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Attraction, Entrance, and Passage Efficiency of Arctic Grayling, Trout, and Suckers at Denil Fishways in the Big Hole River Basin, Montana

Ben Triano*

Fish and Wildlife Ecology and Management Program, Ecology Department, Montana State University, Post Office Box 173460, Bozeman, Montana 59717, USA

Kevin M. Kappenman*

U.S. Fish and Wildlife Service, Bozeman Fish Technology Center, 4050 Bridger Canyon Road, Bozeman, Montana 59715, USA

Thomas E. McMahon

Fish and Wildlife Ecology and Management Program, Ecology Department, Montana State University, Post Office Box 173460, Bozeman, Montana 59717, USA

Matt Blank

Western Transportation Institute, Montana State University, 2327 University Way, Bozeman, Montana 59717, USA

Kurt C. Heim

U.S. Fish and Wildlife Service, Western New England Complex, 11 Lincoln Street, Essex Junction, Vermont 05452, USA

Albert E. Parker

Center for Biofilm Engineering, Department of Mathematical Sciences, Montana State University, 304 Barnard Hall, Bozeman, Montana 59717, USA

Alexander V. Zale

U.S. Geological Survey, Montana Cooperative Fishery Research Unit, Fish and Wildlife Ecology and Management Program, Department of Ecology, Montana State University, Post Office Box 173460, Bozeman, Montana 59717, USA

Nolan Platt

U.S. Department of Agriculture Forest Service, Lolo National Forest, 24 Fort Missoula Road, Missoula, Montana 59804, USA

Katey Plymesser

Department of Civil Engineering, Montana State University, 223 Cobleigh Hall, Bozeman, Montana 59717, USA

*Corresponding authors: benjamintriano@gmail.com; kevin_kappenman@fws.gov

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Abstract

The Big Hole River basin in southwestern Montana supports the only indigenous, self-sustaining fluvial population of Arctic Grayling *Thymallus arcticus* in the conterminous United States, but the basin is fragmented by numerous low-head irrigation diversion dams. Denil fishways at 63 diversion dams provide Arctic Grayling and other fishes opportunities for year-round access to critical habitats; however, their efficiency has not been evaluated. We quantified attraction, entrance, and passage for hatchery-reared Arctic Grayling, wild trout (Brook Trout *Salvelinus fontinalis* and Brown Trout *Salmo trutta*), and wild suckers (White Sucker *Catostomus commersonii* and Longnose Sucker *C. catostomus*) during 14 field trials conducted at six Denil fishways over a representative range of fishway slopes and hydraulic conditions using passive integrated transponder telemetry. Attraction (60.4–84.3%) and entrance (44.3–78.6%) efficiencies were variable across test conditions and reduced overall fishway efficiencies (19.1–55.8%). In contrast, upon entry, passage efficiencies were high (96.2–97.0%) for all taxa across all test conditions. Attraction of hatchery-reared Arctic Grayling increased with upstream depth (a surrogate for fishway discharge) and attraction flow, but attraction of wild fish was less affected by these conditions. Entrance of Arctic Grayling, Brook Trout, and Brown Trout decreased with upstream depth and fishway slope, especially when plunging entrance conditions associated with shallow downstream depths were present. However, entrance of Arctic Grayling and both trout species increased with downstream depth, and submerged fishway entrances demonstrated promise for increasing entrance efficiency at fishways with high discharges and steep slopes. We demonstrate that comprehensive evaluations of fishway efficiency components can identify specific solutions that improve fishway efficiency; application of these engineering solutions at individual fishways (as needed) could improve their efficiency and further enhance aquatic connectivity for fishes in the Big Hole River basin and elsewhere.

Connectivity in rivers facilitates migration of fish to meet life history requirements and respond to biological and environmental cues (Northcote 1984; Baras and Lucas 2001). However, anthropogenic barriers such as dams, diversions, culverts, and road crossings can impede fish migration and negatively affect populations (Morita et al. 2000; Alò and Turner 2005). Barrier removal can restore fish populations (Roni et al. 2008) but is not always feasible because of overriding socioeconomic benefits and high costs (O'Hanley and Tomberlin 2005; Januchowski-Hartley et al. 2013). Alternatively, fishways are often installed at potential migration barriers to restore connectivity (Bunt et al. 1999; Schmetterling et al. 2002), but relatively few fishways have been evaluated in the field to determine their efficiency in passing fish (Noonan et al. 2012; Cooke and Hinch 2013).

A comprehensive evaluation of fishway efficiency requires the systematic assessment of three distinct efficiency components (attraction, entrance, and passage) of approaching fish, any of which can reduce overall fishway efficiency (Bunt et al. 2012, 2016). However, previous studies have typically defined success rates by combining multiple efficiency components (Forty et al. 2016; Hodge et al. 2017), precluding assessment of each distinct component. “Approach” describes the number of fish that encounter a potential barrier and is an index of potential population use (Hodge et al. 2017). “Attraction efficiency” is the percentage of approaching fish that locate the fishway entrance, “entrance efficiency” is the percentage of attracted fish that enter the fishway, and “passage efficiency” is the percentage of entering fish that successfully pass (Cooke and Hinch 2013). “Overall efficiency” is the

percentage of approaching fish that are attracted to, enter, and successfully pass a fishway (Baker et al. 2019).

Quantifying these metrics individually provides important insight as to how each component limits overall fishway efficiency (Bunt et al. 2012). For example, large numbers of approaching fish may be attracted to a fishway, but few may enter. Alternatively, few approaching fish may be attracted to the entrance, but those that are attracted may have high entrance and passage success. The time it takes a fish to become attracted to, enter, and pass a fishway is also of interest because delays at barriers and passage structures can detrimentally affect reproduction and fish health (Mesa and Magie 2006; Newton et al. 2018). Understanding how fish are limited in using a fishway provides a basis for strategic improvements to fishway design that address specific limiting factors and enhance overall efficiency.

Denil fish ladders (Katopodis 1992) are commonly used to restore connectivity in rivers (Clay 1995; Bunt et al. 1999; Haro et al. 1999; Schmetterling et al. 2002); however, their efficiency for passing many fish species under different slopes and hydraulic conditions is not well understood (Haro et al. 1999; Mallen-Cooper and Stuart 2007). Seasonal hydrologic variation alters entrance and exit water depths (hereafter downstream and upstream depths, respectively, or collectively fishway depths) at Denil fishways (Platt 2019), and fishway depths markedly affect hydraulic conditions inside a Denil fishway, thereby affecting passage success (Haro et al. 1999; Blank et al., [In press](#)). Fishway depths are directly influenced by fishway slope, which has variable effects on passage success through Denil fishways; slope had little effect on passage

success of Arctic Grayling *Thymallus arcticus* through an Alaska Steeppass fish ladder (a type of Denil fishway) (Tack and Fisher 1977) but increasing slope negatively affected passage of nonsalmonid fishes through Denil fishways (Haro et al. 1999; Mallen-Cooper and Stuart 2007).

Denil fishways were installed throughout the Big Hole River basin in Montana to improve aquatic connectivity for imperiled Arctic Grayling. Big Hole River Arctic Grayling are the last remaining indigenous, self-sustaining fluvial Arctic Grayling population in the conterminous United States (Shepard and Oswald 1989; Kaya 1992) and have been considered for protection under the Endangered Species Act since 1982 (USOFR 2014). Big Hole River Arctic Grayling make seasonal migrations exceeding 80 km to access critical main-stem and tributary habitats for spawning, feeding, wintering, and thermal refuge (Shepard and Oswald 1989; Lamothe and Magee 2003); however, the basin is fragmented by numerous low-head irrigation diversion dams (pin-and-plank style; Schmetterling et al. 2002) that impound and divert water for agriculture. The Candidate Conservation Agreement with Assurances (CCAA) for Fluvial Arctic Grayling in the upper Big Hole River was established in 2006 (MTFWP and USFWS 2006), with a primary focus being mitigation of barriers to Arctic Grayling migration. Since 2001 and following the establishment of the CCAA, standard-type Denil fishways have been installed at 63 irrigation diversions in the basin to improve aquatic connectivity; however, their efficiency for passing Arctic Grayling and other fishes has not been evaluated comprehensively.

We evaluated the efficiency of Denil fishways for facilitating upstream passage of Arctic Grayling and other species in the Big Hole River basin using passive integrated transponder (PIT) telemetry. Our main objectives were to (1) quantify all three efficiency components (attraction, entrance, and passage) to determine which components limit overall efficiency and (2) evaluate how fishway depths and slope affect each efficiency component. Achieving these objectives allowed us to provide specific recommendations for improving the overall efficiency of existing and future Denil fishway installations, which could contribute to enhancing aquatic connectivity in the Big Hole River basin and elsewhere.

METHODS

Study Area

The Big Hole River originates in the Beaverhead Mountains of southwestern Montana and flows 250 km to its confluence with the Beaverhead River (DNRC 1979). The river and its tributaries provide a variety of critical habitats for a diverse assemblage of native (Arctic Grayling, Westslope Cutthroat Trout *Oncorhynchus clarkii*

lewisi, Mountain Whitefish *Prosopium williamsoni*, Burbot *Lota lota*, White Sucker *Catostomus commersonii*, Longnose Sucker *C. catostomus*, Mountain Sucker *C. platyrhynchus*, Longnose Dace *Rhinichthys cataractae*, and Rocky Mountain Sculpin *Uranidea* sp. cf. *bairdii*) and nonnative (Brook Trout *Salvelinus fontinalis*, Brown Trout *Salmo trutta*, and Rainbow Trout *O. mykiss*) fishes (Oswald 2000).

Seasonal hydrologic variation and irrigation practices in the Big Hole River basin result in highly variable fishway depths at Denil fishways (Platt 2019). The river is fed by spring snowmelt that results in peak stream discharges during June and early July and low base flows during August and September (Sladek 2013; Vatland 2015). Land use in the basin is predominantly agricultural, with about 1,000 water rights allocated for seasonal diversion of surface water to irrigate hay fields and support livestock (MTFWP and USFWS 2006). Low base flows are often exacerbated by irrigation withdrawals (Vatland 2015) and potentially limit connectivity through Denil fishways. Fishways typically operate at deep upstream depths (45.0–60.0 cm) and high fishway discharges (0.075–0.20 m³/s) during peak stream discharges, but fishway discharges can decrease to nearly zero during base flows and periods of irrigation withdrawal.

Study Sites

Fishway efficiency was evaluated in 14 field trials at six Denil fishways in the upper Big Hole River basin from June to October of 2018. Seventeen fishways were initially evaluated in 2017 to assess seasonal hydrologic and hydraulic variation and physical differences among fishway installations (Platt 2019). Three primary study sites (multiple field trials) and three secondary study sites (single trials) were selected for fishway efficiency evaluations in 2018 (Figure 1; Table 1) to best represent the range of fishway depths and slopes observed in 2017. Primary sites were on Steel Creek, upper Warm Springs Creek, and the main-stem Big Hole River, with respective slopes of 5.0, 10.7, and 15.6%; three or four trials were conducted at each primary site over a range of fishway depths. Secondary sites were included to represent other conditions observed among Big Hole River Denil fishways, such as submerged fishway entrances at Rock Creek and Swamp Creek (Figure 2) and a near 0.0% slope and plunging entrance conditions at lower Warm Springs Creek (Figure 3). All Denil fishways tested were standard type with identical width and depth dimensions of 61 × 61 cm (Katopodis et al. 1997).

Hydraulic Conditions

Upstream and downstream depths and water temperatures were recorded every 5 min by data loggers (Model U20L-04; Onset Computer Corporation, Bourne,

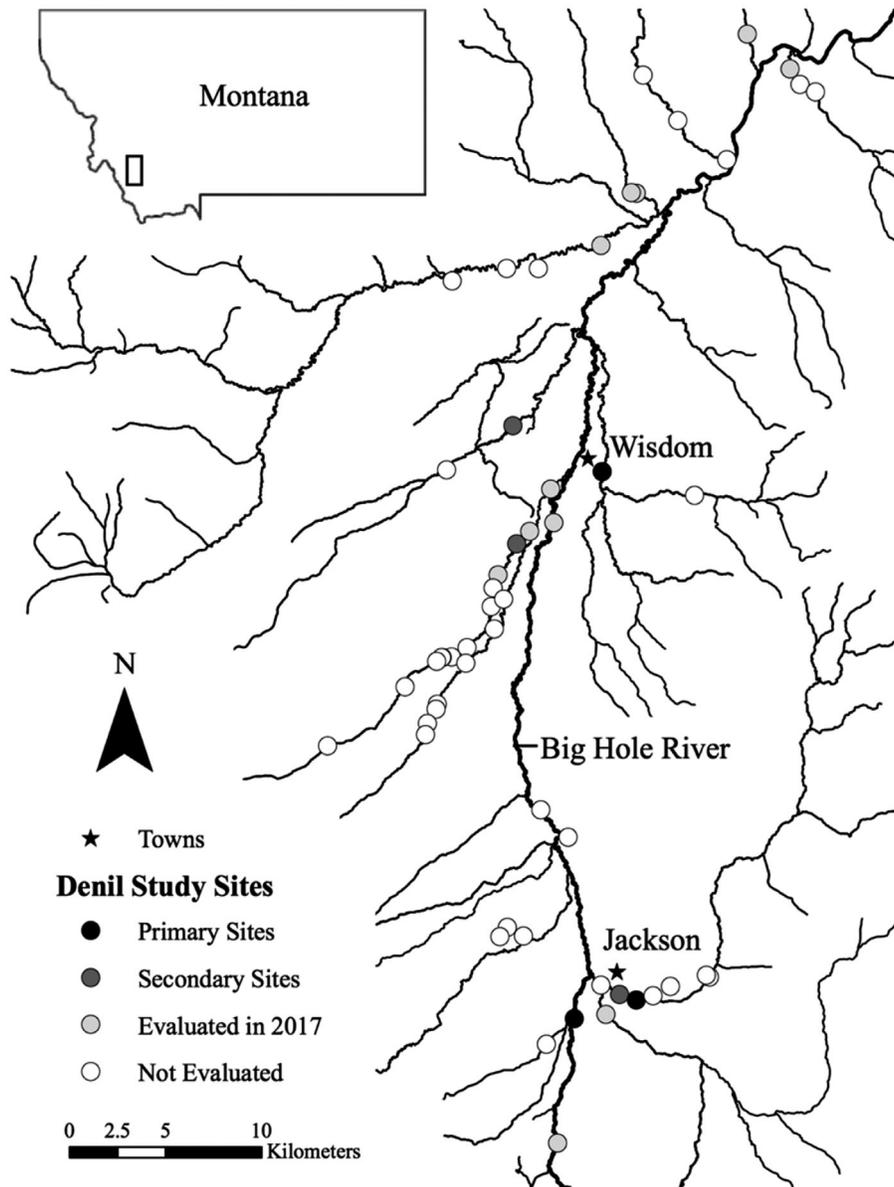


FIGURE 1. Map of the upper Big Hole River basin study area, depicting locations of the 63 Denil fishways currently installed under the CCAA program.

Massachusetts) installed in stilling wells positioned at the exit and entrance of the fishway. Fishway depths were measured relative to the bottom (or “invert”; Figure 4) of the fishway exit and entrance (i.e., upstream and downstream depths describe how full the fishway is at the exit and entrance, respectively). Fishway discharge was calculated every 5 min as the average estimate of five laboratory-derived rating curves for standard-type Denil fishways (Katopodis 1992; Katopodis et al. 1997; Rajaratnam et al. 1997; FAO and DVWK 2002; Odeh 2003) that predicted discharge from upstream depth (measured relative to the v-notch of the most upstream baffle; Figure 4)

and slope (Platt 2019). Total stream discharge downstream of the diversion structure was estimated daily using stage–discharge relationships developed by Platt (2019). Fishway attraction flow (%) was calculated as the relative contribution of fishway discharge to the total stream discharge downstream of the diversion dam.

Test Fish

Field trials were run with wild fish present at each site, including Brook Trout (mean TL \pm SD = 231 \pm 58 mm) and other taxa as available: Longnose Sucker (194 \pm 34 mm), White Sucker (230 \pm 57 mm), Brown Trout (285 \pm

TABLE 1. Average physical and hydraulic conditions in trials 1–14; the variation in hydraulic conditions observed during each trial is reported in parentheses, and overall means represent the average conditions observed across all trials. Abbreviations are as follows: slope = fishway slope, and length = fishway length.

Study site	Trial	Slope (%)	Length (m)	Upstream depth (cm)	Fishway discharge (m ³ /s)	Downstream depth (cm)	Water temperature (°C)	Attraction flow (%)
Steel Creek	4	5.0	2.77	47.1 (45.0–50.1)	0.067 (0.061–0.077)	19.7 (18.9–20.7)	17.5 (12.1–23.8)	74.0
	6	5.0	2.77	25.0 (23.6–26.6)	0.013 (0.011–0.016)	12.1 (11.3–13.1)	16.6 (11.2–22.2)	77.0
	9	5.0	2.77	36.6 (33.3–38.8)	0.037 (0.029–0.043)	15.8 (14.9–16.8)	13.0 (8.6–17.9)	68.0
	10	5.0	2.77	20.5 (19.7–21.4)	0.007 (0.006–0.008)	12.6 (11.9–13.7)	12.2 (7.7–17.7)	30.0
Warm Springs Creek (upper)	3	10.7	3.66	65.4 (58.4–69.6)	0.209 (0.165–0.239)	44.7 (41.8–53.9)	16.2 (13.0–19.8)	29.0
	7	10.7	3.66	23.8 (22.8–25.2)	0.019 (0.017–0.022)	26.5 (24.7–27.7)	14.0 (10.0–18.6)	21.0
	12	10.7	3.66	18.1 (15.0–21.5)	0.008 (0.004–0.014)	28.9 (27.4–30.8)	6.4 (3.5–10.1)	6.0
	14	10.7	3.66	37.1 (35.7–42.4)	0.059 (0.054–0.081)	26.4 (25.0–28.0)	4.3 (2.0–7.4)	80.0
Big Hole River	8	15.6	3.66	22.1 (17.5–26.8)	0.022 (0.011–0.035)	20.7 (19.2–24.4)	10.8 (8.0–14.3)	10.0
	11	15.6	3.66	52.8 (50.2–55.1)	0.165 (0.148–0.180)	23.8 (21.0–25.9)	9.1 (5.3–11.8)	52.0
	13	15.6	3.66	36.9 (35.4–38.6)	0.075 (0.068–0.083)	19.8 (18.3–21.9)	8.4 (4.8–12.2)	46.0
Rock Creek	1	13.4	3.66	55.0 (51.4–61.5)	0.167 (0.143–0.210)	80.4 (76.7–86.4)	14.1 (10.7–18.5)	105.0
Warm Springs Creek (lower)	5	0.6	3.66	54.1 (47.9–57.5)	0.083 (0.057–0.099)	5.7 (4.0–9.1)	17.3 (13.2–21.9)	33.0
Swamp Creek ^a	2 ^a	15.7 ^a	3.66	49.4 (45.6–52.5) ^a	0.145 (0.123–0.165) ^a	70.7 (69.8–71.7) ^a	19.0 (14.0–23.5) ^a	80.0 ^a
Overall means		9.5	3.39	38.0	0.072	25.9	12.3	49.0

^aTrial 2 was not included in overall mean calculations because of a considerable change in hydraulic conditions that occurred 20 h into the trial; hydraulic conditions reported here are from the first 20 h of trial 2. Trial 2 test fish were not included in data analyses and are only discussed in anecdotal comparisons.



FIGURE 2. Photo of the submerged fishway entrance during trial 2. The submerged entrance demonstrated promise for increasing entrance efficiency under the otherwise-limiting high fishway discharge and steep slope (Table 1) by creating presumably more favorable entrance conditions than those in trial 11 (Figure 10).



FIGURE 3. Photo of plunging entrance conditions during trial 5. The deep upstream depth, shallow downstream depth, and shallow slope (Table 1) resulted in an entrance plunge that presumably restricted the entrance of Arctic Grayling (0.0% entrance of 14 attracted Arctic Grayling).

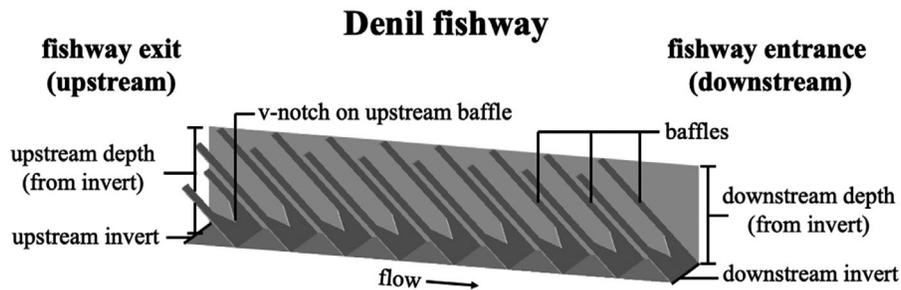


FIGURE 4. Denil fishway schematic identifying key components and depth measurements.

73 mm), Burbot (282 ± 55 mm), and Mountain Whitefish (206 mm). We included 50 Brook Trout in all trials except trial 1 ($n = 36$) and up to 30 fish combined of other taxa. Wild fish were collected on the first day of each trial by backpack electrofishing the stream segment immediately upstream of the diversion structure. Short-term displacement trials in which fish are captured upstream of a potential barrier and relocated downstream are effective for rapid evaluations of passage structures by invoking a homing response that increases motivation and participation of fish (Armstrong and Herbert 1997; Schmetterling et al. 2002; Burford et al. 2009). Captured fish were anesthetized with AQUIS anesthetic (Aquatics Fish Health, Kirkland, Washington), measured (TL), and tagged with half-duplex (HDX) PIT tags (Oregon RFID, Portland, Oregon). Fish longer than 130 mm were tagged with 23-mm \times 3.65-mm tags (0.6 g); shorter fish were tagged with 12-mm \times 2.12-mm tags (0.1 g) (Larsen et al. 2013; Forty et al. 2016). Tags were inserted into the abdomen through a 2–5-mm incision on the ventral surface anterior to the pelvic girdle (Forty et al. 2016); sutures were not necessary for tag retention with such small incisions (Bolland et al. 2009; Larsen et al. 2013). Tagged fish were placed in 19-L buckets of clean stream water for about 15 min to regain equilibrium and then transferred to holding pens in the stream prior to release.

Thirty-two age-1, hatchery-reared Arctic Grayling (212 ± 23 mm) were released simultaneously with wild fish in all trials because of the low availability of wild Arctic Grayling. Test Arctic Grayling originated from a population in Axolotl Lake, Montana, that was established from Big Hole River Arctic Grayling stock. Arctic Grayling were spawned at Axolotl Lake, and embryos were transported to the Yellowstone River Trout Hatchery in Big Timber, Montana, where they were incubated and reared at 12°C. Test Arctic Grayling were exercised in a flowing raceway at about 0.3 m/s for at least 1 month prior to use in trials; exercise training of 4–6 weeks increases swimming performance in captive-reared fish (Davison 1989, 1997). Test Arctic Grayling were PIT-tagged (23 mm) at least 1 month prior to field testing. On the day before each trial, 32 fish

were randomly netted from the raceway, scanned for tags, anesthetized, measured, and transported about 350 km to study sites in a 340-L insulated, oxygenated holding tank at 12°C. Test Arctic Grayling remained in the holding tank for 18–24 h prior to transfer to holding pens at each study site; temperature differences between the holding tank and study streams were $<2^\circ\text{C}$.

Test Protocol

All test fish were kept in holding pens for at least 1 h before simultaneous release downstream of the fishway and diversion dam. Release times were near midday (1145–1430 hours) except in trial 1 when release time was 1750 hours. Release locations were in the second pool downstream (15–40 m) of the diversion dam (Figure 5) so test fish had to volitionally leave the “release pool” and move upstream (“approach”) through a riffle to reach the “approach pool” directly below the fishway. Plastic fencing (6.35-mm mesh) was positioned at the downstream end of the release pool to prevent emigration from the study area; downstream emigration of test fish has been hypothesized as a cause for low participation in passage studies (Hodge et al. 2017). Fencing was also installed along the diversion dam spillway such that the fishway was the only path upstream. After release, fish movement was monitored for 72 h using PIT telemetry. Previous passage studies have shown movement of displaced fish within hours of release (Armstrong and Herbert 1997; Burford et al. 2009), and we observed 60.8% participation ($n = 74$ fish) during a 72-h pilot study in 2017.

Antenna Construction and Operation

We used four stationary PIT antennas (modified from Hodge et al. 2017) to track the approach, attraction, entrance, and passage of fish (Figure 5). Antennas were constructed as vertically oriented swim-through loops; antenna 1 consisted of one or two loops of 8-gauge copper-clad aluminum cable, and antennas 2–4 consisted of four loops of 12-gauge copper wire attached to a 0.6-m \times 0.6-m wooden frame. Approaching fish were detected at antenna 1 (A1), which spanned the stream channel

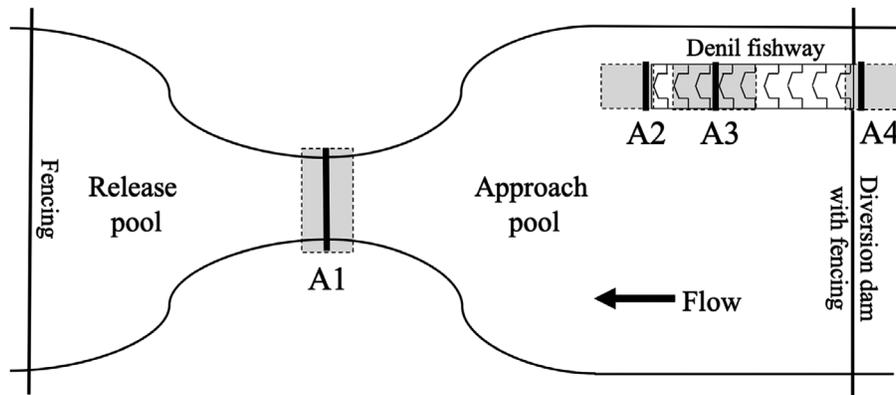


FIGURE 5. General schematic of the study site and PIT array configuration, including locations of four PIT antennas used to record the approach (A1), attraction (A2), entrance (A3), and passage (A4) of fish; the additional antenna (A5) is not pictured. Approximate detection ranges of A1–A4 are depicted by gray boxes. Schematic is not to scale.

between the release pool and approach pool. Attracted fish were detected at antenna 2 (A2), which was positioned 1–3 cm downstream of the fishway entrance and detected fish that staged within 0.6 m of the entrance. Entering fish were detected at antenna 3 (A3), which was positioned on the third baffle inside the fishway and detected fish as they first entered the fishway. Passing fish were detected at antenna 4 (A4), which was positioned just upstream of the fishway exit and detected fish as they passed the final baffle of the fishway. Each antenna was connected to a standard remote tuner board and all four tuner boards were linked to a multiantenna HDX reader (Oregon RFID, Portland, Oregon) that recorded the tag number, antenna, date, and time of each detection. The array was powered by two 12-V 80-Ah absorbed glass mat batteries connected in parallel. A fifth antenna (A5), which spanned the stream channel 30–50 m upstream of the diversion dam, was linked to a separate multiantenna HDX reader and was used to estimate detection probability at A4.

Detection Probability

We conducted two in-situ detection tests prior to each trial to ensure proper function of each PIT antenna. First, separate plastic pipes (3 m long, 1.9 cm in diameter) were placed through both A1 and the fishway (A2–A4). A single 23-mm PIT tag attached to parachute cord was pulled through each pipe with a fishing rod at about 1.5 m/s to simulate a single fish moving through the PIT array (single-tag test). A similar test was conducted with three 23-mm PIT tags spaced 0.4 m apart to simulate multiple fish moving through the PIT array simultaneously (multitag test) and evaluate the potential for missed detections due to tag collision from overlapping signals (<http://support.oregonrfid.com>). Ten single-tag and ten multitag tests were conducted prior to each trial, and antenna-specific detection probability estimates for each trial were

calculated as the percentage of total test tags successfully detected at each antenna. Estimates from single-tag tests were averaged among 13 trials to generate a single estimate of detection probability at each antenna position (A1, A2, etc.) across all trials. A separate estimate was calculated similarly for each antenna position from multitag tests.

We also analyzed the encounter history of each test fish to generate antenna-specific detection probability estimates from observed fish movements (Hodge et al. 2017). For example, if a fish was released and only detected at A5 (a “recorded” detection), its encounter history would be 100001 (the first “1” representing release, the 0s representing missed detections at A1–A4, and the last “1” representing detection at A5). Because this fish was detected at A5, it was assumed to have passed through all downstream antennas (A1–A4), and “adjusted” detections were inserted to complete the adjusted encounter history for this fish (111111). Adjusted encounter histories were built for every fish, including both “recorded” and “adjusted” detections for all upstream and downstream movements. The number of “recorded” detections was compared to the number of expected detections (recorded plus adjusted) at each antenna to calculate antenna-specific detection probability estimates for each trial (Heim et al. 2016). Antenna-specific estimates were averaged among the 13 trials to generate a single estimate of detection probability at each antenna position.

Data Analyses

Species groups.—We considered three species groups (Arctic Grayling, trout, and suckers) to increase sample sizes within groups for data analyses. Brown Trout, White Suckers, and Longnose Suckers were not tested in all trials, so we combined Brook Trout and Brown Trout (“trout” species group) and White Suckers and Longnose

Suckers (“suckers” species group). We expected similar performance within these groups because the swimming abilities of Brook Trout and Brown Trout and that of White Suckers and Longnose Suckers are comparable (Jones et al. 1974; Castro-Santos et al. 2013). Furthermore, similar life histories within each group provided expectations of similar motivation and behavior during trials.

Transit times.—We calculated transit time between each pair of sequential antennas to evaluate how long it took fish to approach, attract, enter, and pass through fishways. Approach time was calculated as the time between release and first approach, attraction time as the time between first approach and first attraction, entrance time as the time between first attraction and first entrance, and passage time as the time between first entrance and first passage. Only “recorded” detections with known detection times were considered in these analyses.

Summarized fishway efficiency.—We summarized attraction, entrance, and passage efficiencies for each species group across 13 trials (Table 2) to generally assess which components were most limiting to overall efficiency. Attraction, entrance, and passage efficiencies were quantified for each species group during each 72-h trial by analyzing adjusted encounter histories. We first omitted fish that did not volitionally reach the approach pool; the number of approaching fish was used only as a metric of participation to calculate attraction efficiency. Attraction, entrance, and passage efficiencies were then calculated as the percentages of fish reaching an antenna that later reached the next upstream antenna. For example, if 100 fish approached the fishway and 60 were attracted, attraction efficiency was 60.0%. If 30 of 60 attracted fish entered the fishway, entrance efficiency was 50.0%. Lastly, if 15 of

30 entering fish passed, passage efficiency was 50.0%. Overall efficiency in this example was 15.0%, with 15 of 100 approaching fish successfully passing the fishway.

Statistical Analyses

We conducted three separate statistical analyses to (1) estimate attraction, entrance, and passage efficiency for each species group (efficiency estimates and species comparisons); (2) predict attraction, entrance, and passage efficiency over the range of upstream depths tested (fishway efficiency versus upstream depth); and (3) determine what factors affected attraction, entrance, and passage efficiency (multiple regression analysis). All statistical modeling was performed using mixed-effects logistic regressions, with individual fish as the sampling unit and attraction, entrance, and passage as three separate binary outcomes. In all analyses, the log odds of each outcome (attraction, entrance, and passage) were modeled as linear combinations of fixed effects; random effects for study site and trial were included in all models to account for nonindependent observations of test fish within each trial (Zuur et al. 2009). Fish were frequently detected passing antennas multiple times during a trial; however, we only included a single observation per fish for each outcome (attraction, entrance, or passage) that included its farthest upstream progress relevant to that outcome by the end of the trial (Goerig et al. 2016). Hydraulic conditions fluctuated minimally during each trial, and fish were assigned the average hydraulic conditions present during their respective trials (Table 1).

Efficiency estimates and species comparisons.—Attraction, entrance, passage, and overall efficiencies were estimated for each species group using logistic regression, with species group as the single fixed effect in these

TABLE 2. Summarized fishway efficiencies over 13 trials; total counts (n) and fishway efficiencies (%) are reported for each species group tested (trout = Brook Trout and Brown Trout, suckers = White Sucker and Longnose Sucker).

Species group	Released (n)	Approached (n)	Attracted (n)	Entered (n)	Passed (n)	Attraction efficiency (%)	Entrance efficiency (%)	Passage efficiency (%)	Overall efficiency (%)
Arctic Grayling	416	335 (332) ^a	178	86 (83) ^a	79	53.1	48.3	95.2	23.8
Trout	668	618 (601) ^a	468	350 (333) ^a	319	75.7	74.8	95.8	53.1
Suckers	175	154 (151) ^a	79	60 (57) ^a	55	51.3	75.9	96.5	36.4
Burbot	8	7	4	2	2	57.1	50.0	100.0	28.6
Mountain Whitefish	1	1	1	1	1	100.0	100.0	100.0	100.0
All species combined	1,268	1,115 (1,092) ^a	730	499 (476) ^a	456	65.5	68.4	95.8	41.8

^aTwenty-three fish with unknown passage fate (i.e., fish that entered fishways but were not detected exiting at A2 or A4) were omitted from passage and overall efficiency analyses; total counts of entering and approaching fish listed in parentheses represent the number of entering and approaching fish used in passage and overall efficiency analyses, respectively, to account for uncertainty about those 23 fish.

models. From the odds of success for each outcome, the probability of success was calculated by

$$P(\text{success}) = \frac{\exp(\beta_i)}{[1 + \exp(\beta_i)]},$$

where $P(\text{success})$ is the efficiency estimate for each outcome and β_i is the model intercept coefficient for each species group (Zuur et al. 2009). Wald 95% confidence intervals were calculated for each β_i . We primarily discuss the efficiency estimates generated by these mixed-effects models as opposed to the summarized efficiencies in Table 2 because these estimates included random effects to account for non-independent observations of test fish within each individual trial. Efficiency estimates for each species group are reported as percentages, and odds ratios with P -values adjusted for multiple tests by the “single step method” (Hothorn et al. 2008) were calculated to identify statistically significant differences in the odds of attraction, entrance, or passage among species groups (Zuur et al. 2009).

Fishway efficiency versus upstream depth.—We used logistic regression to predict attraction, entrance, and passage efficiencies over the range of upstream depths tested without considering potential effects of additional explanatory variables. We focused on upstream depth in these single covariate models because upstream depth is an easily measurable surrogate for fishway discharge, and the amount of water needed to facilitate passage through Denil fishways is a key management question in the Big Hole basin. The models included fixed effects for upstream depth and species group and an upstream depth \times species group interaction to account for potentially different associations with upstream depth among species groups. The probability of success for attraction, entrance, and passage was predicted for each species group over the continuous range of upstream depths tested (18.1–65.4 cm) by

$$P(\text{success}) = \frac{\exp(\beta_{0,i} + \beta_{1,i} \times US)}{[1 + \exp(\beta_{0,i} + \beta_{1,i} \times US)]},$$

where $P(\text{success})$ is the predicted efficiency for each outcome, $\beta_{0,i}$ is the model intercept for the i th species group, US is upstream depth, and $\beta_{1,i}$ is the coefficient for upstream depth for the i th species group (Zuur et al. 2009).

Multiple regression analyses.—We evaluated the effects of slope and hydraulic conditions (and two-way interactions) on the odds of attraction, entrance, and passage for each species group using separate, multiple regression analyses. Each model included the explanatory variables hypothesized to be most relevant for that outcome. A Pearson's correlation analysis was performed on all pairs of the explanatory variables; for strongly correlated variables ($r > 0.70$) we included the single variable with the most likely functional significance for that response

(Dormann et al. 2013). As expected, the two variables describing fishway discharge (upstream depth and fishway discharge) were strongly correlated ($r = 0.91$). We included upstream depth in our models because of its ease of measurement in the field; however, we discuss upstream depth and fishway discharge synonymously. Explanatory variables for attraction included upstream depth, downstream depth, attraction flow, water temperature, and fish length. Explanatory variables for entrance included upstream depth, downstream depth, fishway slope, water temperature, and fish length. Explanatory variables for passage included upstream depth, fishway slope, water temperature, and fish length.

We compared four types of models for each outcome and species group using Akaike information criterion corrected for small sample sizes (AIC_c): (1) a *main effects* model that included the additive combination of explanatory variables plus random effects (for study site and trial), (2) a *full model* that included all main effects and all two-way interactions of the variables plus random effects, (3) a *reduced model* obtained by backward selection of the interactions from the full model ($P > 0.05$), and (4) an *intercept model* that included only an intercept term and random effects. Main effects of variables were not removed from reduced models regardless of their significance to explicitly account for potential effects of all relevant explanatory variables (Wasserman et al. 1996; Ramsey and Schafer 2002). Hence, all variables were always included in our models (except the intercept models); importantly, we did not perform variable selection, which has several limitations (Lukacs et al. 2010). We considered models with ΔAIC_c less than or equal to 2 to be competitive (Burnham and Anderson 2002) and selected the most parsimonious of competitive models as the top model for each analysis. Explanatory variables in top models were centered on their overall mean values (Table 1). Exponentiation of the model coefficient of each statistically significant explanatory variable predicted the effect on the odds ratio of a one-unit increase in that variable, while all other variables were held constant at their overall mean values (Sen and Srivastava 1990).

We identified outliers and assessed goodness of fit for all top models. Outliers were defined as observations >4 SDs from the mean (Ramsey and Schafer 2002). We tested the influence of outliers on parameter and standard error estimation in all models; no outliers were removed before any analysis because none were identified as influential in any model. Goodness of fit of the mixed-effect logistic regression models was confirmed by residual plots, chi-squared tests of deviance, and Hosmer–Lemeshow tests ($P < 0.05$). All models were fit using the statistical software R (R Core Team 2018) package lme4 (Bates et al. 2015), adjusted P -values were calculated using R package

multcomp (Hothorn et al. 2008), and AIC_c was calculated using R package AICcmodavg (Mazerolle 2019).

RESULTS

Detection Probability

Detection probability of PIT arrays was high throughout the study. Detection probability estimates from single-tag tests ranged from 99.3% to 100.0% at A1–A4, suggesting near-perfect detection if a single fish passed through the array. In contrast, estimates from multitag tests ranged from 76.2% to 86.4%, illustrating potential for missed detections resulting from tag collision. However, detection probability estimates generated from encounter histories of test fish ranged from 92.9% to 98.4%, suggesting that tag collision was

infrequent during trials. Potential tag collision occurred at A2 and A4 as a low percentage of entering fish (4.6%; $n = 23$ of 499) were not subsequently detected exiting the fishway at either end. These 23 fish were omitted from passage and overall efficiency analyses because we could not confirm their success or failure in passing fishways.

Transit Times

Transit times varied among efficiency components and taxa (Figure 6). In general, approach and attraction times were longer than entrance and passage times. Wild fish approached fishways more quickly than hatchery-reared Arctic Grayling; over 91.0% of approaching trout and suckers approached within 24 h after release compared with 67.9% of approaching Arctic Grayling. Trout were attracted to the fishway more quickly than Arctic

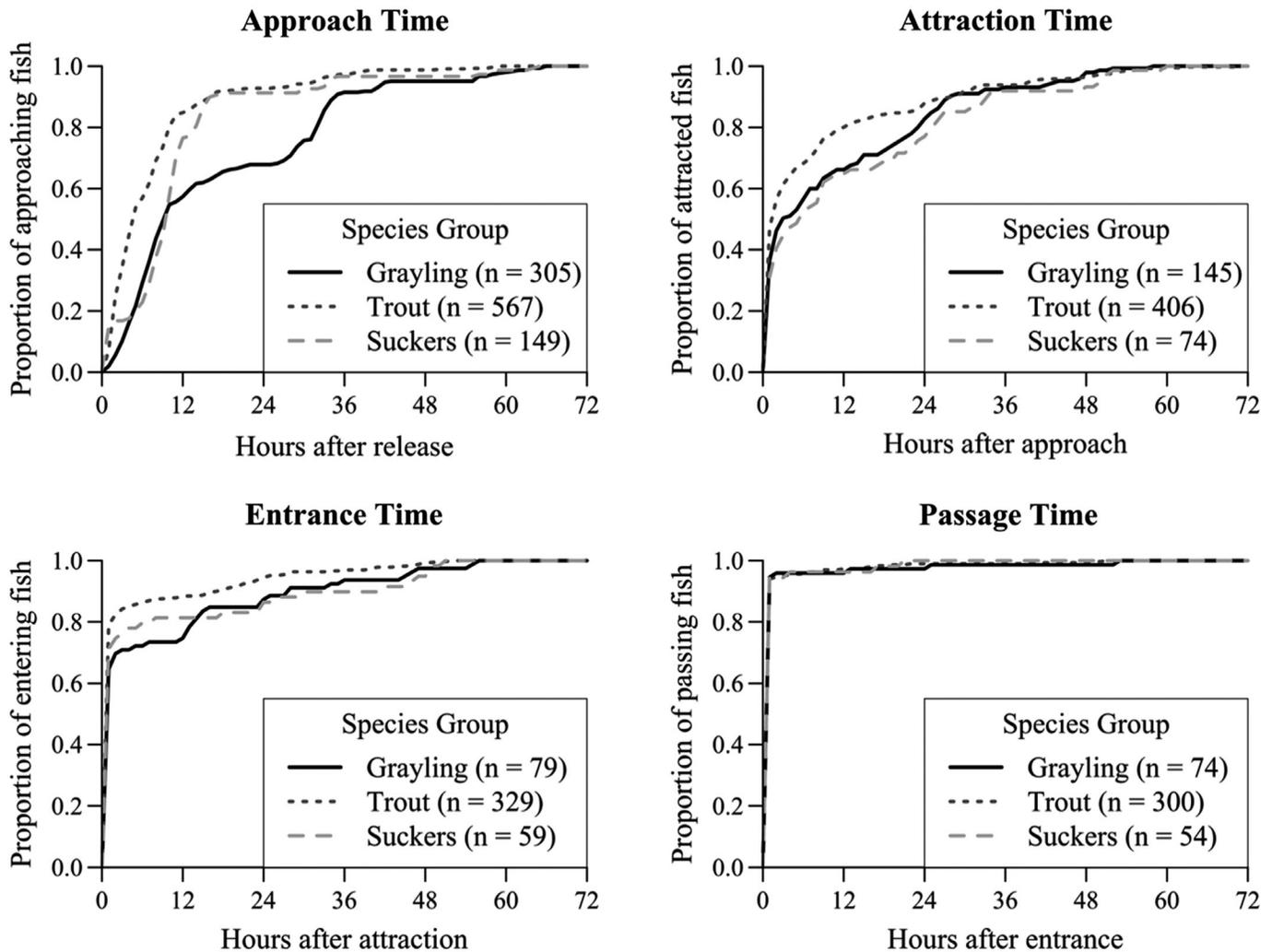


FIGURE 6. Transit times (approach, attraction, entrance, and passage times) for Arctic Grayling, trout (Brook Trout and Brown Trout), and suckers (White Sucker and Longnose Sucker).

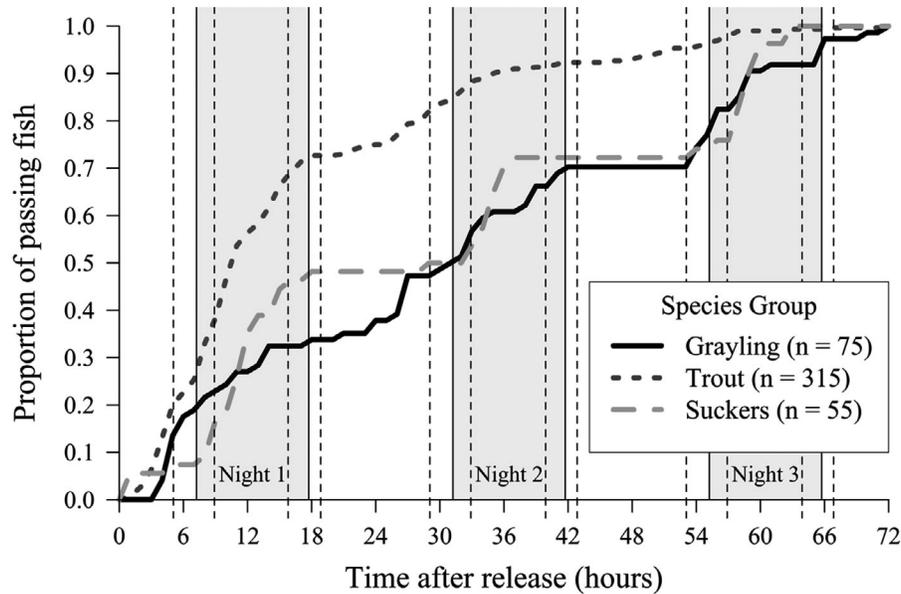


FIGURE 7. Cumulative proportions of times between release and passage of 445 passing fish. Nights 1–3 are depicted as shaded areas bounded by solid vertical lines representing the average time from release until sunset and sunrise calculated over 12 trials (trial 1 was not included in these calculations because of its delayed release time); dashed vertical lines represent the variation in time after release until sunset and sunrise over those 12 trials, given the different release times.

Grayling and suckers, with 47.0% of attracted trout, 36.6% of attracted Arctic Grayling, and 31.1% of attracted suckers being attracted to fishways within 1 h after their first approach. About 80.0% of all attracted fish were attracted within 24 h after their first approach. Entrance times were shorter than attraction times for all taxa. The majority of entering trout (79.0%), Arctic Grayling (64.6%), and suckers (71.2%) entered fishways within 1 h after their first attraction. Of those fish, mean entrance times were 5.2, 5.3, and 3.1 min for trout, Arctic Grayling, and suckers, respectively. Upon entrance, passage times were brief, with 82.7% of all passes ($n = 354$) occurring in less than 1 min and 57.7% of all passes ($n = 247$) occurring in less than 10 s. Passage times were particularly brief for Arctic Grayling; 78.4% of passing Arctic Grayling passed in less than 10 s compared with 53.7% of passing trout and 51.9% of passing suckers.

Trout passed fishways more quickly after release than suckers and Arctic Grayling, and diel periodicity appeared to affect timing of passage (Figure 7). The majority of passing trout (73.3%) and 47.3% of passing suckers passed within 24 h after release, whereas Arctic Grayling passed at a slower and more consistent rate throughout the 72-h trials (37.3, 33.3, and 29.3% on days 1–3, respectively). Passage by all species peaked during sunset and at night (70.3% of all passes), which was most evident for suckers, with 89.1% of passing suckers passing during sunset or at night compared with 66.9% of passing trout and 70.6% of passing Arctic Grayling.

Summarized Fishway Efficiency

Of 1,092 approaching fish with known passage fates, 456 (41.8%) successfully passed through fishways (Table 2). Reductions in overall efficiency were mostly due to attraction (65.5%; $n = 730$ of 1,115) and entrance (68.4%; $n = 499$ of 730) failures because nearly all fish that entered fishways successfully passed (95.8%; $n = 456$ of 476). We observed only 4 failed passage attempts by Arctic Grayling ($n = 83$), 2 by suckers ($n = 57$), and 14 by trout ($n = 333$). Moderate attraction (53.1%) and entrance (48.3%) efficiencies accounted for the low overall efficiency of Arctic Grayling (23.8%), whereas suckers (36.4% overall efficiency) were limited primarily by attraction (51.3%). Trout had the highest overall efficiency (53.1%) and were less limited by attraction (75.7%) and entrance (74.8%) than Arctic Grayling and suckers.

Efficiency Estimates and Species Comparisons

Efficiency estimates derived from mixed-effects logistic regressions exhibited a consistent pattern when comparisons were made across species groups (Figure 8). They were always highest for trout, intermediate for suckers, and lowest for Arctic Grayling for each efficiency component considered (attraction [trout, suckers, and Arctic Grayling, respectively] = 84.3, 72.8, and 60.4%; entrance = 78.6, 69.3, and 44.3%; passage = 97.0, 96.4, and 96.2%; overall = 55.8, 38.5, and 19.1%). Most comparisons were statistically significant ($P < 0.05$; Figure 8), except for passage efficiency; nearly all fish that entered Denil fishways successfully passed.

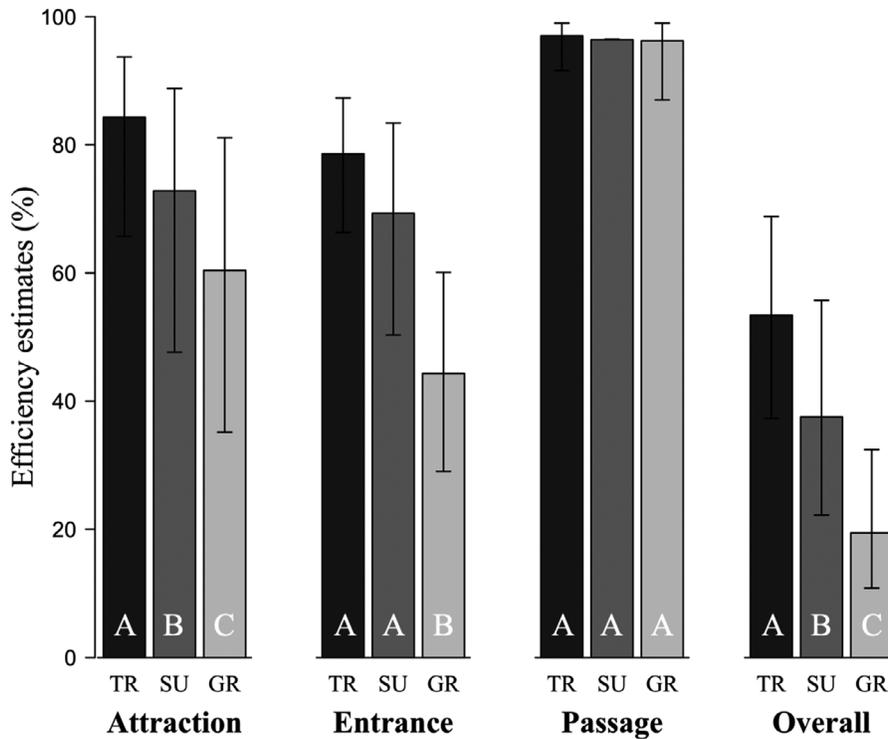


FIGURE 8. Efficiency estimates (attraction, entrance, passage, and overall) and Wald 95% confidence intervals for trout (TR; Brook Trout and Brown Trout), suckers (SU; White Sucker and Longnose Sucker), and Arctic Grayling (GR) from mixed-effects logistic regression. Different letters (A, B, C) denote significant differences ($P < 0.05$) among species groups for each efficiency component.

Fishway Efficiency versus Upstream Depth

Upstream depth was positively associated with attraction and negatively associated with entrance, whereas passage was predicted to be high across all upstream depths tested (Figure 9). Predicted attraction efficiencies of all species groups increased with upstream depth, particularly for Arctic Grayling, with attraction efficiency more than doubling from about 30.0% at an 18-cm upstream depth to about 80.0% at 65 cm. Attraction efficiencies differed among species groups at shallower upstream depths; however, attraction efficiencies of all species groups were about 80.0% at a 65-cm upstream depth, which corresponded to a full fishway. Predicted entrance efficiencies of trout and suckers were between 60.0% and 80.0% across all upstream depths tested. In contrast, entrance efficiency of Arctic Grayling was predicted to decrease considerably at deeper upstream depths, from about 80.0% at an 18-cm upstream depth to about 20.0% at 65 cm. Predicted passage efficiency of all species groups across all upstream depths tested was high (>85.0%).

Multiple Regression Analyses

Attraction.—The top models for attraction of Arctic Grayling, trout, and suckers (Table 3) included significant effects of upstream depth, attraction flow, water temperature, and downstream depth as well as several interactive

effects (Table 4). Attraction of Arctic Grayling increased with upstream depth and attraction flow. A 1-cm increase in upstream depth was associated with a 7.8% increase in the odds of attraction of Arctic Grayling, and a 1.0% increase in attraction flow was associated with a 2.9% increase in odds of attraction of Arctic Grayling. In contrast, upstream depth and attraction flow had varied effects on attraction of trout. A 1-cm increase in upstream depth was associated with a 5.9% decrease in the odds of attraction of trout, and a 1.0% increase in attraction flow was associated with a 5.7% decrease in the odds of attraction of trout. However, an interaction between upstream depth and attraction flow indicated that increased attraction flow had a positive effect on attraction of trout at fishways with shallow upstream depths; alternatively, increased upstream depth had a positive effect on attraction of trout at fishways with low attraction flows.

Attraction of all species groups increased with water temperature, and attraction of trout increased with downstream depth (Table 4). A 1°C increase in water temperature was associated with increased odds of attraction of Arctic Grayling (by 28.9%), trout (by 31.1%), and suckers (by 44.5%). A 1-cm increase in downstream depth was associated with a 22.5% increase in odds of attraction of trout.

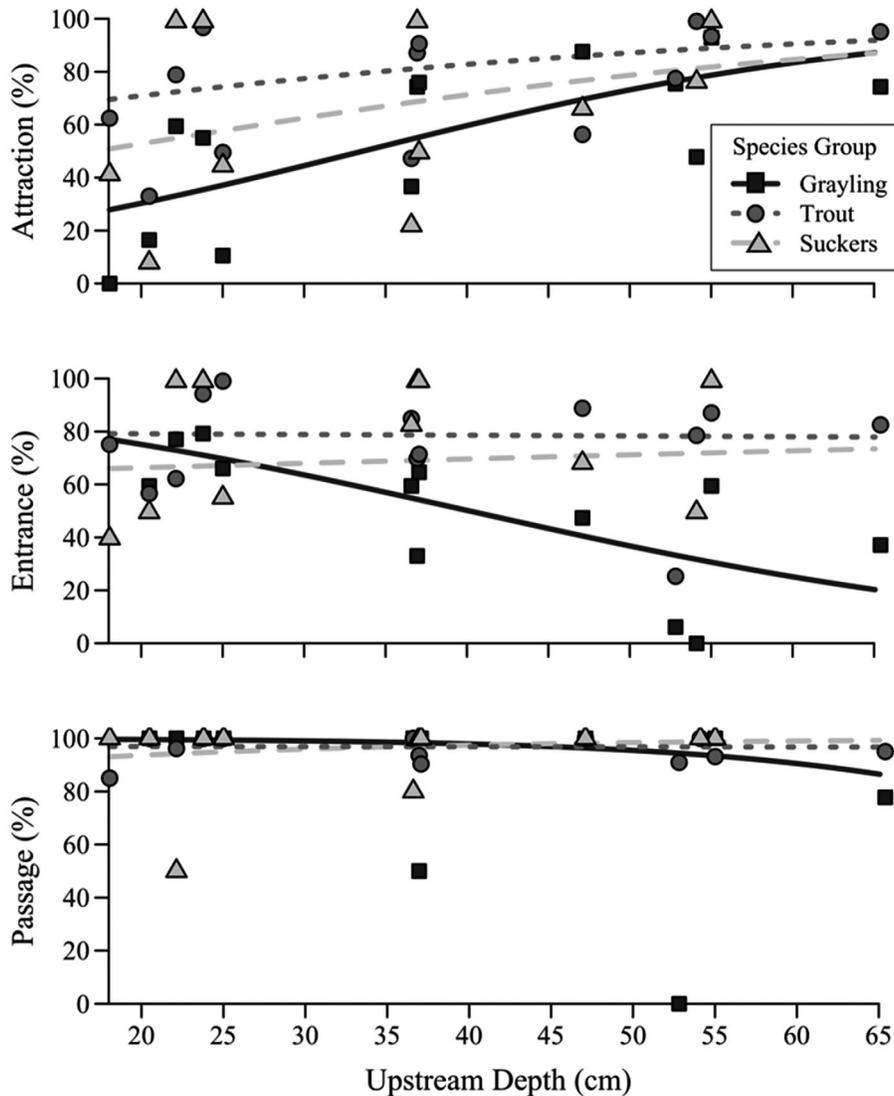


FIGURE 9. Relationships between fishway efficiencies (attraction, entrance, and passage) and upstream depth for Arctic Grayling, trout (Brook Trout and Brown Trout), and suckers (White Sucker and Longnose Sucker). Lines represent predicted efficiencies from mixed-effects logistic regressions, and each point represents an observed efficiency for one species group during an individual trial. Observed efficiencies are calculated on 1 to 58 fish; passage efficiencies $\leq 50.0\%$ are based on 1 or 2 fish.

Entrance.—The top models for entrance of Arctic Grayling and trout (Table 3) included significant effects of upstream depth, downstream depth, slope, and water temperature as well as several interactive effects (Table 4). Entrance of Arctic Grayling and trout decreased with upstream depth, and this association was strongest at fishways with steep slopes. A 1-cm increase in upstream depth was associated with decreased odds of entrance of Arctic Grayling (by 9.8%) and trout (by 5.0%). For trout, deeper upstream depths were more limiting to entrance at fishways with steep slopes than at fishways with gradual slopes. Entrance of Arctic Grayling and trout also decreased with slope; a 1% increase in slope was associated with decreased odds of entrance of Arctic Grayling

(by 34.8%) and trout (by 37.0%). In contrast, entrance of Arctic Grayling and trout increased with downstream depth. A 1-cm increase in downstream depth was associated with increased odds of entrance of Arctic Grayling (by 12.2%) and trout (by 16.3%). The positive effect of downstream depth was stronger at fishways with gradual slopes than at fishways with steep slopes, probably because fishways with gradual slopes often had shallow downstream depths that limited entrance. Entrance of trout increased with water temperature (Table 4). A 1°C increase in water temperature was associated with a 9.4% increase in the odds of entrance of trout.

Passage.—The top models for passage of Arctic Grayling and suckers (Table 3) showed no statistically

TABLE 3. Akaike information criterion (AIC_c) model selection for attraction, entrance, and passage of Arctic Grayling, trout (Brook Trout and Brown Trout), and suckers (White Sucker and Longnose Sucker) at Denil fishways in the Big Hole River basin, Montana. The number of parameters (K), AIC_c scores (AIC_c), ΔAIC_c describing the difference between AIC_c of model $_i$ and the best model, and the Akaike weights (w_i) describing the relative likelihood of being the best model among those tested are reported for each model; all tested models included random effects. The top models from each analysis are highlighted in bold. Abbreviations are as follows: U = upstream depth, A = attraction flow, D = downstream depth, T = water temperature, L = fish total length, and S = fishway slope.

Efficiency	Species group	Model	Parameters	K	AIC_c	ΔAIC_c	w_i
Attraction	Arctic Grayling ($n = 335$)	Reduced	$U + A + T + L + D + U \times A + A \times T$	10	356.71	0.00	0.81
		Full	$U + A + T + L + D$ + all two-way interactions	18	360.22	3.51	0.14
		Main effects	$U + A + T + L + D$	8	363.1	6.39	0.03
		Intercept	Random effects only	3	365.09	8.38	0.01
	Trout ($n = 618$)	Reduced	$U + A + T + L + D + U \times A + U \times L + U \times D + A \times T + A \times D$	13	547.77	0.00	0.77
		Full	$U + A + T + L + D$ + all two-way interactions	18	550.23	2.46	0.23
		Main effects	$U + A + T + L + D$	8	569.88	22.11	0
		Intercept	Random effects only	3	571.66	23.89	0
	Suckers ($n = 154$)	Full ^a	$U + A + T + L + D$ + all two-way interactions	16	168.27	0	
		Main effects	$U + A + T + L + D$	8	169.00	0.73	0.91
		Intercept	Random effects only	3	173.53	5.26	0.09
		Intercept	Random effects only	3	173.53	5.26	0.09
Entrance	Arctic Grayling ($n = 178$)	Reduced	$U + S + T + L + D + S \times D$	9	215.9	0.00	0.99
		Main effects	$U + S + T + L + D$	8	226.18	10.28	0.01
		Full	$U + S + T + L + D$ + all two-way interactions	18	230.02	14.12	0
		Intercept	Random effects only	3	234.52	18.63	0
	Trout ($n = 468$)	Reduced	$U + S + T + L + D + U \times S + U \times A + S \times A + S \times D$	12	476.52	0.00	0.83
		Main effects	$U + S + T + L + D$	8	480.59	4.07	0.11
		Full	$U + S + T + L + D$ + all two-way interactions	18	482.38	5.86	0.04
		Intercept	Random effects only	3	484.13	7.61	0.02
	Suckers ($n = 79$)	Main effects	$U + S + T + L + D$	8	86.62	0	0.69
		Full ^a	$U + S + T + L + D$ + all two-way interactions	16	87.63	1.01	
		Intercept	Random effects only	3	88.19	1.57	0.31
		Intercept	Random effects only	3	88.19	1.57	0.31
Passage	Arctic Grayling ($n = 83$)	Full ^a	$U + S + T + L$ + all two-way interactions	11	31.52	0.00	
		Main effects	$U + S + T + L$	7	32.03	0.51	0.68
		Intercept	Random effects only	3	33.52	2.00	0.32
	Trout ($n = 333$)	Main effects	$U + S + T + L$	7	108.61	0.00	0.91
		Full	$U + S + T + L$ + all two-way interactions	13	113.21	4.60	0.09
		Intercept	Random effects only	3	121.34	12.73	0.00
	Suckers ($n = 57$)	Intercept	Random effects only	3	23.31	0.00	0.98
		Main effects	$U + S + T + L$	7	31.01	7.70	0.02
		Full ^a	$U + S + T + L$ + all two-way interactions	11	31.38	8.07	

^aModels could not be fit with random effects for study site and trial; no interactions were significant in these models so reduced models were identical to main-effects models for these analyses. Akaike weights were not compared between fixed and mixed-effects models.

TABLE 4. Parameter estimates from top models for attraction, entrance, and passage of Arctic Grayling, trout (Brook Trout and Brown Trout), and suckers (White Sucker and Longnose Sucker). Parameter estimates (β), standard errors (SEs), P -values (P), and odds ratios (ORs) are reported for the top models in each analysis. All explanatory variables have been centered on their overall mean values (Table 1). Significant parameter estimates ($P < 0.05$) are denoted by an asterisk. Odds ratios describing the effect of a one-unit increase in each parameter are computed for all statistically significant main effects by exponentiation of parameter estimates (β). Explanatory variables are abbreviated as in Table 3.

Efficiency	β	Parameter	Trout			Arctic Grayling				Suckers				
			SE	P	OR	β	SE	P	OR	β	SE	P	OR	
Attraction	β_0	Intercept	3.841*	0.675	<0.001		-0.483	0.602	0.422		1.970	1.091	0.071	
	β_1	U (cm)	-0.061*	0.024	0.009	0.941	0.075*	0.022	<0.001	1.078	-0.004	0.032	0.888	
	β_2	A (%)	-0.059*	0.015	<0.001	0.943	0.029*	0.010	0.003	1.029	0.011	0.015	0.444	
	β_3	D (cm)	0.203*	0.038	<0.001	1.225	-0.011	0.026	0.667		0.112	0.073	0.125	
	β_4	T (°C)	0.271*	0.094	0.004	1.311	0.254*	0.087	0.004	1.289	0.368*	0.094	<0.001	1.445
	β_5	L (cm)	-0.005	0.020	0.787		0.090	0.065	0.167		0.016	0.043	0.711	
	β_6	U (cm) \times A (%)	-0.007*	0.002	<0.001		0.003*	0.001	<0.001					
	β_7	A (%) \times T (°C)	-0.005*	0.002	0.006		-0.010*	0.003	0.002					
	β_8	D (cm) \times U (cm)	-0.013*	0.004	<0.001									
	β_9	U (cm) \times L (cm)	0.004*	0.002	0.008									
Entrance	β_{10}	D (cm) \times A (%)	0.003*	0.001	0.004									
	β_0	Intercept	1.633*	0.281	<0.001		0.776*	0.314	0.014		1.461*			
	β_1	U (cm)	-0.051*	0.015	<0.001	0.950	-0.103*	0.022	<0.001	0.902				
	β_2	S (%)	-0.462*	0.101	<0.001	0.630	-0.427*	0.136	0.002	0.652				
	β_3	D (cm)	0.151*	0.035	<0.001	1.163	0.115*	0.030	<0.001	1.122				
	β_4	L (cm)	0.028	0.022	0.205		0.146	0.086	0.088					
	β_5	T (°C)	0.090*	0.044	0.042	1.094	0.031	0.056	0.577					
	β_6	S (%) \times D (cm)	-0.025*	0.007	<0.001		-0.019*	0.007	0.004					
	β_7	U (cm) \times S (%)	-0.006*	0.003	0.046									
	β_8	U (cm) \times T (°C)	-0.010*	0.004	0.025									
Passage	β_9	S (%) \times T (°C)	-0.073*	0.028	0.010									
	β_0	Intercept	4.176*	0.555	<0.001		8.566*				4.182*			
	β_1	U (cm)	-0.971	0.730	0.184									
	β_2	S (%)	-0.113	0.094	0.231									
	β_3	T (°C)	0.221*	0.087	0.011	1.247								
	β_4	L (cm)	0.179*	0.063	0.005	1.196								

significant effects by any explanatory variable; however, the top model for passage of trout included significant positive effects of water temperature and fish length (Table 4).

DISCUSSION

Knowledge of fishway efficiency is limited by a lack of comprehensive field evaluations and the use of nonstandardized efficiency components (Bunt et al. 2012; Kemp 2016). Attraction efficiency estimates may be biased by crowding of test fish to induce participation (Haro et al. 1999; Mallen-Cooper and Stuart 2007), and studies that quantify attraction and passage efficiencies often fail to consider entrance efficiency. Hodge et al. (2017) defined “attraction” as the probability that an approaching fish located the entrance and defined “passage” as the probability that an entering fish passed the structure; however, they did not distinguish between attracted and entering fish. Forty et al. (2016) used “proportion of displaced fish attempting passage” as a metric of motivation but combined approach, attraction, and entrance into a single efficiency component. Such inconsistent methodology and terminology have prevented comparisons among studies and limited our understanding of the distinct components of overall fishway efficiency (Bunt et al. 2012, 2016; Kemp 2016; Williams and Katopodis 2016; Hershey 2021).

We identified where fish were limited in using fishways by quantifying approach, attraction, entrance, and passage as four distinct components of overall fishway efficiency. Our PIT array allowed us to distinguish between four types of potential failure: (1) released fish that never approached the fishway (approach failure), (2) approaching fish that never located the entrance (attraction failure), (3) attracted fish that never entered the fishway (entrance failure), and (4) entering fish that failed to pass the fishway (passage failure). By explicitly evaluating each component of overall efficiency, we determined that attraction and entrance failure reduced overall efficiency, whereas nearly all fish that entered fishways successfully passed. High detection probabilities of our and similar PIT arrays (Goerig et al. 2016; Hodge et al. 2017) strengthen these results and confirm PIT telemetry as an accurate means to distinguish between potential causes of failure. Further, we ameliorated less than perfect detection probabilities by incorporating known missed detections into our encounter histories to improve the accuracy of our results.

Attraction failure reduced overall efficiency; however, our attraction efficiency estimates (60.4–84.3%) were similar to, and considerably higher than, the mean attraction efficiency (61.0%) reported in a multispecies meta-analysis by Bunt et al. (2012). Further, we think our estimates may be conservative compared with those expected from naturally motivated wild fish (Hodge et al. 2017). Attraction

of hatchery-reared Arctic Grayling was limited at low fishway discharges and low attraction flows, presumably because fish are attracted to areas of high discharge (Bunt et al. 2012) and discharge occurring away from the fishway entrance can distract approaching fish (Bunt et al. 1999). In contrast, attraction of wild test fish was less limited by low discharges and low attraction flow. Attraction can be driven by biological characteristics of fish, behavior, and motivation (Bunt et al. 2012), and our test Arctic Grayling were naïve to study streams and lacked the homing motivation expected from displaced wild test fish.

Ours is the first study of Denil fishways to quantify entrance as a distinct efficiency component, and we found that entrance failure contributed significantly to reductions in overall efficiency. Our entrance efficiency estimates were between 44.3% and 78.6%, and entrance of Arctic Grayling and trout was limited at fishways with deep upstream depths and steep slopes. Deep upstream depths and steep slopes are correlated to high velocities and turbulence that have limited passage efficiency (Bunt et al. 1999; Haro et al. 1999; Mallen-Cooper and Stuart 2007); however, low passage efficiencies previously reported may have been a result of both entrance and passage failure (Bunt et al. 2012). Previous studies did not distinguish between entrance and passage, and we provide evidence that deep upstream depths and steep slopes limited entrance but did not affect passage. These results highlight entrance as a distinct limiting component of overall efficiency and direct attention to entrance conditions related to downstream depth.

Entrance of Arctic Grayling and trout was limited at shallow downstream depths, presumably because shallow downstream depths can create plunging conditions at fishway entrances (Figure 3). When upstream depth is greater than downstream depth, water accelerates and plunges through the fishway and out of the entrance, a condition that limits upstream passage of Arctic Grayling through Denil fishways (Blank et al., *In press*) and appeared to limit entrance of Arctic Grayling (6.3%; $n = 16$) and trout (25.6%; $n = 43$) during trial 11 (Figure 10). Entrance during trial 11 may have also been limited by high discharge and steep slope (Table 1), but entrance efficiencies during trial 2 at a nearly identical steep slope and high discharge were higher (37.5% and 73.3% by Arctic Grayling [$n = 16$] and trout [$n = 30$], respectively), probably because the entrance was submerged. A submerged entrance prevents plunging and presumably improves entrance conditions (Figure 2), emphasizing the potential benefits of deep downstream depths at steep fishways during high discharges.

Our passage efficiency estimates (96.2–99.0%) were higher and less variable than previous Denil passage efficiencies (mean = 51.0%, range = 0.0–97.0%; Bunt et al. 2012) despite testing a wide range of conditions.



FIGURE 10. Photo of the plunging entrance conditions during trial 11. The deep upstream depth, shallow downstream depth, and steep slope (Table 1) resulted in this entrance plunge that presumably limited the entrance of Arctic Grayling, Brook Trout, and Brown Trout during this trial.

Consistently high passage success was not unexpected because Denil fishways create favorable low-velocity zones inside the fishways over a wide range of discharges (USFWS 2017). We observed highly efficient passage at discharges between 0.007 and 0.209 m³/s (i.e., a nearly empty fishway to a completely full fishway), demonstrating their versatility for providing year-round passage opportunities. Moreover, we identified entrance as a significant bottleneck separate from passage. Therefore, our passage efficiency estimates more accurately depict actual passage than do earlier estimates, which combined entrance and passage failure.

We suspect that the attraction and entrance estimates for our test Arctic Grayling were conservative compared with what could be reasonably expected from wild Big Hole River Arctic Grayling. Moderate attraction efficiency (60.4%) of test Arctic Grayling may have been due to behavioral differences stemming from hatchery rearing, naïveté to study streams, lack of homing motivation, and short trial durations. Test Arctic Grayling were typically slower to approach fishways and approached in lower numbers than wild test fish, which appeared to have a strong homing motivation. Low entrance efficiency (44.3%) of test Arctic Grayling could reflect behavioral or physiological limitations; however, their high passage efficiency (96.2%) and brief passage times suggest they had swimming abilities comparable to wild fish. Arctic Grayling are strong burst swimmers (Northcote 1995; Cahoon

et al. 2018), and swimming performance of hatchery-reared Arctic Grayling and captive wild Brook Trout and Brown Trout (Castro-Santos et al. 2013; Dockery et al. 2020) are comparable. Therefore, the low entrance efficiency of test Arctic Grayling probably reflects behavioral differences associated with hatchery-rearing conditions or the innate behavioral preferences of Arctic Grayling, which may avoid turbulent fishway entrances because they prefer to swim around barriers rather than to jump over them (Cutting et al. 2018). Future testing of wild Arctic Grayling at Big Hole Denil fishways is important to address these uncertainties.

Denil fishways provide upstream passage opportunities through artificial barriers in the Big Hole River basin; however, we determined that enhancing attraction flows and maintaining deep downstream depths could improve attraction and entrance efficiency. Attraction flows could be enhanced by ensuring that any discharge escaping over and through the diversion dam is redirected through the fishway (Triano 2020). Modifications to improve entrance could be prioritized at fishways with shallow slopes ($\leq 5.0\%$), where shallow downstream depths and plunging entrance conditions were typically observed, and at fishways with steep slopes ($\geq 15.0\%$), where deep downstream depths could increase entrance efficiency during high fishway discharges. Fluctuations in fishway depths could be estimated by seasonal monitoring or hydraulic modeling to guide fishway modifications and installations; the

downstream invert elevation could be set to provide deep downstream depths and favorable entrance conditions throughout the year (Clay 1995; Platt 2019).

Our results could be applied to a basinwide connectivity assessment for Arctic Grayling in the Big Hole River. Access to critical habitats could be essentially precluded considering the potential compounding effects of passing multiple sequential barriers with limited overall efficiencies (Cutting et al. 2018; Keefer et al. 2021); our results could be extrapolated to barriers throughout the basin based on their hydraulic characteristics to estimate these effects. Designation of critical habitats and determination of specific Arctic Grayling movement patterns would help prioritize where fishway modifications would be most useful. Lastly, effective downstream passage and prevention of entrainment in irrigation ditches are critical for overall connectivity (Gale et al. 2008; Calles and Greenberg 2009) and our comprehensive methods can be applied to downstream passage.

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