AN EVALUATION OF PREDATOR CONTROL AND HATCHERY OPERATIONS AS MANAGEMENT ACTIONS TO ASSIST WITH RECOVERY OF THE ENDANGERED CULTUS LAKE SOCKEYE SALMON

by

Jeff Amos
BSc. Trent University 2002

PROJECT SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIRMENTS FOR THE DEGREE OF

MASTER OF RESOURCE MANAGEMENT

In the
School of Resource and Environmental Management

Project No. 447

SIMON FRASER UNIVERSITY
Spring 2008

APPROVAL

Name:	Jeff Amos
Degree:	Master of Resource management
Title of Research Project:	An evaluation of predator control and hatchery operations as management actions to assist with the recovery of the endangered Cultus Lake sockeye salmon
Project Number:	447

Supervisory Committee:

Chair: Garret Cooper

____

Dr. Randall Peterman
Senior Supervisor
Professor, School of Resource and Environmental Management
Simon Fraser University

____

Dr. Michael Bradford
Supervisor
Adjunct Professor, School of Resource and Environmental Management
Simon Fraser University

Date Defended/Approved ______________________________

ABSTRACT

The Cultus lake sockeye salmon (*Oncorhynchus nerka*) population has declined dramatically over the past few decades, and was classified as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2003. There are currently three major initiatives underway for assisting the recovery of this population (harvest management, predator control, and hatchery operations). I use a stochastic simulation model within a decision analysis framework to evaluate management strategies associated with these three initiatives. I estimate the probability of meeting pre-specified survival and recovery objectives for four alternative management strategies. My results suggest that the probability of recovery for Cultus Lake sockeye salmon is low under current marine survival rates. I also describe trade-offs between probability of achieving the conservation objectives and reductions in the commercial sockeye salmon fishery to help evaluate the relative merits of these initiatives.

Keywords: recovery planning, predator control, hatchery supplementation, decision analysis

Subject Terms: conservation biology, simulation modelling, predator-prey dynamics, decision analysis

ACKNOWLEDGEMENTS

I thank my supervisory committee, Randall Peterman and Michael Bradford, for their encouragement, advice, and patience during the completion of this work. I would also like to thank members of the fisheries research group at Simon Fraser University for providing a stimulating learning environment during the past three years. I thank the staff at the Cultus Lake salmon Research Laboratory who introduced me to the world of sockeye salmon research and motivated me to complete this project. Special thanks to Jeremy Hume for providing data and whose comments on an earlier version of this paper were helpful. Finally, thanks to Rachelle Lalonde for her encouragement and support when it was most helpful. Funding for this research was provided by an NSERC operating grant awarded to Randall Peterman.

TABLE OF CONTENTS

Approval ii

Abstract iii

Acknowledgements iv

Table of Contents v

List of Figures vi

List of Tables viii

1.0 Introduction 1

- 1.1 A brief history of Cultus Lake 7

2.0 Methods 12

- 2.1 Overview 12
- 2.2 Management Objectives 14
- 2.3 Alternative Management Strategies 15
- 2.4 Uncertainties to be resolved 19
- 2.5 Model to determine consequences 20
  - 2.5.1 Model Initialization 20
  - 2.5.2 Sockeye sub-model 20
  - 2.5.3 Northern pikeminnow sub-model 31
- 2.6 Performance measures 35
- 2.7 Sensitivity Analysis 37

3.0 RESULTS 38

- 3.1 Survival Objective 38
- 3.2 Recovery Objective 40
- 3.3 Harvest Objective 40
- 3.4 Sensitivity Analysis 41

4.0 DISCUSSION 49

- 4.1 Management Implications 51
  - 4.1.1 Predator control 51
  - 4.1.2 Hatchery operations 54

Literature Cited 58

LIST OF FIGURES

Figure 1 Cultus lake sockeye escapement and harvest rate estimates (1925- 2005). Low harvest rates after 1997 are in response to conservation concerns and reduction in fishing fleet size. 4

Figure 2 Decision tree illustrating alternative management actions, uncertain states of nature, and outcomes in this study. Expected probabilities of meeting each management objective are calculated for each of the four alternative management actions (see text). 13

Figure 3 (A) Cultus sockeye smolt and spawner data for years that were not likely affected by either predator control efforts, hatchery operations, or high pre-spawning mortality (solid circles). Years that followed predator control are indicated by open circles. (B) Log_e(Sm/Sp) for standard Ricker model (k = 0) and the two alternative models used in this study. (C) Resulting spawner-to-smolt relationships from assuming low *k* (low consumption rate of sockeye smolts per pikeminnow) at three different northern pikeminnow abundances. (D) Spawner-to-smolt relationships assuming high *k* (high consumption rate of sockeye smolts per pikeminnow) at three different northern pikeminnow abundances. 21

Figure 4 Frequency distributions of marine survival rates for observed Cultus Lake sockeye data (A) and Beta distribution used in Monte Carlo trials for generating annual marine survival rate (B). Bars represent a sample frequency distribution of simulated values with parameters estimated from the historical data; lines represent alternative distributions. 22

Figure 5 Harvest rules used to prescribe annual harvest rate (HR_t) in any given year for Cultus Lake sockeye based on the number of Cultus sockeye adults estimated to be returning. Bottom line (Rule 1) is the base rule; top line (Rule 2) is used in sensitivity analyses. 24

Figure 6 Length-at-age, weight-at-age, and catchability-at-age models (lines) fit to data (circles) and used to simulate the northern pikeminnow population (see text). Parameter values are given in Table 1. 33

Figure 7 Simulated northern pikeminnow abundance under alternative levels of control, with (A) low recruitment compensation, and (B) high recruitment compensation. Notice that all four trajectories begin with the same abundance up to 2007, which represents predator control efforts to date. 36

Figure 8 Simulation results based on Harvest rule 1 (H_{min} = 0.12, H_{max} = 0.50). Top panel shows survival (mean spawners/year ≥ 1000) and recovery (mean spawners/year ≥ 8000) probabilities for four alternative management strategies (A = status quo hatchery operations combined with terminated predator control; B = status quo hatchery operations combined with continued predator control; C = extended hatchery operations combined with terminated predator control; D = extended hatchery operations combined with continued predator control), at four alternative mean marine survival rates (MMS). Bottom panel shows the proportion of simulated years where the harvest rate was set at H_{min} as a result of low Cultus Lake sockeye abundance. Error bars represent two standard deviations. 39

Figure 9 Same as Figure 8 except results are based on using harvest rule 2 (H_{min} = 0.30, H_{max} = 0.60) as opposed to harvest rule 1. 42

Figure 10 Prescription tables showing which management strategies (A-D) meet the survival (left) and recovery (right) objectives with at least 90% probability across a range of mean marine survival rates and different degrees of belief for the RHMS of sockeye. Moving down each column mean that greater belief (from 10% to 90%) is placed on high RHMS (0.8) as the true state of nature, rather than RHMS being only 0.2. These results are based on using harvest rule 1 (H_{min}=0.12, H_{max}=0.5). 45

Figure 11 Same as Figure 10 except results are based on using harvest rule 2 (H_{min} = 0.30, H_{max} = 0.60) as opposed to harvest rule 1. 46

Figure 12 Prescription tables showing which management strategies meet the survival (left) and recovery (right) objectives with at least 90% probability across a range of mean marine survival rates and different degrees of belief for the impact of Northern pikeminnow on the sockeye Sm/Sp relationship. Moving down each column means that greater belief (from 10% to 90%) is placed on the high *k* value (15×10^{-06}) as the true state of nature. These results are based on using harvest rule 1 (H_{min} = 0.12, H_{max} = 0.50). 47

Figure 13 Same as Figure 12 except results are based on using harvest rule 2 (H_{min} = 0.30, H_{max} = 0.60) as opposed to harvest rule 1. 48

LIST OF TABLES

Table 1 Description of parameters used in the simulation model and definition of scenarios and terms. 17

1.0 INTRODUCTION

Management means making choices, but making choices when there is considerable uncertainty and/or conflicting objectives is not an easy task. Making the correct choice involves making reliable forecasts about what will happen in the future as a result of a decision, and deciding what future outcomes are preferred (Walters and Martel 2004). Often in resource management, objectives are not explicitly stated and this, combined with our inability to precisely forecast what will happen in the future, makes decision making difficult. For the management of species at risk, these problems become especially difficult, where deciding among management strategies is a key component of species recovery programs. These actions often have economic and social implications such as restrictions on human activities.

At Cultus Lake, British Columbia, there is a high probability of extinction for a unique population of sockeye salmon (*Oncorhynchus nerka*) (Cultus Sockeye Recovery Team 2004). Thus, urgent but difficult management decisions need to be made to rebuild this population, despite considerable uncertainty. Furthermore, there are budgetary constraints and socially acceptable limits (i.e., severity of harvest reductions) that bound the potential recovery options. Reductions in the catch of Cultus Lake sockeye salmon (hereafter referred to as Cultus sockeye) requires a reduction in fishing effort targeting other, much more productive and abundant sockeye populations that migrate through the fishery at the same time as Cultus sockeye. Closure or reductions in these fisheries would reduce impacts on Cultus sockeye, but would also reduce catches for the more abundant sockeye populations, resulting in social and economic impacts (Irvine et al. 2005, GSGislason & Associates Ltd. 2004, Gross et al. 2004, Pestes et al. 2008).

For work on species at risk, the decision-making process can be assisted by the combined use of population viability analysis (PVA) and decision analysis (DA). These techniques have been recognized as useful partners and are methods that have been widely accepted and used in conservation biology (Drechsler 2000, Harwood 2000, Drechsler and Burgman 2004, Peters et al. 2001, VanderWerf et al. 2006). PVA involves constructing models that are used to assess the persistence of populations. PVA was initially developed to estimate long-term extinction probabilities in small populations while taking into account genetic, demographic, and environmental stochasticity (Shaffer 1981). DA is a framework used to synthesize expert knowledge and assist in the decision making process. One common use of DA methodology is to determine the rank order, from best to worst, of management actions based on forecasted outcomes and specified management objectives. The main benefit of using DA is that it provides a transparent protocol for assessing and comparing management options while explicitly taking various sources of uncertainty into account.

Currently there are three main management strategies that are being used to aid recovery of the Cultus sockeye population. These are reducing harvest rates, reducing predator abundance, and supplementing the population with hatchery releases. Unfortunately, the benefits from reductions in harvest rates since 1998 have been reduced by higher-than-normal pre-spawning mortality (PSM), and more recently by lower-than-average marine survival (Ann-Marie Huang, Fisheries and Oceans Canada, Delta, B.C., personal communication). The reduction in commercial fishery harvest rates on the adult Cultus sockeye population in recent years is substantial (Figure 1) and undoubtedly this will help in population recovery. However, this carries a considerable cost in foregone harvest of other, more abundant and commercially valuable, co-migrating sockeye populations.

A current predator control program targets adult northern pikeminnow *(Ptychocheilus oregonensis),* a large piscivorous cyprinid native to Cultus Lake (Bradford et. al. 2007). Northern pikeminnow control programs have previously been shown to increase freshwater survival of juvenile sockeye at Cultus Lake (Foerster and Ricker 1941) and other salmonids in the Columbia River system (Friesen and Ward 1999). However, in both of these cases, increases in freshwater survival of salmon occurred at times when juvenile salmon abundance was high. The benefits at low abundances (as is the current situation at Cultus Lake) are uncertain. It is unclear whether removals of northern pikeminnow will cause a concurrent increase in sockeye freshwater survival for two main reasons. First, there is no practical way to directly measure northern pikeminnow predation rates on juvenile sockeye, so it is unclear whether pikeminnow predation is even a limiting factor at such low sockeye abundances. Second, there is a large amount of uncertainty about the potential for a compensatory

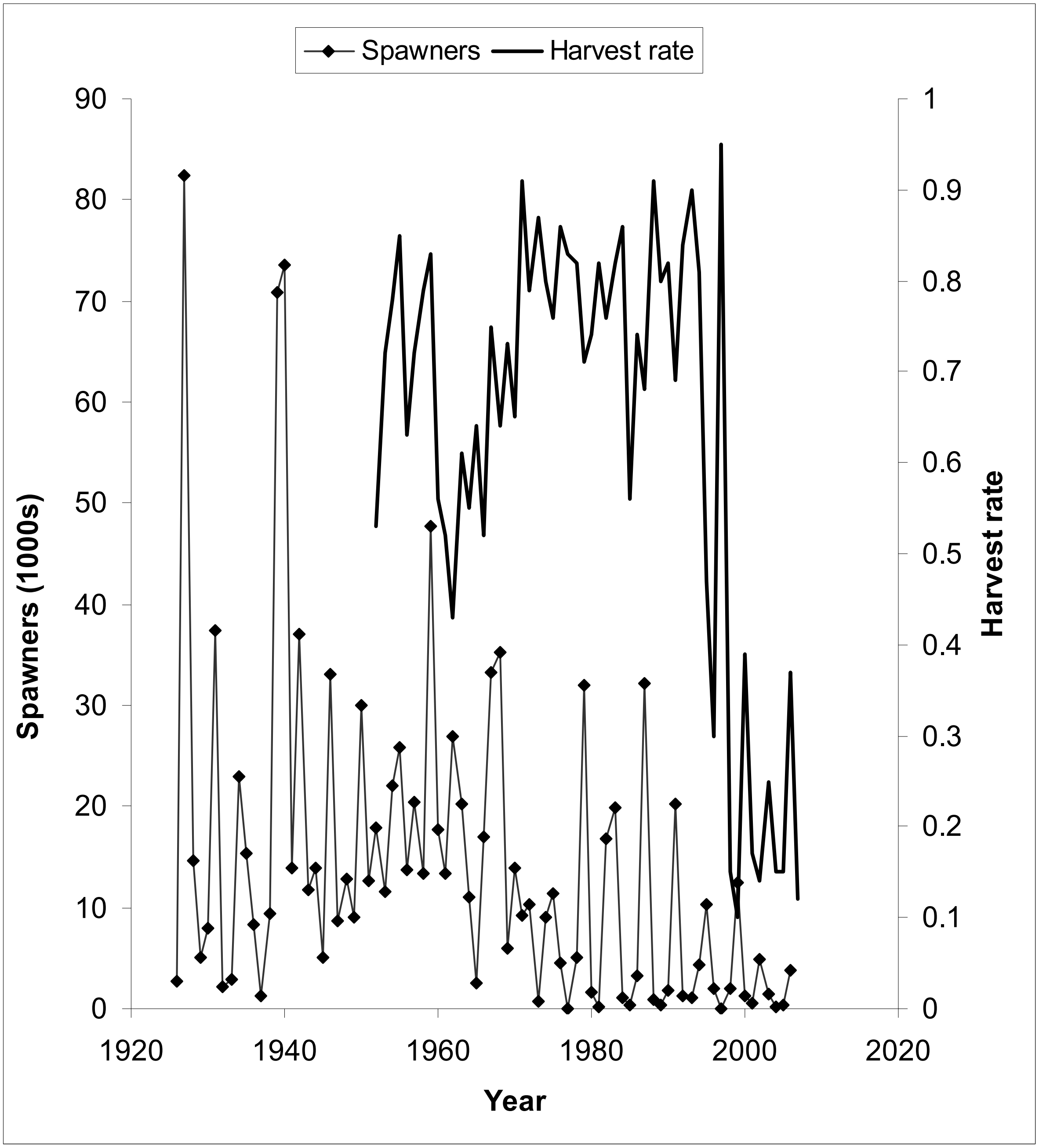

Figure 1 **Cultus lake sockeye escapement and harvest rate estimates (1925- 2005). Low harvest rates after 1997 are in response to conservation concerns and reduction in fishing fleet size.**

response in the predator population (i.e., the ability to quickly rebuild abundance). In the Columbia River system, compensation in the pikeminnow population is considered unlikely, because the pikeminnow removal program exploits a small (12%) proportion of the total population (Beamesderfer et al. 1996). During the past two summers (2006 and 2007), the Cultus Lake northern pikeminnow removal program captured over 30,000 adult northern pikeminnow, a catch representing nearly 50% of the estimated 2004 adult abundance (C. Tovey, Fisheries and Oceans Canada, Cultus lake, B.C., personal communication).

Hatchery operations, which are already underway at Cultus Lake for sockeye, include a captive broodstock program and a supplementation program. Captive broodstock is the maintenance of selected individuals in a hatchery environment for their entire life in order to establish a captive population parallel to the natural population. Supplementation is the release of hatchery-raised fry and smolts into the natural environment. At Cultus Lake, the released fish are derived from genetic contributions of both wild fish and hatchery maintained broodstock. The potential benefits and losses associated with captive broodstock and supplementation programs are widely debated and uncertain (Waples and Drake 2004, Utter 1998, Waples and Do 1994). The main concerns relate to inbreeding depression and unintentional artificial selection that may reduce fitness in the wild. Recent studies have shown large declines in fitness and relative reproductive success in Pacific salmon as a function of number of generations in captivity (Ford et al. 2005, Araki et al. 2007).

A key question that managers are facing is “What management strategy will provide a reasonably high probability of population recovery but will also allow for a socially acceptable level of harvest?” Population recovery planning can be assisted by a quantitative evaluation of the relative merits of predator control and hatchery operations, such as I report here, to ensure that limited resources for operating the programs are used most efficiently. It is also useful to explore alternative sockeye harvest rates and quantify the potential contribution towards population recovery these can make, as overexploitation has been the major contributing factor to the population decline (COSEWIC 2003).

My goal was to rank alternative management strategies for achieving recovery of the endangered Cultus sockeye population. I used decision analysis to evaluate those strategies by forecasting outcomes resulting from each action or combination of actions. I evaluated alternative levels of predator control and hatchery operations by combining PVA and DA. The DA explicitly accounted for several uncertainties and quantified indicators of management objectives. This approach also helped to quantify tradeoffs (probability of recovery vs. number of years with low harvest rates) that are considered by managers when making decisions about recovery planning.

An analysis of management actions for rebuilding Cultus sockeye has been conducted by Pestes et al. (2008). My evaluation is similar to that one in that both studies evaluate alternative levels of harvest as a management action, and both explicitly account for uncertainties in both the spawner-to-smolt relationship and marine survival rates. However, my analysis differs from Pestes et al. (2008) in several ways. First, I evaluated three different recovery activities (predator control, hatchery operations, and alternative harvest rates), whereas Pestes et al. (2008) only evaluated different harvest rates as a recovery action. Second, they explicitly included uncertainty in the implementation of harvest rates and uncertainty in prespawning mortality (PSM) of Cultus sockeye, whereas I did not. Instead, I explicitly included uncertainty in predator/prey dynamics and in marine survival of hatchery fish.

1.1 A brief history of Cultus Lake

Cultus Lake is small, with a surface area of 6.3 km^2 and a mean depth of 31 m. Only 6% of the lake area is considered littoral (Schubert et al. 2002). The lake is drained by Sweltzer Creek, which flows approximately 3 km north to the Chilliwack/Vedder River, which in turn flows 20 km northwest to the Fraser River, entering approximately 100 km from the Pacific Ocean. There is a long history of salmon research at Cultus Lake with a research facility currently located near the lake outlet and a salmon counting fence on Sweltzer Creek. Past research on Cultus Lake has included spawner counts since 1925, smolt counts intermittently since 1926, and fishery catch statistics since 1952. This represents the longest running data set of any Fraser River salmon.

The Cultus sockeye population is unique among Fraser River sockeye populations. They are a locally adapted population with unusual spawning characteristics; they spawn in the lake as opposed to the river and they have the latest (from late November through December) spawning time of all the Fraser sockeye populations (COSEWIC 2003).

The long-standing role of Cultus sockeye salmon as a subject of scientific study means that the population has special interest for naturalists and for the scientific community. The population is also important to First Nations, especially the Soowahlie Band of the Sto:lo Nation. Historic colonization of the area by humans was strongly influenced by the presence of sockeye in the lake and Sweltzer Creek (Schubert et al. 2002).

In 1925, R.E. Foerster and W.E. Ricker began a program at Cultus Lake to help understand the factors limiting the production of sockeye salmon. They found that the losses of juvenile salmon in the lake (egg-to-smolt stage) amounted to over 95% of each brood, and hypothesized that these losses were largely due to predation. Consequently, they subjected the Cultus sockeye salmon population to two large-scale manipulations over the next 15 years. The first was the use of a hatchery to evaluate the potential benefits of artificial production, and the second was a predator removal program targeting the large piscivorous fish inhabiting the lake (Foerster and Ricker 1941).

Although the hatchery efforts were not considered worthwhile and were terminated after a few years, the predator control program continued. Between 1932 and 1942 nearly 22,000 northern pikeminnow and over 7,000 trout (*Oncorhynchus mykiss*, *O. clarki*) and char (*Salvelinus confluentus*) were removed from the lake. Increased returns of sockeye salmon from the experiment were strong enough for Foerster and Ricker to consider the approach a cost-effective means to increase salmon abundance. The result of this program was an increase in average egg-to-smolt survival rate of sockeye from 3.13% for the 8-year period prior to predator removal to 9.95% for the 3-year period after predator removal (Foerster and Ricker 1941). It was estimated that the cost of predator control amounted to 20 cents for each additional returning adult, which was worth $6 in the commercial fishery at the time (Foerster and Ricker 1941).

The number of Cultus sockeye salmon that have returned to spawn has steadily declined since the 1960’s (Figure 1), and has resulted in the current spawner population being less than 4% of the long-term average (Schubert et al. 2002). On October 25th, 2002 the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) conducted an emergency assessment and listed Cultus sockeye as endangered, and this assessment was confirmed in 2003. An endangered designation means that a species faces imminent extirpation or extinction (COSEWIC 2003). In response to the trend in abundance and in anticipation of the species being listed under the Species at Risk Act (SARA), a Cultus Lake Recovery Team was formed in early 2002. The role of the Recovery Team was to document the status of this population and to develop a recovery plan.

Three principal causes for the decline in Cultus sockeye were identified in both the COSEWIC report and in the National Recovery Strategy (Cultus Lake Recovery Team 2004). The first was high harvest rates, which frequently exceeded 80% from the late 1960s to the mid-1990s (Figure 1); second was low recruitment rates associated with poor marine survival from 1991 to 1996; third was the high pre-spawning mortality that occurred during 1995 to 2001 (Schubert et al. 2002). In addition to the above threats, the two reports recognized that there was likely an abundant predator population in Cultus Lake and it was likely having an impact on the population’s ability to recover.

Ultimately, the Cultus sockeye population was not listed under SARA. The Minister of Environment, who is responsible for SARA listings, proposed in January 2005 that the Cultus and Sakinaw populations of Pacific sockeye salmon not be listed because of the unacceptably high social and economic costs. Extensive closures in the mixed-stock commercial fisheries would be required to ensure the protection of the small Cultus Lake population if it had been listed under SARA (Irvine et al. 2005). Thus, the Cultus Lake sockeye population has received no protection under SARA, but Fisheries and Oceans Canada (FOC) has committed to its protection and rebuilding.

Efforts to protect and rebuild the Cultus Lake population began in 2000 with the captive breeding project, which collected five females and ten males. In 2002 the project was redesigned with larger broodstock targets, and significant fry and smolt releases began in 2003 (Cultus Sockeye Recovery Team 2004). Freshwater survival of released fry was poor in the first few years but has improved with changes made to release strategies (J. Hume, Fisheries and Oceans Canada, Cultus Lake, B.C., personal communication). Currently, the program aims to collect 50% of the run to a maximum of 250 adult spawners each year. The program produces approximately 100,000 smolts (smolts released plus fry that have survived to the smolt stage) migrating seaward past the counting fence each year, and a captive broodstock population is maintained (A. Stobbart, Fisheries and Oceans Canada, Inch Creek / Pitt River Hatchery, B.C., personal communication). The hatchery was scheduled to take its last broodstock in late 2007 with final smolt releases in 2014, but this may be extended for at least one more sockeye generation (four years).

The Cultus Sockeye Recovery Team (2004) identified the need for a better understanding of the potential impact of northern pikeminnow on sockeye production. A series of northern pikeminnow mark-recapture studies were conducted by FOC during 2004-2005. This work revealed that the northern pikeminnow population is much larger (approximately 60,000 adult fish) than previously estimated (Bradford et al*.* 2007). These recent studies also documented a high degree of site fidelity that northern pikeminnow have for summer feeding and spawning locations within Cultus Lake. Foerster and Ricker (1938), Steigenberger (1972), and Hall (1992) estimated the adult population to be 9000, 20,000, and 40,000 fish, respectively. The site fidelity behaviour was previously unrecognized and likely led to underestimates of population size in the past because it violates assumptions (equal capture probability of marked and unmarked fish) of the estimation method (Bradford et al*.* 2007). The current northern pikeminnow removal program is scheduled to operate during the summer of 2008, but its future is uncertain beyond that date.

2.0 METHODS

2.1 Overview

I built a stochastic model to simultaneously simulate the Cultus sockeye and northern pikeminnow populations. The purpose of the model was to determine likely outcomes (related to sockeye recovery management objectives) of two main management strategies (predator control and hatchery supplementation). The modelled abundance of northern pikeminnow directly affected freshwater survival rates of juvenile sockeye (wild and hatchery) through predation. Different levels of predator control were included, as well as simulated hatchery production of sockeye. Random variation in sockeye smolt production and sockeye marine survival rates was incorporated in the model. The model simulated both populations (sockeye and northern pikeminnow) forward for 15 years, from 2008 to 2022.

A decision analysis framework was used to rank alternative management strategies. Decision analysis is often characterized by eight parts (Peterman and Anderson 1999) as detailed in the next sections: (1) define management objectives, (2) describe alternative management actions, (3) determine uncertainties to be resolved, (4) synthesize these components in a decision tree (Figure 2), (5) estimate the probability of occurrence for each uncertain state of nature, (6) construct a model to determine consequences for each combination of actions and uncertain states of nature, (7) determine the rank order of

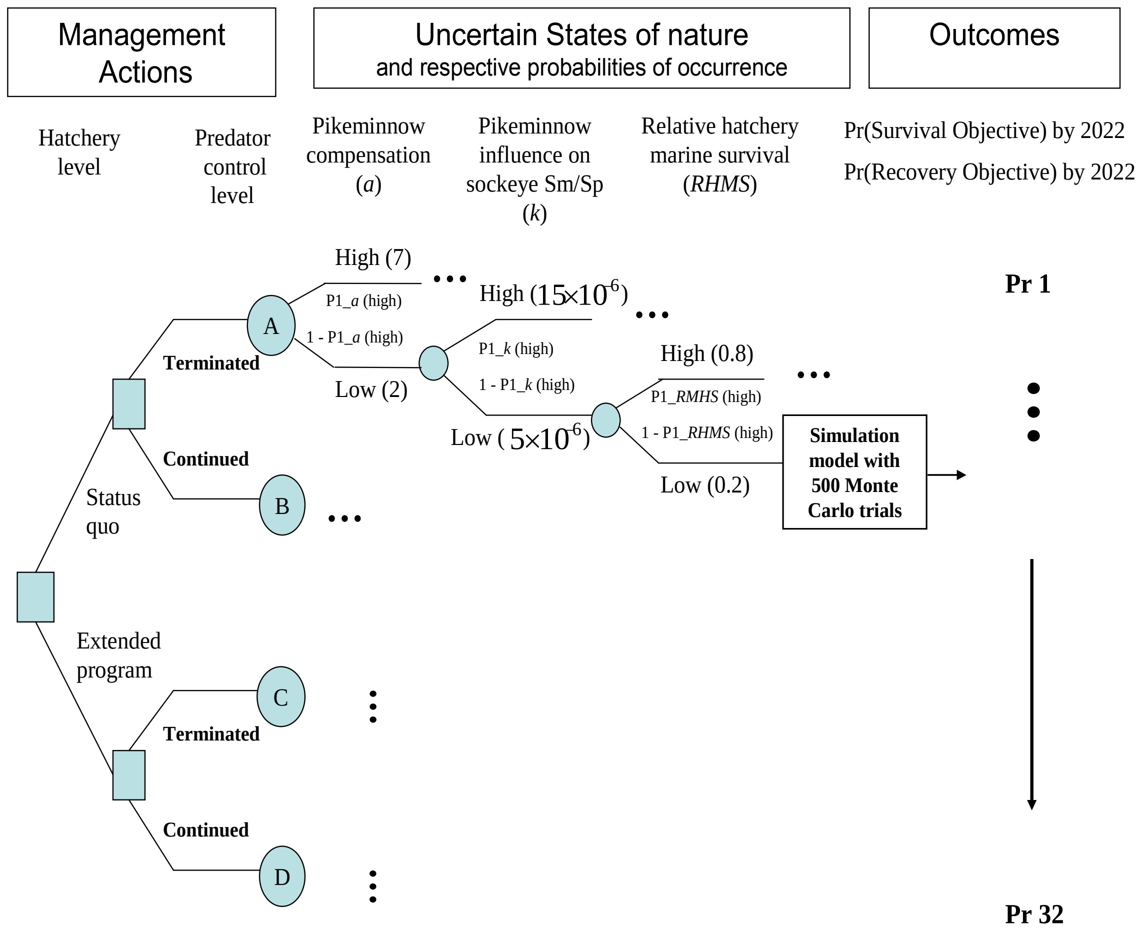

Figure 2 Decision tree illustrating alternative management actions, uncertain states of nature, and outcomes in this study. Expected probabilities of meeting each management objective are calculated for each of the four alternative management actions (see text).

management actions based on performance indicators of how well objectives are met, and (8) conduct sensitivity analyses.

2.2 Management Objectives

The management objectives used in this study are loosely based on objectives developed for the National Recovery Strategy (Cultus Lake Recovery Team 2004). The goal is to halt the decline of the Cultus sockeye population and return it to the status of a viable, self-sustaining, and genetically robust wild population that will contribute to its ecosystems and have the potential to support sustainable use. Four quantitative objectives that are sequential steps toward the recovery of the population are identified in the National Recovery Strategy and I used two of them as the first two objectives in my analysis.

The three management objectives I used are best described as survival, recovery, and harvest objectives. The survival objective is designed to ensure the genetic integrity of the population and therefore its survival. It requires that the four-year arithmetic mean number of spawners in the year 2022 be greater than 1000, and that there be no fewer than 500 spawners in any one year. The recovery objective is related to deciding when the population is "recovered". Meeting this objective requires that the four-year arithmetic mean number of spawners in the year 2022 be greater than 8000, and that there be no fewer than 500 spawners in any one year. This objective was determined based on the observation that the Cultus Lake population shows less potential for rebuilding, or sustaining harvest, when abundance is below the threshold of about 7000 spawners (Bradford and Wood 2004, Cultus Lake Recovery Team 2004). In my model, the calculation of performance measures did not include those fish collected at the fence that were to be used for hatchery broodstock, nor did it include fish that were released from the hatchery and have returned to spawn (see section 2.5.2 for description)

Since reductions in harvest for the protection of Cultus sockeye might result in significant losses of fishing opportunities (commercial, recreational, and aboriginal), I also included a third management objective in my analysis. The third objective was to minimize the number of years with a low ($\leq H_{min}$, see section 2.5.2) harvest rate for Cultus sockeye, which would affect opportunities to exploit other, more abundant salmon populations.

2.3 Alternative Management Strategies

I evaluated recovery actions (strategies) that either closely approximated strategies currently being used or that are likely to be used within realistic time frames and budgetary constraints. These strategies were two alternative levels of hatchery operations (status quo and extended) and two alternative levels of northern pikeminnow control (terminated and continued), producing four combinations of actions for aiding recovery of the Cultus sockeye population. These four alternatives are referred to as strategies A-D throughout this paper (Figure 2); A = status quo hatchery operations combined with terminated predator control efforts that end after 2007; B = status quo hatchery operations combined with continued predator control efforts for 2008 through to the end of 2022; C = extended hatchery operations combined with terminated predator control efforts that end after 2007; D = extended hatchery operations combined with continued predator control efforts for 2008 through to the end of 2022. Specific parameter values and time frames are given in Table 1.

I simulated two scenarios of hatchery production using the current schedule of releases (A. Stobbart, personal communication) and the most recent estimates for freshwater survival of hatchery fish (J. Hume, personal communication). The status quo hatchery strategy had a capacity to produce 450,000 fed fry to be released in the lake and 50,000 yearling smolts to be released in Sweltzer Creek annually for 2006 through 2014. The extended program was assumed to be able to produce 1,000,000 fry and 100,000 smolts annually for 2006 through 2018. Hatchery facilities are limited for this population and the extended hatchery strategy would likely require construction of new facilities. In the model, both hatchery strategies collect spawners annually at the Sweltzer Creek fence for the maintenance of broodstock, ending in 2007 for the status quo hatchery strategy and in 2011 for the extended strategy.

The terminated predator control strategy assumed no pikeminnow removals after 2007 and simulated approximately 25% reduction up through that year in the adult population of 60,000 fish based on the 2004 estimate. For the continued predator control strategy the removal of pikeminnow occurred annually to the final simulation year (2022).

Table 1 Description of parameters used in the simulation model and definition of scenarios and terms.

Parameter/ Scenario	Description	Estimate/Statistic
Sockeye		
α	Log_e(smolts/spawner) at low spawner abundance when influence of pikeminnow in sockeye smolts/spawner relationship is high/low	5.05/4.45
β	Density dependence in smolt production	7.4×10^{-6}
k	Reduction in Log_e(smolts/spawner) per pikeminnow when influence of pikeminnow in sockeye smolts/spawner relationship is high/low	0.000015/0.000005
σ	Standard deviation of Log_e(smolts/spawner)	0.62
RHMS	Marine survival rate of hatchery smolts as a fraction of survival rate of wild smolts (high/low)	0.8/0.2
MMS	Mean marine survival rate used in alternative marine survival scenarios	Range from 1% to 6%
S_{FW}	Baseline freshwater survival rate of hatchery released fry	9%
Hatchery terms		
Broodtake	Number of adult returns collected at the fence for broodstock	MIN (0.5*escapement, 250)
Status quo hatchery	Duration and magnitude of hatchery operations	50,000 smolts and 450,000 fry annually between 2007 and 2014. Final Broodtake in 2007
Extended hatchery	Duration and magnitude of hatchery operations	100,000 smolts and 1,000,000 fry annually between 2007 and 2018. Final Broodtake in 2011

Northern pikeminnow		
PM_{init}	60,000	Initial abundance of age 5+ pikeminnow in 2004
M	Natural mortality rate of age 5+ pikeminnow	0.36
b	Density dependence in pikeminnow recruitment (high/low)	Calculated by rearranging Beverton-Holt function (Equation 11) and solving for *b* given *a* (22050,/50400)
F_{init}	Fishing mortality rate in initialization years (2004/2005/2006/2007)	0.02/0.2/0.5/0.9
F_{rest}	Fishing mortality rate in years 20078 to 2022 (extended predator control only)	0.5
L_{∞}	Asymptotic length	500cm
K_{VB}	Brody growth coefficient	0.085
t_{OVB}	Hypothetical length of fish at t = 0	-2.0
a_w	Weight at age multiplier	0.0052
b_w	Allometric growth coefficient	3.28
c	Catchability shape parameter	11
d	Catchability shape parameter	6.3
Harvest Rule		
H_{min}	Minimum harvest rate (rule 1/rule 2)	0.12/0.3
H_{max}	Maximum harvest rate (rule 1/rule 2)	0.50/0.6
L	Number of adult sockeye returns below which H_{min} applies (rule1/rule 2)	1000/1000
U	Number of adult sockeye returns above which H_{max} applies (rule 1/rule 2)	8000/8000

2.4 Uncertainties to be resolved

I evaluated three crucial uncertainties that scientists may be able to better estimate in the future, thereby providing an idea of how worthwhile it might be to invest in research to resolve such uncertainties. The first uncertainty was the influence of northern pikeminnow predation on freshwater productivity of sockeye (*k* parameter in equation 1). The second source of uncertainty was northern pikeminnow recruitment compensation (the *a* parameter in equation 4), which represents the strength of density-dependent mortality in early life history. The third uncertainty was relative hatchery marine survival (*RHMS*), which is the ratio of the marine survival rate of hatchery fish compared to that of wild fish. The *RHMS* was important to include because little is known about what marine survival rates can be expected from hatchery releases, although it is expected that they are lower than that of wild fish (Ford 2005, Araki et al. 2007, Frits et al. 2007).

I ran simulations using alternative parameter values that represent a range from high to low for each of these three uncertain states of nature. This allowed me to evaluate the relative differences in model outcomes under the alternative values for the uncertainties. These uncertainties are described quantitatively below (summarized in Table 1). I initially assumed that each value of the uncertain state of nature (high or low) was equally likely (50% degree of belief that each was the true state of nature). In my sensitivity analyses, I evaluated different degrees of belief.

2.5 Model to determine consequences

2.5.1 Model Initialization

The total simulation period in each Monte Carlo run was 24 years from 1999 through 2022. The first nine years (1999 through 2007) were the initialization years where the model used observed data from the Cultus Lake program. Thus, each simulation began with the same Cultus sockeye spawner numbers, smolt numbers, hatchery releases and northern pikeminnow removals for the first nine years. The remaining 15 years (2008 through 2022) represent the simulation period over which performance measures were computed, and where stochasticity was applied to the model.

2.5.2 Sockeye sub-model

The operation of a counting fence at the lake outlet, which counts the number of returning sockeye spawners each fall and emigrating smolts each spring, has provided Cultus smolts per spawner (Sm/Sp) and marine survival data for many years between 1925 and 2006, allowing for the modelling of this population using spawner-to-smolt and smolt-to-adult recruit relationships. These data are summarized in Cultus Lake Recovery Team (2004). Many years were likely affected by predator control programs, hatchery operations, or high pre-spawning mortality (PSM), producing data not representative of natural production, and they were not included in the data set used in this study. I used 26 years (1951-1952, 1954-1961, 1965-1972, 1974-1976, 1988-1990, and 2002-2003) of Sm/Sp (Figure 3) and marine survival (Figure 4) data to parameterize the sockeye component of my model.

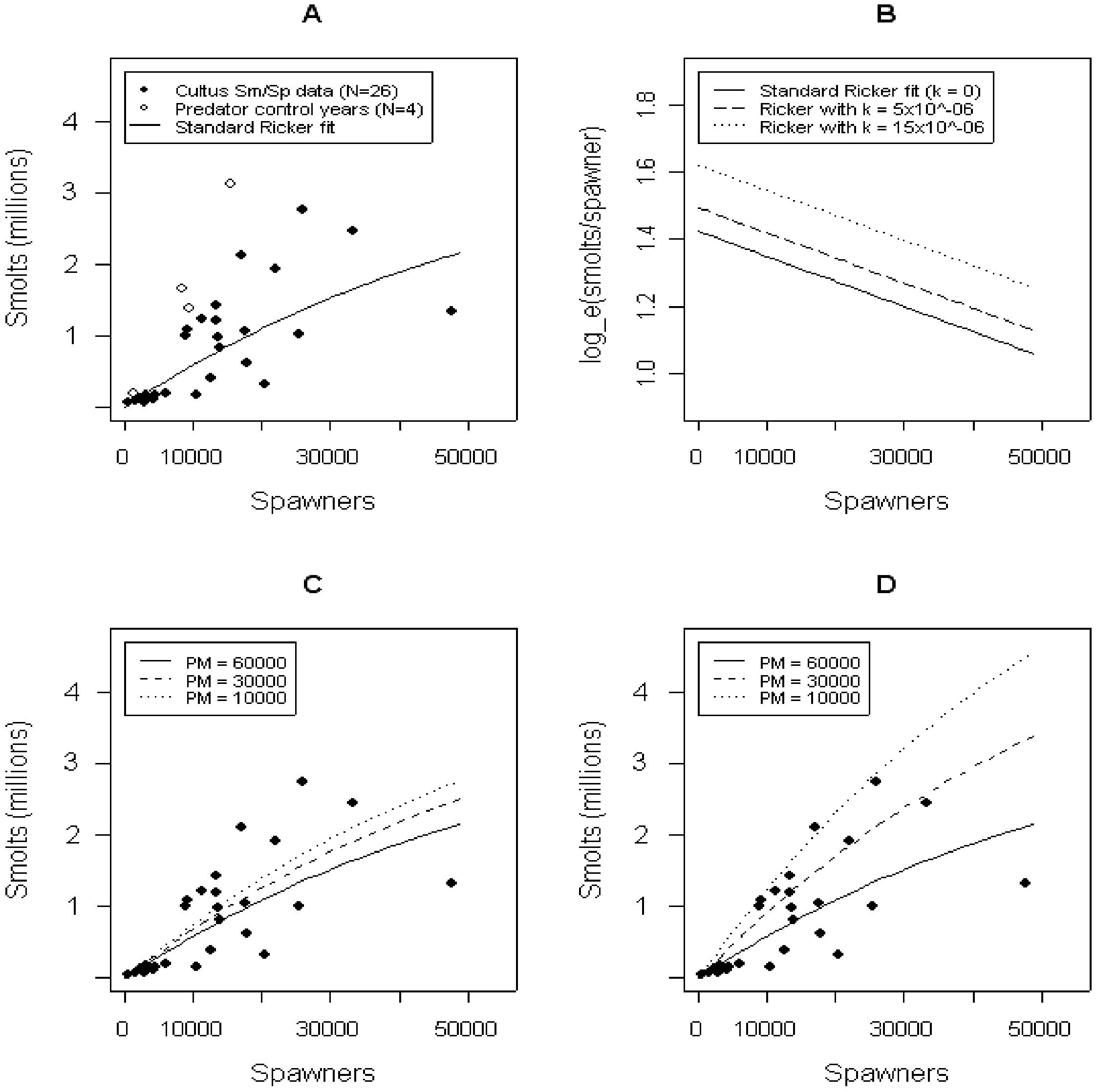

Figure 3 (A) Cultus sockeye smolt and spawner data for years that were not likely affected by either predator control efforts, hatchery operations, or high pre-spawning mortality (solid circles). Years that followed predator control are indicated by open circles. (B) Log_e(Sm/Sp) for standard Ricker model (*k* = 0) and the two alternative models used in this study. (C) Resulting spawner-to-smolt relationships from assuming low *k* (low consumption rate of sockeye smolts per pikeminnow) at three different northern pikeminnow abundances. (D) Spawner-to-smolt relationships assuming high *k* (high consumption rate of sockeye smolts per pikeminnow) at three different northern pikeminnow abundances.

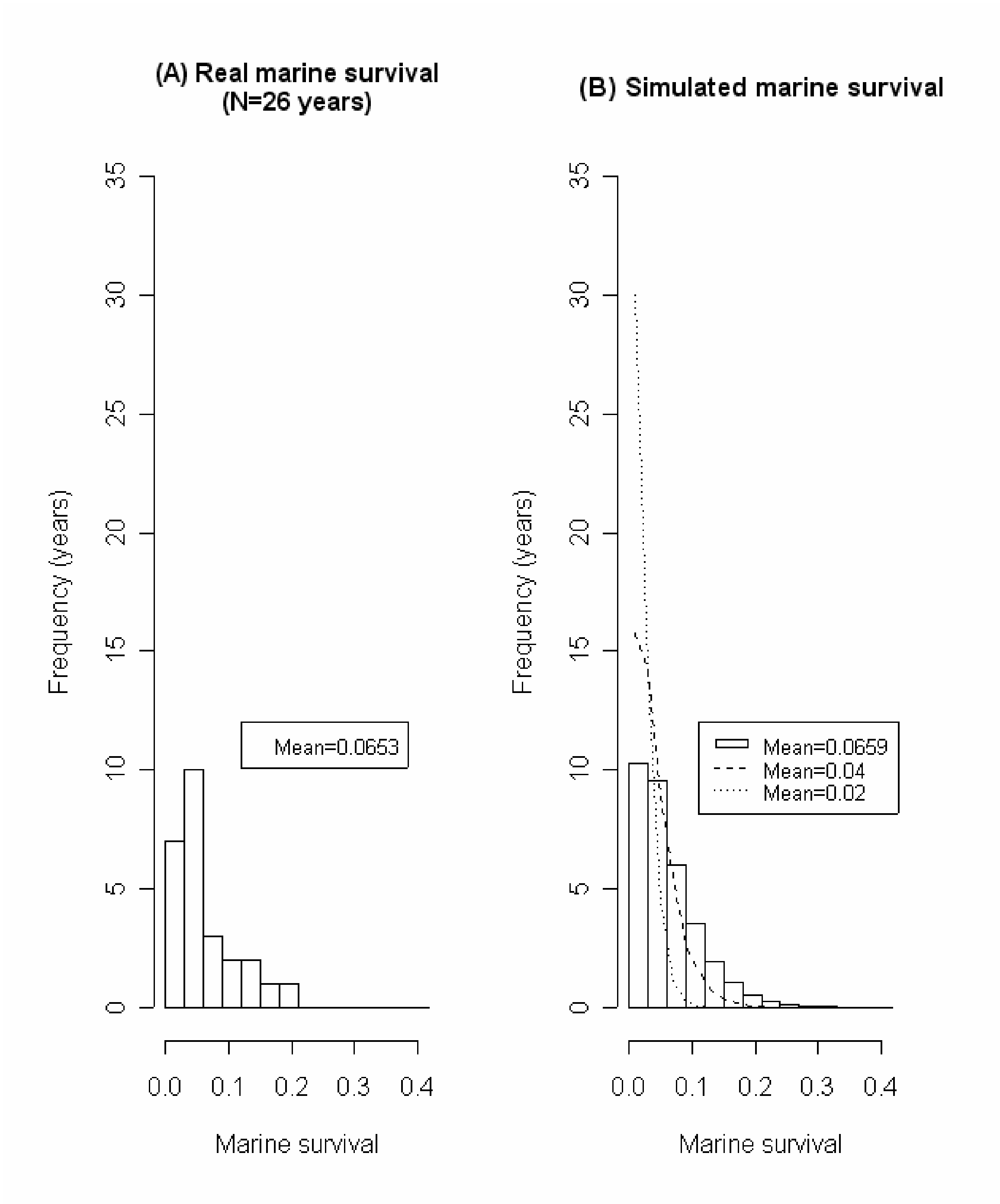

Figure 4 **Frequency distributions of marine survival rates for observed Cultus Lake sockeye data (A) and Beta distribution used in Monte Carlo trials for generating annual marine survival rate (B). Bars represent a sample frequency distribution of simulated values with parameters estimated from the historical data; lines represent alternative distributions.**

Within the sockeye sub-model, the annual number of smolts emigrating from Cultus Lake and the annual number of returning adults was simulated based on a two-stage life history model. The first stage used a spawner-to-smolt model to predict the number of smolts emigrating each year from the lake based on the number of spawners reaching the spawning grounds one and a half years previous.

The model assumed that all juveniles migrate to the ocean in the spring after spending 1.5 years in the lake after egg fertilization. It also assumed that all adult sockeye return at age 4 to spawn after spending 2.5 years in the Pacific Ocean. These assumptions are based on the observations that spawners are >95% age-4 fish and emigrating smolts are >95% age-1 (Cultus Sockeye Recovery Team 2004). My model did not include any pre-spawning mortality (PSM) of adults after they pass the fence, and did not include any outcome uncertainty in harvest (difference between target and achieved harvest rates).

The second stage of the sockeye sub-model predicted the number of spawners each year in three sequential steps: (1) the number of pre-fishery recruits based on density-independent marine survival of smolts (Equation 3); (2) adult escapement at the Sweltzer Creek counting fence derived from a state-dependent fishery harvest rule (Equation 4, Figure 5); and (3) the number of spawners reaching the spawning grounds based on number of fish taken as broodstock (Equation 6).

The sockeye sub-model tracked the abundance of 3 “stock types” (wild, naturalized hatchery fish, and hatchery fish). Wild fish were those that met the

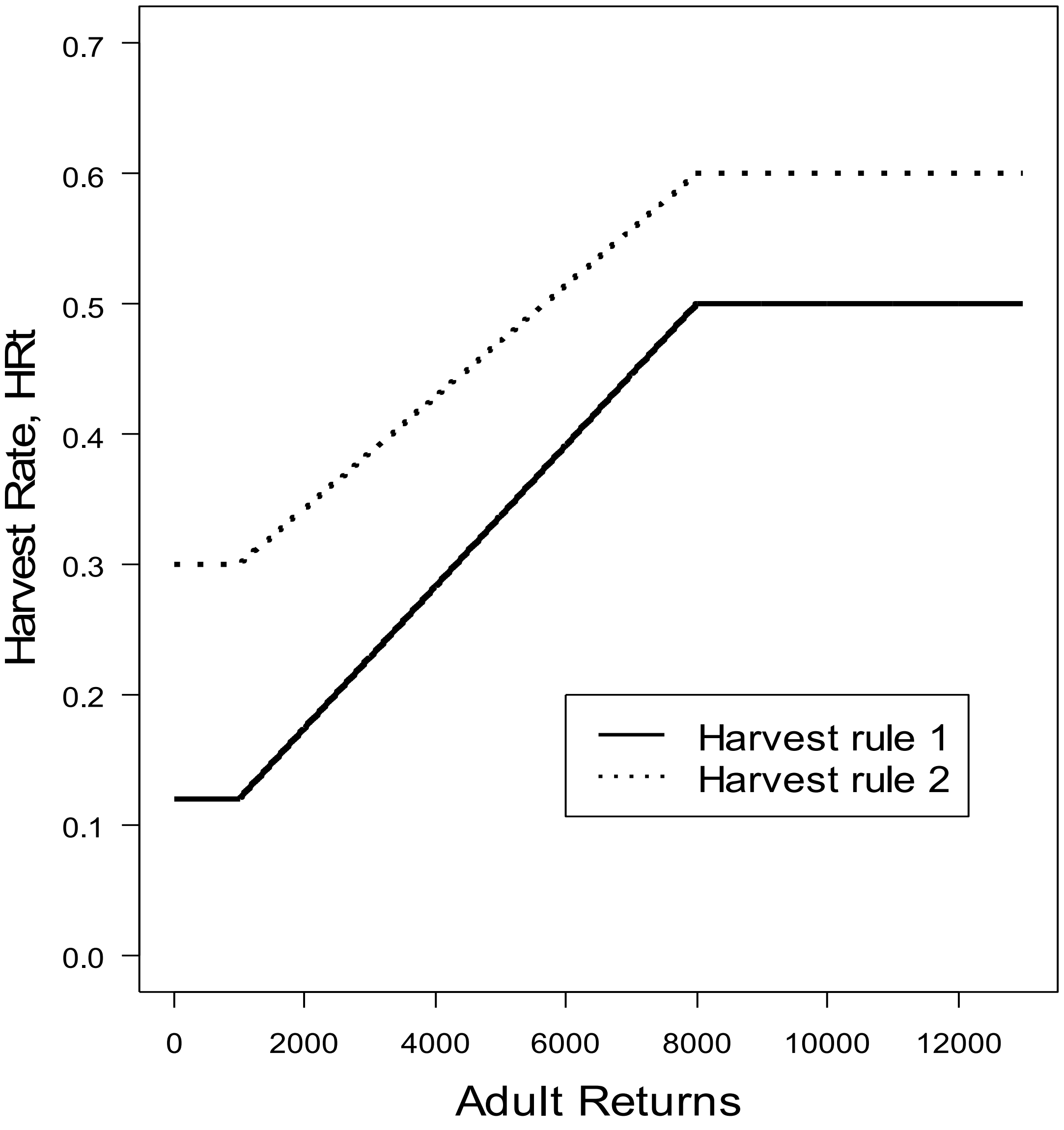

Figure 5 **Harvest rules used to prescribe annual harvest rate (HR_t) in any given year for Cultus Lake sockeye based on the number of Cultus sockeye adults estimated to be returning. Bottom line (Rule 1) is the base rule; top line (Rule 2) is used in sensitivity analyses.**

requirements for wild fish as defined in the Wild Salmon Policy (DFO 2004), where they must be the progeny of parents that spent their entire life cycle in the wild. Hatchery fish were fish that were released from the hatchery. Naturalized hatchery fish (NHF) were the progeny of hatchery released fry or smolts that returned and spawned naturally. It was necessary to track the abundance of hatchery fish and NHF because, although neither is considered wild under the Wild Salmon Policy, the progeny of NHF are considered wild. Keeping track of the contribution of each stock type to the total population size may be important to managers as they consider the potential deleterious effects of an increasing contribution of hatchery fish to the total population. In this model wild fish and NHF had the same freshwater and marine survival rates (Figure 4), whereas the freshwater survival rate of hatchery-released fry and smolts was assumed to follow recent empirical data from the Cultus Lake program (J. Hume personal Communication; Table 1). Marine survival of hatchery fish was simulated as a fraction of the survival rate of wild fish each year (Table 1).

I assumed that predation on sockeye by northern pikeminnow is proportional to adult northern pikeminnow abundance. A linear functional response was used, where northern pikeminnow encounter fry or smolts at random and the per capita encounter rate increases with smolt density (Ricker 1941). This linear relation, rather than the more traditional nonlinear one, is based on the observation that Cultus sockeye smolt abundances are so low that encounter rates are also likely low.

The total number of wild and naturalized hatchery smolts produced for a given number of wild and hatchery spawners (wild and hatchery spawners were assumed to have equal reproductive success), was predicted as,

$$(1) \quad Sm_{i,t} = \alpha * Sp_{i,t-2} * e^{-\beta * Sp_{i,t-2} - k * PM_t + \nu_t},$$

where $Sm_{i,t}$ is the number of smolts of stock type i passing the fence in year t, $Sp_{i,t-2}$ is the total number of fish spawning in year $t-2$, PM_t is the total number of age 5+ northern pikeminnow in the lake at time t. α, β and k are parameters of the stock recruitment relationship and ν_t is a randomly generated error term drawn from a normal distribution with a mean of zero and a standard deviation of σ_ν (see Table 1) . The α parameter represents freshwater productivity at low stock size (maximum Sm/Sp), 1/β is the spawning stock size where smolt production is maximized, and k represents the reduction in Log_e(Sm/Sp) for each age 5+ northern pikeminnow present in the lake in year t.

Although recent investigations have provided current estimates of adult northern pikeminnow abundance (Bradford et al. 2007), there is considerable uncertainty in estimates of historical abundance and therefore also in the relative influence that northern pikeminnow have had on the Cultus Sm/Sp time series. Based on the most recent published estimates, the adult northern pikeminnow population appears to have more than quadrupled since the first estimate (Foerster and Ricker 1938) and has nearly tripled since the estimate provided by Steigenberger (1969). This is difficult to justify, however, given that past studies did not recognize the strong site fidelity behaviour of pikeminnow, which likely affected the abundance estimates (Bradford et al. 2007). If northern pikeminnow are significant predators of sockeye, then sockeye Sm/Sp should have declined over the past 70 years. However, a regression of Sm/Sp on year (using all available data) showed no significant trend ($R^2 = 0.0005$, $p = 0.91$). I therefore assumed the northern pikeminnow population has remained relatively stable over the years, and that the Sm/Sp time series represents sockeye productivity in Cultus Lake with an adult northern pikeminnow abundance of 60,000 individuals.

I fit a Ricker-type model (Equation 1) to the 26 years of smolt and spawner data, and estimated the parameters α and β via least squares regression of Sm/Sp on Sp, assuming that $k = 0$ for this first fit. I then fixed the k value in Equation 1 at one of two values representing high (k= 15 x10^{-6}) and

low (k= 5x10^{-6}) predation rates, assumed 60 000 adult northern pikeminnow, and estimated the respective Ricker α parameters holding β constant. Figure 3 illustrates the modified Ricker model in the context of observed data and how a decrease in northern pikeminnow abundance increases sockeye spawner-to-smolt productivity. This is how predator control results in increased sockeye production in the model.

The current Cultus sockeye hatchery program is a complex operation and I made some simplifying assumptions for my analysis but captured its essential features. In the model, eggs and milt are taken from broodstock collected at the Sweltzer Creek fence. A small portion of eggs are raised to adults (captive broodstock) in the hatchery. Surplus eggs are used in the hatchery to produce a variable number of fry released into the lake in their first summer, and smolts which are released directly into Sweltzer Creek after spending one and a half years in the hatchery. The mature captive broodstock population is used to produce additional fry, which are released along with those mentioned above to meet the annual total fry release target.

I have no reliable estimates of the relative success of hatchery origin fish in either the freshwater or the ocean environment. Recent estimates available from the Cultus Lake hatchery program have been confounded because of the complicated release strategies used by hatchery operators. The model assumed that freshwater survival of smolts released is 100%, as these fish are assumed to migrate immediately to the ocean following release released below the Sweltzer Creek counting fence. The model assumed a freshwater survival rate for hatchery fry that are released in the lake were a function of *k* and abundance of adult northern pikeminnow (Equation 2; a variant of equation 1 used to simulate hatchery smolt production). Based on recent experience, this survival rate is 9% when 60,000 northern pikeminnow are in the lake and it was modelled to increase as northern pikeminnow are removed from the lake (Equation 2). Thus, as predators were removed from the lake, a concomitant increase in freshwater survival of hatchery released fry occurred, similar to that of wild fry. For example, using parameters for the status quo hatchery strategy:

$$(2) \quad Sm_{h,t} = 50{,}000 + \left(450{,}000 * e^{-2.408 + k*(60{,}000 - PM_t)}\right)$$

Data for Cultus sockeye show that marine survival rate is log-normally distributed (Figure 4). I used random draws from a beta distribution to generate future marine survival rates because it confined the marine survival rate to be between zero and one and it can be parameterized to have a similar shape as a log-normal distribution. The two parameters of the beta distribution (β_1 and β_2) were determined by the method of moments (Morgan and Henrion 2003) using the mean marine survival (MMS) and standard deviation from the 26 years of data (Figure 4). Alternative marine survival rate distributions (different means) were simulated for sensitivity analyses. All of the simulated marine survival distributions were parameterized to have the same general shape and coefficient of variation as the real data series and were truncated so that MS_t was never <0.01 and never >0.5. This truncation, however, increased the mean survival rate for simulations with low MMS.

The number of wild and naturalized hatchery pre-fishery recruits was predicted using equation 3, where R_t was the number of pre-fishery recruits in year t and MS_t was the marine survival rate for this cohort of fish and was randomly drawn in each simulation from the beta distribution with a specified mean.

$$(3) \quad R_t = Sm_{t-2} * MS_t ,$$

For marine survival of hatchery fish, the most recent estimates available have been 20% and 65% of the survival rate for wild smolts, for the 2001 and 2002 brood years respectively (M. Bradford, Fisheries and Oceans Canada, Simon Fraser University, personal communication). However, these were based on very small release groups and may not be representative of larger releases.

Given these large uncertainties, I simulated two alternative RHMS rates for hatchery fish, low (0.2) and high (0.8) fractions of wild survival.

In my simulations, the commercial fishery for late-run Fraser river sockeye followed a state-dependent harvest rule that set a target harvest rate based on the number of returning Cultus Lake sockeye (Figure 5). This rule was parameterized based partially on results from Pestes et al. (2008), but was modified to better approximate target harvest rates recently set by FOC. The harvest rule was represented by 4 parameters (L, H_{min}, U, and H_{max}), where L is the lower abundance threshold at which H_{min} is the target harvest rate, and U is the upper abundance threshold at or above which H_{max} is the target harvest rate. Rule 1 had $H_{min} = 0.12$, $H_{max} = 0.5$, $L = 1000$, and $U = 8000$. An alternative harvest rule was explored in sensitivity analyses (Rule 2 in Figure 5; Table 1).

The number of adult sockeye returning to the Sweltzer Creek counting fence was:

$$(4) \quad Esc_t = R_t * (1 - HR_t) \text{ ,}$$

where Esc_t is the number of returning fish in year t that made it past the fishery, reaching the fence at Cultus Lake, and HR_t is the harvest rate in year t, which was determined by the harvest rule. Hatchery fish were assumed to mix with the wild fish and harvested at the same rate in the fishery.

The number of wild and naturalized hatchery spawners (indistinguishable from wild fish) was calculated from,

$$(5)\quad Sp_t = Esc_t - Broodtake_t\ ,$$

where Sp_t is the number of spawners in year t and $Broodtake_t$ is the number of fish collected at the fence to be used for hatchery purposes. No hatchery fish are collected for broodstock and all returning hatchery fish are allowed to spawn naturally in the lake. My model used the rule currently in use for the Cultus Lake hatchery program:

$$(6)\quad Broodtake_t = \min(Esc_t * 0.5, 250)\ ,$$

that is, the number of spawners taken is the minimum of either 50% of the escapement or 250 fish, with a sex composition of 50% females.

2.5.3 Northern pikeminnow sub-model

I used a stochastic age-structured model to simulate the Cultus Lake northern pikeminnow population. The model simulated the effects of a removal program on adult pikeminnow abundance, which affects sockeye productivity through equation 1.The model considered ages 5 through 20+ year-old fish, and did not include sex-specific differences in size or age. The annual change in the number of adults was:

$$(7)\quad N_{a,t} = N_{a-1,t-1} e^{-M + q_a * F_{t-1}}\ ,$$

where N is the number of northern pikeminnow at age a in year t, M is the natural mortality rate, F is the fishing mortality of a predator control program on fully vulnerable age classes, and q is the age-specific catchability that scales F according to the selectivity of the fishing gear used in the predator control program.

The parameterization of the northern pikeminnow sub-model was based on work conducted during 1989-1991 (Hall 1992) and 2004-2005 (Bradford et al. 2007). Length and age data were used to estimate natural mortality rate for the age 5+ population, as well as Von Bertalanffy growth parameters and age specific catchabilities (Figure 6, Table 1). Length (cm) at age was determined using Von Bertalanffy's equation (Ricker 1975),

$$(8) \quad L_a = L_\infty * (1 - e^{-k_{VB} * (a - t_{OVB})}),$$

where L_a the length for age class a, L_∞ is the asymptotic length, k_{VB} is the Brody growth coefficient, and t_{OVB} is the hypothetical length at $t=0$. From the lengths determined in Equation 8, the weight at age was determined as,

$$(9) \quad W_a = a_w * (L_a * 0.1)^{b_w},$$

where W_a is the weight for age class a, a_w is a scalar, L_a is the length (cm) at age a, and b_w is the allometric growth coefficient. Note here that the parameters in the formula convert length from cm to mm for use in the weight-at-age calculation.

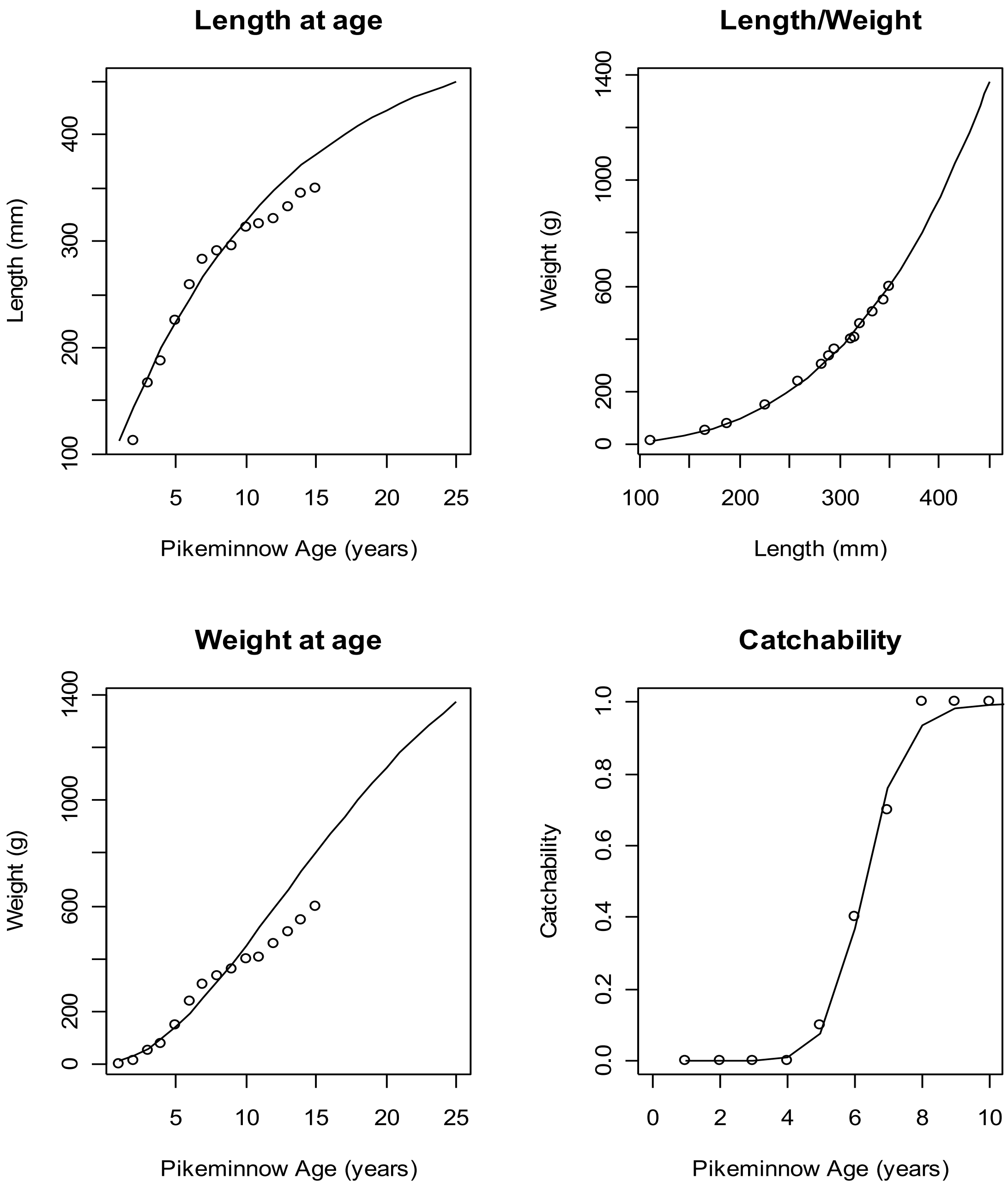

Figure 6 **Length-at-age, weight-at-age, and catchability-at-age models (lines) fit to data (circles) and used to simulate the northern pikeminnow population (see text). Parameter values are given in Table 1.**

The age-specific catchability was determined by fitting a two-parameter ogive function to data contained in Bradford et al. (2007),

$$(10) \quad q_p = \frac{p^c}{p^c + d^c},$$

where q_p is the catchability of age class p, and c and d are parameters that describe the shape of the ogive.

Recruitment to the adult pikeminnow population was derived from a Beverton-Holt recruitment function that calculated the number of age-5s in year t+5 from the age-6+ spawning biomass (S) in year t as:

$$(11) \quad N_{5,t-5} = \frac{aS_t}{1 + \frac{a}{b} S_t}$$

I assumed that prior to predator control, pikeminnow recruitment was constant and the population was at equilibrium such that recruitment was balanced by mortality. Using a recent estimate of the age 5+ population size from mark-recapture experiments (Bradford et al. 2007), and an estimate of natural mortality (M=0.36) for the age 5+ population (Hall 1992), Beverton-Holt parameters (Equation 11, Table 1) were estimated for a population that has an age 5+ population of 60,000 individuals and an age 6+ spawning biomass of 14,000 kg. This became my pre-predator-control baseline population.

No information is available on the degree of compensation (density-dependent mortality in the recruitment phase) in northern pikeminnow populations, so I used two values that resulted in high (a = 7) and low (a = 2) compensation (Figure 7). For each value of a, a corresponding value of b that resulted in 18 000 pikeminnow recruits being produced by a spawning biomass of 14 000 kg was found (Table 1) by rearranging equation (11) and solving for b. No demographic stochasticity was incorporated in the northern pikeminnow model because preliminary analyses showed it to be inconsequential.

2.6 Performance measures

The performance measures are the probability of meeting the management objectives. The model recorded the number of simulations (out of a total of 500) where management objective 1 (survival) and objective 2 (recovery) were met, producing a probability of meeting each objective. The third management objective (harvest) is a measure of the variability in harvest among the alternative management strategies. The model recorded the proportion of years (out of 15) in each simulation where the harvest rate was $\leq H_{min}$. This produced a vector of 500 values from which the mean and standard deviation could be determined. The mean is the proportion of years with the harvest rate $\leq H_{min}$ (15 years per simulation multiplied by 500 simulations equals 7500 simulated years) and the standard deviation is a measure of the variability among simulations. I presented results this way because it allows decision makers to assign appropriate weights to each objective (i.e., probability of recovery vs. number of years with low harvest), and evaluate the tradeoffs associated with alternative recovery actions.

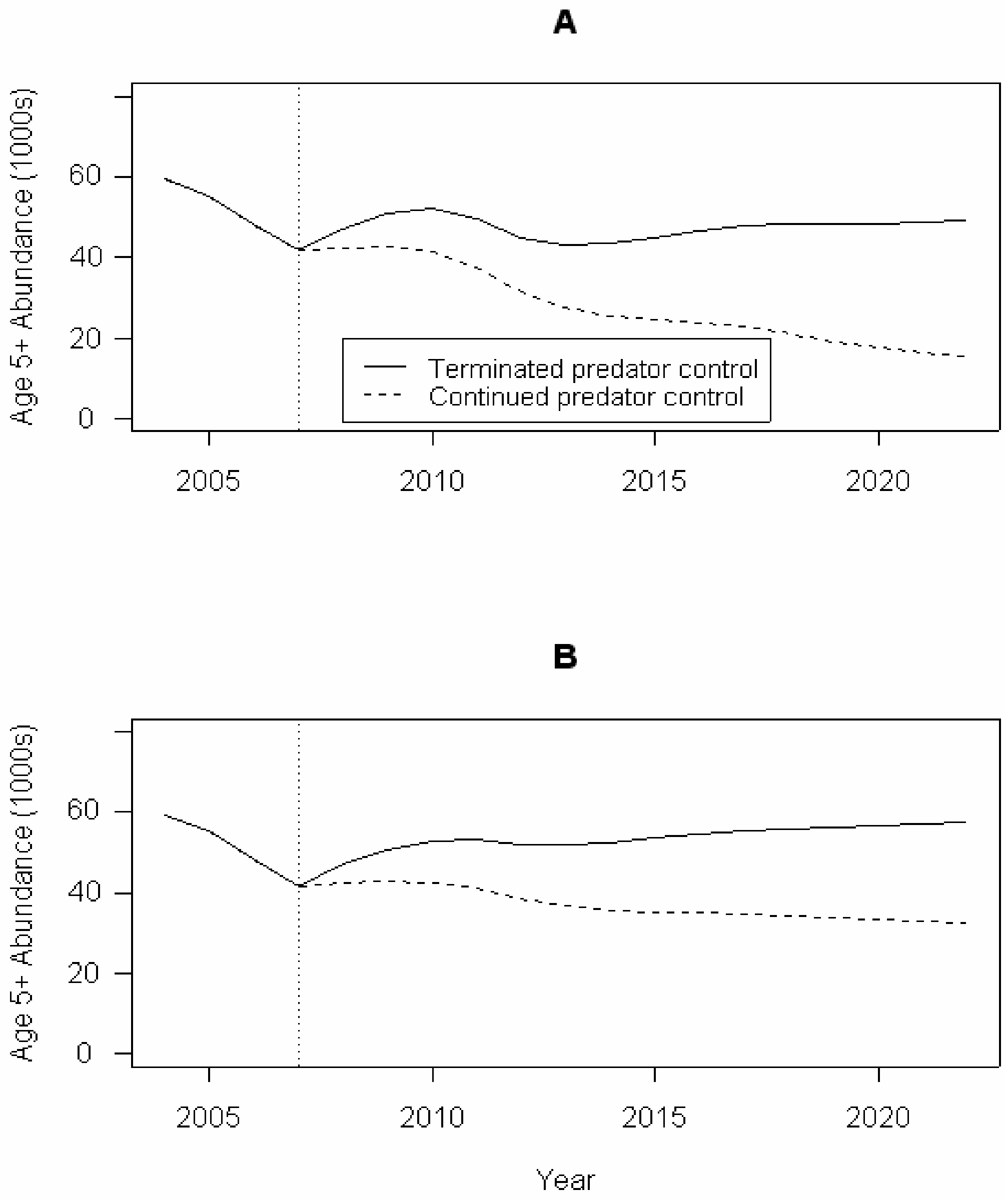

Figure 7 Simulated northern pikeminnow abundance under alternative levels of control, with (A) low recruitment compensation, and (B) high recruitment compensation. Notice that all four trajectories begin with the same abundance up to 2007, which represents predator control efforts to date.

2.7 Sensitivity Analysis

Sensitivity analyses on some key parameters identified which uncertainties had the greatest effect on performance of management strategies.

I examined how alternative mean marine survival rates (used to generate MS_t in Equation 3) affected the performance measures. I also performed sensitivity analysis on RHMS (relative marine survival of hatchery fish to wild fish) and *k* (northern pikeminnow predation) parameters. The performance measures were not very sensitive to changes in the northern pikeminnow compensation parameter (*a*), so this parameter was not considered further.

I also produced results from the alternative harvest rule (Figure 5, Table 1) which may be more representative of harvest rates that have occurred recently (different than target harvest rates) and that might be expected if a more aggressive harvest strategy is adopted in the future.

3.0 RESULTS

3.1 Survival Objective

The probability of meeting the survival objective by 2022 for the Cultus sockeye population under the proposed actions and harvest rule 1 was high, even for relatively low marine survival scenarios (Figure 8). When the mean marine survival rate (MMS) was expected to be at least 4%, all 4 combinations of management strategies produced probabilities of meeting the survival objective >90% (i.e., >450/500 Monte Carlo simulations). If MMS was less than 4%, then more aggressive strategies (C and D) are required. With a MMS rate of 1%, and status quo hatchery operations, the model predicted a 20% increase (from 20% to 40%) in the probability of meeting the survival objective by continuing the predator control program (strategy B) versus the termination of predator control (strategy A). This difference diminished with increasing MMS rates.

Extended hatchery operations were more effective than predator control at low marine survival rates. With a MMS rate of 1%, and terminated predator control, the extended hatchery program (strategy C) increased the probability of meeting the survival objective by 36% (from 20% to 56%) over strategy A. Extended hatchery operations and continued predator control together (strategy D) resulted in a 54% increase in the probability of meeting the survival objective compared with strategy A.

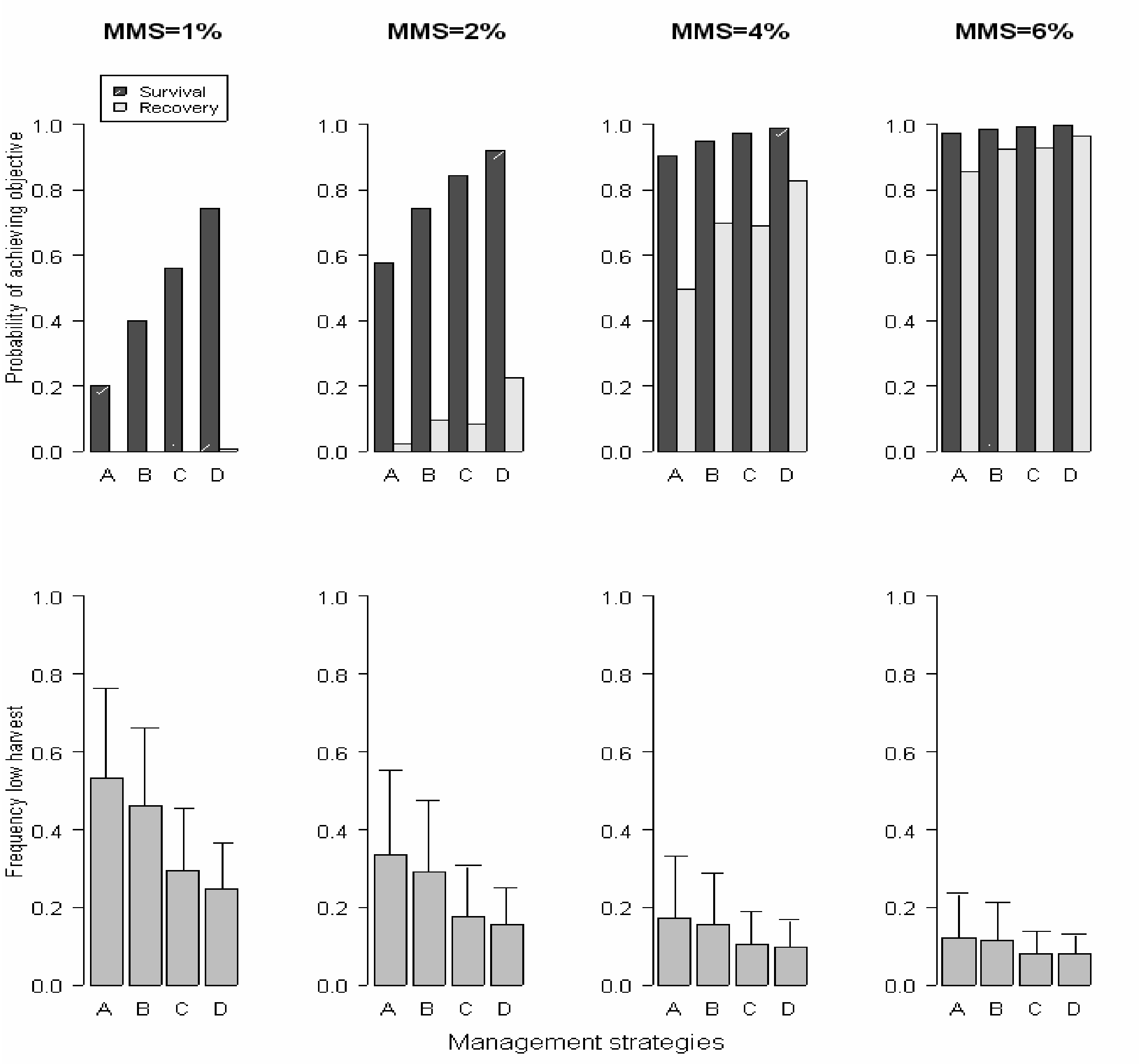

Figure 8 Simulation results based on Harvest rule 1 (H_{min} = 0.12, H_{max} = 0.50). Top panel shows survival (mean spawners/year ≥ 1000) and recovery (mean spawners/year ≥ 8000) probabilities for four alternative management strategies (A = status quo hatchery operations combined with terminated predator control; B = status quo hatchery operations combined with continued predator control; C = extended hatchery operations combined with terminated predator control; D = extended hatchery operations combined with continued predator control), at four alternative mean marine survival rates (MMS). Bottom panel shows the proportion of simulated years where the harvest rate was set at H_{min} as a result of low Cultus Lake sockeye abundance. Error bars represent two standard deviations.

My results demonstrated that the greatest increases in survival probability of the Cultus sockeye population occur under low marine survival rates and that with high marine survival rates, the differences among strategies is small.

3.2 Recovery Objective

Unlike the survival objective, the probability of meeting the recovery objective will be much more difficult if low marine survival rates occur in the future. I found that only under high (6%) MMS will the recovery objective be reached with >90% probability under any of the four strategies (Figure 8).

An interesting result was that the rank order (best to worst) of strategies for meeting the recovery objective was different than that for the survival objective. Although the difference between strategies B and C was relatively large for the survival objective, it was inconsequential for the recovery objective. With a MMS of 2%, strategy B slightly outperformed strategy C (9.7% and 8.5% respectively), and with a MMS of 6%, the rank order is virtually the same, as strategy C only slightly outperformed strategy B (93% and 92% respectively).

3.3 Harvest Objective

The model predicted a large difference across the four alternative management strategies in the harvest rate for Cultus sockeye. The general trend was that the more aggressive strategies allowed for more harvesting. Under strategy A with a MMS rate of 1%, 53% (8 out of 15) of simulated years are expected to have a low harvest rate (H_{min}), compared with only 26% (4 out of 15 years) for strategy D (Figure 8 bottom panel). There was only a slight difference in number of years with low harvest rates among the four strategies at the highest marine survival rates evaluated.

3.4 Sensitivity Analysis

The first sensitivity analysis I performed was an evaluation of model results using harvest rule 2 (higher harvest rates for a given abundance of returning Cultus sockeye; Figure 9) in place of harvest rule 1. Using harvest rule 2 resulted in large decreases in probabilities of meeting objectives 1 and 2 (differences were greatest under low marine survival), but did not change the rank order of management strategies. A comparison of Figures 8 and 9 (strategy A under 1% MMS) revealed a decrease of one order of magnitude (from 20% to 2%) in the probability of meeting the survival objective. The model predicted that under harvest rule 2, none of the strategies simulated will meet the recovery objective with a probability >70%, even with MMS of 6%. Using harvest rule 2 resulted in increased proportion of years with low harvest rate compared with harvest rule 1, although the minimum harvest rate (H_{min}) was much higher under rule 2 (30%) than for rule 1 (12%).

The rank order of management strategies was not very sensitive to changes in the degree of belief for the two key uncertainties (*k, RHMS*) when compared with the effects of changes in marine survival. These results are presented in the form of prescription tables (Figures 10 -13). Each cell of the prescription table shows the management action(s) that meet the objective with at least 90% probability. Vertical axes in these tables indicate the range of

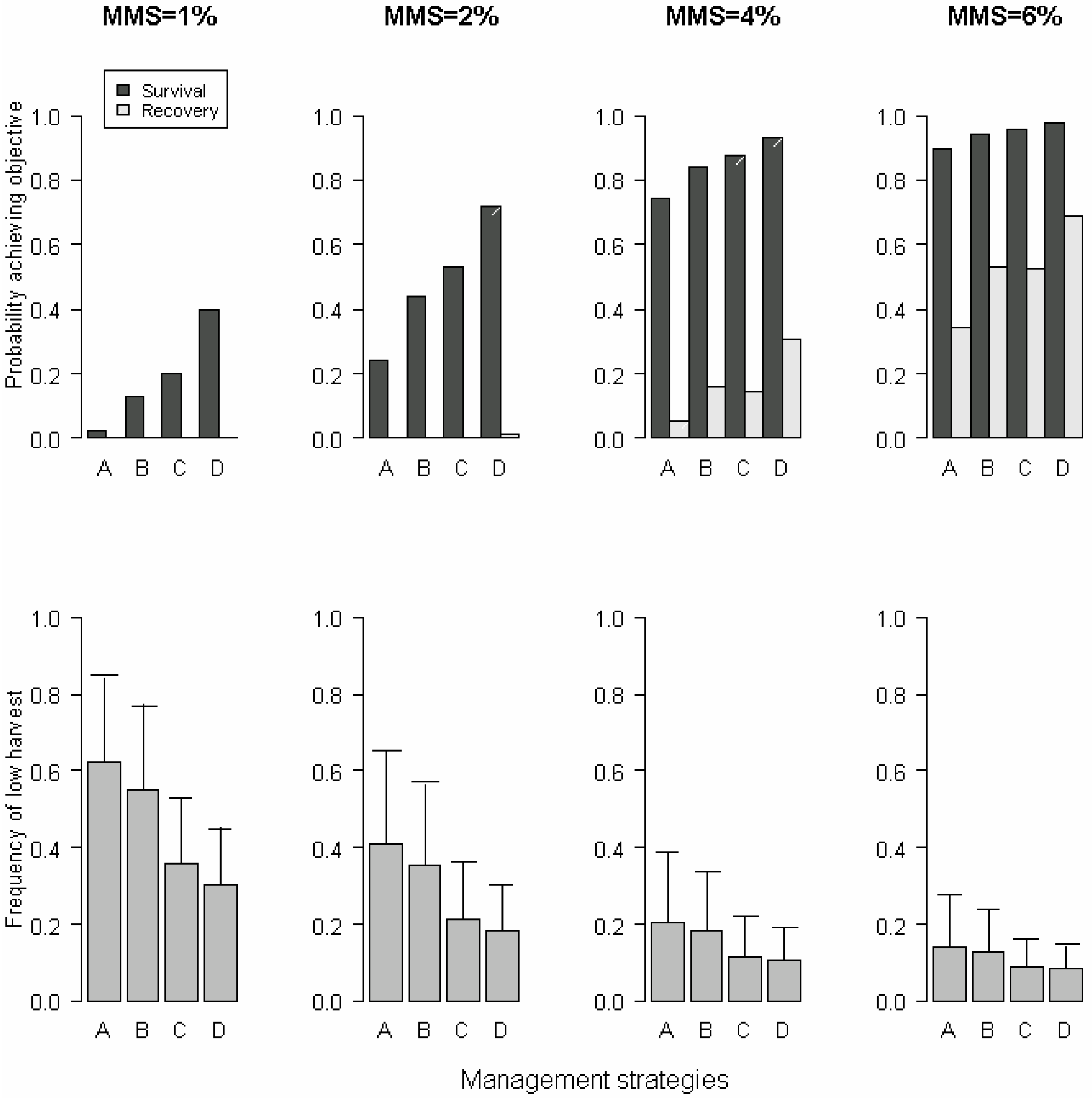

Figure 9 Same as Figure 8 except results are based on using harvest rule 2 (H_{min} = 0.30, H_{max} = 0.60) as opposed to harvest rule 1.

probabilities (from 90% belief in the low value of the uncertain parameter to 90% belief in the high value) of alternative states of the parameter in question. For example, if one is confident that the RHMS is most likely 0.8 instead of 0.2, then the focus would be in the final row of Figure 10. Information in the cells of this row represents 90% belief that the true value of RHMS is 0.8 and only 10% belief that the true value of RHMS is 0.2. Of the two uncertainties considered, my results were most sensitive to the RHMS parameter.

Changes in the degree of belief in *RHMS* (Figures 10 and 11) had a moderate effect in determining the optimal management strategy. Using harvest rule 1 (Figure 10), the level of uncertainty in RHMS was large enough to create a range of strategies that achieved the survival objective with ≥90% probability, particularly under MMS rates of 2% and above. My results also show that when there was a 90% degree of belief in *RHMS* being high (0.8), strategy D met the survival objective with a MMS of only 1%. Results for the recovery objective were much less sensitive to changes in *RHMS*, with changes in strategies occurring only under a MMS ≥4% (right side of Figure 10). When harvest rule 2 was used (Figure 11), results for the survival objective were most sensitive under MMS rates of 4% and 6%. Recovery results were completely insensitive to changes in the degree of belief in RHMS while using the more aggressive harvest rule 2 because none of the strategies achieved the objective with 90% probability under any of the MMS rates evaluated.

Changes in the degree of belief in the *k* parameter, which relates predation losses of sockeye to pikeminnow abundance, did not affect the optimal action (Figures 12 and 13). Using harvest rule 1 (Figure 12), the level of uncertainty in *k* was not large enough to change the optimal management strategy for either the survival or the recovery objective. The model results for the survival objective were only slightly sensitive to changes in *k* when harvest rule 2 was used (Figure 13). With a 6% MMS rate, a minimum of 40% degree of belief in the high *k* was required for strategy A to meet the survival objective (Figure 13). Results were completely insensitive to changes in *k* for the recovery objective under harvest rule 2, where none of the strategies achieved the objective with 90% probability under any of the MMS rates evaluated.

A	**sq hatchery and terminate predator control**
B	**sq hatchery and continued predator control**
C	**extend hatchery and terminate predator control**
D	**extend hatchery and continue predator control**

Degree of belief

	Mean marine survival rate			
P1_RHMS (0.8)	**1%**	**2%**	**4%**	**6%**
0.1	None	None	B/C/D	All
0.2	None	None	B/C/D	All
0.3	None	None	B/C/D	All
0.4	None	D	B/C/D	All
0.5	None	D	All	All
0.6	None	D	All	All
0.7	None	C/D	All	All
0.8	None	C/D	All	All
0.9	D	C/D	All	All

Survival

	Mean marine survival rate			
P1_RHMS (0.8)	**1%**	**2%**	**4%**	**6%**
0.1	None	None	None	B/C/D
0.2	None	None	None	B/C/D
0.3	None	None	None	B/C/D
0.4	None	None	None	B/C/D
0.5	None	None	None	B/C/D
0.6	None	None	None	B/C/D
0.7	None	None	None	B/C/D
0.8	None	None	None	All
0.9	None	None	D	All

Recovery

Figure 10 Prescription tables showing which management strategies (A-D) meet the survival (left) and recovery (right) objectives with at least 90% probability across a range of mean marine survival rates and different degrees of belief for the RHMS of sockeye. Moving down each column mean that greater belief (from 10% to 90%) is placed on high RHMS (0.8) as the true state of nature, rather than RHMS being only 0.2. These results are based on using harvest rule 1 (H_{min}=0.12, H_{max}=0.5).

A	**sq hatchery and terminate predator control**
B	**sq hatchery and continued predator control**
C	**extend hatchery and terminate predator control**
D	**extend hatchery and continue predator control**

Degree of belief

	Mean marine survival rate			
P1_RHMS (0.8)	**1%**	**2%**	**4%**	**6%**
0.1	None	None	D	B/C/D
0.2	None	None	D	B/C/D
0.3	None	None	D	B/C/D
0.4	None	None	D	B/C/D
0.5	None	None	D	All
0.6	None	None	D	All
0.7	None	None	C/D	All
0.8	None	None	C/D	All
0.9	None	None	B/C/D	All

Survival

	Mean marine survival rate			
P1_RHMS (0.8)	**1%**	**2%**	**4%**	**6%**
0.1	None	None	None	None
0.2	None	None	None	None
0.3	None	None	None	None
0.4	None	None	None	None
0.5	None	None	None	None
0.6	None	None	None	None
0.7	None	None	None	None
0.8	None	None	None	None
0.9	None	None	None	None

Recovery

Figure 11 Same as Figure 10 except results are based on using harvest rule 2 (H_{min} = 0.30, H_{max} = 0.60) as opposed to harvest rule 1.

A	**sq hatchery and terminate predator control**
B	**sq hatchery and continued predator control**
C	**extend hatchery and terminate predator control**
D	**extend hatchery and continue predator control**

Degree of belief

	Mean marine survival rate			
P1_k (15x10^-6)	**1%**	**2%**	**4%**	**6%**
0.1	None	D	All	All
0.2	None	D	All	All
0.3	None	D	All	All
0.4	None	D	All	All
0.5	None	D	All	All
0.6	None	D	All	All
0.7	None	D	All	All
0.8	None	D	All	All
0.9	None	D	All	All

Survival

	Mean marine survival rate			
P1_k (15x10^-6)	**1%**	**2%**	**4%**	**6%**
0.1	None	None	None	B/C/D
0.2	None	None	None	B/C/D
0.3	None	None	None	B/C/D
0.4	None	None	None	B/C/D
0.5	None	None	None	B/C/D
0.6	None	None	None	B/C/D
0.7	None	None	None	B/C/D
0.8	None	None	None	B/C/D
0.9	None	None	None	B/C/D

Recovery

Figure 12 Prescription tables showing which management strategies meet the survival (left) and recovery (right) objectives with at least 90% probability across a range of mean marine survival rates and different degrees of belief for the impact of Northern pikeminnow on the sockeye Sm/Sp relationship. Moving down each column means that greater belief (from 10% to 90%) is placed on the high *k* value (15×10^{-06}) as the true state of nature. These results are based on using harvest rule 1 ($H_{min} = 0.12$, $H_{max} = 0.50$).

A	**sq hatchery and terminate predator control**
B	**sq hatchery and continued predator control**
C	**extend hatchery and terminate predator control**
D	**extend hatchery and continue predator control**

Degree of belief

	Mean marine survival rate			
P1_k (15x10^-6)	**1%**	**2%**	**4%**	**6%**
0.1	None	None	D	B/C/D
0.2	None	None	D	B/C/D
0.3	None	None	D	B/C/D
0.4	None	None	D	All
0.5	None	None	D	All
0.6	None	None	D	All
0.7	None	None	D	All
0.8	None	None	D	All
0.9	None	None	D	All

Survival

	Mean marine survival rate			
P1_k (15x10^-6)	**1%**	**2%**	**4%**	**6%**
0.1	None	None	None	None
0.2	None	None	None	None
0.3	None	None	None	None
0.4	None	None	None	None
0.5	None	None	None	None
0.6	None	None	None	None
0.7	None	None	None	None
0.8	None	None	None	None
0.9	None	None	None	None

Recovery

Figure 13 Same as Figure 12 except results are based on using harvest rule 2 (H_{min} = 0.30, H_{max} = 0.60) as opposed to harvest rule 1.

4.0 DISCUSSION

I have demonstrated that large increases in probability of achieving survival and recovery objectives are possible through predator control and hatchery operations, but ultimately the survival/recovery of this population is highly dependent on factors that are not controllable (i.e. marine survival). The model predicts that achieving the survival objective with at least 90% probability is possible under poor (2%) mean marine survival using harvest rule 1, but achieving the recovery objective will be unlikely unless marine survival rates average 6%. The observed long-term average marine survival is 6.8%, but the average marine survival for the period 1999 through 2006 has been <3% (J. Hume, personal communication). My results suggest that the Cultus sockeye population will never recover under the current harvest rule and any of the management strategies evaluated. This conclusion is consistent with recent returns, which continue to decline despite the ongoing recovery efforts. However, recovery of the population is possible if marine survival rates average 4% or greater when the most intensive strategy (continued predator control and extended hatchery operations) is adopted under harvest rule 1.

My results demonstrate the importance of maintaining conservative harvest rates in combination with the other recovery actions. Harvesting at higher levels, as represented here by harvest rule 2, will prevent sustainable growth of the population, counteracting any gains in productivity of the population resulting from the predator control and hatchery operations. Pestes et al. (2008) also demonstrated the importance of maintaining conservative harvest rates, particularly when considering uncertainty in future pre-spawning mortality (PSM) rates. Although I did not include PSM in my simulations of Cultus sockeye, its effect can be seen as one mechanism by which MMS rates would decline to levels as low as the ones I simulated (e.g. 1%).

The sensitivity of results to alternative management strategies, as well as uncertainty in model parameters, was inconsequential compared with sensitivity to uncertainty in future marine survival rates. It is important to remember, however, that the range of MMS rates evaluated here represents a 6-fold increase from lowest (1%) to highest (6%). The difference in survival/recovery probabilities is small among the alternative management strategies at high marine survival rates; this therefore may make the more intensive strategies not worth the extra cost if future marine survival is expected to be high, but I have not done the economic analyses related to that question.

The model predicts a different rank order of management strategies for meeting the recovery versus the survival objective. For instance, my results suggest that, individually, continued predator control (strategy B) and status quo hatchery operations (strategy C) contribute equally towards achieving the recovery objective (Figures 8 and 9). However, this is not true for the survival objective, particularly at MMS rates <4%, where the extended hatchery operations contribute a greater amount than does continued predator control.

4.1 Management Implications

4.1.1 Predator control

Predator control has a long history in natural resource management, but efforts have not always resulted in the desired effect. Past failures of predator control programs are mainly related to the lack of understanding of the complexities of ecological systems and a lack of monitoring of results of management strategies and subsequently learning from them (Lessard et al. 2005, Meacham and Clark 1979). At Cultus Lake, continued active control of northern pikeminnow may have unpredictable consequences in the lake ecosystem, such as an increase in abundance of a sockeye competitor that would otherwise be maintained by northern pikeminnow presence in the lake. For instance, past predator control programs at Cultus Lake likely led to an increase in the threespine stickleback (*Gasterosteus aculeatus*) population, a competitor of juvenile sockeye salmon (Foerster 1968). Thus, an important component of the recovery efforts at Cultus Lake should be the monitoring of other fish species in order to identify and document if an undesirable ecosystem response occurs.

There is a general lack of knowledge about the nature of the relationship between juvenile sockeye salmon survival and northern pikeminnow predation rates. For Cultus Lake the problem lies in the reliability of predator abundance estimates over the past 70 years and in limited knowledge of predator diet. It has been suggested that northern pikeminnow predation may be a source of depensatory mortality in juvenile Cultus sockeye (Steigenberger 1972, COSEWIC 2003) and that this likely happens during smolt out-migration when northern pikeminnow may aggregate at the lake outlet. However, there is no conclusive evidence for such a relationship and recent investigations (Bradford et al. 2007) into movements of northern pikeminnow within Cultus Lake revealed that an aggregation of northern pikeminnow at the lake outlet does not seem to occur during years with very low sockeye abundance. This leads one to believe that encounters between northern pikeminnow and juvenile sockeye occur randomly during years of low sockeye abundance and that northern pikeminnow likely switch to other, more abundant, prey such as redside shiner (*Richardsonius balteatus*) and threespine stickleback during these times. This line of thinking is supported by Ricker (1941) at Cultus Lake, where it was observed that in years of small sockeye populations, consumption of alternative prey by northern pikeminnow increases.

It is important to recognize that the assumptions made here about northern pikeminnow predation represent a conservative approach, from the standpoint of sockeye recovery, in that the simulated predation rates are relatively small and do not represent a source of depensatory mortality on sockeye. The benefits of predator control would be even greater if northern pikeminnow are a source of depensatory mortality in sockeye. The model simulates a relationship where predation occurs randomly and increases with predator abundance. The nature of this relationship is largely unknown, and better methods of collecting data for northern pikeminnow diets are necessary so that the real impacts of predation can be illuminated.

The effects of the pikeminnow removal on the survival of juvenile sockeye salmon in Cultus Lake is being assessed by DFO and results from the current program will be available in the next few years by comparing the freshwater survival index (fall fry or smolts per spawner) in years with and without predator removal. However, due to the highly variable nature of freshwater and marine survival, many years of northern pikeminnow removal may be necessary to increase confidence in effectiveness of the predator removal program.

Ricker and Foerster (1941) noticed that after predator removals, freshwater survival of sockeye juveniles increased and that the average size of sockeye smolt migrants increased. They hypothesized that this was a result of less competition because fewer newly hatched fry were required to produce a given number of migrants. However, in light of newer hypotheses about species interactions between predators and their prey (foraging arena theory; Walters and Martell 2004), it seems that a likely cause of this phenomenon would be that there is reduced predator avoidance and therefore increased feeding and growth among sockeye fry in the lake. This type of interaction has been demonstrated for other sockeye lakes (Eggers 1978).

To achieve the recovery objective, I recommend that FOC continue with predator control efforts and monitor not only the northern pikeminnow population but the whole lake system. Monitoring the whole system will help to determine if undesired changes in the ecosystem, resulting from predator control, have occurred. To achieve the survival objective (i.e. maintaining a persistent low abundance of Cultus Lake sockeye), extended hatchery operations appear to be more effective than predator control.

In his review of the theory, Soule (1985) identifies that conservation biology is a crisis-oriented discipline where sometimes action must be taken before knowing all the facts. At Cultus Lake northern pikeminnow removals are ongoing, but the long term consequences of removing so many large fish from the lake are difficult to predict. Likewise, the hatchery program designed to aid in the recovery of Cultus sockeye has significant momentum and will likely continue for at least the next ten years. However, the long-term effects of the program are uncertain.

4.1.2 Hatchery operations

There are many potential benefits of broodstock/supplementation programs, such as reducing short-term extinction probability through increased recruitment, maintaining a reserve of genetic material, and maintaining the population until causes of the decline are addressed. My results suggest that extending the hatchery program results in the highest probability of all management strategies for meeting the objectives (survival and recovery) and allows for more harvest. However, extending the hatchery program may pose other problems associated with the increase of hatchery origin fish in the population. Thus, it is important to consider the potential negative consequences. Waples and Drake (2004) summarize the major problems associated with supplementation programs, such as loss of genetic diversity, increased disease susceptibility, and increased straying. These are all related to genetic changes in the population resulting from supplementation programs.

The most likely mechanism for genetic change in hatchery environments is domestication (i.e. natural selection in artificial environments; Fritts et al. 2007). A recent study a steelhead (*Oncorhynchus mykiss*) reared in captivity showed that genetic effects of domestication reduced subsequent reproductive capabilities by approximately 40% per captive-reared generation (Araki et al. 2007). Domestication selection may be most extreme when ecological conditions such as predation are different between natural and hatchery environments (Waples and Drake 2004, Frits et al. 2007). The relaxation of predator-induced mortality in hatcheries can result in genetic differences that are maladaptive in natural environments and ultimately result in reduced survival.

Frits et al. (2007) found that reduced survival of Chinook salmon (*Oncorhynchus tshawytscha*) fry, when exposed to piscivorous predators, occurred after only one generation of state-of-the-art hatchery culture. The potential for this type of response in the Cultus sockeye population, coupled with the predator control efforts, presents a unique but dangerous situation. The danger here is in the potential loss of genotypes with specific predator avoidance behaviours, as a result of supplementation into an environment which lacks large numbers of predators. Maintaining the selective pressure of a predator-rich environment may be important to maintain genotypes that will be important in future generations, when predators in the lake return to original levels of abundance.

In my analysis, I have identified management options and have quantified their potential effects on the recovery of the Cultus sockeye salmon. I evaluated the major uncertainties in sockeye life history and used best available knowledge to simulate likely outcomes of alternative management strategies. Accounting for the uncertainties brings greater transparency and also facilitates logical system-scale thinking (management choices).

When there are competing goals, in this case between maximizing survival and recovery probabilities and minimizing harvest restrictions, the task is to find a solution that provides a best compromise. This involves making decisions about the preferences of society which are usually undertaken by managers. The major difficulty in determining the best compromise for the Cultus situation is that the tradeoffs are so large. Maintaining the population has significant cultural and biological importance, but the competing economic tradeoffs involved are substantial. Pestes et al. (2008) showed that, by using alternative harvest rules, probability of recovery of the Cultus Lake sockeye salmon population could be increased from 60% to 90%, but in one of their scenarios this resulted in a reduction in expected annual gross revenue of at least $6.7 million per year (13%) for the commercial fleet that targets all late-run Fraser River sockeye salmon.

Ultimately only time will tell if our actions result in the recovery of the Cultus sockeye population, but continued monitoring is necessary to ensure that we can recognize whether the management actions or some other factors enable rebuilding of the population. Our ability to control the situation is limited and it is not easy to identify an optimal policy, mainly because the system is driven by the uncertainty in marine survival.

LITERATURE CITED

Allendorf, F.W., Bayles, D., Bottom, D.L., Currens, K.P., Frissell, C.A. Lichatowich, J.A., Nehlsen, W., Trotter, P.C., Williams, T.H. 1997. Prioritizing pacific salmon stocks for conservation. Conservation biology. 11(1): 140-152.

Araki, H., Cooper, B., Blouin, M.S. 2007. Genetic effects of captive breeding cause a rapid cumulative fitness decline in the wild. Science. 318: 100-103.

Beamesderfer, R.C.P., Ward, D.L., Nigro, A.A. 1996. Evaluation of the biological basis for a predator control program on northern squawfish (*Ptychocheilus oregonensis*) in the Columbia and snake rivers. Canadian journal of fisheries and aquatic sciences. 53: 2898-2908.

Bradford, M.J., Amos, J.,Tovey, C.P., Hume, J.M.B., Grant, S., Mossop, B. 2007.. Abundance and migratory behaviour of Northern pikeminnow (*Ptychocheilus oregonensis*) in Cultus Lake, British Columbia and implications for predator control. Canadian technical report of fisheries and aquatic sciences. 2723: vii+47 pp.

Bradford, M.J., Wood, C.C. 2004. A review of biological principles and methods involved in setting minimum population sizes and recovery objectives for the September 2004 drafts of the Cultus and Sakinaw Lake sockeye salmon and interior Fraser coho salmon recovery plans. DFO Can. Sci. Advis. Sec. res. Doc. 2004/128.

COSEWIC. 2003. COSEWIC assessment and status report on the sockeye salmon *Oncorhynchus nerka* (Cultus population) in Canada. Committee on the status of Endangered Wildlife in Canada. Ottawa. ix + 57 pp.

Cultus Sockeye Recovery Team. 2004. National recovery strategy for sockeye Salmon (*Oncorhynchus nerka*), Cultus Lake population, in British Columbia. National Recovery Strategy No. XXX. Recovery of Nationally Endangered Wildlife (RENEW). Ottawa, Ontario, 57 pp.

Drechsler, M. 2000. A model-based decision aid for species protection under uncertainty. Biological Conservation. 94: 23-30.

Drechsler, M. Burgman, M.A. 2004. Combining population viability analysis with decision analysis. Biodiversity and Conservation. 13:115-139.

Eggers, D.M. 1978. Limnetic feeding behavior of juvenile sockeye salmon in Lake Washington and predator avoidance. Limnology and Oceanography. 23 (6):1114-1125.

Fisheries and Oceans Canada. 2004. A policy framework for conservation of wild Pacific salmon. Vancouver, B.C. DFO.

Foerster, R.E. and Ricker, W.E. 1938. The effectiveness of predator control in decreasing the mortality of young sockeye salmon (*Oncorhynchus nerka* Walbaum). Verh. Int. Verein. Limnol. 8:151-167.

Foerster, R.E. and Ricker, W.E. 1941. The effect of reduction of predaceous fish on survival of young sockeye salmon at Cultus Lake. J. Fish. Res. Bd. Canada 5:315-336.

Foerster, R.E. 1968. The sockeye salmon (*Oncorhynchus nerka*). Fish. Res. Board Can. Bull. 162. Ottawa.

Ford, M.J. 2005. Selection in captivity during supportive breeding may reduce fitness in the wild. Conservation Biology. 16(3): 815-825.

Frits, A.L., Scott, J.L., Pearsons, T.N. 2007. The effects of domestication on the relative vulnerability of hatchery and wild origin spring Chinook salmon (Oncorhynchus tshawytscha) to predation. Can. J. Fish. Aquat. Sci. 64: 813-818.

Friesen, T.A., and Ward, D.L. 1999. Mangement of northern pikeminnow and implications for juvenile salmonid survival in the lower Columbia and Snake rivers. N. Am. J. Fish. Manage. 19:406-420.

Gross, M. R., Montagnes, P., Parkes, M., Riis, P., Roberts, B., Turner, M.A. 2004. Extinction by miscalculation: The threat to Sakinaw and Cultus Lake Sockeye. University of Toronto. Toronto, Canada.

GSGislason & Associates Ltd. 2004. socio-economic implications of the species at risk act: Sakinaw and Cultus sockeye. Prepared for Canada department of Fisheries and Oceans.

Hall, D.L. 1992. Summary of 1991 and 1992 squawfish removal program, Cultus Lake British Columbia. Contract report FP 91-5001, Dept. Fish. Oceans, Pacific Biological Station, Nanaimo, B.C. 30pp.

Harwood, J. 2000. Risk assessment and decision analysis in conservation. Biological conservation. 95: 219-226.

Irvine, J.R., Gross, M.R., Wood, C.C., Holtby, L.B., Schubert, N.D., Amiro, P.G. 2005. Canada's species at risk act: An opportunity to protect endangered salmon. Fisheries 30 (12) 11:19.

Lessard, B.R., Martell, S.J.D., Walters, C.J., Essington, T.E., Kitchell, J.F. 2005. Should ecosystem management involve active control of species abundances? Ecology and Society 10 (2).

Morgan, M.G. and Henrion, M. 1990. Uncertainty: a guide to dealing with uncertainty in quantitative risk and policy analysis. Cambridge University Press, Cambridge, United Kingdom.

Meacham, C.P. and Clark, J.H. 1979. Management to increase anadromous salmon production *In* predator-prey systems in fisheries management. *Edited by* H. Clepper. Sport Fishing Institute, Washington, D.C. pp. 377-386.

Mossop, B., Bradford, M.J., and Hume, J.M.B., 2004. Review of northern pikeminnow (*Ptychocheilus oregonensis*) control programs in western North America with special reference to sockeye salmon (*Oncorhynchus nerka*) production in Cultus Lake, British Columbia. Report prepared for the Cultus Sockeye Recovery Team. Vancouver. 58 p.

Pestes, L.R., Peterman, R.M., Bradford, M.J., Wood, C.C. 2008. Bayesian decision analysis for evaluating management options to promote recovery of a depleted salmon population. Conservation Biology. In Press. doi:10.1111/j.1523-1739.2007.00875.x

Peterman, R.M., and Anderson, J.L. 1999. Decision analysis: a method for taking uncertainties into account in risk-based decision making. Human and Ecological Risk Assessment. 5: 231-244

Peters, C.N., Marmorek, D.R. Deriso, R.B. 2001. Application of decision analysis to evaluate recovery actins for threatened Sanke River fall Chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. 58: 2447-2458.

Ricker, W.E. 1941. The consumption of young sockeye salmon by predaceous fish. J. Fish. Res. Board. Can. 5:293-313.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations.Bulletin of the Fisheries Research Board of Canada, 191: 382pp.

Scott, W.B., and Crossman, E.J. 1998. Freshwater fishes of Canada. Galthouse publications Ltd. Oakville, Ont. Canada. 966 pp.

Shaffer, M.L. 1981. Minimum population sizes for species conservation. Bioscience. 31 (2): 131-134.

Soule, M.E. 1985. What is conservation biology? Bioscience 35 (11): 727-734.

Schubert, N.D., Beacham, T.D., Cass, A.J., Cone, T.E., Fanos, B.P., Foy, M., Gable, J.H., Grout, J.A., Hume, J.M.B., Johnson, M., Morton, K.F., Shortreed, K.S., Staley, M.J. 2002. Status of Cultus Lake sockeye salmon (*Oncorhynchus nerka*). Canadian Science Advisory Secretariate Res. Doc. 2002/064. Fisheries and Oceans Canada, Ottawa, Ont.

Steigenberger, L.W. 1972. Observations on the predation by squawfish (*Ptychocheilus oregonensis*) on sockeye salmon (*Oncorhynchus nerka*), with particular reference to Cultus Lake, British Columbia. M.Sc. Thesis, University of British Columbia, 111 pp.

Utter, F. 1998. Genetic problems of hatchery-reared progeny released into the wild, and how to deal with them. Bull. Mar. Sci. 62: 623-640.

VanderWerf, E.A., Groombridge, J.J., Fretz, J.S., Swinnerton, K.J. 2006. Decision analysis to guide recovery of the po'ouli, a critically endangered Hawaiian honeycreeper. Biological conservation 129: 383-392.

Walters, C.J. and Martell, J.D. 2004. Fisheries ecology and Management. Princeton University press. Princeton, New Jersey. 399 pp.

Waples, R. and Do, C. 1994. Genetic risk associated with supplementation of Pacific salmonids: Captive broodstock programs. Can. J. Fish. Aquat. Sci. 51(suppl. 1) 310:329.

Waples, R. and Drake 2004. Risk/Benefit considerations for marine stock enhancement: A Pacific salmon perspective. In Stock enhancement and sea ranching: Developments, pitfalls and opportunities. Edited by Leber, K.M., Kitada, S., Blankenship, H.L., and T. Svasand. Blackwell publishing. Ames, Iowa, USA.