

residence time, and depositional areas for sediments. The increased storage attenuates hydrographs (Gurnell, 1998) and can increase base flow (Nyssen et al., 2011). Specifically in the beaver ponds, water infiltration through the bed and adjacent banks influences local groundwater elevations (Hill and Duval, 2009). Within the stream channel, beaver dams alter hydraulic gradients (Lautz and Siegel, 2006) that increase the potential for hyporheic exchange (Lautz and Siegel, 2006). Such changes in channel morphology and hydrology alter stream temperature regimes. Warming due to solar radiation can be a key factor due to increased water surface area (Cook, 1940). Further, foraging and extensive inundation can lead to loss of riparian vegetation that decreases riparian canopy and the associated shading influences (Beschta et al., 1987). Changes in groundwater–surface water interactions can also impact the overall temperature regime (e.g., upwelling zones decrease temperatures below beaver dams (Fanelli and Lautz, 2008; White, 1990). Regardless of this implied connection between hydrologic and stream temperature changes due to beaver dam construction, most studies have investigated these changes separately. Furthermore, the temporal and spatial scales considered within individual studies vary widely, leading to inconsistent conclusions regarding beaver dam impacts on stream systems (Kemp et al., 2012).

When considering hydrologic influences at the beaver dam scale (which includes the beaver dam structure, the upstream ponded area, and the section below the dam), Briggs et al. (2012) found a connection between streambed morphologies formed upstream of beaver pond and hyporheic flow patterns. Similarly, Lautz and Siegel (2006) showed that beaver dams promoted higher infiltration of surface water into the subsurface. Janzen and Westbrook (2011) found enhanced vertical recharge between stream and underlying aquifer upstream of the dams. They also found that the hyporheic flowpaths surrounding beaver dams were longer than expected. Nyssen et al. (2011) studied impacts of beaver dams at a larger reach scale and throughout a series of beaver dams. Similar to other literature (Gurnell, 1998; Burns and McDonnell, 1998), they found that a series of beaver dams retained water during high flows and increased low flows through drier periods. The authors found that the recurrence interval for major

floods increased over 20 years and peak flows were decreased and delayed by approximately a day. In contrast, some argue that while beaver dams affect downstream delivery, they provide minimal retention during large runoff events (Burns and McDonnell, 1998).

The documented impacts of beaver dams on temperature are more variable. Some studies found that beaver dams and beaver ponds cause overall increases in downstream temperatures (Andersen, 2011; Margolis et al., 2001; Salyer, 1935; McRae and Edwards, 1994; Shetter and Whalls, 1955) with reported values as high as 9 °C during summer months (Margolis et al., 2001). Fuller and Peckarsky (2011) also observed increases in temperatures below low-head beaver dams, but a cooling effect below high-head beaver dams. At the longer reach scale (22 km), Talabere (2002) found no significant influence of beaver dams on stream temperature. A recent literature review regarding the impacts of beaver dams on fish further summarizes such inconsistent findings. Kemp et al. (2012) cited 13 articles that argued beaver dams provided thermal refugia and 11 articles that argued negative impacts from altered thermal regime (i.e., detrimental increases in summer temperatures). Interestingly, this review also pointed out that of the 13 articles claiming temperature benefits of beaver dams, only seven were data driven and the remaining six were speculative. By contrast, of the 11 articles showing temperature impairments, only one was data driven while the rest were speculative. Another recent literature review regarding the effects of beaver activity in stream restoration and management further revealed that a majority of studies cover small spatial scale areas (e.g., small reach scales), are mainly qualitative, and many hypotheses are supported only by anecdotal or speculative information (Gibson and Olden, 2014). Particularly in the context of stream management, where beaver have recently been considered as a potential restoration tool (e.g., Utah Beaver Management Plan), a more quantitative understanding of the hydrologic and thermal impacts of beaver within stream systems is critical.

Variability in hydrologic and thermal responses in streams with beaver dams and the subsequent inconsistent conclusions found in the literature highlight the need for more

data driven studies across multiple spatial and temporal scales. In an effort to link hydrologic and temperature responses due to beaver dam development, we present data from different spatial (reach, sub-reach, and beaver dam) and temporal scales (instantaneous to continuous three-year time series) that span a period prior to and during the establishment of 10 beaver dams. We illustrate how the development of beaver dams shifts instream hydrologic and thermal responses. More specifically, a losing reach (pre-beaver) was transformed to a gaining reach (post-beaver) while simultaneously increasing stream temperatures.

Site description

Curtis Creek, a tributary of the Blacksmith Fork River of Northern Utah drains a portion of the Bear River Range. Curtis Creek is a first-order perennial mountain stream with intermittent tributaries. The mountainous watershed includes a combination of hard sedimentary rock, Paleozoic and Precambrian limestone bedrock that is strongly indurated. The valley broadens in the lower portion of Curtis Creek and is primarily dominated by remnant low-angle alluvial fans. The valley bottom is comprised of a mix of longitudinally stepped floodplain surfaces and channel that are both partly confined by coarse-grained alluvial fan deposits with gravel, cobble, boulders and some soil development. These stepped floodplains are infrequently inundated by the modest spring-snowmelt flow regime, and reflect surfaces created by relic beaver ponds and beaver dam flooding.

Data were gathered in a 750 m long study site on the lower portion of Curtis Creek that is located about 15 mi east of Hyrum, Utah at Hardware Ranch (an elk refuge operated by the Utah Division of Wildlife Resources – UDWR). The study reach has a relative steep streambed slope of 0.035, supporting a bed of coarse gravel to large cobble with some man-made boulder vortex weirs placed within the new channel with a meandering planform. In 2001, the UDWR conducted a stream relocation project within the study reach and some segments of the channel were moved and reconstructed, leav-

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ing portions of the original channel abandoned. The banks of the realigned channel were stabilized with boulders, root wads, logs, and erosion control blankets.

The riparian area surrounding the channel prior to and following relocation was heavily grazed by elk and did not support woody riparian vegetation. Roughly around 2005, grazing pressure was lessened and the area was fenced (though some grazing was still allowed). This facilitated some modest recovery of the riparian woody vegetation which was enough to attract beaver. In early summer of 2009, beaver colonization began with beaver dam 7 constructed in the middle of the study reach (Fig. 1). Beaver dams 4 and 5 were also completed during summer 2009. New beaver dams (3 and 8) were established early-summer 2010 and by the late summer-early fall, dams 2, 6, 9, and 10 were completed. By the end of fall 2010, beaver dam 1 was built at the upstream end of the study reach resulting in a total of 10 beaver dams with an average height of 1 m. In addition, two small (less than 0.5 m in height) beaver dams were constructed in the old channel (Fig. 1, dams without numbers). Beaver built seven of their dams using the artificial restoration structures as foundations. By the end of fall 2010, the channel consisted of sections with flowing water (main channel and side channels), ponded water (beaver ponds), and beaver dam structures (Figs. 1 and 7). The resulting dam density by 2010 was $13.3 \text{ dams km}^{-1}$.

2 Methods

The field site was originally instrumented with pressure transducers, temperature sensors, and groundwater observation wells to investigate groundwater–surface water interactions in the absence of beaver. After one year of data collection, beaver colonization occurred within the study reach, changing the objectives of the study. In short, it produced the perfect accidental experiment and a unique opportunity to quantify fundamental hydrologic and thermal impacts of beaver dam construction on stream systems. In an effort to specifically investigate these impacts, three primary data types were collected over a three-year period spanning pre- and post- beaver colonization

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(Table 1, Fig. 1). Flow information was collected at the reach and sub-reach scale to compare influences of individual beaver dams and cumulative impacts. In addition, groundwater levels were observed within the floodplain of the study reach. To explore the corresponding impacts of dams on thermal regimes, stream temperature data were collected and analyzed at the reach, sub-reach and beaver dam scales. Both the hydrologic and temperature data collection took place over different temporal scales and the frequency varied from instantaneous measurements to continuous data throughout the three-year period.

2.1 Data collection

The study reach boundaries were set following a previous study (Schmadel et al., 2010) and locations along the reach were denoted by distance downstream from an arbitrary datum set upstream of the study reach (Fig. 1). Water level and temperature were measured using KWK Technologies[®] SPXD[™] 610 (0–5 psig) (Spokane, Washington) pressure transducers (PT) with vented cables and Campbell Scientific[®] CR-206 data loggers (Logan, Utah) at the upstream (PT515, Fig. 1) and downstream study reach limit (PT1252, Fig. 1). Water level and temperature were measured at 30 s intervals and five-minute averages were recorded. Discharges were measured at each PT under the full range of flow conditions using the velocity-area method to establish rating curves. The flow velocity was recorded with a Marsh McBirney Inc.[®] Flo-Mate[™] (Model 200, Frederick, Maryland). To provide a local comparison of hydrologic responses due to beaver activity, continuous discharge data were similarly collected at the bounds of a control reach approximately 535 m long without any beaver activity located immediately upstream from our study reach (PT0).

The study reach was further divided into six sub-reaches, ranging from 56 to 168 m and numbered sequentially downstream (Fig. 1). The six sub-reaches spanned individual dams (e.g., sub-reach 4), multiple dams (e.g., sub-reach 2 and 5), and a non-impounded sub-reach that received return flows from an upstream beaver dam (sub-

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reach 3). Dilution gaging was conducted at the sub-reach scale on 16 July 2008 (pre-beaver) and 19 July 2010 (post-beaver) to provide a longitudinal understanding of flow variability. As described within Schmadel et al. (2010, 2014), chloride (from NaCl) was used as a conservative tracer (Zellweger, 1994) and rhodamine WT was used as a visual indicator for a qualitative assessment of mixing. Tracer responses were measured following an instantaneous tracer injection starting at the downstream end of the study reach and then moving upstream to individual sub-reach limits. Each response was measured with specific conductance (SC) (electrical conductivity normalized to 25 °C as a surrogate to chloride concentrations) at one-second intervals using YSI[®] sondes (models 600 LS and 600 XLM, Yellow Springs, Ohio) calibrated in the field. The background SC was corrected to zero (Gooseff and McGlynn, 2005; Payn et al., 2009) and each corrected response was correlated to chloride concentrations with calibration regressions.

To capture changes in groundwater levels throughout the reach, groundwater observation wells were installed in June 2008 (Fig. 1). These wells were constructed from half inch polyvinyl chloride (PVC), 2 m in length with 40 cm of perforation covered with 2 mm flexible nylon screen to exclude soil. Elevations were established for individual wells using a total station and later using differential rtkGPS (Trimble[®] R8, Global Navigation Satellite System, Dayton, Ohio). Groundwater levels were determined by measuring distance from the top of each well to the groundwater surface level in each well using a Solinst[®] electronic well sounder (Model 101 Mini, Georgetown, Ontario, Canada).

At the finer, beaver dam scale, temperature measurements were collected above and below individual beaver dams at 10 min intervals using Onset[®] HOBO[®] Temp Pro V2 (Bourne, Massachusetts) deployed from 2 September to 15 October 2010 (Fig. 1, Tables 1 and 2). The temperature sensors were wrapped in aluminum foil to reduce solar radiation influence in slower moving water.

Aerial imagery was used to delineate and compare pre- and post-beaver colonization flowing and ponded water area. Pre-beaver colonization conditions (2006) were

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There were no groundwater elevation data collected in 2010 and thus post-beaver colonization period was represented by the 2011 data. Due to the established groundwater observation wells not being distributed evenly throughout the study reach, changes in groundwater over the study period are only available for sub-reaches 2, 3, and 5.

5 The temperature impacts at the beaver dam scale were quantified from the data above and below individual beaver dams (3, 4, 5, 7, and 8) from fall 2010 (Fig. 1 and Table 2). In case of beaver dam 7 and 8, the ponded water from beaver dam 8 extended to beaver dam 7. Therefore, we used data above dam 7 and below dam 8. A 24 h moving average was calculated from the data to detect temporal trends other than diurnal patterns. The net temperature change, ΔT , for each individual beaver dam was calculated by subtracting the temperature above the beaver dam from the temperature below the beaver dam. A positive change represented net warming, while a negative change represented net cooling below the beaver dams. The area of flowing water (represented by the stream channel) and ponded water from the beaver dams was digitized and calculated from the 2006 (pre-beaver conditions) and 2010 (post-beaver colonization conditions) imagery (Table 3). The main channel water volume for pre- and post-beaver dams were also estimated based on one-dimensional HEC-RAS hydraulic model built to replicate the two different states (Table 3).

3 Results

20 3.1 Reach scale responses

At the reach scale, the average daily discharge (Fig. 2) illustrates the seasonal variations and changes in flow conditions at PT515 (inflow) and PT1252 (outflow) for 2008 through 2010. The 2008 and 2009 flows were fairly comparable with peak flows at PT1252 of 1698 and 1549 Ls^{-1} , respectively. The 2010 flows were, however, one third of peak flow in comparison to previous years (592 Ls^{-1} at PT1252). The impacts of beaver dam building activities are directly reflected in the reach scale flow conditions

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and in the year-to-year variability in net ΔQ and % ΔQ (Fig. 3). Negative changes indicate a net losing reach while positive values indicate net gains in flow. The daily average value for March–October of 2008 (pre-beaver) was -5.6Ls^{-1} for ΔQ and -4.4% for % ΔQ . As the beaver dams were built and increased in number, the average values of ΔQ and % ΔQ increased to 51.2Ls^{-1} and 13.2% in 2009 and to 81.2Ls^{-1} and 53.1% in 2010, respectively.

Across shorter temporal scales, variability within each season of each year was also apparent. Even though data are only available for short portion of the spring period in 2008, the reach was gaining. In July 2008, the % ΔQ became negative suggesting that the reach was losing during the spring flood recession. In early spring of 2009, the reach shifted from losing to gaining. However, the reach did not switch back to losing conditions during lower flows and gains were approximately 10 % during the months of June, July, and August. In September 2009, the % ΔQ further increased to 30 % over one week and was followed by a slow decrease of approximately 20 % the following two weeks before increasing again. Similar gaining conditions continued throughout 2009 and into 2010. In 2010, another increase in % ΔQ was observed in April at the beginning of snowmelt and reached up to 60 %. The greatest % ΔQ occurred at the end of June 2010 reaching approximately 80 % (Fig. 3). This sort of drastic change may be partially affected by irrigation patterns in nearby fields during summer months.

20 At the reach scale, stream temperatures consistently increased during the summer with peaks occurring at the end of July and beginning of August, and some periods of cooling within the reach in the fall and winter for all three years (Fig. 4). Net and percent changes in temperature (ΔT and % ΔT) show a warming trend from 2008 to 2010 corresponding to the increase in the number of dams (Fig. 5). In 2008, the average daily ΔT was 0.22°C and in 2010 the average ΔT was 0.43°C . The average increase from 2008 to 2010, difference based on daily ΔT (not on their yearly averages), was 0.38°C (% $\Delta T = 3.8\%$). The maximum difference in ΔT between these years was 0.77°C (% $\Delta T = 8.5\%$) and occurred on 1 August (Fig. 5).

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Reach scale data from a smaller temporal scale (a five-day period in July) illustrates the links between discharge and temperature patterns associated with beaver dam construction (Fig. 6). Comparison of ΔQ and $\% \Delta Q$ show similar trends to those in Fig. 3 (i.e., an increase in the amount of water gained over the reach each year), but with diurnal patterns. The $\% \Delta Q$ for 2010 shows approximate 80% increase in discharge when compared to 2008 (Fig. 6b). The transformation from losing in 2008 to gaining in 2010 is also more pronounced at this shorter five-day scale. Similarly, when comparing ΔT and $\% \Delta T$ values there is an average increase of 0.6 °C and 4.6% from 2008 to 2010, respectively. The data also contain a diurnal pattern with a maximum difference of 1.1 °C (8%) between 2008 and 2010 (Fig. 6c and d). The ΔT values show that the range of temperature differences during the day doubled in 2010. With this transition from a losing to gaining reach, one might expect a decrease in temperature during the summer due to the addition of colder groundwater. However, there was instead increased warming over the study reach. In 2008, the flowing water surface area was estimated to be 1776 m² with no ponded area. In 2010, the flowing water surface area decreased to 1211 m² with the ponded area covering about 2830 m². In the end, the water surface area in 2010 had more than doubled (Fig. 7, Table 3).

3.2 Sub-reach scale responses

With an increase in the number of beaver dams for each consecutive year, the groundwater elevation increased in sub-reaches as shown by the changes in the annual distribution and median values (Fig. 8, Fig. SI2 in the Supplement). The response was greatest for sub-reach 2, where median groundwater levels increased approximately 0.03 m during the first year (2008–2009) and by another 0.34 m from 2009 to 2011. For sub-reaches 3 and 5, median groundwater levels increased by 0.02 and 0.12 m from 2008 to 2009, respectively. From 2009 to 2011, these levels increased further by 0.10 m in sub-reach 3 and by 0.15 m in sub-reach 5. Based on the positive head gradient between groundwater and surface water, sub-reach 2 and sub-reach 3 is primarily

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gaining over the study period. However, sub-reach 5 is generally neutral in 2008 and is more commonly losing in surface water in 2009 and 2010 (Fig. 8, Supplement Fig. 2).

Groundwater–surface water exchanges in the study reach prior to beaver dam influences were documented in Schmadel et al. (2014). Discharge estimated at various locations longitudinally illustrates the variability in flows prior to beaver dam influences (Fig. 9a) and the sub-reach scale $\% \Delta Q$ showed some sub-reaches gaining while others losing (Fig. 9b). The 2010 discharge values showed greater variability after beaver dams were constructed in the reach (Fig. 9a). In contrast with the yearly average head gradient (Fig. 8), the net $\% \Delta Q$ in sub-reach 2 shows a transition from gaining in 2008 to losing in 2010, sub-reach 3 from neutral to gaining, and sub-reach 5 from neutral to losing in 2010 (Fig. 9b). Mass recoveries from the dilution gaging show the percent of mass loss and gain changed significantly from 2008 to 2010. In 2008, the mean percent mass losses for individual sub-reaches from 2 to 6 were –3.1, –13.2, –19.7, –20.7, and –9.7%, respectively. In 2010, the mean percent mass losses were –103.7, –0.3, –9.5, –62.0, and –15.4% for the same sub-reaches.

Mean residence times estimated from the 2008 and 2010 tracer studies show an increase for all sub-reaches containing beaver dams (Table 4). The biggest change was observed in sub-reach 2 where beaver dam 4, with the largest pond area, was located (Fig. 1). The second greatest increase occurred in sub-reach 5 where a series of dams and ponds covered approximately 50% of the sub-reach length. The increase in sub-reach scale residence times translates into an overall reach scale increase of 62 min or 230%.

3.3 Beaver dam scale responses

The spatial and temporal temperature differences observed between individual beaver dams from a two-day period show that each dam influences the system differently throughout each day (Fig. 10). A comparison of absolute temperatures above and below individual beaver dams, where a positive change represents net warming and negative change represents net cooling below the beaver dam, illustrates a general down-

stream warming trend which cumulatively propagated downstream below beaver dam 8 (Supplement Fig. 3). Although, the temperature increase for each dam was generally within the accuracy of the temperature sensor ($\pm 0.2^\circ\text{C}$), the cumulative impact of multiple dams showed more significant downstream warming.

5 Based on the data shown within Fig. 10, daily ranges (daily maximum minus daily minimum values) of temperature differences below and above each beaver dam (ΔT) provide additional information regarding the spatial variability among individual dams within each day (Fig. 11a). However, when looking at 24 h moving averages (Fig. 11b), ΔT values fall within the accuracy of the sensors and highlight the importance of the
10 temporal scale (frequency) of measurements when determining the impacts of beaver dams on stream systems.

4 Discussion

While many studies exist regarding the influence of beaver dams on the local hydrologic and temperature regimes, the majority of these studies lack sufficient quantitative
15 field measurements across appropriate spatial (beaver dam to reach scale) and temporal scales (instantaneous to continuous over a period of years) to draw meaningful conclusions (Kemp et al., 2012; Gibson and Olden, 2014). Furthermore, the results are often inappropriately generalized beyond the scales of the observations. Our results quantify the influences of beaver dams on a stream flow and temperatures while
20 demonstrating how beaver dams impact stream hydrologic and temperature regimes at different spatial and temporal scales.

The reach scale results of our study suggest an overall increase in ΔQ from 2008 to 2010 based on changes in flow conditions due to beaver dam building activity (Fig. 2). The increases in gains during the spring can be attributed to surface and subsurface
25 lateral inflows. However, the impacts of the beaver dams are more apparent during low flow conditions when the study reach slowly transitions from losing in 2008 to gaining in 2010 (Fig. 3). As the number of beaver dams increases, the impact on reach scale

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discharge is more evident. In summer and fall of 2008, the reach is in equilibrium or slightly losing water. In contrast, the reach is gaining water during these same summer and fall months of 2009. This trend continues and is more pronounced as beaver dams continue being built and the cumulative impact of multiple beaver dams results
5 in constant gains in 2010 (Fig. 3b). The dominant hydrologic processes influencing the study reach clearly changed over the period of three years. To provide a comparison, we can use baseline ΔQ and $\% \Delta Q$ from the control reach just upstream for the same three-year period (Table 3). These data show that the control reach was losing water for all three years except for summer of 2008. In contrast to the beaver impacted study
10 reach, the losing trend in the control reach is more pronounced with each year and it is at its maximum in 2010.

When considering the smaller spatial scales (sub-reach, beaver dam) there is great variability in terms of losses and gains that are not fully understood from the reach scale observations in the study reach with beaver dams (Figs. 8 and 9, Table 4). This
15 variability is due to many different mechanisms occurring in and around beaver dams, including groundwater–surface water exchanges (Lautz and Siegel, 2006; Janzen and Westbrook, 2011). However, the sub-reach scale variability in this study (Fig. 9) was primarily due to high crest dams forcing year round overbank flow. Much of the overbank flow was either returned to the main channel through side channels or was diverted to the off-channel beaver ponds. These changes in flowpaths influenced the mass recovery in our tracer study in 2010, when the highest mass loss occurred in
20 sub-reaches with big beaver dams and multiple side channels. The dynamic activity of beaver, through construction and maintenance of dams, and natural seasonal changes in flow lead to a diverse range of hydrologic responses resulting in the spatial and temporal variability of gains and losses through the study reach. The dilution gaging results show that at the two points in time we sampled, sub-reach 2 transitioned from gaining to losing (Fig. 9). However, if groundwater and channel surface water elevation data are aggregated over a year, the same reach was shown to be dominantly gaining over the study period (Fig. 8). These opposing results highlight the importance of temporal scale
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and repeated measurements, and also show that the differences in measurement techniques can lead to different conclusions as discussed within Schmadel et al. (2014).

Our temperature results demonstrate the considerable spatial and temporal variability in stream temperature caused by beaver dams. We captured the warming effect at the reach scale over a period of three years (Figs. 4 and 5). However, the data at this scale do not portray the thermal heterogeneity illustrated by the beaver dam scale temperatures (Figs. 10 and 11). Similarly, the temporal scale is of importance when determining impacts of beaver dams. For example, the 5 min-interval temperature record captured temperature fluctuations during the day that may play an important role in fish habitat management and restoration (Fig. 6c and d). This daily variability would not be captured if only daily averages or instantaneous measurements were recorded. The lag times in peak temperatures from 2008 to 2010 (more apparent at shorter temporal scales (Supplement Fig. 1) are likely due to different flow conditions, air temperatures, solar radiation, precipitation, and channel morphology.

To understand the significance of simultaneously considering the spatial and temporal scale of measurements, Figs. 10 and 11 illustrate the temperature variability for five beaver dams while providing a comparison between the dams. Individual beaver dams introduce more variability than that observed at the reach scale with warming and/or cooling effects during different times of the day. These individual responses are likely due to the diverse beaver dam morphology, size of the beaver dam, and size of the beaver pond (Fuller and Peckarsky, 2011; McGraw, 1987). However, considering a longer temporal scale, the temperature variability associated with a 24 h moving average falls within a measurement error ($\pm 0.2^{\circ}\text{C}$) (Fig. 11b).

Based on the expectation that a gaining reach should be cooling, it is important to discuss the different heat transfer mechanisms influencing instream temperature responses. It is well established that surface heat fluxes (shortwave radiation, incoming and outgoing longwave radiation, conduction/convection, and evaporation/condensation) and bed processes (bed conduction, groundwater/hyporheic exchanges) are the primary factors dictating stream temperature responses (e.g. Car-

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denas et al., 2014; Evans et al., 1998; Moore et al., 2005; Neilson et al., 2010a, b; Sinokrot and Stefan, 1993; Webb and Zhang, 1997; Westhoff et al., 2007; Younus et al., 2000). When considering the transition between pre and post-beaver colonization, the doubling of the channel surface area is critical because surface heat fluxes are scaled with the area (Neilson et al., 2010a). The influence of these fluxes on temperature is also dependent on the difference in the volume of water in the channel and the residence time within the study reach. Based on the observed temperature increases, the doubling of the surface area (Fig. 7, Table 3) and the tripling of the residence time (Table 4) negate the buffering effects of an almost quadrupled main channel water volume (Table 3) and the cooling effects associated with groundwater inflows. As found within other prior studies, the general downstream warming is due primarily to influences of solar radiation (Cook, 1940; Evans et al., 1998; Johnson, 2004; Webb and Zhang, 1997).

To further illustrate the thermal heterogeneity and complexity of flow paths resulting from beaver colonization, a thermal image of surface stream temperature in May 2012 shows that temperatures range from 11 to 18°C along the study reach (Supplement Fig. 4). It is most important to note the difference in the temperature ranges in areas with and without beaver ponds. Such thermal heterogeneity is typically overlooked when larger scale (e.g., reach scale) measurements are collected. From a stream restoration point of view, when beavers are used to restore riparian areas (Albert and Trimble, 2000; Barrett, 1999; Shields Jr. et al., 1995) and/or enhance fish habitat (Billman et al., 2013; Pollock et al., 2004), small spatial scales (e.g., sub-reach, beaver dam, and even microhabitat units) are key for understanding the influences on the aquatic ecosystem (e.g., Billman et al., 2013; Westbrook et al., 2011). This study emphasizes the need to understand the variability in flow and temperatures at different spatial and temporal scales. Furthermore, these data begin to provide an explanation as to why the current literature provides inconsistent information regarding the influences of beaver colonization.

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Although it is difficult to make any generalizations about the hydrologic and thermal impacts of beaver dams (e.g., beaver dams increase temperature), we measured an increased variability in flow and temperature that have been qualitatively discussed in previous studies. Our quantification of the variability across different spatial and temporal scales provides a context for better interpreting the inconsistent information found in the literature. In a given locality or under specific circumstances, we contend that the patterns of increasing variability in flows and temperatures should create and maintain more heterogeneous habitat that has a greater probability of providing multiple niches and supporting greater biodiversity. We believe that this observed hydrologic and thermal variability is an important and more generalizable attribute of beaver dams. Variability in temperature, flow properties, and the associated increase in microhabitat complexity are often restoration goals. However, if beaver is being considered as a restoration tool (e.g., Utah Beaver Management Plan), the importance of further understanding and predicting their impacts on stream systems at different spatial and temporal scales is a necessity. Based on these findings, future efforts in understanding the impacts of beaver dams on hydrologic and temperature regimes should begin by identifying the spatial and temporal scales of data required to address specific questions and/or restoration goals. Ultimately, more quantitative field and modeling studies are needed to fully understand impacts of beaver on stream ecosystems for the potential use of beaver as a restoration tool.

5 Conclusion

This study quantified the impacts of beaver on hydrologic and temperature regimes, as well as highlights the importance of understanding the spatial and temporal scales of those impacts. Based on the flow and temperature data we collected over period of pre- and post-beaver colonization, we found a general increase in stream discharge and stream temperatures at the reach scale. The reach transitioned from slightly losing in 2008 (pre-beaver colonization period) to gaining in 2010 (post-beaver, second year

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into beaver colonization). Similarly, we observed a downstream warming effect over the 3 year study period. We found that the reach scale hydrologic and temperature changes do not reflect the variability captured at smaller sub-reach and beaver dam scales. For example, temperature measurements at finer temporal scale (5 to 10 min records throughout each day) revealed significant within-day variability at smaller spatial scales not captured at the reach scale. Our most important and likely transferable findings are with regards to the increase in hydrologic and thermal variability that beaver dams produce. We captured natural variability of hydrologic and thermal processes at the sub-reach scale prior to beaver dam influences and show how this variability increased after beaver colonization. While some sub-reaches showed gaining trends from 2008 to 2010, some began losing due to flow being rerouted by dam construction. In addition, daily stream temperature variability increased from 2008 to 2010. Furthermore, these data illustrate the influence of individual beaver dams that can cumulatively contribute to the downstream warming and/or cooling. Such hydrologic and temperature variability would be lost if only reach scale measurements were collected. In the context of ecosystem impacts and potentially using beaver as a restoration tool, where habitat heterogeneity and increased system resilience is achieved through higher rates of biodiversity, we argue that quantifying the range and increase in variability may be far more important than measuring a minor and often inconsistent change in mean conditions.

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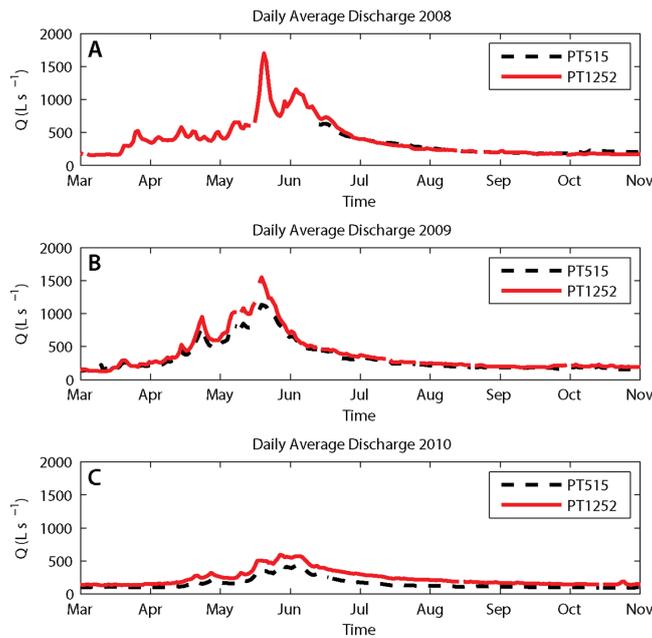


Figure 2. Daily average discharge estimated from continuous pressure transducer records spanning 2008–2010 (a–c). The black dashed line represents upstream, inflow conditions at PT515 and the red solid line represents downstream, outflow conditions at PT1252.

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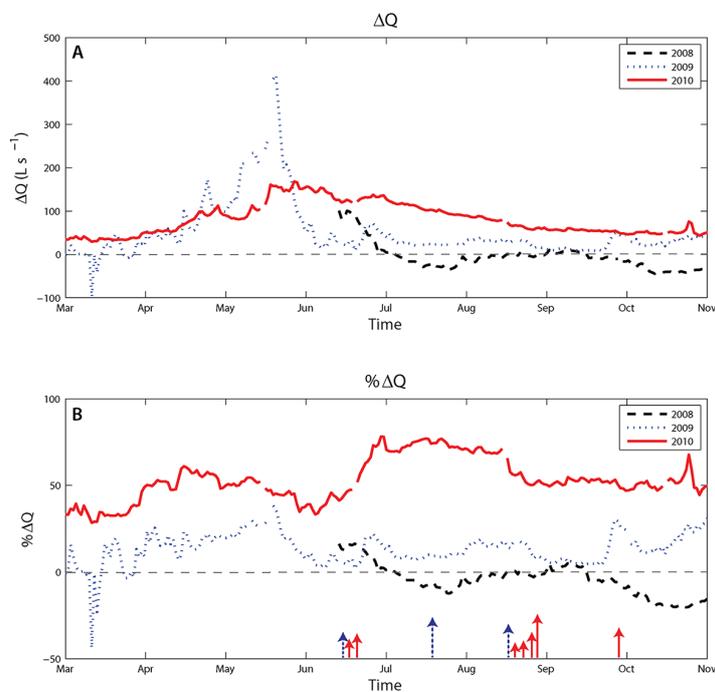


Figure 3. (a) Change in discharge over the study reach calculated from daily average flows where ΔQ is the discharge at PT1252 minus the upstream discharge at PT515. Positive values represent increases in discharge and negative values represent decreases in discharge. **(b)** $\% \Delta Q$ is the percent change relative to the discharge at PT515. Arrows represent time of individual beaver dam construction. Blue and red arrows correspond with year 2009 and 2010, respectively, while the arrow size is proportional to size of the dam.

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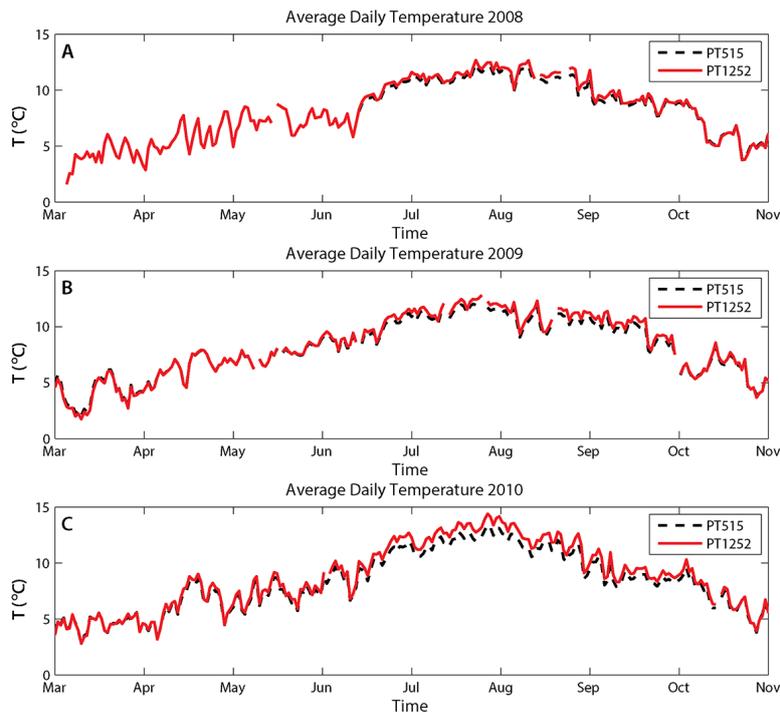


Figure 4. Average daily temperature (absolute) representing reach scale responses at PT515 (black dashed line) and PT1252 (red solid line) during 2008 (a), 2009 (b), and 2010 (c).

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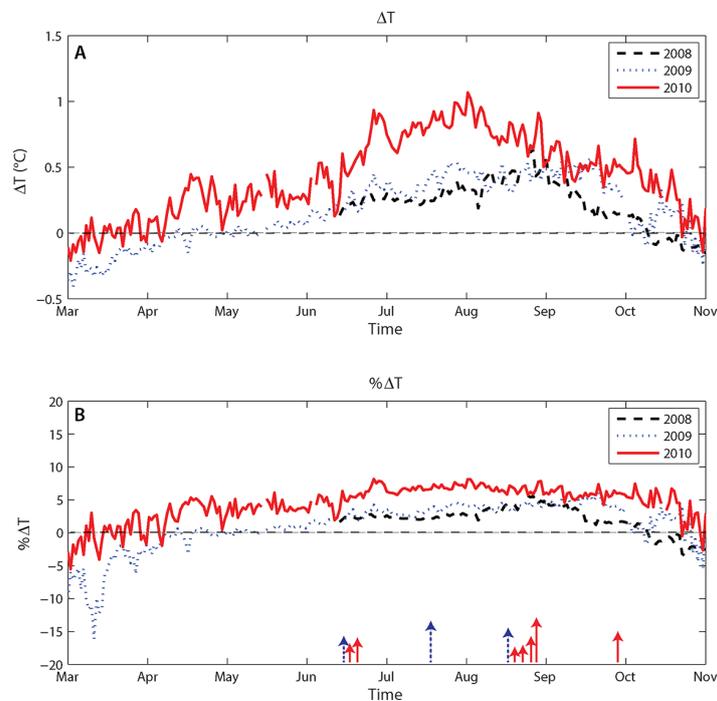


Figure 5. (a) Reach scale change in temperature (ΔT) calculated from temperatures at PT1252 minus the temperature at PT515. (b) % ΔT is the percent change relative to the temperature at PT515. Positive values represent warming throughout the reach and negative values represent cooling relative to the upstream boundary temperature at PT515. Arrows represent time of individual beaver dam construction. Blue and red arrows correspond with year 2009 and 2010, respectively, while arrow size is proportional to size of the dam.

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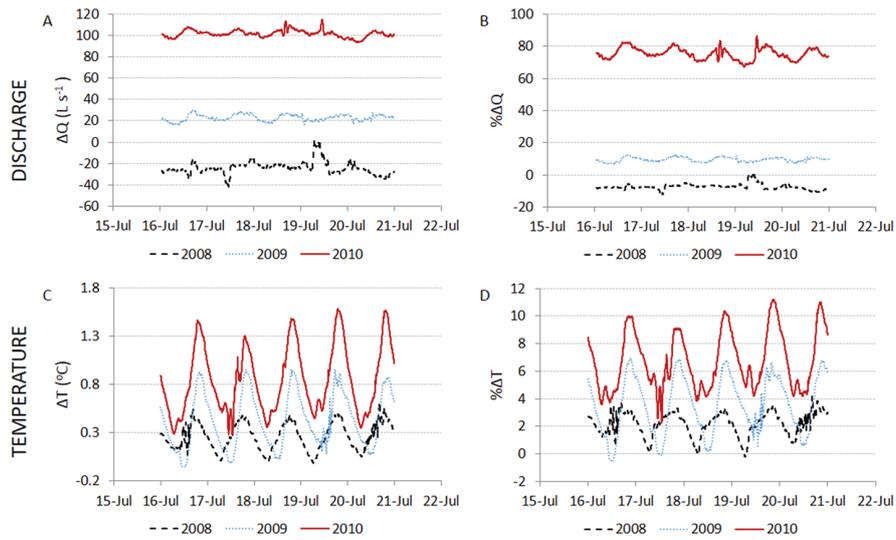


Figure 6. Change in discharge (ΔQ) and temperature (ΔT) over the study reach from 2008 to 2010. Five day period in July was used as an example of shorter temporal scale. The $\% \Delta Q$ and $\% \Delta T$ are relative to the discharge and temperature at the upstream PT515. The $\% \Delta Q$ were averaged over a one hour interval, while $\% \Delta T$ represents 5 min temperature values.

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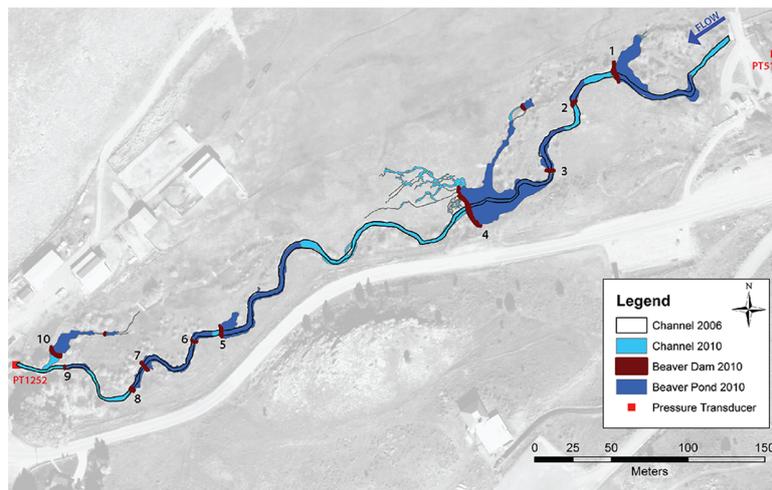


Figure 7. Aerial image of Curtis Creek study reach showing the channel in 2006 (before beaver colonization) and 2010 (after beaver colonization). New beaver dams, ponds, and side channels were created over the study period. The 2006 channel is outlined in a solid black line. Much of the original channel corresponds with the 2010 channel, however there is a significant increase in ponded water and side channels. The overall water surface area more than doubled from 2006 to 2010.

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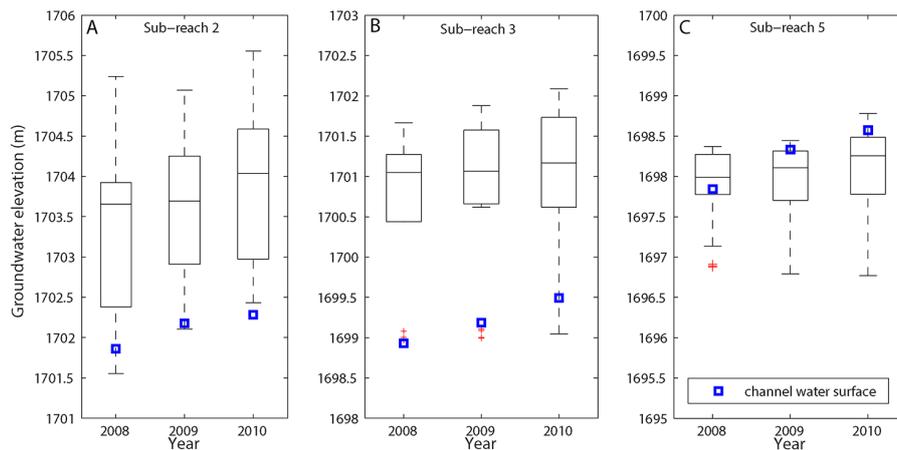


Figure 8. Groundwater elevation throughout the study reach grouped by individual sub-reaches and water surface elevation in the channel for each sub-reach. The water surface elevation in the channel represents the average yearly value for each sub-reach. There is a gradual increase in groundwater elevation and channel water surface elevation in all sub-reaches over the years.

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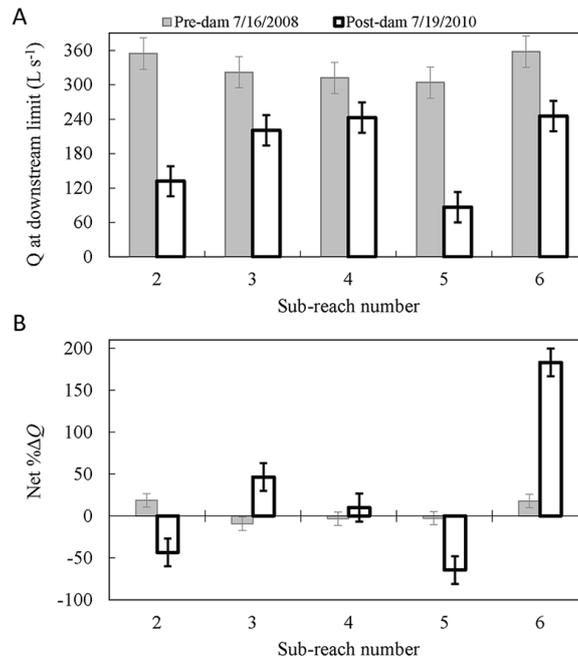


Figure 9. Sub-reach stream discharge (Q) estimates for 2008 and 2010 representing longitudinal flow variability before and after beaver colonization. $\% \Delta Q$ is calculated from flow at the end of the sub-reach minus the flow at the beginning of the sub-reach relative to the upstream value.

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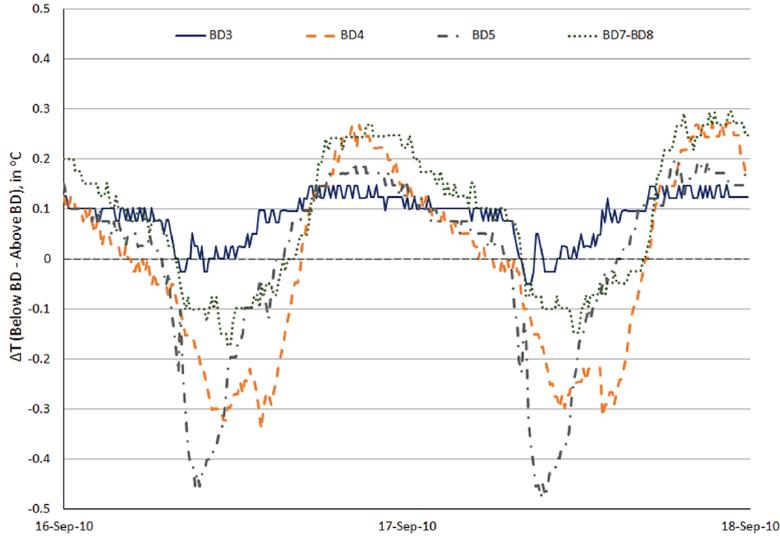


Figure 10. Spatial variability in stream temperature throughout individual beaver dams (BD). Temperature differences (ΔT) values were calculated based on 10 min temperature records from locations below and above the beaver dam and pond. These data illustrate that there can be measurable differences in temperatures at the beaver dam spatial scale that vary diurnally. It further shows the variability in temperature differences between the dams.

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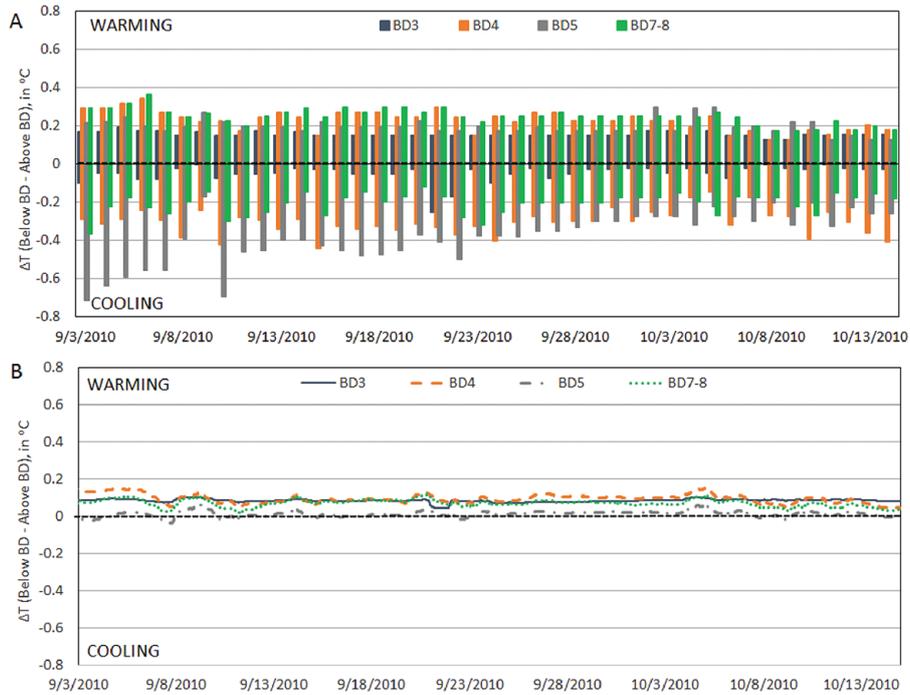


Figure 11. (a) Daily ranges (daily maximum minus daily minimum values) of temperature differences below and above (ΔT) each beaver dam (BD) based on 10 min temperature records. Beaver dam 7 and 8 were considered to be one complex. **(b)** 24 h moving average of ΔT .

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