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> Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative Independent Expert Panel

# Changes in Quality of Chinook Salmon Escapement in the AYK Region

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Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative Independent Expert Panel

# Analysis of

# Changes in Quality of Chinook Salmon Escapement in the AYK Region

# Commissioned by:

Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative

821 N Street, Suite 103, Anchorage, AK 99501

# **AYK SSI Independent Expert Panel**

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An Illustrated Summary presenting main findings of this report is available for download here: https://www.aykssi.org/project/escapement-quality-expert-panel/

## SUMMARY

The demographic structure of Chinook salmon in the AYK region has changed significantly over the past 40-50 years. The length-at-age and proportion of older fish have decreased over time such that the overall mean length of fish returning to AYK rivers has declined markedly. Since the early 1970s, mean body length of female spawners in the Yukon and Kuskokwim rivers has declined by roughly 6% (5-8%) and 9% (8-12%), respectively. The trends in mean length are relatively consistent across sub-populations within watersheds, though some differences by location exists. The changes in mean length of Chinook salmon returning to AYK rivers are similar to trends reported for this species further south along much of the west coast.

Location-specific models for Chinook salmon sampled from fisheries catches or near spawning grounds showed that the mean length of fish caught in commercial and subsistence fisheries has changed more dramatically than that of spawners, particularly since the 2000s. This difference is largely explained by changes in the gillnet mesh sizes used to catch the fish. In the Yukon River the mean length of fish recorded in upper river subsistence catches has declined by 10%, while the mean length of fish caught in lower river commercial fisheries has declined by 18%.

The loss of older and larger fish and the decline in mean size suggest a reduction in reproductive potential of spawners. It was estimated that the average drainage-wide decline of about 6% in mean length of Chinook salmon in the Yukon River has resulted in a decline in mean fecundity of 15% (13-20%) and a decline in mean egg mass per female spawner of 28% (24-35%). Female spawners in the Kuskokwim River were estimated to carry 21% (18-28%) fewer eggs, and 35% (32-45%) lower egg mass than four decades ago. These estimates were based on relationships between size and fecundity or egg mass for Canadian-origin fish from the Yukon River.

Changes in the population sex ratios differed between the two drainages. In the Yukon River, the proportion female has varied around a mean of 40% with a weak declining trend. The apparent trend towards increasing male dominance in the fishery catches was mostly driven by changes in capture methods, i.e. smaller mesh sizes of gillnets used in recent years. Trends in the sex ratio appeared negligible once mesh size selectivity was accounted for in the models. By contrast, the proportion female in the Kuskokwim River has declined by about 7.5% since the early 1970s.

The potential consequences of reduced reproductive potential in spawner populations for the management of Chinook salmon population in the AYK region was explored using a previously developed stock-recruitment model for Canadian-origin Chinook salmon in the Yukon River, and similar analyses were performed using a stock-recruitment model for Chinook salmon in the Kuskokwim River. These analyses suggest that female length has a considerable effect on expected recruitment, but that the uncertainty in the relationship between recruitment and total egg mass is large compared to the effect of female length on escapement at MSY.

The reported decline in productive potential of females and thus the quality of the escapement may have contributed to recent declines in population productivity. Further research is needed to shed light on the relative contribution of changes in spawner abundances, average length, and environmental effects to the reduced run sizes of AYK Chinook salmon populations.

# GLOSSARY

ADF&G	Alaska Department of Fish & Game
ASL	Age-sex-length
АҮК	Arctic Yukon Kuskokwim
AYK SSI	AYK Sustainable Salmon Initiative
AYKDBMS	AYK Database Management System
BSFA	Bering Sea Fishermen's Association
DFO	Fisheries and Oceans Canada
MSY	Maximum Sustained Yield
SR	Stock-recruitment

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## **INTRODUCTION**

### Chinook salmon and the AYK region

Chinook salmon (*Oncorhynchus tshawytscha*) are widely distributed across the North Pacific Ocean and connected freshwater habitats, ranging from southern California to western Alaska and from northern Japan to north-east Siberia. Chinook salmon are anadromous fish that hatch and rear in freshwater, migrate to the ocean to feed and mature, and return to their natal rivers to spawn and then die (Healey 1991; Quinn 2005). This species displays remarkable inter- and intrapopulation diversity in their life-history strategies, particularly with respect to habitat use (freshwater and marine), growth trajectories and maturation schedules (Healey and Heard 1984; Healey 1991; Beacham and Murray 1993; Unwin 2000; Quinn 2005; Scheuerell 2005; Narum et al. 2007; Bourret et al. 2016). Chinook salmon from Western Alaska typically spend one year in freshwater and two to five years in the ocean, primarily in the central/western Bering Sea and the North Pacific Ocean (Weitkamp 2010; Larson et al. 2013).

The Arctic-Yukon-Kuskokwim (AYK) region is at the northern end of the North American distribution range of Chinook salmon, which occur in all major drainages in this region, including the Yukon, Kuskokwim, and Unalakleet rivers. Their watersheds serve as spawning and nursery habitats for Chinook salmon (e.g. Brown et al. 2017), which have provided a key food and cultural resource to indigenous communities for millennia, and currently support commercial, recreational, and subsistence fisheries. The Yukon River is one of the largest rivers in North America with a length of over 3000 kilometers (~2000 miles), and a drainage area about the size of Washington, Oregon and California combined. The Chinook salmon populations in the Yukon and Kuskokwim Rivers are among the largest wild populations in the world.

Chinook salmon populations in the AYK region, and throughout Alaska, have experienced precipitous but poorly understood declines in run abundance and productivity over the last decade (Schindler et al. 2013, Ohlberger et al. 2016). Several factors have been suggested to contribute to the declines in productivity and run abundances of Alaskan Chinook salmon. The Arctic-Yukon-Kuskokwim Chinook Salmon Research Action Plan (Schindler et al. 2013) proposed seven hypotheses that might explain recent abundance declines, including: (i) density dependence effects and overcompensation, (ii) increased freshwater mortality related to suitability and productivity of spawning habitats, (iii) increased ocean mortality related to physical and biological ocean conditions, (iv) anthropogenic impacts to ecological processes in the ocean, (v) marine bycatch in non-salmon ocean fisheries, (vi) pathogens, specifically during upstream migration, and (vii) changes in escapement quality, specifically related to size, sex ratio, and life history types.

Concurrent with the declines in population abundance of Chinook salmon in western Alaska rivers, have been widespread changes in the demographic structure of these populations. Both anecdotal observations and site-specific data sets suggest that the average size of fish on the spawning grounds has declined, as has the proportion of females in the population. While these trends are widely acknowledged, there has been no systematic review and quantification of the causes and magnitude of these apparent trends. Furthermore, current management focuses on the

numerical abundance of fish on the spawning grounds, without explicit consideration of changes in the demographic profile of populations, how these changes affect the quality of escapement, or how this information could inform management.

While it is typically assumed that the number of spawning females limits stock abundance in Pacific salmon, declines in the average age and size of females can cause a reduction in the per capita reproductive potential of female spawners, as reproductive potential depends on body size (Healey & Heard 1984), which may affect the total reproductive potential and thus recruitment of a population. In other words, it is important to consider not only the quantity but also the quality of spawners when investigating potential causes of declines in run abundance.

# **AYK SSI Independent Expert Panel**

In 2016 an Independent Review Panel on escapement quality of Chinook salmon was established by the AYK-SSI to synthesize the existing data and quantify the magnitude of changes in the demographic characteristics of Chinook salmon in the AYK region rivers. The intention was also to investigate the hypothesis that selective fishing and natural mortality have altered the genetic character of stocks and changed the expression of size, sex ratio, and composition of life history types that have contributed to declines in egg deposition in AYK Chinook salmon populations. The main concern, as stated by this hypothesis, is the contribution of declining trends in spawner mean age and size to reductions in population productivity and abundance of Chinook salmon in the AYK region. Further, a potential problem for managers is that changes in age-size structure can introduce bias into run reconstruction and spawner-recruit models that form the basis for current fishery management in this region, i.e. development of appropriate escapement goals.

Specifically, the aim of the Expert Panel was to quantify how changes in population demography have resulted in changes in per capita fecundity and total egg mass in AYK rivers using the best data available. One of the original project objectives was to compile and organize an extensive open-source database on Chinook salmon age-sex-length (ASL) observations from fisheries and escapement projects across the AYK region. Yet, extensive efforts by AYK Region ADF&G Commercial Fish Division staff to collect and publish a comprehensive ASL database that includes most of the available data for Chinook salmon negated the need for development of an additional database. This has allowed the Expert Panel to shift the focus of the analytic work for this project from compiling and organizing data to the second core project objective: a detailed analysis to quantify changes in escapement quality of Chinook salmon in the AYK region.

The goals of the Expert Panel were to (i) understand historical changes in location-specific and drainage-wide age, sex, and length compositions, (ii) estimate potential effects of these changes on the average reproductive potential of the populations in terms of potential number of eggs in the gravel, and (iii) explore potential management implications of changes in escapement quality of Chinook salmon.

In addition to this report and as part of the objectives of the AYK SSI Expert Panel, a synthesis of trends in average length and reproductive potential for Chinook salmon in the Yukon River is currently under consideration for publication as a journal article.

### Previous work on changes in demographic characteristics

The age and size composition of Chinook salmon returning to freshwater habitats to spawn has changed over the past few decades. Several studies have reported reductions in the mean age and length-at-age of returning Chinook salmon in many Alaskan populations (Hyer and Schleusner 2005; Howard et al. 2009; Kendall and Quinn 2011; Lewis et al. 2015). Moreover, the loss of the largest and oldest individuals has been reported for populations throughout the west coast of North America (Ohlberger et al. 2018). Specifically, Chinook salmon are returning to spawn at younger ages and are smaller at a given age compared to previous decades. Here, we estimate changes in demographic structure and resulting trends in per capita reproductive potential based on a comprehensive collection of age-sex-length samples of Chinook salmon in the AYK region. Importantly, while previous large-scale analyses primarily relied on commercial harvest data for the Yukon and Kuskokwim rivers (Lewis et al. 2015), the analyses presented here make use of data from a variety of sampling efforts, including spawner surveys such as weir and carcass sampling, test fisheries, and commercial and subsistence harvests, and they include data for the Canadian portion of the Yukon River.

### Overview of main analytical approaches

This report presents analyses to quantify changes in the escapement quality of Chinook salmon in the AYK region. The analyses are based on a comprehensive collection of age-sex-length samples of Chinook salmon in the Yukon, Kuskokwim, and Unalakleet rivers, and additional data on the fecundity and total egg mass of Yukon River Chinook salmon. The data were analyzed to understand changes in the age, sex, and length composition of specific spawner populations. Trends in mean body length of all fish sampled in a given location were estimated to calculate the resulting change in mean body size. Drainage-wide models were used to reveal trends in mean length and sex ratio for entire watersheds. Fecundity and egg mass data from Canadian-origin Chinook salmon samples were used to establish empirical relationships between reproductive potential and female size. These relationships were used to estimate changes in spawner reproductive potential over time, and were applied to existing stock-recruitment models to evaluate the importance of accounting for changes in reproductive potential on stockrecruitment relationships and management reference points.

# **METHODS**

### Data

The analyses described in this report are based on data from age-sex-length (ASL) samples for Chinook salmon in the Arctic-Yukon-Kuskokwim (AYK) region. We obtained the majority of data from the AYK Database Management System (AYKDBMS) maintained by the Alaska Department of Fish & Game (ADF&G). Additional ASL data for Chinook salmon sampled in the Canadian portion of the Yukon River were obtained from Fisheries and Oceans Canada (DFO). Data on fecundity and egg mass of Chinook salmon were obtained from published and unpublished sources. The ASL and fecundity data sources are described in more detail below.

### AYK Database Management System

Age-sex-length data were first downloaded from the AYKDBMS in September 2017 and were updated in June 2018 (provided by Holly Krenz, ADF&G). ASL data were available starting in the late 1960s, though sample sizes were small until the early 1970s such that most of the time series analyses presented in this report start in 1971 or later. This dataset contains individual observations from sampling projects throughout the AYK region, which is comprised of the Yukon River, the Kuskokwim River, and Norton Sound including the Unalakleet River. The dataset includes samples taken from commercial catches, subsistence catches, test fisheries, weir operations, handpicked or carcass surveys, and less common sampling types such as mark recapture and acoustic telemetry. The full ASL dataset for the AYK region (prior to filtering) contained roughly 573,000 samples; about 397,000 from the Yukon River (85% U.S. and 15% Canadian portion), 162,000 from the Kuskokwim River, and 14,000 from Norton Sound.

The ASL data were filtered prior to analysis. For all analyses that relied on length information, we excluded samples (1) without length information (~2.5% of samples), (2) lengths smaller than 100mm (<0.01% of samples), (3) lengths larger than 1500mm (<0.01% of samples), (4) with unknown measurement type (~6% of samples) or uncommon length measurement type (~0.5% of samples). We kept all samples for which length was recorded as either mid-eye to fork of tail (MEF) or tip of snout to fork of tail (SNF). The vast majority of length measurements was recorded as mid eye to fork of tail, and samples measured as tip of snout to fork of tail were converted to mid eye to fork of tail lengths using an empirically derived formula (Pahlke 1988, see below). For analyses that relied on age information, we excluded samples (1) without age information (~4% of samples), (2) with a recorded aging error in the database (~15% of samples), and (3) from rare age groups younger than four and older than seven years old ( $\sim 0.5\%$ of samples). Finally, for analyses that relied on sex information, we corrected historical data from the weir sampling projects on the Andreafsky and Gisasa rivers, which reported high proportions of females among 4-year-olds (over 20%) in some years. In line with confirmed sex data showing that the proportional female contribution to 4-year-olds is less than 5% and in line with recent sampling protocols used at the Andreafsky and Gisasa weirs (Mears 2012; Carlson 2012), we reassigned age-4 females to males.

# Additional age-sex-length data

Additional datasets with ASL information on Chinook salmon were collected to supplement those data available through the AYKDBMS. We obtained data from Blind Creek weir and the Canadian commercial fishery at Dawson in the Canadian portion of the Yukon River (provided by DFO). The Blind Creek ASL data (<2,000 samples) consist of high quality weir sampling data with reliable sex information and were available from 2003 to present. The Dawson commercial catch data (~17,000 samples) were available for the period 1975-2006. These data have more reliable sex information than samples from the lower river mainstem due to apparent secondary sexual characteristics, and are representative of the majority of the Canadian-origin Yukon River Chinook salmon stock (mainstem fishery).

# Fecundity data

We collected data on the number of eggs and total egg mass per female from different sources, mostly available for Yukon River Chinook salmon, that were used to estimate relationships between female body size and reproductive potential. The dataset we gathered includes previously unpublished data on reproductive potential of Canadian-origin Yukon River Chinook salmon (i) sampled at Eagle during the years 2008-2010 (provided by Lara Horstmann, UAF), (ii) sampled at Eagle in 2018 (provided by AYK-SSI), and (iii) sampled in the Takhini and Tatchun rivers in the Canadian portion of the Yukon River (provided by DFO).

We gathered data on various Alaska Chinook salmon populations from the published literature, including data from (i) the Tanana River (Yukon subdistrict Y6) sampled in 1989 (Skaugstad and McCracken 1991), (ii) the Unalakleet River sampled in 2008-2010 (Bell and Kent 2012), (iii) the Tanana and upper U.S. mainstem of the Yukon River (subdistricts Y5/Y6) sampled in 2005 (Jasper and Evenson 2006), and (iv) the Kenai River sampled in 1989 (Fleischman and Reimer 2017). These data included information on the number of eggs and/or total egg mass per female along with information on female length and in some cases age and body mass.

# Data analysis

Inferring changes in the age, sex, and/or length composition over time is challenging when a large portion of the available data were collected for purposes other than estimating trends in demographic characteristics. The data used here originated from various types of projects (e.g., commercial catches, escapement projects, test fisheries, etc.) that sample fish in different locations throughout a watershed, using different methods (e.g., gillnets, fishwheels, carcasses, weir traps, etc.) and gear types that are often selective with respect to fish size (e.g., gillnets of varying mesh sizes). Furthermore, the relative effort and proportion of fish sampled by the different projects and thus locations, gear types, and mesh sizes, vary from year to year. Accounting for differences between locations, gear types, and mesh sizes, is therefore critical when estimating trends in the age, sex, and/or length composition over time.

An additional challenge when analyzing data with sex information that has been collected using external examination of the fish is the potential for misclassification of sex. Previous studies have shown that external sex determination can be associated with substantial observation error. Previous work using samples from the lower Yukon River test fishery found that ~30% of males and ~36% of females were misclassified (Lozori and McIntosh 2014). The probability of misclassification is likely lower when sampling live fish closer to spawning grounds, e.g. at weirs, due to the development of visually apparent secondary sexual characteristics, and is likely negligible for post-spawner surveys such as carcass sampling. However, the reported error for lower river samples is large enough to be considered during data analysis. Furthermore, while sex misclassification can potentially bias estimates of sex-specific changes in mean size (if sexes differ in mean size and the probability of misclassification depends on size), misclassification was largely independent of body size (Lozori and McIntosh 2014).

### Analyses

### Standardizing length measurements

To standardize length measurements, we converted samples measured as tip of snout to fork of tail (SNF) to mid eye to fork of tail (MEF) lengths using the empirically estimated formula:

### MEF = a + b SNF,

where *a* is the intercept and *b* is the slope of the regression (a=44.126, b=0.846, Pahlke 1988).

### Relationships between body size and reproductive potential

We analyzed data on female fecundity and total egg mass using non-linear least squares and loglinear regressions. These two regression approaches performed similarly with respect to residual normality and homoscedasticity. We present estimates for non-linear least squares regressions:

$$R = a S^b$$
,

where R is a measure of reproductive potential (egg number or egg mass), S is body size (female length or mass), a is the estimated allometric scalar, and b is the estimated allometric exponent. Inclusion of other explanatory variables such as age or year was not supported in the models.

### Location-specific changes in mean body length over time

To analyze location-specific changes in mean length of female Chinook salmon over time, we fit multiple linear regression models of the form:

$$L_{\rm i} = \beta_0 + \beta_{\rm y} Y + \beta_{\rm g} G + \beta_{\rm m} M + \beta_{\rm d} D + \epsilon_{\rm i},$$

where  $L_i$  is the length of an individual, Y is year, G is gear type, M is mesh size, D is day of year of capture,  $\beta_0$  is the intercept,  $\beta_y$ ,  $\beta_g$ ,  $\beta_m$  and  $\beta_d$  are regression coefficients of the fixed effects for year, gear type, mesh size (factors), and capture date (continuous), and  $\epsilon_i \sim N(0, \sigma^2)$  is a normally distributed error term. We fit two sets of models of increasing complexity and report estimated time trends in the results. For escapement samples (weir operations and handpicked or carcass surveys), we fit models with a year effect only and models with effects for year and date of capture. For catch based samples (commercial, subsistence, and test fisheries), we fit models with year effect only and models with effects for year, date of capture, gear type, and mesh size. Due to different time series lengths, we compared mean size estimates before 1990 to after 2010.

#### Drainage-wide trends in mean length of females

To analyze drainage-wide changes in mean length of female Chinook salmon over time, we fit linear mixed effects models of the form:

$$L_{i} = \beta_{0} + \beta_{y}Y + \beta_{c}C + b_{u|y} + \epsilon_{i},$$

where  $L_i$  is the length of an individual, Y is year, C is capture method,  $\beta_0$  is the intercept,  $\beta_y$  and  $\beta_c$  are regression coefficients of the fixed effects for year and capture method,  $b_{y|u} \sim N(0, \sigma_b^2)$  is a normally distributed random effect for year nested in location (*u*), and  $\epsilon_i \sim N(0, \sigma^2)$  is a normally distributed error term. The capture method effect was a combined factor of gear type and mesh size (e.g., 'handpicked or carcass', 'drift gillnet 6.5 in mesh'). Nested random effects were used to account for the lack of independence of the data within years and locations. Inclusion of nested random effects was determined by comparing models with and without random effects by AIC model selection (compared using restricted maximum likelihood estimation, REML). Inclusion of fixed effects (compared using maximum likelihood estimation, ML). The final models were fit using REML. Julian date was not included in drainage-wide models because it was highly confounded with sampling location. Changes in mean body length over time were calculated as the percent difference between the average annual estimates of the first compared to the last five years of the time series.

The same models were fit using egg number or total egg mass as response variable, where individual lengths were converted to a measure of reproductive potential using the previously established relationships between female body length and egg number or total egg mass. We also fit these models by converting individual lengths to total energy in kcal per fish. While equations specific to Yukon or Kuskokwim River populations do not exist, we used a formula developed for southern (BC to CA) populations (O'Neill et al. 2014; Energy = 0.00001.1 Length<sup>3.122</sup>). This estimate was adjusted by a utility factor (dressed head off) of 0.72 for Chinook salmon (Crapo et al. 1993). Future research should use length to energy conversions specific to AYK Chinook salmon. For drainage-wide models, relative changes in mean length, reproductive

potential of females, and caloric value over time were calculated as the difference between mean annual point estimates for the first and last five years. Because the choice of reference time periods is arbitrary, we calculated the difference between mean annual estimates for the first and last three and ten years of the time series, and report these as our estimated ranges of percent change in mean length or reproductive potential.

### Changes in sex ratio over time

We used two approaches for analyzing changes in sex ratio over time. The two approaches differed fundamentally in how individual age and sex information in the available data was used. In the first approach, we relied on the sex information in the historical data and model proportion female using all available samples while estimating a potential bias in the proportion females due to external sex determination. In the second approach, we assumed that sex information in the historical samples, primarily collected using visual/external examination, is not reliable and we instead used sex-by-age proportions from a subset of known sex data collected using internal sex determination (since 2000 as part of the Lower Yukon Test Fishing project), to hindcast the proportion female in other long-term subsets of the data (specific locations and capture methods).

# Estimating changes in the proportion female using sex information of all historical samples

We modeled the proportion female in the population as a random walk process while accounting for differences in sampled proportions by location, gear type, and mesh size. Changes in the proportion females over time were modeled using individual observations of sex as follows:

$$o_{t,u,c,i} \sim Bernoulli(ilogit(y_{t,u,c}) + a_s(1 - 2 ilogit(y_{t,u,c}))),$$

where  $o_{t,u,c,i}$  is the observed sex of an individual *i* sampled at time *t* in location *u*, with capture method *c*, and  $a_s$  is a bias term for observed sex, which was assumed to be zero for internal examination  $(a_{int})$  and was estimated in the model for external examination  $(a_{ext})$ . This bias term reflects observation error in sex determination that is independent of sex, i.e. where the probability of misclassifying males as females is equal to the probability of misclassifying females as males. The capture method effect was a combined factor of gear type and mesh size, as described for the linear mixed effects model of mean length. The process part of the model is estimated in logit space  $[logit(x) = \exp(x)/(1 + \exp(x))]$ , where  $y_{t,u,c,i}$  is the probability of being female for individual *i* sampled at time *t* in location *u*, with capture method *c* given by:

 $y_{t,u,c} = x_t + u + c,$ 

where  $u \sim N(0, \sigma_u)$  and  $c \sim N(0, \sigma_c)$  are normally distributed offsets for location and capture method, with means zero and standard deviations  $\sigma_u$  and  $\sigma_c$ , and  $x_t$  is the average proportion females in the population (in logit space) in a given year, modeled as a random walk process:

# $x_t = x_{t-1} + \epsilon_t,$

where  $\epsilon_t \sim N(0, \sigma_t)$  is a normally distributed error with mean zero and standard deviation  $\sigma_t$ . The standard deviations  $\sigma_u$ ,  $\sigma_c$ , and  $\sigma_t$  were estimated in the model.

### Hindcasting the proportion female using sex-by-age proportions from recent known sex data

We estimated changes in sex ratio over time probabilistically by using known sex samples from recent years (available since the early 2000s) to calculate the proportion females in each agegroup and assuming that sex proportions by age-length group are constant through time. Known sex refers to individual samples for which sex was determined by internal examination (lethal sampling). We first computed the proportion females by age group in the known sex data for each year and fit logit-normal distributions to the annual estimates of each age group. We applied these sex-by-age proportions from the known sex data to the historical age composition data in other datasets with externally determined sex by drawing randomly from the fitted logit-normal distributions. This hindcasting approach was performed assuming that age information in the historical data is reliable while the sex information may not be reliable due to potential sex misclassification.

## Changes in sex ratio and mean length of the largest Chinook salmon

We selected the largest 5% of individuals in a given year and location and computed the mean length and proportion female in this subset of the data to estimate length trends and changes in sex ratio over time for the largest Chinook salmon. We selected locations that either represent specific spawner populations or aggregates of spawner populations that share similar in-river migration distances. We calculated location-specific mean length and proportion female of the largest 5% of fish sampled in each year, and fit dynamic factor analyses (DFA) to the time series to search for common trends (Zuur et al. 2003). The z-scored time series ( $y_t$ ) were modeled as:

$$\mathbf{y}_{t} = \mathbf{Z} \, \mathbf{x}_{t} + \mathbf{v}_{t},$$

where, **Z** are factor loadings on the hidden trends and  $\mathbf{v}_t \sim MVN(0, \mathbf{R})$  is a multivariate normal error with mean zero and variance-covariance matrix **R**, and  $\mathbf{x}_t$  are shared hidden trends that are modeled as random walk processes:

# $\mathbf{x}_{t} = \mathbf{x}_{t-1} + \mathbf{w}_{t},$

where  $\mathbf{w}_t \sim \text{MVN}(0, \mathbf{I})$  is the process noise assumed to be normally distributed with mean zero and identity matrix  $\mathbf{I}$  as variance-covariance structure such that the hidden trends have a variance of 1 and no covariance structure. Because we were interested in the most common trend shared among the time series, we only fit one-trend models. We fit the DFA in a Bayesian framework using an implementation of the model in STAN (Ward et al. 2018). We ran 10000 iterations and examined convergence across parameters using the effective sample size.

# RESULTS

This section presents the main findings of five major analyses used to assess:

- 1. Location-specific age, sex, and length compositions of selected spawner populations
- 2. Relationships between body size and reproductive potential
- 3. Location-specific changes in mean length of spawner populations and landed catch
- 4. Drainage-wide trends in mean length and reproductive potential of females
- 5. Drainage-wide trends in sex ratio over time
- 6. Sex ratio and mean length of the largest Chinook salmon
- 7. Effects of reduced reproductive potential on stock-recruitment relationships

## Location-specific age, sex, and length compositions of selected spawner populations

This analysis was focused on selected Chinook salmon spawning populations for which longterm data series of high quality ASL observations (sufficient number of samples each year) were available and that have been collected using weakly selective sampling methods such as from weirs and carcass surveys. The locations are the Salcha River (Figure 1), Chena River (Figure 2), Gisasa River (Figure 3), and Andreafsky River (Figure 4) in the Yukon drainage, and the Kogrukluk River (Figure 5) in the Kuskokwim drainage. These results describe general characteristics of the ASL compositions of each spawner population as well as their changes over time as reflected in the sampling data. Ages are reported as brood year age, i.e. the number of years between egg deposition and adult return. Note that sex compositions might be slightly biased due to misclassification because sex was determined externally for most samples. The spawning populations analyzed here have similar characteristic ASL compositions and have experienced similar changes in ASL composition over time (letters below refer to figure panels):

- Females are typically larger at a given age, except at age-7 (a)
- The most common age groups in males and females were age 5 and 6, respectively (b)
- The proportion female within ages increases from 1-5% at age-4 to around 75-90% at age-7 (c)
- Length-at-age has declined for ages 6 and 7, and has remained stable for age-5 and age-4 (d)
- The proportion female in Yukon River populations has remained relatively stable over time, while the proportion female in the Kogrukluk River showed a declining trend over time (e)
- The proportion female within the common ages 5 and 6 has typically increased over time (f)
- The mean age of both males and female spawners has decreased over time (g)
- The mean age of the population has declined due to an overall shift toward younger ages, i.e. decreasing proportion of ages 6 and older and increasing proportion of ages 5 and younger (h)

These location-specific trends thus suggest that the major spawning populations in the Yukon and Kuskokwim Rivers have experienced declines in mean age, by ~0.5 years, and declines in the length-at-age of older fish, especially ages 6 and 7, by up to ~100mm since the 1970s or 1980s. The sex ratio has remained relatively stable in Yukon River populations but has declined over time in the Kogrukluk River population (see section on drainage-wide trends for details).





















### Relationships between body size and reproductive potential

We analyzed the relationship between body size and reproductive potential in Chinook salmon using available datasets from the Yukon River, and the Kenai River in southcentral Alaska. We established relationships between female size and number of eggs (fecundity) or total egg mass. We pooled data collected at a specific location over multiple years, because sample sizes in any given year were small, models including year effects were not supported, and it was not known whether the relationship between reproductive potential and size varies interannually. We fit location-specific relationships because the relationship between fecundity and female size has been reported to differ between rivers (Healey and Heard 1984) and between locations within large drainages such as the Yukon River (Bromaghin et al. 2011).



**Figure 6: Relationships of female size against reproductive potential for Chinook salmon.** Shown are data points and non-linear fits for fecundity (top) and egg mass (bottom) as a function of female length (left) and body mass (right). Allometric scaling exponents are shown at the top. These Canadian-origin fish were sampled at Eagle in the Yukon River in 2008 to 2010 (data provided by Lara Horstmann, UAF). Note: the exponent of 1.3 for total egg mass as a function of body mass suggests hyper-allometric scaling and matches the average scaling exponent for marine fishes found in a recent meta-analysis (Barneche et al. 2018).

The most comprehensive dataset of female length, body mass, fecundity, and total egg mass was collected in the Yukon River at Eagle during 2008-2010 using consistent methods (Figure 6). Analyses of this dataset showed that reproductive potential of female Chinook salmon measured as total egg mass scales hyper-allometrically with body mass (exponent >1), while reproductive potential measured as number of eggs scales hypo-allometrically with body mass (exponent <1).

We compared the relationships of egg number and egg mass as a function of length to other datasets sampled at different locations within the upper US portion and the Canadian portion of the Yukon River, as well as a dataset collected on Kenai River Chinook salmon. The comparison showed some variation between the estimated exponents, due to either (i) differences in sampling protocols and associated observation error, (ii) location-specific differences in the relationship between reproductive potential and female size, or (iii) interannual variation in the relationships, for those datasets that were collected over multiple years (though year was not supported as covariate in the models). These scaling relationships suggest that fecundity scales to length with an exponent of 2.2-2.5 (Figure 7). In contrast, total egg mass, which accounts for variation in the number and size of eggs and thus reflects the total reproductive potential of a female, scales to length with an exponent of 2.9-4.8 (Figure 8). A potential limitation of measuring reproductive potential as total egg mass produced by a female is that egg mass can change during upstream migration due to changes in water content that do not reflect changes in energy investment, thus making comparisons difficult.



### Figure 7: Relationship of female length versus number of eggs by location. Shown are data points and non-linear fits (for each location, colors) for fecundity versus female length in Chinook salmon. In addition to the main dataset used in this study (red, b=2.4), length-fecundity relationships were fit to samples from the Tanana and upper U.S. mainstem of the Yukon River sampled in 2005 (green, b=1.9, Jasper and Evenson 2006), the Tanana River sampled in 1989 (yellow, b=1.8, Skaugstad and McCracken 1991), the Takhini and Tatchun rivers in the Canadian portion of the Yukon River sampled between 1990 and 2009 (blue, b=1.7, data provided by Fisheries and Oceans Canada), and the Kenai River sampled in 1989 (gray, b=2.0, Fleischman and Reimer 2017).



**Figure 8: Relationship of female length versus total egg mass by location.** Shown are data points and non-linear fits (for each location, colors) for egg mass versus female length in Chinook salmon. In addition to the main dataset used in this study (red, b=4.8), length-fecundity relationships were fit to samples from the Yukon River at Eagle sampled in 2018 (aquamarine, b=3.1, data provided by AYK-SSI), and the Kenai River sampled in 1989 (gray, b=3.6, Fleischman and Reimer 2017).

Length-adjusted fecundity may decrease with migratory distance (Beacham and Murray 1993). For instance, using data on number of eggs per female in combination with genetic information, Bromaghin et al. (2011) showed that female fecundity at a given body length differed between locations within the Yukon River. Females spawning in the upper river carried a smaller number of eggs compared to females of the same size that spawn in the lower river. These differences likely reflect local adaptations to location-specific selection regimes and life-history trade-offs related to in-river migration distances. This is in line with our data (Figure 7), which suggest the lowest fecundity values for upper river fish that migrate farthest to reach their spawning grounds, and likely invest more energy in somatic tissues than populations with less arduous migrations, or resorb egg mass during their migration.

Age may have an effect on female fecundity in addition to length. Skaugstad and McCracken (1991) reported that previous results on the effects of age on fecundity of Chinook salmon are ambiguous and appear to be location-specific. While no differences in age-specific fecundity were found for Yukon River Chinook salmon, a positive relationship between age and fecundity has been reported in other populations such as for Chinook salmon in the nearby Nushagak River (Skaugstad and McCracken 1991). We tested age as a covariate in the log-linear fecundity models where age data were available and found no support for an age effect in the Yukon River samples. This apparent discrepancy may be related to differences in life-history characteristics between populations or may be attributable to the lack of contrast in the Yukon River Chinook salmon data given the large variance in fecundity within age-groups and the relatively low variance in age at reproduction (over 90% of females mature at age 5 or 6), in contrast to other populations that show larger variance in age at reproduction (Healey and Heard 1984).

### Location-specific changes in mean length of spawner populations and landed catch

This analysis addresses the concern that salmon stocks that are sampled in particular locations within the watersheds may have experienced differing exploitation rates or other ecological change across the time series, such that the trends in age, length, and sex composition cannot be represented by one temporal trend. We therefore selected specific locations from the full list of candidate data sets based on a target number of total samples and length of the available ASL time series. In addition, we pooled subsistence samples along the main stem of the upper U.S. portion of the Yukon River where most of the subsistence catch on the Yukon River occurs (Subdistricts Y4 and Y5). Trends in mean length can then be used to calculate the resulting change in average mass, egg production, or caloric value of fish returning to a specific location to evaluate the social and ecological consequences of declines in the mean length of Chinook salmon. The analysis includes location-specific time series based on weirs or handpicked/carcass samples and those based on samples taken from commercial, subsistence, or test fisheries. As illustrated below, changes in the mean length of fish caught in the fisheries can be explained in part by changes in capture methods. Most importantly, over time there has been a shift in the lower Yukon commercial fishery from large (8.5 in) to small (5.5-6 in) mesh sizes (Figure 9).



**Figure 9: Changes in mean date and mesh size proportions of the lower Yukon River fishery.** Shown are the median date (Julian day) in each year when fish were sampled at Emmonak (left), and the proportions among the most common mesh sizes (>100 samples total) used to capture the fish.

The mean length of Chinook salmon caught in the fisheries at Emmonak in the lower Yukon River has declined by ~17%. However, a linear model that accounts for changes in capture date, gear type, and mesh size suggests that the decline in mean length when keeping these factors constant is approximately 6% (Figure 10). Similarly, the mean length of fish caught in subsistence catches on the main stem of the Yukon River has declined by ~10%, while a model accounting for changes in gear type and mesh size suggests an actual length decline in the population of about 6% (Figure 10). In contrast, samples taken in the test fishery at Big Eddy in the Yukon River historically reflected a mix of 5.5 inch and 8.5 inch mesh nets, but have become dominated by large mesh samples since the late 1990s. A year only model suggests a mean length decline of 4%, whereas a model that accounts for changes in mesh size estimates a decline of 7-8% (Figure 10).





Included are locations with catch-based samples from the Yukon (Emmonak, Big Eddy, Subsistence Y4/Y5) and Kuskokwim (Bethel) drainages. Shown are predictions for linear models including only year as categorical variable (gray) and models including year, capture date, gear type and mesh size as variables (blue). Thick lines illustrate long-term trends using a loess smoother. Year predictions for models that accounted for changes in capture methods were made by setting other predictors to the median value (capture date) or the most common category (gear type, mesh size). These categories were 8.5 inch set gillnet for the commercial fishery at Emmonak, the test fishery at Big Eddy, and the subsistence fishery in Subdistricts Y4/Y5, and 8 inch drift gillnet for the commercial fishery at Bethel.

Accounting for changes in gear type, mesh size, and date of sampling, brings the estimated decline for locations based on catch samples much closer to that estimated using weir or handpicked/carcass samples, which is ~5%, 6%, and 8% in the Chena, Salcha, and Kogrukluk Rivers, respectively. This range likely reflects the biological change in the populations sampled, and the remainder of the change observed in the catch samples is not attributable to demographic or life-history changes in these populations. Consequently, the estimated decline in mean length from before 1990 to after 2010 that is not accounted for by changes in capture methods is consistently below 10% across locations in both drainages (Figure 11).



# Figure 11: Percent change in mean length of Chinook salmon sampled at different locations.

Shown are locations with catch-based (blue) or escapement-based (green) samples from the Yukon and Kuskokwim drainages, and the upper U.S. Yukon subsistence catch. Gray bars show the estimated percent decline for models that include only year as categorical variable. Green bars show estimates for models that include year and date of capture (weir/carcass samples). Blue bars show estimates for models that include year, capture date, gear type and mesh size (catch samples). Percentages were computed by comparing years prior to 1990 to years after 2010.

The same models were run using mass (g) instead of length (mm) as response variable based on a length to mass conversion established for Yukon River Chinook salmon ( $M = 8.88e^{-7}L^{3.4}$ ). As expected, the estimated decline was much larger for mean mass compared to mean length. The mean mass of Chinook salmon caught in the commercial fisheries declined by about 46%. However, accounting for changes in capture methods over time resulted in estimates of 17-22%, similar to the estimated change of 18-24% for samples from weir or handpicked/carcass surveys, suggesting that this range reflects the actual biological change in these populations (Figure 12).



# Figure 12: Percent change in mean mass of Chinook salmon sampled at different locations.

Shown are locations with catch-based (blue) or escapement-based (green) samples from the Yukon and Kuskokwim drainages, and the upper U.S. Yukon subsistence catch. Gray bars show the estimated percent decline for models that include only year as categorical variable. Green bars show estimates for models that include year and date of capture (weir/carcass samples). Blue bars show estimates for models that include year, capture date, gear type and mesh size (catch samples). Percentages were computed by comparing years prior to 1990 to years after 2010.

In conclusion, changes in age-sex-length composition of Chinook salmon returning to the Yukon and Kuskokwim rivers account for declines in the mean length of roughly 40-70 mm or 5-8%. However, the mean length of fish captured by subsistence fishers has decreased by about 10%, and commercial fishers have experienced substantially larger reductions between 14% and 17%. The additional reduction in the mean length of fish caught in fisheries can largely be explained by a shift to smaller mesh sizes, especially in recent years. Percent reductions in mean body mass amount to 18-24% in the spawning populations, ~32% in upper U.S. Yukon subsistence catches, and 37-47% in fish caught in commercial fisheries.

### Drainage-wide trends in mean length and reproductive potential of females

### Changes in mean length of females

Models were developed to evaluate demographic shifts at the drainage-wide scale for the Yukon and Kuskokwim Rivers. The analysis of trends in mean length of females over time showed that changes in age composition and length-at-age of Yukon River Chinook salmon are similar, though slightly weaker, compared to trends suggested by the Alaska and coastwide analyses (Lewis et al. 2015; Ohlberger et al. 2018). The length-at-age of older fish is declining and the mean age of all returning fish has declined over time due to lower proportions of those older age groups. The decreasing proportion of older fish and smaller sizes at a given age have led to a reduction in average length of returning females by about 6% (5-8%) since the early 1970s (Figure 13). The combined gear and mesh size effects suggest that the average length of females sampled is smallest for fishwheels, largest for large-mesh (8-8.5 inch) gillnets, and intermediate for smaller-mesh gillnets and spawner surveys (weir or handpicked/carcass samples) (Figure 14).



Figure 13: Changes in mean length of female Chinook salmon returning to the Yukon River. Shown are annual predictions of mean female length based on a mixed effects model that accounts for differences in mean length by gear types (e.g. drift net, set net, fishwheel, weir sampling, etc.) and mesh sizes. Location was included in the model as random effect. Annual predictions were made for gear type 'Weir' (no mesh size). The gray line illustrates the trend in mean length using a loess smoother. The estimated decline in mean length of female Chinook salmon in the Yukon River is 6% (5-8%). Gray bars at the top indicate the relative number of samples each year.

# Figure 14: Fixed gear type and mesh size effects for the Yukon River model.

Shown are estimates for the combined fixed effect of gear type and mesh size. Gear types associated with different mesh sizes were 'Set Gillnet' and 'Drift Gillnet'. Gear type by mesh size combination with at least 500 samples across at least ten years were used in the model. Horizontal lines are medians and bars 95% confidence intervals. Gray bars at the top indicate the relative number of samples in each category. We also estimated changes in mean length of female Chinook salmon in the Kuskokwim River. The average length of females in the Kuskokwim River has declined by roughly 9% (8-12%) since the early 1970s (Figure 15). The combined gear and mesh size effects were uncertain with largely overlapping confidence intervals (Figure 16). The effects estimates might be uncertain because mesh size information was available for a smaller proportion of gillnet fishery samples in the Kuskokwim River (~70%) compared to the Yukon River (~95%). Changes in mesh sizes used to capture the fish might thus not be fully accounted for in this model, and the estimated year effects and resulting time trend are uncertain compared to those for the Yukon River.



# Figure 15: Changes in mean length of females returning to the Kuskokwim River.

Shown are annual predictions of mean female length based on a mixed effects model that accounts for differences in mean length by gear types (e.g. drift net, set net, weir sampling, etc.) and mesh sizes. Location was included in the model as random effect. Annual predictions were made for gear type 'Weir' (no mesh size). The gray line illustrates the trend in mean length using a loess smoother. The estimated decline in mean length of female Chinook salmon in the Kuskokwim River is 9% (8-12%). Gray bars at the top indicate the relative number of samples each year.

# Figure 16: Fixed gear type and mesh size effects for the Kuskokwim River model.

Shown are estimates for the combined fixed effect of gear type and mesh size. Gear types associated with different mesh sizes were 'Set Gillnet' and 'Drift Gillnet'. Gear type by mesh size combination with at least 500 samples across at least ten years were used in the model. Horizontal lines are medians and bars 95% confidence intervals. Gray bars at the top indicate the relative number of samples in each category.

These models were developed to evaluate drainage-wide demographic shifts for river basins that have multiple distinct spawning populations. Hence, a potential limitation of the approach is that it averages trends across a complex of Chinook salmon populations sampled in discrete locations within the watersheds that have distinct local adaptations and may experience different environmental changes, e.g. related to freshwater conditions or ocean distribution, and/or selection regimes over time, for instance related to time of arrival at the river mouth where commercial harvests occur.

### Expected mean length in fishery catches given mesh size

The mean length of fish caught using gillnets depends on the mesh size used to capture the fish and the length distribution of the fish that the gear encounters. To compare the estimated mesh size effects from the mean length models, we simulated the expected mean length caught by a given mesh size in gillnet fisheries using previously estimated mesh size selectivity curves for Yukon River Chinook salmon (Figure 17) taken from Bromaghin (2005). The expected mean length in fisheries catches was simulated for various mesh sizes used in the lower Yukon River gillnet fisheries and for different length distributions of returning fish. We ran simulations across a range of mean lengths in the return with some random variation in the variance and skewness of the length distribution to reflect uncertainty in the estimates (Figure 18).



**Figure 18: Expected mean length in catch depending on mesh size and mean length in return.** The simulation results shown on the right were based on a standard deviation in length of 80mm and a slight skewness of 0.75, which resembles the typical length distribution of female Chinook salmon in the Yukon River. The diagonal dotted line on the left indicates equal mean lengths in catch and return, and the gray vertical line is the example length used for the other two plots. The center plot shows the full length distribution for a mean of 825mm. The right plot shows the expected mean length in the catch based on the 100 simulations (large circles, black bars) in comparison with the estimated effect size from the statistical mean length model (small circles, gray bars). Error bars represent uncertainty that was simulated by drawing random variance and skewness parameters within reasonable ranges (n=100).

The expected mean length in the fishery catches given a mean length in the return of about 825mm (the average value of the predicted year effects for gear type 'Weir' in the Yukon River model) matched closely with the mesh size effects for drift gillnets estimated the linear mixed models of the mean length of female Chinook salmon in the Yukon River (Figure 14).

#### Changes in female reproductive potential

We used the same models to estimate changes in mean fish mass, fecundity, and total egg mass over time. This was done by converting individual observations of length to female body mass, number of eggs, or egg mass, to accurately account for variation in length among individuals sampled in a given year. The estimated change over time depended on how each of these metrics was related to fish length, i.e. the allometric relationships, which were estimated using data for Canadian-origin Yukon River Chinook salmon. The allometric scaling exponents were 3.4 for mass, 2.4 for fecundity, and 4.8 for egg mass. The resulting declines, calculated as the difference between the means for the first and last five years of the time series, were 15% in mean fecundity and 28% in mean egg mass per female for Yukon River Chinook salmon (Figure 19).



# Figure 19: Changes in reproductive potential of female Yukon River Chinook salmon.

Shown are annual predictions of mean female fecundity (number of eggs) and total egg mass based on mixed effects model that account for differences in mean length by gear types and mesh sizes. Individual observations of length were converted to fecundity, body mass, and egg mass using relationships estimated from empirical data for Canadian-origin Yukon River Chinook salmon. The decline in each metric is indicated at the top right, which was calculated as the percent difference between the average of the last five years compared to the average of the first five years (using the point estimates). Annual predictions were made for the gear type 'Weir' (no mesh size). Gray lines illustrate the long-term trend using a loess smoother.

Changes in fecundity and egg mass of Chinook salmon in the Kuskokwim River were estimated using size-fecundity relationships established for Canadian-origin Yukon River Chinook salmon, because river-specific data were not available. The estimated decline was 21% in mean fecundity

and 35% in mean egg mass per female for Kuskokwim River Chinook salmon (Figure 20). As pointed out for the mean length model, effects estimates were uncertain, such that changes in mesh sizes used to capture the fish might thus not be fully accounted for in this model, and the estimated year effects and resulting time trend are less certain than those for the Yukon River.



Figure 20: Changes in reproductive potential of female Kuskokwim River Chinook salmon. Shown are annual predictions of mean female fecundity (number of eggs) and total egg mass based on mixed effects model that account for differences in mean length by gear types and mesh sizes. Individual observations of length were converted to fecundity, body mass, and egg mass using relationships estimated from empirical data for Canadian-origin Yukon River Chinook salmon. The decline in each metric is indicated at the top right, which was calculated as the percent difference between the average of the last five years compared to the average of the first five years (using the point estimates). Annual predictions were made for the gear type 'Weir' (no mesh size). Gray lines illustrate the long-term trend using a loess smoother.

#### Changes in caloric value

In addition to estimating changes in mean length and reproductive potential, we estimated the relative change in energy content of the fish using an established formula to convert length to energy (eqn. 4, O'Neill et al. 2014) and utility factor (dressed head off) for Chinook salmon (Crapo et al. 1993). By applying these relationships, the estimated decline in fish energy content, from the early 1970s to the most recent years, was 16-24% in the Yukon River and 22-33% in the Kuskokwim River. Such changes in caloric value are of particular concern to Alaska Native and First Nation communities that rely on Chinook salmon for their livelihood. In other words, 100 fish caught in the early 1970s provided on average the same amount of energy as roughly 125 or 138 fish caught in recent years in the Yukon River and Kuskokwim River, respectively.

### Drainage-wide trends in proportion of females

### Changes in the proportion of females over time

The analysis of temporal changes in the proportion females of Yukon River Chinook salmon suggests strong interannual variation in the proportion of females but no clear trend over time (Figure 21). The percent females in the population has varied between 31% and 50% since the early 1970s with an average of 40% (based on median values) and a weak declining trend. An apparent trend toward increasing male dominance in the raw samples was mostly driven by changes in the gillnet mesh sizes used in the lower Yukon commercial fisheries. Accounting for mesh size selectivity thus reveals that the underlying change over time in the true population sex ratio is weak for Yukon River Chinook salmon. This model does not allow for location-specific trends in sex ratio, however, and thus identifies the common drainage-wide trend representative of the entire population.



Figure 21: Changes in the proportion female of Yukon River Chinook salmon.

Shown is the proportion female in the population based on an autocorrelated random walk process (top) and effect sizes for various capture methods, i.e. combinations of gear type and mesh size (bottom left), and locations, subdistricts Y1-Y6 and Canada (bottom right). Grey bars at the top indicate the relative number of samples per year. The model offsets further showed significant effects of gear type and mesh size, and location on the proportion females in the samples (Figure 21). The proportion female was smaller than average in samples taken by fishwheels, electrofishing, and small-mesh (5.25-6 inch) drift or set gillnets, larger than average for large mesh (8-8.5 inch) drift or set gillnets, and average in weir samples, handpicked or carcass samples, and samples from medium-sized drift (6.5 inch) or set (7.5 inch) gillnets. The proportion female was close to average in lower Yukon River samples (Y1), average or below average for middle Yukon River samples (Y2-Y5), and above average in upper Yukon River samples (Y6 and Canada). This effect likely results from a combination of sampling design and ecological differences. The proportion female could increase with distance upstream if the smallest fish (predominantly males) cannot migrate as far up the river. On the other hand, lower river samples are primarily from the mainstem commercial fisheries that catch a mix of populations, including those that migrate to upper portions of the watershed. Samples from the lower river are therefore representative of the entire population, whereas samples from the middle and upper river largely represent local populations that spawn in specific tributaries.

For most of the samples in our dataset sex has been determined by external (visual) examination, which can be associated with misclassification error and can introduce bias in the estimated proportion females. The presented model accounts for misclassification error and thus provides an unbiased estimate of the proportion females in the sampled populations. The estimated bias for external sex determination was statistically significant but biologically negligible at the drainage-wide scale, with a median value of -0.02 which corresponds to a bias in the observed proportion female of less than 1%. While considerable error in external sex determination has been reported for lower Yukon River samples (Jasper and Evenson 2006), the probability of sex misclassification is likely small for post-spawner surveys and visual examination of live fish close to the spawning grounds, which make up a large proportion of the data used in this study.



**Figure 22: Comparison of observed and predicted proportion female for the Yukon River.** Shown are the proportion female as observed in the data (black lines/circles) and as predicted by the model (orange, medians and 90% confidence bands) for the two most common combinations of sampling method and location, fish caught using 8.5 inch set gillnets in Subdistrict Y1 (left) and fish sampled in handpicked/carcass surveys in Subdistrict Y6 (right). Average proportions across the time series are shown by dotted horizontal lines. The gray horizontal line indicates a 1:1 sex ratio.

Model predictions were compared to the proportion female in the data for specific sampling methods and locations (by subdistrict). The two most common categories represented throughout most of the time series were fish sampled in the lower river (Subdistrict Y1) commercial fishery using 8.5 inch set gillnets and fish sampled using handpicked or carcass surveys in the upper U.S. portion of the river (Subdistrict Y6), which together accounted for over 50% of all samples. The model accurately predicted the average proportion female across years and the variability in the proportion female for these subsets of the data (Figure 22).

We also compared the model prediction to the proportion female observed in sampling projects that use handpicked/carcass surveys or weirs (Figure 23). The model-predicted proportion female of 0.4 matched the average proportion female observed in these sampling projects. While weir data are unselective with respect to sex, carcass samples have been suggested to be biased toward larger fish and females.



Figure 23: Observed proportion female in Yukon River weir and carcass surveys. Shown is the proportion female for locations with at least 15 years of data that use weirs (red) or handpicked or carcass surveys (yellow). Boxplots represent the distribution of values across years (thick lines are medians, boxes are the interquartile range, and whiskers extend to extreme values). The vertical dotted line is the model-predicted average proportion female, and the gray line is the 1:1 sex ratio.

Moreover, a previous study on the effects of mesh size on capture probability of Chinook salmon in the Yukon River in 2007-2009 compared the age, length, and sex composition of catches using 7 or 8.5 inch mesh gillnets in the lower river drift net fishery, and concluded that while the age and length compositions clearly differed, differences in sex composition were marginal between the two mesh sizes (Howard and Evenson 2010). Specifically, the proportion female in the catch differed between mesh sizes as it changed from 0.33 using 5.5 inch to 0.53 using 8.5 inch mesh sizes. Our model estimates the average proportion female caught in a lower Yukon River drift gillnet fishery using 5.5 and 8.5 inch mesh sizes during those years (2007-2009) as 0.37 and 0.53, respectively (based on median values), in line with previous work.

For the Kuskokwim River our analysis suggests strong interannual variation in the sex ratio and a declining trend over time (Figure 24). The percent female in the population has varied between 23% and 53% since the early 1970s with an average of 37% (based on median values) and shows a declining trend (~7.5% decline between the first and last five years of the time series). Effect sizes for known capture methods were similar to those estimated for the Yukon River.



### Figure 24: Changes in the proportion female ratio of Kuskokwim River Chinook salmon.

Shown is the proportion female in the population based on an autocorrelated random walk process (top) and effect sizes for various capture methods, i.e. combinations of gear type and mesh size (bottom left), and locations, subdistricts 1, 2, 4, undefined, and Goodnews Bay (bottom right). Grey bars at the top indicate the relative number of samples per year. Note the different x-axis scale for the method effect compared to the Yukon River.

Sex-specific marine survival has been documented in Pacific salmon. Decreasing proportions of females from the juvenile to the adult stage have been reported for Chinook salmon, indicating that females experience higher total mortality in the ocean (Olsen et al. 2006). In addition to different maturation schedules, differences in overall marine survival could be caused by sex-specific annual mortality rates. Holtby and Healey (1990) hypothesized sex-specific differences in boldness of coho salmon, i.e. willingness to risk predation to obtain food, with females taking higher risks when foraging at sea in order to attain a larger size. The hypothesis was based on the observation that the difference between female and male size was greatest when the sex ratio was most biased towards males.

An important consequence of a declining trend in the proportion of females in the population is that it is further compounding the negative effects of declining female reproductive potential. Declines in the average reproductive potential of females and in the proportion of females in the population are expected to reduce population production unless spawner abundance increases sufficiently to offset the reduction in total egg potential.

### Hindcasting sex ratios using sex-by-age proportions from known sex data

We applied an alternative approach to estimating the proportion female for specific subsets of the data using sex-by-age proportions calculated from recent known sex data, i.e. samples for which sex was determined internally. We first computed the proportion female by age in the known sex data for each year and fit logit-normal distributions to the age-by-sex proportions across years (Figure 26). We then applied the estimated sex-by-age proportions from the known sex data to other subsets of the data for which age was considered known but sex was considered uncertain.





Hindcasting for subsets of the historical data was performed by repeatedly drawing values from the logit-normal distributions to account for interannual variation in sex-by-age proportions. Example datasets included fishery samples taken in the lower river (Subdistrict Y1) fisheries using 8.5 inch mesh set gillnets, and handpicked/carcass samples taken in the upper U.S. portion of the river (Subdistrict Y6), mainly in the Chena and Salcha rivers (Figure 27). The proportion female in the data and the hindcasted proportion female using sex-by-age proportions from known sex data for these datasets matched, although uncertainty in the hindcast was large.





### Sex ratio and mean length of the largest Chinook salmon

In addition to trend analyses of the sex ratio and mean length of all returning fish, we analyzed changes in sex ratio and mean length of the largest fish that return to specific locations in a given year. On average, females mature later and are larger at age than males. However, in some years and/or locations the oldest males (7 and 8 year-olds) are known to outsize females of the same age. Individuals of total age 7 or older typically account for about 5% of fish sampled. The largest 5% of fish sampled in a given location may differ depending on the sex ratio and the shape of the sex-specific length distributions, and may have changed over time. The female and male length distributions differ primarily because of the different ages at maturation. We used a total of roughly 35,000 samples for which sex was determined using internal examination and is thus considered known to illustrate the characteristics of the male and female length distributions is more skewed toward smaller individuals (primarily age-4 males), and is broader than that of females, suggesting weaker selection on size in males compared to females.



**Figure 28: Length distributions of male and female Yukon River Chinook salmon.** Shown are length distributions of known sex samples for male (gray) and female (orange) Chinook salmon sampled in various locations throughout the Yukon River drainage.

For this analysis, we selected locations that either represent specific spawner populations or aggregates of spawner populations that share similar in-river migration distances. We included mainstem sampling locations in the Canadian portion of the river and those near the border but excluded locations on the lower river mainstem that sample a mixture of stocks bound to various terminal reaches throughout the watershed. None of these sampling projects have experienced substantial changes in capture methods over time. Gear/mesh selectivity was assumed to be independent of sex within the narrow length range analyzed.

We found that the proportion male among the largest 5% of fish is larger further upstream and has declined over time in all locations. The average proportion male across years was low for spawner populations in the lower portion of the watershed (Andreafsky and Gisasa rivers), intermediate for spawner populations in the upper U.S. portion (Chena and Salcha rivers), and high for spawner populations from the Canadian portion of the Yukon River (Figure 29). Only location-specific time series with at least 15 years of data were used for the spatial comparison.



**Figure 29: Proportion male in the largest 5% of fish sampled by location vs distance upstream.** Shown is the proportion male (left) and the logit-transformed proportion male (right) in the largest 5% of fish. Circles and bars represent means and standard deviations across years in a given location. The gray line and shaded area represent a linear regression fit to the median values on logit scale. Not included are lower river mainstem locations that sample a mixture of populations bound to terminal reaches throughout the drainage.

All locations showed a trend toward decreasing male proportions and thus an increasing proportion of females among the largest 5% of all fish (Figure 30). For the Yukon River, the temporal trend and the spatial pattern weaken as a larger portion of the length distribution is considered (e.g. the largest 25% of all fish), and across individuals of all lengths, no trend is detectable and the proportion female slightly increases with distance upstream (see section on drainage-wide model of changes in proportion female over time).



Figure 30: Changes in proportion male in the largest 5% of fish sampled by location. Shown are location-specific time series of proportion male in the largest 5% of all fish sampled. Not included are lower river mainstem locations that sample a mixture of populations bound to terminal reaches throughout the drainage.

We ran a Bayesian Dynamic Factor Analysis of the standardized (z-scored) time series of the proportion male in the largest 5% of all fish sampled in a given location to extract the common time trend and assess how strong each location was associated with that trend. The results clearly revealed a negative trend over time that was shared among all locations, i.e. each location loaded similarly onto the common trend (Figure 31).



Figure 31: Common trend in proportion male in the largest 5% of fish sampled by location.

Shown is the most common trend among the time series (left, median and 90% confidence bands) along with the location-specific loadings (right) from a dynamic factor analysis (DFA). Loadings indicate whether a time series is positively or negatively associated with the trend (sign of loading) and how closely each time series follows the trend (value of loading). Time series were z-scored and only single-trend models were evaluated.

We also found that the mean length of the largest 5% of individuals sampled declined over time (Figure 32). Mean length of the largest fish may be affected by the selectivity of the different gear types, such that we did not compare mean lengths across locations. We analyzed trends in mean length of the largest fish for locations with long-term data series that have used consistent capture methods, i.e. for which size-selectivity was assumed to not have changed over time.



Figure 32: Changes in mean length of the largest 5% of fish sampled by location. Shown are location-specific time series of mean length of the largest 5% of all fish sampled. Not included are lower river mainstem locations that sample a mixture of populations bound to terminal reaches throughout the drainage.

### Effects of reduced reproductive potential on stock-recruitment relationships

A constant proportion of females in combination with declining mean length of females, due to changes in length-at-age and age composition, implies a reduction in total egg mass and hence per capita reproductive potential, as shown here, because reproductive potential increases with body size. This effect of declining size trends on productivity is not accounted for in traditional approaches to analysis of productivity in the AYK region based on recruits per spawner which are based solely on total numbers of returning salmon. We investigated potential management implications of changes in the average reproductive potential of female spawners by comparing the results of two different stock-recruitment analyses. The analyses were built on an existing stock-recruitment model for Canadian-origin Chinook salmon in the Yukon River developed by Jones et al. (2018). Their work included a conventional escapement quantity model that did not consider changes in population demographic structure, and a second model that accounted for changes in female fecundity, i.e. number of eggs, and its effect on recruitment. Here, we updated this model using total egg mass as a measure of the reproductive potential of females, assuming that it would be a better proxy of recruitment success than fecundity.

As a first step, we refit the escapement quantity model using the same model code, data input, and number of iterations as described in Jones et al. (2018) to ensure that the model output was consistent with previously reported results. The original model used a Ricker stock-recruitment function with overcompensation, such that recruitment is assumed to increase up to a maximum and then decline as spawner abundance increases. We extended the spawner quality model and fitted a stock-recruitment function where stock size was expressed in egg mass instead of number of spawners. We used the Ricker model for comparability, and did not test for support of this functional form compared to other models such as Beverton-Holt. The egg mass model showed that maximum recruitment is achieved at an egg mass of about 27 metric tons (Figure 33).



### Figure 33: Relationship between egg mass and recruitment for Canadian-origin fish.

Shown are fitted relationships for the posterior median estimates (thick line) of alpha and beta, and 50 random draws from the posterior samples (thin lines). Estimated data points and their 90% credible intervals are shown in red. Maximum recruitment is achieved where the fitted curve reaches its maximum. We used the fitted model to calculate female abundance that would produce escapement at maximum sustained yield (MSY) for a range of mean female body lengths by applying the same relationship between body length and total egg mass per female that was used to calculate total egg production in the model. We then calculated the spawner escapement at MSY for different proportions of females in the population (Figure 34). This analysis showed that the escapement at MSY increased considerably as mean female length declines. For instance, at a proportion of females in the population of 0.4 (the historical average from the proportion female model), the estimated median escapement at MSY increased by an average of about 2400 spawners for every 10mm decline in mean female length. These numbers are based on posterior medians for the estimated alpha and beta parameters from the stock-recruit relationship. The estimated spawner abundance required to produce maximum sustained yield (using a proportion female of 0.4) was about 45,000 spawners at a mean length of 850mm and about 56,000 spawners at a mean length of 800mm, which is equivalent to a 25% increase in escapement at MSY.



Figure 34: Escapement at MSY as a function of mean length and proportion females. Shown are median posterior estimates (thick lines) and 50% credible intervals (shaded areas) of the spawner escapement that produces maximum sustained yield across a range of mean female body lengths for three different proportions of females in the population: 0.3 (yellow), 0.4 (red), and 0.5 (blue). Note the large uncertainty around these estimates.

We performed a sensitivity analysis of the expected change in escapement at MSY with female length for different scaling relationships between female length and reproductive potential. Instead of using a measure of uncertainty from the fit to the empirical data (Figure 6), which would account for uncertainty in this particular dataset only, we tested a considerably larger range of scaling exponents. We set a lower limit of b=3.4 which corresponded to the scaling exponents of body mass against length, thus reflecting isometric scaling of reproductive output with body length, and an upper limit of b=6.2 to obtain symmetrical uncertainty about the fitted value of b=4.8 used in the stock-recruitment model.

The resulting dependencies of the spawner escapement at MSY as a function of proportion female and mean female length for different assumptions about the size scaling exponent and considering uncertainty in the estimated relationship between egg mass and recruitment showed that the statistical uncertainty of the SR model was much larger compared to uncertainty in the size scaling exponent (Figure 35). The implications of these results are that female length has a measurable effect on expected recruitment, but that the uncertainty in the relationship between recruitment and egg mass is large compared to the effect of female length on escapement at MSY, even given hyper-allometric scaling of reproductive output with female body length.





Shown is the spawner escapement that produces maximum sustained yield ( $S_{MSY}$ ) as a function of mean length and proportion of females for three different exponents of how total egg mass scales with female length (rows) and three different quantiles of the estimated recruitment (columns) using the posterior distributions of the alpha and beta parameters. The center plot reflects the median estimates from the SR model for the empirically estimated size scaling exponent of b=4.8.

Finally, the importance of considering female reproductive potential in stock recruitment models is also discussed in an appendix to this report that summarizes results of a comparison between spawner quality and quantity models for Kuskokwim River Chinook salmon (see Appendix).

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### APPENDIX

# Incorporating Escapement Quality into Spawner-Recruit Analyses for Kuskokwim River Chinook

### A Report to the AYKSSI Escapement Quality Expert Panel

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### Overview

We evaluated the sensitivity of estimates of Smsc for Kuskokwim River Chinook Salmon to the inclusion of measures of escapement quality into spawner-recruit analyses. We define Smsc traditionally as the total number of spawning salmon, regardless of sex, that would be expected to produce maximum sustainable harvest. We explored four different models, two of which did not account for escapement quality and two that did. The two models that did not account for escapement quality were the current Alaska Department of Fish and Game stock-recruitment analysis (ADFG model) and an age- and sex-structured model that used escapement abundance as the measure of reproductive output (i.e., spawners; AS-N Model). For the two escapement quality models, one model used mean age-specific fecundity as the measure of spawners (AS-Fecundity model) and the other used mean age-specific ovary mass, which is hypothesized to be a better predictor of reproductive output because it has the potential to account for egg quality (AS- Ovary Mass model). We had originally considered a fifth model that would account for individual variation in ovary mass, but this model was dropped when simulation analyses indicated that individual variation in ovary mass would not be expected to influence spawnerrecruit analyses and resulting Smsc estimates because individual variation caused a consistent proportional bias in estimates of age specific reproductive output (Appendix A). The models were fitted to Kuskokwim River Chinook Salmon data from 1976 to 2017i n a Bayesian statespace framework using Markov Chain Monte Carlo simulation.

### The Models

### ADFG Model

This model is currently used by ADF&G to perform spawner-recruit analysis for Kuskokwim Chinook. We included this model in the analysis to provide a baseline and frame of reference for comparison with estimates from additional candidate models that attempted to account for escapement quality. The parameters that were estimated by the ADFG model were brood year recruitment, brood year maturity (age-specific proportion of salmon returning to spawn), annual commercial and subsistence fishing mortality rates, and spawner-recruit parameters. The spawner-recruit parameters included alpha, beta, a residual autocorrelation parameter, and the recruitment process variance. The spawner units in the ADFG model was the escapement abundance, which assumed that per capita reproductive output was independent of age, size or sex and was therefore constant over time (Table A1). This assumption also precluded the model from accounting for the effects of size selective harvest on the size/age/sex composition of the escapement. Thus, the model assumed that all age classes were equally vulnerable to harvest.

Age specific maturity was allowed to vary among brood years by sampling from a Dirichlet distribution via a "white noise" process, but the model assumed that mean age-specific maturity was constant over time. Therefore, the model could accommodate some temporal trends in age-at-maturity via the interannual white noise variation, but the hierarchical nature of this process tended to dampen temporal maturity trends via reversion to the mean maturity. The model was fitted to total annual escapement, subsistence harvest, commercial harvest, and aggregate annual age composition estimates that were obtained by pooling all available escapement and harvest age composition data. Escapement estimates were obtained from a run reconstruction model that was recently reviewed by the ADF&G model development team and an independent AYKSSI-funded review panel. Harvest data were obtained from post-season subsistence harvest surveys and commercial trip tickets.

### AS-N Model

The AS-N model (the "AS" stands for age-sex structured and the N stands for escapement abundance) was developed as an age- and sex-structured analog to the ADFG model. We developed this model to serve as a point of reference that, similar to the ADFG model, used escapement abundance as the spawner units, but that could be fitted to the same data as the agesex structured escapement quality models (AS-Fecundity and AS-Ovary Mass; Table A1). The AS-N model was identical to the ADFG model in how it estimated brood year recruitment, spawner recruit parameters, and commercial and subsistence fishing mortality rates. The model was fitted to the same annual escapement and harvest data as the ADFG model. However, the AS-N model differed from the ADFG model in how it handled maturity. The AS-N model also estimated sex composition and vulnerability to harvest, which the ADFG model did not. The model was fitted to the ADFG composition data that were disaggregated into separate age- and sex-specific tables for escapement, commercial harvest, and subsistence harvest. To accommodate the disaggregated composition data, the model estimated a time-invariant sex ratio and sex-specific maturity schedules to facilitate model predictions of the sex-specific composition data. The model also estimated age-, sex-, and gear-specific vulnerability to harvest to as a function of the ratio of age- and sex- specific mean length to the length of the perimeter of the gill net mesh (Bromaghin 2005). The model estimated four parameters of the relationship between vulnerability and the fish length:mesh perimeter ratio, which was assumed constant over time and between gears, sexes, and ages. From this relationship, vulnerability was predicted for two different gear types: an unrestricted gill net mesh fishery for the years and fisheries (commercial or subsistence) in which mostly 8-inch stretch mesh were used, and a restricted mesh case for years and fisheries that used mainly 6-inch mesh. The particular mesh size for each fishery varied over time for both the commercial and subsistence fisheries depending on management actions but generally unrestricted mesh was more common early in the time series and for subsistence fisheries, except for recent years in which mesh size was mostly restricted even for the subsistence fishery. Annual mean length-at-age and sex estimates were obtained from ADFG ASL sampling of the escapement at weirs. These data were obtained from the AYK Database Management System. We would have preferred to use a more representative estimate of mean length because escapement mean length is likely biased from downriver harvest. However, harvest ASL data were too sparse to be useful. We wrote a simulation to explore the potential bias in escapement mean length due to size-selective harvest and found that these biases were generally less than 5%. We re-ran the model after correcting the mean length data for the

bias and the resulting estimates were essentially unchanged. Thus, were moved forward with the escapement mean length estimates to predict vulnerability to harvest.

# AS-Fecundity Model

The AS-Fecundity model was fitted to the identical data as the AS-N model, but this model used the mean age-specific fecundity of the female escapement as the spawner units. Therefore, this model assumed that only the females in the population contributed to reproduction and that total reproductive output was proportional to the number of eggs that were carried by spawning females (Table A1). Mean age-specific fecundity was estimated as a deterministic linear function of escapement mean body mass which was developed from Yukon River Chinook Salmon (Jasper and Evenson 2006) because raw data or published body mass-fecundity relationships do not exist for Kuskokwim Chinook. Mean body mass was predicted as a power function of mean body length (mm) from the same Yukon Chinook data in Jasper and Evenson (2006). Mean body length was estimated from escapement ASL data collected at weirs throughout the Kuskokwim River drainage since 1976. Maturity was handled differently in the AS-Fecundity model than the AS-N model. In the AS-Fecundity model, age- and sex-specific brood year maturity vectors were again assumed drawn from a Dirichlet distribution, but the estimated mean maturity proportions were allowed to follow a time trend via a baseline-category logit model that estimated additional slope parameters, one for each sex and age class. The time trend in mean maturity allowed the model to better accommodate observed reductions in age-at-maturity for Kuskokwim Chinook since the beginning of the data time series. In addition to the maturity trend, the AS-Fecundity model allowed for a logistic time trend in sex ratio (i.e., proportion females in each cohort). All other components of the model were identical to the AS-N model.

# AS-Ovary Weight Model

The AS-Ovary Weight model was identical to the AS-Fecundity model except that the spawner units were mean age-specific ovary mass (g) of the females in the escapement (Table A1). Mean ovary mass was deterministically predicted as a power function of mean length-at-age according to data from the Kogrukluk River weir (J. Ohlberger personal communication). The mean length data were identical to those used in the AS-Fecundity model.

# Analysis

# Model Fitting

All models described above were fitted using Bayesian integration with MCMC methods to sample from the joint posterior probability distribution. MCMC sampling was conducted using parallel computing with the JAGS software implemented through R. MCMC sampling was conducted using five chains with different initial values to verify convergence and to detect potential multiple solutions. Convergence of the chains was assessed with visual inspection of the posterior distribution sampled by each chain, trace plots, and the Brooks-Gelman-Rubin statistic. MCMC sampling for all model runs involved a burn-in period of 100,000 iterations, 500,000 post-burn-in iterations, and a thinning interval of 250 iterations. These specifications resulted in 10,000 posterior samples retained for analysis.

# Estimation of Reference Points

The management implications from the models were compared by evaluating differences in estimates of the biological reference point Smsc, the equilibrium escapement abundance (number

of salmon regardless of sex) that produces maximum sustained harvest. Smsc was obtained via iterative numerical search by finding the instantaneous fishing mortality of fully-vulnerable fish (Fmax) that maximized equilibrium harvest using an equilibrium spawner-recruit model. Separate equilibrium models were developed for each spawner-recruit model. Equilibrium harvest was a function of the spawner-recruit parameters and the fishing mortality rate, and for the AS- models, it was also a function of mean maturity, mean sex ratio, mean vulnerability, and the mean per capita spawners. Per capita spawners was set at a constant value of 1.0 for the ADFG and AS-N models. Equilibrium recruitment was partitioned into numbers-at-age/sex according to the maturation schedule. Fishing mortality was applied on an age- and sex-specific basis to obtain equilibrium escapement and total harvest. Total harvest was maximized by iteratively changing the fishing mortality Fmax. When a maximum was found, convergence was verified and equilibrium escapement was accepted as Smsc. This model was fitted individually for all posterior samples so that posterior uncertainty in the input quantities from the spawnerrecruit model could be propagated into Smsc. The model was run under the different gears (restricted and unrestricted) separately to allow for derivation of Smsc under the different vulnerability scenarios. To assess the effects of temporal trends in age/sex composition and mean length-at-age/sex on Smsc in the AS-Fecundity and Ovary Mass models, three versions of this routine were run for each gear scenario and estimation model: one using age/sex-specific maturity, fecundity, and vulnerability averaged across the first 10 years of the time series, one scenario using the last 10 years, and one scenario using the average of all years. Iterative derivation of Smsc using posterior samples was implemented via numerical optimization using the optim() function in R.

### Results

Relative reproductive output among age classes in the escapement quality models depended on whether fecundity or ovary mass was used as the spawner units (Figure A1). Older age classes contributed considerably more to reproduction than younger age classes when using ovary mass units when compared with fecundity units. Thus, it appears that under ovary mass units, the value of older females would be much higher than when using fecundity as the spawner units. Older females also contributed relatively more to reproduction early in the time series rather than late and this pattern was consistent between the two types of spawner units.

Vulnerability was dome-shaped and highest for age-5 females under unrestricted mesh (Figure A2). Under the restricted mesh, vulnerability declined with age and was highest for age-4 males. Temporal variation in vulnerability was evident owing to variation in mean length-at-age and sex. Vulnerability was generally higher early in the time series than late for the unrestricted mesh, and the opposite was true under restricted mesh.

Estimates of total annual reproductive output (i.e., spawners) varied over time from a low of around 20% (0.2) and a high of around 140% (1.4) of the unfished level (Figure A3). All of the models depicted a similar general pattern in reproductive output over time but the AS-Fecundity and Ovary Mass models tended to produce larger estimates than the other two models early in the time series and smaller estimates later in the time series. This finding is consistent with data indicating that per capita fecundity has declined over time for this stock as a result of smaller size-at-age, lower relative abundance of females, and younger age-at-maturity, all of which were accounted for by the AS-Fecundity and AS-Ovary Mass models, but not the ADFG and AS-N

models. In recent years, the AS-Ovary Mass model consistently produced the smallest estimates of reproductive output presumably because the AS-Ovary Mass model places higher value on the older female age classes that have become less abundant and smaller since 2000. Figure A4 more clearly depicts the time trends in per capita fecundity as estimated by the AS-Fecundity and Ovary Mass models. Both of the escapement quality models estimated that per capita reproductive output has declined over time. The AS-Fecundity model indicated a 35% decline from an average of around 81% of the maximum in the first 10 years of the time series to around 52% in the last 10 years (Figure A4). The AS-Ovary Mass model indicated a steeper decline of 47% from an average of around 75% of the maximum in the first 10 years of the time series to around 40% in the last 10 years. Inspection of spawner-recruit scatter plots revealed no substantial differences in the overall patterns although the locations of individual spawner-recruit pairs varied somewhat across models (Figure A5).

Estimates of Smsc were similar between the ADFG (mean Smsc = 69,000; 95% CI: 69,000 -100,000) and AS-N models (mean Smsc = 67,000; 95% CI: 54,000 - 93,000; Figure A6). For the AS-Fecundity and Ovary Mass models, Smsc depended on gear and the time period over which maturity, mean length-at-age, and sex ratios were considered. Specifically, Smsc for the unrestricted mesh gear was 59% and 66% larger for the AS-Fecundity and AS-Ovary Mass models, respectively, when considering the most recent 10 years of data compared with the first 10 years of data. Smsc did not increase as strongly as a function of time for the restricted mesh gear and was 20% higher for the AS-Fecundity model and 40% higher for the AS-Ovary Mass model in the last vs. the first 10 years. Thus, there are strong effects of temporal changes in per capita fecundity on Smsc, and these effects are not available for consideration from the ADFG and AS-N models. Overall the AS-Ovary Mass model produced slightly larger Smsc estimates than the AS-Fecundity model, but both models produced substantially larger Smsc than the other two models for the unrestricted mesh gear and slightly smaller Smsc for the restricted mesh. The effect of gear on Smsc when considering escapement quality suggests a trade-off whereby lower escapement goals could perhaps be implemented if stakeholders were willing to accept consistently using smaller restricted-mesh gear. These sorts of trade-offs are important to consider but are only available from spawner-recruit analyses such as the AS-Fecundity and Ovary Mass models that account for escapement quality.

### References

Bromaghin, J. F. 2005. A versatile net selectivity model, with application to Pacific salmon and freshwater species of the Yukon River, Alaska. Fisheries Research 74(1-3):157-168.

Jasper, J. R., and D. F. Evenson. 2006. Length-girth, length-weight, and fecundity of Yukon River Chinook salmon Oncorhynchus tshawytscha. Alaska Department of Fish and Game, Division of Sport Fish, Research and Technical Services.

	Model				
Model Component	ADFG	AS-N	AS-Fecundity	AS-Ovary Mass	
Data					
escapement	time	time	time	time	
harvest	time, fishery	time, fishery	time, fishery	time, fishery	
run composition	age, time				
escapement		age, sex, time	age, sex, time	age, sex, time	
composition					
harvest composition		age, sex, time, fishery	age, sex, time, fishery	age, sex, time, fishery	
spawner units	escapement (M+F)	escapement (M+F)	fecundity (F only)	ovary mass (F only)	
mean total length		age, sex, time	age, sex, time	age, sex, time	
Model					
vulnerability		f(length age,sex,time,gea	f(length age,sex,time,gea	f(length age,sex,time,gea	
		r)	r)	r)	
mean maturity	f(a)	f(age, sex)	f(age, sex, time)	f(age, sex, time)	
maturity time variation	white noise	white noise	logit-linear trend	logit-linear trend	
sex ratio		constant	logit-linear trend	logit-linear trend	
mean recruitment	Ricker	Ricker	Ricker	Ricker	
recruitment variation	ar1	ar1	ar1	ar1	

Table A1. Summary of the data and essential components of four Kuskokwim River Chinook Salmon spawner-recruit models.



Figure A1. Relative age-specific female reproductive output (i.e., spawners) as a proportion of mean age-4 spawners for mean fecundity (solid lines) and ovary mass (dashed lines), and for the first 10 years of the time series (blue lines), all years (black lines), and the last 10 years (red lines).



Figure A2. Age specific vulnerability to harvest for females (solid lines) and males (dashed lines) from the AS-Ovary Mass model for the first 10 years of the time series (blue), all years (black), and last 10 years (red) under unrestricted (upper panel) and restricted mesh gear (lower panel). Vulnerability estimates from the AS-N and AS-Fecundity models were nearly identical to the AS-Ovary Mass models as were therefore not shown here for the sake of efficiency.



Figure A3. Time series of spawners for each of four Kuskokwim River Chinook Salmon stockrecruitment models that differed in terms of model structure and/or the units of spawners. Models ADFG and AS-N used the number of spawning salmon (i.e., escapement) as the units of spawners; model AS-Fecundity used mean age- sex- and year-specific fecundity, and model AS-Ovary Mass used mean age- sex- and year-specific ovary mass. All three of the AS models were fitted to age- sex- and year-specific escapement and harvest data whereas the ADFG model was fitted to pooled age- and year-specific population age composition data.



Figure A4. Time series of per capita spawners as a proportion of the maximum value for two age- and sex- structured Bayesian state-space spawner-recruit models. Annual per capita spawners was obtained by dividing the total annual spawners by the escapement (total number of spawning salmon regardless of age and sex). The units of spawners was mean age-specific fecundity for the AS-Fecundity model as was mean age-specific ovary mass for the AS-Ovary Mass model.



Figure A5. Recruitment (number of returning salmon as a proportion of the theoretical unfished recruitment, R0) as a function of spawners (proportion of the theoretical unfished spawners, S0) for each of four Bayesian state-space spawner-recruit models fitted to Kuskokwim River Chinook Salmon data. The spawner-recruit pairs were plotted as the median of the posterior distributions with error bars representing the 95% credible intervals. The estimated spawner recruit relationship is depicted as the solid black line with the grey shaded area representing the 95% credible interval of predicted recruitment. The dashed line depicts the 1:1 replacement line. The numbers associated with the spawner-recruit pairs indicate the brood year.



Figure A6. Escapement (thousands of salmon) associated with maximum sustainable harvest (Smsc) estimated from four different spawner-recruit models: ADFG, AS-N, AS-Fecundity, and AS-Ovary Mass. Smsc depends on per capita reproductive output, which varies over time, and as a function of the differential exploitation across age/sex classes (i.e., vulnerability). Therefore, separate Smsc estimates were obtained for restricted (<=6" stretch mesh) and unrestricted (>6" stretch mesh) mesh size cases to depict the effects of gear-specific vulnerability. For each vulnerability scenario, three separate Smsc estimates were otained to represent the effects of time varying maturity, sex ratios, and size-at-age on per capita fecundity. The first case estimated Smsc using the maturity, sex ratios, and length-at-age from the first 10 brood years of the tmie series (1976-1985; blue boxes), the second used those quantities from all brood years (1976-2013; black boxes), and the third used only the 10 most recent brood years of maturity, sex ratios, and length-at-age (2004:2013; red boxes). The midpoint of each box depicts the median, the box indicates the central 50<sup>th</sup> percentile, and the whiskers show the 95% credible intercal of the posterior distribution of Smsc.