THE EFFECT OF THERMAL EXPERIENCE ON THE SURVIVAL OF SOCKEYE SALMON (ONCORHYNCHUS NERKA) DURING THEIR SPAWNING MIGRATION IN THE FRASER RIVER, BC

by

Emily Mason

B.Sc., University of British Columbia, 2016

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
IN
NATURAL RESOURCES AND ENVIRONMENTAL STUDIES

UNIVERSITY OF NORTHERN BRITISH COLUMBIA

April 2025

Abstract

Sockeye salmon (*Oncorhynchus nerka*) hold tremendous cultural, economic, and ecological value. The Fraser River, in British Columbia supports the largest return of sockeye salmon in Canada. The water temperature in the Fraser River has been increasing in recent decades, with an estimated increase of 1.5°C and 3°C in mean and maximum temperatures, respectively, since the 1950s and a significant increase in the number of days above critical thermal threshold for sockeye salmon. Sockeye salmon are ectotherms, meaning their physiology is highly dependent on their external environment and driven by changes in external temperature. Previous studies have shown that sockeye salmon experience significant impairment and mortality between 18°C and 21°C, and that the impacts of water temperature on survival vary between sexes and populations. Data for this study were collected by LGL Limited, UBC, Kintama, and DFO researchers and their partners. 3265 sockeye salmon were captured and either tagged with radio or acoustic transmitters in 2002, 2003, 2006, 2010, and 2011 and their migration was tracked using receiver arrays. Field-based studies that aim to investigate how water temperature affects survival during the adult spawning migration pose several challenges: 1) what aspect of the thermal experience is assessed, 2) imperfect detection can influence the outcome of studies relying on tagged fish, and 3) populations with small numbers of tagged fish can create unreliable estimates. I aim to address these challenges by 1) comparing the effect of three components of thermal experience, 2) by using an integrated travel time model and state-space version of the Cormack Jolly Seber (CJS) model to differentiate survival and detection, and 3) using a hierarchical mixed effects model to improve the survival probability estimates of populations with low sample sizes. The three aspects of thermal experience that were tested were: 1) the average temperature of the first 10 days following entry into the Fraser River, 2) the moving average of river temperature up to the final detection, and 3) the number of days above 18°C up to the final detection. The best fitting model, of the moving average river temperature prior to the final detection, was selected. The highest overall migration survival probability was found in the Harrison River Conservation Unit (CU), while the lowest overall migration survival probability was estimated in the Anderson-Seton CU. Across all CUs the overall migration survival probability estimate was lower for females than males. Male and female sockeye salmon reached 50% survival probability at ~18.5-20°C and ~18°C-19°C average temperature, respectively. These results align with previous research indicating sockeye salmon survival is significantly impaired between 18°C-21°C. These results also provide evidence to support conservation and enhancement of thermal refuges as well as conservation unit and sex-specific escapement targets and management adjustments.

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Acknowledgements

I wouldn’t have been able to complete this Master’s program without the support of many wonderful people. I would like to start by thanking my supervisor, Dr. Eduardo Martins, for his patient and kind guidance. Eduardo has been understanding and generous with his time and knowledge. I would also like to thank my committee members Dr. Mark Shrimpton and Dr. David Patterson for their guidance.

The data used in this thesis were collected by many researchers from UBC, DFO, Kintama, and LGL Limited along with their partners. I’m grateful for their hard work, and for allowing me to use these data.

I’m grateful to my family and my amazing partner for their loving support and encouragement. Thank you to my fellow students in the Freshwater Fish Ecology Lab for their camaraderie. I’m very thankful to Erin Hall for making weekend work sessions much more enjoyable and to Bryce O’Connor for putting up with all my questions.

I started this Master’s program collaborating on a project with the Lake Babine Nation Fisheries Department. For health reasons, I was unable to complete that project, but I would be remiss if I didn’t express my deep gratitude to those that were involved. Thank you to Cassie Allen for digging through mountains of spawned salmon with me to recover a handful of radio tags, and to Brandon West, Andy Rosenberger, and Elissa Sweeney-Bergen for your assistance with other fieldwork. Finally, thank you to Donna Macintyre, whose determination and passion were an inspiration. She is deeply missed.

INTRODUCTION

Pacific salmon (*Oncorhynchus sp.*) provide great value to the social, economic and ecological systems with which they interact. Sockeye salmon (*Oncorhynchus nerka*), in particular, are highly valued in the Pacific Northwest. They hold great cultural importance and support First Nations Food, Social and Ceremonial Fisheries (Earth Economics, 2021). Sockeye salmon also provide the basis for marine and in river commercial fisheries and recreational fisheries. For example, a special report prepared for the Pacific Salmon Commission found that commercial and recreational wild salmon fisheries contributed $1.364 billion (USD) in gross revenue to the Canadian economy and 12,400 full time equivalent jobs between 2012 and 2015 (Gislason et al. 2017). Salmon also bring essential marine derived nutrients to the watersheds in which they spawn, supporting healthy ecosystems throughout their range (Naiman et al. 2002). Pacific salmon are a food source for many fish and wildlife species including grizzly bears *(Ursus arctos horribilis*)*,* black bears *(Ursus americanus*), and gray wolves *(Canis lupus*) (Dairmont et al. 2003; Gende et al. 2001). Terrestrial wildlife will consume varying amounts of the salmon and distribute the remaining carcass in the riparian ecosystems (Gende et al. 2001; Harding et al. 2019). The influx of marine-derived nutrients can support increased plant productivity up to 125m from the stream banks in years of high salmon abundance and can increase berry production on salmon berry shrubs, leading to increased food availability for terrestrial wildlife (Kieran et al. 2021; Siemens et al. 2020). Increased salmon abundance is also positively related to diversity and abundance of birds in riparian ecosystems (Wagner and Reynolds 2019).

The Fraser River, covering approximately one third of British Columbia, is an incredibly important system for sockeye salmon production. It supports the largest sockeye salmon return in Canada and at one time could have returns of 100 million sockeye salmon in a single year (Ricker 1987). Sockeye salmon have high fidelity to their natal streams and return to those streams to spawn using magnetic fields and their olfactory senses (Dat et al. 1995; Fraser Basin Council 2011). This means Fraser River sockeye salmon have developed genetically unique spawning populations that migrate between 100km and 1200km to reach their spawning grounds in the Fraser River Watershed (Beacham et al. 2005; Cooke et al. 2004). The Fraser River sockeye salmon populations have declined over the past several decades, with returns between 1980 and 2014 averaging approximately 9.6 million (Grant et al 2017). In recent years, returns have declined further with only ~300,000 sockeye salmon returning in 2020 (PSC 2020).

Fraser River sockeye salmon face a variety of challenges that may be contributing to their decline, such as overfishing, climate change leading to changes in water temperature and flow regimes, habitat degradation, parasites, pathogens, and human-caused and natural barriers to migration (Beacham et al. 2004; DFO 2020a; DFO 2020b; Farrell et al. 2008; Godwin et al. 2015; Martins et al. 2012; Peterman et al. 2010, Ricker et al. 1987). The Fraser River has increased in mean and maximum summer temperatures by 1.5°C and 3°C, respectively, since the 1950s (Patterson et al 2007). Furthermore, retrospective modelling indicated that the number of days above the critical thermal thresholds of 18°C and 20°C for Pacific salmon have also increased over the period from 1950-2015 in 13 out of 17 sites along the Fraser River and tributaries, with the number of days between July and September exceeding 20°C being highest at the Stuart River at Fort St. James (Islam et al. 2019).

There is a growing body of research investigating the effects of river temperature and climate warming on the energetics, health, and physiology and their impacts on survival of adult migrating sockeye salmon (Mayer et al. 2024). The most energetically demanding portion of the spawning migration of sockeye salmon occurs in fresh water. As sockeye salmon stop feeding when they leave salt water, they must complete their upriver migration with finite energy reserves (Rand et al 2006; Wilson et al. 2022). Increased water temperatures during the upriver migration period can lead to an exponential increase in standard metabolic rate and therefore energy use, which causes increased rates of exhaustion and pre-spawn mortality (Eliason and Farrell 2016; Rand et al. 2006). Forecasts of energy depletion given projected climate change in the Fraser River Watershed indicate that these effects may intensify in the future (Rand et al. 2006). In addition to modulating the energy used for migration, high water temperatures may reduce the energy allocated to reproductive maturation, especially in female Pacific salmon. Indeed, experimental studies have shown that sockeye salmon held at warm temperatures experienced a lower rate of reproductive maturation than those held at a cooler temperature (Jeffries et al. 2012; Teffer et al. 2019).

Warm river temperatures can also accelerate the development of parasites and pathogens, which can cause disease and lead to mortality and reduced fitness of adult migrating salmon (Godwin et al. 2015; Teffer et al. 2019; Wagner et al. 2005). In cases where high water temperatures lead to increased stress, sockeye salmon may be more susceptible to microparasites (Miller et al. 2014). Indeed, the higher level of stress exhibited by females make them more susceptible to succumb to pathogens than males toward the end of the upstream migration (Hinch et al. 2021; Martins et al. 2012). The capture and associated handling that may occur during fisheries can further exacerbate salmon mortality (Teffer et al. 2019; Teffer et al. 2022).

Variability in survival at elevated water temperatures exists between populations of sockeye salmon in the Fraser River (Eliason et al. 2011; Farrell et al. 2008; Lee et al. 2003; Martins et al. 2011; Mayer et al. 2024). These variations may be linked to factors such as higher aerobic scope in populations with more arduous migratory routes (e.g. high migration gradient) and the historical thermal experience of each population (Eliason et al. 2011; Farrell et al. 2008; Farell 2009; Fry 1947; Lee et al. 2003; Mayer et al. 2024). The collapse of cardiac performance, specifically heart rate, of sockeye salmon and the resulting inability to circulate enough oxygen to swimming muscles in water above an individual's thermal threshold likely causes the collapse in aerobic scope at higher water temperatures (Eliason et al. 2013).

In addition to variability between populations, there is variability in survival at high water temperatures within populations, notably between male and female sockeye salmon. Females tend to experience higher rates of mortality at warmer temperatures than males, which may result in altered sex ratios on spawning grounds and lead to lower recruitment (Hinch et al. 2021; Jeffries et al. 2012; Martins et al. 2012). Research into understanding the mechanisms behind the elevated mortality of female sockeye salmon and other Pacific salmon during their spawning migration is ongoing. Possible mechanisms include higher resource allocation to gonad development, reduced immune function, physiological impairment following stressors that are exacerbated in higher water temperatures (Crossin 2004; Eliason et al. 2020; Gale et al. 2014; Teffer et al. 2017; Teffer et al. 2019). Physiological factors such as the plasma glucose levels, which indicates stress, can also lead to intrapopulation variability in survival (Minke-Martin et al. 2017). Finally, Minke-Martin et al. (2017) showed that challenges experienced during a fish's spawning migration, such as spending time outside the preferred range of water temperatures, and experiencing physical challenges, such as increased discharge from a dam, may lead to survival variability within a population.

Significant progress has been made in understanding how temperature causes mortality in migrating adult sockeye salmon, however, further work is still needed to quantify the relationship between thermal experience and survival. Field-based studies investigating the relationship between thermal experience and survival in upstream migrating sockeye salmon pose several challenges. First, the aspect of thermal experience used to assess survival varies between studies. There are many ways that thermal experience can influence health and survival of salmon, such as magnitude, duration, or frequency of exceeding temperature thresholds, and these metrics can vary as fish migrate upstream. Thus, the challenge is to identify a representative metric that can be used to estimate survival of an individual throughout its migration (Steel et al. 2017). Second, these studies are often based on either acoustic or radio telemetry or both, and receiver array design and extent will vary between tracked populations and can also vary across years. This makes it challenging to fit a single model to the entire dataset and take full advantage of the information contained in it. Furthermore, classic mark-recapture models typically applied to these datasets cannot separate survival from detection probability at the last receiver array for a population. Finally, survival estimates tend to be possible only for populations with high numbers of tagged individuals (Martins et a. 2012), leaving us with an incomplete understanding of the effects of temperature on survival of less abundant populations.

In this study, I address these challenges to improve our understanding of the effects of temperature on the survival probability of sockeye salmon from 20 Conservation Units as they migrate upstream in the Fraser River (Holtby and Ciruna 2008). Specifically, I (1) assess several metrics of thermal experience to identify which may better describe survival, (2) use an integrated travel time model and state-space version of the Cormack Jolly Seber (CJS) model (based on the model developed by Muthukumarana et al. 2008) to accommodate various telemetry approaches and array designs between populations and across years, as well as to differentiate between detection and survival probabilities at the last receiver array for each population (possible with the integration of the a travel time model and the CJS model as described in Muthukumarana et al 2008), and (3) employ hierarchical mixed effects modelling to improve survival probability estimates obtained from data limited conservation units by "borrowing strength from the ensemble" (Schaub and Kéry 2012).

METHODS

Study System

The Fraser River extends 1375 km from its headwaters in the Rocky Mountains to its mouth near Vancouver, British Columbia (Martins et al. 2023). The over 100 populations of Fraser River sockeye salmon are grouped into 24 conservation units (CU) consisting of individuals that are genetically or geographically distinct from other populations (Holtby and Ciruna 2007, Grant et al. 2011). These are further grouped, for management purposes, into four stock management units based on the timing of their return to the Fraser River. From earliest to latest these are the Early Stuart (peaking in early July), Early Summer (peaking in late July), Summer (peaking in August), and Late runs (peaking in September/October) (Beacham et al. 2004, Cooke et al. 2004). This study focuses on sockeye salmon from the following run-time groups and CUs: (1) Early Summer: Early Shuswap, Anderson-Seton, Bowron, Kamloops, Nahatlatch, North Barriere, Pitt, and Nadina-Francois (includes Francois (first run)) (2) Summer:

Seton, Francois-Fraser, Harrison River, Quesnel, and Takla-Trembleur-Stuart, (3) Late: Harrison (Downstream), Harrison (Upstream), Lillooet-Harrison, Shuswap Complex and Cultus. There are two Chilko CUs, the Early Summer and Summer (Grant et al. 2011, Figure 1). As tagged individuals cannot be distinguished between these two CUs, I grouped them for the analysis and assumed they are from the Summer CU, which is the most abundant.

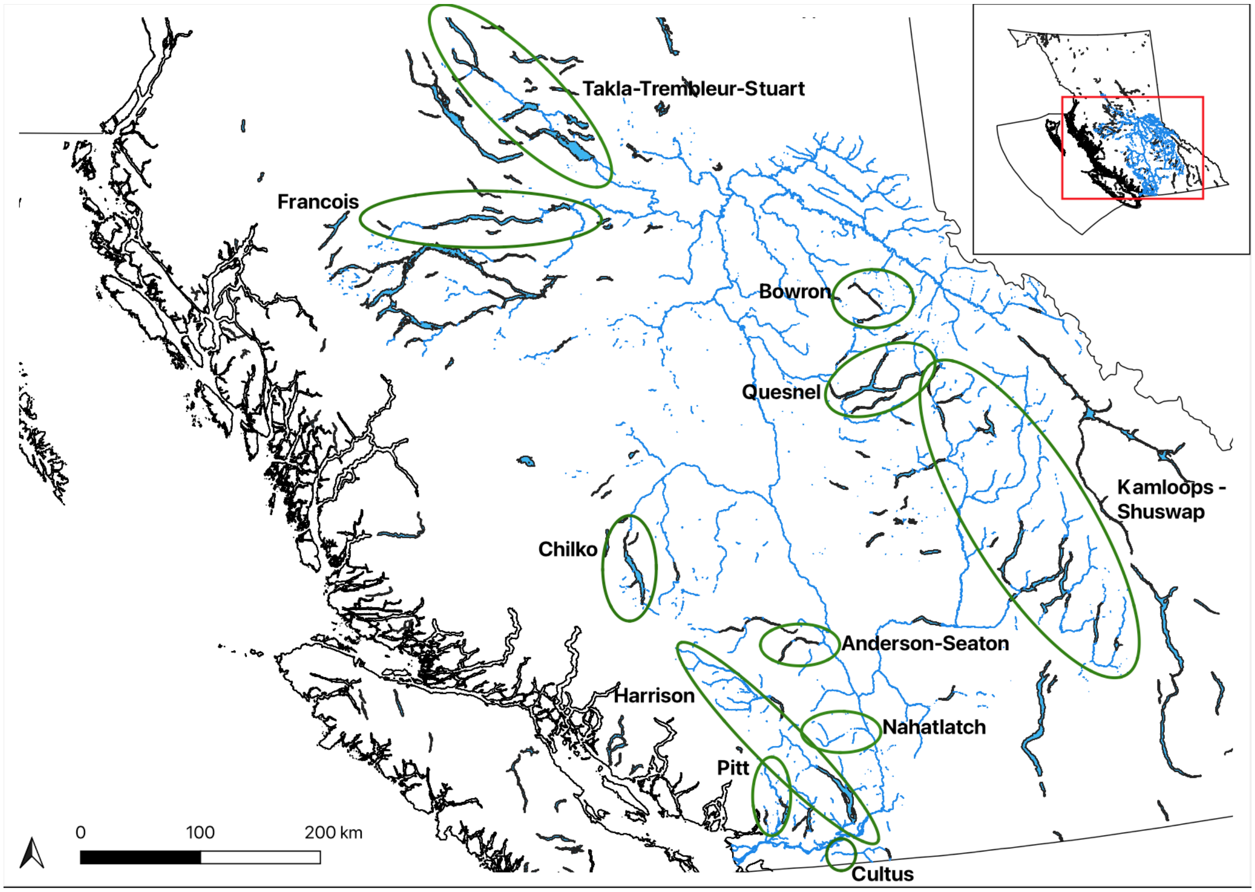

Figure *1*: Map of the Fraser River watershed. CUs included in this study are circled in green. “Francois” represents the Francois-Fraser, Francois (first-run), and Nadina-Francois conservation units. “Kamloops-Shuswap” represents Kamloops, North Barriere, Shuswap, and Shuswap-complex conservation units. “Harrison” represents Harrison upstream, Harrison downstream, Harrison river, and Lillooet-Harrison. “Anderson-Seton” represents Anderson-Seton and Seton conservation units. QGIS.org (2023).

Tagging and monitoring

The data used in this study were collected from previously published studies on sockeye salmon (n = 3265) that were captured and tagged with radio or acoustic transmitters in the marine environment in 2002 (n = 873), 2003 (n = 611), 2006 (n = 656), 2010 (n = 1060) and 2011 (n = 65); Drenner 2014; English et al. 2004; English et al. 2005; Robichaud 2007; Wilson 2014; Wilson 2022). The data were collected in various studies by LGL Limited, Kintama, DFO, and the University of British Columbia (UBC) researchers. The number of tags applied to each CU ranged from one in the François (first run) CU to 1313 in the Shuswap Complex CU (Table 1). All tagged individuals were biopsied, and their CU of origin was identified through DNA analysis. The upriver migration of tagged sockeye salmon was monitored with arrays of radio or acoustic receivers deployed throughout the Fraser River Watershed in the study years.

Table 1: The number of individuals from each conservation unit tagged across study years, summarized by region within the Fraser River Watershed.

Region	**Number of Tags (Region)**	**Conservation Unit**	**Number of Tags (CU)**
Lower Fraser	314	Cultus	2
		Harrison (DS)	3
		Harrison (US)	110
		Harrison River	112
		Lillooet-Harrison	74
		Pitt	13
Mid-Fraser	35	Anderson-Seton	5
		Nahatlatch	2
		Seton	28
Thompson	1721	Kamloops	17
		North Barriere	6
		Shuswap	385
		Shuswap Complex	1313
Upper Fraser	1124	Bowron	15
		Chilko	473
		Francois (First Run)	1
		Francois-Fraser	179
		Nadina-Francois	8
		Quesnel	407
		Summer Takla-Trembleur-Stuart	41
Unknown	71	Unknown	71

In 2002, sockeye salmon were captured in the Juan de Fuca and Johnstone Straits using a seine net (English et al. 2005). This study was targeting late-run sockeye salmon, so tagging did not begin until more than 20% of the sockeye salmon being caught in the test fishery were identified through DNA testing as being from late-run populations. Radio transmitters (MCFT-3A, Lotek Wireless, Inc., of Newmarket, Ontario, Canada) programmed to transmit for 154 days were gastrically implanted into 873 sockeye salmon. A total of 17 fixed radio receiver stations were installed along the Fraser River, the first being installed at Barnston Island and the last at the confluence of the Quesnel River and the Fraser River (SRX400 or SRX400A radio receivers with 3 or 4-element Yagi antennas).

In 2003, sockeye salmon were tagged using the same method as 2002. Tagging, however, only occurred in Johnstone Strait (English et al. 2004; English et al. 2005). A total of 611 radio tags were applied between August 11th and 28th in three sessions. A total of 16 SRX400 and SRX400A receivers with 3 or 4 element Yagi antenna were installed in 15 locations. Two were installed on either side of the river at Mission to get the maximum coverage of the 730 m span. Mobile tracking was conducted at Weaver Creek, Birkenhead River, Portage Creek, Horsefly River, lower Shuswap River, and Shuswap Lake.

In 2006, sockeye salmon were captured, tagged and released both in the marine (660) and in-river (378) environments (Robichaud et al. 2007). In the marine environment, tagging initially occurred in the Juan de Fuca Strait but after the initial four days of tagging the crew relocated to the Johnstone Strait to target a higher proportion of Late-run Fraser sockeye salmon. Marine and in-river tagging was conducted between August 6th and 27th and July 9th and September 1st, respectively. Sockeye salmon were tagged with Lotek MCFT-3A radio transmitters programmed to transmit for 154 days and several biological samples were collected. Marine-tagged fish were initially immediately released, but after fish exhibited stress upon their release, they were held in a continuous flow holding tank until they could right themselves. Only marine-tagged fish were included in my analysis, as it was assumed that if they survived until river entry they were sufficiently recovered from the stress of capture and handling. A total of 24 stationary receivers were installed on the Fraser River mainstem and tributaries. There were two stations installed at the Fraser River at Mission on each side of the river to cover as much of the channel as possible. Mobile receivers were used to search the tributaries that were not monitored by stationary receivers. All stationary and mobile receivers were SRX400, SRX400A and SRX600 models with 3- or 4-element Yagi antenna.

Additional tagging occurred in 2006, 2010, and 2011 (Drenner et al. 2014; Wilson et al. 2014; Wilson et al. 2022). Sockeye salmon were captured by commercial purse seine or commercial trolling in the Johnstone Strait and Discovery Passage. Fish were held in flow through recovery tanks prior to sampling then tagged and biopsied using non-lethal anaesthetised sampling procedures (Cooke et al. 2005). Sockeye were gastrically tagged with either acoustic (VEMCO Model V13AP-1H or VEMCO V16) or radio (Lotek MCFT-3A-3V) tags. Full description of methods can be found in Drenner et al. (2014), Wilson et al. (2014) and Wilson et al. (2022).

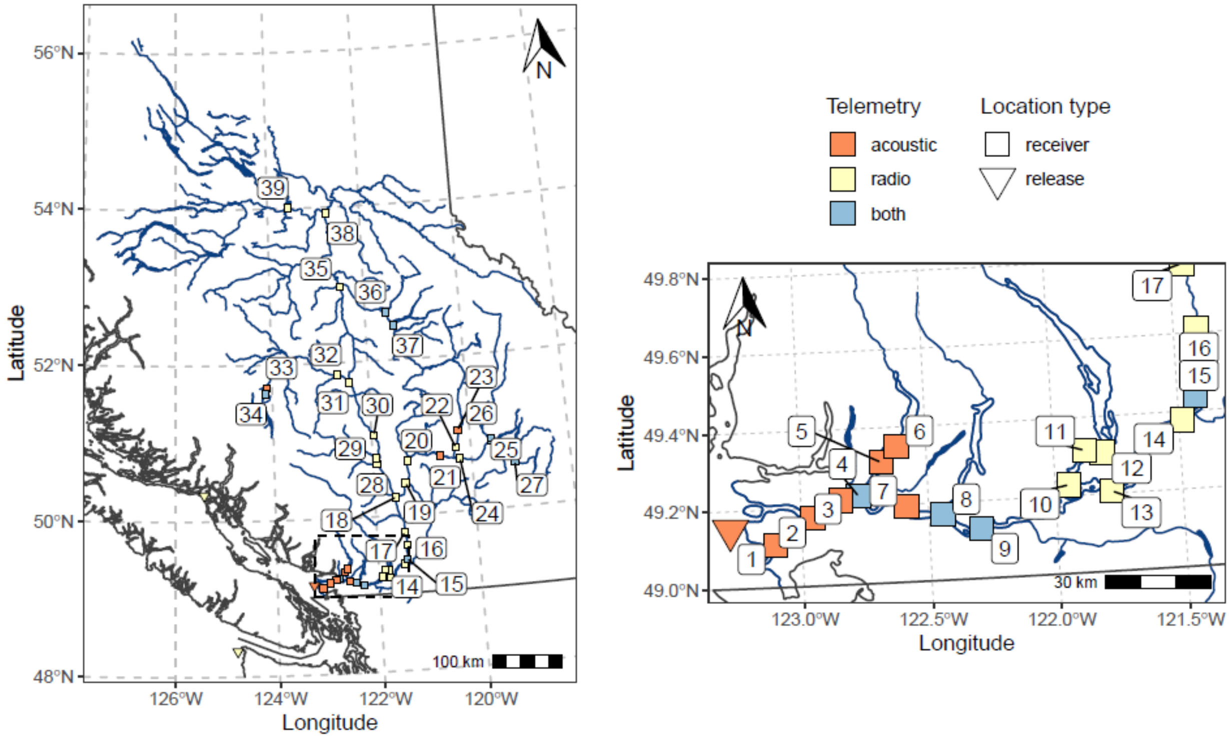

Figure 2: Map of Fraser River Watershed with locations of fish releases (triangles), and stationary receiver sites with acoustic (orange), radio (yellow), or both (blue) telemetry types. The sites are: 1) Fraser Mouth, 2) Fraser Arms, 3) Port Mann, 4) Pitt Confluence, 5) Pitt (river kilometer 16), 6) Pitt Lake Mouth, 7) Derby, 8) Crescent Island, 9) Mission, 10) Harrison Confluence, 11) Weaver Creek, 12) Upper Harrison Downstream, 13) Rosedale, 14) Hope, 15) Qualark, 16) Sawmill, 17) Hells Gate, 18) Thompson Confluence, 19) Spences Bridge, 20) Ashcroft, 21) Kamloops Lake (west), 22) North Thompson (lower), 23) North Thompson (upper), 24) Timber House, 25) Little River, 26) Adams River, 27) Lower Shuswap, 28) Seton Confluence, 29) Bridge River, 30) Kelly Creek, 31) Chilcotin Confluence, 32) Farwell Canyon, 33) Chilko Didson, 34) Chilko, 35) Quesnel Confluence, 36) Likely, 37) Horsefly, 38) Nechako Confluence, and 39) Stuart Confluence.

Data Processing

The telemetry data collected in 2002, 2003, 2006, 2010, and 2011 were processed as follows: detections at each stationary receiver were summarized into the first and last detection indicating when a fish arrived and left the receiver station site. This information was used to determine travel time within each river section defined between receiver station sites and converted to migration rate by dividing the distance of the river section by the amount of time it took the fish to migrate the section. If a fish was detected at a site downstream of the previous detection, this was assumed to be due to mortality (carcass) floating downstream and that detection was not included in the analysis. If a fish fell back to a downstream receiver, then proceeded upstream, the final detection at the upstream receiver was used. If a fish was detected up a tributary that was not on its migratory path based on its CU identification, those detections were excluded and generally resulted in a longer travel time for that fish to reach the next receiver on their migratory path. All reported harvested fish were removed from the data set. Detection data were summarized into a detection history for each fish where 0 indicated the fish was not detected, 1 indicated it was detected, and NA indicated a station was not operational in the year that fish was migrating.

Water Temperature

The thermal experience of sockeye salmon during their freshwater migration was reconstructed using temperatures recorded in the lower Fraser River at Qualark, which has been shown to be well correlated to river temperatures throughout the system, with a few exceptions (Hague et al. 2008). However, the thermal experience of populations entering the river after mid-August or migrating more than 500 km may not be well represented by lower-river conditions, which includes Horsefly (r = 0.52), Nechako (r = 0.65 - 0.78 depending on run timing), and Late Stuart (r = 0.55) CUs. Water temperature data were provided by the Department of Fisheries and Oceans Environmental Watch Program.

Model Description

The analysis was based on an integrated model of travel time and capture-recapture (Cormack-Jolly-Seber) developed by Muthukumarana et al. (2008). Briefly, the CJS component of the model is formulated to estimate *daily* survival probabilities within a given migration section, and the probability of surviving while migrating through the section is estimated by raising the estimated daily survival probability to a power equal to the observed (or predicted in cases where fish was not detected in one or both receivers defining a section) number of days it took a fish to traverse the section. An important outcome of this model formulation is that it enables survival to be parsed out from detection efficiency at the final detection (receiver) station, which is not possible with the use of the CJS model alone. The model used in this study differs from the one developed by Muthukumarana et al. (2008) in two important ways. First, because accounting for intra-individual correlation in travel times with individual random effects is not appropriate given that sections in this study had different lengths, I modeled migration rates instead as they are independent of section length (i.e. section length is divided by travel time yielding a rate of km/day). After model fitting, section length was then divided by observed and model predictions of migration rate to yield travel times as a derived quantity. Second, a state-space formulation of the CJS model was used, which combines an equation for the process of interest (survival) with an equation for the observation process (detection at a receiver arrays; Gimenez et al. 2007). The state-space approach is more flexible than a multinomial likelihood approach as it can accommodate different receiver arrays across years and time-varying covariates (e.g., thermal experience) while fish migrated upriver.

The migration rate model is formulated as

$$M_{i,j,k,l} \sim \text{Gamma}\left(\kappa_M, \frac{\kappa_M}{\bar{M}_{i,j,k,l}}\right)$$

(1)

where $M_{i,j,k,l}$ and $\overline{M}_{i,j,k,l}$ are, respectively, the observed and expected migration rate for individual i from conservation unit j while migrating through river section k in year l; and κ_M is the shape parameter. The expected migration rate is modeled with the following linear predictor and log-link function

$$\log\left(\overline{M}_{i,j,k,l}\right) = \left(\alpha_M + \delta_{M,i} + \delta_{M,j} + \delta_{M,k} + \delta_{M,l}\right) + \beta_{M,zLEN} \cdot zLEN_i$$

(2)

where α_M is the intercept; $\delta_{M,i}$, $\delta_{M,j}$, $\delta_{M,k}$, and $\delta_{M,l}$ are, respectively, random effects for individual, conservation unit, river section and year, which are assumed to be normally distributed with mean zero and independent standard deviations estimated from the data; and $\beta_{M,zLEN}$ is the slope for the effect of z-scored (mean = 0, sd = 1) fish size (fork length), denoted by $zLEN_i$ for individual i. Observed and predicted migration rate was then converted into travel time $T_{i,j,k,l}$ via the relationship below to be compatible with the integrated CJS model estimating daily survival probability in a section of length d_k (in km).

$$T_{i,j,k,l} = \frac{d_k}{M_{i,j,k,l}}$$

(3)

The state-space CJS model is formulated as

$$Z_{i,j,k,l} | Z_{i,j,k-1,l} \sim \text{Bernoulli}\left(Z_{i,j,k-1,l} \cdot \Phi_{i,j,k,l}\right)$$

(4)

where $Z_{i,j,k,l}$ is the state (alive = 1 or dead = 0) of individual i from conservation unit j at the upper receiver station defining section k in year l. The state follows a conditional Bernoulli process, which illustrates the dependence of the fish state at the upper receiver defining section k on their state at the upper receiver defining river section $k-1$ and the apparent survival in river section k (i.e., $\Phi_{i,j,k,l}$). The latter is derived by integrating the estimate of *daily* survival probability while migrating through section k (i.e., $\phi_{i,j,k,l}$) with the observed or estimated travel time through the same section via the relationship

$$\Phi_{i,j,k,l} = \phi_{i,j,k,l}^{T_{i,j,k,l}}$$

(5)

Daily survival probability was modeled with the following linear predictor and logit link function

$$\operatorname{logit}(\phi_{i,j,k,l}) = (\alpha_{\phi} + \delta_{\phi,j} + \delta_{\phi,k} + \delta_{\phi,l}) + \beta_{\phi,SEX} \cdot SEX_i + \\ (\beta_{\phi,zTEMP} + \zeta_{\phi,zTEMP,j}) \cdot zTEMP_{i,k} + \beta_{\phi,SEX\cdot zTEMP} \cdot SEX_i \cdot zTEMP_{i,k}$$

(6)

where α_{ϕ} is the intercept; $\delta_{\phi,j}$, $\delta_{\phi,k}$, and $\delta_{\phi,l}$ are, respectively, intercept random effects for conservation unit, river section and year, which are assumed to be normally distributed with mean zero and independent standard deviations estimated from the data; and $\beta_{\phi,SEX}$ is the effect of sex ($SEX_i = 0$ for females and $SEX_i = 1$ for males); $\beta_{\phi,zTEMP}$ is the slope for the effect of temperature on survival; $\zeta_{\phi,zTEMP,j}$ is a random effect of conservation unit on the slope of temperature effects (this allows for different temperature effects on survival across conservation units; Eliason et al. 2011; Martins et al. 2011), which is assumed to be normally distributed with mean zero and standard deviation estimated from the data; and $\beta_{\phi,SEX\cdot zTEMP}$ is the effect of the interaction between sex and temperature (this allows for different thermal effects on survival of males and females (Hinch et al. 2021; Martins et al. 2012).

Three different temperature variables were constructed dynamically within the model fitting process to reconstruct the thermal experience of each fish while migrating upstream:

1) the average temperature of the first 10 days following entry into the Fraser River,
2) the moving average of river temperature up to the final detection, and
3) the number of days above 18°C up to the final detection.

Temperature variable number 1 can be easily constructed for fish whose time of entry into the Fraser River is known (i.e. fish tagged in 2010 and 2011, when acoustic receiver arrays were deployed at the river mouth) and is provided as data to the model. For fish tagged in 2002, 2003, and 2006, time of entry into the river was calculated dynamically within the model fitting process by subtracting the predicted number of days to migrate from river mouth to Mission (provided by the travel time variable) from the date that they were detected at the Mission receiver station (or an adjacent receiver station which is less than 1 day from Mission). A 10-day average temperature was used from river entry date as an estimation of the average amount of time fish from most conservation units spent in the Fraser River mainstem – a period that is typically the warmest for many fish. Temperature variables number 2 and 3 also use the observed or predicted day of entry into the river to dynamically compute a moving average of mean daily water temperature and the cumulative number of days when temperature was > 18°C between river entry and their last detection. All three variables were z-scored (mean = 0, SD = 1) by subtracting the observed or predicted thermal experiences by their mean (17.2°C for 1 and 2; 2.2 days for 3) and standard deviation (1.67°C for 1 and 2; and 3.7 days for 3), which were computed from the reconstructed thermal experience of all the fish during preliminary runs of the models. These variables aim to investigate the effects of magnitude (all), frequency (temperature variable 3), and duration (all) of warming river temperatures on the survival probability of migrating adult sockeye salmon.

To estimate the parameters of the survival model, the process model was linked to an observation model fitted to a matrix of observations (detections) throughout the river system. The observation model also follows a conditional Bernoulli process, where detection depends on the latent state of the individual (i.e., the individual can only be detected if it is alive) and the detection probability at a receiver station at the upper end of section k. The observation process is modeled as

$$Y_{i,j,k,l} | Z_{i,j,k,l} \sim \text{Bernoulli}\left(Z_{i,j,k,l} \cdot p_k\right) \tag{7}$$

where $Y_{i,j,k,l}$ is the observation (detected = 1 or undetected = 0) of individual i from conservation unit j at the upper receiver station defining section k in year l; and p_k is detection probability at that receiver station, which is modeled with the following linear predictor and logit link function

$$\text{logit}(p_k) = \left(\alpha_p + \delta_{p,k}\right) + \beta_{p,TEL} \cdot TEL_i$$

(8)

where α_p is the intercept; $\delta_{p,k}$, is the intercept random effects for receiver station at the upper end of section k, which are assumed to be normally distributed with mean zero and standard deviation estimated from the data; and $\beta_{p,TEL}$ is the effect of telemetry technology of the tag carried by individual i ($TEL_i = 0$ for radio and $TEL_i = 1$ for acoustic).

Because the sex of 1928 (59%) fish was not determined, I modeled sex as a Bernoulli random variable and used the model to input missing values in the dataset using

$$SEX_i \sim \text{Bernoulli}(m_i)$$

(9)

where m_i is the probability that an upstream migrating individual i is a male, which is a function of the individual's fork length (males are on average longer than females) and modeled as

$$\text{logit}(m_i) = \left(\alpha_m + \delta_{m,j}\right) + (\beta_{m,zLEN} + \zeta_{m,j}) \cdot zLEN_i$$

(10)

where α_m is the intercept; $\beta_{m,zLEN}$ is the slope for the effect of z-scored (mean = 0, sd = 1) fish length; and $\delta_{m,j}$ and $\zeta_{m,j}$ are, respectively, the intercept and slope random effects for conservation unit, which are assumed to be normally distributed with mean zero and independent standard deviations estimated from the data. These random effects account for the variable sex ratio (intercept) and variable relationships with length (slope) across conservation units.

Given that the fork length of 55 fish (1.7%) were not measured, missing values were also input (in the z-score scale) by modeling it as

$$zLEN_i \sim \text{Normal}(0, \sigma_{zLEN})$$

(11)

where $\mu_{zLEN,i,j}$ and σ_{zLEN} are, respectively, the expected standardized fork length of individual i from conservation unit j and associated standard deviation; α_{zLEN} is the intercept; and $\delta_{zLEN,j}$ is the intercept random effects for conservation unit, which is assumed to be normally distributed with mean zero and standard deviation estimated from the data, and accounts for variable mean size across conservation units (Appendix C).

The models were fit using a Bayesian approach. Weakly informative priors were used to exclude implausible values for the parameters (Appendix D), but not unduly influence the outcomes within the range of plausibility (McElreath 2020). The posterior distributions were approximated using a Markov chain Monte Carlo algorithm implemented in JAGS 4.3 (Plummer 2003) implemented in R (R Core Team 2023) via package jagsUI 1.5.2 (Kellner 2021). Four Markov chains were run with 75,000 iterations in each, the first 50,000 iterations of each chain were considered the burn in and not used. Of the remaining 25,000 iterations, every 25th iteration was kept, resulting in 1000 samples of the posterior distributions of model parameters. Convergence of the chains was assessed visually using traceplots and by checking that the $\hat{R}$-statistic was < 1.1 (Gelman & Rubin 1992). The fit of all models (migration rate, CJS, sex, and size) were assessed using Bayesian *P*-values and posterior predictive checks (Gabry et al. 2019), indicating the models fit the data adequately (Appendix A).The Deviance Information Criterion (DIC), a measure of approximate out-of-sample predictive accuracy that balances model fit and model complexity, was used to compare the three models (Spiegelhalter et al. 2002). Ideally, the model selection would be tested under different priors, however, this was not practical given the length of time required to run each model. Therefore, model comparison is primarily based on models fit with vague or regularizing priors.

RESULTS

Detection Efficiency

Most of the stationary receivers had high and uncertain detection efficiency, with 36 out of 40 stations having detection efficiencies between 0.8 and 1.0 (Figure 3). Most stationary radio receivers with lower detection efficiencies were located in the lower Fraser River, specifically, Harrison Confluence (0.39), Pitt Confluence (0.55), Weaver Creek (0.61), and Crescent Island (0.72). However, several stations higher up in the watershed also had relatively low detection efficiencies including the Chilko Didson site (0.67), and Kelly Creek (0.63). All acoustic receivers had detection efficiencies between 0.76 and 1.0, except the Chilko Didson site (0.29), and most exhibited highly uncertain estimates (Figure 4).

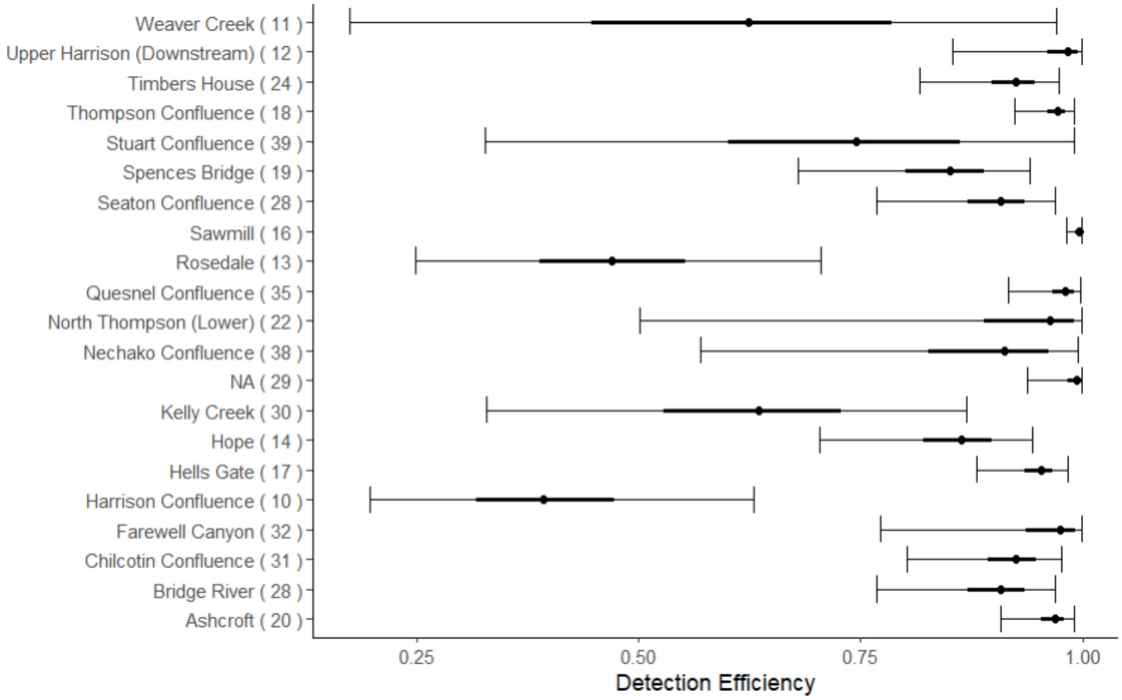

Figure *3*: Detection efficiency of stationary radio receivers along the migratory route of sockeye salmon in the Fraser River with a 50% credible interval (thick line) and a 95% credible interval (thin line).

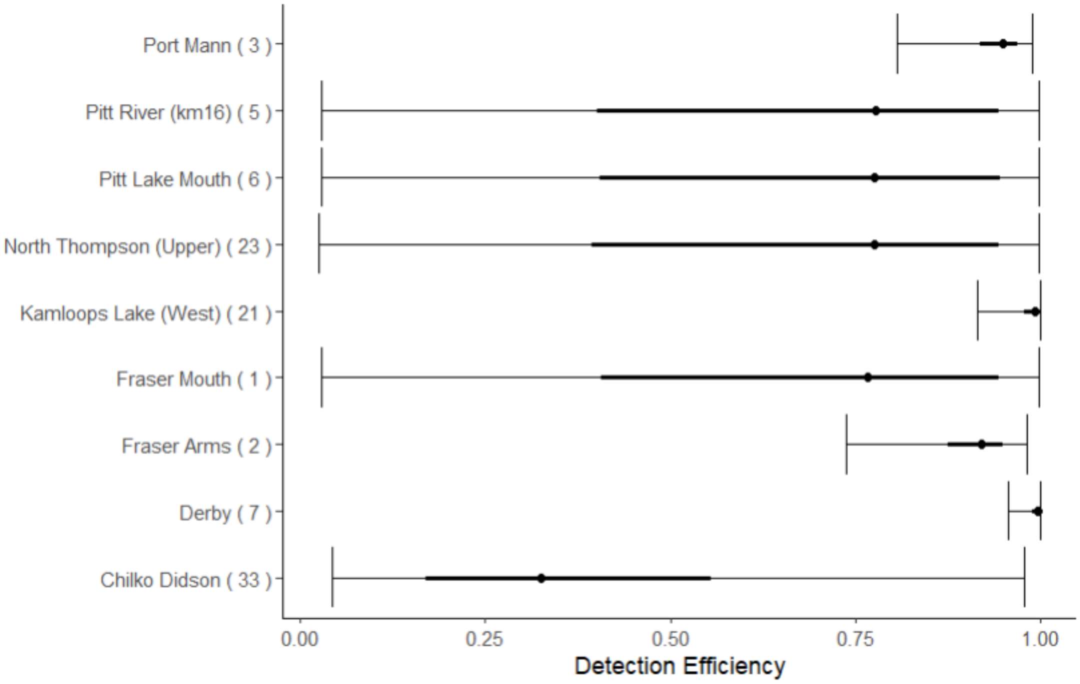

Figure 4: Detection efficiency of stationary acoustic receivers along the migratory route of tagged sockeye salmon in the Fraser River with a 50% credible interval (thick line) and a 95% credible interval (thin line).

Migration Rate and Travel Time

Median migration rates across all conservation units was 27.8 km/day (median absolute deviation (MAD) = 13.7 km/day; Figure 5), and there was no evidence of a relationship between fish length and migration rate ($\beta_{M,zLEN}$ = 0.00, 95% CI[-0.1, 0.2]). The fastest migrating conservation units were Quesnel (median = 45.6 km/day, MAD = 10.5 km/day, n = 407) and Bowron (median = 43.0 km/day, MAD = 9.1 km/day, n = 15). The slowest migrating populations were Seton (median = 21.0 km/day, MAD = 11.2 km/day, n = 28), Harrison (DS) (median = 21.6 km/day, MAD = 6.7 km/day, n = 3), and Shuswap Complex (median = 22.7 km/day, MAD = 10.0 km/day, n = 1313).

Across all conservation units, the slowest migration rates were observed in the Thompson confluence to Spences Bridge (median = 15.6 km/day, MAD = 4.3, n = 857), Seton confluence to Bridge confluence (median = 16.1 km/day, MAD = 7.4, n = 480), and Hope to Qualark (median = 16.4 km/ day, MAD = 5.5, n = 1342) (Figure 6). The fastest sections included the Chilcotin confluence to Quesnel confluence (median = 52.6 km/day, MAD = 6.4, n = 270), the Bridge confluence to Kelly confluence (47.6km/day, MAD = 17.1, n = 480), and Thompson confluence to the Seton confluence (median = 44.1 km/day, MAD = 7.1, n = 480).

The Late run timing populations tended to have slower median migration rates than populations from the Summer and Early Summer run timings (Figure 5). The Hope to Qualark, Thompson Confluence to Spences Bridge, and Thompson Confluence to Seton Confluence river sections appear to be amongst the slowest for all populations that pass through them (Figure 9 and Figure 14).

The Upper Fraser CUs of Francois-Fraser and Takla-Trembleur-Stuart both migrated relatively quickly through the Mission to Harrison confluence and Chilcotin confluence to

Quesnel confluence river sections (Figure 9 and Figure 10). The Shuswap and Shuswap Complex conservation units exhibited similar patterns in migration rates throughout their migration routes, however, the Shuswap CU had slightly faster migration rates throughout (Figure 11 and Figure 12). For the upper Fraser populations of Chilko and Quesnel, the fastest median migration rate occurred in the river section between Bridge Confluence and Kelly Confluence (Figure 13 and Figure 14).

The effect of conservation unit on migration rate was variable (σ= 0.15, Figure 15). The strongest effect on migration rate was observed in the Kamloops (negative, meaning slowest average migration rate compared to other conservation units), Bowron, and Shuswap Complex (both positive, meaning fastest average migration rate compared to other conservation units) conservation units. There was even greater variability in migration rate across river section (σ = 0.34, Figure 16). The river section that had the strongest effect on migration rate were Seton Confluence to Bridge Confluence, Hope to Qualark, and Thompson Confluence to Spences Bridge (all negative, meaning slowest average migration rates compared to average migration rate), and Timber's House to Little River (positive, meaning fastest average migration rate compared to average migration rate). However, this section is only navigated by the Shuswap conservation units.

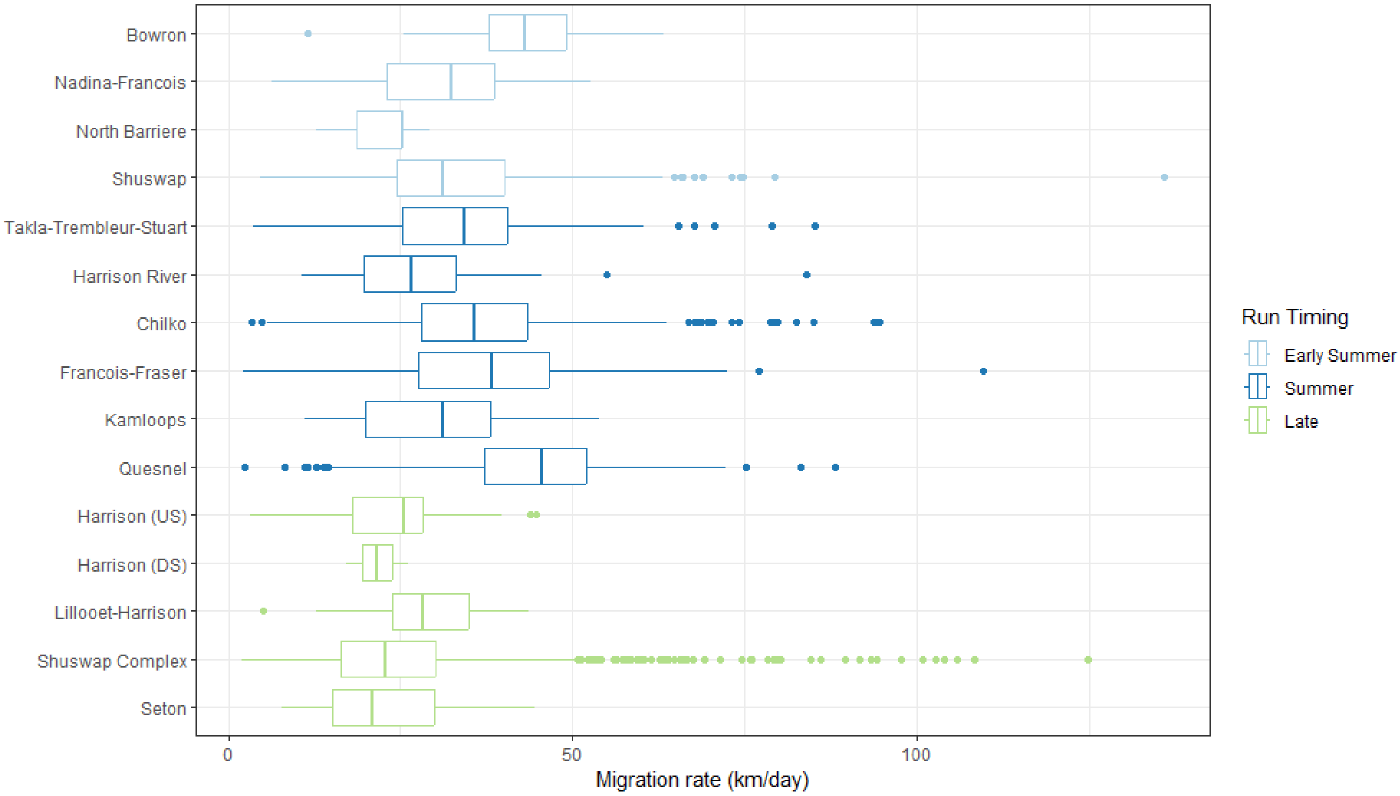

Figure 5: Migration rates for 16 different conservation unit in the Fraser River watershed. Points are migration rates for an individual fish in a specific river section.

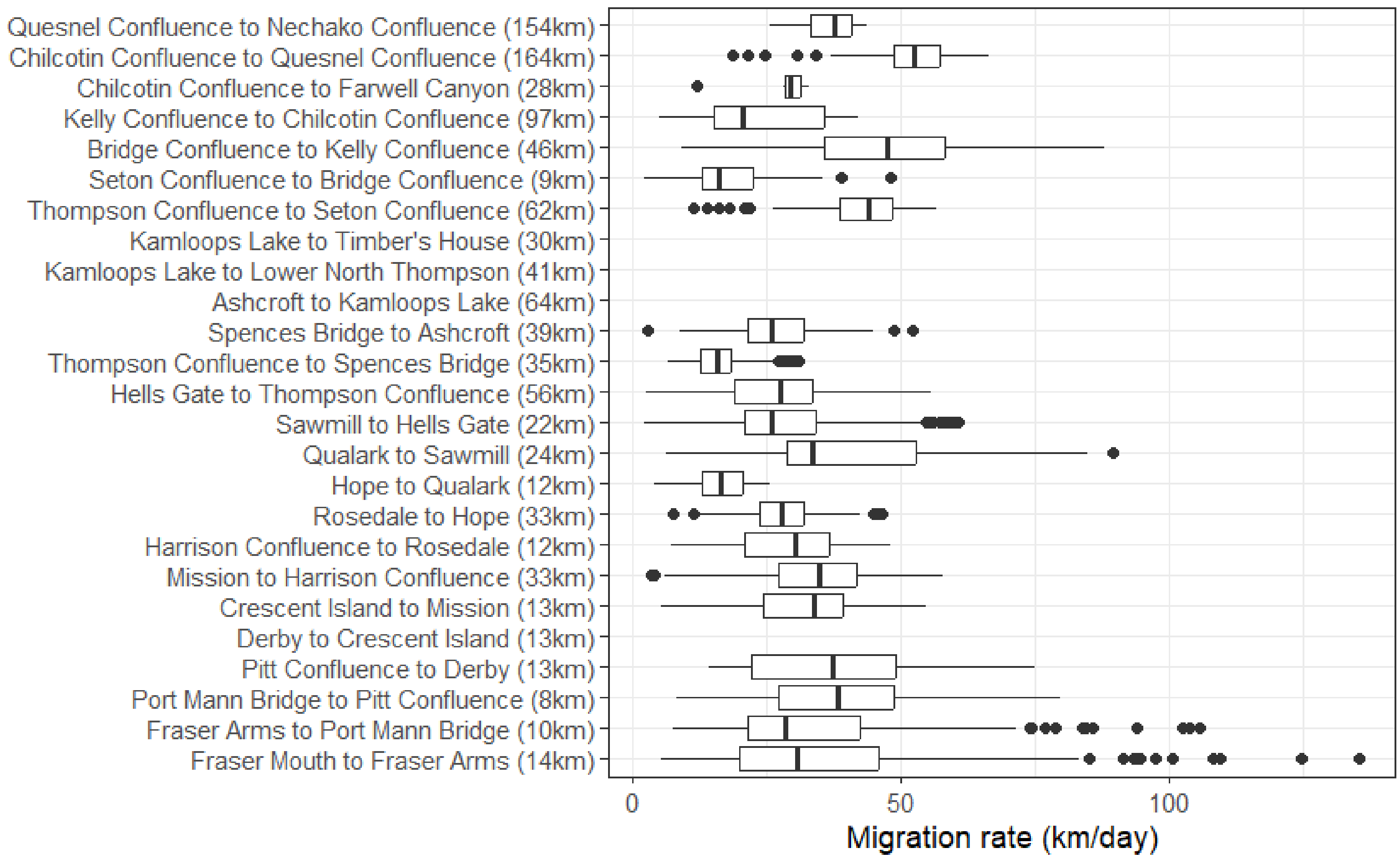

Figure 6: Migration rates for all 16 conservation units in the different river sections of the Fraser River. Points are migration rates for an individual fish.

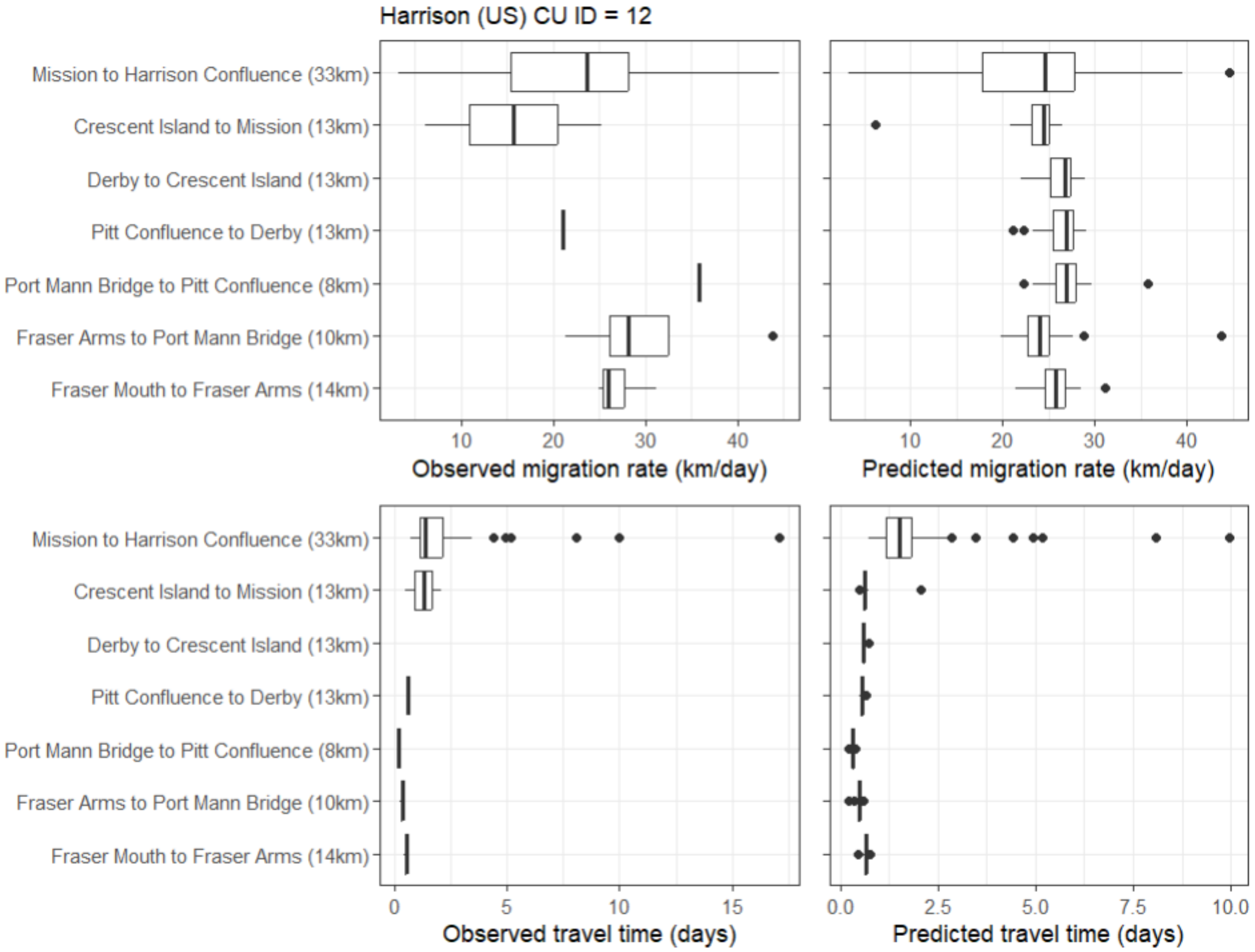

Figure 7: Observed and predicted migration rate (km/day) and travel time (days) in each river section navigated by sockeye salmon in the Harrison (US) conservation unit. Travel time is used to convert estimated daily survival to predicted section survival.

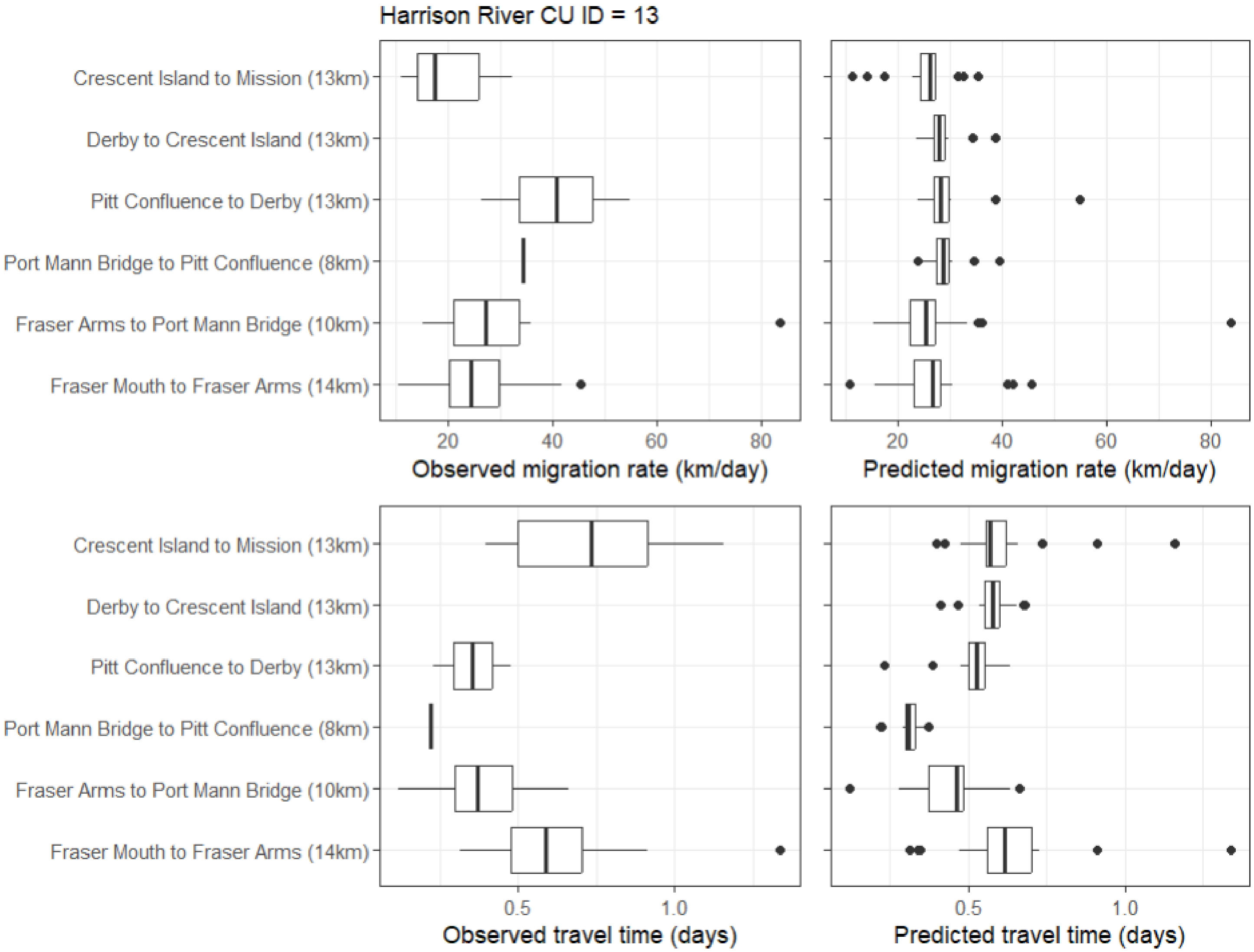

Figure 8: Observed and predicted migration rate (km/day) and travel time (days) in each river section navigated by sockeye salmon in the Harrison River conservation unit. Travel time is used to convert estimated daily survival to predicted section survival.

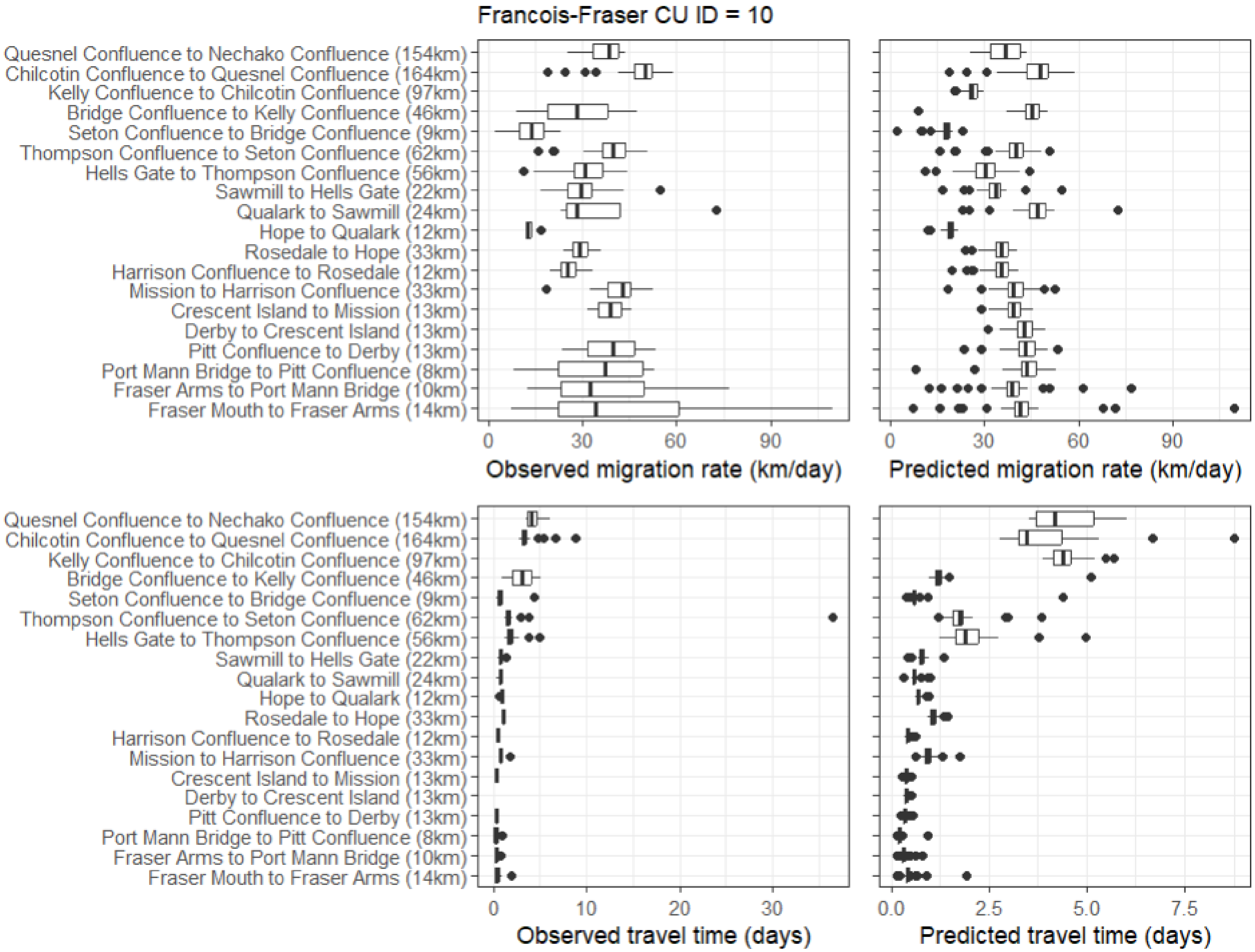

Figure 9: Observed and predicted migration rate (km/day) and travel time (days) in each river section navigated by sockeye salmon in the Francois-Fraser conservation unit. Travel time is used to convert estimated daily survival to predicted section survival.

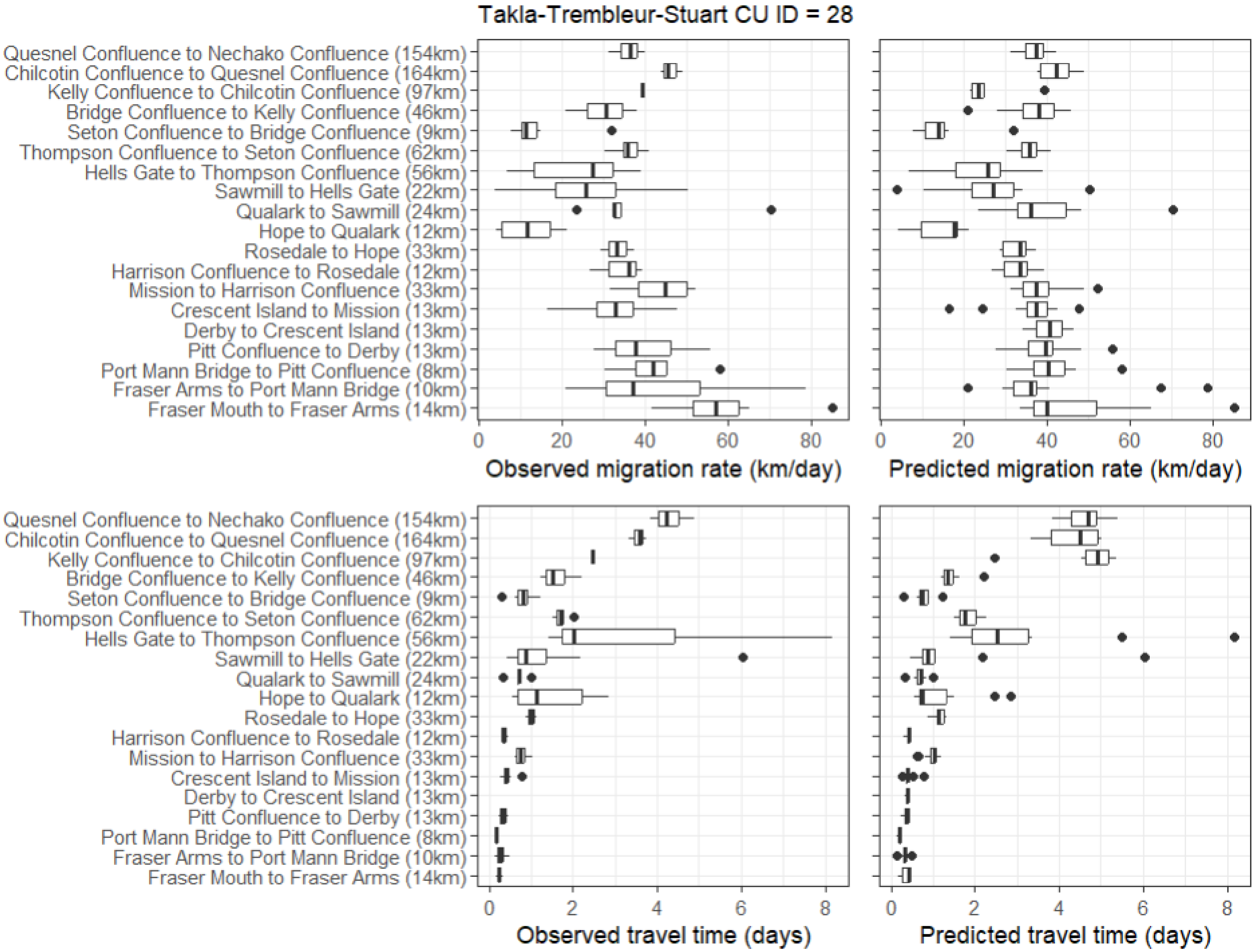

Figure 10: Observed and predicted migration rate (km/day) and travel time (days) in each river section navigated by sockeye salmon in the Takla-Trembleur-Stuart conservation unit. Travel time is used to convert estimated daily survival to predicted section survival.

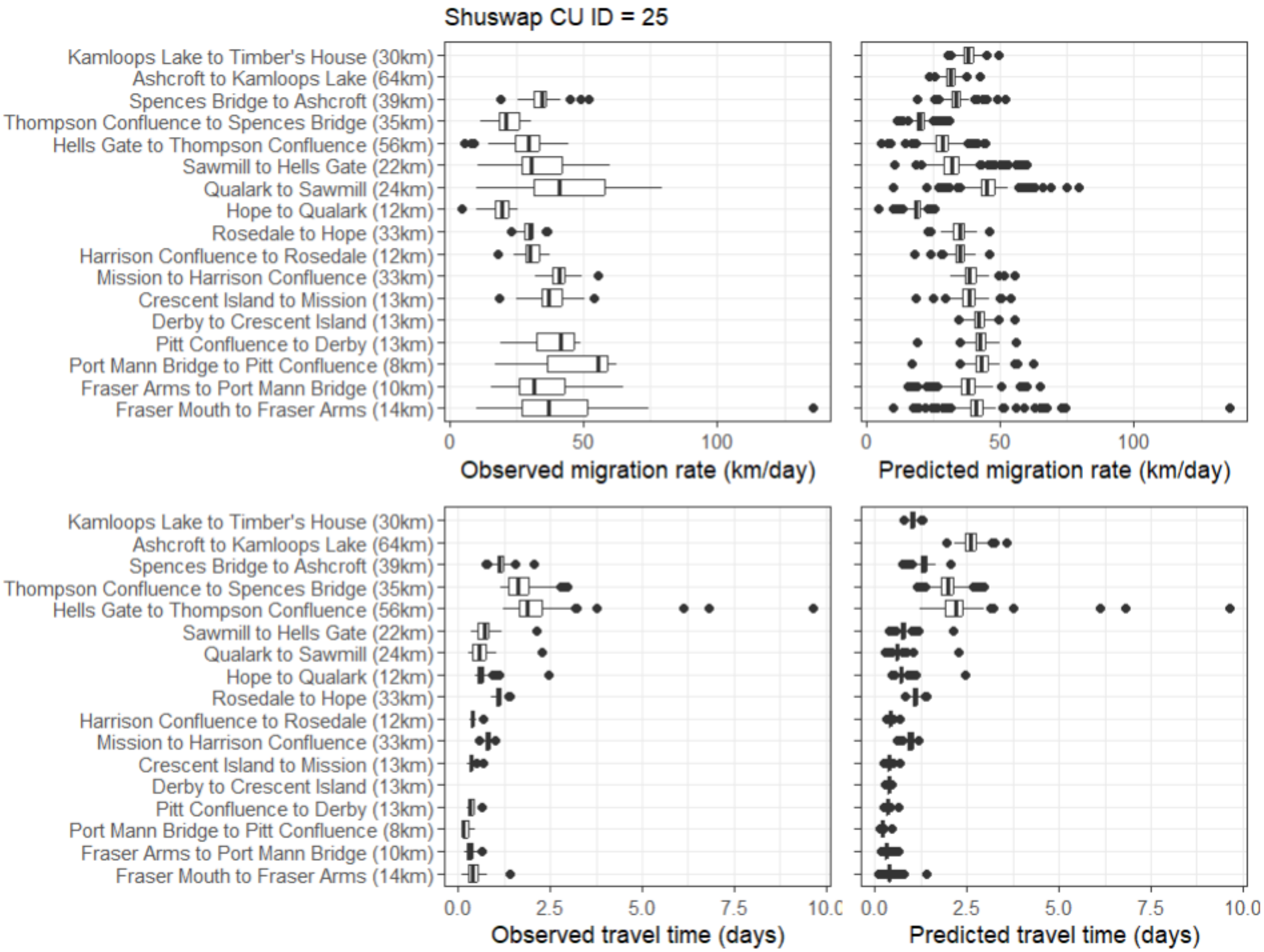

Figure 11: Observed and predicted migration rate (km/day) and travel time (days) in each river section navigated by sockeye salmon in the Shuswap conservation unit. Travel time is used to convert estimated daily survival to predicted section survival.

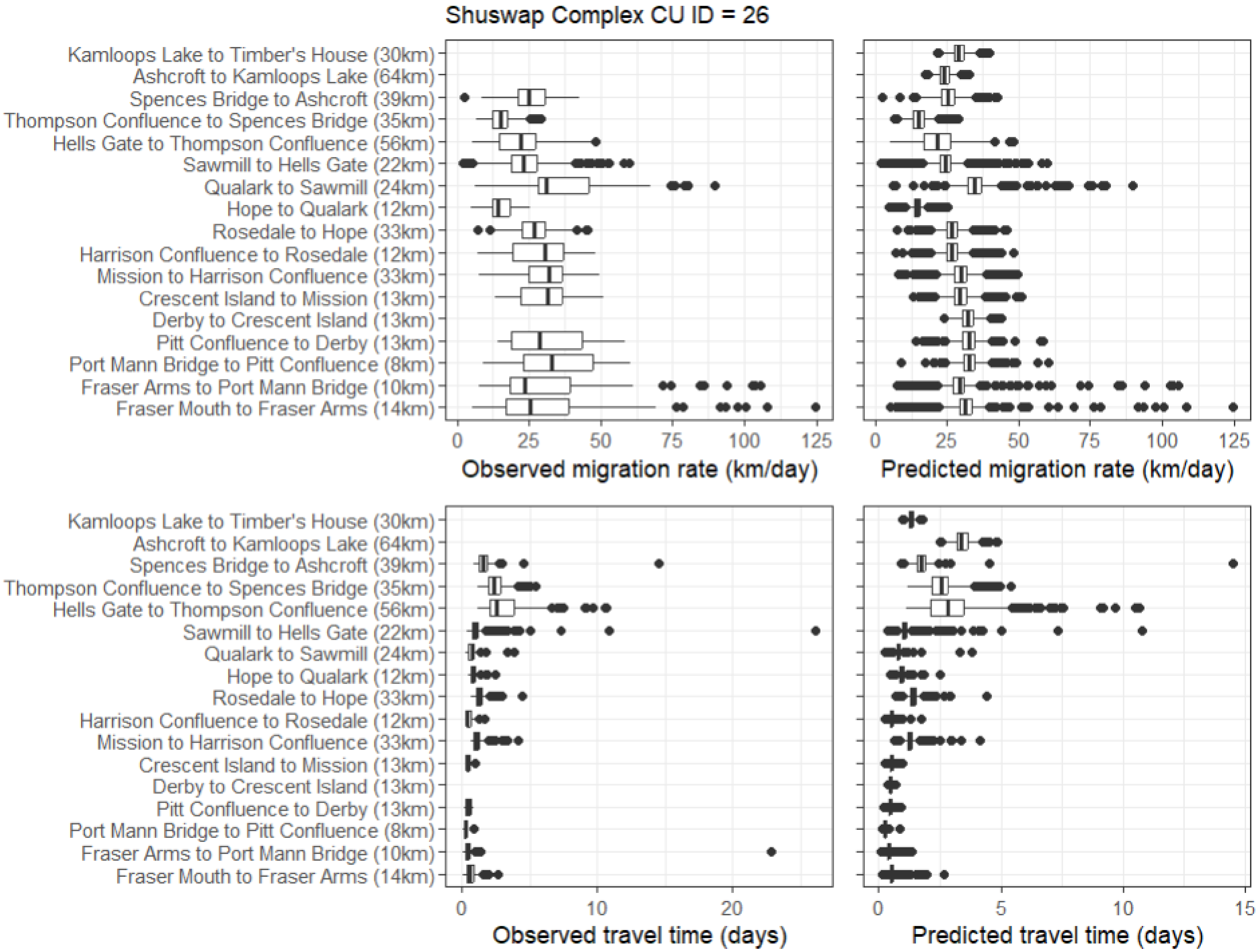

Figure 12: Observed and predicted migration rate (km/day) and travel time (days) in each river section navigated by sockeye salmon in the Shuswap Complex conservation unit. Travel time is used to convert estimated daily survival to predicted section survival.

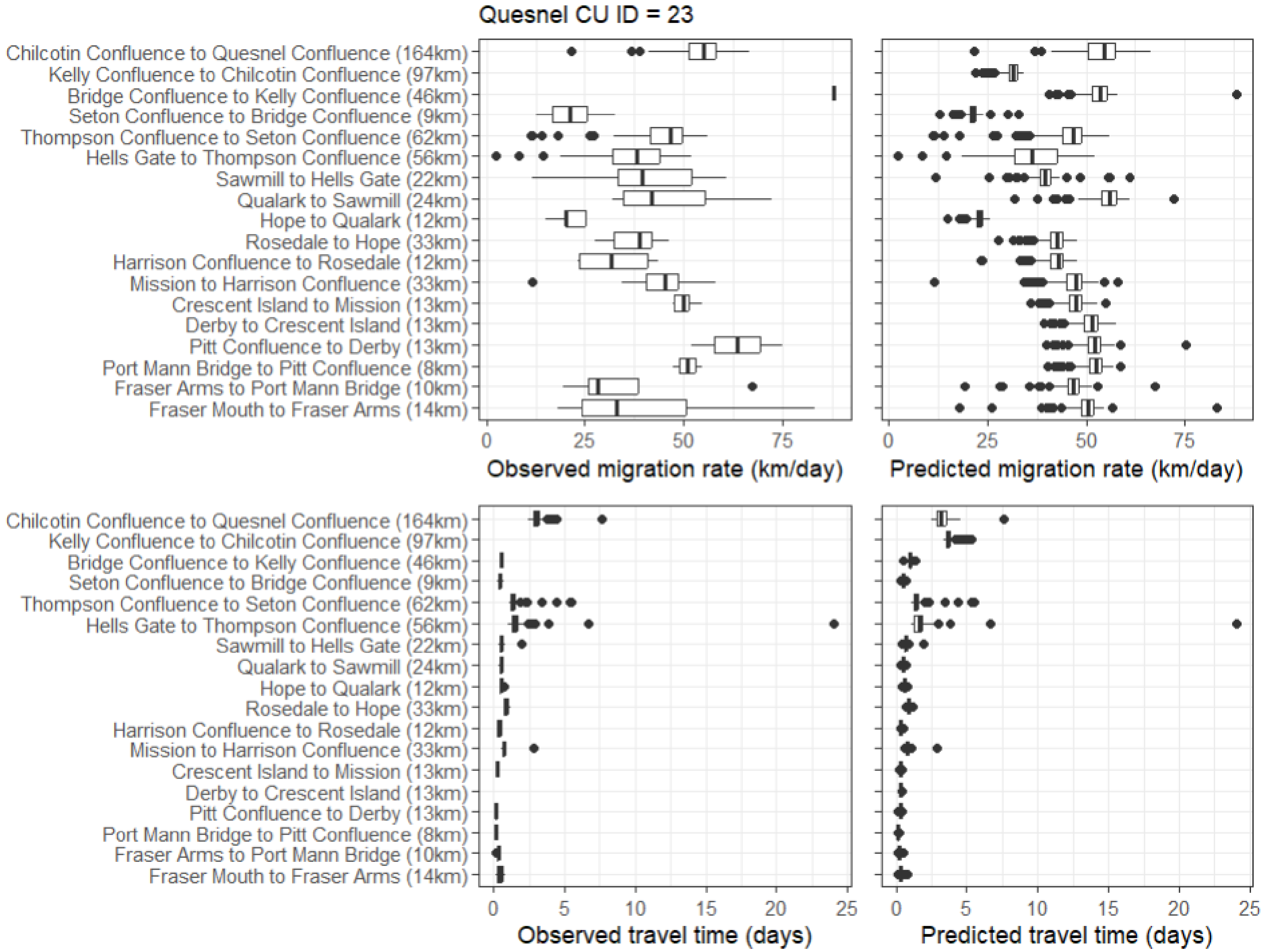

Figure 13: Observed and predicted migration rate (km/day) and travel time (days) in each river section navigated by sockeye salmon in the Quesnel conservation unit. Travel time is used to convert estimated daily survival to predicted section survival.

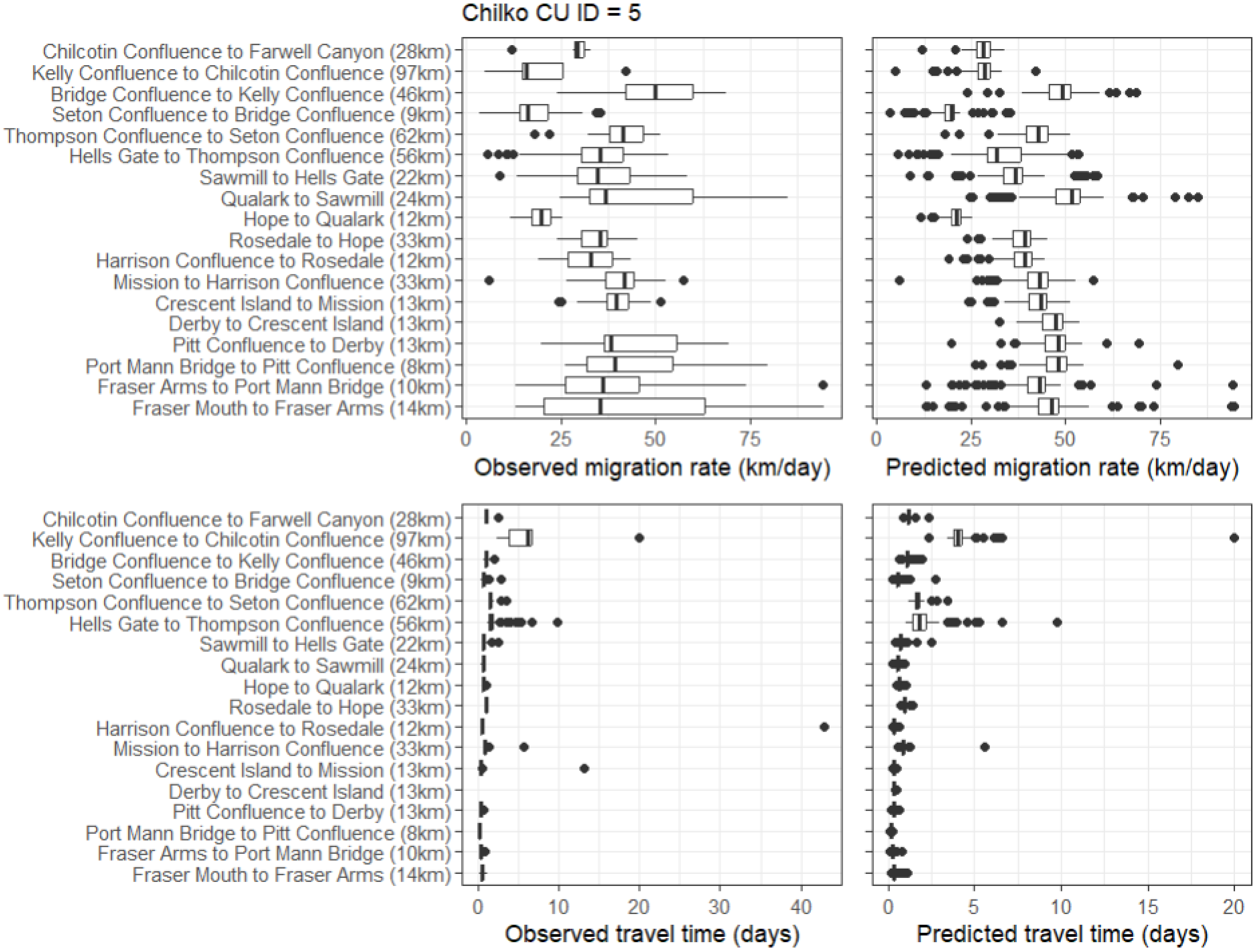

Figure 14: Observed and predicted migration rate (km/day) and travel time (days) in each river section navigated by sockeye salmon in the Chilko conservation unit. Travel time is used to convert estimated daily survival to predicted section survival.

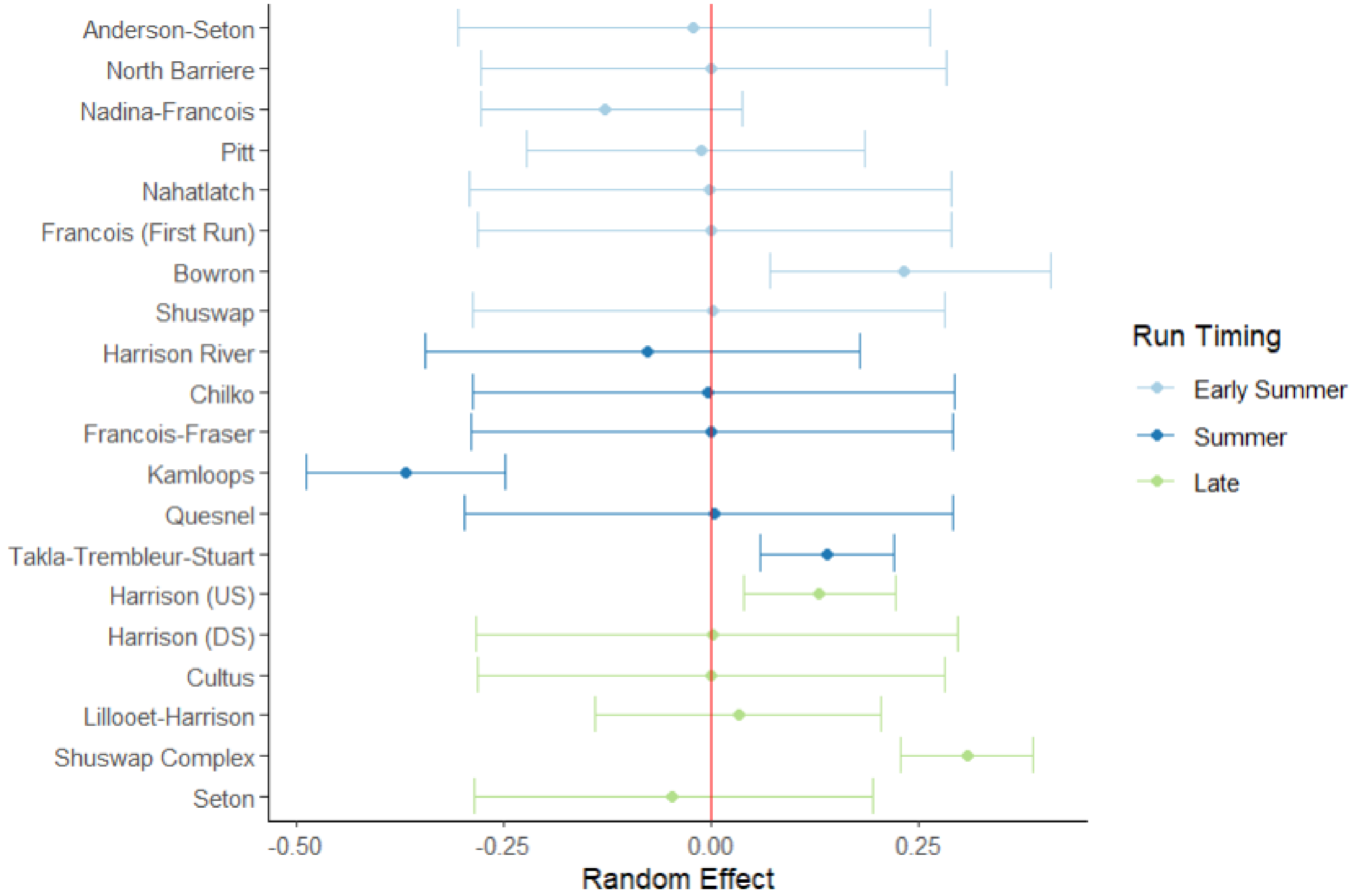

Figure 15: Plot of the random effect of conservation unit on migration rate with 95% credible intervals.

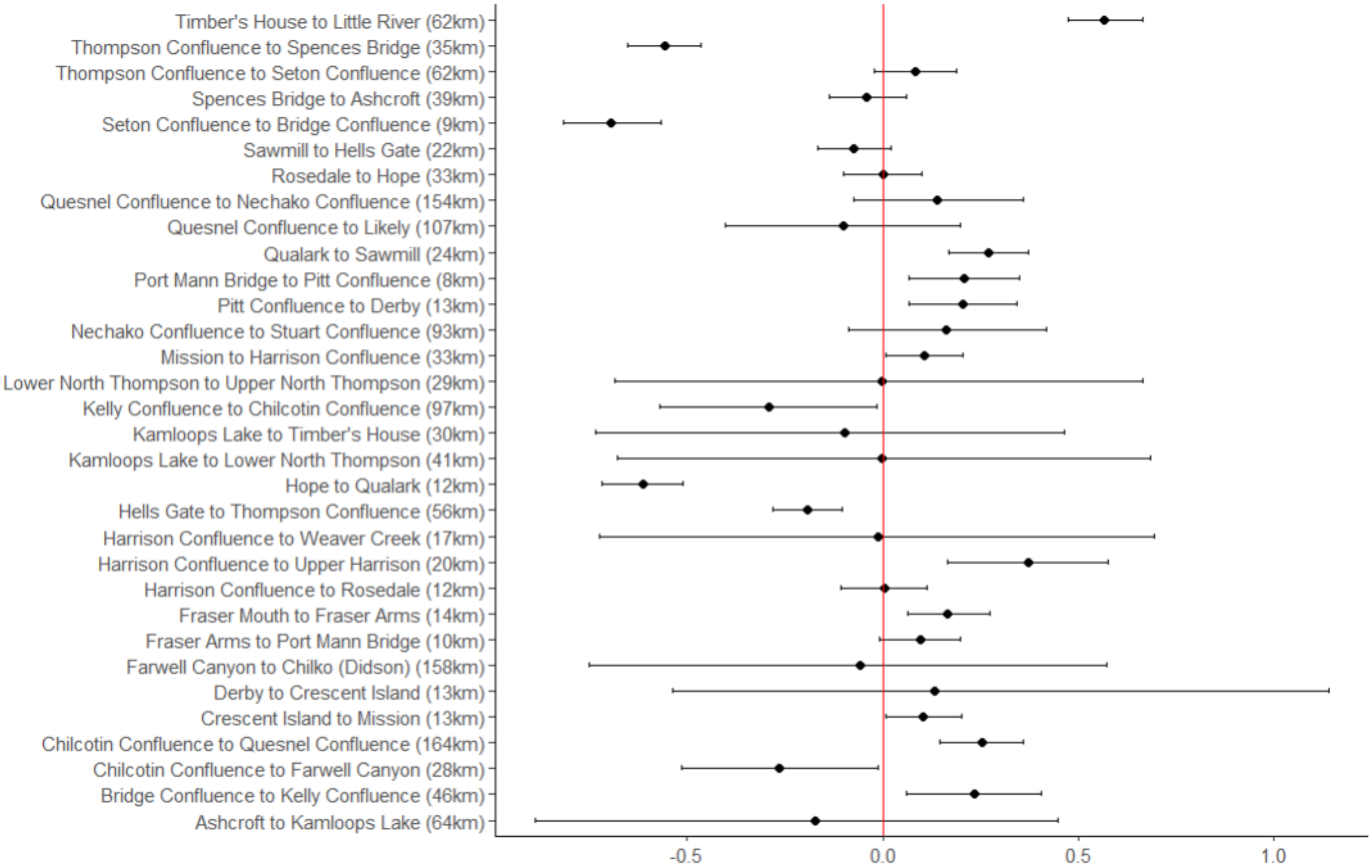

Figure 16: Plot of the random effect of river section on migration rate with 95% credible intervals.

Temperature Effects on Survival Probability

Model 2, which modeled the effect of the moving average of river temperature prior to the final detection of an individual, was selected based on the deviance information criterion (model 1 DIC: 51391.39, model 2 DIC: 51141.16, model 3 DIC: 51364.96; see results of models 1 and 3 in Appendix B). Generally, there was a negative relationship between survival probability and the moving average water temperature following river entry, with the interaction between sex and temperature indicating a slightly steeper relationship occurring for females than males (Figure 17).

There was no consistent deviation from the global slope for the random effect of temperature by CU for the Summer conservation units, while some Early Summer CUs had a slightly negative deviation, and some Late CUs had a slightly positive deviation (Figure 18). However, the credible intervals for all conservation units are wide and include 0, which indicates there is high uncertainty in these results.

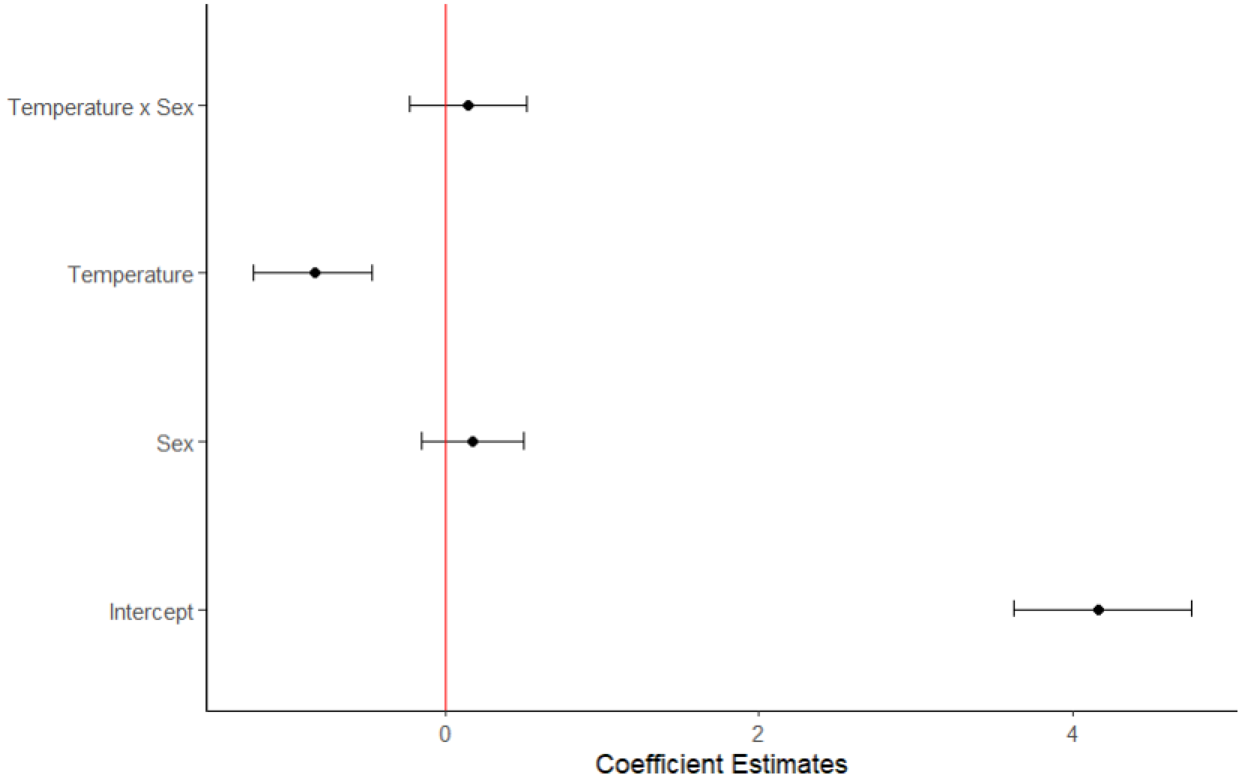

Figure 17: Coefficient estimates (sex, temperature, and the interaction between sex and temperature) for daily survival.

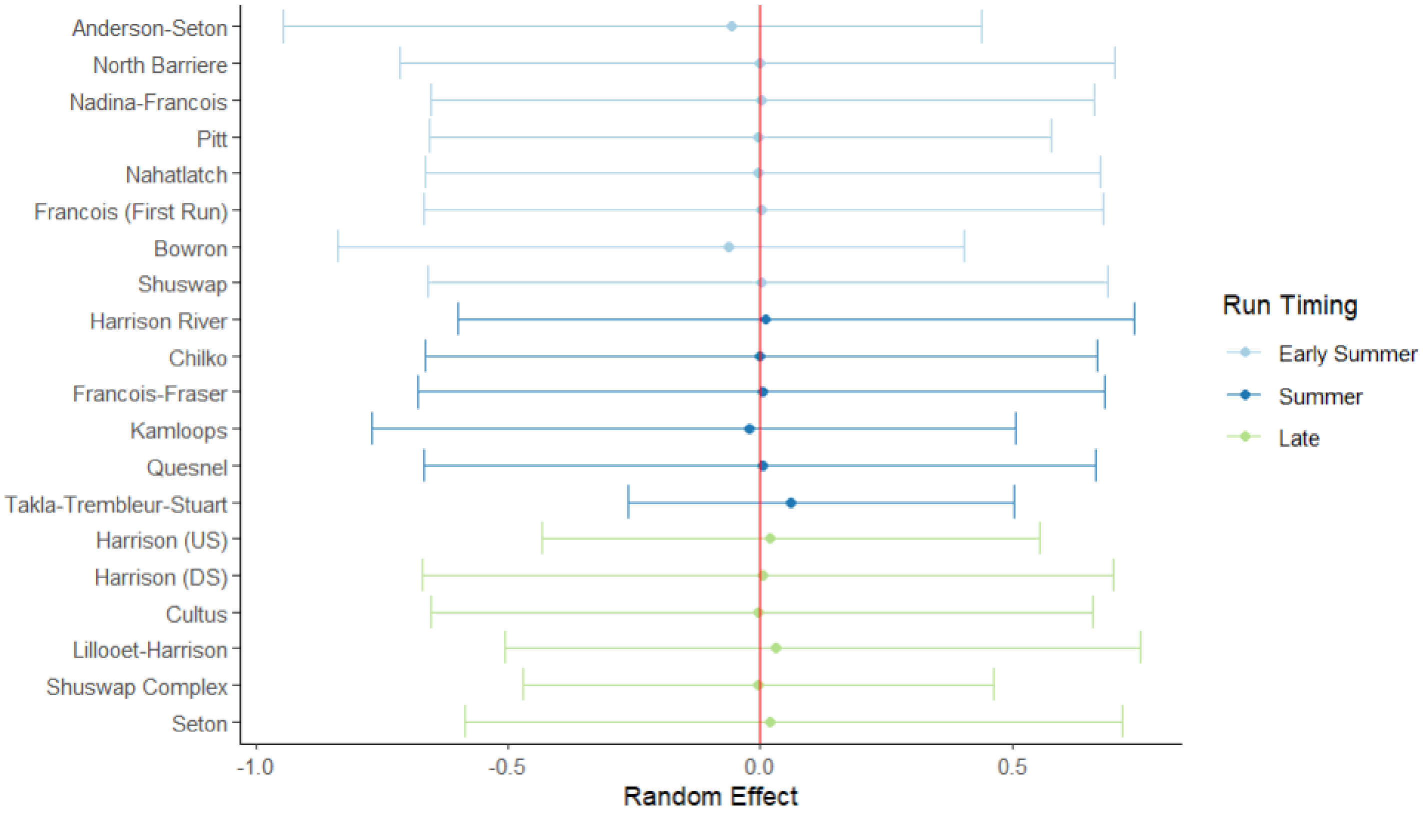

Figure 18: Plot random effect of temperature on survival probability by conservation unit and sex. Overall migration survival probability is based on the moving average water temperature (recorded at Qualark) prior to an individual's final detection.

The Harrison conservation units (Harrison (upstream), Harrison (downstream), Harrison River, and Lillooet-Harrison) had high daily survival probabilities throughout their migration, with median survival probabilities between 0.966 and 0.999 (Figure 19 - Figure 22). Those populations experienced their lowest median daily survival probabilities in the Port Mann Bridge to Pitt Confluence and the Fraser Mouth to Fraser Arms river sections. The Middle Fraser populations (Seton and Anderson-Seton) also experience the lowest daily survival rates in those river sections (Figure 23 - Figure 24). The difference between daily survival and section survival is due to the amount of time fish spend in each river section. Hells Gate to Thompson Confluence (56km) and Rosedale to Hope (33km) are the second and third longest river sections that the Anderson-Seton and Seton conservation units navigate during their migration routes, which may explain why fish are spending more time in those sections. In addition, the narrow canyon of Hells Gate is a difficult feature for sockeye to navigate, they may therefore spend time recovering in the Hells Gate to Thompson Confluence (Ricker 1947). The Thompson conservation units (Shuswap, Shuswap Complex, Kamloops, and North Barriere) all had relatively low daily survival in the Ashcroft to Kamloops Lake river section (Figure 25 - Figure 28). The Shuswap and Shuswap Complex conservation units also experienced relatively low daily survival in the Timber's House to Little River section. All upper Fraser conservation units (Quesnel, Takla-Trembleur, Nadina-Francois, Francois-Fraser, Chilko and Bowron), except Chilko, appear to have experienced their lowest median daily survival in the Fraser Mouth to Fraser Arms, and Port Mann Bridge to Pitt Confluence river sections (Figure 29 - Figure 34).

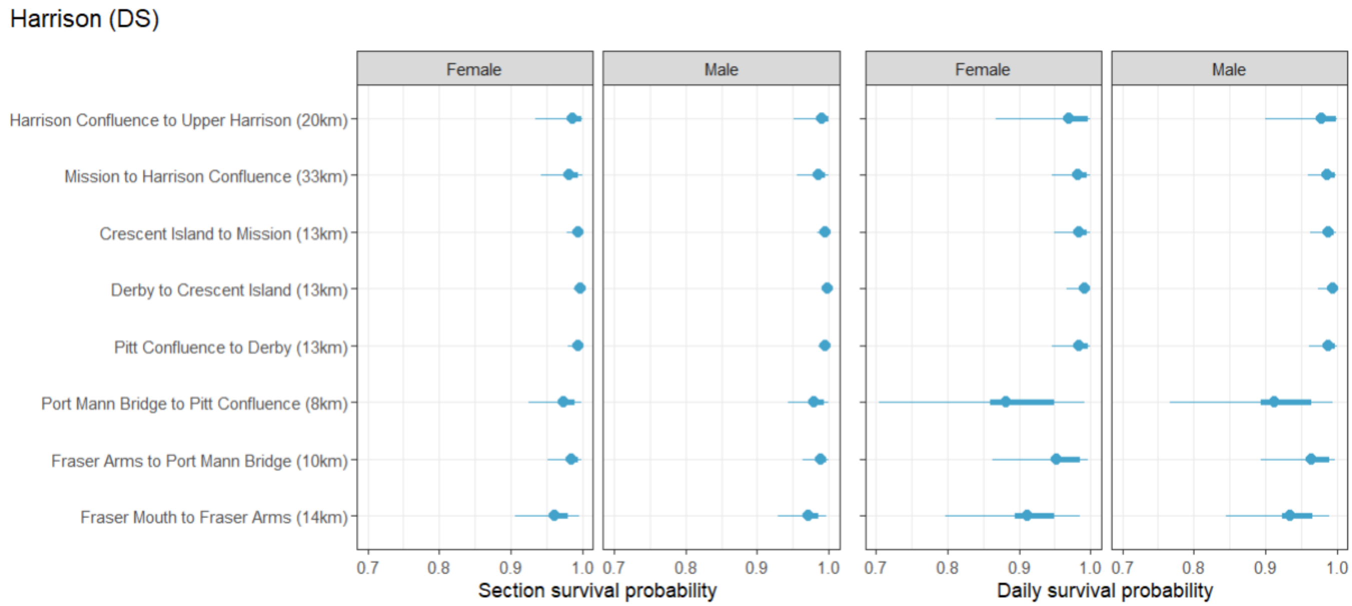

Figure 19: Section and daily survival probability for the Harrison (DS) conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

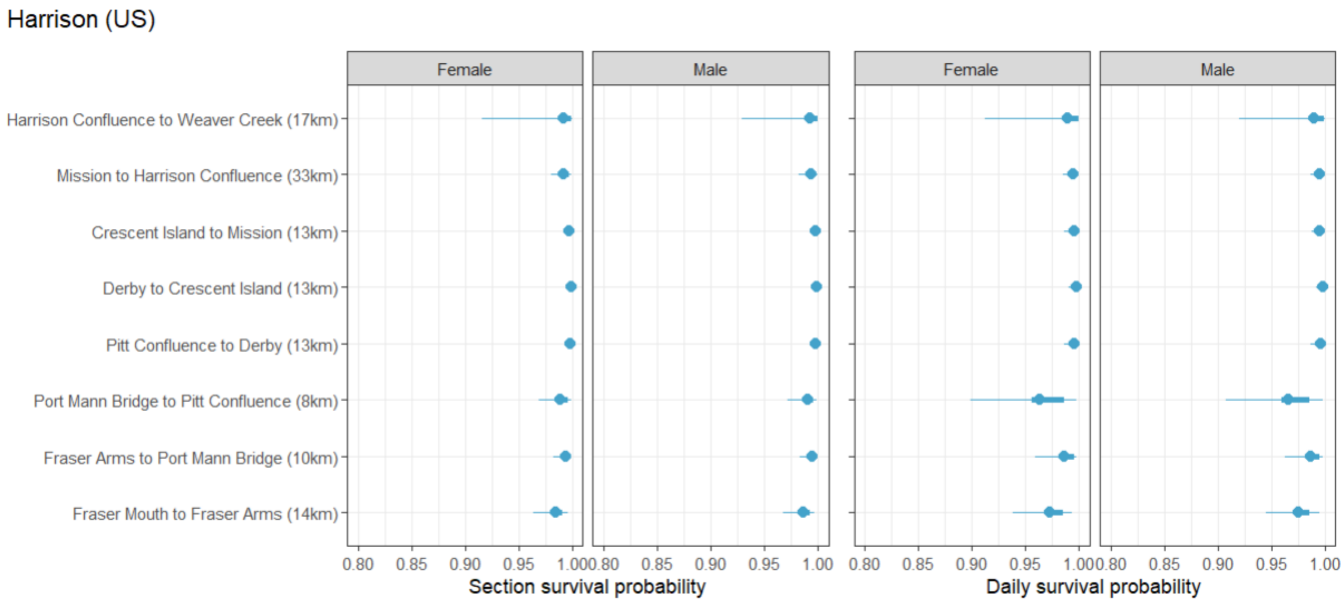

Figure 20: Section and daily survival probability for the Harrison (US) conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

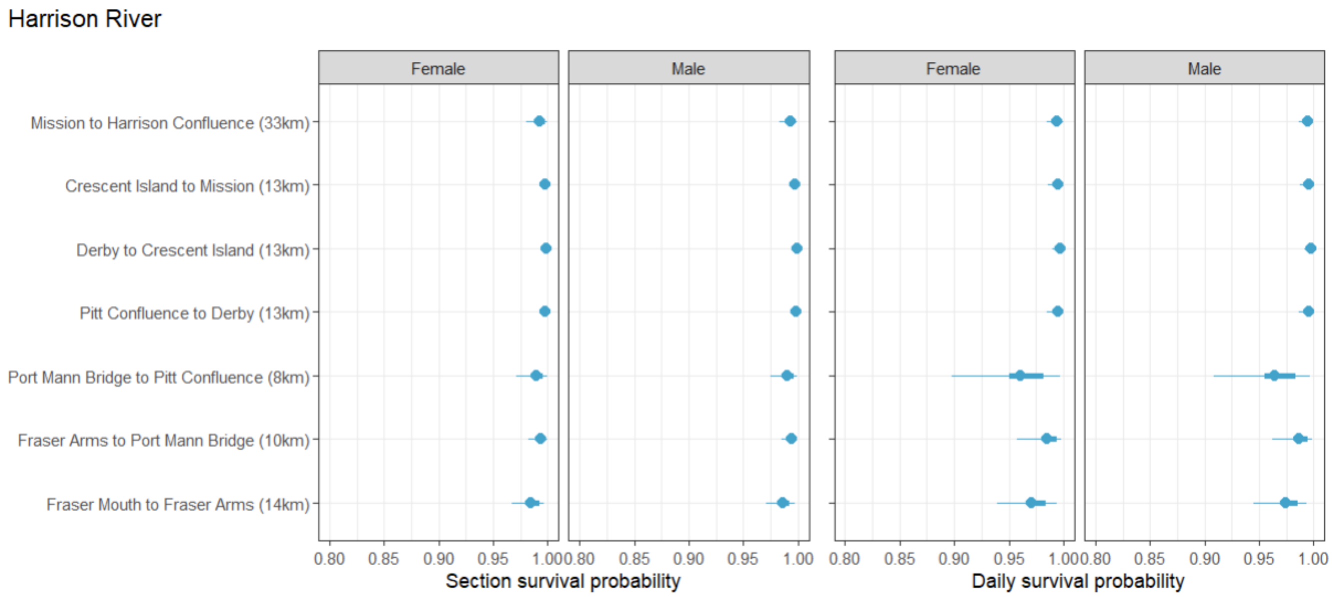

Figure 21: Section and daily survival probability for the Harrison River conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

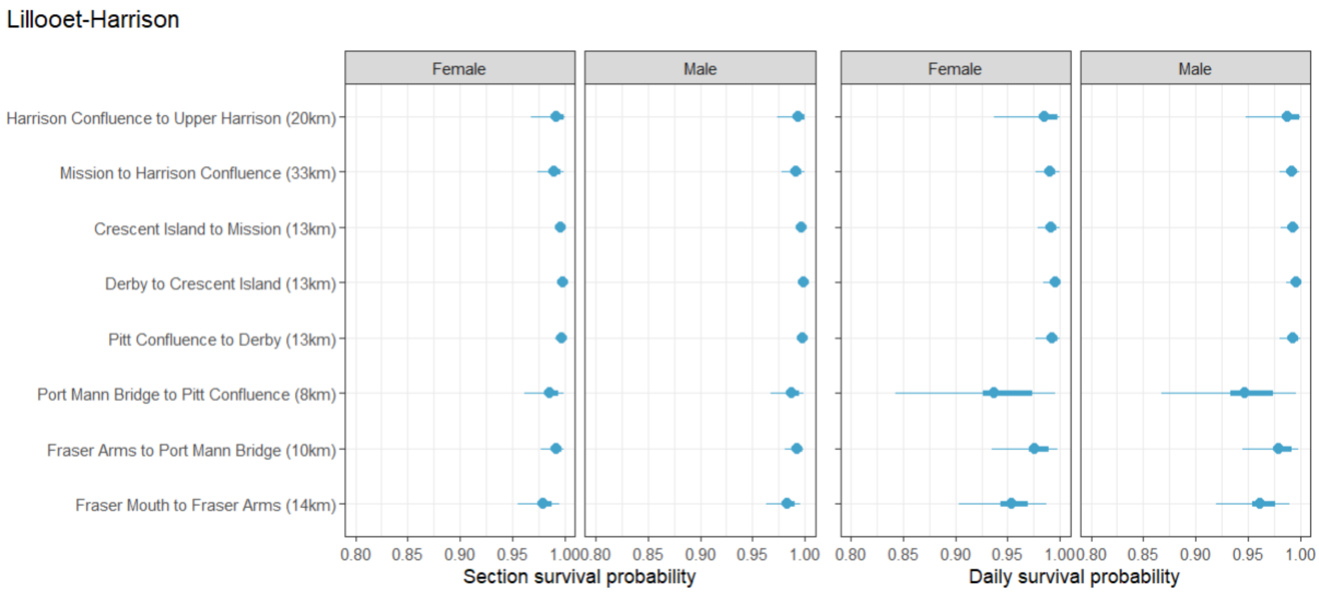

Figure 22: Section and daily survival probability for the Lillooet-Harrison conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

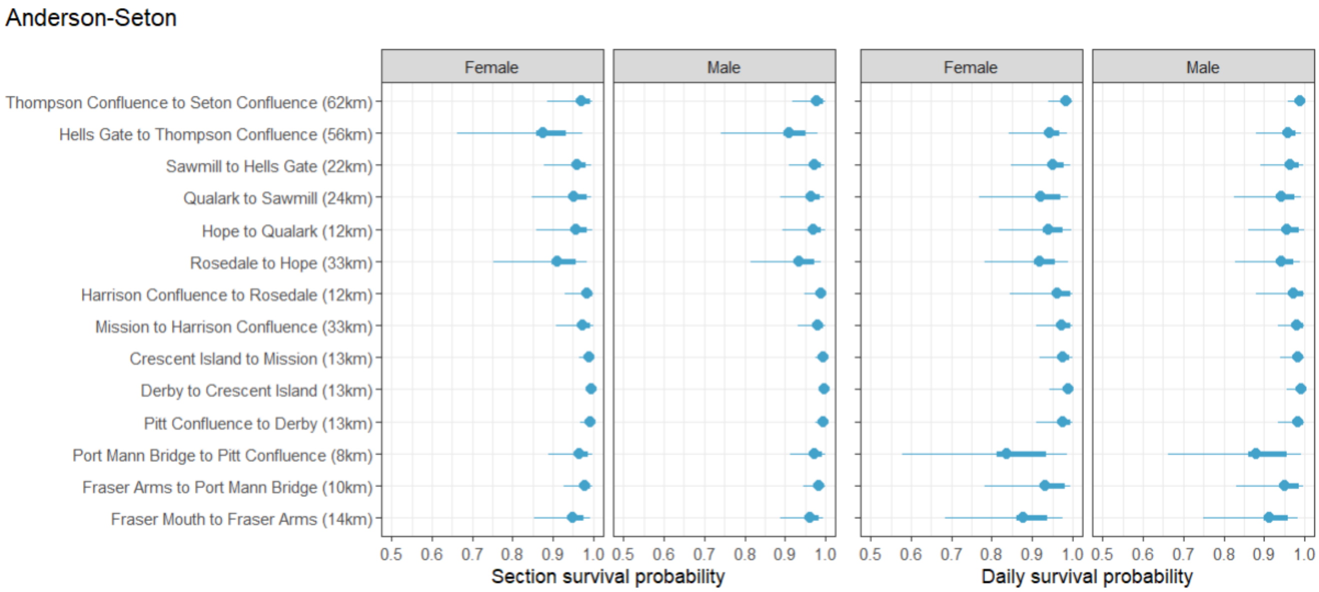

Figure 23: Section and daily survival probability for the Anderson-Seton conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

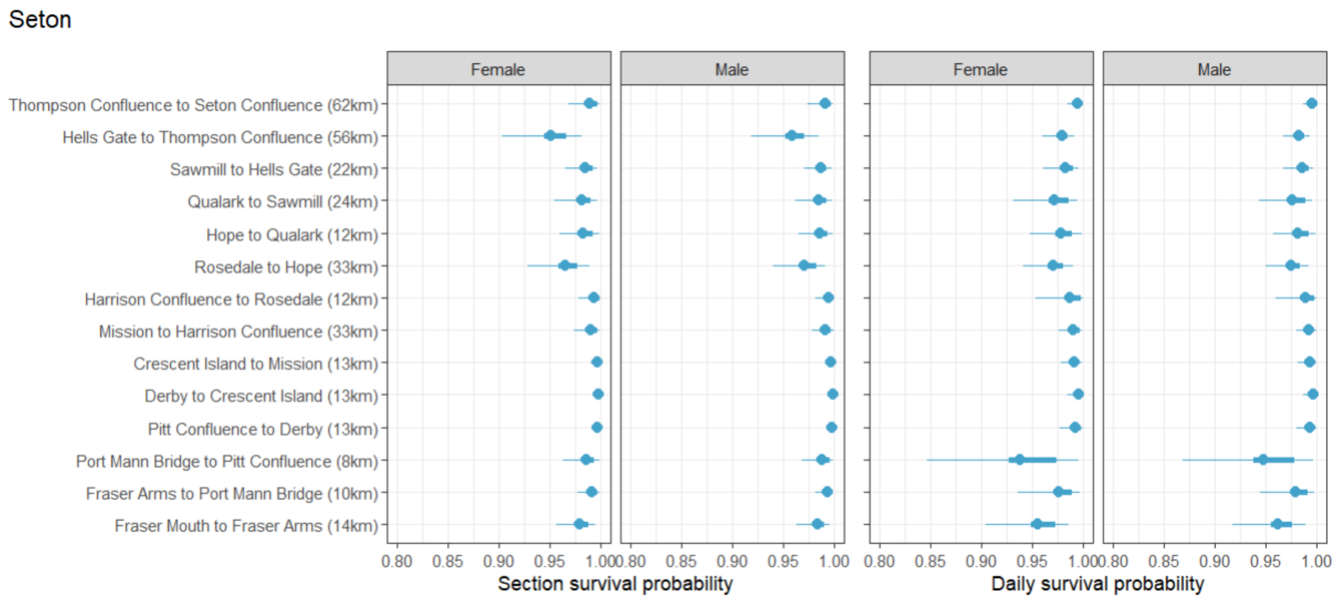

Figure 24: Section and daily survival probability for the Seton conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

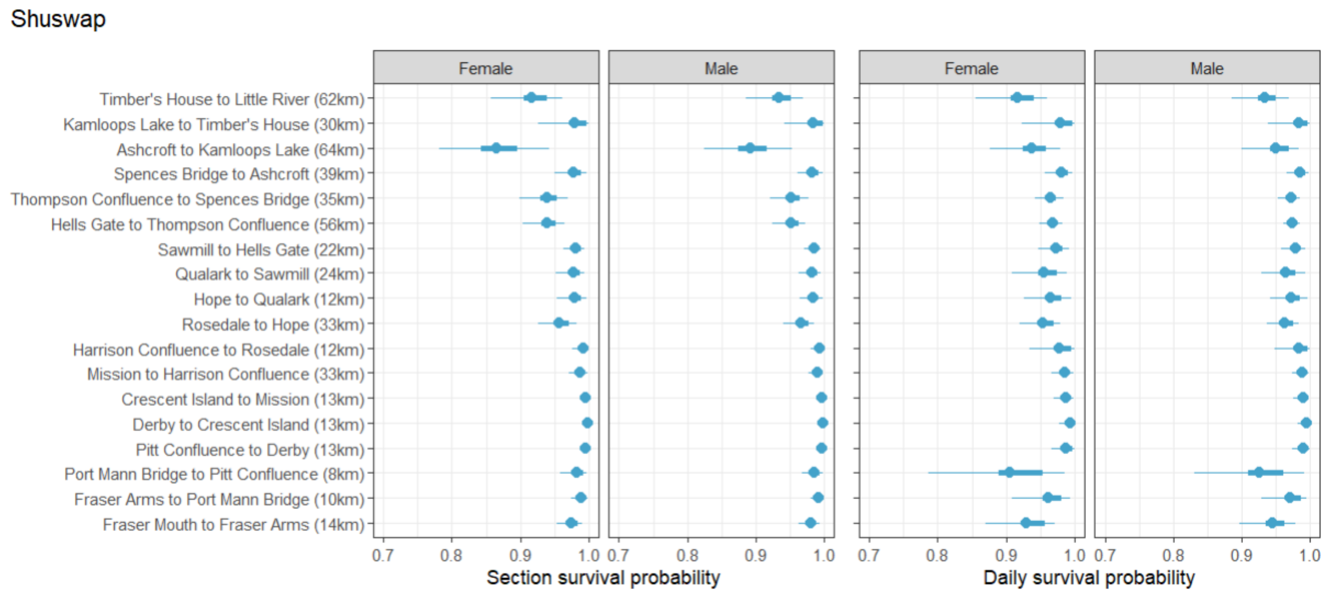

Figure 25: Section and daily survival probability for the Shuswap conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

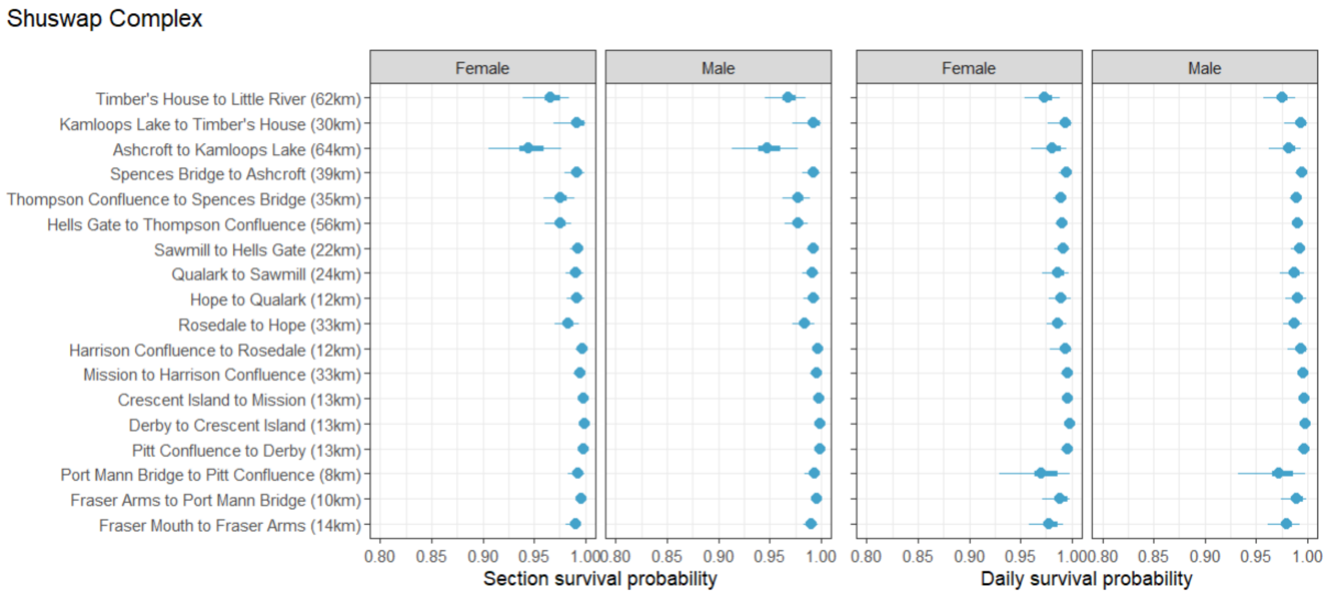

Figure 26: Section and daily survival probability for the Shuswap Complex conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

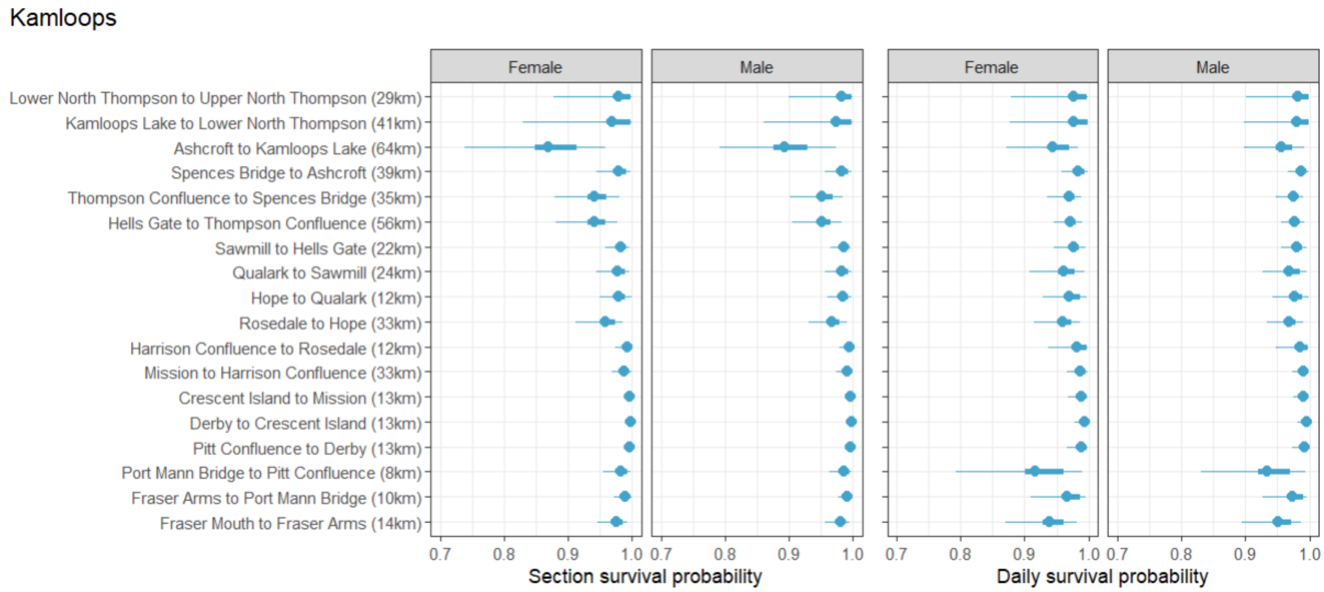

Figure 27: Section and daily survival probability for the Kamloops conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

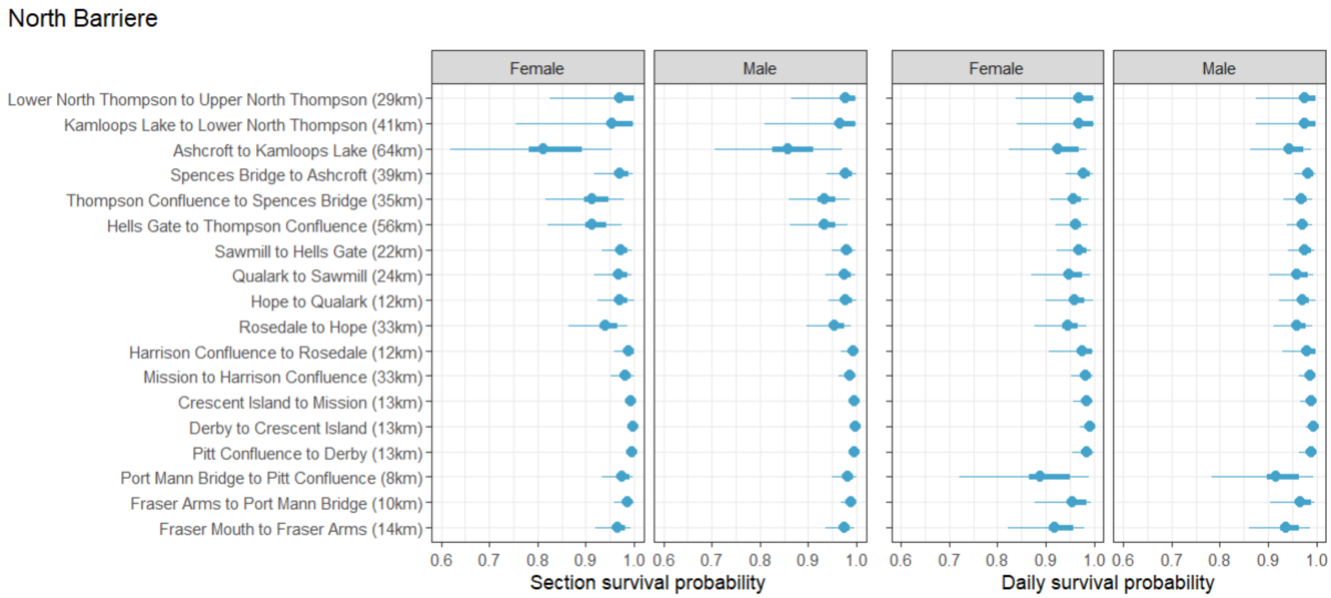

Figure 28: Section and daily survival probability for the North Barriere conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

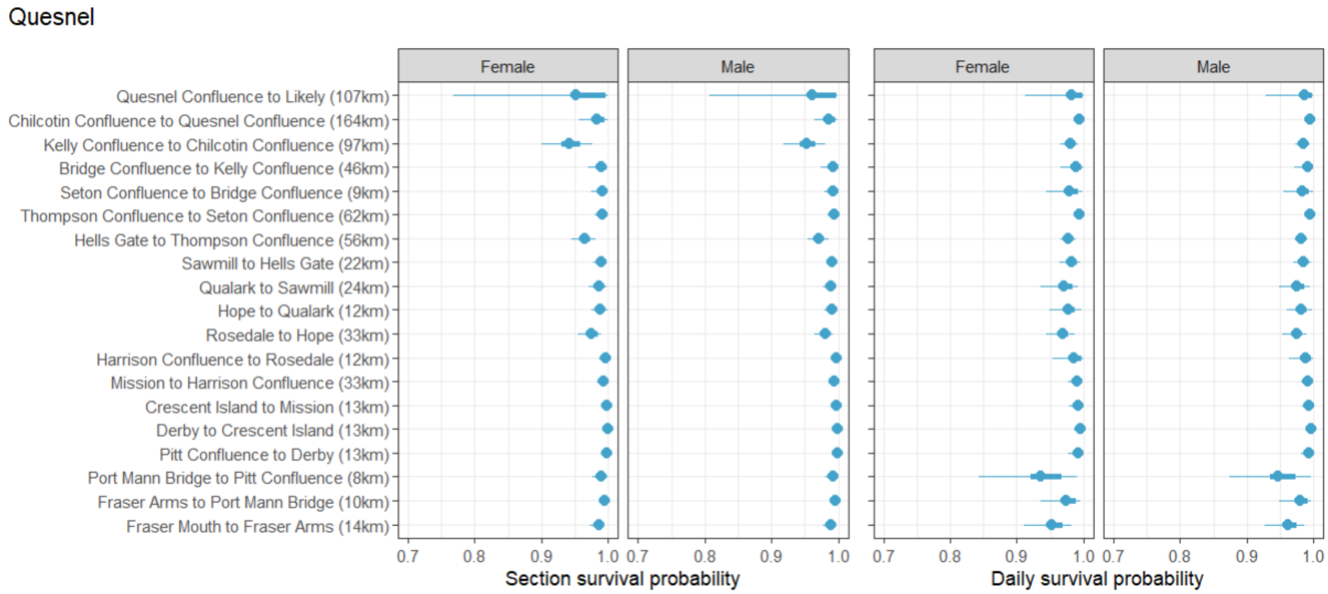

Figure 29: Section and daily survival probability for the Quesnel conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

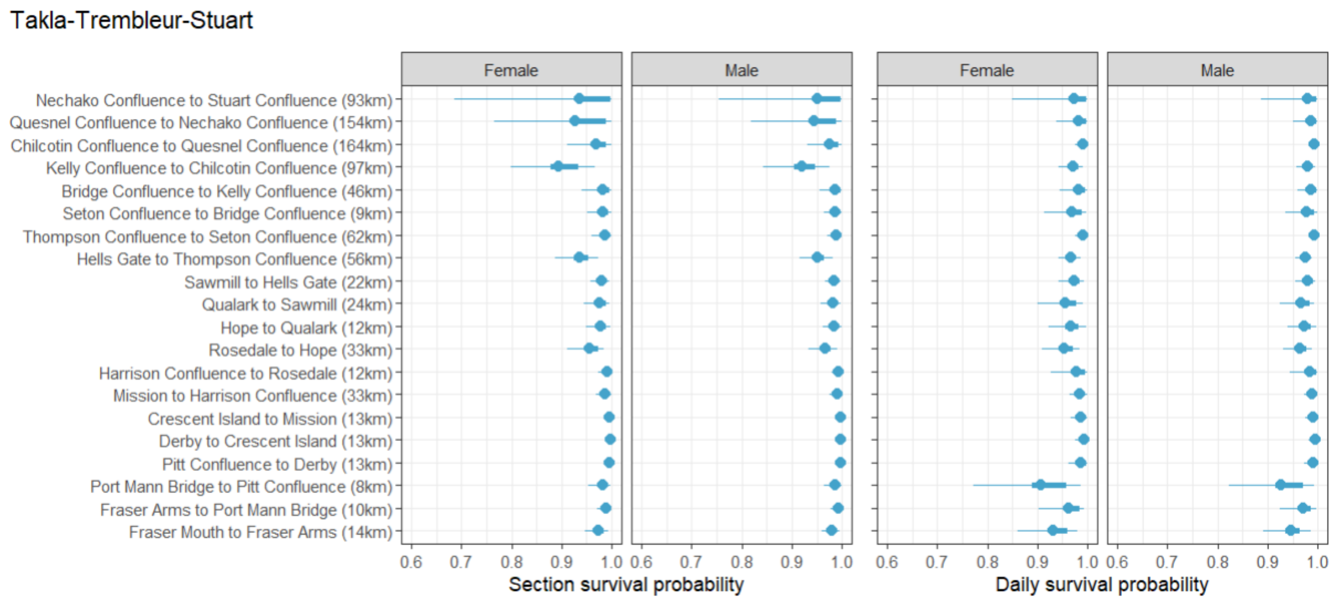

Figure 30: Section and daily survival probability for the Takla-Trembleur-Stuart conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

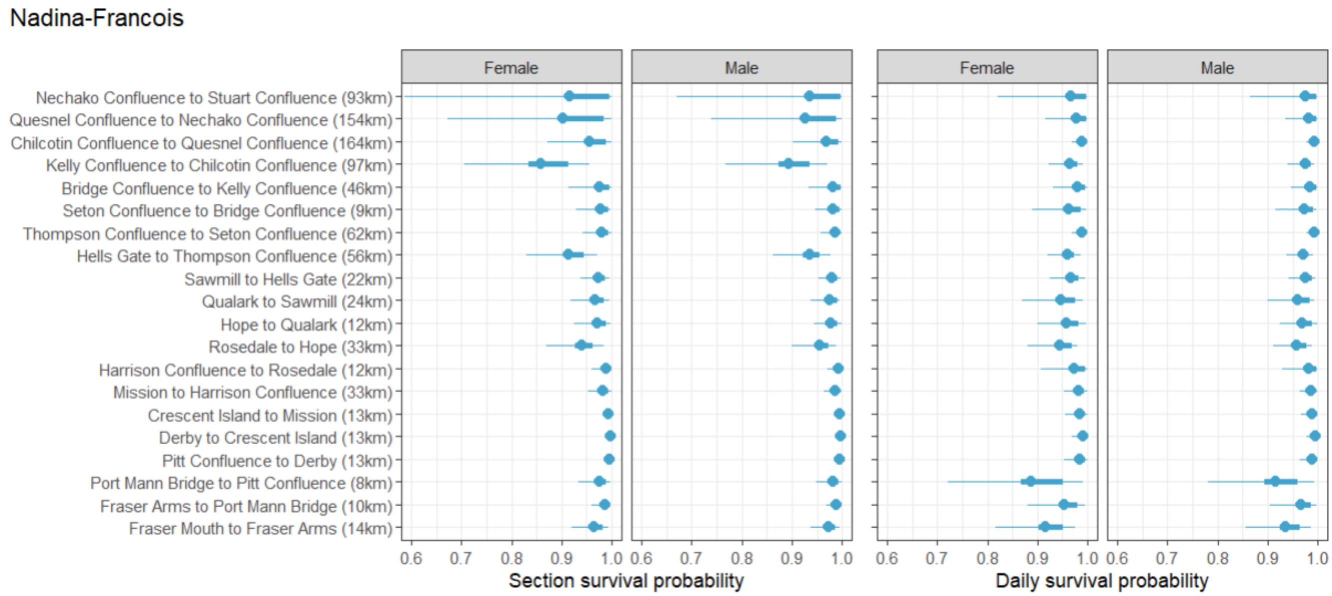

Figure 31: Section and daily survival probability for the Nadina-Francois conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

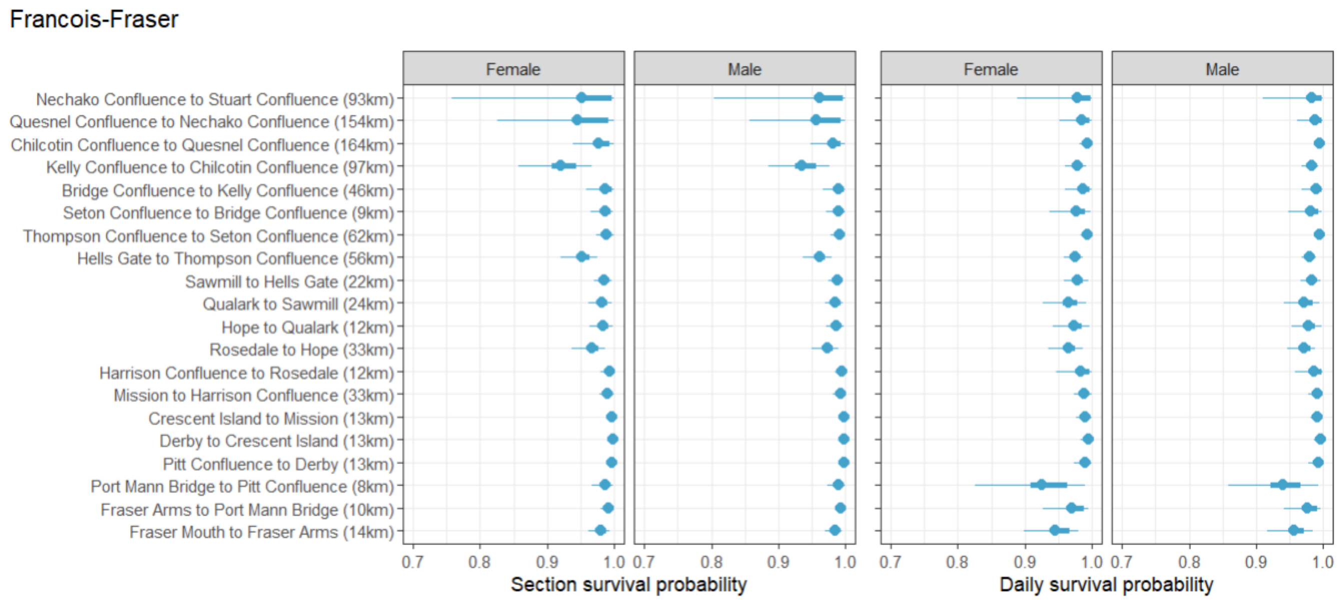

Figure 32: Section and daily survival probability for the Francois-Fraser conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

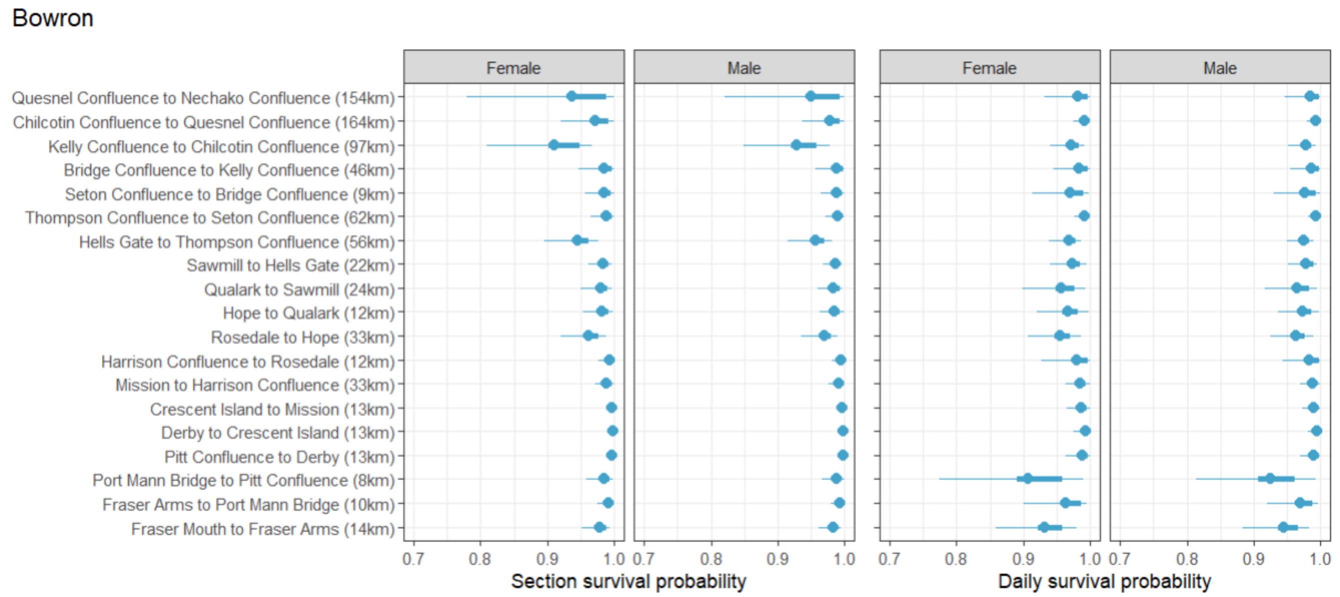

Figure 33: Section and daily survival probability for the Bowron conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

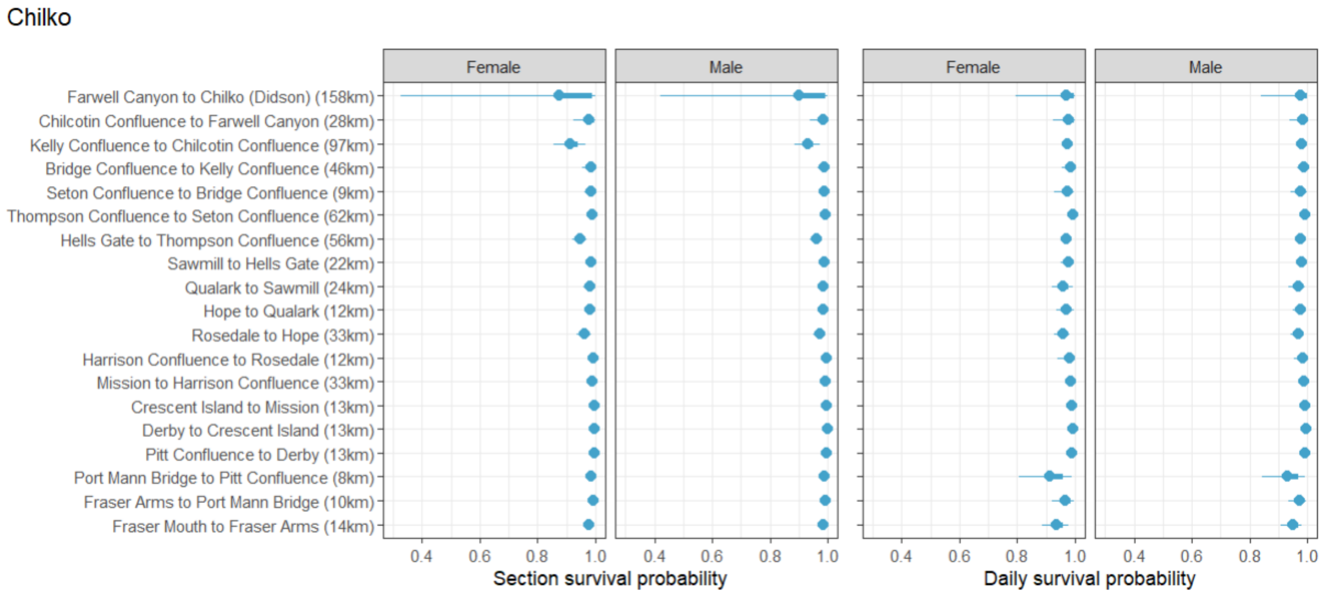

Figure 34: Section and daily survival probability for the Chilko conservation unit with 50% (thick), and 95% (thin) credible intervals. Section survival probability is used to calculate overall migrations survival probability.

Overall migration survival probability is based on the moving average water temperature (recorded at Qualark) prior to an individual’s final detection. The overall migration survival probability of the Harrison conservation units (Harrison (US), Harrison (DS), Harrison River, and Lillooet-Harrison) varied little and thus remained relatively high across the range of moving average temperatures they were exposed to (Figure 35). There were only three individuals tagged from the Harrison (DS) conservation unit, therefore, their modelled daily survival probabilities are highly uncertain. Predictions for the other study conservation units show a much steeper negative relationship between survival and moving average of temperature, with declines in daily survival probability ranging from 0.35 to 0.75 units between the lowest and highest moving average temperature experience by tagged fish in a conservation unit. Generally, daily survival exhibited a slight decline with temperature moving averages < 15°C (a notable example being the Shuswap Complex; Figure 35) and the relationship became steeper and approximately linear at temperature moving averages > 15°C (Figure 35).

Females generally had lower median overall migration survival than males of the same conservation unit (Figure 36). Anderson-Seton conservation unit had the lowest overall migration survival probability for both females (median = 0.40, MAD = 0.17) and males (median = 0.52, MAD = 0.16), while Harrison River conservation unit had the highest median survival probability for both females (median = 0.89, MAD = 0.06) and males (median = 0.90, MAD = 0.04). Other than the Harrison River conservation unit, which has a summer run timing, Late run sockeye had the highest survival probability.

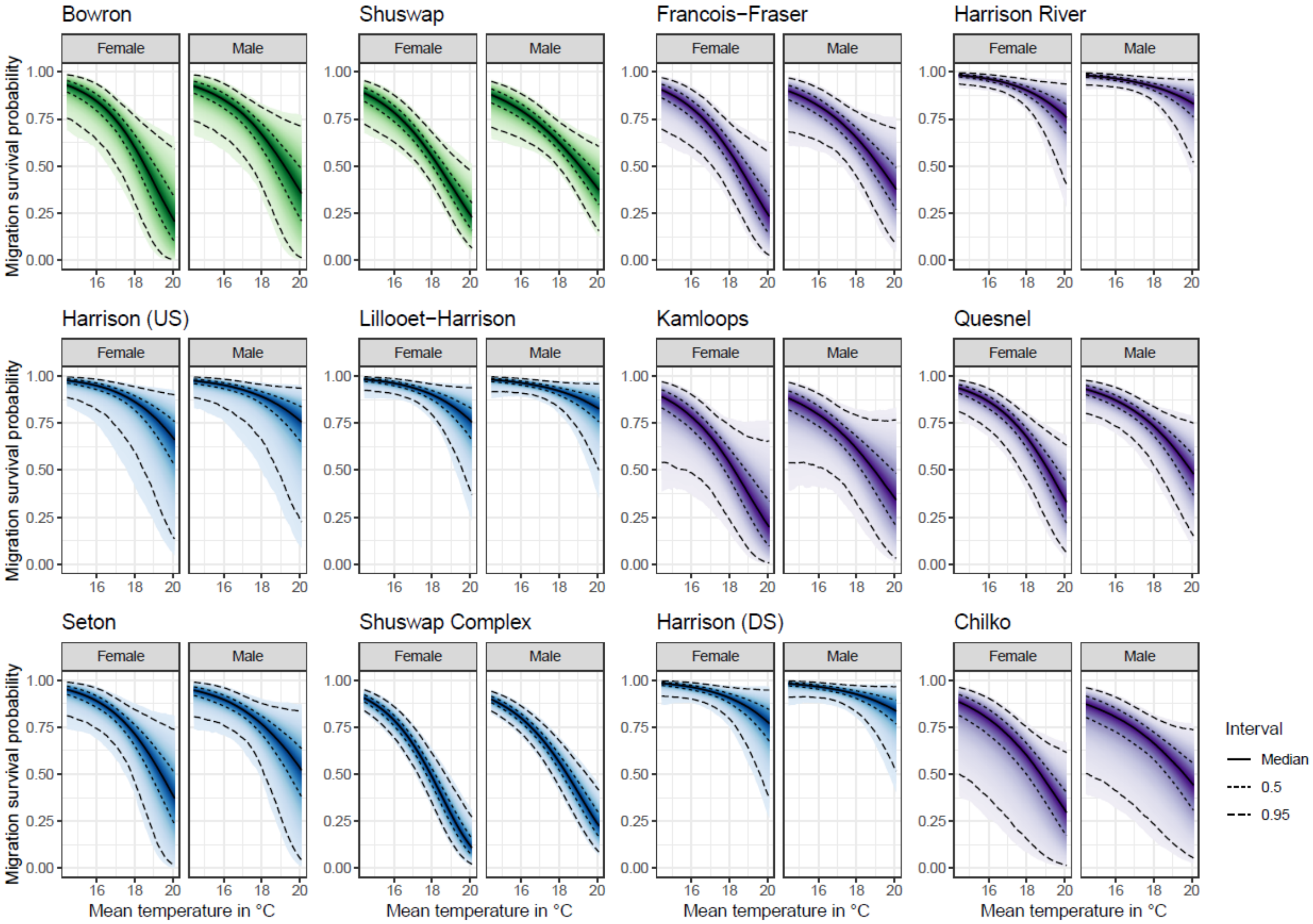

Figure *35*: Modeled effect of the moving average water temperature before the final detection on survival of female and male sockeye salmon. Conservation units coloured by run timing (green = Early Summer, purple = Summer, blue = Late).

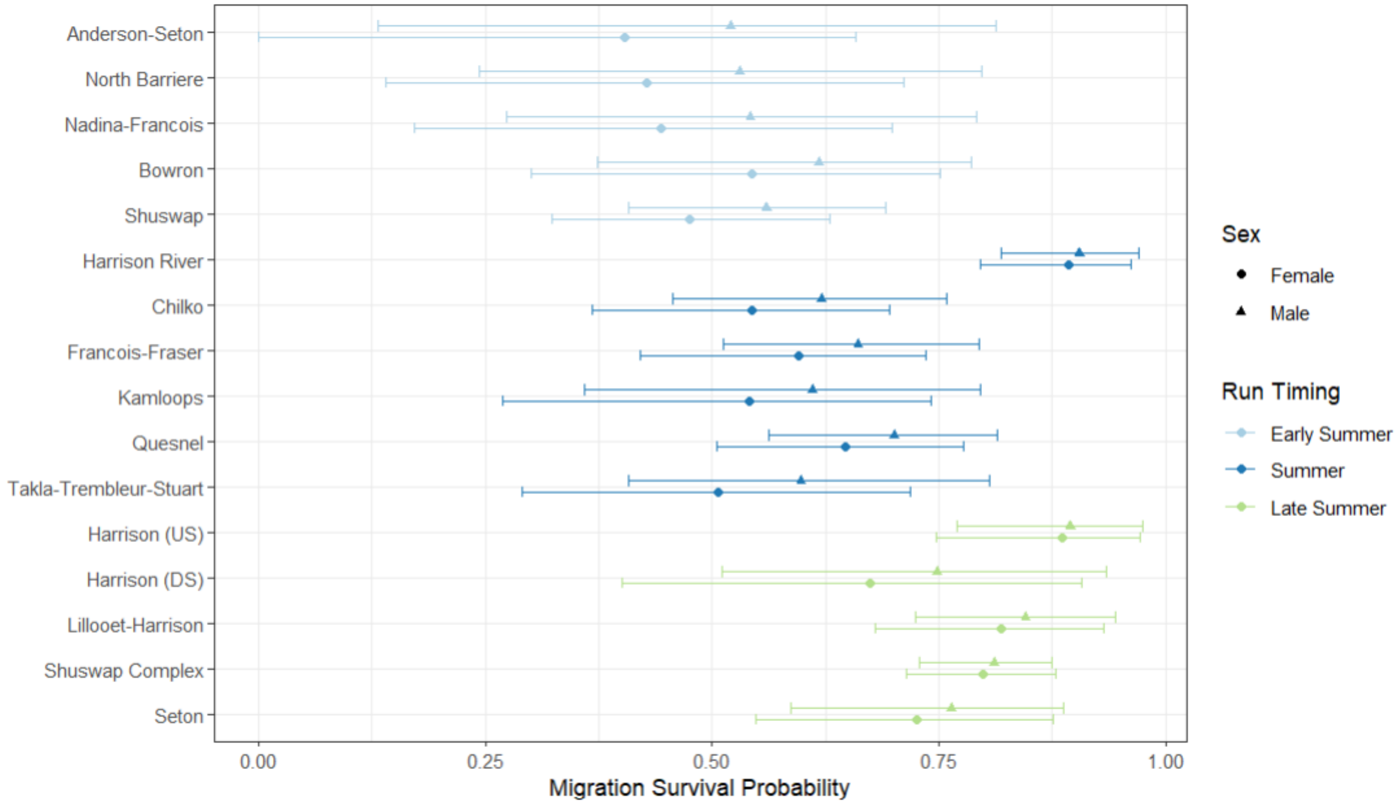

Figure 36: Overall migration survival probability for each conservation unit with 95% credible intervals, colours indicate run timing. Overall migration survival probability is based on the moving average water temperature (recorded at Qualark) prior to an individual's final detection.

DISCUSSION

In this research, I set out to improve our understanding of how the survival probabilities of different conservation units of sockeye salmon in the Fraser River are impacted by their thermal experience, as well as how migration rate and survival probability vary throughout their migration routes. Using a novel analytical approach integrating a model of migration rate with a state-space formulation of a CJS model, my findings identified moving averages of temperatures as the best predictor of survival among other candidate metrics. Furthermore, my findings highlight the variability in migration rates and survival probabilities among different river sections and conservation units. Importantly, the hierarchical modeling approach I used allowed me to obtain reasonable estimates of survival probability for CUs whose data had not been analyzed previously due to the low number of tagged individuals. In most cases, my results demonstrate that survival probability of migrating adult sockeye salmon in the Fraser River decreases with warmer temperatures. However, the strength of the temperature effect varied between different conservation units (CU) and between male and female sockeye in each CU. The Shuswap Complex, Bowron, and Anderson-Seton CUs were the most negatively affected by increasing the moving average temperature. Females consistently experienced lower survival probabilities than the males in the same CU.

Migration rates through each river section varied by conservation unit, however, there were river sections that tended to be consistently navigated faster or slower for conservation units. Migration rates can be influenced by several factors including river flow, water temperature, and run size (Carey et al. 2017; Quinn et al. 1996). Variation in migration rates of different populations has previously been reported, with populations travelling the longest distances migrating slower than those with shorter migration routes (Hanson et al. 2008). Hanson et al. (2008) used the 2003 data also included in this thesis and focussed on three stock complexes (Quesnel, Chilcotin, and Nechako). They found that one population with a longer migration route consistently migrated slower than two others with shorter migration routes, and that all populations migrated significantly slower through an energetically difficult river section containing Hell's Gate Canyon. Interestingly, Hope to Qualark, Thompson Confluence to Spences Bridge, and Thompson Confluence to Seton Confluence were a relatively slow section for several populations, while individuals were able to migrate faster through the sections around Hells Gate, which is generally considered one of the most challenging portions of the migration for many populations. It is possible that the river conditions in 2003 were such that migration through Hell’s Gate was slowed more than in the other years included in this study. The Seton confluence to Bridge confluence also appeared to be slower for several populations. Faster sections included Chilcotin confluence to Quesnel Confluence, and Mission to Harrison confluence. The Fraser Canyon ends part of the way between the Chilcotin Confluence and Quesnel Confluence so hydraulic conditions are favourable in the upstream portion of this section. The Mission to Harrison confluence is tidal, so it is possible that sockeye salmon took advantage of tides and experienced reduced encounter flows. Despite the possibility of tidal assistance, some observed migration rates were very high. It is possible that issues with receiver time syncing or recording receiver coordinates may have led to errors in migration rate computations.

In all three survival models that tested different thermal predictors, female sockeye salmon tended to have a steeper decline in survival with increasing temperatures or time spent in higher temperatures. In the selected model, survival probability declined as the moving average temperature increased, and there was a slightly steeper decline in survival probability for females than males. In most conservation units except Harrison River, Harrison (US), Harrison (DS), and Lillooet-Harrison, male and female sockeye salmon reached 50% survival probability at ~18.5-20°C and ~18°C-19°C, respectively. This is similar to findings of other studies, which showed heightened rates of mortality at 18°C or 19°C (Crossin et al 2008, Jeffries et al 2012, Martins et al. 2011, Mathes et al 2010). The higher energetic cost of reproductive development for females has been suggested as a mechanism of comparatively lower survival in migrating adult female sockeye compared to males (Crossin et al 2008). Other mechanisms suggested include reduced immune function and physiological impairment following stressors (Crossin 2004; Eliason et al. 2020; Gale et. al 2014; Little et al. 2020; Teffer et al. 2019; Teffer et al. 2017). Historically, it was thought that returning adult sockeye populations in the Fraser River have been skewed toward females, and that males experienced higher rates of mortality during their ocean-dwelling life stage (Foerster 1954); however, this is not supported by current sex ratios observed at the lower-river test fishery (Patterson, personal communication, April 2025). The disproportionately high mortality rate of female sockeye salmon during their migration has the potential to negatively affect recruitment and is likely to be exacerbated with projected rises in water temperature.

Also consistent in the three models, the Harrison conservation units (Harrison River, Harrison (US), Harrison (DS), and Lillooet-Harrison) did not appear to respond very strongly to any of the thermal predictors used, whereas all other CUs did. Based on the short migration distance and observed migration rates, it is possible that Harrison sockeye populations were not exposed to elevated river temperatures in the Fraser River mainstem long enough to experience mortality during migration. This is supported by the finding that the random effect of temperature on survival for the Harrison populations showed little deviation from the global effect of temperature, indicating that temperature did not have a smaller or larger effect on those CUs than it did on Fraser sockeye salmon at a whole. Population-specific responses to thermal stress have been observed in other studies (Eliason et al 2011). Eliason et al. (2011) suggested a higher thermal tolerance was likely present in populations with a more challenging migration route, this is consistent with my findings that the Takla-Trembleur-Stuart CU, which has one of the longest migration routes in this study, had the largest positive deviation from the global slope of the random effect of temperature of survival.

In the time since the data were collected for the present study (between 2002 and 2011) water temperatures in the Fraser River have continued to rise, with both magnitude and duration of periods of elevated water temperature. The Canadian Climate Change Report (2019) estimated that air temperature in Canada has increased by an average of 1.7˚C between 1948 and 2016, and found that it is “virtually certain” that air temperatures will continue to rise (Zhang et al. 2019). This is reflected in Fraser River water temperatures, which have increased during the migration periods of all four sockeye salmon run timings since the 1940s (Patterson et al. 2007). Over the same period the proportion of streamflow originating from snowmelt has also decreased, causing further changes to the hydrology of the Fraser River (Kang et al. 2014). Water temperatures in many parts of the Fraser River exceed 20˚C twice as often as they did in the 1950s (Islam et al. 2019). The present study modelled survival probability across the range of temperatures that individuals experienced in 2002, 2003, 2006, 2010, and 2011. All conservation units exhibited negative relationships between survival probability and water temperature before their final detection. It is therefore likely that if water temperature continues to rise survival probability during upstream migration will decline further, unless the conservation units are able use thermal refuges during migration to adapt (Mayer et al. 2024). Although there is evidence of sockeye salmon seeking thermal refuge during their spawning migration (Armstrong et al. 2016), it has not been observed in the Fraser River during river migrations (Donaldson et al. 2009) only with lake residence periods (Mathes et al. 2010).

There are several considerations when addressing the effects of climate change and rising water temperatures on the survival of migrating adult sockeye salmon in the Fraser River. Behavioural thermoregulation, or how an organism uses its thermal environment to regulate its body temperature and physiological processes, may act as a buffer to short periods of high water temperatures (Armstrong et al. 2016; Baldwin 1974). Several studies have shown that different sockeye salmon populations use thermal refuge in lakes to moderate physiological processes prior to spawning (Katinic et al. 2015; Mathes et al. 2010; Newell and Quinn 2005). However, as temperatures continue to rise access to thermal refuge may become more limited (Armstrong et al. 2016). Maintaining areas of thermal refuge through land management practices is essential and may become increasingly important as overall river temperatures are projected to rise. Redirecting cold groundwater has also been trialled to enhance or create areas of cold water refugia (Kurylyk et al 2015; Smith and Kurylyk 2024). The second consideration when addressing the effects of climate change and rising water temperatures on the survival of migrating adult sockeye in the Fraser River is their potential capacity to adapt to rising water temperatures (Crozier et al. 2019; Monaco et al. 2017; Sinclair et al. 2016). There is significant difference in various populations' survival in warmer water temperatures, and historical thermal experience is cited as a potential explanation. This indicates that there may be some capacity for adaptation in the face of continually rising temperatures, although this may not be possible given the current rapid rate of warming (Hague et al. 2011; Reed et al. 2011).

LIMITATIONS AND RECOMMENDATIONS

There were several limitations that may have implications on the results of the present study. First, the sample sizes were variable across the different conservation units included in the study, ranging from 1 in the Francois (first-run) CU to 1313 in the Shuswap Complex CU. This is due to the timing of tagging, which was intended to target late-run sockeye salmon in three out of the five years (English et al. 2004; English et al. 2005; Robichaud et al. 2006; Robiachaud et al. 2007; Robichaud et al. 2008). The use of a hierarchical model allowed the results for data – poor conservation units to be supplemented by information from data rich populations. One limitation is that this can lead to the results for data-poor conservation units being overly influenced by the overall population mean (Schaub and Kéry 2012). As one of the goals of this study was to investigate the differences in the effects of water temperature on survival probability for each conservation unit, this may lead to an underestimation of the variation in response to temperature by each conservation unit (Schaub and Kéry 2012).

Another limitation of this study is that water temperature data collected at Qualark in the Lower Fraser River were used to approximate temperatures throughout the Fraser River Watershed. Although temperatures at Qualark have been found to have a strong correlation ($r > 0.6$) to temperatures throughout the watershed, the relationship is not as strong for conditions in the upper watershed and there is also variation in the magnitude of temperatures experienced (Hague et al. 2008). This should be considered when viewing results for Upper Fraser populations or those entering the river after mid-August. There are several options to address this issue in the future. First, future studies could include more temperature monitoring, for example having a temperature station in each river section or attaching temperature loggers to the fish tags would provide a better understanding of the thermal experience of fish. There are also a growing number of initiatives with the goal of cataloguing water temperature and flow data collected by many different organizations and making it publicly available, for example, the Pacific Salmon Foundation's Pacific Freshwater Monitoring Map for BC and the Yukon[1]. These tools may provide the data necessary as well as identifying potential collaborators to increase the availability of water temperature throughout the Fraser River network in future modelling efforts. Second, a spatial stream network model (SSNM) could be used to better understand the thermal experience of migrating adult sockeye in the Fraser River. Spatial stream network models combine sample site data, distance between sites, and stream flow to predict stream temperature throughout the stream network (Isaak et al. 2014; Ver Hoef et al. 2006). A spatial

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[1] https://experience.arcgis.com/experience/c435a5188ec54d5bbc10b85f6af99d05

stream network model has been developed for one of the Fraser River's major tributaries, the Thompson River (Chezik 2019). Models have also been developed to provide higher resolution temporal changes in water temperature (Siegel et al. 2023). To improve on the present study, water temperature data for available locations along the migratory route for each conservation unit could be compared to those at Qualark to better understand the potential error introduced by only using temperatures from the lower river.

Another limitation is that sex was modelled for 1928 fish that were not sexed in the field. Although sex was assigned using a multiple imputation model based on fork length and including a random intercept (account for differences in mean fish size among CUs) and random slope for fork length (accounting for differences in the effect of fork length on the probability of a fish being male among CUs), it is possible that the difference between male and female survival probabilities is reflecting the effect of size on survival probability rather than sex. Finally, there are other sources of mortality that were not accounted for, which may have confounded the results. Tagged fish that were harvested and reported were removed from the dataset, however, it is possible some harvested fish were not reported, or mortality may have been caused by other factors such as predation or disease. It is also possible that tag loss or failure affected the results. Not accounting for these forms of mortality or missed detections could confound results or lead to an over estimation of the impact of temperature on survival and mortality.

To build upon the findings of the present study, future work should include expanding the protocol to other Fraser populations migrating earlier in the season (Early Stuart) and potentially experiencing warmer river temperatures, and using temperature data from throughout the watershed to create a more accurate approximation of the thermal experience for each conservation unit. In this study, I investigated how certain aspects of magnitude, duration, and timing of high mean water temperatures affected the survival of migrating adult sockeye salmon in the Fraser River. However, investigation into how other aspects of Fraser River sockeye salmon's thermal experience impacts their survival probability, such as frequency of extreme temperatures and the rate of change in water temperature during their migration, could also be beneficial in understanding the implications of a changing climate on sockeye salmon (Steel et al. 2012; Steel et al. 2017).

MANAGEMENT IMPLICATIONS

Management implications resulting from this work could include consideration for current and predicted climatic conditions when developing management adjustments for each population as well as considering sex-specific escapement targets to account for the disproportionate mortality of female sockeye salmon following thermal stress. In the Fraser River, management adjustments are applied to the allowable harvest in each run timing group (Early Stuart, Early Summer, Summer, and Late) to account for the difference between estimates of sockeye salmon entering the lower river and the number of sockeye salmon that reach their spawning grounds. The difference in estimates at the mouth of the Fraser River and the spawning grounds can be attributed to error in either estimate, natural mortality, and/or unreported catch (Macdonald et al. 2010). Refining management adjustments to account for the variable effect of temperature on each conservation unit and sex could be considered (Hinch et al. 2021). My findings align with other studies that show survival probability, and the effect of temperature varies between conservation units and sexes (Eliason et al. 2011; Hinch et al. 2021). Under current mixed-stock harvesting practices differentiation of conservation units is challenging. Single-stock fisheries may be an option to achieve certain management objectives, however, several studies have indicated their success requires detailed consideration of the unique circumstances (Freshwater et al. 2020; Moore et al. 2021). Hinch et al. (2021) discuss the potential benefit of implementing sex-specific escapement targets to ensure returns of female sockeye are sufficient to maintain the population. In addition, they suggested using sex ratios may be an indicator of stress in a population, which is supported by our findings. In this model, the differential effect of temperature on sex was assumed to be consistent between conservation units. Future models may benefit from testing whether the sensitivity of females to high water temperatures is different between conservation units. To address the negative impact of high water temperatures on sockeye, as well as the disproportionate impact on females, temporary pauses to commercial fisheries during periods of high water temperature could also be considered. My findings also emphasize the importance of moderating land use in a way that maintains or reduces river temperature. Maintaining riparian vegetation that provides sufficient shade is a key component of this, even in the face of rising air temperature and decreasing summer stream flows (Wondzell et a. 2019). Specifically, increasing riparian protection in small headwater streams, that do not currently have mandatory riparian reserves in BC, may help maintain cooler temperatures throughout stream networks (O’Connor 2023).

As discussed, sockeye salmon are facing a variety of challenges due to rising water temperatures during their spawning migration. Possible management actions may include population and sex specific responses to rising water temperatures; temporarily pausing commercial fisheries during periods of high water temperature; and mitigating the impacts of land use on water temperature.

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Appendix A

Model discrepancy statistics and posterior predictive checks

Model 1: The effect of ten-day average of river temperature following river entry

Deviance of simulated and observed data for model 1, the effect of the ten-day average of river temperature following river entry, is displayed below (Figure A 1). This model has a Bayesian p-value of 0.49. Posterior predictive checks show that the observed data overlaps with the posterior estimate (Figure A 2 and Figure A 3).

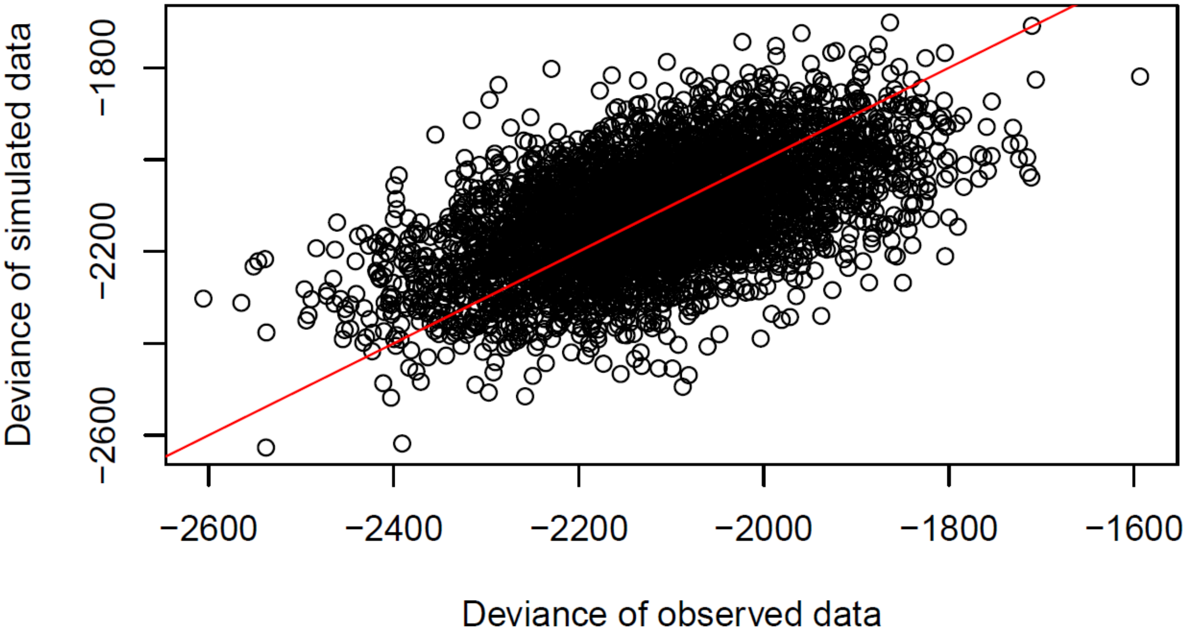

Figure A 1: Deviance of simulated and observed data for Cormack Jolly Seber model 1.

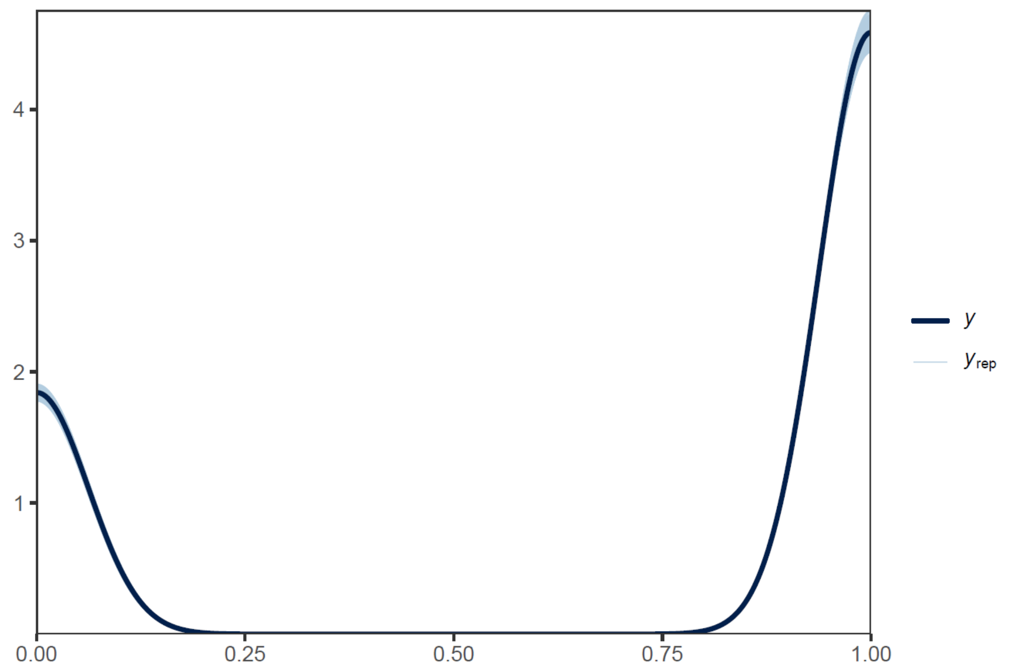

Figure A 2: Density distribution of observed data (dark blue line) and posterior estimate (light blue shading).

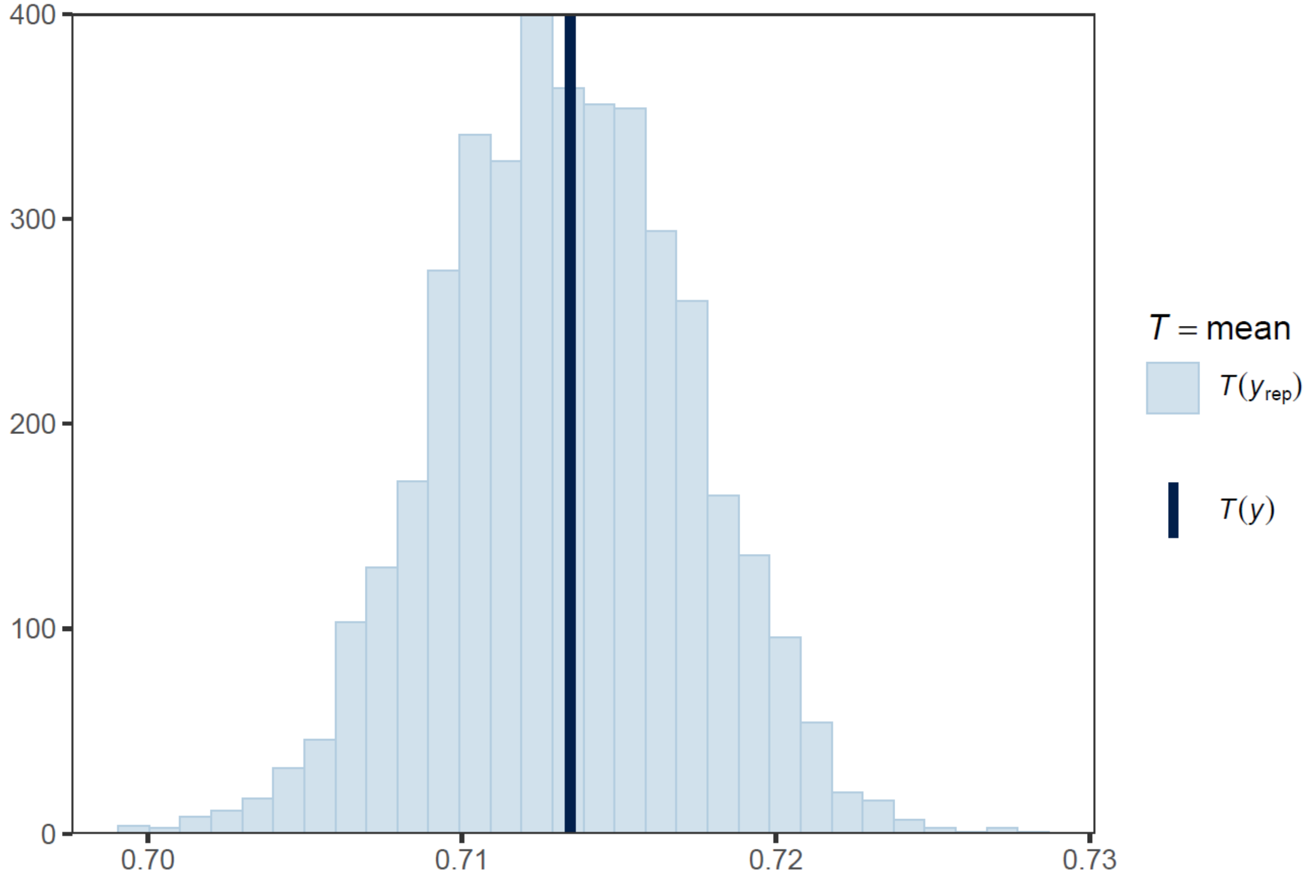

Figure A 3: Histogram of posterior estimate (light blue shading) with overlaid mean of observed data (dark blue line).

Model 2: The effect of average water temperature prior to final detection

Deviance of simulated and observed data for model 1, the effect of the ten-day average of river temperature following river entry, is displayed below (*Figure A 4*). This model has a Bayesian p-value of 0.51. Posterior predictive checks show that the observed data overlaps with the posterior estimate (*Figure A 5* and *Figure A 6*).

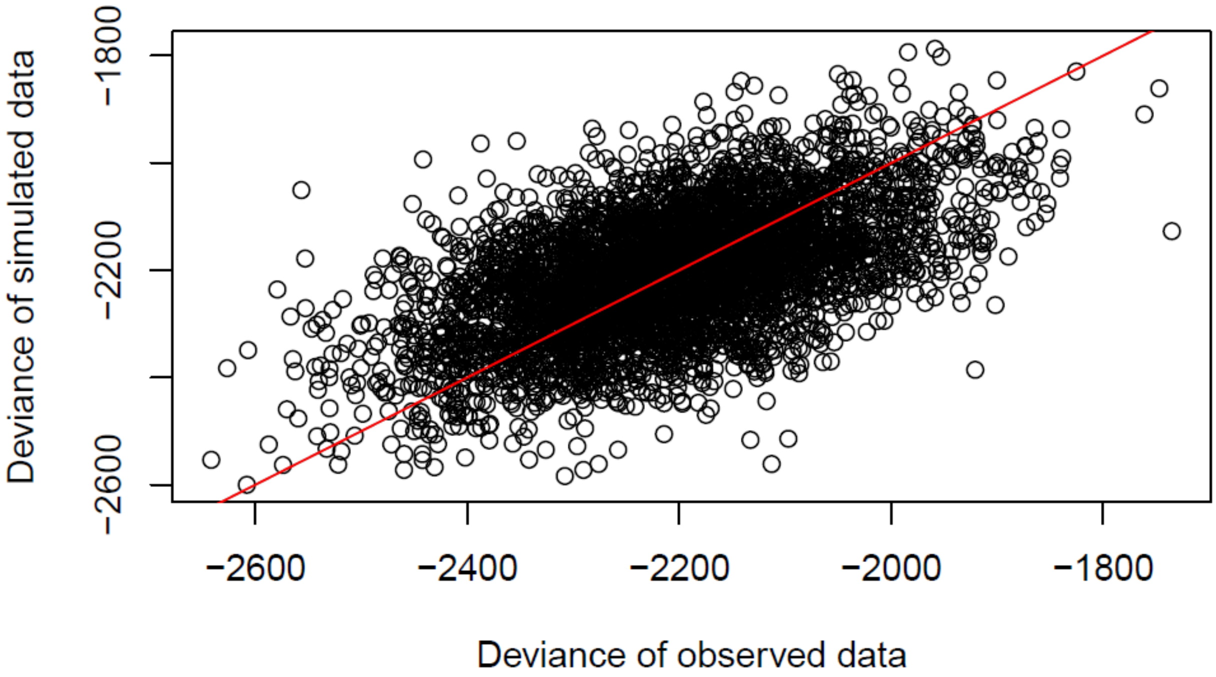

Figure A 4: Deviance of simulated and observed data for Cormack Jolly Seber model 2.

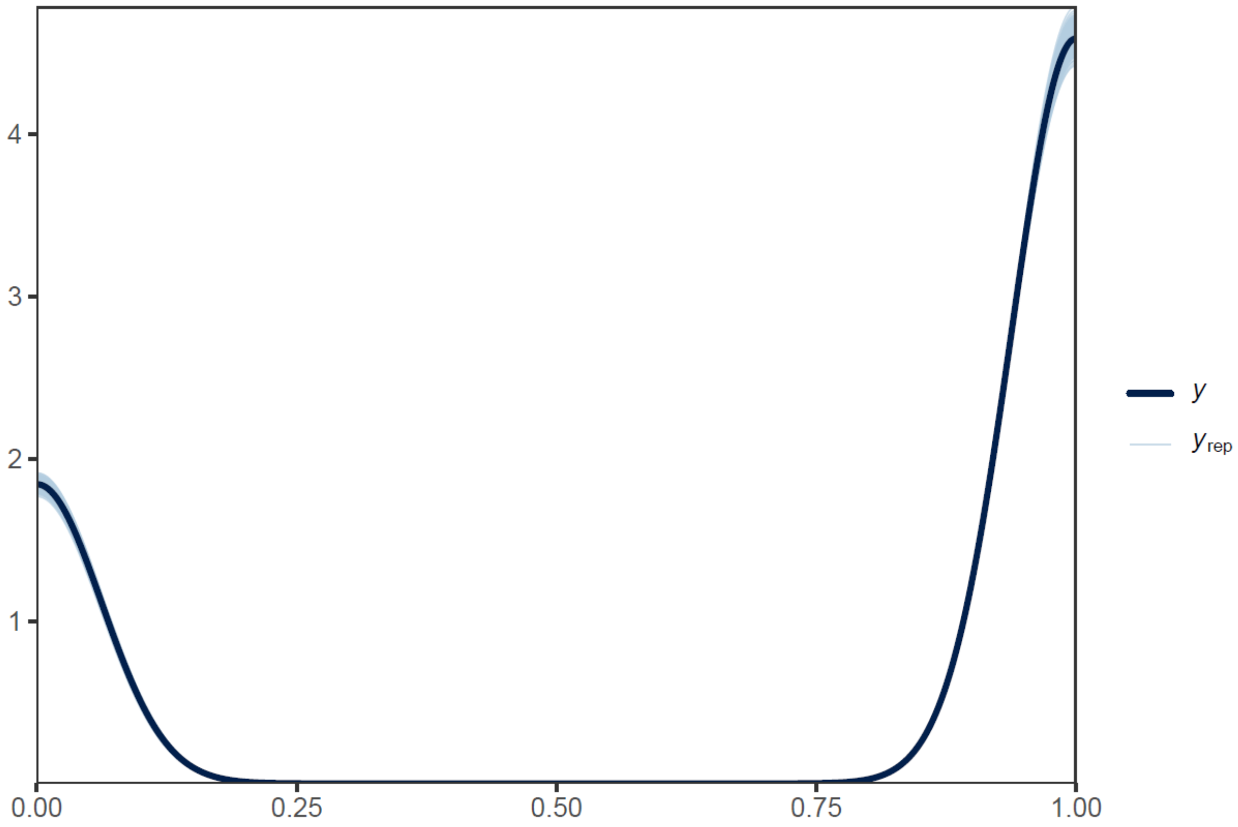

Figure A 5: Density distribution of observed data (dark blue line) and posterior estimate (light blue shading).

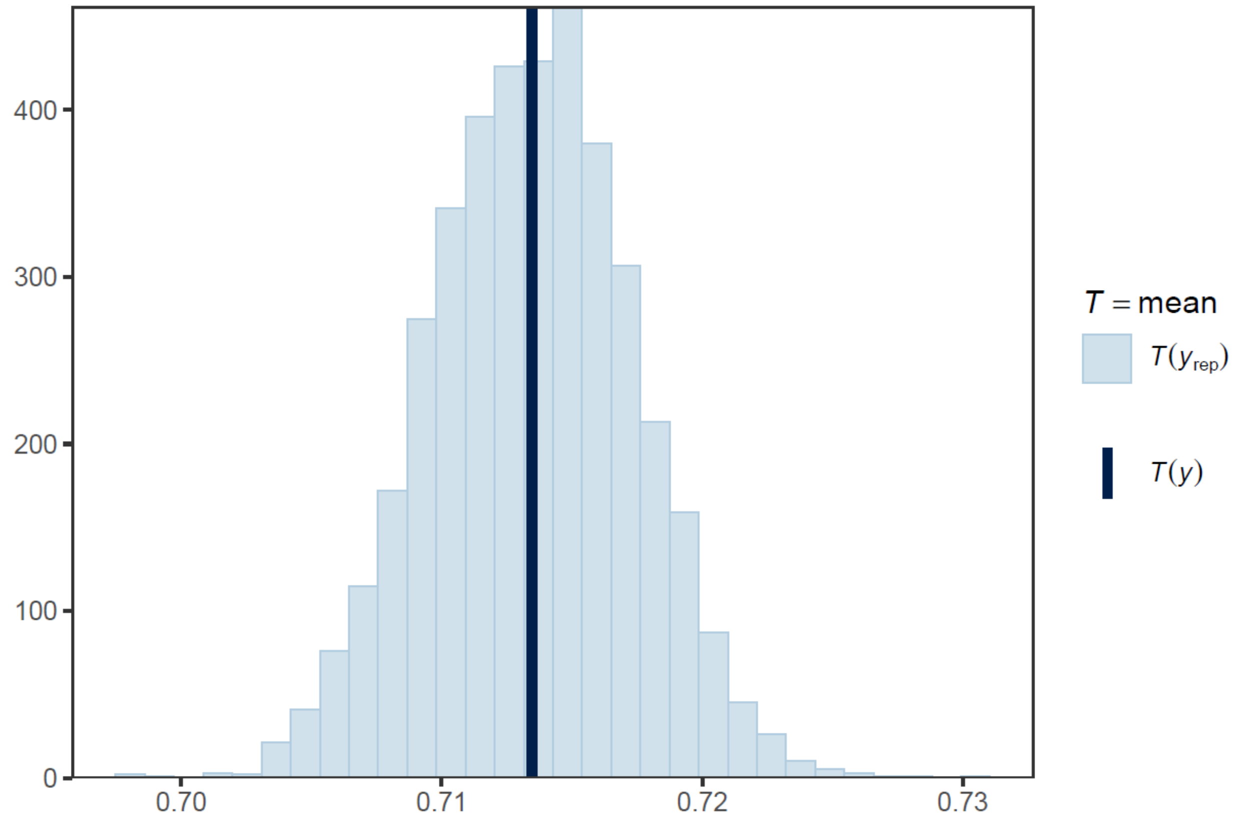

Figure A 6: Histogram of posterior estimate (light blue shading) with overlaid mean of observed data (dark blue line).

Model 3: The effect of number of days above 18° C on survival

Deviance of simulated and observed data for model 1, the effect of the ten-day average of river temperature following river entry, is displayed below (*Figure A 7*). This model has a Bayesian p-value of 0.5. Posterior predictive checks show that the observed data overlaps with the posterior estimate (*Figure A 8* and *Figure A 9*).

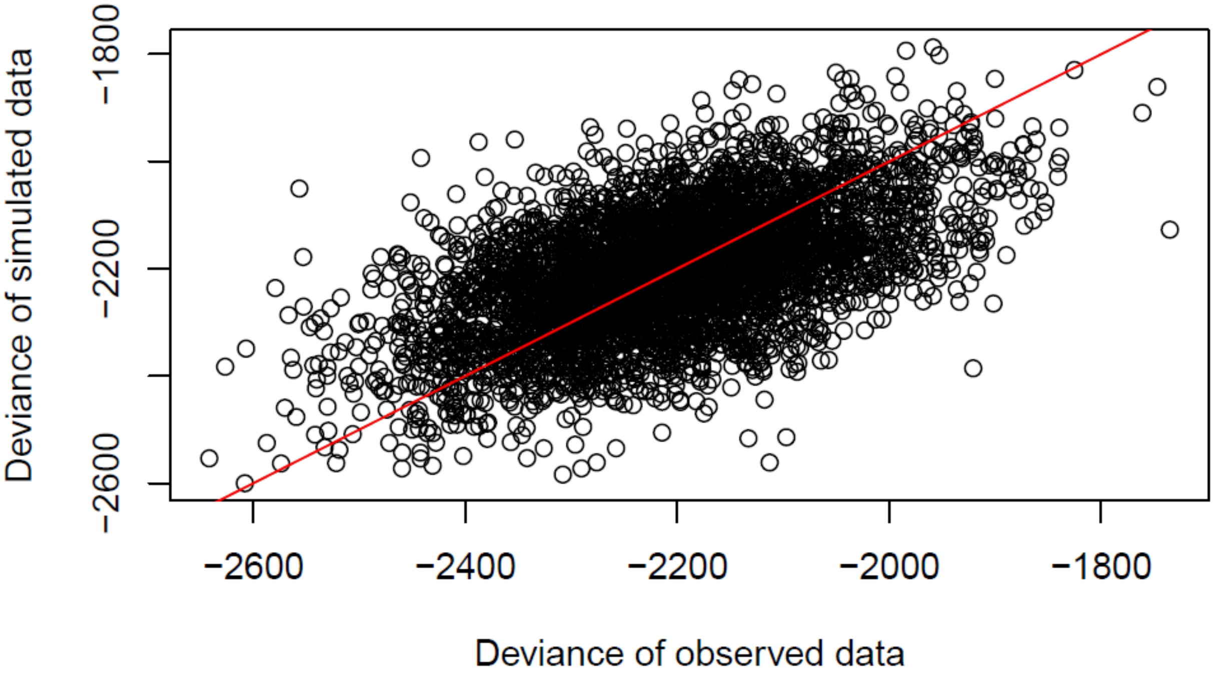

Figure A 7: Deviance of simulated and observed data for Cormack Jolly Seber model 3.

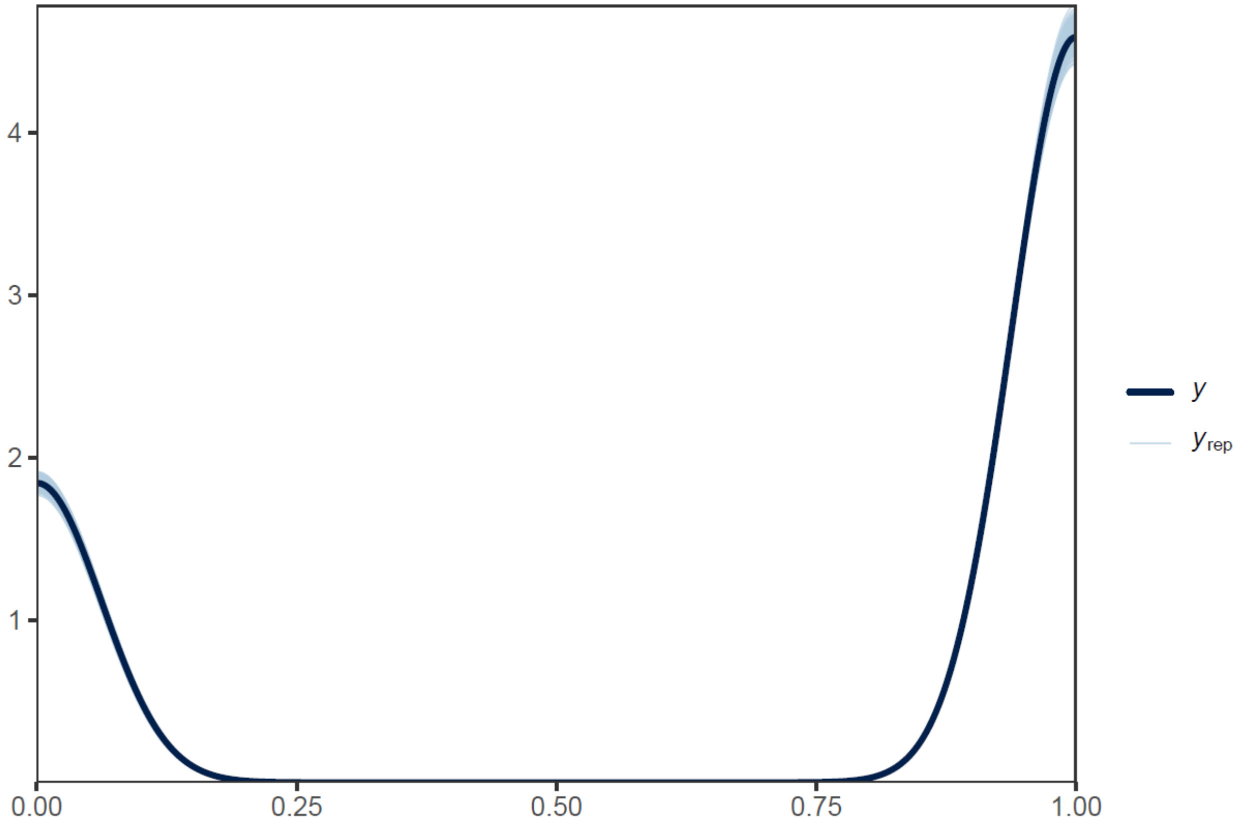

Figure A 8: Density distribution of observed data (dark blue line) and posterior estimate (light blue shading).

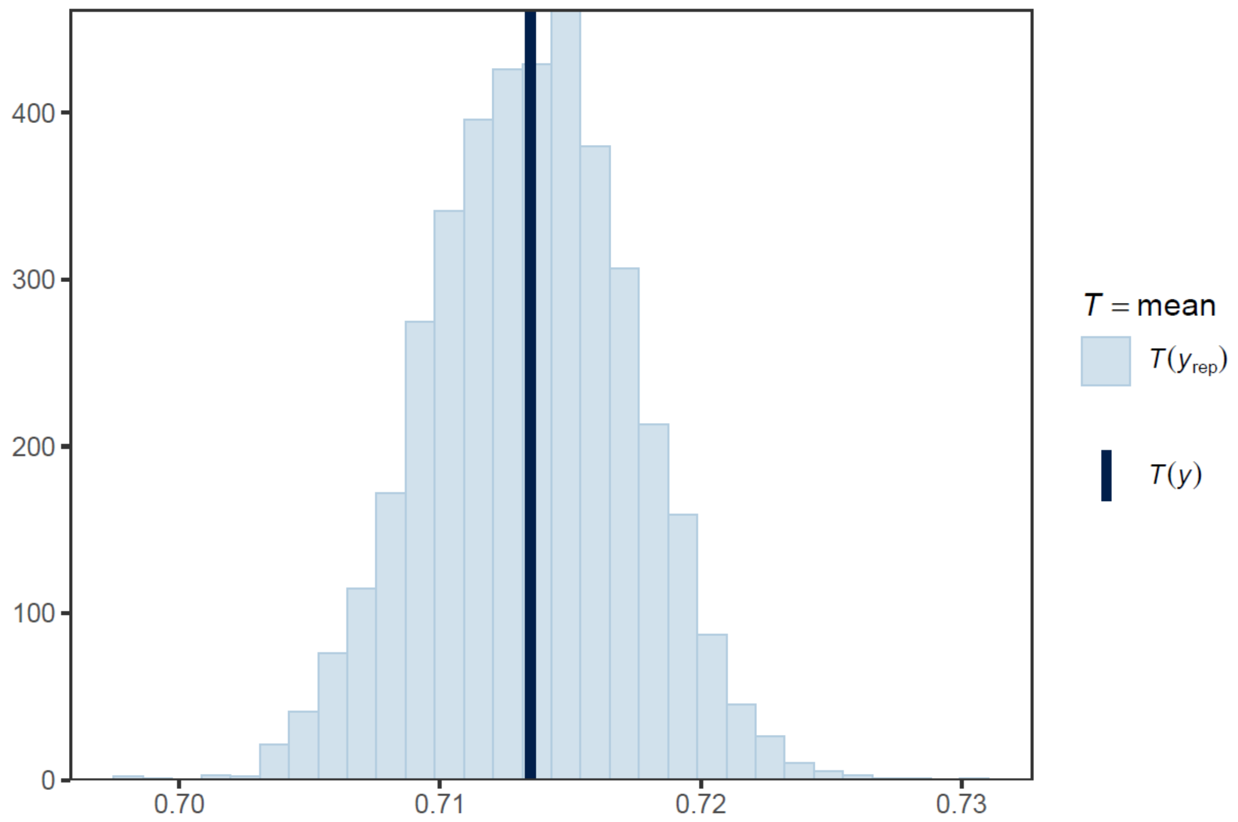

Figure A 9: Histogram of posterior estimate (light blue shading) with overlaid mean of observed data (dark blue line).

Appendix B

Model 1 – Effect of ten-day average of river temperature following river entry

Generally, there is a negative relationship between survival probability and the ten-day average water temperature following river entry, with a steeper relationship occurring for female sockeye salmon than males (Figure B 1). The Lower Fraser conservation units of Harrison River (n = 112), Harrison (US)(n = 110), and Lillooet-Harrison (n = 74) exhibited relatively high survival probability across the range of ten-day average temperatures after river entry that they were exposed to.

Predicted survival probability for females reached 50% at approximately 17°C for the Bowron (n = 15), Chilko (n = 473), Francois-Fraser (n = 179), Kamloops (n = 17), Shuswap (n = 385), Shuswap Complex (n = 1313), and Quesnel (n = 407) conservation units.

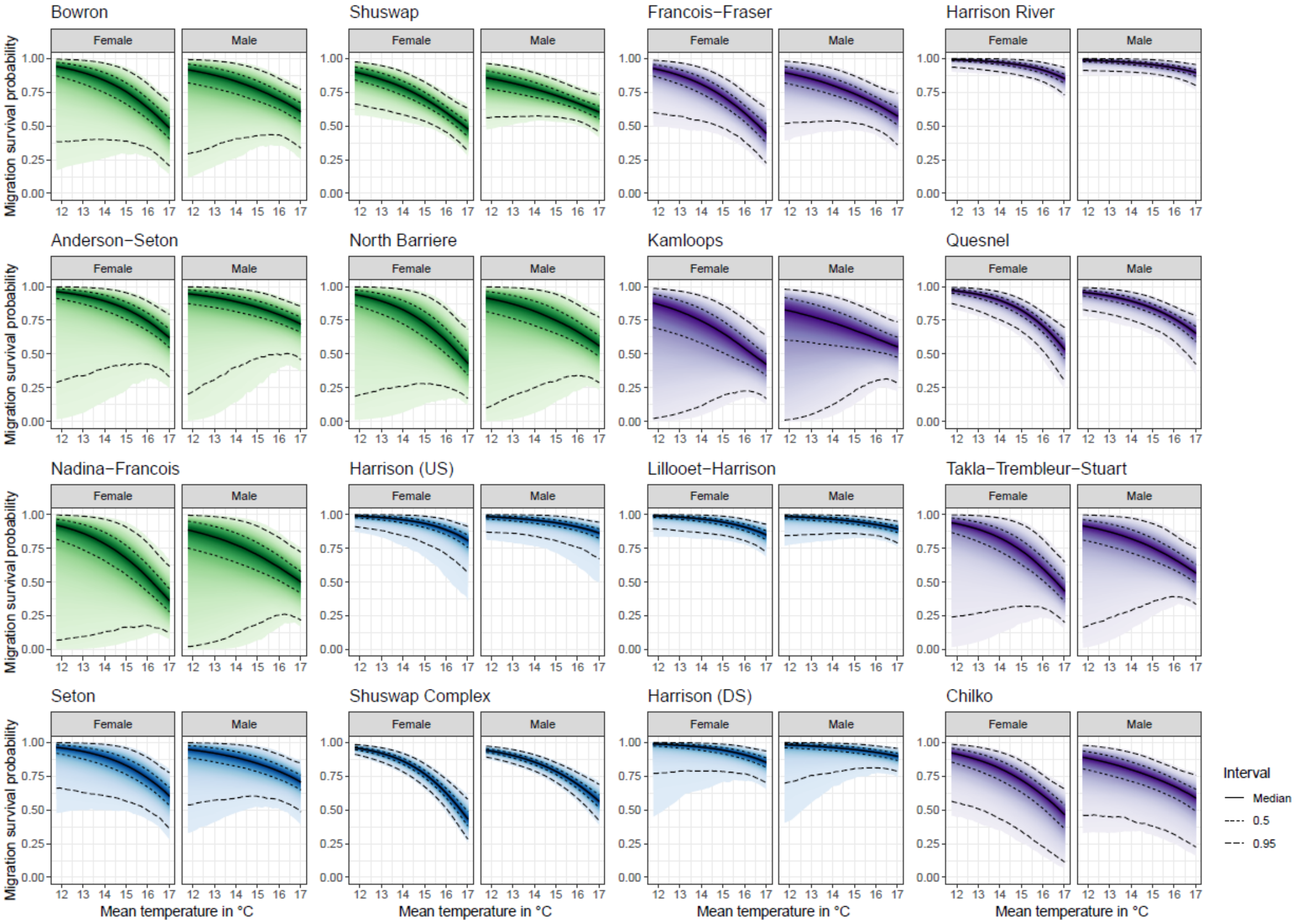

Figure B 1: Modeled effect of the average water temperature during the first ten days after river entry on survival of female and male sockeye salmon. Colour indicates run timing (green = early summer, purple = summer, blue = late).

Model 3- the effect of number of days above 18˚ C on survival

As with the previous two models, the survival probability of the Harrison conservation units remained high over the number of days that individuals were exposed to average water temperatures of above 18˚ C (*Figure B 2*). The predicted survival probabilities of the middle and upper Fraser conservation units exhibit a negative relationship with the number of day a fish experiences above 18˚ C, with females experiencing a steeper decline in survival than males. Several conservation units reached 0% survival probability within the number of days that were modelled. These include Females from Shuswap complex, Bowron, and Nadina-Francois, which reach 0% survival probability at approximately 18, 18 and 20 days respectively.

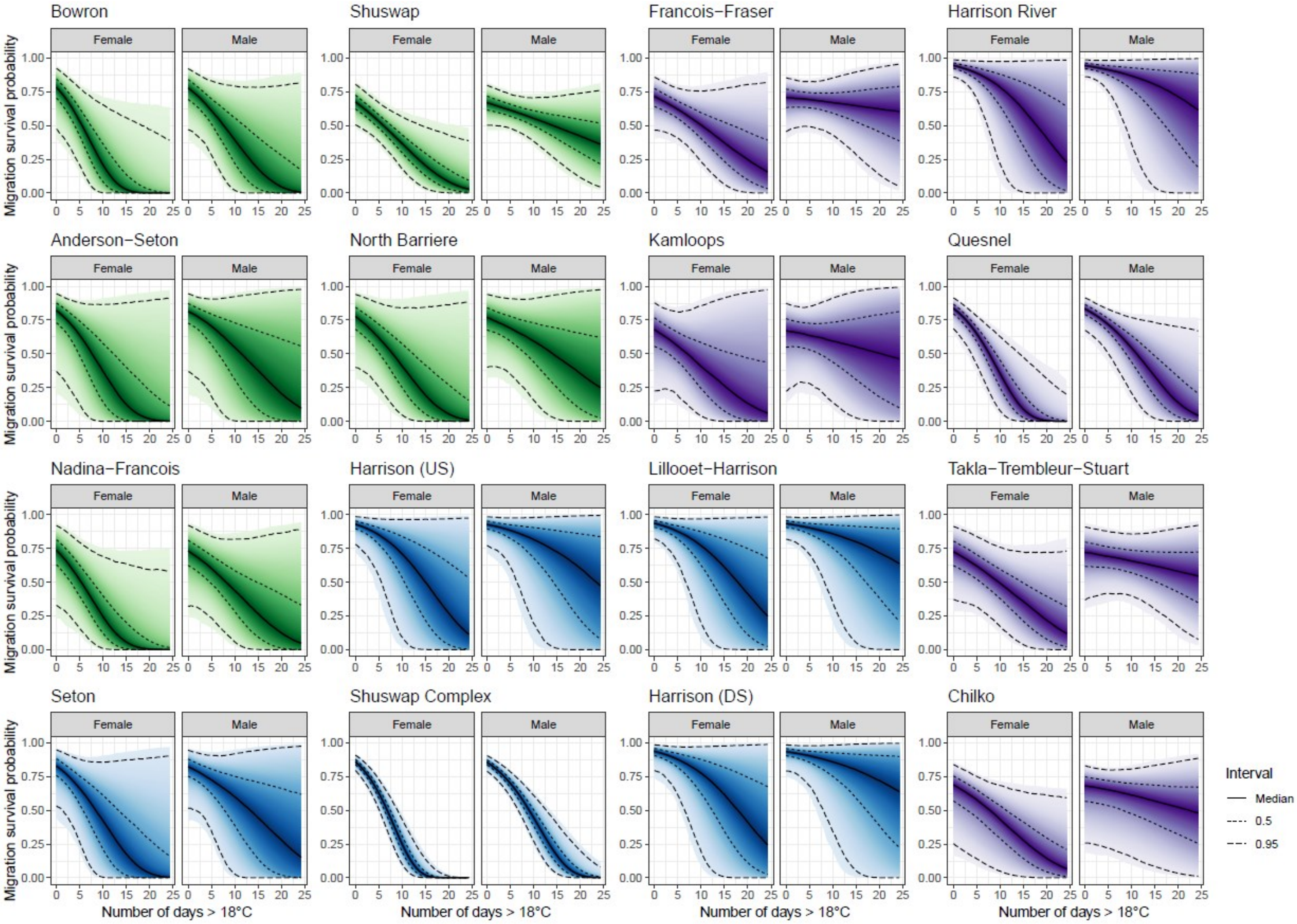

Figure B 2: Modeled effect of the average water temperature during the first ten days after river entry on survival of female and male sockeye salmon. Colour indicates run timing (green = early summer, purple = summer, blue = late).

Appendix C

Fork Lengths

Fork lengths were measured for each tagged individual. The male sockeye tended to have non-significantly longer median fork lengths than females in the same population and year (Figure B 1 and Figure B 2). Due to the number of individuals captured in each population, this comparison as not possible for all populations and years. The smallest median fork length for females was observed in females from the Takla-Trembleur-Stuart conservation unit (54 cm, MAD = 1.48 cm), while the largest median fork length was observed in females from the Pitt conservation unit (63.5 cm, MAD = 2.97 cm). The longest males occurred in the Seton (62 cm, MAD = 1.48 cm), Harrison River (62 cm, MAD = 2.97 cm) and Harrison (US) (62 cm, MAD = 2.97 cm) conservation units, while the smallest males occurred in the Talka-Trembleur-Stuart conservation unit (57 cm, MAD = 1.48 cm). The largest variation in the fork length of males within a population occurred in the Chilko (range = 16.5 cm) and Shuswap Complex (range = 16 cm) conservation units, these were also the conservation units with the largest sample sizes, so that may influence this outcome. However, the largest variation in fork length for females occurred in the Francois-Fraser (range = 14 cm) and Lillooet-Harrison (range = 12.5 cm) conservation units. Sex was not determined for 1928 individuals.

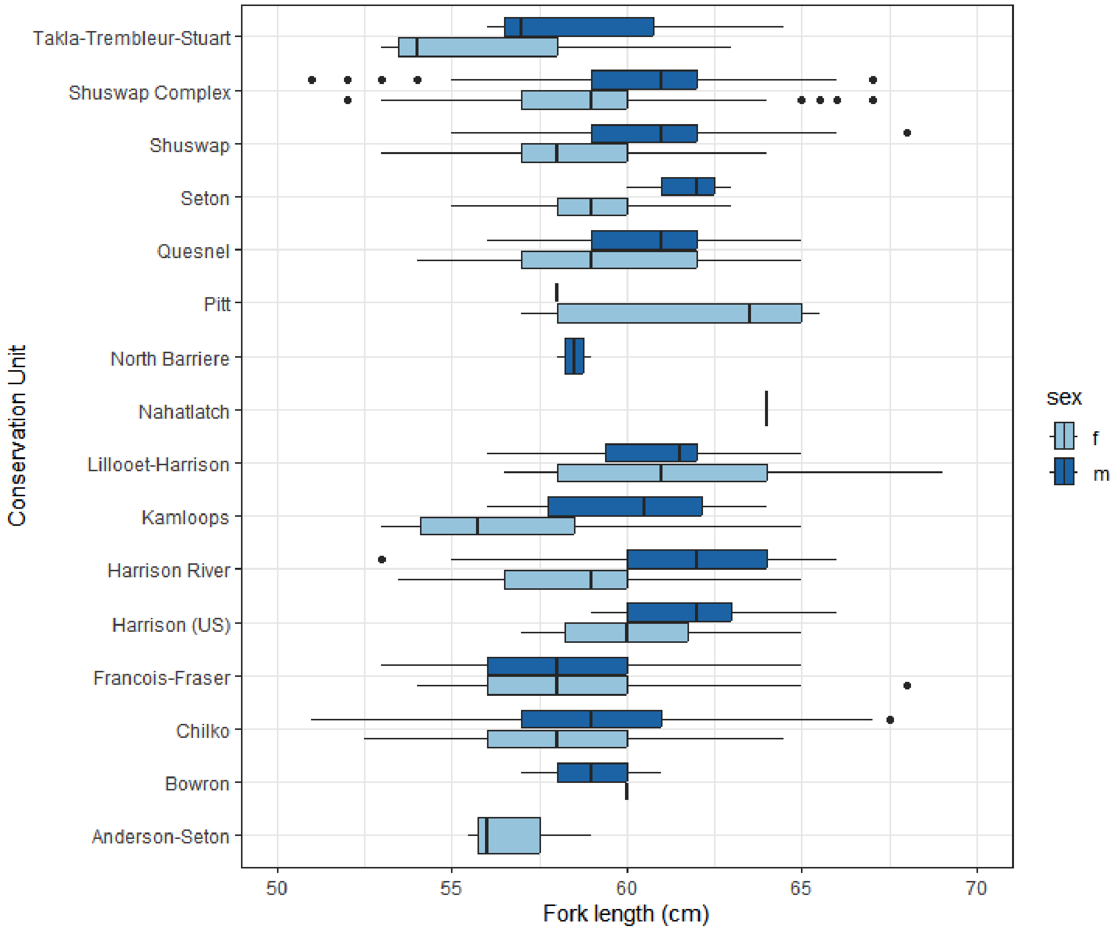

Figure C 1: Fork lengths of females (light blue) and males (dark blue) in 16 conservation units of sockeye salmon in the Fraser Watershed.

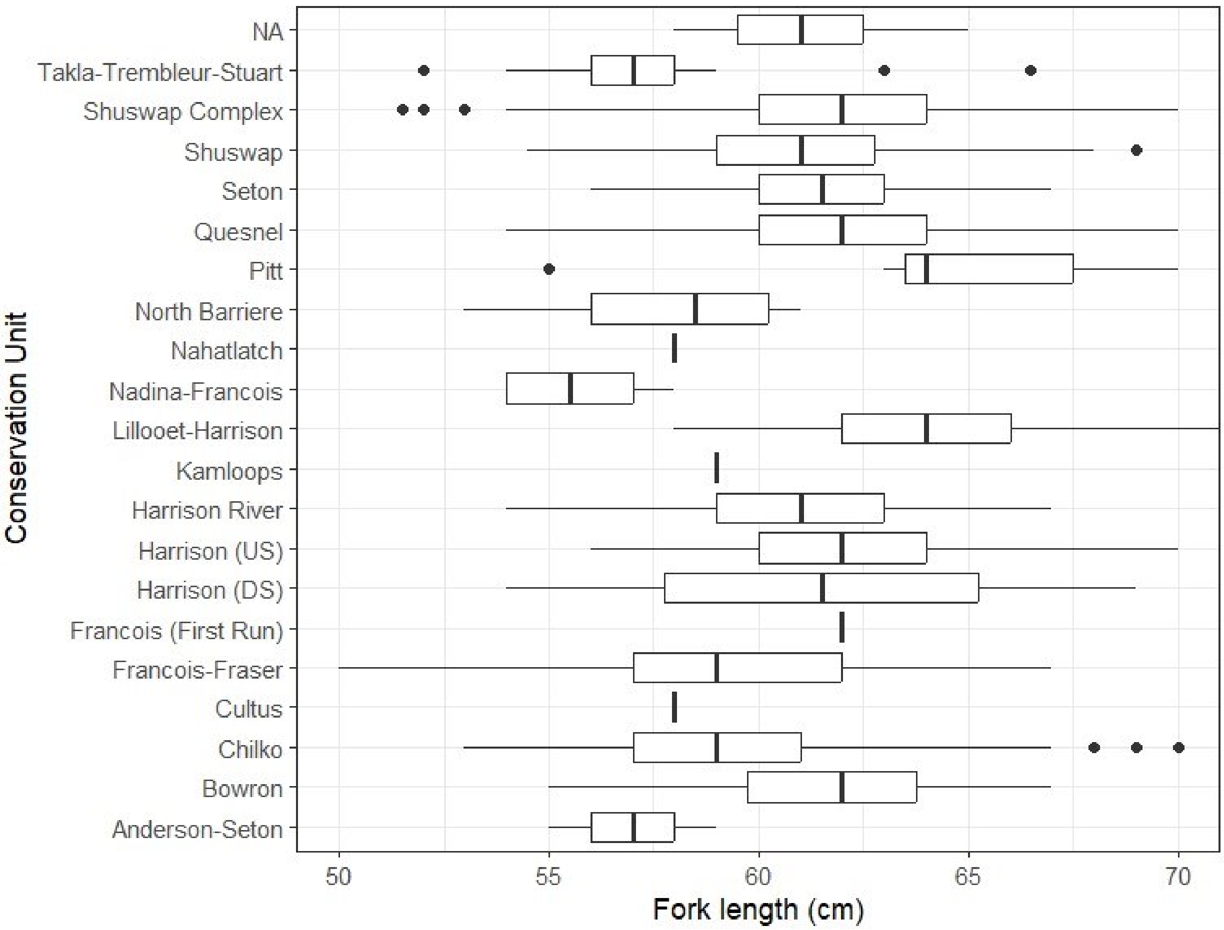

Figure C 2: Fork lengths for 20 CUs for non-sexed individuals.

Appendix D

Table D 1: Prior distributions used for each model parameter.

Equation	Parameter	Parameter Description	Prior	Prior Justification
1	κ_M	Shape parameter of the migration rate model.	Gamma(2, 1)	This prior is weakly informative, allowing for the posterior distribution to be guided by the data, while keeping the mode away from 0.

2	α_M	Intercept of the migration rate model.	Normal(0, 3.2)	This prior was selected to regularize the posterior distribution while excluding implausible values.
2	$zLEN_i$	Effect of fork length on migration rate.	Normal (0, 3.2)	This prior was selected to regularize the posterior distribution while excluding implausible values.
2	$\sigma_{\delta_{M,i}}$	Standard deviation of the random effect of individual on migration rate	Gamma (2, 1)	This prior is weakly informative, allowing for the posterior distribution to be guided by the data, while keeping the mode away from 0.
2	$\sigma_{\delta_{M,j}}$	Standard deviation of the random effect of conservation unit on migration rate.	Gamma (2, 1)	Same as above
2	$\sigma_{\delta_{M,k}}$	Standard deviation of random effect of river section on migration rate.	Gamma (2, 1)	Same as above
2	$\sigma_{\delta_{M,l}}$	Standard deviation of random effect of year on migration rate.	Gamma (2, 10)	Same as above, with larger rate parameter due to the small number of years (avoids unrealistic extreme values that are common when number of random effects is small).
6	α_ϕ	Intercept of expected survival model.	Normal(0, 3.2)	This prior was selected to regularize the posterior distribution while

				excluding implausible values.
6	$\beta_{\phi,SEX}$	Effect of sex on survival.	Normal (0, 3.2)	This prior was selected to regularize the posterior distribution while excluding implausible values.
6	$\beta_{\phi,zTEMP}$	Effect of temperature on survival.	Normal (0, 3.2)	This prior was selected to regularize the posterior distribution while excluding implausible values.
6	$\beta_{\phi,SEX\cdot zTEMP}$	Effect of the interaction between sex and temperature on survival.	Normal (0, 3.2)	This prior was selected to regularize the posterior distribution while excluding implausible values.
6	$\sigma_{\delta_{\phi,i}}$	Standard deviation of random effect of conservation unit on survival.	Gamma (2, 1)	This prior is weakly informative, allowing for the posterior distribution to be guided by the data, while keeping the mode away from 0.
6	$\sigma_{\delta_{\phi,k}}$	Standard deviation of random effect of river section on survival.	Gamma (2, 1)	Same as above
6	$\sigma_{\delta_{\phi,l}}$	Standard deviation of random effect of year on survival	Gamma (2, 10)	Same as above, with larger rate parameter due to the small number of years (avoids unrealistic extreme values that are common when number of random effects is small).

6	$\sigma_{\beta_{\phi,zTEMP}}$	Standard deviation of random effect conservation unit on the slope of temperatures in the survival model.	Gamma (2, 1)	This prior is weakly informative, allowing for the posterior distribution to be guided by the data, while keeping the mode away from 0.
8	α_p	Intercept of the detection probability model.	Normal (0, 3.2)	Same as above.
8	$\beta_{p,TEL}$	The effect of telemetry technology on detection probability.	Normal (0, 3.2)	This prior was selected to regularize the posterior distribution while excluding implausible values.
8	$\sigma_{\delta_{p,k}}$	Standard deviation of random effects for receiver station at the upper end of section k	Gamma (2, 1)	This prior is weakly informative, allowing for the posterior distribution to be guided by the data, while keeping the mode away from 0.
10	α_m	Intercept of sex model.	Normal (0, 3.2)	Same as above.
10	$\beta_{m,zLEN}$	Effect of standardized length on sex.	Normal (0, 3.2)	This prior was selected to regularize the posterior distribution while excluding implausible values.
10	$\sigma_{\delta_{m,j}}$	Standard deviation of random effect of conservation unit on intercept of sex model.	Gamma (2, 1)	This prior is weakly informative, allowing for the posterior distribution to be guided by the data, while keeping the mode away from 0.

10	$\sigma_{\zeta_{m,j}}$	Standard deviation of random effect of conservation unit on slope of standardized length in the sex model.	Gamma (2, 1)	This prior is weakly informative, allowing for the posterior distribution to be guided by the data, while keeping the mode away from 0.
11	σ_{zLEN}	Standard deviation of the expected standardized fork length.	Gamma (2, 1)	Same as above.