

Insights into Chinook salmon (*Oncorhynchus tshawytscha*) movement ecology in the terminal reaches of the upper Yukon River during the spawning migration

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Abstract

Chinook salmon (*Oncorhynchus tshawytscha* (Walbaum, 1792)) from the upper Yukon River are highly unique, with some populations migrating nearly 3000 km to spawning habitat near the northern range limit for the species. We conducted a 4-year study to understand the behaviour of Chinook salmon in the terminal reaches of their migration by tagging salmon with acoustic and radio transmitters in Whitehorse, Yukon, Canada, ~2800 km from the ocean. Various migration characteristics were quantified for Chinook salmon, including en route mortality, diel behaviour, migration rates, and homing patterns, and associations with salmon origin (wild vs. hatchery), sex, size, and migration timing were explored. Salmon had high survival to spawning grounds (>98%) and migrated throughout all hours of the day, with higher proportions of nighttime movements in a smaller spawning tributary than in the Yukon River mainstem. Migration rates were faster for larger salmon as well as late-arriving salmon, which was likely necessary to ensure they had sufficient time and suitable conditions on spawning grounds to reproduce. Non-direct homing movements (e.g., tributary exploration) were more common in male salmon and considerably increased migration distance through the study area. Findings from this study may help to inform the complex international and inter-nation management of these increasingly threatened Chinook salmon populations.

Key words: Chinook salmon, *Oncorhynchus tshawytscha*, behaviour, range limit, long distance, Pacific salmon, passage

Résumé

Les saumons chinooks (*Oncorhynchus tshawytscha* (Walbaum, 1792)) du cours supérieur du fleuve Yukon sont très singuliers, certaines de leurs populations migrant sur près de 3000 km vers des habitats de frai situés près de la limite septentrionale de l'aire de répartition de l'espèce. Nous avons mené une étude de quatre ans afin de comprendre le comportement de saumons chinooks dans les tronçons terminaux de leur migration en dotant des spécimens d'émetteurs acoustiques et de radioémetteurs à Whitehorse (Yukon, Canada), à ~2800 km de l'océan. Différentes caractéristiques de la migration ont été quantifiées pour les saumons chinooks, dont la mortalité en route, le comportement nyctéméral, les vitesses de migration et les motifs de retour, et nous avons examiné les associations avec l'origine (sauvage ou d'élevage), le sexe, la taille et le moment de la migration des saumons. Les saumons présentaient un fort taux de survie (>98 %) jusqu'aux frayères et se déplaçaient à toute heure de la journée, la proportion de déplacements nocturnes étant plus grande dans un petit affluent de frai que dans le bras principal du fleuve Yukon. Les vitesses de migration étaient plus grandes pour les saumons plus gros ainsi que pour les saumons à arrivée plus tardive, probablement pour leur assurer suffisamment de temps et des conditions convenables dans les frayères pour se reproduire. Les déplacements de retour non directs (p. ex. exploration d'affluents) étaient plus répandus chez les saumons mâles et accroissaient considérablement la distance de migration à travers la région étudiée. Les constatations de l'étude pourraient être utiles pour la gestion internationale et entre nations complexe de ces populations de plus en plus menacées de saumon chinook. [Traduit par la Rédaction]

Mots-clés : saumon chinook, *Oncorhynchus tshawytscha*, comportement, limite d'aire de répartition, longue distance, saumon du Pacifique, passage

Introduction

Pacific salmon (*Oncorhynchus* spp.) comprise several anadromous fish species that are well recognized for their iconic migrations inland to complete their single lifetime reproductive events (Quinn 2018). Pacific salmon are philopatric, and follow imprinted olfactory, conspecific, and environmental cues in the river to navigate to natal habitats upstream (Ueda 2011; Bett and Hinch 2016). Though salmon are known to have strong homing ability to spawning sites, non-direct homing movements can be common (Keefer et al. 2008a). Salmon may travel downstream between upstream movements, temporarily enter non-natal tributaries, overshoot (swim beyond) intended spawning habitat, or permanently stray away from natal habitat (Keefer and Caudill 2014; Bett et al. 2017). These movements may have an adaptive role for salmon related to thermoregulation, maturation, or colonization of new habitats, but it is also possible these movements reflect difficulties sensing olfactory cues in the river (Keefer et al. 2006). Salmon movement may differ in response to environmental conditions (Berman and Quinn 1991), and it is known that the biotic characteristics of salmon can shape migratory behaviours. For example, hatchery salmon often have higher rates of straying from intended spawning sites (Keefer and Caudill 2014). Characterizing salmon movements (and their underlying drivers) during critical life-history periods such as spawning migrations can help to inform conservation actions and management decisions for these species.

The life-history characteristics of Pacific salmon (anadromy, semelparity, and philopatry) make these species vulnerable to various threats during their lifecycle, including during their adult spawning migrations. Returning adult salmon may be exposed to elevated water temperatures, pathogens, capture in fisheries, predation, and barriers to movement, among many other threats decreasing their likelihood of arriving at spawning sites. As such, salmon sometimes fail to complete their spawning migrations (i.e., en route mortality) or arrive at spawning locations but fail to successfully spawn (i.e., prespawn mortality); resulting in complete loss of lifetime fitness (Young et al. 2006; Hinch et al. 2012; Bowerman et al. 2016; Twardek et al. 2022). Many salmon populations are in decline throughout their native range (Schoen et al. 2017), in many cases because of the challenges these animals face during freshwater spawning migrations (Cooke et al. 2004). Chinook salmon (*Oncorhynchus tshawytscha* (Walbaum, 1792)) are known for completing longer migrations than any other anadromous salmon species (Groot and Margolis 1991), with some populations travelling thousands of kilometres upstream. Some of the most impressive migrations include those of the upper Yukon River Chinook salmon that collectively undertake the longest inland salmon migrations on Earth, near the northern range limit for the species.

Upper Yukon River Chinook salmon comprise several populations of salmon terminating in the Canadian waters of the Yukon River. Some of these populations travel ~3000 km from the Bering Sea to return to natal spawning habitat, including salmon from the Takhini River, Teslin River, and Yukon River upstream of Whitehorse, YT, Canada

(Brown et al. 2017). Various lines of evidence suggest the Yukon River population upstream of Whitehorse, YT, once had high abundance, with one report stating that 25 Indigenous families would each harvest 300–400 salmon per year (Cox 1997). This population has undergone serious declines over the past century or two and over the last few decades returns have averaged just 950 salmon and continue to decline (JTC 2021). Returns in 2019, 2020, and 2021 were the lowest recorded in consecutive years since monitoring began nearly six decades ago (JTC 2021). Traditional Knowledge has long stated that salmon abundance is in decline, and now, local Indigenous Governments have advised their citizens to limit salmon harvest from the river. While the exact timing and magnitude of historic declines remains unclear, it is believed that overharvest during the Klondike Gold Rush (1896–1899) and in subsequent commercial fisheries were partially responsible for severe declines. Further, in 1958, the Whitehorse Hydro Plant (WHP) was constructed ~100 km downstream of the primary spawning habitat for this population. The WHP created a barrier to both upstream and downstream movement, potentially limiting the capacity for the salmon population to recover to historic levels of abundance. Since 1988, the population has been supplemented by hatchery-reared Chinook salmon to compensate for juvenile mortality through the turbines.

Given concern over low abundance of this population, the objectives of this study were to document survival to spawning grounds, and where possible, the behaviour of Chinook salmon in the terminal reaches of their migration through the upper Yukon River. From 2017 to 2020, salmon were implanted with acoustic and radio transmitters in Whitehorse, YT, and tracking data were compiled to infer individual fate and behaviour. Behaviours quantified focused on those described previously for Chinook salmon (e.g., Keefer et al. 2004, 2008a, 2013; Keefer and Caudill 2014), including diel behaviour, migration rates, spawning site choice, tributary exploration, non-direct homing, and colonization of new habitat. It was hypothesized that behaviours would be associated with individual fish characteristics and environmental conditions, so the influence of fish origin, sex, size, relative migration timing, and migration year, as well as water temperature, were predicted to explain behavioural patterns and were tested as main effects. Results from this study provide insight into the behaviour of Chinook salmon completing one of the world's longest inland salmon migrations near the northern range limit for the species. Further, findings may help support the complex international and inter-nation fisheries management processes regarding this increasingly threatened Chinook salmon population.

Materials and methods

Study site

The upper Yukon River extends ~2948 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. Our study area consisted of the final few hundred kilometres of this salmon migration, from the confluence of the Yukon and

Takhini rivers to upstream spawning sites on the Yukon River (Fig. 1). Within this reach of the migration, most salmon must pass the 40 MW, 18 m high Whitehorse Hydro Plant (2841 km inland) via the Whitehorse Rapids Fishladder (henceforth referred to as “the fishway”) to reach natal spawning sites upstream. The fishway (366 m long) has a pool-and-weir design, and salmon can swim through submerged slots or over baffles between each pool. Known spawning sites upstream of the WHP include Wolf Creek (14 km from the WHP), the M’Clintock River upstream of Michie Creek (80 km), and Michie Creek (80–107 km; Brown et al. 2017). The Yukon River (mainstem section) is a large river with discharge of $\sim 475 \text{ m}^3/\text{s}$ during the migration, while the M’Clintock River (primary tributary) is much smaller. Michie Creek (secondary tributary) is a small, shallow, fluvial system and is the primary spawning tributary upstream of the WHP. Most of the spawning habitat in this system is upstream of Byng Creek, though spawning habitat can be found throughout its entirety. The creek has an abundance of beaver dams potentially obstructing salmon migration and permitted dam breaching is attempted each year by local biologists and Kwanlin Dün First Nation. Since 1988, a hatchery located immediately downstream of the WHP has collected eggs from adult salmon in the fishway and raised and released fry into each (at times) of these spawning tributaries upstream of the WHP to compensate for juvenile mortality through the WHP turbines (Yukon Energy Corporation 2018). Hatchery staff clip the adipose fin off all hatchery-reared fish so they can be distinguished from their wild counterparts. Hatchery salmon comprise approximately 50% of the return, though recently the hatchery component has declined (JTC 2021). Hatchery fish are primarily ocean type (enter marine habitat within their first year and have a freshwater age of zero) while wild fish are stream type (typically remain in freshwater for 1 year before migrating to the ocean; discussed in von Finster et al. 1998; JTC 2021) which may influence their behaviour as adults (Westley et al. 2013). Chinook salmon runs on the Yukon River are typically dominated by age-5 and age-6 fish (JTC 2021).

Fish capture and tagging

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”. A license to fish for scientific, experimental, educational, or public display purposes, under Section 52 of the Fishery (General) Regulations (Yukon/Transboundary Rivers Area) was obtained from Fisheries and Oceans Canada (XR 229 2017-2020).

Chinook salmon ($n = 56$) were captured from the Yukon River downstream of Whitehorse, by gill net and within a fish trap (henceforth “viewing chamber”) within the fishway ($n = 162$) in August each year. Gill netting was completed approximately 8 km upstream of the confluence of the Yukon and Takhini rivers (2818 km), 15 km downstream of the WHP. Fishing practices aligned with those used previously on the Yukon River, which found that 98% of salmon resumed upstream migration after capture and tagging (as assessed by a site ~ 62 km upstream; Eiler et al. 2014) and were further

guided by Traditional Knowledge and other local expertise. Upon capture, fish were cut out of the gill net and placed into a tote filled with river water. An air stone was set in the tote to replenish respired oxygen.

Chinook salmon were gastrically implanted (Naughton et al. 2018) with either a single V16 acoustic transmitter (V16-4H-R64K coded tags, Innovasea, Shad Bay, Nova Scotia, Canada; 10.3 g; diameter = 16 mm \times length = 68 mm; 90 s randomized interval) or with a V13 transmitter (6 g; diameter = 13 mm \times length = 36 mm; 60 s (2019) and 30 s (2020) randomized interval) attached to a TX-PSC-I-80 radio transmitter (Sigma Eight, Newmarket, Ontario, Canada; 150 MHz; battery = 150 days; 4.2 g; diameter = 10 mm \times length = 27 mm; 2.6 s interval). Acoustic and radio transmitters were affixed together with a marine-grade adhesive for ease of application (combined mass = 10.2 g, diameter = 13 mm \times length = 63 mm). A transmitter was placed into a hollow PVC pipe, which was inserted into the fish’s mouth and pushed to the stomach. A wooden plunger was then inserted into the pipe to release the transmitter, and the pipe and dowel were withdrawn from the stomach. Subjects were also externally tagged behind the dorsal fin with a coloured Floy tag and marked with a hole punch on the edge of the caudal fin. External tags and markings allowed visual identification to avoid double tagging with acoustic transmitters if recaptured at the fishway. Anesthesia was not used during tagging procedures. Salmon captured and tagged using the approaches described above had a 93% survival rate to spawning grounds in the nearby, free-flowing Takhini River (Twardek et al. 2021).

Chinook salmon were tagged at the 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 salmon selected for this study 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 to account for differences in the run composition during any given year. The total number of salmon tagged each year was adjusted based on the run size enumerated at the fishway. Sex (based on morphology), origin (hatchery or wild), and fork length (to the nearest 5 mm) were recorded for each tagged salmon at the time of capture.

Receiver array

An array of up to 51 acoustic telemetry receivers (VR2w, InnovaSea, Shad Bay, Nova Scotia, Canada) was used to monitor fish movement to known and suspected spawning tributaries upstream of the confluence of the Yukon and Takhini rivers (Fig. 1; Table 1). In general, three receivers were placed within 200 m of each river confluence to determine the direction of salmon movement (i.e., one receiver within each tributary upstream of the confluence and another located downstream of the confluence). Receiver locations remained mostly consistent over the 4 years of study, though some receivers were moved, added, or removed based on improved knowledge of fish behaviour and array performance each year. Acoustic receivers were generally anchored with a cement block

Fig. 1. Map of part of the upper Yukon River watershed upstream of Lake Laberge, highlighting locations of the Whitehorse Hydro Plant (WHP; primary tagging site) and telemetry receivers (white circles) deployed from 2017 to 2020. Panel plots depict representative reaches of the migration corridor, including the Yukon River (mainstem section), M'Clintock River (primary tributary), and Michie Creek (secondary tributary), and are presented at the same scale for comparison. Known spawning areas include Wolf Creek, the upper M'Clintock River, and Michie Creek. White arrow heads indicate flow direction. ArcGIS Pro was used to create the map. Sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community. [Colour online.]

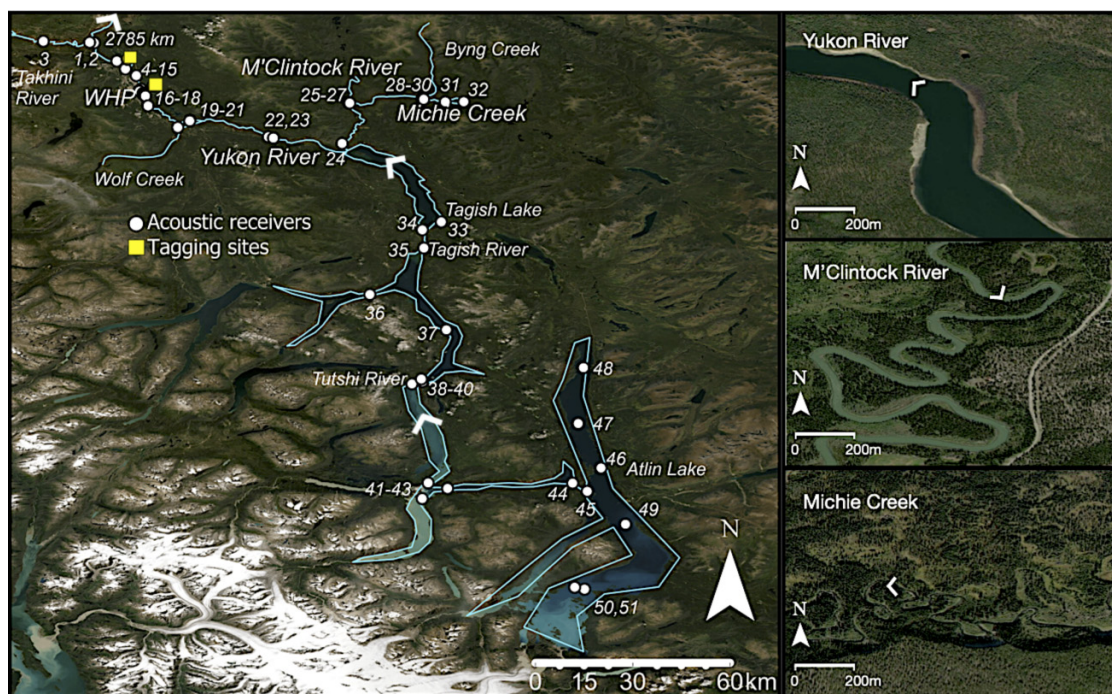


Table 1. Summarized location of and rationale for acoustic receivers deployed throughout the upper Yukon River watershed to monitor the migration of Chinook salmon (*Oncorhynchus tshawytscha*) to spawning sites.

Site (#)	Location	Rationale with respect to postpassage movement	Detection efficiency (%)
1–15	Downstream of the WHP	Fallback at the WHP	—
16–18	WHP Fishway	Movement from the tagging site out of the fishway and through the reservoir	92 ($n = 114$)
19–21	Wolf Creek	Movement past and into a spawning tributary upstream of the WHP	—
22, 23	Yukon River mainstem	Movement upstream of the WHP	100 ($n = 104$)
24	M'Clintock River	Movement into the M'Clintock River	100 ($n = 106$)
25	M'Clintock River (upper)	Movement into a spawning tributary upstream of the WHP	—
26–31	Michie Creek	Movement in the primary spawning tributary upstream of the WHP	100 ($n = 83$)
32	Michie Lake inlet	Movement upstream of the primary spawning tributary	—
33–51	Southern Lakes	Movement away (straying) from known spawning tributaries	—

Note: Site numbers correspond to those shown in Fig. 1. Where applicable, detection efficiency (% detected of all fish known to have passed a receiver) and sample size are presented as an average for all receivers within each site grouping. WHP, Whitehorse Hydro Plant.

or sand bag and were tethered to a rope extending up to a subsurface buoy. Radio telemetry was combined with acoustic telemetry in 2019 and 2020 to enable active tracking on spawning grounds and monitoring at the fishway. The radio receivers (SRX 800s, Lotek Wireless, Newmarket, Ontario, Canada) scanned three frequencies, each for 3.2 s, meaning every tagged salmon was searched for over a 9.6 s period. All receivers were deployed prior to the arrival of the first fish at the Whitehorse Hydro Plant and were removed approximately 2 weeks after the last fish was tagged at the hydro

plant (no changes in fish locations were detected in the few days preceding receiver removal). Receivers 33–51 were deployed and maintained by the governments of Yukon and British Columbia, Canada, as part of a separate study. To assess the performance of receivers, detection efficiency was calculated at each receiver or group of receivers as the proportion of fish detected of those known to have passed a receiver (or receiver group). Although detection efficiencies could not be calculated at the most upstream receivers, it was assumed that detection efficiencies were similar to that

of other receivers within each system. Hourly water temperature throughout the migration was recorded in the fishway (using a single Hobo® Water Temperature Pro data logger) and in Michie Creek (using a Solinst combination water level and temperature data logger deployed 3 km downstream of receiver 31) as part of a long-term monitoring program (Fig. 1; de Graff 2017, 2018, 2019, 2020). Due to technical challenges, temperature was not recorded in Michie Creek in 2018.

Statistical analysis

Analyses focused on salmon movements to spawning sites upstream of the WHP, so all fish that failed to pass the WHP or fell back after passage were excluded (for fishway movement see Twardek et al. 2021). Fish that fell back generally spent multiple days upstream of the WHP, suggesting their fallback through the WHP was related to “overshoot” of spawning grounds rather than “disorientation” (Naughton et al. 2006), though the reason for fallback remains unclear and downstream passage through the WHP could nonetheless lead to injury and mortality (Wagner and Hilsen 1992). Various aspects of migration success and behaviour were quantified including en route mortality, diel movement, migration rates, spawning locations, tributary exploration, non-direct homing, and colonization of new habitat (defined in Table 2). When possible, we assessed the relationship between each migration variable and various biotic characteristics of upper Yukon River salmon as predictor variables including fish origin, sex, size, relative migration timing, and migration year (Table 3). Relative migration timing was calculated as a proportion based on the date of arrival at the WHP viewing chamber relative to the first and last fish to do so each year. Year was included in models as a fixed effect to account for interannual differences in migration conditions (the study was too short to include “year” as a random effect). Relationships between predictor variables were assessed through correlation, *t* tests, and χ^2 tests (depending on the variable types compared) while multicollinearity was assessed using the variance inflation factor (VIF) function (no instances of multicollinearity existed; all VIF < 1.5).

Migration rates through various sections of the migration (Yukon River, M’Clintock River, and Michie Creek) were modeled using multiple regression. Non-direct homing (see Table 2) was converted to a binomial response with all salmon having a degree of non-direct homing greater than 1.11 classified as “non-direct” (1.11 reflected a natural break in the data; Supplementary Table S1). Non-direct homing was then modeled using a generalised linear model with a binomial distribution. *P* values were adjusted using the false discovery rate method (*R stats* package). A zero-inflated Poisson generalized additive model (specifying individual as a random effect) was then used to evaluate whether hour of the day or temperature were significant predictors of movement rate (i.e., number of detections per hour) in the primary spawning tributary (Michie Creek). For this model, a value of “0” was applied to all hours that fish were in the tributary but were undetected. Both predictors were modeled with smooth functions given that salmon movement rates are expected to peak at a thermal optimum (Salinger and Anderson 2006) and that most

diel patterns likely to influence fish behaviour are cyclic (e.g., light intensity) rather than linear. Model diagnostics were assessed using the “gam.check” function (*mgcv*). To assess whether the diel period (i.e., day or night) affected movement rates in Michie Creek and the Yukon River, the proportions of observed nighttime detections in each river were compared to that expected based on the proportion of nighttime hours at this location (*sunclac* package in R; Thieurmel and Elmarhraoui 2019). Only summary statistics were reported for en route mortality, spawning locations, tributary exploration, and colonization of new habitat, for which models evaluating predictors could not be developed (e.g., en route mortality; *n* = 2). All statistical analyses were conducted in R statistical software (R Core Team 2021). Data exploration was conducted with *ggplot2*, while model assumptions were assessed using diagnostic plots of residuals. No model reduction was attempted from the initial candidate model. Where applicable, data are presented as mean \pm SD.

Results

Across 4 years of study, 56 salmon were tagged following gill net capture while 162 were tagged at the fishway. All but one salmon tagged at the viewing chamber migrated through the remainder of the fishway, tag failure occurred for one salmon that was not detected after release in the fishway, and 11 gill net salmon successfully passed the fishway, resulting in a total of 171 tagged salmon passing the WHP (782 ± 87 mm). Fish that fell back through the WHP spillway after passage (whose migration success remains unclear) were excluded from all analyses (*n* = 21 fish). None of the fish that fell back reascended the fishway and terminated upstream. Characteristics of tagged salmon were similar among years, such that most of the tagged sample was male, wild origin, and tagged approximately halfway through the run (Table 3). Wild fish (804 ± 85 mm) tended to be longer than hatchery fish (762 ± 92 mm), while females (842 ± 49 mm) were typically longer than males (777 ± 93 mm), though no other significant relationships existed between predictor variables. Average Yukon River water temperature was highest in 2018 while discharge was highest in 2020 (Table 3). Water temperature tended to decline while discharge remained relatively stable throughout the migratory period.

Survival and diel behaviour

En route mortality upstream of the WHP was estimated to be 2.0% (of *n* = 150), though this excludes fish that fell back at the WHP (whose fate remains unknown). In the Yukon and M’Clintock rivers, salmon movement rates (i.e., number of detections) were similar throughout the diel cycle (*n* = 879 detections), while in the primary spawning tributary (Michie Creek) salmon movement rates tended to vary more throughout the day (*n* = 1008 detections; Fig. 2). Mean August water temperatures were similar in Michie Creek (14.9 °C) and the Yukon River (15.0 °C) though daily temperatures fluctuated much more on average in Michie Creek (1.7 °C) compared to the Yukon River (0.4 °C; Fig. 2). In Michie Creek, hour of the day ($\chi^2 = 63.38$, *P* < 0.01) was a significant predictor of salmon

Table 2. Descriptions of the migratory behaviours and outcomes described for Chinook salmon (*Oncorhynchus tshawytscha*) from the upper Yukon River from 2017 to 2020.

Variable	Units	Description
En route mortality	—	Assigned to all salmon that were last detected along the migration corridor but not at a known spawning location (i.e., Wolf Creek, the upper M'Clintock River, or Michie Creek; as per Cooke et al. 2006; Brown et al. 2017). Carcasses were not recovered; thus, the ultimate fate of these fish was assumed
Diel movement	—	The number of new detections at acoustic receivers occurring in each hour of each day was calculated as an indication of diel movement patterns (per Keefer et al. 2013). Only the initial of consecutive detections at a receiver for each fish was included. Diel movements were considered separately for the mainstem Yukon River and the primary spawning tributary
Yukon River migration rate	km/h	Calculated as the elapsed time between first detections at receivers positioned at the fishway exit (site 25) and the Lewes Dam (site 30), divided by the distance between these receivers
M'Clintock River migration rate	km/h	Calculated as the elapsed time between first detections at receivers positioned at the mouth of the M'Clintock River (site 32) and the confluence of Michie Creek and the M'Clintock river (site 34), divided by the distance between these receivers
Michie Creek migration rate	km/h	Calculated as the elapsed time between first detections at receivers positioned at the confluence of Michie Creek and the M'Clintock river (site 34) and the confluence of Byng Creek and Michie Creek (site 37), divided by the distance between these receivers
Spawning location	—	Spawning locations were assigned as the last tributary/reach entered by migrating salmon (as per Eiler et al. 2014), excluding downstream movements that occurred near the end of the spawning period (assumed to be postspawn movements) after salmon had spent three or more days in an upstream spawning location (assumed to be enough time for spawning; Berejikian et al. 2007)
Tributary exploration	—	Tributary exploration was defined as detection within a tributary before terminating migration in a different known spawning tributary
Non-direct homing	—	The degree of non-direct homing was quantified as the minimum movement length (sum of all detected location differences; including both up and downstream movements) divided by the minimum migration length to terminal locations for each fish. Distances were described as minimum movements because the actual movement path of fish between receivers was unknown
Colonization of new habitat	—	Assigned to all salmon that terminated in a location outside spawning tributaries and migration corridors identified in a previously developed catalogue of spawning habitat in the Yukon River (Brown et al. 2017)

Table 3. Characteristics of acoustically tagged Chinook salmon (*Oncorhynchus tshawytscha*) from the upper Yukon River, and river conditions from 2017 to 2020.

Year	<i>n</i>	Fish size (mm)	Sex (% female)	Origin (% hatchery)	Relative migration timing	Average tagging date	Water temperature (°C)	Discharge in Michie Creek (m ³ /s)	Run size through the fishway
2017	50	748 ± 80	20	32	0.52 ± 0.16	16 August	15.3 ± 1.3	1.2	1226
2018	55	780 ± 91	27	24	0.46 ± 0.15	16 August	15.7 ± 1.4	—	691
2019	40	800 ± 79	20	10	0.63 ± 0.19	19 August	15.1 ± 1.8	1.3	282
2020	26	788 ± 88	15	12	0.56 ± 0.20	19 August	14.3 ± 0.8	2.8	216

Note: Characteristics included proportions by size, sex, and origin (hatchery or wild), relative migration timing, average tagging date, August water temperature, and August discharge (de Graff 2017, 2019, 2020). Data are presented as mean ± SD where applicable.

movement rate ($n = 17\,759$ h) when accounting for individual fish as a random effect ($\chi^2 = 94.83$, $P < 0.01$), though temperature was not significant ($\chi^2 = 1.17$, $P = 0.28$). In Michie Creek, a significantly higher proportion of movements occurred at night than expected (49% vs. 36%) based on the proportion of nighttime hours at this latitude ($\chi^2 = 30.72$, $P < 0.01$), while in the Yukon and M'Clintock rivers this proportion was similar to that expected (34% vs. 36%; $\chi^2 = 0.56$, $P = 0.45$). Mean August water temperatures were slightly cooler at night (14.4 ± 1.7 °C) than during the day (15.1 ± 1.8 °C) in Michie Creek, while night (15.1 ± 1.4 °C) and day (14.9 ± 1.4 °C) temperatures were more similar in the Yukon River.

Migration rates

Migration rates were fastest in the mainstem Yukon River ($n = 132$; 2.42 ± 1.05 km/h) followed by the M'Clintock River ($n = 117$; 1.61 ± 0.53 km/h), and Michie Creek ($n = 90$; 0.39 ± 0.19 km/h). Fork length was significantly and positively correlated with migration rates in the Yukon River and M'Clintock River but had a varying influence on migration rates in Michie Creek across years (Table 4; Fig. 3). Migration rate was also significantly and positively correlated with relative migration timing, a finding consistent for all reaches of the migration (Table 4; Fig. 4; note that fork length did not vary by timing: $R^2 < 0.01$). Origin was not a

Fig. 2. Diel movement of acoustically tagged Chinook salmon (*Oncorhynchus tshawytscha*) (A) en route to spawning grounds and (B) in the primary spawning tributary (Michie Creek) as indicated by the proportion of detections across all hours of the day (combined detections from 2017 to 2020). Mean hourly August water temperatures ($\pm 95\%$ confidence intervals) are presented for (C) the Yukon River and (D) Michie Creek from 2017 to 2020. Consistent nighttime hours are shown in black, while shifting nighttime hours are shown in grey.

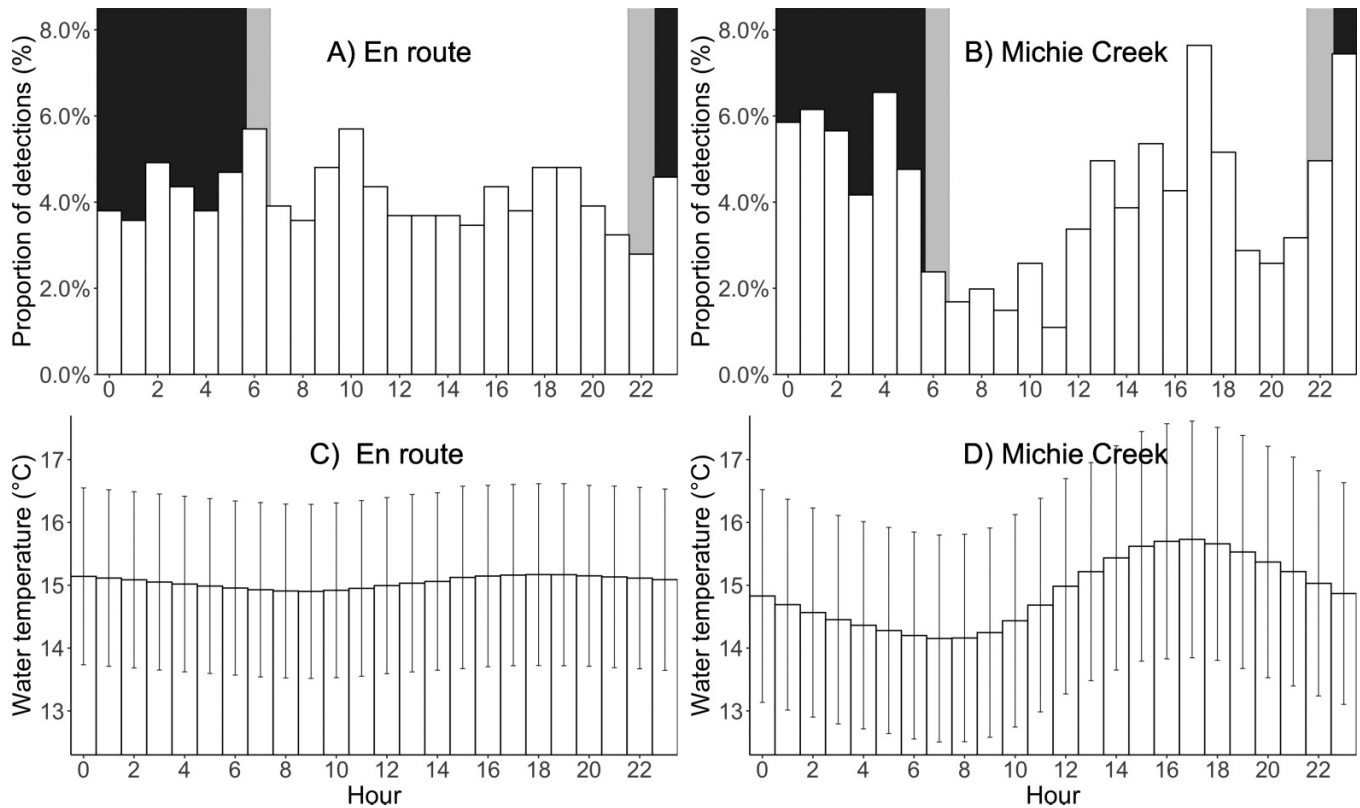


Table 4. Statistical outputs of models evaluating the effects of fish size (fork length), relative migration timing, origin, and sex on reach-specific migration rates, and non-direct homing for Chinook salmon (*Oncorhynchus tshawytscha*) in the upper Yukon River.

Response	Yukon river migration rate				M'Clintock River migration rate				Michie Creek migration rate				Non-direct homing			
	Multiple regression				Multiple regression				Multiple regression				GLM (binomial)			
	Est.	t	n	P-adj	Est.	t	n	P-adj	Est.	t	n	P-adj	Est.	z	n	P-adj
Fish size	0.05	5.32	132	<0.01	0.02	3.58	117	<0.01	-0.01	0.77	90	0.71	-0.05	-1.69	143	0.19
Relative migration timing	2.50	5.56	132	<0.01	1.65	7.10	117	<0.01	0.52	4.81	90	<0.01	-0.95	-0.63	143	0.75
Origin: wild	0.05	0.26	132	0.89	<0.01	<0.01	117	0.99	-0.03	-0.86	90	0.66	-0.16	-0.29	143	0.89
Sex: male	-0.13	-0.67	132	0.75	0.53	5.58	117	<0.01	0.02	0.46	90	0.87	1.40	1.71	143	0.19
Year: 2018	0.04	0.22	132	0.89	0.70	-0.38	117	0.89	-0.12	-2.75	90	0.02	1.65	2.59	143	0.03
Year: 2019	0.30	1.34	132	0.35	-0.28	-2.74	117	0.02	-0.11	2.31	90	0.06	-0.16	-0.18	143	0.89
Year: 2020	0.26	1.00	132	0.57	—	—	—	—	-0.01	-0.22	90	0.89	2.06	2.76	143	0.02

Note: Inferences for factors are presented relative to reference levels ("female" for sex, "hatchery" for origin, and "2017" for year). The acoustic receiver in the M'Clintock River was not retrieved in 2020. P-adj values in boldface type are significant ($P < 0.05$). GLM, generalised linear model.

significant predictor of migration rate through any of the three stretches. Sex was not a significant predictor of migration rate in the Yukon River or Michie Creek, although males had significantly higher migration rates in the M'Clintock River (Table 4).

Homing patterns

Most of the population upstream of the WHP terminated migration in Michie Creek in 2017 (81%), 2018 (80%), 2019 (85%), and 2020 (94%). Approximately 11% of the 90 salmon that migrated to upper Michie Creek (upstream of

Fig. 3. Relationship between fork length (cm) and migration rate (km/h) for acoustically tagged Chinook salmon (*Oncorhynchus tshawytscha*) in the (A) Yukon River (mainstem), (B) M'Clintock River (primary tributary), and (C) Michie Creek (secondary tributary) in 2017 (purple circle), 2018 (blue triangle), 2019 (green square), and 2020 (yellow cross). The acoustic receiver in the M'Clintock River was not retrieved in 2020. [Colour online.]

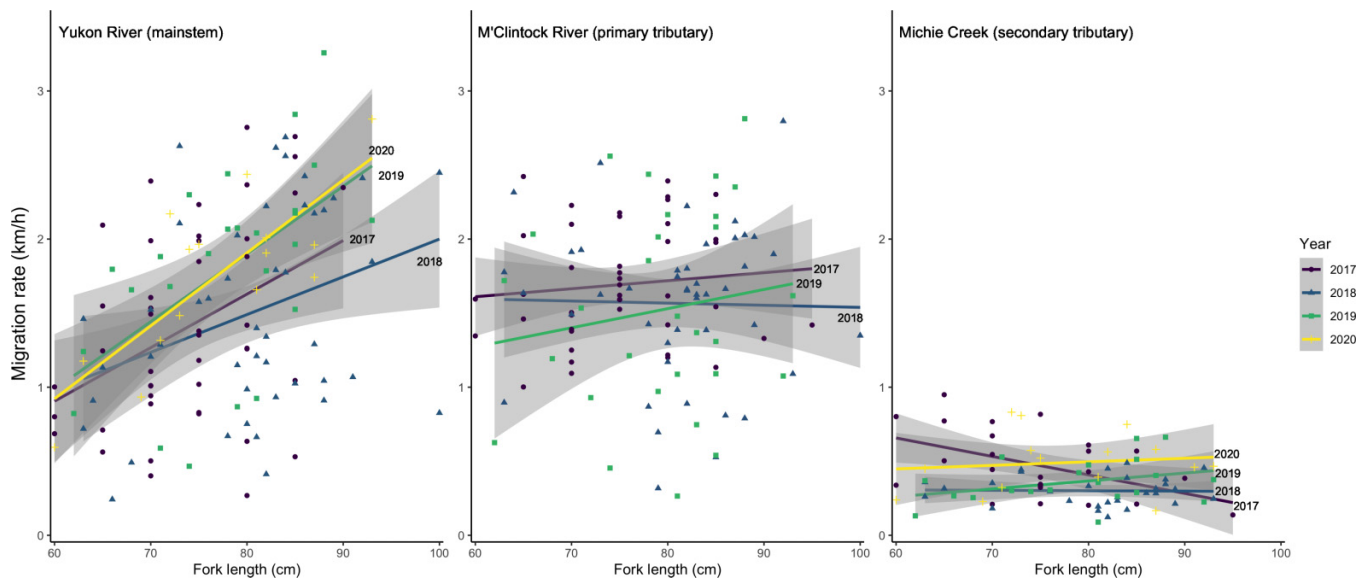
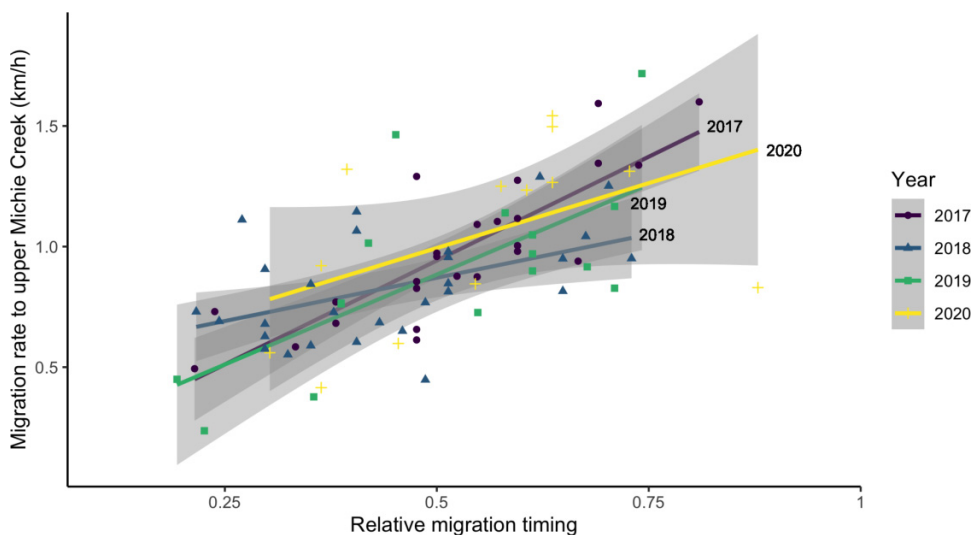


Fig. 4. Migration rate to the upper Michie Creek spawning area in relation to relative migration timing for acoustically tagged Chinook salmon (*Oncorhynchus tshawytscha*) in the upper Yukon River in 2017 (purple circle), 2018 (blue triangle), 2019 (green square), and 2020 (yellow cross). Relative migration timing was defined as the date of arrival at the fishway viewing chamber relative to the first and last fish to do so each year. [Colour online.]



Byng Creek, a small tributary located 22 km from the outlet of Michie Creek) explored tributaries before completing their migration. Exploration rates were similar into Wolf Creek (2.2%; 88 km downstream), the upper M'Clintock River (4.4%; 22 km downstream), and Byng Creek (4.4%; 0 km downstream). No upper Michie Creek salmon explored more than one tributary before arriving at natal sites. Tributary exploration was only undertaken by male salmon (of both wild and hatchery origin). Non-direct homing was observed in 23.4% of salmon migrating to the three known spawning areas (Michie Creek, upper M'Clintock River, and Wolf

Creek) based on our binomial classification of homing behaviour. Non-direct homing increased migration distances in the terminal reaches of this migration by a mean of at least 22.5 ± 8.1 though this was driven by markedly higher non-direct homing by salmon terminating in Wolf Creek (mean of $260 \pm 206\%$; additional 38 km of migration; $n = 8$), compared to the upper M'Clintock River (mean of $15 \pm 49\%$; additional 11.6 km of migration; $n = 61$), and Michie Creek (mean of $3 \pm 11\%$; additional 3 km of migration; $n = 74$). None of sex, origin, size, or relative migration timing was significant predictors of whether salmon undertook non-direct

Table 5. Mortality rates reported for Pacific salmon (*Oncorhynchus* spp.) in the terminal reaches of their spawning migrations.

River	Species (population)	Terminal reach length (km)	Mortality rate (%)	Mortality rate by distance (% per km)	Source
Snake River	Sockeye salmon	242	27.55	0.11	Keefer et al. 2008b
Willamette River	Chinook salmon	~260	16.50	0.06	Keefer et al. 2017
Fraser River	Sockeye (Chilcotin)	379	18.67	0.05	Cooke et al. 2006
Fraser River	Sockeye (Quesnel)	473	11.11	0.02	Cooke et al. 2006
Fraser River	Sockeye (Nechako)	715	4.34	<0.01	Cooke et al. 2006
Yukon River	Chinook salmon	80	1.33	0.03	Current study

Note: For each study, the river, species, length of terminal reach assessed, mortality rate (%), and mortality rate by distance (% per km) are reported.

homing behaviours during migration. Colonization of new habitats was infrequent (<2%) and was a behaviour only observed in males. New habitats were located 80 km (Tutshi River) and 180 km (Atlin Lake) beyond the confluence of the closest known spawning tributary (M'Clintock River). The salmon migrating to Atlin Lake first made an 80 km movement upstream, returned to the WHP reservoir, and then progressed 250 km upstream to Atlin Lake.

Discussion

Chinook salmon from the upper Yukon River have experienced immense declines from their once historic abundance (Cox 1997). Given concern over the low abundance of this population, we conducted a study to describe the survival and migration behaviour of Chinook salmon in the terminal reaches of their migration upstream of Whitehorse, YT. We found that en route survival was high for these fish in this stretch of the migration, and that various biotic and environmental characteristics were associated with differences in migration behaviours. Here, we discuss potential mechanisms underlying these associations and link our findings to the broader literature on Chinook salmon migration behaviour.

En route mortality

Estimated en route mortality was relatively low for Chinook salmon in the terminal reaches of the upper Yukon River compared with that for Pacific Salmon populations in other systems (Table 5). It might be hypothesized that en route mortality would be relatively high for a population undertaking one of the world's longest inland salmon migrations, though a synthesis of prespawn mortality data for Chinook salmon revealed little to no relationship between mortality and migratory work (elevation gain and migration distance; Bowerman et al. 2021). Warm water temperature (Cooke et al. 2004; Naughton et al. 2005; Crossin et al. 2008; Hinch et al. 2012), fisheries (Keefer et al. 2005; Naughton et al. 2013), and natural predation (Peirce et al. 2013; Sorel et al. 2021) are common causes of en route mortality in Pacific salmon throughout their range, though these threats tend to be much less severe in the upper Yukon River, perhaps explaining the low mortality rates observed in this study. Further, salmon included in this study were those that had been successful migrating beyond the WHP via the fishway. Fishways can be selective for fish with certain morphological,

physiological, and behavioural traits that make them more likely to pass the fishway (Castro-Santos et al. 2009) and it is conceivable that these traits may be correlated with greater swimming ability and migration success. A concurrent study at the WHP showed most salmon approaching the fishway fail to pass and that salmon that do pass tend to be those attempting passage for longer periods of time (perhaps an indication of greater condition/fitness; Twardek et al. 2021). As such, it is possible the weaker salmon that may otherwise have succumbed to en route or prespawn mortality in the terminal reaches of the migration never made it past the fishway to become part of the sample. It is also unclear what the mortality rate is for this population in the preceding stretches of this migration, though in general it appears mortality rates near the end of migrations are similar to those earlier in migration (Cooke et al. 2006; Keefer et al. 2008b).

Diel behaviour and migration rates

Salmon movement over the diel period is thought to be context-specific, and to vary based on migratory conditions (Keefer et al. 2013). In the upper Yukon River, movement occurred consistently throughout the day in the mainstem, but in the spawning tributary (Michie Creek), movement rates became more nocturnal. This is contrary to what has previously been reported in the Columbia River, where no significant differences were observed in diel movement between mainstem and tributary habitats, though movement became more diurnal in hydraulically complex areas (fishways), presumably due to an increased reliance on visual cues for navigation (Keefer et al. 2013). However, fish may also shift to more nocturnal behaviour to decrease the likelihood of predation while in shallow, high-vulnerability habitats (discussed in Keefer et al. 2013). In southwestern Alaska, spawning sockeye salmon (*Oncorhynchus nerka* (Walbaum, 1792)) had greater activity in spawning streams at night when grizzly bear (*Ursus arctos* Linnaeus, 1758) activity tended to be lowest (Bentley et al. 2014). Further, Bald Eagles (*Haliaeetus leucocephalus* (Linnaeus, 1766)) are diurnal and tend not to hunt at night (Watson et al. 1991). Both predators are common in Michie Creek, such that it may be advantageous for salmon to reduce their activity during the day when predation risk is highest.

Migration behaviour also differed based on the size of migrating salmon, though the influence of size tended to vary by migratory reach. Size was positively correlated with migration rate in the Yukon River, had a slightly positive

relationship with migration rate in the M'Clintock River, and had little influence on migration rate in Michie Creek (spawning tributary). Larger Chinook salmon have lower energy expenditure for a given swim speed (Geist et al. 2000), which may allow them to migrate at faster rates than smaller fish. However, this size-migration rate relationship was no longer apparent in Michie Creek, where migration rates were much slower than in other larger sections of their migration. Most spawning habitat in Michie Creek is in its upper reaches (between Byng Creek and Michie Lake), though spawning habitat is present throughout the entirety of the creek, which may cause salmon to slow their migration as they begin searching for spawning habitat and mates. Compared to the rest of their migration, Michie Creek is considerably shallower, of higher velocity, and has an abundance of beaver dams that could pose barriers to salmon movement (de Graff 2019) and increase energy expenditure (Hinch and Rand 1998). In 1998, a telemetry study found none of 35 radio-tagged Chinook salmon reached the primary spawning area in Michie Creek, and it was deemed this was likely due to a beaver dam downstream of this habitat (Matthews 1999a, 1999b). For Michie Creek, we hypothesize that differences in migratory behaviour (ie. searching for spawning opportunities) and migratory conditions (e.g., large beaver dams; Kemp et al. 2012) have a greater influence on migration rate than body size.

Relative migration timing was the strongest predictor of migration rate in all three reaches, with salmon migrating later in the season having faster migration rates (despite water temperatures decreasing below thermal optima; Salinger and Anderson 2006). This behavioural pattern is consistent with observations of late-migrating Chinook salmon from the Columbia River, though in this system most salmon arrive at spawning sites before water temperatures reach annual maxima (Keefer et al. 2004). The arrival timing of salmon on spawning grounds has implications for reproductive fitness (Dickerson et al. 2005), such that salmon may need to adjust their migration rates to maximize spawning opportunities. Various factors will influence timing on spawning grounds for an individual fish including its physiological state, reproductive development, availability of mates and habitat, and the suitability of environmental conditions for spawning, among other factors (discussed in Keefer et al. 2008b). Salmon arriving later at spawning grounds may have less access to mates and habitat (Quinn et al. 1996) but reduce their chances that another salmon will dig up their redd (and eggs); a risk associated with early arrival (McNeil 1964; Fukushima et al. 1998). While the association between arrival timing and spawning success is uncertain for this specific population, faster migration rates for salmon migrating later in the season highlight the importance of arrival timing for access to suitable spawning conditions.

Homing patterns

A considerable proportion of the population made non-direct movements to spawning areas that included behaviours such as tributary exploration, downstream movement, and overshoot. These movements increased overall migration distances through the study area by at least 23%,

which inherently has energetic costs. This value is an underestimate given that our receiver array could only capture movements at certain locations and fish would have undoubtedly made smaller scale movements that went undetected. It is unclear why some salmon explored tributaries prior to arriving at terminal locations though multiple potential explanations exist. Salmon are known to enter tributaries to avoid warm temperatures (Gonia et al. 2006), though temperatures typically remained below thermal optima in our study area. Adult salmon may also recognize and enter non-natal tributaries that they used for rearing as juveniles (Bradford et al. 2001; Keefer and Caudill 2014). Salmon may also be attracted to the odours of conspecifics from non-natal tributaries (Bett and Hinch 2016) which could lead to temporary exploration of these sites. In addition to these temporary non-direct movements, a small proportion of salmon (<2%) strayed to areas outside of currently recognized spawning habitat. It is possible that the salmon we classified as colonizers of new habitat had actually returned to natal spawning tributaries given that Traditional Knowledge suggests both stray locations (tributaries off Atlin Lake and the Tutshi River) once supported salmon spawning (Brown et al. 1976). However, these populations would likely have to persist at very low levels based on the number of fish we tagged relative to the population size upstream of the WHP. In addition to colonization of new habitat, it is also possible salmon strayed between known tributaries (e.g., Wolf Creek, M'Clintock River, Michie Creek), though we were unable to quantify this without knowledge of natal streams for each fish.

All salmon that explored tributaries and colonized new habitat were male, consistent with previous studies that have found males to be more exploratory and to have lower levels of homing than females (Neville et al. 2006; Anderson and Quinn 2007; Marklevitz and Morbey 2017). Differences in migration behaviour between the sexes likely reflect their various reproductive strategies. Unlike males, females dig redds and protect offspring until mortality and are unlikely to move away from redd sites and compromise their fitness (Healey et al. 2003). As such, spawning site choice is critical to female reproductive success (Foote 1990). In contrast, males contribute much less to parental care (Healey et al. 2003; Esteve 2005), but face high reproductive competition, making it advantageous to move to different locations along the spawning ground (or between spawning grounds) to attempt spawning with multiple females (Healey and Prince 1995; Quinn et al. 1996; Quinn 1999; Esteve 2005). As an extreme example of this, one male salmon moved downstream ~85 km from Michie Creek and entered another known spawning area (Wolf Creek). Interestingly, salmon movement patterns did not differ by salmon origin, despite consistent evidence that homing ability in hatchery salmon is generally weaker than that of wild salmon (Ford et al. 2015). The collection of hatchery salmon carcasses ($n = 29$) with coded wire tags from the M'Clintock River and Michie Creek in 2005 suggests fidelity to release locations is high in the study area (93%; N.M. de Graff, Canic-a-nick Environmental Services, personal communication, 2022).

Conclusion

This 4-year telemetry study on Chinook salmon from the upper Yukon River provided insight into the behaviour of salmon in the terminal reaches of one of the world's longest inland salmon migrations. We observed low rates of en route mortality, and generally found that salmon homed directly to spawning areas, with some exceptions, mostly among male fish. Salmon migration rates were considerably slower in the primary spawning tributary Michie Creek, compared to larger rivers preceding this system. Migration rates en route to Michie Creek were correlated with salmon size, though this association diminished with proximity to spawning grounds. Late-migrating salmon also tended to have faster migration rates, which was likely necessary to ensure they had sufficient time and suitable conditions on spawning grounds to reproduce. Although no behavioural differences were observed between hatchery and wild salmon, only males explored non-terminal tributaries and the two fish that colonized new habitat were male. It is our hope that findings from this work will contribute to our collective understanding of salmon movement ecology during spawning migrations and will provide important knowledge to support salmon management discussions in the Yukon River, including decisions pertaining to future hatchery practices, harvesting, habitat restoration, and monitoring.

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Data availability

Data are available upon request from the corresponding author.

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Competing interests

The authors declare that there are no competing interests.

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Supplementary material

Supplementary table is available with the article at <https://doi.org/10.1139/cjz-2022-0012>.

References

- Anderson, J.H., and Quinn, T.P. 2007. Movements of adult coho salmon (*Oncorhynchus kisutch*) during colonization of newly accessible habitat. *Can. J. Fish. Aquat. Sci.* **64**: 1143–1154. doi:10.1139/f07-087.
- Bentley, K.T., Schindler, D.E., Cline, T.J., Armstrong, J.B., Macias, D., Ciepiela, L.R., and Hilborn, R. 2014. Predator avoidance during reproduction: diel movements by spawning sockeye salmon between stream and lake habitats. *J. Anim. Ecol.* **83**(6): 1478–1489. doi:10.1111/1365-2656.12223. PMID: 24702169.
- Berejikian, B.A., Endicott, R.C., Van Doornik, D.M., Brown, R.S., Tatara, C.P., and Atkins, J. 2007. Spawning by female Chinook salmon can

- be detected by electromyogram telemetry. *Trans. Am. Fish. Soc.* **136**: 593–605. doi:10.1577/I06-114.1.
- Berman, C.H., and Quinn, T.P. 1991. Behavioural thermoregulation and homing by spring chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), in the Yakima River. *J. Fish. Biol.* **39**: 301–312. doi:10.1111/j.1095-8649.1991.tb04364.x.
- Bett, N.N., and Hinch, S.G. 2016. Olfactory navigation during spawning migrations: a review and introduction of the Hierarchical Navigation Hypothesis. *Biol. Rev.* **91**: 728–759. doi:10.1111/brv.12191. PMID: 25923999.
- Bett, N.N., Hinch, S.G., Burnett, N.J., Donaldson, M.R., and Naman, S.M. 2017. Causes and consequences of straying into small populations of Pacific salmon. *Fisheries*, **42**: 220–230. doi:10.1080/03632415.2017.1276356.
- Bowerman, T., Keefer, M.L., and Caudill, C.C. 2016. Pacific salmon pre-spawn mortality: patterns, methods, and study design considerations. *Fisheries*, **41**(12): 738–749. doi:10.1080/03632415.2016.1245993.
- Bowerman, T.E., Keefer, M.L., and Caudill, C.C. 2021. Elevated stream temperature, origin, individual size influence Chinook salmon pre-spawn mortality across the Columbia River basin. *Fish. Res.* **237**: 105874. doi:10.1016/j.fishres.2021.105874.
- Bradford, M.J., Grout, J.A., and Moodie, S. 2001. Ecology of juvenile chinook salmon in a small non-natal stream of the Yukon River drainage and the role of ice conditions on their distribution and survival. *Can. J. Zool.* **79**(11): 2043–2054. doi:10.1139/z01-165.
- Brown, R.F., Elson, M.S., and Steingenberg, L.W. 1976. Catalogue of aquatic resources of the upper Yukon River. PAC/T-76-4. 172 pp. Available from <https://waves-vagues.dfo-mpo.gc.ca/Library/16715.pdf> [accessed August 2022].
- Brown, R.J., von Finster, A., Henszey, R.J., and Eiler, J.H. 2017. Catalog of chinook salmon spawning areas in Yukon river basin in Canada and United States. *J. Fish. Wildl. Manag.* **8**: 558–586. doi:10.3996/052017-JFWM-045.
- Castro-Santos, T., Cotel, A., and Webb, P.W. 2009. Fishway evaluations for better bioengineering: an integrative approach. *In* Proceedings of the Challenges for Diadromous Fishes in a Dynamic Global Environment. American Fisheries Society Symposium, **69**. pp. 557–575.
- Cooke, S.J., Hinch, S.G., Farrell, A.P., Lapointe, M.F., Jones, S.R., Macdonald, J.S., et al. 2004. Abnormal migration timing and high en route mortality of sockeye salmon in the Fraser River, British Columbia. *Fisheries*, **29**: 22–33. doi:10.1577/1548-8446(2004)29%5b22:AMTAHE%5d2.0.CO;2.
- Cooke, S.J., Hinch, S.G., Crossin, G.T., Patterson, D.A., English, K.K., Healey, M.C., et al. 2006. Mechanistic basis of individual mortality in Pacific salmon during spawning migrations. *Ecology* **87**(6): 1575–1586. doi:10.1890/0012-9658(2006)87%5b1575:MBOIMI%5d2.0.CO;2. PMID: 16869433.
- Cox, J. 1997. Archival research—salmon in the Upper Lakes region, Yukon Territory. Yukon Conservation Society, Whitehorse, YT. 75 pp.
- Crossin, G.T., Hinch, S.G., Cooke, S.J., Welch, D.W., Patterson, D.A., Jones, S.R.M., et al. 2008. Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. *Can. J. Zool.* **86**(2): 127–140. doi:10.1139/Z07-122.
- de Graff, N.M. 2017. KDFN Michie Creek Monitoring Project. Kwanlin Dün Government Report for the Yukon River Panel. Project No. CRE-51-17. 18p + 1 appendix. Available from <https://www.yukonriverpanel.com/restoration-enhancement-fund/r-e-project-reports/> [accessed August 2022].
- de Graff, N.M. 2018. KDFN Michie Creek Monitoring Project. Kwanlin Dün Government Report for the Yukon River Panel. Project No. CRE-51-18. 21p + 1 appendix. Available from <https://www.yukonriverpanel.com/restoration-enhancement-fund/r-e-project-reports/> [accessed August 2022].
- de Graff, N.M. 2019. KDFN Michie Creek Monitoring Project. Kwanlin Dün Government Report for the Yukon River Panel. Project No. CRE-51-19. 22p + 1 appendix. Available from <https://www.yukonriverpanel.com/restoration-enhancement-fund/r-e-project-reports/> [accessed August 2022].
- de Graff, N.M. 2020. KDFN Michie Creek Monitoring Project. Kwanlin Dün Government Report for the Yukon River Panel. Project No. CRE-51-20. 18p + 1 appendix. Available from <https://www.yukonriverpanel.com/restoration-enhancement-fund/r-e-project-reports/> [accessed August 2022].
- Dickerson, B.R., Brinck, K.W., Willson, M.F., Bentzen, P., and Quinn, T.P. 2005. Relative importance of salmon body size and arrival time at breeding grounds to reproductive success. *Ecology*, **86**(2): 347–352. doi:10.1890/03-625.
- Eiler, J.H., Masuda, M.M., Spencer, T.R., Driscoll, R.J., and Schreck, C.B. 2014. Distribution, stock composition and timing, and tagging response of wild Chinook salmon returning to a large, free-flowing river basin. *Trans. Am. Fish. Soc.* **143**(6): 1476–1507. doi:10.1080/00028487.2014.959997.
- Esteve, M. 2005. Observations of spawning behaviour in Salmoninae: *Salmo*, *Oncorhynchus* and *Salvelinus*. *Rev. Fish Biol. Fish.* **15**: 1–21. doi:10.1007/s11160-005-7434-7.
- Foote, C.J. 1990. An experimental comparison of male and female spawning territoriality in a Pacific salmon. *Behaviour*, **115**: 283–314. doi:10.1163/156853990X00617.
- Ford, M.J., Murdoch, A., and Hughes, M. 2015. Using parentage analysis to estimate rates of straying and homing in Chinook salmon (*Oncorhynchus tshawytscha*). *Mol. Ecol.* **24**: 1109–1121. doi:10.1111/mec.13091. PMID: 25626589.
- Fukushima, M., Quinn, T.J., and Smoker, W.W. 1998. Estimation of eggs lost from superimposed pink salmon (*Oncorhynchus gorbuscha*) redds. *Can. J. Fish. Aquat. Sci.* **55**: 618–625. doi:10.1139/f97-260.
- Geist, D.R., Abernethy, C.S., Blanton, S.L., and Cullinan, V.I. 2000. The use of electromyogram telemetry to estimate energy expenditure of adult fall chinook salmon. *Trans. Am. Fish. Soc.* **129**(1): 126–135. doi:10.1577/1548-8659(2000)129(0126:TUOETT)2.0.CO;2.
- Gonia, T.M., Keefer, M.L., Bjornn, T.C., Peery, C.A., Bennett, D.H., and Stuehrenberg, L.C. 2006. Behavioral thermoregulation and slowed migration by adult fall Chinook salmon in response to high Columbia River water temperatures. *Trans. Am. Fish. Soc.* **135**(2): 408–419. doi:10.1577/T04-113.1.
- Groot, G., and Margolis, J. 1991. Pacific salmon life histories. UBC Press, Vancouver, BC.
- Healey, M.C., and Prince, A. 1995. Scales of variation in life history tactics of Pacific salmon and the conservation of phenotype and genotype. *In* Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society Symposium 17. Edited by J.L. Nielsen. pp. 176–184. American Fisheries Society Symposium, Bethesda, MD.
- Healey, M.C., Lake, R., and Hinch, S.G. 2003. Energy expenditures during reproduction by sockeye salmon (*Oncorhynchus nerka*). *Behaviour*, **140**: 161–182. doi:10.1163/156853903321671488.
- Hinch, S.G., and Rand, P.S. 1998. Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): role of local environment and fish characteristics. *Can. J. Fish. Aquat. Sci.* **55**(8): 1821–1831. doi:10.1139/f98-067.
- Hinch, S.G., Cooke, S.J., Farrell, A.P., Miller, K.M., Lapointe, M., and Patterson, D.A. 2012. Dead fish swimming: a review of research on the early migration and high premature mortality in adult Fraser River sockeye salmon *Oncorhynchus nerka*. *J. Fish. Biol.* **81**: 576–599. doi:10.1111/j.1095-8649.2012.03360.x. PMID: 22803725.
- Joint Technical Committee of the Yukon River U.S./Canada Panel (JTC). 2021. Yukon River salmon 2020 season summary and 2021 season outlook. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 3A17-01, Anchorage, AK. 166pp. Available from <https://www.adfg.alaska.gov/FedAidPDFs/RIR.3A.2021.01.pdf> [accessed August 2022].
- Keefer, M.L., and Caudill, C.C. 2014. Homing and straying by anadromous salmonids: a review of mechanisms and rates. *Rev. Fish Biol. Fish.* **24**: 333–368. doi:10.1007/s11160-013-9334-6.
- Keefer, M.L., Peery, C.A., Jepson, M.A., and Stuehrenberg, L.C. 2004. Upstream migration rates of radio-tagged adult Chinook salmon in riverine habitats of the Columbia River basin. *J. Fish. Biol.* **65**(4): 1126–1141. doi:10.1111/j.0022-1112.2004.00522.x.
- Keefer, M.L., Peery, C.A., Daigle, W.R., Jepson, M.A., Lee, S.R., Boggs, C.T., et al. 2005. Escapement, harvest, and unknown loss of radio-tagged adult salmonids in the Columbia River Snake River hydrosystem. *Can. J. Fish. Aquat. Sci.* **62**(4): 930–949. doi:10.1139/f04-246.
- Keefer, M.L., Caudill, C.C., Peery, C.A., and Bjornn, T.C. 2006. Route selection in a large river during the homing migration of Chinook salmon (*Oncorhynchus tshawytscha*). *Can. J. Fish. Aquat. Sci.* **63**(8): 1752–1762. doi:10.1139/f06-068.

- Keefer, M.L., Caudill, C.C., Peery, C.A., and Boggs, C.T. 2008a. Non-direct homing behaviours by adult Chinook salmon in a large, multi-stock river system. *J. Fish. Biol.* **72**: 27–44. doi:10.1111/j.1095-8649.2007.01652.x.
- Keefer, M.L., Peery, C.A., and Heinrich, M.J. 2008b. Temperature-mediated en route migration mortality and travel rates of endangered Snake River sockeye salmon. *Ecol. Freshw. Fish.* **17**(1): 136–145. doi:10.1111/j.1600-0633.2007.00267.x.
- Keefer, M.L., Caudill, C.C., Peery, C.A., and Moser, M.L. 2013. Context-dependent diel behavior of upstream-migrating anadromous fishes. *Environ. Biol. Fishes* **96**: 691–700. doi:10.1007/s10641-012-0059-5.
- Keefer, M.L., Jepson, M.A., Naughton, G.P., Blubaugh, T.J., Clabough, T.S., and Caudill, C.C. 2017. Condition-dependent en route migration mortality of adult Chinook salmon in the Willamette River main stem. *N. Am. J. Fish. Manag.* **37**(2): 370–379. doi:10.1080/02755947.2016.1269032.
- Kemp, P.S., Worthington, T.A., Langford, T.E., Tree, A.R., and Gaywood, M.J. 2012. Qualitative and quantitative effects of reintroduced beavers on stream fish. *Fish. Fish.* **13**(2): 158–181. doi:10.1111/j.1467-2979.2011.00421.x.
- Marklevitz, S.A., and Morbey, Y.E. 2017. Habitat use and arrival timing of hatchery and naturalized Chinook salmon spawning in a Great Lakes tributary. *Trans. Am. Fish. Soc.* **146**(4): 567–583. doi:10.1080/00028487.2017.1300606.
- Matthews, I.P. 1999a. Radio tagging adult Chinook Salmon (*Oncorhynchus tshawytscha*) returning to the Whitehorse Fishway 1998. Unpublished report. Yukon River Restoration and Enhancement Project No. CRE-28-98. Whitehorse, YT. 28pp. Available from <https://www.yukonriverpanel.com/restoration-enhancement-fund/r-e-project-reports/#6-32-1998> [accessed August 2022].
- Matthews, I.P. 1999b. Wolf and Michie Creek enumeration weirs, 1998. Unpublished report. Yukon River Restoration and Enhancement project No. CRE-27-98. Whitehorse, YT. 25pp. Available from <https://www.yukonriverpanel.com/restoration-enhancement-fund/r-e-project-reports/#6-32-1998> [accessed August 2022].
- McNeil, W.J. 1964. Redd superimposition and egg capacity of pink salmon spawning beds. *J. Fish. Board Can.* **21**(6): 1385–1396. doi:10.1139/f64-119.
- Naughton, G.P., Caudill, C.C., Keefer, M.L., Bjornn, T.C., Stuehrenberg, L.C., and Peery, C.A. 2005. Late-season mortality during migration of radio-tagged adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. *Can. J. Fish. Aquat. Sci.* **62**: 30–47. doi:10.1139/f04-147.
- Naughton, G.P., Caudill, C.C., Keefer, M.L., Bjornn, T.C., Peery, C.A., and Stuehrenberg, L.C. 2006. Fallback by adult sockeye salmon at Columbia River dams. *N. Am. J. Fish. Manag.* **26**: 380–390. doi:10.1577/M05-015.1.
- Naughton, G.P., Caudill, C.C., Clabough, T.S., Keefer, M.L., Knoff, M.J., and Jepson, M.A. 2013. Migration behavior and spawning success of spring Chinook salmon in Fall Creek and the North Fork Middle Fork Willamette River: relationships among fate, fish condition, and environmental factors, 2012. Technical Report 2013-2, University of Idaho, Department of Fish and Wildlife Sciences, Moscow.
- Naughton, G.P., Keefer, M.L., Clabough, T.S., Knoff, M.J., Blubaugh, T.J., and Caudill, C.C. 2018. Tag effects on prespawn mortality of chinook salmon: a field experiment using passive integrated transponder tags, radio transmitters, and untagged controls. *N. Am. J. Fish. Manag.* **38**(1): 96–103. doi:10.1002/nafm.10034.
- Neville, H., Isaak, D., Dunham, J., Thurow, R., and Rieman, B. 2006. Fine-scale natal homing and localized movement as shaped by sex and spawning habitat in Chinook salmon: insights from spatial autocorrelation analysis of individual genotypes. *Mol. Ecol.* **15**(14): 4589–4602. doi:10.1111/j.1365-294X.2006.03082.x. PMID: 17107485.
- Peirce, J.M., Otis, E.O., Wipfli, M.S., and Follmann, E.H. 2013. Interactions between brown bears and chum salmon at McNeil River, Alaska. *Ursus*, **24**: 42–53. doi:10.2192/URSUS-D-12-00006.1.
- Quinn, T.P. 1999. Variation in pacific salmon reproductive behaviour associated with species, sex and levels of competition. *Behaviour*, **136**: 179–204. doi:10.1163/156853999501270.
- Quinn, T.P. 2018. The behavior and ecology of Pacific salmon and trout. 2nd ed. University of Washington Press, Seattle, WA.
- Quinn, T.P., Adkison, M.D., and Ward, M.B. 1996. Behavioral tactics of male sockeye salmon (*Oncorhynchus nerka*) under varying operational sex ratios. *J. Ethol.* **102**: 304–322. doi:10.1111/j.1439-0310.1996.tb01127.x.
- R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.R-project.org/>.
- Salinger, D.H., and Anderson, J.J. 2006. Effects of water temperature and flow on adult salmon migration swim speed and delay. *Trans. Am. Fish. Soc.* **135**(1): 188–199. doi:10.1577/T04-181.1.
- Schoen, E.R., Wipfli, M.S., Trammell, E.J., Rinella, D.J., Floyd, A.L., Grunblatt, J., et al. 2017. Future of Pacific salmon in the face of environmental change: lessons from one of the world's remaining productive salmon regions. *Fisheries*, **42**(10): 538–553. doi:10.1080/03632415.2017.1374251.
- Sorel, M.H., Zabel, R.W., Johnson, D.S., Wargo Rub, A.M., and Converse, S.J. 2021. Estimating population-specific predation effects on Chinook salmon via data integration. *J. Appl. Ecol.* **58**: 372–381. doi:10.1111/1365-2664.13772.
- Thieurmel, B., and Elmarhraoui, A. 2019. Compute sun position, sun-light phases, moon position and lunar phase. Package 'suncalc'. 10pp. Available from <https://cran.r-project.org/web/packages/suncalc/suncalc.pdf> [accessed 28 April 2022].
- Twardek, W.M., Lapointe, N.W.R., and Cooke, S.J. 2021. Assessing the fate of returning upper Yukon River Chinook salmon (2017–2020). Technical Report. 30pp. Available from <https://cwf-fcf.org/en/resources/research-papers/ASSESSING-THE-FATE-OF-RETURNING-UPPER-YUKON-RIVER-CHINOOK-SALMON-2017-2020.pdf> [accessed August 2022].
- Twardek, W.M., Lapointe, N.W.R., and Cooke, S.J. 2022. High egg retention in Chinook salmon *Oncorhynchus tshawytscha* carcasses sampled downstream of a migratory barrier. *J. Fish Biol.* **100**: 715–726. doi:10.1111/jfb.14985. PMID: 34958124.
- Ueda, H. 2011. Physiological mechanism of homing migration in Pacific salmon from behavioral to molecular biological approaches. *Gen. Comp. Endocrinol.* **170**(2): 222–232. doi:10.1016/j.ygcen.2010.02.003. PMID: 20144612.
- Von Finster, A., Ricks, W.R., and Viksten, J. 1998. Juvenile chinook salmon downstream migration investigation. Unpublished report. Yukon River Chinook Salmon Restoration and Enhancement Project #Re-19-98. 58pp. Available from <https://www.yukonriverpanel.com/restoration-enhancement-fund/r-e-project-reports/#6-32-1998> [accessed August 2022].
- Wagner, P., and Hilsen, T. 1992. 1991 Evaluation of adult fallback through the McNary Dam juvenile bypass system. Washington Department of Fisheries, Olympia, WA.
- Watson, J.W., Garrett, M.G., and Anthony, R.G. 1991. Foraging ecology of bald eagles in the Columbia River estuary. *J. Wildl. Manage.* **55**: 492–499. doi:10.2307/3808981.
- Westley, A.P., Quinn, T.P., and Dittman, A.H. 2013. Rates of straying by hatchery-produced Pacific salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss*) differ among species, life history types, and populations. *Can. J. Fish. Aquat. Sci.* **70**(5): 735–746. doi:10.1139/cjfas-2012-0536.
- Young, J.L., Hinch, S.G., Cooke, S.J., Crossin, G.T., Patterson, D.A., Farrell, A.P., et al. 2006. Physiological and energetic correlates of en route mortality for abnormally early migrating adult sockeye salmon (*Oncorhynchus nerka*) in the Thompson River, British Columbia. *Can. J. Fish. Aquat. Sci.* **63**(5): 1067–1077. doi:10.1139/f06-014.
- Yukon Energy Corporation. 2018. Whitehorse Rapids fish ladder and hatchery. Available from https://yukonenergy.ca/media/site_documents/fish_ladder_brochure_eng_new_logo_2018.pdf [accessed August 2022].