0.8 (±0.2)	846 (±150)

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

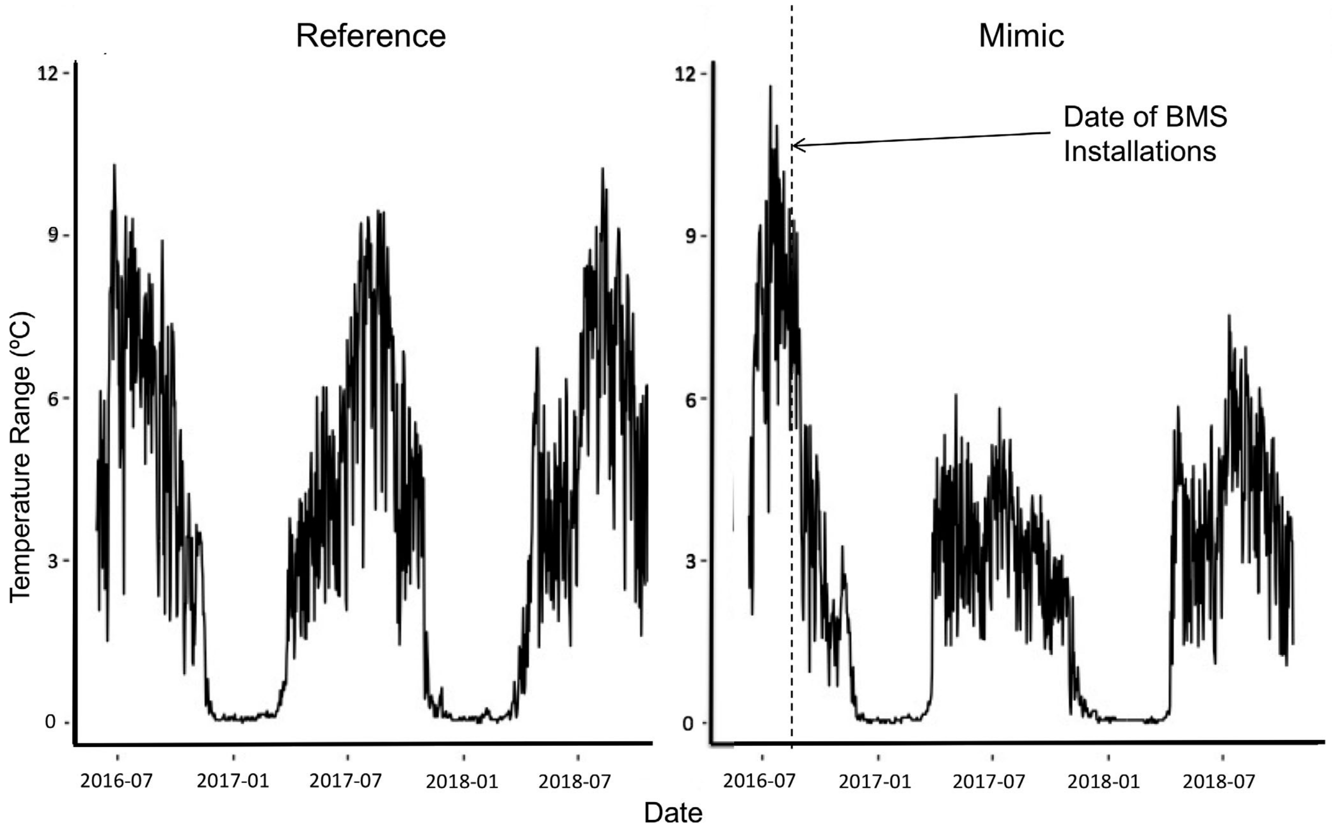

FIGURE 3 Diel temperature ranges (°C), estimated as daily maximum minus daily minimum, for Reference (a) and Mimic (b) treatments across the duration of the study. Structures were installed in the reach with our Mimic sites in the fall of 2016

function in the "Vegan" package to confirm if differences among groups were attributable to the multivariate position of samples rather than heterogeneous variances among treatments.

RESULTS

Physical characteristics

Beaver mimicry had substantial effects on physical characteristics of Long Creek (Table 1). Daily maximum temperatures were statistically higher in Mimic treatments (8.9°C) compared to Reference (8.7°C; Wilcoxon; $v = 201,850$, $p = 0.026$), and averaged 7.4°C for the Mimic and 7.1°C for the Reference. Diel temperature range was smaller within the Mimic treatment compared to the Reference (Wilcoxon; $v = 234,930$, $p < 0.001$; Figure 3). Fine sediment standing stock varied among the three treatments (ANOVA; $F_{2,21} = 11.921$, $p = 0.021$; Figure 4a), with higher levels of fine sediment at Beaver (10,391 ± 2328 mg m^{-2}) and Mimic treatments (20,438 ± 3105 mg m^{-2}) compared to the Reference (846 ± 150 mg m^{-2}).

Basal resources

Benthic CPOM was different among treatments (ANOVA; $F_{2,21} = 5.3871$, $p = 0.007$) with the Reference treatment having the highest mean benthic CPOM (155,00 mg AFDM m^{-2}; Figure 4b), followed by Mimic (71,300 mg AFDM m^{-2}) and Beaver (36,900 mg AFDM

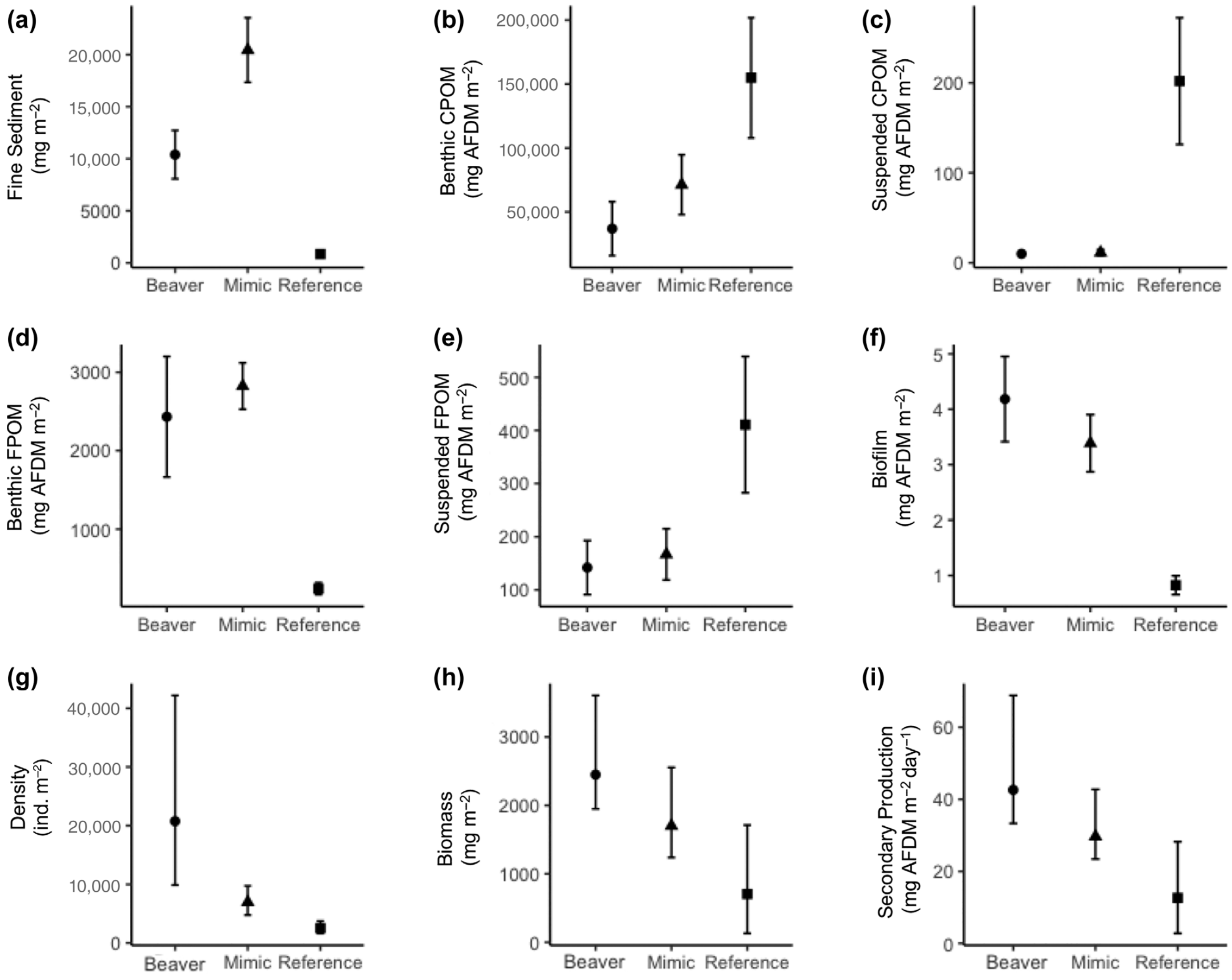

FIGURE 4 Fine sediment accrual (a), benthic CPOM (b), suspended CPOM (c), benthic FPOM (d), suspended FPOM (e), biofilm standing crop (f), macroinvertebrate density (g), macroinvertebrate biomass (h), and secondary production (i) among Beaver (closed circles), Mimic (closed triangles), and Reference (closed squares) treatments (mean ± SEM). Error bars not visible are subsumed within the symbol. Macroinvertebrate density (g), biomass (h), and community secondary production (i) among treatments (bootstrapped median ± 2.5% and 97.5% quantiles)

m^{-2}). Post hoc comparisons showed moderate statistical differences in benthic CPOM only between Beaver and Reference treatments ($p = 0.07$). Suspended CPOM also differed (ANOVA; $F_{2,21} = 14.794$, $p < 0.001$; Figure 4c). The reference treatment had the highest suspended CPOM (202 ± 71 g m^{-2}) followed by Mimic (11 ± 3 mg AFDM m^{-2}) and Beaver (10 ± 2 mg m^{-2}). Differences in suspended CPOM were found between Beaver and Reference treatments ($p = 0.001$), and Mimic and Reference treatments ($p < 0.001$), but not between Beaver and Mimic ($p = 0.23$).

Benthic FPOM was statistically different among treatments (ANOVA; $F_{2,21} = 19.85$, $p < 0.001$; Figure 4d). There were significant differences between Beaver (2431 ± 779 mg AFDM m^{-2}) and Reference treatments (242 ± 76 mg AFDM m^{-2}; $p < 0.001$) and Mimic (2823 ± 296 mg AFDM m^{-2}) and Reference treatments ($p < 0.001$). Suspended FPOM was marginally different among treatments (ANOVA; $F_{2,21} = 2.83$, $p = 0.06$; Figure 4e).

Biofilm standing crop differed among treatments (ANOVA; $F_{2,21} = 19.85$, $p < 0.001$; Figure 4f), with differences between Mimic (3.0 ± 0.5 mg AFDM m^{-2}) and Reference (0.8 ± 0.2 mg AFDM m^{-2}; $p < 0.001$) and between Beaver (4.0 ± 0.8 mg AFDM m^{-2}) and Reference ($p < 0.001$). There was no difference in biofilm standing crop between Beaver and Mimic treatments ($p = 0.97$).

Macroinvertebrate density, biomass, and production

Macroinvertebrate median density was 20,756 individuals (ind.) m^{-2} (95% CI: 9883–42,185) in the Beaver treatment, 6959 ind. m^{-2} (95% CI: 4760–9725) in the Mimic treatment, and 2525 ind. m^{-2} (95% CI: 1636–3743) in the Reference treatment (Figure 4g). Nonoverlapping CIs show differences in median densities across all treatments. Median biomass estimates were 2449 mg AFDM m^{-2} (95% CI: 1949–3605) for Beaver, 1701 mg AFDM m^{-2} (95% CI: 1238–2552) for Mimic, and 704 mg AFDM m^{-2} (95 CI%: 130–1712) for Reference treatments (Figure 4h). CIs at Beaver and Reference treatments did not overlap, indicating substantial differences in median biomass estimates.

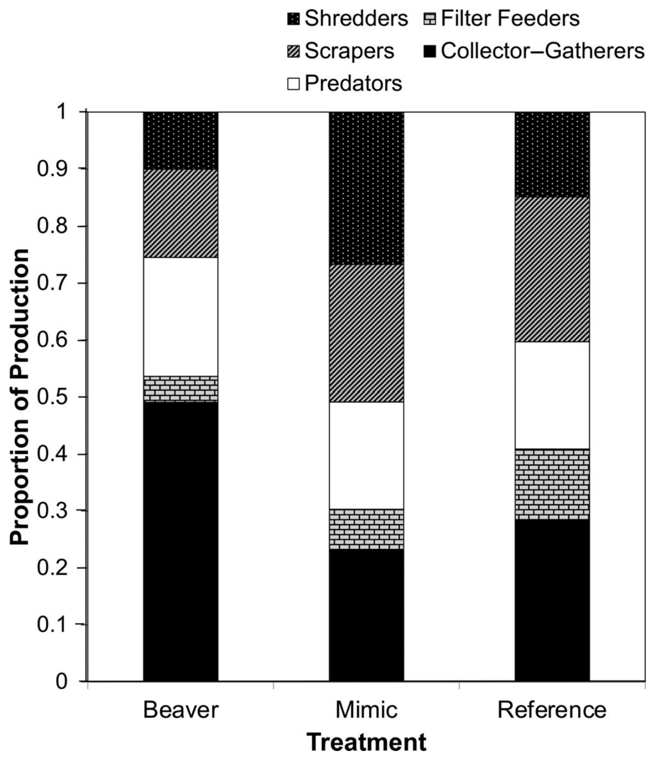

FIGURE 5 Proportion of functional feeding group (FFG) contribution to daily secondary production (mg m^{-2} day^{-1}) across treatments

Community daily secondary production differed among some of our treatments (Figure 4i; Appendix S1: Table S1). Median production by treatments were as follows: Beaver 42.6 mg AFDM m^{-2} day^{-1} (95% CI: 33.3–68.8), Mimic 29.7 mg AFDM m^{-2} day^{-1} (95% CI: 23.4–32.7), and Reference 12.6 mg AFDM m^{-2} day^{-1} (95% CI: 2.8–28.2). Overlapping quantiles between Mimic and Reference treatments, and Beaver and Mimic treatments, suggest statistically similar values. Nonoverlapping quantiles showed a significant difference in daily production between Beaver and Reference treatments. Production of collector–gatherers contributed almost half of the daily production in the Beaver treatment (Figure 5), compared to a quarter of the daily production at Mimic and Reference treatments. Increased shredder production was observed in the Mimic treatment (Figure 5).

To investigate potential drivers of secondary production, we explored linear relationships between basal resources and secondary production. Suspended CPOM ($p = 0.065$, $R^2 = 0.56$; Figure 6a) and benthic CPOM were negatively related ($p = 0.051$, $R^2 = 0.60$; Figure 6b) to secondary production. Suspended FPOM ($p = 0.311$, $R^2 = 0.21$; Figure 6c), benthic FPOM ($p = 0.282$, $R^2 = 0.19$; Figure 6d), biofilm ($p = 0.130$, $R^2 = 0.42$; Figure 6e), and fine sediment ($p = 0.184$, $R^2 = 0.34$; Figure 6f) were not strongly related to secondary production.

Macroinvertebrate community structure

Multivariate analyses of macroinvertebrate community structure (Appendix S1: Figure S1) revealed subtle, yet distinct communities among Beaver, Mimic, and Reference treatments (NMDS; 2D stress = 0.22). The one-way PERMANOVA showed differences in community structure based on densities among treatments

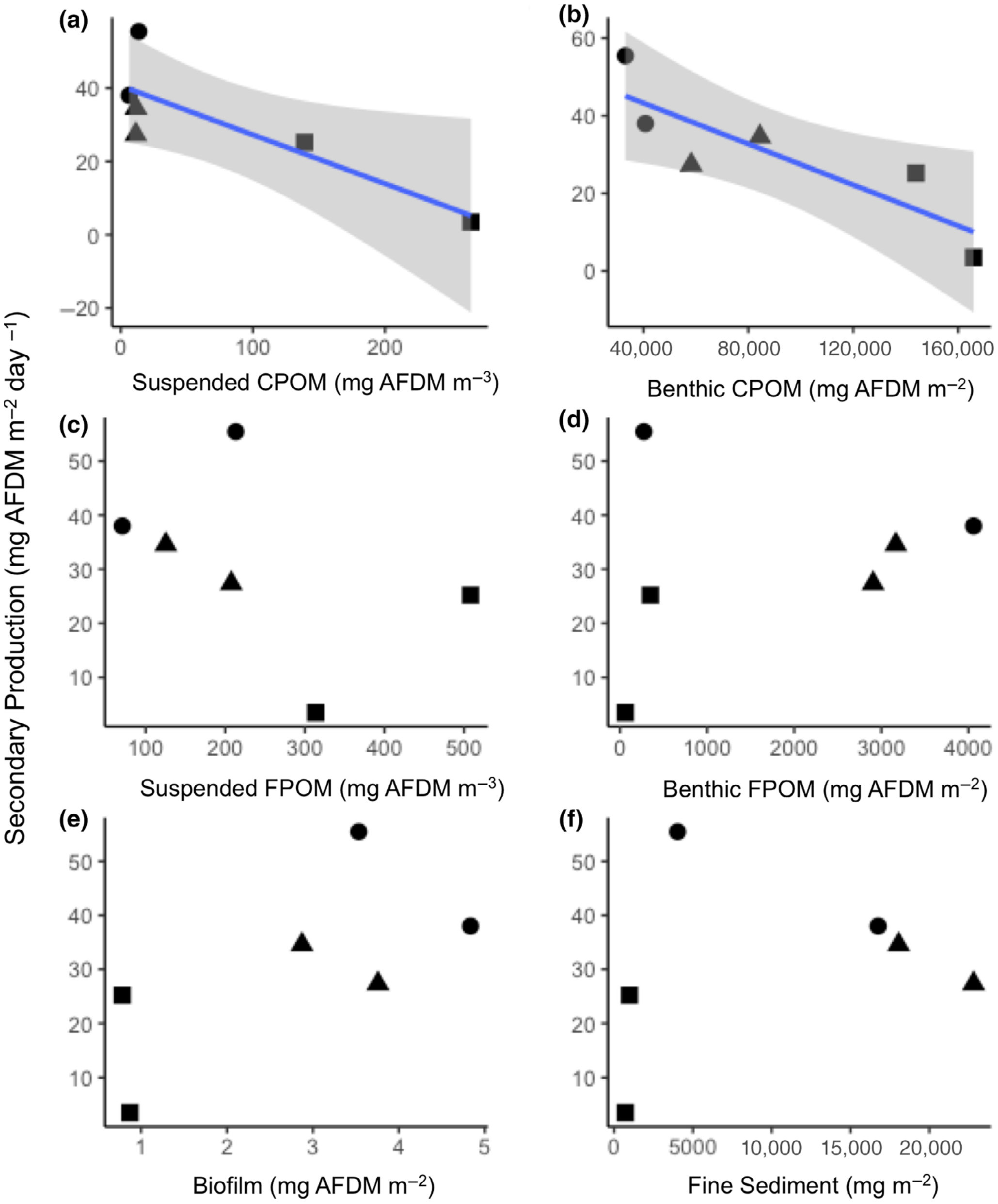

FIGURE 6 Relationships between daily secondary production and suspended CPOM (a), benthic CPOM (b), suspended FPOM (c), benthic FPOM (d), biofilm standing crop (e), and fine sediment accrual (f) among Beaver (closed circles), Mimic (closed triangles), and Reference (closed squares) treatments. Regression lines and gray shading show significant relationships ($p < 0.1$) with CIs

(Appendix S1: Figure S1; $F_{2,69} = 2.0229$, $p = 0.004$). Pairwise comparisons revealed differences in community composition between Beaver and Reference treatments ($t = 1.6959$, $p = 0.002$), and between Mimic and Reference treatments ($t = 1.3758$, $p = 0.032$). However, no difference in community structure was found between Beaver and Mimic treatments ($t = 1.1419$, $p = 0.188$). Species richness did not differ among treatments (PERMANOVA; $F_{2,2.3} = 0.146$, $p = 0.872$). There was no detectable difference in multivariate dispersion among treatments (PERMDISP $F_{2,69} = 0.485$, $p = 0.638$); however, dispersion was slightly higher, although not significant, in the Beaver treatment (43.46 ± 1.58) compared to the Mimicry treatment (41.53 ± 1.23) or Reference treatment (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.

DISCUSSION

Calls to measure ecosystem processes postrestoration work are on the rise, and refining goals and outcomes for stream restoration projects that include ecosystem functions is increasingly emphasized (Beechie et al., 2008; Layman & Rypel, 2020; Palmer & Ferbia, 2012); 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 habitat, resource availability, primary consumer density, biomass, and secondary production patterns. These findings support our prediction that in the 2 years since the structures were installed, secondary production of macroinvertebrates would be similar to actual beaver dams. However, the negative relationship between CPOM and secondary production contradicted our predictions for the role that basal resource availability would play on the secondary production of macroinvertebrates.

Our study had a unique opportunity to compare BMS to both reference riffles and to natural beaver dams. These comparisons among the three treatments are valuable because they monitor differences across multiple common and often neighboring habitat types, including riffles, mimicry pools, and beaver dam pools. Beaver dam pool features broadly represent the hydrologic and geomorphologic water storage goal of many BMS restoration projects. The comparison between Beaver and Mimic treatments is especially informative because natural beaver complexes are dynamic. For example, in 2018, the beaver treatment on Long Creek experienced several dam failures followed by a rebuilding stage. These dam failures are typical of naturally occurring beaver complexes (Levine & Meyer, 2014). Fine sediment standing stock 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 and mimics both experienced that year (Pollock et al., 2014). This increase in sedimentation is important to the aggradation phase of channel evolution in incised streams (Pollock et al., 2007, 2014). Understanding how BMS installations compare to beaver dams that are considered the target conditions is important if BMSs continue to be installed frequently.

Water temperature was different at the BMSs compared to the reference riffles during the time of monitoring. Diel temperature fluctuations were buffered at Mimicry sites and showed more homogenous temperature regimes compared to Reference sites. This finding aligns with 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); however, spatially variable thermal patches have been observed above natural beaver dams (Majerova et al., 2015). The patterns of water temperature that we observed could have consequences for metabolic rates of organisms (Brown et al., 2004), community composition and size structure (Nelson et al., 2017a), and species' distribution (Bouwes et al., 2016; Isaak et al., 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 et al., 2015; Lohr et al., 1996). However, although there was a statistical difference in temperatures measured, the magnitude of difference was small (0.2°C in maximum temperatures), and future work is needed to address how both the range and the absolute temperatures resulting from BMSs influences species of concern. Combined with a warming climate, the effects of BMSs may have important implications for thermal regimes in northern Rocky Mountain streams (Nelson et al., 2016).

We predicted that physical conditions altered by BMS would cascade to the river's biological structure and function. Indeed, we found that secondary production estimates were higher within the beaver complex and the mimic sites than the reference riffles. These larger rates of secondary production measured in our study are congruent with patterns observed in one other study (Anderson & Rosemond, 2007). Higher 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. This provides insight into the wide-ranging factors than can affect secondary production in streams. Previous research has shown how differences in secondary production can be driven by differences in basal resource availability (Huryn & Wallace, 1987; Wallace et al., 1995), allochthonous inputs from riparian vegetation (Albertson et al., 2018; Junker & Cross, 2014), and more stable thermal regimes (Benke et al., 1984; Tumbiolo & Downing, 1994). We attribute the dominance of collector–gatherers and shredders to habitat created by elevated fine sediment and benthic FPOM standing stock, two factors that are positively related to the presence of these FFGs (McDowell & Naiman, 1986; Washko et al., 2020). Negative relationships between secondary production and benthic and drifting CPOM were unexpected and further show the complexity of drivers of secondary production. Our findings from these sites in the Rocky Mountains, which is an area relatively understudied compared to other geographic regions such as the southeast and northwest, are consistent with those from streams in other regions. 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 group such as fish; however, a common issue in stream restoration is the difficulty of defining and assessing the exact suite of parameters that will qualify as “improved” (Bernhardt et al., 2005). One of the biological goals of this restoration project, for example, was to improve in-stream conditions for Arctic grayling. Improvement could mean not only direct effects on fish such as thermally suitable habitat (Liknes & Gould, 1987; Lohr et al., 1996) or access to spawning locations (Cutting et al., 2018), but also indirect effects such as food resource availability (Cutting et al., 2016; Wipfli & Baxter, 2010). Restoration projects often ignore nontarget taxa that provide a food resource, but these taxa are critical components of food webs that may support the species of concern (Lipsey et al., 2007; Naiman et al., 2012). Capturing dynamic, functional responses, such as secondary production, of food resource for fishes provides a more comprehensive outlook on the effects of restoration practices (Dolbeth et al., 2012; Frainer et al., 2018) since static measurements, such as macroinvertebrate density or biomass, do not always offer insight into changes occurring over time within a stream (Miller et al., 2010). Future research might evaluate multiple, competing direct and indirect requirements for target taxa such as Arctic grayling, link food availability to Arctic grayling body condition and reproductive success and consider how the time scale needed to achieve these conditions varies depending on land use, degree of degradation, and catchment geology (Boyd et al., 2018; Dobson et al., 1997).

Although we clearly demonstrate the influence 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 preinstallation monitoring, which is a common reality in many restoration 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. However, 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 during follow-up projects. Future research could consider how these responses occur on a watershed scale, with attention to position within a watershed and changes to different sizes of organic matter and subsequent effects on production, and how to involve multiple stakeholders, such as upstream or downstream landowners, in an effort to potentially expand the influence of BMS in multiple reaches (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 investigate trends in physical and biotic conditions during other seasons. Additional temporal sampling to include multiple seasons over multiple years could be important to capture winter production, which can be lower than in other seasons (Junker & Cross, 2014), and changes to organic material processing from more established pools. The physical form of the constructed riffle structures used in this study is quite different from that of structures made of woven willow between wooden posts with mud and rock at the base of the dam more commonly used for beaver mimicry restoration (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) with potential consequences to terrestrial ecosystems via resource subsidies (Baxter et al., 2005) or riparian vegetation communities (Orr et al., 2020). A comparison across structure types could be an area for future research. Even given these limitations, our findings clearly demonstrate the benefits of increased postinstallation monitoring of BMS on understanding ecosystem functioning.

Incorporating ecosystem engineers, a process-based sampling approach, and monitoring of functional response metrics are major improvements in restoration design (Johnson et al., 2020). Our results show that BMS can initiate physical responses similar to natural beaver dams and create functional responses that resemble 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 feasible. Functional responses like secondary production allow a mechanistic approach for assessing whether rivers can recover from stressors such as riparian land-use change, grazing, droughts, or scour and should be used in future studies to assess viability of restoration work.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from Dryad: https://doi.org/10.5061/dryad.nvx0k6dtf.

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