

Multiple environmental drivers across life stages influence Yukon River Chinook salmon productivity

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Abstract

Recent declines of Yukon River Chinook salmon (*Oncorhynchus tshawytscha*) populations have severely impacted people residing in the Yukon and Alaska. Evidence-based conservation strategies focused on stock recovery and adaptation are urgently needed but are limited by our understanding of what is driving declines, particularly in Canadian portions of the Yukon River basin. We examined how multiple environmental drivers may be influencing Canadian-origin Yukon River Chinook salmon productivity for eight populations over a 28-year period. We found that productivity was related to various environmental and ecosystem processes acting cumulatively over multiple life stages and across broad geographic scales. Productivity decreased in association with warmer upriver migration temperatures, wetter freshwater juvenile rearing habitats, and increasing abundances of potential marine competitors. In contrast, productivity increased in years with warmer and snowier winters and earlier spring onset. We found that different populations had similar relationships with environmental drivers, with potentially negative implications for regional fisheries stability. Our findings provide insight into how Chinook salmon are responding to rapid environmental change and can help inform salmon conservation initiatives and sustainable harvest strategies.

Key words: climate change, subsistence, cumulative effects, spawner recruitment, management

Introduction

Global environmental change is a complex, growing threat to Pacific and Atlantic salmon populations (Schoen et al. 2017; Lehnert et al. 2019; Crozier et al. 2021). During their freshwater residency (i.e., migration, spawning, and rearing), salmon are encountering wide-ranging environmental changes including warmer spawning migration conditions (Martins et al. 2011; Howard and von Biela 2023), lower water flows (Tillotson and Quinn 2017; Warkentin et al. 2022), increased flooding and erosion (Grant et al. 2019), and the transformation of cold, glacier-fed systems (Pitman et al. 2020). At sea, salmon are experiencing major ecosystem shifts such as generally warmer and more competitive conditions (Todd et al. 2008; Connors et al. 2020; Oke et al. 2020; Crozier et al. 2021), changes in prey quality (Mills et al. 2013; Garcia and Sewall 2021), and the alteration of nearshore habitats following sea-level rise (Thorne et al. 2018). Collectively, these shifting environmental conditions present a considerable challenge for understanding and forecasting salmon population dynamics, particularly as environmental effects may vary widely across life stages, populations, regions, and species (Price et al. 2017; Schoen et al. 2017; Grant et al. 2019) and change over time (Litzow et al. 2018). However,

understanding what is driving this variation is critical for developing timely, evidence-based salmon conservation and harvest strategies amid increasing environmental change (Pepin et al. 2022).

Northern salmon populations in Alaska and adjacent Canada are experiencing rapid environmental change, providing a prime opportunity for understanding salmon–environment connections that may be relevant to salmon populations elsewhere as climate changes. Near their northern limits, salmon have endured warming rates more than two times greater than salmon at the southern extent of their range (e.g., United States Northwest) over the past 60 years (Melillo et al. 2014), with direct consequences for salmon growth, reproduction, and survival already being observed (e.g., Kovach et al. 2013; Cline et al. 2019; Howard and von Biela 2023). Given the historically cooler climate, many northern populations are experiencing changes with directly opposing (i.e., positive and negative) consequences for survival and population productivity (Cunningham et al. 2018; Jones et al. 2020; Oke et al. 2020). In particular, warming temperatures may be temporarily benefiting specific life stages that have been historically limited by cooler conditions such as incubation, overwintering, and juvenile rearing

(Leppi et al. 2014; Cunningham et al. 2018; Cline et al. 2019; Murdoch et al. 2020). In contrast, recent evidence of heat stress and widespread pre-spawning mortality events suggest that warming may already be negatively impacting older life stages for some Alaskan salmon populations (Mauger et al. 2017; von Biela et al. 2020, 2022). Changing hydrological regimes have also been linked to both positive and negative outcomes for salmon survival and productivity in Alaskan salmon systems (e.g., Ohlberger et al. 2016; Cunningham et al. 2018; Jones et al. 2020). Importantly, there is growing evidence that fisheries supported by multiple populations encompassing a range of responses to environmental change may be more resilient over time, as some populations may temporarily persevere, while others decline (Anderson et al. 2015; Cline et al. 2017). As northern systems continue to experience rapid and complex changes, understanding why certain populations have fared worse than others may prove useful for preventing and mitigating further declines.

Canadian-origin Yukon River Chinook salmon support a highly valued northern Pacific salmon fishery that began experiencing serious declines in the late 1990s, with current run sizes (2015–2021) depleted to 60% of historical numbers (1985–2014) (JTC 2022). As a result, the fishery has faced numerous restrictions and closures over the past several decades, with immense repercussions for thousands of Yukon First Nations citizens, Alaskan Natives, and non-Indigenous people across the Canadian and American western Arctic that have historically relied on salmon for their food, livelihood, and culture (Moncrieff 2017). Yukon First Nation citizens are ensured a proportion of the overall harvest under the trans-boundary Pacific Salmon Treaty with the United States; however, as a result of depressed returns, these obligations have not been met during eight of the past 15 years (JTC 2022). In recent years, several Yukon First Nations have taken the extraordinary step to refrain from or severely limit fishing even when legally permitted to do so despite the devastating hardship this entails for their community members (Brown and Godduhn 2015).

Over the past several decades, many environmental and anthropogenic stressors have been hypothesized to have contributed to Yukon River Chinook salmon declines (AYK SSI 2006; Connors et al. 2016). In their freshwater habitats, Yukon River Chinook salmon have experienced numerous environmental changes, including warmer temperatures, earlier spring melt, extensive permafrost thaw, and increased precipitation, particularly in the summer months (Bush and Lemmen 2019; Pepin et al. 2022). In addition to changes in freshwater habitats, the Bering Sea where these salmon spend 2–6 years has experienced notable ecosystem shifts, including the potential for increasing abundances of natural and hatchery-origin salmon, changes in prey quality, and increased predation by salmon sharks among other species (Cunningham et al. 2018; Seitz et al. 2019; Garcia and Sewall 2021). In recent years, salmon pathogens, such as the parasite *Ichthyophonus hoferi*, represent an additional growing threat that may be amplified in warmer years (von Biela et al. 2020). Cumulatively, these environmental stressors may be combining and interacting with other anthropogenic stressors such as resource development (Sergeant et al. 2022), migration

impediments such as dams (Twardek et al. 2022), and fishing pressure (Connors et al. 2022), although harvest has drastically decreased in recent years owing to very low returns (JTC 2022). Notably, mixed-stock fisheries, such as the Yukon River Chinook salmon fishery, have the potential to overfish or extirpate the least productive (or “weak”) stocks over time (Connors et al. 2022), as well as impact per capita female reproductive potential and overall population productivity due to the use of size-selective fishing gear targeting older, larger age classes (Ohlberger et al. 2020; Oke et al. 2020).

In this study, we examine the evidence for relationships between multiple environmental and ecosystem processes (local and regional climate drivers, and competition at sea) and Canadian-origin Yukon River Chinook salmon productivity. Canadian watersheds contain over 50% of the known Yukon River Chinook salmon spawning areas (Brown et al. 2017) and have historically supported one half of the overall Chinook salmon harvest (years 1981–2021; JTC 2022); yet very few studies have examined potential local- or regional-level environmental effects on Canadian-origin salmon to date. Historically, there was little information on Canadian-origin Yukon River Chinook salmon populations except at the scale of the single Yukon River Canadian-origin stock aggregate. However, recent genetic and statistical advances have allowed for the dynamics of Chinook salmon to be reconstructed at finer and more biologically relevant scales (Connors et al. 2022). Here, we leverage these advances to gain insight into the drivers of changes in productivity at both population specific and regional scales. Our findings provide insight into the drivers of a declining salmon population complex that may serve as an early-warning case study for northern salmon systems.

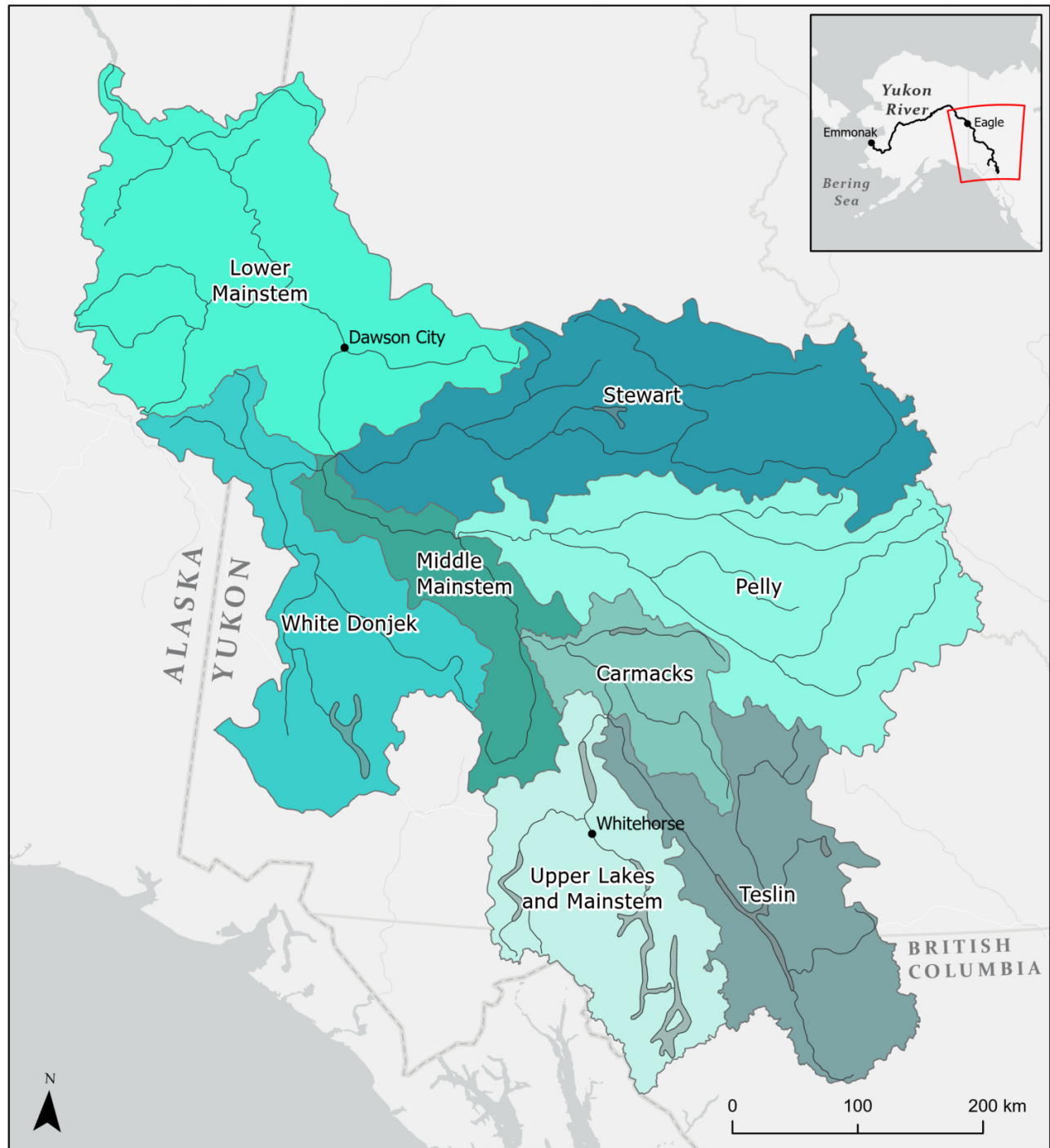
Materials and methods

Study area and species overview

The Yukon River drainage is a major North American river system that flows from its headwaters in British Columbia, Canada, through the Yukon Territory and Alaska, before exiting into the northeastern Bering Sea (Fig. 1). Canadian-origin Yukon River Chinook salmon exhibit one of the longest freshwater migrations in the world, with some populations travelling over 3000 km before reaching their spawning grounds (Brown et al. 2017; Twardek et al. 2022). Canadian-origin Chinook salmon habitats have historically spanned the Traditional Territories of 10 Yukon First Nations.

Chinook salmon destined for Canadian spawning areas generally begin their ascent up the Yukon River in late May or June, although migration timing varies by population and among years (Gilbert 1922; Eiler et al. 2014; Connors et al. 2022). After travelling for over 30 days, salmon begin to enter Canadian waters and will continue their journey to over 100 documented Canadian spawning areas (Brown et al. 2017). Spawning generally occurs from mid-July to September in streams to larger rivers with suitable substrate and oxygen requirements for overwinter incubation (Brown et al. 2017). Following spring emergence, most Canadian-origin Chinook salmon display a stream-type life-history strategy, with

Fig. 1. Local sub-basins for eight geographically and genetically distinct Canadian-origin Yukon River Chinook salmon populations. Salmon conservation unit shapefiles are from [DFO \(2018\)](#). Light gray basemap service layer credits include Northwest Territories, State of Alaska, Esri, HERE, Garmin, FAO, NOAA, USGS, EPA, NRCAN, and Parks Canada. Map projection is Yukon Albers.



juveniles spending approximately 1 year in freshwater before migrating out to the Bering Sea ([Gilbert 1922](#)). During their first summer, some juveniles undergo extensive freshwater migrations to non-natal rearing habitats, including migrations into Alaskan tributaries ([Bradford et al. 2008](#); [Daum and Flannery 2011](#)). Although juvenile migrations into non-natal habitats have been observed for other Pacific salmon

populations, Canadian-origin Chinook salmon are unique in displaying some of the longest juvenile migrations ever documented ([Bouret et al. 2016](#)). The following year, outmigration to the marine environment typically occurs after ice break up ([Bradford et al. 2008](#)), when smolts enter coastal marine habitats in the northeastern Bering Sea ([Murphy et al. 2017](#)). Canadian-origin Chinook salmon typically spend 2–6

summers in the Bering Sea before returning to freshwater for spawning (Bradford et al. 2001; Connors et al. 2022).

Environmental variables

We quantified associations between Yukon River Chinook salmon productivity and 12 freshwater and marine environmental and ecosystem variables based on their hypothesized relationships (Table 1). Of these 12 variables, we selected eight freshwater variables as the time spent in freshwater habitats has been emphasized as an important period regulating cohort survival for northern populations and remains relatively understudied (Daum and Flannery 2011; Murphy et al. 2017; Jones et al. 2020). To calculate precipitation, snowpack, rearing degree days, and winter air temperature in freshwater habitats, we extracted gridded 1 km resolution daily air temperature, precipitation, and snow-water equivalent data from Daymet (Thornton et al. 2020). In addition, water temperature data were obtained for estimating thermal conditions during spawning migrations in the lower Yukon River (ADFG 2022), as well as during the spawning and incubation period within local spawning watersheds (see below for further details regarding water temperature data processing). Gridded marine sea surface temperature data (NOAA OI SST V2) were used for estimating summer and winter thermal conditions during the first year of marine residency in the eastern Bering Sea (Reynolds et al. 2007). We estimated mean summer sea surface temperature (SST) for the northeastern Bering Sea basin, which was defined as areas less than 50 m deep and bounded by 60°–65°N and east of 172.5°W following Yasumiishi et al. (2020). Winter SST was estimated for marine regions along the Bering Sea shelf bounded by 58°N and between 162° and 174°W (Myers et al. 2010; Larson et al. 2013). We note that SST is likely a simplification of temperatures experienced by Chinook salmon, which have been documented frequenting deeper waters. However, we have opted to use SSTs given that past studies demonstrated relationships between seasonal surface temperatures and Chinook salmon (see Table 1), and because SST has been used as an index of overall climate conditions due to its correlation with relevant indices such as bottom temperature and cold pool extent (Oke et al. 2022). We used annual reconstructions of North Pacific-wide pink and chum salmon abundance as independent indices of potential interspecific competitors with Chinook salmon at sea (Table 1). It has been hypothesized that increasing abundances of these species in recent decades may negatively impact Chinook salmon via direct or indirect competition for resources at sea (Table 1), though we note that the evidence in support of this hypothesis is mixed and stronger for pink salmon (e.g., Davis et al. 2005). All environmental covariates were calculated for each year and at the major sub-basin or population level (except the marine variables) to represent the varied conditions experienced by Chinook salmon as summarized in Table 1.

Calculating environmental variables related to juvenile freshwater rearing (rearing degree days and precipitation) required some extra consideration as juvenile Canadian-origin Yukon River Chinook salmon are known to disperse up to 1200 km into non-natal rearing habitats in early-mid sum-

mer of their first year of life (Bradford et al. 2008; Daum and Flannery 2011). However, it is not currently known what proportion of juveniles undergo these rearing migrations versus stay in their immediate sub-basin, and how much rearing migration strategies vary within and among populations year-to-year (Daum and Flannery 2011). Due to these uncertainties, we quantified the effects of precipitation and temperature on the juvenile freshwater rearing period using two methods. First, we calculated rearing variables at the sub-basin scale, which assumed that the majority of juveniles remained within their major sub-basin of origin. Then, we compared our results using rearing variables calculated at a broader spatial area that combined all Canadian sub-basins and adjacent areas of Alaska where Canadian-origin juveniles have been previously documented as indicated by the sub-basins in Fig. 1 (lower boundary at Circle, Alaska; Daum and Flannery 2011). Because our results from the stock-recruitment analyses were similar between methods, for brevity, we present the results from variables derived at the sub-basin scale here.

Prior to model fitting (see below), all environmental variables were examined for multicollinearity using pairwise Pearson's correlation tests and found to be less than 0.6. Variables were then standardized by centering to zero and dividing by one standard deviation to allow for relative effect size comparisons. Covariates were standardized across all sub-basins to preserve any environmental variation present across space (populations) and time (years).

Water temperature data processing

We used water temperature data collected at Emmonak near the Yukon River mouth to estimate migration temperature (Fig. 1), as it comprised the most complete long-term dataset that included all years between 1985 and 2012 (ADFG 2022). As multiple stations were monitored with varying year-to-year coverage, we selected the station and time of day (Big Eddy station at 8:00 A.M.) with the most consistent coverage to reduce the potential influence of location and timing on measurements. When required, missing temperature data were estimated using the most representative and complete dataset available (i.e., from Big Eddy at 8 P.M. or from Middle Mouth at 8 A.M.), or interpolated (2% of data). In addition, we substituted daily population-specific means averaged over the study period for missing data in 2000.

Migration temperature was calculated as a weekly maximum temperature over the first 30 days of the salmon return migration. The first day of the return migration in freshwater was estimated using population and year-specific border passage timing data from Eagle (Connors et al. 2022). As it takes approximately 30 days for salmon to travel from the river mouth to Eagle (Eiler et al. 2015), we subtracted this value to estimate the start of the freshwater return migration. To capture the main migration pulses rather than the first passing of fish, we defined the first day of migration as when 25% of salmon in each population would have started moving upriver.

Due to a lack of historical water temperature data in Yukon watersheds, we approached spawning and incubation temperatures during the August–September period in two

Table 1. Overview of environmental and ecosystem variables used in analyses.

Variable	Description	Prediction	Rationale	References	Data source	Brood year offset
Freshwater						
Migration temperature	Maximum weekly water temperature over the first 30 days of the salmon upriver migration	Negative	Warmer migration temperatures (>18 °C) are linked to heat stress that may reduce spawning success and productivity	(Hinch et al. 2012; Jones et al. 2020; von Biela et al. 2020; Howard and von Biela 2023)	ADFG 2022	0
Spawning and incubation temperature	Estimated mean daily water temperature over the August–September period at spawning sites	Mixed	Warmer spawning and incubation temperatures (>13 °C) may lead to increased chronic and sublethal effects, as well as faster rates of development and earlier spring emergence; cooler incubation temperatures may reduce egg-fry survival	(US EPA 2003; Quinn 2004; Leppi et al. 2014)	Daymet; von Finster 2022	0
Spawning and incubation precipitation	Maximum monthly precipitation in spawning area drainages during the August–October period.	Negative	Higher flows have been associated with negative effects on Alaskan salmon due to the potential risks of dislodging or embedding incubating eggs	(Leppi et al. 2014; Neuswanger et al. 2015; Jones et al. 2020)	Daymet	0
Snowpack	Mean watershed snowpack on April 1st of each year in spawning area drainages	Positive	Snow-dominated watersheds maintain lower water temperatures and more consistent streamflows over the migration and early spawning period	(Mauger et al. 2017; Schoen et al. 2017)	Daymet	0
Freshwater winter temperature	Mean daily winter air temperature at spawning sites over the embryonic period (November–April)	Positive	Longer and colder winters experienced during incubation may limit salmon survival in northern regions	(Dunmall et al. 2016; Murdoch et al. 2020)	Daymet	0
Rearing degree days	Mean watershed growing degree days over 5 °C	Positive	Juvenile fish in northern ecosystems may benefit from longer and warmer seasons that allow them to achieve sufficient growth for overwinter survival	(Shuter and Post 1990; Venturelli et al. 2010; Leppi et al. 2014)	Daymet	1
Rearing precipitation	Maximum monthly precipitation in major sub-basins during the June–August period	Mixed	Precipitation and streamflow variables during the rearing period have been linked to changes (both positive and negative) in Alaskan salmon survival and productivity	(Neuswanger et al. 2015; Cunningham et al. 2018; Jones et al. 2020)	Daymet	1
Ice out date	Day of year of Yukon River ice break up at Dawson, Yukon	Negative	Ice out timing (a proxy of the onset of spring) has been related to Yukon River Chinook salmon smolt outmigration timing; earlier ice out has been linked with increased survival and productivity	(Bradford et al. 2008; Ohlberger et al. 2016; Cunningham et al. 2018)	https://yukonriverbreakup.com/statistics	2
Marine						
Summer sea surface temperature (SST)	Mean summer sea surface temperature in the northeastern Bering Sea basin (depths <50 m) during June–August	Mixed	Water temperatures during the first summer at sea have been associated with differences in juvenile diet and abundances	(Garcia and Sewall 2021; Murphy et al. 2021)	NOAA OI SST V2	2
Winter sea surface temperature (SST)	Mean winter sea surface temperature over the southeastern Bering Sea shelf during January–March	Positive	Juvenile survival may benefit from warmer temperatures during the first winter at sea	(Cunningham et al. 2018)	NOAA OI SST V2	3
Pink and chum salmon abundances	Annual estimated abundances of combined natural and hatchery-born salmon in the North Pacific	Negative	Higher densities of pink and chum salmon may negatively impact Chinook salmon via direct or indirect competition for resources	(Ruggerone and Nielsen 2005; Myers et al. 2010; Cunningham et al. 2018; Oke et al. 2020)	Ruggerone and Irvine 2018	3

Note: Predictions indicate the hypothesized effect on Chinook salmon productivity. A mixed prediction is provided where there is evidence for positive, negative, or unimodal effects on productivity based on the literature.

Table 2. Prior distributions for model parameters.

Parameter	Description	Prior
α_p	Intrinsic productivity at low spawner abundance	\sim Uniform(0,50)
β_p	Within brood-year density-dependent effects	\sim Normal(0,1000)[0,]
τ_p	Recruitment error	\sim Normal(0,1)[0.001,]
φ_p	First-order autoregressive correlation	\sim Uniform(-0.99,0.99)
μ_c	Hyperparameter: mean covariate effect for all populations combined	\sim Normal(0,25)
σ_c	Hyperparameter: standard deviation of all populations combined	\sim Normal(0,5)[0.001,]

Note: Values within square brackets indicate prior distribution boundaries.

ways. First, we used air temperatures at 98 documented Canadian spawning locations (Brown et al. 2017) as a proxy for water temperatures. Using a recent water temperature dataset from 20 sites over the 2011–2020 period (von Finster 2022), we found that the best predictor of water temperature was a lagged air temperature value over the previous 14 days ($R^2 = 0.53$). Second, we built a more complex mixed model to predict historical water temperatures at the same 98 spawning locations that also included other landscape, geographic, and sampling variables such as upstream drainage area, mean drainage elevation, the proportion of discontinuous permafrost upstream, latitude, sampling year, and sub-basin as a random intercept (marginal $R^2 = 0.79$, conditional $R^2 = 0.92$; see Supplementary material A for further details). As both methods deriving spawning and incubation temperatures produced similar results with respect to response direction and overall interpretation, we present results using the model based on estimates of historical water temperatures.

Spawner–recruitment data

Estimates of spawner abundance and subsequent recruitment were obtained for eight different Canadian-origin population complexes (hereafter referred to as populations) over the 1985–2019 period (Fig. 1). These populations roughly encompass the boundaries of nine proposed conservation units as defined under Canada’s Wild Salmon Policy (DFO 2005). Specific details for how these data were derived are provided in Connors et al. (2022). Briefly, annual population-specific spawner abundance and resulting recruitment were estimated using run–reconstruction and state–space spawner–recruitment models fit to data on border passage, genetic stock assignments, age-composition, and aggregate Canadian Chinook salmon harvest. Complete spawner–recruitment estimates (i.e., years with complete information on recruits across all ages at maturity for a given spawner brood year) were available for 28 brood years from 1985 to 2012.

Salmon productivity analysis

Using the spawner–recruitment estimates as inputs, we analysed the relationships between spawner productivity and environmental covariates using a hierarchical Bayesian stock–recruitment model. A hierarchical approach was selected as it allowed us to estimate productivity–covariate relationships at the individual population level as well as with all populations combined (“regional level”) within the same model (e.g., Jones et al. 2020). The model estimated

recruitment as a function of spawner abundance using linearized Ricker spawner–recruitment relationships and additive terms for each environmental covariate:

$$(1) \quad R_{p,y} = S_{p,y} \exp \left(\alpha_p - \beta_p S_{p,y} + \sum_c (\theta_{p,c} X_{p,t,c}) + \omega_{p,y} \right) \\ \omega_{p,y} = \varphi_p \omega_{p,y-1} + \varepsilon_{p,y}$$

where $R_{p,y}$ is the predicted recruitment for population p in brood year y , $S_{p,y}$ is spawner abundance, and α_p and β_p are estimates of population-specific intrinsic productivity and strength of within population density-dependence, respectively. Each environmental covariate term (c) was estimated by multiplying the population-specific covariate coefficient for all years ($\theta_{p,c}$) by the covariate value for each population and calendar year ($X_{p,t,c}$). Individual environmental covariates were lagged by 0–3 calendar years (t) to align with the respective life stages they were hypothesized to influence (Table 1). Population-specific covariate coefficients were assumed to be drawn from a normally distributed prior distribution with covariate-specific hyperparameters (Table 2):

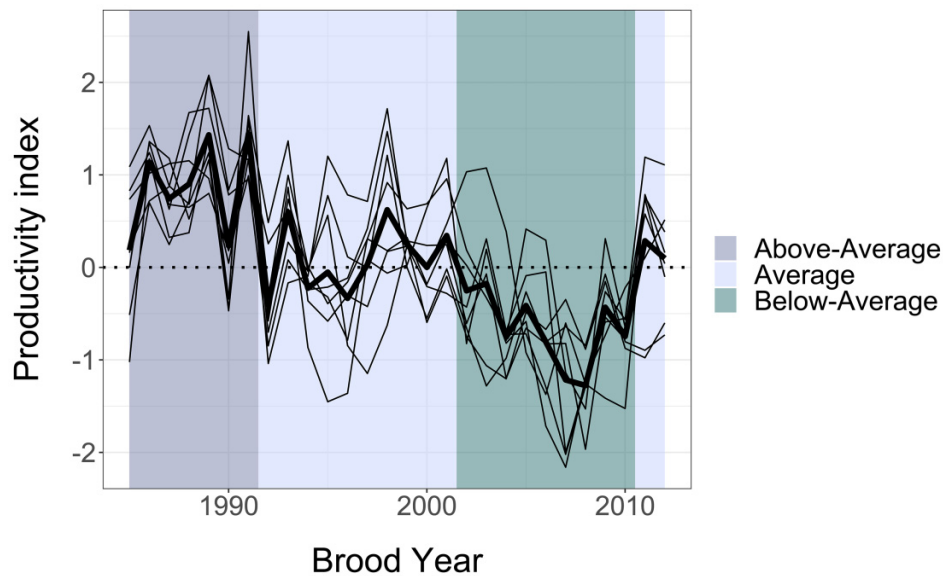
$$(2) \quad \theta_{p,c} \sim \text{Normal}(\mu_c, \sigma_c)$$

Recruitment deviations ($\omega_{p,y}$) represent the model residuals after fitting with environmental covariates for each population p and brood year y . To account for autocorrelation in recruitment deviations (ω) over time, recruitment residuals were assumed to be first-order autocorrelated with residuals in the previous time step $\omega_{p,y-1}$ as estimated by the correlation parameter φ_p , where $\varepsilon_{p,y}$ reflects the portion of the recruitment deviation that is temporally independent (i.e., white noise). Observed recruitment ($R_{obs,p,y}$) was assumed to be log-normally distributed:

$$(3) \quad \ln(R_{obs,p,y}) \sim \text{Normal}(\ln(R_{p,y}), \tau_p)$$

The hierarchical stock–recruitment model outlined in eqs. 1–3 was fit using Markov Chain Monte Carlo methods implemented in JAGS (Plummer 2003). We ran three chains each with 250 000 iterations, a burn-in rate of 15 000, and a thinning rate of 20, resulting in 35 250 posterior samples. We assessed model convergence using standard diagnostics, including effective sample sizes (approximately 7000–35 000) and potential scale reduction factor (<1.002) for all parameters in the model (Gelman et al. 2004). As an additional check on the model results, we examined pairwise correlations between each environmental covariate and recruitment residuals from individual spawner–recruitment models without

Fig. 2. Canadian-origin Yukon River Chinook salmon productivity index (log recruitment deviations from inferred spawner–recruitment relationships) for brood years 1985–2012. General time periods of consecutive above-average, average, or below-average productivity years are indicated by the legend background colouring. Mean productivity for all populations is indicated by the thick black line, whereas thin gray lines represent median population-specific trends for eight Canadian-origin Yukon River Chinook salmon populations.



covariates fit to data from each population (Supplementary material B; Figs. SB1–SB12).

Sensitivity analyses

Our analyses relied on modelled spawner–recruitment data that were generated using run–reconstruction and state–space spawner recruitment models as detailed in Connors et al. (2022). These analyses were based on numerous simplifying assumptions. As such, we carried out two sensitivity analyses to understand how sensitive our inference was to (1) uncertainty in the estimates of spawners and recruitment our models were fit to, and (2) the assumption of shared common exploitation rates among populations.

To examine sensitivity to uncertainty in the estimates of spawners and recruitment we fit our models to, we ran a sensitivity analysis where we took 100 random samples from the joint posterior distribution of estimates of spawner abundance and recruitment (as estimated in Connors et al. 2022), and for each joint set of posterior samples refit the hierarchical stock–recruitment model outlined above (eqs. 1–3). We then summarized the resulting posterior samples for covariate effects ($\theta_{p,c}$) across each of the 100 iterations (Supplementary material B; Figs. SB13–SB14).

The run–reconstruction and state–space spawner–recruitment models from which our spawner–recruitment data were derived assumed populations experienced a shared common exploitation rate within years. While this was considered a reasonable assumption, it has the potential to impose greater covariation among populations in recruitment from year to year than truly exists. Therefore, as an additional sensitivity analysis, we also fit the hierarchical model (eqs. 1–3) to spawner and recruitment data

derived from another set of models that somewhat relaxed the assumption of a shared common exploitation rate (see “integrated” model in Appendix B of Connors et al. (2022) for details). Detailed results from this analysis and further justification for our choice of data presented in the main text are provided in Supplementary material C.

Interpreting environmental covariate effects

We inferred the effects of environmental variables based on the magnitude, direction, and uncertainty in their individual parameter estimates. Relationships between productivity and covariates at the regional and population levels were interpreted as being relatively “strong” if the 95% credible interval of the effect size did not overlap zero, whereas relationships with 75% credible intervals that did not overlap with zero were interpreted as relatively “weak”. Variables with more than 75% overlap were not considered to have a relationship with productivity.

To understand how environmental variables may be influencing productivity over specific time periods of relatively high or low productivity, we subdivided the brood years into three general categories including above-average, average, and below-average periods. Above- and below-average time periods represented years where mean regional productivity remained elevated above or below the long-term mean for greater than 5 years, whereas “average” years were defined as longer periods of fluctuation around the long-term mean (Fig. 2). We further subdivided each environmental variable into the three time periods and ran analyses of variance with post-hoc Tukey’s tests to determine whether certain variables were significantly different among high or low productivity periods.

To translate the observed relationships between Chinook salmon productivity and environmental variables into predicted changes in recruitment, we calculated the predicted change in recruitment associated with a one standard deviation unit change in each covariate. To do this, we sampled model posteriors including population parameters α_p , β_p , and population-specific covariate coefficient estimates $\theta_{p,c}$, and then predicted resulting recruitment at median spawner abundances with and without each covariate of interest. Recruitment changes were then summed over each population to estimate the regional-level impact for all Canadian-origin Yukon River Chinook salmon combined.

For comparison with the hierarchical Bayesian model, we also fit a linear mixed model using the *nlme* package that included a random intercept for population and a first-order autoregressive correlation coefficient (Pinheiro et al. 2022; Supplementary material B; eq. B1, Table SB1). As the response variable, we used recruitment residuals (i.e., productivity) generated from the Bayesian model specified above (eqs. 1–3) but without covariates or an autocorrelation correction. Covariate effect sizes and interpretation from the mixed model were generally similar to results from our hierarchical modelling approach, giving us additional confidence in our inference from the Bayesian model.

Results

General productivity and environmental trends

At the regional scale, Chinook salmon productivity declined over the 28-year period of study (Fig. 2). On average, productivity was higher than the long-term mean prior to 2000 and depressed for brood years 2002–2010. The most recent 2 years of data (2011–2012) displayed an uptick in productivity in comparison to the previous time period.

We characterized the study period as having above-average productivity from brood years 1985–1991, below-average productivity from 2002–2010, and average or fluctuating productivity from 1992–2001 and again from 2011–2012 (Fig. 2). Below-productivity years occurred in conjunction with prolonged periods of cooler winter SSTs, more juvenile degree days, and warmer migration temperatures (Fig. SB15). In contrast, above-average productivity years were snowier and had significantly lower abundances of pink and chum salmon in the North Pacific Ocean.

Environmental and ecosystem drivers of productivity at the regional scale

We found that multiple environmental and ecosystem effects (local and regional climate, and competition at sea) were associated with Chinook salmon productivity over the 1985–2012 brood years. These effects were complex and included both positive and negative relationships that occurred over multiple life stages and across broad geographical habitats from local spawning watersheds in the Yukon to the Bering Sea (Fig. 3). Plots comparing observed versus predicted recruitment demonstrated that variation in recruitment was generally well captured for all populations with no substantial bias or overfitting (Fig. SB16).

Chinook salmon productivity declined in association with warmer spawning migration temperatures (–10%), wetter juvenile rearing conditions (–12%), warmer and longer juvenile growing seasons (–9%), later ice out (–8%), and increased North Pacific wide pink salmon abundance in the marine environment (–7%) (values represent percent change per one standard deviation unit increase in each covariate; Table 3, Fig. 3). When translated into absolute predicted changes in recruitment, each of these environmental variables (+1 SD) were associated with median annual recruitment losses ranging from approximately 8000–13 000 salmon for combined Canadian-origin populations (Table 3, Fig. 4). For context, the mean annual run size was approximately 120 000 salmon during the 1985–2012 period. However, we note that there is substantial variation in these recruitment loss estimates with lower 95% credible interval bounds that spanned from approximately –30 000 to –22 000 salmon and upper bounds from –4000 to 200 salmon.

In contrast, Chinook salmon productivity increased with warmer winters during early development in freshwater (11%) and the marine environment (17%), and snowier pre-season conditions (11%) (Table 3, Fig. 3). Changes in each of these environmental variables (+/–1 SD) were linked to median annual recruitment gains between 12 000 and 19 000 salmon (Fig. 4). Estimates for recruitment gains were highly variable with lower 95% credible intervals spanning –600 to 6000 salmon and upper bounds from 35 000 to 46 000 salmon.

Environmental variables that were weakly related to productivity included spawning and incubation temperature and precipitation (Fig. 3). In contrast, summer SST and North Pacific wide chum salmon abundance were unrelated to productivity.

Environmental and ecosystem drivers of productivity at the population scale

We found that all eight populations demonstrated similar associations between productivity and environmental and ecosystem variation ($\sigma_c = 0.03$ – 0.11 ; Fig. 5). In particular, more consistent and stronger population-specific relationships were observed between productivity and spawning migration temperature ($\sigma_c = 0.03$), ice out date ($\sigma_c = 0.03$), and winter SST ($\sigma_c = 0.04$). In contrast, relatively more variable relationships were observed with productivity and spawning and incubation temperature ($\sigma_c = 0.11$), freshwater winter temperature ($\sigma_c = 0.07$), rearing degree days ($\sigma_c = 0.06$), and rearing precipitation ($\sigma_c = 0.05$). Overall, population-specific productivity–environment relationships mirrored those observed at the regional level, but effect sizes were often classified as more uncertain and therefore relatively weaker.

Sensitivity analyses

Our results were generally robust to uncertainty in spawner and recruitment estimates (Supplementary material B; Figs. SB13–SB14). We observed near-identical patterns for most covariates when compared with results derived using median spawner and recruitment values (Figs. 3 and 5). However, the inference for a few covariates changed from strong to weak (i.e., freshwater winter temperature, pink salmon).

Fig. 3. Changes in Canadian-origin Yukon River Chinook salmon productivity (log (recruits/spawner)) per one standard deviation increase of each environmental variable at the regional scale. Bars represent the 50% (thick black) and 95% credible intervals (thin black). Variables that do not overlap zero with their 95% credible intervals were interpreted as having relatively strong relationships with productivity. SST = sea surface temperature, FW = freshwater.

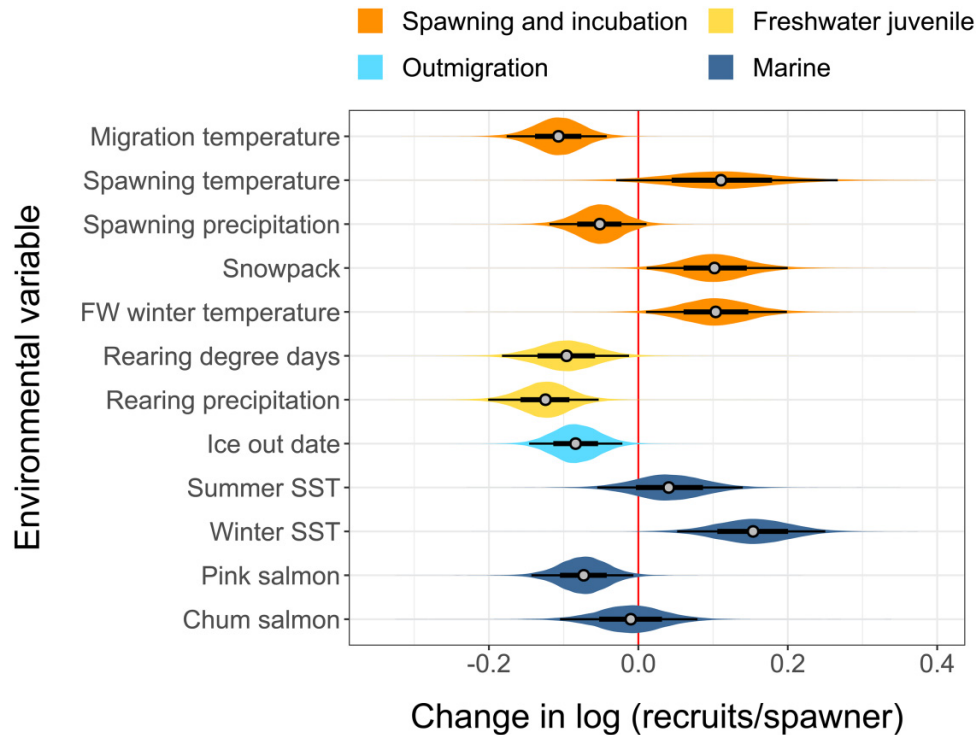


Table 3. Changes in Canadian-origin Yukon River Chinook salmon productivity and total recruitment at the regional level in association with a one standard deviation increase in each environmental variable.

Variable	Change in productivity (%)	Change in recruitment (# salmon)*
Positively related		
Snowpack	11 (1, 22)	11646 (−615, 34 979)
Freshwater winter temperature	11 (1, 22)	12181 (−551, 35 253)
Spawning and incubation temperature**	12 (−3, 31)	14820 (−3167, 52 479)
Winter sea surface temperature (SST)	17 (5, 28)	19425 (5878, 45 776)
Negatively related		
Rearing precipitation	−12 (−18, −5)	−13211 (−29 717, −4025)
Migration temperature	−10 (−16, −4)	−11728 (−27 424, −3907)
Rearing degree days	−9 (−17, −1)	−10 060 (−26 706, −191)
Ice out date	−8 (−14, −2)	−9112 (−21 657, −1863)
Pink salmon abundance	−7 (−13, −1)	−8123 (−21 885, 175)
Spawning and incubation precipitation**	−5 (−11, 1)	−5773 (−17 814, 1264)
Unrelated		
Summer sea surface temperature (SST)	4 (−5, 15)	3986 (−8263, 20 401)
Chum salmon abundance	−1 (−10, 8)	−1063 (−14 002, 10 770)

Note: Variables are grouped by their association with productivity (positive, negative, or unrelated). Median changes are presented followed by the lower and upper 95% credible interval bounds in brackets.

*Based on median spawner estimates of 47 000 salmon.

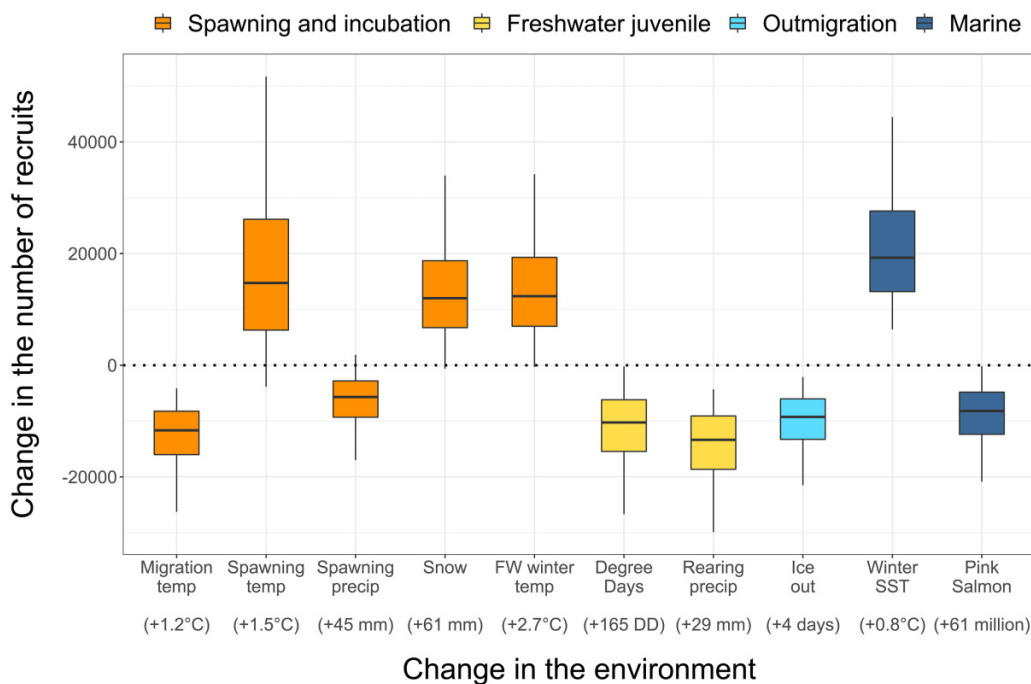
**Variables with relatively weak relationships with productivity.

These covariates had 95% credible interval bounds very close to the zero threshold for determining strong versus weak patterns in the original results, and the sensitivity analysis results produced slightly overlapping distributions with zero.

Using the alternative integrated dataset that was based on a relatively relaxed assumption of shared exploitation rates among populations within year, we found that most environment–productivity relationships remained relatively similar in their overall direction and general inference,

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Fig. 4. Estimated change in total Canadian-origin Yukon River Chinook salmon recruitment for each one standard deviation increase of an environmental covariate value (indicated in brackets), while holding all other covariates at their long-term mean. Predictions are based on a median aggregate spawner abundance of 47 000 salmon. Only variables that had relationships with productivity are displayed. SST = sea surface temperature, FW = freshwater.



although more variation led to generally weaker relationships overall (Figs. SC1–SC2). These results were not unexpected given that the integrated data contained higher recruitment variability estimates relative to the original “separated” dataset, including some estimates that appeared to be spuriously high. Given greater confidence in the original separated dataset (Connors et al. 2022), we provide detailed results from the alternative analysis in Supplementary material C as a supplement to demonstrate which environmental covariates may be more sensitive to the assumption of shared exploitation and may therefore warrant further study.

Discussion

As one of the most northerly Chinook salmon stock complexes in the world, Canadian-origin Yukon River Chinook salmon have experienced a host of complex environmental changes that may negatively or positively influence productivity depending on the specific year-to-year conditions. Our modelling revealed that environmental and ecosystem processes may have resulted in changes in Canadian-origin Yukon River Chinook salmon recruitment on the scale of tens of thousands of salmon from year to year. These potential effects on run size and subsequent allowable harvest are not trivial, as Canadian-origin Chinook salmon had a mean annual run size of approximately 64 000 salmon over the past decade (JTC 2022). Notably, the most recent period of below-average productivity (2002–2010) was associated with colder than average marine winters, warmer temperatures during spawning migrations, and warmer and longer summers for

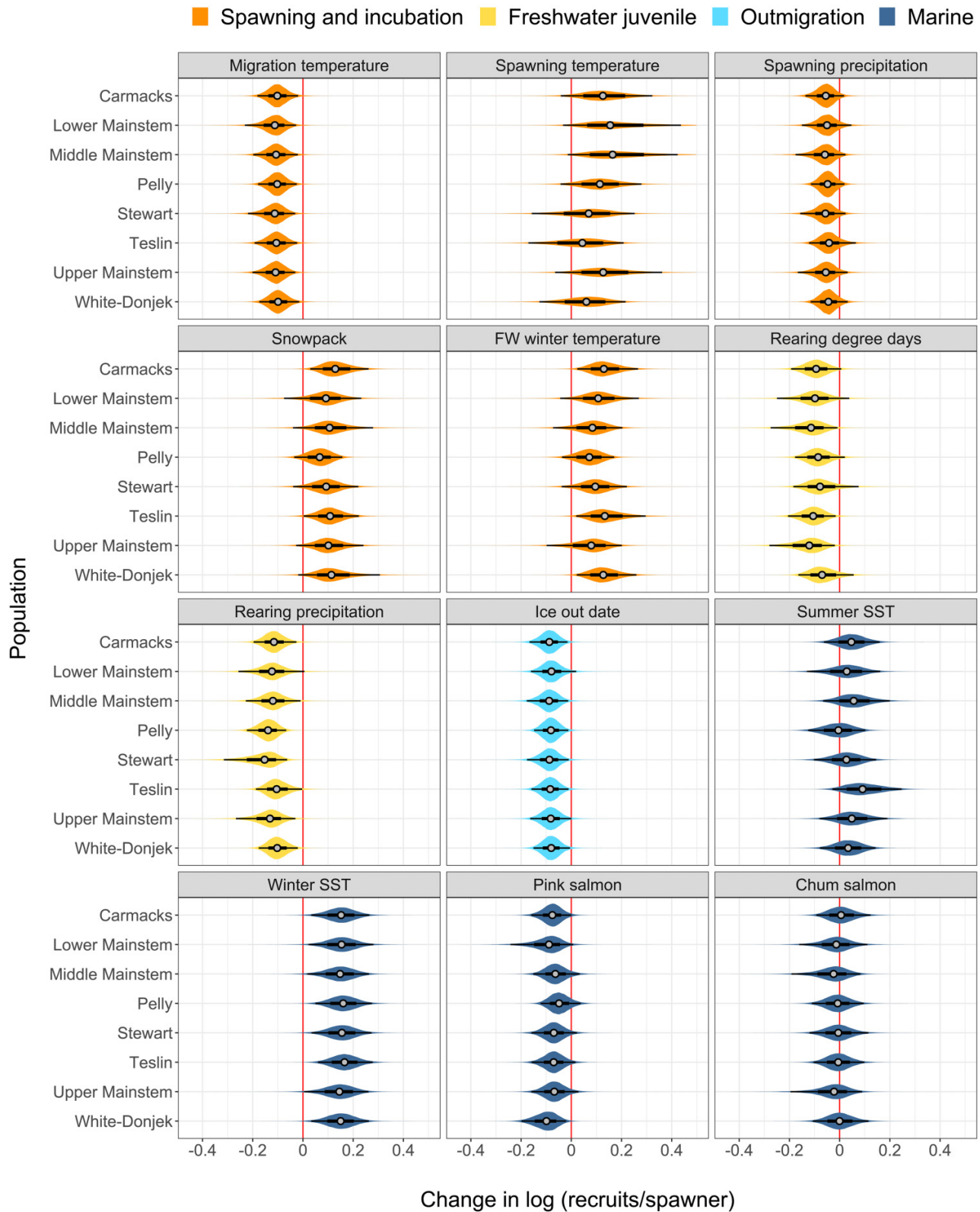
juveniles rearing in freshwater. In comparison, high productivity brood years (1985–1991) experienced snowier early spring conditions and lower abundances of pink and chum salmon in the marine environment. Based on our results, we outline potential opportunities for informing evidence-based conservation and management strategies focused on salmon stock recovery amid increasing environmental change.

Warming during outmigration and early marine residency may increase salmon productivity

Our results supported the hypotheses that earlier ice out and warmer conditions during the first winter at sea are associated with increased productivity, as has been observed for Yukon River Chinook salmon populations that spawn in the lower Alaskan reaches of the Yukon River basin (Ohlberger et al. 2016; Cunningham et al. 2018). Given the remarkable journey that Canadian-origin Chinook salmon smolts make to the Bering Sea, earlier ice out may allow juveniles to reach productive marine feeding areas earlier, increasing their growth opportunities during this life stage (Howard et al. 2016). Similarly, warmer Bering Sea conditions during the first winter may facilitate increased salmon feeding and growth, reducing the potential for size-selective marine mortality (Cunningham et al. 2018).

Our findings suggest that warming marine conditions may be expected to boost Chinook salmon productivity in the coming years, with the caveat that warming may produce concurrent ecosystem shifts with the potential to counter

Fig. 5. Changes in Canadian-origin Yukon River Chinook salmon productivity (log (recruits/spawner)) per one standard deviation increase of each environmental variable at the population level. Bars represent the 50% (thick black) and 95% credible intervals (thin black). SST = sea surface temperature and FW = freshwater.



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positive effects observed here. For example, warming may promote more marine interspecific competition, which we found was a potential threat to Canadian-origin Yukon River Chinook salmon productivity possibly via declining body sizes and resultant lowered fecundity (Oke et al. 2020). Prior research has suggested that high numbers of Bering Sea pink salmon may lead to indirect trophic effects on Chinook salmon (Batten et al. 2018), potentially lowering size-at-age and abundance of Chinook salmon (Lewis et al. 2015; Ruggerone et al. 2016), and reducing Yukon River Chinook salmon survival (Cunningham et al. 2018), which our analysis also found some support for. However, we did not find support for potential Chinook–chum salmon interactions which was in agreement with a recent study examining environmental drivers of salmon body size across Alaska (Oke et al. 2020). In contrast, Cunningham et al. (2018) found that Yukon River Chinook salmon productivity decreased with increasing hatchery chum salmon abundance. Chum salmon likely have relatively low diet overlap with Chinook salmon (~30%) compared to pink salmon (~60%) (Davis et al. 2005), which may help explain our result, though we caution against overinterpreting our correlative findings given the strong time trends in abundances time series and potential for spurious relationships to emerge. Other warming-induced ecosystem shifts may include changes in prey quality (Yasumiishi et al. 2020; Garcia and Sewall 2021) and increased predation pressure in the northern Bering Sea (Seitz et al. 2019; Ohlberger et al. 2019). Notably, our understanding of the influence of warming marine waters on more southerly salmon populations (e.g., Crozier et al. 2021) may help to shed light on how Bering Sea salmon may respond to future rapid environmental change.

Variable temperature effects during spawning and incubation

We found that warmer migration temperatures in the lower Yukon River were associated with reduced productivity despite weekly maximum migration temperatures generally remaining below the established threshold for thermal stress (<18 °C; US EPA 2003). Stress during the migration period can reduce spawning success via carryover effects on progeny or by reducing spawning success directly if salmon are unable to complete their spawning migrations (Martins et al. 2012; Sopinka et al. 2016). Our results suggest that thermal stress may begin at even lower temperatures for Canadian-origin Yukon River Chinook in comparison to more southern salmon populations, perhaps owing to their extensive spawning migrations and (or) less evolutionary selective pressure on thermal tolerance. Although there was no temporal trend in migration temperature over our study period (1985–2012), more recent years have seen evidence of anomalously high temperatures negatively affecting Alaskan salmon systems (von Biela et al. 2022; Howard and von Biela 2023). In addition to direct heat stress, warmer temperatures may also exacerbate other stressors such as disease associated with *Ichthyophonus* (Kocan et al. 2009), which is currently being investigated as a potential driver of Yukon River Chinook salmon declines.

We found that productivity increased in association with warmer spawning and incubation temperatures, although this effect was highly uncertain. However, we caution that our water temperature estimates may not reflect true in situ temperatures as we inferred past conditions from more recent datasets due to a lack of historical temperature data available for Canadian spawning areas. Further, characterizing thermal habitat diversity in spawning systems is complex as salmon may be able to seek preferred thermal conditions within microhabitats such as areas with groundwater influence (Mauger et al. 2017). Despite these caveats, the possibility that spawning and incubation success increased owing to warmer conditions remains plausible as our estimated temperatures were generally below the 13 °C threshold associated with negative effects (US EPA 2003). In addition, warmer incubation temperatures have been linked to increased egg-fry survival for northern salmon populations that are typically limited by long and cold winter conditions (Leppi et al. 2014). Although our estimated spawning temperatures did exceed 13 °C on occasion, we suggest that the benefits from warmer incubation conditions may have outweighed negligible thermal stress occurring during our study period. However, as temperatures in Yukon watersheds continue to rise (Bush and Lemmen 2019), we expect that salmon productivity may eventually decline as freshwater thermal optima are surpassed, as has been observed for declining populations in warmer and more southerly locales (FitzGerald et al. 2021).

Direct and indirect effects of changing juvenile freshwater habitats

Environmental drivers acting on the juvenile freshwater rearing phase emerged as potentially important determinants of Canadian-origin Yukon River Chinook salmon productivity. We found that productivity declined for cohorts experiencing wetter freshwater rearing conditions, as well as longer and warming growing seasons. The influential role of precipitation and discharge on the juvenile life stage has been well documented for Alaskan Chinook salmon, although varying results across populations suggest that local conditions may mediate ecological pathways. Notably, our observation that wetter rearing conditions may reduce Canadian-origin Chinook salmon productivity aligned with studies of other Yukon River populations in adjacent Alaska (Neuswanger et al. 2015; Cunningham et al. 2018). In these studies, it was suggested that higher flows may lead to reduced feeding efficiency, growth, and resultant survival during this critical life stage. We note that this proposed mechanism may be particularly relevant for salmon systems in permafrost-laden regions that may be more vulnerable to flashy and turbid streamflows following rain events (Brabets et al. 2000; Dugan et al. 2009). Further, heavy rainfall events may displace juvenile salmon from rearing tributaries into larger and less productive habitats (Daum and Flannery 2011). As Yukon watersheds are projected to experience wetter summers in the coming decades (Bush and Lemmen 2019), understanding the link to juvenile salmon ecology and survival may be increasingly important for informing local conservation actions.

Given the relatively low historical temperatures in Yukon spawning watersheds, we were surprised that productivity declined in years with longer and warmer freshwater rearing conditions. However, it should be noted that our results are based on the general assumption that juveniles remained within the eight major Yukon sub-basins, including adjacent Alaska, which we acknowledge may have oversimplified juvenile distributions given the uncertainty of where Canadian-origin Chinook salmon rear (Daum and Flannery 2011). Given that temperatures are unlikely to have exceeded thermal criteria for when juvenile salmon may begin to experience chronic or sublethal effects (16–18 °C; US EPA 2003), we suggest that negative relationships observed here may be instead due to indirect warming mechanisms. For example, more growing degree days could result in ecosystem shifts, including higher predation pressure, habitat degradation from algal growth, lowered habitat connectivity including beaver dam obstruction, or reduced water and substrate quality following a higher risk of sedimentation and erosion (Schindler and Smol 2009; Malison et al. 2015; Wrona et al. 2016). An additional consideration is the possibility that warming may be increasing juvenile freshwater growth, leading to carry-over effects on other life stages with potential implications for productivity. For example, warming during the freshwater period for Bristol Bay sockeye has resulted in a life history strategy shift towards earlier outmigration and resultant negative effects on marine growth and population diversity (Cline et al. 2019). We recommend that future studies focus on characterizing juvenile habitat distributions and available thermal conditions to provide much needed insight into how environmental changes are influencing juvenile rearing migrations, habitat use, ecology, and survival.

Limited population response diversity to environmental effects

Overall, we found that Canadian-origin Yukon River Chinook salmon populations exhibited limited response diversity, suggesting that populations may be similarly vulnerable to cumulative stressors. There is increasing evidence that aggregate salmon runs with more population diversity may be more robust to ongoing environmental changes, highlighting the need to preserve heterogeneity in salmon ecosystems (Rogers et al. 2013; Anderson et al. 2015; Moore and Schindler 2022). Population-specific responses to environmental changes have been noted in many Pacific salmon systems that may arise due to differences in available habitats and adaptive processes working to optimize fitness under current and historical conditions (Crozier and Hutchings 2014). For example, Alaskan sockeye populations have been shown to exhibit wide response diversity to regional climate change (Rogers et al. 2013), and Fraser River sockeye demonstrate differing thermal tolerances and physiological traits related to the historical freshwater environmental conditions they experience (Eliason et al. 2011).

There are several potential reasons for the observed lack of response diversity in Canadian-origin Yukon River Chinook salmon populations. First, it is possible that relatively similar environmental conditions were experienced among populations within the river basin and that these shared

conditions are the dominant environmental driver of year-to-year variation in survival. Further, following decades of sustained high exploitation rates of Yukon River Chinook salmon, it is possible that some response diversity has been extirpated along with populations that were relatively less productive. Another consideration that may have contributed to a lack of response diversity is that the spawner–recruitment data we used to quantify relationships with environmental covariates were derived from models that assumed that all populations were equally vulnerable to harvest. While this is likely a reasonable assumption, it is possible that it imposes more shared covariation in recruitment deviations/survival than what truly exists. To partially examine this effect, we ran a sensitivity analysis using an alternative spawner–recruitment dataset derived from models that relaxed this assumption. We observed that most environment–productivity relationships had similar patterns with some noted exceptions owing to increased among-population variation (i.e., freshwater winter temperature and rearing degree days). Lastly, we acknowledge that each “population” examined in our study represents an aggregate of several spawning populations, each of which may respond differently to environmental changes. Future initiatives to create relevant datasets at the individual spawning population level could provide valuable additional insight into the magnitude of response diversity within Canadian-origin Chinook salmon systems.

Study limitations

Studies of environmental drivers in historically data-poor regions often face trade-offs between information needs for guiding timely conservation efforts and data availability. Although relevant datasets for Yukon River Chinook salmon have expanded in recent years, we still faced some limitations in our analyses. We used the only available spawner–recruitment data for Canadian-origin Yukon River Chinook salmon that currently exists at a population complex level. These data are derived from statistical models that attempted to account for numerous sources of observation error and true underlying population variability. However, as with any model, they are predicated upon numerous simplifying assumptions, including similar exploitation rates among populations and a shared age-at-maturity schedule for all populations over the 1985–2005 period due to insufficient population-specific data (Connors et al. 2022). In addition, we note that there is the potential for uncertainty in genetic stock assignments to further confound the reconstructions of spawner–recruitment dynamics and among population correlations in them, which form the bases of our analyses. The consequences of this simplifying assumption are hard to predict but given that the mean classification error was relatively low (approximately 8%; see Appendix A1 and Table S2 of Connors et al. 2022), we expect the influence of this assumption on our overall results to be relatively minor. Lastly, our productivity estimates may have been underestimated in some years as the model did not account for potential pre-spawning mortality upstream of the Yukon–Alaska border.

We necessarily made several assumptions due to inadequate or incomplete historical environmental data used to

characterize salmon habitats. For example, weekly maximum migration temperature was based on water temperatures solely from the Yukon River mouth due to limited datasets that covered our entire study time period further upstream. However, as Yukon River water temperatures may be warmest in the lower river during the predicted spawning migration period (ADFG 2022; Eiler et al. 2023) and another study has linked Yukon River Chinook productivity with lower river water temperatures (Howard and von Biela 2023), we reasoned that the lower river dataset may be representative of the potential for thermal stress during migration. Spawning water temperatures also required estimation due to a lack of historical water temperature data in Yukon watersheds, although we found comparative results using air temperature proxies to support our presented findings. The winter distribution of Yukon River Chinook salmon along the Eastern Bering Sea shelf is uncertain, given that our knowledge is based on relatively few winter surveys, and the possibility that distributions vary from year to year. We additionally examined comparative results for rearing degree days to help navigate uncertainty about freshwater rearing habitat distributions. Finally, there were several hypothesized environmental effects that may be important for driving productivity that we did not incorporate due to limited data availability such as discharge, disease prevalence, human disturbance, and changes in permafrost or groundwater over time.

Opportunities to inform evidence-based conservation and management

The breadth of potential productivity drivers revealed in our study highlights the need for coordinated salmon conservation strategies that consider the impacts of environmental change on Yukon River Chinook salmon across life stages and their entire range. Currently, there are many local and regional efforts in Yukon watersheds to conserve salmon and salmon culture, including the development of regional land use (e.g., Dawson Regional Land Use Plan) and stock restoration plans (Connors et al. 2016), Indigenous-led salmon stewardship and management plans, and the Yukon River Panel's annual call for salmon restoration and enhancement proposals. In addition, the Yukon First Nations Salmon Stewardship Alliance has recently launched a 5-year strategic plan to support a concerted watershed-based approach for salmon in all Yukon habitats. Our findings highlight potential opportunities for refining existing programs (where applicable) as well as developing new collaborative, evidence-based conservation programs in local Canadian watersheds and beyond. First and foremost, we recommend that conservation efforts focus on a habitat protection strategy given the unique opportunity to do so in many relatively undisturbed northern regions. As summer rainfall emerged as a key stressor in local Yukon watersheds (particularly during the juvenile rearing phase), wetter areas could be afforded more protection when designing land use plans, or when making decisions about newly proposed infrastructure or resource development. Complementary stewardship activities could also focus on mitigating the negative effects of high runoff and flows, for example, by

restoring disturbed streamside habitats or enhancing spawning areas that have been silted due to high runoff.

Given that recruitment may fluctuate on the scale of tens of thousands of salmon year-to-year based on environmental conditions, we suggest that it may no longer be sufficient to manage the Canadian-origin Yukon River Chinook salmon stock aggregate without explicitly considering a potential buffer for rapid environmental change. Moreover, recent changes to Canada's *Fisheries Act* now stipulate that environmental conditions affecting major fish stocks shall be taken into account as part of fisheries management decisions (Pepin et al. 2022). Historically, Canadian-origin Yukon River Chinook salmon have been managed to a relatively narrow escapement goal range, with harvested salmon averaging 50% of the total salmon return run size (roughly 59 000 salmon/year) during the 1985–2021 period (JTC 2022). While many productive salmon populations can sustain relatively high harvest rates, historical Yukon River Chinook salmon harvest rates are likely to have resulted in overfishing some of the less productive Chinook salmon population complexes within the stock aggregate, with consequences for local subsistence fisheries (Connors et al. 2022). Although harvest rates have drastically declined in recent years owing to extremely low returns (JTC 2022), future escapement goals are currently under discussion by the transboundary Yukon River Panel and its Joint Technical Committee. Based on our findings, we suggest that the influence of environmental conditions both in freshwater and marine environments could be more directly considered when setting management targets for the system to promote long-term sustainability of individual spawning populations supporting valued subsistence fisheries throughout the watershed. Further, shifting from a maximum sustainable yield approach at the aggregate level to one that considers the viability of more discrete population units (Connors et al. 2022) may be additionally valuable for facilitating population recovery and resilience within rapidly changing northern environments.

Environmental effects may be integrated into run size forecasts and used to identify sustainable escapement goals in various ways. These methods range from more simple, precautionary approaches to more detailed simulation-based analyses that quantify the ability of alternative escapement goals to meet conservation and harvest objectives in the face of environmental change and uncertainty. For example, BC Fraser River Sockeye managers consider various climate scenarios when setting escapement goals and may reduce harvest recommendations in years that salmon are expected to experience more environmental stress during their freshwater return migrations (DFO 2016, 2017). Another way to integrate environmental conditions is to rely more heavily on forecasts that implicitly account for recent environmental conditions such as the dynamic sibling model or juvenile abundance forecast developed for Yukon River Chinook salmon (JTC 2022). However, we note that forecasts are only used to generate pre-season expectations of run size and that in-season assessment is used to guide in-river harvest decisions. In addition, even these types of forecasts have been less reliable in recent years (DFO 2022) and could therefore potentially benefit from a precautionary buffer for additional

sources of environmentally driven change and variability. For example, expectations for allowable Yukon River Chinook salmon harvest could be lowered in years experiencing potential stressors such as warmer spawning migration temperatures.

Conclusion

Although many northern Pacific salmon populations remain productive, our study reveals an informative counter example of a highly valued northern fishery in decline. We conclude that Canadian-origin Yukon River Chinook salmon are potentially influenced by numerous, cumulative environmental changes occurring in their habitats that span a vast geographical area from local Yukon watersheds to conditions in the Bering Sea. Collectively, these environmental changes may be substantially altering the number of recruits produced by each spawning cohort, with implications for pre-season run size forecast accuracy and sustainable harvest goals. Given projections for continued rapid environmental change in northern ecosystems, our findings suggest that it may no longer be sufficient to manage valued aggregate fisheries without considering environmental change. Finally, we highlight the urgent need for coordinated, large-scale salmon conservation plans that encompass the entire Canadian-origin Yukon River Chinook salmon habitat range to effectively address the breadth of potential productivity drivers revealed here. Our findings contribute to a growing collection of knowledge that highlight the importance of understanding how environmental change pathways may yield differing impacts on salmon populations depending on the local and regional context. In turn, this improved knowledge of salmon systems across watersheds and regions is critical for informing timely evidence-based conservation strategies amid rapid environmental change.

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Data availability

Data used in the analyses, along with code to reproduce the analyses, are available at <https://github.com/murdoch1/Multiple-stressor-impacts-on-Yukon-River-Chinook>.

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfas-2022-0254>.

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