

Incorporating harvest–population diversity trade-offs into harvest policy analyses of salmon management in large river basins

Brendan M. Connors, Benjamin Staton, Lewis Coggins, Carl Walters, Mike Jones, Daniel Gwinn, Matt Catalano, and Steve Fleischman

Abstract: Accounting for population diversity can be critical to the sustainable management of mixed-stock fisheries because harvest rates that can be sustained by productive populations may come at the cost of overfishing less productive ones. While these harvest–diversity trade-offs are well-recognized, their consequences for harvest policy performance are not often explicitly evaluated in contemporary fisheries management. We use closed-loop simulations to evaluate the ability of alternative harvest policies to meet population diversity and fishery objectives for one of the largest subsistence Chinook salmon (*Oncorhynchus tshawytscha*) fisheries in the world (Kuskokwim River Basin in western Alaska). We found clear evidence of population diversity that resulted in asymmetric trade-offs among fishery and conservation objectives whereby policies that forgo relatively small amounts of harvest result in relatively large increases in equitable access to Chinook and elimination of risk of weak stock extirpation. The performance of alternative harvest policies, and the magnitude of trade-offs, were sensitive to regime shifts and uncertainty in the drivers of recruitment variation. However, we found that harvest policies that prioritized meeting minimum subsistence needs were unlikely to jeopardize long-term sustainability.

Résumé : La prise en considération de la diversité des populations peut revêtir une importance clé pour la gestion durable des pêches de stocks mélangées, puisque les taux de prises pouvant être soutenus par les populations productives pourraient entraîner la surexploitation de populations moins productives. Si ces compromis entre les prises et la diversité sont bien établis, leurs conséquences sur la performance de politiques sur les prises ne sont pas, dans bien des cas, évaluées explicitement dans la gestion des pêches. Nous avons utilisé des simulations en boucle fermée pour évaluer la capacité de différentes politiques sur les prises d'atteindre des objectifs de diversité des populations et de pêche pour une des plus importantes pêches de subsistance au saumon chinook (*Oncorhynchus tshawytscha*) du monde (dans le bassin de la rivière Kuskokwim de l'ouest de l'Alaska). Nous avons relevé des preuves claires d'une diversité de la population qui se traduit par des compromis asymétriques entre les objectifs de pêche et de conservation, selon lesquels des politiques qui excluent des quantités de prises relativement faibles entraînent des augmentations relativement importantes de l'accès équitable aux saumons chinooks et l'élimination du risque de disparation de stocks faibles. La performance de différentes politiques sur les prises et l'ampleur des compromis sont sensibles à des changements de régime et à l'incertitude concernant les facteurs de variation du recrutement. Nous avons toutefois relevé que les politiques sur les prises dont la priorité est de répondre à des besoins de subsistance minimums sont peu susceptibles de poser un risque pour la pérennité à long terme. [Traduit par la Rédaction]

Introduction

Maintaining variation in life history characteristics among species, populations, and individuals is increasingly recognized as a hallmark of sustainable and resilient fisheries management. In addition to the inherent importance of protecting such diversity, fisheries that integrate across species and population diversity are often more stable (Sethi 2010; Schindler et al. 2015; Anderson et al. 2017), provide increased food security (Nesbitt and Moore 2016), and are more resilient to environmental change (Anderson et al. 2015; Cline et al. 2017). Considerable progress has been made quantifying the fisheries benefits of species and population diversity, and recognition of the importance of protecting population

diversity is now common in national and regional fisheries management policies, such as Canada's Wild Salmon Policy (DFO 2005) and Alaska's Sustainable Salmon Policy. However, protecting population diversity can come at a cost to yield, leading to complex trade-offs among fisheries and conservation objectives, which we refer to as harvest–diversity trade-offs.

Harvest–diversity trade-offs occur when fisheries for individual populations overlap in space and time. This overlap leads to conflict between harvest and the protection of population diversity because unproductive populations will be unable to sustainably withstand the harvest rates that maximize long-term yield from productive stocks. This gives rise to a trade-off between harvests and the protection of diversity, known as the weak stock problem

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B.M. Connors. Institute of Ocean Sciences, Fisheries and Oceans Canada, 9860 W Saanich Rd., Sidney, BC V8L 5T5, Canada.

B. Staton. Auburn University, 217 Swingle Hall, Auburn, AL 36849, USA; Columbia River Inter-Tribal Fish Commission, 700 NE Multnomah St., Portland, OR 97232, USA.

L. Coggins. US Fish and Wildlife Service, 807 Chief Eddie Hoffman Hwy., Bethel, AK 99559, USA.

C. Walters. The University of British Columbia, 2202 Main Mall, Vancouver, BC V6T 1Z4, Canada.

M. Jones. Michigan State University, 80 Wilson Road, East Lansing, MI 48824, USA.

D. Gwinn. Biometric Research, 3 Hulbert Street, South Fremantle, WA 6162, Australia.

M. Catalano. Auburn University, 217 Swingle Hall, Auburn, AL 36849, USA.

S. Fleischman. Alaska Department of Fish and Game, 333 Raspberry Rd., Anchorage, AK 99518, USA.

Corresponding author: Brendan M. Connors (email: brendan.connors@dfw-mpo.gc.ca).

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

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

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

Furthermore, harvest–diversity trade-offs may also be influenced by the specific drivers of variation in recruitment in salmon systems. For example, many salmon spawner–recruitment relationships are assumed to exhibit overcompensation with declining total recruitment at high spawner abundances (i.e., a Ricker-type spawner–recruitment relationship; Peterman and Dorner 2012; Fleischman et al. 2013; Dorner et al. 2017). Such overcompensation may occur because, for example, at high spawner densities spawning success is reduced due to competition on the spawning grounds. However, low frequency cyclical variation in environmental forcing can also give rise to the appearance of overcompensation in spawner–recruitment data (Parma and Deriso 1990). Such cyclical environmental forcing may also exacerbate harvest–diversity trade-offs because weak stocks are more susceptible to overharvest in years of low productivity than they would be if the primary drivers of recruitment variation were intrinsic. These alternative hypotheses, which are not easily distinguished from each other based on typical spawner–recruit datasets, give rise to structural uncertainty that may impact the evaluation of management strategies and perceptions of their ability to meet both harvest and diversity objectives.

Despite the increasing recognition of the importance of salmon biodiversity, there are few published examinations of the performance of alternative harvest policies designed to meet a range of fishery and conservation objectives that incorporate harvest and diversity considerations (but see Hawkshaw and Walters 2015; Walters et al. 2008). Additionally, quantitative evaluations of the performance of alternative harvest policies in the face of large uncertainty in the drivers, magnitudes, and trajectories of recruitment dynamics have been limited to date (but see Collie et al. 2012; Cunningham et al. 2019). These knowledge gaps were recently highlighted by an Arctic–Yukon–Kuskokwim Sustainable Salmon Initiative independent expert panel (Schindler et al. 2019)

that identified the need for empirically grounded closed-loop simulation studies that quantify (i) the predicted consequences of alternative harvest policies in large river basins for both sustainable production over the long term as well as preserving bio-complexity and (ii) trade-offs among fishery and conservation objectives in an attempt to understand the consequences of regime shifts and weak mechanistic understanding of drivers of recruitment.

To help close these knowledge gaps, we characterized salmon population diversity and trade-offs due to mixed-stock harvest in Kuskokwim River Chinook salmon (*Oncorhynchus tshawytscha*), which support one of the largest subsistence salmon fisheries in the world. We then developed and empirically parameterized a multipopulation closed-loop simulation model of the system to evaluate the ability of alternative harvest policies to meet both fishery and conservation objectives. We do this across a range of alternative hypotheses about drivers of recruitment dynamics and nonstationarity in population diversity (i.e., changes in productivity and capacity) to quantify how robust alternative harvest policies and how sensitive harvest–diversity trade-offs are to a variable environment. We find that the inherent Chinook population diversity present in the system gives rise to an asymmetric trade-off between harvest and conserving diversity and that the fishery and biological performance of harvest policies, and the magnitude of resulting trade-offs, are sensitive to directional changes in population diversity and uncertainty in the underlying drivers of recruitment variation. Our work provides a general framework for characterizing salmon population diversity and evaluating the ability of alternative harvest policies to meet multiple biological and fishery objectives in large salmon-producing river systems.

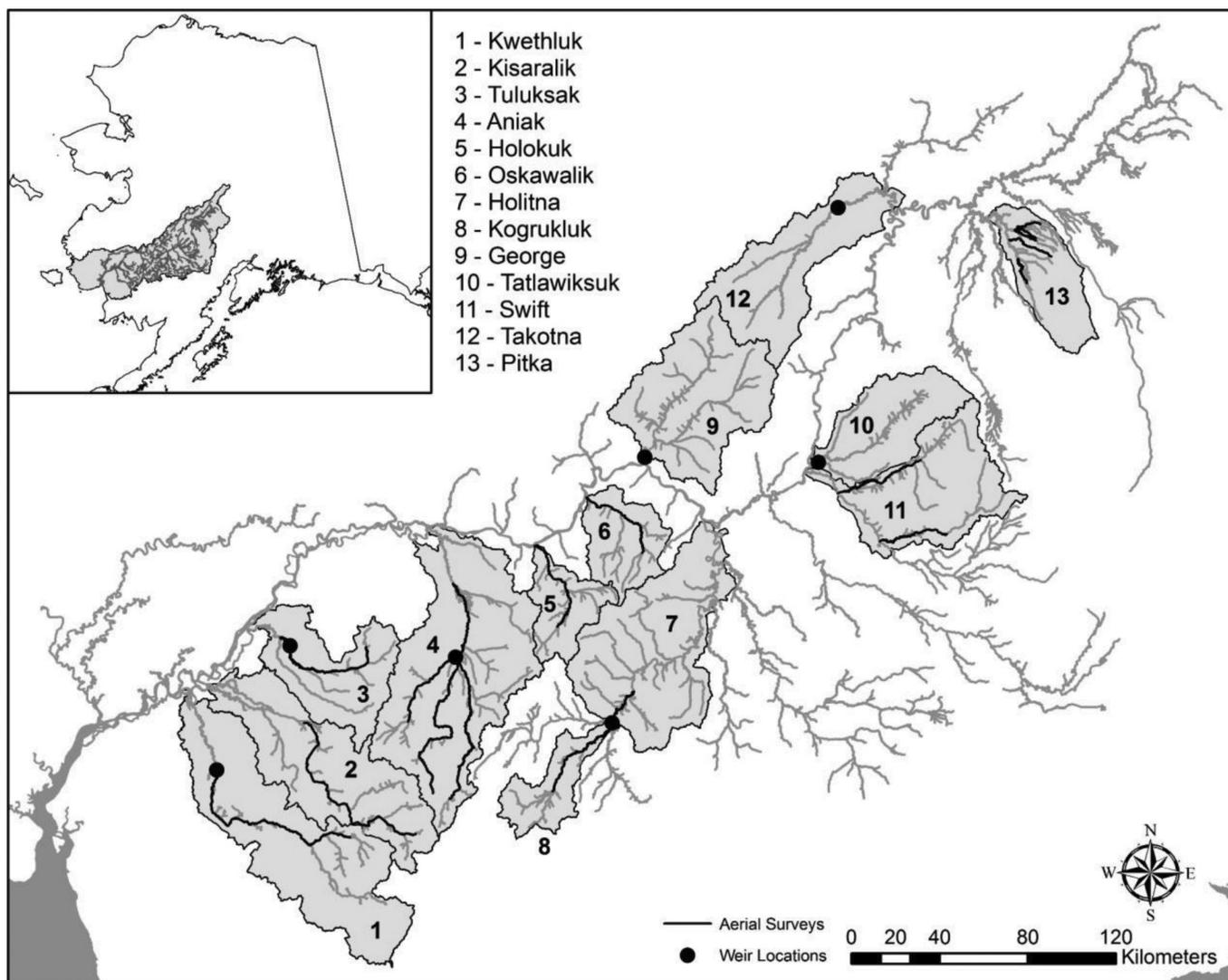
Methods

Our approach consisted of four steps: (1) establish fishery and population diversity objectives as well as alternative harvest policies through workshops with regional stakeholders, subsistence users, and management agencies (US Fish and Wildlife Service and Alaska Department of Fish and Game); (2) characterize population diversity by fitting an age-structured, multipopulation, state-space spawner–recruitment model to available data on spawners, harvests, and age composition at a population level; (3) quantify the performance of the alternative harvest policies against objectives using closed-loop simulations across a range of hypotheses representing alternative states of nature; and (4) characterize the trade-offs between harvest and diversity that emerge from step 3 and illustrate how alternative harvest policies perform relative to them. We use the term “population” to denote spawning populations that have been the subject of separate assessment related activities within the system (see Fig. 1); they are neither a purely biologically or management-based unit. All code and data required to reproduce our analyses are archived in Connors (2019), and all model terms are described in Table 1.

Study area

Chinook populations across western Alaska have declined in abundance and productivity over the past decade (Ohlberger et al. 2016; Dorner et al. 2017). These declines have been particularly pronounced in the Kuskokwim River Basin (Fig. 1), where some recent years (e.g., 2012–2014) have seen record low escapement to Chinook spawning grounds. Although returns have increased since 2014, they remain well below the long-term average. Chinook spawn across at least two dozen tributaries of the mainstem Kuskokwim, and monitoring of harvest, escapement, and age composition for Chinook has occurred since the mid-1970s with a focus on 13 sub-basins monitored by weir or aerial surveys (Fig. 1). The Kuskokwim River system historically supported one of the world’s largest Chinook subsistence fisheries, which is of importance to dozens of communities along the river that have some

Fig. 1. The Kuskokwim River basin. General spawning distribution of the 13 Chinook populations for which there are estimates of spawner abundance based on either weir or aerial surveys. Map data are taken from the US Geological Survey (watershed boundaries), Alaska Department Natural Resources (main stem and state boundaries), and Alaska Department Fish and Game (tributary boundaries).



of the highest levels of subsistence dependence in the state of Alaska. Declines in Kuskokwim Chinook abundance have sharply reduced subsistence harvest, closed commercial fisheries, prompted widespread stakeholder concern about the future of the subsistence fishery, and led to disagreement among managers and stakeholders about the most appropriate way to manage Kuskokwim Chinook.

Fishery objectives and alternative management actions

As part of a broader exercise focused on building capacity among Kuskokwim stakeholders to engage in salmon management, we held a series of workshops with influential community members from throughout the river basin with a long history of active engagement in fishery management, as well as US Fish and Wildlife Service and Alaska Department of Fish and Game biologists and fishery managers. These workshops included discussion of existing and potential Kuskokwim Chinook fishery and biological objectives and alternative management actions associated with them. From these discussions, we identified a suite of long-term objectives against which to quantify the performance of alternative management actions (Table 2), as well as key biological and

fishery characteristics to incorporate into our closed-loop simulations (see section below on Closed-loop forward simulations).

Multistock state-space spawner–recruit model

We used the multistock state-space spawner–recruit model described by Staton et al. (in press) to characterize Chinook population diversity and dynamics in the Kuskokwim Basin. This model is an extension of single-stock models (Fleischman et al. 2013; Staton et al. 2017) that simultaneously fits separate stock–recruitment curves to incomplete population-specific escapement time series and mixed-stock harvest. Our base formulation of the state-space model for this paper was the most complex state-space model evaluated by Staton et al. (in press; referred to as SSM-VM). The model assumed that all populations are equally vulnerable to harvest, but in sensitivity analyses we relaxed this assumption. The model was fitted to time series of spawner abundance, harvest, and age composition in a Bayesian estimation framework using Markov chain Monte Carlo methods to sample from the joint posterior distribution of all unknown quantities (implemented in JAGS; Plummer 2017).

Table 1. States, biological and policy parameters, and associated values.

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

Note: Description of states and parameters in the closed-loop simulation model are described in the main text along with their associated values where appropriate.

Table 2. Fishery and conservation objectives, along with alternative management actions, identified by Kuskokwim River stakeholders.

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

The key quantities estimated by the state-space model included population productivity (i.e., maximum recruits-per-spawner), carrying capacity, latent recruitment states, lag-one temporal correlation in recruitment, variance and covariance in recruitment within and among populations, and time-varying maturity schedules. We used the posterior samples of population productivity and carrying capacity to quantify the range of predicted equilibrium trade-offs between aggregate harvest and conservation of population diversity across a range of mixed-stock harvest rates (Walters and Martell 2004; Walters et al. 2008). Full details of data processing and the structure of the state-space model, including model code and detailed outputs, are provided in Staton et al. (in press), as well as our associated online Supplementary material¹.

Closed-loop forward simulations

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

was to key structural uncertainties in the system, we simulated the biological and fishery dynamics across alternative states of nature (i.e., temporal changes in population diversity or alternative drivers of recruitment dynamics).

Operating model

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

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

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0282>.

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

where $R_{y,j}$ is recruitment from brood year y for population j ; α_j and β_j are population-specific intrinsic rate of growth (productivity) and within-population density dependence, respectively; $S_{y,j}$ is spawner abundance; ϕ is the degree of temporal correlation in recruitment from one year to the next; $\hat{R}_{y-1,j}$ is the expected recruitment in the previous year; and $r_{y,j}$ is residual variation in recruitment that is correlated among populations according to a common correlation parameter (ρ) following a multivariate normal (MVN) distribution:

$$(2) \quad \begin{aligned} r_{y,j} &\sim \text{MVN}(0, \Sigma) \\ \Sigma &= \begin{bmatrix} \sigma_1 \sigma_1 & \dots & \sigma_1 \sigma_j \rho \\ \vdots & \ddots & \vdots \\ \sigma_j \sigma_1 \rho & \dots & \sigma_j \sigma_j \end{bmatrix} \end{aligned}$$

where Σ is the variance-covariance matrix. Returns in year t ($N_{t,j}$) were then modeled a function of the proportion of individuals that mature and return to spawn at each age:

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

where π is a maturity schedule composed of four age classes (4 through 7 for Kuskokwim Chinook). To incorporate the effects of small population size on reproductive success (e.g., allele effects and depensation), we set a quasi-extinction threshold at 50 spawners (Holt and Bradford 2011) such that if spawner abundance fell below this threshold, recruitment from that brood year was assumed to be zero. For simplicity, we assumed that straying among populations did not occur.

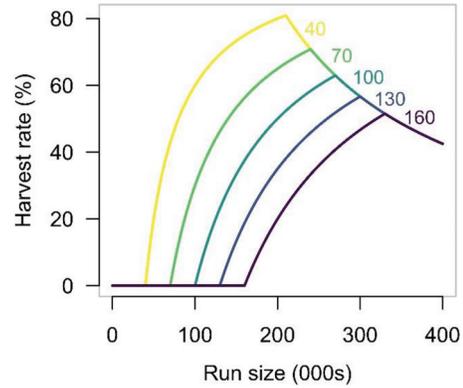
In each year of the forward simulation, the number of spawners in eq. 1 ($S_{y,j}$; where brood year y is equal to calendar year t) was calculated as the harvest ($H_{t,n}$) subtracted from the return ($N_{t,n}$), where the harvest was determined according to the harvest control rules described in the following section (Management procedure model). To simulate the dynamics for the entire Kuskokwim system, in each Monte Carlo trial we expanded spawner abundance, harvest, and recruitment by $1/D$, where D is normally distributed with a mean of 0.56 and standard deviation of 0.05 and represents an estimate of the proportional contribution of the 13 monitored populations to total Kuskokwim Chinook production (Staton et al., in press). This assumes that the monitored populations are a representative sample of all Kuskokwim Chinook populations with respect to population characteristics and time series properties, but was necessary so that the harvest policies we evaluated were on a scale salient to management entities.

Management procedure model

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

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

Fig. 2. Kuskokwim Chinook harvest control rule. Illustration of mixed-stock harvest rate as a function of true run size across a range of escapement goals (coloured lines) assuming a relatively high (175 000 fish) harvest goal (eq. 4). The deterministic harvest control rule is shown, but in the closed-loop simulations the realized harvest rate in any given year deviates from this relationship as a function of forecast error and outcome uncertainty. [Colour online.]



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

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

where ε_H reflects incomplete management control over the harvesting process and outcome uncertainty (Holt and Peterman 2006) and was assumed to be normally distributed with mean zero and standard deviation equal to 0.1. This harvest control rule prioritizes the escapement goal over subsistence needs and subsistence needs over nonsubsistence harvest. It results in exploitation rates that increase from zero at run sizes less than the escapement goal to a maximum when run size is equal to the escapement goal and target harvest, with the exploitation rate declining thereafter at larger run sizes (Fig. 2). Further, it assumed that execution of the fishery was nonselective; the exploitation rate applied to all subpopulations in the harvest mixture was equal each year.

Harvest policies

We quantified the performance of harvest policies across a broad range of basin-wide escapement goals and target harvest. We then considered three contrasting harvest policies (that emerged from the workshops; Table 3) in more detail to illustrate how policies that prioritize different objectives are predicted to perform across a range of biological and fishery performance measures. The first policy sought to maximize potential harvest from the system by setting a basin-wide escapement goal and target harvest (subsistence and commercial) equal to that predicted to produce maximum sustained yield under equilibrium conditions (termed “MSY policy”). The second was a fixed harvest policy without any escapement goal where the target harvest goal is equal to that required to meet minimum subsistence needs (termed “subsistence policy”). This policy is meant to reflect a situation where fishery managers decide to solely focus on meeting subsistence needs and minimize interannual variation in harvest, regardless of forecasted returns, with the assumption that harvests at the level of subsistence needs will not jeopardize long-term prospects for basin-wide sustainable use. The third policy sought to maximize yield from the system but only once biological risks of extirpation to the least productive populations are

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

Policy	Basin-wide escapement goal (\bar{E})	Subsistence needs (H_{sub})	Harvest goal after subsistence needs are met (H_{sub+})
1. Maximize basin-wide harvest (MSY policy)	75 000	65 000	105 000
2. Fixed harvest at levels needed for subsistence and maximize harvest stability (subsistence policy)	5 000	65 000	0
3. Maximize harvest while minimizing biological risk (conservation policy)	135 000	65 000	105 000

minimized (termed “conservation policy”). Under this policy the harvest goal was set to equal that in the MSY policy, but the escapement goal was increased to a level that is predicted to result in no risk of driving the weakest populations towards extinction. The MSY policy is similar to the basin-wide escapement goal approach to management that is currently in place in the Kuskokwim Basin where fishery managers seek to ensure that the aggregate number of Chinook that make it to the spawning grounds fall within the range predicted to provide expected yields greater than 100 000 while also meeting subsistence needs (recommended sustainable escapement goal range of 65 000 – 120 000; Hamazaki et al. 2012). However, policy 1 differs from current management because harvesting capacity is constrained in the Kuskokwim Basin due to household processing and consumption constraints.

Performance measures

We quantified the relative ability of the alternative harvest policies to meet the management objectives that were identified through a series of workshops with fishery managers and stakeholders (Table 2). To achieve this, we summarized our simulation outputs into a set of performance measures that could be assessed against the stated objectives. Performance measures related to harvest objectives included average catch and the interannual coefficient of variation (CV) in catch, both over the last 20 years of the 50-year simulations. We quantified performance relative to the objective of maximizing spatial equity in access to salmon across the river basin as the proportion of populations whose average spawner abundance over the last 20 years of each Monte Carlo trial was greater than or equal to the population-specific estimate of S_{MSY} (the spawner abundance predicted to maximize yield under equilibrium conditions). Lastly, we quantified biological performance as the proportion of populations whose average spawner abundance over the last 20 years of the Monte Carlo trial dropped below an extinction threshold of 5% of equilibrium population size. Each performance measure was summarized across 500 Monte Carlo trials, each parameterized by a unique draw from the posterior distribution of the state-space model fitted to Kuskokwim data (Staton et al., in press).

Uncertain states of nature

We simulated the biological and fishery dynamics of the Kuskokwim system across three alternative states of nature. This allowed us to evaluate how robust a given harvest policy is to key structural uncertainties in the system, something that is recognized as a best practice in the application of closed-loop simulation models to inform decision making (Punt et al. 2016).

As a baseline, we assumed that recruitment dynamics were governed by stationary spawner–recruitment dynamics that follow a Ricker-type relationship with overcompensation at high spawner abundances (eqs. 1–3). This is the spawner–recruitment relationship that is currently assumed by fishery managers in the Kuskokwim system (Hamazaki et al. 2012) and widely across other salmon fisheries. We also considered an alternative recruitment hypothesis that assumed that low frequency regime shifts occur that 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 pro-

ductivity. To do this we transformed the Ricker spawner–recruitment relationship in eq. 1 to a Beverton–Holt form (table 7.2 in Hilborn and Walters 1992) with time-varying productivity:

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

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

where population productivity ($\alpha_{y,j}$) is time-varying following a cycle with a period equal to f and amplitude equal to A . The term δ is a scalar that adjusts productivity such that long-term population equilibrium abundance in the absence of fishing is approximately the same as those assuming a Ricker spawner–recruitment relationship. We fixed f , A , and δ at 14, 0.6, and 1.4, respectively, based on exploratory simulations that showed that this combination of parameters generated spawner–recruitment relationships with apparent overcompensation that approximates that observed in the Kuskokwim Basin (Appendix A). Note that these values may depend on the spawner–recruit relationships used and should therefore be obtained separately for analyses of different populations in other systems.

Lastly, we considered a scenario where climate variation led to long-term directional changes in population productivity and carrying capacity such that halfway through the simulations the least productive stocks became more productive and the most productive stocks became less productive. In this scenario, the productivity (α_j) and carrying capacity (α_j/β_j) of individual stocks was assumed to be time-varying and to change over the course of a decade (from $t = 20$ to $t = 30$ in the simulations). These changes were meant to reflect a situation involving large changes in the productive capacity in some stocks and commensurate declines in others (e.g., due to changes in hydrology, geomorphology, or life history characteristics) such that the overall production of the system remains unchanged but relative population contributions to production does change. The magnitude of change we considered under this scenario is biologically plausible and is within the ranges of changes in productivity and capacity seen in other salmon systems, albeit at coarser spatial scales (Hilborn et al. 2003; Peterman and Dorner 2012; Dorner et al. 2017).

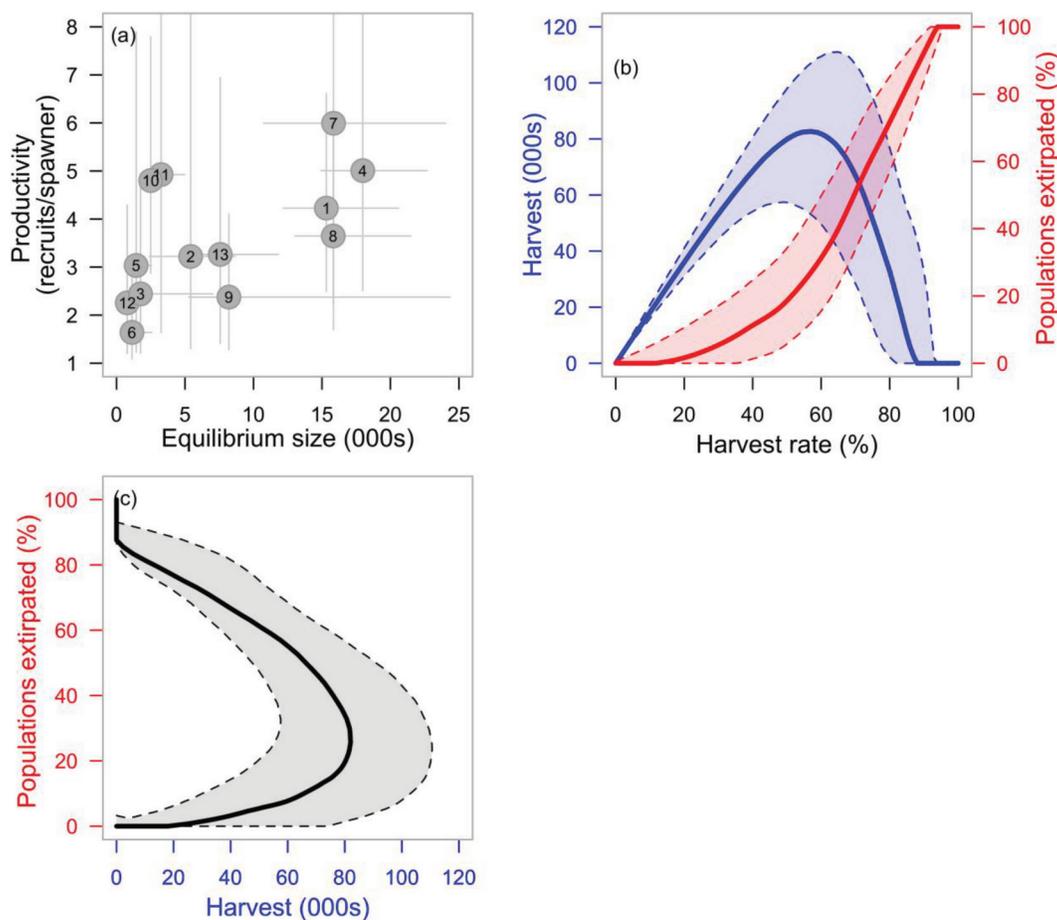
Results

Population diversity

We found clear evidence of heterogeneity in productivity and carrying capacity across the Kuskokwim Chinook populations for which there were data (Fig. 3a). Kuskokwim Chinook populations ranged in equilibrium size from approximately 1000 to 18 000 spawners (x axis of Fig. 3a) and in productivity from 1.65 to 6 recruits-per-spawner (median posterior estimates, y axis of Fig. 3a). There was a weak tendency for larger populations to be more productive; however, no strong spatial patterns in productivity and carrying capacity were found (Figs. 1 and 3a). This population diversity resulted in the equilibrium trade-off between harvest and protection of population diversity depicted in Fig. 3b, which illustrates that the relatively high harvest rates that can be sustained by the most productive populations come at the cost of increased risk of over-exploitation for those that were found to be less productive.

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Fig. 3. Kuskokwim Chinook population diversity and trade-offs with harvest. (a) Posterior distributions of intrinsic productivity (α – recruits per spawner at small population size) for individual population along with corresponding estimates of equilibrium population size. (b) Predicted basin-wide equilibrium yield across a range of fixed harvest rates and corresponding risks to population diversity. Overall yield from the system is predicted to be maximized at a harvest rate of $\sim 50\%$, but this comes at the cost of putting $\sim 20\%$ of the populations at risk of extirpation. (c) Relationship between basin-wide equilibrium yield and risks to population diversity, illustrating asymmetry in the relationship. In all panels, uncertainty around median values is depicted with 10th and 90th percentiles. [Colour online.]



Performance of alternative harvest policies and trade-offs among objectives

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

There was strong asymmetry in trade-offs between harvest and biological or social objectives, with the strength of the asymmetry in trade-offs dependent on the harvest policy that was applied. The harvest policy that sought to maximize mixed-stock harvest (MSY policy) did so at the costs of increased interannual variation in harvest, reduced chances of meeting tributary spawner goals, and elevated risk of weak stock extirpation (Figs. 4 and 5). In contrast, relative to the MSY policy, the fixed harvest approach

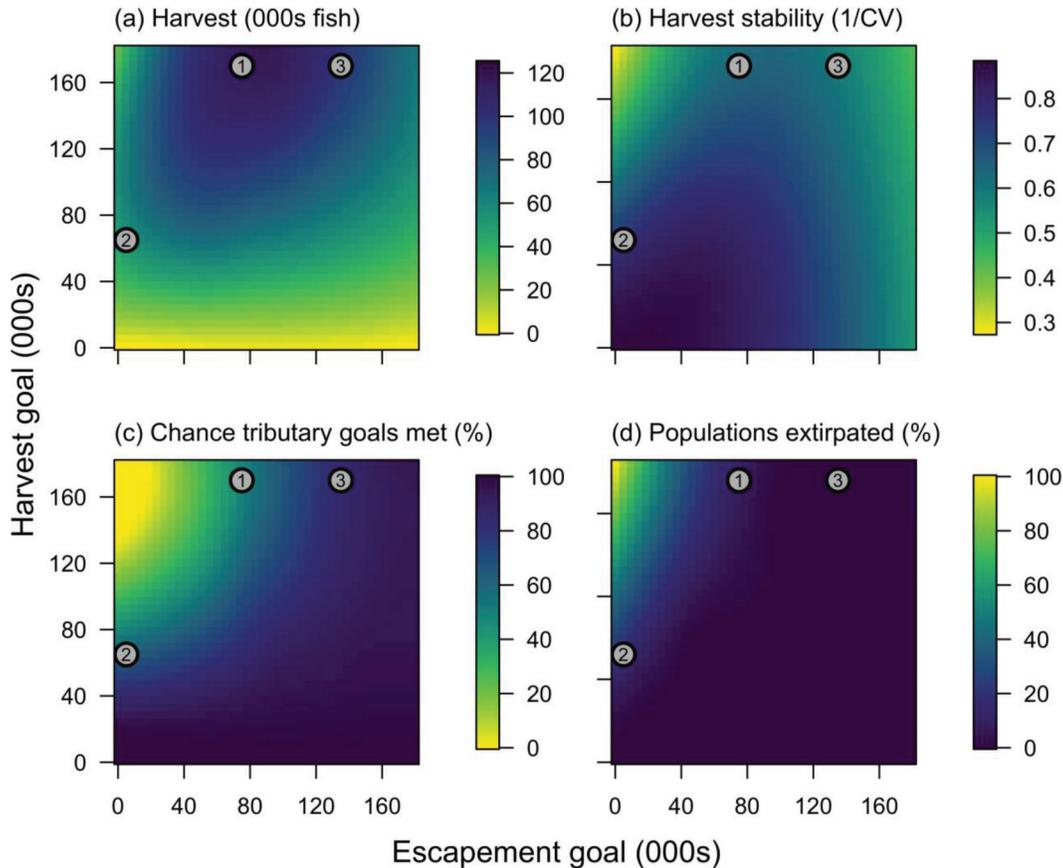
(subsistence policy) increased interannual stability in harvest by 22%, increased the chances of meeting tributary spawner goals by 84%, and reduced median extirpation risk (Figs. 3 and 4). This came at the cost, on average, of a 46% reduction in realized overall harvest. The harvest policy that sought to minimize the risk of driving weak stocks to extirpation (conservation policy) did so at the cost of a 20% reduction in harvests and 16% reduction in interannual stability in harvests, but with the benefit of increasing the chances of ensuring equitable access to Chinook salmon (i.e., meeting tributary goals) by 84% (from 46% to 85%).

Though there was large uncertainty in the predicted performance of alternative policies, by propagating uncertainty through the closed-loop simulations, we can interpret fishery and biological outcomes probabilistically. For example, we found that there was a 41% chance that at least 90% of tributary-level spawner goals would be met if conservation policy was chosen compared with a 1% or 35% chance if the MSY or subsistence policies were chosen, respectively. Alternatively, from a protection of biocomplexity perspective, there was less than a 20% chance of causing at least one population to become extirpated under the conservation policy, but a 70% or 24% chance if the MSY or subsistence policies were chosen, respectively.

Effects of alternative states of nature

The performance of alternative policies, and their resulting trade-offs, were sensitive to the underlying drivers of recruitment vari-

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



ation (Fig. 6). When recruitment dynamics were driven by a time-varying Beverton–Holt-type relationship, absolute harvest and to a lesser extent interannual variation in harvest were predicted to be higher relative to the alternative spawner–recruitment dynamic scenarios (Fig. 7; compare green bars to grey and blue bars in online version), and the magnitude of reduction in harvest between harvest policies was smaller (4% versus 20%–27%). However, the chances of meeting tributary goals and extirpation risk were generally similar across all three spawner–recruitment dynamic scenarios, and so the resulting asymmetry in harvest–diversity trade-offs was greater; a 4% reduction in predicted harvest from the MSY to conservation policies was predicted to result in a 80% increase in the chances of meeting tributary goals, compared with 20% and 84%, respectively, under the stationary Ricker scenario.

We also found that the strength of trade-offs between harvest and stability, equity, or extirpation risk were mediated by temporal changes in population diversity. When there were large shifts in population productivity and size over time (Fig. 6), we found that similar magnitudes of reductions in harvest must be sacrificed to protect diversity (~26%) but that commensurate increases in equity in access to Chinook were larger than when there were not regime shifts in the system (120% versus 84%; Fig. 7; compare change from policy 1 to policy 3 for both grey and blue bars). In addition, we found that regardless of the harvest policy overall,

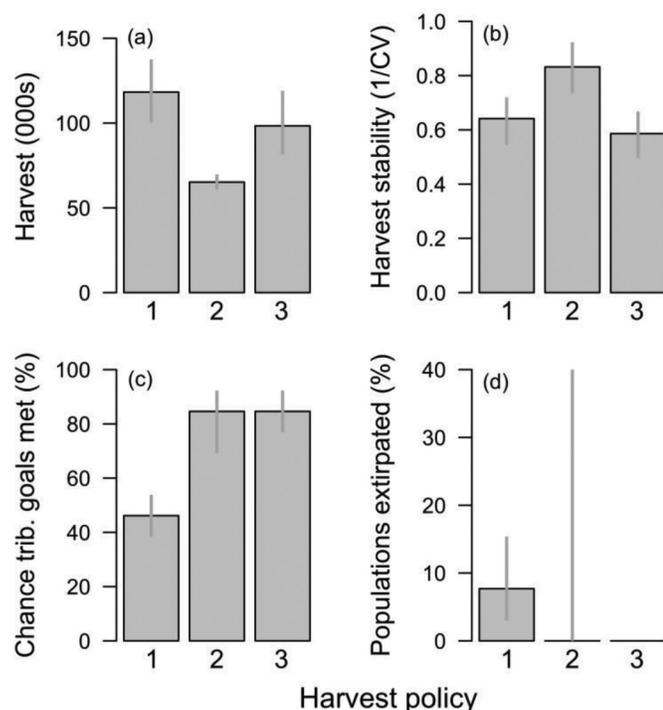
extirpation risk was elevated where there were pronounced regime shifts in the system.

Discussion

Four key findings emerged from our analyses of Kuskokwim River Chinook population diversity and harvest policy performance. First, we found clear evidence of population diversity where productivity and carrying capacity vary by as much as 3-fold and 18-fold among populations, respectively. This diversity gave rise to a clear trade-off between mixed-stock harvest and population diversity conservation where high harvest rates, which can be sustained by the most productive populations, can come at the cost of overfishing less productive populations. Second, this trade-off was strongly asymmetric, whereby giving up relatively small amounts of harvest resulted in both large reductions in risk to weak stocks and large gains in spatial equity among subsistence communities in access to the Chinook. For example, shifting from a policy focused on mixed-stock yield (MSY policy) to one that considered risk to population diversity (conservation policy) resulted in a 20% reduction in average annual mixed-stock harvest, an 84% increase in the probability of equitable access to the fishery, and a near complete elimination of risk of driving weak populations to extinction.

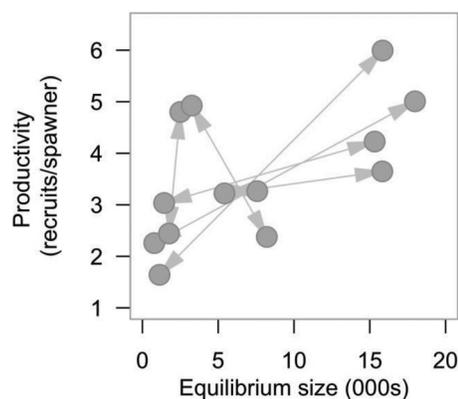
Third, we found that the performance of harvest policies, and their resulting trade-offs, were sensitive to the true underlying

Fig. 5. Trade-offs among harvest policies. Predicted ability of three alternative harvest policies (see Fig. 4 and Table 3) to meet fishery (a: harvest and b: harvest stability), equity (c: proportion of population tributaries with spawner abundances that exceeded a tributary-specific spawner goals), and conservation (d: proportion of populations extirpated) objectives. 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). Policies 1, 2, and 3 refer to the MSY, subsistence, and conservation harvest policies, respectively. Contrasting policies within and among panels illustrate trade-offs in the system among harvest, equity, and conservation, as well as asymmetry in them, but it is important to recognize that these policies are only three points in the policy space as defined by this analysis.



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

Fig. 6. Time-varying population diversity. Example of simulated changes (arrows) in the productivity and size of individual Chinook populations beginning 20 years into the 50-year forward simulations. Each point is the median estimated productivity and equilibrium size for a given population as estimated from the multistock state-space spawner–recruit model presented in Staton et al. (in press). The arrows indicate how a given population was simulated to change under this scenario, where populations connected by arrows “switch positions” over the course of the simulation.

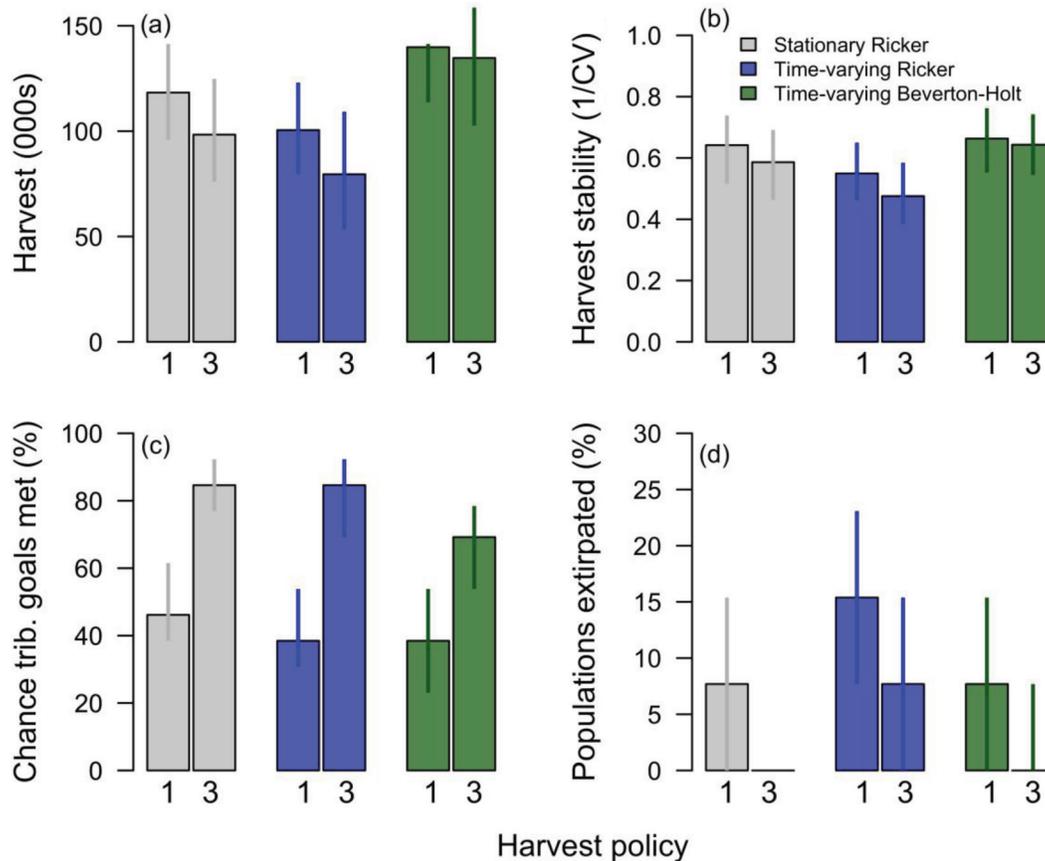


Fourth, we found that it is possible for the strength of these harvest–population diversity trade-offs to be mediated by external changes in the environment. When the environment drives pronounced shifts over time in the size and productivity of populations (e.g., a regime shift), giving up a specific amount of harvest results in larger gains in spatial equity in access to salmon for subsistence needs relative to scenarios where there is no regime shift. These predicted benefits are dependent on the magnitude of change in population size and productivity over time. While the magnitude of change we considered was within the ranges of changes in productivity and carrying capacity seen in other salmon systems (Hilborn et al. 2003; Peterman and Dorner 2012; Dorner et al. 2017), they were of a large magnitude and occurred over a short (10-year) time period (Fig. 6). As a result, our findings might be appropriately considered an upper bound to the potential benefits of protecting population diversity within the system from a harvest–diversity trade-off perspective.

As is inevitable with any analysis of a complex socioecological system, we made a number of simplifying assumptions. First, because of incomplete monitoring coverage, we were only able to model the dynamics of Chinook populations that comprise approximately half of the production from the system (Fig. 1). This implicitly assumes that monitored stocks are a representative sample of all populations with respect to population characteristics and time series properties and that the total proportion of production represented by these populations will not change over time. If this assumption is severely violated, then our inference about trade-offs and aggregate yield may be biased. For example, if only the most productive populations are monitored, then we would have underestimated risks to population diversity. Nonetheless, given that the populations with data are distributed across the basin (Fig. 1) and range widely in both their productivity and size, we suspect that we have captured the general bounds of the system. It should also be noted that the weakest (least productive) spawning populations in the Kuskokwim Basin may have been extirpated early in the development of the fishery for this river and are thus absent from our dataset.

Second, our simulations treated each population as a closed spawning population because we did not consider the effects of straying between and within basins. Straying is a fundamental characteristic of salmon and clearly an important contributor to

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



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

Lastly, our closed-loop simulations are empirically parameterized from a multipopulation spawner–recruit analysis (Staton et al., in press) that assumes all populations in the system have historically been equally vulnerable to harvest, which was also made in our analysis. While the vast majority of harvest has

historically occurred in the lower river near the community of Bethel, differences in run timing and the timing of the fishery (typically front-loaded due to drying weather) are likely to have led to headwater fish being more vulnerable to harvest than lower river populations (Hamazaki 2008). The key findings from our closed-loop simulations are robust to this assumption (Fig. S1¹), but modelling population variation in run timing and the timing of fisheries are logical extensions to the work we present here.

We chose three simple and contrasting harvest policies to illustrate their predicted performance against Chinook fishery and population diversity objectives in the Kuskokwim Basin. While the contrasting policies were not intended to exactly match the current approach to management, there are some general insights that emerge from our analysis that are of relevance for management of the Chinook fishery moving forward. We find that a relatively low overall harvest rate is more important than a strict, high escapement goal, with respect to minimizing extirpation risk. This is because our simulations suggest that subsistence needs, and spatial equity in access to fish, can be met with relatively low risk to population diversity even when the escapement goal is very low. However, as harvest goals increase above those required to meet subsistence needs, the importance of an escapement goal becomes more pronounced to the point where if target harvest is at or near its historical maximum (~150 000), managing for the upper end of the basin-scale escapement goal derived from optimal yield profiles (e.g., ~130 000 fish; Hamazaki et al. 2012) is necessary and adequate to minimize extirpation risk. An obvious

next step in the Kuskokwim system would be to implement a management strategy evaluation that incorporates short-term within-season dynamics and decision making, population differences in run-timing (Smith and Liller 2017), and harvest vulnerability (Hamazaki 2008) with the formal engagement of decision makers and stakeholders in the process (e.g., Cunningham et al. 2019).

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

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

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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 (eqs. 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 gov-

erned by Beverton–Holt dynamics with cyclical variation in population productivity (eq. 6 in main text; hereinafter 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 relationship² generated by eq. 6 with $f = 14$, $A = 0.6$, and $\delta = 1.4$. To simulate time-varying Beverton–Holt spawner–recruitment relationships with apparent overcompensation that approximates that observed in the Kuskokwim system, 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 Kuskokwim 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., $\ln(\text{recruits/spawners}) \sim \text{spawners}$) and compared the estimates of intrinsic productivity (α) and magnitude of density dependence (β) from the model fit with the true values. We did this 1000 times across 20 values of f (1–20), three levels of A (0.2, 0.4, 0.6), and 20 values of δ (0.2–2).

The results of these simulations (Fig. A2) 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 f , A , and 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 Kuskokwim relationship. To do this we simulated 1000 spawner–recruit datasets under the BH_cycl formulation with f , A , and δ equal to 14, 0.6, and 1.4, respectively (Fig. A3a 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 Kuskokwim 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 Kuskokwim system (Fig. A3b).

²Code to reproduce these examples is available at <https://github.com/brendanmichaelconnors/Kusko-harvest-diversity-tradeoffs>.

Fig. A1. Spawner–recruitment data simulated by a Beverton–Holt-type relationship with time-varying productivity (colours). 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. [Colour online.]

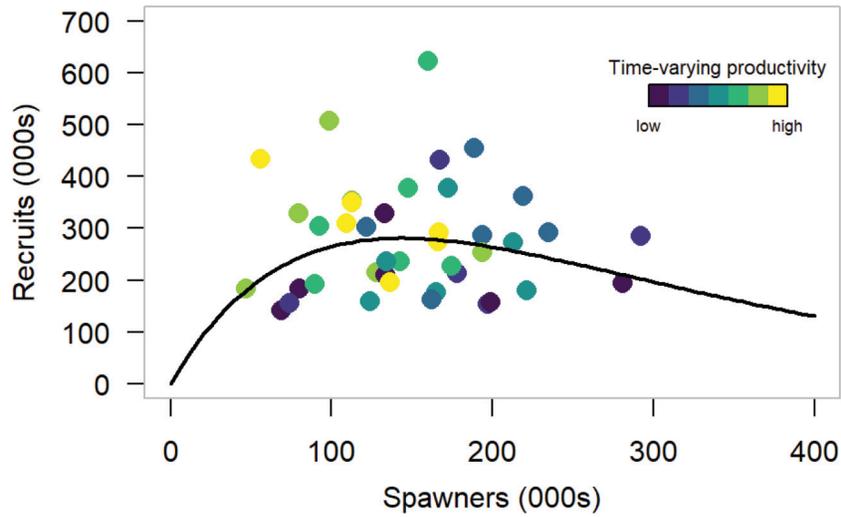
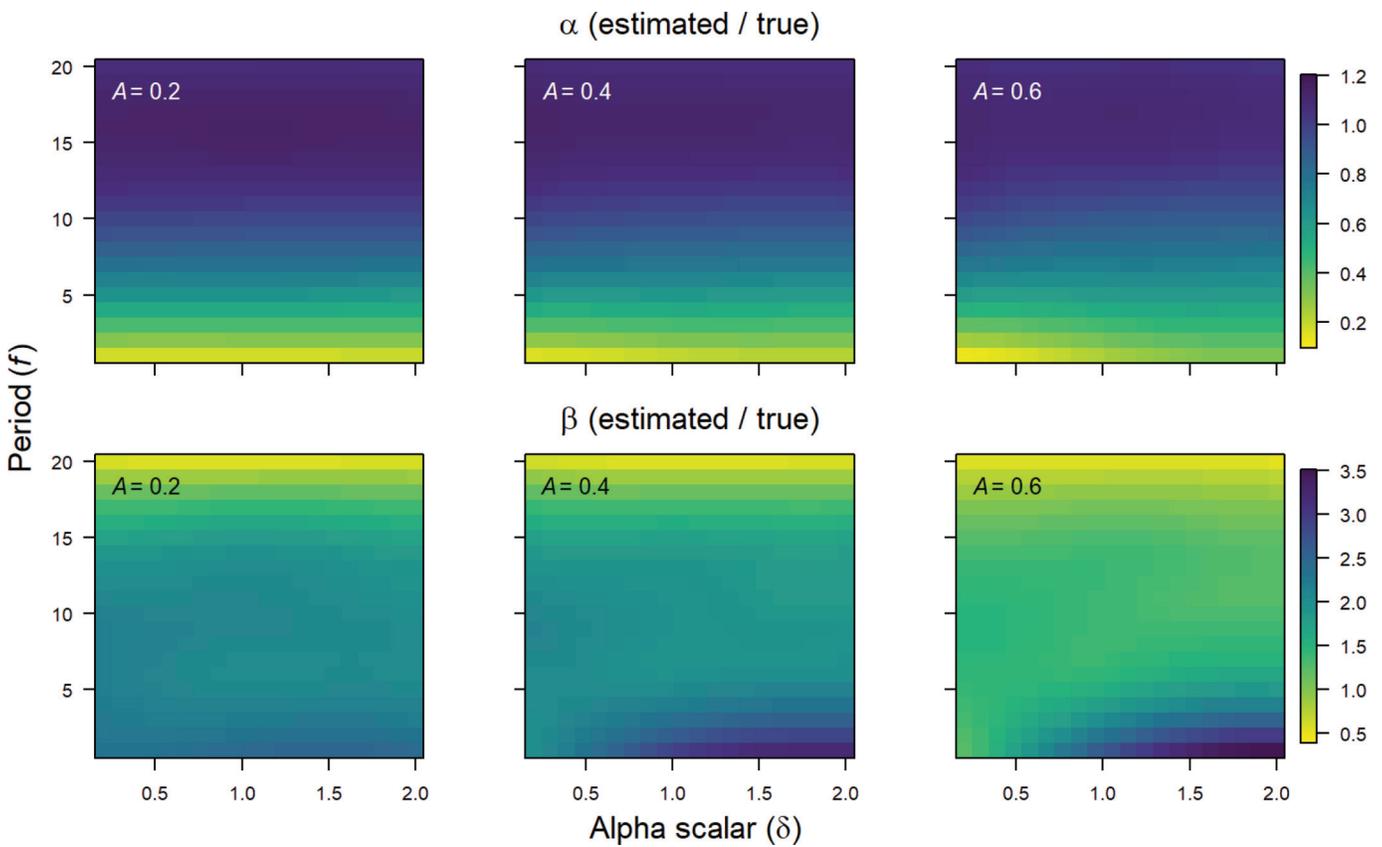
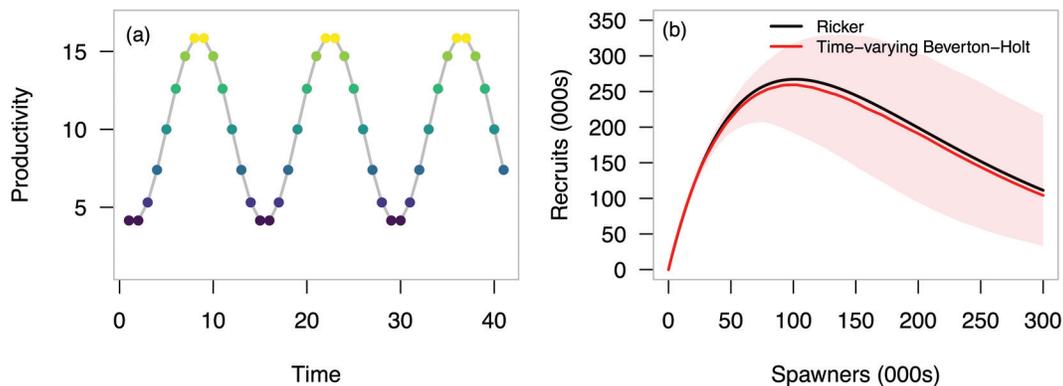


Fig. A2. Effects of f (y axis), A (panels), and alpha scalar (x axis) on model-based (Ricker) estimates of intrinsic productivity (top row) and magnitude of density dependence (bottom row) fit to simulated spawner–recruit data from a model with time-varying Beverton–Holt relationship. The z axis is the median magnitude of proportional error (i.e., estimated/true) across 1000 trials for each combination of f , A , and alpha scalar. [Colour online.]



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Fig. A3. (a) Time-varying productivity and (b) observed (Ricker, black line) spawner–recruitment relationship in the Kuskokwim and simulated relationship (median and 95th percentiles) assuming a Beverton–Holt spawner–recruitment relationship with time-varying productivity. [Colour online.]



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