MANAGEMENT BRIEF

Multispecies Fish Passage Evaluation at a Rock-Ramp Fishway in a Colorado Transition Zone Stream

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Abstract

Stream habitat fragmentation caused by manmade structures is ubiquitous in Colorado, creating a need for passage solutions that accommodate multiple fish species. This study tested the effectiveness of a rock-ramp fishway for passing nine fish species with a range of swimming abilities. The target species for the fishway design included Brassy Minnow *Hybognathus hankinsoni* (weakest swimming), Longnose Dace *Rhinichthys cataractae*, Longnose Sucker *Catostomus catostomus*, and Brown Trout *Salmo trutta* (strongest swimming). Testing included a 46-h enclosure study and 3-month extended study, during which fish passage was evaluated using PIT tags. All of the species exhibited successful passage through the fishway during the enclosure study, but movement probabilities varied by species. Five species were not detected at the fishway during the extended study, possibly due to issues with attraction flows, entrance conditions, or motivation. Hydraulic conditions within the fishway were also evaluated. Roughness elements maintained a benthic, low-velocity zone across a range of flows, even when surface and depth-averaged velocities surpassed the design criteria for the weakest swimming species. The methods from this study could be replicated at other locations to evaluate design criteria (e.g., slope, capacity, roughness, and configuration) and performance for a variety of fish species and fishway types.

Infrastructure that is related to water development and transportation has fragmented aquatic habitat along major rivers and many tributaries in the United States (Warren and Pardew 1998; Malmqvist and Rundle 2002; Sheer and Steel 2006; Fencl et al. 2015), including Colorado. As the persistence of fish populations at the watershed scale may be the result of repeated upstream colonization, habitat fragmentation is a direct threat to the conservation of fish species (Nehlsen et al. 1991; Fausch and Bestgen 1997; Scheurer et al. 2003). Habitat connectivity is critically important for the life cycle of stream fishes that rely on a mosaic of habitats that may be patchy in space and time, including essential habitats for spawning, feeding, and refuge from harsh environmental conditions (Schlosser and Angermeier 1995; Fausch and Bestgen 1997; Rosenberg et al. 2000). Moreover, stream habitat fragmentation has reduced genetic diversity in fish populations, making adaptation to environmental changes less likely (Van Leeuwen et al. 2018; Eschenroeder and Roberts 2019). As increasing water demands and climate change are expected to exacerbate water shortages in the western United States (Ficke et al. 2007; Richter et al. 2020), restoring longitudinal connectivity should benefit fish populations by increasing access to upstream habitats, enhancing genetic diversity, and improving resilience to warming stream temperatures.

Instream structures with the potential to create fish migration barriers include dams and water diversions (Malmqvist and Rundle 2002; Sheer and Steel 2006; Fencl et al. 2015), road crossings (Warren and Pardew 1998), grade control structures (Ficke and Myrick 2009), and whitewater parks (Stephens et al. 2015; Fox et al. 2016). Barriers to fish movement can be attributed to dry-up points, inadequate water depth, elevated water velocity, and/or vertical obstacles. Elevated water velocities can present a barrier to fish movement when they exceed burst

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swimming speeds that can only be maintained for seconds due to the anaerobic energy requirements (Beamish 1978; Peake et al. 1997). Exhaustive barriers can occur when velocities are lower than burst swimming speeds but exceed prolonged swimming speeds over a given distance. Prolonged speeds can be maintained for minutes to hours and use energy from both anaerobic and aerobic metabolism (Beamish 1978; Peake et al. 1997). Swimming speeds vary by species and length, with larger fish typically exhibiting higher swimming speeds than smaller fish (Peake et al. 1997; Aedo et al. 2009; Dockery et al. 2016). Vertical barriers represent an obstacle that requires a fish to jump, and they occur when the height of the structure exceeds the jumping ability of a particular fish (Kondratieff and Myrick 2006). Many small-bodied fish species are not adapted to jumping over any vertical obstacle (Ficke et al. 2011; Ficke 2015).

Various fishway designs have been used to restore fish passage at instream structures, and they can generally be categorized as conventional or nature-like (Katopodis et al. 2001; Katopodis and Williams 2012). Conventional fishways use in-channel devices and openings to create hydraulic conditions that fish can navigate, and they were primarily developed for anadromous salmonids (Katopodis et al. 2001). Nature-like fishways, which are designed to simulate natural stream channels (Katopodis et al. 2001), have become increasingly popular for restoring fish passage at low-head dams (Steffensen et al. 2013). These fishways include bypass channels and channel-spanning or partial-width rock ramps (Wildman et al. 2003). As nature-like fishways may offer advantages for locations with diverse species and associated movements (Katopodis and Williams 2012), they have been the focus of research and evaluation for fisheries with high species diversity in Colorado (Ficke 2015; Swarr 2018). However, an improved understanding of hydraulic conditions and successful passage for target species will further advance the design and effectiveness of these fishways (Steffensen et al. 2013; Landsman et al. 2018).

The Fossil Creek Reservoir Inlet Diversion (FCRID) is a water diversion structure on the Cache la Poudre River, Colorado. The structure was considered a vertical, velocity, and/or depth barrier to upstream fish movement during low to moderate flows, depending on the species in question. During high flows when the diversion structure was completely submerged, a channel-spanning hydraulic wave with elevated velocities formed downstream of diversion crest, which likely inhibited upstream passage for most species. The FCRID was severely damaged during flooding in September 2013. Reconstruction provided an opportunity to incorporate a rock-ramp fishway into the new structure and restore connectivity for 15.6 km of river. As the goal of the project was to restore upstream passage for all small-bodied fish that are endemic to the site and introduced

trout, a partial-width rock ramp was selected by the North Poudre Irrigation Company, Colorado Parks and Wildlife (CPW) and City of Fort Collins Natural Areas for the fishway design. The objectives of this study were to (1) validate that the target fish species could ascend the fishway, (2) validate that the fishway hydraulics met the design criteria, (3) determine whether fishway efficiency varied by species, and (4) investigate the utility of a short-term enclosure method for evaluating fish passage structures. These objectives were tested using a combination of biological and hydraulic assessments.

METHODS

Study site.— There are three major stream habitat zones within the South Platte River basin in Colorado: coldwater mountain streams, warmwater streams on the eastern plains, and a transition zone in between (Figure 1; CPW 2015; Fausch and Bestgen 1997). The transition zone and eastern plains encompass a dynamic gradient of thermal and physical habitat, supporting a range of uniquely suited fish species (Fausch and Bestgen 1997). Our study site is located within the transition zone on the Cache la Poudre River, which is a tributary to the South Platte River in the Southern Rocky Mountains (Figure 1).

The Cache la Poudre River is representative of many rivers within Colorado that have been heavily modified to meet high water demands and infrastructure needs. For the 32-km section of the Cache la Poudre River that extends upstream from the confluence with the South Platte, there is a water diversion structure every 1.5 km on average (Figure 1). Water diversion, grade control, and whitewater park structures are more prevalent in the transition zone than the eastern plains. Although diversion structures are common along the South Platte River, ditch crossings and flood-control structures increase in prevalence for plains streams that are tributary to the South Platte.

At the study site, the Poudre River is a sixth-order stream in an unconfined alluvial valley, with a drainage area of 3,212 km². Elevation in the basin ranges from 1,490 to 4,145 m, and the watershed is approximately 50% forested, 21% grassland, and 3.5% impervious (USGS 2016). The hydrology is snowmelt dominated, but it is highly altered by agricultural and urban water uses (Bestgen et al. 2019). The average annual precipitation is 0.52 m, and the average annual discharge is 4.4 m³/s. The FCRID is located within a reach that historically supported approximately 20 warmwater and coolwater fish species, but half of those species are now thought to be extirpated (F. B. Wright III, unpublished data). Target species for the fishway design were selected from the known assemblage at the study site to represent a range of swimming abilities and morphologies and included Brassy Minnow
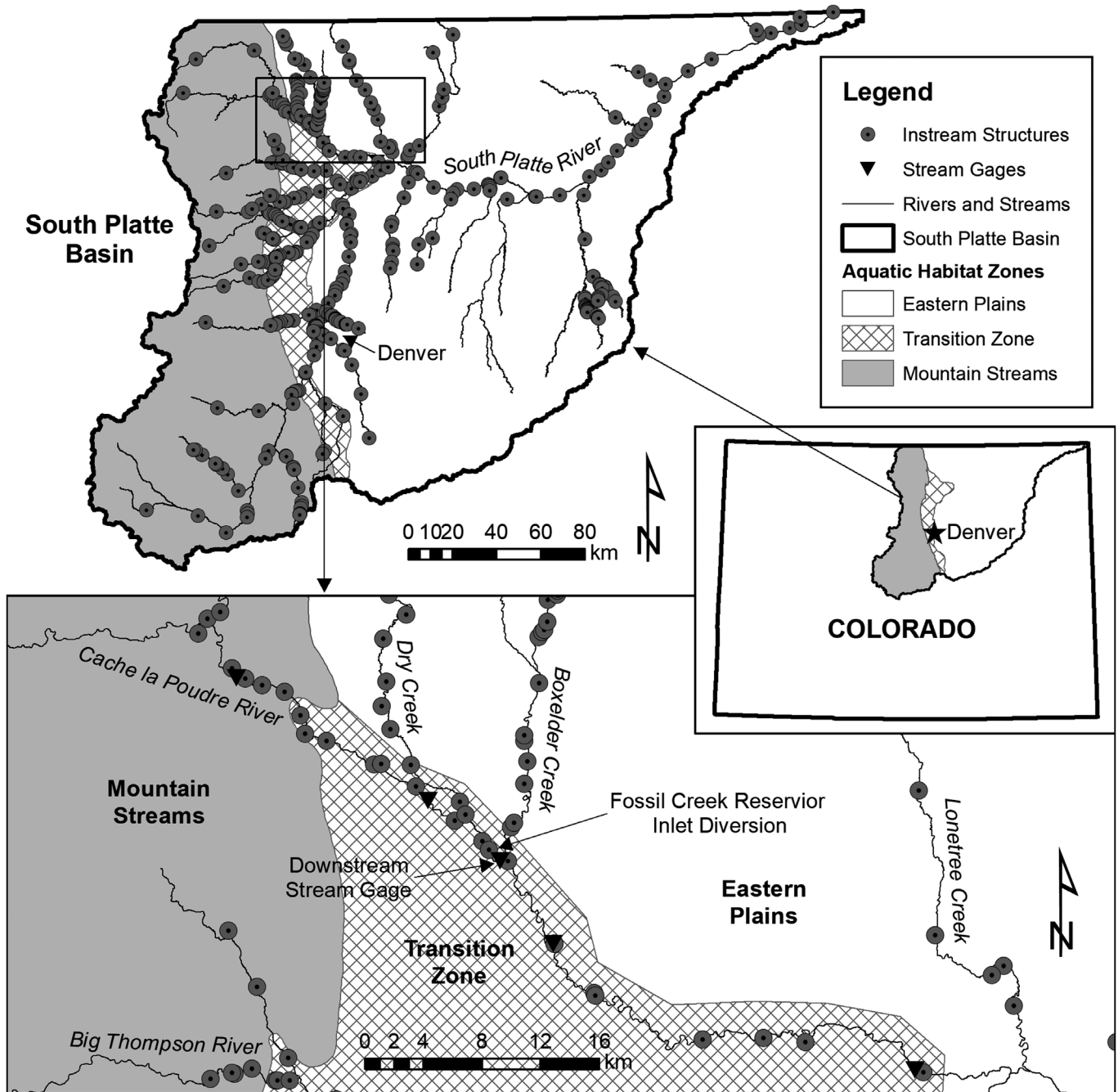
FIGURE 1. Location of the South Platte basin, Colorado, associated aquatic habitat zones, and the Fossil Creek Reservoir Inlet Diversion on the Cache la Poudre River. The instream structures include water diversions, dams, ditch crossings, and grade-control structures that were identified from aerial images along fourth-order or higher rivers and streams within the South Platte basin.

Hybognathus hankinsoni (weakest swimming), Longnose Dace *Rhinichthys cataractae*, Longnose Sucker *Catostomus catostomus*, and Brown Trout *Salmo trutta* (strongest swimming; Table 1).

Fishway design.— The vertical drop over the reconstructed low-head dam was 0.46 m with a flat concrete apron extending 3 m downstream from the base of the dam. The rock-ramp fishway was constrained to a trapezoidal notch in the diversion dam with a top width of approximately 1.2 m and bottom width of 0.6 m to ensure that it did not affect the capacity of the structure to divert water. The fishway was set at a 5% slope, which was

TABLE 1. Summary of published prolonged and burst swimming speeds with associated range in mean total lengths (MTL) for all fish species included in the enclosure and extended studies.

Species	Prolonged swimming[b]		Burst swimming[b]	
	Speed (m/s)	MTL (mm)	Speed (m/s)	MTL (mm)
Brassy Minnow[a]	0.44	62	0.64	62
Brown Trout[a]	0.50–2.35	98–457	1.33–3.12	98–457
Creek Chub *Semotilus atromaculatus*	0.52	70	0.44–0.90	57–70
Green Sunfish *Lepomis cyanellus*	0.11–0.49	63–75	0.79	75
Largemouth Bass *Micropterus salmoides*	0.35–0.50	107	NA	NA
Longnose Dace[a]	0.44–0.73	65–72	0.78–1.75	65–72
Longnose Sucker[a]	0.62	239	0.71–1.82	238–253
Rainbow Trout *Oncorhynchus mykiss*	0.52–0.91	89–387	1.05–2.77	96–387
White Sucker *Catostomus commersonii*	0.33–0.47	77–174	0.53–0.83	77–173

[a]Target species selected for fishway design.

[b]Swim speeds and associated MTL for each species were obtained from the following references: Brassy Minnow (Ficke et al. 2011), Brown Trout (Aedo et al. 2009; Peake et al. 1997), Creek Chub (Ficke 2015; Leavy and Bonner 2009), Green Sunfish (Ficke 2015; Prenosil 2014; Scott and Magoulick 2008; Ward et al. 2003), Largemouth Bass (Farlinger and Beamish 1978), Longnose Dace (Aedo et al. 2009; Dockery et al. 2016; Ficke 2015), Longnose Sucker (Jones et al. 1974; Underwood et al. 2014), Rainbow Trout (Bainbridge 1960; Burgetz et al. 1998; Gregory and Wood 1998; Harper and Blake 1990; Hawkins and Quinn 1996; Jones et al. 1974; Webb 1975, 1976, 1977, 1978), and White Sucker (Ficke 2015; Underwood et al. 2014). NA indicates that data were not available.
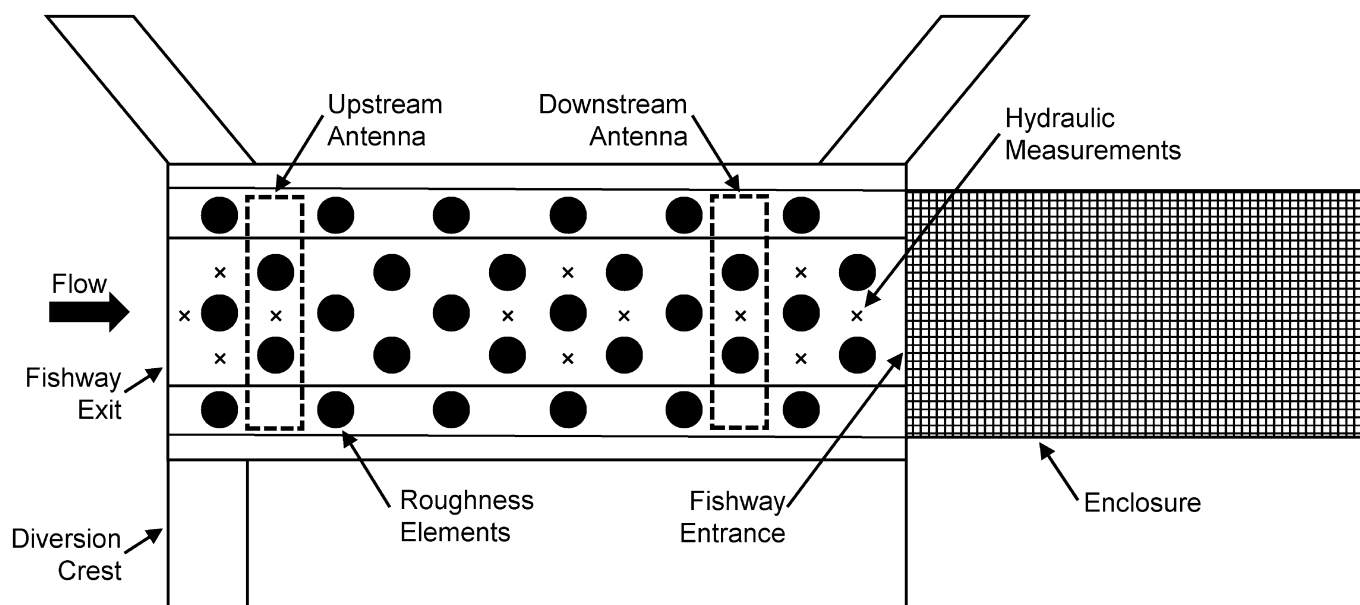

FIGURE 2. Conceptual schematic of the rock-ramp fishway during the enclosure study at the Fossil Creek Reservoir Inlet Diversion on the Cache la Poudre River, Colorado, including the location of roughness elements (black circles), PIT-tag antennas (dashed rectangles), and hydraulic measurements (x).

considered the maximum slope for a rock-ramp fishway of this size (Ficke 2015), and it extended 3 m downstream from the crest of the dam. The design specifications for the roughness elements included a height of 15–20 cm, with a spacing of one particle diameter arranged in a chevron pattern (Figure 2). Conceptual design drawings for the fishway

and photos of the structure are included with the Supplement available in the online version of this article.

Passage criteria included a minimum depth of 0.15 m and water velocity ≤0.64 m/s to support passage for the weakest swimming species (Brassy Minnow; Ficke et al. 2011). These criteria were evaluated for a single design

flow of 0.085 m³/s, which was considered representative of baseflow conditions. The roughness coefficient (Manning 1891) used for the design calculations (0.070) was based on the results from laboratory rock-ramp studies (Ficke 2015) and resulted in an average depth of 0.15 m and cross-sectional velocity of 0.73 m/s for the design flow. We hypothesized that lower velocities ($\leq$0.64 m/s) would occur along the bottom and sides of the fishway based on the depth-velocity profiles and cross-sectional isovels (Chow 1959; Ficke 2015).

Antenna construction and operation.— Radio frequency identification antennas were placed at the entrance and exit of the fishway to detect the movement of the PIT-tagged fish and determine their directionality (upstream or downstream) during both the enclosure and extended studies (Figure 2). Antennas were constructed from two loops of 12-gauge thermoplastic high-heat-resistant nylon-coated wire that was encased in schedule-40 polyvinyl chloride pipe. Each antenna was connected to a tuning board, which was then connected to a half-duplex multiplexing antenna reader (Oregon RFID, Portland, Oregon). The reader recorded the tag number, antenna number, date, and time for each detection. The maximum continuous detection distance (Fetherman et al. 2014) was measured every 10–14 d with both 12- and 32-mm PIT tags, using a perpendicular orientation at the center of each antenna.

Enclosure study.— We conducted a 46-h enclosure study at the fishway during August 17–19, 2016. Fish were collected from two locations: the South Platte River in northeastern Colorado and onsite. The fish that were collected from the South Platte River tested negative for all regulated pathogens by the CPW Aquatic Animal Health Laboratory (Brush, Colorado). To ensure that tag weight was less than 12% of individual body weight (Brown et al. 1999), fish between 55 and 198 mm TL received 12-mm tags and fish between 177 and 448 mm received 32-mm tags, with the majority (70%) of fish that were larger than 177 mm TL receiving a 32-mm tag. Similar fish lengths and associated tag sizes have been used in other studies previously conducted in Colorado (Fetherman et al. 2015; Ficke 2015; Fox et al. 2016; Richer et al. 2017). Eight species were tagged for the enclosure study, including Brassy Minnow, Brown Trout, Creek Chub, Green Sunfish, Largemouth Bass, Longnose Dace, Longnose Sucker, and White Sucker. Although four target species were selected for the fishway design, additional species that were captured during fish collection were included in the study to provide more information on the effectiveness of nature-like fishways for comparable fisheries in Colorado.

The tagged fish were given up to 4 h to recover before being placed in a small enclosure (3 m²) that was open only to the downstream entrance of the fishway (Figure 2). The enclosure was constructed from a cage of wire mesh that was attached to the fishway entrance with a seine. Fish were released into the enclosure in two groups. The first group included eight species and 73 fish (Table 2). To minimize the potential for predation within the enclosure, only small Largemouth Bass (<82 mm TL) and Brown Trout (<100 mm TL) were included in the initial group. The second group, consisting of four species and 48 fish, was released 24 h into the trial and included large Brown Trout (Table 2). The enclosure was removed after 46 h, and all of the fish that were recovered from the enclosure were retained for inclusion in the extended study.

TABLE 2. Number of fish by species for the initial enclosure release at 0 h (n_1), second enclosure release at 24 h (n_2), total number of fish released (n_T) for each study, passage success (PS; the percentage of fish released downstream of the structure that were detected at the upstream antenna), the number of upstream (US) and downstream (DS) movements observed during the extended study, and the range in total length (TL) for all of the fish that were released during both studies. Cells that are marked NA indicate that no individuals for that species were released downstream of the structure at the start of the study.

Species	Enclosure study				Extended study				All fish TL (mm)
	n_1	n_2	n_T	PS (%)	n_T	PS (%)	US	DS	
Brassy Minnow[a]	13	0	13	23	13	0	0	0	55–83
Brown Trout[a]	2	13	15	87	72	49	39	8	94–448
Creek Chub	1	0	1	100	1	NA	0	0	106
Green Sunfish	6	10	16	50	19	0	0	0	84–124
Largemouth Bass	1	0	1	100	1	NA	0	0	82
Longnose Dace[a]	28	4	32	50	42	15	7	0	63–110
Longnose Sucker[a]	21	21	42	71	127	12	13	4	79–198
Rainbow Trout	0	0	0	NA	1	0	0	0	264
White Sucker	1	0	1	100	9	25	2	0	100–286
All	73	48	121	60	285	22	61	12	55–448

[a]Target species selected for fishway design.

Movement out of the enclosure was considered an attempt to move up through the fishway. To evaluate upstream movement through the fishway, encounter histories were created for each species with more than one individual included in the study. Encounter histories consisted of a set of three binary responses: (1) initial release into the enclosure (1 for all fish), (2) detection at the downstream antenna (1 if detected, 0 if not detected), and (3) detection at the upstream antenna (1 if detected, 0 if not detected). Because fish size can influence passage success (Forty et al. 2016; Hatry et al. 2016) and detection probability (Richer et al. 2017), length was included as an individual covariate.

The encounter histories were used to fit a variation of the Cormack–Jolly–Seber (CJS) model that estimated the apparent success (ψ) of upstream movement i using the following equation:

$$\psi_i = \varphi_i \quad p_i, \tag{1}$$

where φ_i is the probability of movement past antenna i, and p_i is the probability of detection at antenna i (Burnham et al. 1987). Estimates of φ and p were obtained by using the CJS open capture–recapture estimator in program MARK (White and Burnham 1999). One model set was run per species (five sets total), and an additional set evaluated the overall passage efficiency of the fishway (all species included). The model sets consisted of intercept-only models (.) as well as models in which φ or p varied by antenna (A), fish length (L), or both ($A + L$) for a total of 16 models per set: (1) $\varphi.p.$, (2) $\varphi.p_A$, (3) $\varphi.p_L$, (4) $\varphi.p_{A+L}$, (5) $\varphi_A p.$, (6) $\varphi_L p.$, (7) $\varphi_{A+L}p.$, (8) $\varphi_A p_A$, (9) $\varphi_A p_L$, (10) $\varphi_A p_{A+L}$, (11) $\varphi_L p_A$, (12) $\varphi_L p_L$, (13) $\varphi_L p_{A+L}$, (14) $\varphi_{A+L}p_A$, (15) $\varphi_{A+L}p_L$, and (16) $\varphi_{A+L}p_{A+L}$. The models were ranked using Akaike's information criterion corrected for small sample sizes (AIC_c), compared using AIC_c differences (ΔAIC_c), and ranked using the model weights (w_i; Burnham and Anderson 2002). Models with $w_i > 0$ were examined for goodness of fit by evaluating the Pearson c-hat statistic for dispersion. The model-averaged parameter estimates and associated unconditional standard errors were reported from each model set ($w_i > 0$ and Pearson c-hat = 1.00; Anderson 2008). In addition, cumulative AIC_c weights were used to assess the relative importance of each covariate on φ or p.

Model-averaged parameter estimates were used to quantify fishway efficiency for each species (Hodge et al. 2017). The probability of entering the fishway was obtained from the downstream antenna (φ_E), and passage efficiency, the probability that a fish successfully ascended the fishway, was obtained from the upstream antenna (φ_P). Total fishway efficiency (φ_T) is the product of the entrance probability and passage efficiency ($\varphi_E \times \varphi_P$). Similarly, total detection probability (p_T), the probability that

a fish was detected by both antennas when passing the fishway, is the product of the downstream and upstream antenna estimates ($p_{DA} \times p_{UA}$).

Extended study.— Following removal of the enclosure, the antennas were left in place from August 19 to November 14, 2016, to evaluate use of the fishway under natural conditions. All of the fish that were recovered from the enclosure ($n = 48$) were released downstream of the structure at the start of the extended study. Additional fish ($n = 164$) were collected from a site located 2.6 km upstream, tagged, and released downstream of the diversion using the same tagging methods as were used in the enclosure study. Relocating fish from upstream reaches exploits homing behavior that motivates individuals to return to upstream capture sites (Halvorsen and Stabell 1990). Fish that ascended the fishway during the enclosure study ($n = 73$) were also available for detection during the extended study, but as their initial disposition was upstream of the structure these fish were only used for analyses of downstream passage.

Upstream and downstream movement through the fishway was monitored over the course of the extended study. Fish that moved downstream could do so through the fishway (detectable) or over the diversion crest (undetectable). Encounter histories were constructed to determine the probability of fishway use for upstream and downstream movements over the course of the extended study regardless of when the movement occurred, and these consisted of the same set of three binary responses that were described for the enclosure study. The same variation of the CJS model that was used for the enclosure study was used to fit the encounter histories for the extended study, using the CJS open capture–recapture estimator in program MARK (White and Burnham 1999). The model sets that were used to estimate the upstream movement probabilities were run separately by species or the fishway (all species), whereas only one model set including all of the species was used to determine the downstream movement probabilities. Each model set included the same 16 models as were described for the enclosure study, with an intercept-only model, as well as models where φ or p differed by antenna, fish length, or both. Entrance probability (φ_E), passage efficiency (φ_P), and total fishway efficiency (φ_T) or detection probability (p_T) are represented in the same way as they were in the enclosure study.

Hydraulic evaluation.— Hydraulic conditions in the fishway were measured over a range of flows between February 24 and November 14, 2016. The amount of flow in the fishway is affected by river discharge, operation of head gates to the ditch, and operation of a radial gate, which makes it difficult to correlate stream discharge to fishway discharge. Therefore, stage was recorded from a staff gauge that was installed just upstream of the fishway exit and discharge was measured at the upstream edge of

the fishway (Figure 2) to develop a stage–discharge relationship for the fishway. Streamflow records from a downstream U.S. Geological Survey stream gauge near Timnath, Colorado (#06752280; Figure 1) were used to evaluate the range of flows during the enclosure and extended studies compared with the period of record.

Point measurements for depth and velocity were collected at 12 locations to evaluate the hydraulic conditions within the fishway (Figure 2). All of the point measurements included water depth, bottom velocity, depth-averaged velocity, and surface velocity. Bottom velocity was measured by lowering the flow meter to the bottom of the wading rod, which corresponded to a depth of 6 cm. Depth-averaged velocity was measured by setting the flow meter to 0.6 of the measured depth from the water surface. Surface velocity was measured by placing the flow meter at the top of the water column at a depth where the sensor remained fully submerged. All of the point velocity measurements represent an average velocity over a 10-s interval. Average depths and velocities for the fishway were calculated from the point measurements for each discharge.

Depth and velocity measurements were also used to calculate the Froude number (F) with the following equation:

$$F = V / \sqrt{gh}, \qquad (2)$$

where V is depth-averaged water velocity, g is the gravitational constant, and h is water depth. The F is the ratio of inertial to gravitational forces and distinguishes between subcritical ($F < 1$; tranquil), critical ($F = 1$), and supercritical ($F > 1$; rapid) flow states (Chow 1959). Critical flow is characterized by a standing wave that can create turbulence and unsteady flow profiles, and it is considered undesirable in fish swimming studies (Dockery et al. 2016). Some plains species (e.g., minnows, suckers, and catfish) may avoid areas where $F > 0.3$ (Yu and Peters 1997). As maintaining optimal hydraulic conditions within the fishway and at the fishway entrance is important for effective fish passage, an $F = 0.3$ was selected as a threshold for potential avoidance behavior. The F was calculated for individual point measurements and averaged across all points within the fishway for each flow measurement.

RESULTS

Enclosure Study

At least one individual from each species exhibited successful passage through the fishway during the enclosure study (Table 2). The majority of fish that entered the fishway ascended the fishway, and probability of success increased with fish length for all species except Green Sunfish (Table 3). The overall probability that a fish entered and successfully passed the fishway during the enclosure study was 0.81 (SE, 0.07). Brassy Minnow and Longnose Dace were less likely to enter the fishway compared with the other three species (Table 4). All of the Longnose Dace that entered the fishway successfully ascended the fishway. However, this was not the case for Brassy Minnow or Green Sunfish, despite Green Sunfish having a

TABLE 3. Cumulative AIC$_c$ weights for antenna (C$\varphi_{antenna}$; C$p_{antenna}$) or length (Cφ_{length}; Cp_{length}) effects on movement (φ) or detection (p) probability and magnitude and direction of effect ($\beta_{antenna}$; β_{length}) from the top model in which it appeared for both the enclosure and extended studies. A negative value for $\beta_{antenna}$ indicates that $\varphi_E < \varphi_P$ or $p_{DA} < p_{UA}$. For β_{length} a negative value indicates that φ or p decreased with an increase in fish length; the opposite is true for positive β values.

	C$\varphi_{antenna}$	Cφ_{length}	$\beta\varphi_{antenna}$	$\beta\varphi_{length}$	C$p_{antenna}$	Cp_{length}	$\beta p_{antenna}$	βp_{length}
Enclosure study								
Brassy Minnow[a]	0.20	0.12	19.91[b]	21.91[b]	0.12	0.54	−10.47[b]	8.32[b]
Brown Trout[a]	0.20	0.80	0.76	4.34[b]	0.48	0.22	513.69[b]	0.02
Green Sunfish	0.25	0.65	−0.95	0.11	0.21	0.30	−16.85[b]	0.11
Longnose Dace[a]	1.00	0.82	−21.80	0.14[b]	0.36	0.36	−20.29[b]	−0.16
Longnose Sucker[a]	0.64	1.00	−1.79	0.16[b]	0.57	0.29	−24.24[b]	0.02
Fishway	1.00	1.00	−5.02	0.05[b]	0.26	0.39	−0.09	0.01
Extended study								
Brown Trout[a]	0.99	0.94	−30.65	0.01[b]	0.03	0.54	−1.14	0.01
Longnose Dace[a]	0.00	0.91	NA	0.13[b]	0.01	0.25	−16.72	0.10
Longnose Sucker[a]	1.00	0.58	−27.65	0.01	0.00	0.43	NA	0.03
White Sucker	0.04	0.13	−30.21	0.01	0.09	0.09	−18.02[b]	0.04
Fishway	1.00	1.00	−30.09	0.01[b]	0.00	0.37	NA	0.01

[a]Target species selected for fishway design.
[b]Confidence intervals for beta estimates do not include zero.

TABLE 4. Movement (φ) and detection (p) probability estimates   unconditional standard errors for Brassy Minnow, Brown Trout, Green Sunfish, Longnose Dace, Longnose Sucker, White Sucker, and the fishway for both the enclosure and extended studies. The variable φ_E is the probability that a fish entered the fishway, φ_P is the probability of successful upstream passage, and φ_T is the total fishway efficiency ($\varphi_E \times \varphi_P$). Total detection probability (p_T), the probability that a fish was detected by both antennas when passing the fishway, is the product of the detection probabilities for the downstream and upstream antennas ($p_{DA} \times p_{UA}$).

	φ_E		φ_P		φ_T		p_{DA}		p_{UA}		p_T	
Enclosure study												
Brassy Minnow[a]	0.45	0.16	0.54	0.20	0.24	0.18	1.00	0.01	1.00	0.02	1.00	0.02
Brown Trout[a]	0.98	0.04	0.98	0.04	0.96	0.07	1.00	0.00	0.97	0.06	0.97	0.06
Green Sunfish	0.72	0.12	0.77	0.13	0.56	0.20	0.87	0.13	0.90	0.13	0.78	0.23
Longnose Dace[a]	0.51	0.10	1.00	0.02	0.51	0.10	0.97	0.04	0.98	0.03	0.95	0.07
Longnose Sucker[a]	0.98	0.03	0.99	0.01	0.98	0.04	0.91	0.06	0.97	0.04	0.88	0.09
Fishway	0.81	0.06	1.00	0.01	0.81	0.07	0.93	0.03	0.93	0.03	0.87	0.05
Extended study												
Brown Trout[a]	0.51	0.08	1.00	0.02	0.51	0.09	0.89	0.06	0.90	0.05	0.80	0.10
Longnose Dace[a]	0.22	0.12	0.22	0.12	0.05	0.05	0.96	0.17	0.97	0.16	0.93	0.32
Longnose Sucker[a]	0.12	0.04	1.00	0.00	0.12	0.04	0.96	0.05	0.96	0.05	0.92	0.10
White Sucker	0.40	0.16	0.43	0.19	0.17	0.14	0.99	0.18	1.00	0.00	0.99	0.18
Fishway	0.19	0.03	1.00	0.00	0.19	0.03	0.93	0.03	0.93	0.03	0.86	0.06
Downstream[b]	0.76	0.09	0.82	0.13	0.62	0.17	0.91	0.08	0.89	0.13	0.82	0.19

[a]Target species selected for fishway design.

[b]Probability that a fish that started upstream of the fishway entered (φ_E) and passed the fishway moving downstream (φ_P), versus going over the structure (undetectable), and was detected (p_{UA} occurs before p_{DA} for downstream movements).

higher probability of entering the fishway. Longnose Sucker and Brown Trout not only had a higher probability of entering the fishway, but were also more likely to ascend the fishway (Table 4). Although p varied by antenna and species, p was relatively high, with $p_T \geq 0.78$ for all of the species and the fishway (Table 4). Brassy Minnow was the only species for which there was a length effect on p (Table 3), with p increasing as fish size increased.

Extended Study

Upstream movements through the fishway during the extended study were only observed for Brown Trout, Longnose Dace, Longnose Sucker, and White Sucker (Table 2). Given estimates of $p_T \geq 0.80$ (Table 3), it is unlikely that the other species passed through the fishway undetected. Lower passage success was observed during the extended study when compared to the enclosure study (Table 2). The fish that were translocated from the upstream collection site exhibited higher passage success (28%) than the fish that were recovered from the enclosure (2%). Brown Trout used the fishway most frequently, with one individual making four different upstream movements. Repeated upstream movements by individual fish were also observed for Longnose Dace and Longnose Sucker. Downstream movements were only documented for Brown Trout and Longnose Sucker during the extended study (Table 2).

The overall probability that a fish released downstream of the structure found, entered, and successfully passed the fishway during the extended study was 0.19 (SE, 0.03). There was a positive effect of length on upstream movement probabilities for Brown Trout and Longnose Dace but not Longnose Sucker or White Sucker (Table 3). Longnose Dace and Longnose Sucker were less likely to
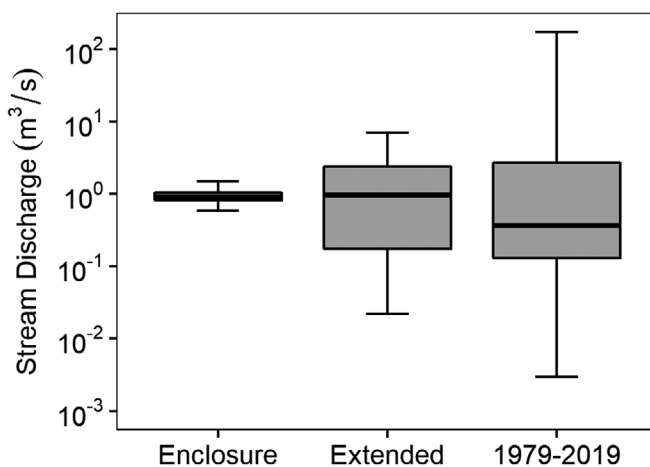

FIGURE 3. Discharge at the downstream stream gauge during the enclosure and extended studies compared with that during the period of record (1979–2019). The boxplots show the minimum, quartiles, median, and maximum values for each period.
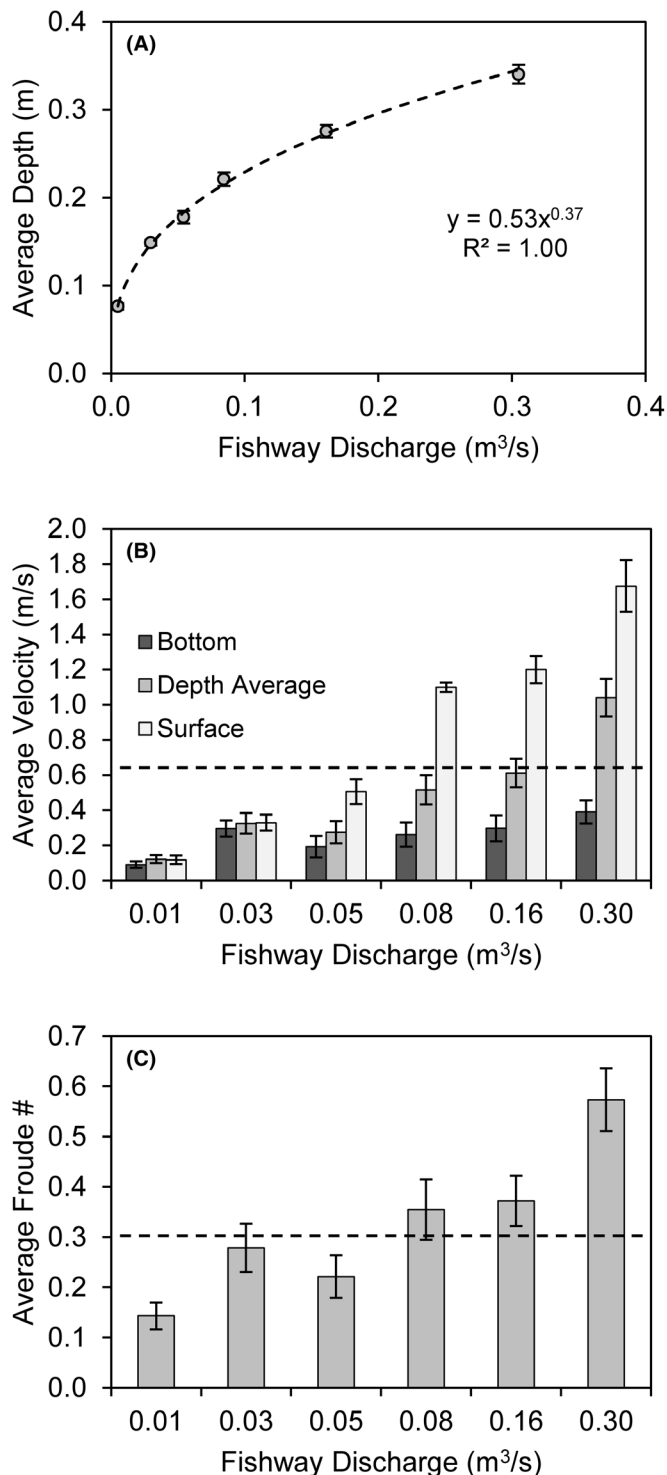
FIGURE 4. Results from hydraulic measurements within the rock-ramp fishway, including comparisons of **(A)** mean ± SE water depth; **(B)** bottom, depth-averaged, and surface water velocity; and **(C)** Froude number to fishway discharge. The dashed lines represent the stage–discharge relationship for the fishway (A), passage criteria for water velocity (0.64 m/s; B), and the potential avoidance threshold for Froude numbers (0.3; C).

enter the fishway than White Sucker and Brown Trout (Table 4). Additionally, not all Longnose Sucker, Longnose Dace, and White Sucker that entered the fishway successfully ascended the fishway, resulting in relatively low estimates of φ_T for these species. A larger proportion of Brown Trout found and entered the fishway, and all of them successfully ascended the fishway. Estimates of downstream φ_T suggest that not all of the fish that moved downstream during the extended study did so by moving through the fishway (Table 4).

Hydraulic Evaluation

Median stream discharge during the enclosure and extended studies was higher than the period of record, but the ranges in discharge varied by orders of magnitude, with the most limited range occurring during the enclosure study (Figure 3). Due to the timing of the study, fish passage was not evaluated during the peak flows that occur in spring and early summer. Average water depths ranged from 0.08 to 0.34 m (Figure 4) while the detection distance for 12- and 32-mm PIT tags ranged from 0.19 to 0.25 m and 0.38 to 0.41 m, respectively. Water depths exceeded the detection distances for the 12-mm tags when discharge in the fishway surpassed 0.06–0.13 m³/s. However, the detection probabilities were similar across species (Table 4), despite differences in fish and tag sizes, which suggests that tag size did not affect our ability to detect the fish. The fishway reached full capacity at an average water depth of 0.29 m, which corresponded to a fishway flow of 0.18 m³/s. The average water depth dropped below the design depth of 0.15 m when the fishway flows were less than 0.03 m³/s.

As hypothesized, bottom velocities within the fishway remained below the target passage velocity of 0.64 m/s for Brassy Minnow (Figure 4). Linear regression analysis indicated that the depth-averaged velocities remained below the target velocity when the flows in the fishway were less than 0.16 m³/s. An empirical analysis of the design flow (0.085 m³/s) indicated that the observed depths (0.21 m) were deeper than anticipated (0.15 m) and observed depth-average velocities (0.42 m/s) were lower than expected (0.73 m/s). These observations validate that the fishway met the hydraulic design criteria and suggest that the Manning's n value that was used for the fishway design (0.070) was underestimated and could be as high as 0.120 for the design flow.

Analysis of the F indicated that the flows were typically tranquil ($F < 1$) within the fishway (Figure 4). However, the average F within the fishway surpassed the potential avoidance threshold ($F > 0.3$) when fishway flows reached 0.08 m³/s (Figure 4). Critical flow ($F = 1$) in the fishway was estimated to occur at 0.61 m³/s. Water velocity and F both increased longitudinally within the fishway, with lower values observed near the upstream exit and higher

values observed near the downstream entrance. Point measurements downstream of the fishway entrance resulted in values for F that ranged from 1.03 to 1.41 during the highest flow measurement, indicating that flow conditions had transitioned from subcritical within the fishway to supercritical at and downstream of the fishway entrance.

DISCUSSION

All four of the target species ascended the fishway during the enclosure trial, but only three of the four species successfully passed the fishway during the extended trial. Passage success was lower for weaker-swimming species (e.g., Brassy Minnow), which suggests that lower rock-ramp slopes (<5%) may be needed to optimize passage for all of the species at the study site. Decreasing the rock-ramp slope has been shown to improve hydraulic conditions (Baki et al. 2014) and accommodate passage for more fish species (Swarr 2018). Incorporating resting pools into rock-ramp designs may also be necessary to improve passage success, particularly as the length of the fishway increases.

Hydraulic measurements indicated that roughness elements within the fishway effectively maintained a benthic, low-velocity zone across a range of flows, even when surface and depth-averaged velocities had surpassed criteria for the weakest swimming species. As diverse species may use different pathways for passage (Swarr 2018), some fish could be excluded when passable conditions are limited to a low-velocity benthic zone. The effect of roughness elements on water velocities diminished as fishway depth increased and the elements were submerged, resulting in fishway hydraulics that would not support passage of all target species during higher flows. This suggests that similar rock-ramp designs may only provide passage for weaker-swimming species during lower flows. Performance at higher flows could be improved by increasing the height of the roughness elements to equal the maximum water depth at fishway capacity. As managing water levels within fishways can improve passage (Pennock et al. 2018), conditions in the FCRID fishway could be optimized for a wider range of flows by regulating the fishway discharge with the radial gate.

As flows through the fishway increased, a hydraulic jump ($F > 1$) formed at the downstream entrance. Chaotic flows with fluctuating velocities can repel fish, while flows that have a component of predictability can attract fish (Liao 2007). Furthermore, increased turbulence can decrease the swimming performance of fish, with smaller fish being more affected than larger fish (Lupandin 2005). Supercritical flows at the fishway entrance may have impaired the ability of some fish to find and enter the fishway during higher flows. During very low flows, a vertical drop formed at the fishway entrance. The height of the drop was not considered a vertical barrier to trout due to their jumping ability (Kondratieff and Myrick 2006), but it was considered an obstacle for small-bodied fish species with limited to no jumping ability (Ficke et al. 2011; Ficke 2015). To address these concerns, the FCRID rock-ramp was extended 6 m downstream during February 2018, which greatly improved the hydraulic conditions at the fishway entrance.

Attraction efficiency is a critical component of fishway performance (Steffensen et al. 2013), with a reported range of 0–100% (mean, 48%) for 21 nature-like fishways studied by Bunt et al. (2011). The entrance probabilities for individual species ranged from 12% to 51% during our extended study, which were lower than the range in attraction efficiency (58% to 100%) reported by Steffensen et al. (2013). We observed species-specific passage efficiencies that ranged from 5% to 51% during the extended study, which was comparable to values that have been reported by others (0–100%, mean, 70%, Bunt et al. 2011; 0–57%, Steffensen et al. 2013), suggesting that the FCRID rock-ramp performed similarly to other nature-like fishways.

Ontogeny or life history may have played a role in the observed fish movements, as indicated by the length effect on movement probabilities. Brown Trout were more likely to find and use the fishway than other species during the extended study, which was conducted in the fall and encompassed the Brown Trout spawning season (Nehring and Andersen 1993). As such, greater use of the fishway by Brown Trout may have been associated with spawning movements. Similarly, species that do not spawn in the fall, along with smaller (i.e., immature) fish, may have lacked the motivation to make movements during this time. Some of the native fish species that are found in the transition zone and eastern plains will move upstream in the spring prior to spawning semibuoyant eggs that are dispersed downstream during high flows (Fausch and Bestgen 1997). Although the sample size was relatively small, no Brassy Minnow (a target species) were detected during the extended study. Brassy Minnow and similar species may become most active in late spring as flows recede and water temperatures warm (Copes 1975). Due to the timing of the study, water temperatures were likely colder than the optimal physiological range for some of the warmwater species, which may have affected their swimming performance and motivation. Therefore, long-term studies that elucidate movement patterns for species with diverse life histories and habitat needs would be informative.

One of the objectives of the study was to investigate the strengths and limitations of the short-term enclosure method for evaluating fishway performance. The enclosure method represents a novel approach for evaluating fish passage structures with a diverse array of species over a relatively short study period, reducing maintenance, monitoring, and evaluation costs when compared with long-

term studies. Releasing fish into an enclosure at the fishway entrance eliminates potential issues with attraction flows or seasonal motivation, which allows managers to validate that target species and life stages are physically capable of ascending the fishway. Increasing fish density is known to motivate upstream movement (Tsukamoto et al. 1985; Kondratieff and Myrick 2006), and fish densities were much higher during the enclosure study than during the extended study. This likely resulted in known passage of species (e.g., Brassy Minnow) during the enclosure study that may not have been observed otherwise.

The enclosure method presented here also has a number of limitations, and we recommend the following considerations for strengthening study design and testing small-bodied fish passage efficiency. First, the enclosure method alone is insufficient for evaluating attraction to the fishway entrance under natural conditions, but this limitation can be addressed by integrating the results from enclosure and extended studies. Second, incomplete recovery from the invasive PIT-tagging procedure may have affected the passage efficiency for species that were transported to the study site (e.g., Brassy Minnow). The mortality rate for tagged Brassy Minnow was 46% compared with 17% for all of the tagged fish, both of which were higher than the mortality rates ($\leq 7\%$) that were reported in a similar study (Pennock et al. 2018). Although all mortalities were noted and removed from the data set prior to analysis, increasing recovery and acclimation times from hours to days would minimize the potential effects of tagging on the passage results. Third, larger sample sizes are recommended for future studies, and similar sample sizes for each species could strengthen the comparison of results across species. In some cases, it may not be practical to PIT-tag smaller fish (<50 mm TL), in which case we recommend placing a second enclosure at the upstream end of the fishway to capture fish that successfully ascend. Finally, the enclosure study was limited to a relatively narrow window of time (2 d) and associated flows. Maintaining an enclosure for extended periods could be difficult due to debris accumulation and increased water velocities during higher flows. Continuous monitoring of fishway discharge during extended studies would support the evaluation of fish passage in relation to streamflow magnitude and frequency.

The FCRID fishway represents the first effort to restore longitudinal connectivity in the transition zone of the Cache la Poudre River. Overall, the FCRID fishway met the objective of passing a variety of fish species, including weaker-swimming species like Brassy Minnow and stronger-swimming species like Brown Trout. The results from this study were used to identify optimal flows in the fishway to support passage, modify the structure to improve hydraulic conditions at the fishway entrance, and inform design criteria (e.g., slope, capacity, roughness, and configuration) for similar structures. Additional research investigating fish movement patterns, attraction flows, species-specific behavioral traits, and various design configurations would further optimize the performance of nature-like fishways. Other variables, such as water temperature and dissolved oxygen, could also be monitored to improve our understanding of fish movement ecology and provide guidelines for the operation of fish passage structures. As more demand is placed on our infrastructure due to growing populations in Colorado and other western states, the maintenance and modernization of instream structures will provide opportunities to restore fish passage. Given the vast number of instream structures, potential project sites should be prioritized based on the current distribution of fish species and the length of restored connectivity to assure that limited funding is used to maximize the benefits of restored habitat connectivity on fishery resources.

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REFERENCES

Aedo, J., M. Belk, and R. Hotchkiss. 2009. Morphology and swimming performance of Utah fishes: critical information for culvert design in Utah streams. Utah Department of Transportation, Research Division, Report UT-09.12, Salt Lake City.

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York.

Bainbridge, R. 1960. Speed and stamina in three fish. Journal of Experimental Biology 37:129–153.

Baki, A. M., D. Z. Zhu, and N. Rajaratnam. 2014. Mean flow characteristics in a rock-ramp-type fish pass. Journal of Hydraulic Engineering 140:156–168.

Beamish, F. W. H. 1978. Swimming capacity. Pages 101–187 *in* W. S. Hoar and D. J. Randall, editors. Fish physiology, volume 7. Academic Press, New York.

Bestgen, K. R., N. L. Poff, D. W. Baker, B. P. Bledsoe, D. M. Merritt, M. Lorie, G. T. Auble, J. S. Sanderson, and B. C. Kondratieff. 2019. Designing flows to enhance ecosystem functioning in heavily altered rivers. Ecological Applications 30:e02005.

Brown, R. S., S. J. Cooke, W. G. Anderson, and R. S. McKinley. 1999. Evidence to challenge the "2% rule" for biotelemetry. North American Journal of Fisheries Management 19:867–871.

Bunt, C. M., T. Castro-Santos, and A. Haro. 2011. Performance of fish passage structures at upstream barriers to migration. River Research and Applications 28:457–478.

Burgetz, I. J., A. Rojas-Vargas, S. G. Hinch, and D. J. Randall. 1998. Initial recruitment of anaerobic metabolism during sub-maximal swimming in Rainbow Trout (*Oncorhynchus mykiss*). The Journal of Experimental Biology 201:2711–2721.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis of fish survival experiments based on release-recapture data. American Fisheries Society, Monograph 5, Bethesda, Maryland.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.

Chow, V. T. 1959. Open-channel hydraulics. The Blackburn Press, Caldwell, New Jersey.

Copes, F. A. 1975. Ecology of the Brassy Minnow, *Hybognathus hankinsoni* (Cyprinidae). Reports on the fauna and flora of Wisconsin. Museum of Natural History. University of Stevens Point, Stevens Point, Wisconsin.

CPW (Colorado Parks and Wildlife). 2015. State wildlife action plan: a strategy for conserving wildlife in Colorado. CPW, Denver.

Dockery, D. R., T. E. McMahon, K. M. Kappenman, and M. Blanks. 2016. Evaluation of swimming performance for fish passage of Longnose Dace *Rhinichthys cataractae* using an experimental flume. Journal of Fish Biology 90:980–1000.

Eschenroeder, J. C., and J. H. Roberts. 2019. Habitat loss, fragmentation, and the genetic status of Roanoke Bass. Canadian Journal of Fisheries and Aquatic Sciences 77:375–387.

Farlinger, S., and F. W. H. Beamish. 1978. Changes in blood chemistry and critical swimming speed of Largemouth Bass, *Micropterus salmoides*, with physical conditioning. Transactions of the American Fisheries Society 107:523–527.

Fausch, K. D., and K. R. Bestgen. 1997. Ecology of stream fishes indigenous to the central and southern Great Plains. Pages 131–166 *in* F. L. Knopf and F. B. Samson, editors. Ecology and conservation of Great Plains vertebrates. Springer-Verlag, New York.

Fencl, J. S., M. E. Mather, K. H. Costigan, and M. D. Daniels. 2015. How big of an effect do small dams have? Using geomorphological footprints to quantify spatial impact of low-head dams and identify patterns of across-dam variation. PLoS (Public Library of Science) ONE [online serial] 10(11):e0141210.

Fetherman, E. R., B. W. Avila, and D. L. Winkelman. 2014. Raft and floating radio frequency identification (RFID) antenna systems for detecting and estimating abundance of PIT-tagged fish in rivers. North American Journal of Fisheries Management 34:1065–1077.

Fetherman, E. R., D. L. Winkelman, L. L. Bailey, G. J. Schisler, and K. Davies. 2015. Brown Trout removal effects on short-term survival of *Myxobolus cerebralis*-resistant Rainbow Trout. Transactions of the American Fisheries Society 144:610–626.

Ficke, A. D. 2015. Mitigation measures for barriers to Great Plains fish migration. Doctoral dissertation. Colorado State University, Fort Collins.

Ficke, A. D., and C. A. Myrick. 2009. A method for monitoring movements of small fishes in urban streams. North American Journal of Fisheries Management 29:1444–1453.

Ficke, A. D., C. A. Myrick, and L. J. Hansen. 2007. Potential impacts of global climate change on freshwater fisheries. Reviews in Fish Biology and Fisheries 17:581–613.

Ficke, A. D., C. A. Myrick, and N. Jud. 2011. The swimming and jumping ability of three small Great Plains fishes: implications for fishway design. Transactions of the American Fisheries Society 140:1521–1531.

Forty, M., J. Spees, and M. C. Lucas. 2016. Not just for adults! Evaluating the performance of multiple fish passage designs at low-head barriers for the upstream movement of juvenile and adult trout *Salmo trutta*. Ecological Engineering 96:214–224.

Fox, B. D., B. P. Bledsoe, E. Kolden, M. C. Kondratieff, and C. A. Myrick. 2016. Eco-hydraulic evaluation of a whitewater park as a fish passage barrier. Journal of the American Water Resources Association 52:420–442.

Gregory, T. R., and C. M. Wood. 1998. Individual variations and interrelationships between swimming performance, growth rate, and feeding in juvenile Rainbow Trout (*Oncorhynchus mykiss*). Canadian Journal of Fisheries and Aquatic Sciences 55:1583–1590.

Halvorsen, M., and O. B. Stabell. 1990. Homing behaviour of displaced stream-dwelling Brown Trout. Animal Behaviour 39:1089–1097.

Harper, D. G., and R. W. Blake. 1990. Fast-start performance of Rainbow Trout *Salmo gairdneri* and Northern Pike *Esox lucius*. Journal of Experimental Biology 150:321–342.

Hatry, C., J. D. Theim, D. Hatin, P. Dumont, K. E. Smokorowski, and S. J. Cooke. 2016. Fishway approach behavior and passage of three redhorse species (*Moxostoma anisurum, M. carinatum*, and *M. macrolepidotum*) in the Richelieu River, Quebec. Environmental Biology of Fishes 99:249–263.

Hawkins, D. K., and T. P. Quinn. 1996. Critical swimming velocity and associated morphology of juvenile Coastal Cutthroat Trout (*Oncorhynchus clarkia clarkii*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. Canadian Journal of Fisheries and Aquatic Sciences 53:1487–1496.

Hodge, B. W., E. R. Fetherman, K. B. Rogers, and R. Henderson. 2017. Effectiveness of a fishway for restoring passage of Colorado River Cutthroat Trout. North American Journal of Fisheries Management 37:1332–1340.

Jones, D. R., J. W. Kiceniuk, and O. S. Bamford. 1974. Evaluation of the swimming performance of several fish species from the Mackenzie River. Journal of the Fisheries Research Board of Canada 31:1641–1647.

Katopodis, C., J. A. Kells, and M. Archarya. 2001. Nature-like and conventional fishways: alternative concepts? Canadian Water Resources Journal 26:211–232.

Katopodis, C., and J. G. Williams. 2012. The development of fish passage research in a historical context. Ecological Engineering 48:8–18.

Kondratieff, M. C., and C. A. Myrick. 2006. How high can Brook Trout jump? A laboratory evaluation of Brook Trout jumping performance. Transactions of the American Fisheries Society 135:361–370.

Landsman, S. J., N. McLellan, J. Platts, and M. R. van den Heuvel. 2018. Nonsalmonid versus salmonid passage at nature-like and pool-and-weir fishways in Atlantic Canada, with special attention to Rainbow Smelt. Transactions of the American Fisheries Society 147:94–110.

Leavy, T. R., and T. H. Bonner. 2009. Relationships among swimming ability, current velocity association, and morphology for freshwater lotic fishes. North American Journal of Fisheries Management 29:72–83.

Liao, J. C. 2007. A review of fish swimming mechanics and behaviour in altered flows. Philosophical Transactions of the Royal Society B 362:1973–1993.

Lupandin, A. I. 2005. Effect of flow turbulence on swimming speed of fish. Biology Bulletin 32:461–466.

Malmqvist, B., and S. Rundle. 2002. Threats to the running water ecosystems of the world. Environmental Conservation 29:134–153.

Manning, R. 1891. On the flow of water in open channels and pipes. Transactions of the Institution of Civil Engineers of Ireland 20:161–207.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21.

Nehring, R. B., and R. M. Andersen. 1993. Determination of population limiting critical salmonid habitats in Colorado streams using the Physical Habitat Simulation Systems. River 4(1):1–19.

Peake, S., R. S. McKinley, and D. A. Scruton. 1997. Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design. Journal of Fish Biology 51:710–723.

Pennock, C. A., D. Bender, J. Hofmeier, J. A. Mounts, R. Waters, V. D. Weaver, and K. B. Gido. 2018. Can fishways mitigate fragmentation effects on Great Plains fish communities? Canadian Journal of Fisheries and Aquatic Sciences 75:121–130.

Prenosil, E. J. 2014. Tests to determine the effects of culverts on fish and macroinvertebrates in central Nebraska streams. Master's thesis. University of Nebraska, Kearney.

Richer, E. E., E. R. Fetherman, M. C. Kondratieff, and T. A. Barnes. 2017. Incorporating GPS and mobile radio frequency identification to detect PIT tagged fish and evaluate habitat utilization in streams. North American Journal of Fisheries Management 37:1249–1264.

Richter, B. D., D. Bartak, P. Caldwell, K. F. Davis, P. Debaere, A. Y. Hoekstra, T. Li, L. Marston, R. McManamy, M. M. Mekonnen, B. L. Ruddell, R. R. Rushforth, and T. J. Troy. 2020. Water scarcity and fish imperilment driven by beef production. Nature Sustainability 3:319–328.

Rosenberg, D. M., P. McCully, and C. M. Pringle. 2000. Global environmental effects of hydrological alteration: introduction. BioScience 50:746–751.

Scheurer, J. A., K. D. Fausch, and K. R. Bestgen. 2003. Multiscale processes regulate Brassy Minnow persistence in a Great Plains river. Transactions of the American Fisheries Society 132:840–855.

Schlosser, I. J., and P. L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. Pages 392–401 in J. L. Nielsen, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society, Bethesda, Maryland.

Scott, M. K., and D. D. Magoulick. 2008. Swimming performance of five warmwater stream fish species. Transactions of the American Fisheries Society 137:209–215.

Sheer, M. B., and E. A. Steel. 2006. Lost watersheds: barriers, aquatic habitat connectivity, and salmon persistence in the Willamette and lower Columbia River basins. Transactions of the American Fisheries Society 135:1654–2006.

Steffensen, S. M., J. D. Thiem, K. M. Stamplecoskie, T. R. Binder, C. Hatry, N. Langlois-Anderson, and S. J. Cooke. 2013. Biological effectiveness of an inexpensive nature-like fishway for passage of warmwater fish in a small Ontario stream. Ecology of Freshwater Fish 22:374–383.

Stephens, T. A., B. P. Bledsoe, B. D. Fox, E. Kolden, and M. C. Kondratieff. 2015. Effects of whitewater parks on fish passage: a spatially explicit hydraulic analysis. Ecological Engineering 83:305–318.

Swarr, T. R. 2018. Improving rock ramp fishways for small-bodied Great Plains fishes. Master's thesis. Colorado State University, Fort Collins.

Tsukamoto, K., K. Uchida, Y. Murakami, M. Endo, and T. Kajihara. 1985. Density effect on jumping behavior and swimming upstream in the Ayu juveniles. Bulletin of the Japanese Society of Scientific Fisheries 51:323.

Underwood, Z. E., C. A. Myrick, and R. I. Compton. 2014. Comparative swimming performance of five Catostomus species and Roundtail Chub. North American Journal of Fisheries Management 34:753–763.

USGS (U.S. Geological Survey). 2016. The StreamStatsprogram. Available: http://streamstats.usgs.gov. (November 2019).

Van Leeuwen, C. H. A., K. Dalen, J. Museth, C. Junge, and L. A. Vollestad. 2018. Habitat fragmentation has interactive effects on the population genetic diversity and individual behavior of a freshwater salmonid fish. River Research and Applications 34:60–68.

Ward, D. L., A. A. Schultz, and P. G. Matson. 2003. Differences in swimming ability and behavior in response to high water velocities among native and nonnative fishes. Environmental Biology of Fishes 68:87–92.

Warren, M. L., and M. G. Pardew. 1998. Road crossings as barriers to small-stream fish movement. Transactions of the American Fisheries Society 127:637–644.

Webb, P. W. 1975. Acceleration performance of Rainbow Trout Salmo gairdneri and Green Sunfish Lepomis cyanellus. Journal of Experimental Biology 63:451–465.

Webb, P. W. 1976. The effect of size on fast-start performance of Rainbow Trout Salmo gairdneri and a consideration of piscivorous predator-prey interactions. Journal of Experimental Biology 65:157–177.

Webb, P. W. 1977. Effects of median fin amputation on fast-start performance of Rainbow Trout (Salmo gairdneri). Journal of Experimental Biology 68:123–135.

Webb, P. W. 1978. Fast-start performance and body form in seven species of teleost fish. Journal of Experimental Biology 74:211–226.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(Supplement):120–138.

Wildman, L., P. Parasiewicz, C. Katopodis, and U. Dumont. 2003. An illustrated handbook on nature-like fishways—summarized version. American Rivers, Washington, D.C.

Yu, S. L., and E. J. Peters. 1997. Use of Froude number to determine habitat selection by fish. Rivers 6(1):10–18.

SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.