**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 for upstream communities who 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. 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 in the Kuskokwim River-basin to reconstruct spatiotemporal patterns of Chinook salmon natal origin distribution at the sub basin scale. 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**

**\* discuss raw water values\***

Strontium isotope ratios in the basin ranged from 0.7042 to 0.7107, with significant variation at multiple spatial scales. More enriched values closer to the 0.7107 ( Figure 1, light oranges and yellow) are primarily found in the upper reaches of the watershed near McGrath. In contract, the lower reaches of the watershed near Bethel, Alaska contain much lower values closer to 0.7040. Associated isoscape error values ranged from \_\_\_ to \_\_\_, with lower error values present along the mainstem and major tributaries where sampling efforts were completed and larger error found \_\_\_\_\_\_.

**Spatiotemporal trends in stock contribution**

Across all years of our dataset (2017-2021), returns to the 21 stock units exhibited distinct temporal patterns in contribution and an progression from upstream to downstream stock as the season progressed. Early season returns (Q1: start of run through June 11) were dominated by stocks from the upper portions of the watershed. The largest contributors were Big River (median: ~12%, range: 8-18%), Upper Kusko Main (median: ~10%, range: 6-16%), and Swift (median: ~8%, range: 4-14%), with moderate contributions from Takotna and Nixon Fork (~8%) and some middle-watershed stocks including Stony (~6%) and Holitna (~5%). Upper watershed stocks exhibited substantially higher inter-annual variability during Q1 as compared to the other three quartiles.The distribution of returns became more balanced across the watershed during Q2 (June 12-21), with contributions more evenly distributed among management units compared to the upper-watershed dominance of Q1. Upper watershed contributions remained important but began declining: Big River decreased from 12% to 10%, Upper Kusko Main from 10% to 9%, and Swift from 8% to 7%. Simultaneously, middle-watershed stocks increased their relative importance, with Holitna rising from 5% to 7%, Middle Kusko Main from 4% to 6%, and Aniak from 3% to 5%. Stony River emerged as a consistently strong contributor (median: ~8%, range: 6-10%) with reduced variability compared to Q1 patterns (range: 4-12%). Q3 returns (June 22-July 1) marked a clear transition toward middle-watershed stocks and represented the most consistent period across years. Upper Kuskokwim stocks showed substantial declines - Big River dropped from 12% to 6%, Upper Kusko Main from 10% to 7%, and Swift from 8% to 4%. Conversely, middle-watershed stocks peaked in importance: Stony maintained ~8% contribution, Holitna increased to ~8%, and Middle Kusko Main reached ~7%. This quartile exhibited the most consistant distribution (smallest interquartile ranges) for most stocks. Late-season returns (Q4: July 2 onward) demonstrated the most dramatic compositional shift, with several stocks showing 3-5 fold changes from their Q1 contributions. Upper-watershed contributions reached their seasonal minimum; Big River declined to ~4%, Upper Kusko Main to ~6%, and Swift to ~3%. Middle-watershed stocks maintained substantial but increasingly variable contributions, with wider distributions than Q3. Most notably, lower-watershed stocks reached their peak contributions during Q4: Aniak increased from ~3% in Q1 to ~9% in Q4, Kwethluk from ~2% to ~8%, and Kisaralik from ~1% to ~6%. These lower-watershed stocks also exhibited the highest variability in Q4, with outliers suggesting some years had more significant late-season contributions from these stocks.

**Cumulative Distribution functions**

Cumulative distribution plots further illustrate the pattern of consistently early returning upper Kuskokwim stocks and late-returning lower Kuskokwim stocks. As compared to the relatively coarse spatial scale of quartile analysis, these data illustrate variation in run timing among stocks at a finer spatial scale that is independent of the binning of values into quartiles based on consistent dates. This analysis reveals whether the timing of stock contribution varies based on the relative timing of the run (i.e. early returning vs late returning or short vs long run), and is independent of the total contribution of the stock to the overall run.Upper watershed stocks demonstrated characteristically steep early-season curves, with populations like Big River, Swift, and Upper Kusko Main (Figure 4, Dark red) reaching 50% of their annual contribution more quickly than lower stocks (Figure 4, Blue). The steepness of these curves indicates highly predictable and concentrated returns for upper Kuskokwim stocks within a relatively narrow window. In most years, fish are predictably arriving within a narrow 10-15 day window at the start of the season. As compared to the quartile analysis, cumulative distribution plots also reveal subtle differences at finer temporal scales. For example, Big river stocks consistently peak 2-3 days before Swift, indicating predictable fine-scale differences in stock contribution timing. Lower watershed stocks, in contrast, exhibited markedly different cumulative patterns with gradual, extended curves reflecting protracted run timing that spans the entirety of the run. Populations such as Aniak, Kwethluk, and Kisaralik showed minimal contributions (0-10%) through mid-June, with their steepest accumulation occurring after DOY 180. Typically, these stocks reach 50% of their annual contribution 10-15 days later than upper watershed populations, with some continuing substantial contributions through DOY 200+ .

**Front end closure protections**

Analysis of the protection offered to stocks across the basin based on a front-end closure illustrated a range of protection across stocks with clearly higher protection afforded to upper Kuskokwim stocks Upper watershed stocks showed the highest closure protection rates, with North Fork Kusko receiving the greatest benefit (median: ~25%, range: 20-35%). Despite North Fork Kusko contributing minimally to the total watershed run (~2-3% annually), approximately 25-35% of the production it does contribute occurs during the Q1 closure window. Several populations showed similarly high proportional protection including the East Fork Kuskokwim (median: ~20%, range: 15-30%), South Fork Kusko (median: ~15%, range: 10-25%), Upper Kusko Main (median: ~15%, range: 10-20%), Tatlawiksuk (median: ~15%, range: 10-25%), and Swift (median: ~12%, range: 8-18%). Of the stocks with the highest protection (>10% median), all were found in the upper portions of the watershed. Several upper watershed stocks also exhibited notable outliers, with Big River, Swift, and East Fork Kuskokwim showing years where protection exceeded 25-30%, suggesting occasional years with exceptionally early timing for these populations.Notably, Takotna and Nixon Fork received relatively little protection (median: ~8%, range: 5-12%) despite its position at the top of the watershed

In contrast, stocks positioned lower in the watershed received less protection from the front end closure. Stony and Holitna river stocks, which are positioned in the middle of the watershed, show low median protection (~5% and ~3% respectively), but with outliers reaching ~22% and ~19% respectively, indicating generally low protection but occasionally higher protection in years with particularly early returns for these stocks. Lower watershed stocks, however, received consistently minimal protection. Aniak, Tuluksak, Kisaralik, Kwethluk, and Lower Kusko all demonstrated consistently low protection rates (medians: 2-5%, ranges: 1-8%), indicating that the vast majority of these stocks' contributions are subject to fishing pressure outside of the front-end closure window.

**Discussion**

* We provided an estimate of spatiotemporal patterns over a longer timescale and at a finer spatial resolution than previously available
* Clear and consistent pattern of early returning stocks to the upper portion of the watershed
* Variation among upper river stocks at finer temporal scales via cumulative distribution
* Pattern holds regardless of the timing (early vs late) or duration of the run.
* Early returning to the upper kusko contain both high contributors (i.e. Big River) and low contributors (i.e. north fork Kuskokwim).
* However, all upper stocks were most protected by the front end closure
* Limitations and assumptions of data collection and assignments using otoliths
  + Including lack of verification
  + Extrapolation of sample size
  + Binning of Quartiles creating inconsistancies among years
* However, clear and consistant patterns follow what we expect based on anecdotal evidence and other studies
* These data provide a tool to assess the impact of a front-end closure and to continue to develop strategies to conserve stock diversity
* Front end closure protection to upper stocks
  + helps guarantee resources to upper kusko communities
  + Protects stock diversity and stabilizes downstream fisheries
* Generally, understanding spatial ecology is key to maintaining diversity through harvest and conservation strategies