### Working Title: Understanding marine and freshwater processes affecting the survival 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 experiencing unprecedented declines in abundance. Yukon River fall Chum salmon are at the northern end of the species’ range, and these runs (*Oncorhynchus keta*) recently collapsed to 10% of their long-term average abundance. This collapse resulted in closure of subsistence fisheries and detrimental impacts on food security and cultural tradition for Alaska Native peoples already facing longer-term declines in Chinook salmon resource. While recent work has linked this decline to climate-driven impacts at specific life stages, there remains a need for stage-structured life cycle modeling approaches that can quantitatively assess how stage-specific mortality and survival interact to shape emergent population-level outcomes.

Here, we use an integrated population model to evaluate the influence of environmental covariates on Yukon River fall chum salmon survival during two distinct periods: survival from egg to the first marine summer and from the first marine summer to adulthood. Using data collected during multiple life stages and environmental covariates hypothesized to influence those life stages, we found that recent declines in abundance are associated with reduced survival across both periods. We found a weak but positive relationship between winter snow depth and egg to juvenile survival. We found a strong negative relationship between survival from first marine summer to terminal harvest and Chum salmon North Pacific-wide hatchery releases. Additionally, we found evidence for a positive relationship between juvenile stomach fullness and later marine survival suggests that fish condition before their first winter at sea is an important predictor of survival. These findings highlight how multiple stressors - from changing freshwater and marine conditions to increased competition – can compound to reduce salmon survival and eventually on 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 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 change across multiple ecosystems. As anadromous species, salmon integrate and reflect the cumulative effects of freshwater and marine warming, such as altered precipitation and river flow patterns and changing ocean conditions, across vast geographic scales. In many cases, this complicates efforts to estimate or anticipate ecosystem change impacts 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 watershed in particular, is experiencing a multi-species salmon collapse. While all 5 species of Pacific salmon spawn in the Yukon River, Chinook and Chum salmon are the primary species targeted for subsistence harvest along the Yukon River and the approximately 50 Alaska Native communities along its length. There have been commercial and subsistence fishery closures on the Yukon River for Chinook salmon since 2007 and since 2019 for Chum salmon (Krueger et al. 2009, Brown & Godduhn 2015, 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. The loss of both Chinook and Chum salmon harvests is particularly devastating for the over 50 rural communities that rely on them, as Chum have historically served as a critical food source when Chinook returns were low, making this collapse a profound threat to both food security and traditional ways of life (Alliance for a Just Society & Council of Athabascan Tribal Governments 2013).

Yukon River 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). Yukon River Chum salmon are comprised of two genetically distinct runs, an early summer run that primarily spawns in the lower river and a fall run that enters the river later and migrates farther upstream (hereafter, fall Chum salmon). Fall Chum salmon are genetically distinct from summer Chum salmon, which enter the river earlier and typically spawn 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). Fall chum salmon primarily spawn in the fall in the upper regions of the Yukon River. Fry out-migrate rapidly after emergence and typically reach the Bering Sea and smolt by July, the juveniles spend their early marine residence in the shallow waters of the northern Bering Sea and immature fish migrate seasonally between the GOA and Bering Sea. Fall Chum salmon 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. The various habitats utilized by Fall Chum salmon necessitates the application of multistage lifecycle models to better understand the drivers of variation in survival across these unique life history periods. Understanding stage-specific survival is particularly crucial given the recent dramatic declines in run abundance and can help identify critical periods where environmental change have the strongest impacts on population dynamics.

Mechanistic understanding of the processes regulating Yukon River Chum salmon population dynamics, inferred from past population crashes, remains limited. Multiple stressors operate across this species' complex life cycle, making it challenging to disentangle their relative impacts on survival. Declines in other salmonid species on the same river, such as Chinook salmon, have been linked to reductions in the body size of spawning individuals, increased daily river temperatures for both the upriver spawning adults and juvenile out migration stages, and interspecific competition in the marine environment (Cunningham et al. 2018, Howard & von Biela 2023, Murdoch et al. 2024, Feddern et al. 2024). However, unlike Chinook salmon, Chum salmon begin their outmigration to the Bering Sea immediately after hatching, often reaching the estuarine environment within six months. Thus, the mechanisms driving changes in abundance may be less heavily influenced by freshwater habitat conditions compared to Chinook salmon that spend 1-2 years in freshwater ecosystems prior to outmigration. Previous studies have focused on understanding Chum salmon population dynamics in either freshwater or marine ecosystems, and separately; 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, , which can provide a more comprehensive understanding of population dynamics compared with single-stage stock-recruitment analyses. Further, this flexibility allows testing of multiple hypotheses around possible ecosystem drivers while accounting for observation error in different data sources and process variation in demographics. 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 salmon populations, and the influence of ocean conditions on population productivity (Cunningham et al. 2018, Scheuerell et al. 2020). IPMs are well-suited for investigating the mechanisms behind recent Yukon River 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 and anthropogenic impacts influence survival across different life stages of Yukon River fall Chum salmon. By incorporating multiple data sources spanning brood years 2002-2021, including juvenile abundance surveys, adult returns, and age composition data, we quantify associations between ecosystem covariates and survival at two stages: from egg to the first marine summer and from the first marine summer to terminal harvest. We tested seven covariates across these stages to evaluate hypotheses about the effect of key environmental and anthropogenic drivers on stage-specific survival. Specifically, we hypothesized that recent population declines are driven by multiple 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 statistical 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 developed here incorporates multiple data sources to estimate the relationships between ecosystem covariates and fall Chum salmon survival. Data used to fit the IPM include juvenile abundance data from marine surveys in the Bering Sea, run reconstruction data from adult fall Chum salmon returning to the Yukon River to spawn, and environmental covariates spanning brood years 2002 – 2021 (Table 1, Table S1). The model was fit within a Bayesian framework as described below.

The IPM tracked fall Chum salmon cohorts 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 number of eggs produced by spawners, 2) “marine juvenile”, which tracks individuals from eggs to the end of their first summer in the marine environment, 3) “marine immature”, which tracks individuals from the end of their first summer through to maturity, 4) “total returns”, which tracks the amount of fish in each calendar year that return to the Yukon River mouth and are vulnerable to terminal harvest, and 5) “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 fall 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 marine 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 of the environment can support at each life stage. The productivity parameter was estimated conditional on stage-specific 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, describing 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 fall Chum salmon cohort and the environmental or ecosystem process (Table 1).

Upon surviving their first summer at sea, fall Chum salmon migrate to the Eastern Aleutian Islands (spring and summer habitat) and Western Gulf of Alaska (GOA) (winter habitat), 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 after the first summer at sea to maturity, including the first winter, 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 hypothesized to be important to the marine life stage 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 is tracked by calendar year and indexed by , where , where the addition of 1 includes the year where fish are eggs in the gravel. 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 annual 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 cumulative marine mortality than younger fish but that overall ocean mortality after the first winter at sea was low (Beamish 2018). We tested this assumption and discuss this further in the results.

The maturity schedule for fall 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, . Fishery selectivity is implicitly assumed to be uniform across ages.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, we estimated the mean fishing mortality in log space, and annual process deviations around the mean, .

Eq. 4.8

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

Eq. 4.9

The number of eggs produced by each spawner, *,* was assumed to follow a Ricker function which includes parameters for the log of the maximum recruitment per spawner at low spawner abundances, , and the capacity, (Ricker 1954, Hilborn 1985). Age-specific Ricker parameters were estimated to account for the difference in realized fecundity for female fall Chum salmon of different ages. Due to difficulties in estimating the density dependence parameter,we fixed at 0.001 for all ages, representing a low level of density dependence. The proportion of female offspring, , 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

The IPM was fit to juvenile abundance data from marine surface trawl surveys conducted by the NOAA National Marine Fisheries Service and the Alaska Department of Fish and Game (ADF&G) in the Bering Sea, run reconstruction model outputs that estimate the number of adult fall Chum salmon returning to the Yukon River to spawn, and environmental covariates spanning brood years 2002 – 2021. We fit the IPM to these datasets using Bayesian methods through 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). Models were fit to data for each life stage, with four chains run for 30,000 iterations with an additional 16% burn-in period, resulting in 100,800 saved 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 (Figure S2). Further, no divergent transitions occurred. We used the *priorsense* package in R to evaluate how sensitive the posterior distribution was to prior and likelihood perturbations (Kallioinen et al. 2023). Finally, we conducted multiple sensitivity tests to understand assumptions about natural mortality and covariate inclusion (Figure S5 and S6).

#### 2.3 Population Data

The marine juvenile abundance predicted by the IPM (Nt,s=j) was fit to a juvenile fall Chum salmon abundance index estimated from data collected by surface trawl surveys conducted annually in the Northern Bering Sea and biennially in the Southeastern Bering Sea (NBS, SEBS) (Figure 1). The surveys use surface trawl gear to sample juvenile salmon at stations across both Bering Sea regions (Figure 1; Murphy et al. 2025) The surveys are conducted between August and September, and encounter 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. Juvenile chum salmon caught in the surveys are allocated to five genetic reporting groups, including Yukon River fall Chum, using a spatial mixed stock analysis (MSA) (Murphy et al. 2021). To account for spatial and temporal variability in survey coverage, a vector autoregressive spatial temporal (VAST) model (Thorson 2019) was fit to station-specific catch per unit effort (#/km2) and used to estimate the relative abundance of juvenile Yukon River fall Chum salmon (Cunningham et al., personal communication 2025). To translate the juvenile abundances estimated by the IPM to the scale of the observed juvenile abundance, we estimated a catchability constant *q* for the juvenile surveys. We fit the IPM to the juvenile abundance index, *Jt,* ranging from brood years 2002 to 2021. To incorporate known error in juvenile abundance estimates from the Bering Sea surveys within the model fitting process, we fixed the estimate of uncertainty in the abundance index, , at the average (across years) standard deviation for the index.

Eq. 4.11

Total return, harvest and spawner abundances 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. In the marine environment, Yukon River fall Chum salmon are caught as bycatch in the Bering Sea pollock fishery. However, the impact is estimated to be less than 2% from 2011-2022, except 2021 where it was estimated higher at 5% (National Marine Fisheries Service, Alaska Region 2024). Due to a shorter timeseries and low impact rate, we have not included these bycatch removal estimates in the model. Age composition information was collected from lower river fisheries and test fisheries (Fleischman & Borba 2009). We used the estimated total return abundance by calendar year and age (Ny,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 using a multinomial likelihood.

Eq. 4.12

We fit the IPM to the return, harvest, and spawner estimates ranging from brood years 2002 to 2021. Here, we incorporated error from the run reconstruction into the total observation error. We fixed sigma in each likelihood using the average of annual standard deviations estimated by the fall Chum salmon run reconstruction (Table 2) (Fleischman & Borba 2009). For all likelihoods, sigma acts as a weighting factor 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

We employed uninformative or weakly informative priors for most model parameters (Table 2). The key exception was for covariate coefficients, , where we applied regularizing priors with a normal distribution, Normal(0,0.1). This regularization approach was implemented to prevent spurious correlations between environmental covariates and productivity estimates by shrinking coefficient estimates toward zero (i.e., no effect) unless the data provided strong evidence for a relationship (McElreath 2020). This technique helps control model complexity and reduces the risk of overfitting while still allowing meaningful covariate effects to emerge when supported by the data.

#### 2.5 Ecosystem Covariates

Covariates included in the IPM represent specific hypotheses about processes associated with variation in Chum salmon survival at various life stages and were developed based on peer reviewed literature (Table 1, Figure 2). All covariates were normalized to a mean of zero and standard deviation of 1, i.e. Z-scored.

##### 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, winter snowpack, cumulative degree days for sea surface temperatures (SSTs) 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 where fall chum salmon spawn (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 (Table 1). As with many covariates in this analysis, this snowpack covariate serves as a regional indicator due to the large spatial area covered in the Yukon watershed. The Circle, AK dataset was chosen because of the longer timeseries available and the proximity to upriver spawning habitat. For salmon smolt leaving the river, increased river flow can negatively impact survival in freshwater as it makes foraging more difficult (Neuswanger et al. 2015). A majority of fall 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). However, river flow data is highly colinear with the snowpack data and was not included in the final analysis.

Empirical studies in the Bering Sea and bioenergetics modeling in Japan have suggested a positive relationship between water temperature and survival during the first summer at sea (Iino et al. 2022, Farley et al. 2024). The hypothesized positive relationship is based on the idea that increases as warmer temperatures enhance juvenile salmon growth rates as they enter the marine environment which can reduce size-selective mortality and lead to greater survival (Beamish & Mahnken 2001, Farley et al. 2024). To address this, we included NBS cumulative degree days (CDD) to represent the Bering Sea surveys thermal conditions for juvenile Chum salmon during their first summer at sea. To calculate CDD we used the daily mean NBS sea surface temperature, publicly available on the Alaska Fisheries Information Network (AKFIN). Temperatures provided by AKFIN are based on satellite data curated by NOAA's Coral Reef Watch Program (https://coralreefwatch.noaa.gov/). We summed daily temperature from June to August for each year to align with when juvenile salmonids would experience the temperature conditions (brood year +1) to yield the cumulative degree day (CDD) covariate.

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). Age-0 pollock represent a high-quality prey source for juvenile Chum salmon in the Bering Sea (Farley & Moss 2009, Moss et al. 2009, Kaga et al. 2013), thus we included the time series of estimated Eastern Bering Sea (EBS) walleye pollock recruitment estimated by the integrated stock assessment for this species (Ianelli et al. 2023). The stock assessment estimates a recruitment index for age-1 pollock, we lagged this index by a 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 time series of estimated pollock recruitment represents a robust prey index for juvenile Chum salmon.

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

We considered three covariates hypothesized to impact marine survival, including the period from the end of the first summer at sea until 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, , including a stomach fullness index (SFI) estimated during juvenile salmon surveys, temperature (CDD) experienced by fall Chum salmon during their first winter in the ocean as indexed by a representative location including the Eastern Aleutian Islands, and annual total Chum salmon hatchery releases from Alaska, Japan, Korea and Russia. We included SFI to reflect foraging conditions experienced by juvenile 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 two Bering Sea juvenile salmon surveys. Stomach content data are collected from juvenile Chum salmon at each SEBS/NBS survey station and recorded on a per station basis after a subsequent analysis. 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 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 annual differences from the average and generate an index across time. 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 the winter Eastern Aleutian CDD to represent the temperature conditions that immature Yukon River Chum salmon experienced during their first winter at sea. To calculate CDD we used the daily mean Eastern Aleutian SST, publicly available on AKFIN, summed from November to February to represent winter conditions.

Large numbers of hatchery salmon released in the North Pacific have been shown to exhibit negative associations with Pacific salmon growth and survival, which are hypothesized to reflect increased competition for prey resources (Cunningham et al. 2018, Scheuerell et al. 2020, Ruggerone et al. 2023, 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 (Krueger et al. 2009). 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 (Connors et al. 2025). To address the impact of competition on Yukon River fall Chum salmon, we included an annual Chum salmon hatchery release abundance, calculated as the sum 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 to represent the timing at which hatchery fish would overlap with Yukon River fall Chum salmon in the ocean. For example, Yukon River fall Chum salmon from brood year 2000, would first encounter marine competition from hatchery fish in their first winter at sea, which would be winter 2001/2002. Due to the overlapping age structure of both wild and hatchery populations, Yukon River fall Chum from brood year 2000 may continue to interact with hatchery fish from subsequent release years (2001, 2002) as different age classes occupy the same marine habitat. To capture this multi-year interaction period, we include a three-year rolling average of hatchery releases starting from the same brood year (t) through brood year t+2. This approach accounts for scenarios such as age-0.2 hatchery fish interacting with age-0.3 Yukon Chum, and age-0.3 hatchery fish interacting with age-0.4 Yukon Chum, etc. While migration distances and timing certainly vary among different release points, we include hatchery releases to represent a coarse index of possible marine competition during the primary ocean rearing period.

#### 2.6 Sensitivity Testing

We conducted two sets of sensitivity testing, one to understand the sensitivity of each covariate included in the model and a second to evaluate the assumption of annual natural mortality. To quantify the sensitivity of model estimates to each covariate, 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 S5). 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 S5).

## 3. Results

#### 3.1 Model Estimation

Brood year abundances for juvenile and returning fish fluctuated by 199% and 187% relative to the mean, respectively, throughout the timeseries (Figure 3). Brood year 2016 had the lowest abundances in the time series for both life stages. 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.

#### 3.2 Population Dynamics

The stage structure of the IPM used to explore the population dynamics of Yukon River fall Chum salmon provided valuable insights into several key aspects of population dynamics and demographic rates. With survival amongst sequential life stages structured as Beverton-Holt transition functions, both maximum survival rates (i.e. basal productivities) and carrying capacities were estimated for both the juvenile and marine life stages. The estimated values for the juvenile basal productivity parameters () was -1.07 with a 95% credible interval of -1.94 to -0.19, which equates to a maximum survival rate of 25.5% (12.5-45.3%) from egg to the fall after ocean entry (Table 2). Conversely, the maximum annual survival rate for Chum salmon in the marine environment was estimated at 12.6% (0.04 - 25.3%). Stage-specific carrying capacities were estimated at very high values (e.g., and ), implying that there is limited evidence for density-dependent capacity limitations in either life stage. Finally, the age-specific Ricker density-independent parameters () increased with Chum salmon age (age-3: 3.07, age-4: 5.92, age-5: 6.57, and age-6: 8.07; Table 2), following expectations for increased female fecundity at age.

#### 3.3 Estimated Covariate Effects

Covariate effects represent how each environmental covariate is associated with fall Chum salmon survival at various life stages. The covariate effect sizes presented here are the estimated percent change in survival resulting from 1 standard deviation increase in the covariate, conditional on the basal productivity (i.e. maximum survival) rate, maximum carrying capacity for a given life stage and the estimated covariate coefficient (Table 2). We interpreted the credible intervals and estimates as follows: 95% credible intervals that do not overlap zero indicate strong support, and 50% credible intervals that do not overlap zero indicate moderate support. We found a strong positive relationship between winter snowpack and juvenile survival, suggesting that a 12-inch (1 SD) increase in mean winter snowpack depth is associated with a 19.40% increase in survival (19.40% 95% CI: (6.90, 35.40),Table 2, Figure 4). In the marine stage, we found a strong negative relationship between marine survival and Chum salmon hatchery release abundance, suggesting that for every increase in North Pacific Chum salmon hatchery releases of 158,735 fish (1 SD), Yukon River Chum survival declines by 15.20% (95% CI: -23.09, -6.78). We also found a strong negative relationship between marine survival and winter CDD in the Aleutians Islands (-24.75, 95% CI: (-32.85, -17.78)) (Table S2, Figure 4), indicating that for an increase of 91.7°C cumulative degree days over the course of the winter, survival declines by ~25%. Finally, we found a strong positive effect of juvenile stomach fullness on marine survival, meaning that an increase in 1 SD of the SFI (141.6, units are (prey weight\*10,000)/Predator biomass, see Murphy et al 2021 for further detail) relates to a 34.06% increase in marine survival (34.06%, 95% CI: (22.75, 46.59), Table 2, Figure 4).

#### 3.4 Sensitivity Analysis

Covariate coefficient estimates did not change by greater than one standard deviation when other covariates were removed in either life stage. These sensitivity results indicate that estimated covariate effects on survival were quite insensitive to the absence of other hypothesized processes and suggests limited potential for strong unmodeled covariate interactions. To quantify the sensitivity of the model to the annual mortality assumption of M = 0.06 (Beamish et al. 2018), we also ran the model using M=0.1 and M = 0.2. We found that population estimates and parameters were not highly sensitive to changes in annual mortality rate (Figure S6).

### 4.0 Discussion

Application of an integrated population model revealed that variation in Yukon River fall Chum salmon abundances, including recent declines, can be explained in part by changing ecosystem conditions at multiple stages within the species’ anadromous life cycle. Our analyses suggest that reduced survival across the life cycle is correlated with 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 (Cunningham et al. 2018, Feddern et al. 2024, Ohlberger et al. 2025).

By examining factors hypothesized to affect Yukon River fall Chum salmon survival throughout their lifecycle, we found the strongest support for covariates describing conditions experienced by subadult Chum salmon after the first summer at sea but before they become vulnerable to terminal harvest. Covariates linked to survival from egg to juvenile stages generally lacked strong model support, except for the positive relationship with winter snowpack depth. 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 survival, particularly as survival bottlenecks during the critical period after ocean entry may mask upstream covariate effects earlier in the life history. 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 does not capture the range of brood years explored in this study (Miller & Weiss 2023). Future research would benefit from including smolt outmigration abundance data to better discern how ecosystem processes relate to juvenile survival in freshwater and outmigration phases. Chum salmon’s abbreviated freshwater residency relative to other species likely reduces their exposure to freshwater environmental pressures.

Yukon River fall Chum salmon are adapted for a long migration 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 salmon spawning habitat is characterized by upwelling through the gravel that allows for consistent temperatures (Beacham et al. 1988, Burril et al. 2010). 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). We found weak support for a positive relationship between winter snowpack and egg to juvenile survival (Figure 4, Table 1), suggesting that a 12-inch increase in the snowpack depth at Circle, Alaska between January and March confers a 19.40% increase in egg to subadult survival. 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 the entire range of fall Chum salmon spawning habitats throughout the upper Yukon River that could cause significant egg mortality. Thus, while snow depth at Circle may represent regional conditions, local effects could increase variability in this relationship.

As with other Pacific salmonid populations, Yukon River fall Chum salmon body sizes have decreased through time across all age classes (Figure S1) (Oke et al. 2020, Ohlberger et al. 2023, Freshwater et al. 2023). This decline in size represents a concerning trend that may affect reproductive potential, migration success, and population resilience to environmental stressors. However, when we accounted for age-specific differences in eggs per spawner in the model through the estimation of age-specific Ricker parameters, the coefficient for spawner size is not different from zero. While the general increase in the expected egg output per spawner with increasing age aligns with life history theory and available fecundity data, these results suggest that there is a limited additional impact of body size overall. This suggests possible compensatory mechanisms in reproductive allocation, where females may be maintaining egg numbers despite reduced body size, potentially at the cost of egg size or energy content—a trade-off that merits further investigation. Alternatively, fecundity may vary spatially across the watershed, with fish spawning farther upriver being less fecund due to the energetic cost of longer migrations (Bromaghin et al. 2011). These spatial differences are not captured by the watershed-wide grouping of Fall Chum.

A reliable predictive relationship between juvenile abundance and adult returns often indicates relatively consistent marine survival rates in salmon populations (Murphy et al. 2025). However, this relationship does not exist for juvenile Chum salmon in the Bering Sea as: juvenile abundance fails to effectively forecast adult returns (Farley et al. 2024). This disconnect suggests that there is significant variation in survival in the marine environment after 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 salmon hatchery release abundances had negative relationships with survival in the same period. This suggests that in years with better than average foraging conditions as indexed by SFI (i.e. greater stomach fullness), are associated with an increase in marine survival of 36.22% (Figure 4, Table 2). The magnitude of this effect underscores the importance of early marine feeding conditions in determining cohort success. This supports the hypothesis that juvenile Chum salmon in poor condition at the end of their first summer experience reduced survival in subsequent migration stages (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). We used SFI as a proxy for the marine foraging experience due to the length of the time series that captured brood years used in this study. However, a more direct proxy for condition such as Chum salmon energy density may better capture the relationship between ecosystem conditions and fish condition. Further, it is important to note that the SFI used here is an index for all juvenile Chum, not just specifically Yukon River fall Chum, however current use of individual genetic assignment will allow for a more specific SFI as well.

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). In this work, we included SST as an indicator of direct (metabolic) and indirect (changes to prey base) processes in both the juvenile and marine stages. During the juvenile stage, we hypothesized a positive relationship between NBS CDD and juvenile survival, however we did not find evidence to support this hypothesis (Figure 4) (Mueter et al. 2005, Iino et al. 2022, Farley et al. 2024). Observed correlations between SST and Chum salmon marine survival likely represent latent effects of other ecosystem processes that drive the observed SST and survival relationships. SST is often used as a covariate because of the accessibility of these datasets. We did find a negative relationship between Aleutian CDD and marine survival, where increases in marine temperature (e.g. an increase of 91.7°C degree days) are correlated with a 24.61% decrease in Chum salmon survival (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 prey 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 was negatively correlated with Japanese hatchery Chum salmon 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 15.20% decrease in Yukon River fall Chum salmon survival. Negative impacts of increased competition at sea for Alaskan salmon have been highlighted recently in the literature, and linked to decreased salmon body sizes (Oke et al. 2020) and decreases in population productivity (Feddern et al. 2024). A negative relationship between hatchery Chum and Yukon River chum could result from intraspecific competition between the groups (Connors et al. 2025). 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). Such coordination would require cooperation across jurisdictional boundaries but could represent a critical step toward coordinated adaptive management in an era of climate change and increasing resource competition.

While we did find strong relationships with covariates, there are limitations in our analytical approach that constrain our inference into Yukon River fall Chum salmon population dynamics. 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. This scale mismatch represents a persistent challenge in large river salmon ecology, where management units often encompass multiple spawning populations experiencing heterogeneous environmental conditions (Hutchinson 2008). 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 life cycle modeling with a broad population that traverses remote areas. While our model's regularized 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 stage-specific survival 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, our results 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. 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 length 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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