## Yukon River Fall Chum Salmon Integrated Population Model

Working title: TBA

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Keywords:

### 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. While climate change across the anadromous migration route likely linked to this decline, it has not been evaluated in an integrated quantitative context. Towards the northern end of the chum salmon range, Yukon River chum salmon runs (*Oncorhynchus keta*) have collapsed to below 90% of their long-term average. 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. 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, we used abundance indices for juveniles at the end of their first marine summer, total return abundances, and age composition from 2002 – 2022. We estimate covariate influence on 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 effects, we found that decreasing spawner body size negatively impacts offspring survival from the egg to juvenile stage. Additionally, there was a positive relationship between Fall snow depth and egg to juvenile survival, as snow can insulate and regulate the egg incubation temperature. We found negative effects of warmer winter temperatures in the Aleutian Islands and increased competition from hatchery-origin salmon on marine survival. Finally, we found 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 (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

#### Study Area

#### 2.1 Population Dynamics Model

We used an IPM to estimate the influence of environmental and ecological covariates on the survival of Yukon River Chum salmon at multiple stages throughout their lifecycle (Figure 1, Figure 2). IPMs are a class of models, also called lifecycle models, that 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 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, , 4) “spawners”, which are the fish that return back to the spawning grounds and is 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 ocean summer, Nt,s=j depended upon 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*, were multiplied by an associated coefficient which described the influence of each covariate, *c*, on stage specific survival rates.

Upon surviving their first summer at sea, Chum salmon migrate to the Eastern Aleutian Islands and Western Gulf of Alaska, where they spend up to five years at sea before returning to the Yukon River (Farley et al. 2024). The first winter in the GOA is hypothesized to be a critical life stage step. Thus, survival was estimated during the first winter at sea, t,s=m.  Survival during the first winter at sea was estimated 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 environmental covariates described in Table 1 for the marine stage. 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 return to spawn from each brood year, .

= Eq. 4.5

We assumed a fixed natural mortality for ages 4-6, , where the annual mortality rate was 0.06. This represents the assumption that older fish had a higher marine mortality than younger fish (Beamish 2018), but that overall ocean mortality after the first winter at sea was low. The maturity schedule for Chum salmon was assumed to vary over time randomly, relative to an average maturity schedule. The proportion of fish returning to the Yukon River at each ocean age in 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 capturing 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 spawner across age classes, yielding the eggs produced in each brood year, .

Eq. 4.11

#### 2.2 Model Estimation

We fit the IPM to multiple datasets using Bayesian inference and implemented the model in STAN (Carpenter et al. 2017) using the rstan package in R (Stan Development Team 2024). The model was fit using 4 chains, 8000 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 arising from data collected in the Northern Bering Sea (NBS) survey. The NBS survey is a collaborative survey run by ADFG, NOAA Alaska Fishery Science Center to better understand the Northern Bering Sea Ecosystem (Murphy et al. 2021). The survey has collected a wide array of ecosystem information, including juvenile salmon abundance from surface trawls that are conducted at multiple stations across the NBS. The survey is conducted annually in Summer/Fall (typically between August and September), which is the termination of juvenile Chum salmon first summer at sea before they migrate to the Gulf of Alaska/Eastern Aleutians.

To account for spatial and temporal survey imbalances, Chum salmon CPUE data were used to estimate a juvenile Chum salmon index (**Garcia et al in prep?**). A Vector Autoregressive Spatio-Temporal modeling approach was used to create an independent index of juvenile chum salmon, and methods are detailed by Cunningham et al (Thorson 2019). The NBS survey includes multiple stocks of juvenile chum salmon that spend their first summer in the NBS. Chum salmon caught in this survey are allocated to genetic reporting groups using a spatial mixed stock analysis (MSA) (**CITE**, **Lee et al..?).** The MSA has five reporting groups, including Yukon River fall chum salmon. Genotype and analysis are further detailed by **XX et al**. We multiplied the mean annual estimated annual proportion of Yukon River fall chum salmon by the total index of juvenile Chum salmon to yield a fall Chum stock-specific juvenile index.

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

Eq. 4.11

Total return, harvest and spawner estimates for Yukon River fall Chum salmon were provided by the Alaska Department of Fisheries and Game (ADFG) run reconstruction (Fleischman & Borba 2009). A full discussion of the run reconstruction model is available in Fleischman and Borba 2009. Model methods have remained the same, while the reconstruction model estimates have been updated with new data annually. Spawner abundances were estimated based on data from escapement monitoring projects that cover 95% of the drainage and yields drainage wide estimates. Harvest data to inform the run reconstruction was compiled from commercial fish tickets and subsistence surveys. In the reconstruction, the total run size was assumed as the sum of the spawners and harvest. We fit the model to the return, harvest and spawner estimates ranging from brood years 2002 to 2022. We assumed observation error was log-normally distributed for all stages. Here, observation error, , acts as a weighting factor for the likelihood, where smaller sigma’s contribute more to the complete likelihood which helps account for the contributions of different sources of information.

Eq. 4.12

Eq. 4.13

Eq. 4.14

Age composition data that informed the run reconstruction was collected from lower river fisheries and test fisheries (Fleischman & Borba 2009). We fit the estimation model to age composition estimates from each calendar year provided by the run reconstruction. We used predicted run size 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 distribution.

Eq. 4.15

#### 2.4 Priors

Priors were selected as generally weak or uninformative for a majority of parameters (Table 1). The exception were regularized priors applied to covariate coefficients, . We 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 and timeseries availability (Table 2, Figure 2). All covariates were mean-scaled.

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

We considered six 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, fall air temperature, fall snow depth, Yukon River flow rates, cumulative degree days for sea surface temperatures in the Northern Bering Sea and pollock recruitment index. We included the mean trend in spawner size at age for spawners that returned during the juvenile brood year. Size at age can impact reproduction potential and affect productivity. We hypothesized a positive relationship between size and productivity where bigger fish produce more offspring and have greater reproductive success (Ohlberger et al. 2020, Oke et al. 2020, Feddern et al. 2024). The Alaska Department of Fish and Game (ADFG) conducts standardized salmon escapement surveys across Alaska where they have recorded salmon length, sex and age since the 1990’s. This information is publicly available (Supplemental Table 1). We compiled Yukon River Chum salmon age and length data spanning 2000-2021 from project sites with current timeseries and estimated a common trend in size at age using a dynamic factor analysis (DFA) (Text S1.1, Table S**XX**).

We included fall snow depth from Circle Alaska (October – December) (Figure 1) to represent regional egg incubation conditions. We hypothesized that years with low snow levels early in the season could lead to high egg mortality, as lower snowpacks have less insulating ability for eggs (Raymond-Yakoubian 2009, Burril et al. 2010, Jallen et al. 2022). In addition to temperature variability, reduced snow could lead to deep freezes into the spawning habitat reducing suitable spawning habitat or lead to dewatering (Jallen et al. 2022). We included the Yukon River mainstem mean flow for May and June as a covariate. We hypothesized that increased river flow has a negative relationship with productivity as it makes juvenile foraging more difficult (Neuswanger et al. 2015). A majority of juvenile Chum migrate to 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 juvenile feeding and address this hypothesis. We acquired monthly flow data (cubic feet per second) from a gage hosted by the USGS at Pilot Station, AK, along the Lower Yukon River (Table 2, Table S1).

We included Northern Bering Sea Summer (NBS) cumulative degree days (CDD) to represent the temperature conditions preceding the NBS survey and represent ecosystem conditions for the first couple months fish are at sea. We hypothesized a positive relationship between temperature and juvenile productivity, as suggested by empirical studies in the Bering Sea and bioenergetics modeling in Japan (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 calculate CDD we used the daily mean NBS SST, publicly available on the Alaska Fisheries Information Network (AKFIN). We summed temperature from June to August for each year brood year +1 to align with when juvenile salmonids would experience the temperature conditions.

We included the EBS walleye pollock (*Gadus chalcogrammus*) recruitment index from the pollock stock assessment to represent changes in salmon prey availability during the first summer at sea (Ianelli et al. 2023). Young pollock represent a high-quality prey source for juvenile Chum (Farley & Moss 2009, Moss et al. 2009, Kaga et al. 2013). High quality prey sources are important for lipid accumulation and can lead to greater growth and productivity (Myers et al. 2009, Kaga et al. 2013, Farley et al. 2024). While juvenile Chum salmon consume multiple fish species, forage fish typically have patchy distributions making them difficult to survey and estimate reliable indices, thus the pollock recruitment index represents robust prey index for juvenile Chum salmon, and typically are the most abundant species in the forage fish biomass (Hollowed et al. 2012).

##### 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 2, 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, : fullness index, 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 a juvenile stomach fullness index (SFI), to represent the conditions fish experience when they begin their first winter at sea and we hypothesized that a higher SFI, which represents better fish condition, would be positively related to adult productivity. The SFI is estimated from fullness data collected by the NBS survey (discussed in more detail below) and data collection methods are detailed in Murphy et al 2021. Briefly, stomach fullness data are collected from salmon at each station and recorded on a per station basis. We used a generalized additive model to estimate an SFI and included a smoothed spatial field to account for differences in the survey through space and time. We also used model weighting to account for differences in the number of stomachs examined at each station. 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. is 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 index model was assessed for convergence and residuals were assessed for homogeneity.

We included winter Eastern Aleutian CDD to represent the temperature conditions that young Yukon River Chum salmon experienced during their first winter at sea. To calculate CDD we used the daily mean E Aleutian SST, publicly available on the Alaska Fisheries Information Network (AKFiN), summed from November to February. We hypothesized that CDD would have a negative relationship with productivity. Mechanistically, high temperatures can alter the prey base and can be compounded by higher metabolic demands created by warm temperatures (Farley et al. 2024).

Finally, we included Chum and Pink hatchery release abundances, separately, from Alaska, Japan, Korea and Russia. We hypothesized a negative relationship between hatchery release abundances and adult marine productivity as increases in marine competition negatively impacts salmon stocks (Ruggerone et al. 2003, Cunningham et al. 2018, Scheuerell et al. 2020, Feddern et al. 2024). International hatchery release information is publicly available from the North Pacific Anadromous Fish Commission (Table S1). We use a lagged tolling average of hatchery releases so that they occur in the model at a timestep where releases would overlap with Fall chum salmon in the ocean. For example, Chum salmon hatchery releases in brood year 2000 could begin to interact 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. While migration distances and times certainly vary from these different release points, we include hatchery releases to represent a coarse marine competition index. 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.

## 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 dataset 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 with limited bias (Figure 3, Figure S3, Figure S4). Posterior predictive checks confirmed that models could simulate observations similar to those it was fit to (PB, juvenile = 0.5,PB, total return= 0.44,PB, harvest= 0.74, PB, spawners= 0.3). R-hat values were <1.05, indicating that chains have mixed well and provide consistent parameter estimates (Table S2). Further, visual inspection of trace plots indicate 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 many covariates in the juvenile stage did not have an effect that was different from zero, however we found a positive effect of mean spawner size on juvenile productivity (**estimate mean and CI,** Table S2, Figure 4). Further, we found a weak positive effect of fall snowpack on juvenile survival (**estimate mean and CI,** Table S2, Figure 4). Covariates applied to the second phase, from 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 that a negative relationship between Chum salmon hatchery release abundance 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.

#### 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 smaller spawner sizes, 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 relationship between spawner size and juvenile survival. However, there is limited information on out-migrating Chum salmon abundance prior to their first summer at sea that could be used to parameterize this component of the model and perhaps elucidate strong drivers of freshwater survival. During outmigration, salmon experience multiple capacity limited life stages. Further, limited outmigration abundance indices hamper our ability to parse out impacts of freshwater ecosystem change at such large scales. 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). We used length data collected by ADFG from Chum spawning populations on the Yukon River in a DFA to estimate a trend in spawner size at age that we used to inform juvenile survival estimates. We found that spawner size has decreased across all age classes, which aligns with observations from Yukon River communities (Figure S1). Further, we found that a trend toward smaller spawners has led to a 20% (+/- XX) decrease in egg to juvenile productivity since brood year 2002. 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). While identifying drivers in Fall Chum size at age is beyond the scope of this paper, this decreasing size trend has a negative relationship with stock productivity.

Compared to other chum populations, Yukon River fall chum have adapted for long migrations and colder 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 (Beacham et al. 1988). This allows fish to develop in time for spring emergence and ample food availability (2°C is likely the lower temperature limit) (Beacham et al. 1988). Suitable fall chum spawning habitat is characterized by upwelling through the gravel that allows for consistent temperatures (Burril et al. 2010). Based on this information, we hypothesized that low snowpack, especially in the early season where conditions are more variable, could have reduced insulating capacities leading to greater 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 2), suggesting that years with high snowpack confer a weak positive relationship with stock productivity. However, we were likely limited in detecting an effect as the snowpack metric was relatively course. We used snow depth in Circle AK as a regional indicator of snowpack, however, Fall Chum spawning habitat spans range of locations in the upper Yukon. Thus, while snow depth at circle may be representative of regional conditions, the local effects that would likely impact significant egg mortality are not accounted for here.

For many salmon stocks, juvenile abundance can reliably predict adult returns. This predictive relationship indicates that a population doesn’t experience unusually high or variable mortality rates at sea. However, this predictive relationship doesn't occur for juvenile chum salmon in the Bering Sea, where juvenile numbers don't effectively forecast adult returns (Farley et al. 2024). This suggests survival bottlenecks occur in the marine environment after the first summer at sea. Our findings support this hypothesis as well. We tested hypotheses for a number of processes that could impact marine survival and found a strong positive relationship between SFI and survival from juvenile to total return stage. We estimated a positive covariate coefficient for SFI during the marine survival stage. 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, juvebile 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). 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. Estimated relationships between SST and chum growth or productivity are variable in the literature. 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). 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 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 our work, it appears more complex ecosystem processes related to prey availability and fish condition are impacting marine productivity.

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. Additionally, Sockeye salmon that return to the Bristol Bay region have consistently had high abundance returns, which could represent an additional source of marine competition. However, sockeye diets have minimal overlap with Chum salmon for the duration of their marine residency. While there could certainly be cascading trophic impacts from these record high abundances, identifying these effects are beyond the scope of this paper.

Yukon River Fall chum salmon migrate and spawn over a wide spatial range in Interior Alaska and Canada. This means many covariates we included serve as large-scale regional indicators that appear to capture weak relationships but could be underestimating. Notably, the strongest covariate effect size comes from the SFI, which is a result of information collected directly from the fish rather than an ecosystem indicator. This further suggests that such large-scale indicators could be underestimating the relationships and highlights the difficulty in lifecycle modeling with a broad population that traverses remote areas. While we incorporated priors in our model that avoid spurious correlations, it is certainly possible that other mechanisms not evaluated in this study are also contributing to population declines. Covariates that aligned with the length of this timeseries, or data on Chum abundances at additional life stages, were limited and if present, typically existed more frequently for the marine lifecycle component.

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 survival, 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 region collected between 2000-2021. Data from 2000 to 2016 was collated by Oke et al, and more recent years were downloaded from the Alaska Department of Fish and Game Age Sex Length Database ((Alaska Department of Fish and Game 2024)) for all escapement projects with recent data (Table SXX). We filtered the data to include only escapement samples and marine ages ranging 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. 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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