AN EVALUATION OF THE MANAGEMENT IMPLICATIONS OF DEPENSATORY PREDATION MORTALITY IN PACIFIC SALMON USING BAYESIAN DECISION ANALYSIS

by

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ABSTRACT

Management of Pacific salmon is often based on the Ricker stock-recruitment model. However, estimates of the parameters of the Ricker model are usually imprecise and such uncertainties are frequently ignored when harvests are based solely on the best point estimates of model parameters. In addition, it is uncertain whether the Ricker model is the appropriate form for describing the shape of the stock-recruitment curve. In some stocks of Pacific salmon, there is considerable anecdotal and empirical evidence to support including depensatory predation mortality (high proportion dying at low abundance) in the stock-recruitment relationship. Given these uncertainties, several fisheries scientists have advocated adjusting the harvest level downward to account for uncertainty, but the appropriate size of these "uncertainty adjustments" is unclear. For several stocks of Fraser River sockeye salmon (*Oncorhynchus nerka),* I used Bayesian decision analysis to compare the benefits of harvest strategies based on the commonly used Ricker model to those based on a stock-recruitment model that accounted for the possibility of depensatory predation mortality. This approach explicitly incorporated uncertainties in the model parameters and quantified the management implications (e.g. expected yield) of using a Ricker or depensatory stock-recruitment model over a range of management policies. For a constant escapement policy, the optimal escapement target was generally unaffected by the possibility of depensation. However, large "uncertainty adjustments" (i.e. increases to the escapement target) may be beneficial for stocks with a high degree of uncertainty about the fit of the stock-recruitment curve at high abundances of spawners. In contrast, under a constant harvest rate policy, the optimal harvest rate depends on the initial abundance of spawners. For a *small* abundance of spawners (e.g. 2,000) the possibility of depensatory predation mortality required lower harvest rates to maximize the expected yield over 10 generations. Additionally, if depensation actually exists, significantly lower yields

are expected compared to the case where depensation is absent. Preliminary analyses that included uncertainty in the shape of the stock-recruitment curves for both the Ricker and depensatory models also indicated that a rebuilding strategy (where harvest rates were reduced from 80% to 50% for four generations to allow rebuilding) for cycle lines with small numbers of spawners should increase the expected yield compared with a constant 80% harvest rate. This analysis also shows that dramatic increases in yield may be possible if depensatory mortality actually does exist in these stocks and a rebuilding strategy is followed.

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INTRODUCTION

Several major fisheries have suffered unexplained collapses (Gulland 1988; Hilborn and Walters 1992). Overfishing, environmental changes, or a combination of both may push the abundance of a stock below an abundance where biological processes, such as depensation or the Allee effect, may drive the stock to extinction, maintain it near a commercially unproductive lower equilibrium, or substantially delay its recovery. A depensatory effect can cause recruitment to decline dramatically as the spawning stock decreases to a low abundance. However, the exact mechanisms producing these declines in recruitment are uncertain and, as a result, management strategies often fail to safeguard against the possibility of stock collapses.

The possibility of detrimental biological processes has led to some attempts to manage conservatively, especially in light of uncertainties in a stock's abundance estimates and biological parameters. Several efforts have been made to estimate a minimum spawning stock biomass to safeguard against overfishing that could reduce the abundance of a stock to a commercially unproductive level (Thompson 1993; Myers et al. 1994). Commonly, a relatively arbitrary "safety margin" or "uncertainty adjustment" to the optimal best-fit harvest strategy may be applied to account for uncertainty (e.g. using an escapement target that is 20% greater than the one based on the best available point estimates of biological parameters). However, recent research on the suitability of "uncertainty adjustments" has shown that the expected yield of harvests associated with different magnitudes of "uncertainty adjustments" depends on the specific stock and the possibility of depensation (Frederick and Peterman 1995). In some stocks, a moderately conservative harvest strategy (i.e. lower than the one based on the best point estimates) produces the highest yields, whereas in other stocks, a much more conservative strategy may be required when depensation exists.

Although there is little direct empirical evidence to support the existence of depensatory effects, there is considerable circumstantial evidence that suggests that depensation may exist. Depensatory effects can result from several mechanisms ranging from nonlinear functional or numerical feeding responses (where either the feeding rate or the abundance of predators become limited at high prey levels) to the inability of spawners to find mates at low population densities, an effect known as the Allee effect (Allee 1931; Peterman 1977, 1980; Peterman and Gatto 1978; Eggers and Rogers 1987). Models of these depensatory population dynamics predict that populations may show multiple equilibria and can rapidly shift from one equilibrium to another. For example, a depensatory predation model showed that the reduction in the abundance of the Georges Bank haddock, *Melanogrammus aeglefinus*, from a high to a low equilibrium state was likely caused by increased fishing pressure (Collie and Spencer 1993). However, little work has been done to determine the management implications of these depensatory mechanisms.

In addition, a recent statistical study based on estimates of spawner and recruit abundance for 128 fish stocks indicated that only three stocks had significant depensation (Myers et al. 1995). Although there was a lack of evidence for depensation in most of the fish stocks, two of the three stocks with significant depensation were pink salmon (*Oncorhynchus gorbuscha*). This suggests that managers of Pacific salmon should consider the effects of depensation on management strategies for these species.

The purpose of this study is to use Bayesian decision analysis to evaluate the possible management implications (e.g. on expected yield) of using an alternative stock-recruitment model that takes into account the possibility of depensatory predation mortality, instead of the more commonly used Ricker model. In particular, Bayesian statistics allows various shapes of stock-recruitment curves to be considered by giving each a probability weighting. This information will then be used in decision analysis to explicitly incorporate uncertainties in the shape of the stock-recruitment curve (i.e. model parameters) and quantify the optimal harvest or rebuilding strategies predicted by the Ricker and depensatory stock-recruitment models. Specifically, I will compare the optimal harvest strategies for the Ricker and depensatory models found using Bayesian and best-fit approaches (where only best-fit parameter estimates are considered) to evaluate differences in model performance for constant escapement, constant harvest rate, and stock rebuilding policies.

A case for depensation in some B.C. salmon populations

A striking feature of Fraser River sockeye salmon and pink salmon is the regular 'cyclic' fluctuations in annual abundance. These 'cyclic' fluctuations are particularly pronounced for some pink salmon populations and many Fraser River sockeye stocks because the recruits are predominately of a single age class (2 years old for pink salmon, and 4 years old for sockeye). This leads to relatively discrete populations (called cycle lines) in each stock. In Fraser River sockeye, the most abundant cycle line in a 4-year cycle is called the "dominant" line, followed by a lower abundance "sub-dominant" line, and two "off-year" lines of extremely low abundance (Cass and Wood 1994). This cyclic pattern in which one cycle line is more abundant than the others is referred to as cyclic dominance. Of approximately 20 sockeye stocks in the Fraser River watershed that are estimated regularly, 8 exhibit persistent 4-year cycles with a predictable dominant cycle line every 4 years (for example, Adams, Late Stuart, and Gates runs) and another 6 stocks show an apparent 4 year cycle but have not exhibited persistent cyclic patterns (for example, Chilko and Raft runs) (Cass and Wood 1994).

There is considerable debate about the mechanism(s) responsible for maintaining these population cycles, particularly for sockeye salmon (Ward and Larkin 1964; Collie and Walters 1987; Eggers and Rogers 1987; Walters and Staley 1987; Levy and Wood 1991; Walters and Woodey 1992; Cass and Wood 1994). Early investigations suggested that cyclic dominance was maintained by depensatory agent(s) independent of the fishery that suppressed recruitment of the smaller escapements of 'off-year' lines (Neave 1953). Ward and Larkin (1964) hypothesized that cyclic dominance in Adams River sockeye was caused by depensatory freshwater predation of salmon fry and smolts by rainbow trout. This hypothesis is supported by estimates of high predation mortality on sockeye fry and smolts by other vertebrate species (Steigenburger and Larkin 1974; Groot and Margolis 1991) and studies suggesting predation mortality is generally depensatory in nature (Ricker 1950,1954; Ward and Larkin 1964; Meacham and Clark 1979; Ruggerone and Rogers 1984). There is also some support for the idea that the formation of fish schools, {e.g. as is done by sockeye fry and migrating smolts (Petersen and DeAngelis 1992; Wood et al. 1993)}, can lead to a powerful depensatory effect, especially in species such as sockeye salmon that are subject to high predation rates (Clark 1974; Gulland 1975).

Several other studies have concluded that recent cyclic fluctuations could be maintained by depensatory fishing by the native Indian or commercial fisheries (Eggers and Rogers 1987; Walters and Staley 1987). In addition, Peterman (1980) suggests that depensatory mortality is a common effect for native Indian food fisheries and recent commercial harvest rates on Adams River sockeye appear to have been depensatory (Collie and Walters 1987). However, in their review, Levy and Wood (1991) conclude that although depensatory fishing may help maintain cycles in the Adams River sockeye, there is no compelling evidence that depensatory fishing generated the prominent historical cycles in Fraser River sockeye in the first place. More recent work also concludes that depensatory fishing is unlikely to be the only explanation for cyclic dominance in Fraser River sockeye stocks (Cass and Wood 1994).

Compelling evidence in support of a depensatory agent independent of the fishery was found for pink salmon in the Atnarko River, B.C., although conclusive evidence on the exact depensatory mechanism was not found (Peterman 1977, 1987). The odd-year population dropped from 2.5 million in 1961 to 80,000 in 1967 due to overexploitation and poor environmental conditions. The spawning population remained at low abundance for 6 generations, varying around an equilibrium of 120,000 fish. However, a subsequent reduction in the fishing mortality rate failed to promote a recovery of the stock, indicating that the lower stable equilibrium abundance was likely maintained by some natural depensatory agent. Artificial enhancement was needed to increase the spawner population to get it back to the more productive upper domain of stability of about 760,000 fish. The population has remained in this upper domain despite harvesting rates as high as 71% and elimination of enhancement efforts. This work indicates that it may not be reasonable to assume that Pacific salmon populations that are affected by depensatory dynamics can recover on their own after being forced to low levels.

The Ricker stock-recruitment model, which is used by most managers of Pacific salmon, implicitly assumes that populations will always return to their unfished equilibrium once fishing pressure is removed. However, this may not be the case if depensatory mechanisms can maintain a stock at a low population abundance, even after fishing pressure has been removed, and may prevent small stocks from rebuilding. This important management consequence, combined with the above evidence concerning the existence of depensatory mortality processes, suggests that managers should use models that explicitly account for depensatory mechanisms, even if their existence is not readily detectable from available data. Indeed, the 1994 Fraser River Sockeye Public Review Board (p. xiii, 1994) has recommended that the Department of Fisheries and Oceans (DFO) develop a "...system for risk aversion management given the uncertainties inherent to various estimation techniques". One component of risk-averse management is to explicitly consider the possibility of depensatory mortality when making decisions about harvest policies, which is the focus of this paper.

Bayesian decision analysis

Fishery managers are often faced with the task of choosing from different strategies for managing fisheries. For example, managers of salmon need to determine escapement goals that balance objectives such as maintaining high yields while adequately protecting stocks against overexploitation. Managers may also be interested in choosing the appropriate harvesting strategy for rebuilding an off-year line to a more commercially productive level. If the manager has perfect information and all of the parameter values of the stock-recruitment model are known precisely, then the appropriate harvesting strategy can be set to achieve the maximum sustainable yield or some other objective, such as rebuilding of an off-year stock to some specified level of spawners. But, because parameter values can never be known precisely, managers often base their decisions solely on the best point estimates of parameters (the best-fit approach) or use an arbitrary adjustment to the escapement goal or harvest rate that accounts for uncertainty in a qualitative fashion. These approaches fail to account for uncertainty in parameter estimates in a quantitative manner and, therefore, assume that the best estimate for a parameter is the only one possible.

Managers should quantitatively consider the uncertainty in parameters of the stock-recruitment model. In this way they can assess the potentially lower yield associated with managing as if a given state of nature (such as the one described by best-fit parameter estimates) is true, when there is some non-zero probability that it is not true. For example, for a constant escapement policy, this decision involves balancing the risks (e.g. losses in yield) of overescapement and those of underescapement. Overescapement may be undesirable because fewer fish are harvested in the current year and the extra fish reaching the spawning ground may reduce future recruitment because of density-dependent processes. Underescapement is potentially more serious because although more fish may be caught in the current year, spawner abundance may be reduced to the point where recruitment overfishing or depensatory processes can drive the stock to extinction or to a low, commercially unproductive equilibrium. Managers are often poorly equipped to make explicit choices among various escapement targets because of the high uncertainty associated with key components, such as the form of the stock-recruitment model or parameter estimates.

Decision analysis has been developed specifically to deal with such problems and has been used in several fisheries case studies (Walters 1981, 1986; Francis 1992; McAllister and Peterman 1992; McAllister et al. 1994; Frederick and Peterman 1995; McAllister and Pikitch 1996). In contrast to a best-fit approach that uses only point estimates of parameters, a Bayesian decision analysis approach explicitly accounts for uncertainty in parameter estimates by making management decisions based on a consideration of the probability distributions associated with uncertain parameters (Walters 1986). The optimal "uncertainty adjustment" (Frederick and Peterman 1995) for a constant escapement policy, for instance, is the difference between the escapement target set using Bayesian decision analysis, which accounts for uncertainty in parameter estimates, and the target based on a best-fit approach.

A Bayesian decision analysis approach involves several steps which are often summarized in a decision tree (Fig. 1, which is described below in greater detail in the methods section). A decision tree allows the performance of alternative management actions (e.g. harvest strategies) to be ranked according to their ability to meet a specified performance level taking into account a range of hypothesized responses of the managed system. For instance, the uncertainty in the shape of the stock-recruitment curve is described by alternative hypotheses, or states of nature, that are represented by different parameter combinations. The degree of belief in a particular parameter combination is quantified using Bayesian statistics (Box and Tiao 1973) to generate a posterior probability distribution. The outcomes (e.g. average yield, as numbers of fish per year) for a particular uncertainty adjustment and parameter set are simulated using a model of population dynamics. Then, the outcomes for each parameter set are weighted by their probabilities of occurrence and summed to give an "expected" (weighted average) value of yield for a particular uncertainty adjustment. The expected value represents the average outcome of a particular management option given the underlying uncertainty associated with the states of nature and represents our present expectation of what the future will give. The expected value does not specify a value that will occur (such a forecast is not possible given the uncertainties), but is simply a measure that can be used in decision analysis to allow the selection of the management option that produces the most favorable result *relative to the other management options evaluated.*

Methods

This section describes the Bayesian decision analysis approach I used to evaluate the management implications of depensatory predation mortality in several stocks of Fraser River sockeye. This paper was not directed toward the management of any of these stocks specifically because the analysis relies on past spawner-recruitment data up to and including the 1990 brood year and new data may alter parameter estimates. Rather, the purpose here was to show how this approach can be used generally to improve management decisions.

I used the Bayesian decision analysis approach to evaluate constant escapement, constant harvest rate and stock rebuilding policies for both stock-recruitment models. Table 1 summarizes the analyses done for each policy and stock to determine the optimal management strategy for the Ricker and depensatory models using the best-fit parameters (i.e. best-fit analysis) and also the parameter distributions from the Bayesian analysis (i.e. uncertain parameters analysis). Each analysis was done following the six basic steps of decision analysis (steps 3 through 6 are expanded upon later) described below. The analyses for the best-fit models differed somewhat from the method outlined below because only the best point estimates of parameters were used. For the best-fit models there was only one state of nature which hence had a probability, $P_i = 1.0$, so steps 3 and 4 were considerably simplified compared to the method followed for the uncertain parameters case. For the rest of this section, I will refer mainly to the analysis done for depensatory model with uncertain parameters for the constant escapement policy (see X* in Table 1). I analyzed the uncertain parameters case of the Ricker model using a similar procedure that only differed from the procedure for the uncertain parameters case of the depensatory model in step 3 because I took into account different parameter values of the Ricker model.

1. *Specify management objective.* I used an objective of maximizing the average yield, in numbers of fish caught annually (averaged over the 10 generations in the simulation). I used this management objective to evaluate constant escapement, constant harvest rate, and stock rebuilding policies. I only refer to the constant escapement policy in the rest of the methods section, but the same procedure was followed for the other policies.
2. *Identify alternative management options.* I assumed that a range of alternative management options could be taken for each policy. Henceforth I will use "policy" to refer to either the constant escapement, constant harvest rate, or rebuilding policies and "strategy" to refer to the different management options within the policy category (e.g. the amount of adjustment for uncertainty applied to the escapement goal). For example, I used the best point estimates of the parameters (best-fit) for the Ricker model *without a depensatory effect* to set a baseline escapement target (see Table 1) that maximized the average yield. Alternative management options consisted of a range of "uncertainty adjustments" that modified the baseline escapement target calculated for the best-fit Ricker model. I made the "uncertainty adjustments" to the baseline escapement target so that the results from all the analyses for a given policy could be compared to a common reference

point. (For the constant harvest rate policy a range of harvest rates from 0 to 95% was used).

3. *Identify the uncertain states of nature.* For the best-fit analyses, I only used the best-fit parameter estimates for the Ricker or depensatory model to define the shape of the stock-recruitment curve. However, to account for uncertainty, I also considered different combinations of the parameter values (i.e. different shapes of the stock-recruitment curve) for the Ricker and depensatory stock-recruitment models as possible states of nature.
4. *Quantify uncertainty using Bayesian statistics.* I used Bayesian statistics to estimate the posterior probabilities for different combinations of stock-recruitment parameters, based on the historical stock-recruitment data.
5. *Predict outcomes with a model of salmon population dynamics.* I used a simulation model to estimate the average yield for each uncertainty adjustment and each possible shape of the stock-recruitment relationship.
6. *Use a decision analysis framework to determine the optimal management strategy.* I calculated the expected average yield for each uncertainty adjustment using the decision tree in Figure 1. The uncertainty adjustment with the highest expected yield was optimal.

Identifying alternative states of nature

I assumed for my analysis that there was one true, but unknown, stock-recruitment relationship for each sockeye stock. However, because the true form of the relationship was unknown, I considered several possible parameter combinations describing the form of the relationship as states of nature. Each state of nature corresponds to a branch from the uncertainty node (circle) of the decision tree in Fig. 1.

For several Fraser River stocks of sockeye salmon, I fit a Ricker and a depensatory stock-recruitment model to adult spawner-recruit data obtained from the International Pacific Salmon Commission (Jim Woodey, Pacific Salmon

Commission, Vancouver, B.C., pers. comm.). I analyzed the following sockeye stocks for the brood years indicated in parentheses: Adams River (1948-1990), Gates Creek (1952-1990), Late Stuart (1949-1990), Raft River (1948-1990) and Chilko River (1948-1990).

Ricker model

The Ricker model is thought to approximate the compensatory mortality (i.e. a reduction in recruits-per-spawner as the number of spawners increases) that acts mainly on the egg-to-fry stage in Pacific salmon (Ricker 1950,1954). All other mortality after predation and up to recruitment was assumed to be density-independent here. The Ricker stock-recruitment model was defined by the following equation:

$$(1) \quad R = Se^{\alpha\left(1-\frac{S}{\beta}\right)}e^{v}$$

where, S denotes the total number of adult sockeye on the spawning ground, R is the total number of adult recruits, e^{α} is the median number of recruits per spawner at low spawner abundance, and β is the unfished equilibrium spawner population (i.e. where recruitment is equal to spawning stock abundance), and e^{v} is defined as a multiplicative log-normally distributed error term (where v has mean = 0 and standard deviation = σ). The use of a multiplicative log-normal error structure has been demonstrated to be the most appropriate for Pacific salmon (Peterman 1981).

Depensatory model

I also evaluated a depensatory model because after the egg-to-fry stage, subsequent mortality on fry and smolts may be depensatory (i.e. reduced recruits-per-spawner at extremely low numbers of spawners) (Ricker 1950, 1954; Ward and Larkin 1964; Peterman and Gatto 1978; Meacham and Clark 1979; Ruggerone and Rogers 1984). Depensatory predation mortality during the life of the salmon was simulated by first using a compensatory process described by a Ricker model for the spawner-to-fry stage (Fry = $Se^{a(1-S/b)}$). This fry abundance was then modified by a Type III total response predation function to reflect depensatory predation mortality on the fry or smolts. Use of a Type III predation function has been justified for vertebrates (Peterman 1977), which are the main predators of salmon. A Type III predation function is characterized by a dome-shaped relationship between fry or smolt abundance and percent mortality caused by predation. The percent mortality increases rapidly at low abundance of fry or smolts as their abundance increases, and then the mortality rate decreases above intermediate abundances. As a result, a Ricker model modified by the Type III predation function is characterized by a "dip" in the net recruitment curve at low levels of spawners. All other mortality after predation and up to recruitment was assumed to be density-independent. Therefore, recruits were determined by the number of fry surviving compensatory mortality minus the number of fry or smolts eaten by predators. The resulting depensatory stock-recruitment model was defined by the following equation (Peterman 1977):

$$(2) \qquad R = \left[Se^{a\left(1-\frac{S}{b}\right)} - \frac{c\left(Se^{a\left(1-\frac{S}{b}\right)}\right)^2}{d^2 + \left(Se^{a\left(1-\frac{S}{b}\right)}\right)^2} \right] e^{v}$$

where, e^a is the median number of fry per spawner at low spawner abundance, *b* is the unfished equilibrium population abundance of fry prior to predation, *c* is the maximum number of fry or smolts consumed by the total predator population, *d* is the number of fry or smolts that results in c / 2 prey lost to predation, and v is defined as in Eqn. 1.

I estimated the best-fit parameters for the best-fit depensatory model using nonlinear parameter estimation based on the relationship of $\log_e$ (recruits / spawner) and spawners. I picked the Adams, Gates, Late Stuart, and Raft sockeye stocks for further analysis because the best-fit relationships for the depensatory model (Eqn. 2) had evidence of depensatory predation mortality at a low abundance of spawners. For example, Fig. 2A and B show the shape of the best-fit curves for the Ricker and depensatory models for the Raft and Late Stuart stocks, respectively. In addition, I included the Chilko sockeye stock where the depensatory and Ricker model fits were nearly identical (indicating no evidence of depensation) as a control case to check that the optimal management strategies were similar for both models when the fits of the two types of curves were the same.

The best-fit parameter estimates and the mean square error (MSE) estimates for the Ricker and depensatory models are shown in Appendix A. In all cases except Chilko, the MSE was slightly lower for the depensatory model, indicating that even with the penalty on MSE from the two additional parameters, the depensatory model explained slightly more of the observed variation than the Ricker model. However, the Ricker and depensatory best-fit curves fit the observed stock-recruitment data poorly because of the high variability in the data points (see Fig. 2A-B).

Quantifying Uncertainty Using Bayesian Statistics

I used Bayesian statistics to evaluate the uncertainty in the spawner-recruit relationship (reflected by the scatter around the best-fit of $\log_e$(R/S) on S). For each salmon stock data set, I quantified the uncertainty in the shape of the stock-recruitment model by calculating a posterior probability for each hypothesized combination of the parameters in Eqn. 1 (α, β, and σ) or Eqn. 2 (*a*, *b*, *c*, *d* and σ). I obtained the probability of each hypothesis, i, using Bayes' formula (Box and Tiao 1973):

$$(3) \quad P(hypothesis_i | data) = \frac{L(data | hypothesis_i) \times P(hypothesis_i)}{\sum_{j=1}^{n}\left[L(data | hypothesis_j) \times P(hypothesis_j)\right]}$$

where, "$hypothesis_i$" was a particular combination of parameters defining the shape of a stock-recruitment curve, P($hypothesis_i$) was the prior probability placed on $hypothesis_i$ independent of the data, L(data | $hypothesis_i$) was the likelihood of the observed data given that $hypothesis_i$ was true, and P($hypothesis_i$ | data) was the posterior probability for a given hypothesis, i. The set of all posterior probabilities is the posterior probability density function (pdf), which sums to one. I assumed that the prior distributions of the stock-recruitment parameters in Eqn. 1 and 2 were described by uniform distributions (i.e. all of the possible parameter values within a given range were given an equal chance of being the true state of nature *a priori*). When stock-recruitment data contain little information about the possible 'true' shape of the stock-recruitment curve, the posterior pdf tends to reflect the prior. But, as the amount of information contained in the data (e.g. tightness of the scatter around a particular shape of the stock-recruitment relationship) increases, the likelihood function has a greater influence on the posterior pdf.

For the likelihood function, I assumed that the natural logarithm of the differences between the observed and predicted recruits-per-spawner were normally distributed with a mean of zero and variance, σ^2, as follows from Eqns. 1 and 2 (i.e. $\log_e(R/S) = f(S) + v$). I therefore first calculated the likelihood of each data point using the following normal equation (Box and Tiao 1973):

$$(4) \quad L_k\left(data\ point_k \middle| a_i, b_i, c_i, d_i, \sigma_i\right) = \frac{1}{\sigma_i\sqrt{2\pi}} e^{-\left(\frac{\delta_k^2}{2\sigma_i^2}\right)}$$

where, L_k was the likelihood of data point k, which represents one year of spawner-recruit data for the given stock, and δ_k^2 is the squared deviation of the difference between the logarithms of the observed recruits-per-spawner, k, and the predicted recruits-per-spawner calculated with Eqn. 1 or Eqn. 2 for a particular set of parameter values. I used the negative natural logarithm of the likelihood values to prevent extremely small values from being lost from the calculation due to a lack of computer precision. The joint likelihood for the entire data set (= $L_1 * L_2 * L_3 ... L_k$) for a given hypothesis ($L(data|hypothesis_i)$ in Eqn. 3) was then the exponentiation of the sum of negative log-likelihoods for each data point from Eqn. 4, computationally:

$$(5) \quad L(data|hypothesis_i) = \exp\left[\sum_{k=1}^{m} -\ln(L_k)\right]$$

I calculated the Bayesian posterior probabilities (Eqn. 3) for the alternative hypotheses using a sampling/importance resampling (SIR) algorithm (Rubin 1988; Smith and Gelfand 1992). This algorithm has recently been used in fisheries problems to provide Bayesian posterior pdfs of multiple uncertain model parameters (McAllister et al. 1994; McAllister and Ianelli 1995). The SIR algorithm is computationally superior to grid search approaches for problems that have large numbers of parameters, as is the case here. Grid searches require a time consuming search where parameter combinations are compared over all of the intervals for each parameter. The computation time increases exponentially for each additional parameter added to the grid search and the computation becomes relatively intractable for cases with large numbers of parameters (e.g. 5 parameters with 10 intervals each would require 10^5 comparisons to evaluate each combination). The SIR algorithm is a much more efficient method for dealing with these computational problems.

The SIR algorithm procedure was as follows (Rubin 1988): (1) Choose an importance function that represents the joint prior probability density function of the input parameters. I used the joint distribution of uniform priors of the input parameters (e.g. on *a, b, c, d* and $1/\sigma$) as the importance function. The use of a prior of $1/\sigma$ has been justified as a better natural prior for the standard deviation of the error term (Press 1989). Using the joint prior pdf for the importance function has often been used for simplicity (Kinas 1993; Punt et al. 1994). (2) Randomly generate a large number of parameter sets (e.g. q = 30,000 samples) from the joint prior pdf. (3) Calculate the likelihood of each parameter set using Eqn. 5. (4) Calculate the weight of each parameter set, which is its likelihood divided by the sum across all parameter sets of all the likelihoods. (5) Check the sampling efficiency of the above steps by finding the parameter set with the highest weighting. This step was done to make sure the importance function was not too inefficient for estimating the posterior. McAllister and Ianelli (1996) suggest that a maximum weight ratio (i.e. the weight of a single parameter set, taken as a proportion of the sum of the weightings for the other parameter sets over all of the draws) of less than 1% is acceptable. For weight ratios above 1%, I examined the marginal posterior pdfs on model parameters to ensure the distributions were not cut off by narrow boundaries on the prior. If this was the case, I repeated the analysis using wider boundaries on the prior distributions for the input parameters to avoid biases that can result from using ranges of parameter values in the prior distributions that are too narrow (Adkison and Peterman 1996). (6) Resample randomly with replacement (e.g. s = 5,000 resamples) from the distribution of weighted parameter sets to approximate the posterior probability density function. The posterior probability for any one parameter set was obtained from the ratio of the number of resamples drawn for that parameter set to the total number of resamples taken (i.e. 5,000). The posterior probabilities generated with the SIR algorithm were used in the decision analysis (described below) to quantify the uncertainty associated with the model parameters.

Decision Analysis Framework

For each stock, I used decision analysis to calculate the optimal management strategy given the objective of maximizing the expected yield. This process is described below for calculating the optimal "uncertainty adjustment" to the baseline escapement target for the constant escapement policy and the uncertain parameters case for the depensatory model. A similar process was used for the decision analysis for the case where parameters of the Ricker model were considered uncertain. The steps of the analysis are shown in Figure 3 and are as follows:

(1) Estimate the baseline escapement target that maximizes the sustainable yield (in numbers of fish) using the best point estimates of the parameters for the Ricker model *without a depensatory effect.* I used linear regression of $\log_e(R/S)$ on S to obtain the best fit parameter estimates because Korman et al. (1995) showed that it was not necessary to adjust for Walters' (1985) "time series bias".

(2) Pick an uncertainty adjustment that refers to an escapement target different from the baseline escapement target. For instance, an "uncertainty adjustment" of +10% would increase escapement and is conservative because more fish escape to the spawning ground, whereas, an "uncertainty adjustment " of −10% would decrease escapement and is therefore permissive. (3) Use a parameter combination and its corresponding posterior probability generated by the SIR algorithm. (4) Set the initial spawner abundance (S_0). Initial spawner

abundance was set at a very small number to reflect a depleted salmon stock. Here, an initial escapement of 2,000 spawners for a single cycle line was small enough to be affected by the depensatory region of the stock-recruitment curve predicted by the best-fit parameters for the depensatory model. An abundance of 2,000 spawners also approximated the lower limits on run sizes seen in the stock-recruitment data for each stock and, therefore, represented a plausible escapement for an off-year line. For example, the average spawning escapement for the 10 lowest escapement years in the data for the Adams, Gates, Late Stuart and Raft stocks was less than 2,000 spawners. (5) Use Eqn. 1 or Eqn. 2 to estimate recruitment using the particular parameter combination and number of spawners. I assumed that the recruits were all age 4 because most Fraser River sockeye return at this age (Welch and Noakes 1991). (6) Harvest the stock in excess of the escapement goal, E (i.e. average yield = R – E, as numbers of fish per year). I assumed a perfect harvest where all of the recruits in excess of the escapement goal were caught. (7) The spawning stock for the next generation was equal to the number of fish specified by the escapement goal except in generations when the number of recruits was less than the escapement goal. If this happened, I assumed that all of the recruits reached the spawning grounds and harvesting did not take place. I repeated steps 5 through 7 for 10 generations (i.e. 40 years). (8) Weight the average yield for a particular parameter combination by its posterior probability. Steps 3 through 8 were repeated until all of the parameter combinations were simulated. (9) Using Eqn. 6, sum the weighted yields across all *n* hypothesized stock-recruitment parameter sets, i, to determine the *expected value* of the "uncertainty adjustment" chosen.

$$(6) \quad EV(Yield) = \sum_{i=1}^{n} \left(probability_i \times Yield_i \right)$$

This process was repeated for each "uncertainty adjustment". (10) The adjustment that maximized the *expected yield* was optimal for the given stock.

RESULTS AND DISCUSSION

Constant Escapement Policy

The optimal escapement strategies for the Ricker and depensatory models are summarized in Table 2 for best-fit and Bayesian analyses. I compared each model under no uncertainty or full parameter uncertainty to the best-fit Ricker model (the types of comparisons are shown in Table 1). The best-fit Ricker model was used to find a baseline escapement target that was the starting point for analyses of the other scenarios. The optimal escapement strategies for the other models are shown in Table 2 as a percentage "uncertainty adjustment" to that baseline escapement target. Also, note that the optimal escapement targets in number of fish for the other scenarios are shown in parentheses in Table 2; they are a function of an "uncertainty adjustment" applied to the baseline escapement target for a given stock. Only the best point estimates of parameters were used for the best-fit models. I used the results from Table 2 to show how different the optimal escapement target would be in three scenarios that differ from the approach of estimating an escapement target from the best-fit Ricker model. These three scenarios were for a best-fit depensatory model where uncertainty was ignored and for Ricker and depensatory models where parameter uncertainty was considered.

Differences between the best-fit models

The optimal "uncertainty adjustments" for the best-fit depensatory model are just corrections to the baseline escapement target from the Ricker model. Because parameter uncertainty was not included in this step, any differences in the escapement targets between the best-fit Ricker and depensatory models should be based only on differences in model structure. For all five stocks, lower escapement targets were optimal for the best-fit depensatory model compared to the best-fit Ricker model (Table 2). This is because the depensatory model has a different shape compared to the Ricker model. For example, this is shown over the full range of spawner abundances for the Raft stock-recruitment data (Fig. 2B). Lower escapement targets are optimal for the depensatory model because the right limb of the stock-recruitment curve falls off rapidly and, as a result, lower spawning escapements fall into a range of higher productivity (measured by $\log_e(R/S)$) in the stock-recruitment curve where yield is maximized (i.e. total recruits minus spawners is maximized). For the Raft stock, the best-fit depensatory model produces an escapement target of 13,000 fish compared to an escapement target of 25,000 fish for the best-fit Ricker model. These results show that the fit of the depensatory model is different than the Ricker model using the same data for the best-fit case. In the next sections, I also determine whether this is the case when parameter uncertainty is explicitly incorporated into the analysis.

Expected Value of Including Uncertainty (EVIU) in the Parameters of the Stock-Recruitment Model

Next, the Ricker and depensatory stock-recruitment models were analyzed taking into account the uncertainty in their parameters. The expected yields for each uncertainty adjustment for these models are shown for the Late Stuart and Raft stocks, respectively (Fig. 4A-B). Although not shown here, the results for the Gates stock were similar to Fig. 4A and the results for the Adams stock were similar to Fig. 4B. The uncertainty adjustments for Late Stuart are extended to much larger values than for Raft to illustrate the peaks in the curves for the uncertain parameters cases. An optimal uncertainty adjustment of 0% corresponds to the baseline escapement target for the best-fit Ricker model.

For a given model, the difference between the expected yields of a decision based on a Bayesian analysis (uncertain parameters case) and a decision that ignores uncertainties (best-fit case) is called the *expected value of including uncertainty* (EVIU) (Morgan and Henrion 1990). For all stocks, the optimal uncertainty adjustment (i.e. the escapement target) for a given model had a higher expected yield under a Bayesian approach compared to the best-fit approach (Fig. 4A and B). However, the EVIU was not necessarily large. For a given stock and model, if a manager used the optimal best-fit strategy, the best estimate of expected yield is at the position on the uncertain parameters curve that corresponds to that optimal best-fit strategy. For example, the EVIU for the depensatory model for the Raft stock was 754 fish per year (i.e. the difference between the expected yield for the optimal uncertainty adjustment (e.g. –41%) and the expected yield on the uncertain parameters curve corresponding to the optimal best-fit strategy (e.g. –48%) in Fig. 4B), or a 2% increase in the expected yield from including parameter uncertainty. The EVIU for the Ricker model was equal to an increase of just 66 fish per year in the expected yield for this stock. Similarly, for the Adams stock, the EVIU was equal to a 2% increase in the expected yield for the depensatory model and a negligible increase for the Ricker model.

However, unlike the Raft and Adams sockeye salmon stocks, values of EVIU were large for both models for the Gates and Late Stuart stocks. For the Ricker model, there was a 24% increase (from 242,496 to 301,103 fish per year) in the expected yield of the Gates stock and a 68% increase (from 5.83 to 9.79 million fish) for the Late Stuart stock. The depensatory models also forecast large values of EVIU equal to increases of 59% and 92% for the Gates and Late Stuart stocks, respectively. The optimal adjustments for uncertainty for the Chilko stock resulted in more modest values of EVIU corresponding to increases in expected yield of 4% and 13% for the Ricker and depensatory models.

These findings are similar to those of Frederick and Peterman (1995) who showed that large uncertainty adjustments may be optimal if there is a highly asymmetric loss function or a highly asymmetric probability distribution describing the range of possible optimal escapement strategies. In this study, large uncertainty adjustments are likely a result of a combination of both a slightly asymmetric loss function (e.g. losses in yield are larger for underescapement than for overescapement when compared to the optimal escapement target) and highly asymmetric probability distributions describing the model parameters which determine the optimal escapement target. For example, for the Late Stuart stock the probability distributions of the 'β' and 'b' parameters are highly asymmetric (Fig. 5B) while the distributions on the other model parameters are fairly symmetric (Fig. 5A, C, and D). Note the difference between these 'β' and 'b' parameter distributions and the more symmetric distributions for the Raft stock where the EVIU is small (Fig. 6). For both models, the 'β' or 'b' parameter dictates the strength of density-dependent mortality at high abundance of spawners. Increases in the 'β' or 'b' parameter tend to flatten out the stock-recruitment curve (i.e. increase the number of recruits-per-spawner) at high abundance of spawners.

In the Late Stuart stock the wide scatter in the stock-recruitment data points at high abundance of spawners (Fig. 2A) contributes to the uncertainty over the strength of density-dependence. In other words, the value of the 'β' or 'b' parameter is uncertain because the shape of the right limb of the stock-recruitment curve is not clearly defined by the stock-recruitment data. Therefore, a consideration of parameter uncertainty in the stock recruitment models resulted in a broadly diffuse and highly asymmetrical distribution on the 'β' or 'b' parameter (Fig. 5B). As a result, there is a large probability that the 'β' or 'b' parameter may be much larger (and therefore, density-dependent survival processes may be much weaker) than predicted by the best-fit parameters. This causes the expected yields to increase for large uncertainty adjustments and is shown by the relatively flat expected yield curves for the uncertain parameters cases for both models(Fig. 4A). For this reason, a large uncertainty adjustment is optimal for the Late Stuart stock.

Conversely, for the Raft stock the uncertainty adjustments for each of the two types of models were much smaller than those for the Late Stuart stock (Table 2). The reason for this difference is that the stock-recruitment data points for the Raft more clearly indicate the shape of the downward bending right limb of the stock-recruitment curve (e.g. Fig. 2B at 15,000 to 20,000 spawners). Therefore, when uncertainty in the stock-recruitment models was considered, only the 'β' and 'b' parameters that produced curves that had a large probability of fitting the data points at high numbers of spawners were selected. This is shown in Fig. 5B by the distributions on the 'β' and 'b' parameters, which are much more symmetrical than they were for the Late Stuart. (The 'b' distribution is significantly more peaked than the 'β' distribution because the ability of the depensatory model to bend downwards at high spawner abundance constrains the range of curves that fit the data in this case.) As a result, both stock-recruitment models are fairly well defined for the right limb of the stock-recruitment curve. This causes the expected yields to decrease for large uncertainty adjustments (note the difference between the curves for uncertainty adjustments above each respective UA* in Fig. 4B for the uncertain parameters cases of the Ricker and depensatory models) and, therefore, uncertainty adjustments are much smaller than for the Late Stuart stock. For the depensatory model, the dramatic decrease in expected yields for large uncertainty adjustments results in a negative optimal uncertainty adjustment (where the optimal escapement target is below the best-fit Ricker optimum) because lower spawning escapements result in higher productivity (i.e. $\log_e(R/S)$).

These results suggest that for some stocks, large conservative uncertainty adjustments may be optimal if there is a high degree of uncertainty over the strength of density-dependent survival. The lack of a strongly downward bending right limb of the stock-recruitment model means that there will be little cost to high escapements. For these stocks, a failure to incorporate the uncertainty of model parameters can result in sub-optimal uncertainty adjustments and large drops in the expected yield (Fig. 4A) if the best fit parameters are assumed to be correct when they may not be. There may be a high probability that density-dependent processes are weaker than predicted in the best-fit analysis. Therefore, escapement targets set based on best-fit parameter analyses may be much too low and higher yields could be realized for higher numbers of spawners. As a result, managers should carefully consider uncertainty in the fit of the stock-recruitment curve to the data at a high abundance of spawners and the consequences of few stock-recruitment data points for these high abundances. An approach such as active adaptive management (Walters 1986) (e.g. where escapement targets are experimentally increased to obtain stock-recruitment data points outside the range of natural variation) would be required to determine the actual benefits of increased escapement levels.

Implications of model selection for the case of uncertain parameters

In this section, I evaluate the implications of choosing the Ricker model over the depensatory model when a full consideration of uncertainty is taken into account. Where parameter uncertainty was included, the Ricker and depensatory models produced positive uncertainty adjustments for the Chilko, Gates, and Late Stuart stocks. For these stocks, the expected yield curves for the Ricker and depensatory models have similar shapes and are flat over a wide range of uncertainty adjustments around the one that is optimal (Fig. 4A). It is clear in Fig. 4A that for both models when parameters are considered uncertain there is not a large drop in the expected yield associated with a wide range of sub-optimal uncertainty adjustments (e.g. ± 100% around the respective UA* values) compared to the optimal uncertainty adjustment. However, the implications (i.e. losses in yield) associated with using the incorrect model to derive the optimal uncertainty adjustment could be much more serious for the Adams and Raft stocks because the expected yield curves are not as flat (Fig. 4B).

For the Adams and Raft stocks, the optimal uncertainty adjustment depends on the model. For the depensatory model, expected yield is highest for a large negative uncertainty adjustment (i.e. lower escapements than the best-fit Ricker case), but a positive adjustment is optimal for the Ricker model (Table 2). What is the impact of choosing one model form over the other in a case like this?

To evaluate the performance of the estimation procedure, I compared how using a particular model performed if in fact the other model was correct. Specifically, I compared the expected loss in yield that would result from using the optimal uncertainty adjustment predicted by a depensatory model when depensatory predation mortality *does not* actually exist (but a Ricker model does), to the expected loss in yield caused by using the optimal uncertainty adjustment predicted by a Ricker model when depensatory mortality actually exists. Each of these losses was estimated for the uncertain parameters cases using the expected yield for the particular optimal uncertainty adjustment, which is the best estimator of the model outcome. For the Raft stock, the optimal uncertainty adjustment for the uncertain parameters case for the depensatory model shown in Fig. 4B was –41% (i.e. to decrease escapement below the baseline target by 41%). If that were the actual model in nature then there would be no loss in yield associated with that approach (hence, the expected loss would be 0 for an uncertainty adjustment of –41% as shown in Fig. 7). However, if the stock actually behaved like a Ricker model without depensation, then the loss would be 6,753 fish per year (indicated as *Loss 1* on Fig. 7). Similarly, if one incorrectly assumed a Ricker model when a depensatory model actually was correct, then the loss would be 17,571 fish per year (indicated as *Loss 2* on Fig.

7). The expected losses as a percentage of the expected yields estimated for the optimal uncertainty adjustment with the correct model were 13% for Loss 1 (i.e. 6,753 / 50,719 fish per year if the Ricker model was correct) and 38% for Loss 2 (i.e. 17,571 / 46,532 fish per year if the depensatory model was correct). In other words, by assuming a Ricker model to determine the optimal uncertainty adjustment when in fact depensatory mortality does exist leads to a larger expected loss in yield (in both absolute and percentage terms) than if a depensatory model were used.

The Raft was the only stock where the losses were expected to be larger if a manager incorrectly assumed that a Ricker model was appropriate. For the Raft for the uncertain parameters case, the losses for incorrectly assuming a Ricker model were larger than incorrectly assuming a depensatory model because at a high abundance of spawners, the expected yield predicted by the depensatory model decreases more rapidly than the Ricker model for sub-optimal uncertainty adjustments above the uncertainty adjustment that is optimal (note the difference between the curves for uncertainty adjustments above UA* in Fig. 4B for the uncertain parameters cases of the Ricker and depensatory models).

For 4 out of 5 stocks evaluated, differences in performance (i.e. expected loss in yield) between the Ricker and the depensatory models were extremely small for a constant escapement policy. Uncertainty over the existence of depensatory predation mortality at a low abundance of spawners does not appear to affect the choice of an optimal uncertainty adjustment. (Note in Fig. 4B that depensatory predation mortality reduces the yield but only at very low uncertainty adjustments of –80% to –100%). For the Adams, Chilko, Late Stuart, and Gates stocks, the differences between Loss 1 and Loss 2 (as percentages of the expected yield estimated with the correct model) was not greater than 1%. In addition, losses (either Loss 1 or 2) not greater than 4% of the expected yield from the correct model resulted from incorrectly using the optimal uncertainty adjustment estimated with the wrong model. These losses are insignificant compared to other sources of error not considered here such as the inability to precisely achieve escapement targets because of imprecise in-season forecasting and imperfect control of the fleet during harvesting.

By choosing the 5 stocks that I did, a situation was created where, because of the strength of depensation, the chances of seeing a big difference between using the Ricker and depensatory models should have been maximized. The fact that these differences were not seen in 4 out of 5 stocks suggests that for the performance criterion used here (e.g. expected loss in yield), the differences between models are inconsequential. These results were expected for the Chilko sockeye because there is not a strong indication of depensation in the spawner-recruit data for this stock. However, the negligible differences between the losses for the Adams, Gates, and Late Stuart stocks are inconsistent with other work that indicates that the presence of a threshold (e.g. such as one created by depensation) may dictate extremely conservative uncertainty adjustments and, hence, acting as if a threshold does not exist when in fact it actually does could result in large losses in yield (Frederick and Peterman 1995). To the contrary, the extremely conservative uncertainty adjustments seen here for some stocks are contingent on the strength of density-dependent survival at high spawner abundance and not on the possibility of a threshold created by depensatory predation.

For a manager who uses a constant escapement policy to manage these stocks, the use of a Ricker model *or* a depensatory model appears to be approximately optimal. Ideally, under this policy, stocks are not harvested unless the number of recruits is above the escapement target. In such cases in the simulation model, very small stock sizes were able to increase rapidly until they reached numbers of spawners above levels that might be susceptible to depensatory mortality. As a result, the optimal uncertainty adjustment was not affected by the spawner abundance used to initialize the model. This suggests that depensatory dynamics *alone* (e.g. in the absence of an additional mechanism such as harvesting) are not responsible for keeping a stock at a commercially unproductive, lower equilibrium.

However, the absence of harvest on small off-year runs is not a realistic situation in the field because of imperfect control of the fishing fleet and the mixed-stock nature of the Fraser River fishery where small off-year runs are harvested along with other larger runs returning at the same time. In the Pacific salmon fishery, high harvest rates of up to 80% are often imposed on small off-year runs (Collie and Walters 1986; Walters and Staley 1987). In addition, high harvest rates may be responsible for maintaining the small spawning escapements of the off-year cycle lines (Walters and Staley, 1987; Collie et al, 1989). This suggests that the implications of depensatory mortality may be more serious for a constant harvest rate policy.

Constant Harvest Rate Policy

In this and the following sections, references to the Ricker and depensatory models are for the uncertain parameters cases unless stated otherwise.

I modified the simulation model to examine the effect of a constant harvest rate policy on the expected yields predicted by the Ricker and depensatory models. I examined a range of harvest rates on the simulated stock. The yield for each year was a fixed proportion of the available recruits; the unharvested recruits spawned. Unlike the constant escapement policy, harvests were taken from all returns, regardless of the size of the run. I based these results on initial escapements of 2,000 spawners so that the results here could be compared to those for the constant escapement policy.

The harvest rates that maximized the expected average yield over 10 generations are shown in Table 3. For the best-fit parameters cases, harvest rates are 5% to 22% lower for the depensatory model than for the Ricker model (except for the Chilko) for reasons I discuss later for the uncertain parameters case. I do not discuss here the EVIU, but in contrast to some stocks that had a high EVIU for the constant escapement policy, the EVIU was small for *all* stocks for the constant harvest rate policy because the differences between the expected yields at optimal harvest rates for the best-fit and uncertain parameters cases for a given model differed only slightly.

For the uncertain parameters cases, the possibility of depensatory mortality dictates optimal harvest rates on the order of 5% to 13% lower than those predicted for the *no depensation* case (i.e. Ricker model) for all of the stocks (except Chilko) (Table 3). Lower harvest rates are optimal for the depensatory model because they allow a stock to slowly rebuild out of the depensatory pit (i.e. the region of reduced productivity at a low abundance of spawners).

However, for all 5 stocks the choice of a particular harvest rate (i.e. management option) for the uncertain parameters cases was relatively insensitive to whether a Ricker or a depensatory stock-recruitment model was used in the analysis. Note that the harvest rates that maximized the expected yields for the Ricker and depensatory models differ by 13% or less (and by 5% or less for the Raft, Chilko, and Gates) (Table 3). In addition, the differences in performance (i.e. expected loss in yield) between the Ricker and depensatory models were small. For example, for the Adams stock, the expected loss in yield associated with applying the optimal harvest rate from the depensatory model when in fact a Ricker model should have been used was 338,458 fish per year (*Loss 1* in Fig. 8). This represents a loss of 10% compared to the expected yield that was estimated with the optimal harvest rate from the Ricker model (e.g. 338,458 / 3,522,835). This compares with an expected loss of 196,566 fish per year (*Loss 2* in Fig. 8) associated with the wrong application of the Ricker model. This represents a loss of 13% compared to the expected yield estimated with the optimal harvest rate from the depensatory model (e.g. 196,566 / 1,525,483). While the absolute value of the Loss 1 is significantly larger than Loss 2, the difference between the expected losses in yield is relatively small (in percentage terms). This result is typical of the small percentage differences between the expected losses in the 5 stocks. So if the fishery is managed under a constant harvest rate policy, the performance of the harvest rate estimated by the Ricker model should *not* be significantly different than the performance of the harvest rate estimated by the depensatory model.

In contrast to the small differences in performance of the optimal harvest rates for the Ricker and depensatory models for the uncertain parameters case, the expected yield that will be realized by the fishery critically depends on the model that is correct. Notice that if depensatory dynamics actually do exist (i.e. the depensatory model is correct), then the expected yield for the optimal harvest rate may be 57% less than is estimated by the optimal harvest rate from the Ricker model (e.g. the difference in expected yield between the models at H* in Fig. 8). This could have serious implications for people dependent on the fishery for their income. However, these results only apply to small initial run sizes of 2,000 spawners. For a high initial abundance of spawners, the expected yields predicted by the Ricker and depensatory models are similar. But, because small escapements are a reality, the question is what to do about them.

Implications of small run sizes under a constant harvest rate policy

While initial conditions do not affect the optimal harvest rates for a Ricker model, this contrasts with a depensatory model where the harvest rate is sensitive to how long the population is in the lower unproductive region of the stock-recruitment curve. If the initial abundance of spawners is high, then the stock will never be in the depensatory region and can be harvested at a higher rate than if it starts out in that region and remains there for some period. The harvest rates that maximized the expected average yield over the 10 simulated generations are shown in Fig. 9 for different spawner abundances used to initialize the simulation. The lowest harvest rates were produced for an initial abundance of spawners in the region of depensatory predation mortality. However, the expected yield over 10 generations is not the same as the optimum long-term sustainable yield that results once the population is above the lower unproductive region caused by depensatory mortality. For a larger initial abundance of spawners (e.g. above 50,000 in Fig. 9), the harvest rates that maximized the expected average yield predicted by the depensatory model were much higher and are relatively insensitive to changes in the initial number of spawners. On the other hand, the harvest rates predicted by the Ricker model were relatively insensitive to the initial abundance of spawners (Fig. 9) because there is not a depensatory region in the Ricker model.

For a constant harvest rate strategy, the 'optimal' harvest rate for a *small* off-year run maximizes the expected yield for that run given that the harvest rate is not changed over the duration of the simulation. For the depensatory model, one could argue that the harvest rate predicted for a higher abundance of spawners is a much better estimate of the long-term 'optimal' harvest rate because the harvest rate asymptotes just above a harvest rate of 80%. Several authors have suggested that higher yields could be obtained for an off-year run by decreasing the harvest rate until the stock rebuilds to a higher level and then imposing a higher harvest rate (Collie et al. 1990; Welch and Noakes 1991).

Stock Rebuilding under a Constant Harvest Rate Policy

In this section, I evaluated several different constant harvest rate strategies to estimate the number of generations it would take for the abundance of spawners from an off-year cycle line to rebuild for a Ricker or depensatory model for the uncertain parameters case. I considered rebuilding to have occurred when an arbitrary number of spawners equivalent to 50% of the best-fit optimal escapement for the Ricker model (as in Table 2) was reached. Then, in the following section (*"Benefits of implementing a rebuilding policy"*), I evaluated whether lowering the harvest rate and then applying a higher harvest rate after some period of rebuilding produced any benefits, in terms of a yield maximizing objective.

I used the Adams stock in the analyses for stock rebuilding because it represents the most extreme example of rebuilding among the 5 stocks. A spawning escapement of 2,000 fish for the Adams stock must undergo a roughly 850-fold increase in abundance to achieve the rebuilding target escapement specified above. The rebuilding required for the 4 other stocks is not as pronounced; increases ranging from 12-fold for the Raft to 275-fold for the Late Stuart are needed for initial spawning escapements of 2,000 fish. Results for the other stocks are qualitatively similar to those for the Adams discussed below.

The number of generations to rebuild an off-year cycle line depended on the initial abundance of the line as well as the harvest rate (Fig. 10). For the Adams stock, the number of generations required to rebuild the stock to 50% of the baseline escapement target decreases as the number of spawners used to initialize the simulation increases. Both models forecast regeneration times less than 5 generations for an initial abundance of spawners above 100,000, for harvest rates less than 70% (Fig. 10). This is because the productivity of the depensatory model is roughly the same as the Ricker model for large abundances of spawners above levels where depensatory mortality reduces productivity. However, for numbers of spawners less than 80,000 rebuilding took significantly longer under the depensatory model compared with the Ricker model for a given harvest rate. For example, for a harvest rate of 70% and an initial abundance of 10,000 spawners, rebuilding would be expected to take 3 to 4 times longer if depensatory dynamics actually *do exist* (Fig. 10). In addition, higher harvest rates dramatically increased the number of generations to rebuild the stock for the depensatory model. Increases in the number of generations required for rebuilding the stock were also realized for the Ricker model for a harvest rate of 70% because even if depensation *does not* exist, high harvest rates lead to recruitment overfishing. These results confirm the obvious effect, that regardless of which model is correct, a reduction in harvest rates can increase the rate at which a stock rebuilds. But in addition, if depensatory dynamics do exist, then rapid rebuilding of a stock (e.g. in under 5 generations) may not be possible unless harvest rates are substantially reduced.

These results are consistent with the widespread conclusion that harvest rates should be lowered to allow off-year cycle lines to rebuild (Walters and Staley 1987; Collie et al. 1990; Welch and Noakes 1991). These results also support the evidence (Walters and Staley 1987; Welch and Noakes 1991) that high harvest rates may help maintain cyclic dominance by preventing the off-year cycle lines from recovering.

I caution readers not to conclude that depensatory predation mortality in conjunction with high harvest rates is responsible for cyclic dominance. Note that the expected number of generations required for rebuilding under the Ricker model can approach 10 cycles (or 40 years) for small numbers of spawners exposed to a 70% harvest rate and thus, small run sizes could also be maintained by *non*-depensatory dynamics. The only way to distinguish between the two models is to experimentally decrease harvest rates. If the Ricker model is correct, the off-year runs should recover rapidly. If the depensatory model is correct, the off-year runs should remain depressed for a much longer time (Collie and Walters 1986). Reducing the harvest rate on off-year runs is thus of primary management importance regardless of whether depensatory dynamics actually do exist. In addition to harvest rate reduction, other experiments such as predator removal would be required to determine the exact mechanism causing depensation (Collie et al. 1990).

Benefits of implementing a rebuilding policy

The benefits of increased yield associated with rebuilding off-year cycle lines through harvest rate reduction has been widely suggested (Walters and Staley 1987; Collie et al. 1990; Welch and Noakes 1990). On the other hand, reducing the harvest rate may result in a short-term loss in yield to the fisheries. The question is whether the short-term loss in yield associated with reducing the harvest rate to rebuild an off-year run is justified given the uncertainty over whether depensatory predation mortality actually exists.

To answer this question, I compared the benefits (i.e. expected yield) associated with a *rebuilding* policy to the benefits from maintaining a *constant harvest rate* policy for the Ricker and depensatory models, explicitly taking the uncertainty in parameter estimates of those models into account through the Bayesian analysis, unlike previous authors. Under the *constant harvest rate* policy, a constant harvest rate of 80% predicted by the best-fit Ricker model was applied for 10 generations. For the *rebuilding* policy, a constant harvest rate of 50% was applied for 4 generations to allow rebuilding and then increased to 80% for the remaining 6 generations (this was similar to the policy used in Collie et al. 1990). I used a 50% harvest rate for the rebuilding policy because it has been suggested as the lowest harvest rate that the fishing industry could consistently find acceptable (K. McGivney, D.F.O., *in* Collie et al. 1990).

Large increases in the expected yield resulted for the depensatory model under the rebuilding policy compared to the constant harvest rate policy. For the Adams stock and an initial abundance of 2,000 spawners, the rebuilding policy produced a 17-fold increase (from 30,000 to 515,000) in the expected yield. A 5-fold increase (from 450,000 to 2.1 million) resulted from following a rebuilding policy for the Ricker model. Obviously, the benefits of pursuing a rebuilding policy are positive for both models, but if depensatory predation mortality actually does exist, then the rebuilding policy increases the yield dramatically. Therefore, it appears that the benefits of increased yield are sufficiently high to justify rebuilding through reduction of harvest rates.

Clearly rebuilding is beneficial but, because of the mixed stock nature of the fishery, harvest rate reductions for the purpose of rebuilding frequently affect more than one stock. For example, attempts to rebuild off-year Adams River sockeye runs would also affect the co-migrating Weaver Creek sockeye and to some extent the Fraser River pink salmon run (Welch and Noakes 1990). Therefore, the problem is how to accomplish rebuilding of off-year runs while minimizing the loss in yield for larger runs that are harvested at the same time as the off-year run(s). This problem is beyond the scope of this study, but some attempts have been made to identify which off-year runs could be targeted for rebuilding while minimizing the loss in yield (e.g. from larger co-migrating stocks) that is associated with reduced harvest rates (Collie et al. 1990; Welch and Noakes 1990)

Improvements to the decision analysis approach

In addition to the stock-recruitment data used in the Bayesian decision analysis, other information sources could be included in the analysis. I used a uniform prior, which placed equal probability on a wide range of reasonable combinations of stock-recruitment parameters for the models. However, other information can be used to assign higher prior probabilities to certain parameter values based on information about environmental variables such as spawning site conditions or lake productivity (Geiger and Koenings 1991; Hume et al. 1996). In addition, information from biologists or managers familiar with salmon life history or the Ricker model can be used to form prior probability distributions on model parameters. In this analysis, the use of an informative prior might dramatically alter the results for some stocks. For stocks where there was considerable uncertainty about the 'β' or 'b' parameters, an informative prior could dramatically change the optimal harvest strategy. For example, if an informative prior was used for the Late Stuart or Gates stocks that specified that large values for the 'β' or 'b' parameters were extremely unlikely (i.e. there was *a priori* information that density dependence was strong at high numbers of spawners), then the optimal escapement targets produced by the decision analysis would probably be considerably lower. However, the choice of an informative or uninformative prior should be made with caution and only if there is a defensible justification (Walters 1986; Adkison and Peterman 1996).

Decision analysis can also be improved upon by evaluating how updating the Bayesian analysis with new stock-recruitment data points each year would alter the optimal harvest decision. Passive adaptive management involves adding new years of stock-recruitment data to the analysis as they become available. This approach may help to further define the shape of the stock-recruitment curve by showing the extent of depensation at low abundance of spawners or the strength of density-dependence at high abundance. This approach relies on the natural variability in the abundance of spawners for contributing new information to the analysis. Another approach, active adaptive management, involves experimentally changing the harvest rate to gain information outside of the range of natural variation (Walters 1986). For example, experimentally increasing the spawning escapement might be favorable when there is high uncertainty about strength of density-dependence in a stock (such as the Late Stuart or Gates) (Walters and Ludwig 1987). However, active adaptive management is often not acceptable to fishery participants because it involves reducing the current harvest in return for information about the stock that will not benefit the participants until some time in the future. My analysis shows that the expected benefits of increasing the escapement of stocks with weak density-dependence such as the Late Stuart may be large compared to maintaining lower escapements.

To select optimal management strategies, I used management objectives of maximizing the expected yield or minimizing the number of years required for a small off-cycle line to rebuild. However, these management objectives are just two of several that managers may wish to consider when using decision analysis. Other objectives might include minimizing the probability that the stock will become commercially extinct (i.e. drop below some pre-determined threshold), reducing the between-year variability of the commercial harvest, or minimizing the chance that duration of commercial fishing drops below some predetermined value. Decision analysis can be used to address the trade-off between any of these other objectives or even multiple objectives of managers.

Limits of the Decision Analysis Approach

Managers using decision analysis must be aware that they are making a decision based on an expected yield and not on a particular prediction of the yield that will be achieved. The optimal management action calculated by decision analysis does not necessarily guarantee a favorable outcome in any particular year. Decision analysis uses expected values to take into account the uncertainty in the natural system and aids the selection of an optimal management action. In any given year, undesirable outcomes may be realized due to natural variability, but this does not necessarily mean a bad decision has been reached. For example, given an optimal uncertainty adjustment of 311% (Ricker model) for the Late Stuart stock, the expected yield is 68% higher than if the best-fit Ricker escapement was used (Fig. 4A). These results do not imply that an optimal uncertainty adjustment of 311% will definitely result in a 68% increase in yield compared to the best-fit Ricker case. Rather the difference is between "expected" yields, which are weighted averages of predicted yields across all of the uncertain states of nature (i.e. parameter combinations) considered in the model. An optimal uncertainty adjustment of 311% is more likely, given the uncertainties in the shape of the stock-recruitment curve, to result in a higher yield than the optimal strategy for the best-fit Ricker case.

Managers must therefore be careful not to assume that the expected yields predicted will actually be realized if a particular management strategy is followed. Over the long-term, a carefully conducted decision analysis guarantees that the results predicted for a given management strategy will be superior to management decisions based on intuition or an incomplete acknowledgment of uncertainty. For this reason, it is important that managers who advocate Bayesian decision analysis do so based on the resulting long-term performance, rather than on any particular year's results.

CONCLUSIONS

This research graphically illustrates when there are benefits from using a depensatory model instead of a Ricker model and from including uncertainty in parameter estimates. This approach was more comprehensive than other studies because Bayesian decision analysis was used to explicitly incorporate uncertainties in the model parameters and also to quantify the management implications (e.g. expected yield) of depensatory predation mortality over a range of management policies. Although there are no general rules for when to use a depensatory model instead of a Ricker model, Bayesian decision analysis provides a rational basis for determining the best approach on a stock-by-stock basis.

The inclusion of uncertainty in stock-recruitment parameters may significantly improve management performance in some circumstances. For example, for some stocks for the constant escapement policy, large "uncertainty adjustments" (i.e. increases to the target escapement) may be beneficial for stocks with a high degree of uncertainty about the fit of the stock-recruitment curve at high abundances of spawners. The calculation of the expected value of including uncertainty (EVIU) illustrates how large the benefits associated with including uncertainty in the decision making process can be compared to a best-fit approach which ignores uncertainty. The EVIU was small for all stocks for the constant harvest rate policy because expected yields of the optimal harvest rates for the best-fit and uncertain parameters cases for a given model differed only slightly.

In general, the inclusion of uncertainty in stock-recruitment parameters means that harvest strategies are more robust to uncertain states of nature than strategies formulated based solely on a best-fit approach which essentially ignores uncertainty. In addition, including uncertainty in the parameters of the depensatory stock-recruitment model allowed the model to have varying degrees of depensation including no depensation (e.g. such as a Ricker model) depending on the stock-recruitment data and thus the possibility of depensation could be quantified for a given stock. A comparison of the benefits of harvest strategies based on the depensatory model to those based on the Ricker model showed that the possibility of depensatory predation mortality may have important management implications for stocks with few spawners (e.g. 2,000) but this depends on the type of harvest policy used.

For example, for a constant escapement strategy, the possibility of depensation at a small spawner abundance did not affect the optimal uncertainty adjustment because small spawning escapements below the escapement target were not harvested. Therefore, very small stock sizes were able to increase rapidly until they reached numbers of spawners above levels that might be susceptible to depensatory predation mortality. Consequently, differences in performance (i.e. expected loss in yield) between the Ricker and depensatory models for the uncertain parameters cases were extremely small for this policy. In addition, this also suggests that a depensatory predation mortality mechanism alone (e.g. in the absence of another mechanism such as harvesting) is not strong enough to maintain an off-year line at a low abundance and thus is likely not the sole explanation for cyclic dominance in Fraser River sockeye salmon.

In contrast, under a constant harvest rate policy, the possibility of depensatory predation mortality generally required lower harvest rates compared to the Ricker model to maximize the expected yield over 10 generations when initial abundances of spawners were small (e.g. 2,000). Although the differences in performance between the Ricker and depensatory models were relatively small, if depensation actually exists, then the absolute value of the expected yield may be much lower than if depensation does not exist for stocks with few spawners. The expected yield for the depensatory model was comparable to the Ricker model when the initial abundance of spawners was large because the stock was rarely at risk of being in the depensatory region and could be harvested at a harvest rate comparable to the optimal harvest rate estimated for the Ricker model. Preliminary analyses of stock-rebuilding policies indicated that high harvest rates similar to historic levels (e.g. 80%), in conjunction with the possibility of depensatory predation mortality, may prevent the rebuilding of small abundances of spawners characteristic of off-year lines. Hence, for small off-year runs, a reduction in the harvest rates are necessary to allow the spawning stock size to rebuild and should result in increases in expected yield. Lower harvest rates benefit small numbers of spawners even if depensatory mortality does not exist because the stock is allowed to rebuild much more quickly. However, dramatic increases in yield may result if depensatory mortality actually exists.

I have reached a similar conclusion to others about the importance of reducing harvest rates on small off-year runs to allow the spawning stock to rebuild. If in fact cyclic dominance is caused in part by depensatory predation mortality in Fraser River sockeye stocks, then dramatic increases in the expected yield could be realized from reducing harvest rates on off-year runs to allow stock rebuilding. Thus, these results are consistent with other recommendations to reduce harvest rates on off-year runs (Walters and Staley 1987; Collie et al 1990; Welch and Noakes 1991).

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Table 1. Summary of the analyses done (denoted by an X) for each policy and level of uncertainty considered in the stock-recruitment model.

		Stock-recruitment model and level of uncertainty considered			
Policy	**Sockeye salmon Stocks Analyzed**	Best-fit Ricker model	Best-fit Depensatory model	Uncertain Parameters, Ricker model	Uncertain Parameters, Depensatory model
Constant escapement	Adams, Raft, Late Stuart, Gates, Chilko	X (baseline escape-ment target)	X	X	X*
Constant harvest rate	Adams, Raft, Late Stuart, Gates, Chilko	X	X	X	X
Stock rebuilding	Adams 'off-cycle' years			X	X

* Denotes the scenario detailed in the methods section

Table 2. Optimal uncertainty adjustments for the constant escapement policy and different admissions of uncertainty in the Ricker and depensatory stock-recruitment models for several Fraser River sockeye stocks. The optimal uncertainty adjustment (as a percentage change in the best-fit Ricker escapement target) maximizes the expected yield over 10 generations for an initial abundance of 2,000 spawners. A positive (or negative) % change indicates an increase (or decrease) in the escapement target relative to the baseline target estimated for a best-fit Ricker model. Optimal escapement targets in number of fish are shown in parentheses for each scenario.

	Stock-recruitment model and level of uncertainty considered			
Sockeye salmon stock	Best-fit Ricker model –baseline escapement target	Best-fit Depensatory model	Uncertain Parameters Ricker model	Uncertain Parameters Depensatory model
		Optimal uncertainty adjustment as a % change in the baseline target escapement (actual escapement)		
Adams	1.7 million	**– 30%** (1.190 million)	**8%** (1.836 million)	**– 16%** (1.428 million)
Raft	25,000	**– 48%** (13,000)	**5%** (26,250)	**– 41%** (14,750)
Late Stuart	550, 000	**– 21%** (434,500)	**311%** (2.261 million)	**261%** (1.986 million)
Gates	31, 000	**– 6%** (29,140)	**129%** (70,990)	**171%** (84,010)
Chilko	530, 000	**– 15%** (450,500)	**35%** (715,500)	**48%** (784,400)

Table 3. Harvest rates that maximized expected yield for the constant harvest rate policy for several Fraser River sockeye salmon stocks and different admissions of uncertainty in the Ricker and depensatory stock-recruitment models. The table shows the results for 10 generations for an initial abundance of 2,000 spawners.

	Stock-recruitment model and level of uncertainty considered			
Sockeye salmon stock	Best-fit Ricker model	Best-fit Depensatory model	Uncertain Parameters Ricker model	Uncertain Parameters Depensatory model
Adams	**68%**	**46%**	**67%**	**54%**
Raft	**62%**	**57%**	**61%**	**57%**
Late Stuart	**81%**	**73%**	**77%**	**69%**
Gates	**82%**	**77%**	**79%**	**74%**
Chilko	**71%**	**75%**	**67%**	**66%**

Figure 1. Decision tree showing the calculation of an example performance measure, average annual yield (across t generations), for different management strategies. For simplicity, only a subset of branches is shown here. Each (...) indicates a repetition of the branch shown for that category. The management options emanating from the square decision node are variations from a best-fit Ricker escapement target modified by uncertainty adjustments that ranged from –99% to +100% in increments of 1%. Different states of nature emanate from the circular uncertainty node and consist of discrete parameter sets for the stock-recruitment model (depensatory model in this example) each with probability, P_i. Each state of nature is defined by particular values for the parameters of that model (*a, b, c, d,* σ). For each branch of the decision tree, a model of salmon population dynamics is used to estimate a value for the average annual yield from catching salmon ($yield_i$). The $yield_i$'s are then weighted by the probability associated with each branch (i.e. P_i) and summed across all branches to give an expected value (EV), or weighted average, of average annual yield for each uncertainty adjustment.

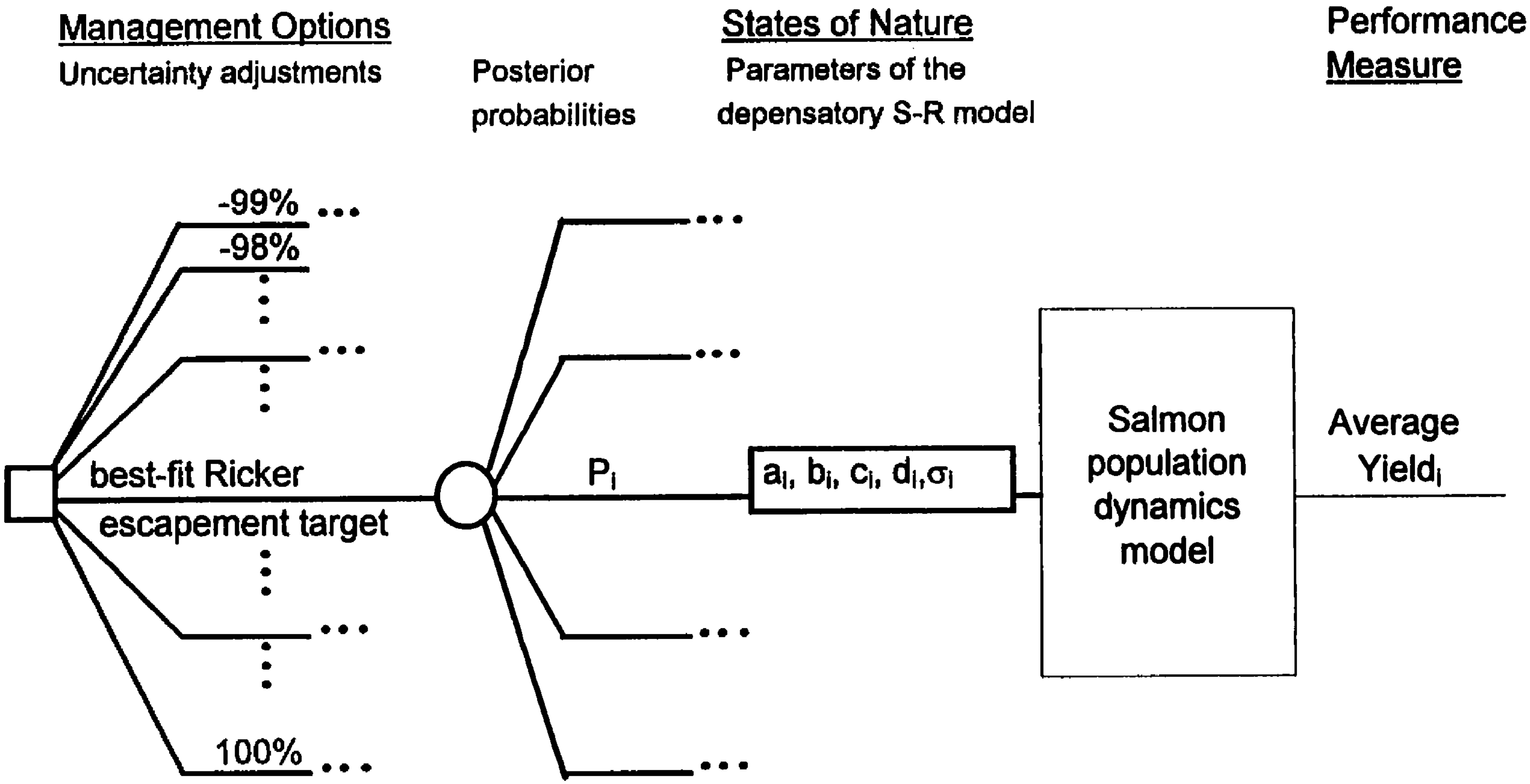
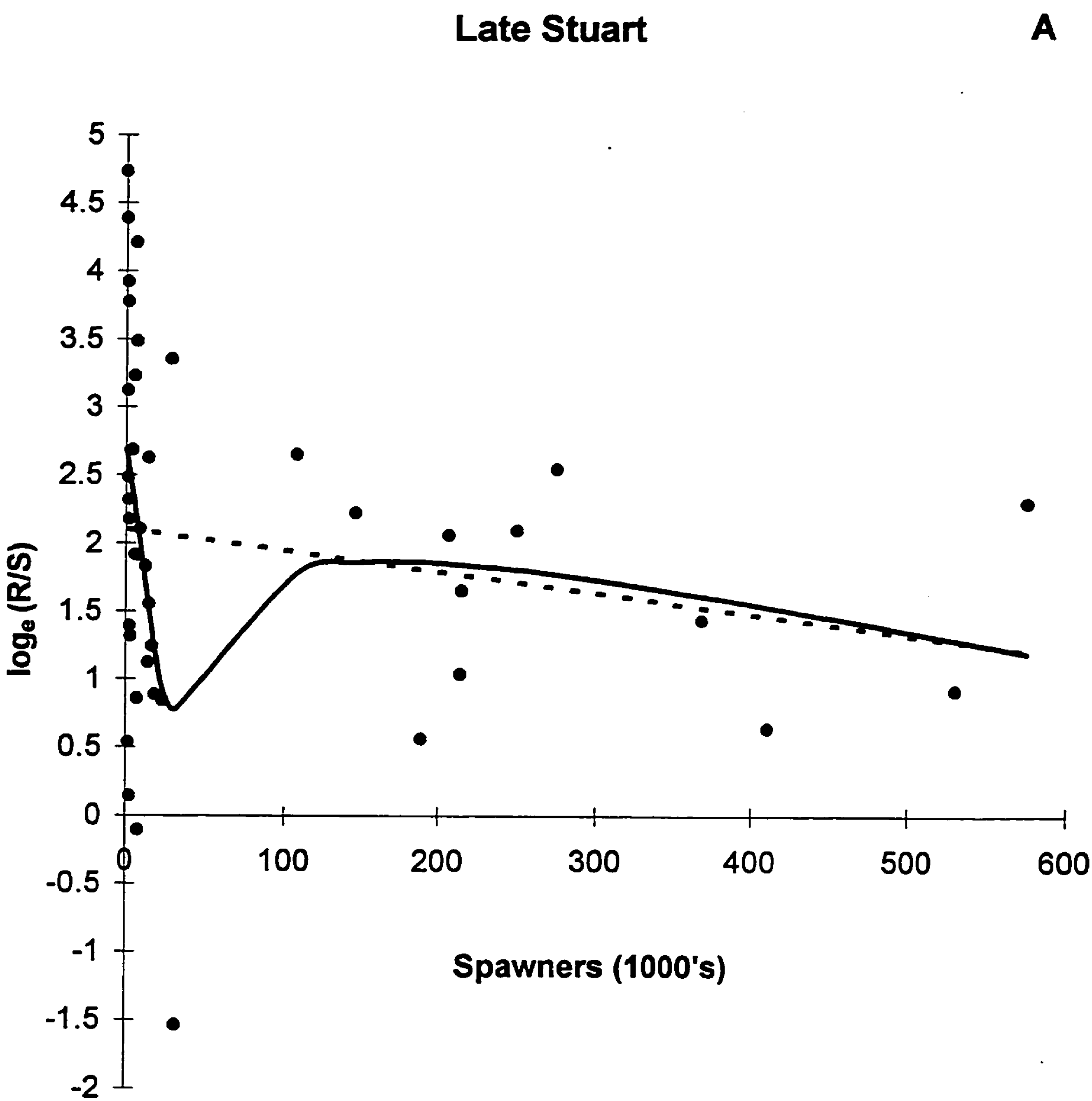

Management Options
Uncertainty adjustments
Posterior probabilities
States of Nature
Parameters of the depensatory S-R model
Performance Measure
-99%
-98%
best-fit Ricker
escapement target
100%
P_i
a_i, b_i, c_i, d_i, σ_i
Salmon population dynamics model
Average Yield$_i$

Figure 2. Stock-recruitment data for the Late Stuart sockeye (1949-1990 brood years (Panel A) and the Raft River sockeye (1948-1990 brood years) (Panel B). The relationships shown are the Ricker (dashed line) and depensatory (solid line) models using best-fit parameters for the relationship between $\log_e$ (recruits/spawner) and spawners.



Late Stuart
A
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
loge (R/S)
0
100
200
300
400
500
600
Spawners (1000's)

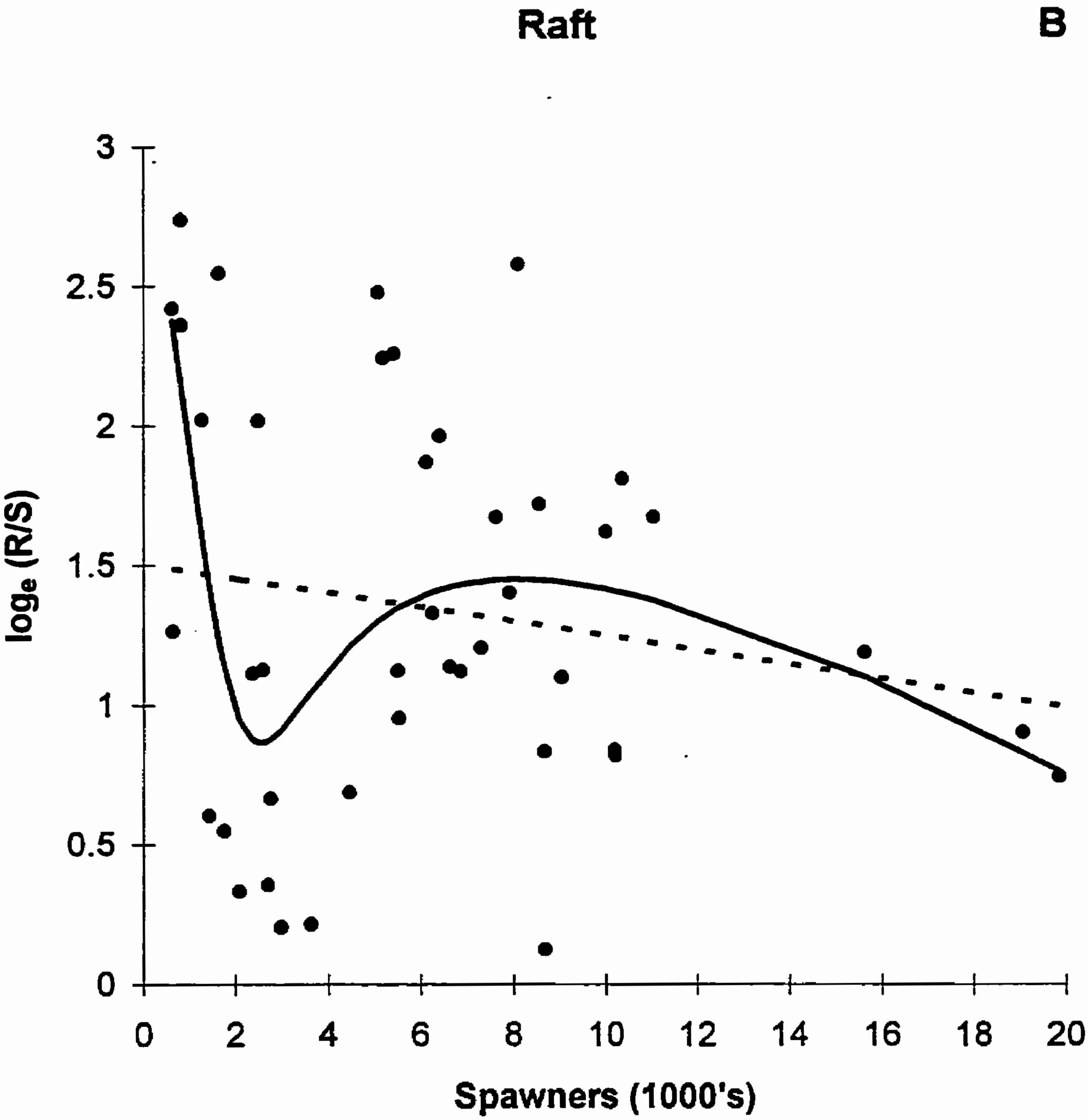

Raft
B
3
2.5
2
1.5
1
0.5
0
$\log_e$ (R/S)
0
2
4
6
8
10
12
14
16
18
20
Spawners (1000's)

Figure 3. Flow chart of the simulation model used in the decision analysis for the case where the admission of uncertainty in the parameters of the depensatory stock-recruitment curve (Eqn. 2) was considered. The same decision analysis framework was also used to consider uncertainty in the parameters of the Ricker stock-recruitment curve (Eqn. 1).

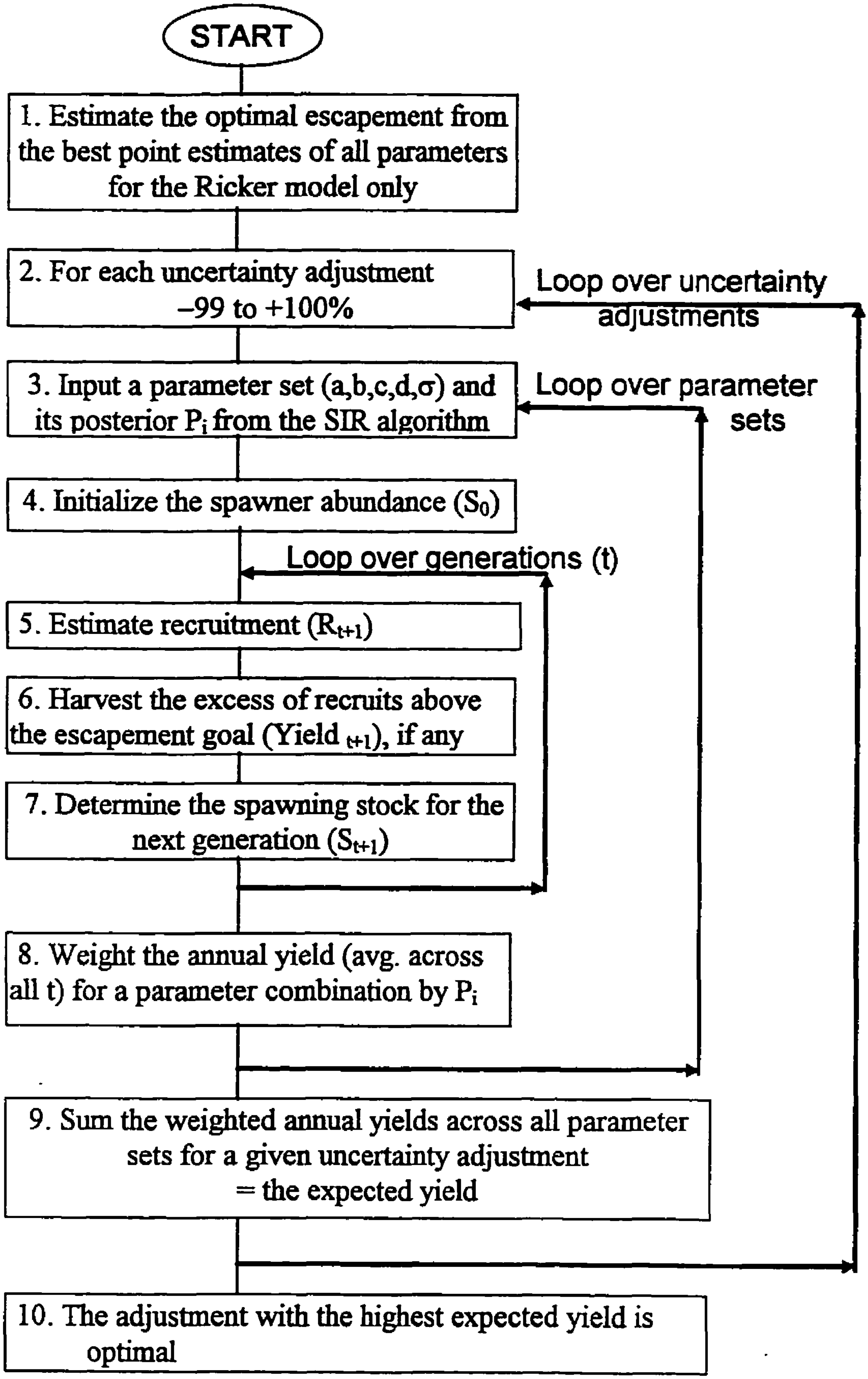
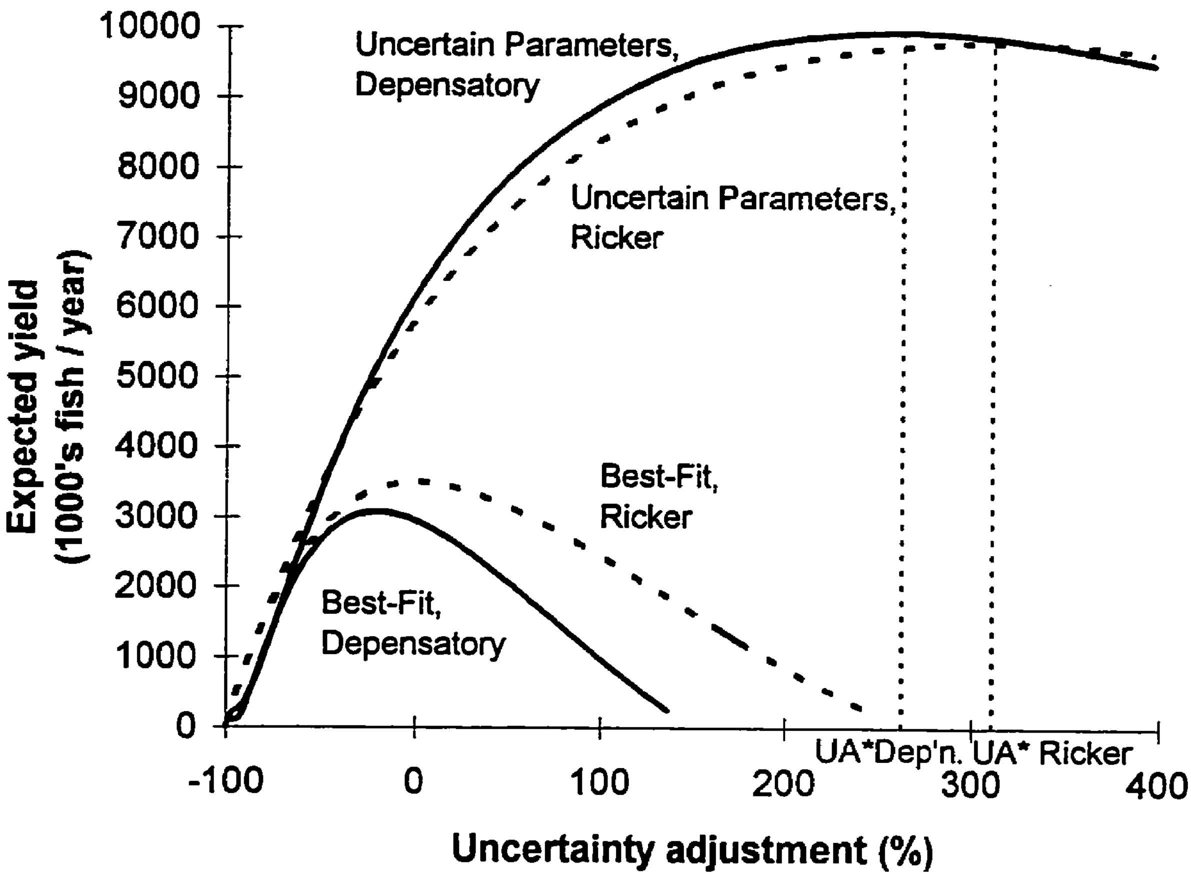

START
1. Estimate the optimal escapement from the best point estimates of all parameters for the Ricker model only
2. For each uncertainty adjustment −99 to +100%
Loop over uncertainty adjustments
3. Input a parameter set (a,b,c,d,σ) and its posterior Pi from the SIR algorithm
Loop over parameter sets
4. Initialize the spawner abundance (S0)
Loop over generations (t)
5. Estimate recruitment (Rt+1)
6. Harvest the excess of recruits above the escapement goal (Yield t+1), if any
7. Determine the spawning stock for the next generation (St+1)
8. Weight the annual yield (avg. across all t) for a parameter combination by Pi
9. Sum the weighted annual yields across all parameter sets for a given uncertainty adjustment = the expected yield
10. The adjustment with the highest expected yield is optimal

Figure 4. Expected yield (in thousands of fish per year) for each uncertainty adjustment for a constant escapement policy. The *x-axis* represents the amount of adjustment (% change) in the optimal escapement goal from the one estimated for the best-fit Ricker case. The dashed line is for the Ricker model and the solid line is for the depensatory model (results for the uncertain parameters and best-fit cases are shown for each). Figure 4A is for the Late Stuart sockeye stock and Figure 4B is for the Raft sockeye stock. Optimal uncertainty adjustments are indicated by UA* for both models. These results are for an initial abundance of 2,000 spawners.

Late Stuart

A



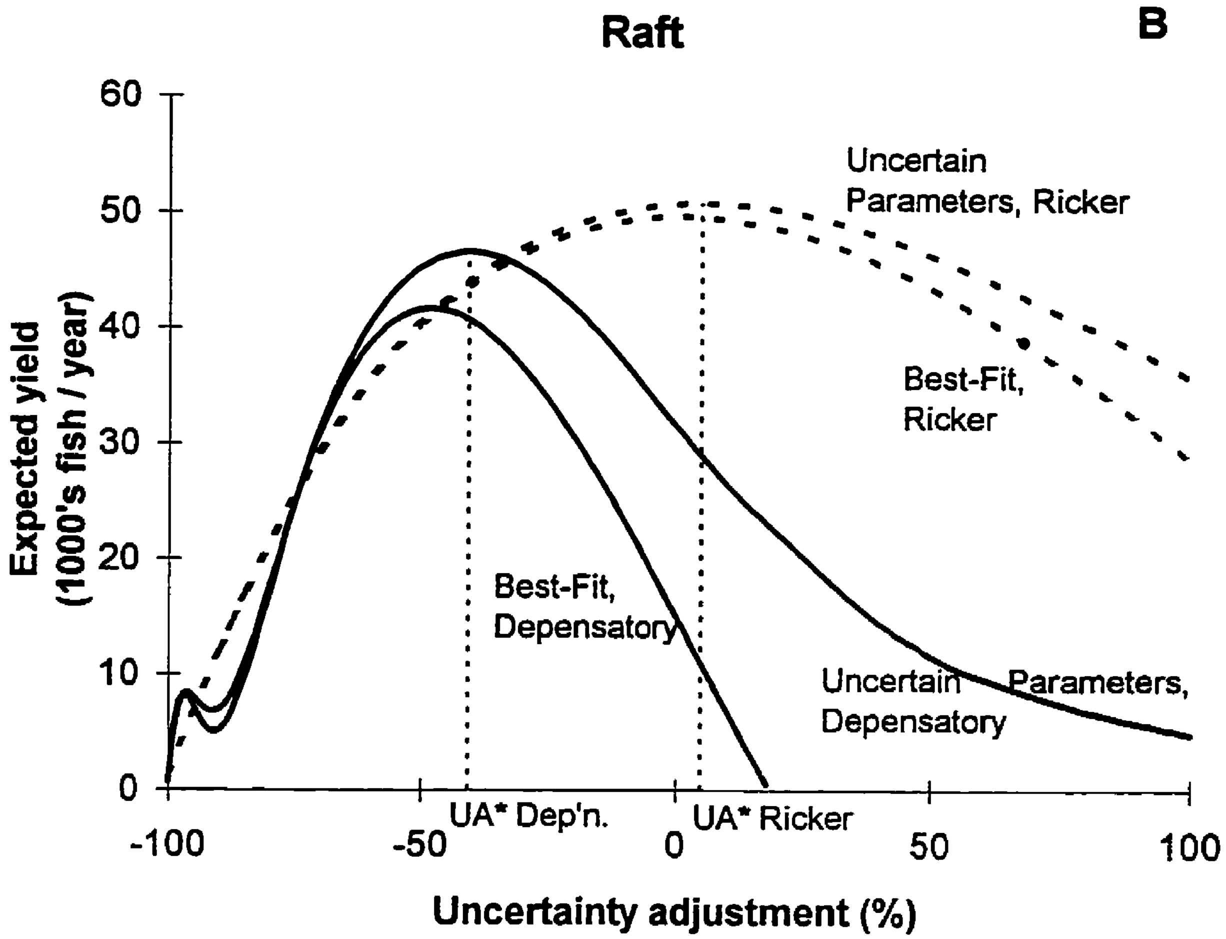

Raft
B
Uncertain Parameters, Ricker
Best-Fit, Ricker
Best-Fit, Depensatory
Uncertain Parameters, Depensatory
UA* Dep'n.
UA* Ricker
Expected yield (1000's fish / year)
Uncertainty adjustment (%)
60
50
40
30
20
10
0
-100
-50
0
50
100

Figure 5. Marginal posterior probability distribution for the parameters of the Ricker (dashed line) and depensatory (solid line) models for the Late Stuart stock. These distributions reflect the posterior probability distributions that were used in the Bayesian analysis to quantify the probabilities associated with different states of nature. The marginal posterior pdfs are for the α (panel A) and β (panel B) parameters of the Ricker model and for the *a* (panel A), *b* (panel B), *c* (panel C) and *d* (panel D) parameters for the depensatory model.

Late Stuart

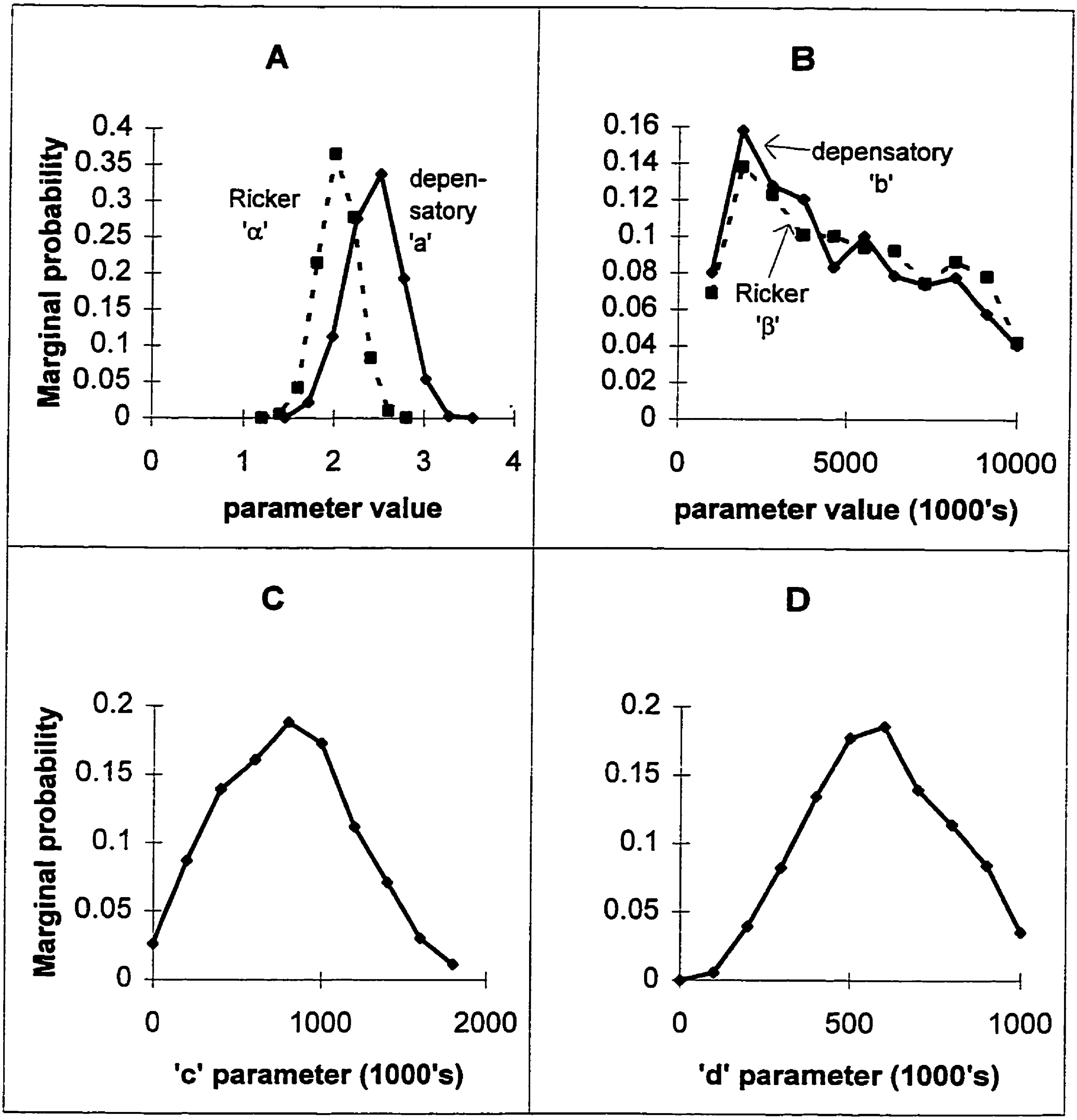

A
Marginal probability
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Ricker
'α'
depen-
satory
'a'
0
1
2
3
4
parameter value
B
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
depensatory
'b'
Ricker
'β'
0
5000
10000
parameter value (1000's)
C
Marginal probability
0.2
0.15
0.1
0.05
0
0
1000
2000
'c' parameter (1000's)
D
0.2
0.15
0.1
0.05
0
0
500
1000
'd' parameter (1000's)

Figure 6. Similar to Fig. 5, except the marginal posterior pdfs are for the Raft stock-recruitment data.

Raft

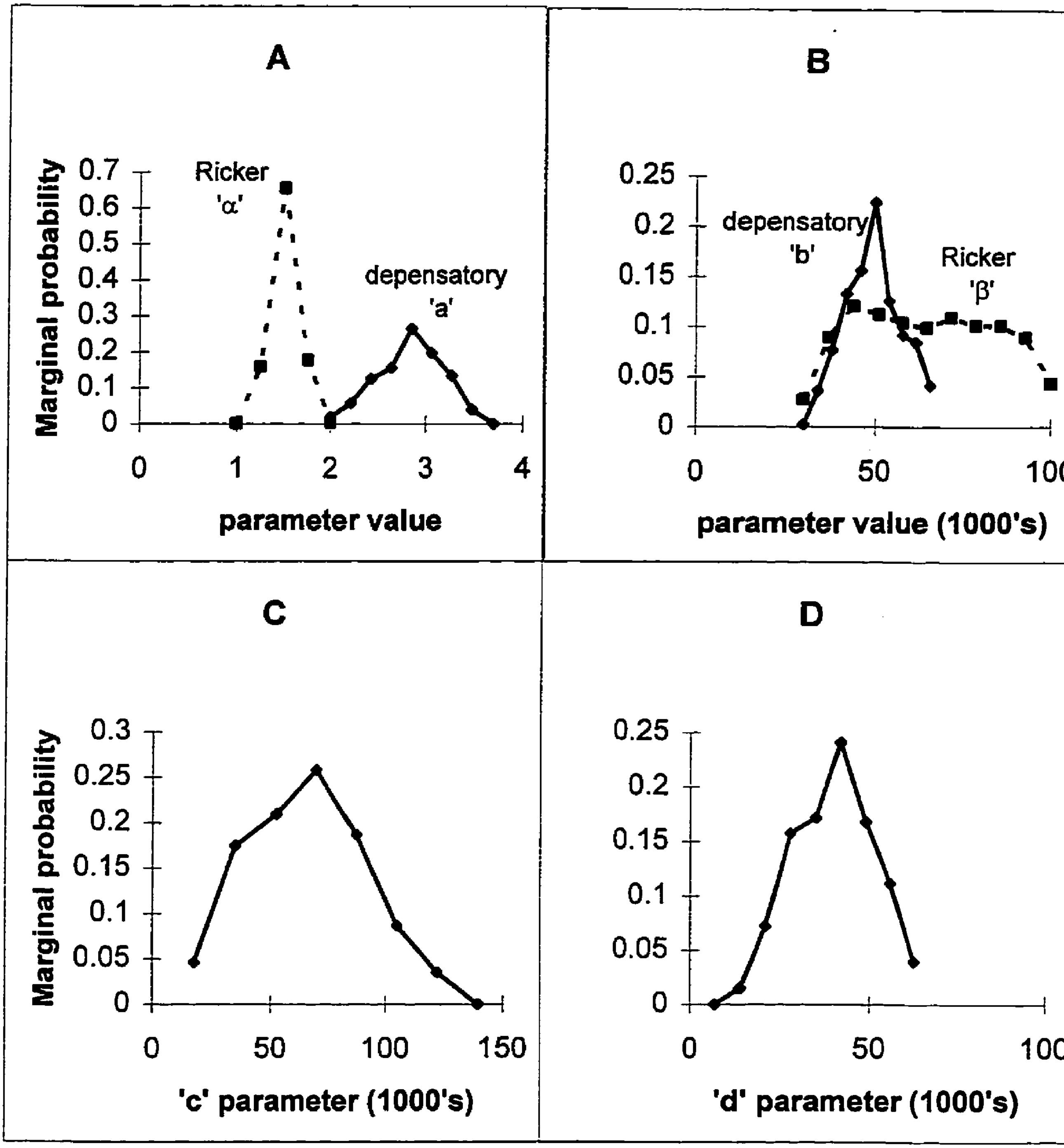

A
Marginal probability
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Ricker
'α'
depensatory
'a'
0
1
2
3
4
parameter value
B
0.25
0.2
0.15
0.1
0.05
0
depensatory
'b'
Ricker
'β'
0
50
100
parameter value (1000's)
C
Marginal probability
0.3
0.25
0.2
0.15
0.1
0.05
0
0
50
100
150
'c' parameter (1000's)
D
0.25
0.2
0.15
0.1
0.05
0
0
50
100
'd' parameter (1000's)

Figure 7. Expected loss in yield (in thousands of fish per year) for each uncertainty adjustment for the Raft River sockeye and a constant escapement policy. The *x-axis* represents the amount of adjustment (% change) in the escapement goal from the best-fit Ricker case. The dashed line is for the Ricker model and the solid line is for the depensatory model, both for the uncertain parameters case only. Solid circles are the optimal uncertainty adjustments for the Ricker and depensatory models, taking uncertainty into account. Open circles designate the expected loss if the optimal strategy *for the wrong model* was applied (see text for explanation).

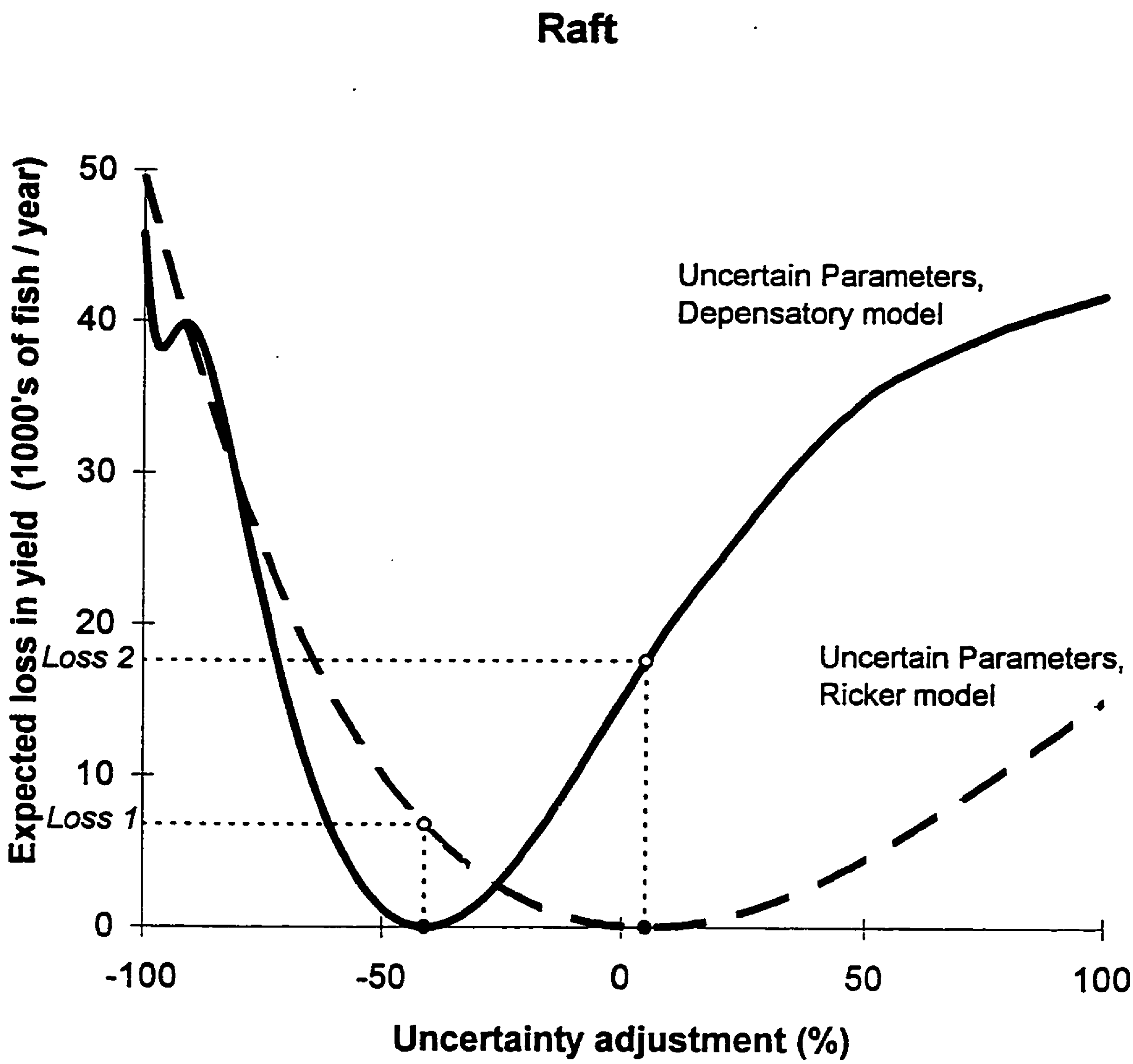
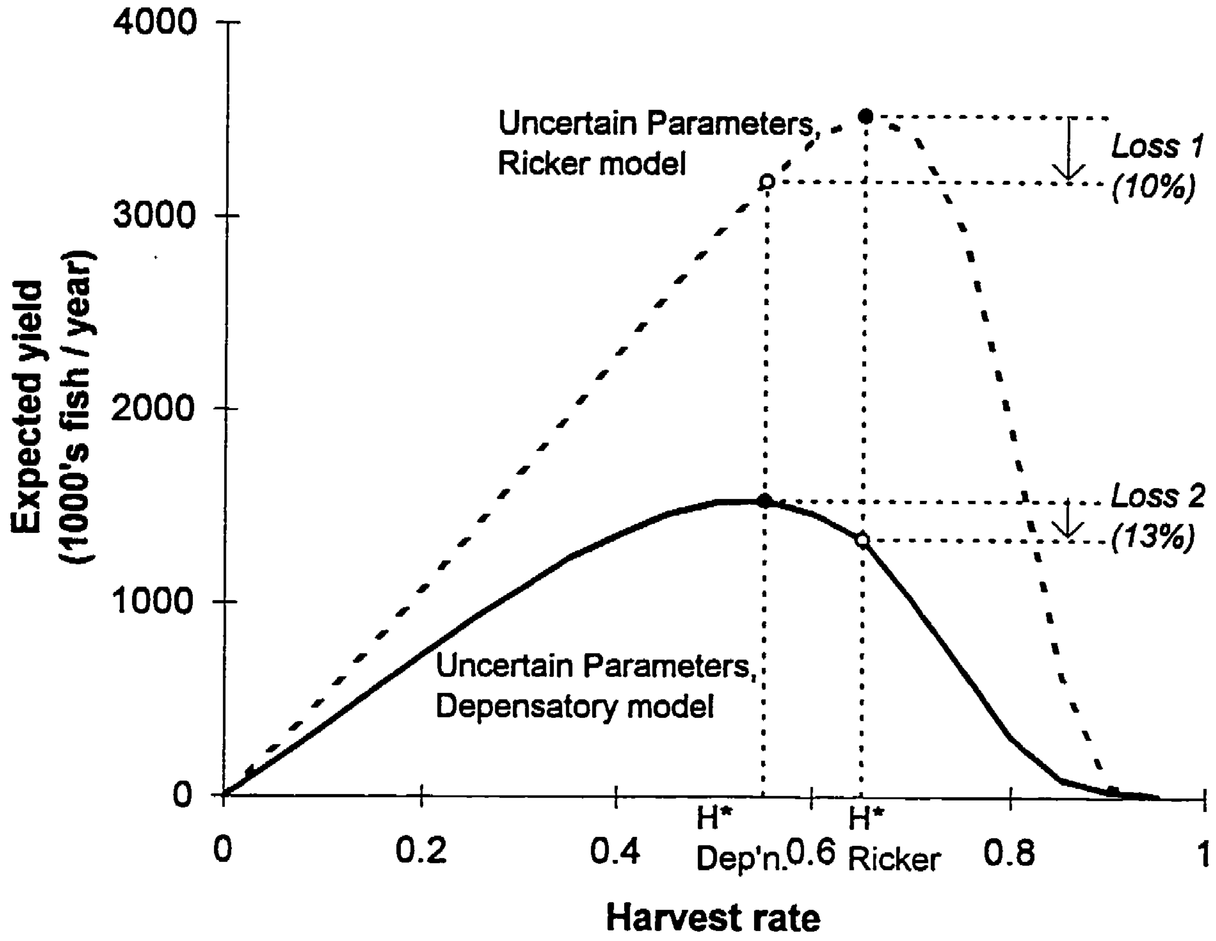

Raft
Expected loss in yield (1000's of fish / year)
50
40
30
20
Loss 2
10
Loss 1
0
-100
-50
0
50
100
Uncertainty adjustment (%)
Uncertain Parameters,
Depensatory model
Uncertain Parameters,
Ricker model

Figure 8. Expected yield (in thousands of fish per year) as a function of the harvest rate applied for the Adams River sockeye for a constant harvest rate policy. The dashed line is for the Ricker model and the solid line is for the depensatory model, both for the uncertain parameters case. The constant harvest rate that generated the highest expected yield is indicated by H* for each model. These results are for an initial abundance of 2,000 spawners.

Adams



4000
3000
2000
1000
0
Expected yield (1000's fish / year)
Uncertain Parameters, Ricker model
Loss 1 (10%)
Loss 2 (13%)
Uncertain Parameters, Depensatory model
0
0.2
0.4
H* Dep'n.
0.6
H* Ricker
0.8
1
Harvest rate

Figure 9. Sensitivity of the optimal harvest rate on the Adams River stock to the initial abundance of spawners for the uncertain parameters cases of the Ricker (dashed curve) and depensatory (solid curve) models. The horizontal line is the optimal harvest rate for the best-fit Ricker model at an escapement target of 1.7 million spawners.

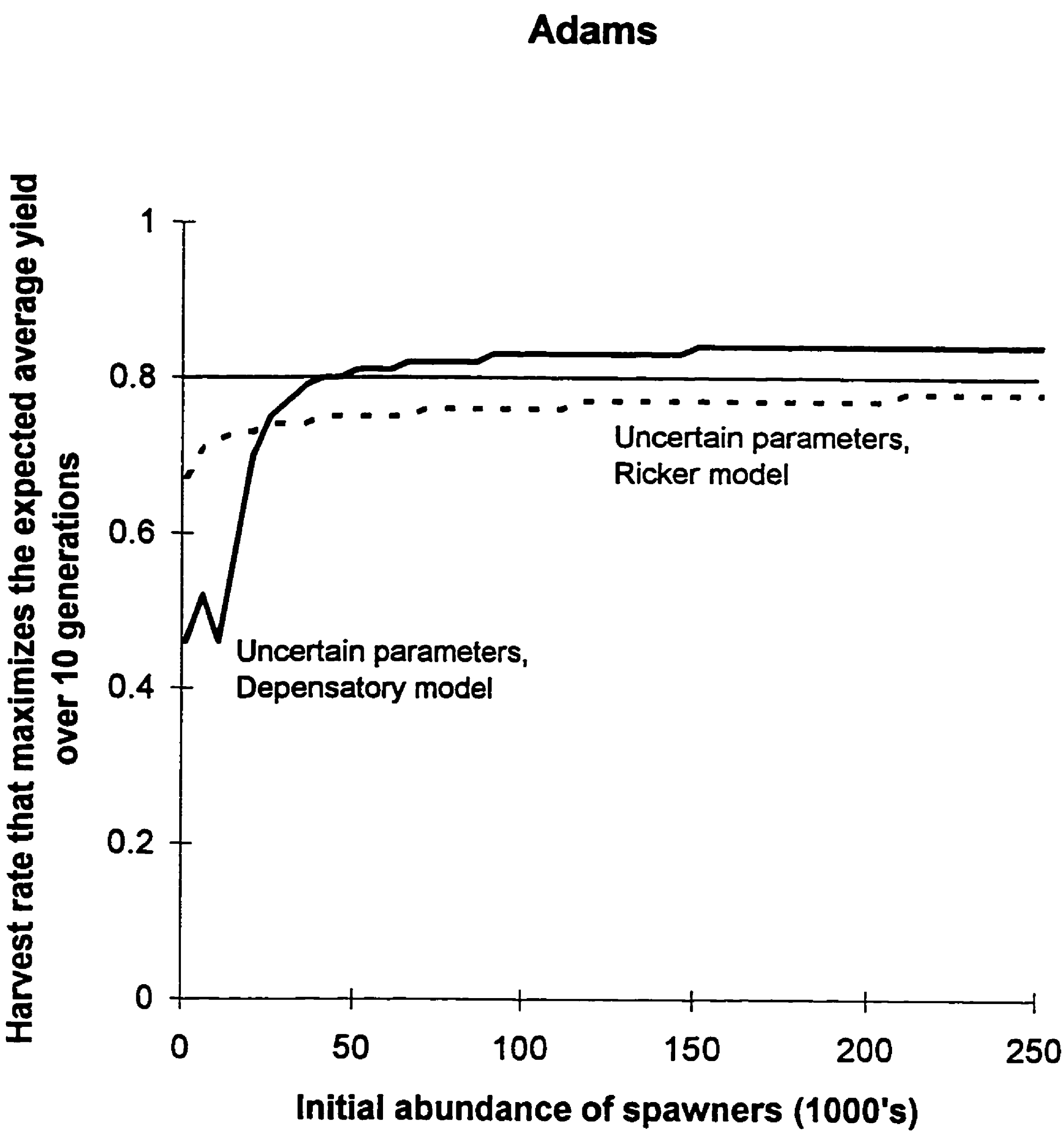
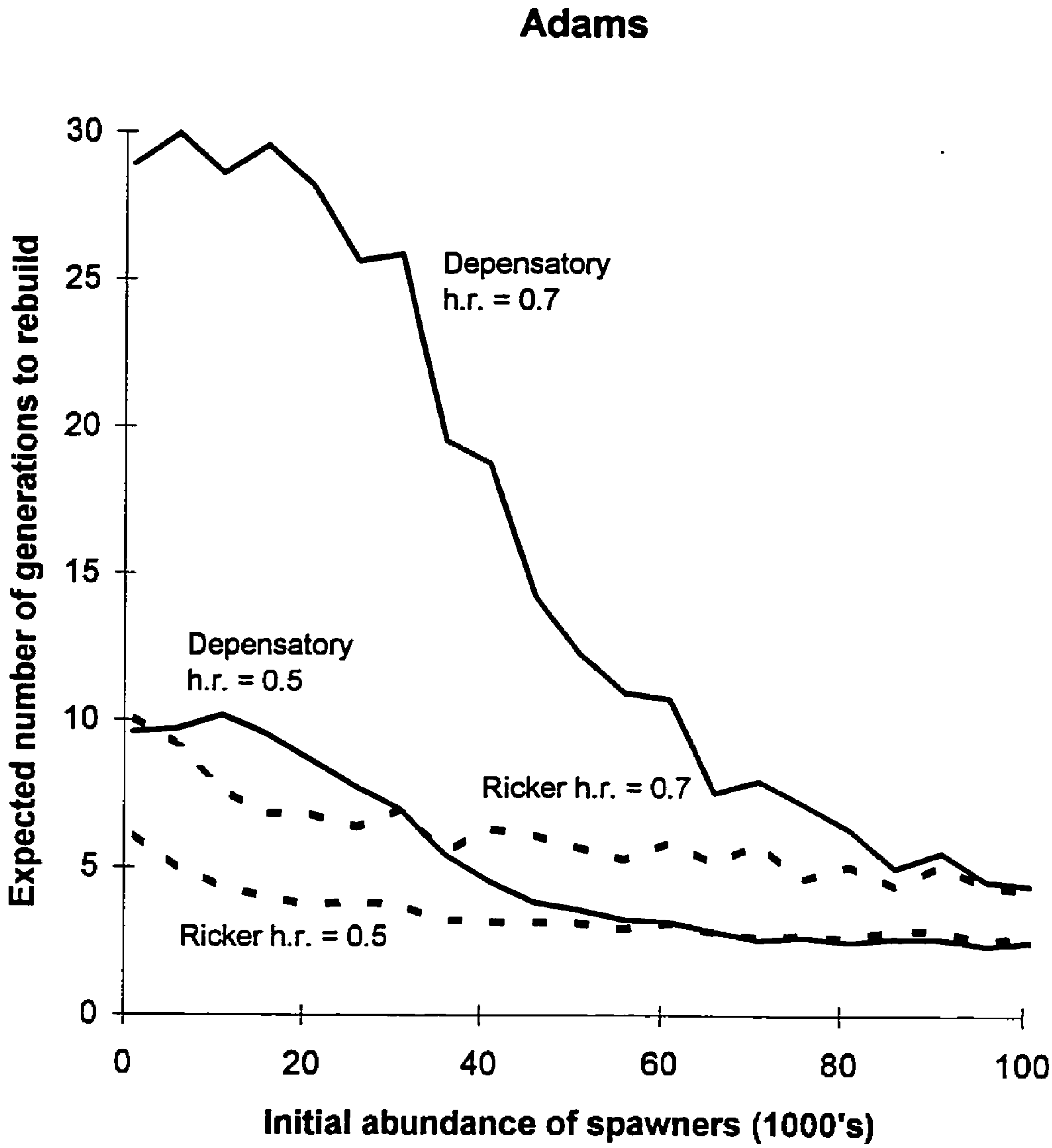

Adams
Harvest rate that maximizes the expected average yield over 10 generations
1
0.8
0.6
0.4
0.2
0
Uncertain parameters, Ricker model
Uncertain parameters, Depensatory model
0
50
100
150
200
250
Initial abundance of spawners (1000's)

Figure 10. The expected number of generations required to rebuild one cycle line of the Adams River sockeye as a function of the initial abundance of spawners in the cycle line. The cycle line was considered to be rebuilt when it reached a spawning escapement equivalent to 50% of the escapement target (of 1.7 million, Table 2) calculated for the best-fit Ricker model. The curves for several different harvest rates (h.r.) are shown for the Ricker (dashed line) and the depensatory models (solid line) for the uncertain parameters cases.

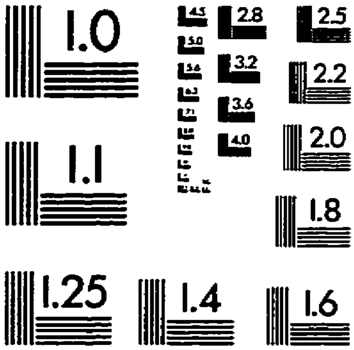

Adams
Expected number of generations to rebuild
30
25
20
15
10
5
0
Depensatory
h.r. = 0.7
Depensatory
h.r. = 0.5
Ricker h.r. = 0.7
Ricker h.r. = 0.5
0
20
40
60
80
100
Initial abundance of spawners (1000's)

Appendix A:

Best-fit parameters for the Ricker and depensatory stock-recruitment models

Stock	Ricker Model		MSE	Depensatory Model				MSE
	α	β (1000's)		*a*	*b* (1000's)	*c* (1000's)	*d* (1000's)	
Adams 1948-1990	1.97	4362.71	**0.85**	2.50	3535.48	251.87	144.42	**0.70**
Raft 1948-1990	1.50	58.84	**0.53**	3.02	44.53	73.93	42.82	**0.43**
Late Stuart 1949-1990	2.11	1353.32	**1.67**	2.70	1301.35	709.65	420.20	**1.47**
Gates 1952-1990	2.23	83.47	**0.91**	2.76	90.86	48.63	35.10	**0.81**
Chilko 1948-1990	2.14	1468.44	**0.48**	2.69	1418.92	757.31	776.20	**0.50**

TEST TARGET (QA-3)



150mm

6″

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