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Project Final Report

Using strontium isotopes in otoliths to determine natal origins, freshwater habitat use, and production patterns of Chinook salmon in the Yukon River

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ABSTRACT

It is currently unclear which regions of the Yukon River produce the most Chinook salmon and if the production from certain regions varies through time in response to changing environmental conditions. Also unknown is the extent to which different juvenile freshwater life history patterns are exhibited by returning adult salmon and how the relative expression of these changes year-to-year. This information, however, is crucial to the effective management and conservation of western Alaska Chinook salmon stocks.

Here, we developed a geospatial analytical framework that uses naturally occurring variation in strontium (Sr) isotope ratios ($^{87}Sr/^{86}Sr$) across the Yukon River to delineate natal origins, freshwater habitat use, and production patterns of Chinook salmon at relatively fine spatial scales. First, we built a predictive model using a new class of geostatistics designed for stream networks to analyze the spatial patterns in measured $^{87}Sr/^{86}Sr$ ratios across the Yukon River (180 different sites) to generate a river 'isoscape'. Within a geographical continuous Bayesian assignment framework, we used this isoscape model, and measurements of $^{87}Sr/^{86}Sr$ ratios recorded in otoliths, to determine the natal origins of adult Chinook salmon sampled at the river's terminus in 2010 (n=150), 2015 (n=250), and 2016 (n=250) during their return to the basin to spawn.

Chinook salmon production across the Yukon River was heterogenous for all return years analyzed. The spatial configuration of locations characterized by high and low production across the basin shifted substantially year-to-year. There was also an array of freshwater life histories that were expressed during each return indicating that juvenile Chinook salmon exploit a variety of different habitats to achieve the total amount of growth needed before migrating to the ocean. Overall, these results suggest that some habitats and populations can be disproportionately important to any given return year and highlight the need to design conservation and management frameworks that explicitly account for the shifting patterns in production across the Yukon River basin. The analytical framework developed here provides relevant information of Chinook salmon dynamics from relatively small spatial scales (e.g., individual tributaries) to large spatial scales (e.g., the major sub-basins of the Yukon). Currently, we do not have mechanistic understanding for why production patterns of the Yukon River shift through time, but analyses such as these conducted across a range of environmental conditions could provide key insights.

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I.INTRODUCTION

Chinook salmon populations have declined for more than a decade across western Alaska (ADF&G 2013, Schindler et al. 2013). The majority of the land surface area of the AYK (Arctic-Yukon-Kuskokwim) region is within the Yukon River basin, a vast watershed that supports commercially and socially important fisheries for Chinook salmon. Since 2000, the Alaska Board of Fisheries has listed the Yukon River Chinook as a stock of yield concern. Although it is clear that Yukon River Chinook salmon as a whole are declining, it remains unclear i) if all Yukon populations are declining at the same rate, ii) which sub-watersheds produce the majority of fish, and iii) whether the relative production from different tributaries varies through time. Also unknown is the range of freshwater life history strategies, and how the expression of these in returning adults changes through time. These questions are central to understanding the recent declines in Chinook salmon production across the region. They also represent critical insights needed for effective management and conservation in the face of increasingly uncertain futures due to the rapidly changing environments of the Arctic and Subarctic. The tools needed to accurately assess these questions, however, are lacking.

Over the last two decades, research has demonstrated that naturally occurring geochemical tracers recorded in the calcified structures of fish (e.g., otoliths) can be used to reconstruct a fish's natal origins (Kennedy et al. 1997, Campana and Thorrold 2001, Barnett-Johnson et al. 2008, Walther et al. 2008) and lifelong movement patterns (Koch et al. 1992, Kennedy et al. 2000, Hegg et al. 2013). These methods generally involve linking up the known variation of geochemical tracers in potential environments used by fish with their corresponding measurements in sequentially growing biogenic tissues (Elsdon et al. 2008). The otolith is the most commonly used structure to accomplish this because it grows incrementally via concentric rings of $CaCO_3$ (Campana 1999). Although the primary constituents of the otolith $CaCO_3$ mineral are calcium, carbon, and oxygen, other 2+ cations (e.g., the trace elements $Sr^{2+}$and Ba^{2+}) present within the ambient environment can substitute for Ca^{2+}. The incorporation of these trace elements into the otolith is primarily a reflection of the element-to-calcium ratios (e.g., Sr/Ca) of the ambient environment (Campana 1999). However, the incorporation of these non-calcium cations into the otolith is also regulated by physiology, ontogeny, and environmental parameters (Walther et al. 2010, Sturrock et al. 2015), the extent of which can also vary with species.

Arguably, the most powerful geochemical tracer is the ratio of two isotopes of the trace element strontium (Sr; denoted as $^{87}Sr/^{86}Sr$). Its power derives from the well-established fact that otolith $^{87}Sr/^{86}Sr$ ratios correspond to the ambient water $^{87}Sr/^{86}Sr$ ratios in which fish reside via a 1:1 relationship (Barnett-Johnson et al. 2008, Muhlfeld et al. 2012, Brennan et al. 2015a). Unlike trace element to calcium ratios in otoliths (e.g. Sr/Ca) (Campana 1999, Walther et al. 2010), $^{87}Sr/^{86}Sr$ ratios are not affected by physiological or environmental factors during incorporation of Sr. As such, otoliths provide an unadulterated $^{87}Sr/^{86}Sr$ history of each fish's entire life, and allow for the assessment of two fundamental ecological dimensions of anadromous fish populations: natal origins and life history patterns.

Although $^{87}Sr/^{86}Sr$ ratios have been used to study the ecology of numerous fish populations worldwide, their use in Alaska as of 2015 (when the project began) was limited to a few studies (Zimmerman et al. 2013, Brennan et al. 2015a, Brennan et al. 2015b). This was largely due to a paucity of data describing spatial variation in $^{87}Sr/^{86}Sr$ ratios across Alaska, especially in the Yukon River. Geological models of the $^{87}Sr/^{86}Sr$ variation across Alaska were available, but they were based on a limited number of $^{87}Sr/^{86}Sr$ measurements of rivers and their poor accuracy limited their application to isotope-based provenance studies of Pacific salmon (Bataille et al. 2014a, Brennan et al. 2014). Recent work on the Nushagak River during the last five years, however, has demonstrated a new analytical framework that integrates geostatistical models of $^{87}Sr/^{86}Sr$ ratios across rivers (Brennan et al. 2016) with $^{87}Sr/^{86}Sr$ ratios in otoliths to delineate fine scale natal origins (Brennan and Schindler 2017), life histories (Brennan et al. 2019a), and production dynamics of Chinook salmon (Brennan et al. 2019b). This project developed and applied this framework to the Yukon River basin.

The primary goal of this project was to develop a strontium isotopic map to delineate the natal origins and movement patterns of Chinook salmon throughout the Yukon River basin. Currently, the genetic structure of Chinook salmon stocks produced from within the Yukon River and of all Western Alaska Rivers is shallow, enabling the discrimination of only 7 unique reporting groups within the Yukon (Templin et al. 2008) and 3 across Western Alaska (Larson et al. 2014). As such, determination of the annual production of Chinook salmon from the Yukon is at a spatial scale much coarser than that of the individual stock-units producing fish. Determination of the relative production at smaller spatial scales (e.g., sub-basins or tributaries) within the Yukon River is currently not possible, primarily because no tools exist to answer this question.

It is well known that the total sum of habitat complexity and intra-specific biodiversity, which characterize salmon population structure, impart temporal stability to the overall annual production of salmon from a given region (Schindler et al. 2010, Brennan et al. 2019b). Schindler et al. (2010) showed that complete fishery closures would be 10 times the current frequency in Bristol Bay (one every 100 years) if the biocomplexity of sockeye salmon were collapsed down to one homogenous population. This analysis was made possible because individual populations contributing to the entire stock portfolio have been monitored in-stream and at the ocean-termini of the major watersheds since the 1940s. In the vast Yukon watershed, such research programs are prohibitive. However, returns of high-latitude Chinook salmon stocks, such as those in the AYK region, are substantially more reliable (less variable) than low-latitude stocks (Griffiths et al. 2014) suggesting there is substantial within-basin diversity in Yukon River Chinook salmon. Further, current genetic mixed stock analysis (MSA) techniques of Chinook salmon have been limited to coarse spatial scales due to the shallow genetic structure within the Yukon (DeCovich and Howard 2010, Larson et al. 2014). However, as demonstrated in the recent work completed in the Nushagak River, developing a robust $^{87}Sr/^{86}Sr$ map of all potential natal and rearing habitats in the Yukon, provides a complementary and accurate way to monitor the relative production of Yukon River Chinook salmon stocks throughout the entire basin. The ability to assign returning adults to their natal tributaries will greatly enhance efforts to construct accurate brood tables – which provide the foundation for sustainable harvests of salmon, and it will improve understanding of the role of population diversity in sustaining Chinook salmon fisheries in the Yukon River.

II. OBJECTIVES

Objective 1: Characterize the $^{87}Sr/^{86}Sr$ variation in waters from across the Yukon River.

Objective 2: Evaluate site-specific temporal variability in $^{87}Sr/^{86}Sr$ ratios across the Yukon River using the sedentary resident fish species, slimy sculpin (*Cottus cognatus*).

Objective 3: Generate geospatial model of $^{87}Sr/^{86}Sr$ ratios throughout Yukon River.

Objective 4: Determine the relative production of Chinook salmon from different tributaries of the Yukon River for the 2010, 2015 and 2016 return years.

Objective 5: Determine the freshwater life history patterns of adult Chinook salmon recruits caught in the lower Yukon River in 2010, 2015 and 2016.

III. METHODS

Characterization of the strontium isotope variation in water throughout the Yukon River

Water samples were collected from tributaries and main stem channels from across the Yukon River watershed (n = 180 different observation sites). Sites were chosen based on i) known spawning and rearing areas of Chinook salmon (Brown et al. 2017), ii) geologic heterogeneity, and iii) areas identified by a geospatial model of $^{87}Sr/^{86}Sr$ water ratios that need to be constrained due to poor model-performance (Bataille et al. 2014a, Brennan et al. 2014). Water samples were collected upstream of the collector in acid-washed 250 ml low-density polyethylene (LDPE) wide-mouth bottles. Within 48 hours of collection, each sample was filtered through a 0.45 mm Luer-lock syringe filter (polypropylene membrane) using a 50 cm^3 polypropylene syringe into a clean acid-washed 125 ml LDPE narrow-mouth bottle. Within a maximum of 16 days of collection, samples were acidified with 2 ml ultra pure concentrated HNO_3 (BDH Aristar Ultra). To evaluate consistency in field collection methods one every 10 samples were collected as a field triplicate. To evaluate contamination due to field collection methods, every tenth sampling-event we collected a blank in the field using the same methods as above, but using MilliQ water.

Site-specific temporal variability: Chena River as a detailed case study

To evaluate the influence of site-specific temporal variability in the Yukon River on using $^{87}Sr/^{86}Sr$ to reconstruct natal origins and life histories of Chinook salmon, we conducted a detailed study on the Chena River using a published high-resolution time-series of water

$^{87}Sr/^{86}Sr$ ratios from a location where we also collected slimy sculpin. The older fish (5 years or older) within this sample set were also living during the period covered during the time-series. The Chena River is also an ideal setting to evaluate the effect of site-specific temporal variability, because of its geologic and hydrologic setting. It drains some of the most radiogenic (i.e., high $^{87}Sr/^{86}Sr$ ratios) rocks of Alaska ($^{87}Sr/^{86}Sr$ ratios > 0.7300), which are juxtaposed to calcareous-rich rocks including limestone and marble, which when weathered should contribute Sr to river water with ratios close to the Precambrian to Paleozoic oceans $^{87}Sr/^{86}Sr$ ratios ~ 0.707-0.709. The basin is also characterized by discontinuous permafrost, which contributes to highly variable surface and groundwater flow paths among the summer and winter months. Previous research demonstrated a large seasonal signal in the $^{87}Sr/^{86}Sr$ ratios, where during the winter, river ratios were ~0.720 but during the summer these increased to ~0.725 (Douglas et al. 2013). This winter-time decrease was driven by increased carbonate weathering. The time-series within this paper spanned the years 2005-2006 and 2008-2009.

The 13 sculpin otoliths measured here were collected in 2013 at the same site of the time-series, plus two other sites within 5 km of the water sampling location (3-5 fish per site). The sculpin collected ranged in age from 1-7 years old (ages estimated using otoliths). Thus, the Chena River is an ideal place to evaluate site-specific variability as it represents a location where we would expect to see the largest degree of site-specific temporal variability. Furthermore, because of the time-series and otolith data available, it is particularly well-suited to address the questions of how site-specific temporal variability of river water is filtered through the lens of otolith chemistry and how it may influence our isotope-based geographic assignments.

Generating a strontium isotope geospatial assignment model for Chinook salmon

To build the strontium isotope geospatial model of the Yukon River (the river network 'isoscape'), we analyzed the water isotope measurements made throughout the basin using a new class of geostatistical models - Spatial Stream Network (SSN) models (Peterson and Ver Hoef 2010, Ver Hoef and Peterson 2010). We followed a similar modeling framework as was done for the Nushagak River (Brennan et al. 2016), and modeled variation in $^{87}Sr/^{86}Sr$ river water ratios as being driven by the percent upstream watershed area composed by different lithologies (e.g., young mafic rocks versus old felsic rocks). The geologic covariates tested during the SSN modeling of $^{87}Sr/^{86}Sr$ ratios were derived from the Global Lithological Map Database (GLiM) (Hartmann and Moosdorf 2012). This database is a globally consistent database that classifies rock types based on their geochemical, mineralogical, and physical properties. Specifically, using the custom STARS toolbox in ArcGIS (Peterson and Ver Hoef 2014) we calculated the percent area of all of the major lithological units within the Yukon basin (i.e., all units that compose >0.8% of the total land surface area within the basin) upstream of all sites with $^{87}Sr/^{86}Sr$ river water measurements. We also tested the mean upstream rock age as a covariate. This set of covariates were then used as the fixed effects within the spatial linear mixed modeling framework of SSNs.

An SSN model describes the extent to which a random variable, y (i.e., $^{87}Sr/^{86}Sr$ ratios), measured within a river network can be explained by a set of fixed effects, or covariates, and random effects. The below equation describes the general SSN model we used.

$$y = X\beta + z_{TU} + z_E + \epsilon,$$

X is a matrix of covariates, and $\beta$is a vector of parameters for each fixed effect included in the model. The random effects of the SSN models we tested were described by two different spatial autocorrelation functions, z_{TU} and z_E, which modeled the spatial autocorrelation among sites via flow-connections along the network (i.e., tail-up) and the straight-line (i.e., Euclidean) distance among sites, respectively. ϵ is the independent random error term. By modeling spatial autocorrelation in this way, SSN models consistently perform better than non-spatial models or models that only account for Euclidean spatial autocorrelation during out of sample prediction and when predicting unsampled locations (e.g., kriging) (Brennan et al. 2016, Ver Hoef 2018). Both of which are particularly important when developing an isoscape. SSN models require clean stream network topologies, which we generated and have made publicly available through one of our recent AYK SSI-funded projects (Whited et al. 2018). The resulting model is a map of predicted Sr isotope ratios of river waters throughout the network.

Because of the 1:1 relationship between river water and otolith $^{87}Sr/^{86}Sr$ ratios (Kennedy et al. 1997, Barnett-Johnson et al. 2008, Brennan et al. 2015a, Brennan et al. 2015b), we turned the river water isoscape into a map of the predicted isotopic compositions of otoliths synthesized at any location within the Yukon River. This was done by assuming otolith $^{87}Sr/^{86}Sr$ ratios recorded at a location were equal to the river water ratios predicted at that location, plus random error (Wunder 2010, Brennan and Schindler 2016). This procedure allowed us to transparently incorporate the principal variance-generating processes that affect how the isotopic composition in river water is reflected in otoliths synthesized at any site (e.g., within population variance), and our ability to predict the correct river water isotope ratio (i.e., isoscape prediction error). This forms the basis of an analytical framework that can determine the natal origins of individual adult Chinook salmon captured in the lower river fishery but bound for some unknown tributary within the Yukon River basin. The analytical procedure used here is described in detail in Brennan and Schindler (2017).

Quantifying the spatial production patterns of Chinook salmon across the Yukon River

Otoliths were collected from individual adult Chinook salmon harvested during the Lower Yukon Test Fishery (LYTF) for years 2010 (n=150), 2015 (n=424), and 2016 (n=250). Samples were collected by the Alaska Department of Fish and Game. Adult Chinook salmon in each year of the project were sampled over the course of the entire run. Our target sample size of otolith measurements was 250 fish per year. Thus, we analyzed all fish from the 2010 and 2016 sample. In 2015, we took a stratified random sample of the 424 fish to get a total sample for otolith analyses of 250 fish.

We used otolith chemistry and river isoscapes to reconstruct the production patterns of the 2017 Chinook salmon run returning to the Yukon River (Brennan and Schindler 2016). The sagittal otoliths from each return year were dissected in the field and stored dry until sectioning and isotope analysis. Fork length and sex of the fish were noted, and a tissue sample was collected for archival purposes for future genetics analysis. All otoliths collected were sectioned in the transverse plane with a low-speed Isomet saw and polished with 1μm aluminum powder. Prior to isotopic analyses, otoliths were sonicated for five minutes in MilliQ water, rinsed, and dried in a laminar flow hood. $^{87}Sr/^{86}Sr$ ratios of Chinook salmon otoliths were measured from the otolith core towards the otolith's edge of each individual otolith using laser ablation (LA) (193 nm Excimer Laser, Photo Machines) multi-collector inductively coupled plasma mass-spectrometry (MC-ICPMS) at the University of Utah, Department of Geology and Geophysics ICPMS laboratory. By measuring the $^{87}Sr/^{86}Sr$ ratio from the core towards the edge of the otolith - a transect which was perpendicular to the otolith growth axis - we were able to determine both i) the natal stream of origin, and ii) the entire freshwater life history of juvenile Chinook salmon before their migration to the ocean. Thus, each 87Sr/86Sr profile encompasses the otolith core, the entire freshwater residence, and migration into the marine environment. Based on previous work in the Nushagak River (Brennan et al. 2015b) we considered the freshwater residence within each otolith to be the region between the distal extant of the core (~ 250 μm from primordia) and the distal extent of the 1st annulus (i.e., before marine migration). Specifically, we determined the freshwater residence portion of each transect by inspecting i) the $^{87}Sr/^{86}Sr$ ratio profile, ii) the corresponding 88Sr intensity (V) profile, and iii) superimposing transects on respective otolith images (taken in reflected light).

To reconstruct production patterns, the $^{87}Sr/^{86}Sr$ ratios of otoliths recorded in the natal region were computed for all fish and then used to determine the natal origin of each individual using a geographically continuous Bayesian assignment framework (Wunder 2010, Brennan and Schindler 2017). For each fish, we calculated the probability of origin for all locations within the entire potential spatial domain from which it could have originated (assumed to be the entire river basin). The locations with the highest probabilities corresponded to the most likely natal source region of each fish based on isotope data. Thus, for each fish we generated a probability surface, or map, across the river basin.

The probability maps of all Chinook salmon analyzed for each return year (2010, 2015, and 2016) were then summed to reconstruct the relative production of each location relative to all other locations in the basin. For each return year, we assessed whether our sample was in proportion to the catch per unit effort (CPUE) over the course of the entire run. If it was not, then we split the run into time strata and weighted each stratum to account for the imbalance between otolith sampling and CPUE. The samples from the 2010, 2015, and 2016 return years were not in proportion to CPUE over the course of each respective run. Thus, we split the run into strata (ranging from 3-5 days per stratum depending on the year) and calculated weights for each stratum, which were computed as the ratio of the mean proportion of CPUE for each stratum to the mean proportion of otoliths sampled (daily otoliths sampled/daily catch). We then weighted each fish's natal origin map by their corresponding stratum weight. Doing so allowed us to account for the fact that different populations likely enter the system at different times during the run.

Integrating isotopes and genetics

Although not explicitly one of the objectives of this specific project, in 2015 and 2016, we also collected tissue samples for genetic analyses from the same individuals from which we collected otoliths. Although the Chinook salmon genetic structure is shallow within the Yukon River, genetic techniques are able to distinguish populations at broad geographic scales. For example, Lower Yukon River populations are distinguishable from the Canadian Upper Yukon River populations (Templin et al. 2008, DeCovich and Howard 2010, Larson et al. 2014).

Using these samples, we built a new analytical framework that integrates genetics and isotopes to delineate natal origins of Chinook salmon and reconstruct interannual production patterns across the Yukon. This framework and its findings are reported in a related recent final report to the AYK SSI (Brennan et al. 2019c).

Life history variation

Because we measured the $^{87}Sr/^{86}Sr$ ratios during each fish's entire juvenile freshwater residence prior to migrating to the ocean, we also inferred general assessments of life history variation of Yukon River Chinook salmon. These general assessments were made in a similar way to (Brennan et al. 2015b) and identified patterns of natal site-fidelity, non-natal habitat use, and forays in the Lower Yukon River prior to moving into the ocean. Natal site-fidelity is inferred from a $^{87}Sr/^{86}Sr$ profile that does not change during freshwater residence. Non-natal habitat use of fish was inferred by $^{87}Sr/^{86}Sr$ profiles that show distinct departures from a fish's natal $^{87}Sr/^{86}Sr$ ratio prior to entering the ocean. Fish that exhibited forays in the lower river prior to ocean entrance, where identified by changes in the $^{87}Sr/^{86}Sr$ ratios towards ratios characteristic of the lower Yukon River main stem proximate to the end of freshwater residence.

IV. RESULTS

$^{87}Sr/^{86}Sr$ ratios across the Yukon River

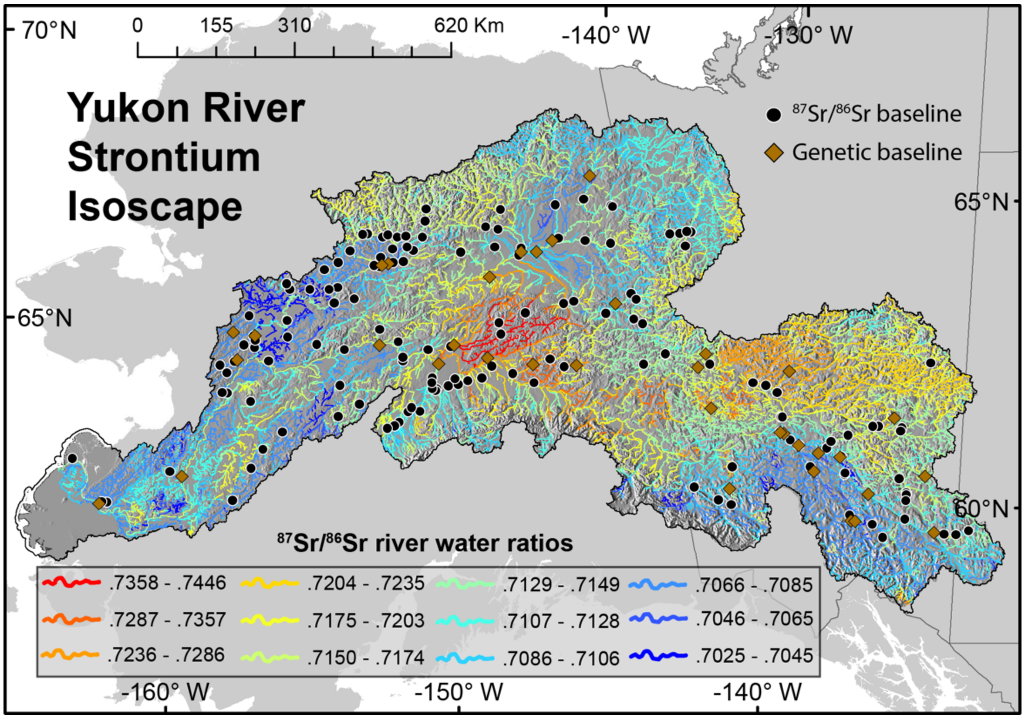
The range of $^{87}Sr/^{86}Sr$ ratios measured from across the Yukon River was 0.70537-0.74463, which is a large range in the $^{87}Sr/^{86}Sr$ ratio. This range is much greater than the range found in the Nushagak and Kuskokwim rivers, where we have also been developing strontium isoscapes (Brennan et al. 2016). Analytical uncertainty for water isotope ratios was ±0.00002 2SE (standard error). Within-site $^{87}Sr/^{86}Sr$ variability among individual juvenile Chinook salmon captured at the same locations within river systems as measured via laser ablation of otoliths is ±0.00031 2SD (standard deviation) (Brennan et al. 2015b, Brennan and Schindler 2017). Thus, the above isotopic range within the Yukon River is approximately 130-times larger than within-site variability as estimated by otoliths of fish captured at the same location. This affords ample power to distinguish isotopically distinct habitats using $^{87}Sr/^{86}Sr$ ratios recorded in the otoliths of Chinook salmon in the Yukon River.

Yukon River $^{87}Sr/^{86}Sr$ isoscape

The SSN model with the best out-of-sample predictive performance (estimated via leave-one-out cross validation) had a root mean square prediction error (RMSPE) of ±0.0028 (Figure 1). This means the total range in observed ratios (above) within the basin was approximately 15-times greater than the uncertainty associated with isoscape prediction, affording ample power for the isoscape to delineate natal origins of individual fish. This RMSPE is substantially larger than the isoscapes of the Nushagak and Kuskokwim Rivers, which were also generated using SSNs (RMSPE=0.00051 and RMSPE=0.00048, respectively) (Brennan et al. 2016) (Brennan and Schindler 2019). That said, the RMSPE of all of these models is more comparable when the total range in isotope ratios within each system is considered. For example, the observed range within the Nushagak and Kuskokwim is ~20 times greater than the prediction error of their respective isoscape models. Furthermore, the Yukon River is a much larger basin, draining approximately 900,000 km^2. It is also characterized by a larger degree of geologic heterogeneity and complexity, as reflected in its isotopic range. Although the model was fit with 180 observation sites, kriging across a network as vast as the Yukon resulted in a large range in prediction errors across all sites (0.0001-0.0067 in the $^{87}Sr/^{86}Sr$ ratio). The lowest prediction errors always occur proximate to observation sites and only 25% of locations within the network had prediction errors less than 0.0033 (the 25% quantile of prediction errors of all locations). The total number of locations with isotope predictions made via kriging in the Yukon was 20,989 (the number of unique stream reaches within the network).

As covariates, the top Yukon isoscape models all included rock age and several different lithological classes. Consistently included in top models were the geologic units of the older, continentally derived (and therefore more felsic in composition) meta-sedimentary units associated with the progressive growth of the North American continental margin during the Precambrian to the Mesozoic (e.g., mt____ and mtpu__ in the GLiM). These are situated in the Yukon-Tanana Uplands between the Denali and Tintina Faults (Colpron et al. 2007, Brennan et al. 2014). The highest $^{87}Sr/^{86}Sr$ ratios were observed in tributaries draining these lithologies (e.g., the Chatanika River and Beaver Creek). The models also consistently included geologic units that were younger and more mafic in composition, such as the mafic siliciclastic and igneous Cretaceous to Cenozoic volcanic and plutonic rocks situated in the western portions of the basin in the lower river and also the southern portions of the Upper Yukon basin (e.g., vi____ and pi____ in GLiM). The rivers draining these regions had the lowest $^{87}Sr/^{86}Sr$ ratios measured in the basin (e.g., the Dakli and Takhini Rivers).

Figure 1: $^{87}Sr/^{86}Sr$ isoscape of the Yukon River generated using Spatial Stream Network (SSN) models. Streamlines are color coded on the basis of the predicted $^{87}Sr/^{86}Sr$ ratio of river water. Black-filled circles are locations where we measured $^{87}Sr/^{86}Sr$ ratios in river water. Brown diamonds denote locations of the genetic baseline.



All of the best performing models included both a tail-up and Euclidean spatial autocorrelation model, and geologic terrane as random effects. The former two model the spatial dependency in the residuals in flow-connected and 2-dimensional space, respectively. Because dissolved Sr and its isotopic composition act as conservative tracers of passive particles being transported downstream, we only considered the tail-up spatial autocorrelation functions when modeling spatial dependency in the network. This allowed us to account for the mixing processes that are occurring throughout the network as water and dissolved constituents are routed downstream. The Euclidean autocorrelation functions were able to model the finer scale variation in isotope ratios that was most likely due to geologic processes and heterogeneity present across the landscape not described by the GLiM geospatial database or rock ages.

The geologic terrane random effect through which a river carves was also consistently selected in the top models. Geologic terranes delineate distinct landforms that have a shared tectonic evolution (Colpron et al. 2007). This is an important consideration for $^{87}Sr/^{86}Sr$ ratios of rivers that route through large sedimentary and metamorphic lithological units that typically span across multiple distinct geologic terranes (e.g., those of the GLiM across the Yukon). Although the unit may share principal lithological similarities, differences in the recycling history of sedimentary and metamorphic rock units among different terranes can drive large differences in

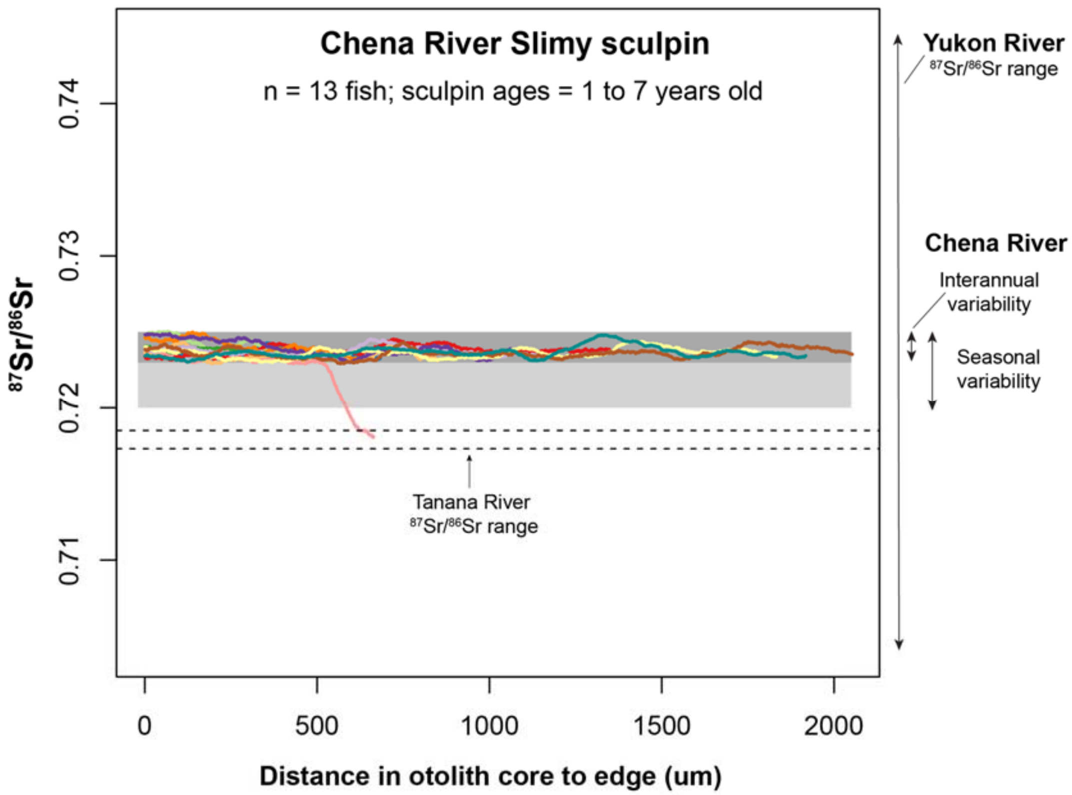
^{87}Sr/^{86}Sr ratios of bedrock and rivers (Arth 1994, Bataille et al. 2014b). The importance of accounting for these geologic and tectonic processes in our SSN models is reflected in the fact that all models that included terrane as a random effect outperformed models that did not (based on RMSPE, but also AIC too).

The model selected for the isoscape presented here and used in subsequent analyses included the following covariates: mean rock age, percent mt____, percent vi____, percent smpyvr, percent ssmxcl, per ssmx__, and percent pi____. It included a Linear-Sill tail-up and Gaussian Euclidean autocovariance (Ver Hoef and Peterson 2010) and terrane as random effects. The covariates explained 44% of the variation, tail-up 25%, Euclidean 18%, and the terrane random effect explained 12%. The remaining independent random error accounted for <0.1% of the variation.

Chena River: a case study of ^{87}Sr/^{86}Sr site-specific variation

The range of ^{87}Sr/^{86}Sr ratios recorded in individual sculpin lifelong (1-7 years old) profiles ranged from 0.0004-0.0019 (Figure 2). These ranges do not include the range from the single fish that showed ratios near the edge of its otolith that dropped well below any of the measured water values from the Chena River (Douglas et al. 2013) (Figure 2). The lifelong ^{87}Sr/^{86}Sr profiles of all other fish fell entirely within the interannual range of measured ^{87}Sr/^{86}Sr ratios of river water. This individual's ^{87}Sr/^{86}Sr profile likely does not reflect site-specific temporal variability, but instead reflects fine scale movements among isotopically different habitats. A plausible hypothesis is that this individual moved into habitats that were influenced by the Tanana River (^{87}Sr/^{86}Sr ratios = 0.7173-0.7185). There are multiple sloughs near our sampling locations that originate from the Tanana River and connect the Tanana and Chena River floodplains. Groundwater upwelling could also be a source of water that is characteristic of Tanana River ^{87}Sr/^{86}Sr ratios, as the sampling locations were within the connected floodplains. Both scenarios involve fine scale spatial variability that is relevant to the scale of movements and habitat use of slimy sculpin (Brennan et al. 2015a). That said, 12 out of the 13 fish measured appear to reflect the site-specific temporal variability as filtered through the lens of otolith chemistry, which is clearly weighted towards isotope ratios characteristic of the warmer summer months when fish are growing (Figure 2).

Figure 2: Life-long $^{87}Sr/^{86}Sr$ records of slimy sculpin otoliths collected from the Chena River (n=13 fish) compared to the total range across the Yukon (i.e., the scale of y-axis). Different colored lines indicate individual fish. The gray boxes correspond to the seasonal range of $^{87}Sr/^{86}Sr$ ratios observed in river water over the course of two two-year long time series of water measurements (made ~ twice per month) (Douglas et al. 2013). The dark gray box corresponds to the interannual variability of the summer period.

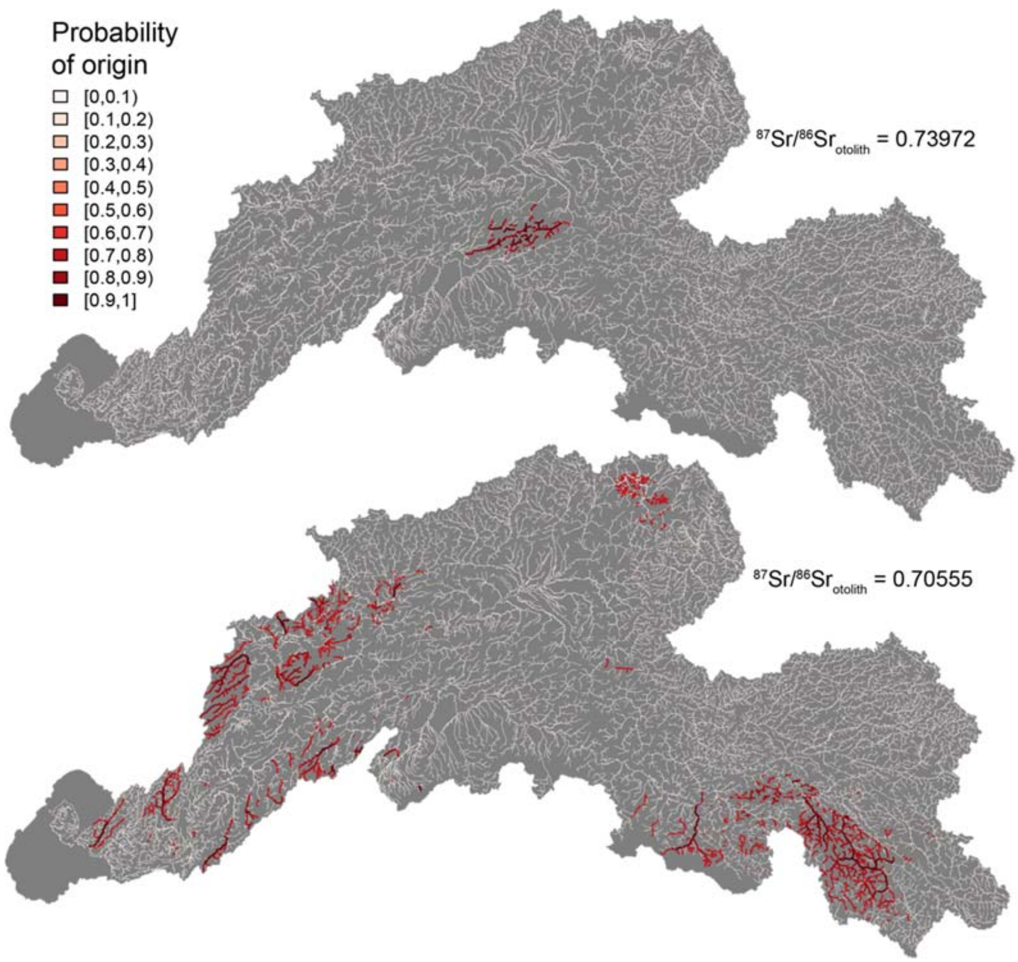


Spatial production patterns of 2010, 2015 and 2016 Chinook salmon returns to the Yukon River

The $^{87}Sr/^{86}Sr$ ratios recorded in the natal region of the otolith indicate that fish originate and use a wide range of habitats within the basin. Using the isoscape in Figure 1 and otolith measurements we were able to determine the natal origin of each individual Chinook salmon with relatively high precision, sometimes to a single tributary. Because of the large range in kriging prediction errors across the basin, during geographic assignment, we set all locations with a prediction error less than the 25% quantile (0.0033) to have a prediction error of this value. Not doing so results in probability surfaces that only determine locations near observation sites as probable, which is unrealistic. We think this is the most conservative approach to capturing the uncertainty in the model's ability to determine the true natal origin given isotope data.

The precision (i.e., the spatial scale of likely locations relative to entire basin) of isotope-based assignments depended on the isotope ratio. Some ratios were able to determine single tributaries as a fish's natal origin (Figure 2 top panel), whereas other ratios exhibited substantial geographic overlap (Figure 2 bottom panel). This overlap is due to isotopic similarities on the landscape (e.g., the blue colored stream lines in Figure 1).

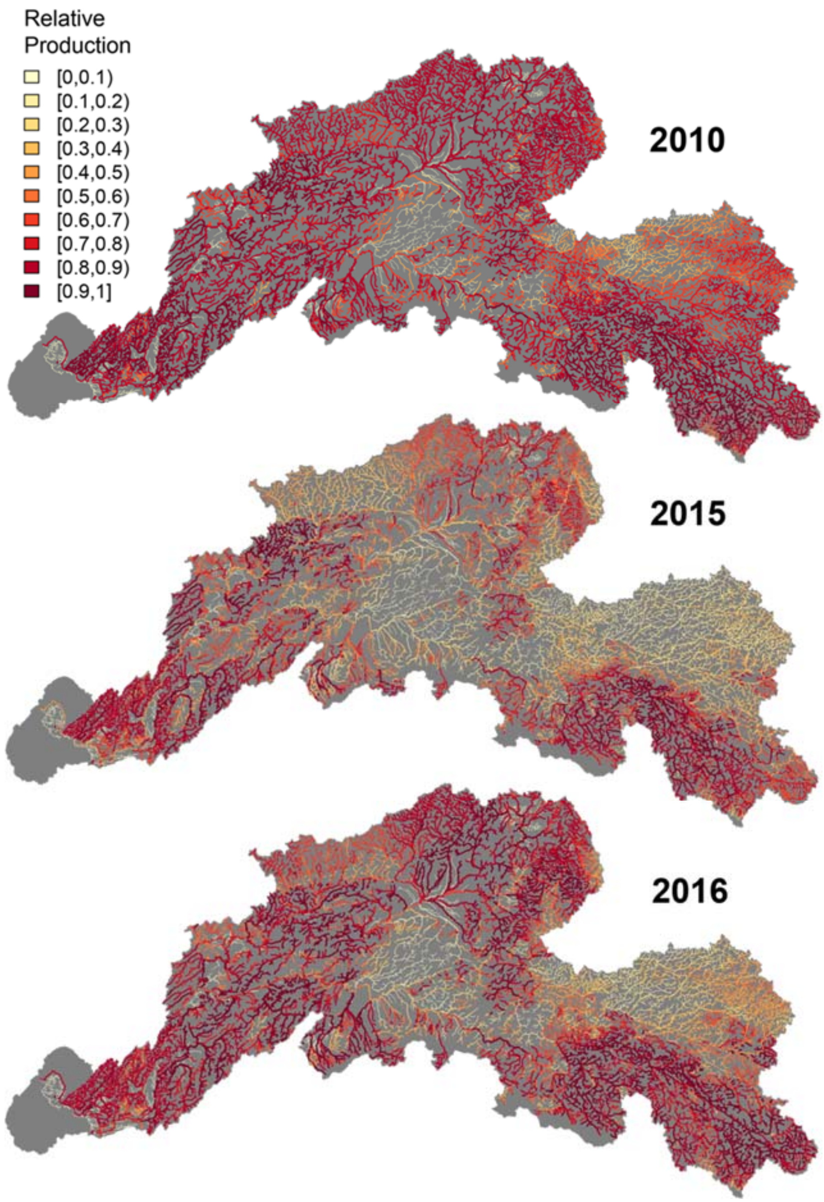
Figure 3: Probability of origin of two individual adult Chinook salmon caught in the Emmonak Test Fishery (only showing locations with probabilities >0.70). The $^{87}Sr/^{86}Sr$ ratio of each fish is shown. In the top panel, the isotope-based assignment model determined the most likely natal origin to be the Chatanika River north of Fairbanks, AK (the dark red streamlines). The bottom panel shows a fish where the isotope model determined the fish was just as likely to be from tributaries of the Lower Yukon as the southern tributaries of the Upper Yukon.



Overall, the large amount of isotopic variability that does exist across the Yukon enabled relatively fine scale estimates of natal origins of individual fish (Figure 3). As a result, the model also generated relatively fine scale estimates of the spatial pattern in production across the basin for each return year (Figure 4).

Production for all return years was heterogeneously distributed across the river basin. However, the spatial configuration of locations characterized by high and low Chinook salmon production shifted interannually. In 2010, the production pattern was more evenly distributed across the basin, except from tributaries such as the Chatanika River and Beaver and Birch creeks, which produced few fish. In 2015, locations of relatively high production shifted to rivers with low isotope ratios, such as those ratios characteristic of tributaries draining into the Lower Yukon River (e.g., Innoko, Gisasa, Anvik, and Andreafsky rivers) and the southern tributaries of the Upper Yukon in Canada (e.g., Takhini, Nordenskiold, and M'Clintock rivers). The spatial production pattern in 2016 was similar to 2015, however tributaries with intermediate isotope ratios (e.g., Chandlar, Porcupine, and Teslin rivers) increased in their relative production. The tributaries with the highest and most unique $^{87}Sr/^{86}Sr$ ratios, such as the Chatanika River, were not represented in the Emmonak Test Fishery in 2010 and 2015 (Figure 5). In 2016, however, at least three fish had radiogenic ratios consistent with the Chatanika River (>0.738) (Figure 5).

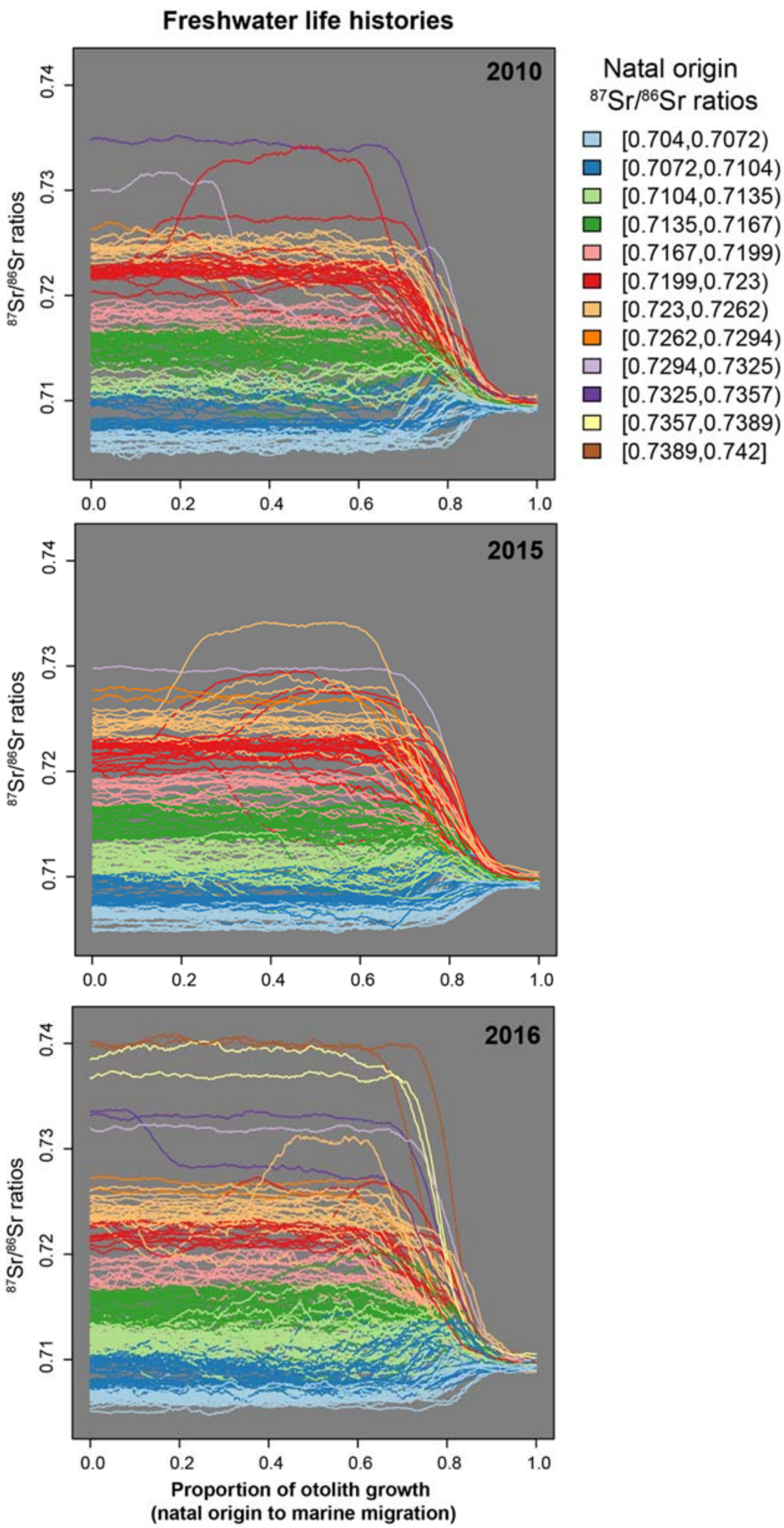
Figure 4: Spatial production patterns of Chinook salmon returning to the Yukon River in 2010, 2015, and 2016.



Freshwater life history variation of Yukon River Chinook salmon

For all return years (2010, 2015, and 2016), the $^{87}Sr/^{86}Sr$ profiles recorded in the freshwater growth region of Chinook salmon indicated that individual fish exhibited an array of freshwater life histories before migrating to the ocean (Figure 5). Many Yukon River fish exhibited site-fidelity to their natal origin during their entire freshwater residence, which is illustrated by the flat $^{87}Sr/^{86}Sr$ ratios of some fish recorded during this time. However, many fish showed profiles that suggest multiple habitats were used to achieve the total amount of freshwater growth needed prior to their seaward migration. For example, in each return year, numerous individuals migrated into non-natal habitats, as indicated by fish in Figure 5 that trace into isotopically different environments from their natal site (i.e., profiles that start at one color and then trace into different color bands). The extent to which fish used non-natal habitats differed among years as well. For example, more of the fish that originated at ratios between 0.720-0.723 (the red lines in Figure 2) migrated into non-natal habitats (i.e., the red lines cross into different color bands) to achieve large fractions of their total freshwater growth in 2015 as compared to the 2010 and 2016 return years. Furthermore, a large fraction of fish from each return year used the main stem Yukon River to achieve a portion of the freshwater growth prior to migrating to the ocean. This is evident in fish with isotope profiles that show distinct shifts towards the Yukon River mainstem ratios ($^{87}Sr/^{86}Sr$ = 0.7130-0.7140) just prior to entering the ocean (e.g., many of the the blue lines in Figure 5 show such forays). These same general life history patterns were also found in Chinook salmon of the Nushagak River (Brennan et al. 2015b, Brennan et al. 2019b).

Figure 5: Variation in freshwater life histories is reflected in the $^{87}Sr/^{86}Sr$ profiles recorded in the freshwater growth region of Chinook salmon otoliths.



V.DISCUSSION

$^{87}Sr/^{86}Sr$ ratios as a new analytical tool to manage and conserve Yukon River Chinook salmon

This project produced a new analytical framework for identifying the natal origins, life histories, and production patterns of Yukon River Chinook salmon. The framework is based on the variation in $^{87}Sr/^{86}Sr$ ratios across the basin. It relies on a geospatial model that predicts $^{87}Sr/^{86}Sr$ ratios across the network and integrates this model with measured $^{87}Sr/^{86}Sr$ ratios in otoliths.

Previous work has shown that this approach can accurately and precisely (i.e., accuracies of >90% for precisions <4%) determine the correct natal origins of known origin juvenile Chinook salmon (Brennan and Schindler 2017). Furthermore, our detailed case study of site-specific temporal variability in $^{87}Sr/^{86}Sr$ ratios in the Chena River shows that even in a system known to exhibit large seasonal variation, this variability is not reflected in the otoliths of the sedentary fish living in the river. The lifelong variability recorded in the otoliths of slimy sculpin (1-7 years old), instead, fell within the range of the observed interannual variability of the system (Figure 2). The magnitude of this variability is largely negligible compared to the among-site isotopic variation across the Yukon River (Figure 2) and the uncertainty associated with isoscape predictions, which is accounted for in the natal origin assignment model. These findings are consistent with other studies in Alaska (Brennan et al. 2015a, Brennan and Schindler 2017) and further highlight that the interannual scale is the most important temporal scale to evaluate and constrain isotopic variability, especially when using $^{87}Sr/^{86}Sr$ ratios to determine natal origins of fish returning in different years. The case study on the Chena River and previous work on the Nushagak River suggests that $^{87}Sr/^{86}Sr$ ratios are relatively stable at this scale.

With respect to production patterns, the isotope-based geographic assignment framework essentially samples the entire basin by delineating the natal origins of hundreds of individual fish (Figure 3 and 4) intercepted by the Lower Yukon Test Fishery during their migration to some unknown upstream location within the basin. By aggregating all of these natal origin maps from fish sampled over the course of the run, we can then reconstruct the spatial pattern in production across the basin at fine spatial scales. A power analysis used to evaluate this approach's ability to determine the correct population size (i.e., the proportion of total annual return) across a range of potential population sizes (proportions ranging from 0.01-0.99) given a sample size of n=250 fish determined that the error in our population size estimates ranged from ±0.015-0.032 (Brennan et al. 2019b). Thus, the smallest proportion of the total run that could be resolved was approximately 0.02. Given this level of uncertainty, the isotope-based framework produced here has ample power to quantify how Chinook salmon production is distributed across the basin annually.

The two principal limitations of the isotope-based assignment model presented here relate to isotopic overlap of geographically disparate tributaries (e.g., Figure 1 and Figure 3, bottom panel), and the relatively large prediction errors of the isoscape model during kriging. We have improved the former significantly by integrating the isotope baseline with existing genetic baselines across the Yukon River to further refine the natal origin assignments of individual Chinook salmon. What genetic structure exists across the Yukon is highly complementary to the isotopic variation across the system. We report these finding and resulting framework in a related final report to AYK SSI (Brennan et al. 2019c).

The limitation concerning the large prediction errors during kriging is inherent to building a geostatistical model of a 900,000 km^2 basin. Prior to this project only a handful of $^{87}Sr/^{86}Sr$ ratio measurements existed in the Yukon River basin (~5 sites total). The baseline now includes measurements at 180 different sites. Nonetheless, in comparison to the Nushagak (100 sites; 35,000 km^2 basin) and the Kuskokwim (120 sites; 124,000 km^2) rivers, where we have developed similar isoscape models, the Yukon River baseline sampling density is approximately an order of magnitude lower. Thus, it is likely that increasing the number of measurements across the basin would improve the model's performance substantially. Furthermore, the large portion of variation that was explained by the tail-up random effect model, which models the mixing processes as Sr is routed downstream, also suggests that the kriging model would improve from sampling aimed at downstream locations within the network from current observation sites. The current baseline focused on characterizing all known spawning locations in headwater reaches. Any future sampling efforts that focused on measurements made downstream as tributaries flow into larger order streams would improve model performance significantly. Updating the baseline and incorporating new measurements into the model is straightforward given that the geospatial data products and modeling framework is now in place.

Ultimately, given the large range of isotopic variability across the Yukon, the current isoscape model has ample power to delineate natal origins of individual fish and reconstruct interannual production patterns at relatively fine spatial scales (Figure 3 and 4).

Production of Chinook salmon across the Yukon River

The shifting spatial patterns in production of Chinook salmon across the Yukon River (Figure 4) reflect the fact that different parts of the basin are disproportionately important to the total return of fish year-to-year. This is shown in the shifts in production among the 2010, 2015, and 2016 return years, where some tributaries that were relatively productive one year, such as the tributaries characterized by intermediate to high $^{87}Sr/^{86}Sr$ ratios (>0.714) in 2010, can experience relatively large decreases in production in following years, especially in 2015.

The Yukon River basin is a complex mosaic of habitats whose conditions vary across space and time as landscape features (e.g., topography) filter the overriding environmental forcing of the region. This means that optimal biological conditions for fish communities tend to shift across the basin through time (Stanford et al. 2005, Armstrong and Schindler 2013, Baldock et al. 2016). The locally adapted populations of Chinook salmon that spawn and rear throughout the entire basin must respond and adapt to the ever-changing spatial configuration of conditions produced by the dynamics of shifting habitat mosaics. Currently, we do not have a mechanistic understanding for why some habitats are more productive than others for any given year. However, we do know that watersheds with an intact portfolio of habitat spread the risk of poor performance or low production across the entire riverscape, its locally adapted populations, and variable life histories (Schindler et al. 2010, Brennan et al. 2019b).

With only three years of data for the Yukon River, we do not have the ability to assess how freshwater conditions influence interannual variability in fish returns to the basin. With additional years of data, using the analytical framework and geospatial data products developed by this project, it may be possible to constrain interannual variability in production across the Yukon River and potentially its key environmental drivers. In the Nushagak River, these shifting patterns in production were not random across the basin and appeared to be driven by the multiscale climate forcing of environmental variables, such as the amount of precipitation, snowpack, and air temperature, which influence biologically important features of riverscapes for fish (e.g., stream flow and stream temperature) (Brennan et al. 2019b). Currently, AYK SSI has funded projects (including this one) to reconstruct production patterns of the 2010 and 2015-2018 return years using the analytical framework presented here and in a related report. Continuing this time-series across a range of environmental conditions, especially in the face of ongoing climate change, will provide critical insights into Chinook salmon dynamics of western Alaska and their effective conservation into the future.

VI.REFERENCES

ADF&G, C. R. T. 2013. Chinook salmon stock assessment and research plan, 2013. **Special Publication No. 13-01**.

Armstrong, J. B., and D. E. Schindler. 2013. Going with the Flow: Spatial Distributions of Juvenile Coho Salmon Track an Annually Shifting Mosaic of Water Temperature. Ecosystems **16**:1429-1441.

Arth, J. G. 1994. Isotopic composition of the igneous rocks of Alaska.*in* G. Plafker, Berg, H.C., editor. The Geology of Alaska. Geological Society of America, The Geology of North America, Boulder, Colorado.

Baldock, J. R., J. B. Armstrong, D. E. Schindler, and J. L. Carter. 2016. Juvenile coho salmon track a seasonally shifting thermal mosaic across a river floodplain. Freshwater Biology **61**:1454-1465.

Barnett-Johnson, R., T. E. Pearson, F. C. Ramos, C. B. Grimes, and R. B. MacFarlane. 2008. Tracking natal origins of salmon using isotopes, otoliths, and landscape geology. Limnology and Oceanography **53**:1633-1642.

Bataille, C. P., S. R. Brennan, J. Hartmann, N. Moosdorf, M. J. Wooller, and G. J. Bowen. 2014a. A geostatistical framework for predicting variations in strontium concentrations and isotope ratios in Alaskan rivers. Chemical Geology **389**:1-15.

Bataille, C. P., S. R. Brennan, J. Hartmann, N. Moosdorf, M. J. Wooller, and G. J. Bowen. 2014b. A geostatistical framework to predict strontium isotopes variations in Alaska Rivers. Chemical Geology **389**:1-15.

Brennan, S. R., T. J. Cline, and D. E. Schindler. 2019a. Quantifying habitat use of migratory fish across riverscapes using space-time isotope models. Methods in Ecology and Evolution **10**:1036-1047.

Brennan, S. R., D. P. Fernandez, G. Mackey, T. E. Cerling, C. P. Bataille, G. J. Bowen, and M. J. Wooller. 2014. Strontium isotope variation and carbonate versus silicate weathering in rivers from across Alaska: Implications for provenance studies. Chemical Geology **389**:167-181.

Brennan, S. R., D. P. Fernandez, C. E. Zimmerman, T. E. Cerling, R. J. Brown, and M. J. Wooller. 2015a. Strontium isotopes in otoliths of a non-migratory fish (slimy sculpin): Implications for provenance studies. Geochimica Et Cosmochimica Acta **149**:32-45.

Brennan, S. R., and D. E. Schindler. 2016. Linking otolith microchemistry and dendritic isoscapes to map heterogeneous production of fish across river basins. Ecological Applications.

Brennan, S. R., and D. E. Schindler. 2017. Linking otolith microchemistry and dendritic isoscapes to map heterogeneous production of fish across river basins. Ecological Applications **27**:363-377.

Brennan, S. R., and D. E. Schindler. 2019. Quantifying Chinook salmon production at fine spatial scales and mercury concentrations in resident fish across the Kuskokwim River. Arctic-Yukon-Kuskokwim Sustainable Salmon Iniative.

Brennan, S. R., D. E. Schindler, T. J. Cline, T. E. Walsworth, G. Buck, and D. P. Fernandez. 2019b. Shifting habitat mosaics and fish production across river basins. Science **364**:783-786.

Brennan, S. R., L. W. Seeb, and D. E. Schindler. 2019c. Integrating genetics with otolith chemistry to reconstruct production patterns of Chinook salmon throughout the Yukon River. Arctic-Yukon-Kuskokwim Sustainable Salmon Iniative.

Brennan, S. R., C. E. Torgersen, J. P. Hollenbeck, D. P. Fernandez, C. K. Jensen, and D. E. Schindler. 2016. Dendritic network models: Improving isoscapes and quantifying influence of landscape and in-stream processes on strontium isotopes in rivers. Geophysical Research Letters **43**:5043-5051.

Brennan, S. R., C. E. Zimmerman, D. P. Fernandez, T. E. Cerling, M. V. McPhee, and M. J. Wooller. 2015b. Strontium isotopes delineate fine-scale natal origins and migration histories of Pacific salmon. Sci Adv **1**:e1400124.

Brown, R. J., A. von Finster, R. J. Henszey, and J. H. Eiler. 2017. Catalog of Chinook Salmon Spawning Areas in Yukon River Basin in Canada and United States. Journal of Fish and Wildlife Management **8**:558-587.

Campana, S. E. 1999. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Marine Ecology Progress Series **188**:263-297.

Campana, S. E., and S. R. Thorrold. 2001. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? Canadian Journal of Fisheries and Aquatic Sciences **58**:30-38.

Colpron, M., J. L. Nelson, and D. C. Murphy. 2007. Northern Cordilleran terranes and their interactions through time. GSA Today **17**.

DeCovich, N. A., and K. G. Howard. 2010. Genetic Stock Identification of Chinook Salmon Harvest on the Yukon River 2009. Alaska Department of Fish and Game **Fishery Data Series No. 10-58**.

Douglas, T. A., J. D. Blum, L. D. Guo, K. Keller, and J. D. Gleason. 2013. Hydrogeochemistry of seasonal flow regimes in the Chena River, a subarctic watershed draining discontinuous permafrost in interior Alaska (USA). Chemical Geology **335**:48-62.

Elsdon, T. S., B. K. Wells, S. E. Campana, B. M. Gillanders, C. M. Jones, K. E. Limburg, D. H. Secor, S. R. Thorrold, and B. D. Walther. 2008. Otolith chemistry to describe movements and life-history parameters of fishes: Hypotheses, assumptions, limitations and inferences. Oceanography and Marine Biology: An Annual Review, Vol 46 **46**:297-+.

Griffiths, J. R., D. E. Schindler, J. B. Armstrong, M. D. Scheuerell, D. C. Whited, R. A. Clark, R. Hilborn, C. A. Holt, S. T. Lindley, J. A. Stanford, and E. C. Volk. 2014. Performance of salmon fishery portfolios across western North America. Journal of Applied Ecology **51**:1554-1563.

Hartmann, J., and N. Moosdorf. 2012. The new global lithological map database GLiM: A representation of rock properties at the Earth surface. Geochemistry Geophysics Geosystems **13**.

Hegg, J. C., B. P. Kennedy, P. M. Chittaro, and R. W. Zabel. 2013. Spatial structuring of an evolving life-history strategy under altered environmental conditions. Oecologia **172**:1017-1029.

Kennedy, B. P., J. D. Blum, C. L. Folt, and K. H. Nislow. 2000. Using natural strontium isotopic signatures as fish markers: methodology and application. Canadian Journal of Fisheries and Aquatic Sciences **57**:2280-2292.

Kennedy, B. P., C. L. Folt, J. D. Blum, and C. P. Chamberlain. 1997. Natural isotope markers in salmon. Nature **387**:766-767.

Koch, P. L., A. N. Halliday, L. M. Walter, R. F. Stearley, T. J. Huston, and G. R. Smith. 1992. Sr Isotopic Composition of Hydroxyapatite from Recent and Fossil Salmon - the Record of Lifetime Migration and Diagenesis. Earth and Planetary Science Letters **108**:277-287.

Larson, W. A., J. E. Seeb, C. E. Pascal, W. D. Templin, and L. W. Seeb. 2014. Single-nucleotide polymorphisms (SNPs) identified through genotyping-by-sequencing improve genetic stock identification of Chinook salmon (Oncorhynchus tshawytscha) from western Alaska. Canadian Journal of Fisheries and Aquatic Sciences **71**:698-708.

Muhlfeld, C. C., S. R. Thorrold, T. E. McMahon, and B. Marotz. 2012. Estimating westslope cutthroat trout (Oncorhynchus clarkii lewisi) movements in a river network using strontium isoscapes (vol 69, pg 906, 2012). Canadian Journal of Fisheries and Aquatic Sciences **69**:1129-1130.

Peterson, E. E., and J. M. Ver Hoef. 2010. A mixed-model moving-average approach to geostatistical modeling in stream networks. Ecology **91**:644-651.

Peterson, E. E., and J. M. Ver Hoef. 2014. STARS: An ArcGIS Toolset Used to Calculate the Spatial Information Needed to Fit Spatial Statistical Models to Stream Network Data. Journal of Statistical Software **56**:1-17.

Schindler, D. E., R. Hilborn, B. Chasco, C. P. Boatright, T. P. Quinn, L. A. Rogers, and M. S. Webster. 2010. Population diversity and the portfolio effect in an exploited species. Nature **465**:609-612.

Schindler, D. E., C. C. Krueger, P. Bisson, M. Bradford, B. Clark, J. Conitz, K. Howard, M. Jones, J. Murphy, K. Myers, M. Scheuerell, E. C. Volk, and J. Winton. 2013. Arctic-Yukon-Kuskokwim Chinook Salmon Research Action Plan: Evidence of Decline of Chinook Salmon Populations and

Recommendations for Future Research. AYK Sustainable Salmon Initiative (Anchorage, AK) **v + 70 pp.**

Stanford, J. A., M. S. Lorang, and F. R. Hauer. 2005. The shifting habitat mosaic of river ecosystems. Int Ver Theor Angew **29**:1123-1136.

Sturrock, A. M., E. Hunter, J. A. Milton, R. C. Johnson, C. P. Waring, C. N. Trueman, and E. Leder. 2015. Quantifying physiological influences on otolith microchemistry. Methods in Ecology and Evolution **6**:806-816.

Templin, W. D., N. A. DeCovich, and L. W. Seeb. 2008. Genetic Stock Identification of Chinook salmon Harvest on the Yukon River 2006. Alaska Department of Fish and Game **Fishery Data Series No. 08-15**.

Ver Hoef, J. M. 2018. Kriging models for linear networks and non-Euclidean distances: Cautions and solutions. Methods in Ecology and Evolution **9**:1600-1613.

Ver Hoef, J. M., and E. E. Peterson. 2010. A Moving Average Approach for Spatial Statistical Models of Stream Networks. Journal of the American Statistical Association **105**:6-18.

Walther, B. D., M. J. Kingsford, M. D. O'Callaghan, and M. T. McCulloch. 2010. Interactive effects of ontogeny, food ration and temperature on elemental incorporation in otoliths of a coral reef fish. Environmental Biology of Fishes **89**:441-451.

Walther, B. D., S. R. Thorrold, and J. E. Olney. 2008. Geochemical signatures in otoliths record natal origins of American shad. Transactions of the American Fisheries Society **137**:57-69.

Whited, D., S. R. Brennan, and D. E. Schindler. 2018. 2018 Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative Project Final Report. Arctic-Yukon-Kuskokwim Sustainable Salmon Iniative.

Wunder, M. B. 2010. Using Isoscapes to Model Probability Surfaces for Determining Geographic Origins. Pages 251-270 *in* J. B. West, G. J. Bowen, T. E. Dawson, and K. P. Tu, editors. Isoscapes: Understanding Movement, Pattern, and Process on Earth Through Isotope Mapping. Springer, Berlin, Germany.

Zimmerman, C. E., H. K. Swanson, E. C. Volk, and A. J. R. Kent. 2013. Species and Life History Affect the Utility of Otolith Chemical Composition for Determining Natal Stream of Origin for Pacific Salmon. Transactions of the American Fisheries Society **142**:1370-1380.

VII.DELIVERABLES

Geospatial data products:

1) Strontium isoscape and baseline of the Yukon River
2) Spatial production pattern of the 2010, 2015, and 2016 Chinook salmon return years to the Yukon River

Eight semi-annual reports were generated over the course of this project documenting the progress of our work over time:

1) SAPR #1515 SchindlerJun-Dec2015
2) SAPR #1515 SchindlerJan-Jun2016
3) SAPR #1515 SchindlerJul-Dec2016
4) SAPR #1515 SchindlerJan-Jun2017
5) SAPR #1515 SchindlerJul-Dec2017
6) SAPR #1515 SchindlerJan-Jun2018
7) SAPR #1515 SchindlerJul-Dec2018
8) SAPR #1515 SchindlerJan-Jun2019

Several oral presentations on this work were delivered at international, national and regional meetings over the course of this project:

Brennan, S.R. and Schindler, D.E. (Jan 2020) *Invited plenary talk*. Shifting habitat mosaics of free-flowing rivers and the conservation of Pacific salmon in an uncertain future. *Upper Columbia Science Conference, 2020, Wenatchee, WA.*

Brennan, S.R. and Schindler, D.E. (Dec 2019) *Oral presentation*. Shifting habitat mosaics of free-flowing rivers and fish production in an uncertain future. *American Geophysical Union, Fall Meeting 2019, San Francisco, CA.*

Brennan, S.R. and Schindler, D.E. (Sep 2019) *Oral presentation*. Shifting habitat mosaics and salmon production across Alaska's largest rivers. *American Fisheries Society and Wildlife Society Joint Conference, 2019, Reno, NV.*

Brennan, S.R. (March 2019) *Invited speaker*. Shifting habitat mosaics and salmon production across Alaska's largest rivers. *2019 Early Career Scientists Symposium, University of Michigan.* Theme: "Stable Isotopes in Ecology, Evolution, and Conservation."

Brennan, S., Schindler, D., French, D., Whited, D. (Spring 2018) *Invited talk*. "Strontium isoscapes as a tool to quantify production dynamics and life history variation of Yukon and Kuskokwim Chinook salmon", Session: Understanding the drivers of Chinook salmon decline in western Alaska & exploring new approaches to sustainable salmon management & stakeholder engagement. *American Fisheries Society, Western Division 2018 Annual Meeting, Anchorage, AK.*

Brennan, S. (Spring 2018) *Invited talk*. "Spatial Stream Network models and isoscapes", Session: Spatial-stream-network (SSN) models: Recent technical advances and a diversifying set of applications. *American Fisheries Society, Western Division 2018 Annual Meeting, Anchorage, AK.*

Brennan, S., Schindler, D. (Spring 2018) *Invited talk.* "Quantifying habitat use of anadromous fish using space-time isotope models", Session: Evolving methods for specifying anadromous waters in Alaska. *American Fisheries Society, Western Division 2018 Annual Meeting, Anchorage, AK.*

French, D., Brennan, S., Whited, D., Schindler, D. (Spring 2018) *Invited talk.* "Controls on the spatial variation of mercury in the Kuskokwim River", Session: Spatial-stream-network (SSN) models: Recent technical advances and a diversifying set of applications. *American Fisheries Society, Western Division 2018 Annual Meeting, Anchorage, AK.*

Schindler, D. (Spring 2018) *Invited talk.* "The regional and global significance of Alaska's rivers and their fisheries. Plenary presentation." *American Fisheries Society, Western Division 2018 Annual Meeting, Anchorage, AK.*

We published four related papers integral in building the analytical framework produced here for the Yukon River:

Brennan, S.R., Schindler, D.E., Cline, T.J., Walsworth, T.E., Buck, G., Fernandez, D.P. (2019) Shifting habitat mosaics and fish production across river basins. *Science*. 364 (6442), 783-786.

Brennan, S.R., Cline, T.J., Schindler, D.E. (2019) Quantifying habitat use of migratory fish across riverscapes using space-time isotope models. *Methods in Ecology & Evolution.* 10, 1036-1047.

Brennan, S. R., and D. E. Schindler (2017) Linking otolith microchemistry and dendritic isoscapes to map heterogeneous production of fish across river basins. *Ecological Applications.* 27:363-377.

Brennan, S. R., C. E. Torgersen, J. P. Hollenbeck, D. P. Fernandez, C. K. Jensen, D. E. Schindler (2016) Dendritic network models: Improving isoscapes and quantifying influence of landscape and in-stream processes on strontium isotopes in rivers. *Geophysical Research Letters.* 43:5043-5051

VIII. PROJECT DATA

The geospatial data products produced here: (i) the strontium isoscape, and (ii) 2010, 2015, and 2016 production maps, and the associated data to generate these products will be stored in the University of Washington Alaska Salmon Program database. Access to these data will be made available upon request, and after the data and associated maps have been published in peer-reviewed journals.

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X. PRESS RELEASE

We have modified a press release related to our recent paper in *Science* that discusses overall results of our three final reports to AYK SSI in 2019.

Press release below:

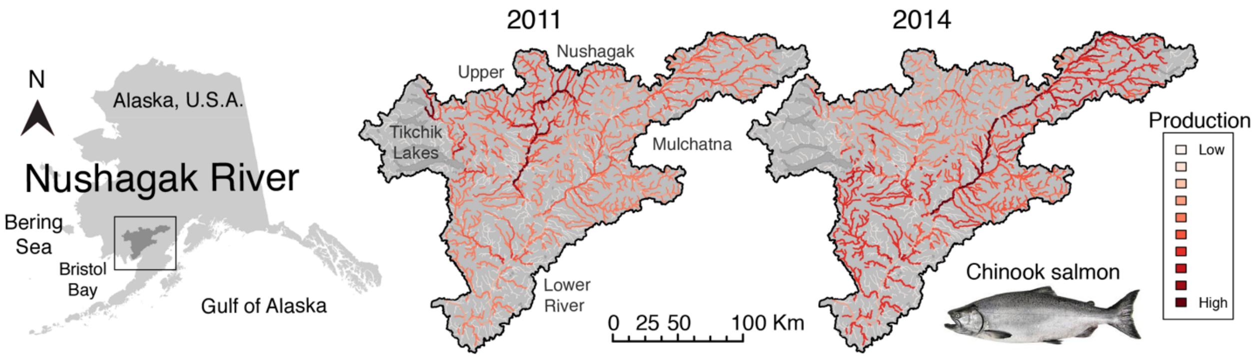
Hot spots of salmon production shift across Western Alaska's largest rivers and stabilize the region's critical fisheries

Chemical signatures imprinted on tiny stones that form inside the ears of fish show that Alaska's most productive salmon populations, and the fisheries they support, depend on the entire watershed and the diversity of populations and habitats represented at the ecosystem scale.

Chinook salmon born in the Yukon and Kuskokwim rivers, and sockeye and Chinook salmon of the Nushagak River and their network of streams, rivers, and lakes in western Alaska use the whole basin for spawning. As juveniles they use these habitat networks for the best places to find prey, shelter and safety from predators. From birth until the fish migrate to the ocean a year later is a critical period for young salmon to eat and grow.

By analyzing each fish's ear stone — called an otolith — scientists have found that different parts of these large watersheds are hot spots for salmon production and growth, and these favorable locations change year to year depending on how climate conditions interact with local landscape features like topography to affect the value of habitats.

A new study, led by the University of Washington, appeared May 24, 2019 in Science. This study quantified how Chinook and sockeye salmon production shifts across the Nushagak River basin (Figure 1).



<u>Figure 1:</u> Hot spots of Chinook salmon production shift across the Nushagak River basin year to year. The Nushagak's portfolio of habitats, life histories, and locally adapted populations makes the fisheries of this region more reliable [redrawn from Brennan et al., *Science* 364, 783-786, (2019)]

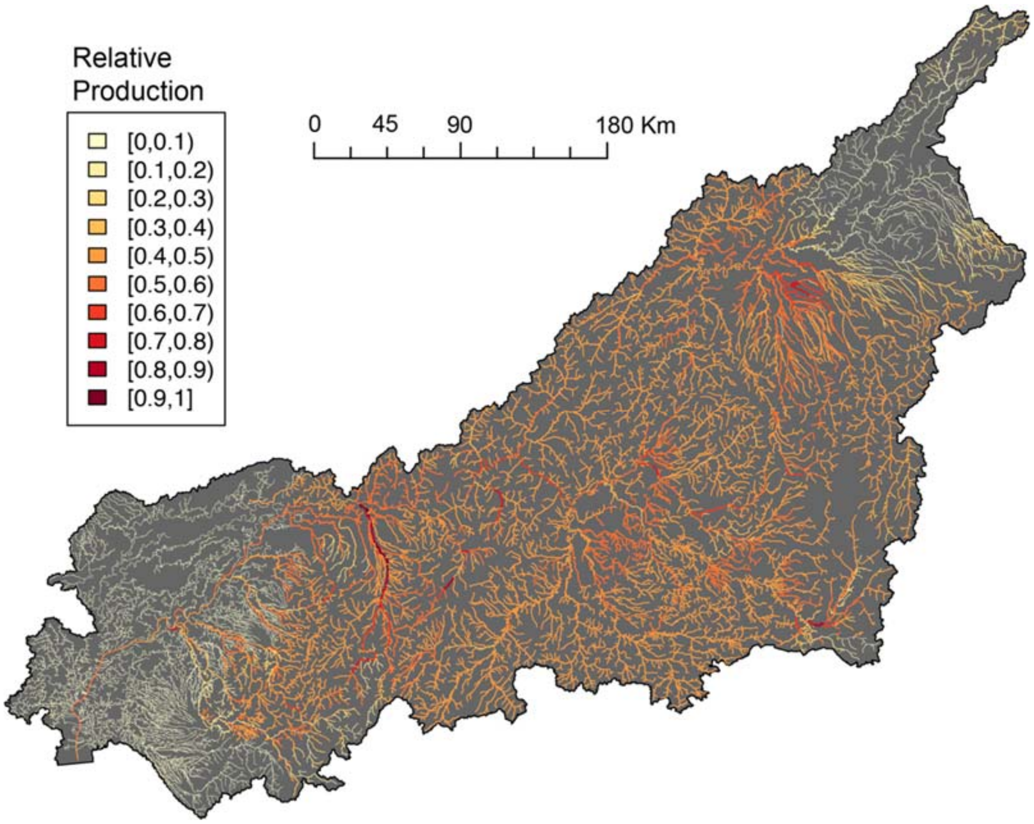
The research team, with funding from the AYK-SSI, has developed and applied this analytical framework to quantify how Chinook salmon production shifts across the Yukon and Kuskokwim rivers as well. In all three of these vast rivers systems, the production of salmon is patchy across the landscape. Some habitats are more productive than others for any given year (see Figure 1-3).

"We found that the areas where fish are born and grow flicker on and off each year in terms of productivity," said lead author Sean Brennan, a postdoctoral researcher at the UW School of Aquatic and Fishery Sciences. "Habitat conditions aren't static, and optimal places shift around. If you want to stabilize fish production over the years, the only strategy is to keep all of the options on the table."

The Yukon, Kuskokwim, and Nushagak river watersheds are the largest river basins in western Alaska. Together, these basins support the production of approximately 50 percent of the wild Chinook salmon globally.

The new *Science* study on the Nushagak, plus the ongoing studies in the Yukon and Kuskokwim, show that key salmon habitat shifts year to year, and how productive one area is for a short period might not represent its overall value to the fish population or larger ecosystem.

<u>Figure 2:</u> Results showing the spatial pattern of production of Chinook salmon across the Kuskokwim River from the 2017 return. The production is not spread evenly across the basin.



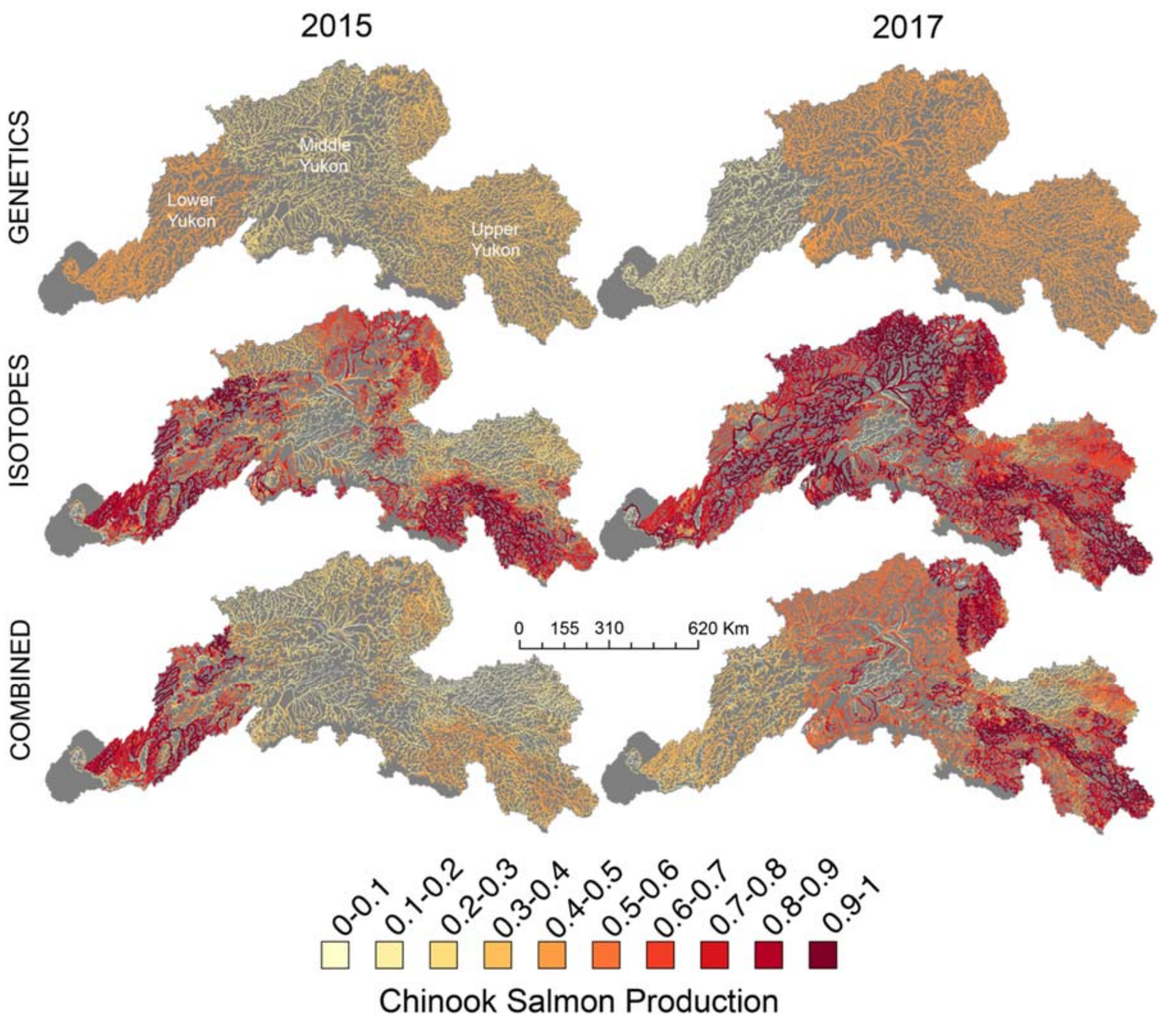
"The overall system is more than just the sum of its parts, and small pieces of habitat can be disproportionately important," said senior author Daniel Schindler, a professor at the UW School of Aquatic and Fishery Sciences. "The arrows point to the need to protect or restore at the entire basin scale if we want rivers to continue to function as they should in nature." The ecosystem is relatively stable because different stocks originating from areas of the watershed compensate for each other's booms and busts.

The research team has reconstructed the likely geographic locations of nearly 3,650 adult salmon (~250 fish per species per river per year) from their birth in a Yukon, Kuskokwim, or Nushagak stream until they migrated to the ocean. These annual production estimates span from 2010-2018 in the Yukon, 2017-2018 in the Kuskokwim, and 2011-2015 in the Nushagak. By looking at each fish's otolith — which accumulates layers as the animal grows — researchers can tell where the fish lived by matching the chemical signatures imprinted on each "growth ring" of the otolith with the chemical signatures of the water in which they swam.

These chemical signatures come from isotopes of the trace element strontium, found in bedrock. Strontium's isotopic makeup varies geographically from one tributary to another, particularly in the Yukon and Kuskokwim basins, making it easy to tell where and when a fish spent time.

"The otolith is this natural archive that basically provides a transcript of how a fish moved downstream through the river network," Schindler said. "Essentially, we're sampling the entire watershed and letting the fish tell us where the habitat conditions were most productive in that year."

Figure 3: Yukon River results showing the spatial pattern of production of Chinook salmon across the Yukon River from the 2015 and 2017 return years. The different rows correspond to quantifying the spatial pattern of production using different methods (only genetics, only isotopes, and combining genetics and isotopes). The genetics-only maps depict the proportion of production for each year, whereas the isotope-only and combined maps are scaled by the maximum relative production value.



In the Yukon River, the team is integrated both genetic and isotopic analyses to delineate the birth place of Chinook salmon (Figure 3). Combining these two natural tags provided much more fine scale and detailed information about the birth place of individual salmon than using any one of these two tags alone.

Results from the Kuskokwim River (Figure 2) and the Yukon River (Figure 3) support the results reported in the May 24 study in *Science* on the Nushagak River salmon ecosystem. Entire riverscapes are involved in producing Chinook salmon. When the biocomplexity of free-flowing rivers, and the processes that maintain it through time, remain intact – the critical fisheries of the region are more reliable. In the Nushagak, the researchers noticed significant shifts in production patterns when comparing where fish lived year to year (Figure 1). The ongoing projects in the Yukon and Kuskokwim are quantifying how these shifts play out in these other large river basins.

Similar types of shifts have been documented in a number of land- and water-based animal populations, but these studies on the Yukon, Kuskokwim, and Nushagak are the first to show the phenomenon at a watershed-wide scale, the authors said.

"The big thing we show is these types of dynamics are critical for stabilizing biological production through time. When you have a range of habitat available, the total production from the system tends to be more stable, reliable and resilient to environmental change," Brennan said.

The Yukon and Kuskokwim studies have been funded by the Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative (AYKSSI). The Nushagak study was funded by Bristol Bay Regional Seafood Development Association, the Bristol Bay Science Research Institute and the AYKSSI.

Chinook salmon drying at a fish camp along the Kuskokwim River. *Photo credit*: Janessa Esquible, Orutsararmiut Native Council

A fish camp on the Kuskokwim River. *Photo credit*: Janessa Esquible, Orutsararmiut Native Council