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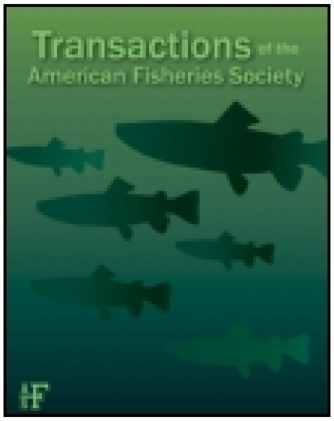

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ARTICLE

Do Beaver Dams Impede the Movement of Trout?

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Abstract
Dams created by North American beavers *Castor canadensis* (hereafter, "beavers") have numerous effects on stream habitat use by trout. Many of these changes to the stream are seen as positive, and many stream restoration projects seek either to reintroduce beavers or to mimic the habitat that they create. The extent to which beaver dams act as movement barriers to salmonids and whether successful dam passage differs among species are topics of frequent speculation and warrant further research. We investigated beaver dam passage by three trout species in two northern Utah streams. We captured 1,375 trout above and below 21 beaver dams and fitted them with PIT tags to establish whether fish passed the dams and to identify downstream and upstream passage; 187 individual trout were observed to make 481 passes of the 21 beaver dams. Native Bonneville Cutthroat Trout *Oncorhynchus clarkii utah* passed dams more frequently than nonnative Brown Trout *Salmo trutta* and nonnative Brook Trout *Salvelinus fontinalis*. We determined that spawn timing affected seasonal changes in dam passage for each species. Physical characteristics of dams, such as height and upstream location, affected the passage of each species. Movement behaviors of each trout species were also evaluated to help explain the observed patterns of dam passage. Our results suggest that beaver dams are not acting as movement barriers for Bonneville Cutthroat Trout or Brook Trout but may be impeding the movements of invasive Brown Trout.

Before settlement by Europeans, North American beavers *Castor canadensis* (hereafter, "beavers") played a significant role in shaping the habitats of North American fishes (Naiman et al. 1988). The extensive removal of beavers beginning in the 17th century affected native fish, such as Brook Trout *Salvelinus fontinalis* in the east and Cutthroat Trout *Oncorhynchus clarkii* in the west. With the recent recovery of beavers in some western streams (Naiman et al. 1988), the reintroduction of beavers into other streams, and restoration projects that seek to mimic the effects of beavers on stream processes (DeVries et al. 2012; Pollock et al. 2011), a better understanding of the interactions between beavers and native fish is needed. This understanding would permit improved choices and prioritization in how and where these types of restoration activities are used, especially in the presence of declining native populations of Cutthroat Trout (Budy et al. 2012) and Brook Trout (Marschall and Crowder 1996; Fausch 2008).

It has been suggested that the increased habitat complexity found in reaches (especially lower-stream-order reaches) with beaver dams benefits salmonid species in western North America (Neff 1957; Gard 1961; Collen and Gibson 2001; Kemp et al. 2012) and provides vital habitats for threatened or imperiled fish species. Deeper water with low velocities and high wood abundances provides important rearing habitat for Endangered Species Act (ESA)-listed Coho Salmon *O. kisutch* (Pollock et al. 2004). White and Rahel (2008) showed that complementation of different habitat types, including beaver ponds, supported the needs of multiple life stages of imperiled Bonneville Cutthroat

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Trout *O. clarkii utah* and increased their recruitment. Beaver ponds provide vital overwinter habitat in streams that otherwise may freeze throughout their entire depth (Cunjak 1996; Lindstrom and Hubert 2004). Collen and Gibson (2001) identified other benefits to fish dwelling within the beaver pond, such as cover created by the beaver lodge and food cache; stabilization of streamflows; increased sediment storage in the pond, thus creating spawning habitats below the dam; and an increase in lentic invertebrates. These benefits may also be exploited by numerous pool-dwelling, ESA-listed Pacific salmon (Murphy et al. 1989). We postulate that native fish are more likely to benefit from the habitat heterogeneity created by beavers if they are adept at passing beaver dams to access those different habitats.

Even in small streams, beaver dams can be up to 2.5 m tall, and it is logical that such dams might act as barriers to the upstream migration of fish (Kemp et al. 2012). However, the diversity of flow paths over, through, under, and around (e.g., side channels that act as fish ladders) such dams provides a number of plausible pathways for upstream movement (Schlosser 1995). Moreover, these flow paths change regularly with beaver maintenance and construction activities and with fluctuations in discharge.

Whether beaver dams act as barriers to fish and the extent to which they impede the movement of different species are questions in need of clarification. Kemp et al. (2012) reviewed 108 studies evaluating the effects of beaver dams on fish and fish habitat; beaver dams were cited as "barriers to fish movement" in 43% of the papers, and this was the most common adverse effect discussed. However, the putative negative effect of beaver dams as barriers was speculative in that 78% of the studies did not support this claim with data (Kemp et al. 2012).

The objective of our study was to evaluate whether trout can pass beaver dams. The Logan River, Utah, serves as an ideal study area, as it contains native Bonneville Cutthroat Trout that compete with two nonnative species—the Brook Trout and Brown Trout *Salmo trutta*—in beaver-altered habitats. Differences in passage behaviors among the three trout species may provide information that is crucial to the future conservation of Bonneville Cutthroat Trout. Knowledge of dam passage by trout may also have implications for fisheries and land managers in streams where beaver dams exist or where beaver dam surrogate structures are being implemented as a means of stream restoration (Pollock et al. 2011; DeVries et al. 2012).

STUDY SITE

Temple Fork (watershed area = 41.5 km^2) is a third-order tributary to the Logan River, and Spawn Creek (14.6 km^2) is a second-order tributary to Temple Fork (Figure 1). The Temple Fork watershed is a good analog for lower-order, montane trout streams in the intermountain west. The annual hydrograph consists of peak flows that are dominated by spring snowmelt and base flow (0.28–1.39 m^3/s) that is supported by spring flow (Seidel 2009). Peak streamflows usually occur in May to June

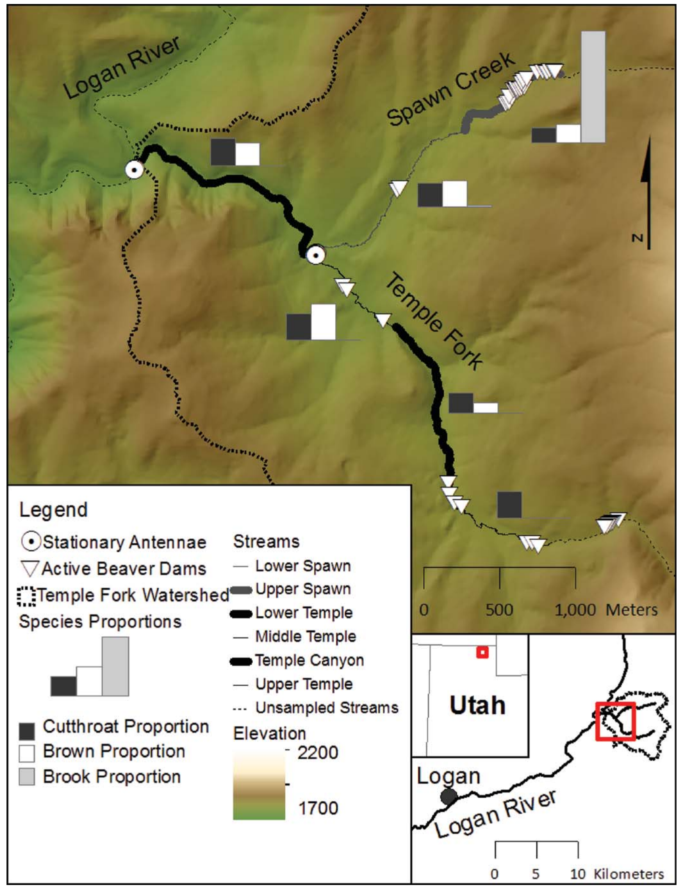

FIGURE 1. Map of the Temple Fork and Spawn Creek study area in Utah. Stream line widths and colors indicate different stream reaches. Bar graphs show the proportion of each trout species among the fish that were initially captured in each reach (Cutthroat = Bonneville Cutthroat Trout; Brown = Brown Trout; Brook = Brook Trout). Brook Trout were almost exclusively found in the upper reach of Spawn Creek. Only Bonneville Cutthroat Trout were found in the upper reach of Temple Fork. The uppermost beaver dams in each stream were not evaluated for fish passage in this study. [Figure available online in color.]

and are approximately five times base flow (de la Hoz Franco and Budy 2005; Seidel 2009). At base flow, wetted widths in reaches without beaver dams are approximately 5.0 m in Temple Fork above Spawn Creek and 2.5 m in Spawn Creek.

From 2008 to 2011, beavers maintained 27 dams along Temple Fork and Spawn Creek (Figures 2, 3). It is worth noting that just upstream of our study site boundary on Temple Fork, beavers built 12 new dams within a 200-m reach during 2012. Of the 21 beaver dams that were evaluated in this study, three were constructed during the study period and four others were breached or blown out during the 2011 spring runoff floods (Table 1). Of the four dams that were impacted by the 2011 floods, all were on Temple Fork: two dams (T3 and T9) were completely blown out and have not been repaired, while the other two (T4 and T8) had only minor breaches and have not been repaired. Many of the ponds in the upper portion of Spawn Creek are part of a major beaver dam complex that has been

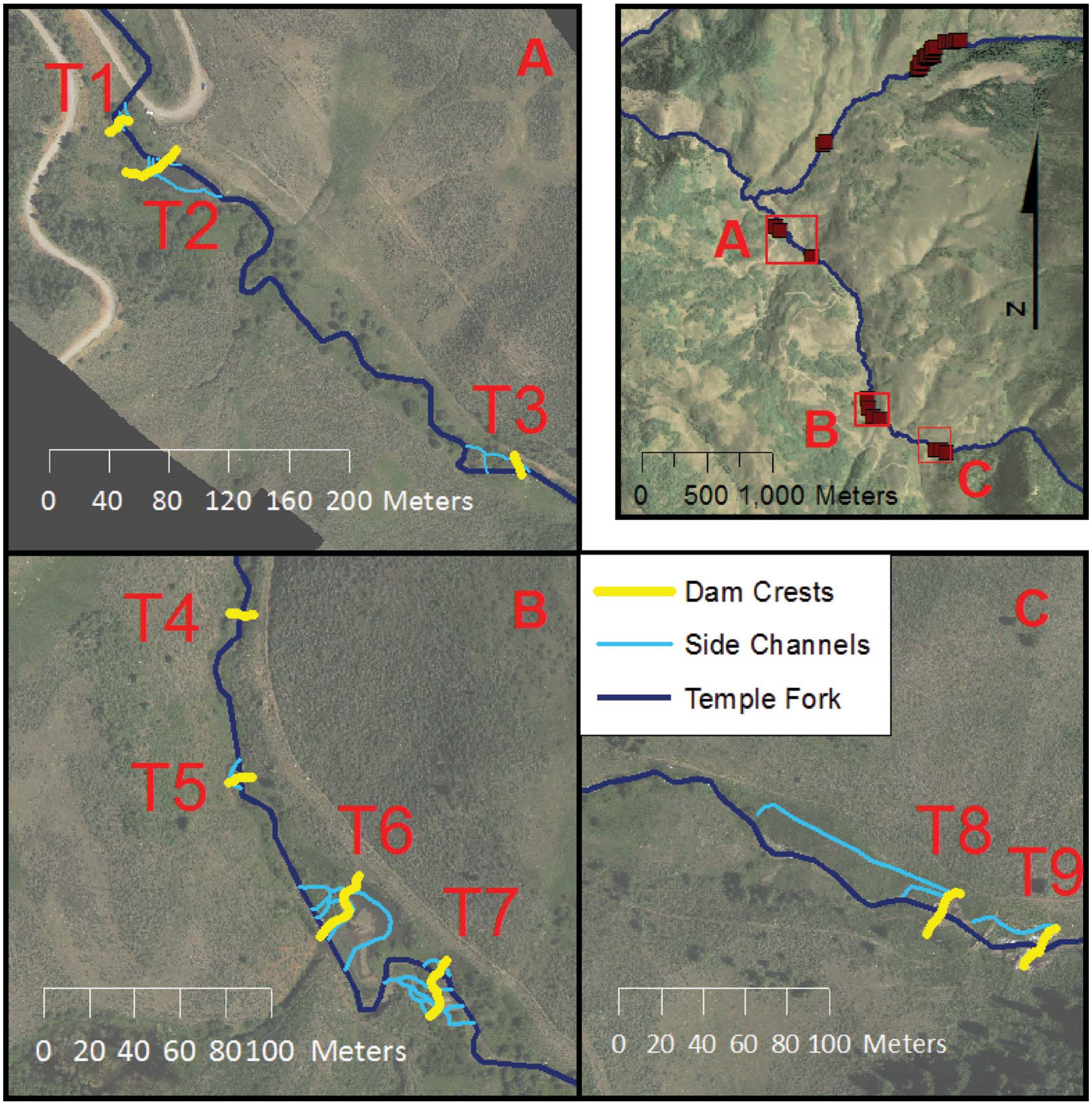

FIGURE 2. Locations of beaver dams in Temple Fork. Dams are numbered in the upstream direction; side channels are indicated (A, B, and C locations in the upper right panel correspond to panels A–C). Brown Trout were not observed above dam T4, and Brook Trout were not present in Temple Fork. [Figure available online in color.]

present for over 30 years (Bernard and Israelsen 1982). By contrast, the valley bottom road up Temple Fork, which was not removed until the mid-1990s, minimized development of beaver ponds in this area until recently. The uppermost dams on Spawn Creek and Temple Fork were not included in this study because they were above the area where fish were marked and they were not consistently scanned for fish presence.

METHODS

Between 2008 and 2011, we captured 1,375 trout in Spawn Creek and Temple Fork and fitted them with PIT tags, which permitted us to track unique fish (Moore 1992). Some fish that were originally tagged in the Logan River were also detected in the study streams, and these individuals were included in our study. Fish were captured during summer months by electrofishing and angling. Upon initial capture of a trout, a Biomark full-duplex, 12-mm PIT tag was placed subcutaneously behind the dorsal fin. The capture location was recorded with a handheld GPS unit. The numbers of tagged fish varied within and among streams (Table 2). In addition to their use in evaluating beaver dam passage by trout, these PIT-tagged fish were part of a larger study to evaluate trout movement, growth, and habitat use within these streams.

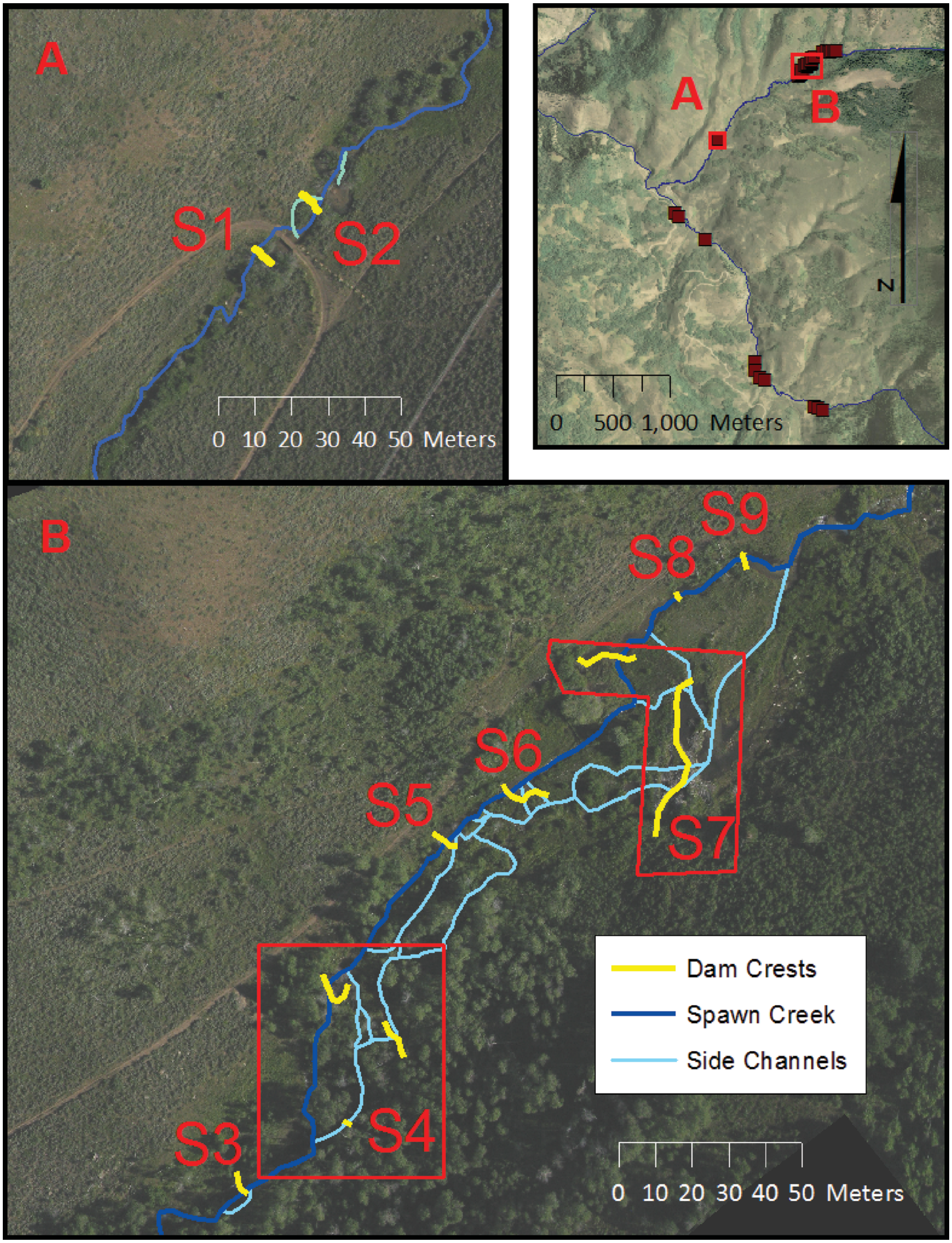

FIGURE 3. Locations of beaver dams in Spawn Creek. Dams are numbered in the upstream direction; side channels are indicated (A and B locations in the upper right panel correspond to panels A, B). Dams S4 and S7 have left and right components. Brown Trout did not pass S7. [Figure available online in color.]

TABLE 1. Physical characteristics of beaver dams evaluated in Temple Fork and Spawn Creek, Utah. Dam codes correspond to those in Figures 2 and 3 (in the dam code, T = Temple Fork, S = Spawn Creek; R = right component, L = left component). "Height" is beaver dam height measured from the downstream side of the dam. "Max depth" is the maximum depth of the pool created by the beaver dam. "Flow" is the dominant flow path at the dam during spring 2011 (over = flow spilled over the dam; under = flow spilled at the bottom of the dam; through = flow leaked through the entire structure; all = all flow paths). "Side channels" indicates whether there was a path of water that circumvented the dam structure. "Dam built" indicates the period in which beavers started construction on a dam. Two dams failed during the spring of 2011.

Dam code	Height (cm)	Max depth (cm)	Flow	Side channels?	Dam built
T1	35	50	Over	Yes	Pre-study
T2	200	125	Under	Yes	Pre-study
T3	100	60	Under	Yes	Pre-study; failed in 2011
T4	50	50	Over	No	Pre-study
T5	75	100	Through	Yes	Pre-study
T6	125	75	Under	Yes	Pre-study
T7	90	75	Under	Yes	Pre-study
T8	125	85	Through	Yes	Pre-study
T9	200	125	Under	Yes	Pre-study; failed in 2011
S1	110	70	All	No	Nov 2010
S2	135	70	All	Yes	Nov 2010
S3	60	25	Over	Yes	Pre-study
S4R1	70	40	Under	No	Pre-study
S4R2	65	60	Under	Yes	Pre-study
S4L	65	65	All	Yes	Pre-study
S5	110	50	All	Yes	Pre-study
S6	75	40	All	Yes	Pre-study
S7R	85	55	Under	Yes	Pre-study
S7L	100	15	All	Yes	Pre-study
S8	75	65	All	No	June 2010
S9	120	85	All	Yes	Pre-study

To determine whether the fish passed beaver dams, we used a variety of spatially explicit data collected for individual fish. The GPS coordinates of fish locations were taken from capture locations, stationary antennas, and mobile antennas. Stationary PIT tag antennas were located (1) in Temple Fork just upstream from its confluence with the Logan River, (2) in Temple Fork just upstream from its confluence with Spawn Creek, and (3) in Spawn Creek just upstream from its junction with Temple Fork (Figure 1). The Temple Fork–Spawn Creek antenna array began operation in May 2009 and identified fish that moved into or out of the area with beaver ponds. Active scanning upstream of the stationary antennas in both creeks by using a mobile antenna commenced on a monthly basis in May 2009. Mobile efforts entailed one or two observers moving upstream with PIT tag receivers attached to a wand that detected fish in the stream. Detection of individual fish in this small stream system was aided by the use of two observers with mobile antennas to actively search all available habitat (Randall 2012). During mobile scanning, locations of tagged fish were determined by synchronizing the location of a handheld GPS unit when each fish was recorded by the PIT tag receiver.

TABLE 2. Numbers of trout that were captured and tagged during each year and in each study stream. Tagging numbers were lower in 2011 due to near-record-high flows. Some trout were tagged in the Logan River and migrated into the study streams.

Year or stream	Bonneville Cutthroat Trout	Brown Trout	Brook Trout
2008	39	3	1
2009	491	161	66
2010	478	199	22
2011	150	60	62
Temple Fork	602	190	NA
Spawn Creek	308	124	151
Logan River	248	109	NA

Initial and resight locations of trout were plotted by snapping the GPS point to the nearest location on a stream layer that was digitized from 1-m aerial imagery using ArcGIS version 10.0. A fish was designated as having passed a beaver dam if we recorded that fish at locations both above and below a given dam. Each pass was summarized by pass direction, dam, and species. Statistical differences in beaver dam passes among the trout species were determined by comparing the number of dam passes made by each species against the expected number of dam passes based on the proportional representation of each species among the tagged fish. We used a chi-square test to determine whether passage differed among the species. The null hypothesis was that the number of passes for a given species reflected the proportion of tagged fish of that species. The expected number of passes for a given species was calculated by multiplying the total number of passes (i.e., for fish of all species) by that species' proportion among the tagged fish. This was done for both streams (overall) as well as for each stream. Additionally, we evaluated whether fish passage at a beaver dam was equally likely to occur in upstream and downstream directions.

Movement direction (upstream or downstream) was determined based on the locations and dates of the observations. The date of fish passage at a beaver dam was estimated by assigning the month representing the midpoint between two successive observations. For situations in which the period between the two observations exceeded 6 months, we disregarded those data in our evaluation of fish movement timing. The null hypothesis for fish movement was that movement was independent of month.

To determine whether dam passage was affected by differences in the propensity of each trout species to move, we summed the absolute values of minimum observed distances traveled by each individual fish over all observations. These sums provide information on minimum travel distances because we only recorded movement between two observations and not actual fish movement during unobserved periods. The total movement distances of each fish were used to determine the median of total movement distance for each species.

To determine the size of fish that passed beaver dams, fish length on the predicted date of dam passage was estimated. Growth in length (TL; mm/d) was based on all fish that had been captured multiple times and was calculated by dividing the observed growth by the time period between captures. Daily growth rates were calculated for each species. Average growth rates were applied to the length of time between the most recent capture event and the estimated date of beaver dam passage to determine the length of each fish at the time of passage. To reduce error with these predictions, we used size-class distributions consisting of 50-mm bins ($<$150, 151–200, 210–250, 251–300, and $>$300 mm). The size-classes for the tagged population of each species and the size-classes of fish that passed dams were compared by using a chi-square test.

The physical characteristics of the beaver dams within both streams were determined during spring 2011. Attributes that were recorded included dam height (from the streambed on the downstream side), maximum pond depth, and whether side channels were present (Figure 4). In addition, side channels and dam crests were mapped as polylines, and the upstream backwater of the pond from the dam was mapped as a point with a Juniper Archer map-grade GPS unit and ArcPad. Spawn

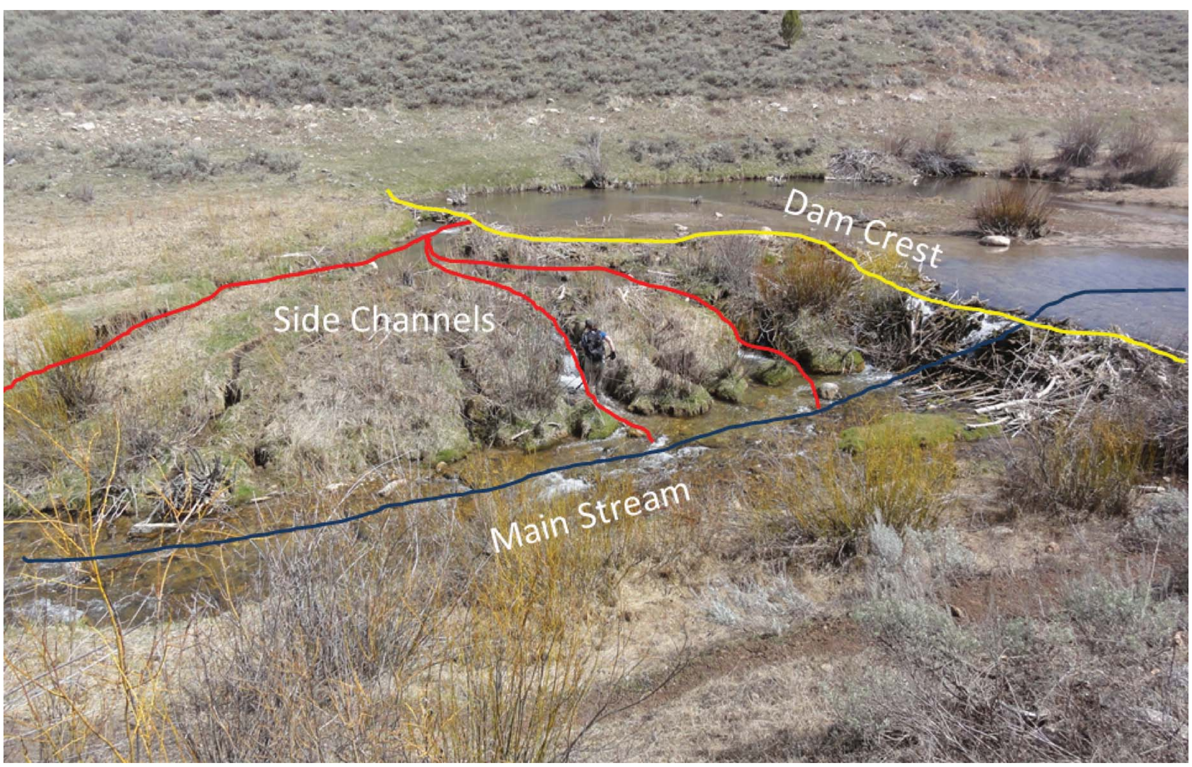

FIGURE 4. Photo of Temple Fork beaver dam 6 (T6). This dam has been in place since 2004 and contains multiple side channels; it was passed in both directions (upstream and downstream) by Bonneville Cutthroat Trout. [Figure available online in color.]

Creek dam 4 (S4) represented a set of three dams built on two channels (Figure 3). These dams were grouped for the analysis to avoid ambiguities arising from the fact that fish located above and below this complex could have passed the dams in either channel. A similar situation occurred at Spawn Creek dam 7 (S7). For each group of dams, the dam with the shortest height was used in the analysis of dam height.

We used linear regression to determine which beaver dam characteristics affected fish passage at the dams. We assumed that dam height, stream (Spawn Creek or Temple Fork), and side channels (present or absent) would be the primary dam characteristics governing fish passage. As such, we considered six models explaining passage by each trout species: (1) passage was affected by dam height; (2) passage was affected by the presence of a side channel around the dam; (3) passage was affected by dam number, which reflected dam position in the stream (i.e., higher numbers, such as T7 or S9, represented dams that were located further upstream); (4) passage was affected by dam height, with separate intercepts for each stream; (5) passage was affected by the presence of a side channel, with separate intercepts for each stream; and (6) passage was affected by dam number, with different intercepts for each stream. We used these models to evaluate all passes as well as only upstream passes. Because five of the dams (T3, T9, S1, S2, and S8) were not in place for the entire time frame of the study, the number of fish that would have passed each of those dams was estimated by expanding the number of fish detected as passing a dam to the 3.5-year study period. The best model for each species was chosen by using Akaike's information criterion corrected for small sample size (AIC_c; package MuMIn in R software; Barton 2012). The best model was averaged across all models for which AIC_c values differed by less than 2.0 (Burnham and Anderson 2002). An attribute with a model weight of 1.0 meant that it was included in all competing models. The closer a model weight was to 0.0, the less evidence that inclusion of the attribute improved the understanding of the data. We present adjusted R^2 values for the best model to reflect the explained variation in the data.

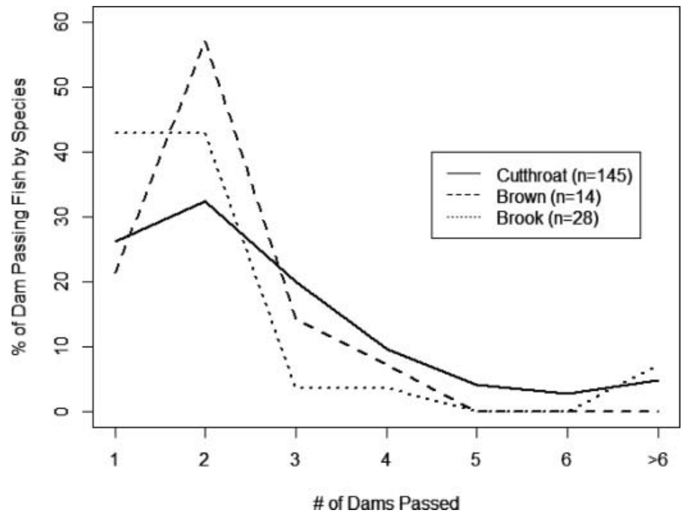

FIGURE 5. Number of beaver dams that were passed by tagged trout within Temple Fork and Spawn Creek (Cutthroat = Bonneville Cutthroat Trout; Brown = Brown Trout; Brook = Brook Trout). This graph only includes fish that passed at least one dam in any direction; it excludes the 84.1% of Bonneville Cutthroat Trout, 95.5% of Brown Trout, and 81.3% of Brook Trout that were never detected as passing any beaver dam.

RESULTS

We recorded 481 individual passage events by trout at beaver dams. Of those passes, 53 were single passes by unique individuals, whereas the remaining 428 passes were from fish that passed multiple dams (Figure 5). Overall, passage at beaver dams differed significantly among the three species ($P < 0.001$; Table 3). Relative to each species' proportional representation among the tagged fish, Bonneville Cutthroat Trout were more likely to pass beaver dams, while Brown Trout were less likely to pass dams. Brook Trout passed dams as often as expected given the number of tagged fish.

Among the fish that were tagged in Temple Fork and Spawn Creek, at least 15.9% of the Bonneville Cutthroat Trout, 4.5% of the Brown Trout, and 18.7% of the Brook Trout passed at least one dam. These values represent minimum estimates because (1) not all tagged fish were relocated and (2) some fish could have moved over a dam and back to their previous location between detections and thus would not have been recorded as passing the dam. Of the fish that passed at least one dam, the majority were detected as exhibiting passage events at two or more dams (Figure 5).

TABLE 3. Beaver dam passage by the three trout species in Temple Fork, in Spawn Creek, and overall (both streams). The total number of passes in both upstream and downstream directions is shown, along with the number expected (Exp; in parentheses) based on the number of tagged fish. The P-values are the results of chi-square tests.

	Species			
Location	Bonneville Cutthroat Trout (Exp)	Brown Trout (Exp)	Brook Trout (Exp)	P-value
Overall	394 (312)	29 (107)	58 (55)	<0.001
Temple Fork	251 (197)	8 (62)	NA	<0.001
Spawn Creek	143 (112)	21 (45)	58 (55)	<0.001

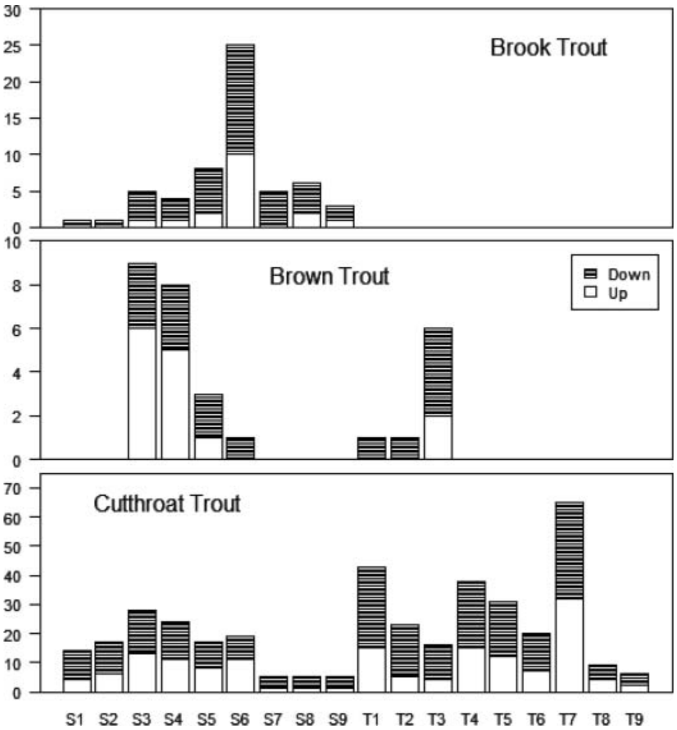

FIGURE 6. Direction of movement (downstream or upstream) by tagged trout at each of the beaver dams studied in Temple Fork (T1–T9) and Spawn Creek (S1–S9; see Figures 2, 3 and Table 2). For each stream, the *x*-axis presents dams in order from downstream to upstream. Note that the scale of the *y*-axis (number of passes) differs among species.

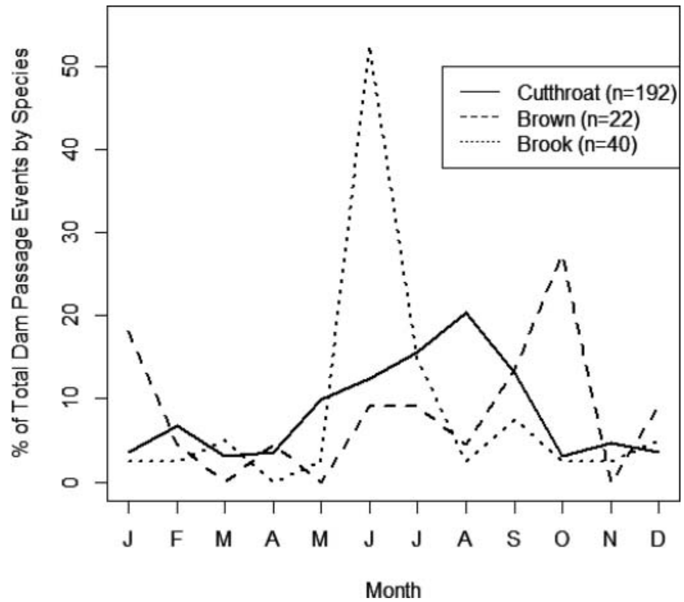

FIGURE 7. Timing of beaver dam passage events (in both upstream and downstream directions) by each trout species within Temple Fork and Spawn Creek (Cutthroat = Bonneville Cutthroat Trout; Brown = Brown Trout; Brook = Brook Trout). Only fish that had repeat observations within 6 months and that passed a dam are included in this figure. The month of passage was determined based on the middle date between two successive resight events; passage events that were separated by a period greater than 6 months were not used. Percentage of dam passes was calculated separately for each species (i.e., the total for each species sums to 100%).

Every evaluated dam was passed by trout, and each dam was associated with both upstream and downstream passage events (Figure 6). We found that Bonneville Cutthroat Trout and Brook Trout were significantly ($P < 0.001$) more likely to move downstream over dams than to move upstream. The few Brown Trout that we detected as moving past dams seemed to have an equal likelihood of moving upstream and moving downstream.

Timing of fish movement differed among the trout species (Figure 7). Bonneville Cutthroat Trout passed beaver dams more often than expected from May to September and less often than expected during the remaining months ($P < 0.001$). Brown Trout passed dams more often than expected in January, September, and October and less often than expected during the remaining months ($P = 0.053$). Brook Trout passed dams more often than expected in June and July and less often than expected in other months ($P < 0.001$).

Dam passage could be partially explained by the difference in movement proclivities among species. The median movement distance of fish tagged within the study area was 227 m for Bonneville Cutthroat Trout, 48 m for Brown Trout, and 8 m for Brook Trout. The high median movement distance of Bonneville Cutthroat Trout and the extended tail of their movement distribution (Figure 8) corresponded to the more frequent dam passage of this species. The lower median movement distance and narrower movement distribution for Brown Trout could partially explain their lower frequency of beaver dam passage. The very limited distance traveled by Brook Trout did not correspond well with their dam passage counts in Spawn Creek. The combination of a low movement distance with a relatively high frequency of dam passage indicates the redistribution of Brook Trout within a dam complex rather than passage at multiple dams related to longer migratory movements.

The sizes of fish that passed beaver dams (upstream and downstream passes combined) differed by species. Our results indicate that for Bonneville Cutthroat Trout, fewer fish smaller than 200 mm and more fish greater than 300 mm passed dams than would be expected based on the size-class distribution of this population (chi-square test: $P \leq 0.001$). The size of Brown Trout that passed dams was different than expected based on the population's size-class distribution ($P = 0.011$). The number of Brown Trout larger than 300 mm that passed dams was lower than expected. In contrast, Brown Trout in the 201–250-mm size-class passed dams nearly 2.5 times more often than expected. Size was not related to dam passage for Brook Trout ($P = 0.70$).

Physical attributes of individual beaver dams differed slightly between the two evaluated streams (Table 1). Beaver ponds in Temple Fork were taller on average than those in Spawn Creek (111 cm versus 89 cm). The depths of pools formed by beaver

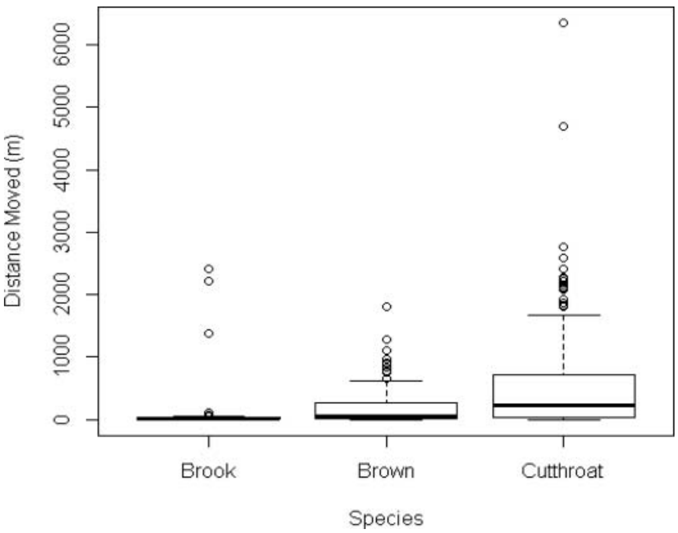

FIGURE 8. Movement distance by trout species within Temple Fork and Spawn Creek (Brook = Brook Trout; Brown = Brown Trout; Cutthroat = Bonneville Cutthroat Trout). The line within each box represents the median; the ends of the box represent the 25th and 75th percentiles; whiskers represent 1.5 times the interquartile range; and circles represent outliers.

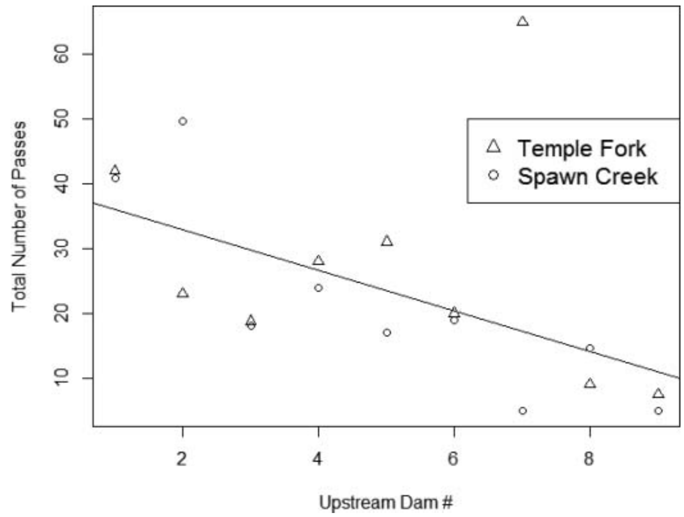

FIGURE 9. Graph depicting the best model for Bonneville Cutthroat Trout passage at beaver dams in Temple Fork and Spawn Creek. The *x*-axis presents dam number (T1–T9 or S1–S9) from downstream to upstream. The regression line shows that dams located further upstream were less likely to be passed. The number of passes at each dam includes both upstream and downstream passes and was adjusted for dams that were not in place during the entire study period.

ponds were greater in Temple Fork (83 cm) than in Spawn Creek (53 cm). Almost every beaver pond in both streams could be circumnavigated by a side channel; in Temple Fork, 89% of beaver ponds had side channels, whereas in Spawn Creek 75% of beaver ponds had side channels.

All of the study dams were passed by Bonneville Cutthroat Trout, regardless of the physical characteristics of the dam. Even the dams exceeding 2 m in height (T2 and T9) had 5 and 2 upstream passes, respectively, and 18 and 4 downstream passes, respectively.

The best model for total dam passage by Bonneville Cutthroat Trout included a single significant ($P = 0.03$; adjusted $R^2 = 0.22$) slope for dam number (model weight = 1.0; Figure 9). The further upstream a dam was in each river (i.e., as reflected by the dam number), the fewer fish passed that dam. The best model had the same negative slope for both streams. When only upstream passes were assessed for Bonneville Cutthroat Trout, three attributes were present in the best model ($R^2 = 0.21$): dam height (model weight = 0.44), dam number (model weight = 0.39), and side channel presence (model weight = 0.17). All of these predictors had a negative slope, indicating that dam passage decreased (1) as dam height increased, (2) as dam number increased, and (3) if side channels were present. Even though these predictors were included in the best model using AIC_c, the slope for each predictor was not significant ($P > 0.10$).

The best model for Brown Trout included dam number (model weight = 0.48) as well as dam height (model weight = 0.33) and side channel presence (model weight = 0.19). Passage at dams decreased as dam number increased and as dam height increased; passage increased at dams when side channels were absent. However, the best model did a poor job in explaining the data ($P > 0.10$; adjusted $R^2 = 0.06$). When only upstream passes of Brown Trout were considered, the same three attributes were present in the best model ($R^2 = 0.15$): dam height (model weight = 0.41), dam number (model weight = 0.33), and side channel presence (model weight = 0.26). Again, these predictors were not significant ($P > 0.10$).

We found that the best model for Brook Trout included stream (model weight = 1.0), dam number (model weight = 0.37), side channel presence (model weight = 0.37), and dam height (model weight = 0.26). The large weight due to stream was attributable to the absence of Brook Trout in Temple Fork. For Spawn Creek, the best model indicated that (1) dams higher in the system (i.e., higher dam number) were more likely to be passed; (2) the presence of side channels resulted in more Brook Trout passage events; and (3) as dam height increased, dam passage by Brook Trout decreased. This model was significant ($P = 0.02$; $R^2 = 0.35$), but this was mainly due to the lack of Brook Trout in Temple Fork. When only upstream passes were evaluated for Brook Trout, stream was identified as the most important predictor (model weight = 1.0) and the same three dam attributes were present in the best model ($R^2 = 0.29$): dam height (model weight = 0.30), dam number (model weight = 0.39), and side channel presence (model weight = 0.31). The slopes of dam number and side channel presence were both positive, indicating that dams with side channels and dams located further upstream were more likely to be passed by Brook Trout.

DISCUSSION

All three species of trout evaluated in our study passed beaver dams. Our observations show that Bonneville Cutthroat Trout and Brook Trout passed beaver dams more than expected. Brown Trout passed dams less than expected, and the majority of passes we observed were at smaller dams where Brown Trout concentrations were relatively high. Our results indicate that Bonneville Cutthroat Trout and Brook Trout are readily capable of negotiating large beaver dams. Brown Trout movements are more restricted, as shown by a lack of passage at larger dams. It appears that beaver dams benefit Bonneville Cutthroat Trout in the presence of Brown Trout by impeding the movements and migrations of Brown Trout and by keeping these nonnative fish out of upstream reaches. Still, questions remain regarding dam passage timing, movement behavior, specific mechanisms of dam passage, and restoration implications. We discuss each of these below.

Dam Passage Timing

We found that peak passage at beaver dams coincided with spawning migrations for Bonneville Cutthroat Trout and Brown Trout but not for Brook Trout. Bonneville Cutthroat Trout passed beaver dams at high frequencies during their spawning season in May to July (Seidel 2009), but their passage was also high in the months after spawning. Movement during these months spanned the breadth of streamflow conditions, ranging from peak flows to base flows. Movement in the upstream and downstream directions was approximately equal during May–August (54 upstream passes, 58 downstream passes), but movement was decidedly greater in the upstream direction during September (17 upstream passes, 8 downstream passes). Such movement patterns suggest that Bonneville Cutthroat Trout are seeking areas in which to recover after spawning. Movement during late summer indicates that these fish can pass beaver dams in both directions during times of the year with low base flows.

Elevated dam passage by Brown Trout coincided with spawning; the highest passage rate occurred just prior to their late-fall and early winter spawning season (Wood and Budy 2009). The number of dam passes made by Brown Trout in September and October was low (4 upstream passes, 5 downstream passes) because 95.5% of the Brown Trout tagged for this study were never detected as passing a beaver dam. Observed passage by Brown Trout during fall low-streamflow periods suggests that they are able to pass dams at that time. The low passage rate provides some support to the assertion that passage by Brown Trout at beaver dams is hindered by low flows (Schlosser and Kallemeyn 2000; Rosell et al. 2005; Taylor et al. 2010). However, our sample size of Brown Trout passing beaver dams was limited, so further research is needed to test whether Brown Trout are able to pass dams at low flows.

Brook Trout passed beaver dams in June, when streamflows were high and when Bonneville Cutthroat Trout were spawning. Movement during this time of year would be facilitated by side channels with sufficient flow and by increased flows passing over and through dams. Brook Trout movement in June may correspond to Bonneville Cutthroat Trout spawning; Brook Trout could be relocating to benefit from foraging on Bonneville Cutthroat Trout eggs and on insects that are displaced during spawning by the native trout. Although Brook Trout passage was not related to their fall spawning season, it could reflect an adaptive history of Brook Trout to redistribute during times of high flow (Peterson and Fausch 2003). Within the Brook Trout's native range, movement in relation to changing flows in small streams is likely related to rainfall events that are less predictable than the snowmelt-dominated runoff found in the Spawn Creek watershed (Scruton et al. 2003). Since this system has predictable snowmelt-mediated high-flow events, higher passage rates during these periods provide evidence that Brook Trout are being aided in dam passage by flashy, higher-peaked, rain-dominated flow events.

Dam-Influenced Movement Behaviors

Understanding beaver dam passage as it relates to movement patterns for each species is complicated. Behaviors inherent to each of these trout species could affect beaver dam passage, but the dams could be modifying these behaviors. Based on movement distances, Bonneville Cutthroat Trout encountered dams more frequently than Brook Trout or Brown Trout, yet approximately the same percentage of tagged Brook Trout passed at least one dam even though this species demonstrated the most restricted movement. All three species appeared to be adept at passing multiple dams (Figure 5). However, only 14 individual Brown Trout passed any dam at all. The majority of Brown Trout that passed more than one beaver dam did so in the upper Spawn Creek dam complex, where dams are closely spaced. This pattern of passing multiple dams is the same for Brook Trout in upper Spawn Creek. A higher number of individual Bonneville Cutthroat Trout ($n = 145$) passed at least one beaver dam, and a larger proportion of these fish passed more than two dams (Figure 5). Future research is needed to determine whether beaver dams restrict fish movement or whether fish exhibiting a higher propensity to migrate will pass multiple dams simply because they encounter more dams.

Beaver dams in downstream locations have the potential to restrict the movements of Brown Trout. In the Temple Fork area where Brown Trout are the dominant species, there are two large dams (T2 and T3) that were passed only seven times. We have yet to document a Brown Trout that has successfully passed T2 while moving in an upstream direction. This same pattern was seen in Spawn Creek at S1 and S2 (which were only in place during the last year of our study period), where we have yet to document any passage of Brown Trout. The lack of upstream passes by Brown Trout over these recently built beaver dams indicates that the dams have so far impeded the upstream movements of Brown Trout. Therefore, large dams in the downstream areas of these streams may slow the movement of Brown Trout into habitats that are occupied by Bonneville Cutthroat Trout.

The size-class distributions of fish that passed beaver dams differed among the three species. Brook Trout appeared to have the ability to pass dams regardless of fish size. In contrast, we observed only one large (>300-mm) Brown Trout passing a beaver dam in the downstream direction. The high number of 201–250-mm Brown Trout passing dams in both directions (4 upstream passes, 6 downstream passes) may be the result of an increase in spawning-related movement as the fish reached sexual maturity. This observation suggests that younger Brown Trout would be more able to invade stream systems with beaver ponds. The higher-than-expected passage by large sizes of Bonneville Cutthroat Trout supports the idea that size does not affect the passage of this species at beaver dams. The largest size-class of Bonneville Cutthroat Trout (>350 mm) passed dams in both directions (4 upstream passes, 2 downstream passes) over three times more often than expected based on their frequency in the tagged population.

The high level of passage by Bonneville Cutthroat Trout at S1 and S2 is remarkable considering the height of these dams and the relatively short duration for which they were in place. Bonneville Cutthroat Trout passed S1 14 times and passed S2 17 times, even though the two dams were in place only for the final 16 months of the study period. High passage frequency at S1 and S2 is necessary since most of the spawning locations within Spawn Creek are upstream of these dams. Recently, spawning activity by Bonneville Cutthroat Trout has increased within the 75 m above the pool of S2 (Brett B. Roper, unpublished data).

Dam Passage Mechanisms

To fully understand the mechanisms of beaver dam passage, broader samples of streams and beaver ponds are needed. Measuring the geometry of scour pools at the base of dams could contribute to an understanding of whether it is possible for a fish to leap over a dam. We need a better understanding of how and when fish pass beaver dams as well as the characteristics of dam passage attempts that are unsuccessful. Placement of stationary antennas along the face of the dam and in side channels could be configured to provide a more direct measurement of whether some fish are attempting to pass dams and whether they are successful. The evaluation of trout passage at beaver dams is complicated by the dynamic nature of these dams. Beavers frequently reengineer their habitat. Over the course of this study, beavers constructed two new dams (S1 and S2), and two dams failed (T3 and T9). Two dams (T2 and S9) increased in height and length, and their ponds increased in depth. For a number of dams, flow patterns around (side channels) and through (over the dam to under the dam) the dams also changed during the study period. These physical changes can alter whether and how fish movement is facilitated on a daily to annual basis. The dramatic and subtle changes we observed in beaver dam configuration suggest that dam characteristics must be examined more closely over time rather than measuring them at a single point in time (i.e., as was done in this study).

Restoration and Conservation Implications

Our findings of the apparent ease with which Bonneville Cutthroat Trout and Brook Trout passed beaver dams are of fundamental importance to restoration and conservation efforts aimed at restoring native trout populations. Our results refute the largely speculative concerns about beaver dams acting as migration barriers. This is timely in light of an increasing number of examples in which dam-building beavers are used to reconnect floodplains and restore fish habitat (e.g., Pollock et al. 2011) or in which beaver activity is mimicked to bring about desired changes in stream habitat (DeVries et al. 2012). Our results also have positive implications for the management and conservation of declining native Brook Trout in eastern North America (Petty et al. 2005). Reintroducing beavers or promoting the beaver as a conservation species—instead of treating them as a nuisance—may provide a means to conserve and restore Brook Trout populations. If nonnative Brown Trout movement is indeed constrained by the presence of beaver dams, then beaver reintroduction may have the added advantage of shifting the competitive advantage back to native trout species.

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