

Relocated beaver can increase water storage and decrease stream temperature in headwater streams

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Abstract

Many areas are experiencing increasing stream temperatures due to climate change, and some are experiencing reduced summer stream flows and water availability. Because dam building and pond formation by beaver can increase water storage, stream cooling, and riparian ecosystem resilience, beaver have been proposed as a potential climate adaptation tool. Despite the large number of studies that have evaluated how beaver activity may affect hydrology and water temperature, few experimental studies have quantified these outcomes following beaver relocation. We evaluated changes in temperature and water storage following the relocation of 69 beaver into 13 headwater stream reaches of the Skykomish River watershed within the Snohomish River basin, Washington, USA. We evaluated how beaver dams affected surface and groundwater storage and stream temperature. Successful relocations created 243 m³ of surface water storage per 100 m of stream in the first year following relocation. Dams raised water table elevations by up to 0.33 m and stored approximately 2.4 times as much groundwater as surface water per relocation reach. Stream reaches downstream of dams exhibited an average decrease of 2.3°C during summer base-flow conditions. We also assessed how dam age, condition, maintenance frequency, and pond morphology influenced stream temperature at naturally colonized wetland complexes. Our findings demonstrate that dam building can increase water storage and reduce stream temperatures in the first year following successful beaver relocation. Fluvial and floodplain morphology of candidate reaches for relocation is an important consideration because it determines the type and magnitude of response. Relocation to reaches with existing small, abandoned ponds may address thermal criteria by conversion from warming to cooling reaches, whereas relocation within large, abandoned complexes or vacant habitat may result in greater water storage. Although beaver relocation can be an effective climate adaptation strategy to retain more stable hydrologic regimes and water quality in our study area, there appear to be regionally specific environmental and geomorphic factors that influence how beaver affect water storage and temperature. More research is needed to investigate how

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and why these regional differences affect water storage and stream temperature response in beaver-influenced systems.

KEYWORDS

beaver, *Castor canadensis*, climate change, dam, groundwater, hydrology, reintroduction, relocation, salmonid, stream, temperature, wetland

INTRODUCTION

The Pacific Northwest region of the United States is undergoing considerable hydrologic change and will continue to do so over the next century (CIG, 2009; Huss et al., 2017; Littell et al., 2013). Summer precipitation, stream flow, and snowpack are all decreasing (Mauger et al., 2015). Snow melt is projected to occur earlier in the year, and winter precipitation, storm intensity, and stream temperatures will likely continue to increase (Das et al., 2011). These changes have the potential to disrupt physical, hydrologic, and ecosystem processes, which may threaten sensitive species and habitats and affect farmlands and human communities through increased flooding and decreased summer water availability (Van Vliet et al., 2013).

The North American beaver (*Castor canadensis*) has long been recognized for creating pond and wetland complexes, thereby altering hydrologic processes and conditions in aquatic ecosystems. The impoundment of surface water in beaver ponds allows for increased groundwater recharge and thermal variability (Smith et al., 2020). These effects, coupled with the increased habitat complexity found within beaver complexes (Burchsted et al., 2010; Consolati-Machen, 2016; Polvi & Wohl, 2013; Westbrook, 2021), can lead to greater biodiversity (Naiman et al., 2000; Pollock et al., 1995; Robinson et al., 2020; Wright et al., 2002) and ecosystem resilience to environmental perturbations (Bailey et al., 2018; Fairfax & Small, 2018; Fairfax & Whittle, 2020; Hood & Bayley, 2008; Johnston & Naiman, 1987; Naiman et al., 2000; Pilliod et al., 2018; Puttock et al., 2017; Silverman et al., 2019). The potential for increasing water storage and reducing in-stream temperatures may make beaver reintroduction an effective climate change adaptation strategy (Beechie et al., 2013; Dittbrenner et al., 2018; Lawler, 2009; Pollock et al., 2018; Rosemond & Anderson, 2003).

Beaver complexes have been shown to substantially increase surface and groundwater storage potential. It is estimated that, worldwide, beaver complexes store up to 11 km³ of surface water (Karran et al., 2016) with up to 30% of a stream's surface water stored in beaver ponds (Duncan, 1984). Studies have found that beaver increase the width of riparian areas along streams from 11 to 34 m (McKinstry et al., 2001), and in reaches downstream of dams, pool volume also increased (Stack & Beschta, 1989).

Dammed stream reaches have been found to extend the lateral extent of the hyporheic zone by up to 8 m beyond control reaches from a width of 0.2 m prior to dam construction (Shaw, 2009), whereas larger ponds extended groundwater extent by over 50 m (10 m in control reaches; Lowry, 1993). Due to the complexity and high variability of local geology, landform, soil type, and other morphological features, however, estimates of total storage are difficult to quantify. While most existing studies have documented storage at well-established beaver complexes, the effects of relocated beaver on surface and groundwater storage remain understudied.

The effects of beaver dams on stream temperature are also highly variable among studies depending on location and study methodology. Past research has found evidence of warming (Avery, 2002; Patterson, 1951), cooling (White, 1990), warming or cooling depending upon season (Avery, 1983), or no relationship between dam presence and temperature (McRae & Edwards, 1994). In higher elevation headwater systems, where streams are relatively cold, temperature increases of 6–9°C were observed downstream of beaver ponds (Margolis et al., 2001). More recent studies have evaluated stream temperatures at larger scales and found that beaver ponds can also have a net cooling effect (Weber et al., 2017; White & Rahel, 2008) due to groundwater recharge and upwelling (Pollock et al., 2007).

Beaver relocation has been increasingly proposed as a habitat restoration and climate adaptation approach (Babik & Meyer, 2015; Goldfarb, 2019; Kornse & Wohl, 2020; Law et al., 2016, 2017; MBP, 2014; TU, 2022; Tulalip Tribes, 2022; Wohl, 2021). Relocation allows practitioners to target specific priority stream reaches and may be more feasible than traditional restoration approaches in headwater streams. In some cases, naturally dispersing beaver may eventually colonize these same reaches, but relocation accelerates this process and facilitates colonization within areas that may have constraints preventing or slowing natural establishment. There is limited experimental evidence, however, documenting how newly introduced beaver affect water storage and temperature, especially in headwater riparian systems where climate change impacts are predicted to be most pronounced (CIG, 2009; Huss et al., 2017). We sought to address this knowledge gap by evaluating how newly established beaver colonies affect the hydrology and

temperature of stream systems in headwater riparian areas. Specific objectives were to (1) quantify the surface and sub-surface storage potential and influence of beaver complexes, (2) identify how beaver complexes affect stream temperature, and (3) evaluate the restoration potential of beaver reintroduction as a tool to increase ecosystem resilience to climate impacts.

METHODS

Study area and site selection

The Skykomish River watershed (2160 km²) is located on the west slope of the Cascade Mountain range in Washington State, USA (Figure 1). This area is representative of upland basins in the western Cascades. The hydrology in the region is highly variable spatially and temporally due in part to abundant precipitation in the winter and sporadic precipitation in the summer. Mountainous areas contain narrow, glacially carved valleys and high-gradient streams, which transition to low-gradient streams across a wide, hilly plateau, and a large river floodplain. The basin is representative of other watersheds in the region in terms of habitat conditions, importance for threatened and endangered salmonids, and potential climate refugia for wildlife

(Bartz et al., 2015; Scheuerell et al., 2006; Snohomish Basin Salmon Recovery Forum, 2005).

In 2013 and 2014, we conducted a survey of potential beaver habitat within the Skykomish River watershed and developed a beaver intrinsic potential (BIP) habitat model to predict where beaver habitat could exist based on extrinsic landscape variables (i.e., stream gradient and width, and valley width) (Dittbrenner et al., 2018). Within the Skykomish basin, we found that of the 1652 km of streams with high and moderate quality beaver habitat, 73% of the reaches were vacant and could be used as potential relocation sites.

We narrowed this initial set of potential relocation reaches to 25 sites using criteria such as proximity to other known beaver populations, ease of relocation (e.g., proximity to a road), and size of vacant reaches that were predicted by the BIP model to contain high- or moderate-quality habitat. We then conducted detailed site surveys at proposed relocation sites. Prior to relocation, proposed sites were monitored for beaver occupation using a combination of wildlife cameras (Bushnell model 119875C) and repeated site visits to evaluate whether there were signs present, such as dam building, herbivory, or scent mounds (following Snodgrass & Meffe, 1998). In proposed relocation reaches that contained evidence of historical beaver activity, such as unmaintained dams or lodges, we notched dam structures and noted

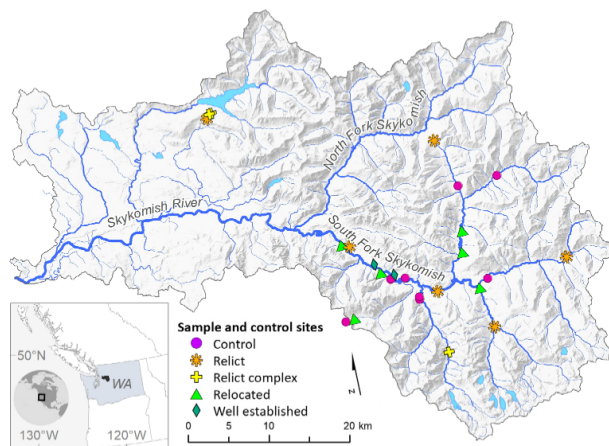


FIGURE 1 Sampling locations within the Skykomish River watershed, Washington, USA. Of the 25 sites sampled between 2014 and 2016, 8 were free-flowing control reaches with no evidence of beaver modification, 6 were relict reaches consisting of a single small pond with an unmaintained dam, 4 were relict complexes consisting of a series of unmaintained dams and ponds, 2 were naturally colonized and well-established beaver complexes, and 5 were relocation sites at which beaver successfully built dams that formed wetland or pond complexes.

whether rebuilding took place. In all cases, no active beaver sightings or sign was evident in proposed relocation reaches for at least a year prior to relocation.

Experimental design

We designed this experiment using a before, after, control, impact (BACI) experimental design (Figure 2; Downes et al., 2002; Stewart-Oaten et al., 1992; Stewart-Oaten & Bence, 2001) to measure how beaver affect stream temperature, and surface and groundwater impoundment. Twenty-five sites were instrumented with continuous water temperature loggers at the upstream and downstream extent of the site. Sampling sites were selected, in part, based on uniformity along sufficiently long stream reaches to ensure that site variability was minimized. Paired upstream and downstream groundwater monitoring well arrays were installed in three of these sites. The lower

groundwater monitoring array at each site was located at the planned relocation site (i.e., impact array). The upper arrays, intended as controls, were located sufficiently far upstream to avoid influences of anticipated dam and pond creation, but they shared similar hydrology and morphology as the impact array.

Beaver relocation

Between 2014 and 2016, we trapped 91 beaver from lowland areas of the study basin. We attempted to trap and relocate all members of a colony to increase site relocation fidelity (Pollock et al., 2018). After capture, colony members were held at a husbandry facility until all members of a family were trapped from a site. In cases where only one beaver was captured, we grouped singly trapped beaver into mating pairs. Prior to relocation, sites were prepared by constructing a temporary relocation lodge of

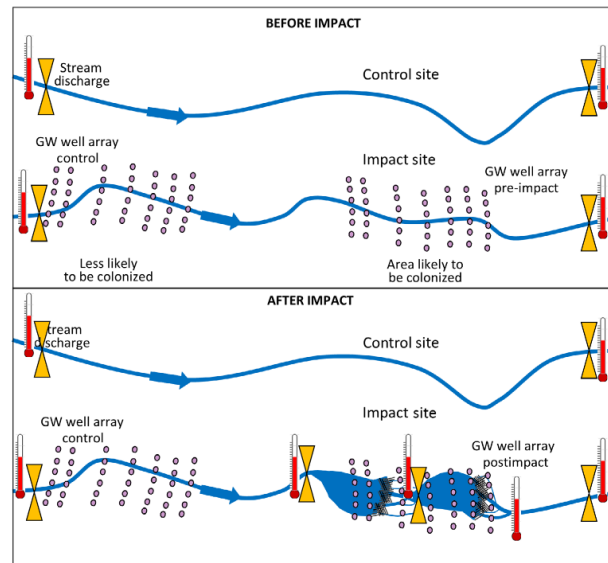


FIGURE 2 Before, after, control, impact (BACI) design for monitoring the effects of beaver relocation on hydrology and stream temperature. Red thermometer symbols indicate locations of in-stream continuous temperature probes, and orange triangles show flow discharge measurement locations. Additional temperature probes and discharge collection points were installed after a colony was successfully relocated. Arrays of groundwater (GW) wells were installed at anticipated dam sites and in the area upstream of the anticipated impact site.

logs and supplementing the site with cuttings if necessary. Following relocation, the site was monitored using a combination of wildlife cameras and surveys to track occupancy and dam building. Beaver were relocated to new sites until half of the sites contained established colonies. Sites were initially designated as controls until a relocated colony was ostensibly established according to two criteria: (1) A colony persisted for at least one season following relocation, and (2) there was dam construction sufficient to create a pond or wetland complex that expanded the stream width to at least twice that prior to beaver relocation. A site retained its designation as impact once these criteria were met, regardless of subsequent colony presence or activity.

Over 3 years, we relocated 23 beaver in seven colony groups at six sites (2014), 24 beaver in eight groups to six sites (2015), and 22 beaver in seven groups to six sites (2016). In cases where an initial relocation failed (i.e., beaver emigrated from the site or were depredated), we relocated another colony to the same site either later in the season or in the following year. Of the 22 colonies relocated to 13 unique sites, 11 relocations were considered successful because beaver remained onsite for a year or longer (Appendix S1: Table S1). During the period of this study, 5 out of 11 established relocations had dam-building activity that resulted in enough impounded stream water to form a pond or wetland complex for a year or longer. In some cases, beaver persisted onsite following relocation but initiated dam construction only after we had completed our study (i.e., during or after 2017); these cases are not reported as part of this study. It is unknown why these six colonies did not immediately build dams. These colonies originated as “nuisance beavers,” having built large dams at their origin sites prior to relocation, and the sites that they were relocated to all had sufficient dam-building material and topography to support pond formation.

In addition to the five successfully established relocation sites, we monitored conditions at 20 other sites included in the initial pool of 25 sites (Table 1). Of these, eight consisted of control sites, which were free-flowing streams containing no historical dams or active sign of beaver activity during the study period. These sites were all ranked as high-quality potential habitat by both the BIP model (Dittbrenner et al., 2018) and subsequent field-based site ranking protocols (Pollock et al., 2018). Six sites were categorized as relict pond reaches, containing a single, small historical, but breached dam with no sign of an active colony, recent beaver occupancy, or dam maintenance. Relict ponds impounded little to no water. Four sites were categorized as relict complexes. These sites contained either one large historical pond or a large pond-wetland complex with no sign of recent activity. Here, dams were breached or porous and impounded little water. The remaining two sites were well-established complexes with large dams, ponds, and wetland habitat that had been colonized for many years.

Surface and groundwater estimation

We monitored surface water storage at all relocation sites using a combination of survey-based and remote sensing techniques. At each site, all surface water was mapped and digitized with surveys (Topcon QS Total Station), GPS (Topcon GR3 GPS and Trimble TNJ31), and unmanned aerial vehicle (UAV)-derived imagery. Georeferenced and digitized UAV imagery was collected again in subsequent years after relocation and dam building to track changes in surface water area. Pond area was also measured at each site during each annual site assessment by walking the pond perimeter or measuring using a range finder (TruPulse Laser Rangefinder model 360). Pond depth was measured at the

TABLE 1 Study sites grouped by beaver occupancy, condition of complex, and morphology.

Site category	Site type	No. sites	Description
Control	Control	8	No preexisting colony, introduction, or subsequent natural colonization
Vacant sites with preexisting, historical dams	Relict ponds	6	Sites vacant. Historical, unmaintained, breached dams and often shallow ponds present
	Relict complex	4	Similar to relict sites, but evidence of large historical complex of dams and ponds
Active sites with established dams and ponds	Established relocation	5 ^a	Relocation sites with established colonies and sufficient damming to form pond/wetlands
	Well-established complex	2	Beaver-maintained dams and ponds already present upon initial inspection for many years and through the duration of study

^aBeaver constructed dams at one additional reintroduction site, but this site became inaccessible in 2015 after the access road washed out. See Appendix S1: Table S4 for additional details.



dam and at the location of maximum depth. We estimated pond volume using the methods of Karran et al. (2016).

Groundwater elevations were characterized at established relocation sites using mini-piezometers (Baxter et al., 2003). We installed arrays of approximately 30–40 wells at relocation sites prior to beaver relocation throughout the area expected to be affected by dam construction (Figure 2). We installed a control array in the same reach above the zone of influence of the beaver colony. Three pairs of arrays were installed, and each was related to an arbitrary datum. Groundwater levels were monitored at least monthly during low-flow periods using a Solinst 101P7 water-level meter.

Variation in groundwater depth at control and relocation arrays was used to identify changes in groundwater storage following established relocation. Interannual variation in groundwater elevation at each site was normalized by subtracting mean groundwater elevation at the treatment site from the mean elevation of the upstream control array. We assessed elevation change during low-flow conditions, generally from 15 July through 15 September 2014–2016 (Dunham et al., 2005; see Appendix S1: Table S2 for focal periods of data collected). Total storage change after established relocation was calculated by multiplying the mean normalized groundwater elevation change by the area affected by damming and the soil porosity of the soil at each site (Woo & Waddington, 1990). Although we used a constant porosity at each site, as damming increases pond height and saturation within the riparian zone, we expected that the alteration of localized conditions (e.g., soil characteristics, sedimentation, and organic matter decomposition rates) would lead to increased variability in storage potential throughout the site.

Stream temperature

Stream temperature was measured using continuous temperature data loggers, recording every 30 min, placed at all 25 sites at the upstream and downstream extent of each sample reach (Figure 2). After relocated beavers were established at treatment sites, additional stream temperature loggers were installed along colonized areas to detect small-scale temperature fluctuations. We calculated the net warming or cooling effect (ΔT) within each reach by subtracting the mean daily stream temperature at the upstream data logger location from the downstream location. Negative values indicated that stream temperature was cooling over that reach, and positive values indicated warming.

The effect of dam building and pond formation on stream temperature before and after relocation ($\Delta T_{\text{after}} - \Delta T_{\text{before}} = \Delta T_{\text{relocation}}$) was evaluated at the five established relocation sites using a linear mixed model BACI analysis (Schwarz, 2015). We used a mixed model approach to evaluate the relative importance of non-beaver-related environmental

factors influencing temperature at individual sites. The use of a linear mixed-effect modeling approach accounts for serial autocorrelation in time series and allows for separation among means between fixed and random explanatory variables (Seltman, 2014). Site colonization timing and success (e.g., before and after) were used as fixed effects, and random effects included sites, sample year, and environmental variables (Table 2). We evaluated competing models with covariates hypothesized to influence beaver's influence on stream temperature, selecting the most parsimonious model. Akaike information criterion for small samples (AIC_c) was used to correct for small sample bias. Models were fit to the response data using the R package “nlme” (Pinheiro et al., 2018). We focused our analysis within an annual window of 27 July through 28 August 2014–2016 (Appendix S1: Table S2) to avoid confounding effects of heavy precipitation events on stream temperature that often occurred later in the summer each year.

Spatial and climate data

We acquired site-level environmental data from public datasets and analyzed them in a GIS (ESRI, 2014). Stream

TABLE 2 Candidate linear mixed-effects models predicting the influence of beaver pond formation and other covariates on stream temperature between 2014 and 2016.

Model	AIC_c	ΔAIC_c	w_i
1. R + AirT + Precip3	670	0.00	0.47
2. R + Slope + Precip3	671	0.90	0.30
3. R + Slope + Vol/m	673	2.69	0.12
4. R + Slope + AirT	675	4.64	0.05
5. R + Slope	675	5.04	0.04
6. R + Slope + DA	676	5.95	0.02
7. R + Precip3	682	12.29	0.00
8. R + Precip3 + DA	683	12.71	0.00
9. R + Precip3 + Vol/m	683	13.03	0.00
10. R + Vol/m	686	15.70	0.00
11. R + AirT	686	16.06	0.00
12. R (null model)	686	16.51	0.00
13. R + DA	687	16.85	0.00

Notes: Parsimonious models, describing the most variation with fewest variables, and the null model are included. ΔAIC_c represents the difference between a given model and the highest ranked model and w_i (Akaike weight) indicates the most probable model. Abbreviations in the model column correspond to the following environmental variables: R = before/after relocation, AirT = air temperature, Precip3 = 3-day average precipitation, Slope = log of site elevation change/site length, Vol/m = surface water volume in ponds and streams per meter, DA = drainage area contributing to site from lowest extent of stream reach.



gradient was calculated from 10-m digital elevation models (USGS, 2014a). Hydrogeomorphic data (e.g., stream lines, stream size, and contributing area) were obtained from online datasets (USGS, 2014b). We used publicly available remotely sensed color infrared orthoimagery from 2013 to 2015 (USDA, 2014a) to measure surface water area change over time. Higher-resolution imagery was collected annually using UAVs (SZ DJI Technology Co.; 3DR, Inc.), and imagery was postprocessed using Hugin (D'Angelo, 2014) for photo mosaicking. We used GIS for georeferencing and Pix4D Mapper (Pix4D SA, Inc.) for mapping and image creation. Daily precipitation and hourly air temperature were obtained from National Weather Service weather stations closest to each site below 1500 m elevation (i.e., stations SKKW1, TINDX; NOAA, 2014). Hourly air temperature for sites above 1500 m was collected with a Hobo Pendant temperature data logger (Onset Computer Corp.) deployed at site OLN02. Total daily solar irradiance data were obtained from weather station KWAGOLDB6 (WU, 2016) located near the center of study sites. We used spatially explicit data on climate (annual precipitation and air temperature) (PRISM, 2004) and soils (USDA, 2014b).

RESULTS

Surface and groundwater storage

Within the first year following relocation, beaver constructed 14 dams at five successful relocation sites. These five sites stored roughly 22 times as much surface water as control sites. At these relocation sites, dam building led to the retention and impoundment of 243 m³ of water per 100-m stream reach in 2014–2016 (Figure 3) with a mean pond volume of 983 m³. During this period, control reaches remained relatively constant with a mean volume of 11 m³/100 m (SD = 8). New ponds experienced no observable levels of sediment deposition within the year following establishment; however, it is likely that some pond volume may be lost over time as ponds accumulate sediment and aggrade (Polvi & Wohl, 2012).

Relocation sites with established ponds stored 2.4 times more ground water than surface water in ponds. At relocation sites fitted with groundwater well arrays (sites SFS02 and FOS02), mean normalized groundwater elevations increased 0.18 and 0.26 m, respectively, following pond formation (Figure 4). Additionally, one naturally colonized and well-established complex site (SFS08) had a 0.33-m mean normalized groundwater elevation increase after transitioning from having limited beaver activity in 2015 to very active dam construction in 2016. This increase in groundwater elevation at established relocation sites equated to an increase in groundwater volume of 581 m³ per 100 m

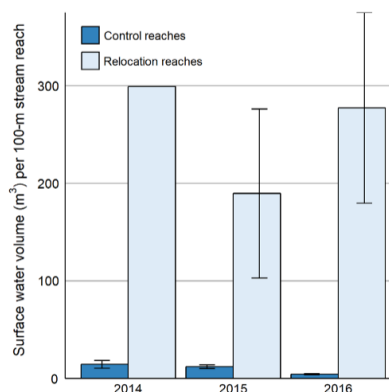


FIGURE 3 Mean and SE of surface water storage at control and established relocation reaches during August 2014–2016. In 2014, the mean and SE were not calculated because there was only one relocation reach.

in the first year following relocation. Beaver ponds capture fine sediments and organic matter, both of which affect water storage capacity over time (e.g., fine sediments could decrease storage, while organic matter could increase storage). Given the short-term nature of this study, we acknowledge this potential error in our calculation but did not observe substantial aggradation in the year following pond creation.

Stream temperature

Frequent and periodic heavy precipitation events occurring throughout the summers of 2014–2016 had a substantial effect on stream temperature. Cold weather fronts associated with these events brought cooler air, precipitation, and increased cloud cover, leading to substantial stream cooling. Some of the relocation sites showed shifts in the relationship between stream temperatures at upper and lower probes. We analyzed the effect of relocation on stream temperature within the focal period 27 July through 28 August 2014–2016 to avoid the confounding effect of heavy precipitation events that occurred during other periods of summer base-flow conditions.

During the focal period, the construction of beaver ponds resulted in an increased stream cooling effect of $\Delta T_{\text{relocation}} = 2.3^{\circ}\text{C}$ among sites (Figure 5). The BACI analysis using a linear mixed-effects model showed that this cooling effect observed at relocation sites was

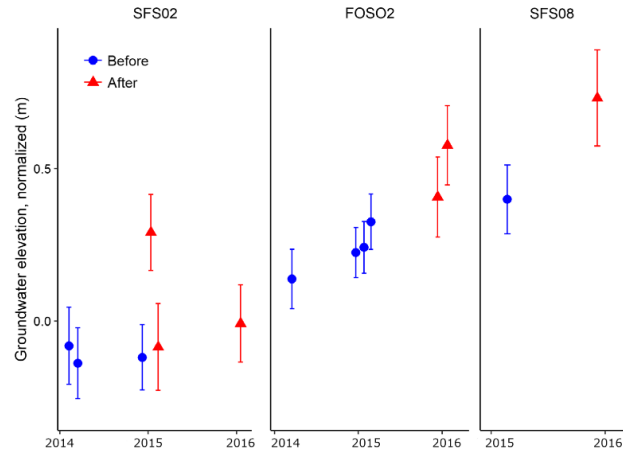


FIGURE 4 Normalized groundwater elevation at release sites during low-flow conditions, before and after beaver relocation. Each point represents the normalized site mean elevation of all groundwater wells on the sampling date, which were collected in August of each year. Normalized groundwater elevation at each treatment site was calculated by subtracting the mean groundwater elevation from the upstream mean groundwater elevation (i.e., control array) at that site. Elevations are relative to each other within sites only.

significant ($p = 0.009$). Prior to beaver relocation, stream reaches exhibited a mean cooling effect over the length of the site of $\Delta T_{\text{before}} = 0.1^{\circ}\text{C}$ ($\text{SD} = 1.9^{\circ}\text{C}$) over the extent of the reach. Following relocation and dam construction, sites showed an increased mean cooling effect of $\Delta T_{\text{after}} = 2.4^{\circ}\text{C}$ ($\text{SD} = 1.9^{\circ}\text{C}$) from the upper to lower extent of the beaver-influenced reach. Four of the five established relocation sites had an increase in cooling following dam building (Figure 5; see Appendix S1: Figures S1 and S2 for maximum cooling and warming effect per site). Temperature shifts at these sites ranged from $\Delta T_{\text{relocation}} = -6.0^{\circ}\text{C}$ (site BEC02) to $\Delta T_{\text{relocation}} = -0.3^{\circ}\text{C}$ (BEC04). One site (SFS02) exhibited a diminished cooling effect following relocation, $\Delta T_{\text{relocation}} = +1.1^{\circ}\text{C}$, but the site retained an overall cooling effect ($\Delta T_{\text{SFS02,after}} = -1.6^{\circ}\text{C}$, $\text{SD} = 0.9^{\circ}\text{C}$).

We used a linear mixed-effects model to evaluate how environmental factors not related to beavers may influence stream temperature at individual sites. These results indicated that the differences we observed in stream temperature at established relocation sites were associated with air temperature, 3-day mean precipitation, stream slope, and stream volume (Table 2). The most parsimonious model included air temperature and 3-day precipitation, both of which were negatively correlated with differences in upstream and downstream temperature.

When we broadened our analysis to include the entire summer base-flow period (i.e., 15 July–15 September), four of the five relocation sites showed downstream warming prior to pond creation (i.e., higher temperatures downstream compared to upstream temperature; Figure 6a). Following beaver relocation, dam building, and pond formation, this pattern reversed and streams were cooler downstream (Figure 6b). One established relocation site (FOSO2) differed from this trend. Here, stream temperatures were cooler downstream prior to establishment (Figure 6c). Following dam construction, this site experienced a decrease in the magnitude of cooling (Figure 6d). Additionally, the amplitude of diel stream temperature was substantially dampened after established relocation within this reach.

Heavy summer storm events had a dramatic effect on stream temperature. For example, prior to beaver relocation at site SFS02 (Figure 6a), the warming trend observed throughout most of the summer was temporarily suppressed during heavy precipitation events (e.g., 224 mm between 29 August and 3 September 2014). After dam building at SFS02 (Figure 6b), the downstream cooling trend observed for much of the summer was reversed during large precipitation events (e.g., 538 mm between 29 August and 4 September 2015) when high flows pushed warm surface water in

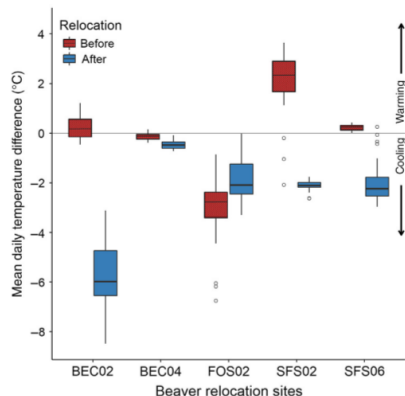


FIGURE 5 Before- and after-relocation temperature differences at relocation sites. The data represented in the box plots are the daily mean of all synoptic differences between stream temperature at the upper and lower extent of each site, collected in 30-min intervals, 27 July–28 August 2014–2016. Positive values represent an increase in stream temperature from the site's upper to lower extent, whereas negative values represent a temperature decrease. Mean pre-relocation stream temperature for all sites was $\Delta T_{\text{before}} = -0.10^{\circ}\text{C}$ ($\text{SD} = 1.85^{\circ}\text{C}$, $n = 5$) and mean postrelocation temperature was $\Delta T_{\text{after}} = -2.44^{\circ}\text{C}$ ($\text{SD} = 1.93^{\circ}\text{C}$, $n = 5$). The mean of change in daily mean temperature from before relocation to after was BEC02: -6.0°C , BEC04: -0.3°C , FOS02: -4.2°C , SFS02: $+1.1^{\circ}\text{C}$, and SFS06: -2.2°C . Boxes are interquartile ranges, horizontal lines are medians, whiskers are interquartile range, and dots are outlying data points.

the ponds over the dam and past the downstream temperature logger.

Temperature effects in multiple beaver pond classes

When we broadened our investigation to include additional site categories of small, abandoned ponds, large abandoned complexes, long-established sites, relocation sites, and control streams, we observed an increasingly stronger cooling trend as pond sites became more complex, increased in size, and were more actively maintained (Figure 7). Control streams with no beaver structures exhibited a warming effect of $\Delta T_{\text{control}} = 0.8^{\circ}\text{C}$ ($\text{SD} = 1.5^{\circ}\text{C}$) between downstream and upstream temperature probes. Vacant relict ponds had a greater warming effect than control streams ($\Delta T_{\text{relict}} = 2.2^{\circ}\text{C}$, $\text{SD} = 2.4^{\circ}\text{C}$)

and also had fewer overall cooling days. By contrast, vacant relict complexes, established relocation reaches, and well-established beaver pond complexes all exhibited cooling effects of $\Delta T_{\text{relict-complex}} = 1.2^{\circ}\text{C}$ ($\text{SD} = 1.3^{\circ}\text{C}$), $\Delta T_{\text{relocation}} = 2.0^{\circ}\text{C}$ ($\text{SD} = 1.8^{\circ}\text{C}$), and $\Delta T_{\text{complex}} = 1.9^{\circ}\text{C}$ ($\text{SD} = 2.5^{\circ}\text{C}$, $n = 2$ sites), respectively. We did not perform additional tests on these categories due to limitations in sample size.

Potential effect of relocation on salmonids

Over the duration of this study, maximum daily stream temperature correlated closely with ambient air temperature, which was highly variable among years. Prior to relocation, study reaches had a mean maximum daily temperature of 15.0°C during base-flow conditions and showed a small decrease in maximum daily stream temperature of 0.5°C between upstream and downstream temperature probes (Table 3). In the year following relocation, seasonal ambient temperature was substantially warmer than in previous years, which was reflected in a higher mean maximum stream temperature of 16.1°C during the study's focal period. Despite a much hotter summer, however, streams downstream of dams following relocation exhibited a 2.8°C decrease in mean maximum temperature.

We evaluated the potential effect of beaver relocation on salmonids by quantifying the number of days that maximum stream temperature exceeded thermal tolerances of species within this study region (i.e., $\geq 17^{\circ}\text{C}$ daily mean) and lethal levels (i.e., $>23^{\circ}\text{C}$ daily mean) (Hicks, 2002). The summer prior to relocation was relatively mild and, although pre-relocation sample reaches rarely exceeded thermal thresholds, we observed a downstream increase in mean days per site (Table 3). The summer following relocation was much warmer, and we observed that above beaver ponds 9.4 mean days per site met or exceeded salmonid thermal tolerances. Downstream of these ponds, however, there was a reduction of 9.2 mean days above thermal thresholds, with only 0.2 mean days during the focal period.

DISCUSSION

This study demonstrates that the creation of beaver wetland complexes has the potential to increase water storage and decrease stream temperatures, suggesting that relocated beaver could play a role in climate change adaptation. Beaver can rapidly construct dams following relocation that create ponds sufficient to store large amounts of surface water and increase groundwater elevations near

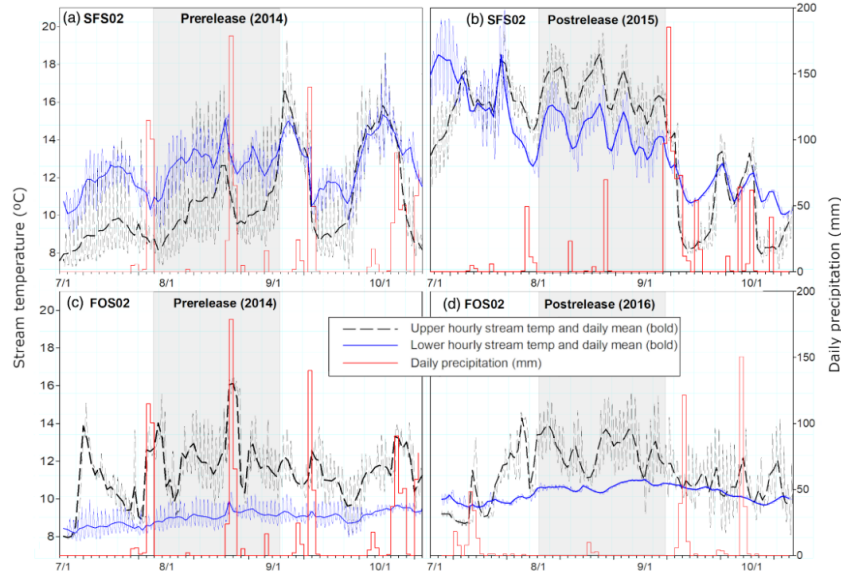


FIGURE 6 Example of the two types of stream temperature effects from beaver relocation and precipitation observed during low-flow conditions (i.e., 1 July–1 October). In four of five sites, downstream temperature was greater than upstream prior to relocation. Site SFS02 is an example of this trend (a). Following relocation, stream temperature was cooler downstream of impoundments sites; site SFS02 demonstrates this reversal (b). In one case (c), stream temperature was cooler downstream than upstream prior to relocation. Following relocation (d), this site had a diminished cooling effect. Upstream temperature is dashed black, downstream is solid blue, precipitation is red, and the gray box is the period of focus for this study.

beaver ponds. Stream temperatures downstream of dams were substantially cooler than temperatures above dams, especially during summer low-flow conditions. In ponds created from both newly relocated beaver colonies and well-established wetland complexes, site complexity had a strong effect on stream temperature.

Dams constructed by relocated colonies were initially small in the first few years of our study compared to dam structures in well-established colonies. However, their associated ponds were still able to impound substantial amounts of surface water. Relatively new dams (i.e., constructed within the first year of site colonization) had the potential to impound greater volumes than previously reported. Many studies have quantified pond storage at well-established complexes and found ponds ranging from very small (e.g., 15 m³) to over 10,000 m³, with a mean pond size near 1000 m³ (Karran et al., 2016). The relatively small dams created in our study within the first year following

relocation led to the impoundment of 983 m³ per pond on average. While regional morphology (e.g., gradient and valley width) is a strong predictor of pond size potential, our findings suggest that, even in areas such as the Snohomish Basin, with relatively high gradient and relatively narrow valley width, beaver relocation as a restoration measure has the potential to increase water storage relatively quickly.

The impoundments at our sites led to an increase in groundwater elevation and overall groundwater storage equivalent to approximately 2.4 times that of the surface water storage at each site. Although there have been no previous studies that have reported the effects of beaver on groundwater storage at relocation sites, some have quantified the effects of beaver damming on groundwater at established beaver sites and found an increase in the water table when compared to control reaches (Hill & Duval, 2009; Lowry & Beschta, 1994; Westbrook et al., 2006). Our findings of groundwater increases of between 0.18 and 0.33 m are

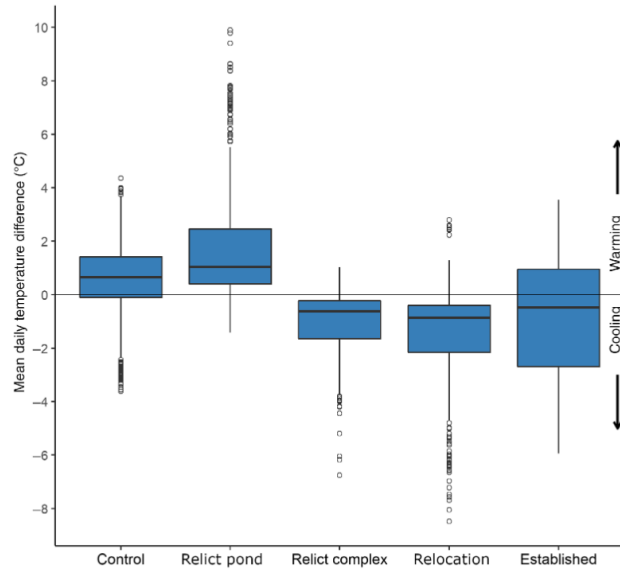


FIGURE 7 Daily mean stream temperature differences between upstream and downstream at control reaches and in four categories of beaver complexes. Control sites were free-flowing streams. Relict sites were vacant of beaver and contained small ponds with historical, unmaintained dams. Relict complexes were also vacant but contained multiple or large ponds behind historical, unmaintained dams. Relocation sites had newly constructed dams and ponds, and established sites possessed well-maintained and long-established dams and ponds. Ponds at established sites tended to be much larger than those at relocation sites. Boxes are interquartile ranges, horizontal lines are medians, whiskers are interquartile range, and dots are outlying data points.

TABLE 3 Mean maximum daily stream temperature and number of days that stream temperature exceeded salmonid impairment limits at beaver relocation sites.

Sample location relative to beaver relocation	Mean and SD of maximum temperature (°C)				Mean and SD of days impaired per site			
	Before	SD	After	SD	Before	SD	After	SD
Upstream	14.96	1.48	16.08	1.95	0.60	0.03	9.40	0.09
Downstream	14.42	2.50	13.28	1.94	1.40	0.04	0.20	0.02
Change	-0.54		-2.80		0.80		-9.20	

Notes: Stream temperature was assessed at the upper and lower extent of beaver-influenced stream reaches before and after beaver relocation during core summer base flow, 27 July–28 August 2014–2016. Impairment to salmonids from single-day extremes was defined as stream temperatures $\geq 17^\circ\text{C}$. Stream temperatures never exceeded lethal limits $>23^\circ\text{C}$ during this study.

similar to studies at naturally colonized beaver dam sites with documented increases of 0.25 m (Bouwes et al., 2016) to 0.34 m (Majerova et al., 2015). Although all our successful relocation sites were located within mountainous areas with moderately sized valley cross-sections, we observed a positive

relationship between valley width and groundwater storage. Thus, we expect beaver impoundments within areas with wider floodplains to store substantially more groundwater, but given that our study was not designed to explore this relationship, further research is needed to better understand

the lateral extent to which beaver can raise groundwater tables.

Beaver complexes in our study basin had an overall mean cooling effect of -2.3°C on streams. Four of these sites exhibited a mean change of -3.18°C from before to after relocation. One site, SFS02, exhibited a change of $+1.1^{\circ}\text{C}$ following relocation. This trend was observed in the summer of 2015, which was particularly hot, and highlights the role of environmental factors on temperature outcomes at a given site. Previous studies report a range of effects from overall warming to cooling of streams below beaver dams. The nature and magnitude of temperature effects tend to vary with environmental factors and dam size and age, but this relationship has only been more recently investigated. For example, early studies (Patterson, 1951; Rasmussen, 1941; Reid, 1952) and recent research (Majerova et al., 2015) have found a warming trend downstream of dams. Other studies that have considered geomorphology have found dams to produce both warming and cooling depending on stream complexity and dam height (Fuller & Peckarsky, 2011a). Furthermore, some studies have found a cooling effect and often a dampening of diel variability as beaver occupied a stream reach (Błdzki et al., 2011; Bouwes et al., 2016; Pollock et al., 2007). Given the range of temperature effects observed in different beaver studies, we were curious to identify which environmental factors lead to downstream cooling rather than warming. Within our study basin, we found that the strongest site-specific environmental variables influencing stream cooling were decreasing site gradient and increasing pond volume. Lower gradient sites have the potential to impound greater surface water volume than steeper sites with a similar dam height. Complexes with larger surface water storage, and presumably hydraulic head, may promote greater groundwater infiltration and downstream upwelling.

Newly created beaver ponds demonstrated a reduction in the daily maximum stream temperature among sites. The year following relocation was a particularly hot summer, and we observed over 9 days per site of maximum daily temperatures exceeding salmonid thermal tolerances (i.e., 17°C). Below beaver complexes within these same streams, however, the number of mean maximum days above threshold levels, fell to 0.2 days per site, representing a substantial moderating effect for aquatic species. These trends have been observed in other systems with both natural beaver dams (Bouwes et al., 2016; Fuller & Peckarsky, 2011b) and after construction of beaver dam analogues (Weber et al., 2017).

In the Pacific Northwest, periodic heavy precipitation events occurred throughout the summers of 2014–2016, supplementing streamflow and decreasing ambient temperature. Although no relationship was observed between dam height and temperature at relocation sites, it is likely that

late-season precipitation events and snowmelt drive cooling in beaver ponds in our study region; these events keep ponds filled and allow for groundwater recharge throughout the summer. It is possible that variation in temperature response depends on whether dams are creating a sufficiently strong hydraulic gradient to drive groundwater upwelling downstream of dams. Regions with periodic precipitation events that continue to supplement ponds and stabilize groundwater tables may have consistently cooler downstream temperature. Contrary to beaver ponds in more arid areas, which may have less supplementation of flow during low-flow periods (e.g., Majerova et al., 2015), we observed cooling trends following relocation. This finding further supports our assertion that beaver-influenced systems in our study area maintain sufficient flow and hydraulic gradient to drive downstream cooling throughout low-flow periods.

When we expanded our temperature analysis to include beaver site categories of relict ponds, relict complexes, established relocations, well-established sites, and control sites, we identified a notable pattern. Although active beaver sites (i.e., established relocation and well-established sites) and relict complexes had a greater cooling effect than control streams, relict ponds were substantially warmer. The differing temperature effect between small relict ponds and large relict complexes—warming versus cooling—supports previous findings that, when normalized by area, ponds with low dam height to pond area ratio produce more frequent downstream warming (Fuller & Peckarsky, 2011a, 2011b). This pattern has several management implications for beaver-based restoration strategies. Relocation practitioners often prioritize large, abandoned beaver complexes over small relict ponds to create ponds with large surface water and groundwater storage. Our findings suggest that focusing on these areas may enhance storage but will not necessarily address temperature goals, particularly for streams that face heightened concerns of elevated temperatures. Focusing relocation efforts on relict beaver ponds that are small, shallow, and abandoned may be more effective in some instances because restoration in these areas will encourage increases in dam heights, which will drive greater hydraulic gradients and potentially have a greater likelihood of reducing downstream temperatures.

The role of beaver in stream restoration and climate adaptation has received increased attention in recent years (Fairfax & Whittle, 2020; Hood & Bayley, 2008; Johnston, 2014; Lawler, 2009; McKay et al., 2012; Naiman et al., 1988; Pollock et al., 2018; Stoll & Westbrook, 2020). Many low-order streams in North America were once inhabited by beaver prior to widespread trapping and extirpation, and legacy dams and complexes can be found in many places (Wohl, 2021). Dispersing beaver will often colonize these areas, but permanent colonization can take a long time if local conditions are not immediately ideal and sites that

beaver choose to colonize do not always correlate with restoration priorities (Dittbrenner et al., 2018). Additionally, natural colonization may occur in areas with elevated conflict potential, such as reaches adjacent to infrastructure or areas sensitive to flooding. Relocation allows for targeted colonization in reaches that are degraded or have been prioritized for various conservation goals, and have a lower likelihood to create human–beaver conflict. If beaver relocation is to be an effective restoration and climate change adaptation strategy, however, it is critical to consider whether long-term site fidelity of beaver colonies is a prerequisite to achieving stream temperature and storage restoration goals. Our relocation success rate was consistent with past relocation programs conducted in the American West (Babik & Meyer, 2015; MBP, 2014; McKinstry & Anderson, 2002; Pollock et al., 2018). Despite relocating active, dam-building beaver to sites with high habitat quality potential and food availability, it was often necessary to introduce multiple colonies to a site over several years before permanent colonization could be achieved. In some cases, colonies that abandoned the site may have colonized nearby reaches. Emigration from relocation reaches to nearby areas has been observed in other relocation programs as well (Babik & Meyer, 2015; Hoffman & Recht, 2013; McKinstry & Anderson, 2002). However, depending upon the goals of the relocation program, this may still be considered a success. In other cases, colonies that initially emigrated from a site eventually returned in following seasons. Multiple practitioners have observed that some initially successful colonization efforts eventually succumbed to high predation rates or dam breaches during heavy precipitation events leading to emigration from the site. In these cases, successful colonization and long-term site fidelity were contingent on dam structures with large, stable ponds that reduced predation risk and withstood high winter storms and streamflow. The potential for dam breaches may be exacerbated by climate change, as winter flows increase in intensity in the Pacific Northwest (Das et al., 2011); this emerging concern needs to be considered when prioritizing reaches for relocation.

Habitat quality and water quantity were important factors affecting relocation success and long-term site fidelity. We observed substantial variability in streamflow among sites, with some sites experiencing extreme winter flow events and others nearly drying out during summer. Major sources of site variation included lithology and substratum type (e.g., colluvial material), soil composition, landscape position (e.g., high and low elevation), hydrogeomorphic variation (e.g., slope, BFW, and valley width), and vegetation composition and structure. These factors affect beaver colonization preference, dam and pond size, and the resulting magnitude of hydrologic and temperature change between sites.

Despite repeated relocation at individual sites, permanent colonization and dam building was only achieved at one-third (5 of 15) of the attempted relocation sites. To our knowledge, no previous studies exist that document the hydrologic or temperature effects of targeted beaver relocation. Of those that have monitored the initial environmental effects at naturally colonized sites, sample size is generally low, most often consisting of a single site (Pilliod et al., 2018). Thus, although the sample size of five sites, including 19 dams and ponds among sites, is still relatively small, it represents an increase in replication from previous studies. Nonetheless, greater replication would have improved our statistical power to determine which site-specific environmental and physical factors are most important in affecting stream temperature. Limited sample size also constrained our ability to evaluate the relatively high temperature variability among sites. Despite these limitations, our 15 randomly selected candidate relocation sites were classified as “highly suitable” by the BIP model (Dittbrenner et al., 2018) and were representative of similar headwater and low-order streams considered for relocation within the region.

This study focused on beaver relocation within free-flowing streams and did not include relocation within wetland or side-channel habitats. The hydrology and morphology of free-flowing versus wetland and side-channel habitats have different responses to dam building by beaver. Furthermore, our study sites were located in a mountainous area, often with localized patches of high-quality potential habitat. This environmental setting differs from lowland areas that have larger, contiguous habitats and potentially dissimilar site characteristics (e.g., lower gradient, broader floodplains, and potentially higher dam and colony density). There may be differences in the hydrologic and temperature effects observed between beaver ponds in upland versus lowland sites, as well as among sites with other sources of variation (e.g., ecoregion, climate regime, lithology, and geomorphology).

Despite greater understanding of beaver influences on stream hydrology (Brazier et al., 2020; Larsen et al., 2021; Rosell et al., 2005), there remains considerable uncertainty about how regional factors affect water storage and stream temperature. Given the highly variable results of studies exploring the effects of beaver on stream temperature, additional research is needed to elucidate the underlying mechanisms that drive temperature in beaver-influenced systems and to better understand why such variability exists among regions and in different ecological and hydrologic contexts. More experimental studies are needed to quantify how thermal heterogeneity is affected within and among beaver pond complexes over time. Sites with older dams often have more pronounced effects on hydrology than newer dams (Meentemeyer & Butler, 1999), suggesting that field observations from



newly constructed dams may yield a relatively weak signal in some instances. Long-term studies are needed to identify how river systems change over time in response to the dynamics of beaver colonization and movement.

We examined how beaver may offset some climate-related impacts on water storage and stream temperature, but beaver themselves may be affected directly and indirectly by climate change (Campbell et al., 2012; Stoll & Westbrook, 2020). For example, reduced summer precipitation in the Pacific Northwest has the potential to cause perennial streams to become intermittent (Reidy Liermann et al., 2011; Van Vliet et al., 2013). In these cases, beaver will likely abandon intermittent reaches and move downstream to find more suitable habitat. Climate projections also predict higher-magnitude winter storm events, increased peak stream flows, erosion, and sediment mobilization (CIG, 2009). Beaver dams are more likely to fail during these events. Similarly, rates of aggradation are also likely to increase, potentially accelerating beaver pond to meadow succession following abandonment. In some cases, this may promote recovery of riparian ecosystems, but it is unknown how these impacts will affect beaver population and colony dynamics.

Beaver reintroduction provides opportunities for ecosystem restoration and climate adaptation. The creation of wetlands by beaver colonies increases hydrologic stability, thermal variability, geomorphic complexity, species and habitat diversity, and resilience. In our study, active beaver ponds constructed by both long-established and newly relocated colonies caused stream cooling and increased surface and groundwater storage during summer low-flow conditions. Our findings in free-flowing streams differ from some other beaver pond-related temperature studies, and further research could advance our understanding of regional drivers of stream temperature. When identifying potential reaches for relocation, potential changes in the future need to be considered as well as regional context and existing habitat and hydrologic conditions, but also to potential changes in the future. Variability in environmental and hydrologic effects caused by beaver damming is likely to increase in a changing climate. In watersheds with similar conditions and climate trajectories as those in our study area, beaver relocation may be an effective climate adaptation tool to ameliorate elevated temperature and reduced watershed storage.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Dittbrenner, 2022) are available from Figshare: <https://doi.org/10.6084/m9.figshare.14384936>.

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