







RESEARCH ARTICLE

Partial dam removal restores passage for a threatened salmonid

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Funding information

Natural Sciences and Engineering Research Council of Canada

Abstract

Dams represent one of the major forms of river alteration. As these structures reach the end of their lifespan, they often require extensive refurbishments or removal. A small-scale water supply dam in Banff National Park (Alberta, Canada) was partially removed, creating a breach that allowed water to scour a new passage resembling a nature-like fishway. We investigated the permeability of the partially removed dam as a means of validating the conservation benefits of the partial dam removal. We quantified the proportion of bull trout (*Salvelinus confluentus*), a threatened species in Canada, that approached and passed the fishway using radio telemetry receiver stations. The proportion of bull trout that approached the fishway was low (37.0%; $N = 27$ of 73), but was consistent with upstream reference sites (33%; $N = 20$ of 60). For those that did approach, the proportion of bull trout that passed yielded a high passage efficiency (77.8%; $N = 21$ of 27 that approached). The probability that a fish passed the fishway was related to water depth and time of day. Bull trout were more likely to pass when water depths were high (>0.40 m), and at night. Passage duration ranged from 5-mins to 13-days, suggesting that this resident species used the fishway for a variety of purposes (e.g., station holding and foraging) and not just transiting. Some individuals underwent large-scale movements 2-km upstream (15.1%; $N = 11$ of 73), or 2-km downstream (2.7%; $N = 2$ of 73) following a successful passage event. This study provides new insight on how, in some instances, a breach in a dam can function as a nature-like fishway, accommodating year-round stream flows and providing hydraulic conditions suitable for fish passage without costly engineering or construction.

KEYWORDS

bull trout, connectivity, dam removal, fish, fish passage, nature-like fishway, telemetry

1 | INTRODUCTION

Human-made water diversion facilities (e.g., dams and water mills) have influenced stream connectivity for centuries. In the past few decades, their negative ecological and environmental effects have been recognized (e.g., Ligon, Dietrich, & Trush, 1995; Rosenberg et al., 1997; Weaver, 1963). Of particular concern are migrating fishes that may be limited or have lost complete connection to upstream

waters associated with spawning or rearing habitats (Lucas & Baras, 2000; Peter, 1998). Resident riverine fishes also require upstream and downstream access for food, habitat, and/or various life stage requirements (Burroughs, Hayes, Klomp, Hansen, & Mistak, 2010; Fullerton et al., 2010). Generally speaking, longitudinal connectivity in fluvial ecosystems is important for gene transfer, nutrient cycling, and population persistence (Pringle, 2003; Wiens, 2002). As such, contemporary perspectives on river restoration call for efforts to re-

establish or enhance ecological connectivity in fragmented systems (Cooke, Paukert, & Hogan, 2012; Jansson, Nilsson, & Malmqvist, 2007).

Negative effects arising from river fragmentation have been mitigated through strategies such as dam removal (ranging from partial removal to full removal) and construction of different types of fishways. Fishways have been used in various forms for decades (See Clay, 1994; Katopodis & Williams, 2012) and range in appearance from highly engineered structures (e.g., Denil or vertical slot fishways) to designs that mimic natural channels (i.e., nature-like fishways; Katopodis, Kells, & Acharya, 2001). Complete dam removal has become more common in the past few decades, especially for ageing structures, which pose a liability or are impractical to maintain due to high costs (Hart & Poff, 2002). However, a complete dam removal requires substantial efforts to not only remove the structure but also restore the system itself (e.g., Hart et al., 2002; Stanley & Doyle, 2002).

In some instances, complete dam removal is not possible due to limited funding or high environmental risk. In these scenarios, a partial dam removal may be a suitable alternative to a complete dam removal. During a partial removal, a section of the dam is breached (i.e., broken and/or removed) to enhance connectivity (e.g., Maloney, Dodd, Butler, & Wahl, 2008). If the passage through the breach no longer impedes the river, allows for a natural flow regime, and facilitates fish passage, the breach has the potential to act as a fishway and restore ecological connectivity. If the channel through the breach mimics the natural stream with minimal engineered infrastructure (i.e., has some natural substrate and depths similar to the areas immediately upstream and downstream of the dam), partial dam removal can be considered akin to a nature-like fishway. However, to our knowledge the use of dam breaches as fishways has not been evaluated (e.g., Maloney et al., 2008; Raabe & Hightower, 2014a, 2014b). Given that only a part of the dam is breached, channel constriction through the dam infrastructure is likely, and hydraulic conditions suitable for passage may not be possible without additional engineering.

The benefits of nature-like fishways vary, but often include habitat for resident species and familiar environments that may attract individuals to the entrances (Acharya, Kells, & Katopodis, 2000; Katopodis et al., 2001). Understanding how different species interact with nature-like fishways is of utmost importance for advancing the science of river restoration and for informing species at risk recovery. This is also imperative for ageing structures, where decommissioning could result in the partial or full removal of the obstruction leaving the streambed in various states of connectivity (e.g., Helms, Werneke, Gangloff, Hartfield, & Feminella, 2011).

The purpose of this study was to evaluate the conservation benefits of removing a portion of the Forty Mile Creek Dam in Banff National Park, Alberta, Canada. We defined the breach and the resulting channel through the breach, as a nature-like fishway, specifically a "rocky ramp fishway" (Katopodis et al., 2001). The Forty Mile Creek Dam was built in several stages, starting in the early 1900s, to create a reservoir, which was used as the source of Banff's drinking water and for fire protection. However, in the mid-1980s, the dam

ceased to have a function after deep-water wells were drilled in the area. The Town of Banff expressed interest in removing the dam as it was rendered a liability because of costs associated with continued dam maintenance (e.g., routine inspections and maintaining road access to the dam). The dam stood without purpose until 2013 when the access road was washed away during an exceptionally large flood. Managers wanted to invest funds to demolish the dam instead of rebuilding the access road. However, the budget was insufficient to remove the full concrete structure. Furthermore, removing the complete dam would require fluming the entire creek while simultaneously demolishing 8-m high and 2-m thick concrete walls.

An existing bypass channel within the dam acted as a flume managing the flow of Forty Mile Creek while the fishway was created in the spring of 2014 (Figure 1). The fishway was created in a section of the dam separate from the bypass channel and therefore could be constructed in a dry environment. This effort mitigated the need for complicated sediment control measures. The fishway itself was 50-m in length, with an average wetted width of 6.8-m. The downstream entrance and the interior of the fishway were characterized by natural substrate, whereas the upstream entrance was characterized by a cement slab with baffles. The mean velocity in the fishway taken in the fall was 0.11 m/s higher than the upstream channel and 0.9 m/s higher than the downstream channel, with a slope of 1.3% at the upstream entrance, 4.9% in the interior of the fishway, and 5.3% at the downstream entrance.

The objectives of this study were to: (a) assess the proportion of bull trout (*Salvelinus confluentus*) that approached the fishway, the proportion that successfully passed the fishway and their associated passage durations; (b) identify if biotic factors (i.e., fork length) or abiotic factors (i.e., water depth, water temperature, or time of year) influenced the probability of a fish to approach, probability of a fish to pass, or their passage duration; and (c) determine the distance travelled by fish following a passage event. Bull trout are currently protected under the Alberta Wildlife Act (Alberta Sustainable Resource Development, 2012) and have been assessed as threatened by Canada's Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2012). In Alberta, this species has declined in distribution by 33%, and populations in the Bow River Watershed have experienced the greatest declines due to habitat fragmentation (Alberta Sustainable Resource Development, 2012). In recognition of this, we believed that a restored system would likely benefit this threatened species and thus used them as our focal species in this study.

2 | METHODS

2.1 | Study site

This study was conducted in Forty Mile Creek in Banff National Park, Alberta. The dam is located approximately 2-km north of the town of Banff at 51°12'25.7" North and 115°34'51.9" West. The fishway is 50-m in length, with an average wetted width of 6.8-m. The average

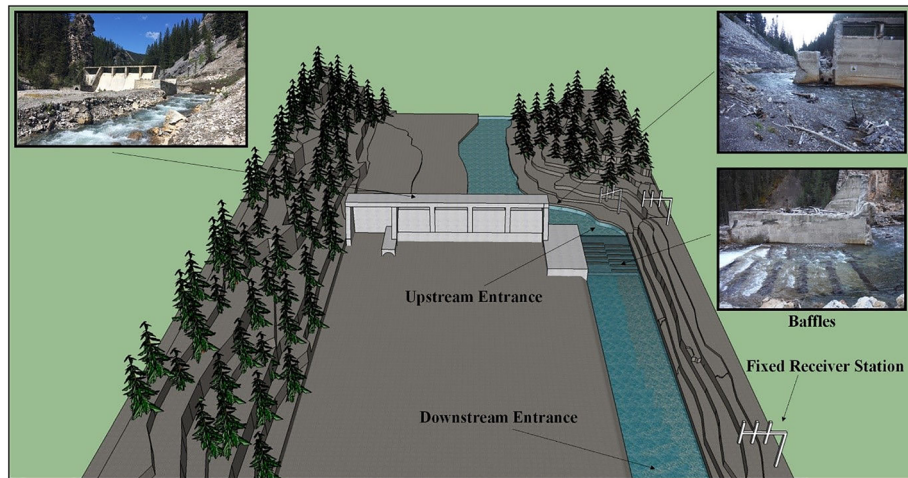


FIGURE 1 Schematic drawing of nature-like fishway in Forty Mile Creek, Banff National Park, the upstream entrance of the fishway is characterized by 11 evenly spaced baffles to control flow and reduce potential bank erosion, the interior of the fishway and downstream entrance are characterized by natural rocky substrate (e.g., cobble and boulders). Fixed receiver stations are represented by antennas at the upstream and downstream entrance of the fishway. The two antennas depicted at the upstream entrance account for one fixed receiver station, whereas the single antenna at the downstream entrance accounts for a separate fixed receiver station

wetted width of the channel upstream of the fishway was 8.8-m and downstream was 7.8-m. The fishway had minimal in-stream engineering and the upstream entrance was a concrete apron (8.5-m \times 10.4-m) from the foundation for the dam. The concrete apron was not a design feature of the fishway, yet it was required to maintain stability in the remaining structure. There were 11 evenly spaced baffles (0.38-m width, 3.8-m length, and 0.20-m spacing) added to the apron to disrupt laminar flow. The remaining length of the fishway had natural cobbles and boulders (2.5-cm to 71.3-cm diameter from intermediate axis), and boulder spacing (1.8-m to 7.8-m). The slope of the channel upstream was 1.3%, downstream was 4.9%, and within the fishway was 5.3% (see Figure 1). Overall, the structure was akin to a “rocky ramp fishway” (Katopodis et al., 2001). Mean velocity in the fishway was 0.11-m/s higher than the upstream channel and 0.9-m/s higher than the downstream channel, as measured in the fall.

2.2 | Experimental design

This study was conducted over a 9-month period between the fall of 2015 to the fall of 2016 (Oct 29 to November 15 2015 and March 13 to Oct 29 2016); no monitoring occurred in the winter months and the reason for this is explained later in this section. All fish were captured with a pulsed DC backpack electrofisher (Smith Root, Vancouver, WA). Once caught, fish were temporarily held in a stream-side holding facility (diameter = 243-cm, depth = 90-cm, and volume = 2839-L) supplied with ambient fresh water and oxygen. Fish were anaesthetised with clove oil (one part clove oil to 10 parts ethanol) and then were measured (mm), weighed (g), and transferred to a V-shaped surgery trough in the supine position to be implanted with a uniquely-coded radio transmitter (Sigma-Eight Inc., Markham, ON; Model PSC-I-80, 1.5-V, 150-mHz; 2.5 (length) \times 1.0-cm (width);

4.2-g (mass); 5-second ping rate; 9-month battery life). While fresh water was continuously pumped across their gills, a transmitter was inserted into the body cavity through a 10-mm incision made on the ventral body surface of the fish, posterior to the girdle, using a scalpel (number 3 blade, rounded cutting point). The incision was closed with two simple interrupted sutures (PDS II, 3/0, Ethicon Inc). Fish were then returned to a recovery tank and held for a short time (<15-mins) before their release. All transmitters were programmed to turn off during the winter (November 16, 2015–March 12, 2016) to conserve battery life (which ensured a 9-month monitoring period), and because large-scale movements were not expected during the winter months based on previous overwintering salmonid studies (Jakober, McMahon, Thurow, & Clancy, 1998; Muhlfeld, Glutting, Hunt, Daniels, & Marotz, 2005).

Bull trout movement was monitored within a 12-km reach of Forty Mile Creek from Oct 29 to November 15, 2015 and March 13 to Oct 29, 2016, using six fixed radio-telemetry receiver stations at a total of five locations. Each fixed receiver station included one solar powered SRX 800 radio tracking receiver (Lotek Wireless, Newmarket, ON) with one or two 3-element yagi antennas (AF Antronics, Urbana, IL) secured to a tree (e.g., pointed upstream or downstream) to record passage events. Two fixed receiver stations were used at the site of the nature-like fishway, one was placed at the upstream entrance with two antennas, one antenna recorded fish that approached or entered from upstream or exited the fishway from downstream. The second antenna was used to record movements in the interior of the fishway. The other station was placed at the downstream entrance with only one antenna to record fish that approached or entered from downstream or exited from upstream. Collectively, the two fixed receiver stations placed at the fishway were referred to as Site 3 (S3), which provided the opportunity to track a fish's location as it passed through the fishway in its entirety.

There were four additional fixed receiver stations at 2-km and 6-km distances from the dam (both upstream and downstream). The downstream stations were referred to as Site 1 (S1; 6-km downstream) and Site 2 (S2; 2-km downstream from the fishway). The two upstream sites referred to as Site 4 (S4; 2-km upstream) and Site 5 (S5; 6-km upstream from the fishway; see Figure 2). S1, S2, S4 and S5 had two yagi-antennas in both the upstream and downstream direction to quantify fish movement. Range testing was conducted on a weekly basis at S3 and a bi-weekly basis at S1, S2, S4 and S5. This involved recording the relative signal strength of a tester tag at pre-defined distances to allow for signal strength recordings to take place. The weekly and bi-weekly signal strength recordings allowed us to quantify movement based on the terminology defined in the *Data Analysis* section of this study.

Our study involved two groups of fish. We knew from historical sampling that bull trout existed at very low densities downstream of the dam (Parks Canada, unpublished data). Thus, we enhanced the downstream population by transporting upstream residents below the partial dam removal in order to improve sample sizes (Parks Canada, unpublished data). While translocating fish could have artificially stimulated upstream movement (i.e. "homing"; Cooke & Hinch, 2013), the goal was to quantify as many approaches and passages as possible, not document natural movements of resident bull trout. The translocated group of fish were caught upstream (~14 km upstream of the nature-like fishway) and transported within 1-km downstream of the fishway (S3) by helicopter in a Bambi bucket in the fall of 2015 ($N = 52$; October, 29–30, 2015; Fork Length (FL), 180-mm to 317-mm; 143-g to 250-g) and spring of

2016 ($N = 21$; May 2–3, 2016; Fork Length (FL), 210-mm to 320-mm; 136-g to 264-g) where they were tagged and released.

A reference group of non-translocated fish ($N = 60$; October 29–November 3, 2015, FL, 238-mm to 388-mm; 128-g to 354-g) were caught, tagged, and released within 1-km downstream of the upstream fixed receiver stations (S4 and S5; released within ~100-m of their capture site). This approach allowed us to compare movement at the reference sites (S4, S5) with the fishway (S3) as a measure of fishway permeability. The upstream (S4, S5) and downstream sites (S1, S2) also provided a method of quantifying coarse-scale movement of fish following a passage event (2-km or 6-km upstream or downstream).

Water level loggers (model U20 L, Onset Hobo Inc.) were used to collect depth (to the nearest cm) and temperature (to the nearest 0.02°C) at 30-min intervals within a 100-m distance downstream of the fishway. Passage events were matched with the closest water depths and temperature measurements in our dataset.

2.3 | Data analysis

A number of terms were developed to define bull trout movement activity at the fishway or upstream reference sites in order to meet all three of our objectives. We describe the terms related to each objective and then explain those that were used to calculate these values below.

For our first objective, we wished to assess the proportion of bull trout that approached, the proportion that passed the fishway, and their passage duration. For fishway studies, attraction efficiency is

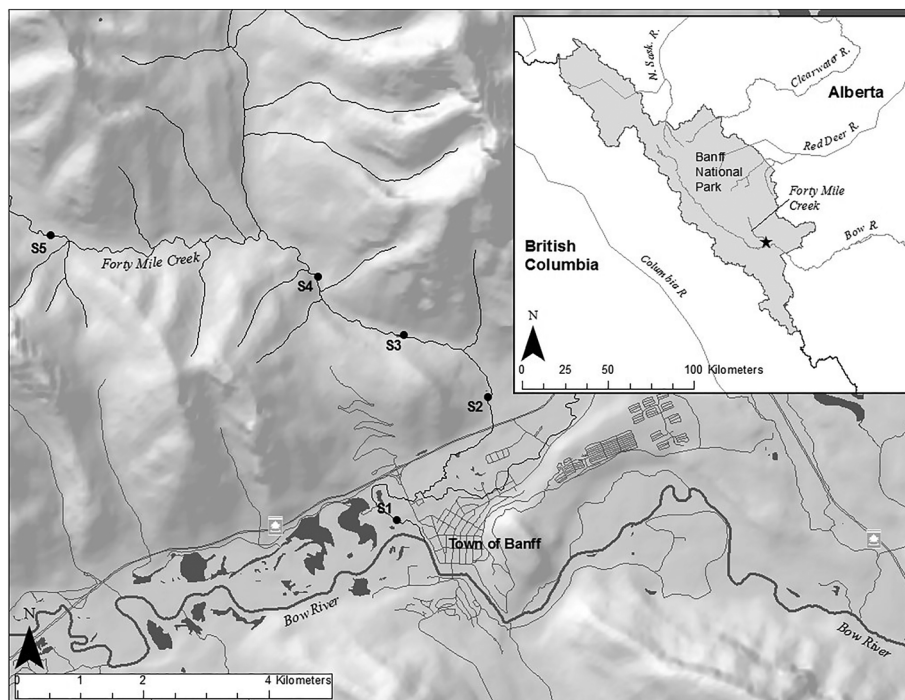


FIGURE 2 Radio telemetry fixed receiver stations along Forty Mile Creek in Banff National Park. S3 represents the site of the nature-like fishway, S4 and S2 are stations positioned 2 km upstream and downstream of the nature-like fishway, respectively, whereas S5 and S1 are 6 km upstream and downstream of the fishway, respectively

often used to assess “the proportion that approached” under natural fish movement. For our study, we recognized that this term would not be appropriate as the translocation of fish could have altered their natural behaviour (Cooke & Hinch, 2013). Instead, we used “proportion that approached” as its own term. The proportion that approached was calculated as the proportion of translocated fish that approached the fishway (within 10-m), in comparison with the total number of translocated, tagged, and released below the fishway. To assess the proportion of fish that passed the fishway, the common metric of “passage efficiency” was used, which was calculated as the proportion of translocated fish that passed through the fishway in comparison with the proportion of fish that approached the fishway.

An “approach” event was defined as a fish that was recorded within 10-m of the upstream or downstream entrance of the fishway or reference sites based on signal strengths. An “enter” event was the time in which a fish’s presence corresponded with an entrance into the fishway based on signal strengths. An “exit” event was when a fish passed through the fishway exit based on signal strengths. All signal strengths were based on range testing which was done on a weekly or bi-weekly basis as described previously. A “passage” event was when a fish successfully entered and exited the fishway, and the “passage duration” was the time span (provided as days:hours:minutes) of the passage event.

For our second objective, we intended to identify if biotic factors (i.e., fork length) or abiotic factors (i.e., water depth, water temperature, and season) influenced the probability of a fish to approach, the probability to pass, and the passage duration. “Probability” was used rather than “proportion” here for modeling purposes. For this objective, we modelled the total number of approach and passage events as well as passage duration as three separate models described in Section 2.4. Please note that we used the total number of upstream and downstream passages and passage durations in the analyses. We used the total number of events rather than total number of fish because translocated fish that approached and passed the fishway often did so more than once. Each of these events were matched with recordings for water depth, water temperature, and season, along with the fork length.

For our third objective, we wished to determine the distance travelled by fish following a passage event. This was calculated based on the number of approach events fish made at the upstream or downstream sites (throughout the 12-km reach) following their passage through the fishway. This was calculated in both the upstream and downstream direction using the same metrics described earlier in this section.

2.4 | Statistical analysis

To account for two separate release dates for translocated fish, we ran a chi-square test to compare the proportion of individuals that approached the fishway by release date. This analysis failed to detect a significant difference ($\chi^2 = 1.97$, $df = 1$, $p = 0.16$) between the two release groups, so we combined the groups for subsequent modelling purposes. In addition, fish that approached or passed the fishway were

likely to do so more than once making the data not independent (Heck, Thoma, & Tabata, 2010); as such, we incorporated fish ID as a random effect in mixed effects regression models. We used backward model selection with Akaike’s information criterion (AIC, Akaike, 1974) to objectively compare model fits and determine the most parsimonious model with the lowest AIC value. Prior to modelling, we used Pairwise Spearman’s rank correlation plots and variance inflation factors to assess multicollinearity between predictor variables. It was found that fish weight and fork length were collinear thus fish weight was removed from any further analyses, recognizing that fish length provided an equivalent metric to evaluate fish size. To describe the relationships between predictor variables in the models, we relied on predicted probabilities using the predict function in R statistical environment. For all models, residual plots were used to test for model assumptions that included normality and homogeneity of fixed effects residuals when applicable (R Studio version 3.3.3; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Where heterogeneity of variance between fixed effects was observed, the variance weighting function varIdent from the nlme package (Pinheiro, Bates, DebRoy, & Deepayan, 2014) was applied (Zuur et al., 2009).

To determine the probability to approach the fishway (and upstream reference sites), we ran a generalized linear mixed effects model (GLMM) with a binomial response (i.e., approach or no approach). Data were analysed with glmer function in lme4 package in R statistical environment (R Studio version 3.3.3; Bates, Maechler, Bolker, & Walker, 2015). This model included presence/absence data for each fish (i.e., translocated and non-translocated) by season and fork length at the upstream reference sites or nature-like fishway. Season was treated as a fixed factor with three levels: spring (March 21–June 20), summer (June 21–September 22), and fall (September 23 and October 30). We used spring as baseline from which the other seasons were compared. Location was treated as a fixed factor with two levels that included the treatment group (the fishway, S3) and upstream reference sites (S4 and S5). We compared a “location effect” for the purpose of identifying potential bias between the translocated and reference group in addition to testing “fishway permeability.” We also tested for the interaction between location and season to determine if fish approached the fishway at the same rate as the reference sites seasonally. Fish ID was included as a random effect as there could be more than one approach per fish. For seasons, we acknowledge that fall only captures 1 month in this model, whereas spring and summer capture 3 months. It was not possible to compare approaches on a monthly basis due to sample size limitations, however, we were able plot these relationships to illustrate that the seasonal effect can also be clearly shown at monthly intervals, which is likely interchangeable with changes in water level (see Figure 3).

To determine the probability to pass the fishway itself, we used a second binomial GLMM (passage or no passage) and tested for fixed effects of water depth, water temperature, time of day, passage direction (upstream or downstream), and fork length. In this model, we only included fish that entered the fishway in comparison with those that approached the fishway. Time of day was included as a binary predictor of night or day, which was based on local sunset and sunrise times

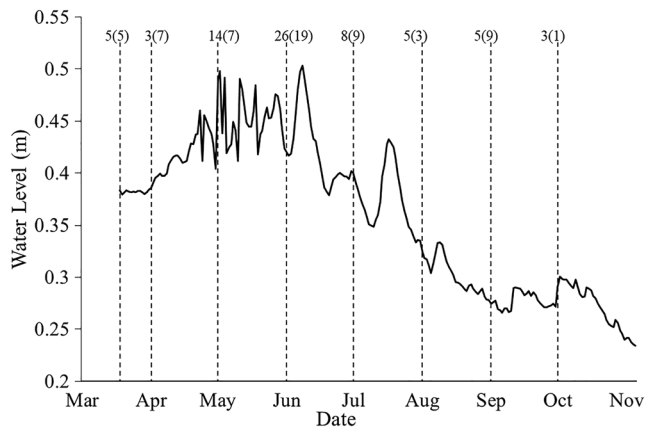


FIGURE 3 Water level measurements (interchangeable with season) for the nature-like fishway in Forty Mile Creek, Banff National Park (March–October 2016). The number of approach events are provided on a monthly basis at the fishway and the upstream control sites in brackets to show the relative changes in movement activity in the study system over varying water levels

in the geographic area. Water temperature and water depth were included as continuous predictors and fish ID was included as a random effect as there could be more than one passage per fish.

To determine if passage duration was influenced by biotic and/or abiotic factors, we used a linear mixed model. The response (i.e., passage duration) was modelled as a continuous variable with a Gaussian error distribution. We included: water depth and water temperature, time of day as a factor with two levels as night and day based on local sunrise and sunset times in the geographic area, and fork length in our model. Fish ID was specified as a random effect as there could be more than one passage duration per fish. Data were analysed using lme function in nlme package implemented in R statistical environment (R Studio version 3.3.3; Pinheiro et al., 2014).

3 | RESULTS

The proportion of translocated fish that approached the fishway was low (37%; 27 of 73 translocated individuals), but was consistent with upstream reference sites (33%; 20 of 60 non-translocated individuals). However, most translocated fish that approached the fishway also successfully passed through the fishway with a high passage efficiency (77.8%; 21 of 27 translocated individuals). In the event that a fish did not pass, it was likely not due to a lack of motivation because the velocities were well within the range that migrating salmonids are able to traverse (e.g., Weaver, 1963; Reiser, Huang, Beck, Gagner, & Jeanes, 2006).

Our best ranked model for probability to approach either the fishway or reference sites included the predictors of season, location (i.e., fishway or reference sites), fork length, and an interaction term between location * fork length. The interaction term between location and season was not included in the final model ($R^2 = 0.54$; $\Delta AIC_{full} = 314.7$, $\Delta AIC_{reduced} = 311.4$; Table 1). The AIC did not change when location was included or excluded from the model

TABLE 1 Parameter estimates for a generalized linear mixed effects model to understand the probability to approach the nature-like fishway and the upstream reference sites (i.e., S4 and S5) in Forty Mile Creek Banff National Park

	Estimate \pm SE	z value	p value
Intercept	-1.66 ± 0.44	-3.81	0.00014
Summer	-0.98 ± 0.38	2.61	0.0091
Fall	-2.59 ± 0.55	-4.68	$2.89e^{-06}$
Location	-0.58 ± 0.48	-0.12	0.90
Fork Length	-0.80 ± 0.39	-2.06	0.040
Fork Length * Location	1.32 ± 0.49	2.68	0.0074

($\Delta AIC_{reduced} = 311.4$). Including location in the model showed that the fishway was indeed as permeable as the upstream reference sites because the model rendered the location effect (i.e., reference sites vs. fishway) as insignificant ($p = 0.90$). There was a seasonal effect on the probability to approach, but the seasonal effect was consistent for both translocated and non-translocated fish (i.e., reference fish; interaction between location and season was insignificant; $p = 0.43$ (summer); 0.74 (fall)). The probability to approach was highest in the spring ($N = 41$, $N = 35$), followed by summer ($N = 21$, $N = 18$; $p = 0.009$), and further declined in the fall ($N = 4$, $N = 4$; $p = 2.9e^{-06}$; see Figure 3) when the fishway and reference sites were compared.

There was a significant interaction between location (i.e., the fishway and upstream reference sites) and fork length ($p = 0.007$), where the probability to approach for large non-translocated individuals was higher at the upstream reference sites (240-mm to 388-mm approached, 238-mm to 388-mm tagged), whereas the probability to approach was higher for small translocated individuals at the fishway (180-mm to 300-mm approached, 180-mm to 320-mm tagged; Figure 4). For example, the probability to approach the upstream

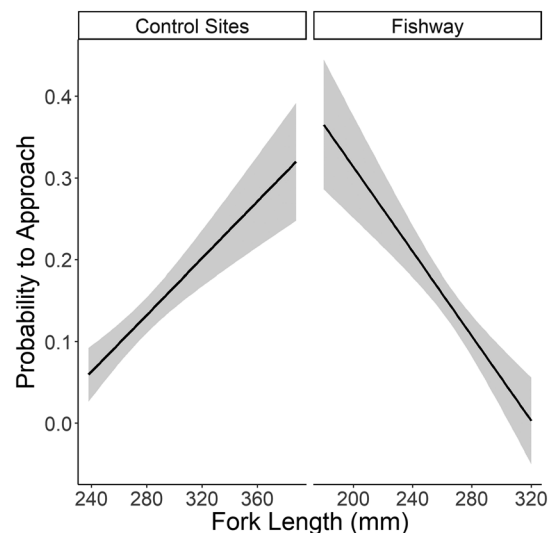


FIGURE 4 The probability to approach the upstream reference sites ($N=60$) by non-translocated (ie. control) individuals and the probability to approach the fishway by translocated individuals ($N=73$) based on fish fork length in Forty Mile Creek, Banff National Park. Shaded area accounts for 95% confidence intervals

reference receivers increased by 0.30 for a large non-translocated individual (FL 360-mm) in comparison with a small non-translocated individual (FL 240-mm). At the fishway, the probability to approach was 0.40 higher for a small translocated individual (FL 200-mm) than a large translocated individual (FL 320-mm). Although the probability to approach for small individuals was higher at the fishway, there was no size limitation for those that passed the fishway ($p = 0.34$).

The best ranked model for the probability to pass the fishway included both water depth and time of day ($R^2 = 0.25$; $\Delta AIC_{full} = 56.3$, $\Delta AIC_{reduced} = 52.9$; Table 2). The probability to pass was higher at night ($p = 0.005$). For example, the probability to pass the fishway at night increased by 0.30 compared with during the day at the mean water level (0.40-m). The probability to pass was also higher at greater water depths ($p = 0.0007$; Figures 3 & 5). For instance, there was a probability of 0.80 that a fish passed at a water depth of 0.40-m, whereas at a water depth of 0.30-m, the probability that a fish passed was 0.40 (see Figure 6). Fork length ($p = 0.34$), temperature ($p = 0.31$), and direction of passage ($p = 0.61$) were not included in the top ranked model, with insignificant p values.

Passage duration through the fishway varied between 5-min to 13-days, with an average of 1.80-days \pm 2.87-days (\pm SE; Table 3). Passage

TABLE 2 Parameter estimates for a generalized linear mixed effects model to understand the probability of passage for bull trout through a nature-like fishway in Forty Mile Creek Banff National Park

	Estimate \pm SE	z value	p value
Intercept	-9.60 \pm 3.02	-3.17	0.002
Water Depth	26.00 \pm 7.62	3.41	0.0007
Time of Day	3.15 \pm 1.11	2.84	0.005

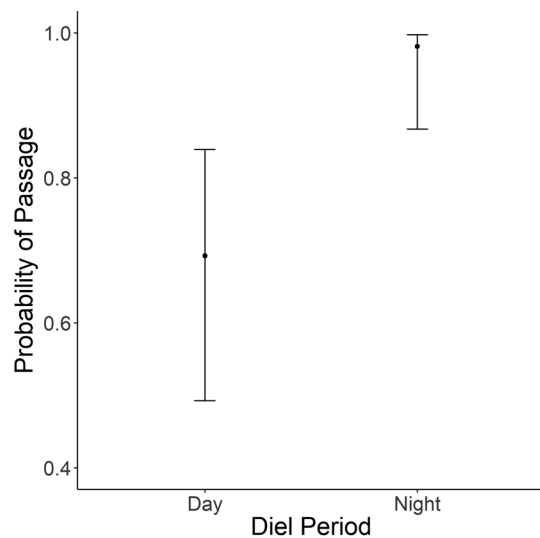


FIGURE 5 Predicted probability of passage through the nature-like fishway by bull trout in Forty Mile Creek, Banff National Park. There were 69 events by translocated ($N=27$) and non-translocated ($N=2$) individuals. Night and day with standard error bars (\pm SE) were categorized based on local sunset and sunrise times during our study period, whereas water level was held at its mean (0.40 m)

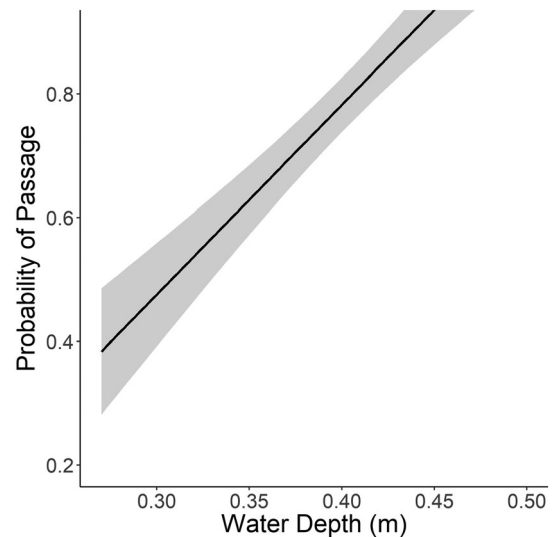


FIGURE 6 Predicted probability of passage through the nature-like fishway by bull trout in Forty Mile Creek, Banff National Park for water level. Shaded area accounts for 95% confidence intervals

TABLE 3 Parameter estimates for a linear mixed effects model to understand biotic and abiotic factors influencing passage duration with standard error (\pm SE) for bull trout through a nature-like fishway in Forty Mile Creek Banff National Park

	Estimate \pm SE	t value	p value
Intercept	-2.07 \pm 6.38	-0.32	0.75
Fork Length	3.23 \pm 20.60	0.16	0.88
Temperature	-0.16 \pm 0.25	-0.66	0.52
Water Depth	8.11 \pm 7.01	1.16	0.26
Time of Day	1.24 \pm 0.78	1.59	0.12

duration was not significantly influenced by water depth ($p = 0.26$), time of day ($p = 0.12$), water temperature ($p = 0.52$), or fork length ($p = 0.88$).

Some translocated individuals underwent large-scale movements by travelling 2-km upstream (15.1%; $N = 11$ of 73) or 2-km downstream (2.7%; $N = 2$ of 73; Table 4 & Figure 7). However, no translocated individuals exhibited homing behaviour, as they did not pass 6-km (S5) upstream of the fishway, which was required to reach their initial upstream capture sites.

4 | DISCUSSION

Our study showed that the breach in Forty Mile Creek dam was passable for bull trout with a high passage efficiency. Although the proportion of translocated bull trout that approached the fishway was low, the hydraulic conditions in the fishway appeared to enable passage for those motivated to do so at all seasons tested. We recognized that water levels were a predictor of success, but the water level effect on bull trout movements was consistent with upstream reference fish, therefore, the reduced probability to pass during low water periods

TABLE 4 A subsample of the individuals that used the fishway for multiple upstream and downstream passes (S3) and/or made large-scale movements 2-km upstream or downstream (S4 and S2), transit times are provided as dd:hh:mm:ss, adopted from (Cahill et al., 2015)

Fish ID	Station passed	Number of passes	Median transit time (S3)	(Min) Max transit time (S3)
10	S3	4	00:14:13:19	(00:03:02:23)
	S4	1		8:22:17:17
144	S3	5	00:01:35:44	(00:00:33:20) 00:04:44:08
55	S3	7	02:21:16:21	(00:01:31:30) 07:23:33:40
161	S3	2	0:3:04:55	(0:0:54:26)
	S4	2		1:1:38:51
61	S3	2	4:0:09:40	(0:0:20:12)
	S4	1		7:23:59:08
37	S2	1	00:03:19:40	(0:0:57:54)
	S3	4		1:2:49:52
	S4	2		

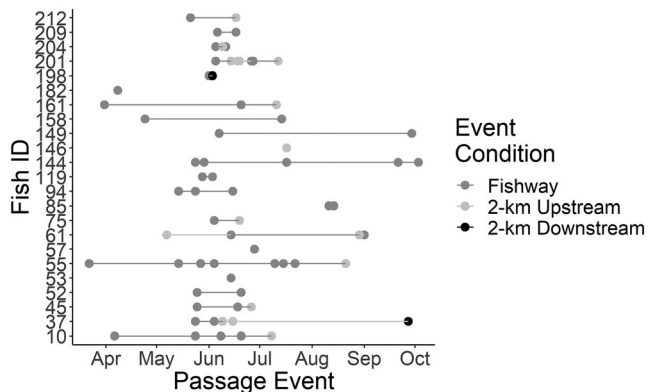


FIGURE 7 The successful passage events captured by a fish (represented by fish ID) through the fishway and/or 2-km upstream and downstream of the fishway. Each successful passage event is depicted by a dot that is shaded based on the location of the successful passage event. The first passage event depicted in this figure for all fish is provided as an upstream passage event, with the exception of fish ID 61 that passed upstream of the fishway when the transmitters were turned off for winter and is therefore first depicted descending the fishway. The direction of the passage events should be inferred with respect to the initial upstream passage

was likely due to seasonal changes in motivation and behaviour rather than conditions at the fishway. Additionally, it is worth noting that passage duration was long enough for some individuals that the habitat within the fishway was likely suitable for other aspects of their life history (e.g., station holding and presumed foraging). Furthermore, some individuals that successfully passed went on to travel at least 2-km further upstream suggesting that the fishway should enable upstream and downstream mixing of individuals and thus enable gene flow.

We translocated fish below the dam to encourage bull trout to make an attempt at passing the dam. This was an important aspect

of the study design because we would not have been able to tag enough fish using only below-dam residents. Therefore, it allowed for sufficient data to achieve the objectives over a realistic time frame. Although translocated fish may have a strong desire to home and bias our understanding of the “natural” movements, the main objective of the study was to quantify bull trout proportion and probability to approach and proportion and probability to pass, which was not biased by our study design. We tested for a location effect (fishway versus reference sites) on the probability to approach and it was not significant, which suggested that bull trout were approaching the fishway at the same rate as the upstream reference sites. In addition, the seasonal effect on probability to approach was consistent between locations, suggesting that the translocated fish were behaving the same as non-translocated fish on a seasonal basis.

Previous studies on resident bull trout have shown an increase in downstream overwintering movements (>1-km) in the fall with declining temperatures (e.g., Jakober et al., 1998). Our study found that temperature did not influence the probability to approach or pass, likely because our system did not experience a wide enough difference in water temperatures ($0.5\text{--}9.0 \pm 1.8^\circ\text{C}$) during the study. Despite the literature suggesting that stream salmonids tend to restrict movement during the winter (Brown & Mackay, 1995; Jakober et al., 1998; Muhlfeld et al., 2005), it is possible that the fish could have moved downstream later on (as noted in Jakober, 1995), when temperatures were at their lowest. To maximize transmitter life and keep the tag size small, the transmitters were turned off between November 16, 2015 and March 12, 2016 so we were unable to capture such movements. Nonetheless, manual radio tracking in spring of 2016 suggests that such large-scale winter movements were unlikely to have occurred.

Changes in water depths have been associated with large-scale fish movements (Alabaster, 1970; Egglisshaw & Shackley, 1982; Taylor & Cooke, 2012), and are often an important predictor of the probability to pass fishways (e.g., Cahill et al., 2015; Mallen-Cooper & Brand, 2007). The probability to pass was positively correlated to water depth. Most passes occurred at water depths >0.40-m in the spring and declined into the fall (see Figure 3). This suggests the lack of passage events at low water depths was not characteristic of the fishway, but rather the seasonal changes in the system.

The probability of fish to pass a fishway has often been associated with body size for many fishway types with which we compare the partial dam removal (e.g., Denil or vertical slot fishways; see Schwalme, Mackay, & Lindner, 1985; Noonan, Grant, & Jackson, 2012; Podgorniak, Angelini, De Oliveira, Daverat, & Pierron, 2016). Here, we observed that the probability to approach the fishway was higher for small translocated individuals than their larger counterparts (Figure 4). It is likely that large translocated individuals were able to secure a “new” home range downstream, requiring small individuals to use the remaining potentially suboptimal downstream habitat or move upstream. We suggest this as the fishway was likely not a physical impediment given that it was short in length (50-m) and had a relatively low gradient (5.3%). A strikingly different pattern was observed at the reference sites where the probability to approach was higher for

large non-translocated bull trout when compared with small individuals (see Figure 4). We suggest that the large non-translocated individuals were able to use their home range more effectively by frequently transitioning between home sites (see Clapp, Clark, & Diana, 1990), whereas small individuals may not have had access to same opportunities limiting their home range (see Clapp et al., 1990). In addition, the overall movement of fish at the reference sites (33%; $N = 20$ of 60) and the partial removal (37%; $N = 27$ of 73) were comparable.

In this study, some translocated individuals underwent large-scale movements and travelled 2-km upstream or 2-km downstream following a passage event (See Table 4 & Figure 7). It is possible that these fish exhibited searching behaviour where they attempted to locate and secure a new home range. This behaviour tends to occur when foraging conditions become suboptimal (Gowan & Fausch, 2002; Rodríguez, 2002). We suggest that non-translocated individuals upstream did not frequent the fishway ($N = 2$) as they may have already had an established home range given that the dam was present for over 100-years.

Stream-dwelling bull trout tend to exhibit diel habitat partitioning and often emerge from cover at night, where they shift towards using low cover and/or shallow habitats (Jakober, McMahon, & Thurow, 2000). In our study, movements often occurred after dusk when this species would be less vulnerable to predation (e.g., birds; Alvarez & Nicieza, 2003; Railsback, Harvey, Hayse, & LaGory, 2005), and would potentially have more foraging opportunities (e.g., Furey, Hinch, Lotto, & Beauchamp, 2015; Metcalfe, Fraser, & Burns, 1999). This also explains the extended periods of time that fish spent in the fishway, as they may have been able to access sufficient foraging opportunities and/or cover to hide under and settle into before moving upstream or downstream at a later time.

Our study has provided quantitative evidence of restored ecological connectivity for a threatened salmonid at a nature-like fishway created by a partial dam removal. The dam had blocked upstream bull trout passage for at least 100-years. The challenge of removing the dam in the past was the cost as well as concern for the environment. The damage to the dam infrastructure during a large flood in 2013 required capital investment to maintain the asset, and the cost of rebuilding the access road was equal to the cost of removing a portion of the dam. The cost of a full dam removal would have been prohibited given that a full removal would have also been considerably more challenging with regards to sediment control. Minimal work was done to prepare the nature-like fishway for water; a pilot channel was excavated, some boulders were added, and water shaped the channel naturally. The channel resembles a "rocky ramp fishway" and our approach to creating it required no engineering. This honours one of the main principles of nature-like fishways: The idea of self-design and self-regulation which respects nature as a collaborator (Katopodis et al., 2001).

Nature-like fishways provide an innovative way of restoring fragmented systems and have improved connectivity for both resident (e.g., Calles & Greenberg, 2007; Steffensen et al., 2013) and migratory species (e.g., Calles & Greenberg, 2009; Franklin, Haro, Castro-Santos, & Noreika, 2012), although to our knowledge, this has not previously

been done in the context of partial dam removal. The partial dam removal approach to generate a nature-like fishway should be especially relevant for low-head dams when financial resources for complete dam removal are lacking, thus providing another tool for those engaged in river restoration.

ACKNOWLEDGEMENTS

We would like to thank several Parks Canada employees, including Colby Whelan, Kayla Eykelboom, Brenna Stanford, Fonya Irvine, Sarah Fassina, and Hedin Nelson-Chorney, as well as volunteer Colin Maclean who devoted a number of hours towards this project, ultimately making this study possible. We would like to thank Natural Sciences and Engineering Research Council of Canada (NSERC) summer student Shannon Clarke for her dedication towards this project in the 2016 field season, and Phillip Harrison and Lee Gutowsky for R coding advice. Cooke is supported by NSERC and the Canada Research Chairs Program. We thank several referees for providing valuable input on the manuscript.

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How to cite this article: Sullivan BG, Taylor MK, Carli C, Ward TD, Lennox RJ, Cooke SJ. Partial dam removal restores passage for a threatened salmonid. *River Res Applic.* 2019;1–11. <https://doi.org/10.1002/rra.3426>