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

**Introduction:**

Chinook salmon populations are experiencing unprecedented declines across much of their range. 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. 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. 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. 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 shaped by the statistical averaging of multiple distinct, semi-independent sub-units distributed across space and time. 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. 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. 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. 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., \_). 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. Consequently, long-term resilience is better assessed by the health and viability of contributing subunits rather than by total run size alone.

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 the timing of harvest throughout the season. Strategies that concentrate 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.

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. While this strategy supports basin-wide escapement goals, it does not account for the relative stock composition of fish protected by the closure versus those exposed to harvest afterward. Moreover, assessments of basin health are typically conducted on annual timescales and focus primarily on total returns over time. This overlooks 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 set**

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.

**Sample Prep and LA-ICPMS**

Otoliths were sectioned along the transverse plane, mounted on microscope slides, and polished to expose internal growth structures (CITE). 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. The result is a continuous measurement of Sr87/86 from early development until movement to the marine environment. From these data, the Sr8786 value associated with the natal freshwater rearing period was manually extracted by examining changes in Sr8786 and Sr88 from the core region and morphological features of the otolith visible among the ablation path.

**Isoscape Development**  
Isoscapes were constructed to estimate 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, Sr8786 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. The result is a spatially continuous estimate of Sr87/86 and associated uncertainty for all tributaries in the basin

**Assignment framework and priors**

For each fish, a posterior probability of origin was calculated by comparing its extracted natal Sr8786 value to values predicted across the isoscape using a Bayesian probabilistic framework. This approach incorporates both spatial variation in isotopic ratios and associated error;

[ Insert Model Here]

In which..

[ Describe the Model Here]

Presence and habitat priors

Several priors were included to limit assignments to areas within the river basin suitable for spawning Chinook salmon. First, a stream order prior 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 includes in assignments (assigned a prior value of 1), while smaller tributaries were excluded (assigned a value of 0). Second, a habitat suitability prior 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 (CITE, CITE, CITE) 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.

**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 [insert list of tributaries, e.g., the Salcha, Chena, Tanana, etc.]. For each of these systems, all upstream stream segments were grouped together and assigned a common management unit identifier. Additional tributaries not explicitly identified in ADFG’s management priorities were organized into units of comparable size or hydrological significance, including [insert remaining groupings here].

**Production estimates and time binning**

Basin-scale estimates of natal origin distribution were generated for each year by summing posterior probabilities across all individuals at each spatial location. To examine temporal patterns within the run, the dataset was divided into four temporal quartiles. The first quartile extended through June 11th, corresponding to the end of the front-end fishing closure on the Kuskokwim River. The second and third quartiles each spanned 10 days, while the final quartile included the remainder of the run. Minor variation in the duration of the fourth quartile occurred among years due to differences in run timing and length; however, these deviations were limited to a few days and represented a negligible portion of the overall CPUE. For each quartile, tributary-specific production estimates were normalized to sum to one, enabling visual comparison of the relative natal origin distribution within each quartile across the basin (Figure X). These values were then aggregated by management unit and rescaled to sum to one within each quartile. This process produced a five-point time series (Q0–Q4) for each year, where each value represents the relative contribution of a management unit *within* that specific quartile.

**Dynamic Factor Analysis**

To identify underlying temporal patterns in salmon run timing across management units, we applied Dynamic Factor Analysis (DFA) to management unit timeseries representing within-quartile proportions. DFA is a dimension-reduction technique that decomposes multivariate timeseries into a smaller number of underlying common trends, allowing us to identify shared patterns of variability among contributing metapopulations over time.

Our analysis examined the proportion each management unit contributed within each specific timing quartile across years (2017-2021). This metric captures how the relative contributions of different management units change within timing windows—revealing, for example, whether certain management units consistently contribute more during early-run periods while others are more prominent during late-run timing, and how these patterns vary from year to year.

We modeled each management unit's timeseries as a linear combination of *m* latent trends:

*y\_t = Z × x\_t + v\_t*

where *y\_t* represents the observed within-quartile proportions at time *t*, *Z* is a matrix of factor loadings indicating how strongly each management unit responds to each underlying trend, *x\_t* contains the *m* common trends, and *v\_t* represents observation error.

We fit a 4-state DFA model, which is reasonable given that there are four unique quartiles in our timing framework. We used a "diagonal and unequal" observation error variance structure because variance likely differs among management units due to the unequal spatial distribution of prediction error in the underlying isoscape across the basin. All models were fit using maximum likelihood estimation in the MARSS package in R. We checked model convergence and examined model residuals using autocorrelation function (ACF) plots to ensure model assumptions were met.

To enhance interpretability, we applied varimax rotation to the final model. This rotation produces factor loadings that reveal which management units respond similarly over time and trends that show the underlying temporal dynamics driving these co-varying patterns. We mapped the factor loadings onto spatial maps of the watershed to visualize the spatial distribution of relative contribution towards each of the four extracted underlying trends.

**Results:**

**Discussion:**