Uncertainties in population dynamics and outcomes of regulations in sockeye salmon (*Oncorhynchus nerka*) fisheries: implications for management

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Abstract: Fisheries managers usually have multiple options available but are often unclear on how to choose among them owing to uncertainties in biological and management components of fisheries systems. We evaluated the performance of current and possible future assessment and management practices for sockeye salmon (*Oncorhynchus nerka*) in British Columbia and Alaska by using a computer model that included major biological and management components and their associated uncertainties (interannual variability in recruitment, age-at-maturity, and sex ratio, as well as uncertainty in observations of spawner abundances, forecasts of recruitment, and outcomes from implementing management regulations). One option for management practices that we evaluated was designed to make the forecasting model more realistic by accounting for long-term trends in age-at-maturity. A second option was designed to reduce deviations between management targets and actual or "realized" harvest levels. We found that compared with practices that ignore those sources of uncertainty, the second option produced annual catches that were higher, on average, and less variable over time while maintaining recruitment above critical conservation levels. Contrary to our expectations, the first modification did not result in comparable benefits. Our results demonstrate the value of using simulation models to evaluate potential modifications to Pacific salmon management practices.

Résumé : Les gestionnaires de la pêche se retrouvent fréquemment face à plusieurs marches à suivre possibles, mais ne voient souvent pas clairement comment choisir entre elles, à cause des incertitudes qui existent au sujet des composantes de biologie et de gestion dans les systèmes de pêche. Nous évaluons la performance des pratiques présentes et des pratiques futures potentielles d'évaluation et de gestion du saumon rouge (*Oncorhynchus nerka*) en Colombie-Britannique et en Alaska à l'aide d'un modèle informatique qui comprend les principales composantes de la biologie et de la gestion ainsi que leurs incertitudes associées (la variabilité d'une année à l'autre du recrutement, de l'âge à la maturité et du rapport mâles–femelles, de même que les incertitudes des observations des abondances de reproducteurs, des prédictions du recrutement et des effets de la mise en vigueur des règlements de gestion). L'une des modifications possibles de gestion que nous avons examinées a été calculée pour rendre le modèle prédictif plus réaliste en tenant compte des tendances à long terme de l'âge à la maturité. Une seconde modification visait à réduire les déviations entre les cibles de gestion et les niveaux actuels ou « réalisés » de la récolte. Nous observons que, par comparaison avec les pratiques de gestion qui ignorent ces sources d'incertitude, la seconde option donne des récoltes annuelles qui sont en moyenne plus élevées et moins variables dans le temps, tout en maintenant le recrutement au-dessus des niveaux critiques pour la conservation. Contrairement à nos attentes, la première modification ne génère pas d'avantages comparables. Nos résultats démontrent l'avantage d'utiliser des modèles de simulation pour évaluer les modifications potentielles des pratiques de gestion des saumons du Pacifique.

[Traduit par la Rédaction]

Introduction

Uncertainties, which are pervasive in biological, human, and management components of fisheries systems, arise because of variability within each component and complex interactions among components (Peterman 2004). The consequences of proposed management actions are usually unclear because of these uncertainties, which are often only incompletely considered by stock assessment scientists when evaluating the effects of proposed management actions. Particularly neglected are uncertainties in both long-term trends in life history characteristics and accuracy with which management targets are typically achieved.

"Management procedures" are sets of rules used by man-

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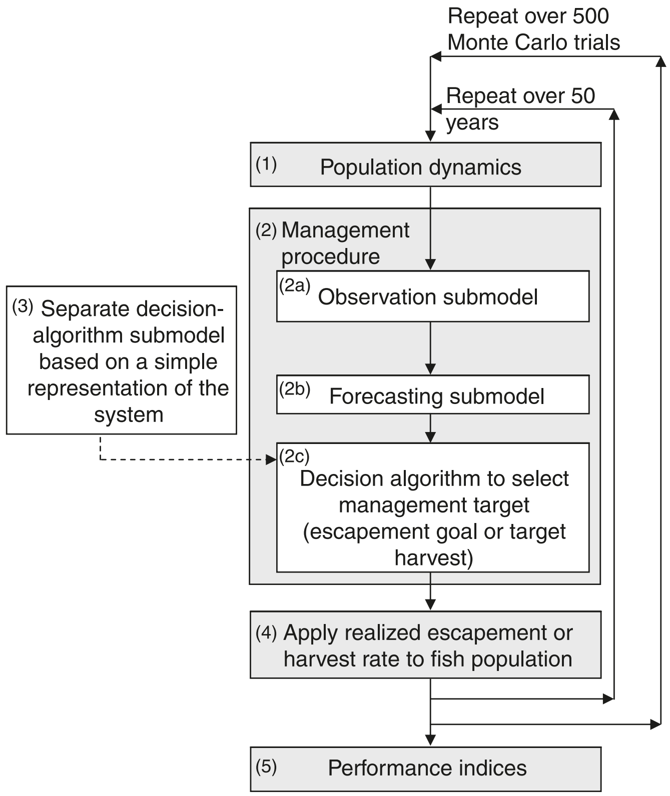
Fig. 1. Simplified outline of the simulation model used to evaluate management procedures for sockeye salmon (*Oncorhynchus nerka*) fisheries in British Columbia and Alaska.



agers that specify how data are collected on the state of a fishery, how population status is assessed, and how decisions are made (Butterworth et al. 1994; Cochrane et al. 1998). We would expect management procedures that account for uncertainties to better achieve management objectives than those that do not. However, such improvement is not guaranteed. Feedback loops and interactions among system components may offset some of the benefits. Furthermore, derivations of management procedures have to rely on imperfect models of the real world when identifying appropriate decision-making algorithms.

A practical approach to evaluating management procedures is to simulate an entire fisheries system in a computer model ("operating model") that includes biological, human, and management components (i.e., "management strategy evaluation"; Sainsbury et al. 2000) (Fig. 1). This approach differs from traditional simulation modelling commonly used in stock assessment because it incorporates most known major components of the system and their associated uncertainties, including biological processes, surveys of abundance, scientific assessment of a stock, subsequent management actions, responses of harvesters to those actions, and effects on fish population dynamics. Furthermore, these operating models attempt to reflect reality by basing choices of management actions on estimates of the "true" population (i.e., from simulated surveys of abundance), but in contrast to the real world, it is possible to compare the simulated "true" abundance in a computer model with the simulated estimate of abundance. When management actions are evaluated prospectively in this way, the degree to which objectives are achieved can therefore be identified and the relative performances of different management procedures can be assessed (de la Mare 1996).

Fisheries managers often have many options for changes to current management practices. These options usually pertain to different steps in a management procedure. For example, recent evidence suggests that forecasting accuracy might be improved by newly developed forecasting models that account for uncertainty in age-at-maturity of sockeye salmon (*Oncorhynchus nerka*) (Holt and Peterman 2004). Furthermore, harvest rules that account for the commonly observed types and magnitudes of uncertainty in outcomes from implementing fishing regulations, i.e., outcome uncertainty, may improve the accuracy with which management targets are achieved for sockeye salmon (Holt and Peterman 2006). A simulated comparison of practices that use these modifications with practices that ignore them (i.e., the base case) may help scientists and managers focus efforts on actions that will best achieve management objectives.

Our research objective was to use computer simulations to evaluate the respective benefits of two modifications to the base case, one that improved realism (and potentially the accuracy) of one type of forecasting model and another that took into account outcome uncertainty for sockeye salmon fisheries in British Columbia and Alaska. This paper emphasizes a more comprehensive method for evaluating performance of different modifications to management practices for Pacific salmon than is normally the case. Our two examples of salmon populations demonstrate the method rather than make recommendations for specific practices to be applied to particular fisheries on sockeye salmon.

More specifically, the first modification to the base case (i.e., the procedure that ignored those two sources of uncertainty) pertained to forecasts of recruitment of sockeye salmon prior to the fishing season (the number of adults that return to freshwater every year and become vulnerable to the fishery). Forecasting models such as the "sibling model" (Peterman 1982; Wood et al. 1997) are used by industry to help prepare for the fishery and by management to set early-season regulations. We developed a new Kalman-filter version of this model that in a retrospective analysis, improved forecasts for some stocks by accounting for long-term time trends in age-at-maturity (Holt and Peterman 2004). However, any tendency to improve achievement of management objectives (e.g., escapement goals or the target number of spawners) owing to more accurate forecasts could be swamped by large natural variation in recruitment or deviations between management targets and outcomes from fishing regulations (outcome uncertainty), negating the usefulness of this new forecasting model. In other words, it is not clear whether, in practice, this modification to the forecasting method will help managers more accurately achieve management objectives when that method is embedded in a larger fisheries system with its inherent complexity.

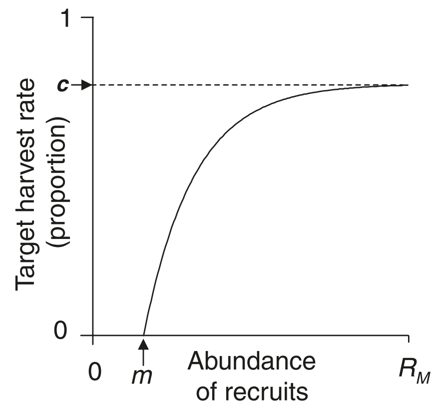
Our second modification to the base case pertains to how target escapements or target harvest rates are identified by stock assessment scientists. One way to set a target is to simulate the fisheries system in a simple computer model and use an optimization routine to search for the escapement goal or state-dependent harvest rule (e.g., Fig. 2) that best achieves a given management objective. However, the fact that actual harvest levels often deviate substantially from targets (Bocking and Peterman 1988; Eggers 1992; Holt and Peterman 2006) is rarely accounted for when comparing performances of various escapement goals or harvest rules in these types of simulation models (McAllister et al. 1999; Kell et al. 2005). Such deviations (outcome uncertainties) arise from, for example, incomplete compliance by harvesters and incomplete control over outcomes by management agencies after issuing fishing regulations (''implementation uncertainty'' or ''implementation error''; Rosenberg and Brault 1993; Kell et al. 1999), temporal variability in catchability of fish (Cass et al. 2003), and numbers of fishing vessels, as well as errors in estimating fish abundance (Rosenberg and Restrepo 1994). Intuitively, we might expect that management performance could be improved by taking these factors into account prior to setting fishing regulations (e.g., by appropriately adjusting escapement goals or harvest rules). However, again the extent to which improvements are possible is unknown because of the system's complexity and feedback loops. Thus, to clarify the relative merits of these two modifications to the base case, we conducted simulations to determine the net effect of accounting for uncertainties in age-at-maturity in the forecasting model and outcomes of fishing regulations.

Materials and methods

Data

To parameterize the simulation model for evaluating management procedures, we used previously compiled data on age-specific escapement and total recruitment for two sockeye salmon stocks: Togiak River, Bristol Bay, Alaska (brood years 1952–1998) (Michael Link, LGL, Alaska Research Associates, 1101 East 76th Avenue, Anchorage, AK 99518, USA, personal communication), and Chilko Lake, Fraser River (part of the summer run-timing group), British Columbia (brood years 1948–1998) (Michael LaPointe, Pacific Salmon Commission, 600 – 1155 Robson Street, Vancouver, BC V6E 1B5, Canada, personal communication). For Togiak, estimates of recruitment included the sum of spawning escapement (estimated visually from counting towers) and catch from commercial, recreational, subsistence, personal-use, and test fisheries (Plotnick and Eggers 2004). For Chilko, estimates of recruitment included the sum of spawning escapement (estimated from mark–recapture studies), catch from marine and in-river commercial and test fisheries, Fraser River First Nations harvests, and recreational fisheries, as well as estimates of en-route mortality (Pacific Salmon Commission 2001). Parameters for observation errors in escapement were estimated from repeated tower counts in Bristol Bay, Alaska (2004–2005) (Tim Baker, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518-159, USA, personal communication), and from unpublished mark–recapture studies in the Fraser River, British Columbia (2001–2004) (Timber Whitehouse, Fisheries and Oceans Canada, B.C. Interior Area Science Branch, 985 McGill Place, Kamloops, BC V2C 6X6, Canada, personal communication). Parameters for the outcome-uncertainty component were estimated from empirical records of target and actual (''realized'') escapements for the Togiak River (1962–2004) and from target and realized harvest rates for Chilko Lake (estimated from harvest rates on the summer run-timing group of Fraser River sockeye salmon, 1986–2003) (Holt and Peterman 2006). For Chilko sockeye only, we used previously compiled data on the proportion of spawners that were effective females (1948–1998) (Michael LaPointe, personal communication) to convert total spawner abundance to effective female spawners, as is the standard practice for Fraser River sockeye salmon.

Fig. 2. Example of a harvest rule used to identify target harvest rates for sockeye salmon (*Oncorhynchus nerka*) fisheries in the Fraser River, British Columbia. Parameter m is the protection level in abundance of recruits below which target harvest rate is zero, c is the maximum target harvest rate at high recruitment, and R_M is the maximum observed recruitment. In many salmon fisheries (depending on the management objective), m is the escapement goal, or target number of spawners.



Current management approaches differ for these two stocks. Togiak sockeye salmon are managed for an escapement goal and Chilko sockeye salmon are managed, in part, using a harvest rule (as in Fig. 2). Therefore, the simulation models used to evaluate management options for these populations also differed.

Simulation model for evaluating management procedures

The simulation model used to evaluate management procedures had five components that simulated different aspects of the fishery: population dynamics, the management procedure (which contained an observation submodel, a forecasting submodel, and a decision algorithm to select the management target), steps taken to choose the decision algorithm, the effects of harvesting on the population (including outcome uncertainty), and a performance module (Fig. 1). We describe each component (boxes in Fig. 1) in more detail below. All equations are in Appendix A (Table A1).

Population dynamics component

We simulated the dynamics of hypothetical true sockeye salmon populations for 50 years, repeated over 500 Monte Carlo trials to incorporate stochastic variability in recruitment, age-at-maturity, and proportion of escapement that was effective female spawners (the latter for Chilko only) (box 1 of Fig. 1). That number of Monte Carlo trials was

Table 1. Description of the three management procedures that we evaluated in the simulation model.

	Components of management procedure	
	Forecasting submodel	Decision-algorithm submodel
Base case	Assumes that parameters are constant	Assumes that management targets are achieved exactly
VM procedure	Time-varying parameters accounted for by using a Kalman filter	Assumes that management targets are achieved exactly
OU procedure	Assumes that parameters of the forecasting submodel are constant	Management targets are adjusted for outcome uncertainty

Note: The VM (variable-maturity) procedure is a modification to the base case that accounts for uncertainty in age-at-maturity in the forecasting submodel. The OU (outcome-uncertainty) procedure is a modification to the base case that accounts for outcome uncertainty through a decision-algorithm submodel. The second and third columns describe our modifications to these two components of the management procedure: the forecasting submodel and the decision-algorithm submodel.

necessary to stabilize output metrics recorded in the performance component of the model.

For Togiak, true spawner abundance in a given brood year was used to calculate recruitment resulting from that spawning using a standard Ricker model, which included lognormally distributed, autocorrelated random variation (the latter with a one-year time lag) (Appendix A, Table A1, eq. A1). For this and all subsequent relations, parameters (Appendix A, Table A1, right side of table) were estimated from historical data using maximum likelihood methods, unless stated otherwise.

For Chilko, we used the slightly more complex Larkin spawner–recruit relation (Walters and Staley 1987) because this relation captures this stock's four-year cyclic pattern in abundance of recruits (Appendix A, Table A1, eq. A2). The abundance of the "dominant" line of Chilko Lake sockeye that occurs every fourth year consistently exceeds that of the subsequent "subdominant" line and the following two "off-cycle" lines.

For both Togiak and Chilko simulations, historical recruitment data were used to estimate the mean proportion of fish of a given freshwater age that matured at each ocean age, as well as to estimate a time trend to reflect the simulated rate of increase in mean ocean age observed for these stocks over the last 50 years (Appendix A, Table A1, eq. A3). For example, for the base case for Togiak for the fish that spent two winters in freshwater, our data show that the proportion that returned after only two winters in the ocean instead of three declined from 0.53 to 0.39 from 1952 to 1998 (and the proportion that returned after three ocean winters increased from 0.47 to 0.61). When combined over all age classes, the increase in mean age-at-maturity for Togiak was 0.186 years, but for Chilko (1948–1998), this increase was much smaller (0.049 years). The simulation model also included natural interannual variation in age-at-maturity according to a multivariate logistic distribution (as in Schnute and Richards 1995) (Appendix A, Table A1, eqs. A4 and A5). Finally, for Chilko Lake sockeye salmon, we calculated the proportion of effective female spawners and incorporated interannual variability into that proportion using a beta distribution parameterized using historical spawner data (Appendix A, Table A1, eqs. A6–A8).

Management procedure

Management actions were broken down into three submodels (box 2 of Fig. 1): (2*a*) observations of abundances of recruitment from total catch and surveys of escapement, (2*b*) forecasts of recruitment using the sibling model, and (2*c*) selection of escapement goal or target harvest rate as specified by a decision algorithm. We evaluated three different management procedures in simulations of the fisheries system (Table 1). The first management procedure represented the base case. The second was a modification of the base case in which the forecasting submodel accounted for time-varying parameters associated with age-at-maturity using a Kalman-filter technique (the variable-maturity or VM procedure). The third was another modification to the base case that adjusted management targets for outcome uncertainties (the outcome-uncertainty or OU procedure), rather than assuming that targets were met exactly.

Observation submodel

The observed number of spawners each year was calculated from the "true" (i.e., simulated abundances in the population dynamics component of the simulation model) number of spawners and multiplicative, lognormally distributed random variability (as in Cass et al. 2003) (box 2*a* of Fig. 1; Appendix A, Table A1, eq. A9). The latter random deviations represent both errors in visual observations of spawner abundance and sampling variability. We assumed that catch was known perfectly and that errors due to stock misidentification were negligible for the Togiak and Chilko sockeye stocks, as determined by analyses of scale patterns and locations of catch that are separate from other stocks (T. Baker, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518-159, USA, personal communication; T. Whitehouse, Fisheries and Oceans Canada, B.C. Interior Area Science Branch, 985 McGill Place, Kamloops, BC V2C 6X6, Canada, personal communication). In addition, we assumed perfect knowledge of fish age and proportion of spawners that was effective females.

To properly parameterize natural process variation in recruitment (ν or γ, depending on the stock, in eqs. A1 and A2 of Appendix A, Table A1) and observation error (κ, eq. A9 of Appendix A, Table A1), we estimated variability from those two specific sources of the total observed variability in recruitment (see Appendix B for more details).

Forecasting submodel

We implemented two different forecasting submodels. For the base case and OU procedure, we applied the widely used standard linear sibling model that assumed constant parameters over time to forecast age-specific recruitment (box 2*b* of Fig. 1 and Appendix A, Table A1, eq. A10). However, for the VM procedure, we modified that standard sibling model to account for temporal changes in age-at-maturity using a Kalman-filter estimation scheme (see Holt and Peterman (2004) for a description of these two parameterizations of the sibling model and Appendix A, Table A1, eqs. A10 and A11). To forecast the abundance of the youngest age class for each freshwater age, we simply used recruitment in the previous generation, instead of the sibling model (as in Haeseker et al. 2007). The standard or Kalman-filter models were used to forecast all older age classes.

Selection of escapement goal or target harvest rate

An annual management target was then chosen based on a decision algorithm (i.e., an escapement goal or target harvest rule) (box 2*c* of Fig. 1) that was identified in the decision-algorithm submodel (box 3 of Fig. 1, described below). For Chilko, a management target was identified from a target harvest rule, and for Togiak, an escapement goal was used.

Decision-algorithm submodel

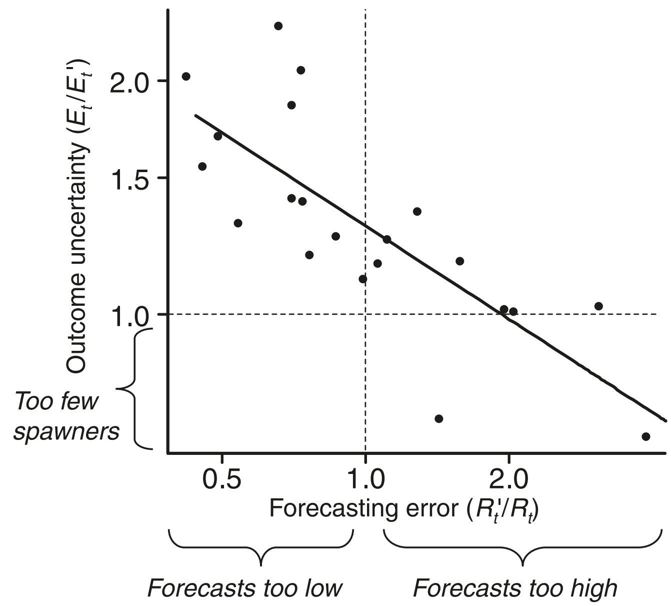
The decision algorithm was selected in a submodel, which was simulated separately from the main model used to evaluate management options (i.e., it was run once for each management procedure and stock in our experimental design) (box 3 of Fig. 1). Specifically, in the decision-algorithm submodel, we simulated the biological system and management actions using various targets to identify the one that best met management objectives among those considered.

For both stocks, we assumed that the objective was to maximize yield while meeting two constraints: allowing no more than a 10% chance of catch dropping below 10% of maximum sustainable yield (MSY) and no more than a 10% chance of spawner abundances dropping below 10% of the spawner abundance associated with maximum recruitment (SMR) in each year. Although the latter reference point is unusual, it is similar to what was used for the Sockeye Salmon Spawning Initiative, a recent project aimed at revising management procedures for Fraser River, British Columbia, sockeye fisheries (Cass et al. 2003). Such management constraints are often not explicitly documented, so our two constraints represent only one example of possible trade-offs between maximizing catch and minimizing population declines.

This decision-algorithm submodel was similar to the overall simulation model, with some simplifying assumptions. These assumptions (described in Appendix C) reflect factors commonly considered by managers when choosing decision algorithms. However, comprehensive quantitative analyses of decision-algorithm submodels, such as ours in box 3 of Fig. 1, are not routinely performed for Fraser River or Bristol Bay sockeye salmon when identifying decision algorithms.

We ran the decision-algorithm submodel twice for each stock. First, we ran it to identify management targets that ignored outcome uncertainty (an escapement goal for Togiak and a state-dependent harvest rule with parameters c, d, and m for Chilko, as shown in Fig. 2) (Appendix A, Table A1, eq. A12). Second, we ran it to identify targets that took outcome uncertainty into account (a revised escapement goal for Togiak and a harvest rule with parameters c^*, d^*, and m^* for Chilko) (Appendix A, Table A1, eq. A13). For Togiak, the decision-algorithm submodel simulated the bias

Fig. 3. Relation between annual preseason forecasting error in abundance of adult recruits (R_t'/R_t) and outcome uncertainty (E_t/E_t') plotted on a logarithmic scale, where R_t' is the forecast of recruitment in year t, R_t is realized recruitment, E_t is realized escapement, and E_t' is the escapement goal for Togiak River sockeye salmon (*Oncorhynchus nerka*), Bristol Bay, Alaska (1984–2004) ($r^2 = 0.65$, $P < 0.001$). The vertical broken line represents a perfect forecast ($R_t'/R_t = 1.0$) and the horizontal broken line represents an escapement goal that is achieved exactly ($E_t/E_t' = 1.0$). This relation is equivalent to that between $\{\log_e(R_t') - \log_e(R_t)\}$ and $\{\log_e(E_t) - \log_e(E_t')\}$.



in deviations between realized and target escapement that appears in the historical data. Specifically, preseason forecasting errors were negatively related to deviations between realized and target escapements for that stock (Fig. 3; $p < 0.001$). For example, when preseason forecasts underestimated the actual, realized recruitment (i.e., to the left of 1.0 on the x axis of Fig. 3), more fish returned to spawning grounds than targeted by the escapement goal. Fewer fish escaped the fishery than targeted in only 2 out of 21 years (i.e., 2 points fell below 1.0 on the y axis of Fig. 3). This tendency towards over-escapement arises because of incentives for Togiak managers to meet or exceed the escapement goal (Hilborn 2006). In the decision algorithm that accounted for outcome uncertainty for Togiak sockeye, we used the relation in Fig. 3 and calculated escapement deviations (i.e., $\log_e(E_t/E_t')$, where E_t is realized escapement and E_t' is target escapement) as a linear function of forecasting errors (i.e., $\log_e(R_t'/R_t)$, where R' is the forecast of recruitment and R is realized recruitment) plus normally distributed variability (Appendix A, Table A1, eq. A14).

In contrast, data for Chilko Lake sockeye show no evidence of consistent bias in realized harvest rates compared with targets (as part of the summer run-timing group of the Fraser River; Holt and Peterman 2006), so we simulated imprecision in the outcome from the target harvest rule without bias. Specifically, we included beta-distributed random variability in the realized harvest rate of Chilko sockeye between zero and one to simulate imprecision in outcomes (Appendix A, Table A1, eqs. A15–A17).

Harvesting and escapement

In the simulation model's fourth component, we simulated escapement to spawning grounds after harvesting (box 4 of Fig. 1) while adding the effect of uncertainty in outcomes of applying management targets (as described above for the decision-algorithm submodel; Appendix A, Table A1, eq. A14 for Togiak rearranged to solve for realized escapement, E_t, and eqs. A15–A18 for Chilko). For Togiak, that outcome uncertainty was based on the stochastic relation in Fig. 3, which reflects the historical association between outcome uncertainty and forecasting error. We do not imply that this is a direct causal relation, but rather that it is the net result of interactions among accuracy of forecasts of recruitment, the timing and magnitude of in-season updates of abundance, and management actions (Holt and Peterman 2004). Such associations are commonly observed in salmon fisheries. When forecasts overestimate recruitment (which tends to happen at low abundances) (Appendix C, eq. C2), by the time in-season updates are available, it is often too late to restrict harvest pressure to achieve management goals (Bocking and Peterman 1988). In contrast, when forecasts underestimate recruitment, by the time in-season updates are available, it tends to be too late to allow sufficient harvest pressure to achieve goals (Bocking and Peterman 1988). Other sources of uncertainty in outcomes compared with targets are accounted for implicitly by stochastic variability parameterized with historical data. Unlike Togiak, management targets for Chilko are derived from a target harvest rule and forecasts of recruitment, and deviations between management targets and outcomes are not associated with forecasting accuracy. Therefore, forecasts of abundance of adult recruits (not accuracy of those forecasts) were used to identify management targets from the harvest rule for the Chilko stock, and outcome uncertainties were stochastic deviations from that target, parameterized with empirical data (Appendix A, Table A1, eqs. A15–A17).

Historical escapement data that were used to parameterize this component of the model contain observation error as one component of outcome uncertainty. For the overall simulation model that evaluated management options, we separated observation error (as it was already simulated in the observation submodel) using the same method as that used for separating observation error in recruitment from natural variability (see Appendix B).

Performance component

To evaluate how well management procedures achieved objectives, the following metrics were averaged over each 50-year simulation period and over Monte Carlo trials (box 5 in Fig. 1): (1) mean annual catch; (2) proportion of years when catch dropped below 0.1·MSY; (3) proportion of years when escapement dropped below 0.1·SMR (10% of spawner abundance at maximum recruitment); (4) median percent change in catch between successive years; (5) root-mean-square (RMS) forecasting error; (6) mean absolute forecasting error; and (7) mean of the absolute deviations between target and realized escapements or harvest rates.

In addition to those attributes described by the initial management objective (performance metrics 1 through 3), harvesters may prefer reductions in variability of catch among years (captured by metric 4), whereas scientists and managers may be more concerned about forecasting errors (metrics 5 and 6, referred to as RMS forecasting error and bias of forecast, respectively) and deviations between management targets and outcomes (metric 7).

Sensitivity analyses

We evaluated the sensitivity of the rank order of the three management procedures to different assumptions: (*i*) larger increases in age-at-maturity over time than those previously observed in past field data, (*ii*) sinusoidal time trends in age-at-maturity, (*iii*) constant age-at-maturity, and (*iv*) larger magnitudes of observation errors than typically seen for these stocks relative to natural variation in recruitment and outcome uncertainty. We also identified the maximum potential improvement in mean annual catch that would occur over the base case if we assumed that the forecasting model was perfectly accurate.

Finally, we examined the potential consequences of adjusting harvest regulations for outcome uncertainties when such uncertainties do not exist in the "true" population. Specifically, we omitted outcome uncertainty from the simulation model used to evaluate management options and calculated the difference in mean annual catch between a practice that used the OU procedure and the base case that did not. In other words, we evaluated the potential reductions in performance when outcome uncertainty was mistakenly accounted for (when it did not occur in the "true" population), compared with the base case. Although this scenario is unlikely, it provides an upper bound on the magnitude of losses incurred by incorrectly accounting for outcome uncertainty.

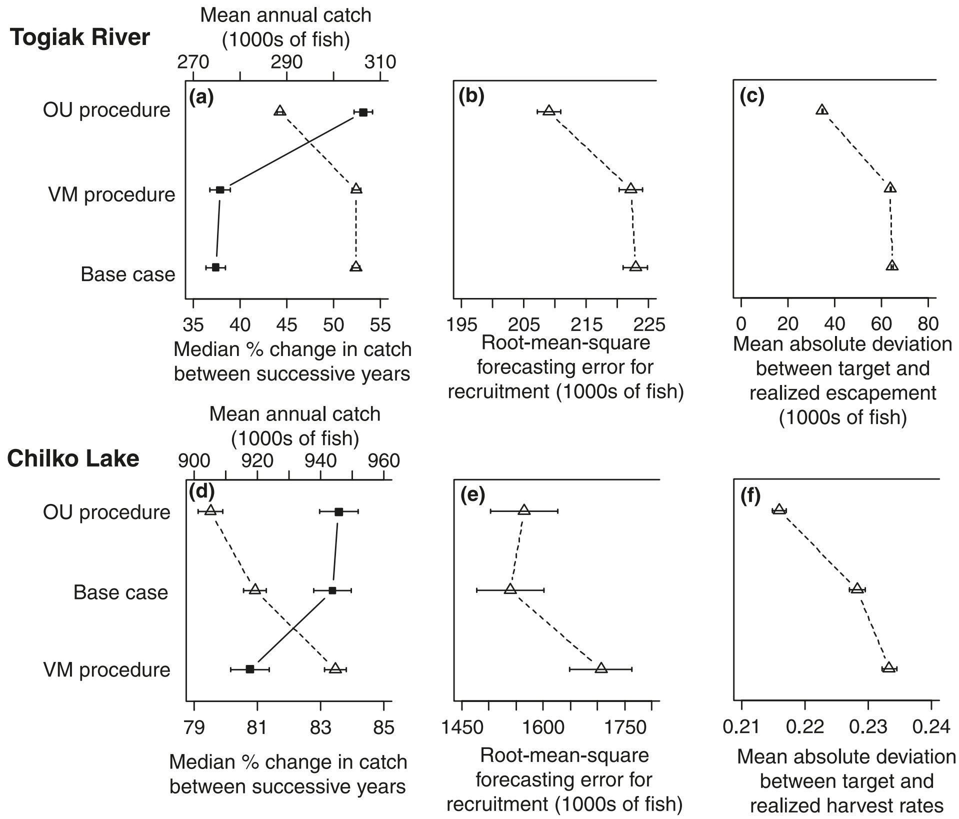
Results

We expected that the procedure that accounted for outcome uncertainty when identifying a target escapement or harvest rule (the OU procedure) would have higher mean abundance and annual catch and hence would better achieve management objectives than the procedures that ignored that source of uncertainty. Similarly, because our scenarios assumed long-term trends in age-at-maturity in the "true" population, we expected that when simulated over years and Monte Carlo trials, the management procedure that forecasted recruitment using a sibling model that accounted for those trends in age-at-maturity (the VM procedure) would have lower forecasting errors, improved accuracy of achieving management targets, and therefore higher mean annual catch than the base case that used a standard sibling model (which assumed a constant proportion of maturing fish in each age class).

Togiak

We present results first for Togiak and then for Chilko. As expected, compared with the base case, mean annual catch for Togiak sockeye salmon was higher for the OU procedure by 31 418 fish (11.4%) (Fig. 4*a*). For this OU procedure, the escapement goal (132 660 spawners) was lower than the goal that ignored that source of uncertainty

Fig. 4. Trade-offs in performance metrics for (*a*, *b*, and *c*) salmon fisheries on Togiak River, Bristol Bay, Alaska, and (*d*, *e*, and *f*) Chilko Lake, Fraser River, British Columbia, sockeye salmon (*Oncorhynchus nerka*) for three management procedures: outcome-uncertainty (OU) procedure, variable-maturity (VM) procedure, and base case, arranged on the vertical axis according to their rank in mean annual catch (different rankings for Togiak and Chilko). (*a* and *d*) Mean annual catch in 1000s of fish (solid lines and solid squares); median percent change in catch between successive years (i.e., catch variability; broken lines and open triangles); (*b* and *e*), root-mean-square forecasting error for recruitment (i.e., RMS forecasting error); (*c*) mean absolute deviation between target and realized escapement; and (*f*) mean absolute deviation between target and realized harvest rates (proportions). Error bars represent ± one standard error of the mean result across 500 Monte Carlo trials, except in (c) where the error bars are too narrow to distinguish from the mean.



(179 176 spawners); that lower goal compensated for the observed tendency for over-escapement (Fig. 3). Compared with the base case, mean annual catch tended to be higher for the VM procedure, i.e., the one that accounted for long-term trends in age-at-maturity, but this difference was small (943 fish or 0.3% of mean annual catch for the base case). For this and the subsequent five plots in Fig. 4, management procedures are placed on the *y* axis according to their rank in mean annual catch, with the highest on top (Figs. 4*a* and 4*d*). To show trade-offs between mean annual catch and other performance metrics, values for additional metrics are included in Figs. 4*a*–4*f*, scaled according to the bottom *x* axis.

The mean proportion of years when annual catch dropped below 0.1·MSY was consistently low for all three procedures and so is not shown here (<0.07, i.e., less than the 0.1 stated in the management objective). This was also true for the mean proportion of years in which spawning abundance dropped below 0.1·SMR (<0.001, i.e., less than the 0.1 management objective). Because sockeye spawning stocks of Bristol Bay, Alaska, are often compared with their expected spawner abundance at the unfished equilibrium, S_{eq}, we further calculated the mean proportion of years when spawning abundance dropped below $0.1 \cdot S_{eq}$. Again, this value was low for all procedures (<0.001).

For the remaining four performance metrics (interannual variability in catch, RMS forecasting error, bias in forecasts, and deviations between targets and outcomes), the rank orders of management procedures for Togiak were consistent with the rank order for mean annual catch. For example, management procedures that had the highest mean annual catch also had the lowest catch variability (i.e., performance improved on both metrics) (Fig. 4*a*). In contrast to our initial expectations, the RMS forecasting error for Togiak sockeye was not consistently smaller for the VM procedure compared with the base case, even though long-term trends in age-at-maturity occurred in the simulated “true” population (Fig. 4*b*). However, compared with the base case, the RMS forecasting error was consistently smaller for the OU procedure (Fig. 4*b*). Forecasts for the OU and VM procedures were also less negatively biased than the base case and the absolute magnitude of bias was reduced (not shown). As expected, compared with the base case, deviations between target and realized escapement were smaller (performance improved) for the OU procedure (i.e., by 29 856 spawners or 46% of the mean deviation for the base case) (Fig. 4*c*). That metric was also lower for the VM procedure compared with the base case, but only by 855 spawners or 1.3% of the mean deviation for the base case.

To summarize results for Togiak, the OU procedure outperformed the base case on all performance measures and either outperformed or performed as well as the VM procedure.

Chilko

Chilko results were qualitatively similar to those of Togiak; mean annual catches were higher for the OU procedure compared with the base case, but this increase was small (1944 fish or 0.2% of mean annual catch for the base case) (Fig. 4*d*). In contrast to our initial expectations, compared with the base case, mean annual catches were lower for the VM procedure (by 25 967 fish, or a 2.8% decrease in mean annual catch).

As was the case for Togiak, the mean proportion of years when annual catch of Chilko Lake sockeye dropped below 0.1·MSY, and the mean proportion of years when spawning abundance dropped below 0.1·SMR, were consistently low for all procedures (<0.07 and <0.06, respectively, i.e., less than the 0.1 in the management objective).

The time series of catches were least variable for the OU procedure, followed by the base case, and VM procedure in order of increasing variability (Fig. 4*d*). However, the range of percent change in catch across those cases was small (<4%). Counter to expectations, the RMS forecasting errors of the VM and OU procedures were larger (i.e., had worse performance) than those errors for the base case (Fig. 4*e*). In contrast, the two modified management procedures had forecasts with smaller positive bias by 4% to 41% compared with the base case (not shown). Deviations between target and realized harvest rates were about 1% smaller for the OU procedure compared with the base case, and the VM procedure was 0.5% greater (Fig. 4*f*).

Although the OU procedure outperformed the VM procedure and the base case on many performance metrics for Chilko, these improvements were small compared with those observed for Togiak (e.g., 1% increase in mean annual catch for the OU procedure over the base case for Chilko compared with an 11% increase for Togiak). The base case outperformed the VM procedure on all performance metrics for Chilko Lake sockeye salmon.

Sensitivity analyses

For both stocks, the rank order of management procedures did not change during our sensitivity analyses. First, there was no change in ranking when evaluating different time trends in age-at-maturity (annual increases twice as large as those observed historically, sinusoidal changes, or no long-term trends). For example, for Togiak sockeye salmon, the relatively small (<1%) increase in catch for the VM procedure over the base-case management procedure occurred regardless of the trends in age-at-maturity in the "true" population. Furthermore, for both stocks, the rank order of management procedures was not sensitive to increases in the magnitude of observation error relative to natural variation in recruitment and outcome uncertainty. When we assumed that the forecasting submodel was perfectly accurate, mean annual catches increased over the base case by 16% and 13% for Togiak and Chilko, respectively.

In a final sensitivity analysis, we asked what would happen if, in the management of the simulated "true" population, targets were achieved exactly, yet the management procedure mistakenly assumed that the target would be missed due to outcome uncertainty and adjusted management actions accordingly. For such cases where management procedures "mistakenly" accounted for outcome uncertainties, the mean annual catches were lower than the base-case management procedure by 2% and 5% for Togiak and Chilko, respectively.

Discussion

Although accounting for key biological and outcome uncertainties in stock assessments may a priori seem justifiable for improving the assessment and management of sockeye salmon, alterations to any one component of our simulated fisheries system did not necessarily enhance performance overall. For example, accounting for outcome uncertainty with the OU management procedure improved management performance, especially for Togiak, but accounting for uncertainty in age-at-maturity in the forecasting submodel with the VM procedure did not. Although our primary interest was to demonstrate a method for evaluating management options, our results suggest that scientists and managers should consider evaluating management practices that adjust management targets to reflect outcome uncertainty instead of (or in addition to) practices that only attempt to improve forecasts of abundance.

Improvements from accounting for outcome uncertainty

Compared with the base case, the management procedure that accounted for outcome uncertainty resulted in larger catches that were less variable from year-to-year for both Togiak and Chilko. This result can be explained for Togiak by the bias that causes realized escapements to exceed targets, as evident in the historical record for that stock. When target escapements are adjusted downwards to compensate for that bias, a larger proportion of the recruitment can be harvested (so mean annual catches increase). Not surprisingly, deviations between target and realized escapements were lower for the OU management procedure compared with the base case. Therefore, by ignoring the historical differences between management targets and outcomes, managers of Togiak sockeye salmon may be inadvertently foregoing some long-term catch. However, if objectives differ from those implied by historical data (e.g., due to incentives by managers to allow over-escapement; Hilborn 2006), then adjustments to the targets such as our simulated ones may be inappropriate. Nevertheless, those deviations should be quantified and explained.

Similarly, for Chilko, the management procedure that accounted for outcome uncertainties was better able to maintain high levels of catch. However, in contrast to Togiak, the outcome of harvest rates for Chilko sockeye was unbiased both in the historical record and in the "true" population in our simulation model of the fisheries system. Thus, improvements in mean annual catch were due only to accounting for the imprecision in achieving target harvest rates, and those benefits were relatively small.

In our base-case analysis, we assumed that the outcomes from applying management regulations differed from targets in the "true" population. In the sensitivity analysis, when we instead assumed that outcomes exactly matched targets but managers (incorrectly) accounted for outcome uncertainty, the reduction in mean annual catch over the base case for Togiak (2%) was much less than the increase in catch (11%) when the opposite occurred (i.e., when managers correctly assumed that outcomes differed from targets). However, the opposite was true for Chilko. The losses from mistakenly adjusting target harvest rates (5% reduction in mean annual catch) were larger than the gains associated with adjusting target harvest rates when they were, in fact, implemented with uncertainty in the "true" population (0.1% increase in mean annual catch).

Improvements from accounting for long-term trends in age-at-maturity

For Togiak, the management procedure that accounted for time-varying age-at-maturity (the VM procedure) improved forecasting accuracy only slightly over the base case, and for Chilko, such forecasts were consistently less accurate. The latter inaccurate forecasts were due, in part, to the tendency of the forecasting submodel that used a Kalman filter (the VM procedure) to track random variability in age-specific recruitment ("noise") and the cyclic patterns in Chilko recruitment instead of long-term trends in age-at-maturity, which reflected relatively small changes for that stock. This situation resulted in large interannual variability in parameters of the Kalman-filter version of the forecasting submodel and, hence, relatively inaccurate forecasts of recruitment and reductions in mean annual catch. Furthermore, the rank order of management procedures was independent of long-term trends in age-at-maturity in the "true" population (as shown in our sensitivity analyses), also suggesting that the VM procedure was unable to appropriately capture these trends for Chilko Lake sockeye salmon.

For the standard sibling model for Chilko Lake sockeye, forecasting accuracy improved when outcome uncertainties were ignored (i.e., the base case was better than the OU procedure). This result may be due to increased variability in recruitment and catch, resulting in larger contrast in simulated observed data and therefore better estimates of parameters of the forecasting submodel. However, any increases in such forecasting accuracy for Chilko did not result in increased mean annual catch. For Togiak, management procedures that ignored outcome uncertainties (and reduced management control) did not improve forecasting.

Nevertheless, larger improvements in forecast accuracy with other future modifications to the sibling or other models that were not considered here (e.g., Haeseker et al. 2007) may result in improved mean annual catch. For example, the potential increase in mean annual catch over the base case with a completely accurate forecasting submodel ranged from 13% to 16%. However, given large natural variability in population dynamics, ecological interactions within and among stocks, and effects of changing climate, such large improvements in forecasting accuracy may be unlikely in the foreseeable future.

We also evaluated the performance of a procedure that accounted for both variable maturity in the forecasting submodel as well as outcome uncertainties in the harvest rule or target escapement. Results were dominated by the influence of only one modification, i.e., either the VM or OU procedure, depending on the stock as reported above; the combination did not perform better.

Comparison with previous research: outcome uncertainty

Despite repeated recommendations to incorporate implementation uncertainties (one component of outcome uncertainties) into simulation models when evaluating management options for various fisheries (e.g., Rice and Richards 1996; McAllister et al. 1999), fisheries models that include them are the exception rather than the rule. Previous studies that incorporated outcome uncertainties into simulation models assumed that those differences were either deterministic (i.e., a fixed bias) (Kell et al. 1999) or, if stochastic, that they were unbiased with respect to the target (Johnston et al. 2000). In the few cases where both imprecision and bias have been included, they have been parameterized qualitatively either using only limited empirical data (Kell et al. 1999; Peterman et al. 2000) or expert opinion (Kell et al. 1999). Furthermore, with one exception (Cass et al. 2003), previous studies have not evaluated decision algorithms that specifically account for these deviations. Cass et al. (2003) identified harvest rules for two Fraser River stocks that accounted for uncertainty in achieving management targets by assuming that differences between realized harvest rates and targets were characterized by a random normal deviation around the target, as parameterized by expert judgment. Similar to our results for Chilko, those authors found that accounting for imprecision in this type of uncertainty resulted in relatively small changes in the form of the target harvest rule (Cass et al. 2003). However, in contrast to our study, Cass et al. (2003) took into account only imprecision in outcome uncertainty, and not bias plus imprecision, when evaluating management options.

Comparisons with previous research: evaluating forecasting models

Several studies have quantitatively evaluated the performance of a wide range of forecasting models for sockeye salmon (Wood et al. 1997; Peterman et al. 2000; Haeseker et al. 2007), but none has prospectively evaluated sibling forecasting models that use a Kalman filter, let alone by using a simulation model of an entire fishery system. A common assumption in these other studies is that improvements in forecasting accuracy will result in higher yields and economic gains, but our results show that this is not necessarily the case.

One example of a study that supported the assumption that more accurate forecasts improve management performance used a computer simulation model to evaluate another type of forecasting model, the spawner–recruit relation (Peterman et al. 2000). That study compared parameter estimation methods that did not account for long-term trends in productivity with a Kalman-filter method that did. In contrast to our results, they found that the forecasting model that used a Kalman filter had higher cumulative catches compared with the standard forecasting model. However, Peterman et al. (2000) used a different derivation of outcome uncertainty (for both bias and imprecision) than we did in our study. Furthermore, they simulated much larger temporal changes in the variable being estimated (the Ricker *a* parameter) than we did for our variable (the *y* intercept of the sibling model, representing relative ages-at-maturity).

Limitations

Interpretations of our results are affected by at least four limitations. First, the performance of the two modifications to current practices depends on our assumptions about dynamics and structure of the fishery, including assumptions about which components to consider uncertain. For example, for Togiak, we assumed that the realized number of spawners exceeded escapement goals when forecasts underestimated actual run size, and vice versa, and that forecasts overestimated run size when abundance of returns was low, and vice versa. Our results may change if outcomes of fishing regulations vary in ways not captured by those two relations. Although these relations were empirically based, forecasting accuracy may act as a surrogate for other factors that determine outcome uncertainties.

Second, large stock-to-stock differences in population dynamics and management approaches preclude generalizing our results to other sockeye salmon stocks with confidence, let alone to other species. However, it is more likely that the OU procedure will outperform the base-case management procedure when outcome uncertainty in the "true" population creates a bias between targets and realized outcomes, rather than just imprecision. In addition, it is unlikely that the VM procedure will perform well in other sockeye salmon stocks that show large among-year variability in recruitment (e.g., for cyclic stocks such as Chilko).

Third, within-season forecasts of recruitment of sockeye salmon often replace preseason forecasts fairly early in the fishing season as more accurate estimates of abundance become available, but these within-season forecasts were not explicitly incorporated into our management procedures. However, within-season forecasts were implicit in our relations used to calculate outcome uncertainty in the "true" population because parameters of these relations were estimated from empirical data for years in which management agencies used within-season updates of recruitment. Nevertheless, it is unclear how our results would have changed if we had simulated complex within-season management.

Fourth, although we updated the forecasting submodel with annual recruitment data, we did not incorporate learning into our choice of management targets. Further improvements in performance may be expected with periodic updates of the decision-algorithm submodel (i.e., in a fully closed management feedback loop, sensu Walters 1986), especially if the management procedure and (or) natural variation creates sufficient contrast in spawner abundance to more accurately estimate parameters. Management procedures that include learning when identifying decision algorithms can be evaluated in a simulation model such as the one described here.

Management recommendations

This study shows that assessment methods with more realistic assumptions about the presence and nature of uncertainties may or may not result in improved performance when put in the context of an entire fishery. We therefore recommend that holistic simulations of fisheries be used to evaluate new assessment methods. Although few researchers have applied this approach to salmon, we are not alone in this recommendation. Many previous authors (e.g., de la Mare 1998; Cooke 1999; Punt 2006) suggested that proposed management procedures (including forecasting and decision-algorithm models) should be evaluated in as comprehensive of a simulation model as possible prior to applying them in a fishery. This simulation process was demonstrated for other fisheries such as North Sea plaice (Kell et al. 1999) and the Australian gemfish fishery (Punt and Smith 1999), to name two examples of many. By simulating a fishery over various future scenarios, such evaluations avoid the constraint of assuming that "history will repeat itself", as is implicitly assumed by retrospective analyses of historical data or real-time experiments. Furthermore, as suggested by many of the authors listed above, sensitivity analyses should be used to evaluate management procedures in the face of uncertainties in underlying models that describe system dynamics (McAllister et al. 1999; Punt and Smith 1999). For example, Cooke (1999) recommends considering different assumptions about spatial structure of stocks, trends in productivity over the medium and long terms, and interactions among species, as well as management scenarios with misleading data (i.e., observations and (or) assessments that do not reflect the state of the "true" population). In this way, managers can choose procedures that are relatively robust to structural uncertainty.

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Appendix A. Equations, notations, and parameters used in the simulation model

Table A1 follows.

Table A1. Description of equations, parameters, and variables used in the simulation model to evaluate management procedures. Para-
tion model in which that equation is used (boxes in Fig. 1). Values are given for parameters in the last two columns. NA represents

Description	Equation
Ricker spawner–recruit relation (used to simulate population dynamics, box 1)	(A1) $R_y = a_r S_y e^{-b_r S_y + \varphi_y},\ \varphi_y = \rho\varphi_{y-1} + \nu_y,\ \nu \sim N\left(-\frac{\sigma_r{}^2}{2}, \sigma_r{}^2\right)$, where the normal deviates are centered around $-\sigma^2/2$ to make the arithmetic mean of the lognormally distributed recruitment multiplier equal to 1
Larkin spawner–recruit relation (to simulate population dynamics, box 1)	(A2) $R_y = a_L S'_y e^{(-b_{L0}S'_y - b_{L1}S'_{y-1}) + \gamma_y},\ \gamma \sim N\left(-\frac{\sigma_L{}^2}{2}, \sigma_L{}^2\right)$
Mean proportion of recruits-at-age (used to simulate time trends, box 1)	(A3) $\overline{p}_{i,j,t} = a_{i,j} + b_{i,j}t$
Proportion of recruits-at-age calculated from a multivariate logistic distribution (Schnute and Richards 1995) (used to simulate population dynamics, box 1)	(A4) $p_{i,j,t} = \frac{e^{x_{i,j,t}}}{\sum_{j_i=1}^{J_i} e^{x_{i,j,t}}}$
Dummy variable used in eq. A4 above	(A5) $x_{i,j,t} = \log_e\left(\overline{p}_{i,j,t}\right) + \varpi_i\varepsilon_{i,t} - \frac{1}{J_i}\sum_{j_i=1}^{J_i}[\log_e(\overline{p}_{i,j,t}) + \varpi_i\varepsilon_{i,t}],\ \varepsilon \sim N(0, 1)$
Proportion of spawners that are effective females (used to simulate population dynamics, box 1)	(A6) $q_y = \mathrm{Beta}(\beta_{q_1}, \beta_{q_2})$
First parameter for eq. A6 above (Morgan and Henrion 1990)	(A7) $\beta_{q_1} = \frac{\mu_q{}^2 - \mu_q{}^3 - \sigma_q{}^2 \cdot \mu_q}{\sigma_q{}^2}$
Second parameter for eq. A6 above	(A8) $\beta_{q_2} = \frac{\mu_q(1-\mu_q)^2 - \sigma_q{}^2(1-\mu_q)}{\sigma_q{}^2}$
Uncertainty in observed spawner abundance (used to simulate observations of abundances, box 2*a*)	(A9) $S_{O,y} = S_y e^{\kappa_y},\ \kappa \sim N\left(-\frac{\sigma_\kappa{}^2}{2}, \sigma_\kappa{}^2\right)$

meters and variables are defined only at their first occurrence. The description in the first column includes the component of the simula-
parameters that were not used for that stock; blank cells in the last two columns correspond to variables.

Parameter or variable	Definition	Values: Togiak	Values: Chilko
y	Brood year		
r	Index designating parameters of the Ricker stock–recruitment relation		
R	Abundance of recruits		
S	Abundance of spawners		
a_r, b_r	Parameters of the Ricker spawner–recruit relation	5.55, 3.75×10^{-6}	NA
φ, ν	Stochastic terms		
ρ	Autocorrelation coefficient for the residual errors	0.25	NA
σ_r	Standard deviation in residuals	0.51	NA
L	Index designating parameters of the Larkin stock–recruitment relation		
S'	The number of effective female spawners ($S\times q$, see eq. A6)		
a_L, b_{L0}, b_{L1}	Parameters	NA	19.84, 2.25×10^{-6}, 2.33×10^{-6}
γ	Stochastic term		
σ_L	Standard deviation in residuals	NA	0.63
i	Number winters spent in freshwater		
j	Number of winters spent in the ocean		
$\overline{p}_{i.j}$	Mean proportion of recruits that spend i winters in freshwater and j in the ocean		
t	Simulated calendar year at return (t = 1–50)		
$a_{i.j}$, $b_{i.j}$	Y intercept and slope of relation between year t and $\overline{p}_{i.j}$	$a_{1.2} = 0.36$, $b_{1.2} = -3.8\times10^{-3}$, $a_{1.3} = 0.64$, $b_{1.3} = 3.7\times10^{-3}$, $a_{2.2} = 0.51$, $b_{2.2} = -3.5\times10^{-3}$	$a_{1.1} = 0.016$, $b_{1.1} = -1.7\times10^{-4}$, $a_{1.2} = 0.99$, $b_{1.2} = -2.0\times10^{-3}$
p	Proportion of recruits-at-age including multivariate logistic error		
j_i	Number of winters spent in the ocean for i winters spent in freshwater		
J_i	Maximum number of winters spent in the ocean for i winters spent in freshwater	4 for i = 1 and 3 for i = 2	3 for i = 1
$x_{i.j,t}$	Defined by eq. A5 below		
ϖ_i	Standard deviation in the multivariate logistic distribution of proportions-at-age	0.4 for i = 1 and 0.6 for i = 2	0.9 for i = 1
ε	Stochastic term		
q	Proportion of spawners that are effective females		
β_{q1}, β_{q2}	Described in eqs. A7 and A8 below		
μ_q	Mean proportion of spawners that are effective females	NA	0.53
σ_q	Standard deviation in proportion of spawners that are effective females	NA	0.092
S_O	Observed abundance of spawners		
κ	Stochastic term		
σ_κ	Standard deviation in observation error of spawner abundances	0.02	0.02

Table A1 (*concluded*).

Description	Equation
Sibling model (used to forecast age-specific recruitment, box 2*b*)	(A10) $\log_e(R_{i,j,t}) = a^s{}_{i,j,t} + b^s{}_{i,j}\log_e(R_{i,j-1,t-1}) + \omega_{i,j,t},\ \omega_{i,j} \sim N(0, \sigma_{\omega_{i,j}}{}^2)$
Sibling model, system equation (used along with eq. A10 in the Kalman filter version to forecast age-specific recruitment, box 2*b*)	(A11) $a^s{}_{i,j,t} = a^s{}_{i,j,t-1} + \xi_{i,j,t},\ \xi_{i,j} \sim N(0, \sigma_{\xi_{i,j}}{}^2)$
Target harvest rule ignoring outcome uncertainty (generated from decision-algorithm submodel, box 3, and used to apply target harvest rates, box 4)	(A12) $h'_t = c\{1 - \exp[d(m - R'_t)]\}$
Same as eq. A12 except that this target harvest rule accounts for outcome uncertainty	(A13) $h'_t = c^*\{1 - \exp[d^*(m^* - R'_t)]\}$
Deviation of realized escapement from target for Togiak only (used to simulate realized escapements in the decision-algorithm submodel, box 3, and when applying target escapements, box 4)	(A14) $\log_e\left(\dfrac{E_t}{E'_t}\right) = \lambda_0 + \lambda_1 F_t + \delta_t,\ \delta \sim N(0, \sigma^2_\delta)$
Outcome uncertainty in harvest rates for Chilko only (used to simulate realized harvest rates in the decision-algorithm submodel, box 3, and when applying target harvest rates, box 4)	(A15) $h_t = \mathrm{Beta}(\beta_{h_1,t}, \beta_{h_2,t})$
First parameter for eq. A15 above (Morgan and Henrion 1990)	(A16) $\beta_{h_1,t} = \dfrac{h'^2_t - h'^3_t - \sigma^2_h \cdot h'_t}{\sigma^2_h}$
Second parameter for eq. A15 above	(A17) $\beta_{h_2,t} = \dfrac{h'_t(1 - h'_t)^2 - \sigma^2_h(1 - h'_t)}{\sigma^2_h}$
Escapement after harvest (used to simulate realized escapements in the decision-algorithm submodel, box 3, and when applying target escapements, box 4)	(A18) $E_t = R_t(1 - h_t)$

Appendix B. Separating sources of uncertainty

Separating observation error from natural variability

Historical recruitment data used to estimate parameters of eqs. A1 and A2 (Appendix A, Table A1) contain both natural process variation and observation error; hence, recruitment calculated from these equations contained both ν or γ (eqs. A1 and A2, respectively) and κ (eq. A9). To separately estimate their respective contributions to variability, we first set the standard deviation in observation error of the natural logarithm of spawner abundance, σ_κ, to 0.02, the mean estimate for observation error in visual surveys of escapement for Togiak in 2004 and 2005 (T. Baker, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518-159, USA, personal communication). For that stock, the precision of the sampling method was reported as coefficients of variation (CV = standard deviation/mean) and were converted to variance, σ^2 (for the error term in eq. A9), using the well-known relationship

$$\text{(B1)} \qquad \sigma^2 = \log_e(\mathrm{CV}^2 + 1)$$

Parameter or variable	Definition	Values: Togiak	Chilko
$R_{i,j}$	Abundance of recruits that spent i winters in freshwater and j winters in the ocean		
$a^{s}_{i,j,t}$	Time-varying parameter	Estimated annually using the Kalman filter	
$b^{s}_{i,j}$	Constant parameter	Estimated for each stock and age class separately	
ω	Stochastic term		
$\sigma_{\omega_{i,j}}$	Standard deviation of "observation error"	Estimated for each stock and age class separately	
ξ	Stochastic term		
$\sigma_{\xi_{i,j}}$	Standard deviation of "process error"	Estimated for each stock and age class separately	
h'	Target harvest rate		
R'	Forecast of recruitment		
c	Maximum harvest rate (proportion) at high R' for the target harvest rule that ignores outcome uncertainty	NA	0.93
d	Shape parameter for that harvest rule	NA	1.20×10^{-6}
m	Protection level (spawner abundance below which harvest rates are zero for that harvest rule)	NA	1
c^*, d^*, m^*	Same as c, d, and m in eq. A12, except this model accounts for outcome uncertainty	NA	0.93, 9.07×10^{-6}, 1
F	Forecasting error ($\log_e(R'/R)$)		
δ	Stochastic term		
E	Realized escapement		
E'	Target escapement that ignores outcome uncertainty	179 176	NA
	Target escapement that accounts for outcome uncertainty	132 660	NA
λ_0, λ_1	Parameters	0.26, –0.40	NA
σ_δ	Standard deviation in residuals	0.19	NA
h	Realized harvest rate		
$\beta_{h_1,t}$, $\beta_{h_2,t}$	Described in eqs. A16 and A17 below		
σ_h	Standard deviation in harvest rates	NA	0.18

The standard deviation ($\sqrt{\sigma_\kappa{}^2}$) in observed error for Togiak corresponded to a relatively low level of observation error for Chilko, as shown by mark–recapture studies on 10 Fraser River stocks, where annual estimates of σ_κ ranged from 0.02 to 0.19 between 2001 and 2004 (T. Whitehouse, Fisheries and Oceans Canada, B.C. Interior Area and Science Branch, 985 McGill Place, Kamloops, BC V2C 6X6, Canada, personal communication). In a simple simulation model, we then estimated the standard deviations of the natural process variation, σ_r and σ_L (for eqs. A1 and A2 for Togiak and Chilko, respectively), which in combination with the above observation errors in the simulation resulted in standard deviations in total recruitment equal to those observed historically (σ_ψ). Note that those variances were not additive (i.e., $\sigma_\psi{}^2 \neq \sigma_r{}^2 + \sigma_\kappa{}^2$ for Togiak and $\sigma_\psi{}^2 \neq \sigma_L{}^2 + \sigma_\kappa{}^2$ for Chilko), indicating that the sources of variability were not independent. For both of our study populations, we found that the total combined uncertainty (ψ) was dominated by large, natural variability in recruitment. Specifically, the standard deviation in natural process variation was equal to 99% of the standard deviation in total combined recruitment for both stocks (i.e., $\sigma_r = 0.99\sigma_\psi = 0.51$ in eq. A1 for Togiak, and $\sigma_L = 0.99\sigma_\psi = 0.63$ in eq. A2 for Chilko). In a sensitivity analysis, we increased the magnitude of observation errors to σ_κ = 0.19, which corresponded to standard deviations in natural process variation that were equal to 94% of the standard deviation in total observed recruitment for Togiak (i.e., $\sigma_r = 0.94\sigma_\psi = 0.48$) and 90% for Chilko (i.e., $\sigma_L = 0.90\sigma_\psi = 0.57$).

Separating observation error from outcome uncertainty

We separated observation error (σ_κ, eq. A9) from outcome uncertainty (σ_δ, eq. A14, for Togiak and σ_h, eqs. A15–A17, for Chilko) using the same method as described above. For Togiak, the standard deviation in outcome uncertainty not included in observation error was 94% of the standard deviation in total observed outcome uncertainty that included observation error (resulting in σ_δ = 0.19), and that proportion was 99% for Chilko (resulting in σ_h = 0.18). When we increased observation errors in a sensitivity analysis (σ_κ = 0.19 instead of 0.02), these values (σ_δ and σ_h) were 70% and 88% for Togiak and Chilko, respectively (resulting in σ_δ = 0.14 and σ_h = 0.16, respectively).

Appendix C. Decision-algorithm submodel

The decision-algorithm submodel used the following five simplifications of the overall simulation that evaluated management options.

(1) Assumptions about recruitment

For Togiak, the decision-algorithm submodel assumed that all recruits were age 5 years at maturity, because from 1956 through 2001, on average, 67% of recruits were age 5. For Chilko, the decision-algorithm submodel assumed that adults returned at ages 4 and 5 because ecological interactions between fish that return in subsequent years, in part due to differential age-at-maturity, are an important component of cyclic population dynamics of Chilko Lake sockeye salmon (Ricker 1997). The proportion of recruits that were age 4 in year t, $p_{4,t}$, was calculated from the proportion of spawners that were age 4 in the parent generation, $p'_{4,t}$ (Walters and Woodey 1992), using the following logistic model:

$$\text{(C1)} \qquad p_{4,t} = (1 + f_0 f_1{}^{p'_{4,t}})^{-1} + \tau_t$$

and

$$\tau \sim N(0, \sigma_\tau{}^2)$$

where f_0 and f_1 are parameters and τ represents normally distributed random variation with variance $\sigma_\tau{}^2$. The dependent variable, $p_{4,t}$, was always between zero and one.

(2) Assumptions about time trends in age-at-maturity

In contrast to the overall simulation model, we did not incorporate long-term trends in age-at-maturity in the decision-algorithm submodel.

(3) Assumptions about forecasts of recruitment

In the decision-algorithm submodel, we did not explicitly simulate forecasts of recruitment. Instead, for Togiak, we simulated only errors in forecasts, and for Chilko, we did not simulate forecasts or errors in forecasts because historical data showed that outcomes of fishing regulations were independent of those factors. Specifically, for Togiak, we simulated a stock assessment procedure that took into account forecasting error from an empirically based relation with realized recruitment. Our analyses of historical data for that stock show that forecasts of recruitment tend to underestimate realized recruitment when recruitment is large and overestimate realized recruitment when recruitment is small. Therefore, we calculated forecasting error (the natural logarithm of the ratio of forecasts of recruitment, R_t', to realized recruitment, R_t) from the natural logarithm of realized recruitment:

$$\text{(C2)} \qquad \log_e\left(\frac{R'_t}{R_t}\right) = \eta_0 + \eta_1 \log_e(R_t) + \alpha_t$$

and

$$\alpha \sim N(0, \sigma_\alpha{}^2)$$

where η_0 and η_1 are parameters (equal to 13.5 and –1.02, respectively), and α represents normally distributed variability in forecasting errors with variance, $\sigma_\alpha{}^2$ (= 0.35). We used log-transformed abundances because of empirical and theoretical support for lognormally distributed variation in recruitment (Peterman 1981; Hilborn and Walters 1992).

(4) Assumptions about observation errors

In the decision-algorithm submodel, observation errors were not separated from outcome uncertainty and natural variability (as described for the overall model that we used to evaluate management options, see Appendix B) because estimates of observed abundance were not explicitly simulated.

(5) Number of Monte Carlo trials

The decision-algorithm submodel was repeated over 1000 iterations instead of the 500 used for the overall simulation model because the decision-algorithm submodel did not included time trends in age-at-maturity and therefore was not iterated over years. Therefore, a larger sample of Monte Carlo trials was required to stabilize output metrics in this decision-algorithm submodel.

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