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 quinquin (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 autogressive 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–recruit (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...
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 *K* 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:

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

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* is the model residual,

\[
\omega_y = \ln(R_y) - \ln(S_y) - \ln(\alpha) + \beta S_y + \phi \omega_{y-1} + \varepsilon_y
\]

and the *ε*′s are independent normally distributed process errors with standard deviation σε.

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, MSY is always higher under the assumption of a Ricker...
model than under a Beverton–Holt model. We allowed productiv-
ity, 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 ≤ 1, q ≤ 1) were sufi-
cient to explain the variation in stock–recruit model residuals,
and we have found that an AR(1) model is almost always suffi-
cient to explain the variation in stock–recruit model residuals,
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 propor-
tions \( \{ \pi_a \} \) returning at age:

\[
\pi_a = \frac{\gamma_a}{\sum \gamma_a}
\]

The sum of the \( \{ \gamma_a \} \) can be interpreted as the inverse dispersion
(\( D \)) of the Dirichlet distribution. This parameter governs the vari-
ability 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 Supplement). 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:

\[
N_y = \sum_a N_{y,a}
\]

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:

\[
W_y = N_y - H_{By}
\]

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

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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.

<table>
<thead>
<tr>
<th>Year</th>
<th>Esc</th>
<th>Annual abundance (run) by age ( N_{y,a} )</th>
<th>Run</th>
<th>Return</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>S_1</td>
<td>( N_{1,3}, N_{1,4}, N_{1,5}, N_{1,6}, N_{1,7} )</td>
<td>( R_{1} )</td>
<td>( N_{1} )</td>
</tr>
<tr>
<td>2</td>
<td>S_2</td>
<td>( N_{2,3}, N_{2,4}, N_{2,5}, N_{2,6}, N_{2,7} )</td>
<td>( R_{2} )</td>
<td>( N_{2} )</td>
</tr>
<tr>
<td>3</td>
<td>S_3</td>
<td>( N_{3,3}, N_{3,4}, N_{3,5}, N_{3,6}, N_{3,7} )</td>
<td>( R_{3} )</td>
<td>( N_{3} )</td>
</tr>
<tr>
<td>4</td>
<td>S_4</td>
<td>( N_{4,3}, N_{4,4}, N_{4,5}, N_{4,6}, N_{4,7} )</td>
<td>( R_{4} )</td>
<td>( N_{4} )</td>
</tr>
<tr>
<td>5</td>
<td>S_5</td>
<td>( N_{5,5}, N_{5,6}, N_{5,7} )</td>
<td>( R_{5} )</td>
<td>( N_{5} )</td>
</tr>
<tr>
<td>6</td>
<td>S_6</td>
<td>( N_{6,6}, N_{6,7} )</td>
<td>( R_{6} )</td>
<td>( N_{6} )</td>
</tr>
<tr>
<td>7</td>
<td>S_7</td>
<td>( N_{7,7} )</td>
<td>( R_{7} )</td>
<td>( N_{7} )</td>
</tr>
<tr>
<td>8</td>
<td>S_8</td>
<td>( N_{8,8} )</td>
<td>( R_{8} )</td>
<td>( N_{8} )</td>
</tr>
<tr>
<td>9</td>
<td>S_9</td>
<td>( N_{9,9} )</td>
<td>( R_{9} )</td>
<td>( N_{9} )</td>
</tr>
<tr>
<td>10</td>
<td>S_{10}</td>
<td>( N_{10,10} )</td>
<td>( R_{10} )</td>
<td>( N_{10} )</td>
</tr>
</tbody>
</table>
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:

$$S_y = W_y - H_{Ay}$$

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

$$H_{Ay} = N_y U_{Ay}$$

$$H_{By} = N_y U_{By}$$

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 as-
seSSments of observation error due to sampling were available, 
the analysis was run for three values of weir sampling error coef-
icient 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 
estimates of inriver abundance. Observed weir counts ($W_y$) 
were assumed to be lognormally distributed with parameters $ln(W_y)$ 
and $\sigma_{W_y}$. CVs were converted to lognormal variance parameters as 
follows (Evans et al. 1993):

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

Annual harvests below the weir ($H_{By}$) were taken by recrea-
tional (mean harvest rate 7%), commercial (also 7%), and subsis-
tence 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 esti-

dated from postseason interviews. Standard errors were available 
for mail survey estimates (CVs of 0.14 to 0.79; Jennings et al. 2010). We 
used very large observation errors for the (very small) subsis-
tence harvests ($CV = 1.0$) and small errors for the commer-
cial harvests ($CV = 0.05$). Again, CVs of 0.025 and 0.075 for the 
commercial harvests did not produce discernibly different re-
sults. Squared standard errors were summed across the three fish-
eries, then divided by the squared summed harvest estimates to 
obtain annual (squared) observation error CVs. Observed harvest 
below the weir ($H_{By}$; sum of recreational, commercial, and subsis-
tence harvests, as described above) was assumed to be lognor-
mally distributed with parameters $ln(H_{By})$ and $\sigma_{H_y}$. The mail survey 
estimates of recreational harvest contributed the largest com-
ponent of observation error for harvest below the weir. Annual har-
vests 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 $\sigma_{H_y}$. Observation error variances $\sigma_{H_y}^2$ and 
$\sigma_{W_y}^2$ were obtained from their respective CVs 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 (unob-
served) 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 esti-
mates of age proportions from the time-stratified design were 
used to obtain annual “effective sample sizes” $n_y$, where $n_y$ is the 
multinomial sample size that would produce uncertainty equiva-

tent to that indicated by the time-stratified analysis (Hulson et al.
2011; McAllister and Ianelli 1997). Surrogate scale age counts $n_{Sy}$ 
were obtained that summed to $n_y$, rather than to $n_y$. The $n_{Sy}$ were 
modeled as multinomially distributed, with order parameter $n_{Sy}$ 
and proportion parameters as follows:

$$q_y,a = \frac{N_{Sy,a}}{\sum a N_{Sy,a}}$$

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

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

$$S_{MSY} = \frac{a}{\beta} \left( 0.5 - \frac{0.65a^{127}}{8.7 + a^{127}} \right)$$

where $a = \ln(\alpha)$ (Peterman et al. 2000). This approximation is more 
accurate than that of Hilborn (1985) for large values of $\alpha$, 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

$$\alpha(1 - \beta S_{MSY}) e^{-\beta S_{MSY}} = 1.$$
Table 1. Prior distributions for model parameters and alternate priors tested for sensitivity.

<table>
<thead>
<tr>
<th>Text</th>
<th>BUGS</th>
<th>Prior</th>
<th>Alternate Priors</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\ln(\alpha)$</td>
<td>lnalpha</td>
<td>$\ln(\alpha) \sim \text{Uniform}(\omega, \omega)$&lt;/br&gt;$\beta$</td>
<td>$\beta \sim \text{Uniform}(0, \omega)$</td>
</tr>
<tr>
<td>$\sigma_R$</td>
<td>sigma.R</td>
<td>$\sigma_R \sim \text{Uniform}(0, 100)$</td>
<td>$1/\sigma_R^2 \sim \text{gamma}(0.001, 0.001)$</td>
</tr>
<tr>
<td>$\phi$</td>
<td>phi</td>
<td>$\phi \sim \text{Uniform}(-1, 1)$</td>
<td>$\gamma_e \sim \text{gamma}(0.001, 0.001)$</td>
</tr>
<tr>
<td>$D$</td>
<td>D</td>
<td>$1/\sqrt{D} \sim \text{Uniform}(0, 1)$</td>
<td>$1/\sigma_{\phi}^2 \sim \text{gamma}(1.25, 0.4)$</td>
</tr>
<tr>
<td>$\pi_{n-t}$</td>
<td>pij</td>
<td>$\pi \sim \text{Dirichlet}(0.2, 0.2, 0.2, 0.2, 0.2)$</td>
<td>$\pi_{n-t} \sim \text{Uniform}(1.5)$</td>
</tr>
<tr>
<td>$\omega_0$</td>
<td>log.resid.0</td>
<td>$\omega_0 \sim \text{Normal}(0, \sigma_0^2/\phi^2)$</td>
<td>$\gamma_e \sim \text{gamma}(0.001, 0.001)$</td>
</tr>
<tr>
<td>$R_1$</td>
<td>R[1:7]</td>
<td>lognormal($\ln(R_0), \sigma_{\phi0}$)</td>
<td>$\gamma_e \sim \text{gamma}(0.001, 0.001)$</td>
</tr>
<tr>
<td>$\ln(R_0)$</td>
<td>mean.log.R0</td>
<td>$\ln(R_0) \sim \text{Uniform}(w, \omega)$</td>
<td>$\gamma_e \sim \text{gamma}(0.001, 0.001)$</td>
</tr>
<tr>
<td>$\sigma_{\phi0}$</td>
<td>sigma.R0</td>
<td>$1/\sigma_{\phi0}^2 \sim \text{gamma}(0.001, 0.001)$</td>
<td>$\gamma_e \sim \text{gamma}(0.001, 0.001)$</td>
</tr>
</tbody>
</table>

<sup>a</sup>Where “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.<br>

<sup>b</sup>For the age-at-maturity submodel, an alternate parameterization was tested. Parameters ($\gamma_e/\alpha = 3.7$) are described in the text (eqs. 5 and 6).

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 $\beta$ excluded negative values, thus reflecting the biological reality of natural populations. A population with a negative $\beta$ 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 (Miller 2002). For some parameters ($\ln(\alpha), \beta, \phi$), adoption of a uniform prior caused computational disruptions during MCMC sampling. 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 $\sigma_R$, following the advice of Su and Peterman (2012). The vector of age proportion hyperparameters ($\pi_{n-t} \approx 3.7$) 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 supplement<sup>1</sup> 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 $D$, $\sigma_{\phi0}$, and $R_{1969}^{K_{975}}$. 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 supplement<sup>1</sup> 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 $\sigma_R$, we adopted an inverse gamma(0.001, 0.001) distribution for $\sigma_R$, which is a commonly used diffuse conjugate prior. A uniform prior for the standard deviation $\sigma_{\phi0}$ of log initial brood year returns performed poorly, resulting in implausible values of the initial state parameters $R_{1969}^{K_{975}}$. Therefore, an informative prior was constructed for $\sigma_{\phi0}$ 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.
with mean 0.54. For an alternate prior, we used an inverse gamma(1.25,0.4) prior distribution on \( \sigma_{BO} \) with mean 1/0.54² and dispersion sufficient to bracket the 10 individual estimates. Finally, for the age-at-maturity submodel, an alternate parameterization was adopted, where \( (\gamma, \alpha) = (3.7) \) 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 \( \alpha, \beta, S_{0Q} \), 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 \( \alpha \) implies a lower \( U_{MSY} \). Other alternate priors had only negligible effects on key model parameters (Table 2). The informative prior on \( \sigma_{BO}^2 \) had a large effect on \( \sigma_{BO} \) itself (Table 2), and it also affected initial states \( R \). However the prior had no effect on key model quantities (Table 2) because \( \sigma_{BO} \) is a hyperparameter far removed from the data, with little bearing on the SR parameters. The large difference in \( \sigma_{BO} \) 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 supplement 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 \( \alpha \) of 1.7 recruits per spawner (posterior median; 95% CI: 0.2–11.8). The estimate of expected productivity \( \alpha \) 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 \( \beta \) was \( 9.3 \times 10^{-5} \) (CI: 1.3–17.8 \times 10^{-5}), which suggests an equilibrium stock size \( S_{0Q} \) 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 well as affected initial states.

<table>
<thead>
<tr>
<th>Base prior</th>
<th>Alternate prior for</th>
<th>( \alpha )</th>
<th>1.70</th>
<th>2.00</th>
<th>1.72</th>
<th>1.69</th>
<th>1.73</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \beta )</td>
<td>9.3E-05</td>
<td>9.8E-05</td>
<td>9.4E-05</td>
<td>9.2E-05</td>
<td>9.2E-05</td>
<td>9.3E-05</td>
<td></td>
</tr>
<tr>
<td>( \sigma_{BO} )</td>
<td>0.52</td>
<td>0.51</td>
<td>0.50</td>
<td>0.52</td>
<td>0.52</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \phi )</td>
<td>0.82</td>
<td>0.81</td>
<td>0.83</td>
<td>0.82</td>
<td>0.82</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( S_{0Q} )</td>
<td>11 080</td>
<td>11 870</td>
<td>10 970</td>
<td>11 200</td>
<td>11 190</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( S_{MSY} )</td>
<td>4 580</td>
<td>4 819</td>
<td>4 501</td>
<td>4 562</td>
<td>4 590</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( D )</td>
<td>21</td>
<td>21</td>
<td>21</td>
<td>22</td>
<td>22</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \sigma_{BO} )</td>
<td>0.25</td>
<td>0.25</td>
<td>0.28</td>
<td>0.24</td>
<td>0.54</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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

**Note:** Noteworthy differences are in bold.

### Additional Quantities

**Parameter** | **Percentile** | **Percentile** | **Percentile**
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>( \alpha )</td>
<td>0.21</td>
<td>1.70</td>
<td>11.8</td>
</tr>
<tr>
<td>( \beta )</td>
<td>1.3E-05</td>
<td>9.3E-05</td>
<td>1.8E-04</td>
</tr>
<tr>
<td>( \sigma_{BO} )</td>
<td>0.37</td>
<td>0.52</td>
<td>0.76</td>
</tr>
<tr>
<td>( \phi )</td>
<td>0.48</td>
<td>0.82</td>
<td>0.99</td>
</tr>
<tr>
<td>( S_{0Q} )</td>
<td>0</td>
<td>11 080</td>
<td>97 520</td>
</tr>
<tr>
<td>( S_{MSY} )</td>
<td>4 580</td>
<td>17 275</td>
<td></td>
</tr>
<tr>
<td>( D )</td>
<td>14</td>
<td>21</td>
<td>32</td>
</tr>
<tr>
<td>( \pi_{sp} )</td>
<td>0.02</td>
<td>0.03</td>
<td>0.05</td>
</tr>
<tr>
<td>( \pi_{MSY} )</td>
<td>0.09</td>
<td>0.12</td>
<td>0.16</td>
</tr>
<tr>
<td>( \pi_{spec} )</td>
<td>0.25</td>
<td>0.30</td>
<td>0.35</td>
</tr>
<tr>
<td>( \pi_{t} )</td>
<td>0.43</td>
<td>0.48</td>
<td>0.54</td>
</tr>
<tr>
<td>( \pi_{f} )</td>
<td>0.04</td>
<td>0.21</td>
<td>0.54</td>
</tr>
</tbody>
</table>

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

The large difference in \( \sigma_{BO} \) 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 supplement to this article.

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 \( \alpha \) and \( \beta \) (Fig. 4). Uncertainty about \( \alpha \) is reflected as diversity, among these curves, in their slopes at the origin, whereas uncertainty about \( \beta \) is reflected as diversity in the escapement leading to maximum recruitment \( S_{MSR} = 1/\beta \). As noted above, uncertainty about both \( \alpha \) and \( \beta \) is very large for this stock (Table 3). This is partially due to the substantial observation error in \( k \) 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 \( (\alpha < 1; \ln(\alpha) < 0) \) 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
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).
The reconstructed values of \( R \) 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 \( \lambda_{MSY} \) 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. 3a) 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-
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 ($U_{\text{MAX}} = 1 - 1/e$) that it exceeds the productive potential of the stock. By tallying whether or not specified incremental levels of harvest rate exceed $U_{\text{MAX}}$ 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 $\alpha$, 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.

<table>
<thead>
<tr>
<th>Output</th>
<th>For each MCMC sample:</th>
<th>Comments</th>
<th>Source–examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Probability of not exceeding X% of maximal yield <strong>due to fishing too hard</strong>, as a function of escapement</td>
<td>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 $S &lt; S_{MSY}$, or 0 otherwise.</td>
<td>Probability of recruitment overfishing, which is defined as setting goal too low, and thereby reducing yield to less than X% of MSY.</td>
<td>“Overfishing profiles” of Bernard and Jones 2010</td>
</tr>
<tr>
<td>2. Probability of exceeding X% of maximal yield, as a function of harvest rate $\mu$</td>
<td>At incremental values of $\mu$ (0 to 0.99 by 0.01), calculate $S$ and $Y$, then compare $Y$ with X% of the value of MSY for that sample.</td>
<td>Where $S = 1/\beta \left[ \ln(\alpha) + \ln(1 - \mu) \right]$</td>
<td>Online supplement, Fig. S6a</td>
</tr>
<tr>
<td>3. Probability of exceeding maximum harvest rate $U_{\text{MAX}} = 1 - 1/\alpha$</td>
<td>At incremental values of $\mu$ (0 to 0.99 by 0.01), calculate maximum harvest rate, record 0 if less than $\mu$, 1 if greater.</td>
<td>Risk of zero yield and eventual extirpation, especially important for a fixed harvest rate policy on a low productivity stock</td>
<td>Online supplement, Fig. S6a</td>
</tr>
<tr>
<td>4. Probability of exceeding X% of maximal production, as a function of escapement</td>
<td>At incremental values of $S$, calculate $R$ and compare with X% of the value of MSR for that sample.</td>
<td>Useful when absolute abundance and catch rate are an important consideration (recreational and subsistence fisheries)</td>
<td>Hamazaki et al. 2012</td>
</tr>
<tr>
<td>5. Sustained yield as a function of escapement</td>
<td>At incremental values of $S$, plot percentiles of posterior distribution for sustained yield.</td>
<td>Expected yield curve</td>
<td>Fleischman et al. 2011</td>
</tr>
<tr>
<td>6. Closed-loop simulations of population dynamics, such as management strategy evaluations (Collie et al. 2012)</td>
<td>Base each simulation rep on a different MCMC sample of relevant quantities subject to uncertainty, e.g., $\alpha$, $\beta$, $\phi$, $\sigma$.</td>
<td>Injects realistic uncertainty about stock production characteristics into such analyses</td>
<td>Jones and Volk 2011</td>
</tr>
</tbody>
</table>

**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.

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

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 idiosyncrasies, 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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