Received: 7 May 2024 | Revised: 12 August 2024 | Accepted: 2 September 2024

DOI: 10.1111/gcb.17508

RESEARCH ARTICLE

Global Change Biology WILEY

Body size and early marine conditions drive changes in Chinook salmon productivity across northern latitude ecosystems

Megan L. Feddern[1] | **Rebecca Shaftel**[1,2,3] | **Erik R. Schoen**[4] | **Curry J. Cunningham**[1] | **Brendan M. Connors**[5] | **Benjamin A. Staton**[6] | **Al von Finster**[7] | **Zachary Liller**[8] | **Vanessa R. von Biela**[9] | **Katherine G. Howard**[8]

[1]College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Juneau, Alaska, USA

[2]Alaska Center for Conservation Science, University of Alaska Anchorage, Anchorage, Alaska, USA

[3]BLM Alaska, Anchorage, Alaska, USA

[4]International Arctic Research Center, University of Alaska Fairbanks, Fairbanks, Alaska, USA

[5]Institute of Ocean Sciences, Fisheries and Oceans Canada, Sidney, British Columbia, Canada

[6]Columbia River Inter-Tribal Fish Commission, Portland, Oregon, USA

[7]Fisheries and Oceans Canada, Whitehorse, Yukon, Canada

[8]Alaska Department of Fish and Game, Anchorage, Alaska, USA

[9]U.S. Geological Survey, Alaska Science Center, Anchorage, Alaska, USA

Correspondence

Megan L. Feddern, Northwest Fisheries Science Center, National Marine Fisheries Service, NOAA Fisheries, 2725 Montlake Boulevard East, Seattle, Washington 98112 USA.

Email: megan.feddern@noaa.gov

Funding information

Alaska Sustainable Salmon Fund, Grant/Award Number: 53018 and 54016

Abstract

Disentangling the influences of climate change from other stressors affecting the population dynamics of aquatic species is particularly pressing for northern latitude ecosystems, where climate-driven warming is occurring faster than the global average. Chinook salmon (*Oncorhynchus tshawytscha*) in the Yukon-Kuskokwim (YK) region occupy the northern extent of their species' range and are experiencing prolonged declines in abundance resulting in fisheries closures and impacts to the well-being of Indigenous people and local communities. These declines have been associated with physical (e.g., temperature, streamflow) and biological (e.g., body size, competition) conditions, but uncertainty remains about the relative influence of these drivers on productivity across populations and how salmon–environment relationships vary across watersheds. To fill these knowledge gaps, we estimated the effects of marine and freshwater environmental indicators, body size, and indices of competition, on the productivity (adult returns-per-spawner) of 26 Chinook salmon populations in the YK region using a Bayesian hierarchical stock-recruitment model. Across most populations, productivity declined with smaller spawner body size and sea surface temperatures that were colder in the winter and warmer in the summer during the first year at sea. Decreased productivity was also associated with above average fall maximum daily streamflow, increased sea ice cover prior to juvenile outmigration, and abundance of marine competitors, but the strength of these effects varied among populations. Maximum daily stream temperature during spawning migration had a nonlinear relationship with productivity, with reduced productivity in years when temperatures exceeded thresholds in main stem rivers. These results demonstrate for the first time that well-documented declines in body size of YK Chinook salmon were associated with declining population productivity, while taking climate into account.

KEYWORDS

Bayesian model, Chinook salmon, climate change, Kuskokwim River, northern latitudes, productivity, spawner-recruitment, Yukon River

1 | INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) are adapted to live in freshwater and marine environments from California to the Arctic, survive in the open ocean, and migrate up to 3200km as they home back to natal rivers to spawn. Each spawning population adapts traits to habitat use and environmental conditions which contributes to meta-population stability and resilience through time (Connors et al., 2022; Schindler et al., 2010). In the northern extent of Pacific salmon range in the North American Arctic, air temperature warming is four times the rate of the global average, and has led to sea ice loss, permafrost thaw, increased ocean temperatures, and altered hydrologic regimes that have caused unprecedented ecological, cultural, and socioeconomic consequences (Hicke et al., 2022). As extreme conditions become increasingly frequent and severe (Hicke et al., 2022), there is more evidence that climate threatens many high latitude bird (Choy et al., 2021), fish (von Biela et al., 2020), and mammal (Thompson et al., 2020) species. Among Northern Pacific salmon populations, both marine and freshwater habitats are affected by extreme climate events (e.g., heatwaves) that likely contribute to salmon declines (Carey et al., 2021; Farley Jr et al., 2024; von Biela et al., 2022).

Chinook salmon (*O. tshawytscha*) are influenced by the physical and biological conditions in which they incubate as embryos; rear (including overwintering), and migrate as juveniles; and grow, migrate, and spawn as adults (Crozier et al., 2021). The impacts of environmental conditions are complex and produce both positive and negative effects on Chinook salmon abundance and productivity, which vary based on life stage and across spatial scales. For example, stream temperature has been shown to positively impact juvenile growth during the first summer in freshwater (Falke et al., 2019) but increased stream temperatures during migration and spawning are associated with heat stress (von Biela et al., 2020), which can lead to reduced reproductive success and premature mortality (Hinch et al., 2021; von Biela et al., 2022). For freshwater and anadromous species like Chinook salmon, responses to climate are increasingly dependent on the local conditions because warmer air temperatures do not result in a uniform change across aquatic habitats. For example, stream temperatures are becoming warmer and more variable in response to climatic warming and altered hydrologic inputs (Mauger et al., 2017; Shaftel et al., 2020) such as permafrost thaw and decreased glacial melt (Pitman et al., 2020). Similarly, streamflow regimes include increasing flows in winter and spring (Brabets & Walvoord, 2009) and decreasing flows in the summer (Ge et al., 2013). Many of these complex physical and biological conditions likely influence adult body size which determines reproductive potential as larger fish carry more eggs (Ohlberger et al., 2020; Oke et al., 2020). Thus, body size is a key intrinsic indicator of spawner quality and reproductive potential that represents fecundity associated with growth and age structure that complements extrinsic environmental indicators.

Declines in abundance and productivity are particularly pronounced for Chinook salmon in the Yukon-Kuskokwim (YK) region, which includes both the Yukon (United States and Canada), and Kuskokwim (United States) drainages (Schoen et al., 2023). Chinook salmon have supported subsistence ways of life in the YK region since time immemorial, as well as commercial and recreational fisheries during much of the twentieth century (Carothers et al., 2021). Since the 1990s, Chinook salmon abundance in the region has been below historical averages prompting closures of commercial fisheries and restrictions of salmon-directed subsistence fishing opportunities (Schoen et al., 2023). Record low abundances throughout the past decade resulted in progressively restricted harvest opportunities. Extraordinarily low abundance of Chinook and other salmon species in 2020–2023 resulted in no salmon-directed fishing opportunities for any user group in the Alaska portion of the Yukon River Basin (JTC 2023). Adult returns up the Yukon River into Canada failed to reach the minimum objective established by the United States/Canada Yukon River Panel under the Pacific Salmon Treaty Yukon Salmon Agreement for six of the past 11years (2013–2023; JTC 2023). The Kuskokwim watershed has fared somewhat better; Chinook salmon runs have been below their long-term average since 2010, resulting in severe subsistence fishery restrictions, but have remained large enough to meet the established escapement goal since 2013 (KRITFC, 2022; Larson, 2023). Understanding how changing conditions have impacted Chinook salmon productivity throughout their life cycle in the YK region is vital for an informed response to this crisis.

Here, we analyze the effects of regional and watershed-scale physical and biological drivers across marine and freshwater habitats on the productivity of Chinook salmon populations in the Kuskokwim River and Yukon River watersheds in the United States (US) and Canada (CA). Our objectives were to compile time series of environmental conditions (physical and biological) with hypothesized links to Chinook salmon productivity to determine which conditions explain observed variation in YK Chinook salmon productivity (i.e., adult returns-per-spawner). We also aimed to characterize the coherence or diversity in the responses of individual populations to these drivers within and across watersheds. To identify associations between the environment and the productivity of YK Chinook salmon, we quantified the relationship between spawning abundance and recruitment for 26 Chinook salmon populations while estimating the influence of 4 regional-, 3 subregional-, and 4 watershed-scale indicators. Each indicator represented a hypothesized effect on Chinook salmon during a particular life stage (Table 1) that were developed in collaboration with regional experts (Feddern et al., 2023). There is particular interest to better understand what environmental conditions contributed to the declines in the early 2000s (Feddern et al., 2023); given available data (Table S1); this time period (1980–2016) is the focus of our analysis.

2 | MATERIALS AND METHODS

2.1 | Study area and species

The Yukon-Kuskokwim is an arctic–subarctic region that covers 980,000 km^2 of the United States and Canada, draining west to the Bering Sea (Figure 1). The Yukon River is the fourth largest river

TABLE 1 Hypothesized effects of environmental indicators on Chinook salmon life stages used in the stock-recruitment model.

Covariates	Temporal domain	Hypothesis	Life stage	Brood year offset	Scale
Incubation and juvenile rearing					
Maximum daily streamflow	August–November	High streamflow reduces egg survival through streambed scour	Incubation	0	Population
Median daily streamflow	May–September	High streamflow negatively impacts juvenile foraging efficiency and positively impacts channel connectivity	Juvenile rearing	+1	Population
Stream temperature rearing	May–September (cumulative degree days)	Cumulative degree days during the summer positively impacts juvenile growth during the first summer in freshwater	Juvenile rearing	+1	Population
Juvenile migration and early marine					
Ice breakup timing	Day of year	Later ice breakup negatively impacts survival by preventing optimal migration timing and reducing survival via physical interaction with ice	Smolt outmigration	+2	Subregional
Ice concentration index	January 1–March 15	Winter sea ice conditions negatively impact juvenile growth via prey quality and/or juvenile ocean entry timing	Early marine	+2	Regional
Summer sea surface temperature	June–August	Warmer sea surface temperature reduces early marine growth or survival by impacting availability and/or quality of prey	Early marine	+2	Subregional
Wind	June–August	Greater mixing improves prey availability and/or quality increasing growth and survival	Early marine	+2	Regional
Winter sea surface temperature	January–March	Warmer temperature increases over-winter survival	First marine winter	+3	Regional
Adult marine and spawning migration					
Marine competitors	Annual mean	Greater competition with walleye pollock, and pink and chum salmon through competitive exclusion from optimal habitat, reduces marine growth, adult size, and survival	Immature marine	+ 3	Regional
Maximum daily migration temperature	June–July	Maximum mean daily stream temperatures increase heat stress in spawners and reduce survival and/or reproductive success	Adult migration	0	Population
Body size	Annual mean	Larger body size increases migration survival, fecundity, or egg quality	Adult migration/spawning	0	Subregional

Notes: Temporal domain is the time period for which each covariate was derived, while brood year offset indicates the lag from the brood year. Scale describes whether indicators are standardized across region (Yukon-Kuskokwim), subregion (Yukon [US], Yukon [CA], or Kuskokwim) or population. Covariates are ordered based on the life stage within each category (Incubation and Juvenile Rearing, Juvenile Migration and Early Marine, Immature Marine and Spawning Migration). See Table S4 for additional details on each covariate.

in North America (basin area of 855,000 km^2) and extends from Canada's British Columbia and Yukon Territory through Alaska where it drains into the northeastern Bering Sea. The Kuskokwim River is the ninth largest river in the United States (basin area of 124,319 km^2) and drains into Kuskokwim Bay in the southeastern Bering Sea. The region is characterized by extensive areas of pristine habitat and is sparsely populated with two dense population centers (Fairbanks North Star Borough Alaska, population ~95,000; Whitehorse Yukon Territory, population ~30,000) in the Yukon Basin.

Chinook salmon in the YK region deposit eggs in freshwater during August–September (brood year) that hatch the following spring. Juveniles rear and grow throughout the year as age-1 parr and migrate to sea the following spring as age-2 smolts. Adults return after spending 1–6 (predominantly 2–4) years at sea, such that returning adults are between 3 and 8 (predominantly 4–6) years old. In the Kuskokwim basin, Chinook salmon spawn across at least two-dozen tributaries of the main stem Kuskokwim River. Monitoring of harvest, escapement, and age composition for Chinook salmon has occurred since the mid-1970s with a focus on 16 subbasins monitored by weir or aerial surveys. In the Yukon basin, Chinook salmon spawn across dozens of tributaries (Brown et al., 2017) and are primarily monitored as they migrate upriver through the main stem and in select tributaries in Alaska and Canada (JTC 2023).

2.2 | Chinook salmon productivity

A Bayesian hierarchical stock-recruitment model was used to quantify evidence for heterogeneity in environmental effects on Chinook salmon productivity across population units. The goal of this analysis was to quantify population-specific and subregional (across populations within subregion: Yukon [US], Yukon [CA], Kuskokwim) impacts of environmental conditions on relative indices of Chinook salmon productivity, represented as natural log recruits-per-spawner. The advantage of the hierarchical structure is that it allows for the inclusion of population units with shorter time series, while providing a novel synthesis of the diversity in population-level responses to a common set of environmental processes. Notably, the relative indices

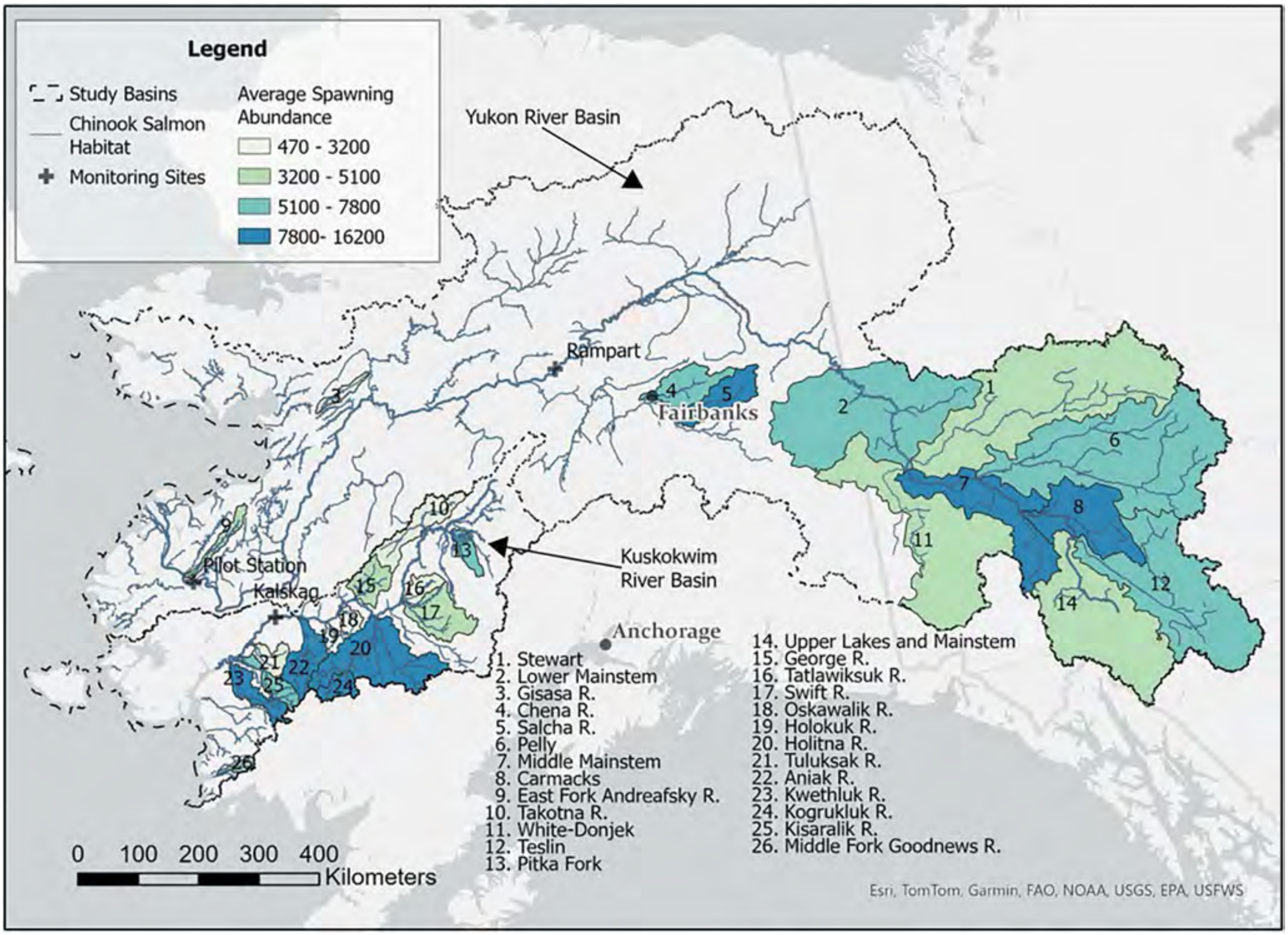

FIGURE 1 The Kuskokwim and Yukon River basins. General spawning distribution of the 26 Chinook salmon population units included in the hierarchical Ricker model to investigate environmental drivers of productivity. Color represents mean spawning abundance for each population during the study period. Dashed outline represents the study area, which is the region of Chinook salmon habitat that was considered for inclusion in this analysis. Temperature monitoring sites at Kalskag, Pilot Station, and Rampart were used to estimate main stem water temperature during migration. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

are not suitable for analyses that require absolute metrics (i.e., stock assessments, comparing population productivity among stocks).

2.2.1 | Spawner-recruit time series compilation

Estimates of salmon population productivity require brood tables which relate the number of adult fish that return to freshwater to spawn each brood year (spawning stock) to the number of offspring (recruits) that were produced. Recruits are estimated as the number of surviving adult offspring that return to freshwater habitat (spawners plus harvest) in the years following the brood year. Chinook salmon in the YK region have a complex life history; therefore, the population-specific age composition of returning fish is necessary to assign the number of recruits in subsequent years to the correct brood year. We compiled existing stock-recruitment datasets (Brown et al., 2020; Connors et al., 2022; Joy et al., 2024; Staton et al., 2020) that were modeled from annual population-specific spawner abundance and associated recruitment estimated from age structured run-reconstructions which applied Ricker stock-recruitment functions in either state-space or regression-based frameworks. Nearly all data that contributed to run reconstructions were collected by projects managed by the Alaska Department of Fish and Game, US Fish and Wildlife Service, and the Department of Fisheries and Oceans Canada; complete list of sources can be found in Table S1.

Suitability of data and modeling approaches for this analysis were identified during a 2022 workshop that included harvesters, Indigenous community members, researchers, and agency scientists (Feddern et al., 2023). During this workshop, it was determined stock-recruitment datasets from previous modeling efforts were of sufficient quality capable of capturing interannual variability that could identify relationships between productivity and environmental conditions (Tables S1 and S2). Time series of 26 Chinook salmon populations across the YK region had at least 10 years of modeled spawner and associated recruitment data which was considered sufficient overlap with covariate data (Figure 1, S1–S3). It was also determined that model approaches should: (1) use a linearized Ricker function to align with the models that generated the time series, (2) incorporate model estimates of uncertainty, (3) apply a hierarchical structure to minimize spurious correlations between productivity and environmental conditions, (4) exclude model data with no associated empirical observations, and (5) validate model structure using simulated data.

2.2.2 | Stock-recruitment analysis

A hierarchical stock-recruitment model (Equation 1, 2) was fit to spawner and recruit abundance data by applying Bayesian methods implemented in Stan using the R package (R Core Team, 2023) 'rstan' (Stan Development Team, 2023). Recruitment was assumed to follow a Ricker function (Hilborn, 1985; Ricker, 1954) and hypothesized relationships with environmental and biological drivers were assumed to affect density-independent processes.

$$\hat{R}_{p,y} = \hat{S}_{p,y}\exp\left(\alpha_p - \beta_p \hat{S}_{p,y} + \sum_c \left(\theta_{p,c}X_{p,t,c}\right)\right), \quad (1)$$

$$\ln\left(R_{p,y}\right) \sim \text{Normal}\left(\ln\left(\hat{R}_{p,y}\right), \sigma_{p,y,\text{recruits}} * \phi_p\right), \quad (2)$$

where $\hat{R}_{p,y}$ is the predicted recruitment for population p in brood year y which is a function of spawner abundance $\hat{S}_{p,y}$, the natural log of maximum recruitment per spawner in the absence of density dependence α_p, and the strength of density-dependent compensation β_p. $R_{p,y}$ is the model derived estimate of recruitment from previous studies (Brown et al., 2020; Connors et al., 2022; Joy et al., 2024; Staton et al., 2020). To ensure uncertainty in estimated $R_{p,y}$ was properly incorporated, $\sigma_{p,y,\text{recruits}}$ was assumed to be known based on the error estimated by the source model of $R_{p,y}$. To ensure sufficient flexibility in observation uncertainty, φ_p represents the stock-specific observation error correction factor not accounted for in the uncertainty in previous models, $\sigma_{p,y,\text{recruits}}$, which allows error to be greater than $\sigma_{p,y,\text{recruits}}$ but not less.

To incorporate error in spawner abundance from the compiled time series, $\hat{S}_{p,y}$ was estimated using an informative prior (see Table 2 for complete list of priors) based on estimated spawner abundance, $S_{p,y}$ and estimated error for spawner abundance, $\sigma_{p,y,\text{spawners}}$.

$$\hat{S}_{p,y} \sim \text{lognormal}\left(S_{p,y}, \sigma_{p,y,\text{spawners}}\right). \quad (3)$$

Less than 2% of spawner and recruit observations had missing error data. For years or populations that error data was missing, the observation error standard deviation (SD) was assumed to be 0.3 on the log scale (mean observed $\sigma\sigma_{p,y,\text{recruits}}$ for observed populations and years).

Environmental covariates were specified to have an additive effect on productivity where the value of covariate c for population p in calendar year t ($X_{p,t,c}$) is multiplied by population specific covariate effect, $\theta_{p,c}$ which is estimated by the model. Covariate effects, $\theta_{p,c}$, and maximum recruitment, α_p, were hierarchically structured across populations within subregions (i.e., Kuskokwim River, Canadian Yukon River, and United States Yukon River),

$$\theta_{p,c} \sim \text{Normal}\left(\mu_{r,c}, \sigma_{r,c}\right), \quad (4)$$

$$\alpha_p \sim \text{Normal}\left(\mu_\alpha, \sigma_\alpha\right), \quad (5)$$

where hyperparameters, $\mu_{r,c}$ and $\sigma_{r,c}$, describe the expected value and variation of each covariate effect among population units for each subregion r, and hyperparameters, μ_a and σ_a, were used to describe the distribution of population-specific maximum recruitment rates across the entire YK region (Table 2). The calendar year for each covariate, t, was offset by 0–3 years to align with the stage of the Chinook salmon life cycle hypothesized to be impacted by each covariate (Table 1). Prior distributions for estimated model parameters

TABLE 2 Description of model parameters and specified prior distributions.

Parameters	Description	Prior
$\theta_{p,c}$	Covariate effect	~ Normal($\mu_{r,c}$, $\sigma_{r,c}$)
α_p	Ricker: max productivity	~ Normal(μ_α, σ_α)
β_p	Ricker: density dependence	~ Normal(0, 0.01)[0,]
μ_α	Hyperparameter: group mean max productivity	~ Uniform(0, 5)
σ_α	Hyperparameter: group SD of max productivity	~ Normal(0, 5)[0,]
$\mu_{r,c}$	Hyperparameter: group mean covariate effect	~ Normal(0, 5)
$\sigma_{r,c}$	Hyperparameter: group SD of covariate effect	~ Normal(0, 5)[0,]
$\hat{S}_{p,y}$	Predicted spawning abundance	~lognormal($S_{p,y}$, $\sigma_{p,y,spawners}$)
φ_p	Parameter: observation error correction factor	~ Normal(1, 1.25)[1,]

Note: Values indicate mean and SD for each distribution; brackets indicate lower and upper bounds.

and hyperparameters (Table 2) were chosen to be diffuse or weakly informative (Table 2). All covariates were standardized by subtracting the population-, subregion-, or region-specific mean and dividing by the SD (Table 1) for the time period 1980–2018 such that each population (or subregion or region) covariate time series had a mean of 0 and SD of 1. As such, covariate coefficients can be interpreted as the percent change in productivity (expressed as natural log recruits-per-spawner; ln[$R_{p,y}/S_{p,y}$]) for a 1 SD increase in a given covariate.

Markov Chain Monte Carlo (MCMC) methods were used to sample from the joint posterior distribution using three chains with 10,000 iterations each. The initial 1000 iterations were discarded as a burn-in period. Convergence of the algorithm was diagnosed using the Gelman–Rubin statistic (Brooks & Gelman, 1998), effective sample size, and visual inspection of trace plots for each chain. We performed a posterior predictive check to assess the model's ability to reproduce properties of the data (Gelman, 2004), wherein we simulated $ln(R_{p,y})$ values from the model and calculated the Bayesian *p*-value (p_B) as the proportion of MCMC iterations in which observed recruitment was greater than the simulated recruitment.

Subregional posterior distributions for $\mu_{r,c}$ represent the mean overall effect of covariate *c* across populations included in this analysis for a given subregion *r* (i.e., Kuskokwim, Yukon [CA], or Yukon [US]), but may not represent other populations in the YK region. We considered posterior estimates with an absolute magnitude >0.1 to be strong, indicating a change in the covariate by +1 SD from the mean resulted in an expected change in population productivity (natural log recruits-per-spawner) of >10%. When the 80% highest density credible intervals (HDI) excluded 0, associations were considered to be meaningful and statistically different than the effect of a null covariate (Text S1; Figures S4–S6).

2.3 | Environmental indicators

2.3.1 | Incubation and juvenile rearing

High streamflow events during the fall spawning and incubation period can reduce egg survival through streambed scour or sedimentation (Goode et al., 2013; Montgomery et al., 1996). We extracted modeled discharge from the Global Flood Awareness System (GloFAS, Harrigan et al., 2020) for 0.1° grid cells that most closely matched each tributary outlet (Text S2 and see Shaftel et al., In Prep). An evaluation of GloFAS performance showed good predictive accuracy against observed streamflow from sites in the study area with flow gages (mean normalized Nash-Sutcliffe Efficiency = 0.67 for 49 sites). A fall streamflow indicator was calculated as the annual maximum of mean daily streamflows in the fall of the brood year (August through November).

Higher than normal streamflow conditions during summer juvenile rearing may reduce foraging efficiency and overall growth (Neuswanger et al., 2015). We extracted modeled discharge from GloFAS for each tributary habitat and calculated a summer streamflow indicator as the annual median of mean daily streamflows in the summer of juvenile rearing (May through September) 1 year after the brood year.

Warm stream temperatures can increase juvenile growth (and presumably subsequent survival) in streams where temperatures are normally below thermal optima (Falke et al., 2019). Stream temperature data were received from 5 main stem and 27 tributary sites from the Alaska Department of Fish and Game, the US Fish and Wildlife Service, and Al von Finster (personal communication; retired biologist with the Department of Fisheries and Oceans Canada; see von Finster, 2023) and combined with U.S. Geological Survey data from stream gages that were directly downloaded using the “dataRetrieval” R package (De Cicco et al., 2022). Stream temperature data were not available for all years with productivity information, and we developed site-specific models of daily stream temperatures that could be used to impute missing data (Text S2 and Figure S7). For each stream temperature time series associated with a population, we calculated an annual indicator (cumulative degree days, base temperature of 0°C) during the summer growing season (May–September) 1 year after the brood year (Honsey et al., 2023).

2.3.2 | Juvenile migration and early marine

We considered several conditions during the juvenile migration and early marine life stages, both 2 years after the brood year, as potential drivers of Chinook salmon productivity. Later main stem river ice breakup has been associated with reduced smolt survival in Yukon River Chinook salmon populations (Chena and Salcha rivers; Cunningham et al., 2018). River ice data were compiled for the Yukon and Kuskokwim Rivers from Arp and Cherry (2022) at three locations. Breakup dates on the Kuskokwim River at Bethel, on the Tanana River at Nenana, and the Yukon River at Dawson were assigned to Chinook salmon population units in the Kuskokwim, Yukon (US), and Yukon (CA) subregions, respectively.

Sea ice cover and the timing of its retreat is an important component of primary productivity and food web dynamics in the eastern Bering Sea (Lomas et al., 2012), potentially impacting the survival and productivity of Chinook salmon (Miller et al., 2013). We included an index of sea ice concentration during the winter before outmigration from Bering Climate Data (Hunt et al., 2011). This index represents the average ice concentration in a 2° by 2° box in the eastern Bering Sea (56° N-58° N, 163° W-165° W) from January 1 to March 31.

Summer sea surface temperature (SST) during the first summer at sea has been associated with salmon productivity (Mueter et al., 2002), adult size (Oke et al., 2020), and growth (Yasumiishi et al., 2020). Seasonal means for summer (June–August) during smolt outmigration were calculated using monthly SST from NCEP/NCAR reanalysis data (Kalnay et al., 1996). We used two indices to represent the northeastern Bering Sea (60.1° N - 65° N and 165° W - 172.5° W) and the southeastern Bering Sea (67° N - 60° N and 162° W-172.5° W) following Yasumiishi et al. (2020). Conditions in southeastern Bering Sea were assigned to populations in the Kuskokwim subregion and conditions in northeastern Bering Sea were assigned to populations in the Yukon (US) and Yukon (CA) subregions to align with the location of ocean entrance for juveniles in each region.

Wind mixing in the eastern Bering Sea is associated with primary productivity, sea ice formation and retreat, and juvenile recruitment of many fish species (Stachura et al., 2014). Wind mixing was expected to integrate aspects of multiple favorable conditions for early marine growth and survival during the first year at sea (Table 1). Monthly zonal westerly winds (u-wind) were acquired for NCEP/NCAR Reanalysis for June–August at 60° N and 170° W at the surface as an approximation for cross-shelf wind for the region during the summer of outmigration. Average summer wind speed vectors were all positive (range: 1.39–5.53) such that standardized values can be interpreted as strength of westerly wind.

Warmer winter SST during the first marine winter coincided with higher survival for the Yukon River Chinook salmon populations analyzed by Cunningham et al. (2018). A seasonal mean (January–March) during the first marine winter was calculated using monthly SST in the southeastern Bering Sea (Siddon, 2022) corresponding to 3 years after the brood year. Winter SST data was not available for the brood years 1980 and 1981 and were assigned to the mean water temperature (i.e., a standardized value of 0). This impacted only two observations for four populations in the Kuskokwim subregion (Table S1).

2.3.3 | Immature marine and adult spawning migration

In subsequent years of marine feeding, there is potential for competition, predation, and interspecific interactions with other fishes. Adult walleye pollock (*Gadus chalcogrammus*) is a highly abundant consumer in the eastern Bering Sea that overlaps spatially with Chinook salmon as inferred by bycatch of western Alaska Chinook salmon in the pollock fishery (Ianelli & Stram, 2015). Some stocks of other species of Pacific salmon such as pink salmon (*O. gorbuscha*) and chum salmon (*O. keta*) may also interact directly or indirectly with YK Chinook for resources in the Bering Sea and North Pacific, potentially impacting survival, growth, and fecundity of Chinook salmon (Cunningham et al., 2018; Oke et al., 2020; Ruggerone et al., 2023).

We derived a “marine competitor” index representing both direct and indirect interspecific interactions. Time series of annual biomass of adult (age 3+) walleye pollock and annual recruits of juvenile walleye pollock were compiled from stock assessment reports (Ianelli et al., 2020). Annual abundance estimates of the total of wild- and hatchery-origin pink salmon (*O. gorbuscha*) and chum salmon (*O. keta*) in the Bering Sea and North Pacific Ocean were compiled from the North Pacific Anadromous Fish Commission database and North Pacific Fisheries Commission documents by Ruggerone and Irvine (2018) and summarized by Oke et al. (2020). Because of high collinearity across these biological times series, we applied dynamic factor analysis, a dimension reduction technique that identifies common processes underlying a set of time series, to identify a single underlying trend representing an index of overall abundance of marine competitors which we then used as a covariate (Text S3, Figures S8, S9).

Warm stream temperatures may negatively affect spawning adults in shared migration corridors that regularly exceed thresholds known to induce thermal stress (e.g., 18°C; von Biela et al., 2020) or in warmer spawning tributaries. The final stream temperature time series (described above) for each migration corridor was used to estimate thermal conditions affecting adult migration. We used migration timing information from escapement monitoring projects and radiotelemetry studies (Eiler et al., 2015) to identify the time period when each population was exposed to maximum temperatures as they moved through the main stem and into their respective spawning tributary. Stream temperatures experienced by adults along the upstream migration were then estimated by calculating the annual maximum of mean daily stream temperatures of main stem and tributary habitats occupied by each population during migration in the return year of adults (spawners) which corresponds to the brood year of offspring (recruits) (Text S2 and Figure S7, see Shaftel et al., In Prep).

Body size is linked to reproductive success and fecundity of Chinook salmon (Malick et al., 2023; Ohlberger et al., 2020; Oke et al., 2020). Data on Chinook salmon body size (nearest mm, mid eye to fork of tail) were collated and archived by Clark et al. (2018) from age, sex, and length projects across Alaska and Canada. Observations for body size of escaped salmon were available for some population units in this study and a dynamic factor analysis (DFA) was performed to derive overall trends in body size for each of the Yukon (United States and Canada) and Kuskokwim subregions (Text S3; Figures S10–S13). This approach allowed us to include size from as many populations as possible, despite variability in time series length. We used a single time series, the latent trend of the subregion-specific DFA representing the dominant trend among all populations within a subregion, as a covariate. Body size and the marine competitor index are both biological (as opposed to physical) conditions and as such are subject to cumulative effects of environmental processes and processes at previous life stages. Given that the size of spawning individuals likely represents the cumulative effects of processes several years prior to the brood year, and size of the spawning population is related to offspring survival up to 3 years after the brood year, these process are suitably separate in time so as to not confound interpretation of estimated body size effects. The impact of competition at sea and body size were of particular interest to communities in the region (Feddern et al., 2023) and our objective was to identify the relative effects of multiple drivers which warranted the inclusion of biological conditions in the model despite these distinct properties compared to the other environmental drivers.

Finally, we conducted two post hoc analyses. First, we characterized nonlinear or threshold patterns in covariate effects by examining the residuals from simple linearized Ricker models fit without environmental effects, as these provided a standardized metric of relative productivity after accounting for density dependence that was comparable across all populations and brood years. We plotted these Ricker residuals against unstandardized covariates at appropriate time lags to reveal whether salmon responded similarly to environmental conditions expressed in absolute terms (e.g., migration temperature,°C). Second, we tested the model sensitivity to two moderately correlated covariates ($R^2=0.54$), body size and marine competitors (Text S4), by omitting each individually from the model and comparing the results to model results that included all 11 covariates.

3 | RESULTS

The length of spawner and recruit time series ranged from 14 to 31 years spanning brood years 1980–2016. Spawning abundance fluctuated annually, and most populations had their lowest spawning abundance around 2010 (Figure S1). Eleven covariates were included in the final model (Text S4 and Table S4) and did not indicate multicollinearity based on variance inflation factors (Table S5) and R^2 (Figures S14–S17). Most populations exhibited density dependence where the productivity index declined with an increase in spawner abundance (Figure S3). The impact of density dependence varied across populations and was highly uncertain—a 1 SD increase in spawner abundance resulted in a decrease in productivity as small as 4% in the Takotna (50% HDI: −6% to −2%) to a decrease as large as 91% (50% HDI: −119% to −63%) in the Kwethluk (Table S6). Most populations experienced low productivity during brood years in the mid-1990s, followed by a period of improvement, with a second decrease in the early 2000s (Figure 2). However, the magnitude and timing of this change varied across populations (Figure 2).

The posterior predictive check confirmed that the model could simulate observations similar to those it was fit to ($P_B=0.46$; Figure S18). Effective sample sizes were all >1000, indicating high precision in summary statistics such as the posterior mean and various quantiles. R-hat values were < 1.05, indicating chains were well mixed and approximated the same stationary distribution.

3.1 | Environmental indicators

Mean estimated covariate effects (Figure 3, $\mu_{r,c}$) varied across subregions and only winter SST substantially differed from 0 for all subregions and populations (positive effect; Figure 3). For most freshwater conditions, the estimated covariate effect varied by population (e.g., maximum daily migration temperature; Figure 4) while marine conditions had consistent covariate effects within each subregion (e.g., summer SST, predominantly negative effect; Figure 4).

3.1.1 | Incubation and juvenile rearing

Maximum daily streamflow during egg incubation was negatively associated with productivity for populations in both the CA and US Yukon subregions and positively associated with populations in the Kuskokwim subregion but did not differ from 0 (Figure 3). Both the strength and uncertainty of the effect of maximum daily streamflow during egg incubation varied by population across the Yukon subregion (Figure 4). Subregional posteriors describing the effect of maximum daily streamflow did not exclude 0 for any subregion (Figure 3), but posteriors for five of the eight Yukon (CA) populations did (Figure 4). Across the Yukon (CA) subregion, a 1 SD increase in maximum daily streamflow resulted in a 10% decrease in Chinook salmon productivity on average (80% HDI: −19% to 0%).

Subregional posterior distributions did not exclude 0 for median daily streamflow and cumulative stream temperature during juvenile rearing (Figure 3). At the population level, the association between cumulative stream temperature and Chinook salmon productivity varied across populations with both positive and negative associations in each subregion but were highly uncertain (Figure 4).

3.1.2 | Juvenile migration and early marine

River ice breakup date was not associated with Chinook salmon productivity in the Yukon (US) and Kuskokwim but was negatively associated for the Yukon (CA) subregion (Figure 3). Both positive and negative associations between river ice breakup date and productivity that excluded 0 were observed in the Yukon (US) subregion (Figure 4). Sea ice cover was strongly, negatively associated with Chinook salmon productivity in the Kuskokwim and weakly, negatively associated with Yukon (CA) subregions and

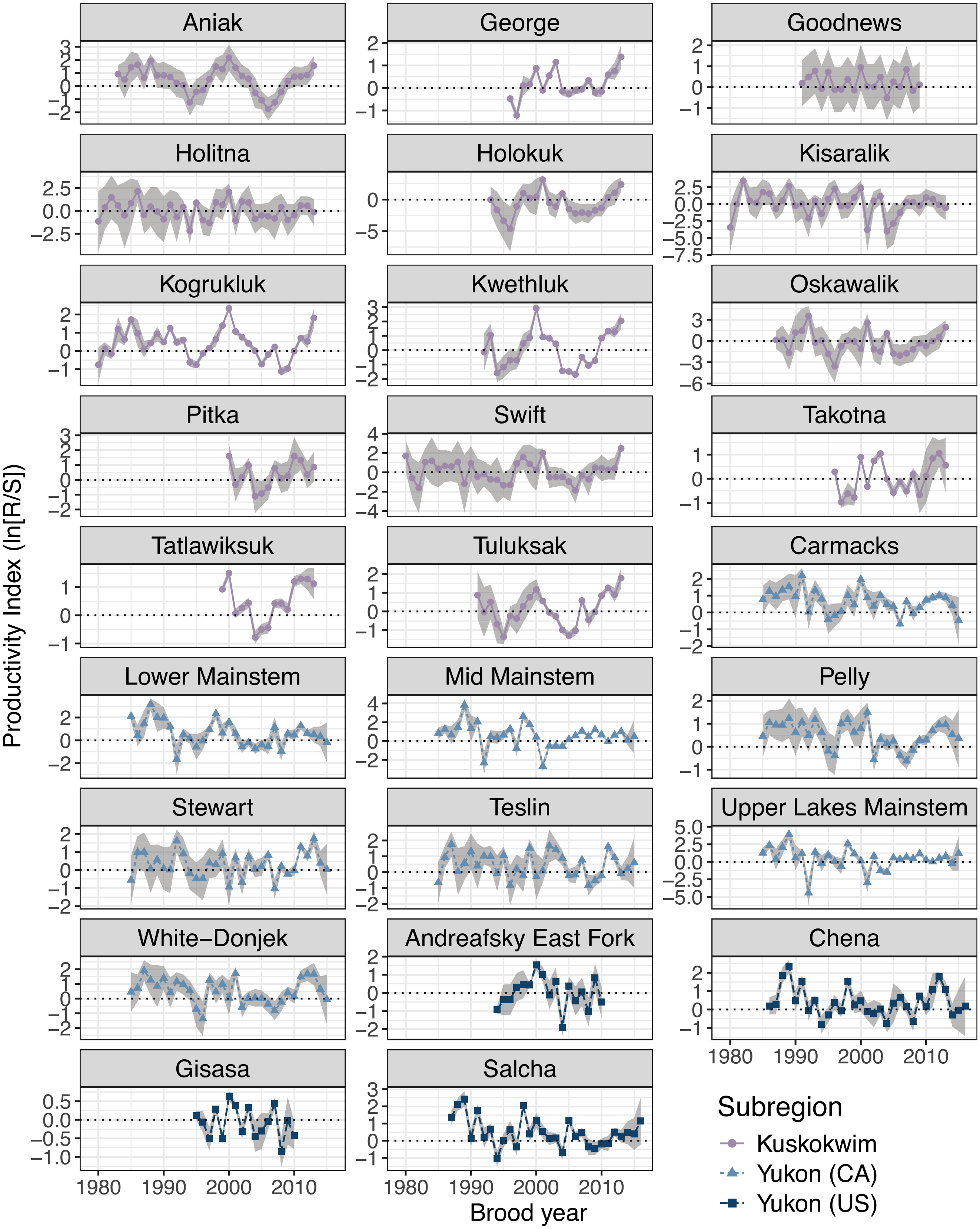

FIGURE 2 Chinook salmon population productivity (natural log recruits-per-spawner) by brood year for population units in the Kuskokwim River drainage (pink) and Yukon River drainage (blue). Dotted lines at zero represent the long-term mean productivity levels of each population and shaded area represents 2 SD.

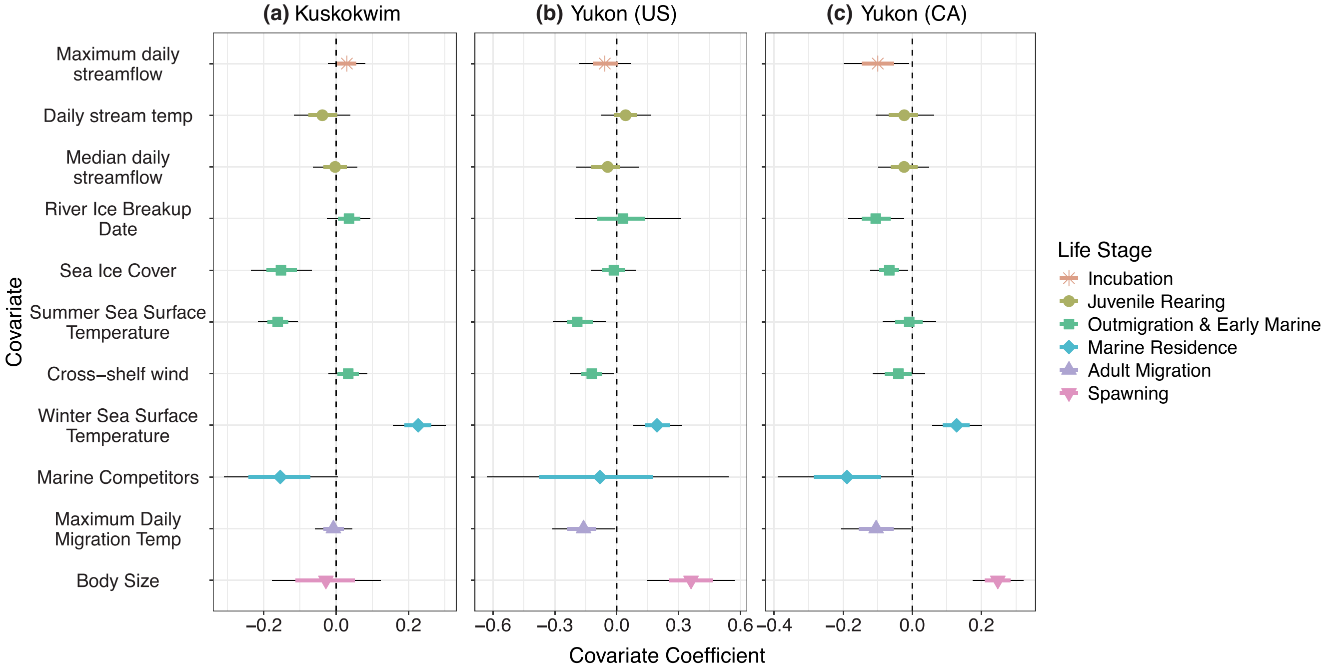

FIGURE 3 Posterior summaries of subregion-level covariate coefficients ($\mu_{r,c}$), (a) Kuskokwim, (b) Yukon (US), and (c) Yukon (CA) for each environmental covariate. Points show the posterior median of each $\mu_{r,c}$, while the thick colored and thin black lines describe the posterior uncertainty/spread (50% and 80% credible intervals, respectively). Colors and shapes denote the life stage impacted by the covariate and the dashed line at zero represents a null effect on productivity. See Table 1 for a description of covariates and Table S6 for numerical values of these estimates.

excluded 0 (Figure 3a,c) but was not associated with productivity in the US Yukon subregion (Figure 3b). Across populations, 13 of 14 Kuskokwim populations had negative associations with sea ice cover, eight of which excluded 0. A 1 SD increase in sea ice cover resulted in a 15% decrease (80% HDI: −23% to −7%) in Chinook salmon productivity in the Kuskokwim subregion (Figure 3; Table S7).

Summer sea surface temperature during the early marine life stage was strongly, negatively associated with productivity and excluded 0 for the Kuskokwim and Yukon (US) subregions where a 1°C increase (1 SD) resulted in a 16%–19% decrease (80% HDI Kuskokwim: −21% to −11%; Yukon [US]: −31% to −8%) in Chinook salmon productivity (Figure 3; Table S7). The association with summer SST was consistently, strongly negative at the population level for the Kuskokwim and Yukon (US) subregions (Figure 4). The association between population productivity and wind was weak and only excluded 0 for the Yukon (US) subregion. Winter sea surface temperature during the first marine winter had a strong, positive association with Chinook salmon productivity (Figure 4). A 1°C increase (1 SD) resulted in a 13% (Yukon CA; 80% HDI: 5%–20%) to 23% (Kuskokwim; 80% HDI: 16%–30%) increase in Chinook salmon productivity that excluded 0 for all subregions (Figure 4; Table S7).

3.1.3 | Immature marine and adult spawning migration

Record high abundance of some Pacific salmon species has been associated with reduced growth and survival across numerous species and trophic levels in the northeast Pacific (Ruggerone et al., 2023). We found the marine competitor index had a strong, but highly uncertain negative association with Chinook salmon productivity but did not exclude 0 (Figures 3a and 4). Smaller body size has been attributed to competition at sea in several studies (e.g., Oke et al., 2020) and body size was moderately correlated with marine competitors. Our post hoc sensitivity analysis wherein size was removed from the model revealed a stronger association between the marine competitor index and productivity across all three subregions (Figure S19) with reduced uncertainty compared to the full model (Figure 3). Similarly, when the marine competitor covariate was omitted from the model a stronger relationship with body size was estimated (Figure S20); these changes did not alter the overall interpretation of other drivers compared to the full model.

Maximum daily migration temperature during the adult spawning migration was negatively associated with productivity at the subregional scale and excluded 0 for both of the Yukon subregions (Figure 3) but was variable across populations (Figure 4). Some populations had strong, negative associations that excluded 0 in both the Yukon (US) and the Yukon (CA) subregions (Figure 4). The post hoc analysis of the relationship between Ricker residuals and absolute stream temperature during migration showed limited evidence for a nonlinear relationship (Figure 5) that might align with initial hypotheses of a threshold effect near 18°C (Table 1). This decline was most apparent when maximum daily temperatures reached 18.5°C for the Yukon (US), 20°C for Yukon (CA), and 16°C for the Kuskokwim basin (Figure 5).

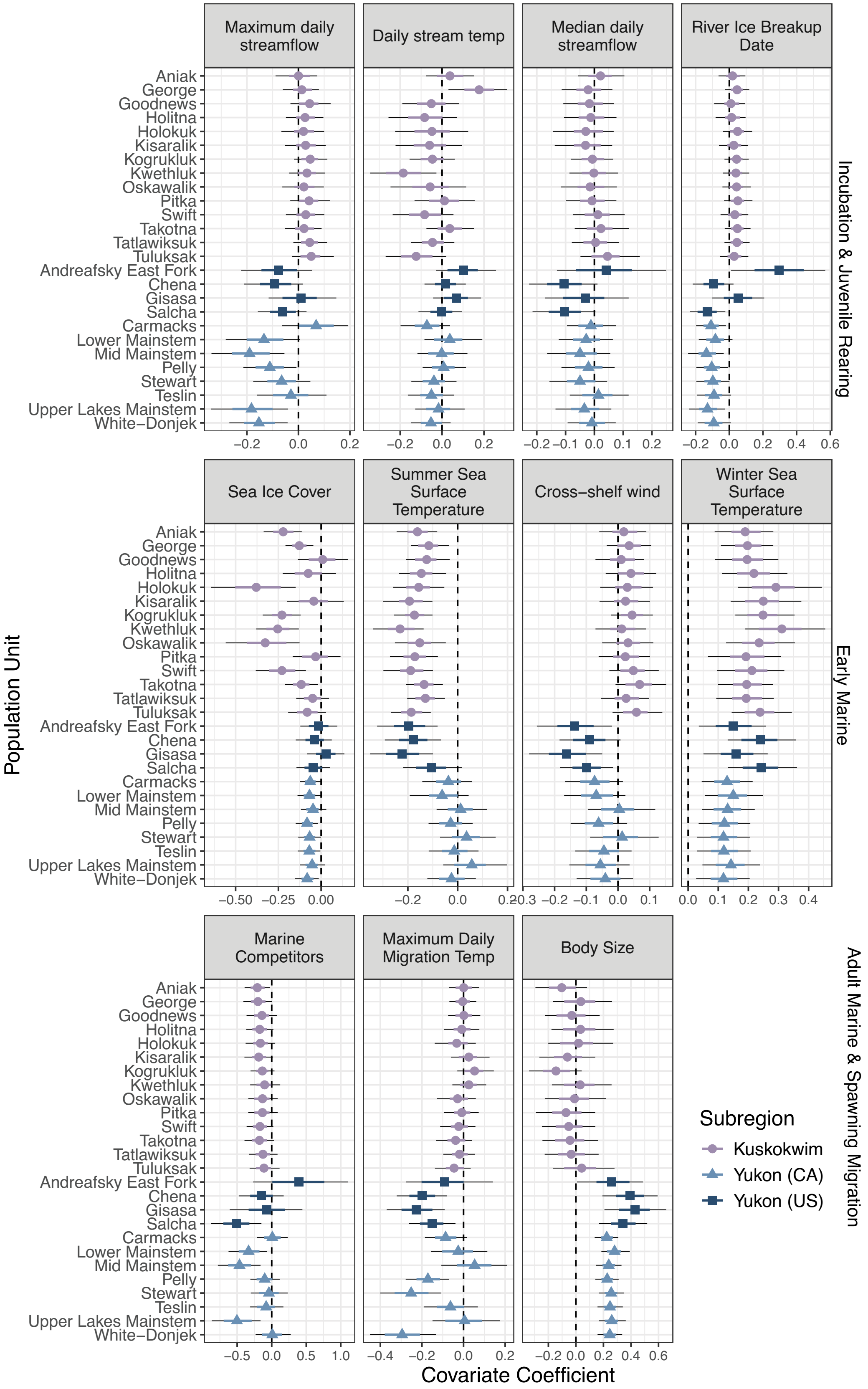

FIGURE 4 Posterior summaries of the population-level covariate coefficient ($\theta_{p,c}$) between environmental covariates and Chinook salmon population productivity (natural log recruits-per-spawner). Points and lines have the same interpretation as Figure 3.

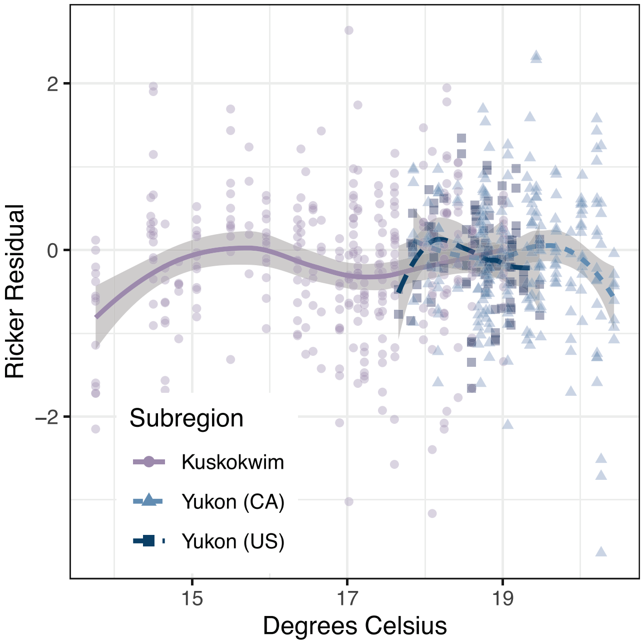

FIGURE 5 Relationships between Ricker residuals and maximum daily migration temperature. The vertical axis represents an index of population productivity after accounting for density dependence (excluding covariates). Each circle represents the productivity of one population in one brood year, colored curves represents a LOESS regression fit to the data for each region, and the gray band represents the 95% confidence interval (see Figure S19 for additional relationships).

Size of adult Chinook salmon migrating to the freshwater environment to spawn had a strong positive association with productivity that excluded 0 across the Yukon subregions but not the Kuskokwim subregion (Figure 3). At the subregional scale, a 68 mm decrease in size (1 SD) in the Yukon subregions, was associated with a 25%–36% decline in population productivity (Figure 3; Table S7). At the population scale, Yukon populations had consistently positive associations between body size and production (Figure 4).

4 | DISCUSSION

The results of our spatially comprehensive stock-recruitment analysis revealed that YK Chinook salmon declines are likely a response to multiple factors throughout their life history including the effects of adult body size and of physical environmental conditions in freshwater and marine ecosystems. Freshwater conditions tended to show population-specific responses during the incubation and juvenile life stages that likely result from heterogeneous freshwater habitat (e.g., high streamflow) and local adaptations which may produce asynchronous responses to environmental change that can stabilize salmon production at larger spatial scales (e.g., Brennan et al., 2019). In contrast, across populations, early marine conditions had a consistent, strong influence on productivity supporting previous research that identified this life stage as a critical period (Howard et al., 2016). Collectively, our results show favorable conditions for YK Chinook salmon productivity coincide with moderate flows during incubation, low sea ice cover prior to smolt outmigration, below average summer SST and above average winter SST during the first year in the marine environment. Adult body size and migration temperatures have particularly strong influence on the productivity of Yukon populations and may partially explain the exceptionally low abundance in recent warm years compared to Chinook salmon populations within the Kuskokwim River watershed.

4.1 | Heterogeneous responses to freshwater conditions

Freshwater conditions had variable effects on juvenile life stages across populations (Figure 4) and subregions (Figure 3), which may partially explain asynchronous dynamics in the Yukon basin (Connors et al., 2022). Negative impacts of high streamflow on productivity in the Chena and Salcha populations were observed during juvenile rearing, in agreement with Neuswanger et al. (2015) and Cunningham et al. (2018) that found higher streamflow led to reduced feeding efficiency, growth, or survival in the same populations. However, no other populations exhibited similarly strong effects. Greater precipitation during spawning and rearing has also been shown to reduce productivity in Yukon (CA) populations (Murdoch et al., 2024), in agreement with our streamflow results although our results show more variable responses across populations. Underlying heterogeneity in tributary conditions, including habitat complexity and local adaptations, may protect some incubating eggs from high streamflow events in certain watersheds.

Environmental conditions during juvenile rearing had a minimal impact on Chinook salmon productivity, contrary to our expectations that warmer temperatures would increase growth and survival based on temperature-dependent growth potential (Falke et al., 2019) and that higher streamflows would reduce foraging efficiency. It is possible that the hypothesized benefits of enhanced juvenile growth on survival are counteracted by indirect impacts of warm conditions, such as increased predation rates by warm-adapted predators such as northern pike (Dunker et al., 2018; Öhlund et al., 2015; Schoen et al., 2022) or lower availability and quality of food resources. Many subsistence fishermen and field researchers have reported seeing greater numbers of northern pike in salmon habitats in the YK region, especially during warm summers (Godduhn et al., 2020; Raymond-Yakoubian & Raymond-Yakoubian, 2015; Schoen et al., 2022). Similarly, higher stream flows during juvenile rearing may improve side channel connectivity, potentially mitigating negative effects of reduced foraging efficiency in main stem habitats. Rearing in non-natal streams is common across the region, particularly in the Canadian Yukon (Bradford et al., 2001; Daum & Flannery, 2011), which limits our ability to summarize relevant hydrological conditions. Notably, drivers during early life stages will always be challenging to detect without intermediate indices of juvenile abundance to separate mortality among different stages in the life cycle.

Our results showed limited evidence for the effect of river ice breakup date with a few notable exceptions. River ice breakup had a positive effect on the East Fork Andreafsky River population (later river ice breakup is more productive) and a negative effect on the Chena and Salcha populations (earlier river ice breakup is more productive). Previous studies also found that earlier breakup was better for some Yukon (US) populations (Cunningham et al., 2018; Ohlberger et al., 2016) and Yukon (CA) populations (Murdoch et al., 2024). Later breakups can be more dynamic, sometimes resulting in large ice jams and flooding which may harm smolts due to physical interactions with the ice or stranding when floodwaters recede. The East Fork Andreafsky River is located close to the mouth of the Yukon River, and populations lower in the river may encounter less adverse effects of dynamic breakups due to shorter migrations.

4.2 | Early marine conditions: a critical period for productivity

Previous research suggested that Yukon River Chinook salmon population dynamics are predominantly driven by factors occurring between the adult spawner life stage and their offspring's first summer at sea (2 years after the brood year; Howard & von Biela, 2023, Murphy et al., 2017). This window includes juvenile outmigration and early marine residence that have been the focus of several studies that identified size-dependent mortality when juvenile salmon enter estuaries and nearshore environments (Duffy & Beauchamp, 2011; Healey, 1982; Moss et al., 2005) and condition-dependent mortality prior to the first marine winter (Howard et al., 2016). Our results show that environmental factors impacting growth and body condition during this critical period also impact overall population productivity across the region. We found that low sea ice cover during outmigration, cool summer marine temperatures, and warm winter marine temperatures are the best conditions during early marine residence for the productivity of Chinook salmon populations.

This combination of environment–productivity relationships during the early marine critical period suggests that cold winters continue to limit northern salmon productivity even as summers may be too warm. The evidence of cold limitation on productivity is consistent with several other studies (Cunningham et al., 2018; Murdoch et al., 2024; Murphy et al., 2021). Warmer winter conditions may facilitate feeding opportunities via increased prey quality or an increase in the spatial extent of potential foraging habitat via reduced sea ice extent (Cunningham et al., 2018; Murdoch et al., 2024). Relationships between northern salmon production and summer temperatures vary among studies and likely reflect differences in the absolute temperature range considered relative to optimums. For example, previous work determined summer sea surface temperature was negatively associated with growth of juvenile Chinook salmon in the southeastern Bering Sea and was particularly pronounced during warm stanzas (2002–2010), but the relationship was not present in the northeastern Bering Sea (Yasumiishi et al., 2020). These differences appear to track shifting bottom-up relationships as warming summer SSTs become associated with reduced diet mass and lower piscivory for juvenile Chinook salmon (Garcia & Sewall, 2021; Murphy et al., 2021).

4.3 | Influence of crowded seas

The combined biomass of both natural and hatchery released salmon in the North Pacific Ocean has increased since the 1980s (Ruggerone & Irvine, 2018), and this has initiated trophic cascades across ecosystems (Ruggerone et al., 2023). The underlying trend in walleye pollock and pink and chum salmon abundance (Marine Competitors Index panel in Figure 6) was negatively associated with the productivity of Chinook salmon in the Kuskokwim subregion and some populations in the Yukon subregions (Figures 3 and 4) consistent with negative direct or indirect interactions among species in the marine environment. Spatial and dietary overlap between western Alaska Chinook salmon and pink and chum salmon varies throughout the year, and between stocks of pink and chum salmon (Myers et al., 2009). Previous research identified competition for food and density-dependent growth effects occurring when salmon feed in offshore waters (Myers et al., 2009). Complex interactions can impact growth opportunities such as avoidance of other species that limits access to resources or favorable environmental conditions, increased movement, or trophic cascades. This may explain the moderate negative correlation between spawner body size and the marine competitors index (Figure S16). Collectively, these results highlight the potentially important interplay between marine conditions and interactions at sea impacting body size of spawners, which may ultimately influence productivity via changes in juvenile survival and condition, body size, and fecundity of adults as they leave marine habitats to spawn. This finding is consistent with other studies that have identified competition at sea as a likely driver of declining body size (Oke et al., 2020), survival (Cunningham et al., 2018), and productivity (Ohlberger et al., 2018) among YK Chinook salmon. Notably, these dynamics warrant further investigation to disentangle the impacts of individual species; additionally, not all North Pacific chum and pink salmon populations forage in the Bering Sea, and the inclusion of a more spatially explicit marine competitor index could improve our ability to test this hypothesis.

4.4 | Smaller spawner size in Yukon Chinook salmon

Decline in the average body size of spawning individuals was identified as having the strongest negative effect on population productivity of Chinook salmon in the Yukon subregions (Figures 3 and 4). In many fish species including Pacific salmon, the body size

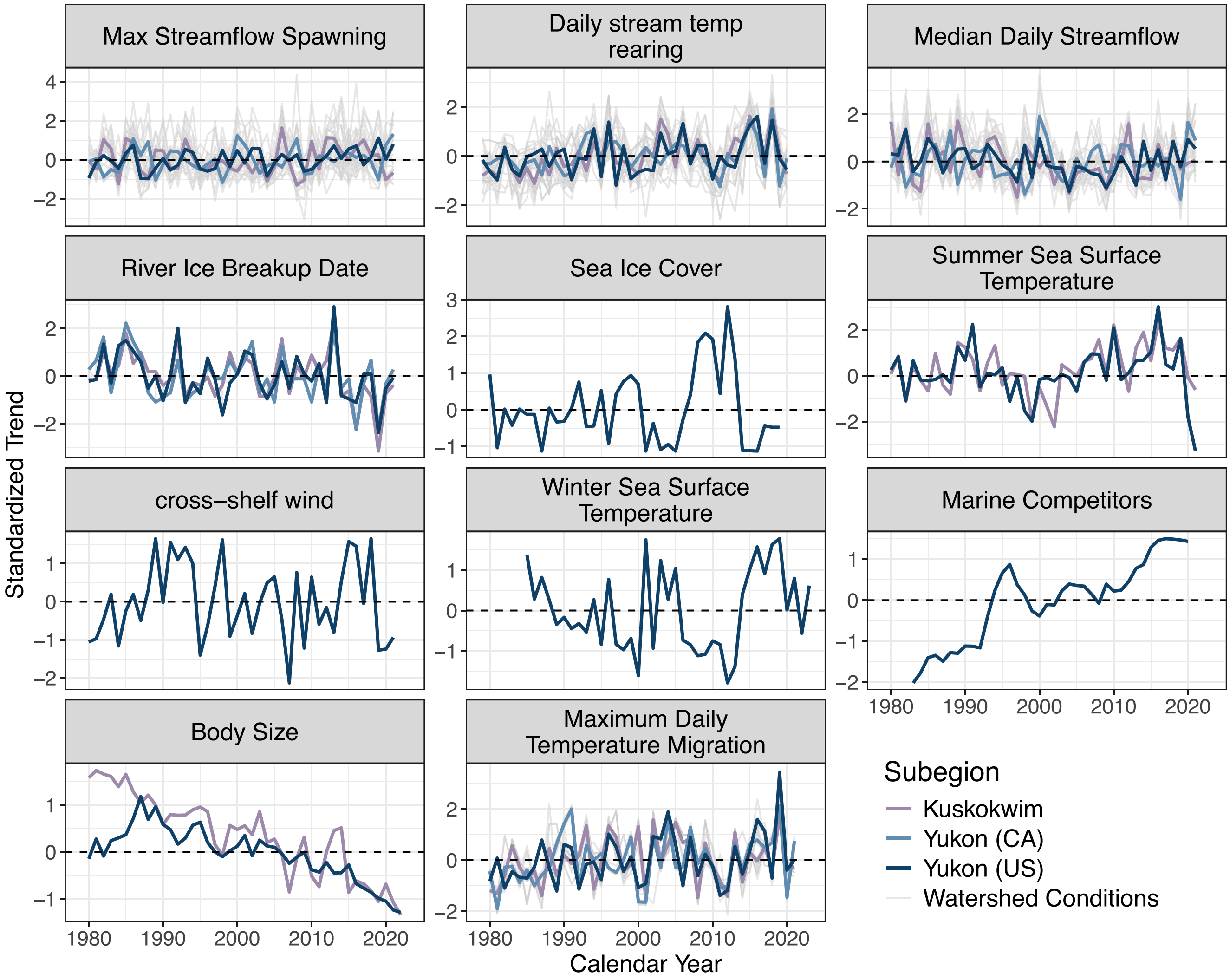

FIGURE 6 Standardized time series of environmental conditions for the Kuskokwim River drainage (pink) and Yukon River drainage (blue) experienced by Chinook salmon from a given brood year. The horizontal dashed line indicates the long-term mean between the years 1980 and 2016.

of spawners can affect future population abundance and productivity because larger females disproportionately contribute to replacement due to higher egg production and higher egg quality (Barneche et al., 2018; Ohlberger et al., 2020). Body size of Pacific salmon can also impact susceptibility to other stressors during spawning and migration such as streamflow and temperature which interact with migration distance (Braun et al., 2013; Tuor et al., 2020). For Yukon River Chinook salmon, the decline in size since the 1970s is estimated to have reduced female reproductive potential by 24%–34% (Ohlberger et al., 2020). Our results show that the decline in body size corresponded to a 30% decline in productivity across the Yukon since the 1980s. Changes in size have not only been driven by demographic changes, specifically declines in mean age of adult spawners (Ohlberger et al., 2020) but also reduced size at older ages (Ohlberger et al., 2018). Previous work has identified declines in body size of Pacific salmon across Alaska (e.g., Lewis et al., 2015; Ohlberger et al., 2018), which has largely been attributed to changing environmental conditions, competition, and late-stage mortality at sea (Manishin et al., 2021; Ohlberger et al., 2023; Oke et al., 2020). Size-selective harvest may also be driving earlier maturation and declines in size, but the evidence is not conclusive (Lewis et al., 2015).

4.5 | Nonlinear dynamics may obscure drivers

Evidence of heat stress during freshwater spawning migrations and reduced productivity in years of warm freshwater migrations have emerged as important stressors in recent years for high latitude Pacific salmon populations (Howard & von Biela, 2023; Jones et al., 2020; Murdoch et al., 2024; von Biela et al., 2020; von Biela et al., 2022). River temperatures that exceed 18°C induce heat stress in spawning Yukon River Chinook salmon (von Biela et al., 2020) that is more prevalent in warm years. Howard and von Biela (2023) estimated that 45% of the variability in production of juvenile Chinook salmon per adult spawner can be attributed to conditions that adults experienced during the spawning migration (either temperature, discharge, or a combination). Record-breaking temperatures and prolonged drought in 2019 caused premature mortality events for all five Pacific salmon species across Alaska, including the Yukon River (von Biela et al., 2022).

Our model results identified a negative linear relationship between spawning migration temperature and productivity (Figure 3), with greater among-population heterogeneity in relationships exhibited by Yukon River populations than Kuskokwim River populations (Figure 4). Post-hoc analyses indicated a potential nonlinear, threshold relationship between productivity and absolute water temperatures that aligned with the hypothesized relationship (Figure 5). Water temperatures >20°C for Canada Yukon Chinook salmon were associated with declines in productivity (Figure 5) and compare favorably to the understanding that heat stress begins at ~18°C and intensifies >21°C (von Biela et al., 2020, 2022). The difference in water temperatures associated with the decline in productivity may be the result of locally adapted thermal tolerances for heat stress as a result of their longer, warmer, migration, as previously shown in sockeye salmon (Eliason et al., 2011). Simulation testing identified that our analysis was not suitable for detecting non-linear relationships between productivity and drivers (Text S1). We may underestimate the impact of drivers that exhibit underlying nonlinear relationships with productivity and are unable to fully resolve the impact of thresholds by modeling them as linear associations.

4.6 | Study limitations and future research

We characterized regional and population-specific conditions using downscaled climate models and subregional summary statistics to quantify their association with Chinook salmon productivity. This approach is limited in its ability to characterize within-watershed habitat complexity that is a component of survival and productivity during freshwater life stages. For example, thermal refugia, side channel/minor tributary connectivity, and gravel quality for redds are important habitat characteristics for salmon production; however, habitat data with sufficient spatial and temporal resolution do not exist. Individual watersheds have also experienced other changes over the study period such as wildfire, placer mining, and human development (Wohl et al., 2022). We tested hypotheses relevant to high streamflows, but low streamflows can also impact habitat availability and connectivity, however, events such as dewatering

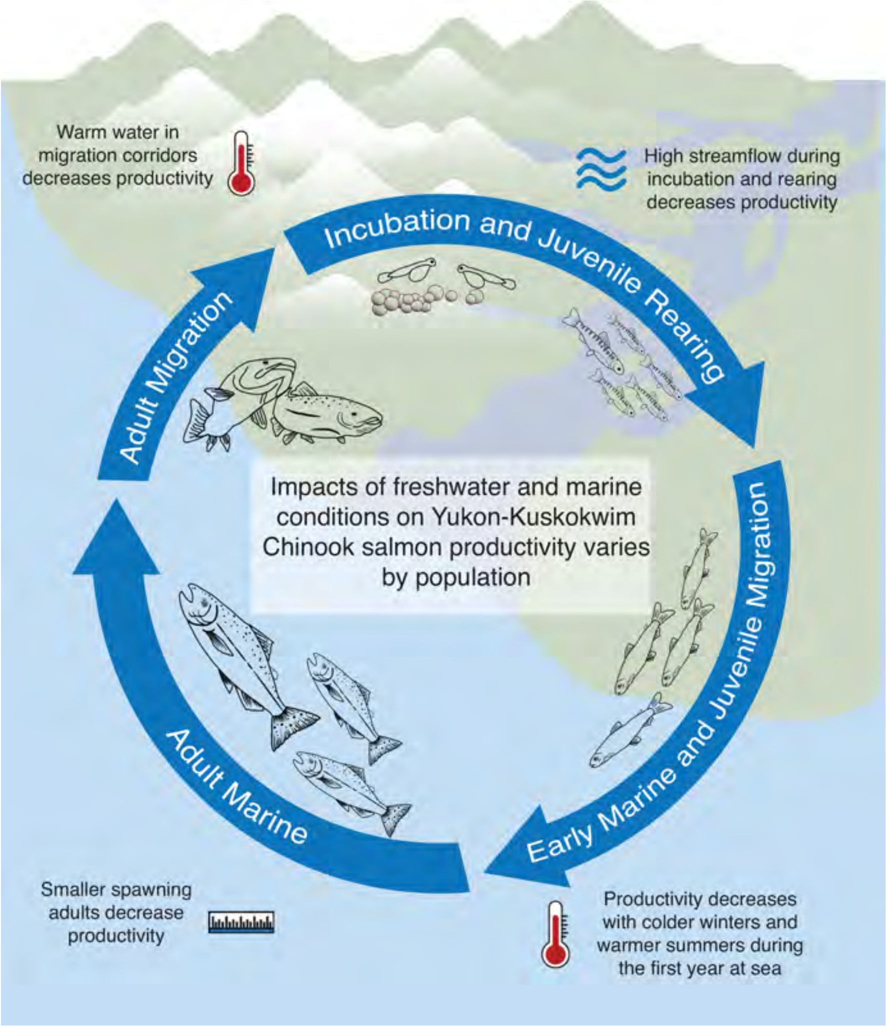

FIGURE 7 Summary of overall impacts of freshwater and marine conditions on Yukon-Kuskokwim Chinook salmon productivity throughout their life cycle.

are challenging to document in remote regions and may not be captured by regional indices (i.e., streamflow, precipitation, or drought). Altogether, this highlights the challenge in characterizing important freshwater conditions in remote high latitude regions.

The YK region has experienced particularly extreme environmental conditions in recent years (2015–2022; Figure 6), including marine heatwaves, freshwater heatwaves, and droughts (Farley Jr et al., 2024; von Biela et al., 2022). Unfortunately, returns of these brood years were not complete in time for this analysis. As a result, we were unable to characterize responses in productivity to the most recent extreme environmental conditions. However, Chinook salmon returns to the YK region declined by 45% between 1998 and 2010 (relative to 1982–1997; Schoen et al., 2023), a period our analysis is well suited to address. While recent drought and high water temperatures during the 2019 heatwave are of particular concern (von Biela et al., 2022), communities in the region are also keen to identify drivers that led to fishery closures and disaster declarations in the early 2000s.

A general question remains about the extent to which retrospective analyses relating past Chinook salmon survival and population dynamics to environmental processes provide inference for future ecosystems outside the bounds of past conditions. Historically, the range-wide view of Pacific salmon demonstrated that warm conditions on a regional scale tend to favor Alaska's salmon populations and cool conditions favor west coast (British Columbia to California) salmon populations (Hare et al., 1999). As these relationships have been reevaluated under new climate conditions, evidence for non-stationary salmon–environmental relationships has grown (e.g., Litzow et al., 2020; Malick, 2020) where prior relationships no longer hold as new environmental extremes are reached. As such, analysis of past climate–salmon relationships may have limited reliability in predicting future responses to ongoing climate change within this region. While the range of contrast in past environmental observations may suggest linear associations, the underlying salmon–climate relationship may in fact be highly nonlinear and the utility of predictions for future responses of salmon to yet unobserved, or infrequently observed, climatic or hydrologic conditions may be limited. Life cycle models incorporating nonlinear responses may be useful tools to explore how salmon may respond to future climate scenarios. The future of this complex and dynamic salmon–climate system may be inherently less predictable than the uncertainty described by statistical models detecting these relationships (Schindler & Hilborn, 2015).

4.7 | Conclusion

Chinook salmon in the YK region are culturally important and contribute to the food security and wellbeing of subsistence-dependent communities throughout the region. We conclude that Chinook salmon productivity in the YK region is associated with co-occurring ecological factors in both the freshwater and marine environment. The magnitude of the effect of each environmental condition varies based on population and subregion. These heterogeneous responses may buffer some populations to future change relative to others, but many responses were similar across subregions and populations indicating regional synchrony in response to climate change. In the future, streamflow is expected to be more variable (higher highs, lower lows) with warmer temperatures in the freshwater and marine environments. These conditions will have both positive (warmer winters, less sea ice) and negative (increased stream temperatures and variable streamflow) effects on YK Chinook salmon (Figure 7). As new environmental extremes are reached, it will be important to reevaluate conditions that impact Chinook salmon, as these relationships may change if environmental conditions reach new states, which is likely as permafrost and glaciers continue to thaw and sea ice extent continues to diminish. Collectively, our work provides valuable long-term, historical, context for interpreting the effects of rapid environmental change on Chinook salmon in northern latitudes and important insights to environmental factors that contributed to Chinook salmon declines.

AUTHOR CONTRIBUTIONS

Megan L. Feddern: Conceptualization; data curation; formal analysis; methodology; project administration; visualization; writing – original draft. **Rebecca Shaftel:** Conceptualization; data curation; formal analysis; funding acquisition; methodology; writing – review and editing. **Erik R. Schoen:** Conceptualization; data curation; funding acquisition; methodology; writing – review and editing. **Curry J. Cunningham:** Conceptualization; funding acquisition; methodology; supervision; writing – review and editing. **Brendan M. Connors:** Conceptualization; data curation; funding acquisition; methodology; writing – review and editing. **Benjamin A. Staton:** Data curation; methodology; writing – review and editing. **Al von Finster:** Conceptualization; data curation; funding acquisition; writing – review and editing. **Zachary Liller:** Conceptualization; data curation; funding acquisition; writing – review and editing. **Vanessa R. von Biela:** Conceptualization; funding acquisition; writing – review and editing. **Katherine G. Howard:** Conceptualization; funding acquisition; writing – review and editing.

ACKNOWLEDGEMENTS

We thank the Alaska Department of Fish and Game and Fisheries and Ocean Canada for providing much of the information necessary to complete this analysis. Funding for this research was provided by the Alaska Sustainable Salmon Fund projects #53018 and #54016 with matching funds from the state of Alaska, Fisheries and Oceans Canada, and the Salmon Science Network. This project was supported by the Interdisciplinary Reseasch for Arctic Coastal Environments (InteRFACE) project through the U.S. Department of Energy, Office of Science, Biological and Environmental Research. We offer our gratitude to the 2022 workshop participants (Feddern et al., 2023) who shared their knowledge and experiences to shape and develop this analysis. We also thank Alyssa Murdoch, Bill Templin, and Dylan Cunningham for their helpful feedback and two anonymous reviewers who saw value in this synthesis and provided thoughtful insight. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

CONFLICT OF INTEREST STATEMENT

There is no conflict of interest declared in this article.

DATA AVAILABILITY STATEMENT

The freshwater indices used in this study are openly available in Dryad at https://doi.org/10.5061/dryad.9w0vt4bqm. Model input, output and code that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.13696302 and GitHub at https://github.com/mfeddern/Yukon-KuskokwimChinook/.

ORCID

Megan L. Feddern https://orcid.org/0000-0002-5863-7229
Rebecca Shaftel https://orcid.org/0000-0002-4789-4211
Erik R. Schoen https://orcid.org/0000-0001-8301-6419
Curry J. Cunningham https://orcid.org/0000-0002-1234-1297
Benjamin A. Staton https://orcid.org/0000-0002-2342-3482
Vanessa R. von Biela https://orcid.org/0000-0002-7139-5981

REFERENCES

Arp, C., & Cherry, J. (2022). River and lake ice phenology data for Alaska and Northwest Canada from 1882 to 2021. *Arctic Data Center*. https://doi.org/10.18739/A28W38388

Barneche, D. R., Robertson, D. R., White, C. R., & Marshall, D. J. (2018). Fish reproductive-energy output increases disproportionately with body size. *Science*, *360*(6389), 642–645. https://doi.org/10.1126/science.aao6868

Brabets, T. P., & Walvoord, M. A. (2009). Trends in streamflow in the Yukon River basin from 1944 to 2005 and the influence of the Pacific decadal oscillation. *Journal of Hydrology*, *371*(1), 108–119. https://doi.org/10.1016/j.jhydrol.2009.03.018

Bradford, M. J., Grout, J. A., & Moodie, S. (2001). Ecology of juvenile chinook salmon in a small non-natal stream of the Yukon River drainage and the role of ice conditions on their distribution and survival. *Canadian Journal of Zoology*, *79*(11), 2043–2054.

Braun, D. C., Patterson, D. A., & Reynolds, J. D. (2013). Maternal and environmental influences on egg size and juvenile life-history traits in Pacific salmon. *Ecology and Evolution*, *3*(6), 1727–1740. https://doi.org/10.1002/ece3.555

Brennan, S. R., Schindler, D. E., Cline, T. J., Walsworth, T. E., Buck, G., & Fernandez, D. P. (2019). Shifting habitat mosaics and fish production across river basins. *Science*, *364*(6442), 783–786.

Brooks, S. P., & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, *7*(4), 434–455.

Brown, R. J., Bradley, C., & Melegari, J. L. (2020). Population trends for Chinook and summer chum salmon in two Yukon River tributaries in Alaska. *Journal of Fish and Wildlife Management*, *11*(2), 377–400. https://doi.org/10.3996/072019-JFWM-064

Brown, R. J., von Finster, A., Henszey, R. J., & Eiler, J. H. (2017). Catalog of Chinook salmon spawning areas in Yukon River basin in Canada and United States. *Journal of Fish and Wildlife Management*, *8*(2), 558–586. https://doi.org/10.3996/052017-JFWM-045

Carey, M. P., von Biela, V. R., Dunker, A., Keith, K. D., Schelske, M., Lean, C., & Zimmerman, C. E. (2021). Egg retention of high-latitude sockeye salmon (*Oncorhynchus nerka*) in the Pilgrim River, Alaska, during the Pacific marine heatwave of 2014–2016. *Polar Biology*, *44*(8), 1643–1654. https://doi.org/10.1007/s00300-021-02902-8

Carothers, C., Black, J., Langdon, S. J., Donkersloot, R., Ringer, D., Coleman, J., Gavenus, E. R., Justin, W., Williams, M., Christiansen, F., Samuelson, J., Stevens, C., Woods, B., Clark, S. J., Clay, P. M., Mack, L., RaymondYakoubian, J., Sanders, A. A., Stevens, B. L., & Whiting, A. (2021). Indigenous peoples and salmon stewardship: A critical relationship. *Ecology and Society*, *26*(1), 16. https://doi.org/10.5751/ES-11972-260116

Choy, E. S., O'Connor, R. S., Gilchrist, H. G., Hargreaves, A. L., Love, O. P., Vézina, F., & Elliott, K. H. (2021). Limited heat tolerance in a cold-adapted seabird: Implications of a warming Arctic. *Journal of Experimental Biology*, *224*(13), jeb242168. https://doi.org/10.1242/jeb.242168

Clark, J., Brenner, R., & Lewis, B. (2018). Compiled age, sex, and length data for Alaskan salmon, 1922–2017. *Knowledge for Network Biocomplexity*. https://doi.org/10.5063/F1707ZTM

Connors, B. M., Siegle, M. R., Harding, J., Rossi, S., Staton, B. A., Jones, M. L., Bradford, M. J., Brown, R., Bechtol, B., Doherty, B., Cox, S., & Sutherland, B. J. G. (2022). Chinook salmon diversity contributes to fishery stability and trade-offs with mixed-stock harvest. *Ecological Applications*, *32*(8), e2709. https://doi.org/10.1002/eap.2709

Crozier, L. G., Burke, B. J., Chasco, B. E., Widener, D. L., & Zabel, R. W. (2021). Climate change threatens Chinook salmon throughout their life cycle. *Communications Biology*, *4*(1), 222. https://doi.org/10.1038/s42003-021-01734-w

Cunningham, C. J., Westley, P. A. H., & Adkison, M. D. (2018). Signals of large scale climate drivers, hatchery enhancement, and marine factors in Yukon River Chinook salmon survival revealed with a Bayesian life history model. *Global Change Biology*, *24*(9), 4399–4416. https://doi.org/10.1111/gcb.14315

Daum, D. W., & Flannery, B. G. (2011). Canadian-origin Chinook salmon rearing in nonnatal US tributary streams of the Yukon River, Alaska. *Transactions of the American Fisheries Society*, *140*(2), 207–220. https://doi.org/10.1080/00028487.2011.545004

De Cicco, L. A., Lorenz, D., Hirsch, R. M., Watkins, W., & Johnson, M. (2022). dataRetrieval: R packages for discovering and retrieving water data available from U.S. federal hydrologic web services. https://doi.org/10.5066/P9X4L3GE

Duffy, E. J., & Beauchamp, D. A. (2011). Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*(2), 232–240. https://doi.org/10.1139/F10-144

Dunker, K. J., Sepulveda, A. J., Massengill, R. L., & Rutz, D. S. (2018). The northern pike, a prized native but disastrous invasive. In C. Skov & P. A. Nilsson (Eds.), *Biology and ecology of pike* (pp. 356–398). CRC Press.

Eiler, J. H., Evans, A. N., & Schreck, C. B. (2015). Migratory patterns of wild Chinook Salmon (*Oncorhynchus tshawytscha*) returning to a large, free-flowing river basin. *PLoS One*, *10*, e0123127.

Eliason, E. J., Clark, T. D., Hague, M. J., Hanson, L. M., Gallagher, Z. S., Jeffries, K. M., Gale, M. K., Patterson, D. A., Hinch, S. G., & Farrell, A. P. (2011). Differences in thermal tolerance among sockeye salmon populations. *Science*, *332*(6025), 109–112. https://doi.org/10.1126/science.1199158

Falke, J. A., Huntsman, B. M., & Schoen, E. R. (2019). Climatic variation drives growth potential of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) along a subarctic boreal riverscape. *American Fisheries Society Symposium*, *90*, 57–82.

Farley, E. V., Jr., Yasumiishi, E. M., Murphy, J. M., Strasburger, W., Sewall, F., Howard, K., Garcia, S., & Moss, J. H. (2024). Critical periods in the marine life history of juvenile western Alaska chum salmon in a changing climate. *Marine Ecology Progress Series*, *726*, 149–160. https://doi.org/10.3354/meps14491

Feddern, M. L., Schoen, E. R., Shaftel, R., Cunningham, C. J., Chythlook, C., Connors, B. M., Murdoch, A. D., von Biela, V. R., & Woods, B. (2023). Kings of the north: Bridging disciplines to understand the effects of changing climate on Chinook Salmon in the Arctic-Yukon-Kuskokwim region. *Fisheries*, *48*, 331–343. https://doi.org/10.1002/fsh.10923

Garcia, S., & Sewall, F. (2021). Diet and energy density assessment of juvenile Chinook salmon from the northeastern Bering Sea, 2004–2017. Alaska Department of Fish and Game, fishery data series, (21-05).

Ge, S., Yang, D., & Kane, D. L. (2013). Yukon River basin long-term (1977–2006) hydrologic and climatic analysis. *Hydrological Processes*, *27*(17), 2475–2484. https://doi.org/10.1002/hyp.9282

Gelman, A. (2004). Parameterization and Bayesian modeling. *Journal of the American Statistical Association*, *99*(466), 537–545. https://doi.org/10.1198/016214504000000458

Godduhn, A. R., McDevitt, C. R., Kostick, M. L., Brown, C. L., & Runfola, D. M. (2020). Subsistence harvest and use of nonsalmon fish in coastal Yukon-Kuskokwim Delta communities, 2017. Alaska Department of Fish and Game, Division of Subsistence Technical Paper No. 458, Fairbanks.

Goode, J. R., Buffington, J. M., Tonina, D., Isaak, D. J., Thurow, R. F., Wenger, S., Nagel, D., Luce, C., Tetzlaff, D., & Soulsby, C. (2013). Potential effects of climate change on streambed scour and risks to salmonid survival in snow-dominated mountain basins. *Hydrological Processes*, *27*(5), 750–765. https://doi.org/10.1002/hyp.9728

Hare, S. R., Mantua, N. J., & Francis, R. C. (1999). Inverse production regimes: Alaska and west coast Pacific salmon. *Fisheries*, *24*(1), 6–14.

Harrigan, S., Zsoter, E., Alfieri, L., Prudhomme, C., Salamon, P., Wetterhall, F., Barnard, C., Cloke, H., & Pappenberger, F. (2020). GloFAS-ERA5 operational global river discharge reanalysis 1979–present. *Earth System Science Data*, *12*(3), 2043–2060. https://doi.org/10.5194/essd-12-2043-2020

Healey, M. C. (1982). Juvenile Pacific salmon in estuaries: The life support system. In *Estuarine comparisons* (pp. 315–341). Academic Press. https://doi.org/10.1016/B978-0-12-404070-0.50025-9

Hicke, J. A., Lucatello, S., Mortsch, L. D., Dawson, J., Domínguez Aguilar, M., Enquist, C. A. F., Gilmore, E. A., Gutzler, D. S., Harper, S., Holsman, K., Jewett, E. B., Kohler, T. A., & Miller, K. A. (2022). North America. In: Climate Change 2022: Impacts, Adaptation and Vulnerability. In H.-O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, & B. Rama (Eds.), *Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1929–2042). Cambridge University Press. https://doi.org/10.1017/9781009325844.016

Hilborn, R. (1985). Apparent stock recruitment relationships in mixed stock fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*(4), 718–723. https://doi.org/10.1139/f85-230

Hinch, S. G., Bett, N. N., Eliason, E. J., Farrell, A. P., Cooke, S. J., & Patterson, D. A. (2021). Exceptionally high mortality of adult female salmon: A large-scale pattern and a conservation concern. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*(6), 639–654. https://doi.org/10.1139/cjfas-2020-0385

Honsey, A. E., Rypel, A. L., & Venturelli, P. A. (2023). Guidance for selecting base temperatures when using degree-days in fish growth analyses. *Canadian Journal of Fisheries and Aquatic Sciences*, *80*(3), 549–562.

Howard, K., Murphy, J., Wilson, L., Moss, J., & Farley, E. (2016). Size-selective mortality of Chinook Salmon in relation to body energy after the first summer in nearshore marine habitats. *North Pacific Anadromous Fish Commission Bulletin*, *6*(1), 1–11. https://doi.org/10.23849/npafcb6/1.11

Howard, K. G., & von Biela, V. (2023). Adult spawners: A critical period for subarctic Chinook salmon in a changing climate. *Global Change Biology*, *29*(7), 1759–1773. https://doi.org/10.1111/gcb.16610

Hunt, G. L., Coyle, K. O., Eisner, L. B., Farley, E. V., Heintz, R. A., Mueter, F., Napp, J. M., Overland, J. E., Ressler, P. H., Salo, S., & Stabeno, P. J. (2011). Climate impacts on eastern Bering Sea foodwebs: A synthesis of new data and an assessment of the oscillating control hypothesis. *ICES Journal of Marine Science*, *68*, 1230–1243. https://doi.org/10.1093/icesjms/fsr036

Ianelli, J., Fissel, B., Holsman, K., De Robertis, A., Honkalehto, T., Kotwicki, S., Monnahan, C., Siddon, E., & Thorson, J. (2020). Chapter 1: Assessment of the walleye Pollock stock in the eastern Bering Sea. In *Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions*. Alaska Fisheries Science Center, National Marine Fisheries Service.

Ianelli, J. N., & Stram, D. L. (2015). Estimating impacts of the pollock fishery bycatch on western Alaska Chinook salmon. *ICES Journal of Marine Science*, *72*(4), 1159–1172.

Jones, L. A., Schoen, E. R., Shaftel, R., Cunningham, C. J., Mauger, S., Rinella, D. J., & St. Saviour, A. (2020). Watershed-scale climate influences productivity of Chinook salmon populations across south-central Alaska. *Global Change Biology*, *26*, 4919–4936. https://doi.org/10.1111/gcb.15155

Joy, P. J., Ocaña, M., Savereide, J. W., & Tyers, M. (2024). Run reconstruction, spawner–recruit analysis, and escapement goal recommendation for Chinook salmon in the Chena and Salcha Rivers. Alaska Department of Fish and Game, fishery manuscript series No. 24-02, Anchorage.

JTC (Joint Technical Committee of the Yukon River U.S./Canada Panel). (2023). *Yukon River salmon 2020 season summary and 2021 season outlook*. Game, Division of Commercial Fisheries, Regional Information Report.

Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Leetman, A., Reynolds, B., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K. C., Ropelewski, C., … Dennis, J. (1996). The NCEP/NCAR 40-year reanalysis project. *Bulletin of the American Meteorological Society*, *17*, 437–471. https://doi.org/10.1175/15200477(1996)077<0437:TNYRP>2.0.CO;2

KRITFC (Kuskokwim River Inter-Tribal Fish Commission). (2022). Kuskokwim River salmon situation report. https://www.kuskosalmon.org/documents

Larson, S. (2023). *2022 Kuskokwim River Chinook salmon run reconstruction and 2023 forecast*. Alaska Department of Fish and Game, division of commercial fisheries, Regional Information Report 3A23-01, Anchorage.

Lewis, B., Grant, W. S., Brenner, R. E., & Hamazaki, T. (2015). Changes in size and age of Chinook salmon *Oncorhynchus tshawytscha* returning to Alaska. *PLoS One*, *10*(6), e0130184. https://doi.org/10.1371/journal.pone.0130184

Litzow, M. A., Malick, M. J., Bond, N. A., Cunningham, C. J., Gosselin, J. L., & Ward, E. J. (2020). Quantifying a novel climate through changes in PDO-climate and PDO-salmon relationships. *Geophysical Research Letters*, *47*(16), e2020GL087972.

Lomas, M. W., Moran, S. B., Casey, J. R., Bell, D. W., Tiahlo, M., Whitefield, J., Kelly, R. P., Mathis, J. T., & Cokelet, E. D. (2012). Spatial and seasonal variability of primary production on the eastern Bering Sea shelf. *Deep Sea Research Part II: Topical Studies in Oceanography*, *65*, 126–140. https://doi.org/10.1016/j.dsr2.2012.02.010

Malick, M. J. (2020). Time-varying relationships between ocean conditions and sockeye salmon productivity. *Fisheries Oceanography*, *29*(3), 265–275.

Malick, M. J., Losee, J. P., Marston, G., Agha, M., Berejikian, B. A., Beckman, B. R., & Cooper, M. (2023). Fecundity trends of Chinook salmon in the Pacific northwest. *Fish and Fisheries*, *24*, 454–465. https://doi.org/10.1111/faf.12738

Manishin, K. A., Cunningham, C. J., Westley, P. A., & Seitz, A. C. (2021). Can late stage marine mortality explain observed shifts in age structure of Chinook salmon? *PLoS One*, *16*(2), e0247370.

Mauger, S., Shaftel, R., Leppi, J. C., & Rinella, D. J. (2017). Summer temperature regimes in southcentral Alaska streams: Watershed drivers of variation and potential implications for Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(5), 702–715. https://doi.org/10.1139/cjfas-2016-0076

Miller, J. A., Teel, D. J., Baptista, A., & Morgan, C. A. (2013). Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook salmon (Oncorhynchus tshawytscha). *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(4), 617–629. https://doi.org/10.1139/cjfas-2012-0354

Montgomery, D. R., Buffington, J. M., Peterson, N. P., Schuett-Hames, D., & Quinn, T. P. (1996). Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(5), 1061–1070. https://doi.org/10.1139/f96-028

Moss, J. H., Beauchamp, D. A., Cross, A. D., Myers, K. W., Farley, E. V., Jr., Murphy, J. M., & Helle, J. H. (2005). Evidence for size-selective mortality after the first summer of ocean growth by pink salmon. *Transactions of the American Fisheries Society*, *134*(5), 1313–1322. https://doi.org/10.1577/T05-054.1

Mueter, F. J., Peterman, R. M., & Pyper, B. J. (2002). Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. *Canadian Journal of Fishery and Aquatic Sciences*, *59*, 456–463. https://doi.org/10.1139/F02-020

Murdoch, A. D., Connors, B. M., Lapointe, N. W., Mills Flemming, J., Cooke, S. J., & Mantyka-Pringle, C. (2024). Multiple environmental drivers across life-stages influence Yukon River Chinook salmon productivity. *Canadian Journal of Fisheries and Aquatic Sciences*, *81*, 97–114.

Murphy, J. M., Howard, K. G., Gann, J. C., Cieciel, K. C., Templin, W. D., & Guthrie, C. M. (2017). Juvenile Chinook Salmon abundance in the northern Bering Sea: Implications for future returns and fisheries in the Yukon River. *Deep Sea Research Part II: Topical Studies in Oceanography*, *135*, 156–167. https://doi.org/10.1016/j.dsr2.2016.06.002

Murphy, M. M., Howard, K., Garcia, S., Moss, J. H., Strasburger, W. W., Sewall, F., & Lee, E. (2021). Juvenile Yukon River Chinook salmon in a warming Arctic. *North Pacific Anadromous Fish Commission, Technical Report No*, *17*, 97–101.

Myers, K. W., Walker, R. V., Davis, N. D., Armstrong, J. L., & Kaeriyama, M. (2009). High seas distribution, biology, and ecology of Arctic–Yukon–Kuskokwim salmon: Direct information from high seas tagging experiments, 1954–2006. *In American Fisheries Society, Symposium*, *70*, 201–239.

Neuswanger, J. R., Wipfli, M. S., Evenson, M. J., Hughes, N. F., & Rosenberger, A. E. (2015). Low productivity of Chinook salmon strongly correlates with high summer stream discharge in two Alaskan rivers in the Yukon drainage. *Canadian Journal of Fisheries and Aquatic Sciences*, *72*(8), 1125–1137. https://doi.org/10.1139/cjfas-2014-0498

Ohlberger, J., Cline, T. J., Schindler, D. E., & Lewis, B. (2023). Declines in body size of sockeye salmon associated with increased competition in the ocean. *Proceedings of the Royal Society B: Biological Sciences*, *290*, 2248. https://doi.org/10.1098/rspb.2022.2248

Ohlberger, J., Scheuerell, M. D., & Schindler, D. E. (2016). Population coherence and environmental impacts across spatial scales: A case study of Chinook salmon. *Ecosphere*, *7*(4), e01333. https://doi.org/10.1002/ecs2.1333

Ohlberger, J., Schindler, D. E., Brown, R. J., Harding, J. M., Adkison, M. D., Munro, A. R., Horstmann, L., & Spaeder, J. (2020). The reproductive value of large females: Consequences of shifts in demographic structure for population reproductive potential in Chinook salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(8), 1292–1301. https://doi.org/10.1139/cjfas-2020-0012

Ohlberger, J., Ward, E. J., Schindler, D. E., & Lewis, B. (2018). Demographic changes in Chinook salmon across the Northeast Pacific Ocean. *Fish and Fisheries*, *19*(3), 533–546. https://doi.org/10.1111/faf.12272

Öhlund, G., Hedström, P., Norman, S., Hein, C. L., & Englund, G. (2015). Temperature dependence of predation depends on the relative performance of predators and prey. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1799), 20142254. https://doi.org/10.1098/rspb.2014.2254

Oke, K. B., Cunningham, C. J., Westley, P. A. H., Baskett, M. L., Carlson, S. M., Clark, J., Hendry, A. P., Karatayev, V. A., Kendall, N. W., Kibele, J., Kindsvater, H. K., Kobayashi, K. M., Lewis, B., Munch, S., Reynolds, J. D., Vick, G. K., & Palkovacs, E. P. (2020). Recent declines in salmon body size impact ecosystems and fisheries. *Nature Communications*, *11*(1), 4155. https://doi.org/10.1038/s41467-020-17726-z

Pitman, K. J., Moore, J. W., Sloat, M. R., Beaudreau, A. H., Bidlack, A. L., Brenner, R. E., Hood, E. W., Pess, G. R., Mantua, N. J., Milner, A. M., & Radić, V. (2020). Glacier retreat and Pacific salmon. *Bioscience*, *70*(3), 220–236. https://doi.org/10.1093/biosci/biaa015

R Core Team. (2023). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Raymond-Yakoubian, B., & Raymond-Yakoubian, J. (2015). *Always taught not to waste: Traditional knowledge and Norton sound/Bering Strait Salmon populations*. Kawerak Inc.

Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Board of Canada*, *11*(5), 559–623. https://doi.org/10.1139/f54-039

Ruggerone, G. T., & Irvine, J. R. (2018). Numbers and biomass of natural- and hatchery-origin pink salmon, chum salmon, and sockeye salmon in the north Pacific Ocean, 1925–2015. *Marine and Coastal Fisheries*, *10*(2), 152–168. https://doi.org/10.1002/mcf2.10023

Ruggerone, G. T., Springer, A. M., van Vliet, G. B., Connors, B., Irvine, J. R., Shaul, L. D., Sloat, M. R., & Atlas, W. I. (2023). From diatoms to killer whales: Impacts of pink salmon on North Pacific ecosystems. *Marine Ecology Progress Series*, *719*, 1–40.

Schindler, D. E., & Hilborn, R. (2015). Prediction, precaution, and policy under global change. *Science*, *347*(6225), 953–954.

Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., & Webster, M. S. (2010). Population diversity and the portfolio effect in an exploited species. *Nature*, *465*, 609–612.

Schoen, E. R., Howard, K. G., Murphy, J. M., Schindler, D. E., Westley, P. A. H., & von Biela, V. R. (2023). Divergent Responses of Western Alaska Salmon to a changing climate. NOAA Technical Report OAR ARC 23-13. https://doi.org/10.25923/f2hv-5581

Schoen, E. R., Sellmer, K. W., Wipfli, M. S., López, J. A., Ivanoff, R., & Meyer, B. E. (2022). Piscine predation on juvenile salmon in sub-arctic Alaskan rivers: Associations with season, habitat, predator size and streamflow. *Ecology of Freshwater Fish*, *31*(2), 243–259. https://doi.org/10.1111/eff.12626

Shaftel, R., Feddern, M. L., Schoen, E. R., McAfee, S., Cunningham, C. J., von Biela, V. R., Falke, J. A., Schwenke, J., & Paul, J. (In Prep). Integrating climate data and river modeling to reveal influences on declining Chinook salmon in the Sub-Arctic river basins.

Shaftel, R., Mauger, S., Falke, J., Rinella, D., Davis, J., & Jones, L. (2020). Thermal diversity of salmon streams in the Matanuska-Susitna Basin, Alaska. *Journal of the American Water Resources Association*, *56*(4), 630–646. https://doi.org/10.1111/1752-1688.12839

Siddon, E. (2022). Ecosystem status report 2022: Eastern Bering Sea, stock assessment and fishery evaluation report, North Pacific fishery management council, 1007 west 3rd Ave., suite 400, Anchorage, Alaska 99501.

Stachura, M. M., Mantua, N. J., & Scheuerell, M. D. (2014). Oceanographic influences on patterns in North Pacific salmon abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, *71*(2), 226–235. https://doi.org/10.1111/fog.12458

Stan Development Team. (2023). RStan: The R interface to Stan. R Package Version 2.21.8. https://mc-stan.org/

Staton, B. A., Catalano, M. J., Connors, B. M., Coggins, L. G., Jr., Jones, M. L., Walters, C. J., Fleichman, S. J., & Gwinn, D. C. (2020). Evaluation of methods for spawner-recruit analysis in mixed-stock Pacific salmon fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(7), 1149–1162. https://doi.org/10.1139/cjfas-2019-0281

Thompson, D. P., Crouse, J. A., Jaques, S., & Barboza, P. S. (2020). Redefining physiological responses of moose (*Alces alces*) to warm environmental conditions. *Journal of Thermal Biology*, *90*, 102581. https://doi.org/10.1016/j.jtherbio.2020.102581

Tuor, K. M., Heath, D. D., & Shrimpton, J. M. (2020). Spatial and environmental effects on Coho Salmon life history trait variation. *Ecology and Evolution*, *10*(23), 13198–13210. https://doi.org/10.1002/ece3.6912

von Biela, V. R., Bowen, L., McCormick, S. D., Carey, M. P., Donnelly, D. S., Waters, S., Regish, A. M., Laske, S. M., Brown, R. J., & Larson, S. (2020). Evidence of prevalent heat stress in Yukon River Chinook salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, *77*(12), 1878–1892. https://doi.org/10.1139/cjfas-2020-0209

von Biela, V. R., Sergeant, C. J., Carey, M. P., Liller, Z., Russell, C., Quinn-Davidson, S., Rand, P. S., Westley, P. A., & Zimmerman, C. E. (2022). Premature mortality observations among Alaska's Pacific salmon during record heat and drought in 2019. *Fisheries*, *47*(4), 157–168. https://doi.org/10.1002/fsh.10705

von Finster, A. (2023). Final report: Water temperature monitoring of Yukon River Chinook Salmon spawning and migration habitats in Canada. Report to the Yukon River Panel, Project CRE22-20. 33 pp.

Wohl, E., Kramer, N., & Lininger, K. B. (2022). *The Yukon and the Mackenzie: Large Arctic Rivers of North America* (2nd ed., pp. 368–387). Geomorphology and Management.

Yasumiishi, E. M., Farley, E. V., Maselko, J., Aydin, K. Y., Kearney, K. A., Hermann, A. J., Ruggerone, G. T., Howard, K. G., & Strasburger, W. W. (2020). Differential north–south response of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) marine growth to ecosystem change in the eastern Bering Sea, 1974–2010. *ICES Journal of Marine Science*, *77*(1), 216–229. https://doi.org/10.1093/icesjms/fsz166

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Feddern, M. L., Shaftel, R., Schoen, E. R., Cunningham, C. J., Connors, B. M., Staton, B. A., von Finster, A., Liller, Z., von Biela, V. R., & Howard, K. G. (2024). Body size and early marine conditions drive changes in Chinook salmon productivity across northern latitude ecosystems. *Global Change Biology*, *30*, e17508. https://doi.org/10.1111/gcb.17508