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Estimates of biological reference points for the Canadian-origin Yukon River mainstem Chinook Salmon (*Oncorhynchus tshawytscha*) stock aggregate

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The Yukon River Basin is one of the largest salmon producing river basins in the world and Chinook salmon (*Oncorhynchus tshawytscha*) from the river have historically supported commercial, subsistence, and First Nations fisheries in both Alaska and Canada. The Yukon River Chapter of the Pacific Salmon Treaty specifies a spawning escapement goal for Canadian-Origin Mainstem Yukon River Chinook salmon which has been revised over time and considered interim in nature until a comprehensive review and analysis of available data could be completed. To inform a biologically based aggregate escapement goal we developed a semi integrated state-space run reconstruction and spawner-recruitment model fit to data (1981-2019) from various assessment projects that estimate mainstem passage, harvests, tributary escapements, stock-proportions, and age-composition, under a single Bayesian estimation framework. We found that the Canadian-origin Yukon River Chinook salmon stock aggregate is moderately productive. Equilibrium stock size (S_{EQ}) was estimated to be 110,601 (95% CRI: 81,708-234,252, the spawner abundance expected to maximize long-term sustainable yield (S_{MSY}) was estimated to be 43,125 (29,874-93,070) and the spawner abundance expected to maximize recruitment (S_{MSR}) was estimated to be 70,447 (41,094-186,200). Female Chinook salmon age at maturity, and to a lesser extent the proportion of females in the spawning population, has declined over time. We adapted the integrated state-space run reconstruction and spawner-recruitment model to account for these demographic changes and found that the spawner abundance expected to maximize yield or recruitment was estimated to be on average 13% and 19% greater, respectively, in recent years than in our baseline analysis that did not take demographic changes in escapement into consideration. We outline key considerations when developing an escapement goal based on the information we provide and conclude with recommendations for future work. These include a more comprehensive consideration of the consequences of demographic change in the spawning stock and explicit consideration of trade-offs between the harvest rates, and escapement goals, predicted to maximize aggregate yield (or recruitment) and risk to individual weak (less productive) populations within the Canada stock aggregate. We also recommend undertaking a Management Strategy Evaluation that quantifies trade-offs among a broad range of objectives and evaluates the ability of alternative management strategies to meet them as part of a collaborative process with fishery participants, Traditional Knowledge holders, and resource managers.

1. INTRODUCTION

1.1. BACKGROUND

The Yukon River is one of the largest and most isolated river systems in North America, draining over 850,000 square kilometers and flowing from its headwaters in northern British Columbia through the Yukon Territory and Alaska before emptying into the Bering Sea. The Yukon River is also one of the largest salmon producing river basins in the world and Chinook salmon (*Oncorhynchus tshawytscha*) spawn throughout it. Within the Canadian portion of the basin, Chinook salmon spawn in hundreds of streams (Brown et al. 2017) which, under Canada's Wild Salmon Policy (DFO 2005), are considered to make up nine genetically and ecologically unique groups of salmon or Conservation Units (Holtby and Ciruna 2007). These Chinook salmon have a stream-type life history in which juveniles emerge from spawning beds in the spring, remain in freshwater for a year or two (Bradford et al. 2009), migrate from freshwater to the Bering Sea in the spring and summer as 1- or 2-year-old smolts, and remain in the ocean for 2-6 years before returning to the Yukon River as adults in May-July (Gilbert 1922). Returning adults migrate upstream to spawning areas during the summer months and die after spawning in the fall. Chinook salmon from the Canadian portion of the basin enter the Yukon River earlier than those that spawn in Alaska and migrate upstream for up to 3,200km to reach their spawning grounds. As a result of their long freshwater migrations, Canadian origin Yukon Chinook salmon are generally thought to have relatively larger body size, proportionally older age-classes, and proportionally more females that are less fecund than Chinook salmon that spawn in the lower, Alaskan, portions of the river (Bromaghin et al. 2011).

Yukon River Chinook salmon historically supported commercial, subsistence, recreational, and First Nations fisheries. In 2002, Canada and the United States finalized the Yukon River Chapter of the Pacific Salmon Treaty (1985) where a spawning escapement goal for Canadian-Origin Mainstem Yukon River Chinook salmon was set at 33,000 to 43,000. At the time, this escapement goal was considered optimal for the intended purpose of preventing long-term declines in salmon productivity (JTC 1987a, pg. 22) and stabilizing long-term expected harvest over a 20-year period (JTC 1987b, pg. 47). The escapement goal was based on available data and understanding of the dynamics of the stock at that time. Since then, the number and type of assessment projects for Chinook salmon within the Yukon River have increased, and run sizes have generally declined, resulting in variations in the spawning escapement goal over the last two decades. These revised spawning escapement goals have always been considered interim in nature, until such time that a comprehensive review and analysis of available data could be completed, and the Yukon River Salmon Agreement could be updated to reflect a new goal. There have been multiple analyses of Yukon River Chinook salmon dynamics relevant to escapement goal considerations over the years including run reconstructions, spawner-recruitment analyses, and closed-loop simulations (summarized in Appendix A). However, to date there have not been any formal joint Canada and U.S. efforts to comprehensively review and analyze available data to inform the development of a revised escapement goal.

The U.S. / Canada Yukon River Joint Technical Committee (JTC) is composed of multiple Canadian and U.S. entities and provides technical support to the Yukon River Panel (Panel). The JTC is charged with investigating alternative approaches to determining total run size and escapement and making recommendations on spawning escapement objectives. Furthermore, based on recommendations of the JTC, the Panel may recommend spawning escapement objectives

for implementation by the Canadian and U.S. governments through their management entities (Canada Department of Fisheries and Oceans [DFO] and Alaska Department of Fish and Game). In April 2019, the JTC decided to undertake a quantitative review of the Canadian-origin Chinook salmon escapement goal. This action was in response to the Panel's expressed desire to explore the possibility of establishing a biologically-based escapement goal for this stock. As a first step, the JTC formed a bilateral working group to review available data, develop statistical models, and estimate key biological reference points for the purpose of informing subsequent discussions and escapement goal recommendations.

This report documents the methods used to estimate biological reference points for the Canadian-origin Mainstem Yukon River Chinook salmon stock. The JTC requested bilateral peer review and science advice to ensure the models and results presented in this report are technically sound and appropriate for informing escapement goal recommendations consistent with the State of Alaska's Policy for the Management of Sustainable Salmon Fisheries (Alaska Board of Fisheries 2000) and Policy for Salmon Escapement goals (Alaska Board of Fisheries 2001), Canada's Policy for Conservation of Wild Pacific Salmon (DFO 2005), DFO's Precautionary Approach (DFO 2009), and emerging requirements under the 2019 amendments to Canada's Fisheries Act (DFO 1985).

1.2. OBJECTIVES

The specific objectives of this research document are to:

1. Develop a Bayesian integrated state-space run reconstruction and spawner-recruitment model and fit it to available data.
2. Derive estimates of biological reference points (e.g., S_{MSY} , S_{EQ} , S_{MSR} , S_{GEN}) and associated profiles (e.g., yield and recruitment).
3. Document and examine the consequences of key data and methodological assumptions related to data weighting, biases in data, priors, and model structure.
4. Explore, to the extent possible with available data, the sensitivity of biological reference points to change in escapement quality (e.g., total fecundity and egg mass) over time.
5. Provide guidance on key considerations for next steps to identify an escapement goal and recommendations for future analyses and research to further develop them.

2. METHODS

2.1. OVERVIEW OF ANALYTICAL APPROACH

We developed an integrated state-space run reconstruction and spawner-recruitment model (Figure 1) that was adapted from the multi-stock run reconstruction and state-space spawner-recruitment frameworks of Hamazaki (2021) and Fleischman et al. (2013), respectively. The model combines historical data (1981-2019) from various assessment projects that estimate mainstem passage, harvests, tributary escapements, stock-proportions, and age-composition, under a single Bayesian estimation framework. The run reconstruction component of the model reconstructs historical harvest and escapement for three Chinook salmon stock aggregates: the lower, middle, and upper (Canada) portions of the Yukon River basin. The key quantities estimated by the spawner-recruitment component of the model applied only to the Canadian aggregate stock, and included estimates of intrinsic productivity and the magnitude of density dependence from which biological benchmarks and inference about expected yield and recruitment across a range of future spawning escapements were derived.

We used a multi-stock run reconstruction model, as opposed to reconstructing only the Canada stock, in order to take full advantage of available assessment information. The multi-stock approach allowed our estimates of Canada-origin abundance to be informed by a wide range of projects: those designed to assess the Canada stock; multi-stock assessment projects; and projects directed at other stocks that exist in concert with the Canada stock. By simultaneously estimating all three of the major stock components, the estimates of Canada stock total run, harvest, and escapement were expected to be better informed and prevent conflicting estimates between drainage wide and stock-specific run sizes.

We chose to develop and fit an integrated run reconstruction and spawner-recruitment model, as opposed to sequential analyses, in order to preserve the complete information content of the data (Staton et al. 2017). The model simultaneously reconstructs the annual run size of Canadian-origin Chinook salmon by partitioning harvest and escapement, estimates parameters describing the relationship between observed spawning abundance and estimated recruitment, and quantifies derived parameters of interest (i.e., biological reference points). This allowed for more complete propagation of uncertainty in the analysis due to missing information, measurement error, and process variation. It also enhanced our diagnostic ability by allowing us to more seamlessly evaluate the influence of specific data types and assessment projects on biological reference points. While we refer to our model as “integrated” throughout this document, the manner in which we integrated the run reconstruction and spawner-recruitment model is best described as “semi” or “partially” integrated because it was not as fully integrated as it could (i.e., it did not share leading parameters among sub-models) and describe and justify our approach further in Section 2.3.4.

2.2. DATA SOURCES

A comprehensive review of available data that is potentially useful for reconstructing the abundance and dynamics of Canadian-origin Yukon River Chinook salmon was undertaken as part of a complimentary effort to this report (Pestal et al. 2022). The data review spanned assessment projects for Chinook salmon across the Yukon River Basin including mainstem passage (e.g., sonar, fishwheels, and mark-recapture projects), tributary escapement (e.g., weir, tower, aerial, and sonar projects), harvest estimation, and associated biological sampling (e.g., genetics and age, sex, and length information for stock apportionment). The individual sources of data,

including types and years, that were used to fit the integrated (run reconstruction and spawner-recruitment) model are provided in Figure 2 and specific details on how they were incorporated into the analysis are provided in Section 2.3.

The data sources we fit the run reconstruction sub-model to represent nearly all long-running (i.e., generally >10 yrs.) assessment projects in the U.S. and Canada, for which large numbers (i.e., >1,000) of Chinook salmon have been observed at least once, and for which data were readily available. The specific datasets that we decided not to use are detailed in Pestal et al. (2022) (see Table 8, Table 9, and section 4.1.1) along with rationale for their exclusion. The most common reasons a dataset was not incorporated into the run reconstruction model was due to missing data, inconsistent assessment methodology, too short of a time series, or data not readily available.

Known, and potential, biases in the data sources we used exist. A review of the most likely biases is provided in Appendix B along with an exploratory analysis into their potential implications for estimation of biological reference points.

2.3. INTEGRATED RUN RECONSTRUCTION AND SPAWNER RECRUITMENT MODEL

The integrated run reconstruction and state-space stock-recruitment analysis (RR-SRA) framework we developed for Canadian-origin Yukon River Chinook salmon is comprised of two components: (1) a run reconstruction sub-model that partitions harvest and estimates of annual run size for the Lower, Middle, and Canada stocks, and (2) a stock-recruitment analysis sub-model that quantifies the relationship between reconstructed recruitment and spawning abundance for the Canada stock, and estimates quantities of interest for management based on attributes of the theoretical stock-recruitment relationship. Here we describe each sub-model separately as well as their points of integration. Variable definitions for the integrated model are provided in Table 1.

2.3.1. Run reconstruction sub-model structure

The run reconstruction sub-model is based on the methods described in Hamazaki (2021) and are excerpted below. The model leverages a wide range of spawning abundance and river passage indices, along with harvest and genetic composition of harvest data to estimate annual run size for the Lower, Middle, and Canada stocks.

For simplicity, we describe the run reconstruction model in three steps. First, we present an overview of a single-stock run reconstruction framework, introduce the necessary extensions to accommodate multiple stocks, and present a conceptual multi-stock run reconstruction. Then, we describe how the conceptual multi-stock model was applied to Yukon River Chinook salmon by introducing each stock component's progression, from entry into the river mouth to the spawning grounds. This progression of stocks through the drainage aligns with the model structure and available data. Finally, we describe the specific observational model and statistical models associated with inriver run assessment, harvest, and escapement.

2.3.1.1. Single-stock run reconstruction model

In a single-stock run reconstruction modeling framework (e.g., Bue et al. 2012; Bue and Hamazaki 2014), the observed quantities consist of yearly (y) total harvest (H_y), tributary (i) escapements ($e_{y,i}$), and at least a few years of total run size estimates (N_y).

In this framework, for each year, harvest (H_y) is modeled as a fraction (i.e., fishing harvest rate) (U_y) of the total run (N_y):

$$H_y = U_y N_y \quad (1)$$

total escapement (E_y) is modeled as the run minus harvest:

$$E_y = N_y - H_y \quad (2)$$

and observed escapements from the subset of monitored tributaries ($e_{y,i}$) are modeled as time-invariant scalars (K_i) of the drainage-wide escapement:

$$e_{y,i} = \frac{E_y}{K_i} \quad (3)$$

Note that monitored tributary escapements are not required to sum to the total escapement. Predicted model quantities of \hat{N}_y , \hat{H}_y , and $\hat{e}_{y,i}$ are fit to observed quantities of N_y^{obs} , H_y^{obs} , and $e_{y,i}^{obs}$, respectively, using appropriate log-normal distributional assumptions (Equ. 4). By doing so, the annual harvest rates U_y and tributary fractions of total escapement K_i may be estimated.

The full single-stock run reconstruction is therefore described by log-normal distributions for escapement, harvest, and the total run ($q = 1$) or total run index ($0 < q < 1$):

$$\begin{aligned} \ln(e_{y,i}^{obs}) &\sim N(\ln(\hat{e}_{y,i}), (\sigma_i^{obs})^2) \\ \ln(H_y^{obs}) &\sim N(\ln(\hat{H}_y), (\sigma_{(H)y}^{obs})^2) \\ \ln(N_y^{obs}) &\sim N(\ln(q\hat{N}_y), (\sigma_{(N)y}^{obs})^2) \end{aligned} \quad (4)$$

where σ_i^{obs} is an observed lognormal standard deviation of tributary escapement i , $\sigma_{(H)y}^{obs}$ is an observed lognormal standard deviation of the drainagewide harvest in year y , and $\sigma_{(N)y}^{obs}$ is an observed lognormal standard deviation of the drainagewide run size in year y . Allowing for a systematic underestimate in the observed total run size, q estimates the fraction of the true total run size observed through assessment and is restricted to values between 0 and 1.

2.3.1.2. Multi-stock run reconstruction model

In a multi-stock run reconstruction framework, additional required observed quantities consist of tributary escapements by stock, total harvest by stock or harvest stock proportions, and at least a few years of total or stock-specific run and run stock proportion data. In this framework, total run, escapement, and harvest consist of the sum of individual stocks (s):

$$\begin{aligned} N_y &= \sum_s N_{y,s} \\ E_y &= \sum_s E_{y,s} \\ H_y &= \sum_s H_{y,s} \end{aligned} \quad (5)$$

In the multi-stock framework, harvest (H) and run (R) stock proportions are additional observed quantities. Harvest stock proportions ($P_{(H)y,s}$) are modeled as fractions of each stock's harvest to total harvest:

$$P_{(H)y,s} = \frac{H_{y,s}}{H_y} \quad (6)$$

Run stock proportions ($P_{(R)y,s}$) are modeled as fractions of a stock-specific run to a total run:

$$P_{(R)y,s} = \frac{N_{y,s}}{N_y} \quad (7)$$

The model estimated stock proportions ($\hat{P}_{(H)y,s}$ and $\hat{P}_{(R)y,s}$) are fit to observed proportions of each stock ($P_{(H)y,s}^{obs}$ and $P_{(R)y,s}^{obs}$) assumed to have a multinomial distribution with effective input sample sizes $n_{(H)y}$ and $n_{(R)y}$, respectively (Equ. 8). When at least one stock-specific run estimate ($N_{y,s}$) is available, Hamazaki and DeCovich (2014) showed that total run (N_y) could be estimated by applying genetic mark-recapture techniques ($N_y = \frac{N_{y,s}}{P_{(R)y,s}}$). Equ. 8 (below) is equivalent to fitting to the observed stock-specific run (L2) and stock proportions (L4) simultaneously. Additionally, total run size may be observed through annual survey methods (L6).

As in the single-stock model, observed data is modeled as realizations of underlying distributions with expectations equal to model predicted values. We assumed a log-normal distribution for escapement, harvest, and inriver counts to accommodate the expectation that estimation error is proportional to the mean. A multinomial distribution is assumed for observed counts of fish from each stock in harvest and passage monitoring programs to model the expectation that each stock comprises different proportions of the total annual run.

$$\begin{aligned}
 & \text{Tributary escapements (L1)} \\
 & \ln(e_{y,s,i}^{obs}) \sim N(\ln(\hat{e}_{y,s,i}), (\sigma_{y,s,i}^{obs})^2) \\
 & \text{Stock-specific run (L2)} \\
 & \ln(N_{y,s}^{obs}) \sim N(\ln(\hat{N}_{y,s}), (\sigma_{(N)y,s}^{obs})^2) \\
 & \text{Harvest (L3)} \\
 & \ln(H_{y,s}^{obs}) \sim N(\ln(\hat{H}_{y,s}), (\sigma_{(H)y,s}^{obs})^2) \\
 & \text{Run stock proportion (L4)} \\
 & n_{(R)y} P_{(R)y,s}^{obs} \sim \text{Multinomial}(n_{(R)y}, \hat{P}_{(R),y,s}) \\
 & \text{Harvest stock proportion (L5)} \\
 & n_{(H)y} P_{(H)y,s}^{obs} \sim \text{Multinomial}(n_{(H)y}, \hat{P}_{(H),y,s}) \\
 & \text{Total run (q=1) or total run index (0<q<1) (L6)} \\
 & \ln(N_y^{obs}) \sim N(\ln(q\hat{N}_y), (\sigma_{(N)y}^{obs})^2)
 \end{aligned} \quad (8)$$

where $\sigma_{y,s,i}^{obs}$ is a standard deviation of a tributary escapement observation, $\sigma_{(N)y,s}^{obs}$ is a standard deviation of a stock-specific run size, $\sigma_{(H)y,s}^{obs}$ is a standard deviation of a stock-specific harvest, and $\sigma_{(N)y}^{obs}$ is a standard deviation of a total run size. As described in the single-stock framework, q allows for a systematic underestimate in the observed total run size and is restricted to values between 0 and 1.

The key assumptions of both the single and multi-stock run reconstruction models are:

1. estimates of inriver run and harvest are accurate or the degree of bias can be estimated,
2. tributary escapements, as a whole, are indices of drainagewide escapement,
3. there is no covariance in the observation errors of the tributary escapement estimates (i.e. errors in tributary assessments are independent), and

-
4. there is no temporal pattern (i.e. autocorrelation) in the observation errors within individual tributary assessment estimates.

In addition, the multi-stock model assumes:

1. accurate estimates of harvest stock proportions, and
2. accurate estimates of run stock proportions.

2.3.2. Run reconstruction sub-model applied to Yukon River Chinook salmon

Harvest of Chinook salmon occurs throughout the mainstem Yukon River and many of its tributaries. In applying the multi-stock model to Yukon River Chinook salmon from the Canada, Middle Yukon, and Lower Yukon stocks, we made following simplifying assumptions.

1. Yukon River Chinook salmon consists of three stocks (Canada, Middle Yukon, and Lower Yukon) with defined geographic boundaries (Figures 3 and 4).
2. All harvest downriver of the Pilot Station sonar occurs at the mouth of the Yukon River.
3. Lower Yukon stock escapement downriver of the Pilot Station sonar site consists only of the Andreafsky River (Figures 3 and 4). Escapements to other tributaries downstream of Pilot Station are negligible (Brown et al. 2017), and were assumed zero.
4. All harvest between upriver of the Pilot Station sonar site and downriver of the U.S.-Canada border occurs immediately upriver of the Pilot Station sonar site.
5. Canada stock escapement consists only of tributaries upriver of the mainstem U.S.-Canada border (Figures 3 and 4). Escapements to other spawning tributaries to Canada, such as the Porcupine River, were assumed to be zero.

2.3.2.1. Conceptual structure

In the following equations, the three major Yukon River Chinook salmon stocks (s) are represented as: $s = c$ for Canada, $s = m$ for Middle Yukon, $s = l$ for Lower Yukon. Conceptually, the three stocks returning annually to Yukon River ($N_{y,s}$) follow eight stages from entry into the river mouth to the spawning grounds (Figure 4). In the following model description, the final subscript is often used to designate location (L) (d : downriver from Pilot Station, pl : Pilot Station, u : upriver from Pilot Station, b : U.S./Canada border, and c : Canada).

1. Returning fish are harvested at the mouth of the river downstream of Pilot Station ($H_{y,s,L=d}$).
2. A portion of the Lower Yukon stock migrates to the Andreafsky River ($e_{y,s=l,i=ad}$) to spawn.
3. The remaining Lower Yukon stock and the entire Middle Yukon and Canada stocks are monitored at Pilot Station ($N_{y,L=pl}$), where abundance and stock proportions are estimated.
4. Fish passing upriver of Pilot Station are harvested ($H_{y,s,L=u}$) in Alaska fisheries (i.e., harvest occurring upriver from Pilot Station and downriver from the U.S.-Canada border).
5. The remaining Lower and Middle Yukon stocks migrate to spawning tributaries upriver from Pilot Station ($E_{y,s=l,L=u}$, $E_{y,s=m,L=u}$). Their escapements are monitored at several tributaries in Alaska ($e_{y,s,i}$ where $s = l, m$).
6. The remaining Canada stock migrates to the U.S.-Canada border ($N_{y,s=c,L=b}$) where abundance is estimated.
7. A portion of the Canada stock is harvested in Canada ($H_{y,s=c,L=c}$).

-
8. The remaining Canada stock migrates to spawning tributaries ($E_{y,s=c,L=c}$). The escapements are monitored at several tributaries in Canada ($e_{y,s,i}$ where $s = c$).

Mathematical expressions describing the stages above are as follows:

1. Harvest at the mouth of the river ($H_{y,s,L=d}$).

Harvest at the mouth of the river is a fraction ($U_{y,s,L=d}$: fishing harvest rate) of the run:

$$\begin{aligned} H_{y,s,d} &= U_{y,s,d} N_{y,s} \\ U_{y,s,d} &= 1 - \exp^{-F_{y,s,d}} \end{aligned} \quad (9)$$

where $F_{y,s,d}$ is an instantaneous fishing mortality rate, by year and stock.

The total lower river harvest is then the sum of the stock-specific harvests, and the proportion of each stock in the lower river harvest ($P_{(H)y,s,L=d}$) is a ratio of the stock-specific harvest to the total harvest:

$$\begin{aligned} H_{y,d} &= \sum_s H_{y,s,d} \\ \text{and} \\ P_{(H)y,s,d} &= \frac{H_{y,s,d}}{H_{y,d}} \end{aligned} \quad (10)$$

2. Escapement to the Andrafsky River to spawn ($e_{y,s=l,i=ad}$).

Escapement to the Andrafsky River ($e_{y,s=l,i=ad}$) was modeled as a fraction of the Lower Yukon stock run ($N_{y,s=l}$) after harvest occurred in the lower river fishery ($H_{y,s=l,L=d}$):

$$e_{y,l,ad} = \frac{N_{y,l} - H_{y,l,d}}{K_{ad}} \quad (11)$$

where K_{ad} is a model estimated parameter and $K_{ad} > 1$.

3. Stock-specific passage and proportions monitored at Pilot Station.

Inriver passage of the Middle Yukon and Canada stocks at Pilot Station ($N_{y,s,L=pl}$) was modeled as the returning run ($N_{y,s}$) minus the harvest that occurred in the lower river ($H_{y,s,L=pl}$). For the Lower Yukon stock, escapement to Andrafsky River was also subtracted:

$$N_{y,s,pl} = \begin{cases} N_{y,s} - H_{y,s,d} & s = c, m \\ N_{y,s} - H_{y,s,d} - e_{y,s,ad} & s = l \end{cases} \quad (12)$$

Total inriver passage at Pilot Station ($N_{y,L=pl}$) is then the sum of the stock-specific passage, and the proportion of the total passage that was each stock ($P_{(R)y,s,L=pl}$) is a ratio of stock-specific passage to total passage:

$$\begin{aligned} N_{y,pl} &= \sum_s N_{y,s,pl} \\ \text{and} \\ P_{(R)y,s,pl} &= \frac{N_{y,s,pl}}{N_{y,pl}} \end{aligned} \quad (13)$$

4. Stock-specific harvest in Alaska, upriver from Pilot Station ($H_{y,s,L=u}$).

Stock-specific harvest upriver from Pilot Station is a fraction ($U_{y,s,L=u}$: fishing harvest rate) of the corresponding stock passage monitored at Pilot Station:

$$\begin{aligned} H_{y,s,u} &= U_{y,s,u} N_{y,s,pl} \\ U_{y,s,u} &= 1 - \exp^{-F_{y,s,u}} \end{aligned} \quad (14)$$

The total U.S. harvest above Pilot Station is the sum of stock-specific harvest:

$$H_{y,u} = \sum_s H_{y,s,u} \quad (15)$$

and the proportion of each stock in that harvest ($P_{(H)y,s,L=u}$) is a ratio of the stock-specific harvest to the total harvest:

$$P_{(H)y,s,u} = \frac{H_{y,s,u}}{H_{y,u}} \quad (16)$$

5. Lower and Middle Yukon stocks migrate to spawning tributaries upriver from Pilot Station ($E_{y,s=l,L=u}$, $E_{y,s=m,L=u}$). Their escapement is monitored at several tributaries ($e_{y,s,i}$ where $s = l, m$).

6. Canada stock migrates to U.S.-Canada border and is monitored ($N_{y,s=c,L=b}$).

Escapement of Lower and Middle Yukon stocks upriver from Pilot Station ($E_{y,s=l,L=u}$, $E_{y,s=m,L=u}$) and the abundance of Canadian stock passing the U.S.-Canada border ($N_{y,s=c,L=b}$) were modeled as the stock-specific passage at Pilot Station ($N_{y,s,L=pl}$) minus harvest in Alaska upriver from Pilot Station ($H_{y,s,L=u}$):

$$\begin{aligned} E_{y,s,u} &= N_{y,s,pl} - H_{y,s,u} & s = l, m \\ N_{y,s,b} &= N_{y,s,pl} - H_{y,s,c} & s = c \end{aligned} \quad (17)$$

Escapement of the Lower and Middle Yukon stocks monitored at an individual tributary (i) ($e_{y,s,i}$) is a fraction of the corresponding stock escapement ($E_{y,s}$):

$$e_{y,s,i} = \frac{E_{y,s}}{K_i} \quad (18)$$

where K_i is a model estimated parameter and $K_i > 1$.

7. Canada stock is harvested in Canada ($H_{y,s=c,L=c}$).

Harvest of Canada stocks in Canada is a fraction ($U_{y,s=c,L=c}$, fishing harvest rate) of the border passage:

$$\begin{aligned} H_{y,c,c} &= U_{y,c,c} N_{y,c,b} \\ U_{y,c,c} &= 1 - \exp^{-F_{y,c,c}} \end{aligned} \quad (19)$$

8. Canada stock migrates to spawning tributaries in Canada ($E_{y,s=c}$). The escapement is monitored at several tributaries.

Escapement of Canada stock ($E_{y,c,c}$) is equal to the border passage ($N_{y,s=c,L=b}$) subtracted by harvest in Canada ($H_{y,s=c,L=b}$):

$$E_{y,c,c} = N_{y,c,b} - H_{y,c,c} \quad (20)$$

Escapement to an individual tributary (i) ($e_{y,s,i}$) is a fraction of the corresponding stock escapement ($E_{y,s}$) (Equ. 18).

2.3.1.2. Observation model

For the reconstruction of Yukon River Chinook salmon the observed data consisted of inriver run assessments and stock proportions, tributary escapements, harvest, and stock proportions of harvest. Within each stock, positive correlations were observed among tributary escapements (Figures A1, A20, and A37 in Pestal et al. 2022), supporting the assumption that tributary escapements represent relative indices of total and stock-specific escapement, and that individual tributary

contributions to total escapement are approximately constant through time (i.e. time-invariant K_i parameters). However, as noted by Hamazaki (2021) positively correlated tributary escapements are not definitive support for this assumption; rather, they provide evidence that the assumption may be reasonable for the intended purpose of the run reconstruction. Nonetheless, simulations suggest that run-reconstruction based estimates of total run-size are only moderately sensitive to violating the assumption of synchronous dynamics among tributaries (Schindler et al. 2019).

Inriver Run Assessments

Inriver run assessment data consisted of Canada stock passage estimates at the U.S.-Canada border, passage estimates for all stocks at Pilot Station, and estimates of stock proportions at Pilot Station.

The Canada stock passage at the U.S.-Canada border has been estimated since 1982 using various methods (j). From 1982–2008, passage was estimated using fishwheel mark–recapture data and either Petersen-Chapman (1982-1998, 2008) or stratified mark-recapture analytical methods (1999-2007) by the Department of Fisheries Oceans (DFO) (Milligan et al. 1984; Johnson et al. 2002). Since 2005, passage has been estimated using sonar methods by the ADF&G and DFO (e.g., McDougall and Brodersen 2020). For the years 2002–2004, passage was also estimated by radiotelemetry mark–recapture (Spencer et al. 2009). The JTC uses the sonar data and radiotelemetry mark–recapture passage estimates as a basis for informing escapement goal recommendations (JTC 2020), and thus those data were treated as accurate. Fishwheel mark–recapture estimates were treated as an underestimate of total border passage.

Observed U.S.-Canada border passage data was modeled as realizations of log-normal distributions:

U.S.-Canada border Eagle sonar and radiotelemetry mark-recapture

$$\ln(N_{y,c,b}^{obs}) \sim \mathcal{N}(\ln(\hat{N}_{y,c,b}), (\sigma_{(N)y,c,b,j}^{obs})^2) \quad (21)$$

U.S.-Canada border fishwheel mark-recapture

$$\ln(N_{y,c,b}^{obs}) \sim \mathcal{N}(\ln(q_{fw}\hat{N}_{y,c,b}), (\sigma_{(N)y,c,b,j}^{obs})^2)$$

where j = method (sonar, radiotelemetry mark-recapture, fishwheel Chapman-Petersen mark-recapture, or fishwheel stratified mark-recapture), q_{fw} is an index of survey accuracy and $0 < q_{fw} < 1$, $(\sigma_{(N)y,c,b,j}^{obs})^2 = \ln((CV_{y,b,j}^{obs})^2 + 1)$ for j = sonar and radiotelemetry mark-recapture and $(\sigma_{(N)y,c,b,j}^{obs})^2 = \ln((CV_{y,b,j}^{obs})^2 + 1) + \sigma_{add,c,b,j}^2$ for j = fishwheel Chapman-Petersen and stratified mark-recapture estimates. Given deviations from mark-recapture assumptions (see project description in Pestal et al. 2022), we estimated an additional variance term $\sigma_{add,c,b,j}^2$ for each fishwheel mark-recapture method (j). The observed coefficient of variation (CV) was considered proper for the radiotelemetry mark–recapture and sonar estimates. CVs of the annual fishwheel mark–recapture estimates were available in years using Chapman-Petersen estimates, and assumed to be 0.20 otherwise.

At Pilot Station, total passage ($N_{y,pl}^{obs}$) has been monitored using various methods (j): sonar (feasibility: 1985 - 1994; operational but biased low: 1995 - 2001; operational and unbiased: 2002 - 2019), spaghetti-tag mark–recapture (2000–2001) and radiotelemetry mark-recapture (2002-2004). Sonar passage between 1986 and 1994 was estimated as part of a feasibility study and was considered an underestimate. Full-scale sonar passage monitoring started in 1995 (Pfisterer et al. 2017). The sonar estimate is not always accurate. For example, sonar passage in 2001 was lower than the sum of observed harvest and escapements upriver of Pilot Station.

Mark–recapture experiments were conducted just above Pilot Station using spaghetti-tag (2000–2001) and radiotelemetry techniques [2002–2004; Spencer et al. (2009)]. Mark-recapture estimates

above Pilot Station were germane to large fish (generally > 650 mm mid-eye-to-tail-fork), and the number of small fish were estimated separately using a proportional approach based on age-class information from spawning ground surveys (Spencer et al. 2009). For our purposes we combined the large and small fish estimates and uncertainties to represent all fish that passed Pilot Station. This step was necessary so that the mark–recapture estimates were directly comparable to all other assessment projects used in the model, which reported total fish.

During the 2002–2004 period, estimates from both sonar and mark–recapture were similar (Spencer et al. 2009), and sonar passage estimates since 2005 were similar to those estimated from genetic mark–recapture methods (Pfisterer et al. 2017). Based on these comparisons and judgments about data accuracy, sonar passage estimates for 1986–1994 and 1995–2001 were considered an underestimate, but probably by differing degrees. Sonar estimates since 2002 were considered accurate. Abundance estimates from radiotelemetry mark–recapture (2002–2004) were considered accurate; however, the accuracy of the external tagging studies (2000–2001) is unknown.

Fish have been apportioned to the three stocks ($P_{(R)y,s,pl}^{obs}$) by genetic stock identification (GSI) using allozymes (2002–2003) and SNPs (2005–2019) with various degrees of accuracy and precision.

Given these data considerations, observations of passage and stock proportions at Pilot Station were modeled with log-normal and multinomial distributions, respectively:

Pilot Station mark-recapture

$$\ln(N_{y,pl,j}^{obs}) \sim \mathcal{N}(\ln(\hat{N}_{y,pl,j}), (\sigma_{(N)y,pl,j}^{obs})^2)$$

Pilot Station sonar passage

$$\ln(N_{y,pl,j}^{obs}) \sim \mathcal{N}(\ln(q_{pl}\hat{N}_{y,pl,j}), (\sigma_{(N)y,pl,j}^{obs})^2) \quad (22)$$

Pilot Station stock proportion

$$n_{(R)y,pl} P_{(R)y,s,pl}^{obs} \sim \text{Multinomial}(n_{(R)y,pl}, \hat{P}_{(R)y,s,pl})$$

where j = method (spaghetti-tag mark-recapture, radiotelemetry mark-recapture, or sonar periods) and q_{pl} is an index of survey accuracy ($0 < q_{pl} < 1$ [indicating an underestimate] during the 1986–1994 and 1995–2001 periods, $q_{pl} = 1$ [indicating an accurate estimate] during the 2002–2019 periods).

The variance term, $(\sigma_{(N)y,pl,j}^{obs})^2 = \ln((CV_{y,pl,j}^{obs})^2 + 1) + \sigma_{add,pl,j}^2$, included added variance for all methods j except the DIDSON sonar period where the observation error was considered proper. An observed coefficient of variance was not available for the sonar estimates between 1986 and 1994 and was assumed to be 0.20.

The effective sample size ($n_{(R)y,pl}$) weighting the run stock proportion data was set to 200.

Tributary escapements

Throughout the Yukon River drainage, Chinook salmon escapements are assessed at various tributaries using varying methods (Figures 2 and 3). Modeling of most tributary escapement surveys followed Equ. 18. However, several cases needed additional modeling considerations. These include (1) aerial survey counts conducted on the same tributary where a ground survey (e.g., weir, tower, or sonar) operated, (2) Nulato River, and (3) Andrefsky River.

In the Big Salmon River (Canada), Chena and Salcha Rivers (Middle Yukon), and Gisasa River (Lower Yukon), escapement was assessed by both ground (weir, tower, or sonar) and aerial

surveys (aer). In those cases, the annual aerial survey count ($e_{y,s,i,aer}^{obs}$) was modeled as a fraction of the ground survey count ($e_{y,s,i}^{obs}$):

$$e_{y,s,i,aer}^{obs} = \frac{e_{y,s,i}^{obs}}{K_{i,aer}} \quad (23)$$

where $K_{i,aer}$ is a scalar and $K_{i,aer} > 1$, indicating that the aerial survey successfully enumerated some fraction of the escapement that would have been observed by a ground survey project (weir, tower, or sonar).

The Nulato River (Lower Yukon) (*nlt*) is made up of the North (*N*) and South (*S*) Forks. An escapement counting tower ($e_{y,l,nlt}^{obs}$) has been operated at the main tributary confluence, and aerial surveys (*aer*) have been conducted within each fork ($e_{y,l,nlt,aer,N}^{obs}$, $e_{y,l,nlt,aer,S}^{obs}$). Ground survey escapement to the entire Nulato River was modeled using Equ. 18. Escapement to the North Fork was modeled as a fraction (p_N) of the Nulato River tower count, and the remainder ($1 - p_N$) was assigned to the South Fork such that North Fork escapement was $p_N e_{y,l,nlt}^{obs}$, and the South Fork escapement was $(1 - p_N) e_{y,l,nlt}^{obs}$. Then, each aerial escapement survey count was modeled as a fraction of each fork's escapement,

$$e_{y,l,nlt,aer,N}^{obs} = \frac{p_N e_{y,l,nlt}^{obs}}{K_{nlt,aer}} \quad (24)$$

$$e_{y,l,nlt,aer,S}^{obs} = \frac{(1 - p_N) e_{y,l,nlt}^{obs}}{K_{nlt,aer}}$$

The Andreafsky River (Lower Yukon) is made up of the West (*W*) and East (*E*) Forks. East Fork escapement is monitored by both weir ($e_{y,l,ad,w,E}^{obs}$) and aerial ($e_{y,l,ad,aer,E}^{obs}$) survey. Escapement to the West Fork is monitored by an aerial survey ($e_{y,l,ad,aer,W}^{obs}$).

East Fork weir escapement is a fraction (p_E) of the total Andreafsky River escapement:

$$e_{y,l,ad,w,E}^{obs} = p_E e_{y,l,ad}^{obs} \quad (25)$$

Applying Equ. 18, aerial escapement of East ($e_{y,l,ad,aer,E}^{obs}$) and West ($e_{y,l,ad,aer,W}^{obs}$) Forks are therefore:

$$e_{y,l,ad,aer,E}^{obs} = \frac{p_E e_{y,l,ad}^{obs}}{K_{ad,aer}} \quad (26)$$

$$e_{y,l,ad,aer,W}^{obs} = \frac{(1 - p_E) e_{y,l,ad}^{obs}}{K_{ad,aer}}$$

All tributary escapement data were assumed to be realizations of underlying log-normal distributions:

$$\ln(e_{y,s,i,j}^{obs}) \sim \mathcal{N}(\ln(\hat{e}_{y,s,i,j}), (\sigma_{y,i,j}^{obs})^2) \quad (27)$$

where $(\sigma_{y,i,j}^{obs})^2 = \ln((CV_{y,i,j}^{obs})^2 + 1) + \sigma_{add,s,j}^2$ and j is survey method (aerial, foot, tower, weir, sonar, fishway).

Where available (Figure 2), estimated annual CVs were used to represent observation error variability. However, these were not available in many cases. Based on observed CVs and information provided in the data report (Pestal et al. 2022), in those cases the CV was assumed

to be 0.25 for an aerial or foot survey and fishway data, 0.15 for sonar data, and 0.10 for tower and weir data. Additional variance terms ($\sigma_{add,s,j}^2$) for each survey method were model estimated to account for unestimated observation error.

Harvests

Our consideration of annual harvest was limited to fisheries occurring within the Yukon River drainage, and did not account for incidental harvest in marine fisheries. See Appendix B for discussion of the potential implications of ignoring incidental harvest in marine fisheries for estimation of biological reference points.

Fishery harvests occurring throughout Yukon River drainage can be separated into three geographic areas (Figure 4): (1) lower U.S. harvests, occurring from the Yukon River mouth to below Pilot Station, (2) upper U.S. harvests occurring from Pilot Station to the U.S.-Canada border, and (3) harvests occurring in Canada. Of those, our model assumed that all lower U.S. harvests occur below the confluence of Andreafsky River, and all the upper U.S. harvests occur below the confluence of Koyukuk River. These harvest assumptions were necessary to ensure that all stock-specific harvest removals were accounted for prior to considering escapement information for Lower and Middle stocks or border passage estimates for the Canada stock.

Log-normal and multinomial distributions modeled observed harvest counts and stock proportions, respectively:

$$\begin{aligned} & \text{Harvest} \\ \ln(H_{y,L}^{obs}) & \sim \mathcal{N}(\ln(\sum_s \hat{H}_{y,s,L}), (\sigma_{(H)L}^{obs})^2) \end{aligned} \tag{28}$$

Harvest stock proportion

$$n_{(H)y,s,L} P_{(H)y,s,L}^{obs} \sim \text{Multinomial}(n_{(H)y,s,L}, \hat{P}_{(H)y,s,L})$$

where $(\sigma_{(H)L}^{obs})^2 = \ln((CV_{(H)L}^{obs})^2 + 1)$ and L denotes harvest locations: downriver (d), upriver (u), and Canada (c).

The CV of the annual harvests is unknown but considered relatively precise. Harvest by commercial fisheries are reported to fish tickets, and subsistence fishery harvests are estimated from annual postseason household surveys. Individual households may under or over report, or not report at all. However, historical knowledge of household harvest patterns and survey level checks (i.e., cross-validation of group harvest to household harvest), coupled with the stratified sampling methods used to estimate U.S. subsistence harvest, are believed to result in unbiased overall estimates of harvest. Within the integrated RR-SRA, the total harvest CV was set to 0.20 for all years. The precision of harvest stock proportions is not reported and so an input multinomial sample size ($n_{(H)y,L}$) was set to 100 for all years, which provided precise fits to harvest stock compositions while providing generally unbiased fits to tributary escapement data. See Appendix B for discussion of the potential implications of biased harvest estimates for estimation of biological reference points.

2.3.3. Spawner-recruitment analysis sub-model

The spawner-recruitment sub-model represents true underlying population dynamics (i.e., free of measurement error) and specifies productivity, density-dependence, and age-at-maturity by cohort (i.e., brood year, y). Adult recruits (R) from 1981 to 2019 were treated as unobserved states and modeled as a function of Canada spawner abundance (E_c) assuming a Ricker (1954)

spawner-recruitment relationship with serially auto-correlated log-normal process variation:

$$\ln(R_y) = \ln(E_{y,s=c}) + \ln(\alpha) - \beta E_{y,s=c} + v_y \quad (29)$$

where α is productivity (intrinsic rate of growth), β is the magnitude of within brood-year density-dependent effects and v is inter-annual variation in survival from egg to adulthood which was assumed to be correlated with lag-1 (ϕ) over time (AR1 process):

$$v_y = \phi v_{y-1} + \varepsilon_y, \varepsilon_y \sim N(0, \sigma_R) \quad (30)$$

where ε_y is temporally independent white noise. At least one age in the first seven years of returns lacked recruitment abundance linked to spawner abundance (Equ. 29) and so recruitment in these years was modeled as random draws from a log-normal distribution with mean $\ln(R_0)$ and standard deviation σ_{R_0} .

The number of Chinook salmon that returned in year y and age a ($a \in 4 : 7$) was the product of the total recruitment in year $y - a$ and the proportion of fish from brood year $y - a$ that returned at age a :

$$N_{y,a,s=c}^{SRA} = R_{y-a,a} p_{y-a,a} \quad (31)$$

where $p_{y,a}$ is the proportion of fish that spawned in brood year y and matured at age a , and the SRA superscript differentiates this value from total run size in the run-reconstruction sub-model. We modeled brood year variation in age at return as Dirichlet random vectors drawn from a common hyperdistribution characterized by a mean age-at-maturity probability vector (π) and an inverse dispersion parameter ($1/D^2$):

$$p_{y,a} \stackrel{\text{iid}}{\sim} \mathcal{D}(\pi(\frac{1}{D^2})) \quad (32)$$

2.3.4. Observation model

Separate time series of age composition data were available from (1) lower river harvest, (2) upper river harvest (e.g., Larson et al. 2020) and (3) Canadian border passage (Hamazaki 2018a). Together these age compositions provide the best available estimates of the total age composition of Canadian-origin Chinook salmon returning in a given calendar year. The average of annual age compositions from these three model components was weighted by the salmon abundance estimated for each within the RR sub-model such that the total run abundance by age for the Canada stock was calculated as:

$$N_{y,a}^{obs} = (p_{y,a,L=d}^{obs} H_{y,s=c,L=d}) + (p_{y,a,L=u}^{obs} H_{y,s=c,L=u}) + (p_{y,a,L=bp}^{obs} N_{y,s=c,L=b}) \quad (33)$$

where $H_{y,s=c,L=d}$ is the harvest of the Canadian stock in the lower Yukon River, $H_{y,s=c,L=u}$ is the harvest of this stock in the upper river, and $N_{y,s=c,L=b}$ is the Canadian border passage abundance. $p_{y,a,L=d}^{obs}$ is the observed age composition proportions at age a , in year y , from lower river harvests, while $p_{y,a,L=u}^{obs}$ and $p_{y,a,L=bp}^{obs}$ are the observed age composition proportions from upper river harvests and border passage, respectively. The total abundance age composition was subsequently converted into proportions, as:

$$p_{y,a}^{obs} = \frac{N_{y,a}^{obs}}{\sum_a N_{y,a}^{obs}} \quad (34)$$

The SRA sub-model predicted run size by calendar year and age ($N_{y,a,s=c}^{SRA}$) was used to calculate the predicted proportions at age by calendar year: $\tau_{y,a}^{age} = \frac{N_{y,a,s=c}^{SRA}}{\sum_a N_{y,a,s=c}^{SRA}}$. The difference between the annual age composition predicted by the RR sub-model ($p_{y,a}^{obs}$) and by the SRA sub-model ($\tau_{y,a}^{age}$) was minimized by relating the two through a multinomial distribution:

$$ESS_y p_{y,a}^{obs} \sim \text{Multinomial}(ESS_y, \tau_{y,a}^{age}) \quad (35)$$

with a time-varying effective multinomial sample size ESS_y of 50 pre-2007 and 100 thereafter. These values are lower than the likely observed sample sizes to account for the non-independence of observation within a given sampling event (Maunder 2011) and were chosen to reflect the reduced confidence in age composition data prior to the Eagle test fishery sampling program which was standardized beginning in 2007.

Next, the difference between the RR sub-model estimated annual run size for Canadian-origin Chinook salmon ($N_{y,s=c}$) and the SRA sub-model estimate ($N_{y,s=c}^{SRA} = \sum_a N_{y,a,s=c}^{SRA}$) was minimized by fitting the predicted RR sub-model annual run size to a log-normal distribution with expectation equal to the estimated SAR sub-model annual run size:

$$\ln(N_{y,s=c}) \sim \mathcal{N}(\ln(N_{y,s=c}^{SRA}), \sigma_{RR-SRA}^2) \quad (36)$$

where σ_{RR-SRA} is the standard deviation describing the residual difference across calendar years y between RR and SRA sub-model estimates of annual run size for Canadian-origin Yukon River Chinook salmon. The prior distribution assumed for this residual standard deviation term was uninformative, specified as a broad normal distribution with a lower bound at zero ($\sigma_{RR-SRA} \sim N(0, 20^2)$). The value for this residual standard deviation term was freely estimated so as to provide equal weight to the data informing both the RR and SRA sub-models.

We chose to couple the run-reconstruction and spawner-recruitment sub-models this way, as opposed to fully integrating the two by having them share a single run abundance in each year ($N_{y,s=c}$), in order to handle uncertainty in observed annual run age composition (i.e., $N_{y,a}$) by deriving it within the model (Equ. 34-35). There are two alternatives to this approach. The first is to ignore uncertainty in the age composition data by running the run-reconstruction model first and then deriving observed age composition from it but this ignores uncertainty due to uncertainty in run-size. The second is to directly model harvest and escapement age-composition and fit the model directed to separate time series of observation of it in harvest and escapement. However, this latter approach requires accounting for size (age) selectivity in fisheries which is difficult in the Yukon River because selectivity has varied tremendously in space (by river section) and time (within and among years) due to management measures (e.g., space-time closures, mesh size restrictions) and nature of fisheries (e.g., commercial vs. subsistence).

2.4. MODEL FITTING AND DIAGNOSTICS

We fit the model described in Section 2.3 in a Bayesian estimation framework with Stan (Carpenter et al. 2017; Stan Development Team 2020), which implements the No-U-Turn Hamiltonian Markov chain Monte Carlo algorithm (Hoffman and Gelman 2014) for Bayesian statistical inference to generate the joint posterior probability distribution of all unknowns in the model. In our main model run, we sampled from 4 chains with 10,000 iterations each and discarded the first half as warm-up. We assessed chain convergence visually via trace plots and by ensuring that \hat{R} [potential scale reduction factor; Vehtari et al. (2021)] was less than 1.01 and that the effective sample size was greater than 200.

Prior distributions are detailed in Table 2 and Table 3. In most cases, parameters in the run reconstruction were modeled as uniformly distributed on the log scale, consistent with the parameter definitions provided in Hamazaki (2021) where the model was fit in a maximum likelihood estimation framework. Bounds were either constrained to the range of possible values for the parameter, e.g. proportions, or mildly informative and constructed from intuition regarding specific data types, e.g. added variance terms. After fitting the model to the data we plotted prior and posterior distributions for each parameter in the run reconstruction to check for evidence of prior influence on model parameter estimates, specifically related to bounding issues.

We examined the relative fit to the data from each index in the run reconstruction sub-model by calculating the normalized root mean squared error (NRMSE) of each, where the NRMSE is the RMSE divided by the mean of the data. To assess the appropriateness of the assumption of time-invariant tributary contributions to stock-specific escapement, we checked for evidence of temporal trends in the standardized residuals of each index fit. We also explored the importance of each index to the reconstructed estimates of Canadian stock escapement by rerunning the sub-model with each index removed in turn (i.e., leave-one-out) and calculating the RMSE in the escapement estimates between the full (all indices included) and reduced models.

2.5. BIOLOGICAL REFERENCE POINTS, YIELD, AND RECRUITMENT PROFILES

We calculated biological reference points for each MCMC sample and then summarized them across MCMC samples. The spawning abundance expected to maximize sustainable yield over the long-term under equilibrium conditions (S_{MSY}) was derived as:

$$S_{MSY} = \frac{1 - W(e^{1-\ln(\alpha)})}{\beta} \quad (37)$$

where W is the Lambert function (Scheuerell 2016), and α and b are intrinsic productivity and the magnitude of within stock density dependence, respectively. We chose to apply this exact solution for S_{MSY} instead of the commonly applied Hilborn (1985) approximation because the approximation only holds for $0 < \ln(\alpha) \leq 3$ and so infrequent, but large, posterior samples of α can result in biased estimates of the posterior distribution of S_{MSY} .

The spawner abundance expected to maximize recruitment over the long-term under equilibrium conditions (S_{MSR} , also commonly referred to as S_{MAX}) was estimated as:

$$S_{MSR} = \frac{1}{\beta} \quad (38)$$

Equilibrium spawner abundance, where recruitment exactly replaces spawners, was estimated as:

$$S_{EQ} = \frac{\ln(\alpha)}{\beta} \quad (39)$$

We did not estimate the spawner abundance required to recover to S_{MSY} within one generation under equilibrium conditions in the absence of fishing [S_{GEN} ; Holt et al. (2009)] because it is only relevant as a biological reference point at the scale of Conservation Units and not aggregate population (or Conservation Unit) abundances.

Lastly, the harvest rate expected to lead to maximum sustainable yield (U_{MSY}) was derived according to the solution proposed by Scheuerell (2016) as:

$$U_{MSY} = 1 - W(e^{-\ln(\alpha)}) \quad (40)$$

The reference points above are germane to median yield and recruitment, but because of the assumption that recruitment is lognormally distributed this differs from expected (i.e., mean) yield and recruitment. Therefore, to provide inference about expected yield and recruitment we applied a lognormal bias correction by substituting α' for α in equations 37-40, where:

$$\ln(\alpha') = \ln(\alpha) + \frac{\sigma_R}{2(1 - \phi^2)} \quad (41)$$

Applying this lognormal bias correction is common in ADF&G and transboundary escapement goal analyses (Bernard and Jones 2010; Eggers and Bernard 2011; Hamazaki et al. 2012; Fleischman et al. 2013; Pestal et al. 2016; Miller and Pestal 2020; Reimer and Decovich 2020) and in marine fish stock assessments but is not consistently done in Canadian analyses that estimate biological reference points. For the remainder of the main text we report results based on the bias correction but we also report estimates of biological reference points derived from the uncorrected estimates of α to illustrate their sensitivity to the bias correction in Appendix F.

The probability that a given spawning abundance would produce average yield or recruitment exceeding X% of MSY and MSR , respectively, was obtained by calculating yield and recruitment at incremental values of spawning abundance (0 to 150,000 in increments of 15,000) for each MCMC sample (based on bias corrected α'), and then comparing them with X% of MSY and MSR for that sample. The resulting proportion of samples in which yield and recruitment exceeded X% of MSY and MSR were then plotted against the range of spawner abundances as optimal yield and recruitment probability profiles (Fleischman et al. 2013).

We also derived the inverse of the optimal yield probability profile when spawner abundance is less than S_{MSY} , which indicates the probability yield would be less than X% of MSY by supplying too few spawners. This was done calculating yield at incremental values of spawning abundance and tallying the number of MCMC samples for which yield was less than X% of MSY and spawning abundance was less than S_{MSY} . A plot of spawning abundance versus the fraction of MCMC samples in which this condition was met has been referred to as an “overfishing” profile (Bernard and Jones 2010) though we note that instances where spawner abundances are less than those predicted to maximize yield can occur for reasons other than overfishing (e.g., environmental change).

2.6. ESCAPEMENT QUALITY

Our baseline analysis assumed that demographic attributes of spawning escapement have not changed over time such that reproductive output is homogeneous among individuals and has been static over the past 40 years. However, changes in age, sex, and length-at-age of returning Chinook salmon, including in the Yukon (Lewis et al. 2015; Ohlberger et al. 2018, 2020), have been widely observed, suggesting concurrent declines in per capita reproductive output as smaller females carry disproportionately fewer eggs of a smaller mass compared to larger females (i.e., fecundity and total egg mass scale exponentially with female size) (Ohlberger et al. 2020). While changes in age, sex, and length-at-age (aka “escapement quality”) are not typically considered when deriving spawner-recruitment based reference points and setting escapement goals, recent research on Chinook salmon in the Kuskokwim River of western Alaska suggests that failing to account for declines in escapement quality may result in underestimating the escapement needed to maximize long-term sustainable yield (Staton et al. 2021).

To evaluate the potential consequences of changes in escapement quality over time (which we operationalized as total eggs or egg mass) we translated time trends in sex ratios, age composition,

and size-at-age to annual estimates of total egg or total egg mass production. We then refit our integrated model to these alternative time-series, replacing the spawner abundance term (E_y) in Equ. 29 with:

$$Z_{m,y} = \sum_a E_y \cdot q_{y,a} \cdot w_{m,y,a} \quad (42)$$

where $Z_{m,y}$ is the year-specific reproductive metric m (total eggs or total egg mass), E_y is the year specific total spawner abundance, $q_{y,a}$ is the year- and age-specific proportion females, and $w_{m,y,a}$ is the average for each reproductive metric (m) per individual in each year (y) and age (a).

For each joint posterior sample of α' and b (Equ. 41 and 29, respectively) we then back calculated the spawner abundance expected to maximize yield and recruitment for a given set of assumptions about escapement age, sex, and length-at-age. The specific assumptions we considered for female age composition, proportion females, and female length at age, were either the long-term average or the average over the first (1982-1992) or last (2009-2019) decade with data.

To model changes in escapement quality, we needed to consider two additional sources of data: (i) annual age and sex composition as well as mean length derived from assessment projects at the U.S.-Canada border, and (ii) allometric relationships between female Chinook salmon size and total eggs, or total egg mass, to translate female size to expected reproductive output by age. Estimates of annual age and sex composition, and mean length were derived from records of individual fish sampled by fishwheels (pre-2007), and more recently by multi-mesh size gill net test fishery, near the Alaska-Yukon border (ADF&G AYK Database Management System). These data were corrected for the known size selectivity of fishwheels using the length selectivity method described in Hamazaki (2018a). The allometric relationships between female Chinook salmon size and total eggs, or total egg mass, were based on 140 samples of female fish with paired measurements of length (mid-eye to tail fork; METF), egg count and egg (ovary) mass, based on collections in the gill net test fishery between 2008 and 2010 (Ohlberger et al. 2020).

2.7. SENSITIVITY ANALYSES

2.7.1. Age composition effective sample sizes

Our base formulation of the integrated model assumed an age composition effective sample size for the multinomial distributions of 50 pre-2007 and 100 thereafter. Because these values were not directly informed by data, we explore the sensitivity of our estimates of S_{MSY} and S_{MSR} to alternative age composition effective sample size assumptions. Specifically, we fit three alternative models with:

1. an ESS_y (Equ. 35) of 100 across all years to reflect equal confidence in age composition across the entire time series;
2. an ESS_y of 25 pre-2007 and 100 thereafter to reflect reduced confidence in age composition in the early (pre-2007) portion of the time series; and lastly
3. an ESS_y of 25 pre-2007 and 200 thereafter to reflect reduced confidence in age composition in the early (pre-2007) portion of the time series and increased confidence thereafter.

We then compared estimates of S_{MSY} and S_{MSR} across each of these alternative data weightings and the base model formulation.

2.7.2. Stock composition effective samples sizes

In our base integrated model we assumed a constant ESS of 200 for the multinomial distribution modeling stock composition at Pilot Station ($n_{(R)y,pl}$, Equ. 22). Because this value was not directly informed by data, we tested the sensitivity of S_{MSY} and S_{MSR} estimates to this choice by refitting the model using ESS of 50 and 400, bounding reasonable values for this parameter.

We did not explore alternatives to the choice of ESS in the U.S. harvest stock composition model ($n_{(H),y,s,L}$, Equ. 28) because it was derived from fishing mortality which was a free (unconstrained) parameter and so its influence was considered negligible.

2.7.3. Run reconstruction indices weighting

Most passage and escapement indices included in the run reconstruction did not have empirically based estimates of uncertainty [Figure 2; Pestal et al. (2022)]. Where values were missing, coefficients of variation were asserted for mark-recapture estimates (0.20), aerial and foot surveys (0.25), fishway estimates (0.25), sonar estimates (0.15), and weir and tower estimates (0.10). These values represent relative confidence in the precision of abundance estimates based on various assessment methods following the data review. We refit the run reconstruction without the observed or asserted measures of uncertainty included, such that the model estimated additional variance terms ($\sigma_{add,s,j}^2$, Table 1) were the sole source of index weighting. We then compared estimates of the reconstructed Canadian-origin run size under both conditions to examine model sensitivity to the asserted weights.

2.7.4. Alternative functional form to the spawner-recruitment relationship

One of the central assumptions in stock-recruitment analysis is the functional form of the underlying relationship between spawning abundance and expected recruitment. Our base analyses assumed a Ricker-type spawner–recruitment relationship (Equ. 29) that exhibited overcompensation with declining total recruitment at high spawner abundances. To explore the sensitivity of our estimates of S_{MSY} to structural uncertainty in the functional form of the spawner-recruitment relationship we fit an alternative version of the integrated model that assumed a Beverton-Holt type spawner–recruitment relationship that exhibits asymptotic behavior at high levels of spawning abundance (Appendix F.5)

3. RESULTS

3.1. MODEL FITS AND DIAGNOSTICS

We estimated a total of 148 model parameters. Visual inspection of trace plots indicated all chains were well mixed for leading parameters, all parameters had $\hat{R} < 1.01$, and almost all had effective sample sizes $> 1,000$ suggesting reasonable model convergence. The parameters that were the most difficult to estimate were (σ_{RR-SRA}^2 ; Equ. 36), the variance in residual difference between RR and SRA sub-model estimates of annual run size, and ($1/D^2$; Equ. 32), which governed the variability of the age proportion vectors across cohorts (effective sample size = 706), both of required a relatively large number of iterations to be well mixed and estimated reliably.

Plots of the prior and posterior distributions of parameters fit in the run reconstruction indicate no significant issues related to prior specifications (Appendix C). In two cases, the Tincup Creek aerial survey and the Wolf River aerial survey, posterior estimates of the time-invariant tributary fractions of total escapement, K_i , approach the upper bounds of the prior. However, because this is a fractional scalar, large values of K_i indicate that the tributary is a very small contributor to the overall stock-specific escapement. The upper bound of the prior is equivalent to a tributary contributing about 0.25% to the total and increasing prior bounds would only allow that contribution to lessen. Therefore, we determined that this was not significant to the overall model results. Alternatively, the fractional scalar could be recast as a proportion to the total escapement and the prior could be specified with a uniform or beta distribution strictly bounded by 0 and 1. We chose to maintain the structure as specified in Hamazaki (2021), but this could be pursued in the future.

Visual examination of plots of observed and estimated values for each index included in the run reconstruction submodel (Appendix C) did not reveal any significant issues with fit. Model fits to reported upriver harvest, however, were poor in several recent years (2017 and 2019; Figure C.7) as a result of data conflicts between the Pilot Station and Eagle Sonar assessment projects. These conflicting estimates may have been due, at least in part, to enroute mortality due to heat stress and are discussed in more detail in Appendix E. Examination of the residual plots also indicated no persistent temporal trends in lack of fit (Appendix C), suggesting that the assumption of time-invariant tributary proportionality to stock-specific escapement to be a reasonable one. NRMSE indicated that the fit to the U.S.-Canadian border passage data was precise (sonar < 0.001 , radiotelemetry mark-recapture = 0.156, fishwheel mark-recapture = 0.137). Passage estimates made at Pilot Station were less closely fit by the model (radiotelemetry mark-recapture = 0.236, sonar = 0.141). Among tributary assessment projects, model estimates of tower, weir, and sonar projects (mean NRMSE = 0.386, $n = 10$) were more precise than estimates of aerial and foot survey data (mean NRMSE = 0.478, $n = 17$), consistent with *a priori* weights given to the different assessment project types.

Dropping any tributary assessment project in Canada, with the exception of the Big Salmon River sonar project, was more impactful (RMSE range: 1,296 - 4,179; Appendix C) to the Canadian escapement estimates than dropping lower or middle U.S. assessment projects (max RMSE: 629 [Salcha River tower]; Appendix C). Because the fishwheel mark-recapture project was the only border passage inriver assessment project informing the Canadian run reconstruction prior to 2005, we also examined the consequences of dropping it from the run reconstruction. This resulted in the largest change in Canadian escapement estimates from the full model (RMSE: 6,148).

3.2. RUN-SIZE, ESCAPEMENT, AND HARVEST

We estimated the average basin-wide run-size to be approximately 288,000 fish per year (range of median estimates: 98,000 in 2013 to 466,000 in 1995; Figure 5a; Appendix D). The Canadian portion of the Yukon was estimated to produce the largest average annual run-sizes of the three stocks at approximately 124,000, followed by the lower river stock at 85,000, and then middle river stock at 64,000 (Figure 5a). Annual run-size was moderately correlated among stocks (median pairwise correlation in run-size = 0.61).

All stocks experienced relatively large run-sizes from 1982-1995, followed by a sharp decline (particularly for the Canada stock) with the lowest observed run-sizes in 2000 and 2013. In recent years (2015-2019), run sizes have averaged approximately half of what they were from 1982-1995 (orange bands Figure 5). In contrast to run size, spawning escapements for all three stocks have been relatively consistent over time (grey bands in Figure 5a).

Aggregate harvest and harvest by stock varied considerably over time, and realized harvest rates ranged from 3%-82%, 2%-87%, and 26%-52% for the Canada, Middle and Lower stocks respectively (Figure 5b). The Canadian stock experienced the highest harvest rates (54%), on average, of the three stocks (Figure 5b).

3.3. PRODUCTIVITY, CAPACITY, YIELD, AND RECRUITMENT

Posterior means, medians and credible intervals for leading spawner-recruitment parameters and biological reference points are summarized in Table 4. We found that the Canadian-origin Yukon Chinook salmon stock aggregate is moderately productive with intrinsic productivity estimated to be 4.92 recruits per spawner (median posterior of α' ; 95% CRI: 2.73-9.36). Recruitment was estimated to be moderately positively correlated through time ($\phi= 0.39$; CRI: -0.06-0.85) and realized recruits produced per spawner was above average in the 1980s, variable in the 1990s, below average in the 2000s with several years at replacement, and has since increased back towards the long-term average in the most recent decade (Figure 6b).

Equilibrium stock size (S_{EQ}), which is a function of intrinsic productivity (α') and the strength of within stock density dependence (β), was estimated to be 110,601 (CRI: 81,708-234,252; Table 4, Figure 7). As a result of relatively weak density dependence, expected yield (i.e., “surplus” production above replacement) and recruitment was relatively flat across a wide range of spawner abundances (Figure 6a). Nonetheless, the spawner abundance expected to maximize long-term sustainable yield (S_{MSY}) was estimated to be 43,125 (CRI: 29,874-93,070) while the spawner abundance expected to maximize recruitment (S_{MSR}) was estimated to be 70,447 (CRI: 41,094-186,200). Lastly, the harvest rate expected to lead to maximum sustainable yield (U_{MSY}) was estimated to be 62% (CRI: 43% - 77%), and the harvest rate expected to result in maximum recruitment (U_{MSR}) was estimated to be 45% (CRI: 4% - 71%).

Estimates of intrinsic productivity were moderately sensitive to whether or not a lognormal bias correction was applied; not applying the bias correction resulted in a median estimate of intrinsic productivity that was 12% lower than when the bias correction was applied (4.33 vs. 4.92 recruits per spawner; Table F.1). This in turn resulted in small reductions in estimates of equilibrium stock size (S_{EQ}), S_{MSY} , and U_{MSY} (Table F.1).

There was relatively large uncertainty in leading parameters, the overall shape of the spawner-recruitment relationship, and associated biological reference points, as illustrated by their large credible intervals (Table 4). It is presumably desirable to identify an escapement goal that is robust to this uncertainty as opposed to based solely on the point (e.g., median) estimate of

the spawner-recruitment relationship. We therefore generated “optimal” yield (Figure 8a) and recruitment (Figure 8b) profiles that illustrate the expected probability that a given number of spawners will achieve some percentage of maximum sustainable yield or recruitment, respectively. These profiles integrate over all of the uncertainty in true spawner abundance and intrinsic productivity of the stock, and can be used to quantify the expected yield and recruitment performance of prospective escapement goals. For example, based on the yield profile in Figure 8a there is a greater than 4 in 5 chance (prob. > 0.8) that escapements between 35,000 and 55,000 fish will produce yields greater than 80% of maximum sustainable yield. Similarly, there is a greater than 4 in 5 chance that escapements between 40,000 and 90,000 fish will produce recruitments greater than 80% of maximum recruitment (Figure 8b). Figure 8 provides additional profiles across a range of thresholds (70%, 80%, and 90%) that could define optimal yield and recruitment as well as yield based risk associated with supplying too few spawners.

3.4. ESCAPEMENT QUALITY

Female Chinook salmon age composition, as measured at the Alaska-Yukon border, has declined over time. In the 1980s, approximately 20% of females were seven year olds, 70% were six year olds, and fewer than 10% of females returned on average as five year olds (Figure 9c). By the 2010s an average of 5% of females returned as seven year olds, 70% as six year olds and 25% as five year olds. In addition, the proportion of returning fish that were female has declined over time from an average of approximately 53% in the 1980s to 44% in the 2010s, with considerable interannual variation (as high as 59% in 1989 and low as 32% in 2016; Figure 9a). In contrast to these changes in age and sex over time, there was no evidence of directional change in female length at age over this same time period (Figure 9b).

Collectively, these observed demographic changes have likely resulted in declines in per capita output of eggs and total egg mass over time such that for the same number of spawners, early years produced an above average number of eggs or total egg mass, whereas recent years produced a below average number of eggs and total egg mass (Figure 9d). These changes result in modest differences in the inferred shape of the relationship between reproductive output and recruitment across the three measures (i.e., total spawners, total eggs, or total egg mass; Figure 10) resulting in lower estimates of intrinsic productivity and weaker estimates of within stock density dependence which in turn translate into slightly larger estimates of the spawner abundance expected to maximize long-term sustainable yield (“Average” period in Table 5, Figure 11) or recruitment (“Average” period in Table 6, Figure 11). We note, however, that these alternative measures of reproductive output did not explain more year-to-year variation in recruitment than simply considering total spawner abundance (R^2 of $\ln(R/Z) \sim Z$ was 0.28, 0.22, and 0.22 when Z was equal to total spawners, total eggs, and total egg mass, respectively).

As a result of these observed declines in total eggs and egg mass, the spawner abundance expected to maximize yield was estimated to be about 10% greater on average in recent years (2009-2019) than in the 1980s and was slightly greater when considering total egg mass (13%) as the units of reproductive output instead of total eggs (“Early” vs. “Recent” periods in Table 5, Figure 11). The consequences of declines in total eggs and egg mass were more pronounced for estimates of spawner abundance associated with maximum recruitment which was estimated to be on average about 19% greater in recent years (2009-2019) than in the 1980s and also slightly greater when considering total egg mass (23%) as the units of reproductive output instead of total eggs (“Early” vs. “Recent” periods in Table 6, Figure 11).

3.5. SENSITIVITY ANALYSES

3.5.1. Age composition effective sample sizes

We found that fits to lower river harvest and age composition data, as well as estimates of both S_{MSY} and S_{MSR} , were moderately sensitive to assumptions about age composition data weighting. As assumed confidence in age composition pre-2007 declined (from an ESS of 50 to 25) fits to lower river harvest improved but at the cost of poorer fits to age composition (Figures F.2 and F.3) and estimates of S_{MSY} and S_{MSR} both increased (Figure F.6). When assumed confidence post-2007 increased (from an ESS of 100 to 200), both reference points further increased (Figure F.6) with little influence on fits to lower river harvest and age composition (Figures F.3 and F.4). Conversely, when confidence in age composition pre-2007 increased (from an ESS of 50 to 100) reference points remained essentially unchanged (Figure F.6), but at the cost of poorer fits to lower river harvest in the early part of the time series (Figures F.2 and F.5).

3.5.2. Stock composition effective sample sizes

We found that fits to the stock composition data and estimates of S_{MSY} and S_{MSR} were robust to assumptions about stock composition data weighting. Lower U.S. stock proportion estimates were most closely fit to the observed data regardless of the ESS asserted in the model (Figure F.7, Table F.4). However, among the alternatives explored here, there were minimal changes observed in the resultant S_{MSY} and S_{MSR} estimates (Figure F.8, Tables F.5 and F.6).

3.5.3. Run reconstruction indices weighting

Removing the observed and assumed measures of index uncertainty in the run reconstruction and allowing the model-estimated added variance terms to be the sole measure of index uncertainty had little impact on estimates of the Canadian run size (Figure F.9). Point estimates of the added variance terms, $\sigma_{add,s,j}^2$, fit to index type (i.e. weir, aerial survey, etc) and stock (Table 1) increased to compensate for the data loss without an associated increase in parameter uncertainty (Figure F.10, Table F.7). However, we maintained empirical estimates of index uncertainty, and asserted values where such information was unavailable, in the integrated model to make full use of the data and maintain model flexibility.

3.5.4. Alternative functional form to the spawner-recruitment relationship

Both the Ricker and Beverton-Holt formulations of the integrated model resulted in estimates of spawning abundance and recruitment that were largely consistent. However, the estimated shape of the underlying stock-recruitment relationship were distinctly different between the two model formulations, with the Beverton-Holt version estimating a much more rapid increase in recruitment at low spawning abundances (Figure F.11). These much more optimistic expectations for population productivity at low spawning abundances under the Beverton-Holt model resulted in substantially lower estimates of the spawning abundance necessary to produce maximum sustainable yield (S_{MSY}), as compared with the Ricker model (Figure F.12). Estimates of potential yield under the Beverton-Holt model were also lower, compared with the potential yield estimated by the Ricker model (Figure F.13). These findings were not unexpected given the overall uncertainty in the stock-recruitment relationship for Yukon River Canadian-origin Chinook salmon and the asymptotic behavior of the Beverton-Holt model. Given the unrealistically high estimated intrinsic productivity of the Beverton-Holt model, we considered the Ricker version of the integrated stock-recruitment model to serve as a better basis for deriving estimates of biological reference points.

4. SUMMARY OF KEY FINDINGS

In this report we describe an integrated state-space run reconstruction and spawner-recruitment model that was fit to historical data from various assessment projects that estimate mainstem passage, harvests, tributary escapements, stock-proportions, and age-composition. From this model we estimated biological reference points and associated yield and recruitment profiles for Canadian-origin Yukon Chinook salmon, and examined how sensitive they are to key data and methodological assumptions as well as potential change in escapement quality (e.g., total spawning cohort fecundity and egg mass) over time.

We found that the Canadian-origin Yukon Chinook salmon stock aggregate is moderately productive with positively correlated survival from year to year that was above average in 1980s, variable in the 1990s, below average in the 2000s and has since increased back towards the long-term average in the most recent decade. Equilibrium stock size (S_{EQ}) was estimated to be 110,601 (CI: 81,708-234,252; all reference points reported here are based on log-normal bias correction where applicable), the spawner abundance expected to maximize long-term sustainable yield (S_{MSY}) was estimated to be 43,125 (CI: 29,874-93,070) and the spawner abundance expected to maximize recruitment (S_{MSR}) was estimated to be 70,447 (CI: 41,094-186,200). Despite large credible intervals, the posterior estimates combined with probability profiles (Figure 8), demonstrate there is sufficient information content to evaluate tradeoffs and expected outcomes across a range of potential spawner abundances

Our estimates of biological reference points were moderately sensitive to age composition data weighting where reduced confidence in age composition data pre-2007, and/or increased confidence post-2006, resulted in increased estimates of both S_{MSY} and S_{MSR} . Estimates of Canada stock run-size and biological reference points were otherwise generally robust to assumptions about stock composition data and index weighting and to potential biases in data they were based on. As is inevitable with any complex analysis, we made a number of simplifying assumptions and future analyses could consider expanding our analytical framework to explore their consequences in more detail. From a run-reconstruction perspective, future considerations include allowing for spatial and temporal correlation in observation errors across and within assessment projects and allowing for time-varying tributary contributions to total escapement. From a spawner-recruitment perspective, future extensions could include time-varying productivity (e.g., as a random walk) and incorporation of environmental covariates that might help inform assessment of future states of nature and reference points that are most relevant to them.

Female Chinook salmon age at maturity, and to a lesser extent the proportion of females in the spawning population, has declined over time. These demographic changes have likely resulted in declines in potential measures of per capita reproductive output such that for the same number of spawners, early years (1980s) produced above average total eggs or eggs mass, whereas recent years (2010s) produced below average total eggs and egg mass. Our exploratory analyses of the consequences of these demographic changes suggest that the spawner abundance expected to maximize yield or recruitment is on average 13% or 19% greater, respectively, in recent years than in our baseline analysis that did not take changes in escapement quality into consideration. These estimates are generally similar to those found by Staton et al. (2021) for Chinook salmon in the Kuskokwim River basin. However, the magnitude of the impact of accounting for demographic change on biological reference points (i.e., S_{MSY}) was smaller in the Canadian-origin Yukon stock aggregate than in the Kuskokwim. This is likely a result of the less exaggerated time trends in sex ratio and particularly size-at-age in the Yukon and because our analysis assumed a flat age-specific selectivity function for all reference point calculations. When

compared to a subset of the Kuskokwim analyses that assumed flat selectivity and no length-at-age trends, the percent change in S_{MSY} is more consistent between the systems. We note, however, that our estimates should be considered exploratory in nature as the suitability of the age, sex, length data we utilized, and approach taken to correct for size selectivity of fishwheels used to collect the data in some years, has not been rigorously evaluated.

Our spawner-recruitment models with total eggs, or total egg mass, as the measure of reproductive output implicitly assumed that total reproductive output is limited by females and that male abundance is always sufficient to fertilize all eggs (Staton et al. 2021). We believe this was a reasonable assumption across the range of aggregate spawner abundances that have been observed in the Canada stock, and at the scale at which we are modelling spawner-recruitment dynamics, though at very low abundances and in small populations, male abundance will also presumably limit reproductive output. Lastly, these models assume that only eggs, or egg mass, contribute to within-stock density effects whereas total spawners (males and females) contribute to density effects in the base model.

5. CONCLUSIONS

5.1. CONSIDERATIONS FOR DEVELOPING AN ESCAPEMENT GOAL

Our analyses provide a quantitative foundation upon which to base the development of an escapement goal recommendation for Canadian-origin Yukon Chinook salmon, but they do not prescribe one. Here we describe three key considerations when developing an escapement goal based on the information we provide.

The **first consideration** is defining the objectives of the escapement goal, and the decision context in which they are embedded.

Chapter 8 of the Pacific Salmon Treaty, The Yukon River Agreement, which defines the international obligations under which Canadian-origin Yukon Chinook are managed, does not specify an objective for spawning escapement beyond calling for “optimal spawning escapement”. However, both Alaskan and Canadian fisheries policy provide institutional frames of reference [i.e., the yardstick being applied to biological information; Pestal et al. (2016)] that can be considered when developing an escapement goal recommendation.

The Alaska Sustainable Salmon Fisheries Policy states that “salmon escapement goals. . . should be established in a manner consistent with sustained yield; unless otherwise directed, the department will manage Alaska’s salmon fisheries, to the extent possible, for maximum sustained yield.” (Alaska Board of Fisheries 2000). Under the Policy, when sufficient data are available, a Biological Escapement Goal (*BEG*) is established based on the estimated range of escapements expected to maximize yield (S_{MSY}) and when a *BEG* cannot be estimated (e.g., due to lack of stock specific catch data) a Sustainable Escapement Goal (SEG), which is known to provide for sustained yield over a 5 to 10 year period, may be established. In practice, however, SEGs have been established for numerous fisheries with sufficient data to estimate S_{MSY} but maximum yield was not the preferred objective (e.g., subsistence fisheries). An Optimal Escapement Goal may then be established that takes additional biological and allocative considerations into account while ensuring sustainability, and though not directly related to escapement goal setting per se, a Sustained Escapement Threshold may be identified as the level below which sustainability is jeopardized (set below the lower end of the *BEG* range).

In contrast, Canadian fisheries policy, including Canada's Policy for Conservation of Wild Salmon (Wild Salmon Policy, DFO 2005), Sustainable Fisheries Framework (DFO 2009) and Fisheries Act (DFO 1985) are less prescriptive. The Wild Salmon Policy (WSP) calls for "healthy, diverse, and abundant wild salmon populations . . . sustainable fisheries to meet the needs of First Nations and contribute to the current and future prosperity of all Canadians." Under the policy the biological status of Conservation Units is assessed based on a suite of metrics (e.g., relative abundance, short- and long-term trends in abundance), as well as upper and lower biological benchmarks for each metric to delineate three status zones (red/amber/green). For the relative abundance metric, the biological benchmark is often set at 80% of the point estimate of S_{MSY} , and the lower reference point at S_{GEN} (Holt et al. 2009; Holt and Bradford 2011), though other metrics like trends through time and spatial distribution may be considered. Importantly, however, the WSP applies to Conservation Units, and not stock aggregates like Canadian-origin Yukon Chinook salmon that are comprised of multiple Conservation Units.

Canada's Sustainable Fisheries Framework and Fisheries Act, which are broader policies concerning all exploited fishes under DFO's jurisdiction, rely on the definition of biological reference points which define an abundance (or biomass) target (Upper Stock Reference; USR) as well as a low abundance (or biomass) threshold (Limit Reference Point; LRP) to be avoided with high probability. Formal guidance is currently being developed for LRP for Pacific salmon at stock aggregate scales. While a LRP is based on biological considerations, the USR can be determined by productivity objectives for the stock, broader biological considerations, and social and economic objectives. In practice, the USR point is often set at 80% of S_{MSY} (or B_{MSY} for non-salmonid fisheries). The Fisheries Act requires that fish stocks be managed at sustainable levels, specifically at levels above the LRP and that harvest rates can be highest when the stock is at or above the USR and then must be progressively reduced to promote stock growth as abundance declines towards the LRP. When a stock is at or below the LRP, management actions must promote stock growth and removals from all sources must be kept to the lowest possible level until the stock has cleared the zone.

What the summaries above highlight is that while fisheries policy in both countries is guided by the concept of sustainable use, the specifics of how it is defined and implemented for Pacific salmon varies hence the need to clearly articulate the objectives of an escapement goal before trying to develop recommendations for it. Nonetheless, both jurisdictions delineate spawner abundance ranges based on biological reference points, including the identification of a threshold of concern, and in both cases S_{MSY} can (but does not have to) serve as a common anchor point.

The **second consideration**, once the objective(s) of the escapement goal(s) are clarified, is the magnitude of acceptable risk (i.e., risk tolerance) of not meeting the stated objectives. The yield or recruitment profiles we provide (Figure 8) have both descriptive and prescriptive utility. For example, the probability of failing to meet a yield or recruitment objective can be determined for any escapement goal range under consideration (i.e., descriptive). The results allow one to consider if the proposed escapement goal is acceptable relative to the desired performance. Conversely, one might specify an explicit risk tolerance and use the profiles to identify the corresponding upper and lower escapement values as the basis for recommending a goal range (i.e., prescriptive). In addition, it is often necessary to specify a hierarchy to objectives (e.g., maximize recruitment and then maximize yield), as well risk tolerances that vary depending on whether one is identifying an upper or lower bound to an escapement goal.

The **final consideration** is additional uncertainties that need to be accounted for when developing an escapement goal recommendation. These uncertainties can help ground the degree of

precaution that should be taken when establishing an escapement goal in the face of imperfect information. While our state-space integrated modelling framework attempts to more completely represent and propagate uncertainty attributable to observation error and true underlying process variation than traditional spawner-recruitment analyses, there may be other uncertainties that need to be taken into consideration. These might include, but are not necessarily limited to, whether the past is expected to be a good predictor of the future, whether demographic change in the spawning population is taken into account, and whether there are risks associated with not considering the underlying biological diversity of the stock aggregate that the escapement goal recommendations are based on.

Time-varying population processes (e.g., survival) are common in Pacific salmon (Peterman and Dorner 2012; Dorner et al. 2018), and rapid changes in the freshwater and marine environments that Yukon Chinook salmon utilize brought on by climate change may result in conditions in the future that have not been seen in the recent past. These changes may challenge the assumptions that the conditions experienced over the past 35 years, which our analyses are based on, will hold for the next 35 years. In general, declines in survival and consequently intrinsic productivity (i.e., recruits per spawner at low spawner abundance) lead to a reduction in MSY and MSR , as well as the escapement associated with them, which means that escapement goals based on a period of relatively high productivity should, all other things being equal, be biologically precautionary in periods where productivity is depressed or declining. However, if there is reason to believe that there is high uncertainty about future conditions that may impact the stock, then it may be important to take this into consideration.

In addition to changes in survival, there is widespread evidence of changes in Chinook salmon demographic characteristics over time (Ohlberger et al. 2018). Our analyses suggest that estimates of biological reference points are sensitive to temporal trends in demographic characteristics of the spawning population, consistent with research in other systems (e.g., Staton et al. 2021). Specifically, as the proportion of spawners that are female and their age at maturity declines (i.e., shift to younger ages at maturity), the spawning escapements associated with MSY and MSR increase. As a result, whether observed trends of declining escapement quality (i.e., age, sex, and length-at-age) are expected to continue into the future should also be taken into consideration when developing an escapement goal recommendation.

Lastly, our analyses did not explicitly consider fine scale Chinook salmon population diversity within the Canadian portion of the Yukon. As a result there is considerable uncertainty about the risks, if any, that an escapement goal based on maximizing yield, for example, might pose to individual populations within the stock aggregate and the communities that depend on them for subsistence and cultural use. Uncertainty about risks to individual component populations of the stock aggregate may therefore be a further consideration when developing an escapement goal recommendation.

Based on the considerations above we recommend the following steps be followed as an escapement goal recommendation is being formulated:

1. Define the objective(s) of an escapement goal and document the decision context in which it is being implemented.
2. Identify the key attributes required of the escapement goal. For example:
 - Has a reasonably high probability of achieving objectives (e.g., near-optimal yields or recruitments; with stated risk tolerance)
 - Consistent with previous bi-lateral development of escapement goals

-
- Precautionary in the face of:
 - recent low run-sizes,
 - uncertainties about future production due to demographic (escapement quality) and environmental (water temperature, ocean conditions) change, and
 - uncertainty about risks to individual component populations of the stock aggregate.
 - 3. Formulate and document an escapement goal recommendation that meets the key attributes identified in step 2, along with recommendation on the frequency and nature of future reviews of the escapement goal recommendation.

5.2. RECOMMENDATIONS FOR FUTURE WORK

5.2.1. Escapement quality

Our consideration of the consequences of demographic change (e.g., younger age-at-return) for expectations around yield and recruitment were based on readily available data and a number of simplifying assumptions. We therefore recommend a more thorough consideration of changes in escapement quality moving forward. Specific considerations include:

1. Carry out a detailed review of all available data on Yukon Chinook salmon age, sex and length as well as reproductive output (e.g., relationship between female size and total eggs or egg mass). This could build on several recent efforts to compile and review this data (Ohlberger et al. 2020), and follow an approach that is similar to the process followed for the bi-lateral data review completed to support this report (Pestal et al. 2022).
2. Revise our integrated model to explicitly model sex-ratios, length-at-age, and relationships between female length and fecundity and egg mass as being observed with error as opposed to as fixed inputs so as to better propagate uncertainty, and potentially time trends, in these dimensions of escapement quality.
3. Explicitly account for fishery selectivity by making the spawner-recruitment model we describe in this report sex structured with ability to estimate age/sex-based selectivity by multiple fisheries (e.g., commercial and subsistence fisheries) using different gears and resulting in differing exploitation rates (e.g., Staton et al. 2021). This would allow for better representation of uncertainty in age and sex-based selectivity and provide for the ability to quantify the consequences of size selective harvests on the estimation of biological reference points.
4. Consider an expanded set of structural forms of the spawner-recruitment relationship that allow for incorporation of alternative hypotheses about how within stock density-dependent processes affect survival (e.g., model with and without considering the effects of males in addition to female reproductive output, allowing for depensation, and alternative spatial scales at which density-dependence occurs) and potential for additional sources of information [e.g., accessible spawning habitat; Liermann et al. (2010)] to inform priors for density-dependence parameters. This should include quantifying the statistical support for the alternative structural forms of the spawner-recruitment relationship that are considered.

5.2.2. Population diversity and mixed-stock fishery tradeoffs

Alaska's Sustainable Salmon Policy and Canada's Wild Salmon Policy both recognize the importance of considering and protecting salmon population diversity. However, our analyses treated Chinook salmon that spawn in the Canadian portion of the Yukon River as a single homogeneous population complex. Yukon Chinook salmon spawn in hundreds of streams within the watershed (Brown

et al. 2017), which in turn likely comprise at least a dozen reproductively isolated populations. These spawning populations have likely adapted traits (e.g., juvenile habitat use, residence time, adult spawning duration, and spawn-timing) related to specific locations. These adaptations likely contribute to variability in intrinsic productivity and sustainable harvest rates among populations, while variation in overall habitat size (e.g., area of spawning and/or rearing habitats) contributes to variation in population abundance. This heterogeneity in population productivity and size complicates the development of escapement goals because the higher harvest rates that can be sustained by the most productive populations come at the risk of overfishing and potential extirpation of the less productive populations (Ricker 1958; Walters et al. 2008; Hilborn and Walters 2013). In addition, an uneven distribution of these populations among watersheds may lead to uneven impacts of aggregate management across the communities that rely upon salmon for subsistence and cultural needs (Connors et al. 2020).

Molecular analysis of decades-old scale samples collected at the Alaska-Yukon border, coupled with population level run reconstruction and spawner-recruitment models, suggests that intrinsic productivity and carrying capacity varies approximately 2- and 3-fold respectively among Canadian-origin Yukon Chinook salmon populations (Connors et al. 2019). This heterogeneity gives rise to trade-offs between the harvest rates, and escapement goals, predicted to maximize aggregate yield and risk to individual weak (less productive) populations that could be formally considered in the future when formulating escapement goal recommendations. This could be accomplished by extending the integrated modelling framework we describe in this report to separately model the reproductively isolated spawning populations within the Canadian portion of the Yukon River.

5.2.3. Management Strategy Evaluation

There are several limitations to our analyses that were inevitable given the approach we took to reconstructing stock dynamics and estimating a spawner-recruitment relationship for Canadian-origin Chinook salmon. These limitations included:

- We assumed long-term equilibrium conditions, which implicitly assumes that the past is a good predictor of the future. Rapid changes in both freshwater (e.g., changes in flow and river temperatures) and marine environments (e.g., timing of sea ice loss in Bering Sea and change in primary production and food web structure) brought on by climate change may result in conditions in the future that have not been seen in the recent past which may challenge the assumptions that the conditions experienced over the past 35 years will hold for the next 35 years.
- We only considered a narrow range of potential objectives (i.e., yield and recruitment) that may matter to managers, First Nations, subsistence users, and stakeholders. Additional objectives might include the chances of meeting target harvest over the short and long-term, stability in harvests from year-to-year, chances of stock growth, equity among subsistence and Indigenous users in access to fish, or other cultural values.
- We did not consider all common sources of uncertainty in salmon fishery systems. While our analyses explicitly accounted for uncertainty due to measurement error and process variation, and to a lesser extent structural uncertainties (demographic change, density dependence at high spawner abundance), they did not take into account the consequences of incomplete management control in the system (aka. “outcome uncertainty” sensu Holt and Peterman 2006), which can result in realized outcomes that deviate from management targets. Outcome uncertainty can be large in salmon systems, increase with declining

salmon abundance, and affect the true ability of an escapement goal, and the management strategy it is embedded in, to meet objectives.

All of these limitations could be addressed by quantitatively evaluating the performance of alternative management strategies (e.g., escapement goals, or harvest objectives within an escapement goal, or other management actions) using closed-loop simulation as part of a Management Strategy Evaluation. Closed-loop simulation modelling is widely considered to be the gold standard for quantifying trade-offs among objectives and evaluating the ability of alternative management strategies to meet objectives in the face of multiple sources of uncertainty (Punt et al. 2016). When developed and interpreted as part of a collaborative process with fishery participants, Traditional Knowledge holders, and resource managers, such simulations form a key part of a broader Management Strategy Evaluation.

Our work provides a foundation upon which closed-loop simulations of the system could be developed to quantitatively evaluate how alternative management strategies (e.g., aggregate escapement goals and harvest policies) affect the ability of the system to meet a broader diversity of conservation and socio-economic objectives (e.g., Cunningham et al. 2019; Connors et al. 2020; Freshwater et al. 2020) while also explicitly accounting for all key sources of uncertainty. Key steps in the development and application of a Management Strategy Evaluation include (adapted from Punt et al. 2016; Anderson and Keppel 2021):

1. **Define the decision context** including specifying (a) what is the decision(s) to be made, by whom and over what time frame, (b) what are the specific roles and responsibilities of parties involved, and (c) how final decisions will be made and how the process will be governed.
2. **Identify objectives and associated performance metrics**, which can be expressed as the metric, the desired probability of success, and a time frame to achieve the objective. These objectives may need to be prioritized at this stage based on, for example, legal requirements (e.g., stock may not be overfished).
3. **Develop a set of ‘operating models’** that provide a mathematical representation of the system under consideration including the biological components of the system, the fisheries which operate on the modelled population, how data are collected and how they relate to the modelled population (including the effect of measurement error and outcome uncertainty). These operating models should capture key axes of uncertainty representing hypotheses about how the system operates (e.g., multi-population population dynamics models with time trends in escapement quality) and what future conditions may be like, and should be conditioned on observed data.
4. **Identify candidate management procedures** that are the alternative management strategies to be evaluated.
5. **Simulate** each management procedure for each operating model over a time frame defined in step 1.
6. **Summarize results** including visualizing trade-offs among objectives (e.g., short- vs. long-term harvest, aggregate harvest vs. biological risk to individual populations) and, based on the performance of management procedures relative to the hierarchy of objectives, **select the preferred management procedure**.

6. ACKNOWLEDGEMENTS

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7. FIGURES

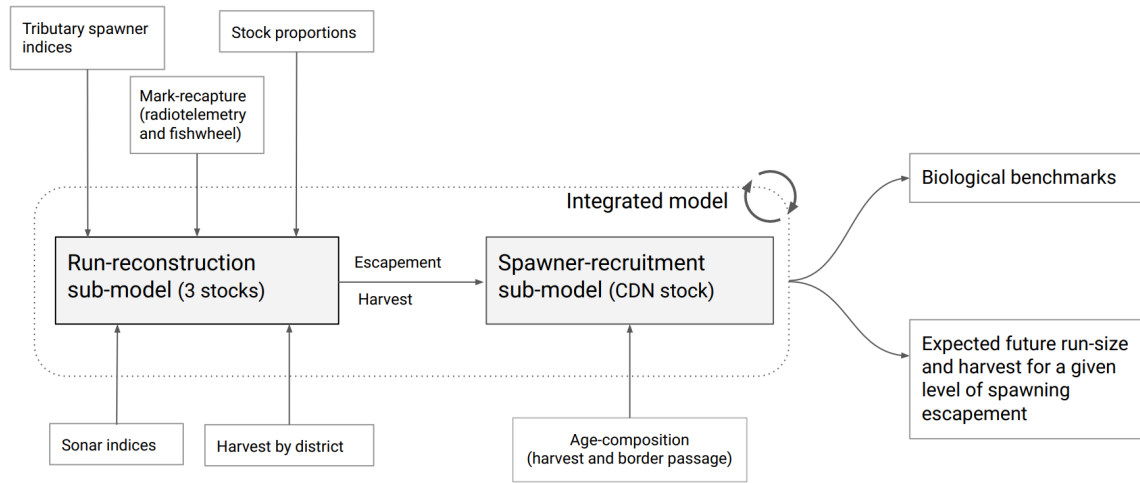


Figure 1. Schematic of integrated model illustrating key data inputs, model components, and inferential outputs.

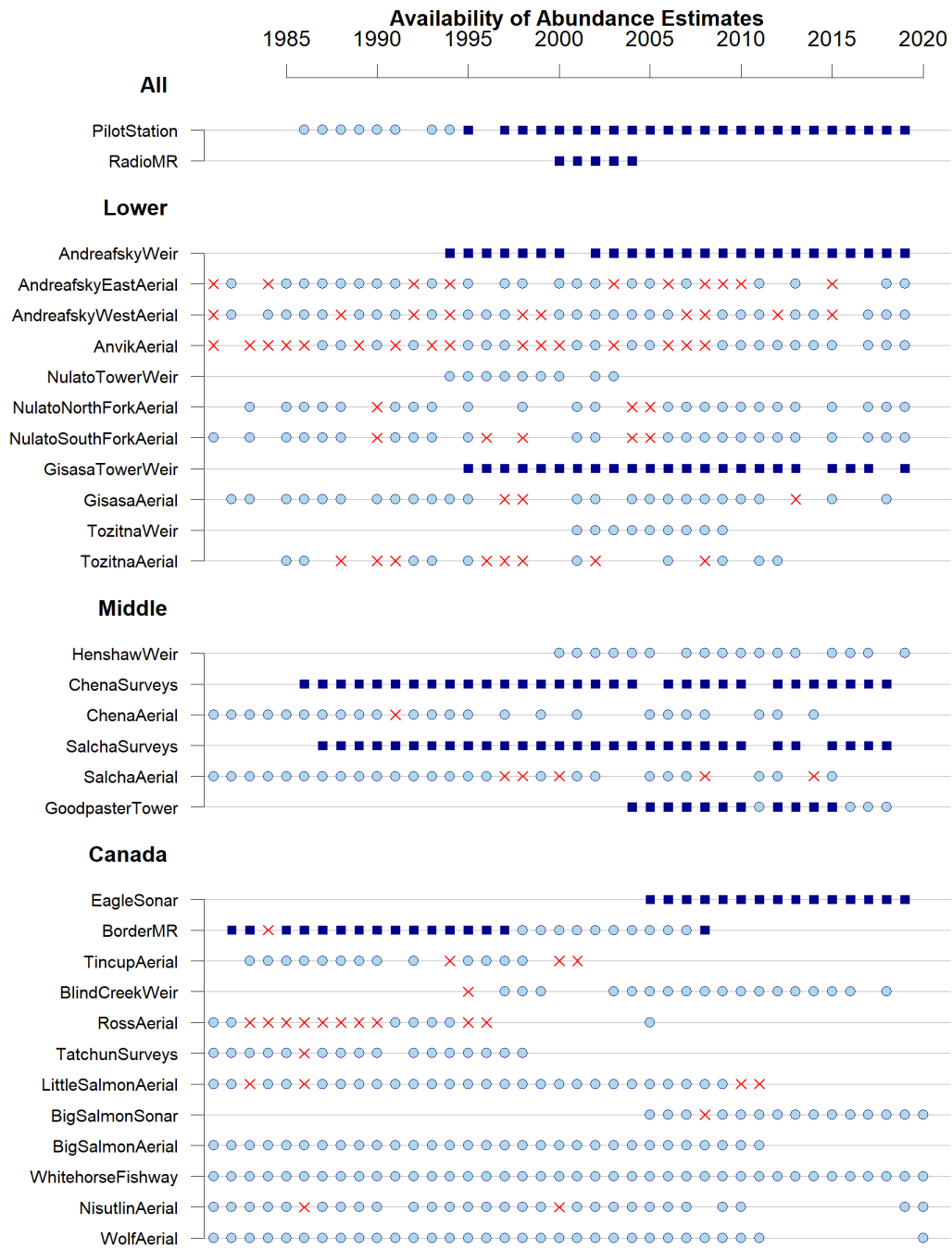


Figure 2. Data types and years that the integrated model was fit to. Dark blue squares mark years where estimates included measures of uncertainty that were accounted for. Light blue circles are years where only point estimates were available. Years where data exist, but were not used due to data concerns, are marked with a red "x." Additional data sets not shown in the figure are: Harvest age composition (available all years as point estimates), harvest stock composition (available all years as point estimates), and age-sex-length sampling at the border (available all years as point estimates, except 1981 and 1984).

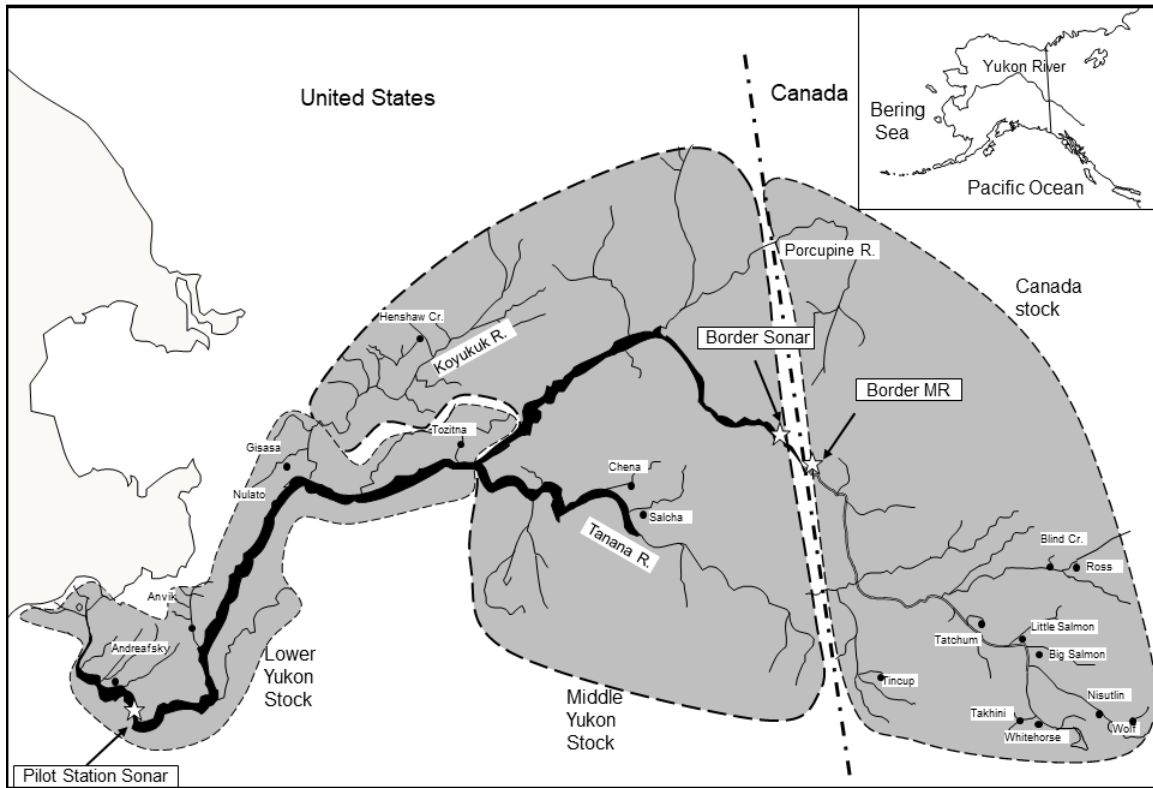


Figure 3. Yukon River drainage, mainstem monitoring projects locations (stars), escapement monitoring project locations (black dots), and Chinook salmon stocks groups (grey shading). Reproduced from Hamazaki (2021).

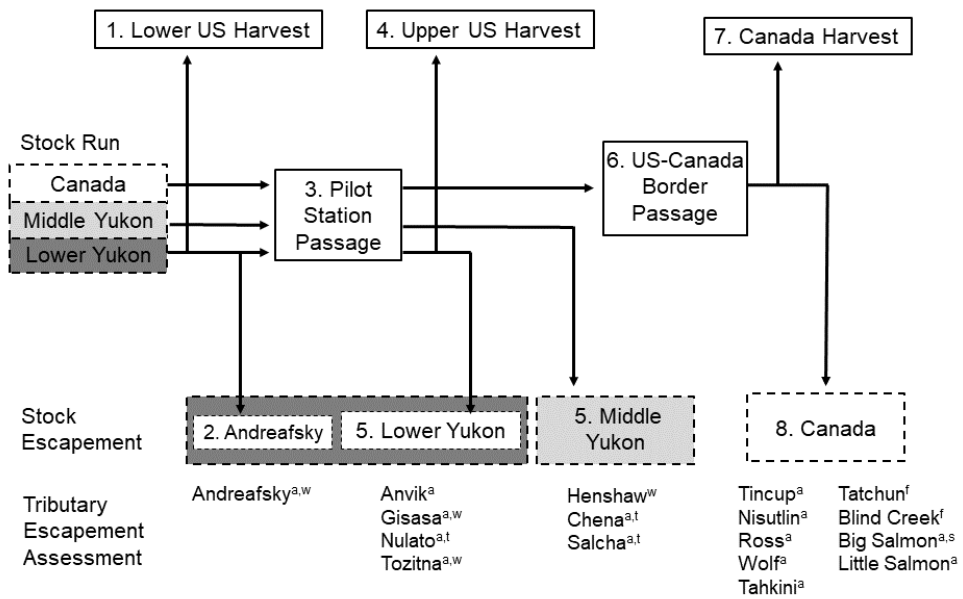


Figure 4. Schematic of multi-stock run reconstruction model structure and key sources of data (a: aerial survey; f: foot survey; t: tower; s: sonar; w: weir). Numbers in boxes correspond to the eight stages in the run reconstruction model. Adapted from Hamazaki (2021).

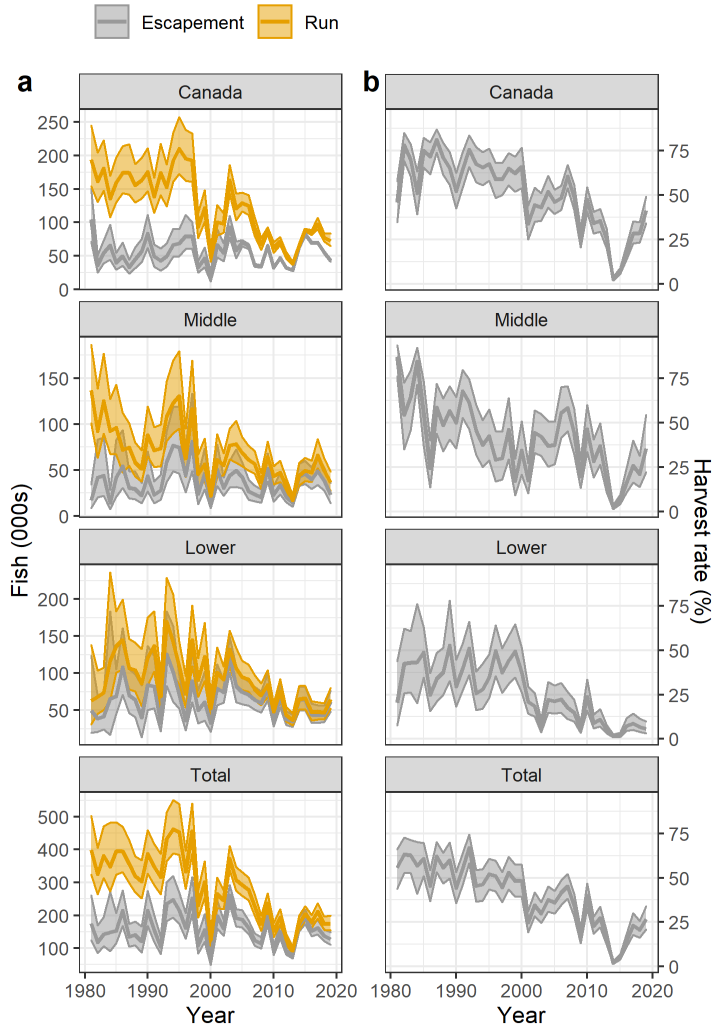


Figure 5. Reconstructed (a) total run size (orange) and spawning escapement (grey), and (b) harvest rates for Yukon River Chinook salmon by stock and for all stocks combined. Thick lines are medians and shaded areas indicate 95% credible intervals.

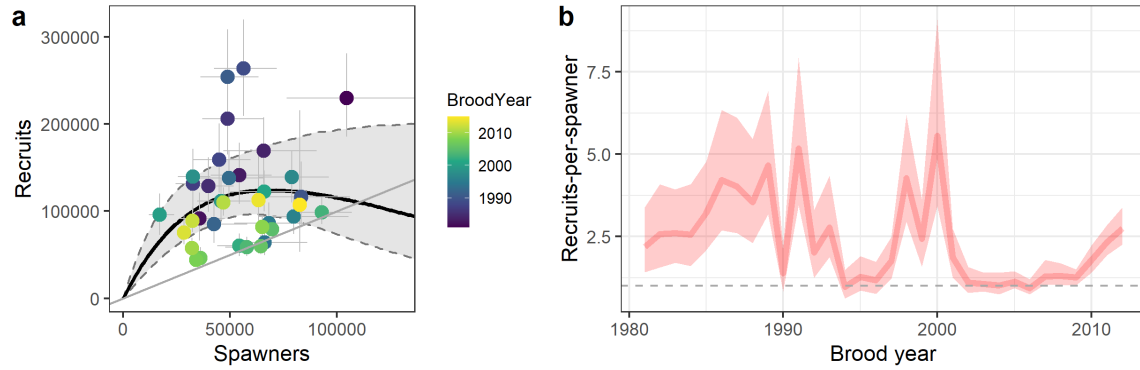


Figure 6. Spawner-recruitment relationship and productivity over time. (a) Relationship between recruitment and spawner abundance for Canada-origin Yukon Chinook salmon from 1982 to 2019. Error bars and grey band are 90% credible intervals, thick black line is the expected relationship. (b) Realized recruits produced per spawner over time (median and 95% credible intervals) with dashed line at replacement.

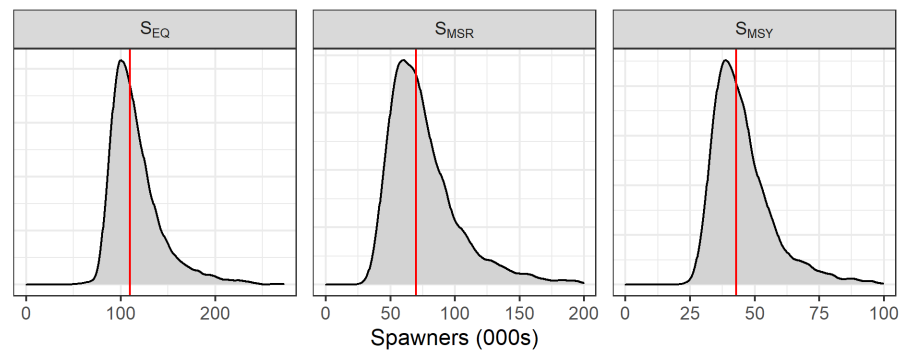


Figure 7. Posterior distributions of reference points including equilibrium spawning abundance (S_{EQ}), spawning abundance expected to maximize recruitment (S_{MSR}), and spawning abundance expected to maximize sustainable yield (S_{MSY}). Vertical red lines denote posterior means.

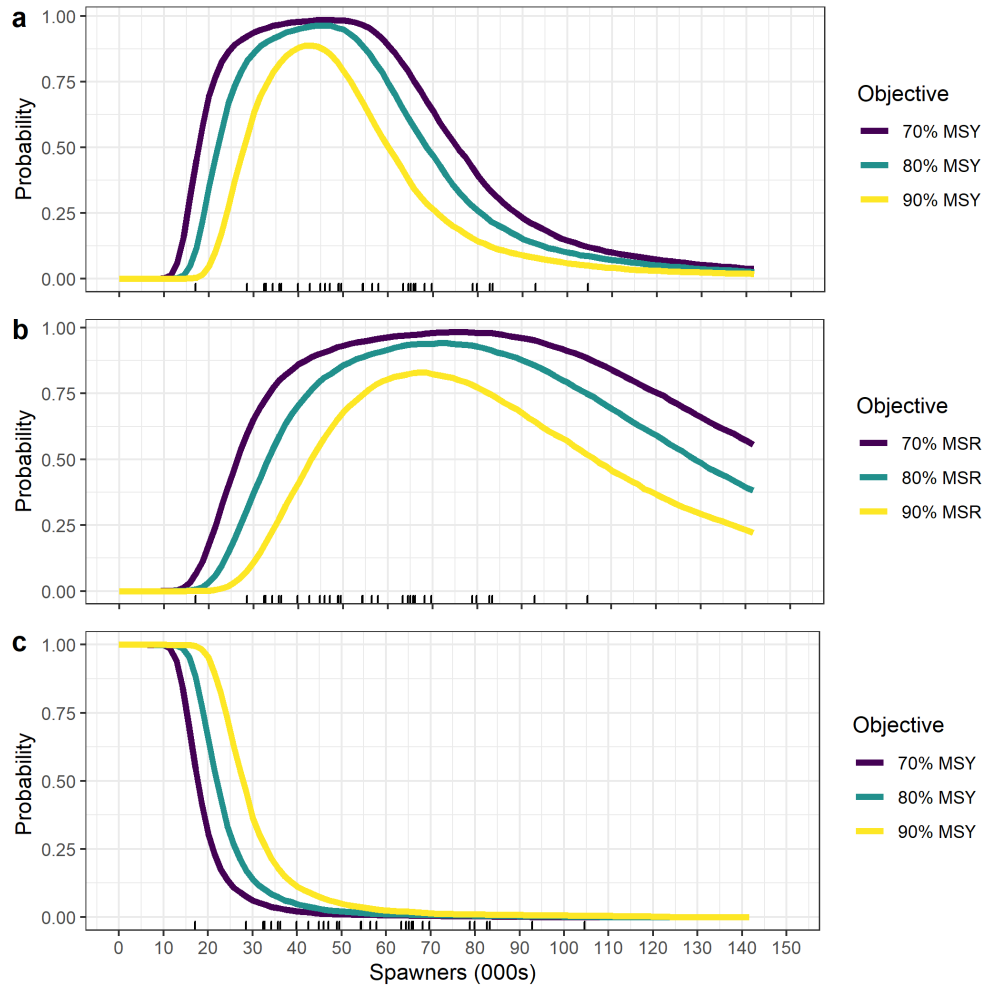


Figure 8. Optimal yield, recruitment, and “overfishing” probability profiles. (a) Optimal yield profile showing the probability that a given spawner abundance is expected to achieve 70%, 80%, or 90% of maximum sustainable yield (MSY). (b) Optimal recruitment profile showing the probability that a given spawner abundance is expected to achieve 70%, 80%, or 90% of maximum sustainable recruitment (S_{MSR}). Historical spawning escapements are shown along x-axis. (c) Overfishing profile, calculated as $1 - P(SY > X\% \text{ of } MSY)$ at $S < S_{MSY}$, and 0 at $S > S_{MSY}$, showing the probability that, at a given spawner abundance, sustained yield (SY) is reduced to less than a percentage (70%, 80%, or 90%) of MSY by supplying too few spawners.

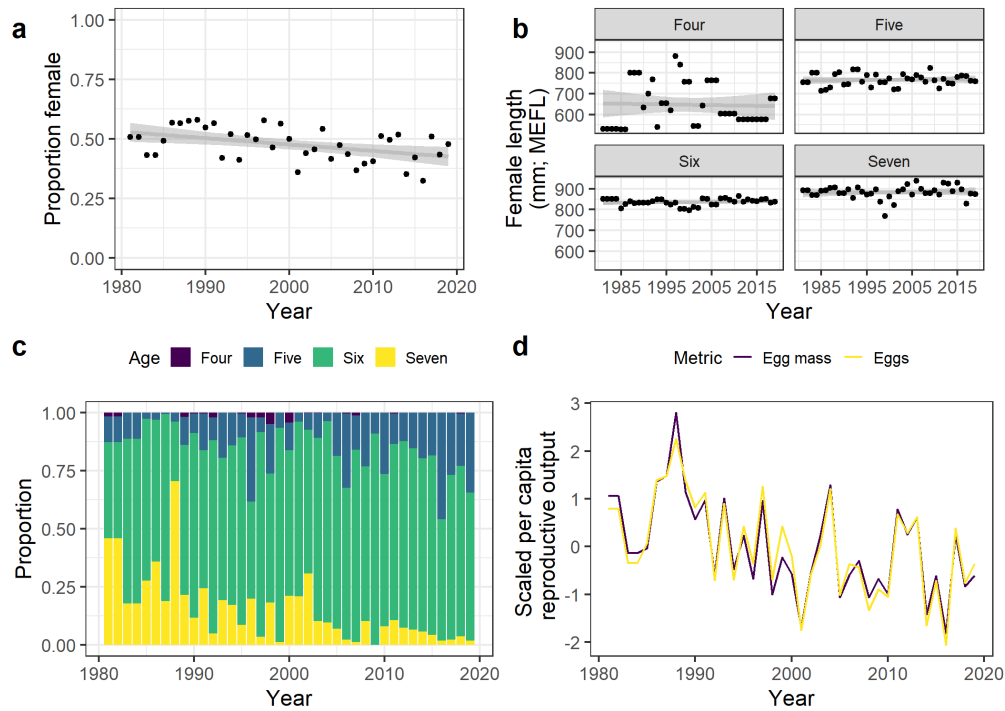


Figure 9. Female Chinook salmon age, sex, and size composition over time and implications for reproductive output. (a) Proportion of returning Chinook salmon that are female. (b) Average female length at age with years without data infilled with last year with estimates of length. (c) Proportion of females returning to spawn as 4-7 year olds. (d) Standardized reproductive output for two separate metrics (egg mass and eggs) based on the age, sex, length information in panels a-c, length-fecundity/egg mass relationships, and estimates of total spawning escapement from the base case integrated RR-SRA model. Note: 3 and 8 year olds were combined with 4 and 7 year olds, respectively, and age 4 female lengths are based on very small sample sizes in most years and so should be interpreted with caution. However, because 4 year old females make up so little of the spawning population these estimates have little influence on time series of reproductive output.

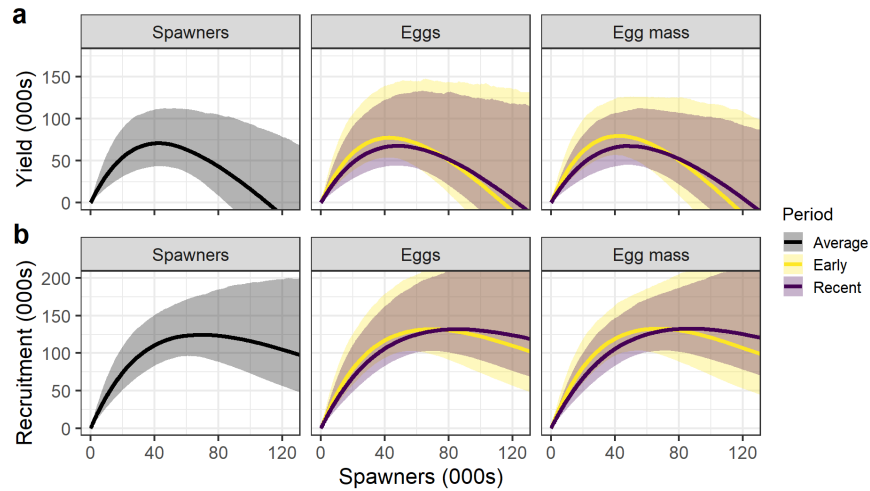


Figure 10. Expected (a) yield (i.e., surplus production) and (b) recruitment across a range of spawner abundances based on spawner-recruitment models fit to three alternative measures of reproductive output (total egg mass, total eggs, or total spawners). Shown is median \pm 90% credible intervals. The time period represents which years were used to calculate the average demographic qualities (sex-ratio, female age, and female length-at-age) used in equilibrium calculations; “Recent” corresponds to 2009-2019 and “Early” corresponds to 1982-1992.

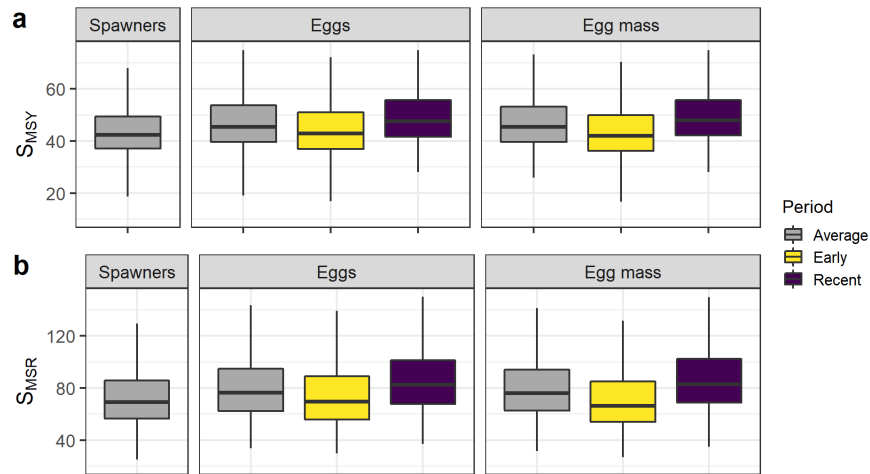


Figure 11. Spawner abundance expected to maximize long-term sustainable yield (S_{MSY}) and recruitment (S_{MSR}) based on spawner-recruitment models fit to three alternative measures of reproductive output (Total egg mass, total eggs, or total spawners). Boxplots show median and 25th and 75th quartiles with whiskers extending to the lowest/highest value up to 1.5 times the interquartile range. The time period represents which years were used to calculate the average demographic qualities (sex-ratio, female age, and female length at age) used in equilibrium calculations; “Recent” corresponds to 2009-2019 and “Early” corresponds to 1982-1992.

8. TABLES

Table 1. Variables in the run reconstruction (RR) submodel. Stock (s) is lower Yukon (l), middle Yukon (m), or Canada (c). Location (L) is downriver from Pilot Station (d), Pilot Station (pl), upriver from Pilot Station (u), the U.S./Canada border (b), or Canada (c). Method (j) references various assessment methods in use at locations and tributaries throughout the Yukon River drainage. Methods may change over time and more than one method may be used at a location.

Variable	Description
$H_{y,s,L}$	Total harvest in year y , stock s , location L
$e_{y,s,i,f}$	Escapement in year y , stock s , tributary i , using method j
$N_{y,s,L}$	Total run size in year y , stock s , location L
$U_{y,s,L}$	Fishing harvest rate in year y , stock s , location L
$E_{y,s,L}$	Total escapement in year y , stock s , location L
K_i	Time-invariant fraction of total escapement in tributary i
$\sigma_{y,i,j}$	Observed log-normal standard deviation of tributary i in year y , using method j
$\sigma_{(H)L}$	Time-invariant asserted log-normal standard deviation of the harvest in location L
$\sigma_{(N)y,s,L,j}$	Observed log-normal standard deviation of the total run in year y , stock s , location L , using method j
$P_{(H)y,s,L}$	Observed harvest proportions of stock s in year y , location L
$P_{(R)y,s,L}$	Observed run proportions of stock s in year y , location L
$n_{(H)y,L}$	Effective samples size asserted for the harvest stock proportions likelihood in year y , location L
$n_{(R)y,L}$	Effective samples size asserted for the run stock proportions likelihood in year y , location L
R_y	Total recruitment in year y
$p_{y,a}$	Proportion of fish spawned in brood year y that matured at age a , where $a \in 4:7$
$N_{y,a,s}^{SRA}$	Number of Chinook salmon that are predicted in the spawner-recruitment submodel to return to stock s in year y and age a
$p_{y,k,a}^{obs}$	Observed harvest age composition proportion for age a , in river section k and year y
$\tau_{y,a}^{age}$	Predicted run age (a) proportions for year y
$q + y, a$	Female sex ratio in spawner escapement in year y and age a
$w_{j,y,a}$	Per capita reproductive output for metric j in year y and age a
$Z_{j,y}$	Total reproductive output for metric j in year y

Table 2. Prior probability distributions for run reconstruction parameters. Normal distributions are in SD units.

Parameter	Prior	Bounds	DescriptionNotes
$F_{y,s,L}$	$\sim N(0, 2)$	$[0, \text{inf}]$	Instantaneous fishing mortality rate: Lower Yukon, Upper Yukon, Canadian Yukon
$N_{y,s}$	$\ln(N_{y,s}) \sim U(9, 13)$		Stock run sizes (natural log space)
K_i	$\ln(K_i) \sim U(0, 6)$		Escapement fraction scalars (natural log space)
q_{pl}	$\ln(q_{pl}) \sim U(-10, 1)$		Pilot Station sonar catchability
q_{fw}	$\ln(q_{fw}) \sim U(-5, 0)$		Survey catchability for fish wheel mark-recapture
p_N	$\ln(p_N) \sim U(-5, 0)$		Proportion of Nulato River escapement to North Fork
p_E	$\ln(p_E) \sim U(-5, 0)$		Proportion of Andreafsky escapement to East Fork
$\sigma_{add,s=c,j}$	$\ln(\sigma_{add,s=c,j}) \sim U(-5, 5)$		Additional escapement variance for Canadian tributary projects
$\sigma_{add,s=c,L=b,j}$	$\ln(\sigma_{add,s=c,L=b,j}) \sim U(-15, 2)$		Additional escapement variance for border fishwheel mark-recapture project
$\sigma_{add,s=l,m,j}$	$\ln(\sigma_{add,s=l,m,j}) \sim U(-5, 1)$		Additional escapement variance for US weir and tower projects
$\sigma_{add,s=l,m,j}$	$\ln(\sigma_{add,s=l,m,j}) \sim U(-10, 1)$		Additional escapement variance for US aerial surveys
$\sigma_{add,pl,j}$	$\ln(\sigma_{add,pl,j}) \sim U(-10, 10)$		Additional variance for Pilot Station sonar and mark-recapture

Table 3. Prior probability distributions for spawner-recruit parameters.

Parameter	Prior	Bounds	DescriptionNotes
$\ln(\alpha)$	$\sim N(0, 3)$	$[0, \text{inf}]$	Natural log of intrinsic rate of growth
β	$\sim N(0, 1)$	$[0, \text{inf}]$	Magnitude of within brood-year density-dependence
ϕ	$\sim U(-1, 1)$		Lag-one correlation in interannual variation in survival
σ_R	$\sim N(0, 2)$	$[0, \text{inf}]$	White noise process standard deviation in survival.
$\ln(R_0)$	$\sim N(0, 20)$	$[0, \text{inf}]$	Natural log of unobserved recruitment in the first seven years of process model.
σ_{R_0}	$\sim \text{Inv} - \text{Gamma}(2, 0)$	$[0, \text{inf}]$	Standard deviation in unobserved recruitment in the first seven years of process model. Based on meta-analysis of other AK Chinook stocks (Fleischman et al. 2013), less informative priors resulted in divergent transitions in sampler during initial attempts to code the model in Stan.
π	$\sim \text{Dir}(0.25, 0.25, 0.25, 0.25)$		Mean maturation-at-age probability for ages 4:7.
D	$\sim \text{beta}(1, 1)$		Dispersion parameter that governs variability in maturation-at-age probabilities across cohorts.

Table 4. Posterior means, medians and credible intervals for leading spawner-recruitment parameters and associated biological reference points. Also shown are estimates of the effective sample size (n_{eff}) and potential scale reduction factor (\hat{R}) for parameters and reference points estimated by the model.

Variable	Mean	Median	p2.5	p97.5	n_{eff}	\hat{R}
$\ln(\alpha)$	1.848	1.594	1.003	2.236	3,348	1.001
β	1.440E-05	1.420E-05	5.371E-06	2.433E-05	3,882	0.9999
σ_R	0.441	0.435	0.314	0.602	4,531	1.0016
ϕ	0.389	0.393	-0.055	0.850	1,898	1.0005
S_{MSR}	82,918	70,447	41,094	186,200	2,893	1.0006
S_{EQ}	146,576	110,601	81,708	234,252	3,855	1.0009
S_{MSY}	48,443	43,125	29,874	93,070	3,089	1.0006
U_{MSY}	62%	62%	43%	77%	4,529	1.0001
U_{MSR}	43%	45%	4%	71%		

Table 5. Posterior means, medians and credible intervals for the spawner abundance expected to maximize long-term sustainable yield (S_{MSY}) across three different measures of reproductive output (total spawners, total eggs, and total egg mass) and three time periods. "Recent" corresponds to 2009-2019 and "Early" corresponds to 1982-1992. Note that minor differences in estimates for total spawners between this table and Table 4 are due to iterative search algorithm used to derive the estimates presented in this table.

Variable	Mean	Median	p2.5	p97.5
1	47,253	42,946	29,987	93,882
2	53,536	46,995	32,795	126,958
3	50,020	44,070	30,075	117,038
4	56,213	49,224	34,659	133,485
5	51,981	46,568	32,226	105,004
6	47,885	42,891	29,090	97,942
7	55,162	49,479	34,616	111,093

Table 6. Posterior means, medians and credible intervals for the spawner abundance expected to maximize long-term sustainable recruitment (S_{MSR}) across three different measures of reproductive output (total spawners, total eggs, and total egg mass) and three time periods. "Recent" corresponds to 2009-2019 and "Early" corresponds to 1982-1992. Note that minor differences in estimates for total spawners between this table and Table 4 are due to iterative search algorithm used to derive the estimates presented in this table.

Variable	Mean	Median	p2.5	p97.5
1	77,096	69,919	41,285	150,537
2	86,927	78,945	46,319	168,878
3	76,560	69,529	40,794	148,736
4	94,801	86,096	50,514	184,175
5	86,796	78,086	46,209	176,888
6	73,514	66,137	39,138	149,820
7	95,867	86,246	51,039	195,374

9. REFERENCES CITED

- Alaska Board of Fisheries. 2000. Policy for the Management of Sustainable Salmon Fisheries. 5 AAC 39.222.
- Alaska Board of Fisheries. 2001. Policy for Statewide Salmon Escapement Goals. 5 AAC 39.223.
- Anderson, F., S. C., and Keppel, E.A. 2021. A management procedure framework for groundfish in British Columbia. DFO Can. Sci. Advis. Sec. Res. Doc. 2021/007. 139 p.
- Bernard, D.R., and Jones, E.L. 2010. Optimum escapement goals for Chinook salmon in the transboundary Alsek River. Alaska Department of Fish & Game, Fishery Manuscript Series No. 10-02, Anchorage.
- Biela, V.R. von, Bowen, L., McCormick, S.D., Carey, M.P., Donnelly, D.S., Waters, S., Regish, A.M., Laske, S.M., Brown, R.J., Larson, S., Zuray, S., and Zimmerman, C.E. 2020. Evidence of prevalent heat stress in Yukon River Chinook salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 77(12): 1878–1892.
- Biela, V.R. von, Sergeant, C.J., Carey, M.P., Liller, Z., Russell, C., Quinn-Davidson, S., Rand, P., Westley, P.A.H., and Zimmerman, C.E. In press. Premature mortality observations among Alaska's Pacific salmon during record heat and drought in 2019. *Fisheries*.
- Bradford, M.J., Finster, A. von, and Milligan, P.A. 2009. Freshwater life history, habitat, and the production of chinook salmon from the upper yukon basin. *In American fisheries society symposium*. pp. 19–38.
- Bromaghin, J.F., Evenson, D.F., McLain, T.H., and Flannery, B.G. 2011. Using a genetic mixture model to study phenotypic traits: Differential fecundity among yukon river chinook salmon. *Transactions of the American Fisheries Society* 140(2): 235–249. Taylor & Francis.
- Brown, C.L., and Deena, M.J. 2019. 2019 Pilot inseason monitoring of subsistence salmon harvests in the Yukon River drainage. Alaska Department of Fish and Game Division of Subsistence, Technical Paper 448.
- Brown, R.J., Finster, A. von, Henszey, R.J., and Eiler, J.H. 2017. [Catalog of Chinook salmon spawning areas in Yukon River basin in Canada and United States](#). *Journal of Fish and Wildlife Management* 8(2): 558–586.
- Bue, B.G., and Hamazaki, T. 2014. Yukon River Chinook salmon run reconstruction. Final Report to the US Fish and Wildlife Service Office of Subsistence Management Study: 10–200.
- Bue, B., Schaberg, K.L., Liller, Z.W., and Molyneaux, D.B. 2012. Estimates of the historic run and escapement for the Chinook salmon stock returning to the Kuskokwim River, 1976–2011. Alaska Department of Fish; Game, Fishery Data Series No. 12-49, Anchorage.
- Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., and Riddell, A. 2017. [Stan : A probabilistic programming language](#). *J. Stat. Soft.* 76(1).

-
- Connors, B.M., Siegle, M.R., and Harding, J. 2019. Yukon harvest-population diversity trade-offs. Arctic-Yukon-Kuskokwim sustainable salmon initiative project final report: 85 p.
- Connors, B.M., Staton, B., Coggins, L., Walters, C., Jones, M., Gwinn, D., Catalano, M., and Fleischman, S. 2020. [Incorporating harvest–population diversity trade-offs into harvest policy analyses of salmon management in large river basins](#). *Can. J. Fish. Aquat. Sci.* 77(6): 1076–1089.
- Cunningham, C.J., Anderson, C.M., Wang, J.Y.-L., Link, M., and Hilborn, R. 2019. A management strategy evaluation of the commercial sockeye salmon fishery in Bristol Bay, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 76(9): 1669–1683.
- DFO. 1985. [Canada’s Fisheries Act, Revised Statutes of Canada \(1985, c. F-14\)](#).
- DFO. 2005. Canada’s Policy for Conservation of Wild Pacific Salmon.
- DFO. 2009. A fishery decision-making framework incorporating the precautionary approach.
- Dorner, B., Catalano, M.J., and Peterman, R.M. 2018. [Spatial and temporal patterns of covariation in productivity of Chinook salmon populations of the northeastern Pacific Ocean](#). *Can. J. Fish. Aquat. Sci.* 75(7): 1082–1095.
- Eggers, D.M., and Bernard, D.R. 2011. Run reconstruction and escapement goals for Alsek River sockeye salmon. Alaska Department of Fish; Game, Fishery Manuscript Series No. 11-01, Anchorage.
- Fleischman, S.J., Catalano, M.J., Clark, R.A., and Bernard, D.R. 2013. [An age-structured state-space stock–recruit model for Pacific salmon \(*Oncorhynchus* spp.\)](#). *Can. J. Fish. Aquat. Sci.* 70(3): 401–414.
- Freshwater, C., Holt, K.R., Huang, A.-M., and Holt, C.A. 2020. [Benefits and limitations of increasing the stock-selectivity of Pacific salmon fisheries](#). *Fisheries Research* 226: 105509.
- Gilbert, C.H. 1922. The salmon of the yukon river. US Government Printing Office.
- Hamazaki, T. 2018a. Estimation of U.S.-Canada border age-composition of Yukon River Chinook salmon, 1982 - 2006. Alaska Department of Fish and Game, Fishery Data Series 18-21.
- Hamazaki, T. 2018b. Estimation of US-Canada border age-composition of Yukon River Chinook salmon, 1982-2006. Alaska Department of Fish; Game, Fishery Data Series No. 18-21, Anchorage.
- Hamazaki, T. 2021. Stock-specific run and escapement of Yukon River Chinook salmon 1981–2019. Alaska Department of Fish and Game, Fishery Data Series No. 21-15, Anchorage.
- Hamazaki, T., and DeCovich, N. 2014. [Application of the genetic mark–recapture technique for run size estimation of Yukon River Chinook Salmon](#). *North American Journal of Fisheries Management* 34(2): 276–286.
- Hamazaki, T., Evenson, M., Fleischman, S., and Schaberg, K. 2012. Spawner–recruit analysis and escapement goal recommendation for Chinook salmon in the Kuskokwim River drainage. Fishery Manuscript (12).

-
- Hilborn, R. 1985. Simplified calculation of optimum spawning stock size from Ricker's stock recruitment curve. *Canadian Journal of Fisheries and Aquatic Sciences* 42(11): 1833–1834. NRC Research Press Ottawa, Canada.
- Hilborn, R., and Walters, C.J. 2013. *Quantitative fisheries stock assessment: Choice, dynamics and uncertainty*. Springer Science & Business Media.
- Hoffman, M.D., and Gelman, A. 2014. The No-U-Turn sampler: Adaptively setting path lengths in Hamiltonian Monte Carlo. *J. Mach. Learn. Res.* 15(1): 1593–1623.
- Holt, C.A., and Bradford, M.J. 2011. [Evaluating benchmarks of population status for Pacific salmon](#). *North American Journal of Fisheries Management* 31(2): 363–378.
- Holt, C.A., Cass, A., Holtby, B., and Riddell, B. 2009. Indicators of status and benchmarks for Conservation Units in Canada's Wild Salmon Policy. DFO Can. Sci. Advis. Sec. Res. Doc.
- Holt, C.A., and Peterman, R.M. 2006. [Missing the target: Uncertainties in achieving management goals in fisheries on Fraser River, British Columbia, sockeye salmon \(*Oncorhynchus nerka*\)](#). *Can. J. Fish. Aquat. Sci.* 63(12): 2722–2733.
- Holtby, L.B., and Ciruna, K.A. 2007. Conservation Units for Pacific Salmon under the Wild Salmon Policy. DFO Canadian Science Advisory Secretariat Research Document 2007/070: 358.
- Ianelli, J.N., and Stram, D.L. 2018. [Chinook bycatch mortality update](#). Discussion paper presented to the North Pacific Fishery Management Council, April 2018.
- Johnson, Y., Boyce, I., and Waugh, B. 2002. Estimation of the abundance of Chinook salmon, *Oncorhynchus tshawytscha*, in the upper Yukon River basin using mark-recapture methods, 1990-95. Fisheries & Oceans Canada, Pacific Region, Science Branch.
- JTC. 1985a. Yukon River Technical Report, October 1985. U.S./Canada Yukon River Joint Technical Committee, Joint Technical Report.
- JTC. 1985b. Yukon River Technical Report, November, 1990. U.S./Canada Yukon River Joint Technical Committee, Joint Technical Report.
- JTC. 1987a. Yukon River Technical Report, April 1987. U.S./Canada Yukon River Joint Technical Committee, Joint Technical Report.
- JTC. 1987b. Yukon River Technical Report, October 1987. U.S./Canada Yukon River Joint Technical Committee, Joint Technical Report.
- JTC. 2002. Yukon River salmon season review for 2002 and technical committee report. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 3A02-44.
- JTC. 2010. Yukon River salmon 2009 season summary and 2010 season outlook. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 3A10-01.
- JTC. 2011. Yukon River salmon 2010 season summary and 2011 season outlook. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 3A11-01.
-

-
- JTC. 2020. Yukon River salmon 2019 season summary and 2020 season outlook. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 3A20-01.
- JTC. 2021. Yukon River salmon 2020 season summary and 2021 season outlook. Alaska Department of Fish and Game, Division of Commercial Fisheries, Regional Information Report 3A21-01.
- Larson, S., DuBois, L., and Wood, E. 2020. Origins of Chinook salmon in Yukon area fisheries, 2015. Alaska Department of Fish and Game, Fishery Data Series, Anchorage No. 20-21.
- Lewis, B., Grant, W.S., Brenner, R.E., and Hamazaki, T. 2015. [Changes in size and age of Chinook salmon *Oncorhynchus tshawytscha* returning to Alaska](#). PLoS ONE 10(6): e0130184.
- Liermann, M., Sharma, R., and Parken, C. 2010. Using accessible watershed size to predict management parameters for chinook salmon, *Oncorhynchus tshawytscha*, populations with little or no spawner-recruit data: A Bayesian hierarchical modelling approach. Fisheries Management and Ecology 17(1): 40–51. Wiley Online Library.
- Maunder, M.N. 2011. [Review and evaluation of likelihood functions for composition data in stock-assessment models: Estimating the effective sample size](#). Fisheries Research 109(2): 311–319.
- McCullough, D.A. 1999. A review and synthesis of effects of alterations to the water temperature regime on freshwater life stages of salmonids, with special reference to Chinook salmon. US Environmental Protection Agency, Region 10.
- McDougall, M.J., and Brodersen, N.B. 2020. Sonar estimation of Chinook and fall chum salmon passage in the Yukon River near Eagle, Alaska. Alaska Department of Fish and Game, Fishery Data Series 20-26.
- Miller, S.E., and Pestal, G. 2020. Estimates of a biologically-based spawning goal and management benchmarks for the Canadian-origin Taku River sockeye salmon stock aggregate.
- Milligan, P., Rublee, W., Cornett, D., and Johnston, R. 1984. The distribution and abundance of Chinook salmon (*Oncorhynchus tshawytscha*) in the upper Yukon River Basin as determined by a radio-tagging and spaghetti tagging program, 1982-1983. Department of Fisheries & Oceans.
- Ohlberger, J., Schindler, D.E., Brown, R.J., Harding, J.M.S., Adkison, M.D., Munro, A.R., Horstmann, L., and Spaeder, J. 2020. [The reproductive value of large females: Consequences of shifts in demographic structure for population reproductive potential in chinook salmon](#). Can. J. Fish. Aquat. Sci. 77(8): 1292–1301.
- Ohlberger, J., Ward, E.J., Schindler, D.E., and Lewis, B. 2018. [Demographic changes in Chinook salmon across the Northeast Pacific Ocean](#). Fish Fish 19(3): 533–546.
- Pestal, G., Etherton, P., Boyce, I., Richards, P., and Jaecks, T. 2016. Exploration of data and methods for developing estimates of a biologically-based spawning goal and biological benchmarks for Little Tahltan Chinook (Stikine River drainage). DFO Can. Sci. Advis. Sec. Res. Doc. 2016/110. 141 p.

-
- Pestal, G., Mather, V., West, F., Liller, Z., and Smith, S. 2022. Review of available abundance, age, and stock composition data useful for reconstructing historical stock specific runs, harvest, and escapement of Yukon River Chinook salmon (*Oncorhynchus tshawytscha*), 1981-2019. Pacific Salmon Commission Technical Report 48: iii + 347 p.
- Peterman, R.M., and Dorner, B. 2012. [A widespread decrease in productivity of sockeye salmon \(*Oncorhynchus nerka*\) populations in western North America](#). Can. J. Fish. Aquat. Sci. 69(8): 1255–1260.
- Pfisterer, C.T., McIntosh, B.C., and Hamazaki, T. 2017. Updated passage estimates for the pilot station sonar project, 1995-2015. Alaska Department of Fish; Game, Division of Sport Fish, Research; Technical Services.
- Punt, A.E., Butterworth, D.S., Moor, C.L. de, De Oliveira, J.A.A., and Haddon, M. 2016. [Management strategy evaluation: Best practices](#). Fish Fish 17(2): 303–334.
- Reimer, A.M., and Decovich, N.A. 2020. Susitna River Chinook salmon run reconstruction and escapement goal analysis. Alaska Department of Fish; Game, Fishery Manuscript No. 20-01,.
- Ricker, W. 1958. Maximum sustained yields from fluctuating environments and mixed stocks. Journal of the Fisheries Board of Canada 15(5): 991–1006.
- Ricker, W.E. 1954. Stock and recruitment. Journal of the Fisheries Board of Canada 11(5): 559–623.
- Scheuerell, M.D. 2016. [An explicit solution for calculating optimum spawning stock size from Ricker's stock recruitment model](#). PeerJ 4: e1623.
- Schindler, D.E., Walsworth, T.E., Adkison, M.D., Peterman, R.M., and Punt, A.E. 2019. Kuskokwim River Chinook salmon run-reconstruction and stock recruitment models: A review by an independent expert panel. Arctic-Yukon Kuskokwim Sustainable Salmon Initiative, Anchorage.
- Spencer, T.R., Eiler, J.H., and Hamazaki, T. 2009. Mark–recapture abundance estimates for Yukon River Chinook salmon in 2000–2004. Alaska Department of Fish and Game, Fishery Data Series 09-32.
- Stan Development Team. 2020. [RStan: The R interface to Stan](#).
- Staton, B.A., Catalano, M.J., and Fleischman, S.J. 2017. From sequential to integrated Bayesian analyses: Exploring the continuum with a Pacific salmon spawner-recruit model. Fisheries Research 186: 237–247.
- Staton, B.A., Catalano, M.J., Fleischman, S.J., and Ohlberger, J. 2021. [Incorporating demographic information into spawner–recruit analyses alters biological reference point estimates for a western Alaska salmon population](#). Can. J. Fish. Aquat. Sci. 78(12): 1755–1769.
- Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., and Burkner, P.-C. 2021. Rank-normalization, folding, and localization: An improved \hat{R} for assessing convergence of MCMC (with discussion). Bayesian analysis 16(2): 667–718. International Society for Bayesian Analysis.

Walters, C.J., Lichatowich, J., Peterman, R.M., and Reynolds, J.D. 2008. Report of the Skeena independent science review panel. A report to the Canadian Department of Fisheries and Oceans and the British Columbia Ministry of the Environment.

APPENDIX A. HISTORY OF ANALYTICAL WORK RELEVANT TO ESCAPEMENT GOALS FOR CANADIAN-ORIGIN YUKON CHINOOK SALMON

The following synopsis provides a brief history of Canadian-origin Chinook salmon escapement goals and analytical work conducted by the Yukon River Joint Technical Committee, associated agencies, and academic researchers which were relevant to previous escapement goal discussions. Readers should refer to Appendix A9 in JTC (2021) for a complete record of escapement goals recommended by the Yukon River Panel (YRP) for this stock. Table A.1 lists key analytical work in chronological order.

Since 1985, the U.S. and Canada have bilaterally agreed to annual escapement objectives for Canadian-origin Mainstem Yukon River Chinook salmon based on recommendations from the JTC. Goal recommendations have been based, in part, on five key sources of information: 1) tributary escapement indices in Canada, 2) estimates of U.S./Canada border passage, 3) harvest in Canada, 4) harvest of Canadian-origin fish in U.S. fisheries occurring within the Alaska portion of the river, and 5) age-structured brood tables.

The quantity, quality, and methods used to assess Canadian-origin mainstem Chinook salmon has changed over time. From 1982–2007, border passage was estimated using fish wheel mark–recapture techniques at tagging and recapture locations in Canada. Beginning in 2008, the JTC transitioned to using sonar estimates from a project located downriver from the Alaska community of Eagle, and border passage was estimated by subtracting the U.S. harvest that occurred between the sonar location and the U.S./Canada border. Harvest of Canadian-origin Chinook salmon throughout the entire Alaska portion of the drainage was assessed using commercial fish tickets, postseason subsistence harvest surveys, and stock-separation techniques based on scale pattern analyses (1981–2004) or genetic analysis (2005–present). Harvest in Canada was reported annually through commercial fishery documents and reports from First Nations. Escapement in Canada has been monitored with aerial surveys, ground surveys, weirs, and sonars, but various aerial survey indices have been used extensively to inform escapement goal analyses. With these sources of information, the Canadian-origin Chinook salmon run size has been estimated annually by the JTC by adding the estimates of border passage and U.S. harvest of Canadian-origin fish. Escapement of Canadian-origin Chinook salmon has been assessed by the JTC by subtracting the estimated harvest in Canada from the border passage (e.g., JTC 2021).

In 1985, the JTC began bilateral efforts to recommend an escapement goal for the mainstem Canadian-origin Chinook salmon stock (i.e., not including the Porcupine River). An analysis based on the average ratio of the annual 3-area (Whitehorse fishway, Big Salmon, and Nisutlin River) index count to total escapement was used to propose an escapement target of 55,000 (JTC 1985a). The analysis utilized limited escapement data from 1980–1984 and leveraged the 3-area index counts for years 1980, 1981, and 1984, because those years were assumed to represent above average escapements. The three-year average escapement index of 4,735 was expanded to the entire Canada stock by dividing the index value by an escapement ratio of 0.0881. The escapement ratio was based on the average 3-area index value divided by total escapement for years 1982 and 1983. The result ($4,735/0.0881 = 53,746$) was rounded up to 55,000 but was not implemented as a formal management objective.

In 1987, after two years of discussion, the JTC recommended the first escapement goal range for Canadian-origin mainstem Chinook salmon. It was determined that the 1985 analysis used non-standardized data for the Big Salmon and Nisutlin rivers, and the 3-area index counts for years 1980, 1981, and 1984 were not comparable. The analysis was redone using standardized

3-area index counts and an updated expansion factor which included newly available 1985 data. The result was a refined total Canada mainstem stock escapement objective of 37,912. Alternate tributary escapement index values were explored resulting in a range of total escapement objectives from 31,979–37,912.

Ultimately, the JTC agreed that an escapement objective for this stock should be represented as a range to reflect different interpretations of the limited data and to better align with management needs. The JTC recommended a range of 33,000–43,000 which was informed by the range of updated analyses and a desire to evaluate future run sizes from elevated escapements. There was consensus that the recommended goal range was biologically sound but should be considered an interim objective until additional information is available to refine the goal (JTC 1987a).

Evaluation of the newly established escapement objective was based on annual assessment using fish wheel mark-recapture techniques implemented in Canada near the Bio-Island site upriver from the U.S./Canada border. The fish wheel program provided the most complete and best available information about the annual abundance of mainstem Yukon River Chinook salmon entering Canada. Total annual escapement was estimated annually by subtracting harvest in Canada from the mark-recapture estimate of border passage.

During the 1987–1989 period, the estimated Canadian spawning escapements were well below the established escapement goal range of 33,000–43,000 (JTC 1985b). However, recent-year average productivity was estimated to be 4.39 recruits per spawner, based on estimates from 1978–1983 brood years (see Table 4 in JTC 1985b). Biologists believed recent-year production was adequate to support the population and continue fishing on a limited basis.

From 1990–2001, the Yukon River Panel implemented minimum escapement objectives that were less than the lower bound of the established escapement goal range of 33,000–43,000. A “stabilization escapement objective” of 18,000 fish was recommended in 1990 as part of a rebuilding plan, and that objective remained in place until 1995. In 1996, the Yukon River Panel established a minimum escapement objective of 28,000 Chinook salmon as part of a rebuilding plan which was effective until 2001.

In 2002, the Yukon River Salmon Agreement (YRSA) was ratified by the U.S. and Canada and included as Chapter 8 in the Pacific Salmon Agreement. The 33,000–43,000 Chinook salmon interim escapement objective was incorporated into Appendix II of the YRSA. Specific language identifies 33,000–43,000 as the “spawning escapement objective for the rebuilt chinook salmon stock in the Mainstem Yukon River”. While the YRSA makes no mention of this goal range as an interim objective, the JTC recommended that this goal range be considered and Interim Management Escapement Goal (IMEG) when it was developed in 1987.

Following the signing of the YRSA, the JTC discussed the possibility of developing a biological escapement goal and determined that available data were inadequate at that time, according to Chinook Technical Committee (CTC) standards. Data shortcomings were listed as short time series, low contrast in escapements, and no escapements having recruit-per-spawner ratios less than 1:1 (JTC 2002). The rebuilding goal of 28,000 fish remained in place as the annual management objective until 2006.

A need to revise the escapement goal became progressively clearer over the 2002–2007 period. After decades of using the DFO mark-recapture border program as the sole U.S./Canada border passage estimator on the Yukon River, the cooperative ADF&G-NOAA drainagewide radiotelemetry project and ADF&G-DFO sonar project (operated near Eagle Alaska) provided independent estimates of border passage for 2002–2004 and 2005–2007, respectively. Notable and variable

differences between the annual DFO mark-recapture estimates and the estimates derived from radiotelemetry and sonar projects strongly suggests that the DFO mark-recapture results were biased low. A revised goal was necessary.

In 2008, the JTC and YRP undertook a transition from assessing border passage using fish wheel mark-recapture to assessing passage using sonar operated near Eagle, Alaska. This transition necessitated that the escapement time series based on biased mark-recapture data and the bilateral escapement goal be rescaled to align with Eagle sonar counts. The JTC formed an escapement goal working group to address the change in assessment. Although members could justify IMEG targets ranging from 45,000–50,000, consensus was achieved, and a new IMEG of 45,000 Chinook salmon was established (JTC 2008). This goal was recommended for one year, recognizing the need for further analysis to establish a biologically based escapement goal, but this IMEG remained in place for both 2008 and 2009 (JTC 2010).

Beginning in 2008, an exploratory analysis was conducted to determine a statistically sound method to correct for bias in the 1982–2001 mark-recapture estimates (Sandone 2010). Sandone proposed a 3-area (Little Salmon, Big Salmon, and Nisutlin River) index count approach to reconstruct the escapement time series. In this approach a linear regression model was constructed between the estimated total spawning escapements (Eagle Sonar: 2005–2007 and radiotelemetry mark-recapture: 2002–2004). The model was applied to the 3-area aerial survey index to estimate historical spawning escapement estimates back to 1982. Sandone presented the results of his work to the YRP, and the YRP made the decision to adopt the revised estimates of border passage. The JTC did not review or approve the revised dataset before it was adopted by the YRP, but the JTC began using the updated timeseries of escapement estimates (see Appendix D in JTC 2021).

In 2010, following the revision of the historical timeseries of Canadian-origin Yukon River Mainstem Chinook salmon, the JTC recommended a new IMEG for this stock. As part of his prior work, Sandone conducted a Ricker spawner-recruitment analysis and determined a biological escapement goal range based on maximum sustained yield (S_{MSY}) of 23,000–41,000 fish. He ultimately recommended a more conservative lower bound, based on maximum recruits per spawner (S_{MSR}), of 40,000 fish and an upper bound of 60,000 fish, above which data had indicated poor recruitment. The JTC reached consensus that the IMEG should be established as a range to allow for uncertainty of information from assessment projects. The JTC reached consensus for an upper bound of 55,000. The JTC was not able to reach consensus on the lower bound and presented two options to the YRP, 40,000 and 45,000 (JTC 2010). After consultation with the YRP, the JTC reached consensus on a recommended escapement goal range of 42,500–55,000 Canadian origin Chinook salmon (JTC 2011).

Since 2010, the JTC has made no formal recommendations to modify the Canadian-origin Chinook salmon IMEG of 42,500–55,000; however, there has been substantial new information developed independent of JTC activities. In 2014, Bue and Hamazaki (funded by the USFWS in 2010) developed a run reconstruction model and spawner-recruit analysis for the entire drainagewide and Canadian-origin Chinook salmon stocks. This new model was based on run reconstruction modeling techniques developed for Kuskokwim River Chinook salmon (Bue et al. 2012). Also in 2014, Hamazaki and DeCovich developed an approach to using Yukon River Chinook salmon genetic mixed-stock analysis and border passage data to estimate total stock-specific run size by applying genetic mark-recapture techniques. Fleischman (ADF&G Retired, Unpublished) expanded on methods and developed a state-space approach that combined run reconstruction and spawner-recruit analysis simultaneously within a single modeling framework. Jones et

al. (2018) expanded Fleishman's unpublished model and developed a closed loop simulation to evaluate the performance of alternative harvest strategies that also incorporated quality of escapement (i.e., Management Strategy Evaluation). In 2018, Hamazaki corrected historical border age-sex composition to account for selectivity bias associated with fishwheel sampling. In 2019, the JTC agreed to use the revised age composition estimates presented by Hamazaki (2018b) for subsequent production analyses but did not approve use of the revised sex composition (see Appendix D1 in JTC 2020). In 2020, Ohlberger et al. (2018) used available age, sex, size, and fecundity data to investigate the consequences of declines in Yukon River Chinook body size for production, and concluded that changes in spawner quality should be considered when developing management reference points. In 2021, Hamazaki (2021) developed methods to consider a diverse range of mainstem passage, tributary escapement, harvest, and stock separation data to simultaneously estimate total annual run size for all major Yukon River stock components.

Table A.1. A brief timeline of analytical work related to Canadian-origin Yukon Chinook salmon escapement goals.

Year	Description	Escapement goal range	Citation
1982	Fish wheel mark-recapture border passage assessment began.		Milligan et al. 1984
1985	First escapement objective proposed. Based on expanded 3-river index (Whitehorse fishway, Big Salmon, Nisutlin aerial survey).	55 000 (fish wheel MR)	JTC 1985
1987	Bilateral escapement objective established.	33 000-43 000 (fish wheel MR)	JTC 1987
1990	First brood table for Canadian-origin Chinook salmon (assumed fixed age composition).		JTC 1990
1996	Brood table revised to incorporate annual estimates of age composition.		JTC 1997
2001	Brood table for Canadian origin Chinook salmon updated through 1997 brood year. JTC concluded a comprehensive Biological Escapement Goal could not be developed based on Pacific Salmon Commission, Chinook Technical Committee (1999) guidelines.		JTC 2001
2005	Border passage first estimated by sonar operated at Eagle (Eagle Sonar).		Carroll et al. 2007
2008	Border passage assessment transitioned from fish wheel mark-recapture to Eagle Sonar.		JTC 2008
2008	3-area aerial survey (Big Salmon, Little Salmon, Nisutlin) index was used to reconstruct and standardize historical escapement to be equivalent to Eagle Sonar count.		Sandone 2010
2008	Spawner-Recruitment analyses conducted.		Sandone 2010
2010	Interim management escapement goal (IMEG) range was established.	45,000-50,000 (Eagle Sonar)	JTC 2010
2010	Drainagewide and Canadian-origin run reconstruction model developed.		Bue and Hamazaki 2014
2011	Canadian-origin run reconstruction state-space model developed.		Fleischman Unpublished
2014	Genetic mark-recapture method developed to estimate drainagewide and stock-specific run.		Hamazaki and DeCovich 2014

Year	Description	Escapement goal range	Citation
2018	Canadian origin management strategy evaluation (MSE) model developed.		Jones et al. 2018
2018	Border age-sex composition 1982–2006 revised.		Hamazaki 2018
2019	Brood table for Canadian origin Chinook salmon updated to include revised border age composition data.		JTC 2020
2020	Evaluation of consequences of shifts in escapement quality on Yukon River Chinook salmon productivity.		Ohlberger et al. 2020
2021	Drainagewide and stock-specific run reconstruction model developed.		Hamazaki 2021

APPENDIX B. IMPLICATIONS OF KNOWN OR POTENTIAL BIASES IN DATA USED TO ESTIMATE RUN, HARVEST, AND ESCAPEMENT OF CANADIAN-ORIGIN YUKON CHINOOK SALMON

We were faced with several data limitations that likely resulted in relatively minor biases in estimation of Canadian-origin mainstem Chinook salmon run size, and which may have implications for the estimation of biological reference points.

1. Small-scale hatcheries have operated annually since 1984 to facilitate a wide range of stock restoration efforts throughout the Canadian portion of the Yukon River Basin. As such, some unknown number of the annual run is hatchery-origin.
2. The Canada mainstem stock cannot be differentiated from the Canada Porcupine stock in U.S. harvests using conventional scale pattern and genetic multiple sequence alignment (MSA) methods. As such, some unknown number of Porcupine River fish are harvested in U.S. fisheries and incorrectly assigned to the Canada mainstem stock.
3. Prior to 2004 it was incorrectly assumed that all Chinook salmon harvested in Alaska's fishing District 5 (i.e., the portion of the mainstem Yukon River drainage in Alaska upriver of the Tanana River confluence) were Canada stock. As such, some unknown number of fish of U.S. stock-origin were incorrectly assigned to the Canada Stock.
4. Canadian-origin Chinook salmon are harvested as bycatch in Bering Sea Aleutian Island (BSAI) groundfish fisheries, but these fish were not accounted for in our run reconstruction model. As such, the total number of brood-year recruits was biased low.
5. Canadian-origin Chinook salmon are subject to a broad range of cumulative stressors that may result in natural premature mortality at any point along their upriver migration from the mouth of the Yukon River to their spawning grounds in Canada. Natural mortality is not monitored in U.S. or Canadian assessment programs. As such, non-harvest removals from the system were not accounted for in our models.
6. Harvest uncertainty in U.S. or Canada.

The cumulative implications of these data limitations is that our reconstruction of the Canada Stock may be biased relative to the true abundance of wild Canadian-origin mainstem Chinook salmon. The direction and degree of bias is not known with certainty but can be generalized based on limited data available. The following narrative discusses the most likely potential sources of bias in more detail, followed by results of an exploratory analysis to investigate the implications of possible biases on estimates of biological reference points.

B.1. HATCHERY VS. WILD PRODUCTION

There are currently no annual assessment programs that allow for accurate estimation of hatchery contribution to the total run size of the Canada Stock, but data from the Whitehorse Hatchery coded-wire tag (CWT) program provides some insight into the proportion of the total run that is hatchery versus wild origin. Since 1985, the Whitehorse Hatchery has released approximately 7,800,000 Chinook salmon fry, (average 140,000 per year, range: 83,000–441,000) of which about 85% are CWT. The average contribution of Whitehorse Hatchery CWT fish to Yukon Fisheries was informally investigated in 2007 at the request of the JTC. Assuming no straying or en-route mortality of hatchery fish, all returning adult CWT fish would be encountered in fisheries or counted as escapement at the Whitehorse Hatchery Fish Ladder. The investigation determined that harvest sampling programs had not been robust enough to reliably estimate the

proportion of hatchery fish, especially in Alaskan subsistence and Canadian fisheries. However, rough estimates of 1%-2% hatchery contribution to each Yukon fishery were postulated and supported by CWT recoveries from the Alaska District 1 fishery. A rough estimate of 2% was postulated as the average contribution of hatchery fish past the U.S./Canada border. Given this limited information, we determined that the hatchery bias associated with the estimates of Canadian Stock harvest and border passage used in our multi-stock run reconstruction model was likely small, and the time required to investigate this issue further was not warranted at this time. Further, investigation of the influence of the Whitehorse Dam data to the run reconstruction through the leave-one-out sensitivity analysis (Appendix C) indicated that the data had little influence on estimated Canada stock escapement despite the project being one of few with data available throughout the time frame of the reconstruction. We concluded that it was acceptable to include hatchery fish in our analyses since adult returns from hatchery fry releases have been part of the total run subject to harvest, hatchery releases are expected to continue in the future, and hatchery fish cannot be managed separately from wild fish within the context of the Yukon River Salmon Agreement.

B.2. MAINSTEM VS. PORCUPINE RIVER STOCKS

Stock separation methods that were available from 1981-2019 were not capable of differentiating between Chinook salmon that originated from the Canada Mainstem and those from the Porcupine River in Canada. Assuming the mainstem and Porcupine River stock components are harvested in proportion to their abundance, the Porcupine Sonar escapement and Eagle Sonar passage estimates provides some insight into the magnitude of U.S. harvest mis-assignment. There are six years of paired observations between the two assessment projects (2014–2019, Pestal et al. 2022), and the Porcupine sonar passage has made up 2%–9% (average 6%) of the total Chinook salmon estimated by both projects combined. On average (1981–2019), the U.S. commercial and subsistence fisheries were composed of 43% and 59% Canada Stock (mainstem and Porcupine stock combined), respectively. Given these averages, it is reasonable to speculate that the Canada Stock proportions used to apportion U.S. harvest may be biased high by 2.5%–3.5% on average, relative to the true Canada Mainstem Stock proportions. Revisions to the Yukon River Chinook salmon genetics baseline were completed by ADF&G in 2021 (Restoration and Enhancement Fund project #163-19), and the new baseline can accurately separate Canada Porcupine from Canada Mainstem stocks. External funding would be required to reanalyze stock of origin for historical U.S. harvest samples so as to be able to apportion the U.S. harvest to the Canada Mainstem and Porcupine stocks. We therefore chose to ignore the likely small contribution of Porcupine Chinook salmon to estimates of U.S. harvest of the Canada Mainstem stock.

B.3. U.S. HARVEST APPORTIONMENT IN DISTRICT 5

Prior to 2004, there were no U.S. harvest sampling programs in the mainstem portions of District 5, and all Chinook salmon harvested in local fisheries were assumed to be Canada stock. Given the lack of data, this simplifying assumption was likely reasonable for general stock harvest apportionment purposes; however, the assumption was known to be violated to some degree. There are several U.S. tributaries that drain into District 5, two are known to support large numbers of Chinook Salmon (i.e., Teedriinjik and Sheenjek rivers), and 12 are known to produce small numbers of Chinook salmon (Brown et al. 2017). Additionally, the potential for Lower and Middle

Stocks to swim into District 5 before dropping back to locate the confluence with their downriver natal streams is consistent with Chinook salmon migratory behavior in large rivers. From 2006–2018, District 5 subsistence harvests downriver from Fort Yukon were sampled and approximately 25% of the sampled harvest was not Canada stock. Violation of the historical assumption decreased further upriver, and four years of sampling indicated >90% of the subsistence harvest near Fort Yukon was Canada Stock (Pestal et al. 2022). The majority of the harvest that occurs in District 5 is for subsistence and personal uses, and about half of that harvest occurs downriver from Fort Yukon, where violation of the historical assumption was assumed to be greatest. However, the impact of this assumption on estimates of total Canada stock harvest is likely small. For the years of concern (1981 – 2003), the District 5 subsistence harvest downriver from Fort Yukon made up about 17% of the total Yukon River subsistence harvest in Alaska. Given the available information, it is reasonable to suspect that the annual number of U.S. subsistence harvested fish that were incorrectly assigned to the Canada stock from 1981– 2003 is biased high by about 5% on average. However, given a lack of empirical data that spanned a longer period we determined that a retrospective analysis to correct the historical estimates was not possible.

B.4. BERING SEA ALEUTIAN ISLAND BYCATCH

Yukon River Canadian-origin salmon are caught as bycatch in Bering Sea Aleutian Island (BSAI) groundfish fisheries along with other salmon stocks from Alaska, the west coast of Canada and the United States, eastern Asia, and Russia. The number of salmon captured as bycatch each year is always more than the number of adult salmon that would have returned to the Canadian portion of the Yukon River drainage in that year for two reasons. First, the bycatch is composed of multiple stocks, and the Canadian stock comprises a relatively small percentage (2%–5%) of the total catch by year [2011–2016; Ianelli and Stram (2018)]. Second, salmon are predominately captured as bycatch during their immature life-history stage and will spend one or more additional years in the ocean before returning to freshwater. Stock-specific bycatch numbers of immature salmon require an adjustment for natural mortality before an accurate impact assessment can be conducted. Bycatch estimates that are adjusted for natural mortality are referred to as Adult Equivalent (AEQ) bycatch. Bycatch impacts to Canadian-origin Chinook salmon by the BSAI pollock fishery is estimated by run year. The 2017 run is the most recent year for which bycatch impact estimates are available for Canadian-origin Chinook salmon. The average (1994–2017) bycatch impact rate by the pollock fishery on the Canadian-origin Chinook salmon run is estimated to be 1.0% with an annual impact rate less than 3.1% (Ianelli and Stram 2018)].

B.5. PREMATURE MORTALITY

Environmental and biological stressors have been implicated as potential causes of natural premature mortality of Canadian-origin Yukon River Chinook salmon, which can occur enroute losses along the Yukon River mainstem or pre-spawn losses in tributaries. Premature mortality is not assessed by any research or monitoring program in the U.S. or Canadian portions of the Yukon drainage. The magnitude of premature mortality exhibited by Canadian Yukon Chinook on an annual basis is therefore not known, and likely varies substantially in space and over time. Premature mortality of Canadian fish may occur while the fish is in the U.S. or Canada portions of the drainage, and an inability to account for these “removals” from the system has different implications for estimation depending on where the mortality occurred. Unaccounted mortalities

in the U.S. could cause unexplained differences in run size indices across projects, but it is unlikely to substantially impact total run estimates. Unaccounted mortalities in Canada would result in overestimating escapement and underestimating production by some unknown amount.

Elevated water temperatures and *Ichthyophonus hofori* disease have been identified as two relatively common stressors that may result in premature mortality of Yukon Chinook salmon throughout the U.S. or Canadian portions of the drainage. Field experiments demonstrated that Yukon River Chinook salmon display signs of heat stress when subject to water temperatures $>18^{\circ}\text{C}$ (Biela et al. 2020). Portions of the Yukon River mainstem in Alaska have recorded water temperatures $>18^{\circ}\text{C}$ in 85% of years (1996–2019), suggestive of routine and prevalent heat stress that may be related to decreases in production and run sizes over a similar timeline. *Ichthyophonus hofori* is a parasite that infects Yukon River Chinook salmon via their marine diet and can cause disease at levels that have been suspected of causing enroute mortality (see JTC 2011 for a summary of relevant work). *Ichthyophonus* was studied extensively from the late 1990's until about 2011. Prevalence of infections is cyclical and reached a peak in 2003 and 2004, before declining to relatively low levels. The disease progression is known to be related to water temperature, possibly resulting in a synergistic impact on the host fish.

B.6. HARVEST UNCERTAINTY

Errors when estimating harvest in both the U.S. and Canada are possible but the degree to which errors occur and their magnitude are not known. Required reporting associated with commercial, sport, and personal use fisheries in the U.S. and commercial, recreational, and domestic fisheries in Canada are likely highly accurate. Subsistence and First Nations harvest estimates are more difficult to quantify, but they are generally considered unbiased. While there has been no formal assessment of response bias in the U.S. (Alaska) subsistence estimates, there have been several independent comprehensive subsistence surveys conducted by the Division of Subsistence which support the accuracy of the harvest estimates used in the model with subsistence survey annual harvest CVs around 0.1 (e.g., Brown and Deena 2019). While estimates of First Nations harvest in Canada are believed to be unbiased, a systematic assessment of this assumption has not been undertaken.

B.7. IMPLICATIONS OF POTENTIAL BIASES FOR ESTIMATES OF BIOLOGICAL REFERENCE POINTS

We conducted an exploratory analysis to generalize the possible implications each of the known or potential data biases for estimates of biological reference points (Figure B.1). For each scenario, a magnitude of bias was assumed that was somewhat larger than what was thought to be most likely. This “bias adjusted” dataset was then used to derive a spawner recruitment (SR) relationship and estimate associated reference points. These alternative results were visually compared to the original base model estimates.

Scenario A assumed a 15% unaccounted removals upriver from the U.S. Canada border, but before spawning, due to either natural premature mortality or undocumented harvest. If scenario A were true, our base model estimates of spawner abundance would be biased high, but there would be no bias associated with our estimates of run size or recruitment. To correct for this, all SR points would be shifted to the left, and estimates of S_{MSY} and S_{MSR} would be smaller compared to our base model. If escapement goal recommendations were based on bias-adjusted

estimates, the recommendation would likely be for a lower goal than if uncorrected data had been used.

Scenario B assumed a 10% underestimate of U.S. harvest of the Canadian stock due to undocumented harvest or errors in stock apportionment. If scenario B were true, our base model estimates of annual run and brood year recruitment would be biased low, but there would be no bias associated with our estimates of escapement. To correct for this, all SR points would be shifted up, and there would be little or no change in estimates of S_{MSY} or S_{MSR} . U.S. harvest of Canada stock could also be biased high due to the incorrect pre-2004 assumption that all Chinook salmon harvest in District 5 were bound for Canada. In this case (not shown), all SR points would be shifted down, and there would be little or no change in estimates of biological reference points.

Scenario C assumed that bycatch in the Bering Sea Aleutian Island pollock fishery reduces total run size by 5% annually. If scenario C were true, our base model estimates of run size and brood year recruitment would be biased low. Like scenario B, there would be no consequential implications for estimates of biological reference points.

Scenario D assumed that 7% of the annual Canadian run is of Porcupine River origin. If scenario D were true, our estimates of Canadian mainstem run size used in our base model would be biased high, but estimates of escapement would remain unbiased. To correct for this, all SR points would be shifted down. If this scenario were true, there would be little or no change in our estimates of S_{MSY} or S_{MSR} . Scenario E assumed that hatchery-origin Chinook salmon comprise 3% of the total annual Canada stock run. If scenario E were true, our estimates of wild Chinook salmon run size and escapement used in our base model would be biased high. To correct for this, the SR points would be shifted down and to the left, resulting in smaller estimates of S_{MSY} and S_{MSR} . Like Scenario A, an escapement goal recommendation centered around smaller reference points would result in a lower goal.

This illustrative example provides some assurances that the data used in our base model likely resulted in reasonable, and possibly higher (i.e., conservative), estimates of biological reference points regardless of our inability to fully address all potential sources of bias. These scenarios also provide a general framework for thinking about alternative biases not explored here. Errors that affect estimates of run size and brood-year recruitment are unlikely to result in meaningful changes in estimates of biological reference points. However, run size errors will have implications for model predictions of future recruitment and yield that would be expected from a range of spawning abundance. Errors affecting spawning escapement are substantially more likely to result in meaningful changes to estimates of biological reference points, with possible implications for escapement goal setting. Our base model assumes that run size minus harvest equals escapement, and escapement in Canada is driven almost exclusively by border passage estimates and harvest in Canada. As such, unaccounted removals in Canada due to natural premature mortality or undocumented harvest are expected to have larger implications for estimates of biological reference points than data errors associated with U.S. harvest or run accounting.

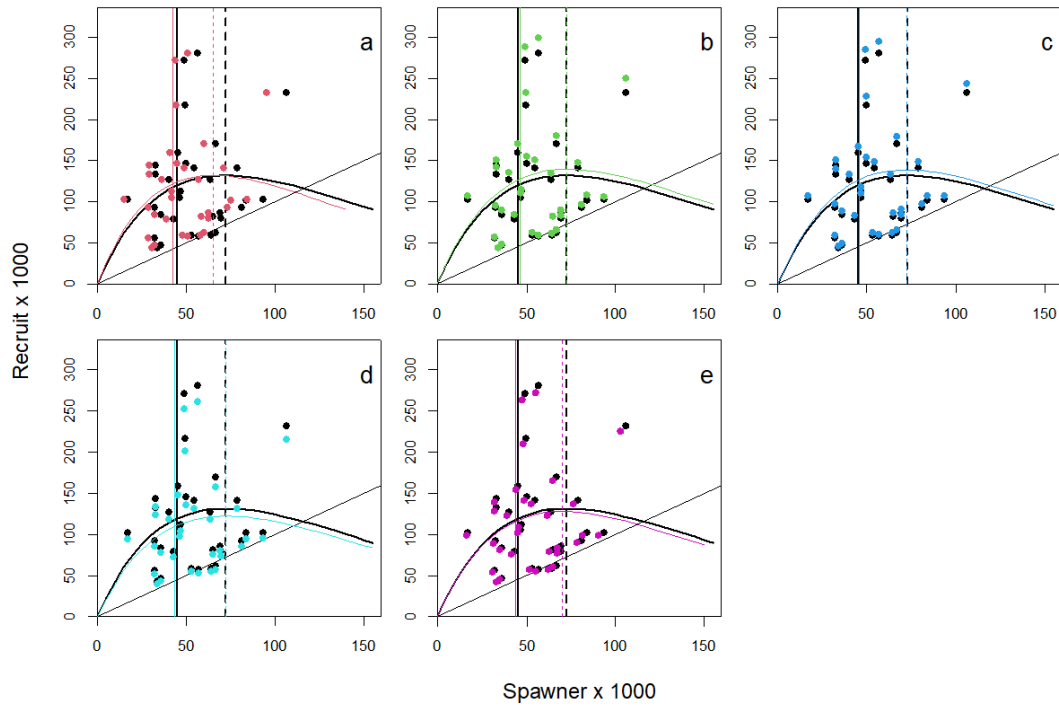


Figure B.1. Implications of possible data biases on estimates of biological reference points due to (a) 15% unaccounted removals in Canada; (b) 10% under reporting of U.S. harvest; (c) 5% reduction of total run due to bycatch in the Bering Sea Aleutian Island pollock fishery; (d) 7% over estimation run size due to inability to separate Mainstem and Porcupine stocks; (e) 3% overestimation of run size and escapement due to inability to separate wild from hatchery origin fish. In each panel, black dots and lines are the base model and colored dots and lines are bias adjusted data. Solid and dashed vertical lines represent median estimates of S_{MSY} and S_{MSR} , respectively.

APPENDIX C. MODEL FIT AND DIAGNOSTICS

C.1. MODEL FITS TO PASSAGE AND ESCAPEMENT DATA

We examined the fit to observed passage and escapement data in the run reconstruction. The normalized root mean squared error (NRMSE) was calculated for each fit. NRMSE values are comparable between projects, such that lower NRMSE values indicate data are better fit in the model than data with higher NRMSE values. We also examined plots of the standardized residuals for each fit as a check for temporal trends. Projects are presented roughly in spatial order from most downstream (Lower Yukon, Andreafsky River) to most upstream (Canada, Whitehorse Dam Fishway).

C.1.1. Lower Yukon River

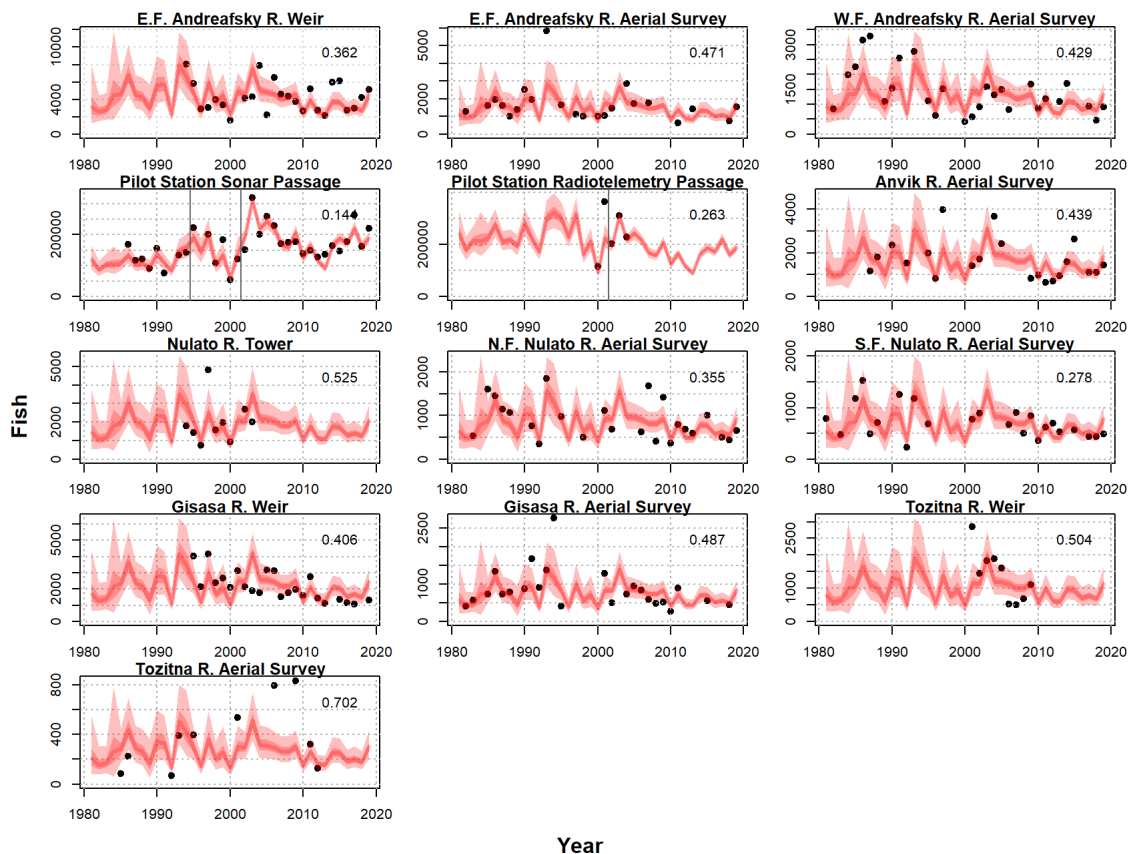


Figure C.1. Observed data (black points) at Lower Yukon River passage and escapement projects used in the run reconstruction. Model estimated numbers of fish (red line), 50% credible intervals (dark red shaded area) and 95% credible intervals (light red shaded areas) are presented for each project. The normalized root mean squared error (NRMSE) for each fit is in the upper right hand corner. Note that solid black lines in the Pilot Station sonar and radiotelemetry plots divide the data into time periods where differing degrees of bias and/or variance were allowed to be fit in the run reconstruction.

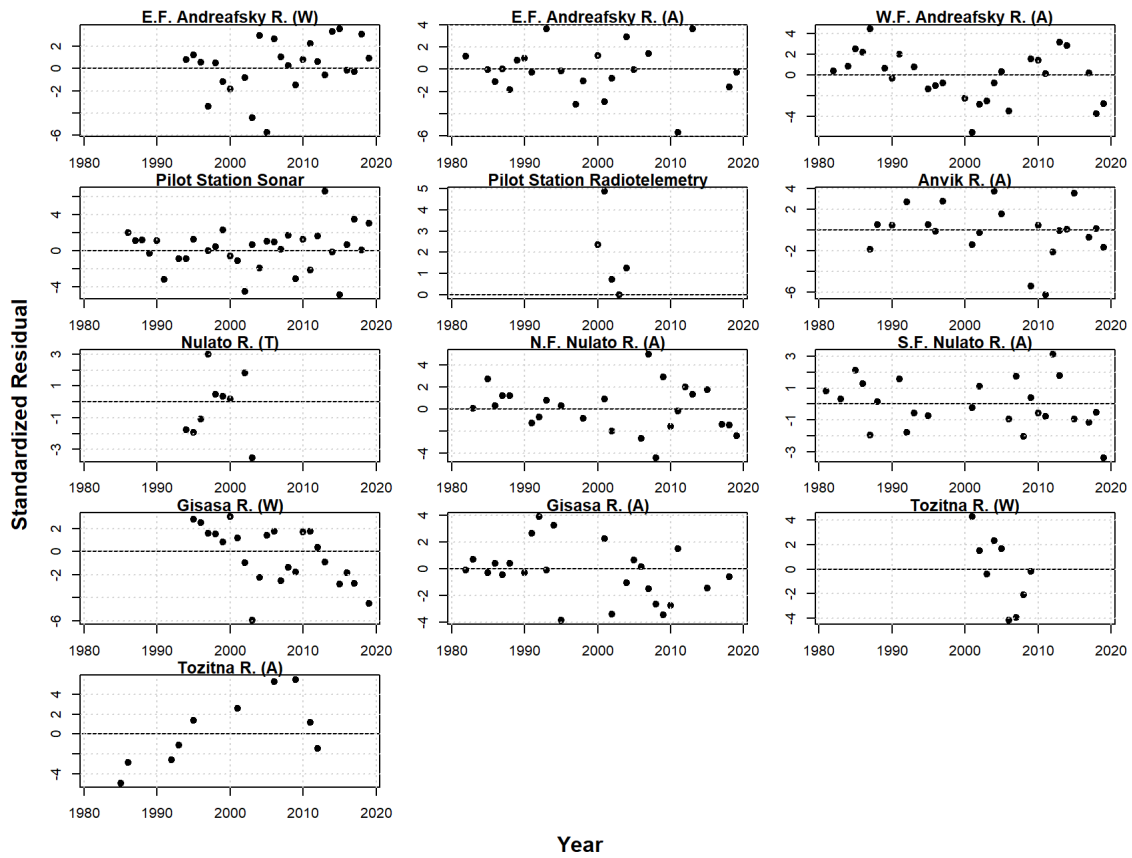


Figure C.2. Standardized residuals from the model fit to Lower Yukon River passage and escapement projects used in the run reconstruction (log scale).

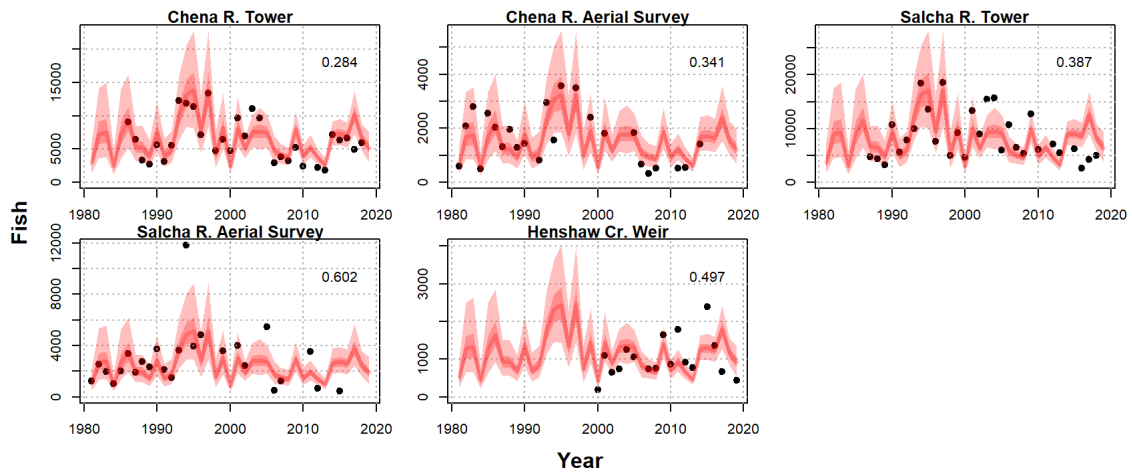


Figure C.3. Observed data (black points) at passage and escapement projects in the Middle Yukon River used in the run reconstruction. Model estimated numbers of fish (red line), 50% credible intervals (dark red shaded area) and 95% credible intervals (light red shaded areas) are presented for each project. The normalized root mean squared error (NRMSE) for each fit is in the upper right hand corner.

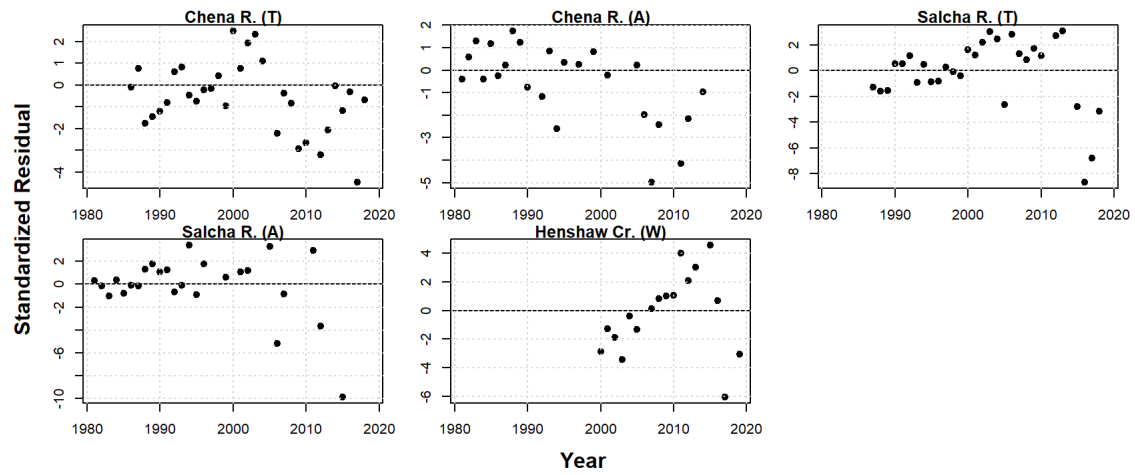


Figure C.4. Standardized residuals from the model fit to Middle Yukon River passage and escapement projects used in the run reconstruction (log scale).

C.1.2. Canada

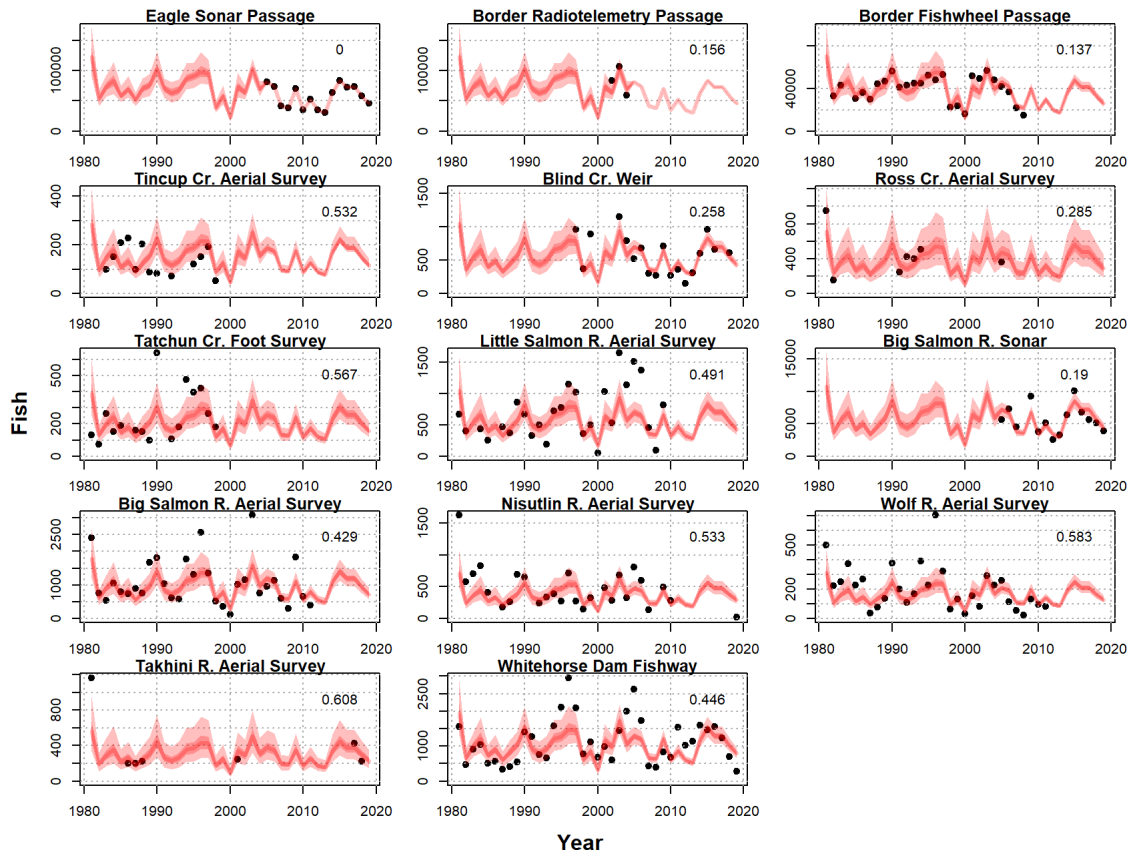


Figure C.5. Observed data (black points) at Canadian passage and escapement projects used in the run reconstruction. Model estimated numbers of fish (red line), 50% credible intervals (dark red shaded area) and 95% credible intervals (light red shaded areas) are presented for each project. The normalized root mean squared error (NRMSE) for each fit is in the upper right hand corner.

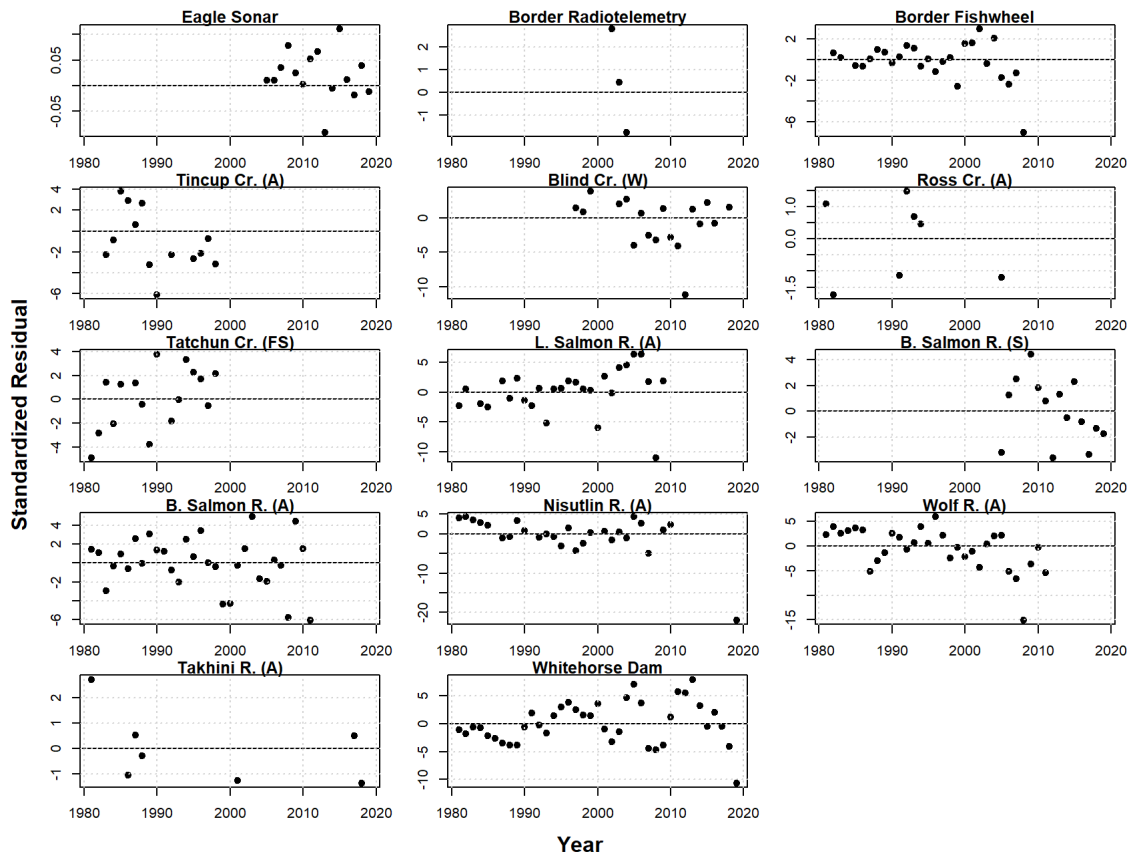


Figure C.6. Standardized residuals from the model fit to Canadian passage and escapement projects used in the run reconstruction (log scale).

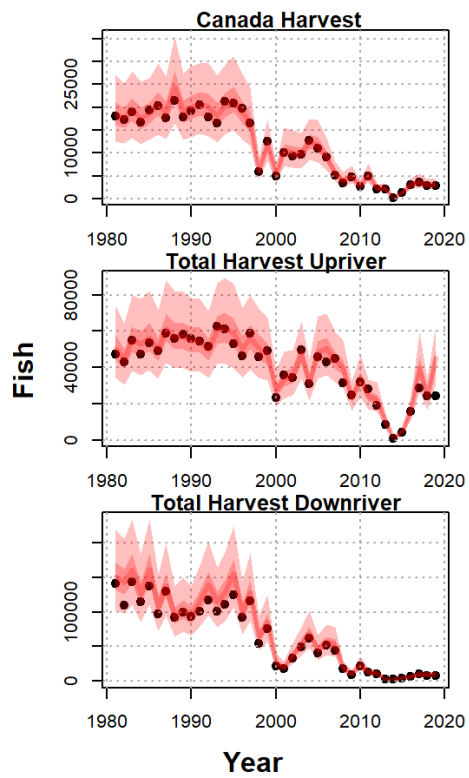


Figure C.7. Observed point estimates (black points) of total harvest in Canada, upriver of Pilot Station, and downriver of Pilot Station as used in the run reconstruction. Model estimated numbers of fish (red line), 50% credible intervals (dark red shaded area) and 95% credible intervals (light red shaded areas) are presented for each area.

C.1.3. Harvest stock composition

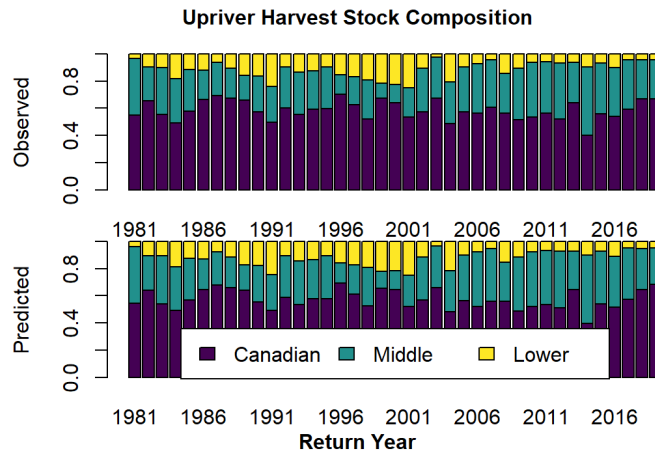


Figure C.8. Observed (top) and model predicted (bottom) stock composition in the harvest upriver of Pilot Station.

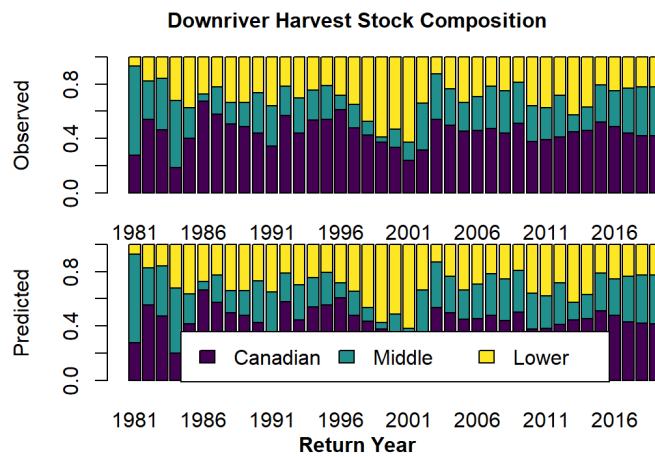


Figure C.9. Observed (top) and model predicted (bottom) stock composition in the harvest downriver of Pilot Station.

C.2. INTEGRATION OF THE RUN RECONSTRUCTION AND SPAWNER-RECRUIT MODELS

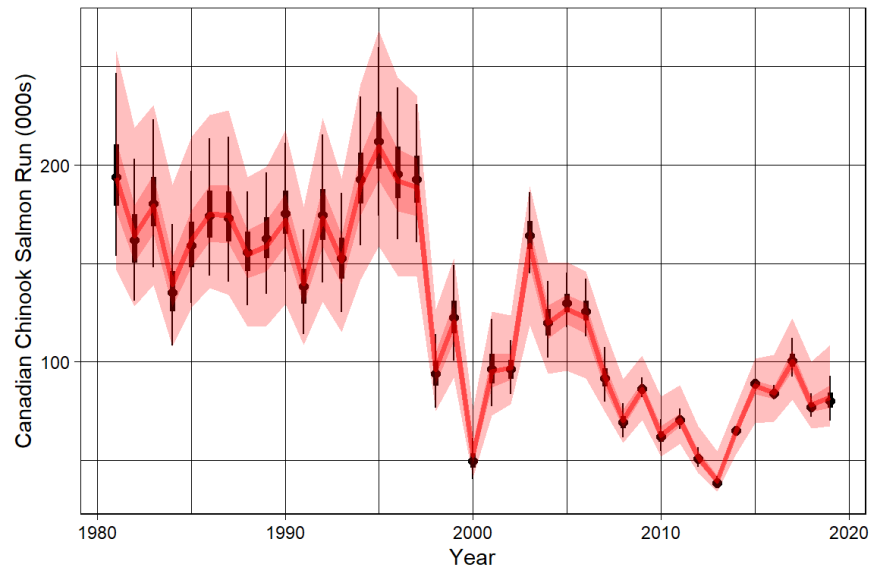


Figure C.10. Run reconstruction estimates for the Canadian run are in black and stock-recruitment analysis estimates of the run for this stock are in red. Black points are posterior medians from the run reconstruction, and the thick red line is the posterior median from the stock-recruit model. Thin lines and outer red bounds are 95% credible intervals. Thick lines and inner red bounds are 50% credible intervals.

C.3. MODEL PARAMETERS

The table below provides summary statistics for a subset of model parameters. Parameters described elsewhere in the text, as well as annual estimates of run size, stock proportions, etc., are not shown here.

Table C.1. Posterior means, medians and credible intervals for a subset of model parameters not summarized elsewhere in this report. Estimates of the effective sample size and potential scale reduction factor (\hat{R}) for parameters estimated by the model are also given. The first column uses the parameter notation consistent with the main text, the second column provides the parameter notation as it appears in the model code for reference.

	Var	VarModelName	Mean	p2.5	Median	p97p5	n_{eff}	\hat{R}
σ_{RR-SRA}^2		sigma_can_run	0.08	0	0.07	0.23	220.2	1.01
D		D_scale	0.21	0.17	0.21	0.25	706.16	1.01
$K_{TincupAir}$		atinc	366.04	297.43	372.42	402.09	8079.22	1
$K_{TatchunFoot}$		ftatc	272.19	199.11	269.62	359.97	6266.38	1
$K_{LSalmonAir}$		alsal	99.92	79.1	99.22	124.67	5774.11	1
$K_{BSalmonAir}$		absal	6.09	4.65	6.04	7.81	7459.48	1
$K_{NisulAir}$		anstl	147.26	116.79	146.26	183.62	6355.8	1
$K_{RossAir}$		aross	150.33	94.55	146.53	225.26	6905.41	1
$K_{GisasaAir}$		agisa	2.99	2.25	2.96	3.89	8387.1	1
$K_{AnvikAir}$		aanvk	36.53	28.96	36.29	45.51	7173.59	1
$K_{AndreAir}$		aandr	2.83	2.12	2.81	3.66	8618.36	1
$K_{WolfAir}$		awolf	332.88	269.8	332.64	394.02	5810.89	1
$K_{TakhiniAir}$		atakh	188.77	120.03	184.08	284.26	6824.06	1
$K_{TozitnaAir}$		atoz	3.9	2.47	3.81	5.85	8570.25	1
$K_{ChenaAir}$		achen	4.31	3.29	4.27	5.55	7642.14	1
$K_{SalchaAir}$		asalc	3.37	2.57	3.34	4.36	7884.56	1
$K_{NulatoAir}$		anult	1.22	1.01	1.19	1.64	8170.7	1
$K_{TozitnaWeir}$		wtoz	58.74	42.66	57.92	79.24	8928.03	1
$K_{BlindWeir}$		wblnd	99.45	87.35	99.29	112.14	7444.22	1
$K_{BSalmonSonar}$		sbsal	9.69	8.4	9.67	11.13	8255.24	1
$K_{WhiteDam}$		dwhte	54.15	44.73	53.92	64.75	5884.31	1
$K_{GisasaAir}$		wgisa	26.82	21.72	26.72	32.64	7638.27	1
$K_{AndreWeir}$		wandr	9.33	7.65	9.28	11.34	8783.26	1
$K_{NulatoTower}$		tnult	32.11	23.72	32.18	40.49	7377.57	1
p_N		nultp	0.54	0.47	0.54	0.6	7106.29	1
p_E		andrep	0.55	0.48	0.55	0.61	7851.53	1
$\sigma_{add,s=l,m,j=weir,sonar}$		rtower	0.44	0.37	0.43	0.51	7428.22	1
$\sigma_{add,s=l,m,j=aerial}$		raerial	0.41	0.34	0.41	0.48	7902.01	1
$\sigma_{add,s=c,j=aerial}$		rcair	0.48	0.42	0.48	0.55	7541.54	1

Var	VarModelName	Mean	p2.5	Median	p97p5	n_{eff}	\hat{R}
$\sigma_{add,s=c,j=weir}$	rcang	0.21	0.12	0.21	0.32	4427.62	1
$\sigma_{add,s=c,l=b,j=fishwheel}$	rwmr[1]	0.14	0	0.15	0.29	2392.69	1
$\sigma_{add,s=c,l=b,j=fishwheel}$	rwmr[2]	0.03	0	0	0.27	8195.2	1
$\sigma_{add,pl,j=sonar,early}$	rspilt[1]	0.03	0	0	0.23	8836.87	1
$\sigma_{add,pl,j=sonar,mid}$	rspilt[2]	0.1	0	0.06	0.42	4888.65	1
$\sigma_{add,pl,j=mr,early}$	rspilt[3]	0.55	0	0.36	2.2	9228.09	1
$\sigma_{add,pl,j=mr,late}$	rspilt[4]	0.01	0	0	0.1	9746.13	1
$q_{pl,early}$	qplt[1]	0.49	0.41	0.49	0.58	7831.19	1
$q_{pl,mid}$	qplt[2]	0.63	0.51	0.63	0.77	6965.79	1
$q_{pl,late}$	qplt[3]	0.25	0	0.01	2.02	5983.91	1

C.4. LEAVE-ONE-OUT SENSITIVITY CHECK

We checked the influence of each contributing tributary assessment project, as well as the Border fishwheel mark-recapture passage project, to the estimate of the Canadian escapement by dropping each project in turn, rerunning the run reconstruction, and comparing the resulting estimates. We calculated the root mean squared error (RMSE) between the full and reduced models in each instance using the median estimates of the predicted escapements. Projects with higher influence on the Canadian escapement estimates should have a higher RMSE. Projects are presented roughly in spatial order from most downstream (Lower Yukon, Andreafsky River) to most upstream (Canada, Whitehorse Dam Fishway).

C.4.1. Lower Yukon River

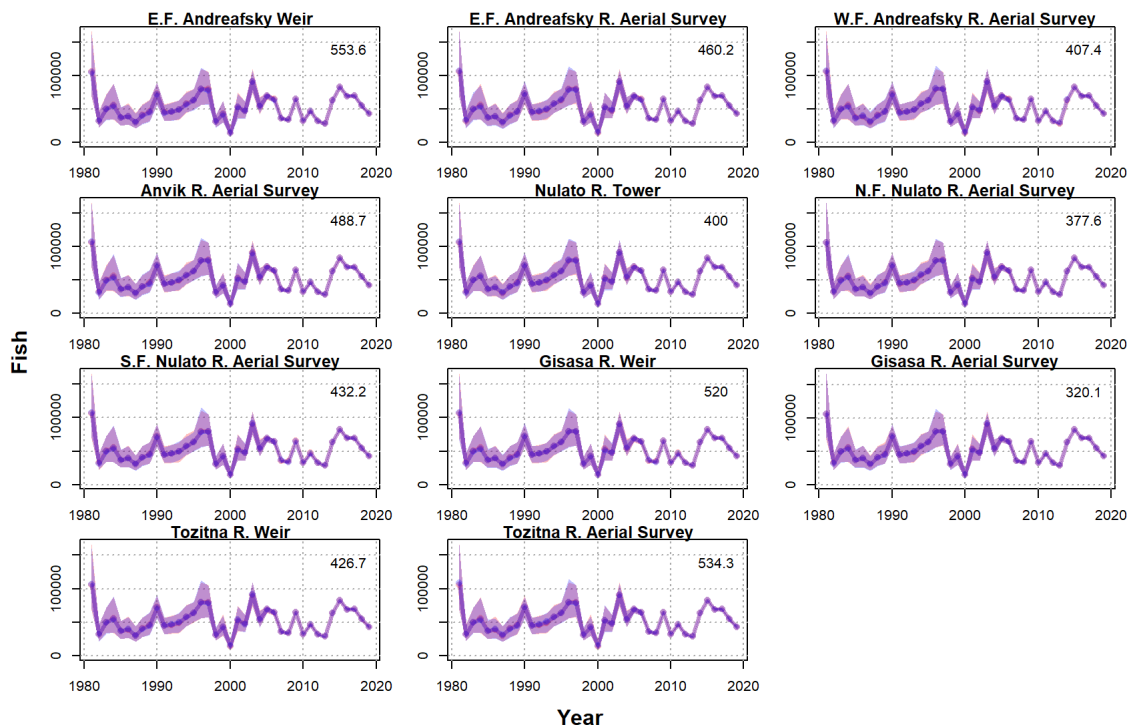


Figure C.11. Estimates of the Canada stock escapement using all (red) and dropping each project from the Lower Yukon in turn from the run reconstruction (blue). Overlapping areas appear purple. Points are the posterior median run estimates and shaded areas represent 95% CI. The normalized root squared error (NRMSE) between the full and reduced models dropping each project is in the upper right hand corner.

C.4.2. Middle Yukon River

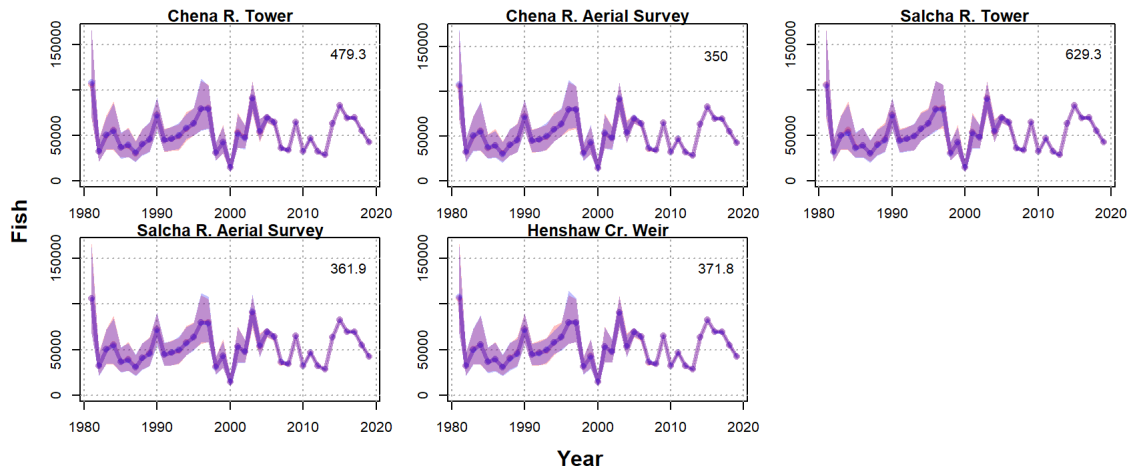


Figure C.12. Estimates of the Canada stock escapement using all (red) and dropping each project from the Middle Yukon in turn from the run reconstruction (blue). Overlapping areas appear purple. Points are the posterior median run estimates and shaded areas represent 95% CI. The normalized root squared error (NRMSE) between the full and reduced models dropping each project is in the upper right hand corner.

C.4.3. Canada

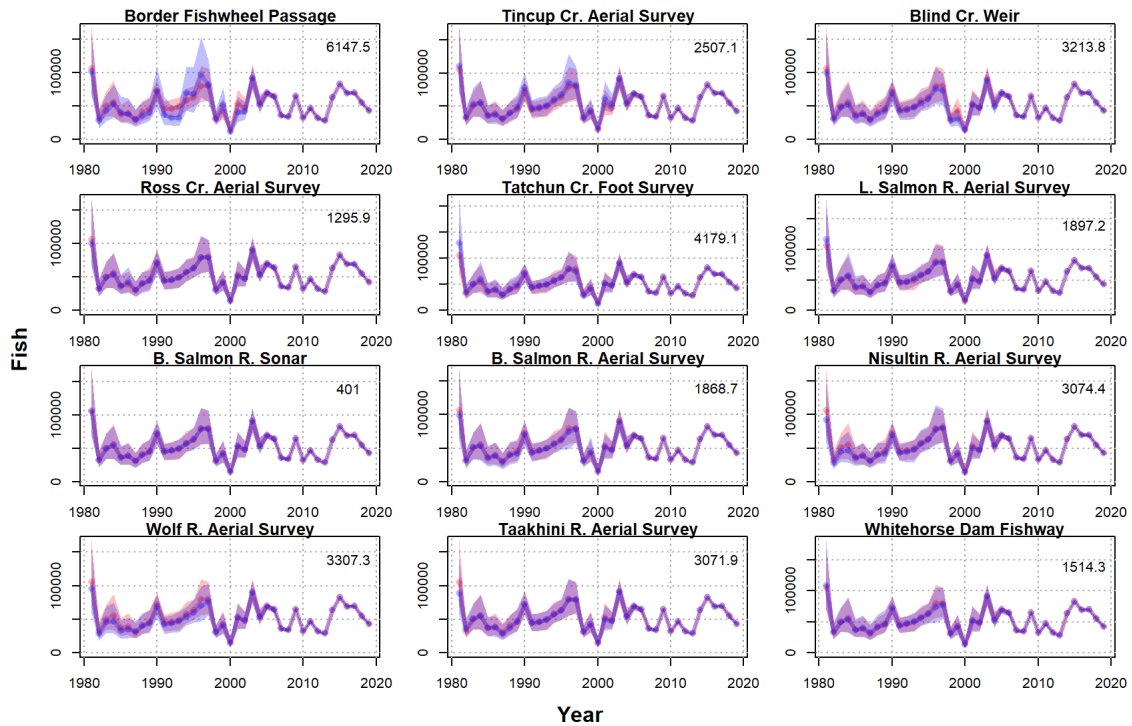


Figure C.13. Estimates of the Canada stock escapment using all (red) and dropping each project from the Canadian Yukon in turn from the run reconstruction (blue). Overlapping areas appear purple. Points are the posterior median run estimates and shaded areas represent 95% CI. The normalized root squared error (NRMSE) between the full and reduced models dropping each project is in the upper right hand corner.

C.5. RUN RECONSTRUCTION PARAMETER PRIOR AND POSTERIOR DISTRIBUTIONS

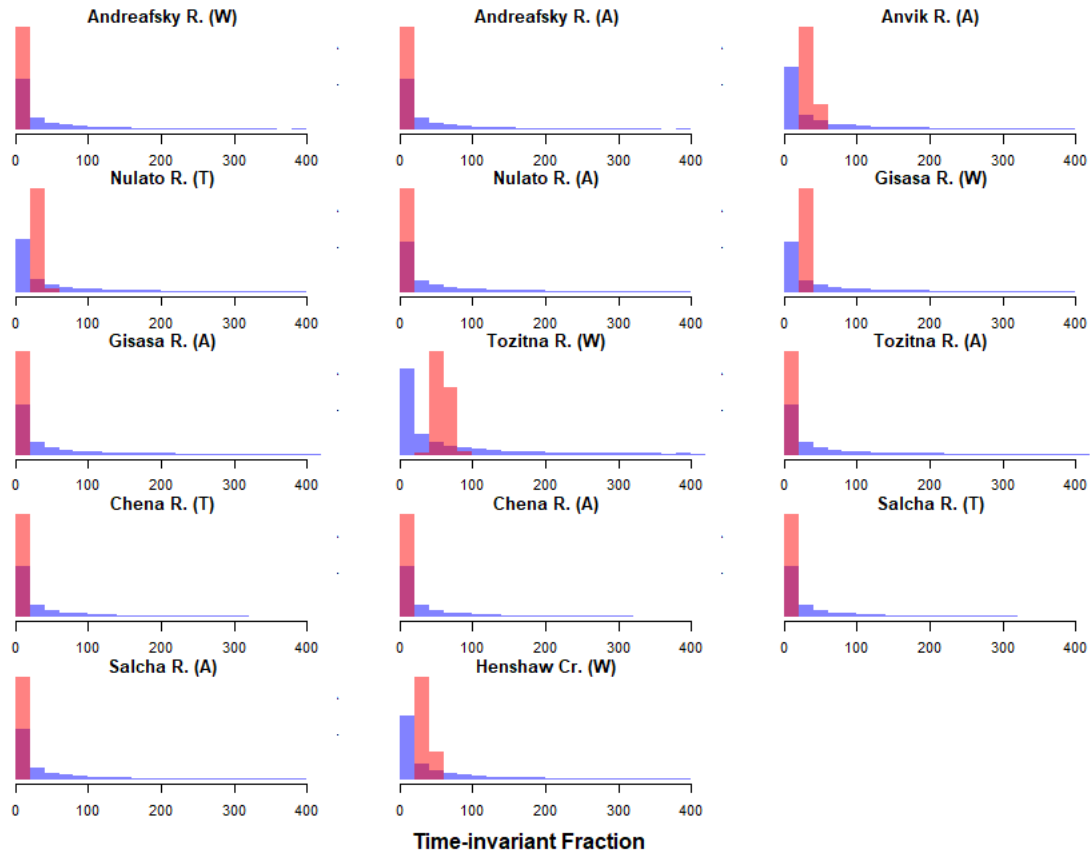


Figure C.14. Prior (blue) and posterior (red) distributions of the time-invariant fraction of total stock-specific escapement in tributary i , K_i , for indices in the Lower and Middle Yukon. Parameter values presented on the real scale, exponentiated from the log-scale used in the prior specifications. W = weir, A = aerial, and T = tower.

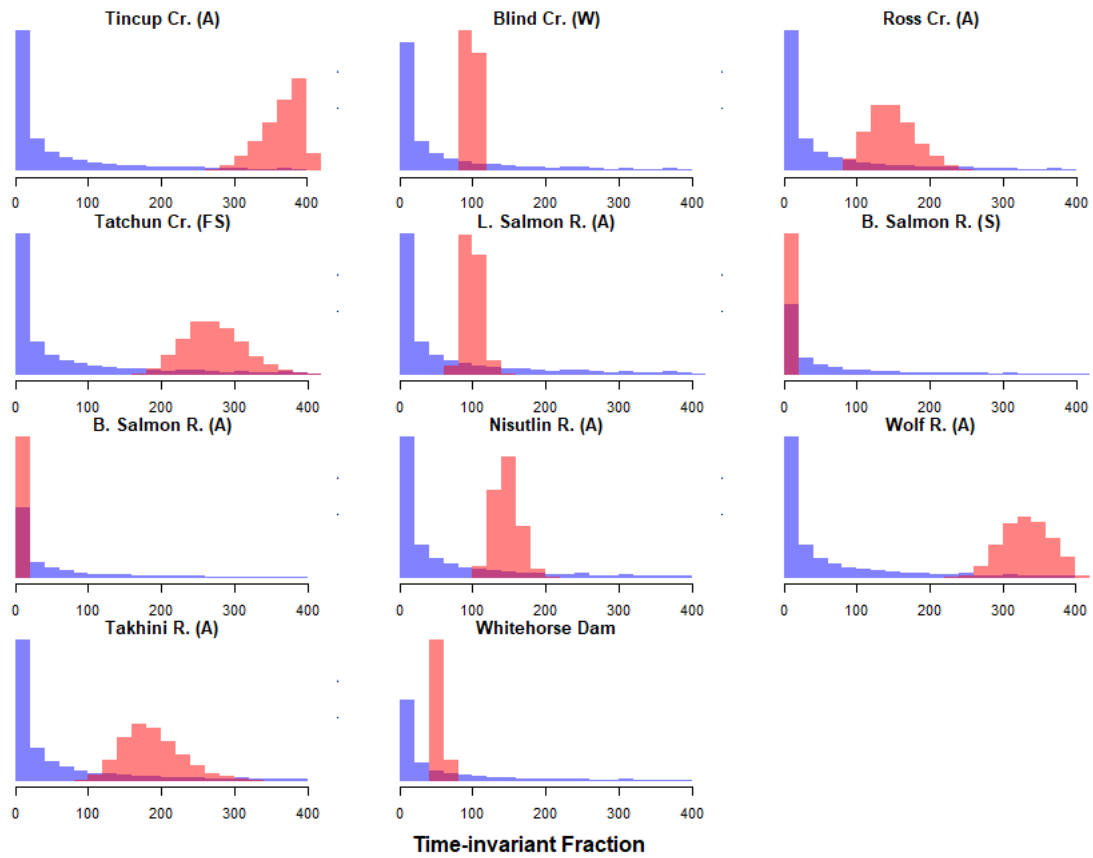


Figure C.15. Prior (blue) and posterior (red) distributions of the time-invariant fraction of total stock-specific escapement in tributary i , K_i , for indices in the Canadian Yukon. Parameter values presented on the real scale, exponentiated from the log-scale used in the prior specifications. W = weir, A = aerial, S = sonar, and FS = foot surveys.

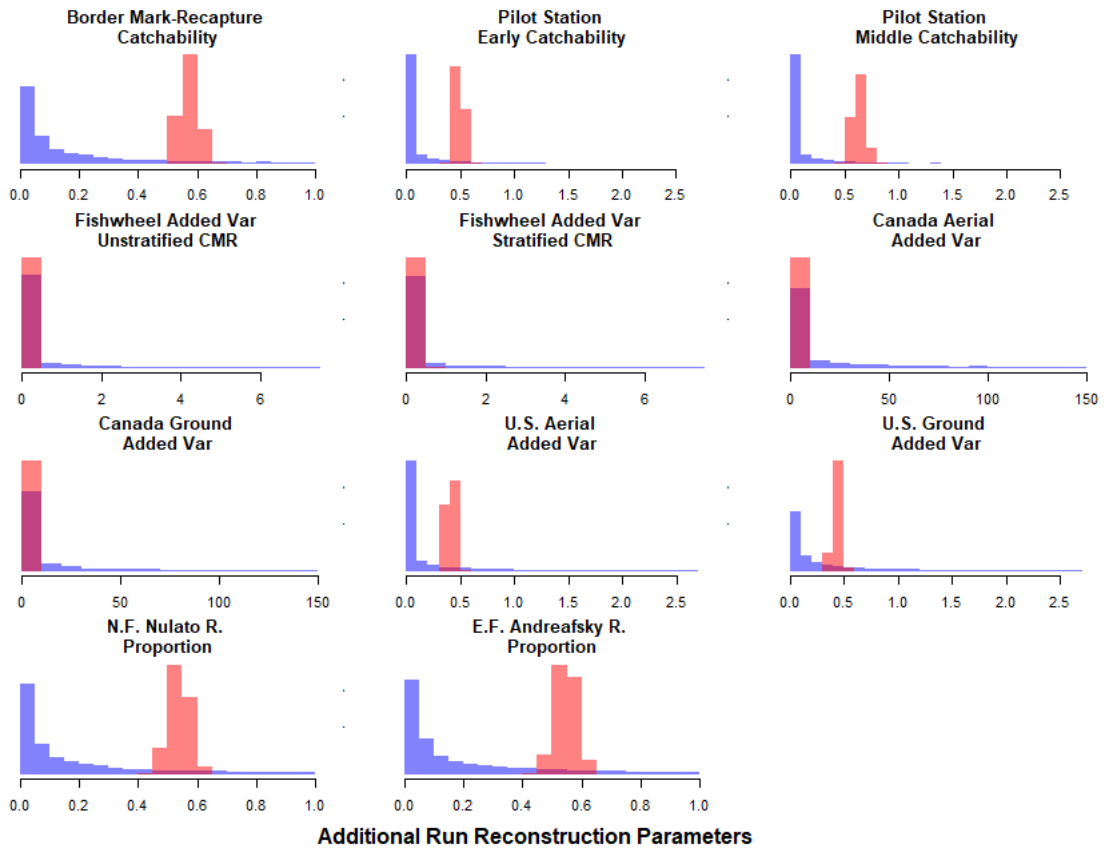


Figure C.16. Prior (blue) and posterior (red) distributions of estimated run reconstruction parameters not shown in Figures C15 and C16. Note that the x-axis varies by the scale of the parameter. Parameter values presented on the real scale, exponentiated from the log-scale used in the prior specifications. Further description and prior specifications for each parameter can be found in Table 2 in the main text.

APPENDIX D. RUN RECONSTRUCTION OUTPUTS

Table D.1. Run reconstruction based estimates (median) of total run size, escapement, harvest and harvest rate (%) by year for the Canada stock.

Year	Total run	Escapement	Harvest	Harvest rate (%)
1981	193880	104596	88067	46
1982	161653	35668	125773	78
1983	180775	54387	125973	70
1984	135294	65716	68931	51
1985	159025	39872	118818	75
1986	174082	48906	124129	72
1987	173796	32740	140783	81
1988	155564	44865	110107	71
1989	163003	56424	105962	65
1990	175405	83297	91322	52
1991	138371	48978	88732	64
1992	174092	42487	130686	76
1993	152719	49535	102268	67
1994	192562	66113	125523	65
1995	210026	68185	141633	68
1996	195526	79845	114125	59
1997	192621	78844	113247	59
1998	93577	32644	60623	65
1999	121721	45919	75305	62
2000	50260	17055	32834	66
2001	100162	66072	33722	34
2002	98020	54312	43312	44
2003	163181	92871	69967	43
2004	120883	57830	62744	52
2005	128745	69692	59346	46
2006	124409	64491	60119	48
2007	91368	36182	55359	61
2008	66585	34190	32459	49
2009	86967	65071	21979	25
2010	61466	32326	29191	47
2011	71061	47023	24171	34
2012	50104	32406	17755	35
2013	37925	28524	9433	25
2014	65105	63370	1714	3

Year	Total run	Escapement	Harvest	Harvest rate (%)
2015	88837	82695	6133	7
2016	83828	69219	14663	17
2017	96893	69572	27414	28
2018	76909	54929	22057	29
2019	72405	42507	29999	41

Table D.2. Run reconstruction based estimates (median) of total run size, escapement, harvest and harvest rate (%) by year for the Lower Yukon stock.

Year	Total run	Escapement	Harvest	Harvest rate (%)
1981	63185	49592	12771	20
1982	68465	38832	28742	43
1983	73445	41413	30986	43
1984	116790	65421	49556	43
1985	136478	69076	65843	49
1986	145082	108402	35632	25
1987	107197	70282	35886	34
1988	103978	64384	38459	37
1989	86464	40511	44872	53
1990	120766	84453	35385	29
1991	137012	82305	53857	40
1992	68656	33192	34646	51
1993	169261	125319	43015	26
1994	142238	101813	39466	28
1995	110418	71644	37977	35
1996	72377	36029	35619	50
1997	144871	89674	53722	37
1998	90709	50334	39500	44
1999	122217	61129	60007	49
2000	53240	32978	19838	38
2001	101236	79950	21179	21
2002	91682	74512	16809	18
2003	131966	123040	8639	7
2004	106654	82798	23442	22
2005	95147	74627	20129	21
2006	91475	70748	20213	22
2007	78913	64547	13870	18
2008	70368	59613	10547	15
2009	84522	79676	4728	6
2010	48060	36471	11317	24
2011	75433	68405	6818	9
2012	43487	38626	4761	11
2013	36942	35044	1855	5
2014	65265	64153	1087	2
2015	66010	64614	1337	2
2016	47760	44160	3512	7

Year	Total run	Escapement	Harvest	Harvest rate (%)
2017	48000	43677	4161	9
2018	47244	43968	3259	7
2019	65212	61344	3700	6

Table D.3. Run reconstruction based estimates (median) of total run size, escapement, harvest and harvest rate (%) by year for the Middle Yukon stock.

Year	Total run	Escapement	Harvest	Harvest rate (%)
1981	136952	17383	118356	87
1982	92625	41663	49699	54
1983	125174	43868	79406	65
1984	92345	14267	77162	84
1985	96162	41995	52728	56
1986	72158	54203	17529	24
1987	74904	30775	43299	58
1988	58329	29673	28075	49
1989	51813	22269	28875	57
1990	88105	43638	43668	50
1991	71561	22901	47918	68
1992	73661	28160	44635	61
1993	108720	58816	48952	45
1994	123248	76740	45533	37
1995	130627	74610	54665	42
1996	62841	44098	18195	29
1997	116668	81349	34378	30
1998	45529	24234	20762	46
1999	56358	46273	9691	17
2000	21857	14167	7447	34
2001	61306	50395	10583	17
2002	55505	30759	24468	44
2003	76884	44156	32287	42
2004	78529	49459	28505	37
2005	68490	42549	25654	38
2006	61380	27072	33815	56
2007	57087	23739	33080	58
2008	37214	20633	16447	44
2009	64227	51552	12642	20
2010	43239	23107	19897	46
2011	47121	33677	13204	28
2012	33473	20981	12227	37
2013	17342	14264	2991	17
2014	44148	43177	959	2
2015	49166	46057	3026	6
2016	47394	39545	7735	16

Year	Total run	Escapement	Harvest	Harvest rate (%)
2017	66173	48923	16883	26
2018	49163	38731	10294	21
2019	36385	23304	12852	35

Table D.4. Run reconstruction based estimates (median) of total run size, escapement, harvest and harvest rate (%) by year for all stock combined.

Year	Total run	Escapement	Harvest	Harvest rate (%)
1981	399495	175524	220350	56
1982	325669	118804	205006	63
1983	381442	142073	237709	63
1984	348386	148518	196595	57
1985	394213	153453	238595	61
1986	394372	214449	178199	45
1987	357366	135244	221062	62
1988	319378	140779	177402	56
1989	302826	120742	180537	60
1990	386517	214047	170879	44
1991	348405	155297	191199	55
1992	317140	105270	210773	67
1993	432955	235696	194825	45
1994	461823	247845	211437	46
1995	453129	216098	235380	52
1996	332794	162501	168584	51
1997	456678	252178	202179	44
1998	230764	108574	121357	53
1999	301796	155580	145522	48
2000	126121	65270	60399	48
2001	265019	198436	65840	25
2002	245504	159962	84837	35
2003	372559	260547	111390	30
2004	307090	191445	115225	38
2005	293006	187027	105370	36
2006	277643	162554	114564	41
2007	227864	124680	102624	45
2008	174480	114533	59644	34
2009	236280	196620	39546	17
2010	153121	92039	60689	40
2011	194058	149122	44456	23
2012	127392	92256	34911	27
2013	92413	77996	14334	16
2014	174916	171056	3782	2
2015	204423	193908	10538	5
2016	179382	153083	26002	15

Year	Total run	Escapement	Harvest	Harvest rate (%)
2017	211669	162382	48682	23
2018	173838	137790	35754	21
2019	174708	127429	46707	27

APPENDIX E. MODEL FITS TO U.S. HARVEST AND POTENTIAL ENROUTE MORTALITY

Our run reconstruction sub-model provides a convenient framework for balancing abundance estimates from multiple projects and generating a single estimate of Canada stock run size that attempts to rectify what otherwise may be considered conflicting sources of information. For example, the 2019 model fits provided a unique opportunity to evaluate how the model performed when information about Canada stock run size from three different assessment projects, which are all highly influential within the model, was not well aligned. If it were possible to perfectly account for the entire Canada stock as it progresses upriver, then the Eagle Sonar estimate would be exactly equal to the Pilot Station sonar estimate minus removals between the two projects. In 2019, the Canada stock passage estimated by the Eagle Sonar program was notably smaller than what was expected based on information from the Pilot Station Sonar program after accounting for U.S. harvest of the Canada stock. On the surface, comparison of point estimates from each of these three assessment projects suggested that over 33,000 fish were “missing”. Multiple explanations for “missing” fish could be formulated, but there was no evidence that Pilot Station sonar or the associated GSI program overestimated Canada stock passage, that U.S. harvest of Canada Stock was underreported, or that the Eagle Sonar project underestimated Chinook salmon passage.

A leading hypothesis to explain the apparent discrepancy between estimates of Canada stock size past Pilot Station and Eagle Sonar was that fish died enroute due to heat stress (JTC 2020). Heat stress has been documented in Yukon River Chinook Salmon when spawning migration water temperatures exceed 18°C (Biela et al. 2020). In 2019, an unprecedented, sustained period of water temperatures exceeding 18°C occurred throughout the Yukon River mainstem, including a shorter duration exceeding the suggested upper thermal limit for migrating Chinook salmon (21°C, McCullough 1999). Both periods of elevated water temperature overlapped with the upriver migration timing of Chinook salmon – albeit to different extents. Small numbers of pre-spawn Chinook salmon enroute mortalities were reported by residents along the mainstem of the Yukon River in 2019 (Biela et al. In press). The relatively few opportunistic reports of enroute Chinook salmon mortalities likely underrepresented the impact of elevated water temperatures on the upriver migration success of the Canada stock in 2019. Nevertheless, attributing all 33,000-missing fish to enroute mortality in 2019 is tenuous. An alternative hypothesis is that the apparent “missing” fish is best explained by a combination of factors that consider sonar and harvest estimation uncertainty in addition to elevated natural enroute mortality, possibly caused by heat stress.

The model fit available data in 2019 as expected. Fits to observed data in 2019 suggests that Eagle Sonar was an accurate estimate of Canada stock passage, Pilot Station Sonar modestly overestimated Chinook salmon passage, and more fish were removed between the sonar locations than can be explained by U.S. harvest alone (Figure E.1). Compared to Eagle sonar, the Pilot Station Sonar/GSI and U.S. harvest assessment programs are considerably more complicated resulting in a higher degree of data uncertainty (i.e., less precise). The model “mis-fit” to the Pilot Station Sonar data in 2019 was within the range of what had been observed since 2002, and we consider the degree of overestimation by the Pilot Station Sonar to be reasonable given the level of data uncertainty associated with that project. On the surface, the model “mis-fit” to the upriver U.S. harvest estimate would suggest that U.S. harvest was underreported in 2019; however, we do not think that is an accurate interpretation. The U.S. harvest estimation program is considered statistically robust, and its accuracy has been confirmed by several independent

comprehensive harvest surveys conducted at the community level (e.g., Brown and Deena 2019). Instead, we believe the difference between reported and model estimated U.S. harvest is due to unaccounted for enroute mortality (likely due to heat stress). The current model structure attributes all “removals” from the system to harvest. In the future, however, the model could be revised to separately estimate harvest and natural enroute mortality.

The 2017 model fits displayed a similar pattern to that observed in 2019, although the magnitude of the mis-fits was smaller. The model suggested that Pilot Station sonar overestimated Chinook salmon passage. The 2017 sonar operations were successful with no known issues, and the degree of overestimation was within the range of what is reasonable for this project. The model suggests that more fish were “removed” from the system upriver from Pilot Station Sonar than can be explained by U.S. harvest alone. There were no known issues with U.S. harvest assessment in 2017, and no evidence of systematic underreporting. Elevated water temperatures were experienced in 2017, but temperatures exceeding 18°C in the lower Yukon River were largely associated with the later portion of the Chinook salmon migration. Enroute mortality due to disease has been implicated in some years, but there is no evidence disease prevalence or severity was abnormal in 2017. Higher than average contribution of Canadian Porcupine Chinook salmon could also have in theory contribute to a difference between estimates, but 2017 was characterized by the smallest Porcupine River contribution to total Canada Stock based for the six years (2014–2019) with data (Pestal et al. 2022). As a result, unlike 2019, there is no clear explanation for the 2017 model mis-fits to the reported data.

The model provides an alternative and improved framework for quantifying the magnitude of “missing” fish in any single year, in contrast to simply comparing point estimates from individual assessment projects. However, our assumptions about the accuracy and precision of the data from these assessment projects determine whether those fish are attributed to overestimation by Pilot Station Sonar or unreported removals upriver from Pilot Station. We made *a priori* decisions about the relative reliability of the data to inform the Canada stock run size, based on an extensive data review (Pestal et al. 2022). Specifically, we placed a high degree of trust in the Eagle sonar dataset based on relatively small survey CVs and input from agencies who utilize the data for management purposes. We assumed the Pilot Station Sonar/GSI dataset was accurate and unbiased in the 2002–2019 strata and did not include an additional variance term as was done for earlier strata, but we did assume Eagle Sonar was more precise compared to the Pilot Station Sonar. As such, Eagle Sonar estimates were considered highly informative and they anchor the model, providing context for fitting to the less precise Pilot Station/GSI and U.S. harvest data. We set the survey CV for U.S. harvest at 20%, which was notably larger than both sonar programs, thus allowing U.S. harvest upriver from Pilot Station to absorb much of the differences between sonar estimates. The model fit to the reported data largely conformed to expectation and aligned with our understanding of the relative accuracy and precision associated with the highly influential sonar and harvest datasets. This reality, however, underscores the importance of careful *a priori* decisions pertaining to data treatment.

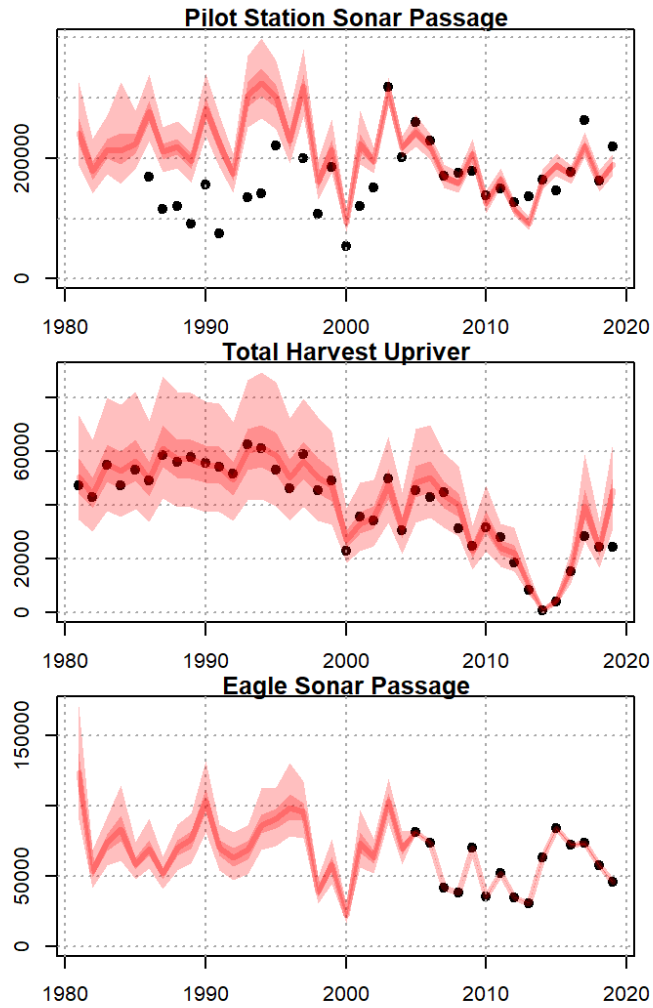


Figure E.1. Observed data (black points) and model estimated number of fish (median with 50% and 95% credible intervals) for Pilot Station sonar, harvest upriver of Pilot Station and downriver of Eagle, and Eagle sonar.

APPENDIX F. SENSITIVITY ANALYSES

F.1. SENSITIVITY ANALYSIS: LOG-NORMAL BIAS CORRECTION

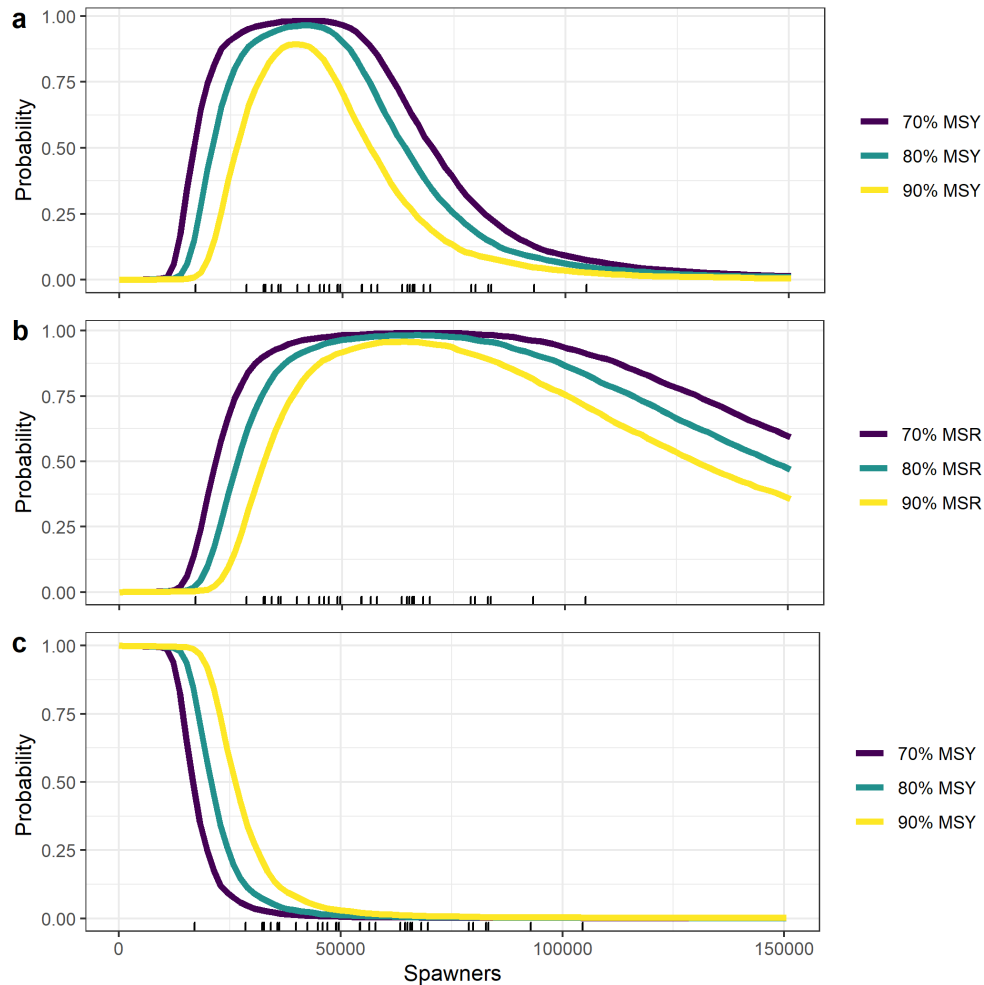


Figure F.1. Optimal yield, recruitment, and “overfishing” probability profiles without log-normal bias correction applied (compare to Figure 8). (a) Optimal yield profile showing the probability that a given spawner abundance is expected to achieve 70%, 80%, or 90% of maximum sustainable yield (MSY). (b) Optimal recruitment profile showing the probability that a given spawner abundance is expected to achieve 70%, 80%, or 90% of maximum sustainable recruitment (S_{MSR}). Historical spawning escapements are shown along x-axis. (c) Overfishing profile, calculated as $1 - P(SY > X\% \text{ of } MSY)$ at $S < S_{MSY}$, and 0 at $S > S_{MSY}$, showing the probability that, at a given spawner abundance, sustained yield (SY) is reduced to less than a percentage (70%, 80%, or 90%) of MSY by supplying too few spawners.

Table F.1. Posterior means, medians and credible intervals for biological reference points that have not been log-normal bias corrected (compare to Table 3). Also shown are estimates of the effective sample size (n_{eff}) and potential scale reduction factor (\hat{R}) for parameters and reference points estimated by the model.

Variable	Mean	Median	p2.5	p97.5	n_{eff}	\hat{R}
$\ln(\alpha)$	1.461	1.465	0.813	2.061	3,924	1.0007
S_{EQ}	111,128	101,502	73,238	194,555	3,284	1.0008
S_{MSY}	44,620	40,501	27,997	81,664	3,144	1.0006
U_{MSY}	58%	59%	36%	73%	3,596	1.0003
U_{MSR}	34%	37%	-16%	66%		

F.2. SENSITIVITY ANALYSIS: AGE COMPOSITION EFFECTIVE SAMPLE SIZES

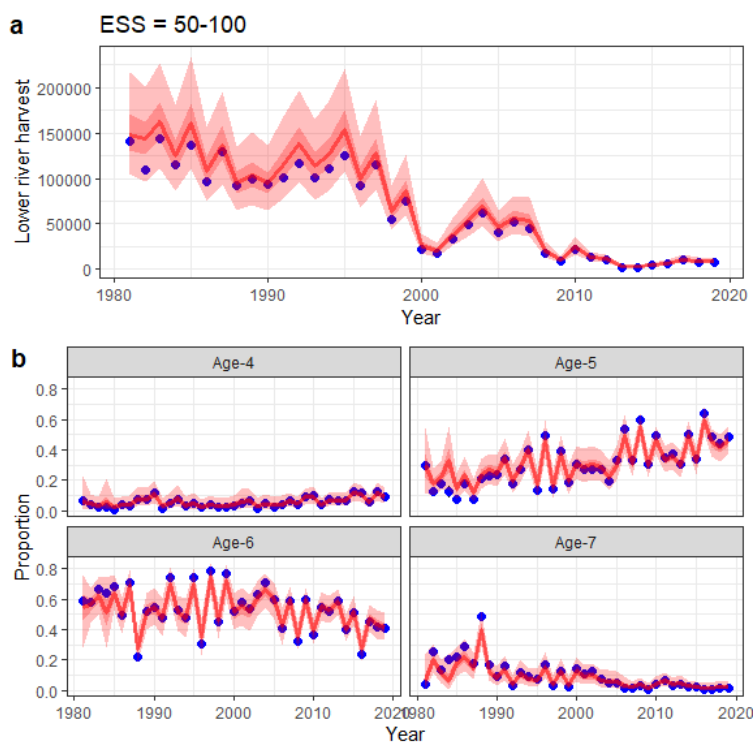


Figure F.2. Model fits to harvest and age composition under **base model** effective sample size assumption of 50 pre-2007 and 100 thereafter. (a) Lower river total harvest observations (blue points) and model predictions (median, 50th and 97.5th quantiles). (b) Observed (blue points) and model predicted (median, 50th and 97.5th quantiles) age composition.

Table F.2. Influence of alternative assumptions about age composition effective sample size on estimates of S_{MSY} .

Scenario	Mean	Median	p2.5	p97.5
1	45,935	41,982	28,793	85,552
2	50,611	45,182	29,157	98,970
3	68,495	48,133	31,388	114,464

Scenario	Mean	Median	p2.5	p97.5
4	46,199	42,006	28,845	87,865

Table F.3. Influence of alternative assumptions about age composition effective sample size on estimates of S_{MSR} .

Scenario	Mean	Median	p2.5	p97.5
1	76,055	67,637	39,135	165,395
2	87,077	76,118	39,532	203,812
3	133,892	84,083	45,453	219,293
4	77,163	67,298	38,332	170,696

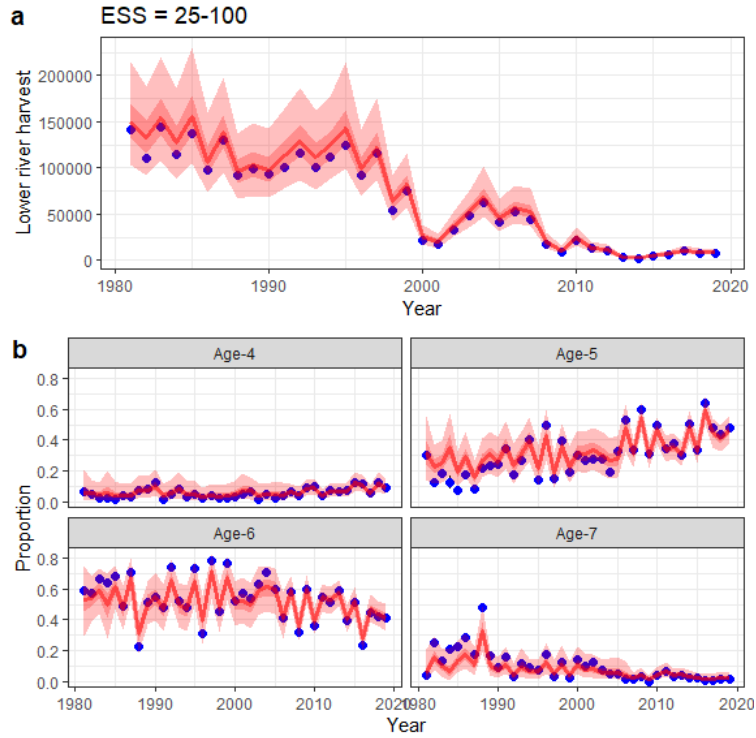


Figure F.3. Model fits to harvest and age composition assuming an effective sample size of **25** pre-2007 and **100** thereafter. (a) Lower river total harvest observations (blue points) and model predictions (median, 50th and 97.5th quantiles). (b) Observed (blue points) and model predicted (median, 50th and 97.5th quantiles) age composition.

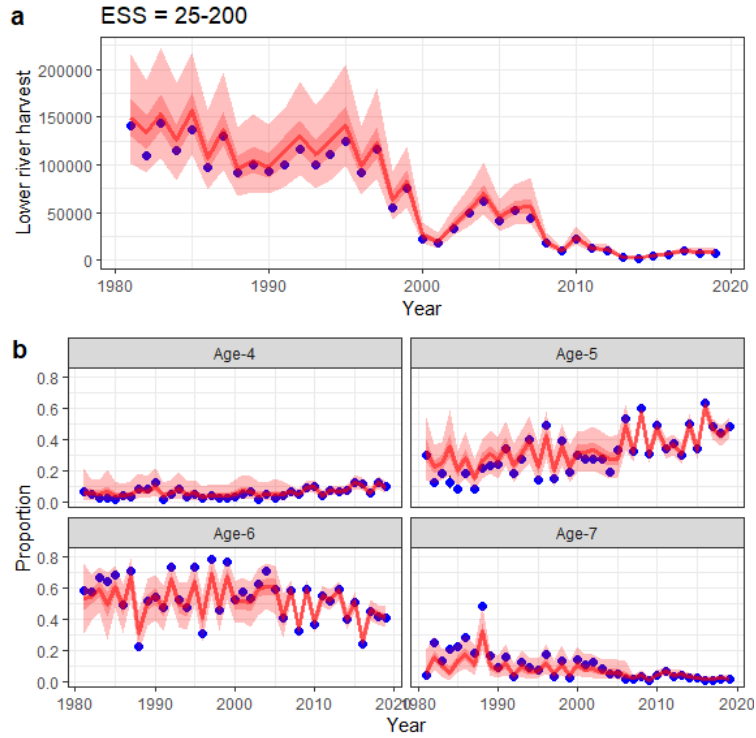


Figure F.4. Model fits to harvest and age composition assuming an effective sample size of **25** pre-2007 and **200** thereafter. (a) Lower river total harvest observations (blue points) and model predictions (median, 50th and 97.5th quantiles). (b) Observed (blue points) and model predicted (median, 50th and 97.5th quantiles) age composition.

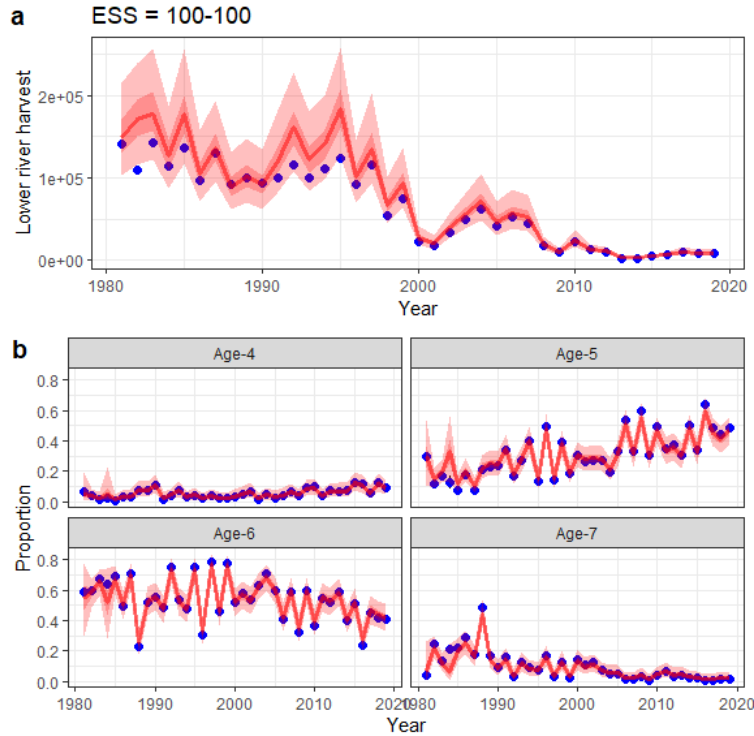


Figure F.5. Model fits to harvest and age composition assuming an effective sample size of **100**. (a) Lower river total harvest observations (blue points) and model predictions (median, 50th and 97.5th quantiles). (b) Observed (blue points) and model predicted (median, 50th and 97.5th quantiles) age composition.

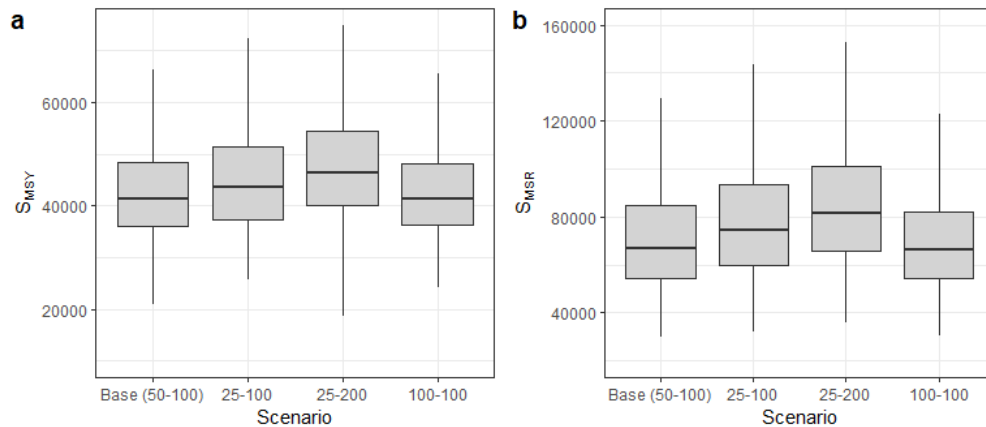


Figure F.6. Influence of alternative assumptions about age composition effective sample size on estimates of (a) S_{MSY} and (b) S_{MSR} . Boxplots show median and 25th and 75th quartiles with whiskers extending to the lowest/highest value up to 1.5 times the interquartile range.

F.3. SENSITIVITY ANALYSIS: STOCK COMPOSITION EFFECTIVE SAMPLE SIZES

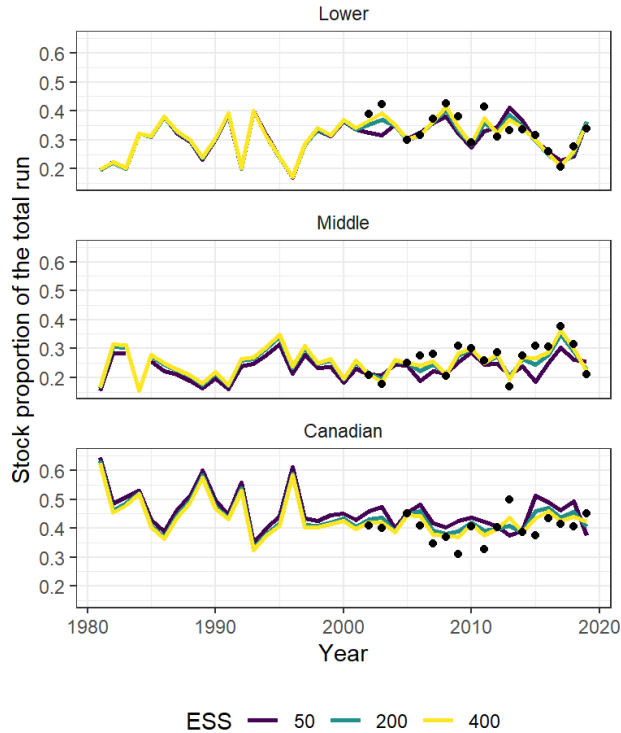


Figure F.7. Model fits to observed stock composition (black points) under effective sample size assumption of 50 (purple), 200 (green, **base model**), and 400 (yellow).

Table F.4. Normalized root mean squared error (NRMSE) for the stock composition estimates under alternative assumptions of effective sample size.

ESS	Lower	Middle	Canadian
50	0.146	0.202	0.187
200	0.089	0.107	0.119
400	0.061	0.07	0.083

Table F.5. Influence of alternative assumptions about stock composition effective sample size on estimates of S_{MSY} .

ESS	Mean	Median	p2.5	p97.5
50	48,916	43,746	30,334	96,538
200	48,715	43,364	29,764	97,664
400	52,629	42,972	29,663	96,742

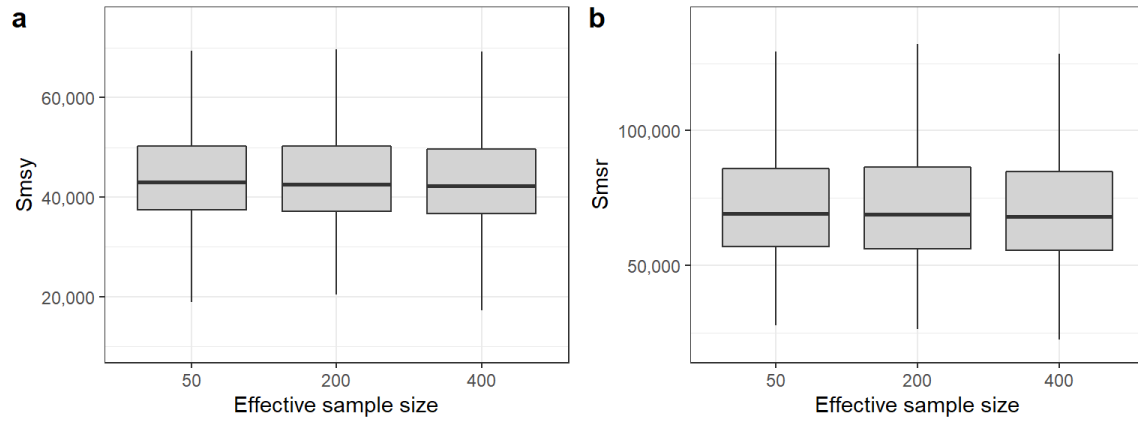


Figure F.8. Estimates of (a) S_{MSY} and (b) S_{MSR} under alternative assumptions about stock composition effective sample size. Boxplots show median and 25th and 75th quartiles with whiskers extending to the lowest/highest value up to 1.5 times the interquartile range.

Table F.6. Influence of alternative assumptions about stock composition effective sample size on estimates of S_{MSR} .

ESS	Mean	Median	p2.5	p97.5
50	83,383	71,133	41,491	188,866
200	83,088	70,834	40,638	192,642
400	93,267	69,856	40,508	193,335

F.4. SENSITIVITY ANALYSIS: RUN RECONSTRUCTION INDICES WEIGHTING

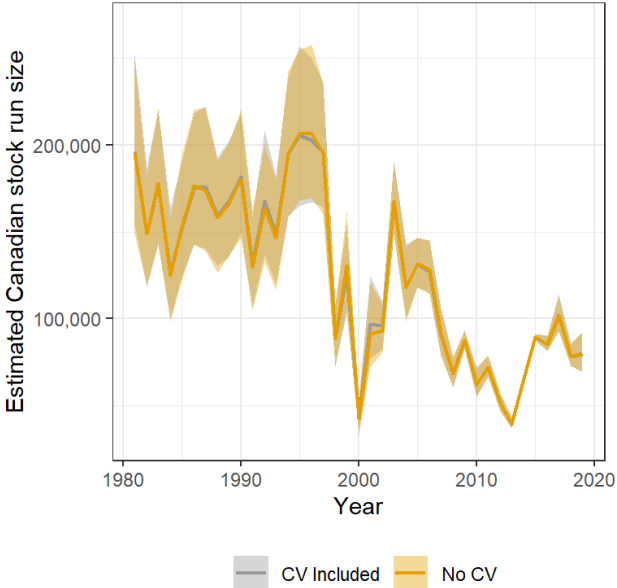


Figure F.9. Comparison between model predicted Canadian stock run sizes where index weights (CV) were estimated by the model only (yellow) and where weights were included as data (grey) in addition to model-estimated dispersion. Shaded areas indicate 95% credible intervals.

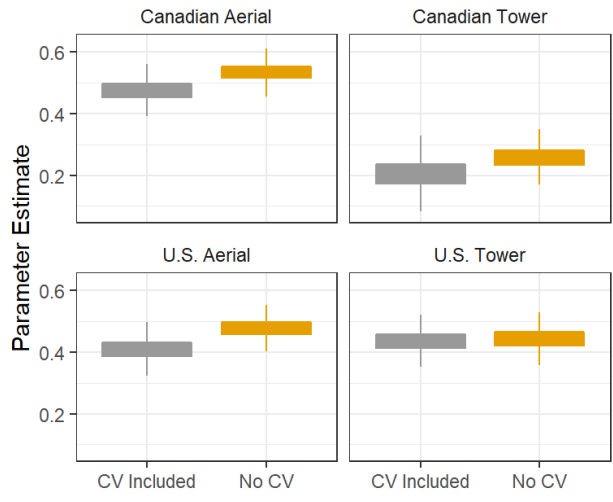


Figure F.10. Estimates of dispersion parameters where index weights (CV) were estimated by the model only (yellow) and where weights were included as data (grey) in addition to model-estimated dispersion. Parameters for aerial surveys also applied to foot survey and fishway data. Parameters for tower surveys also applied to weir data. Boxplots show median and 25th and 75th quartiles with whiskers extending to the lowest/highest value up to 1.5 times the interquartile range.

Table F.7. Mean and standard deviation of dispersion parameter estimates under alternative model specifications where index weights (CV) were estimated by the model only (No CV) and where weights were included as data (CV Included) in addition to model-estimated dispersion. Parameters for aerial surveys also applied to foot survey and fishway data. Parameters for tower surveys also applied to weir data.

Surveys	CV Included		No CV	
	Mean	SD	Mean	SD
Canadian Aerial	0.475	0.034	0.535	0.030
Canadian Tower	0.205	0.049	0.259	0.039
U.S. Aerial	0.409	0.034	0.478	0.030
U.S. Tower	0.435	0.032	0.445	0.032

F.5. ALTERNATIVE FUNCTIONAL FORM TO THE SPAWNER-RECRUITMENT RELATIONSHIP

One of the central assumptions in stock-recruitment analysis is the functional form of the underlying relationship between spawner abundance and resulting recruitment. The Ricker model was selected as the primary basis for estimation of biological reference points given its flexibility and potential to account for overcompensation, and its general tendency to provide more biologically risk adverse estimates of reference points including S_{MSY} . However, there was interest in understanding the sensitivity of our estimates of biological reference points to alternative assumptions about the structural form of the spawner recruitment relationship such as the Beverton-Holt stock-recruitment model which, unlike the Ricker model, exhibits asymptotic behavior at high levels of spawning abundance. We therefore revised Equ. 29 to:

$$\ln(R_y) = \ln(E_{y,s=c}) + \ln(\alpha) - \ln(1 + (\alpha/\beta)E_{y,s=c}) + v_y \quad (\text{F.1})$$

where α is productivity (intrinsic rate of growth), β is the equilibrium recruitment as spawner abundance approaches infinity instead of the magnitude of within stock density dependence as in Equ. 29 and v is inter-annual variation in survival from egg to adulthood which was assumed to be correlated with lag-1 (ϕ) over time (Equ. 30). This version of the Beverton-Holt model was selected because the interpretation of the α parameter is consistent with that of the Ricker model used in our base analyses, and as such the same prior distribution (Table F.8) could be applied thus allowing more direct comparison among model parameterizations. In all other ways the structure of this Beverton-Holt formulation of the integrated model was consistent with the Ricker version described in Section 2.3.

The spawning abundance expected to maximize sustainable yield over the long-term under equilibrium conditions (S_{MSY}), was derived as:

$$S_{MSY} = \beta\sqrt{1/\alpha} - \beta/\alpha \quad (\text{F.2})$$

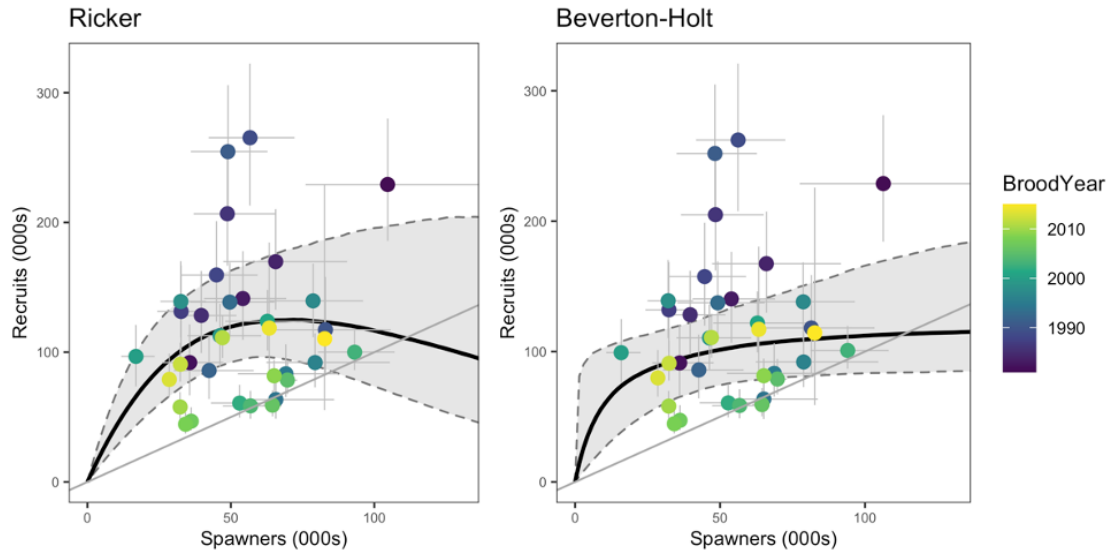


Figure F.11. Relationship between recruitment and spawner abundance for Canadian-origin Yukon River Chinook salmon under Ricker and Beverton-Holt models. Error bars and grey bands are 90% credible intervals, and the thick black line is the expected relationship for each form of the stock-recruitment model.

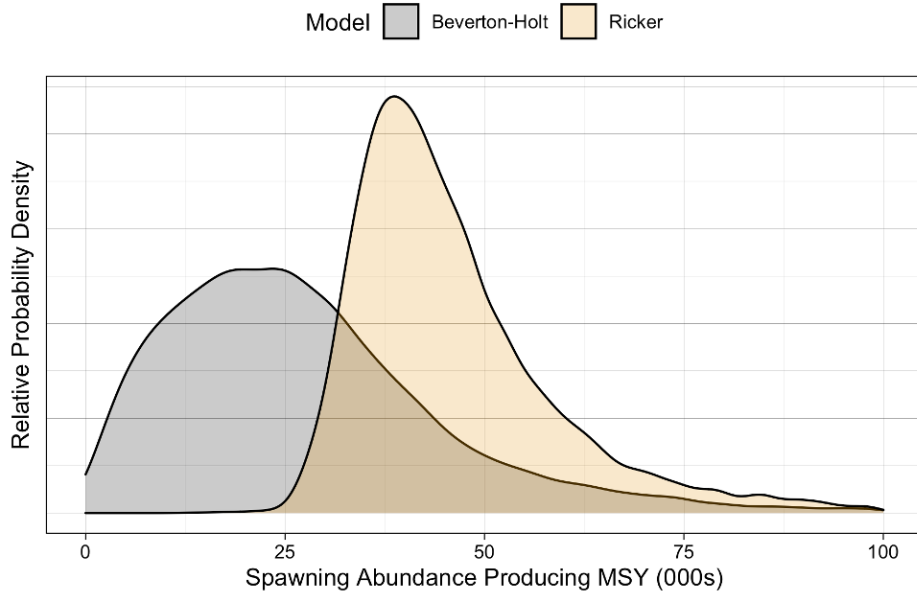


Figure F.12. Comparison of posterior distributions for the spawning abundance expected to maximize sustainable yield (S_{MSY}), as estimated by the Beverton-Holt and Ricker models.

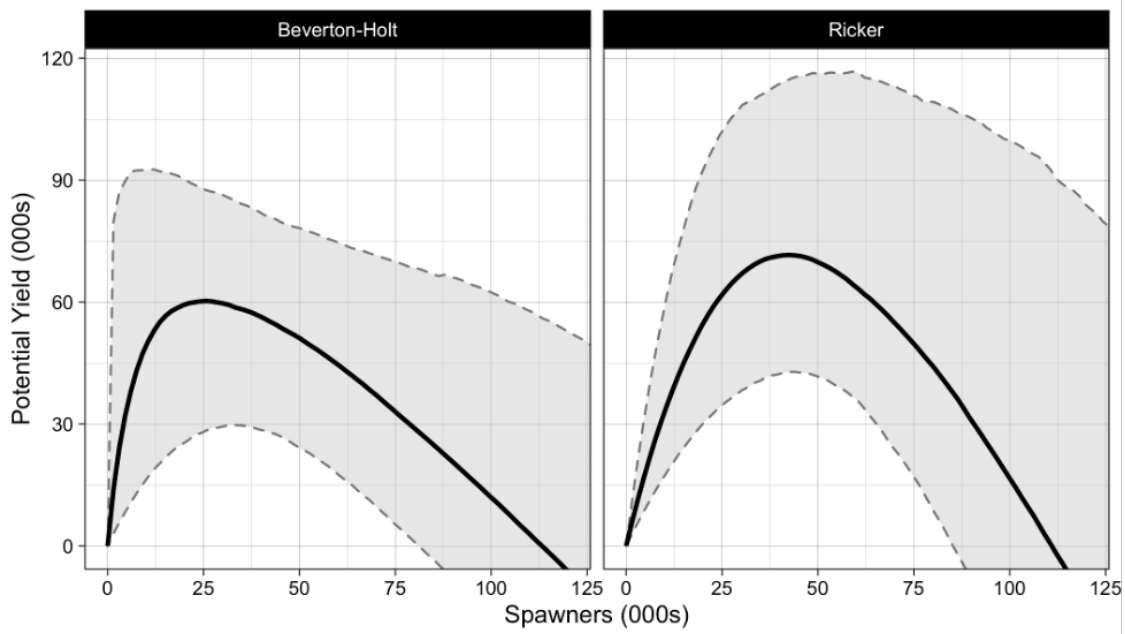


Figure F.13. Expected yield (i.e. surplus production) across a range of spawner abundances based on Beverton-Holt and Ricker spawner-recruitment models fit to the same data. Shown is the median \pm 90% credible intervals.

Table F.8. Prior probability distributions for spawner-recruit parameters.

Parameter	Prior	Bounds	DescriptionNotes
$\ln(\alpha)$	$\sim N(0, 3)$	$[0, \text{inf}]$	Natural log of intrinsic rate of growth
$\ln(\beta)$	$\sim N(0, 10)$	$[0, 15]$	Natural log of asymptotic recruitment
ϕ	$\sim U(-1, 1)$		Lag-one correlation in interannual variation in survival
σ_R	$\sim N(0, 2)$	$[0, \text{inf}]$	White noise process standard deviation in survival.
$\ln(R_0)$	$\sim N(0, 20)$	$[0, \text{inf}]$	Natural log of unobserved recruitment in the first seven years of process model.
σ_{R_0}	$\sim \text{Inv} - \text{Gamma}(2, 0)$	$[0, \text{inf}]$	Standard deviation in unobserved recruitment in the first seven years of process model. Based on meta-analysis of other AK Chinook stocks (Fleischman et al. 2013), less informative priors resulted in divergent transitions in sampler during initial attempts to code the model in Stan.
π	$\sim \text{Dir}(0.25, 0.25, 0.25, 0.25)$		Mean maturation-at-age probability for ages 4:7.
D	$\sim \text{beta}(1, 1)$		Dispersion parameter that governs variability in maturation-at-age probabilities across cohorts.