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Watershed-scale climate influences productivity of Chinook salmon populations across southcentral Alaska

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Abstract

The ecosystems supporting Pacific salmon (*Oncorhynchus* spp.) are changing rapidly as a result of climate change and habitat alteration. Understanding how—and how consistently—salmon populations respond to changes at regional and watershed scales has major implications for fisheries management and habitat conservation. Chinook salmon (*O. tshawytscha*) populations across Alaska have declined over the past decade, resulting in fisheries closures and prolonged impacts to local communities. These declines are associated with large-scale climate drivers, but uncertainty remains about the role of local conditions (e.g., precipitation, streamflow, and stream temperature) that vary among the watersheds where salmon spawn and rear. We estimated the effects of these and other environmental indicators on the productivity of 15 Chinook salmon populations in the Cook Inlet basin, southcentral Alaska, using a hierarchical Bayesian stock-recruitment model. Salmon spawning during 2003–2007 produced 57% fewer recruits than the previous long-term average, leading to declines in adult returns beginning in 2008. These declines were explained in part by density dependence, with reduced population productivity following years of high spawning abundance. Across all populations, productivity declined with increased precipitation during the fall spawning and early incubation period and increased with above-average precipitation during juvenile rearing. Above-average stream temperatures during spawning and rearing had variable effects, with negative relationships in many warmer streams and positive relationships in some colder streams. Productivity was also associated with regional indices of streamflow and ocean conditions, with high variability among populations. The cumulative effects of adverse conditions in freshwater, including high spawning abundance, heavy fall rains, and hot, dry summers may have contributed to the recent population declines across the region. Identifying both coherent and differential responses to environmental change underscores the importance of targeted, watershed-specific monitoring and conservation efforts for maintaining resilient salmon runs in a warming world.

KEYWORDS

Chinook salmon, climate change, fisheries, population dynamics, precipitation

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1 | INTRODUCTION

Ecosystems supporting Alaskan salmon (*Oncorhynchus* spp.) populations are changing rapidly due to climate change and habitat alteration. Alaska is warming at more than twice the rate of the contiguous United States (IPCC, 2018), leading to a myriad of habitat changes including increasing ocean, stream, and lake temperatures (Cline, Ohlberger, & Schindler, 2019; Di Lorenzo & Mantua, 2016; Mauger, Shaftel, Leppi, & Rinella, 2017), altered hydrologic regimes (Stewart, Cayan, & Dettinger, 2005; Wobus et al., 2015), earlier ice breakup (Cline et al., 2019), and increased melting of glaciers (O'Neel et al., 2015; Pitman et al., 2020). Salmon are an immensely valued resource for Alaskans (Lord, 2016; McDowell Group, 2015; NRC, 2004), and the effects of these changes on salmon productivity have major implications for jobs, food security, cultural well-being, and the persistence of salmon-dependent communities.

Salmon are strongly influenced by environmental conditions in the watersheds where they spawn as adults and rear as juveniles. For example, high water temperatures during spawning runs can block migratory corridors and cause pre-spawn mortality (Bowerman, Roumasset, Keefer, Sharpe, & Caudill, 2018; Richter & Kolmes, 2005). Temperature also strongly influences juvenile growth rates (Beauchamp, 2009; Brett, 1971), which can, in turn, affect survival due to size-selective mortality in freshwater and the ocean (Howard, Murphy, Wilson, Moss, & Farley, 2016; Thompson & Beauchamp, 2014). Likewise, heavy rains during spawning or egg incubation can increase mortality due to high flows dislodging embryos or sedimentation of spawning redds (Greene, Jensen, Pess, Steel, & Beamer, 2005; Lapointe, Eaton, Driscoll, & Latulippe, 2000), and greater variability in streamflow can reduce population growth rates (Ward, Anderson, Beechie, Pess, & Ford, 2015). Through these and other mechanisms, climate-driven changes in Alaskan watersheds are likely to reduce the productivity of some salmon populations while benefiting others (Leppi, Rinella, Wilson, & Loya, 2014; Mantua, Crozier, Reed, Schindler, & Waples, 2015; Pitman et al., 2020; Schoen et al., 2017).

Chinook salmon (*O. tshawytscha*) populations across Alaska have suffered declines since the mid-2000s (ADFG, 2013; Dorner, Catalano, & Peterman, 2017; Ohlberger, Scheuerell, & Schindler, 2016; Schindler et al., 2013). As a result, fishing restrictions and closures have caused severe hardship in fishing communities and exacerbated conflicts among user groups (Brown & Godduhn, 2015; Loring, 2016; Schindler et al., 2013). The causes are not fully understood, but retrospective studies have linked regional-scale environmental indicators to the dynamics of particular populations. For example, the productivity of two Chinook salmon populations in the Yukon River basin is associated with the timing of river ice breakup, winter temperatures in the Bering Sea, and the abundance of hatchery-origin chum salmon (*O. keta*) in the North Pacific Ocean (Cunningham, Westley, & Adkison, 2018). More broadly, shared regional trends in Chinook salmon productivity are associated with the North Pacific Gyre Oscillation, an index of ocean conditions (NPGO; Dorner et al., 2017; Kilduff, Di Lorenzo, Botsford, & Teo, 2015; Ohlberger et al., 2016). However, much of the variability in productivity remains unexplained by regional-scale indicators, suggesting local conditions within spawning watersheds may have also contributed to these declines (Ohlberger et al., 2016).

Few studies have linked local climatic conditions to the dynamics of Alaskan Chinook salmon populations, due to a scarcity of environmental time-series data from watersheds where populations are monitored. Notably, reduced productivity of two neighboring populations in the Yukon River basin was linked to high streamflow during the summer juvenile rearing period, potentially due to reduced foraging efficiency (Neuswanger, Wipfli, Evenson, Hughes, & Rosenberger, 2015). A subsequent study also concluded high streamflow had a potentially large negative effect, although it was highly uncertain (Cunningham et al., 2018). More generally, it remains unknown how Chinook salmon in other rivers across the state have responded to variations in streamflow, as well as stream temperature, precipitation, and other local conditions; how synchronous or diverse these responses have been among individual spawning populations; and whether these changes in local watersheds can help to explain the recent population declines. However, recent developments in downscaled climate products and a proliferation of stream temperature monitoring data present a novel opportunity to quantify climatic variables in many remote watersheds, providing more relevant population-specific metrics of freshwater conditions for analyses of salmon productivity.

Here, we conducted the first analysis of the effects of regional and watershed-specific climate drivers on the productivity of a diverse group of Alaskan Chinook salmon populations. We focused on the Cook Inlet basin of southcentral Alaska, where a federal fishery disaster was declared following record-low Chinook salmon returns in 2012. Several rivers in this region are among the warmest in Alaska, where temperatures already exceed criteria designed to protect salmon (Mauger et al., 2017; Shaftel et al., 2020). To quantify associations between climate and the productivity of Cook Inlet Chinook salmon, we modeled the relationship between spawning abundance and recruitment for 15 populations while estimating the influence of nine regional- and watershed-scale indicators. Each indicator represented a hypothesized effect on Chinook salmon during a particular life stage. Specifically, we hypothesized that high stream temperatures and high or flashy flows during the spawning and early incubation periods would reduce fertilization rates and embryo survival; that flashy flows during the spring emergence period would reduce fry survival; and that high temperatures or high flows during the rearing season would reduce juvenile growth and subsequent survival. We further hypothesized that late ice breakup during the year of ocean entry would reduce survival and that survival during the early marine life stage would be associated with the NPGO index.

2 | MATERIALS AND METHODS

2.1 | Study area

The Cook Inlet basin covers 121,700 km^2 of southcentral Alaska draining southward to the Gulf of Alaska (Figure 1). The region

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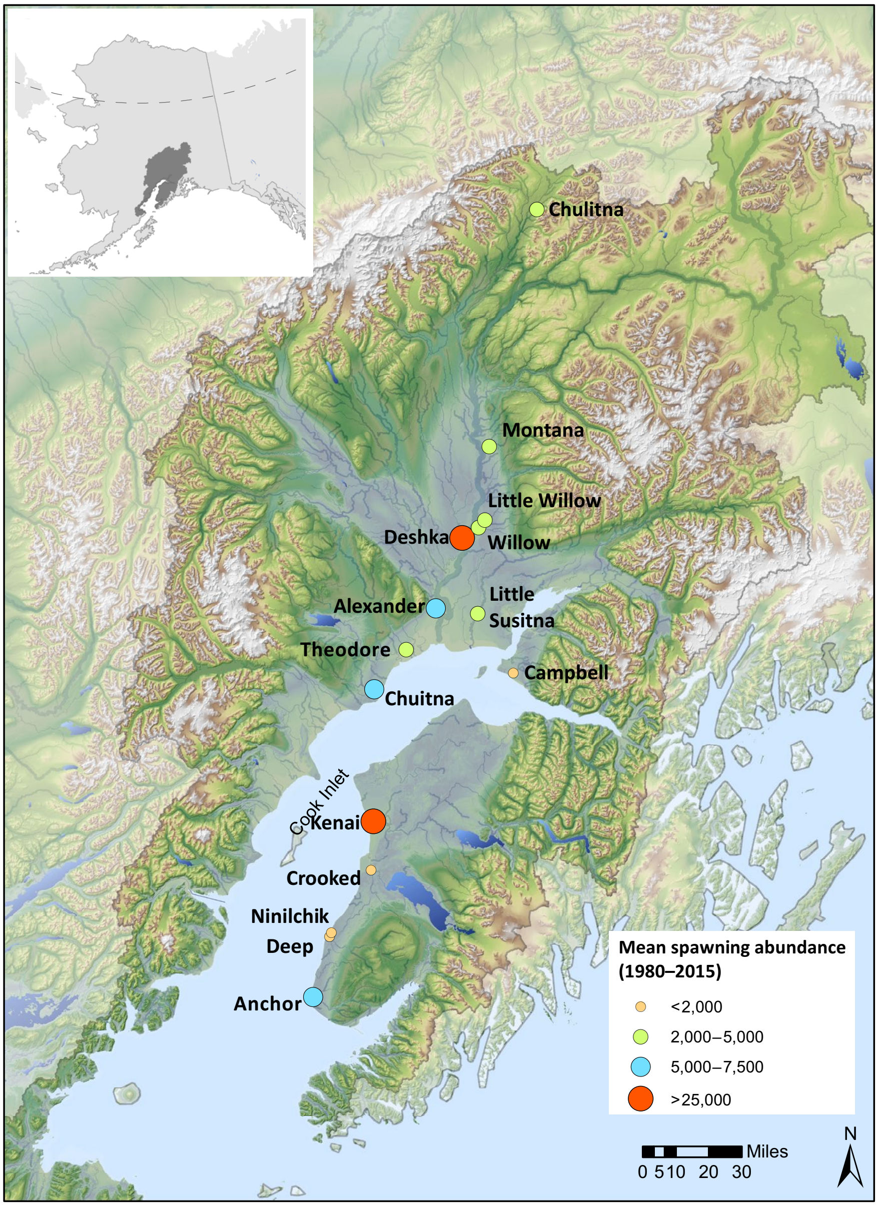

FIGURE 1 Study populations included in the stock-recruitment model to investigate environmental drivers of Chinook salmon productivity in the Cook Inlet basin. Dark shading on inset map indicates the location of Cook Inlet basin in southcentral Alaska. Circle size represents mean spawning abundance for each population during the 1980–2015 period

consists of coastal and valley lowlands surrounded by rugged mountains including some of North America's highest peaks. The climate ranges from continental to maritime, with mean annual temperatures between −6 and 6°C (Brabets, Nelson, Dorava, & Milner, 1999). Precipitation ranges annually from 50 cm across the continental zone to 180 cm across the maritime zone, with the greatest accumulation in mountainous areas (Brabets et al., 1999). The basin's major river systems drain alpine glaciers and therefore have high sediment loads and turbidity (Lloyd, Koenings, & LaPerriere, 1987), although many of the tributary streams have clear waters with little or no glacial influence. The basin has 12,000 km of documented salmon streams and supports substantial wild runs of Chinook, chum, coho (*O. kisutch*), pink (*O. gorbuscha*), and sockeye (*O. nerka*) salmon, as well as other anadromous and resident fishes (Johnson & Coleman, 2014).

Chinook salmon is a highly valued species harvested in recreational, commercial, subsistence, and personal-use fisheries in the Cook Inlet basin. In this region, Chinook salmon adults typically spawn during July–August and die shortly thereafter. Their embryos incubate in the gravel streambed during the fall and winter, and juveniles emerge during the following spring. Juveniles typically rear in freshwater for 1 year before migrating to the ocean as smolts, where they spend 1–5 years before returning to spawn in their natal streams. The Alaska Department of Fish and Game (ADF&G) monitors 24 Chinook salmon spawning populations in the Cook Inlet basin (Erickson, Willette, & McKinley, 2017; Otis, Erickson, Kerkvliet, & McKinley, 2016). We analyzed data from 15 of these populations for which co-located stream temperature data were available, which together accounted for roughly 75% of the monitored spawning escapement (Figure 1; see Supporting Information). These 15 populations span a diverse range of stream and watershed characteristics, including low-elevation wetland streams, high-elevation snow-fed streams, and one glacial river.

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2.2 | Environmental indicators

2.2.1 | Stream temperature

We used regression models to hindcast stream temperatures for each of the 15 streams, based on site-specific relationships with air temperature. Stream temperature data were collected in main-stem channels between 1999 and 2016 and each stream had 4–14 years of data. Time series of water temperature logged at 15- and 30-min intervals from June 1 to September 30 were aggregated to weekly means (Mauger et al., 2017). We fit linear regression models describing weekly mean stream temperatures as a function of concurrent weekly mean air temperatures from the nearest long-term airport weather station (Homer, Kenai, Anchorage, or Talkeetna; Menne et al., 2012). Site-specific model coefficients and air temperature data from the closest airport were used to model weekly mean stream temperatures from May–September for the years 1980–2016. Air temperature explained 52%–89% of the variation in weekly mean stream temperatures across the 15 streams. For 10 of the 15 streams, regression models explained more than 70% of the variation, and only one site had an r^2 value below .6 (Theodore River). To investigate stream temperature trends over the 37-year period, we aggregated hindcasted weekly temperature time series to means for June–August (warmest months of the year) across all sites and regressed against year. Using the modeled weekly stream temperatures, we generated thermal indicators for Chinook (a) adult spawning and early stage embryonic development and (b) juvenile rearing. We did not include any indicators related to delayed adult migration (20°C; Hicks, 2000) or lethal temperatures (24°C; Richter & Kolmes, 2005) because modeled weekly stream temperatures only exceeded 20°C in the Deshka River and Alexander Creek.

Our first thermal indicator represented potential effects of stream temperature on fertilization rates and subsequent embryo survival, both of which decrease when temperatures exceed 13.5–14.5°C (Hicks, 2000; McCullough, Spalding, Sturdevant, & Hicks, 2001; Richter & Kolmes, 2005). We calculated this indicator as the maximum weekly average temperature during the spawning months of July and August (Covariate name: maxT_spawn; Table 1). A second thermal indicator represented potential effects on juvenile Chinook salmon growth, which under natural levels of food intake is optimized around 15°C (McCullough et al., 2009; Richter & Kolmes, 2005). We calculated this indicator as the average weekly temperature from June to August (avgT_rear; Table 1), the core of the rearing season. We lagged this indicator by 1 year to align juvenile freshwater rearing with the corresponding brood years (Table 1). It is important to note that although our stream temperature indicators were specific to watersheds (i.e., populations) in our study, the location of most monitoring sites was in the lower reaches of the watershed. For this reason, the thermal characteristics of our indicators do not reflect the range of thermal diversity available within

TABLE 1 Hypothesized effects of environmental indicators on salmon life stages used in stock-recruitment model. Temporal domain is the months for which each covariate was derived, while brood year offset indicates the lag from the brood year

Covariate		Temporal domain	Hypothesis	Life stage	Brood year offset
Stream temperature					
maxT_spawn	Maximum weekly stream temperature	July–August	Above-optimal temperatures negatively affect fertilization rates and embryo survival	Spawning and incubation	0
avgT_rear	Average weekly stream temperature	June–August	Above- and below-optimal temperatures negatively affect juvenile growth	Juvenile rearing	+1
Precipitation and discharge					
maxP_spawn	Maximum monthly precipitation	August–November	High rainfall negatively affects egg survival through streambed scour or sedimentation	Spawning and incubation	0
RB_spawn	R-B Index		Flashy streamflow negatively affects egg survival through redd dewatering		
RB_emerge	R-B Index	May–June	Flashy streamflow during fry emergence negatively affects survival rates	Juvenile rearing	+1
avgP_rear	Average precipitation	May–August	Rainfall affects juvenile growth (positively or negatively) by influencing foraging efficiency or habitat connectivity		
medianQ_rear	Median discharge		High flows negatively affect juvenile growth through reduced foraging efficiency		
Ice breakup					
Breakup	River ice breakup date	Day of year	Late ice breakup negatively affects survival rates	Smolt outmigration	+2
Marine					
NPGO	North Pacific Gyre Oscillation	Year (annual mean)	Ocean conditions influence growth or survival (positively or negatively)	First year of marine residence	+2

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each watershed. They do, however, characterize relative differences among sites and years.

2.2.2 | Precipitation and streamflow

Due to sparse placement and intermittent operation of stream gages in the study region (Curran, Barth, Veilleux, & Ourso, 2016), streamflow data were not available for the majority of sites and years included in this study. Thus, we derived streamflow indices using two complementary approaches: (a) watershed-specific precipitation metrics based on downscaled climate models and (b) regional streamflow metrics based on daily measurements from a single index gage with continuous temporal coverage. Climate models use empirical data from weather stations to interpolate climate conditions across space and time. One difference between observed streamflow and modeled climate data is the measure of time (i.e., temporal scale) over which they describe hydrologic processes. The downscaled climate predictions were available at a monthly resolution for all watersheds and years, but do not capture weather events that typically occur over short time periods (Lader, Walsh, Bhatt, & Bieniek, 2017). Although measurements at the index gage were used to assess short-term changes in discharge, they did not reflect spatial differences among watersheds. Watersheds were assumed to represent distinct spawning populations, and juvenile salmon were assumed to rear within their natal watershed. Each population-specific watershed was delineated in ArcGIS by aggregating USGS Hydrologic Units (Code 10).

We calculated watershed-scale precipitation indicators using downscaled (1 km resolution) estimates of monthly total precipitation (mm; SNAP, 2017) to describe interannual variation in precipitation during the spawning and juvenile rearing life stages of each population. Our two precipitation indicators included (a) mean precipitation during May–August (avgP_rear; Table 1) to describe overall streamflow conditions during the juvenile rearing season and (b) maximum monthly precipitation during August–November (maxP_spawn; Table 1) to capture effects of above-average precipitation (i.e., high flows) during spawning and early incubation. We lagged avgP_rear by 1 year to align juvenile freshwater rearing with the corresponding brood years (Table 1).

Regional streamflow indicators were calculated using daily discharge data from an index gage on the Little Susitna River (USGS 1529000). Daily discharge values at this gage correlated with those of 14 other gages in the Cook Inlet basin (Pearson's *r* from .55 to .96; Curran, 2012), suggesting it to be a representative regional index. To characterize short-term changes in streamflow in response to precipitation events (i.e., flashiness), we calculated the Richard-Baker Index (R-B Index) of flashiness (Baker, Richards, Loftus, & Kramer, 2004) over the August–November spawning and early incubation period (RB_spawn) and May–June fry emergence period (RB_emerge). The R-B Index reflects changes in short-term daily flows relative to average flows over a specified period. To describe winter snow accumulation, seasonal melt rates, and the overall magnitude of discharge during the juvenile rearing season (Neuswanger et al., 2015), we calculated median discharge during May–August (medianQ_rear). We found medianQ_rear to be positively correlated ($r = .51$) with May 1st snow-water equivalent at the Independence Mine Snow Telemetry site (SNOTEL site 1091) located upstream of the Little Susitna River gage, where the highest (2005) and lowest (1996) medianQ_rear years coincided with high and low snowpack years for the Talkeetna Mountains. The RB_emerge and medianQ_rear indicators were lagged 1 year after the brood year to correspond with the year of fry emergence and juvenile rearing in freshwater (Table 1).

2.2.3 | River ice breakup and ocean conditions

Although our study focused on stream temperature and discharge, we also included two regional-scale indicators strongly associated with productivity of Alaskan Chinook salmon populations in prior studies (Cunningham et al., 2018; Kilduff et al., 2015; Ohlberger et al., 2016): the date of river ice breakup (NOAA, 2018) and the North Pacific Gyre Oscillation Index (NPGO; Di Lorenzo et al., 2008) during the year of ocean entry. Breakup observations were only available for a small subset of rivers and years in the Cook Inlet region, so we developed a regional indicator of breakup timing from the Susitna River at Sunshine (USGS 15292780). We used linear regression models to predict breakup for six missing years on the Susitna River using time series from nearby Alexander Creek ($r^2 = .95$; 4 years) and the Yentna River ($r^2 = .55$; 2 years). Breakup dates of rivers across Alaska are highly correlated (Bieniek et al., 2011), so this regional proxy likely explained most of the interannual variability across our study streams. Time series of monthly NPGO (Di Lorenzo, 2019) were used to calculate annual mean values and used as a regional-scale indicator of marine conditions. The breakup and NPGO indicators were lagged 2 years after the brood year to correspond with the year of smolt outmigration and ocean entry (Table 1).

To avoid multicollinearity among indicators (e.g., stream temperature and discharge), all indicators were prescreened to ensure that absolute Pearson correlations among indicators did not exceed .6 (Cunningham et al., 2018). Prior to analysis, each indicator time series was standardized by subtracting the mean and dividing by the *SD*.

2.3 | Chinook salmon productivity

We used a hierarchical stock-recruitment approach to quantify environmental effects on Chinook salmon productivity while accounting for density dependence in survival. Stock-recruitment models relate the numbers of fish that escape ocean and freshwater fisheries to spawn in each brood year (spawning stock) to the numbers of their offspring (recruits) that return as adults and are harvested or spawn in subsequent years (Quinn & Deriso, 1999). Estimates of adult returns (spawners plus harvest) and samples of ages are required to assign recruits to the correct spawning stock. We compiled spawning

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abundance, harvest, and age composition data collected by ADF&G and used a run reconstruction approach (Branch & Hilborn, 2010; Cunningham et al., 2017) to estimate recruitment and productivity. We excluded hatchery-origin salmon from our estimates of spawning abundance and harvest, so our results were based on recruitment of natural-origin salmon only.

The goal of the run reconstructions was to estimate unbiased relative indices of productivity (log-transformed recruits per spawner; $\ln[R/S]$) for each population to quantify the effects of environmental indicators. The productivity indices were highly correlated with absolute estimates of productivity generated with traditional run reconstruction models (Erickson et al., 2017; Fleischman & Reimer, 2017) for two data-rich populations (Deshka: $r = .99$; Kenai late run: $r = .93$). The advantage of using the relative approach was that it allowed us to estimate productivity for 13 additional data-limited populations. This relative approach, however, would not necessarily be suitable for stock assessments, setting spawning escapement goals, or comparing population productivity or capacity among stocks, when absolute metrics are required.

2.3.1 | Run reconstructions

Chinook salmon spawning abundance (escapement) is monitored in Cook Inlet using two primary methods. Many populations are monitored using single aerial or foot surveys conducted near the peak of the spawning run, which provide an annual index of spawning abundance. For a smaller number of populations, weir and sonar projects provide an approximate census of spawning abundance (Erickson et al., 2017; Otis et al., 2016; St. Saviour, 2017). We expanded aerial survey counts by dividing by a 45% mean visibility rate to estimate total spawning abundance (Oslund, Ivey, & Lescanec, 2017). Spawning abundance was estimated for 12–35 return years across each of the 15 study populations (Figure S1).

The run reconstructions accounted for salmon harvested in the sport, personal-use, subsistence, and educational fisheries conducted in freshwater, as well as the largest commercial fishery in Cook Inlet in terms of Chinook salmon harvest (Figure S2). Harvest in this mixed-stock commercial fishery was allocated to individual populations using genetic stock-identification data (Eskelin & Barclay, 2017). We did not include harvest from smaller mixed-stock fisheries because stock composition data were inadequate to assign harvest to individual study populations. In total, the run reconstructions accounted for the majority (87% mean, 69%–95% range) of Chinook salmon harvested in the Cook Inlet basin in each of the 1980–2015 return years. As a consequence of excluding a small fraction of the mixed-stock harvest, our estimates of recruitment were conservative.

ADF&G monitors the age composition of salmon by sampling from commercial harvests, sport harvests, and spawning escapement, but not all populations and components are sampled in each year. Gaps in the age composition data for Chinook salmon in the spawning escapement and harvest were filled by fitting a multinomial logistic regression model to the empirical data and using AIC_c model selection (Burnham & Anderson, 2002; Hosmer, Lemeshow, & Sturdivant, 2013). The most parsimonious model included fixed effects of run component (commercial harvest, sport harvest, or spawning escapement), subregions within Cook Inlet, return year, and a subregion × return year interaction. We used this model to estimate missing age compositions (see Supporting Information for additional details on the run reconstruction methods). To maximize the length of population-specific time series available for analysis, we only included recruits from the three most common age classes, which expanded the size of the stock-recruitment dataset from 301 to 332 population-years. Ninety-four percent of all aged fish spent 1 year rearing in freshwater and 2–4 years in the ocean, returning at ages 3–5. Recruitment of these age classes, termed “core-age recruitment,” was highly predictive of total recruitment (linear regression: $r^2 = .999$, $p < .00001$). The resulting time series of stock-recruitment data ranged from 6 to 29 years in duration among the 15 study populations (Figure S3). When the natural log of population productivity ($\ln[R/S]$) was regressed against spawning abundance, the majority of these populations showed evidence for density-dependent compensation or a progressive reduction in population productivity with increased spawning abundance (Figure S4). These observations suggested that a hierarchical time-varying Ricker approach to modeling stock-recruitment dynamics with environmental effects was appropriate.

2.3.2 | Stock-recruitment analysis

Hierarchical Bayesian stock-recruitment models were used to quantify the effects of hypothesized freshwater and marine indicators on Chinook salmon productivity. We use “effect” to refer to a statistical association between an indicator and productivity, which does not necessarily imply causation. Hierarchical models benefit from sharing information among groups, salmon stocks in the present context, to identify common responses (Cressie, Calder, Clark, Ver Hoef, & Wilke, 2009; Ogle, 2009) while averaging out process errors (Thompson & Page, 1989). The effects of environmental indicators on productivity of each Chinook salmon population were estimated by assuming population-specific effects arise from a common prior distribution representing all populations in the Cook Inlet region. This hierarchical structure permitted us to address two primary questions:

1. What is the association between each environmental indicator and the productivity of Chinook salmon in the Cook Inlet basin?
2. What are the estimated covariate effects for individual spawning populations and how much variation is exhibited among populations?

The strength of the association between a covariate and productivity was evaluated from the Bayesian posterior probability distribution of the estimated effect size, which describes the relative probability of different covariate effects given the data. If the 95% credible interval did not overlap zero, we presumed the covariate had a *strong* association with productivity (either positive or negative). If

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the upper or lower tails (within the 50%–95% bounds) of the distribution overlapped zero, the covariate was presumed to have a *weak* association with productivity, which would not be considered significant in the classical frequentist statistical framework (Ward et al., 2015). The covariate was presumed to have little or no association with productivity if the 50% credible interval overlapped zero.

Recruitment was assumed to follow a Ricker function (Hilborn, 1985; Ricker, 1954),

$$\hat{R}_{p,y} = S_{p,y} \exp\left(\alpha_p - \beta_p S_{p,y} + \sum\nolimits_c (\theta_{p,c} X_{p,t,c})\right), \tag{1}$$

where $\hat{R}_{p,y}$ is the predicted recruitment for population p in brood year y, and it is a function of the spawning stock size $S_{p,y}$ and population-specific Ricker parameters α_p and β_p. The exponent of α_p describes the maximum recruitment rate at low spawning stock size in the absence of density-dependent compensation, while β_p describes the strength of density dependence or the rate at which recruitment declines as spawning stock size increases.

Environmental covariates were specified to have an additive effect on the log recruitment rate. Specifically, the value of covariate c, for population p, in calendar year t ($X_{p,t,c}$) is multiplied by the population-specific covariate effect $\theta_{p,c}$ estimated by the model. A normally distributed prior distribution was specified for population-specific covariate effects:

$$\theta_{p,c} \sim \mathrm{Normal}(\mu_c, \sigma_c), \tag{2}$$

where hyperparameters μ_c and σ_c describe the distribution of covariate effects across all Cook Inlet Chinook salmon populations. μ_c is the average effect for each covariate across populations, while σ_c reflects the level of variation among populations in estimated covariate effects (Table 2). The calendar year for each covariate t was offset from the brood year y by 0–2 years, depending on the hypothesized period in the salmon life cycle during which the covariate was expected to influence survival (Table 1).

The hierarchical model was fit to reconstructed stock-recruitment data for the 15 populations of Chinook salmon using Bayesian methods. Combined observation and process error was assumed log-normally distributed:

$$\ln(R_{p,y}) \sim \mathrm{Normal}(\ln(\hat{R}_{p,y}), \tau_p), \tag{3}$$

with population-specific log-normal *SD* τ_p, where $\hat{R}_{p,y}$ is the predicted and $R_{p,y}$ the observed recruitment in the likelihood calculation. Bayesian models were implemented with the JAGS software (Plummer, 2013), with posterior samples generated using Gibbs Markov Chain Monte Carlo (MCMC) sampling. Three chains were run for 2,000,000 iterations, with a 50% burn-in and saving every 200th iteration, resulting in 15,000 posterior samples. Standard convergence diagnostics were used including effective samples sizes (2,600–15,000 for all model parameters), potential scale reduction factors (<1.002 for all parameters), and visual assessment of traceplots for lack of trend and mixing (Gelman, Carlin, Stern, & Rubin, 2004; Gelman & Rubin, 1992).

TABLE 2 Description of model parameters and specified prior distributions. Values in parentheses indicate means and *SD* of each distribution. Square brackets indicate the prior distribution was truncated at a lower and upper bound

Parameter	Description	Prior distribution
$\theta_{p,c}$	Covariate effect	$\sim \mathrm{Normal}(\mu_c, \sigma_c)$
α_p	Ricker: max productivity	$\sim \ln(\mathrm{Uniform}(0,25))$
β_p	Ricker: equilibrium abundance	$\sim \mathrm{Normal}(0,0.1)[0,]$
τ_p	Ricker: process error	$\sim \mathrm{Normal}(0,1)[0.001,]$
μ_c	Hyperparameter: Group mean covariate effect	$\sim \mathrm{Normal}(0,25)$
σ_c	Hyperparameter: Group *SD* of covariate effect	$\sim \mathrm{Normal}(0,5)[0.001,]$

Finally, we conducted a post-hoc exploratory analysis to characterize any nonlinearities or thresholds in the covariate effects. We examined 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 the two temperature indicators (maxT_spawn and avgT_rear), using unstandardized indicator values to reveal whether salmon responded similarly to absolute temperatures (as compared to the standardized temperatures relative to each population's long-term mean, which were used in the model). We also plotted the Ricker residuals against the four environmental indicators with the largest regional mean effect sizes. For this comparison, we left the environmental indicators unstandardized, except that precipitation indicators were standardized by population to allow comparison across watersheds receiving different amounts of precipitation.

3 | RESULTS

3.1 | Chinook salmon spawning abundance, harvest, and productivity

Chinook salmon spawning abundance and harvest fluctuated by roughly an order of magnitude during the 1980–2015 return years. Spawning abundance declined during the early 1990s for many populations and during the mid-2000s for all populations. Spawning abundance partially recovered for some populations after 2010 (Figure S1). Spawning abundance was most variable in Alexander Creek, ranging from a high of 10,455 in 1988 to a low of 250 in 2008. Total harvest of Cook Inlet Chinook salmon peaked at 134,489 in 1993 and later declined by 89% over 7 years from 99,462 in 2005 to only 10,838 in 2012 (Figure S2). Despite the partial recovery in spawning abundance of some populations during 2010–2015, overall harvest reached a 30-year low. Most harvest (65% mean, 45%–83% range) took place in freshwater. The freshwater sport fishery harvested the most Chinook salmon in all years, followed by the commercial fishery. The marine

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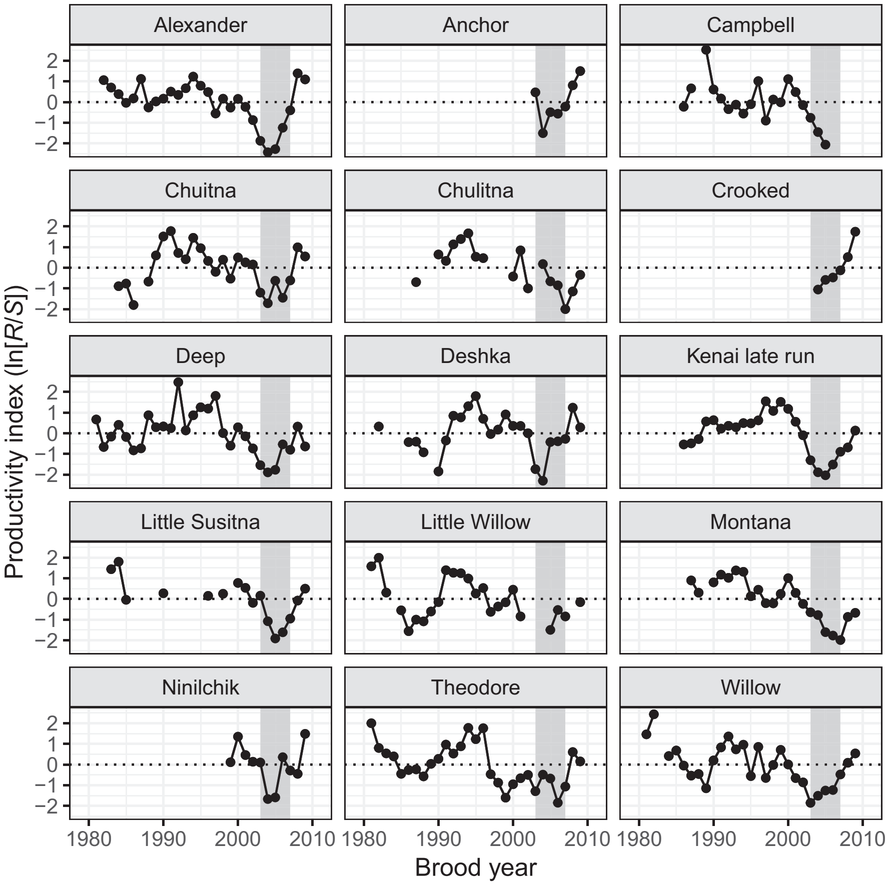

FIGURE 2 Standardized index of Chinook salmon population productivity (natural log of recruits per spawner) by brood year. Dotted lines at zero represent the long-term mean productivity levels of each population. In all, 13 of 15 populations exhibited their single lowest productivity level during 2003–2007 (shaded vertical bands)

sport fishery represented the third largest harvest in most years, although an unknown, but potentially large fraction of this harvest was made up of Chinook salmon from populations outside Cook Inlet (see Supporting Information). Subsistence, personal-use, and educational fisheries combined represented a small fraction of the harvest. Age composition data indicated Chinook salmon returned at younger ages over time throughout the Cook Inlet region (Figure S5).

Chinook salmon populations across the region suffered a low productivity period beginning with the 2003 brood year. Recruitment of the 2003–2007 broods averaged 57% lower than the long-term (pre-2003) mean. Individual populations exhibited recruitment declines ranging from 38% to 93%. On average, density dependence explained only a 10% decline in recruitment during this period, based on linearized Ricker models lacking environmental covariates. In all, 13 of the 15 populations exhibited their single lowest brood year productivity level (natural log of core-age recruits per spawner) during 2003–2007 (Figure 2).

3.2 | Environmental effects on Chinook salmon productivity

Maximum monthly precipitation during the spawning and early incubation season (maxP_spawn) had the strongest association with productivity of all indicators at the regional scale (i.e., all populations

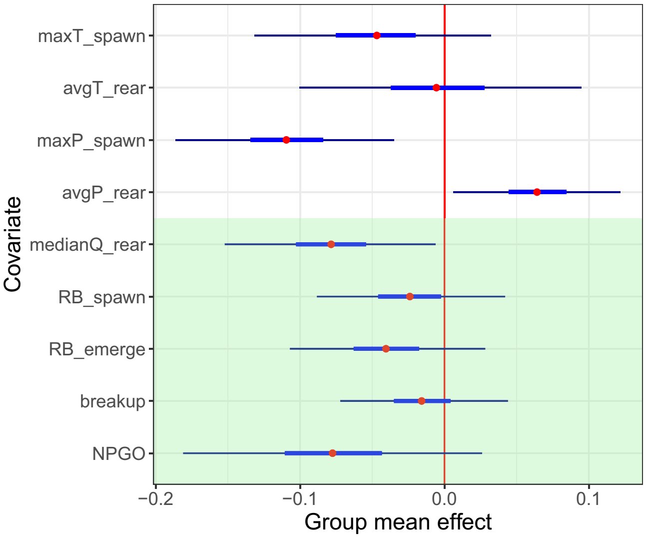

FIGURE 3 Regional mean effects of environmental covariates on Chinook salmon population productivity (log recruits per spawner). Red dots describe the median estimated effect of each covariate on productivity, while the thick and thin blue lines describe the uncertainty (50% and 95% credible intervals, respectively) in estimated effect sizes. The red line centered at zero represents a null effect on productivity. Background color differentiates watershed- (white) and regional-scale (green) indicators. See Table 1 for description of covariates

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across the Cook Inlet region). We found a strong negative association (Figure 3), which was consistent among populations. Each 1 *SD* increase in maximum monthly precipitation from its long-term average was associated with a 10.4% decrease in population productivity (recruits-per-spawner; 95% highest density interval [HDI]: 3.4%–17.0% decrease). Effect sizes estimated for individual populations varied only slightly from the regional mean effect size (Figure 4; *SD* = 3.6 percentage point difference in productivity among populations). Across all populations and brood years, productivity was reduced markedly when maxP_spawn exceeded a threshold of roughly 1 *SD* above-average, based on examination of the Ricker residuals (Figure S6).

Mean precipitation during the juvenile rearing period (avgP_rear) had a strong positive association with productivity across the Cook Inlet region (Figure 3). At the regional scale, each 1 *SD* increase in mean monthly precipitation was associated with a 6.6% increase in population productivity (mean; 95% HDI: 0.6%–13.0% increase). Estimated effect sizes for individual populations were weakly positive (Figure 4), differing very little from the regional mean effect size (*SD* = 2.7 percentage points), but with greater uncertainty. The effect of precipitation during juvenile rearing appeared to be dome-shaped, with the greatest productivity at average or slightly above-average precipitation levels, based on the Ricker residuals (Figure S6). Productivity decreased when precipitation was either more than 2 *SD* above or 1 *SD* below average during juvenile rearing.

Above-average temperatures during the spawning season had a weak negative association with salmon productivity at the regional scale (mean 4.7% decrease per 1 *SD* increase in maxT_spawn; 95%

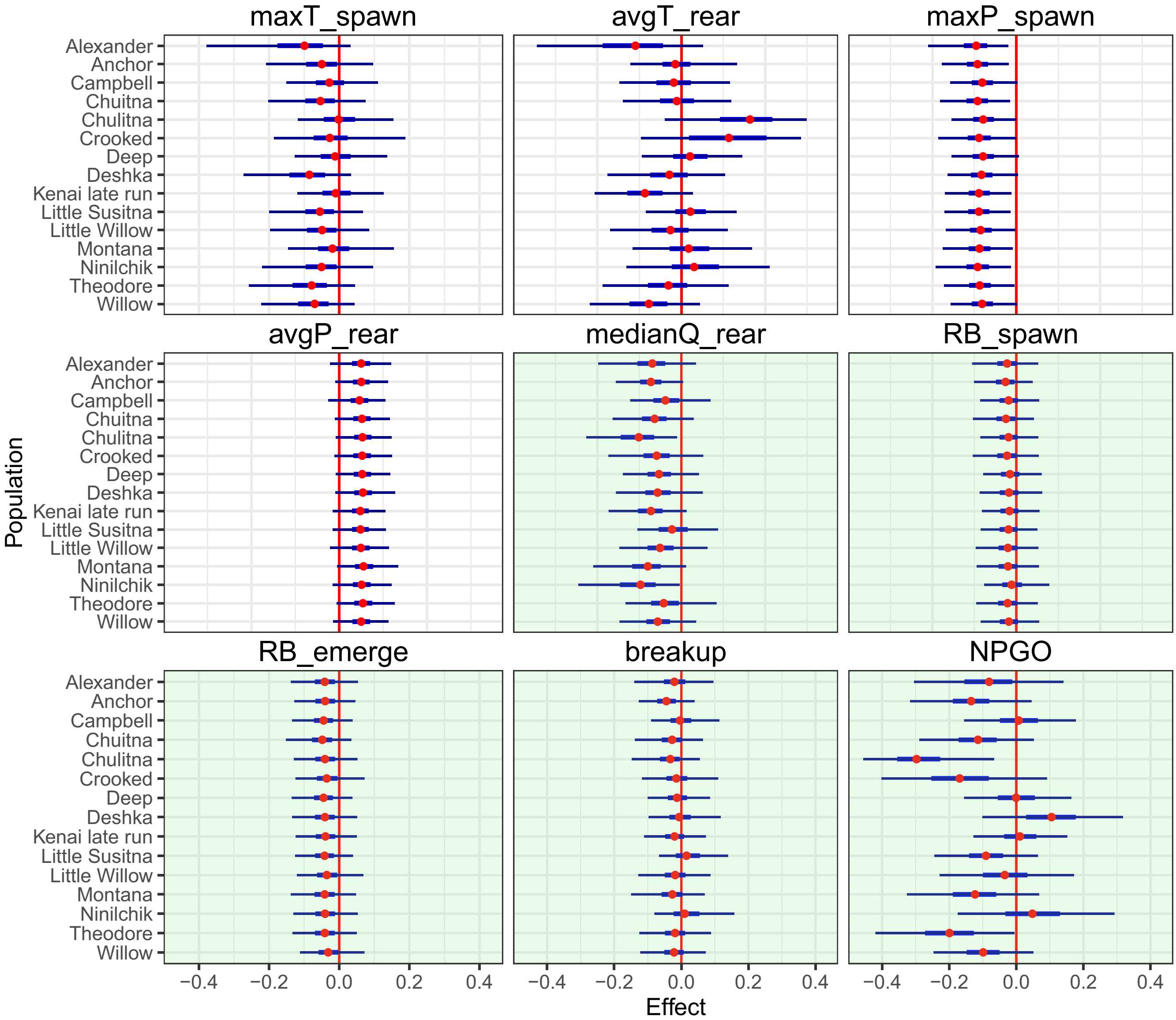

FIGURE 4 Population-specific effects of environmental covariates on Chinook salmon population productivity (log recruits per spawner). Red dots describe the median estimated effect of each covariate on the productivity of each population, while the thick and thin blue lines describe the uncertainty (50% and 95% credible intervals, respectively) in estimated effect sizes. Red lines centered at zero represent null effects on productivity. Background color differentiates watershed- (white) and regional-scale (green) indicators

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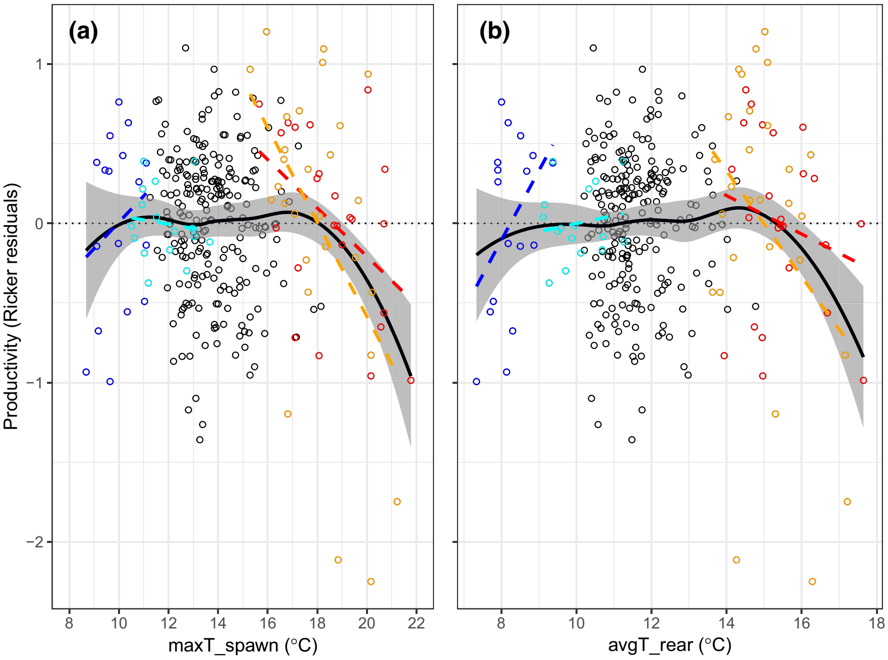

FIGURE 5 Relationships between population productivity, (a) maximum weekly temperature during spawning and early incubation (maxT_spawn), and (b) mean weekly temperature during juvenile rearing (avgT_rear). The vertical axis represents an index of population productivity after accounting for density dependence. Each circle represents the productivity of one population in one brood year, black curve represents a loess regression fit to the data from all populations, and the gray band represents the 95% confidence interval. The two coolest (Chulitna, blue; Little Susitna, cyan) and two warmest (Deshka, red; Alexander, orange) study sites are highlighted. Colored dashed lines represent simple linear regression models fit to the data from each highlighted site

HDI: 12.3% decrease–3.3% increase; Figure 3). Effects varied from negligible to weakly negative among populations (Figure 4). Mean temperature during the summer of juvenile rearing had no consistent association with productivity at the regional scale (mean 0.5% decrease per 1 *SD* increase in avgT_rear; 95% HDI: 9.6% decrease–9.9% increase). Population-specific effect sizes for avgT_rear were highly variable (Figure 4; *SD* = 13.9 percentage points) among populations, ranging from weakly negative (15% decrease) to weakly positive (19% increase).

Our results showed that individual populations responded variably to *standardized* temperature indicators (relative to the long-term average for each stream), but we found coherent nonlinear patterns when the responses of all populations were examined with respect to the temperature indicators expressed in *absolute* terms (°C). These emergent responses were revealed by post-hoc examination of population productivity (Ricker residuals without environmental effects) plotted against unstandardized maxT_spawn and avgT_rear covariates (Figure 5). Across all populations and years, productivity decreased when maximum weekly temperatures exceeded ~18°C during spawning and incubation and ~15°C during rearing. The nonlinear relationships were strongly influenced by data from the coldest and warmest streams. In particular, salmon productivity in the coldest stream (Chulitna River) was positively associated with both maxT_spawn and avgT_rear, whereas productivity in the two warmest streams (Deshka River and Alexander Creek) was negatively associated with both covariates.

Two regional indicators were negatively associated with productivity: the NPGO index of ocean conditions and the median discharge of the Little Susitna River during juvenile rearing (medianQ_rear). The NPGO had a weak negative association with productivity at the regional scale (Figure 3; mean 7.4% decrease per 1 *SD* increase in NPGO; 95% HDI: 16.5% decrease–2.6% increase). Population-specific effects, however, were highly variable ranging from strongly negative to weakly positive (Figure 4; *SD* = 15.9 percentage points). Despite the weakly negative relationship between NPGO and productivity at the regional scale, a residuals plot indicated cohorts that entered the ocean during years with the highest NPGO values (>1.5 *SD*) tended to exhibit above-average productivity (Figure S6). Median discharge (medianQ_rear) had a strong negative association with the productivity of populations across the region (Figure 3; mean 7.6% decrease per 1 *SD* increase in discharge; 95% HDI: 14.1% decrease–0.6% decrease). Effects on individual populations were more variable ranging from negligible to strongly negative (Figure 4; *SD* = 6.5 percentage points).

The regional indicators of river flashiness and ice breakup timing had weakly negative or negligible associations with productivity (Figure 3). Higher flashiness of the Little Susitna River during the spawning season (RB_spawn) had a weak negative association with productivity (mean 2.4% decrease for a 1 *SD* increase in RB_spawn; 95% HDI: 8.8% decrease–4.2% increase), as did higher flashiness during fry emergence (mean 4.0% decrease for a 1 *SD* increase in RB_emerge; 95% HDI: 10.7% decrease–2.8% increase). The effects of both indicators were highly consistent among individual populations (Figure 4; *SD* = 2.9–3.1 percentage points for both indicators). Later, ice breakup on the Susitna River during the year of smolt outmigration had no association with productivity.

Productivity model fit differed substantially among populations (Figure S7). Alexander Creek had the greatest model error, suggesting that our models were missing important drivers of productivity for this population. In contrast, the precise recruitment predictions for the Anchor River, which had one of the shortest time series, suggest that the population-specific model was over-parameterized. A year-by-year comparison of model predictions to the observed data for each population (Figure 6) showed that the models generally captured the variation in recruitment with no apparent bias. The models predicted a decrease in recruitment during the mid-2000s for most populations, although they failed to predict the full extent of the

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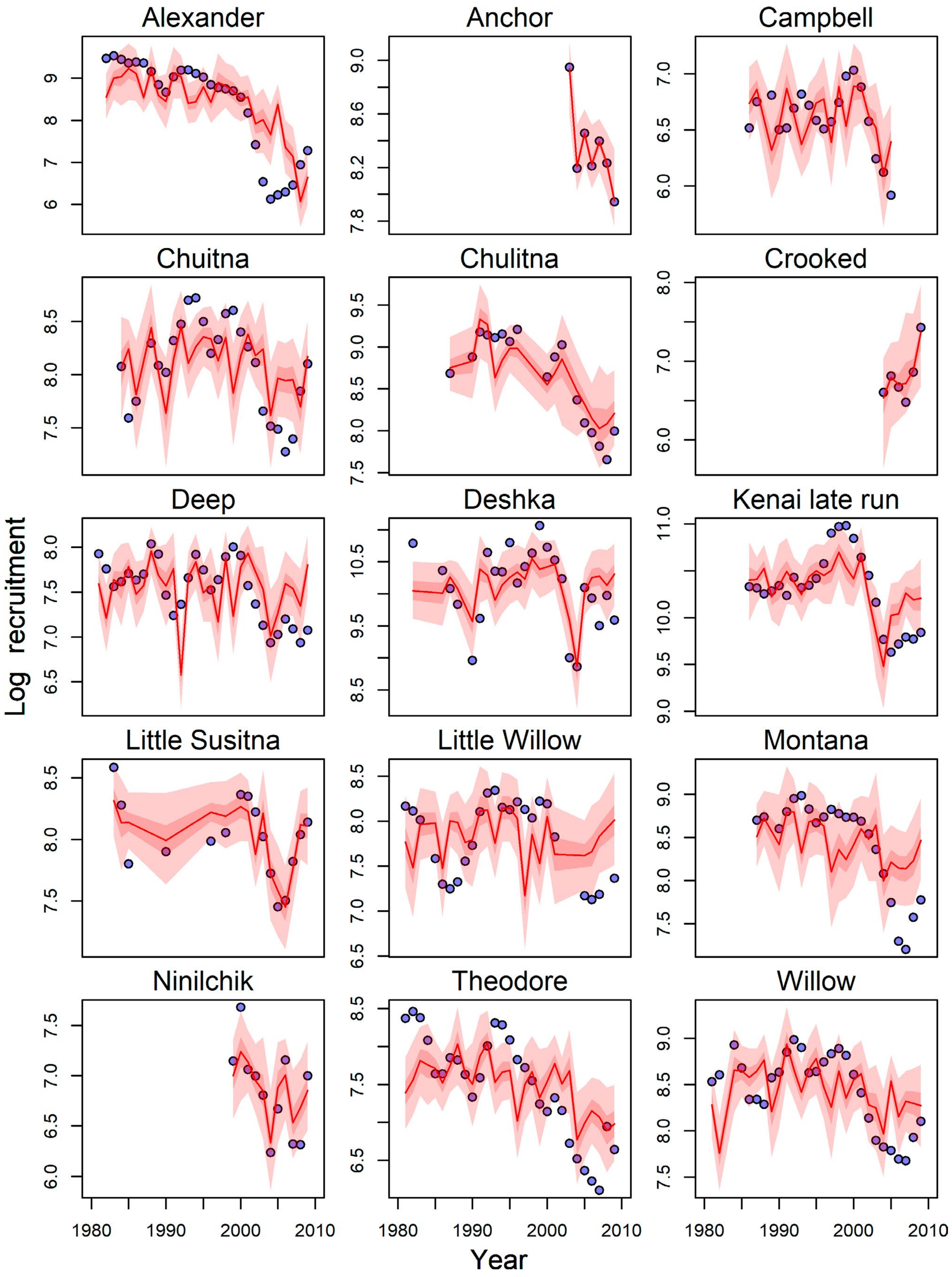

FIGURE 6 Productivity model results for all Chinook salmon populations. Blue points show observed data and red line represents the median, dark red 50%, and light red 95% credible intervals for predicted recruitment

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decline of some populations. This suggested that the models may not have incorporated all of the drivers involved in the decline. For example, the models failed to fully replicate the rapid decline in recruitment in the Alexander Creek population from the late 1990s to the early 2000s. Alternatively, the lack of fit could have been due to the linear constraints of the model, when some of the effects appeared to be nonlinear in nature (Figure 5; Figure S6).

4 | DISCUSSION

Salmon productivity has long been known to fluctuate in association with regional climate patterns (Mantua, Hare, Zhang, Wallace, & Francis, 1997; Mueter, Peterman, & Pyper, 2002), but the influence of climate at watershed scales remains less studied, especially in data-sparse regions like Alaska. However, understanding the strength and coherence of both regional- and watershed-scale effects is crucial for making effective land-use, management, and conservation decisions in a changing world. By quantifying habitat conditions specific to individual rivers across the Cook Inlet basin (i.e., at the watershed scale), our study revealed important similarities and differences in how individual spawning populations respond to a changing climate. In particular, the negative effect of above-average precipitation during spawning and the positive effect of above-average precipitation during juvenile rearing were consistent across all 15 populations. However, stream temperature effects were highly variable and ranged from positive to negative. These results confirm the influence of freshwater conditions on salmon population dynamics and provide new insights into population-specific responses to a suite of climate drivers.

4.1 | Precipitation and discharge effects

High precipitation during the fall spawning and early incubation period had the strongest negative effect on salmon productivity and was consistent across all populations in our study. The ecological mechanisms explaining this effect might include flooding following heavy rain events, which can scour the streambed and damage or displace embryos (Lapointe et al., 2000; Montgomery, Buffington, Peterson, Schuett-Hames, & Quinn, 1996), thereby reducing egg-to-fry survival and population productivity (Greene et al., 2005; Healey, 1991). Heavy precipitation events can also limit embryo survival via siltation of redds, where high levels of fine sediments deposited in the streambed reduce intra-gravel water flow and dissolved oxygen levels (Reiser & White, 1988; Tappel & Bjornn, 1983). Several studies have linked river discharge to the survival and population dynamics of Chinook salmon (e.g., Greene et al., 2005; Michel, 2019; Neuswanger et al., 2015; Ward et al., 2015), but such analyses are rare in Alaska where long-term, paired stream gage and spawning abundance data are scarce. Although Kovach, Ellison, Pyare, and Tallmon (2015) found that salmon migration timing was associated with precipitation, as far as we are aware, this is the first study to link watershed-scale precipitation patterns to salmon population dynamics.

Above-average precipitation during the juvenile rearing period had a strong positive effect on productivity at the regional level, with little variability among populations. The post-hoc analysis suggested this relationship was dome-shaped, with the greatest productivity at slightly above-average precipitation levels, and reduced productivity when precipitation was below average or extremely high (Figure S6). Moderate rainfall and associated increases in streamflow during the summer months likely increase invertebrate drift (Naman, Rosenfeld, & Richardson, 2016), which could benefit juvenile salmon rearing in main-stem habitats. Moderate increases in flow also allow juveniles to access off-channel habitats, which can confer advantages for growth and survival due to favorable temperatures, high invertebrate production, and cross-ecosystem resource subsidies (Baldock, Armstrong, Schindler, & Carter, 2016; Huntsman & Falke, 2019; Rine, Wipfli, Schoen, Nightengale, & Stricker, 2016; Sommer, Nobriga, Harrell, Batham, & Kimmerer, 2001). At the extreme, however, heavy rains and associated high flows likely increase water velocity, turbidity, or inedible debris densities to levels that reduce drift foraging efficiency (Donofrio, Simon, Neuswanger, & Grossman, 2018; Gregory & Northcote, 1993; Neuswanger, Wipfli, Rosenberger, & Hughes, 2014).

Median discharge during the juvenile rearing period had a strong negative effect on productivity at the regional level, in accordance with prior research (Neuswanger et al., 2015). This result was surprising, given the strong positive effect of precipitation during juvenile rearing. The apparent contradiction might be explained by the different spatial scales of the indicators: watershed-specific (precipitation) versus regional (discharge). In addition, median discharge at the regional index gage on the Little Susitna River was positively correlated with winter snow accumulation, which can have significant effects on the sensitivity of stream temperatures to air temperature. Cline, Schindler, Walsworth, French, and Lisi (2020) found that, during low snow years, streams draining high-elevation watersheds were more responsive to variation in air temperature and that summer water temperatures were 4°C warmer than during high snow years. Given the positive relationship between snowpack and median discharge, years with high median discharge may have had colder stream temperatures than predicted by our hindcasting models, leading to a reduction in juvenile salmon growth and productivity. The relative influence of snowmelt on summer stream temperatures will vary across watersheds depending upon catchment geomorphology and summer climate (air temperature and cumulative precipitation; Cline et al., 2020). These results suggest populations may respond differently to changing snowpack conditions, mediated in part by varying stream temperatures and their associated effects on productivity.

In the Cook Inlet basin, average monthly rainfall peaks during August through October (SNAP, 2019), the spawning and early incubation period for Chinook salmon. Although rainfall during this period is important for moderating temperatures and providing access to critical spawning habitats, heavy rains can have detrimental effects on spawning success. There were no trends in maximum

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monthly rainfall during the fall spawning period over our study years (1980–2010), but precipitation is projected to increase for August and September in the future under all emission scenarios (RCP 4.5, 6.0, and 8.5) and decadal timeframes (2040–2049, 2060–2069, and 2090–2099). Additionally, the frequency and severity of storm events (Graham & Diaz, 2001) including short-duration heavy rainfall events are expected to increase by over 50% across Alaska (Lader et al., 2017). Overall, high-flow events are expected to increase during the time of the year when salmon eggs are incubating (Shanley & Albert, 2014; Wobus et al., 2015), which may increase the potential for adverse effects from scouring, sedimentation, and reduced oxygen levels. Furthermore, many Alaskan watersheds are projected to transition from snow-dominated to rain-dominated during winter months (Littell, McAfee, & Hayward, 2018; Wobus et al., 2015), exposing salmon to winter flooding and increased mortality risk during the incubation period. This climatic transition has already occurred in much of the Pacific Northwest, leading to increased hydrologic variability and reduced Chinook salmon population growth rates (Ward et al., 2015).

4.2 | Stream temperature effects

Warmer stream temperatures during the spawning and early incubation period were weakly associated with reduced productivity at the regional scale, and this effect tended to be stronger in warmer streams. Temperatures were highest for Alexander Creek and the Deshka River, where maximum weekly temperatures exceeded 20°C for three consecutive years during the early 2000s (2002, 2003, 2004; Figure S8). Accordingly, high temperatures during spawning had negative effects on productivity for Alexander Creek and the Deshka River but no effect on several of the coldest streams in our study (e.g., the Chulitna and Kenai Rivers; Figure S8 and Figure 4). High temperatures may have reduced productivity through prespawn mortality (Bowerman et al., 2018), reduced egg survival (Raleigh, Miller, & Nelson, 1986), or changes in embryonic development rates leading to a mismatch between the timing of emergence and optimal foraging conditions (Crozier et al., 2008). Productivity declined steeply for both the Deshka River and Alexander Creek as maximum weekly temperatures increased from 18 to 22°C during spawning (Figure 5a), corresponding to temperatures associated with substantial prespawn mortality in Oregon rivers (Bowerman et al., 2018).

The effects of stream temperature during juvenile rearing were highly variable among populations. Above-average temperatures during juvenile rearing were most negatively associated with productivity in warm, low-elevation Alexander Creek, in the cool, glacially influenced Kenai River, and in moderately cool Willow Creek. In contrast, above-average temperatures during rearing were positively associated with productivity for the coldest stream in our study (Chulitna River) and in moderately cool Crooked Creek (Figure S9). Warm conditions in the snow-fed Chulitna River likely increase the production of invertebrate prey and juvenile salmon growth rates. Warm years in the glacial Kenai River lead to greater rates of glacial melt and increased turbidity, which may reduce invertebrate production and the foraging efficiency and growth rates of juvenile salmon (Edmundson et al., 2003). It is possible that salmon responded differently in Willow Creek and Crooked Creek, despite their similar mean temperatures because of the high daily and seasonal variability of temperatures in Willow Creek (Shaftel et al., 2020). The thermal performance of fish and other ectotherms is nonlinear, so growth rates can be substantially reduced under a variable temperature regime relative to a stable one (Ruel & Ayres, 1999; Vasseur et al., 2014). Across all sites and brood years, productivity declined sharply when mean weekly temperatures during rearing exceeded 15°C (Figure 5b), which was consistent with the literature (McCullough et al., 2001).

The highly variable response of population productivity to stream temperatures underscores the importance of thermal habitat diversity to salmon. Salmon streams in Cook Inlet exhibit a variety of stream thermal regimes driven by hydrologic and climatic factors that are rapidly changing (Mauger et al., 2017; Shaftel et al., 2020). Modeled average weekly stream temperatures warmed at rates of 0.22–0.39°C per decade over our 37-year study period (1980–2016, Figure S10). Alaska experienced a record heatwave in 2019, when 7-day average maximum daily stream temperatures in the Deshka River reached 26.9°C (Mauger, 2019), indicating an imminent risk of mortality for salmonids (Richter & Kolmes, 2005). Our findings support the predictions of previous studies that the effects of climate warming will vary across watersheds and habitats, harming some populations while benefiting others (Lynch et al., 2016; Mantua et al., 2015; Schoen et al., 2017). For example, further warming will likely reduce productivity in low-elevation or wetland-dominated systems such as the Deshka River and Alexander Creek, where temperatures already frequently exceed optimal conditions (Figures S8 and S9). Conversely, warming in cooler, high-elevation systems such as the Chulitna River may result in more favorable thermal regimes, increasing juvenile growth potential. However, thermal heterogeneity within watersheds and other, more complex ecological processes may blur these patterns. Our results demonstrate how heterogeneous responses of individual populations to environmental effects can be obscured in analyses conducted at the regional scale that assume a consistent response among populations (Rogers & Schindler, 2011).

4.3 | Ocean conditions and ice breakup effects

The NPGO showed a weak negative regional effect, and population-specific effects were highly variable in direction and size, in accordance with prior studies (Dorner et al., 2017; Kilduff et al., 2015; Ohlberger et al., 2016). While recent research has suggested that productivity and survival of Chinook salmon populations have become more synchronous over time (Dorner et al., 2017) in association with broad-scale oceanographic conditions such as the NPGO, heterogeneity in localized population dynamics continues to be

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observed. In some cases, regional differences between salmon productivity and ecosystem conditions are primarily reflected in differences in the relationship between early marine survival and nearshore temperature patterns (Mueter et al., 2002; Sharma & Liermann, 2010; Sharma, Velez-Espino, Wertheimer, Mantua, & Francis, 2013). Although the hierarchical model estimated a negative regional effect of the NPGO, the residuals plot (Figure S6) suggested that the highest NPGO values were associated with above-average productivity. This seemingly paradoxical result may be explained by non-stationarity in the relationship between NPGO and productivity, whereby the ecological mechanisms underlying the association have changed over time (Litzow et al., 2018).

The timing of ice breakup during the year of ocean entry was not associated with productivity in the Cook Inlet basin. Ice breakup data from the Susitna River show a trend toward earlier breakup over the last 18 years (NOAA, 2018). These trends are even more pronounced in higher latitudes of Alaska, where earlier breakup timing is strongly associated with increased Chinook salmon productivity (Cunningham et al., 2018; Ohlberger et al., 2016). The lack of a breakup effect in our study may be due in part to the longer growing season in southcentral Alaska, which could result in reduced sensitivity to variation in food availability or less risk of mismatch with marine prey availability.

4.4 | Trade-offs between spatial scale and ecological complexity

Like most studies relating environmental drivers to the productivity of wild populations, our analysis lacked experimental controls and relied on correlational evidence. It is possible the effects identified by the model were driven by other causal processes (Myers, 1998). However, we found the results plausible because they were based on ecological mechanisms that influence Chinook salmon populations in other regions (e.g., fall flooding: Greene et al., 2005; extreme temperatures: Richter & Kolmes, 2005). Furthermore, by integrating environmental indicators and productivity time series for 15 populations, we reduced the possibility of identifying spurious “false-positive” correlations (Mueter et al., 2002; Myers, 1998). However, our hierarchical approach may have had reduced sensitivity to detecting population-specific effects by assuming all populations shared a region-wide, linear response to each indicator. This analytical trade-off meant the hierarchical model may have underestimated some of the population-specific temperature and NPGO effects that appeared nonlinear and were highly variable across populations (Rogers & Schindler, 2011). To avoid overlooking important ecological patterns (i.e., “false negatives”; Tillotson & Quinn, 2016), we explored the diversity of population-specific responses with post-hoc analysis.

In addition to its direct effects, climate can influence salmon populations indirectly via their food supply (Schindler, Rogers, Scheuerell, & Abrey, 2005), competitors (Schoen, Beauchamp, Buettner, & Overman, 2015), predators (Lawrence et al., 2014), and pathogens (Kocan, Hershberger, Sanders, & Winton, 2009). Our analysis did not include multi-species interactions due to a lack of time-series data, but we recognize they could have contributed to Chinook salmon population declines. In particular, predation by invasive northern pike (*Exos lucius*) was likely a primary driver of the decline in Alexander Creek (Dunker, Sepulveda, Massengill, & Rutz, 2018; Sepulveda, Rutz, Dupuis, Shields, & Dunker, 2015; St. Saviour, 2017). Alexander Creek exhibited greater model error than the other populations in our analysis, most obviously during the 2000s, when observed productivity declines were not replicated by the model (Figure 6). Invasive northern pike also consume salmon in the Deshka River and many other salmon streams across northern Cook Inlet, but it is unclear how strongly predation affects salmon population dynamics in these systems. Future warming in the Cook Inlet region could cause pike metabolic rates to increase and facilitate an expansion of their range, thereby increasing predation of juvenile salmon (Dunker et al., 2018; Hein, Öhlund, & Englund, 2014). Further research to integrate biological drivers into productivity analyses would be valuable.

4.5 | Population declines and cumulative effects

Our results suggest that cumulative effects from 5 years of adverse freshwater conditions, including high spawning abundance, heavy fall rains, and above-optimal spawning and rearing temperatures, reduced the productivity of the 2003–2007 broods and contributed to the diminished returns of Chinook salmon to Cook Inlet during the late 2000s and early 2010s. Spawning abundance was relatively high across the region during 2003–2005 (Figure S1), and density dependence explained a small portion (10 percentage points) of the 57% average decline in recruitment suffered by the 2003–2007 broods. In addition, these broods faced a combination of unusually high fall precipitation and warm summer stream temperatures. Specifically, maximum monthly precipitation during the fall spawning and early incubation period (maxP_spawn) was more than 1 *SD* greater than the long-term mean for the majority of the 15 study streams during the 2004, 2005, and 2006 brood years (Figure S11). In addition, 2003–2007 was the longest period on record in Cook Inlet with average July air temperatures above 12°C; 1.2°C warmer than the previous 5-year period (1998–2002) and 1.7°C warmer than the following 5-year period (2008–2012; NOAA, 2015). This regional climate signal was reflected in maximum weekly stream temperatures during spawning (maxT_spawn), which were well above the long-term average across all sites during 2003 and 2004.

In contrast to these unusually poor freshwater conditions, the 2003–2007 broods experienced variable marine conditions, as indicated by the NPGO index (Figure S12). During their respective years of ocean entry, the NPGO was >1 *SD* below average (regionally favorable, according to our model) for the 2003 brood, >1 *SD* above average (regionally unfavorable) for the 2006 brood, and near average for the 2004, 2005, and 2007 broods. Although our analysis estimated separate (additive) effects for each indicator, it is possible that conditions interacted to compound the effects on productivity. Future studies should pursue the possibility of interacting impacts from both freshwater and marine environments.

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Synchronous declines of Chinook salmon populations across Alaska prompted a multi-faceted research effort to determine the cause(s) (e.g., ADFG, 2013; Schindler et al., 2013). In principle, these concurrent declines could be explained more parsimoniously by adverse conditions in the ocean, where all populations overlap, than by adverse conditions occurring in synchrony across their many distinct spawning and rearing streams (Schindler et al., 2013). However, recent studies show unfavorable freshwater conditions (i.e., late breakup, heavy fall rains, and high stream temperatures) often do occur simultaneously across many watersheds (Bieniek et al., 2011; Mauger et al., 2017; this study), suggesting that the potential importance of freshwater drivers cannot be ruled out based on synchrony in population dynamics alone.

A growing body of evidence now links the productivity of Alaskan Chinook salmon populations to multiple drivers in both the freshwater and marine environments, including river discharge and temperature (Neuswanger et al., 2015; this study), precipitation (this study), river ice breakup timing and the NPGO (Cunningham et al., 2018; Ohlberger et al., 2016; this study), winter sea surface temperature and competition with hatchery salmon in the ocean (Cunningham et al., 2018), and growth rates during the first year in the ocean (Graham, Sutton, Adkison, McPhee, & Richards, 2019). No single driver or life stage has been identified that can fully explain these declines, suggesting that multiple drivers are involved, individual populations are responding differently, or both. Further research examining the relationships between climate and productivity at finer scales, leveraging advances in monitoring, remote sensing, and climate modeling, is necessary to provide valuable watershed-specific guidance for conserving habitats and managing fisheries.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Cook_Inlet_Chinook repository at https://github.com/curryc2/, reference number d3a1b75.

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REFERENCES

ADFG (Alaska Department of Fish and Game). (2013). Chinook salmon stock assessment and research plan. Alaska Department of Fish and Game Special Publication No. 13-01. Anchorage, AK.

Baker, D. B., Richards, R. P., Loftus, T. T., & Kramer, J. W. (2004). A new flashiness index: Characteristics and applications to midwestern rivers and streams. *Journal of the American Water Resources Association*, *40*(2), 503–522. https://doi.org/10.1111/j.1752-1688.2004.tb01046.x

Baldock, J. R., Armstrong, J. B., Schindler, D. E., & Carter, J. L. (2016). Juvenile coho salmon track a seasonally shifting thermal mosaic across a river floodplain. *Freshwater Biology*, *61*(9), 1454–1465. https://doi.org/10.1111/fwb.12784

Beauchamp, D. (2009). Bioenergetic ontogeny: Linking climate and mass-specific feeding to life-cycle growth and survival of salmon. *American Fisheries Society Symposium*, *70*, 53–72.

Bieniek, P. A., Bhatt, U. S., Rundquist, L. A., Lindsey, S. D., Zhang, X., & Thoman, R. L. (2011). Large-scale climate controls of interior Alaska river ice breakup. *Journal of Climate*, *24*(1), 286–297. https://doi.org/10.1175/2010JCLI3809.1

Bowerman, T., Roumasset, A., Keefer, M. L., Sharpe, C. S., & Caudill, C. C. (2018). Prespawn mortality of female Chinook salmon increases with water temperature and percent hatchery origin. *Transactions of the American Fisheries Society*, *147*(1), 31–42. https://doi.org/10.1002/tafs.10022

Brabets, T. P., Nelson, J. M., Dorava, J. M., & Milner, A. M. (1999). Water-quality assessment of the Cook Inlet basin, Alaska-environmental setting. U.S. Geological Survey Open-File Report 2010–1236, Water-resources investigations report 99–4025. 66 pp.

Branch, T. A., & Hilborn, R. (2010). A general model for reconstructing salmon runs. *Canadian Journal of Fisheries and Aquatic Sciences*, *67*(5), 886–904. https://doi.org/10.1139/F10-032

Brett, J. R. (1971). Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *American Zoologist*, *11*(1), 99–113.

Brown, C. L., & Godduhn, A. R. (Eds.). (2015). *Socioeconomic effects of declining salmon runs on the Yukon River*. Fairbanks, AK: Alaska Department of Fish and Game, Division of Subsistence.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer.

Cline, T. J., Ohlberger, J., & Schindler, D. E. (2019). Effects of warming climate and competition in the ocean for life-histories of Pacific salmon. *Nature Ecology & Evolution*, *3*(6), 935–942. https://doi.org/10.1038/s41559-019-0901-7

Cline, T. J., Schindler, D. E., Walsworth, T. E., French, D. W., & Lisi, P. J. (2020). Low snowpack reduces thermal response diversity among streams across a landscape. *Limnology and Oceanography Letters*.

Cressie, N., Calder, C. A., Clark, J. S., Ver Hoef, J. M., & Wilke, C. K. (2009). Accounting for uncertainty in ecological analysis: The strengths and limitations of hierarchical statistical modeling. *Ecological Applications*, *19*(3), 553–570. https://doi.org/10.1890/07-0744.1

Crozier, L. G., Hendry, A. P., Lawson, P. W., Quinn, T. P., Mantua, N. J., Battin, J., … Huey, R. B. (2008). Potential responses to climate change in organisms with complex life histories: Evolution and plasticity in Pacific salmon. *Evolutionary Applications*, *1*(2), 252–270. https://doi.org/10.1111/j.1752-4571.2008.00033.x

Cunningham, C. J., Branch, T. A., Dann, T. H., Smith, M., Seeb, J. E., Seeb, L. W., & Hilborn, R. (2017). A general model for salmon run reconstruction that accounts for interception and differences in availability to harvest. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(3), 439–451. https://doi.org/10.1139/cjfas-2016-0360

Cunningham, C. J., Westley, P. A., & 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

13652486, 2020, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.15155 by Cochrane Canada Provision, Wiley Online Library on [13/02/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

life history model. *Global Change Biology*, *24*(9), 4399–4416. https://doi.org/10.1111/gcb.14315

Curran, J. H. (2012). Streamflow record extension for selected streams in the Susitna River Basin, Alaska. U.S. Geological Survey Scientific Investigations Report 2012-5210. Anchorage, AK. 36 pp.

Curran, J. H., Barth, N. A., Veilleux, A. G., & Ourso, R. T. (2016). Estimating flood magnitude and frequency at gaged and ungaged sites on streams in Alaska and conterminous basins in Canada, based on data through water year 2012. U.S. Geological Survey Scientific Investigations Report 2016-5024. Anchorage, AK. 47 pp.

Di Lorenzo, E. (2019). *North Pacific Gyre Oscillation*. Retrieved from http://www.o3d.org/npgo/

Di Lorenzo, E., & Mantua, N. (2016). Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nature Climate Change*, *6*(11), 1042.

Di Lorenzo, E., Schneider, N., Cobb, K. M., Chhak, K., Franks, P. J. S., Miller, A. J., … Rivere, P. (2008). North Pacific Gyre Oscillation links ocean climate and ecosystem change. *Geophysical Research Letters*, *35*(L08607), 1–6.

Donofrio, E., Simon, T., Neuswanger, J. R., & Grossman, G. D. (2018). Velocity and dominance affect prey capture and microhabitat selection in juvenile Chinook (*Oncorhynchus tshawytscha*). *Environmental Biology of Fishes*, *101*(4), 609–622. https://doi.org/10.1007/s10641-018-0723-5

Dorner, B., Catalano, M. J., & Peterman, R. M. (2017). Spatial and temporal patterns of covariation in productivity of Chinook salmon populations of the northeastern Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences*, *75*(7), 1082–1095. https://doi.org/10.1139/cjfas-2017-0197

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). Boca Raton, FL: CRC Press.

Edmundson, J., Willette, T., Edmundson, J., Schmidt, D., Carlson, S., Bue, B., & Tarbox, K. (2003). Sockeye salmon over escapement (Kenai River component). Alaska Department of Fish and Game Restoration Project 96258A-1. Anchorage, AK.

Erickson, J. W., Willette, T. M., & McKinley, T. (2017). Review of salmon escapement goals in Upper Cook Inlet, Alaska, 2016. Alaska Department of Fish and Game Fishery Manuscript Series No. 17-03. Anchorage, AK.

Eskelin, A., & Barclay, A. (2017). Mixed stock analysis and age, sex, and length composition of Chinook salmon in the Eastside Set Gillnet Fishery in Upper Cook Inlet, Alaska, 2016, Including an Examination of Large Fish (>= 75 cm) Harvest for 2015 and 2016. Alaska Department of Fish and Game Regional Information Report 2A17-03. Anchorage, AK.

Fleischman, S. J., & Reimer, A. M. (2017). Spawner-recruit analyses and escapement goal recommendations for Kenai River and Chinook salmon. Alaska Department and Fish and Game Fishery Manuscript Series No. 17-02. Anchorage, AK.

Gelman, A., Carlin, J. B., Stern, H. S., & Rubin, D. B. (2004). *Bayesian data analysis* (2nd ed.). Boca Raton, FL: Chapman & Hall/CRC.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, *7*(4), 457–511. https://doi.org/10.1214/ss/1177011136

Graham, C. J., Sutton, T. M., Adkison, M. D., McPhee, M. V., & Richards, P. J. (2019). Evaluation of growth, survival, and recruitment of Chinook salmon in southeast Alaska rivers. *Transactions of the American Fisheries Society*, *148*(2), 243–259. https://doi.org/10.1002/tafs.10148

Graham, N. E., & Diaz, H. F. (2001). Evidence for intensification of North Pacific winter cyclones since 1948. *Bulletin of the American Meteorological Society*, *82*(9), 1869–1893. https://doi.org/10.1175/1520-0477(2001)082<1869:Efionp>2.3.Co;2

Greene, C. M., Jensen, D. W., Pess, G. R., Steel, E. A., & Beamer, E. (2005). Effects of environmental conditions during stream, estuary, and ocean residency on Chinook salmon return rates in the Skagit River, Washington. *Transactions of the American Fisheries Society*, *134*(6), 1562–1581. https://doi.org/10.1577/T05-037.1

Gregory, R. S., & Northcote, T. G. (1993). Surface, planktonic, and benthic foraging by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. *Canadian Journal of Fisheries and Aquatic Sciences*, *50*(2), 233–240.

Healey, M. C. (1991). Life history of chinook salmon (*Oncorhynchus tshawytscha*). In C. Groot & L. Margolis (Eds.), *Pacific salmon life histories* (pp. 311–393). Vancouver, BC: University of British Columbia Press.

Hein, C. L., Öhlund, G., & Englund, G. (2014). Fish introductions reveal the temperature dependence of species interactions. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1775), 20132641. https://doi.org/10.1098/rspb.2013.2641

Hicks, M. (2000). *Preliminary review draft discussion paper evaluating standards for protecting aquatic life in Washington's surface water quality standards temperature criteria*. Olympia, WA: Washington State Department of Ecology, Water Quality Program, Watershed Management Section.

Hilborn, R. (1985). Simplified calculation of optimum spawning stock size from Ricker's stock recruitment curve. *Canadian Journal of Fisheries and Aquatic Sciences*, *42*(11), 1833–1834. https://doi.org/10.1139/f85-230

Hosmer, D. W. J., Lemeshow, S., & Sturdivant, R. X. (2013). *Applied logistic regression* (3rd ed.). Hoboken, NJ: John Wiley & Sons.

Howard, K. G., Murphy, J. M., Wilson, L. I., Moss, J. H., & Farley, E. V. Jr. (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*, 1–11. https://doi.org/10.23849/npafcb6/1.11

Huntsman, B. M., & Falke, J. A. (2019). Main stem and off-channel habitat use by juvenile Chinook salmon in a sub-Arctic riverscape. *Freshwater Biology*, *64*(3), 433–446. https://doi.org/10.1111/fwb.13232

IPCC (Intergovernmental Panel on Climate Change). (2018). Summary for policymakers. In V. Masson-Delmotte, P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P. R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J. B. R. Matthews, Y. Chen, X. Zhou, M. I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, & T. Waterfield (Eds.), *Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty* (pp. 1–24). Geneva, Switzerland: World Meteorological Organization and the United Nations Environment Program.

Johnson, J., & Coleman, J. (2014). Catalog of waters important for spawning, rearing or migration of anadromous fishes – Southcenteral Region. Alaska Department of Fish and Game Special Publication No. 14-03. Anchorage, AK.

Kilduff, D. P., Di Lorenzo, E., Botsford, L. W., & Teo, S. L. H. (2015). Changing central Pacific El Niños reduce stability of North American salmon survival rates. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(35), 10962–10966. https://doi.org/10.1073/pnas.1503190112

Kocan, R., Hershberger, P., Sanders, G., & Winton, J. (2009). Effects of temperature on disease progression and swimming stamina in Ichthyophonus-infected rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Journal of Fish Diseases*, *32*(10), 835–843. https://doi.org/10.1111/j.1365-2761.2009.01059.x

Kovach, R. P., Ellison, S. C., Pyare, S., & Tallmon, D. A. (2015). Temporal patterns in adult salmon migration timing across southeast Alaska. *Global Change Biology*, *21*(5), 1821–1833. https://doi.org/10.1111/gcb.12829

Lader, R., Walsh, J. E., Bhatt, U. S., & Bieniek, P. A. (2017). Projections of twenty-first-century climate extremes for Alaska via dynamical downscaling and quantile mapping. *Journal of Applied Meteorology and Climatology*, *56*(9), 2393–2409. https://doi.org/10.1175/JAMC-D-16-0415.1

Lapointe, M., Eaton, B., Driscoll, S., & Latulippe, C. (2000). Modelling the probability of salmonid egg pocket scour due to floods. *Canadian*

13652486, 2020, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.15155 by Cochrane Canada Provision, Wiley Online Library on [13/02/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Journal of Fisheries and Aquatic Sciences, *57*(6), 1120–1130. https://doi.org/10.1139/cjfas-57-6-1120

Lawrence, D. J., Stewart-Koster, B., Olden, J. D., Ruesch, A. S., Torgersen, C. E., Lawler, J. J., … Crown, J. K. (2014). The interactive effects of climate change, riparian management, and a nonnative predator on stream-rearing salmon. *Ecological Applications*, *24*(4), 895–912. https://doi.org/10.1890/13-0753.1

Leppi, J. C., Rinella, D. J., Wilson, R. R., & Loya, W. M. (2014). Linking climate change projections for an Alaskan watershed to future Coho salmon production. *Global Change Biology*, *20*(6), 1808–1820. https://doi.org/10.1111/gcb.12492

Littell, J. S., McAfee, S. A., & Hayward, G. D. (2018). Alaska snowpack response to climate change: Statewide snowfall equivalent and snowpack water scenarios. *Water*, *10*(5), 668. https://doi.org/10.3390/w10050668

Litzow, M. A., Ciannelli, L., Puerta, P., Wettstein, J. J., Rykaczewski, R. R., & Opiekun, M. (2018). Non-stationary climate–salmon relationships in the Gulf of Alaska. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1890), 20181855. https://doi.org/10.1098/rspb.2018.1855

Lloyd, D. S., Koenings, J. P., & Laperriere, J. D. (1987). Effects of turbidity in fresh waters of Alaska. *North American Journal of Fisheries Management*, *7*(1), 18–33. https://doi.org/10.1577/1548-8659(1987)7<18:EOTIFW>2.0.CO;2

Lord, N. (Ed.). (2016). *Made of salmon: Alaska stories from the salmon project*. Fairbanks, AK: University of Alaska Press.

Loring, P. A. (2016). Toward a theory of coexistence in shared social-ecological systems: The case of Cook Inlet salmon fisheries. *Human Ecology*, *44*(2), 153–165. https://doi.org/10.1007/s10745-016-9806-0

Lynch, A. J., Myers, B. J. E., Chu, C., Eby, L. A., Falke, J. A., Kovach, R. P., … Whitney, J. E. (2016). Climate change effects on North American inland fish populations and assemblages. *Fisheries*, *41*(7), 346–361. https://doi.org/10.1080/03632415.2016.1186016

Mantua, N. J., Crozier, L. G., Reed, T. E., Schindler, D. E., & Waples, R. S. (2015). Response of Chinook salmon to climate change. *Nature Climate Change*, *5*(7), 613. https://doi.org/10.1038/nclimate2670

Mantua, N. J., Hare, S. R., Zhang, Y., Wallace, J. M., & Francis, R. C. (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, *78*(6), 1069–1080. https://doi.org/10.1175/1520-0477(1997)078<1069:APICOW>2.0.CO;2

Mauger, S. (2019). Deshka River [online]. Provisional data. Retrieved from https://inletkeeper.org/our-work/healthy-habitat/real-time-temperature-sites/deshka-river/

Mauger, S., Shaftel, R., Leppi, J. C., & Rinella, D. (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*, 702–715. https://doi.org/10.1139/cjfas-2016-0076

McCullough, D. A., Bartholow, J. M., Jager, H. I., Beschta, R. L., Cheslak, E. F., Deas, M. L., … Wurtsbaugh, W. A. (2009). Research in thermal biology: Burning questions for coldwater stream fishes. *Reviews in Fisheries Science*, *17*(1), 90–115. https://doi.org/10.1080/10641260802590152

McCullough, D., Spalding, S., Sturdevant, D., & Hicks, M. (2001). Summary of technical literature examining the physiological effects of temperature on salmonids. U.S. Environmental Protection Agency EPA-910-D-01-005.

McDowell Group. (2015). *The economic impact of the seafood industry in Southcentral Alaska*. Retrieved from aksalmonalliance.org/wp-content/uploads/2015/06/Economic-Impact-of-Southcentral-Seafood-Industry-online-version.pdf

Menne, M. J., Durre, I., Korzeniewski, B., McNeal, S., Thomas, K., Yin, X., … Houston, T. G. (2012). Global Historical Climatology Network – Daily (GHCN-Daily), Version 3.

Michel, C. J. (2019). Decoupling outmigration from marine survival indicates outsized influence of streamflow on cohort success for California's Chinook salmon populations. *Canadian Journal of Fisheries & Aquatic Sciences*, *76*(8), 1398–1410. https://doi.org/10.1139/cjfas-2018-0140

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/cjfas-53-5-1061

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 Fisheries and Aquatic Sciences*, *59*(3), 456–463. https://doi.org/10.1139/f02-020

Myers, R. A. (1998). When do environment–recruitment correlations work? *Reviews in Fish Biology and Fisheries*, *8*(3), 285–305. https://doi.org/10.1023/A:1008828730759

Naman, S. M., Rosenfeld, J. S., & Richardson, J. S. (2016). Causes and consequences of invertebrate drift in running waters: From individuals to populations and trophic fluxes. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*, 1292–1305.

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

Neuswanger, J., Wipfli, M. S., Rosenberger, A. E., & Hughes, N. F. (2014). Mechanisms of drift-feeding behavior in juvenile Chinook salmon and the role of inedible debris in a clear-water Alaskan stream. *Environmental Biology of Fishes*, *97*(5), 489–503. https://doi.org/10.1007/s10641-014-0227-x

NOAA (National Oceanic and Atmospheric Administration). (2015). Climate at a glance [online]. National Oceanic and Atmospheric Administration. Retrieved from http://www.ncdc.noaa.gov/cag/time-series

NOAA (National Oceanic and Atmospheric Administration). (2018). National Oceanic and Atmospheric Administration – National Weather Service. Break Up Database. Retrieved from https://www.weather.gov/aprfc/breakupDB

NRC (National Research Council). (2004). *Developing a research and restoration plan for Arctic-Yukon-Kuskokwim (Western Alaska) salmon*. Washington, DC: National Academy Press.

Ogle, K. (2009). Hierarchical Bayesian statistics: Merging experimental and modeling approaches in ecology. *Ecological Applications*, *19*(3), 577–581. https://doi.org/10.1890/08-0560.1

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

O'Neel, S., Hood, E., Bidlack, A. L., Fleming, S. W., Arimitsu, M. L., Arendt, A., … Pyare, S. (2015). Icefield-to-ocean linkages across the northern Pacific coastal temperate rainforest ecosystem. *BioScience*, *65*(5), 499–512. https://doi.org/10.1093/biosci/biv027

Oslund, S., Ivey, S., & Lescanec, D. (2017). Area management report for the recreational fisheries of Northern Cook Inlet, 2014–2015. Alaska Department of Fish and Game Fisheries Management Report No. 17-07. Anchorage, AK.

Otis, E. O., Erickson, J. W., Kerkvliet, C., & McKinley, T. (2016). A review of escapement goals for salmon stocks in Lower Cook Inlet, Alaska, 2016. Alaska Department of Fish and Game Fishery Manuscript Series No. 16-08. Anchorage, AK.

Pitman, K. J., Moore, J. W., Sloat, M. R., Beaudreau, A. H., Bidlack, A. L., Brenner, R. E., … Whited, D. C. (2020). Glacier retreat and Pacific salmon. *BioScience*, *70*(3), 220–236. https://doi.org/10.1093/biosci/biaa015

Plummer, M. (2013). JAGS Version 3.4.0 user manual. Retrieved from http://www.stats.ox.ac.uk/~nicholls/MScMCMC15/jags_user_manual.pdf

13652486, 2020, 9, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/gcb.15155 by Cochrane Canada Provision, Wiley Online Library on [13/02/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Quinn, T. J., & Deriso, R. B. (1999). *Quantitative fish dynamics*. New York, NY: Oxford University Press.

Raleigh, R. F., Miller, W. J., & Nelson, P. C. (1986). Habitat suitability index models and instream flow suitability curves: Chinook salmon. U.S. Fish and Wildlife Service Biological Report 82 (10.122). Fort Collins, CO.

Reiser, D. W., & White, R. G. (1988). Effects of two sediment size-classes on survival of steelhead and chinook salmon. *North American Journal of Fisheries Management*, *8*(4), 432–437.

Richter, A., & Kolmes, S. A. (2005). Maximum temperature limits for chinook, coho, and chum salmon, and steelhead trout in the Pacific Northwest. *Reviews in Fisheries Science*, *13*(1), 23–49. https://doi.org/10.1080/10641260590885861

Ricker, W. E. (1954). Stock and recruitment. *Journal Fisheries Research Board of Canada*, *11*, 556–623.

Rine, K. M., Wipfli, M. S., Schoen, E. R., Nightengale, T. L., & Stricker, C. A. (2016). Trophic pathways supporting juvenile Chinook and coho salmon in the glacial Susitna River, Alaska: Patterns of freshwater, marine, and terrestrial food resource use across a seasonally dynamic habitat mosaic. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*, 1626–1641.

Rogers, L. A., & Schindler, D. E. (2011). Scale and the detection of climatic influences on the productivity of salmon populations. *Global Change Biology*, *17*(8), 2546–2558. https://doi.org/10.1111/j.1365-2486.2011.02415.x

Ruel, J. J., & Ayres, M. P. (1999). Jensen's inequality predicts effects of environmental variation. *Trends in Ecology & Evolution*, *14*, 361–366.

Schindler, D., Krueger, C., Bisson, P., Bradford, M., Clark, B., Conitz, J., … Myers, K. (2013). *Arctic-Yukon-Kuskokwim Chinook salmon research action plan: Evidence of decline of Chinook salmon populations and recommendations for future research*. Anchorage, AK: AYK Sustainable Salmon Initiative, 70 pp.

Schindler, D. E., Rogers, D. E., Scheuerell, M. D., & Abrey, C. A. (2005). Effects of changing climate on zooplankton and juvenile sockeye salmon growth in southwestern Alaska. *Ecology*, *86*(1), 198–209. https://doi.org/10.1890/03-0408

Schoen, E. R., Beauchamp, D. A., Buettner, A. R., & Overman, N. C. (2015). Temperature and depth mediate resource competition and apparent competition between *Mysis diluviana* and kokanee. *Ecological Applications*, *25*(7), 1962–1975. https://doi.org/10.1890/14-1822.1

Schoen, E. R., Wipfli, M. S., Trammell, E. J., Rinella, D. J., Floyd, A. L., Grunblatt, J., … Witmer, F. D. W. (2017). Future of Pacific salmon in the face of environmental change: Lessons from one of the world's remaining productive salmon regions. *Fisheries*, *42*(10), 538–553. https://doi.org/10.1080/03632415.2017.1374251

Sepulveda, A. J., Rutz, D. S., Dupuis, A. W., Shields, P. A., & Dunker, K. J. (2015). Introduced northern pike consumption of salmonids in Southcentral Alaska. *Ecology of Freshwater Fish*, *24*(4), 519–531. https://doi.org/10.1111/eff.12164

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*, 1–17. https://doi.org/10.1111/1752-1688.12839

Shanley, C. S., & Albert, D. M. (2014). Climate Change sensitivity index for pacific salmon habitat in Southeast Alaska. *PLoS ONE*, *9*(8), e104799. https://doi.org/10.1371/journal.pone.0104799

Sharma, R., & Liermann, M. (2010). Using hierarchical models to estimate effects of ocean anomalies on north-west Pacific Chinook salmon *Oncorhynchus tshawytscha* recruitment. *Journal of Fish Biology*, *77*(8), 1948–1963. https://doi.org/10.1111/j.1095-8649.2010.02779.x

Sharma, R., Velez-Espino, L. A., Wertheimer, A. C., Mantua, N., & Francis, R. C. (2013). Relating spatial and temporal scales of climate and ocean variability to survival of Pacific Northwest Chinook salmon (*Oncorhynchus tshawytscha*). *Fisheries Oceanography*, *22*(1), 14–31. https://doi.org/10.1111/fog.12001

SNAP (Scenarios Network for Alaska and Arctic Planning), University of Alaska. (2017). Scenarios network for Alaska and Arctic Planning, University of Alaska. 2018. Historical Monthly and Derived Precipitation Products - 771m CRU TS. Retrieved from http://ckan.snap.uaf.edu/dataset/historical-monthly-and-derived-precipitation-products-771m-cru-ts

SNAP (Scenarios Network for Alaska and Arctic Planning), University of Alaska. (2019). *Community climate charts*. Retrieved from https://snap.uaf.edu/tools/community-charts

Sommer, T. R., Nobriga, M. L., Harrell, W. C., Batham, W., & Kimmerer, W. J. (2001). Floodplain rearing of juvenile chinook salmon: Evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(2), 325–333. https://doi.org/10.1139/f00-245

St. Saviour, A. (2017). Alexander Creek chinook and coho salmon stock assessment, 2014 and 2015. Alaska Department of Fish Fishery Data Series No. 17-06. Anchorage, AK.

Stewart, I. T., Cayan, D. R., & Dettinger, M. D. (2005). Changes toward earlier streamflow timing across western North America. *Journal of Climate*, *18*(8), 1136–1155. https://doi.org/10.1175/JCLI3321.1

Tappel, P. D., & Bjornn, T. C. (1983). A new method of relating size of spawning gravel to salmonid embryo survival. *North American Journal of Fisheries Management*, *3*(2), 123–135. https://doi.org/10.1577/1548-8659(1983)3<123:ANMORS>2.0.CO;2

Thompson, J. N., & Beauchamp, D. A. (2014). Size-selective mortality of steelhead during freshwater and marine life stages related to freshwater growth in the Skagit River, Washington. *Transactions of the American Fisheries Society*, *143*(4), 910–925. https://doi.org/10.1080/00028487.2014.901253

Thompson, K. R., & Page, F. H. (1989). Detecting synchrony of recruitment using short, autocorrelated time series. *Canadian Journal of Fisheries and Aquatic Sciences*, *46*, 1831–1838. https://doi.org/10.1139/f89-230

Tillotson, M. D., & Quinn, T. P. (2016). Beyond correlation in the detection of climate change impacts: Testing a mechanistic hypothesis for climatic influence on sockeye salmon (*Oncorhynchus nerka*) productivity. *PLoS ONE*, *11*(4), e0154356. https://doi.org/10.1371/journal.pone.0154356

Vasseur, D. A., Delong, J. P., Gilbert, B., Greig, H. S., Harley, C. D. G., Mccann, K. S., … Connor, M. I. O. (2014). Increased temperature variation poses a greater risk to species than climate warming. *Proceeding of the Royal Society B*, *281*(1799). https://doi.org/10.1098/rspb.2013.2612

Ward, E. J., Anderson, J. H., Beechie, T. J., Pess, G. R., & Ford, M. J. (2015). Increasing hydrologic variability threatens depleted anadromous fish populations. *Global Change Biology*, *21*(7), 2500–2509. https://doi.org/10.1111/gcb.12847

Wobus, C., Prucha, R., Albert, D., Woll, C., Loinaz, M., & Jones, R. (2015). Hydrologic alterations from climate change inform assessment of ecological risk to Pacific salmon in Bristol Bay, Alaska. *PLoS ONE*, *10*(12), e0143905. https://doi.org/10.1371/journal.pone.0143905

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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