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### Working Title: Understanding marine and freshwater 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 detrimental impact on food security and cultural tradition for Alaska Native peoples faced with 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. Specifically, we 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 associated with reduced survival across multiple life stages. While most freshwater covariates showed limited association with survival, we found that decreasing spawner body size is correlated with reduced productivity to the juvenile stage in addition to the direct impacts of age structure on the number of eggs deposited. Additionally, there was a weak positive relationship between Fall snow depth and egg to juvenile survival. We found evidence that hatchery released Chum salmon have a negative relationship with Yukon River chum salmon marine productivity. Finally, a positive relationship between juvenile stomach fullness and marine survival suggests 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 exhibit a compounding affect on population productivity. 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 environments changing at different rates over the course of their life history. Pacific salmon exemplify this vulnerability as they traverse freshwater, estuarine, and marine habitats, 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 both of 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 have historically provided 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 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 both river migration stages, 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 may be less heavily influenced by outmigration conditions compared to fish that spend 1-2 years in freshwater ecosystems. 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 (Burril et al. 2010, Farley et al. 2024).

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 stock-recruitment analyses. Further, this flexibility allows testing of multiple hypotheses around possible 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 from brood years 2002-2021, 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 or offspring provisioning, shifting egg incubation conditions, warming ocean temperatures altering prey availability and metabolic demands during critical 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 Bering Sea, run reconstruction data from adult chum salmon returning to the Yukon River to spawn, and environmental covariates spanning brood years 2002 – 2021. The model was fit within a Bayesian framework as described below.

The IPM tracked cohorts of fall chum salmon by brood year, *t*, life stage, *s* and age, *a*. The model includes five stages for Yukon river fall chum: 1) “eggs”, which tracks the amount of eggs produced by spawners, 2) “marine summer”, which tracks individuals from eggs to the end of their first summer in the marine environment, 3) “marine winter”, which tracks individuals from the end of their first summer past their first winter in the marine environment, 4) “total returns”, which tracks individuals after 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 maximum 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. The time reference for each covariate value is offset from the brood year by a stage-specific value , indicating the appropriate calendar year of reference for the interaction between the chum salmon cohort and the environmental or ecosystem process.

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 from the first winter at sea to maturity, t,s=m using the Beverton-Holt transition function described above (Eq. 4.2). 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 to maturity, 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 and mature, .

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

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

= 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 with 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, as:

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 to which the IPM was fit included juvenile abundance data from marine surface trawl surveys conducted by NOAA National Marine Fisheries Service in the Bering Sea, run reconstruction model outputs describing adult chum salmon returning to the Yukon River to spawn, and environmental covariates spanning brood years 2002 – 2022. The Yukon River fall chum salmon run reconstruction model was developed and is implemented by the Alaska Department of Fish and Game (ADF&G) and is informed by data collected through the extensive efforts of ADF&G monitoring and assessment programs. We fit the IPM to these datasets using Bayesian inference using the STAN platform and implemented the model using the rstan package in R (Carpenter et al. 2017, R Core Team 2021, Stan Development Team 2024). Four chains for 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 trace plots to ensure all chains converged to a stationary distribution (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

The marine juvenile abundance predicted by the IPM (Nt,s=j) was fit to a juvenile fall chum salmon index estimated from data collected by surface trawl surveys conducted in the Northern and Southeastern Bering Sea (NBS, SEBS). These data come from 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, and encounters juvenile chum salmon at the end of the first summer at sea 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 temporal (VAST) model (Thorson 2019) was fit to station-specific abundance per unit area swept and used to estimate the relative abundance of juvenile chum salmon Cunningham et al.

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 catchability 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 by a run reconstruction using a state-space modeling approach that 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. 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 proportions, 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 2021 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 regularizing priors applied to covariate coefficients, , where we applied a prior with a normal distribution, mean of 0 and standard deviation of 0.1. This regularizing prior was imposed to avoid spurious correlations among covariates and productivity estimates, by penalizing coefficient estimates toward zero (i.e. no effect) in the absence of strong information from the data.

#### 2.5 Ecosystem Covariates

Covariates included in the IPM represent specific hypotheses about processes suspected to be associated with variation in chum salmon survival a various life stages, and were developed based on 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 survival from the egg stage to the end of their first summer at sea, including the mean spawner size trend from the parent generation, and winter snowpack, Yukon River flow rates, cumulative degree days for sea surface temperatures in the NBS, and an index of Alaska pollock (*Gadus chalcogrammus*) recruitment. We included the mean trend in spawner size-at-age for spawners based on the hypothesis that larger fish produce more offspring and thus are likely to exhibit greater relative reproductive success (Ohlberger et al. 2020, Oke et al. 2020, Feddern et al. 2024). We compiled 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 (DFA) to estimate a common trend in size at age (Text S1.1). These age and length data are collected routinely by ADF&G monitoring and assessment projects, 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). Further, increased river flow can negatively impact juvenile survival in freshwater as it makes foraging more difficult (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 chum salmon population 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 temperature 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 survival (Myers et al. 2009, Kaga et al. 2013, Farley et al. 2024). Juvenile pollock 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 timeseries of estimated Eastern Bering Sea (EBS) walleye pollock recruitment estimated by the integrated stock assessment for this species (Ianelli et al. 2023). 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 timeseries of estimated pollock recruitment represents a robust prey index for juvenile Chum salmon.

##### 2.5.1 First winter at sea to maturity

We considered four covariates hypothesized to impact marine salmon survival, which included the period from the end of the first summer at sea until the individuals are vulnerable to terminal harvest when they mature and return to the Yukon River (Table 1, Figure 2). At the end of their first summer at sea, individuals leave the Bering Sea and 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 initial marine stage, : a stomach fullness index (SFI), temperature (CDD) experienced by chum salmon during their first winter in the ocean 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 reflect the result of foraging conditions experienced by chum salmon during the early marine portion of their life cycle just prior to their first winter at sea. We hypothesized that a higher SFI would be positively associated with overwinter survival and ultimately the return abundance of adult chum salmon. The SFI is estimated from stomach content data collected during the NBS survey. Stomach content data are collected from juvenile chum salmon at each in EBS/NBS survey 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 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 control 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 subadult 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 have been shown to exhibit negative associations with Pacific salmon productivity and survival, which are hypothesized to reflect 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 North Pacific scale hatchery competition with Yukon River chum salmon, we included Chum and Pink salmon hatchery release abundances, separately, as annual sums of releases 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 timing at which hatchery fish would overlap with Yukon River fall chum salmon in the ocean. For example, chum salmon hatchery releases in brood year 2000 may 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 2 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 index of plausible inter- and intraspecific marine competition.

## 3. Results

#### 3.1 Model Estimation

Brood year abundances for juvenile and returning fish fluctuated by 199% and 187%, respectively, during the timeseries where brood year 2016 had the lowest abundances in the time series across both life stages (Figure 3). Plots of observed and predicted abundance indices indicate that the model generally captured trends in both juvenile and spawning abundance indices (Figure 3, Figure S4) and returning age composition (Figure S3). 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).

#### 3.2 Estimated Covariate Effects

Covariate effects represent how ecosystem change is associated with Chum salmon survival at various life stages. 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 survival (0.17, 95% CI: (0.02, 0.24), 0.09, 95% CI: (-0.04, 0.15), respectively,Table S2, Figure 4). Covariates applied to the second stage, first winter at sea to maturity, appeared to have a stronger association with survival. We found a negative relationship between Chum salmon hatchery release abundance (mean: -0.12, 95% CI: (-0.30, 0.01)) and marine survival during the first winter at sea, and winter SST (mean: -0.13, 95% CI: (-0.31, 0.02)) and survival through this life stage **(**Table S2, Figure 4). We also found a positive effect of juvenile stomach fullness on marine survival, meaning that juveniles in better condition are more likely to survive their first winter at sea (0.16, 95% CI: (0.03, 0.35), Table S2, Figure 4).

#### 3.3 Sensitivity Analysis

To quantify the sensitivity of model estimates to each covariate included, we iteratively refit the model with one covariate removed at a time, and evaluated the resulting changes in the remaining coefficients describing covariate effects on maximum stage-specific survival rates (Figure S4). We expressed the changes as relative differences, dividing the change in each retained coefficient by the uncertainty (posterior standard deviation) in that coefficient’s estimate when the full model containing all covariates was originally fit to the data. As such, the standardized covariate sensitivity values can be interpreted as the change in effect sizes, relative to their uncertainty, in number of standard deviations higher or lower than the estimate from the full model containing all covariates (Figure S4). Most estimates did not change by greater than one standard deviation when other covariates were removed. However, estimates for the effect of Pink hatchery fish abundance decreased by -1.3 and -1 standard deviation units, respectively, when temperature and fullness covariates were removed, indicating moderate sensitivity to this covariate. 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 are associated with changing ecosystem conditions at multiple stages within the species’ anadromous life cycle. Our analyses suggest that reduced survival through important life stages can be explained by decreased spawner sizes, decreased regional winter snowpack, increased marine competition, and poor juvenile feeding conditions resulting in low stomach fullness. These findings contribute to a growing body of evidence suggesting that Pacific salmon populations are increasingly vulnerable to ecosystem change across the freshwater and marine ecosystems they inhabit during their anadromous life cycle.

We explored a range of hypotheses about processes associated with Yukon river fall chum salmon survival throughout their lifecycle and found the strongest support for covariates describing conditions experienced by subadult chum salmon after the first summer at sea, before maturation and to return to freshwaters where they are vulnerable to terminal harvest. Covariates linked to survival from egg to juvenile stages generally lacked strong model support, except for the positive survival effects of spawner size and winter snowpack. A lack of direct estimates for Chum salmon abundance during smolt outmigration makes it challenging to disentangle key drivers of freshwater survival from those impacting early marine summertime survival, particularly as survival bottlenecks during the critical period after ocean entry may mask upstream effects. While outmigration monitoring projects have been developed, the time series for which paired genetic composition data can be used to separate Yukon summer and fall run Chum salmon is insufficient to capture the range of brood years explored in this study (Miller & Weiss 2023). Future research would benefit from including smolt outmigration abundance data alongside surface trawl survey data indexing Chum salmon at the end of their first summer at sea and information on adult return abundance and harvest. However, overall 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 found that spawner size has decreased across all age classes (Figure S1). Further, we found that a trend toward smaller average body size for spawning adults has resulted in a 17% (+/- -2% to 36%) decrease in egg to juvenile survival. We included size as a covariate, rather than as a size-specific fecundity estimator, as the body size of spawning female salmon may influence both realized fecundity and the provisioning of offspring on a per-egg basis. 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). Conserved spawn timing in conjunction with the accumulated degree days allow salmonids to develop in time for spring emergence and overlap with the onset of primary and secondary production in freshwater ecosystems, thus ensuring sufficient food resources are available (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 9% increase in productivity (95% CI: -0.04, 0.15). 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 often fails to effectively forecast adult returns (Farley et al. 2024). This disconnect suggests that significant survival bottlenecks occur in the marine environment after the early marine stage (i.e. the first summer at sea). Our results support this hypothesis, as we identified a positive relationship between the SFI and subadult marine survival, while winter Aleutian temperature and chum hatchery release abundances had negative relationships with survival after juvenile surveys indexing Yukon River chum salmon during their first fall in the ocean. This suggests that in years with lower average SFI (i.e. lower stomach fullness), are associated with a reduction in marine survival of 16% (95% CI: 0.03, 0.35) (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 periods of warmer marine 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 the marine foraging experience and individual chum condition prior to the first winter at sea due to its long time series, a more direct proxy for condition such as chum energy density, may better capture the relationship between ecosystem conditions and fish condition.

Regional SST is often correlated with Pacific salmon productivity and survival across their range; however, the strength and direction of the relationship depend on species, region and life stage (Pyper et al. 2002, Mueter et al. 2005, Litzow et al. 2018). Further, as warming increases to unprecedented levels and interpretation of climate indices shift, SST-salmon productivity relationships can exhibit nonstationarity (Litzow et al. 2018, 2019, 2020). While 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. In this work, we included SST as an indicator of direct (metabolic) and indirect (changes to prey base) processes. While we hypothesized a positive relationship between NBS CDD and juvenile productivity, we did not find evidence to support this hypothesis (Figure 4) (Mueter et al. 2005, Iino et al. 2022, Farley et al. 2024). However, there was a negative relationship between Aleutian CDD and marine productivity, where increases in marine temperature relate are correlated with a 13% decrease in chum productivity (95% CI: -0.31, -0.02) (Figure 4). Mechanistically, increases to marine temperatures could impact prey quality and alter the distribution of the prey base while simultaneously increasing metabolic demands of immature salmon (Farley et al. 2024).Warming temperatures in the Bering Sea, and North Pacific more broadly, are associated with reduced prey availability and reduced nutritional content for salmonids (Mackas et al. 2007, Garzke et al. 2023, Farley et al. 2024).

Increased competition in the marine environment has been associated with changes in survival and productivity for many Pacific Salmon stocks, including Yukon River Chinook salmon, Norton Sound chum salmon, and Bristol Bay sockeye salmon (Ruggerone et al. 2012, Cunningham et al. 2018, Ohlberger et al. 2023, Feddern et al. 2024). Growth of Kuskokwim River chum salmon has previously been shown to negatively correlate with Japanese hatchery chum salmon [harvest? Return abundance? Releases?] (Frost et al. 2021). We found weak support for the hypothesis that increases in aggregate North Pacific scale Chum salmon hatchery releases are associated with a 12% (-95% CI: 0.30, 0.01) 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 for Alaskan salmon have been highlighted recently in the literature, and linked to decreased salmon body sizes and decreases in population productivity (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. Increasing evidence supporting negative impacts of crowded seas resulting from increased hatchery releases on wild salmon populations has led to calls for more coordinated international hatchery management (Connors et al. 2025).

The broad spatial distribution of Yukon River fall chum salmon across Interior Alaska and Canada presents challenges for detecting relationships with biotic or abiotic environmental processes. Most covariates in our analysis serve as regional indicators that may obscure 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 the covariate data matching our time series, particularly for freshwater life stages, with most available data focused on the marine phase of the life cycle.

Overall, our 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 appear to contribute to changes in marine survival, including changing ocean conditions that impact stomach fullness and increased competition from hatchery-origin chum salmon. Together with the estimated negative association between marine survival and overwinter temperatures suggest that a bioenergetic interaction between foraging conditions and temperature may play an important role in regulating the survival of Yukon River fall Chum salmon cohorts. Further, declining body sizes across age classes appear to influence realized offspring production on a per-spawner basis. 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 production or reduced offspring survival. 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.

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#### 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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