**Spatiotemporal trends in salmon metapopulation contribution to the Kuskokwim river**

**Introduction:**

Chinook salmon populations are experiencing unprecedented declines across much of their range (Atlas et al., 2023; Ohlberger et al., 2018). This trend is especially severe in western Alaska watersheds, which contain some of the world's last pristine Chinook salmon habitat but have seen steep declines in returning Chinook and chum salmon in recent years (Lamborn et al., 2025; Murdoch et al., 2024). Salmon from this region have supported lucrative commercial fisheries, and have historically provided the cultural and nutritional foundation for dozens of subsistence communities in the region. As runs have collapsed, however, harvest has been completed restricted or upstream communities have voluntarily reduced or ceased subsistence fishing altogether, triggering a region-wide crisis of food insecurity, cultural loss, and the potential disappearance of a critical economic resource (Brown & Godduhn, 2015). As a result, resource managers face the difficult task of designing management strategies which balancing ongoing harvest opportunities with the urgent need to rebuild salmon populations and strengthen their resilience to future perturbations.

There is growing recognition of the critical role that intrapopulation variability plays in fostering resilience at the ecosystem scale in both terrestrial and aquatic ecosystems (Luck et al. 200X, Schindler et al. 2015). In salmon populations, substantial variation in both return timing and spatial distribution of habitat use produces significant complexity in life history strategies within and among populations (Hilborn et al. 2003). Overall population performance in salmon ecosystems is therefore shaped by the statistical averaging of multiple distinct, semi-independent sub-units distributed across space and time (Schindler et al. 2010; Connors et al., 2022). Weak or negative covariance among these stocks helps buffer the broader population against the poor performance of any individual subunit, whose success may fluctuate in response to a dynamic mosaic of multi-dimensional environmental conditions (Brennan, Schindler, et al., 2019; Schindler et al., 2010). This “portfolio effect” dampens ecosystem variability by distributing risk across its components, much in the same way that financial diversification of a portfolio spreads investment risk across sectors to reduce overall volatility (Griffiths et al., 2014; Markowitz, 1952; Schindler et al., 2015). The reliability of salmon resources to communities is a product of the health of stock components throughout the watershed. For Pacific salmon fisheries, which harvest stocks as the migrate upstream, the duration and reliability of this resource is the result of the aggregate dynamics of upstream stocks. For example, healthy stock components with unique spatiotemporal patterns may allow for more diverse set of harvest opportunities over a longer time period (Nesbitt & Moore, 2016). Further, distributing risk across space and time in several stocks may buffer basin-wide returns to local or short-term changes to habitat conditions, thereby enhancing both the accessibility and reliability of downstream harvest opportunities (Schindler et al. 2010). The health of salmon populations in terms of long-term resilience and reliability of ecosystem services is therefore better assessed by the health and viability of contributing subunits rather than by total run size alone (Griffiths et al. 2014; Connors et al., 2022).

Downstream fisheries which harvest migrating stocks face a difficult challenge to design harvest methods which consider both overall harvest opportunity as well as stock specific exploitation rates. For example, strategies which concentrate harvest in periods of peak abundance (e.g., highest CPUE per day) may fail to account for whether this peak consists of a mix of vulnerable, weak stocks or a single, more robust stock that can sustain higher exploitation (Connors et al. 2022). Fishing which disproportionally exploits weak stocks as they migrate upstream may threaten the availability of resources to upstream communities and threaten the reliability of downstream resources in subsequent years as upstream stock health degrades. Management strategies which maintain reliable fishery resources should therefore aim to allow harvest opportunities on healthy stocks while minimizing the risk of overexploitation for co-migrating weak stocks (Connors et al., 2020). In practice, however, implementing such stock-specific management approaches requires detailed data on the spatiotemporal ecology of salmon populations; information that has historically been limited at sufficiently fine spatial and temporal scales (Connors et al., 2020, 2022).

Lack of stock-specific spatial ecology of Chinook salmon populations in western Alaska, has necessitated that management strategies be implemented at relatively coarse spatial scales. A salient example of this is in the Kuskokwim River where managers implement a front-end closure strategy that heavily restricts fishing during the beginning of the salmon migration season to protect early returning fish (e.g. Bechtol et al., 2025). This strategy aims to support basin-wide escapement goals while allowing for a significant number of fish to return to stocks in the upper portions of the river basin , thereby protecting access to harvest opportunities for upstream communities and bolstering the health of upstream stocks which have a general tendency to migrate early in the season (Clark et al., 2015). However, little data exist which quantifies the spatiotemporal patterns among stocks. The impact of front-end closure strategies on individual stock components is not well understood, and a more complete understanding of stock contribution to the overall run both within and among years is currently not readily available. However, these data may be important to assessing the impact of current management strategies and designing new strategies which maintain stock health across all components of the watershed and maintain a reliable resource for communities and industry in the region.

Here, we apply otolith microchemistry from fish caught at different times of the migration season over 6 years to reconstruct spatiotemporal patterns of Chinook salmon natal origin distribution at the sub basin scale in the Kuskokwim River-basin. In doing so, we will: (1) identify the spatiotemporal structure of returning populations in the Kuskokwim river-basin, and (2) evaluate the potential impacts of harvest strategies such as a front-end closure on stocks across these systems.

**Methods:**

**Otolith Sample sets**

Otoliths were collected over several years from the Bethel Test Fishery (BTF) near Bethel, Alaska by \_\_\_\_\_\_\_\_\_ . Both fisheries are designed to sample the stock composition of returning salmon throughout the duration of the season to assess relative contribution over the course of the run. Approximately 500 otoliths were collected over the full duration of the run from the Kuskokwim River between 2017 and 2022. From these, about 250 otoliths were selected for analysis to ensure coverage across the full sampling period and to provide proportional representation relative to catch per unit effort (CPUE) throughout the run. Selected samples were sectioned along the transverse plane, mounted on microscope slides, and polished to expose internal growth structures (Donohoe & Zimmerman, 2010; Zimmerman & Reeves, 2002). Prepared samples were analyzed at the University of Utah Strontium Isotope Laboratory using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS). Laser ablation was conducted along a transect from the otolith core to just beyond the onset of marine growth using a 53 μm diameter beam and scanning at 2μm/second (Brennan et al., 2015). The resulting data represent a continuously integrated measurement of Sr87/Sr86 from early development until marine entry (Brennan et al., 2015; Campana, 1999; Capo et al., 1998). From these data, the Sr87/86 value associated with the natal freshwater rearing period was extracted by examining patterns of change in Sr87/Sr86 and Sr88 between the core and freshwater region, morphological features of the otolith visible among the ablation path, and known distances from the core to onset of the freshwater signal (cite).

**Isoscape Development**

An isoscape of the Kuskokwim river was constructed to model spatial variation in Sr87/Sr86 ratios across the river basin, following the methodology described in Brennan et al., (2016) and Makhlouf et al., (2025). Briefly, Sr87/Sr86 values were derived from water samples (N= ? ) collected throughout both river basins (Supp. 1) and modeled via spatial stream network modeling using the STARRS package in R (add more). This approach considered several geologic and hydrological covariates as well as Euclidian distance and hydrological connectivity between sampling sites (Ver Hoef & Peterson, 2010). The resulting isoscape provides a spatially continuous estimate of Sr87/Sr86 values and their associated uncertainties for roughly every ~1km stretch of tributaries across the basin (Figure 1). To prevent over-assignment to tributaries with exceptionally low prediction error, minimum error values were constrained to 0.0006. This threshold was selected through systematic evaluation to minimize assignments driven primarily by uncertainty differences rather than isotopic similarity, while preserving broad-scale production patterns across the basin

**Assignment framework and priors**

Posterior probability values were calculated for all fish and for all tributary segments across the river-basin using a geographically continuous Bayesian framework (Brennan, Cline, et al., 2019). This approach considers the relationship between extracted natal origin otolith Sr87/Sr86 values as well as several variance generating processes including analytical, within-population, and isoscape prediction error. We assumed all errors were normally distributed, and combined them through the equation:

Posterior probability values for each tributary (j) were then calculated using Bayes theorem (Brennan & Schindler, 2017; Wunder, 2010) ;

The probability of an individual assigning to tributary j is defined as the product of the probability of the isotope ratio in the otolith of an individual (o) given the isotope ratio in tributary j (r\_j). The probability of the isotope ratio (rj) was assumed to be normally distributed with a mean represented by the otolith isotope ratio (o) and an error of . Several priors were included to limit assignments to areas within the river basin suitable for spawning Chinook salmon. First, a stream order prior (PStreamOrder) was applied to limit assignments to tributaries with a stream order of 3 or greater, , reflecting Chinook Salmon’s known preference for spawning in larger streams (cite). Reaches with a stream order of 3 or greater were included in assignments (assigned a prior value of 1), while smaller tributaries were excluded (assigned a value of 0). Second, a habitat suitability prior (PHabitat) was used to exclude regions below a threshold contributing slope value, thereby preventing assignment to exceedingly slow or flat reaches determined to be unsuitable for spawning Chinook salmon. Finally, data was included on observed locations of spawning chinook presence derived from USGS Arctic-Yukon-Kuskokwim (AYK) Chinook Salmon Intrinsic potential mapping. This dataset synthesizes several sources of data on observed Chinook salmon spawners to provide a binary 0 or 1 value for locations with or without observations across the dataset (Falke & Paul, 2025). To avoid biasing regions without observations but with low sampling effort, this prior was only applied to the two highest stream orders in the dataset (Stream order >= 6). From these tributaries, reaches identified in the intrinsic potential dataset as lacking observed Chinook spawning were assigned as a value of 0.

Natal origin distributions were estimated by summing posterior probability values across individuals and locations, retaining only the top 30% of posterior values for each individual to prevent low-probability assignments from confounding spatial patterns. Estimates were produced for predefined temporal quartiles based on capture date: Q1 (run start through June 11), Q2 (June 12-21), Q3 (June 22-July 1), and Q4 (July 2 onward).These dates were chosen to roughly split the full run into four equal quartiles while allowing for direct comparison among years. Due to differences in the total run duration among years the duration of the fourth quartile bin varies slightly among years. For the most part, these deviations were minimal and included a negligible portion of the CPUE. Finally, estimates were produced for the full run in each year by including all four quartiles of data.

Twenty-one management units were defined to aggregate tributary-level estimates into units relevant to current management practices (Figure 2). Management units of interest to the Alaska Department of Fish and Game were identified by \_\_\_\_], with all upstream segments from the most downstream point of each tributary assigned to common management identifiers. Remaining basin areas were manually grouped into units of comparable size to ensure complete basin coverage.

**Spatial and Temporal patterns**

For each quartile, return estimates were normalized to sum to one across the watershed, displaying proportional contribution patterns independent of among-quartile abundance differences. Mean contributions across all years were calculated for each management unit and quartile and visualized by coloring all tributaries assigned to the same unit by their relative contribution (Figure x). Corresponding boxplots for each quartile illustrate temporal variability in contribution patterns, ordered from upstream to downstream locations. Cumulative distribution functions were produced by subsetting the full dataset into every third day. From each subset total summed estimates of production for each tributary was produced and aggregated into management units. These values were then compared against the raw values for the entire dataset. Lines are colored in order of distance up the watershed with deeper red values displaying the furthest upstream populations and deep blue illustrating the furthest downstream populations. Cumulative distribution functions were constructed using 3-day intervals throughout each run. For each interval, tributary-level production estimates were aggregated into management units and compared against full-season totals. Management units were color-coded by watershed position, with upstream populations in red transitioning to downstream populations in blue, providing a visual representation of the temporal progression of returns across the basin.

To assess the protective effectiveness of front-end closure strategies on upstream stock components, we quantified the proportion of each management unit's annual production that occurs within the current closure window. We calculated the ratio of estimated returns during Q1 (run start through June 11) to the total annual returns for each management unit and year. This metric represents the fraction of each stock's production that would be protected by implementing a front-end closure, independent of that unit's overall contribution to basin-wide returns.

**Results**

**Isoscape variation**

Sr87/Sr86 values in the isoscape ranged from \_\_\_ to \_\_\_, with relatively enriched values in the upper reaches of the watershed and progressively lower values towards the downstream terminus. Isoscape error varied from \_\_\_\_ to \_\_\_\_ . etc. etc.

Spatiotemporal trends

* Q1 high production in \_\_\_ , \_\_\_, and \_\_\_.