**Spatiotemporal trends in salmon metapopulation contributions to portfolio effects in Western Alaska**

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**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 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 support lucrative commercial fisheries, contribute billions of dollars to regional and global economies, and have historically supported subsistence harvests for dozens of communities in the region. As runs have collapsed, however, many 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 (Bolnick et al., 2011). 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. 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 (Connors et al., 2022; Ohlberger et al., 2016). 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 (Cline et al., 2017; Griffiths et al., 2014; Markowitz, 1952; Schindler et al., 2015). Ecosystems composed of numerous negatively or weakly correlated “assets” are therefore better equipped to withstand both localized and system-wide disturbances, as such events may favor some components while disadvantaging others. Additionally, both the duration and magnitude of resources available to communities depend on preserving this natural phenotypic diversity. For example, fisheries that harvest downstream stocks during their upstream migration, such as commercial Pacific salmon fisheries, rely on the aggregate dynamics of multiple upstream populations. The stability of downstream harvests, therefore, hinges on preserving response diversity across these upstream metapopulations, which in turn enhances both the accessibility and reliability of harvest opportunities (Nesbitt & Moore, 2016).

In many salmon populations, particularly those at lower latitudes, this natural complexity has been eroded due to poor management and anthropogenic impacts on salmon ecosystems (Griffiths et al., 2014). As a result, many systems now exhibit increased synchrony across subunits, leading to greater covariance in performance and generating “boom-or-bust” cycles in ecosystem productivity. This homogenization increases ecosystem vulnerability, even if aggregate return numbers appear stable or even more productive than more diversified ecosystems in the short term (Schindler et al., 2010). Consequently, the health of salmon populations at the riven-basin scale in terms of long-term resilience is better assessed by the health and viability of contributing subunits rather than by total run size alone (Connors et al., 2022). Efforts to rebuild and conserve the long-term resilience of Western Alaska Chinook salmon must therefore account for this spatiotemporal complexity and design management strategies which maintain it in the long term. These include designing harvest methods which consider both overall exploitation rate as well as stock specific exploitation rate, which may vary throughout the season (Schindler et al., 2010). Strategies that concentrate on harvest in periods of peak abundance (e.g., highest CPUE per day), for example, 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. Instead, management strategy should aim to allow harvest opportunities on healthy stocks while minimizing the risk of overexploitation for co-migrating weak stocks. 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., 2020b, 2022).

In the absence of fine-scale data on stock-specific spatial ecology in Western Alaska, management strategies have been implemented at relatively coarse spatial scales across large river basins. In the Yukon River Basin, for example, decisions are based on broad stock aggregates defined by the resolution of available genetic baselines. As a result, large portions of the watershed (e.g. Canadian-origin salmon) are managed as a single aggregate stock. This approach obscures the presence of multiple contributing sub-stocks, each of which may exhibit substantial variation in life history traits both within and across seasons (Connors et al., 2023). In contrast, the Kuskokwim River Basin employs front-end closure strategies aimed at allowing an estimated number of early-returning fish to escape before harvest begins (e.g. Bechtol et al., 2025) While this strategy supports basin-wide escapement goals, it does not account for the relative stock composition of fish protected by the closure and is likely to favor fish returning to the furthest upstream portions of the watershed (Clark et al., 2015). Moreover, assessments of basin health are typically conducted on annual timescales and focus primarily on total returns over time, which may overlook the relative health of individual sub-stocks and shifts in their spatiotemporal distribution or contribution to the broader metapopulation portfolio. In both cases, managing based on aggregate spatial or temporal patterns risks obscuring underlying trends which may very independently from the aggregate and respond differently to environmental pressures or management actions. Here, we apply otolith-based methods to reconstruct spatiotemporal patterns of Chinook salmon natal origin distribution in the Kuskokwim River basins to: (1) identify the spatiotemporal structure of returning populations in Alaska’s most productive salmon-bearing watersheds; (2) assess how this structure varies with overall run dynamics; and (3) evaluate the potential impacts of harvest strategies, including front-end closures, on stocks across these systems.

**Methods:**

**Otolith Sample sets**

Otoliths were collected over multiple years from both the Yukon and Kuskokwim River basins. Sampling was conducted continuously at the Lower Yukon Test Fishery (LYTF) near Emmonak, Alaska, and at the Bethel Test Fishery (BTF) near Bethel, Alaska. Both fisheries are designed to monitor the stock composition of returning salmon throughout the duration of the run. Approximately 500 otoliths were collected over the full duration of the run from the Kuskokwim River between 2017 and 2021, and from the Yukon River in 2015, 2016, and 2021. 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 inferred onset of marine growth using a 53 μm diameter beam and scanning at 2μm/second (Brennan et al., 2015) The result data represent a continuously integrated measurement of Sr87/Sr86 which is expected to be minimally fractionated during incorporation into the otolith and represents the experienced Sr8786 of the fish from early development until marine entry (Brennan et al., 2015; Campana, 1999; Capo et al., 1998). From these data, a discrete value associated with the natal freshwater rearing period was manually extracted by examining known patterns of changes in Sr8786 and Sr88 between the core and freshwater region as well as morphological features of the otolith visible among the ablation path.

**Isoscape Development**

Isoscapes were constructed to model spatial variation in Sr87/86 ratios across the river basin, following the methodology described in Brennan et al., (2016) and Makhlouf et al., (2025). Briefly, Sr87/86 values were derived from water samples collected throughout both river basins (Supp. 1) and modeled using spatial stream network modeling, which considers 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 Sr8786 values and their associated uncertainties for roughly every ~1km stretch of tributaries across the basin (Figure 2). To avoid overrepresentation of regions with very low uncertainty—which could lead to inflated assignment probabilities—each site was assigned a minimum error value of 0.0006. This threshold was selected based on the distribution of uncertainty values across the basin and systematic evaluation of thresholds that minimized overassignment to a limited number of tributaries, while preserving broad-scale production patterns. Implementing a minimum error value ensures that assignments are primarily driven by isotopic similarity between otolith and isoscape values rather than by differences in local uncertainty. This approach balances the need to consider uncertainty in isoscape prediction without allowing this variation to drive assignments.

**Assignment framework and priors**

For each fish, a posterior probability of origin was calculated using a geographically continious Bayesian framework (Brennan, Cline, et al., 2019). This approach considers the relationship between extracted natal origin otolith Sr8786 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 of provenance 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) and 3 separate habitat priors. 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 higher-order tributaries, reflecting Chinook Salmon’s known preference for spawning in larger streams. Only reaches with a stream order of 4 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 (threshold to be inserted from [source]), thereby preventing assignment to exceedingly slow or flat reaches determined to be unsuitable of spawning Chinook. 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 (Falke & Paul, 2025) to provide a binary 0 or 1 value for locations with or without observations across the dataset. To avoid biasing regions without observations but with low sampling effort, this prior was only applied to mainstream tributaries and those with the second highest stream order. From these tributaries, reaches identified in the IP dataset as lacking observed Chinook spawning were assigned as a value of 0.

**Natal origin distribution estimates.**

Posterior probability estimates of origin were generated for each individual across all tributaries in the basin. To retain only the most likely natal habitats, the top 30% of posterior values were preserved while the bottom 70% were discarded. This filtering reduced the influence of diffuse, low-probability values and improved the spatial resolution of basin-scale patterns.

Full-run estimates of the spatial distribution of natal origins were calculated by summing the thresholded posterior probabilities for all individuals at each tributary location. To assess temporal patterns within the run, individuals were grouped into predefined quartiles based on their capture date. The first quartile spanned from the beginning of the run through **June 11**, corresponding to the current front-end block closure on the Kuskokwim River. The second quartile covered **June 12–21,** the third spanned **June 22–July 1,** and the final quartile included all individuals captured from **July 2 onward.** Although the duration of the fourth quartile varied slightly among years due to interannual differences in run timing, these deviations were minimal and had negligible impact on overall CPUE. Quartile-specific natal origin distributions were calculated by summing the thresholded posterior probabilities of all individuals captured within each quartile window. For both full-run and quartile-specific estimates, values were normalized to sum to one. For visualization purposes, these values were then rescaled to a 0–1 range to depict the relative distribution of natal origins across the basin.

**Management units and timeseries construction**

Tributaries across the basin were grouped into management units based on regions of management concern identified by the Alaska Department of Fish and Game (ADFG). These included key tributaries such as the Aniak, Kwethluk, Takotna, and Holitna rivers, which are subject to active management goals. For each of these systems, all upstream stream segments were grouped and assigned a common management unit identifier. Additional tributaries not explicitly highlighted in ADFG’s management priorities were grouped into units of comparable size or hydrological significance. These included units such as “Upper Kusko Main,” “George,” and “Lower Kusko,” ensuring that the entire basin was binned into management categories that could be reasonably compared across regions (Figure X). Production estimates across the basin were aggregated by management unit and rescaled to sum to one for each quartile. This process was repeated for all quartiles across all years in the dataset (2017–2021), resulting in a time series of proportional contributions for each of the 20 management regions.

**Dynamic Factor Analysis**

To identify shared temporal patterns in salmon run timing across management units, we applied Dynamic Factor Analysis (DFA) to time series data of proportional contributions within each quartile. DFA is a multivariate time series technique that models observed series as linear combinations of a smaller set of latent trends, capturing underlying structure in the data while accounting for observation error. The model consists of two main equations, an observation equation:

And a state equation;

In the observation equation, represents the vector of observed proportional contributions at time t, while contains m latent trends that drive the observed patterns. The loading matrix Z quantifies how strongly each observed time series responds to each underlying trend, with larger absolute values indicating stronger associations with a given trend. The matrix D contains coefficients for covariates , the intercept term d captures the mean level of each series, and represents observation error with covariance matrix R. The State equation is modeled as a random walk, where the process error covariance matrix Q determined variability in trend evolution. This approach is particularly well suited for dimensionality reduction across multiple time series and provides a systematic framework for identifying the optimal number of underlying trends, estimating their influence (loadings), and exploring the effects of potential covariates.

**Model Selection**

All timeseries were Z normalized to allow comparison of trends irrespective of absolute production values. We then used a three-stage approach to model selection where we first identified the optimal *m* number of underlying states, then tested several R covariance matrix, and finally tested the influence of covariates against a null model. We compared *m* model fit for a 1-4 state model by calculating a partial R2, defined as;

This metric lets us quantify the extra variation explained by the addition of each additional trend. R covariance structure and the inclusion of covariates were compared using AIC. We compared two common R matrix options including “diagonal and equal”, which assumes all timeseries have the same observation error variance and are uncorrelated, and “diagonal and unequal”, which also assumes no correlation between timeseries but allows each one to have its own error variance. Finally, we tested the effect of two covariates related to the size of returning cohorts in the year of analysis. These include a “run size” , which is the full run size for the given year of analysis and a CPUE covariate which is the proportion of CPUE contained within each quartile for a given datapoint. From the best-fitting model, we extracted the underlying latent trends and the corresponding loadings for each time series on each trend and applied a varimax rotation. Factor loadings were mapped onto their corresponding management units within the watershed to provide a clearer, spatially explicit understanding of the spatiotemporal patterns.

**Results:**

Model selection based on partial R² identified two underlying trends as optimal. These two trends together explained 89% of the variance among time series, while adding a third trend contributed only an additional 2.4% of explained variance. Comparison of observation error structures strongly favored a structure of "diagonal and unequal" over “diagonal and equal” (AIC 332.16 vs 521.75) meaning each management unit time series was allowed to have its own unique observation error variance while maintaining the assumption that observation errors are uncorrelated between units. This result tracks with our expectation that observation error across the basin would vary based in part on isoscape prediction error variance among management unit regions. Finally, the best model contained neither CPUE or run size covariates based on AIC.

**Underlying Trends and spatial loadings**

Trend 1 (Figure X) is characterized by an increase in mean proportional contribution starting in 2019, driven by increased Q3 and Q4 contributions. This trend is led by strong positive loadings from management units such as the Hoholitna, Takotna, Nixon Fork, and Stony Rivers. In contrast, several tributaries in the northernmost portion of the basin have strong negative loadings, including the East, North, and South Fork Kuskokwim as well as the Kwethluk and Big Rivers, indicating the opposite trend of decreasing mean proportional contribution, particularly in the latter half of the run.

Trend 2 (Figure X) contains a more stable mean across the dataset but shows a shift from patterns driven by relatively equal contributions from Q1 and Q2 to an increasing contribution from only the first quartile in the last two years of the dataset (2020 and 2021). This trend is driven by strong positive loadings from most tributaries in the upper portion of the river basin, including the Upper Kuskokwim mainstem, South Fork Kuskokwim, Kwethluk, Big River, and Tatlawiksuk Rivers. In contrast, the lower reaches of the Kuskokwim, including the Oskawalik, Tuluksak, Swing, Aniak, and Holokuk Rivers, contain strong negative loadings on this trend, indicating a shift towards higher proportional contribution away from the first quartile.

**Discussion:**

Our analysis identified two major underlying trends in the spatiotemporal ecology of Chinook salmon in the Kuskokwim River basin. Both trends reveal shifts in spatiotemporal patterns that have important implications for rebuilding Chinook salmon populations.

Trend 1 shows production shifting away from [X, Y, Z management units] toward [X, Y, Z management units], with particularly notable increases in late-season contributions (Q3-Q4) beginning around 2019. This redistribution may significantly impact both the timing and magnitude of fish available to upstream communities such as McGrath, Alaska, which relies on runs from tributaries near the confluence of [specific tributary] and the mainstem Kuskokwim River. [Add 1-2 sentences about specific implications - e.g., timing mismatch with traditional harvest windows, changes in stock availability, etc.]

Trend 2 reveals a steady increase in Q1 contributions throughout the dataset, with a notable decoupling from Q2 production patterns. Management units with strong positive loadings on this trend—primarily upper Kuskokwim tributary groups including [X, Y, Z]—showed dramatically higher Q1 contributions in 2021 compared to 2017. This shift suggests that the early portion of the run is becoming increasingly dominated by these upper basin stocks, with their peak contribution window moving earlier in the season.

This temporal concentration has important implications for both ecological resilience and management effectiveness. The growing dominance of upper Kuskokwim stocks in Q1 may reflect [environmental drivers/competitive release/habitat changes], while the decoupling from Q2 suggests a compression of run timing that could reduce overall temporal diversity. This trend is further supported by the decreasing contribution of the upper Kuskokwim region during the latter half of the run, as is evident by their negative loadings onto Trend 1. Taken together. Thes trends suggest that upper Kuskokwim stocks are increasingly dominant in the first quartile and absent towards the latter half of the run, where the proportional contribution is more rapidly coming from X,Y,Z.

**Implications for Management**

**Implications for ecosystem resilliance**

Nesbitt et al., predicted that communities with access to more diversity may have longer fishing seasons

Chinook salmon (*Oncorhynchus tshawytscha*) populations returning to the Yukon River of Alaska provide vast cultural and economic value to indigenous people of the region that subsist on the resource (Brown & Godduhn, [**(Makhlouf et al., 2025)**](https://onlinelibrary.wiley.com/doi/full/10.1111/gcb.14315#gcb14315-bib-0006)).

The need to understand what is driving Chinook salmon dynamics is especially urgent, as many populations have experienced an abrupt shift to chronically low productivity and abundance (Atlas et al. 2023; ADFG – DCF 2022; Joint Technical Committee of the Yukon River U.S./Canada Panel 2021).

Declines in abundance and mean body size have a range of social and ecological implications, like decreased fecundity and a weakened portfolio effect (Staton et  al.  2021; Ohlberger et  al.  2020; Dorner et  al.  2018). A reduced portfolio effect increases a species' risk to adverse events across space and time (Carvalho et  al.  2023).

Furthermore, restricting access to fisheries in Alaska threatens cultures, livelihoods, well-being, and the sovereignty of rural and Indigenous communities (Connoy et  al.  2024; Carothers et  al.  2021).