PRESS RELEASE

October 23, 2019

# 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.**

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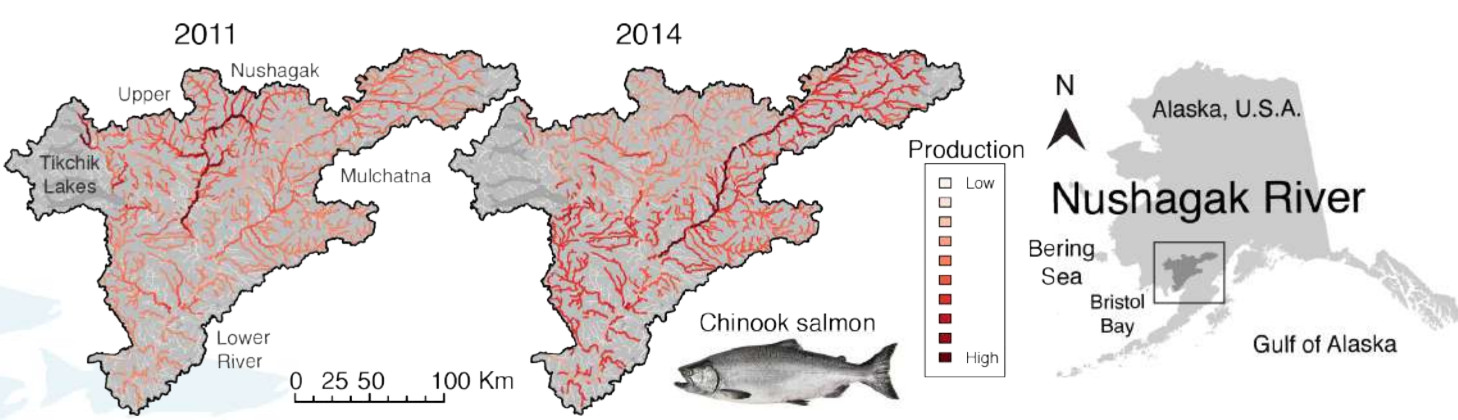
Chinook salmon born in the Yukon and Kuskokwim rivers, and sockeye and Chinook salmon of the Nushagak River and their network of streams, rivers, and lakes in western Alaska use the whole basin for spawning. As juveniles they use these habitat networks for the best places to find prey, shelter and safety 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).

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 2-5).

"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."




**<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 Yukon, Kuskokwim, and Nushagak river watersheds are the largest river basins in western Alaska. Together, these basins support the production of approximately 80 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.

"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. This also has important implications for the fisheries of these river basins because it leads to more stable harvests year-to-year (Figure 2).

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.

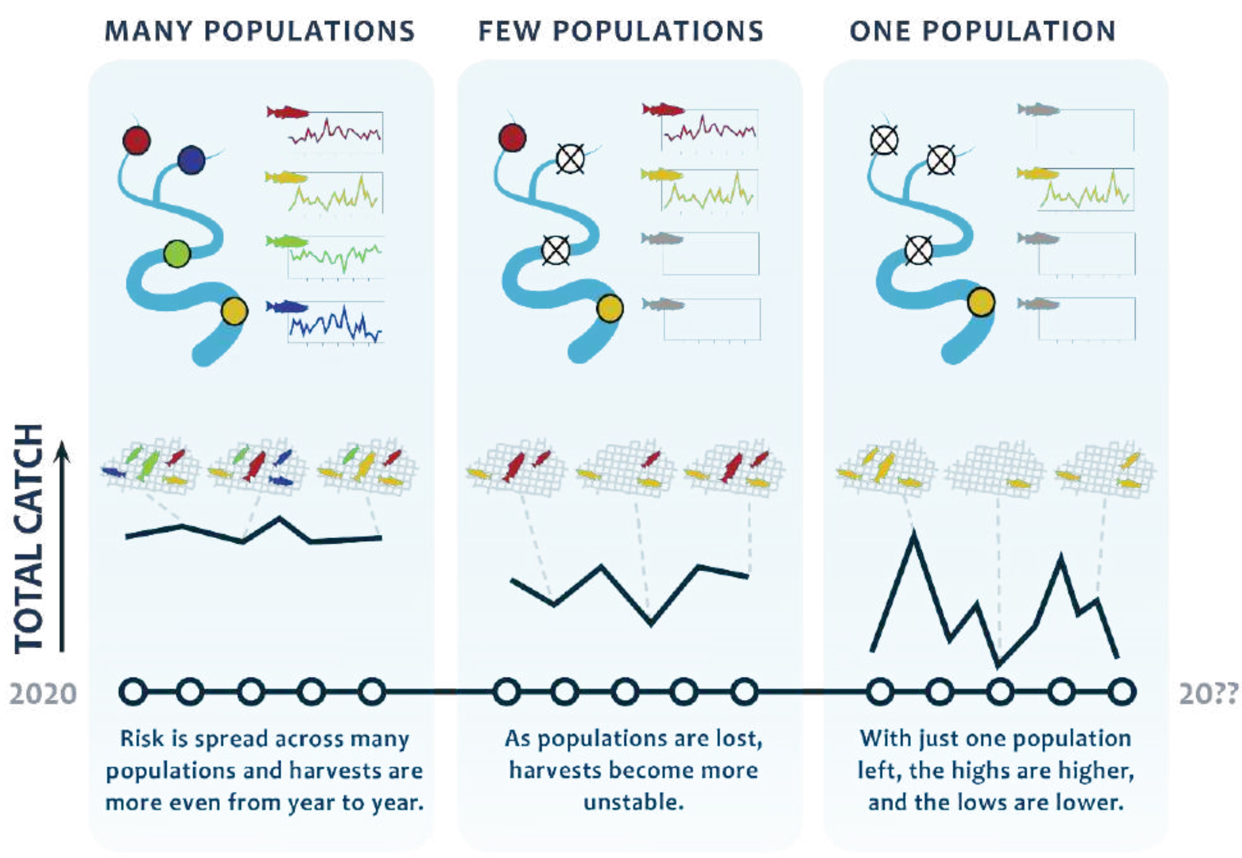



**Figure 2: Illustration of how population diversity contributes to harvest stability. When diversity is high, individual populations doing very well can compensate for those that are doing badly, leading to a more stable average harvest over time. When diversity is low, all your eggs are in one basket and so harvest is more unpredictable from year to year**

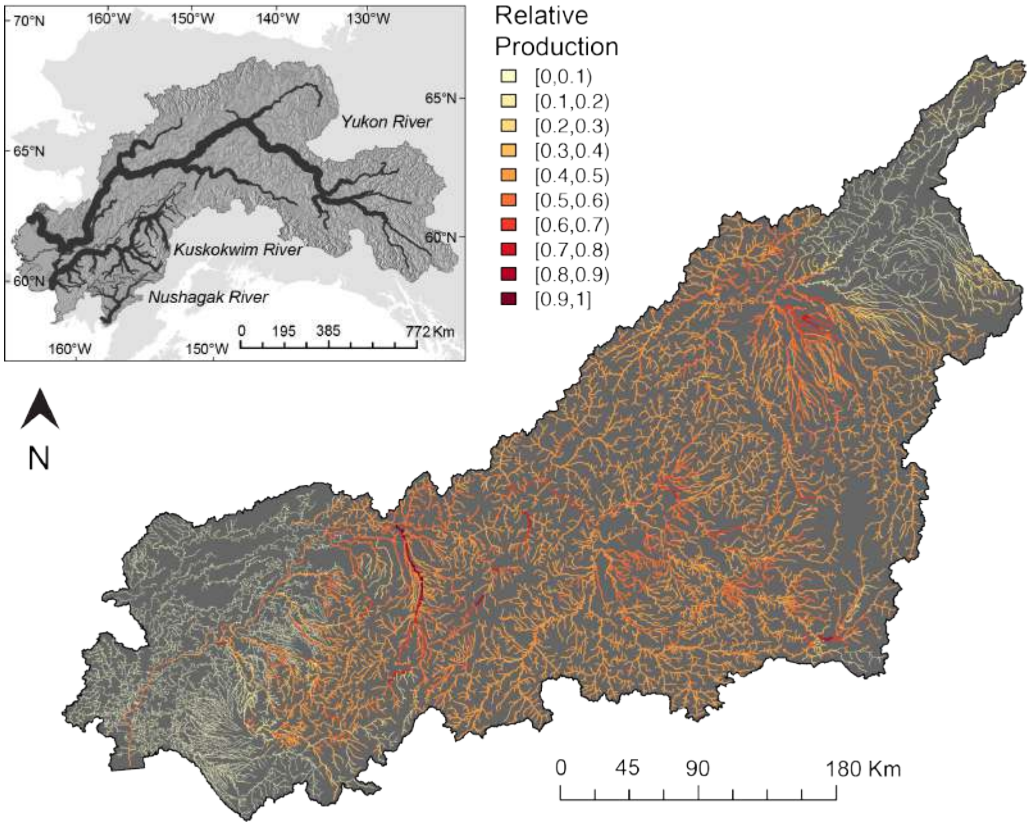



**Figure 3:** Results showing the spatial pattern of production of Chinook salmon across the Kuskokwim River from the 2017 return. The production is not spread evenly across the basin

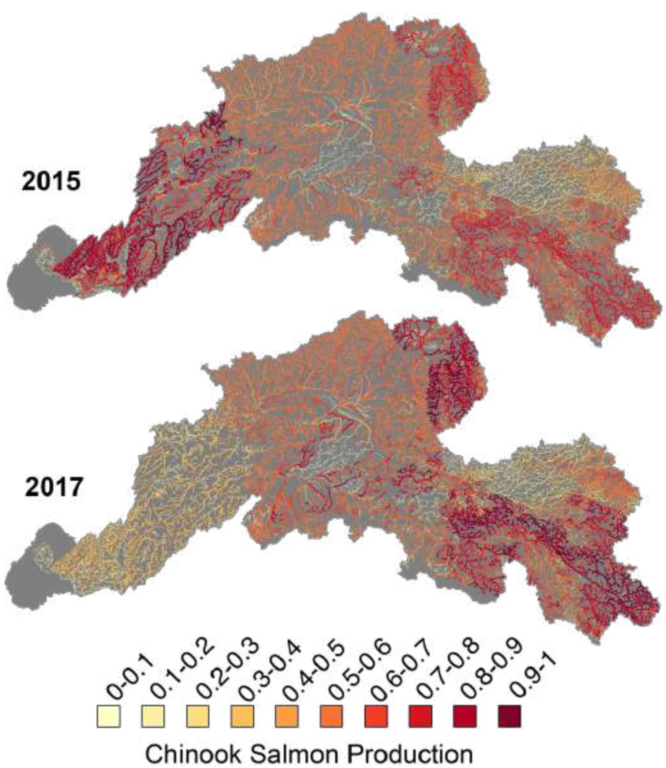



**Figure 4: Shifts in the spatial pattern of Chinook salmon production among return years in the Yukon River basin. These estimates are based on the run composition up to the peak of each run.**

"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."

In the Yukon River, the team has integrated both genetic and isotopic analyses to delineate the birth place of Chinook salmon (Figure 4 and 5). 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 3) and the Yukon River (Figure 4) 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.

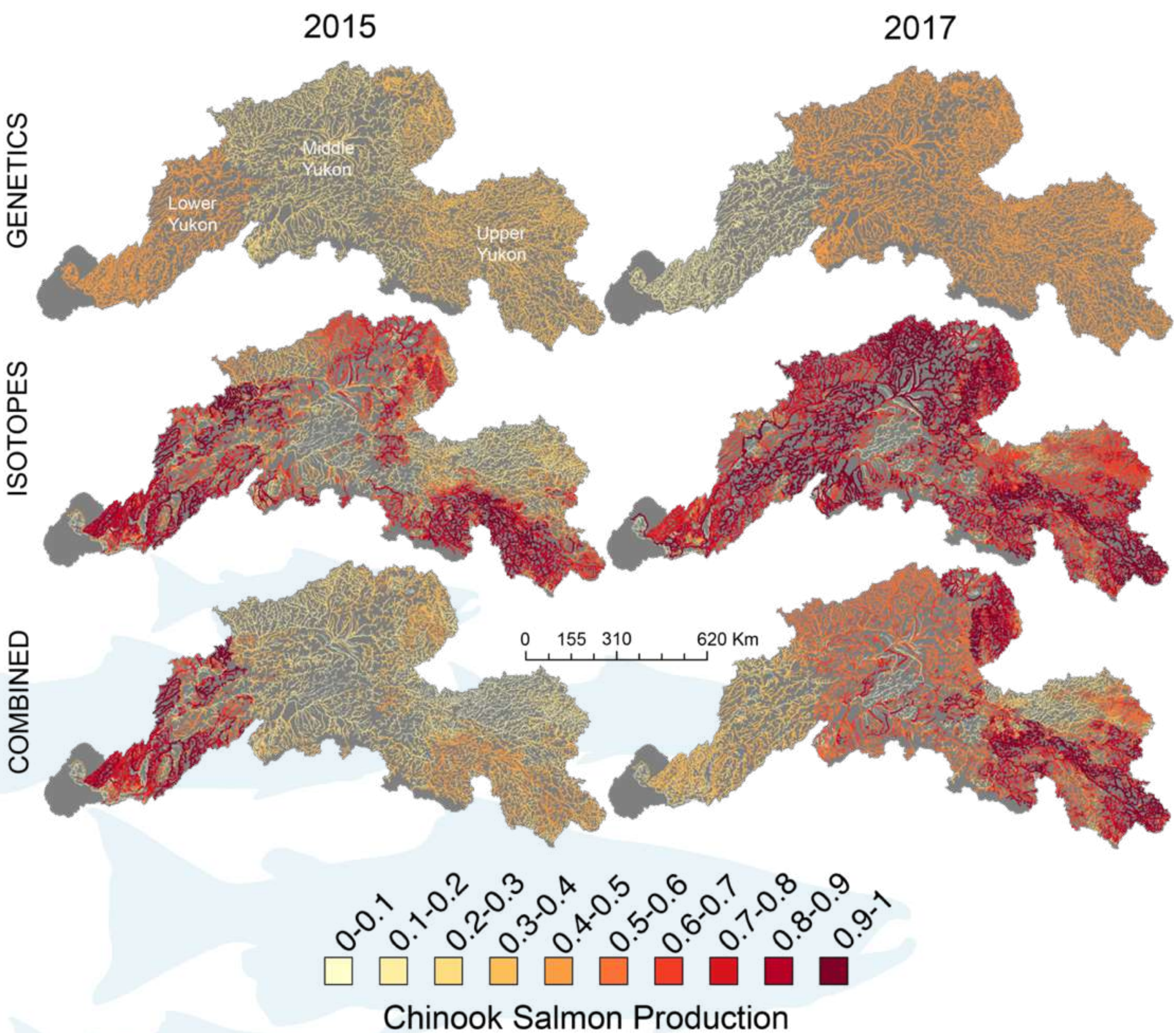



**Figure 5:** **Yukon River results showing the power of integrating isotopes and genetics to quantify the spatial patterns of production of Chinook salmon across the Yukon River for the 2015 and 2017 return years. The 2015 return reflects fish sampled over the course of the entire run, whereas in 2017, the map shows the pattern from fish sampled up to the peak of the run. 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.**

This research was made possible with support from AYK-SSI

Download the full project report using this LINK

**2019 Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative**

**Project Final Report**

# Quantifying Chinook salmon production at fine spatial scales and mercury concentrations in resident fish across the Kuskokwim River

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## ABSTRACT

Kuskokwim River Chinook salmon have experienced low returns during the last decade, critically challenging commercial fishing and subsistence-based human communities of this watershed. Fundamental knowledge gaps concerning the ecology of its Chinook salmon populations remain unknown but are critical to their effective management. In particular, it is unknown how Chinook salmon production is distributed across the Kuskokwim's diverse tributaries and habitats, and how these production patterns change over time in response to climate forcing and fishery interceptions lower in the river. Spatial variability in salmon production patterns across large river basins and how these patterns shift through time are integral to the resilience of populations and fisheries to environmental change. This largely stems from intact watersheds being able to distribute the risk of low production across a variety of distinct populations, habitats, and life history strategies.

We currently lack the tools to easily delineate how production patterns change over time across the Kuskokwim River basin. Here, we built a strontium isoscape (the spatial variation in $^{87}Sr/^{86}Sr$ ratios) of the Kuskokwim River that is able to determine Chinook salmon production patterns and life histories at small spatial scales. Using the isoscape and a geographically continuous Bayesian assignment framework, we determined the natal origins of 262 fish caught in the Bethel Test Fishery based on a match between the strontium isotopes in their otoliths and the spatial variation across the watershed. By aggregating the natal origin maps of these fish, we estimated the spatial pattern in production for the 2017 return year. Production of Chinook salmon returning in 2017 to the Kuskokwim was heterogenous across the river network, with most fish being produced from tributaries such as the Aniak River and Salmon Fork of the Pitka River. This information can be used to inform stock assessments that are currently hampered by a distinct lack of data describing the distribution of returning fish among tributary populations.

In addition to analyzing $^{87}Sr/^{86}Sr$ ratios across the Kuskokwim River, we also analyzed concentrations in mercury (Hg) in slimy sculpin tissues, plus a suite of other dissolved constituents in river waters (e.g., dissolved organic carbon) known to covary with bioavailable Hg concentrations. We constructed a spatial hydrology model which quantified the patterns of mercury contamination in slimy sculpins throughout the ecosystem. Hg concentrations varied across the basin at multiple spatial scales reflecting the influence of multiple biological, chemical, and physical landscape processes. The baseline map of the spatial variation in fish tissue Hg can be used to better assess the potential risk of consuming resident fish to human communities and the influence of proposed industrial development in the basin.

## Table of Contents

## List of Tables and Figures

# I.INTRODUCTION

During the last decade Chinook salmon populations have declined precipitously across western Alaska rivers (ADF&G 2013, Schindler et al. 2013), including in the Kuskokwim River – which supports the largest subsistence fishery in the state. Since 2007, the Kuskokwim River Chinook salmon have experienced multi-year periods of critically low productivity resulting in years where there were not enough fish for subsistence, as established by the Alaska Board of Fisheries (Schindler et al. 2013). Although the decline in abundance is clear, its causes, and how the decline has been expressed across the diverse habitats and tributaries of the Kuskokwim River are largely unknown. Such knowledge gaps are primarily due to the fact that it is extremely difficult to reconstruct the variation in production patterns of Chinook salmon across this vast basin at spatial and temporal scales relevant to Chinook salmon biology, and the mismatch with the scales at which management and assessment occur. For example, stock assessments of Kuskokwim Chinook salmon have relied heavily on weirs located on a small number of tributaries, with very little data beyond highly uncertain aerial surveys on most of the watershed. This paucity of reliable information on the Kuskokwim stock complex makes stock assessments prone to substantial uncertainty that seriously challenges management intending to balance conservation and fisheries outcomes.

Production patterns and life history strategies of salmon are often heterogeneous across space and time (Hilborn et al. 2003, Schindler et al. 2010, Griffiths et al. 2014). Such heterogeneity, in combination with habitat diversity, acts to buffer populations from unpredictable environmental change. Harnessing the capacity of these attributes to impart resilience to populations, especially in terms of their future conservation and management, requires the ability to quantify how these fundamental features of Chinook salmon biology vary across space and through time. These questions are central to multiple research themes identified in this RFP. However, the tools needed to easily and accurately assess these questions are lacking, but remain critical to our understanding and management of AYK Chinook salmon.

Since 2009, we have been developing the use of strontium isotope ratios ($^{87}Sr/^{86}Sr$), which are naturally occurring in Alaska's river waters and recorded in the otoliths of its fish populations, to illuminate the production patterns and life-history variation of western Alaska Chinook salmon. This work has been motivated by two decades of research demonstrating the power of this particular tracer to distinguish the movement patterns and provenance of animals among and within geologically diverse ecosystems (Koch et al. 1992, Kennedy et al. 1997, Barnett-Johnson et al. 2008, Britton et al. 2009, Copeland et al. 2011); variation in $^{87}Sr/^{86}Sr$ ratios scale with geologic heterogeneity (Bataille and Bowen 2012). It was also motivated by the fact that current methodologies, such as genetic Mixed Stock Analysis (MSA) on fishery harvests, are often limited to apportioning Chinook salmon to stocks at relatively coarse spatial scales, especially in the Kuskokwim River (Larson et al. 2014). Western Alaska, including the Kuskokwim River, is characterized by an immense amount of geologic and isotopic diversity and supports the world's largest wild Chinook salmon populations. Recently, we demonstrated that by integrating $^{87}Sr/^{86}Sr$ information recorded in the otoliths of Chinook salmon with riverine $^{87}Sr/^{86}Sr$ isoscape models, the heterogeneous production of Chinook salmon across a complex river basin (the Nushagak River) could be resolved at small spatial scales (Brennan et al. 2015b, Brennan and Schindler 2016, Brennan et al. 2019a, Brennan et al. 2019b). We are also extending this work to the Yukon River basin, where AYK SSI has funded three related projects to generate the $^{87}Sr/^{86}Sr$-baseline model in order to reconstruct the production patterns of Chinook salmon within this large river basin annually.

**The primary goal of this project was to develop a $^{87}Sr/^{86}Sr$ isoscape of the Kuskokwim River basin that would be able to reconstruct patterns of Chinook salmon production across this large, free-flowing watershed annually.** By including the Kuskokwim River in these efforts, the largest three producers of Chinook salmon in western Alaska (the Yukon, Kuskokwim and Nushagak Rivers) will have $^{87}Sr/^{86}Sr$ isoscapes. These can be used to reconstruct the production patterns and life history strategies of Chinook salmon at fine spatial scales throughout each of these vast rivers. Here, we present results of (*i*) the isoscape model for the Kuskokwim River, and (*ii*) the production patterns of the 2017 Chinook salmon run. The overall result is an analytical framework that can assess two fundamental features of Chinook salmon biology simultaneously (production patterns of individual populations and life-history variation), which will provide important insights when trying to develop and implement effective conservation strategies for an uncertain future.

**Additionally, this project also determined a baseline of bioavailable mercury (Hg) throughout this watershed**. Doing so was motivated by two reasons: i) Hg is a known contaminant that is biomagnified up food chains and can have detrimental health impacts on human communities that consume fish with high Hg-concentrations, and ii) mining activity within watersheds can dramatically alter natural levels of Hg in river waters; the Kuskokwim River has several currently operating, and proposed mines. The variation in the levels of Hg throughout the Kuskokwim River and how this is reflected in fish populations is not known. It is known, however, that the presence of mines within tributaries of this watershed substantially increase the levels of Hg relative to tributaries without mining activity (Wang 1999). By characterizing the spatial variation of bioavailable Hg across the entire Kuskokwim River we now have a better understanding of the current levels, how existing mining activity shapes Hg throughout the basin, and how future mining activity may change Hg throughout the Kuskokwim River. The spatial framework we used for modeling Sr isotopes throughout the Kuskokwim enabled spatial analysis of Hg throughout the river. This should translate directly to a more rigorous assessment of the risks of consumption of resident fish species by subsistence communities in this river basin and how this risk may change in the face of industrial development.

## II.OBJECTIVES

**Objective 1:** Characterize the variability in strontium isotope ratios in river waters across the Kuskokwim River basin.

**Objective 2:** Generate a baseline geospatial model of strontium isotope variation in river water across the entire Kuskokwim River basin to enable the reconstruction of production patterns of Chinook salmon

**Objective 3:** Reconstruct the production patterns of Chinook salmon that returned to the Kuskokwim River watershed in 2017.

**Objective 4:** Determine the spatial distribution of mercury (Hg) throughout the Kuskokwim River in order to determine how this distribution is influenced by mining activity and may affect subsistence human communities via consumption of resident fish species.

## III.METHODS

### Characterization of the strontium isotope baseline of rivers in the Kuskokwim basin

In 2017, in collaboration with ADF&G and US-FWS, water samples were collected from tributaries and main stem channels from across the Kuskokwim River watershed (n=120 sites). Target sites were chosen based on i) known spawning and rearing areas of Chinook salmon, and ii) geologic heterogeneity (Bataille et al. 2014, Brennan et al. 2014) in order to capture the full extent of the isotopic variation that exists in the watershed and how this relates to Chinook salmon habitat. 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.

### A strontium isotope geospatial assignment model for Chinook salmon

To build the strontium isotope geospatial model of the Kuskokwim 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 lithological units within the Kuskokwim basin (n=16 lithological classes) upstream of all sites with $^{87}Sr/^{86}Sr$ river water measurements. 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. $\epsilon$ 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 Kuskokwim 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 Kuskokwim River basin. The analytical procedure used here is described in detail in Brennan and Schindler 2016)

**Reconstructing the 2017 production patterns across the Kuskokwim River Basin**

We used otolith chemistry and river isoscapes to reconstruct the production patterns of the 2017 Chinook salmon run returning to the Kuskokwim River (Brennan and Schindler 2016). Otoliths were collected from individual adult Chinook salmon harvested during the lower river test fisheries in Bethel, AK during the 2017 run (n=262 fish). These collections were stratified temporally across the run in an attempt to capture all potential source populations in the stock complex. Sagittal otoliths 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. 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 87Sr/86Sr 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 information. Thus, for each fish we generated a probability surface, or map, across the river basin. The probability maps of all 262 Chinook salmon from the 2017 run were then summed to reconstruct the relative production of each location relative to all other locations in the basin. We confirmed that this otolith sample was in proportion to the catch per unit effort (CPUE) over the course of the entire run. Therefore, the sample reflects any temporal structure that may exist in terms of run-timing among different populations entering the Kuskokwim River.

**Determining the spatial variation in Hg across the Kuskokwim River**

We used SSNs to model the spatial patterns in Hg across the Kuskokwim River basin. To avoid complications related to site-specific temporal variability in Hg concentrations in rivers (i.e., only analyzing a 'snapshot' in time of the Hg distribution by collecting and analyzing water samples), we analyzed the Hg concentrations in the tissues of slimy sculpin. Slimy sculpin are a well-established sentinel species that is able to track these types of contaminants, whereby the chemical composition of their tissues reliably reflects that of the river environment they inhabit (Gray et al. 2004, Cunjak et al. 2005). Furthermore, by focusing on fish tissues of a sedentary organism we avoided analytical problems related to naturally low levels of Hg in some river waters (Wang 1999). Last, by using the time-integrated tissues of a non-migratory fish species, we were better able to assess how this contaminant is stored in resident fish populations and its implications for the health of human communities dependent on consuming such species. Although, slimy sculpins are not known to be directly consumed by these communities, we assumed sculpin to be a better proxy than water samples for the reasons listed above, but also due to the fact that such contaminants are biomagnified up food chains as they are consumed by higher trophic level predators.

Slimy sculpin (*Cottus cognatus*) were collected using a stick seine with 7 mm mesh net along river banks at 68 of the sites sampled for water. A total of 272 sculpin were collected across all sites, with a mean of 5 fish per site, and all but 10 sites having 2 or more fish collected for duplicate tissue measurements. Sculpin were euthanized immediately following removal from the stream, placed in Whirl-Pak bags, and frozen. All samples were stored frozen in the dark until lab processing. At sites with active mining nearby, fish were collected upstream and downstream of observed activity, and in the middle of the actively mined reach where accessible.

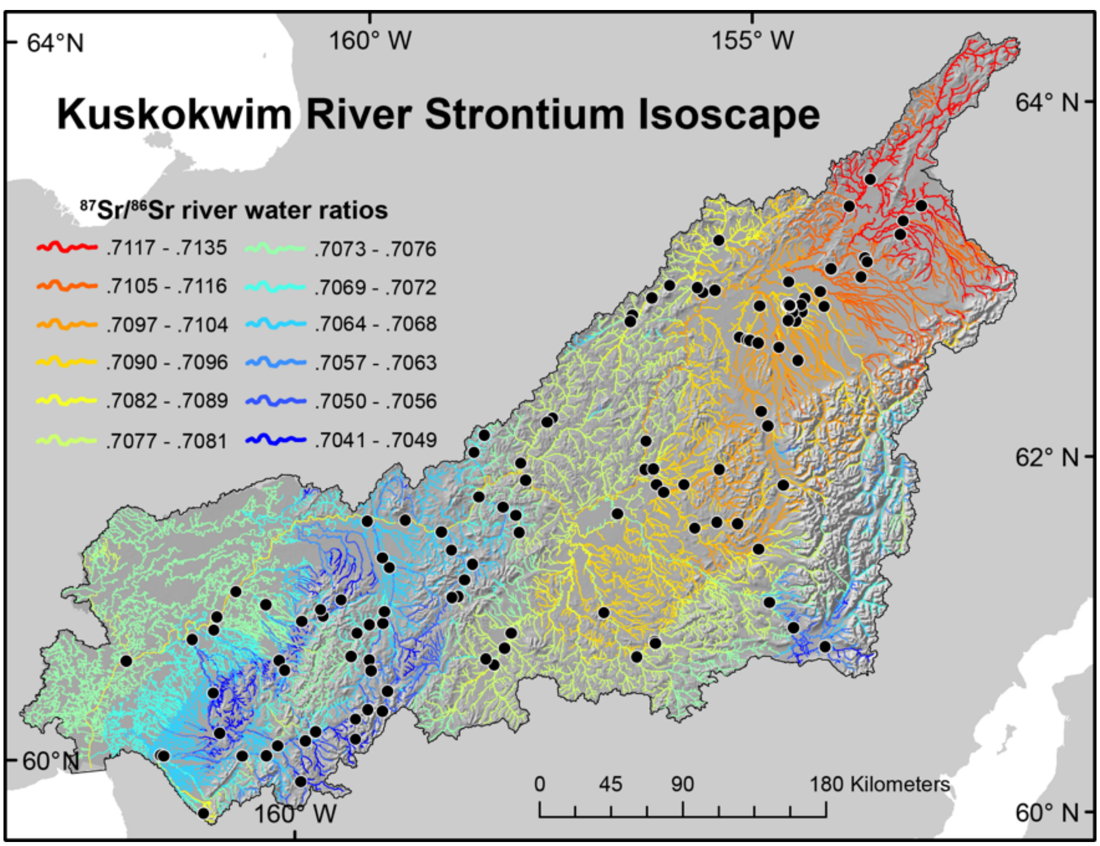
Total body burden of fish was determined from muscle total Hg (THg) and converted to methyl Hg (MeHg) based on existing empirical relationships (Bevelhimer et al. 1997, Baker et al. 2009). Sculpin were weighed, freeze-dried, and then re-weighed in a clean environment at the University of Washington School of Aquatic and Fishery Sciences. Freeze-dried samples were analyzed by thermal decomposition atomic adsorption direct mercury analyzer (DMA) following a modified EPA standard method 7473, lab method TM.0813 (www.standardmethods.org) at the Biotron Analytical Laboratory at Western University in London, Ontario. Samples were analyzed on a Milestone DMA-80 (Milestone Scientific, Inc., Shelton, Connecticut), with a LoD of 0.08 ng and a method reporting limit of 0.24 ng. Mean relative percentage difference in sample duplicates was 2 percent, with a calibration curve coefficient of determination equal to 0.995. Analysis of a certified reference material (DORM-4) indicated recovery of 97 – 102 percent, with a relative percentage difference of 1 percent between duplicate samples.

## IV.RESULTS

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

The range of $^{87}Sr/^{86}Sr$ ratios measured from across the Kuskokwim River was large (0.70418-0.71310) relative to the analytical uncertainty of measuring this isotope ratio in water (Figure 1). This measured range is similar to the range found in the Nushagak River (Brennan et al. 2016). Analytical uncertainty for water isotope ratios is typically ±0.00002 2SE (standard error), as was for the Kuskokwim River samples here. 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 Kuskokwim River is approximately 30-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 Kuskokwim River.

**Figure 1: $^{87}Sr/^{86}Sr$ isoscape for the Kuskokwim 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.**

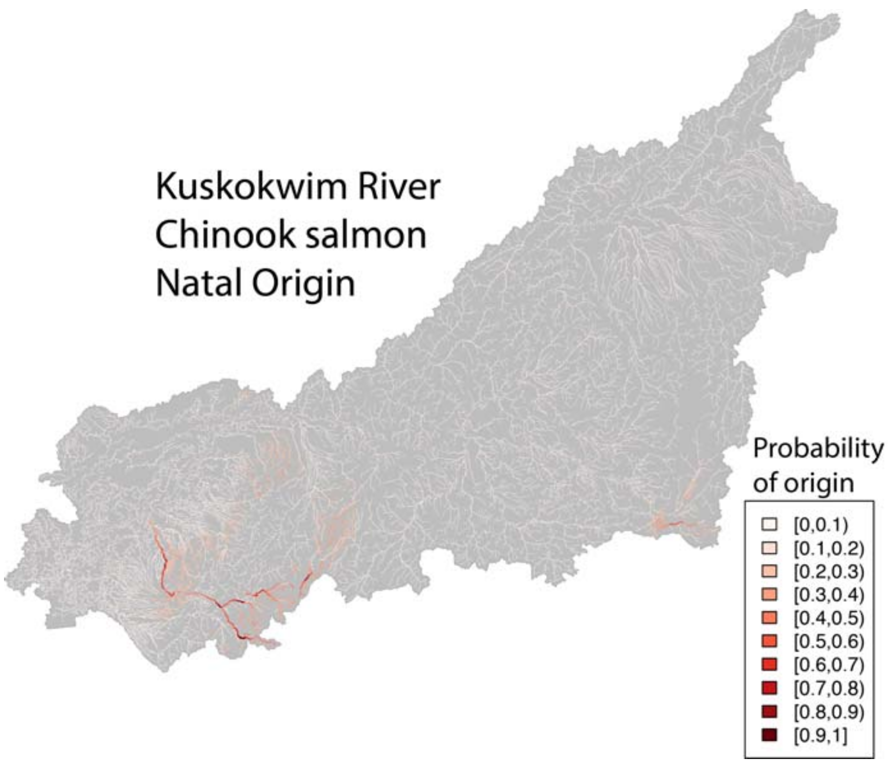


**Kuskokwim River $^{87}Sr/^{86}Sr$ isoscape**

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 ±0.00048 (Figure 1). This means the total range in observed ratios within the basin was approximately 20-times greater than the uncertainty associated with isoscape prediction, affording ample power for the isoscape to delineate natal origins of individual fish. This was also similar to the prediction error of the Nushagak River isoscape (RMSPE=0.00051) (Brennan et al. 2016). The Kuskokwim model included five different lithological classes as fixed effects. These included geologic units of the older, continentally derived (and therefore more felsic in composition) meta-sedimentary units of the Paleozoic Farewell Terrane (e.g., smmxmt in the GLiM), which is situated in the eastern portion of the basin. The highest $^{87}Sr/^{86}Sr$ ratios were observed in tributaries draining these lithologies. The model also included geologic units that were much younger, such as the mafic siliciclastic and igneous Mesozoic to Cenozoic volcanic and plutonic rocks situated in the southwestern portions of the basin associated with the Ahklun and Kilbuck Mountains (e.g., vi____ and sspyvr in GLiM). The rivers draining this region were the lowest $^{87}Sr/^{86}Sr$ ratios measured in the basin (e.g., the Kwethluk and Kisaralik Rivers). This general geologic pattern across the basin resulted in a strong east-west gradient with high ratios in the east and progressively much lower ratios to the west. It also produced a strong geographic pattern, not only among the upper and lower river regions, but also among specific tributaries. In some cases, individual tributaries are distinguishable based on $^{87}Sr/^{86}Sr$ ratios (e.g., the Kwethluk River) (Figure 2).

All of the best performing models included both a tail-up and Euclidean spatial autocorrelation model, which modeled the spatial dependency in the model 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 most likely due to geologic processes and heterogeneity present across the landscape but not described by the GLiM geospatial database.

**Figure 2: Probability of origin of an individual adult Chinook salmon caught in the Bethel Test Fishery in 2017. The $^{87}Sr/^{86}Sr$ ratio of this fish was 0.70481. The isotope-based assignment model determined the most likely natal origin to be the Kwethluk River (the dark red streamlines).**

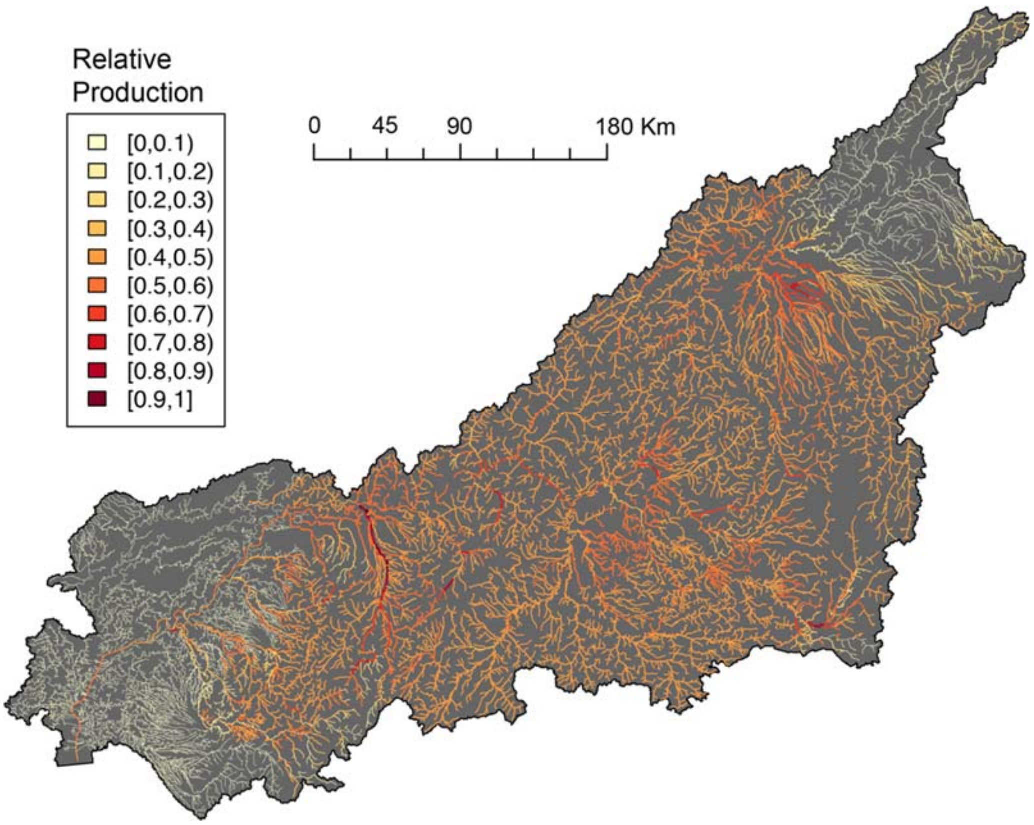



**Spatial production patterns of the 2017 Chinook salmon return to the Kuskokwim River**

The $^{87}Sr/^{86}Sr$ ratios recorded during freshwater residence in adult Chinook salmon otoliths collected from the Bethel Test Fishery 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 (e.g., Figure 2).

The spatial pattern in production for the 2017 return year indicated that production was heterogenous across the river basin. For example, the Aniak River was particularly productive (Figure 3). On the other hand, some habitats produced few fish, such as the tributaries in the northeastern portion of the basin draining the western slope of the Alaska Range and the North Fork of the Kuskokwim River. We assumed that the low gradient streams (streams with mean upstream watershed slope of <2°) draining the low-lying regions of the lower Kuskokwim River (e.g., the Johnson River and the other small streams draining the tundra) do not produce Chinook salmon.

**Figure 3: Spatial production pattern of Chinook salmon returning to the Kuskokwim River, caught in the Bethel Test Fishery, in 2017. Production was heterogeneously distributed across the basin, with high production coming from places like the Aniak River. This map assumes that the Bethel Test Fishery catches no fish returning to the Eek River, whose confluence with the Kuskokwim is 100 km downstream.**




There was also a general east-west geographic pattern in whether tributaries produced more or less Chinook salmon compared to an assumption that all tributaries produce salmon in proportion to their size (proportion of total stream length in basin) (Table 1). In 2017, tributaries to the west situated in the lower Kuskokwim River produced more fish than expected based on their size, whereas the eastern tributaries in the upper river, especially the East and North forks of the Kuskokwim, produced fewer fish than expected. These results are presented in Table 1 alongside the total run sizes for all of the major tributaries of the Kuskokwim River. Because the Bethel Test Fishery occurs approximately 100 km upstream from where the Eek River flows into the Kuskokwim, we also report estimates that assume that the fishery does not catch any fish returning to the Eek River. Using the estimates that assume no Eek River-bound fish were caught, indicates that the top-producing tributaries for the 2017 return were the Kwethluk, Kisaralik, Aniak, Holitna, and Stony rivers (Table 1).

**Table 1: Chinook salmon production from the major tributaries of the Kuskokwim River for the 2017 return year. Rivers highlighted in red are those that produced more fish than expected based on the amount of habitat in them. Rivers highlighted in blue are those that produced fewer fish than expected based on the amount of available habitat.**

| | Habitat amount | | 2017 Kuskokwim Chinook salmon Production (assuming Bethel TF caught zero Eek River fish) | | | 2017 Kuskokwim Chinook salmon Production (includes Eek River) | | |
|---|---|---|---|---|---|---|---|---|
| **River** (arranged ~ closest to furthest from river's terminus) | **Total stream length in tributary** (km) | **Proportion of total stream length in basin** | **Proportion of production** (based on isotope model) | **Total Run** (1000s of fish) | **Percent difference** between isotope production estimate and production assumed to be proportional to habitat amount | **Proportion of production** (based on isotope model) | **Total Run** (1000s of fish) | **Percent difference** between isotope production estimate and production assumed to be proportional to habitat amount |
| **Total Run** | | | | **166.9** | | | **166.9** | |
| Eek | 1250 | 3.0% | - | - | - | 6.2% | 10.3 | 107% |
| Kwethluk | 1168 | 2.8% | 6.4% | 10.7 | 130% | 4.3% | 7.2 | 56% |
| Kisaralik | 1434 | 3.4% | 6.4% | 10.7 | 88% | 5.5% | 9.2 | 61% |
| Tuluksak | 798 | 1.9% | 3.3% | 5.5 | 73% | 3.0% | 5.0 | 58% |
| Aniak | 2341 | 5.6% | 8.4% | 14.0 | 51% | 7.9% | 13.1 | 41% |
| Holokuk | 409 | 1.0% | 1.2% | 2.0 | 24% | 1.1% | 1.9 | 15% |
| Oskawalik | 479 | 1.1% | 1.4% | 2.3 | 18% | 1.3% | 2.1 | 11% |
| George | 1150 | 2.7% | 2.0% | 3.4 | -26% | 2.0% | 3.3 | -28% |
| Holitina | 7057 | 16.8% | 16.7% | 27.9 | -1% | 16.1% | 26.9 | -4% |
| Stony River | 3395 | 8.1% | 11.1% | 18.5 | 37% | 10.7% | 17.9 | 32% |
| Swift | 2173 | 5.2% | 5.8% | 9.6 | 11% | 5.7% | 9.5 | 10% |
| Tatlawiksuk | 917 | 2.2% | 2.1% | 3.5 | -4% | 2.1% | 3.5 | -5% |
| Cheneetnuk | 702 | 1.7% | 1.9% | 3.2 | 14% | 1.9% | 3.2 | 13% |
| Gagariah | 314 | 0.7% | 1.0% | 1.6 | 32% | 1.0% | 1.6 | 31% |
| Takotna | 2307 | 5.5% | 4.3% | 7.2 | -21% | 4.2% | 7.0 | -23% |
| Salmon R Pitka Fork | 175 | 0.4% | 0.2% | 0.4 | -44% | 0.2% | 0.4 | -44% |
| Pitka Fork | 968 | 2.3% | 1.5% | 2.5 | -35% | 1.5% | 2.5 | -35% |
| Middle Fork | 3145 | 7.5% | 6.0% | 10.0 | -20% | 5.9% | 9.9 | -21% |
| South Fork | 2455 | 5.9% | 5.2% | 8.7 | -10% | 5.1% | 8.4 | -14% |
| East Fork | 1726 | 4.1% | 1.0% | 1.7 | -75% | 1.0% | 1.7 | -75% |
| North Fork twrds AK range | 1451 | 3.5% | 1.0% | 1.7 | -70% | 1.0% | 1.7 | -70% |

## Spatial variability in Hg in slimy sculpin across the Kuskokwim River

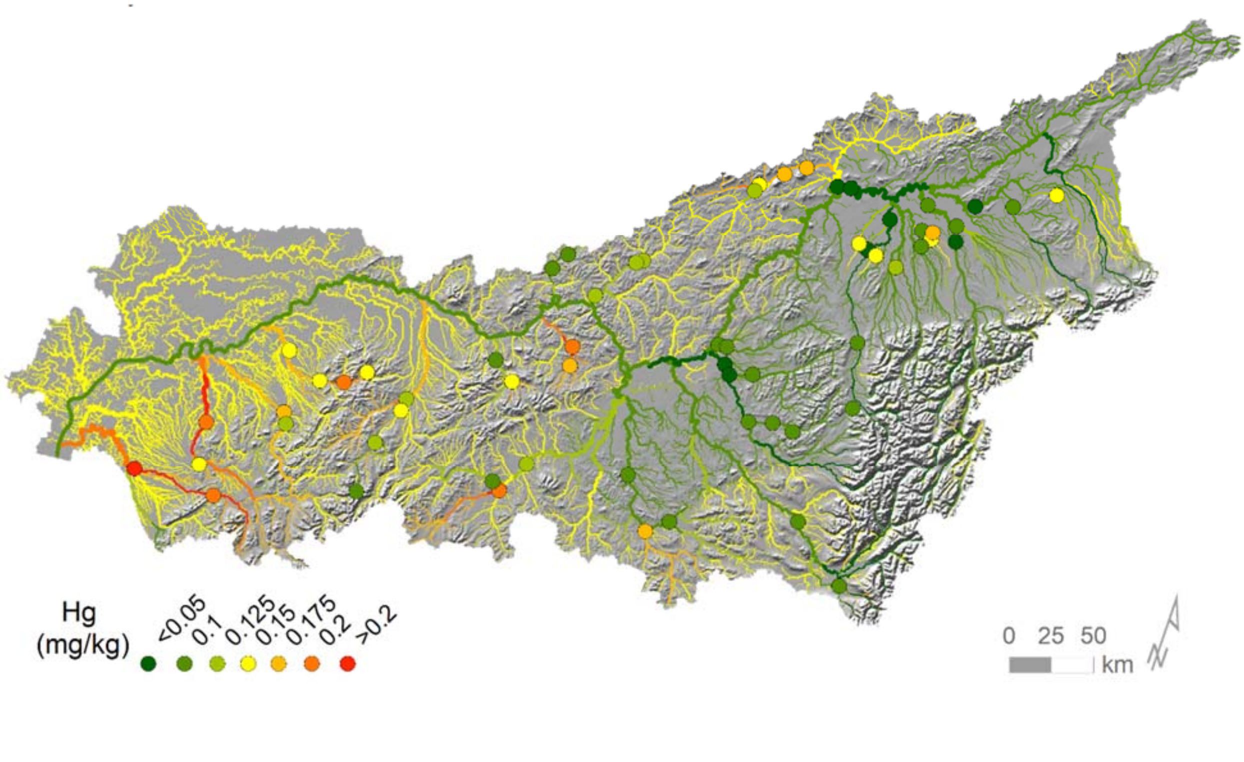
Mercury concentrations [Hg] in slimy sculpin tissues analyzed from across the Kuskokwim River ranged from 0.02 to 0.50 mg/L (wet weight). [Hg] in slimy sculpin tissues varied across the Kuskokwim River basin at fine to broad spatial scales, suggesting multiple processes were involved in shaping variation in [Hg].

The [Hg] in slimy sculpin was positively related to the mass of individual fish, where larger fish on average had higher [Hg] in their tissues. To account for the effect of body size on [Hg] in sculpin, we included it as a covariate in all SSN models. Doing so allowed us to isolate the influence of environmental drivers of the spatial variation in Hg across the basin.

The best candidate SSN models (i.e., models within 3 AIC points of the model with the lowest AIC score) included covariates of body mass, watershed slope and relief, carbonate-rich mixed meta-sedimentary rocks, active glaciers, and the concentration of dissolved organic carbon [DOC]. Specifically, these covariates were: log(body mass), the mean upstream watershed slope and relief, the percent area upstream underlain by the SMMXMT and IG____ lithological units of the GLiM, and log([DOC]) measured at the site, respectively.

These covariates explained approximately 35% of the spatial variability across the Kuskokwim basin. A tail-up autocovariance model accounted for approximately 55% of the variation. The remaining 10% was attributed to independent random error (the nugget) in the model. None of the top models included a Euclidean autocovariance function, and all of the non-spatial models performed substantially worse than any of the spatial models (>20 AIC points). These results suggest that the covariates in the model effectively captured the landscape processes driving spatial patterns in Hg that are typically expressed in Euclidean space (the closest straight-line distance between locations). They also support the use of only a tail-up model to account for the spatial dependency driven by connectivity among flow-connected locations throughout the Kuskokwim River.

**Figure 4: Spatial patterns in the mercury concentrations for the average sized slimy sculpin across the Kuskokwim River. Colored circles indicate the [Hg] concentrations measured in slimy sculpin after accounting for the effect of body (mass). The colored lines depict the predicted [Hg] concentrations for the average size fish using one of the top SSN models identified here with covariates that capture the variation in watershed slope, geology, and the upstream area covered in bare ice and rock.**



## V.DISCUSSION

### Production of Chinook salmon in 2017 across the Kuskokwim River

The spatial pattern in production of Chinook salmon in 2017 was heterogeneously distributed across the Kuskokwim River basin. Some tributaries, such as the Aniak River, were relatively productive, whereas other parts of the river, such as the upper northeastern part of the basin, produced very few fish. This result demonstrates that some habitats can be disproportionately important to the total return of Chinook salmon to the Kuskokwim River for any given return year. Furthermore, some tributaries produced substantially more fish (up to 25-70%) than expected based on their size; while others produced less. This further demonstrates the patchy spatial distribution of Chinook salmon production across the Kuskokwim in 2017.

The Kuskokwim 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 one year of data for the Kuskokwim River (2017), we do not have the ability to assess how freshwater conditions influence inter-annual 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 will be possible to constrain interannual variability in production across the Kuskokwim River and potentially its key environmental drivers. The former is one of the objectives of a recently funded project by AYK SSI. In the neighboring 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).

### $^{87}Sr/^{86}Sr$ ratios to reconstruct spatial patterns of Chinook salmon production

This project built a new analytical framework for the Kuskokwim River that is able to quantify the spatial pattern in production of the annual returns of Chinook salmon to the basin. Alternative methods to quantify how production is distributed across the basin include fish counting weirs, telemetry studies, aerial counts, and genetics. In the Kuskokwim, all of these methods have drawbacks related to spatial resolution, accuracy, and logistical constraints. For example, there is not enough genetic differentiation in the Kuskokwim River to distinguish different populations of Chinook salmon (Larson et al. 2014). Aerial surveys tend to be inaccurate ways to innumerate fish within rivers as large and as complex as the Kuskokwim River. Similarly, although counting weirs can provide better estimates of fish counts within individual tributaries, they are only operated in a limited number of locations (Smith and Liller 2018). Telemetry studies can be integral for distinguishing migration routes of returning adult fish, and in the Kuskokwim River, for estimating total run size via mark-recapture studies (Smith and Liller 2017a, b). But these studies are difficult to execute every return year.

The isotope-based geographic assignment framework produced by this project essentially samples the entire basin by delineating the natal origins of hundreds of individual fish (Figure X) intercepted by the Bethel 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. 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 et al. 2015b). Because $^{87}Sr/^{86}Sr$ ratios of a fish's habitat are directly recorded in their otoliths and site-specific temporal variability in $^{87}Sr/^{86}Sr$ ratios tends to be stable (Brennan et al. 2015a), especially interannually, this framework can be used to reconstruct interannual variation in production patterns across the basin by analyzing the otoliths of fish sampled over the course of the run during the lower river fisheries. Furthermore, we conducted a power analysis 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 (Brennan et al. 2019b). The error in our population size estimates ranged from ±0.015-0.032. The smallest proportion of the total run that we could resolve 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.

## Hg concentrations in fish across the Kuskokwim River

The SSN models produced here suggest that the spatial pattern in Hg across the Kuskokwim River is related to variation in broad landscape features and water chemistry. In particular, the average size slimy sculpin living in stream reaches and tributaries that are characterized by steep watersheds, or high relief, have lower [Hg] in their tissues. The influence of landscape characteristics is also evident from the fact that the spatial pattern in DOC across the Kuskokwim was also one of the important covariates identified in the SSN models. Previous work has shown that stream chemistry, such as DOC concentrations and pH, appear to be related to the bioavailability of Hg at the base of aquatic food webs and identify the central role of wetlands in the production and supply of methyl Hg (Hurley et al. 1995, Selvendiran et al. 2008, Yu et al.

2011). Wetlands are widespread throughout the low-lying regions of the Kuskokwim and are an important driver of the spatial pattern in DOC across the basin.

Nonetheless, the two steepest regions of the watershed (rivers draining the Kilbuck/Ahklun Mountains and the Alaskan Range) exhibit different patterns in sculpin [Hg]. Although there is fine spatial scale variation within both regions, the average size sculpin living in tributaries of the Kilbuck/Ahklun Mountains have substantially higher concentrations than those of the Alaska Range. This general pattern sets up a discernable east-west gradient in body mass-corrected [Hg] variation across the basin (Figure 4). The presence of geologic covariates in all of the best SSN models, suggests that this pattern appears to be related to geologic differences among these two regions. The calcareous rocks of the meta-sedimentary units of the Farewell Terrane (SMMXMT included in all top SSN models) are only present in the eastern part of the basin. Rivers draining this lithology tend to have relatively high concentrations of strontium and calcium, in addition to high pH (7-8.5) and alkalinity (90-179 mg/L), which are all indicators of a strong influence of carbonate weathering on stream chemistry (Jacobson et al. 2003, Brennan et al. 2014).

The covariates of the SSN models presented here accounted for only 35% of the variation in [Hg] across the Kuskokwim River. The tail-up model, however, accounted for nearly 55% of the variation, which highlights the importance of downstream transport on the spatial pattern in [Hg] across the network. This likely reflects the finer scale processes of how the general landscape features and river water chemistry influence downstream locations on the bioavailability of Hg that our current models unable to explain with covariates.

The data presented here and the SSN modeling effort, however, do provide a useful baseline of [Hg] in fish tissues and the general processes shaping its variability across the Kuskokwim River basin. The Kuskokwim faces numerous challenges in the future related to proposed industrial development and a rapidly warming climate. This baseline provides important information that can guide future monitoring and efforts to assess the risk of Hg as a contaminant in resident fishes.

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## VII. DELIVERABLES

Geospatial data products:

1) Strontium isoscape of the Kuskokwim River
2) Spatial production pattern of the 2017 Chinook salmon return to the Kuskokwim River
3) Baseline map of Hg concentrations in resident fish tissues across the Kuskokwim River

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

1) SAPR #1704 SchindlerJun-Dec2017
2) SAPR #1704 SchindlerJan-Jun2018
3) SAPR #1704 SchindlerJul-Dec2018

Five oral presentations were delivered at the American Fisheries Society, Western Division 2018 Annual Meeting held in Anchorage in May 2018:

**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 two related papers integral in building the analytical framework produced here for the Kuskokwim 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.

## VIII. PROJECT DATA

The geospatial data products produced here: (i) the strontium isoscape, (ii) 2017 production map, and (iii) [Hg] shapefile, 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.

## IX. ACKNOWLEDGEMENTS

We thank our critical collaborators on this project including Zachery Liller (ADFG), Nick Smith (ADFG), Lewis Coggins (USFWS), Diego Fernandez (University of Utah), Christian Zimmerman (USGS), Gordon Holtgrieve (University of Washington), David French (University of Washington), Madeline Jovanovich (University of Alaska-Fairbanks), Dan Young (NPS), and Diane Whited (University of Montana). We also thank all of the ADFG and USFWS researchers and technicians that assisted in the collection of water and fish samples throughout the Kuskokwim River in 2017. Thank you to Alex Shapiro and Alaska Land Exploration for supporting all helicopter-based sampling.

## 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:

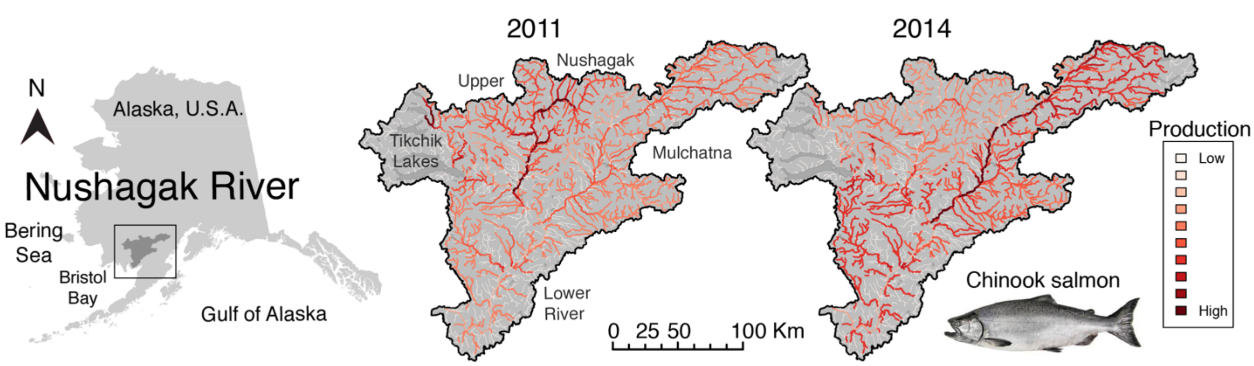
**Hot spots of salmon production shift across Western Alaska's largest rivers and stabilize the region's critical fisheries**

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)]**

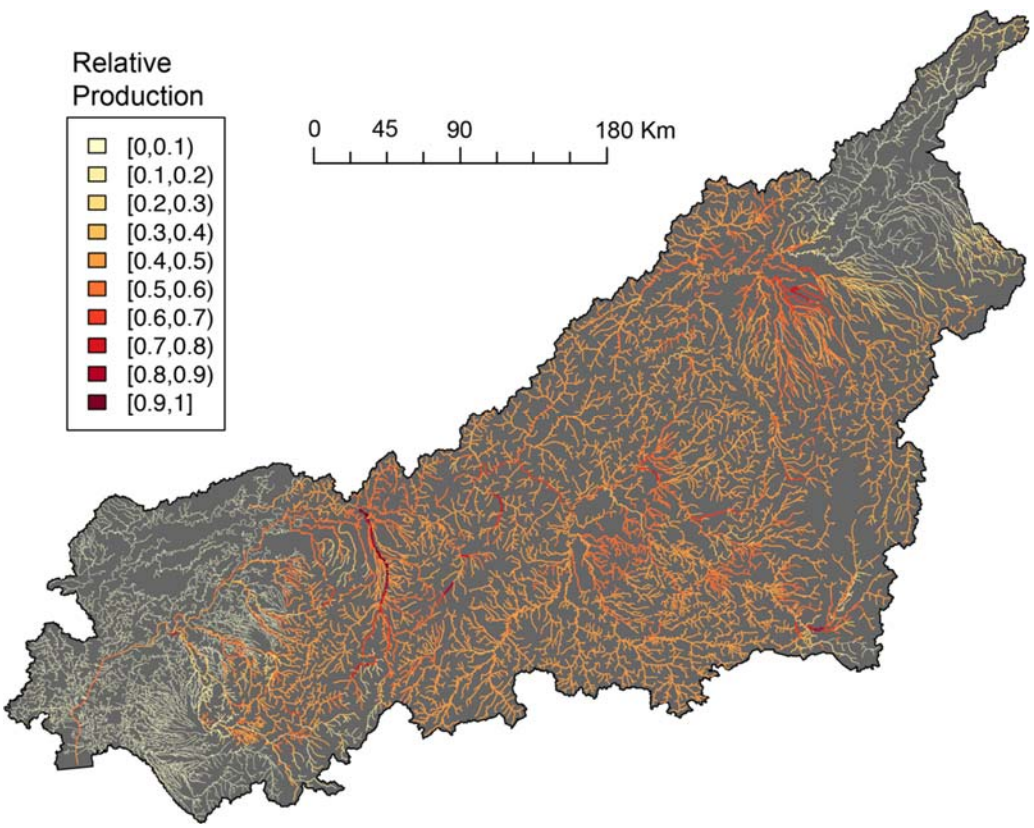
The research team, with funding from the AYK-SSI, has developed and applied this analytical framework to quantify how Chinook salmon production shifts across the Yukon and Kuskokwim rivers as well. In all three of these vast rivers systems, the production of salmon is patchy across the landscape. Some 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.**



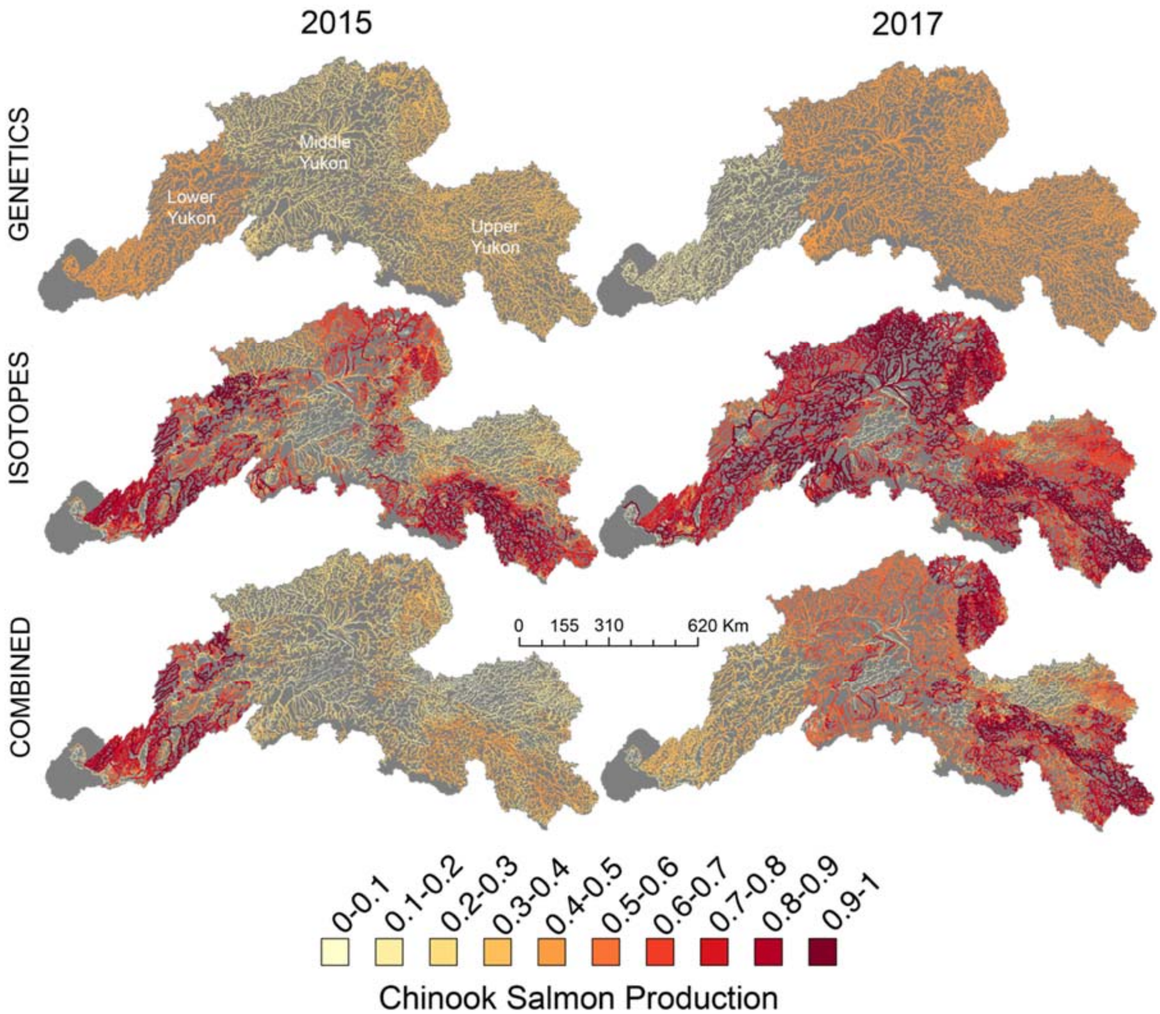

"The overall system is more than just the sum of its parts, and small pieces of habitat can be disproportionately important," said senior author Daniel Schindler, a professor at the UW School of Aquatic and Fishery Sciences. "The arrows point to the need to protect or restore at the entire basin scale 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