I.   AYK SSI TITLE PAGE:

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

Yukon harvest-population diversity trade-offs

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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 6- and 4-fold, respectively. 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. 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 ~ 60%, but this comes at the cost of overfishing ~ 70% 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 findings underscore how population diversity can support food security across a large remote river basin and suggest that protecting fine-scale population 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: Canadian Yukon Chinook population diversity and its consequences for fisheries management.

Yukon Chinook population diversity and its consequences for fisheries management

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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 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 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 6- and 4-fold, respectively. 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. 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 ~ 60%, but this comes at the cost of overfishing ~ 70% 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

47 highly sensitive to uncertainty in the underlying drivers of recruitment variation (i.e., whether or not

48 overcompensation occurred in the system), as well as to numerous assumptions that had to be made in

49 order to conduct the analyses. Nonetheless, our findings underscore how population diversity can

50 support food security across a large remote river basin and suggest that protecting fine-scale population

51 diversity can help promote food security for Indigenous peoples in a region where salmon are of

52 immense cultural and subsistence value. Our work provides a blueprint for future quantitative

53 evaluations of the ability of alternative harvest policies to meet a diversity of fishery, social, and

54 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 (Bolnick et al., 2011). 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), provide increased 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 increasingly recognized as a hallmark of sustainable and resilient natural resource management (R. Hilborn et al., 2003; Hutchinson, 2008; Schaffer & Elson, 1975).

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

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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 a stochastic environment (Chapin III et al., 2000; Elmqvist et al., 2003)

Understanding how biodiversity influences ecosystem function and service, and how human activities mediate these benefits, requires 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. Logistical challenges to characterizing biodiversity increase as the target area increases in size and degree of remoteness. In areas that are more distant from human population centres and contain challenging terrain, access becomes increasingly restrictive and the ability to study these areas more difficult. However, many services are derived from ecosystems in these vast, isolated areas. The boreal and sub-arctic regions of North America exemplify these characteristics as they contain enormous swaths of forest, wetland and aquatic habitat, responsible for the provisioning of countless ecosystem services. These areas are also undergoing rapid change due to the effects of climate change (Sagarin & Micheli, 2001; Zhang et al., 2019), and as such it could be argued have an urgent need to characterize 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 over 3,000 kilometres from its headwaters in northern British Columbia through the Yukon Territory and Alaska before emptying into the Bering Sea. It drains over 850,000 square kilometres that span over 20 different ecoregions (Gallant, Binnian, Omernik, & Shasby, 1995)(Figure 1).

Chinook populations across Western Alaska and the Yukon Territory have declined in abundance and productivity over the past decade. These declines have been particularly pronounced in the Yukon River Basin which experienced near record low returns in some recent years (JTC 2016). 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 biocomplexity 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 within the

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

129   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   Under the Treaty, they are managed as a single aggregate stock with an interim management escapement

132   goal, set by the Yukon River Panel, that establishes the number of Chinook that need to make it into the

133   CDN portion of the Yukon and onto spawning grounds in each year. The consequences of managing CDN

134   origin Chinook as a single aggregate stock, both for the protection of Chinook population diversity and for

135   the communities and First Nations in the CDN portion of the Yukon that depend upon them, are currently

136   unknown.

137   Here, we use genetic analysis of archived scale samples to reconstruct Chinook salmon population

138   diversity within the CDN portion of the Yukon River Basin and then quantify how alternative fisheries

139   management policies are predicted to affect it. Specifically we (1) use genetic stock identification from

140   archived scale samples to reconstruct population specific returns to Canada over the past three decades,

141   (2) fit multi-population Bayesian state-space spawner-recruit models to the run reconstructions to

142   characterize Chinook population diversity (i.e., productivity and carrying capacity), (3) quantify the

143   consequences of population diversity for portfolio effects (i.e. variance dampening due to asynchronous

144   dynamics) and equilibrium trade-offs in mixed-stock fisheries, (4) use closed-loop simulation models of

145   the socio-ecological system to evaluate how alternative harvest policies affect the ability of the system to

146   meeting conservation and socio-economic objectives.

147   **Methods**

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

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

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

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

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

Chinook salmon spawn in over one-hundred locations in the CDN portion of the Yukon River Basin (Brown et al., 2017). 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 considered genetically and ecologically unique groups of salmon under Canada's Wild Salmon Policy (DFO, 2005). These populations also correspond to the traditional territories of many of the First Nations along the Yukon River.

Monitoring and assessment

The number of Chinook salmon migrating into the Yukon territory (hereafter referred to as border passage) has been estimated with a variety of methods since the early 1980s. From the early 1980s to the mid 2000s a mark-recapture program and fish wheels were operated in several locations near the border to sample fish and collect biological samples (Figure 1). In 2005, sonar along with a drift gillnet test fishery was implemented to estimate border passage and collect biological samples. The sonar site at Eagle, Alaska consists of a DIDSON and 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 assumed to be 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 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 stock-recruitment relationship (JTC 2018).

On average, 1300 Chinook scale samples have been collected annually from fish wheels (1982–2008) and gillnets (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 ID 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. For each year with scale samples that could be recovered we haphazardly selected approximately 150 scales, genomic DNA was extracted from each scale, and allelic variation at a suite of 15 microsatellite loci was used to assign individuals to one of the eight populations.

Population level run-reconstructions

We estimated the daily passage (9 Jun – 12 Oct) of Chinook into Canadian waters from 1985 to 2016 using multi-stock run reconstruction (RR) models. The RRs 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, indexed by *s* (Table 1). Annual, population-specific run size was the main parameter of interest estimated by the model, though we also estimated parameters for run timing and catchability

198 (T3.1). We separately model catchability to two fishing "gears" (index by g): sonar and fish wheels. Model

199 notation and equations are listed in Table 2 and 3 respectively.

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

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

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

203 equivalent to standard deviations.

204 *Population dynamics*

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

206 assumed to be normally disturbed around mean μ_{sy} with variance σ_s^2 (T3.4). Numbers of salmon arriving

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

208 proportions and run size (T3.5). To model interannual variability in mean run timing, we assume that the

209 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

210 the previous year, i.e.,

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

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

212 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

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

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

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

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

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

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217   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

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

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

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

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

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

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

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

225   at the potentially steep cost of 27 additional parameters.

226   *Observation model and objective function*

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

228   specific catchability factor (T3.6). Catchability to the fish wheel was estimated while catchability to sonar

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

230   invariant catchability factor (T3.7). While catchability may vary across populations for a variety of reasons

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

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

233   present on each day (T3.8).

234   Daily salmon counts were assumed to arise from negative-binomial (NB) distributions (T3.11). The

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

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

237   parameterize the NB distribution in terms of the mean count η and the dispersion ϕ (T3.9). The variance

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

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

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

241   low perceived reliability of these counts.

242   Population-composition data were fitted using a multinomial likelihood (T3.12). For each

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

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

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

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

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

248   were already relatively small.

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

250   τ_y, which was equal to the product of the externally estimated CV (0.06) and the index (T3.13-T3.14).

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

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

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

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

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

256   fits to the index.

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

258   distribution with covariance $\mathbf{\Sigma}$ (T3.15).

259   *Simulation-estimation experiments*

260   We tested model performance using simulation-estimation experiments. Specifically, we quantified

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

262   comparing the estimated border passage to the "true" border passage used to generate the data. We

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

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

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

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

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

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

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

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

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

Multi-population spawner-recruit model

273   We used multi-population state-space spawner-recruit models (Staton et al., Under review) to

274 characterize Chinook population diversity and dynamics in the CDN portion of the Yukon River Basin. This

275 model is an extension of single-stock models (Fleischman, Catalano, Clark, Bernard, & Chen, 2013; Staton,

276 Catalano, & Fleischman, 2017) that simultaneously fits separate stock-recruitment curves to population-

277 specific time series of escapement and aggregate mixed-stock harvest. The model was fitted to time series

278 of spawner abundance, harvest, and age composition in a Bayesian estimation framework using Markov

279 Chain Monte Carlo methods to sample from the joint posterior distribution of all unknown quantities

280 (implemented in JAGS; Plummer, 2017).

281   The formulation of the model we used assumed that all populations are (a) equally vulnerable to

282 harvest and (b) share the same maturity schedule. The spawner abundance estimates we used were

283 derived from the multi-population run-reconstruction models. To account for Canadian harvest – the run-

284 reconstruction model estimated border passage, and not escapement – we applied an annual Canadian

285 exploitation rate (Canadian commercial, First Nations and recreational harvests) to the population specific

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

287   estimates of age – composition were taken from JTC (2018), with age – composition assumed to be equal

288   across populations.

289   The key quantities estimated by the state-space model included population productivity (i.e.,

290   maximum recruits-per-spawner), carrying capacity, latent recruitment states, lag-one temporal

291   correlation in recruitment, variance and covariance in recruitment within and among populations, and a

292   common time-varying maturity schedule. To account for, and propagate, structural uncertainty arising

293   from the alternative run-reconstruction models we combined posterior samples from models fitted to the

294   spawner abundance estimates from the three alternative run-reconstructions thereby generating an

295   unweighted ensemble of posterior samples that captures both estimation and structural uncertainty.

296   We then used the ensemble posterior samples of population productivity and carrying capacity to

297   quantify the range of predicted equilibrium trade-offs between aggregate harvest and conservation of

298   population diversity across a range of mixed-stock harvest rates (C J Walters, Lichatowich, Peterman, &

299   Reynolds, 2008; Carl J Walters & Martell, 2004). Full details of data processing and the structure of the

300   state-space model, including model code and detailed outputs, are provided in a supplement to this paper.

301   *Portfolio effects*

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

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

304   2010). We calculated the portfolio effect (*PE*) according to (Nesbitt & Moore, 2016) for region *i* as the

305   difference between the predicted coefficient of variation of run size (CV$_j$) assuming synchronous

306   variance dampening (weighted by the proportional run size, X_j) and the observed CV of the aggregate

307   run (CV$_{obs}$).

$$PE_i = \sum_{j-1}^{n} X_j CV_j - CV_{obs} \tag{3}$$

14

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

309   the individual populations (Nesbitt & Moore, 2016). When the PE is positive, the predicted CV is greater

310   than the observed CV, and is evidence that asynchronous dynamics are stabilizing the aggregate run. We

311   quantified PE with a rolling 10-year average of run size, generating PE estimates from 1995 to 2016 for

312   all populations (represented by fishing near Dawson City, with the possibility of harvesting fish from any

313   of the eight populations) and for three populations (represented by fishing near Carmacks, with the

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

315   *Closed-loop simulations*

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

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

318   components: (1) an empirically parameterized multi-population operating model that simulated the

319   dynamics of Chinook populations over time, (2) a management procedure model that assessed the state

320   (i.e., total returning abundance) of the system each year and (3) applied a given harvest policy, and (4) a

321   performance model that tracked the outcomes of the management procedure for quantitative

322   performance measures related to a suite of fishery and conservation objective. To evaluate how robust a

323   given harvest policy was to key structural uncertainties in the system we simulated the biological and

324   fishery dynamics across alternative states of nature (i.e., alternative drivers of recruitment dynamics). The

325   approach we describe here closely matches that taken in (Connors et al., Under review).

326   *Operating model*

327   Our operating model was used to simulate future population trajectories for the eight CDN-origin

328   Yukon Chinook populations by projecting their dynamics forward over 50 years (approximately eight

329   generations starting in 2017). By simulating the Chinook dynamics in this manner, we ensured that

330   predicted future spawner abundance and age structure were conditioned on the incomplete cohorts at

331   the end of the data series (i.e., those cohorts from which one or more older age classes have not yet

332   returned to spawn) and that uncertainties in the spawner-recruit relationships were propagated through

333   time (i.e., by drawing from the ensemble posterior distributions of each estimated parameter and

334   abundance state in each iteration of the simulation).

335   The simulated population complex was comprised of j populations whose dynamics were governed

336   by Ricker type stock recruitment relationships (Ricker, 1954):

$$R_{y,j} = \alpha_j S_{y,j} e^{-\beta_j S_{y,j} + \phi \log(R_{y-1,j}/\hat{R}_{y-1,j}) + r_{y,j}} \tag{4}$$

337   where $R_{y,j}$ is recruitment from brood year y for population j, α_j and β_j are population specific intrinsic

338   rate of growth (productivity) and within-population density dependence, respectively; $S_{y,j}$ is spawner

339   abundance; ϕ is the degree of temporal correlation in recruitment from one year to the next; $\hat{R}_{y-1,j}$ is

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

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

342   normal distribution:

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

$$\mathbf{\Sigma} = \begin{bmatrix} \sigma_1\sigma_1 & \cdots & \sigma_1\sigma_j\rho \\ \vdots & \ddots & \vdots \\ \sigma_j\sigma_1\rho & \cdots & \sigma_j\sigma_j \end{bmatrix} \tag{5}$$

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

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

$$\dot{N}_{t,j} = \sum_{a=4}^{7} R_{t-a,j}\pi_{a-3} \tag{6}$$

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

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

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

16

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

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

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

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

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

353 *Management procedure model*

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

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

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

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

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

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

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

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

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

$$TAC_t = \widehat{N}_t - G \tag{7}$$

363 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

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

365 forecast error in the Yukon).

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

367 allocation defined in the Yukon River Salmon Agreement:

$$TAC_{CDN,t} = \begin{cases} 0.24TAC_t, & TAC_y \leq 110000 \\ 0.24 \; x \; 110000 + 0.5(TAC_t - 110000), & TAC_t > 110000 \end{cases} \tag{8}$$

and

$$TAC_{US,t} = TAC_t - TAC_{CDN,t} \tag{9}$$

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

$$H_{US,C,t} = \dot{U}_C e^{\varepsilon_C} \begin{cases} TAC_{US,t} - \dot{H}_{US,S}, & TAC_{US,t} - \dot{H}_{US,S} > 0 \\ 0, & TAC_{US,t} - \dot{H}_{US,S} \leq 0 \end{cases} \tag{10}$$

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 target US subsistence harvest. We assumed that commercial harvest occurs before US subsistence harvest and so realized US subsistence harvest ($H_{US,Sy}$) was:

$$H_{US,S,t} = \begin{cases} (\dot{N}_t - H_{US,C,t})e^{\varepsilon_{US,S}}, & \dot{H}_{US,S} > \dot{N}_t - H_{US,C,t} \\ \dot{H}_{US,S}e^{\varepsilon_{US,S}}, & \dot{H}_{US,S} \leq \dot{N}_t - H_{US,C,t} \end{cases} \tag{11}$$

where $\varepsilon_{US,S}$ is US subsistence fishery outcome error $\sim N(0,0.05)$. These harvest control rules (equation 10-11) are intended to reflect the priority placed on meeting subsistence needs over commercial harvests, the fact that commercial harvest occurs before subsistence harvest, and the extent to which there is imperfect control over managing harvests to their target levels.

Canadian harvest depended on estimated Chinook border passage ($\hat{P}_t$) which was a function of US commercial and subsistence harvest:

$$\hat{P}_t = [\dot{N}_t - (H_{US,C,t} + H_{US,S,t})]e^{\varepsilon_P} \tag{12}$$

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

18

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

383   a given year, which was:

$$\dot{H}_{CDN,S,t} = \begin{cases} 0, & \hat{P}_t \leq 42{,}500 \\ 1{,}000, & 42{,}500 \leq \hat{P}_t < 48{,}750 \\ 4{,}000, & 48{,}750 \leq \hat{P}_t < 55{,}000 \\ 10{,}000, & 55{,}000 \leq \hat{P}_t \end{cases} \tag{13}$$

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

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

$$\dot{H}_{CDN,C,t} = \dot{U}_C e^{\varepsilon_C}(P_t - G - \dot{H}_{CDN,S,t}) \tag{14}$$

386   The resulting realized CDN First Nations harvest was therefore:

$$\dot{H}_{CDN,S,t} = \dot{H}_{CDN,S,t} e^{\varepsilon_{CDN.S}} \tag{15}$$

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

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

$$H_{t,j} = U_t \dot{N}_{t,j} \tag{16}$$

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

$$U_t = (H_{US,C,t} + H_{US,S,t} + H_{CDN,C,t} + H_{CDN,S,t})/ \dot{N}_{t,j} \tag{17}$$

390   *Harvest policies*

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

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

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

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

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

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

more detail (Table 5) to illustrate how policies that prioritize different objectives are predicted to perform

across a range of biological and fishery performance measures.

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

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

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

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

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

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

Performance measures

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

422   *Alternative drivers of recruitment*

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

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

425   abundances (equations 4-6). This is the state of nature that is currently assumed by fishery managers in

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

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

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

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

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

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

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

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

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

435   relationship in equation 3 to a Beverton-Holt form (Table 7.2 in Hilborn and Walters 1992) with time-

436   varying productivity:

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

(16)

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

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

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

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

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

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

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

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

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

445 other systems.

446 **Results**

447 *Genetic stock composition*

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

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

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

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

452 respectively; Table S1). In general, the distribution of scale samples corresponds with the annual run

453 distribution (Figure 3). On average, the daily proportion of scale samples differs from the daily proportion

454 of the total annual run by less than 5%. However, for some years there are substantial gaps in scale sample

455 coverage, most notably for 1991, 1992, 2001, and 2007. There are also a handful of years (1984, 1988-

456 1990, 1998) for which no scale samples exist.

457

458 *Population level run-reconstructions*

459   *Model fits*

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

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

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

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

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

465   three models. The count likelihood L_E was smallest for RR_oneCor (Table 6), though the discrepancy in

466   likelihood values mostly came from the 2005 fish wheel counts where the count likelihood was 235 units

467   smaller for RR_oneCor than the other models.

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

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

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

471   (Figure S4). Setting α to a relatively low value (e.g., 10) allows the model to chase spuriously high fish

472   wheel counts in 2001, resulting in unreliable estimates of border passage. Increasing α to higher values

473   (e.g., 500) may be expected to tighten the model fits to the mark-recapture estimates in all years, though

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

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

476   abundance data (i.e., sonar) becomes available in 2005, the mark-recapture index has essentially no effect

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

478   While the three models fit the data similarly, RR_oneCor was highly preferred by AIC (Table 7). We

479   note, however, that AIC rankings for these models are somewhat dubious, as RR_oneCor is preferred due

480   to the closer fits of that model to a relatively low-value dataset.

481   *Border passage estimates*

482   The model-based estimates of border passage were broadly similar across the three RRs, though

483   reconstructed border passage estimates did vary for some populations/year combinations due to a lack

484   of data for distinguishing between populations with overlapping run timing (Figure 6). As an example,

485   consider the population-specific arrival timing curves from RR_base (Figures 6 and 7). The Lower and

Upper Mainstem populations tend to pass the border earlier and later, respectively, than the other populations for which peak timing tends to occur within the same 30-day range. As a result, Lower and Upper Mainstem border passage are well-estimated by the reconstructions, with the three models converging on similar estimates. In contrast, the remaining populations had several years where reconstructed border passage varied greatly among the 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.

Teslin had the highest median annual border passage at around 10,800, followed by Pelly (8,300) and Middle Mainstem (7,000). The most modest returns were to the Upper Lakes (median: 2,600), which in comparison is about 25% of the median Teslin run size (Figure 8).

The Pelly population exhibited the least interannual variability in run timing, followed by Carmacks (Figure S5). Run timing was most variable for populations that tended to arrive later in the run (i.e., Teslin, Middle Mainstem, Upper Mainstem). Parameterization of run timing correlation appeared to have no systematic effect on run timing variability.

The RR_oneCor model estimated moderate correlation among the populations (c=0.384). The RR_fullCor model estimated similar levels of correlation among most of the populations, though some population pairs had zero or negative correlation in run timing (Table 7). For instance, Upper Mainstem run timing was not correlated with Lower Mainstem or White-Donjek, and was negatively correlated with Pelly.

The duration of population level return migrations, as estimated at the US-CDN border, 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 Mainstem) (Figure 6 and 7). This run-timing variation results in an average aggregate CDN-origin Yukon Chinook return migration that spans 75 days which is 2.15 times longer than if the system was comprised of a single homogenous population.

510   Not surprisingly these model-based estimates of spawner abundances differ from those derived from

511   data-based estimates (i.e., by simply applying the population composition estimates from the genetic

512   stock ID methods to the aggregate Canadian brood table used by the JTC) (Figure S4). For most

513   populations, there was no obvious systemic bias in spawner abundance estimates between the model-

514   based or data-based methods. However, model-based estimates of spawner abundance for White-Donjek

515   were lower than data-based ones and for the Teslin population model-based estimates tended to be

516   higher than data-based ones. There was no evidence of systematic temporal bias in the difference

517   between the data-based and model-based methods.

518   *Simulation-estimation trials*

519   The three RRs had similar performance in simulation tests (Figure 9). In general border passage

520   estimates were reasonably unbiased when fitting to data generated by OM_base; Lower Mainstem,

521   Carmacks, Teslin, and Upper Mainstem were estimated with little bias while Stewart, Pelly, and Middle

522   Mainstem tended to be slightly underestimated (0.03-0.1 median relative error), and White-Donjek

523   tended to be slightly overestimated (0.04 median relative error). Increasing population composition

524   sample sizes for the fish wheel to 250 per year reduced bias in border passage estimation for White-

525   Donjek, Pelly, and Stewart, although MRE for Stewart still remained high at 6%. Increasing population

526   composition sample sizes for sonar counts to 1250/year reduced bias in border passage estimation for

527   Lower Mainstem, White-Donjek, Pelly, and Stewart, and produced estimates with low MREs for all

528   populations. There is little difference between OM_incS and OM_incFWS scenarios, indicating that

529   increasing the historical samples sizes for the fish wheel do little to reduce bias in RR model estimates

530   when the sonar is increased to 1250/year. Increased sonar sample sizes were also associated with sharp

531   reductions in bias and variability in Upper Mainstem border passage estimates and increased bias for

532   Teslin.

533   *Population Diversity*

534   We found clear evidence of heterogeneity in population productivity and size in CDN-origin Yukon

535   Chinook (Figures 10 and 11; Table S2) where populations ranged in average spawner abundance from

536   approximately 3,300 to 13,300 spawners and in productivity from 2.5 to 16 recruits-per-spawner (median

537   posterior estimates, y-axis of Figure 10). There was a tendency for larger populations to be less productive

538   than smaller ones, however, we caution against over-interpreting these patterns due to the very large

539   uncertainty in these estimates (Figure 10).

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

541   term yield (i.e., U_{MSY}) that range from ~25% to 80% (median posterior estimates; Figure 12). We used the

542   posterior estimates of productivity and carrying capacity to quantify the predicted equilibrium trade-offs

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

544   rates (e.g., Walters et al. 2008). The resulting picture illustrates that the relatively high harvest rates that

545   can be sustained by the most productive populations come at the cost of increased risk to less productive

546   ones (Figure 13). Overall yield from the system is predicted to be maximized at a harvest rate of ~ 60%,

547   but this comes at the cost of overharvesting ~ 70% of the populations (i.e., harvest rate is > U_{MSY} for a

548   given population) and putting a quarter of populations at risk of extirpation). Furthermore, there is clear

549   asymmetry in these trade-offs where relatively small (~20%) reductions in predicted yield (e.g., from

550   55,000 to 45,000) correspond to relatively large (~60%) reductions in biological risk (e.g., from ~70% to

551   30% overfished).

552   *Portfolio effects*

553   The Chinook population diversity we uncovered gives rise to strong portfolio effects whereby the

554   asynchronous dynamics of Chinook populations stabilize overall returns (Figure 14). For example,

555   variability in annual returns of CDN-origin Chinook is 2.15 times more stable than if the system consisted

556   of a single homogenous population (CV of 30% vs 65% [average CV across individual populations; SD =

557   0.15]). However, the stabilizing effects of Chinook population diversity were diminished as you move up

558   river and integrate across fewer populations (Figure 14). As a result fisheries that integrate across Chinook

559   population diversity (e.g., in Alaska or lower section of the CDN portion of the river such as near Dawson)

560   are predicted, on average, to be ~1.5 more stable than those in the middle section of the CDN portion of

561   the river (e.g., Carmacks) and ~2 times more stable than those in the headwaters (e.g., Teslin).

562   *Closed loop simulations*

563   The closed-loop simulations indicated that mixed-stock harvests are predicted to be maximized at

564   intermediate basin scale escapement goals (~40,000-60,000) when the target harvest rate on surplus

565   production (i.e., production above and beyond which is predicted to be required to meet the escapement

566   goal plus US subsistence and First Nation harvest targets) is high (80-90%) (Figure 15a and b). At higher

567   basin scale escapement goals harvest is predicted to decline because of more frequent fishery closures

568   while at lower escapement goals it declines due to due to the loss of production from overfishing the

569   weaker (i.e., less productive) populations in the system (Figure 16d) and driving the weakest populations

570   to extirpation (Figure 15e). Harvest stability was predicted to be greatest at both low escapement goals

571   and target harvest rates (Figure 15f) while the chances of meeting population level escapement goals and

572   minimizing risks of driving individual populations to extirpation were greatest when target harvest rates

573   were low and/or basin-wide escapement goals were high (Figure 15i and e).

574   Contrasting the three alternative harvest policies illustrates asymmetries in trade-offs between

575   harvest and biological or conservation objectives. We found that the harvest policy that sought to

576   maximize mixed-stock harvest (MSY policy) did so at the costs of an increased proportion of populations

577   that were overfished, reduced chances of meeting population-level escapement goals and elevated risk

578   of weak population extirpation (Figure 16). In contrast, relative to the MSY policy, the conservation policy

579   was predicted to increase the chances of meeting tributary spawner goals by 40%, (from 62% to 87%), to

580   cut the proportion of populations that are overfished in half (from 75% to 37.5%) and eliminate the risk

581   of extirpating the least productive populations (Figure 16). This came at the cost, on average, of only a

582 20% reduction in realized overall harvest and no change in inter-annual stability in harvests. The harvest

583 policy that approximated the current approach to management (status quo policy) was predicted to have

584 higher chances of meeting tributary spawner goals and a lower proportion of populations that are

585 overfished but, as expected, this came at the cost of much lower harvests (Figure 16). All three policies

586 had a very high probability (~90%) of meeting First Nations harvest targets but much lower probabilities

587 of meeting US subsistence needs (50%, 50%, and 60% for the conservation, MSY and status quo policies,

588 respectively).

589   The performance of harvest policies, and their resulting trade-offs, were sensitive to the underlying

590 drivers of variation in recruitment in the system. When recruitment dynamics were driven by time-varying

591 Beverton-Holt type relationships, basin – wide escapement and to a lesser extent harvest were predicted

592 to be higher relative to the alternative Ricker spawner-recruitment dynamic scenario (compare Figure 15

593 and 16 to Figure S6 and S7). In contrast, risks to population diversity across the range of escapement goals

594 and harvest rates we considered were generally similar across the two spawner-recruitment scenarios.

595 Mixed-stock yield was predicted to occur at a higher escapement goal under the time-varying Beverton-

596 Holt scenario. As a result the shape of the harvest – diversity trade-offs differed dramatically between the

597 two scenarios and mixed-stock harvest were predicted to be greater under the conservation policy than

598 the MSY policy when dynamics were driven by time-varying Beverton-Holt type relationship but harvest

599 policies assumed Ricker dynamics (Figure S7).

600 **Discussion**

601   Five key findings emerge from our analyses of CDN-origin Yukon Chinook population diversity and

602 harvest policy performance. First, our molecular analyses of archived scale samples, run-reconstructions,

603 and spawner-recruit analyses uncovered clear evidence of Chinook population diversity in the system.

604 Populations varied in their productivity and average spawner abundance by 6, and 4-fold, respectively.

605 Variation among populations in run-timing and run-size results in return migrations that are 2.15 times

28

longer, and 2.15 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 ~ 60%, but this comes at the cost of overfishing ~ 70% of the populations and putting 25% 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 harvest rates that also reduced risks to population diversity compared to a harvest policy that was predicted to maximize yield assuming Ricker type dynamics.

There are at least two reasons to temper our interpretation of the findings above. First, our analyses are predicated upon being able to generate unbiased estimates of annual population composition through time from archived scale samples. However, because of the small samples sizes for our composition

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

650 Pacific salmon like pink and chum (Quinn, 2018), and the populations we considered typically had

651 spawning locations that were greater than 100 km away from the nearest other populations. We therefore

652 considered the magnitude of straying to likely be negligible but nonetheless consider this an area that

653 warrants future study. Our multi-stock spawner-recruit analysis and closed-loop simulations assumed all

654 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 results in return migrations that are 2.15 times longer, and 2.15 times more stable, than if they were comprised of a single homogenous population thereby stabilizing and extending 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 management escapement goal, set by the Yukon River Panel, that establishes the number of Chinook that need to make it into the CDN portion of the Yukon and onto spawning grounds in each year. Since 2010 the Interim Management Escapement Goal has been 42,500-55,000. We chose three simple and

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

707   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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831   **Table 1.** Model notation for multi-population run-reconstruction model.

Symbol	Description
Indices	
s	Populaiton, 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

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Table 2. Model equations for multi- population run-reconstruction model.

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

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837   **Table 3.** 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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840 **Table 5.** 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

841 [+]Maximum, see equation 13.

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843 **Table 6.** Likelihood and AIC values for the three run reconstruction models.

Model	No. of parameters	$\Delta AICc$	L	L_E	L_x	L_I	L_ε
RR_base	522	1340.3	69690.9	20920.8	47356.8	12.7	-486.8
RR_oneCor	523	0	69019.6	20768.3	46873.8	12.6	-520
RR_fullCor	550	37.7	69005.2	20969.3	46749.2	12.6	-610.8

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847 **Table 7.** Correlation matrix estimated by RR_fullCor.

	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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852 **Table 8.** Median relative error in run size estimates from simulation-estimation experiments.

RR model	Operating model			
	OM_base	OM_incFW	OM_incS	OM_incFWS
RR_base	0.00908	0.01052	0.00336	0.00474
RR_oneCor	0.00896	0.00951	0.00386	0.00429
RR_fullCor	0.00755	0.00913	0.00227	0.00340

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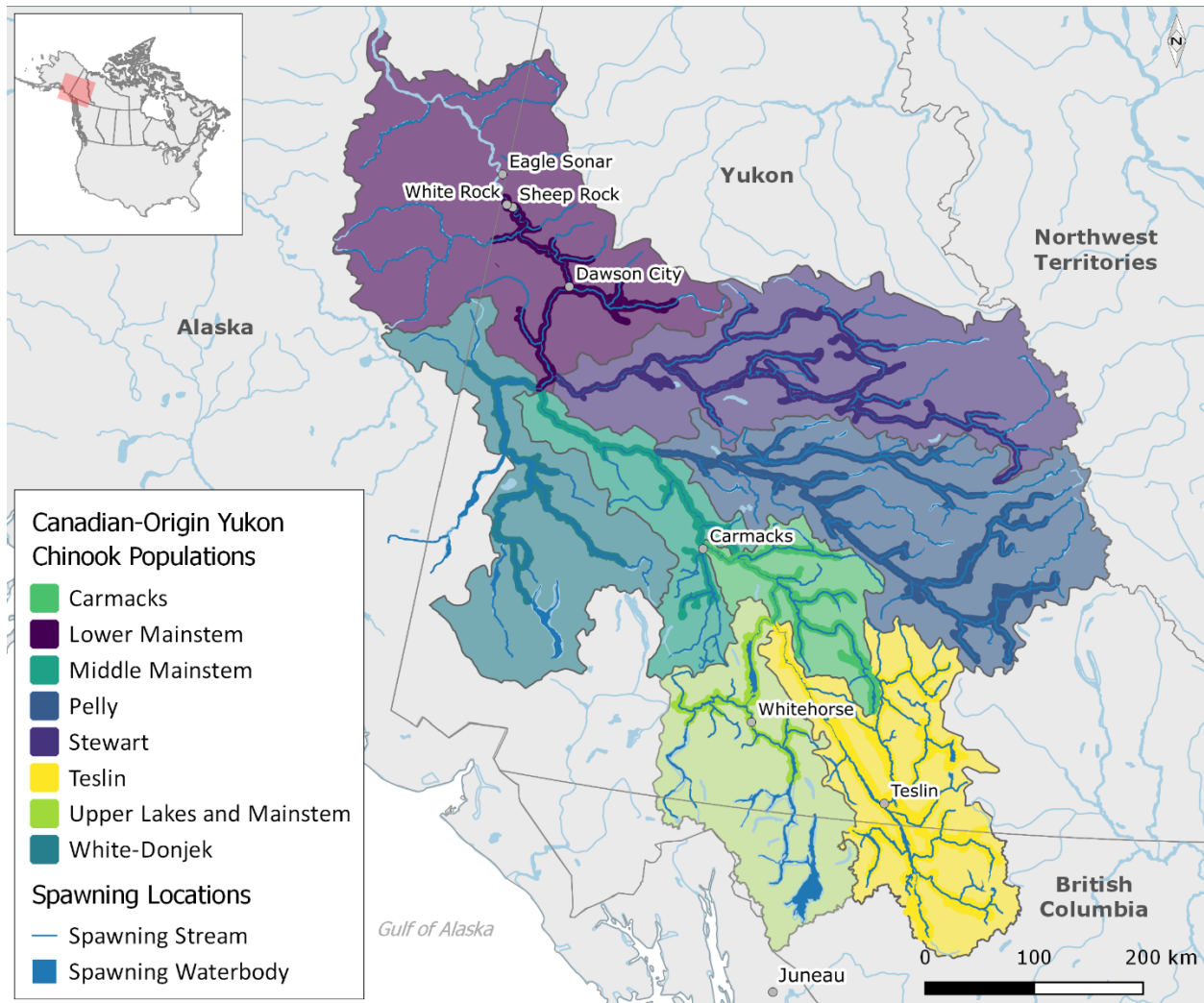
Figure 1. Location of the eight major sub-basins of the Yukon River in Canada corresponding to the populations that individual fish have been assigned to through genetic stock ID. Spawning streams and waterbodies are from Brown et al. (2017).

Archived scale samples → 1. Genetic stock identification → Population assignments

Daily (and annual) aggregate border passage → 2. Multi-population run-reconstruction model → Population specific border passage

Annual aggregate harvest (US and CDN) and age-composition → 3. Multi-population spawner-recruit model → Population characteristics (spawner abundance, recruitment, productivity, capacity, covariation in survival, etc.)

Biological and socio-economic objectives (and associated performance measures) → 4. Closed-loop simulation model → Performance of policies against objectives

Inputs / outputs
Modelling step

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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.

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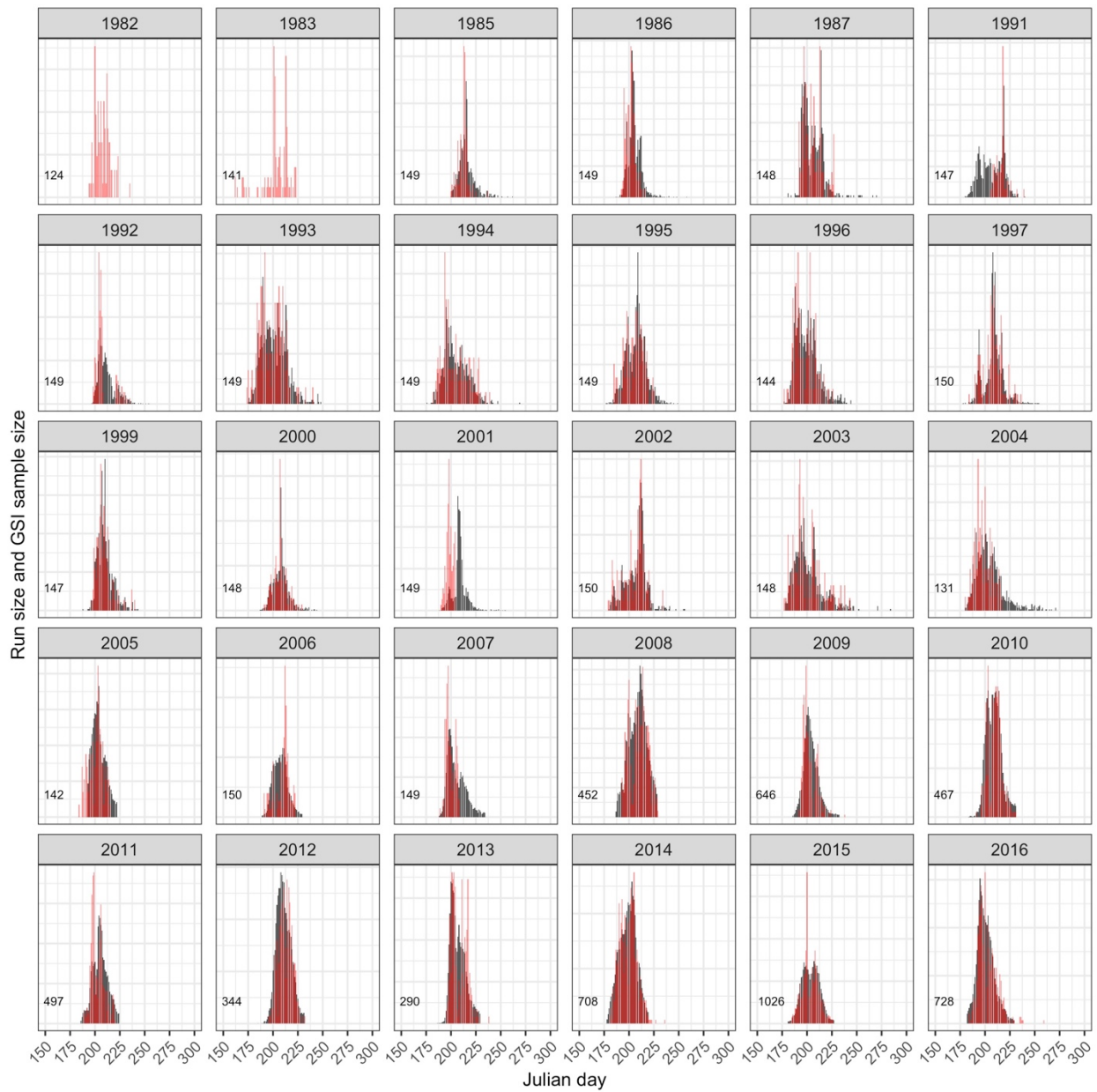
Figure 3. Daily estimates of Chinook border passage (grey bars) and distribution of scales sampled from the run to determine genetic stock ID (GSI). Overall, the scale sub-sampling is generally representative of the observed run. However, there are some clear mismatches between the observed run our scale 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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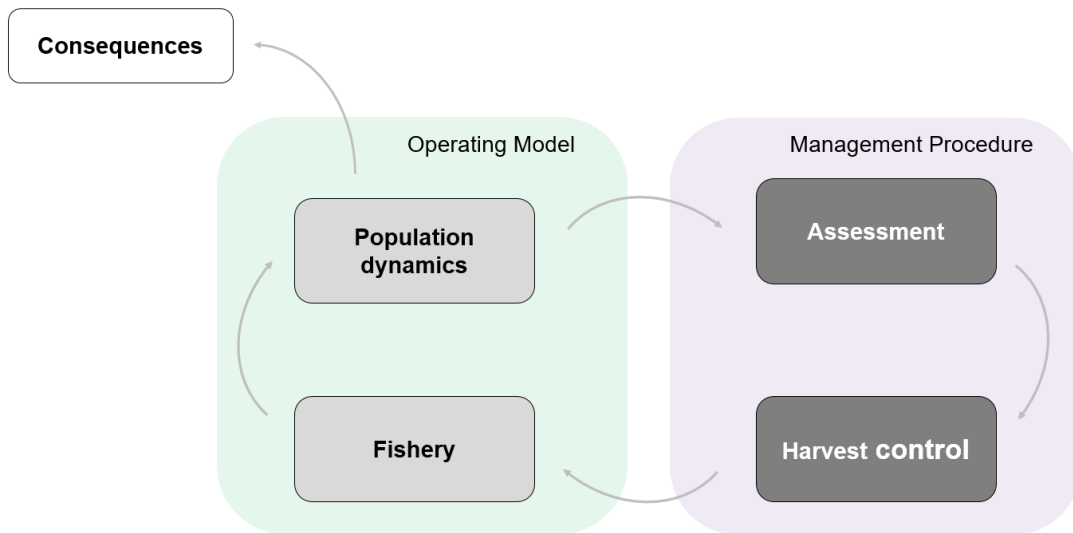
Figure 4. Illustration of the structure of the closed-loop simulation model.

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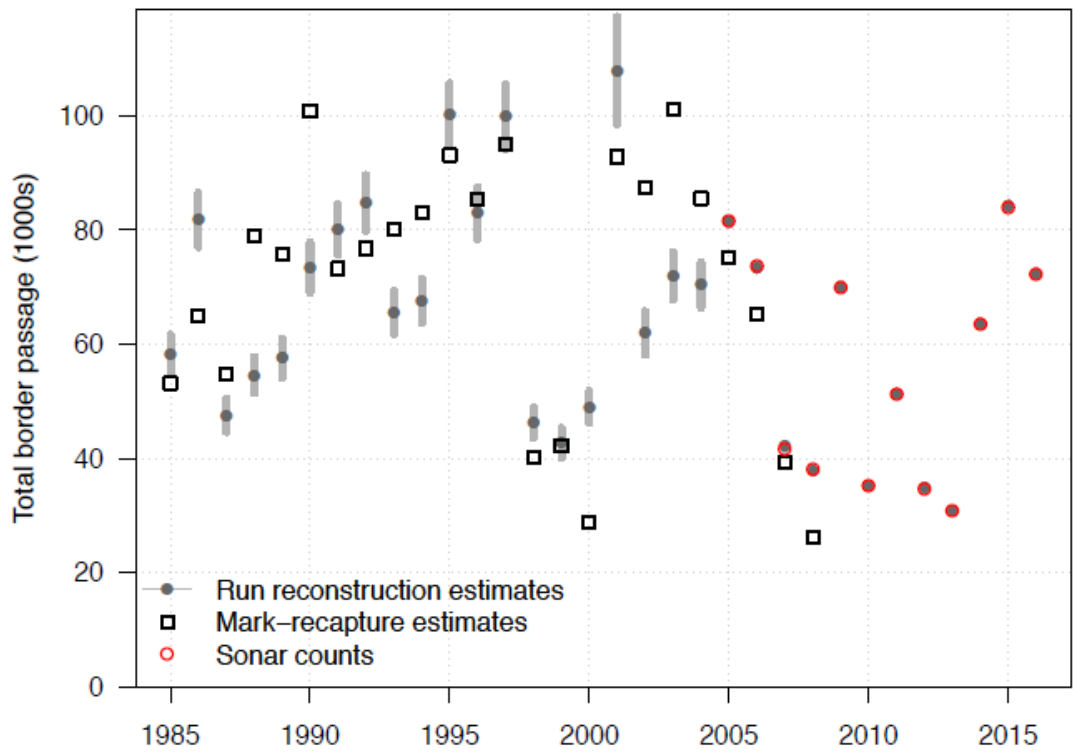
Figure 5. Total border passage estimates from RR_base (closed grey circles with grey bars to indicate the central 95% uncertainty interval), mark-recapture analysis (boxes), and the Eagle sonar (open red circles).

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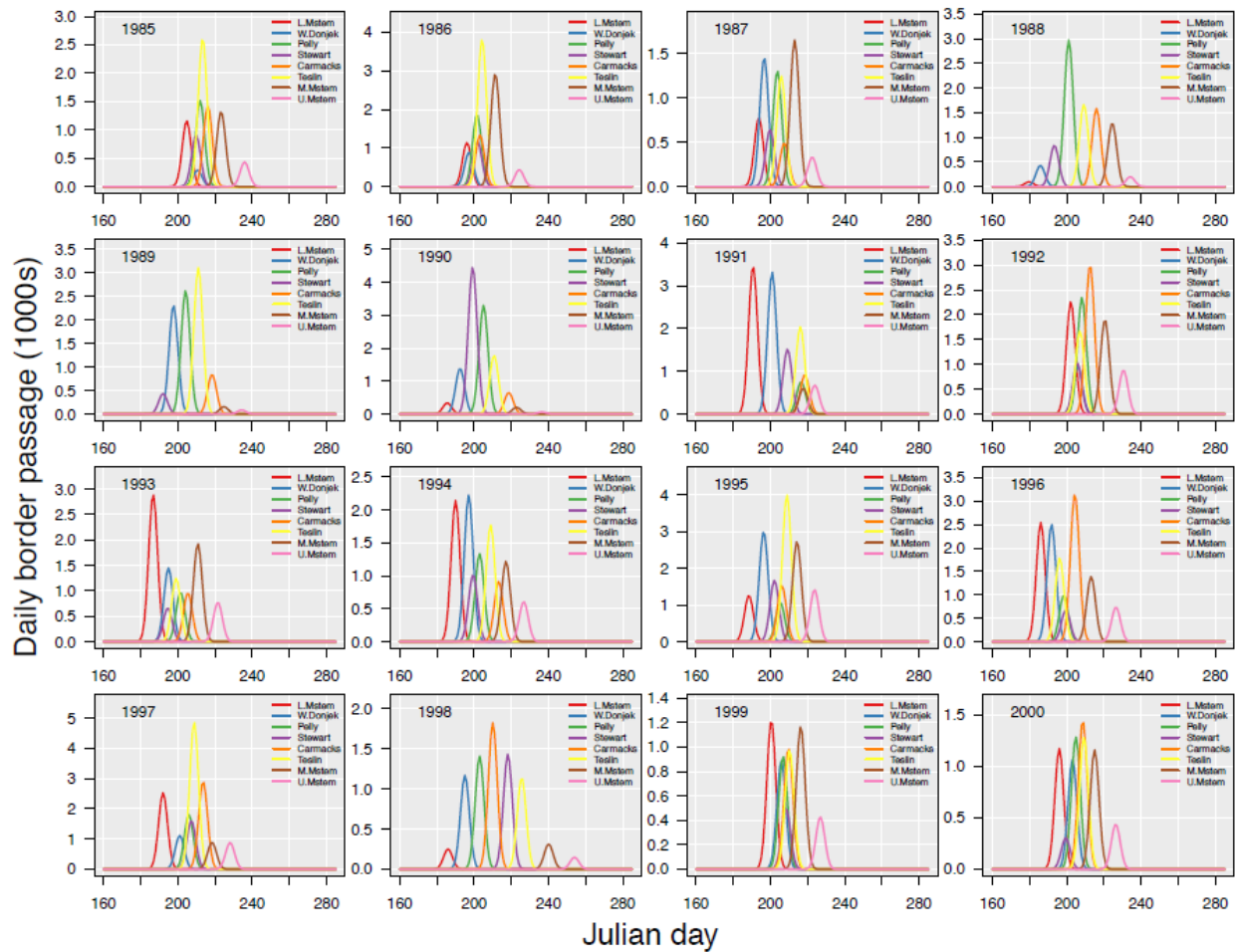
Figure 6. Estimates of daily border passage for the eight Yukon River Chinook populations (1985-2000)
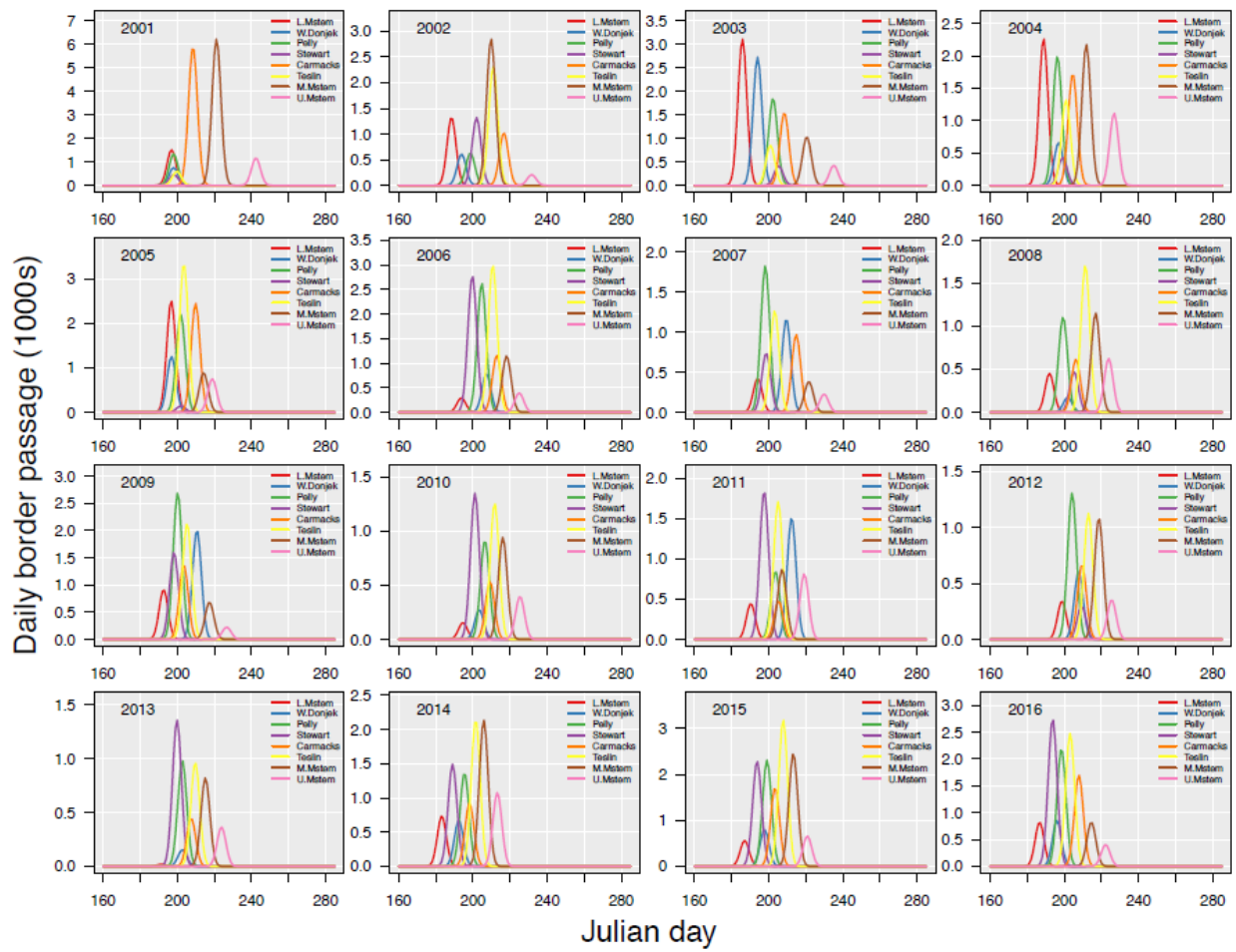
Figure 7. Estimates of daily border passage for the eight Yukon River Chinook populations (2001-2016).

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Figure 8. 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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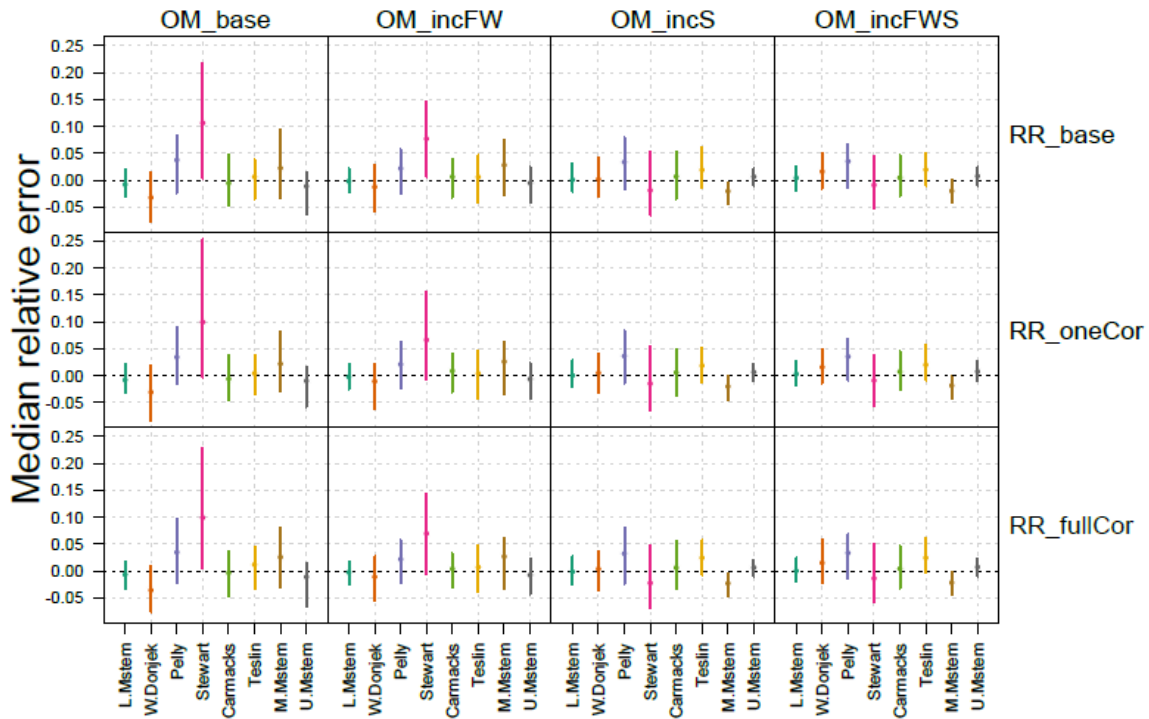
Figure 9. Median relative error (MRE) in run size estimates from three RRs (rows), which were each fitted to 100 datasets generated by four OMs (columns). A positive MRE indicates model estimate was less than the true value from simulation (i.e., underestimate), while a negative MRE indicates model estimate 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.

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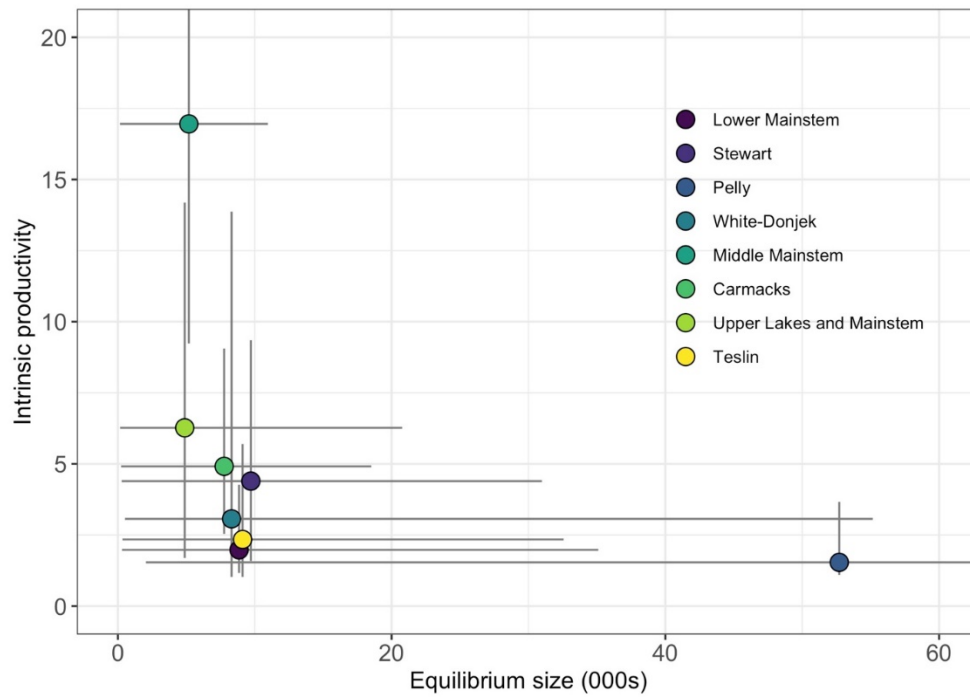
Figure 10. Posterior distributions of intrinsic productivity (alpha – recruits per spawner at small population size) for individual populations along with corresponding estimates of equilibrium population size. Points are colored to increase visual contrast.

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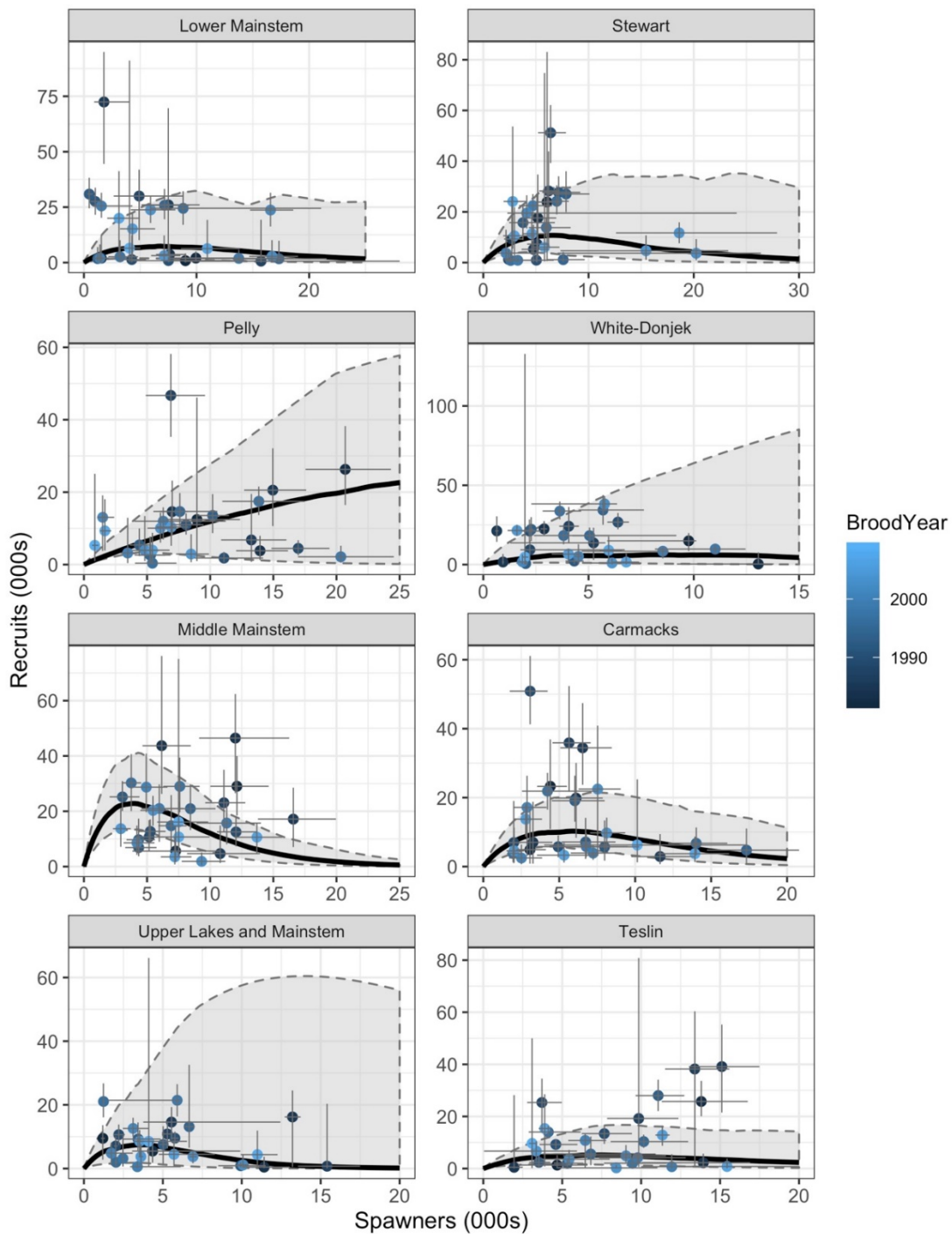
Figure 11. Relationship between recruitment and spawner abundance for Canadian-origin Yukon Chinook populations. Individual spawner-recruitment pairs are colored coded according to time. The black line is the predicted relationship between spawner abundance and recruitment along with 95% credible intervals in the shaded region.

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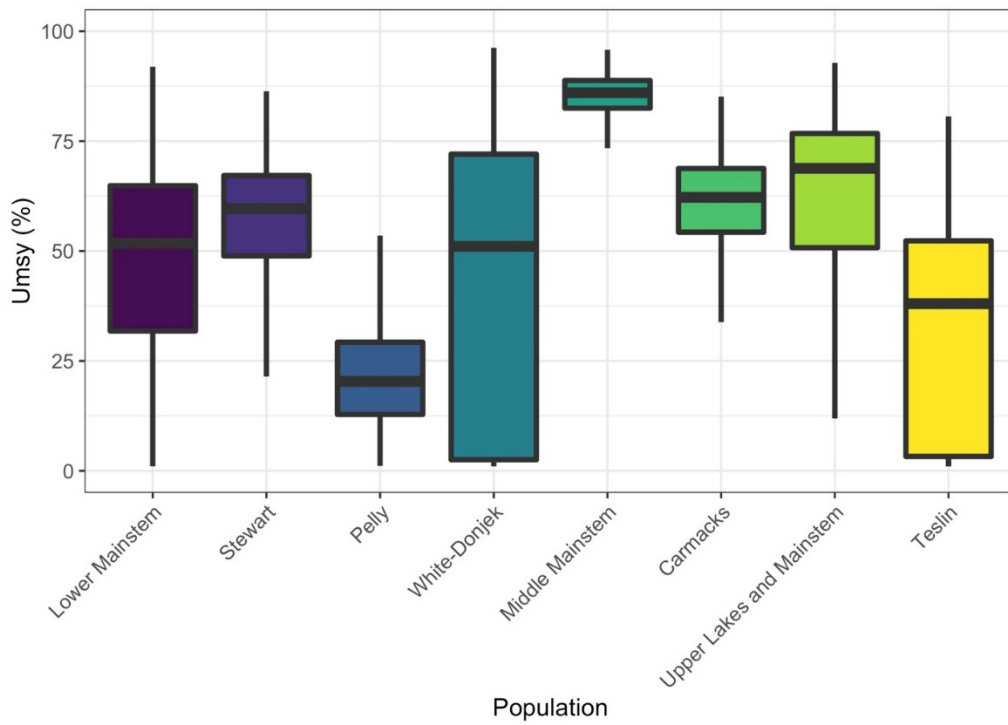
**Figure 12.** Posteriors distributions of the harvest rate predicted to maximize yield (U_{MSY}) for the Canadian populations.

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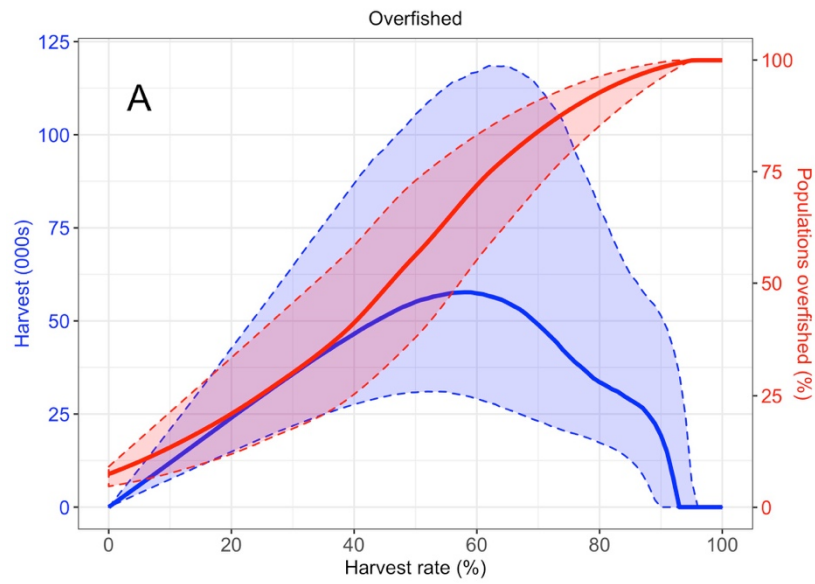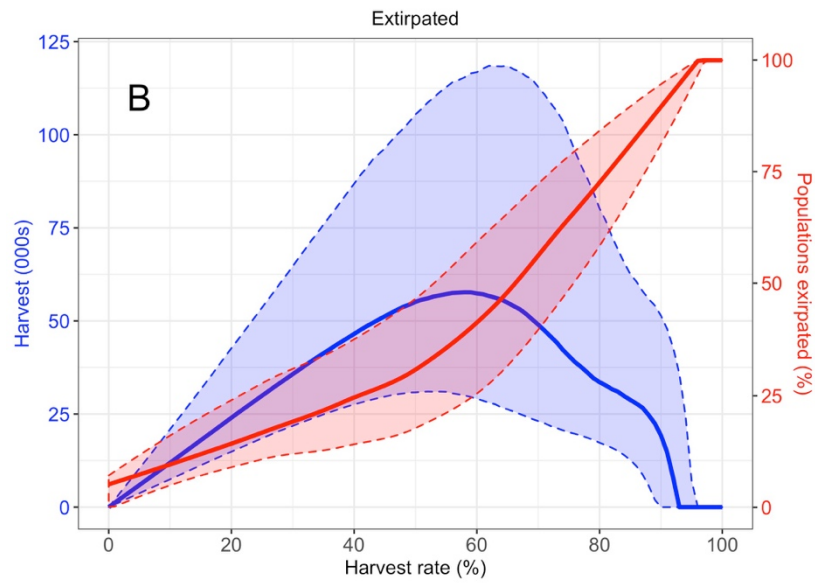
Figure 13. Predicted yield under equilibrium conditions across a range of fixed harvest rates. The corresponding consequences for population diversity, in terms of the percentage of populations predicted to be (A) overfished or (B) driven to extirpation, are plotted on the secondary y-axes.

Year (last year of 10-year rolling window)
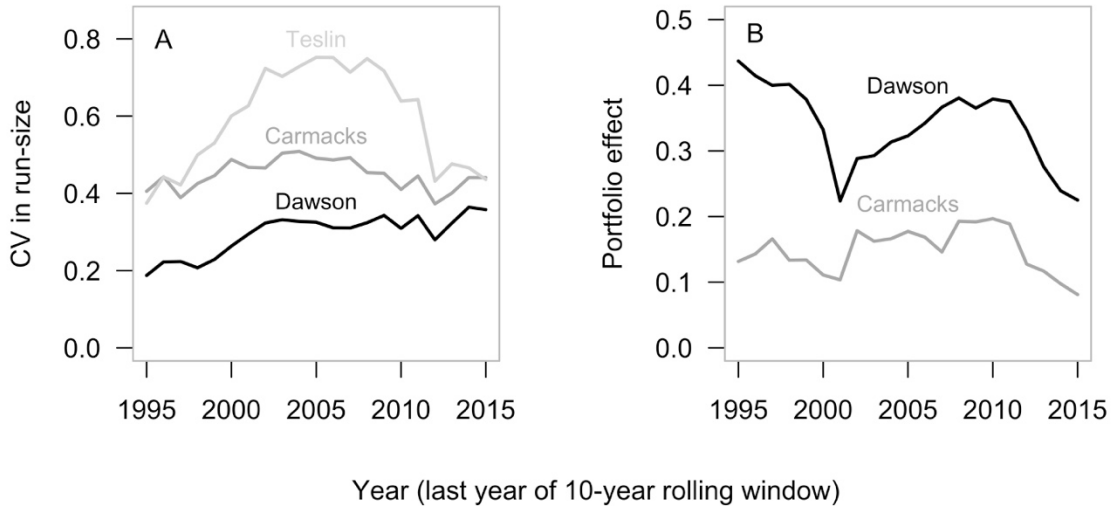
Figure 14. Ten year running average coefficient of variation (CV, Panel A) and Portfolio effects (Panel B) for the aggregate run-size (represented by fish passing Dawson) and smaller spatial scales at the middle of the CDN basin (represented by Carmacks; including populations Carmacks, Upper Lakes and Mainstem, and Teslin) and the headwaters (represented by just Teslin). See Figure 1 for locations of communities.
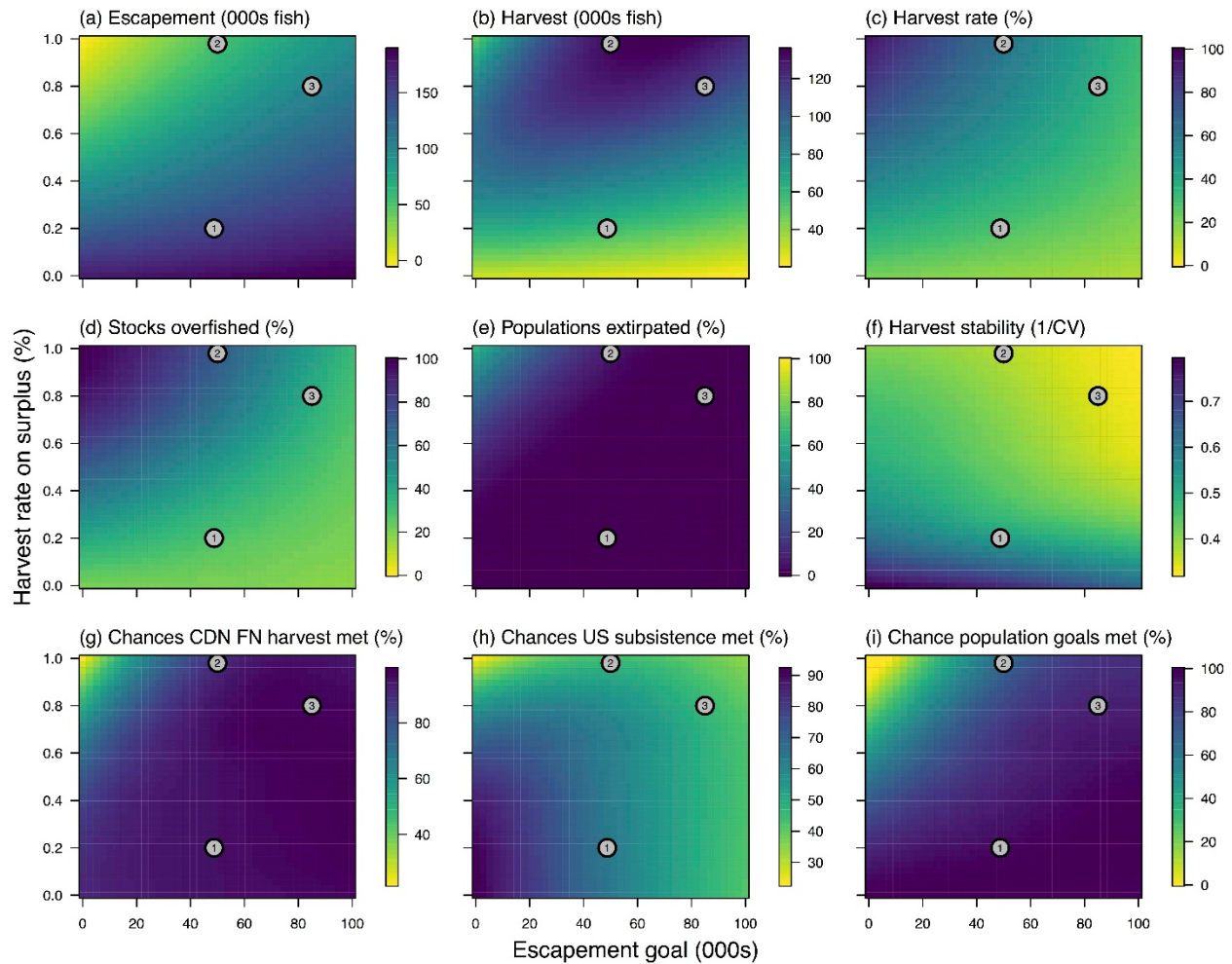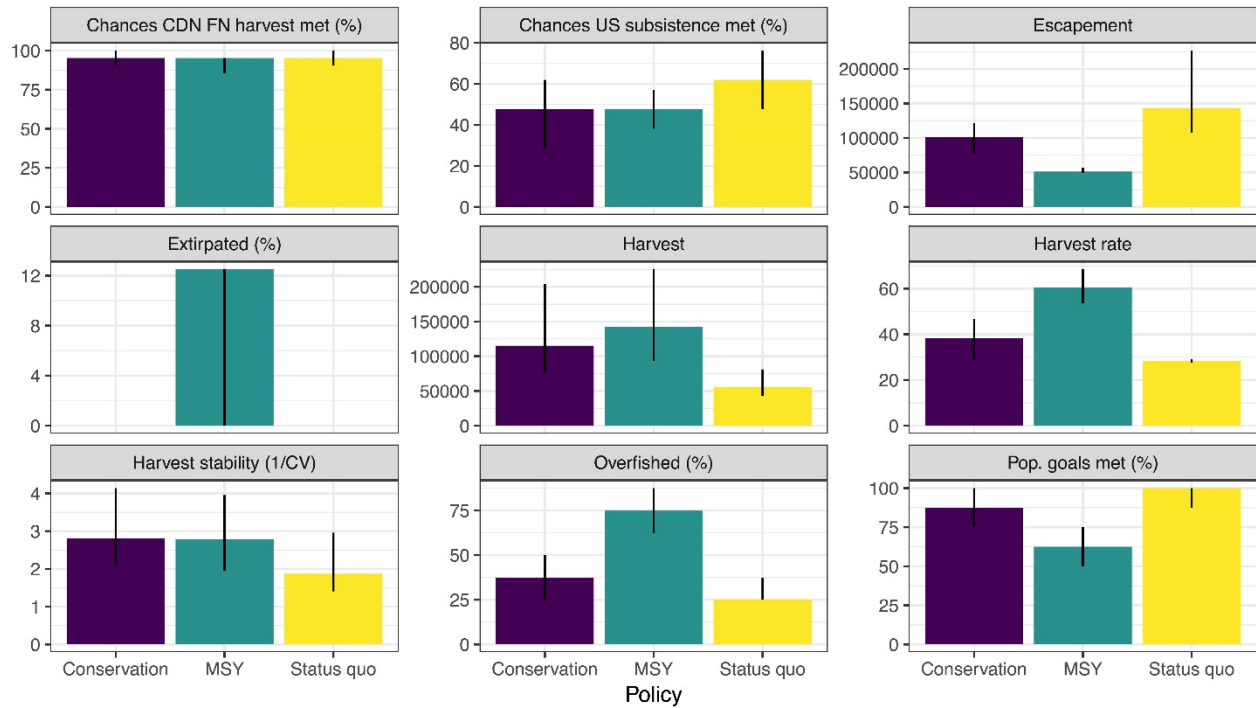
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Figure 15. Predicted consequences of alternative harvest policies. Each policy is defined by a combination of target harvest on surplus (y-axis; surplus above escapement, subsistence and First Nations harvest targets) and basin-wide escapement goals (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.

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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).

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

Year	Population															
	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
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

Year	Population															
	LM		S		P		WD		MM		C		ULM		T	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
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. Productivity (alpha) and size (1/beta) by population +/- 95% credible intervals.

Population	Productivity	Equilibrium
Lower Mainstem	1.98 (1.1-4.2)	8854 (303-35101)
Stewart	4.39 (1.5-9.3)	9715 (282-30982)
Pelly	1.54 (1.0-3.6)	52707 (2043-414586)
White-Donjek	3.07 (1.0-13.)	8307 (522-55151)
Middle Mainstem	16.95 (9.2-31)	5185 (149-10964)
Carmacks	4.91 (2.5-9.0)	7764 (237-18511)
Upper Lakes and Mainstem	6.27 (1.6-14)	4883 (158-20770)
Teslin	2.34 (1.0-5.6)	9113 (333-32564)

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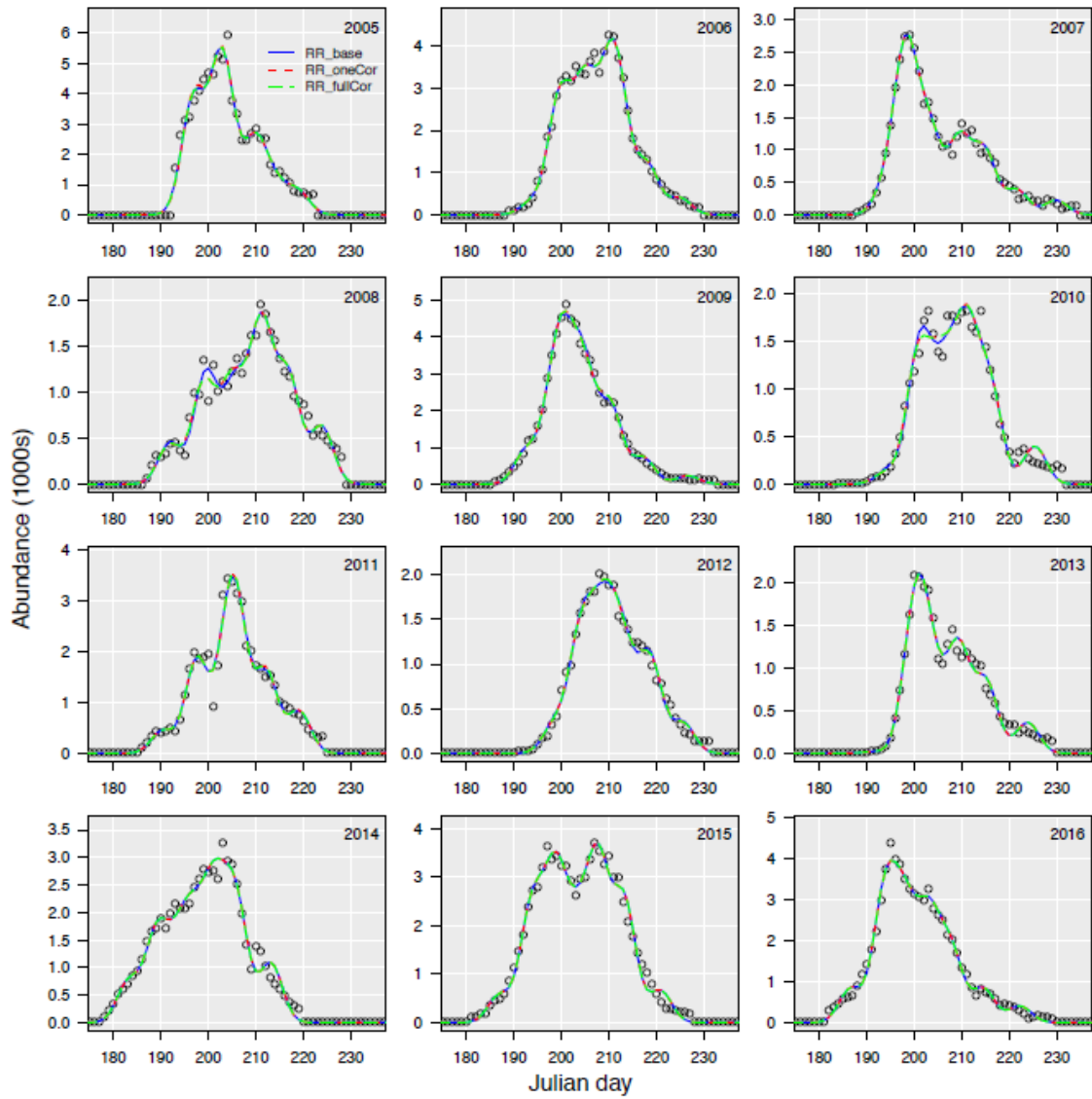
Figure S1. Fits of the three run-reconstruction models (lines) to daily Eagle sonar counts (circles).

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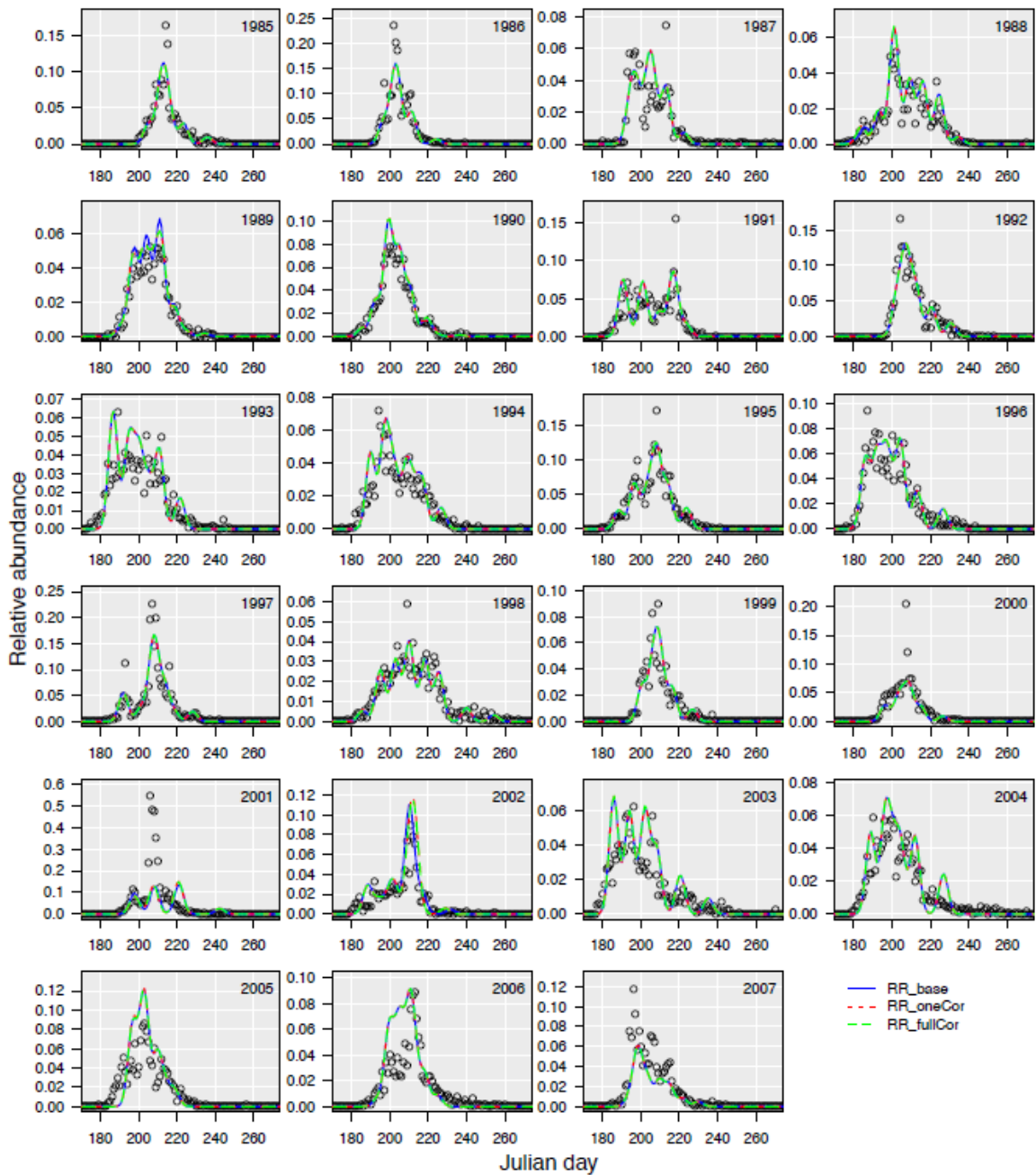
Figure S2. Fits of the three run-reconstruction models (lines) to daily fish wheel counts (circles).
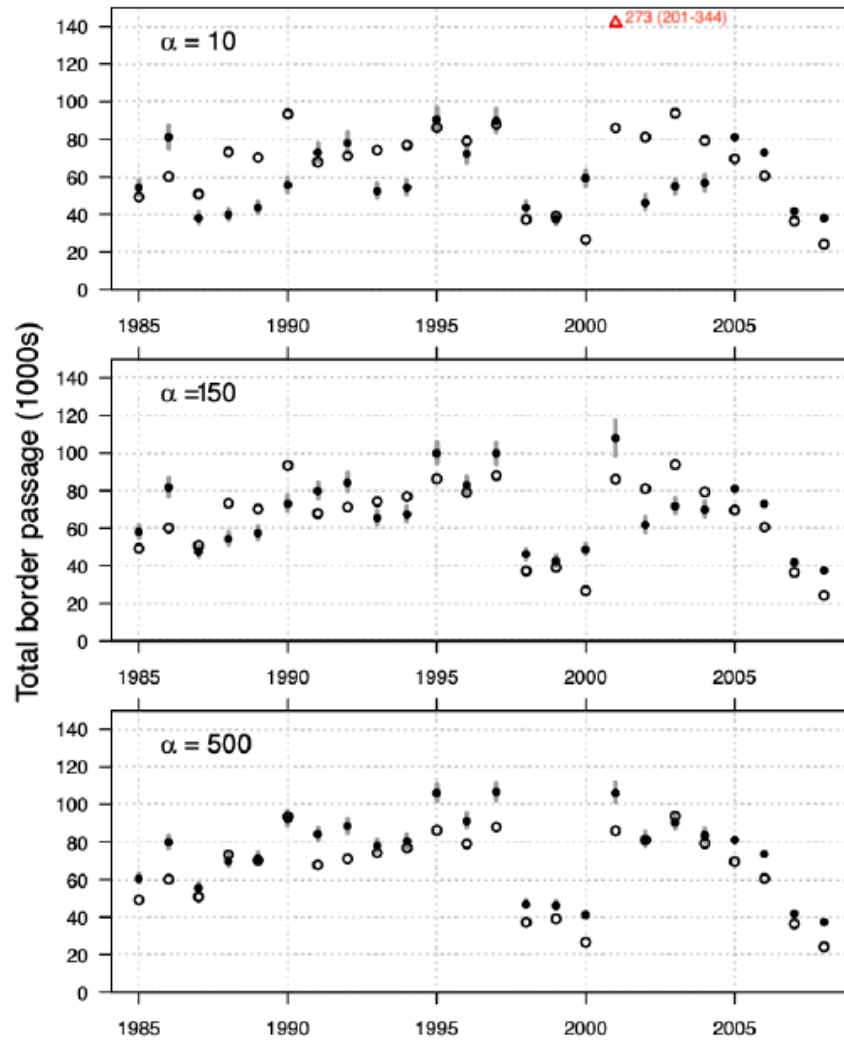
Figure S3. Sensitivity analysis of total border passage estimates (1000s) from RR_base for three likelihood weights (α) in years where mark-recapture is the only source of total border passage data. Closed circles indicate run reconstruction MLEs, grey bars indicate the associated central 95% uncertainty 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).
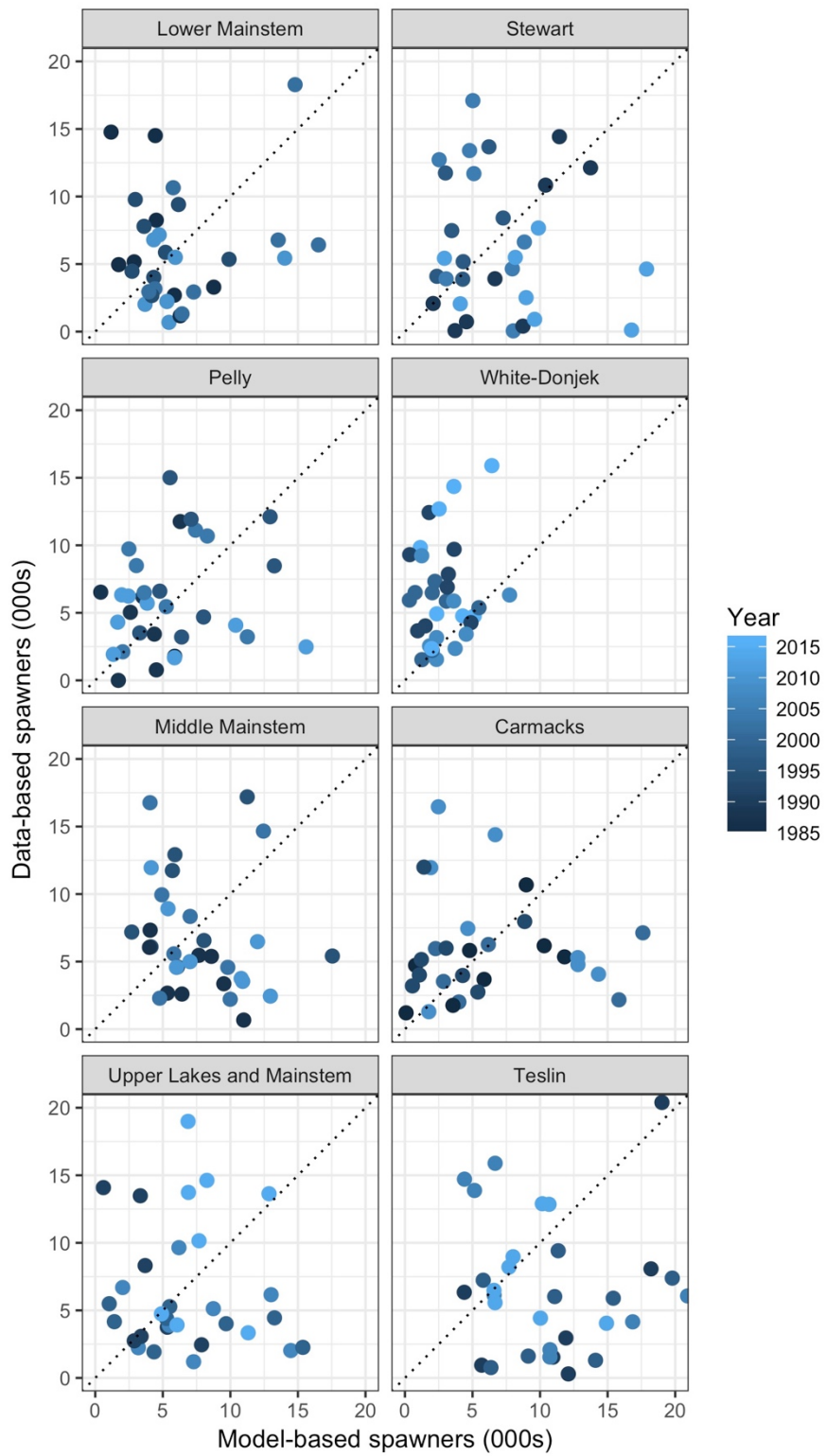
Figure S4. Comparison of data- and model-based estimates of population-level spawner abundance.

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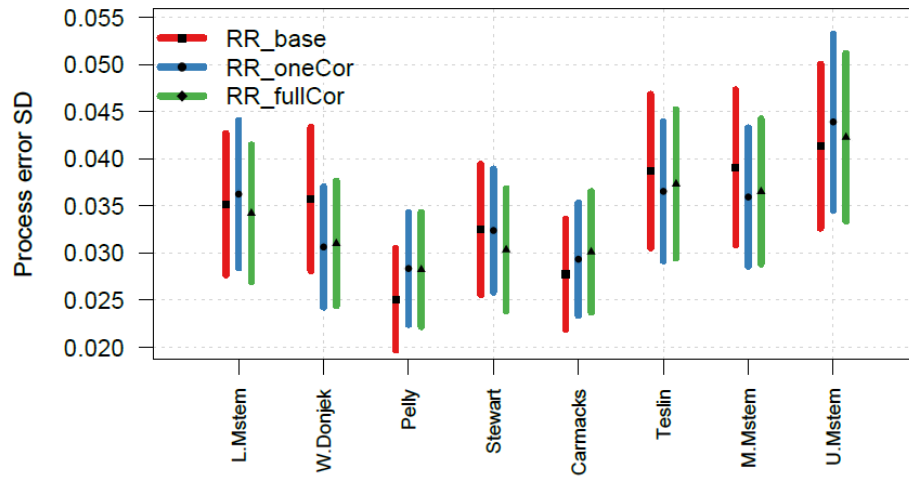
Figure S5. Standard deviation of process errors in arrival timing for each model and stock. Points indicate the maximum likelihood estimates while lines indicate the central 95% uncertainty interval.
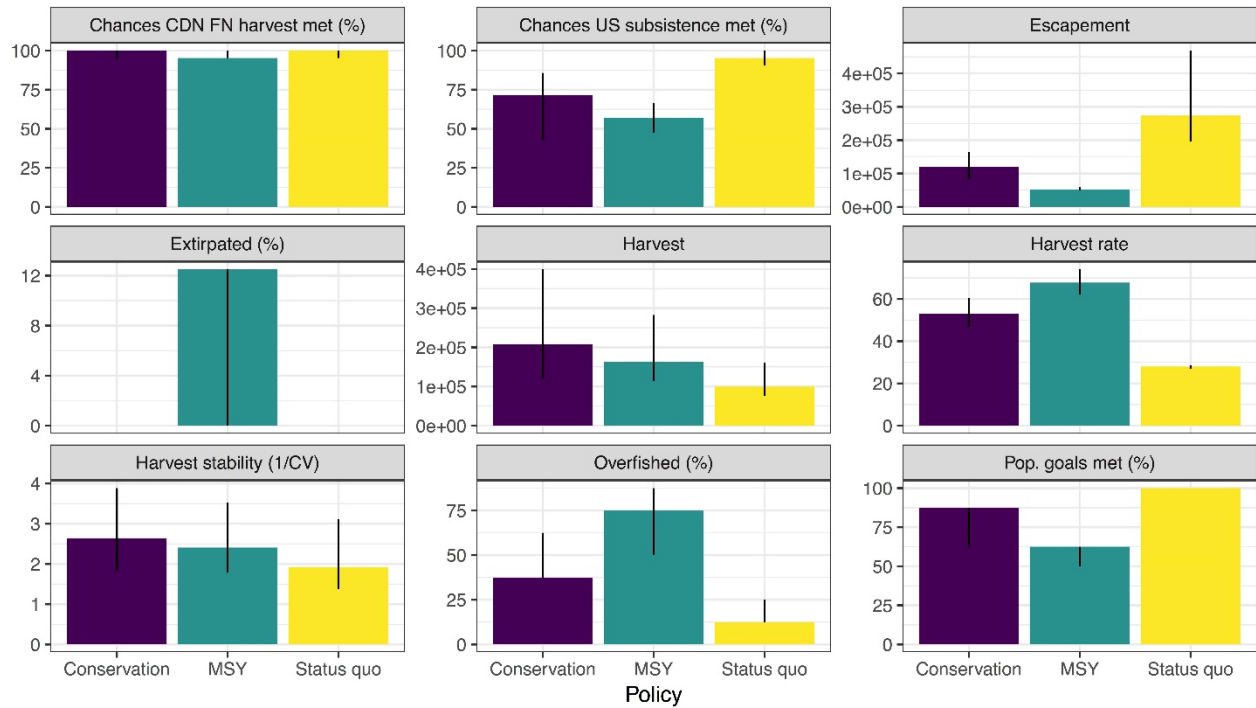
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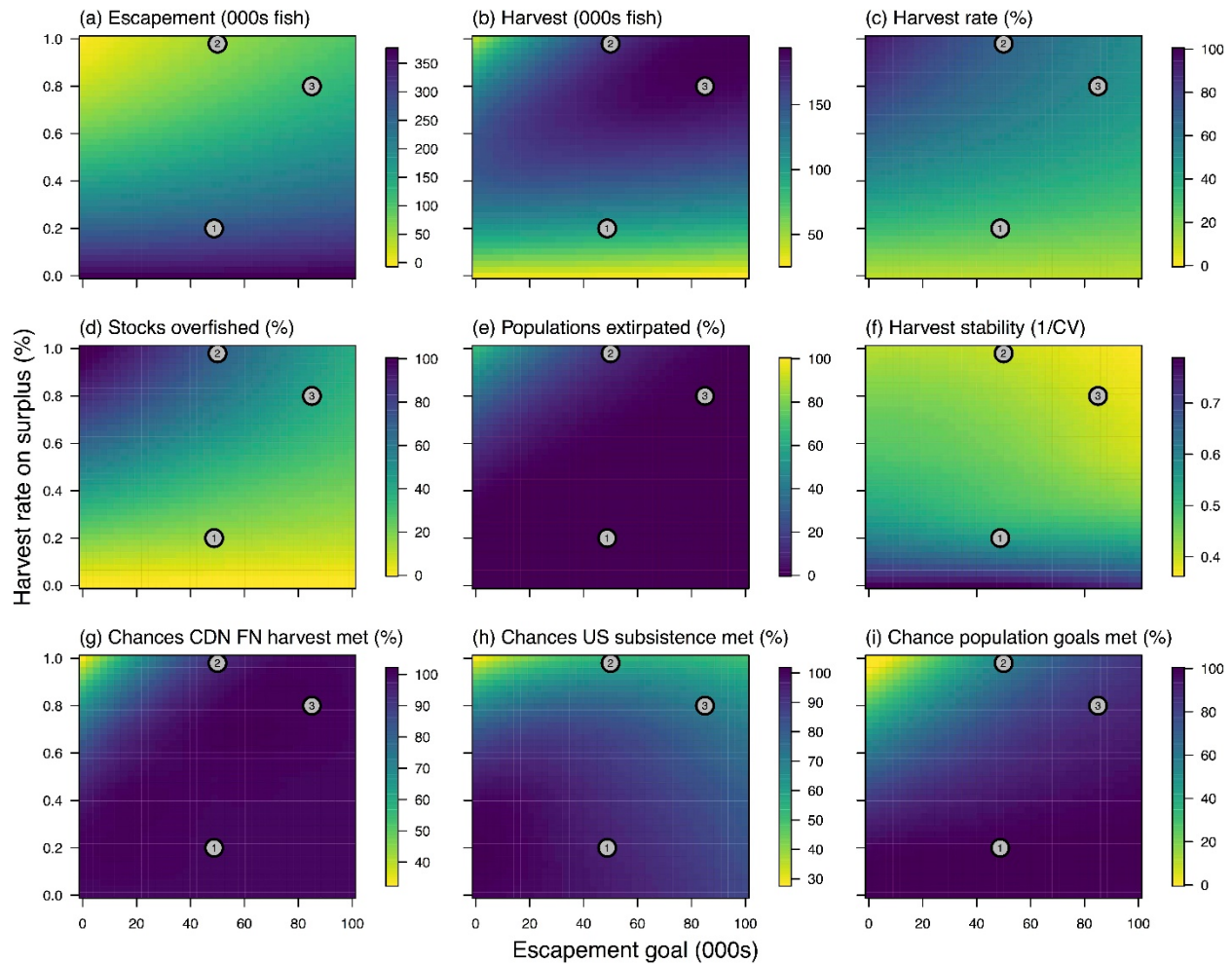
Figure S6. Predicted consequences of alternative harvest policies when recruitment is driven by time-varying Beverton=Holt type spawner-recruitment relationship. Each policy is defined by a combination of target harvest on surplus (y-axis; surplus above escapement, subsistence and First Nations harvest 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.

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Figure S7. 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.

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 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 20 values of δ (0.2-2).

The results of the simulations suggest that estimates of α are biased low at periods (f) less than 10 years, but were otherwise relatively unbiased across a range of values in A and δ. Estimates of β were more sensitive to parameter combinations, but generally appeared to be the least biased when the period (f), amplitude (A) and productivity scalar (δ) were approximately 14, 0.6 and 1.4, respectively. We then further explored the extent to which this combination of parameter values generates an apparent spawner-recruit relationship that qualitatively matches the empirical Yukon one. To do this we simulated 1000 spawner-recruit datasets under the BH_cycl formulation with the period (f), amplitude (A) and productivity scalar (δ) equal to 14, 0.6 and 1.4, respectively (Figure A2a illustrates the resulting time-series of productivity). For each simulation we then fit a Ricker spawner-recruit relationship to the data and summarized the predicted relationship across the 1000 simulations relative to the observed Ricker spawner-recruit relationship for the Yukon aggregate. These simulations suggest that this combination of parameter values result in a spawner-recruitment relationship with apparent overcompensation of a magnitude similar to that observed in the Yukon (Figure A2b).
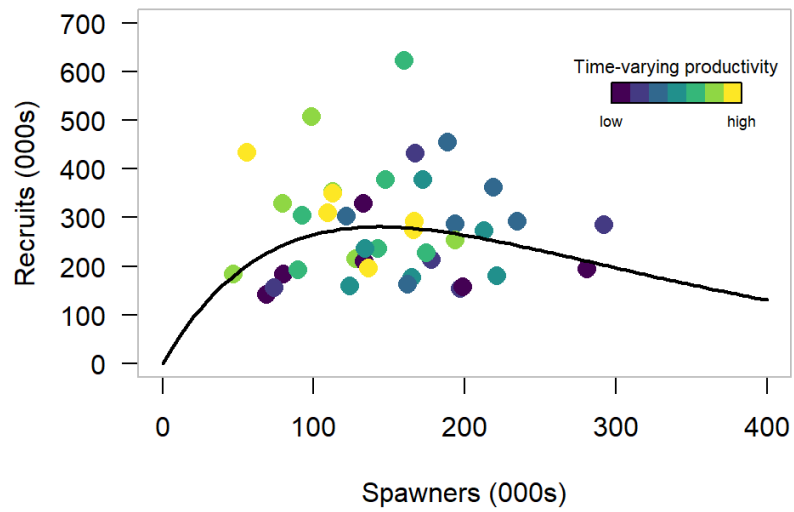
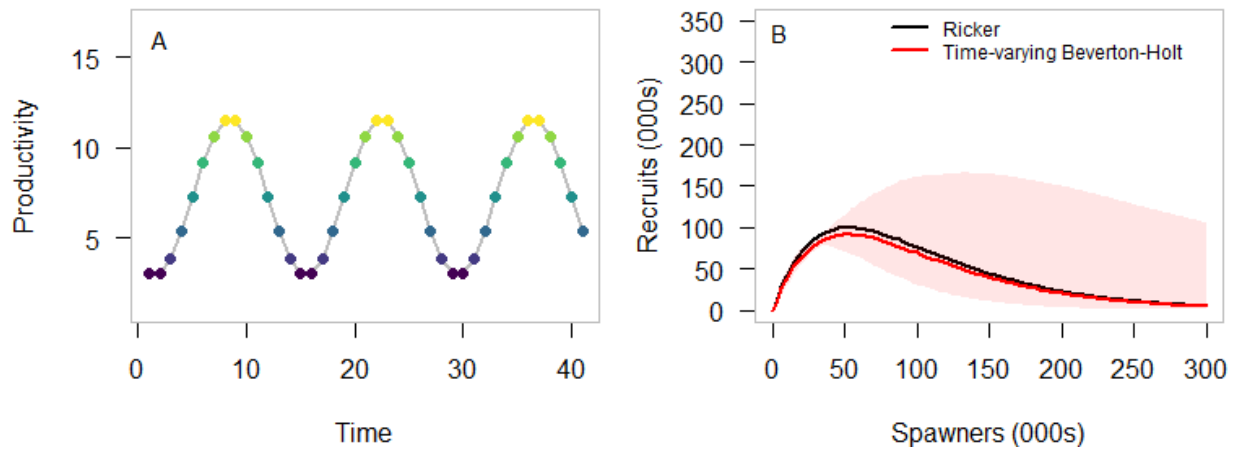**Figure A1.** Spawner-recruitment data simulated by a Beverton-Holt type relationship with time-varying productivity (colors). The black line is the Ricker type spawner-recruitment relationship estimated from the data, which implies that there is overcompensation when in fact there is none.

1052 **Figure A2.** (A) Time-varying productivity and (B) observed (Ricker black line) spawner-recruitment

1053 relationship in the Kuskokwim and simulated relationship (median and 95th percentiles) assuming a

1054 Beverton-Holt spawner-recruitment relationship with time-varying productivity.

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