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An age-structured state-space stock–recruit model for Pacific salmon (*Oncorhynchus* spp.)

Steven J. Fleischman, Matthew J. Catalano, Robert A. Clark, and David R. Bernard

Abstract: We describe an age-structured state-space model for stock–recruit analysis of Pacific salmon data. The model allows for incorporation of process variation in stock productivity, recruitment, and maturation schedules, as well as observation error in run abundance, harvest, and age composition. Explicit consideration of age structure allows for realistic depiction of system dynamics and sample design, more complete use of recent data, and forecasts that consider sibling relationships. A Bayesian framework is adopted, implemented with Markov chain Monte Carlo methods, which provides an enhanced ability to incorporate auxiliary information, convenient and rigorous consideration of measurement error and missing data, and a more complete assessment of uncertainty. We fit the model to annual upstream weir counts, commercial and recreational harvest estimates, and age composition data from Chinook salmon (*Oncorhynchus tshawytscha*) in Karluk River, Alaska. For the case study, the model is configured with a Ricker stock–recruit relationship, autoregressive lag-1 productivity, and Dirichlet age-at-maturity. Details of alternate configurations are also described. We introduce the optimal yield probability profile as an objective tool for informing the selection of escapement goals based on yield considerations and describe alternative versions useful for addressing other management questions.

Résumé : Nous décrivons un modèle d'espace d'états structuré selon l'âge pour l'analyse stock–recrutement de données sur le saumon du Pacifique. Le modèle permet l'intégration de la variation des processus touchant à la productivité des stocks, au recrutement et au moment de l'atteinte de la maturité, ainsi que des erreurs d'observation concernant l'abondance de la montaison, les prises et la composition selon l'âge. La prise en compte explicite de la structure selon l'âge permet une détermination de la dynamique du système et d'un plan d'échantillonnage réaliste, l'utilisation plus exhaustive de données récentes et des prévisions qui tiennent compte des liens de fratrie. Un cadre bayésien est adopté et mis en application avec des méthodes de Monte Carlo par chaîne de Markov. Cette approche permet une capacité accrue d'intégration d'information connexe, la prise en compte pratique et rigoureuse des erreurs de mesure et des données manquantes et une évaluation plus complète de l'incertitude. Nous avons ajusté le modèle à des données de dénombrement annuel en fascine en amont, à des estimations des prises commerciales et récréatives et à des données de composition par âge pour le saumon quinnat (*Oncorhynchus tshawytscha*) de la rivière Karluk, en Alaska. Pour l'étude de cas, la configuration du modèle comprend une relation stock–recrutement de Ricker, un modèle de productivité autorégressive de retard 1 et une courbe de maturité à l'âge de type Dirichlet. Les détails d'autres configurations sont également présentés. Nous introduisons le profil de probabilité du rendement optimal comme outil objectif pour éclairer le choix des objectifs d'échappées à la lumière de considérations relatives au rendement et décrivons d'autres versions utiles pour aborder d'autres questions de gestion. [Traduit par la Rédaction]

Introduction

Pacific salmon (*Oncorhynchus* spp.) spawn only once and are harvested primarily as adults. Therefore, the essentials of their population dynamics can be almost entirely described by the stock–recruitment (SR) relationship (Quinn and Deriso 1999). Because they are anadromous and exhibit homing behavior, Pacific salmon are often subjected to targeted fishing mortality as they approach and enter their natal streams. Management of Pacific salmon fisheries can thus benefit greatly from information about the SR relationship, in the form of management reference points derived to satisfy maximum yield or other criteria (Hilborn and Walters 1992).

Reference points for Pacific salmon fisheries are commonly derived under the assumption of a stationary SR relationship, with parameters estimated from linearized transformations of Ricker or, less commonly, Beverton–Holt models (Quinn and Deriso 1999). Such methods are convenient and can be effective (Clark

et al. 2009); however, they are subject to important shortcomings. For instance, the assumption of a stationary, time-invariant SR relationship is questionable, especially for exploited populations (Walters 1987). Serially correlated variation in productivity is well documented, manifested as decadal-scale swings in abundance (Adkison et al. 1996; Peterman et al. 2003; Walters 1987), which can have large economic and social consequences (Bue et al. 2008). Furthermore, the traditional analysis approach assumes that spawner abundance is an independent variable, when in fact it is linked to previous recruitment. Failure to consider time-varying productivity and this “R–S linkage” can lead to biased estimates of SR parameters (“time series bias”; Walters 1985) and poorly performing reference points, especially for stocks with low productivity (Korman et al. 1995). Another potential shortcoming of conventional SR analysis is errors-in-variables bias (Kehler et al. 2002; Kope 2006; Walters and Ludwig 1981), which can arise when spawning escapement is measured with error. Caputi (1988) found that time-series bias and errors-in-variables bias are not additive

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and must be considered simultaneously. Finally, Pacific salmon (of all species except pink salmon (*Oncorhynchus gorbuscha*)) return at multiple ages to spawn, and the maturity schedule differs among cohorts. Traditionally, the complexity introduced by age structure is not fully considered in the SR analysis, leading to an oversimplified model that cannot accurately depict measurement error and missing data.

These shortcomings stem largely from failure to acknowledge the multiple sources of variation and time-dependent linkage of Pacific salmon life history data. State-space models offer a robust, flexible framework for characterizing uncertain temporal measurements of dynamic natural systems, including fisheries (Millar and Meyer 2000; Peterman et al. 2000; Rivot et al. 2004). The state-space approach simultaneously models temporal process variation and observation error. Process variation (often called process error) is incorporated by modeling dynamic quantities, such as stock size or productivity, as unobserved “states” that are linked in time and subject to stochastic fluctuation. Observation error is incorporated by specifying the relationship of observable data to the unknown states. Explicit specification of co-occurring process variation and observation error permit realistic depiction of system dynamics and sample design. State-space models can be fit using either a Kalman filter or Bayesian approach. For complex nonlinear models, the Bayesian approach is preferable because of the restrictive assumptions of the Kalman filter (Millar and Meyer 2000). Markov chain Monte Carlo (MCMC) methods (Gelman et al. 2004), used for sampling from the posterior distribution of such Bayesian models, facilitate a clear depiction of parameter uncertainty and provide a basis for prospective simulations that account for uncertainty.

Bayesian state-space models have been successfully developed for Pacific salmon stocks; however, few age-structured models that incorporate measurement error and time-varying productivity have been published that are suitable for widespread application. Meyer and Millar (2000) fitted a Bayesian state-space model with measurement error and R-S linkage to pink salmon data, and Su and Peterman (2012) conducted extensive simulations using a similar model. These models assumed constant age of maturity and did not accommodate time-varying productivity. Peterman et al. (2003) used Kalman filter methodology to fit autoregressive and random walk productivity models to sockeye salmon (*Oncorhynchus nerka*) data, and Liermann et al. (2010) fitted a Bayesian hierarchical model with random walk productivity to SR data from 26 Chinook salmon (*Oncorhynchus tshawytscha*) stocks; however, these models were not age-structured and did not incorporate R-S linkage. Savereide and Quinn (2004) and Lessard et al. (2008) fitted age-structured models, in a non-Bayesian framework, to Chinook and sockeye salmon data, respectively. Newman and Lindley (2006) developed a Bayesian age- and sex-structured life history model for winter-run Chinook salmon in the Sacramento River. The models of Lessard et al. (2008) and Newman and Lindley (2006) estimated separate survival and maturation processes and required data on juvenile abundance that are seldom available. Newman and Lindley (2006) employed a variation of sequential importance sampling that must be manually programmed and thus would be difficult to adapt to stocks with other data configurations. There remains a need for a basic representation of an age-structured Pacific salmon population in a Bayesian state-space framework.

In this paper, we describe an improved method of selecting escapement goals and other harvest policy parameters for Pacific salmon stocks for which escapement and age-specific return data are available. We formulate a state-space model that explicitly allows for serial correlation in productivity as an autoregressive (AR) or random walk (RW) process and variable age at maturity as a Dirichlet process. The age-structured state-space framework allows for proper representation of process variation and observation error, permits full utilization of data, and provides forecasts

that incorporate multiple sources of uncertainty. A Bayesian statistical framework is adopted, implemented with MCMC methods. The analysis was conducted with the noncommercial software WinBUGS (version 1.4.3; Spiegelhalter et al. 1999), which provides a powerful, convenient modeling environment and exceptional versatility in model specification. We also introduce optimal yield probability profiles, an objective tool for quantifying uncertainty and informing the choice of an escapement goal based on sustained yield considerations. For illustration, the proposed model and methodology are applied to 25 years of weir counts, harvest estimates, and age composition data from Karluk River Chinook salmon on Kodiak Island in western Alaska. Pacific salmon stocks in Alaska are managed with an escapement goal policy, so we focus primarily on estimation of optimal escapement reference points. However, we also provide details on how the model and associated methods can be extended and adapted to other harvest policies and data configurations. For the Karluk case study, we calculate retrospective estimates of escapement and harvest reference points to illustrate potential trade-offs between harvest policies based on cumulative versus recent data.

Methods

The process variation component of the state-space model specifies productivity and age at maturity by cohort, identified by the “brood year” of the spawning event. Salmon produced from a single brood year return to their natal stream during multiple calendar years. The observation error component operates in calendar year steps, in the form of annual harvest surveys, weir counts, and age composition sampling. Observed annual quantities from these programs make it possible to reconstruct the returns from individual spawning events, indexed by brood year, from components staggered across multiple calendar years (Fig. 1). In this paper, we use the term “return” to describe the total production (recruitment) of fish from a single cohort, or brood year. The term “run” describes all fish, of multiple ages and from multiple brood years, that arrive back at their natal river during a particular calendar year (Fig. 1). The model described below is configured for Karluk River Chinook salmon, which mature and return to spawn at ages 3 to 7, and are counted at a weir as they ascend the river. Karluk River Chinook salmon are managed under the state of Alaska’s escapement goal policy (Clark et al. 2009), in which Pacific salmon goals are reviewed and considered for revision every 3 years.

Process model

Returns R of Chinook salmon from the 1976–2008 cohorts were treated as unobserved states, modeled as a function of spawning escapement S in year y using a Ricker (1954) stock–recruit function with AR lognormal process error:

$$(1) \quad \ln(R_y) = \ln(S_y) + \ln(\alpha) - \beta S_y + \phi \omega_{y-1} + \varepsilon_y$$

where α is the productivity parameter and β the (inverse) capacity parameter of the Ricker stock–recruit relationship, ϕ is the AR lag-1 coefficient, ω_y is the model residual,

$$(2) \quad \omega_y = \ln(R_y) - \ln(S_y) - \ln(\alpha) + \beta S_y = \phi \omega_{y-1} + \varepsilon_y$$

and the $\{\varepsilon_y\}$ are independent normally distributed process errors with standard deviation σ_R .

The Ricker model is, by far, the most common choice for Pacific salmon SR analyses, probably because (i) it can accommodate overcompensation, which is evident in many Pacific salmon data sets, and (ii) it is conservative with respect to optimal escapement levels (for fixed values of the productivity parameter and carrying capacity, S_{MSY} is always higher under the assumption of a Ricker

Fig. 1. Abundance of adults by year and age, the diagonal reconstruction of brood year returns, and key notation for age-structured stock-recruitment model, as described in the text.

Year	Esc	Annual abundance (run) by age $N_{y,a}$					Run	Return
y	S_y	3	4	5	6	7	$N_y = \sum_{a=3}^7 N_{y,a}$	$R_t = \sum_{a=3}^7 N_{y+a,a}$
1	S_1	$N_{1,3}$	$N_{1,4}$	$N_{1,5}$	$N_{1,6}$	$N_{1,7}$	N_1	R_1
2	S_2	$N_{2,3}$	$N_{2,4}$	$N_{2,5}$	$N_{2,6}$	$N_{2,7}$	N_2	R_2
3	S_3	$N_{3,3}$	$N_{3,4}$	$N_{3,5}$	$N_{3,6}$	$N_{3,7}$	N_3	R_3
4	S_4	$N_{4,3}$	$N_{4,4}$	$N_{4,5}$	$N_{4,6}$	$N_{4,7}$	N_4	R_4
5	S_5	$N_{5,3}$	$N_{5,4}$	$N_{5,5}$	$N_{5,6}$	$N_{5,7}$	N_5	R_5
6	S_6	$N_{6,3}$	$N_{6,4}$	$N_{6,5}$	$N_{6,6}$	$N_{6,7}$	N_6	R_6
7	S_7	$N_{7,3}$	$N_{7,4}$	$N_{7,5}$	$N_{7,6}$	$N_{7,7}$	N_7	R_7
8	S_8	$N_{8,3}$	$N_{8,4}$	$N_{8,5}$	$N_{8,6}$	$N_{8,7}$	N_8	R_8
9	S_9	$N_{9,3}$	$N_{9,4}$	$N_{9,5}$	$N_{9,6}$	$N_{9,7}$	N_9	R_9
10	S_{10}	$N_{10,3}$	$N_{10,4}$	$N_{10,5}$	$N_{10,6}$	$N_{10,7}$	N_{10}	R_{10}

model than under a Beverton–Holt model). We allowed productivity, rather than capacity, to vary because it is the more plausible explanation of serially correlated production residuals (Peterman et al 2000). We used an AR(1) model because Noakes et al. (1987) concluded that simple ARMA(p, q) models ($p \leq 1$, $q \leq 1$) were sufficient to explain the variation in stock-recruit model residuals, and we have found that an AR(1) model is almost always sufficient for Pacific salmon. We confirmed the choice of an AR(1) for the Karluk data by inspecting autocorrelation function and partial autocorrelation function plots of model residuals (not shown). A summary of criteria for identifying an underlying ARMA(p, q) process in time series data can be found in Pankratz (1983).

The seven initial returns R_{1969} – R_{1975} , which were not linked to previous monitored escapements via the SR relationship, were modeled as draws from a common lognormal distribution with parameters $\ln(R_0)$ and σ_{R0} .

The abundance (number returning to spawn, $N_{y,a}$) of age a Chinook salmon in year y was the product of the total return from brood year $y - a$ and the proportion of mature fish from cohort $y - a$ returning at age a :

$$(3) \quad N_{y,a} = R_{y-a} p_{y-a,a}$$

The vectors of age-at-maturity proportions ($p_{y,a}: a = 3:7$) were drawn from a common Dirichlet distribution, implemented by generating independent gamma variates ($g_{y,a}: a = 3:7$) and dividing each by their sum (Evans et al. 1993):

$$(4) \quad p_{y,a} = \frac{g_{y,a}}{\sum_a g_{y,a}}$$

$$(5) \quad g_{y,a} \sim \text{gamma}(\text{shape} = \gamma_a, \text{inverse scale} = 1)$$

where the gamma distribution is parameterized following Gelman et al (2004), and the $\{\gamma_a\}$ are age-specific hyperparameters of the Dirichlet distribution that determine the expected proportions $\{\pi_a\}$ returning at age:

$$(6) \quad \pi_a = \frac{\gamma_a}{\sum_a \gamma_a}$$

The sum of the $\{\gamma_a\}$ can be interpreted as the inverse dispersion (D) of the Dirichlet distribution. This parameter governs the variability of the age proportion vectors across cohorts, with smaller D leading to more variability and vice versa. The inverse scale parameter of the gamma distribution in eq. 5 acts as a scaling factor and has no effect on the mean or dispersion of the age proportions, although it can have important effects on MCMC sampling (online Supplement¹). Similar fisheries applications of the Dirichlet distribution are described by Høst et al. (2002) and Rivot et al. (2004).

The total run abundance in calendar year y was the sum of abundance-at-age across all ages:

$$(7) \quad N_y = \sum_a N_{y,a}$$

The number of Chinook salmon reaching the weir each calendar year (W_y) was the difference between the total run abundance and the harvest (H_{By}) below the weir:

$$(8) \quad W_y = N_y - H_{By}$$

We assume no natural mortality between the (terminal) harvest area and the spawning grounds because observed harvest occurs

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2012-0112>.

near the river mouth (commercial fishery) or inriver (recreational fishery). Spawning escapement (S_y) was the difference between the number of salmon reaching the weir and the harvest (H_{Ay}) above the weir:

$$(9) \quad S_y = W_y - H_{Ay}$$

Harvests H_{By} and H_{Ay} were modeled as the products of abundance (N_y or W_y) and harvest rates ($0 < U_{By} < 1$; $0 < U_{Ay} < 1$), which serves to constrain W_y and S_y to be non-negative:

$$(10) \quad H_{By} = N_y U_{By}$$

$$(11) \quad H_{Ay} = W_y U_{Ay}$$

From a state-space model perspective, eqs. 1–11 represent the “system” equations, and the data relationships in the following section constitute the “observation” equations of this model.

Data and observation model

Returning salmon were counted at a weir in the lower Karluk River (4 km from the mouth) from 1976 to 2010. Estimates of harvest above and below the weir were also available from 1976 to 2010. Fish passing the weir were sampled for age composition from 1993 to 2010.

With one exception (1998, see below), weir-based estimates of passage were assumed to be precise. Because no quantitative assessments of observation error due to sampling were available, the analysis was run for three values of weir sampling error coefficient of variation $CV(W_y)$ (0.025, 0.05, and 0.075) that bracketed the range of plausible values. Because the three values of CV yielded results that were only negligibly different, only the $CV = 0.05$ results are presented. In 1998, the weir was inoperable for 17 days in midseason because of high water. Weir counts in that year were expanded based on historical run-timing data (e.g., Schmidt and Polum 2011), resulting in a CV of 0.19 for the 1998 estimate of inriver abundance. Observed weir counts (w_y) were assumed to be lognormally distributed with parameters $\ln(W_y)$ and σ_{W_y} . CV s were converted to lognormal variance parameters as follows (Evans et al. 1993):

$$(12) \quad \sigma_{W_y}^2 = \ln[CV^2(w_y) + 1]$$

Annual harvests below the weir (H_{By}) were taken by recreational (mean harvest rate 7%), commercial (also 7%), and subsistence fisheries (0.1%). Total annual harvest rate averaged 15%, ranging from 0% to 51%. Recreational harvests were estimated by mail survey, commercial harvests were tallied from fish sale receipts, and subsistence harvests (less than 1% of total harvest) were estimated from postseason interviews. Standard errors were available for mail survey estimates (CV s of 0.14 to 0.79; Jennings et al. 2010). We assumed very large observation errors for the (very small) subsistence harvests ($CV = 1.0$) and small errors for the commercial harvests ($CV = 0.05$). Again, CV s of 0.025 and 0.075 for the commercial harvests did not produce discernibly different results. Squared standard errors were summed across the three fisheries, then divided by the squared summed harvest estimates to obtain annual (squared) observation error CV s. Observed harvest below the weir (h_{By} , sum of recreational, commercial, and subsistence harvests, as described above) was assumed to be lognormally distributed with parameters $\ln(H_{By})$ and σ_{By} . The mail survey estimates of recreational harvest contributed the largest component of observation error for harvest below the weir. Annual harvests above the weir (H_{Ay}) consisted solely of recreational harvest, estimated by mail survey (Jennings et al. 2010). Observed harvest above the weir (h_{Ay}) was assumed lognormally distributed with

parameters $\ln(H_{Ay})$ and σ_{Ay} . Observation error variances σ_{Ay}^2 and σ_{By}^2 were obtained from their respective CV s using eq. 12.

For this analysis, we assume no unreported harvest of Karluk River Chinook salmon. Commercial fishers are required by law to report all such harvest, whether sold commercially or not. Mail survey estimates of recreational harvest have not been shown to exhibit large bias. Some Karluk River fish are probably caught in other marine fisheries in the region. We believe that unreported harvest is small, but to the degree that it does exist, estimates of productivity would be biased low. The degree of such bias could be investigated by configuring the model with an additional (unobserved) fishery and placing a prior distribution on the associated harvest rate.

Age composition was estimated by counting scale annuli (Mosher 1969) from fish sampled ($n_y = 21$ –373) as they passed the weir, beginning in 1993. Because age composition changes during the course of the annual run (younger fish tend to arrive later in the season), estimates of proportion by age were stratified by 2- to 3-week time periods (Schmidt and Polum 2011). Variance estimates of age proportions from the time-stratified design were used to obtain annual “effective sample sizes” n_{E_y} , where n_{E_y} is the multinomial sample size that would produce uncertainty equivalent to that indicated by the time-stratified analysis (Hulson et al. 2011; McAllister and Ianelli 1997). Surrogate scale age counts x_{ya} were obtained that summed to n_{E_y} rather than to n_y . The x_{ya} were modeled as multinomially distributed, with order parameter n_{E_y} and proportion parameters as follows:

$$(13) \quad q_{y,a} = \frac{N_{y,a}}{\sum_a N_{y,a}}$$

Reference points, optimal yield profile (OYP), time-varying productivity, and forecasts

Reference points were calculated for each individual MCMC sample. S_{MSY} was approximated by

$$(14) \quad S_{MSY} \cong \frac{a}{\beta} \left(0.5 - \frac{0.65a^{1.27}}{8.7 + a^{1.27}} \right)$$

where $a = \ln(\alpha)$ (Peterman et al. 2000). This approximation is more accurate than that of Hilborn (1985) for large values of $\ln(\alpha)$, which is important given the need to calculate it for widely dispersed MCMC samples. Equation 14 cannot be evaluated for $\ln(\alpha) < 0$; therefore, for stocks with positive probability of $\ln(\alpha) < 0$ (e.g., Karluk Chinook salmon), S_{MSY} must be obtained by assuming $\ln(\alpha)$ is non-negative, or by iterative solution of

$$(15) \quad \alpha(1 - \beta S_{MSY}) e^{-\beta S_{MSY}} = 1.$$

Sustained yield at a specified level of S was obtained by subtracting spawning escapement from the return:

$$(16) \quad Y_s = R - S = S e^{\ln(\alpha) - \beta S} - S$$

Other relevant quantities include harvest rate leading to maximum sustained yield, approximated by U_{MSY} (Peterman et al. 2000):

$$(17) \quad U_{MSY} \cong a \left(0.5 - \frac{0.65a^{1.27}}{8.7 + a^{1.27}} \right)$$

again where $a = \ln(\alpha)$; maximum harvest rate

Table 1. Prior distributions for model parameters and alternate priors tested for sensitivity.

Text	BUGS	Prior	Alternate Priors]
$\ln(\alpha)$	lnalpha	$\ln(\alpha) \sim \text{"Uniform"}(\infty, \infty)^a$	$\ln(\alpha) \sim \text{"Uniform"}(0, \infty)^a$
β	beta	$\beta \sim \text{"Uniform"}(0, \infty)^a$	
σ_R	sigma.R	$\sigma_R \sim \text{Uniform}(0, 100)$	$1/\sigma_R^2 \sim \text{gamma}(0.001, 0.001)$
ϕ	phi	$\phi \sim \text{"Uniform"}(-1, 1)^a$	
D	D	$1/\sqrt{D} \sim \text{Uniform}(0, 1)$	$\gamma_a \sim \text{gamma}(0.001, 0.001)^b$
$\pi_1 - \pi_5$	pi[1:5]	$\pi \sim \text{Dirichlet}(0.2, 0.2, 0.2, 0.2, 0.2)$	
ω_0	log.resid.0	$\omega_0 \sim \text{Normal}(0, \sigma_R^2/(1 - \phi^2))$	
$R_1 - R_7$	R[1:7]	$\text{lognormal}(\ln(R_0), \sigma_{R0}^2)$	
$\ln(R_0)$	mean.log.R0	$\ln(R_0) \sim \text{"Uniform"}(\infty, \infty)$	
σ_{R0}	sigma.R0	$1/\sigma_{R0}^2 \sim \text{gamma}(0.001, 0.001)$	$1/\sigma_{R0}^2 \sim \text{gamma}(1.25, 0.4)$

^aWhere "Uniform" is in quotes, a normal distribution with mean 0 and extremely large variance was used. These distributions were designed to be equivalent to uniform distributions over the range of the likelihood. Normal distributions were less likely to cause computational disruptions during MCMC sampling.

^bFor the age-at-maturity submodel, an alternate parameterization was tested. Parameters $\{\gamma_a; a = 3:7\}$ are described in the text (eqs. 5 and 6).

$$(18) \quad U_{\text{MAX}} = 1 - \frac{1}{\alpha}$$

maximum sustained production R

$$(19) \quad \text{MSR} = \frac{\alpha}{\beta e^{(1)}}$$

escapement leading to maximum production

$$(20) \quad S_{\text{MSR}} = \frac{1}{\beta}$$

and equilibrium spawning abundance, where return exactly replaces spawners:

$$(21) \quad S_{\text{EQ}} = \ln(\alpha)/\beta$$

The probability that a given spawning escapement S would produce average yields exceeding $X\%$ of MSY was obtained by calculating Y_S at incremental values of S (0 to 10 000 by 100) for each MCMC sample, then comparing Y_S with $X\%$ of the value of MSY for that sample. The proportion P_Y of samples in which Y_S exceeded $X\%$ of MSY is an estimate of the desired probability, and the plot of P_Y versus S is termed an optimal yield probability profile.

Equations 14–19 and 21 are germane to "median" production R and "median" yield Y . Because we assume that production conditional on spawning abundance has a lognormal distribution, which is skewed, this differs from "mean", or expected production. To obtain inference about expected production and yield, α' must be substituted for α in eqs. 14–19 and 21, where

$$(22) \quad \ln(\alpha') = \ln(\alpha) + \frac{\sigma_R^2}{2(1 - \phi^2)}$$

corrects for the difference between the median and the mean of a lognormal error distribution from an AR(1) process (Pacific Salmon Commission 1999; Parken et al. 2006). The optimal yield plots in Figs. 6 and 7 describe expected yield, obtained using the correction in eq. 22. Because there is no equivalent correction for the random walk model, Fig. S5 in the online supplement¹ is based on median production (no correction applied).

A run size forecast for 2011 was generated by running the model forward an additional year beyond the last year of data (2010). The quantity N_{2011} constituted a posterior prediction of run size 1 year into the future.

Prior distributions and MCMC simulation

Bayesian analyses require that prior probability distributions be specified for all unknowns in the model (Table 1). For this analysis, most prior distributions were designed to be noninformative. One exception was that the prior for β excluded negative values, thus reflecting the biological reality of natural populations. A population with a negative β would grow at an increasing rate as the population expanded, which is not sustainable. The censored prior is also a reference prior for the Ricker model (Millar 2002). For some parameters ($\ln(\alpha)$, β , ϕ), adoption of a uniform prior caused computational disruptions during MCMC sampling in WinBUGS. For these parameters, a normal distribution with mean 0 and extremely large variance was substituted. Because of the large variances, these distributions were flat over the range of the likelihood. We used a uniform distribution for σ_R , following the advice of Su and Peterman (2012). The vector of age proportion hyperparameters $\{\pi_a; a = 3:7\}$ was given a Dirichlet(0.2, 0.2, 0.2, 0.2, 0.2) prior distribution, implemented as a series of nested beta distributions. WinBUGS code for the AR(1) and RW versions of the model can be found in the online supplement¹ to this article.

MCMC methods (Spiegelhalter et al. 1999; Lunn et al. 2000) were used to generate the joint posterior probability distribution of all unknowns in the model. Three Markov chains were initiated. After a 10 000-sample burn-in period was discarded, 80 000 MCMC updates were retained from each chain. Samples were not thinned, because thinning provides no advantage other than to reduce storage requirements. Bayesian credible intervals (CIs, 95%) were obtained from percentiles 2.5 and 97.5 of the marginal posterior distribution. The slowest mixing parameters (those with the highest autocorrelation) were D , σ_{R0} , and $R_{1969} - R_{1975}$. For these quantities, it took 1–3 h to get smooth estimates of posterior densities on a 2.66 GHz personal computer. History plots and Gelman–Rubin convergence diagnostic plots for key parameters are provided in the online supplement¹ to this article.

The analysis was run with alternate priors for some parameters as a means to test for sensitivity (Table 1). For productivity parameter $\ln(\alpha)$, the analysis was re-run with negative values censored (Su and Peterman 2012). As an alternative to the uniform prior on σ_R , we adopted an inverse gamma(0.001, 0.001) distribution for σ_R^2 , which is a commonly used diffuse conjugate prior. A uniform prior for the standard deviation σ_{R0} of (log) initial brood year returns performed poorly, resulting in implausible values of the initial state parameters $R_{1969} - R_{1975}$. Therefore, an informative prior was constructed for σ_{R0} as an alternative. Estimates of the standard deviation of log R were compiled from 10 other Alaskan Chinook salmon stocks for which reconstructed brood year returns were available. These quantities ranged from 0.29 to 0.76,

Table 2. Posterior medians of key model quantities, with base and alternate versions of prior distributions.

	Base prior	Alternate prior for			
		$\ln(\alpha)$	σ_R	D, π	σ_{R0}
α	1.70	2.00	1.72	1.69	1.73
β	9.3E-05	9.8E-05	9.4E-05	9.2E-05	9.3E-05
σ_R	0.52	0.51	0.50	0.52	0.52
ϕ	0.82	0.81	0.83	0.82	0.82
S_{EQ}	11 080	11 870	10 970	11 200	11 190
S_{MSY}	4 580	4 819	4 501	4 562	4 590
D	21	21	21	22	22
σ_{R0}	0.25	0.25	0.28	0.24	0.54

Note: Noteworthy differences are in bold.

with mean 0.54. For an alternate prior, we used an inverse gamma(1.25, 0.4) prior distribution on σ_{R0}^2 with mean $1/0.54^2$ and dispersion sufficient to bracket the 10 individual estimates. Finally, for the age-at-maturity submodel, an alternate parameterization was adopted, where $\{\gamma_a: a = 3:7\}$ were root parameters (see eqs. 5 and 6), and given independent gamma(0.001, 0.001) prior distributions.

Negative values of $\ln(\alpha)$ ($\alpha < 1$) represent inability of the stock to sustain itself, even in the event of no harvest. Under the base model, with the uncensored prior on $\ln(\alpha)$, posterior probability of unsustainability was 20% for the Karluk stock, although after accounting for lognormal production (eq. 22), this probability was only 4%. Under the alternate censored prior (Su and Peterman 2012), quantities α , β , S_{EQ} , and S_{MSY} increased slightly (Table 2). It is worth noting that under escapement goal management, the censored prior on $\ln(\alpha)$ is more biologically conservative because the slightly (8%) higher estimate of S_{MSY} favors a higher escapement goal. Under harvest rate management, the uncensored prior is more conservative because the lower estimate of α implies a lower U_{MSY} . Other alternate priors had only negligible effects on key model parameters (Table 2). The informative prior on σ_{R0}^2 had a large effect on σ_{R0} itself (Table 2), and it also affected initial states R_y (not shown). However the prior had no effect on key model quantities (Table 2) because σ_{R0} is a hyperparameter far removed from the data, with little bearing on the SR parameters. The large difference in σ_{R0} between the two prior distributions reflects lack of information in the data regarding the dispersion of the returns from early unmonitored escapements. Kernel density estimates of posterior distributions for key parameters are provided in the online supplement¹ to this article.

Results

Posterior medians and credibility intervals for key model parameters are summarized in Table 3. Karluk River Chinook salmon exhibited low productivity with an estimated α of 1.7 recruits per spawner (posterior median; 95% CI: 0.2–11.8). Corrected for the skewness in lognormal production (eq. 21), the estimate of expected productivity α was 2.8 recruits per spawner, and there is 4.3% probability that the stock is not self-sustaining ($\alpha < 1$). The estimated density dependence parameter β was 9.3×10^{-5} (CI: 1.3 – 17.8×10^{-5}), which suggests an equilibrium stock size S_{EQ} of 11 080 (CI: 0–97 520). S_{MSY} was estimated (eq. 15) to be 4580 (CI: 0–17 275). Residual deviations from the Ricker model exhibited strong serial correlation, as evidenced by AR(1) correlation coefficient near 1 ($\phi = 0.82$; CI: 0.48–0.99). Note that estimates of α , β , S_{EQ} , and S_{MSY} are extremely imprecise (Table 3).

Posterior percentiles of selected state variables are plotted in Fig. 2. Estimates of escapement S were precise, except for 1998, when the weir failed for part of the season (Fig. 2a). Estimates of brood year returns R were less precise (Fig. 2b), being subject to

Table 3. Posterior percentiles of key model quantities, Karluk River Chinook salmon.

	Percentile		
	2.5%	50%	97.5%
α	0.21	1.70	11.8
β	1.3E-05	9.3E-05	1.8E-04
σ_R	0.37	0.52	0.76
ϕ	0.48	0.82	0.99
S_{EQ}	0	11 080	97 520
S_{MSY}	0	4 580	17 275
D	14	21	32
π_3	0.02	0.03	0.05
π_4	0.09	0.12	0.16
π_5	0.25	0.30	0.35
π_6	0.43	0.48	0.54
π_7	0.04	0.06	0.09

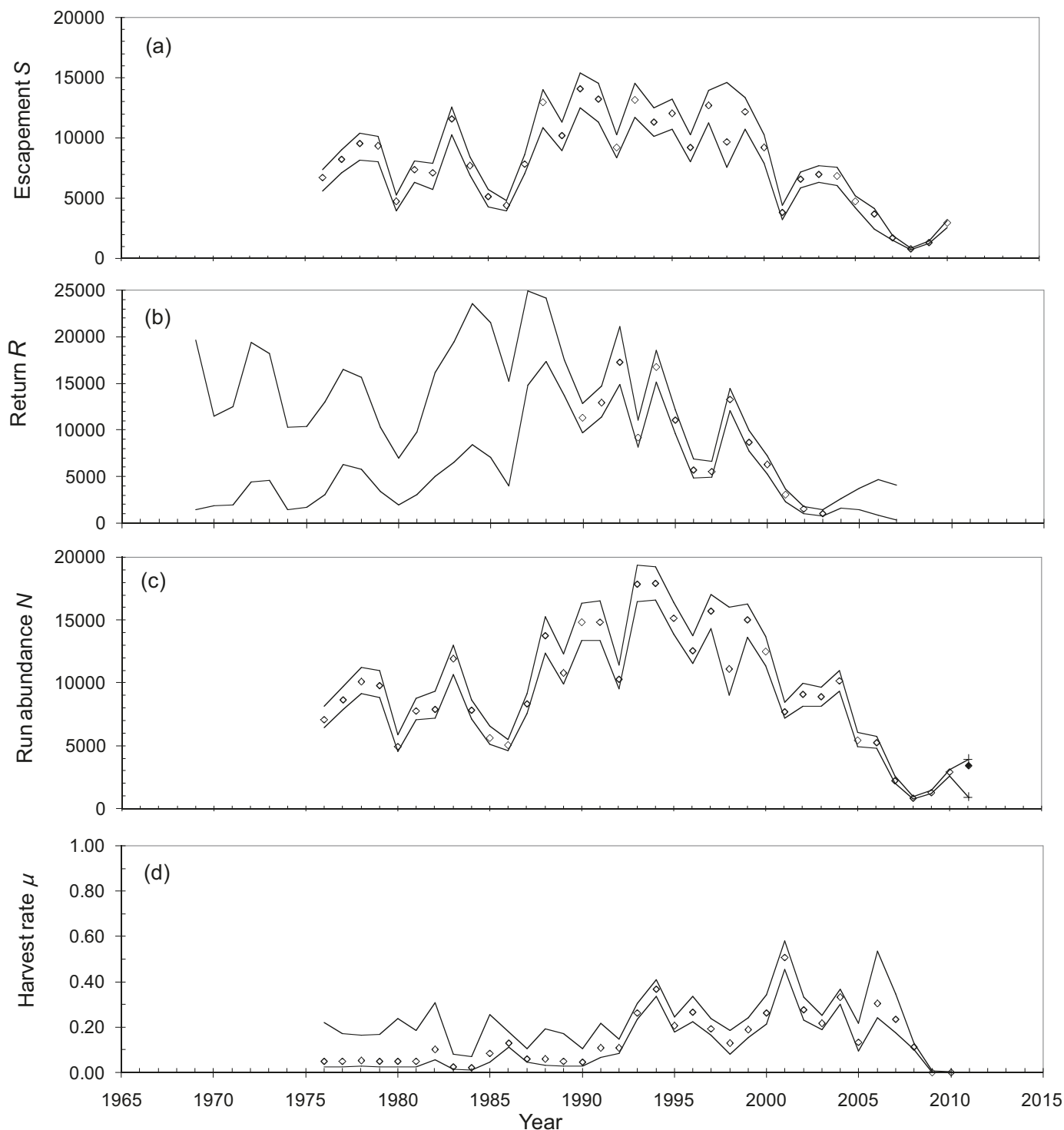
additional uncertainty from harvest estimates and age composition assessments. Total annual run abundance N ranged from 864 (CI: 793–943) salmon in 2008 to 17 870 (CI: 16 610–19 220) in 1993; and the stock underwent more than a 10-fold decline beginning in the late 1990s (Fig. 2c). Harvest rates (Fig. 2d) ranged from 0.03 (1984) to 0.51 (2001) until 2009, at which point all harvest ceased in response to declining abundance.

On average, nearly half ($\pi_6 = 0.48$; CI: 0.43–0.54) of Karluk River Chinook salmon matured and returned to spawn at age 6, but a substantial proportion also matured at age 5 ($\pi_5 = 0.30$; CI: 0.25–0.35; Table 3). Relative uncertainty was higher for age classes with small proportions (Table 3), which is a property of Dirichlet-multinomial processes. The amount of process variation in age at maturity is reflected in the value of the Dirichlet inverse dispersion parameter D (median: 21; CI: 14–32; Table 3). Such variation can be seen in Fig. 3 for brood years 1988–2004, which are informed by the age composition data collected in 1993–2010. Information about age-at-maturity proportions for brood years before 1988 is, appropriately, much less precise (gray dashed lines in Fig. 3). The same is true for cohorts after 2004, which had yet to complete their return in 2010. It is this imprecision that causes the wide recruitment intervals for the last several cohorts in Fig. 2b. Age at maturity showed no evidence of trend or serial correlation (Fig. 3).

Inference about the true Ricker relationship was very imprecise, as reflected by the wide diversity of plausible Ricker curves produced by paired posterior samples of α and β (Fig. 4). Uncertainty about α is reflected as diversity, among these curves, in their slopes at the origin, whereas uncertainty about β is reflected as diversity in the escapement leading to maximum recruitment ($S_{MSR} = 1/\beta$). As noted above, uncertainty about both α and β is very large for this stock (Table 3). This is partially due to the substantial observation error in R for early cohorts (Fig. 4). Another factor is the strong serial correlation ($\phi = 0.82$, CI: 0.48–0.99; Table 3) in the model residuals, which reflects the nonstationary productivity of the population (Fig. 5). Annual productivity, as approximated by the sum of $\ln(\alpha)$ and annual residuals, declined steeply to less than replacement ($\alpha_y < 1$; $\ln(\alpha_y) < 0$) after the 2001 cohort and has been recovering slowly since 2004 (Fig. 5). Annual productivity estimates from a random walk submodel, designed to be comparable to those of Peterman et al. (2000), are included in Fig. 5 for comparison. These estimates show a trend similar to that from the AR(1) submodel, except that they are smoother, because extraneous high-frequency process variation and observation error has been reduced. Also, the RW model did not detect an increase in productivity during the last several cohorts.

With respect to yield considerations, information pertaining directly to choice of an escapement goal is summarized in the

Fig. 2. Point estimates (open symbols) and 95% credibility intervals (lines) of (a) spawning escapement, (b) return by brood year, (c) run abundance, and (d) harvest rate for Karluk River Chinook salmon, 1969–2010. In panel (c), the interval bounds for 2011 run abundance (+ symbols) constitute a posterior prediction, and the filled symbol for 2011 is the realized run size.



OYP (Fig. 6). Despite the great uncertainty about the true SR relationship and reference points, there exists useful information in the data about the values of S that over the long term would result in optimal yield. For example, one can state that there is greater than 68% probability that escapements between 2700 and 6000 will produce expected yields at least 70% of maximum sustained yield (Fig. 6; dotted gray lines).

Discussion

Benefits of including age structure in the SR model

Under the traditional protocol for analyzing Pacific salmon SR data (e.g., Clark et al. 2009), recruitment originating from individual cohorts is first reconstructed by summing estimates of escapement-at-age and harvest-at-age across calendar years (Fig. 1).

Fig. 3. Area graph of age-at-maturity proportions, Karluk River Chinook salmon, brood years 1969–2008. Distances between the solid lines are posterior medians of proportions of fish returning by age for the specified cohort. Dashed grey lines bracket 95% credible intervals for the proportion returning at age 5 or younger.

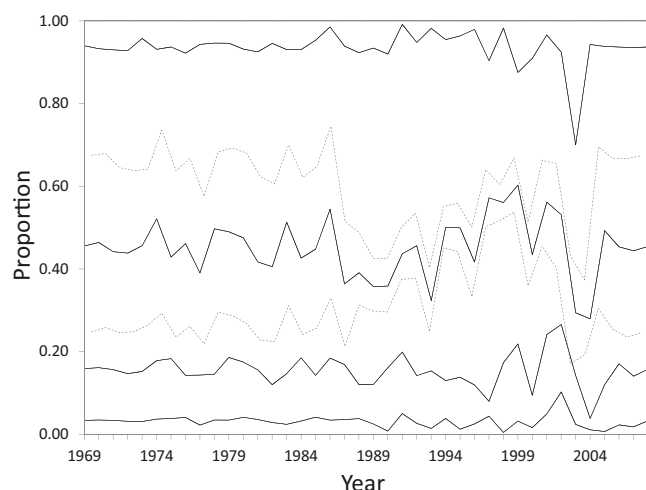


Fig. 4. Brood year return (recruitment) versus escapement for Karluk River Chinook salmon, 1976–2008. Error bars are 95% credible intervals from the Bayesian state-space age-structured model. Gray lines represent 50 curves drawn at random from the posterior distribution of the stock–recruitment parameters α and β , depicting the uncertainty in the relationship between stock and recruitment for the stock.

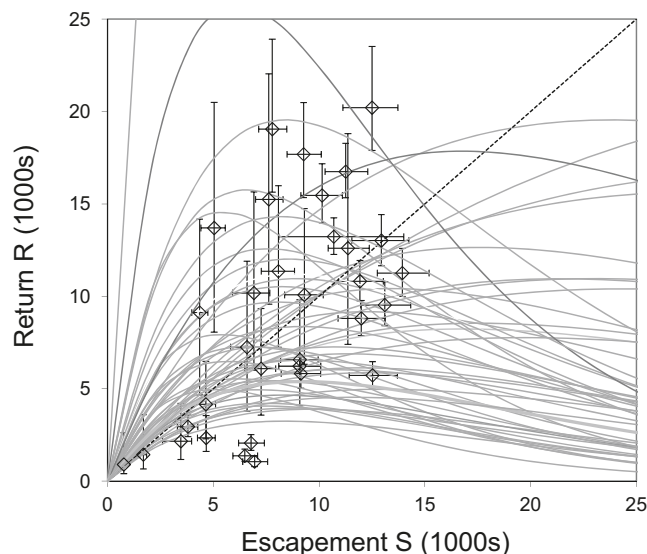
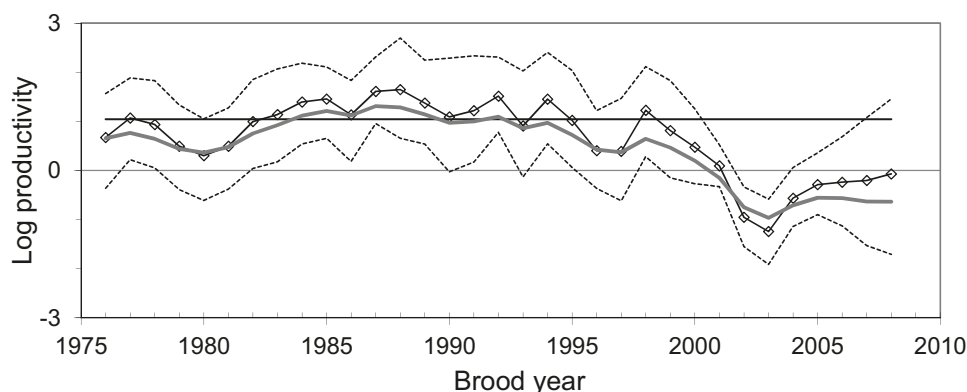


Fig. 5. Approximate annual values of time-varying (log) productivity (sum of $\ln(\alpha)$ and log residuals) for Karluk River Chinook salmon, brood years 1976–2008 (2008 values constitute a posterior prediction). Overall mean log productivity $\ln(\alpha)$, corrected for lognormal production, is represented by the horizontal reference line. Deviations of productivity from the mean value are the model residuals ω_t . Also plotted (gray line, no symbols) are annual log productivity values from a random walk version of the state-space model.

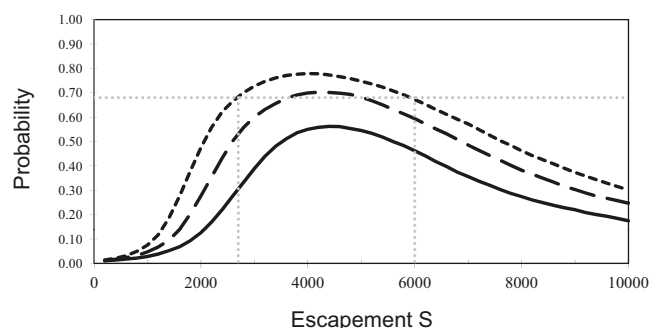


The reconstructed values of R_t are then directly input to the SR analysis. Under this protocol, failure of an assessment project during a single year (e.g., weir failure on the Karluk River) prevents the estimation of returns from multiple brood years (five brood years for Karluk Chinook salmon). Failure to obtain age composition data in one or more calendar years (e.g., Karluk River 1976–1992) presents a similar obstacle. Although values can feasibly be imputed for missing data such as these, imputation of age composition estimates may introduce bias to estimates of population parameters (Zabel and Levin 2002), and it is difficult to quantify the additional uncertainty introduced, especially for S_{MSY} and other derived quantities.

By properly accounting for age structure in the Bayesian state-space model, missing data such as these no longer present any special difficulty. The stochastic model of age at maturity permits estimation of model quantities in the context of the specified relationships of abundances across time and age. Like parameters, missing data constitute unknown quantities for which posterior

samples are automatically generated, and the additional uncertainty flows through to the remaining model parameters as appropriate. In the Karluk River example, the imprecise 1998 estimate of escapement S (Fig. 2a) automatically leads to parallel uncertainty in the 1998 run abundance N (Fig. 2c), which in turn increases uncertainty in the returns R from the 1992, 1993, and 1994 cohorts, contributors of 6-, 5-, and 4-year-old fish, respectively, to the 1998 run. This scenario also highlights the fact that individual quantities of S and R are not independent, but independence must be assumed in non-age-structured analyses. In the case study, the 1998 escapement is positively correlated with 1992–1994 recruitments (this can be seen by plotting these quantities versus one another using the MCMC samples; not shown). By employing an age-structured model, the full complexity of this covariance structure is automatically taken into account when making inferences about parameters and reference points. Given the prevalence of missing data among Pacific salmon stock assessments, this constitutes an important advantage of an age-

Fig. 6. Optimal yield profiles for Karluk River Chinook salmon, showing the probability that a specified spawning abundance will achieve 70% (short dashes), 80% (long dashes), and 90% (solid line) of maximum sustained yield (MSY). For example, escapements between 2700 and 6000 have at least 68% probability of yielding 70% of MSY over the long term.



structured approach. In a retrospective analysis described in the online supplement¹, the 1995 version of the Karluk River data set would have included only 3 years of scale age data, yet it still produced estimates of reference points that would have been useful for management.

A second advantage of an age-structured model is the ability to consider information from recent, incomplete brood years. Under the assumption of nonstationary productivity (see below), recent information has the greatest relevance and value. Especially for long-lived species, it may be helpful to detect changes in productivity as soon as possible to support timely management responses. In addition, the ability to forecast run size 1 year in advance (N_{2011} in the Karluk River example) depends largely upon information about the number of young fish returning from the incomplete 2004–2007 cohorts. The forecast from the age-structured state-space model uses such information to maximum advantage, yet with realistic uncertainty, in the context of the Ricker SR relationship, time-specific productivity, and stochastic maturity at age. Such forecasts can be useful for establishing realistic expectations in advance of the upcoming fishing season. On the Karluk River, the 2011 run eventually came in at 3420, within the 95% prediction interval of 921–3862 (Fig. 2c).

Evaluating conditions across states of nature as a general approach

The ability to draw samples from the posterior distribution for any quantity or condition of interest imparts great power and flexibility to the Bayesian MCMC modeling environment. Under the Bayesian framework, each MCMC sample includes a value for each model parameter and thus represents a completely specified “state of nature” that plausibly could have resulted in the data that were ultimately observed. Posterior draws thus represent a collection of such states of nature, across which any relevant condition or quantity can be evaluated. By carefully specifying quantities of interest and considering them across MCMC samples, it is possible to make useful probability statements tailored to specific questions or hypotheses. For example, Alaska stocks of Pacific salmon are managed with a fixed escapement policy and, where appropriate, a maximum yield objective. By setting optimal yield criteria such as 70%, 80%, or 90% of MSY, and tallying success or failure of specified levels of escapement to meet such criteria across plausible states of nature, one can quantify the probabilities of achieving optimal yield at different prospective levels of escapement. Such OYPs provide an objective appraisal of the quality of information about optimal escapement levels contained in the data, and actual probabilities are available to help weigh risks and benefits of alternative management choices. The steeper the limbs of the OYP and the higher the maximum probability, the

better the information about sustained yield at different levels of escapement. Compared with other Alaska stocks of Pacific salmon that have been analyzed in a similar manner, Karluk River Chinook salmon data contain a modest amount of information about optimal escapement for sustained yield (Fig. 7), due largely to great uncertainty about the SR relationship. Nevertheless, such information is valuable when it becomes necessary to develop or revise harvest policy parameters such as escapement goals. There are often considerations other than yield that drive selection of an escapement goal, for example, the composition of user groups (subsistence vs recreational vs commercial fishers), the resilience of the fisheries to prolonged closures, and (or) the timeliness of stock assessment data. Given the ability to assess the quality of information about production characteristics of the stock (as summarized by the OYP), such information can be weighted appropriately when considered in the context of the other factors. In the absence of other compelling considerations, escapement goal ranges can be chosen such that a stated probability of meeting an optimal yield criterion is achieved. The current escapement goal range for the Karluk River (3000–6000 spawning adults) provides at least 68% probability of achieving greater than 70% of MSY, given the current state of knowledge about the stock (Fig. 6).

Examples of other possible applications of this approach are summarized in Table 4. For instance, with a fixed harvest rate policy, it is crucial that the harvest rate not be set so high ($>U_{\text{MAX}} = 1 - 1/\alpha$) that it exceeds the productive potential of the stock. By tallying whether or not specified incremental levels of harvest rate exceed U_{MAX} across plausible states of nature, one can quantify the probability of exceeding this threshold for any prospective harvest rate. Such a graphic could be called an extirpation risk profile (ERP). The more precise the information about stock productivity α , the steeper the ERP and the more resolution one has in determining which harvest rates are safe. An ERP for the Karluk stock is provided in the online supplement¹, along with OYPs as a function of harvest rate (Table 4, rows 2, 3).

Considerations related to nonstationary productivity

Nonstationary productivity has become more evident in Pacific salmon as longer time series of stock assessment data have accumulated (Dorner et al. 2008; Peterman et al. 2003; Collie et al. 2012). Although the AR(1) submodel accommodates annual changes in productivity (Hilborn and Walters 1992), it is important to note that it assumes an underlying central tendency, from which annual productivity values may deviate substantially but to which they eventually return. Inference about yield characteristics and other attributes of the stock is centered on values that reflect “average” productivity, so when productivity veers far away from average, the performance of harvest policies based on the central tendency can degrade (Collie et al. 2012). A potential alternative is to use a random walk (RW) submodel (Peterman et al. 2000), which estimates annual productivity values without assuming a central tendency, and to base harvest policy on the most recent annual estimates. Collie et al. (2012) demonstrated with simulated data that an adaptive, time-varying policy such as this may result in greater long-term yields. A simple retrospective analysis of the Karluk River data suggests that under an escapement goal policy, important trade-offs may exist that counter some of the benefits of such an approach (online supplement¹ to this article). These trade-offs include greater volatility in management advice and greater biological risk for low-productivity stocks. More work is needed to devise policies that make optimal use of annual estimates of productivity such as those generated by these models.

Fig. 7. Optimal yield profiles (OYPs; probability of achieving 90% of MSY) from similar Bayesian age-structured state-space analyses of spawner–recruit data for Anchor River Chinook salmon (Szarzi et al. 2007), Andreafsky River summer chum salmon (Fleischman and Evenson 2010), Chilkat River coho salmon (Ericksen and Fleischman 2006), Blossom River Chinook salmon (Fleischman et al. 2011), Keta River Chinook salmon (Fleischman et al. 2011), Taku River Chinook salmon (McPherson et al. 2010), and Yukon River fall chum salmon (Fleischman and Borba 2009). (The 90% OYP for Karluk River Chinook salmon from Fig. 6 is shown with a solid line.) Horizontal axis is scaled differently for each stock, such that the range of escapements bracket the value of optimal escapement S_{MSY} .



Table 4. Additional ways to evaluate conditions across plausible states of nature (i.e., across MCMC samples) to extract management advice from the data.

Output	For each MCMC sample:	Comments	Source—examples
1. Probability of not exceeding X% of maximal yield due to fishing too hard , as a function of escapement	At incremental values of S , calculate Y , compare with X% of the value of MSY for that sample. Record 1 if Y is smaller and $S < S_{\text{MSY}}$, or 0 otherwise.	Probability of recruitment overfishing, which is defined as setting goal too low, and thereby reducing yield to less than X of MSY	“Overfishing profiles” of Bernard and Jones 2010
2. Probability of exceeding X% of maximal yield, as a function of harvest rate μ	At incremental values of μ (0 to 0.99 by 0.01), calculate S and Y_S , then compare Y_S with X% of the value of MSY for that sample.	Where $S = 1/\beta [\ln(\alpha) + \ln(1 - \mu)]$	Online supplement, Fig. S6 ^a
3. Probability of exceeding maximum harvest rate $U_{\text{MAX}} = 1 - 1/\alpha$	At incremental values of μ (0 to 0.99 by 0.01), calculate maximum harvest rate, record 0 if less than μ , 1 if greater.	Risk of zero yield and eventual extirpation, especially important for a fixed harvest rate policy on a low productivity stock	Online supplement, Fig. S6 ^a
4. Probability of exceeding X% of maximal production, as a function of escapement	At incremental values of S , calculate R and compare with X% of the value of MSR for that sample.	Useful when absolute abundance and catch rate are an important consideration (recreational and subsistence fisheries)	Hamazaki et al. 2012
5. Sustained yield as a function of escapement	At incremental values of S , plot percentiles of posterior distribution for sustained yield.	Expected yield curve	Fleischman et al. 2011
6. Closed-loop simulations of population dynamics, such as management strategy evaluations (Collie et al. 2012)	Base each simulation rep on a different MCMC sample of relevant quantities subject to uncertainty, e.g., α , β , ϕ , σ .	Injects realistic uncertainty about stock production characteristics into such analyses	Jones and Volk 2011

Note: The base case is the optimal yield profile (Fig. 6), which quantifies the probability of exceeding a stated percentage of maximal yield as a function of escapement. See text.

^aAvailable through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2012-0112>.

Table 5. Alternate configurations for state-space model described in the text.

Base configuration	Modification–enhancement	Details	Comments	Source/Examples
1. Ricker stock–recruitment relationship (eq. 1)	Beverton–Holt (B–H)	Several parameterizations are available	We find that the B–H model can be unstable when fitted to Pacific salmon data See Discussion section	Michielsens and McAllister 2004
2. Production R subject to autoregressive lag-1 process variation (eqs. 1, 2)	Production R subject to random walk process variation	$\ln(R) = \ln(S) + \ln(\alpha_y) - \beta S + \varepsilon_{2y};$ $\ln(\alpha_y) = \ln(\alpha_{y-1}) + \varepsilon_{3y}$		Online supplement ^a ; Jones and Volk 2011
3. Direct, unbiased estimates of absolute abundance, such as those from weirs, sonar, towers, mark–recapture experiments	Substitute indices of relative abundance such as tributary abundance or aerial or foot survey counts for some years	$\text{Index}_y = \text{lognormal}(\ln(qN_y), \sigma_I^2)$	One or more time series of relative abundance indices anchored by less frequent direct estimates of absolute abundance	Fleischman and McKinley 2013 ; Ericksen and Fleischman 2006
4. Direct, unbiased estimates of absolute abundance, such as those from weirs, sonar, towers, mark–recapture experiments	Additional catch and effort data from inriver or terminal marine fishery to quantify relative abundance	$C_y = \exp(-qE_y)N_y$	Baranov catch equation	Szarzi et al. 2007
6. Unbiased estimates of age composition of total run observed	Biased estimates of age composition from multiple components of total run observed	Age count data modeled as function of true age composition and selectivity parameters	Enables estimation of fishery selectivity and harvest rate by age	Bernard and Jones 2010 ; S. Fleischman (unpublished)
7. Noninformative priors on SR parameters	Informative priors based on hierarchical habitat model (Liermann et al. 2010)	Equilibrium escapement S_{EQ} is function of watershed size	Applies to Chinook salmon only	Fleischman et al. 2011

^aAvailable through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2012-0112>.

Informative prior distributions

The Bayesian framework provides a convenient platform for incorporating auxiliary information through the use of prior probability distributions for model parameters. Such distributions summarize available information about the parameters outside the framework of the observed data. Although not used in the current analysis, informative priors could have been formulated for several quantities. For example, [Parken et al. \(2006\)](#) found a useful relationship between watershed area and Chinook salmon stock size, and [Liermann et al. \(2010\)](#) developed a Bayesian hierarchical model based on the relationship. Using the model of [Liermann et al. \(2010\)](#) to formulate an informative prior for equilibrium stock size would result in greater posterior precision for α , β , and S_{MSY} . The OYP would also become steeper and higher, indicating better information about which levels of escapement provide optimal yield. There exists much potential for development of useful priors for α , ϕ , σ , and D from meta-analyses (e.g., [Myers et al. 1999](#)) of Pacific salmon stock–recruitment dynamics, including those that account for spatial and temporal correlations ([Dorner et al. 2008](#); [Su et al. 2004](#)).

Generality of the model

[Newman and Lindley \(2006\)](#) acknowledged the need for off-the-shelf software capable of fitting complex Bayesian state-space models. The WinBUGS software (which continues to undergo development under the OpenBUGS moniker; [Lunn et al. 2009](#)) begins to fill that need in providing a flexible platform for models of moderate complexity. In the BUGS environment, the state-space model framework presented herein can be readily adapted to other Pacific salmon species and submodels (Table 5). The Karluk River data set is simple, but it can serve as a template for other more complex sample designs and data configurations. Details for many alternative configurations have already been worked out (Table 5). The Karluk case study features precise estimates of escapement based on weir data, but the benefits of fitting a state-space model are greater when escapement is estimated with substantial observation error ([Su and Peterman 2012](#)). Such data, originating from run reconstructions, mark-recapture experiments, sonar, aerial and foot surveys, and other stock assessment methods, are very common for Pacific salmon.

Potential for reduced bias

The age-structured state-space approach described here provides a complete probability model for observations of escapement, catch, and age composition in the context of (i) the complex temporal dependence of those quantities and (ii) observation error. Because these factors are taken into account, the approach has the potential for reducing time-series and (or) errors-in-variables bias ([Meyer and Millar 2000](#)), as well as bias due to imputation of age composition estimates ([Zabel and Levin 2002](#)). [Su and Peterman \(2012\)](#) demonstrated that a Bayesian state-space approach produces improved estimates of S_{MSY} in the presence of observation error in S , under most combinations of productivity and harvest regime. Compared with a traditional linear regression approach, point estimates (posterior medians) from their state-space model were less biased and interval estimates had better coverage probability. Like that of [Su and Peterman \(2012\)](#), our model provides explicit consideration of observation error in S , and of R-S linkage, and therefore should provide similar performance advantages with respect to bias reduction and interval coverage. Our model differs from that of [Su and Peterman \(2012\)](#) in that it includes annual process variation in productivity and age at maturity. As discussed earlier, these features allow the model to better reflect biological reality and to better characterize the age-structured nature of the data and its information content. For these reasons and others (see below), it is possible that our model may provide some improvement in performance over that of [Su and Peterman \(2012\)](#). Unfortunately, the simulation studies

required to confirm such advantages would be very cumbersome because computational time is greatly increased for our model. For instance, for the Karluk data, WinBUGS requires >1 h to run our model versus <1 min for a non-age-structured version similar to that of [Su and Peterman \(2012\)](#).

[Su and Peterman \(2012, their table 7\)](#) found that information about the relative magnitude of process and observation error led to improvement in performance of their state-space model. For Alaska stocks, we have found that it is usually not difficult to quantify the observation error associated with escapement estimates. Many stock assessment projects (e.g., mark-recapture, sonar) that produce estimates of abundance also provide estimates of sampling error. For assessments of relative abundance that are biased and do not come with standard errors (e.g., aerial and foot surveys), it is common to run a parallel assessment of absolute abundance for several years and to include both relative and absolute measurements as observations in the state-space model, structuring an appropriate relationship between them directly into the model (Table 5, modification number 3). By doing so, information about relative and absolute abundance is synthesized, providing inference about escapement to the SR model in such a way that the uncertainty flows through to the SR parameters, and process and observation error are appropriately partitioned.

Outlook

We conclude by noting caveats about use of the methods described herein as well as areas of potential work. First, we have not addressed structural uncertainty or model selection issues. Second, although there is strong reason to believe that these methods provide improved estimates of biological reference points, we have not provided direct evidence that this is so. [Su and Peterman's \(2012\)](#) work suggests that time-linked full probability models do not remove all effects of time-series and errors-in-variables bias. Third, although we have found the WinBUGS modeling environment to be flexible and powerful, we caution that there exist many idiosyncracies, technical obstacles, and time constraints associated with the application of MCMC methods, and we recommend that appropriate care be taken when using such methods. Fortunately, although Bayesian statistics and software have nontrivial learning curves, there is an increasing amount of instructive material available. In the online supplement¹ to this article, we provide some advice about a common technical mishap encountered while fitting these models. Finally, the age-structured model described herein builds on the work of [Peterman et al. \(2000\)](#) and [Collie et al. \(2012\)](#) by enhancing the ability to detect ambient changes in stock productivity and by providing such information with an appropriate assessment of uncertainty. We believe that the potential for harvest policy improvements in the light of their work has not been adequately tapped, and more work is needed to devise policies that make the best use of timely stock assessment information.

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