

RESEARCH ARTICLE

Low summer river flows associated with low productivity of Chinook salmon in a watershed with shifting hydrology

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Abstract

1. Climate change and human activities are transforming river flows globally, with potentially large consequences for freshwater life. To help inform watershed and flow management, there is a need for empirical studies linking flows and fish productivity.
2. We tested the effects of river conditions and other factors on 22 years of Chinook salmon productivity in a watershed in British Columbia, Canada.
3. Freshwater conditions during adult salmon migration and spawning, as well as during juvenile rearing, explained a large amount of variation in productivity.
4. August river flows while salmon fry reared had the strongest effect on productivity—our model predicted that cohorts that experience 50% below average flow in the August of rearing have 21% lower productivity.
5. These contemporary relationships are set within long-term changes in climate, land use, and hydrology. Over the last century, average August river discharge decreased by 26%, air temperatures warmed, and water withdrawals increased. Seventeen percent of the watershed was logged in the last 20 years.
6. Our results suggest that, in order to remain stable, this Chinook salmon population being assessed for legal protection requires substantially higher August flow than previously recommended. Changing flow regimes—driven by watershed impacts and climate change—can threaten imperilled fish populations.

KEYWORDS

Chinook salmon, climate change, cumulative effects, drought, environmental flows, flow regime, hydrology

1 | INTRODUCTION

Coincident changes in climate, land cover and water use are altering the natural flow regimes of the world's rivers (Palmer & Ruhí, 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; Grondahl et al., 2019; Perry & Jones, 2017). As a result, some systems are experiencing

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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 for 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). Fish-flow relationships are a key foundation of effective flow regulation (Rosenfeld, 2017; Rosenfeld & Ptolemy, 2017), but instream flow regulations 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 to inform flow management (Chen & Olden, 2017; Sabo et al., 2017).

Empirical studies of fishes and flows are especially important for species of cultural and economic 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 *Oncorhynchus tshawytscha* (Sturrock et al., 2020) and coho salmon *Oncorhynchus 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 and other variables influenced 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. 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 demographics. We discovered that low summer flows, which have decreased over the last century, are correlated with low productivity of this imperilled population and quantified empirical fish-flow relationships that can inform the management of cumulative effects on hydrology.

2 | MATERIALS AND METHODS

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, Canada. The watershed is a part of the traditional, ancestral and unceded territories of the Nlaka'pamux and Syilx Nations. It drains 7184 km² and supports imperilled stream-rearing Chinook salmon, coho salmon and steelhead (*Oncorhynchus 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 on the Status of Endangered Wildlife in Canada is currently assessing whether to recommend Nicola Chinook salmon for listing under the *Species at Risk* Act. Recruitment has been below replacement for more than half of the cohorts since 1992 (Figure 1). Chinook salmon 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).

This study focuses on the early summer run Chinook salmon of the Nicola, one of several populations in the watershed. The early summer run leaves the ocean to enter the Fraser River from May to July and spawns in the Nicola River in September, mainly in the mainstem Nicola River and 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 British Columbia 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 m³s⁻¹, while summer base flow can be less than 3 m³s⁻¹. Natural mean annual discharge (MAD; long-term mean annual discharge plus estimated water withdrawal) is 29.8 m³s⁻¹ (unpublished data, Ptolemy). Floods can occur in the fall, winter and early spring. Flows usually decrease and reach base flows in

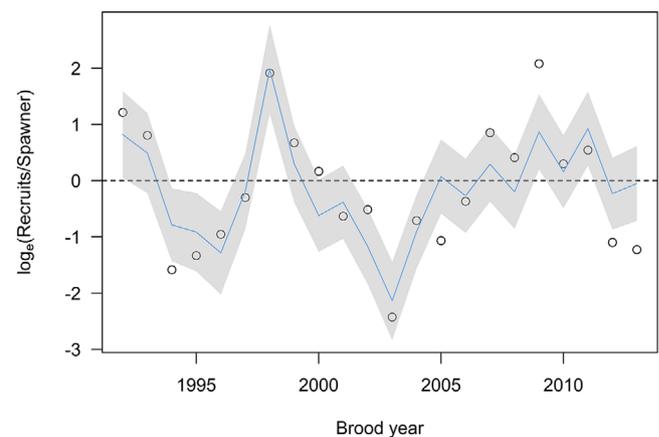


FIGURE 1 Observed (points) and predicted mean (blue line) and 90% credible intervals (grey area) of $\log_e(\text{Recruits/Spawner})$ for Nicola Chinook salmon, 1992–2013. The predictions are based on the model averaged posteriors based on stacking. The horizontal line shows the replacement level of one recruit per spawner

August, and remain low into September. The river was assessed as typically having no surplus flows in August to September unless supported by water storage (Kosakoski & Hamilton, 1982).

2.2 | Data

2.2.1 | Escapement and spawners

We used escapement data from the cohorts spawned in 1992–2013 (22 cohorts), collected by Fisheries and Oceans Canada (DFO). 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.

2.2.2 | 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 Supporting Information for details.

2.2.3 | 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 Supporting Information; 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 (Supporting Information). We summed recruits from each brood year to estimate the number of wild recruits for each cohort.

2.2.4 | Covariates

We examined the influence of five covariates on the productivity of each cohort of Chinook salmon (Table 1, Figure S1). 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 et al., 2019; Rodenhuis et al., 2007). We also did a preliminary analysis of river flows to determine the amount of correlation between average monthly flows. If two variables were highly correlated, we avoided choosing one.

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 also examined metrics of flow regime as potential predictors. We used hydrometric data from Nicola River near Spences Bridge (Water Survey of Canada station 08LG006). For each Chinook salmon cohort, we calculated mean August flow when the spawners were migrating upstream and waiting to spawn in the 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 salmon were rearing (brood year + 1). We centred and standardized these five covariates to mean = 0 and SD = 1 to aid the comparison of relative effect sizes. We note that August flows during spawning and rearing are the same value offset by 1 year. The correlation coefficient of these two variables is -0.14 , so we do not suspect any issues from multi-collinearity.

2.3 | Stock recruit model

We used a loglinear 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 1). The coefficients for the five environmental variables were b_1, b_2, b_3, b_4 , and b_5 , respectively. We used the loglinear form of the Ricker equation because it has a normal distribution of residuals (Equation 2).

$$R = S\alpha e^{-\beta S + b_1 \text{smoltsurv} + b_2 \text{spawnflow} + b_3 \text{flood} + b_4 \text{ice} + b_5 \text{rearflow}}, \quad (1)$$

$$\log\left(\frac{R}{S}\right) = \log(\alpha) - \beta S + b_1 \text{smoltsurv} + b_2 \text{spawnflow} + b_3 \text{flood} + b_4 \text{ice} + b_5 \text{rearflow}. \quad (2)$$

The full Bayesian model was defined as follows (Equations 3–9), with similar priors to Connors et al. (2019).

$$\log\left(\frac{R}{S}\right) \sim \text{Normal}(\mu, \tau), \quad (3)$$

TABLE 1 Environmental variables used to explain variation in productivity. Mean and standard deviations are for the time series associated with Nicola Chinook salmon cohorts that spawned in 1992–2013

Variable		Mean	SD
smoltsurv	Smolt-to-age 3 survival of hatchery smolts	0.026	0.030
spawnflow	Mean August river flow during brood year, when parents of cohort migrated up-river to spawn (m^3s^{-1})	8.6	5.6
flood	Discharge of maximum fall flood during incubation in brood year (m^3s^{-1})	60.8	57.2
ice	Number of days of river ice cover in winter of incubation	55	32.9
rearflow	Mean August river flow during rearing year (brood year + 1; m^3s^{-1})	8.7	5.6

$$\mu = \log(\alpha) - \beta S + b_1 \text{smoltsurv} + b_2 \text{spawnflow} + b_3 \text{flood} + b_4 \text{ice} + b_5 \text{rearflow}, \quad (4)$$

$$\log(\alpha) \sim \text{Uniform}(0, 3), \quad (5)$$

$$\beta \sim \text{Uniform}(0, 10), \quad (6)$$

$$b_1, b_2, b_3, b_4, b_5 \sim \text{Normal}(0, 1), \quad (7)$$

$$\tau \sim \text{Gamma}(0.01, 0.01), \quad (8)$$

$$\mu = \log(\alpha) - \beta_W S_W - \beta_H S_H + b_1 \text{smoltsurv} + b_2 \text{spawnflow} + b_3 \text{flood} + b_4 \text{ice} + b_5 \text{rearflow}. \quad (9)$$

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 9, with the same priors for β_W and β_H as for β . See Supporting Information for details on model fitting.

2.4 | Model selection

We wanted to find out whether there were relationships between river conditions and the productivity of Chinook salmon, while accounting for density dependence and variable ocean survival. We took several steps to achieve this. To compare the effects of different covariates and separate β terms, we compared 24 models (Table 2). We then compared these models using several methods that rank models based on their ability to explain the data while penalizing models with more variables: the widely applicable information criterion (WAIC) and leave-one-out cross-validation (LOO) (Vehtari et al., 2017). We used the rethinking package (McElreath, 2016) for WAIC and the loo package (Vehtari et al., 2019) for LOO. The top set of models (8, 7b, 8b, 11b) were very close in both WAIC and LOO scores, and depending on the random draws of initial values and the MCMC sampling results, several different models were ranked as the top model, and the estimated differences between the next-best models were not significantly greater than 0 (Table S1). To account for multiple models being ranked similarly, we used model stacking, which is a form of model averaging for

Bayesian models (Yao et al., 2018). Each of the 24 candidate models were assigned model weights based on LOO using the loo package (Vehtari et al., 2019). Model weights were consistent with different random initial values. Then the posterior distributions from each model were multiplied by these model weights and summed across all models to get a weighted average posterior distribution. These stacked posterior distributions of model variables were used for the results. WAIC comparisons are not reported because they were similar to those from LOO, and because using LOO is more aligned with the model stacking approach. We tested for autocorrelation and partial autocorrelation of residuals, and compared predictions to observations (Figure S2). We also looked at the stability of posterior estimates of effect terms across models (Figure S3) and R^2 values.

2.5 | 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 Supporting Information for data sources. Water allocations represent the maximum possible water allocation and should be viewed as a metric of demand on water—data on actual withdrawals were not available. We note that precipitation and air temperature data were from one station located in Merritt, the geographic centre of the catchment. Thus, it should serve as an indicator of conditions in the watershed.

3 | RESULTS

Freshwater conditions, ocean survival, and density dependence were the main drivers of population dynamics for Chinook salmon. Parameter estimates (before model averaging) were mainly stable when comparing between models, with the exception of the effect of smolt-to-age 3 survival (b_1 ; Figure S3). After using stacking to model-average the posterior estimates of parameters based on model weights (Table 2), mean flow in August during rearing had the strongest relationship with productivity, followed by ice days, smolt-to-age 3 survival, fall flooding and August flow during spawning (Figure 2, Table S2). All of these posterior estimates had 90% credible intervals (CI) that

TABLE 2 The 24 candidate models used in model comparison. Points indicate which variables were included in each model. Model weight is from Bayesian model weighting based on stacking and leave-one-out cross-validation. Models with weights > 0.05 are in bold

Model name	Model weight	Environmental parameters included					β parameters included		
		smoltsurv	spawnflow	flood	ice	rearflow	β (total spawners)	β_W	β_H
0b	0.0000	●					●		
1b	0.0000	●	●				●		
2b	0.1976	●		●			●		
3b	0.0000	●				●	●		
4b	0.0000	●				●	●		
5b	0.2314	●	●			●	●		
6b	0.0562	●		●	●		●		
7b	0.2694	●		●	●	●	●		
8b	0.0000	●	●		●	●	●		
9b	0.0000	●	●	●		●	●		
10b	0.0000	●	●	●	●		●		
11b	0.0000	●	●	●	●	●	●		
0	0.0000	●						●	●
1	0.0000	●	●					●	●
2	0.0000	●		●				●	●
3	0.0000	●			●			●	●
4	0.0000	●				●		●	●
5	0.0587	●	●			●		●	●
6	0.0000	●		●	●			●	●
7	0.0000	●		●	●	●		●	●
8	0.1865	●	●		●	●		●	●
9	0.0000	●	●	●		●		●	●
10	0.0000	●	●	●	●			●	●
11	0.0000	●	●	●	●	●		●	●

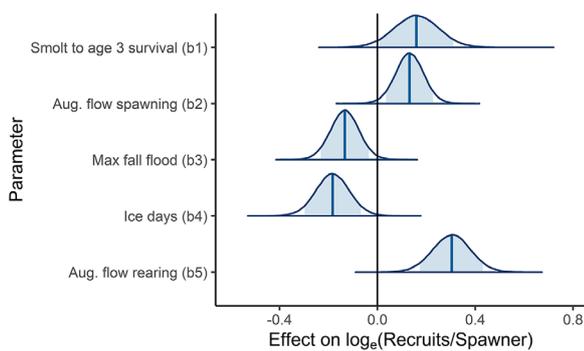


FIGURE 2 Posterior estimates (with means and 90% credible intervals in shaded region) of effect terms for five environmental variables, from the model averaged posteriors based on stacking. Note that all environmental variables were standardized (mean = 0, SD = 1)

did not overlap with 0 (Figure 2). From now on, discussion of parameter estimates and predictions refers to the stacked model averages.

Of the variables examined, mean August flows during Chinook salmon rearing had the strongest relationship with productivity;

cohorts with greater flows in their rearing summers had higher productivity (Figure 3). Our model predicts Chinook cohorts whose juveniles rear during summers with 50% below average flow have 21% (CI 13%–29%) lower productivity, where the CI uses the lower and upper bounds of the 90% CI for the effect of August rearing flows from the stacked model average (see Supporting Information for details on model predictions). Comparing across candidate models, the posterior estimates for this parameter had the most consistently high magnitudes (Figure S3a). In addition, all years with August rearing flows > 10.6 m³s⁻¹ had positive residuals from the mean Ricker curve (observed minus predicted recruits; Figure 4f). August flows when spawners were returning were also important. Chinook that spawned during summers with 50% below average flow have 10% (CI 3%–16%) 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 29% (CI 15%–40%) lower productivity.

River conditions during fall and winter also explained variation in salmon productivity. Cohorts that incubated in winters with more ice days tended to have lower recruitment; for every 10 additional days of

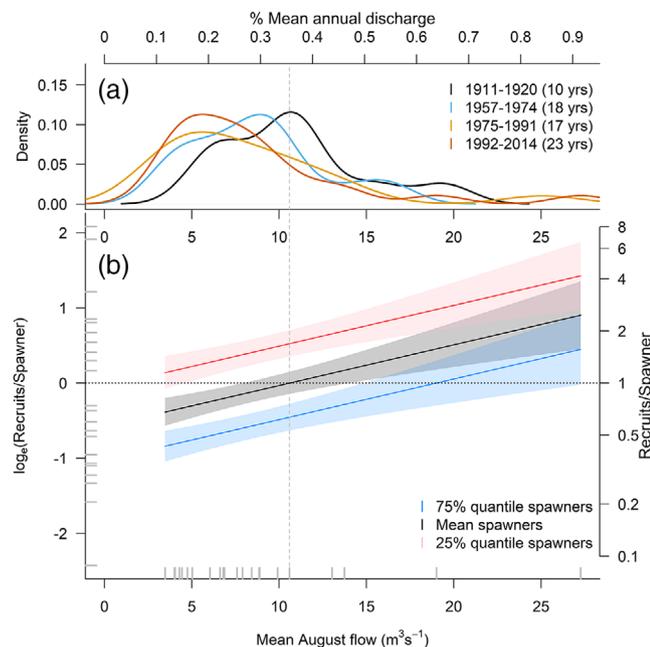


FIGURE 3 (a) Empirical cumulative density function of mean August flows in four periods. (b) Effect of mean August flow during rearing on recruitment of Nicola River Chinook salmon. The three shaded regions represent 90% credible intervals of model predictions based on three spawner abundances (mean, 25th percentile and 75th percentile). The dotted horizontal line shows the replacement level of one recruit per spawner at mean spawner abundance. The vertical dashed grey line indicates the model-predicted value of $10.6 \text{ m}^3\text{s}^{-1}$ flow during the rearing summer that results in replacement (recruits/spawner = 1). Rugplots (grey ticks along inside of x and y axes) show distribution of observations. Natural mean annual discharge (discharge plus estimated withdrawal) is $29.8 \text{ m}^3\text{s}^{-1}$ (unpublished data, Ptolemy)

river ice, recruits were predicted to decrease by 5% (CI 2%–9%). There was also evidence that cohorts that experienced large fall floods during incubation had lower productivity (Figure 4d), with an effect size of nearly equal magnitude to August spawning flows (Figure 2, Table S2).

Survival during downstream migration and early marine growth also accounted for some variation in productivity. If a cohort's smolt-to-age 3 survival was 1 SD above average—5.5% compared to 2.6%—productivity increased by 17% (CI 1%–36%). Among models, this relationship was the most variable of the covariates tested, and its magnitude decreased as more variables were included (Figure S3a). The model averaged posterior also had the highest uncertainty (SD) among covariates tested (Table S2).

There was limited evidence that density dependence was stronger for hatchery spawners compared to wild spawners. Comparing estimates across all models, the mean of β_H posteriors were consistently higher than for β_W (Figure S3b). However, the CI overlapped and the 95% CI for β_W was contained by the 95% CI for β_H .

The positive relationships between summer flows and Chinook salmon productivity reveals challenges for water management (Figure 3). A transect-based modelling approach recommended an environmental flow for the Nicola River mainstem (from Spius Creek down to

confluence with the Thompson River) of $5.66 \text{ m}^3\text{s}^{-1}$ year-round, and concluded there was no surplus flows for withdrawal in August and September in the 1980s (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 $5.66 \text{ m}^3\text{s}^{-1}$ during both spawning and rearing, every 100 spawners would only produce 72 (CI 64–82) recruits, and the population would decline even in the absence of any harvest.

The flow regimes of the Nicola River that explain contemporary variation in Chinook salmon productivity (1992–2013) have changed substantially over the last century. Average August flow decreased by 26% when comparing flows from 100 years ago with the past two decades (Figure 3a). From 1911 to 1920, average August discharge never fell below 15% MAD of $4.47 \text{ m}^3\text{s}^{-1}$, whereas from 1992–2014, it fell below this value five times (Figure 5). More broadly, summer river discharge (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 S4). Fall flows during incubation are also increasing (Figure S4). Such changes occurred progressively over the last century.

The setting for these shifting flow regimes is a changing watershed and climate system. Climate, land use and water withdrawal in the Nicola watershed have changed substantially over the past century (Figure 6). Winters are warming, from 1920–1980, daily average air temperatures in January never exceeded 0°C , but rose above freezing 5 years 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 S3).

4 | DISCUSSION

We found that the flow regime of an interior watershed, likely altered by the cumulative effects of climate change, land use and water withdrawals, is strongly associated with the productivity of an imperilled fish population. Analysis of 22 years of Chinook salmon life cycle data from 1992 to 2013 revealed that low summer flows have a strong link with lower 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 $10.6 \text{ m}^3\text{s}^{-1}$ (or 36% MAD) during the rearing summer (Figure 3). These contemporary challenges posed by low summer flows on Chinook salmon are set within long-term patterns of watershed and climate change. Low summer flows are now 26% lower than they were 100 years ago and air temperatures, rainfall, logging pressure and water demand have all increased over the last 100 years. Although there are no equivalent Chinook productivity data for earlier than 1992 when summer flows

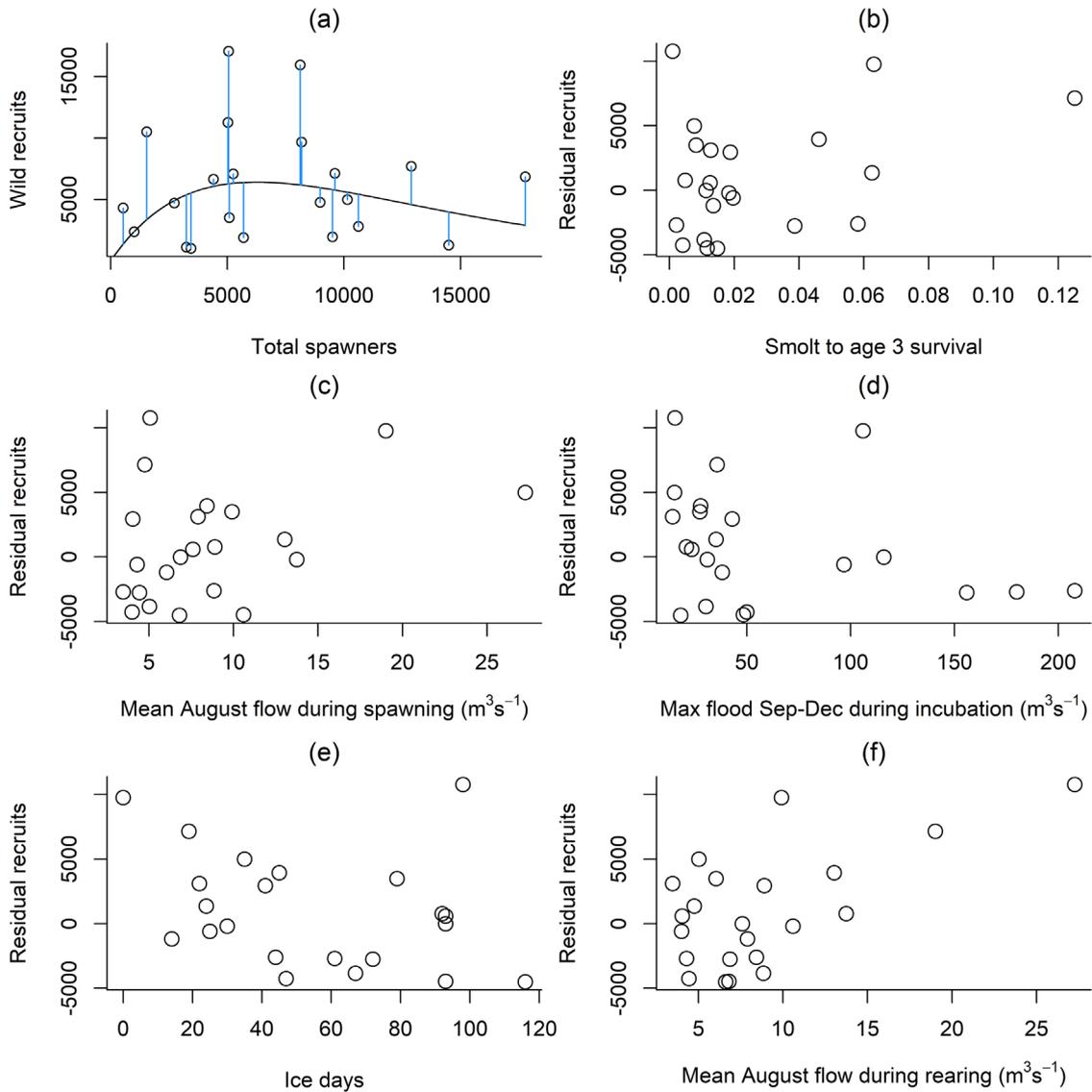


FIGURE 4 (a) Observed wild recruits plotted against total spawners (points). The black line is the Ricker curve based on α and β values, and the blue lines are the residuals. (b–f) Residuals of observed total recruits and predictions from mean Ricker curve in panel a, plotted as a function of the five 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

were higher, these findings provide empirical evidence that lower summer flows can decrease salmon productivity.

Summer low flows have been shown to influence the productivity and growth of 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). 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). Summer rearing flows in the Nicola will directly impact the juveniles that remain in

the Nicola system, and may indirectly affect those that disperse downstream and rear in nonnatal habitats (Lauzier & McPherson, 1987; Murray & Rosenau, 1989). We also found that low flows during adult migration appeared to impair productivity, an effect that could be compounded by warm stream temperatures. 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 present (Figure S3b). Cohorts that experienced more ice cover also appeared to have lower productivity, which aligns with evidence that anchor ice and ice scour can kill incubating eggs and alevins (Cunjak et al., 1998; Huusko et al., 2007). Large fall and winter floods can have negative consequences for coastal salmon populations

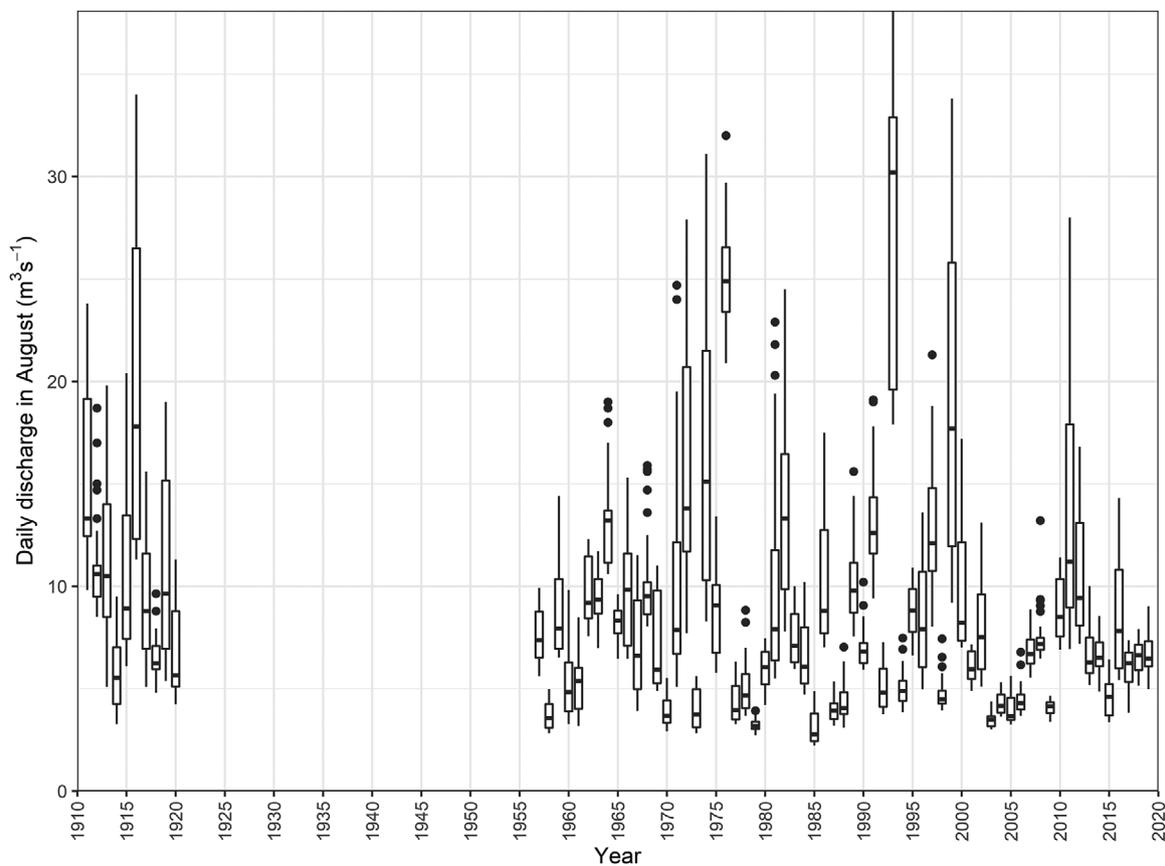


FIGURE 5 Boxplots of August daily discharge of the Nicola River, 1911–2019

(Greene et al., 2005; Jones et al., 2020; Seiler et al., 2003), and we found further evidence for this relationship. Productivity appeared lower for cohorts that incubated during years with fall floods greater than $\sim 150 \text{ m}^3 \text{ s}^{-1}$ (Figure 4d). Flows over this threshold could mobilize gravel and scour incubating eggs (Gendaszek et al., 2018). Untangling the effects of seasonal extremes from other factors over the salmonid life cycle is challenging, but is essential for understanding population dynamics and informing appropriate planning and conservation.

Freshwater conditions explained as much or more of the variation in lifetime productivity than survival of fish during downstream 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 affected wild smolts. However, productivity for the 1992 cohort was well-predicted (Figure 1). Other studies found a strong positive 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 use of hatchery smolt survival as a proxy for wild smolt ocean survival.

There was also a weak pattern of stronger density dependence for hatchery fish, which is consistent other research on wild and hatchery salmon (Buhle et al., 2009; Ward et al., 2015; Williamson et al., 2010).

4.1 | 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 habitat model-based environmental flow recommendation of 19% MAD (Kosakoski & Hamilton, 1982) is associated with predicted productivity levels which fall below replacement and eliminate the possibility of 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. Based on our model, mean August flow during rearing would need to be $17.2 \text{ m}^3 \text{ s}^{-1}$ (58% MAD) to allow a harvest of 30% and escapement to spawning grounds at replacement levels. 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

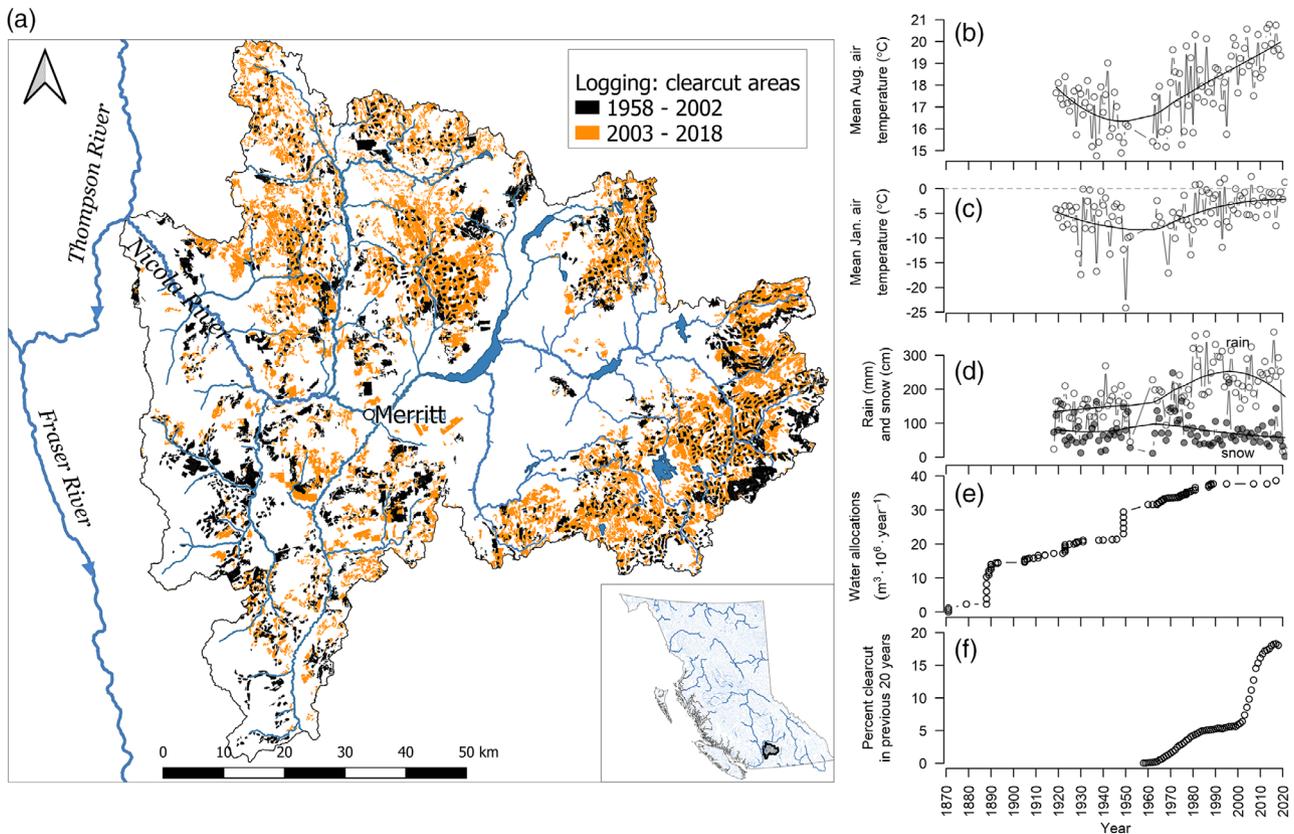


FIGURE 6 (a) The Nicola River watershed with clearcut areas in two time periods. (b and c) Historical changes in annual mean August and January air temperatures, (d) rain and snow, (e) water allocations for the mainstem Nicola River (not including conservation and dam storage licenses), and (f) percent of Nicola watershed clearcut in previous 20 years (rolling sum). Average total annual water yield of the Nicola River is 831,103,760 m³. Black lines in panels b, c, and d are LOESS best fit lines

(Tennant, 1976). Instead, we observed a variable but approximately linear relationship between summer flows and the natural logarithm of productivity over the observed range of flows (Figures 3 and 4f; Beecher et al., 2010). Rearing flows exceeded 36% MAD for only four of the 22 cohorts we examined, highlighting the contemporary 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 (Water Sustainability Act, 2014). Thus, our study provides an empirical relationship that links flows and fish productivity, a critical foundation of setting effective instream flow thresholds.

These contemporary challenges of low summer flows and Chinook salmon conservation are set within longer-term shifts in flow regimes. Average August flows decreased by 26% from 10.83 m³s⁻¹ to 6.87 m³s⁻¹ over the last century (Figure 3a), despite considerable development of storage reservoirs to offset withdrawals during the same period. Although equivalent Chinook productivity data is not available before 1992, it appears that historic flow regimes may have been more favourable for Chinook salmon than current flow regimes. These shifting flow regimes are likely driven by the combined impacts of increasing water withdrawals for agricultural and municipal uses, shifting precipi-

tation patterns, increasing air temperatures that hasten snowmelt, and forestry. For example, clearcut logging can cause a lagged, long-term reduction in summer flows starting approximately 15 years after harvest (Coble et al., 2020; Gronsdahl et al., 2019; Perry & Jones, 2017). Thus, the contemporary challenges of instream flow management are likely the product of a century or more of cumulative effects of water withdrawal, land-use, and climate change. Such cumulative effects and shifting baselines of flow likely pose an underappreciated challenge for salmon (Healey, 2011) and other freshwater species (Palmer & Ruhí, 2019).

There are many options for conserving Chinook salmon and flow regimes, each with potential trade-offs. Chinook salmon are economically and culturally important in this region and have been and remain vital to Indigenous fisheries (Nesbitt & Moore, 2016). Reduction in Chinook salmon harvest would allow more fish to spawn even when productivity is lowered by low summer flows. However, local fisheries have already been severely restricted in many years with cultural and economic consequences. 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). Watersheds with large increases in logging in the last 10–20 years, such as the Nicola and much of interior British Columbia, 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, we need a holistic appreciation for shifting flow regimes and their consequences (Palmer & Ruhi, 2019).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

All authors conceived the project; LW and CP designed the methodology; RB and CP collected data; LW analyzed data with assistance from CP; LW led writing. JM contributed to project scoping and writing. All authors contributed to drafts and approved submission.

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DATA AVAILABILITY STATEMENT

Data is available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.ffbg79crv> (Warkentin et al., 2021). Analysis code is available at <https://doi.org/10.5281/zenodo.5778307> (Warkentin, 2021).

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SUPPORTING INFORMATION

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