DEVELOPMENT OF METHODS TO EVALUATE MANAGEMENT OPTIONS FOR ACHIEVING THE RECOVERY OF ENDANGERED SALMON STOCKS

by

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Abstract

I developed a stochastic population model in a Bayesian decision analysis framework to evaluate management options for the depleted Cultus Lake, British Columbia, sockeye salmon stock. I sought state-dependent harvest rules that met three management objectives reflecting the probability of recovery within a specified period, the probability of abundance remaining above a conservation threshold, and the economic value of the harvest. This method produced quantitative information about tradeoffs between competing objectives. I found that recovery is feasible for the Cultus Lake sockeye stock under a number of harvest rules that allow harvesting in most years. Results were highly sensitive to pre-spawning mortality rate, indicating the need for a better understanding of that factor. Allowing the Cultus stock to recover may permit other late-run stocks to rebuild, thus partially offsetting the economic losses associated with reduced catches during recovery of the Cultus stock.

Keywords

recovery planning, Bayesian decision analysis, salmon management, fisheries simulation model, conservation

To Dr. G. H. McMorland

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Introduction

In recent years, numerous local populations of Pacific salmon (*Oncorhynchus* spp.) in the Pacific Northwest have become extinct, and abundances of many others have been severely reduced (Konkel and McIntyre 1987; Nehlsen et al. 1991; Slaney et al. 1996). Reasons for these depletions include, among others, overharvesting, poor oceanographic conditions for marine survival, and human activities that reduce the quality and quantity of freshwater habitat (Knudsen et al. 2000). However, in many cases, a combination of such factors occurred simultaneously, so that it is not possible to clearly attribute a cause to the observed reduction in abundance (Deriso et al. 2001; Peters and Marmorek 2001). This confounding of causal factors has thus created considerable uncertainty about appropriate management strategies for both attaining recovery of depleted salmon stocks and preventing severe depletion of other salmon stocks in the future.

Agencies responsible for management of salmon on the west coast of North America have responded to this situation by generally becoming more cautious about regulating both the harvest of salmon and activities that could affect freshwater habitat (Knudsen et al. 2000). Also, compared to several decades ago, more risk assessments are being conducted for harvesting plans, proposed habitat alterations, and other activities that could potentially threaten the survival of salmon stocks.

These responses have in part been legally mandated or promoted through the United States' Endangered Species Act (ESA) or Canada's Species at Risk Act (SARA). Both acts require evaluation of management options that will improve chances of recovery or prevent further depletion of stocks facing conservation challenges.

Most such evaluations of management options and population viability have been conducted using quantitative models (Botsford and Brittnacher 1998; Nickelson and Lawson 1998). Stochastic models of population dynamics have been used to classify species under ESA, SARA, or criteria set forth by the World Conservation Union (IUCN) (Taylor et al. 2002), as well as to set target harvest rates and spawner abundances for stocks that are not yet in “threatened” or “endangered” categories (Mace 1994; Bradford et al. 2000). To the extent that models used to evaluate recovery options take uncertainties in model components into account explicitly, they are considered as one component of broader risk assessments (U.S. EPA 1998).

Relatively few models developed to date for evaluating options for recovery of depleted salmon stocks have tied together the major dynamic processes that have been incorporated singly into other, separate models. For example, uncertainty about how effectively management regulations are implemented has rarely been included in salmon models, but such processes may critically affect the chance of success of proposed recovery options.

Research goal

My research goal was to fill some of these gaps by developing a more elaborate quantitative method for evaluating management options: a method capable of identifying options that increase the chance that a salmon stock will recover from a depleted state and providing managers with quantitative information on tradeoffs between competing management objectives, such as probability of recovery and revenue from harvest. I used the sockeye salmon (*O. nerka*) stock from Cultus Lake, British Columbia (B.C.), Canada, as a case example.

Cultus Lake sockeye

Cultus Lake is part of the Fraser River system, and the Cultus Lake sockeye salmon are managed as part of the late-run Fraser River sockeye group, which is harvested in a fishery that has normally generated catches worth millions of dollars annually. This stock is also of cultural and economic importance to First Nations, particularly the Soowahlie Band and other Sto:lo nations. Cultus Lake sockeye escapement to the spawning grounds has declined dramatically from historical levels, particularly in recent years (Schubert et al. 2002) (Figure 1). An excellent overview of Cultus Lake sockeye life history and management can be found in Schubert et al. (2002), and the Cultus Sockeye Recovery Team (2004) described the population's distribution, habitat, and threats to its persistence.

The Cultus Sockeye Recovery Team identified three main causes for the population's decline in abundance: "over-exploitation in mixed stock fisheries prior to 1995, poor marine survival in the early- to mid-1990s, and, since 1995, high pre-spawning mortality (PSM) caused by unusually early migrations into freshwater and an associated parasite infection" (Cultus Sockeye Recovery Team 2004). Other possible threats to the recovery of the Cultus stock, in addition to exploitation, early migration, and PSM, include other parasitic infections and diseases, natural variability in freshwater and ocean conditions, and human alterations to the freshwater conditions for spawners and smolts (Cultus Sockeye Recovery Team 2004). The area around Cultus Lake has been developed for recreational properties and the lake is heavily used. An exotic plant, Eurasian watermilfoil (*Myriophyllum spicatum*), has spread through the lake, encroaching on spawning grounds and providing habitat cover for juvenile northern pikeminnow

(*Ptychocheilus oregonensis*) (Schubert et al. 2002). Adult pikeminnow are known to be predators of sockeye fry and smolts in Cultus Lake (Ricker 1941; Steigenberger 1972; Mossop et al. 2004).

Concern about the unusually high PSM rate and the dramatic decline in Cultus spawner abundance prompted increased assessment by Fisheries and Oceans Canada (DFO) (Schubert et al. 2002), as well as a public petition for emergency assessment by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). COSEWIC designated the population as Endangered by emergency assessment in November 2002 and by full committee in May 2003 (COSEWIC 2003), prompting DFO to form a Recovery Team for this stock. The COSEWIC assessment was sent to the Federal Government for the Cultus Lake sockeye salmon to be considered for listing under SARA. However, in 2004 the Canadian Minister of the Environment chose not to list this stock under SARA, because listing the Cultus sockeye stock would have triggered a ban on "killing, harming, harassing, capturing or taking" Cultus sockeye, unless these activities were specifically authorized through a permit under SARA or as part of the recovery strategy or action plan for the Cultus sockeye stock (Canada Gazette 2005). Any resulting reduction in the harvest rate of Cultus Lake sockeye would have also decreased opportunities to harvest co-migrating late-run Fraser River sockeye in the mixed-stock fishery in marine and estuarine waters, potentially reducing the value of that fishery by millions of dollars annually. The resulting social and economic costs were deemed unacceptably high.

Regardless of the legal status of the Cultus Lake sockeye salmon stock under SARA, DFO committed to continue developing a recovery strategy and subsequent action plan for this stock. No matter what DFO subsequently does with that recovery strategy, the research reported here developed methods to help inform fisheries managers about the relative merits of management options in terms of the probability of recovery for this stock and the revenues from harvests on co-migrating salmon stocks. Furthermore, the procedures used here, as well as some qualitative findings, may be more widely applicable to recovery planning for other fish populations.

Population modeling

Most models of salmon population dynamics that have been used in analyses of conservation issues have been stochastic, PVA-type models (population viability analyses) that focused on estimating the chance that a population would either go extinct or reach some other undesirable level of abundance. A few of those models were developed to identify recovery strategies for achieving recovery goals for various Pacific salmon populations or to identify de-listing criteria (to define when to safely remove a stock from formal listing as "endangered"). Examples of such models are Botsford (1994), Botsford and Brittnacher (1998), McElhany et al. (2000), Peters and Marmorek (2001), Peters et al. (2001), Ford et al. (2001), and Ruckelshaus et al. (2002). It is clear from these and other cases that stock-specific, as opposed to general, models are needed to evaluate rebuilding options in the context of fully-specified, stock-specific recovery goals (Botsford 1994; Peters and Marmorek 2001; MacCall 2002). My research project aimed to meet this need for Cultus Lake sockeye salmon by developing a model to determine harvest strategies that have a high probability of meeting recovery goals in a timely manner.

The research reported here also extended previous salmon risk assessment models by incorporating into one analysis several factors that may have an important influence on the chance that any fish population, including the Cultus Lake sockeye population, will recover under a given set of natural and harvesting conditions. These factors are:

(1) Implementation uncertainty in the fishery;
(2) Changing, complex, and conflicting management objectives;
(3) Biological factors such as pre-spawning mortality; and
(4) Structural uncertainty in functional forms of model components, in particular, depensatory mortality in fresh water.

Each of these factors is important to include in analyses of Cultus Lake sockeye for several reasons. First, implementation uncertainty (i.e., deviation from the annual target escapement or target percent harvest rate) is important but is still not often included in models (Bocking and Peterman 1988; Rice and Richards 1996; Robb and Peterman 1998). Implementation uncertainty can occur in salmon fisheries for multiple reasons. First, the annual preseason forecast of recruit abundance, on which the target harvest rate is based, is imperfect, and in-season updates are often difficult. Second, the actual harvest rate in a fishery usually deviates from the target harvest rate. For example, large recruitment tends to lead to over-escapement because by the time in-season estimates indicate high salmon abundance, it is usually too late to harvest all the desired fish and the escapement goal is exceeded (Rosenberg and Brault 1993; Robb and Peterman 1998). The converse is true when recruitment is low; by the time a low recruitment is identified, even a complete closure of fisheries may not be enough to achieve the escapement target.

As well, although models often assume no discarding or unreported catch, this assumption is likely incorrect (Pitcher et al. 2002). If implementation uncertainty is not explicitly considered in a model, the conservation and economic objectives for a stock may not be met because the actual outcomes from a given management action will deviate from the mean predicted outcomes (Rice and Richards 1996). My model included a stochastic function in the harvesting sub-model to reflect such implementation uncertainty.

Second, fisheries management is difficult because objectives held by different user groups are often uncertain, changing, or conflicting (Smith 1993; Marmorek and Peters 2001; Walters and Martell 2004). An effective model must be able to produce appropriate indicators for a variety of management objectives and show tradeoffs between different objectives. Specifically, in the case of conservation problems such as those dealt with here, managers, user groups, and the public may like to see, for instance, how much of a gain in the chance of recovery of the Cultus Lake sockeye stock will be obtained for each reduction of 100,000 fish caught in the late-run sockeye salmon fishery. The model developed here permits such comparisons.

Third, many biological uncertainties are often overlooked in models. For instance, pre-spawning mortality rates for Cultus Lake sockeye have been unusually high in the last decade. However, future PSM rates are quite uncertain, and causes of variation are unknown (Gilhousen 1990; PSC 2003; Cooke et al. 2004). Thus, I examined the effect of this uncertainty through a sensitivity analysis.

The fourth factor accounted for here reflects the observation that structural uncertainty in functional forms of processes included in models can be very important, perhaps even more important than uncertainty in parameters (McAllister and Kirchner 2002). This type of uncertainty can potentially greatly alter the choice of an optimal management action (Punt and Hilborn 1997; Robb and Peterman 1998; Runge and Johnson 2002). Despite this viewpoint, relations among variables in most models are usually represented by a single function without any other functional form being investigated. In contrast, I considered here different shapes of a key model component that reflect various intensities of depensatory mortality in the spawner-to-smolt relation for the Cultus Lake sockeye.

Depensatory mortality (an increasing percent mortality rate as abundance decreases) can arise from several mechanisms, especially predation. Although past papers have discussed the possibility of, and the theory behind, depensation at low salmon abundance (Neave 1953; Peterman 1977), unequivocal empirical evidence to support this theory for salmon populations is rare (Peterman 1977, 1991; Peterman and Steer 1981; Myers et al. 1995; Liermann and Hilborn 1997; Myers 2001). Several authors conclude that although there is still considerable uncertainty about whether depensation occurs in specific salmon populations, or to what degree, they recommend allowing for the possibility of depensation in models (Peterman et al. 1985; Liermann and Hilborn 1997; Chen et al. 2002). Depensation should receive particular attention in the case of low-abundance stocks such as the Cultus Lake sockeye, because it can slow or prevent recovery or help push stocks to extinction (Peterman 1977; Routledge and Irvine 1999; Petersen and Levitan 2001).

When depensation is accounted for by salmon managers, it is often handled only indirectly through a quasi-extinction threshold, rather than through a depensatory function in the model of population dynamics (e.g., Schubert et al. 2002; Lindley and Mohr 2003). However, an arbitrary quasi-extinction threshold may lead to the choice of a harvest rule that is overly conservative biologically and thus decreases economic benefits, or overly aggressive in terms of harvest, thereby not providing the stock with adequate protection against depletion to levels where depensation may occur. In contrast, an appropriate harvest rule (i.e., one that guards against unacceptable and unnecessary decreases in economic value or benefits of biological conservation) can be estimated from a model such as mine that explicitly accounts for depensatory mortality.

At least two models have already been developed and applied to the Cultus Lake sockeye salmon stock as part of the evaluations by PSARC and the Recovery Team. However, neither model explicitly deals with depensation or implementation uncertainty (Schubert et al. 2002; Cultus Sockeye Recovery Team 2004). Instead, they account for the possibility of depensation through the just-described approach of using an arbitrary quasi-extinction threshold, rather than through structural uncertainty in the population dynamics. Those models were applied assuming that the condition to avoid is four consecutive years with less than 100 successful adult Cultus sockeye spawners. By merely accounting for uncertainty about depensation through this quasi-extinction threshold, the assumption is made that depensation will not come into play at abundances above 100 spawners. Such an exact threshold is unlikely. Furthermore, although these models examined the possibility of stock recovery, they have not sought optimal harvest rules that allow for both “recovery” (increased abundance to a desired level) and “long-term survival” (maintenance of abundance above some level of concern).

The model developed here incorporates aspects of the management and population biology of the Cultus Lake sockeye stock to examine tradeoffs between probability of recovery of the stock and gross commercial revenue from the harvest of late-run Fraser River sockeye. The results of this work should not be construed as making specific recommendations for the Cultus Lake sockeye stock, but rather as illustrating a useful tool for recovery planning in general. Before making final decisions on the Cultus Lake situation, managers must consider a broader range of factors, such as human effects on freshwater habitat, that are beyond the scope of this study. Also, although this study focuses on commercial revenue as a conventional illustrative example, there are non-commercial values that should be considered in a more thorough analysis. These include, among others, non-extractive values such as existence value and value to the ecosystem, and First Nations' food, social, and ceremonial values.

Methods

Overview

There were two research objectives: (1) determine the rank order of various harvesting options for the Cultus Lake sockeye population while taking into account uncertainties in the population's dynamics by using Bayesian decision analysis, and (2) identify harvesting options that are robust to changes in various assumptions, while also meeting the management objectives.

The main framework for this research, decision analysis, is a formal method for taking uncertainties into account when evaluating management options (Walters 1986; Punt and Hilborn 1997; Peterman and Peters 1998; Peterman and Anderson 1999). Decision analysis has been used for about 40 years in business and has been applied to various problems in fisheries management (Lord 1976; Walters 1986; Robb and Peterman 1998; Schnute et al. 2000; Macgregor et al. 2002). Both risk assessment and decision analysis have also been applied in the management of endangered species (Maguire 1986; Ludwig 1996; Taylor et al. 1996; Marmorek and Peters 2001; Peters and Marmorek 2001; Peters et al. 2001).

My decision analysis for the management of Cultus Lake sockeye had eight components, as detailed in the next sections: (1) management objectives, (2) alternative management actions, (3) models for estimating consequences or outcomes for each combination of management action and uncertain state of nature, (4) uncertain states of nature to consider explicitly, (5) probabilities on each uncertain state of nature, (6) rankings of management actions, and (7) sensitivity analyses (Peterman and Anderson 1999). The eighth component, a decision tree, illustrates connections among these components for a limited subset of example management options, uncertain states of nature, and outcomes (Figure 2).

Management objectives

In endangered species planning, the definitions and time frames of "recovery" and "long-term survival" are somewhat arbitrary and are typically left to the discretion of the recovery planners (Tear et al. 2005), as was the case for the Cultus Sockeye Recovery Team. Thus, for the purpose of this paper, I deemed the Cultus Lake sockeye stock to be "recovered" if the 4-year running average (arithmetic mean) of spawner abundance (*S*) exceeded a recovery goal (*X*) by some year (*T*). I defined "long-term survival" as the 4-year running average of spawner abundance (*S*) remaining above a quasi-extinction level (*Q*) for (*Y*) years after "recovery" had been achieved. Use of the 4-year arithmetic mean guarded against the stock being boosted above the recovery goal by one dominant cycle line while the other cycle lines had not recovered. Similarly, the stock was not considered quasi-extinct if three cycle lines had high abundances and only one dropped below the quasi-extinction threshold.

I characterized the Cultus Lake sockeye situation by three hypothetical management objectives. The general structure of these objectives was as follows:

(1) A *recovery objective*, which stated that the probability must be greater than Z_1 that the Cultus spawner abundance, S, will reach some recovered level, X, by some year, T, symbolized as Pr ($S > X$ by year T) > Z_1, or $Pr_{rec} > Z_1$;

(2) A *long-term survival objective*, which stated that once the recovery target, X, was reached, the probability must be less than Z_2 that the number of Cultus spawners will fall below some level Q over the next Y years, or Pr ($S < Q$ over next Y years) < Z_2, or $Pr_{qext} < Z_2$; and

(3) An *economic objective*, which sought to maximize the long-term gross commercial revenue from the harvest of late-run Fraser River sockeye under the condition that the first two management objectives were met.

Specific desired values of the components of the first two objectives (e.g., X, T, Z_1, Q, Y, and Z_2) have yet to be determined by any decision-making body. Therefore, my analyses examined a range of these parameter values to reflect a range of plausible management objectives (baseline values listed in Table 1). The specific indicators, or performance measures, that reflected how well each management objective was met under a given simulated management option were Pr_{rec} (the probability of recovery estimated via Monte Carlo simulation), Pr_{qext} (the probability of quasi-extinction, also estimated by simulation), and the expected long-term and annual gross commercial revenue from the catch.

For this research project, I defined the baseline recovery goal (*X*) as a 4-year average of 20,000 spawners and the recovery time frame (*T*) as 20 years, or 5 generations of Cultus Lake sockeye salmon. The recovery goal of 20,000 spawners is roughly the average spawner abundance for Cultus sockeye during a period of low exploitation rates (1925-1952) (Cultus Sockeye Recovery Team 2004). Elsewhere, long-term salmon management goals have sometimes been set according to such historical criteria (Knudsen 1999). I selected 20 years or 5 generations as the time frame for the recovery goal because the Cultus stock is severely depleted and may require several generations for substantial population growth to occur. Some studies have chosen even longer periods (e.g., Peters and Marmorek 2001).

I defined the baseline quasi-extinction level (*Q*) as 1000 spawners and the time frame (*Y*) for the long-term survival objective as 100 years or 25 generations. A 4-year average of 1000 spawners is the minimum genetically effective population size for Cultus sockeye, below which genetic integrity of the stock cannot be ensured (Lynch and Lande 1998, Allendorf and Ryman 2002, Waples 2002, Bradford and Wood 2004, Cultus Sockeye Recovery Team 2004).

Alternative management actions and implementation uncertainty

I sought harvest rules that met the management objectives for Cultus Lake sockeye. Each harvest rule was represented by four parameters: L, H_{min}, U, and H_{max} (Figure 3). L was the Cultus recruit abundance below which no harvest was taken and at which the minimum proportional harvest rate, H_{min}, was the management target, and *U* was the Cultus recruit abundance above which the maximum proportional harvest rate, H_{max}, was the target. Between *L* and *U*, targets were a linear function of abundance. This state-dependent, time-independent harvest rule generated the desired, or target, harvest rate, H_{tar}, from the simulated annual abundance of Cultus sockeye recruits. Alternative management actions (different harvest rules) were defined by different combinations of values for *L*, H_{min}, *U*, and H_{max}.

I did a preliminary analysis in which I explored a wide range of shapes of harvest rules, as defined by these ranges of parameters: $1000<L<50{,}000$, $0.1<H_{min}<0.95$, $1000<U<200{,}000$, and $0.1<H_{max}<0.95$. This preliminary analysis indicated that values of *L* and H_{min} at the higher ends of these ranges resulted in lower long-term gross commercial revenues than other parameter values, even though the biological conservation objectives may have been met. Those harvest rules were thus sub-optimal and were not considered further. Therefore, I more thoroughly explored parameter values in these ranges: $1000<L<10{,}000$, $0.1<H_{min}<0.2$, $1000<U<140{,}000$, and $0.1<H_{max}<0.95$ and only report those results here.

Ideally, implementation uncertainty would be represented as a relation between annual recruitment and the resulting actual escapement (e.g., Robb and Peterman 1998) with stochastic variation around it. However, the available data for the late-run Fraser River sockeye stocks showed no such relation. Instead, to generate random implementation uncertainty on the target harvest rate, I used a *beta* distribution (Morgan and Henrion 1990) to represent the deviation of the actual harvest rate, H_{act}, from the target proportional harvest rate, H_{tar}, which was calculated each year from the harvest rule. This distribution constrained the actual proportional harvest rate to between 0 and 1:

(1) $H_{act} = beta(\beta_h , \gamma_h)$

where values of β_h and γ_h were the *beta* distribution's shape parameters, with $\beta_h = H_{tar}$ for a given year and $\gamma_h = 0.1$. In years with Cultus recruit abundance less than *L*, H_{tar} and H_{act} were both set to zero to simulate a closure of the fishery.

Model to calculate outcomes, taking into account uncertainties

I first provide a general overview of the model; details follow in the next sections. I simulated annual changes in abundance of the Cultus Lake sockeye stock using a stochastic population model that incorporated uncertainties in each life stage and implementation uncertainty in harvest rate (Figure 4). I also modeled the population dynamics of other major late-run Fraser River sockeye stocks that migrate through fishing areas along with Cultus sockeye. The model calculated the abundance of, and harvest taken from, each stock at the end of every year. At the end of each year during the recovery period (1 to *T*, or 20 years, for the baseline recovery objective), the model determined whether the Cultus stock had recovered (whether the 4-year running average of spawner abundance reached *X*, or 20,000). If the Cultus stock successfully recovered within *T* years, the model continued to simulate and check the stock's abundance at the end of each year (*T* to *T* + *Y* years, as indicated in the long-term survival objective) to determine whether the 4-year running average of spawner abundance had dropped below the quasi-extinction threshold *Q*, or 1000. At the end of a simulation of 120 (*T* + *Y*) years, the model calculated the long-term gross commercial revenue from the price and harvest of all late-run stocks over *T* + *Y* years, as well as the mean annual gross revenue.

The above life history model was embedded in a stochastic simulation framework to calculate values for the three main indicators of the objectives (Pr_{rec}, Pr_{qext}, and expected gross commercial revenue from the catch) using the methods described below. Various management options (i.e., sets of parameter values that determined the shapes and axis scales of state-dependent harvest rules, as in Figure 3) were evaluated in the context of stochastic processes that represented several uncertain states of nature. Uncertainties included here were (1) parameters of the spawner-to-smolt relation for the Cultus stock, which reflected uncertainty about depensatory mortality, (2) a stochastic process for the smolt-to-adult relation for the Cultus stock, (3) a stochastic process in the stock-recruit relation for each non-Cultus sockeye stock, and (4) implementation uncertainty affecting the outcome of applying the harvest rule. These uncertainties are described below along with the basic model components.

Data sources

Historical abundances for all late-run Fraser River sockeye stocks came from a database maintained by the Pacific Salmon Commission (Michael Lapointe, personal communication, Pacific Salmon Commission, 1155 Robson St., Vancouver, B.C.). Stock-recruit data for the main six non-Cultus stocks were from brood years 1948-1996 (Weaver, Harrison Rapids, Adams, Portage, Shuswap, and Birkenhead). Cultus spawner-to-smolt data and smolt-to-adult data included all brood years for which the abundances of both 1- and 2-year-old smolts were estimated, for years when freshwater productivity was unlikely to be affected by predator-control projects, and for years in which spawner estimates were unlikely to be confounded by excessive pre-spawning mortality. These criteria left 1951, 1954-60, 1965-71, 1974-54, and 1988-89. I excluded the 1920s and

1930s because large predator-control projects and hatchery experimentation took place at Cultus Lake during those years. I did not use data from 1995 to the present because of extremely high pre-spawning mortality rates during those years (Schubert et al. 2002, PSC 2003). Also, the spawner abundances for 1988 and 1989 were adjusted upward because the counting fence was in operation for an unusually brief time in those years (Mike Bradford, personal communication, DFO, Burnaby, B.C.). Although predator-control projects could have affected smolt production for the 1967 and 1989-1991 brood years, M. Bradford (personal communication) concludes that these projects were small enough that they likely had little-to-no effect on the smolt-per-spawner ratio for those years. Estimates of pre-spawning mortality rates for the Cultus Lake sockeye stock were from Schubert et al. (2002).

Cultus stock

The model of the Cultus Lake sockeye stock was divided into several life stages. First, it was initialized with spawner abundances from 1998-2001 (Table 2). A modified Beverton-Holt model (Myers et al. 1995) incorporated depensation into the Cultus sockeye spawner-to-smolt relation:

(2) $Sm_t = ((a*S_t^d)/(1 + (S_t^d/K)))*\exp(v_t)$

where Sm_t is the abundance of smolts generated from the spawners, S_t, in a given brood year t, and a, d, and K are parameters; v_t is assumed to be a normally distributed error term with a mean of 0 and a variance of σ^2_v. Equation 2 represents a standard Beverton-Holt curve when $d = 1$; depensation occurs when $d > 1$, and hypercompensation occurs when $d < 1$ (Myers et al. 1995). The three parameters of this model were considered to be uncertain states of nature in the analysis, as estimated by a Bayesian joint posterior probability distribution (Gelman et al. 2004) based on historical spawner-to-smolt data for the Cultus stock. These data and the best-fit relation are shown in Figure 5. Appendix 1 gives details of the Bayesian calculations that produced marginal posterior probability distributions for the parameters a, d, and K (Figure 6).

The Cultus smolt-to-adult-recruits relation was

(3) $R_t = c\, Sm_t^b \exp(g_t)$

where R_t is the abundance of Cultus adult recruits from brood year t, Sm_t is Cultus smolts from brood year t, c and b are parameters, and the error term, g_t, is $\sim N(0, \sigma^2_g)$. Parameters c, b, and σ^2_g (Table 3) were estimated via least squares regression.

The number of recruits to the Cultus spawning stock in a given calendar year (R_{yr}) was composed of 4-year-old recruits from brood year t and 5-year-old recruits from brood year t-1:

(4) $R_{yr} = (p_4 * R_t) + (p_5 * R_{t-1})$

where p_4 and p_5 are the probabilities that a Cultus fish will return at age 4 or age 5, as calculated from the average annual proportions in the historical data (Table 3). Here, $p_5 = 1 - p_4$. Escapement past the fishery, E, was the abundance of recruits minus fish harvested:

(5) $E_{t+4} = R_{yr} - (R_{yr} * H_{act})$

where the actual harvest rate, H_{act}, reflected the beta-distributed random implementation uncertainty described in equation 1. Spawner abundance was escapement minus fish that die from pre-spawning mortality:

(6) $S_{t+4} = E_{t+4} - (E_{t+4} * PSM)$

where *PSM* is a fixed proportional pre-spawning mortality rate that was assumed constant due to lack of a predictive model. The baseline PSM rate of 0.1 (Table 1) is similar to historical PSM rates in decades prior to the elevated rates of the mid-1990s.

Other late-run stocks

Spawner abundance for non-Cultus stocks was initialized with historical data from 1998-2001 (Table 2), except for the Harrison Rapids stock, which was initialized with data from 1998-2000 because it recruits mainly as 3- and 4-year-olds, as opposed to the other late-run stocks, which recruit mainly at ages 4 and 5. The Ricker stock-recruit relation for each non-Cultus late-run stock was

(7) $$RL_{t,s} = \alpha_s * SL_{t,s} * \exp((-\beta_s * SL_{t,s}) + w_t)$$

where $RL_{t,s}$ is the abundance of adult recruits for a given non-Cultus stock, s, from a given brood year t, $SL_{t,s}$ is the same except for spawners rather than adult recruits, α_s and β_s are parameters for a given stock s (or cycle-line specific for cyclic stocks: Shuswap, Adams, and Portage), and w_t is an autocorrelated error term,

(8) $$w_{t,s} = \rho_s * w_{t-1,s} + u_s$$

where the parameter ρ_s is the autocorrelation coefficient for stock s, $w_{t-1,s}$ is the error from the previous year (or previous year of that cycle line for cyclic stocks) for stock s, and u_s is $\sim N(0, \sigma^2_{u,s})$. Parameters were estimated via least squares regression based on historical data for each non-Cultus stock (Table 4).

As with the Cultus stock, recruits in a given year for each non-Cultus stock were composed of a given proportion of age-4 and age-5 returns (eq. 4), except for the Harrison Rapids stock, which recruited mainly at age 3 and age 4 (Table 4). Escapement past the fishery and escapement to the spawning grounds for each stock were calculated as for the Cultus stock (eq. 5 and 6). The actual harvest and pre-spawning mortality rates for the Cultus stock in a given year were also applied to all other late-run stocks in that year.

Performance measures

The gross commercial revenue from harvesting late-run Fraser River sockeye in each year was the sum of fish harvested from each stock multiplied by a fixed price per fish (estimated in Appendix 2). During a simulation of 120 ($T + Y$) years, the model recorded whether the Cultus stock recovered and, if so, the year of recovery (to determine whether the stock met the recovery objective, objective #1), as well as whether the Cultus stock went quasi-extinct and, if so, the year of quasi-extinction (to determine whether the stock met the long-term survival objective, objective #2). The model also recorded the long-term gross commercial revenue from the harvest of all late-run Fraser River sockeye stocks over the 120 years.

Monte Carlo trials for decision analysis

The Monte Carlo procedure for this decision analysis (Figure 7) began with calculating a posterior probability for every combination of parameters a, d, and K of the Cultus spawner-to-smolt relation (one combination = a “scenario”). As illustrated in Figure 6 and described in Appendix 1, I used 16 different values for a, 14 for d, and 15 for K, for a total of 3360 different combinations of these parameters, or different “scenarios”.

I simulated the life history and harvest of all late-run stocks for 120 years using Monte Carlo (MC) trials for each scenario of Cultus spawner-to-smolt parameters in order to account for uncertainty in other parameters and relations in the model, as described above. Only 40 MC trials were necessary for each scenario because the coefficient of variation in the probability of recovery over the test runs was less than 0.05 at ≥ 40 MC trials, and the probability of recovery was the output measure with the greatest amount of variation. Once the model completed the MC trials for a given scenario of Cultus spawner-to-smolt parameters, it calculated the proportion of trials in which the Cultus stock recovered (Pr_{rec}), the proportion in which it recovered and then went quasi-extinct (Pr_{qext}), and the mean gross commercial revenue from the harvest of all late-run stocks across trials. For a single harvest rule (defined by the 4 parameters in Figure 3), the 120-year simulation ran 40 times for each of 3360 scenarios, or a total of 134,400 times (Figure 7). The model calculated the expected (weighted average) probability of those three performance measures by weighting results for each scenario by the Bayesian posterior probability for that scenario (i.e., combination of *a*, *d*, and *K*). The model then determined whether the recovery and long-term survival objectives were met under that harvest rule by comparing the expected Pr_{rec} and Pr_{qext} to Z_1 and Z_2, respectively.

Ranking of management actions

I repeated these procedures for each new combination of the harvest rule parameters in Figure 3 and re-calculated the expected performance measures (Figure 7). Once simulations were completed for the different harvest rules, the subset of 4-parameter harvest rules that met the first two objectives were ranked according to the third objective (gross commercial revenue).

Sensitivity analyses

To identify key uncertainties that have the greatest effect on the choice of management actions, I performed sensitivity analyses on pre-spawning mortality rate and the parameters of the management objectives (Table 1). This model easily allows for changes to other assumptions and factors that I did not explore because they were beyond the scope of this project. Those factors include the impacts of future changes in adult body size on both fecundity and revenue from harvest, the effect of using different values of the parameters of the beta distribution used to calculate implementation uncertainty, and the inclusion of a more comprehensive economic indicator resulting from a full economic analysis of the costs and benefits associated with the harvest of late-run Fraser River sockeye.

Results

The analysis produced many cases of individual Monte Carlo trials for which, within the first 20 years, the Cultus stock recovered, did not recover, or recovered but then went quasi-extinct (Figure 8). Results of all simulations across different harvest rules can be efficiently described in terms of Pr_{rec}, or the estimated probability of recovery for Cultus sockeye, which was compared to Z_1, the desired probability of recovery (Figure 9). Each harvest rule has four parameters, so to represent different harvest rules in this figure, I fixed H_{min} at either 0.1 or 0.2 and L at either 1000 or 10,000 and varied U and H_{max} for each of these four combinations of L and H_{min}. I used these four combinations of L and H_{min} because, as mentioned previously, preliminary simulations indicated that higher values of L and H_{min} resulted in lower long-term economic values. Therefore, my results show only a subset of the harvest rules that meet the conservation objectives.

Under baseline management objectives (Table 1) and for each combination of L and H_{min}, all harvest rules represented in Figure 9 by the combination of U and H_{max} parameters in the area to the right of the Z_1 = 0.9 isopleth, for example, allowed the Cultus sockeye stock to meet that recovery objective, i.e., produced a probability (Pr_{rec}) greater than 0.9 that the abundance of Cultus spawners will reach 20,000 by year 20. Boundaries of acceptable harvest rules under recovery objectives with different values of Z_1 can be used to determine whether a given combination of U and H_{max} will meet a given value of Z_1 (Figure 9). For example, in Figure 9C, if L = 1000, H_{min} = 0.2, U = 80,000 and H_{max} = 0.6, this harvest rule will meet a recovery objective in which Z_1 = 0.9. However, if U is reduced to 60,000, the harvest rule no longer falls within the range that satisfies Z_1 = 0.9, although it would satisfy Z_1 = 0.8. Also, this figure shows that changes to the values of H_{min} and L among panels A to D cause the boundaries of combinations of U and H_{max} that meet a given Z_1 to shift, but do not change the general pattern of these boundaries. The 52 harvest rules that met objective 1 with Z_1 = 0.9 show a range of shapes (Figure 10).

Under baseline management objectives and simulation parameters, management objective 2, or the probability (Pr_{qext}) of the Cultus stock recovering and then subsequently going below the quasi-extinction abundance of 1000 spawners, proved to be inconsequential. No harvest rule of those examined here (with a $Pr_{rec} > 0.6$) produced a probability (Pr_{qext}) that exceeded the Z_2 value of 0.05 (Tables 5-8).

Because every harvest rule that met a recovery objective (defined by its *X*, *T*, and Z_1) also met the long-term survival objective (defined by *Q*, *Y*, and Z_2), I ranked all harvest rules meeting a given recovery objective according to the expected gross commercial revenue from the harvest of late-run Fraser River sockeye (Tables 5-8 for Z_1 = 0.6, 0.7, 0.8, and 0.9, respectively). Rankings are shown, as well as both the expected long-term and mean annual gross commercial revenue from the harvest for each harvest rule. For the baseline case, when $Z_1 = 0.9$, harvest rule #43 met that recovery goal as well as provided the highest long-term gross revenue from the harvest (Table 5). That rule's shape parameters were $L = 10{,}000$, $H_{min} = 0.2$, $U = 65{,}000$, $H_{max} = 0.63$ (Figure 10). The expected gross revenue from this harvest rule was $5.241 billion over 120 years or a mean of $43.68 million annually.

Although a single expected (weighted average) gross commercial revenue was calculated for each harvest rule, there was a range of possible economic outcomes with varying probabilities of occurrence, such as in Figure 11, which was based on the 3360 scenarios of parameters for the Cultus spawner-to-smolt relation. To calculate the expected gross revenue, each individual outcome was weighted according to the posterior probability for the scenario that produced it.

For harvest rules that allowed the Cultus stock to recover under baseline conditions and management objectives ($Z_1 = 0.9$), the expected year of recovery was consistently around year 14 or 15 (Table 5), but there was a probability distribution of year of recovery under each harvest rule (e.g., Figure 12). The expected percent of years (of a total of 120) with no harvest ranged from 0.2% to 3.6% (due to fishery closures when Cultus recruit abundance was below *L*), while the expected percent of years with small harvest (target proportional harvest rate <0.2) ranged from 0.2% to 13.2% (Table 5).

Sensitivity analyses

Desired probability of recovery (Z_1)

The expected gross commercial revenue from harvesting late-run Fraser River sockeye salmon with the highest-ranked harvest rule decreased nonlinearly with increasing desired probability of recovery (Z_1) for the Cultus stock (e.g., Figure 13). If Z_1 was decreased from 0.9 to 0.8, the expected gross revenue of the highest-ranked harvest rule increased by $2.7 million per year (6%), whereas changing Z_1 from 0.7 to 0.6 increased gross revenue by only $1.7 million per year (3%).

For each value of Z_1 (0.6, 0.7, 0.8, and 0.9), the harvest rule with the highest gross revenue had a relatively low *U* (ranging from 20,000 up to 65,000), which was the abundance at which the maximum percent harvest rate would occur (Figure 3). This was true even though the Cultus stock could still meet the recovery and survival objectives with *U* values as high as 120,000 or 140,000 if H_{max} was correspondingly changed (Figure 10, Tables 5-8). Changes in the estimated probability of recovery (Pr_{rec}) for the Cultus stock also resulted in small changes in the expected year of recovery for that stock. As Pr_{rec} increased, the earliest expected year of recovery decreased (Figure 14).

Alternative management objectives

An additional objective of concern to many fisheries managers is to minimize the number of years with little or no commercial harvest while still meeting the recovery and long-term survival objectives for Cultus sockeye. To achieve this, in the harvest rule of Figure 3, a manager would want to minimize *L*, the number of Cultus recruits below which no harvest is taken, given the other constraints. Many harvest rules with low *L* did not meet the recovery and survival objectives; however, all harvest rules in Tables 5-8 did meet them and had either *L* = 1000 or *L* = 10,000. In most simulations with harvest rules that allowed Cultus sockeye to recover to a spawner abundance of 20,000 by year 20, the trajectory of population growth was such that Cultus sockeye were able to produce 1000 recruits in the first few years. Thus, when *L* = 1000, the expected number of years with no harvest was typically less than 1. However, because the first years of the model were initialized with the low spawner abundances from 1998-2001 (Table 2), and given the population's rate of recovery, the Cultus stock was not often able to produce 10,000 recruits until year 5 or 6, in the second 4-year period. Thus, when *L* was 10,000, the expected number of years with no harvest was typically around 4 or 5.

A harvest rule that was robust to this alternative management concern about years with little or no fishing, while still meeting the other baseline management objectives, was the highest-ranked harvest rule on Table 5 that had *L* = 1000. Harvest rule #22 on Table 5 met these conditions. This harvest rule was ranked fourth according to the economic objective and had an expected mean gross revenue of only $300,000 per year less than rule #43, the highest-ranked harvest rule (a decrease of less than 1%). Rule #22 had the minimum expected number of years with no harvest and so was more robust to the consideration of this alternative management objective.

Tradeoffs between gross commercial revenue from the catch and the frequency of little or no fishing can also be visualized (Figure 15). When the 52 harvest rules that met the conservation objectives for the baseline case (in which Z_1 = 0.9) are ranked by gross revenue from the catch, there is relatively little difference in gross revenue among the top 40 rules but considerable difference in the proportion of years with little or no fishing (Figure 15A). If managers wished to have no closures, the harvest rule that ranked 4th economically (rule #22, Table 5) would be best (no closures). However, if 3% of years with little or no fishing were acceptable, any of the rules ranked 1-3 (rules #43, 44, and 42) would be appropriate, but would produce a less than 1% increase in expected gross revenue when compared with rule #22. Similar logic could be used to make tradeoffs if rules were first ranked based on the proportion of years with little or no catch (Figure 15B).

Another possible management objective could be to allow the Cultus stock to recover as soon as is reasonably possible. This would require managers to make tradeoffs between the expected year of recovery and expected gross commercial revenue. For example, changing the desired probability of recovery (Z_1) from 0.8 to 0.9 led to a small decrease in the earliest possible expected year of recovery for the Cultus stock from about 15.2 to 14.6 (Figure 14). However, this change also led to a decrease in expected mean annual gross revenue from about $47 million to $44 million.

Pre-spawning mortality

In a sensitivity analysis on PSM, the Cultus stock did not meet the baseline recovery goal (recovering to a spawner abundance of 20,000 by year 20) if the constant PSM rate was 0.5 or above, even if no harvest was taken. To test the importance of obtaining a good estimate of PSM, I used the harvest rule that gave the highest gross revenue while satisfying Z_1 = 0.9 when PSM was set at the baseline value of 0.1 (rule

#43, Table 5), but I then performed the analysis with PSM set to 0.2 and 0.3. This represented situations in which PSM is underestimated and, therefore, a sub-optimal harvest rule is used. When the PSM rate was set to 0.2, the Cultus stock had a 0.7 probability of recovery (Pr_{rec}), and when PSM rate was set to 0.3, the probability of recovery dropped to 0.42 (Table 9). Gross revenue also decreased when the actual PSM was higher than estimated. Expected mean annual gross revenue decreased by about $1.2 million when PSM was 0.2 (2.7% less than the baseline expected value), and dropped another $1.5 million when PSM was 0.3 (6.1% less than the baseline expected value).

Price per fish

The estimated price per fish (Appendix 2) was based on body size data from a troll test fishery. The size-selectivity of the gear in that test fishery may differ from that of the gear used in the commercial fishery, which would lead to a somewhat inaccurate estimate of the commercial price per fish. More importantly, future prices for fish cannot be known. Changes in price per fish would not lead to changes in the rank order of harvest rules in Tables 5-8; they would only lead to a change in the magnitude of gross commercial revenue for each harvest rule. For example, a 10% increase from $6.96 to $7.65 in mean processed price per kg round would lead to a corresponding 10% increase in gross revenue for each harvest rule and would cause the curve in Figure 13 to shift upward by 10%. Similarly, if a 2- or 3-decade decrease in body weight per fish were to occur again as observed in the past, a 10% decrease in mean weight per fish from 3.14 kg to 2.83 kg would lead to a corresponding 10% decrease in gross revenue for each harvest rule and would cause the curve in Figure 13 to shift downward by 10%.

Biological feasibility of recovery

Part of the mandate of recovery teams under SARA is to determine whether the recovery of a stock is biologically feasible. I calculated the mean spawner-per-spawner ratio over the first 20 years of the model for the 40 MC trials within a given scenario, and the weighted average of this value across scenarios for a given harvest rule. The first 20 years were when the Cultus stock was increasing the most rapidly and thus give the best estimate of the stock's productive potential. I calculated this ratio for the most biologically conservative harvest rule (no harvest over 120 years) and the least conservative harvest rule presented here, the highest ranked harvest rule when Z_1 = 0.6 (rule #32, Table 8). With no harvest, the average spawner-per-spawner ratio was 7.5, under the least conservative harvest rule the average spawner-per-spawner ratio was 5.7, and other harvest rules presented here presumably fall within this range. These levels of productivity are realistic and indicate that recovery of the Cultus stock, as defined here, is indeed feasible under certain conditions.

Discussion

These analyses lead to two types of conclusions: specific quantitative ones and more general conclusions about the utility of this type of modelling. In the first category, results indicate that, under many of the parameter conditions explored, the two conservation objectives (short-term recovery and long-term survival) can be met by certain harvest rules that still allow fishing in most years (Figure 9, Tables 5-8). Among these harvest rules that met the conservation objectives, there were several that gave similar gross commercial revenues but that differed in the number of years with little or no fishing.

Although the model indicated that recovery of the Cultus stock is biologically feasible, recovery of the Cultus stock has not been seen in recent years. One likely reason for the discrepancy between the modeling results and the actual state of the Cultus stock is that in the model the target harvest rate in each year was based solely on the abundance of Cultus recruits, and the harvest rules were chosen with the purpose of allowing the Cultus stock to recover. In reality, the target harvest rate has historically generally been set by the Fisheries and Oceans Canada with the entire late-run aggregate in mind, particularly the much more abundant stocks, and with much less importance placed on smaller stocks such as the Cultus stock. Also, factors not included in my model, such as unusually low freshwater or marine survival rates, or elevated pre-spawning mortality rates such as those seen in the mid-1990s, can hold the stock at lower abundances in the field than in the model.

The ability of any harvest rule to meet conservation objectives was critically dependent upon the assumed pre-spawning mortality rate (PSM), for which we do not understand the causes of variation. This result emphasizes the need to better understand the elevated PSM rates for late-run Fraser River sockeye in the late 1990s and early 2000s and to improve predictions of PSM. An example is the research being conducted by Cooke et al. (2004). Although at this time little is known about the exact causes and interactions among contributing factors, Cooke et al. are exploring possible causes for early migration to freshwater and its associated elevated PSM. Their hypotheses are related to energetics, osmoregulation, oceanic conditions, in-river conditions, and parasites, among others. Since in my model the Cultus stock did not recover at PSM rates of 0.5 or higher, enhancement may become increasingly important for survival of the

Cultus stock if PSM rates rise above 0.5 again. However, I simulated PSM as a constant. Episodic patterns of PSM rates may permit the Cultus stock to recover if PSM only rises above 0.5 for a few years, although harvest rules may need to be more conservative than when PSM is a constant at 0.1. Because underestimating PSM can severely reduce the probability of recovery and the economic value of harvest, managers may wish to build a conservative safety margin into their choice of harvest rules until scientists are better able to predict PSM rates. These arguments concerning PSM are equally applicable to other factors that are poorly understood and difficult to forecast, such as trends in freshwater productivity, which in these analyses was governed by the spawner-to-smolt relation's joint posterior probability distribution (independent of time), and the marine survival rate of Cultus Lake sockeye smolts, which was reflected as stochastic variation around an underlying smolt-to-adult relation.

As for general conclusions of this work, it is clear that a modelling approach such as the one presented here can be useful in formulating recovery plans for endangered species. For instance, the quantitative statement of a recovery goal, $Pr(S > X \text{ by year } T) > Z_1$, is useful because it translates a general, or aspirational conservation goal, into a specific operational objective (BRWG 1994; Peters and Marmorek 2001; de la Mare 2005). The desired and actual ability to meet the goal in a specified period ($S > X$ by year T) were expressed in probabilistic terms (Z_1 and Pr_{rec}), which reflects the reality that there is uncertainty about reaching the goal. The stochastically generated probability distributions for the performance indicators (Pr_{rec}, Pr_{qext}, and gross commercial revenue) thus permit a richer set of management objectives than would otherwise be possible. Stating the objectives in this format also allows a range of values for the parameters of the objectives to be explored, which is useful because there is no single easily-agreed-upon objective. For example, the quasi-extinction level, *Q*, could be set to equal the minimum viable population level, the "endangered" threshold under IUCN criteria, or some other value at the managers' discretion. Managers can also vary the recovery goal (*X*) and the time frame (both *T* and *Y*) to reflect their preferences. For example, potential recovery targets for Cultus Lake sockeye could be set according to the lake's productive capacity (photosynthetic rate model, Shortreed et al. 2000), S_{MSY} (the spawner abundance at maximum sustainable yield over the long term), historical average abundance, an appropriate level for adequate ecosystem function, or other measures (Cultus Sockeye Recovery Team 2004).

The modelling approach used here can also incorporate several management objectives and can provide results that are useful for examining tradeoffs. Many managers find it difficult to make decisions about recovery planning because of potential decreases in economic benefits that must be traded off against biological conservation objectives. Models like the one developed here allow scientists to present managers with information to make explicit tradeoffs between indicators of economic outcomes and species recovery, for example. Such explicit information about tradeoffs can also assist in discussions and negotiations with user groups.

For example, managers can use information such as the nonlinear relation in Figure 13 to determine whether a $5 million per year (11%) increase in expected mean annual gross revenue is worth the associated decrease in probability of recovery from 0.9 to 0.7. Managers can also take into account an indicator of expected year of recovery (Figure 14). When other management objectives are added, the rank order of harvest rules may change. Ideally, managers may use results from this type of model to find management actions that perform well (are robust to) a variety of management objectives, such as maximizing expected gross revenue while minimizing the expected number of years with no harvest.

For endangered stocks and species for which recovery may have large decreases in economic benefits, such as the Cultus sockeye, these types of results can allow managers to determine the economic value of protecting or not protecting the stock. The Canadian Minister of the Environment cited excessive costs as a reason to not list the Cultus stock as “Endangered” under the Species at Risk Act, but this conclusion was based on analyses (e.g., GSGislason and Associates, Ltd. 2004) that focused on costs and overlooked social and economic benefits associated with protecting and generating recovery of the stock. The Gislason report only examined the economic costs of restricting harvest on the late-run Fraser River sockeye to achieve various levels of Cultus sockeye spawner escapement for one year, 2004. The report did not include corresponding decreases in costs associated with a reduced harvest, such as reduced costs of labor, maintenance, fuel, and boats, and did not include any projections of long-term economic value (Gross et al. 2004). Depending on the economic factors included in the model and the parameter values used, stochastic simulation models such as the one used here may give a more accurate and complete assessment of costs and benefits associated with recovery and may show that the decreased harvest rates necessary to allow Cultus sockeye to recover may also allow other late-run stocks to rise to higher abundances, leading to higher catch and greater benefits in the long run than initially expected.

In this model, the starting abundances for most simulated late-run stocks were below S_{msy} for each given stock (Table 2). Also, the late-run Fraser River sockeye stocks tend to have relatively high harvest rates at MSY (H_{msy}) (Table 2). The lower harvest rates that allowed the Cultus stock to recovery also allowed the other late-run stocks to be rebuilt, which may explain why the expected revenue showed a relatively weak dependence on the choice of harvest rule. As illustrated in Figure 14, when Pr_{rec} declined by 11% from 0.9 to 0.8, expected gross revenue only declined 6% from $46.4 to $43.7 million. If the other late-run stocks were initially at abundances near their respective MSY's, then the low harvest rates that allow the Cultus stock to recover in the first 20 years of the model would not lead to rebuilding of the other late-run stocks. In that case, the low harvest rates in the initial years would lead to decreases in economic revenues, the expected revenue would be more sensitive to changes in the harvest rule, and greater variation would be apparent in the economic indicator, because any decrease in harvest rate would represent a direct decrease in the numbers harvested from the others stocks, rather than an opportunity for rebuilding.

My results also demonstrate decreases in gross revenue associated with high harvest rates. An increase in harvest rate caused the probability of recovery (Pr_{rec}) for the Cultus sockeye stock to decrease, and in most cases this led to an increase in gross revenue (such as when Pr_{rec} decreased from 0.9 to 0.8) (Figure 14). However, below a certain threshold (around Pr_{rec} = 0.57) the harvest rate was high enough that the late-run stocks were kept at lower abundances and the gross revenue began to decline. This demonstrates that caution must be used when putting economic interests before conservation.

In my model, none of the harvest rules I examined that produced an acceptable probability of the Cultus sockeye stock recovering (i.e., met objectives with Z_1 = 0.6, 0.7, 0.8, or 0.9) also had an unacceptable probability ($Pr_{qext} \geq 0.05$) of then subsequently going quasi-extinct (Tables 5-8). This occurred because of the parameter values used for the management objective and population dynamics model. The recovery objective contained a high enough abundance (20,000 Cultus sockeye spawners) and a short enough time-frame (20 years) that if the Cultus stock was able to increase rapidly enough to meet this target, it would rarely drop back below the quasi-extinction level (1000 spawners) under the same harvest rule that allowed it to recover. However, this outcome may only be true within the bounds of the parameters considered in the model. In reality, factors not included dynamically in the model (such as very low marine survival rate or very high pre-spawning mortality rate) could still lead to extinction or quasi-extinction in cases where the model does not forecast such outcomes. Also, as described above, another reason for discrepancies between abundance of the Cultus stock in the model and in reality is that historically the target harvest rate was not adjusted to annual variations in the abundance of the Cultus stock, while in my model, this was the sole consideration in determining the target harvest rate each year. The long-term survival objective would also come into play if the recovery goal (X) was lower, the quasi-extinction level (Q) was higher, and/or the time frame for recovery (T) was longer.

In this model, the expected year of recovery increased as the probability of recovery decreased, because a decrease in probability of recovery was the result of a more aggressive harvest rule with higher harvest rates. The higher harvest rates during the recovery period led to fewer recruits produced per spawner, and as a result the stock took longer to achieve the recovery goal.

For all harvest rules that allowed the Cultus stock to recover to a level of 20,000 spawners by year 20 and achieved a desired probability of recovery of 0.9, the expected year of recovery was consistently around year 15 (Table 5, Figure 14) . This is because the first four years of the model were seeded with actual spawner abundances from 1998-2001 (Table 2). In years 1 and 2 (1998 and 1999) the Cultus stock had relatively high spawner abundances compared to years 3 and 4. These more abundant cycle lines returned in years 5 and 6, 9 and 10, and 14 and 15. The rate of recovery of the population under relatively light fishing was such that these more-abundant cycle lines did not typically exceed the recovery goal until the middle of the second decade of the simulation. Depending on values of stochastic processes and probability of recovery, the weighted average year of recovery across Monte Carlo trials could be shifted forward or back in time, but only by a year or two (Figure 14). Note, though, that compared to that weighted average recovery date, the date was much more variable among individual Monte Carlo trials for a given harvest rule (Figure 12).

My results indicate that a harvest rate that increases along with abundance of Cultus Lake sockeye recruits is economically beneficial up to a certain abundance, above which a constant proportional harvest rate maximizes gross revenue. For example, when Z_1 = 0.9, the harvest rule with the highest gross revenue had U = 65,000 and H_{max} = 0.63 (rule #43, Table 5), even though the stock could still meet the recovery and survival objectives with U as high as 140,000. This occurred because when U was set to a higher value, such as in rule #51 where U = 100,000 (Table 5), H_{max} had to be correspondingly increased, in this case to 0.77, to maximize gross revenue at the higher *U* value. However, this increase in H_{max} led to higher proportional harvest rates in years with recruit abundance above 65,000 than would have been implemented under rule #43, leading to fewer spawners and thus fewer recruits in future generations.

Future research

The model developed here incorporated several key aspects of the life history and management of the Cultus Lake sockeye salmon, such as uncertainty about depensatory mortality in the freshwater life stage and implementation uncertainty for harvest rules. In further extensions and sensitivity analyses, it would be possible to add other features to the model to explore the importance of other uncertain parameters or factors that might have time trends or stochastic variation. For example, I used a simplistic economic measure for illustrative purposes and did not thoroughly examine factors such as discount rate, non-economic benefits of the harvest and recovery of Cultus sockeye, and costs associated with management and harvesting. My model was based on historical data for freshwater productivity, which may be declining or have declined in recent years, in which case these results would be overly optimistic. I did not include human alterations to freshwater habitat that could affect productivity, such as enhancement, predator control, or watermilfoil control. A sensitivity analysis on freshwater productivity could indicate the impacts of such changes, as well as the usefulness and effectiveness of such human intervention. Implementation uncertainty could be represented by a more complex function (e.g., Peterman et al. 2000) than the simple error distribution used here.

Also, the mean length of harvested late-run Fraser River sockeye was based on recent data (2000-2003), but mean body size was larger then than in previous years due to a reversal of oceanographic conditions that persisted during substantial decreases in age-specific body size of Pacific salmon in the previous decades (Bigler et al. 1996; Pyper and Peterman 1999; Lapointe et al. 2004). Sensitivity analyses could be conducted using hypothesized increasing or decreasing body sizes over time, which would affect expected economic yields. These trends in body size are rarely accounted for in models, even though fecundity clearly depends on body size, as should parameters of the spawner-to-smolt relation.

The decision analysis performed here could be a useful tool in recovery planning for the Cultus sockeye. However, as cautioned above, there are still many unknown processes of variation that were not included in this model. Any one of them could potentially affect the ability of harvest rules to meet conservation and harvesting objectives. Furthermore, decisions should never be made based solely on results of models such as this one. Many other factors must be taken into account when making management decisions, including those that cannot be quantified, such as changes in biological diversity or social benefits associated with fishing. Decision analysis is by nature an iterative process, and data collected in the future may necessitate a revision of this decision analysis so that the rank order of management actions will reflect the current state of knowledge.

In conclusion, stochastic modeling and decision analysis can be useful tools for recovery planning, for examining tradeoffs associated with recovery, for examining tradeoffs between conflicting management objectives, and for identifying high-priority research topics. These are therefore important tools for managers.

As Irvine et al. (2005) note in the context of Canada's Species at Risk Act (SARA),

> Unfortunately, making tradeoffs to conserve diversity raises socioeconomic issues that can lead to hesitancy to fully embrace the goal of protecting Canada's salmon diversity.…SARA provides an opportunity and legal means for management to concentrate harvest at the point where it is biologically most appropriate. It highlights that harvest remains possible even if it is not where society has previously wished to operate. SARA requires that Canadians consider the economic and social implications of guaranteeing the protection of biodiversity at these fine levels by evaluating implications prior to making a decision to legally list. In the end, society will decide the level of salmon diversity that it will protect.

These new decisions facing managers and society emphasize the need for tools, such as those applied here, that highlight the tradeoffs associated with species recovery.

Tables

Table 1. Baseline values for parameters of management objectives, which state that the probability must be greater than Z_1 that the Cultus Lake sockeye spawner abundance, *S*, will reach some recovered level, *X*, by some year, *T*; and once the recovery target, *X*, is reached, the probability must be less than Z_2 that the number of Cultus spawners will fall below some level *Q* over the next *Y* years. PSM is the constant proportional pre-spawning mortality rate for all adult late-run Fraser River sockeye stocks, including Cultus.

	Parameter	**Value**
Management objectives	*X*	20,000
	T	20
	Z_1	0.9
	Q	1000
	Y	100
	Z_2	0.05
Biological parameter	*PSM*	0.1

Table 2. Spawner abundances for all simulated late-run Fraser River sockeye stocks, where "Sp. year 1", "2", "3", and "4" are historical spawner abundances from 1998-2001 and are used to initialize the first four years of the model, except for the Harrison Rapids stock, which was initialized with data from 1998-2000 because it returns mainly at ages 3 and 4 years. MSY is the maximum sustainable yield, S_{msy} is the spawner abundance at MSY, and H_{msy} is the proportional harvest rate at MSY. MSY for the Cultus stock was calculated using best-fit parameters for a modified Beverton-Holt relation (eq. 2, Figure 5) and was calculated for the other late-run stocks using stock-specific parameters (Table 4) for a Ricker relation (eq. 7).

Stock	Cycle	Sp. year 1	Sp. year 2	Sp. year 3	Sp. year 4	MSY	S_{msy}	H_{msy}
Cultus	All	1224	867	86	193	37,431	28,000	0.57
Weaver	All	52,831	23,087	5058	13,090	425,989	183,000	0.70
Harrison	All	4451	8564	4343		32,124	10,250	0.76
Birkenhead	All	282,098	47,532	12,923	4341	382,852	112,000	0.77
Shuswap								
	Dominant	293,896				1,876,559	870,000	0.68
	Off-cycle		6398	38	55	26,327	4700	0.85
Portage								
	Dominant	22,787				64,462	13,000	0.83
	Off-cycle		4151	1183	2845	47,085	8600	0.85
Adams								
	Dominant	1,028,458				4,037,495	1,360,000	0.75
	Sub-dominant		223,206			1,421,648	450,000	0.76
	Off-cycle			433	3837	18,418	3500	0.84

Table 3. Parameters of the Cultus smolt-to-adult-recruit relation (eq. 3 and 4), where *c* and *b* are parameters, σ^2_g is the variance of the normally distributed error term *g* (eq. 3) that has a mean of 0, and p_4 is the proportion of the stock that returns at age 4.

Parameter	Value
c	0.686
b	0.620
σ^2_g	0.464
p_4	0.955

Table 4. Stock-specific parameter values for non-Cultus late-run Fraser River sockeye stocks, where α_s and β_s are parameters of the Ricker relation (eq. 7), ρ_s is the autocorrelation coefficient for residuals (eq. 8), $\sigma^2_{u,s}$ is the variance of residuals of equation 8, and $p_{4,s}$ is the proportion of the stock that returns at age 4 (eq. 4). Harrison Rapids sockeye return at age 3 and age 4, so its $p_{4,s}$ corresponds to age 3. For Shuswap and Portage stocks, the sub-dominant lines were combined with off-cycle lines.

Stock	**Cycle-line**	α_s	β_s	ρ_s	$\sigma^2_{u,s}$	$p_{4,s}$
Weaver		6.82	0.004	0.19	1.300	0.912
Harrison		8.79	0.074	0.15	0.693	0.568
Birkenhead		9.61	0.007	0.31	0.512	0.732
Shuswap						0.989
	Dominant	6.28	0.0008	0.40	0.343	
	Off-cycle	15.57	0.1826	0.01	1.304	
Portage						0.951
	Dominant	13.77	0.0644	-0.10	0.341	
	Off-cycle	15.09	0.0984	0.18	1.497	
Adams						0.988
	Dominant	8.41	0.0006	0.18	0.303	
	Sub-dominant	8.90	0.0017	-0.37	0.389	
	Off-cycle	14.63	0.2424	0.04	1.021	

Table 5. Results for the baseline case (Table 1). Harvest rules for which the estimated probability of recovery (Pr_{rec}) for the Cultus stock meets or exceeds a desired probability of recovery (Z_1) of 0.9, where L, H_{min}, U, and H_{max} are parameters of the harvest rule. "Pr_{rec}" is the probability of the Cultus stock recovering (management objective 1), "Pr_{qext}" is the probability of the Cultus stock recovering and then going quasi-extinct (management objective 2), "Long-term revenue" is the expected gross revenue from the harvest of late-run Fraser sockeye over the 120 years of the simulation, "annual revenue" is the expected mean annual gross revenue from the harvest of late-run Fraser sockeye, "Number years no harvest" and "Number years small harvest" refer to the expected number of years out of 120 with a proportional harvest rate of zero or less than 0.2, respectively. "Year of recovery" is the expected year of recovery for the Cultus sockeye. "Economic ranking" is the rank for the harvest rule based on gross revenue from the harvest.

Harvest rule	L (1000s)	H_{min}	U (1000s)	H_{max}	Pr_{rec}	Pr_{qext}	Long-term revenue ($ mil.)	Annual revenue ($ mil.)	Number years no harvest	Number years small harvest	Proportion years no harvest	Proportion years small harvest	Year of recovery	Economic ranking
1	1	0.1	10	0.44	0.901	0.00	4487	37.39	0.2	1.6	0.002	0.013	14.8	47
2	1	0.1	20	0.47	0.902	0.00	4751	39.59	0.2	2.6	0.002	0.022	14.8	42
3	1	0.1	40	0.53	0.906	0.00	5055	42.12	0.2	4.2	0.002	0.035	14.9	26
4	1	0.1	50	0.56	0.908	0.00	5071	42.26	0.2	4.9	0.002	0.041	14.9	24
5	1	0.1	65	0.63	0.907	0.00	5199	43.33	0.2	5.7	0.002	0.047	15.1	5
6	1	0.1	70	0.65	0.909	0.00	5182	43.18	0.2	6.0	0.002	0.050	15.1	9
7	1	0.1	80	0.70	0.906	0.00	5146	42.88	0.2	6.4	0.002	0.054	15.3	18
8	1	0.1	85	0.72	0.906	0.00	5103	42.52	0.2	6.8	0.002	0.057	15.4	22
9	1	0.1	100	0.79	0.901	0.00	4898	40.82	0.2	7.6	0.002	0.063	15.4	37
10	1	0.1	120	0.87	0.905	0.00	4603	38.36	0.2	9.5	0.002	0.079	15.2	44
11	1	0.1	140	0.94	0.903	1.28E-03	4083	34.02	0.4	15.8	0.003	0.132	15.0	50
12	1	0.2	1	0.20	0.995	0.00	1886	15.72	0.2	0.2	0.002	0.002	12.6	52
13	1	0.2	10	0.40	0.936	0.00	4044	33.70	0.2	0.2	0.002	0.002	14.6	51

Table 5 continued.

Harvest rule	L (1000s)	H_{min}	U (1000s)	H_{max}	Pr_{rec}	Pr_{qext}	Long-term revenue ($ mil.)	Annual revenue ($ mil.)	Number years no harvest	Number years small harvest	Proportion years no harvest	Proportion years small harvest	Year of recovery	Economic ranking
14	1	0.2	10	0.42	0.914	0.00	4285	35.71	0.2	0.2	0.002	0.002	14.9	49
15	1	0.2	20	0.43	0.925	0.00	4350	36.25	0.2	0.2	0.002	0.002	14.6	48
16	1	0.2	20	0.45	0.915	0.00	4570	38.08	0.2	0.2	0.002	0.002	14.8	46
17	1	0.2	50	0.50	0.938	0.00	4737	39.47	0.2	0.2	0.002	0.002	14.6	43
18	1	0.2	50	0.52	0.918	0.00	4929	41.07	0.2	0.2	0.002	0.002	14.8	34
19	1	0.2	60	0.56	0.907	0.00	5088	42.40	0.2	0.2	0.002	0.002	15.0	23
20	1	0.2	70	0.60	0.902	0.00	5187	43.22	0.2	0.2	0.002	0.002	15.1	8
21	1	0.2	80	0.63	0.910	0.00	5175	43.12	0.2	0.2	0.002	0.002	15.3	10
22	1	0.2	90	0.67	0.904	0.00	5205	43.38	0.2	0.2	0.002	0.002	15.2	4
23	1	0.2	100	0.70	0.902	0.00	5141	42.84	0.2	0.2	0.002	0.002	15.3	19
24	1	0.2	100	0.71	0.903	0.00	5167	43.06	0.2	0.2	0.002	0.002	15.4	12
25	1	0.2	120	0.77	0.904	0.00	5012	41.76	0.2	0.2	0.002	0.002	15.4	28
26	1	0.2	140	0.84	0.906	0.00	4886	40.71	0.2	0.2	0.002	0.002	15.3	38
27	10	0.1	20	0.48	0.928	0.00	4796	39.96	4.0	5.3	0.034	0.044	14.4	41
28	10	0.1	20	0.49	0.924	0.00	4904	40.86	4.1	5.3	0.034	0.044	14.5	36
29	10	0.1	20	0.50	0.906	0.00	5010	41.75	4.1	5.3	0.034	0.044	14.6	29
30	10	0.1	40	0.56	0.906	0.00	5158	42.98	4.0	7.8	0.034	0.065	14.7	14
31	10	0.1	45	0.58	0.903	0.00	5161	43.01	4.0	8.5	0.034	0.071	14.8	13
32	10	0.1	50	0.60	0.904	0.00	5196	43.30	4.0	9.0	0.033	0.075	14.8	6
33	10	0.1	55	0.62	0.905	0.00	5157	42.97	4.0	9.7	0.034	0.080	14.8	15
34	10	0.1	60	0.64	0.915	0.00	5149	42.91	4.0	10.2	0.033	0.085	14.9	16
35	10	0.1	65	0.66	0.923	0.00	5117	42.64	4.0	10.7	0.034	0.089	14.9	21
36	10	0.1	65	0.67	0.910	0.00	5147	42.89	4.1	10.7	0.034	0.089	15.0	17
37	10	0.1	80	0.73	0.934	0.00	4965	41.38	4.0	12.3	0.033	0.103	14.9	33
38	10	0.1	80	0.75	0.900	0.00	4985	41.54	4.1	12.5	0.034	0.104	15.2	32
39	10	0.1	100	0.84	0.905	0.00	4601	38.34	4.3	15.6	0.036	0.130	15.1	45
40	10	0.2	20	0.48	0.916	0.00	4799	39.99	4.1	4.1	0.034	0.034	14.5	40

Table 5 continued.

Harvest rule	L (1000s)	H_{min}	U (1000s)	H_{max}	Pr_{rec}	Pr_{qext}	Long-term revenue ($ mil.)	Annual revenue ($ mil.)	Number years no harvest	Number years small harvest	Proportion years no harvest	Proportion years small harvest	Year of recovery	Economic ranking
41	10	0.2	20	0.49	0.903	0.00	4907	40.89	4.1	4.1	0.034	0.034	14.7	35
42	10	0.2	60	0.61	0.907	0.00	5229	43.57	4.1	4.1	0.034	0.034	15.0	3
43	10	0.2	65	0.63	0.906	0.00	5241	43.68	4.1	4.1	0.034	0.034	15.1	1
44	10	0.2	70	0.65	0.906	0.00	5234	43.62	4.1	4.1	0.034	0.034	15.1	2
45	10	0.2	80	0.67	0.927	0.00	5134	42.78	4.0	4.0	0.034	0.034	14.9	20
46	10	0.2	80	0.68	0.919	0.00	5172	43.10	4.1	4.1	0.034	0.034	15.1	11
47	10	0.2	80	0.69	0.906	0.00	5192	43.27	4.1	4.1	0.034	0.034	15.1	7
48	10	0.2	100	0.73	0.947	0.00	4986	41.55	4.0	4.0	0.034	0.034	14.8	31
49	10	0.2	100	0.74	0.938	0.00	4998	41.65	4.1	4.1	0.034	0.034	14.9	30
50	10	0.2	100	0.76	0.916	0.00	5020	41.83	4.1	4.1	0.034	0.034	15.1	27
51	10	0.2	100	0.77	0.913	0.00	5056	42.13	4.1	4.1	0.034	0.034	15.2	25
52	10	0.2	120	0.84	0.915	0.00	4821	40.17	4.2	4.2	0.035	0.035	15.1	39

Table 6. Results for the baseline parameters (Table 1), except for Z_1, which is 0.8. Harvest rules for which the probability of recovery (Pr_{rec}) for the Cultus stock meets or exceeds a desired probability of recovery (Z_1) of 0.8. Column headings are as defined in Table 5.

Harvest rule	L (1000s)	H_{min}	U (1000s)	H_{max}	Pr_{rec}	Pr_{qext}	Long-term revenue ($ mil.)	Annual revenue ($ mil.)	Number years no harvest	Number years small harvest	Proportion years no harvest	Proportion years small harvest	Year of recovery	Economic ranking
1	1	0.1	10	0.49	0.825	0	5095	42.45	0.2	1.5	0.002	0.012	15.5	40
2	1	0.1	10	0.50	0.804	0	5211	43.42	0.2	1.4	0.002	0.012	15.6	31
3	1	0.1	20	0.53	0.802	0	5429	45.24	0.2	2.4	0.002	0.020	15.5	12
4	1	0.1	40	0.59	0.801	0	5555	46.29	0.2	3.8	0.002	0.032	15.5	2
5	1	0.1	60	0.65	0.828	0	5419	45.16	0.2	5.1	0.002	0.042	15.5	13
6	1	0.1	60	0.66	0.804	0	5455	45.46	0.2	5.0	0.002	0.042	15.6	9
7	1	0.1	75	0.68	0.895	0	5164	43.03	0.2	6.2	0.002	0.052	15.3	38
8	1	0.1	80	0.72	0.872	0	5200	43.33	0.2	6.3	0.002	0.052	15.5	32
9	1	0.1	80	0.74	0.820	0	5223	43.53	0.2	6.1	0.002	0.051	15.8	30
10	1	0.1	90	0.78	0.827	0	5078	42.32	0.2	6.8	0.002	0.056	15.8	42
11	1	0.1	110	0.86	0.848	0	4734	39.45	0.2	8.6	0.002	0.072	15.6	52
12	1	0.1	110	0.87	0.825	0	4705	39.21	0.2	8.8	0.002	0.074	15.7	53
13	1	0.1	130	0.95	0.808	4.02E-03	3994	33.28	0.6	17.0	0.005	0.142	15.4	58
14	1	0.1	140	0.95	0.886	2.99E-03	3979	33.16	0.5	17.0	0.004	0.142	15.0	60
15	1	0.2	10	0.49	0.803	0	5093	42.44	0.2	0.2	0.002	0.002	15.6	41
16	1	0.2	20	0.46	0.889	0	4703	39.19	0.2	0.2	0.002	0.002	14.9	54
17	1	0.2	40	0.51	0.883	0	4983	41.53	0.2	0.2	0.002	0.002	14.9	48
18	1	0.2	40	0.53	0.860	0	5184	43.20	0.2	0.2	0.002	0.002	15.2	35
19	1	0.2	40	0.56	0.820	0	5439	45.32	0.2	0.2	0.002	0.002	15.4	10
20	1	0.2	40	0.57	0.802	0	5524	46.03	0.2	0.2	0.002	0.002	15.6	4
21	1	0.2	50	0.53	0.894	0	5012	41.77	0.2	0.2	0.002	0.002	15.0	46
22	1	0.2	50	0.54	0.883	0	5095	42.46	0.2	0.2	0.002	0.002	15.1	39
23	1	0.2	60	0.60	0.841	0	5339	44.50	0.2	0.2	0.002	0.002	15.5	17
24	1	0.2	70	0.61	0.891	0	5245	43.71	0.2	0.2	0.002	0.002	15.3	28
25	1	0.2	80	0.67	0.848	0	5359	44.66	0.2	0.2	0.002	0.002	15.6	15
26	1	0.2	80	0.69	0.813	0	5418	45.15	0.2	0.2	0.002	0.002	15.9	14

Table 6 continued.

Harvest rule	L (1000s)	H_{min}	U (1000s)	H_{max}	Pr_{rec}	Pr_{qext}	Long-term revenue ($ mil.)	Annual revenue ($ mil.)	Number years no harvest	Number years small harvest	Proportion years no harvest	Proportion years small harvest	Year of recovery	Economic ranking
27	1	0.2	100	0.71	0.892	0	5171	43.09	0.2	0.2	0.002	0.002	15.4	36
28	1	0.2	100	0.72	0.891	0	5185	43.21	0.2	0.2	0.002	0.002	15.6	34
29	1	0.2	100	0.75	0.836	0	5249	43.74	0.2	0.2	0.002	0.002	15.8	26
30	1	0.2	100	0.76	0.820	0	5262	43.85	0.2	0.2	0.002	0.002	15.9	23
31	1	0.2	100	0.77	0.804	0	5249	43.74	0.2	0.2	0.002	0.002	16.1	25
32	1	0.2	140	0.91	0.821	1.25E-04	4745	39.54	0.2	0.2	0.002	0.002	15.8	51
33	10	0.1	20	0.55	0.817	0	5500	45.83	4.3	5.6	0.036	0.046	15.3	6
34	10	0.1	40	0.61	0.819	0	5506	45.88	4.1	8.0	0.035	0.066	15.4	5
35	10	0.1	50	0.61	0.888	0	5252	43.77	4.0	9.1	0.034	0.075	14.9	24
36	10	0.1	60	0.67	0.851	0	5246	43.72	4.1	10.3	0.034	0.086	15.3	27
37	10	0.1	60	0.68	0.814	0	5278	43.98	4.1	10.3	0.034	0.086	15.4	19
38	10	0.1	65	0.68	0.889	0	5166	43.05	4.1	10.8	0.034	0.090	15.2	37
39	10	0.1	80	0.76	0.874	0	4988	41.56	4.1	12.5	0.034	0.104	15.4	47
40	10	0.1	80	0.78	0.808	0	4953	41.27	4.1	13.0	0.034	0.108	15.6	49
41	10	0.1	100	0.85	0.887	0	4588	38.23	4.4	15.9	0.036	0.132	15.2	56
42	10	0.1	100	0.88	0.804	2.88E-15	4476	37.30	5.2	17.8	0.043	0.148	15.5	57
43	10	0.1	120	0.93	0.879	1.76E-03	3988	33.24	8.4	23.7	0.070	0.198	14.9	59
44	10	0.1	120	0.94	0.855	3.43E-03	3857	32.14	9.9	25.5	0.083	0.212	15.0	61
45	10	0.1	120	0.95	0.820	8.14E-03	3726	31.05	11.4	27.2	0.095	0.227	14.9	62
46	10	0.2	20	0.54	0.828	0	5430	45.25	4.2	4.2	0.035	0.035	15.2	11
47	10	0.2	20	0.55	0.802	0	5527	46.06	4.3	4.3	0.036	0.036	15.2	3
48	10	0.2	40	0.55	0.892	0	5186	43.22	4.1	4.1	0.034	0.034	14.9	33
49	10	0.2	40	0.56	0.886	0	5271	43.93	4.1	4.1	0.034	0.034	15.0	22
50	10	0.2	40	0.57	0.863	0	5353	44.61	4.1	4.1	0.034	0.034	15.1	16
51	10	0.2	40	0.59	0.830	0	5499	45.83	4.1	4.1	0.034	0.034	15.2	7
52	10	0.2	40	0.60	0.807	0	5569	46.41	4.2	4.2	0.035	0.035	15.3	1
53	10	0.2	60	0.62	0.890	0	5284	44.03	4.1	4.1	0.034	0.034	15.1	18
54	10	0.2	60	0.62	0.888	0	5276	43.97	4.1	4.1	0.034	0.034	15.1	20
55	10	0.2	60	0.66	0.802	0	5459	45.49	4.1	4.1	0.035	0.035	15.6	8
56	10	0.2	80	0.70	0.889	0	5240	43.67	4.1	4.1	0.034	0.034	15.3	29

Table 6 continued.

Harvest rule	*L* (1000s)	H_{min}	*U* (1000s)	H_{max}	Pr_{rec}	Pr_{qext}	Long-term revenue ($ mil.)	Annual revenue ($ mil.)	Number years no harvest	Number years small harvest	Proportion years no harvest	Proportion years small harvest	Year of recovery	Economic ranking
57	10	0.2	80	0.73	0.818	0	5272	43.93	4.1	4.1	0.034	0.034	15.6	21
58	10	0.2	100	0.78	0.890	0	5025	41.87	4.1	4.1	0.034	0.034	15.3	45
59	10	0.2	100	0.81	0.837	0	5038	41.98	4.1	4.1	0.035	0.035	15.7	43
60	10	0.2	100	0.82	0.807	0	5026	41.88	4.2	4.2	0.035	0.035	15.8	44
61	10	0.2	120	0.87	0.867	0	4776	39.80	4.5	4.5	0.037	0.037	15.4	50
62	10	0.2	120	0.89	0.813	2.01E-11	4679	38.99	5.1	5.1	0.043	0.043	15.7	55

Table 7. Results for the baseline parameters (Table 1), except for Z_1, which is 0.7. Harvest rules for which the probability of recovery (Pr_{rec}) for the Cultus stock meets or exceeds a desired probability of recovery (Z_1) of 0.7. Column headings are as defined in Table 5.

Harvest rule	L (1000s)	H_{min}	U (1000s)	H_{max}	Pr_{rec}	Pr_{qext}	Long-term revenue ($ mil.)	Annual revenue ($ mil.)	Number years no harvest	Number years small harvest	Proportion years no harvest	Proportion years small harvest	Year of recovery	Economic ranking
1	1	0.1	10	0.52	0.732	0.00	5409	45.07	0.2	1.4	0.0019	0.0114	15.9	21
2	1	0.1	10	0.53	0.703	0.00	5521	46.01	0.2	1.3	0.0019	0.0112	16.0	17
3	1	0.1	40	0.61	0.727	0.00	5668	47.23	0.2	3.7	0.0019	0.0312	15.8	7
4	1	0.1	50	0.64	0.732	0.00	5585	46.54	0.2	4.4	0.0019	0.0364	15.8	12
5	1	0.1	60	0.68	0.717	0.00	5499	45.83	0.2	4.9	0.0019	0.0411	16.0	18
6	1	0.1	80	0.75	0.788	0.00	5232	43.60	0.2	6.1	0.0018	0.0508	15.9	30
7	1	0.1	80	0.77	0.716	0.00	5235	43.63	0.2	6.0	0.0018	0.0502	16.1	29
8	1	0.1	100	0.85	0.753	0.00	4865	40.54	0.2	7.7	0.0017	0.0644	16.0	38
9	1	0.1	100	0.86	0.717	0.00	4831	40.25	0.2	8.0	0.0017	0.0664	16.1	39
10	1	0.2	10	0.50	0.782	0.00	5192	43.27	0.2	0.2	0.0018	0.0018	15.8	31
11	1	0.2	10	0.51	0.738	0.00	5313	44.27	0.2	0.2	0.0018	0.0018	15.9	24
12	1	0.2	20	0.54	0.735	0.00	5568	46.40	0.2	0.2	0.0018	0.0018	15.8	13
13	1	0.2	20	0.55	0.715	0.00	5672	47.27	0.2	0.2	0.0018	0.0018	15.9	5
14	1	0.2	40	0.60	0.710	0.00	5758	47.98	0.2	0.2	0.0018	0.0018	15.9	3
15	1	0.2	60	0.65	0.729	0.00	5622	46.85	0.2	0.2	0.0019	0.0019	16.0	9
16	1	0.2	80	0.70	0.786	0.00	5447	45.39	0.2	0.2	0.0018	0.0018	16.0	20
17	1	0.2	80	0.71	0.758	0.00	5471	45.59	0.2	0.2	0.0017	0.0017	16.1	19
18	1	0.2	100	0.80	0.704	0.00	5271	43.93	0.2	0.2	0.0018	0.0018	16.4	28
19	1	0.2	120	0.85	0.792	0.00	5039	41.99	0.2	0.2	0.0018	0.0018	16.0	32
20	1	0.2	120	0.88	0.703	0.00	4971	41.42	0.2	0.2	0.0017	0.0017	16.4	35
21	1	0.2	140	0.92	0.791	2.59E-04	4687	39.06	0.2	0.2	0.0019	0.0019	15.9	40
22	1	0.2	140	0.95	0.705	6.26E-04	4392	36.60	0.5	0.5	0.0042	0.0042	16.1	44
23	10	0.1	20	0.56	0.791	0.00	5594	46.62	4.3	5.6	0.0360	0.0468	15.4	11
24	10	0.1	20	0.57	0.755	0.00	5672	47.27	4.4	5.7	0.0365	0.0475	15.5	6
25	10	0.1	20	0.59	0.703	0.00	5850	48.75	4.5	5.9	0.0376	0.0491	15.7	1
26	10	0.1	40	0.62	0.792	0.00	5561	46.34	4.2	8.0	0.0347	0.0668	15.5	14

Table 7 continued.

Harvest rule	L (1000s)	H_{min}	U (1000s)	H_{max}	Pr_{rec}	Pr_{qext}	Long-term revenue ($ mil.)	Annual revenue ($ mil.)	Number years no harvest	Number years small harvest	Proportion years no harvest	Proportion years small harvest	Year of recovery	Economic ranking
27	10	0.1	40	0.64	0.716	0.00	5638	46.98	4.3	8.3	0.0356	0.0689	15.6	8
28	10	0.1	60	0.69	0.789	0.00	5308	44.24	4.1	10.3	0.0342	0.0860	15.6	25
29	10	0.1	60	0.70	0.770	0.00	5316	44.30	4.2	10.5	0.0346	0.0872	15.6	23
30	10	0.1	60	0.71	0.728	0.00	5321	44.34	4.1	10.6	0.0345	0.0883	15.7	22
31	10	0.1	80	0.79	0.789	0.00	4958	41.32	4.2	12.9	0.0349	0.1079	15.7	36
32	10	0.1	80	0.81	0.702	0.00	4896	40.80	4.3	13.5	0.0359	0.1126	16.0	37
33	10	0.1	100	0.89	0.762	6.14E-08	4442	37.02	5.6	18.5	0.0466	0.1544	15.6	42
34	10	0.2	20	0.58	0.718	0.00	5801	48.34	4.5	4.5	0.0374	0.0374	15.7	2
35	10	0.2	40	0.61	0.775	0.00	5617	46.81	4.3	4.3	0.0355	0.0355	15.5	10
36	10	0.2	40	0.63	0.726	0.00	5743	47.86	4.3	4.3	0.0354	0.0354	15.6	4
37	10	0.2	60	0.68	0.754	0.00	5529	46.07	4.1	4.1	0.0345	0.0345	15.7	15
38	10	0.2	60	0.69	0.710	0.00	5526	46.05	4.2	4.2	0.0349	0.0349	15.8	16
39	10	0.2	80	0.74	0.792	0.00	5278	43.99	4.1	4.1	0.0343	0.0343	15.8	27
40	10	0.2	80	0.75	0.765	0.00	5295	44.12	4.2	4.2	0.0349	0.0349	15.9	26
41	10	0.2	100	0.83	0.774	0.00	5012	41.77	4.3	4.3	0.0355	0.0355	15.9	33
42	10	0.2	100	0.84	0.745	0.00	4971	41.43	4.4	4.4	0.0368	0.0368	15.9	34
43	10	0.2	120	0.90	0.789	6.44E-07	4638	38.65	5.5	5.5	0.0458	0.0458	15.7	41
44	10	0.2	120	0.93	0.711	6.41E-04	4414	36.78	8.1	8.1	0.0673	0.0673	15.8	43

Table 8. Results for the baseline parameters (Table 1), except for Z_1, which is 0.6. Harvest rules for which the probability of recovery (Pr_{rec}) for the Cultus stock meets or exceeds a desired probability of recovery (Z_1) of 0.6. Column headings are as defined in Table 5.

Harvest rule	L (1000s)	H_{min}	U (1000s)	H_{max}	Pr_{rec}	Pr_{qext}	Long-term revenue ($ mil.)	Annual revenue ($ mil.)	Number years no harvest	Number years small harvest	Proportion years no harvest	Proportion years small harvest	Year of recovery	Economic ranking
1	1	0.1	10	0.56	0.603	0.00	5874	48.95	0.2	1.3	0.0018	0.0107	16.3	8
2	1	0.1	40	0.64	0.636	0.00	5887	49.06	0.2	3.5	0.0018	0.0295	16.0	6
3	1	0.1	60	0.69	0.682	0.00	5526	46.05	0.2	4.9	0.0019	0.0407	16.1	20
4	1	0.1	60	0.71	0.615	0.00	5598	46.65	0.2	4.8	0.0017	0.0399	16.2	17
5	1	0.1	80	0.78	0.677	0.00	5232	43.60	0.2	6.0	0.0018	0.0498	16.2	27
6	1	0.1	80	0.79	0.614	0.00	5218	43.48	0.2	6.0	0.0017	0.0498	16.4	28
7	1	0.1	90	0.82	0.683	0.00	5034	41.95	0.2	6.7	0.0018	0.0559	16.2	29
8	1	0.1	90	0.83	0.637	0.00	5013	41.78	0.2	6.8	0.0018	0.0567	16.3	30
9	1	0.1	100	0.88	0.623	1.10E-14	4744	39.53	0.2	8.6	0.0018	0.0721	16.2	35
10	1	0.1	110	0.92	0.635	6.17E-04	4417	36.81	0.3	12.4	0.0022	0.1030	16.1	36
11	1	0.2	20	0.58	0.623	0.00	5965	49.71	0.2	0.2	0.0017	0.0017	16.3	3
12	1	0.2	40	0.62	0.651	0.00	5891	49.09	0.2	0.2	0.0019	0.0019	16.1	5
13	1	0.2	40	0.63	0.614	0.00	5945	49.54	0.2	0.2	0.0017	0.0017	16.3	4
14	1	0.2	60	0.66	0.694	0.00	5665	47.21	0.2	0.2	0.0018	0.0018	16.1	16
15	1	0.2	60	0.67	0.661	0.00	5704	47.53	0.2	0.2	0.0018	0.0018	16.2	15
16	1	0.2	60	0.68	0.627	0.00	5755	47.96	0.2	0.2	0.0018	0.0018	16.3	12
17	1	0.2	80	0.73	0.692	0.00	5498	45.82	0.2	0.2	0.0018	0.0018	16.3	22
18	1	0.2	80	0.75	0.604	0.00	5512	45.93	0.2	0.2	0.0019	0.0019	16.5	21
19	1	0.2	100	0.82	0.638	0.00	5268	43.90	0.2	0.2	0.0017	0.0017	16.6	25
20	1	0.2	120	0.90	0.626	4.01E-08	4899	40.82	0.2	0.2	0.0019	0.0019	16.5	32
21	1	0.2	140	0.95	0.685	1.86E-03	4409	36.74	0.5	0.5	0.0043	0.0043	16.2	37
22	10	0.1	20	0.61	0.630	0.00	5987	49.90	4.6	6.1	0.0384	0.0505	15.8	2
23	10	0.1	40	0.66	0.653	0.00	5713	47.61	4.3	8.4	0.0362	0.0697	15.9	13
24	10	0.1	40	0.67	0.626	0.00	5705	47.54	4.4	8.5	0.0366	0.0708	16.0	14
25	10	0.1	60	0.72	0.678	0.00	5329	44.41	4.2	10.7	0.0348	0.0891	15.8	23
26	10	0.1	60	0.74	0.609	0.00	5301	44.17	4.3	10.9	0.0359	0.0907	16.1	24

Table 8 continued.

Harvest rule	L (1000s)	H_{min}	U (1000s)	H_{max}	Pr_{rec}	Pr_{qext}	Long-term revenue ($ mil.)	Annual revenue ($ mil.)	Number years no harvest	Number years small harvest	Proportion years no harvest	Proportion years small harvest	Year of recovery	Economic ranking
29	10	0.1	100	0.93	0.603	1.40E-03	4031	33.59	10.1	24.3	0.0840	0.2024	15.8	40
30	10	0.2	20	0.59	0.685	0.00	5878	48.98	4.6	4.6	0.0380	0.0380	15.7	7
31	10	0.2	20	0.61	0.600	0.00	6051	50.43	4.7	4.7	0.0388	0.0388	16.0	1
32	10	0.2	40	0.64	0.677	0.00	5783	48.20	4.3	4.3	0.0362	0.0362	15.8	11
33	10	0.2	40	0.65	0.651	0.00	5833	48.60	4.3	4.3	0.0361	0.0361	15.8	10
34	10	0.2	40	0.66	0.600	0.00	5866	48.88	4.4	4.4	0.0368	0.0368	16.0	9
35	10	0.2	60	0.70	0.665	0.00	5553	46.28	4.3	4.3	0.0357	0.0357	16.0	19
36	10	0.2	60	0.71	0.625	0.00	5558	46.32	4.3	4.3	0.0357	0.0357	16.0	18
37	10	0.2	80	0.77	0.693	0.00	5255	43.79	4.2	4.2	0.0353	0.0353	16.1	26
38	10	0.2	100	0.85	0.694	0.00	4964	41.36	4.5	4.5	0.0373	0.0373	16.1	31
39	10	0.2	100	0.87	0.625	0.00	4865	40.54	5.0	5.0	0.0413	0.0413	16.2	33
40	10	0.2	120	0.95	0.625	3.51E-03	4124	34.37	10.9	10.9	0.0911	0.0911	15.9	39

Table 9. Results when the constant pre-spawning mortality rate (PSM) is 0.2 or 0.3, but when the harvest rule is used that has the highest expected gross revenue satisfying Z_1 = 0.9 in a case where PSM = 0.1 (rule #43, Table 5). The harvest rule parameters are L = 10,000, H_{min} = 0.2, U = 65,000, H_{max} = 0.63. Column headings are as defined in Table 5.

PSM	Pr_{rec}	Pr_{qext}	Long-term revenue ($mil.)	Annual revenue ($mil.)	Number years no harvest	Number years small harvest	Proportion years no harvest	Proportion years small harvest	Year of recovery
0.1	0.906	0.00	5241	43.68	4.1	4.1	0.0339	0.0339	15.07
0.2	0.702	0.00	5095	42.46	4.3	4.3	0.0361	0.0361	16.04
0.3	0.419	0.00	4918	40.98	4.7	4.7	0.0395	0.0395	16.66

Figures

Figure 1. Annual abundance of Cultus Lake sockeye adult spawners (escapement), 1925-2001.

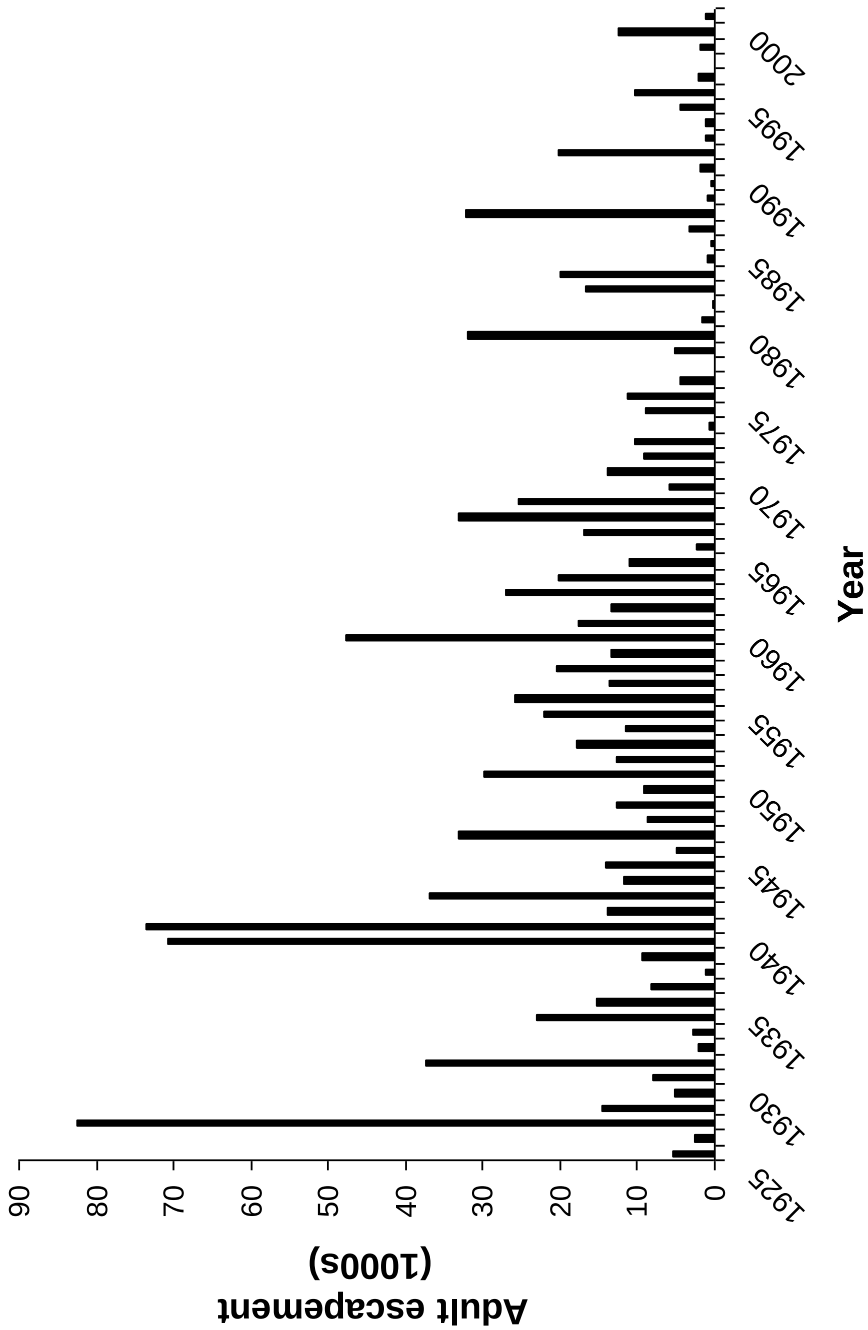
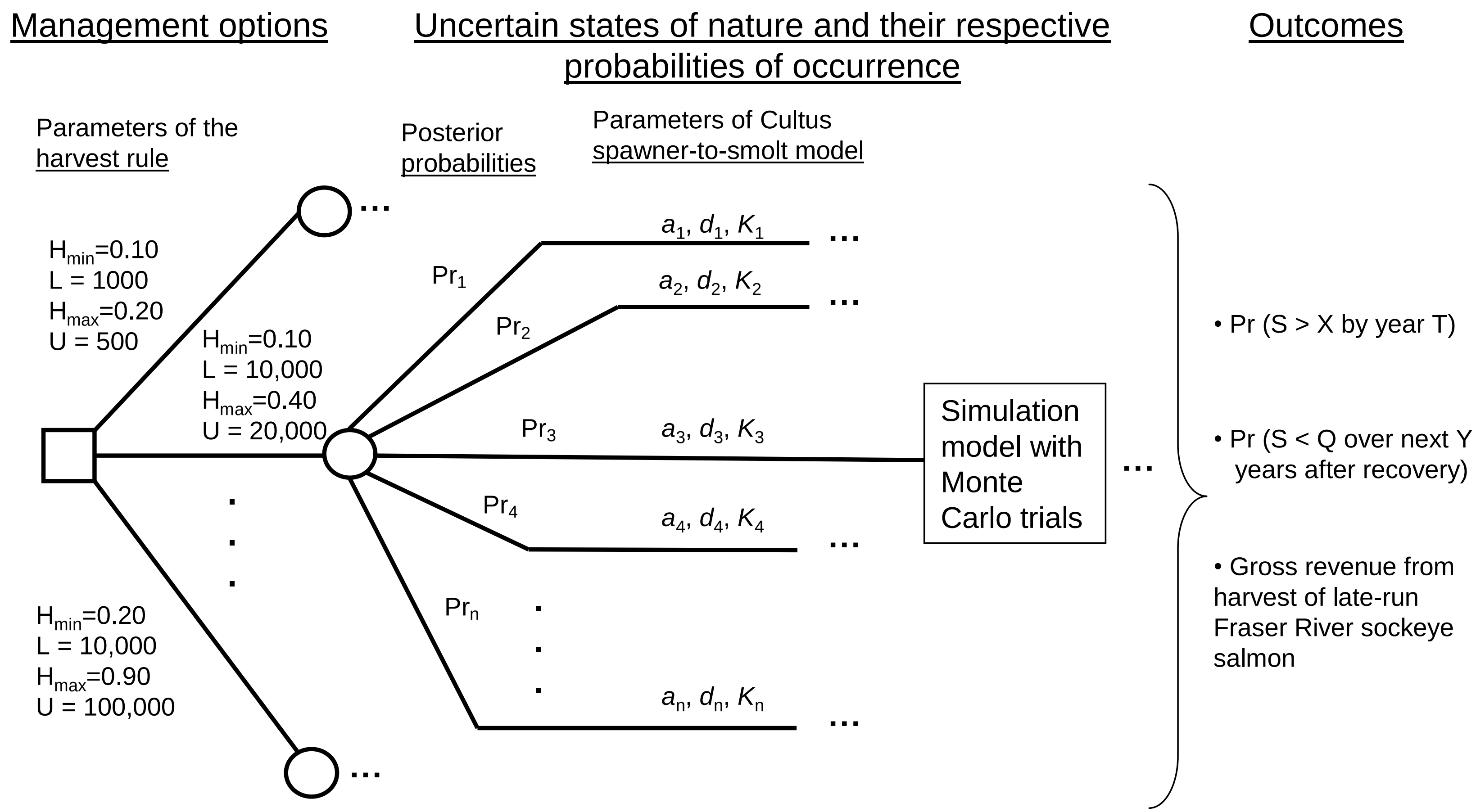

Adult escapement (1000s)
0
10
20
30
40
50
60
70
80
90
1925
1930
1935
1940
1945
1950
1955
1960
1965
1970
1975
1980
1985
1990
1995
2000
Year

Figure 2. Decision tree illustrating the main structure of this analysis. Branches emanating from the square node represent different harvest rules, each one described by a set of parameters as illustrated in Figure 3. Branches emanating from round nodes are uncertain states of nature. For each possible harvest rule, there is an uncertainty node that has a branch for every possible state of nature (combination of parameter values for the Cultus spawner-to-smolt model). The relative weighting (or probability, Pr_n) on each uncertain state is the Bayesian joint posterior probability for a given combination of those parameters. The figure only shows a subset of the many harvest rules and uncertain states of nature.



Management options
Uncertain states of nature and their respective probabilities of occurrence
Outcomes
Parameters of the harvest rule
Posterior probabilities
Parameters of Cultus spawner-to-smolt model
H_{min}=0.10
L = 1000
H_{max}=0.20
U = 500
H_{min}=0.10
L = 10,000
H_{max}=0.40
U = 20,000
H_{min}=0.20
L = 10,000
H_{max}=0.90
U = 100,000
Pr_1
Pr_2
Pr_3
Pr_4
Pr_n
a_1, d_1, K_1
a_2, d_2, K_2
a_3, d_3, K_3
a_4, d_4, K_4
a_n, d_n, K_n
Simulation model with Monte Carlo trials
• Pr (S > X by year T)
• Pr (S < Q over next Y years after recovery)
• Gross revenue from harvest of late-run Fraser River sockeye salmon

Figure 3. Harvest rule to calculate the target harvest rate, H_{tar} (before implementation uncertainty was imposed). *L* is the abundance of Cultus Lake sockeye recruits at which H_{min} was the management target and below which no harvest was taken. The maximum proportional harvest rate, H_{max}, was the target above Cultus recruit abundance *U*.

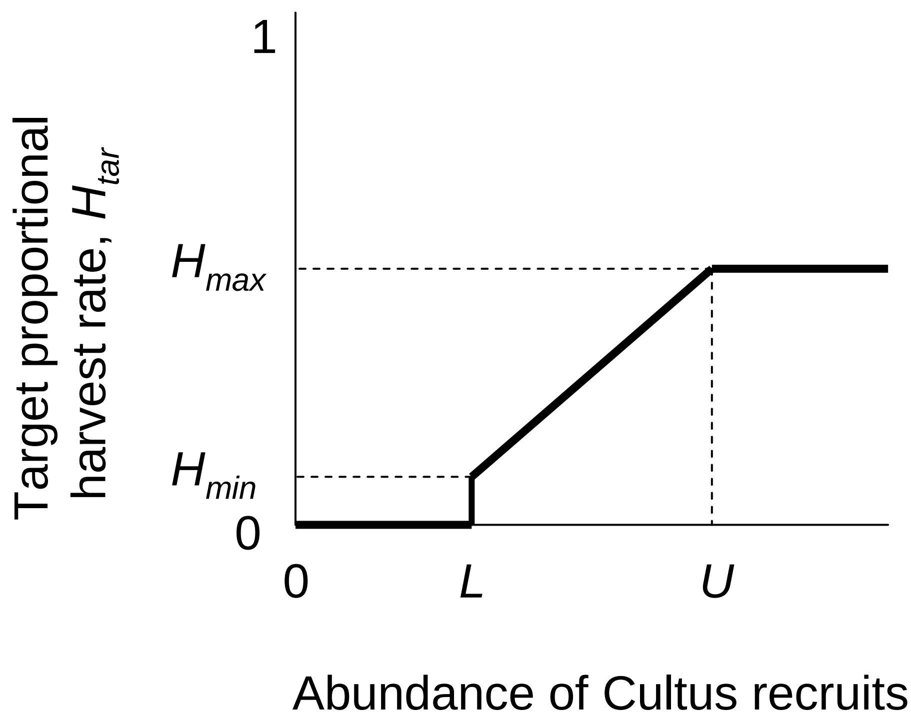

1
Target proportional harvest rate, H_tar
H_max
H_min
0
0
L
U
Abundance of Cultus recruits

Figure 4. Flow chart of the simulation model of life histories and management of the Cultus Lake and other late-run Fraser River sockeye stocks. PSM is pre-spawning mortality of adults that occurs in the lake, *T* is the time frame for recovery, and *Y* is the time frame for long-term survival subsequent to recovery.

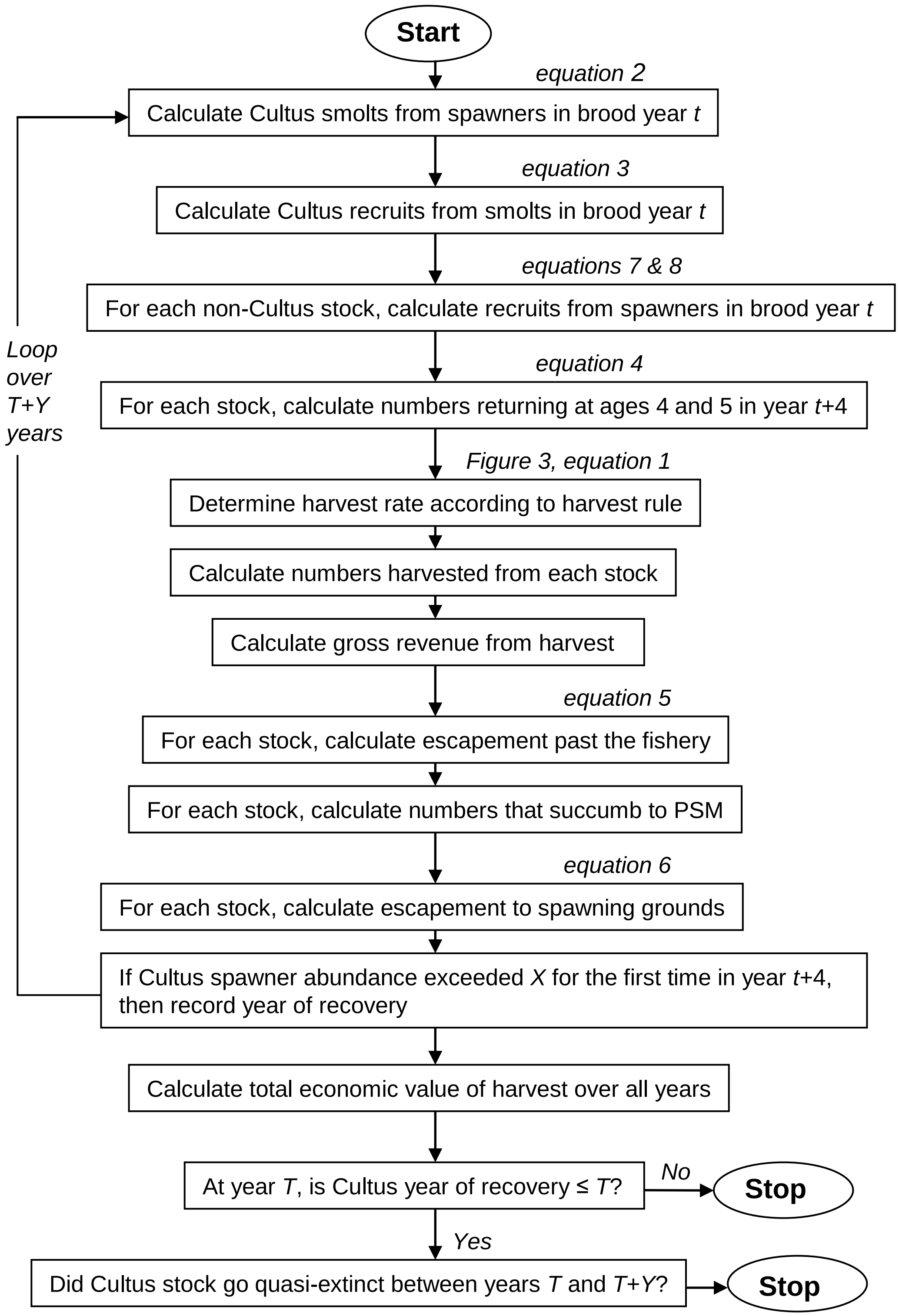

Start
equation 2
Calculate Cultus smolts from spawners in brood year t
equation 3
Calculate Cultus recruits from smolts in brood year t
equations 7 & 8
For each non-Cultus stock, calculate recruits from spawners in brood year t
equation 4
For each stock, calculate numbers returning at ages 4 and 5 in year t+4
Figure 3, equation 1
Determine harvest rate according to harvest rule
Calculate numbers harvested from each stock
Calculate gross revenue from harvest
equation 5
For each stock, calculate escapement past the fishery
For each stock, calculate numbers that succumb to PSM
equation 6
For each stock, calculate escapement to spawning grounds
If Cultus spawner abundance exceeded X for the first time in year t+4, then record year of recovery
Loop over T+Y years
Calculate total economic value of harvest over all years
At year T, is Cultus year of recovery ≤ T?
No
Stop
Yes
Did Cultus stock go quasi-extinct between years T and T+Y?
Stop

Figure 5. Smolt and spawner data for the Cultus Lake sockeye stock (1951, 1954-1960, 1965-1971, 1974-1975, and 1988-1989 brood years). The curve is the best-fit modified Beverton-Holt curve (eq. 2 fit using least squares regression). The best-fit parameter values are a = 55.597, d = 1.153, and K = 69.375.

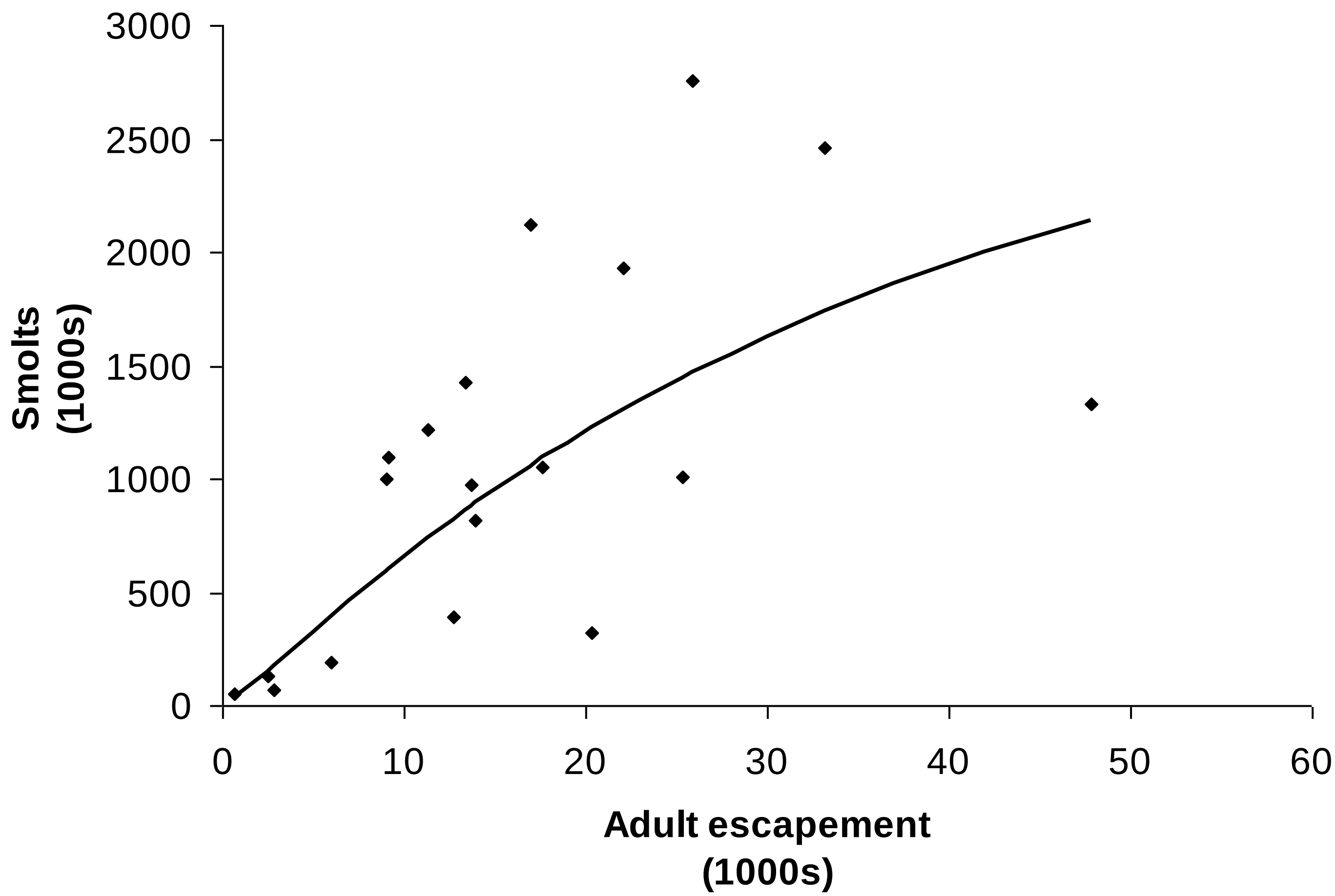

Smolts
(1000s)
3000
2500
2000
1500
1000
500
0
0
10
20
30
40
50
60
Adult escapement
(1000s)

Figure 6. Marginal posterior probabilities for parameters of the modified Beverton-Holt model (eq. 2) used to represent the Cultus spawner-to-smolt relation. The discrete values shown by data points are those considered in the Bayesian analysis: (A) 16 values of the a parameter with a minimum value of 15 and an interval of 10, (B) 14 values of the d parameter with a minimum value of 0.5 and an interval of 0.1, and (C) 15 values of the K parameter with a minimum value of 20 and an interval of 20. Bounds on the uniform prior probabilities are indicated by dashed vertical lines.

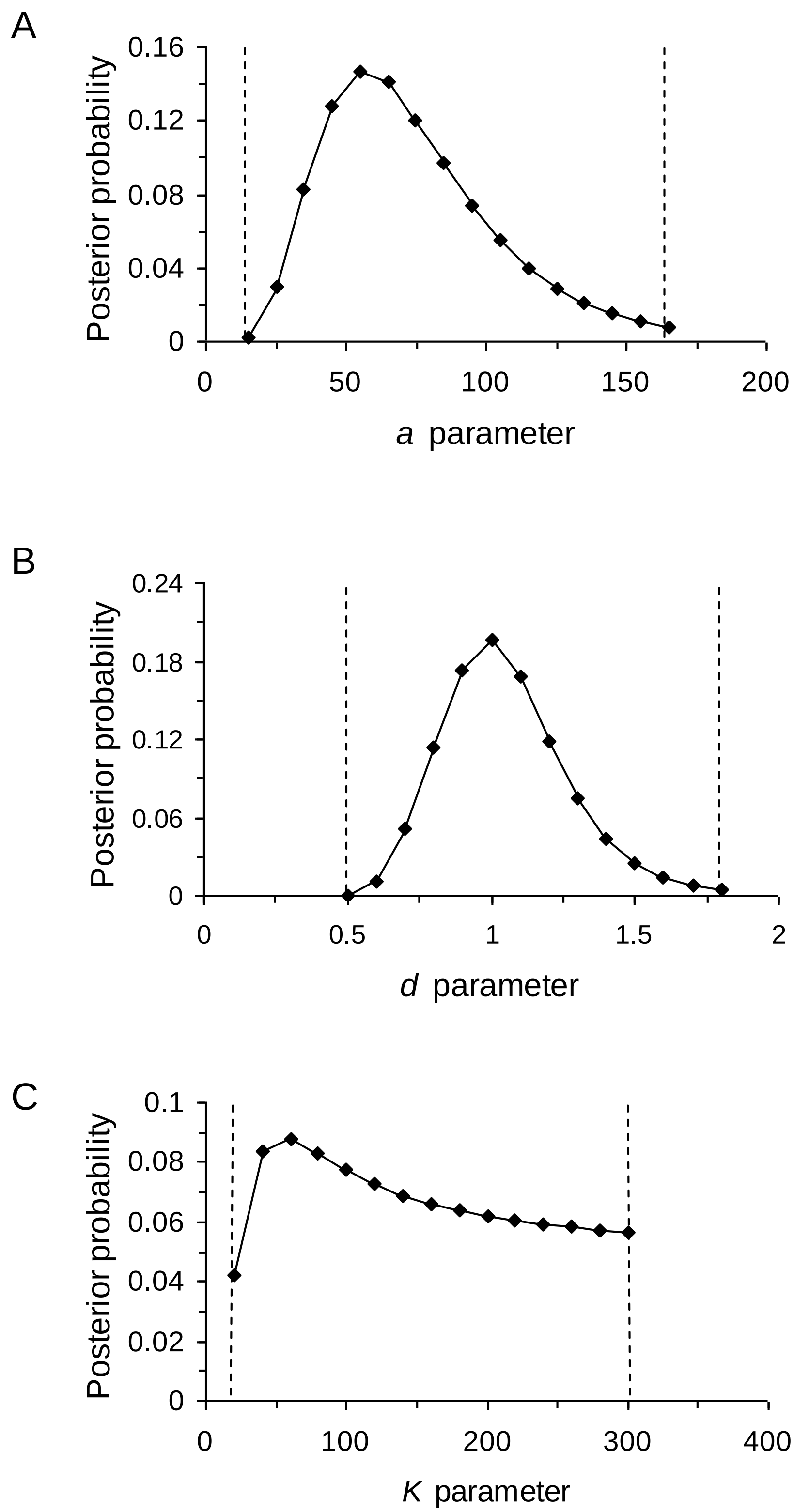

A
Posterior probability
0.16
0.12
0.08
0.04
0
0
50
100
150
200
a parameter
B
Posterior probability
0.24
0.18
0.12
0.06
0
0
0.5
1
1.5
2
d parameter
C
Posterior probability
0.1
0.08
0.06
0.04
0.02
0
0
100
200
300
400
K parameter

Figure 7. Flow chart of the Monte Carlo procedure for finding harvest rules that satisfy the stated management objectives. Symbols are defined in the text.

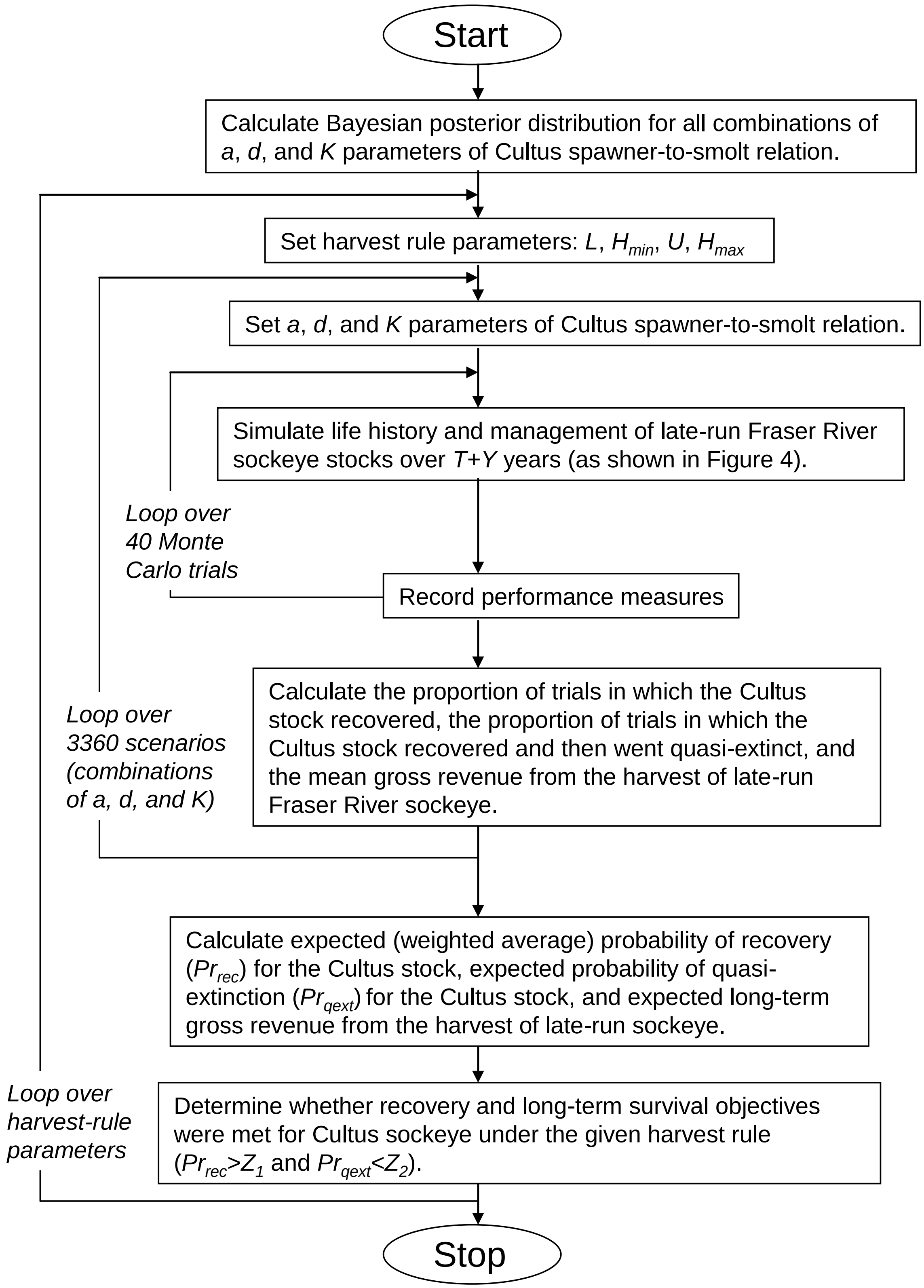

Start
Calculate Bayesian posterior distribution for all combinations of a, d, and K parameters of Cultus spawner-to-smolt relation.
Set harvest rule parameters: L, H_{min}, U, H_{max}
Set a, d, and K parameters of Cultus spawner-to-smolt relation.
Simulate life history and management of late-run Fraser River sockeye stocks over T+Y years (as shown in Figure 4).
Loop over 40 Monte Carlo trials
Record performance measures
Calculate the proportion of trials in which the Cultus stock recovered, the proportion of trials in which the Cultus stock recovered and then went quasi-extinct, and the mean gross revenue from the harvest of late-run Fraser River sockeye.
Loop over 3360 scenarios (combinations of a, d, and K)
Calculate expected (weighted average) probability of recovery (Pr_{rec}) for the Cultus stock, expected probability of quasi-extinction (Pr_{qext}) for the Cultus stock, and expected long-term gross revenue from the harvest of late-run sockeye.
Loop over harvest-rule parameters
Determine whether recovery and long-term survival objectives were met for Cultus sockeye under the given harvest rule ($Pr_{rec}>Z_1$ and $Pr_{qext}<Z_2$).
Stop

Figure 8. Example simulation results of the trajectory of Cultus spawner abundance over time. The lighter line is Cultus spawner abundance. The darker line is the 4-year running average of that abundance, which was used for comparison with management objectives. (A) Case in which the Cultus stock recovers, i.e., the 4-year running average of spawner abundance (*S*) exceeds the recovery threshold of 20,000 (*X*) (horizontal dashed line) by year 20 (*T*) (vertical dashed line). This case used baseline parameters (Table 1); harvest rule parameters were L = 10,000, H_{min} = 0.1, U = 60,000, and H_{max} = 0.75. (B) Case in which the Cultus stock fails to recover by year 20. This case used baseline parameters (Table 1); harvest rule parameters were L = 10,000, H_{min} = 0.1, U = 60,000, and H_{max} = 0.83. (C) Case in which the Cultus stock recovered to a threshold (*X*) of 10,000 before year 20 but then went below a quasi-extinction threshold (*Q*) of 5000 at year 26. Harvest rule parameters were L = 1000, and H_{min} = 0.1, U = 60,000, and H_{max} = 0.94. Panels A, B, and C reflect examples that used, for illustrative purposes only, the best-fit values for parameters of the Cultus spawner-to-smolt relation (Figure 5).

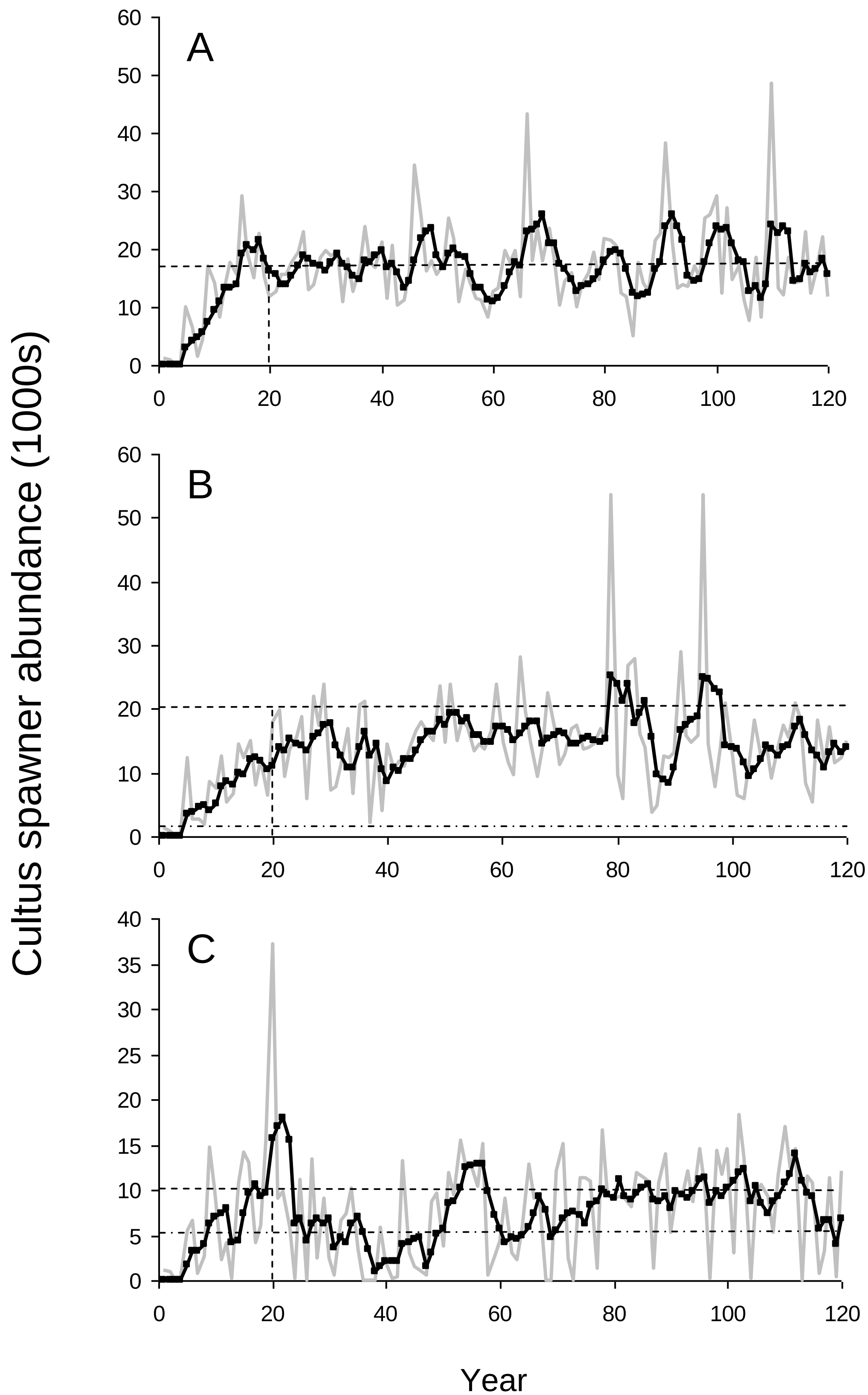
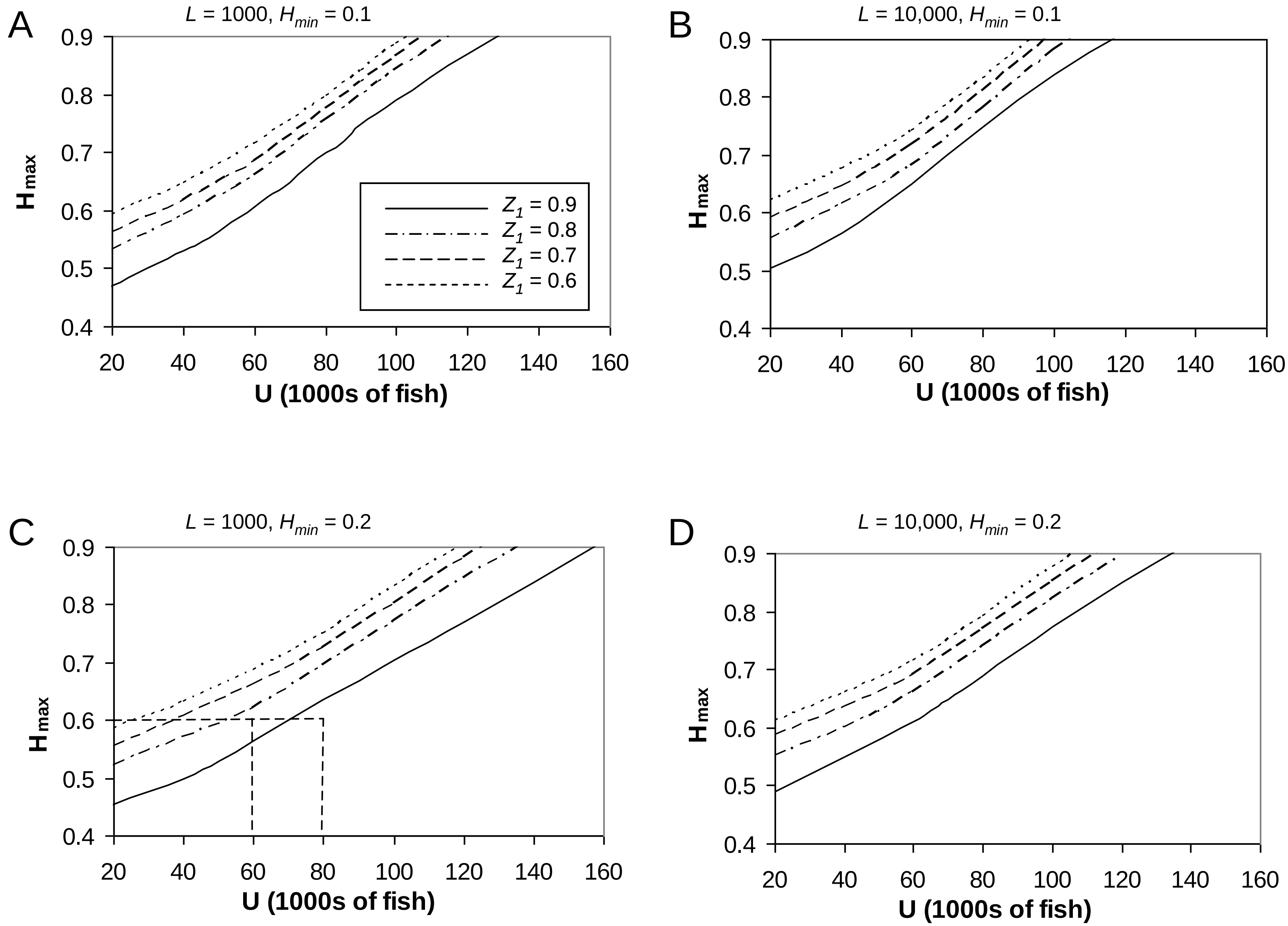
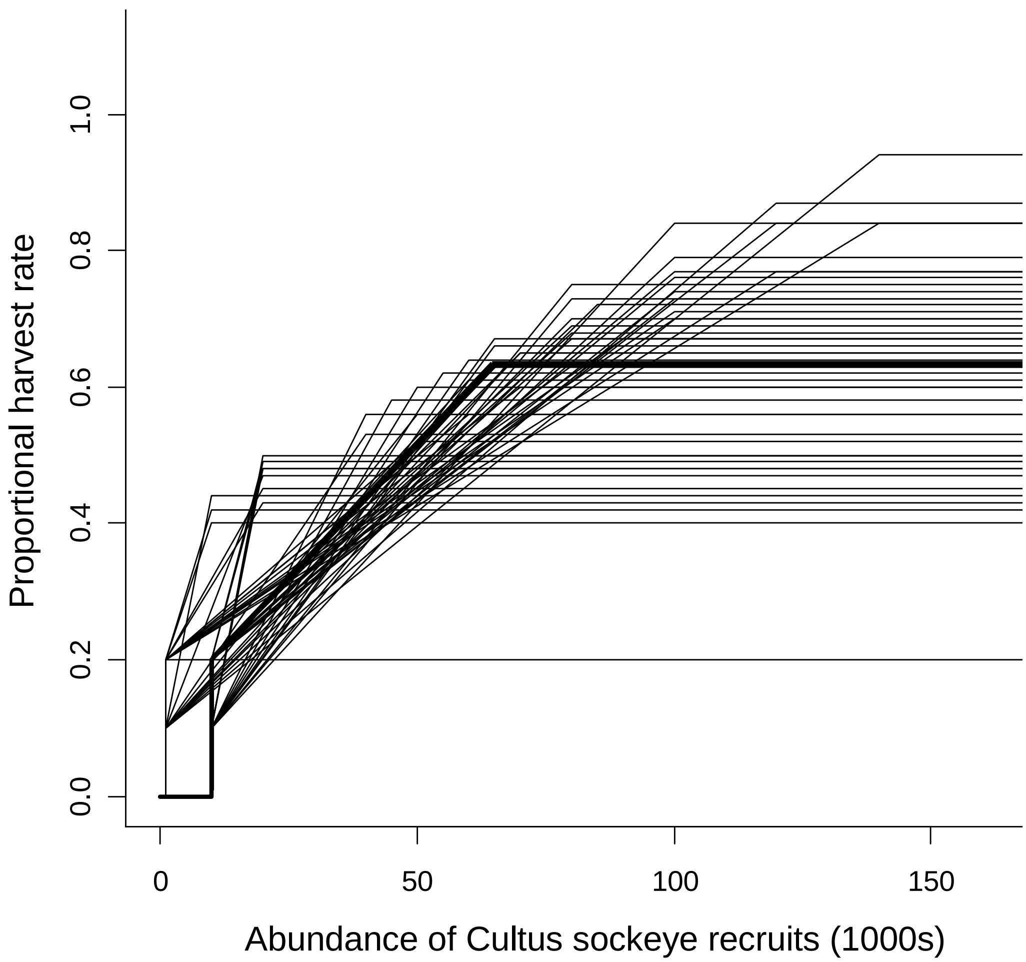

A
B
C
Cultus spawner abundance (1000s)
Year
0
10
20
30
40
50
60
0
5
15
25
35
80
100
120

Figure 9. Isopleths of Pr_{rec}, or estimated probability of recovery for the Cultus stock, compared to Z_1, the desired probability of recovery, for combinations of harvest rule parameters L, H_{min}, U, and H_{max}.



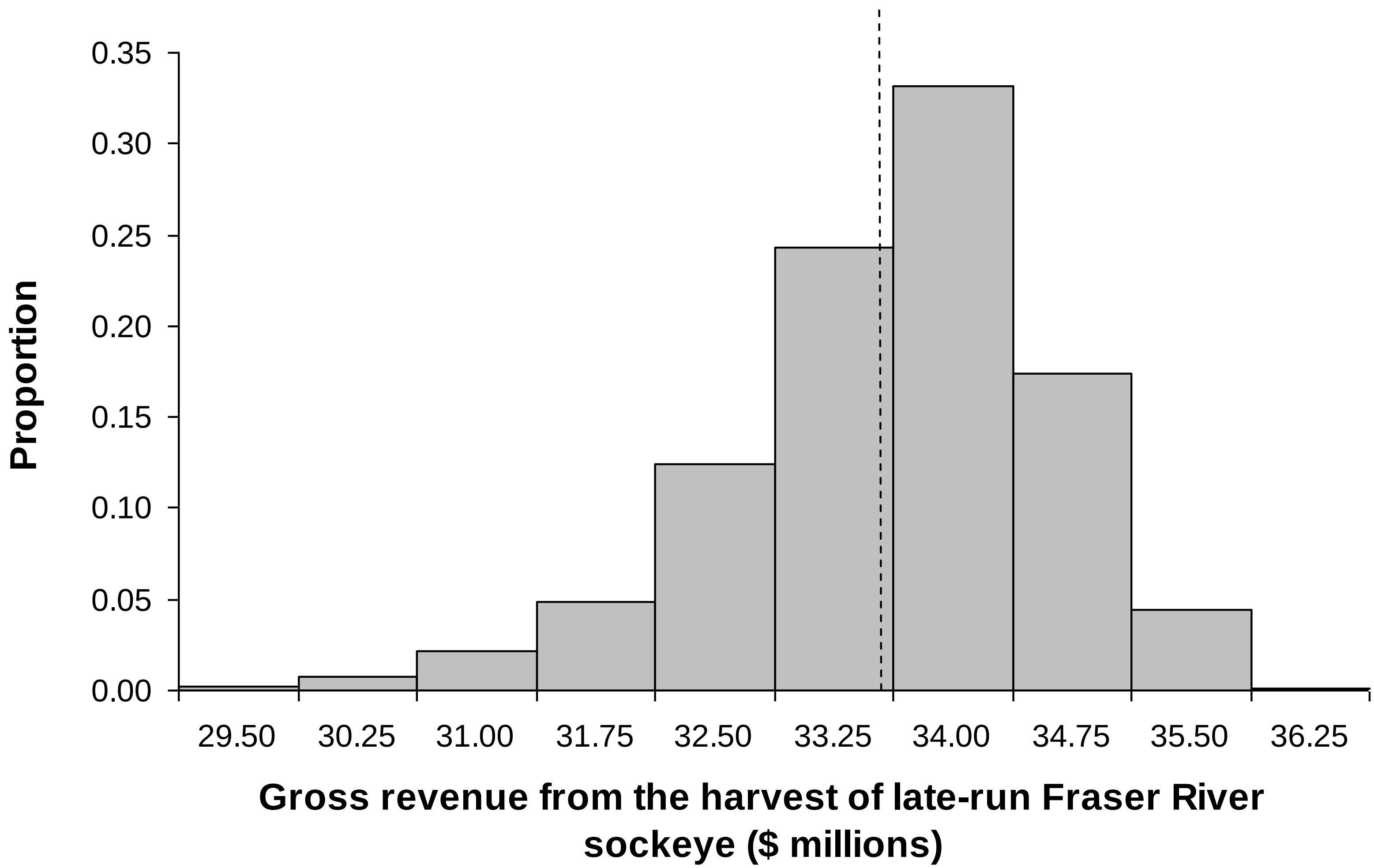
A
L = 1000, Hmin = 0.1
B
L = 10,000, Hmin = 0.1
C
L = 1000, Hmin = 0.2
D
L = 10,000, Hmin = 0.2
Hmax
U (1000s of fish)
0.9
0.8
0.7
0.6
0.5
0.4
20
40
60
80
100
120
140
160
Z1 = 0.9
Z1 = 0.8
Z1 = 0.7
Z1 = 0.6

Figure 10. Shapes of harvest rules that met both the recovery and long-term survival objectives (management objectives 1 and 2) under baseline parameters (Table 1). The boldfaced harvest rule is the highest-ranked harvest rule based on maximizing gross commercial revenue that also achieved Z_1 = 0.9 and is defined by L = 1,000, H_{min} = 0.2, U = 65,000, and H_{max} = 0.63 (rule #43, Table 5).



Proportional harvest rate
0.0
0.2
0.4
0.6
0.8
1.0
0
50
100
150
Abundance of Cultus sockeye recruits (1000s)

Figure 11. Example probability distribution of the expected annual gross revenue from the harvest of late-run Fraser River sockeye (average over 120 years). The distribution is from 134,400 Monte Carlo trials under baseline conditions (Table 1) and a harvest rule where L = 10,000, H_{min} = 0.1, U = 100,000, and H_{max} = 0.93. For economic values not shown on the graph (less than $29.17 million), the cumulative probability is less than 0.01. Labels on the x-axis are the midpoint for each interval. The dashed vertical line represents the expected value of $33.59.



Proportion
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
29.50
30.25
31.00
31.75
32.50
33.25
34.00
34.75
35.50
36.25
Gross revenue from the harvest of late-run Fraser River sockeye ($ millions)

Figure 12. Example probability distribution of year of recovery for the Cultus sockeye stock for the portion of 134,400 Monte Carlo trials in which the stock recovered to a spawner abundance of 20,000 by year 20, based on baseline conditions (Table 1) and a harvest rule where L = 10,000, H_{min} = 0.2, U = 65,000, and H_{max} = 0.63. For years of recovery not shown on the graph (below year nine), the cumulative probability was less than 0.001. The dashed vertical line represents the mean year of recovery, 15.02.

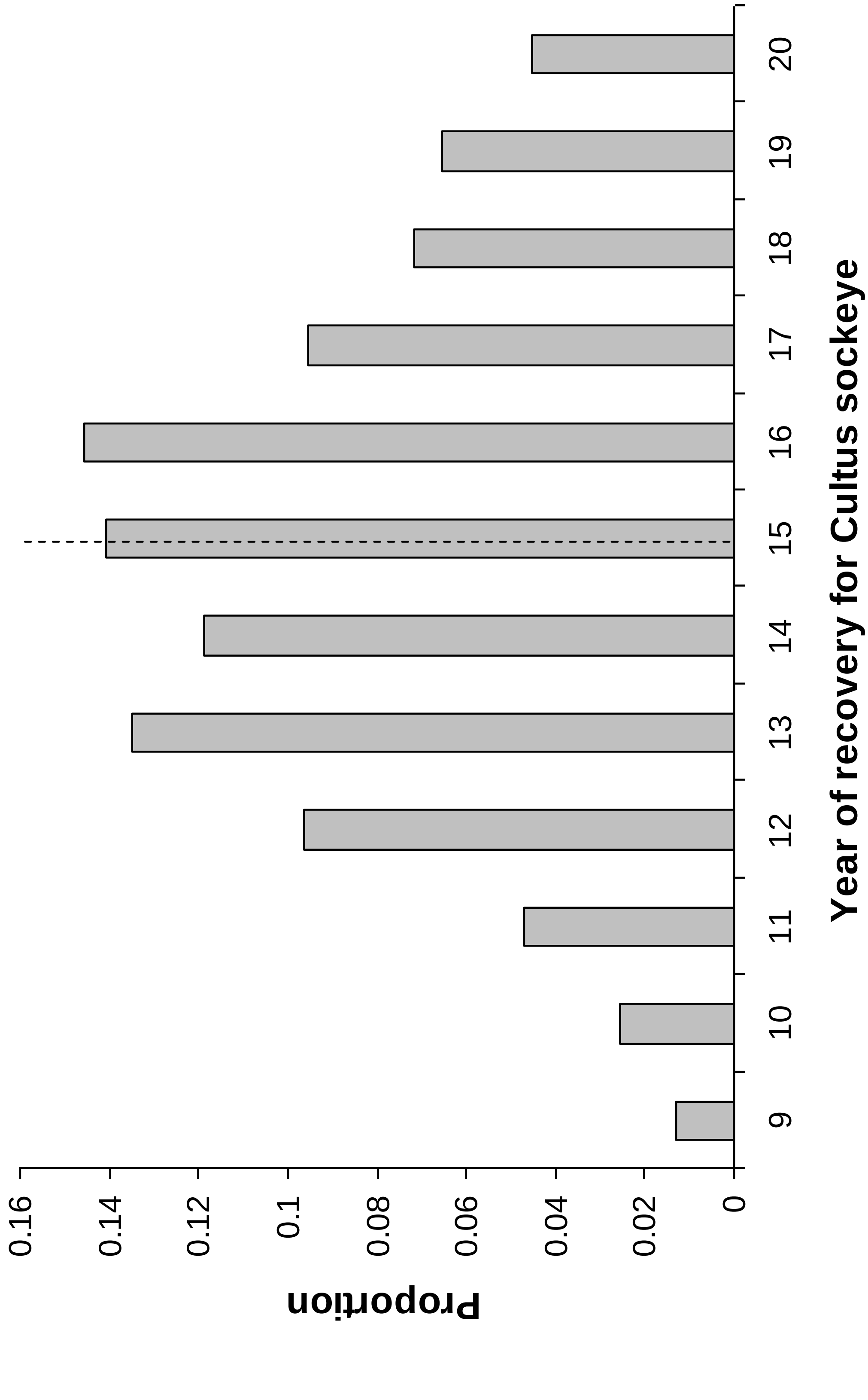
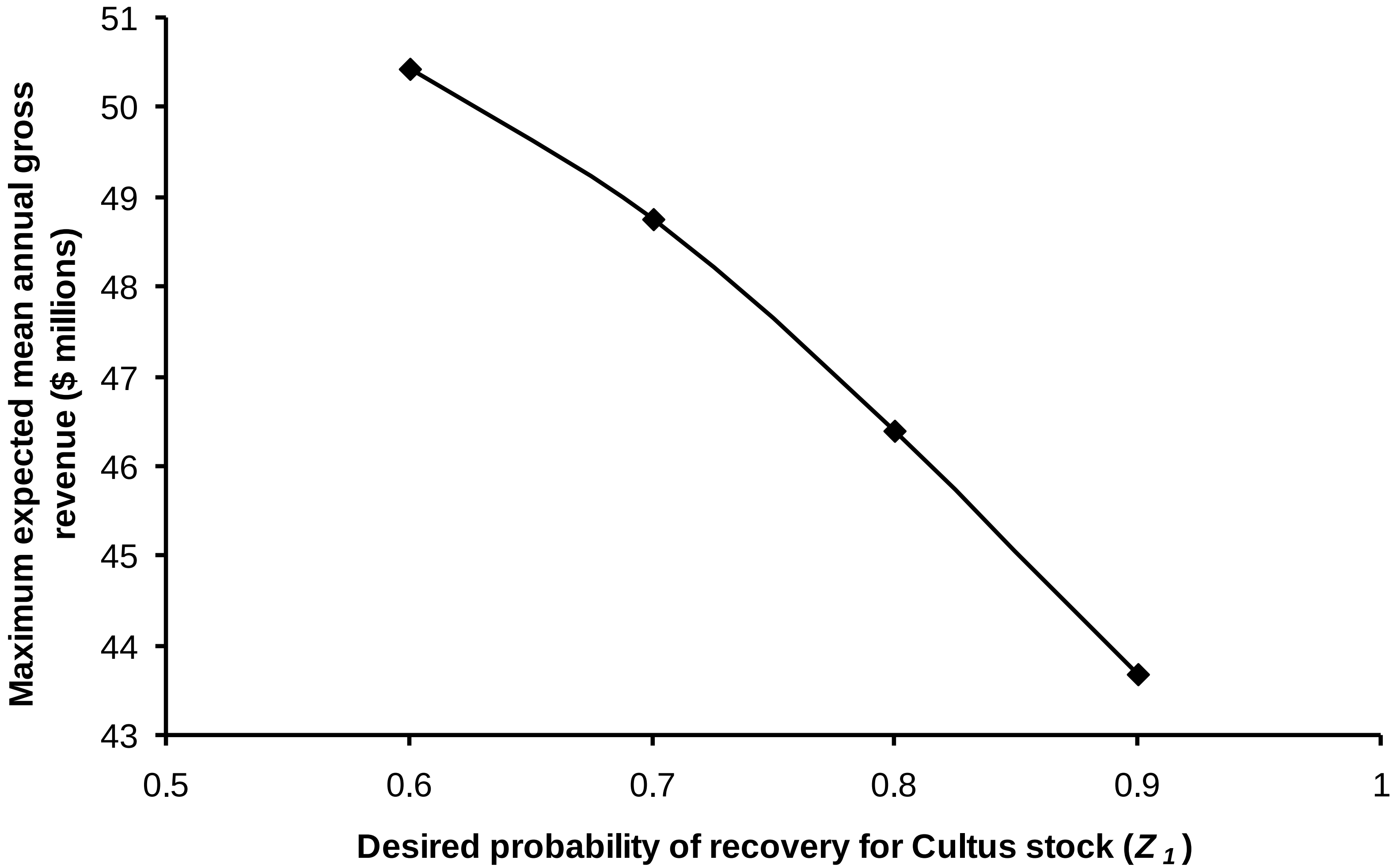
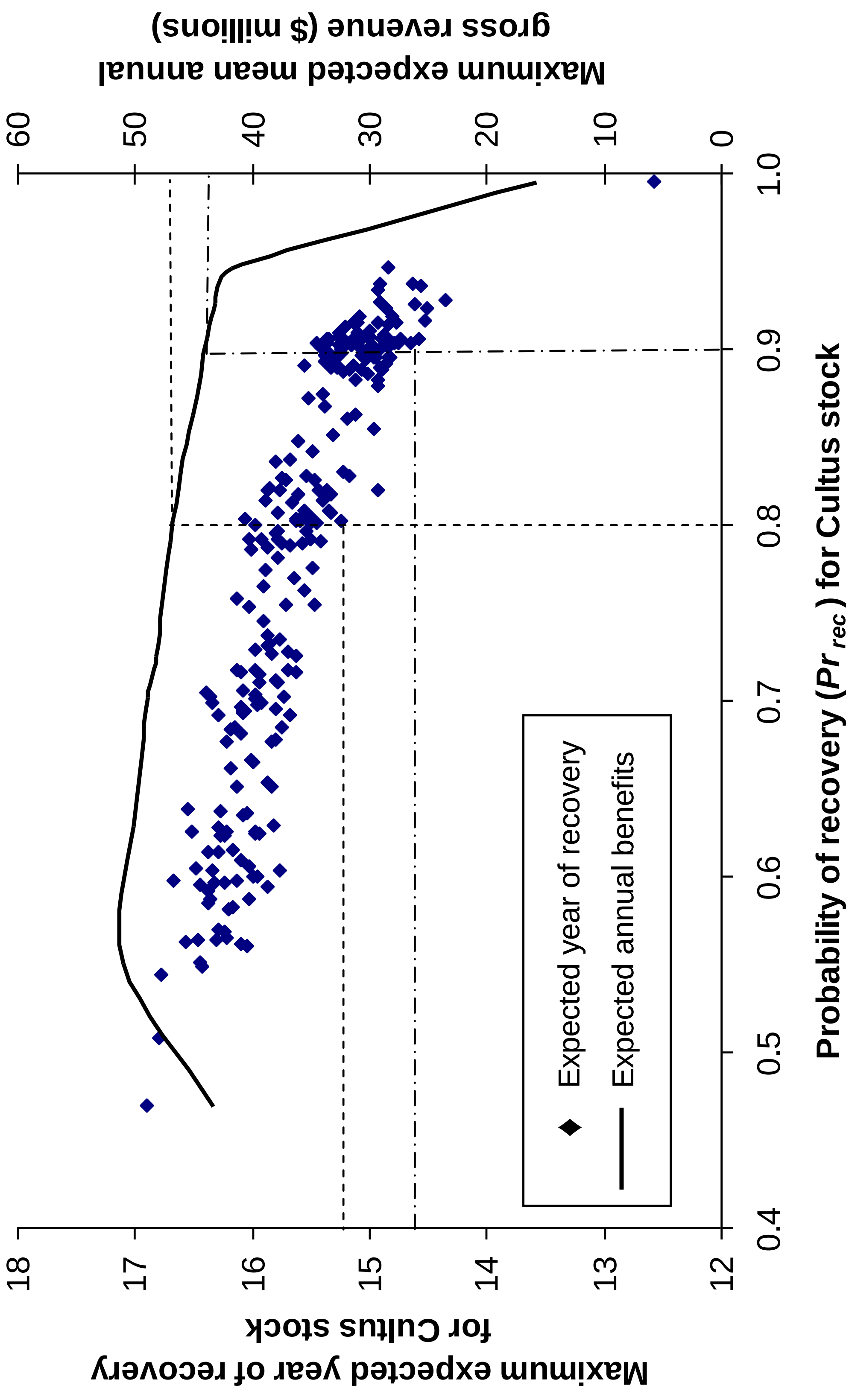

Proportion
0.16
0.14
0.12
0.1
0.08
0.06
0.04
0.02
0
9
10
11
12
13
14
15
16
17
18
19
20
Year of recovery for Cultus sockeye

Figure 13. Expected mean annual gross revenue ($ millions) under the highest-ranked harvest rule (based on expected revenue) from the harvest of late-run Fraser River sockeye over the next 120 years as a function of the desired probability of recovery for the Cultus Lake sockeye salmon stock (Z_1).



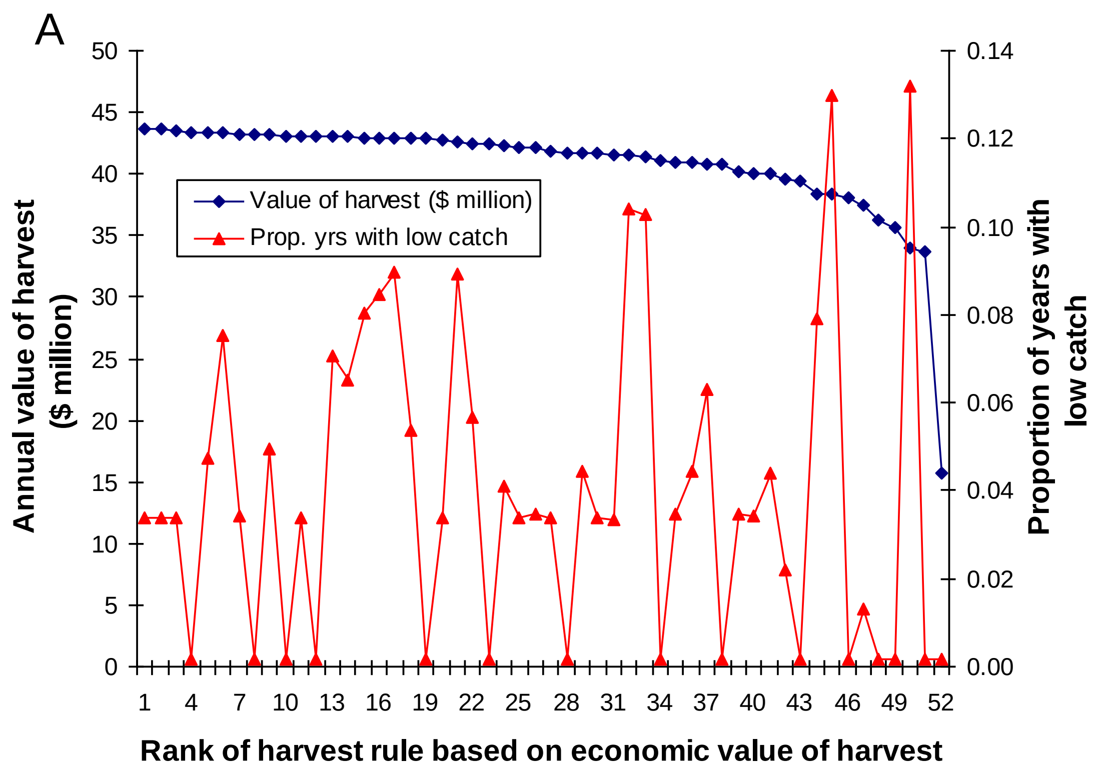
Maximum expected mean annual gross revenue ($ millions)
51
50
49
48
47
46
45
44
43
0.5
0.6
0.7
0.8
0.9
1
Desired probability of recovery for Cultus stock (Z 1)

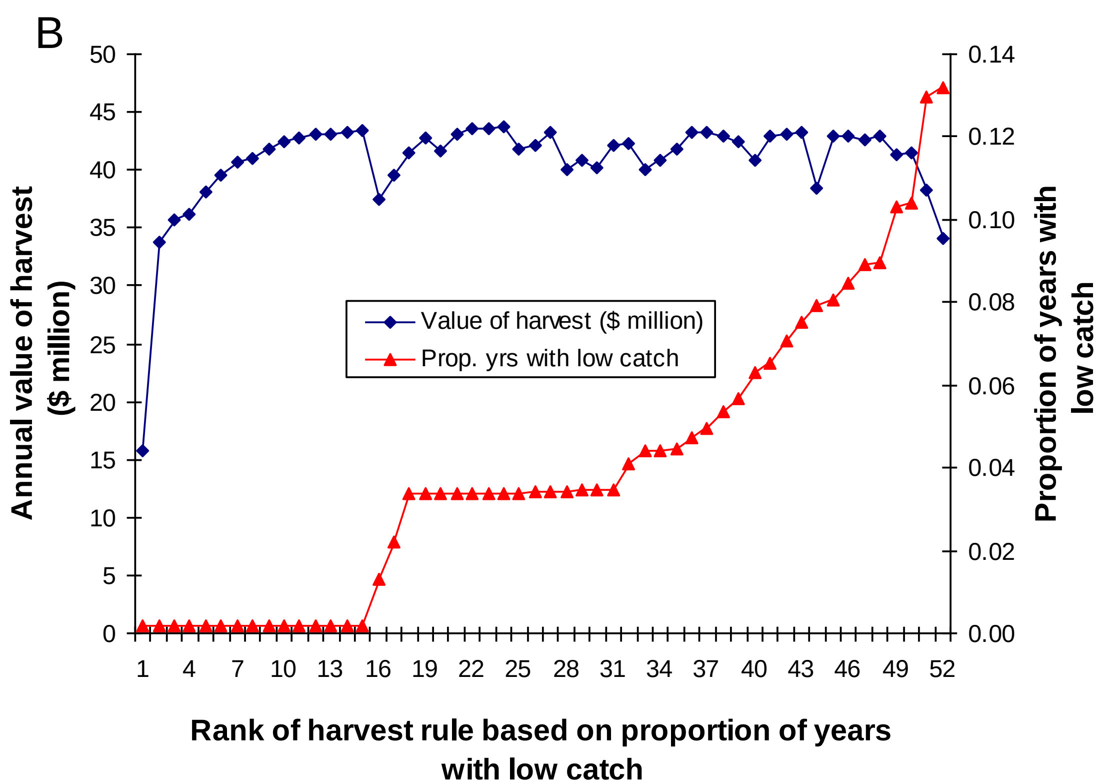
Figure 14. Expected year of recovery for the Cultus sockeye stock and expected mean annual gross revenue ($ millions) from the harvest of the late-run Fraser River sockeye as a function of probability of recovery (Pr_{rec}) for the Cultus stock. Points on the graph represent expected year of recovery, and the solid line represents the expected mean annual gross revenue for a given probability of recovery, as defined in Figure 13. The vertical and horizontal lines intersect to show the expected mean gross revenue and the earliest expected year of recovery for probabilities of recovery equal to 0.8 and 0.9.



Maximum expected mean annual gross revenue ($ millions)
60
50
40
30
20
10
0
Maximum expected year of recovery for Cultus stock
18
17
16
15
14
13
12
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Probability of recovery (Pr_{rec}) for Cultus stock
Expected year of recovery
Expected annual benefits

Figure 15. Expected mean annual gross revenue from the catch ($ millions) and the expected proportion of years with little or no catch (proportional harvest rate ≤ 0.2) for the 52 harvest rules that met the baseline conservation management objectives (Z_1 = 0.9 and Z_2 = 0.05). (A) Harvest rules ranked from left to right based on gross revenue. (B) Harvest rules ranked from left to right based on proportion of years with little or no catch.


A
Value of harvest ($ million)
Prop. yrs with low catch
Annual value of harvest ($ million)
Proportion of years with low catch
Rank of harvest rule based on economic value of harvest


B
Value of harvest ($ million)
Prop. yrs with low catch
Annual value of harvest ($ million)
Proportion of years with low catch
Rank of harvest rule based on proportion of years with low catch

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Appendices

Appendix 1. Bayesian estimation of the Cultus sockeye spawner-to-smolt relation

I generated a Bayesian joint posterior probability distribution for the parameters *a*, *d*, and *K* of the Cultus sockeye spawner-to-smolt relation (eq. 2). A uniform prior probability was specified for each hypothesized parameter value, with bounds illustrated in Figure 6. I calculated the likelihood of spawner-to-smolt data for each of 3360 hypothesized combinations of *a*, *d*, and *K* parameters. The likelihood function for a normal distribution was used for each observed data point for a given hypothesized parameter combination:

(A1) $L_t(\text{data point}_t|a_i, d_i, k_i) = [1/(\sigma(2\pi)^{1/2})]\exp[-(\log_e Sm_o - \log_e Sm_p)^2/2\sigma^2]$

where *t* is brood year, *i* is one combination of hypothesized parameter values *a*, *d*, and *K*, (where $i = 1$ to 3360) and Sm_o and Sm_p are observed and predicted smolt abundance, respectively. The posterior probability for each parameter combination, *i*, was calculated in the usual manner with Bayes' formula (Gelman et al. 2004).

The bounds on the uniform priors were determined through a sensitivity analysis examining the effect of the bounds on the marginal posterior probabilities for the *a*, *d*, and *K* parameters. I initially chose the ranges of the prior distributions based on ±3 standard errors (SE) of the best-fit values for parameters of the Cultus spawner-to-smolt relation that resulted from a least squares regression. The bounds were then adjusted if the resulting marginal posterior distribution appeared truncated or trailed off extensively at low probability. The marginal posterior distribution for the *K* parameter is extremely asymmetrical and so the prior was terminated at 300. At higher *K* values the resulting Cultus spawner-to-smolt relation became illogical and unlikely.

Appendix 2. Gross commercial revenue

To estimate an indicator of the economic value of future late-run Fraser River sockeye harvests, I calculated the average commercial dollar-value per fish, which represents the gross commercial revenue from harvest. In these future projections of economic value, I have not used a discount rate or accounted for costs associated with the harvest, because I was only interested in the relative merits of alternative harvest rules, not the actual dollar benefits. Furthermore, little is know about future discount rates and costs associated with harvesting and processing or technological advances that may occur. I also did not consider social costs and benefits in this model because these are difficult to quantify and beyond the scope of this study.

Using data from Table A1, the mean length of fish is 56.25 cm. Post-orbital-fork (POF) length was converted to weight using the following equation (Steve Latham, Pacific Salmon Commission, Vancouver, B.C., personal communication):

(A2) $WGT = (0.1613 \times POF) - 5.9358$

where WGT is weight in kg and r^2=0.83.

Using this equation, the mean weight per fish came to 3.14 kg.

Using data in Table A2, the mean processed price per kg round was $6.96. Using the mean price per kg and mean weight per fish, the mean gross revenue per fish came to $21.83.

In this analysis I assumed that all sockeye caught are worth the same commercial processed price, whether they were caught in commercial, aboriginal, or other fisheries. I made this assumption because there is little information about how catch will be divided between First Nations and commercial fisheries in the future. Further, there is no accurate estimate of the value of fish to First Nations, because the market price only counts food value and not social or ceremonial value.

Table A1. Mean post-orbital-fork (POF) length (cm) of fish caught in Gulf troll test fisheries in late August and September (S. Latham, personal communication).

Year	Sample size	Mean POF length of fish in catch (cm)
2000	62	56.07
2001	42	56.34
2002	3687	57.23
2003	300	55.36

Table A2. Assumed gross commercial revenue as processed price per kg round (GSGislason & Associates, Ltd. 2004).

Area	$ price/kg round processed value	Proportion of catch
Seine area B	$7.00	0.40
Gillnet area D	$7.00	0.15
Gillnet area E	$6.60	0.30
Troll area H	$7.53	0.15