EFFECTIVENESS OF THE NATURE-LIKE FISHWAY AT HUNTLEY DIVERSION DAM, YELLOWSTONE RIVER, MONTANA

by

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ABSTRACT

We evaluated passage of a diverse fish assemblage through the nature-like fishway built around Huntley Diversion Dam, the uppermost of six low-head diversion dams on the Yellowstone River in Montana. Although nature-like fishways purportedly facilitate the passage of many species, relatively few have been evaluated, particularly on large rivers with unregulated discharge regimes. We examined seasonal and diel use of the Huntley fishway, quantified efficiencies and temporal metrics, and determined which factors influenced attraction and passage. We implanted > 3,500 fish of 14 species with passive integrated transponder tags, released most fish 250 m downstream of the fishway, and used stationary antennas to monitor movements of fish through the fishway in 2019 and 2020. Seasonal use of the fishway was generally associated with pre-spawning movements and occurred from April to August annually, and diel use reflected the known biology of each species. Attraction efficiencies were apparently low (usually < 50%), probably because of low motivation or the inability of fish to locate the entrance. Suckers released on opposite riverbanks downstream of the fishway were similarly successful at locating the entrance. Entrance efficiencies were usually > 90%. Both transit and passage efficiencies were usually > 60%, but fewer individuals (particularly among certain species) successfully passed than were able to transit to near the fishway exit. High river discharges were associated with decreased passage success and increased exit delays, probably because of problematic hydraulic conditions near the exit. Conditions throughout the rest of the fishway were appropriate, as most fish transited to near the exit in < 1 h regardless of discharge. Fourteen species passed upstream, demonstrating the functionality of nature-like fishways on large, unregulated rivers. However, the placement of such fishways must be thoughtfully considered to ensure that they remain effective over a wide range of environmental conditions.

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Introduction

Humans have constructed millions of dams and other barriers on rivers around the globe (Lehner et al. 2011) to enable activities associated with hydropower production, industry, and agriculture, and provide a steady supply of water for human consumption (Katopodis and Aadland 2006). However, these barriers also limit the longitudinal connectivity vital to intact river ecosystems and productive fish populations (Katopodis and Aadland 2006). Many riverine fishes must move to access upstream and downstream habitats to reproduce, grow, and survive, and the habitats they require may differ among life stages (Northcote 1984; Baras and Lucas 2001). In the short term, barriers to fish movement can cause harmful migratory delays (Caudill et al. 2007; Castro-Santos et al. 2017), and over time can fragment populations, decrease genetic diversity, and eventually lead to population extirpations (Katopodis and Aadland 2006). To mitigate these negative effects, structures (hereafter, fishways) have been built to facilitate the movement of fish past barriers (Bunt et al. 2012; Silva et al. 2018).

Technical fishways, the most common design type, are built with artificial materials, feature baffles, slots, or steps, and typically facilitate the passage of strong-swimming fishes (Jungwirth 1996; Katopodis et al. 2001). Conversely, nature-like fishways are built at least partly with natural materials (such as boulders or large woody debris) that increase channel roughness and can be arranged to simulate a pool-riffle sequence or even a meandering, low-gradient side channel or tributary, ideally mimicking the natural river channel (Jungwirth 1996; Katopodis et al. 2001; Bunt et al. 2012). Nature-like fishways can take the form of bypass channels, which are

constructed around barriers, and rock ramps, which incorporate design elements into the existing river channel, thereby allowing fish to remain within the natural riverbanks (Wildman et al. 2003). Both nature-like fishway designs create varied water depths, velocities, and flow patterns that purportedly allow the passage of a wide range of sizes and species of fish (Jungwirth 1996; Katopodis et al. 2001; Aarestrup et al. 2003). However, relatively few nature-like fishways have ever been comprehensively evaluated, and those that have been evaluated have not been shown to be universally effective at passing all fishes studied over the entire range of environmental conditions observed during periods that fish are motivated to move (Schmutz et al. 1998; Aarestrup et al. 2003; Calles and Greenberg 2007; Franklin et al. 2012; Steffensen et al. 2013; Kim et al. 2016; Landsman et al. 2018; Raabe et al. 2019). Consequently, fishway effectiveness must be evaluated on a site-specific basis to identify passage bottlenecks if present and corrective measures if needed.

The effectiveness of any fishway depends first on the ability of a fish to locate its attraction flow among other competing and distracting flows passing over or near the barrier (Katopodis et al. 2001). Limited attraction to a fishway can result from structural deficiencies such as the improper placement of the entrance (Bunt et al. 2012; Williams et al. 2012), a problem that is compounded in large rivers where the quantity of attraction flow coming out of the fishway entrance is often just a small fraction of the total flow passing over the barrier, further accentuating the importance of an appropriate entrance location (Katopodis et al. 2001). Successful attraction is also dependent on biological characteristics of fish, such as migratory tendencies and motivation, which are difficult to quantify (Katopodis et al. 2001; Bunt et al.

2012). Fishway attraction problems are therefore common, particularly among nature-like fishways (Bunt et al. 2012, 2016; Hershey 2021).

After locating the attraction flow, a fish must then enter the fishway, swim its full length, and transition back into the river on the opposite side of the barrier to successfully pass (Williams et al. 2012). Suitable hydraulic conditions must be available to facilitate the successful entry and passage of fish over a wide range of environmental conditions (Katopodis et al. 2001; Williams et al. 2012) without causing excessive temporal delay or energy expenditure (Geist et al. 2000; Castro-Santos et al. 2009; Castro-Santos et al. 2017). Fishway hydraulic conditions such as water velocity, turbulence, and depth (Katopodis et al. 2001) are directly influenced by design characteristics such as slope, cross-sectional geometry, and in-channel structural elements installed to dissipate energy (Larinier 1998; Aarestrup et al. 2003; Castro-Santos et al. 2009). Successful entry and passage are also driven by biological factors such as species morphology, fish length, and individual swimming capabilities (Katopodis et al. 2001; Castro-Santos et al. 2009; Bunt et al. 2012). The potential problems associated with each stage of fish passage (i.e., attraction, entrance, and passage) emphasize the need to evaluate each individually.

Early fishway evaluations relied on counts from fish traps to draw conclusions about fishway use but did not track the movements of individuals and could not account for fish that did not find or fully ascend a fishway (Roscoe and Hinch 2010; Bunt et al. 2012; Cooke and Hinch 2013). Fish passage research has advanced with the use of radio, acoustic, and passive integrated transponder (PIT) telemetry, in which the attachment or implantation of a tag and subsequent detections at antennas allows for the tracking of individual fish and the estimation of fishway “efficiencies,” the percentages of fish moving from one stage of passage to the next

(Castro-Santos et al. 1996; Bunt et al. 2012; Cooke and Hinch 2013). However, fishway evaluations should not end with efficiency measures. Environmental variables, fish characteristics, and temporal factors (i.e., passage durations and delays) should be considered to provide a mechanistic understanding of effectiveness (Castro-Santos et al. 2009). Site-specific hydraulic models can provide evidence of problematic hydraulic conditions and help locate potential bottleneck areas (Khan 2006), particularly when compared to observed telemetry data. Ideally, multiple techniques should be used over multiple years to provide a detailed understanding of fishway efficiency and effectiveness (Cooke and Hinch 2013; Tummers et al. 2016), particularly on rivers with diverse fish assemblages and dynamic hydrology.

The Yellowstone River is the longest free-flowing (i.e., unregulated) river in the contiguous United States (Benke 1990). The river transitions from a coldwater trout fishery to a warmwater prairie fishery as it flows from its headwaters in northwestern Wyoming, through Montana, to its confluence with the Missouri River near the North Dakota border, and is characterized by a diverse fish assemblage, high-quality habitat, and an unregulated, snowmelt-driven discharge regime (White and Bramblett 1993). Despite this, the Yellowstone River is altered by the presence of six low-head, run-of-the-river diversion dams that are distributed from near the Montana-North Dakota border upstream to near Billings, Montana (Helfrich et al. 1999). Some of these dams act as partial or complete passage barriers for Sauger *Sander canadensis*, Paddlefish *Polyodon spathula*, Pallid Sturgeon *Scaphirhynchus albus*, Shovelnose Sturgeon *S. platorynchus*, and others (USACE and YRCDC 2015).

Huntley Diversion Dam is the farthest upstream of the six diversion dams on the Yellowstone River, and is located in the cold-to-warmwater transition zone that contains about

30 fish species (White and Bramblett 1993; Helfrich et al. 1999). Upstream fish movement past the dam occurs, but probably only in limited numbers, during periods of high discharge, and by strong-swimming species such as White Sucker *Catostomus commersonii*, Longnose Sucker *C. catostomus*, Shorthead Redhorse *Moxostoma macrolepidotum*, Flathead Chub *Platygobio gracilis*, Goldeye *Hiodon alosoides*, and Brown Trout *Salmo trutta* (Helfrich et al. 1999). Only White Suckers and Shorthead Redhorses passed downstream, and whether fish movement in either direction occurred over the dam or around the dam via a natural side channel—which runs dry and is impassable at low discharges—is unknown (Helfrich et al. 1999). The dam may limit the upstream distribution of, and angling opportunities for, a population of genetically distinct Saugers (Bingham et al. 2012), which were historically found upstream of the dam in the Yellowstone River and its tributary, the Clarks Fork (McMahon and Gardner 2001), but are now rarely captured there (M. P. Ruggles, Montana Fish, Wildlife & Parks, personal communication). Furthermore, local anglers have claimed that angling opportunities for Burbot *Lota lota* have recently decreased in the area, although the role of the dam in this perceived decrease is unknown (M. P. Ruggles, personal communication). A nature-like bypass channel (hereafter, "nature-like fishway" is used to refer to a bypass channel and not a rock ramp) was constructed around the north side of Huntley Diversion Dam in 1999 to facilitate fish passage. Unfortunately, the fishway did not meet original design specifications and excessive water velocities in the steep gradient channel were thought to prevent passage (M. P. Ruggles, personal communication). Therefore, the nature-like fishway was lengthened in 2015 to reduce gradient and velocities, and rock weirs were constructed perpendicular to the flow of the fishway to create simulated pool-weir sequences (M. P. Ruggles, personal communication). The ability of the fishway to facilitate

passage of the diverse fish assemblage of the Yellowstone River over varying environmental conditions had not been evaluated heretofore.

We performed a multi-year evaluation of the effectiveness of the nature-like fishway at Huntley Diversion Dam by using PIT telemetry to track the movement of tagged individuals of 14 species through the fishway. Our objectives were to 1) quantify fishway efficiencies, 2) examine seasonal and diel use of the fishway, 3) quantify temporal metrics of fishway use, and 4) determine the factors influencing attraction to and passage through the fishway. Addressing these objectives allowed us to locate and determine the mechanisms resulting in bottlenecks, identify potential corrective solutions, and determine the overall effectiveness of the structure at facilitating upstream movement of fishes in the Yellowstone River. Additionally, our results shed light on the general functionality of nature-like fishways on large, unregulated rivers with diverse fish assemblages.

Methods

Study Site

Huntley Diversion Dam (rkm 566) is the farthest upstream of the six low-head, run-of-the-river diversion dams on the Yellowstone River, and is located about 15 km northeast (i.e., downstream) of Billings, Montana (Helfrich et al. 1999). The dam (Figure 1), built in 1934, is 3.2 m high, 99 m wide, and can divert about 17 m^3/s (600 ft^3/s) of water into a canal on the south side of the river to irrigate 12,140 ha (30,000 acres; USACE and YRCDC 2015). The dam is located at a split flow in the river and only spans the main channel; a large, natural side channel that flows on the north side of the island bypasses the dam completely (Helfrich et al. 1999) but is probably impassable to fish when Yellowstone River discharge is less than about 142–198

m^3/s (5,000–7,000 ft^3/s). Discharge of the Yellowstone River in the study area fluctuates greatly during the year. From 1904 to 2018, estimated annual peak discharge at Billings varied from 430 to 2,322 m^3/s (15,200 to 82,000 ft^3/s), whereas estimated mean base discharge was 63 m^3/s (2,227 ft^3/s; USACE and YRCDC 2015).

A nature-like fishway (hereafter, the Huntley fishway) was constructed around the north end of Huntley Diversion Dam (Figure 1) in 1999 to facilitate passage of the diverse fish assemblage of the Yellowstone River. The Huntley fishway was then lengthened and modified in 2015 to create more favorable hydraulic conditions (M. P. Ruggles, personal communication). The modified structure is 125 m long, varies from 6 to 16 m wide, and has an average slope of 1.22%. The banks of the fishway are riprapped for stability and large boulders within the fishway create pool-weir sequences, with water flowing between the boulders at low discharges and completely submerging them at high discharges. The Huntley fishway has one upstream fish exit that is directly adjacent to the north end of the dam and two downstream fish entrances: the primary entrance that was built as part of the 2015 modifications and a secondary entrance that was retained from the original fishway built in 1999. The primary and secondary entrances are located about 75 and 25 m downstream of the dam, respectively. The secondary entrance is only connected to the river at discharges greater than about 255 m^3/s (9,000 ft^3/s). Hydraulic conditions in and adjacent to the fishway are highly variable because of extreme seasonal fluctuations in Yellowstone River discharge. Despite reference herein to fishway entrances and the exit in terms of upstream fish movement, fish can also enter and exit moving downstream.

Sampling Design

We captured and tagged over 3,500 fish of 14 species representing 8 families (Table 1) to assess movements of fish through the Huntley fishway. We captured fish in the Yellowstone River from March 22 to August 24, 2019, and from March 5 to May 29, 2020, from near Laurel, Montana (rkm 626), to near Custer, Montana (rkm 474). We used boat electrofishing to capture most fish of each species except for Burbot, most of which we captured with hoop nets, and Sauger, most of which we captured by drifting trammel nets or angling. We anesthetized fish, recorded their total lengths (TL; mm), and implanted a uniquely coded, half-duplex passive integrated transponder (PIT) tag in the abdominal cavity of each individual. We implanted fish < 150 mm TL and those > 150 mm TL but with a small abdominal area—most of which were Burbot, Flathead Chub, and Mountain Whitefish—with a 12-mm long PIT tag (Oregon RFID, Portland, Oregon, USA). All other fish received a 32-mm long PIT tag (Oregon RFID). We released all tagged fish near shore after a short (< 30 min) recovery period in fresh river water; most fish were captured and released in batches.

We assigned fish to release groups according to capture locations, release locations, and study objectives. The general release group consisted of fish captured within about 5 rkm downstream of the dam and released about 250 m downstream of the primary entrance to the fishway. We released most fish in the general group at site A, which was located along the north riverbank (i.e., the same riverbank as the fishway) about 250 m downstream of the primary entrance (Figure 1). We rarely captured fish intended for the general group between the dam and site A except for Burbot, which we targeted in deep holes directly downstream of the dam; most general-group fish were captured downstream of site A. We released an experimental subset of Longnose Suckers and White Suckers from the general group at site B, which was located on the

south riverbank (i.e., the riverbank opposite the fishway) directly across from site A (Figure 1), to determine if riverbank of approach (i.e., riverbank of release) influenced the attraction of fish to the fishway (Hatry et al. 2016). We captured batches of suckers intended for the experimental subset on select dates from March 28 to April 24, 2020, before or during their putative spawning periods. We PIT-tagged fish, released the first batch each day either at site A or B as determined by a coin flip, sampled the same river section again using the same gear, and then released the second batch of the day on the other riverbank. We captured all Longnose Suckers and White Suckers in 2020 according to this protocol to allow for direct comparisons between fish released at sites A and B. Fish in the general group were the most readily comparable with those from most other fishway evaluations, as they usually had the largest sample sizes and were all released the same distance downstream of the fishway.

The supplemental upstream and downstream release groups consisted of fish released near their capture locations anywhere upstream of the dam or downstream of sites A and B, respectively. The supplemental groups provided information about use of the fishway by fish released up to 60 rkm upstream and 92 rkm downstream of the dam. Most supplemental sampling occurred from March through May each year in association with annual Burbot and Sauger monitoring by Montana Fish, Wildlife & Parks. Therefore, we mainly targeted Burbot during upstream sampling (except from late June to mid July 2019 when we released about 300 fish representing 11 other species about 0.5 rkm upstream of the dam), and Burbot and Sauger during downstream sampling.

We translocated Sauger into the fishway on select dates from April 16 to May 7, 2020, to separate the issue of attraction from passage and help locate passage bottlenecks within the

fishway (Steffensen et al. 2013). We captured Sauger intended for translocations (n = 13; range = 436–615 mm TL; mean = 525 mm TL; SD = 63) downstream of the dam and released them in a 54-m long reach in the upstream half of the fishway (Figure 1).

We reassigned fish to or removed them from release groups based on recaptures and known mortalities but not based on movements through the fishway (i.e., PIT-tag detections) except for fish in the supplemental upstream group that were present in, but did not successfully pass, the fishway in 2019, in which case they were reassigned to the general group in 2020. We assumed that fish that successfully passed the fishway in an upstream direction could return downstream to their original locations either over the dam or through the natural side channel on the north side of the island, as evidenced by fish passing upstream through the fishway multiple times without ever being detected moving downstream through the fishway. For example, fish in the general release group that passed upstream through the fishway in 2019 were still considered to be in the general (not the supplemental upstream) group in 2020.

PIT Telemetry

We used stationary PIT antennas to monitor the movement of PIT-tagged individuals through the Huntley fishway from April 23, 2019, through December 31, 2020, which allowed for the quantification of individual movements and fishway performance metrics (Castro-Santos et al. 1996). We installed antennas horizontally on the substrate (i.e., pass-over antennas) to avoid extreme water velocities and impacts from large woody debris. We deployed PIT antennas at the attraction flow (hereafter, antenna A1), the primary (A2) and secondary (A5) entrances, near the midpoint of the length of the fishway (A3), and just downstream of the fishway exit (A4; Figure 2). Dangerous hydraulic conditions prevented the installation of an antenna at the

true exit until spring 2020. This antenna (A6) operated only from April 10 to May 1 and from May 8 to May 29, 2020, when it was destroyed by debris. Antennas consisted of welding wire encased in protective tubing that was secured to the substrate across the fishway using concrete weights, galvanized cables, and metal clamps. Antennas extended onto the floodplain above the fishway where possible to account for increasing wetted width during high discharge and varied from 6 to 18 m wide, although we sometimes installed smaller antennas that spanned only a portion of the fishway as temporary substitutes for damaged antennas. We tuned (model ATC AutoTuner; Oregon RFID) all antennas to maximize vertical tag read ranges, which varied among antennas and varied from 5 to 25 cm for 12-mm tags and 25 to 75 cm for 32-mm tags during normal antenna function.

We used remotely powered data loggers to store the dates, times, durations, and unique PIT tag codes associated with detections of fish at antennas. We downloaded detection data using a satellite-linked Rockfish unit (Ritter Designs; Lynnwood, Washington, USA) to reduce the number of site visits, and positioned data loggers (model ORSR Single Antenna Reader; Oregon RFID) and power source components above the floodplain to protect them from debris impact and submersion. The primary remote power source, consisting of two 300-W solar panels, eight 92-ampere hour (Ah) batteries, and a solar charge controller, provided continuous power to functioning antennas except during short periods of routine maintenance and from July 6 to July 8, 2019, when a circuit breaker malfunctioned. We installed a smaller, auxiliary power source consisting of a single 300-W solar panel, four 92-Ah batteries, and a solar charge controller on the floodplain above the fishway exit in spring 2020 to increase vertical read ranges of antennas near the exit by reducing the distance between the antennas and their power source.

Several factors negatively affected PIT antenna performance during the study. Extreme water velocities and large woody debris occasionally dislodged or destroyed antennas (e.g., A1, A4, and A6) and reduced or caused a complete loss of functionality (Figure 3). Moreover, curved antennas necessitated by site characteristics (e.g., A1) and long distances between power sources and some antennas (e.g., A5) led to concerns about low read ranges. Therefore, the quantification of antenna performance and detection efficiency was necessary. We performed PIT-tag pull-through tests using a fishing rod and reel in early spring 2020 near base discharge in the Yellowstone River to estimate antenna detection efficiency when antenna detection fields covered the greatest proportion of the water column. However, boulders and other obstructions near antennas made it difficult to simulate the behavior of tagged fish moving through detection fields during pull-through tests. Therefore, we estimated in-situ detection efficiency (hereafter, $E_{in\text{-}situ}$; Zydlewski et al. 2006) of individual antennas using observed detection data from all tagged fish to characterize antenna performance over the full range of study conditions, including periods when antennas were damaged or destroyed. We calculated $E_{in\text{-}situ}$ as the percentage of fish known to have passed an antenna that were detected by the antenna, as informed by detections at other antennas (Zydlewski et al. 2006; Franklin et al. 2012). Consequently, PIT tag read ranges, percentages of fish that swam through detection fields as opposed to around them, and the functionality, or lack thereof, of antennas during the study influenced estimates of $E_{in\text{-}situ}$ (Zydlewski et al. 2006). We calculated $E_{in\text{-}situ}$ of A1, A2, A3, and A4, the antennas that detected fish as they moved upstream through the primary channel, but not A6 because no antennas were located farther upstream of it. We calculated $E_{in\text{-}situ}$ annually for A1, A2, and A3, and used detection data from April 10 to May 1, 2020, the only period when both A4 and A6 were

operational, to calculate $E_{in\text{-}situ}$ of A4 in 2020. Calculations of $E_{in\text{-}situ}$ incorporated upstream and downstream movements but could not account for movements of fish that were last detected in the middle of the fishway. For example, if a fish was last detected at A2 we could not assign missed detections to other antennas because the true direction of the subsequent movement of the fish was unknown. Therefore, we overestimated $E_{in\text{-}situ}$ of all antennas because we could not account for all missed detections. Calculations of $E_{in\text{-}situ}$ excluded data from the 15% of detected fish that were detected at A5 during the study because movement into the secondary entrance channel was generally not required for passage.

Fishway Efficiencies

We calculated fishway efficiencies to broadly describe the performance of the fishway. Efficiencies were calculated only for fish moving in an upstream direction and separately, when applicable, among species, release groups (and release site for the experimental subset), years, and tag statuses. Tag statuses were "new" (fish tagged that year) and "previous" (fish tagged the previous year that, to the best of our knowledge, were still available to use the fishway, excluding known mortalities and fish that were reassigned to a different release group; Nau et al. 2017). Each fish contributed only once to each annual efficiency calculation. In addition to calculating species-specific efficiencies, aggregate efficiencies of all species combined were calculated to generalize the performance of the fishway among release groups, years, and tag statuses. Efficiencies of newly tagged fish in the general group were the most readily comparable with those from most other fishway evaluations and meta-analyses.

Efficiency definitions and criteria from Bunt et al. (2012) and Silva et al. (2018) were modified when necessary to reflect the unique design of the fishway (e.g., multiple entrances and

an exit close to the face of the dam) and address site-specific concerns (e.g., variable hydraulic conditions near the exit). Attraction was defined as any detection of a fish at A1 or an antenna farther into the fishway (to account for missed detections at A1) at any time during the year, whereas attraction efficiency (hereafter, E_{ATT}) was the percentage of released fish that were attracted to the fishway. Entrance was defined as any detection of a fish at A2 (the primary entrance), A5 (the secondary entrance), or an antenna farther into the fishway at any time during the year, whereas entrance efficiency (E_{ENT}) was the percentage of attracted fish that entered the fishway. Fish that were only detected at A1 were considered to have been attracted but not to have entered. Transit was defined as any detection at A4 or A6 at any time during the year, confirming that a fish traveled to near the upstream extent of the fishway. Transit efficiency (E_{TRN}) was the percentage of entering fish that transited the fishway regardless of their eventual passage outcome, and was calculated because of concerns that hydraulic conditions near the exit were preventing fish from transitioning out of the fishway and back into the river upstream of the dam.

Passage occurred when a fish was detected at the farthest upstream functioning antenna (either A3, A4, or A6) and not subsequently detected moving downstream within the fishway. A fish last detected at A5 was never deemed to have passed, even when A3 was the farthest upstream functioning antenna (when A4 or A6 or both were destroyed), because of the close proximity of A5 to the river. Detection histories revealed a pattern wherein some fish were detected by an exit antenna (A4 or A6) and then next by the attraction (A1) or an entrance antenna (A2 or A5). We could not determine with certainty whether these “fallback” events were voluntary (overshooting, Boggs et al. 2004; indirect or exploratory movements, Keefer et al.

2008), involuntary (poor fishway placement, Reischel and Bjornn 2003; disorientation, Naughton et al. 2006), missed detections of fish moving downstream within the fishway (e.g., A4-A2), or merely the movements of fish that were unmotivated or delayed at the exit (e.g., A4-A5-A4-A5). In addition, we were unable to determine the location of each fish in the time between detections because of the discontinuous nature of PIT telemetry. For example, a fish that was detected at an exit antenna and then 24 h later at an entrance antenna could have successfully passed upstream, foraged upstream for almost 24 h, voluntarily swam downstream over the dam or through the natural side channel, and then re-entered the fishway. Alternatively, the fish could have been involuntarily swept downstream over the dam while attempting to pass and then searched for 24 h before re-entering the fishway. Despite this uncertainty, visual observations of hydraulic conditions at the fishway exit and preliminary hydraulic models (Johnson et al. 2021) provided some evidence that involuntary fallback at Yellowstone River discharges < 368 m^3/s (13,000 ft^3/s) was unlikely. Accordingly, we assumed that fish that fell back at discharges < 368 m^3/s had passed upstream and then voluntarily fell back over the dam, whereas those that fell back at discharges ≥ 368 m^3/s had failed to pass upstream (i.e., they fell back involuntarily). Therefore, passage efficiency (E_{PAS}) was defined as the percentage of entering fish that passed the fishway *at least once* during the given year, either according to their last annual detection or a fallback event at a discharge < 368 m^3/s. This fallback adjustment allowed us to account for eight additional fish (three Burbot, two Brown Trout, and one each of White Sucker, Smallmouth Bass, and Rainbow Trout) that presumably passed, fell back, but did not pass according to their last annual detection. The effect of fallback on passage efficiencies would have been small regardless of the discharge threshold used; if all fish that fell back (even

those that did so at near peak discharge) were deemed to have passed, passage outcomes would have changed for only 12.8% (33) of the fish attracted in 2019 and 3.4% (23) of the fish attracted in 2020. Moreover, twenty-five of the 56 (44.6%) fish that fell back during the entire study were Burbot, whereas no more than eight individuals of any other species fell back.

Seasonal and Diel Fishway Use

We examined aggregate and species-specific seasonal and diel use of the fishway by recording the dates, times, and corresponding environmental conditions when fish were present and passed during the study. We defined a presence as any detection of a fish (including stationary fish) at any antenna (including the attraction antenna), and recorded the number of unique individuals (of each species and in aggregate) present each day during the monitoring period. We obtained mean daily and nearest instantaneous water temperatures (°C) and discharges (m^3/s) of the Yellowstone River at the USGS gage 06214500 near Billings, Montana, using the dataRetrieval package (De Cicco et al. 2021) in Program R (R Core Team 2021). We visualized and analyzed all data using base R and the following packages unless otherwise noted: cowplot (Wilke 2020), egg (Auguie 2019), gridExtra (Auguie 2017), and the tidyverse (Wickham et al. 2019) suite.

Trends in seasonal fishway use depended both on the timing of fish releases and the period that the fishway was monitored with PIT antennas. We tagged and released fish beginning in late March 2019, whereas monitoring of the fishway with PIT antennas did not begin until late April 2019. Therefore, we probably failed to detect a portion of tagged fish that used the fishway in 2019, particularly fish motivated to move upstream during the early spring. Conversely, we were able to monitor the fishway for the entirety of 2020. We used data from both years to

describe fishway use and effectiveness but considered efficiencies, seasonal trends in use, and the results of statistical analyses (described hereafter) for 2020 to be more accurate than those for 2019 when they differed greatly between years, unless otherwise noted, and describe potential effects of the lack of monitoring in early spring 2019 on our results when necessary.

Assessment of Attraction

We performed statistical analyses to better understand the factors that influenced two components of the attraction of fish to the Huntley fishway: whether fish were attracted, and their time to attraction. We performed all attraction analyses separately among species and years using data only from newly tagged fish ("new" tag status) in the general group (including the experimental subset of the general group), but excluded fish released after July 31 each year because relatively few fish moved into the fishway after that date. We performed the regression analyses described below only on Longnose Sucker, White Sucker, Burbot, Shorthead Redhorse (2020 only), and Smallmouth Bass because they had adequate sample sizes (Babyak 2004). For other species, we performed two-tailed unequal variance *t*-tests on ranked data (because of non-normality; Ruxton 2006) to determine if total length differed between fish that were and were not attracted (when $n \geq 5$ in each group) and Spearman's rank correlations to determine if total length was related to time to attraction after release (when $n \geq 10$). The *P*-values obtained from all analyses and tests indicated the strength of evidence (on a continuum) against the null hypothesis of no difference between groups, no relationship between variables, or no influence on the response, with small values indicating stronger evidence against the null hypothesis than large values (Murtaugh 2014).

Multiple logistic regression was used to determine the influence of total length and riverbank of release on the probability of a fish being attracted. The response for each fish (the experimental unit) in logistic regression was attracted (1) or not (0). Logistic regression modeled the log odds of success (here, attraction to the fishway) as a function of explanatory variables, or fixed effects, that could affect the upstream movement of fish: total length at tagging (TL; continuous) and water temperature (hereafter, TAR; continuous) and discharge (DAR; continuous) recorded at the USGS gage at the time of release. Attraction models for Longnose Sucker and White Sucker in 2020 also contained the variable riverbank of release (ROR; 2-level categorical; reference level = site A). Attraction models were "mixed" in that they contained a random effect (a random intercept term) for the release batch of fish to account for non-independence among fish within batches owing to differences in handling time (i.e., stress) and batch size (Zuur et al. 2009). Therefore, the log odds of attraction were modeled as

$$\log_e\left(\frac{p_{ij}}{1-p_{ij}}\right) = \beta' \times X_{ij} + b_i,$$

where p_{ij} was the probability of attraction of the j^{th} fish from the i^{th} batch, β was the vector of model coefficients, X_{ij} was the vector of explanatory variables of the j^{th} fish from the i^{th} batch, and b_i was the random intercept for the i^{th} batch (Zuur et al. 2009).

We performed diagnostic procedures for multiple logistic regression models using a process similar to that outlined in Zuur et al. (2010) after first fitting an additive model containing the fixed and random effects. We examined variance inflation factors to assess collinearity between explanatory variables and, when two variables had values > 3 (Zuur et al. 2010), we removed the variable thought to have less mechanistic importance from the model (Dormann et al. 2013). We did not remove any observations because we had no evidence of

recording error. We examined plots of partial residuals for evidence of biologically relevant interactions between riverbank of release and other variables as well as non-linearity between explanatory variables and the response. Plots of partial residuals did not suggest including interactions in the models for Longnose Sucker and White Sucker, but did suggest adding a second order orthogonal polynomial to help linearize the relationship between length of Longnose Suckers and the response in 2020.

We used *P*-values from Wald tests (`summary` function in R) to provide evidence of the influence of total length and riverbank of release on the response. We only interpreted results of the influence of length and riverbank in all attraction models, as water temperature and discharge were included solely to control for environmental conditions at the time of release. We exponentiated model coefficients of influential variables to calculate the estimated change in the mean odds of attraction for a 1-unit increase in the explanatory variable (while controlling for the other variables in the model; Vittinghoff et al. 2012). We converted coefficients into probabilities to aid in visual interpretation using the equation

$$p_{ij} = \frac{e^{\beta \times X_{ij}}}{1 + e^{\beta \times X_{ij}}},$$

where p_{ij} represented the estimated change in the probability of attraction for a 1-unit increase in the explanatory variable, and β was the coefficient for explanatory variable X of the j^{th} fish from the i^{th} batch (Zuur et al. 2009), while controlling for the other variables in the model.

We used multiple linear regression to determine the influence of fish total length and riverbank of release on time to attraction after release (in days; continuous). Initial multiple linear regression models contained the same fixed and random effects as those in logistic regression. We performed the same model diagnostic procedures for linear regression that we

performed for logistic regression but also examined residual plots to assess normality and homogeneity of variance. We ln transformed time to attraction to better meet model assumptions (Matter and Sandford 2003), removed no observations, added no interactions, and added a second-order orthogonal polynomial for discharge in the model for Longnose Sucker in 2020. We used *P*-values (`summary` function with output extended by the lmerTest package in R; Kuznetsova et al. 2017) to provide evidence of the influence of total length and riverbank of release on time to attraction. Model coefficients represented the estimated change in the ln transformed response for a 1-unit increase in the explanatory variable, whereas exponentiated coefficients represented the percentage change in the untransformed response for a 1-unit increase in the explanatory variable (while controlling for other variables).

We created species-specific Kaplan-Meier curves to examine differences in rates of attraction to the fishway of Longnose Suckers and White Suckers released on either riverbank in 2020. We used the survival (Therneau 2021) and survminer (Kassambara et al. 2021) packages to create Kaplan-Meier curves and the lme4 (Bates et al. 2015), effects (Fox 2003; Fox and Weisberg 2018, 2019), and ggeffects (Lüdecke 2018) packages to fit, diagnose, and visualize results from regression models of attraction (and passage, as described below).

Assessment of Passage

We examined temporal metrics and performed analyses on passage data to better understand the factors that may influence travel time and passage through the Huntley fishway. We performed all temporal and passage analyses only on entering fish and separately among species using data pooled between years and among release groups (except for translocated Sauger) to increase sample sizes, and only the first confirmed transit and passage event of each

fish during the study to ensure independence when comparing groups. We only included fish with complete detection histories at the applicable antennas in temporal analyses.

We calculated transit duration of transiting fish as the time elapsed in hours between the departure of a fish from A2 and its arrival at either A4 or A6, and compared transit durations between conspecifics that did and did not pass (when $n \geq 5$ in each group) using two-tailed unequal variance *t*-tests on ranked data (Ruxton 2006). We calculated passage duration of successful fish as the time elapsed in hours between the departure of a fish from A2 and its first passage event. Aggregate transit and passage durations were calculated using data from all species. We performed the following temporal analyses using data from successful Longnose Suckers, White Suckers, Burbot, Shorthead Redhorses, and Smallmouth Bass, the only species with large ($n > 30$) sample sizes of fish with complete detection histories. We calculated exit delay of successful fish as the time elapsed in hours between the arrival of a fish at A4 or A6 and its first passage event, representing the time required to progress from transiting to successfully passing, which we expected to be minimal when fish were able to easily navigate the farthest upstream extent of the fishway. We attempted to use multiple linear regression to model each temporal metric as a function of explanatory variables, but model diagnostics were poor. Therefore, we used scatterplots to examine relationships between the travel times (i.e., transit durations and exit delays) of successful individuals of the five species and total length (at tagging) and water temperature and discharge (recorded at the USGS gage) at the time of entrance to the fishway. Scatterplots were fit with LOESS smooth models with 95% confidence intervals (CI), models were fit using 80% of the neighboring observations (span = 0.8) to minimize variability in the smoothed lines (Cleveland 1979), and travel times were ln

transformed to reduce skew in the data (Matter and Sandford 2003). The width of CIs (i.e., the ability to draw a horizontal line through the CI) and the magnitude of the change in transformed travel times were considered when interpreting relationships (Bigelow et al. 1999).

We performed multiple logistic regression analyses using passage data from Longnose Sucker, White Sucker, and Burbot, the only species with adequate sample sizes (Babyak 2004), to determine the influence of biological and environmental variables on the probability of entering fish passing the fishway (1) or not (0). Logistic regression models of passage, unlike those of attraction, contained only fixed effects, including total length at tagging (TL; continuous) and water temperature (hereafter, TAE; continuous) and discharge (DAE; continuous) recorded at the USGS gage at the time of entrance to the fishway. The passage model for Burbot also contained the variable year (YR; 2-level categorical; reference level = 2019), whereas the models for Longnose Sucker and White Sucker did not contain year because of small sample sizes (Babyak 2004). We fit each initial additive model and performed the same diagnostic procedures that were outlined for the logistic regression analysis of attraction (Zuur et al. 2010). We retained all variables and observations, added no orthogonal polynomials, and added one interaction term to the model for Burbot. We used *P*-values from Wald tests (`summary` function in R) to provide evidence of the influence of each variable on the response while controlling for the other variables. We interpreted all coefficients from passage models because environmental variables were not just included to control for conditions at the time of entrance into the fishway. We performed two-tailed unequal variance *t*-tests on ranked data (Ruxton 2006) from species other than Longnose Sucker, White Sucker, and Burbot, to determine if entering fish that did and did not pass differed in total length at tagging and water

temperature and discharge (recorded at the USGS gage) at the time of entrance (when $n \geq 5$ in each group).

Results

PIT Antenna Performance

In-situ detection efficiency ($E_{in\text{-}situ}$) varied between years and among antennas. Estimates of $E_{in\text{-}situ}$ of A1 (68.3% in 2019 and 83.4% in 2020) were lower than A2 (87.8% in 2019 and 86.2% in 2020) and A3 (89.5% in 2019 and 92.2% in 2020) in both years of the study, and estimates of $E_{in\text{-}situ}$ of A1, A2, and A3 in 2020 were similar to or higher than estimates in 2019. The $E_{in\text{-}situ}$ of the version of A4 operating from April 10 to May 1, 2020, was 75.0%, but probably differed from the efficiencies of the versions of A4 operating at other times because of differences in tag read ranges and functionality. In general, antennas located near entrances or the exit had lower estimates of $E_{in\text{-}situ}$, probably because they were more susceptible to damage by debris and avoidance by fish during high discharge. Antennas located near entrances and the exit, except A4 and A6 starting in spring 2020, were also farther from the primary power source and had lower vertical read ranges than antennas closer to power sources. Antenna 3 was the best performing antenna throughout the study, probably because it was located in a relatively calm part of the fishway and was closest to the primary power source. Despite being unable to estimate $E_{in\text{-}situ}$ of A6 because no antennas were located farther upstream of it, A6 was probably one of the best performing antennas during its short period of functionality in spring 2020 because its read range was similar to that of A3. All estimates of $E_{in\text{-}situ}$ were > 68% despite concerns about low read ranges, suggesting that most fish swam close to the substrate where PIT antennas were located.

Aggregate Fishway Effectiveness

Fish Presences. Individuals of all 14 study species were present (i.e., detected by any antenna) at the Huntley fishway. Fish were first present the day monitoring began on April 23, 2019, and last present on November 7, 2020 (Figure 4). Although seasonal patterns of presences varied among species, most fish were present from April to August each year, few were present each autumn, and none were present from late November 2019 to late February 2020 (Figure 5), when water temperatures were low and ice was present in the fishway. The daily number of fish present during the study peaked at 85 fish on April 21, 2020, when a pulse of Longnose Suckers used the fishway. The number of fish present peaked on the descending limb of the hydrograph in 2019 but on the ascending limb in 2020, probably because of inter-annual differences in the timing of fish releases and the period of fishway monitoring. Although fish were present within a wide range of mean daily water temperatures (0.3–23.3°C) and discharges (81–1,651 m^3/s) (Table 2), most were present at water temperatures from about 12 to 16°C and discharges from about 100 to 700 m^3/s (Figure 6). Fish were present at all hours of the day, and diel patterns of presences varied among species (Figure 7). Diel patterns of presences also differed between years; most presences occurred during the day after water temperatures peaked in 2019, whereas most occurred during the night after temperatures peaked in 2020 (Figure 8).

Attraction. Aggregate attraction efficiencies of newly (i.e., tagged that year) and previously (i.e., tagged the year prior) tagged fish in the general group varied from 11.4 to 32.5% and were higher than those of fish in the supplemental upstream (0.0–9.1%) and downstream (2.5–5.3%) groups (Table 3). Attraction efficiencies of newly tagged fish in all groups in 2019 were probably underestimated because fish were tagged and released up to about a month before

fishway monitoring began and may have been attracted during the interim. Aggregate attraction efficiencies of newly tagged fish were higher than those of previously tagged fish in the general and supplemental downstream groups, probably because some previously tagged fish died, lost their tags, left the area, or lacked motivation. Conversely, the aggregate attraction efficiency of previously tagged fish (9.1%) was higher than that of newly tagged fish in the supplemental upstream group in 2019 (6.0%) and 2020 (0.0%) (Table 3). Most fish released upstream in 2019 were probably not motivated to first move downstream over the dam or through the natural side channel and then back upstream via the fishway that same year. Furthermore, no fish released > 2 rkm upstream of the dam in 2019 (most of which were Burbot) were present until 2020, and most of the 168 newly tagged fish released upstream in 2020 (most of which were Burbot and none of which were attracted) were released > 2 rkm upstream of the dam, and therefore may not have been present until 2021.

The influence of total length on the two components of attraction (whether fish were attracted and their time to attraction) varied among species and between years. The probability of attraction to the fishway was highest for fish of short, long, or intermediate lengths in certain years (Figure 9) among the five species for which data were analyzed using logistic regression (Table 4), whereas length did not differ between fish that were and were not attracted in a given year among all of the other species. Time to attraction increased (Longnose Sucker) or decreased (Smallmouth Bass) with length (Figure 10) for two of the species analyzed using linear regression (Table 5), and time to attraction was positively correlated with length among some salmonid species (Mountain Whitefish and perhaps Brown Trout) in certain years.

Riverbank of release did not influence whether Longnose Suckers or White Suckers in the experimental subset of the general group were attracted (Table 4) or their time to attraction (Table 5) in 2020. Suckers released on both riverbanks were attracted at similar rates during periods of high motivation within each species and trends in the cumulative proportions of suckers attracted did not closely resemble those of suckers released (Figure 11), suggesting that rates of attraction of both species were mostly affected by changing environmental conditions and not riverbank or date of release. Small differences in the cumulative proportions of fish of each species attracted from each riverbank may have been caused by differences in the cumulative proportions of suckers that had been released on each riverbank on a given date.

Entrance. Fish from all release groups were highly successful at entering the fishway after being attracted, as most aggregate entrance efficiencies were > 90% (Table 3). Only 4.9% of entering fish entered the fishway via the secondary entrance.

Transit. Most entering fish were successful transiting to near the upstream extent of the fishway. Aggregate transit efficiencies varied from 80.3 to 82.7% for the general group and were slightly lower or more variable for the supplemental upstream (68.8–79.3%) and downstream (60.0–100.0%) groups (Table 3). Over 68% and 93% of transit durations (the time elapsed between the departure of a fish from A2 and its arrival at either A4 or A6) were < 1 and 24 h, respectively. The median aggregate transit duration was only 0.72 h, and transit durations varied among species (Table 6); although merely a point estimate, the median transit duration of Goldeyes (0.22 h) was lower than those of all other species, whereas the median of Burbot (0.98 h) was higher than those of other species with sample sizes > 20. Transit duration generally changed little with increasing fish total length or water temperature or discharge (recorded at the

USGS gage) at the time of entrance, although Longnose Suckers and White Suckers that entered at high discharges (of which data were sparse) took longer to transit than conspecifics that entered at low discharges (Figure 12).

Passage. At least one individual of each of the 14 study species passed the Huntley fishway. Most fish passed from April to August each year, with the daily number of passages peaking annually on the ascending limb of the hydrograph (Figure 5). Seventy-five passages (mostly of Longnose Suckers) occurred on April 21, 2020, the date on which the daily number of fish present also peaked. Hourly passages peaked between 2000 and 2200 hours and were less evenly spread throughout the day than presences (Figure 7). Diel patterns of passages varied among species and seasonally within species. Most Burbot and Channel Catfish passed at night, whereas most Smallmouth Bass and Mountain Whitefish passed during the day (Figure 7). Most Longnose Suckers, White Suckers, and Shorthead Redhorses that passed during the early spring in 2020 did so at night, whereas most that passed during June 2020, the month during which discharge peaked that year, did so during the day (Figure 8). Only one fish (a Longnose Sucker) passed the fishway in a downstream direction during the entire study period. However, the fishway also facilitated the downstream passage in August 2020 of one spiny softshell turtle *Apalone spinifera*, about one year after it was PIT-tagged in another study and released in the natural side channel on the north side of the island. To our knowledge, this represents the first documented passage of a reptile through a nature-like fishway.

Entering fish from all groups were moderately to highly successful at passing (aggregate passage efficiencies = 58.5–80.3%; Table 3). Aggregate passage efficiencies of both newly and previously tagged fish in the general group in 2020 were higher than the efficiency of newly

tagged fish in 2019. The same was true of efficiencies in the supplemental upstream group but not the supplemental downstream group, which had smaller sample sizes of entering fish than the other groups (Table 3). About 64% and 88% of passage durations (the time elapsed between the departure of a fish from A2 and its first passage event) were < 1 and 24 h, respectively, and the median aggregate passage duration (0.77 h) was just slightly longer than the median aggregate transit duration (Table 6). Passage durations varied among species, with the median (albeit merely a point estimate) passage duration of Goldeyes (0.33 h) being lower than those of all other species and the median of Burbot (0.96 h) being higher than those of other species with sample sizes > 20 (Table 6).

High discharge was consistently detrimental to passage. The probability of Longnose Suckers, White Suckers, and Burbot passing decreased with increasing discharge (Figure 13) even while controlling for length and water temperature (Table 7), and Shorthead Redhorses, Smallmouth Bass, and Mountain Whitefish that passed entered at lower discharges than conspecifics that did not pass. Discharge and water temperature were correlated within the data sets of Shorthead Redhorse and Smallmouth Bass, but differences in effect sizes suggested that passage of the two species was influenced more by discharge than by temperature. Fish passed within a slightly narrower range of mean daily discharges (81–1,532 m^3/s) than when fish were present (Table 2), and the distribution of the number of passages was skewed toward low discharges (Figure 6). Mean daily discharge was > 566 m^3/s (20,000 ft^3/s) for only 37 d in 2020 but 54 d in 2019, which may explain why aggregate passage efficiencies of newly and previously tagged fish in the general and supplemental upstream groups in 2020 were higher than those of newly tagged fish from the same groups in 2019. The amount of time fish of five species spent

delayed at the exit before passing increased at discharges > 300–400 m^3/s, whereas the relationship varied among species at discharges < 300–400 m^3/s (Figure 12).

Fish total length (at tagging) had a positive influence on the passage of some species. Increasing length positively influenced the passage of Longnose Suckers (Figure 13), Smallmouth Bass, and perhaps Saugers. The range of lengths of fish that passed (157–726 mm TL) was just slightly narrower than that of fish that were present (135–726 mm TL) (Table 2), and exit delay of successful fish was not strongly related to total length (Figure 12).

The influence of water temperature on passage varied among species. Goldeyes that passed entered at higher water temperatures than those that did not pass, and Burbot that entered at high water temperatures in 2019 were more likely to pass than those that entered at low temperatures (Figure 13), although the opposite was true among Burbot in 2020. Conversely, individuals that passed of each of the remaining species for which we had at least weak evidence entered the fishway at lower temperatures than those that did not pass. Fish passed within a slightly narrower range of mean daily temperatures (1.4–23.1°C) than when they were present (Table 2). Exit delay increased with increasing water temperature for some species (Figure 12), but temperature was often correlated with discharge within data sets.

Species-specific Fishway Effectiveness

Effectiveness of the fishway varied among species, as did our ability to make conclusions about its effectiveness for certain species because of sample size limitations. Longnose Suckers and White Suckers, the only species released as part of the experimental subset, were released (n > 550 each) and attracted (n > 150 each) in large numbers because of their great abundance near the study site, allowing for rigorous statistical analyses of attraction and passage. Many Burbot,

Shorthead Redhorses, and Smallmouth Bass were released ($n > 250$ each) and attracted ($n > 75$ each) despite not being part of the experimental subset, which allowed for the analysis of attraction or passage or both. Goldeyes, Channel Catfish, and Mountain Whitefish were released in relatively large numbers ($n > 125$ each) and ≥ 25 individuals of each species were attracted, allowing for some analyses to be performed. Therefore, we provide species-specific visualizations of seasonal and diel fishway use only for these eight species, which were the most prevalent. Few Saugers were attracted, but translocations of them into the fishway allowed us to separate the issue of attraction from passage. Brown Trout, Flathead Chubs, River Carpsuckers, Rainbow Trout, and Mountain Suckers were released ($n < 70$ each) and attracted ($n < 25$ each) in relatively low numbers, limiting our ability to analyze their attraction or passage. The effectiveness of the fishway for each of the 14 study species, arranged generally in order of descending sample sizes of released and attracted fish, is described below.

Longnose Sucker. Attraction efficiencies of Longnose Suckers in the general group (23.1–47.2%) were higher than those of suckers released upstream of the dam (2.7–19.4%) (Table 3). Newly tagged suckers in the general group in 2020 had attraction efficiencies that were about twice as high (41.4–47.2%) as those of suckers in the same release group that were initially tagged in 2019 (23.1–23.6%). All entrance efficiencies approached 100%. The transit efficiency of newly tagged suckers in the general group in 2019 (78.0%) was lower than of those either previously or newly tagged in the same group in 2020 (92.1–95.3%). Passage efficiencies of suckers in the general group were higher in 2020 (90.8–95.1%) than in 2019 (68.3%). Ten suckers passed multiple times in the same year, five passed in both years, and one (340 mm TL)

released upstream in 2019 passed downstream through the fishway in April 2020—the only downstream passage event of a fish confirmed during the study.

Longnose Suckers were present primarily throughout the spring and summer but rarely during periods of rapidly increasing discharge associated with annual peak runoff, short periods of rapidly decreasing water temperatures in the spring, or at water temperatures above 20°C (Figure 4). The number of Longnose Suckers, which spawn in the spring at water temperatures from 10 to 15°C (Edwards 1983), that were present peaked on April 21, 2020 (Figure 14), the first day that year when mean daily water temperatures surpassed 12°C. Mean daily water temperatures in 2019 first surpassed 12°C on April 19, 4 days before fishway monitoring began. About 42% of suckers were released and could have used the fishway before monitoring began in 2019. Therefore, a portion of spawning fish was probably not detected in spring 2019 and suckers that did enter the fishway after monitoring began may have had low motivation to move upstream to spawn if the initial spawning temperature threshold had already been surpassed, which could have contributed to lower attraction and transit efficiencies in 2019 than in 2020. Suckers passed within narrower ranges of discharges and water temperatures than when they were present and at lower temperatures than most other species (Table 2). Most presences and passages occurred from late afternoon to early night (Figure 7), although presences and passages occurred more often during the day than at night during periods of high discharge (Figure 8).

The influence of total length of Longnose Suckers on the two components of attraction varied between years, whereas riverbank of release did not influence either component. Length of suckers in 2019 did not influence whether they were attracted (Table 4) or their time to attraction (Table 5). However, length of suckers influenced both components of attraction in

2020; the probability of attraction was highest among fish of intermediate lengths (Figure 9) and time to attraction increased by 0.29% (95% CI = 0.02–0.55%) for each 1-mm increase in length (Figure 10). Conversely, riverbank of release did not influence whether suckers were attracted (Table 4) or their time to attraction (Table 5), and attraction efficiencies did not differ between suckers released on opposite riverbanks in 2020 (chi-square test: $\chi^2 = 1.41$, df = 1, $P = 0.235$). Suckers released on both riverbanks were attracted at similar rates during a period of apparently high motivation in April 2020 and trends in the cumulative proportions of suckers attracted did not mirror trends in releases (Figure 11), suggesting that rates of attraction of suckers in 2020 were influenced more by environmental conditions than riverbank or date of release.

Biological and environmental variables differentially affected the passage of Longnose Suckers, which generally transited and passed the fishway in a timely manner (Table 6). Over 86 and 83% of transit and passage durations, respectively, were < 1 h, and < 5% of suckers had exit delays > 1 h. Transit duration changed little with increasing total length or water temperature (which was positively associated with discharge within the data set; Spearman's rank correlation: $r_s = 0.73$, $P < 0.001$), and exit delay was not related to length but was shortest at low temperatures (Figure 12). Both transit duration and exit delay were longest at high discharges, although data were sparse at discharges > 375 m^3/s. Despite equal ranges of lengths of suckers that passed and that were present (Table 2), longer suckers were more likely to pass than shorter suckers (Figure 13), with the odds of passage increasing by 1.08% (95% CI = 0.25–1.95% increase) for each 1-mm increase in length (Table 7). Additionally, suckers that entered at high discharges were less likely to pass than those that entered at low discharges (Figure 13), with the odds of passage decreasing by 0.53% (95% CI = 0.33–0.75% decrease) for each 1-m^3/s increase

in discharge (Table 7). Water temperature did not influence the probability of passage, while controlling for the other variables.

White Sucker. Attraction efficiencies of newly tagged White Suckers in the general group (22.0–31.5%) were relatively low but were higher than those of previously tagged suckers in the same group (9.4%) (Table 3). Only four suckers released upstream and none in the supplemental downstream group were ever attracted. All entrance efficiencies were near 100%. After entering, suckers in the general group were moderately to highly successful transiting (69.2–83.0%) and passing (54.8–83.0%) the fishway, although the percentage of transiting fish that passed was lower in 2019 (70.4%) than in 2020 (98.9%). Nine suckers passed multiple times in a single year and one sucker passed in both years.

White Suckers, which begin spawning in the spring at water temperatures from 10 to 13°C (Hamel et al. 1997), were present primarily from April through August each year (Figure 4). The number of suckers present on the ascending limb of the hydrograph increased and decreased, respectively, with increases and decreases in water temperature (Figure 14). Passages were rare after water temperatures had peaked each year and during periods of high discharge associated with annual runoff (Figure 4). Water temperatures during the first two peaks of sucker movements in spring 2020 (Figure 14) had already been surpassed in late April 2019 when fishway monitoring began. Therefore, we probably failed to detect a portion of spawning suckers in 2019, although the effect of the lack of monitoring on attraction efficiencies was probably small because only about 20% of suckers in 2019 were released before monitoring began. White Suckers passed within slightly narrower ranges of water temperatures and discharges than when they were present (Table 2) and, despite being present during all hours, mostly passed during the

afternoon and night (Figure 7). Most presences and passages occurred at night during periods of low discharges (Figure 8).

The influence of total length of White Suckers on the two components of attraction varied between years, whereas riverbank of release did not influence either component. Length of suckers did not influence whether they were attracted in 2019 (Table 4) or their time to attraction in either year (Table 5). However, shorter suckers were more likely to be attracted than longer suckers in 2020 (Figure 9), with the odds of attraction decreasing by 0.65% (95% CI = 0.06–1.24% decrease) for each 1-mm increase in length (Table 4). Similar to Longnose Suckers, riverbank of release did not influence whether White Suckers were attracted (Table 4) or their time to attraction (Table 5) while controlling for other variables, and attraction efficiencies did not differ between suckers released on either riverbank in 2020 (chi-square test: $\chi^2 = 0.51$, df = 1, $P = 0.477$). The cumulative proportion of White Suckers attracted after being released on the same riverbank as the fishway (site A) was slightly higher than the proportion attracted from the opposite riverbank (site B) during late April and early May 2020 when motivation was apparently high (Figure 11). However, a greater proportion of fish had been released on the same than the opposite riverbank at the start of this period, and the trends in cumulative proportions of suckers attracted from each riverbank during this period did not hold true the remainder of the year.

High discharge was detrimental to the passage of White Suckers, although most that transited and passed the fishway did so relatively quickly (Table 6). About 66% of passage and transit durations of suckers were < 1 h, and transit durations did not differ between fish that did and did not pass ($t = -1.13$, df = 6.70, $P = 0.296$). Only about 5% of exit delays of successful fish

were > 1 h. Neither transit duration nor exit delay were strongly related to total length or water temperature (Figure 12). Transit duration and exit delay increased starting at discharges > 300–400 m^3/s, although data were sparse at high discharges. The range of lengths of fish that passed was about the same as that of fish that were present (Table 2), and neither length nor water temperature at the time of entrance influenced passage (Table 7). However, suckers that entered at high discharges were less likely to pass than those that entered at low discharges (Figure 13), with the odds of passage decreasing by 0.29% (95% CI = 0.08–0.51% decrease) for each 1-m^3/s increase in discharge (Table 7).

Burbot. Attraction efficiencies varied among Burbot released in the general (10.0–56.2%), supplemental upstream (0.0–21.9%), and supplemental downstream (4.3–8.7%) groups (Table 3). Newly tagged Burbot in the general group in 2020 had the highest attraction efficiency (56.2%) of any species in any group with $n > 20$, although the attraction efficiencies of Burbot in the general group may have been inflated because of the upstream homing behavior (Armstrong and Herbert 1997) of fish captured just downstream of the face of the dam. The attraction efficiency of previously tagged Burbot in the general group (10.0%) was much lower than that of newly tagged Burbot in the general group in either year. Most entrance efficiencies were > 90%, and most entering Burbot in the general group were successful transiting (transit efficiencies = 77.1–90.9%). However, far fewer Burbot in the general group passed than transited, particularly in 2019 when only 17 of 37 (46%) transiting fish passed, which could be attributable to the period of snowmelt runoff (i.e., high discharge) lasting longer in 2019 than in 2020. Passage efficiencies of Burbot in the general group varied but were higher for previously tagged (81.8%)

than newly tagged (37.8–60.2%) fish. Burbot in the supplemental release groups were moderately to highly successful passing. Three Burbot passed multiple times in the same year.

Burbot, which usually spawn at near freezing water temperatures in the winter or spring (McPhail and Paragamian 2000), were present earlier in the year than other species but primarily from March through July (Figure 4). Annual peaks in the daily number of Burbot present occurred outside of their putative spawning period and coincided with increases in water temperature on the ascending limb of the hydrograph (Figure 14). Burbot were present and passed within wide ranges of discharges and at water temperatures up to 19.3°C (Table 2). Burbot were present during all hours but mostly passed at night (Figure 7).

At least some tagged Burbot were highly mobile. Burbot released up to 23 rkm upstream in spring 2019 passed back upstream the following spring, whereas some released downstream of the dam passed upstream in autumn. The farthest migrating fish of the entire study was a Burbot (496 mm TL) that was released about 83 rkm downstream, was attracted 33 days later (~ 2.5 rkm/day), and passed. A smaller Burbot (249 mm TL) was released about 68 rkm downstream, was attracted 34 days later (~ 2 rkm/day), passed, fell back, and then failed to pass according to its last detection. Another (305 mm TL) was released about 61 rkm downstream, was attracted 87 days later (~ 0.7 rkm/day), transited, but did not pass. These three fish, which were released in late March 2020, either passed directly over Waco Diversion Dam (rkm 509) or bypassed it via a natural side channel as they moved upstream toward Huntley Diversion Dam.

The overall influence of total length of Burbot on attraction was minimal. Shorter Burbot were more likely to be attracted than longer Burbot in 2019 (Figure 9), with the odds of attraction decreasing by 0.31% for each 1-mm increase in length, although the evidence was

somewhat weak as the 95% CI for the coefficient contained zero (0.64% decrease to 0.01% increase in the odds of attraction) and the *P*-value (0.0633) was not particularly small (Table 4). Moreover, 79% (95 of 120) of Burbot in the general group in 2019 were released and could have used the fishway before monitoring began in 2019, potentially confounding these results. Length did not influence time to attraction in 2019 (Table 5) or either component of attraction in 2020.

Discharge and, to a lesser extent, water temperature influenced the passage of Burbot, which had the longest median transit and passage durations of any species with sample size > 20 (Table 6). About 51% of transit durations of Burbot were < 1 h and entering fish that eventually passed transited more quickly (median = 0.86 h) than those that did not pass (median = 1.26 h) ($t = -3.97$, df = 81.69, $P < 0.001$), indicating that the mechanisms that influenced their travel times also influenced their passage outcomes. Only about 55% of passage durations were < 1 h, and over 21% of passing Burbot were delayed at the exit for > 1 h. Transit duration was not related to total length, discharge, or water temperature (Figure 12). Exit delay was not related to total length, but did increase steadily with discharge and was shortest at low temperatures, although discharge and temperature were correlated within the data set (Spearman's rank correlation: $r_s = 0.51$, $P < 0.001$). The range of lengths of passing fish was slightly narrower than that of fish that were present (Table 2), but length did not influence whether entering fish passed while controlling for other variables (Table 7). Burbot that entered the fishway at high discharges were less likely to pass than those that entered at low discharges (Figure 13), with the odds of passage decreasing by 0.22% (95% CI = 0.05–0.41% decrease) for each 1-m^3/s increase in discharge. The influence of water temperature on passage differed between years ($P = 0.0487$; Table 7), with Burbot entering at high temperatures being more likely to pass than those entering at low

temperatures in 2019, and the opposite being true in 2020 (Figure 13). However, sample sizes of entering Burbot were larger, the range of temperatures at which they entered was wider, and the period during which the fishway was monitored was longer in 2020 than in 2019, suggesting that model results for 2020 more accurately depict the influence of temperature on passage than those for 2019.

Shorthead Redhorse. Attraction efficiencies of newly tagged Shorthead Redhorses in the general group (13.2–16.6%) were lower than those of other catostomids with $n > 100$ (Table 3). Few redhorses released in the supplemental groups were ever attracted. Most entrance efficiencies of redhorses approached 100%, and most entering redhorses in the general group were successful transiting (transit efficiencies = 73.9–90.9%). Newly tagged redhorses in 2020 had a higher passage efficiency (87.9%) than those newly tagged in 2019 (65.2%), which could be attributable to the period of snowmelt runoff lasting longer in 2019 than in 2020. All redhorses that passed did so only once.

Presences and passages of Shorthead Redhorses, which begin spawning at water temperatures of 10 to 11°C (Reid 2006), occurred on both the ascending and descending limbs of the hydrograph but rarely when discharges or water temperatures peaked annually (Figure 4). The number of fish present daily in 2019 peaked after snowmelt runoff in the spring and well after temperatures had surpassed the spawning threshold (Figure 14). However, few redhorses in 2019 were tagged and released before the putative spawning period. Conversely, most redhorses in 2020 were released before the putative spawning period, and the number of fish present that year peaked before runoff, one day after mean daily water temperatures surpassed 11°C. Passages occurred within slightly narrower ranges of water temperatures and discharges than did

presences (Table 2) and usually during the day (Figure 7), although some redhorses passed at night before discharge peaked each year (Figure 8).

The influence of total length of Shorthead Redhorses on whether they were attracted varied between years, whereas length did not influence time to attraction. Length of redhorses in 2019 did not differ between those that were and were not attracted ($t = 0.36$, df = 35.03, $P = 0.718$), but longer redhorses were less likely to be attracted than shorter redhorses in 2020 (Figure 9), with the odds of attraction decreasing by 1.63% (95% CI = 0.44–2.91% decrease) for each 1-mm increase in length (Table 4). Differences in results between years are probably attributable to differences in the timing of releases of redhorses and the lack of monitoring in early spring 2019. Length was not related to time to attraction in 2019 ($r_s = -0.19$, $P = 0.380$) and had no influence on time to attraction in 2020 (Table 5).

High discharges and, to a lesser extent, high water temperatures negatively affected the passage of Shorthead Redhorses, although most redhorses that transited and passed the fishway did so in a timely manner (Table 6). Over 73% of transit durations of redhorses were < 1 h, and they did not differ between fish that eventually did and did not pass ($t = 0.20$, df = 5.19, $P = 0.846$). In addition, over 63% of passage durations were < 1 h and only about 9% of passing fish had exit delays > 1 h. Transit duration and exit delay were not strongly related to total length or water temperature (Figure 12). Transit duration was not related to discharge, whereas exit delay increased with discharge starting between about 400 and 500 m^3/s. The range of lengths of passing fish was narrower than that of fish that were present (Table 2), but length did not differ between entering fish that did and did not pass ($t = 0.94$, df = 28.73, $P = 0.357$). However, redhorses that passed entered at lower discharges (median = 326 m^3/s) and slightly lower water

temperatures (median = 13.9°C) than those that did not pass (median = 597 m^3/s; median = 14.4°C) (discharge: $t = 2.80$, df = 30.02, $P = 0.009$; temperature: $t = 2.50$, df = 34.23, $P = 0.017$). Despite discharge and water temperature being correlated within the data set ($r_s = 0.42$, $P < 0.001$), the relative difference between the median discharges at which passing and not passing redhorses entered was much greater than the difference between median water temperatures, suggesting that discharge was more important in influencing passage.

Smallmouth Bass. Attraction efficiencies of newly tagged Smallmouth Bass in the general group (29.5–37.0%) were higher than that of previously tagged bass (7.4%) and, similar to most other species in the general group, the attraction efficiency of newly tagged bass in 2019 (29.5%) was lower than that of newly tagged bass in 2020 (37.0%) (Table 3). Both entrance (93.3–100.0%) and transit (82.1–97.1%) efficiencies of bass in the general group were high. Despite most entering bass in the general group passing, the passage efficiency of newly tagged bass in 2019 (68.6%) was lower than those of both previously (77.8%) and newly tagged bass in 2020 (78.6%). Over 31% of transiting bass in all release groups in 2019 failed to pass, whereas only about 6% of transiting bass in 2020 failed to pass. Four bass released in the general group in 2019 passed in both years. Few bass in the supplemental release groups were attracted and their entrance, transit, and passage efficiencies varied widely, although sample sizes were small.

Smallmouth Bass, which begin spawning in the spring at water temperatures from 12.5 to 15°C (Graham and Orth 1986; Rubenson and Olden 2016), were mostly present and passed from late April through August each year (Figure 4). The number of bass present daily generally increased and decreased, respectively, with increases and decreases in water temperature, although few bass were present after temperatures peaked each year (Figure 14). Bass passed on

both the ascending and descending limbs of the hydrograph but rarely during peak runoff (Figure 4), suggesting that high discharges on the Yellowstone River temporarily halted upstream movement during the probable spawning period (Graham and Orth 1986). Bass were present at higher water temperatures than most other species and passed within more narrow ranges of temperatures and discharges than when they were present (Table 2). Nearly all bass presences and passages occurred during the day (Figure 7).

The influence of total length of Smallmouth Bass on the two components of attraction differed between years. Length did not influence whether bass were attracted in 2019 (Table 4), but longer bass that year were attracted more quickly than shorter bass (Figure 10), with time to attraction decreasing by 0.63% (95% CI = 0.08–1.18% decrease) for each 1-mm increase in length (Table 5). Conversely, length did not influence time to attraction in 2020 (Table 5), but longer bass that year were more likely to be attracted than shorter bass (Figure 9), with the odds of attraction increasing by 0.88% for each 1-mm increase in length, although the strength of evidence was not strong as the 95% CI for the model coefficient contained zero (0.03% decrease to 1.89% increase in the odds of attraction) and the *P*-value (0.068) was not particularly small (Table 4). The mean daily water temperature at which bass were first present in 2020 (13.1°C) was surpassed 3 days before monitoring began in 2019, suggesting that the results of attraction analyses for 2020 may be more accurate than those for 2019.

Total length, water temperature, and discharge affected the passage of Smallmouth Bass. Most bass that transited and passed the fishway did so relatively quickly (Table 6), with about 76 and 59% of bass transiting and passing, respectively, in < 1 h. However, about 24% of successful bass were delayed at the exit for > 1 h. Neither transit duration nor exit delay were related to total

length or water temperature; transit duration was also not related to discharge (Figure 12). Conversely, exit delay first decreased but then increased with discharge starting between about 300 and 400 m^3/s. Passing fish were within a narrower range of lengths than those that were present (Table 2), and entering fish that passed were slightly longer (median = 308 mm) than those that did not pass (median = 285 mm) ($t = -2.43$, df = 31.79, $P = 0.021$). Furthermore, passing fish entered at lower discharges (median = 337 m^3/s) and water temperatures (median = 13.5°C) than fish that did not pass (median = 623 m^3/s; median = 15.5°C) (discharge: $t = 3.58$, df = 46.66, $P < 0.001$; temperature: $t = 4.16$, df = 47.88, $P < 0.001$), although discharges and water temperatures at the time of bass entrances were positively associated ($r_s = 0.41$, $P < 0.001$). Longer bass, which are active and spawn earlier in the year than shorter bass (Ridgway et al. 1991), entered the fishway earlier than shorter bass did in both 2019 and 2020. Small sample sizes precluded the use of multiple logistic regression to examine the influence of length on passage while controlling for environmental variables, so we were unable to determine if the difference in length between entering bass that did and did not pass was caused by longer fish having greater swimming abilities or merely entering the fishway at more favorable hydraulic conditions than shorter fish. Regardless, passage of bass through the fishway was size dependent.

Goldeye. Attraction efficiencies of Goldeyes in the general (8.2–17.8%) and supplemental upstream (7.2–11.1%) groups were low, and the one Goldeye released in the supplemental downstream group was not attracted (Table 3). Most entrance efficiencies were 100%. Transit efficiencies varied from 40.0 to 76.2% and passage efficiencies varied from 20.0 to 71.4%, although most sample sizes of entering Goldeyes were ≤ 10. Efficiencies of Goldeyes in the general and supplemental upstream groups were similar, suggesting that Goldeyes released

upstream (which had to first move downstream over the dam or via the natural side channel) were similarly motivated and capable of using the fishway as those released downstream of the dam. One Goldeye in the general group passed in both years.

Most presences and passages of Goldeyes, which spawn from April through early June in the Teton River in Montana (Hill 1965) and the Missouri River in North Dakota (Moon et al. 1998), occurred from June through August on the descending limb of the hydrograph (Figure 4). Passages occurred at higher water temperatures than most other species and within a much narrower range of discharges than did presences (Table 2). Goldeyes were present throughout the day but mostly passed in the afternoon and night (Figure 7).

Total length of Goldeyes did not influence either component of attraction. Length in 2019 did not differ between Goldeyes that were and were not attracted ($t = -0.32$, df = 34.14, $P = 0.747$) and was not related to time to attraction ($r_s = -0.02$, $P = 0.950$). Goldeyes that were and were not attracted in 2020 did not differ in length ($t = 1.47$, df = 4.64, $P = 0.205$). Small sample sizes of attracted Goldeyes in 2020 precluded further analysis.

Water temperature was the main factor affecting the passage of Goldeyes, which moved through the fishway quickly (Table 6). Goldeyes had the lowest median transit and passage durations of any species, and transit duration did not differ between fish that did (median = 0.20 h) and did not pass (median = 0.28 h) ($t = -1.61$, df = 12.78, $P = 0.131$). The range of lengths of fish that passed was slightly narrower than that of fish that were present (Table 2), but neither length ($t = 0.34$, df = 33.20, $P = 0.733$) nor discharge at the time of entrance ($t = 1.20$, df = 27.19, $P = 0.242$) differed between fish that did and did not pass. However, Goldeyes that passed entered at higher water temperatures (median = 19.1°C) than those that did not pass (median =

16.8°C) ($t = -3.53$, df = 34.60, $P = 0.001$), providing additional evidence that most passages of Goldeyes, which spawn at water temperatures from 8 to 15°C (Hilton et al. 2014), were probably related to post-spawn migrations to foraging habitats.

Channel Catfish. Attraction efficiencies of Channel Catfish in the general group (10.8–14.6%) were low, and only one catfish from the supplemental release groups was ever attracted (Table 3). Similar to most other species, all entrance efficiencies of catfish were ≥ 90%. Catfish in the general group were moderately successful transiting (transit efficiencies = 55.6–63.6%). Passage efficiencies of catfish in the general group varied from 53.3 to 66.7% and, although sample sizes of entering catfish were ≤ 15, were similar between newly tagged fish in 2019 and 2020. Three catfish passed multiple times in one year. One catfish (574 mm TL) in the general group passed in July 2019 just a few days after being released and was later found dead in spring 2020 near the town of Billings, Montana, about 12.5 rkm upstream of the fishway.

Catfish were present from about May to September each year (Figure 4), and pulses of movement mostly coincided with increases in water temperature on the descending limb of the hydrograph (Figure 14). The daily number of catfish present peaked annually in mid to late July when mean daily water temperatures first surpassed 21°C, the temperature at which catfish begin spawning (Clemens and Sneed 1957). Presences and passages of catfish occurred at higher water temperatures than nearly all other species and at wide ranges of discharges (Table 2). Catfish only passed during the evening and night but were present during all hours (Figure 7), although daytime presences became less frequent in 2020 as water temperature approached its peak and discharge approached base flow (Figure 8).

Neither biological nor environmental variables seemed to affect the attraction or passage of Channel Catfish, although sample sizes were relatively small. Total length did not differ between catfish that were and were not attracted in 2019 ($t = -1.07$, df = 13.23, $P = 0.306$), and was not related to time to attraction in 2019 ($r_s = -0.02$, $P = 0.968$) or 2020 ($r_s = -0.16$, $P = 0.576$). Evidence was scant ($t = 1.68$, df = 18.38, $P = 0.110$) to suggest that length differed between catfish that were (median = 480 mm TL) and were not attracted (median = 524 mm TL) in 2020. Some catfish were able to transit and pass in under 1 h (Table 6). The ranges of lengths of catfish that were present and passed were the same (Table 2), and entering fish that did (median = 502 mm TL) and did not pass (median = 556 mm TL) did not differ in length ($t = 1.59$, df = 28.03, $P = 0.123$). Additionally, neither discharge ($t = 1.28$, df = 29.04, $P = 0.210$) nor water temperature at the time of entrance ($t = -0.21$, df = 29.66, $P = 0.835$) differed between fish that eventually did and did not pass.

Mountain Whitefish. Attraction efficiencies of Mountain Whitefish in the general group were low (5.3–20.8%), and the one whitefish released upstream was not attracted (Table 3). All attracted whitefish ($n = 25$) entered the fishway and 13 of the entering fish transited and passed. Most presences and passages of Mountain Whitefish, which spawn from October through November in the Yellowstone River (Liebelt 1970), occurred from April through July (Figure 4), probably representing movements to upstream thermal refugia (Pettit and Wallace 1975; Lance 2019). Pulses of movement coincided with increases in water temperature (Figure 14), although fish were rarely present at temperatures above 20°C. The maximum water temperatures and discharges at which Mountain Whitefish passed were among the lowest maximums of all species (Table 2). Nearly all whitefish presences and passages occurred during the day (Figure 7).

Small sample sizes of Mountain Whitefish in 2019 precluded detailed analysis. Total length in 2020 did not differ between fish that were and were not attracted ($t = 1.21$, df = 31.15, $P = 0.235$) but was positively associated with time to attraction ($r_s = 0.53$, $P = 0.013$). All transit and passage durations of whitefish were less than about 2 h (Table 6). The range of lengths of fish that passed was narrower than that of fish that were present (Table 2), but length did not differ between entering fish that did and did not pass ($t = 0.86$, df = 21.21, $P = 0.400$). However, whitefish that passed entered at lower discharges (median = 140 m^3/s) than those that did not pass (median = 374 m^3/s) ($t = 2.53$, df = 22.85, $P = 0.019$). Evidence was weak ($t = 1.90$, df = 21.12, $P = 0.071$) that water temperature at the time of entrance differed between fish that did (median = 11.9°C) and did not pass (median = 14.5°C).

Sauger. Few Saugers were ever attracted to the fishway, particularly those tagged in 2019 (Table 3). Seven Saugers were attracted, six entered, three transited, and three passed. Despite the release of 204 Saugers up to 88 rkm downstream in the supplemental downstream group, only three were attracted and were released < 16 rkm downstream. The farthest moving Sauger of the study (422 mm TL) was released nearly 16 rkm downstream in early spring 2020 and entered the fishway 71 days later, but did not transit or pass. The three Saugers that passed did so in July 2020 as discharge approached base flow and water temperature approached its annual peak, probably representing movements to home locations upstream after previously having moved downstream of the dam to spawn in the spring (Jaeger et al. 2005). Passages occurred between 0030 and 0930 hours and within a narrow range of high water temperatures and low discharges (Table 2).

Small sample sizes precluded the analysis of data from Saugers that moved into the fishway voluntarily. Attracted Saugers varied from 392 to 584 mm TL, and one fish released in general group in May 2020 was attracted seven days later. The one entering Sauger that had a complete detection history transited and passed in just over 10 h (Table 6). However, one Sauger with an incomplete detection history moved from the primary entrance to the midpoint of the length of the fishway in just 9 min, whereas two others traveled from the midpoint to the exit in 22 and 35 min, suggesting that Saugers probably were able to transit and pass the fishway in a timely manner (at least at high water temperatures and low discharges). Passage may have been size dependent, as only the three longest fish (range = 504–545 mm TL) among those attracted in 2020 passed the fishway. However, the fish that was attracted in 2019 was the longest Sauger (584 mm TL) attracted during the study but did not pass, despite entering the fishway at similar water temperatures and discharges as the fish that passed in 2020.

Translocated Saugers released within the fishway seemed unmotivated to pass. None of the 13 translocated Saugers passed and only one transited the fishway, after which it exited the fishway in a downstream direction through the primary entrance. Most translocated fish, which were released between 1130 and 1600 hours, remained in the fishway until exiting in a downstream direction that evening between 2000 and 2300 hours. Saugers voluntarily entered the fishway in the spring and summer but only passed in the latter, suggesting that translocated fish, which were released in the spring, may have had low motivation to pass even if hydraulic conditions were suitable.

Brown Trout. Attraction efficiencies of Brown Trout varied widely, although sample sizes of released trout were usually ≤ 12 (Table 3). Nearly all of the 23 attracted trout entered the

fishway and over half of them transited and passed. Two newly tagged trout in 2020 passed twice that year, and the three trout in the supplemental downstream group that were attracted to the fishway passed, the farthest of which was released 12 rkm downstream. Brown Trout, which spawn in autumn (Brown and Kamp 1942), were present and passed mostly from April through July each year as water temperatures increased, probably representing movements to upstream summer habitats used before spawning (Meyers et al. 1992). One trout (391 mm TL) was present almost every day during the month of May 2019. The maximum mean daily water temperature at which trout presences and passages occurred (17.9°C) was lower than the maximums of nearly all other species (Table 2). Most trout passed during the day.

The detailed analysis of attraction and passage data of Brown Trout was precluded by small sample sizes. Some trout were highly motivated to move upstream, with multiple fish attracted less than 12 min after release. Total length did not differ between trout that were and were not attracted in 2019 ($t = 0.31$, df = 9.50, $P = 0.765$) or 2020 ($t = 1.33$, df = 26.71, $P = 0.196$), and evidence that time to attraction in 2020 increased with length was weak ($r_s = 0.48$, $P = 0.096$). A Brown Trout had the fastest recorded transit duration (0.12 h) and one of the fastest passage durations (0.14 h) during the study (Table 6). The range of lengths of passing trout was the same as that of trout that were present (Table 2), and neither length ($t = -1.37$, df = 7.32, $P = 0.210$), discharge ($t = 0.79$, df = 11.35, $P = 0.448$), nor water temperature at the time of entrance ($t = 0$, df = 5.66, $P = 1$) differed between trout that did and did not pass.

Flathead Chub. Few Flathead Chub were attracted to the fishway, particularly in 2019 (Table 3). All attracted chub ($n = 11$) entered the fishway, six transited, and five passed. Chub were mostly present from late April through August 2020, but also each autumn during periods

of base flow. Passages occurred most often at night and within narrower ranges of water temperatures and discharges than did presences (Table 2).

The analysis of attraction and passage data of Flathead Chub was limited by small sample sizes. One chub released in 2019 was attracted just 2 days after release and another released in 2020 was attracted 4 days after release. Length did not differ between fish that were (median = 177 mm TL) and were not attracted (median = 154 mm TL) in 2020 ($t = -1.58$, df = 11.75, $P = 0.140$), although the sample size was small. One chub transited the fishway in less than 1 h and another passed in less than 13 h. The range of lengths of chub that were present was wider than that of chub that passed (Table 2). Neither length ($t = 0.10$, df = 5.97, $P = 0.925$) nor discharge at the time of entrance ($t = -0.30$, df = 7.55, $P = 0.774$) differed between entering chub that did and did not pass. Despite small sample sizes, passing chub entered at lower water temperatures (median = 15.0°C; range = 11.5–18.0°C) than fish that did not pass (median = 18.3°C; range = 15.1–22.5°C) ($t = 2.29$, df = 8, $P = 0.052$). Therefore, passages of chub, which spawn from July through August at water temperatures from 18 to 25°C in Montana (Gould 1985), may have been related to pre-spawn migrations to upstream habitats (Walters et al. 2014).

River Carpsucker. Only eight River Carpsuckers were attracted to the fishway (Table 3). All attracted fish entered, seven transited, and six passed. Carpsuckers were present and passed during both day and night, on both the ascending and descending limbs of the hydrograph, and within narrower ranges of discharges and water temperatures than many other species (Table 2), although sample sizes were small. The ranges of lengths of fish that were present and passed were the same (Table 2). Most passages of carpsuckers, which spawn at water temperatures from 19 to 23°C (Fuiman 1982), occurred at temperatures from about 18 to 20°C, suggesting that

passages were related to upstream spawning movements. All fish that transited and passed did so in less than 1 h (Table 6).

Rainbow Trout. Seven Rainbow Trout were attracted to the fishway, of which all seven entered, six transited, and five passed (Table 3). Rainbow Trout were present periodically from April through October and passed within narrower ranges of water temperatures and discharges than when they were present (Table 2). Presences and passages occurred during both day and night. One fish transited and passed in less than 30 min (Table 6), and the ranges of lengths of fish that were present and passed were the same (Table 2).

Mountain Sucker. One Mountain Sucker used the fishway in spring 2019. It entered the fishway in the morning and transited and passed less than 1 h later (Table 6).

Discussion

The nature-like fishway at Huntley Diversion Dam on the Yellowstone River markedly improved upstream passage of a diverse assemblage of fishes past the dam. We documented upstream passage of 645 PIT-tagged individuals of 14 species, whereas only a small number of fin-clipped Longnose Suckers, White Suckers, Shorthead Redhorses, Goldeyes, Brown Trout, and Flathead Chub were documented to have moved upstream past the dam (either directly over it or through the natural side channel) before the construction of the fishway (Helfrich et al. 1999). Our study provides another example of the ability of nature-like fishways to pass many species of fish, and even one species of turtle. Other nature-like fishways previously evaluated for their efficiency and effectiveness were of different designs, and their evaluations varied in scope. Our study provides one of the most comprehensive evaluations of a nature-like bypass

channel and, perhaps, the most comprehensive of such on a large river with an unregulated discharge regime influenced predominantly by snowmelt runoff. Our use of PIT telemetry over multiple years sheds light on the factors that affected attraction to and passage through the fishway and helped us identify structural deficiencies and bottleneck areas. Despite facilitating the passage of at least one individual of each of the 14 species, species-specific effectiveness, efficiency, and use of the Huntley fishway varied.

Most use of the fishway was suggestive of pre-spawning movements, and pulses of movements of some species often occurred shortly after increasing water temperatures surpassed known spawning thresholds, particularly among catostomids, Smallmouth Bass, and Channel Catfish. Water temperature can stimulate the movements of riverine fishes (Northcote 1984; Jonsson 1991) and influenced seasonal use of the nature-like fishway. Although use of the fishway by Burbot did not seem to be directly related to spawning, their presence also increased during short periods of rapidly increasing water temperature on the ascending limb of the hydrograph. In fact, the number of fish of many species present increased and decreased, respectively, with increases and decreases in water temperature in the spring. Fish tend to be more active at high rather than low water temperatures within their ranges of tolerance, at least up to a certain temperature (Jonsson 1991; Lucas and Baras 2001). Accordingly, few fish were present or passed at temperatures > 23°C. The close correspondence between spawning thresholds (or increases in water temperature in general) and pulses of fish movement, as well as periodic high rates of attraction of suckers in the experimental subset, suggests that the attraction of some individuals occurred promptly at the onset of suitable environmental conditions.

The movement of some individuals was suggestive of that to apparent home ranges, foraging habitats, and refugia. Autumn-spawning salmonids (Mountain Whitefish, Liebelt 1970; Brown Trout, Brown and Kamp 1942) often passed the fishway months before their spawning periods, presumably seeking cold-water refuge upstream (Pettit and Wallace 1975; Meyers et al. 1992; Lance 2019), whereas most Goldeyes passed at relatively high water temperatures after their spawning period (Hill 1965; Moon et al. 1998), which could be indicative of movement to foraging habitats. Ice apparently halted movement through the fishway from about December through February, the period during which Burbot on the Yellowstone River have their largest seasonal home ranges (Jaeger et al. 2016) and presumably spawn (McPhail and Paragamian 2000). Unexpectedly, most Burbot were present and passed from late April through early June each year. Additionally, six Burbot released up to 23 rkm upstream in early spring 2019 passed back upstream in spring 2020 before runoff, suggesting that some Burbot used the fishway to return to upstream home ranges after spawning downstream of the dam. Saugers in the Yellowstone River move downstream to spawn from March through May and back upstream to home ranges from April through July (Jaeger et al. 2005). However, most radio-tagged Saugers curtailed their movements in July and none traveled as far upstream as Huntley Diversion Dam (Jaeger et al. 2005). We found that Saugers only passed in July, indicating that some individuals had summer home ranges farther upstream and continued moving upstream later in the year than previously known. The extent of such seasonal migrations past Huntley Diversion Dam is largely unknown but could be further elucidated by the tracking of radio-tagged Burbot, Sauger, and other highly mobile fishes in the vicinity of the dam.

Nature-like fishways tend to have lower attraction efficiencies than some other fishway types (Bunt et al. 2012, 2016; Hershey 2021). Attraction efficiencies of newly tagged White Suckers (22.0–31.5%) and Smallmouth Bass (29.5–37.0%) in our general group were lower than those of the same species released downstream of two Denil fishways in Ontario, Canada (Bunt et al. 1999), and attraction efficiencies of newly tagged Shorthead Redhorses in the general group (13.2–16.6%) were much lower than those of redhorses released during the spawning season downstream of a vertical slot fishway in Quebec, Canada (Hatry et al. 2016). However, most fish from both of the aforementioned studies already had experience locating the fishway, making it difficult to determine the true cause of the differences in attraction efficiencies. Regardless, attraction efficiencies of some species to the Huntley fishway were even lower than those reported for the same species at other nature-like fishways. For example, attraction efficiencies of newly tagged White Suckers in our general group were lower than the attraction efficiency of suckers at a nature-like fishway bypassing a dam on a small river in Canada (65.6%; Steffensen et al. 2013). Moreover, species-specific attraction efficiencies of newly tagged fish in our general group with sample sizes ≥ 20 were rarely and only once, respectively, higher than the estimated mean attraction efficiencies of 36% (Hershey 2021) and 48% (Bunt et al. 2016) reported for nature-like fishways in recent meta-analyses, and our aggregate attraction efficiencies never surpassed the estimated mean from either meta-analysis. Factors that may have contributed to the apparently low attraction efficiencies of fish to the Huntley fishway include low motivation, our use of PIT telemetry, possible problematic placement of the fishway entrance, and low attraction flows.

Attraction to fishways is largely driven by the biological characteristics of fish (Bunt et al. 2012), of which motivation may have been the most important at the Huntley nature-like fishway. Migratory motivation can bias efficiency estimates if not accounted for because some individuals may be entirely unmotivated to move upstream or be attracted to a fishway in a given year (Cooke and Hinch 2013; Hershey 2021). Partial migration, in which just a portion of a population migrates (Lack 1943), is widespread among potamodromous fishes (Chapman et al. 2012), and skipped, or non-annual, spawning has been documented in at least 31 fish species (Rideout and Tomkiewicz 2011), including White Sucker (Quinn and Ross 1985), Burbot (McPhail and Paragamian 2000), and Smallmouth Bass (Franckowiak et al. 2017). However, the degree to which partial migration or skipped spawning occurs among fishes in the Yellowstone River is unknown, and we did not sample endocrine levels to determine the spawning phase of fish at their time of release (Thiem et al. 2013a) and were unable to determine the sex of most individuals.

Intra-specific differences in the probabilities of attraction among fish of different total lengths may in part reflect differences in sex-specific lengths and reproductive schedules. For example, male White Suckers matured at and reached shorter lengths than females and were also three times more prevalent during the spawning season in a tributary to a lake in Missouri (Wakefield and Beckman 2005), providing a possible explanation as to why shorter White Suckers had a higher probability of attraction than longer conspecifics at Huntley in 2020. However, female White Suckers in a spawning tributary in Massachusetts spawned more frequently as they aged (Quinn and Ross 1985), which could offset this trend. Therefore, the mechanism behind the intra-specific differences in probabilities of attraction among White

Suckers, and other species, of different lengths remains unclear. Conversely, intra-specific differences in time to attraction among Smallmouth Bass of different lengths were probably attributable to longer bass being more active and spawning earlier in the year (i.e., more motivated) than shorter conspecifics (Ridgway et al. 1991). Longer fish generally have greater swimming performance than shorter conspecifics (Jones et al. 1974; Bunt et al. 1999; Haro et al. 2004). Although longer bass were attracted more quickly and often than shorter bass in certain years, this trend was not consistently evident among the other species, suggesting that attraction was driven more by intra-specific differences in motivation than swimming ability.

Motivation to move upstream may have been limited if fish were able to spawn downstream of the dam (Thiem et al. 2013a), and we possess no empirical evidence that suitable spawning habitat is limited downstream of Huntley Diversion Dam (S. Blackburn, Montana Fish, Wildlife & Park, personal communication). Low motivation to migrate long distances and the availability of suitable spawning habitat downstream of the dam are possible explanations as to why aggregate attraction efficiencies of fish in the supplemental downstream group varied from only 2.5% to 5.3%. Conversely, most fish tagged upstream in 2019 were released just 0.5 rkm away from the dam, which could explain why their aggregate attraction efficiencies that year (6.0%) and the next (9.1%) were higher than those of fish in the supplemental downstream group. Attraction efficiencies of newly tagged fish of seven species in the general group (with sample sizes > 20) were lower, in at least one year of the study, than the mean attraction efficiency estimated by Hershey (2021) for entirely non-migratory fish (25.9%), which presumably have low motivation to move upstream. Therefore, low motivation was probably just one of a few factors contributing to low apparent attraction efficiencies.

Limitations imposed by our use of PIT telemetry may have contributed to low attraction efficiencies. True attraction efficiencies were probably higher than we estimated because we were unable to determine which fish lost their PIT tags, died, or entirely left the study area after being released (Franklin et al. 2012). The installation of an "approach" antenna just downstream of the fishway entrance would have reduced this uncertainty (Dodd et al. 2017) but was not possible because of the width and depth of the Yellowstone River. Additionally, we probably failed to detect some fish that were attracted but did not enter, particularly at high discharges, because of our inability to install the attraction antenna in a large semi-circle farther out into the river, shifts in the direction of the attraction flow as discharges increased, and the occasional reduced or complete loss of attraction antenna functionality. We were also unable to install an antenna at the attraction flow coming out of the secondary entrance.

The ability of fish to locate the attraction flow coming out of the fishway entrance is of the utmost importance in ensuring the overall effectiveness of the structure (Katopodis et al. 2001) but is often limited by insufficient attraction flow and improper placement of the entrance, particularly among nature-like fishways (Bunt et al. 2012; Williams et al. 2012). Fish are attracted to and aggregate in areas of high discharge and water velocities near dams and turbines as they migrate upstream (Bunt et al. 1999; Lundqvist et al. 2008) and therefore, the entrance of any fishway should be as close as possible to the barrier itself (Larinier 1998; Bunt 2001; Williams et al. 2012). Fish that move upstream past the fishway entrance and are attracted to the discharge coming over the dam may be hesitant to move back downstream (Bunt 2001), which may have occurred at Huntley Diversion Dam where the primary entrance of the nature-like fishway is located > 70 m downstream of the face of the dam. The placement of nature-like

fishway entrances distal to barriers is not uncommon (Jungwirth 1996; Schmutz et al. 1998; Calles and Greenberg 2007; Steffensen et al. 2013; Kim et al. 2016; Landsman et al. 2018) and is probably a result of the need to maintain a low gradient within the fishway (Larinier 1998). Such placement of a fishway entrance can be mitigated if the flow coming out of the fishway entrance (i.e., the attraction flow) sufficiently attracts fish to the fishway and away from the competing flow near the barrier (Larinier 1998). The attraction flow at fishways designed to pass anadromous salmonids in the United States is recommended to be 5–10% of the "mean daily average streamflow that is exceeded 5% of the time during periods when fish are normally present at the site" (NMFS 2011), and ≥ 5% of "annual daily flow" of streams and rivers in the United Kingdom (Armstrong et al. 2010), although the effectiveness of a fishway probably continues to increase as the percentage of the flow reaching the barrier that is used to attract fish increases (Armstrong et al. 2010; NMFS 2011). At most, 4.22% of the flow reaching Huntley Diversion Dam flowed out of the nature-like fishway entrance in 2019 (Tupen 2020). That peak occurred simultaneously with peak mean daily discharge (1,475 m^3/s; 52,100 ft^3/s) that year. The percentage averaged only 1.95% from April 18 to November 5, 2019, when mean daily discharges were lower. Despite the aforementioned factors that probably contributed to low apparent attraction efficiencies, almost 900 tagged fish were attracted to the Huntley fishway in two years over a wide range of discharges, suggesting that many thousands of untagged fish also located the fishway entrance each year as they attempted to move upstream past the dam.

The angle of the fishway entrance and the directionality of the resulting attraction flow probably did not affect attraction to the Huntley fishway. The entrance is situated perpendicular to the flow of the river and creates an area of stagnant, low velocity water immediately

downstream of the rock wall that forms the downstream side of the entrance. This area of stagnant water is mainly evident at low discharges when the quantity of attraction flow is also limited, suggesting that fish may have difficulty locating the entrance during periods of low discharge. However, fish tend to be attracted to high water velocities as they migrate upstream, suggesting that the stagnant water, which was located adjacent to the attraction flow, would be avoided and therefore probably did not delay motivated individuals. Furthermore, about 60% of all attracted fish were attracted at mean daily discharges ≤ 348 m^3/s (12,300 ft^3/s), at which the attraction flow was ≤ 2.16% of the flow reaching the dam (Tupen 2020). The area of stagnant water becomes less evident as discharge increases because the rock wall becomes submerged and the discharge coming out of the entrance flows downstream over it along the same riverbank as the fishway, allowing fish to move directly upstream into the structure, presumably benefiting the probability of attraction (Williams et al. 2012). However, nearly the entire fishway becomes submerged when snowmelt runoff is at or near its peak, resulting in a large eddy that "drowns" the entrance (Katopodis et al. 2001), a problem reported at other nature-like fishways (Dodd et al. 2017). The effect of the full submersion of the entrance on attraction to the Huntley fishway is unknown.

The riverbank on which the fishway was located did not affect attraction. Silver Redhorse *Moxostoma anisurum* released on the riverbank opposite a vertical-slot fishway in Canada had a higher probability of detection in the fishway (i.e., attraction) than those released on the same riverbank as the fishway, presumably because the attraction flow was directed more toward the opposite riverbank (Hatry et al. 2016). However, equivalent percentages (61% and 62%, respectively) of Longnose Suckers released on the same and opposite riverbanks as the Huntley

fishway were attracted during three days in April 2020 when mean daily discharges ranged from about 126 to 142 m^3/s (4,460–5,000 ft^3/s) and the attraction flow was only about 1.18% of the flow reaching the dam (at 137 m^3/s; Tupen 2020). Moreover, attraction efficiencies, probabilities of attraction, and times to attraction to the Huntley fishway did not differ among Longnose and White suckers released on opposite riverbanks, indicating that these fish moved about freely downstream of the dam and had similar success locating the entrance despite its perpendicular orientation to the river and low attraction flow. Therefore, a single fishway is probably adequate to attract these two benthic-oriented suckers in situations such as at Huntley.

Entrance was far less limiting than attraction. More than 96% of all attracted fish successfully entered, including about 92% of attracted fish in the supplemental upstream group and about 96% in the supplemental downstream group, some of which migrated long distances before reaching the dam. Most of the downstream half of the fishway was submerged during periods of high discharge, and we therefore probably failed to detect some attracted fish that did enter the fishway. As previously described, we also probably failed to detect some fish that were attracted but did not enter. We therefore probably underestimated and overestimated entrance efficiencies. Entrance efficiencies were consistently high and indicated that most fish—even those that migrated long distances—were able to enter the fishway after locating it. Notably, our ability to distinguish fish that merely located the attraction flow from those that actually entered the structure allowed us to determine that entrance was far less limiting than attraction. Few fishway evaluations explicitly distinguish between attraction and entrance (Hershey 2021), making it difficult to determine if unsuccessful fish were unable to enter or unable to pass (Bunt et al. 2012; Triano 2020).

Most entering fish successfully passed the Huntley fishway. All aggregate passage efficiencies (58.5–80.3%) were higher than the mean passage efficiency for nature-like fishways (55.7%) estimated by Hershey (2021) and half were higher than that (73.0%) estimated by Bunt et al. (2016). Many of our study species had passage efficiencies in at least one year that were similar to or higher than those of the same species at vertical slot (Thiem et al. 2013b; Hatry et al. 2016), Denil (Bunt et al. 1999), or other nature-like fishways (Calles and Greenberg 2007; Steffensen et al. 2013). In fact, most species in release groups and years with sample sizes of entering fish ≥ 20 had passage efficiencies higher than means reported for small (58.4%) and large (57.7%) potamodromous species. Moreover, newly tagged Longnose Suckers, White Suckers, and Shorthead Redhorses in the general group in 2020 had passage efficiencies higher than even large diadromous species (81.9%; Hershey 2021). However, passage efficiencies varied among species and years, and the percentage of all entering fish that passed (73.1%) was lower than that of all entering fish that were able to transit to *near* the upstream extent of the fishway (81.2%). The discrepancy between transit and passage efficiencies also varied among species and years; transit efficiency of newly tagged Burbot in the general group was about 44% higher than passage efficiency in 2019 but only about 17% higher than passage in 2020, with similar trends existing for Longnose Sucker, White Sucker, Smallmouth Bass, and others. Our ability to distinguish between and calculate efficiencies of fish that passed and those that merely transited to near the upstream extent of the fishway allowed us to identify a potential bottleneck area near the fishway exit. Although calculating and comparing efficiencies is useful in its own right, rigorous analyses are necessary to elucidate the biological, environmental, temporal, and

structural mechanisms that influence passage success and lead to the formation of bottlenecks (Castro-Santos et al. 2009; Roscoe and Hinch 2010).

Fishways should maintain functionality and provide hydraulic conditions conducive to passage over the full range of discharges—including at peak snowmelt runoff and base flow—at which fish are motivated to move upstream (Katopodis et al. 2001; Pander et al. 2013), a requirement particularly relevant at the Huntley fishway because of the temporal variability of movements of the diverse fish assemblage found in the area. Although hydraulic conditions in and adjacent to the Huntley fishway varied with discharge, two-dimensional hydraulic models confirmed that a corridor of low water velocities along the channel margins was present throughout most of the length of the fishway over a wide range of discharges (Tupen 2020). About 68% of transit durations (the time elapsed between the departure of a fish from A2 and its arrival at either A4 or A6) were < 1 h, and those of most species changed little with increasing discharge, indicating that most entering fish were able to travel to near the upstream extent of the fishway in a timely manner over a wide range of hydraulic conditions. However, not all transiting fish passed, and exit delays of passing fish increased rapidly at river discharges > 300–400 m^3/s.

Individuals that entered the fishway at high discharges tended to be less successful at passing than conspecifics that entered at low discharges, when exit delays were shorter. When the goal of a fishway is to make the dam "transparent" to migrating individuals (Castro-Santos et al. 2009), any amount of migratory delay at a barrier should be viewed as detrimental, as it can increase energy expenditures of individuals thereby leading to a reduction in subsequent survival (Castro-Santos and Letcher 2010) or passage failure (Castro-Santos et al. 2017). Extensive

delays can lead to total failure to reach spawning habitat (Caudill et al. 2007) or encourage migratory fish to abandon their efforts to move upstream and spawn in less desirable habitat downstream of a barrier (Bunt 2001). An area of turbulent water featuring a large standing wave and plunge pool was present near the Huntley fishway exit starting at discharges between about 300–400 m^3/s, and depth-averaged water velocities near the exit were much higher than in the rest of the fishway and increased dramatically with increasing discharge (Tupen 2020; Johnson et al. 2021). These problematic hydraulic conditions near the fishway exit, which lies in close proximity to the face of the dam, delayed successfully passing fish and probably prevented others from successfully passing upstream.

We may have overestimated the true number of passages that occurred during high discharges. Tupen (2020) predicted the daily passage of four species of fish at the Huntley fishway in 2019 by comparing swimming abilities drawn from the literature to depth-averaged water velocities near the fishway exit that were estimated from two-dimensional hydraulic models. Only three Saugers ever passed, precluding meaningful comparisons between predicted passage windows (Tupen 2020) and apparent passages from PIT telemetry. However, we deemed that Burbot, Smallmouth Bass, and Channel Catfish successfully passed on dates when they were predicted to be unsuccessful as judged by their swimming abilities. The discrepancy between predicted passage windows and apparent passages among the three species was greatest for Burbot, with nine apparent passages in 2019 during periods when they were predicted to be unsuccessful; seven such passages occurred in 2020. Four Smallmouth Bass in 2019 (and one in 2020) and one Channel Catfish in 2019 (and one in 2020) apparently passed during periods when they were predicted to be unsuccessful. Furthermore, apparent passages of fish of any of the 14

species occurred at mean daily discharges of up to 1,532 m^3/s (54,102 ft^3/s), whereas hydraulic models developed subsequently (Johnson et al. 2021) indicated that extreme depth-averaged water velocities (3.0–4.6 m/s; 10–15 ft/s) were present across much of the fishway exit at a discharge of 566 m^3/s (20,000 ft^3/s) and nearly all of it at discharges of 991 m^3/s (35,000 ft^3/s) and 1,416 m^3/s (50,000 ft^3/s). The fishway (excluding the turbulent area near the exit) is entirely inundated by the river at extreme high discharges, and therefore we probably failed to detect some fish that moved back downstream after being detected at the farthest upstream functioning PIT antenna. Fish that were deemed to have passed at high discharges may also have involuntarily fallen back (i.e., been swept) over the dam but failed to later locate the fishway attraction or entrance (Castro-Santos et al. 2017). Moreover, exit antennas were often destroyed during periods of extreme high discharge, limiting our ability to calculate exit delays when hydraulic conditions near the exit were the most problematic.

Two-dimensional hydraulic models, which estimate depth-averaged water velocities, supported our observations of a visually apparent area of turbulent, high velocity water near the fishway exit at high discharges, but could not account for differences in water velocities throughout the water column, meaning that some fish may have been able to proceed upstream of the exit even when depth-averaged velocities appeared excessive. Small fish can pass rocky channels by exploiting low water velocities in the boundary layer above the substrate (Bestgen et al. 2010), and Burbot can proceed upstream in experimental flumes by exploiting areas of low water velocities along the bottom and corners of the structure (Vokoun and Watrous 2009). Other fishes can successfully pass Denil fishways by swimming at burst speeds and then resting between baffles (Schwalme et al. 1985; Bunt et al. 1999), and individuals in nature-like fishways

should be able to choose the most energy-efficient route upstream among the varied turbulence patterns and water velocities created by cobbles and boulders (Bretón et al. 2013). Whether low water velocities exist in a boundary layer above the substrate near the fishway exit at high discharges is unknown, and fish that do successfully transition back into the river upstream of the exit at high discharges are particularly susceptible to fallback because of the close proximity of the exit to the face of the dam. Fishes such as Burbot may have momentarily proceeded upstream of the exit during high discharges by exploiting low water velocities near the boundary layer, only to then be swept downstream over the face of the dam. This could help explain why more Burbot fell back than any other species, and why the discrepancy between predicted passage windows and apparent passages among the three species examined was greatest for Burbot.

Despite some discrepancies between predicted passage windows and apparent passages, evidence exists that passage efficiencies and temporal metrics were mostly accurate and reflected both the challenging hydraulic conditions near the fishway exit at high discharges and interspecific differences in swimming ability. For example, lower aggregate passage efficiencies in 2019 than in 2020 were probably caused by the longer period of snowmelt runoff in 2019. Although the number of fish present in the fishway remained relatively high up to discharges of 600–700 m^3/s, the number of passages in that same range of discharges was relatively low, suggesting that PIT antennas located at the attraction flow, the entrances, and the midpoint of the length of the fishway detected unsuccessful fish as they moved downstream, even though antennas covered just a small fraction of the fishway at high discharges and in-situ detection efficiencies were not 100%. Burbot traveled through the fishway more slowly than other species with sample sizes > 20, and unlike other species, had ln transformed exit delays that increased

somewhat linearly with discharge, indicating that hydraulic conditions near the exit became increasingly difficult for them starting at low discharges. Burbot are generally regarded as weak swimmers (Jones et al. 1974; Vokoun and Watrous 2009); accordingly, passage efficiencies of newly tagged Burbot in the general group were lower each year than those of Longnose and White sucker, Shorthead Redhorse, and Smallmouth Bass. Discharge influenced hydraulic conditions disproportionately near the fishway exit and was a key mechanism driving passage success and delay.

Fish length and water temperature influenced passage less than discharge. Although longer individuals of some species were more successful than shorter conspecifics, fish of a wide range of total lengths transited and passed the fishway expeditiously, and neither transit duration nor exit delay changed with length among conspecifics of five species. Long (> 400 mm TL) individuals of five species (Longnose and White suckers, Burbot, Shorthead Redhorses, and Channel Catfish) passed at low discharges (< 142 m^3/s; 5,000 ft^3/s), indicating that the arrangement of the boulders within the fishway provided ample space for the movement of large fish. The influence of water temperature on passage was difficult to disentangle from that of discharge for many species and in many analyses. However, the water temperature at which passing fish entered generally reflected the period during which the species was motivated to move, rather than acting as a mechanism driving the passage or failure of fish.

Our assumption that all fish that entered the fishway were motivated to move upstream was probably false. Nature-like fishways, in addition to facilitating upstream movement past barriers, can provide habitat for local fish, including juveniles (Jungwirth 1996), those that inhabit nearby tributaries or side channels (Santos et al. 2005), and spawning adults (Landsman

et al. 2018). Some fish that entered but did not pass the Huntley fishway during periods of extreme high discharge, when most of the fishway was submerged and became a large eddy, may have merely been seeking refuge from high water velocities present in the main channel of the river (Reinhold et al. 2016; Dodd et al. 2017). Some tagged individuals were present intermittently for weeks or months before transiting and passing, and some species were present during all hours of the day but only passed during some. Furthermore, backpack electrofishing surveys that occurred inside the fishway mid-day on September 19, 2019 (a date on which no tagged fish were present), confirmed the presence of untagged Longnose and White suckers, Burbot, Smallmouth Bass, Brown Trout, Flathead Chub, and Rainbow Trout, as well as untagged Stonecat *Noturus flavus*, Longnose Dace *Rhinichthys cataractae*, and at least one species in the genus *Hybognathus*, indicating that the fishway itself was suitable habitat for many fishes. However, use of the structure as "compensatory" habitat (Pander et al. 2013) is probably of little consequence to local fish populations given the diversity (Bowen et al. 2003), lateral connectivity (Reinhold et al. 2016), and abundance of high-quality natural habitat in the system (White and Bramblett 1993).

Diel patterns of fishway use largely reflected the known biology of each species. The strongly diurnal Smallmouth Bass (Gerber and Haynes 1988) was present and passed almost exclusively during the day, whereas nocturnal Burbot (Harrison et al. 2013) and Channel Catfish (Bailey and Harrison 1948) were present throughout the day but mostly passed at night. Diel patterns of use were similar to those reported in previous fishway studies for Longnose and White suckers (Thiem et al. 2013b), Shorthead Redhorses (Thiem et al. 2013b; Hatry et al. 2016), and Brown Trout (Calles and Greenberg 2005). Most passages of catostomids during the

early spring in 2020 occurred at night, whereas most during June 2020, the month during which discharge peaked that year, occurred during the day. High turbidity during periods of high discharge probably allowed these fishes to move freely during the day by affording them protection from visual predators (Jacobsen et al. 2004), such as the Great Blue Heron *Ardea herodias* and Bald Eagle *Haliaeetus leucocephalus*, that were often seen hunting within or near the fishway. Regardless of some seasonal differences in diel patterns of use, the nature-like fishway allowed fish to pass at all hours of the day throughout much of the year and species-specific patterns of diel activity were generally consistent with those in the literature.

Neither handling stress nor PIT-tag implantation were assumed to negatively affect swimming ability or alter fish behavior. The weight of the 12-mm long PIT tag (0.1 g) never surpassed 2% of the total body weight of a fish, and the weight of the 32-mm long PIT tag (0.8 g) surpassed 2% of the total body weight of only two fish (two Flathead Chub; tag weight = 2.66% of total body weight; Winter 1996). We observed rapid healing of the PIT-tag implantation wound among recaptured fish, and newly tagged fish had entrance, transit, and passage efficiencies similar to those of previously tagged fish, suggesting that newly tagged fish that were attracted behaved similarly to previously tagged fish, whose tag implantation wounds had mostly or fully healed.

The use of radio telemetry would have further elucidated the movements of fish directly downstream of the dam and fishway, upstream of the dam after passing, and through the natural side channel on the north side of the island, and consequently would have provided more accurate estimates of fishway efficiencies, fallback, and migratory delay. For example, PIT telemetry only allowed us to calculate the amount of time between the release of a fish and its

attraction (i.e., time to attraction), without any knowledge of the location or degree of motivation of the fish in the interim, whereas a well-designed radio telemetry array would have allowed us to calculate the amount of time upstream-searching (i.e., motivated) fish spent directly downstream of the face of the dam before locating the fishway entrance. In addition, some PIT antennas were susceptible to damage or destruction, particularly during high discharges. However, radio telemetry would have resulted in smaller sample sizes, longer handling times, and perhaps greater mortality than PIT telemetry. The concurrent use of both PIT and radio telemetry in future studies would probably result in more accurate estimates of fishway efficiencies, fallback, and delay—particularly on large rivers with dynamic hydrographs—as long as each fish only receives one type of tag or the effect of double-tagging is negligible (Hatry et al. 2016).

The efficiency of the nature-like fishway at Huntley Diversion Dam varied among species, years, and the different stages of passage, and a number of biological, environmental, temporal, and structural mechanisms drove attraction to and passage through the fishway. However, individuals of 14 diverse species of fish passed over a wide range of environmental conditions over two years. Nature-like fishways such as the one at Huntley Diversion Dam can facilitate the prompt upstream passage of diverse fish assemblages on large, unregulated rivers, but the placement of the fishway in relation to the barrier must be thoughtfully considered to ensure that it remains effective over the full range of conditions at which fish are motivated to move upstream.

Management Implications

We documented the upstream passage of 645 PIT-tagged individuals of 14 diverse fish species through the Huntley fishway over two years, and thousands of untagged fish presumably used the fishway annually. However, we identified a few bottlenecks seemingly caused by structural deficiencies that could be addressed to increase the ability of the fishway to attract and pass fish over a wide range of environmental conditions.

Attraction

Repositioning the primary fishway entrance close to the face of Huntley Diversion Dam and orienting it parallel to the flow of the river would probably result in increased attraction. Fishway entrances should be placed as close as possible to the face of the barrier (Larinier 1998; Bunt 2001; Williams et al. 2012) because fish tend to seek areas of high discharges and water velocities, such as those found where water passes over a dam, as they move upstream (Bunt et al. 1999; Lundqvist et al. 2008). Fish may swim past the primary fishway entrance at Huntley and be hesitant to move back downstream to find an alternative route if they are cued into the distracting, competing flows passing over the barrier (Bunt 2001). Although the existing secondary entrance is located relatively close to the dam, it is only connected to the river at Yellowstone River discharges greater than about 255 m^3/s (9,000 ft^3/s). Despite fish being attracted to the existing primary entrance over a wide range of discharges, its orientation perpendicular to the flow of the river is probably not ideal, and orienting it parallel to the flow of the river would allow fish to move directly upstream into the entrance (Williams et al. 2012). Currently, the fishway becomes nearly entirely inundated at high discharges and functions as a large backwater; repositioning the entrance to near the barrier would probably still result in its

"drowning" at high flows (Katopodis et al. 2001). Ensuring that the fishway entrance remains attractive to fish as discharges increase would be necessary.

Increasing the percentage of the flow reaching the barrier that is diverted down the fishway would probably enhance attraction. Currently, diversion percentages (4.22% maximum, 1.95% mean; Tupen 2020) do not meet the recommended guidelines of ≥ 5% for attraction flows (Armstrong et al. 2010; NMFS 2011). Increasing the quantity of attraction flow would probably draw more fish away from the flows passing over the barrier.

The one fishway currently located on the north riverbank is apparently adequate for attracting Longnose and White suckers moving upstream on either riverbank given the similar success of fish released on opposite riverbanks downstream of the fishway in locating the entrance. However, we did not determine if individuals of other species that approached the fishway on opposite riverbanks were similarly successful. An additional fishway on the opposite (i.e., south) riverbank with an entrance near the dam and an exit farther upstream could potentially increase attraction and decrease migratory delay. However, fish successfully passing a fishway situated as such would transition back into the river near two headgates that control the flow of water into the irrigation canal, possibly leading to entrainment or disorientation. A fishway on the south riverbank would be laterally constrained by a nearby railroad track and other irrigation infrastructure. Therefore, several site constraints would need to be addressed to ensure the construction of an efficient and effective fishway on the south riverbank.

Passage

Hydraulic conditions throughout most of the length of the fishway are consistently appropriate for passage but conditions near the fishway exit vary greatly with discharge, delay

fish, and probably prevent their upstream movement at high discharges. Conditions throughout most of the fishway and near the exit were appropriate for the upstream movement of most species at low discharges, and most fish continued to transit to near the upstream extent of the fishway expeditiously as discharge increased. However, delays of fish at the exit began to increase at discharges > 300–400 m^3/s, and visual observations at the exit starting within the same range of discharges indicated the presence of an area of highly turbulent water featuring a standing wave and plunge pool that seem to form because of complex structural elements near the junction of the fishway exit and the face of the dam, which are in close proximity. At high discharges, water flows downstream over a concrete shelf that lies adjacent to the exit and plunges into the fishway itself (Figure 15). Water flowing in the river adjacent to (south of) the shelf enters the fishway and then flows directly over the rock wall that creates the downstream side of the fishway exit, thereby forming a large standing (and possibly vertically recirculating) wave. The rock wall at the downstream side of the fishway exit essentially acts as a continuation of the face of the dam at high discharges. The visually apparent complex, turbulent flow patterns near the exit have been confirmed by two-dimension hydraulic models (Tupen 2020; Johnson et al. 2021); water velocities are not only consistently higher near the exit than in the rest of the fishway, but also increase more severely as discharge increases. Fish attempting to pass the turbulent, high velocity water near the exit at high discharges may be swept downstream directly over the rock wall, whereas fish that manage to make it past this initial challenge may be swept downstream over the face of the dam itself. Passage may be compromised in either of these scenarios.

Repositioning the fishway exit farther upstream of the dam would reduce the complex interactions of turbulent, high velocity water near the concrete shelf, rock wall, and the face of the dam, and probably lead to increased passage success and decreased delay. However, the direction of the exit in relation to the flow of the river would need to be considered carefully. Fish would probably have greater success if they were able to move upstream out of the fishway and directly into the river, with flow entering the fishway nearly parallel to flow in the river. However, this configuration would probably elicit entrainment of large woody debris into the exit that would result in blockages and require increased maintenance. Shifting the exit farther upstream but positioning it perpendicular to the flow of the river would probably result in fewer blockages, but would potentially create an area of turbulence or an eddy at the intersection of the fishway exit and the river, making it difficult for fish to transition back into the river. Either way, the fishway exit would need to be positioned far enough upstream to avoid the high velocity areas near the face of the dam.

An alternative to entirely repositioning the fishway exit is to construct an additional channel that serves as a secondary exit during high discharges (Figure 16). A prefabricated technical fishway, such as a Denil, could be installed with its entrance just downstream of the present fishway exit and its exit in the river itself upstream of the present exit (Johnson et al. 2021), but the ability of this type of fishway to facilitate the passage of the diverse fish assemblage of the Yellowstone River is unknown. Conversely, the existing nature-like design has demonstrated its ability to pass 14 species, and therefore an additional nature-like channel would probably yield the best results. A secondary nature-like exit channel could span from a point in the upstream half of the present fishway to the river upstream of the present exit (Figure

16) and sit at an elevation higher than the existing channel, thereby providing fish with an alternative passage route during high discharges when turbulent, high velocity water is present near the existing fishway exit. This secondary exit channel could contain boulders and roughness elements similar to those in the existing channel.

All fishways feature unique hydraulic conditions that are directly influenced by the placement of the fishway, particularly in relation to the barrier, and structural elements adjacent to and within the fishway itself. Therefore, even minor modifications to the placement and structural elements of the existing Huntley fishway could result in drastically different hydraulic conditions. These hydraulic conditions should not be assumed to facilitate fish movement as well as or better than previous conditions, as even fishways with similar designs can vary greatly in their performance (Bunt et al. 2012, 2016; Hershey 2021). Consequently, modifications to existing fishways should be planned carefully by interdisciplinary teams of biologists and engineers, and fishways should be evaluated post-modification to ensure that they facilitate the passage of target species.

A fishway can be viewed as effective from a management perspective when it meets well-defined passage objectives, which can vary among target species (Larinier 1998). The objective for an anadromous species may be to pass the entire population upstream of a barrier in a timely manner so that individuals can reach suitable spawning habitat well within the reproductive period (Larinier 1998). Conversely, the objective for a potamodromous, facultative, or non-migratory species, such as those found in the Yellowstone River, may be to pass just a fraction of the population annually to preclude population fragmentation (Larinier 1998). The objective defined for each target species should take into account the location of the barrier and

fishway on the landscape (Larinier 1998). For example, fish can bypass both the dam and fishway at Huntley via the natural side channel when Yellowstone River discharges are greater than about 142–198 m^3/s (5,000–7,000 ft^3/s). Although these data were excluded from our analyses, we confirmed that fish released in the main channel both downstream and upstream of the dam moved into the side channel, fish released in the side channel moved back into the main channel, and at least one tagged individual of seven species (White Sucker, Shorthead Redhorse, Smallmouth Bass, Goldeye, Channel Catfish, River Carpsucker, and Mountain Sucker) was later present at the fishway after being released in the side channel, indicating that some fishes in the area moved about freely. In fact, six species were documented to have moved upstream past the dam (either over the dam itself or via the side channel) prior to the construction of the fishway (Helfrich et al. 1999). The aforementioned structural modifications and additions to the existing Huntley fishway should be viewed, first and foremost, as a means to achieve unmet passage objectives for target species in the area, with objectives being framed within the context of the surrounding landscape and while considering the current state of populations both upstream and downstream of the dam.

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APPENDIX A

TABLES AND FIGURES

Table 1. Sample sizes and lengths of 14 species of fish of eight families in three release groups used in the evaluation of the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, in 2019 and 2020.

		General group			Supplemental upstream group			Supplemental downstream group		
			Total length (mm)			Total length (mm)			Total length (mm)	
Family	Species	*n*	Mean ± SD	Range	*n*	Mean ± SD	Range	*n*	Mean ± SD	Range
Catostomidae	Longnose Sucker *Catostomus catostomus*	590	320 ± 60	163–480	37	345 ± 87	203–472			
	Mountain Sucker *Catostomus platyrhynchus*	6	170 ± 34	140–221	2	177 ± 2	175–178			
	River Carpsucker *Carpiodes carpio*	43	402 ± 42	277–473	18	387 ± 56	312–513			
	Shorthead Redhorse *Moxostoma macrolepidotum*	391	381 ± 47	193–513	48	373 ± 72	216–495	3	410 ± 49	376–466
	White Sucker *Catostomus commersonii*	501	370 ± 43	189–485	45	365 ± 54	249–450	11	388 ± 50	297–450
Centrarchidae	Smallmouth Bass *Micropterus dolomieu*	204	299 ± 54	150–422	43	318 ± 56	160–427	6	315 ± 48	244–384
Cyprinidae	Flathead Chub *Platygobio gracilis*	33	172 ± 19	131–203	9	163 ± 13	147–185	1	231	
Gadidae	Burbot *Lota lota*	274	447 ±122	153–820	197	506 ±105	191–878	178	476 ±124	199–771
Hiodontidae	Goldeye *Hiodon alosoides*	171	344 ± 26	250–406	72	350 ± 27	302–419	1	411	
Ictaluridae	Channel Catfish *Ictalurus punctatus*	197	543 ± 74	386–768	26	568 ± 82	391–738	9	629 ± 74	513–721
Percidae	Sauger *Sander canadensis*	22	470 ± 61	304–584	1	635		204	463 ± 67	345–640
Salmonidae	Brown Trout *Salmo trutta*	48	359 ± 60	268–503	3	376 ±150	234–533	9	399 ± 53	335–475
	Mountain Whitefish *Prosopium williamsoni*	125	305 ± 74	163–450	1	361				
	Rainbow Trout *Oncorhynchus mykiss*	12	314 ± 55	232–380						
Total		2,617			502			422		

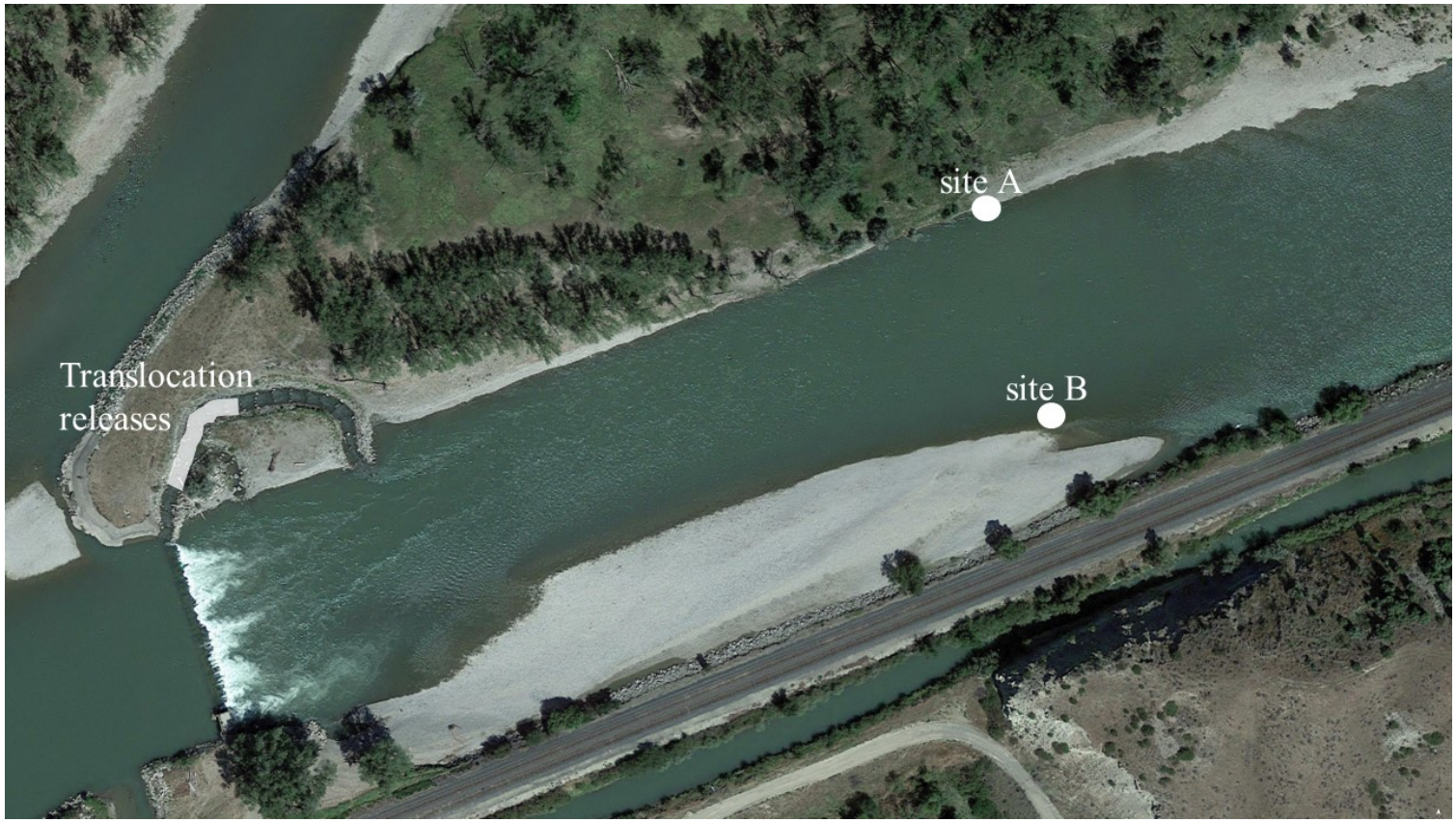

Figure 1. Release sites of PIT-tagged fish in the general group (see Methods for definition) and translocated Saugers used in the evaluation of the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, in 2019 and 2020.

Figure 2. Locations of stationary PIT antennas used to monitor the movement of tagged fish during the evaluation of the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, from April 23, 2019, through December 31, 2020.

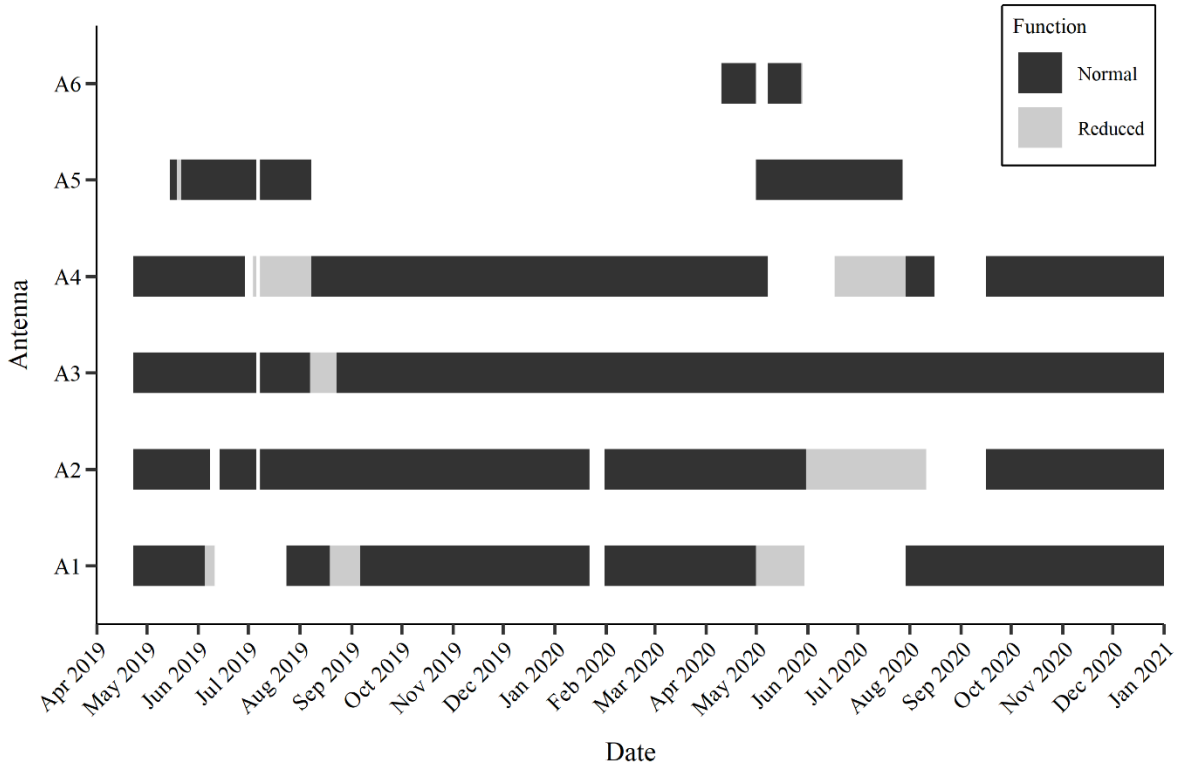

Figure 3. Functionality of PIT antennas used during the evaluation of the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, from April 23, 2019, through December 31, 2020. Black segments indicate normal antenna function, gray segments indicate reduced function, and white segments indicate no antenna function.

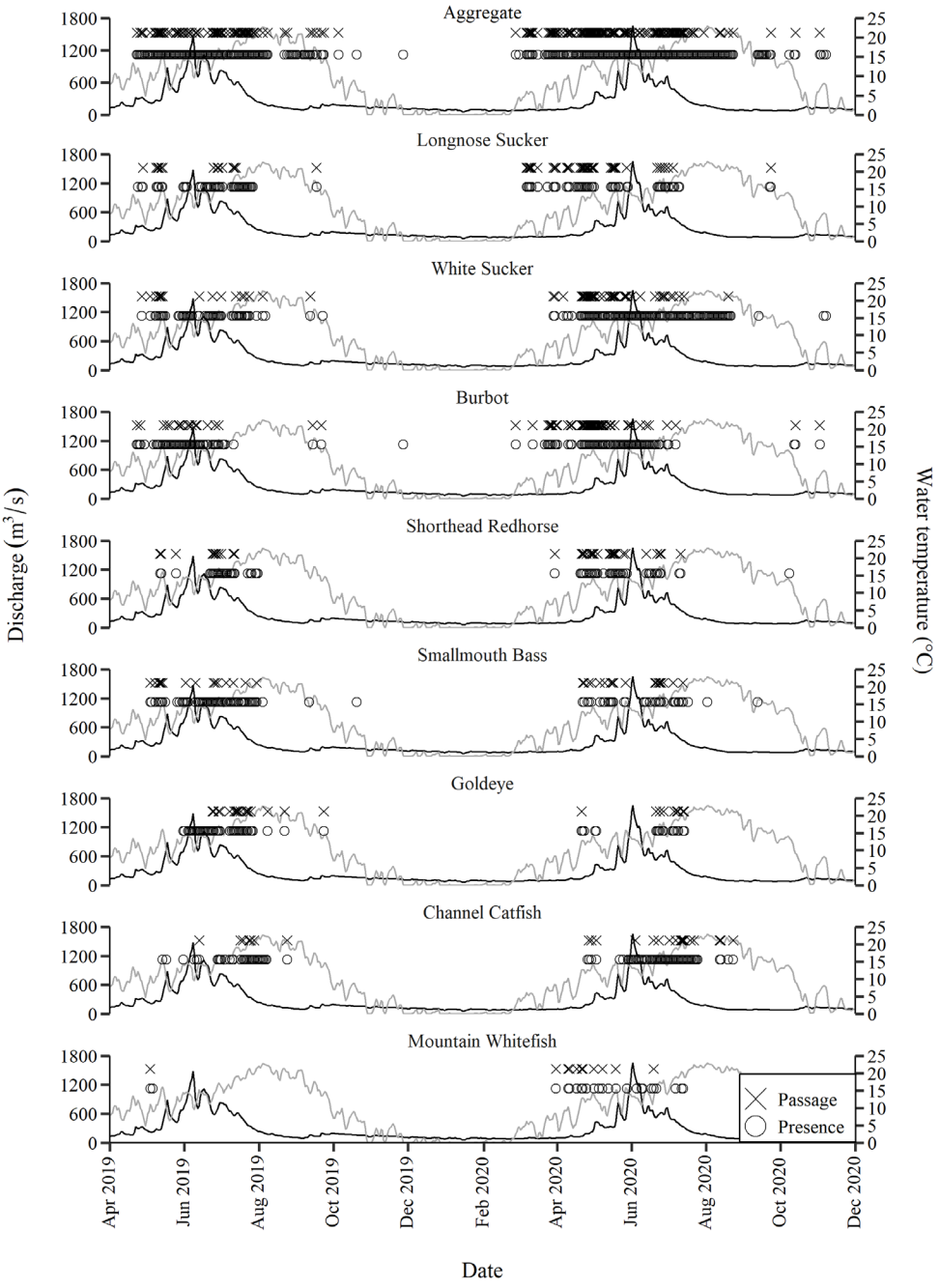

Figure 4. Dates on which one or more individuals of any of the 14 species (in aggregate) and the eight most prevalent species were present (○) and passed (×) the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, during the fishway evaluation in 2019 and 2020, as well as mean daily discharges (—) and water temperatures (—) of the Yellowstone River at USGS gage 06214500 near Billings, Montana, over the duration of the evaluation. The month of December 2020 is not included; no fish were present or passed during that month.

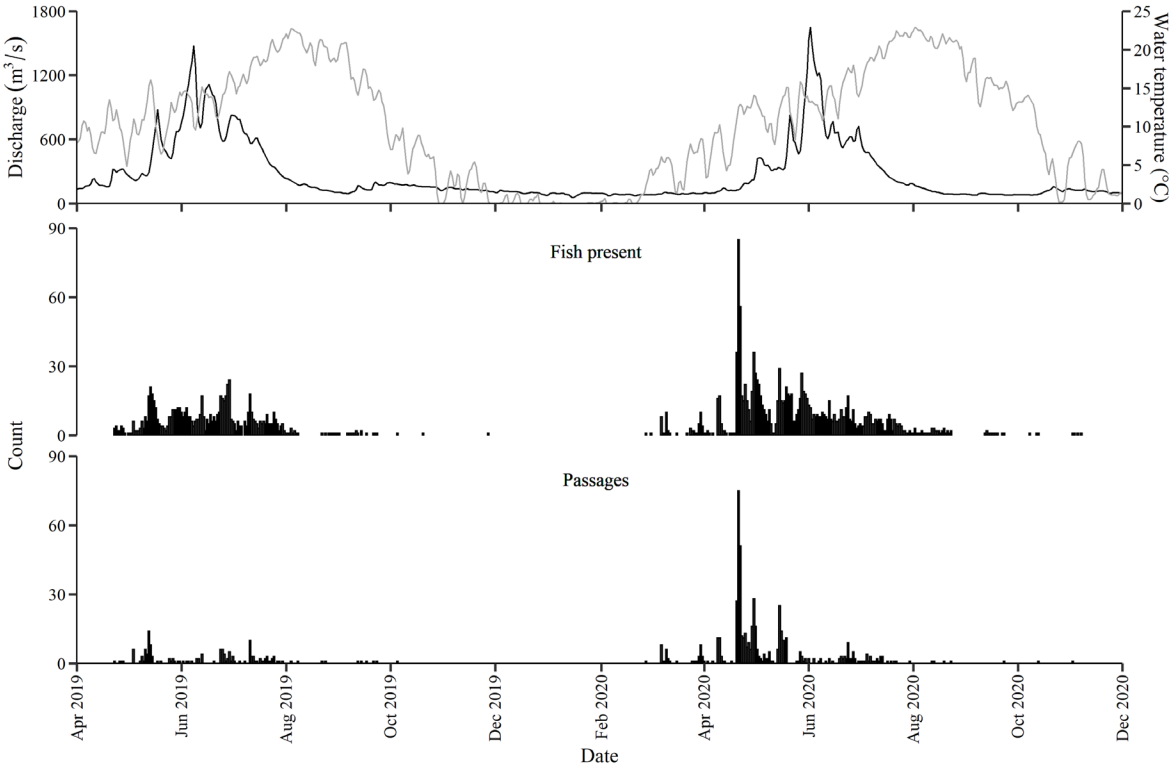

Figure 5. Daily counts of the aggregate number of fish of all 14 study species present, aggregate passages, and mean daily discharges (▬) and water temperatures (▬) of the Yellowstone River at USGS gage 06214500 near Billings, Montana, during the evaluation of the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, in 2019 and 2020. The month of December 2020 is not included; no fish were present or passed during that month.

Table 2. Aggregate and species-specific ranges of total lengths at tagging as well as mean daily water temperatures and discharges of the Yellowstone River at USGS gage 06214500 near Billings, Montana, within which species were present (i.e., detected at antennas) or passed the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, during the fishway evaluation in 2019 and 2020.

Species	Event type	Total length (mm)	Water temperature (°C)	Discharge (m^3/s)
		Aggregate		
14 species	Presence	135 – 726	0.3 – 23.3	81 – 1,651
	Passage	157 – 726	1.4 – 23.1	81 – 1,532
		Species-specific		
Longnose Sucker	Presence	163 – 480	1.4 – 21.7	82 – 1,065
	Passage	163 – 480	1.4 – 19.3	82 – 821
White Sucker	Presence	228 – 448	5.5 – 23.3	89 – 1,651
	Passage	228 – 447	7.9 – 23.1	89 – 1,532
Burbot	Presence	153 – 681	0.3 – 19.3	81 – 1,651
	Passage	193 – 681	2.5 – 19.3	81 – 1,532
Shorthead Redhorse	Presence	257 – 508	8.6 – 21.9	82 – 827
	Passage	257 – 436	8.6 – 19.9	93 – 824
Smallmouth Bass	Presence	160 – 422	7.4 – 23.3	94 – 1,113
	Passage	210 – 422	9.8 – 21.7	142 – 923
Goldeye	Presence	250 – 419	9.7 – 22.5	126 – 1,475
	Passage	287 – 419	12.8 – 22.5	126 – 824
Channel Catfish	Presence	438 – 726	9.7 – 23.1	89 – 1,651
	Passage	438 – 726	12.7 – 22.8	90 – 1,339
Mountain Whitefish	Presence	168 – 423	6.3 – 20.8	96 – 1,254
	Passage	178 – 399	6.3 – 15.3	96 – 595
Sauger	Presence	392 – 584	12.5 – 23.3	170 – 479
	Passage	504 – 545	19.3 – 21.9	185 – 453
Brown Trout	Presence	268 – 481	3.6 – 17.9	84 – 1,651
	Passage	268 – 481	3.6 – 17.9	93 – 1,339
Flathead Chub	Presence	135 – 198	10.6 – 22.6	85 – 1,048
	Passage	157 – 189	12.5 – 20.9	220 – 1,048
River Carpsucker	Presence	340 – 495	14.3 – 20.0	226 – 603
	Passage	340 – 495	14.3 – 20.0	226 – 603
Rainbow Trout	Presence	269 – 380	3.4 – 20.9	96 – 770
	Passage	269 – 380	8.9 – 20.9	183 – 603
Mountain Sucker	Presence	157	16.3	388
	Passage	157	16.3	388

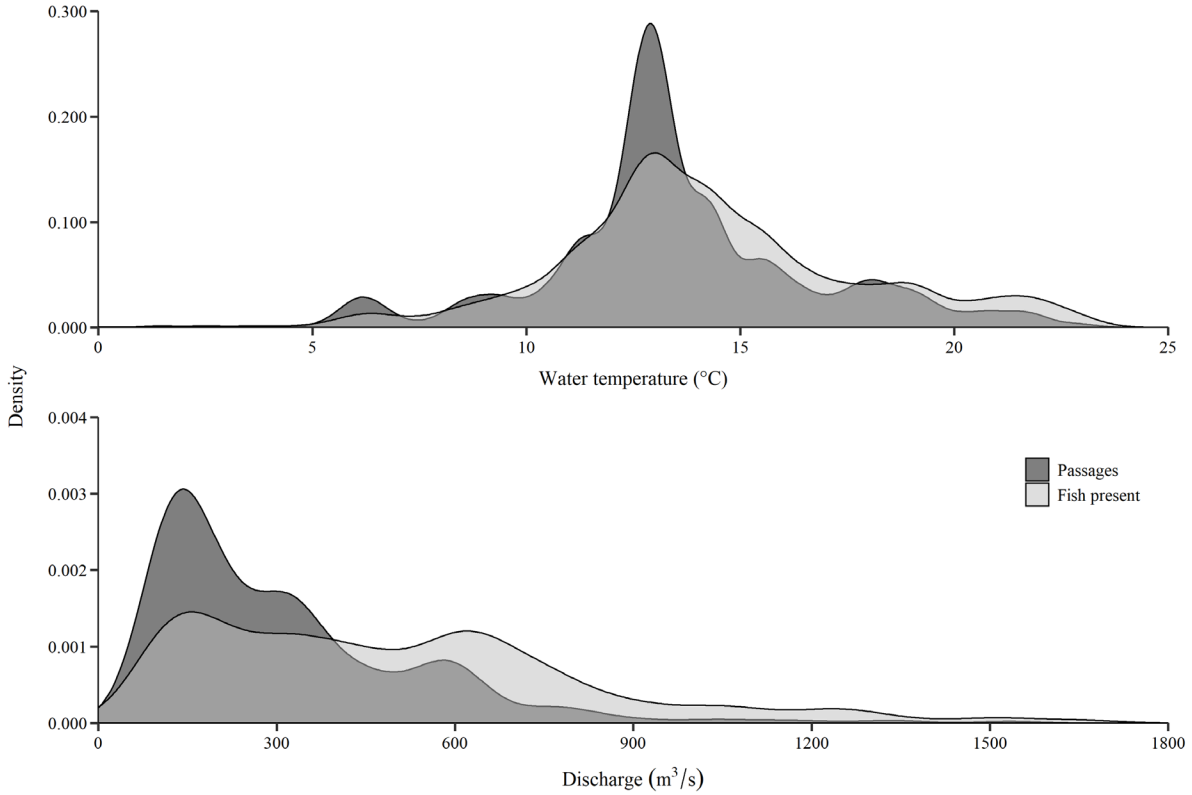

Figure 6. Density plots of the aggregate number of fish of all 14 study species that were present and passed the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, over the range of water temperatures and discharges of the Yellowstone River recorded at USGS gage 06214500 near Billings, Montana, during the fishway evaluation in 2019 and 2020.

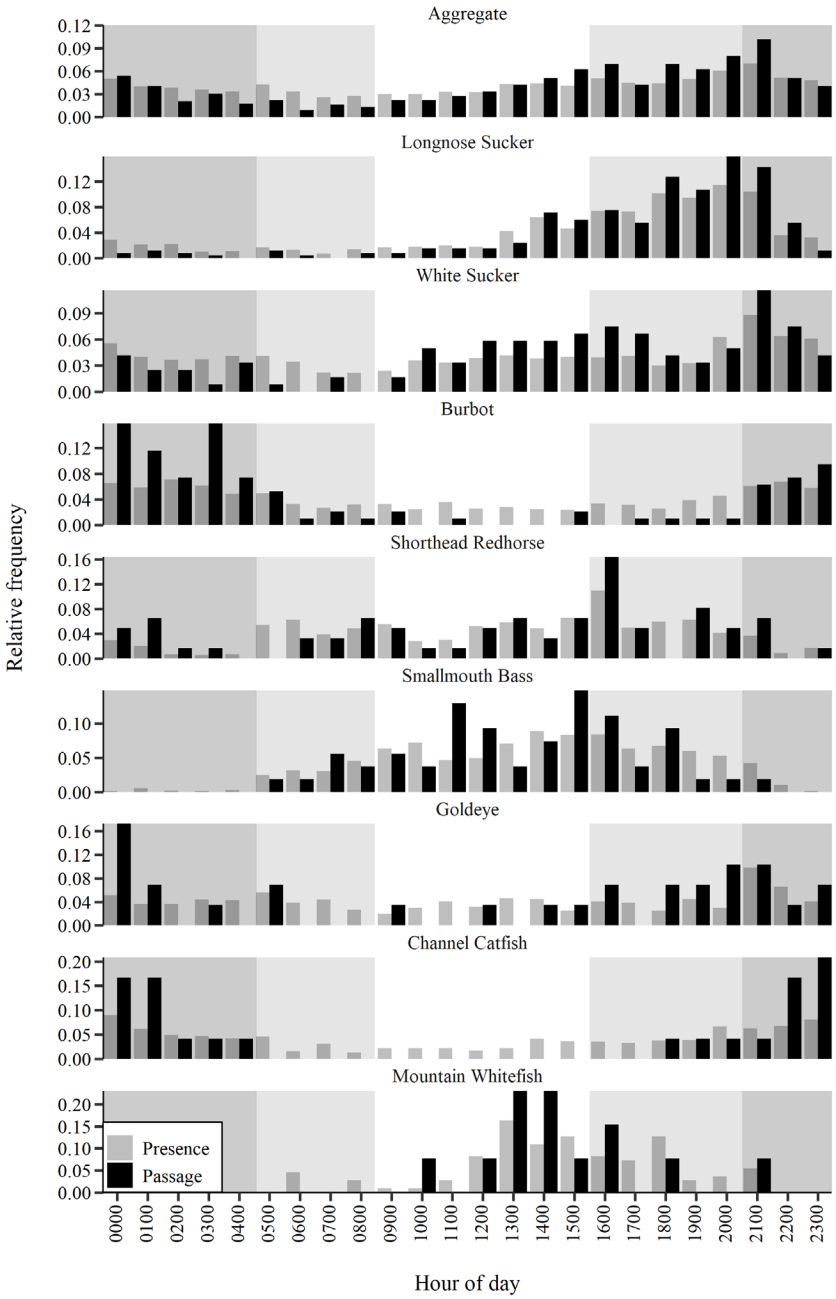

Figure 7. Relative hourly frequencies of presences and passages of all 14 species (in aggregate) and the eight most prevalent species at the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, during the fishway evaluation in 2019 and 2020. The white background indicates the period that was always daytime (i.e., between sunrise and sunset), the light gray backgrounds indicate periods that were either day or night depending on the season, and the dark gray backgrounds indicate periods that were always night. Note differences in *y*-axis scales.

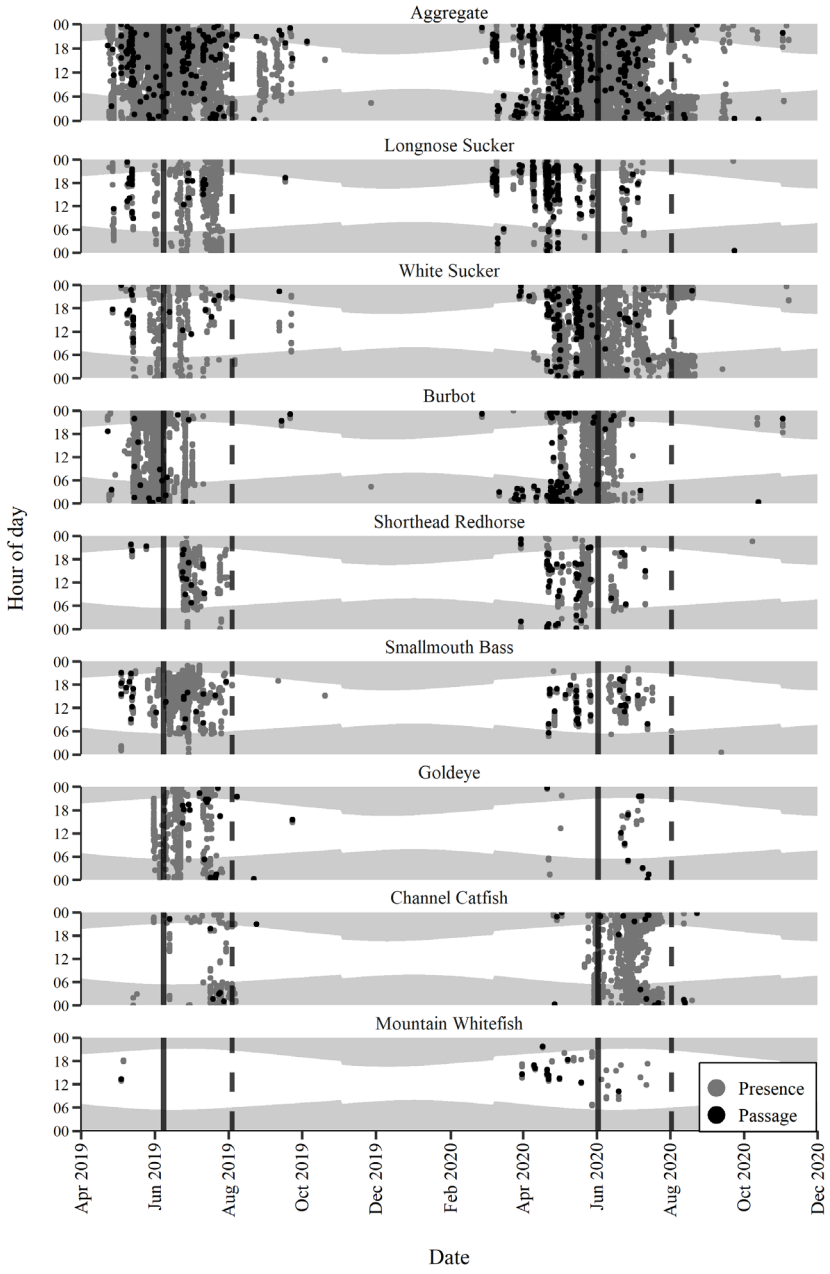

Figure 8. Hour of day of each presence (i.e., detection at any antenna) and passage of fish of all 14 species (in aggregate) and the eight most prevalent species at the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, during the fishway evaluation from April 2019 to December 2020. The white background indicates the period that was daytime (i.e., between sunrise and sunset), whereas the gray background indicates the period that was night. The dates of peak annual discharge and water temperature of the Yellowstone River recorded at USGS gage 06214500 near Billings, Montana, in 2019 and 2020 are indicated by solid and dashed vertical lines, respectively. The month of December 2020 is not included; no fish were present or passed during that month.

Table 3. Fishway efficiencies (%) calculated using aggregated data from all 14 study species and data from each species separately in each of the three release groups. Numbers of fish used to calculate each attraction (E_{ATT}), entrance (E_{ENT}), transit (E_{TRN}), and passage (E_{PAS}) efficiency are in parentheses.

			General group					Supplemental upstream group					Supplemental downstream group				
Species	Year	Tag status	*n*	E_{ATT}	E_{ENT}	E_{TRN}	E_{PAS}	*n*	E_{ATT}	E_{ENT}	E_{TRN}	E_{PAS}	*n*	E_{ATT}	E_{ENT}	E_{TRN}	E_{PAS}
Aggregate																	
14 species	2019	New	1,048	22.1 (232)	96.6 (224)	80.8 (181)	58.5 (131)	336	6.0 (20)	80.0 (16)	68.8 (11)	68.8 (11)	127	3.9 (5)	100.0 (5)	100.0 (5)	80.0 (4)
	2020	Previous	1,046	11.4 (119)	98.3 (117)	80.3 (94)	80.3 (94)	320	9.1 (29)	100.0 (29)	79.3 (23)	75.9 (22)	120	2.5 (3)	100.0 (3)	66.7 (2)	66.7 (2)
		New (all sites)	1,555	32.5 (506)	97.0 (491)	82.7 (406)	78.4 (385)	168	0.0 (0)				300	5.3 (16)	93.8 (15)	60.0 (9)	60.0 (9)
Species-specific																	
Longnose Sucker	2019	New	182	23.1 (42)	97.6 (41)	78.0 (32)	68.3 (28)	37	2.7 (1)	100.0 (1)	100.0 (1)	100.0 (1)					
	2020	Previous	182	23.6 (43)	100.0 (43)	95.3 (41)	93.0 (40)	36	19.4 (7)	100.0 (7)	85.7 (6)	85.7 (6)					
		New (site A)	191	41.4 (79)	96.2 (76)	92.1 (70)	90.8 (69)										
		New (site B)	216	47.2 (102)	100.0 (102)	95.1 (97)	95.1 (97)										
White Sucker	2019	New	141	22.0 (31)	100.0 (31)	80.6 (25)	54.8 (17)	45	4.4 (2)	100.0 (2)	100.0 (2)	100.0 (2)	11	0.0 (0)			
	2020	Previous	138	9.4 (13)	100.0 (13)	69.2 (9)	69.2 (9)	45	4.4 (2)	100.0 (2)	50.0 (1)	50.0 (1)	10	0.0 (0)			
		New (site A)	175	28.0 (49)	95.9 (47)	83.0 (39)	83.0 (39)										
		New (site B)	178	31.5 (56)	96.4 (54)	81.5 (44)	79.6 (43)										
Burbot	2019	New	120	41.7 (50)	90.0 (45)	82.2 (37)	37.8 (17)	36	2.8 (1)	0.0 (0)			23	8.7 (2)	100.0 (2)	100.0(2)	100.0 (2)
	2020	Previous	120	10.0 (12)	91.7 (11)	90.9 (10)	81.8 (9)	32	21.9 (7)	100.0 (7)	100.0 (7)	85.7 (6)	23	4.3 (1)	100.0 (1)	100.0(1)	100.0 (1)
		New	153	56.2 (86)	96.5 (83)	77.1 (64)	60.2 (50)	163	0.0 (0)				155	8.4(13)	92.3(12)	58.3(7)	58.3 (7)
Shorthead Redhorse	2019	New	182	13.2 (24)	95.8 (23)	73.9 (17)	65.2 (15)	48	8.3 (4)	75.0 (3)	33.3 (1)	33.3 (1)	1	0.0 (0)			
	2020	Previous	185	8.6 (16)	100.0 (16)	75.0 (12)	81.3 (13)	45	8.9 (4)	100.0 (4)	75.0 (3)	75.0 (3)	1	100.0 (1)	100.0 (1)	0.0(0)	0.0 (0)
		New	205	16.6 (34)	97.1 (33)	90.9 (30)	87.9 (29)						2	0.0 (0)			
Smallmouth Bass	2019	New	122	29.5 (36)	97.2 (35)	97.1 (34)	68.6 (24)	43	4.7 (2)	50.0 (1)	0.0 (0)	0.0 (0)	4	25.0 (1)	100.0 (1)	100.0(1)	0.0 (0)
	2020	Previous	121	7.4 (9)	100.0 (9)	88.9 (8)	77.8 (7)	39	5.1 (2)	100.0 (2)	50.0 (1)	50.0 (1)	4	0.0 (0)			
		New	81	37.0 (30)	93.3 (28)	82.1 (23)	78.6 (22)						2	0.0 (0)			
Goldeye	2019	New	118	17.8 (21)	100.0 (21)	76.2 (16)	61.9 (13)	72	11.1 (8)	87.5 (7)	71.4 (5)	71.4 (5)	1	0.0 (0)			
	2020	Previous	122	8.2 (10)	100.0 (10)	60.0 (6)	60.0 (6)	69	7.2 (5)	100.0 (5)	60.0 (3)	60.0 (3)	1	0.0 (0)			
		New	49	10.2 (5)	100.0 (5)	40.0 (2)	20.0 (1)										
Channel Catfish	2019	New	95	11.6 (11)	100.0 (11)	63.6 (7)	54.5 (6)	21	0.0 (0)				3	0.0 (0)			
	2020	Previous	93	10.8 (10)	90.0 (9)	55.6 (5)	66.7 (6)	20	5.0 (1)	100.0 (1)	100.0 (1)	100.0 (1)	3	0.0 (0)			
		New	103	14.6 (15)	100.0 (15)	60.0 (9)	53.3 (8)	5	0.0 (0)				6	0.0 (0)			
Mountain Whitefish	2019	New	20	10.0 (2)	100.0 (2)	50.0 (1)	50.0 (1)	1	0.0 (0)								
	2020	Previous	19	5.3 (1)	100.0 (1)	0.0 (0)	0.0 (0)	1	0.0 (0)								
		New	106	20.8 (22)	100.0 (22)	54.5 (12)	54.5 (12)										
Sauger	2019	New	11	9.1 (1)	100.0 (1)	0.0 (0)	0.0 (0)	1	0.0 (0)				75	0.0 (0)			
	2020	Previous	11	0.0 (0)				1	0.0 (0)				70	0.0 (0)			
		New	11	27.3 (3)	66.7 (2)	50.0 (1)	50.0 (1)						134	2.2 (3)	100.0 (3)	66.7(2)	66.7 (2)
Brown Trout	2019	New	12	50.0 (6)	100.0 (6)	100.0 (6)	83.3 (5)	3	0.0 (0)				8	25.0 (2)	100.0 (2)	100.0(2)	100.0 (2)
	2020	Previous	12	8.3 (1)	100.0 (1)	0.0 (0)	100.0 (1)	3	0.0 (0)				7	14.3 (1)	100.0 (1)	100.0(1)	100.0 (1)
		New	36	36.1 (13)	92.3 (12)	58.3 (7)	66.7 (8)						1	0.0 (0)			
Flathead Chub	2019	New	18	11.1 (2)	100.0 (2)	50.0 (1)	0.0 (0)	9	0.0 (0)				1	0.0 (0)			
	2020	Previous	18	16.7 (3)	100.0 (3)	66.7 (2)	66.7 (2)	9	0.0 (0)				1	0.0 (0)			
		New	15	40.0 (6)	100.0 (6)	50.0 (3)	50.0 (3)										
River Carpsucker	2019	New	16	6.3 (1)	100.0 (1)	100.0 (1)	100.0 (1)	18	11.1 (2)	100.0 (2)	100.0 (2)	100.0 (2)					
	2020	Previous	15	0.0 (0)				18	5.6 (1)	100.0 (1)	100.0 (1)	100.0 (1)					
		New	28	14.3 (4)	100.0 (4)	75.0 (3)	50.0 (2)										

Table 3 - continued. Fishway efficiencies (%) calculated using aggregated data from all 14 study species and data from each species separately in each of the three release groups. Numbers of fish used to calculate each attraction (E_{ATT}), entrance (E_{ENT}), transit (E_{TRN}), and passage (E_{PAS}) efficiency are in parentheses.

			General group								Supplemental upstream group					Supplemental downstream group				
Species	Year	Tag status	*n*	E_{ATT}		E_{ENT}		E_{TRN}		E_{PAS}		*n*	E_{ATT}	E_{ENT}	E_{TRN}	E_{PAS}	*n*	E_{ATT}	E_{ENT}	E_{TRN}	E_{PAS}
Rainbow Trout	2019	New	6	66.7	(4)	100.0	(4)	75.0	(3)	75.0	(3)										
	2020	Previous	5	20.0	(1)	100.0	(1)	100.0	(1)	100.0	(1)										
		New	7	28.6	(2)	100.0	(2)	100.0	(2)	50.0	(1)										
Mountain Sucker	2019	New	5	20.0	(1)	100.0	(1)	100.0	(1)	100.0	(1)	2	0.0	(0)							
	2020	Previous	5	0.0	(0)							2	0.0	(0)							
		New	1	0.0	(0)																

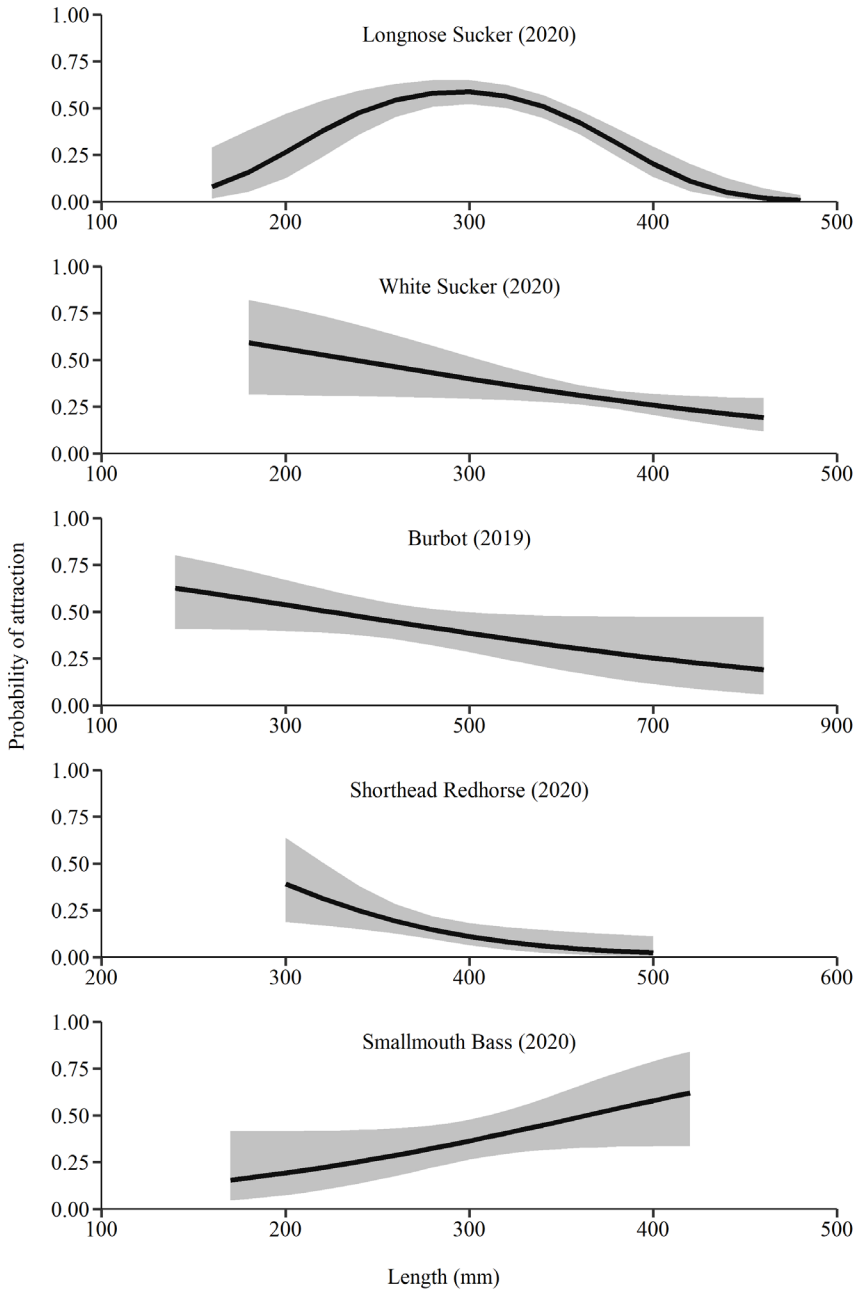

Figure 9. Predicted probability of attraction of five species of fish to the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, in 2019 and 2020 based on total length, while controlling for other variables such as water temperature and discharge recorded at the nearest USGS gage at the time of fish release, riverbank of fish release, and release batch (see Table 4 for the exact variables included in each species-specific multiple logistic regression model). Gray shaded areas are 95% confidence intervals. Note differences in *x*-axis scales.

Table 4. Parameter estimates from multiple logistic regression models of attraction to the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, for five species in 2019 and 2020. Abbreviations of explanatory variables are TL (fish total length, mm), TAR (water temperature recorded at the USGS gage at the time of fish release, °C), DAR (discharge recorded at the USGS gage at the time of fish release, m^3/s), and ROR:siteB (riverbank of fish release: site B). All models also contained a random effect for the release batch of fish. The estimated model coefficient (β), standard error (SE), and *P*-value are reported for each model parameter. The polynomial order of each parameter is reported as a superscript when applicable. Only newly tagged fish in the general group that were released before July 31 each year were included in attraction analyses.

Species	Year	*n*	Parameter	β	SE	*P*
Longnose Sucker	2019	179	TL	−0.0029	0.0029	0.3310
			TAR	0.0138	0.0816	0.8660
			DAR	−0.0001	0.0006	0.8480
	2020	407	TL^1	−11.0451	2.6883	< 0.0001
			TL^2	−14.2337	2.9008	< 0.0001
			ROR:siteB	0.0060	0.2262	0.9790
			TAR	−0.0491	0.0881	0.5776
			DAR	−0.0093	0.0060	0.1239
White Sucker	2019	128	TL	−0.0008	0.0041	0.8410
			TAR	0.0610	0.0631	0.3340
			DAR	−0.0011	0.0007	0.1270
	2020	353	TL	−0.0065	0.0030	0.0310
			ROR:siteB	0.2094	0.2435	0.3898
			TAR	0.1137	0.0666	0.0876
			DAR	−0.0041	0.0052	0.4277
Burbot	2019	113	TL	−0.0031	0.0017	0.0633
			TAR	−0.2219	0.0859	0.0098
	2020	153	TL	0.0005	0.0016	0.7530
			TAR	−0.0237	0.0635	0.7090
			DAR	−0.0007	0.0030	0.8260
Shorthead Redhorse	2020	205	TL	−0.0165	0.0064	0.0098
			TAR	−0.2244	0.1008	0.0260
			DAR	−0.0008	0.0139	0.9544
Smallmouth Bass	2019	114	TL	0.0040	0.0041	0.3280
			TAR	−0.0255	0.0814	0.7540
			DAR	0.0010	0.0010	0.3160
	2020	81	TL	0.0087	0.0048	0.0677
			TAR	0.0169	0.0940	0.8568
			DAR	0.0035	0.0026	0.1778

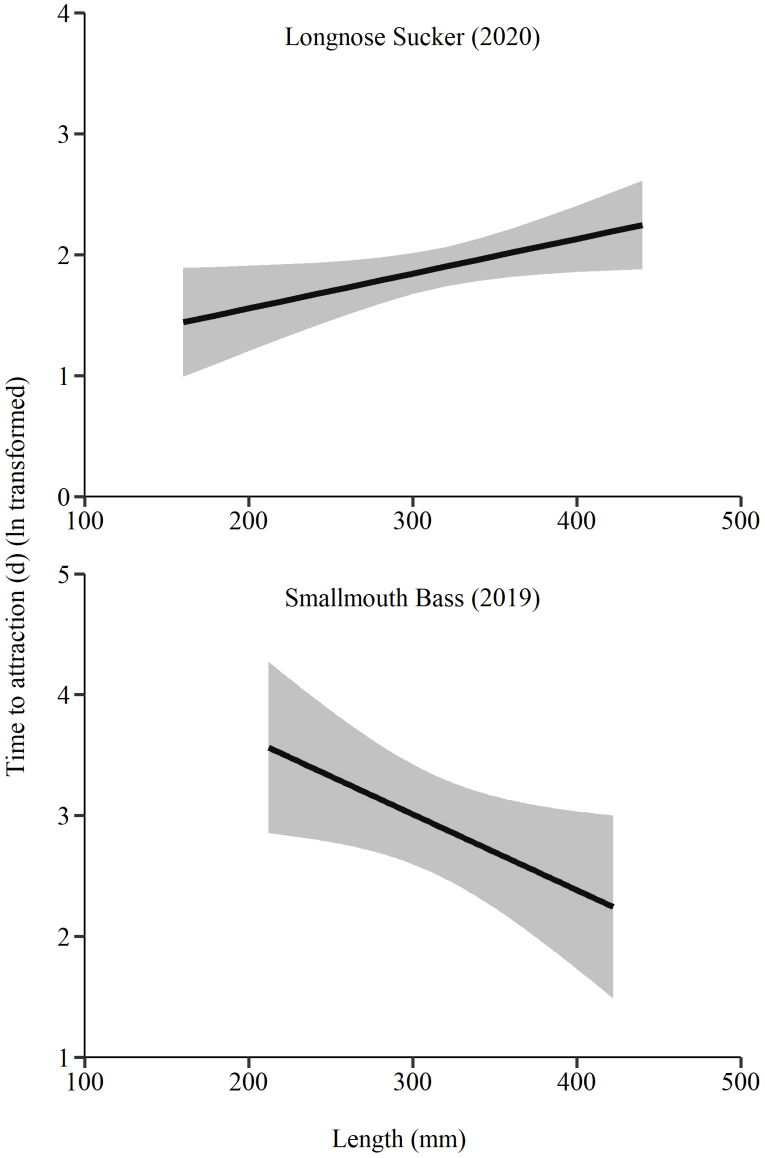

Figure 10. Predicted time to attraction (ln transformed) of Longnose Sucker in 2020 and Smallmouth Bass in 2019 to the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, based on total length, while controlling for other variables such as water temperature and discharge recorded at the nearest USGS gage at the time of fish release, riverbank of fish release, and release batch (see Table 5 for the exact variables included in each species-specific multiple linear regression model). Gray shaded areas are 95% confidence intervals. Note differences in *y*-axis scales.

Table 5. Parameter estimates from multiple linear regression models of time to attraction (ln transformed) to the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, for five species in 2019 and 2020. Abbreviations of explanatory variables are TL (fish total length, mm), TAR (water temperature recorded at the USGS gage at the time of fish release, °C), DAR (discharge recorded at the USGS gage at the time of fish release, m^3/s), and ROR:siteB (riverbank of fish release: site B). All models also contained a random effect for the release batch of fish. The estimated model coefficient (β), standard error (SE), and *P*-value are reported for each model parameter. The polynomial order of each parameter is reported as a superscript when applicable. Only newly tagged fish in the general group that were released before July 31 each year were included in attraction analyses.

Species	Year	*n*	Parameter	β	SE	*P*
Longnose Sucker	2019	42	TL	−0.0025	0.0025	0.3300
			TAR	−0.1108	0.0729	0.1510
			DAR	−0.0006	0.0005	0.3040
	2020	181	TL	0.0029	0.0014	0.0350
			ROR:siteB	−0.0230	0.1359	0.8695
			TAR	0.0143	0.0579	0.8057
			DAR^1	−3.2094	1.1663	0.0125
			DAR^2	7.1474	1.0307	< 0.0001
White Sucker	2019	30	TL	0.0052	0.0043	0.2307
			TAR	−0.1884	0.0523	0.0013
			DAR	−0.0010	0.0007	0.1675
	2020	105	TL	−0.0034	0.0024	0.1600
			ROR:siteB	0.3048	0.1998	0.1300
			TAR	0.0596	0.0576	0.3040
			DAR	−0.0173	0.0042	0.0001
Burbot	2019	50	TL	0.0004	0.0004	0.3440
			TAR	0.0113	0.0260	0.6670
	2020	86	TL	−0.0002	0.0007	0.7099
			TAR	−0.0452	0.0237	0.0598
			DAR	−0.0050	0.0012	0.0001
Shorthead Redhorse	2020	34	TL	0.0015	0.0037	0.6789
			TAR	0.0205	0.0591	0.7309
			DAR	−0.0372	0.0145	0.0153
Smallmouth Bass	2019	36	TL	−0.0063	0.0029	0.0348
			TAR	−0.1261	0.0710	0.1175
	2020	30	TL	−0.0054	0.0035	0.1344
			TAR	−0.0393	0.0616	0.5293
			DAR	−0.0001	0.0018	0.9384

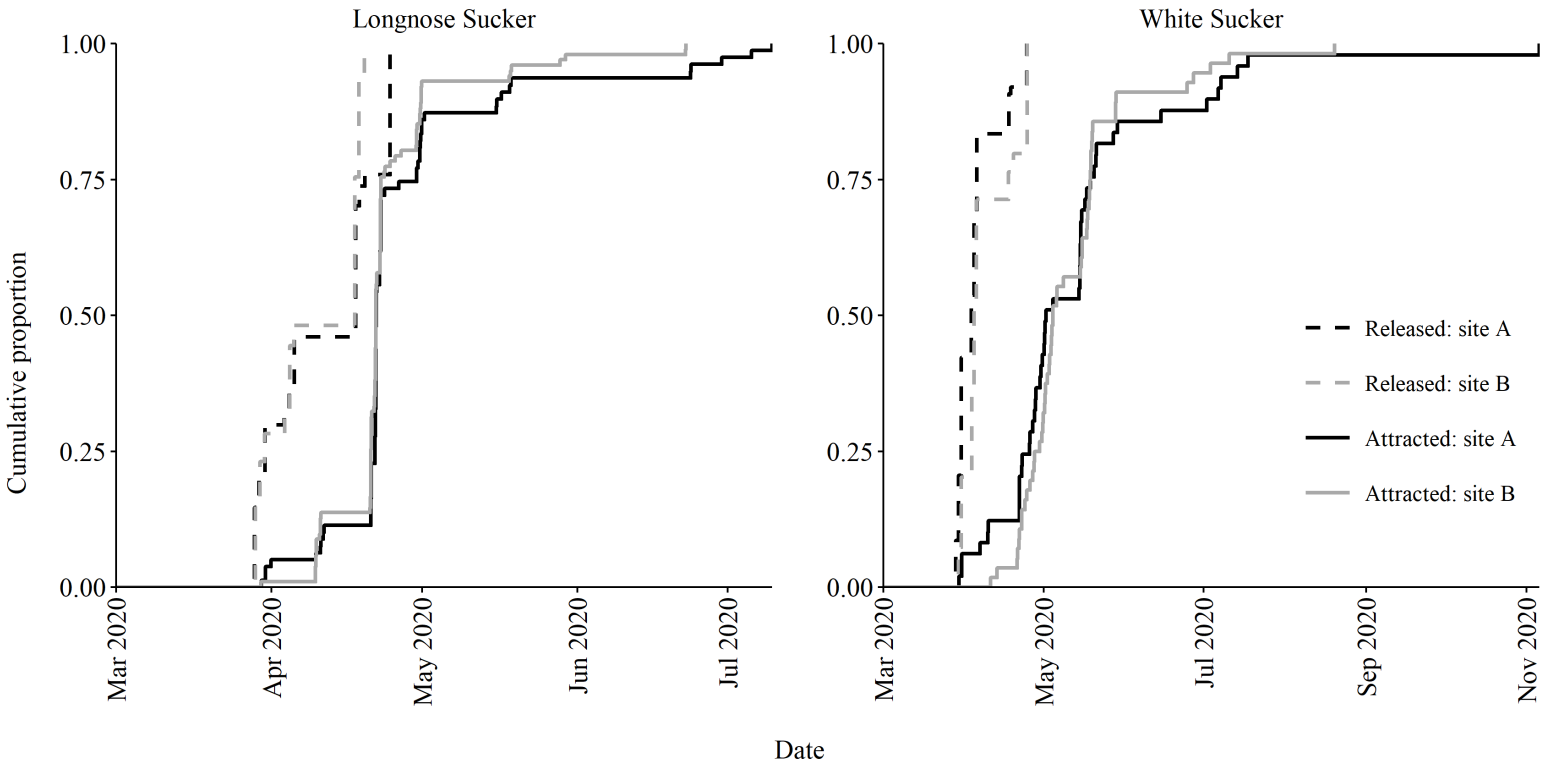

Figure 11. Kaplan-Meier curves of the cumulative proportions of Longnose Suckers (left) and White Suckers (right) released and attracted in 2020 from two release sites located 250 m downstream of the primary entrance to the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana. Site A was located on the same riverbank as the fishway and site B was located on the riverbank opposite the fishway. Note differences in *x*-axis scales.

Table 6. Transit and passage durations (h) calculated using data pooled from 2019 and 2020 for all of the 14 study species (in aggregate) and each species separately at the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana. Sample sizes include entering fish from any release group with complete detection histories at the antennas in question.

	Transit duration (h)			Passage duration (h)		
Species	*n*	Median	Range	*n*	Median	Range
Aggregate						
14 species	619	0.72	0.12 – 1,415.68	560	0.77	0.14 – 1,415.78
Species-specific						
Longnose Sucker	226	0.66	0.29 – 472.65	224	0.70	0.30 – 1,038.04
White Sucker	103	0.65	0.22 – 608.06	97	0.65	0.23 – 1,114.81
Burbot	101	0.98	0.42 – 721.29	71	0.96	0.44 – 1,378.68
Shorthead Redhorse	61	0.64	0.31 – 151.37	55	0.77	0.34 – 408.33
Smallmouth Bass	50	0.65	0.18 – 219.11	46	0.76	0.18 – 670.07
Goldeye	23	0.22	0.14 – 2.51	18	0.33	0.14 – 333.94
Channel Catfish	16	1.01	0.27 – 602.44	13	17.86	0.78 – 604.38
Mountain Whitefish	13	0.34	0.18 – 2.01	13	0.34	0.19 – 2.04
Sauger	1	10.08		1	10.10	
Brown Trout	13	1.04	0.12 – 1,415.68	12	74.61	0.14 – 1,415.78
Flathead Chub	3	5.81	0.62 – 12.56	2	276.38	12.56 – 540.20
River Carpsucker	4	0.49	0.22 – 0.86	4	0.49	0.22 – 0.87
Rainbow Trout	4	115.51	0.44 – 517.42	3	223.23	0.45 – 517.42
Mountain Sucker	1	0.87		1	0.88	

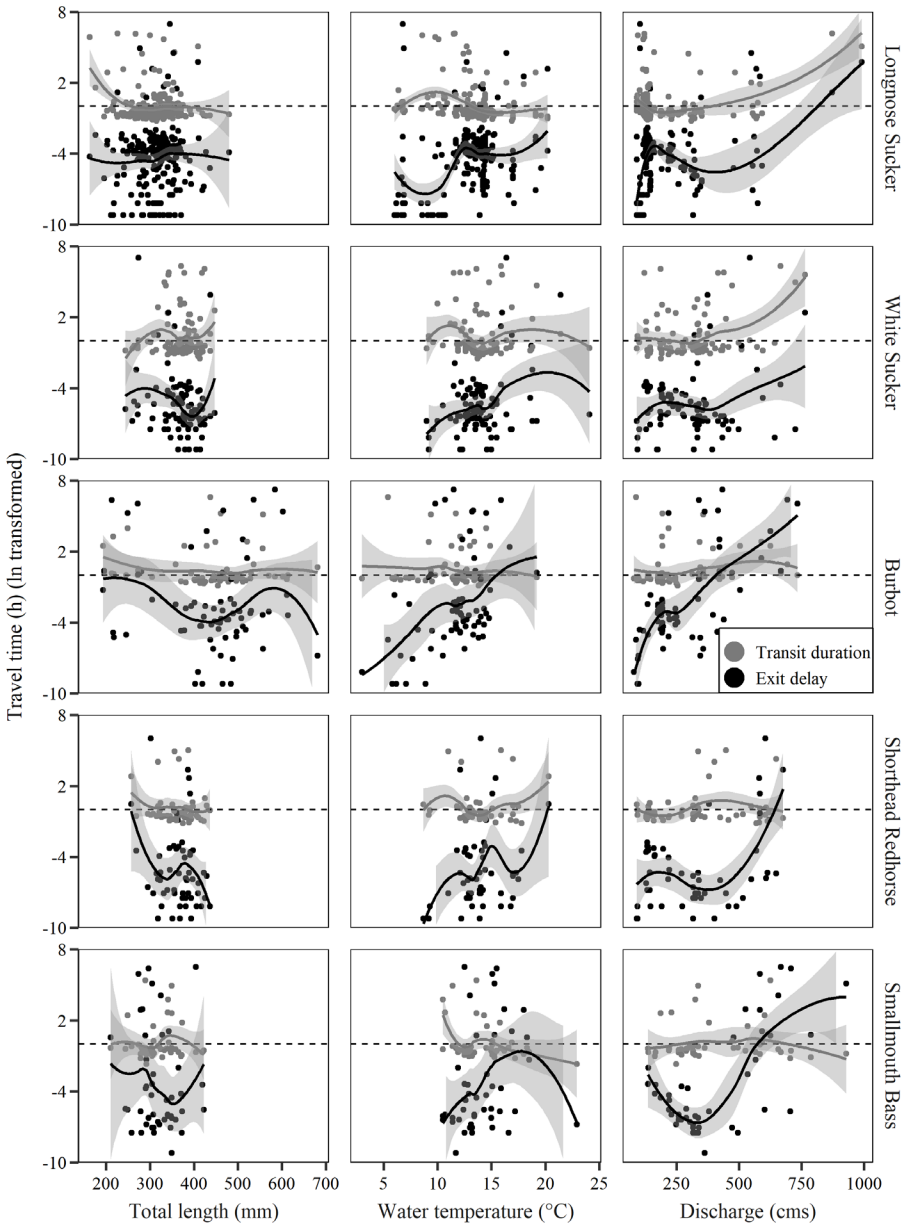

Figure 12. Relationships between transit duration and exit delay (both ln transformed) and three explanatory variables for five species of fish that used the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, during the fishway evaluation from 2019 through 2020. Scatterplots are fit with LOESS smooth models (span = 0.8). Gray areas are 95% confidence intervals from each LOESS model. The horizontal dashed line at $y = 0$ in each plot represents a 1 h (untransformed) transit duration or exit delay.

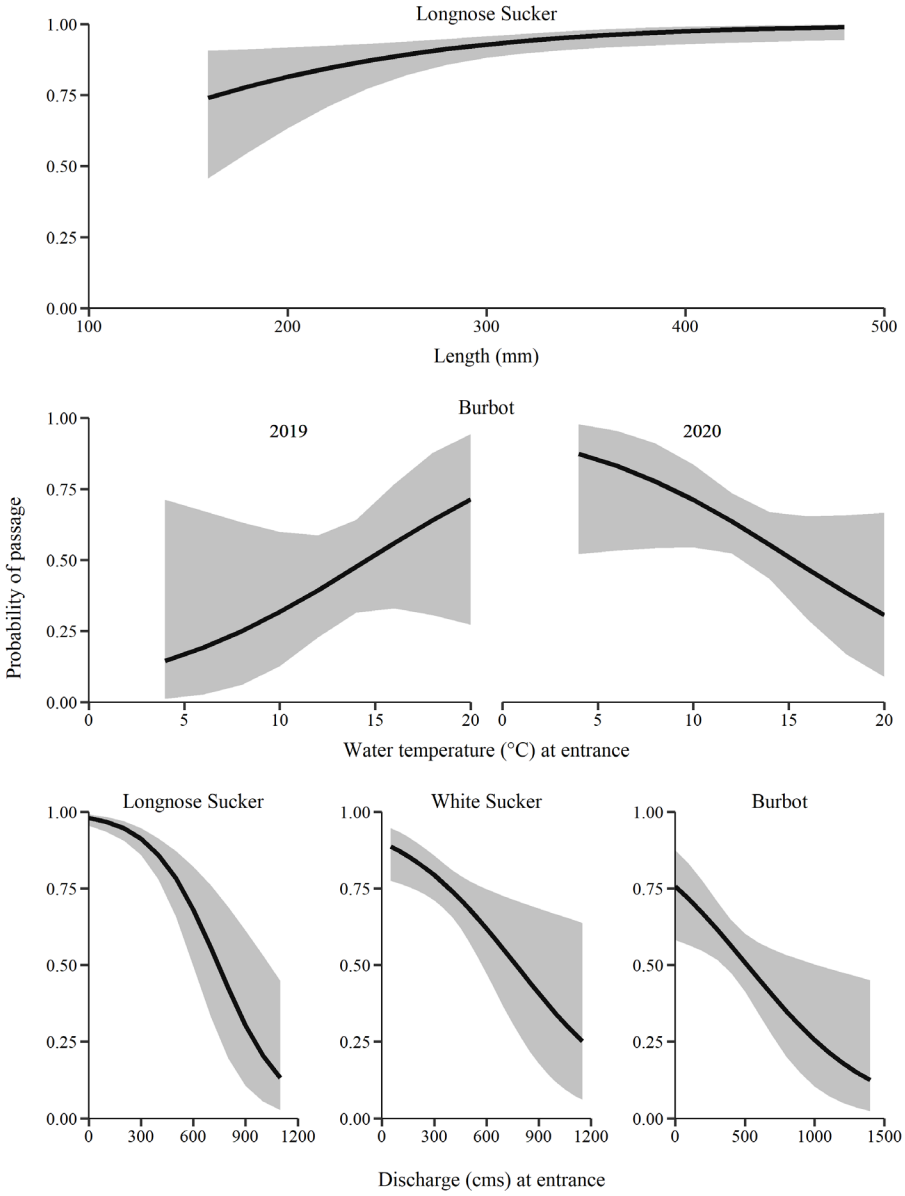

Figure 13. Predicted probability of passage of three species of fish at the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, based on three explanatory variables, while controlling for the other variables in each multiple logistic regression model (see Table 7 for exact variables included in each species-specific model). Data were pooled from 2019 and 2020. Gray shaded areas are 95% confidence intervals. Note differences in *x*-axis scales among discharge plots.

Table 7. Parameter estimates from multiple logistic regression models of passage for three species at the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, using data pooled from 2019 and 2020. Abbreviations of explanatory variables are TL (fish total length, mm), TAE (water temperature recorded at the USGS gage at the time of entrance to the fishway, °C), DAE (discharge recorded at the USGS gage at the time of entrance to the fishway, m^3/s), and YR:2020 (the year 2020). The term YR:2020*TAE is the interaction between study year and water temperature on the response in the model for Burbot. The estimated model coefficient (β), standard error (SE), and *P*-value are reported for each model parameter.

Species	*n*	Parameter	β	SE	*P*
Longnose Sucker	259	TL	0.0108	0.0043	0.0116
		TAE	−0.0024	0.0903	0.9791
		DAE	−0.0053	0.0011	< 0.0001
White Sucker	144	TL	0.0033	0.0046	0.4756
		TAE	−0.0758	0.0734	0.3015
		DAE	−0.0029	0.0011	0.0078
Burbot	156	TL	−0.0020	0.0016	0.2036
		TAE	0.1679	0.1392	0.2280
		DAE	−0.0022	0.0009	0.0134
		YR:2020	5.0705	2.3549	0.0313
		YR:2020*TAE	−0.3398	0.1724	0.0487

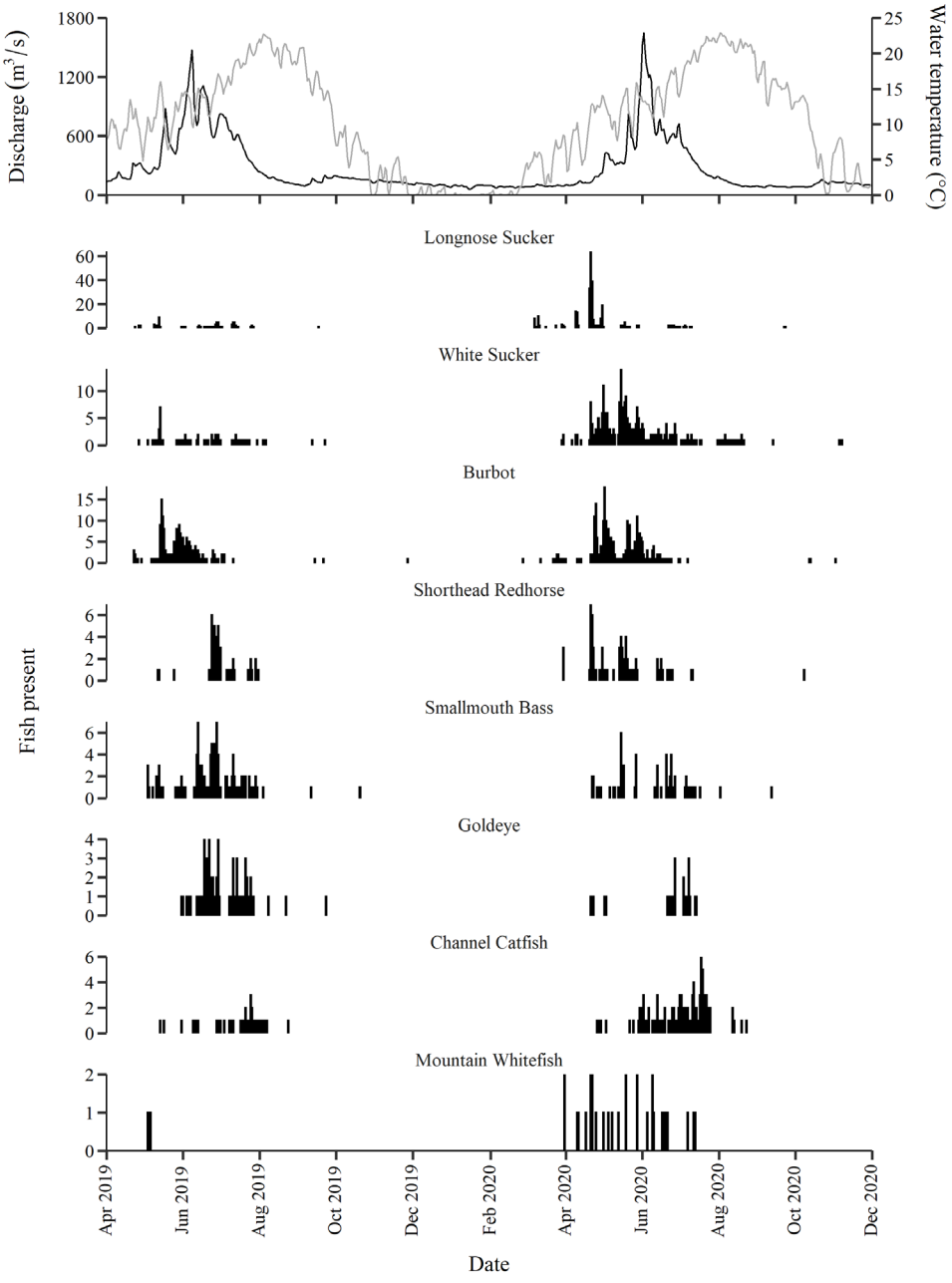

Figure 14. Daily counts of the number of fish of eight species present and mean daily discharges (▬) and water temperatures (▬) of the Yellowstone River at USGS gage 06214500 near Billings, Montana, during the evaluation of the nature-like fishway at Huntley Diversion Dam, Montana, in 2019 and 2020. The month of December 2020 is not included; no fish were present or passed during that month. Note differences in *y*-axis scales.

Figure 15. Photos of the exit of the nature-like fishway at Huntley Diversion Dam, Montana, at low (78 m^3/s; 2,750 ft^3/s; upper panel) and high (1,002 m^3/s; 35,400 ft^3/s; lower panel) discharges of the Yellowstone River. A rock wall forming the downstream side of the fishway exit and a reinforced concrete shelf are visible at low discharges, whereas both become entirely submerged at high discharges. Note the water plunging off of the concrete shelf and into the fishway at high discharges, as well as the standing wave formed where water flows over the rock wall. These problematic hydraulic conditions at high discharges delay successful fish at the exit and probably prevent others from passing.

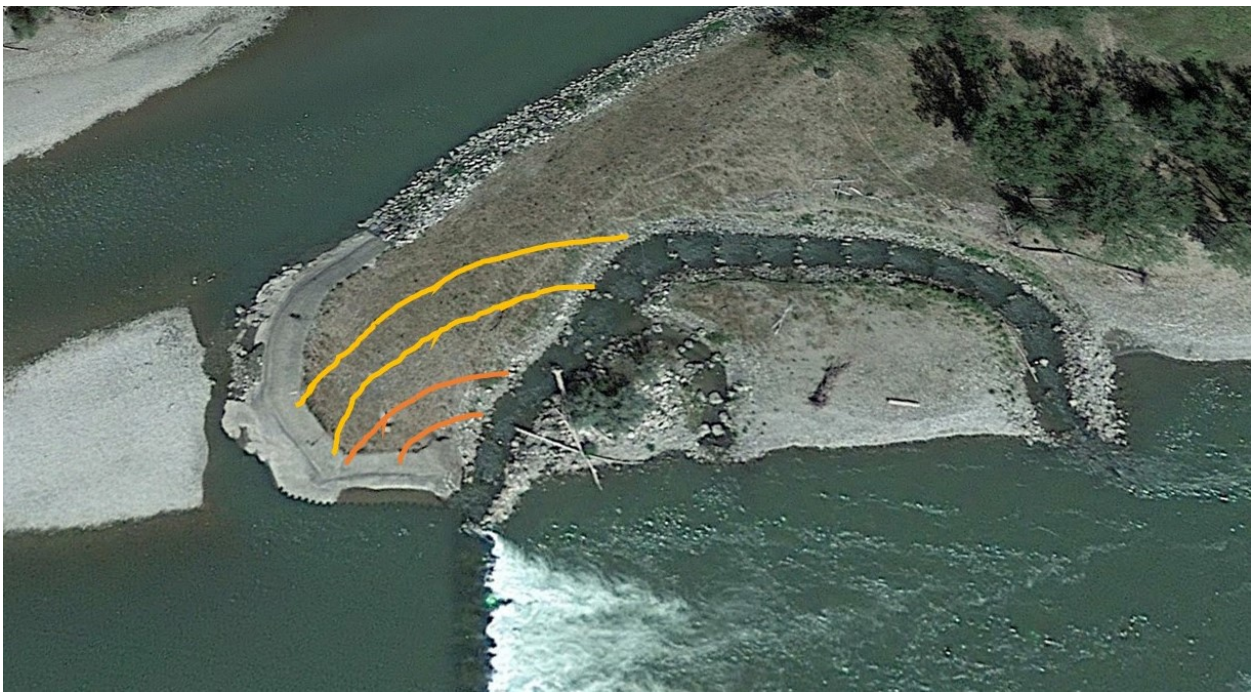

Figure 16. Diagram outlining two potential locations of a secondary nature-like exit channel that could be constructed at the nature-like fishway at Huntley Diversion Dam, Yellowstone River, Montana, to provide an alternative upstream passage route for fish during high discharges when turbulent, high velocity water is present near the existing exit. A secondary exit channel could contain boulders and other roughness elements similar to those in the existing channel.