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High egg retention in Chinook Salmon *Oncorhynchus tshawytscha* carcasses sampled downstream of a migratory barrier

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Abstract

Barriers in rivers have the potential to severely decrease functional connectivity between habitats. Failure to pass barriers and reach natal spawning habitat may compromise individual reproductive success, particularly for semelparous, philopatric species that rely on free-flowing rivers to reach natal habitat during their once-in-a-lifetime spawning migrations. To investigate the consequences of in-river barriers on fish spawning success, we quantified egg retention and spawning effort (caudal fin wear) in female Chinook Salmon *Oncorhynchus tshawytscha* carcasses collected downstream of the Whitehorse Hydro Plant on the upper Yukon River and at a nearby free-flowing tributary (Teslin River) from 2018 to 2020 (~2900 km migrations). Previous studies have demonstrated that a large proportion of fish attempting to reach spawning locations upstream of the hydro plant fail to pass the associated fishway. We estimated nearly all female salmon failing to pass the hydro plant attempted spawning in non-natal habitat downstream, but that these females retained ~34% of their total fecundity compared to ~6% in females from the free-flowing river. Females downstream of the hydro plant also had lower wear on their caudal fin, a characteristic that was correlated with increased egg deposition. Egg retention did not vary across years with different run sizes, and we propose that egg retention downstream of the hydro plant was not driven by density-dependent mechanisms. Findings from this work indicate that female Chinook Salmon can still deposit eggs following failed fish passage and failure to reach natal spawning sites, though egg retention rates are considerably higher and uncertainties remain about reproductive success. We encourage researchers to incorporate carcass surveys into fish passage evaluations for semelparous species to fully account for consequences of failed passage.

KEYWORDS
fish passage, fitness, hydropower, Pacific salmon, spawning success, Yukon River

1 | INTRODUCTION

Salmon spawning migrations constitute some of the most iconic and challenging animal movements on Earth. These migrations often entail long-distance upstream travel that requires bouts of routine (aerobic) and burst (anaerobic) swimming that deplete energy stores and consume aerobic scope (Brett, 1995, Hinch *et al.*, 2002). Both of these scenarios can reduce the capacity for salmon to overcome the challenges of migration, potentially resulting in en route or pre-spawn mortality and complete loss of lifetime reproductive fitness (Bowerman *et al*., 2016). En route and pre-spawn mortality are natural phenomena affecting Pacific salmon *spp*. and may even occur in the absence of additional stressors or challenges (Bowerman *et al*., 2021). For instance, high densities of salmon on spawning grounds can force salmon to compete for mates and spawning habitat, causing some salmon to die without successfully reproducing (Quinn *et al*., 2007). Despite such challenges, salmon typically have high migration and reproductive success. Populations facing additional stressors tend to have the greatest mortality rates (Bowerman *et al*., 2021). These additional threats include warm water temperatures, disease, habitat loss and degradation, fishing encounters, predators, and barriers, among other factors affecting migration and spawning (Hoekstra *et al*., 2007; Miller *et al*., 2014; Schoen *et al*., 2017; Wargo Rub *et al*., 2019). One of the greatest threats to salmon reproduction is the construction of anthropogenic barriers (*e.g*., hydropower dams, water control structures, weirs) that fragment riverine ecosystems and can prevent salmon from reaching natal spawning habitat (Liermann *et al*., 2012).

Fish passage remediation describes human efforts to restore functional connectivity at barriers by facilitating fish movement both up and downstream (Clay, 1995). Fish passage remediation most often involves creating a structure (*i.e*., fishway; Katopodis & Williams, 2012) that provides an alternative route past the barrier. The ideal goal of a fishway is to be 'transparent' and allow all fish to move beyond the barrier without additional delays relative to the pre-barrier condition (Castro-Santos & Haro, 2010). Fishway transparency is rarely achieved, and it is common for a portion of fish to fail to pass these structures (*e.g*., because they cannot find or swim through them; Noonan *et al*., 2012). Failed passage may have severe reproductive impacts on fish, particularly Pacific salmon which are both semelparous and philopatric (Groot & Margolis, 1991). Fish passage can be energetically costly because salmon must navigate high-velocity areas below and within fishways (Burnett *et al*., 2014). As salmon approach death, there may be a fitness benefit to abandoning upstream migration to natal habitat to instead attempt spawning on non-natal habitat (discussed in Turcotte & Shrimpton, 2020). It seems likely that this behavioural flexibility (*i.e*., ability to stray) would be maintained in salmon populations whose habitat changes dynamically in response to natural and anthropogenic disturbances (Hamann & Kennedy, 2012; Liermann *et al*., 2017; Yeakel *et al*., 2018). If spawning locations were fixed, populations would be rapidly extirpated if habitat became inaccessible or unsuitable, and recolonization would be unlikely. It is unclear to what extent salmon that fail to pass barriers can successfully spawn, though this likely depends on them having behavioural plasticity in spawning site choice, having sufficient energy to spawn, and on the availability of suitable spawning habitat and potential mates downstream.

Spawning is an energetically costly process for female salmon as they often dig multiple nests and hold position in the river for long periods of time (Healey *et al*., 2003). Although the actual process of depositing eggs lasts just a few seconds, females generally deposit eggs over multiple spawning events, with successive events typically separated by several hours (or even days; Berejikian *et al*., 2000, 2007). If salmon do not have sufficient energy to complete multiple spawning events, or are unable to find suitable conditions to spawn, they may retain part or all of their fecundity, compromising their lifetime reproductive fitness (Groot & Margolis, 1991). Furthermore, high spawning ground density can increase competition for habitat, elevating egg retention rates in the female population (Quinn *et al*., 2007). Carcass surveys are a useful tool for quantifying egg retention and have been used extensively across the range of Pacific salmon (Bowerman *et al*., 2016). These studies have demonstrated that egg retention is generally low across Pacific salmon populations, though various environmental stressors and fish characteristics (*e.g*., size) can influence egg retention (Bowerman *et al*., 2021). Barriers preventing salmon from reaching natal spawning habitat are likely to increase egg retention, though few studies have actually explored this hypothesis by quantifying egg retention in salmon downstream of barriers. Knowledge of where salmon intend to spawn (*i.e*., natal habitat) can be particularly insightful in contextualizing the impacts of barriers on salmon spawning success. Thus, carcass surveys on fish of hatchery origin can be highly useful as release locations (and therefore natal spawning sites) are known.

Chinook Salmon *Oncorhynchus tshawytscha* (Walbaum 1792) migrating to the headwaters of the Yukon and Teslin rivers complete the longest inland salmon migrations on Earth, at ~3000 km. The upper Yukon River population returning through Whitehorse was once said to support harvest of ~10,000 fish per year, though over the last six decades ~950 fish have returned annually and in recent years ~250 fish (Cox, 1997; Joint Technical Committee of the Yukon River U.S./Canada Panel, 2021). Since 1958, most *O. tshawytscha* migrating through the upper Yukon River have faced the additional challenge of passing the Whitehorse Hydro Plant (WHP) *via* the Whitehorse Rapids Fish Ladder, just 100 km downstream of natal spawning areas. Most salmon attempting passage do not successfully pass the hydro plant after multiple days of attempting to do so and instead terminate downstream of the WHP (Twardek *et al*., 2021). Spawning habitat exists in this area (Access Consulting Group and Yukon Environmental Services, 2002) making it possible for salmon that fail to pass to potentially reproduce downstream of the WHP. Furthermore, some salmon appear to return to this habitat without ever attempting passage at the fishway (*i.e*., natal spawners; Twardek *et al*., 2021). The objective of this study was to evaluate the influence that failed fish passage at a major physical barrier has on spawning success. Given the extraordinary length of this migration it is possible that egg retention may be naturally higher in these fish relative to most other populations. Therefore, we also quantified indicators of spawning success in female salmon from nearby free-flowing rivers, hypothesizing that female salmon terminating downstream of the hydro plant would have lower indicators of spawning success. We also hypothesized that hatchery fish would have higher egg retention downstream of the barrier than wild salmon, given that hatchery salmon found at this location were released at upstream natal spawning sites and were expected to imprint there, whereas wild salmon that terminate downstream of the barrier are a mix of natal spawners and fish that failed to pass the ladder. While our study was not designed to gain insights into the mechanisms behind egg retention at each location, we evaluated the relationships between run year and run timing on indicators of spawning success to investigate whether density-dependent mechanisms were likely contributing to spawning success. Under this hypothesis, it was predicted that egg retention would be highest during years and periods of the run when salmon density was highest.

2 | MATERIALS AND METHODS

2.1 | Study site and survey methods

Carcass surveys were conducted to collect and sample *O. tshawytscha* carcasses downstream of the Whitehorse Hydro Plant in the Yukon River (2841 km from the Bering Sea) and on spawning grounds downstream of Johnson's Crossing in the free-flowing Teslin River (2868 km from the Bering Sea). The Yukon River passes through relatively undisturbed landscapes in Yukon and Alaska, and remains free-flowing downstream of the WHP. The WHP is the main energy source in the Yukon (producing 40 MW) but presents a barrier to salmon movement in both up- and downstream directions. To reach the primary spawning grounds upstream of Whitehorse, YT (Michie Creek, 2946 km from the Bering Sea), salmon must circumvent the WHP *via* the Whitehorse Rapids Fish Ladder, a 366 m-long wooden pool and weir fishway, rising 18 m to the reservoir upstream. Adult salmon are collected from this fish ladder as broodstock to support hatchery production and release of juvenile salmon in spawning sites upstream of the WHP. Hatchery operations have been ongoing since 1988 as a means of compensating for construction of a fourth turbine, contributing to juvenile salmon mortality during downstream migration. Hatchery salmon comprise approximately 50% of the return each year, though the proportion of hatchery salmon returning was much lower during the years of this study (Joint Technical Committee of the Yukon River U.S./Canada Panel, 2021). In contrast, the Teslin River is a free-flowing river branching off the Yukon River 2704 km from the Bering Sea and has no hatchery program.

Surveys occurred during and after the spawning migrations of *O. tshawytscha* each August from 2018 to 2020. Survey frequency in the Yukon River varied across years but occurred at least once every 4 days, with an average of one survey every 1.7 days (a total of 46 survey days across all years). Surveys began before the first carcasses appeared (~3 weeks after the first fish arrived at the Whitehorse Rapids Fish Ladder viewing chamber) and ceased 4 weeks later when carcass deposition became infrequent (see Supporting Information Table S1 for details on annual survey dates and locations). Surveys comprised several locations in each river (Figure 1). In the Yukon River, all sites were between 1.3 and 8.0 km downstream of the hydro plant. Sections of the river that were too deep to detect and retrieve carcasses from were not surveyed. Similarly, fast sections of river that were not likely to retain carcasses were only surveyed once each year. After repeatedly locating carcasses in distinct locations along the river, we restricted our surveys to established sites (Figure 1). These locations generally corresponded to the deposition sites identified in previous carcass surveys near Whitehorse, YT (Sebes & Lapointe, 2017;

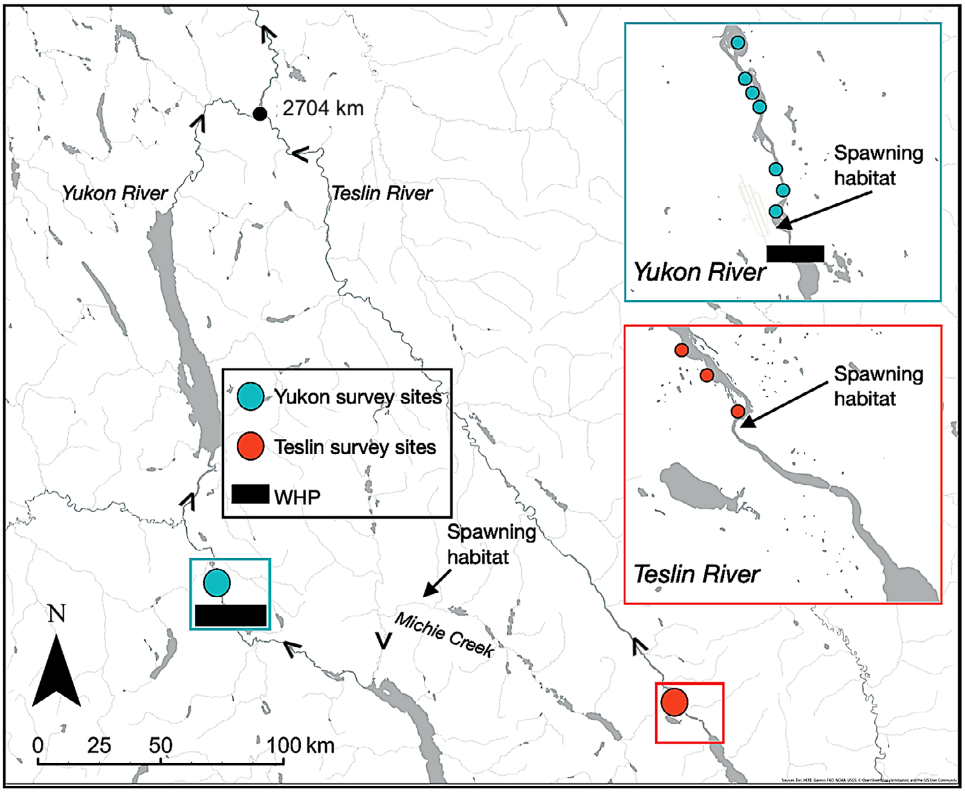

FIGURE 1 Map of the Yukon River watershed upstream of the confluence of the Yukon and Teslin rivers (2704 km from the Bering Sea). Carcass surveys for *Oncorhynchus tshawytscha* were completed in the Yukon River downstream of the Whitehorse Hydro Plant (WHP, blue) and in the free-flowing Teslin River (red) from 2018 to 2020. Major spawning sites are shown for each river, including the primary spawning tributary upstream of the hydro plant (Michie Creek). Most salmon passing the WHP return to natal spawning habitat in Michie Creek (~100 km upstream of the hydro plant)

von Finster, 2005) although additional locations were added. Carcasses collected from the Yukon River comprised fish that spawned there natally and those that failed to pass the WHP and arrive at intended spawning sites upstream. Though we do not have individual movement histories to relate egg retention data to migratory behaviour, we rely on the findings of a concurrent telemetry project (*i.e.*, Twardek *et al*., 2021) to estimate the proportion of our sample downstream of the WHP that was likely to have failed passage. In the Teslin River, surveys were completed approximately 12–13 km downstream of Teslin Lake, YT. Surveys were completed in the Teslin River in 2019 and 2020, with three surveys occurring in the river each year. August water temperatures were collected at the WHP *via* HOBO logger each year (De Graff 2020).

2.2 | Carcass sampling

Female carcasses were sampled on site following the Yukon River protocol for carcass/pre-spawning mortality data (Yukon River Panel, unpub. data). Carcasses were photographed, and sex, fork length, and mid-eye fork length were recorded to the nearest centimetre. Fish were weighed to the nearest 10 g using a digital hanging scale. Fish were classified as having completely spawned, partially spawned, or experienced pre-spawn mortality (as per Quinn *et al*., 2007; see Figure 2). Complete spawning was assigned to fish that had fewer than 100 eggs retained in their body cavity, whereas pre-spawn mortality was assigned to fish with completely intact egg skeins or with loose eggs overflowing from the body cavity on initial dissection. These pre-spawn mortality designations were later corroborated with a length-based fecundity model derived from broodstock fish collected at the Whitehorse Rapids Fish Hatchery (described below). The volume and weight of eggs were quantified using a measuring cup (nearest 25 ml) and hanging scale (nearest 10 g), respectively. A subset of 50 eggs was measured in a 50 ml graduated cylinder to volumetrically estimate the total number of eggs retained [total eggs = 50 eggs × (total egg volume/50 egg volume)]. We refer to egg deposition and retention rather than spawning success given that the site of egg deposition and extent of hatching success are unknown. We assume throughout that higher egg retention is associated with poorer fitness outcomes. Furthermore, our estimate of egg retention in both rivers is inherently an underestimate given that salmon carcasses could have lost eggs through the oviduct while tumbling downstream (although egg loss during carcass retrieval was not frequently observed).

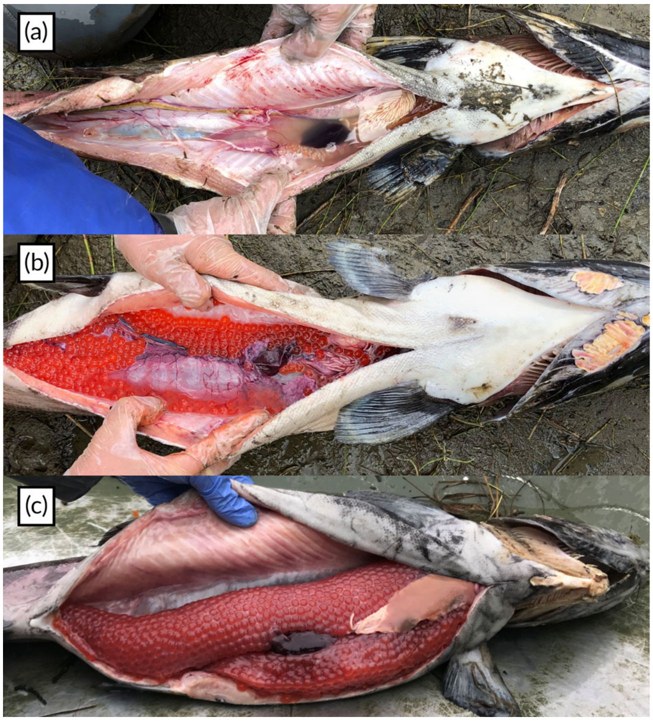

FIGURE 2 Female *Oncorhynchus tshawytscha* carcasses from the upper Yukon River and Teslin River classified as having (a) completely spawned, (b) partially spawned, or (c) experienced pre-spawn mortality

We hypothesized that it was possible some eggs were expelled from the body cavity of female salmon without successfully building a redd or while drifting downstream as a carcass. To evaluate whether egg deposition was associated with spawning effort, we classified the condition of each female's caudal fin, which wears away as they dig redds and protect offspring (Bowerman *et al*., 2016; Burner, 1951). The degree of wear on the caudal fin was scored from photographs on a scale of 1–8 as follows: (1) no fin wear, (2) wear on the edges of the fin, (3) fin worn beyond the edges but not worn completely, (4) fin completely worn, (5) fin completely worn and 25% of the caudal peduncle worn between the caudal and adipose fin, (6) fin completely worn and 50% of the caudal peduncle worn between the caudal and adipose fin, (7) fin completely worn and 75% of the caudal peduncle worn between the caudal and adipose fin, and (8) fin completely worn and 100% of the caudal peduncle worn between the caudal and adipose fin.

2.3 | Ethical statement

The care and use of experimental animals complied with the Canadian Council on Animal Care animal welfare laws, guidelines, and policies as approved by Carleton University under permit 'Cooke Umbrella Tagging'. It is noteworthy that we did not work with live fish, given that salmon are semelparous (die after spawning) and all fish were sampled after completion of their lifecycle.

2.4 | Statistical analyses

To test the hypothesis that spawning success differed between the two rivers, we compared complete spawning rates (proportion of the female population spawning completely) and retained gonadosomatic index (GSI) between Yukon and Teslin river females, and conducted a literature search to find complete-spawning rates for other nearby populations. Retained GSI was calculated as the quotient of retained egg mass divided by fish mass (*i.e.*, soma mass, excluding egg mass).

To estimate the percentage of total fecundity retained within each female (ER_T), we first predicted fecundity for each carcass using a length-based fecundity model developed from broodstock females collected at the Whitehorse Rapids Fish Hatchery from 2018 to 2020. The relationship between length and fecundity was assessed using linear regression. Percentage egg retention was then calculated as the quotient of the number of eggs retained in the body cavity, divided by the total estimated fecundity (as per Cook *et al*., 2011; McConnachie *et al*., 2012; Raby *et al*., 2013). We then estimated the degree of egg retention (% of total fecundity) in the subset of salmon failing to pass the Whitehorse Rapids Fish Ladder in the Yukon River (ER_{FS}; Equation 1). We relied on the assumption that the egg retention rate of natal spawning female *O. tshawytscha* in the Yukon River was equal to that of natal spawning females in the Teslin River (*i.e*., ER_{NS}; 6.3%). We assigned P_{NS} (44%) and P_{FS} (56%) of all carcasses collected downstream of the WHP using concurrent telemetry data that assigned a fish as natal if it did not attempt to pass the WHP (Twardek & Lapointe, 2021). We then solved for ER_{FS} and the same process was undertaken to estimate the proportion of failed passage salmon that spawned completely in the Yukon River.

$$ER_T = P_{NS} \times ER_{NS} + P_{FS} \times ER_{FS}$$

$$21.6\% = 44\% \times 6.3\% + 56\% \times ER_{FS} \qquad (1)$$

where ER_T is the total observed egg retention in females downstream of the WHP (calculated from our carcass survey data and the length-based fecundity model), P_{NS} is the proportion of natal salmon in the population downstream of the WHP, ER_{NS} is the natal salmon egg retention rate downstream of the WHP (% of total fecundity), P_{FS} is the proportion of failed passage salmon in the population downstream of the WHP and ER_{FS} is the failed passage salmon egg retention rate downstream of the WHP (% of total fecundity).

The egg retention rate for hatchery salmon from the Yukon River was presented separately from that of wild fish, given that these fish have known terminal locations upstream and are all assumed to have failed passage. As a final assessment of the hypothesis that spawning success differs between rivers, we compared differences in caudal fin wear (*i.e*., spawning effort) between females from each river. To evaluate the correlation between caudal fin wear and egg retention (and the potential usefulness of fin wear as a future indicator of egg retention), we conducted separate Spearman's rank correlations between caudal fin wear and retained GSI for salmon from each river. To evaluate whether differences in habitat contribute to differences in caudal fin wear between the two rivers, we compared caudal fin wear for the subset of fish that spawned completely from both rivers.

To evaluate whether interannual differences (in environmental and migratory conditions) influenced egg retention, we conducted a Kruskal–Wallis test using year as a predictor of retained GSI. To explore whether density-dependent factors influence egg retention, the relationship between retained GSI and relative carcass collection date was assessed using a generalized additive model (because we did not predict a linear relationship). Only Yukon River *O. tshawytscha* were included in this model given the limited sampling dates for the remotely located Teslin River. Relative collection date was used as a proxy for run density, given that the salmon return tends to follow a bell-shaped curve (Lawrence Vano, pers. comm., Whitehorse Rapids Fish Hatchery). Relative collection date was calculated as the date of carcass collection relative to the first and last carcass found that year in each river. The degree of accuracy of this metric is dependent on how long after mortality we found each carcass, which remains unknown. To evaluate whether fish size influenced egg retention, we evaluated the Spearman's rank correlation between retained GSI and fish mass.

All statistical analyses were completed in R statistical software (R Core Team, 2020) and statistical significance was considered at an alpha level of 0.05. A small number of missing egg retention observations ($n=3$ fish) were imputed using the mean egg retention value for fish with similar characteristics. For instance, when egg mass was not recorded, an average egg mass was calculated based on the egg mass for fish with similar egg volumes. Model assumptions were assessed through visual examination of diagnostic plots of residuals. Differences in various biotic and environmental variables, including fork length (ANOVA), sex proportions (chi-square), and origin proportions (chi-square), were compared among years at each location. There were no significant differences in these variables between years at each location, so data from all years were pooled for analyses. Summary statistics are presented when comparing egg retention and tail wear for females from the two rivers. Inferential tests were avoided when comparing these metrics between rivers as our study lacked true replication of our treatment across sites (*i.e*., pseudoreplication; Hurlbert 1984). One exception was the comparison of retained GSI (relative to fish mass), given the influence mass had on this metric. Retained GSI was not normally distributed (zero-inflated) and was compared between sites using a Kruskal–Wallis rank sum test.

3 | RESULTS

During surveys from 2018 to 2020, 144 carcasses were sampled from the Yukon River and 105 from the Teslin River. Carcasses from the Yukon River were primarily female (90%) and females were typically of wild origin (85%, 825 ± 53 mm fork length). Most fish sampled from the Teslin River were female (83%) and all were of wild origin (902 ± 53 mm fork length). Neither the size, proportion of females, nor proportion of wild fish varied significantly among years at a location (all $P > 0.05$). Mean August water temperature in the Yukon River varied from 14.3 to 15.7°C across years, with mean daily temperature varying from 12.4 to 18.2°C. The run enumerated at the Whitehorse Rapids Fish Ladder viewing chamber was low in 2018 (691 fish), 2019 (282 fish), and 2020 (216 fish) relative to the 60-year average of 950 individuals (Joint Technical Committee of the Yukon River U.S./Canada Panel, 2021). The average fecundity of female *O. tshawytscha* at the hatchery was 5047 eggs (2086–7661 eggs,

$n = 114$) from 2018 to 2020, and was lowest in 2019 (4578 ± 1086 eggs) and highest in 2020 (5592 ± 1150 eggs). Fork length of individual salmon explained about half of the variation in fecundity across female salmon at the hatchery ($R^2 = 0.48$, DF = 112, $P < 0.01$).

3.1 | Egg retention

The proportion of salmon spawning completely was considerably lower in the Yukon River (33%) compared to the Teslin River (78%; $n = 249$).

TABLE 1 A summary of *Oncorhynchus tshawytscha* carcass survey data from downstream of the WHP on the Yukon River and from various free-flowing tributaries of the Yukon River watershed

Location	Migration distance (km)	Year	Female sample	Spawned completely	Spawned completely (%)	Complete spawn criteria	Method	Reference
Yukon River downstream of the WHP								
Yukon River downstream of the WHP	2840	2020	22	9	41%	<100 eggs	Count	Present study
Yukon River downstream of the WHP	2840	2019	43	15	35%	<100 eggs	Count	Present study
Yukon River downstream of the WHP	2840	2018	79	23	29%	<100 eggs	Count	Present study
Yukon River downstream of the WHP	2840	2005	14	7	50%	'none OR almost all of their eggs'	Visual	von Finster, 2005
Total/average	**2840**	**2005–2020**	**158**	**34%**	**90%**	—		
Nearby free-flowing rivers								
Teslin River, YT	2893	2020	28	23	82%	<100 eggs	Count	Present study
Teslin River, YT	2893	2019	77	59	77%	<100 eggs	Count	Present study
Teslin River, YT	2783–2893	2015	347	337	97%	<5% of eggs	Visual	Mercer, 2015
Teslin River, YT	2783–2893	2014	304	292	96%	<5% of eggs	Visual	Mercer, 2015
Big Salmon River, YT	2654–2799	2017	44	28	64%	<5% of eggs	Visual	Mercer & Wilson, 2018
Big Salmon River, YT	2654–2799	2016	73	70	96%	<5% of eggs	Visual	Mercer & Wilson, 2017
Big Salmon River, YT	2654–2799	2015	81	76	94%	<5% of eggs	Visual	Mercer & Wilson, 2016
Big Salmon River, YT	2654–2799	2014	69	66	96%	<5% of eggs	Visual	Mercer & Wilson, 2015
Mayo River, YT	2489	2011	8	8	100%	<1% of eggs	Visual	Wilson, 2011
Little Kalzas River, YT	~2640	2011	10	9	90%	<1% of eggs	Visual	White Mountain Environmental Consulting, 2011
South McQuesten River, YT	2511	2011	33	33	100%	<1% of eggs	Visual	Can-Nic-a-Nick Environmental Sciences, 2011
M'Clintock River, YT[a]	2921	2005	8	8	100%	<1% of eggs	Visual	De Graff, unpub data
Michie Creek, YT[a]	2946	2005	11	11	100%	<1% of eggs	Visual	De Graff, unpub data
Salcha River, AK	1553–1753	2015	224	202	90%	<1% of eggs	Visual	Stark, 2016
Salcha River, AK	1553–1753	2005	311	258	83%	<10% of eggs	Visual	Hamazaki *et al*., 2013
Salcha River, AK	1553–1753	2006	111	94	85%	<10% of eggs	Visual	Hamazaki *et al*., 2013
Chena River, AK	1544–1744	2005	147	125	85%	<10% of eggs	Visual	Hamazaki *et al*., 2013
Chena River, AK	1544–1744	2006	84	70	83%	<10% of eggs	Visual	Hamazaki *et al*., 2013
Total/Average	**1544–2886**	**2005–2020**	**1970**	**90%**	**55%**	—		

Note: Migration distances to each confluence were determined using Brown *et al*. (2017) and individual study references. The total/average values from downstream of the WHP and on nearby free-flowing rivers are shown in bold.

[a] Upstream of the Whitehorse Hydro Plant.

Relative to other nearby spawning populations in the Yukon River watershed, the rate of complete spawning in fish sampled downstream of the WHP was low (Table 1). Three fish were assigned as having retained all their eggs in the Yukon River, compared to two in the Teslin River. Retained GSI in females downstream of the hydro plant in the Yukon River was approximately five times higher than retained GSI in the free-flowing Teslin River ($n = 242$; Figure 3). Retained GSI was significantly and negatively correlated with fish mass ($N = 205$, $S = 2,294,173$, $P < 0.01$), which was higher in the Teslin River (5322 ± 1422 g) than the Yukon River (3421 ± 950 g). However, retained GSI remained highly and significantly different between the two locations when controlling for fish mass ($n = 205$, $\chi^2 = 38.89$, $P < 0.01$). Using our fecundity model, we estimated that egg retention corresponded to 21.6% of total fecundity in female salmon from the Yukon River compared to 6.3% of total fecundity for females from the Teslin River. Under the assumption that natal spawning Yukon River *O. tshawytscha* females have the same egg retention (% of total fecundity) as natal spawning Teslin River *O. tshawytscha* females, it can be estimated that failed passage female salmon have a 0% complete spawning rate and retain 33.6% of their estimated fecundity. Hatchery females ($n = 21$) with known release sites upstream of the WHP (thus presumably failed passage spawners) retained an estimated 36.3% of total fecundity and 14% spawned completely. One telemetry tagged female salmon was recovered after attempting passage for ~50 h before returning downstream and retained an estimated 16% of its eggs.

3.2 | Spawning effort

Female salmon carcasses from the Teslin River had greater caudal fin wear (score of 7.4 ± 1.2, $n = 67$) than female salmon from the Yukon River (score of 5.4 ± 2.1, $n = 102$). Females with greater caudal fin wear had significantly lower rates of egg retention in the Yukon River ($n = 102$, $\rho = -0.44$, $S = 253,818$, $P < 0.01$) but not in the Teslin River ($n = 67$, $\rho = -0.13$, $S = 56,640$, $P = 0.29$; Figure 4). Among

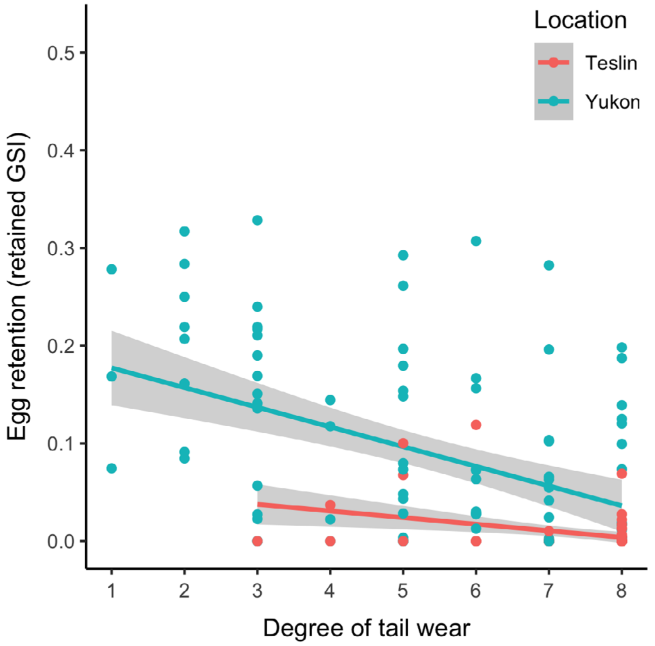

FIGURE 4 The linear relationship between egg retention (retained GSI) and degree of tail wear (indicative of spawning effort) for female *Oncorhynchus tshawytscha* carcasses sampled from the upper Yukon River downstream of the Whitehorse Hydro Plant (blue, $y = -0.020143x + 0.197368$) and the Teslin River (red, $y = -0.006761x + 0.057894$) from 2018 to 2020

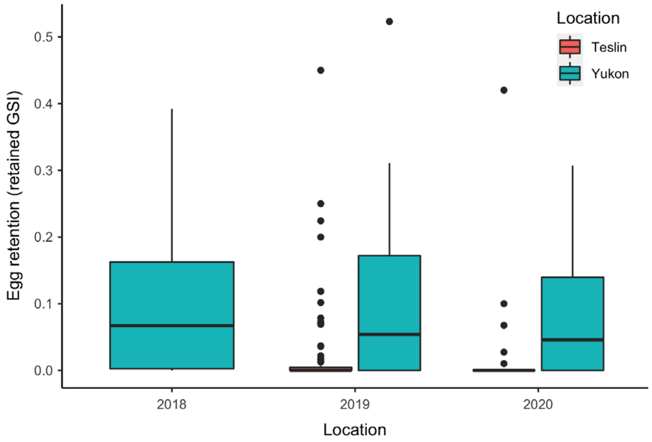

FIGURE 3 Boxplots depicting egg retention of *Oncorhynchus tshawytscha* sampled in the Yukon River downstream of the Whitehorse Hydro Plant (blue) in 2018 ($n = 72$), 2019 ($n = 43$) and 2020 ($n = 22$) and in the Teslin River (red) in 2019 ($n = 77$) and 2020 ($n = 28$). Egg retention was calculated as the mass of eggs remaining in the body cavity relative to the mass of the carcass (*i.e.*, retained gonadosomatic index)

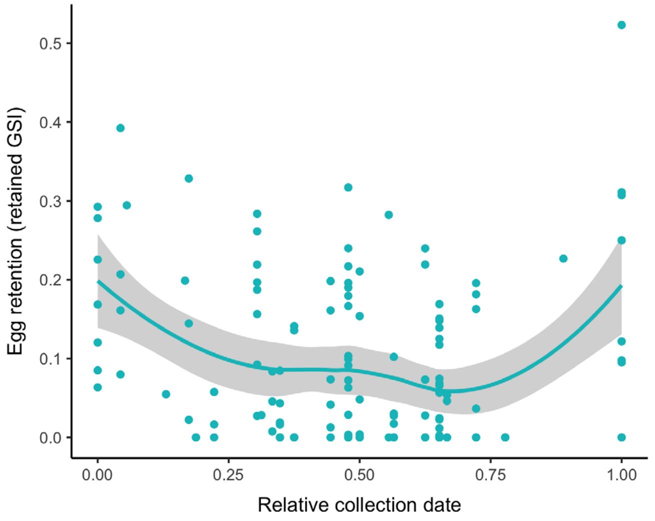

FIGURE 5 The smoothed relationship between egg retention (retained GSI) and relative collection date for female *Oncorhynchus tshawytscha* carcasses sampled from the upper Yukon River downstream of the Whitehorse Hydro Plant from 2018 to 2020 ($R^2 = 0.15$)

completely spawned females in both rivers, tail wear tended to be higher for those in the Teslin River (score of 7.5 ± 1.1, $n = 55$) compared to the Yukon River (score of 6.4 ± 1.7, $n = 34$).

3.3 | Other correlates of egg retention

Retained GSI in female *O. tshawytscha* was similar in the Yukon River in 2018 (0.0954 ± 0.100), 2019 (0.0989 ± 0.115) and 2020 (0.0840 ± 0.0987, $n = 137$, $\chi 2 = 94.68$, $P = 0.60$) despite interannual differences in run size, water temperature, and flow. Egg retention in female Yukon River *O. tshawytscha* was significantly correlated with relative carcass collection date and tended to be lowest during the middle of the collection period ($R^2 = 0.15$, $n = 137$, F value $= 6.35$, $P < 0.01$; Figure 5).

4 | DISCUSSION

4.1 | Overview

Egg retention was variable in the Yukon River downstream of the WHP but was one of the highest reported in the literature (see Quinn *et al*., 2007). Given the extraordinary length of this migration (~3000 km) it could be hypothesized that egg retention may be naturally higher in these fish relative to most other populations; however, egg retention was much lower in female salmon sampled from nearby free-flowing rivers (reviewed in Table 1), including the Teslin River. We do not have individual movement histories to complement the egg retention data presented in this study, so we rely on the findings of a concurrent telemetry project (*i.e*., Twardek *et al*., 2021) to infer the mechanisms behind the observed egg retention in this group of fish. Therefore, we can only hypothesize that the higher proportion of carcasses with elevated egg retention on the Yukon River reflects the large proportion of the population that fails passage at the WHP (Twardek *et al*., 2021). An elevated rate of egg retention observed in female salmon downstream of the WHP is likely to be detrimental if this population is below carrying capacity, which is probable given the low abundance of salmon returning to Whitehorse and the broad-scale declines observed throughout the watershed (Joint Technical Committee of the Yukon River U.S./Canada Panel, 2021). Below, we discuss the potential implications that failed passage at fishways has on salmon reproductive potential.

4.2 | Implications of failed passage at barriers on spawning potential

Dams and other barriers restrict the movement of species through rivers (Silva *et al*., 2018) and this is often only partially overcome with fishways (Noonan *et al*., 2012). In the Yukon River, *O. tshawytscha* passage failure is considerable at the WHP relative to passage rates at other hydro plants in this species' range (Keefer *et al*., 2021; Twardek *et al*., 2021). Though numerous telemetry studies have documented failed salmon passage at dams and other barriers, very few studies have directly measured the reproductive consequences of a fishway, particularly after failed passage (Roscoe & Hinch, 2010). Failed passage beyond barriers is likely to have severe impacts on reproduction when individuals fail to arrive at intended spawning areas. For semelparous, anadromous, and philopatric species like *O. tshawytscha* that have one opportunity to reproduce, it has been stated that failure to complete spawning migrations results in zero life-time fitness (Farrell *et al*., 2008; Roscoe & Hinch, 2010), though our findings potentially suggest otherwise for upper Yukon River salmon. We estimated that none of the females failing passage completely spawned (*i.e*., <100 eggs retained), but that most salmon spawned partially despite failing to reach their assumed natal spawning habitat 80–100 km upstream. Although salmon are known to have high homing rates (Dittman & Quinn, 1996), it seems possible that after repeatedly failing to pass through the fishway, it could be advantageous to divert energy use away from upstream migration and instead attempt spawning at suitable non-natal habitat.

Egg deposition in Yukon River *O. tshawytscha* downstream of the WHP provides evidence that anadromous salmonids have plasticity in spawning site choices. Under the assumption that elevated egg retention downstream of the WHP is the result of failed passage at the WHP, it was estimated *O. tshawytscha* failing passage expelled approximately 67% of their estimated fecundity on downstream spawning grounds. Close alignment of this estimate with the 64% estimated egg deposition in hatchery salmon (with known upstream release locations) supports this assumption. This observation of hatchery salmon egg deposition provides more evidence that salmon have plasticity in spawning site choice. Furthermore, findings from concurrent telemetry work found many of the salmon failing to pass the WHP in the Yukon River tended to move into the braided mainstem spawning habitat 2 km downstream of the dam at least temporarily, sometimes spending multiple days in this habitat (Twardek *et al*., 2021). Of 24 telemetry tagged females that attempted and failed passage at the WHP, one was recovered as a carcass downstream of spawning grounds after attempting passage for ~50 h and had expelled most of its eggs (and had a worn tail indicative of spawning behaviour).

O. tshawytscha have strong homing ability to natal spawning grounds under routine migratory conditions (Keefer & Caudill, 2014), although successful spawning of straying salmon indicates it is possible for salmon to spawn in non-natal habitat (Bett *et al*., 2017). Spawning in non-natal habitat is thought to be partly driven by environmental factors of the non-natal habitat including its physicochemical properties (*e.g*., discharge, temperature, water chemistry; Hasler & Scholz, 2012; Correa & Gross, 2008; Ueda, 2011), chemical or behavioural cues from conspecifics (*e.g*., spawning activity, pheromones; Solomon, 1973; Nordeng, 2009), and its distance from natal tributaries. Bett *et al*. (2017) reviewed the causes of straying in salmon populations, hypothesizing that disrupted flow patterns at dams can make olfactory navigation difficult and that fish may track the conspecific cues of salmon aggregations downstream of a dam (Bett &

Hinch, 2015; Quinn *et al*., 1989). Based on this hypothesis, effluent from the hatchery and cues from a spawning population just downstream of the WHP could increase the likelihood of Yukon River *O. tshawytscha* foregoing their migration after migratory challenges to attempt spawning with downstream conspecifics. This effect may be exacerbated if olfactory and neurological functions decline with senescence such that mature fish with advanced senescence revert to nearby spawning sites rather than complete their migration to natal sites (Keefer & Caudill, 2014; Morbey *et al*., 2005). Though little information exists to evaluate these mechanistic hypotheses, anadromous salmon have demonstrated they will revert to non-natal habitat when faced with migratory obstacles. Wild Coho salmon *Oncorhynchus kisutch* (Walbaum 1792) in the Coldwater River strayed to other nearby spawning locations when they were unable to reach natal spawning sites due to low water levels and beaver dams (Turcotte & Shrimpton, 2020). This behaviour of seeking out alternative spawning sites has also been observed in Atlantic salmon *Salmo salar* (Linnaeus 1758) that are delayed at power stations (Chanseau & Larinier, 1999; Rivinoja *et al*., 2001; Thorstad *et al*., 2003, 2005; Webb, 1990). However, successful spawning of salmon after failed passage may not be additive to the spawning of natal salmon. If female salmon failing passage return to spawning grounds later in the migration, they may build their redds over existing ones from previously spawning females, dislodging the fertilized eggs from the original redd (Fukushima *et al*., 1998; McNeil, 1964).

4.3 | Exploring drivers of egg retention on non-natal spawning grounds

On the Yukon River downstream of the WHP, nearly all (97%) female salmon had some degree of tail wear, indicating that spawning was attempted, although the degree of this wear was lower than in the free-flowing Teslin River. Part of this may be related to habitat composition, as fish that completely spawned wore down their tails less on the Yukon River than in the Teslin River, but this does not fully account for differences in spawning effort between the rivers. This suggests that Yukon River females failing to pass the WHP either could not find suitable spawning locations in the large Yukon River mainstem (that differs considerably from their intended small natal tributaries upstream) or that they did not have the energy to effectively spawn after attempting passage. Following challenging migrations, salmon typically have enough energy to survive for only a short period of time on spawning grounds (typically days; Healey *et al*., 2003; Twardek *et al*., 2021). During this time, female salmon expend most of their energy holding on spawning areas and digging while males spend more energy on holding and posture displays (Healey *et al*., 2003). Challenging fish passage conditions can deplete energy reserves available to salmon to complete these spawning behaviours (Burnett *et al*., 2014; Caudill *et al*., 2007) and ultimately increase egg retention (Minke-Martin *et al*., 2018). These factors could make these females failing passage less competitive on downstream spawning grounds, and they could be relegated to less suitable spawning locations if spawning ground density is high (*e.g*., areas with fine sediment, vulnerability to streambed scour; Chapman, 1988; Rennie & Millar, 2000; Schuett-Hames *et al*., 2000; Schroder, 1981).

High density on spawning grounds has been linked to elevated rates of egg retention in Pacific Salmon populations (Quinn *et al*., 2007). If Yukon River salmon that fail to navigate the fishway revert to alternative spawning areas downstream, then greater salmon density could lead to competition with the natal salmon spawning in this habitat. Salmon abundance in the study area is low and was considerably below the long-term average during each year of the study. As a result, we speculate that the natal downstream population is not at capacity and that density-dependent factors are having a minimal influence on spawning success. Alternatively, if the annual natal population downstream of the WHP is stable and regularly at capacity, then any additional salmon from upstream spawning populations could initiate density-dependent effects. Indeed, if density-dependent mechanisms were contributing to increased egg retention below the hydro plant, we would expect egg retention to be highest during years with greater run size and during parts of the migration with the highest spawning ground density. However, egg retention was consistent between 2018 and 2019/2020 despite the run size being twice as large in the first year of the study, and was lowest during the middle of our survey period when carcass observation rates were highest. This indicates that other density-independent factors may be contributing to egg retention, such as energy depletion after failing to pass the fishway (Minke-Martin *et al*., 2018). Our finding that heavier females had greater egg deposition than lighter females could support either hypothesis: that spawning ground density is high and larger females can outcompete smaller females for habitat, or that larger fish have more energy available to attempt spawning after failed passage (Foote, 1990; van den Berghe & Gross, 1989).

Environmental conditions varied considerably across years, and the influence of these environmental differences cannot be statistically teased apart with our limited time series. For instance, the lower Yukon River was abnormally warm during the migration in 2019 and water levels throughout the river were well below historic averages (ADFG, 2019). This warm water was linked to stress and pre-spawn mortality in *O. tshawytscha* in the lower river (discussed in von Biela *et al*., 2020) and it is possible there were latent effects on those salmon in the upper Yukon River. In 2020, water temperatures were cooler and water levels were well above historic averages (ADFG, 2020). Although our short-term dataset cannot isolate the effects of temperature, water level, and run size, the lack of variation in egg retention across years suggests these variables did not strongly influence egg retention during the observed years. It is possible that these variables acted in a synergistic, additive or antagonistic manner such that the effects of density were muted by interannual variability in environmental conditions or *vice versa*.

5 | CONCLUSIONS

Compared to the Teslin River, female salmon downstream of the WHP had higher egg retention and less wear on their caudal fins (a proxy for spawning effort). We hypothesize that salmon failing to pass the WHP had limited energy reserves, which compromised spawning ability, and ultimately led to the observed egg retention rates. However, partial egg deposition in these females suggests that failed passage at migratory barriers will not always result in complete loss of spawning ability. If the spawning habitat downstream of the WHP is below carrying capacity (as we suspect; Joint Technical Committee of the Yukon River U.S./Canada Panel, 2021), egg deposition from fish failing passage could increase the overall productivity of this population. It is unclear, however, whether these fish failing passage and attempting spawning in non-natal habitat have similar nesting and offspring hatching success as natal spawners. Regardless of egg deposition downstream of the WHP, failure of many Yukon River salmon to spawn in intended natal spawning habitat upstream of the WHP (*i.e.*, Michie Creek) undoubtedly has negative effects on the productivity of that population, given low run sizes to that spawning area in recent years (~250 fish total) relative to historic returns (Cox, 1997; Joint Technical Committee of the Yukon River U.S./Canada Panel, 2021). Future work should seek to quantify egg retention in female salmon upstream of the WHP to evaluate whether there are consequences of delayed and difficult passage on spawning success. In 2005, a small number of females were recovered upstream of the WHP and all had spawned completely (De Graff, unpub data; Table 1), though we were unable to recover any carcasses in this area in 2019 and 2020 when run sizes were small.

Findings from our study also have the potential to inform the use and design of future carcass surveys. Most of the females recovered downstream of the WHP had partially spawned (65%), highlighting that egg retention is best measured as a continuous variable. This contrasts with how egg retention is typically reported in the literature (binary), perhaps because subjective (visual) assessments are often used to characterize spawning success (Bowerman *et al*., 2016). We encourage researchers to quantitatively measure egg retention to better characterize the natural variation in egg retention rates in salmon populations and to better standardize egg-retention estimates among studies that often report pre-spawn mortality with different criteria (reviewed in Bowerman *et al*., 2021). We encourage future research to test the hypotheses presented here, and for carcass surveys to be included in the fish passage 'toolkit' to better understand the reproductive consequences of fish passage at migratory barriers (Katopodis, 2005; Roscoe & Hinch, 2010).

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AUTHOR CONTRIBUTIONS

W.M.T: ideas, data generation, data analysis, manuscript preparation and funding. N.W.R.L: ideas, data generation, data analysis, manuscript preparation and funding. S.J.C: ideas, manuscript preparation and funding.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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