Population diversity in Canadian-origin Yukon Chinook

A research team funded by the Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative used genetic stock identification of archived scale samples and computer models to uncover population diversity and its potential benefits for fisheries and food security in a region where salmon are of immense cultural and subsistence value.

Brendan M. Connors[1,†] Matthew R. Siegle[2], and and Joel M. S. Harding[3]

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 and Canada's Wild Salmon Policy.

However, it is hard for management to account for this underlying diversity because it requires more detailed knowledge than often exists, and because this diversity often occurs at finer spatial scales than the management systems operate over. Nonetheless, 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, may 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 Western Alaska and the Yukon, does not often explicitly consider them. To help address this knowledge gap we used genetic stock identification

Figure 1. Illustration of how population diversity contributes to harvest stability. When diversity is high, individual populations doing 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 ESSA Technologies Ltd., Vancouver, BC
3 Fisheries and Oceans Canada, Whitehorse, YT
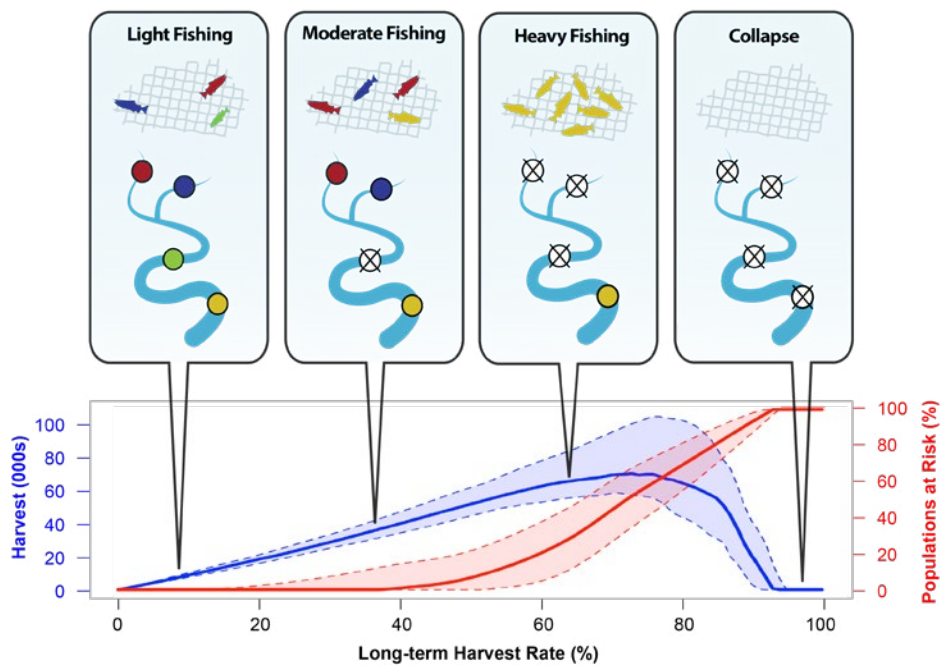† Brendan.connors@dfo-mpo.gc.ca; (250) 858-7028

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.

of archived scale samples collected at the border between Alaska and the Yukon, and run-reconstruction models, to quantify population specific returns of Canadian-origin Yukon Chinook over the past 35 years (**Figure 3**).

We found that the annual duration of population level return migrations averaged ~35 days, and

ranged from as early as late June to as late as early September (**Figure 4**). This run-timing variation results in an average aggregate Canadian Yukon Chinook return migration that is 2.15 times longer (~ 75 days) than if the system was comprised of a single population. We also found that variation among populations in run-size (**Figure 5**) resulted in aggregate annual returns that were 1.8 times
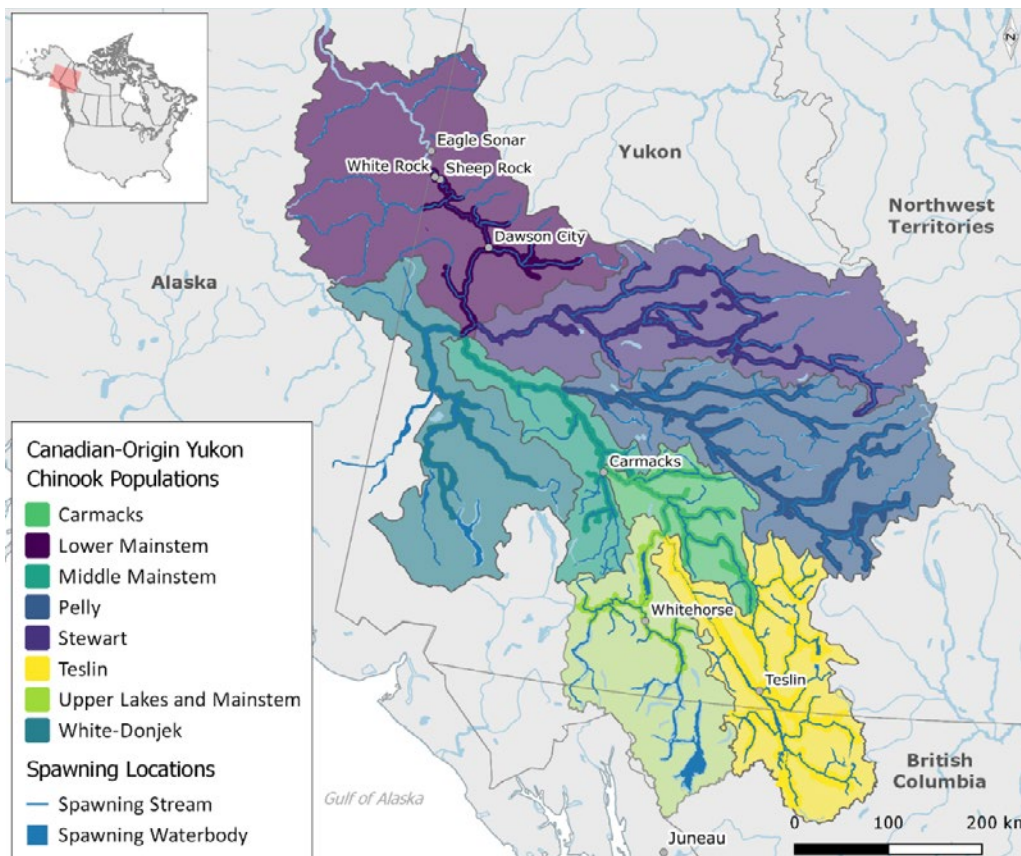

Figure 3. Location of the eight major sub-basins of the Yukon River in Canada corresponding to the populations that individual fish have been assigned to through genetic stock ID. Spawning streams and waterbodies are from Brown et al. (2017) [1]

[1] Brown, R.J., von Finster, A., Henszey, R.J., and Eiler, J.H. 2017. Catalog of Chinook Salmon Spawning Areas in Yukon River Basin in Canada and United States. *J. Fish Wildl. Manag.* 8(2): 558–586. doi:10.3996/052017-jfwm-045

more stable than if they were comprised of a single population.

Next, we used spawner-recruitment analyses of the run-reconstruction data to quantify population diversity in the system and found that productivity and carrying capacity varied across populations by approximately 3.1- and 2-fold, respectively. Variation among Chinook populations in their size and productivity gives rise to a trade-off between mixed-stock harvest and conservation of population diversity. For example, mixed-stock harvest is predicted to be maximized at a harvest rate of ~ 70%, but this comes at the cost of overfishing ~ 50% of the populations.

Lastly, we developed a prototype computer simulation model of the fishery management system to explore how well alternative harvest policies are predicted to meet Chinook conservation and fishery objectives. Though preliminary, these simulations suggest that harvest policies prioritizing the maintenance of population diversity over mixed-stock harvest only need to forgo a relatively small amount of harvest to yield relatively large reductions in the proportion of populations that are overfished and eliminate the risk of driving the least productive populations to extinction.

The run-reconstructions, spawner-recruitment analyses and computer simulation models we developed will continue to be refined as part of a follow up AYK-SSI grant that increases the number of historic scale samples analyzed for genetic stock ID. Nonetheless, our preliminary findings underscore the benefits of Chinook population diversity and suggest that protecting it may help promote food security for Indigenous peoples in a region where salmon are of immense cultural and subsistence value. Our work also provides a blueprint for future quantitative evaluations of the ability of alternative harvest policies to meet a diversity of fishery, social, and biological objectives in the system.
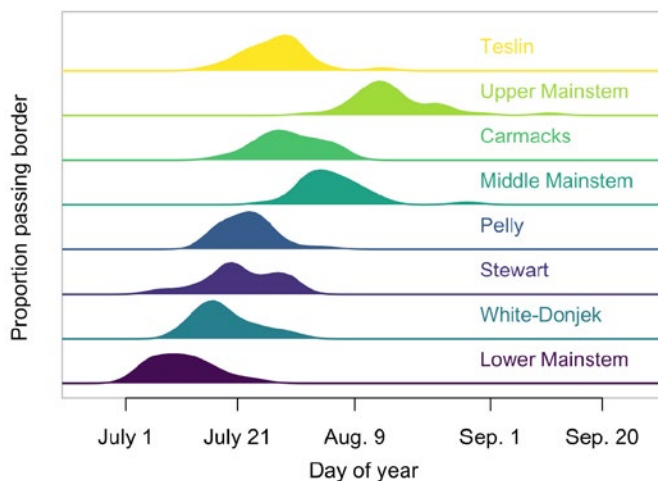

Figure 4. Estimated average daily border passage for the eight Yukon River Chinook populations we considered. Populations are ordered from shortest (bottom) to furthest (top) upriver spawning locations and are color coded according to the legend in Figure 3.
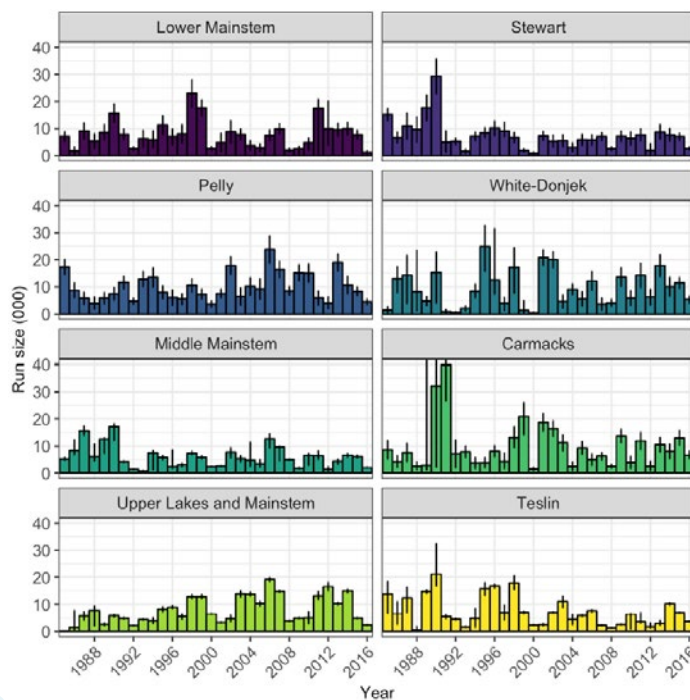

Figure 5. Population-specific estimates of border passage over time. Bars indicate best estimates, while whiskers indicate central 95% uncertainty intervals.

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I.   AYK SSI TITLE PAGE:

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

Yukon harvest-population diversity trade-offs

Brendan M. Connors[1,†], Matthew R. Siegle[2] and Joel M. Harding[3]

[1] Fisheries and Oceans Canada, Sidney, BC
[2] ESSA Technologies Ltd., Vancouver, BC
[3] Fisheries and Oceans Canada, Whitehorse, YT
[†] Brendan.connors@dfo-mpo.gc.ca; (250) 858-7028

December 6, 2019

II.   ABSTRACT:

Population diversity (e.g., variability among fish populations in ecological characteristics and productive capacity) helps maintain resilience to environmental change and reduces year to year variability in harvest for fisheries that depend upon them. As a result, maintaining population diversity is increasingly viewed as a foundation of sustainable and resilient resource management. 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, come at the cost of increased risk of overfishing those that are less productive. We used historic scale samples and genetic analysis to uncover population diversity and trade-offs with mixed-stock harvest in one the largest and most northerly salmon stock complexes in the world: Chinook from the Canadian portion of the Yukon River Basin. We used genetic stock identification, run-reconstructions and spawner-recruitment analyses to characterize Yukon Chinook population diversity over the last 35 years. We found strong evidence of population diversity whereby productivity and average spawner abundance varied across populations by approximately 3.1- and 2-fold, respectively. Variation among populations in run-timing and run-size resulted in return migrations that were 2.2 times longer, and 1.8 times more stable, than if they were comprised of a single homogenous population. However, this diversity gives rise to a trade-off between mixed-stock harvest and conservation of population diversity. For example, mixed-stock harvest is predicted to be maximized at a harvest rate of ~ 70%, but this comes at the cost of overfishing ~ 50% of the populations and putting a quarter of populations at risk of extirpation. We then used closed-loop simulations to evaluate how well alternative harvest policies are predicted to meet Chinook conservation and fishery objectives. We found that harvest policies prioritizing the maintenance of population diversity over mixed-stock harvest need only forgo relatively small amounts of harvest (e.g., 10-20% reduction) in order to yield (1) relatively large increases in the chances of meeting population level escapement goals (40% increase), (2) reductions in the proportion of populations that are overfished (50% decrease), and (3) eliminate the risk of extirpating the least productive populations. The fishery, but not biological, performance of alternative harvest policies was highly sensitive to uncertainty in the underlying drivers of recruitment variation (i.e., whether or not overcompensation occurred in the system), as well as to numerous assumptions that had to be made in order to conduct the analyses. Nonetheless, our preliminary findings underscore how population diversity contributes to stability and resilience in a large remote river basin and suggest that protecting this diversity can help promote food security for Indigenous peoples in a region where salmon are of immense cultural and subsistence value. Our work provides a blueprint for future quantitative evaluations of the ability of alternative harvest policies to meet a diversity of fishery, social, and biological objectives in the system.

III.   PROJECT EVALUATION:

Our original proposal had four objectives. These objectives, and our progress towards meeting them, are described below.

Objective 1: Characterize Chinook population diversity in the CDN portion of the Yukon.

We met this objective by processing over 2,700 historical scale samples from 1982 through 2005. These samples were analysed for allelic variation at a suite of 15 microsatellite loci and genetic stock identification (GSI) methods were used to assign individuals to one of the eight populations in the Canadian portion of the Yukon River watershed. This work extends the population level composition of the annual aggregate Canadian run by 20+ years. We then developed and applied a multi-population run-

reconstruction model and spawner-recruitment analysis to characterize population diversity in the system. We found that population productivity and spawner abundances varied by 6.4- and 4-fold, respectively, and that variation among populations in run-timing and run-size resulted in return migrations that were 2.2 times longer, and 2.2 times more stable, than if they were comprised of a single homogenous population.

Full details of the analyses supporting this Objective can be found in the manuscript in Appendix A (see for example Figures 2, 3, 5, 9 and 10).

Objective 2: Quantify the trade-off between harvest and conservation of population diversity across a range of mixed-stock harvest rates.

We met this objective by using estimates 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. We found that mixed-stock harvest is predicted to be maximized at a harvest rate of ~60%, but this comes at the cost of overfishing ~70% of the populations and threatens 25% of the populations with extirpation (see Figure 13 in Appendix A).

Objective 3: Evaluate the fishery and population diversity performance of current and alternative harvest management actions and their sensitivity to alternative drivers of recruitment.

We met this objective by developing a closed-loop simulation model that was used to evaluate the effect of alternative harvest policies on a suite of performance measures. Full details are provided in Appendix A. These simulations illustrate that the harvest – population diversity trade-offs in the system are asymmetric whereby giving up relatively small amounts of harvest is predicted to result in both large reductions in risk to weak populations and large gains in meeting population level escapement goals. For example, shifting from a policy focused on mixed-stock yield to one that considers risk to population diversity was predicted to result in a 20% reduction in average annual mixed-stock harvest, a 50% reduction in the proportion of populations that are overfished, a 40% increase the proportion of populations that met their escapement goals, and a complete elimination of risk of driving weak populations to extinction.

Objective 4: Determine the harvest and population diversity costs of assuming Yukon Chinook recruitment is driven by (1) over-compensatory processes or (2) extrinsic environmental forcing when the alternative hypothesis is true.

We met this objective by quantifying the performance of alternative harvest policies against objectives 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 the performance of alternative harvest policies were sensitive to the underlying drivers of recruitment in the system. Basin-wide escapement and harvest were predicted to be higher under a Beverton-Holt scenario relative to the Ricker scenario. In contrast, risks to population diversity across the range of escapement goals and harvest rates were generally similar between the two scenarios.

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 2 presentations and attended 3 meetings where we have presented and discussed our research. We anticipate submitting a

manuscript on the research supported by this grant in the winter of 2019/20. Copies of presentations are available from the project PI upon request.

Presentations:

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.

Draft manuscripts:

Yukon Chinook population diversity and its consequences for fisheries management. In preparation. Connors B.M., Siegle M.R., Harding J., Rossi S., Staton B., Jones M., Bradford M., Browne R., Bechtol B., Doherty B., Cox S., and T. Beacham.

Final manuscript(s) will be provided to AYK-SSI once published.

Meetings:

Fisheries and Oceans Canada. Whitehorse. April 2019

Yukon River panel Joint Technical Committee meeting. November 2018

Yukon River panel Joint Technical Committee meeting. November 2017

Reports:

Semiannual progress reports July 2017, January and July 2018 and 2019.

Harvest policy trade-offs web visualization:

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

https://brendanmichaelconnors.shinyapps.io/CDNYukonShinyApp/

V.   PROJECT DATA SUMMARY:

The raw data used in the run-reconstructions and spawner-recruitment analyses described in Appendix A were sourced from Fisheries and Oceans Canada and the Alaska Department of Fish and Game. These data and source code for the analyses performed in Appendix A can be found at: https://github.com/brendanmichaelconnors/Yukon-harvest-diversity

Note that the source code for the manuscript in Appendices A will continue to be refined until the manuscript is published.

VI. APPENDICES:

Appendix A: Yukon Chinook population diversity and its consequences for fisheries management.

1

Yukon Chinook population diversity and its consequences for fisheries management

3

Brendan M. Connors[1], Matthew R. Siegle[2], Joel Harding[3], Stephen Rossi[4,5], Benjamin Staton[6], Mike

Jones[7], Mike Bradford[5,8], Randy Browne[9], Bill Bechtol[10], Beau Doherty[4], Sean Cox[4,5]

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[1] Institute of Ocean Sciences, Fisheries and Oceans Canada, Sidney, BC

[2] ESSA Technologies Ltd., Vancouver, BC

[3] Fisheries and Oceans Canada, Whitehorse, YT

[4] Landmark Fisheries Research, Port Moody, BC

[5] Simon Fraser University, Burnaby, BC

[6] Columbia River Inter-Tribal Fish Commission, Portland, OR

[7] Michigan State University, East Lansing, MI

[8] Fisheries and Oceans Canada, West Vancouver, BC

[9] US Fish and Wildlife Service, Fairbanks, AK

[10] Bechtol Research, Homer, AK

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NOTE: At the time of final reporting to AYK-SSI all co-authors had not reviewed all aspects of this draft; the lead author is therefore solely responsible for any errors of omission, commission or interpretation

Abstract

Population diversity (e.g., variability among fish populations in ecological characteristics and productive

capacity) helps maintain resilience to environmental change and reduces year to year variability in

harvest for fisheries that depend upon it. As a result, maintaining population diversity is increasingly

viewed as a foundation of sustainable and resilient resource management. 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, come at the cost of increased risk of overfishing those that are less productive. We used

historic scale samples and genetic analysis to uncover population diversity and trade-offs with mixed-

stock harvest in one the largest and most northerly salmon stock complexes in the world: Chinook from

the Canadian portion of the Yukon River Basin. We used genetic stock identification, run-reconstructions

and spawner-recruitment analyses to characterize Yukon Chinook population diversity over the last 35

years. We found strong evidence of population diversity whereby productivity and average spawner

abundance varied across populations by approximately 3.1- and 2-fold, respectively. Variation among

populations in run-timing and run-size resulted in return migrations that were 2.2 times longer, and 1.8

times more stable, than if they were comprised of a single homogenous population. However, this

diversity also gives rise to a trade-off between mixed-stock harvest and conservation of population

diversity. For example, mixed-stock harvest is predicted to be maximized at a harvest rate of ~ 70%, but

this comes at the cost of overfishing ~ 50% of the populations and potentially putting ~10% of

populations at risk of extirpation. We then used closed-loop simulations to evaluate how well

alternative harvest policies are predicted to meet Chinook conservation and fishery objectives. We

found that harvest policies prioritizing the maintenance of population diversity over mixed-stock harvest

need only forgo relatively small amounts of harvest (e.g., 10-20% reduction) in order to yield (1)

relatively large increases in the chances of meeting population level escapement goals (40% increase),

(2) reductions in the proportion of populations that are overfished (50% decrease), and (3) eliminate the

risk of extirpating the least productive populations. The fishery, but not biological, performance of

48   alternative harvest policies was highly sensitive to uncertainty in the underlying drivers of recruitment

49   variation (i.e., whether or not overcompensation occurred in the system), as well as to numerous

50   assumptions that had to be made in order to conduct the analyses. Nonetheless, our preliminary

51   findings underscore how population diversity contributes to stability and resilience in a large remote

52   river basin and suggest that protecting this diversity can help promote food security for Indigenous

53   peoples in a region where salmon are of immense cultural and subsistence value. Our work provides a

54   blueprint for future quantitative evaluations of the ability of alternative harvest policies to meet a

55   diversity of fishery, social, and biological objectives in the system.

Introduction

There is a well-established relationship between biodiversity and stability in ecosystem function and service (Hilborn, Quinn, Schindler, & Rogers, 2003; Tilman & Downing, 1994; Yamane, Botsford, & Kilduff, 2018). This relationship can be largely explained by functional diversity, the presence and combination of certain functional traits, rather than solely reflective of species diversity alone (Diaz & Cabido, 2001; Mccann, 2000). Populations within species often exhibit phenotypic and demographic variation that gives rise to heterogeneity in population productivity and population dynamics (Bu et al., 2011) and few species exhibit the high level of intraspecific life-history variation observed within Pacific salmon (Quinn, 2018).

Variation in life-history traits among and within salmon populations, such as migration and spawning timing, underpin the ecosystem services they provide because fisheries that integrate across this diversity are often more stable (Anderson et al., 2017; Schindler, Armstrong, & Reed, 2015; Sethi, 2010), increase Indigenous food security (Nesbitt & Moore, 2016) and are more resilient to environmental change (Anderson, Moore, McClure, Dulvy, & Cooper, 2015; Cline, Schindler, & Hilborn, 2017). Consideration of this population diversity enhances our understanding of the consequence of diversity loss for ecosystem stability and function (Luck, Daily, & Ehrlich, 2003). Maintaining variation in life history characteristics among species, populations and individuals is therefore increasingly recognized as a hallmark of sustainable and resilient natural resource management (Barot, Heino, O'Brien, & Dieckmann, 2004; R. Hilborn et al., 2003; Schaffer, Elson, & Elson, 2019).

Human activities can undermine biodiversity-stability relationships in a number of ways. For example, changes in land use can negatively affect biodiversity directly through intentional habitat removal (e.g., logging), and indirectly through increasing edge effects that reduce habitat quality or genetically, by increasing inbreeding, which reduces the viability of small populations (Hanski, 2011). Fisheries may truncate the age and size structure and run-timing of populations through selective harvest (Charbonneau, Keith, & Hutchings, 2019; Holmlund & Hammer, 1999; Tillotson & Quinn, 2018). They may

also lead to the loss of population diversity through the overharvest of "weak" stocks in mixed stock fisheries (Ray Hilborn et al., 2015; Ray Hilborn & Walters, 1992; Link, 2017). The loss of population diversity can lead to more variable systems that are less resilient to environmental change (Elmqvist et al., 2003; Iii et al., 2000)

A necessary first step towards understanding how biodiversity influences ecosystem function and service, and how human activities mediate these benefits, is characterizing biodiversity within a given system (Luck et al., 2003). This in turn requires information on individual components of biodiversity in both space and time. As the size and remoteness of an area of consideration increases, characterizing biodiversity becomes increasingly challenging. The boreal and sub-arctic regions of North America exemplify these challenges because they contain large remote swaths of forest, wetland and aquatic habitat, that provide numerous ecosystem services. However, these areas are also undergoing rapid transformation as a result of climate change (Sagarin & Micheli, 2001; Zhang et al., 2019), and as such it could be argued there is an urgent need to characterize their biodiversity.

The importance of understanding relationships between biodiversity and ecosystem function and services, as well as the challenges to do so, are well illustrated in Yukon River Chinook salmon (*Oncorhynchus tshawytscha*). The Yukon River is one of the largest and most isolated river systems in North America, flowing from its headwaters in northern British Columbia through the Yukon Territory and Alaska before emptying into the Bering Sea (Figure 1). The Yukon drains over 850,000 square kilometres that span over 20 different ecoregions (Gallant, Binnian, Omernik, & Shasby, 1995). Chinook populations across Western Alaska and the Yukon Territory have declined in abundance and productivity over the past decade (Dorner, Catalano, & Peterman, 2017; Ohlberger, Scheuerell, & Schindler, 2016). These declines have been particularly pronounced in the Yukon River Basin which experienced near record low returns in some recent years (JTC 2018).

Yukon River Chinook have been called the "Kings of Kings" due to their extensive freshwater migrations (up to ~3000 km, the furthest of any salmon) and their high oil content. These salmon have been fished for subsistence for millennia and are at the center of fisheries and fish camps where stories, food, and traditional knowledge are shared (Loring & Gerlach, 2010). Poor returns of Yukon Chinook have severely limited harvest opportunities for the dozens of communities in Alaska and Canada that depend upon these salmon for subsistence and cultural needs. Chinook returns have been so low in recent years that Canadian (CDN) recreational and commercial fishing has been closed and many Indigenous communities have voluntarily stopped subsistence fishing for several decades. This has strained the cultural fabric that Yukon Chinook have historically supported.

Yukon Chinook salmon spawn in hundreds of different locations (Brown, von Finster, Henszey, & Eiler, 2017), with each spawning population likely adapted to the local conditions they experience in traits such as juvenile behavior and residence time and adult spawning duration and timing (Quinn, 2018). The different ecological conditions these individual populations have adapted to have likely given rise to variability in productivity among populations (i.e., the maximum average number of adult recruits expected to be produced per spawner) and the overall carrying capacity of their freshwater habitats (i.e., the maximum number of spawners or juveniles a population's habitat can support). A consequence of this Chinook population diversity is that individual populations will vary in the harvest rates they can sustainably withstand. For example, large capacity, highly productive populations will be able to support high harvest rates and fisheries that capture a large number of fish relative to less productive or less abundant populations. When fisheries for multiple populations overlap in space and time, like the Yukon where 80% of CDN-origin Chinook harvest has historically occurred in the lower, Alaskan, portion of the river (JTC 2018), there can be a conflict between harvest rates and population diversity (i.e., the number of viable populations). Higher harvest rates can be sustained by the most productive populations but come at the cost of increased risk of over-fishing and potential extirpation of the less productive populations. Because these less productive populations are not likely to be evenly distributed among watersheds

128   within the CDN portion of the Yukon Basin, overfishing of these populations can lead to differential

129   impacts across the communities that rely upon these salmon for subsistence and cultural needs.

130   Canadian-origin Yukon Chinook are a transboundary stock managed under the Pacific Salmon Treaty

131   as a single aggregate stock with an interim management escapement goal, set by the Yukon River Panel,

132   that establishes the number of Chinook that need to make it into the CDN portion of the Yukon and onto

133   spawning grounds in each year (JTC 2018). The consequences of managing CDN-origin Chinook as a single

134   aggregate stock, both for the protection of Chinook population diversity and for the communities and First

135   Nations in the CDN-portion of the Yukon that depend upon them, are currently unknown. Here, we use

136   genetic analysis of archived scale samples to reconstruct Chinook salmon population diversity within the

137   CDN portion of the Yukon River Basin and then quantify how alternative fisheries management policies

138   are predicted to affect it. Specifically we (1) use genetic stock identification from archived scale samples

139   to reconstruct population specific returns to Canada over the past three decades, (2) fit multi-population

140   Bayesian state-space spawner-recruit models to the run reconstructions to characterize Chinook

141   population diversity (i.e., productivity and carrying capacity), (3) quantify the consequences of population

142   diversity for portfolio effects (i.e. variance dampening due to asynchronous dynamics) and equilibrium

143   trade-offs in mixed-stock fisheries, (4) use closed-loop simulation models of the socio-ecological system

144   to evaluate how alternative harvest policies affect the ability of the system to meeting conservation and

145   socio-economic objectives.

146   **Methods**

147   Our methodological approach consisted of four key steps (Figure 2): (1) apply molecular analyses to

148   archived scale samples collected at the US-CDN border to determine population composition of annual

149   returns; (2) reconstruct annual border passage and spawner abundance for each population using a state-

150   space run-reconstruction model fit to daily estimates of border passage and population assignments from

151   step 1; (3) characterize population diversity by fitting an age-structured, multi-stock, state-space spawner-

recruitment model to reconstructed data on spawners, aggregate CDN harvest and age composition; and

(4) quantify the performance of alternative harvest policies using closed-loop simulations across a range

of plausible hypotheses representing alternative states of nature to characterize the trade-offs between

harvest and population-diversity in the system.

Study area

For our analyses we considered eight population units (Figure 1), hereafter referred to as

"populations". These populations roughly correspond to nine proposed Conservation Units (Table 1)

which are genetically and ecologically unique groups of salmon under Canada's Wild Salmon Policy (DFO,

2005). These populations spawn in areas spanning the traditional territories of ten Yukon Territory First

Nations.

Monitoring and assessment

The number of Chinook salmon migrating into the Yukon territory (hereafter referred to as border

passage) has been estimated using a variety of methods over the past four decades. From the early 1980s

to the mid 2000s a mark-recapture program and fish wheels were operated in several locations near the

border (White and Sheep rocks: Figure 1) to estimate abundance and collect biological samples. In 2005,

a sonar site at Eagle, Alaska along with a drift gillnet test fishery was established to estimate border

passage and collect biological samples. The system uses a DIDSON sonar with split-beam transducer on

opposing banks, with partial weirs to ensure salmon do not swim behind the transducers. The Eagle sonar

site is located 48 km downstream from the fish wheel site, which is approximately one day of travel

downstream assuming typical Chinook swimming speeds (Eiler, Evans, & Schreck, 2015).

The Yukon River Panel Joint Technical Committee (JTC) uses multiple sources of information to

reconstruct total returns of Chinook to the CDN portion of the Yukon along with harvest and age-

composition (JTC 2018). These sources of information include (1) border passage estimates from a mark-

recapture program (1982-2007), radiotelemetry data (2002-2004) and the mainstem sonar project (2005-2017), (2) aerial spawner surveys from multiple systems as indices of relative abundance (1981-2001), (3) estimates of harvest in both US and CDN fisheries, and (4) age composition data from fish wheel and gillnet test fisheries near the US-Canada border and from US harvest. The resulting brood table forms the basis of the current data used to estimate the basin wide spawner-recruitment relationship (JTC 2018).

On average, 1300 Chinook scale samples have been collected annually from the fish wheels (1982–2008) and gillnet test fishery (2005–present). These samples have typically been taken over most of the duration of the annual upstream adult migration, with the number of samples taken each day roughly proportional to run size (Figure 3). Since 2006 tissue samples have also been collected for genetic stock identification by assigning each fish back to one of the eight populations using microsatellite markers (between 293 and 1026 fish per year) (Beacham et al., 2006). We extended population composition estimates back to 1982 using the archived collection of scale samples. To do this, for each year with scale samples that could be recovered, we haphazardly selected approximately 150 scales, extracted genomic DNA from each scale, and used allelic variation at 15 microsatellite loci to assign individuals to one of the eight populations (Table S1).

Population level run-reconstructions

We estimated daily passage (between June 9th and October 12th) of Chinook into Canadian waters from 1985 to 2016 using multi-population run reconstruction models. The models use a Bayesian state-space framework, which simultaneously accounts for uncertainty in observations and underlying population processes and allows for the inclusion of incomplete datasets. We separately modelled the dynamics of the eight Chinook populations. Annual, population-specific border passage was the main parameter of interest estimated by the model, though we also estimated parameters for run timing and catchability, and separately modeled catchability for the sonar and fish wheel gear types. We fit three

198   alternative run-reconstructions which varied in their parameterization of variance and covariance in

199   arrival timing by population.

200   To quantify the extent to which the run-reconstruction models may yield biased estimates of

201   population specific run-sizes (e.g., due to incomplete sampling of return migrations, and small samples

202   sizes) we conducted a suite of simulation-estimation experiments across a range of different sample sizes

203   for population composition estimates (Table 2). Complete details of the run-reconstruction models,

204   including model notation, equations, and details of the simulation estimation trials, are provided in

205   Appendix A.

206   *Population level spawner-recruitment modelling*

207   To characterize Chinook population diversity within the CDN portion of the Yukon River we fit

208   individual age-structured state-space spawner-recruitment models to all available data for each

209   population (i.e., time series of estimated catch, spawner abundance and age composition). The

210   formulation of the model we used assumed that all populations are (a) equally vulnerable to harvest and

211   (b) share the same maturity schedule. The spawner abundance estimates we used were derived from the

212   multi-population run-reconstruction models described in Appendix A. To account for CDN harvest – the

213   run-reconstruction model estimated border passage, and not escapement – we applied an annual CDN

214   exploitation rate (CDN commercial, First Nations and recreational harvests) to the population specific

215   border passage estimates to derive an estimate of spawner abundance. All harvest data, along with

216   estimates of age – composition were taken from JTC (2018).

217   The key quantities estimated by the state-space model (described in Appendix B) included population

218   productivity (i.e., maximum recruits-per-spawner), carrying capacity, latent recruitment states, lag-one

219   temporal correlation in recruitment, and a time-varying maturity schedule. We used the posterior samples

220   of population productivity and carrying capacity to quantify the range of predicted equilibrium trade-offs

221 between aggregate harvest and conservation of population diversity across a range of mixed-stock harvest

222 rates (C J Walters, Lichatowich, Peterman, & Reynolds, 2008; Carl J Walters & Martell, 2004).

223 *Portfolio effects*

224   We quantified the extent to which inter-annual variation in returns of CDN-origin Chinook were

225 dampened due to asynchronous dynamics (i.e., portfolio effect Hilborn et al., 2003; Schindler et al.,

226 2010) by calculating the coefficient of variation in run size and portfolio effects at various spatial and

227 temporal scales. Specifically we calculated the portfolio effect (*PE*) following Nesbitt and Moore (2016)

228 for region *i* as the difference between the predicted coefficient of variation of run size (CV$_j$) assuming

229 synchronous variance dampening (weighted by the proportional run size, *X$_j$*) and the observed CV of the

230 aggregate run (CV$_{obs}$).

$$PE_i \;=\; \sum_{j-1}^{n} X_j CV_j - CV_{obs} \tag{1}$$

231 PE measures the additional stability of the aggregate than would be expected based on the sum of the

232 individual populations. When PE is positive, the predicted CV is greater than the observed CV, and is

233 evidence that asynchronous dynamics are stabilizing the aggregate run. We quantified PE and CV in

234 returns with a rolling 10-year average of run size, generating estimates from 1995 to 2016 for all

235 populations (indicative of fishing near Dawson City, with the possibility of harvesting fish from any of the

236 eight populations) and for three populations further upriver (represented by fishing near Carmacks, with

237 the possibility of harvesting fish from the Carmacks, Upper Lakes and Mainstem or Teslin populations).

238 *Closed-loop simulations*

239   To quantitatively evaluate the performance of alternative harvest policies relative to both fishery

240 and conservation objectives, we developed a closed-loop simulation (Figure 4) that consisted of four

components: (1) an empirically parameterized multi-population operating model that simulated the dynamics of Chinook populations over time, (2) a management procedure model that assessed the state (i.e., total returning abundance) of the system each year and (3) applied a given harvest policy, and (4) a performance model that tracked the outcomes of the management procedure for quantitative performance measures related to a suite of fishery and conservation objective. To evaluate how robust a given harvest policy was to key structural uncertainties in the system we simulated the biological and fishery dynamics across alternative states of nature (i.e., alternative drivers of recruitment dynamics). The approach we describe here closely matches that taken in (Connors et al., Under review).

Operating model

Our operating model was used to simulate future population trajectories for the eight CDN-origin Yukon Chinook populations by projecting their dynamics forward over 50 years (approximately eight generations starting in 2017). By simulating the 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 through time (i.e., by drawing from the ensemble posterior distributions of each estimated parameter and abundance state in each iteration of the simulation).

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

$$R_{y,j} = \alpha_j S_{y,j} e^{-\beta_j S_{y,j} + \phi \log(R_{y-1,j}/\hat{R}_{y-1,j}) + r_{y,j}} \tag{2}$$

where $R_{y,j}$ is recruitment from brood year y for population j, α_j and β_j are population specific intrinsic rate of growth (productivity) and within-population density dependence, respectively; $S_{y,j}$ is spawner abundance; ϕ is the degree of temporal correlation in recruitment from one year to the next; $\hat{R}_{y-1,j}$ is

263 the expected recruitment in the previous year; and $r_{y,j}$ is residual variation in recruitment that is

264 correlated among populations according to a common correlation parameter (ρ) following a multivariate

265 normal distribution:

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

(3)

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

266 where $\mathbf{\Sigma}$ is the variance covariance matrix. Returns in year t, $\dot{N}_{t,j}$, were then modeled a function of the

267 proportion of individuals that mature and return to spawn at each age:

$$\dot{N}_{t,j} = \sum_{a=4}^{7} R_{t-a,j}\pi_{a-3}$$

(4)

268 where π is a maturity schedule composed of four age classes (4 through 7). To incorporate the effects of

269 small population size on reproductive success (e.g., allele effects and depensation), we set a quasi-

270 extinction threshold at 50 spawners (Holt & Bradford, 2011) such that if spawner abundance fell below

271 this threshold recruitment from that brood year was assumed to be zero. For simplicity, we assumed that

272 straying among populations did not occur. In each year of the forward simulation, the number of spawners

273 in equation 3 ($S_{y,j}$; where brood year y is equal to calendar year t) was calculated as the harvest ($H_{t,n}$)

274 subtracted from the return ($N_{t,n}$), where the harvest was determined according to the harvest control

275 rules described in the following section (Management Procedure model).

276 *Management procedure model*

277 The decision rules governing harvest of CDN-origin Yukon Chinook are complex and have varied over

278 time. We sought to develop a model that captured the general elements and rules governing the fishery

279 so as to be able to approximate it. The management procedure model forecasted returns each year and

280 applied a harvest control rule that was defined by a combination of US and Canadian TAC allocation, US

281   subsistence needs, a commercial target harvest rate on surplus production (after escapement and

282   subsistence needs are accounted for), an aggregate escapement goal, and CDN First Nations harvest needs

283   (referred to in Canada as Basic Needs Allocation).

284   The annual total combined (US and Canada) allowable harvest (TAC) in year t was calculated as the

285   difference between the forecasted run size ($\widehat{N}_t$) and the basin wide escapement goal (G):

$$TAC_t = \widehat{N}_t - G \tag{5}$$

286   where the forecasted run-size ($\widehat{N}_t$) was equal to $\dot{N}_t \varepsilon_N$, where ε_N is forecast error which was assumed to

287   be lognormally distributed with a standard deviation equal to 0.2 (based on retrospective evaluation of

288   forecast error in the Yukon).

289   The TAC was then split into Canadian ($TAC_{CDN,t}$) and US ($TAC_{US,t}$) components based on the

290   allocation defined in the Yukon River Salmon Agreement:

$$TAC_{CDN,t} = \begin{cases} 0.24 TAC_t, & TAC_y \leq 110000 \\ 0.24\ x\ 110000 + 0.5(TAC_t - 110000), & TAC_t > 110000 \end{cases} \tag{6}$$

291   and

$$TAC_{US,t} = TAC_t - TAC_{CDN,t} \tag{7}$$

292   Following the determination of US and CDN TAC allocation, US commercial harvest ($H_{US,C}$) in year t

293   was:

$$H_{US,C,t} = \dot{U}_C e^{\varepsilon_C} \begin{cases} TAC_{US,t} - \dot{H}_{US,S}, & TAC_{US,t} - \dot{H}_{US,S} > 0 \\ 0, & TAC_{US,t} - \dot{H}_{US,S} \leq 0 \end{cases} \tag{8}$$

294   where $\dot{U}_C$ is the target harvest rate on surplus production, ε_C is outcome error (set at 0.1) and $\dot{H}_{US,S}$ is the

295   target US subsistence harvest. We assumed that commercial harvest occurs before US subsistence harvest

296   and so realized US subsistence harvest ($H_{US,Sy}$) was:

14

$$H_{US,S,t} = \begin{cases} (\dot{N}_t - H_{US,C,t})e^{\varepsilon_{US,S}}, & \dot{H}_{US,S} > \dot{N}_t - H_{US,C,t} \\ \dot{H}_{US,S}e^{\varepsilon_{US,S}}, & \dot{H}_{US,S} \leq \dot{N}_t - H_{US,C,t} \end{cases} \qquad (9)$$

297 where $\varepsilon_{US,S}$ is US subsistence fishery outcome error $\sim N(0,0.05)$. These harvest control rules (equation

298 8-9) are intended to reflect the priority placed on meeting subsistence needs over commercial harvests,

299 the fact that commercial harvest occurs before subsistence harvest, and the extent to which there is

300 imperfect control over managing harvests to their target levels.

301   Canadian harvest depended on estimated Chinook border passage ($\hat{P}_t$) which was a function of

302 US commercial and subsistence harvest:

$$\hat{P}_t = [\dot{N}_t - (H_{US,C,t} + H_{US,S,t})]e^{\varepsilon_P} \qquad (10)$$

303 where ε_P is border passage observation error ($\sim N(0,0.05)$) based on evaluations of the precision of sonar

304 estimates at the border.

305   Canadian commercial harvest depended on the anticipated First Nations harvest target ($\dot{H}_{CDN,S,t}$) in

306 a given year, which was:

$$\dot{H}_{CDN,S,t} = \begin{cases} 0, & \hat{P}_t \leq 42{,}500 \\ 1{,}000, & 42{,}500 \leq \hat{P}_t < 48{,}750 \\ 4{,}000, & 48{,}750 \leq \hat{P}_t < 55{,}000 \\ 10{,}000, & 55{,}000 \leq \hat{P}_t \end{cases} \qquad (11)$$

307   Canadian commercial harvest was assumed to occur before First Nations harvest and so CDN

308 commercial harvest ($H_{CDN,C,t}$) was:

$$\dot{H}_{CDN,C,t} = \dot{U}_C e^{\varepsilon_C}(P_t - G - \dot{H}_{CDN,S,t}) \qquad (12)$$

309   The resulting realized CDN First Nations harvest was therefore:

$$\dot{H}_{CDN,S,t} = \dot{H}_{CDN,S,t}e^{\varepsilon_{CDN,S}} \qquad (13)$$

310   where $\varepsilon_{CDN.S}$ is CDN First Nations fishery outcome error ($\sim N(0,0.05)$) and total harvest by population,

311     $H_{t,j}$, is then:

$$H_{t,j} = U_t \dot{N}_{t,j} \tag{14}$$

312   where the realized harvest rate (U_t), common to all populations, was:

$$U_t = (H_{US,C,t} + H_{US,S,t} + H_{CDN,C,t} + H_{CDN,S,t}) / \dot{N}_{t,j} \tag{15}$$

313   *Harvest policies*

314   We quantified the performance of harvest policies across a broad range of two key elements of CDN-

315   origin Yukon Chinook harvest policies: the basin wide escapement goal and the target harvest rate on

316   surplus (above escapement and subsistence and First Nations harvest targets). We chose to focus on these

317   two elements instead of US subsistence and CDN First Nations harvest needs because the harvest

318   requirements of subsistence and indigenous peoples to meet food security and cultural values are not

319   considered a management lever in the system. We then considered three contrasting harvest policies in

320   more detail (Table 3) to illustrate how policies that prioritize different objectives are predicted to perform

321   across a range of biological and fishery performance measures.

322   The first policy sought to approximate the current approach to fishery management in the system

323   (termed "status quo policy"). The second policy sought to maximize potential yield from the system by

324   setting a basin wide escapement and target surplus harvest rate equal to that predicted to produce

325   maximum sustained yield under equilibrium conditions (termed "MSY policy"). The third policy sought to

326   maximize yield from the system but only once there was a high probability (> 80%) that individual

327   population escapement goals were met (see next section for more detail) (termed "conservation policy").

328   *Performance measures*

329   We quantified the relative ability of alternative harvest policies to meet a suite of objectives. To

330   achieve this, we summarized the results of the closed-loop simulations through quantifiable performance

331   measures that could be assessed against the objectives. Performance measures related to harvest

332   objectives included average annual total harvest, harvest rate, inter-annual stability in harvest (i.e., 1 /

333   coefficient of variation in catch) and the proportion of years US subsistence and First Nations harvest

334   needs were met. Performance measures related to conservation objectives included total escapement,

335   the proportion of populations whose average spawner abundance fell below a quasi-extinction threshold

336   of 5% of equilibrium population size (% extirpated) or were overfished (i.e., $U_t > U_{MSY}$), and the

337   proportion of populations whose average spawner abundance was greater than or equal to population

338   specific upper biological benchmarks (i.e., 80% of $S_{MSY,j}$; referred to hereafter as escapement goal). The

339   latter performance measure has been proposed as a biological benchmark delineating "healthy" biological

340   status under Canada's Wild Salmon Policy (Holt & Bradford, 2011) and can also be considered a measure

341   of the extent to which spatial equity in First Nations access to salmon across the CDN portion of the river

342   basin is met. Each performance measure was summarized over the last 20 years of the 50 year simulations

343   and across 500 Monte Carlo trials, with each trial parameterized by a unique draw from the posterior

344   samples from the state-space spawner-recruitment model.

345   *Alternative drivers of recruitment*

346   Our baseline simulations assumed that recruitment was governed by stationary spawner-

347   recruitment dynamics that follow a Ricker-type relationship with overcompensation at high spawner

348   abundances (equations 2-4). This is the state of nature that is currently assumed by fishery managers in

349   the Yukon (JTC, 2018) and widely across other salmon systems. However, cyclical variation in

350   environmental forcing can also give rise to the appearance of overcompensation in spawner-recruit data

351   sets (Parma & Deriso, 1990). Such cyclical environmental forcing may exacerbate harvest – diversity trade-

352   offs because weak stocks are more susceptible to overharvest in years of low productivity than they would

353   be if the primary drivers of recruitment variation were intrinsic. We therefore also considered an

354   alternative recruitment hypothesis that assumed that low frequency regime shifts occur that gave rise to

355   the appearance of overcompensation, when in fact none was present. Under this hypothesis we assumed

356   that individual spawner-recruitment relationships were governed by Beverton-Holt dynamics with cyclical

357   variation in population productivity. To do this we transformed the Ricker spawner-recruitment

358   relationship in equation 2 to a Beverton-Holt form (Table 7.2 in Hilborn and Walters 1992) with time-

359   varying productivity:

$$\overline{R}_{y,j} = \left. \alpha_{y,j} \middle/ 1 + \frac{\alpha_{y,j}}{\beta_j}\, S_{y,j} \right.$$

(16)

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

360   where population productivity ($\alpha_{y,j}$) is time-varying following a cycle with a period equal to f and

361   amplitude equal to A. The term δ is a scalar that adjusts productivity such that long-term population

362   equilibrium abundance in the absence of fishing is approximately the same as those assuming a Ricker

363   spawner-recruitment relationship. We fixed f, A and δ at 14, 0.6, and 1.4, respectively, based on

364   exploratory simulations that showed that this combination of parameters generated spawner-

365   recruitment relationships with apparent overcompensation that approximates that observed in CDN-

366   origin Yukon Chinook (Appendix C). Note that these values may depend on the spawner-recruit

367   relationships used and should therefore be obtained separately for analyses of different populations in

368   other systems.

369   **Results**

370   *Genetic stock composition*

371   In total, we processed over 2,700 archived scale samples thereby extending annual estimates of CDN-

372   origin Yukon Chinook population composition back to 1982. On average, 147 samples were successfully

373   analysed each year. The median assignment probabilities for each year ranged from 53% to 79%, with a

374   median annual assignment probability of 63% (5th and 95th percentile values are 55% and 76%,

18

375 respectively; Table S1). In general, the distribution of scale samples corresponded to the annual run

376 distribution (Figure 3). However, for some years there were substantial gaps in scale sample coverage,

377 most notably for 1991, 1992, 2001, and 2007, and there were also a handful of years (1984, 1988-1990,

378 1998) for which no archived scale samples existed.

379 *Population level run-reconstructions*

380 <u>*Model fits*</u>

381 Each of the RR models fit the count data reasonably well with fits very close for the sonar counts

382 (Figure S1). In contrast, model fits to the fish wheel count were more variable, which is expected due to

383 the relatively imprecise nature of the fish wheel data (Figure S2). In years when sonar and fish wheel

384 counts overlapped (2005-2007), the tight correspondence between model estimates and sonar counts

385 resulted in particularly poor fits to the fish wheel data. Fits to the count data were very similar among the

386 three alternative model formulations of variance-covariance in run-timing.

387 The mark-recapture index tended to stabilize border passage estimates when other data were

388 relatively uninformative (e.g., 2001) but had less influence in other years (Figure 5). We ran a sensitivity

389 analysis to evaluate the effect of the mark-recapture likelihood weight α on border passage estimates.

390 Setting α to a relatively low value (e.g., 10) allows the model to chase spuriously high fish wheel counts in

391 2001, resulting in unreliable estimates of border passage (Figure S3). Increasing α to higher values (e.g.,

392 500) may be expected to tighten the model fits to the mark-recapture estimates in all years, though we

393 found this only occurred in years when data is missing (late 1980s) or unreliable (early 2000s). In the latter

394 half of the 1990s, model fits to the mark-recapture were closer for α = 10 than for a = 500. As reliable

395 abundance data (i.e., sonar) became available in 2005, the mark-recapture index had essentially no effect

396 on model estimates, even for high values of α.

While the three models fit the data similarly, the RR model with a single shared correlation among population in run-timing (RR_oneCor) was highly preferred by AICc (Table S2). We note, however, that AICc rankings for these models are somewhat dubious, as the model with a single shared run-timing correlation (RR_oneCor) was considered the most parsimonious due to the closer fits of that model to a relatively low-value dataset. For this reason we generated an unweighted ensemble prediction of border passage by population that treated all three RR models as equally likely and used these resulting ensemble predictions in all subsequent analyses.

Border passage estimates

Border passage timing was predicted to vary both among populations, and among years within populations. Populations that spawned in the lower sections of the CDN portion of the Yukon River Basin tended to return, on average, earlier than those in the upper sections of the basin (Figure 6), and tended to exhibit the least inter-annual variation in run-timing (Figures S4-S6). However, the upper river mainstem spawning populations (Middle Mainstem and Upper Lakes and Mainstem) tended to return later, and exhibit more inter-annual variation in run-timing, than the Teslin population that spawns the furthest upriver. The estimated annual duration of population level return migrations averaged ~35 days (SD = 11 days) spanning as early as late June (Julian day 175; Lower Mainstem) to as late as early September (Julian day 250; Upper Lakes and Mainstem) (Figures 6 and S4-S5). This run-timing variation results in an average aggregate CDN-origin Yukon Chinook return migration that is 2.15 times longer (~ 75 days) than if the system was comprised of a single homogenous population.

The Pelly population was predicted to have the highest median annual border passage at around 8,440, followed by the White-Donjek (median: 8,350), Carmacks (7,730) and Lower Mainstem (7,660) populations (Figure 7). The most modest returns were to the Middle Mainstem (5,550) and Upper Lakes and Mainstem (5,750) populations. Estimates of border passage tended to be most precise for those populations with the least overlap in run-timing with other populations (e.g., Lower and Upper Lakes and

Mainstem populations tend to pass the border earlier and later, respectively) (Figure 7). Those populations with the most overlap in run-timing had reconstructed border passage that varied the most among the three RR models (i.e., White-Donjek for 2008-2013, Pelly for 1988-1990, Stewart for 1988-1990 and 2009-2013), suggesting that the population-composition data was not always informative enough to distinguish between these populations giving rise to structural uncertainty that was propagated through to the ensemble estimates of border passage.

The run-reconstruction model with a fully estimated run-timing correlation matrix (RR_fullCor) estimated that run-timing was moderately correlated, on average, among populations (median pair-wise correlation of 0.32)(Table 4). However, there was some evidence that the magnitude of correlation in run-timing was inversely related to distance between populations with those that are closest to each other having pair-wise correlations that ranged from 0.7-0.9, while those furthest from each other tended to have uncorrelated run-timing (Table 4).

Simulation-estimation trials

The three RRs had similar performance in simulation tests (Figure S6). In general border passage estimates were reasonably unbiased when fitting to data generated with population composition sample sizes equal to historical levels (OM_base; Table 2); Lower Mainstem, Carmacks, Teslin, and Upper Lakes and Mainstem were estimated with little bias while Stewart, Pelly, and Middle Mainstem tended to be slightly underestimated (3-10% median relative error), and White-Donjek tended to be slightly overestimated (4% median relative error). The simulation tests suggested that increasing population composition sample sizes for the fish wheel to 250 per year (from an average of 150) reduced bias in border passage estimation for White-Donjek, Pelly, and Stewart, although MRE for Stewart remained relatively high at 6%. Increasing population composition sample sizes for sonar counts to 1250 per year (from an average of 500) reduced bias in border passage estimation for Lower Mainstem, White-Donjek, Pelly, and Stewart, and produced estimates with relatively low MREs for all populations.

Population Diversity

446   We found clear evidence of heterogeneity in population productivity and size, where populations

447   ranged in estimated productivity from 3.89 to 12.10 recruits-per-spawner (median posterior estimates, y-

448   axis of Figure 8; Table S3) and predicted equilibrium size from approximately 8,300 to 17,860 spawners

449   (x-axis in Figure 8; Table S3). Most populations showed some visual evidence of overcompensation with

450   the largest recruitments having being observed from brood years with relatively low spawning

451   abundances (Figure 9). Productivity was positively correlated through time within populations (median

452   lag-one correlation in recruitment residuals = 0.55; Table S3), and in space among populations (median

453   pairwise correlation = 0.63; Figure 10).   Most population exhibited some evidence of declines in

454   productivity over time (Figure 11) which translated into an approximately 10% decline in productivity on

455   average (range 3%-20% reduction) across populations.

456   The range of productivities we estimated correspond to harvest rates predicted to maximize long-

457   term yield (i.e., U_{MSY}) that range from ~62% to 85% (median posterior estimates). We used the posterior

458   estimates of productivity and carrying capacity to quantify the predicted equilibrium trade-offs between

459   aggregate harvest and conservation of population diversity across a range of mixed-stock harvest rates

460   (Figure 12). The resulting picture illustrates that the relatively high harvest rates that can be sustained by

461   the most productive populations come at the cost of increased risk to less productive ones. Overall yield

462   from the system is predicted to be maximized at a harvest rate of ~ 70%, but this comes at the cost of

463   overharvesting ~ 50% of the populations (i.e., harvest rate is > U_{MSY} for a given population) and putting a

464   ~10% of populations at risk of extirpation). Furthermore, there is clear asymmetry in these trade-offs

465   where relatively small (~12%) reductions in predicted yield (e.g., ~12% from 90,000 to 80,000) correspond

466   to relatively large reductions in biological risk (e.g., ~ 80% from ~50% to 10% overfished).

467   *Portfolio effects*

The Chinook population diversity we uncovered gives rise to strong portfolio effects whereby the asynchronous dynamics of Chinook populations stabilize overall returns (Figure 13). For example, variability in annual returns of CDN-origin Chinook was 1.81 times more stable than if the system consisted of a single homogenous population (CV of 38% vs 68% [average CV across individual populations; SD = 0.11]). However, the stabilizing effects of Chinook population diversity diminished as you move up river and integrate across fewer populations (Figure 13). As a result fisheries that integrate across the full extent of CDN-origin Yukon Chinook population diversity (e.g., in Alaska or lower section of the CDN portion of the river such as near Dawson) are predicted, on average, to be ~1.5 more stable than those in the middle section of the CDN portion of the river (e.g., Carmacks) and ~2 times more stable than those in the headwaters (e.g., Teslin).

Closed loop simulations

The closed-loop simulations indicated that mixed-stock harvests are predicted to be maximized at intermediate basin scale escapement goals (~40,000-60,000) when the target harvest rate on surplus production (i.e., production above and beyond which is predicted to be required to meet the escapement goal plus US subsistence and First Nation harvest targets) is high (80-90%) (Figure 14a and b). At higher basin scale escapement goals harvest is predicted to decline because of more frequent fishery closures while at lower escapement goals it declines due to due to the loss of production from overfishing the weaker (i.e., less productive) populations in the system (Figure 15d) and driving the weakest populations to extirpation (Figure 14e). Harvest stability was predicted to be greatest at both low escapement goals and target harvest rates (Figure 14f) while the chances of meeting population level escapement goals and minimizing risks of driving individual populations to extirpation were greatest when target harvest rates were low and/or basin-wide escapement goals were high (Figure 14i and e).

Contrasting the three alternative harvest policies illustrates asymmetries in trade-offs between harvest and biological or conservation objectives. We found that the harvest policy that sought to

maximize mixed-stock harvest (MSY policy) did so at the costs of an increased proportion of populations that were overfished, reduced chances of meeting population-level escapement goals and elevated risk of weak population extirpation (Figure 15). In contrast, relative to the MSY policy, the conservation policy was predicted to increase the chances of meeting tributary spawner goals by 40%, (from 62% to 87%), to cut the proportion of populations that are overfished in half (from 75% to 37.5%) and eliminate the risk of extirpating the least productive populations (Figure 15). This came at the cost, on average, of only a 20% reduction in realized overall harvest and no change in inter-annual stability in harvests. The harvest policy that approximated the current approach to management (status quo policy) was predicted to have higher chances of meeting tributary spawner goals and a lower proportion of populations that are overfished but, as expected, this came at the cost of much lower harvests (Figure 15). All three policies had a very high probability (~90%) of meeting First Nations harvest targets but much lower probabilities of meeting US subsistence needs (50%, 50%, and 60% for the conservation, MSY and status quo policies, respectively).

The performance of harvest policies, and their resulting trade-offs, were sensitive to the underlying drivers of variation in recruitment in the system. When recruitment dynamics were driven by time-varying Beverton-Holt type relationships, basin – wide escapement and to a lesser extent harvest were predicted to be higher relative to the alternative Ricker spawner-recruitment dynamic scenario (compare Figure 14 and 15 to Figure S7 and S8). In contrast, risks to population diversity across the range of escapement goals and harvest rates we considered were generally similar across the two spawner-recruitment scenarios. Mixed-stock yield was predicted to occur at a higher escapement goal under the time-varying Beverton-Holt scenario. As a result the shape of the harvest – diversity trade-offs differed dramatically between the two scenarios and mixed-stock harvest were predicted to be greater under the conservation policy than the MSY policy when dynamics were driven by time-varying Beverton-Holt type relationship but harvest policies assumed Ricker dynamics (Figure S8).

Discussion

24

Five key findings emerge from our analyses of CDN-origin Yukon Chinook population diversity and harvest policy performance. First, our molecular analyses of archived scale samples, run-reconstructions, and spawner-recruit analyses uncovered clear evidence of Chinook population diversity in the system. Populations varied in their productivity and carrying capacity by 3.1- and 2-fold, respectively. Variation among populations in run-timing and run-size results in return migrations that are 2.15 times longer, and 1.8 times more stable, than if they were comprised of a single homogenous population. Second, this diversity gives rise to a trade-off between mixed-stock harvest and conservation of population diversity where relatively high harvest rates, which can be sustained by the most productive populations, can come at the cost of overfishing less productive populations and putting the weakest populations at risk of extirpation. For example, mixed-stock harvest is predicted to be maximized at a harvest rate of ~ 70%, but this comes at the cost of overfishing ~ 50% of the populations and putting 10% of populations at risk of extirpation.

Third, these harvest – population diversity trade-offs are asymmetric whereby giving up relatively small amounts of harvest is predicted to result in both large reductions in risk to weak populations and large gains in meeting population level escapement goals. For example, shifting from a policy focused on mixed-stock yield (MSY policy) to one that considers risk to population diversity (conservation policy) resulted in a 20% reduction in average annual mixed-stock harvest, a 50% reduction in the proportion of populations that are overfished, a 40% increase the proportion of populations that met their escapement goals, and a complete elimination of risk of driving weak populations to extinction.

Fourth, the performance of harvest policies, and their resulting trade-offs, were highly sensitive to the true underlying drivers of variation in recruitment in the system (i.e., structural uncertainty). When harvest policies assume the system is driven by Ricker type dynamics (i.e., exhibits over-compensation), but they are truly driven by time-varying Beverton-Holt type dynamics, harvest – diversity trade-offs all but disappeared. Under this scenario harvests were predicted to be maximized at escapement goals and

541   harvest rates that also reduced risks to population diversity compared to a harvest policy that was

542   predicted to maximize yield assuming Ricker type dynamics.

543   There are at least two reasons to temper our interpretation of the findings above. First, our analyses

544   are predicated upon being able to generate unbiased estimates of annual population composition through

545   time from archived scale samples. However, because of the small samples sizes for our composition

546   estimates in many years (e.g., ~125 samples across the duration of the return migration), particularly

547   outside of peak run-timing, as well as gaps in sampling both within and among years, the run-

548   reconstructions are uncertain and potentially biased. Biases in the run-reconstructions then have the

549   potential to impact our ability to characterize the system via multi-population spawner-recruitment

550   analyses. Indeed, structural uncertainty in the run-reconstructions (i.e., assumptions about correlations

551   in run-timing) had significant effects on border passage estimates for some populations in some years

552   which in turn led to considerable variation in leading parameter estimates (e.g., productivity) among

553   spawner-recruitment models fit to the outputs of the three alternative run-reconstructions. To account

554   for this, we combined posterior samples from each of the models thereby generating an unweighted

555   ensemble of posterior samples that captures both estimation and structural uncertainty. In addition,

556   simulation testing suggested that border passage estimates were reasonably unbiased for most

557   populations. However, further consideration of estimation and structural uncertainty is clearly warranted

558   moving forward as are opportunities to increase the inter- and intra-annual coverage of scales samples

559   that are used for genetic stock ID and underpin our analyses.

560   Second, as is inevitable with any analysis of a complex socio-ecological system, we made a number of

561   simplifying assumptions. These include not considering the effects of straying between and within basins,

562   and assuming all populations in the system have historically been equally vulnerable to harvest. Failing

563   to account for straying could lead to overestimating risk of extirpation because populations at low

564   abundance cannot be "rescued" by neighbouring populations. However, straying is considered to occur

565   at lower levels in Chinook (and particularly stream-type Chinook like those in the Yukon) than in other

26

Pacific salmon like pink and chum (Quinn, 2018), and the populations we considered typically had spawning locations that were greater than 100 km away from the nearest other populations. We therefore considered the magnitude of straying to likely be negligible but nonetheless consider this an area that warrants future study. Our multi-stock spawner-recruit analysis and closed-loop simulations assumed all populations in the system have historically been equally vulnerable to harvest. It is possible that differences in run-timing and the timing of the fishery in Alaska (typically front-loaded due to drying weather), are likely to have led to earlier returning fish being more vulnerable to harvest than later returning ones. While simulation testing suggests that the over-all shape of harvest – diversity trade-offs are relatively insensitive to violations of assumptions about population vulnerability to harvest (Staton et al. In review), modelling population variation in run-timing and the timing of fisheries are logical extensions to the work we present here.

Despite these uncertainties, and the need to interpret our analyses with caution, our work has important implications for subsistence and indigenous food security as well as the management of CDN-origin Yukon Chinook. We found that Chinook population diversity stabilizes and extends indigenous access to these salmon. This underscores how population diversity can support food security across a large watershed and suggests that protecting fine-scale population diversity will help promote food security for indigenous peoples in the region. These benefits of maintaining population diversity are strongest for communities that harvest fish in the lower river (both in Canada and Alaska) because these fisheries integrate over multiple populations. However, it is also important to note that harvest policies that prioritized conservation of populations over maximizing mixed-stock yield were also much more likely to meet population level escapement goals, and is likely to subsequently bolster terminal fisheries as well. The outcome of which is predicted to result in more sustainable and equitable access to salmon across communities that depend upon them for both food security and culture.

Canadian-origin Yukon Chinook are a transboundary stock managed under the Pacific Salmon Treaty. Under the Treaty, CDN-origin Chinook are managed as a single aggregate stock with an interim

591   management escapement goal, set by the Yukon River Panel, that establishes the number of Chinook that

592   need to make it into the CDN portion of the Yukon and onto spawning grounds in each year. Since 2010

593   the Interim Management Escapement Goal has been 42,500-55,000. We chose three simple and

594   contrasting harvest policies to illustrate their predicted performance against Chinook fishery and

595   population diversity objectives using a closed-loop simulation model. While the contrasting policies were

596   not intended to exactly match the current approach to management, and we caution against over-

597   interpreting their performance until the limitations outlined earlier are addressed, there are some general

598   insights that emerge from our analysis that are of relevance for management of the Chinook fishery

599   moving forward. First, we found that so long as the target harvest rate on surplus production is relatively

600   low (i.e., ~20%) then the current approach to management is unlikely to jeopardize population diversity

601   in the system. However, this policy is predicted to come at the cost of foregone yield and our analyses

602   suggest that mixed-stock harvest could be doubled by increasing both the escapement goal and target

603   harvest rate, and that this could be achieved while still ensuring population escapement goals are

604   achieved in more than three quarters of the populations. Second, we found that these findings are

605   sensitive to structural uncertainty in the system regarding the true drivers of recruitment variation, which

606   suggests that if/when there is debate about what the true structural form of the spawner-recruitment

607   relationships are it may be more biologically precautionary to increase the escapement goal used.

608   Management Strategy Evaluation (MSE), which is the quantitative evaluation of management

609   strategies using closed-loop simulation models, is widely considered to be the most rigorous way to

610   evaluate the trade-offs achieved by alternative management strategies and to assess the consequences

611   of multiple types of uncertainty on the ability of strategies to meet management objectives (Punt,

612   Butterworth, de Moor, De Oliveira, & Haddon, 2016). The closed loop simulation model we developed,

613   and illustrate the use of here, provides a foundation upon which future decision-making process for CDN-

614   origin Yukon Chinook could be based. In addition to the points raised above, logical extensions to our work

615   that would make it more decision relevant include consideration of future temporal changes in

productivity (e.g., depressed productivity due to climate change); modelling changes in escapement

quality (size/age and sex ratios) which have been observed throughout Western Alaska and the Yukon

(Ohlberger, Ward, Schindler, & Lewis, 2018); increased realism of the harvest control rules that are

evaluated; and engagement of key stakeholders (e.g., subsistence users), Indigenous communities and

decision makers to define biological fishery objectives and evaluate them in an open and transparent

manner.

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Table 1. Canadian-origin Yukon Chinook population units considered and the Conservation Units and stocks they correspond to along with associated Fisheries and Oceans codes. Population Index (*s*) corresponds to index numbers used in the run-reconstruction models.

Population	Population code	Stock code	Stock name	Conservation Unit	Conservation Unit code	Index (*s*)
Carmacks	32	128	Big_Salmon	Big Salmon	CK-70	5
Carmacks	32	393	N_Big_Salmon	Big Salmon	CK-70	5
Carmacks	32	132	L_Salmon	Middle Yukon River and tributaries	CK-73	5
Carmacks	32	131	Tatchun	Middle Yukon River and tributaries	CK-73	5
Middle Mainstem	33	10	Yukon_main	Middle Yukon River and tributaries	CK-73	7
Middle Mainstem	33	356	Nordenskiold	Nordenskiold	CK-71	7
Lower Mainstem	36	255	Chandindu	Northern Yukon River and tributaries	CK-76	7
Lower Mainstem	36	151	Klondike	Northern Yukon River and tributaries	CK-77	7
Pelly	34	139	Blind_Cr	Pelly	CK-72	3
Pelly	34	354	Earn	Pelly	CK-72	3
Pelly	34	359	Glenlyon	Pelly	CK-72	3
Pelly	34	360	Hoole	Pelly	CK-72	3
Pelly	34	390	Kalzas	Pelly	CK-72	3
Pelly	34	357	L_andB_Kalzas	Pelly	CK-72	3
Pelly	34	144	Pelly	Pelly	CK-72	3
Pelly	34	420	Ross_YT	Pelly	CK-72	3
Stewart	35	140	Mayo	Stewart	CK-74	3
Stewart	35	531	McQuesten	Stewart	CK-74	3
Stewart	35	141	Stewart	Stewart	CK-74	3
Upper Lakes and Mainstem	30	14	Whitehorse	Upper Yukon River	CK-69	8
White-Donjek	38	353	Kluane	White and tributaries	CK-75	8
White-Donjek	38	392	Nisling	White and tributaries	CK-75	2
Teslin	31	564	100_Mile_R	Yukon River-Teslin headwaters	CK-68	2
Teslin	31	129	Morley	Yukon River-Teslin headwaters	CK-69	6
Teslin	31	127	Nisutlin	Yukon River-Teslin headwaters	CK-70	6
Teslin	31	133	Takhini	Yukon River-Teslin headwaters	CK-71	6
Teslin	31	22	Teslin	Yukon River-Teslin headwaters	CK-72	6

Population	Population code	Stock code	Stock name	Conservation Unit	Conservation Unit code	Index (s)
Teslin	31	446	Teslin_Lake	Yukon River-Teslin headwaters	CK-73	6
Teslin	31	153	Wolf_R	Yukon River-Teslin headwaters	CK-74	6

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755   **Table 2.** Operating models used in simulation-estimation experiments.

Operating model	Structure/Assumptions
OM_base	Population composition sample sizes (n) equal to historical levels
OM_incFW	OM_base with fish wheel n increased to 250/year
OM_incS	OM_base with sonar n increased to 1250/year
OM_incFWs	OM_incFW with sonar n increased to 1250/year

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758　**Table 3.** Alternative harvest policies considered in the closed loop simulations.

Policy	Basin-wide escapement goal (G)	US subsistence needs ($\dot{H}_{US,S}$)	CDN First Nations basic needs allocation[+] ($\dot{H}_{CDN,S,t}$)	Target harvest rate on surplus ($\dot{U}_{US,C}$)
1. Current harvest management (status quo policy)	48,750	20,000	10,000	0.2
2. Maximize basin wide harvest (MSY policy)	50,000	20,000	10,000	0.98
3. Maximize harvest while minimizing biological risk (conservation policy)	85,000	20,000	10,000	0.8

759　[+]Maximum, see equation 11.

760

761 **Table 4.** Correlation matrix estimated by the run-reconstruction model with a full estimated run-timing
762   correlation matrix (RR_fullCor). Populations are approximately ordered from lowest to furthest
763   upriver, from top to bottom and left to right.

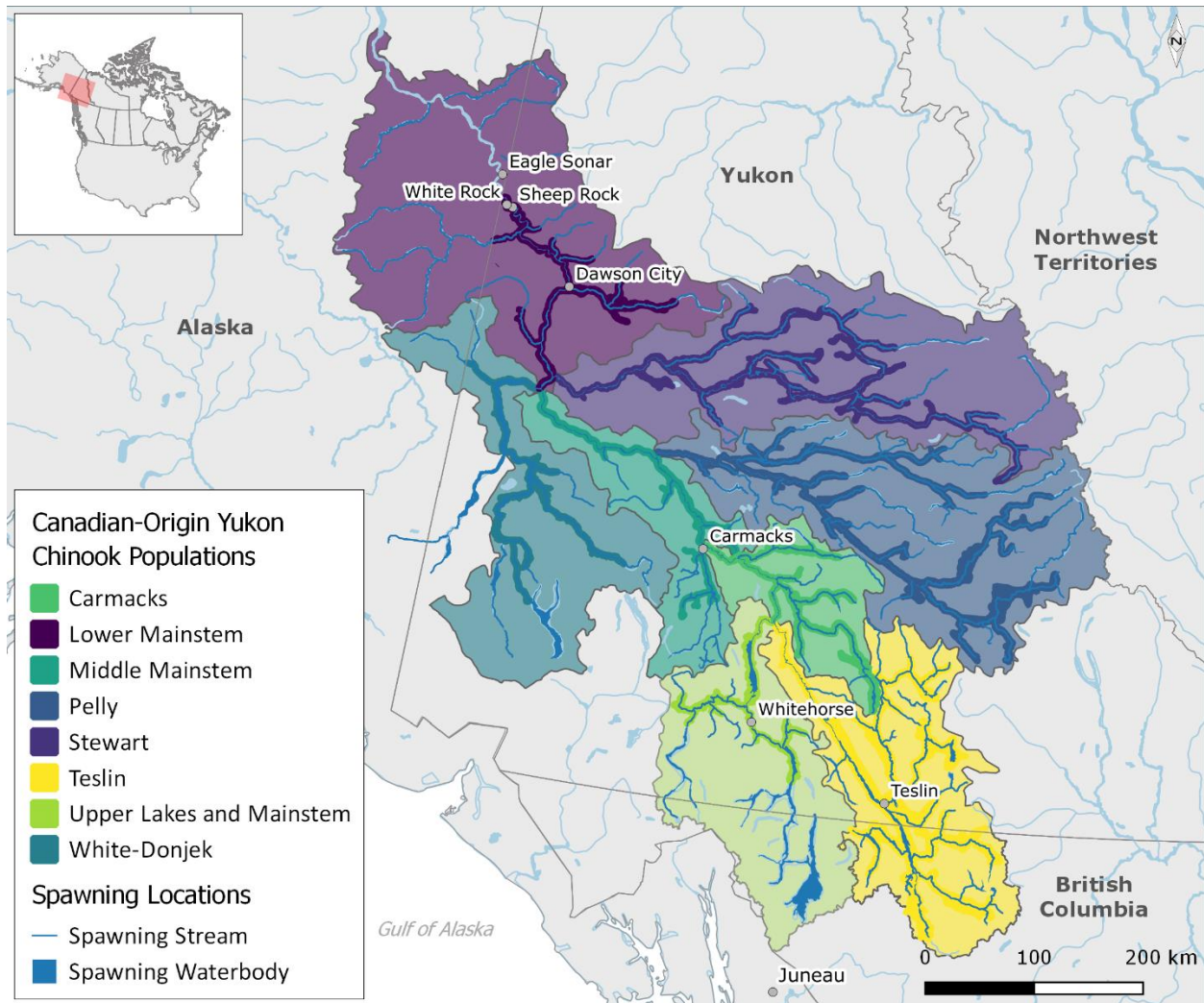|	L.Mstem	W.Donjek	Pelly	Stewart	Carmacks	Teslin	M.Mstem	U.Mstem
L.Mstem	-	-	-	-	-	-	-	-
W.Donjek	0.767	-	-	-	-	-	-	-
Pelly	0.444	0.595	-	-	-	-	-	-
Stewart	0.374	0.37	0.572	-	-	-	-	-
Carmacks	0.153	0.393	0.377	0.664	-	-	-	-
Teslin	0.053	0.255	0.599	0.58	0.509	-	-	-
M.Mstem	-0.024	0.106	0.063	0.533	0.599	0.534	-	-
U.Mstem	-0.091	-0.001	-0.184	0.371	0.388	0.37	0.937	-

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Figure 1. Location of the eight major sub-basins of the Yukon River in Canada corresponding to the populations that individual fish have been assigned to through genetic stock ID. Spawning streams and waterbodies are from Brown et al. (2017).
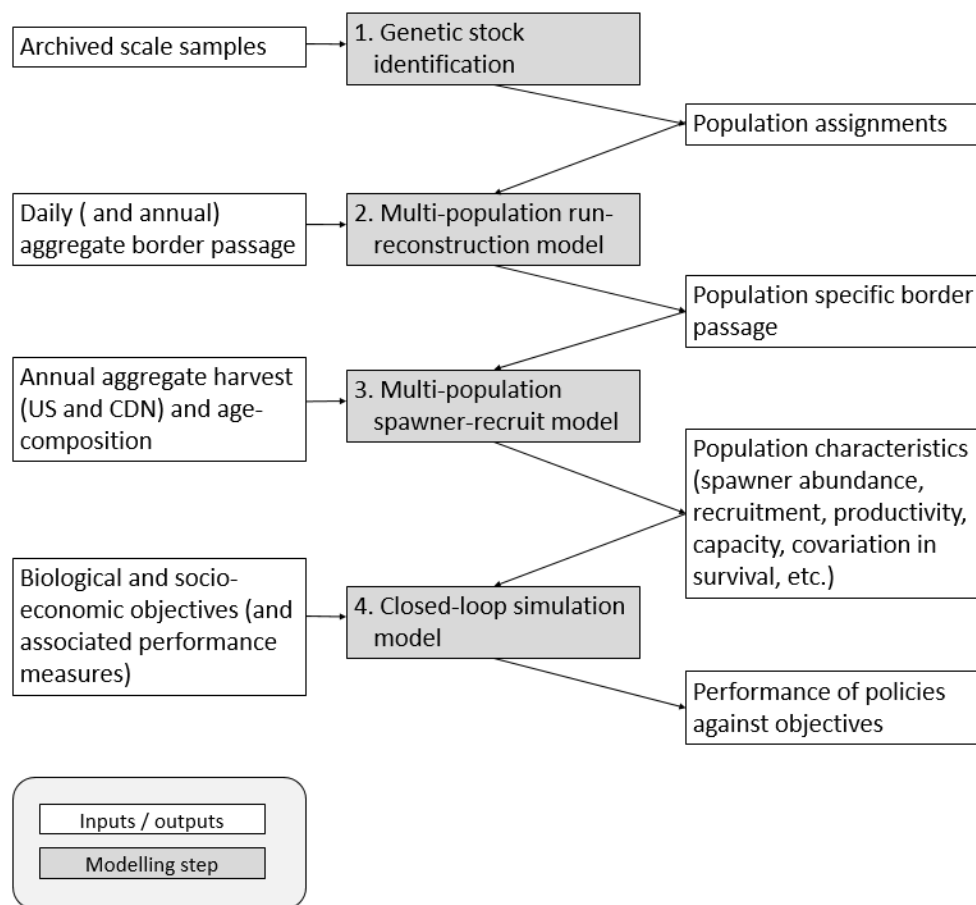
Figure 2. Schematic overview of the analytical approach used to characterize Chinook population diversity and evaluate alternative harvest policies. Data inputs and outputs are denoted by white boxes and key steps to the analysis are in filled boxes.
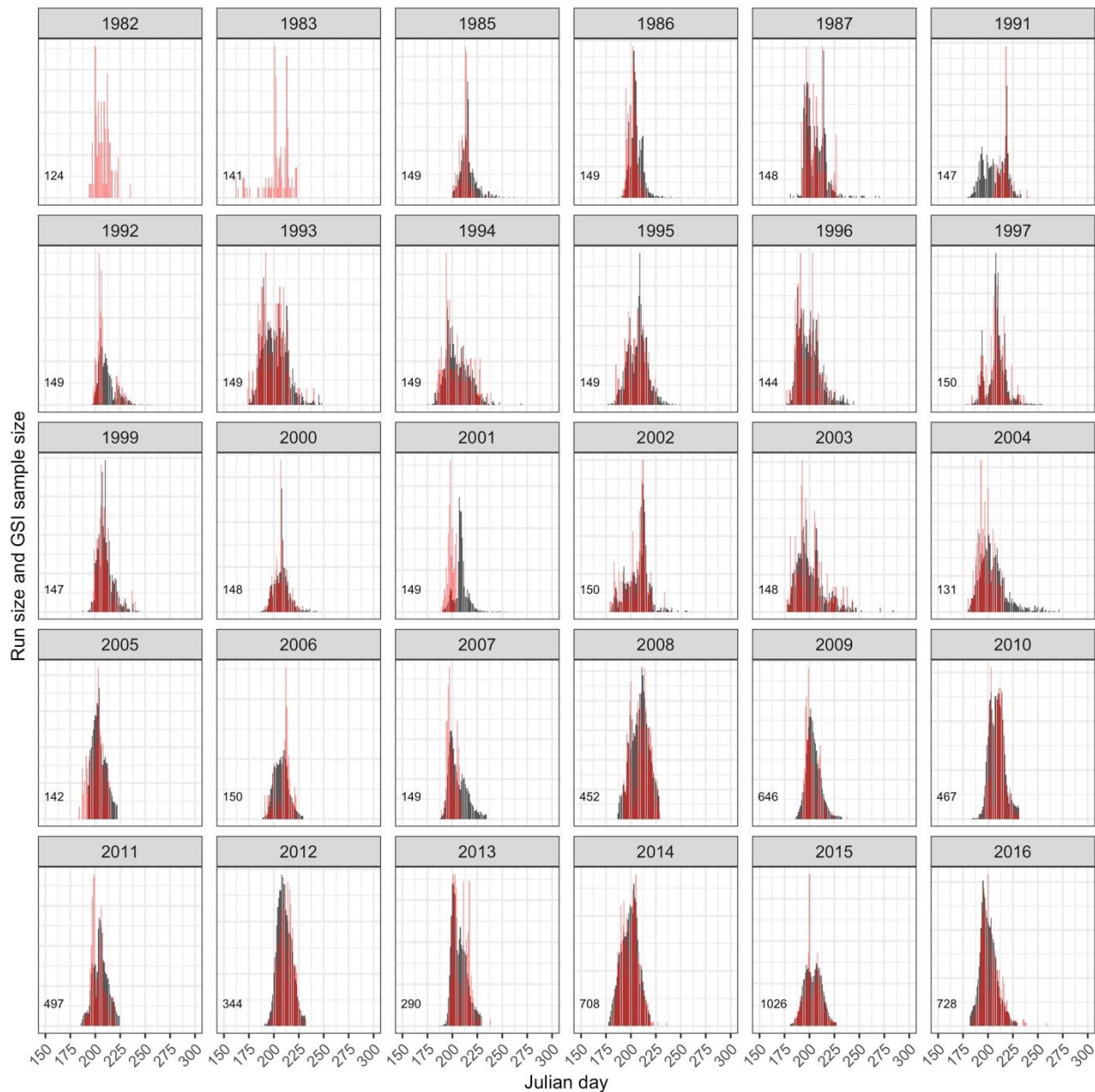
Figure 3. Daily estimates of Chinook border passage (grey bars) and distribution of scales sampled from the run to determine genetic stock ID (GSI). Overall, the scale sub-sampling is generally representative of the observed run. However, there are some clear mismatches between the observed run our scale sub-sampling (e.g., 2001 where the scales sub-sampled for GSI did not overlap with much of the run). The total number of scales analyzed each year to date is in the upper left corner of each panel. Note that scales were unavailable for 1988-1990, and 1998 and we do not currently have information on the distribution of the run in 1982 and 1983. For reference in a non-leap year July 19th is equivalent to Julian day 200.
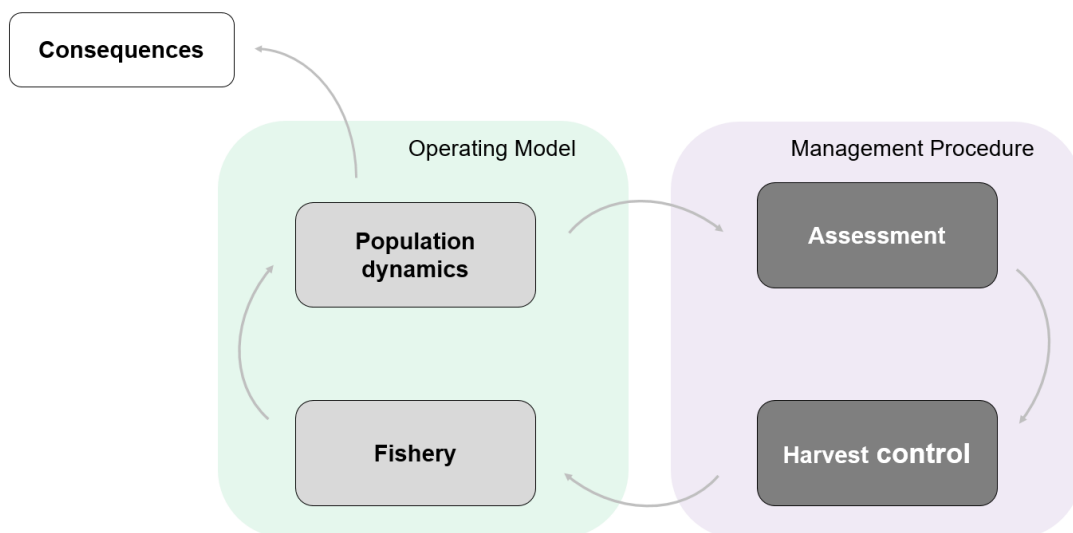
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Figure 4. Illustration of the structure of the closed-loop simulation model.
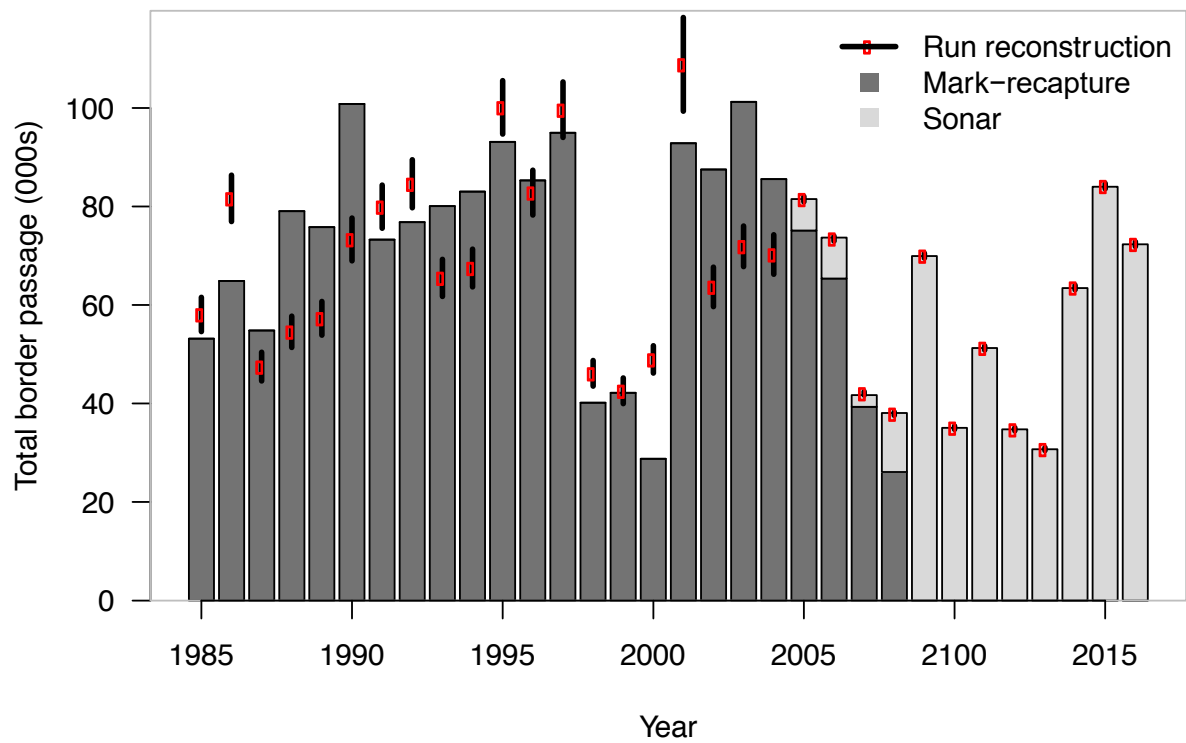
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Figure 5. Total border passage estimates based on the run-reconstruction model (open red circles with black bars indicating the central 95% uncertainty interval), mark-recapture analysis from based on fish sampled from fish wheels (dark grey bars), and the Eagle sonar (light grey bars).
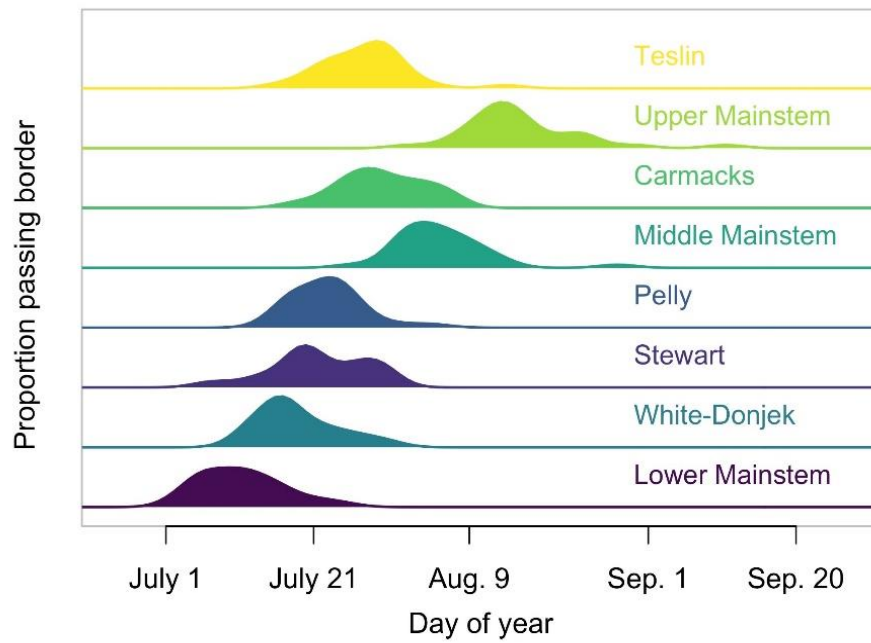
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Figure 6. Estimated average daily border passage for the eight Yukon River Chinook populations. Populations are ordered from earliest (bottom) to latest (top) return timing based on their median run-timing and are color coded according to Figure 1.
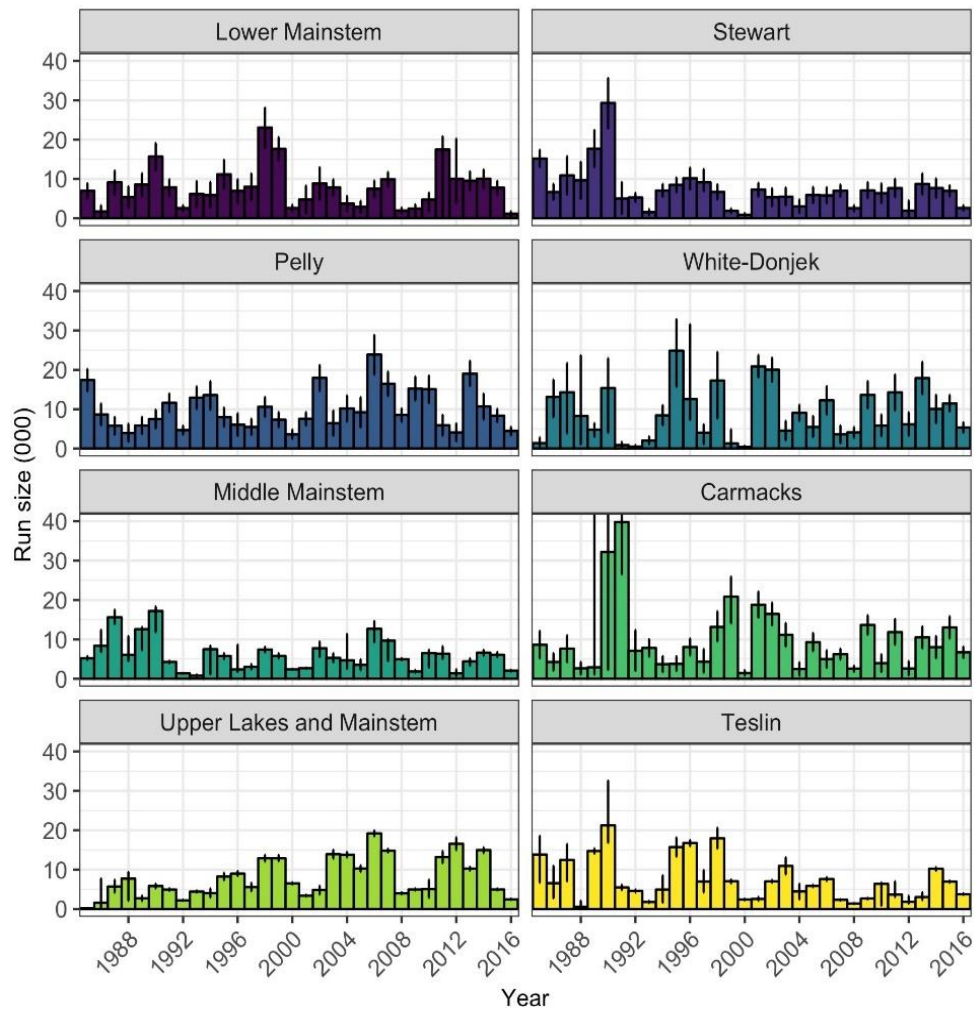
Figure 7. Population-specific border passage run size estimates over time. Bars indicate maximum likelihood estimates while whiskers indicate central 95% uncertainty intervals.
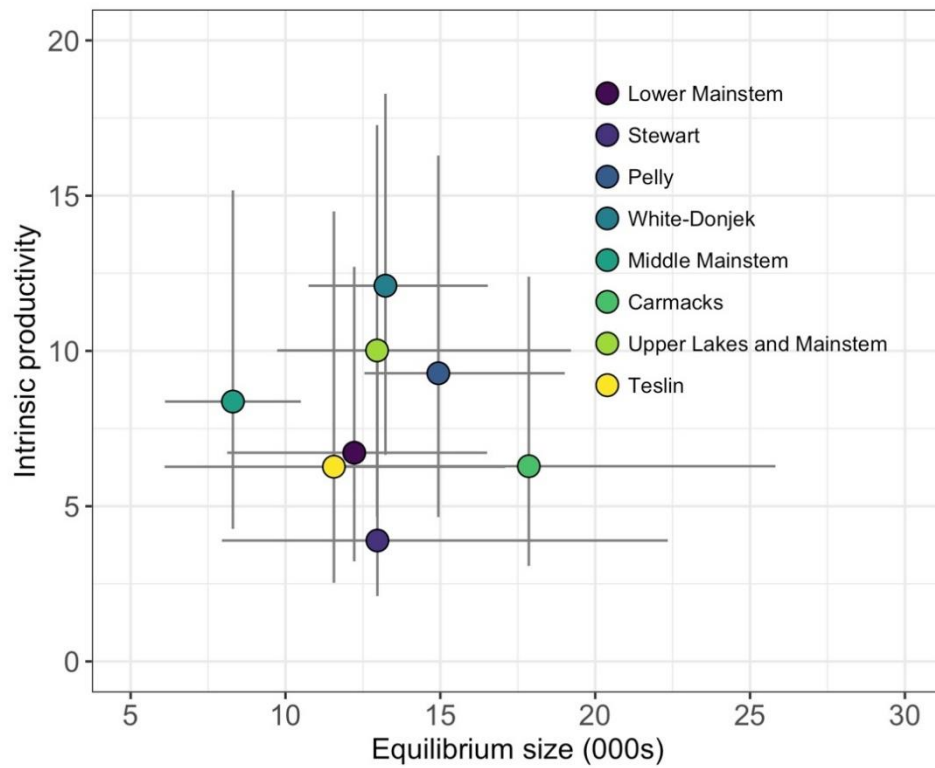
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Figure 8. Posterior distributions of intrinsic productivity (alpha – recruits per spawner at small population size) for individual populations along with corresponding estimates of equilibrium population size. Points are colored coded according to Figure 1.

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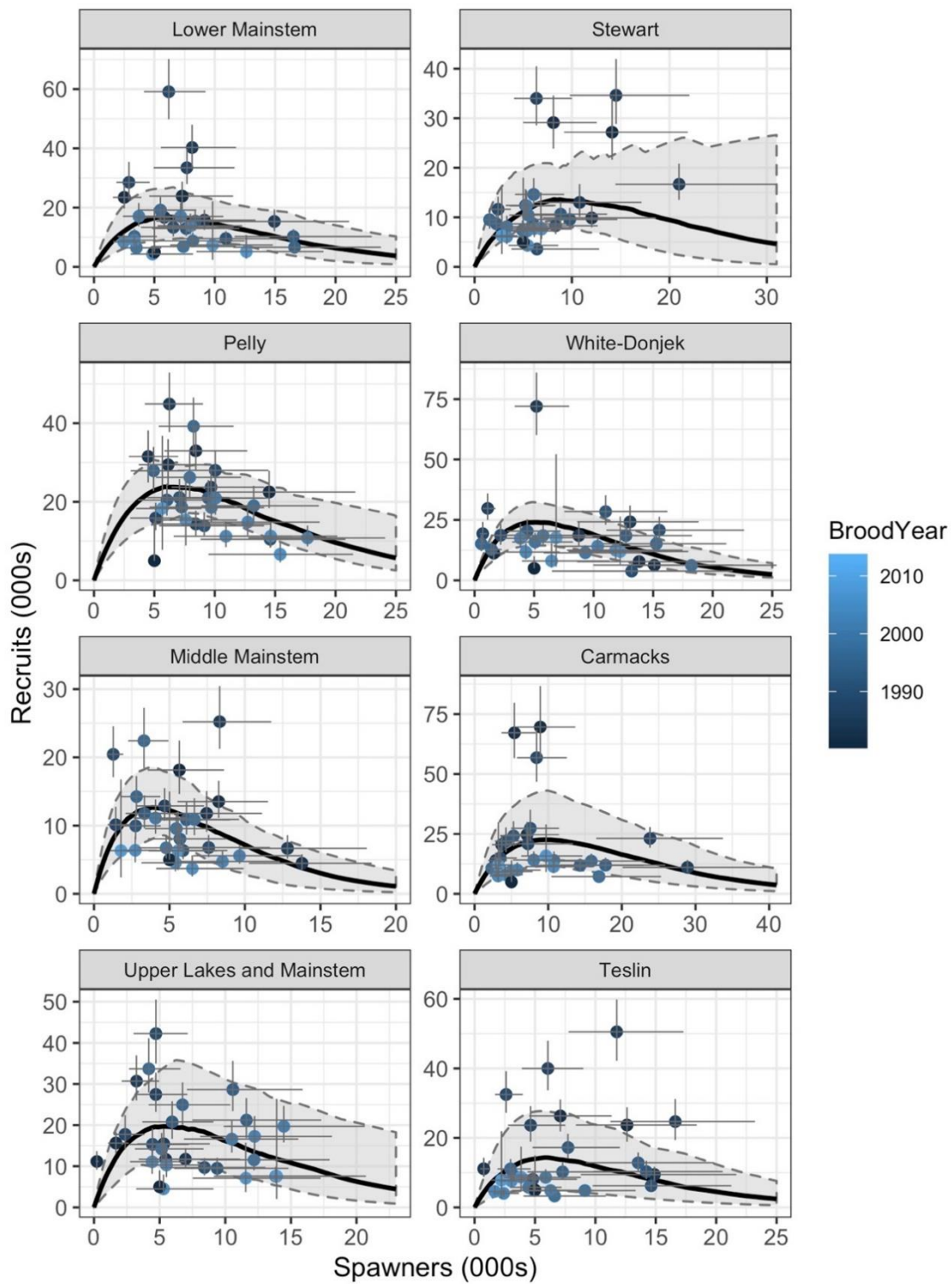
Figure 9. Relationship between recruitment and spawner abundance for Canadian-origin Yukon Chinook populations. Individual spawner-recruitment pairs are colored coded according to time. The black line is the predicted relationship between spawner abundance and recruitment along with 95% credible intervals in the shaded region.
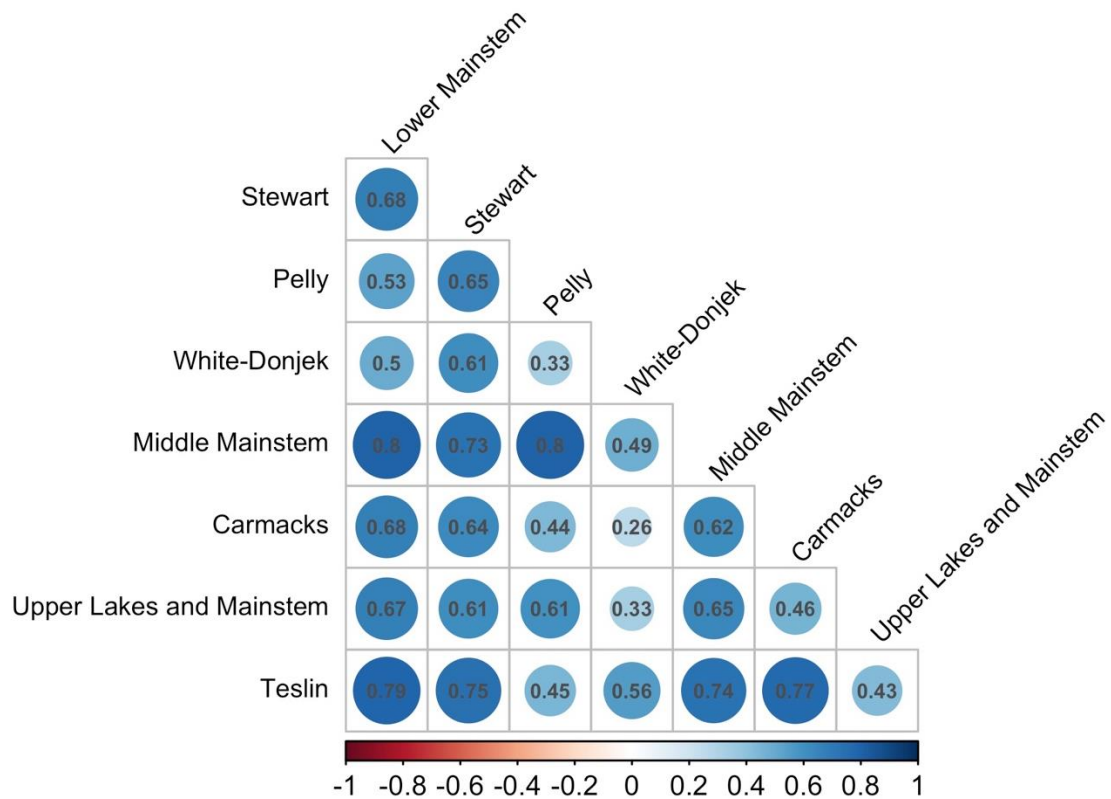
Figure 10. Pairwise correlation in productivity (i.e., log residuals) for each population. Populations are ordered from lower (top) to upper (bottom) river.

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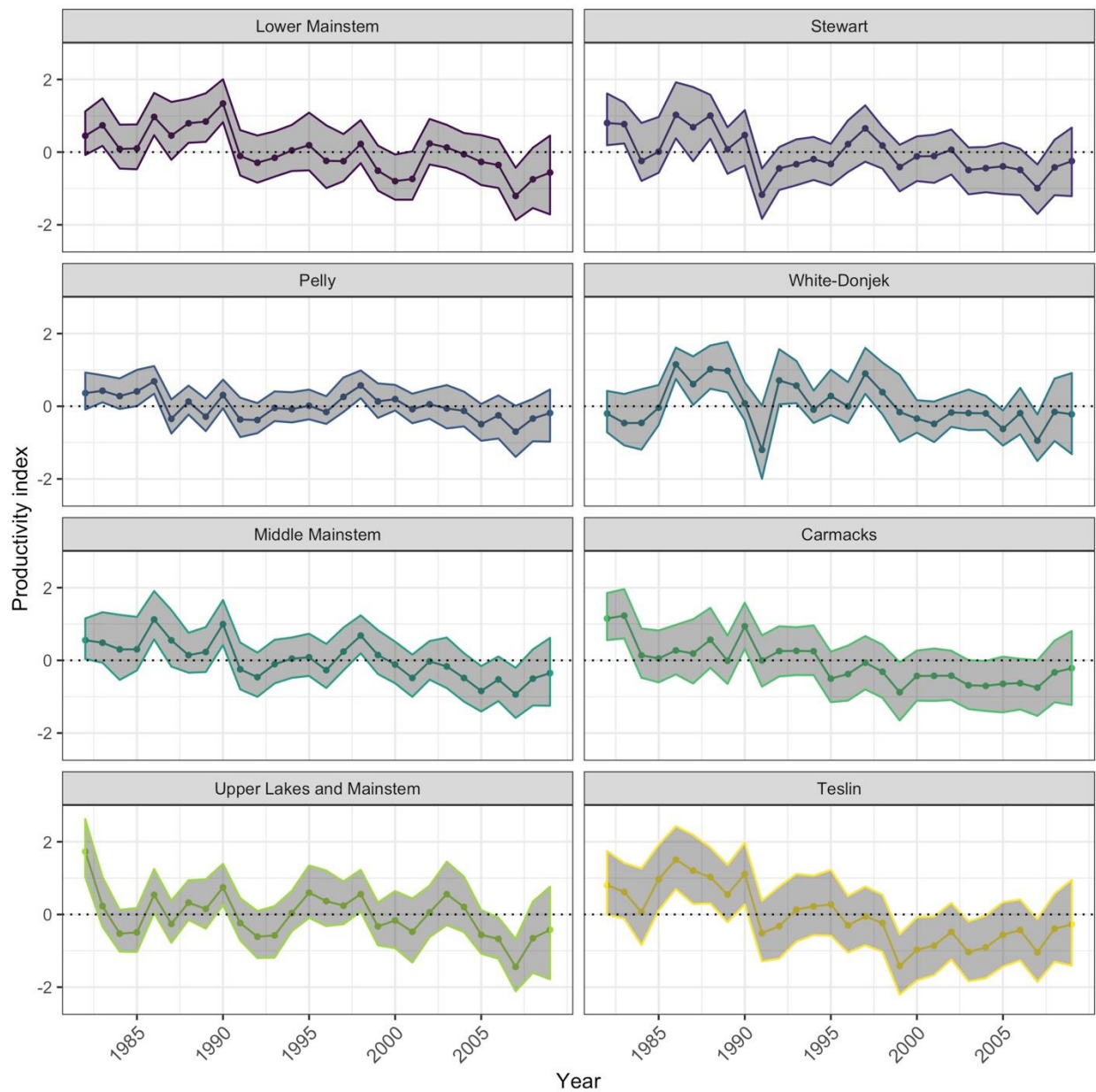
Figure 11. Temporal trends in productivity (i.e., log residuals) for each population +/- 95% credible intervals. Populations are ordered from lower (top left) to upper (bottom right) river.

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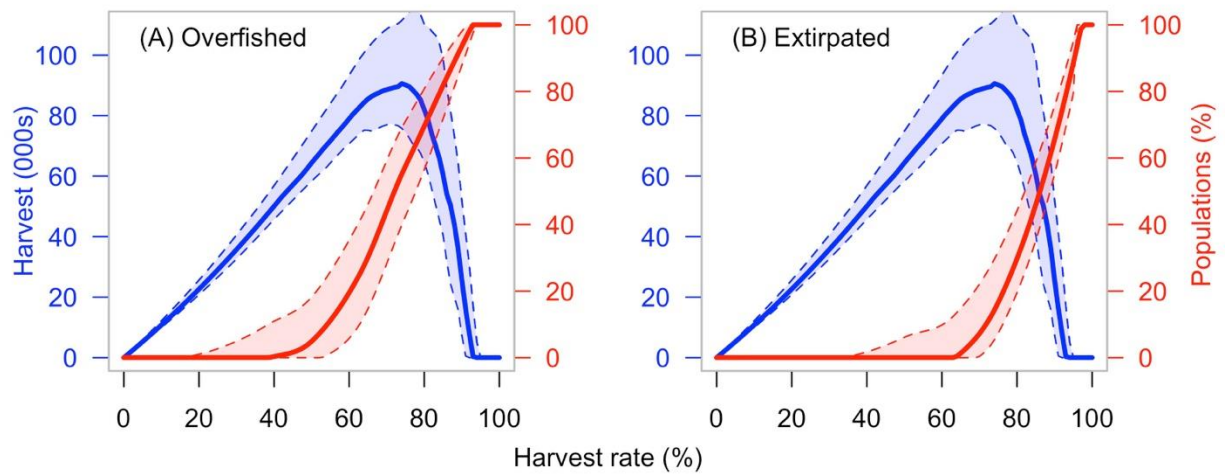
Figure 12. Predicted yield under equilibrium conditions across a range of fixed harvest rates. The corresponding consequences for population diversity, in terms of the percentage of populations predicted to be (A) overfished or (B) driven to extirpation, are plotted on the secondary y-axes.

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Year (last year of 10-year rolling window)
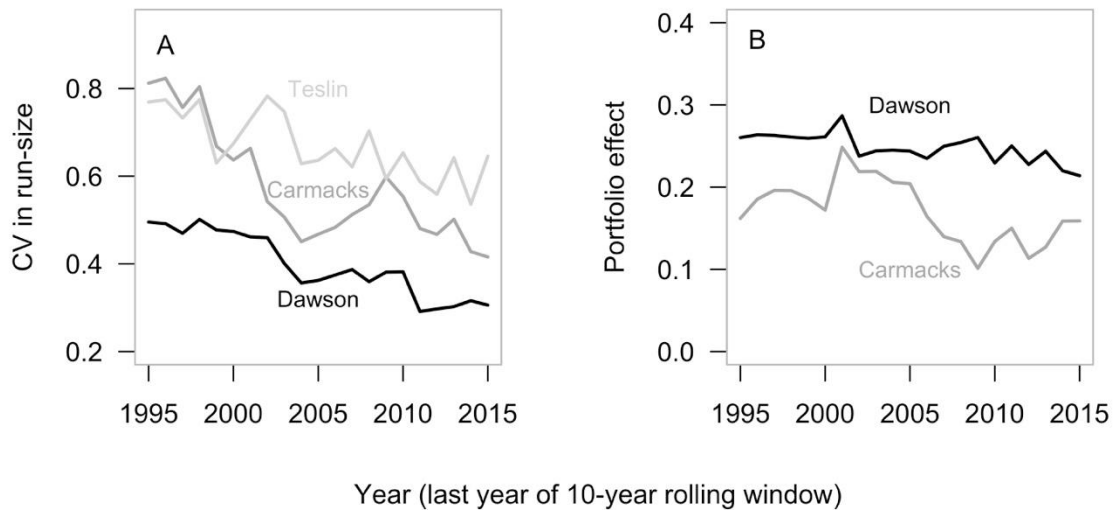
Figure 13. Ten year running average coefficient of variation (CV, Panel A) and Portfolio effects (Panel B) for the aggregate run-size (represented by fish passing Dawson) and smaller spatial scales at the middle of the CDN basin (represented by Carmacks; including the Carmacks, Upper Lakes and Mainstem, and Teslin populations) and the headwaters (represented by just the Teslin population). See Figure 1 for locations of communities.
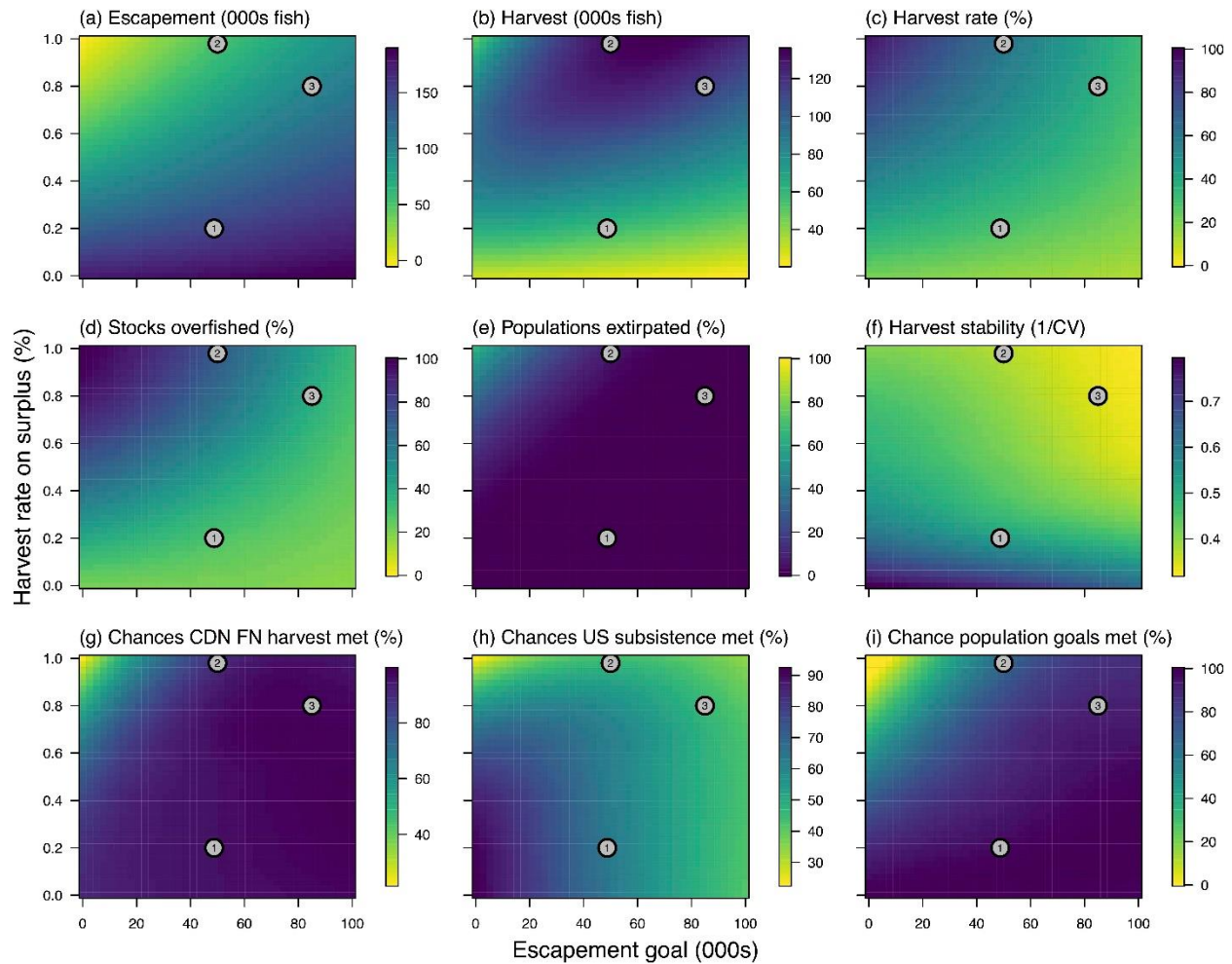
Figure 14. Predicted consequences of alternative harvest policies. Each policy is defined by a combination of target harvest on surplus (y-axis; surplus above escapement, subsistence and First Nations harvest targets) and basin-wide escapement goals (x-axis). Performance measures (z-axis) are calculated over the last 20 years of each Monte Carlo trial (500 in total), which project stock dynamics 50 years forward in time. Three illustrative harvest policies are overlaid on each panel (see Table 5 for more details): (1), a policy similar to the current status-quo (2) a policy that seeks to maximize yield and (3) a policy that seeks to maximize yield once biological risks to populations are minimized.
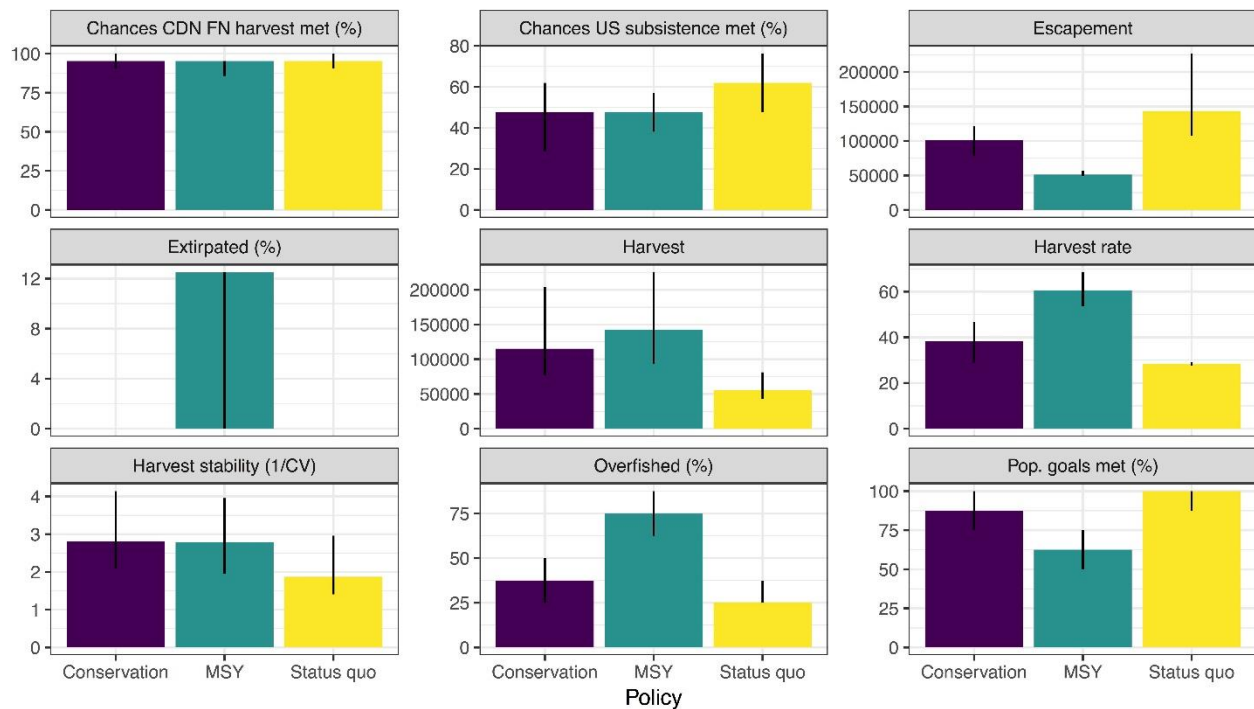
Figure 16. Trade-offs between harvest policies. Predicted ability of three alternative harvest policies (see Figure 16 and Table 5) to meet a diversity of fishery and biological objectives. Each bar is the median (and 25th and 75th percentiles) performance of a given policy as calculated over the last 20 years of each Monte Carlo trial (500 in total).

Supplementary tables and figures

863 **Table S1.** Population, year, # scale samples analyzed (N), and estimate of proportional contribution to
864 total run that year (%). LM = Lower Mainstem; S = Stewart; P = Pelly; WD = White-Donjek; MM =
865 Middle Mainstem; C = Carmacks; ULM = Upper Lakes and Mainstem; T = Teslin.

|	Population															
Year	LM		S		P		WD		MM		C		ULM		T	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
1985	18	12	14	9.3	23	15.7	5	3.1	20	13.6	22	14.8	7	4.5	40	27.1
1986	9	6	14	9.4	22	15	13	9	7	4.9	40	26.9	3	2.1	39	26.5
1987	15	10	12	7.9	24	16.3	27	18.1	32	21.9	12	7.8	3	2	24	16.1
1988	NA	5	NA	0	NA	33.1	NA	9.6	NA	14.2	NA	17.5	NA	2.2	NA	18.4
1989	NA	0.2	NA	24.3	NA	27.2	NA	4.7	NA	1.6	NA	8.8	NA	0.9	NA	32.4
1990	NA	2.8	NA	36.7	NA	27	NA	11.4	NA	1.7	NA	5.3	NA	0.5	NA	14.5
1991	38	26	17	11.4	8	5.7	37	24.9	7	4.5	10	6.9	7	5.1	23	15.4
1992	24	16	11	7.3	25	16.7	10	6.9	20	13.5	32	21.4	9	6.3	18	11.9
1993	40	26.6	9	6.1	13	8.9	20	13.3	26	17.7	13	8.8	11	7.1	17	11.4
1994	28	19.1	14	9.1	18	11.9	30	19.8	16	10.8	12	8.1	8	5.4	24	15.8
1995	11	7.5	15	10	10	6.4	27	18	24	16.4	14	9.2	13	8.5	36	24
1996	27	18.5	7	4.9	11	7.2	27	18.2	15	10.1	33	22.9	8	5.4	19	12.9
1997	23	15.2	15	9.7	16	10.9	10	6.7	8	5	27	17.7	8	5.3	44	29.4
1998	NA	3.3	NA	23.7	NA	18.2	NA	15.2	NA	4.1	NA	18.6	NA	1.9	NA	14.9
1999	25	17.2	10	7.1	19	13	18	12.5	24	16.5	20	13.9	9	6	20	13.8
2000	21	14.4	5	3.7	23	15.8	19	13	21	14.2	26	17.8	8	5.4	23	15.7
2001	12	7.8	4	2.4	10	6.8	6	3.8	56	37.6	3	2.2	10	6.5	49	32.9
2002	18	12.2	19	12.9	9	6	8	5.6	52	34.8	8	5.6	4	2.5	30	20.3
2003	38	26	5	3.4	23	15.5	34	22.8	13	8.7	19	13	5	3.6	11	7.1
2004	25	19.4	5	3.7	22	17	7	5.6	24	18.6	19	14.8	12	9.5	15	11.3
2005	27	19.1	0	0.1	24	16.7	13	9.5	9	6.6	26	18.1	8	5.6	35	24.4
2006	4	2.4	34	22.8	32	21.5	10	6.4	14	9.4	14	9.5	5	3.2	37	24.6
2007	9	6	16	10.6	39	26.1	25	16.7	8	5.5	21	13.9	5	3.2	27	18.1
2008	31	6.8	20	4.5	42	9.2	77	17	83	18.3	33	7.4	45	9.9	121	26.8
2009	47	7.3	52	8.1	141	21.9	73	11.3	40	6.2	118	18.2	13	2	162	25.1
2010	10	2.1	29	6.2	79	16.9	103	22	78	16.7	40	8.5	32	6.8	98	20.9
2011	26	5.2	40	8	53	10.7	69	13.9	95	19.1	38	7.6	49	9.8	127	25.6

Year	Population															
	LM		S		P		WD		MM		C		ULM		T	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
2012	18	5.1	66	19.1	45	13.2	26	7.6	60	17.4	43	12.5	20	5.9	66	19.3
2013	1	0.4	77	26.6	55	19.1	9	3.2	47	16.1	25	8.7	21	7.1	55	18.8
2014	50	7	100	14.1	91	12.9	45	6.4	144	20.3	62	8.8	72	10.2	144	20.3
2015	41	4	168	16.4	169	16.5	58	5.7	181	17.6	125	12.2	48	4.7	234	22.8
2016	50	6.8	166	22.8	132	18.2	52	7.1	50	6.9	103	14.1	25	3.4	150	20.6

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Table S2. Likelihood and AIC values for the three run reconstruction models used to estimate population specific border passage from 1985-2016. Each model differed in the parameterization of the run-timing variance-covariance relationship. Shown are likelihoods for the objective function (L), process error in run-timing (L_E), run-size index (L_I), population composition (L_x), and daily counts (L_ε).

Model	Description	No. of para.	$\Delta AICc$	L	L_E	L_x	L_I	L_ε
RR_base	Uncorrelated run-timing among populations	522	1340.3	69690.9	20920.8	47356.8	12.7	-486.8
RR_oneCor	Shared correlated run-timing among populations	523	0	69019.6	20768.3	46873.8	12.6	-520
RR_fullCor	Unique correlated run-timing among populations	550	37.7	69005.2	20969.3	46749.2	12.6	-610.8

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Table S3. Productivity (alpha), size (alpha/beta), and correlation through time (phi) by population +/- 95%
877   credible intervals.

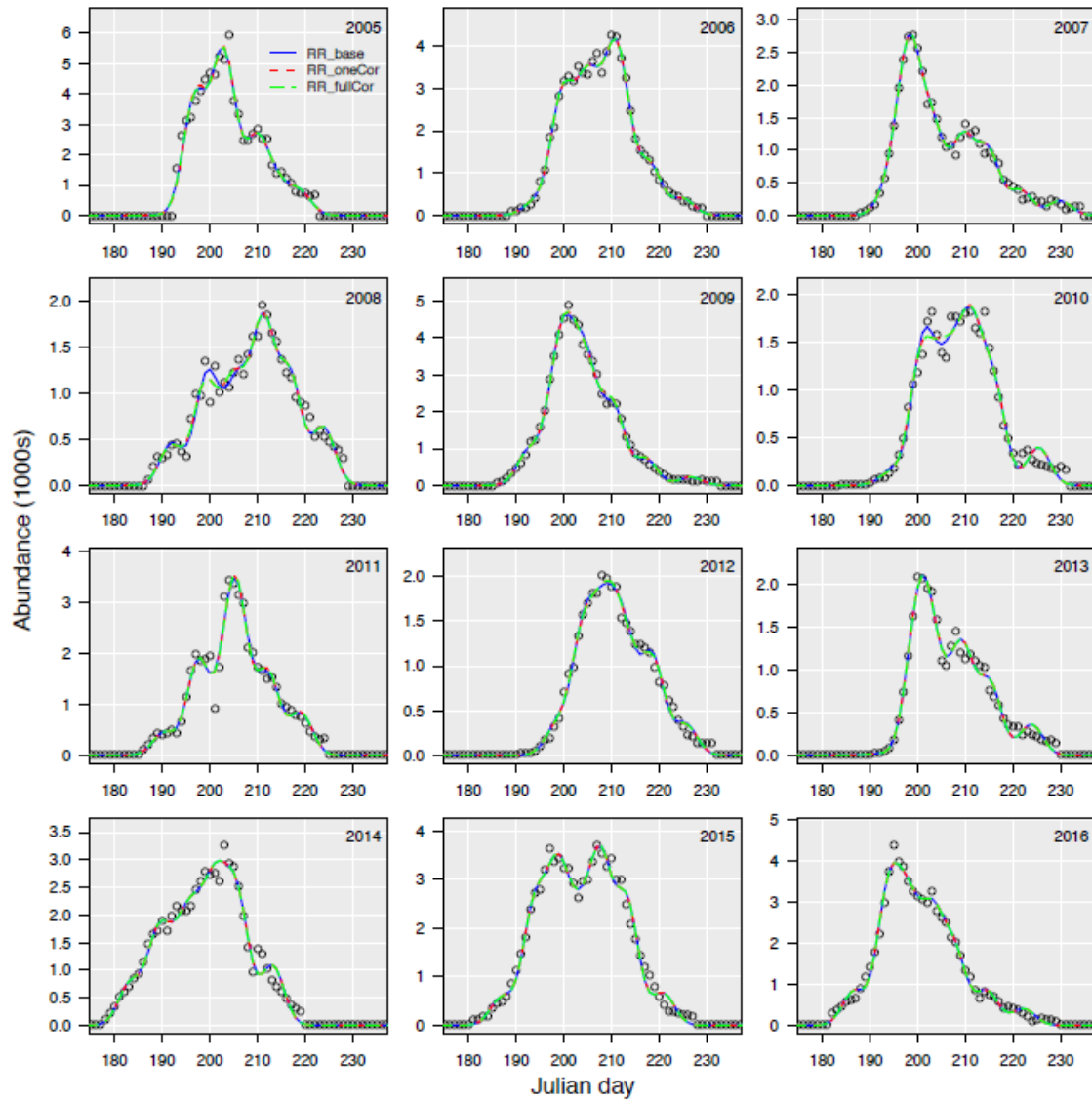| Population	Productivity	Equilibrium	Phi	Sigma
Lower Mainstem	6.72	12220	0.61	0.54
	(3.22-12.70)	(8110-16510)	(0.25-0.90)	(0.42-0.72)
Stewart	3.89	12968	0.52	0.56
	(2.11-9.84)	(7946-22344)	(0.02-0.90)	(0.42-0.75)
Pelly	9.28	14940	0.4	0.38
	(4.64-16.29)	(12550-19018)	(-0.23-0.84)	(0.26-0.53)
White-Donjek	12.10	13226	0.35	0.65
	(6.65-18.28)	(10744-16532)	(-11-0.75)	(0.44-0.93)
Middle Mainstem	8.37	8302	0.58	0.50
	(4.26-15.17)	(6108-10497)	(0.14-0.90)	(0.36-0.69)
Carmacks	6.28	17860	0.71	0.49
	(3.07-12.39)	(11200-25810)	(0.34-0.94)	(0.36-0.68)
Upper Lakes and Mainstem	10.01	12956	0.48	0.64
	(4.66-17.07)	(9731-19218)	(0.01-0.86)	(0.49-0.87)
Teslin	6.26	11564	0.73	0.61
	(2.53-14.49)	(6098-17096)	(0.43-0.94)	(0.45-0.83)

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Figure S1. Fits of the three run-reconstruction models (lines) to daily Eagle sonar counts (circles).
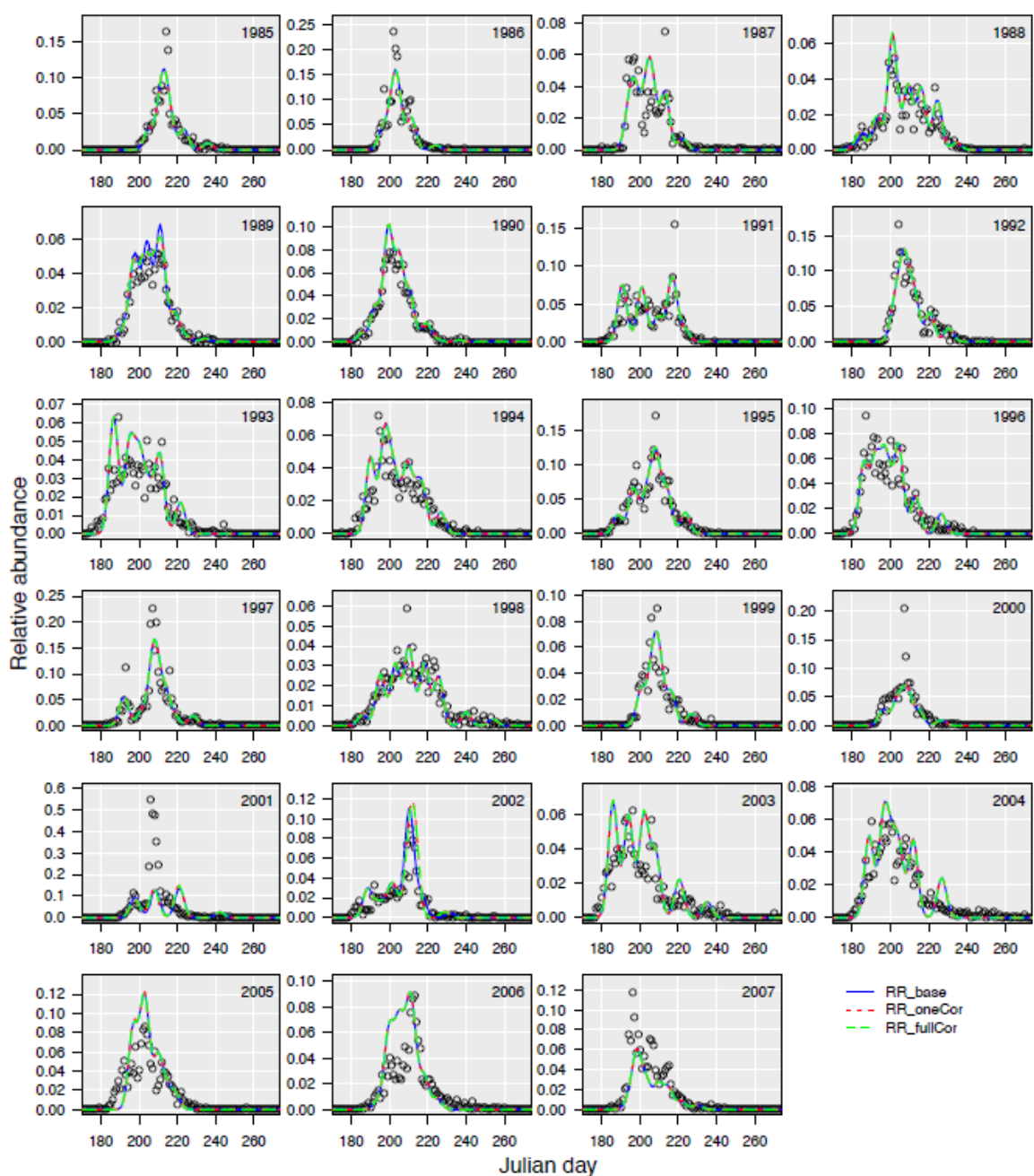
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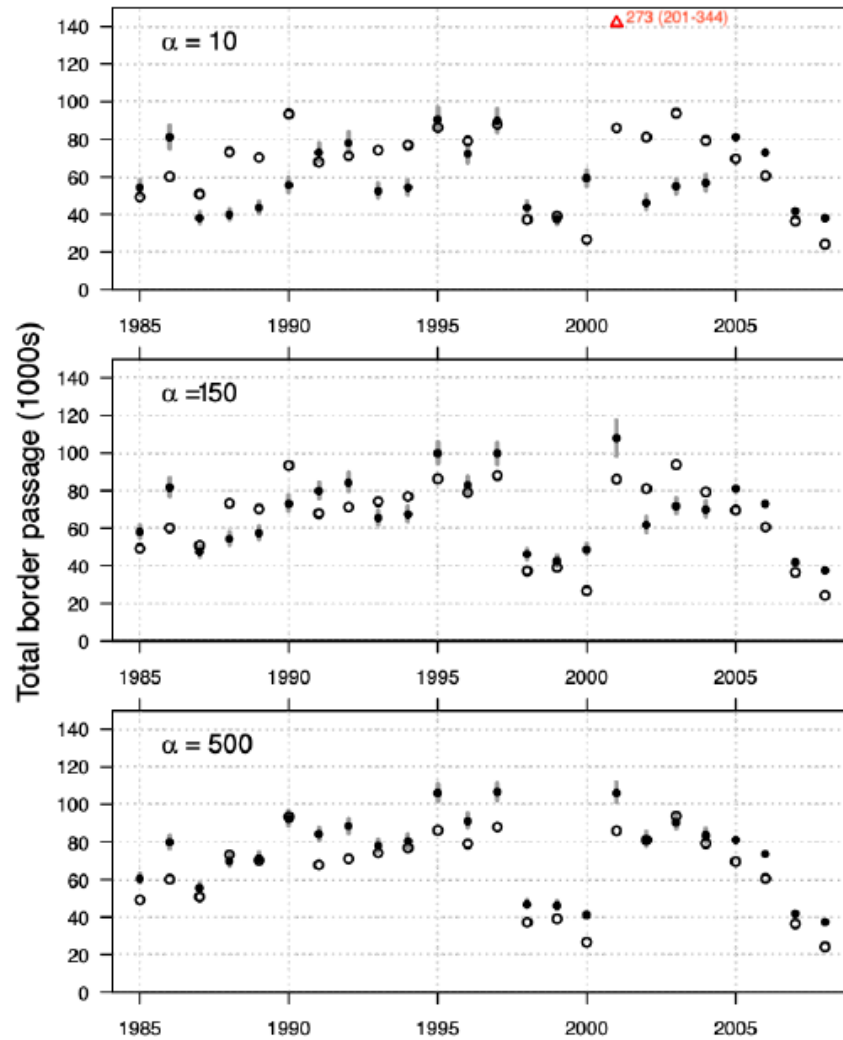**Figure S2.** Fits of the three run-reconstruction models (lines) to daily fish wheel counts (circles).

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Figure S3. Sensitivity analysis of total border passage estimates (1000s) from RR_base for three likelihood weights (α) in years where mark-recapture is the only source of total border passage data. Closed circles indicate run reconstruction MLEs, grey bars indicate the associated central 95% uncertainty interval (UI), and open circles indicate mark-recapture estimates. The red triangle in the top plot indicates that the run reconstruction estimate for that year is outside of plot bounds (MLE: 273; 95% UI: 201-344).
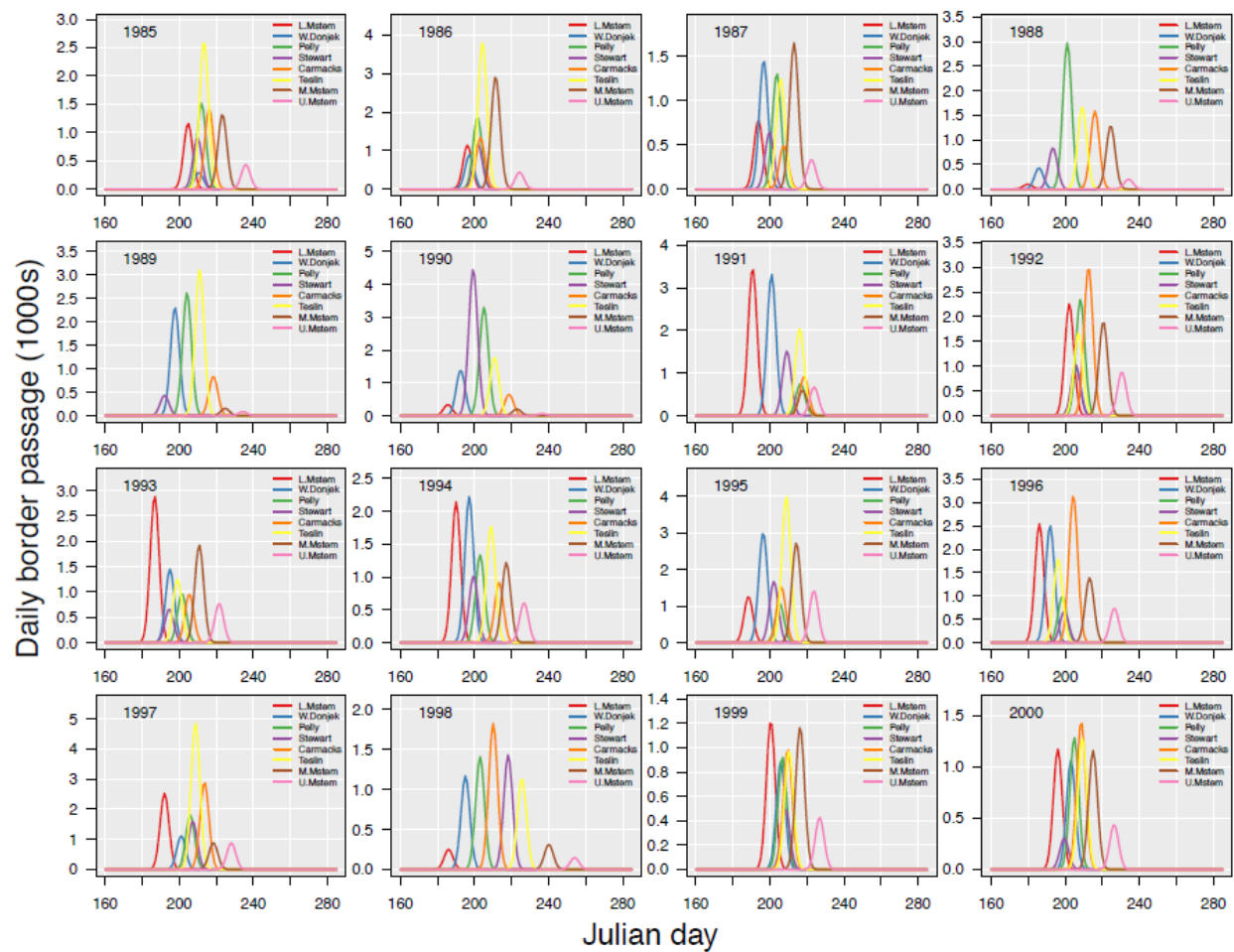
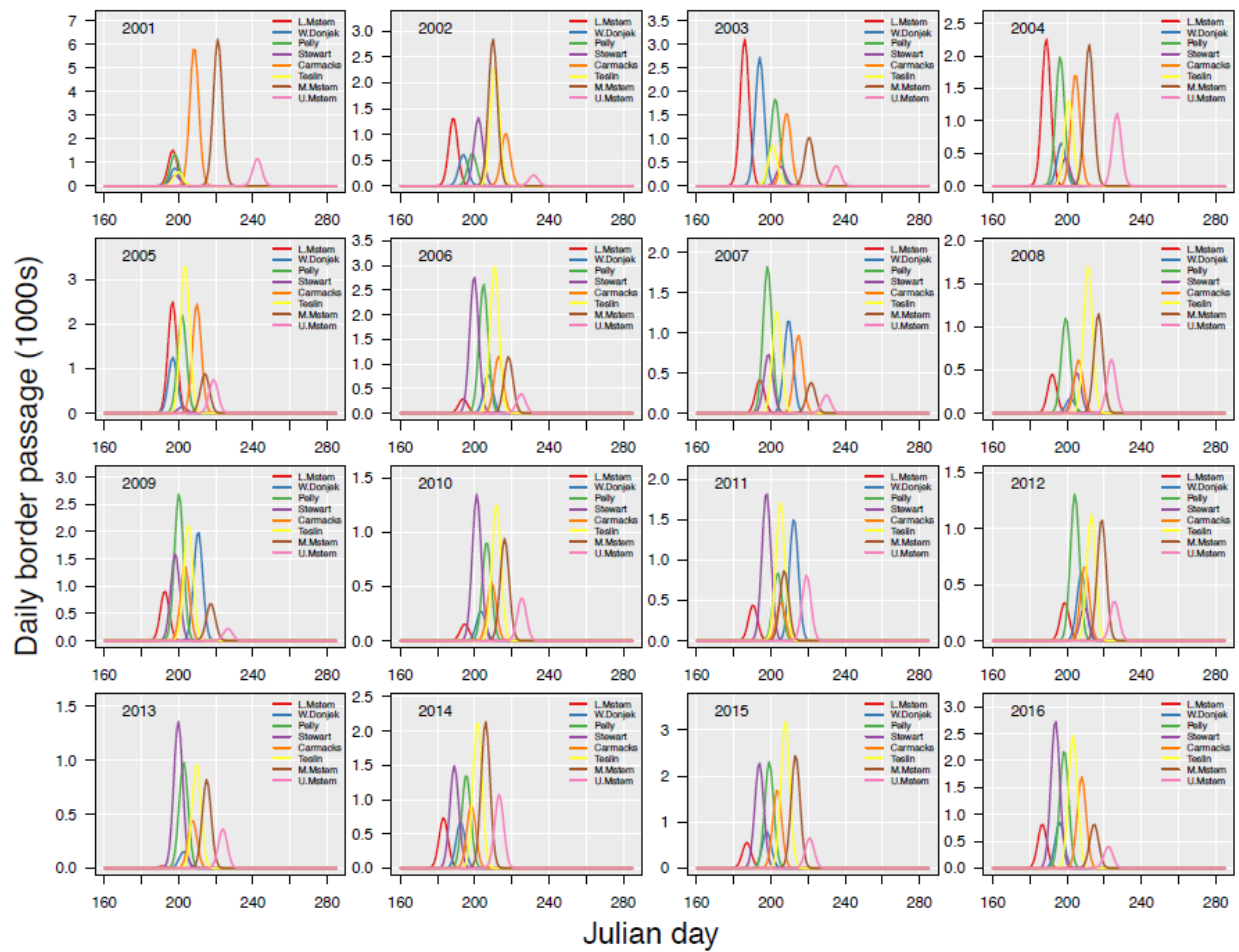Figure S4. Estimates of average daily border passage for the eight Yukon River Chinook populations (1985-2000)

Figure S5. Estimates of daily border passage for the eight Yukon River Chinook populations (2001-2016).

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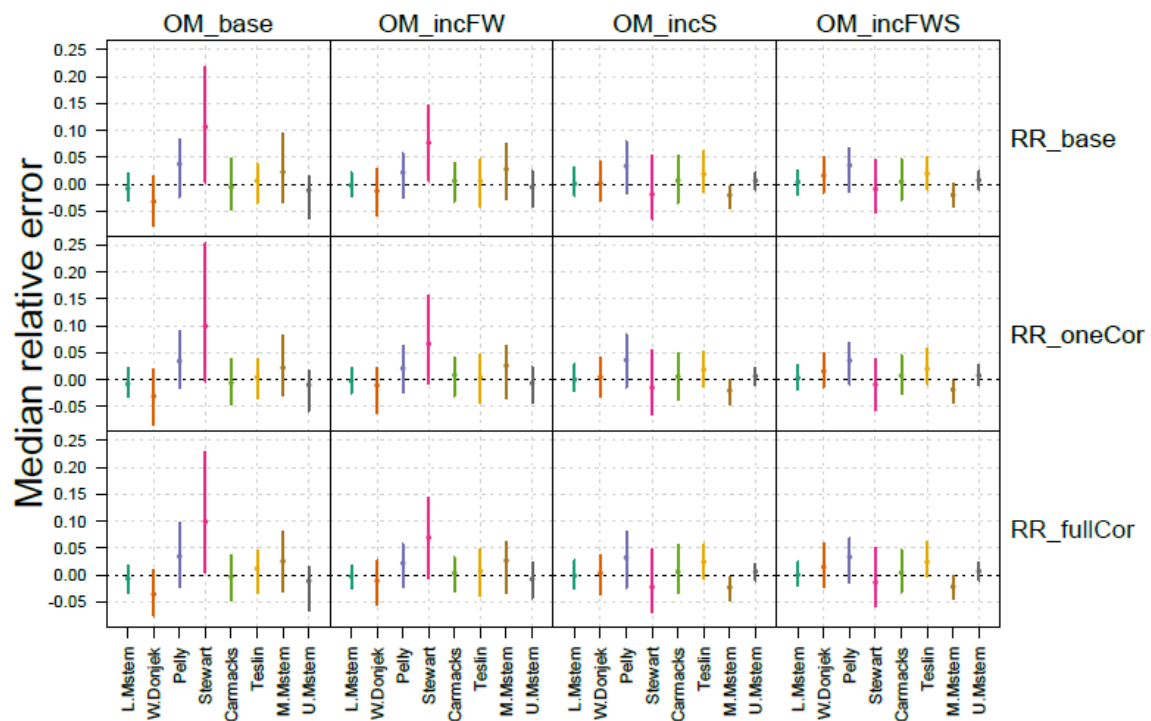
Figure S6. Median relative error (MRE) in run size estimates from three RRs (rows), which were each fitted to 100 datasets generated by four OMs (columns). A positive MRE indicates model estimate was less than the true value from simulation (i.e., underestimate), while a negative MRE indicates model estimate was greater than the true value from simulation (i.e., overestimate). Points indicate the median MRE across the 100 fits, while lines indicate the central 95% interval.

Figure S7. Predicted consequences of alternative harvest policies when recruitment is driven by time-varying Beverton=Holt type spawner-recruitment relationship. Each policy is defined by a combination of target harvest on surplus (y-axis; surplus above escapement, subsistence and First Nations harvest targets) and basin-wide 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. Three illustrative harvest policies are overlaid on each panel (see Table 5 for more details): (1), a policy similar to the current status-quo (2) a policy that seeks to maximize yield and (3) a policy that seeks to maximize yield once biological risks to populations are minimized.
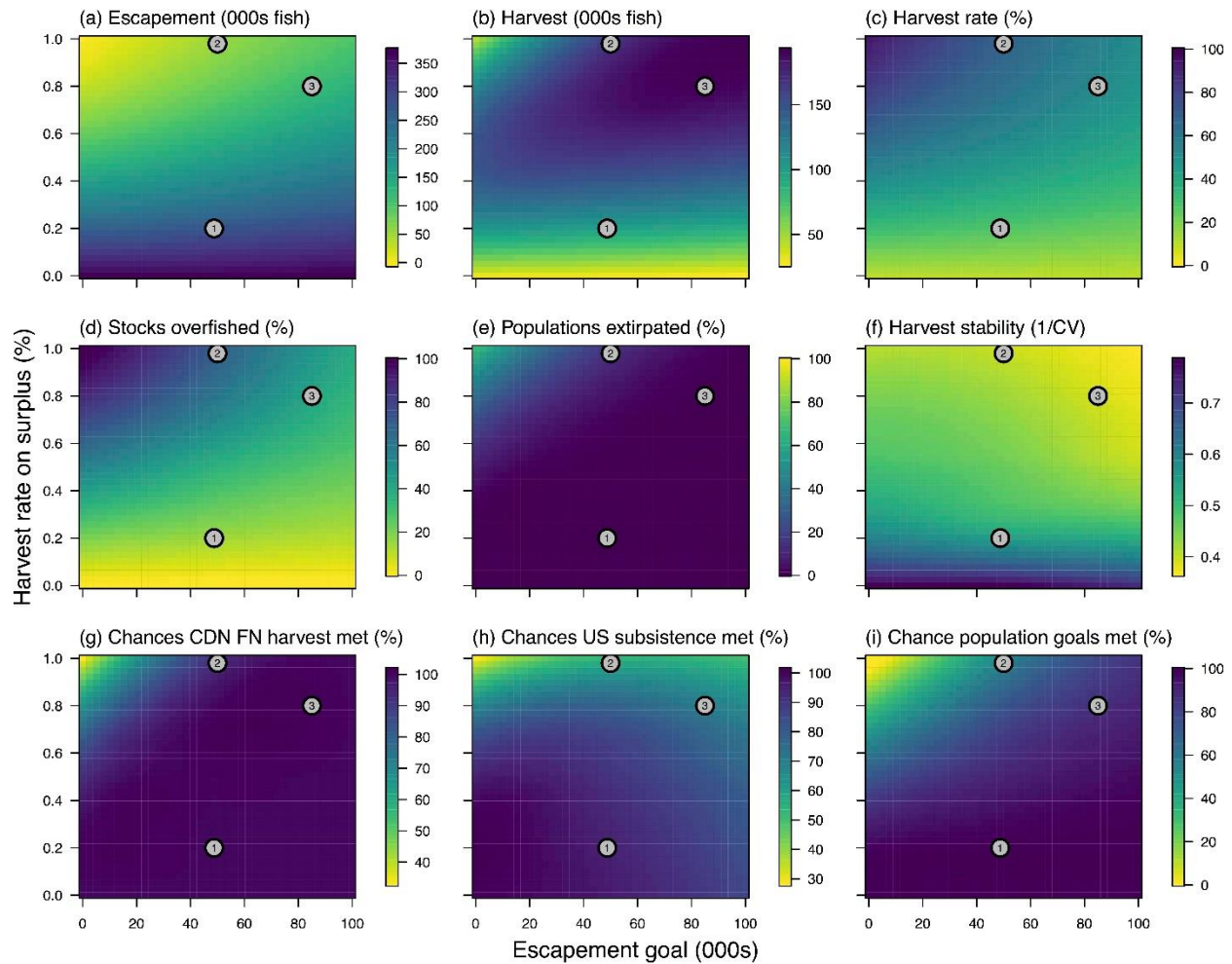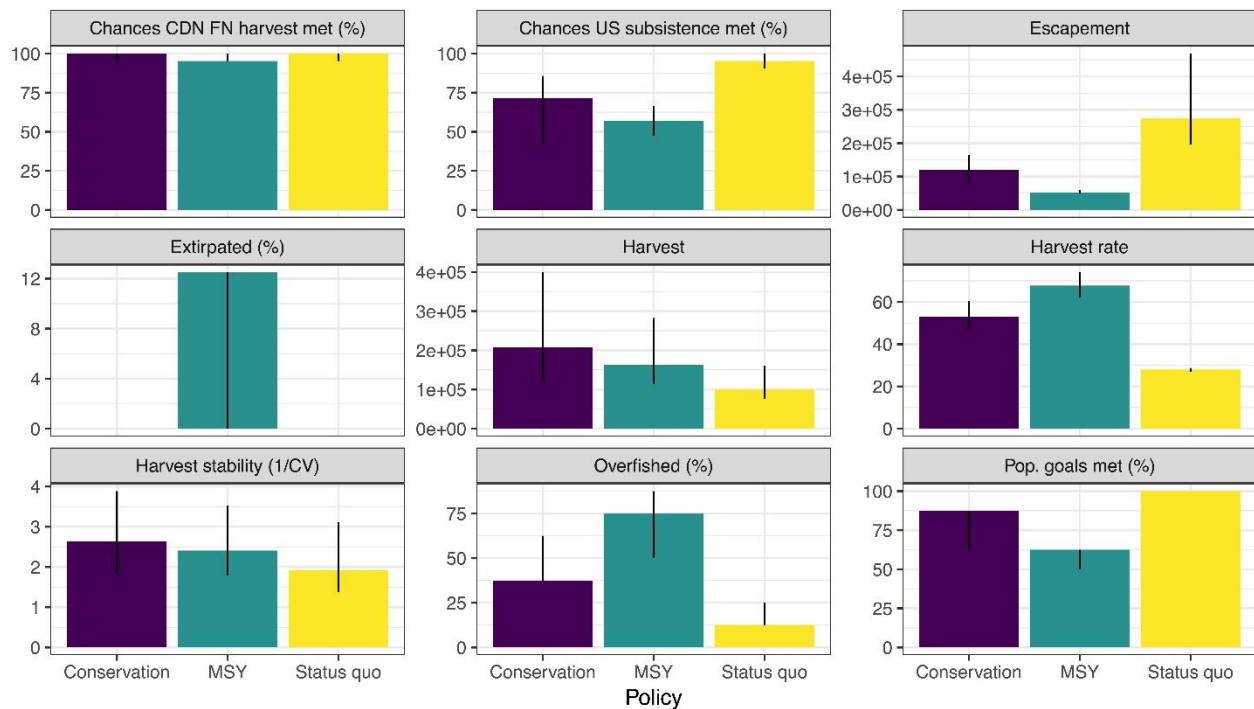
Figure S8. Predicted consequences of alternative harvest policies when recruitment is driven by time-varying Beverton-Holt type spawner-recruitment relationship. Predicted ability of three alternative harvest policies (see Figure S6 and Table 5) to meet a diversity of fishery and biological objectives. Each bar is the median (and 25th and 75th percentiles) performance of a given policy as calculated over the last 20 years of each Monte Carlo trial (500 in total).

Appendix A.

930   We estimated the daily passage of Chinook into Canadian waters using multi-population run

931   reconstruction (RR) models which simultaneously accounts for uncertainty in observations and underlying

932   population processes and allows for the inclusion of incomplete datasets. We separately modelled the

933   dynamics of the eight Chinook populations, indexed by *s* (Table A1). Annual, population-specific run size

934   was the main parameter of interest estimated by the model, though we also estimated parameters for

935   run timing and catchability. We separately model catchability to two fishing "gears" (index by *g*): sonar

936   and fish wheels. Model notation and equations are listed in Table A1 and A2 respectively.

937   We implemented the models using the Template Model Builder package (TMB; Kristensen, Nielsen,

938   Berg, Skaug, & Bell, 2015) within R version 3.5.3 (R Core Team, 2019). Standard error of model parameters

939   and quantities of interest were calculated using a delta method routine within TMB and were treated as

940   equivalent to standard deviations.

941   *Population dynamics*

942   The daily proportion of salmon entering the model (i.e., escaping to Canadian waters) each day is

943   assumed to be normally disturbed around mean μ_{sy} with variance σ_s^2 (TA2.4). Numbers of salmon arriving

944   daily for each population/year combination is subsequently calculated as the product of the daily arrival

945   proportions and run size (TA.5). To model interannual variability in mean run timing, we assume that the

946   population-specific mean dates of arrival in a given year ($\left\{\mu_{s,y}\right\}_{s=1}^8$ or $\boldsymbol{\mu}_y$) are a function of run timing in

947   the previous year, i.e.,

$$\boldsymbol{\mu}_{y+1} = \boldsymbol{\mu}_y \exp(\boldsymbol{\varepsilon}_y) \tag{A.1}$$

948 where $\boldsymbol{\varepsilon}_y$ is a vector of 8 normally distributed process errors with mean 0 and covariance $\boldsymbol{\Sigma}$. The

949 covariance matrix is constructed as $\boldsymbol{\Sigma} = \mathbf{DCD}$, where $\mathbf{D}$ is a diagonal matrix with the variance of $\boldsymbol{\mu}_s$ as the

950 ssth element, and $\mathbf{C}$ is a symmetric correlation matrix, i.e.,

$$\mathbf{C}_{ij} = \begin{cases} 1 & i = j \\ c_{ij} & i \neq j \end{cases} \tag{A.2}$$

951 where c_{ij} is the correlation between arrival timing deviations for population i and j $\left(c_{ij} = c_{ji}\right)$.

952 We constructed alternative run-reconstructions by defining a suite of process models considering

953 alternative parameterizations of $\boldsymbol{\Sigma}$. We first considered a model, RR_base, in which the diagonal elements

954 of $\mathbf{D}$ were estimated while $\mathbf{C}$ was set to the identity matrix (i.e., $c_{ij} = 0$ for $i \neq j$). This model assumes

955 that there is no correlation in run timing deviations among the eight populations. We alternatively

956 considered two models in which the off-diagonal elements of $\mathbf{C}$ were estimated. In one model

957 (RR_oneCor) we constrained all off-diagonal elements of $\mathbf{C}$ to have the same value (i.e., $c_{ij} = 0$ for $i \neq j$)

958 and another model (RR_fullCor) in which all c_{ij} parameters were freely estimated for $i \neq j$. RR_oneCor

959 can account for correlation between run timing deviations using only one more parameter than RR_base,

960 though it may not be appropriate if there are strong discrepancies in the levels of correlation among

961 stocks. In contrast, RR_fullCor can account for more complex patterns of correlation than RR_oneCor, but

962 at the potentially steep cost of 27 additional parameters.

963 *Observation model and objective function*

964 Daily border passage counts were predicted by scaling the daily model-predicted passage by a gear-

965 specific catchability factor (TA2.6). Catchability to the fish wheel was estimated while catchability to sonar

966 was fixed at 1. Similarly, the predicted run size index is the total run size scaled by a gear- and population-

967 invariant catchability factor (TA.7). While catchability may vary across populations for a variety of reasons

968 (i.e., bank orientation, run-timing, etc.), the data were not informative enough to estimate population-

969 specific catchability. Population composition was predicted as the relative proportion of population

970 present on each day (TA2.8).

971   Daily salmon counts were assumed to arise from negative-binomial (NB) distributions (TA2.11). The

972 NB distribution, describing the number of successes in a series of Bernoulli trials before r failures occur

973 (with probability of success p), is broadly applicable as a model for overdispersed count data. We

974 parameterize the NB distribution in terms of the mean count η and the dispersion ϕ (TA2.9). The variance

975 of this distribution is $\tau^2 = \eta + \eta^2\phi$, hence the NB distribution is equivalent to the Poisson when $\phi = 0$.

976 We set $\phi = 0$ for sonar counts, as these counts are believed to be relatively accurate. We set $\phi = 0.02$

977 for the fish wheel counts in all years except for 2001, when dispersion was set to 1.5 to account for the

978 low perceived reliability of these counts.

979   Population-composition data were fitted using a multinomial likelihood (TA2.12). For each

980 year/day/gear combination, the observed number of Chinook by population, $n_1, \dots, n_8$, was assumed to

981 arise from a multinomial distribution with sample size $n = \sum_s n_s$ and probabilities equal to the relative

982 proportions of escapement by population for that year/day. Sample sizes in multinomial distributions for

983 fisheries composition data are typically down-weighted to an "effective" sample size to account for

984 correlations among fish within a given sample. However, we did not down-weight sample sizes as they

985 were already relatively small.

986   Total run size indices were assumed to arise from a lognormal distribution with standard deviation

987 τ_y, which was equal to the product of the externally estimated CV (0.06) and the index (TA2.13-TA2.14).

988 Initial trials indicated that the objective function was overwhelmed by the count and composition

989 likelihoods (i.e., L_E and L_x were respectively about 1000x and 3000x larger than L_I). As a result, the model

990 was overfitting to noise in the population composition at the expense of fitting to the run size index. To

991 increase the influence of the run size index in the likelihood, we applied a scalar α to the total run size

992　index likelihood. We tested a range of values for α and determined that $\alpha = 150$ produced appropriate

993　fits to the index.

994　　　Process errors in arrival timing are assumed to arise from a zero-mean multivariate normal

995　distribution with covariance $\boldsymbol{\Sigma}$ (TA2.15).

996　　　*Simulation-estimation experiments*

997　　　We tested model performance using simulation-estimation experiments (Table A3).. Specifically, we

998　quantified bias in population-specific border passage estimates by fitting the RRs to sets of simulated data,

999　then comparing the estimated border passage to the "true" border passage used to generate the data.

1000　We simulated data from a suite of four operating models (OMs) that were structurally identical to RR_base

1001　but had different sample sizes for population composition to test the effect of population composition

1002　information on run size estimates (Table 4). The sampling structure in the OMs was consistent with

1003　historical patterns; that is, the proportion of annual samples taken daily in OMs was equal to that of the

1004　real data and the sample size was set to 0 for years and gears without data. Border passage and run timing

1005　estimates from RR_base were used to simulate population dynamics in the OMs. We generated 100

1006　datasets from each OM and fit the three RRs to each simulated dataset. For each OM/RR combination,

1007　we calculated the relative error between the true and estimated run sizes. We used the median relative

1008　error (MRE) to measure bias, where relative error is calculated as (true-estimated)/true.

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Table A1. Model notation for multi-population run-reconstruction model.

Symbol	Description
Indices	
s	Population, $s=1,...,8$
y	Year, $y=1985,...,2016$
d	Julian day, $d=160,...,285$
g	Gear type, 1=Sonar, 2=Fish Wheel
Data and inputs	
x_{sgyd}	Observed stock composition by gear/year/day
E_{gyd}	Escapement counts by gear/year/day
I_y	Run size index from mark-recapture
Parameters	
$\hat{R}_{sy}$	Annual run size by population
$\hat{\mu}_{s,y}$	Mean Julian date of arrival by population/year
σ_s	Standard deviation around mean Julian date of arrival by stock
ε_{sy}	Process error in arrival timing by stock/year
Σ	Process error covariance
$q_g^{(E)}$	Daily counts catchability by gear
$q^{(I)}$	Mark-recapture catchability
τ_y	Observation error variance for mark-recapture indices
α	Run size index likelihood weight
Latent variables	
N_{syd}	Daily numbers arriving by population /year
ρ_{syd}	Daily arrival proportions by population /year
μ_{sy}	Mean Julian date of arrival by population /year
$\hat{E}_{sgyd}$	Predicted daily counts by population /gear/year
$\hat{I}_y$	Predicted run size index
p_{sgyd}	Stock composition by gear/year/day

Table A2. Model equations for multi- population run-reconstruction model.

Equation	Formula
Population Dynamics	
(TA.1) Estimated Parameters	$\Theta = \{\hat{R}_{sy}, \hat{\mu}_s, \sigma_s, \varepsilon_{sy}, \boldsymbol{\Sigma}, q_{E,s,g}, q_{I,s}, \tau\}$
(TA2.2) Arrival timing, y=1	$\mu_{s,1} = \hat{\mu}_s$
(TA2.3) Arrival timing, y>1	$\mu_{s,y} = \mu_{s,y-1} \exp(\varepsilon_{s,y-1})$
(T3.4) Daily arrival proportions	$\rho_{syd} = \dfrac{\exp\left(-0.5(d - \mu_{s,y})^2 \sigma_s^{-2}\right)}{\sum_k \exp\left(-0.5(k - \mu_{s,y})^2 \sigma_s^{-2}\right)}$
(T3A.5) Daily arrivals (numbers)	$N_{syd} = \hat{R}_{sy} \rho_{syd}$
Model predictions	
(TA2.6) Predicted daily counts	$\hat{E}_{sgyd} = q_g^{(E)} N_{syd}$
(TA.7) Predicted run size index	$\hat{I}_y = q^{(I)} \sum_s \hat{R}_{sy}$
(TA2.8) Predicted stock composition	$p_{syd} = N_{syd} / \sum_j N_{jyd}$
Objective function	
(TA.9) Mean and variance parameters for N.B. count likelihood	$\eta_{gyd} = \sum_s \hat{E}_{sgyd}$
(TA.10) Reparameterization of N.B. parameters	$\tau_{gyd}^2 = \eta_{gyd} + \eta_{gyd}^2 \phi_{gy}$ $p_{gyd} = \eta_{gyd} / \tau_{gyd}^2$ $r_{gyd} = \eta_{gyd} p_{gyd}(1 - p_{gyd})$
(TA.11) N.B. NLL for daily counts	$L_E = \sum_g \sum_y \sum_d \left[-\ln\Gamma(E_{gyd} + \eta_{gyd}) + \ln\Gamma(\eta_{gyd}) + \ln\Gamma(E_{gyd} + 1) - \eta_{gyd} \ln(1 - p_{gyd})\right]$
(TA.12) Multinomial NLL for stock composition	$L_x = \sum_g \sum_y \sum_d \left[-\ln\Gamma\left(\sum_s x_{sgyd} + 1\right) + \sum_s \ln\Gamma(x_{sgyd} + 1) - \sum_s x_{sgyd} \ln(p_{syd})\right]$
(TA2.13) Run size index std. dev.	$\tau_y = 0.06 I_t$
(T3.14) Lognormal NLL for run size index	$L_I = \sum_{y=1985}^{2008} \left[\ln \tau_y + \dfrac{\ln 2\pi}{2} + \dfrac{(\ln I_y - \ln \hat{I}_y)^2}{2\tau_y^2}\right]$
(T3A2.15) Multivariate-normal prior on process errors	$L_\varepsilon = 0.5\left[\ln|\boldsymbol{\Sigma}| - \boldsymbol{\varepsilon}^T \boldsymbol{\Sigma}^{-1} \boldsymbol{\varepsilon} - S \ln 2\pi\right]$
(TA.16) Objective function	$L = L_E + L_x + \alpha L_I + L_\varepsilon$

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1016   **Table A3.** Operating models used in simulation-estimation experiments.

Operating model	Structure/Assumptions
OM_base	Population composition sample sizes (n) equal to historical levels
OM_incFW	OM_base with fish wheel n increased to 250/year
OM_incS	OM_base with sonar n increased to 1250/year
OM_incN	OM_incFW with sonar n increased to 1250/year

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Appendix B.

Process model

The process model, or system equations, component of our state-space spawner-recruitment

model specifies productivity and age at maturity by cohort (i.e. brood year, *y*). Returns of Chinook (R)

from 1985-2017 were treated as unobserved states and modeled as a function of spawner abundance (S)

assuming a Ricker (1954) spawner-recruitment relationship with serially correlated log-normal process

variation:

$$\ln(R_y) = \ln(S_y) + \ln(\alpha) - \beta S_y + v_y \qquad\qquad (B.1)$$

where α is productivity (intrinsic rate of growth), β is the magnitude of within brood-year density

dependent effects and v reflects inter-annual variation in survival which was assumed to be correlated

(ɸ) over time:

$$v_y = \phi v_{y-1} + \varepsilon_y, \ \ \varepsilon_y \sim N(0, \sigma_R) \qquad\qquad (B.2)$$

where ε_y is independent normally distributed process variation in survival with a standard deviation of

σ_R.

The first 6 years of observed returns that were not linked to observations of spawner abundance

in the spawner-recruitment relationship (eqn. B1) were modelled as draws from a log-normal distribution

with mean $\ln(R_0)$ and standard deviation σ_{R0}.

The number of Chinook that returned to spawn in year y and age a was the product of the total

return in year $y - a$ and the proportion of fish from brood year $y - a$ that returned at age a:

$$N_{y,a} = R_{y-a} p_{y-a,a} \qquad\qquad (B.3)$$

1040   where the vector of age-at-maturity proportions were drawn from a common Dirichlet distribution,

1041   realized by generating independent gamma variates ($\gamma_{y,a}, a \in 3:6$) and dividing by their sum (Fleischman,

1042   Catalano, Clark, Bernard, & Chen, 2013):

$$p_{y,a} = \frac{\gamma_{y,a}}{\sum_a \gamma_{y,a}} \qquad (B.4)$$

1044   where the gamma variates are drawn from a gamma distribution with shape k_a and inverse scale θ equal

1045   to 1. This gamma distribution was parameterized according to Gelman et al. (2013) where the $\gamma_{y,a}$ are the

1046   age-specific hyperparameters of the Dirichlet distribution that determine the expected proportions (π_a)

1047   of salmon returning at age:

$$\pi_a = \frac{\gamma_a}{\sum_a \gamma_a} \qquad (B.5)$$

1049   Lastly, harvest in a given year (H) was modelled as the product of total run size and the harvest

1050   rate (U) experienced:

$$H_y = N_y U_y \qquad (B.6)$$

1052   *Data and observation model*:

1053   We assumed a 30% coefficient of variation (CV) for spawner observations. Observed spawner

1054   abundance was therefore assumed to be lognormally distributed with parameters $\ln(S_{O,y})$ and $\sigma_{S_{O,y}}$, with

1055   the CVs converted to lognormal variance following Forbes et al. (2011):

$$\sigma_{S_{O,y}}^2 = \ln[\text{CV}^2(S_{O,y}) + 1] \qquad (B.7)$$

1057   We assumed that harvest had a 15% CV and so harvest observations were log-normally distributed

1058   with parameters $\ln(H_{O,y})$ and $\sigma_{H_{O,y}}$, with the CV converted to log-normal variance as per equation B.7.

1059   Age composition by return year was assumed to be observed with error, where uncertainty in age

1060   proportions in a given year was generated by specifying an "effective sample size" (ESS) of 100. An ESS

1061   equal to 100 is the multinomial sample size expected to produce uncertainty roughly equivalent to that

1062   which would be anticipated from the average number of fish sampled in a given year from a population

1063   with age proportions and classes similar to that of the CDN-aggregate.

1064   *Model fitting*

1065   We fit the model described in equations B.1-7 in a Bayesian estimation framework. Prior probabilities

1066   for most unknowns in the model were specified so as to be uninformative, with the exception of β which

1067   was constrained to avoid biologically implausible negative values which would imply the population could

1068   grow at an increasing rate as it expanded. Joint posterior probability distributions for all unknowns in the

1069   model were generated using a Markov chain Monte Carlo (MCMC) procedure in the JAGS sampler

1070   interfaced through R (Plummer, 2017). We ran six chains for 250,000 iterations after a burn-in of 50,000,

1071   and thinned every 5th iteration. Convergence was assessed by examining the potential scale reduction

1072   factor ($\hat{R}$) and assumed to have occurred if $\hat{R}$ was less than 1.1 (Gelman & Rubin, 1992). The Gelman-

1073   Rubin statistic compares within-chain variance to between-chain variance to diagnose convergence.

1074

Appendix C.

Our baseline simulations assumed that recruitment dynamics are governed by a stationary Ricker-type spawner-recruitment relationship that exhibits overcompensation at high spawner abundances (equations 1-3 in main text). We also considered an alternative recruitment hypothesis that assumed that low frequency regime shifts gave rise to the appearance of overcompensation, when in fact none was present. Under this hypothesis we assumed that individual spawner-recruitment relationships were governed by Beverton-Holt dynamics with cyclical variation in population productivity (equation 12 in main text; hereafter referred to as "BH_cycl").

In addition to productivity at small population size (α) and magnitude of density dependence (β), there are three additional terms required to parameterize the cyclical Beverton-Holt formulation: f and A which are the period and amplitude of time-varying productivity, respectively, and δ which is a scalar that adjusts productivity such that long-term population equilibrium abundance in the absence of fishing is approximately the same as those under the stationary Ricker spawner-recruitment formulation.

Figure A1 illustrates a simulated spawner-recruit relationship generated by equation 6 with f = 14, A = 0.6, and δ = 1.4. In order to simulate time-varying Beverton-Holt spawner-recruitment relationships with apparent overcompensation that approximate that observed for the CDN Yukon Chinook aggregate we needed to determine what combination of f, A and δ should be used in our closed-loop simulations. What we wanted were combinations of the parameters that generate a spawner-recruit relationship that looks the same as the aggregate Yukon relationship, but that arises from time-varying Beverton-Holt dynamics instead of overcompensation (i.e., Ricker assumption). To do this we simulated spawner-recruit datasets using the BH_cyl formulation across a range of f, A and δ. In each iteration of the simulation we fit a Ricker spawner-recruit relationship to the data (i.e., ln(recruits/spawners)~spawners) and compared the estimates of intrinsic productivity (α) and magnitude of density dependence (β) from the model fit to

1098   the true values. We did this 1000 times across twenty values of f (1-20), three level of A (0.2, 0.4, 0.6) and

1099   20 values of δ (0.2-2).

1100   The results of the simulations suggest that estimates of α are biased low at periods (f) less than

1101   10 years, but were otherwise relatively unbiased across a range of values in A and δ. Estimates of β were

1102   more sensitive to parameter combinations, but generally appeared to be the least biased when the period

1103   (f), amplitude (A) and productivity scalar (δ) were approximately 14, 0.6 and 1.4, respectively. We then

1104   further explored the extent to which this combination of parameter values generates an apparent

1105   spawner-recruit relationship that qualitatively matches the empirical Yukon one. To do this we simulated

1106   1000 spawner-recruit datasets under the BH_cycl formulation with the period (f), amplitude (A) and

1107   productivity scalar (δ) equal to 14, 0.6 and 1.4, respectively (Figure A2a illustrates the resulting time-series

1108   of productivity). For each simulation we then fit a Ricker spawner-recruit relationship to the data and

1109   summarized the predicted relationship across the 1000 simulations relative to the observed Ricker

1110   spawner-recruit relationship for the Yukon aggregate. These simulations suggest that this combination of

1111   parameter values result in a spawner-recruitment relationship with apparent overcompensation of a

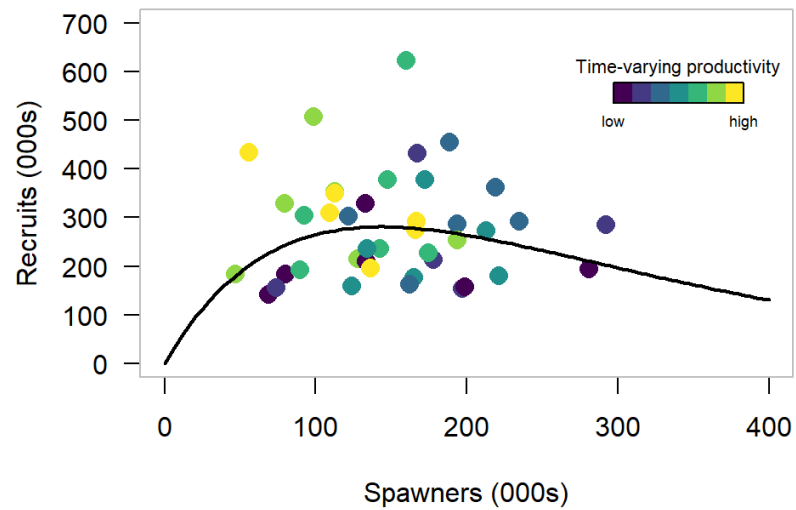1112   magnitude similar to that observed in the Yukon (Figure A2b).

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Figure A1. Spawner-recruitment data simulated by a Beverton-Holt type relationship with time-varying

productivity (colors). The black line is the Ricker type spawner-recruitment relationship estimated from

the data, which implies that there is overcompensation when in fact there is none.

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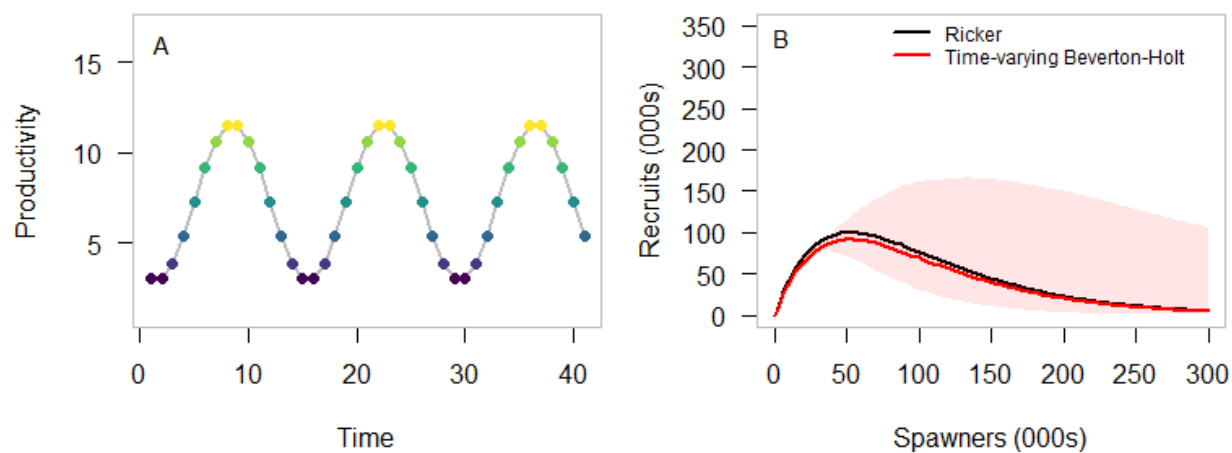
1120

1121 **Figure A2.** (A) Time-varying productivity and (B) observed (Ricker black line) spawner-recruitment

1122 relationship in the Kuskokwim and simulated relationship (median and 95th percentiles) assuming a

1123 Beverton-Holt spawner-recruitment relationship with time-varying productivity.

1124