

# Population diversity in Kuskokwim Chinook: New findings on trade-offs for different harvest strategies

A research team funded by the Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative used estimates of Chinook population diversity to build computer simulations that evaluated how well alternative harvest policies meet Chinook population diversity and fishery objectives in the Kuskokwim.

Brendan M. Connors<sup>1,†</sup> Lew Coggins<sup>2</sup>, Benjamin A. Staton<sup>3</sup>, Mike Jones<sup>4</sup>, Carl Walters<sup>5</sup> and Daniel C. Gwinn<sup>6</sup>

Variation among salmon populations in their productivity, carrying capacity and life history characteristics (population diversity) contributes to stable fisheries as a result of portfolio effects, whereby fisheries that harvest multiple populations benefit from the averaging effects of their variable dynamics (**Figure 1**). This diversity also supports fishery resilience because typically at least some populations will do well when others do not and populations that are less productive today might be more productive under future conditions.

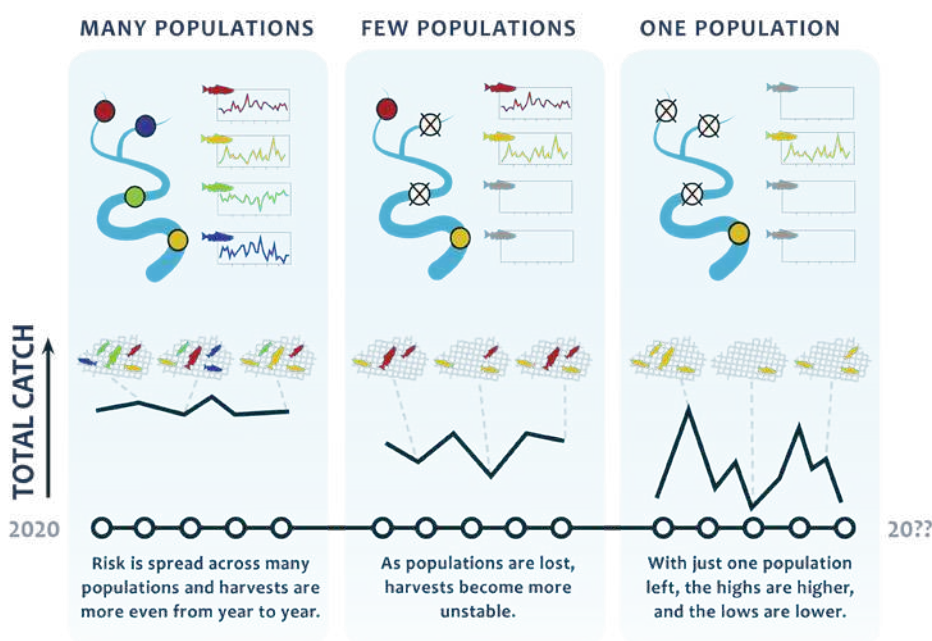
As a result population diversity is increasingly viewed as a foundation of sustainable and resilient resource management and the importance of

protecting population diversity is recognized in fisheries management policies such as [Alaska's Sustainable Salmon Policy](#).

When mixed-stock fisheries for multiple populations overlap in space and time there can be an inherent conflict between harvest rates and population diversity: high harvest rates, which can be sustained by the most productive populations, can come at the cost of increased risk of overfishing less productive ones (**Figure 2**).

Despite the potential importance of these harvest-population diversity tradeoffs, Chinook salmon management, including in the large river basins of

**Figure 1.** Illustration of how population diversity contributes to harvest stability. When diversity is high, individual populations doing very well can compensate for those that are doing poorly, leading to a more stable harvest over time. When diversity is low, harvests are more variable because there are fewer populations to buffer the effects of a variable environment.



## Author Affiliations

1 Fisheries and Oceans Canada, Sidney, BC

2 US Fish and Wildlife Service, Bethel, AK

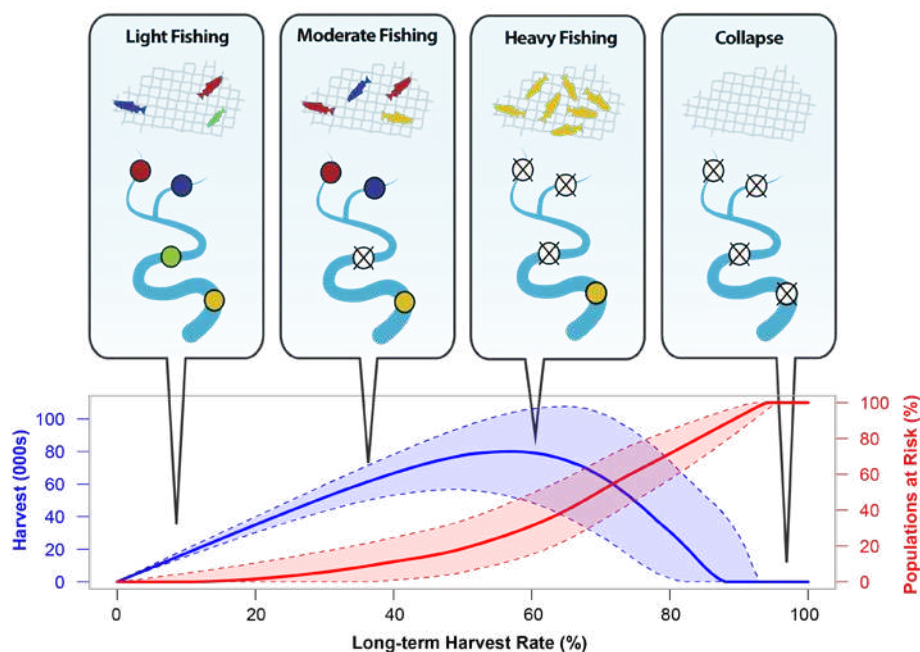
3 Columbia River Inter-Tribal Fish Commission, Portland, OR

4 Michigan State University, East Lansing, MI

5 University of British Columbia, Vancouver, BC

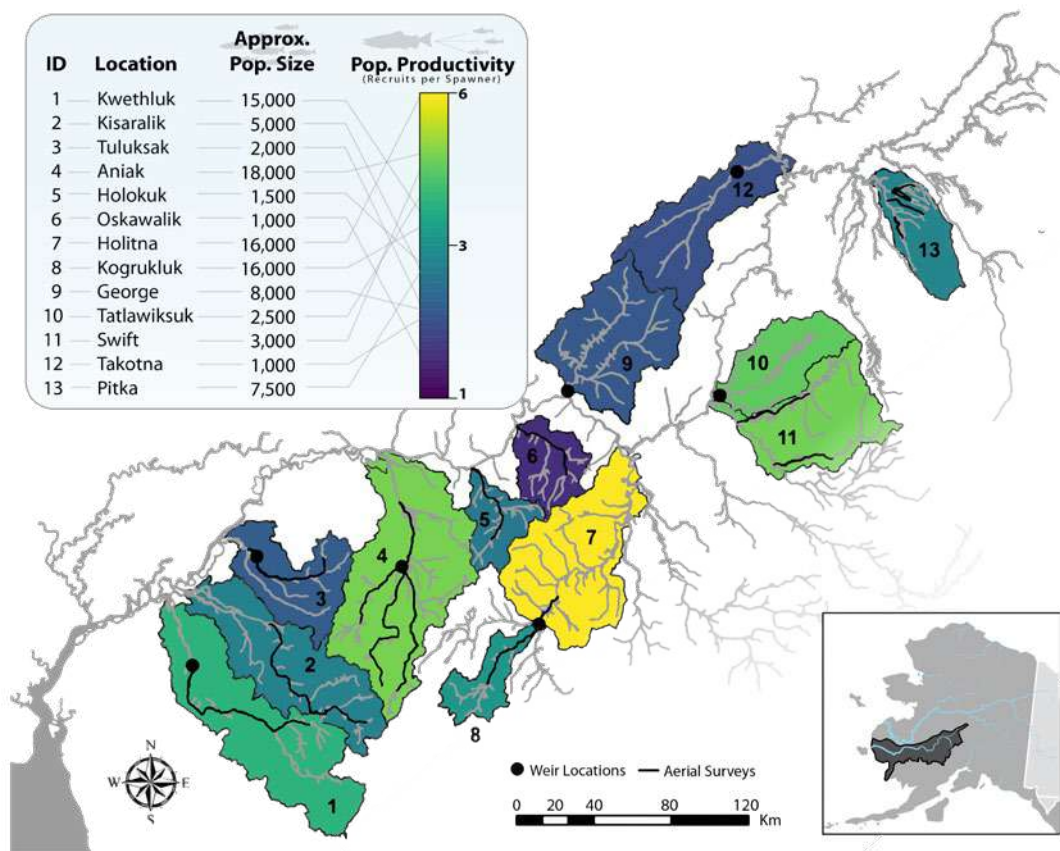
6 Biometric Research LLC, Gainesville, FL

† [Brendan.connors@dfo-mpo.gc.ca](mailto:Brendan.connors@dfo-mpo.gc.ca); (250) 858-7028



**Figure 2.** Relationship between long-term mixed-population harvest and risks to individual populations across a range of long-term average harvest rates. Overall harvest from the system is predicted to increase as the average harvest rate increases up to a point, after which it rapidly declines because most populations are overfished and then driven to extinction. This figure illustrates that you have to be willing to accept some risk to the weakest (least productive) populations if you want to maximize total harvest from the system.

Western Alaska and the Yukon, does not often explicitly consider them. To help address this knowledge gap we characterized the degree of Chinook population diversity within the Kuskokwim River basin by fitting spawner-recruitment models to all available tributary level data on Chinook escapement along with estimates of age composition and total harvest (13 populations accounting for approximately half of the total production from the Kuskokwim). We found clear evidence of population diversity in the system where population productivity and size were estimated to vary by as much as 3-fold and 18-fold among populations, respectively (**Figure 3**).

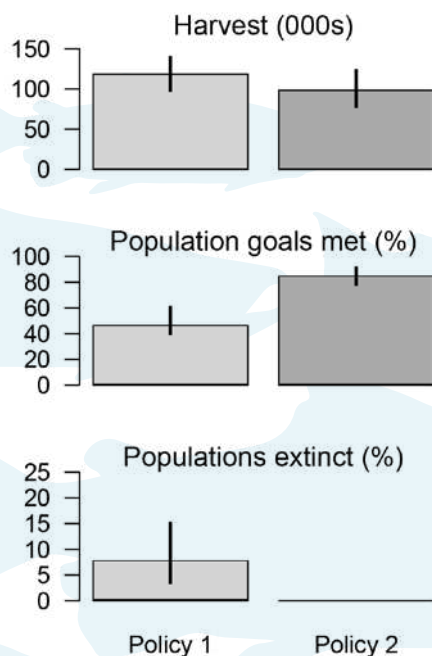


**Figure 3.** Chinook population diversity in the Kuskokwim River basin. Each polygon depicts the general spawning distribution of the 13 Chinook populations for which there are estimates of spawner abundance based on either weir (points) or aerial (thick line) surveys. Populations are color coded by their productivity (recruits produced per spawner at small population size) and estimated average population size (predicted in absence of fishing) is listed next to each system's name. This biodiversity emphasizes that large populations are not necessarily the most productivity, and vice-versa.



We used estimates of Chinook population diversity to build computer simulations that evaluated how well alternative harvest policies (defined by basin wide escapement and harvest goals) meet Chinook population diversity and fishery objectives in the Kuskokwim. We found that harvest policies focused on meeting minimum subsistence needs were unlikely to jeopardize long-term prospects for basin-wide sustainable use. However, Chinook population diversity gives rise to asymmetric trade-offs among fishery and conservation objectives in the Kuskokwim. For example, relative to a harvest policy that seeks to maximize mixed-stock harvests, foregoing relatively small amounts of mixed-stock harvest is predicted to yield relatively large increases in the chances of ensuring equitable access to Chinook (i.e., meeting tributary goals) and to nearly eliminate biological risks to weak populations (**Figure 4**).

The approach we developed for the Kuskokwim provides a general framework for characterizing salmon population diversity in large river basins and evaluating harvest-population diversity trade-offs among alternative harvest policies within them. With support from AYK-SSI we are now exploring Chinook salmon population diversity in the Yukon River basin. Ongoing research analyzing Chinook salmon ear stones (otoliths) in the Kuskokwim and Yukon suggests that different parts of these large watersheds are hot spots for salmon production and growth, and that favorable locations change year to year. Together with our efforts to characterize Chinook population diversity, this research emphasizes the importance of protecting and monitoring salmon habitats and populations (both large and small) throughout these large free flowing river basins to maximize their resilience to environmental change and the benefits communities derive from them.



**Figure 4.** Illustration of the predicted performance of two alternative harvest policies for Kuskokwim Chinook. Policy 1 seeks to maximize total mixed-population harvest while Policy 2 seeks to maximize harvests only once the risk of driving the weakest populations extinct is minimized. Shown for each policy is (1 – top panel) the predicted average harvest, (2 – middle panel) proportion of individual populations whose average spawner abundance is above a population (or tributary) level goal which is also a proxy for equitable access to Chinook, and (3 – lower panel) the proportion of populations predicted to be driven to extinction.

This research was made possible  
with support from AYK-SSI



Download the full project report using this [LINK](#)

## **I. AYK SSI TITLE PAGE:**

---

2019 Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative Project Final Product\*

### **Chinook harvest-population diversity tradeoffs**

Brendan M. Connors<sup>1,†</sup> Lew Coggins<sup>2</sup>, Benjamin A. Staton<sup>3</sup>, Mike Jones<sup>4</sup>, Carl Walters<sup>5</sup> and Daniel C. Gwinn<sup>6</sup>.

<sup>1</sup> Fisheries and Oceans Canada, Sidney, BC

<sup>2</sup> US Fish and Wildlife Service, Bethel, AK

<sup>3</sup> Columbia River Inter-Tribal Fish Commission, Portland, OR

<sup>4</sup> Michigan State University, East Lansing, MI

<sup>5</sup> University of British Columbia, Vancouver, BC

<sup>6</sup> Biometric Research LLC, Gainesville, FL

<sup>†</sup> Brendan.connors@dfo-mpo.gc.ca; (250) 858-7028

July 5, 2019

---

\* Final products of AYK Sustainable Salmon Initiative-sponsored research are made available to the Initiatives Partners and the public in the interest of rapid dissemination of information that may be useful in salmon management, research, or administration. Sponsorship of the project by the AYK SSI does not necessarily imply that the findings or conclusions are endorsed by the AYK SSI.

## II. ABSTRACT:

---

Variability among fish populations in ecological characteristics and productive capacity (i.e., population diversity) can be critical to maintaining resilience to environmental change and to dampening variability in harvest for fisheries that depend upon them. However, when fisheries for multiple populations overlap in space and time there can be an inherent conflict between mixed-stock harvest and population diversity: high harvest rates, which can be sustained by the most productive populations, can come at the cost of increased risk of overfishing those that are less productive. The importance of these harvest-population diversity trade-offs in salmon management is well-recognized, but they are difficult to characterize due to incomplete information, and they are not often explicitly evaluated in contemporary fisheries management. We developed an integrated age-structured multi-population state-space spawner-recruit model and fitted it to data from 13 Chinook salmon populations from the Kuskokwim drainage in western Alaska. We found clear evidence of population diversity in the system where productivity and carrying capacity can vary by as much as 3-fold and 18-fold among populations, respectively. Simulation testing of the model illustrated that it was largely unbiased with respect to leading parameters, abundance states, and derived biological reference points, whereas more commonly applied regression-based approaches showed substantial bias. We used the state-space model to parameterize closed-loop simulations that evaluated how well alternative harvest policies meet Chinook population diversity and fishery objectives in the Kuskokwim. We found that Chinook population diversity gives rise to asymmetric trade-offs among fishery and conservation objectives whereby foregoing relatively small amounts of mixed-stock harvest resulted in relatively large increases in the chances of ensuring equitable access to Chinook (i.e., meeting tributary goals) and nearly eliminated the risk of weak stock extirpation. We also found that harvest policies focused on meeting minimum subsistence needs were unlikely to jeopardize long-term prospects for basin-wide sustainable use. The fishery and biological performance of alternative harvest policies, and the magnitude of resulting trade-offs, were moderately sensitive to potential future changes in population productivity and capacity and to uncertainty in the underlying drivers of recruitment variation. Our approach provides a general framework for characterizing salmon population diversity in large river basins and evaluating harvest-population diversity trade-offs among alternative harvest policies within them.

## III. PROJECT EVALUATION:

---

Our original proposal had six objectives; a seventh objective was added in consultation with the AYK-SSI Science Coordinator as the project was being carried out. These objectives, and our progress towards meeting them, are described below.

**Objective 1:** To determine the shape of the relationship between spawner abundance and adult recruitment for each individual Chinook spawning population in the Kuskokwim watershed.

*We met this objective by developing an integrated age-structured multi-population state-space spawner-recruit model modelling framework that is described in detail in the manuscript in Appendix A. See Figure 5 in the manuscript for an illustration of the inferred shape of these relationships across a range of alternative model formulations. Simulation testing of the model illustrated the state-space model was largely unbiased with respect to leading parameters, abundance states, and derived biological reference points, whereas more commonly applied regression-based approaches showed substantial bias.*

**Objective 2:** To determine the predicted average annual fishery yield across all Kuskokwim Chinook populations - the sum of the equilibrium harvest that each population could sustain, and the proportion of populations that are predicted to not be overexploited - in order to evaluate the

tradeoff between harvest and conservation of population diversity across a range of mixed-population harvest rates.

*We met this objective as detailed in the manuscripts in Appendix A and B (see for example Figure 7 in Appendix A and Figure 3 in Appendix B).*

**Objective 3:** To determine the extent to which the erosion of population diversity resulting from overharvest of weak populations may limit long-term fishery yield under changing environmental conditions that might favor what are now weak populations over those that are currently strong.

*We met this objective by developing empirically parameterized closed-loop simulations of the Kuskokwim system where we evaluated the fishery and biological consequences of alternative harvest policies under a scenario with large future change in Chinook population diversity (i.e., weak populations became strong, and strong ones became weak). We found that when the environment drives pronounced shifts over time in the size and productivity of populations in the system (e.g., a regime shift) giving up a specific amount of harvest results in larger gains in spatial equity in access to the salmon for subsistence needs relative to scenarios where there is not a regime shift. These findings are described in detail in the manuscript in Appendix B.*

**Objective 4:** To determine both fishery manager and stakeholder perspectives on acceptable conservation constraints (i.e., which point[s] on the curve in Figure 1 is acceptable) and fishery objectives (e.g., minimize frequency of fishery closures) in order to inform the estimation of optimal harvest policies in objective 5.

*We met this objective by piggy backing on a broader exercise focused on building capacity among Kuskokwim stakeholders to engage in salmon management through a series of workshops with influential community members from throughout the river basin with a long history of active engagement in fishery management as well as US Fish and Wildlife Service and Alaska Department of Fish and Game biologists and fishery managers. These workshops included discussion of existing and potential Kuskokwim Chinook fishery and biological objectives and alternative management actions associated with them. From these discussions, we identified a suite of long-term objectives against which to quantify the performance of alternative management actions in the system. This is detailed in the manuscript in Appendix B.*

**Objective 5:** To determine optimal harvest policies for Kuskokwim Chinook based upon the magnitude of persistent productivity changes in Kuskokwim Chinook and the conservation constraints and fishery objectives from Objective 4.

*We met this objective by quantifying the performance of alternative harvest policies against objectives from Objective 4 using closed-loop simulations across a range of plausible hypotheses representing alternative states of nature. This is detailed in the manuscript in Appendix B. It is important to note however that our analysis do not identify an “optimal” strategy but instead help uncover trade-offs amongst objectives across a range of strategies.*

**Objective 6:** To determine the harvest and population diversity costs of assuming Kuskokwim Chinook recruitment is driven by (1) over-compensatory processes or (2) extrinsic environmental forcing when the alternative hypothesis is true.

*We fully met this objective by quantifying the performance of alternative harvest policies against the objectives from Objective 4 using closed-loop simulations for scenarios where recruitment is driven by either over-compensatory processes or extrinsic environmental forcing that gives rise to the appearance of overcompensation. We found that absolute harvest and its inter-annual stability were predicted to be lower, and that more harvest had to be foregone to minimize extirpation risk and increase chances of*

*ensuring equitable access to Chinook, under the extrinsic environmental forcing scenario relative to the over-compensatory one. These findings are detailed in the manuscript in Appendix B.*

**Objective 7:** To generate infographics that communicate key insights from the proposed research.

*We met this objective by developing a web-based tool that allow for interactive visualization of the conservation and fishery outcomes of our closed-loop simulations (see deliverables). In addition we generated numerous figures and visuals for the manuscripts and associated presentations that helped to communicate key insights from the proposed research (see figure in Appendix A, B and C).*

#### **IV. DELIVERABLES:**

---

The findings of our project have been, and will continue to be, disseminated via conference presentations, management meetings and peer-reviewed manuscripts. To date we have given six presentations and attended five meetings where we have presented and discussed our research. We anticipate submitting two manuscripts by the fall of 2019 and further refining the web visualization. Copies of presentations are available from the project PIs upon request.

##### **Presentations:**

Staton B., M. Catalano, B.M. Connors, L. Coggins, M. Jones, C. Walters, S. Fleischman and D. Gwinn.

2019. State-space models for estimating population diversity in mixed-stock Pacific salmon fisheries. American Fisheries Society Annual Meeting.

Staton B., M. Catalano, B.M. Connors, L. Coggins, M. Jones, C. Walters, S. Fleischman and D. Gwinn 2019.

Assessment approaches for mixed-stock Pacific salmon fisheries: Empirical and simulation-estimation applications. Auburn University; dissertation seminar

Connors B. M., L. Coggins, B. Staton, C. Walters, M. Jones, M. Catalano and J. Harding. 2018.

Incorporating harvest-population diversity tradeoffs into salmon management in large river basins: insights from Chinook in the Kuskokwim and Yukon River Basins. Western Division American Fisheries Society Meeting.

Connors B. M., L. Coggins, B. Staton, C. Walters, M. Jones, M. Catalano and J. Harding. 2018.

Incorporating harvest-population diversity tradeoffs into salmon management in large river basins: insights from Chinook in the Kuskokwim and Yukon River Basins. Institute of Ocean Sciences.

Staton B., M. Catalano, B.M. Connors, L. Coggins, M. Jones, C. Walters, S. Fleischman and D. Gwinn 2017.

Problems and solutions in the assessment of mixed-stock salmon fisheries. University of British Columbia.

Connors B. M., L. Coggins, B. Staton, C. Walters, and M. Jones. 2016. Incorporating harvest-population diversity trade-offs into salmon management. Canadian Conference for Fisheries Research.

Staton B., M. Catalano, B.M. Connors, L. Coggins, M. Jones, C. Walters, S. Fleischman and D. Gwinn 2016.

Estimation of stock-specific productivity to assess trade-offs in mixed-stock Pacific salmon fisheries. Alabama-Georgia joint American Fisheries Society Meeting.

##### **Draft manuscripts:**

Staton B., M. Catalano, B.M. Connors, L. Coggins, M. Jones, C. Walters, S. Fleischman and D.

Gwinn. In preparation. Evaluation of methods for quantifying population diversity in mixed-stock Pacific salmon fisheries.

Connors B. M., B. Staton, L. Coggins, C. Walters, M. Jones, D. Gwinn, M. Catalano and S. Fleischman. In preparation. Incorporating harvest-population diversity trade-offs into salmon management in large river basins: a case study of Kuskokwim River Chinook.

Final manuscripts will be provided to AYK-SSI once published.

#### **Online visualizations:**

An interactive online visualization of the results of the harvest policy analysis detailed in Appendix B can be found at:

<https://brendanmichaelconnors.shinyapps.io/kuskokwimShinyApp/>

These visualizations will continue to be developed until the manuscript they are associated with is published.

#### **Meetings:**

2015. National Fish and Wildlife Federation Capacity Building Workshop no. 1. Aniak, Alaska

2016. National Fish and Wildlife Federation Capacity Building Workshop no. 2. Anchorage/Bethel, Alaska

2016. National Fish and Wildlife Federation Capacity Building Workshop no. 3. Bethel, Alaska

2017. National Fish and Wildlife Federation Capacity Building Workshop no. 4. Bethel, Alaska

2017. Salmon Harvest Trade-offs workshop. Anchorage, Alaska

#### **Reports:**

Semiannual progress reports July 2015, January and July 2016, 2017, and 2018.

## **V. PROJECT DATA SUMMARY:**

---

The raw data used in the run-reconstructions and spawner-recruitment analyses described in Appendix A were sourced from the Alaska Department of Fish and Game. These data and source code for the analyses performed in Appendix A can be found in the html supplement provided with this report (Appendix\_A\_online\_supplement\_S2.4.html). Source code for the closed-loop simulations performed in Appendix B, can be found at: <https://github.com/brendanmichaelconnors/Kusko-harvest-diversity-tradeoffs>

Note that the source code for the manuscripts in Appendices A and B will continue to be refined until the manuscripts are published.

## **VI. APPENDICES:**

---

**Appendix A:** Evaluation of Methods for Quantifying Population Diversity in Mixed-stock Pacific Salmon Fisheries

**Appendix B:** Incorporating harvest-population diversity trade-offs into salmon management in large river basins: a case study of Kuskokwim River Chinook



---

# Evaluation of Methods for Quantifying Population Diversity in Mixed-stock Pacific Salmon Fisheries

---

**Benjamin A. Staton\***

School of Fisheries, Aquaculture, and Aquatic Sciences, Auburn University, 203 Swingle Hall, Auburn, AL 36849

Fishery Science Department, Columbia River Inter-Tribal Fish Commission, 700 NE Multnomah St., Ste. 1200, Portland, OR 97232, [bstaton@critfc.org](mailto:bstaton@critfc.org)

**Matthew J. Catalano**

School of Fisheries, Aquaculture, and Aquatic Sciences, Auburn University, 203 Swingle Hall, Auburn, AL 36849, [mjc0028@auburn.edu](mailto:mjc0028@auburn.edu)

**Brendan M. Connors**

Institute of Ocean Sciences, Fisheries and Oceans Canada, 9860 W Saanich Rd., Sidney, BC V8L 5T5, [brendan.connors@dfo-mpo.gc.ca](mailto:brendan.connors@dfo-mpo.gc.ca)

**Lewis G. Coggins, Jr.**

Yukon Delta National Wildlife Refuge, U.S. Fish and Wildlife Service, P.O. Box 346, Bethel, AK 99559, [lewis\\_coggins@fws.gov](mailto:lewis_coggins@fws.gov)

**Michael L. Jones**

Quantitative Fisheries Center, Department of Fisheries and Wildlife, 480 Wilson Rd., Michigan State University, East Lansing, MI 48824, [jonesm30@msu.edu](mailto:jonesm30@msu.edu)

**Carl J. Walters**

Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, BC V6T1Z4, [c.walters@oceans.ubc.ca](mailto:c.walters@oceans.ubc.ca)

**Steven J. Fleischman**

*How to list Affiliation*, [sjfleischman2@gmail.com](mailto:sjfleischman2@gmail.com)

**Daniel C. Gwinn**

Biometric Research LLC, South Fremantle, Western Australia, Australia, [dgwinnbr@gmail.com](mailto:dgwinnbr@gmail.com)

**Keywords:** mixed-stock fisheries, Pacific salmon, state-space models, Bayesian inference

**\*Corresponding Author:**

Benjamin A. Staton, [bstaton@critfc.org](mailto:bstaton@critfc.org), (503) 731-1284  
700 NE Multnomah St., Ste. 1200, Portland, OR 97232

# Abstract

Populations harvested in mixed-stock Pacific salmon fisheries show diversity in genotypic, behavioral, and life history characteristics which can lead to heterogeneity in productivity and population size. Methods to quantify this heterogeneity within mixed-stocks are not well-established but are required for full acknowledgement of trade-offs when setting harvest policies. We developed an integrated age-structured state-space model that allows for more complete use of available data and sharing of information than simpler methods. We developed a suite of state-space models of varying structural complexity for comparison to simpler regression-based approaches and fitted them to data from 13 Chinook Salmon populations in the Kuskokwim drainage in western Alaska. We found biological and policy conclusions were largely consistent between state-space models but differed strongly from regression-based approaches. Simulation trials illustrated our state-space models were largely unbiased with respect to leading parameters, abundance states, and derived biological reference points, whereas the regression-based approaches showed substantial bias. These findings suggest our state-space model shows promise for informing harvest policy evaluations in the context of harvest-biodiversity trade-offs in mixed-stock salmon fisheries.

# 1 Introduction

Many Pacific salmon *Oncorhynchus* spp. populations in large drainage systems are commonly harvested in a relatively small spatial area and are managed as a single stock. However, these “stocks” are instead stock-complexes, in which the aggregate stock is composed of several (and sometimes, many) substocks, hereafter referred to as “populations.” These populations can vary in genotypic (Templin et al. 2014), phenotypic (e.g., morphology; Hendry and Quinn 1997), behavioral (e.g., run timing; Clark et al. 2015; Smith and Liller 2017a,b), and life history (e.g., age-at-maturation, Blair et al. 1993) characteristics that are the result of adaptations to local environments after many generations of high spawning-site fidelity and reproductive isolation from conspecifics in other tributaries located within the same basin. It has been widely proposed that maintaining this diversity of local adaptation (hereafter, “biodiversity”) is favorable both from ecosystem and exploitation perspectives. One argument is that in a system where many parts contribute to the whole, the variability in the aggregate characteristics can be dampened due to asynchrony in the subcomponent dynamics, a phenomenon commonly referred to as the “portfolio effect” (Schindler et al. 2010, 2015).

Diversity in these population characteristics can ultimately lead to heterogeneity in their productivity (Walters and Martell 2004). Productivity in this context (hereafter,  $\alpha$ ) is the ability of a population to replace itself after harvesting or some other perturbation, often represented for salmon populations as the maximum number of future returning adults (recruits) produced by one spawner, which is attained at low spawner abundances due to density-dependent survival. Populations  $j$  with higher  $\alpha_j$  values can sustain greater exploitation rates ( $U$ ) than those with smaller  $\alpha_j$  values;  $\alpha_j$  can be expressed in terms of the exploitation rate that maximizes sustained yield from population  $j$  ( $U_{\text{MSY},j}$ ; Schnute and Kronlund 2002):

$$(1) \quad \alpha_j = \frac{e^{U_{\text{MSY},j}}}{1 - U_{\text{MSY},j}}.$$

Given that there is likely some level of heterogeneity in  $\alpha_j$  and  $U_{\text{MSY},j}$  among individual populations, the logical conclusion is that in a mixed-stock fishery where the exploitation rate in year  $t$  is common among all populations, some weaker populations must be exploited at  $U_t > U_{\text{MSY},j}$  in order to fish the more productive populations at  $U_{\text{MSY},j}$ . This of course implies a trade-off, such that it may be necessary to over-exploit some populations in order to maximize harvest benefits from others.

Before these trade-offs can be considered by managers in a well-informed way, the shape and magnitude of the trade-off must first be quantified. These trade-offs are typically expressed as the amount of mixed-stock harvest that must be foregone to reduce the number or fraction of populations at risk of overfishing or extirpation (Walters and Martell 2004; Walters et al. 2018). However, to conduct these assessments, the estimated productivity and carrying capacity of all (or a representative sample) of the populations contributing harvest to a mixed-stock fishery. Using a set of assumptions about the underlying population dynamics, these quantities are obtained via spawner-recruit analysis, which involves tracking the number of recruits produced in each brood year by the number of fish that spawned in that same year and fitting a curve to the resulting pattern. Other methods exist for obtaining estimates of population-level parameters, such as habitat-based methods (e.g., Lierman et al. 2010; Parken et al. 2006), but spawner-recruit analyses provide other information such as estimates of variability in recruitment anomalies and maturation schedules, which may be useful for forecasting (e.g., Murphy et al. 2017) or parameterizing operating models for use in closed-loop policy evaluations (e.g., Cunningham et al. 2018a; Catalano and Jones 2014; Connors et al. nd).

The spawner-recruit literature is extensive, but focuses primarily on assessing popu-

lations or stocks as a whole, as opposed to population components (but see the work on Skeena River, British Columbia sockeye salmon *O. nerka* populations; Korman and English 2013; Walters et al. 2008). Population-specific analyses are uncommon because of two factors: (1) the data to conduct well-informed population-specific spawner-recruit analyses are often unavailable (20 – 30 years of continuous spawner and harvest counts/estimates and age composition for each population) and (2) management actions in large mixed-stock fisheries may not be dexterous enough to deliberately exert higher exploitation rates on more productive populations even if the nature of the trade-off was known perfectly. Regarding the former reason, there are some cases where the data do exist to perform these kinds of analyses (e.g., the Kuskokwim River Chinook salmon *O. tshawytscha* stock in western Alaska is used here as case study), however methods to conduct mixed-stock spawner-recruit analyses are not well-developed. Regarding the latter, even in cases where management cannot target particular populations over others, understanding the nature of the trade-offs can be informative for evaluating candidate harvest policies for the mixed-stock in the context of population biodiversity (Walters et al. 2018).

Methods to fit spawner-recruit models can be grouped into two broad categories: regression-based approaches (e.g., Clark et al. 2009) and state-space (i.e., time series) models (e.g., Fleischman et al. 2013; Su and Peterman 2012). The regression-based approaches treat spawner-recruit pairs as independent observations, and are thus subject to the pitfalls of dealing with the inherent time-dependent properties and oftentimes large amounts of observation error found in spawner-recruit data sets (Walters and Martell 2004, Ch. 7). The consequence of ignoring the first issue is “time-series bias”, which causes positive biases in  $\alpha$  and negative biases in  $\beta$ , resulting in the same directional biases in  $U_{\text{MSY}}$  and  $S_{\text{MSY}}$ , respectively (i.e., spuriously providing too aggressive harvest policy recommendations; Walters 1985). The second is known as “errors-in-variables bias” and is known to cause an apparent scatter which inserts additional variability that commonly used regression estimators do not account for and can also lead to positive biases in  $\alpha$  (Ludwig and Walters 1981). Though



these methods have been known for their problems for over 30 years, they are still somewhat widely used (e.g., Clark et al. 2009; Korman and English 2013). Unlike the regression-based approaches, the state-space class of models attempts to capture the process of recruitment events leading to future spawners while simultaneously accounting for variability in the biological and measurement processes that gave rise to the observed data (de Valpine and Hastings 2002; Fleischman et al. 2013). For these reasons, state-space spawner-recruit analyses have rapidly gained popularity, particularly in Alaska (Fleischman et al. 2013; Staton et al. 2017; Su and Peterman 2012). This level of additional model complexity comes at computational costs, as these models are well-suited for Bayesian inference with Markov Chain Monte Carlo (MCMC) methods (Newman et al. 2014, Ch. 4), but have been shown to reduce bias in estimates in some circumstances relative to regression-based approaches (Su and Peterman 2012; Walters and Martell 2004).

In cases where data are available to perform mixed-stock spawner-recruit analyses on a population-specific basis, it is difficult to know which assessment method is most appropriate. Two prevalent issues arise which may benefit from the development of a mixed-stock state-space spawner-recruit model that simultaneously estimates population dynamics parameters, recruitment states, and biological reference points on a single population and aggregate mixed-stock basis. First, reconstructing population-specific recruitment time series is difficult without genetic stock identification (Cunningham et al. 2018b; Michielsens and Cave 2018; Beacham et al. 2004) of the populations contributing to in the mixed-stock harvest, because they are otherwise assessed primarily in aggregate. This situation requires assumptions about the relative exploitation rates experienced by each population, and an approach that integrates the population-specific dynamics into one model can provide flexibility and transparency in how these simplifications are made. Second, available population-specific data are generally escapement time series, whether they are censuses, indices, or estimates. In cases where reasonably long time series (20+ years) are available for a significant portion (>50%) of the populations in a mixed-stock, it is common to have non-contiguous sampling

data. An additional benefit of integrating the analysis in a time series framework may be the ability to share information between populations by exploiting patterns in their recruitment covariance. Inappropriate treatment of either factor may render the final estimates of population parameters inappropriate for management use, thus the sensitivity and performance of a variety of approaches should be assessed, including an integrated state-space model.

In this article, we evaluate the performance of a range of assessment models for mixed-stock salmon fisheries via simulation-estimation and apply them to Chinook salmon populations in the Kuskokwim River in western Alaska as a case study. Our objectives were to:

- (1) develop a set of varyingly complex mixed-stock versions of state-space spawner-recruit models,
- (2) determine the sensitivity of biological and trade-off conclusions to assessment model complexity (including those obtained using regression-based approaches) using empirical data from Kuskokwim River Chinook salmon populations, and
- (3) test the performance of the assessment models via simulation-estimation trials.

## 2 Methods

We conducted our analysis in two parts to evaluate the sensitivity and performance of assessment strategies for the mixed-stock Pacific salmon fisheries. First, all assessment methods (two regression-based and four state-space models) were fitted to observed data from the Kuskokwim River populations ( $n_j = 13$ ) to determine the extent to which the choice of assessment model structure influences biological and management conclusions with real data. Next, a hypothetical salmon system composed of several age-structured populations and with known properties, subjected to observation with error and inconsistent sampling

frequencies, and then all models were fitted to each simulated data set. Lastly, we quantified model performance based on the bias and precision of quantities with relevance to mixed harvest management (e.g.,  $U_{\text{MSY}}$  and  $S_{\text{MSY}}$ ).

## 2.1 Mixed-stock spawner-recruit models

### 2.1.1 Regression-based models

Two regression-based approaches for estimating Ricker (1954) spawner-recruit parameters on a population-specific basis were assessed: (a) a single mixed-effect regression model with random intercepts (also referred to as a hierarchical model) and (b) independent regression models. The Ricker spawner-recruit model can be written as:

$$(2) \quad R_y = \alpha S_y e^{-\beta S_y + \varepsilon_y}$$

where  $R_y$  is the total recruitment produced by escapement  $S_y$  in brood year  $y$ ,  $\alpha$  is the maximum expected recruits per spawner (RPS),  $\beta$  is the inverse of the escapement that is expected to produce maximum recruitment ( $S_{\text{MAX}}$ ), and  $\varepsilon_y$  are mean zero deviations from the expected curve often assumed to be attributed to environmentally driven fluctuations in juvenile survival. Primary interest lies in estimating the population dynamics parameters  $\alpha$  and  $\beta$  as they can be used to obtain biological reference points from which sustainable harvest policies can be developed. The Ricker function in (2) is increasing at small escapements and declining at large ones, and it can be linearized:

$$(3) \quad \log_e(\text{RPS}_y) = \log_e(\alpha) - \beta S_y + \varepsilon_y,$$

allowing for estimation of the parameters  $\log_e(\alpha)$  and  $\beta$  in a linear regression framework using the least squares method or likelihood methods under the assumption that  $\varepsilon_y \sim N(0, \sigma_R^2)$  (Clark et al. 2009; Hilborn and Walters 1992). This relationship is nearly always declining, implying a compensatory effect on juvenile survival (i.e., RPS) with reductions in spawner abundance (Rose et al. 2001). Obtaining the  $R_y$  component of  $RPS_y$  can be problematic for salmon populations that mature at multiple ages (like Chinook salmon, for which we have incorporated ages four to seven) given the prevalence of non-consecutive sampling years of either age composition or escapement data. For fitting regression models, only brood year recruitment events were used in which all contributing ages were observed. For example, to include brood year recruitment for 2010 in the model, escapement data must have been available for calendar years 2014 – 2017, as well as in 2010 to complete the pair.

A mixed-stock formulation of this model can be expressed by including population-specific random effects on the intercept  $[\log_e(\alpha)]$ :

$$\begin{aligned}
 \log_e(RPS_{y,j}) &= \log_e(\alpha_j) - \beta_j S_{y,j} + \varepsilon_y, \\
 \log_e(\alpha_j) &= \log_e(\alpha) + \varepsilon_{\alpha,j}, \\
 \varepsilon_{\alpha,j} &\sim N(0, \sigma_\alpha^2).
 \end{aligned}
 \tag{4}$$

It would be nonsensical to include population-level random effects on the slope, given that  $\beta$  is a capacity parameter related to the compensatory effect of habitat and resource limitation experienced by juveniles, likely in the freshwater environment (i.e., amount of habitat as opposed to quality of habitat). Fitting the individual population models in this hierarchical fashion allows for the sharing of information such that the more intensively assessed populations can help inform those that are more data-poor.

The mixed-effect model may have the benefit of sharing information to make some populations more estimable, but it should also have the tendency to pull the extreme  $\alpha_j$

(those in the tails of the hyperdistribution) toward  $\alpha$ . This behavior may not be preferable for policy recommendations, as it should tend to dampen the extent of heterogeneity estimated in  $\alpha_j$ . For this reason, independent regression estimates for each population were also obtained for evaluation. In estimating the parameter  $\log_e(\alpha)$ , a lower bound constraint of zero was used in all regression models. This was necessary to prevent the models from estimating biologically implausible parameters: if  $\log_e(\alpha) < 0$ , then no amount of spawners would be expected to replace themselves (let alone provide surplus) in their most productive state, in which case the population would not likely be in existence.

### 2.1.2 State-space models

We developed four versions of the state-space formulation. As three versions were simplifications of a more full model, the full model is presented completely here and the changes resulting in the other three model structures are described following the description of the full model.

The state-space formulation of the mixed-stock spawner-recruit analysis developed and evaluated here is an extension of various single-stock versions (e.g., Fleischman et al. 2013). Walters et al. (2008) used a similar model using maximum likelihood methods to provide estimates of >50 populations in the Skeena River drainage, British Columbia. The model presented here was fitted with Bayesian methods using program JAGS (Plummer 2017), and allows for relaxation of certain assumptions made by Walters et al. (2008) such as the important notion of all populations having the same recruitment residual time series (i.e., anomalies – deviations from the expected population response).

The state-space model is partitioned into two submodels: (a) the process submodel which generates the latent (i.e., true but unobserved) states of  $R_{y,j}$  and the resulting calendar year states (e.g.,  $S_{t,j}$ ) and (b) the observation submodel which fits the latent states to the observed data (notation summarized in Tables 1, 2). Note that this method does not require



206 excluding brood year recruitment events that were not fully observed as was necessary for  
 207 the regression-based models.

208 The recruitment process operated by producing a mean prediction from the deterministic  
 209 portion of the Ricker relationship in (2) for  $n_y$  brood years for each of the  $n_j$  populations.  
 210 From these deterministic predictions, auto-correlated process variability was added to generate  
 211 the realized latent recruitment states. To populate the first  $n_a$  calendar year abundance  
 212 states with recruits of each age  $a$ , the first  $a_{max}$  brood year expected recruitment states  
 213 were not linked to a spawner abundance through (2) (because the  $S_y$  component was not  
 214 observed), but instead were assumed to have a constant mean equal to the unfished equilibrium  
 215 recruitment (where non-zero  $S_j$  produces  $R_j = S_j$  when unexploited and in the absence of  
 216 process variability):

$$(5) \quad \dot{R}_{y,j} = \frac{\log_e(\alpha_j)}{\beta_j},$$

217 where  $\dot{R}_{y,j}$  is the expected (i.e., deterministic) recruitment in brood year  $y$  from population  
 218  $j$  with Ricker parameters  $\alpha_j$  and  $\beta_j$ . The remaining  $n_y - a_{max}$  brood years had an explicit  
 219 time linkage:

$$(6) \quad \dot{R}_{y,j} = \alpha_j S_{t,j} e^{-\beta_j S_{t,j}},$$

220 where  $t = y - a_{max}$  is the  $t^{\text{th}}$  calendar year index in which the escapement produced the  
 221 recruits in the  $y^{\text{th}}$  brood year index.

222 From these deterministic predictions of the biological recruitment process, lag-1 auto-  
 223 correlated process errors were added to produce the latent states:

$$(7) \quad \log_e(R_{y,1:n_j}) \sim \text{MVN}(\log_e(\dot{R}_{y,1:n_j}) + \omega_{y,1:n_j}, \Sigma_R),$$

224 where

$$(8) \quad \omega_{y,1:n_j} = \phi \left( \log_e(R_{y-1,1:n_j}) - \log_e(\dot{R}_{y-1,1:n_j}) \right),$$

225 and  $R_{y,1:n_j}$  is the vector of latent recruitment states across the  $n_j$  stocks in brood year  $y$ ,  
 226  $\omega_{y,1:n_j}$  is the portion of the total process error attributable to serial auto-correlation,  $\phi$  is  
 227 the lag-1 auto-correlation coefficient (constant across populations), and  $\Sigma_R$  is a covariance  
 228 matrix representing the white noise portion of the total recruitment process variance. In the  
 229 full model,  $\Sigma_R$  was estimated such that each population was assigned a unique variance and  
 230 covariance with each other population. This was achieved by using an inverse Wishart prior  
 231 distribution, with degrees of freedom equal to  $n_j + 1$  and the scale matrix populated with  
 232 zero-value elements along the off-diagonals and each diagonal element equal to one, which  
 233 inserts little information about the covariance matrix  $\Sigma_R$  (Plummer 2017). The multivariate  
 234 normal errors were on the logarithmic scale so the variability on  $R_{y,j}$  was lognormal, which  
 235 is the most commonly used distribution for describing recruitment variability (Walters and  
 236 Martell 2004). Further, the multivariate normal was used as opposed to  $n_j$  separate normal  
 237 distributions so the degree of synchrony in brood year recruitment deviations (i.e., recruitment  
 238 process errors) among populations could be captured and freely estimated in  $\Sigma_R$ .

239 The maturity schedule is an important component of age-structured spawner-recruit  
 240 models, as it determines which calendar years the brood year recruits  $R_{y,j}$  return to spawn  
 241 (and be observed). Recent state-space spawner-recruit analyses have accounted for brood  
 242 year variability in maturity schedules as Dirichlet random vectors drawn from a common

hyperdistribution characterized by a mean maturation-at-age probability vector ( $\pi_{1:n_a}$ ) and an inverse dispersion parameter ( $D$ ) (see Fleischman et al. 2013; Staton et al. 2017, for implementation in JAGS), and the same approach was used for the full model with maturity schedules shared perfectly among populations within a brood year. Brood year-specific maturity schedules were treated as random variables such that:

$$(9) \quad p_{y,a} \stackrel{\text{iid}}{\sim} \text{Dirichlet}(\pi_{1:n_a} \cdot D).$$

where  $p_{y,a}$  is the probability a fish spawned in brood year  $y$  will mature and make the spawning migration at age  $a$ .

In order to link  $R_{y,j}$  with calendar year observations of escapement from each population,  $R_{y,j}$  was allocated to calendar year runs-at-age ( $N_{t,a,j}$ ) based on the maturity schedule:

$$(10) \quad N_{t,a,j} = R_{t+n_a-a,j} p_{t+n_a-a,a},$$

and the total run returning to population  $j$  in year  $t$  was the sum of mature fish within a calendar year across ages:

$$(11) \quad N_{t,j} = \sum_{a=1}^{n_a} N_{t,a,j}.$$

The harvest process was modeled using a freely estimated annual exploitation rate ( $U_t$ ) time series, which was assumed to apply equally to all populations (but see Section 2.2.3 for a relaxation of this assumption):

$$(12) \quad H_{t,j} = N_{t,j}U_t,$$

257 and escapement was obtained as:

$$(13) \quad S_{t,j} = N_{t,j}(1 - U_t).$$

258 The quantity  $H_t$  (mixed-stock harvest) was obtained by summing  $H_{t,j}$  within a  $t$  index  
 259 across the  $j$  indices. The true age composition returning in year  $t$  to population  $j$  ( $q_{t,a,j}$ ) was  
 260 obtained as:

$$(14) \quad q_{t,a,j} = \frac{N_{t,a,j}}{N_{t,j}}.$$

261 Three data sources were used to fit the state-space model: (a) observed escapement  
 262 from each population ( $S_{obs,t,j}$ ) with assumed known coefficients of variation (CV), (b) total  
 263 harvest arising from the aggregate stock ( $H_{obs,t}$ ) with assumed known CV, and (c) the age  
 264 composition of populations with these data each calendar year ( $q_{obs,t,a,j}$ ; which had associated  
 265 effective sample size  $ESS_{t,j}$  equal to the number of fish successfully aged for population  $j$  in  
 266 year  $t$ ). The CVs were converted to lognormal variances:

$$(15) \quad \sigma_{\log}^2 = \log_e(\text{CV}^2 + 1),$$

267 and used in lognormal likelihoods to fit the time series  $S_{t,j}$  to  $S_{obs,t,j}$  and  $H_t$  to  $H_{obs,t}$ . Calendar

year age composition was fitted using independent multinomial likelihoods with parameter vectors  $q_{t,1:n_a,j}$  and observed vectors of  $(q_{obs,t,1:n_a,j} \cdot ESS_{t,j})$ .

Three alternative formulations of the state-space model were evaluated, and all were simplifications of the full model described above regarding the structure of (a) the covariance matrix on recruitment residuals ( $\Sigma_R$ ) and (b) the maturity process (see Table 3 for a summary of the models fitted in this analysis). The simplest state-space model did not include brood year variability in maturity schedules and  $\Sigma_R$  was constructed by estimating a single  $\sigma_R^2$  and  $\rho$  (common across all populations and population pairs) and populating the diagonal elements with  $\sigma_R^2$  and off-diagonal elements with  $\rho\sigma_R^2$ . This simplest model is denoted as SSM-vm (lower case letters indicate simple versions; v = recruitment covariance; m = maturity variability). In one intermediate model (SSM-vM), brood year maturation variability was included but  $\Sigma_R$  was constructed as in the simplest model. In the other intermediate model (SSM-Vm), brood year variability in maturation was not included but  $\Sigma_R$  was fully estimated as in the full model (SSM-VM). These two structural uncertainties (complexity in recruitment covariance and maturity variability) were chosen for evaluation here because they are two key areas where an analyst might question if the available data are adequate for model fitting and inference. In other words, these are two key model components where it may be important to know if the complex versions are reliably estimable with a reasonable amount of data.

## 2.2 Kuskokwim empirical analysis

### 2.2.1 Study system

All six assessment models (two regression-based and four state-space models) evaluated were fitted to empirical data from Chinook salmon populations of the Kuskokwim River located in western Alaska (Figure 2). The Kuskokwim River is one of the largest subsistence salmon fisheries in the state, and the largest for Chinook salmon (Fall et al. 2018). Commercial harvests have been historically important to the region, but have not been directed toward



Chinook salmon since 1984. The fishery can very well be described as operating on a mixed-stock, both for multiple salmon species (predominately Chinook, chum *O. keta*, and sockeye salmon) and for multiple populations of the same species. Rigorous monitoring of harvest, escapement, and age composition for Chinook salmon began in the mid-1970s with efforts expanding significantly in the early-1990s and 2000s (Figure 1). Approximately 90% of the subsistence salmon harvest in the drainage occurs in the main-stem Kuskokwim River using primarily drift gillnet gear, downstream of the confluence with the Aniak River (Hamazaki 2011). Migrating adult fish originating from and returning to the various tributaries (of which there are at least 20 that support salmon; Figure 2) enter through this bulk of the fishery as a mixed-stock: first Chinook in early June, then chum and sockeye later in June and July but with substantial overlap in entry timing. Chinook salmon stocks migrating to the headwaters have been illustrated to enter the main-stem earliest in the summer migration (Smith and Liller 2017a,b) so a limited ability to direct harvest toward or away from these populations may exist by manipulating the front portion of the fishery. It is acknowledged that the assessment program does not sample all tributaries within the Kuskokwim River where Chinook salmon spawn (Figure 2), but total run size between 1976 and 2017 has been estimated via run reconstruction (Liller et al. 2018) and large-scale mark-recapture studies (Schaberg et al. 2012; Smith and Liller 2017a,b; Stuby 2007).

### 2.2.2 Data sources

The data set used included counts of Chinook salmon at many locations throughout the Kuskokwim River drainage (Figure 2). Nearly all data were collected by projects managed by the Alaska Department of Fish and Game (ADF&G) and a complete description of data needs and preparation procedures is provided in Online Supplement S1. The raw escapement data set spanned 20 different escapement monitoring projects (six weirs and 14 aerial surveys) and 42 calendar years from 1976 – 2017; see Head and Smith (2018) for details on tributary escapement monitoring. Some pre-processing was required to convert the aerial survey

index counts to estimates of total escapement so that abundance-based reference points could be calculated. Annual estimates of Chinook salmon harvest originating from both subsistence and commercial fisheries in each year was also available, as were the estimated exploitation rates of the aggregate stock. Finally, age composition data were available for the six populations monitored via weir programs (complete details on data processing are provided in Online Supplement S1).

### 2.2.3 Sensitivity Analyses

Two analyses were conducted to test the sensitivity of inference from state-space models fitted to Kuskokwim data. First, the default assumption that all populations have been fished at the same rate each year is tenuous. We therefore included a term in the model that allowed for populations to have differential vulnerability to harvest ( $v_j$ ) by replacing  $U_t$  with  $U_t v_j$  in (12) and (13) which allowed acknowledgement of heterogeneous exploitation rates. This alteration changes the interpretation of the parameter vector  $U_t$  to be the exploitation rate of fully vulnerable populations. Without additional information on what portion of  $H_{obs,t}$  was attributable to each population going back in time, the  $v_j$  elements are not estimable. In the absence of this information for Kuskokwim River Chinook salmon,  $v_j$  was assigned by calculating the fraction of the fishing households residing along the main-stem of the river that each population must travel past in order to reach their natal spawning grounds. Fishing household data were available from post-season interviews conducted by ADF&G (e.g., Hamazaki 2011; Shelden et al. 2016). Although this method ignores the temporal overlap of the fishery (Hamazaki 2008) with the arrival timing of particular population groups (Smith and Liller 2017a,b), it was intended as a first step at determining how much the conclusions might depend on how the internal harvest accounting was specified. No attempt was made to alter how harvest was apportioned for use in the regression-based models.

As a secondary sensitivity analysis, the information content of the age composition data was reduced. In the default case, each annual multinomial age composition vector had sample

size equal to the number of fish successfully aged for that population/year combination. For some populations/years, this number was quite high from a multinomial sampling perspective when the number of categories is small (e.g.,  $\approx 1,200$  samples across four age categories). To assess whether this strength of information had an impact on the inference, the effective sample size was manipulated such that the maximum number of fish sampled for a population was assigned  $ESS_{t,j} = 100$ , and the other years with data were scaled proportionately.

#### 2.2.4 Comparisons of model output

Key population dynamics parameters and biological reference points were compared among the six assessment models wherever possible to determine the extent to which the management conclusions for Kuskokwim River Chinook salmon populations might change based on the model structure used. Where appropriate, quantities were averaged across populations to facilitate comparisons and included indicators of the average population's productivity ( $\bar{U}_{MSY,j}$ ; the "bar" denotes average across populations) and size ( $\bar{S}_{eq,j}$  and  $\bar{S}_{MSY,j}$ ). Reference points for the aggregate mixed-stock included  $U_{MSY}$  and  $S_{MSY}$ .

Model fits to the data ( $S_{obs,t,s}$ ,  $H_{obs,t}$ , and  $q_{obs,t,a,j}$ ) were examined for all state-space models and noteworthy differences among model structures were identified. Estimates of synchrony in recruitment anomalies were examined, both between two average populations ( $\bar{\rho}_{i,j}$ ), and among all population pairs. For the simple recruitment variance models (SSM-vm and SSM-vM), correlations between each population pair were conducted by applying Pearson's  $r$  coefficient to two populations' estimated recruitment anomaly time series; in the complex variance models these correlations were captured in the freely estimated covariance matrix ( $\Sigma_R$ ), and they were extracted and summarized. Although the state-space models were ignorant of spatial relationships among the populations, visual comparisons were made to determine if populations closer in proximity showed higher synchrony than those spaced more distantly, as might be expected. The auto-correlation parameter ( $\phi$ ) and characteristics of the maturity schedules ( $\pi_a$  and  $D$ ) were also compared among state-space models.

Harvest-biodiversity trade-offs were assessed visually using estimated equilibrium mixed-stock states and metrics of biodiversity. First, the equilibrium escapement and harvest were calculated (Schnute and Kronlund 2002) for each population at each level of an exploitation rate that affected all populations equally, then summed to obtain the mixed-stock expected states at each level. The fraction of populations overfished and trending towards extirpation (defined as the case where equilibrium  $S_j \leq 0$ ) were also calculated. Some populations could not be fitted using the regression approach because they had fewer than three observed pairs of  $RPS_{y,j}$ . When comparing quantities to the estimates from the state-space models, the populations that could not be fitted with regression approaches were removed from state-space model outputs.

### 2.3 Simulation-estimation trials

To test the performance of these models, we simulated 160 data sets designed to mimic the Kuskokwim River empirical data set. Each of the 160 data sets were passed to each of the six assessment models to evaluate which methods return estimates closest to the true parameters.

Given that the state-space model is a much more natural model of this system (which has intrinsic time series properties) than the regression-based versions, it was used as the foundation of the operating model (i.e., state-generating model). The biological submodel was more complex than the most complex estimation model – namely with regards to the maturity schedule, which had a modest level of population variability in mean maturity but with highly correlated brood year variability. In order to serve as the state-generating model for the simulation, the state-space model needed only to be populated with true parameters, initial states, and a harvest control rule. A fixed exploitation rate policy was used (chosen to maximize yield without overfishing more than 30% of the populations) with a modest amount of implementation error to ensure the escapement data time series were generated with contrast.  $n_j = 13$  populations were simulated with different parameters  $U_{MSY,j}$  and  $S_{MSY,j}$  which took on the values of random posterior draws from the most complex

state-space model fitted to the Kuskokwim River Chinook salmon population data. All other parameters were chosen to mimic the estimated values from the Kuskokwim analysis, with the exception of  $\Sigma_R$ , which was set to have a modest amount of population recruitment variability ( $\bar{\sigma}_{j,j} \approx 0.4$ );  $\rho_{i,j}$  for each pair of populations was simulated randomly to be between -1 and 1, but approximately zero when averaged across all populations.

For a given set of simulated true states, a set of observed states ( $S_{obs,t,j}$ ,  $H_{obs,t}$ ,  $q_{obs,t,a,j}$ ) was generated by adding sampling error to each year following a fifty year “burn-in” period of the harvest policy into the population dynamics. This was intentionally done to violate the assumption made by the state-space estimation model that sampling was initiated under unfished conditions, as shown in (5). Sampling errors in escapement and harvest estimates were generated with lognormal variability and multinomial sampling for the age composition, as assumed in the state-space estimation model. Frequency of sampling on each population was set to approximately mimic the Kuskokwim River historical monitoring program (Figure 1). The sampling frequency was designed to continue to generate random sampling schedules until one was found that ensured no population had fewer than three observations of  $RPS_{y,j}$  which allowed the regression-based models to be fitted to all populations. Aggregate harvest data ( $H_{obs,t}$ ) were assumed to be available every year as were annual estimates of the mixed-stock exploitation rate.

Estimation performance in terms of accuracy among assessment models was calculated using the proportional error ( $\frac{x_{est} - x_{true}}{x_{true}}$ ). Key quantities of interest for comparison between the regression approaches and the state-space models included:  $S_{MSY}$ ,  $U_{MSY}$ ,  $\alpha_j$ ,  $U_{MSY,j}$ , and  $S_{MSY,j}$ , as well as two metrics that incorporate population biodiversity considerations:  $S_p^*$  and  $U_p^*$ . These quantities represent the equilibrium mixed-stock escapement or exploitation rate, respectively, that would result in no more than  $p \cdot 100\%$  of populations expected to be overfished. “Overfished” is defined here as the case where a population would be fished at  $U > U_{MSY,j}$ . Three levels of  $p$  were extracted: 0.1, 0.3, and 0.5. For the state-space models, the ability to accurately estimate the abundance states of  $R_{y,j}$ ,  $S_{t,j}$ , and  $H_t$  was also

assessed, summarized for early years and all years separately to investigate the influence of the assumption that the observation time series began at unfished equilibrium, as described by (5). Coverage of the 95% equal-tailed credible interval was assessed for these quantities by determining the fraction of obtained credible intervals that captured true values. Additionally, model run times and convergence diagnostics were summarized for all models that were successfully fitted to the simulated data sets.

## 2.4 Computation

All parameter estimation was conducted in the Bayesian framework using the MCMC engine JAGS (Plummer 2017) invoked through R (R Core Team 2018) using the package “jagsUI” (Kellner 2017). All priors for the regression-based methods were uniform and sufficiently non-informative to exclude only highly implausible values (e.g.,  $\log_e(\alpha_j) \sim U(0, 5)$ ). Priors were selected with the same intent for state-space models, though other distributional forms were required in some cases (Table 4).

MCMC sampling was conducted using sufficiently long chains (Table 5) to ensure adequate sampling of the posterior parameter space for inference and was assessed using visual inspection of MCMC sampling behavior and the convergence diagnostic proposed by Brooks and Gelman (1998). Adequate sampling was further verified for key estimated quantities using the effective sample size and the Raftery-Lewis diagnostic (Raftery and Lewis 1992). All posterior distributions were summarized using the median and 95% equal-tailed credible intervals. In all cases where a quantity was derived from estimated parameters, (e.g.,  $S_p^*$ ), the calculation was conducted for each sample from the joint posterior, then the resulting marginal posterior was summarized, which proved to be a straightforward approach to carry the uncertainty forward from the model estimates to other quantities of interest. All code for simulation, JAGS models, data processing, making use of High Performance Computing resources, and output summarization is documented in Staton (YYYY; *a Github repository that stores code and data, will have a DOI associated with it*).

## 3 Results

### 3.1 Kuskokwim River empirical analysis

#### 3.1.1 State-space models fit to data

The four state-space models produced generally similar latent escapement state time series, especially in years with observed escapement data (Figure 3). For several populations, there were no escapement data prior to the mid-1990s, and this is one area the various state-space models produced different escapement estimates. In this early portion of the time series, models with brood year variability in maturity (SSM-vM and SSM-VM) tended to estimate higher escapement abundance than the models with time-constant maturity (SSM-vm and SSM-Vm). For example, populations spawning in the Kwethluk, George, Holokuk, and Takotna rivers all showed this pattern (Figure 3).

There were several cases where extremely high (and seemingly unrealistic) escapement states were estimated by the state-space model, though these only occurred in models with simple maturation schedules (Figure 3). The period in the late-1980s and the early 1990s had much (i.e., 5 – 10 times) higher estimated escapement than ever observed for the Holitna, Pitka, and Tatlawiksuk populations under either models SSM-vm or SSM-Vm. The George River population had abnormally large escapements in the mid-1990s, and was again most exaggerated for the SSM-vm and SSM-Vm versions. All of these cases occurred when no escapement data were available; in years with data all state-space models fitted the escapement data quite well (Figure 3).

In general, the fit to the aggregate harvest data was good, though the time-varying maturity schedule versions (SSM-vM and SSM-VM) fitted the data nearly perfectly. Constant maturity schedule models resulted in a harvest state that was greater than twice as large as the observed state in 1976 (the first observed year) but never showed discrepancies nearly this large for the rest of the time series. Additionally, the state-space models generally fitted

the age composition data well. The only differences among model structures came in the distinction of how maturity was treated. Complex maturity models tended to have better fit than simple maturity models for most populations and ages. Far more detailed model output and model fits from each of the state-space models can be found in the Online Supplements S2 – S5.

### 3.1.2 Comparisons of estimated spawner-recruit dynamics

There were large discrepancies in estimates of population productivity between the regression models and the state-space models. Both regression approaches suggested the maximum productivity of the average population ( $\bar{\alpha}_j$ ) was far higher than any of the state-space models. The independent regression approach provided an estimate of  $\bar{\alpha}_j = 7.74$  ( $4.47 - 20.22$ ; 95% credible limits) and the mixed-effect regression approach suggested  $\bar{\alpha}_j = 4.63$  ( $3.16 - 7.45$ ). Most state-space models suggested  $\bar{\alpha}_j < 3$ , with the highest upper 95% credible limit being 5.01, obtained by SSM-vM. These differences in estimated productivity translated directly to the maximum sustainable exploitation rate for the average population ( $\bar{U}_{\text{MSY},j}$ ; Figure 4a) and even more so for the mixed-stock ( $U_{\text{MSY}}$ ; Figure 4b). Among state-space models, those that included complex maturity variability tended to suggest the populations were more productive (Figure 4a,b). In comparing state-space model estimates from the 10 substocks able to be fitted with all methods to the complete set of 13 substocks, the average maximum sustainable exploitation rates were quite similar, indicating the stocks with insufficient data for regression were missing at random in this regard (Figure 4a,b; compare squares and circles).

One metric of substock size is the spawner abundance expected to exactly replace itself under unfished equilibrium conditions ( $S_{\text{eq},j}$ ). When averaged across substocks ( $\bar{S}_{\text{eq},j}$ ), the regression approaches suggested the Kuskokwim River substocks were approximately 2,500 fish (~25%) smaller than the state space models.  $\bar{S}_{\text{MSY},j}$  followed a similar pattern: smaller values for the regression approaches than the state-space models (Figure 4c). In



terms of the mixed-stock escapement expected to produce maximum sustained yield ( $S_{\text{MSY}}$ ), regression approaches suggested much smaller escapements were necessary than did state-space models; by a margin of 12,000 – 15,000 fish ( $\sim 25 - 50\%$ ; Figure 4d). State-space models with time-constant maturity had much greater uncertainty in  $\bar{S}_{\text{MSY},j}$  and  $S_{\text{MSY}}$  than the complex maturity models (Figure 4c,d). In comparing state-space model estimates from the 10 substocks able to be fitted with all methods to the complete set of 13 substocks, the average substock-specific escapement values were quite similar, indicating the stocks with insufficient data for regression were missing at random in this regard (Figure 4c; compare squares and circles). However, the mixed-stock  $S_{\text{MSY}}$  estimates were quite different between the 10 and 13 substock outputs (Figure 4d; compare squares and circles). It seems the three additional substocks (Holitna, Kisaralik, and Oskawalik) should make up approximately 25% of the escapement among the substocks included in this analysis if the management objective is to maximize long-term yield.

These similarities and differences in population size and productivity between approaches are well-illustrated at the population-level by visualizing the expected recruitment at each spawner abundance suggested by each model (Figure 5). It is evident that the four state-space models behaved similarly near the origin (which is governed by  $\alpha_j$ ), whereas in many cases the regression models suggested steeper slopes near the origin (corresponding to higher values of  $\alpha_j$ ). State-space models tended to disagree in expected recruitment more at larger spawner abundances (Figure 5), suggesting that inferences about stock size and the strength of compensation are dependent on the details of how recruitment variance and maturity are modeled for some substocks. The mixed-effect regression approach differed from the independent regression estimates the most for substocks with fewer observations due to shrinkage (e.g., Pitka versus Kogruklu; Figure 5).

In terms of recruitment variability, the regression-based approaches suggested that the average standard deviation of the lognormal distribution that describes randomness in the recruitment process ( $\bar{\sigma}_{R,j}$ ) was 0.78 and 0.52 for the independent and mixed-effects versions,

528 respectively (Figure 4e). The state-space models estimated that the average amount of  
529 recruitment process variability by substock was higher: point estimates ranged from 0.85 –  
530 1.11 (Figure 4e). The models with time-varying maturity had estimates on the lower end  
531 of this range, which could be explained by the inclusion of additional process variability in  
532 maturity that could describe variability in the data.

533 Unlike the regression models, the state-space models estimated the degree of covariance  
534 between substock recruitment residuals. All state-space models estimated a moderate amount  
535 of correlation in recruitment variance (i.e., synchrony) between two average substocks ( $\bar{\rho}_{i,j}$ ):  
536 point estimates ranged between 0.18 and 0.28, and none of the models suggested 95% credible  
537 limits that encompassed zero. The simple variance models (SSM-vm and SSM-vM) estimated  
538 a single correlation parameter, whereas the complex versions (SSM-Vm and SSM-VM)  
539 estimated a unique value for each substock combination. One might expect that substock  
540 pairs belonging in the same region to show higher degrees of synchrony than substock pairs  
541 in different regions, though this analysis suggested this was not necessarily the case (the  
542 state-space models did not take into account spatial relations among substocks). Large  
543 correlations (e.g.,  $>0.5$ ) were found between pairs of lower versus upper river substocks, lower  
544 versus lower, and upper versus upper substocks (Figure 6). Relatively few large correlations  
545 were found among middle river substocks with other substocks, though both SSM-Vm and  
546 SSM-VM suggested that the Holokuk and Oskawalik substocks have highly synchronous  
547 recruitment dynamics, which is interesting given their close proximity (Figure 2; substocks #5  
548 and #6, respectively). Conversely, all models suggested the Holitna and Kogrukluk substocks  
549 have little synchrony, and they fall within the same subdrainage (Figure 2; substocks #7  
550 and #8, respectively). Most correlations were positive, especially those that were large  
551 in magnitude (Figure 6). A notable exception was the correlation between the Kisaralik  
552 substock and the Holokuk and Oskawalik substocks: their dynamics were suggested to be  
553 largely opposite.

### 3.1.3 Trade-off comparisons

With increasing mixed-stock exploitation rates, the equilibrium mixed-stock escapement declined, but did so more rapidly for the state-space models than the regression models (Figure 7). State-space models that included time-varying maturity suggested higher equilibrium escapement and harvest would be available at most exploitation rates than models with time-constant maturity. Regression models suggested that MSY was much larger and occurred at a higher exploitation rate than for the state-space models, as would be expected based on comparing the estimated biological reference points between these methods (Figure 4). In terms of substock diversity, the time-varying maturity models suggested fewer substocks would be overfished or trending towards extirpation at low exploitation rates than the time-constant maturity models, and the regression approaches suggested even more biologically optimistic conclusions (Figure 7).

### 3.1.4 Sensitivity analyses

The alternative vulnerability schedule ( $v_j$ ) based on the spatial distribution of fishing households resulted in lower river substocks (those spawning in the Kwethluk, Kisaralik, and Tuluksak rivers) having the lowest  $v_j$  ranging between 0.7 – 0.8, the middle river substocks ranging between 0.9 and 0.95, and those in the upper river between 0.95 and 1. When these  $v_j$  terms were incorporated in the state-space models, most changes in substock specific  $U_{\text{MSY},j}$  and  $S_{\text{eq},j}$  were small ( $\pm 10\%$ , range:  $-20\% - 30\%$ ), and most (eight of 13) substocks showed increases in  $U_{\text{MSY},j}$ . Changes in  $U_{\text{MSY},j}$  occurred randomly with respect to changes in vulnerability: some substocks in the three regions showed both increases and decreases. Changes with respect to substock size ( $S_{\text{eq},j}$ ) showed more of a pattern: lower river substocks (i.e., those that became less vulnerable in this sensitivity analysis) tended to become smaller by 5 – 15%, whereas upper river substocks showed increases of 5 – 25%. Middle river substocks showed a mix of increases and decreases in  $S_{\text{eq},j}$ . Despite these changes in substock-specific

estimates, derived biological reference points for the aggregate mixed-stock showed a high degree of similarity: escapement-related quantities were  $\sim 3,000$  fish smaller ( $<5\%$  change) and harvest-related quantities were  $\sim 3,000$  fish ( $\sim 10\text{-}15\%$ ) larger for the alternative vulnerability assumption. Additionally, the conclusions about substock diversity at MSY were nearly identical: approximately 60% of substocks would be overfished and 23% would be trending towards extirpation.

The alternative age composition weighting resulted in more substantial differences from the default case. Twelve of the 13 substocks showed increases in  $U_{\text{MSY},j}$ , with two substocks showing increases of approximately 100%. Most substock-specific  $S_{\text{eq},j}$  were estimated to be smaller when the alternative scheme was used, with eight of 13 substocks showing decreases between 10 and 35%. Derived biological reference points for the aggregate mixed-stock substantially differed as well: escapement-related quantities were  $\sim 6,000 - 10,000$  fish smaller ( $\sim 10\text{-}15\%$  change) and harvest-related quantities were  $\sim 6,000 - 12,000$  fish larger ( $\sim 35\%$  change) for the alternative age composition weighting scheme, however the conclusions about substock biodiversity at MSY were nearly identical, just as for the alternative vulnerability analysis.

### 3.2 Simulation-estimation trials

State-space models took between 1.3 and 2.9 days to fit on average (range: 0.8 – 5.1 days), with longer run times associated with more complex models; regression-based models took less than an hour in all cases. The state-space models fitted successfully to the majority of simulated data sets (136 out of 160) and the regression-based models were fitted successfully in all cases. No attempts were made to try different initial values for the relatively few data sets that failed in fitting for the state-space models. MCMC diagnostics suggested that sampling was adequate in the vast majority of cases:  $>99\%$  of all data sets met the convergence criterion for all parameters in all models and  $>95\%$  met the criterion for adequate number of samples.

Regression models were found to systematically overestimate the population-specific quantities of  $\alpha_j$  and  $U_{\text{MSY},j}$  and in some cases they produced wildly erroneous estimates. The mixed-effect model was more accurate than the models that fitted independent regressions to each population (Figure 8). State-space models far more accurately and precisely estimated these productivity-based quantities than the regression-approaches, though there was still a slight positive bias (median proportional error  $\sim 5\%$ ; Figure 8). Additionally, regression approaches tended to underestimate  $S_{\text{MSY},j}$  more than the state-space models. All state-space models tended to overestimate  $\sigma_{R,j}$  by approximately 5% regardless of the assumed covariance structure, though the degree of serial auto-correlation ( $\phi$ ) was accurately estimated. The individual state-space models showed essentially no differences in bias for  $\sigma_{R,j}$  or  $\phi$  (Figure 8). However, models with simple covariance structure tended to overestimate the correlation among populations and vice versa for the complex covariance structure.

All state-space models returned unbiased estimates of abundance-related states ( $R_{y,j}$ ,  $S_{t,j}$ , and  $H_t$ ) when including all years. The early portion of the time series had a slight tendency to be overestimated by all models (primarily for  $R_{y,j}$ ) by approximately 5%. This was likely a result of the assumption that data collection began when the populations were unfished.

Just as for the population-specific quantities, the regression-based methods provided generally poorer estimates of mixed-stock biological reference points than state-space models and there was no loss in performance with state-space model complexity (Figure 9). The mixed-effect regression produced more positively biased estimates of  $U_{0.1}^*$  and  $U_{0.3}^*$  than the independent regression model approach, but this pattern switched for  $U_{0.5}^*$  and  $U_{\text{MSY}}$ , likely as a result of the estimated shape of the distribution of population productivity. The mixed-effect version was less dispersed, meaning that productivities in the lower tail would have been closer to the mean (i.e., larger) than for the independent regression approach. State-space models tended to produce slight underestimates of  $U_{0.1}^*$  and  $U_{0.3}^*$  and slight overestimates of  $U_{0.5}^*$  and  $U_{\text{MSY}}$  (Figure 9).

Credible interval coverage was better for the state-space models than for regression approaches as well. For population-specific parameters, the regression approaches had lower coverage than the state-space models and the models that had the complex recruitment variance structure had more parameters close to the optimal level of 95% (Table 6). All state-space models had low coverage for  $\pi$  which resulted from highly narrow credible intervals, not from inaccurate estimates, though complex maturity models did have slightly better coverage (16% versus 11%; Table 6). In terms of mixed-stock biological reference points, the state-space model provided much better coverage than the regression approaches, particularly for exploitation rate-based points (Table 6). All state-space models exhibited poor coverage for abundance-related states (49 – 66%; Table 6).

## 4 Discussion

We presented a novel extension of the age-structured state-space spawner-recruit analytical framework, which has increasingly been applied to single stocks (e.g., Su and Peterman 2012; Hamazaki et al. 2012; Fleischman et al. 2013; Staton et al. 2017; DeFilippo et al. 2018), to the mixed-stock realm. This state-space model was shown to (1) have much less bias and better coverage in key management quantities than regression-based approaches, (2) be robust to structural uncertainty in assumed recruitment covariance and maturity variability, (3) provide good fits to the data, and (4) make more full use of the available data for policy and ecological conclusions. Though it was developed and simulation-tested in the context of Kuskokwim River Chinook salmon, we expect that the mixed-stock state-space framework presented here is general enough to be applied to other systems with similar (and possibly dissimilar) properties and data availability.

The simulation-trials illustrated that the state-space model performed superiorly to both evaluated regression-based approaches, regardless of the assumptions made regarding recruitment covariance structure and variability in maturity. Furthermore, the directionality

of the regression biases were consistent with expectations from time-series bias (Walters 1985): positive biases in  $U_{\text{MSY},j}$  and downward biases in  $S_{\text{MSY},j}$ , as well as for the respective aggregate mixed-stock quantities ( $U_{\text{MSY},j}$  and  $S_{\text{MSY},j}$ ). These biases all but disappeared in comparison for the state-space models for  $U_{\text{MSY},j}$  and to a lesser degree for  $S_{\text{MSY},j}$ . These results speak strongly in favor of the use of the state-space model over the regression-based approaches assessed here. The superior performance of state-space models was likely a result of its ability to (1) explicitly account for the time-series properties in the data, (2) parse observation from process uncertainty, and (3) make more full use of the available data.

With respect to the fuller use of the available data, there were 35 brood years for each population in which it was possible to jointly observe spawners and recruits across all four ages (if all calendar years between 1976 and 2017 were monitored). The average Kuskokwim River population fitted using the regression approaches had 17% of the possible observations because partially observed recruitment events were not considered. Conversely, the average population fitted using the state-space model had 31% of possibly observable pairs where the recruitment was observed for three out of four ages, 39% with two ages out of four, and 42% for one age out of the possible four observed. Ignoring whether recruitment and escapement were observed jointly, the average population fitted using the state-space model had 48%, 65%, and 76% of possibly observable recruitment events observed for the same ages combinations, respectively. Clearly, the use of the regression approaches resulted in a severe loss of information. It could be argued that the rule we employed to only use completely observed recruitment pairs for fitting the regression approaches was too strict and that alternative approaches to impute missing observations could be devised. While this may be true, the state-space model provides a comprehensive, rational, and rigorous method to completely reconstruct the brood tables with latent states informed with partial information by fitting to solely observed data.

Although the simulation results suggested the state-space model is an unbiased estimator, to reduce the dimensionality of our analyses it was assessed under relatively limited conditions.

Su and Peterman (2012) illustrated that state-space models can still show bias under some combinations of measurement error, intrinsic productivity, and fishing intensity. We attempted to evaluate performance across a range of true parameters by randomly sampling leading parameters from the joint posterior from one of the empirical model fits. Though it is possible the model could perform more poorly if (1) population size and productivity were more or less heterogeneous than assumed, (2) fewer populations were used, (3) available data time series were much shorter or sparser, or (4) the magnitude of observation error was incorrectly assumed. All of these scenarios remain exciting avenues for future research, but were beyond the scope of this study. As it currently stands, our analysis suggests that it is reasonable to conclude that the state-space model developed here can be an appropriate estimator for mixed-stock fishery data, though future applications to specific cases should be simulation-tested if the properties of the system and available data differ significantly from the Kuskokwim and the operating model and simulated sampling scheme designed roughly off of it.

The policy and trade-off conclusions from the state-space model were generally robust to an alternative assumption regarding relative vulnerability of the populations to harvest, although population-specific estimates did change moderately (primarily  $U_{\text{MSY},j}$ ). The alternative vulnerability vector used was a first attempt at assessing sensitivity to the assumption that all populations have been equally vulnerable to harvest; other more complex approaches to determining this vector could also be assessed in the future. For example, the fishery has historically been focused in on the early portion of the Chinook salmon run in the Kuskokwim River (Hamazaki 2008), and upper river populations have been illustrated to arrive earliest in the summer migration (Smith and Liller 2017a,b). This indicates that upper river populations may be even more vulnerable than what was captured by the vector I used, which was based solely on the spatial distribution of harvesters. Although no data sources were available to directly estimate the vulnerability vector for the Kuskokwim River data, other systems may have these data that could be incorporated, particularly those with



precise genetic stock identification programs. One would expect larger discrepancies in policy conclusions to arise when vulnerability covaries more strongly with either population size or population productivity; coupled with methods to incorporate information on population-specific harvest data, this provides an provides an interesting avenue for future research.

The conclusions from the state-space models were less robust to alterations in the assumed weighting of age composition data. Specifically, policy recommendations became more aggressive when age composition data received less weight: higher estimates of  $U_{\text{MSY}}$  and lower  $S_{\text{MSY}}$ . It is unsurprising that the estimates changed, as this often happens in stock assessment models when the assumed data weighting structure is altered (Hulson et al. 2011), but it is unclear as to why weakening the confidence in the age data had the effect of increasing perceived population productivity. Regardless of the cause, this finding suggests that policy conclusions may be conditional on the weighting of the data, and that careful thought should be given to the appropriate weighting scheme. It is likely that the optimal weighting scheme falls somewhere between the two schemes assessed here, given that effective sample size is nearly always less than the true sample size due to violations to the multinomial sampling distribution (e.g., sampled individuals show similarities that result in clustering, non-independence, and overdispersion; Maunder 2011).

Regarding state-space model complexity, the important findings were (1) there was no loss in estimation performance with increasing model complexity, (2) credible interval coverage of the complex recruitment covariance models was better than that of the models with simple structures for population-level parameters of interest, and (3) the time-varying maturity models never resulted in wildly large estimates of escapement or harvest as the time-constant maturity models sometimes did for the Kuskokwim data. Based on these findings, it seems that the most complex model is most appropriate, however, as previously stated, the simulation-trials were limited in the scope of biological and sampling scenarios considered, and as such the appropriate model may change if applied to other systems with differing characteristics.

The conclusion that the most complex model is most appropriate is contrary to the traditional dogma of assessment model complexity and management performance. Walters and Martell (2004) advise that more complex models may provide more accurate estimates of management quantities, but that their uncertainty will be much greater rendering them less useful for setting harvest policies (see Figure 5.2 and the corresponding discussion therein). These claims have been supported through closed-loop evaluations that have shown simple models known to be wrong but that give conservative advice can provide better management outcomes than complex models that better approximate the true model (e.g., Hilborn 1979; Ludwig and Walters 1985). The simplest model (fewest freely estimated parameters) evaluated here was the mixed-effect regression approach. Although it did provide more conservative and more confident advice than the independent regression approach, the simulation-trials showed that it was biased with respect to  $U_{\text{MSY}}$  and  $S_{\text{MSY}}$  in the direction that would lead to more aggressive than optimal harvest policies relative to the state-space models.

In some cases, harvest on strong and highly profitable fisheries has been severely curtailed in the name of conserving a few small and unproductive populations. Walters et al. (2018) discuss an example of British Columbia commercial salmon fisheries, where large declines in harvest beginning in the early-1990s and continuing to the present were (in part) a result of intentional reductions in exploitation rates intended to minimize the risk of extinction of a few small and unproductive stocks. The authors argue that fisheries managers have not adequately considered the harvest-biodiversity trade-off in their decision-making processes, and have instead focused on managing for the weakest stocks in the portfolio. Among the authors' four (mostly controversial) recommendations to address this situation, first on their list is for managers to conduct trade-off analyses so that costs and benefits to both fishery and conservation interests can more fully inform decision-making. Our state-space approach shows promise for informing these policy analyses. Particularly for those that involve closed-loop stochastic simulation (e.g., Catalano and Jones 2014), the state-space model provides rich biological estimates to populate the operating models and understand the strength of the

portfolio effect (which is inversely related to the magnitude of shared recruitment trends;  
Schindler et al. 2010, 2015). The model not only provides estimates of leading parameters ( $\alpha_j$   
and  $\beta_j$ ), but also estimates of the extent to which recruitment anomalies are shared among  
populations and the strength of serial auto-correlation in these time series, all of which would  
be valuable in populating operating models for policy evaluation. Furthermore, it is possible  
to use the estimated states of recruitment and spawner abundance and recruitment anomalies  
at the end of the time series to populate forward simulations from the present to determine  
which policies might be most likely to achieve short-term objectives in addition to those more  
focused on the long-term (Connors et al. nd).

## Acknowledgments

- Alabama Supercomputer Authority
- AYKSSI
- ADF&G: data
- Workshop attendees

## References

- Beacham, T. D., Lapointe, M., Candy, J. R., and Withler, K. M. M. R. E. 2004. DNA in action: Rapid application of DNA variation to sockeye salmon fisheries management. *Conservation Genetics*, 5(3):411–416.
- Blair, G. R., Rogers, D. E., and Quinn, T. P. 1993. Variation in life history characteristics and morphology of sockeye salmon in the Kvichak River system, Bristol Bay, Alaska. *Transactions of the American Fisheries Society*, 122.
- Brooks, S. P. and Gelman, A. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, 7(4):434.
- Catalano, M. J. and Jones, M. L. 2014. A simulation-based evaluation of in-season management tactics for anadromous fisheries: Accounting for risk in the Yukon River fall chum salmon fishery. *North American Journal of Fisheries Management*, 34(6):1227–1241.
- Clark, R. A., Bernard, D. R., and Fleischman, S. J. 2009. Stock-recruitment analysis for escapement goal development: A case study of Pacific salmon in Alaska. In Krueger, C. C. and Zimmerman, C. E., editors, *Pacific Salmon: Ecology and Management of Western Alaska’s Populations*, American Fisheries Society Symposium 70, pages 743–757, Bethesda, MD.
- Clark, S. C., Tanner, T. L., Sethi, S. A., Bentley, K. T., and Schindler, D. E. 2015. Migration timing of adult Chinook salmon into the Togiak River, Alaska, watershed: Is there evidence for stock structure? *Transactions of the American Fisheries Society*, 144(4):829–836.
- Connors, B. M., Staton, B. A., Coggins, Jr., L. G., Walters, C. J., Jones, M. L., Gwinn, D. C., Catalano, M. J., and Fleischman, S. J. n.d. Incorporating harvest-population diversity trade-offs into salmon management in large river basins: a case study of Kuskokwim Chinook.
- Cunningham, C. J., Anderson, C. M., Wang, J. Y.-L., Link, M., and Hilborn, R. 2018a. A management strategy evaluation of the commercial sockeye salmon fishery in Bristol Bay, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*.
- Cunningham, C. J., Branch, T. A., Dann, T. H., Smith, M., Seeb, J. E., Seeb, L. W., and Hilborn, R. 2018b. A general model for salmon run reconstruction that accounts for interception and differences in availability to harvest. *Canadian Journal of Fisheries and Aquatic Sciences*, 75(3):439–451.
- de Valpine, P. and Hastings, A. 2002. Fitting population models incorporating process noise and observation error. *Ecological Monographs*, 72(1):57–76.
- DeFilippo, L. B., Schindler, D. E., Ohlberger, J., Schaberg, K. L., Foster, M. B., Ruhl, D., and Punt, A. E. 2018. Recruitment variation disrupts the stability of alternative life histories in an exploited salmon population. *Evolutionary Applications*, 12(2):214–229.
- Fall, J. A., Godduhn, A., Halas, G., Hutchinson-Scarborough, L., Jones, B., Mikow, E., Sill, L., Trainor, A., Wiita, A., and Lemons, T. 2018. Alaska subsistence and personal use salmon fisheries 2015 annual report. Technical Paper 440, Alaska Department of Fish and Game, Anchorage, AK. Available at: <http://www.adfg.alaska.gov/techpap/TP440.pdf> [last accessed 2/20/2019].

- 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.). *Canadian Journal of Fisheries and Aquatic Sciences*, 70(3):401–414.
- Hamazaki, T. 2008. “When people argue about fish, the fish disappear.” Fishery closure “windows” scheduling as a means of changing the Chinook salmon subsistence fishery pattern: is it an effective tool? *Fisheries*, 33(10):495–501.
- Hamazaki, T. 2011. Reconstruction of subsistence salmon harvests in the Kuskokwim Area, 1990 – 2009. Fishery Manuscript Series 11-09, Alaska Department of Fish and Game, Anchorage, AK. Available at: <http://www.adfg.alaska.gov/FedAidPDFs/FMS11-09.pdf> [last accessed 2/20/2019].
- Hamazaki, T., Evenson, M. J., Fleischman, S. J., and Schaberg, K. L. 2012. Spawner-recruit analysis and escapement goal recommendation for Chinook salmon in the Kuskokwim River drainage. Fishery Manuscript Series 12-08, Alaska Department of Fish and Game, Anchorage, AK. Available at: <http://www.adfg.alaska.gov/FedAidPDFs/FMS12-08.pdf> [last accessed 2/20/2019].
- Head, J. M. and Smith, N. J. 2018. Salmon escapement monitoring in the Kuskokwim Area, 2017. Fishery Data Series 18-11, Alaska Department of Fish and Game, Anchorage, AK. Available at: <http://www.adfg.alaska.gov/FedAidPDFs/FDS18-11.pdf> [last accessed 2/20/2019].
- Hendry, A. P. and Quinn, T. P. 1997. Variation in adult life history and morphology among Lake Washington sockeye salmon (*Oncorhynchus nerka*) populations in relation to habitat features and ancestral affinities. *Canadian Journal of Fisheries and Aquatic Sciences*, 54(1):75–84.
- Hilborn, R. 1979. Comparison of fisheries control systems that utilize catch and effort data. *Journal of the Fisheries Research Board of Canada*, 36(12):1477–1489.
- Hilborn, R. and Walters, C. J. 1992. *Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty*. Springer US.
- Hulson, P.-J. F., Hanselman, D. H., and Quinn, T. J. 2011. Determining effective sample size in integrated age-structured assessment models. *ICES Journal of Marine Science*, 69(2):281–292.
- Kellner, K. 2017. *jagsUI: A Wrapper Around ‘rjags’ to Streamline ‘JAGS’ Analyses*. R package version 1.4.9.
- Korman, J. and English, K. 2013. Benchmark analysis for Pacific salmon conservation units in the Skeena watershed. A report to Pacific Salmon Foundation.
- Lierman, M. C., Sharma, R., and Parken, C. K. 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.
- Liller, Z. W., Hamazaki, H., Decossas, G., Bechtol, W., Catalano, M., and Smith, N. 2018. Kuskokwim River Chinook salmon run reconstruction model revision – executive summary. Regional Information Report 3A.18-04, Alaska Department of Fish and Game, Anchorage, AK. Available at: <http://www.adfg.alaska.gov/FedAidPDFs/RIR.3A.2018.04.pdf> [last accessed 2/20/2019].

- Ludwig, D. and Walters, C. J. 1981. Measurement errors and uncertainty in parameter estimates for stock and recruitment. *Canadian Journal of Fisheries and Aquatic Sciences*, 38(6):711–720.
- Ludwig, D. and Walters, C. J. 1985. Are age-structured models appropriate for catch-effort data? *Canadian Journal of Fisheries and Aquatic Sciences*, 42(6):1066–1072.
- 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(2-3):311–319.
- Michielsens, C. G. and Cave, J. D. 2018. In-season assessment and management of salmon stocks using a Bayesian time-density model. *Canadian Journal of Fisheries and Aquatic Sciences*.
- Murphy, J. M., Howard, K. G., Gann, J. C., Ciciel, K. C., Templin, W. D., and Guthrie, C. M. 2017. Juvenile Chinook salmon abundance in the northern Bering Sea: Implications for future returns and fisheries in the Yukon River. *Deep Sea Research Part II: Topical Studies in Oceanography*, 135:156–167.
- Newman, K. B., Buckland, S. T., Morgan, B. J. T., King, R., Borchers, D. L., Cole, D. J., Besbeas, P., Gimenez, O., and Thomas, L. 2014. *Modelling Population Dynamics*. Springer New York.
- Parken, C. K., McNichol, R. E., and Irvine, J. R. 2006. Habitat based methods to estimate escapement goals for Chinook salmon stocks in British Columbia, 2004. Research Document 2006/083, Canadian Science Advisory Secretariat, Ottawa, ON.
- Plummer, M. 2017. *JAGS Version 4.3.0 User Manual*.
- R Core Team 2018. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Raftery, A. E. and Lewis, S. 1992. How many iterations in the Gibbs sampler? In *Bayesian Statistics 4*, pages 763–773. Oxford University Press.
- Ricker, W. E. 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, 11(5):559–623.
- Rose, K. A., Cowan, J. H., Winemiller, K. O., Myers, R. A., and Hilborn, R. 2001. Compensatory density dependence in fish populations: Importance, controversy, understanding and prognosis. *Fish and Fisheries*, 2(4):293–327.
- Schaberg, K. L., Liller, Z. W., Molyneaux, D. B., Bue, B. G., and Stuby, L. 2012. Estimates of total annual return of Chinook salmon to the Kuskokwim River, 2002–2007. Fishery Data Series 12-36, Alaska Department of Fish and Game, Anchorage, AK. Available at: <http://www.adfg.alaska.gov/FedAidPDFs/FDS12-36.pdf> [last accessed 2/20/2019].
- Schindler, D. E., Armstrong, J. B., and Reed, T. E. 2015. The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment*, 13(5):257–263.
- Schindler, D. E., Hilborn, R., Chasco, B., Boatright, C. P., Quinn, T. P., Rogers, L. A., and Webster, M. S. 2010. Population diversity and the portfolio effect in an exploited species. *Nature*, 465(7298):609–612.

- Schnute, J. T. and Kronlund, A. R. 2002. Estimating salmon stock-recruitment relationships from catch and escapement data. *Canadian Journal of Fisheries and Aquatic Sciences*, 59(3):433–449.
- Shelden, C. A., Hamazaki, T., Horne-Brine, M., and Roczicka, G. 2016. Subsistence salmon harvests in the Kuskokwim Area, 2015. Fishery Data Series 16-55, Alaska Department of Fish and Game, Anchorage, AK. Available at: <http://www.adfg.alaska.gov/FedAidPDFs/FDS16-55.pdf> [last accessed 2/20/2019].
- Smith, N. J. and Liller, Z. W. 2017a. Inriver abundance and migration characteristics of Kuskokwim River Chinook salmon, 2015. Fishery Data Series 17-22, Alaska Department of Fish and Game, Anchorage, AK. Available at: <http://www.adfg.alaska.gov/FedAidPDFs/FDS17-22.pdf> [last accessed 2/20/2019].
- Smith, N. J. and Liller, Z. W. 2017b. Inriver abundance and migration characteristics of Kuskokwim River Chinook salmon, 2016. Fishery Data Series 17-47, Alaska Department of Fish and Game, Anchorage, AK. Available at: <http://www.adfg.alaska.gov/FedAidPDFs/FDS17-47.pdf> [last accessed 2/20/2019].
- 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.
- Stuby, L. 2007. Inriver abundance of Chinook salmon in the Kuskokwim River, 2002 – 2006. Fishery Data Series 07-93, Alaska Department of Fish and Game, Anchorage, AK.
- Su, Z. and Peterman, R. M. 2012. Performance of a Bayesian state-space model of semelparous species for stock-recruitment data subject to measurement error. *Ecological Modelling*, 224(1):76–89.
- Templin, W. D., Smith, C. T., and D. Molyneaux, L. W. S. 2014. Genetic diversity of Chinook salmon from the Kuskokwim River. USFWS Office of Subsistence Management, Fisheries Resource Monitoring Program, Final Report 01-070, Alaska Department of Fish and Game, Anchorage, AK. Available at: [http://www.adfg.alaska.gov/static/fishing/pdfs/research/fis01-070\\_final\\_report.pdf](http://www.adfg.alaska.gov/static/fishing/pdfs/research/fis01-070_final_report.pdf) [last accessed 2/20/2019].
- Walters, C., English, K., Korman, J., and Hilborn, R. 2018. The managed decline of British Columbia’s commercial salmon fishery. *Marine Policy*. Pre-print as of 2/18/2019; DOI: 10.1016/j.marpol.2018.12.014.
- Walters, C. J. 1985. Bias in the estimation of functional relationships from time series data. *Canadian Journal of Fisheries and Aquatic Sciences*, 42(1):147–149.
- Walters, C. J., Lichatowich, J. A., 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.
- Walters, C. J. and Martell, S. J. D. 2004. *Fisheries Ecology and Management*. Princeton University Press.

TABLE 1. Description of the various index notation used in the description of state-space models.  $n_t$  is the number of years observed for the most data-rich stock.

Index	Meaning	Dimensions
$y$	Brood year index; year in which fish were spawned	$n_y = n_t + n_a - 1$
$t$	Calendar year index; year in which observations are made	$n_t$
$j$	Population index	$n_j$
$a$	Age index; $a = 1$ is the first age; $a = n_a$ is the last age	$n_a$



TABLE 2. Symbology used in the presentation of the state-space models.

Symbol	Description
<b>Dimensional Constants</b>	
$n_y$	Number of brood years
$n_t$	Number of calendar years for the population with the longest data time series
$n_j$	Number of populations
$n_a$	Number of possible ages of maturation
$a_{min}$	The first age recruits can mature
$a_{max}$	The last age recruits can mature
<b>Parameters</b>	
$\alpha_j^a$	Maximum recruits per spawner for population $j$
$\beta_j^a$	Capacity parameter for population $j$ ; inverse of $S_{MAX,j}$
$\sigma_{R,j}^2$	Recruitment white noise process variance for population $j$
$\rho_{i,j}$	Correlation in process variance between substocks $i$ and $j$
$\Sigma_R$	Recruitment white noise process covariance matrix
$\phi$	Lag-1 serial autocorrelation coefficient
$\omega_{y,j}$	Serially autocorrelated portion of recruitment process anomalies (residuals)
$\pi_a$	Mean probability a juvenile matures at age $a$
$D^b$	Dirichlet dispersion parameter for brood year-specific maturity schedules
$p_{y,a}^b$	Probability a juvenile belonging to brood year $y$ matures at age $a$
$U_t^c$	Exploitation rate experienced by fully vulnerable populations in calendar year $t$
$v_j^c$	Relative vulnerability term for population $j$
<b>Biological Reference Points</b>	
$U_{MSY,j}$	Exploitation rate expected to produce MSY for population $j$
$U_{MSY}$	Exploitation rate expected to produce MSY for the mixed-stock aggregate
$S_{MSY,j}$	Spawner abundance expected to produce MSY for population $j$
$S_{MSY}$	Spawner abundance expected to produce MSY for the mixed-stock aggregate
$S_{MAX,j}$	Spawner abundance expected to produce maximum recruitment for population $j$
$S_{eq,j}$	Spawner abundance expected to produce the same number of recruits for population $j$
$S_p^{*d}$	Mixed-stock escapement expected to result in no greater than $p \cdot 100\%$ of populations overfished
$H_p^{*d}$	Same as $S_p^*$ , but for mixed-stock harvest
$U_p^{*d}$	Same as $S_p^*$ , but for mixed-stock exploitation rate
$p_{OF,MSY}^d$	Fraction of populations expected to be overfished at MSY
$p_{EX,MSY}^e$	Fraction of populations expected to be trending towards extinction at MSY
<b>States</b>	
$\hat{R}_{y,j}$	Deterministic (expected) recruitment in brood year $y$ for population $j$
$R_{y,j}$	Realized latent (true) recruitment in brood year $y$ for population $j$
$N_{t,j}$	Run abundance returning to spawn in calendar year $t$ for population $j$

TABLE 2. Symbology used in the presentation of the state-space models. (*continued*)

Symbol	Description
$S_{t,j}$	Spawner abundance in calendar year $t$ for population $j$
$H_t$	Mixed-stock aggregate harvest in calendar year $t$
$q_{t,a,j}$	Fraction of the run mature at age $a$ in year $t$ for population $j$

<sup>a</sup> In the state-space models,  $U_{\text{MSY},j}$  and  $S_{\text{MSY},j}$  were estimated as leading parameters,  $\alpha_j$  and  $\beta_j$  were derived from them using equations found in Schnute and Kronlund (2002).

<sup>b</sup> Used only in complex maturity models: SSM-vM and SSM-VM. For simple maturity models,  $p_{y,a}$  took the value  $\pi_a$ .

<sup>c</sup> In the default case, all populations were assumed to be fully vulnerable,  $v_j$  was used in a sensitivity analysis to this assumption.

<sup>d</sup> Overfished is defined here as the case where the mixed-stock or any given population is fished with exploitation rate greater than is expected to produce MSY.

<sup>e</sup> Trending towards extirpation is defined here as the case where expected equilibrium escapement is less than or equal to zero.

TABLE 3. Summary of evaluated models in this analysis. Regression models are described in Section 2.1.1 and state-space models are described in Section 2.1.2.

Model	$n_j$	Unique $\sigma_j$	AR(1)	Recruitment Covariance	Time-Varying Maturity
<b>Regression-Based Models</b>					
LM	10	Yes	No	None	Yes
LME	10	No	No	None	Yes
<b>State-Space Models</b>					
vm	13	No	Yes	Single $\rho$ bounded by $[-0.05 - 1)$	No
Vm	13	Yes	Yes	Unique $\rho_{i,j}$	No
vM	13	No	Yes	Same as vm	Yes
VM	13	Yes	Yes	Same as Vm	Yes

TABLE 4. Prior distributions used for all parameters in the state-space models for both empirical and simulation analyses. In all cases, priors were selected to be minimally informative while also preventing the sampler from exploring highly unlikely areas of the parameter space. Differences among versions of the state-space model (e.g., SSM-vm and SSM-Vm; Table 3) are described by footnotes.

Parameter	Prior	Description
$U_{\text{MSY},j}$	Uniform(0.01, 0.99)	Exploitation rate that produces MSY
$S_{\text{MSY},j}$	Lognormal(0, 0.001)	Spawner abundance that produces MSY
$\phi$	Uniform(-0.99, 0.99)	Lag-1 auto-correlation coefficient
$\Sigma_R^{-1a}$	Wishart( $R, n_j + 1$ )	Inverse covariance matrix for white-noise recruitment process variability
$\sigma_R^b$	Uniform(0, 2)	White-noise recruitment process standard deviation
$\rho^b$	Uniform(-0.05, 1)	Correlation in recruitment process variability among populations
$\pi$	Dirichlet( $\alpha = [1, 1, 1, 1]$ )	Average probability of maturing at each age
$D^{-0.5c}$	Uniform(0.03, 1)	Dispersion of brood year-specific maturity schedules
$p_y^c$	Dirichlet( $\alpha = \pi \cdot D$ )	Brood year-specific probability of maturing at each age
$U_t$	Beta(1,1)	Annual exploitation rate of fully vulnerable populations

<sup>a</sup> Only for SSM-Vm and SSM-VM

<sup>b</sup> Only for SSM-vm and SSM-vM,  $\Sigma_R$  was constructed using  $\sigma_R$  and  $\rho$  as described at the end of Section 2.1.2.

<sup>c</sup> Only for SSM-vM and SSM-VM, all  $p_y$  took on  $\pi$  for SSM-vm and SSM-Vm.

TABLE 5. Dimensions for the Markov Chain Monte Carlo algorithms used in this analysis. State-space models were sampled much more intensively than the regression models. Fewer chains were used for the simulation analysis to maximize High Performance Computing efficiency. Oversampling of models fitted to empirical data was intentional to ensure adequate inference.

	Regression Models		State-Space Models	
	Empirical	Simulation	Empirical	Simulation
<b>Burn-in</b>	20,000	20,000	50,000	50,000
<b>Post Burn-in</b>	200,000	200,000	800,000	600,000
<b>Thin Interval</b>	50	50	400	100
<b>Chains</b>	10	5	10	5
<b>Total</b>	<b>2,200,000</b>	<b>1,100,000</b>	<b>8,500,000</b>	<b>3,250,000</b>
<b>Retained</b>	<b>40,000</b>	<b>20,000</b>	<b>20,000</b>	<b>30,000</b>

TABLE 6. Posterior coverage for key quantities in the simulation-estimation trials. Coverage was calculated as the percentage of all estimated 95% credible intervals across simulated data sets that contained the true value. Bold numbers are those that fall greater than 5 percentage points from the optimal coverage.

Quantity	Regression		State-space			
	LM	LME	vm	Vm	vM	VM
<b>Parameters</b>						
$\alpha_j$	<b>84</b>	<b>68</b>	95	94	95	95
$\beta_j$	<b>83</b>	<b>73</b>	90	<b>88</b>	90	<b>89</b>
$U_{\text{MSY},j}$	<b>84</b>	<b>68</b>	95	94	95	95
$S_{\text{MSY},j}$	<b>85</b>	<b>76</b>	<b>85</b>	<b>84</b>	<b>85</b>	<b>85</b>
$\sigma_{R,j}$	—	—	<b>44</b>	93	<b>45</b>	95
$\phi$	—	—	<b>87</b>	97	<b>88</b>	97
$\pi$	—	—	<b>12</b>	<b>11</b>	<b>16</b>	<b>16</b>
$\bar{\rho}_{i,j}$	—	—	<b>86</b>	93	<b>88</b>	93
<b>Mixed-stock reference points</b>						
$S_{0.1}^*$	99	94	93	92	93	93
$S_{0.3}^*$	99	94	96	96	96	96
$S_{0.5}^*$	94	91	91	90	91	90
$S_{\text{MSY}}$	100	<b>88</b>	94	90	94	91
$U_{0.1}^*$	<b>79</b>	<b>38</b>	96	97	96	96
$U_{0.3}^*$	<b>66</b>	<b>32</b>	99	99	99	99
$U_{0.5}^*$	<b>21</b>	<b>38</b>	95	95	96	96
$U_{\text{MSY}}$	<b>75</b>	<b>80</b>	95	91	95	93
<b>Abundance states</b>						
$U_t$	—	—	<b>64</b>	<b>64</b>	<b>66</b>	<b>66</b>
$R_{y,j}$	—	—	<b>59</b>	<b>58</b>	<b>60</b>	<b>59</b>
$S_{t,j}$	—	—	<b>50</b>	<b>49</b>	<b>51</b>	<b>51</b>
$H_t$	—	—	<b>51</b>	<b>51</b>	<b>55</b>	<b>55</b>

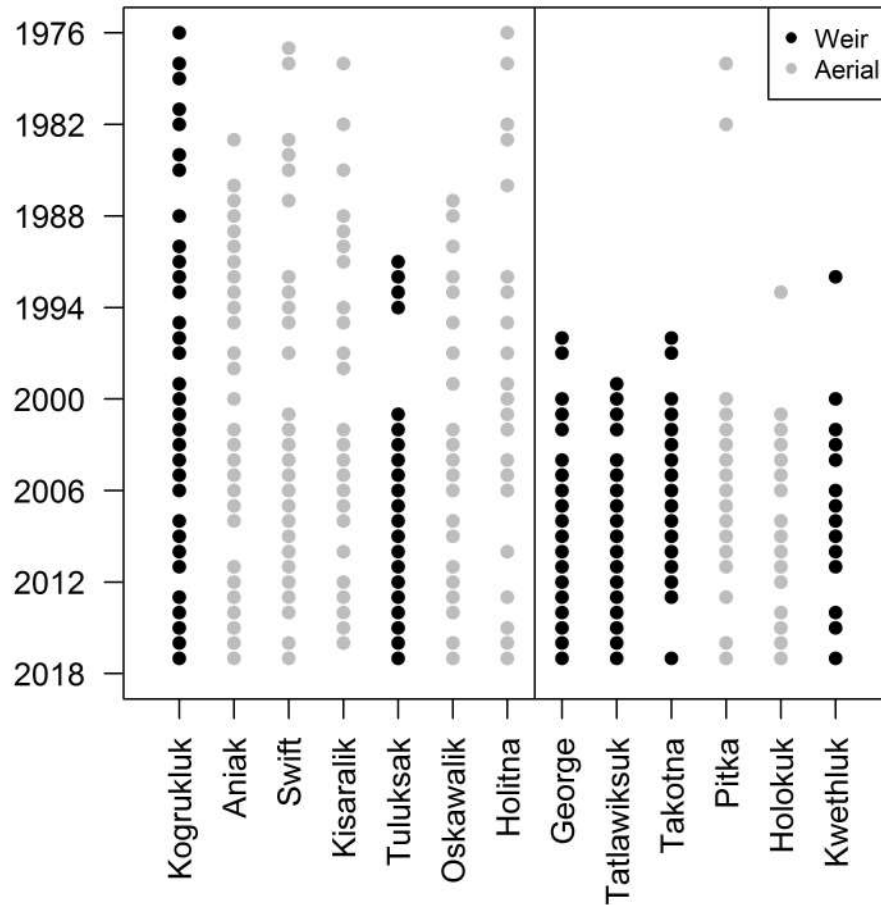


FIGURE 1. The frequency of escapement sampling for each Chinook salmon population monitored in the Kuskokwim River. Black points indicate years that were sampled for populations monitored with a weir and grey points indicate years sampled for populations monitored with aerial surveys. The vertical black line shows a break where  $> 50\%$  of the years were monitored for a population

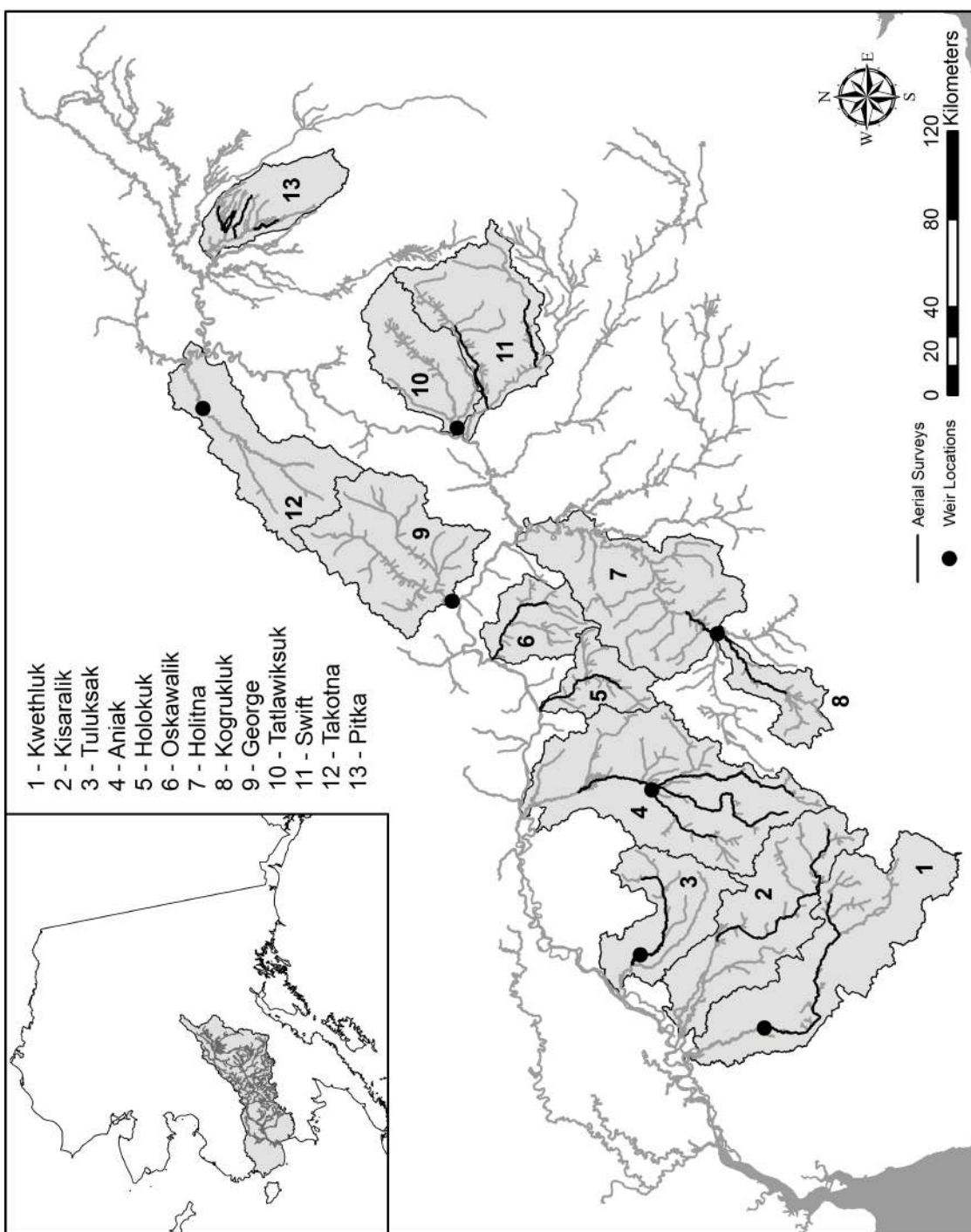


FIGURE 2. Map of the Kuskokwim River drainage, with the 13 drainage basins representing unique spawning units (populations) used in this analysis. Black points show the location of weir projects, black sections of river indicate the reaches flown as part of aerial surveys. Drainages monitored via both aerial survey and weir used the weir counts to inform escapement estimates in this analysis, with the exception of the Aniak drainage (#4), for which aerial survey data were much more abundant than available weir data.



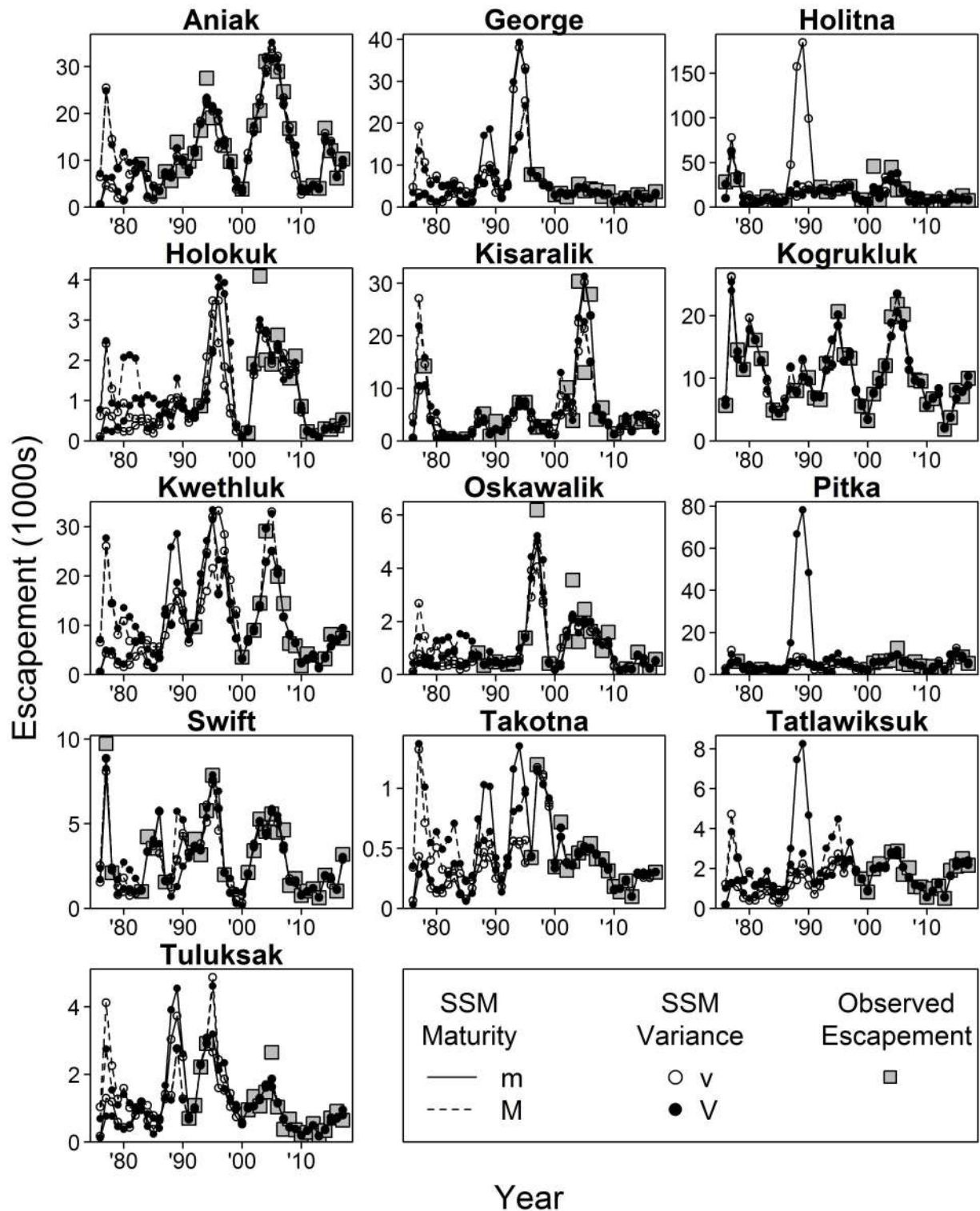


FIGURE 3. Observed and fitted escapement time series for each Kuskokwim River population. Line/symbol types denote the particular state-space model and grey squares denote observed weir counts or expanded aerial survey indices.

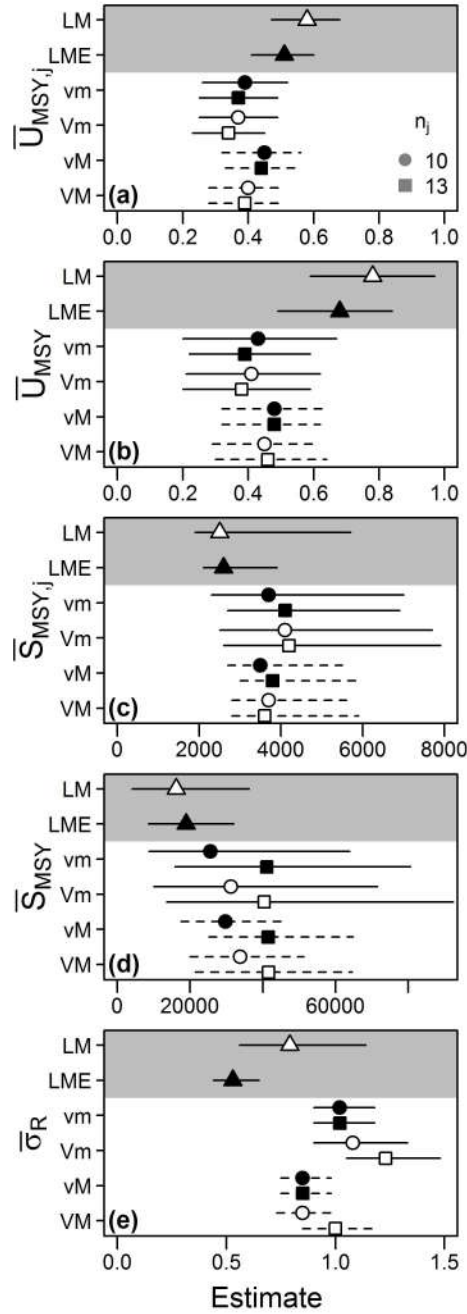


FIGURE 4. Estimates of biological reference points serving as indicators of productivity ( $\bar{U}_{MSY,j}$  – exploitation rate producing MSY from the average population;  $U_{MSY}$  – exploitation rate producing mixed-stock MSY) and size ( $\bar{S}_{MSY,j}$  and  $S_{MSY}$  – same symbology but for escapement), as well as the variability of recruitment anomalies for the average population ( $\bar{\sigma}_R$ ). Six models are shown: two regression models (LM and LME – triangles) and four state-space models (vm, Vm, vM, and VM – circles/squares; models summarized in Table 3). For state-space models, circles represent the values calculated with only the 10 populations able to be fitted with regression approaches included; squares represent the values calculated with all 13 populations.

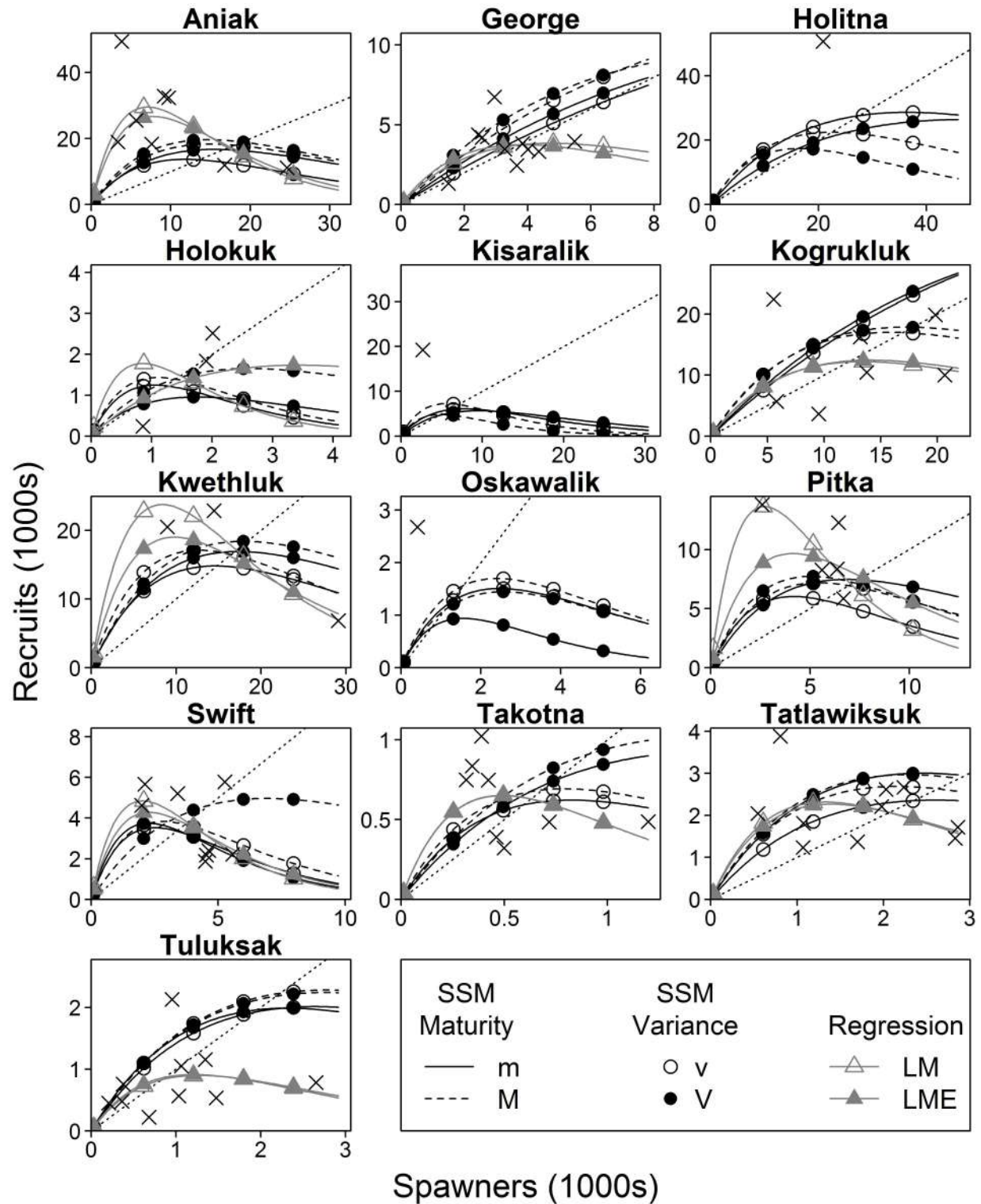


FIGURE 5. Fitted spawner-recruit relationships for the 13 populations monitored in the Kuskokwim River subdrainage included in this analysis. Line and point types denote to different models; crosses are completely observed spawner-recruit pairs. Note that the regression approaches (grey lines/triangles) fitted only to these data, the state-space models (black lines/circles) fitted to all observations of population-specific escapement, aggregate harvest, and age composition.

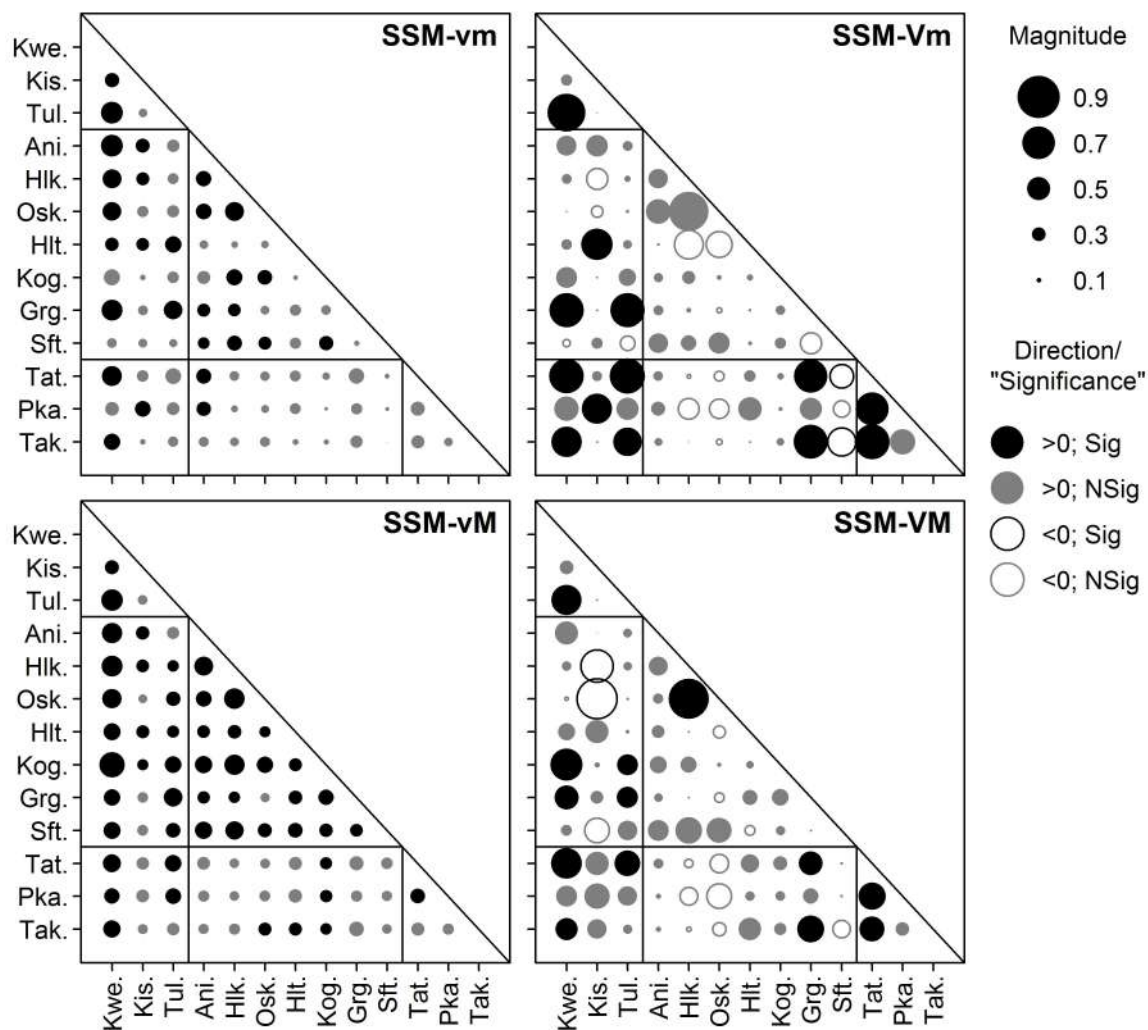


FIGURE 6. Correlation coefficients for recruitment residuals for each pair of populations. The size of each circle represents the magnitude of the correlation, the shade represents significance (whether 95% credible interval included 0), and the fill represents directionality as described in the legend. Populations are ordered from downriver to upriver on both axes, and vertical/horizontal lines denote the boundaries between what are generally considered to be lower, middle, and upper river populations.

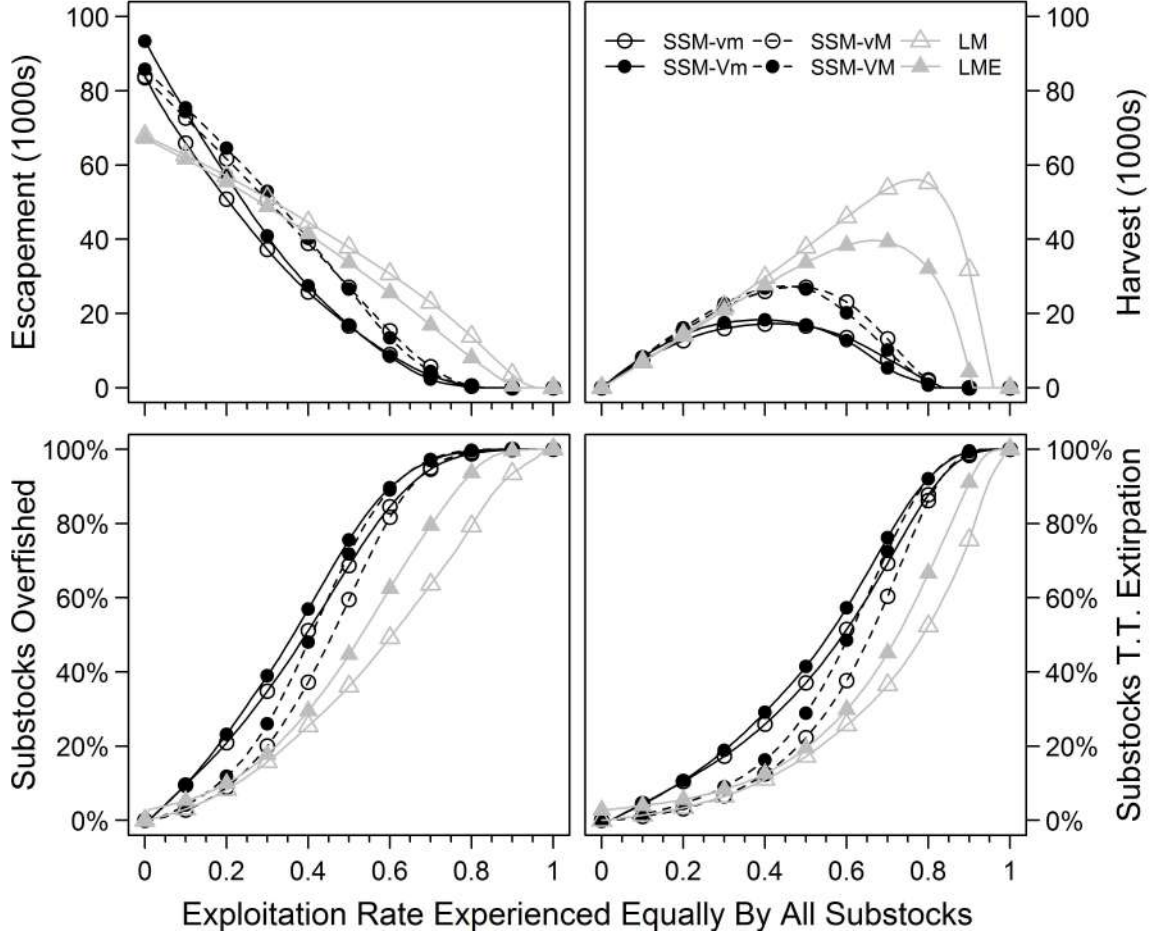


FIGURE 7. Harvest-biodiversity trade-offs based on equilibrium states (escapement and harvest) of the mixed-stock and the percentage of populations expected to be in an undesirable state as a function of the exploitation rate under the assumption that all populations are fished at the same rate. “Overfished” is defined here as  $U > U_{MSY,j}$ . “T.T.” stands for “trending toward”, and represents the case where equilibrium escapement would be  $\leq 0$ . To facilitate comparisons with the regression approaches (grey lines/triangles), the three populations with insufficient data for fitting regression models were excluded from summaries of the state-space models (black lines/circles).



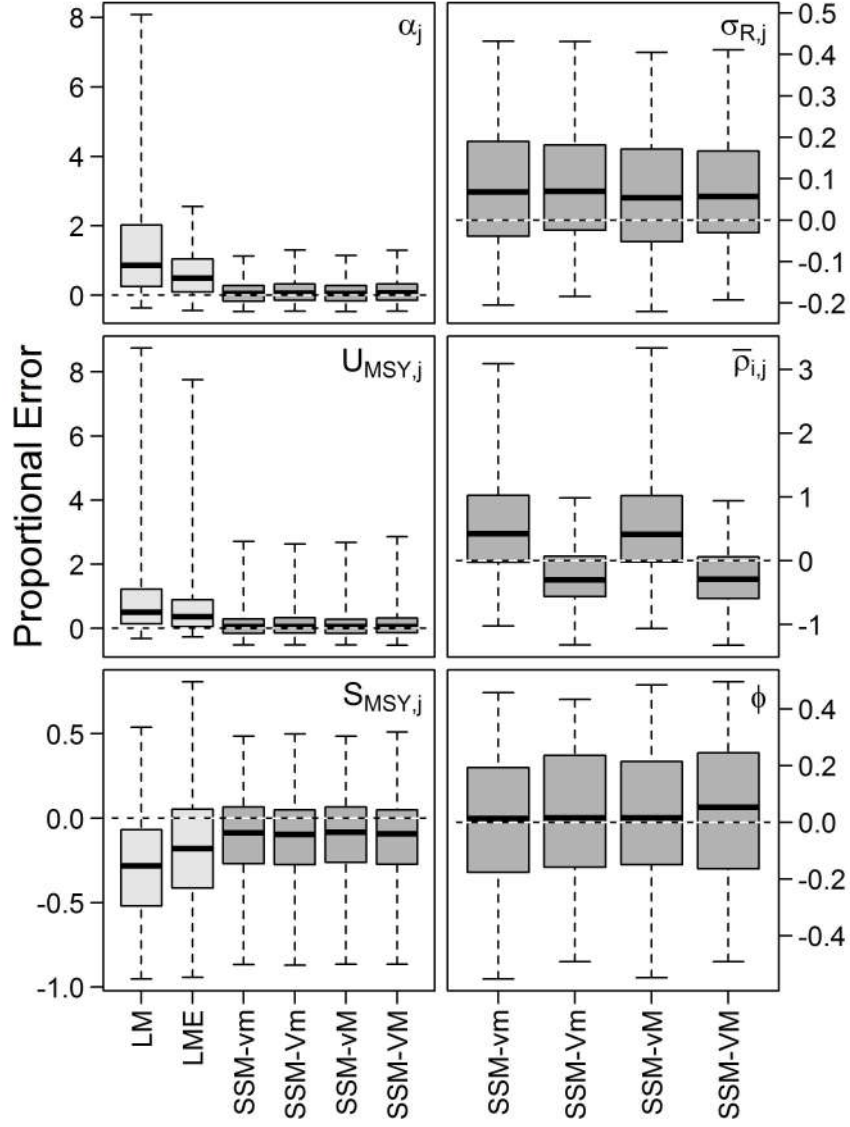


FIGURE 8. Proportional error for key parameters in the multi-stock spawner-recruit models from the simulation-estimation trials. Point estimates used were posterior medians.

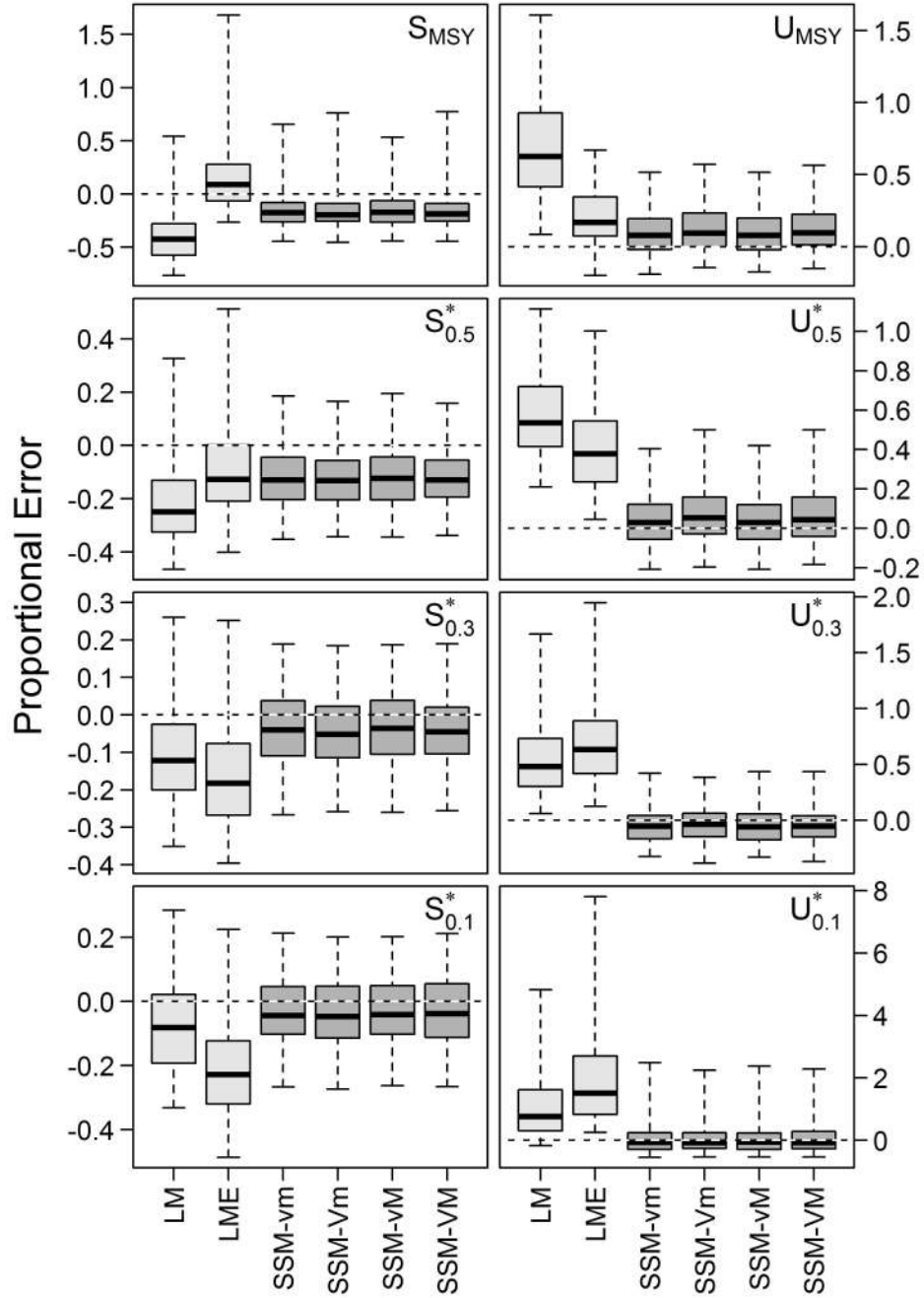


FIGURE 9. Proportional error for key biological reference points of the aggregate mixed stock.  $S^*_p$  and  $U^*_p$  are the aggregate escapement and fully vulnerable exploitation rate that would ensure no more than  $p \cdot 100\%$  of populations are overfished, respectively. Point estimates used were posterior medians.

1 Incorporating harvest-population diversity trade-offs into salmon management in large river basins: a  
2 case study of Kuskokwim River Chinook

3 Brendan M. Connors<sup>1</sup>, Ben Staton<sup>2,3</sup>, Lew Coggins<sup>4</sup>, Carl Walters<sup>5</sup>, Mike Jones<sup>6</sup>, Dan Gwinn<sup>7</sup>, Matt Catalano<sup>2</sup>  
4 and Steve Fleischman<sup>8</sup>

5 <sup>1</sup> Institute of Ocean Sciences, Fisheries and Oceans Canada, Sidney, BC

6 <sup>2</sup> Auburn University, Auburn, AL

7 <sup>3</sup> Columbia River Inter-Tribal Fish Commission, Portland, OR

8 <sup>4</sup> US Fish and Wildlife Service, Bethel, AK

9 <sup>5</sup> University of British Columbia, Vancouver, BC

10 <sup>6</sup> Michigan State University, East Lansing, MI

11 <sup>7</sup> Biometric Research LLC, Gainesville, FL

12 <sup>8</sup> Alaska Department of Fish and Game, Anchorage, AK (retired)



## Abstract

Variability among fish populations in ecological characteristics and productive capacity (i.e., population diversity) can be critical to maintaining resilience to environmental change and to dampening variability in harvest for fisheries that depend upon them. However, when fisheries for multiple populations overlap in space and time there can be an inherent conflict between harvest and population diversity: high harvest rates, which can be sustained by the most productive populations, can come at the cost of increased risk of overfishing those that are less productive. While the importance of these harvest-population diversity trade-offs in salmon management is well-recognized, they are not often explicitly evaluated in contemporary fisheries management. We used recently obtained estimates of Chinook salmon population diversity within the Kuskokwim River basin of western Alaska, which supports one of the largest subsistence salmon fisheries in the world, to parameterize closed-loop simulations that evaluated how well alternative harvest policies meet population diversity and fishery objectives. We found clear evidence of Chinook population diversity that gives rise to asymmetric trade-offs among fishery and conservation objectives. For example, relative to policies that sought to maximize mixed-stock harvest, policies that sought to minimize the risk of driving weak stocks to extirpation did so at the cost of a 20% reduction in harvests and 16% reduction in inter-annual stability in harvests, but with the benefit of increasing the chances of ensuring equitable access to Chinook (i.e., meeting tributary goals) by 84% and nearly eliminating the risk of weak stock extirpation. We also found that harvest policies focused on meeting minimum subsistence needs were unlikely to jeopardize long-term prospects for basin-wide sustainable use. The fishery and biological performance of alternative harvest policies, and the magnitude of resulting trade-offs, were moderately sensitive to potential future changes in population productivity and capacity and to uncertainty in the underlying drivers of recruitment variation. Our approach provides a general framework for characterizing salmon population diversity in large river basins and evaluating harvest-population diversity trade-offs among alternative harvest policies within them.

## Introduction

Maintaining variation in life history characteristics among species, populations and individuals is increasingly recognized as a hallmark of sustainable and resilient fisheries management. In addition to the inherent importance of protecting such diversity, fisheries that integrate across species and population diversity are often more stable (Sethi 2010; Schindler et al. 2015; Anderson et al. 2017), provide increased food security (Nesbitt and Moore 2016) and are more resilient to environmental change (Anderson et al. 2015; Cline et al. 2017). Considerable progress has been made uncovering and quantifying the benefits of species and population diversity, and recognition of the importance of protecting population diversity is now common in national and regional fisheries management policies such as Canada's Wild Salmon Policy (DFO 2005) and Alaska's Sustainable Salmon Policy. However, the tactical incorporation of these considerations into contemporary fisheries management has lagged behind (Walters et al. 2018).

Pacific salmon *Oncorhynchus* spp. provide a classic example of the many dimensions and benefits of species and population diversity. Pacific salmon are broadly distributed across the North Pacific, exhibit a diversity of ecological characteristics and life histories, spawn in thousands of locations across their range and are uniquely adapted to the environmental conditions they experience at fine spatial and temporal scales (Quinn 2018a). This diversity helps to stabilize the aggregate benefits derived from salmon by humans (e.g., Nesbitt & Moore, 2016; Schindler et al., 2010) and wildlife (Schindler et al. 2013; Deacy et al. 2019; Service et al. 2019). For example, sockeye salmon fisheries in Bristol Bay, which integrate across hundreds of discrete spawning populations, are two times more stable than if the system consisted of a single homogenous population (Schindler et al. 2010).

In situations where fisheries for individual populations within a biodiverse system overlap in space and time, there can be a conflict between harvest and the protection of population diversity because unproductive populations will be unable to sustainably withstand the harvest rates that maximize long-term yield from productive stocks. This gives rise to a trade-off between harvests and the protection of

diversity, known as the “weak” stock problem in fisheries management (Hilborn and Walters 1992; Hilborn et al. 2015; Link 2017). Harvest-diversity trade-offs can be acute in large river basins with low levels of management precision and control, where fisheries for multiple species and stocks in the marine environment or lower river overlap both spatially and temporally (Pestes et al. 2008; Walters et al. 2008).

Harvest-diversity trade-offs may be exacerbated by a changing climate. Climate variation, filtered through spatially variable and nonlinear ecological processes, can give rise to changes in salmon abundance and productivity over inter-decadal and centennial scales (Rogers et al. 2013; Malick et al. 2017). These changes are unlikely to be synchronous across populations and so populations that are relatively unproductive and contribute little to fisheries today may become more productive and important contributors to the fisheries of the future (Hilborn et al. 2003; Anderson et al. 2015). It follows that if these weak stocks are traded off for higher harvests today, then their ability to make a greater contribution to harvest in the future may be compromised.

Harvest-diversity trade-offs may also be influenced by non-stationarity in population productivity which may also obscure the drivers of variation in recruitment in salmon systems. Many salmon spawner-recruitment relationships are assumed to exhibit over-compensation with declining total recruitment at high spawner abundances (i.e., a Ricker-type spawner-recruitment relationship)(Peterman and Dorner 2012; Fleischman et al. 2013; Dorner et al. 2017). Such over-compensation may occur because, for example, at high spawner densities spawning success is reduced due to competition on the spawning grounds. However, cyclical variation in environmental forcing can also give rise to the appearance of overcompensation in spawner-recruit data sets (Parma and Deriso 1990). Such cyclical environmental forcing may also exacerbate harvest-diversity trade-offs because weak stocks are more susceptible to overharvest in years of low productivity than they would be if the primary drivers of recruitment variation were intrinsic. These alternative hypotheses, which are not easily distinguished from each other based on

typical spawner-recruit data sets, give rise to structural uncertainty which may impact the evaluation of management strategies and perceptions of their ability to meet both harvest and diversity objectives.

Despite the increasing recognition of the importance of salmon biodiversity, there are few published examinations of the performance of alternative harvest policies designed to meet a range of fishery and conservation objectives that incorporate harvest-diversity considerations (but see Hawkshaw & Walters, 2015; Walters et al., 2008). Additionally, quantitative evaluations of the performance of alternative harvest policies in the face of large uncertainty in the drivers, magnitudes and trajectories of recruitment dynamics, have been limited to date (but see Collie, Peterman, & Zuehlke, 2012).

These knowledge gaps were recently highlighted by an Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative independent expert panel that identified the need for empirically grounded closed-loop simulation studies that quantify (1) the predicted consequences of alternative harvest policies in large river basins for both sustainable production over the long-term as well as preserving biocomplexity, and (2) trade-offs among fishery and biological objectives in an attempt to understand the consequences of regime shifts and weak mechanistic understanding of drivers of recruitment (Schindler et al. 2019).

To help close this knowledge gap we characterized salmon population diversity and trade-offs with mixed-stock harvest in Kuskokwim River Chinook salmon (*O. tshawytscha*), which support one of the largest subsistence salmon fisheries in the world. We then developed and empirically parameterized a multi-stock closed-loop simulation model of the system to evaluate the ability of alternative harvest policies to meet both fishery and conservation objectives. We do this across a range of alternative hypotheses about drivers of recruitment dynamics and non-stationarity in population diversity to quantify how robust alternative harvest policies, and how sensitive harvest-diversity trade-offs, are to a variable environment. We find that the inherent Chinook population diversity present in the system gives rise to an asymmetric trade-off between harvest and conserving diversity and that the fishery and biological performance of

harvest policies, and the magnitude of resulting trade-offs, are sensitive to directional changes in population diversity and uncertainty in the underlying drivers of recruitment variation. Our work provides a general framework for characterizing salmon population diversity and evaluating the ability of alternative harvest policies to meet multiple biological and fishery objectives in large salmon-producing river systems.

## **Methods**

Our approach consisted of four steps: (1) establish fishery and population diversity objectives as well as alternative harvest policies through workshops with regional stakeholders, subsistence users and management agencies (US Fish and Wildlife Service and Alaska Department of Fish and Game); (2) characterize population diversity by fitting an age-structured, multi-stock, state-space spawner-recruitment model to available data on spawners, harvests, and age composition at a population level<sup>1</sup>; (3) quantify the performance of the alternative harvest policies against objectives using closed-loop simulations across a range of plausible hypotheses representing alternative states of nature; and (4) characterize the trade-offs between harvest and diversity that emerge from step 4, and illustrate how alternative harvest policies perform relative to them.

### **1.1 Study Area**

Chinook populations across Western Alaska have declined in abundance and productivity over the past decade (Ohlberger et al. 2016; Dorner et al. 2017). These declines have been particularly pronounced in the Kuskokwim River Basin (Figure 1) where some recent years (e.g., 2012-2014) have seen record low escapement to Chinook spawning grounds, though returns have increased to stable but well below

---

<sup>1</sup> We use the term population to denote spawning populations that have been the subject of separate assessment related activities within the system (See Figure 1), they are neither a purely biologically or management based unit.

average in the years since then. The Kuskokwim historically supported one of the world's largest Chinook subsistence fisheries, which is of importance to dozens of communities along the river that have some of the highest levels of subsistence dependence in the state of Alaska. Declines in Kuskokwim Chinook abundance have sharply reduced subsistence harvest, closed commercial fisheries, prompted widespread stakeholder concern about the future of the subsistence fishery, and led to disagreement among managers and stakeholders about the most appropriate way to manage Kuskokwim Chinook.

Chinook spawn across at least two-dozen tributaries of the main-stem Kuskokwim, and monitoring of harvest, escapement, and age composition for Chinook has occurred since the mid-1970s with a focus on 13 sub-basins monitored by weir or aerial surveys. These populations account for approximately half of annual escapement to the system, and total run size from 1976 and 2017 has been estimated via run reconstruction (Liller and Hamazaki 2016) scaled to drainage-wide mark-recapture estimates of total abundance (e.g., Smith and Liller 2017).

## 1.2 Fishery objectives and alternative management actions

As part of a broader exercise focused on building capacity among Kuskokwim stakeholders to engage in salmon management we held a series of workshops that included influential community members from throughout the river basin with a long history of active engagement in fishery management as well as US Fish and Wildlife Service and Alaska Department of Fish and Game biologists and fishery managers. These workshops included discussion of existing and potential Kuskokwim Chinook fishery and biological objectives and alternative management actions associated with them. From these discussions, we identified a suite of long-term objectives against which to quantify the performance of alternative management actions in the system (Table 1).

## 1.3 Multi-stock state-space spawner-recruit model

We used a multi-stock state-space spawner-recruit model to characterize Chinook population diversity and dynamics in the Kuskokwim Basin (Staton et al. n.d.). This model is an extension of various single-stock models (Fleischman et al. 2013; Staton et al. 2017) that simultaneously fits separate recruitment curves to incomplete population-specific escapement time series and mixed-stock harvest. We fit the model to time series of spawner abundance, harvest, and age composition in a Bayesian estimation framework using Markov Chain Monte Carlo methods to sample from the joint posterior distribution of all unknown quantities (implemented in JAGS; Plummer, 2017).

The key quantities estimated by the state-space model included population productivity (i.e., maximum recruits-per-spawner), carrying capacity, latent recruitment states, lag-one correlation in recruitment, variance and covariance in recruitment within and among populations, and time-varying maturity schedules. Full details of data processing and the structure of the state-space model, including model code and detailed outputs, are provided in (Staton et al. n.d.) and associated supplements. Our base formulation of the state-space model assumed that all population are equally vulnerable to harvest, but in sensitivity analyses we relaxed this assumption. We chose to use posterior draws obtained from the most complex state-space model evaluated by Staton et al. (n.b). (SSM-VM) with a maximum effective sample size of 100 for the age composition data because (1) effective sample size is nearly always less than the true sample size due to violations to the multinomial sampling distribution (2) their simulations showed no loss in estimation performance with the additional complexity, and (3) it afforded us the ability to parameterize the model more fully with respect to recruitment variance.

We used the posterior samples of population productivity and carrying capacity to quantify the range of predicted equilibrium trade-offs between aggregate harvest and conservation of population diversity across a range of mixed-stock harvest rates (Walters and Martell 2004; Walters et al. 2008).

#### 1.4 Closed loop forward simulations

To prospectively evaluate the performance of alternative harvest policies with respect to both fishery and conservation objectives, we developed a closed-loop simulation that consisted of three components: (1) an empirically parameterized multi-stock operating model that simulated the dynamics of Kuskokwim Chinook populations over time, (2) a management procedure model that assessed the state (i.e., total returning abundance) of the system each year, and applied a given harvest policy (defined by subsistence needs and basin-wide target harvest and spawner abundances), and (3) a performance model that tracked the outcomes of the management procedure for quantitative performance measures related to each fishery and conservation objective.

#### *Operating model*

We simulated future population trajectories for the 13 Kuskokwim populations for which we had data by projecting stock dynamics forward over 50 years (approximately eight generations starting in 2017), thereby generating a posterior predictive distribution of future states conditioned on the historical data. By simulating Kuskokwim Chinook dynamics in this manner, we ensured that predicted future spawner abundance and age structure were conditioned on the incomplete cohorts at the end of the data series (i.e., those cohorts from which one or more older age classes have not yet returned to spawn) and that uncertainties in the spawner-recruit relationships were propagated (i.e., by drawing from the posterior distributions of each estimated parameter and abundance state in each iteration of the simulation). We chose to use posterior draws obtained from the most complex state-space model evaluated by Staton et al. (n.b.), because their simulations showed no loss in estimation performance with the additional complexity, and it afforded us the ability to parameterize the model more fully with respect to recruitment variance.

The simulated population complex was comprised of  $n$  populations whose dynamics were governed by Ricker type stock recruitment relationships (Ricker 1954):



$$R_{y,j} = \alpha_j S_{y,j} e^{-\beta_j S_{y,j} + \phi \log(R_{y-1,j}/\hat{R}_{y-1,j}) + r_{y,j}} \quad (1)$$

195 where  $R_{y,n}$  is recruitment from brood year  $y$  for population  $j$ ,  $\alpha_n$  and  $\beta_j$  are population specific intrinsic  
 196 rate of growth (productivity) and within population density dependence, respectively,  $S_{y,j}$  is spawner  
 197 abundance,  $\phi$  is the degree of temporal correlation in recruitment from one year to the next,  $\hat{R}_{y-1,j}$  is  
 198 the expected recruitment in the previous year, and  $r_{y,j}$  is white noise variation in recruitment that is  
 199 correlated among populations according to a common correlation parameter ( $\rho$ ) following a multivariate  
 200 normal distribution:

$$r_{y,j} \sim \text{MVN}(0, \mathbf{\Sigma}),$$

$$\mathbf{\Sigma} = \begin{bmatrix} \sigma_1 \sigma_1 & \cdots & \sigma_1 \sigma_j \rho \\ \vdots & \ddots & \vdots \\ \sigma_j \sigma_1 \rho & \cdots & \sigma_j \sigma_j \end{bmatrix} \quad (2)$$

201 Returns in year  $t$ ,  $N_{t,j}$ , were then a function of the proportion of individuals that mature and return to  
 202 spawn at each age:

$$N_{t,n} = \sum_{a=4}^7 R_{t-a,n} \pi_{a-3} \quad (3)$$

203 where  $\pi$  is a maturity schedule composed of four age classes (4 through 7 for Kuskokwim Chinook). To  
 204 incorporate the effects of small population size on reproductive success (e.g., allele effects and  
 205 depensation), we set a quasi-extinction threshold at 50 spawners such that if spawner abundance fell  
 206 below this threshold recruitment from that brood year was assumed to be zero. For simplicity, we  
 207 assumed that straying among populations did not occur.

208 In each year of the forward simulation, harvest ( $H_{t,n}$ ) was subtracted from the return ( $N_{t,n}$ ) according to  
 209 the harvest control rules described in the following section (Management Procedure model). To simulate

the dynamics for the entire Kuskokwim system in each iteration of our forward simulations we expanded spawner abundance, harvest and recruitment by  $1/D$ , where  $D$  is normally distributed with a mean of 0.56 and standard deviation of 0.05 and represents an estimate of the proportional contribution of the 13 monitored populations to total Kuskokwim Chinook production (Staton et al. n.d.). This assumes that the monitored populations are a representative sample of all Kuskokwim Chinook populations with respect to population characteristics and time series properties, but was necessary so that the harvest policies we evaluated were on a scale salient to management entities.

#### *Management procedure model*

The harvest policies we explored were defined by two key management objectives: a basin-wide escapement goal ( $\tilde{E}$ ) and a harvest goal. Due to the priority placed on subsistence fishing, the harvest goal can be further defined as minimum harvests required to meet subsistence needs ( $H_{sub}$ ) and a commercial harvest goal ( $H_{com}$ ) that specifies desired harvest once subsistence needs have been met. These goals, along with the predicted run size in a given year ( $N_t$ ) determine the harvest rate ( $U_t$ ) experienced by each population in the forward simulations:

$$U_{t,j} = \begin{cases} (\dot{N}_t - \tilde{E})/\dot{N}_t, & \hat{N}_t - \tilde{E} \leq H_{sub} \\ [H_{sub} + (\dot{N}_t - \tilde{E} - H_{sub})]/\dot{N}_t, & \hat{N}_t - \tilde{E} > H_{sub} \wedge \hat{N}_t - \tilde{E} \leq H_{sub} + H_{com} \\ (H_{sub} + H_{com})/\dot{N}_t, & \hat{N}_t - \tilde{E} > H_{sub} \wedge \hat{N}_t - \tilde{E} > H_{sub} + H_{com} \end{cases} \quad (4)$$

where  $\dot{N}_t = \sum_j N_{t,j}$ . The forecasted run-size is  $\hat{N}_t = \dot{N}_t \varepsilon_N$ , where  $\varepsilon_N$  is forecast error which is assumed to be lognormally distributed with a standard deviation equal to 0.27 (based on retrospective evaluation of forecast error in the Kuskokwim) (Staton and Catalano 2018). Total harvest by population,  $H_{t,j}$ , is then

$$H_{t,j} = U_t N_{t,j} (1 + \varepsilon_H) \quad (5)$$

where  $\varepsilon_H$  reflects incomplete management control over the harvesting process and outcome uncertainty (Holt and Peterman 2006) and was assumed to be normally distributed with mean zero and standard deviation equal to 0.1. This harvest control rule results in exploitation rates that increase from zero at run sizes less than the escapement goal to a maximum when run size is equal to the escapement goal and target harvest, with the exploitation rate declining thereafter at larger run sizes (Figure 2). Further, it assumed that execution of the fishery was non-selection: the exploitation rate applied to all sub-stocks in the harvest mixture was equal each year.

#### *Harvest policies*

We quantified the performance of harvest policies across a broad range of basin wide escapement and harvest goals and then considered three contrasting harvest policies (Table 2) in more detail to illustrate how policies that prioritize different objectives are predicted to perform across a range of biological and fishery performance measures. The first policy sought to maximize potential harvest from the system by setting a basin wide escapement goal equal to that predicted to produce maximum sustained yield under equilibrium conditions. The second was a fixed harvest policy without any escapement goal where the harvest goal is equal to that required to meet minimum subsistence needs. This policy is meant to reflect a situation where fishery managers decide to solely focus on meeting subsistence needs, and minimize inter-annual variation in harvest, regardless of forecasted returns, with the assumption that harvests at the level of subsistence needs will not jeopardize long-term prospects for basin-wide sustainable use. The third policy sought to maximize yield from the system but only once biological risks of extirpation to the least productive populations are minimized. Under this policy the harvest goal was set to equal that in policy 1 but the escapement goal was increased to a level that is predicted to result in no risk of driving the weakest populations towards extinction (see performance measures below). Policy 1 is similar to the basin wide escapement goal approach to management that is currently in place in the Kuskokwim where fishery managers seek to ensure that the aggregate number of Chinook that make it to the spawning

grounds fall within the range predicted to provide expected yields greater than 100,000 while also meeting subsistence needs (recommended sustainable escapement goal range of 65,000-120,000)(Hamazaki et al. 2012). However, policy 1 differs from current management because harvesting capacity is constrained in the Kuskokwim due to household processing and consumption constraints.

#### *Uncertain states of nature*

We simulated the biological and fishery dynamics of the Kuskokwim system across three alternative states of nature. This allowed us to evaluate how robust a given harvest policy is to key structural uncertainties in the system, something that is recognized as a best-practice in the application of closed-loop simulation models to inform decision making (Punt et al. 2016). The first state of nature assumed stationary spawner-recruitment dynamics that follow a Ricker-type relationship with overcompensation at high spawner abundances (equations 1-3). This is the state of nature that is currently assumed by fishery managers in the Kuskokwim (Hamazaki et al. 2012) and widely across other salmon fisheries.

The second state of nature we considered assumed there were long-term directional changes in population productivity and carrying capacity such that half way through the simulations the least productive stocks became more productive and the most productive stocks became less productive (Figure 5). In this scenario the productivity ( $\alpha_n$ ) and carrying capacity ( $\alpha_n/\beta_n$ ) of individual stocks was assumed to be time-varying and to change over the course of a decade (from  $t=20$  to  $t=30$  in the simulations). These changes were meant to reflect a situation involving large changes in the productive capacity in some stocks and commensurate declines in others (e.g., due to changes in hydrology, geomorphology or life history characteristics) such that the overall production of the system remains unchanged but relative population contributions to production does. The magnitude of change we considered under this scenario is biologically plausible; it is within the ranges of changes in productivity

and capacity seen in other salmon systems, albeit at coarser spatial scales (Hilborn et al. 2003; Peterman and Dorner 2012; Dorner et al. 2017).

The third state of nature we considered assumed that low frequency regime shifts occur that gave rise to the appearance of overcompensation, when in fact none was present. Under this scenario we assumed that individual spawner-recruitment relationships were governed by Beverton-Holt dynamics with cyclical variation in population productivity. To do this we transformed the Ricker spawner-recruitment relationship in equation 1 to a Beverton-Holt form (Hilborn and Walters 1992):

$$\bar{R}_{y,j} = \frac{\alpha_{y,j}}{1 + \frac{\alpha_{y,j}}{\beta_j} S_{y,j}} \quad (6)$$

$$\alpha_{y,j} = \sin(2\pi \left(\frac{y}{f}\right)) ((\alpha_j \delta + (\alpha_j \delta A)) - \alpha_j \delta) + \alpha_j \delta$$

where population productivity ( $\alpha_{y,j}$ ) is time-varying following a cycle with a period equal to  $f$  and amplitude equal to  $A$ . We fixed  $f$  and  $A$  at 12 and 0.4, respectively based on exploratory simulations, to generate spawner-recruitment relationships with apparent overcompensation that approximates that observed in the Kuskokwim. The term  $\delta$  is a scalar that adjusts productivity such that long-term population equilibrium abundance in the absence of fishing is approximately the same as those assuming a Ricker spawner-recruitment relationship. We fixed  $\delta$  at 0.76 based on further exploratory simulations that showed that long-term basin-wide equilibrium spawner abundances were the same under the alternative spawner-recruitment formulations when average productivity in the Beverton-Holt formulation is scaled by 0.76. Note that this scalar may depend on the spawner-recruit relationships used, and should therefore be obtained separately for analyses of different populations in other systems.

### *Performance measures*

Biological and fishery objectives were identified through workshops with fishery managers and stakeholders (Table 2), and we quantified the relative ability of the alternative harvest policies to attain

them according to a set of performance measures. Performance measures related to harvest objectives included average catch and the inter-annual coefficient of variation (CV) in catch, both over the last 20 years of the 50 year simulations. We quantified performance relative to the objective of maximizing spatial equity in access to salmon across the river basin as the proportion of populations whose average spawner abundance over the last 20 years of each Monte Carlo trial was greater than or equal to the population specific estimate of  $S_{MSY}$ . Lastly, we quantified biological performance as the proportion of populations whose average spawner abundance over the last 20 years of the Monte Carlo trial dropped below a quasi-extinction threshold of 5% of equilibrium population size. Each performance measure was summarized across 500 Monte Carlo trials, each parameterized by a unique draw from the posterior distribution of the state-space model fitted to Kuskokwim data (Staton et al. n.b).

## Results

### 2.1 Population diversity

We found clear evidence of heterogeneity in productivity and carrying capacity across the Kuskokwim Chinook populations for which there were data (Figure 3a). Kuskokwim Chinook populations ranged in equilibrium size from approximately 1000 to 18,000 spawners and in productivity from 1.65 to 5 recruits-per-spawner (median posterior estimates). There was a weak tendency for larger populations to be more productive, however, no strong spatial patterns in productivity were found (Figure 1 and 3a). We used this observed heterogeneity to quantify equilibrium trade-off between harvest and protection of population diversity in the system (Figure 3b). This illustrates that the relatively high harvest rates that can be sustained by the most productive populations come at the cost of increased risk of over-exploitation for those that were found to be less productive. The large uncertainty in our estimates of productivity and carrying capacity result in large uncertainty in these predicted trade-offs.

### 2.2 Performance of alternative harvest policies and trade-offs among objectives

Our closed-loop simulations indicated that mixed-stock harvest was maximized at intermediate basin scale escapement goals (~60,000-120,000)(Figure 4a, which is consistent with independent yield analyses from the stock aggregate (Hamazaki et al. 2012). At escapement goals greater than 120,000, harvests are reduced due to more frequent fishery closures, and at escapement goals lower than 60,000 harvests are reduced due to the loss of production from the weakest (i.e., least productive) populations in the system. Harvest stability was predicted to be greatest at both low escapement goals and target harvests (Figure 4b) and the chances of meeting tributary spawner goals and minimizing risks of driving individual populations to extirpation were greatest when target harvests were low and/or basin-wide escapement goals were high (Figure 4c and d).

There was strong asymmetry in trade-offs between harvest and biological or social objectives, with the strength of the asymmetry in trade-offs dependent on the harvest policy that was applied. The harvest policy that sought to maximize mixed-stock harvest (policy 1) did so at the costs of increased inter-annual variation in harvest, reduced chances of meeting tributary spawner goals and elevated risk of weak stock extirpation (Figures 4 and 5). In contrast, relative to policy 1, the fixed harvest approach (policy 2) increased inter-annual stability in harvest by 22%, increased the chances of meeting tributary spawner goals by 83%, and reduced median extirpation risk (Figure 3 and 4). This came at the cost, on average, of a 46% reduction in realized overall harvest. The harvest policy that sought to minimize the risk of driving weak stocks to extirpation (policy 3) did so at the cost of a 20% reduction in harvests and 16% reduction in inter-annual stability in harvests, but with the benefit of increasing the chances of ensuring equitable access to Chinook (i.e., meeting tributary goals) by 84% from 46% to 85%.

Though there was large uncertainty in the predicted performance of alternative policies, by propagating uncertainty through the closed-loop simulations we can interpret fishery and biological outcomes probabilistically. For example, we found that there was a 41% chance that at least 90% of tributary-level spawner goals would be met if policy 3 was chosen compared to a 1% or 35% chance if policy 1 or 2 were

chosen, respectively. Or from a protection of biocomplexity perspective, there was less than a 20% chance of causing at least one population to become extirpated under policy 3, but a 70% or 24% chance if policy 1, or 2 were chosen, respectively.

## 2.3 Effects of alternative states of nature

We found that the strength of trade-offs between harvest and stability, equity, or risk to diversity were mediated by non-stationarity in the system. When there were large shifts in population diversity over time (Figure 6), we found that similar magnitudes of reductions in harvest must be sacrificed to protect diversity (~30%) but that commensurate increases in equity in access to Chinook were larger than when there were not regime shifts in the system (55% vs 45 %; Figure 7; compare grey and blue bars). In addition, we found that regardless of the harvest policy overall, extirpation risk was elevated where there were pronounced regime shifts in the system.

The performance of harvest policies, and their resulting trade-offs, were also sensitive to the underlying drivers of recruitment variation. When recruitment dynamics were driven by a time-varying Beverton-Holt type relationship, absolute harvest and its inter-annual variation were predicted to be lower relative to the alternative spawner-recruitment dynamic scenarios (Figure 7; compare green bars to grey and blue bars), and the magnitude of reduction in harvest between harvest policies was greater (50% vs 27%). However, the chances of meeting tributary goals, and extirpation risk, were generally similar across all three spawner-recruitment dynamic scenarios and asymmetry in harvest-diversity trade-offs was dampened: a 50% reduction in predicted harvest from the maximize yield to minimize risk policies was predicted to result in a 45% increase in the chances of meeting tributary goals, compared to 26% and 45%, respectively, under the stationary Ricker scenario.



## Discussion

Four key findings emerge from our analyses of Chinook population diversity and performance of alternative harvest policies in the Kuskokwim system. First, we found clear evidence of population diversity where productivity and carrying capacity can vary by as much as 3-fold and 18-fold among populations, respectively. This population diversity gave rise to a clear trade-off between mixed-stock harvest and conserving population diversity: high harvest rates, which can be sustained by the most productive populations, can come at the cost of increased risk of overfishing those that are less productive. Second, this trade-off was strongly asymmetric: our analysis showed that giving up relatively small amounts of harvest resulted in both large reductions in risk to weak stocks and large gains in spatial equity among subsistence communities in access to the resource. For example, a 20% reduction in average annual mixed-stock harvest by shifting from a policy focused on mixed-stock yield to one that also considers risk to population diversity resulted in an 84% increase in the chances of ensuring equitable access to Chinook across the communities in the river basin and a near complete elimination of risk of driving weak populations to extinction.

Third, we found that it is possible for the strength of these harvest-population diversity trade-offs to be mediated by external changes in the environment. When the environment drives pronounced shifts over time in the size and productivity of populations in the system (e.g., a regime shift) giving up a specific amount of harvest results in larger gains in spatial equity in access to the salmon for subsistence needs relative to scenarios where there is not a regime shift. These predicted benefits are dependent on the magnitude of change in population size and productivity over time. While the magnitude of change we considered was within the ranges of changes in productivity and capacity seen in other salmon systems (Hilborn et al. 2003; Peterman and Dorner 2012; Dorner et al. 2017), they were of a large magnitude and occurred over a short (10-year) time period (Figure 5). As a result, our findings might be appropriately

considered an upper bound to the potential benefits of protecting population diversity within the system from a harvest-diversity trade-off perspective.

Fourth, we found that the performance of harvest policies, and their resulting trade-offs were sensitive to the true underlying drivers of recruitment variation. Many salmon systems, including the Kuskokwim are assumed to exhibit strong overcompensation where survival declines at high spawner abundance (i.e., a Ricker type spawner-recruitment relationship). However, cyclical environmental forcing can lead to apparent overcompensation in observed spawner-recruitment relationships because years of high recruitment due to favourable environmental conditions are followed by years of low recruitment due to unfavourable conditions (Parma and Deriso 1990). The true drivers of recruitment in a system are rarely known; this uncertainty can fuel debate about the fishery and ecological consequences of alternative assumptions about the structural form of spawner-recruitment relationships when providing harvest advice (Schindler et al. 2019). It is well known that fishery reference points are more biologically conservative (e.g.,  $S_{MSY}$  is higher) when one assumes a Ricker type spawner-recruitment relationship rather than a Beverton-Holt one (Fleischman et al. 2013); however, the performance of alternative harvest policies across these uncertain states of nature are rarely fully evaluated. We found that absolute harvest and its inter-annual stability were predicted to be lower, and that more harvest had to be foregone to minimize extirpation risk and increase chances of ensuring equitable access to Chinook, under the time-varying Beverton-Holt scenario relative to the Ricker ones. As a result, the asymmetry in harvest-diversity trade-offs was weaker under the Beverton-Holt scenario.

As is inevitable with any analysis of a complex socio-ecological system, we made a number of simplifying assumptions. First, due to incomplete monitoring coverage we were only able to model the dynamics of Chinook populations that comprise approximately half of the production from the system (Figure 1). This implicitly assumes that monitored stocks are a representative sample of all populations with respect to population characteristics and time series properties. If this assumption is severely violated then our

inference about trade-offs and aggregate yield may be biased. For example, if only the most productive populations are monitored then we would have underestimated risks to population diversity. Nonetheless, given that the populations with data are distributed across the basin (Figure 1) and range widely in both their productivity and size we suspect that we have captured the general bounds of the system. It should also be noted that the weakest (least productive) spawning populations in the Kuskokwim may have been extirpated early in the development of the fishery for this river, and are thus absent from our dataset.

Second, our simulations treated each population as a closed spawning population because we did not consider the effects of straying between and within basins. Straying is fundamental characteristic of salmon and clearly an important contributor to adaptation and fitness. Failing to account for straying could lead to overestimating risk of extirpation because populations at low abundance cannot be “rescued” by neighbouring populations. In general, it is hypothesized that the relative frequency of straying in wild salmon is related to stability of habitat quality, extent of specialization for freshwater habitat, and variation in age at maturity (Quinn 2018b). As a result, straying is considered to occur at lower levels in Chinook (and particularly stream-type Chinook like those in the Kuskokwim) than in other Pacific salmon like pink and chum. Empirical estimates of Chinook stray rates are available for hatchery fish and range from 0.1 to 10% for stream-type Chinook in the Columbia Basin (Westley et al. 2013). In light of the above magnitude of straying, and the fact that the populations we considered typically had spawning locations that were greater than 100 km away from the nearest other populations, we considered the magnitude of straying to likely be negligible but nonetheless consider this an area that warrants future study. Strontium isotopes, which have recently been used to uncover fine-scale natal origins and migration histories of Chinook in western Alaska (Brennan et al. 2019), offer a potentially useful tool to quantify the magnitude of straying in the large river basins.

431 Lastly, our closed-loops simulations are empirically parameterized from a multi-stock spawner-recruit  
432 analysis (Staton et al. n.d.) that assumes all populations in the system have historically been equally  
433 vulnerable to harvest, which was also made in our analysis. While the vast majority of harvest has  
434 historically occurred in the lower river near the community of Bethel, differences in run-timing and the  
435 timing of the fishery (typically front-loaded due to drying weather), are likely to have led to headwater  
436 fish being more vulnerable to harvest than lower river populations (Hamazaki 2008). The key findings from  
437 our closed-loop simulations are robust to this assumption (Figure S1) but modelling population variation  
438 in run-timing and the timing of fisheries are logical extensions to the work we present here.

439 We chose three simple and contrasting harvest policies to illustrate their predicted performance against  
440 Chinook fishery and population diversity objectives in the Kuskokwim. While the contrasting policies were  
441 not intended to exactly match the current approach to management, there are some general insights that  
442 emerge from our analysis that are of relevance for management of the Chinook fishery moving forward.  
443 We find that a relatively low overall harvest rate is more important than a strict, high escapement goal,  
444 with respect to minimizing extirpation risk. This is because our simulations suggest that subsistence needs,  
445 and spatial equity in access to fish, can be met with relatively low risk to population diversity even when  
446 the escapement goal is very low. However, as harvest goals increase above those required to meet  
447 subsistence needs the importance of an escapement goal becomes more pronounced to the point where  
448 if target harvest is at or near its historic maximum (~150,000) managing for the upper end of the basin  
449 scale escapement goal derived from optimal yield profiles (Hamazaki et al. 2012) is necessary and  
450 adequate to minimize extirpation risk. An obvious next step in the Kuskokwim would be to implement a  
451 Management Strategy Evaluation that incorporates short-term within-season dynamics and decision  
452 making, population differences in run-timing (Smith and Liller 2017b) and harvest vulnerability (Hamazaki  
453 2008), with the formal engagement of decision makers and stakeholders in the process (e.g., Cunningham  
454 et al. 2018).

The performance, and merits, of alternative harvest policies in salmon management have been debated for years. Many salmon systems are managed with escapement goals based on basin scale yield predictions, as in the case in many parts of Alaska and British Columbia. Time varying policies have been shown through simulations to yield improved performance against fishery and conservation objectives when there is low frequency changes in the productivity of salmon stocks over time (Collie et al. 2012). However, these types of harvest policies can lead to relatively high variability in harvest, and require precise information on run size to inform annual harvest rates. In instances where stability in harvest and large errors in forecasts dominate, fixed harvest policies (with caps based on conservation constraints) can perform well against fishery and conservation objectives (Hawkshaw and Walters 2015).

Maintaining population diversity is increasingly recognized as a hallmark of sustainable and resilient fisheries management. However, in large river basins (e.g., Kuskokwim, Yukon, Skeena, and Fraser) with relatively little fine spatial and temporal management control doing so can be challenging. Our work provides a blueprint for characterizing salmon population diversity in large river basins with relatively limited management control and evaluating harvest-population diversity trade-offs among alternative harvest policies within them.

## **Acknowledgements**

We are grateful for the efforts of the many technicians and biologists who gathered and processed the salmon data used in this manuscript and to Z. Liller and N. Smith for sharing them with us. This work benefitted greatly from discussions with a group of Kuskokwim River residents and government agency staff that shared their knowledge and perspectives with us in a series of capacity-building workshops in Bethel and Aniak AK between 2015 and 2018; we are particularly grateful for contributions from Lamont Albertson, Bill Bechtol, Barb Carlson, James Charles, Dave Cannon, Lisa Feyereisen, Dan Gillikin, Ken Harper, Nick Kamaroff, Zach Liller, Mary Paltola and Kevin Whitworth. This project was funded by the

Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative (<http://www.aykssi.org/>) and we thank J. Spaeder for his insights and support.

## References

- Anderson, S.C., Moore, J.W., McClure, M.M., Dulvy, N.K., and Cooper, A.B. 2015. Portfolio conservation of metapopulations under climate change. *Ecol. Appl.* **25**(2): 559–572. Wiley Online Library.
- Anderson, S.C., Ward, E.J., Shelton, A.O., Adkison, M.D., Beaudreau, A.H., Brenner, R.E., Haynie, A.C., Shriver, J.C., Watson, J.T., and Williams, B.C. 2017. Benefits and risks of diversification for individual fishers. doi:10.1073/pnas.1702506114.
- Brennan, S.R., Schindler, D.E., Cline, T.J., Walsworth, T.E., Buck, G., and Fernandez, D.P. 2019. Shifting habitat mosaics and fish production across river basins. *Science* (80-. ). **364**(6442): 783–786. American Association for the Advancement of Science.
- Cline, T.J., Schindler, D.E., and Hilborn, R. 2017. Fisheries portfolio diversification and turnover buffer Alaskan fishing communities from abrupt resource and market changes. *Nat. Commun.* **8**: 14042. Nature Publishing Group.
- Collie, J.S., Peterman, R.M., and Zuehlke, B.M. 2012. A fisheries risk-assessment framework to evaluate trade-offs among management options in the presence of time-varying productivity. *Can. J. Fish. Aquat. Sci.* **69**(2): 209–223. doi:10.1139/f2011-148.
- Cunningham, C.J., Anderson, C.M., Wang, Y.-L.J., Link, M.R., Hilborn, R., Wang, J.Y., Link, M.R., and Hilborn, R. 2018. A management strategy evaluation of the commercial sockeye salmon fishery in Bristol Bay, Alaska. *Can. J. Fish. Aquat. Sci.* **15**(ja): 1–15. NRC Research Press.
- Deacy, W.W., Leacock, W.B., Stanford, J.A., and Armstrong, J.B. 2019. Variation in spawning phenology within salmon populations influences landscape-level patterns of brown bear activity. *Ecosphere* **10**(1): e02575. Wiley Online Library.
- DFO. 2005. Canada's policy for conservation of wild Pacific salmon.
- Dorner, B., Catalano, M.J., and Peterman, R.M. 2017. Spatial and temporal patterns of covariation in productivity of Chinook salmon populations of the Northeastern Pacific. *Can. J. Fish. Aquat. Sci.* **1095**(September 2017): cjfas-2017-0197. doi:10.1139/cjfas-2017-0197.
- Fleischman, S.J., Catalano, M.J., Clark, R.A., Bernard, D.R., and Chen, Y. 2013. An age-structured state-space stock–recruit model for Pacific salmon (*Oncorhynchus* spp.). *Can. J. Fish. Aquat. Sci.* **70**(3): 401–414. doi:10.1139/cjfas-2012-0112.
- Hamazaki, T. 2008. When people argue about fish, the fish disappear. *Fisheries* **33**(10): 495–501. Wiley Online Library. doi:10.1577/1548-8446-33.10.495.
- Hamazaki, T., Evenson, M.J., Fleischman, S.J., and Schaberg, K.L. 2012. Spawner-recruit analysis and escapement goal recommendation for Chinook salmon in the Kuskokwim River Drainage. Alaska

Department of Fish and Game. Fish. Manuscr. Ser. (12-08).

Hawkshaw, M., and Walters, C. 2015. Harvest control rules for mixed-stock fisheries coping with autocorrelated recruitment variation, conservation of weak stocks, and economic well-being. *Can. J. Fish. Aquat. Sci.* **72**(5): 759–766. NRC Research Press. doi:10.1139/cjfas-2014-0212.

Hilborn, R., Fulton, E.A., Green, B.S., Hartmann, K., Tracey, S.R., and Watson, R.A. 2015. When is a fishery sustainable? *Can. J. Fish. Aquat. Sci.* **72**(9): 1433–1441. doi:10.1139/cjfas-2015-0062.

Hilborn, R., Quinn, T.P., Schindler, D.E., and Rogers, D.E. 2003. Biocomplexity and fisheries sustainability. *Proc. Natl. Acad. Sci.* **100**(11): 6564–6568. National Acad Sciences.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Springer.

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. NRC Research Press.

Liller, Z.W., and Hamazaki, T. 2016. Kuskokwim River Chinook salmon run reconstruction, 2015. Alaska Department of Fish and Game, Division of Commercial Fisheries.

Link, J.S. 2017. System-level optimal yield: increased value, less risk, improved stability, and better fisheries. *Can. J. Fish. Aquat. Sci.* **75**(1): 1–16. NRC Research Press.

Malick, M.J., Cox, S.P., Mueter, F.J., Dorner, B., and Peterman, R.M. 2017. Effects of the North Pacific Current on the productivity of 163 Pacific salmon stocks. *Fish. Oceanogr.* **26**(3): 268–281. Wiley Online Library.

Nesbitt, H.K., and Moore, J.W. 2016. Species and population diversity in Pacific salmon fisheries underpin indigenous food security. *J. Appl. Ecol.* **53**(5): 1489–1499. doi:10.1111/1365-2664.12717.

Ohlberger, J., Scheuerell, M.D., and Schindler, D.E. 2016. Population coherence and environmental impacts across spatial scales: A case study of Chinook salmon. *Ecosphere* **7**(4): 1–14. doi:10.1002/ecs2.1333.

Parma, A.M., and Deriso, R.B. 1990. Experimental harvesting of cyclic stocks in the face of alternative recruitment hypotheses. *Can. J. Fish. Aquat. Sci.* **47**(3): 595–610. NRC Research Press.

Pestes, L.R., Peterman, R.M., Bradford, M.J., and Wood, C.C. 2008. Bayesian decision analysis for evaluating management options to promote recovery of a depleted salmon population. *Conserv. Biol.* **22**(2): 351–361. Wiley Online Library.

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. doi:10.1139/f2012-063.

Plummer, M. 2017. JAGS version 4.3. 0 user manual.

- Punt, A.E., Butterworth, D.S., de Moor, C.L., De Oliveira, J.A.A., and Haddon, M. 2016. Management strategy evaluation: Best practices. *Fish Fish.* **17**(2): 303–334. doi:10.1111/faf.12104.
- Quinn, T.P. 2018a. From magnets to bears: Is a career studying salmon narrow or broad? *ICES J. Mar. Sci.* **75**(5): 1546–1552. doi:10.1093/icesjms/fsy055.
- Quinn, T.P. 2018b. The behavior and ecology of Pacific salmon and trout. University of Washington press.
- Ricker, W.E. 1954. Stock and recruitment. *J. Fish. Board Canada* **11**(5): 559–623. NRC Research Press.
- Rogers, L.A., Schindler, D.E., Lisi, P.J., Holtgrieve, G.W., Leavitt, P.R., Bunting, L., Finney, B.P., Selbie, D.T., Chen, G., and Gregory-Eaves, I. 2013. Centennial-scale fluctuations and regional complexity characterize Pacific salmon population dynamics over the past five centuries. *Proc. Natl. Acad. Sci.* **110**(5): 1750–1755. National Acad Sciences.
- Schindler, D.E., Armstrong, J.B., Bentley, K.T., Jankowski, K., Lisi, P.J., and Payne, L.X. 2013. Riding the crimson tide: mobile terrestrial consumers track phenological variation in spawning of an anadromous fish. *Biol. Lett.* **9**(3): 20130048. The Royal Society.
- Schindler, D.E., Armstrong, J.B., and Reed, T.E. 2015. The portfolio concept in ecology and evolution. *Front. Ecol. Environ.* **13**(5): 257–263. Wiley Online Library. doi:10.1890/140275.
- Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species. *Nature* **465**(7298): 609–612. Nature Publishing Group. doi:10.1038/nature09060.
- Schindler, D.E., Walsworth, T.E., Adkison, M.A., 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.
- Service, C.N., Bateman, A.W., Adams, M.S., Artelle, K.A., Reimchen, T.E., Paquet, P.C., and Darimont, C.T. 2019. Salmonid species diversity predicts salmon consumption by terrestrial wildlife. *J. Anim. Ecol.* Wiley Online Library.
- Sethi, S.A. 2010. Risk management for fisheries. : 341–365. doi:10.1111/j.1467-2979.2010.00363.x.
- Smith, N.J., and Liller, Z.W. 2017a. Inriver abundance and migration characteristics of Kuskokwim River Chinook salmon, 2015. *Fish. Data Ser.* 17-22, Alaska Dep. Fish Game, Anchorage, AK. Available from <http://www.adfg.alaska.gov/FedAidPDFs/FDS17-22.pdf>.
- Smith, N.J., and Liller, Z.W. 2017b. Inriver abundance and migration characteristics of Kuskokwim River Chinook salmon, 2015. *Fish. Data Ser.* 17-22, Alaska Dep. Fish Game, Anchorage, AK.
- Staton, B.A., and Catalano, M.J. 2018. Bayesian information updating procedures for Pacific salmon run size indicators: Evaluation in the presence and absence of auxiliary migration timing information. *Can. J. Fish. Aquat. Sci.* (ja). NRC Research Press.
- Staton, B.A., Catalano, M.J., Connors, B., Coggins, L., Jones, M.L., Walters, C.J., Fleischman, S.J., and Gwinn, D. (n.d.). Evaluation of Methods for Quantifying Sub-population Diversity in Mixed-stock Pacific



Salmon Fisheries.

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. *Fish. Res.* **186**: 237–247. Elsevier B.V. doi:10.1016/j.fishres.2016.09.001.

Walters, C., English, K., Korman, J., and Hilborn, R. 2018. The managed decline of British Columbia's commercial salmon fishery. *Mar. Policy.* Elsevier.

Walters, C.J., Lichatowich, J.A., Peterman, R.M., and Reynolds, J.D. 2008. Report of the Skeena independent science review panel. A Rep. to Can. Dep. Fish. Ocean. Br. Columbia Minist. Environ. **15**.

Walters, C.J., and Martell, S.J.D. 2004. Fisheries ecology and management. Princeton University Press.

Westley, P.A.H., Quinn, T.P., and Dittman, A.H. 2013. Rates of straying by hatchery-produced Pacific salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss*) differ among species, life history types, and populations. *Can. J. Fish. Aquat. Sci.* **70**(5): 735–746. NRC Research Press.

**Table 1.** Fishery and conservation objectives, along with alternative management actions, identified by Kuskokwim River stakeholders.

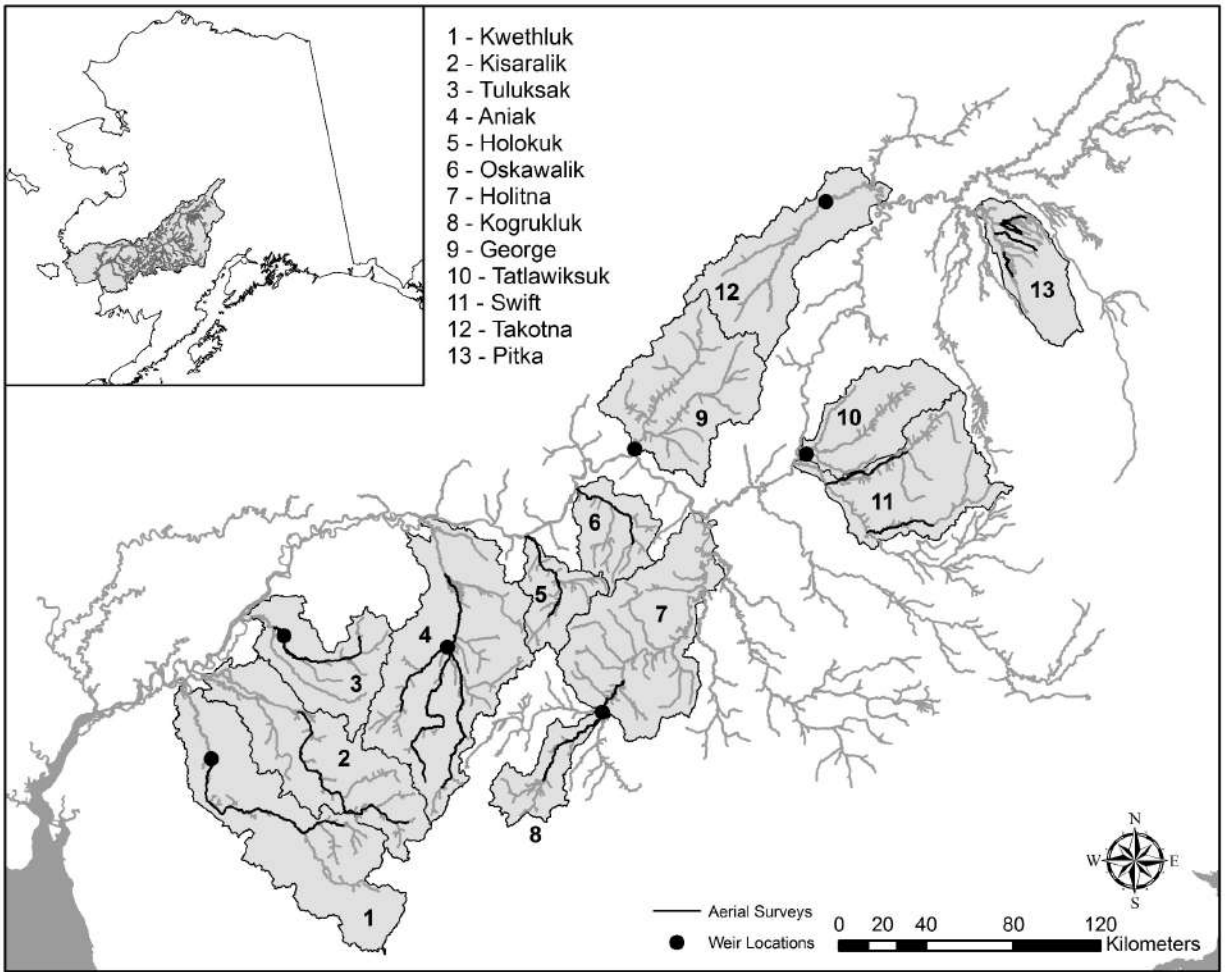
Objectives	Alternatives
<ul style="list-style-type: none"> <li>• Maintain population and species diversity</li> <li>• Maximize equity among villages in access to salmon resource</li> <li>• Ensure and protect food security for subsistence users</li> <li>• Maximize commercial fishing opportunities</li> </ul>	<ul style="list-style-type: none"> <li>• Fixed harvest (i.e., minimum required to meet subsistence needs)</li> <li>• Manage for basin wide maximum sustainable yield</li> <li>• Manage for escapements greater than those predicted to maximize yield so as to protect less productive stocks and ensure equity among villages in access to salmon</li> <li>• Manage for population specific escapement goals</li> </ul>

**Table 2.** Alternative harvest policies considered in the closed loop simulations.

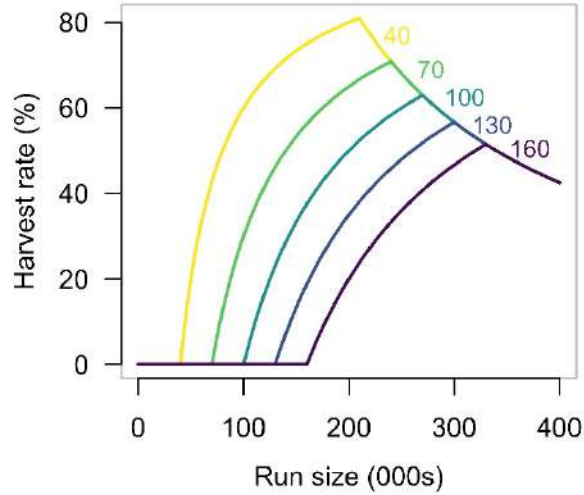
Policy	Basin wide escapement goal ( $\tilde{E}$ )	Subsistence needs ( $H_{sub}$ )	Commercial harvest goal ( $H_{com}$ )
Maximize basin wide harvest	75,000	65,000	105,000
Fixed harvest at levels needed for subsistence and maximize harvest stability	5,000	65,000	0
Maximize harvest while minimizing biological risk	135,000	65,000	105,000

**Table 3. States, biological and policy parameters and associated values.** Description of states and parameters in the close loop simulation model described in the main text along with their associated values where appropriate.

Parameter	Description (with median values for base scenario where appropriate)	Equation at first use
$S_{y,n}$	Spawner abundance in brood year $y$ from population $n$	1
$R_{y,n}$	Recruitment in brood year $y$ from population $n$	1
$\alpha_n$	Productivity (maximum recruits-per-spawner at small population size) for population $n$	1
$\beta_n$	Magnitude of within brood-year density dependent effects on survival for population $n$	1
$\phi$	Strength of lag-one temporal correlation in survival [0.23]	1
$\sigma_n$	Recruitment variation (SD units) for population $n$ [0.69]	2
$\rho_{i,j}$	Correlation in recruitment variation between population $i$ and $j$ [0.18-0.28]	
$\pi_{3:6}$	Age-at-maturity proportions [4yrs=0.25, 5yr=0.36, 6yr=0.35, 7yr=0.4]	3
$N_{t,n}$	Adult salmon returning to spawn prior to any harvest in fisheries in calendar year $t$ from sub- stock $n$	3
$\dot{N}_t$	Total aggregate run-size in calendar year $t$	4
$\hat{N}_t$	Forecasted aggregate run-size in calendar year $t$	4
$\tilde{E}$	Basin-wide escapement goal	4
$H_{sub}$	Basin-wide minimum harvest required to meet subsistence needs	4
$H_{com}$	Basin-wide commercial harvest target	4
$U_{n,t}$	Harvest rate experienced by population $n$ in calendar year $t$	4
$\varepsilon_N$	Forecast error [ $\sim \ln(1, 0.27)$ ]	4
$\varepsilon_H$	Outcome uncertainty [ $\sim N(0,0.1)$ ]	5
$f$	Period of time-varying productivity in Beverton-Holt spawner-recruitment model formulation [12]	6
$A$	Amplitude of time-varying productivity in Beverton-Holt spawner-recruitment model formulation [0.4]	6
$\delta$	Scalar that adjust productivity in Beverton-Holt formulation so that long-term equilibrium abundance is equal to that under the Ricker spawner-recruitment [0.67]	6

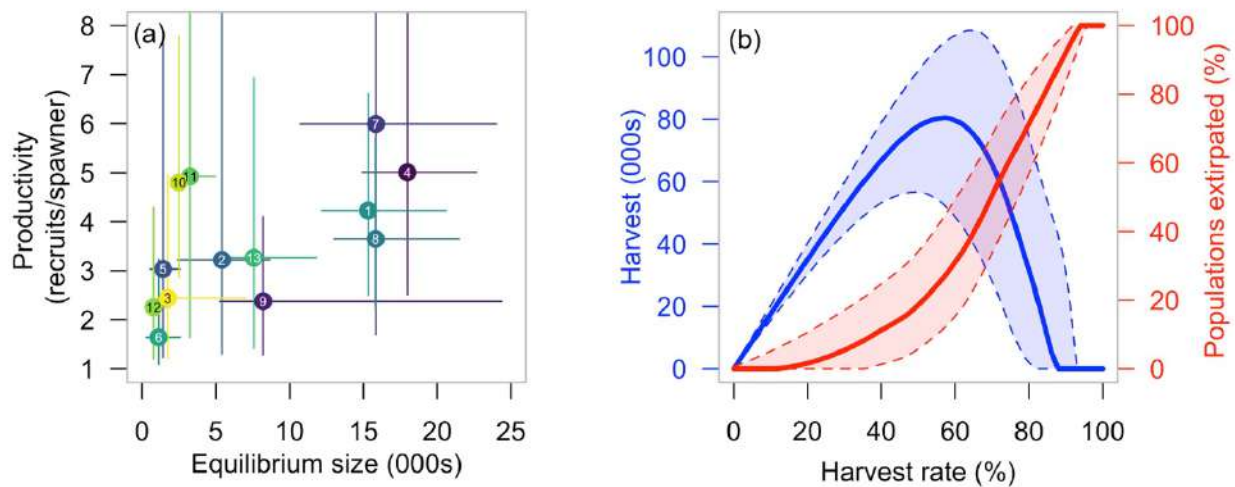


**Figure 1. The Kuskokwim River basin.** General spawning distribution of the 13 Chinook populations for which there are estimates of spawner abundance based on either weir or aerial surveys.

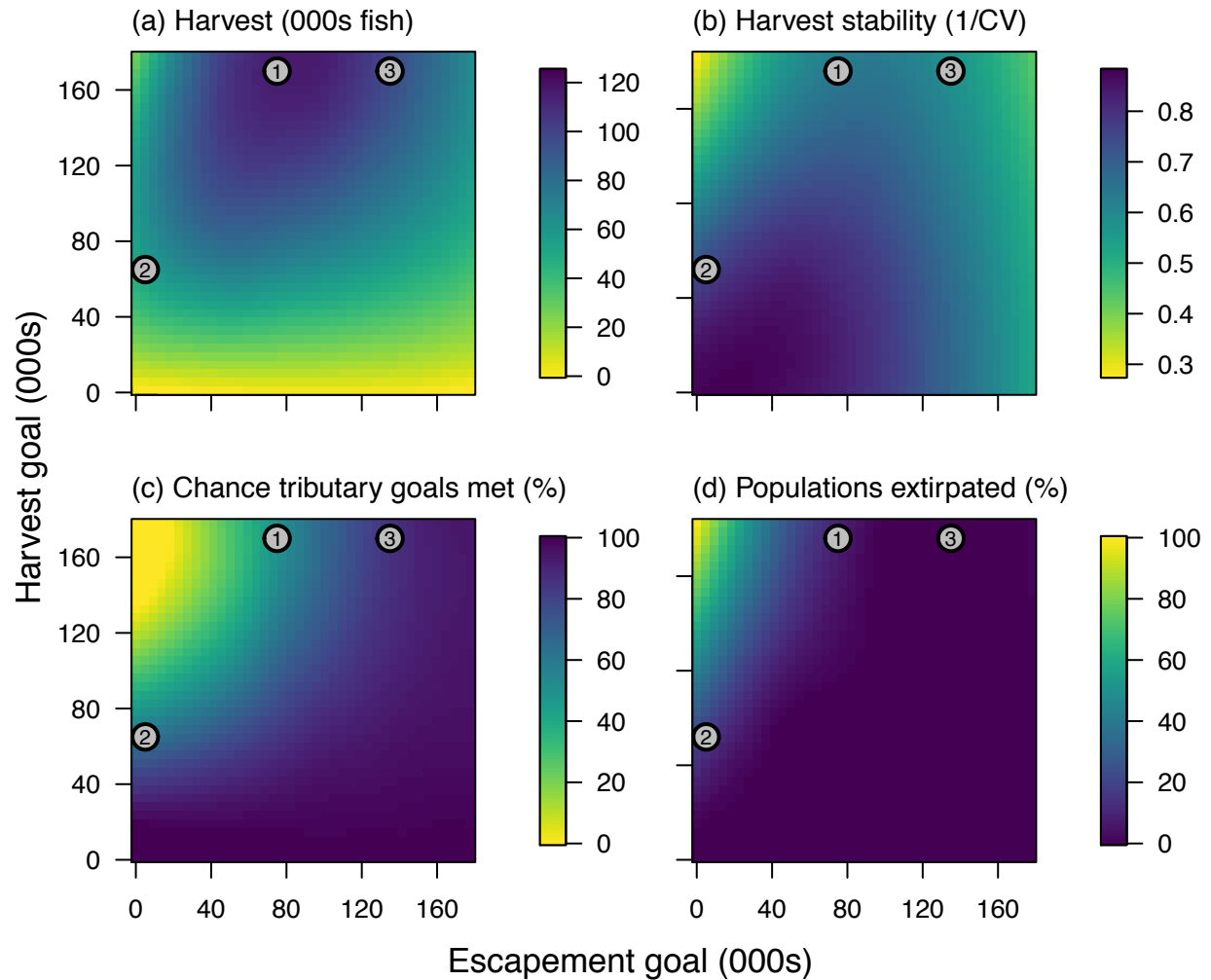


609

610 **Figure 2. Kuskokwim Chinook harvest control rule.** Illustration of mixed-stock harvest rate as a function  
 611 of true run-size across a range of escapement goals (colored lines) assuming a relatively high (175,000  
 612 fish) harvest goal (equation 4). The deterministic harvest control rule is shown but in the closed loop  
 613 simulations the realized harvest rate in any given year deviate from this relationship as a function of  
 614 forecast error and outcome uncertainty.

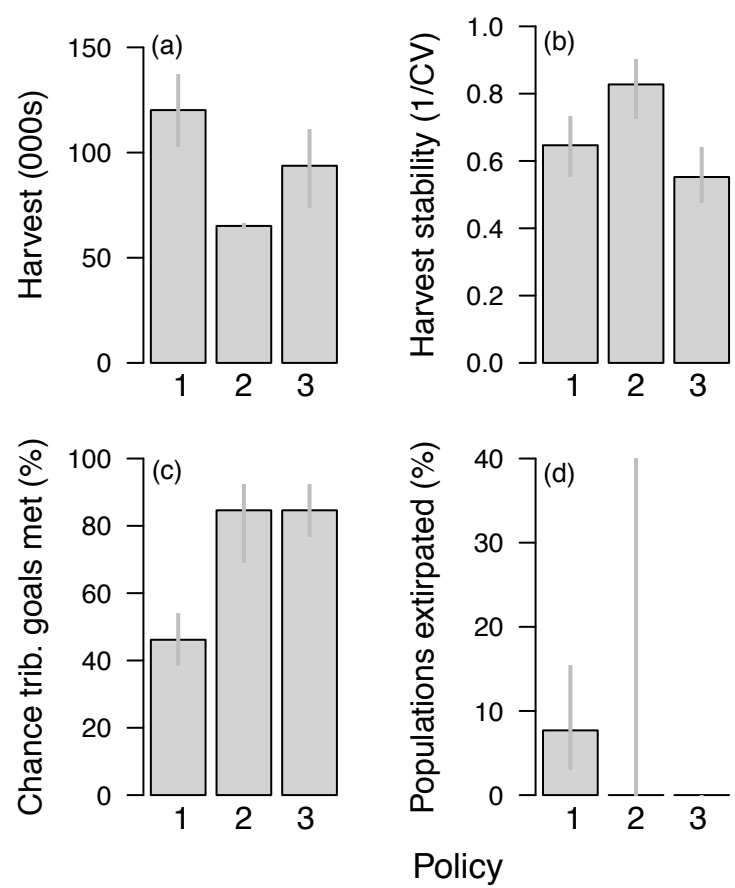


**Figure 3. Kuskokwim Chinook population diversity and trade-offs with harvest.** (a) Posterior distributions of intrinsic productivity (alpha – recruits per spawner at small population size) for individual population along with corresponding estimates of equilibrium population size. Points are colored to increase visual contrast and numbers correspond to the populations in Figure 1; (b) Predicted basin wide equilibrium yield across a range of fixed harvest rates and corresponding risks to population diversity. Overall yield from the system is predicted to be maximized at a harvest rate of ~ 50%, but this comes at the cost of putting ~20% of the populations at risk of extirpation.



**Figure 4. Predicted consequences of alternative harvest policies.** Each policy is defined by a combination of basin scale harvest (y-axis) and escapement goals (x-axis). Performance measures (z-axis) are calculated over the last 20 years of each Monte Carlo trial (500 in total), which project stock dynamics 50 years forward in time, and correspond to (a) median harvest (in thousands of Chinook salmon), (b) harvest stability (1/ coefficient of variation [CV] in harvest), (c) proportion of population tributaries with spawner abundances that exceeded a tributary specific spawner target ( $S_{MSY}$ ) and (d) proportion of populations extirpated. Three illustrative harvest policies are overlaid on each panel (see Table 2 for more details): (1) a policy that seeks to maximize yield, (2) a fixed harvest policy corresponding to minimum subsistence needs and (3) a policy that seeks to reduce biological risks to populations while also achieving relatively high harvests.

635



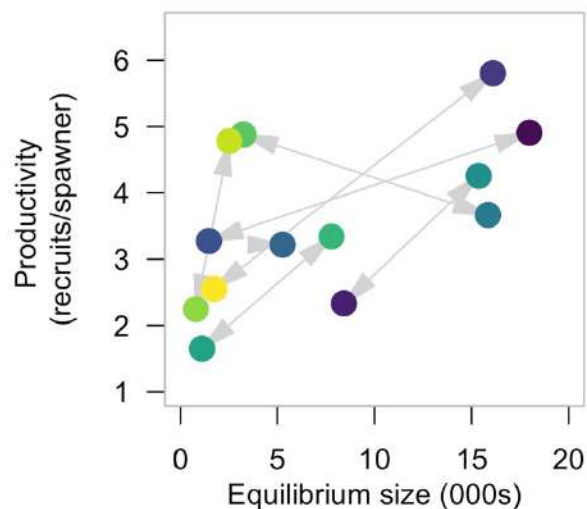
636

637 **Figure 5. Trade-offs between harvest policies.** Predicted ability of three alternative harvest policies (see  
638 Figure 4 and Table 2) to meet fishery (a: harvest and b: harvest stability), equity (c: proportion of  
639 population tributaries with spawner abundances that exceeded a tributary specific spawner goals) and  
640 conservation (d: proportion of populations extirpated) objectives. Each bar is the median (and 25<sup>th</sup> and  
641 75<sup>th</sup> percentiles) performance of a given policy as calculated over the last 20 years of each Monte Carlo  
642 trial (500 in total). Contrasting policies within and among panels illustrates trade-offs in the system  
643 between harvest, equity and conservation, as well as asymmetry in them – but it is important to recognize  
644 that these three policies are only three points in the policy space as defined by this analysis.

645



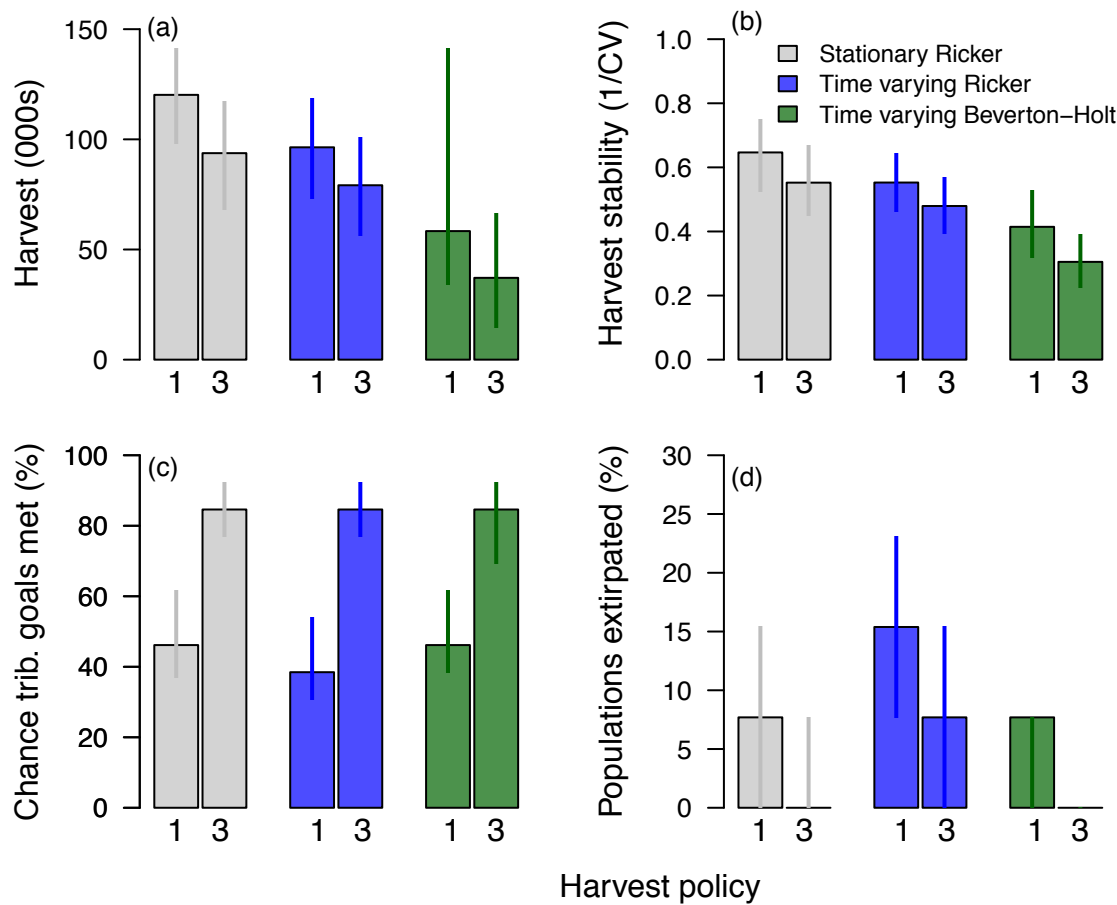
646



647

648 **Figure 6. Time varying population diversity.** Example of simulated changes (arrows) in the productivity  
 649 and size of individual Chinook populations beginning 20 years into the 50 year forward simulations. Each  
 650 point is the median estimated productivity and equilibrium size for a given population as estimated from  
 651 the multi-stock state-space spawner-recruit model presented in Staton et al (n.b).

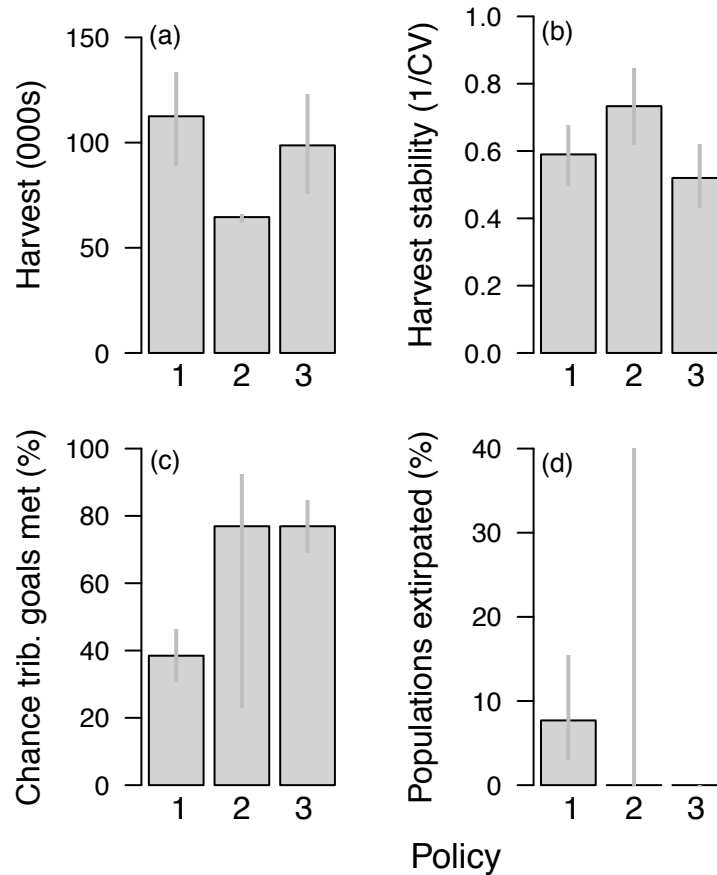
652



655

**Figure 7. Trade-offs between harvest policies across alternative states of nature.** Performance of alternative harvest policies (1 and 3 from Figure 4) across three alternative forms of underlying stock recruitment dynamics (grey bars: stationary Ricker type spawner-recruitment relationship; blue bars: time varying Ricker spawner-recruitment relationship (Figure 6); green bars: time varying Beverton-Holt spawner-recruitment relationship). These plots illustrate that while the general trade-offs are robust to structural uncertainty in the underlying form of the spawner-recruitment dynamics, the magnitude and asymmetry of the trade-offs are sensitive to the underlying drivers of variation in recruitment.

660



**Figure S1. Sensitivity of trade-offs between harvest policies to alternative harvest vulnerability assumptions.** Predicted ability of three alternative harvest policies to meet fishery (a: harvest and b: harvest stability), equity (c: proportion of population tributaries with spawner abundances that exceeded a tributary specific spawner goals) and conservation (d: proportion of populations extirpated) objectives based on simulation parameterized from a multi-population spawner-recruit model that assumes all populations in the system have historically been unequally vulnerable to harvest (in contrast to base model that assumes all populations are equally vulnerable; see Figure 5). Each bar is the median (and 25<sup>th</sup> and 75<sup>th</sup> percentiles) performance of a given policy as calculated over the last 20 years of each Monte Carlo trial (500 in total).