# 3. Materials and Methods

## 3.1 Study Area

The Yukon-Kuskokwim (YK) region covers 980,000 km2 of the US and Canada, draining west to the Bering Sea (Figure 1). The Yukon River is the fourth largest river in North America with a length of 3,185 km and a basin area of 855,000 km2. The Yukon River extends from Canada’s British Columbia and Yukon Territory through Alaska where it drains into the northeastern Bering Sea with a discharge of 700 m3s-1 (Czaya 1983). The Kuskokwim River is the ninth largest in the United States and has a length of 1,130 km, a basin area of 124,319 km2, and a discharge of 1,897 m3s-1 draining into Kuskokwim Bay in the southeastern Bering Sea (Benke and Cushing 2000). Within the Canadian portion of the watershed, the Yukon River and its tributaries flow through both remote and populated environments characterized by extensive areas of pristine habitat intermixed with a patchwork of historic mining and hydroelectric activity. The region as a whole is sparsely populated with two dense population centers (Fairbanks North Star Borough Alaska, population ~95,000; Whitehorse Yukon Territory, population ~180,000) in the Yukon Basin. In the Kuskokwim basin, Chinook spawn across at least two-dozen tributaries of the main-stem Kuskokwim River. Monitoring of harvest, escapement, and age composition for Chinook has occurred since the mid-1970s with a focus on 13 sub-basins monitored by weir or aerial surveys. In the Yukon basin, Chinook salmon spawn across over 180 spawning areas, mostly located in tributaries (Brown et al. 2017), and are primarily monitored as they migrate upriver through the mainstem and in select tributaries in Alaska and Canada (Feddern et al. 2023).

## 3.2 Environmental and Biological Indicators

To identify potential drivers of Chinook salmon productivity across the Yukon-Kuskokwim region we quantified associations with a variety of freshwater conditions, ocean conditions, and biological dynamics. Each explanatory variable was hypothesized to impact salmon abundance, growth, size, or survival at different stages in their life history (Table 1). Variables were included based on previous studies and expert observations of salmon dynamics in the Yukon-Kuskokwim region elicited during a participatory workshop (Feddern et al. 2023).

### 3.2.1 Incubation and Juvenile Rearing

Freshwater covariates were developed to represent hydrologic and thermal conditions specific to habitats used by different life stages and populations of Chinook salmon in the Yukon-Kuskokwim region. We hypothesized that hydrologic indicators of streamflow, temperature and river ice breakup timing could impact Chinook salmon productivity during egg incubation, juvenile rearing, and adult migration (Table 1).

High streamflow during the fall spawning and incubation period can reduce egg survival through streambed scour or sedimentation (Montgomery et al. 1996; Goode et al. 2013). Streamflow data were available for 14 of the tributaries where Yukon-Kuskokwim Chinook Salmon populations spawn and rear, but not for all years with productivity information, so we used modeled streamflow to estimate hydrologic conditions experienced by different life stages. We extracted modeled discharge from the Global Flood Awareness System [(GloFAS, Harrigan et al. 2020)](https://www.zotero.org/google-docs/?9jW52I) for the grid cell that most closely matched each tributary outlet. An annual covariate for each tributary was calculated as the maximum daily streamflow in the fall of the brood year (August through November).

Higher streamflow conditions during summer juvenile rearing may reduce foraging efficiency and overall growth (Neuswanger et al. 2015). Using extracted model discharge from GloFAS an annual covariate was calculated as the median daily streamflow in the summer of juvenile rearing (May through September) one year after the brood year.

Warm stream temperatures can increase juvenile growth in streams where temperatures are normally below thermal optima (Falke et al. 2019). Stream temperature data were available for three sites on the mainstem Yukon River, one site on the mainstem Kuskokwim River, and 27 tributaries used by YK Chinook salmon, but not for all years with productivity information (see below). Stream temperature data were received from the Alaska Department of Fish and Game, the U.S. Fish and Wildlife Service, and Al von Finster (retired biologist with the Department of Fisheries and Oceans Canada) and combined with U.S. Geological Survey data that were directly downloaded using the DataRetrieval package in R [(De Cicco et al. 2022, R Core Team 2022)](https://www.zotero.org/google-docs/?7yfGcT). We used the empirical stream temperature data to develop site-specific models of daily stream temperatures that could be used to fill temporal data gaps (Appendix S4). The final stream temperature time series for each tributary habitat were used to estimate thermal conditions affecting juvenile salmon growth. We calculated an annual covariate using cumulative degree days during the summer growing season (May through September) one year after the brood year for each tributary habitat associated with a population, using a base temperature of 0 degrees C (Honsey et al. 2023). Cumulative degree days during juvenile rearing were expected to be linearly associated with juvenile growth potential.

### 3.2.2 Juvenile Migration and Early Marine

We considered several conditions during the juvenile migration and early marine life stages as potential drivers of Chinook salmon productivity during the marine phase of their lifecycle. Later river ice breakup has been associated with reduced smolt survival (Cunningham et al. 2018) and river ice break up date observed at three locations throughout the region was used as a covariate. River ice data was compiled for the Yukon and Kuskokwim Rivers from Arp and Cherry (2022). Break up dates on the Kuskokwim River at Bethel, on the Tanana River at Nenana, and the Yukon River at Dawson were assigned to Chinook salmon population units in the Kuskokwim, Yukon (US), and Yukon (CA) respectively two years after the brood year.

Sea ice cover and the timing of its retreat is an important component of productivity and food web dynamics in the eastern Bering Sea (Lomas et al. 2012). We included an index of sea ice concentration during the winter before outmigration from Bering Climate Data. This index represents the average ice concentration in a 2 degree by 2 degree box (56°N-58°N, 163°W-165°W) from January 1 to March 31 which impacts the food web dynamics and physical conditions at ocean entry corresponding to 2 years after the brood year. Overall productivity at the base of the food web can also influence resource availability at other trophic levels potentially impacting the survival and productivity of Chinook salmon (Miller et al. 2013).

Summer sea surface temperature (SST) during the first summer at sea has been found to predict salmon productivity (Mueter et al. 2002), size (Oke et al. 2020), and growth (Yasumishi et al. 2020). Seasonal means for summer (June - August) during smolt outmigration were calculated using monthly SST from NCEP/NCAR reanalysis data (Kalnay et al. 1996). Two indices were used to represent the northeastern Bering Sea (60.1°N - 65°N and 165°W - 172.5°W) and the southeastern Bering Sea (67°N - 60°N and 162°W-172.5°W) following Yasumiishi et al. (2020). Conditions in southeastern Bering Sea were assigned to populations in the Kuskokwim region and conditions in northeastern Bering Sea were assigned to populations in the Yukon region.

Wind mixing in the eastern Bering Sea influences primary productivity, sea ice formation and retreat, and juvenile recruitment of many fish species (Stachura et al. 2014). Cross-shelf wind was expected to integrate aspects of multiple favorable conditions for early marine growth and survival during the first year at sea (Table 1). Indices of cross-shelf wind speed were acquired for NCEP/NCAR Reanalysis (u-wind). Mean monthly wind at 60°N and 170°W at the surface were used as an annual average index of overall wind mixing for the region during the year of outmigration.

For some Yukon River Chinook salmon (Chena and Salcha) survival is higher during years of warmer SST during the first marine winter (Cunningham et al. 2018). A seasonal mean (January - March) during the first marine winter was calculated using monthly SST from NCEP/NCAR reanalysis data (Kalnay et al. 1996). One index was used to represent the southeastern Bering Sea (67°N - 60°N and 162°W-172.5°W) corresponding to 3 years after the brood year.

### 3.2.4 Adult Marine and Spawning Migration

Although this study focused primarily on environmental conditions in the marine and freshwater environments, we also considered biological conditions that relate to Chinook salmon growth and productivity during the adult marine and spawning migration lifestages. Adult walleye pollock (*Gadus chalcogrammus*) is a numerically dominant consumer in the eastern Bering Sea that overlaps spatially and dietarily with immature Chinook salmon and may be an important competitor. Some stocks of other species of Pacific salmon such as pink salmon (*O. gorbuscha*) and chum salmon (*O. keta*) spatially overlap with Chinook salmon in the summer and may compete with YK Chinook for resources in the Bering Sea and North Pacific, impacting survival, growth, and fecundity of Chinook salmon (Oke et al. 2020; Cunningham et al. 2018).

Time series of annual biomass of adult (age 3+) Walleye pollock and annual recruits of juvenile walleye pollock were compiled from stock assessment reports (Ianelli et al. 2020). Annual abundance estimates of the total of wild- and hatchery-origin pink salmon (*O. gorbuscha*) and chum salmon (*O. keta*) in the Bering Sea and North Pacific Ocean were compiled from the North Pacific Anadromous Fish Commission database and North Pacific Fisheries Commission documents by Ruggerone and Irvine (2018) and summarized by Oke et al. 2020. These indicators were correlated with each other and other marine and ecological time series (Appendix S5). To reduce multicollinearity a dynamic factor analysis, a dimension reduction technique that identifies common processes underlying a set of time series, was performed to identify a single underlying trend representing an index of overall marine competition (Appendix S3).

In contrast to juvenile rearing, warm stream temperatures may negatively affect adults in shared migration corridors that regularly exceed thresholds known to induce thermal stress [(e.g. 18°C von Biela et al. 2020)](https://www.zotero.org/google-docs/?kb2tmW) or in low elevation spawning tributaries. The final stream temperature time series (described above) for each migration corridor were used to estimate thermal conditions affecting adult migration. We used migration timing information from escapement monitoring projects to identify the time period when each population was exposed to maximum temperatures as they moved through the mainstem and into their respective spawning tributary. Stream temperatures experienced by adults during the upstream migration were estimated by calculating the annual maximum of mean daily stream temperatures of mainstem and tributary habitats occupied by each population during migration which corresponds to the brood year.

Body size is linked to survival and fecundity of Chinook salmon during adult migration and spawning which can have important carry-over effects to offspring (Malick et al. 2023; Oke et al. 2020; Ohlberger et al. 2020). Data of Chinook salmon body size (nearest mm, mid eye to fork of tail) were collated and archived by Clark et al. (2018) from age, sex, and length projects across Alaska and Canada. Observations for size of escaped salmon were available for some but not all population units in this study and a dynamic factor analysis was performed to estimate the overall trends in body size for both the Yukon (US and Canada) and Kuskokwim basins (Appendix S3). The latent trends represented a size index and were used as a covariate for population units in each watershed.

## 3.3 Chinook salmon productivity

A Bayesian hierarchical stock-recruitment model was used to quantify the heterogeneity of environmental and food web effects on Chinook salmon productivity across population units. The goal of this analysis was to quantify the population specific and region wide impacts of environmental and food web conditions on relative indices of Chinook salmon productivity, represented as log-transformed recruits per spawner. The relative productivity indices used here are assumed to be highly correlated with absolute estimates of productivity from traditional run reconstructions. The advantage of this relative approach is it allows for the inclusion of data-limited population units, while providing a novel synthesis of the diversity in population-level responses to a common set of environmental and climate processes. Notably, the relative indices are not suitable for analyses that require absolute metrics (i.e., stock assessments, comparing population productivity among stocks).

### 3.3.2 Run reconstruction compilation

Estimates of salmon population productivity require run reconstructions which relate the number of adult fish that return to freshwater to spawn each brood year (spawning stock) to the number of offspring (recruits) that were produced by the spawning stock. Recruits are estimated as the number of surviving offspring that return to freshwater habitat (spawners plus harvest) in the years following the brood year. Chinook salmon in the YK region return to freshwater at different ages, typically spending 1 year in freshwater and remaining at sea for 2 - 5 years. Therefore, the population-specific age composition of returning fish is necessary to assign the number of recruits in subsequent years to the correct brood year.

Twenty-six run reconstructions of Chinook salmon in the YK region were compiled and considered to be of suitable reliability for inclusion in the hierarchical spawner-recruit model based on the expert opinion of Alaska Department of Fish and Game, US Fish and Wildlife Service, and Department of Fisheries and Oceans Canada scientists (Figure 1, Appendix 1: Table S1). Identifying impacts on Chinook salmon productivity require sufficient temporal overlap between productivity data and environmental and biological indices. Chinook salmon run reconstructions that had enough spawner and recruit data to estimate at least ten years of productivity were considered to have suitable overlap with covariate data (Appendix 1: Table S1). Run reconstructions included in this analysis varied in reconstruction approach (i.e., state-space models versus regression), and data assumptions (i.e., missing harvest data) (Appendix 1: Table S1). All compiled run reconstructions were considered to be of high enough quality by regional experts (Feddern et al 2023) to calculate a relative index of productivity useful for investigating potential environmental and biological drivers.

### 3.3.2 Stock-recruitment analysis

The stock-recruitment model was fit to available data using Bayesian methods, and implemented in Stan using the rstan (Stan Development Team, 2023) package in R (R Core Team 2023). Models were fit to data, with three chains run for 6,000 iterations. The initial 1,000 iterations were discarded as a burn-in period. Convergence of the chains was diagnosed using the Gelman-Rubin statistic (Brooks & Gelman, 1998) and visual inspection of trace plots for each chain. A posterior predictive check estimating the Bayesian P-value (PB) (Gelman et al. 2004), was performed to test whether the model would generate new observations that were similar to or more extreme than the data. PB close to 1 or 0 indicates the model cannot generate new observations that properly resemble the data.

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

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is the predicted recruitment which is a function of the predicted parameters spawning stock biomass , maximum recruitment rate at low spawning stock size , and the strength of density dependence *βp*. For and observation error was assumed to be known based on the estimated error from run reconstructions. *ɸp*represents the stock-specific observation error correction factor not accounted for in the observed uncertainty, 𝝈r,p,y, allowing error to be greater than 𝝈r,p,y but not less. Less than 2% of spawner and recruit observations had missing error data. For years or stocks that error data was missing, the observation error standard deviation was assumed to be 0.5 on the log scale.

Environmental covariates were specified to have an additive effect on log recruitment rate where the value of covariate *c* for population *p*  in calendar year *t* () is multiplied by population specific covariate effect, *p,c* which is estimated by the model. The prior distribution for the population-specific covariate effect was normally distributed,

where hyperparameters, *μθ,c* and *𝝈θ,c*, describe the expected value and distribution of each covariate effect among population units across the region, and hyperparameters, μɑ and 𝝈ɑ, were used to describe the distribution of population-specific maximum recruitment rates across the region (Table 2). The calendar year for each covariate, *t*, was offset by 0-3 years to align with the correct stage of the Chinook salmon life cycle hypothesized to be impacted by each covariate (Table 1). Prior distributions for estimated model parameters and hyperparameters (Table 2) were chosen to be uninformative or weakly informative. All covariates were standardized by subtracting the mean and dividing by the standard deviation for the time period 1980 - 2017. Watershed- and region- specific covariates were standardized within a given watershed or region such that each watershed (or region) had a mean of 0 and standard deviation of 1.