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### Working Title: Understanding marine processes affecting the productivity of Yukon River chum salmon using an integrated population model.

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### Abstract

Climate change is rapidly transforming high-latitude marine and freshwater ecosystems, with Pacific salmon populations in the Yukon River experiencing unprecedented declines in abundance. At the northern end of the species’ range, Yukon River chum salmon runs (*Oncorhynchus keta*) recently collapsed to 10% of their long-term average return abundance. This collapse resulted in closure of subsistence fisheries, and a significant and detrimental impact on food security and cultural tradition for Alaska Native peoples who are facing a multi-species salmon collapse. While the impacts of climate change across the anadromous life stages of chum salmon have been linked to this decline, there remains a need to explore these hypotheses within an integrated quantitative context.

Here, we use an integrated population model to examine how ecosystem change influences survival of Yukon River fall chum salmon across multiple life stages. To evaluate the influence of environmental covariates on survival during two critical life stage periods: survival from egg to first marine summer and from first marine summer to terminal harvest. We found that recent declines are driven by reduced survival across multiple life stages. While most freshwater covariates showed limited association with survival, we found that decreasing spawner body size likely impacts the number of eggs deposited, which is correlated with reduced productivity to the juvenile stage. Additionally, there was a weak positive relationship between Fall snow depth and egg to juvenile survival. We found a negative effect of increased competition from hatchery-origin salmon on marine survival and a positive relationship between juvenile stomach fullness and marine survival, suggesting that fish condition before their first winter at sea is crucial for survival. These findings highlight how multiple stressors - from changing freshwater and ocean conditions to increased competition - can compound to affect population survival rates. Our results underscore the importance of evaluating ecosystem impacts on fish survival across multiple life stages and the challenges in understanding ecosystem- abundance relationships for anadromous fish populations undergoing rapid environmental change.

### 1. Introduction

High-latitude regions are experiencing climate change at twice the global average rate, leading to profound transformations in both marine and freshwater ecosystems (IPCC 2023). These rapid changes are particularly impactful for species that cross ecosystem boundaries during their life cycle, as they must navigate multiple altered environments to complete their life history. Pacific salmon exemplify this vulnerability as they traverse freshwater, estuarine, and marine habitats throughout their lives, making them sentinel species for detecting and understanding ecosystem change. As anadromous species, salmon integrate and reflect the cumulative effects of freshwater and marine warming, altered precipitation and river flow patterns, and changing ocean conditions across vast geographic scales. In many cases, this also adds challenges when estimating or anticipating impacts of ecosystem change on salmon populations. In the Arctic and sub-Arctic regions, where warming is most pronounced, these environmental shifts can affect critical periods in salmon life history. The accelerated rate of change in these northern regions creates unique challenges for species like salmon, which must adapt to rapidly evolving conditions in multiple ecosystems simultaneously.

Western Alaska, and the Yukon River region in particular, is experiencing a multi-species salmon collapse. There have been commercial and subsistence closures of Chinook salmon on the Yukon River since 2007 and chum salmon harvest has been severely restricted or closed since 2019 (Krueger et al. 2009, Jallen et al. 2022). These closures represent the first time in recent history that both subsistence and commercial harvests were prohibited for these species. Impacts of populations crashes and fishing closures extend far beyond the ecological - for thousands of years, Native Alaskan communities along the Yukon River have stewarded and relied on relationships with salmon for food security and maintaining a way of life. The loss of both Chinook salmon and Chum salmon harvests is particularly devastating, as Chum salmon provide a critical food source when Chinook salmon returns are low. With over 50 rural communities depending on these fisheries, the collapse impacts traditional ways of life and food security (Alliance for a Just Society & Council of Athabascan Tribal Governments 2013).

Yukon River Fall Chum salmon undergo one of the longest freshwater migrations for the species, traveling over 2,700 kilometers from the Bering Sea into Interior Alaska and Canadian spawning grounds (Krueger et al. 2009). This migration distinguishes them from the river's summer Chum salmon run, which typically spawns within the lower 800 kilometers of the drainage. Fall Chum begin entering the river mouth from mid-July through early September, with peak migration into Canadian waters occurring in mid-September (Krueger et al. 2009). These populations face distinct survival challenges across multiple life stages: from egg incubation in groundwater-fed areas during harsh subarctic winters, to rapid outmigration as juveniles, followed by their critical first summer feeding in the northern Bering Sea, and subsequent years of ocean residence primarily in the Gulf of Alaska and Aleutian Island regions. After spending up to five years at sea, with age-four and age-five fish as the most abundant age classes, adults return to the Yukon River to complete their life cycle. The genetic distinctness between summer and fall runs, combined with their discrete spawning distributions, enables the application of multistage lifecycle models to better understand the drivers of productivity across these different life history periods. Understanding stage-specific productivity is particularly crucial given the recent dramatic declines in returns and can help identify critical periods where environmental change may be having the strongest impacts on population dynamics.

The recent crashes in Yukon River Chum salmon abundances were largely unexpected andmechanistic understanding of population dynamics as they related to past population crashes that occurred to return years 2003 and 2019, remain limited. Multiple stressors operate across the species' complex life cycle, making it challenging to disentangle their relative impacts on survival. Declines in different salmonid species on the same river, such as Chinook salmon, have been linked to smaller spawner body sizes, increased daily river temperatures for out and return migrations, and competition in the marine environment (Cunningham et al. 2018, Howard & von Biela 2023, Feddern et al. 2024). However, unlike Chinook salmon, Chum salmon immediately begin their outmigration to the Bering Sea after hatching, often reaching the estuarine environment within six-months. Thus, the mechanisms driving their changes in abundance likely vary and may be less heavily influenced by outmigration conditions compared to fish that spend 1-2 years in the freshwater. Many previous studies or hypotheses presented focus on understanding Chum salmon population dynamics in either freshwater or marine ecosystems, we build on this work to identify linkages among these ecosystems that could influence Chum salmon population dynamics.

Integrated population models (IPMs) provide a powerful framework for understanding complex life histories and their relationships with ecosystem change. These models are particularly valuable for anadromous species like salmon, where survival is influenced by conditions across multiple ecosystems and life stages. IPMs can incorporate multiple data sources, from juvenile abundance surveys to adult return estimates and age composition data, which provides a more comprehensive understanding of population dynamics than single-stage analyses. Further, this flexibility allows for multiple hypotheses to be tested about ecosystem drivers while accounting for observation error and process variation in different data sources. The success of IPMs in salmon research has been well demonstrated, with applications revealing climate impacts on Chinook salmon survival, density-dependent effects in sockeye populations, and the influence of ocean conditions on population productivity (Cunningham et al. 2018, Jones et al. 2020, Scheuerell et al. 2020). IPMs are well-suited for investigating the mechanisms behind recent Fall Chum salmon declines, where multiple potential drivers may be operating across different life stages.

Here, we use an IPM to examine how ecosystem change influences productivity across different life stages of Yukon River Fall Chum salmon. By incorporating multiple data sources spanning 2002-2022, including juvenile abundance surveys, adult returns, and age composition data, we quantify associations between ecosystem covariates and productivity at two critical stages: from egg to the first marine summer and from the first marine summer to terminal harvest. We tested nine covariates across these stages to evaluate hypotheses about key environmental drivers affecting productivity. Specifically, we hypothesized that recent declines are driven by multiple interacting factors: decreased spawner size reducing reproductive success, shifting egg incubation conditions, warming ocean temperatures altering prey availability and metabolic demands during critical early marine periods, and increased competition from hatchery-origin salmon during chum salmon ocean residence.

### 2. Methods

#### 2.1 Population Dynamics Model

An integrated population model (IPM) was used to estimate the influence of environmental and ecological covariates on the survival of Yukon River fall chum salmon at multiple stages throughout their lifecycle (Figure 1, Figure 2). IPMs, also called lifecycle models, are well-suited to address the challenge of incorporating environmental predictors into population models (Schaub & Abadi 2011), as demonstrated by successful applications in mammal, bird and fish conservation (Besbeas et al. 2002, Cunningham et al. 2018, Regehr et al. 2018, Crozier et al. 2021, DeFilippo et al. 2021). The flexible IPM framework incorporates multiple data sources to estimate ecosystem covariate impacts on fall chum salmon survival. Data used to fit the IPM include juvenile abundance data from a marine survey in the northern Bering Sea, run reconstruction data from adult chum salmon returning to the Yukon River to spawn, and environmental covariates spanning brood years 2002 – 2022. The model was fit within a Bayesian framework which will be described below.

The IPM tracked cohorts of fall chum salmon by brood year, *t*, life stage, *s* and age, *a*. The model includes four stages for Yukon river fall chum: 1) “eggs”, which tracks the amount of eggs produced by spawners, 2) “juvenile”, which tracks individuals from eggs to the end of their first summer in the marine environment, 3) “total returns”, which tracks individuals from their first winter to when they return to the Yukon River mouth and are vulnerable to terminal harvest, and 4) “spawners”, which are the fish that escape harvest and make it to the spawning grounds and is equal to the difference between total returns and total terminal harvest (Figure 2).

The number of Chum salmon surviving from an egg to the end of their first summer in the ocean, Nt,s=j, depends on the number of eggs spawned in brood year, *t*, Nt,s=e and the survival rate from eggs to ocean juveniles, t,s=j.

Nt,s=j= t,s=j\* Nt,s=e Eq. 4.1

The survival rate, t,s=j, was calculated using a Beverton-Holt transition function (Moussalli & Hilborn 1986).

Eq. 4.2

where the productivity parameter represents time-varying maximum survival rate in the absence of density-dependent compensation, and represents the carrying capacity, or the maximum number of individuals that could survive to the end of each life stage. The productivity parameter was estimated conditional on environmental covariates (Table 1) using an inverse logit function of basal productivity, , which represented the mean survival rate (in logit space) at low density.

Eq. 4.3

Here, a matrix, of mean-scaled covariate values *c*, was multiplied by an associated coefficient vector, which described the influence of each covariate, *c*, on stage-specific survival rates.

Upon surviving their first summer at sea, fall chum salmon migrate to the Eastern Aleutian Islands and Western Gulf of Alaska (GOA), where they spend up to five years at sea before returning to the Yukon River (Farley et al. 2024). The first winter is hypothesized to be a critical period in the life stage of juvenile salmon (Beamish & Mahnken 2001, Farley Jr et al. 2007). Thus, we estimated survival for the first winter at sea, t,s=m using the Beverton-Holt transition function described above (Eq. 4.2), and the productivity parameter, which informs the maximum survival rate, was estimated conditional on covariates as described in Table 1. Survival from the first winter at sea, t,s=m, was multiplied by the number of juvenile fish, Nt,s=j, to yield the number of fish that survive their first winter at sea, .

= t,s=m \* Nt,s=j Eq. 4.4

The number of fish returning to the Yukon River are based on calendar year, which is indexed by . The number of returning fish, Ny,s=r,a, depended on age-structured natural mortality rates, , and the proportion of fish that mature and return to spawn from each brood year, .

= Eq. 4.5

We assumed a fixed natural mortality for fish with a total age of 3-6 years, , where the annual mortality rate was 0.06. This represents the assumption that older fish had a higher marine mortality than younger fish but that overall ocean mortality after the first winter at sea was low (Beamish 2018). The maturity schedule for Chum salmon was assumed to vary randomly over time, relative to an average maturity schedule. The proportion of fish maturing and returning to the Yukon River at each ocean age, from each brood year , was estimated as a Dirichlet hyper-distribution arising from a mean age-at-maturity probability vector, . Annual deviations from the mean age-at-maturity were determined by an inverse dispersion parameter, *D*.

Eq. 4.6

Returning fish, Ny,s=r,a, were subject to terminal harvest determined by annual fishing mortality in each calendar year , , and age-specific selectivity, . The resulting catch-at-age in calendar year is:

Eq. 4.7

To allow ample flexibility in annual fishing mortality rates by calendar year , , we estimated mean fishing mortality and process deviations around the mean, .

Eq. 4.8

Returning fish that were not captured in terminal fisheries were assumed to reach the spawning grounds and reproduce.

Eq. 4.9

The number of eggs produced by each spawner, *,* was assumed to follow a Ricker function which includes parameters for the log of the maximum recruitment per spawner without density dependence, , and the strength of density dependence, (Ricker 1954, Hilborn 1985). The proportion of females, , was fixed at 50% (Gilk et al.2009).

Eq. 4.10

The lifecycle begins again by summing the number of eggs produced by each female spawner across age classes, which yields number of eggs produced in each brood year, .

Eq. 4.11

#### 2.2 Model Estimation

Data used to fit the IPM include juvenile abundance data from a marine survey in the northern Bering Sea, run reconstruction data from adult chum salmon returning to the Yukon River to spawn, and environmental covariates spanning brood years 2002 – 2022. We fit the IPM to these datasets using Bayesian inference and implemented the model using the rstan package in R (Carpenter et al. 2017, R Core Team 2021, Stan Development Team 2024). The model was fit using 4 chains, 8,000 warm up iterations and 24,000 total iterations. We used an adapt-delta of 0.99 to force the model to take smaller steps when searching the parameter space. We diagnosed chain convergence using the Gelman-Rubin statistic (Brooks & Gelman 1998) and visually inspected coherence in the distribution of posterior samples from each chain using trace plots (Figure S2). We used the *priorsense* package in R to evaluate how sensitive the posterior distribution was to prior and likelihood perturbations (Kallioinen et al. 2023).

#### 2.3 Population Data

Marine juvenile abundance estimated in the IPM (Nt,s=j) was fit to a juvenile fall chum salmon index estimated from data collected during Bering Sea surveys that cover the Northern and Southeastern Bering Sea (NBS, SEBS) . The survey are a collaborative survey run by the NOAA Alaska Fishery Science Center and ADF&G to better understand the Bering Sea ecosystem (Murphy et al. 2021). The survey uses surface trawl gear to sample juvenile salmon at stations across both Bering Sea regions (Figure 1). The survey is conducted annually between August and September, at the end of the first summer at sea for juvenile chum salmon and before they migrate to the Gulf of Alaska/Eastern Aleutians for their first winter. To account for spatial and temporal variability in survey coverage, a vector autoregressive spatial temeporal model was used to estimate juvenile chum salmon relative abundance using catch data from the NBS survey and methods are detailed by Cunningham et al (Thorson 2019).

Multiple stocks of juvenile chum salmon spend their first summer in the NBS and are caught during surface trawl operations. Chum salmon caught in this survey are allocated to five genetic reporting groups, including Yukon River fall chum, using a spatial mixed stock analysis (MSA) (Murphy et al. 2021). We multiplied the annual mean stock proportion of Yukon River fall chum salmon by the VAST-generated juvenile Chum salmon abundance index to estimate the stock-specific juvenile fall chum salmon abundance index.

To translate the IPM model-estimated juvenile abundances to the scale of the observed juvenile abundance, we estimated a constant, *q*. We fit the IPM to the juvenile abundance index, Jt, ranging from brood years 2002 to 2022. Observation error was assumed to be log-normally distributed:

Eq. 4.11

Total return, harvest and spawner estimates for Yukon River fall chum salmon are estimated in a run reconstruction using a state-space modeling approach and is updated annually(Fleischman & Borba 2009, United States and Canada Joint Technical Committee 2024). Spawner abundances were estimated using data from escapement monitoring projects that cover 95% of the drainage and yields drainage-wide estimates (Fleischman & Borba 2009). Harvest data to inform the run reconstruction were compiled from commercial fish tickets and subsistence surveys. In the run reconstruction, the total run size was assumed equal to the sum of spawners and harvest and age composition information was collected from lower river fisheries and test fisheries (Fleischman & Borba 2009). We used estimated total return abundance by calendar year and age (Nt+a+1,s=r,a) to calculate the predicted proportions at age by calendar year (). The difference between the annual return age composition predicted by the model, *,* and the observed return age composition, was minimized by relating the two through a multinomial likelihood.

Eq. 4.12

We fit the IPM to the return, harvest, and spawner estimates ranging from brood years 2002 to 2022 and assumed observation error was log-normally distributed for all stages. Here, observation error, , is fixed based on coefficient of variation from respective abundance indices. Sigma acts as a weighting factor for the likelihood which helps account for confidence and uncertainty in contributions of different sources of information to the total likelihood.

Eq. 4.13

Eq. 4.14

Eq. 4.15

#### 2.4 Priors

Priors were selected as weak or uninformative for a majority of parameters (Table 2). The exception were regularized priors applied to covariate coefficients, , wherewe applied a prior with a normal distribution, mean of 0 and standard deviation of 0.1. This regularized prior was imposed to avoid spurious correlations among covariates and productivity estimates.

#### 2.5 Ecosystem Covariates

Covariates included in the IPM were gathered based on support from peer reviewed literature (Table 1, Figure 2). All covariates were mean-scaled and included in the IPM all at once.

##### 2.5.1 Egg to the first summer at sea

We considered four covariates hypothesized to impact juvenile salmon productivity from the egg stage to the end of their first summer at sea, including the mean spawner size trend from the parent generation, winter snowpack, Yukon River flow rates, cumulative degree days for sea surface temperatures in the NBS, and pollock recruitment index. Larger fish produce more offspring and have greater reproductive success (Ohlberger et al. 2020, Oke et al. 2020, Feddern et al. 2024). We included the mean trend in spawner size-at-age for spawners by compiling Yukon River fall chum salmon age and length data spanning brood years 2002-2021 from escapement projects in the Yukon River drainage. We used a dynamic factor analysis to estimate a common trend in size at age (DFA) (Text S1.1). These age and length data are collected routinely by ADF&G and are publicly available (Table S1).

Local knowledge and ecosystem reports have highlighted the insulating impact snowpack has in protecting eggs against extreme cold conditions in interior Alaska and Canada (Raymond-Yakoubian 2009, Jallen et al. 2022). We hypothesized that low snowpack could have reduced insulating capacities leading to greater temperature variability, higher egg mortality and lower stock productivity (Jallen et al. 2022). We compiled snowpack data for brood years 2002 – 2021 from January to March in Circle, Alaska and used mean winter snowpack as a covariate (Figure 1).

Increased river flow can negatively impact productivity as it makes foraging more difficult for smolts (Neuswanger et al. 2015). A majority of Chum smolt leave the lower Yukon River Delta by the end of June and occasionally into July, depending on ice break up phenology (Miller & Weiss 2023). Given this outmigration timing, Yukon River flow rates in May and June are the most likely to impact feeding and address this hypothesis. We acquired monthly flow data for May and June (cubic feet per second) from a gauge hosted by the United States Geologic Survey (USGS) at Pilot Station, AK, along the Lower Yukon River (Table 1, Table S1).

Empirical studies in the Bering Sea and bioenergetics modeling in Japan have suggested a positive relationship between water temperature during the first summer and productivity (Iino et al. 2022, Farley et al. 2024). The hypothesized positive relationship may arise if warmer temperatures enhance juvenile salmon growth rates as they enter the marine environment which can reduce size-selective mortality and lead to greater survival (Beamish & Mahnken 2001, Farley et al. 2024). To address this, we included NBS cumulative degree days (CDD) to represent the temperature conditions preceding the NBS survey and represent ecosystem conditions for the juvenile’s first summer at sea. To calculate CDD we used the daily mean Northern Bering Sea (NBS) sea surface temperature, publicly available on the Alaska Fisheries Information Network (AKFIN). We summed temperature from June to August for each year to align with when juvenile salmonids would experience the temperature conditions (brood year +1).

High quality prey sources are important for juvenile salmonid lipid accumulation which can lead to greater growth and productivity (Myers et al. 2009, Kaga et al. 2013, Farley et al. 2024). Juvenile pollock (*Gadus chalcogrammus*) represent a high-quality prey source for juvenile Chum in the Bering Sea (Farley & Moss 2009, Moss et al. 2009, Kaga et al. 2013), thus we included the Eastern Bering Sea (EBS) walleye pollock recruitment index. While juvenile Chum salmon consume multiple fish species, forage fish typically have patchy distributions making them difficult to survey and estimate reliable indices. Juvenile pollock are typically the most abundant species in the forage fish biomass (Hollowed et al. 2012), thus the pollock recruitment index represents a robust prey index for juvenile Chum salmon.

##### 2.5.1 First winter at sea to terminal river harvest

We considered four covariates hypothesized to impact marine salmon productivity, which included the period from the end of the first summer at sea until the individuals are vulnerable to terminal harvest when they return to the Yukon River (Table 1, Figure 2). At the end of their first summer at sea, individuals leave the Bering Sea and typically migrate to the Gulf of Alaska and the Aleutian Islands, where they feed and mature. We included the following covariates when estimating survival for the marine stage, : stomach fullness index (SFI), winter CDD from the Eastern Aleutian Islands, and annual total Chum and Pink salmon hatchery releases (separately) from Alaska, Japan, Korea and Russia. We included juvenile SFI to represent the fish’s health condition just before their first winter at sea. We hypothesized that a higher SFI, which we used to represent fish condition, would be positively related to overwinter survival and ultimately adult productivity. The SFI is estimated from stomach content data collected during the NBS survey. Stomach content data are collected from juvenile chum salmon at each station and recorded on a per station basis. Stomach fullness indexes the amount of prey weight relative to juvenile salmon weight (see Murphy et 2021 for more details on fullness calculations). To account for differences in the survey spatial coverage and timing and for differences in the number of stomachs examined at each station, we used a generalized additive model to estimate an annual SFI. The model took the following form:

Eq. 4.16

where is the expected log SFI, for the i-th observation in space and time. We included an intercept, to estimate mean SFI and a factor year effect, , to estimate direct annual indices. To account for the location of the stomach samples, we included , a spatial field represented by a tensor product of B-splines for geospatial coordinates (: latitude, : longitude), which allowed for anisotropy in the smoothing process. To generate standardized estimates used in the IPM, we predicted SFI across years for the mean survey latitude and longitude in the dataset (62.0°N, -168.1°W). The SFI model was assessed for convergence and residuals were assessed for homogeneity.

Increased marine temperatures can lower prey quality and alter the distribution of the prey base while simultaneously increasing metabolic demands of immature salmon (Farley et al. 2024). To evaluate the influence of warm winter temperatures, we included winter Eastern Aleutian CDD to represent the temperature conditions that young Yukon River Chum salmon experienced during their first winter at sea. This stage is hypothesized as a critical survival bottleneck in the lifecycle (Farley et al. 2024). To calculate CDD we used the daily mean Eastern Aleutian SST, publicly available on AKFIN, summed from November to February to represent winter conditions.

Hatchery salmon released in large numbers to the North Pacific can have negative impacts on Pacific Salmon productivity and survival by increased competition for prey resources (Ruggerone et al. 2003, Cunningham et al. 2018, Scheuerell et al. 2020, Feddern et al. 2024). The competition primarily centers on key food sources like zooplankton and forage fish, where hatchery fish often having an initial advantage due to their larger size at release. This competition can trigger density-dependent mortality when the combined number of hatchery and wild salmon exceeds the marine environment's carrying capacity, potentially reducing growth and survival rates for both groups but particularly impacting wild populations that enter the ocean in more dispersed patterns. To address the impact of hatchery fish competition for Yukon chum salmon, we included Chum and Pink salmon hatchery release abundances, separately, from Alaska, Japan, Korea and Russia. International hatchery release abundances are publicly available from the North Pacific Anadromous Fish Commission (Table S1). We used a rolling average of hatchery release abundance lagged to represent the timespan hatchery fish would overlap with Yukon River fall chum salmon in the ocean. For example, chum salmon hatchery releases in brood year 2000 could overlap with Yukon River fall chum salmon by 2002 (calendar year, t+2) and due to variation in age structure, brood year 2000 may continue to compete with wild Yukon River fall chum for 3 more years. To capture this, we include a three-year rolling average of hatchery releases from brood year t + 2 through the return year. Since Pink salmon have a different life history than Chum salmon, we did not use a rolling average, we added a t+1 lag so pink salmon from brood year 2000 could compete with Yukon River fall chum in calendar year 2001. While migration distances and times certainly vary from these different release points, we include hatchery releases to represent a coarse marine competition index.

## 3. Results

#### 3.1 Model Estimation

Brood year abundances for juveniles and total returns fluctuated by XX% between 2000-2018, respectively. Total returns in 2019 were XX% lower than the total mean and juvenile abundance in XX was XX% lower than the dataset mean. Plots of observed and predicted abundance indices indicate that the model generally captured trends in all data sources (Figure 3, Figure S3, Figure S4). Posterior predictive checks confirmed that models could simulate observations similar to those it was fit to (PB, juvenile = 0.43,PB, total return= 0.44,PB, harvest= 0.74, PB, spawners= 0.35). R-hat values were <1.05, indicating that chains have mixed well and provide consistent parameter estimates. Further, visual inspection of trace plots indicated model convergence (Figure S2).

We used a Ricker function to estimate spawner to egg recruitment. Ricker parameters were estimated as α = 2.8 (95% CI: 2.81-2.87) and β = 0.05 (95% CI: 0.01-0.13), which indicates a maximum reproductive rate of 2.8 recruits per spawner at low population sizes, suggesting moderate productivity. However, estimates for the beta parameter includes a large amount of uncertainty (95% CI: 0.01-0.13).

#### 3.2 Estimated Covariate Effects

Covariate effects represent how ecosystem change impacts Chum salmon productivity. The effect size presented in the results represents the percent change in juvenile abundance or total returns (depending on the life stage covariate is applied) for 1 standard deviation increase in the covariate. We found that most covariates in the juvenile stage did not have an effect that was different from zero, however we found weak positive effects of mean spawner size and winter snowpack on juvenile productivity (**estimate mean and CI,** Table S2, Figure 4). Covariates applied to productivity in the first summer at sea to when fish return to the river at terminal harvest, appeared to have a stronger impact on productivity. We found a negative relationship between Chum salmon hatchery release abundance and winter SST on marine productivity during the first winter at sea (**estimate mean and CI,** Table S2, Figure 4). We also found a positive effect of juvenile stomach fullness on marine productivity, meaning that juveniles in better condition are more likely to survive their first winter at sea (**estimate mean and CI,** Table S2, Figure 4).

#### 3.3 Sensitivity Analysis

To understand model sensitivity to each covariate included in the model, we iteratively ran the model with one covariate removed and evaluated the changes in theta (Figure S4). We expressed the changes as relative differences standardized by the full model's standard deviation (Figure S4). For the egg to juvenile stage, the mean return size showed the strongest effect when removed, with parameter estimates decreasing by approximately **1.6 standard deviations** relative to the full model. Other covariates (NBS July/August Temperature, Pollock Recruitment, and Yukon River Mainstem Discharge) had minimal impacts when removed, with relative differences close to zero. For the juvenile to return stage, the removal of Pink Salmon Hatchery Release Abundance had the strongest effect, decreasing parameter estimates by approximately **2.5-3.3 standard deviations** compared to the full model. In contrast, the Fullness Index and Chum Salmon Hatchery Release Abundance showed positive effects when removed, with parameter estimates increasing by **roughly 0.9 standard deviations**. The SFI (Stomach Fullness Index) removal showed a smaller negative effect of **approximately -2.3 standard deviations.** Our final model includes all covariates hypothesized to impact fall chum salmon survival. Rather than including only “significant” covariates, we reduced the likelihood of spurious correlations with covariates by using a regularized prior, thus covariate effects are only estimated as different than zero if there is a strong effect.

### 4.0 Discussion

Our integrated population model reveals that recent declines in Yukon River fall chum salmon stem from changing ecosystem conditions along multiple life stage steps. Cumulative impacts of these processes which include decreased spawner sizes, decreased regional winter snowpack, increased marine competition, and poor juvenile feeding conditions resulting in low stomach fullness, have ultimately led to reduced survival during critical life stages. These findings contribute to a growing body of evidence suggesting that Pacific salmon populations are increasingly vulnerable to ecosystem change across their life cycle.

We included a range of covariates focused on hypotheses throughout the lifecycle and found the strongest support for covariates that impact survival after the first summer at sea before fish return to natal rivers and are vulnerable to terminal harvest. Covariates that were included in estimating survival from egg to juvenile stages generally lacked strong model support, with the exception of the positive relationships for spawner size and winter snowpack, with productivity. Limited data on Chum salmon abundance during their outmigration makes it challenging to model and identify key drivers of freshwater survival, particularly during the multiple capacity-limited life stages they experience during this critical period. While outmigration monitoring projects have been developed, the genetically resolved time series does not capture enough brood years for this study (Miller & Weiss 2023). However, compared to other salmonids, juvenile Chum salmon spend minimal time in freshwater as they head to the ocean. Thus, Chum salmon may be less susceptible to change in freshwater covariates as less of their lifecycle is spent in freshwater.

As with other Pacific salmonid populations, Yukon River fall chum salmon body sizes have decreased through time (Figure S1) (Ohlberger et al. 2023, Freshwater et al. 2023). In estimating a trend in spawner size at age we found that spawner size has decreased across all age classes (Figure S1). Further, we found that a trend toward smaller spawners has led to a 20% (+/- XX) decrease in egg to juvenile productivity. We included size as a covariate, rather than as a size-specific fecundity estimator, to evaluate hypotheses surrounding impacts of salmon size on productivity. Changes to body size has been linked to decreased productivity for Chinook salmon in the Yukon and Kuskokwim Rivers (Feddern et al. 2024) and decreases to salmonid size has implications for the cultural and ecological role of salmon (Oke et al. 2020). Large females produce more eggs than expected based solely on linear scaling with size, thus large females contribute disproportionately to population productivity (Barneche et al. 2018). Management strategies and escapement goals that fail to account for nonlinear reproductive scaling can lead to overexploitation, as each fishes reproductive contribution decreases exponentially with declining body size (Barneche et al. 2018).

Compared to other chum populations, Yukon River fall chum have adapted for long migrations and cold incubation temperatures. Local knowledge and ecosystem reports have highlighted how snowpack can insulate and stabilize temperatures by protecting eggs against extreme cold conditions in interior Alaska and Canada (Raymond-Yakoubian 2009, Jallen et al. 2022). Successful egg and alevin development requires stable temperatures, with ideal temperature around 4°C, and most suitable fall chum spawning habitat is characterized by upwelling through the gravel that allows for consistent temperatures (Beacham et al. 1988, Burril et al. 2010). Accumulated degree days allow fish to develop in time for spring emergence and overlap with sufficient food resources (Beacham et al. 1988). We hypothesized that low snowpack could have reduced insulating capacities leading to greater incubation temperature variability, higher egg mortality and lower stock productivity (Jallen et al. 2022). While we did not find strong support for this hypothesis in our analysis, there was weak support for a positive relationship between Fall snowpack and egg to juvenile survival (Figure 4, Table 1), suggesting that years with greater snowpack confer a XX% increase in productivity (+/-). Our ability to detect snowpack effects was likely limited by using a regional indicator of snowpack, as this single location may not capture the variable local conditions across fall Chum spawning habitats throughout the upper Yukon that could cause significant egg mortality. Thus, while snow depth at Circle may represent regional conditions, local effects could increase variability in this relationship.

A reliable predictive relationship between juvenile abundance and adult returns often indicates relatively stable marine survival rates in salmon populations. However, this relationship breaks down for juvenile Chum salmon in the Bering Sea, where juvenile abundance during their first summer fails to effectively forecast adult returns (Farley et al. 2024). This disconnect suggests that significant survival bottlenecks occur in the marine environment after the juvenile stage. Our results strengthen this hypothesis, as we identified a positive relationship between the SFI and productivity from the juvenile to adult return stage, while other potential drivers of marine productivity showed weaker effects. This suggests that lower SFI, meaning fish were less full, has led to decreases in marine productivity by XX% (+/) (Figure 4, Table S2). This supports the hypothesis that juvenile chum feeding on lower quality prey during warmer years adversely impacts their survival throughout migration, particularly during their first winter when fish in poor condition are unlikely to survive (Farley et al. 2024). During warm conditions, juvenile chum salmon are more likely to feed on gelatinous zooplankton, which are less lipid rich than forage fishes or juvenile pollock (Kaga et al. 2013, Farley et al. 2024). While we used SFI as a proxy for marine condition due to its long time series, more recent time series, like chum energy density, may better capture the relationship between ecosystem conditions and fish condition.

Warm winter conditions in the marine environment are hypothesized to enhance growth rates and improve the prey base for many salmonids, however we did not find evidence of this relationship for Yukon River chum salmon. Rather, we found that increased marine temperature led to a XX% decrease in chum productivity. In the literature, estimated relationships between marine temperature conditions and chum growth or productivity are variable. For example, growth estimated using scales for Norton Sound and Western AK Chum salmon did not indicate correlations between SST and growth (Ruggerone & Agler 2008, Agler et al. 2013). [discuss other + or – relationships]. Further, SST relationships between EBS and GOA Chum salmon can be nonstationary. Dampening of Aleutian Low variance that occurred in 1989 is associated with a weakening of positive relationship between EBS and GOA chum salmon productivity to a neutral relationship, which is what our analysis indicated as well (Litzow et al. 2018). It is likely that observed correlations between SST and productivity represent mechanistic effects of other ecosystem processes that drive the observed SST productivity relationships. However, SST is commonly used as it is typically an accessible, spatiotemporal dataset. In this case, SST may be driving latent trends that have negative impacts on chum salmon productivity in the ocean.

Increased competition in the marine environment has been associated with changes in survival and productivity for multiple Pacific Salmon stocks, including Yukon River Chinook salmon, Norton Sound chum salmon, and Bristol bay sockeye (Ruggerone et al. 2012, Cunningham et al. 2018, Ohlberger et al. 2023, Feddern et al. 2024). Growth in Kuskokwim River chum salmon has decreased through time in strong correlation with increases in Japanese hatchery chum (Frost et al. 2021). We found weak support for the hypothesis that an increasing trend in hatchery released chum salmon has led to a XX% (+/- ) decrease in Yukon River fall chum salmon productivity. Similar to other work in the North Pacific, we did not find evidence of competition with hatchery released pink salmon (Frost et al. 2021). Negative impacts of increased competition at sea have been highlighted recently in the literature, and linked to decreased salmon body sizes and decreases in productivity, as we also found here (Oke et al. 2020, Feddern et al. 2024). Increased competition could result from trophic overlap and density dependent impacts among conspecifics in the marine ecosystem.

The broad spatial distribution of Yukon River fall Chum salmon across Interior Alaska and Canada presents challenges for detecting environmental relationships. Most covariates in our analysis serve as regional indicators that may underestimate local effects. The strongest relationship we found was with the SFI, which derives from direct measurements of the fish rather than ecosystem-level indicators. This suggests that our broad-scale environmental metrics may be detecting only weak signals of potentially stronger underlying relationships and highlights the difficulty in lifecycle modeling with a broad population that traverses remote areas. While our model's informed priors help avoid spurious correlations, additional unmeasured mechanisms could be contributing to population declines. Our ability to test alternative hypotheses was constrained by limited covariate data matching our time series, particularly for freshwater life stages, with most available data focused on the marine phase of the life cycle.

This analysis revealed that changes in Yukon River fall chum salmon productivity have occurred across freshwater and marine ecosystems and these changes have contributed to population temporal variability and recent declines. Multiple interacting factors contribute to changes in marine productivity, including changing ocean conditions that impact stomach fullness and increased competition from hatchery-origin Chum salmon. Further, declining body sizes across age classes impact spawner productivity. The significant relationship between spawner size and productivity, coupled with documented size declines, suggests a longer-term process where smaller spawners lead to lower offspring productivity. These findings align with broader patterns of climate-induced changes in Pacific salmon populations, where marine ecosystem change, and increased competition are increasingly linked to reduced survival and productivity. Our results highlight the complexity of managing anadromous fish populations under rapid environmental change.

#### Supplemental Text:

##### Dynamic Factor Analysis for Spawner Size

To estimate a temporal trend for Yukon River fall chum salmon mean size-at-age, we conducted a dynamic factor analysis (DFA) using data from the Yukon River collected between 2000-2021. Data from 2000 to 2016 was collated by Oke et al. (2020), and more recent years were downloaded from the ADF&G Age Sex Length Database (Alaska Department of Fish and Game 2024) for all escapement projects with data through 2021 (Table S1). We used age and lengths data from fish whose total ages ranged from 3-6 years. Prior to analysis, length measurements were standardized within each marine age group to have a mean of 0 and standard deviation of 1.

The DFA was implemented using the MARSS package in R to identify common trends in body size across different ocean residence times (Holmes et al. 2024). Our model treated the standardized lengths as linear combinations of latent trends and relates the observed data to overall estimated length trend. This was expressed in our observation model as:

where represents the observed data (with marine ages as rows and years as columns), **Z** is a matrix of factor loadings (0,1) on the latent trends that determines how observations relate to the estimated trends and represents observation errors. The observation errors were assumed to be multivariate normal with mean zero and variance-covariance matrix **R**.

The process model estimates the latent trend in spawner size across ages as a random walk with process error:

where is the state, or the spawner length trend, for each calendar year, y, and represents process errors assumed to be multivariate normal with mean zero and variance-covariance matrix **Q**. Model parameters and states were estimated using maximum likelihood via the MARSS package with model convergence set to a maximum of 1000 iterations.

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