Regimes of river temperature and flow in an interior watershed, and their implications for Chinook salmon

by

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Abstract

Climate change and human activities are altering river flows and temperatures, with potentially large consequences for aquatic life. I investigated how changing river flows affect salmon productivity, and how climate sensitivity varies across a watershed. First, I tested the effects of shifting river conditions on Chinook salmon productivity in a river where average August river discharge decreased by 26% in the last century. Summer low flows had the greatest negative impact on productivity: cohorts that experienced 50% below average flow in the August of spawning and rearing had 40% lower productivity. Second, I examined whether watershed characteristics could predict which streams were warmest and most sensitive to regional climate. Streams with more riparian forest cover were cooler overall and less sensitive to warmer air temperatures. Overall, this research shows that restoring river flows and watershed-scale forest management are essential parts of salmon conservation.

Keywords: flow regimes; stream temperature; Chinook salmon; hydrology; environmental flows; climate change

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Chapter 1.

Introduction

Rivers are a foundation for much of the integrity of the biosphere (Strayer & Dudgeon, 2010). Each river is an expression of its watershed, transporting and integrating water, sediment, and organic materials across vast distances from mountaintop to sea (Gomi et al., 2002; Naiman et al., 1992). The particular climate, geology, and vegetation of a watershed interact to shape what each river looks like and the variety of habitats it provides for aquatic life (Thorp et al., 2006). Naturally variable, they provide a shifting mosaic of habitats and flows across hours, days, seasons, years, decades, and centuries (Baldock et al., 2016; Bradford & Higgins, 2001; Brennan et al., 2019; Philipsen et al., 2020; Poff et al., 1997). As such, changes to anything that the river integrates, such as precipitation, sediment mobility, organic matter, and heat load can alter its downstream character (DeLong et al., 2018). For example, changes to the plant community in a watershed have implications for its downstream hydrology (Goeking & Tarboton, 2020; Niemeyer et al., 2020; Perry & Jones, 2017).

Aquatic organisms, such as river fishes, have adapted in an incredible diversity to these pulsed ecosystems, taking advantage of niches in environmental gradients over time and space (Crisp, 1996; Mann, 1996). Anadromous salmon demonstrate this pattern well, with a diversity of species, life history types, and populations with variable migration timing, juvenile rearing location and duration, and body size, matched to the qualities of their home rivers (Beechie et al., 2006; Eliason et al., 2011). However, the natural variability of rivers can have dramatic effects on the vital rates – such as growth and survival – of these fishes. For example, temperature and spring rainfall (as a proxy for discharge) explain the majority of the variation in recruitment of stream-rearing salmonids (Lobón-Cerviá & Mortensen, 2005). This natural variability in river character is one factor in determining the natural variability in the population dynamics of river fishes.

Rivers are faced with enormous legacy, current, and projected effects from humans which threaten the ability of rivers to support life – both human and non-human (Meybeck, 2003; Tickner et al., 2020; Wohl, 2019). These changes span from global climate change (Islam, Curry, et al., 2019) to local stream alterations (Wohl, 2019).

Anthropogenic climate change alters patterns of precipitation, temperature, and glacial extent, altering flow regimes and water temperatures (Curry et al., 2019; Islam, Hay, et al., 2019; Mantua et al., 2010; Pitman et al., 2020; van Vliet et al., 2013; Wu et al., 2012). On the regional scale, pervasive changes to the landscape – like forestry and development – change how water moves from the sky to the river mouth, and can lead to reduced flow rates and more intense floods (Cheng & Wang, 2002; Goeking & Tarboton, 2020; Poff et al., 1997, 2006). At the local scale, alterations to the river and its riparian forest have implications for physical habitat and local stream temperature (Garner et al., 2014; Pollock et al., 2009; Wohl, 2019) and the direct extraction of water reduces the amount of water available for freshwater life (Postel, 2000). To complicate matters, interactions across this spectrum are probable and proven (Tockner et al., 2010). For example, altered sediment dynamics can exacerbate changes in hydrology (Collins et al., 2019). These coincident, interrelated changes to rivers – sometimes referred to as cumulative effects – have complex implications for freshwater organisms that are challenging to quantify (Collins et al., 2019; Crozier et al., 2008; Tockner et al., 2010; Zhang et al., 2019). Cumulative effects remain a challenge not only to researchers, but also in policy and governance (Seitz et al., 2011).

Amidst these cumulative effects, flow and water temperature have been identified as critical aspects of river habitat in need of special attention (Reid et al., 2019; Tickner et al., 2020). Natural flow regimes – the patterns of flow volume and variability over time – are essential for diverse, productive rivers (Bestgen et al., 2020; Poff, 2018; Poff et al., 1997). Flow regimes are being recognized as more and more important for population dynamics of salmonids that spend part of their life cycle in fresh water (Jones et al., 2020; Ohlberger et al., 2018; Scheuerell et al., 2020; Vorste et al., 2020). Low summer flows during rearing are linked to lower productivity in coho salmon (*Oncorhynchus kisutch*) in the Pacific northwest (Ohlberger et al., 2018) and California (Vorste et al., 2020), and Chinook salmon (*O. tshawytscha*) in Alaska (Jones et al., 2020). Additionally, high flows during incubation in fall, winter or early spring have been linked with lower productivity in steelhead (*O. mykiss*) (Scheuerell et al., 2020), Chinook (Jones et al., 2020), and brown trout (*Salmo trutta*) (Lobón-Cerviá & Mortensen, 2005). These effects of flow are context specific – for example, in two Alaskan rivers, high summer discharge was associated with lower productivity for Chinook salmon (Neuswanger et al., 2015). In watersheds with both stream-rearing salmonids and stressors on flow regimes, quantifying the relationship between flow and fish productivity is a key step in conserving fishes of economic and cultural value.

As with flow regime, patterns of water temperature are a foundational characteristic of river habitat that influence aquatic organisms in many ways (Allan & Castillo, 2007; Brewitt & Danner, 2014; Claireaux & Lagardère, 1999; Lessard & Hayes, 2003). Warming rivers, whether from local changes or global climate warming, present a threat to freshwater life (Reid et al., 2019). For salmonids, warming water temperatures can have lethal and non-lethal effects across life stages (Hinch et al., 2012; Marine & Cech, 2004; Martin et al., 2017; Richter & Kolmes, 2005). Furthermore, rivers offer complex waterscapes of thermal habitats, with cold-water refuges and areas with lower sensitivity to warming climates (Beaufort et al., 2020; Fullerton et al., 2015; Mauger et al., 2016; Steel et al., 2017). Finding these areas with cooler water temperatures and lower sensitivity to regional climate and identifying ways to mitigate the effects of climate change would benefit already imperilled salmonids (Ebersole et al., 2020)

In my thesis, I investigated key relationships of stream temperatures and flow regimes in an interior watershed of British Columbia, Canada. First, I explored the relationship between flow regimes and fish population dynamics. Second, I investigated the patterns of stream temperature sensitivity to climate, and what watershed characteristics make streams less sensitive to warm air temperatures.

The Nicola watershed in interior British Columbia is an ideal location to explore these specific questions within the broader context of cumulative effects in river systems. The watershed is located in the rain shadow of the Coastal Mountains and is prone to summer droughts and large spring floods. Several important salmonids live in the watershed, including Chinook salmon, coho salmon, steelhead trout, and bull trout (*Salvelinus confluentus*). Assessments for federal protection for some of these species are recent or ongoing. Water temperatures in summer regularly exceed 20°C, when juvenile salmon are rearing and adults are returning to spawn. Drought is a chronic problem, and low flows are a concern despite the construction of storage reservoirs over the past century. There is ongoing concern about the impacts of warm water temperatures and low flows on salmonids. Pine beetle infestation and associated forestry are also changing the landscape at large scales. In this watershed with many pressures, I investigated the linkages between variable flow regimes and Chinook productivity, and the linkages between watershed characteristics and climate sensitivity of streams.

In Chapter 2, I tested the effects of variable river conditions on the productivity of Chinook salmon and review available data on cumulative stressors and hydrology over the last century. Despite the addition of water storage to augment summer flows, average August river discharge has decreased by 26% in the last 100 years. Freshwater processes, namely density-dependence and summer low flows, had the greatest negative impacts on productivity. I found that the altered flow regime is eroding the productivity of a Chinook population with productivity levels below replacement for more than 50% of cohorts since 1992. Analysis of over two decades of Chinook salmon life-cycle data revealed that low summer flow strongly decreases productivity. Specifically, August flow during spawning and fry rearing had the strongest effects – cohorts that experienced 50% below average flow in the August of spawning and rearing had 40% lower productivity. Chinook salmon cohorts are predicted to drop below replacement – and thus unable to sustain fishery mortality – in years with average August discharge less than 10.83 m^3s^{-1} (or 36% mean annual discharge) during the rearing summer. Alarmingly, this flow only occurred for 18% of cohorts examined. Our results suggest that this Chinook population being assessed for legal protection requires almost double the amount of August flow recommended by a model-based study to remain stable, and additional summer flows would be required to sustain fisheries harvest.

In Chapter 3 of my thesis, I asked how watershed characteristics influence patterns of maximum water temperatures and stream temperature sensitivity. Specifically, I identified the influence of riparian forest cover, lakes, elevation, and catchment area on the thermal regime of streams across the watershed. I found that steam locations with larger upstream catchment areas had higher maximum temperatures as well as greater climate sensitivity to air temperatures. In addition, sites with more riparian vegetation cover had lower climate sensitivity. Streams with 100% riparian forest cover had, on average, maximum temperatures 1.2°C lower than streams without riparian cover. Many smaller tributaries were identified as contributing cool water to the mainstem in the warmest days of summer and being less sensitive to warm regional air temperatures. Other geographic features like lakes influenced thermal regimes. Collectively, these results identify factors that are associated with warmer temperatures and greater climate sensitivity that pose risks to cold-water fishes such as

Chinook and coho salmon, steelhead, and bull trout. They also identify feasible actions – such as planting riparian trees around small streams – that may increase the resiliency of stream temperatures to a warming climate.

I discuss the broad implication of my findings in Chapter 4. In particular, I identify how these studies contribute to the growing body of work that emphasizes the importance of freshwater conditions to the life-cycle productivity – and thus recovery – of declining salmon populations. Particularly, these findings provide rare empirical evidence of how different components of flow regimes impact salmon, which are necessary to inform water and land use. I also discuss the opportunity to mitigate some impacts of climate change on thermal regimes using riparian restoration, and the importance of working with the unique characteristics of rivers – rather than against them – for successful conservation of rivers and fishes.

Chapter 2.

Shifting flow regimes erode the productivity of imperiled Chinook salmon[1]

2.1. Introduction

Coincident changes in climate, land cover, and water use are altering the natural flow regimes of the world's rivers (Palmer & Ruhi, 2019). Natural flow regimes are the patterns of "flow quantity, timing, and variability" (Poff et al., 1997) that maintain diverse, productive river ecosystems (Bestgen et al., 2020; Poff, 2018). Yet climate modelling predicts large changes in flow regimes due to shifts in global precipitation (Gerten et al., 2008; van Vliet et al., 2013). Furthermore, human activities such as forestry and irrigation influence the volume and timing of flow in rivers (Goeking & Tarboton, 2020; Gronsdahl et al., 2019; Perry & Jones, 2017). Indeed, empirical studies have already reported earlier freshets, lower discharge in summer, and longer dry periods in fall (Déry et al., 2009). However, the consequences of past, present, and future changes in flow regimes for river ecosystems and fish remain uncertain (Palmer & Ruhi, 2019).

Changing flow regimes are a leading contributor to the current "emergency" in freshwater biodiversity, and understanding the instream flow needs of fish is a global priority (Tickner et al., 2020). Typically, models are used to make predictions about how much water fish need (Tennant, 1976), and these flow-fish relationships are considered in light of human uses and values to set in-stream flow regulations (Rosenfeld & Ptolemy, 2017). While fish-flow relationships are a key foundation of effective flow regulation (Rosenfeld, 2017; Rosenfeld & Ptolemy, 2017), they are often based on habitat models and rarely tested with empirical data at the population level (Beecher et al., 2010; Bradford et al., 2011; Shirvell, 1989). However, emerging examples from around the world are showcasing empirical linkages between flow regimes and fish productivity (Chen & Olden, 2017; Sabo et al., 2017).

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[1] This chapter is currently a manuscript in review: Warkentin, L., C.K. Parken, R. Bailey, and J.W. Moore (2020). Shifting flow regimes erode the productivity of imperiled Chinook salmon. Ecological Solutions and Evidence.

Empirical studies of fishes and flows are especially important for species of economic and cultural importance, such as Pacific salmon (*Oncorhynchus* spp.) (Bradford & Heinonen, 2008). While salmon are adapted to their local flow regime (Beechie et al., 2006), variable or extreme hydrology can impact salmon through a variety of processes during their freshwater life stages. For example, hydrology influences spawning site selection and egg survival (Malcolm et al., 2012), large floods can kill incubating eggs (Gendaszek et al., 2018; Sloat et al., 2017), and reduced summer low-flows can decrease the growth rates of juveniles (Harvey et al., 2006). As a result, changing flow regimes can exert population-level impacts on salmon via summer flows (Jones et al., 2020; Ohlberger et al., 2018; Vorste et al., 2020), floods (Greene et al., 2005; Seiler et al., 2003), flow variability (Sturrock et al., 2020; Ward et al., 2015), and winter ice (Bradford et al., 2001; Cunningham et al., 2018). Flow regimes are likely especially important for salmon that rear in freshwater, such as stream-type Chinook salmon *O. tshawytscha* (Sturrock et al., 2020) and coho salmon *O. kisutch* (Ohlberger et al., 2018). Yet, it has proven challenging to isolate the effects of changing flow regimes from other processes, such as ocean survival, fishing mortality, and interactions with hatchery-origin salmon.

We examined how changing flow regimes influence the productivity (adult offspring per reproducing parent) of stream-type Chinook salmon, which support Indigenous, commercial and recreational fisheries and are prey for endangered Southern Resident Killer Whales (Hanson et al., 2010). Specifically, we investigated how river flow regimes affect the productivity of Chinook salmon in a watershed which exemplifies cumulative effects of human activities and climate change and a hydrograph driven by snow-melt. We focused on average August flow, fall flooding, and duration of winter ice cover and accounted for variable ocean survival, mortality from fishing, and hatchery influence. We discovered that shifting flow regimes are decreasing the productivity of this imperiled population and quantified empirical fish-flow relationships that can inform the management of cumulative effects on hydrology.

2.2. Methods

2.2.1. Study System

The Nicola River is a tributary of the Thompson River, which flows into the Fraser River at Lytton in British Columbia (BC), Canada (Figure 2.1). The watershed drains 7184 km^2 and supports imperiled stream-rearing Chinook salmon, coho salmon, and steelhead *O. mykiss*. The watershed is under pressure from multiple human activities and climate change, emblematic of many semi-arid watersheds in western North America. The Committee for the Status of Endangered Wildlife in Canada is currently assessing whether to recommend Nicola Chinook for listing under the *Species at Risk Act*. Recruitment has been below replacement for more than half of the cohorts since 1992 (Figure S1). Chinook fry from the Nicola are stream-rearing and overwinter in freshwater, either in the Nicola River and tributaries, or downstream in the Thompson and Fraser systems (unpublished data, C. Parken).

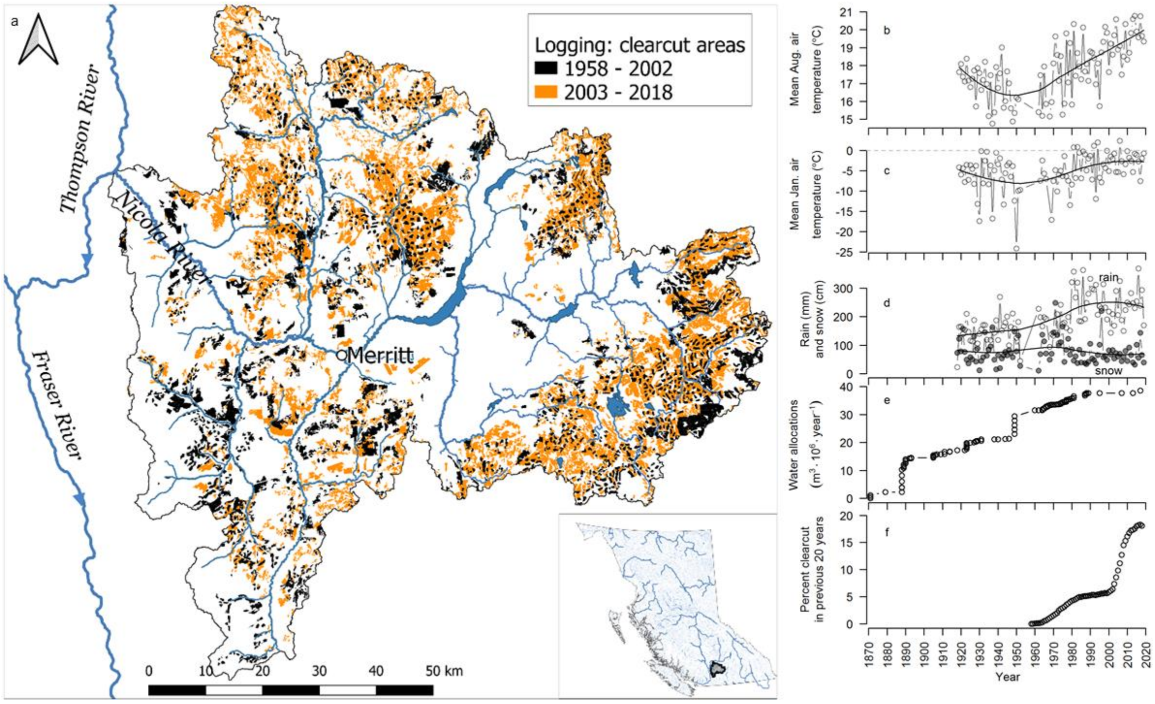

Figure 2.1. (a) The Nicola River watershed with clearcut areas. (b and c) Historical changes in annual mean August and January air temperatures, (d) rain and snow, (e) water allocations for the mainstem Nicola River (not including conservation and dam storage licenses), and (f) percent of Nicola watershed clearcut in previous 20 years (rolling sum).

Average total annual water yield of the Nicola River is 831,103,760 m^3. Black lines in b, c, and d are LOESS best fit lines.

This study focuses on the early summer-run Chinook salmon of the Nicola, one of several populations in this watershed. The early summer run enters the Fraser River from May to July and spawns in the Nicola River in September, mainly in the mainstem Nicola River, and in the lower reaches of the Coldwater River and Spius Creek (Parken et al., 2003, 2008).

The flow regime of the Nicola River is characteristic of interior BC rivers with a hydrograph driven by snow-melt, with a large spring freshet which usually peaks in late April or early May (Figure 2.2). Peak flow during freshet can exceed 200 m^3s^{-1}, while summer base flow can be less than 3 m^3s^{-1}. Natural mean annual discharge (MAD; long-term mean annual discharge plus estimated water withdrawal) is 29.8 m^3s^{-1} (unpublished data, R. Ptolemy). Floods can occur in the fall, winter, and early spring. Flows usually decrease and reach base flows in August, and remain low into September. The river was assessed as having no surplus flows in August to September unless supported by water storage (Kosakoski & Hamilton, 1982).

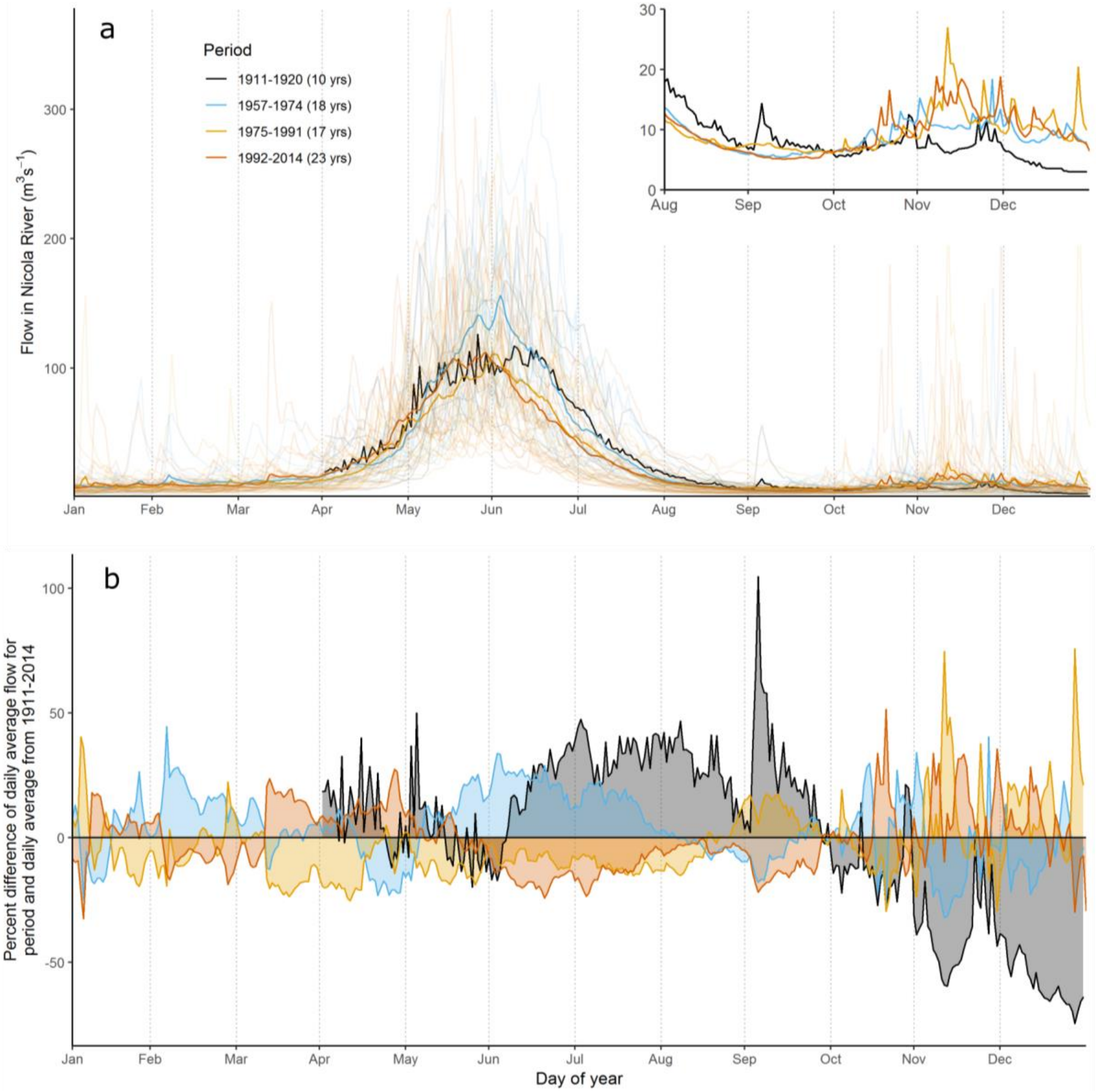

Figure 2.2. **(a) Hydrographs for the Nicola River, 1911-2014, divided into four periods. Bold lines are average daily flows for each day of the year within each period, and faint lines are actual daily flows for each year. (b) Percent difference between average daily flow in the four periods and the long-term historical average for each day of the year.**

There are no data available for 1921-1956. For period 1911-1920, January-March data were not used as these days had less than 6 years of data, to avoid skewed averages.

2.2.2. Data

Long-term Environmental Data

We compiled long-term data on air temperature (1918-2019), precipitation (1918-2019), discharge (1911-1920, 1957-2014), water allocations (1871-2017), and forestry (1958-2018) for the watershed to give context for hydrological change and its potential drivers. See Appendix A for data sources.

Escapement and Spawners

We used escapement data from the cohorts spawned in 1992-2013 (22 cohorts), collected by Fisheries and Oceans Canada (DFO) and Scw'exmx Tribal Council. For cohorts 1992-1994, spawner escapement was estimated by aerial counts, with the proportion of adipose fin-clipped fish estimated from stream walks (Parken et al., 2003). From 1995-2013, data are from a mark-recapture program which estimates spawner escapement by age, sex, and Coded Wire Tag (CWT) code (Nandor et al., 2009), and marine survival and fishery-specific exploitation by age. The total abundance of spawners for a cohort included hatchery- and wild-origin fish that returned to the Nicola River minus any fish that were removed for hatchery brood stock and other purposes.

Unmarked Hatchery Returns

DFO operates the Spius Creek Hatchery on Spius Creek, near the confluence with the Nicola River. This hatchery has released juvenile Chinook since 1984. Since 2005, most releases are 1+ smolts with CWT and adipose fin clips, and a smaller number of fry with no CWT or fin clip. Before 2005, there were releases of fry, sub-yearling and 1+ smolts with no CWT or fin clip. To get an accurate measure of wild recruitment for each brood year, we estimated the number of unmarked hatchery-origin adults (those appearing to be wild, with no CWT or adipose fin clip) returning to the spawning grounds each year. After estimating this number for each cohort in a spawning year, we subtracted this from the unclipped spawners to get an estimate of 'true' wild spawning escapement for each cohort (see Appendix A for details).

Estimating Recruitment

To estimate recruitment (the number of wild adults produced by each year of spawners), we accounted for mortality from fishing. We assumed wild and hatchery fish had equivalent mortality from fishing, by age and cohort, and used estimates of fishing mortality, by age and cohort, from the CWT program (see Appendix A; Nandor et al. 2009, Pacific Salmon Commission 2018). To estimate recruitment, we summed the abundance of wild river spawners plus wild fish removed for hatchery and other purposes by cohort and age, and divided by 1 minus the fishing mortality rate (Appendix A). We summed recruits from each brood year to estimate the number of wild recruits for each cohort.

Covariates

We examined the influence of five covariates on the productivity of each cohort of Chinook salmon (Figure A2):

- Smolt-to-age 3 survival (mean=0.026, SD=0.030)
- Mean August flow during brood year migration of spawners (parents of cohort; mean=8.6 m^3s^{-1}, SD=5.6 m^3s^{-1})
- Discharge of maximum fall flood during incubation in brood year (mean=60.8 m^3s^{-1}, SD=57.2 m^3s^{-1})
- Number of days in winter of incubation with ice cover (mean=55, SD=32.9)
- Mean August flow during rearing year (brood year + 1) (mean=8.7 m^3s^{-1}, SD=5.6 m^3s^{-1})

We chose these covariates based on existing evidence from the literature on stream-rearing salmonids (Jones et al., 2020; Ohlberger et al., 2018; Vorste et al., 2020), and because of predictions and evidence of climate change in this region (Islam, Curry, et al., 2019; Rodenhuis et al., 2007).

To account for variable survival during downstream migration and growth in the ocean, we used the estimated smolt-to-age 3 survival, calculated from the survival of CWT-marked smolts released from the hatchery (Pacific Salmon Commission, 2018). We note that this metric of early marine survival also includes the downstream migration phase of smolts. We used hydrometric data from Nicola River near Spences Bridge (Water Survey of Canada station 08LG006). For each Chinook cohort, we calculated mean August flow when the spawners were migrating upstream and waiting to spawn (brood year), the discharge of the largest flood from September 1 to December 31 of the brood year, the number of days in the winter of incubation when ice covered the river near the hydrometric station (recorded as a backwater effect from ice formation), and the mean August flow in the summer when the juvenile Chinook were rearing (brood year +1). We centered and standardized these five covariates to mean=0 and SD=1 to aid the comparison of relative effect sizes.

2.2.3. Stock Recruit Model

We used a log-linear Ricker equation including environmental effect terms (following Jones et al., 2020; Schick et al., 2016; Sharma & Liermann, 2010; Ward et al., 2015). The standard Ricker equation predicts recruits *R* from spawners *S,* productivity *α*, and the strength of density dependence *β* (Equation 2.1). The five effect term coefficients of smolt-to-age 3 survival, mean August flow (spawning), maximum fall flow, ice days, and mean August flow (rearing) are b_1, b_2, b_3, b_4, and b_5, respectively. We used the log-linear form of the Ricker equation because it has a normal distribution of residuals (Equation 2.2).

$$log\left(\frac{R}{S}\right) = log(\alpha) - \beta S + b_1 ocean\, surv + b_2 Aug\, flow\, spawn + b_3\, fall\, flood + b_4 ice\, days + b_5 Aug\, flow\, rear \qquad (2.1)$$

The full Bayesian model was defined as follows (Equations 2.3-2.9), with similar priors to Connors et al. (2019).

$$\log\left(\frac{R}{S}\right) \sim Normal(\mu, \tau) \qquad (2.2)$$

$$\mu = log(\alpha) - \beta S + b_1 oceansurv + b_2 Augflowspawn + b_3 fallflood + b_4 icedays + b5Augflowrear \qquad (2.3)$$

$$log(\alpha) \sim Uniform(0,3) \qquad (2.4)$$

$$\beta \sim Uniform(0,10) \qquad (2.5)$$

$$b_1, b_1, b_3, b_4, b_5 \sim Normal(0,1) \qquad (2.6)$$

$$\tau \sim Gamma(0.01,0.01) \qquad (2.7)$$

$$\mu = log(\alpha) - \beta_W \cdot S_W - \beta_H \cdot S_H + b_1 oceansurv + b_2 Augflowspawn + b_3 fallflood + b_4 icedays + b5Augflowrear \qquad (2.8)$$

For the models where we used separate β terms for wild and hatchery spawners – β_W and β_H, S_W and S_H – we used Equation 2.8, with the same priors for β_W and β_H as for β. See Appendix A for details on model fitting.

2.2.4. Model Selection

To compare the effects of different covariates and separate β terms, we compared 23 models which were subsets of the full model (Table A1). We used several methods to compare models: the widely applicable information criterion (WAIC) and leave-one-out cross-validation (LOO) (Vehtari et al., 2017); stability of posterior estimates of effect terms; and R^2 values. We used the rethinking package (McElreath, 2016) for WAIC and the loo package (Vehtari et al., 2019) for LOO. We also tested for autocorrelation and partial autocorrelation of residuals.

2.3. Results

Climate and land use in the Nicola have changed substantially over the past century (Figure 2.1). Winters are warming: from 1920-1980, daily average air temperatures in January never exceeded 0°C, but rose above freezing five times since 1980. Daily average air temperatures in August increased by about 2°C. Patterns of precipitation have also shifted: rainfall nearly doubled in some recent years compared with historic values. Water use and forest cover have also changed. Water allocations began in 1871 and increased steadily up to the 1990s. During and after the spread of the Mountain Pine Beetle throughout the region, logging increased substantially: 17% of the entire watershed was logged in the last 20 years. Six major tributaries had over 20% of their area logged in the last 20 years, up to 36% in Clapperton Creek (Table A2).

The hydrology of the Nicola River is responding to these coincident changes (Figure 2.2). From 1911-1920, average August discharge never fell below 15% MAD of 4.47 m^3s^{-1}, whereas from 1992-2014, it fell below this value five times (Figure A3). Average August flow decreased by 26% comparing flows from 100 years ago with the past two decades. River discharge in June-September in the last 23 years was up to 25% lower than the long-term average, compared to 1910-1921, when flows were up to 50% greater than the long-term average (Figure 2.2).

Freshwater flow regimes and density dependence were the main drivers of population dynamics for Chinook salmon (Figure 2.3, Table A3). Mean flow in August during spawning and rearing and ice days were the most important variables. These were present in the most parsimonious model according to WAIC and LOO (model 8b; R^2=0.70), which we use henceforth for predictions and results (Figures A1, A4-A7, Tables A4-A5).

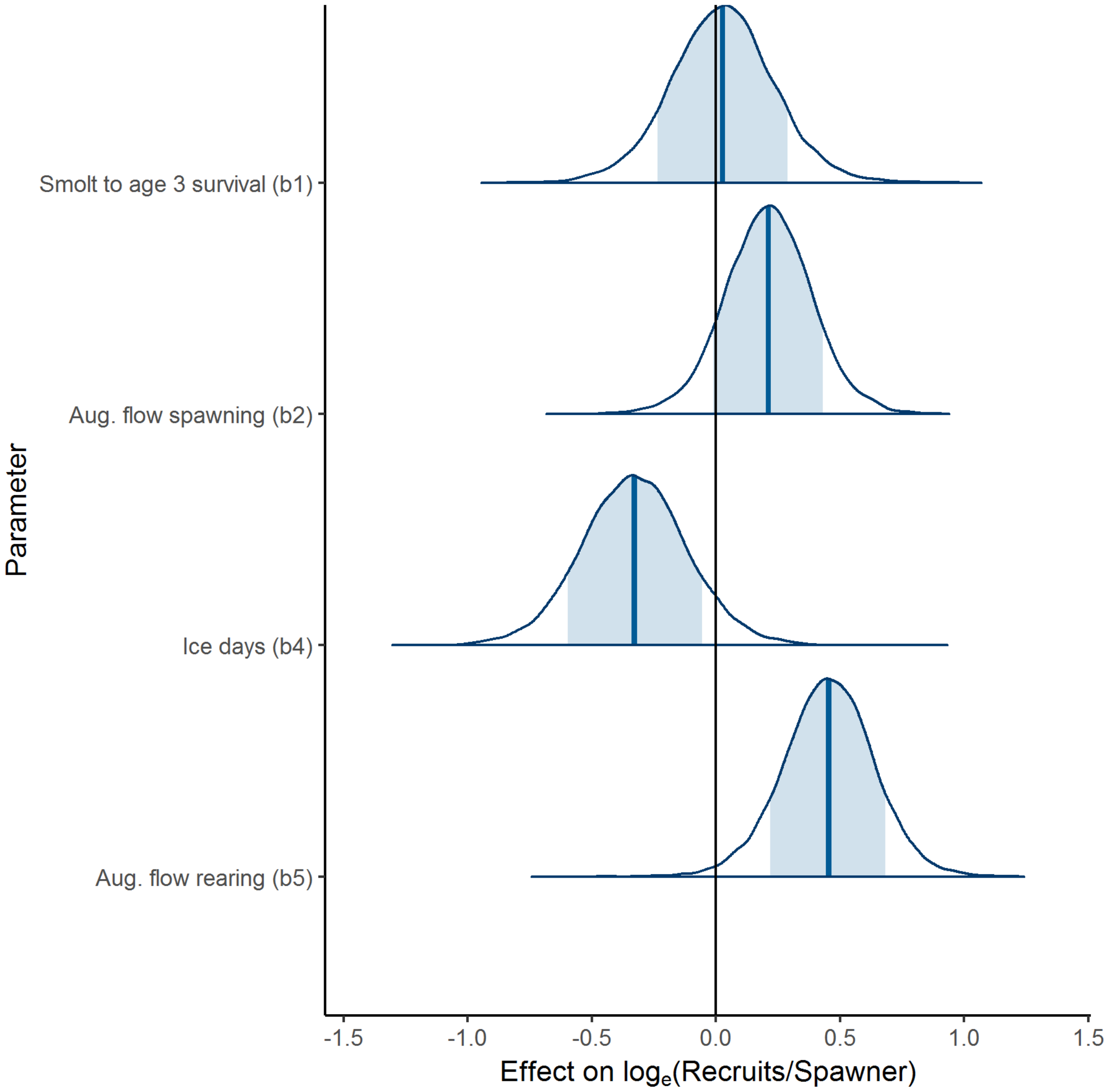

Figure 2.3. Posterior estimates (with means and 80% credible intervals in shaded region) of effect terms for the four environmental variables in the top model, 8b.

Note that all variables were standardized (mean=0, SD=1).

Mean August flows during Chinook rearing had the strongest effect on productivity; cohorts with greater flows in their rearing summers had higher productivity (Figure 2.4). Our model predicts Chinook cohorts whose juveniles rear during summers with 50% below average flow have 30% lower productivity. August flows when spawners were returning were also important. Chinook that spawn during summers with 50% below average flow have 15% lower productivity. In combination, cohorts with 50% below average flow in the August they were spawned and the subsequent August during rearing are predicted to have 40% lower productivity.

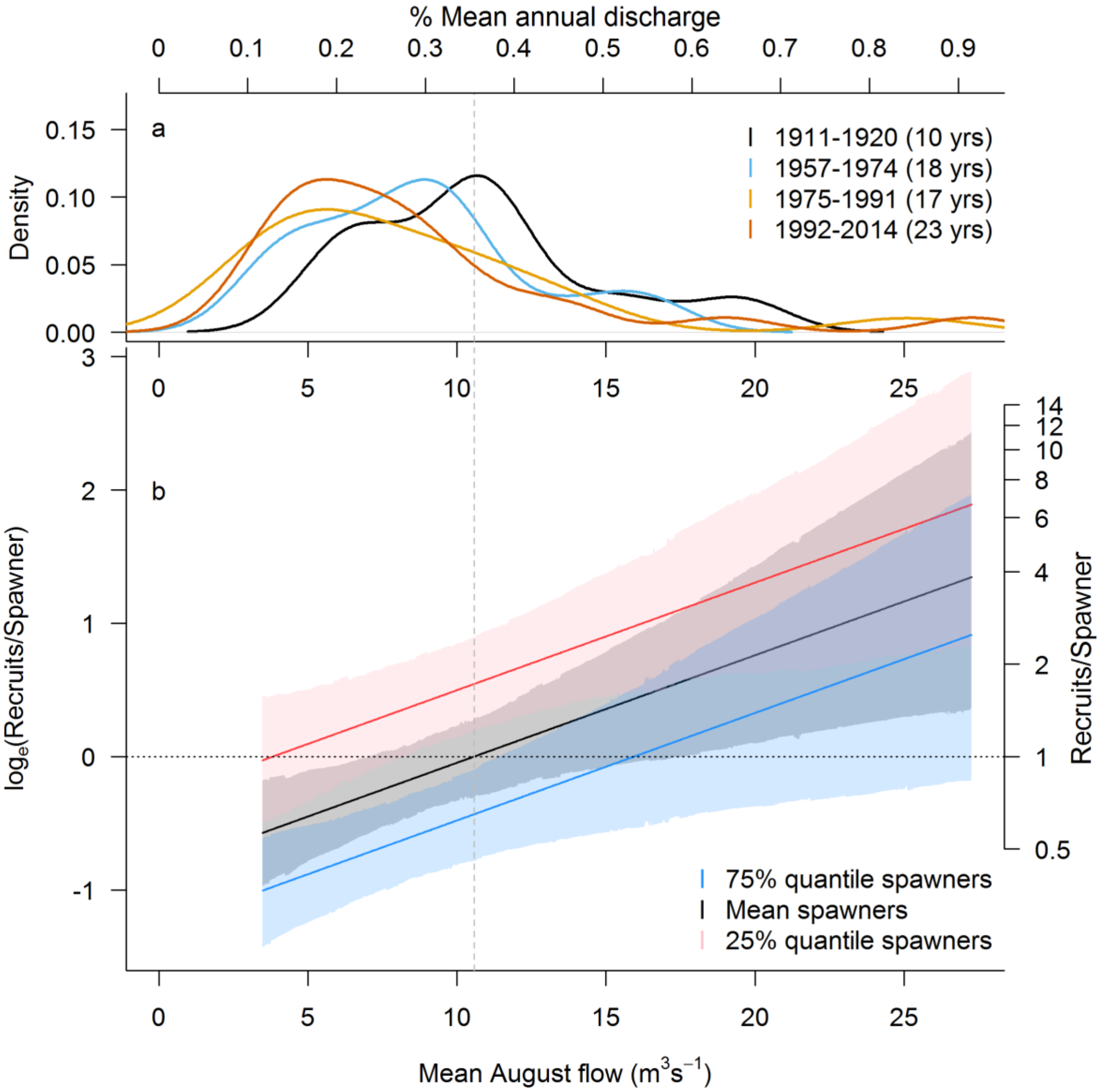

Figure 2.4. **(a) Empirical cumulative density function of mean August flows in four periods. (b) Effect of mean August flow during rearing on recruitment of Nicola River Chinook salmon.**

The three shaded regions represent 90% credible intervals of model predictions based on three spawner abundances (mean, 25th percentile, and 75th percentile). The dotted horizontal line shows replacement level of 1 Recruit/Spawner at mean spawner abundance. The vertical dashed gray line indicates the model-predicted value of 10.83 m^{3}s^{-1} flow during the rearing summer that results in replacement (Recruits/Spawner = 1). Natural mean annual discharge (discharge plus estimated withdrawal) is 29.8 m^{3}s^{-1} (unpublished data, Ptolemy).

Alarmingly, the median of yearly average August flows has decreased by 37% from 10.83 m^{3}s^{-1} to 6.87 m^{3}s^{-1} over the last century (Figure 2.4a), despite considerable development of storage reservoirs to offset withdrawals during the same period. Holding all other variables at their average, this corresponds to a 27% decrease in productivity of

Chinook salmon based on the effect on rearing juveniles, and a 37% decrease in recruitment based on the combined effect on rearing and spawning, to a level where every 100 spawners produces 73 recruits. A transect-based modelling approach recommended an environmental flow for the Nicola mainstem (from Spius Creek down to confluence with the Thompson River) of 5.66 m^3s^{-1} year-round, and concluded there was no surplus flows for withdrawal in August and September (Kosakoski & Hamilton, 1982). Based on our analyses, this flow is insufficient to allow for population replacement in a typical year – if the mean August flow was 5.66 m^3s^{-1} during both spawning and rearing, every 100 spawners would only produce 63 recruits, and the population would decline even in the absence of any fishing mortality.

Cohorts that incubated in winters with more ice days tended to have lower recruitment; for every 10 additional days of river ice, recruitment was predicted to decrease by 10%. Surprisingly, smolt-to-age 3 survival, which includes early marine survival, accounted for little variation in recruitment after accounting for variation in river conditions, with a mean effect size of 0.03 and a credible interval that spans 0 (Figure 2.3).

There is also evidence that fall floods may decrease productivity, as this effect is included in the third most parsimonious model for WAIC and second for LOO. However, this effect had less evidence than August flows and ice days. There was limited evidence that density dependence was stronger for hatchery spawners compared to wild spawners (Figure A8).

2.4. Discussion

We found that the altered flow regime of an interior watershed, likely driven by the cumulative effects of climate change, land use, and water withdrawals, is eroding the productivity of an imperiled fish population. Specifically, air temperatures, rainfall, logging pressure, and water demand have all increased over the last 100 years (Rodenhuis et al. 2007). Low summer flows are now 26% lower than they were 100 years ago. Analysis of 22 years of Chinook salmon life-cycle data revealed that this low summer flow strongly decreases productivity. For example, Chinook salmon cohorts are predicted to drop below replacement – and thus unable to sustain fishery mortality – in years with average August discharge less than 10.83 m^3s^{-1} (or 36% MAD) during the rearing summer. These findings provide rare empirical evidence of how different components of flow regimes impact salmon.

Summer low flows have been shown to influence productivity and growth in stream-rearing salmonids (Beecher et al., 2010; Grantham et al., 2012; Letcher et al., 2015; Ohlberger et al., 2018; Rosenfeld, 2017; Vorste et al., 2020). Rather than assuming that a single mechanism consistently drives the relationship between low flows and fish, the empirical relationship between summer flows and fish we observed could be driven by a variety of mechanisms. Lower flows can decrease the amount of invertebrate food (Harvey et al., 2006), as well as reduce amounts of suitable rearing habitat (Bradford et al., 2011). It is also possible that lower flows may render the system more sensitive to excessively hot weather (van Vliet et al., 2013); water temperatures in the Nicola can exceed 25°C in some summers (unpublished data, L. Warkentin). Given that juvenile Chinook salmon, including a subset of those from the Nicola River watershed, may disperse downstream and rear in non-natal habitats (Murray & Rosenau, 1989), summer rearing flows in the Nicola will directly impact the juveniles that remain in the Nicola system, but only indirectly impact those that disperse to downstream habitats (Figure A9). We also found that low flows during adult migration appeared to impair productivity, an effect that could be compounded by warm stream temperatures. Regardless of the mechanisms, our study provides strong empirical evidence that lower flows during the summer impair the productivity of this population of concern.

Our study evaluated other factors that could affect this population's productivity. Like many salmonids, evidence of density-dependence was strong. In addition, cohorts that experienced more ice cover appeared to have lower productivity; anchor ice and ice scour can kill incubating eggs and alevins (Cunjak et al., 1998; Huusko et al., 2007). Although large fall and winter floods can have negative consequences for coastal salmon populations (Greene et al., 2005; Jones et al., 2020; Seiler et al., 2003), we did not find conclusive evidence for this effect. However, productivity appeared lower for cohorts that incubated during years with fall and winter floods greater than ~150 m^3s^{-1} (Figure A10d). Flows over this threshold could mobilize sediments and scour incubating eggs (Gendaszek et al. 2018), but this is speculative given the sample size and lack of statistical support. Although untangling the effects of seasonal extremes from other factors over the salmonid life cycle is challenging, it is essential for salmon conservation.

Freshwater processes were stronger predictors of life-time productivity than survival during downstream smolt migration and ocean growth. Many recent publications have focused on the influence of ocean conditions on the survival and productivity of Pacific salmon (Connors et al., 2020; Dorner et al., 2017; Sharma & Liermann, 2010). We found that freshwater conditions explain more variation in lifetime productivity than an index of early ocean survival. We were able to incorporate a proxy for marine survival of wild fish based on estimates of smolt-to-age 3 survival of hatchery smolts, which has potential for error. Notably, the lowest observed smolt-to-age 3 survival was for the 1992 hatchery cohort, likely from a pathogen problem, which would not have effected wild smolts. However, productivity for the 1992 cohort was well-predicted (Figure A1), and other studies found good correlation between the inter-annual variability of marine survival for wild and hatchery stocks (Raymond, 1988; Williamson et al., 2010; Zimmerman et al., 2015), supporting our finding that freshwater dynamics can be the dominant driver of some stream-rearing salmon populations.

The influence of hatchery spawners on the dynamics of this population deserves attention. There was some evidence that density dependence for hatchery spawners was higher than for wild fish (see Appendix A). In addition, the proportion of total spawners that were of hatchery origin over time has varied, with hatchery fish making up a significant proportion of spawners in some years (Figure A12). Although this information is dependent on the methods of accounting for unmarked hatchery fish, it deserves attention given the multiple influences that hatchery fish can have on wild populations (Buhle et al., 2009).

Two important assumptions in the analysis were related to fishing mortality and the model formulation that made the environmental effects independent of density-dependence. We assumed that fishing mortality for wild fish was equal to that of hatchery-origin fish, which had an average of 29% and maximum of 60% by brood year for the cohorts examined (1992-2013). Making the effects of the environmental covariates independent of density-dependence makes the interpretation of their effects simpler and has been used by others (Jones et al., 2020; Ward et al., 2015). Specific evidence of how a given environmental variable effects survival of a life stage in a density-dependent way would justify a different model formulation that evaluates such a pattern.

Implications for the Management of Fish and Flows

Our study has specific relevance to environmental flow recommendations for the Nicola River and BC. We found that the older model-based environmental flow recommendation of 19% MAD (Kosakoski & Hamilton, 1982) is associated with productivity levels in a Chinook salmon population that are not only below replacement but also eliminate the possibility of sustainable fishing. Instead, we estimate that for average spawner abundance and current habitat and environmental conditions, 36% MAD during rearing would support a stable population in the absence of fishing. This result adds to the growing evidence that habitat suitability models may underestimate the instream flow needs of fish (Beecher et al., 2010; Bradford et al., 2011; Shirvell, 1989). Furthermore, conventional habitat suitability curves generally assume that fish-flow relationships are asymptotic (Rosenfeld 2017) and that productivity declines sharply below a threshold (Tennant, 1976). Instead, we observed a variable but approximately linear relationship between summer flows and productivity over the observed range of flows (Figure 2.4, A10f; Beecher et al., 2010). Rearing flows exceeded 36% MAD for only four of the 22 cohorts we examined, highlighting the chronic problem of low flows and the importance of higher flows during infrequent, wet summers for the recovery of this population. Our results are also relevant for setting critical environmental flow thresholds under the BC *Water Sustainability Act*, with the aim to prevent “significant or irreversible harm” to fish populations. Thus, our study provides a rare empirical relationship that links flows and fish productivity, a critical foundation of setting effective instream flow thresholds.

Chinook and other stream-rearing salmon support commercial, recreational, and Indigenous fisheries (Nesbitt & Moore, 2016), and restrictions to these fisheries have cultural and economic consequences. We show that consequential decisions about harvest limits can be based on more accurate predictions by accounting for the effects of river conditions. Based on our model, mean August flow during rearing would need to be 15 m^3s^{-1} (50% MAD) to allow a harvest of 30% and escapement to spawning grounds at replacement levels.

There are many options for conserving flow regimes, each with potential trade-offs. Limiting new water licenses and buying back existing licenses would leave more water in the river but would have consequences for licensees. Releases from reservoirs can boost summer flows, although storage capacity is constrained by infrastructure, flood management, and precipitation, and summer reservoir releases can alter downstream temperatures (Olden & Naiman, 2010). We also suggest that forestry's influence on hydrology deserves attention. Forests have a strong influence on hydrology, and forest disturbances can alter the amount and timing of river discharge (Goeking & Tarboton, 2020). Importantly, clearcut logging can cause a lagged, long-term reduction in base flows starting approximately 15 years after harvest (Coble et al., 2020; Gronsdahl et al., 2019; Perry & Jones, 2017). Watersheds with large increases in logging in the last 10-20 years, such as the Nicola and much of interior BC, may be at risk of further decreases in summer discharge from a legacy of forestry. Future impacts of forestry and climate change could be mitigated by adjusting harvest and regeneration (Goeking & Tarboton, 2020). Thus, while climate change and shifting flow regimes present a dour challenge, there are a suite of management options that could aid the survival of stream-rearing fishes.

Changes in climate, land cover and water extraction are profoundly altering river systems and flow regimes for Pacific salmon (Healey, 2011; Schoen et al., 2017) and freshwater life across the world (Palmer & Ruhi, 2019). Globally, adequate river flows are needed to support diverse freshwater ecosystems (Tickner et al., 2020), while climate change pushes conditions beyond historical values (van Vliet et al., 2013). To steward the life of rivers that bear the burden of human work, we need a wholistic appreciation for shifting flow regimes and their real consequences (Palmer & Ruhi, 2019).

2.5. Authors' Contributions

All authors conceived the project; Luke Warkentin and Chuck Parken designed the methodology; Richard Bailey and Chuck Parken collected data; Luke Warkentin analysed data with assistance from Chuck Parken; Luke Warkentin led writing. Jonathan Moore contributed to project scoping and writing. All authors contributed to drafts and approved submission.

2.6. Acknowledgements

We thank Sean Naman, Rich McCleary, and Douglas Braun for comments on an earlier draft and Jordan Rosenfeld and Brendan Connors for helpful suggestions during preparation. Thanks to Scw’exmx Tribal Council and the DFO Nicola tagging program for data collection. We thank the Nicola Basin Collaborative Research and Technical Committee for feedback, and support from the Fraser Basin Council, the National Science and Engineering Research Council, and the DFO Ocean and Freshwater Science Contribution Program.

2.7. Data Availability Statement

Upon publication, data will be available from the Dryad Digital Repository https://doi.org/10.5061/dryad.ffbg79crv (Warkentin et al., 2020). Analysis code will be available at https://github.com/lukewarkentin/nicola_chinook.

Chapter 3.

The relationship between watershed characteristics and stream temperature sensitivity in the Nicola River watershed

3.1. Introduction

Water temperature influences aquatic life at many scales, including individuals, populations, and communities (Allan & Castillo, 2007). On an individual basis, water temperature influences metabolic rates (Claireaux & Lagardère, 1999). At a larger scale, it can explain the distribution of species in river basins (Lessard & Hayes, 2003; Sloat & Osterback, 2013) and changes in distribution of a population across days (Brewitt & Danner, 2014) and seasons (Baldock et al., 2016). As such, changes in stream temperatures based on human influence and climate change may drive expansion of some populations while others shrink (Buisson et al., 2008; Lynch et al., 2016; Ruesch et al., 2012). As climate change continues to warm the world's rivers (Isaak et al., 2012; Islam, Hay, et al., 2019), warming streams present a threat to the viability of some populations and communities of freshwater organisms (Reid et al., 2019).

Warming river temperatures can impact economically- and culturally-important salmonids across their life cycle (Jones et al., 2020; Kovach et al., 2016; Myers et al., 2017; Richter & Kolmes, 2005). While warmer water may have some benefits for specific salmonids life stages – like higher juvenile growth rates and earlier migration (Fullerton et al., 2017) – much attention is given to the negative effects of elevated summertime temperatures on salmon, which can experience various physiological consequences of temperatures that approach or exceed thresholds (Richter & Kolmes, 2005). For adult salmon, warm water during adult migration up-river is associated with delayed migration (Goniea et al., 2006) and pre-spawn mortality (Hinch et al., 2012). Elevated water temperature can also cause mortality during embryo growth (Martin et al., 2017; Tang et al., 1987), alter incubation duration (Whitney et al., 2014), and decrease juvenile growth rate (Marine & Cech, 2004). However, thermal regimes are complex across space and time (Fullerton et al., 2015), and salmon depend on and make use of this thermal diversity. For example, adult salmon utilize thermal refugia during migration (Frechette et al., 2018; Keefer et al., 2018), while juveniles exploit temperature differentials for metabolic benefits (Armstrong et al., 2013; Baldock et al., 2016; Brewitt et al., 2017).

River systems offer complex networks of thermal diversity throughout space and time (Fullerton et al., 2015; Steel et al., 2017). While stream temperature is directly influenced by energy fluxes like short and long wave radiation (Poole & Berman, 2001; Webb et al., 2008), physical watershed characteristics can explain patterns in both maximum stream temperatures and the relationship between air temperature and stream temperature (Beaufort et al., 2020; Chang & Psaris, 2013; Jackson et al., 2018; Mauger et al., 2016). For example, maximum stream temperatures have been positively linked to livestock grazing (Kovach et al., 2018) and riparian forest harvesting (Bladon et al., 2018). Water temperatures in the northern hemisphere generally peak in late summer, and these maximum temperatures are a common focus for studies of water temperatures in salmon watersheds (Madej et al., 2006). Maximum temperatures may indicate stream reaches that are inhospitable or stressful for salmonids (Sloat & Osterback, 2013). Besides maximum temperatures, stream temperature sensitivity to climate is an additional dimension of stream thermal regimes that conveys the relative responsiveness of the system to warmer air temperatures. One metric of stream temperature sensitivity is the relationship between air temperature and water temperature, or thermal sensitivity (TS) (Nelitz et al., 2007). TS is an important characteristic of streams, and indicates the degree to which changes in air temperature over days, weeks, or seasons are reflected by changes in water temperature (Mohseni et al., 1998). As such, TS can be a measure of climate sensitivity, and has been linked to watershed characteristics such stream size, shade, elevation, watershed area, and hydrology (Beaufort et al., 2020; Lisi et al., 2015; Mauger et al., 2016). Streams that show a high correlation between stream temperature and air temperature may be at greater risk of warming if regional air temperatures increase, while streams with lower TS may indicate important areas of resilience to climate change.

Understanding the underlying portfolio of temperatures in a watershed supporting multiple life histories and species that are under threat can help us understand limiting factors and opportunities for conserving and restoring natural thermal regimes. Here, I focus on understanding patterns of stream temperature across an important salmon watershed prone to drought and warm water temperatures. Specifically, I ask two questions. First, how do watershed characteristics influence patterns of maximum water temperatures across a watershed? Second, how do watershed characteristics influence patterns of temperature sensitivity of streams? The watershed characteristics I used were riparian forest cover, the influence of lakes, catchment elevation, and catchment area.

3.2. Methods

3.2.1. Study System

The Nicola River is a tributary of the Thompson River, which flows into the Fraser River at Lytton in British Columbia (BC), Canada (Figure 3.1). The watershed drains 7184 km^2 and supports imperiled stream-rearing Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), steelhead trout (*O. mykiss*), and bull trout (*Salvelinus confluentus*). The watershed is under pressure from multiple human activities and climate change, emblematic of many semi-arid watersheds in western North America. The Committee for the Status of Endangered Wildlife in Canada is currently assessing whether to recommend Nicola Chinook salmon for listing under the *Species at Risk Act* (SARA). COSEWIC assessed Thompson River steelhead as Endangered in an Emergency Assessment in 2018 (COSEWIC, 2020).

The Nicola watershed is representative of many watersheds prone to drought and warm stream temperatures. In the rain-shadow of the Coast Mountains, this interior watershed can reach high summer water temperatures in its main stem that exceed 25°C. Drought is a chronic problem, and low flows are a concern despite the construction of storage reservoirs over the past century. The watershed has no glaciers. The flow regime of the Nicola River is characteristic of interior BC rivers with a hydrograph driven by snow-melt, with a large spring freshet which usually peaks in late April or early May. Peak flow during freshet can exceed 200 m^{3}s^{-1}, while summer base flow can be less than 3 m^{3}s^{-1}. Flows usually decrease and reach base flows in August, and remain low into September.

3.2.2. Data Collection

Stream temperature

I quantified the thermal regimes throughout the study catchment through installation of an extensive network of temperature loggers (Figure 3.1). Temperature loggers were a combination of OnSet© Pendant and Tidbit loggers. These were installed in September 2017 (a small number were installed in September 2018 and July 2019) in well-mixed areas of streams. Deep pools sheltered by boulders were targeted as they are less likely to dewater during low water or be disturbed by floods than shallower reaches. Loggers were set to record once per hour or two hours (depending on memory size) and housed in white PVC cases to protect them from direct sunlight. They were held in place with aircraft cable by either wrapping the cable around a boulder, a tree, or to an anchor bolt with climbing hanger installed into a boulder. The loggers were left in place year-round, and some loss of loggers occurred during floods. For this analysis, 50 sites were used, which had records during the September 2017-September 2019 period (Table 3.1).

Temperature data were downloaded and data were visually inspected for possible dewatering events. Dewatering events were characterized by a sudden large increase in temperature values and an increase in the magnitude of day-to-night fluctuation in the temperature signal. Dewatering was also known if the logger was out of the water when the site was visited to download. Periods suspected of dewatering were removed and not used in the analysis.

Air temperature

To understand the regional air temperatures and how stream temperatures responded to these (i.e., climate sensitivity), I used Environment Canada mean daily air temperature from the Merritt STP station, which is approximately in the centre of the watershed, downloaded with *weathercan* package (LaZerte & Albers, 2018).

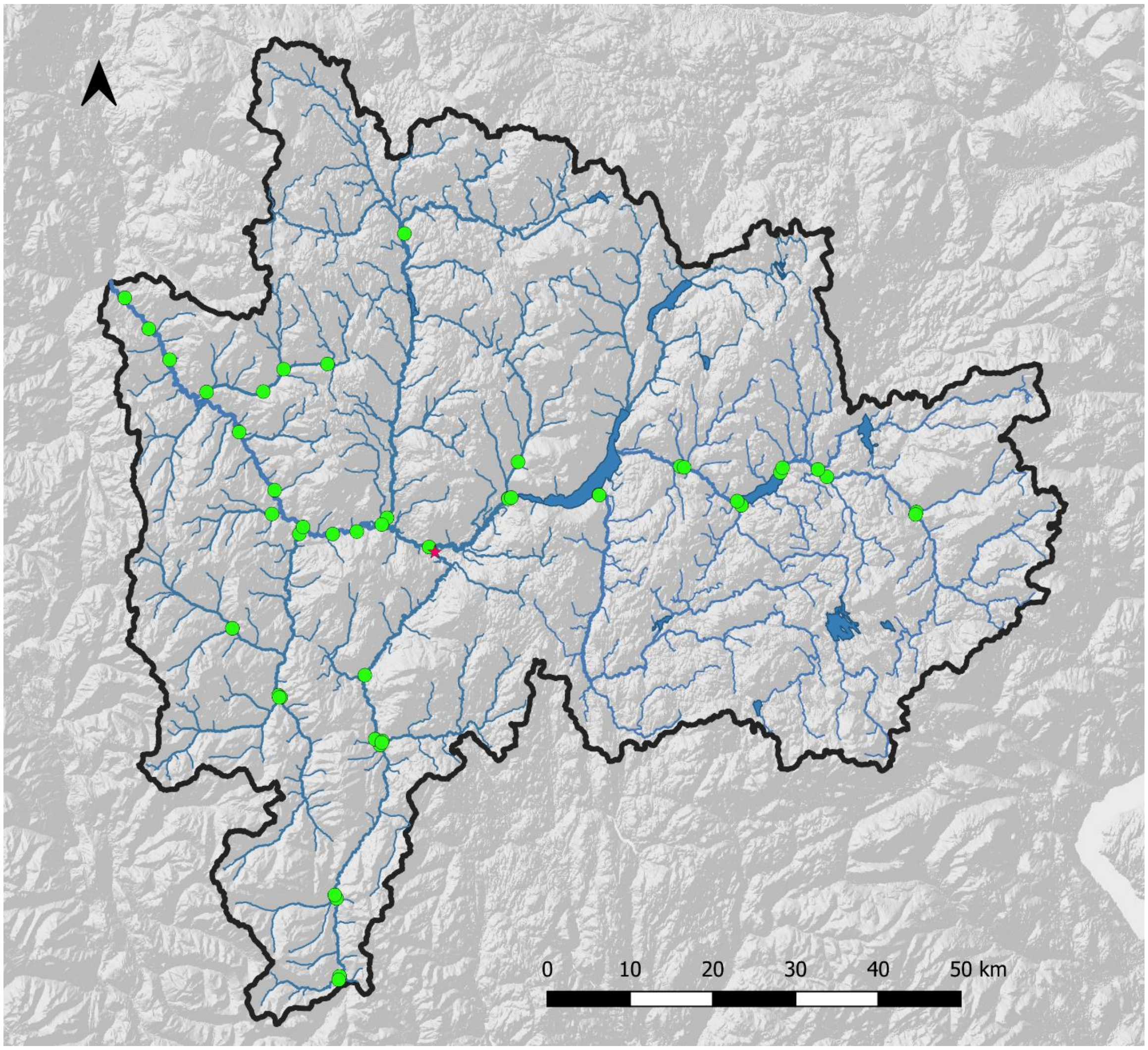

Figure 3.1. Stream temperature monitoring sites (green points) in the Nicola River watershed (outlined in black), with streams and major lakes within the watershed in blue.

The red star indicates the Merritt weather station. The hillshade digital elevation model shows topography.

Table 3.1. Stream temperature monitoring sites with their mean TS slopes and intercepts

Site ID	Site name	Latitude	Longitude	Mean TS slope	Mean TS intercept
200	Clapperton Creek	50.16234	-120.66963	0.56	13.3
201	Nicola River upstream of Clapperton Creek	50.16199	-120.66939	0.71	18.2
202	Quilchena Creek	50.15888	-120.516035	0.75	16.9
203	Nicola River above Nicola Lake 1	50.182583	-120.374983	0.67	16.5
204	Nicola River above Nicola Lake 2	50.181267	-120.368433	0.71	16.7
205	Nicola River above Douglas Lake 1	50.16724	-120.20668	0.42	14.9
207	Nicola River above Douglas Lake 3	50.17212	-120.20241	0.64	16.3
208	Coldwater River above Patchett Road	49.98209	-120.93307	0.65	15.6
209	Coldwater River under Gillis Road	49.90536	-120.91579	0.69	14.8
210	Juliet Creek	49.74369	-121.00843	0.48	12.1
211	Coldwater River above Juliet Creek	49.74206	-121.00715	0.45	11.3
212	Coldwater River below Juliet Creek	49.74602	-121.00972	0.50	11.6
213	Coldwater River at Gravel Pit	49.65744	-121.01124	0.44	10.0
214	Coldwater River Headwaters	49.65367	-121.01328	0.39	10.5
215	Nicola River below Skeikut Creek	50.33898	-121.22566	0.74	18.0
216	Nicola River below Kloklwuck Creek	50.37406	-121.2574	0.69	17.7
217	Nicola River near Spences Bridge	50.40926	-121.29466	0.76	18.3
218	Skuhun Creek 1	50.30125	-121.16675	0.51	13.0
219	Skuhun Creek 2	50.297417	-121.070633	0.42	10.9
220	Skuhost Creek	50.32009	-121.03354	0.36	9.4
221	Nicola River above Manning Creek	50.2554	-121.11617	0.71	17.5
222	Nicola River at Shackelly Creek	50.18963	-121.0631	0.70	17.4
223	Nuaitch Creek	50.16407	-121.07044	0.38	11.0
225	Prospect Creek	50.04303	-121.15062	0.51	11.8
227	Nicola River above Hatchery	50.13767	-120.97016	0.68	17.1
228	Nicola River at Sunshine Valley Road	50.13846	-120.92927	0.67	17.2
229	Guichon Creek at Nicola River	50.150946	-120.876649	0.66	16.0
230	Spius Creek at Maka Creek	49.96693	-121.08054	0.64	13.6
231	Skuhun Creek 3	50.32243	-120.95857	0.46	9.7
232	Guichon Creek above Mamit Lake	50.45771	-120.81185	0.47	11.9
233	Quilchena Creek 2	50.158373	-120.515576	0.75	16.8
234	Nicola Lake at Dam	50.162984	-120.664385	0.68	18.4
235	Clapperton Creek 2	50.201123	-120.648212	0.45	12.0
237	Nicola River at Norgaards	50.115966	-120.809059	0.73	18.2
238	Gillis Creek 1	49.911912	-120.923101	0.41	10.9
239	Gillis Creek 2	49.911828	-120.923437	0.41	10.8
240	Voght Creek 1	49.909316	-120.911425	0.52	12.8
241	Voght Creek 2	49.907712	-120.912797	0.45	12.3
242	Maka Creek 1	49.964606	-121.077311	0.65	13.9
244	Spius Creek above Maka Creek	49.964583	-121.079605	0.66	13.6
245	Spius Creek at Hatchery Intake	50.140333	-121.026582	0.75	15.9

Site ID	Site name	Latitude	Longitude	Mean TS slope	Mean TS intercept
246	Prospect Creek 2	50.043033	-121.150547	0.57	11.8
247	Spaxomin Creek near Douglas Lake	50.135027	-120.276938	0.55	14.6
248	Nicola River at outlet of Douglas Lake	50.139985	-120.283533	0.42	17.8
250	Nicola River above Chaperon Creek	50.158411	-120.128775	0.58	15.6
251	Nicola River below Chaperon Creek	50.167158	-120.14297	0.53	16.2
252	Beaks Creek	50.112014	-119.982919	0.49	12.1
253	Nicola River above Beaks Creek	50.109477	-119.984539	0.51	12.4
300	Nicola River at Guichon Creek confluence	50.144087	-120.886353	0.55	18.1
301	Nicola River at Petit Creek	50.147573	-121.019528	0.57	17.9

Watershed characteristics

As covariates for the analysis to examine how watershed characteristics influence temperature regimes, I chose the following four variables that have been shown to predict stream temperatures and thermal sensitivity in other watersheds (Table B1):

1. Riparian forest cover
2. Lake influence
3. Elevation
4. Watershed area

I calculated percent riparian forest cover upstream of each site. To do this, I combined line and polygon shapefiles for rivers from the BC Freshwater Atlas (GeoBC, 2019). I then made a 30 m buffer on each side of this shapefile, and then clipped this at the site and 600 m upstream of the site. This buffer was used to make a clip of the BC provincial Forest Vegetation Composite Polygons (Ministry of Forests, Lands, Natural Resource Operations, 2019) which classifies land cover into treed, non-tree vegetation, unvegetated land, and water. I calculated the percent of the riparian buffer with treed vegetation for each site, and chose a 30 m by 600 m buffer based on previous research on the amount of riparian forest required to show a detectable effect on stream temperature (Bladon et al., 2018; Pollock et al., 2009; Sullivan et al., 1990). Other studies have used 500 m and 1000 m long buffers (Hrachowitz et al., 2010).

To calculate an index of lake influence weighted by distance upstream of each site, I used lakes with an area >10,000 m^2. For each site, I calculated the distance from the site to each upstream lake. The area of each lake was divided by its distance to the downstream site. These area/distance values were then summed for each site to give the lake index for each site (Mauger et al., 2016). I used the BC Freshwater Atlas lakes polygon layer (GeoBC, 2020b) to calculate this index.

I calculated the mean elevation of the upstream catchment for each site using the DEM and the upstream catchment area. I used a digital elevation model (DEM) for British Columbia to calculate this elevation variable (GeoBC, 2020a). I used ArcGIS to delineate upstream catchment area polygons for each site based on the DEM. All manipulation of spatial data was done in ArcGIS (ESRI, 2020) and QGIS (QGIS Development Team, 2020).

3.2.3. Statistical analyses

Statistical models of water temperature – compared to process-based or physical models – are increasingly used to quantify and analyze stream temperatures (Hague & Patterson, 2014; Isaak et al., 2017). Before analysis, watershed area and lake influence were log-transformed to improve normality (Lisi et al., 2013).

Maximum daily stream temperature

To determine the relationship between watershed characteristics and maximum stream temperatures, I fit a mixed-effect linear model to predict maximum stream temperatures for each site in each year (Equation 3.1). For site *i*, *TWmax* is the maximum of daily mean stream temperatures over each summer, e_{rip} is the effect of riparian forest cover, *riparian* is the percentage of the riparian buffer with trees, e_{lake} is the effect of lakes, *lake* is the lake index for each site, e_{elev} is the effect of elevation, *elevation* is the mean elevation of each catchment, e_{area} is the effect of area, *area* is the area of each catchment, and *b* is the intercept. I included a random effect of year.

$$TWmax_i = e_{rip} \times \ riparian_i + e_{lake} \times \ log(lake_i) + e_{elev} \times \ elevation_i + e_{area} \times log(area_i) + (1|year) + b \qquad (3.1)$$

I also included a spatially autocorrelated error term, based on the latitude and longitude (in decimal degrees) of each site. The spatial autocorrelation term uses the latitude and longitude values to determine linear distance between each pair of sites (in this case, in decimal degrees). Including this term allows the model to account for similarities between sites that are closer together. There was essentially no difference in AIC values between models fit with exponential and linear auto-correlation structures (difference < 0.001), so I used an exponential auto-correlation structure for the analysis.

The model was fit with the *nlme* package (Pinheiro et al., 2020), which was also used to extract confidence intervals for the effect terms.

Stream temperature sensitivity

I used a multi-step linear modelling approach to determine the influence of watershed characteristics on the thermal sensitivity of streams throughout the watershed. This analysis used data for August and September only, as this time period is typically when base flow conditions are present, coincides with the migration and spawning of Chinook salmon, and was shown to be important in terms of flow effects on both spawning and rearing (see Chapter 2). The TS slopes are also similar between these two months, based on visual inspection. Air temperature was centred to reduce the amount of covariation between slope and intercept to aid model fitting. The TS slope indicates the relative change in stream temperature given a change in air temperature at each site. Because air temperature was centred for this analysis, the TS intercept indicates the average stream temperature at each site given a common distribution of regional air temperatures.

This analysis was done in two steps (Beaufort et al., 2020; Mauger et al., 2016). First, I regressed stream temperature as a function of air temperature to get slopes and intercepts for each site. I used a Bayesian approach to fit slope and intercept for each site, as random effects. For each site i, predicted daily mean stream water temperature pTW are predicted by the product of site-specific slope b_i and daily mean air temperature TA plus a site-specific intercept a_i (Equation 3.2). Observed daily mean water temperature TW is assumed to be drawn from a normal distribution with mean pTW and standard deviation σ (Equation 3.3). The prior for σ is a half-cauchy distribution (Equation 3.4). All site-specific slopes b are drawn from a common normal distribution with hyper-parameters μ_b and σ_b specifying their mean and standard deviation, and likewise for site-specific intercepts a (Equations 3.5-3.10). This modelling was carried out using R (R Development Core Team, 2015) and the *rstan* package (Stan

Development Team, 2019). The model was run with 3 chains and 5000 iterations, with a burn-in of 1000.

$$pTW = b_i \times TA + a_i \quad (3.2)$$

$$TW \sim Normal(pTW, \sigma) \quad (3.3)$$

$$\sigma \sim Cauchy(0,\ 1) \quad (3.4)$$

$$b_i \sim Normal(\mu_b, \sigma_b) \quad (3.5)$$

$$\mu_b \sim Normal(1,\ 0.1) \quad (3.6)$$

$$\sigma_b \sim Cauchy(0,\ 1) \quad (3.7)$$

$$a_i \sim Normal(\mu_a, \sigma_a) \quad (3.8)$$

$$\mu_a \sim Normal(12,\ 0.1) \quad (3.9)$$

$$\sigma_a \sim Cauchy(0,\ 1) \quad (3.10)$$

When visually inspecting the data, only a few of the sites exhibited an effect of month or year (e.g., Nooaitch Creek), but these varied by at least two other factors which would have required a three-way interaction term (month×year×site), which would have been prohibitive to model fitting given the sample size. Since the goal of this analysis was detecting overall site-specific patterns and relating these to watershed characteristics that were either static by nature (e.g., elevation, lake influence, area) or within the time period (e.g., riparian forest), as opposed to a predictive model, this was not a large concern. Also, for this part of the analysis, we are interested in the average TS for each site, not in temporal differences.

After determining the site-specific TS slopes and intercepts, linear models were used to predict these variables based on the four watershed characteristics (Equations 3.11-3.12).

$$b_i = b_{rip} \times\ riparian_i + b_{lake} \times\ log(lake_i) + b_{elev} \times\ elevation_i + b_{area} \times\ log(area_i) + intercept_b \quad (3.11)$$

$$a_i = a_{rip} \times riparian_i + a_{lake} \times log(lake_i) + a_{elev} \times elevation_i + a_{area} \times log(area_i) + intercept_a \quad (3.12)$$

I used the *nlme* package (Pinheiro et al., 2020) to fit these models.

I also included spatial autocorrelation terms in these models. I used exponential structure for the slope model as it had a lower AIC score than the same model fit with a linear spatial autocorrelation. I used a linear structure for the intercept model as it had a lower AIC score than the model fit with exponential structure. In order to use the *nlme* package to account for spatial auto-correlation structure, I also included a dummy random effect term, which was identical for all observations.

A preliminary analysis attempted to accomplish the two steps above with a single, hierarchical Bayesian model, where the site-specific slopes and intercepts were fit simultaneously with the effects of watershed characteristics, but even after centering the air temperature variable, the slope and intercept were still correlated, and the model failed to converge. While the two-step approach may be less sophisticated, other two-step approaches have been used successfully (Beaufort et al., 2020; Mauger et al., 2016).

Watershed characteristics with effect terms whose 95% confidence intervals did not span 0 were interpreted as having a detectable relationship with maximum stream temperature, TS slope, and/or TS intercept. The TS slope represents the sensitivity of stream temperature to changes in air temperature, and the TS intercept represents the typical stream temperature at the average air temperature from August-September.

3.3. Results

There were large differences in temperature dynamics across the different portions of the Nicola watershed. In the mainstem Nicola River, summertime maximum temperatures exceeded 25°C in 2018 and 2019 in late July and early August. In comparison, the coldest measured water temperatures in the watershed were smaller creeks and tributaries, and had daily mean temperatures that stayed below 15°C throughout the summer (e.g., Skuhost Creek, Gillis Creek, Coldwater River headwaters, upper Skuhun Creek, upper Clapperton Creek).

Catchment area had a strong positive relationship with maximum stream temperature, and riparian tree cover a weak negative effect (Figure 3.2, Table 3.2). For an increase in the natural logarithm of catchment area by 1, maximum stream temperature increased by 1.5°C. The estimate of the effect of riparian tree cover was more uncertain, with 90% confidence intervals overlapping 0. The mean estimate of the effect size of riparian cover was -1.2, meaning that for a 50% increase in riparian cover, maximum stream temperature decreased 0.6°C. There was no evidence of a relationship between maximum stream temperature and either lake influence or mean watershed elevation. Collectively, these watershed variables explained the majority of the observed variation in maximum stream temperature (R^2 of equation 3.1 was 0.64).

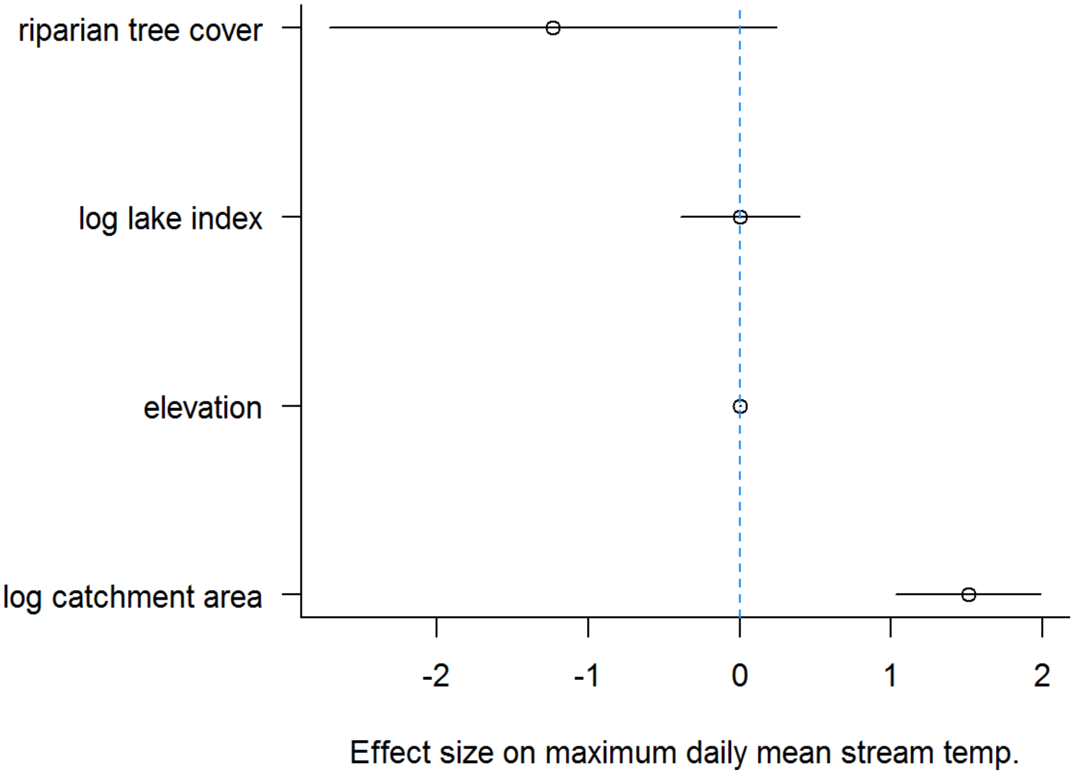

Figure 3.2. **Mean and 95% confidence intervals for the estimated effect sizes of the four watershed characteristics on maximum daily mean stream temperature.**

The sensitivity of streams temperature to regional air temperatures showed a large amount of variation (Figure 3.3). On days when air temperature was 25°C, streams with the lowest TS slopes averaged less than 15°C, while the most sensitive streams were warmer than 20°C.

There was strong evidence that riparian cover, lake influence, and catchment area had relationships with TS slopes – the sensitivity of stream temperature to regional air temperature – during August and September (Figure 3.4, Figure 3.5, Table 3.3). Streams with higher riparian cover of the monitoring site had lower TS slopes. Given a 10°C increase in air temperature, water temperature would increase by 0.8°C less at sites with 100% riparian cover, compared to sites with 0% riparian cover (based on the mean effect estimate). Sites with larger lakes located closer upstream had lower sensitivity slopes, while larger watersheds had higher sensitivity slopes. Mean watershed elevation did not have a clear relationship with sensitivity – the 90% confidence intervals included both positive and negative relationships.

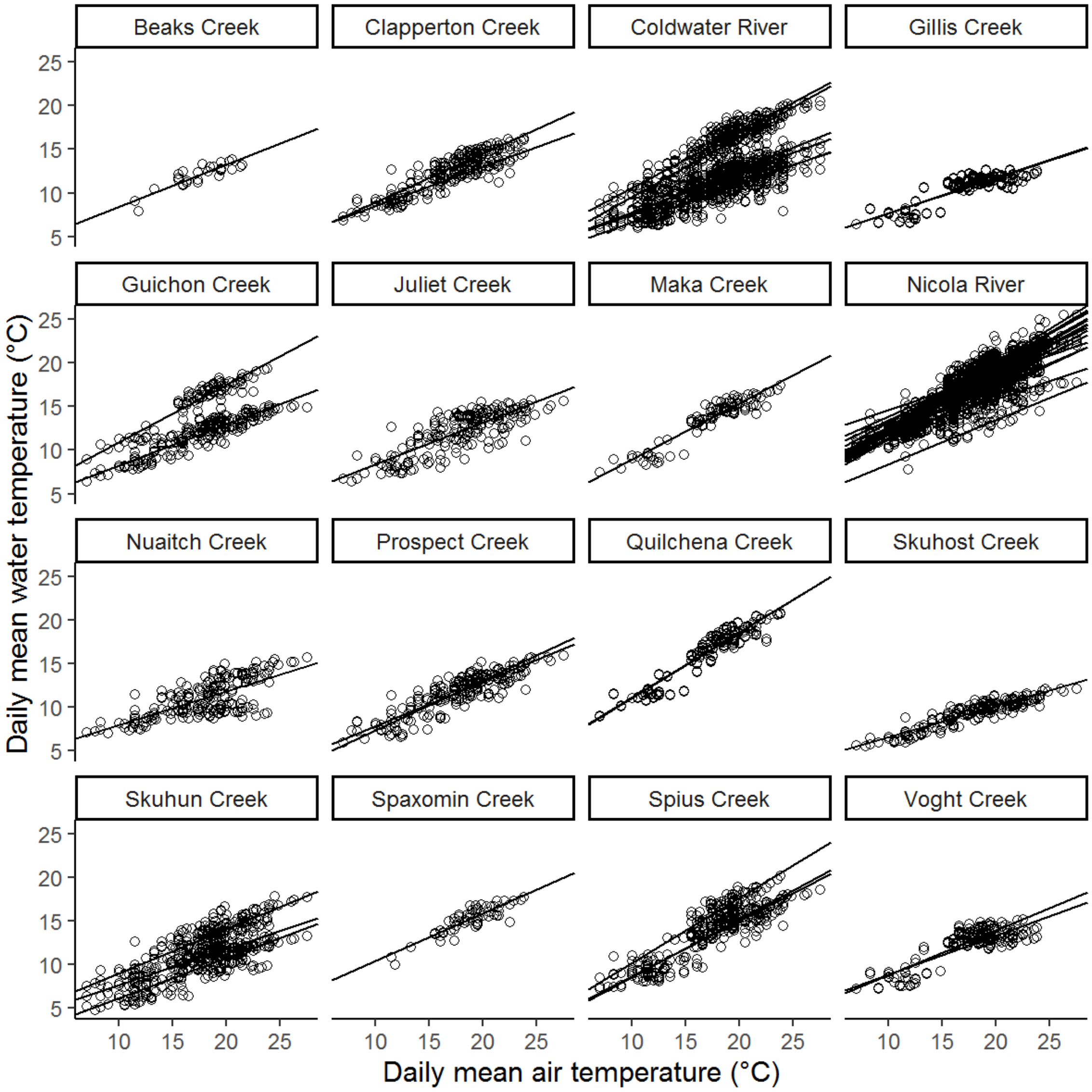

Figure 3.3. **TS relationships for each of the 50 sites (one line per site), for August-September.**

The panels include all sites located along a single stream.

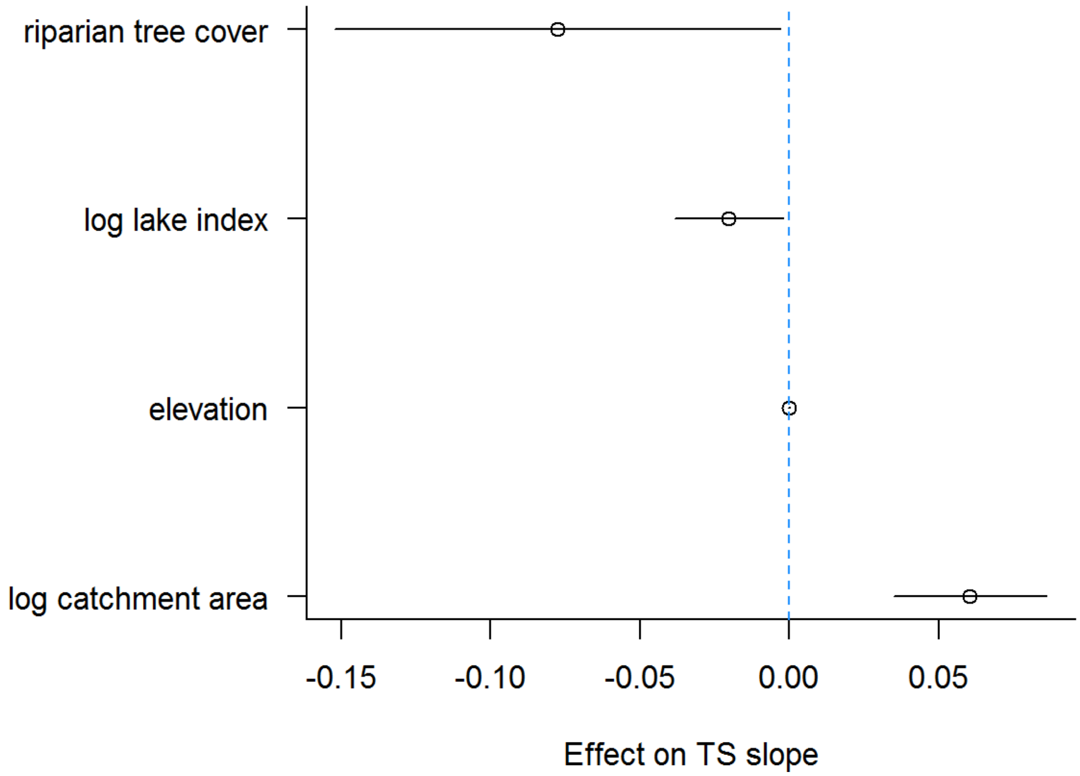

Figure 3.4. **Mean and 95% confidence intervals for the estimated effect sizes of the four watershed characteristics on TS slopes (thermal sensitivity).**

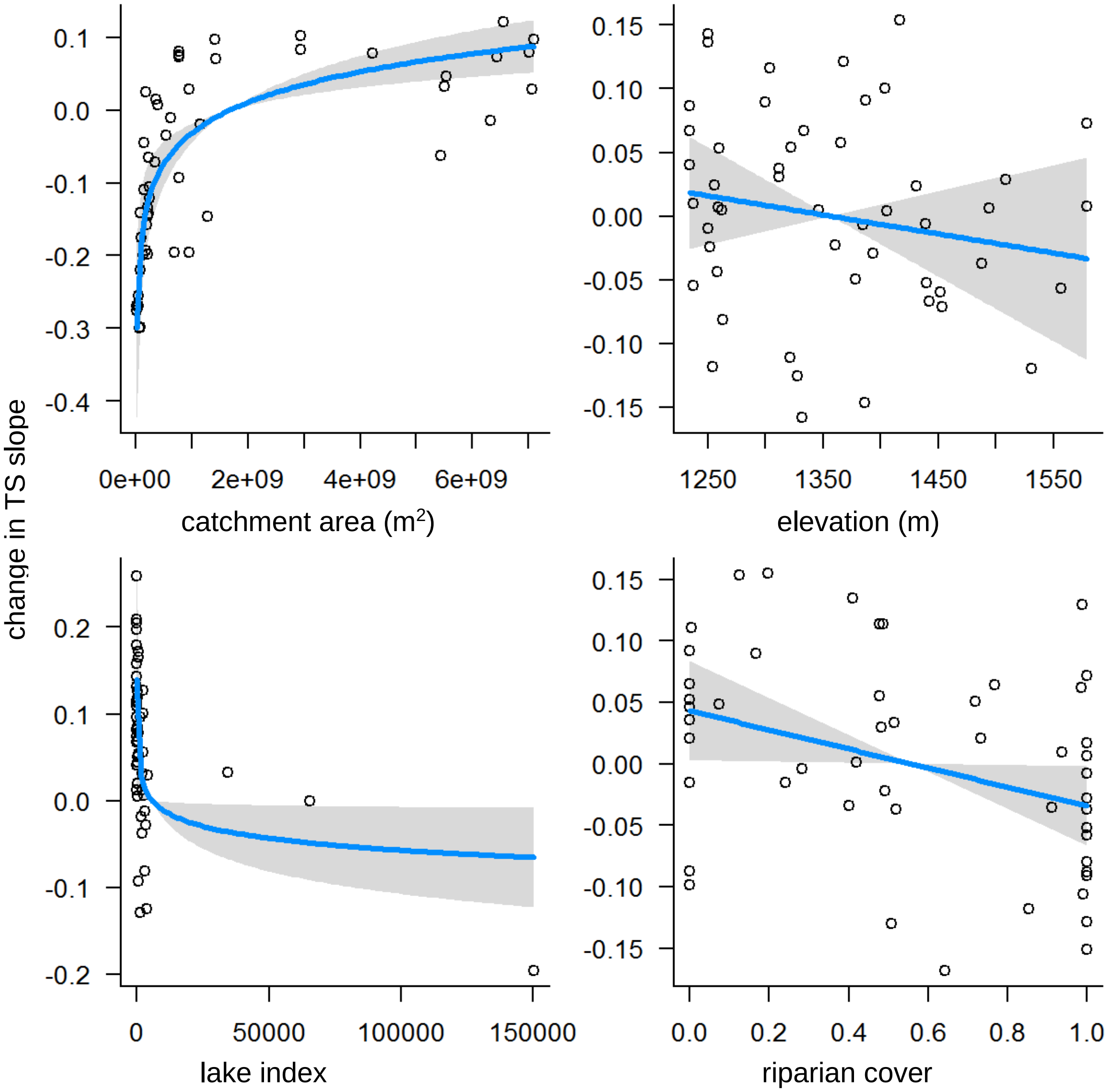

Figure 3.5. **Contrast plots of relationship between TS slopes and watershed characteristics.**
Y axes show the relative change in TS slopes for values of the four watershed characteristics. Each point represents an individual site.

Relationships between watershed characteristics and the TS intercept – the average stream temperature at average air temperature values – were similar to slope, except for the lake area, which had the opposite effect (Figure 3.6, Figure 3.7, Table 3.4). Sites with greater lake influence showed higher intercepts (i.e., the average stream temperature at average air temperatures were greater for more lake-influenced sites). Sites also had higher intercepts if they had larger catchments, and lower intercepts with higher riparian cover (but the upper confidence interval for the latter relationship was just overlapping 0, and uncertainty was higher).

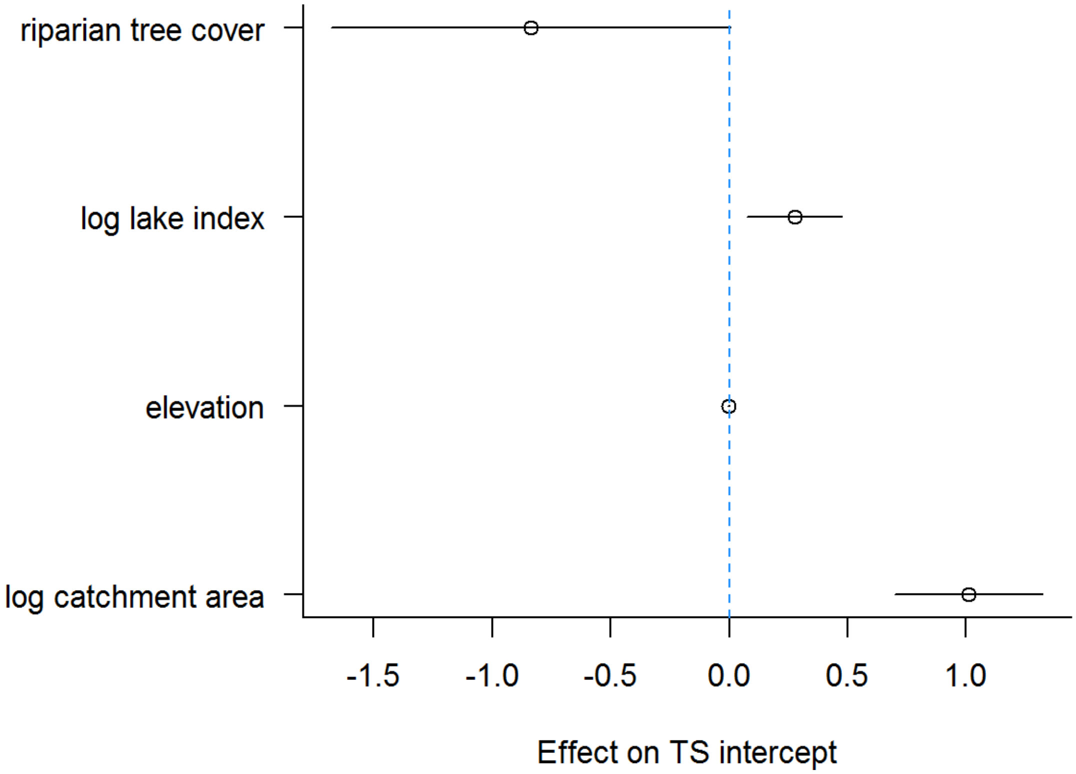

Figure 3.6. **Mean and 95% confidence intervals for the estimated effect sizes of the four watershed characteristics on TS intercepts.**

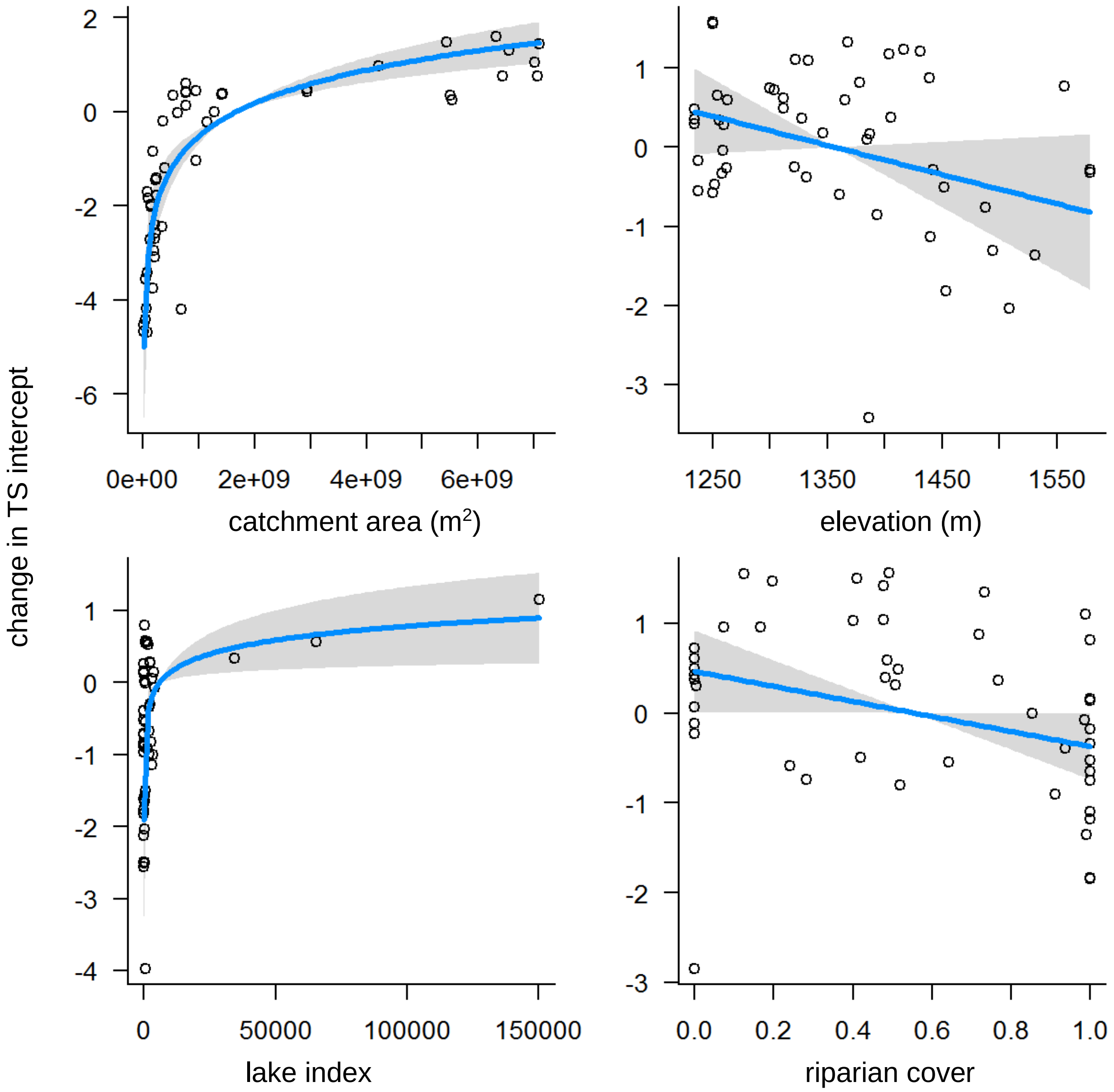

Figure 3.7. **Contrast plots of relationship between TS intercepts and watershed characteristics.**

Y axes show the relative change in TS intercepts for values of the four watershed characteristics. Each point represents an individual site.

Table 3.2. **Mean and 95% confidence intervals of the estimated intercept and fixed effects for the model predicting maximum daily mean water temperature.**

	lower	estimate	upper
intercept	-27.4006	-13.3706	0.659333
log catchment area	1.030987	1.507651	1.984315
elevation	-0.00649	0.000228	0.006944
log lake index	-0.39178	0.003022	0.397824
riparian tree percent cover	-2.70671	-1.23232	0.242059

Table 3.3. **Mean and 95% confidence intervals of the estimated intercept and fixed effects for the model predicting TS slopes.**

	lower	estimate	upper
intercept	-1.08724	-0.28037	0.52651
log catchment area	0.034912	0.06049	0.086068
elevation	-0.00052	-0.00015	0.000219
log lake index	-0.03837	-0.02023	-0.00209
riparian tree percent cover	-0.15216	-0.07752	-0.00287

Table 3.4. **Mean and 95% confidence intervals of the estimated intercept and fixed effects for the model predicting TS intercepts.**

	lower	estimate	upper
intercept	-12.0641	-1.97755	8.108974
log catchment area	0.698063	1.010192	1.322322
elevation	-0.00825	-0.0037	0.000851
log lake index	0.076474	0.275377	0.474281
riparian tree percent cover	-1.67949	-0.83676	0.005975

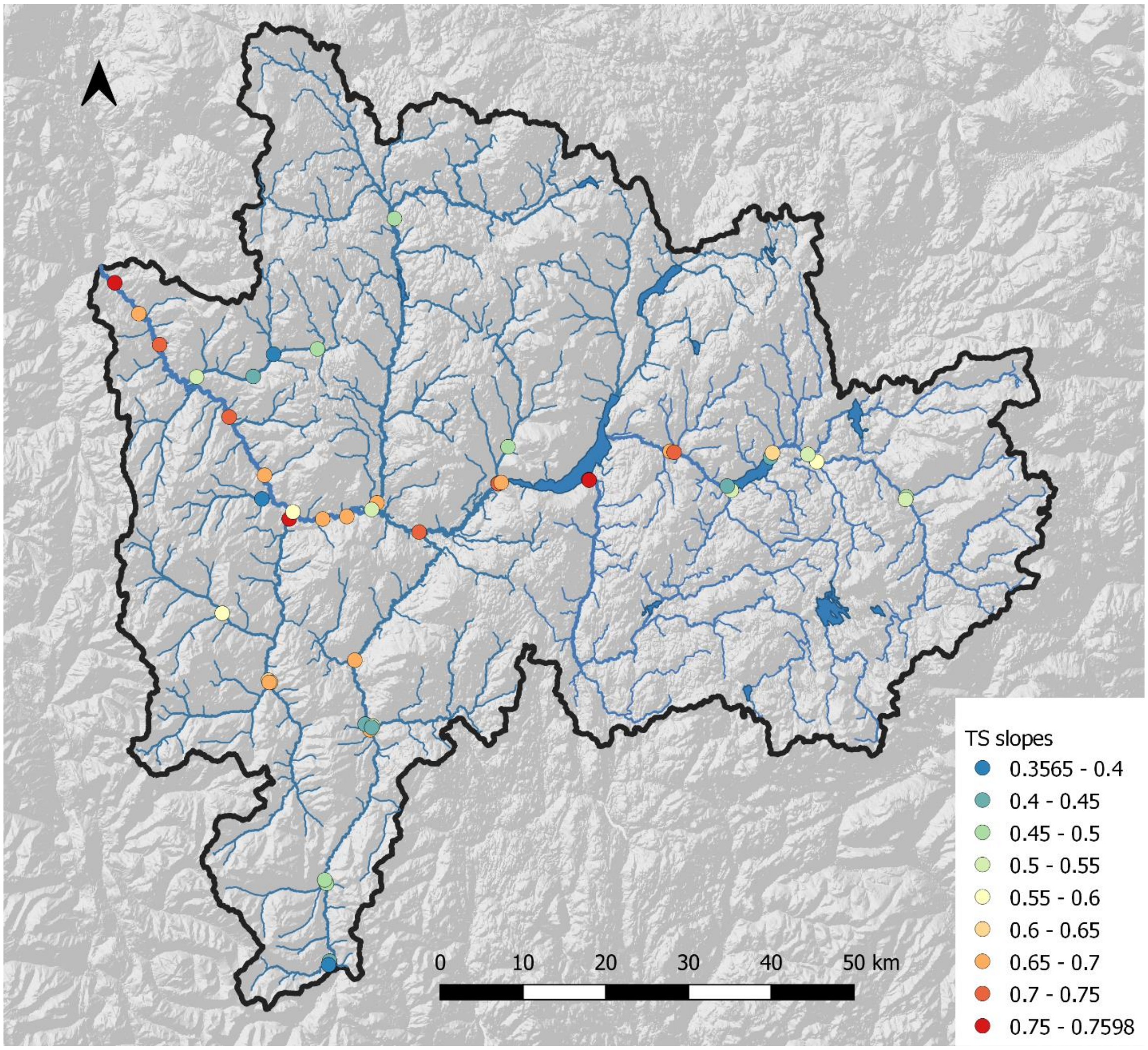

Figure 3.8. **The Nicola watershed, showing the TS slopes of the 50 monitoring sites.**

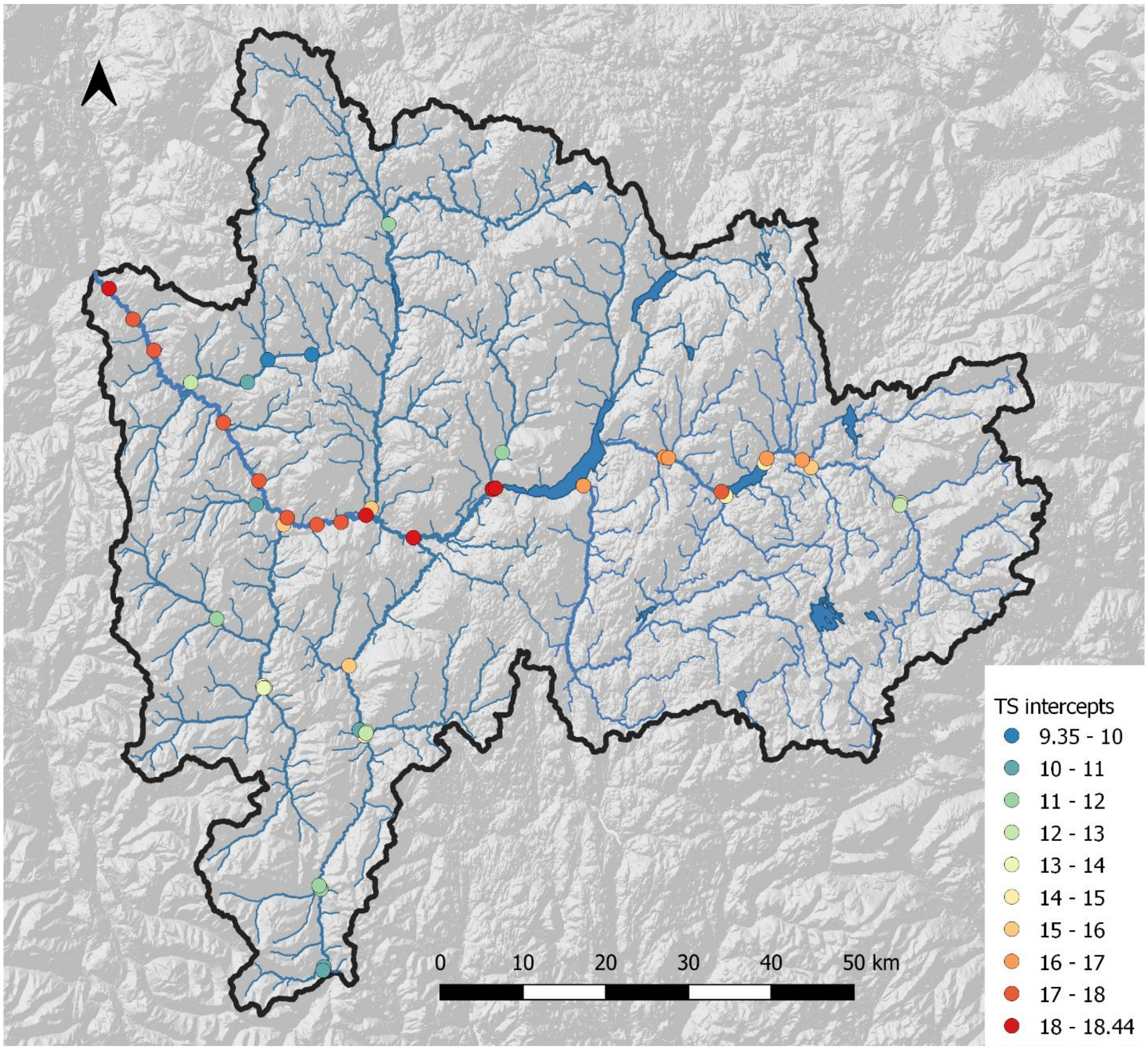

Figure 3.9. The Nicola watershed, showing the TS intercepts of the 50 monitoring sites.

3.4. Discussion

This study quantified how different watershed characteristics influenced the thermal regime of an interior river system with imperiled salmon. Specifically, sites with higher catchment areas had higher maximum temperatures as well as greater thermal sensitivity (TS slope). In addition, sites with greater riparian vegetation cover had lower thermal sensitivity. Other geographic features, namely lakes, also influenced thermal regimes. Collectively, these results identify factors that, even after accounting for spatial autocorrelation, are associated with warmer temperatures and greater climate sensitivity that pose risks to cold-water fishes such as Chinook salmon and bull trout.

The influence of catchment area was the most consistent and strong predictor of the stream thermal regime, having a strong positive relationship with maximum stream temperature and TS slope and intercept. I found that larger catchments had a higher thermal sensitivity (TS slope), or higher sensitivity to regional air temperature. This result is consistent with other studies that show that catchment area has an important influence of stream thermal regime, including positive relationships with TS slope (Chang & Psaris, 2013; Mauger et al., 2016). As catchment area increases, there is more surface area for both insolation of the stream surface and for heat fluxes across the stream-air interface (Poole & Berman, 2001). Summer stream temperatures generally increase downstream (although not always, see Fullerton et al. 2015), as the temperature of water tends toward equilibrium with air temperature (Poole & Berman, 2001). Thus, through impacts on both maximum temperature and climate sensitivity, catchment area is a strong structuring force on stream temperatures. Our study provides additional evidence that small tributaries with smaller catchments can be both cooler and less climate sensitive than downstream rivers, and thus likely reflect important thermal refugia in this warming world (Ebersole et al., 2020).

Riparian tree cover was an important local factor in influence temperature regimes, and decreased thermal sensitivity of stream temperatures, consistent with other studies (Beaufort et al., 2020). More riparian tree cover was associated with lower TS slopes, indicating that loss of riparian habitat may increase climate sensitivity. More riparian tree cover also tended to be associated with somewhat lower maximum stream temperature and TS intercept (an indicator of average stream temperatures). These patterns emerged despite relatively coarse available data on riparian cover; more detailed mapping based on orthophotos or LIDAR data may reveal stronger, more precise relationships between riparian vegetation and stream temperatures (Dugdale et al. 2020). These results illustrate that conservation or restoration of local riparian cover (the reach that extends 600m upstream) could help improve thermal regimes for salmonids in warming rivers. Riparian forest creates a local microclimate around the stream channel, buffering the stream from solar radiation, wind, and meteorological effects (Garner et al., 2015; Poole & Berman, 2001). Other studies have shown that large-scale riparian planting (together with channel restoration), may provide short and long-term benefits to cold-dependent salmonids with climate change (Justice et al., 2017). In addition, protection of riparian forests, such as from rural development, agriculture, logging, and other human impacts found in the Nicola system and elsewhere, will help maintain the climate resilience of stream ecosystems.

Lakes and reservoirs, a common feature in many salmon watersheds, decreased thermal sensitivity (TS slopes) but increased maximum temperatures in this study. It appears that lakes dampen daily fluctuations in temperatures due to their high thermal inertia. This pattern is apparent just downstream of Nicola Lake, where diel variation is lower than in reaches without lake influence or farther downstream. Further, higher TS intercepts with greater lake influence indicates that lakes may elevate the entire distribution of water temperature downstream in August and September, due to the physical properties of lakes (e.g., large surface area, stratification with warm water flowing out of the top layer of the lake). Other studies show complex effects of reservoirs on downstream temperatures which vary across years, seasons and days (Webb & Walling, 1997). While it may be possible to adjust reservoir releases with the goal of enhancing habitat for certain species (Bestgen et al., 2020; Olden & Naiman, 2010; Sabo et al., 2017), context is important. For example, the operation of the Nicola Lake reservoir is constrained by a top-release dam, frequent drought, flood safety management, and a shallow lake mouth that requires a minimum water depth in winter to avoid freezing, which can limit late summer and fall releases during low flows. Other reservoirs in the watershed, such as Mamit Lake reservoir, which is at a higher elevation, may offer more opportunities for cold-water releases during summer. Regardless, the spatial distribution of lakes and reservoirs in watersheds is an important driver of thermal riverscapes.

This study had analytical challenges that are important to discuss. First, this study did not find any relationship between elevation and thermal regime, contrary to other research, but note that study catchments only spanned 300 m in elevation. Other studies of systems with greater elevational ranges (500-1000 m) found that mean catchment elevation was negatively related with average stream temperature (Lisi et al., 2013), maximum weekly maximum temperature, and TS slope (Mauger et al., 2016). Second, while flow is somewhat implicit in the catchment area variable (Hrachowitz et al., 2010), this study also did not examine the potential moderating effect of flow on TS slope (Hague & Patterson, 2014; Sohrabi et al., 2017) because of the lack of hydrometric data for many of the smaller tributary streams, and the current availability of unapproved provisional data that are subject to changes. Third, dealing with spatial autocorrelation and pseudo-replication with stream water quality data is challenging, and the most sophisticated techniques are often complicated analyses unto themselves (Hoef et al., 2014; Peterson et al., 2013). General practice is to avoid sites closer than 5-10 km (Gardner et al., 2003; Hrachowitz et al., 2010). However, it is still possible to introduce error in the estimation of other effects. I used a simple spatial structure based on site latitude and longitude to account for potential spatial autocorrelation, striking a balance between computational intensity and over-simplification. A more robust estimation of spatial auto-correlation would be more important for models that aim to predict temperatures throughout river systems (Isaak et al., 2010). Finally, further research could investigate whether these results are sensitive to which air temperature data are used, comparing a regional air temperature station to site-specific air temperature loggers and downscaled, interpolated climate data (Chezik et al., 2017; Wang et al., 2016).

One factor that could be explored more in future research is the potential interaction between riparian forest cover and stream size. Riparian vegetation shades streams from direct solar radiation, and thus a riparian forest of a given height and density will shade more of a small stream compared to a wider stream. In addition, the buffering effect of riparian vegetation to reduce air speed and thus heat exchange processes over a stream may decrease as channel width increases (Poole & Berman, 2001). Thus, one could expect an interaction between riparian cover and stream size, such that the same percentage of riparian forest cover would have a greater effect on smaller streams compared to larger streams. If this pattern is present in the Nicola watershed, it is possible that my estimates of the effects of riparian forest were over-estimated for larger streams and under-estimated for smaller streams. Although I did not test for this pattern, doing so in further work would be worthwhile.

The low TS slopes and intercepts of many of the smaller tributaries in the Nicola watershed highlight their importance as sources of cold water during the summer, with less sensitivity to regional climate (Figure 3.8, Figure 3.9), thus representing thermal refugia. These results highlight the importance of managing land and water use in order to preserve the favourable thermal regimes of these smaller tributaries. Land use management such as preservation of riparian cover in small tributary streams can keep small streams cooler (Macdonald et al., 2003), while forest harvest practices that aim to reduce rate of snow-melt, such as minimizing logging on steep and south-facing slopes can help to ensure higher base-flows of tributary streams (Goeking & Tarboton, 2020). An approach with increasing popularity, beaver dam analogs have been shown to increase temperature heterogeneity and decrease temperatures downstream (Weber et al., 2017), increase downstream flows (Pollock et al., 2003), and improve habitat for rearing salmonids (Bouwes et al., 2016). Indeed, beaver ponds have been shown to be especially important for rearing coho salmon in the Coldwater River, a major tributary of the Nicola (Swales & Levings, 1989). As such, there are a number of science-based approaches to land and water management that could help preserve and restore thermal regimes for salmonids in climate-stressed watersheds.

Elevated water temperatures can affect fish populations at specific pinch points in their life cycle when they encounter warm water. For example, adults sockeye salmon migrating up the Fraser River have greater mortality with increasing river temperature, with over 90% dying before spawning in the warmest years (Hinch et al., 2012). Non-lethal effects can include reduced growth rate (Marine & Cech, 2004), reduction in cold-water refugia which used by migrating adults (Keefer et al., 2018), and may increase the feeding rate of predators on juvenile salmonids (Petersen & Kitchell, 2001). However, different populations of salmon from warmer watersheds are differently physiologically adapted to elevated water temperatures (Eliason et al., 2011). Furthermore, diverse salmon populations and species have different migration timings and use different portions of river networks, thereby driving divergent exposures to elevated water temperatures (Brennan et al., 2019; Crozier et al., 2019). For example, the Nicola has several different conservation units of Chinook salmon that migrate through the mainstem river at different times and spawn in different locations, ranging from mainstem to tributaries. Studies such as this one represent a step towards understanding the risks posed by climate change to different salmon conservation units.

Climate change poses many risks to the viability of salmon populations throughout their range (Crozier et al., 2008; Healey, 2011; Wade et al., 2013). At the same time, salmon play a critical role in supporting food security of Indigenous Peoples today and for at least the last seven millennia (Campbell & Butler, 2010; Nesbitt & Moore, 2016). Given the cultural, economic and ecological importance of productive salmonid populations and their reliance on specific thermal regimes, research that sheds light on the relationship between the landscape and stream temperature sensitivity provides valuable information for science-based management in the face of accelerating climate change (Ebersole et al., 2020).

Chapter 4.

Conclusion

The relationship between climate, landscapes, rivers, and freshwater communities are intricately linked. In this thesis, I have quantified two important linkages in this chain of relationships: the relationship between freshwater flow conditions and the productivity of salmon (Chapter 2), and the relationship between watershed characteristics and stream temperature regime (Chapter 3). In this chapter, I present an overview of major findings, their key implications and context, and suggestions for future work.

4.1. The importance of freshwater conditions for salmonids

In my first chapter, I showed that low summer flows during the migration of Chinook spawners and rearing of their offspring the following year were correlated with lower lifetime productivity in a population currently being assessed for federal protection. This is particularly relevant because more than half of cohorts since 1992 have produced less than one recruit per spawner. Moreover, I showed that flows during this critical time have decreased by 26% over the last 100 years. These results, based on empirical stock-recruit data, suggest that sufficient flows for a stable population – in the absence of fishing – are nearly double previous estimates of flow requirements based on habitat models. In addition, this flow threshold – 35% of mean annual discharge – only occurred for 18% of cohorts examined. Winter ice conditions also showed a significant relationship with productivity. These results are critical to understand the status of this population and its potential for recovery, especially given the cumulative effects on the landscape, water use, and climate of the region.

This research has important implications for actions that influence hydrology, like forestry and water use Although this has not been a comprehensive hydrological analysis, there is a pattern of declining August base flows over the last century in the Nicola River. This is the same pattern predicted in British Columbia given climate change (Kang et al., 2016) and a legacy of logging (Goeking & Tarboton, 2020; Gronsdahl et al., 2019). In interior BC, clearcut logging has been demonstrated to reduce summer baseflows, but this effect can take at least 15 years to be detected – large stands of young trees with high rates of transpiration the most probable cause (Gronsdahl et al., 2019). Summer baseflow decreased after logging after a similar period of time in Oregon, with no return to pre-disturbance base flows despite 45 years of data after logging (Perry & Jones, 2017). Thus, watersheds with large increases in logging in the last 10-20 years, such as the Nicola, may be at greater risk of decreasing base flows as young forests develop. As has been demonstrated, Nicola Chinook have seldom experienced the river discharge associated with stable population growth – only about one in five of the years examined did flows exceed 35% mean annual discharge in August. If maintaining a stable population is desired, flows in the river need to increase from their current patterns. Achieving this in the Nicola watershed is a challenge, but there are a suite of options to boost summer low flows. For example, the forestry sector could work to keep water on the landscape as long as possible by managing forests to enhance snow accumulation, soil moisture, and infiltration while delaying melt (e.g., minimizing logging on steep and south-facing slopes). This could be informed by water and energy budgets specific to regions and catchments, since the processes that drive runoff vary across forest composition, elevation, slope, aspect, and latitude (Boon, 2012; Ellis et al., 2011; Goeking & Tarboton, 2020; Hubbart et al., 2015; Winkler et al., 2014). Other diverse actions such as beaver dam analogs (Pollock et al., 2003), reassessing historical water licenses and farm subsidy programs for water conservation retrofits could mitigate the effects of rapid climate change on flow regimes critical for salmon productivity.

My results and the growing body of work on the importance of variable flow conditions on salmon productivity are highly important given that many of these species are used by Indigenous, commercial and recreational fisheries (Nesbitt & Moore, 2016; Prince, 2002). Based on our model, mean August flow during rearing would need to be 15 m^3s^{-1} (50% MAD) to allow a harvest of 30% and escapement to spawning grounds at replacement levels. Given that year-to-year variation in freshwater conditions can have major implications for the productivity of some stocks, fisheries that are able to adjust based on these variable conditions will be more adaptable to actual productivity. Because different populations may have different or even opposite reactions to the same change in freshwater conditions (Jones et al., 2020; Neuswanger et al., 2015), fisheries that are able to be population-selective will also be better able to avoid those populations that are more at risk from consistently changing flow regimes (e.g., steady decreases in summer base flow). Further, by incorporating quantified stock-recruit relationships that use freshwater conditions as inputs, fisheries managers can be more accurate in predicting total returns, and thus better match allocations to actual returns and avoid overfishing cohorts that have experienced poor freshwater conditions at critical life stages. For stocks of conservation concern, identifying key, limiting freshwater stages may become more and more important as climate changes continues to alter flow regimes in Canada and across the world.

4.2. Watershed portfolios of temperature regimes

In my second chapter, I showed that both maximum stream temperatures and climate sensitivity of streams across a watershed were related to several watershed characteristics. Stream sites with smaller upstream catchment areas had lower maximum stream temperatures, as did streams with more riparian cover. For a 50% increase in riparian tree cover, maximum temperature was on average 0.6°C lower. Streams with larger catchments had higher climate sensitivity, while those with more riparian cover and higher lake influence were less climate sensitive. My results also identified small tributaries as important sources of cooler water at the height of summer, while also being less sensitive to warm air temperatures.

The link between riparian forest cover and lower maximum stream temperatures and lower climate sensitivity is important considering climate change projections. In combination with the result that smaller streams had lower maximum temperatures and were less sensitive to regional air temperatures, these results highlight the importance of preserving and restoring riparian cover for small streams. As this and other studies show, riparian forests buffer stream temperatures and their removal can increase stream temperatures by 4-6°C (Beakes et al., 2014; Garner et al., 2014; Macdonald et al., 2003). Currently, the British Columbia *Forest and Range Practices Act* and its regulations do not require retention of any riparian trees around fish-bearing streams less than 1.5 m width or non fish-bearing streams less than 3 m width when logging (Forest Planning and Practices Regulation, 2018; Forest Practices Board, 2018). The consequences of small stream management is disproportionate with their individual size, as small stream catchments can make up 70-80% of total watershed area (Gomi et al., 2002). Legislating the protection of riparian buffers around all small streams – whether fish bearing or not – could mitigate some impacts of warming climates on thermal regimes. In combination with large-scale riparian planting programs, this could help struggling salmon populations persist in the coming century (Justice et al., 2017).

Just as the effects of flow are context-specific, the effects of increased stream temperature depend on the overall patterns of temperature present. For example, warmer than average stream temperatures are associated with higher productivity in typically cold streams and lower productivity in typically warm streams (Jones et al., 2020). The Nicola watershed shows signs of typically warm temperatures over the last several decades, with summertime temperatures in the main stem often exceeding 20°C (PSF, unpublished data). However, it also has tributary streams and headwater areas which stay cooler, such as the Coldwater River headwaters, which are used by rearing coho, Chinook, rainbow trout, and Dolly Varden (Swales & Levings, 1989). This study has shown that smaller tributaries and headwater areas with smaller catchment areas are less sensitive to warmer regional air temperatures, which may make them more suitable as cold-water refugia.

4.3. Act like a river: the need for context, connectivity and integration

Preserving complex, interdependent watershed functioning and species in the face of climate change is a dire challenge (Reid et al., 2019; Tickner et al., 2020). The regimes of flow and temperature that freshwater organisms depend on – such as summer base flows for Chinook identified here – are changing rapidly, and are expected to continue to change, with many potential effects on ecosystems with large uncertainty (Ficke et al., 2007; Heino et al., 2009). In this examination of flows and temperatures in the Nicola watershed, I have shown the importance of place-based, specific case studies in understanding the manifestations of global and regional changes to particular rivers and fishes. Indeed, place-based management – reliant on studies such as this – can help conserve fisheries in this era of pervasive changes (Gayeski et al., 2018).

The naturally variable and integrative nature of rivers requires wholistic thinking and action in order to have desirable outcomes not only for fishes, but also wildlife, water supply, flood mitigation, and fire control. Just as rivers connect and integrate water, sediment, wood, and energy, our approach to river conservation must make connections between typically divorced disciplines and integrate knowledge and planning to implement actions that will have the greatest benefits to multiple processes and species. For example, riparian restoration has the potential for multiple benefits (Feld et al., 2018; Seavy et al., 2009), including cooling stream temperatures (Garner et al., 2014; Justice et al., 2017), invertebrate productivity (Zalewski et al., 1998), woody debris input (Wohl et al., 2019), and fire mitigation and recovery (Dwire & Kauffman, 2003). Approached this way, the unique characteristics of river systems, like connectivity and integration, could actually serve to advance efforts to conserve processes and species throughout their networks. Humans would do well to identify the connected benefits that are possible when watersheds are treated as wholistic systems, where changes to the headwaters will have cascading effects downstream, for fishes and people.

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Appendix A.

Supplemental Material for Chapter 2

Long-term Environmental Data

We used the Harvested Areas of BC (Consolidated Cutblocks) layer to calculate areas logged in the Nicola watershed (Ministry of Forests, Lands, Natural Resource Operations and Rural Development, 2019). We used the weathercan package (LaZerte & Albers, 2018) to access air temperature and precipitation data for the Merritt and Merritt STP weather stations from Environment and Climate Change Canada. We used the tidyhydat package (Albers, 2017) to access hydrometric data from the Water Survey of Canada's HYDAT database. There was no hydrometric information from 1921-1956. Naturalized long-term mean annual discharge (mean annual discharge plus estimated water usage) was based on HYDAT hydrometric data and an estimate of annual water usage (unpublished data, Ptolemy; Summit Environmental Consultants Ltd., 2007). We accessed water allocation data from the Water Licenses Query website using stream name = Nicola, and removed licenses for conservation or dam storage purposes (Government of British Columbia, 2020).

We also used the Freshwater Atlas (GeoBC, 2019) and the Atlas of Canada 1:1,000,000 National Scale Data – Boundaries, Rivers, Waterbodies (GeoBC & Natural Resources Canada, 2019) with QGIS (QGIS Development Team, 2020) to make Figure 2.1.

There was no evidence of correlation between the five covariates used in the stock-recruit model. The greatest correlation between these variables was -0.47.

Accounting for Unmarked Hatchery Adults

The period of the analysis includes years when the Spius Creek hatchery released unmarked Chinook into the Nicola River and tributaries. (Marked fish refers to fish that are adipose fin-clipped and have a CWT.) These included unmarked fry, sub-yearling smolts, and yearling smolts. When these unmarked spawners of hatchery origin return to the river, they are not distinguishable from wild origin spawners except by genetic or otolith methods, which were not used. To measure actual recruitment from wild spawners, we needed to estimate how many of the unmarked adults in the study period were actually of hatchery origin. We downloaded hatchery release data from the Regional Mark Information System (Regional Mark Processing Center 2019)

There were four types of hatchery releases that we estimated unmarked adult returns from:

- Type 1: Releases of unmarked fish with complementary releases of marked fish of the same stage, brood year, and stock.
- Type 2: Releases of unmarked fish that did not have complementary releases of marked fish of the same stage; unmarked fish which had a complementary release of marked fish of another stage in the same brood year, where those two stages have paired tagged releases in another brood year.
- Type 3: Hatchery-origin strays from Coldwater and Spius stocks: unmarked fish of Coldwater and Spius stock, which had complementary release of same stage, same brood year of marked fish from Nicola stock, where those stages/stocks have paired tagged releases in another brood year
- Type 4: Releases of unmarked fish that never had coded wire tags or clipped adipose fins for that stage (Coldwater fry, Spius fry and sub-yearling smolts).

Type 1

We calculated a return index – the fraction of CWT adult returns to the river from the total number of CWT fish released from the hatchery, for each combination of return age, stage of hatchery release (fry, sub-yearling, or yearling), brood year, and stock (Nicola, Coldwater, or Spius), which were summed by age, brood year and stock before dividing (Equation A1). These were pooled because CWT tag numbers within a stage, brood year and stock do not represent different treatments but reflect the limited number of CWT tag codes in each tagging wire. For years with paired marked/unmarked releases, we then expanded the return index by the the number of unmarked releases to get an estimate of unmarked hatchery adult returns (Equation A2).

$$ReturnIndex_{age,stage,BY,stock} = \frac{\sum MarkedAdultReturnsToNicola_{age,BY,stock}}{\sum MarkedReleases_{stage,BY,stock}} \qquad \text{(A1)}$$

$$UnmarkedHatcheryAdultReturns_{age,stage,BY} = UnmarkedReleases_{stage,BY,stock} \cdot ReturnIndex_{age,stage,BY,stock} \qquad \text{(A2)}$$

Type 2

For releases of unmarked fish that didn’t have a marked release of the same stage and brood year, we calculated a return index factor which was the ratio of the return index values for the stage of the release to esimate returns for and the stage with a complementary release of marked fish, for each age and brood year (Equation A3). Then, we took an average of these return idex factors by return age, across all years where these stages had shared CWT releases (Equation A4).

$$ReturnIndexFactor_{stage1:stage2,age,BY} = \frac{ReturnIndex_{stage1,age,BY}}{ReturnIndex_{stage2,age,BY}} \qquad \text{(A3)}$$

$$ReturnIndexFactor_{stage1:stage2,age} = \frac{1}{N}\sum_{i}^{N} Return\ IndexFactor_{stage1:stage2,age,BY_i} \quad \text{(A4)}$$

To estimate the unmarked hatchery adult returns for these releases, we then multipled the number of umarked hatchery releases by the return index for the complementary stage and by the return index for that complementary stage for the brood year and age of interest (Equation A5).

$$UnmarkedHatcheryAdultReturns_{age,BY} = UnmarkedReleases_{stage1,BY} \cdot$$
$$ReturnIndex_{age,stage2,BY} \cdot ReturnIndexFactor_{stage1:stage2,age} \qquad \text{(A5)}$$

Type 3

Based on CWT analysis, there is a small number of strays of hatchery releases of Coldwater River and Spius Creek origin that return to the Nicola River late run and are counted in the Nicola late run mark recapture program. Some of these unmarked fish are from years with complementary CWT releases and were estimated as part of the Type 1 category. Others did not have paired releases of CWT fish, but had paired releases of the same age and stage but from Nicola brood stock. To estimate the number of these unmarked adult strays we calculated a return index factor which was a proportion of the return index for stock of interest and the the Nicola origin hatchery release of the same age, stage and brood year (Equation A6).

$$ReturnIndexFactor_{stock_j:stock_{Nicola},stage,age,BY} = \frac{ReturnIndex_{stock_j,age,stage,BY}}{ReturnIndex_{stock_{Nicola},age,stage,BY}} \qquad \text{(A6)}$$

After calculating a return index factor for each pair of Coldwater/Spius and Nicola stocks, we averaged these factors across brood years to get an average proportion of strays to Nicola returns (Equation A7).

$$ReturnIndexFactor_{stock_j:stock_{Nicola},age} = \frac{1}{N}\sum_i^N ReturnIndexFactor_{stock_j:stock_{Nicola},age,stage,BY_i} \quad \text{(A7)}$$

Using this average return index factos, we multiplied the number of unmarked fish by the return index of hatchery releases of the same age, stage and brood year of Nicola origin fish and by the appropriate return index factor (Equation A8).

$$UnmarkedHatcheryAdultReturns_{age,BY} = UnmarkedReleases_{stock_j,stage,BY} \cdot ReturnIndex_{age,stock_{Nicola},stage,BY} \cdot ReturnIndexFactor_{stock_j:stock_{Nicola},stage,age} \quad \text{(A8)}$$

Type 4

There were a very small number of releases of unmarked hatchery fish of Coldwater and Spius stocks of stages that have not had any complimentary CWT release. As such, it is not possible to estimate the number of strays from these fish that end up in the Nicola late run mark-recapture program. We assume that this number is very low.

Accounting for Unmarked Hatchery Adults in Escapement

After estimating the number of unmarked hatchery adults for each brood year and age for each type and summed these estimates for each brood year and age, we subtracted this amount from the number of unmarked adults on the spawning grounds as estimated by the mark-recapture program to get an esimated of wild escapement (Equation A9). If the result was negative, we used 0 instead.

$$Escapement_{BY,age} = UnmarkedAdults_{BY,age} - UnmarkedHatcheryAdultReturns_{BY,age} \quad \text{(A9)}$$

Accounting for Fishing Mortality

We assumed that the rate of fishing mortality of wild fish was equal to that for hatchery fish for each age and brood year. This is possible if there is both escapement and recovery of CWT from fish caught in a fishery. Fisheries and Oceans Canada estimates age-specific mortality from fishing of hatchery fish using CWT recoveries from fisheries. We estimated wild recruitment from these exploitation rates and the wild escapement (Equation A10). The fishing rates are the total fishing mortality, which include landed catch plus incidental mortality. No adjustments were made for any differential mortality that could have occurred from mark selective fishing regulations.

$$WildRecruits_{BY,age} = \frac{WildEscapement_{BY,age}}{1 - CWTExploitationRate_{BY,age}} \qquad \text{(A10)}$$

For ages and brood years where there were 0 fish with CWT counted in escapement:

- If there were CWT fish caught in the fishery, this would imply an exploitation rate of 100%, which would give a recruitment of infinity. Because this is impossible, in these years/ages, we used an expansion factor to estimate the number of wild fish caught in the hatchery and then found total escapement (Equations A11, A12).

$$WildFishMort_{age_i,BY} = CWTFishMort_{age_i,BY} \cdot \frac{WildEsc_{age_j,BY} + WildEsc_{age_k,BY}}{CWTEsc_{age_j,BY} + CWTEsc_{age_k,BY}} \qquad \text{(A11)}$$

$$WildRecruits_{BY,age} = WildFishMort_{age,BY} + WildEscapement_{age,BY} \qquad \text{(A12)}$$

- If there were no CWT caught in the fishery, then an average of the exploitation rate for that age from all other years with both CWT in escapement and fishery was used.

Bayesian Model Details

We used the rstan package (Stan Development Team, 2019) to fit the Bayesian models. Although an informative prior could be chosen for α based on previous research on Chinook populations (Parken et al., 2006), we used a uniform prior to aid model fitting and because the inclusion of covariates in the Ricker equation changes the relative value of α compared to analyses that do not include covariates. We used the following initial values: random draw from a uniform distribution between 0 and 3 for $\log_e(\alpha)$;

random draw from a uniform distribution between 0.0002 and 0.0001 for β, β_W, and β_H; random draw from a normal distribution with mean 0 and SD 0.1 for b_1, b_2, b_3, b_4, and b_5; and random draw from a uniform distribution between 0 and 2 for τ. We ran all models with 3 chains of 10000 iterations, with a warmup (burn in) of 5000 iterations. We did not find any evidence of autocorrelation for model 8b (spurious lag-3 auto-correlation).

Comparison of Effect Sizes Across Models

Estimates of effect terms were mainly stable when comparing between models (Figure A11). This indicates that the effects are not very sensitive to whether certain variables are included or excluded. The most stable effect sizes were for mean August flow for rearing, which adds support that this parameter is important in explaining the variation in the recruitment. The parameter with the most variation in effect sizes across models was smolt to age 3 survival.

Density-dependence of Hatchery and Wild Spawners

There was limited evidence that density dependence was stronger for hatchery spawners compared to wild spawners. The second most parsimonious model from WAIC and third most for LOO included different β terms for wild and hatchery fish. Using α and β terms from this model, the strength of density dependence for wild fish (β = 0.00014) was about half that of hatchery fish (β = 0.00024, Figure A11b), with respective carrying capacities of 8007 and 4339 (Figure A8). However, the credible intervals overlapped and the 90% CI for β_W was contained by the 90% CI for β_H (Figure A11b). This pattern, although weak, is consistent with findings that hatchery salmon have stronger density dependence and lower carrying capacities than wild salmon (Buhle et al., 2009; Ward et al., 2015; Williamson et al., 2010).

Table A1. Candidate models. Note that models with “b” had one β term for total spawners, and models without “b” had two β terms (βW for wild, βH for hatchery spawners).

Model name	Parameters	Number of β parameters (1 for total spawners, or 2 for hatchery and wild spawners)
0	Base model: smolt-to-age 3 survival only	1
1b	Base + spawning flows	1
2b	Base + fall flood	1
3b	Base + ice days	1
4b	Base + rearing flows	1
5b	Base + summer terms	1
6b	Base + fall/winter terms	1
7b	Full - spawning flows	1
8b	Full - fall flood	1
9b	Full - ice days	1
10b	Full - rearing flows	1
11b	Full model (Base + spawning flows + fall flood + ice days + rearing flows)	1
1	Base + spawning flows	2
2	Base + fall flood	2
3	Base + ice days	2
4	Base + rearing flows	2
5	Base + summer terms	2
6	Base + fall/winter terms	2
7	Full - spawning flows	2
8	Full - fall flood	2
9	Full - ice days	2
10	Full - rearing flows	2
11	Full model (Base + spawning flows + fall flood + ice days + rearing flows)	2

Table A2. **Proportion of area clearcut in last 20 years in major catchments in the Nicola watershed.**

Catchment	Stream order	Catchment area (ha)	Clearcut area since 2000 (ha)	Percent clearcut since 2000
Nicola River	8	718379	119977	17%
Guichon Creek	7	119250	27372	23%
Coldwater River	6	91228	11533	13%
Quilchena Creek	6	77953	14426	19%
Spius Creek	6	76756	4503	6%
Meadow Creek	6	30943	6887	22%
Stumplake Creek	5	30473	4217	14%
Spahomin Creek	5	23604	3129	13%
Skuhun Creek	6	23201	6951	30%
Clapperton Creek	5	23189	8505	37%
Chapperon Creek	5	22255	5091	23%
Prospect Creek	5	22154	718	3%
Maka Creek	5	21607	1813	8%
Voght Creek	5	21046	4771	23%

Table A3. **Parameter estimates from top model 8b.**

	Mean	SE	SD	10%	90%
alpha	2.870441	0.010848	0.949462	1.825359	4.06135
beta	0.000165	0	3.90E-05	0.000116	0.000215
b1	0.029556	0.002253	0.203438	-0.22923	0.28449
b2	0.209371	0.001734	0.171638	-0.00457	0.427826
b4	-0.32564	0.002337	0.210528	-0.58604	-0.06327
b5	0.454623	0.001902	0.178372	0.228721	0.68003
tau	0.756471	0.001992	0.142339	0.595594	0.944297

Table A4. WAIC scores for model comparison

Model	WAIC	Estimated effective number of parameters	dWAIC	Akaike weight	SE (WAIC)	SE (dWIAC)	Cumulative weight
Model 8b	55.2	4.81	0	0.13	4.39	NA	0.13
Model 8	55.36	5.34	0.16	0.12	4.67	1.59	0.26
Model 7b	55.41	4.8	0.21	0.12	4.5	2.79	0.38
Model 11b	55.95	5.38	0.74	0.09	4.47	1.53	0.47
Model 5b	56.32	4	1.12	0.08	5.73	3.66	0.55
Model 11	56.61	5.77	1.4	0.07	4.36	1.5	0.61
Model 9b	56.71	4.5	1.51	0.06	5.95	4.18	0.67
Model 7	56.89	5.34	1.69	0.06	4.49	3.09	0.73
Model 5	57.07	4.52	1.87	0.05	5.63	3.78	0.78
Model 4b	57.81	3.34	2.6	0.04	4.41	3.41	0.82
Model 2b	58.11	3.35	2.91	0.03	5.93	5.19	0.85
Model 9	58.27	5.06	3.06	0.03	5.57	3.95	0.88
Model 6b	59.03	4.41	3.83	0.02	5.67	4.9	0.9
Model 4	59.22	3.86	4.01	0.02	4.27	3.78	0.92
Model 2	59.9	3.97	4.7	0.01	5.69	5.18	0.93
Model 0b	60.13	2.95	4.93	0.01	4.66	4.17	0.94
Model 1b	60.45	3.63	5.25	0.01	5.2	4.32	0.95
Model 10b	60.62	4.99	5.42	0.01	5.51	4.6	0.96
Model 3b	60.67	3.97	5.47	0.01	5.26	4.78	0.97
Model 6	60.84	4.91	5.64	0.01	5.37	4.85	0.98
Model 1	60.96	3.92	5.75	0.01	5.02	4.36	0.99
Model 0	61.5	3.48	6.3	0.01	4.52	4.37	0.99
Model 10	62.01	5.34	6.81	0	5.19	4.53	1
Model 3	62.18	4.56	6.98	0	5.22	4.97	1

Table A5. **Estimates from leave-one-out (LOO) cross-validation for Bayesian models using Pareto smoothed importance sampling**

Model	ELPD diff.	SE diff.	ELPD LOO	SE ELPD LOO	p LOO	SE p LOO	LOOIC	SE LOOIC
Model 8b	0	0	-28.03	2.33	5.24	1.01	56.05	4.67
Model 7b	-0.18	1.49	-28.21	2.37	5.3	0.93	56.42	4.75
Model 8	-0.21	0.81	-28.24	2.49	5.89	1.04	56.48	4.98
Model 11b	-0.5	0.79	-28.53	2.37	5.93	1.04	57.05	4.75
Model 5b	-0.51	1.87	-28.53	3.03	4.37	1.14	57.07	6.07
Model 9b	-0.75	2.12	-28.77	3.14	4.91	1.14	57.55	6.28
Model 11	-0.92	0.77	-28.95	2.34	6.41	0.99	57.9	4.67
Model 5	-0.97	1.93	-28.99	2.97	4.97	1.1	57.98	5.95
Model 7	-0.99	1.64	-29.02	2.38	5.92	0.96	58.04	4.76
Model 4b	-1.09	1.73	-29.12	2.27	3.55	0.64	58.24	4.55
Model 2b	-1.21	2.62	-29.24	3.07	3.53	0.8	58.47	6.14
Model 9	-1.7	2.03	-29.73	2.97	5.65	1.11	59.46	5.93
Model 6b	-1.8	2.5	-29.83	2.97	4.72	1.08	59.65	5.94
Model 4	-1.9	1.94	-29.92	2.21	4.18	0.66	59.85	4.41
Model 0b	-2.19	2.1	-30.21	2.41	3.1	0.6	60.43	4.81
Model 2	-2.2	2.63	-30.22	2.95	4.25	0.84	60.45	5.91
Model 1b	-2.48	2.16	-30.51	2.7	3.92	0.82	61.02	5.39
Model 3b	-2.59	2.42	-30.61	2.75	4.25	0.98	61.22	5.51
Model 10b	-2.76	2.33	-30.78	2.92	5.46	1.16	61.57	5.84
Model 1	-2.77	2.18	-30.79	2.59	4.24	0.75	61.59	5.19
Model 6	-2.84	2.5	-30.87	2.86	5.36	1.11	61.74	5.71
Model 0	-2.99	2.22	-31.02	2.34	3.74	0.66	62.03	4.68
Model 10	-3.54	2.28	-31.57	2.75	5.9	1.09	63.13	5.5
Model 3	-3.72	2.57	-31.74	2.79	5.22	1.14	63.48	5.58

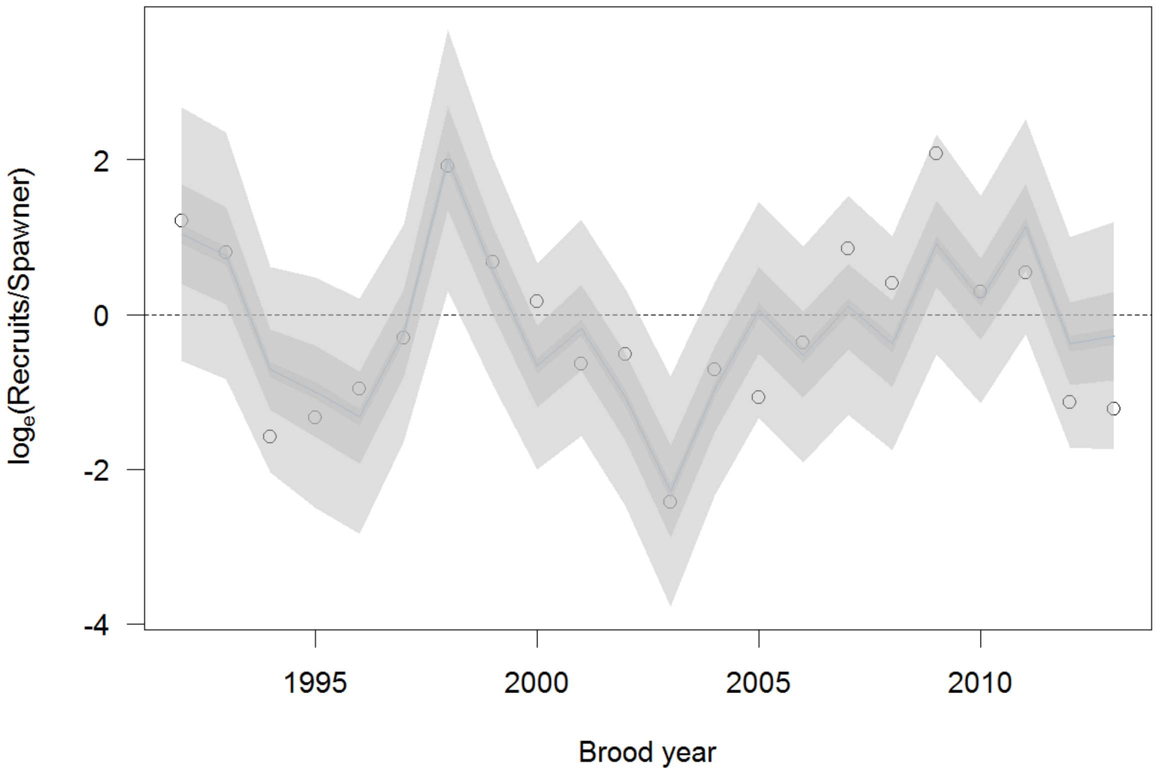

Figure A1. **Observed (points) and predicted (mean, 10%, 50%, and 90% credible intervals) of $\log_e$(Recruits/Spawner) for Nicola Chinook salmon, 1992-2013.**

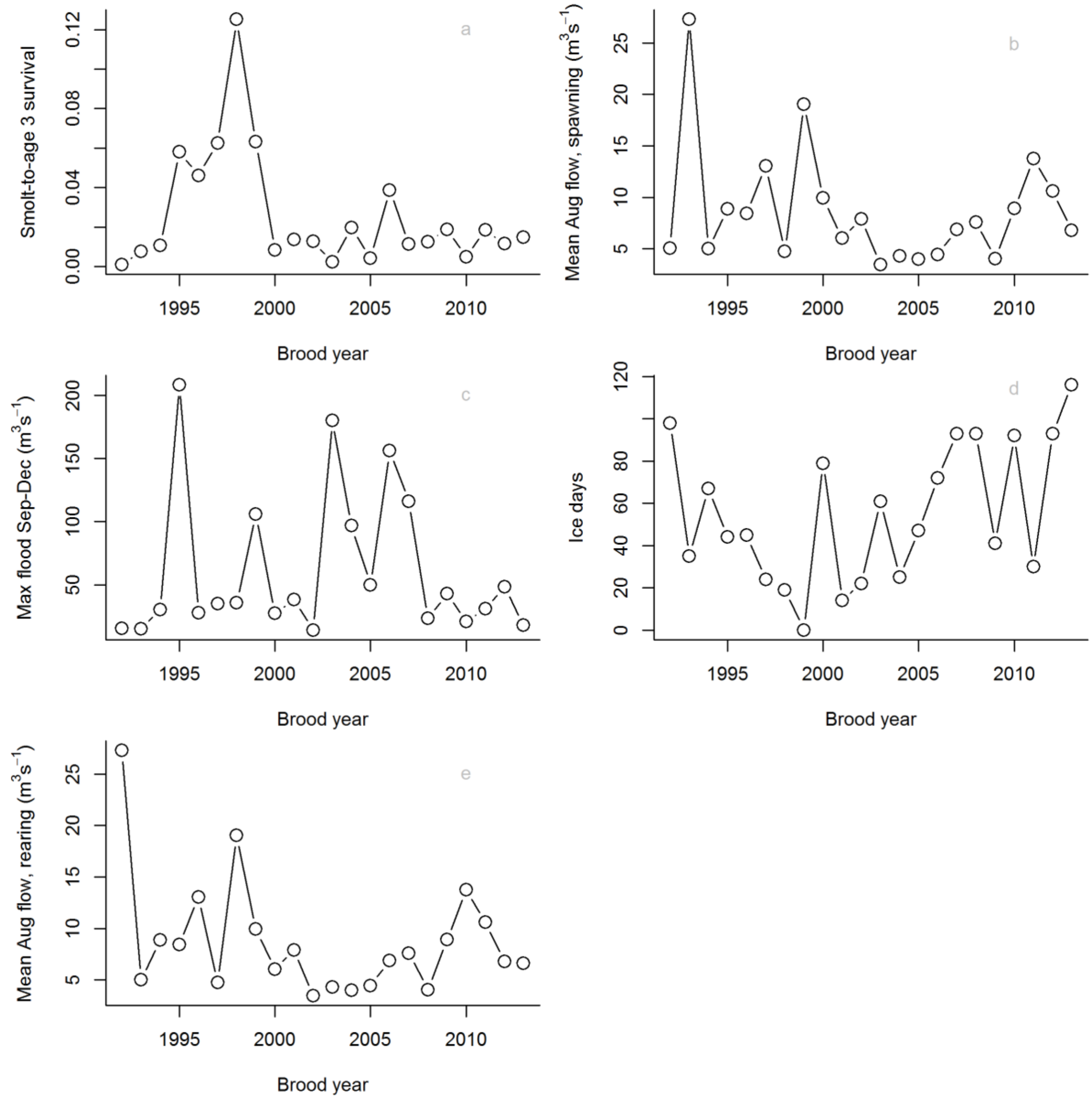

Figure A2. **Unscaled covariates for each of the 22 cohorts. Note that all variables were centered and standardized to mean=0 and SD=1 before analysis.**

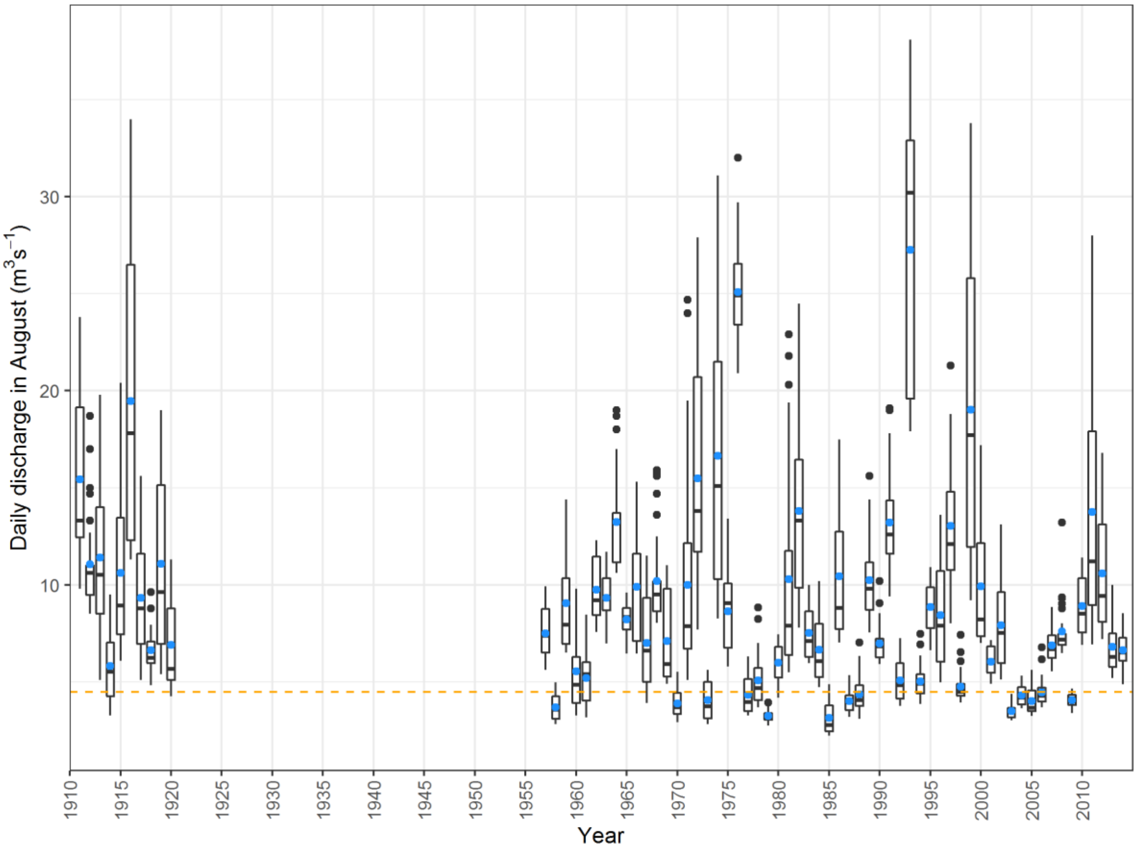

Figure A3. **Boxplots (black) and mean values (blue) of August daily discharge of the Nicola River, 1911-2014. The orange dashed line indicates 15% mean annual discharge (4.47 m3s-1).**

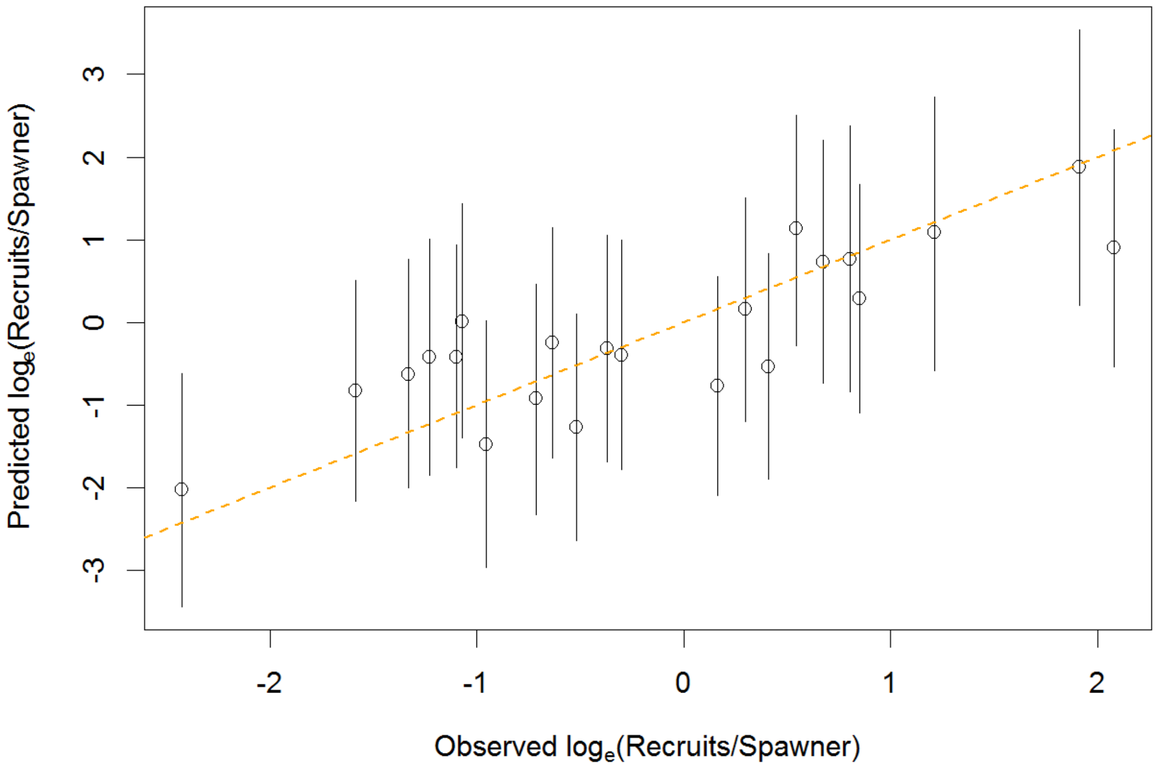

Figure A4. **Predicted (mean with 90% credible intervals) vs. observed $\log_e$(Recruits/Spawner), with 1:1 slope line in orange. Based on top model 8b.**

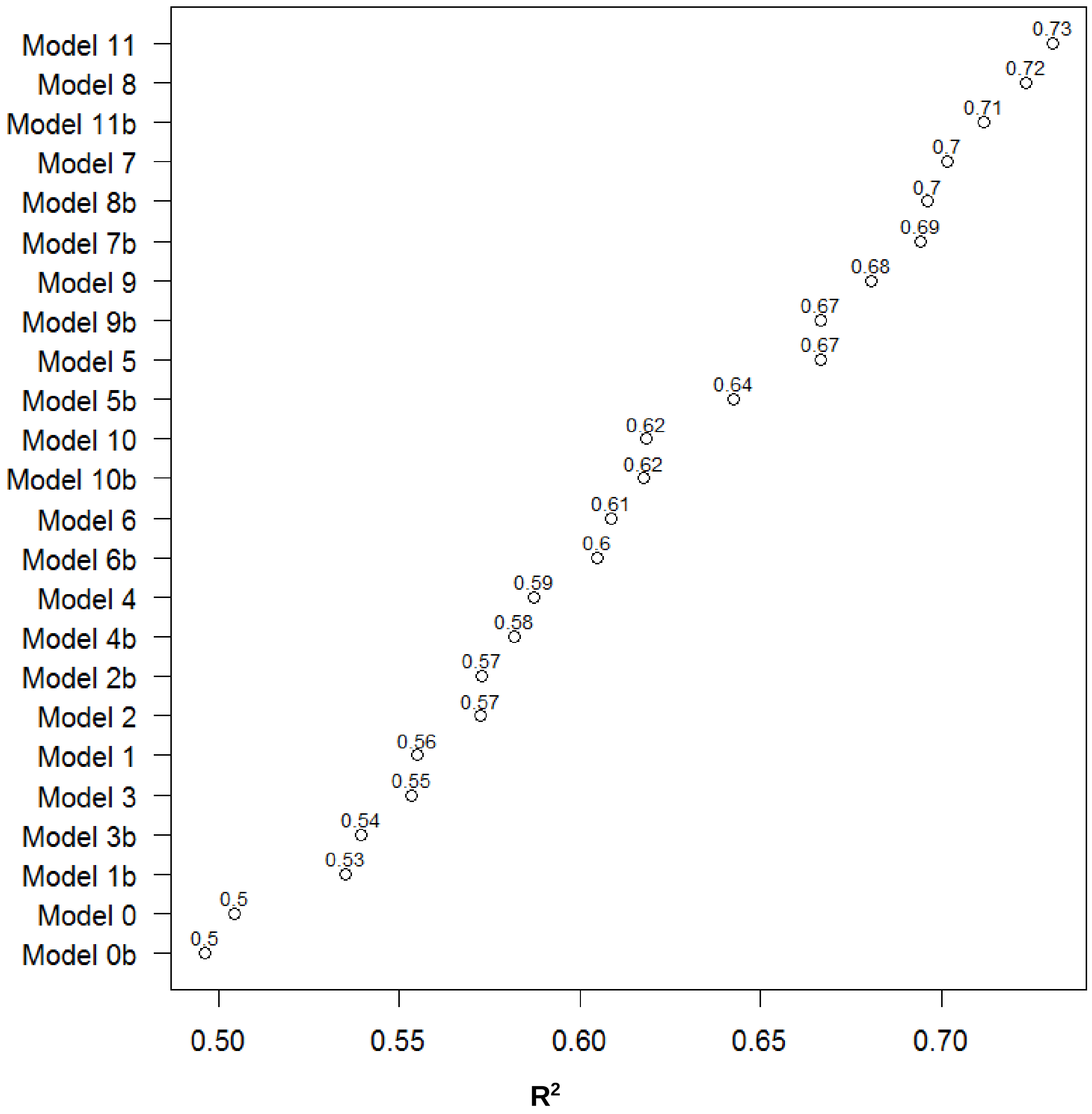

Figure A5. **R^2 values for the 24 candidate models based on predicted $\log_e$(Recruits/Spawner) ~ observed $\log_e$(Recruits/Spawner).**

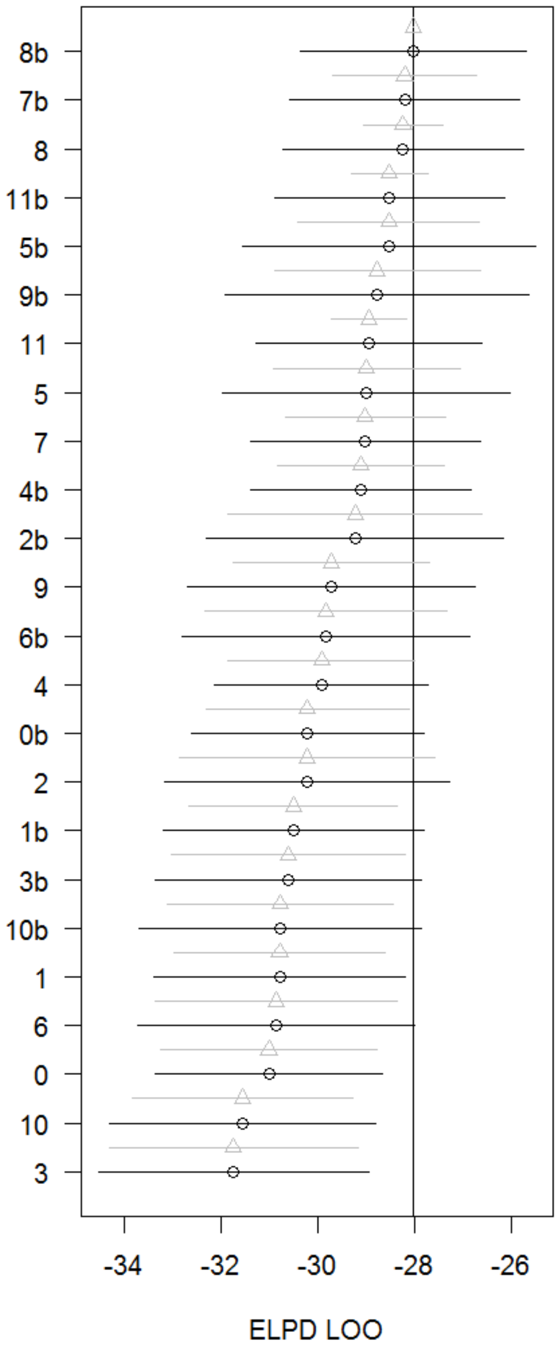

Figure A6. LOO comparison between models. The black circles and horizontal lines are the ELPD LOO and SE. The vertical black line is the ELPD LOO of the top model. The gray triangles and horizontal lines are the difference between each ELPD LOO and the ELPD LOO of the top model, with SE bars. Note that the difference SE for model 11 does not overlap 0.

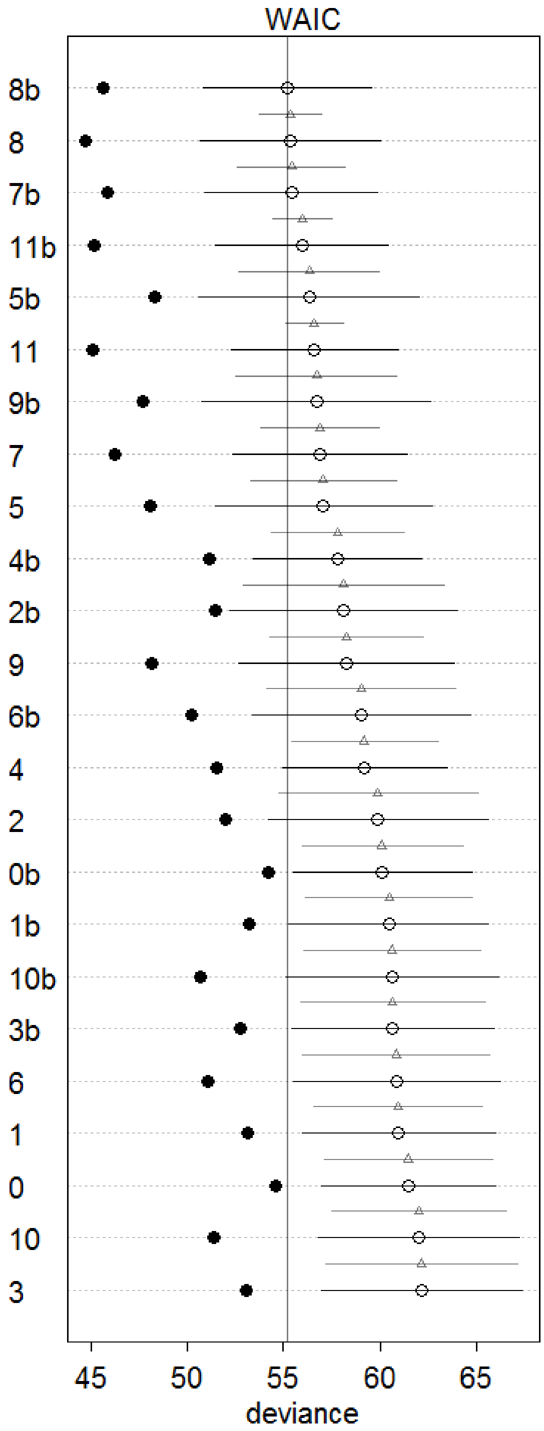

Figure A7. WAIC comparison between models. Black open circles and horizontal lines are the WAIC estimates for each model with SE. The vertical black line is the WAIC of the top model. The Gray triangles and horizontal lines are the difference between the WAIC of each model and the WAIC of the top model with SE. Closed black circles are the in-sample deviance of each model.

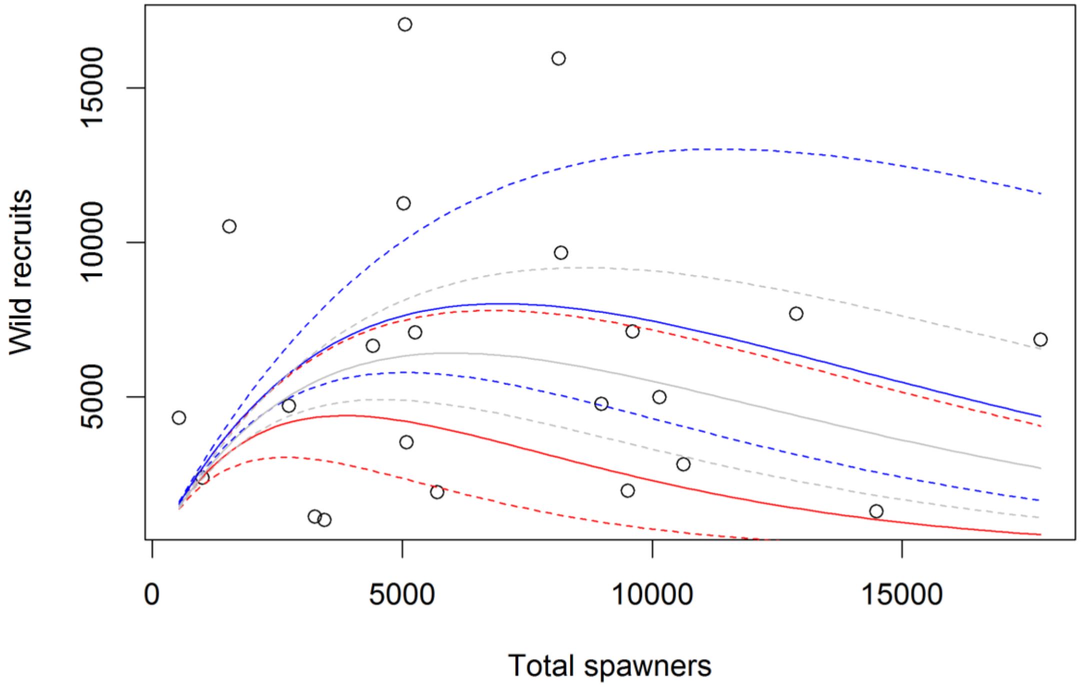

Figure A8. Solid lines show the difference between stock recruit relationship when using the mean estimated beta terms for wild spawners (blue) and hatchery spawners (red) from model 8 and total spawners (gray) from model 8b. Dotted lines use the 80% credible intervals for beta estimates.

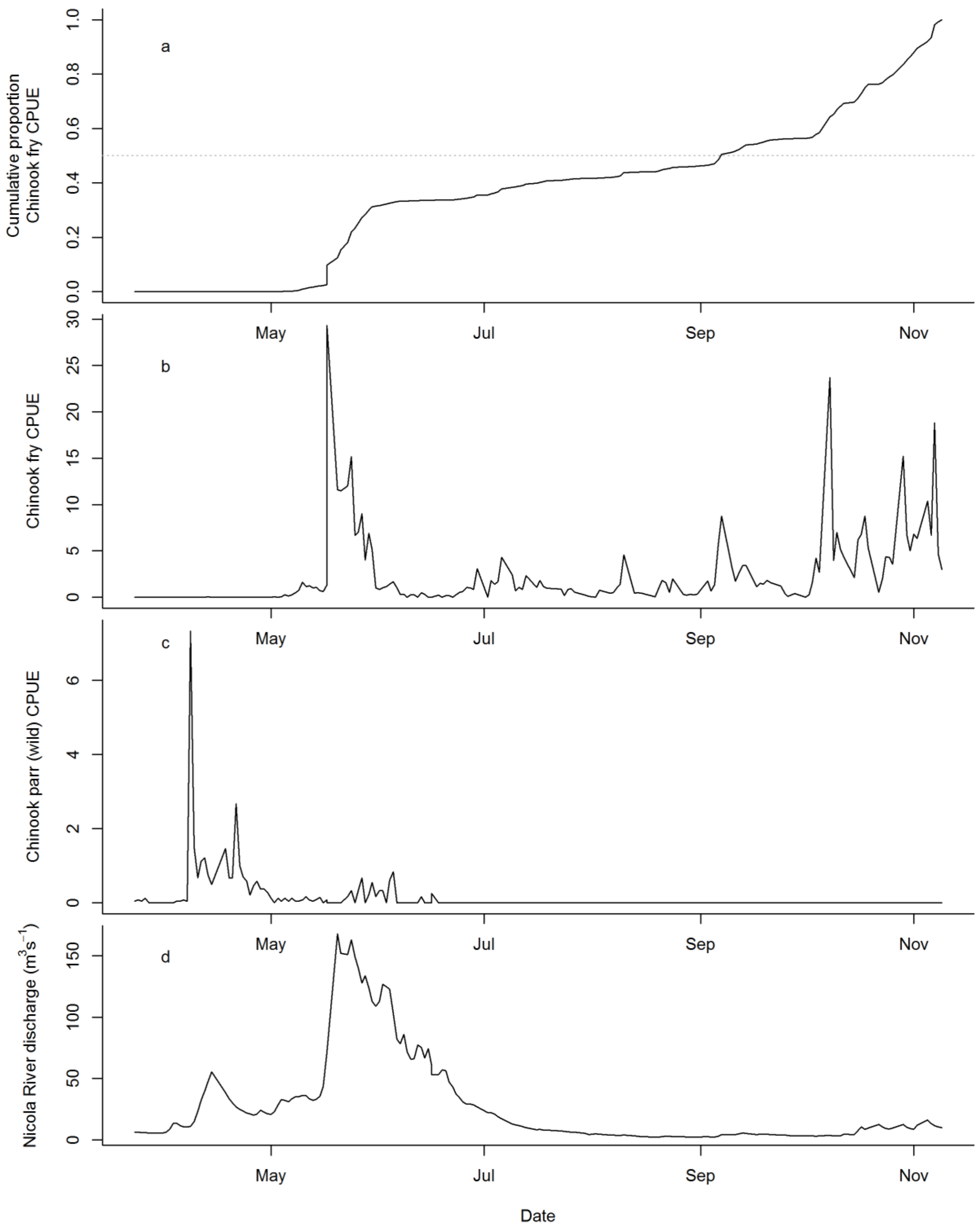

Figure A9. **Data from inclined plane trapping of downstream-migrating juvenile Chinook in 1985 (data from Lauzier and McPherson 1987). (a) Cumulative proportion of total catch per unit effort (number of fish per hours fished; CPUE) of Chinook fry; (b) Chinook fry CPUE; (c) wild Chinook parr CPUE; and (d) daily discharge in the Nicola River, Environment Canada hydrometric station 08LG006 (Nicola River near Spences Bridge).**

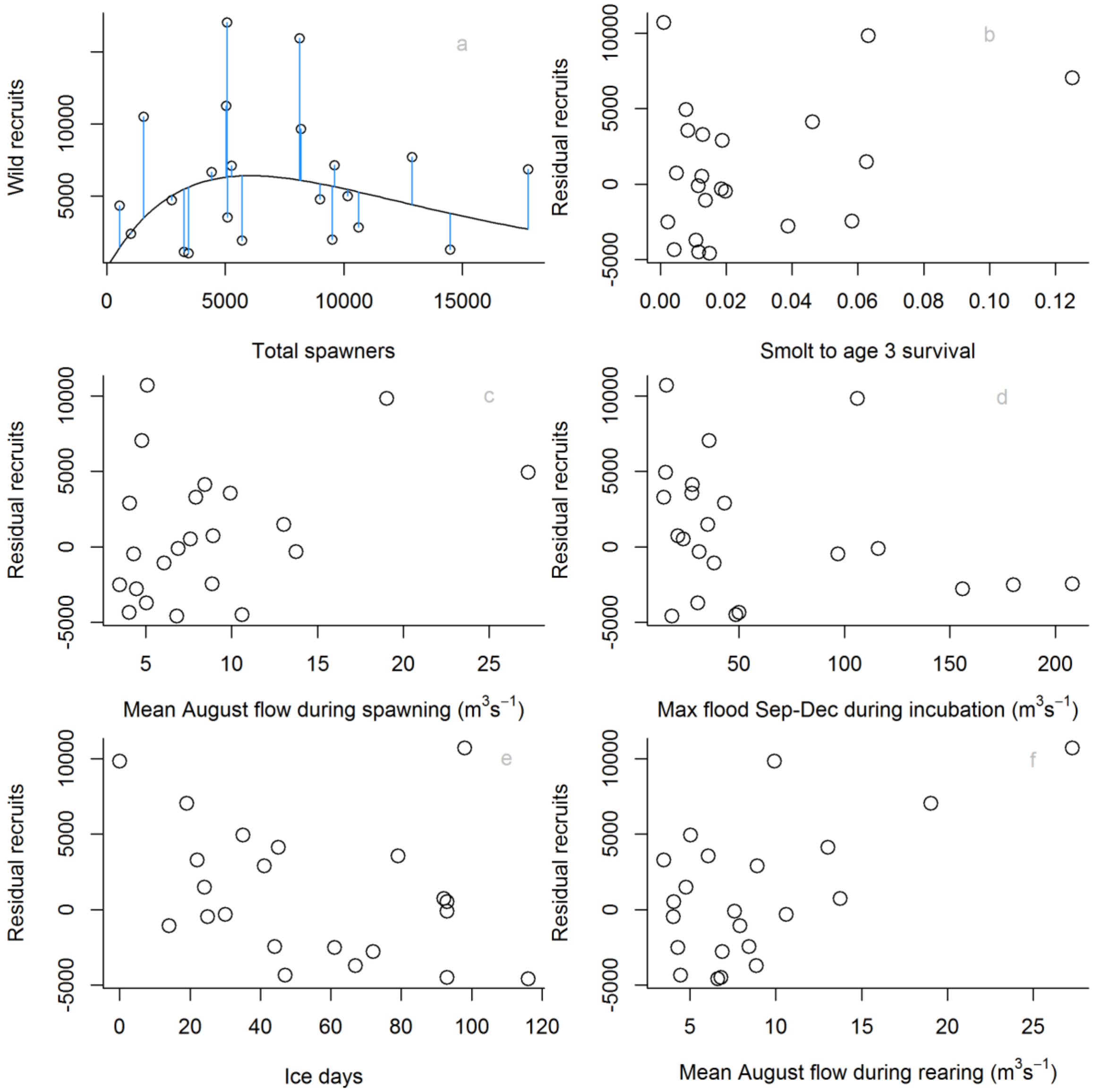

Figure A10. **(a) Observed wild recruits plotted against total spawners (points). The black line is the Ricker curve based on alpha and beta values only (from the top model 8b), and the blue lines are the residuals. (b-f) Residuals of observed total recruits and predictions from mean Ricker curve in panel (a), plotted as a function of the five environmental covariates tested: (b) smolt-to-age 3 survival; (c) mean August flow during spawning; (d) maximum fall flood during incubation; (e) ice days; and (f) mean August flow during rearing.**

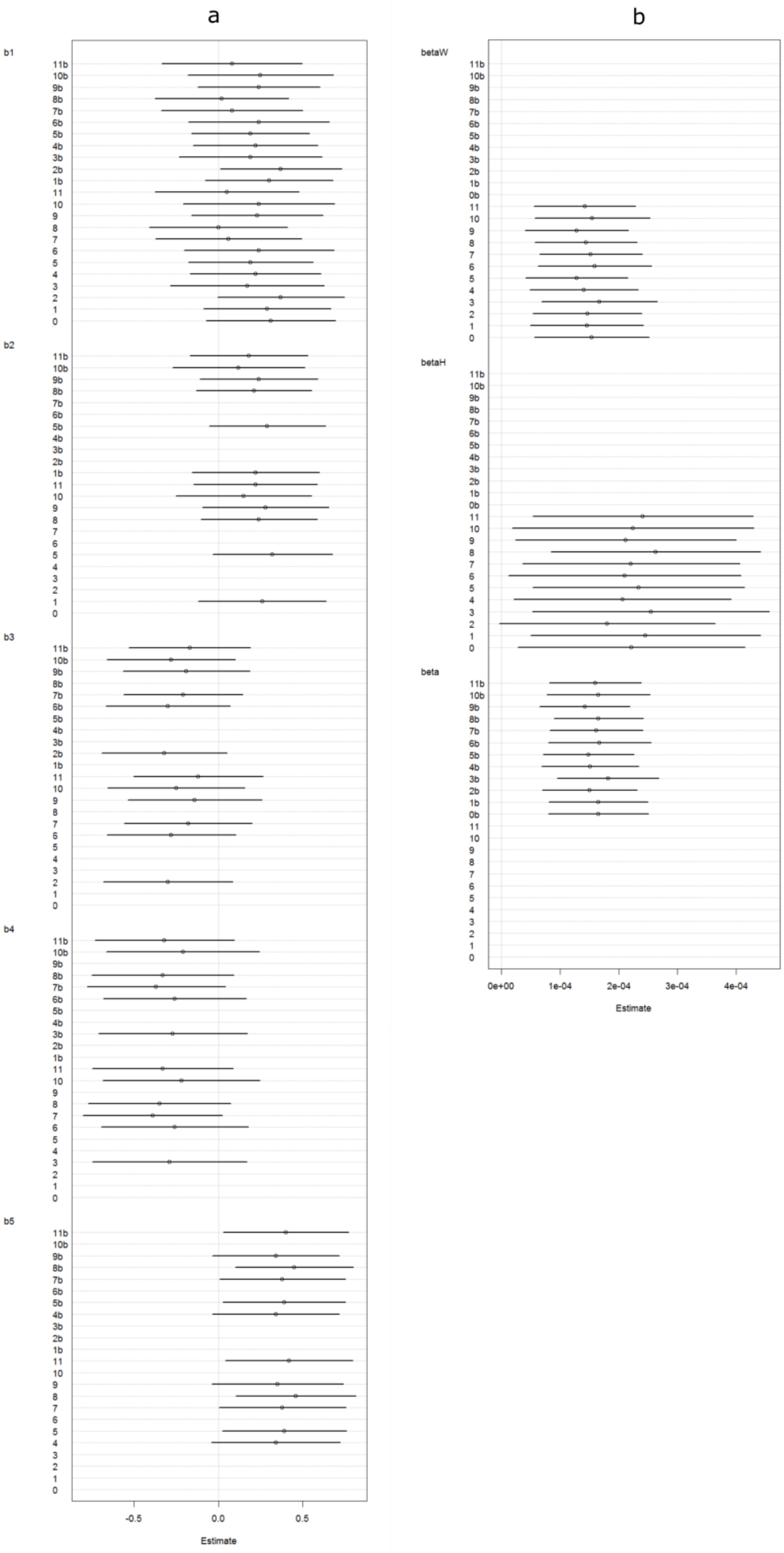

Figure A11. Parameter estimates under the 24 models for (a) environmental covariates and (b) beta terms.

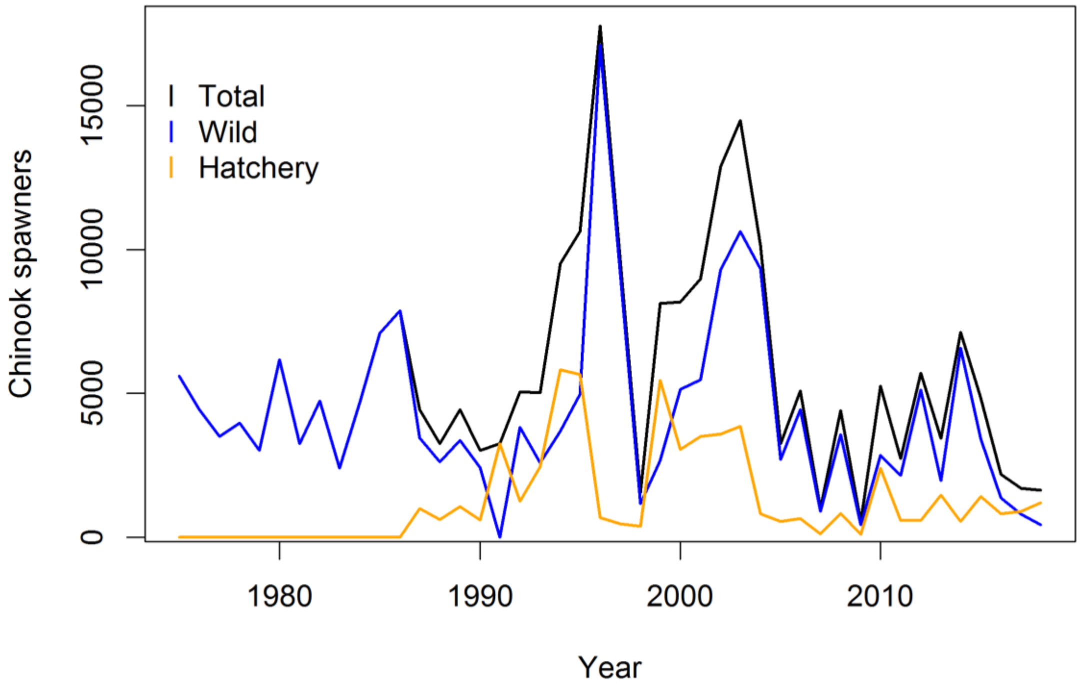

Figure A12. Time series of Chinook total, wild, and hatchery spawners in the Nicola River. Wild and hatchery spawner abundances account for unmarked hatchery as explained in Appendix A.

Appendix B.

Supplemental Material for Chapter 3

Table B1. Watershed characteristics of the 50 stream temperature monitoring sites.

Site ID	Site name	Catchment area (m²)	Mean catchment elevation (m)	Lake index	Riparian tree cover
200	Clapperton Creek	230277918	1361	157	0.000
201	Nicola River upstream of Clapperton Creek	2933482568	1235	34328	0.004
202	Quilchena Creek	771494216	1250	622	0.124
203	Nicola River above Nicola Lake 1	1421302695	1300	2246	0.769
204	Nicola River above Nicola Lake 2	1403240824	1304	2301	0.488
205	Nicola River above Douglas Lake 1	950778425	1332	1160	0.642
207	Nicola River above Douglas Lake 3	947738792	1334	1166	0.720
208	Coldwater River above Patchett Road	617339810	1322	182	0.477
209	Coldwater River under Gillis Road	357120005	1404	69	0.478
210	Juliet Creek	69041409	1557	6	0.493
211	Coldwater River above Juliet Creek	130838439	1452	16	1.000
212	Coldwater River below Juliet Creek	200164186	1488	21	1.000
213	Coldwater River at Gravel Pit	47816104	1440	14	0.520
214	Coldwater River Headwaters	47400859	1442	15	1.000
215	Nicola River below Skeikut Creek	7011327271	1259	2185	0.000
216	Nicola River below Kloklwuck Creek	7067002867	1258	2052	0.000
217	Nicola River near Spences Bridge	7101386082	1256	1945	0.000
218	Skuhun Creek 1	234150265	1385	88	1.000
219	Skuhun Creek 2	173672721	1453	133	1.000
220	Skuhost Creek	54976892	1531	8	1.000
221	Nicola River above Manning Creek	6560153102	1260	2528	0.938
222	Nicola River at Shackelly Creek	6441932323	1262	2717	0.420
223	Nuaitch Creek	82316288	1321	10	1.000
225	Prospect Creek	138314872	1579	37	1.000
227	Nicola River above Hatchery	5535803706	1250	3085	0.283

Site ID	Site name	Catchment area (m^2)	Mean catchment elevation (m)	Lake index	Riparian tree cover
228	Nicola River at Sunshine Valley Road	5507780754	1252	3345	0.240
229	Guichon Creek at Nicola River	1150775548	1346	473	0.000
230	Spius Creek at Maka Creek	386908564	1387	94	0.987
231	Skuhun Creek 3	69222210	1508	145	1.000
232	Guichon Creek above Mamit Lake	684580223	1387	533	0.000
233	Quilchena Creek 2	771487201	1250	624	0.196
234	Nicola Lake at Dam	2933397526	1235	65431	0.000
235	Clapperton Creek 2	183437893	1394	208	1.000
237	Nicola River at Norgaards	4220583866	1234	4078	0.000
238	Gillis Creek 1	11829628	1312	85	0.514
239	Gillis Creek 2	11826348	1312	86	0.481
240	Voght Creek 1	209328863	1238	132	0.911
241	Voght Creek 2	209392917	1238	130	0.990
242	Maka Creek 1	214623884	1365	43	0.167
244	Spius Creek above Maka Creek	170926497	1417	51	0.987
245	Spius Creek at Hatchery Intake	764901113	1368	101	0.411
246	Prospect Creek 2	138303569	1579	37	1.000
247	Spaxomin Creek near Douglas Lake	239230171	1406	751	0.074
248	Nicola River at outlet of Douglas Lake	1273217180	1328	150182	0.000
250	Nicola River above Chaperon Creek	530004642	1431	456	0.732
251	Nicola River below Chaperon Creek	773129294	1378	1521	0.402
252	Beaks Creek	82863881	1439	12	1.000
253	Nicola River above Beaks Creek	330188099	1494	463	1.000
300	Nicola River at Guichon Creek confluence	5446299561	1255	3701	0.508
301	Nicola River at Petit Creek	6330929863	1263	2905	0.854