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Fishway performance of adult Chinook salmon completing one of the world's longest inland salmon migrations to the upper Yukon River

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ABSTRACT

Fishways can restore functional connectivity within rivers for migratory fish where barriers compromise connectivity. Providing fish passage is particularly important for semelparous, anadromous species that require access to upriver habitats to successfully reproduce. From 2017 to 2020, we used a combination of acoustic and radio telemetry to investigate the passage success of Chinook salmon (*Oncorhynchus tshawytscha*) in the upper Yukon River through the wooden Whitehorse Rapids Fishway and compared this to the migration of salmon in the nearby free-flowing Takhini River. The upper Yukon River population of Chinook salmon studied here is highly unique, completing a 2800 km inland migration to Whitehorse, YT, before attempting to pass the Whitehorse Hydro Plant (WHP) to reach spawning sites upstream. We found that upstream passage success was variable across four years of study (0%–66%), was low overall at 31%, and was considerably lower for female salmon. In contrast, salmon migrating up the free-flowing Takhini River had high migration success to spawning grounds and had many times faster migration rates. Attraction (86%), entrance (77%), and passage efficiency (36%) were less than that reported for Chinook salmon at other fishways. Within the fishway, a disproportionately high number of salmon returned downstream upon reaching a daytime-operated viewing chamber (fish trap) located ~115 m up the fishway. Upon passing the fishway, salmon had high migration success to spawning grounds, though 12% of salmon returned downstream of the WHP, typically after multiple days and after traveling dozens of kilometres upstream of the facility. Findings from this study reveal opportunities to improve fishway performance and thus connectivity for one of the world's most impressive animal migrations.

1. Introduction

Fish are dependent on longitudinal connectivity within rivers to access various habitats important for feeding, refuge, and spawning and ultimately to complete their life cycle (Brink et al., 2018). This connectivity has been diminished by human-made barriers (e.g., hydropower facilities) and there are numerous cases in which physical barriers have led to immense population declines affecting fish and fisheries (Nehlsen et al., 1991; WCD (World Commission on Dams), 2000; Santos et al., 2018). For centuries, humans have attempted to overcome these barrier issues by constructing fishways that provide fish alternative routes around obstacles (Clay, 1995). Fishways rely on the premise that fish can find, enter, and ascend the structure with minimal sublethal consequences, though this is not always the case (Castro-Santos et al., 2009). Optimal passage conditions can be highly variable with regards to the species, life stage, barrier height, fishway design, and river (Castro-Santos et al., 2009). Even within a population, fish of different sizes (Keefer et al., 2013), sex (Burnett et al., 2014a; Roscoe et al., 2011), and condition (Cocherell et al., 2011), may have varying abilities to pass through a fishway. These differences highlight the need for context-specific evaluations to accurately quantify passage success at a given site (Roscoe and Hinch, 2010).

Fishways can be challenging for fish to find and enter as the areas approaching fishway entrances may have hydraulic conditions (e.g. high-velocity, turbulence) that overcome swimming abilities or otherwise deter fish (Burnett et al., 2014a). This can be of particular concern at hydropower facilities where fishway entrances may have insufficient water flow to attract fish away from competing flows nearby (e.g. turbine and spillway discharges; Castro-Santos et al., 2009). Once inside a fishway, passage conditions (e.g. velocity, number of rest stops) can greatly influence the likelihood of navigating the fishway (Mallen-Cooper and Brand, 2007). A portion of fish will resultingly not pass a

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given fishway (Bunt et al., 2012), and those that do may have compromised fitness due to delays or excessive burst swimming during the passage event (Burnett et al., 2014b; Roscoe et al., 2011; Caudill et al., 2007). Migratory fish may also fall back after passage through spillways, turbines, or other water passing structures (Boggs et al., 2004), given that they tend to be both rheotactic (orienting towards flow) and bank-oriented which may make them prone to follow the upstream barrier wall towards these areas (Groot and Margolis, 1991). At higher head facilities, fish that fall back may succumb to injury, or death, and are less likely to reascend the fishway and reach intended spawning sites (Boggs et al., 2004; McLaughlin et al., 2013). Reviews of fish-passage literature have found that fishways generally fall short of restoring full functional connectivity at physical barriers (Noonan et al., 2012; Bunt et al., 2012; Hershey, 2021). This is of particular concern for obligatory migratory species such as Pacific salmon (*Oncorhynchus* spp.) that are dependent on free-flowing rivers to successfully complete their lifecycle. Given the value of salmonids to humans (National Research Council, 1996), there has been a disproportionate amount of research undertaken to design and monitor fishways to pass these species (Katopodis and Williams, 2012) and in some cases these efforts have been highly successful. For instance, fishways in the Columbia River Basin appear to pass ~95% of migratory salmonids (Keefer et al., 2021), while 100% of Cutthroat Trout *Oncorhynchus clarkii pleuriticus* were able to pass beyond a small-scale barrier on a Rocky Mountain stream (Hodge et al., 2017).

Chinook salmon (*Oncorhynchus tshawytscha*) are anadromous, semelparous, and philopatric fish that complete long-distance migrations up rivers to spawn (Quinn, 2018; Birnie-Gauvin et al., 2021). These long-distance migrations expose salmon to numerous threats, and productivity of Chinook salmon populations across the west coast of North America has declined severely over the past century (Dorner et al., 2017; Ohlberger et al., 2016). The salmon lifecycle increases population-level risk posed by failed passage, as failure to reach intended spawning sites can have drastic consequences on spawning success (Twardek et al., 2022). However, salmon have strong swimming abilities (including high burst, prolonged, and sustained swimming speeds; Reiser et al., 2006) which increase their likelihood of successful passage through high-velocity areas often associated with hydropower plants and fishways (Burnett et al., 2014a). Pacific Salmon are an ideal model for fish passage research because their motivation to move beyond barriers is known, relative to iteroparous and non-philopatric species that may not be motivated to migrate beyond a barrier (Goerig and Castro-Santos, 2017) and may not pass a fishway due to intrinsic factors rather than fishway performance. Further, fishways across North America have typically been designed specifically for salmonids, and are expected to function better for them than non-target species (Clay, 1995). For salmon and other diadromous fishes, fish passage targets of '90% passage' have been suggested (see Lucas and Baras, 2001), while others have proposed that fishways should ideally allow fish to move freely beyond a barrier without additional delay (Castro-Santos et al., 2009).

The objective of this study was to evaluate the effectiveness of the Whitehorse Rapids Fishway (hereby termed fishway) at restoring migratory connectivity at the Whitehorse Hydro Plant (WHP) for Chinook salmon returning to the upper Yukon River. This population completes one of the world's longest inland salmon spawning migrations (~2900 km) and may be particularly susceptible to the effects of impeded migration given the general decline of animal populations with relatively long migrations (Sanderson et al., 2006; Pearce-Higgins et al., 2015; De Zoeten and Pulido, 2020). Upon migrating nearly 3000 km inland, the ability of upper Yukon River Chinook salmon to find, enter, and move through the fishway was evaluated, along with their passage duration, number of passage attempts, diel passage behaviour, and behaviour at a viewing chamber situated partway through the fishway. Post-passage outcomes were evaluated including fallback, arrival at spawning grounds, and en-route mortality. We further considered the influence of fish and environmental characteristics on passage success and behaviour including fish sex, origin, run timing, size, and water temperature. Where possible, we draw upon additional evidence to evaluate fishway effectiveness including sex ratios downstream of vs. in the fishway, and indicators of spawning success (ie. egg retention) from salmon carcasses downstream of the WHP. Findings from this study may help inform design and operational changes at the WHP and other fishways intended to pass adult salmonids.

2. Methods

2.1. Study site

The upper Yukon River extends ~2900 km upstream from its mouth at the Bering Sea to an elevation of 719 m at the head of spawning tributaries south of Whitehorse, YT. The river passes through relatively remote northern landscapes in the Yukon Territory and Alaska and the mainstem is free of human-made barriers aside from the WHP (~2800 rkm inland). Discharge in the Yukon River near Whitehorse averages 470 m^3/s (Environment Canada, 2022). Our study area consisted of the final 100 km of this salmon migration, from the confluence of the Yukon and Takhini rivers to upstream spawning sites on the Takhini and Yukon rivers (Fig. 1). The Takhini River is free-flowing and supports a run of ~1900 fish (Fisheries and Oceans Canada, 2019). In contrast, the Yukon River is impounded by the WHP, and has an average annual escapement above the facility of 950 fish over the last 60 years (JTC (Joint Technical Committee of the Yukon River U.S./Canada Panel), 2020). Since 1988, a hatchery located ~1 km downstream of the WHP has collected eggs from adult salmon at the WHP and raised and released fry into spawning tributaries located upstream (Wolf Creek, upper M'Clintock River, and Michie Creek). Approximately 50% of the salmon passing the WHP are of hatchery-origin, though the hatchery contribution (28%) was much lower during our study years (JTC (Joint Technical Committee of the Yukon River U.S./Canada Panel), 2020). Chinook salmon runs on the Yukon River are typically dominated by age-5 and age-6 fish, with wild fish being stream type and hatchery fish being ocean type (JTC (Joint Technical Committee of the Yukon River U.S./Canada Panel), 2020). There have been few observations of precocial salmon within this system.

The WHP was constructed in 1958 and is the largest source of energy in the Yukon (40 MW). Energy is generated through four Kaplan (blade-style) turbines with discharge ranging from 90 to 277 m^3/s. Screens prevent adult salmon from moving upstream towards the turbine discharge, while an angled fish weir (45 m wide, 2.5 m high) prevents salmon from approaching the spillway. The Whitehorse Rapids Fishway provides the only means for fish to access habitat upstream of the WHP (Fig. 2). The 366 m-long structure is the longest wooden fishway in the world and rises 18 m from the Yukon River to the Schwatka Lake reservoir (area = 1.5 km^2, length = 2.5 km). Discharge through the fishway is approximately 0.61 m^3/s and flow through the fishway is controlled by stop logs at the fishway exit. The fishway has been managed by the same individual for multiple decades, who generally allocates a consistent amount of water into the fishway each year. The fishway has a pool-and-weir design, where salmon can swim through submerged slots or over baffles between each step. In 2019 (when a Hach FH950 Velocity Flow Meter was available), it was estimated that 56% of discharge passes above the baffles. The fishway has 51 steps (step dimensions of w = 1.22 m, h = 1.93 m, l = 3 m) with slots (slot dimensions of w = 0.4 m, h = 0.6 m) that are offset between successive steps. Attraction flow at the fishway entrance (w = 1.8 m, h = 2.7 m) is controlled by a valve that has remained in a partially open position for the last few decades. The fishway remains as a single low gradient step for ~10 m after the entrance, there is then an ascent (18 steps; 47 m long; 0.09 slope) to a turning basin (3 m), a second ascent to a viewing chamber (15 steps; 39 m; 0.09 slope), a 184 m low-velocity stretch (<0.01 slope), and a final ascent to the fishway exit (18 steps; 83 m; 0.10 slope). The viewing chamber (ie. a fish trap) allows fishway staff to

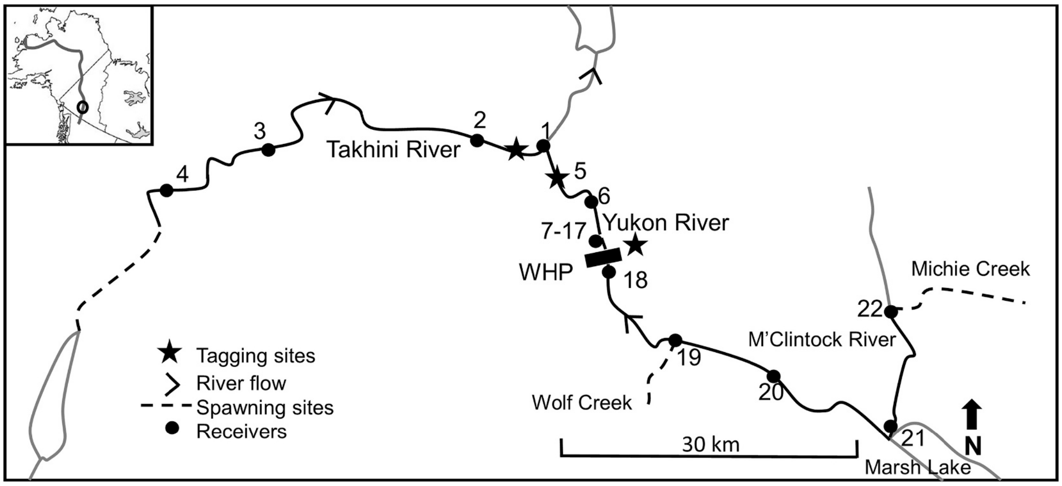

Fig. 1. Map of the upper Yukon River study area from 2017 to 2020, highlighting the locations of the WHP, spawning sites, tagging sites, and telemetry stations.

Fig. 2. Map of the hydroelectric facilities in Whitehorse, YT, and receiver locations from 2017 to 2020. All receivers were acoustic aside from those with a subscript 'R' which were radio telemetry receivers. Subscript numbers indicate the years that receivers were deployed at that location.

count fish, collect salmon for a hatchery program, and facilitate public outreach. Notably, staff must lift a gate on the upstream end of the trap to allow fish to continue their migration. Passage is therefore restricted to opening hours (9:00–20:00) when staff are present to operate the gate. The fishway was designed to pass salmon though other species (e. g., *Thymallus arcticus*, *Salvelinus namaycush*, *Esox lucius*, *Coregonus* spp.) use the fishway occasionally. Hourly water temperature in the fishway was obtained using a HOBO temperature logger (de Graff, Can-Nick-a-Nick Environmental Services, pers. Comm). Mean August daily water temperatures in the fishway remained similar between 2017 (15.3 [13.1–18.2] °C), 2018 (15.7 [13.8–18.2] °C), 2019 (15.1 [12.4–17.6] °C), and 2020 (14.3 [12.9–16.1] °C). Fishway slopes (listed above) were calculated using the ArcticDEM Explorer that hosts high-resolution (~0.5 m) data derived from optical imaging satellites.

2.2. Fish capture and tagging

Short set gill nets were used to capture Chinook salmon from the

Yukon River in August from 2017 to 2020. Gill netting was completed approximately 8 km upstream of the confluence of the Yukon and Takhini rivers (2785 km), 15 km downstream of the WHP. Fishing practices aligned with those used previously on the Yukon River which documented a 98% post-tagging recovery rate (Eiler et al., 2014). The cable-laid gill net measured 30.5 m (100 ft) long, 3.05 m (10 ft) tall, and had a 3:1 hang ratio and 16.5 cm mesh size. The hang ratio encouraged entanglement over gilling to minimize harm and facilitate salmon removal. Nets were set along eddy lines and were constantly watched over a 30 min soak period. Nets were checked immediately if the float line indicated a fish capture, or were checked at the end of the soak period. Fish were lifted on board and were quickly unrolled. Scissors were used to cut the net (typically 1–2 panels per fish) to decrease the amount of time spent entangled. Fish were placed into a plastic bin filled with river water and an oxygen pump was set at 25 mg/L.

Chinook salmon were gastrically implanted (Naughton et al., 2018) with either a single V16 acoustic transmitter (V16-4H-R64K coded tags, Innovsea [formerly Vemco Inc.], Shad Bay, NS, Canada; 10.3 g; diameter = 16 mm x length = 68 mm; 90 s randomized interval) or with a V13 transmitter (6 g; diameter = 13 mm x length = 36 mm; 60 s [2019] and 30 s [2020] randomized interval) attached to a TX-PSC-I-80 radio transmitter (Sigma Eight, Newmarket, ON, Canada; whip antenna; 150 MHz; battery = 150 days; 4.2 g; diameter = 10 mm x length = 27 mm; burst rate = 2.6 s). Acoustic and radio transmitters were affixed together with a marine-grade adhesive for ease of application in salmon (combined weight = 10.2 g, diameter = 13 mm, length = 63 mm). A small-diameter hollow PVC pipe was used to apply transmitters, the end of which was coated in PlastiDip to avoid injury to the viscera. A transmitter was placed in the pipe, which was inserted into the fish's mouth and pushed to the stomach. A wooden dowel plunger was then inserted into the pipe to release the transmitter, and the pipe and dowel were withdrawn from the stomach. Fish were then externally tagged behind the dorsal fin with a coloured anchor tag (Floy Manufacturing Ltd., Washington) and a hole punch was used to collect a genetic sample from the caudal fin. External tags and markings allowed visual identification of treatment groups to avoid double tagging with acoustic transmitters if recaptured at the fishway. Sex (based on external characteristics), origin (hatchery or wild; adipose fins are clipped on all hatchery fish), and fork length (to the nearest 5 mm) were recorded. Fish were kept in a water-filled cooler during sampling except during gastric tagging. Fish were released ~800 m upstream in low-velocity areas to reduce the likelihood of recapture in the gill net and facilitate recovery from tagging. One captured fish was released without a transmitter in 2017 that was not seen entering the net and was in poor condition upon retrieval.

Chinook salmon were also monitored on the Takhini River to control for the potential impacts of capture, tagging, and natural rates of enroute mortality (see Cooke and Hinch, 2013 for a discussion on the need for controls in fish passage research). Salmon were caught in gill nets in the Takhini River and tagged with V16 transmitters using the same methods as for the Yukon River. In 2018, tagging was completed by Fisheries and Oceans Canada (DFO) as part of the Takhini River Chinook salmon Restoration Investigation – 2018 (Fisheries and Oceans Canada, 2019). The cable-laid gill net used by DFO measured 15.2 m (50 ft) long, 2.44 m (8 ft) tall, had a 3:1 hang ratio, and 13.3–19.1-cm mesh size depending on the net. Nets were not actively monitored but were checked every 30 min (so entanglement times are not known).

Chinook salmon were also tagged at the Whitehorse Rapids Fishway viewing chamber by fishway and hatchery staff. Fish were gastrically tagged using the same methods as previously described, except capture was completed by dip net rather than gill net. Target characteristics of study salmon were objectively set a-priori based on historic population averages/frequencies of size, sex, origin, and arrival date (though more wild fish were tagged). Hatchery staff then adapted fish selection (based on these historic values) to account for differences in the run during any given year. Total handling time was ~2 min and air exposure was generally <20 s. Fish were released beyond the upstream gate of the viewing chamber, allowing them to complete the fishway.

2.3. Receiver array

An array of 19 acoustic telemetry stations (VR2ws, Vemco Inc., Shad Bay, NS, Canada) and three radio telemetry stations (Lotek, SRX800, Newmarket, ON, Canada) were used to monitor fish movement to known and suspected spawning tributaries upstream of the confluence of the Yukon and Takhini rivers (Figs. 1 and 2; Table 1). Stations consisted of one to three receivers depending on the location, with a minimum of 12 receivers deployed in 2017 and a maximum of 29 in 2020. Locations remained mostly consistent over the four years of the study, but were adjusted adaptively based on improved knowledge of fish behaviour and telemetry system performance each year. Acoustic receivers were generally anchored with a cement block or sand bag and were tethered to a rope extending up to a sub-surface buoy. Radio telemetry was adopted in addition to acoustic telemetry from 2019 onwards. Radio telemetry receivers (SRX 800 s, Lotek Wireless, Newmarket, ON) replaced acoustic telemetry receivers at the entrance, first step, and turning basin of the fishway due to low acoustic detection efficiency. As such, only data from 2019 and 2020 could be used to calculate attraction, entrance, and passage efficiency of the fishway. Radio telemetry receivers were connected to a 7.6 m piece of coaxial cable that was inserted into a submerged PVC pipe. The end of the cable was stripped (22 cm) and protruded from a joint in the PVC pipe arranged perpendicular to the walls of the fishway (approximately mid-height in the water column; Beeman et al., 2004). The radio receivers scanned three frequencies, each for 3.2 s, meaning every tagged salmon was searched for over a 9.6 s period. The gain was set on the entrance receiver such that fish were not detected upon actually entering the fishway, but were detected consistently at 2 m (93% of transmissions) and never at 20.5 m. The receiver positioned in the first step of the fishway had the gain set such that no fish would be detected outside the fishway, but would be detected consistently in the first step (80% of transmissions) and fairly frequently in the step above and turning area below. The receiver in the turning basin was set such that salmon would be consistently detected in the turning basin (~75% of transmissions) and detected frequently in the step above the turning basin (35% of transmissions). Receivers were tested prior to deployment and range testing was conducted on a subset of acoustic and radio receivers. Range testing was completed at each site by placing a V16 or V13 range test transmitter, or TX-PSC-I-80 radio transmitter at set distances from each receiver for a set time interval (100 potential detections; Kessel et al., 2014). Range test results are presented in Supplemental Material 1. Detection efficiency was calculated as the number of fish successfully detected by a receiver divided by the number of fish known to have passed upstream of the receiver (Table 1). Manual radio tracking was completed approximately every three days in the 5-km stretch downstream of the WHP for two weeks following the final tagging date to supplement fixed-station data.

2.4. Statistical analysis

Tagging conditions were recorded for each fish including entanglement, air exposure, and total tagging durations. Entanglement period (101 vs. 113 s), air exposure (57 vs. 48 s), and total tagging time (524 vs. 527 s) were similar between salmon that attempted passage vs. those that did not. Initial recovery from gill net capture and tagging (96%; n = 71) was based on detection at an upstream receiver (or in some cases manual radio tracking).

Fishway efficiency calculations only included fish that were detected entering the tail race and approaching the WHP (i.e., detected at receivers 400 m from the fishway entrance). Efficiency calculations followed those used previously (Dodd et al., 2017). Overall passage success of the fishway was defined as the proportion of fish that approached the facility (ID 9) which then passed (ID 17). Attraction efficiency was

Table 1
Location and detection efficiency (% detected of those that passed a receiver) of acoustic and radio stations deployed throughout the upper Yukon River watershed from 2017 to 2020 to monitor the migration of Chinook salmon to spawning sites. Distances in the "Location" column represent distance upstream of the confluence of the Yukon and Takhini rivers. Detection efficiencies could not be calculated for 1, 5, 8, and 19 given their positions in the river.

ID #	Type	Location	Rationale	Detection efficiency
1	Acoustic	Confluence Yukon and Takhini River (0 km)	Post-gill netting fallback	–
2	Acoustic	Takhini River, 16.7 km	Similar distance as release site to fishway exit receiver on Yukon River	100% (n = 16)
3	Acoustic	Takhini River, 57 km	Directionality into suspected spawning site (x2 receivers for directionality)	100% (n = 16)
4	Acoustic	Takhini River, 87 km	Lowermost extent of major spawning area (x2 receivers for directionality)	100% (*n* = 12)
5	Acoustic	Yukon River, 8 km	Tagging site	–
6	Acoustic	Yukon River, 16.1 km	Confirm initial post-tagging recovery	77% (*n* = 37)
7	Acoustic	Yukon River, 20.6 km	Progression towards fishway	62% (*n* = 45)
8	Acoustic	Yukon River, 21.2 km	Known spawning site (x1 receiver in 2018 and 2019, x2 in 2020)	–
9	Acoustic	Yukon River, 22.3 km, ~400 m downstream of fishway	Detect fish that enter tail race and approach the dam (x1 receiver in 2018, x2 in 2019, and x3 in 2020)	73% (*n* = 26)
10	Acoustic	Yukon River, 22.4 km, Tail race eddy 1	Detect tail race movements (2018 only)	80% (n = 10)
11	Acoustic	Yukon River, 22.5 km, Tail race eddy 2	Detect tail race movements (2018 only)	28% (n = 7)
12	Acoustic	Yukon River, 22.5 km, Tail race eddy 3	Detect tail race movements (2018 only)	14% (n = 7)
13	Radio	Yukon River, 22.6 km, Fishway entrance	Attraction efficiency	100% (*n* = 11)
14	Radio	Yukon River, 22.6 km, Lower fishway	Entrance efficiency	100% (*n* = 9)
15	Radio	Yukon River, 22.7 km, Fishway turning basin	Progression through the fishway	100% (*n* = 7)
16	Acoustic	Yukon River, 22.8 km, Viewing chamber	Progression through the fishway	97% (*n* = 111)
17	Acoustic	Yukon River, 23.0 km, Reservoir entry	Detects fishway exit and reservoir entry (x2 in 2020)	87% (*n* = 117)
18	Acoustic	Yukon River, 26.2 km, Reservoir exit	Progression past the reservoir	96% (n = 26)
19	Acoustic	Yukon River, 37.6 km, Wolf creek mouth	Known spawning tributary (x1 receiver 2017 and 2018, x2 in 2019 and 2020)	–
20	Acoustic	Yukon River, 52.5 km, Lewes Dam	Detects passage at Lewes Dam (x2 receivers for directionality, x1 in 2018)	100% (*n* = 104)
21	Acoustic	69 km, M'Clintock River mouth	Known spawning tributary	100% (*n* = 106)
22	Acoustic	101.3 km, M'Clintock River Michie Creek confluence	Known spawning tributaries (x3 receivers for directionality)	100% (*n* = 92)

calculated as the proportion of fish that approached the facility (~400 m; receiver ID 9) which then approached the fishway entrance (<10 m; receiver ID 13). Entrance efficiency reflected the proportion of fish arriving outside the fishway entrance (receiver ID 13) that then entered (receiver ID 14), whereas passage efficiency described the proportion of fish that entered the fishway (receiver ID 14) that then passed the fishway (receiver ID 17). We further divided the fishway as the lower fishway (receiver 14 to 15), turning basin (receiver 15), mid-fishway (receiver 15 to 16), viewing chamber area (receiver 16), and upper fishway (receiver 16 to 17) to calculate passage efficiency for each of these reaches. Three fish (one from the Takhini River and two from the Yukon River) were never detected upstream after tagging. These fish were not included in further analysis or any summary statistics. One additional fish was taken by hatchery staff at the fishway viewing chamber because it appeared to be struggling to leave the fishway and was not included in calculation of overall passage success, passage duration, or behaviour at the fishway viewing chamber.

Migration rates were quantified for the first 15 km of the migration after release for both Yukon River and Takhini River Chinook salmon. Migration rates for Yukon River Chinook salmon were also calculated for the overall passage period and for each reach of the fishway and beyond the fishway (i.e., through the reservoir, through the Yukon River mainstem, and to the primary spawning area; Michie Creek). Migration rates both within and outside the fishway were typically calculated using the elapsed time between first detections at the upstream and downstream receivers divided by the distance between these receivers (Similar to Silva et al., 2018). However, migration rates in the turning basin were calculated as the first and last detections in the turning basin during the first attempt at passage, and migration rates in the viewing chamber were calculated as the elapsed time between first and last detections at the chamber receiver. Upper fishway migration rates were calculated as the elapsed time from the last detection in the viewing chamber (indicating fish left the viewing chamber area) and the first detection at the fishway exit (excluding one statistically significant outlier that took 20 h to leave the fishway and fish that went undetected exiting the fishway). The number of approach, attraction, and entrance events was quantified as the number of unique movements to either the tailrace entry (approach), fishway entrance (attraction), or first step (entrance) following detection downstream. The duration between first and last passage attempts (defined as the time elapsed between first and final detections in the tail race; receiver ID 9) was calculated for those fish that failed to pass the fishway. The diel period (categorized as day or night) was determined for all detections at the fishway entrance receiver, first step receiver, and viewing chamber receiver using the *Sunlight* package in R.

Fish were assigned as successful migrants if they were detected passing Lewes Dam (52 km; receiver ID 20), terminating in Wolf Creek (38 km; receiver ID 19), or passing the Takhini River upstream of 57 km (receiver ID 3). These sites have been previously identified as spawning areas or immediately downstream of spawning areas (Brown et al., 2017). One female fish was also assigned as a successful migrant that was recovered as a completely spent carcass at 36 km upstream. Fallback through the WHP was assigned to fish detected in the reservoir that were later detected downstream of the facility. Fish falling back >1 h after entering the reservoir were considered to have returned downstream volitionally. We refer to this volitional fallback as overshoot (Boggs et al., 2004), though the reasons for this fallback behaviour are not clear. The first detection upon entering the reservoir and first subsequent detection downstream of the WHP was used to calculate overshoot duration.

Proportion tests were used to test for differences in diel arrival period (day vs. night) at various points in the fishway relative to the expected proportion based on the amount of daylight hours at this latitude. Sex, size, origin, and relative passage date (date relative to the first and last salmon counted at the fishway) were used as predictors (when sample size allowed) for separate models using fishway passage success, upper fishway migration rate, fall back, and duration of failed passage attempts as response variables (models outlined in Table 3) to evaluate the influence of fish characteristics on these passage metrics. *P*-values were adjusted within these models to account for multiple comparisons using the *p.adjust* function specifying "*fdr*". A logistic regression (*glm,* specifying *family* = *'binomial'*) model was used to evaluate the influence of water temperature on passage outcomes (pass/fail). Gill net sampling downstream of the WHP revealed an even sex ratio in the population (52% female; $n = 56$). Under the assumption that males and females have equal passage success, 52% of females would have been expected to pass through the fishway. A chi-square test was used to compare the sex proportions in salmon sampled by gill net downstream of the WHP and of the total population counted passing through the Whitehorse Rapids Fishway viewing chamber to assess whether sex ratios at the fishway matched those of the population migrating towards the fishway. It was hypothesized that the female proportion at the fishway would be lower given that females often have lower passage success and higher migration mortality than males (Burnett et al., 2014b; Hinch et al., 2021). All statistical analyses were conducted in R Statistical Software (R Core Team, 2020) using an alpha level of 0.05, and model assumptions were assessed through visual examination of diagnostic plots of residuals.

2.5. Carcass surveys

Carcasses were collected downstream of the WHP ($n = 146$) and on the nearby free-flowing Teslin River ($n = 105$) from 2018 to 2020 (as outlined in Twardek et al., 2022). We observed lower levels of complete spawning (ie. <100 eggs retained; Quinn et al., 2007) in female carcasses downstream of the WHP compared to those on the Teslin River. Carcasses downstream of the WHP comprise adults returning to spawn at their natal habitat, and presumably those that failed passage at the fishway. Carcass survey data in combination with telemetry data were used to provide a secondary estimate of passage success at the fishway (see full details of this analysis in Supplemental Material 2). Briefly, we assumed that fish that failed to pass the WHP would not spawn completely, and estimated what proportion of carcasses downstream of the WHP would have to be attributed to failed passage to result in the lower complete spawning rate observed there compared to the Teslin River.

3. Results

3.1. Fishway passage success

Across all years, 56 Chinook salmon were tagged downstream of the WHP on the Yukon River, 36 of which attempted passage (834 ± 74 mm; 40% female), while 15 Chinook salmon (879 ± 63 mm; 40% female) were captured from the free-flowing Takhini River (one tagging mortality). Salmon from the Takhini River were more likely to migrate 15 km upstream of tagging sites (100% of $n = 14$) than salmon on the Yukon River where they had to pass the WHP to migrate 15 km upstream (31% of $n = 35$). Salmon were also more likely to arrive at upstream spawning sites on the Takhini River (100% of n = 14) than on the Yukon River (29% of n = 35). Passage success at the fishway varied considerably across years with the lowest passage rates observed in 2017 (0% of $n = 6$) and 2020 (0% of $n = 5$), which also had the smallest sample sizes. Across all years, attraction (86% of $n = 21$), entrance (77% of $n = 18$), passage (36% of $n = 11$), and overall passage success (31% of n = 35) were recorded for Chinook salmon at the Whitehorse Rapids Fishway. Upon entering the fishway, most salmon reached the turning basin (79% of n = 14), and most moved beyond to the viewing chamber (73% of n = 11). Upon reaching the viewing chamber, 69% of salmon passed the upstream gate and subsequently passed the fishway exit ($n = 16$).

From release, it took Chinook salmon about two additional days to migrate 15 km and pass the WHP on the Yukon River (142.8 ± 180.8 h; median $n = 74.3$ h of $n = 8$) than to migrate a similar distance on the free-flowing Takhini River (27.2 ± 18.8 h; median = 23.4 h of n = 14). Fish spent an average of 118 [27–564] h (median = 50.3 h) passing the fishway upon entering the tail race (n = 8), which included attraction, entrance, and passage times. In comparison, 60.5 ± 40.8 h (median = 50. 3 h of $n = 100$) was the time it took salmon to travel 78 km upstream to Michie Creek (the primary spawning tributary) after passing the WHP. Migration rates varied considerably throughout different components of the passage event (See Table 2) with the slowest passage rates observed for salmon entering the fishway, in the lower fishway, and around the viewing chamber.

Salmon often completed various passage sections more than once. For example, some salmon reapproached the WHP (14% of salmon; 1.3 ± 0.8 approaches of $n = 36$), reapproached the fishway entrance (31% of salmon; 1.5 ± 1.9 entrance approaches of $n = 16$), and reentered the fishway (58% of salmon; 1.5 ± 1.7 entries of $n = 12$). In one instance, a salmon moved 23 km downstream before returning to and passing the fishway 3 weeks later. This salmon had approached and entered the fishway several times prior to its 3 week departure. Salmon that failed to pass spent an average of 44.5 ± 56.6 h (median = 31.3 h of $n = 18$) from their first to last attempts at passage. After failing to pass the fishway, most salmon were detected on the nearest known spawning ground located 1.5 km downstream (66% of n = 18), though 16% were there for only a couple of hours.

3.2. Diel patterns of fishway passage

Salmon arrived at the fishway for the first time both during day light (44%) and at night (56% of n = 16). Given that nighttime comprises just 7–9 h of the day at this latitude, salmon had a disproportionately higher arrival rate at the fishway entrance at night (~2.5 fold), though this was not significant ($\chi^2 = 9.2$, $P = 0.34$ of $n = 16$). Salmon entered the fishway more so during day light (67% of n = 12) though this was proportional to the amount of daylight hours at this latitude. Salmon tended to arrive at the viewing chamber for the first time more so during day light (82% of n = 17), though this was not significantly different than expected ($\chi^2 = 0.40$, $P = 0.53$ of $n = 17$). Of greater relevance to this fishway is whether salmon first arrived at the viewing chamber during hours of operation (9:00–20:00) or during close (when passage through the fishway is impossible). Indeed, more than half of all salmon arrived at the viewing chamber for the first time when the facility was closed (53% of n = 17), and 34% of overall detections in the viewing chamber occurred during closed hours (Fig. 3). Salmon that failed to

Table 2
The timing of various components of passage for upper Yukon River Chinook salmon at the Whitehorse Rapids Fishway, Yukon from 2017 to 2020. Passage time metrics include all salmon tagged downstream that then attempted passage, regardless of whether they ultimately passed the fishway.

Passage time metric	Average ± SD (h)	Median	Distance (m)	Median migration rate (km/h)	n
Overall passage	118 ± 183	50.3	776	0.015	8
• Attraction	1.6 ± 1.7	1.0	410	0.41	13
• Entrance	49.1 ± 149.1	1.3	10	0.008	12
• Passage	34.8 ± 8.3	37.0	356	0.010	3
Lower fishway	*13.8 ± 14.3*	*10.1*	*47*	*0.005*	*9*
Turning basin	*0.1 ± 0.1*	*0.1*	*3*	*0.300*	*9*
Mid-fishway	*4.4 ± 5.9*	*0.7*	*39*	*0.056*	*7*
Viewing chamber area	*28.8 ± 38.9*	*13.7*	*114*	*0.008*	*16*
Upper fishway	*0.8 ± 0.2*	*0.8*	*153*	*0.191*	*6*
Spawning tributary mouth after passage	60.5 ± 40.8	50.3	78,000	1.3	100

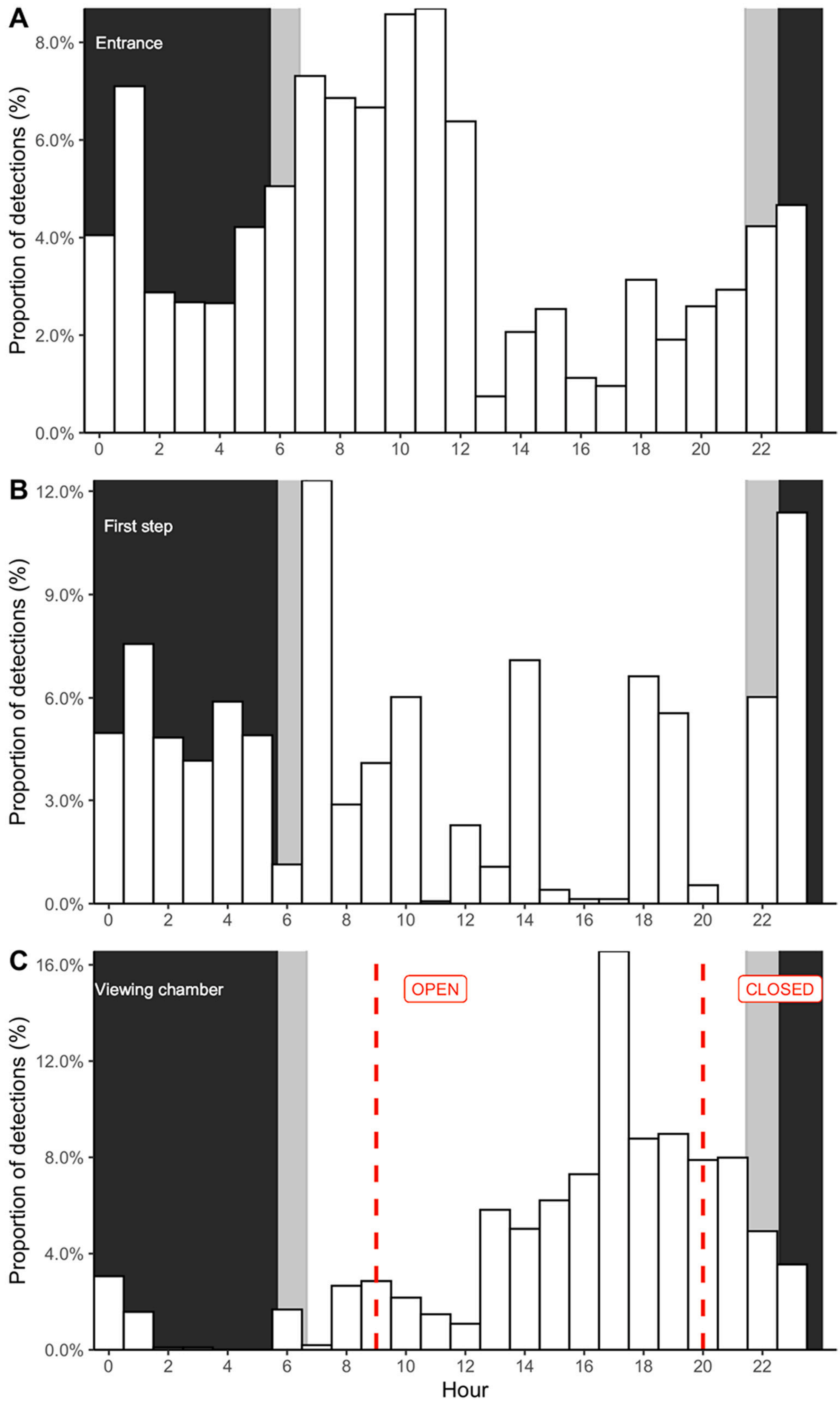

Fig. 3. Fishway use of Yukon River Chinook salmon measured as the proportion of all detections at A) the fishway entrance (n = 10,846) B) the first step of the fishway (n = 1494) and C) the fishway viewing chamber (n = 1014) over a diel period. Constant nighttime hours are shown in black while grey areas reflect the shifting sunrise and sunset times over the course of the migration. Red lines indicate the opening and closing hours for the fishway viewing chamber (9:00–20:00). Data were combined for all fish from 2017 to 2020. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

pass the viewing chamber spent more time attempting passage at the viewing chamber (50.6 [4–121] h; median = 30.9 h of n = 5) than salmon that passed the viewing chamber (18.8 [0.1–105] h; median = 1.7 h n = 11; $t = -1.59$, $P = 0.14$). Salmon that failed to pass typically also entered the chamber during daylight hours when passage should be permitted, though the upstream chamber gate can often remain closed during the day to permit counting, and adult collection for the hatchery.

3.3. Post-passage migration success

160 Chinook salmon were tagged at the viewing chamber from 2017 to 2020 (778 ± 88 mm; 22% female; 79% wild origin) to quantify upper fishway movement, post-passage migration rates, and arrival at spawning sites. Migration rates through the reservoir were 1.1 ± 0.6 km/h ($n = 22$). Migration success (>50 km travel upstream to spawning tributaries; 87.8% $n = 171$) was high for fish that successfully passed the WHP, though three of these fish terminated in Marsh Lake which is not known to support spawning, and two others appeared to stray upstream of known spawning areas. Many fish did fall back however (12.2%), after passing the fishway. Detection data indicated these salmon did not move downstream through the fishway, and it seems likely they returned downstream through the spillway vs. the turbines given they appeared to survive and that turbine intakes are blocked with racks. Only one of these fallback events occurred shortly after passage (<1 h), while most fallback events occurred after multiple days (5.7 ± 6.9 days $n = 20$) and after movement many kilometres upstream (i.e. overshoot). Upon returning downstream of the dam, 73.7% of these salmon (of $n = 19$ that fell back) were detected on a known mainstem spawning area, though only 36.8% were repeatedly detected in this area (suggestive of spawning activity). Passage was attempted for a second time by three salmon that fell back (n = 19), two of which successfully reascended the fishway, and eventually fell back a second time.

3.4. Predictors of fishway passage success, behaviour, and post-passage fate

None of fish size, relative passage date, origin, or sex tended to be significant predictors of passage success (origin not assessed), upper fishway migration rates, fallback, or duration of failed passage attempts (origin not assessed; See Table 3), the exception being that relative passage date was significantly and negatively correlated with the duration of failed passage attempts. In addition, males tended to have higher overall passage success than females (47% vs. 13%) but fell back more often after passage (17.5% vs. 2.8%). Female salmon (55.9 ± 64.2; median = 41.2 h) tended to attempt passage for longer periods than males (26.5 ± 39.8 h; median = 2.6 h) before ceasing upstream migration. Average temperature during passage events was not a significant predictor of passage success ($t = 1.86$, $P = 0.06$ $n = 35$).

3.5. Indirect evidence of overall passage success

Counts by the fishway staff from 2017 to 2020 ($n = 2415$) revealed the female proportion passing through the fishway was significantly lower than expected based on the approximately equal sex ratio observed downstream in gill nets (28.3% female; $\chi^2 = 13.6$, $P < 0.01$). This skewed sex ratio suggests female passage is 54% as successful as male passage.

The combination of telemetry data and carcass survey data resulted in a fishway passage success estimate of 31.2%. Similarly, this combined approach yielded a female passage success estimate of 12.7%.

4. Discussion

4.1. Overview

We evaluated the degree to which a pool-and-weir fishway provides functional connectivity for Chinook salmon at a hydro plant in the upper Yukon River. Passage success was low overall (31%), particularly for females (13%), though annual sample sizes were small and there is considerable and unquantified uncertainty around our estimates. Concurrent carcass surveys revealed that females failing to pass the dam still attempt to spawn, but that estimated egg retention in salmon downstream of the WHP is much greater than that of females naturally spawning in a nearby free-flowing tributary (Twardek et al., 2022). Passage estimates derived from egg retention data resulted in a similar efficiency estimate, and comparison of sex ratios downstream of and within the fishway provided further independent evidence that females are experiencing higher passage failure than males. This result is not surprising, given that female salmon invest more energy into gonads; perhaps limiting the energy available to respond to migratory challenges and increasing their likelihood of mortality relative to males (Brett, 1995; Hinch et al., 2021). Passage delays were also substantial at the WHP and many salmon fell back after passing the dam (12%). For those salmon that remained upstream of the WHP, migration success to spawning sites appeared to be high. Although this population of salmon undertakes an extraordinarily long migration prior to the fishway, our study indicates the idealistic goal of a 'transparent' fishway (Castro-Santos et al., 2009) is not being achieved. Findings from this work highlight that passage success is not always high for Pacific salmon despite strong swimming ability and migratory motivation.

4.2. Drivers of Chinook salmon passage success relative to other systems

Chinook salmon passage success at the Whitehorse Rapids Fishway was considerably lower than that observed in other studies (conducted in the Columbia River; Table 4). Similarly, the duration of passage for Chinook salmon at the Whitehorse Rapids Fishway was relatively slow (median 2.1 days) compared to median passage durations of 0.3–1.1 days for Fall run Chinook salmon at fishways on the Columbia River (that typically have greater heights; Table 4; Keefer et al., 2004). Mechanisms driving lower passage success and delays at the Whitehorse Rapids Fishway are unclear given that it has a similar design (pool-and-weir) and slope (0.05) as more effective fishways (0.06–0.10 slope in the Columbia Basin; Keefer et al., 2021; Table 4). That said, fishway design is complex (US Fish and Wildlife Service, 2019), and design differences can have pronounced effects on passage outcomes. In the Columbia River (albeit a much wider river), each fishway has at least three entrances and typically has two exits (Keefer et al., 2021), which is more likely to accommodate the range of behaviours in migrating fish. Further, each pool in the Whitehorse Rapids Fishway has a single slot to connect it to adjacent pools, whereas pools in Columbia River fishways generally have two openings. These differences would change the hydraulic conditions within each pool (Katopodis, 1992), potentially contributing to the observed increases in passage efficiency and lower passage times in the Columbia River. It is also possible that the creosote-

Table 3
Statistical outputs of models evaluating the correlation between fish size (fork length), relative passage date, origin, and sex with passage success, upper fishway migration rate, fall back, or duration of failed passage. Inferences for factors are presented relative to reference levels ("female" for sex and "hatchery" for origin. Significant effects are highlighted by bold font.

		Fish size			Relative passage date			Origin: wild			Sex: male		
Response	Model	t/z value	N	P-adj	t/z value	N	P-adj	t/z value	N	P-adj	t/z value	N	P-adj
Passage success	GLM (binomial)	0.21	35	0.89	−1.26	35	0.42	–	–	–	1.93	35	0.28
Upper fishway migration rate	ANOVA	−0.55	151	0.74	1.59	151	0.34	1.32	151	0.42	0.21	151	0.89
Fallback	GLM (binomial)	0.61	171	0.74	1.91	171	0.28	−0.01	171	0.99	1.73	171	0.28
Duration of failed passage attempt	ANOVA	0.92	18	0.62	**−5.54**	**18**	**0.01**	–	–	–	−0.87	18	0.62

Table 4
Fall-run Chinook salmon attraction, entrance, passage, and overall efficiencies at pool-and-weir fishways located at hydropower plants throughout the Columbia River Basin from 1997 to 2005 (as summarized in Keefer et al., 2021). Data from the Yukon River are provided for comparison.

Location	Rkm	Head	Attn (%)*	Ent (%)*	Pass (%)*	Overall (%)	n
Bonneville Dam	235	17	96%	98%	96%	94%	4130
The Dalles Dam	308	24	97%	98%	95%	90%	4514
John Day Dam	347	31	99%	98%	93%	92%	3592
McNary Dam	470	22	99%	100%	98%	97%	2771
Ice Harbour Dam	538	29	96%	95%	94%	87%	372
Lower Monumental Dam	589	30	100%	98%	96%	97%	277
Little Goose Dam	635	30	98%	98%	93%	94%	251
Lower Granite Dam	695	30	100%	100%	97%	97%	227
Whitehorse Hydro Plant	**2800**	**18**	**86%**	**77%**	**36%**	**31%**	**35**

* Median annual attraction, entrance, and passage efficiency estimates were extracted from Figs. S5-S7 in Keefer et al. (2021).

treated lumber used to build the Whitehorse Rapids Fishway (vs. poured concrete at most fishways) influenced passage success. It is known that harmful compounds (e.g. PAHs) leach from creosote-treated lumber into the surrounding water (Becker et al., 2001). PAH exposure can induce avoidance behaviours in salmonids (Weber et al., 1981), and more generally, chemicals can influence olfaction through disruptions of the nervous system and masking of biological cues (discussed in Johannessen and Ross, 2002).

Some Yukon River salmon failed to pass the viewing chamber located partway up the fishway. This chamber is essentially a fish trap with a slotted gate that can be lifted to allow passage, and serves as both a tourist attraction and mechanism for counting fish and obtaining hatchery broodstock. Outside opening hours, the gate remains closed and salmon are unable to pass the chamber. Approximately half of all fish reached the chamber during closed hours, and about 30% permanently abandoned further upstream migration attempts after delays in the chamber both during opening and closed hours. Transient barriers such as fish traps are common in fishways, and have been associated with delays for migratory salmonids (Clabough et al., 2014; Murauskas et al., 2014; Morrisett et al., 2019). Further, salmon that were captured in a fish trap overnight at the Lower Granite Dam were significantly less likely to arrive at spawning grounds (Morrisett et al., 2019). Delays at the viewing chamber were substantial for those Yukon River Chinook salmon failing to pass this reach; with salmon spending an average of 2 days between their first and last attempts at passing the chamber. Even when the gate was lifted during the day, Yukon River Chinook salmon appeared hesitant to pass through the relatively small opening in the upstream gate and sometimes needed chasing by means of a pole to move upstream. The presence of humans above the viewing chamber could invoke a predation response in salmon, causing delays or even downstream movement. Salmon may also be disturbed by human movement or light entry in the chamber windows (though they are reflective). Similarly, chase and capture by hatchery staff in the viewing chamber for broodstock collection could potentially result in the release of human cues into the fishway. Chinook salmon appear to avoid fishways when mammalian (including human) cues are introduced (Brett and MacKinnon, 1954; Ferguson et al., 2002). If these disturbances are severe, they could result in chemical alarm cues or stress byproducts being released by fish into the fishway, potentially affecting the behaviour of conspecifics (Bett et al., 2016). Based on the findings of our research, the Whitehorse Rapids Fishway has now made efforts to transition their current counting system to an automated camera that would allow passage throughout all hours of the day.

4.3. Intrinsic biological differences contributing to passage success

Intrinsic biological differences may contribute to relatively low passage success for upper Yukon River Chinook salmon. Exhaustion related to the extraordinary length of the migration prior to the WHP may be partly responsible for longer delays and low passage success at the fishway. While a small number of salmon migrations (those of the Upper Salmon River) involve similar 'work' (combined measure of distance and elevation gain; Bowerman et al., 2021), these populations pass their final fishway after completing ~6% of their migratory work, compared to ~75% for those passing the WHP. The observation that salmon successfully passing the fishway attempted passage for longer periods than those that failed (Supplemental Material 3), and that salmon arriving later in the season attempted passage for shorter periods, suggests that perhaps there is a motivation-related component driving passage outcomes. Further, recent evidence has found that successful fish passage may be driven by collective navigation (whereby social interactions improve an animal's ability to find their way; Okasaki et al., 2020). The sensing of conspecific pheremones is likely an important aspect of collective navigation, particularly in the absence of strong natal cues which may be difficult to follow in dam tail races where flows are complex (Bett and Hinch, 2015). Density is low at the Whitehorse Rapids Fishway compared to other systems where higher Chinook salmon passage has been observed (Table 4), potentially reducing opportunities for collective navigation.

4.4. Spawning habitat downstream of the WHP: impacts on salmon behaviour and passage estimates

Spawning grounds located 1.5 km downstream of the WHP potentially influenced the behaviour of salmon approaching the WHP and our estimate of passage success. As salmon move downstream after failed passage attempts at the Whitehorse Rapids Fishway, they may then be attracted to conspecific cues from the spawning population downstream of the WHP or effluent from the Whitehorse Rapids Fish Hatchery, located 1 km downstream of the WHP. Attraction to these sites could reduce the likelihood of salmon re-attempting passage at the fishway. For these salmon failing passage, it is known that some will spawn in this non-natal habitat with at least partial success (Twardek et al., 2022). We hypothesize there may be a tradeoff between attempting to pass the WHP to arrive at natal spawning sites vs. attempting to spawn on non-natal (potentially less suitable) habitat.

It is also possible that some salmon that approached and entered the fishway simply 'over shot' downstream spawning grounds and that the fishway acted as a partial 'ecological trap' (ie. the fishway attracted salmon to move upstream to the reservoir, though the dam limited movement back downstream to natal habitat; Pelicice and Agostinho, 2008). Overshoot tends to be more likely when upstream dams are in close proximity to downstream spawning habitat (Keefer et al., 2008). In the Yukon River, downstream habitat is much closer to the WHP than on many of the dams studied on the Columbia River (Keefer et al., 2008), increasing the likelihood that salmon with natal habitat downstream could have comprised some of the tagged salmon approaching the fishway that then failed to pass. However, abnormally high levels of egg retention in female salmon downstream of the WHP suggests overshoot towards and into the fishway by salmon spawning downstream was uncommon and did not have a large influence on our passage estimate (See Supplemental Material 2). Although we did not confirm that the specific fish that failed to pass also failed to spawn, our estimate of passage failure is equivalent to what would be expected based on the higher egg retention rates observed in salmon downstream of the WHP compared to other spawning populations on nearby free-flowing rivers. The close alignment of passage failure estimates based on carcass data and telemetry data further suggest that the capture and tagging of individuals had minimal influence on our passage estimate.

4.5. Post-passage fate

Salmon that passed the fishway were generally successful in completing migration to spawning grounds despite moderate passage delays (median of 2.1 days; See (Twardek et al., 2022) for more details on migratory behaviour following passage). During non-fishway migration, upper Yukon River Chinook salmon would have travelled 80 km upstream in that amount of time. Fishway passage is energetically costly particularly because high-flow areas often require individuals to undertake anaerobic (inefficient) burst-swimming (Burnett et al., 2014b; Brown et al., 2006). Further, repeated attempts at passage (i.e., salmon moving downstream in the fishway) would have increased the energy expended by migrating Yukon River salmon. Fish passage can result in substantial delayed en route mortality (Caudill et al., 2007), but we did not observe this for Yukon River Chinook salmon. Fish passage can also reduce energy available to spawn and potentially spawning success (Geist et al., 2000; Mesa and Magie, 2006); however, we did not evaluate this in our study.

Rates of fallback after passing the hydropower plant were high (12%), consistent with studies in preceding decades on this population (Cleugh and Russell, 1980; Matthews, 1999). Migrating fish are positively rheotactic (face oncoming current) and can be attracted to the water passing through a spillway upon entering reservoirs if fishway exits are inappropriately located (discussed in Boggs et al., 2004). Fallback may also occur if fish are exhausted upon exiting the fishway; however, all but one of the fallback events that we observed were delayed and occurred after fish had spent an average of 5.5 days upstream (often after traveling dozens of kilometres). Fallback may also result for fish that ‘overshoot’ downstream spawning grounds (Ricker, 1972). In the Columbia River basin, overshoot beyond natal tributaries averaged 15% for Chinook salmon populations, and typically lasted <5 days (Keefer et al., 2008). In 1997 and 1998, delayed fall back (>24 h) occurred for 8% of Pacific Salmon passing Bonneville Dam (Reischel and Bjornn, 2003). It is believed overshoot may be related to orientation difficulties, the following of conspecifics, or the finding of thermal refugia (discussed in Keefer et al., 2008), though the factors driving this behaviour in Yukon River Chinook salmon are unclear. Rates of fall back at the WHP were nearly identical for hatchery and wild salmon despite evidence that straying and downstream movement are generally more common in hatchery Chinook salmon (Quinn, 1993; Keefer et al., 2004). After falling back, Yukon River Chinook salmon often visited the nearest spawning habitat located 1.5 km downstream of the WHP, though several moved well beyond this location including two who travelled 22 km downstream then >87 km up the Takhini River. No hatchery salmon are stocked on this downstream spawning habitat, so their movements downstream cannot be explained by overshoot of natal spawning grounds, while this explanation is possible for wild salmon. Regardless of the mechanism, fallback through spillways can lead to injuries such as bruising or immediate or delayed mortality (Wagner and Hilsen, 1992; Bjornn et al., 1998). All tagged salmon that moved back, presumably through the spillway, appeared to survive the event based on their detection patterns downstream of the WHP. It is unclear whether these fish suffered injuries, or whether they spawned successfully downstream of the dam.

4.6. Reflections on the approach

Fish passage assessments can be complex given the vast array of behaviours individual fish may undertake at various scales and locations. Over four years, we were able to adapt our experimental approach, based upon knowledge gained on salmon behaviour from prior years of study. This multi-year approach may delay the application of study findings, but is a more robust means of accounting for inter-annual differences in passage outcomes. This approach was not only preferred, but necessary when working with a population of such low abundance (200–1000 adults/year). The inclusion of fish on the Takhini River allowed us to control for natural enroute mortality and impacts of capture and handling on migratory success. Control groups on a suitable free-flowing river are rarely included in passage studies, likely due to the lack of suitable control rivers and cost of additional tagging and receiver deployment (Cooke and Hinch, 2013). Our inclusion of a control group is beneficial, though we recognize that a before-after control-impact design is needed to account for natural rates of passage failure that may have been present prior to the construction of the hydropower facility (e.g. rapids or canyons compromising passage). Our study also highlighted the importance of monitoring fish movement prior to approaching hydropower facilities. For instance, had we assigned fish as attempting passage upon moving within 1.5 km of the dam, rather than once they entered the tail race (within 500 m of the dam), we would have substantially underestimated passage performance (because there is spawning habitat in this reach where salmon terminated without attempting passage).

5. Conclusions

Fishway passage is complex necessitating the integration of many different disciplines to build and operate effective fishways (Silva et al., 2018). While it is impossible to elucidate all the factors governing passage success, every fishway evaluation acts as a natural experiment to help reveal the key factors resulting in passage success or failure (Castro-Santos and Haro, 2010). Here, we evaluated the passage success of Chinook salmon at a pool-and-weir fishway after a long-distance migration. Although there are no quantitative fish passage goals for the fishway, passage was low (~31% overall). Elsewhere, idealistic fishway targets of complete ‘transparency’ or ‘90% passage’ have been suggested (see Lucas and Baras, 2001; Castro-Santos et al., 2009) which were clearly not achieved here. Given the imperiled status of this salmon run, higher levels of passage success would presumably be of conservation benefit. Implementing a fishway design like those of the Columbia River (Keefer et al., 2021) may lead to fish passage improvements, though the extreme length of the migration prior to the WHP may still compromise passage success. Our work also found that a fish trap within the fishway impeded passage and we suggest that care be taken to ensure similar facilities at other fishways are designed and operated such that they do not hinder passage. Further work is needed to understand whether the level of passage failure that appears to occur here has population-level consequences and the extent to which it may constrain recovery of this population. It is our hope that this research will help inform fish passage decision-making and science at a broad scale, and management of the iconic upper Yukon River Chinook salmon.

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CRediT authorship contribution statement

W.M. Twardek: Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition, Project administration. **S.J. Cooke:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition, Supervision. **N.W.R. Lapointe:** Conceptualization, Methodology, Investigation, Writing – review & editing, Funding acquisition, Project administration, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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