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Status of Cultus Lake Sockeye Salmon

État de la population de saumon sockeye du lac Cultus

Bradford, M.J., Hume, J.M.B., Withler, R.E., Lofthouse, D., Barnetson, S. Grant, S., Folkes, M., Schubert, N., Huang, A-M.

Fisheries and Oceans Canada
Science Branch
Cooperative Resource Management Institute
School of Resource and Environmental Management
Simon Fraser University
Burnaby, B.C. V5A 1S6

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ABSTRACT

The sockeye salmon (*Oncorhynchus nerka*) population from Cultus Lake, British Columbia, was assessed as endangered in 2003 as a result of a long term decline in abundance that began in the 1970s. Recovery measures that include a conservation breeding program, harvest management and a predator control program in Cultus Lake have been implemented. This report reviews the current status of the population and the efficacy of the recovery measures. We found that that status of the population has not improved since 2003 largely because of poor smolt-recruit survival, and the average number of spawners remains at about 1000 fish. Harvest rates have been reduced since the 1990s and the predator control program appears to have increased the survival of juveniles in the lake. Supplementation releases of juveniles from the captive breeding program to the lake have resulted in increasing numbers of returning hatchery adults, but their success as spawners in the wild remains unknown. Modelling suggests that under the current low smolt-recuit survival rates, recovery is only possible with the successful implementation of all recovery measures. We conclude that the recovery of the Cultus Lake sockeye salmon population is highly uncertain and that continued monitoring is needed to determine if the recovery actions are indeed reducing risks to the population.

RÉSUMÉ

La population de saumon sockeye (*Oncorhynchus nerka*) du lac Cultus (Colombie-Britannique) a été désignée espèce en voie de disparition en 2003 à la suite d'un déclin à long terme de l'abondance ayant commencé dans les années 1970. Des mesures de rétablissement incluant un programme de conservation et de reproduction, la gestion des prélèvements et un programme de lutte contre les prédateurs dans le lac Cultus ont été mises en œuvre. Le présent rapport examine l'état actuel de la population et l'efficacité des mesures de rétablissement. Nous avons constaté que l'état de la population ne s'est pas amélioré depuis 2003, en grande partie à cause d'une faible survie du stade de saumoneau au stade de recrue et parce que le nombre moyen de reproducteurs est resté environ à 1 000 poissons. Les taux de récolte ont été réduits depuis les années 1990 et le programme de lutte contre les prédateurs semble avoir permis d'augmenter la survie des juvéniles dans le lac. Les libérations de juvéniles à la suite d'ensemencement dans le lac dans le cadre du programme de reproduction en captivité ont permis d'augmenter l'effectif des adultes d'écloserie qui participent à la remonte, mais leur succès en tant que reproducteurs dans la nature demeure inconnu. La modélisation donne à penser que d'après les faibles taux de survie actuels du stade de saumoneau au stade de recrue, le rétablissement est uniquement possible grâce à la mise en œuvre réussie de toutes les mesures de rétablissement. Nous concluons que le rétablissement de la population de saumon sockeye du lac Cultus est très incertain et qu'il faut assurer une surveillance continue pour déterminer si les mesures de rétablissement aident vraiment à réduire les risques pour la population.

INTRODUCTION

Cultus Lake is a small lake (6.4 km^2) located in the lower Fraser valley, and is the natal area for the Cultus Lake sockeye salmon (*Oncorhynchus nerka*) Conservation Unit (CU, Holtby and Ciruna 2007). This population has considerable importance for the Soowahlie Band of the Sto:Lo First Nation, and has been a contributor to commercial and sports fisheries since the late 1800s (CSRT 2009). In addition, there is a significant legacy for Western science from the studies that have been conducted at the lake since 1923 (see Foerster 1968 for entry into the early literature).

The abundance of adult sockeye salmon returning to Cultus Lake began to decline in the 1970s (Figure 1), probably as the result of fishing that exceeded sustainable rates (CSRT 2009). That decline accelerated in the late 1990s, because of a combination of poor smolt-recruit survival and increased rates of premature mortality of adult spawners once they reach the lake (often called pre-spawning mortality, PSM).

These declines prompted a review of the status of the Cultus population in 2002 (Schubert et al. 2002), and a Committee on the Status of Endangered Wildlife in Canada assessment in 2003 (COSEWIC 2003). COSEWIC determined that the population was endangered, however, it was not listed in Schedule 1 under SARA. A recovery team was formed in 2004, whose work ultimately lead to the publication of a Conservation Strategy (CSRT 2009).

The risk of an extended period prespawning mortality and poor survival was considered an immediate risk and a captive breeding was included as an element of the conservation strategy (CSRT 2009). Prior to the recent declines in abundance, the Cultus sockeye salmon population was characterized by unusual allele frequencies and low levels of diversity at allozyme and microsatellite loci for a Fraser River sockeye salmon population (Withler et al. 2000). The effect of ongoing small population size on fitness in this genetically isolated and highly specialized population has been recognized as a threat to its persistence (Schubert et al. 2002). Populations greatly reduced in size during periods of low survival lose genetic diversity due to genetic drift and inbreeding, processes that cause reductions in fitness and lead to even lower survival and the possibility of an extinction vortex (Gilpin and Soulé 1986). Captive breeding, in which individuals are removed from the natural environment for at least one entire life cycle to increase survival and reproductive capacity, is a rapid means of increasing juvenile production in highly fecund species such as sockeye salmon. Pedigreed breeding programs can minimize the loss of genetic diversity due to inbreeding and random processes, but pose their own challenges to maintenance of fitness in the wild environment (Fraser 2008). The alteration or relaxation of natural selection experienced in captivity may engender genetic alterations that impose a cost to fitness upon those individuals ultimately re-introduced to the natural environment (Lynch and O'Hely 2001, Araki *et al*. 2008).

Additional recovery actions include a reduction in harvest rates and the implementation of a predator control program. In addition, a number of studies were conducted at the lake on the biology of the fish and the lake environment. Recognizing the experimental nature of these interventions an intensive assessment program has accompanied the recovery actions.

Here we provide an update on the status of the Cultus Lake sockeye salmon population. The request for Science Advice that initiated this work is:

"What is the current status of the Cultus sockeye population? How has the population responded

to recovery actions to date and what are its prospects for recovery? This will entail an evaluation against the interim goal and objectives of the Conservation Strategy as well as establishing indicators and benchmarks consistent with the Wild Salmon Policy."

We address the request by providing analysis of:

1. recent trends in the population, with focus on the last 2 generations,
2. the current status of the population relative to Conservation Objectives 1 & 2 of the Conservation Strategy and proposed Wild Salmon Policy benchmarks,
3. the efficacy of the major recovery actions: harvest reductions, captive broodstock and predator control, and
4. possible future trajectories of the population as a function of various combinations of recovery actions and environmental conditions (using a population viability model).

The Conservation Goal of CSRT (2009) is *"to halt the decline of the Cultus Lake sockeye population and return it to the status of a viable sell-sustaining and genetically robust wild population that will contribute to ecosystems and have the potential to support sustainable use*"

Objective 1 of the CSRT (2009) is "Ensure the genetic integrity of the population by exceeding a 4-year arithmetic mean of 1 000 successful adult spawners with no fewer than 500 successful adult spawners on any one cycle." Objective 2 is "Ensure growth of the successful adult spawner population for each generation (that is, across 4 years relative to the previous 4 years) and on each cycle (relative to its brood year) for not less than 3 of 4 consecutive years". These objectives were considered intermediate steps in the recovery process towards a larger, sustainable population.

Two other objectives of CRST (2009) were to rebuild the population to allow for a de-listing by COSEWIC (Objective 3), and long term sustainable use (Objective 4). However, CRST (2009) did not provide numerical targets for these objectives. We decided that these Objectives could be supplanted by the lower and upper benchmarks of the Wild Salmon Policy (WSP) (Fisheries and Oceans Canada 2005), and thus they were replaced by these two provisional WSP abundance benchmarks.

The assessment of biological status for each Pacific Salmon CU is a requirement of the WSP. To determine CU status, different classes of indicators (spawner abundance, trends-in-abundance, distribution, and fishing mortality) and associated metrics (e.g. S_{gen}, S_{msy}, trends in abundance over the last three generations, etc.) have been identified (Holt *et al*. 2009). These metrics are used to establish two benchmarks to delineate CU status into one of three categories: red, amber, and green. Conservation unit status changes from green to amber to red signal the need for increased conservation and management actions for the CU (Fisheries and Oceans Canada 2005). Here, only spawner abundance was considered, as surrogates for Objectives 3 and 4 of CRST (2009), thus our analysis is only a subset of the considerations that might be included in a full WSP status evaluation. The other factors, including rates of decline, distribution and fishing mortality trends will be the subject of a Centre for Science Advice-Pacific (CSAP) paper in November 2010.

DATA SOURCES

Much of the data (up to and including the 2001 brood year) were from the previous status report for Cultus sockeye salmon (Schubert et al. 2002). Efforts have been made to verify and document the earlier data, as well as add the newly available information, but that effort has not been completed (Cleary et al., *in prep*). Consequently, comprehensive data tables are not presented in the current report, but will be made available later in 2010.

The escapement of Cultus Lake sockeye salmon returning to Cultus Lake has been estimated from fences located in Sweltzer Creek, 200 – 300 m below the Cultus Lake outlet since 1921. The basic operational procedures were described in Schubert et al. (2002). Fish are visually assessed as jacks or adults, and the sex of the adults is also estimated visually. Hatchery-bred fish, marked by a missing adipose fin began to return in significant numbers in 2006 and a mirror was installed at a 45º angle in the fence gate to enable the status of the adipose fin to be viewed on returning adults without handling. Coded-wire tags (CWT) are present in some adipose-clipped fish, and the proportion of CWT tagged fish was estimated from recoveries in the captive brood population and by the use of a detector wand to subsample some of the fish passing the fence. CWT rates were then expanded to the unsampled population. DNA samples are obtained from all captive broodstock fish, as well as some of those handled at the fence.

Beginning in October the lake shores are surveyed for carcasses by boat and on foot, and some carcasses are recovered from the counting fence. Biological information and spawning success is obtained from carcasses. Spawning success (1-PSM) is estimated from the ratio of spawned to unspawned female carcasses recovered from the lake. In recent years these estimates are likely biased low because the probability of capture of unspawned females appears to be higher than for spawned fish. PSM fish often die 1-2 months prior to spawning (Bradford et al. 2010) and are recovered along the margins of the lake. The probability of recovery of a spawned fish is lower as spawning now takes place at depth along the lake margins and carcasses sink to the bottom after death (Pon et al. 2010). As well, the peak of spawning is at the end of November, and weather conditions often impair recovery efforts of spawned carcasses compared to earlier in the fall when unspawned carcasses are available. Historical (pre-2000) estimates of spawning success may be less biased as there was significant spawning in shallow water at the south end of the lake where spent carcasses could be more readily recovered. As annual estimates of spawning success are required for some analyses, so a composite time series of spawning success was constructed that used direct PSM estimates from lake prior to 1999, and PSM rates from the captive broodstock (Bradford et al. 2010) and Weaver Creek spawning channel for 2000-2009. While these surrogates are likely useful for indicating major trends, the accuracy of annual estimates is unknown.

Estimates of spawner age are obtained in 2 ways: in the field, all fish that pass the fence or are captured for broodstock are visually classed as jacks and adults based on length. For those fish from which biological samples are taken scale and otolith readings are used to estimate age. Age readings are used by the Pacific Salmon Commission for the reconstruction of broods (recruits), but have not been used to correct the field estimates of age from fence or captive broodstock data. For this analysis, we assume that field estimates of “jacks” are age-3 fish, and “adults” are age-4 or age-5 fish. In the past less than 5% of adults are estimated to be age-5s using scales. A preliminary analysis of the 2008 and 2009 age readings indicates about 4.5% of field assessed jacks were age-4 fish, and only 1 of 413 “adults” was an age-3 fish.

Traditionally, jacks are assumed to be all males, but in this sample 13% of age-3 adults were female.

Juvenile sockeye salmon fry and other pelagic fish rearing in Cultus Lake were sampled and their abundance estimated from 1989 to 2009 using standard hydroacoustic and mid-water trawl survey methods (Schubert et al. 2002; MacLellan and Hume 2010). We used estimates of the abundance of age-0 sockeye salmon from surveys conducted in late fall (October 15 to November 30) when the fish are near the end of their growing season for the estimation of overwinter survival rates.

Sockeye salmon smolt emigration from Cultus Lake was first assessed in 1926 (Foerster 1929; Cleary et al. In prep). Counting fences were installed at various locations in Sweltzer Creek (within 500 m of the lake outlet) from 1926 to 1945 and sporadically from 1953 to 1984; more recent assessments have been conducted in 1990-1992 and 2001 to present. The fence and trap were installed at the onset of the migration in mid-March to early April and operated till the near-completion of the run in late-May to mid-June. The fence was operated continuously during the emigration period and was inspected regularly during each 24-hour period. Each day, smolts were removed from the live box, identified to species, counted and released below the fence; a portion of the smolts were systematically sampled for length and weight. In most years, scales were taken to estimate age composition; in some years, however, age composition was estimated from length-frequency distributions rather than scale samples. Procedures changed in 2003 when marked smolts from the supplementary releases started to migrate past the fence. Since then all migrants are passed through a viewing tank where each fish can be examined for clipped adipose fins. For the few days when the number of smolts was too high to allow all fish to be inspected outmigrants were subsampled and examined for clips. A subsample of migrants with a missing adipose fin were anesthetized and examined under an ultraviolet light for the fluorescing mark “Calcein”, which was applied to some of the hatchery release groups.

Estimates of recruitment and harvest are from the Pacific Salmon Commission. In recent years the abundance of Cultus Lake sockeye salmon in the catch is too low to enable a direct estimate of harvest, so the exploitation rate for Weaver Creek sockeye is employed as a surrogate.

METHODS

DEMOGRAPHIC ANALYSIS

Recent trends in the Cultus Lake population were evaluated using the fence counts of smolts and spawners. We broke the life cycle into 2 stages for analysis—spawner-smolt, and smolt-recruit. We estimated productivity during the spawner-smolt stage as the ratio of the unmarked smolts leaving the lake to the count of adults (the parents) entering the lake in year *t*:

$$\textit{Smolts/Spawner}_t = (\textit{age 1 smolts}_{t+2} + \textit{age 2 smolts}_{t+3})/\textit{adults entering the lake}_t$$

Thus prespawning mortality is included as an element of this stage. Smolt-recruit survival is calculated as:

$$\textit{Smolt-Recruit Survival} = \textit{smolts}_t /(\textit{recruits4}_{t+2} + \textit{recruits5}_{t+3})$$

where recruits*N* refers to the estimated number of age-4 or age-5 fish returning to coastal waters. Age-3 fish are not included in this calculation.

The CSRT (2009) conservation objectives are expressed in terms of total numbers of "successful adult spawners" in the lake, regardless of their origin (i.e., whether they were born in the lake or the hatchery). "Successful" refers to spawners that arrive in the lake and are able to spawn successfully, and "adult" refers to the large size category (i.e., not jacks). As noted earlier, robust estimates of prespawning mortality have not been available in recent years, so here we use both the fence counts of adults, and estimates of effective spawners calculated from the provisional PSM estimates.

Objective 1 was satisfied by meeting the 2 criteria:

$$\text{Average}\{N_t, N_{t+1}, N_{t+2}, N_{t+3}\} > 1000 \text{ and Minimum}\{Nt, N_{t+1}, N_{t+2}, N_{t+3}\} > 500$$

where N_t is the total number of adults that either entered the lake, or were presumed to have spawned successfully in year *t*.

Objective 2 was satisfied by meeting the criteria:

$$\text{Average}\{N_{t+4}, N_{t+5}, N_{t+6}, N_{t+7}\} > \text{Average}\{N_t, N_{t+1}, N_{t+2}, N_{t+3}\} \text{ \underline{and} Count}(N_{t+4}/N_t > 1 \text{ for i= 1 to 4}) \geq 3.$$

Abundance-based benchmarks for the WSP recommended by Holt et al. (2009) were estimated using a Ricker model stock-recruitment relationship cast in a Bayesian framework to include prior information on carrying capacity. S_{gen} (abundance that would result in recovery to S_{msy} within one generation in the absence of fishing, under equilibrium conditions) and 80% of S_{msy} were used as the lower and upper benchmarks respectively (Holt et al. 2009). Stock-recruit data for brood years 1950 to 2000 were used to estimate the benchmarks; more recent broods are complicated by hatchery releases. An informative prior on the lake capacity estimate that was based on various estimates of photosynthetic-rate based models was used (Hume et al. 1996; Shortreed et al. 2000; Cox-Rogers et al. 2004). The prior was normally distributed with a mean of 60 000 and a standard deviation of 6 000 effective spawners. The lower benchmark (S_{gen}) was estimated as 10 169 effective spawners and the upper benchmark (80% Smsy) was 28 323 effective spawners. Jacks are not included in these calculations, which may be inconsistent with the WSP criteria for wild spawners. The outcome of the current analysis will be little affected by this assumption, however.

The evaluation of status relative to the WSP-like benchmarks used the generational average:

$$\text{Average}\{NW_t, NW_{t+1}, NW_{t+2}, NW_{t+3}\} > 10\ 200 \text{ or } 28\ 300,$$

where NW is the number of unclipped adult successful spawners entering the lake. Note that this is slightly different from the WSP definition of a wild fish, which requires the parents of a wild fish to have also spawned in the wild. Operationally, this distinction can only be made with an extensive genetic analysis of the unmarked fish to determine if their parents were born in a hatchery or in the lake.

RECOVERY MEASURES

Enhancement

In response to the decline of the Cultus Lake sockeye, impromptu hatchery work was conducted at the Cultus Lake Lab in brood years 2000 and 2001. The Cultus Sockeye Enhancement Work Group was formed in January, 2002 and a formal captive brood program was initiated. Typical hatchery techniques (fry and smolt releases) were considered inadequate because of the threat of continued very high PSM similar to that observed in 1999 and 2000. The goal of the Captive Brood Program was to produce 500 captive spawners annually for at least two cycles. The primary purpose of the program was to preserve the genetic diversity of the Cultus stock in the event of catastrophic losses in the wild population. Fry and smolt supplementation was an important, but secondary objective.

For every brood year since 2000, attempts were made to collect a genetically diverse sample of the Cultus Lake sockeye population for breeding. Wild smolts were collected from brood years 2000 and 2001, eggs from the small 2001 egg take were used, and large-scale, complex egg takes have been conducted since brood year 2002. Initially, only wild fish were taken for broodstock, but the proportion of hatchery fish used for broodstock has increased in 2008 and 2009 because the number of wild spawners returning to the fence was very low.

The program aims to minimize both genetic and operational risks. Genetic concerns about a small founder population are addressed by the use of a semifactorial matrix breeding plan. Operational risks are addressed by the use of multiple rearing locations to reduce exposure to equipment failure. The Cultus Lake Salmon Research Laboratory (the Cultus Lab) is the location of adult holding and egg-take programs. Rosewall Creek Hatchery was chosen as the only suitable facility for a multi-year captive brood program. The Inch Creek Hatchery is the site of the captive brood backup and juvenile production.

Consistent with naming conventions in US agencies, eggs or juvenile fish destined for release to the natural environment are labeled `supplementation' groups. Eggs or juvenile fish destined to be raised to maturity in the hatchery are called 'captive brood' groups. The designation of fish as F1 or F2 (first or second generation hatchery) is uninformative when tracking hatchery groups. In the Cultus program, eggs may be obtained from wild fish returning to Cultus Lake; hatchery-born fish (usually fin-clipped) returning naturally to Cultus Lake; or from captive brood fish reared at Rosewall Creek Hatchery.

In brief, the current protocol for the program is as follows:

Adults are collected from the counting fence, mainly in September and October and kept in ponds supplied with hypolimnetic lake water at the Cultus Lab. A maximum of about 250 spawners (both sexes) is targeted, or 50% of the return for runs less than 500 spawners. Beginning in late November, fish are checked for maturity, and egg takes are conducted on a weekly basis from late November to the end of December.

Eggs are fertilized and incubated until the eyed stage at the Cultus Lab, and then they are surface disinfected and distributed to the rearing facilities. Usually 3 eggs from each mating (a total of 1,500 eggs) are taken to the captive programs at Rosewall Creek and Inch Creek Hatcheries. At the Rosewall Creek Hatchery fish are reared to maturation (about 75% mature at age 3 and 25% at age 4) and are spawned at that site. The Inch satellite is restricted by rearing space and therefore captive fish are held there for only ~1 year as a back-up. If they are not needed these fish are released as smolts in May to Sweltzer Creek. As these fish are large (>75g) they were used for the POST (Pacific Ocean Shelf Tracking) telemetry study in each of the 2003-2006 brood years.

Eggs from broodstock collected at Cultus Lake that are not required for the captive program are used for supplementation (up to 450k annually). At the eyed stage they are pooled and transferred to Inch Creek Hatchery. At that facility the eggs are incubated and fish are reared to the fry or smolt stage, and are released to Cultus Lake (summer fry or fall parr) or Sweltzer Creek (yearling smolts).

Eggs collected from maturing captive-reared fish at Rosewall Creek Hatchery are normally used for supplementation, however in 2004 some eggs were streamed back into the captive program because of the low availability of wild spawners. The captive adults can produce up to 1,300K eggs annually. As the Inch satellite can only accommodate ~300-500K of these in addition to the wild supplementation eggs (750k in total), Rosewall Creek Hatchery eggs in excess of this number are reared at the Rosewall Creek Hatchery until transported to the lake for release as fry.

Since 2006, three main release strategies have been used: fry that are released from June to August to the lake at about 1.0 gram in size, parr that are released in early October to the lake at about 5 grams and smolts that are released in May below the Sweltzer Creek counting fence at 20 grams. Initially releases to the lake were from the shore but beginning with the 2004 brood all releases have been made at dusk in the pelagic zone to minimize exposure to postulated near-shore predators.

In all years except 2005 all hatchery fry released to the lake have adipose fin clips as a mark. In 2005 264K unfed unmarked fry were also released into the lake in addition to the marked release groups. In subsequent life stages the unmarked hatchery fish have been distinguished from wild fish by otolith patterns (as smolts) or genetic parental analysis (for returning adults). An additional mark (calcein) has been used to distinguish part of the fall release group in some years. All yearling smolt releases are marked with a coded wire tag (CWT) as well as an adipose fin clip.

Genetic Sampling

All samples of Cultus Lake sockeye salmon were genotyped at the 14 polymorphic microsatellite loci used to characterize sockeye salmon populations and estimate stock compositions in mixed-stock harvest samples of the Fraser River sockeye salmon complex (Beacham *et al*. 2005). Wild (i.e., naturally-spawned) sockeye salmon returning to Cultus Lake in 1992 and from 1999 through 2008 were sampled for genetic analysis at the Sweltzer Creek fence, after transfer from the fence into the broodstock program, or by carcass sampling in the lake. From 2005 on, marked hatchery-produced fish also returned to Cultus Lake and were sampled in proportion to their abundance. Except for 1992, when liver tissue was sampled, samples for DNA extraction consisted of small punches of operculum tissue, which were stored individually in tubes of 95% undenatured alcohol. Sampling of hatchery broodstock used in the supplementation and captive breeding for future genetic analysis occurred in 2001 and was initiated on an ongoing basis in 2004. In 2008, broodstock fish were sampled prior to spawning.

The genotypes obtained were used to determine parent-offspring relationships between the broodstock fish spawned at Cultus Lake in 2001 and 2002 and their progeny spawned at the Rosewall Creek Hatchery in 2004 and 2005. This group of fish constituted the 'hatchery-born' spawners used at the Rosewall Creek Hatchery. The microsatellite genotypes were also used to determine probable full- and half-sibling relationships among the 2004 and 2005 Rosewall Creek Hatchery parents originating from collections of wild smolts and the wild broodstock spawned at Cultus Lake Lab in 2004 and 2005. This group of fish constituted the 'wild-born' spawners used at Rosewall Creek Hatchery and Cultus Lake Lab. Maximum likelihood analysis in the program COLONY (Wang 2004) was used to identify full- and half-sibling relationships among the fish from each brood year and partition them into families of variable size based on Mendelian inheritance of alleles at unlinked loci.

The identification of the family structure in fish spawned at Rosewall Creek Hatchery and Cultus Lab in 2004 and 2005 and their assignment to wild- or hatchery-spawned parents enabled reconstruction of the grandparental and parental pedigree for hatchery-produced fish that returned to the Cultus Lake sockeye population at age three in 2007 and ages three and four in 2008. Parentage of the primarily captively-bred hatchery-produced fish that returned in 2007 and 2008 was examined in two ways. The first method was to assign each returning fish to its most probable parents based on the 14-locus parental and progeny genotypes and the cross records maintained at both the Cultus Lab and Rosewall Creek Hatchery. The assignment was done with the help of the CERVUS program (Kalinowski et al. 2007), which identifies single and paired parental genotypes compatible (based on exclusion) with progeny genotypes. The second method of estimating parental contributions employed differences in allele frequencies that occurred in 2004 between the hatchery-born and wild-born parents in maximum likelihood (ML) estimation of parental contributions to their returning progeny. The analysis was performed with the LEADMIX (likelihood estimation of admixture) program (Wang 2003). Using the ML method, it was not possible to distinguish the contributions of wild-born parents used at Rosewall Creek Hatchery (primarily maturing wild smolts) and the Cultus Lab (primarily live broodstock).

The two-generation pedigree provided estimates of both the variance and inbreeding effective population sizes for the mature fish that returned to Cultus Lake from the 2004 hatchery program and for the 2008 spawning population in Cultus Lake The pedigree was also used to develop a mating plan to avoid incremental inbreeding in families produced by the broodstock collected and spawned at Cultus Lake Lab during 2008.

More information of the methods used in the genetic analysis will be available in Withler *et al*. (in prep).

Predator Control

Based on studies conducted in the 1930s (Foerster and Ricker 1941), predator reduction experiments in Cultus Lake have occurred in the 1970s, 1990s and most recently beginning in 2004. While the early studies targeted all large fish in the lake, subsequent attempts have focussed on a large piscivorous cyprinid, the northern pikeminnow (*Ptychocheilus oregonensis).* From 2004-2006 a variety of techniques including angling, trapnets and pots were used to capture pikeminnow although many of these were tagged for a study of movements and abundance (Bradford et al. 2007). Beginning in 2007 a modified commercial fishing vessel equipped with a small-meshed seine net was deployed to capture pikeminnow in the lake. The seine vessel operated in the spring months once pikeminnow began to move to the shore, but ceased operations before recreation activity on the lake resulted in excessive operational risks. Aggregations of pikeminnow were searched with the vessel sonar; fish that were landed were examined for tags and subsampled for biological information. All carcasses were cut and returned to the lake.

EVALUATING THE PROSPECTS FOR RECOVERY

The prospect of recovery of the Cultus Lake population was evaluated using the Cultus Lake Sockeye Population Viability Analysis (PVA) model of Korman and Grout (2008). The central structure of the model was retained, but new performance measures and management options were included. Many of the input parameters and the initial conditions were updated (Table 1) with information not available to Korman and Grout (2008). It is important to note that the model does not explicitly account for cumulative genetic effects that may occur as a result of small population sizes or hatchery releases.

The analysis of individual simulations revealed that at times, very large estimates of smolt production, smolt survival or PSM occurred that was consequence of a using the log-normal function to model environmental variation. These estimates were far above the largest observed in the 50-80 years of data for the population. To eliminate these extreme values in the simulations we prevented the model from using random deviates that were more than 2.5 standard deviations from the mean. New deviates were picked if the values exceeded this limit.

The key difference between the version of Korman and Grout (2008) and the revision used here is the form of the relation describing depensatory mortality of juvenile sockeye in the lake. Korman and Grout used a Ricker model to predict smolt production from a given abundance of spawners, but added the Michaelis-Menton function to decrease productivity at low spawner abundance. That function results in a very sharp drop in productivity at small spawner populations (see Figure 11). For example, their model predicts only 2 smolts/spawner when spawners = 100, which is much lower than has been observed empirically at Cultus Lake.

Time did not permit the testing of alternative model forms for depensation in the smolt-spawner relation (e.g., Liermann and Hilborn 2001). Instead a simple step function for productivity was added to the Ricker model, with the location of the step (6 000 spawners) being determined by eye from the data:

$$\mathit{ln}(\text{Smolts}_{t+2}/\text{Spawner}_t) = \alpha + \delta Z_i - \beta \text{ Spawners}_t$$

where Z_i is a dummy variable that codes for years with either Spawners ≤ 6 000 or Spawners > 6 000. The δ parameter changes the intercept of the regression without affecting the slope. Freshwater habitat enhancement was modelled by assuming that predator control could eliminate the effect of depensatory mortality on naturally spawned fish. Details of the model fit are provided in the evaluation of the predator control program.

Prespawning mortality was a key component of earlier analyses (e.g., Schubert et al. 2002), which were conducted shortly after the 2 years of large losses of Cultus Lake spawners. Although we do not have good estimates of PSM, smolt production rates do not suggest that severe outbreaks have occurred in the past 10 years. Consequently we used the average PSM for years 1996-1998, 2001-2009 in our analysis (Table 1). By taking this approach we consider high PSM events to be a rare catastrophic event similar to other disease outbreaks or natural disasters; such events are not considered in the model. We also used a normal error term bounded between 0 and 1; Korman and Grout (2008) used a log-normal form but we found that this resulted in unrealistically frequent occurrences of 100% mortality of spawners.

We considered 2 alternatives for smolt-recruit survival; in the first we used statistics from the 1999-2005 broods of recent low survival (average 2.6%), and for the second we used the 1952-1972 average (5.8%). The survival of hatchery smolts was assumed to be a fixed proportion of wild smolt survival, with estimates based on recent data (Table 1).

Other studies have found that hatchery-born adults may not be as successful as wild fish in spawning successfully in natural environments (Araki *et al*. 2009). Data to evaluate the performance of hatchery-born spawners in the wild are not yet available for Cultus Lake, but results of the 2010 smolt run (see Discussion) highlight the significance of this uncertainty. To evaluate the effect of a difference in reproductive success between hatchery and wild fish in the wild, we modelled the relative spawning success of hatchery fish to wild fish using values of 0.1 and 0.9.

Simulations were run for 20 years to evaluate the short-term prospects for recovery. Primary performance measures considered in the analysis were the proportion of years when abundances met CRST Objectives 1 and 2, the status of the population relative to the WSP lower benchmark in years 17-20 of the simulation, and the probability of extinction defined as 4 consecutive years of 100 or less successful spawners. COSEWIC considers a model prediction of a >20% risk of extinction in 5 generations (20 years) to be consistent with the *endangered* status.

Three hatchery scenarios were considered. In the first, all fish held in facilities were culled and the program was halted in 2009. For the second scenario the captive brood eggtake continued to 2011, and fry releases (of up to 1 000K) from captive population continued to 2016. In the final scenario began like the second, but transitioned to a standard hatchery supplementation program with annual fry releases of about 300 000 fry (from a collection of a maximum of 250 spawners, discounted by 20% to account for PSM in the broodstock). This level of fry release results in the production of about 46 000 smolts annually.

We simulated constant harvest at 5, 20, 30, 40 and 50%, and a cyclic harvest regime of 50% for the dominant late-run cycle (i.e., 2010) and 20% for the other 3 years.

RESULTS

RECENT TRENDS IN THE WILD POPULATION

Since the last assessment in 2002, the abundance of sockeye salmon returning to Cultus Lake has decreased (Figure 1). There has also been a slow decline in the generational average number of fish, with the 4-year average now fluctuating around 1 000 spawners. Some cycle growth (N_{t+4}/N_t) has occurred in the last 2 years as a result of the increasing numbers of hatchery fish in the run and that has caused generational average to increase slightly (Figure 2).

Freshwater productivity (smolts produced per adult spawner entering the lake) has increased steadily since the re-initiation of the smolt fence in 2001 (1999 brood; Figure 3). Low values in the first 2 years were likely the result of high PSM noted in 1999 and 2000 (Cooke et al. 2004). Similarly, a somewhat lower productivity for the 2006 brood may also be the result of PSM observed in that year (Bradford et al. 2010). The recent (2001-2007) rate (56 smolts/spawner) is similar to that observed for the 1951-1972 broods (63 smolts/spawner). Age-0 overwinter survival, calculated from the acoustic estimates of juvenile abundance in the fall and the subsequent smolt estimate, has increased substantially since the 2004 brood (Figure 4).

The increasing productivity in the lake has contributed to an increasing trend in the abundance of wild smolts since 1999, although there is large interannual variation caused by the variation in spawner abundances (Figure 5). Nonetheless the recent (1999-2007 broods) annual average of 54 000 smolts is only 5% of the 1952-1972 average of 1.07 million smolts per year.

The average smolt-to-recruit survival rate for the 1999-2005 broods was 2.6%. However, the trend has been downward and in the last 3 years the average has been 1.1%. In contrast the 1952-1972 average smolt-to-recruit survival is 5.8% (the geometric mean is 4.2%; Figure 6). The recent trend is very similar to that observed for the Chilko Lake population (Figure 7).

Population recovery is only possible when conditions permit a positive population growth rate. Ignoring density-dependent effects on survival (which is reasonable given the current small population size), population growth occurs when this inequality is satisfied:

$$\textit{Spawners}_t * \textit{Smolts}\cdot\textit{Spawner}^{-1} * \textit{Recruits}\cdot\textit{Smolt}^{-1} *(1\text{-}\textit{Harvest Rate}) > \textit{Spawners}_t$$

which compares the production of spawners in the following generation to the size of the parent population. Recruits·Smolt $^{-1}$ is often colloquially (and incorrectly) referred to as the “marine survival rate”. This relation can be simplified as:

$$\textit{Smolts}\cdot\textit{Spawner}^{-1} * \textit{Recruits}\cdot\textit{Smolt}^{-1} *(1\text{-}\textit{Harvest Rate}) > 1$$

Rearrangement of this inequality results in the equation:

$$\textit{Smolts}\cdot\textit{Spawner}^{-1} = 1/\{\textit{Recruits}\cdot\textit{Smolt}^{-1} *(1\text{-}\textit{Harvest Rate})\}$$

which allows for the visual representation of the combinations of freshwater productivity and smolt survival rates as isopleths of zero population growth under differing scenarios of fishing mortality (Figure 8).

Plotting the recent data and comparing it against the zero growth isopleth illustrates how the population has not been in a situation that would permit growth since the 1999 brood, largely due to the poor smolt-recruit survival rates (Figure 8). Although freshwater productivity has been increasing, these gains have been offset by the recent decline in the survival of smolts. In contrast, the average for the 1952-1972 period lies above and to the right of the 60% harvest isocline highlighting that this was a period when the combination of freshwater and marine productivity could sustain a high rate of exploitation, compared to the average for the recent period (Figure 8).

EVALUATION AGAINST OBJECTIVES AND BENCHMARKS

Since 2002, the population has failed to meet Objective 1 of CSRT (2009) of a generational average of 1 000 effective spawners, with no year of less than 500 fish. The generational average for fish entering the lake has fluctuated around 1 000 individuals, but 2 of the 4 cycle ines have consistently remained below 500 spawners. Objective 2, of growth, N_{t+4}/N_t, in 3 of 4 years has also not been met by the population. The outcome of assessment is similar whether total or effective spawners are used (Figure 2).

The population is currently well below the both the upper lower and upper abundance benchmarks that were calculated by WSP procedures. The average number of wild adult spawners entering the lake in the last four years was 997 fish; the lower WSP benchmark is 10 200 spawners.

RECOVERY ACTIONS

ENHANCEMENT

The enhancement program has been success in its first goal of maintaining a captive broodstock population as insurance against the risk of catastrophic loss in the wild. Since 2004 an annual average of 626 spawners matured in captivity and was spawned; 75% of the captive adults were mature as age-3 fish and most of the remainder were age-4s (Table 4).

The first large-scale release of juveniles into Cultus Lake began in 2003 (2002 brood, Table 4), and the number of fry released has gradually increased since then. Release-to-smolt survival rates have generally increased between 2003 and 2009 (Figure 4). In the first 2 years juveniles were released in summer from the shore and this may have increased their exposure to predatory fish that use the margins of the lake in summer for feeding and spawning. Since 2005 all releases have taken place mid-lake from a small boat. With the recent increase in survival rates the lake releases have made significant contributions to the smolt run, and for 2004-2007 broods most of the smolts leaving Cultus Lake are of hatchery origin (Figure 5).

The recent smolt-to-recruit survival rate of smolts resulting from hatchery fry releases have been similar to those of naturally spawned fish (Figure 7). Estimates of survival for the first two years of releases were somewhat lower than those of naturally spawned fish, but are based on few fish and may be less accurate. The survival of yearling hatchery smolts released directly into Sweltzer Creek has averaged only 24% of the wild survival rate (Figure 7).

Since 2007 significant numbers of hatchery-born fish are now returning to Cultus Lake (Figure 2). For 2008 and 2009, the two weak cycles, hatchery fish comprised over 85% of the returns. The contribution of hatchery fish will be smaller for the two more abundant lines that have larger natural production.

The impact of the enhancement program to date can be estimated by using a life cycle model to calculate the number of spawners that would have returned to the late assuming that no enhancement activities had taken place. We used the recent time series of lake productivities (potentially including the effects of predator control), smolt-recruit survival for wild fish and harvest rates. Beginning with 4 years of spawner abundances (1999-2003) we estimated the number of adults that would have returned to the lake to 2009.

The results show that the enhancement program slightly reduced the size of the spawning population in the early years because of the captive brood take (Figure 9); averaged over the past 2 generations the enhancement program has reduced the average annual spawner count by about 100 fish (Figure 9). However the enhancement program has increased the abundance of spawners in 2008 and 2009 by a factor of 3, as the survivors of the large fry releases begin to return as adults.

Allelic diversity and genic diversity

Genic diversity (expected heterozygosity) and allelic richness at the 14 microsatellite loci did not change in wild Cultus sockeye salmon sampled between 1992 and 2007. The hatchery-produced age-4 fish that returned in 2006 and 2007 from the primarily supplemental releases of juveniles from the 2002 and 2003 brood years had similar diversity values (Table 5). However, the hatchery-produced age-3 fish sampled in 2007 had lower levels of both genic diversity and allelic richness. Allele frequencies of these fish, which were primarily the progeny of captive breeding at Rosewall in 2004, were also unusual compared to other samples of naturally- and hatchery-spawned Cultus sockeye. Whereas pairwise F_{ST} values between all other samples of wild fish and fish that returned from hatchery production were less than 0.01, pairwise F_{ST} values involving the age-3 hatchery-produced fish that returned in 2007 ranged up to 0.02.

Analysis of the hatchery-born parents spawned at Rosewall in 2004 revealed the reason for the anomalous allele frequencies and low levels of diversity among their progeny that were sampled in 2007. The parental fish, themselves progeny of crosses made at Cultus Lake in 2001, were primarily members of two large halfsib families (Families A and B), each resulting from the mating of a single female with two different males. The rest were progeny of two single pair crosses and a factorial cross among five female and 5 male parents. Members of these families, arising from only 20 fish spawned at Cultus Lake in 2001, constituted over half the parental fish contributing to progeny production at Rosewall Creek and Cultus Lake in the 2004 brood year (Table 6). The levels of allelic richness and genic diversity in the hatchery-born spawners at Rosewall were low, as expected from a large sample of fish made up from relatively few families. The wild-born spawners at Rosewall (arising from collections of wild smolts) and the wild broodstock at Cultus in 2004 possessed typical levels of genetic diversity for Cultus sockeye salmon (Table 5).

The escapement of Cultus sockeye salmon in 2004 was the lowest on record, consisting of no hatchery-produced and only 90 wild fish, of which 37 were removed for use as broodstock. Coincidentally, 2004 was the first year in which large numbers of fish in the captive breeding program at Rosewall matured and were spawned. The release of large numbers of second generation hatchery juveniles with restricted wild grand-parentage from a brood year in which only 53 wild sockeye had entered Cultus Lake to spawn raised concern about the potential genetic impacts on the population. In particular, if the survival and age structure of juveniles produced from hatchery-born and captively reared parents was similar to that of juveniles produced from supplementation and natural spawning, second generation hatchery fish would be expected to predominate among age-4 returning fish in 2008. Additional genetic diversity could be supplied to the 2008 Cultus sockeye spawning population only by a strong return of age-3 fish (wild and/or hatchery-produced), an uncertain prospect given the prevailing low survival of Cultus sockeye salmon.

A few wild fish were present in the 2008 escapement. However, the 4-yr-old hatchery fish that returned in 2008 from the 2004 brood year encompassed more genetic diversity than their 3-yr-old counterparts. The levels of both allelic richness and genic diversity were similar to those in samples of wild Cultus sockeye salmon (Table 5). This was due to a greater contribution of the wild-born hatchery parents to the age-4 than to the age-3 fish that returned to Cultus Lake.

The hatchery-born parents used at Rosewall in the 2005 and 2006 brood years arose primarily from semi-factorial crosses among larger numbers of wild broodstock spawned at Cultus in 2002 and 2003. Levels of allelic richness and genic diversity in these fish were similar to those in samples of wild Cultus sockeye salmon (Table 5). Therefore, hatchery-produced fish that return to Cultus Lake from brood years subsequent to 2004 are expected to have typical levels of allelic variation.

Parental contributions to fish that returned from the 2004 BY hatchery programs

The two methods of parentage determination, assignment to parents and maximum likelihood analysis of allele frequencies, provided similar results (Table 6). In 2004, the hatchery-born spawners at Rosewall contributed 70% of all gametes and the wild-born Rosewall spawners from the 2002 and 2003 smolt collections contributed 24% of gametes (Table 6). The 25 live broodstock spawned at Cultus contributed almost 6% of gametes, half in the form of eggs and milt used in crosses made at Cultus and half in the form of milt used in egg fertilization at Rosewall. Cryopreserved milt from wild Cultus males of the 2002 brood year was also used in egg fertilization at Cultus (Table 6).

All 3-yr-old fish sampled in 2007, consisting of 56 marked and six unmarked fish, were assigned to hatchery-spawned parents. Estimated parental contributions to these progeny indicated that they returned approximately in proportion to their production in 2004, with their 20 2001 brood year grandparents contributing 59% of their genes (45% from Families A and B alone). Only one was assigned to wild broodstock parents spawned at Cultus in 2004 (and released in the supplemental production); the remainder came from Rosewall crosses although one was sired by a Cultus wild male whose milt was also used at Rosewall (Table 6).

Of 218 age-4 fish sampled in 2008 and attributed to 2004 brood year hatchery production, 198 were marked and 20 were unmarked. Whereas virtually all of the age-3 returns from the 2004 brood year releases originated from captive breeding at Rosewall, this was not true of the age-4 fish. The genetic contributions from Families A and B were only one-third to one-half those expected based on their contributions to egg fertilization in 2004. Based on parental assignment, the hatchery-born spawners cultured at Rosewall accounted for 39% of genes among their age-4 progeny whereas contributions from wild-born spawners at both Cultus Lake and Rosewall increased correspondingly (Table 6).

Assignment methods indicated that about 10% of the hatchery-produced age-4 fish were progeny of crosses made at Cultus in 2004, which contributed less than 5% of the juveniles released from the 2004 brood year (Table 6). Thus fish returning from the supplementation program tended to either mature a year later or survive better than those from the captive breeding program, or both. Unfortunately, because from fish the two hatchery sources develop and mature at different rates they are unavoidably distributed unequally among different release groups. Thus, differences in their rates of survival cannot be interpreted simply in terms of fitness. This was especially true in 2005 when a large early release of (unmarked) unfed fry from the 2004 brood year into Cultus Lake was composed entirely of juveniles produced at Rosewall.

The genetic contribution of wild-born parents at Rosewall also increased in the age-4 fish that returned from the 2004 brood year of hatchery spawning. Their contribution increased from 39% in age-3 fish to 48% in age-4 fish and that from the fresh milt collected at Cultus and used to fertilize eggs at Rosewall increased from 1 to 7%. Maximum likelihood analysis of parental contributions provided similar results; the ML estimates of the contribution of wild-born parents to the age four fish of 2008 was somewhat higher than that based on assignment (Table 6).

These results indicate that the measures implemented to increase genetic variation in the captive broodstock beyond that represented in the limited crosses made at Cultus in 2001 were successful in increasing diversity among the age four 2008 returns from captive breeding. The substantial genetic impact of parents drawn from the wild smolt collections was primarily responsible for the normalization of allele frequencies and levels of genetic diversity among the age-4 returning fish.

Inbreeding and Effective Population Size

Inbreeding occurred during the captive breeding of 2004, primarily as the result of mating of full- and half-sib progeny from Families A and B. Nine inbred progeny from the within family crosses were sampled in 2007 and 2008. Six of them had one parent each in the two Family A half-sibships. Three of them resulted from crosses in which the parents were full-sibs; one each from Families A1 and A2 and one from Family B1. Inbreeding increases by 25% in the progeny of full-sibling parents and 12.5% in progeny of half-sibling parents. However, most fish that returned from hatchery production did not have related parents and the overall increase in mean inbreeding among the returning fish was low (approximately 1% among the age-3 and <0.5% among the age-4 fish).

The pedigree-based estimated variance effective population size (N_{eV}) of the age-4 hatchery-produced fish of 2008 was 54. However, 6% of the spawning population of 2008 was comprised of wild age-3 and age-4 fish and hatchery-produced age-3 fish. Inclusion of these fish increased the N_{eV} to 72 for the total 2008 population. These estimates of N_{eV} were smaller than those based on known inbreeding levels (N_{eI}). The N_{eI} estimates were 93 and 138 for the 2008 hatchery returns and total returns, respectively. These estimates based on known inbreeding levels were likely inflated by the shallowness of the available pedigree (i.e. inbreeding that occurred in the wild before the hatchery program was established and in the 2001 brood year of hatchery spawning count not be accounted for).

2008 Crosses at Cultus Lake

The objective of the mating design developed for 2008 was to avoid additional inbreeding in the progeny of the 2004 brood year hatchery-produced fish. Inbred fish, and potential additional inbreeding in 2008, was expected to be primarily the result of common ancestry in the large Families A and B of 2004. Preliminary classification of the 2008 sockeye taken into the broodstock into three groups was conducted with genotypes obtained prior to spawning. Age-4 fish with parents in Families A and/or B (all derived from six grandparents spawned in 2001) were placed in Group 1. All other age-4 fish were placed in Group 2, so that this group contained all hatchery-produced fish from Rosewall and Cultus that did not have

Family A or B parents and the eight wild fish among unmarked broodstock. All age-3 fish, consisting of ten marked hatchery-produced fish and one unmarked wild fish from the 2005 brood year, were placed in Group 3. As each fish matured, it was to be crossed with as many mature fish of the other gender as were available, with the restriction that Group 1 fish were not to be mated with each other. Ultimately, each female was crossed with between eight and ten males and each male was crossed with between three and fifteen females to make a total of 586 crosses.

Final classification of the 2008 broodstock into the three groups based on parentage analysis took place after spawning. In this process, the classifications of 12 age-4 fish were changed with the result that 23 (4%) of the 586 crosses made involved related parents. The average increase in inbreeding for the 23 inbred crosses was low (5%) and over all crosses the increase in inbreeding was 0.21%.

HARVEST MANAGEMENT

Harvest of late-run sockeye salmon has decreased in recent years as a result of concerns of high rates of en-route and prespawn mortality in the stock complex, and conservation concerns for Cultus Lake sockeye salmon. The recent (2003-2009) harvest rate has averaged 17% compared to the historical (1952-1972) average of 67% (Figure 6). There is an extensive hook and line fishery in the Vedder River during the period of adult migration but the impacts (due to catch and release mortality or illegal retention) are unknown.

PREDATOR CONTROL

The mark-recapture experiment conducted in 2004 and 2005 yielded an estimate of northern pikeminnow population in Cultus Lake of 60 000-70 000 adult fish (Bradford et al. 2007). Since then over 42 000 adult pikeminnow have been removed from the lake mainly by seine net (Figure 10). An additional 17 000 juveniles have also been removed. The adult catch per set for the seine boat decreased linearly between 2006 and 2009 and relatively few adults were caught in 2009 (Figure 10). The capture of juveniles in 2009 increased as effort was directed towards smaller fish.

The efficacy of predator control program was assessed by the change in the production of smolts (as smolts/spawner) from the lake. Considering all the broods potentially impacted by predator control (1935-1941, 1989, 1990, and 2004 to present), it appears that predator control has served to reduce the impacts of depensatory mortality on smolt survival (Figure 11). A general linear model based on the Ricker model was fit to these data using standard least squares as:

$$\mathit{ln}(\text{Smolts}_{t+2}/\text{Spawner}_t) = \alpha + \delta Z_i + \beta\ \text{Spawner}_t$$

where δ is the increment in productivity associated with years of predator control, or depensation (as specified by the dummy variable Z). A brood was considered subject to depensation if there were less than 6 000 effective spawners. The model fit was significant, for both β ($P < 0.017$) and δ ($P < 0.004$) terms. Multiple comparisons showed no significant difference in productivity between broods impacted by predator control and those consisting of >6 000 spawners, but both groups were significantly more productive than the years with small broods subject to depensation (without predator control, $P < 0.002$). The model predicts a more than 2-fold increase in productivity for small broods as a result of predator control (Figure 11).

VIABILITY ANALYSIS AND A COMPARISON OF ALTERNATIVES

To evaluate the relative roles of the key factors affecting the viability of the Cultus population we first modelled 2 levels of five factors (smolt survival, relative reproductive success of hatchery fish in the wild, hatchery alternatives, harvest rate, predator control) in a fully factorial fashion for a total of 2^5, or 32 model runs of 20 years in length. These were displayed in a “heat” diagram with the factors sorted to rank the outcomes (Figure 12).

Smolt–to-recruit survival was the most important factor affecting the probability of reaching CRST Objectives 1 and 2 and the risk of extinction. Under the historical survival rate of 5.8%, the population is predicted grow and at least achieve Objective 1 under most combinations of the other parameters, and the overall risk of extinction is low.

If smolt survival continues at the recent average of 2.6%, the potential for recovery is dependent on the successful implementation of recovery actions. If the harvest is kept low, the predator control program continues, and the hatchery supplementation produces adults that can successfully reproduce in the wild, then the probability of recovery to Objective 1 is reasonably high and the risk of extinction is low. The relative fitness of hatchery fish is a key factor in affecting recovery under low smolt survival conditions, as the hatchery program plays a significant factor in recovery. Similarly, the elimination of depensation through predator control plays a major role in reducing the risk of extinction. The probability of achieving Objective 1 is low under a 50% exploitation rate, and the risk of extinction can be kept below 20% only if depensation can be offset with a predator control program or if the hatchery program is successful.

Further simulations were conducted that explored the range of exploitation rates (Figure 13). Results from the cyclical harvest regime are not shown as they were nearly identical to the constant 30% harvest. Not surprisingly the probability of meeting Objective 1 decreased with increasing harvest, but the impact of harvest strongly depended on the success of the other recovery actions on increasing productivity. For example, if the reproductive success of hatchery fish was high, and smolt survival was good, then the productivity of the population was high enough to allow for population growth under all harvest rates under consideration.

Overall, the simulation results suggest that the probability of achieving Objective 1 is high (>75%) if 2 of the 4 major factors are favourable- harvest ≤ 20%, elimination of depensation, average smolt survival, or a successful hatchery program. Achieving the WSP lower benchmark is unlikely in 20 years under low smolt survival conditions, but is possible if smolt survival is average, and depensation can be eliminated. The hatchery program has a lesser effect on meeting the WSP benchmark as returning hatchery fish are not included in the calculation of mean abundance used in the evaluation.

The three alternatives for the hatchery program differed in their contribution to recovery, but those differences depend on the other parameter choices (Figure 14). If hatchery fish are able to reproduce successfully in the wild, the hatchery program can make some impact on achieving Objective 1 when smolt-recruit survival is low. The benefit of continuing the supplementation program (Option 2) is relatively small compared to Option 3 (terminating the captive brood program in 2011) as the number of additional adults returning to the lake (after the brood take) is relatively small for the supplementation program. The benefits of the option 2 with its continued large fry releases on the first five years of the simulation are sufficient to increase abundance such there is little overall difference between that option and the long-term supplementation program.

The hatchery program can contribute to reducing the risk of extinction if smolt-recruit survival is low, and the reproductive success of hatchery fish is high. The continuous production of smolts by the supplementation program does assist in preventing the spawning population in the lake from falling below the extinction threshold in years of poor survival.

DISCUSSION

The status of the Cultus Lake sockeye CU has changed little in the past 2 generations. None of the six brood years from 1999 to 2005 have encountered conditions that have permitted the population to significantly increase as a result of natural spawning. Although the productivity of some broods was reduced by PSM, the main factor limiting population growth is consistent low smolt-recruit survival. Sustained recovery of this population from natural spawning can only occur when smolt-recruit survival rates are greater than about 3%, which is 2-3 times higher than has been observed recently. Although the population decline has been halted, if current conditions continue, most cohorts will be unable to replace themselves and the Conservation Goal of achieving a self-sustaining wild population is not feasible.

RECOVERY ACTIONS

The information available at this time indicates that the recovery actions have the potential to contribute to the recovery of the Cultus Lake population; however, there remains considerable uncertainty about their long-term utility. Some of that uncertainty will be reduced in the next few years, assuming the recovery and assessment programs continue.

Predator Control

The sharp decline in the seine catches of northern pikeminnow in Cultus Lake suggests that the abundance of this predator has been significantly reduced by the control measures. However, tagging studies in the lake have revealed that pikeminnow have strong home range behaviours (Bradford et al. 2007), so declining trends in catch may partly reflect local depletion of adult fish. Aggregations of adult pikeminnow have probably been most significantly impacted in areas of the lake where the seine boat has been able to operate efficiently and safely. In other parts of the lake where the boat cannot operate, pikeminnow density may be less impacted. Alternative ways of catching pikeminnow, such as longlining have been tested and may have utility in capturing fish from deeper waters, and areas that are otherwise not fishable. Bradford et al. (2007) used a simple population model to show that a relatively modest level of effort (F = 0.2, or an annual catch of about 20%) may be sufficient to suppress the pikeminnow population over the long term.

There is a consistent positive trend in the survival of juvenile sockeye coincident with the removal of predators. We found that the production of wild fish, the survival of hatchery releases, and the estimated winter survival of both wild and hatchery fish as estimated by hydroacoustics have all increased. The observation that all of these groups show a similar increasing trend suggests that survival has improved during the final six months before migration because this is the only period that is common to all of the survival estimates. This finding is consistent with the detailed analyses of Foerster and Ricker (1941) who felt that the impact of pikeminnow predation on juvenile sockeye salmon was greatest in the winter months when both predator and prey spatially overlap in the lake. Pikeminnow remain in shallow water from May to September to feed and reproduce where sockeye are much less common than other food items such as crayfish, cyprinids and other fishes. Based on the statistical analysis of the smolt/spawner data, predator control seems to have had the greatest impact on the smaller broods, as it appears to offset depensatory mortality in the lake.

A possibly confounding factor for inferences about the efficacy of the pikeminnow program is the role that recent large releases of hatchery fish may have on depensatory mortality. In addition to the increasing cumulative effect of pikeminnow removal over the past five years, the number of juvenile sockeye in the lake (resulting from natural spawning and hatchery releases) has also increased. A run of 6 000 natural spawners might be expected to produce about 360 000 smolts in average conditions; the combined abundance of wild and hatchery production has been near this value for the 2008 and 2009 smolt runs. For these broods the combined abundance of wild and hatchery fry may be sufficient to allow them to escape depensatory mortality. Smaller hatchery releases are expected in the next few years which will be useful for distinguishing between these hypotheses.

Removal of a top predator in a lake is expected to produce a cascading effect on the ecosystem. Ward (1953) speculated that that the release of juvenile pikeminnow from cannibalism by adults may in fact lead to a positive recruitment response for pikeminnow, possibly thwarting efforts to decrease the population. However, although no direct evidence of cannibalism in Cultus Lake pikeminnow has been recorded. Increased survival of the other prey species, such as red-side shiner and crayfish might also be expected. Increased survival of other species in the pelagic zone such as stickleback and kokanee may also occur. Baseline data on the abundance and composition of near shore fish species in 1991, 2005 and 2006 and on pelagic fish in many years have been collected but have not yet been analysed.

Enhancement

The captive breeding program has been successful in creating a parallel spawning population in captivity as an insurance against catastrophic losses, and it producing significant numbers of adult returns from the juvenile releases. Whether these returns will contribute to natural production cannot yet be verified.

Genetic analysis has shown that the efforts to capture the molecular genetic diversity present in Cultus Lake sockeye salmon population by the supplementation/captive breeding program have been generally successful. The large numbers of hatchery-born spawners used as parents at Rosewall in the 2004 BY themselves came from only 20 parents, with most being the progeny of only six of those parents. This produced a genetic bottleneck in the hatchery-produced fish released from the 2004 BY that was apparent in the age three sockeye salmon that returned in 2007 but had less influence on the age four fish that returned in 2008. Hatchery-born spawners used at Rosewall Creek in brood years subsequent to 2004 have arisen from the generally greater numbers of fish spawned at Cultus Lake after 2002.

Hatchery supplementation of salmonid populations, even in the absence of captive rearing to adulthood, results most frequently in a single population that occupies two breeding environments, the hatchery and the wild. Hatchery production in 2004 and 2005 generated over 90% of the 2008 return of 521 fish to Cultus Lake, five times as many fish as returned in 2004.

The next significant genetic assessment of the hatchery-produced Cultus Lake sockeye salmon will involve their ability to spawn in the wild and produce progeny that will themselves survive to spawn in the wild. A series of studies examining the spawning success of steelhead trout from a supplementation hatchery has produced variable results in which the measurement of reproductive capacity in the wild for hatchery-produced trout was estimated to decline by up to 30% (Araki *et al.* 2007a, b) for each generation of hatchery rearing. This has been interpreted as a reduction of fitness resulting from altered or reduced natural selection in the hatchery environment that results in impaired performance when hatchery fish reproduce in the wild (Araki et al. 2008, 2009).

Inbreeding, which may cause loss of fitness in wild populations (Frankham 2010), is of particular concern in re-introduced populations (Biebach and Keller 2010). Any ability to manage the breeding structure of a threatened population that was assisted by captivity is likely lost upon re-introduction to the wild and inbreeding may accumulate rapidly while population size remains low (Ewing *et al*. 2008). Additionally, environmental or genetic factors other than inbreeding that reduce the reproductive capacity of hatchery-born animals in the wild (Araki et al. 2007a, Schroder *et al*. 2008) may impact ‘hybrid’ progeny resulting from the mating of hatchery- and wild-born Cultus Lake sockeye salmon, leading to a further decline in population productivity.

The captive broodstock spawned at Rosewall in 2005 and 2006 (and later years) consisted of hatchery-born fish that were drawn from larger numbers of families than those of 2004. Moreover, after the 2001 crosses made at Cultus, the number of fish from each family transferred to Rosewall for captive rearing was limited to between 3 and seven fish that would mature at Rosewall at age three or four. Thus, fish released from hatchery production since 2004 have had higher levels genetic diversity than those of 2004 and are expected to produce returning fish with lower levels of relatedness. As a result, we expect reduced inbreeding in future generations of hatchery-produced fish that spawn in the wild. This is important because hatchery-produced fish constituted 67% of the 2009 escapement of 1392 fish to Cultus Lake and about 60% of the 2008 smolt emigration that will produce the majority of fish in the 2010 escapement.

PROSPECTS FOR RECOVERY

Population viability analysis demonstrated that in the present regime of low smolt-recruit survival rates the Cultus population can be maintained at a low level in the next 20 years (i.e., achieving Objective 1) if 2 or more of the recovery actions are continuously successful. However, there is substantial uncertainty surrounding this condition. The PVA model does not account for the potential deterioration of fitness in hatchery-reared fish, nor any of the risks that are necessarily associated with a long-term hatchery operation, such as disease outbreaks or equipment failures. There is also uncertainty whether the predator control program can be maintained at decadal scales, or if a “surprise” outcome may result from this long term manipulation of the ecosystem (Pine et al. 2009).

However, recovery to the lower WSP benchmark in the next 20 years will require a significant increase in the smolt-recruit survival, low harvest rates, and predator control. If smolt-recruit survival increases for all late run stocks (including Cultus), and harvest rates are increased recovery to the lower WSP benchmark is unlikely (although the population may reach Objective 1).

THE 2010 SMOLT RUN

The 2010 smolt run currently underway at the time of writing provides some insight into the potential uncertainties about the recovery actions and population trajectories. As noted earlier, the nearly all of the 2008 spawning population consisted of hatchery born fish, as only 10-20 of the 338 adults were born in the wild. Many of the hatchery return in 2008 were progeny of parents that had been maintained in captivity for an entire life cycle. These fish were not highly inbred and their levels of allelic richness and genic diversity were similar to those seen in samples of wild Cultus sockeye salmon. However, because there were many related fish in the small escapement, inbreeding may have occurred during natural spawning in Cultus Lake that will impact the number and fitness of progeny produced by natural spawning in 2008. Whether or not the naturally-produced progeny were more inbred than those produced in the controlled broodstock crosses, in which inbreeding was minimized, depends on the extent to which, if any, mate choice in the natural environment resulted in inbreeding avoidance.

Only 365 unmarked age-1 smolts migrated from the lake, and preliminary genetic analysis suggests some of these may have been hatchery fish that with faulty fin clips. Thus the production rate for this brood is less than 1 smolt/spawner, and the run is a very small fraction of the expected 10 000-30 000 smolts. Over 88 000 marked smolts surviving from the 825 000 fry released in 2009 were counted through the fence, indicating a survival rate of about 11% for the fry releases.

A variety of hypotheses could explain these results, including a very high rate of PSM, reproductive failure in the lake, or poor juvenile survival. Parental analysis from smolt samples will assist in determining if any of the hatchery-born fish spawned successfully in 2008 and how many families have contributed to the smolt run. Past experience in Cultus Lake does not indicate that F1 hatchery-born adults that were released as fry in the lake have had difficulty spawning and producing smolts. There were 3 broods in the 1930s for which all returning fish were taken into the hatchery and the resulting fry were released to the lake (Foerster 1968). Adults returning to the lake from the fry releases reproduced successfully and had good rates of smolt production. Recent returns from the captive breeding program in Redfish Lake, Idaho, also do not indicate a failure of hatchery fish to reproduce in the wild (Mike Peterson, IDFG, pers. comm.). However, we do not know if F2 fish can spawn successfully in the wild.

The hypothesis of unusually high rates of PSM or developmental problems in the early life stages are also not supported by the better than average survival rates for broodtake adults and the resulting eggs and fry held in the captive broodstock program for this brood year (Table 6). However, the survival of the fry that were released into the lake in 2009 is significantly lower than in the preceding 2 years, which does support the hypothesis of reduced fitness in the wild (although natural variation in the lake cannot be ruled out). Hypotheses that cannot be readily tested are an in-lake disease outbreak, Allee or imprinting issues that prevented hatchery-born adults from finding mates or suitable spawning areas in the lake, or high rates of mortality in the early life stages resulting from a change in environmental conditions or predation.

Since few wild fish returned to Cultus Lake in 2008, our ability to compare the production and freshwater survival of progeny from wild and hatchery-produced parents that spawned in the lake is limited for this brood year. And, the performance of the 2008 fish may be additionally impacted by inbreeding not likely to affect subsequent brood years. Continuing genetic analysis of emigrating smolts and returning adults until 2014 will enable us to better assess the contributions of hatchery-produced spawners for three brood years in which hatchery fish have formed a majority of the spawning population in Cultus Lake. Nonetheless the 2010 smolt run highlights the uncertainty and perhaps risks associated with recovery actions that have the potential to change the nature of the population or its ecosystem.

CONCLUSIONS

The Cultus Lake sockeye salmon population is still small, and to a large degree recovery hinges on an improvement in the survival of smolts once they leave the lake. As most of the smolts and returning adults are now hatchery-born, the short-term trajectory will also depend on untested assumption that hatchery fish will be able to reproduce successfully in the wild. Given the uncertainty about future survival rates, short and long-term effects of the hatchery program, and the potential changes to the Cultus Lake food web from predator manipulation, the prognosis for the Cultus Lake sockeye population remains highly uncertain**.**

RECOMMENDATIONS

1. Attempts to recover endangered salmon populations through the manipulation of the population or its environment are both risky and experimental and thus require a thorough monitoring program to ensure benefits are being accrued as expected or to allow timely modifications to the recovery protocols as required. These programs should comprise a significant proportion of the overall recovery program.
2. Given that the severe pre-spawn mortality of 1999-2000 has not re-occurred, the apparent lower survival of hatchery raised smolts compared to the wild stock supplementation program, and the risks associated with continuing the captive broodstock program from both a genetic and fish culture perspective, it is recommended that the captive breeding program be phased out of the recovery strategy.
3. Long term supplementation may be an alternative to a captive broodstock program, but this will depend on the relative reproductive success of hatchery fish in the wild. Assessing the reproductive success of hatchery fish in the lake is a high priority information need. Depending on the outcome of this assessment, significant changes to the enhancement program may be warranted.
4. Predator control appears to be increasing juvenile sockeye survival, and efforts to suppress the pikeminnow population are recommended. However, monitoring of the predator population and other components of the lake ecosystem is needed to ensure undesirable side-effects of the predator control program do not occur.
5. To ensure the Cultus population will persist for a decade or longer of poor smolt-recruit survival, continuation of the current recovery measures (harvest management, predator control, and supplementation) is recommended, but the exact nature of those activities should be continually reviewed to take advantage of the findings of the ongoing assessment program.

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Table 1. Revised biological parameters for the Cultus Lake PVA model. Other parameters remain unchanged from Korman and Grout (2008). μ is the mean, SD is the standard deviation, and ρ is the lag-1 autocorrelation coefficient.

Parameter	**Values Used**	**Comments**
Prespawning mortality	μ=0.21, SD = 0.11	Statistics for 1996-2009, except 1999, 2000
Prespawning mortality, broodstock	0.20	Average of recent years
Smolt-recruit survival, recent	μ=0.026, SD = 0.71, ρ = 0.11	Statistics for 1999-2005 broods
Smolt-recruit survival, historical	μ=0.058, SD = 0.86, ρ = 0.01	Statistics for 1952-1972 broods
Egg-fed fry survival for captive brood parents	0.59	Average for 2003-2008 broods
Egg-fed fry survival for parents taken from fence	0.76	Average for 2001-2008 broods
Fry-smolt survival for releases	0.14	Average for 2005-2008 mid-lake releases
Relative smolt-recruit survival for fry releases compared to wild smolts	1.0	Average for 2003-2005 broods
Relative smolt-recruit survival for smolt releases	0.24	Average for 2003-2005 broods

Table 2. Key biological values and policy choices that were used various model runs.

Factor	Values	Comment
Smolt-recruit survival (mean, SD)	0.026 (0.71) “recent” 0.058 (0.86) “historical”	See values in Table 1.
Relative reproductive success of hatchery fish in the wild	0.01 “low” 0.09 “high”	Extreme range motivated by 2010 smolt run
Predator Control-Ricker parameters for smolt-spawner relation	No predator control: $\alpha = 3.635$, $\beta = 1.46x10^{-6}$ for spawners ≤6 000 $\alpha = 4.516$, $\beta = 1.46x10^{-6}$ for spawners >6 000	Depensation occurs without predator control.
	Predator control: $\alpha = 4.516$, $\beta = 1.46x10^{-6}$	Predator control eliminates depensation
Hatchery/CB alternatives	1. 2009 cull of all fish 2. Continue CB to 2011 and release fry to 2016 3. Switch to ongoing hatchery supplementation in 2012	Alternatives 2 and 3 assume all fish released as fry in summer and fall, and are based on a maximum brood take of 250 spawners.
Harvest	Constant at 0.05, 0.2, 0.3, 0.4, 0.5 Cyclic starting in 2010 as 0.5, 0.2, 0.2, 0.2	0.2 and 0.5 used as alternatives spanning likely range. Cyclic targets harvest on dominant late-run cycle.

Table 3. Primary performance measures for model evaluation

Name	Criteria	Calculated as:
CRST Objective 1	4-year average of 1 000 successful spawners, no year <500.	Proportion of years exceeding criteria
CRST Objective 2	Generational growth with 3 of 4 cycles growing	Proportion of years exceeding criteria
WSP lower benchmark	Generational average of spawners that were born in the wild >10 200	During last 4 years of simulation
Extinction	4 consecutive years of <100 spawners (of all types)	Proportion of simulations during which the population goes extinct

Table 4. Summary of captive brood activities, 2000-2009. Upper block are data from the eggtake, middle blocks show the progression of the captive cohorts, and the final block shows the hatchery releases from either the captive adults (Rosewall), or spawners taken at the fence that were surplus to captive broodstock needs (Cultus).

Brood Year:	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
Cultus Adults Captured										
Male	n/r	n/r	89	105	17	85	103	61	83	162
Female	n/r	22	177	141	20	63	169	90	78	120
Cultus Adults Spawned										
Male	10	11	70	100	15	78	76	52	59	117
Female	5	9	120	132	10	60	121	74	69	92
Eggs Taken	13,385	24,458	438,100	464,038	39,976	185,273	430,674	282,261	257,915	320,209
Rosewall Hatchery Captive:										
Brood Year +1	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	
Rls from Cultus Egg Takes	0	3,715	227,029	346,002	21,384	99,727	304,702	196,733	133,130	
Year End Balance	3,892	4,320	3,296	53,406	57,646	52,061	53,356	53,227	58,506	
Brood Year +2	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**		
Smolt Capture	2,014	881	0	0	0	0	0	0		
Smolt Release	3,891	3,166	2,135	47,804	53,760	53,166	51,903	51,645		
sub-Adult Release	0	0	299	0	0	0	0	0		
# Spawned (males only >2004)	0	184	23	0	0	0	18	2		
Eggs Taken	0	16,000	0	0	0	0	0	0		
Year-end Balance	1,070	1,564	738	1,451	1,303	1,270	1,330	1,512		
Brood Year +3	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**			
Number Spawned Male	67	207	43	166	126	204	195			
Number Spawned Female	22	285	135	395	440	366	304			
Eggs Taken	46,000	694,058	256,512	813,291	935,247	879,918	432,537			
Year-end Adult Balance	928	401	241	380	131	214	17			
Brood Year +4	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**				
Number Spawned Male	9	35	34	100	2	18				
Number Spawned Female	196	103	49	85	0	6				
Eggs Taken	631,677	233,638	146,597	183,218	0	5,350				
Year-end Adult Balance	249	110	0	0	0	0				
Brood Year +5	**2005**	**2006**								
Number Spawned Male	96	15								
Number Spawned Female	60	8								
Eggs Taken	230,902	20,380								
Year-end Adult Balance	76	0								

Brood Year Production

Brood Year:	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
Rosewall Eggs - Captive Spawners	-	-	-	62,000	1,325,735	721,052	980,268	1,118,465	879,918	472,418
Cultus Eggs - Natural Returns	13,385	24,458	438,100	464,038	39,976	185,273	430,674	282,261	257,915	320,209
Total Eggs	13,385	24,458	438,100	526,038	1,365,711	906,325	1,410,942	1,400,726	1,137,833	792,627
Total Release Rosewall Captive	-	-	-	17,761	727,317	246,408	640,143	702,320	686,966	
Total Release Cultus Returns	3,891	6,881	229,463	377,154	21,384	154,163	356,605	248,528	189,958	
Total Rls	**3,891**	**6,881**	**229,463**	**394,915**	**748,701**	**400,571**	**996,748**	**950,847**	**876,924**	

Table 5. Allelic richness (AR), genic diversity (HE - expected heterozygosity, Ho observed heterozygosity) for 14 microsatellite loci in wild-born and hatchery-produced Cultus Lake sockeye salmon of sample size N.

Year	N	A_R	H_E	H_O
Wild				
1992	45	6.3	0.60	0.58
1999	76	6.1	0.59	0.61
2001	58	5.9	0.59	0.61
2002	172	6.2	0.59	0.58
2004	28	6.3	0.60	0.61
2005	151	6.1	0.60	0.59
2006	504	6.2	0.60	0.59
2007	169	6.1	0.59	0.58
Hatchery Returns				
2006 (4-yr-old)	72	6.2	0.60	0.59
2007 (4-yr-old)	50	5.8	0.60	0.61
2007 (3-yr-old)	62	5.6	0.57	0.58
2008 (4-yr-old)	218	6.0	0.58	0.59
Hatchery parents				
2004 hatchery-born	469	4.5	0.52	0.55
2004 wild-born	251	6.2	0.60	0.60
2005 hatchery-born	209	6.1	0.59	0.59
2005 wild-born	350	5.9	0.59	0.60

Table 6. Numbers of parental Cultus Lake sockeye salmon and their percentage genetic contributions to successfully fertilized eggs produced at Rosewall Creek and Cultus Lake in 2004 and to their age three and four adult progeny that returned to Cultus Lake in 2007/08. Among the adult progeny, the contributions from hatchery-born and wild-born parents were estimated by both parentage assignment and maximum likelihood analysis of allele frequencies. Confidence intervals (95%) for the ML estimates are given in parentheses.

Broodstock source	Successful Parents	% gametes in 2004	% in 2007 age 3 returns	% in 2008 age 4 returns
Rosewall				
Hatchery (2001 BY: Fam A)	267	35	32	20
Hatchery (2001 BY: Fam B)	141	22	13	7
Hatchery (2001 BY: Other)	61	9	12	8
Hatchery (2002 BY males)	9	3	2	4
Hatchery-born – assignment	**478**	**70**	**59**	**39**
Hatchery-born - ML			**59 (49-68)**	**33 (29-40)**
Wild (mature smolts)	213	24	38	45
Wild (2004 BY fresh milt)	12*	3	1	6
Cultus				
Wild Brood (fresh gametes)	25*	3	2	9
Wild (2002 BY frozen milt)	36	1	0	1
Wild-born – parentage	**274**	**30**	**41**	**61**
Wild-born – ML			**41 (32-51)**	**67 (60-71)**

* milt from 12 of 15 males spawned at Cultus Lake in 2004 was also used to fertilize eggs at Rosewall Creek.

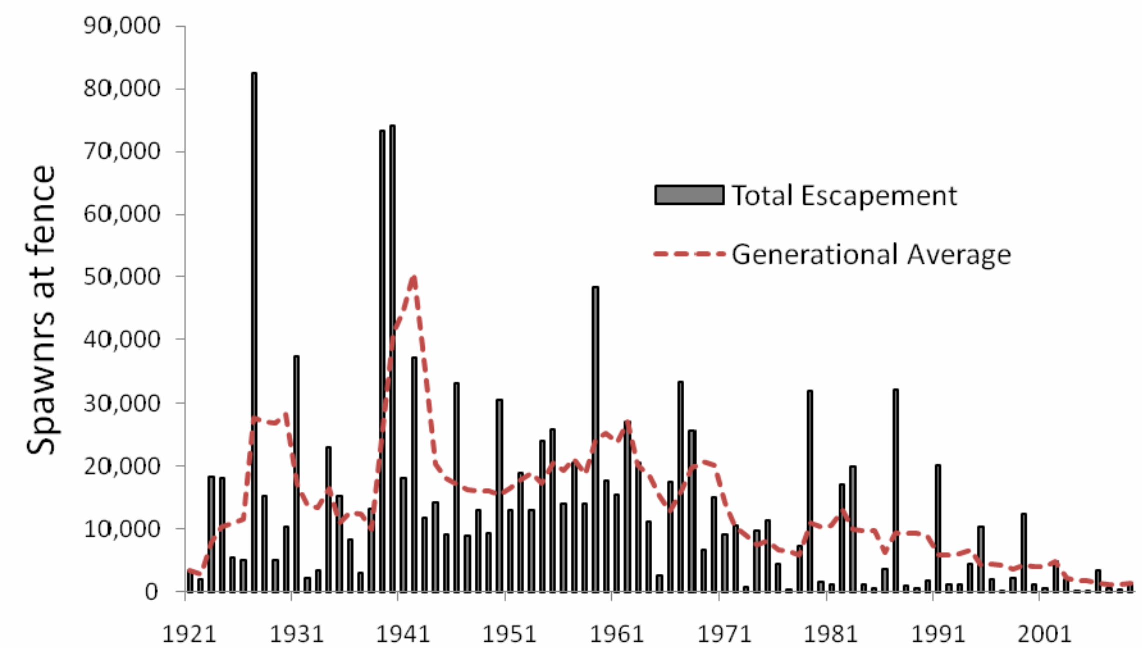

Figure 1. The number of adult sockeye salmon passed into Cultus Lake through the counting fence, by return year. Generational average is the 4 year running average.

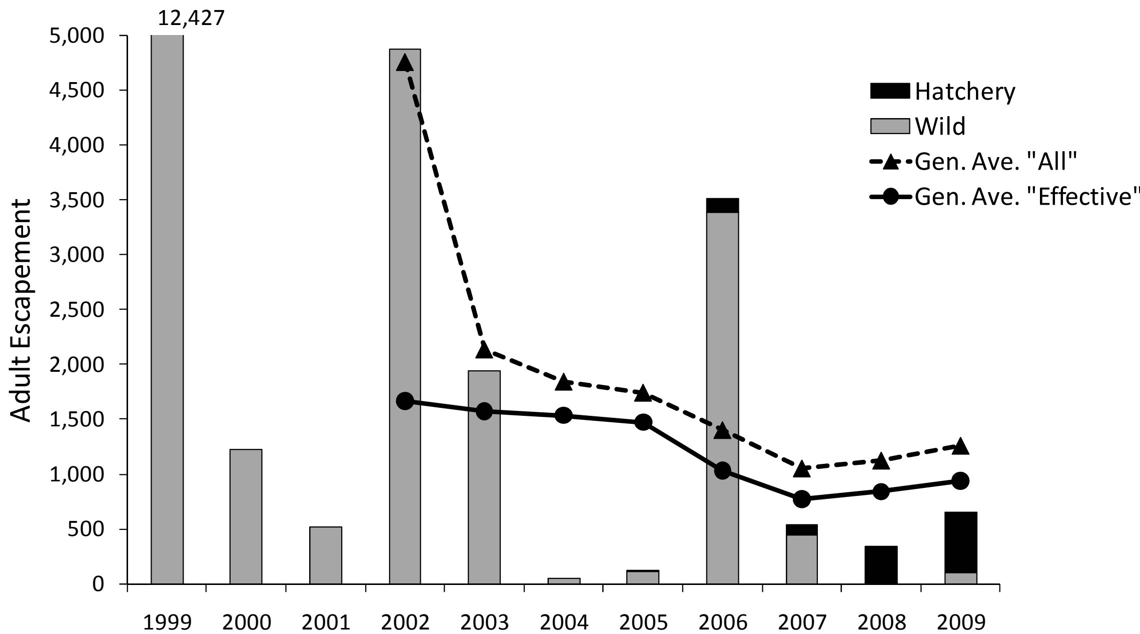

Figure 2. Recent trend in adult escapement to the Cultus Lake fence. The 1999 escapement (12 427) is off the scale. Dashed line is the 4-year running average. Solid line is the 4-year running average of effective spawners (i.e., adjusted for prespawning mortality).

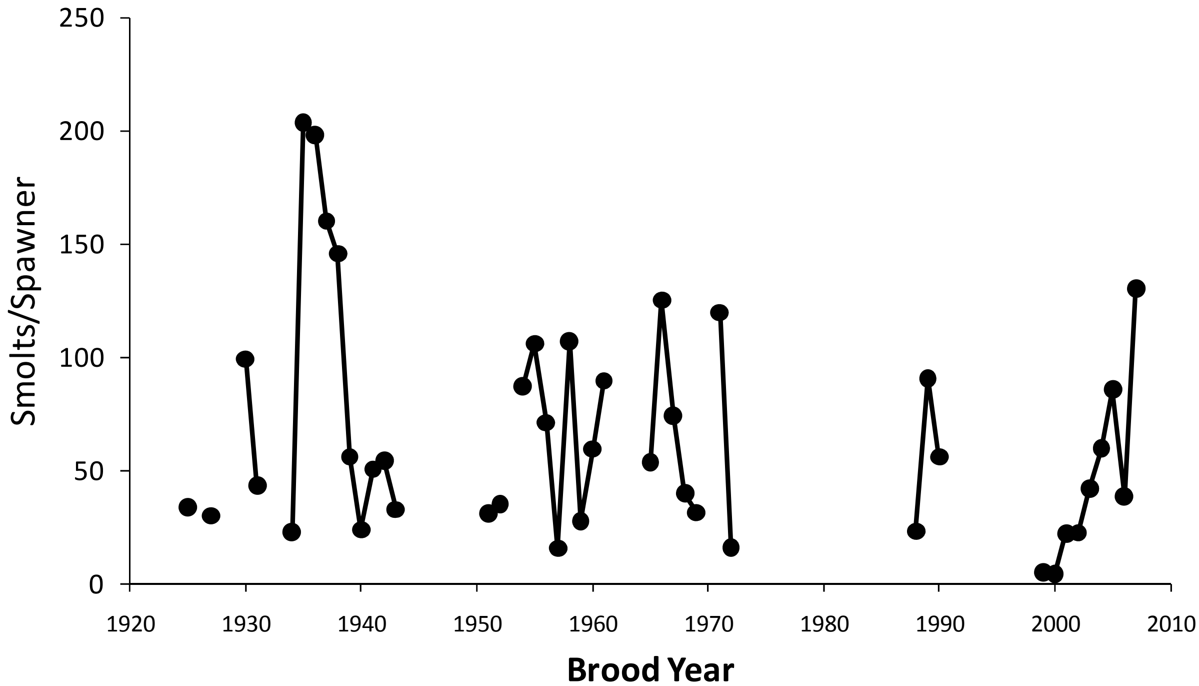

Figure 3. Time series of smolt/spawner ratios for wild Cultus Lake sockeye salmon, by brood year. Spawners in this plot are counts at the fence and are not corrected for PSM.

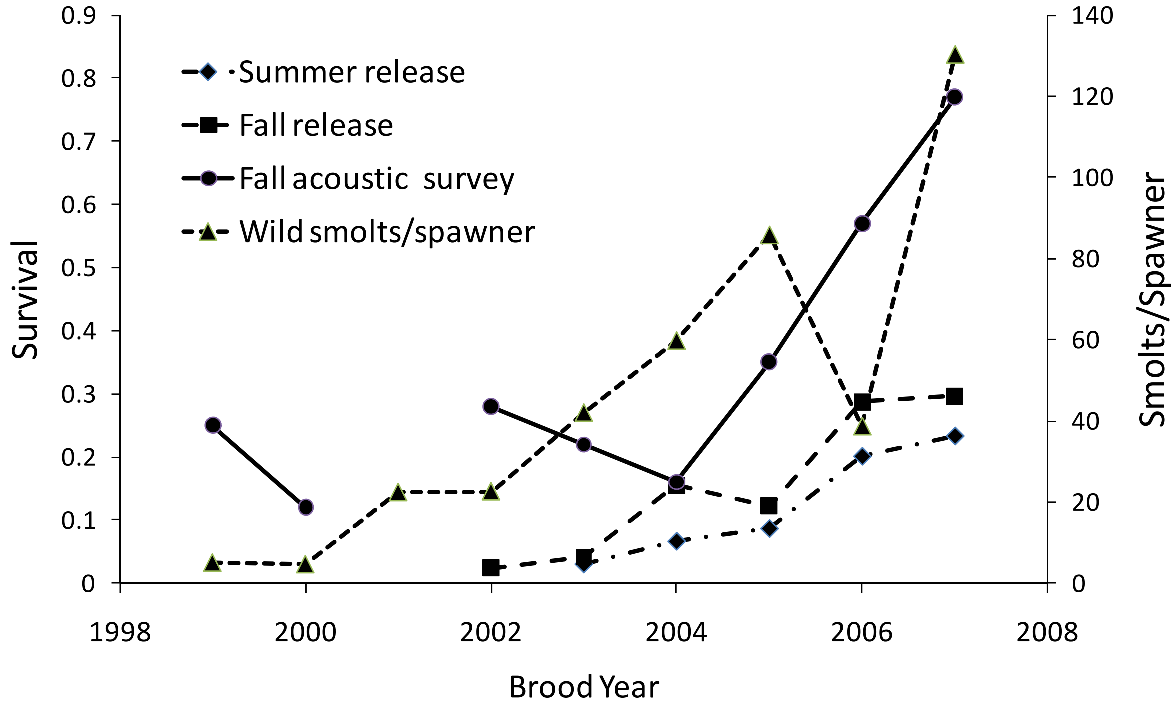

Figure 4. Recent freshwater survival rates by brood year. Data plotted are the release-to-smolt survival rates for summer and fall hatchery releases, and overwinter survival estimated as the ratio of smolt abundance (hatchery and wild) to late fall hydroacoustic estimates. Also shown are the smolt/spawner ratios for fish spawning in the lake (triangles and right vertical axis).

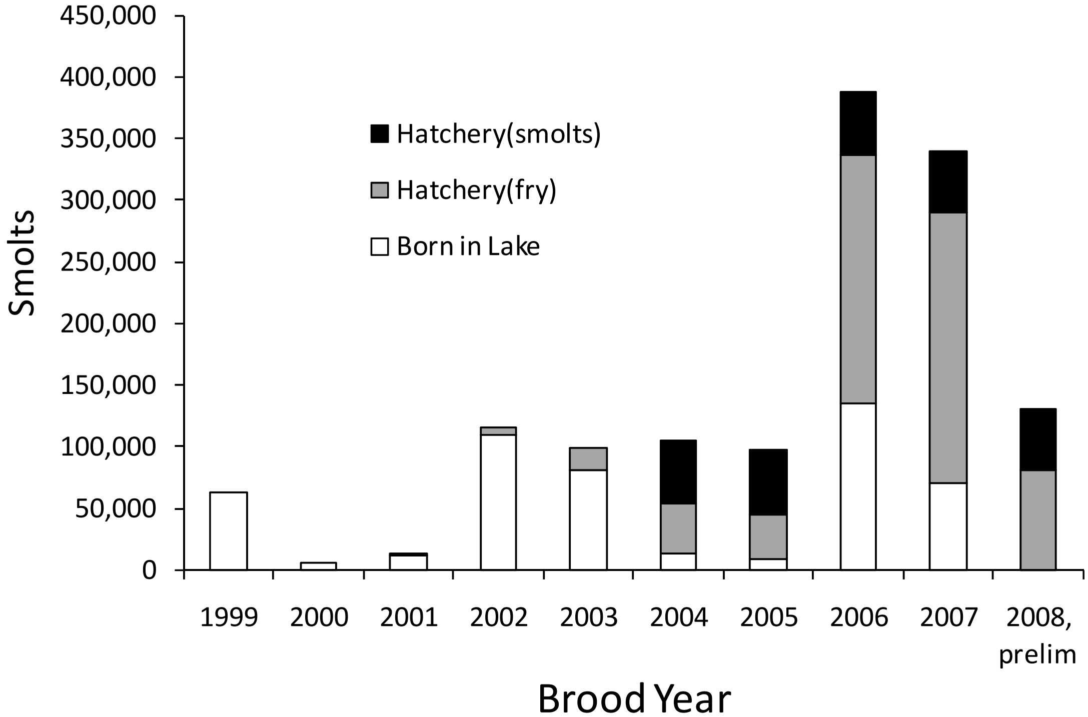

Figure 5. Composition of recent smolt runs from Cultus Lake resulting from spawning in the lake, hatchery fry releases, or hatchery yearling smolt releases in Sweltzer Creek. Data for 2008 brood are incomplete, but represent >90% of the run (May 16, 2010).

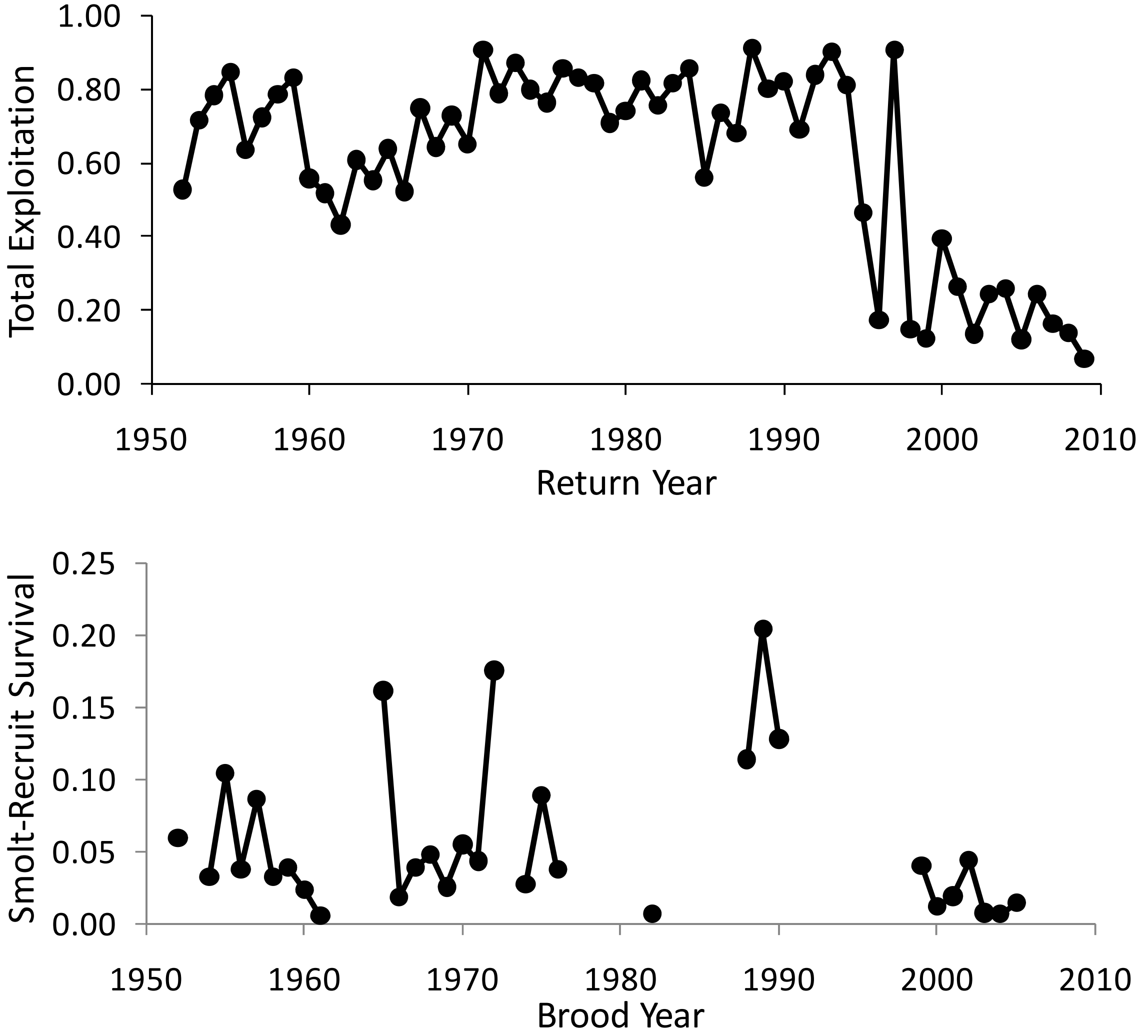

Figure 6. Upper: time series of exploitation rates for Cultus Lake sockeye salmon. Lower panel: time series of smolt-recruit survival rates by brood year. Data from the Pacific Salmon Commission.

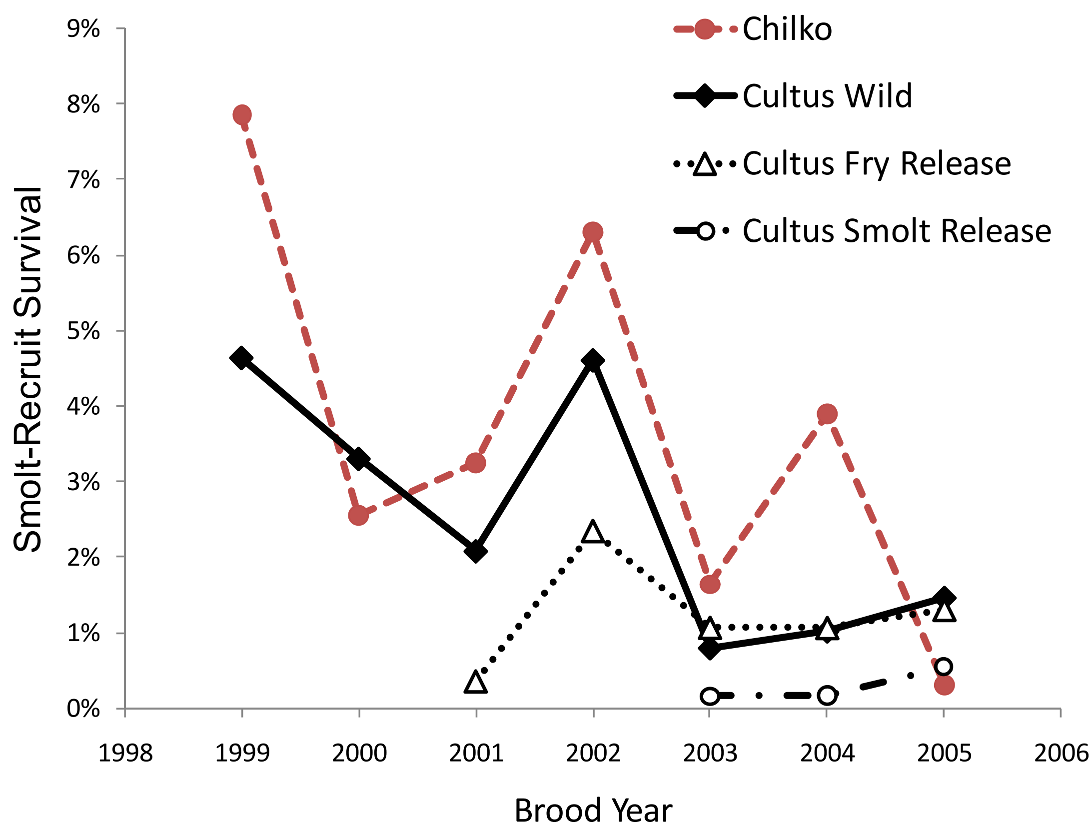

Figure 7. Smolt-recruit survival rates for Cultus wild smolts (born in the lake), smolts resulting from hatchery fry releases, and for hatchery smolt releases. Also shown are smolt-recruit survival estimates for Chilko Lake sockeye salmon (data from PSC).

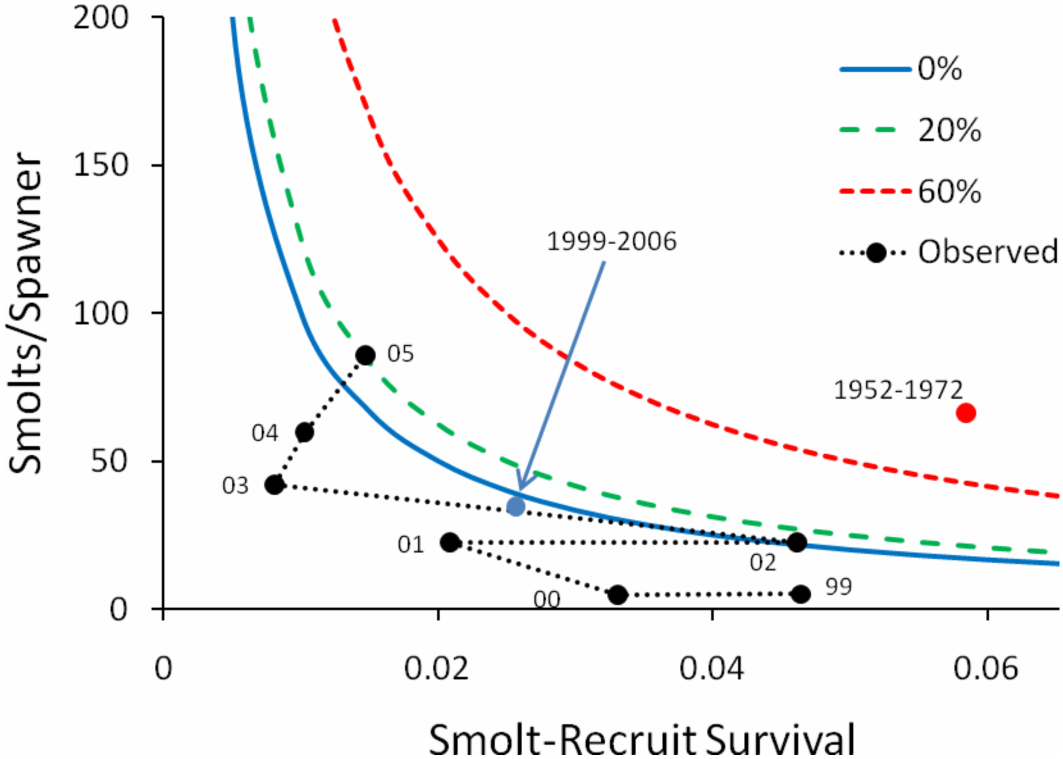

Figure 8. Isopleth diagram showing lines of no population growth under three levels of harvest, as a function of freshwater productivity and smolt-recruit survival. A cohort will increase in size ($N_{t+4}/N_t > 1$) if the point for the brood lies above and to the right of the isopleths for the harvest rate it experiences. Dotted lines connect observed annual values for the 1999 to 2005 brood years. Also shown is the average for the 1952-1972 (red circle) and the 1999-2006 brood years (blue circle).

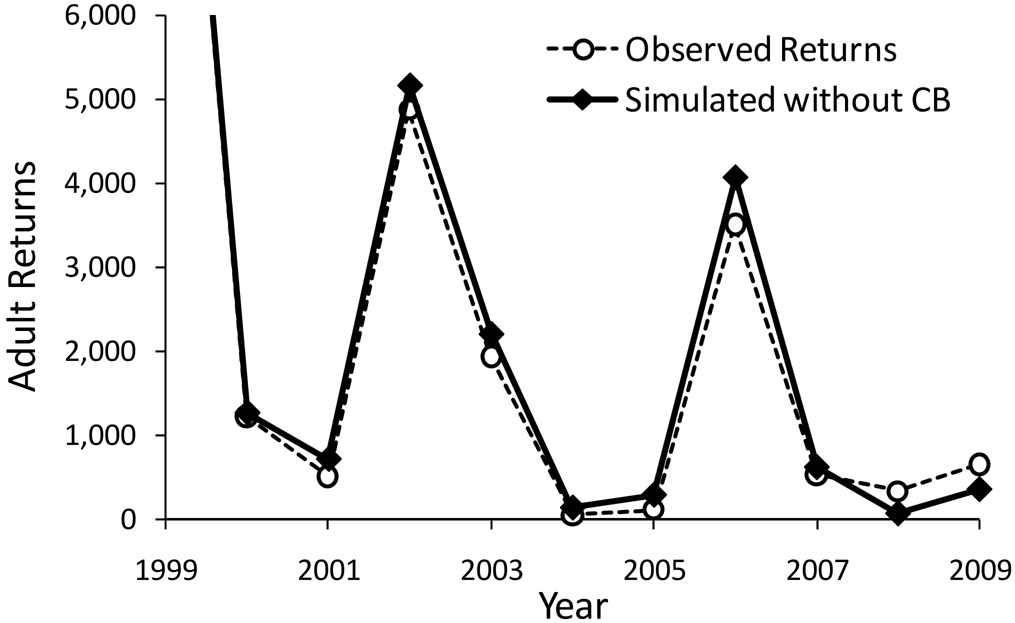

Figure 9. Results of a simulation that uses observed freshwater productivity and smolt-recruit survival rates to retrospectively predict the number of adult salmon that would have returned to the lake if the cative broodstock (CB) program was not in place. The simulation uses the historical estimates of harvest and incorporates the effects of the predator control program.

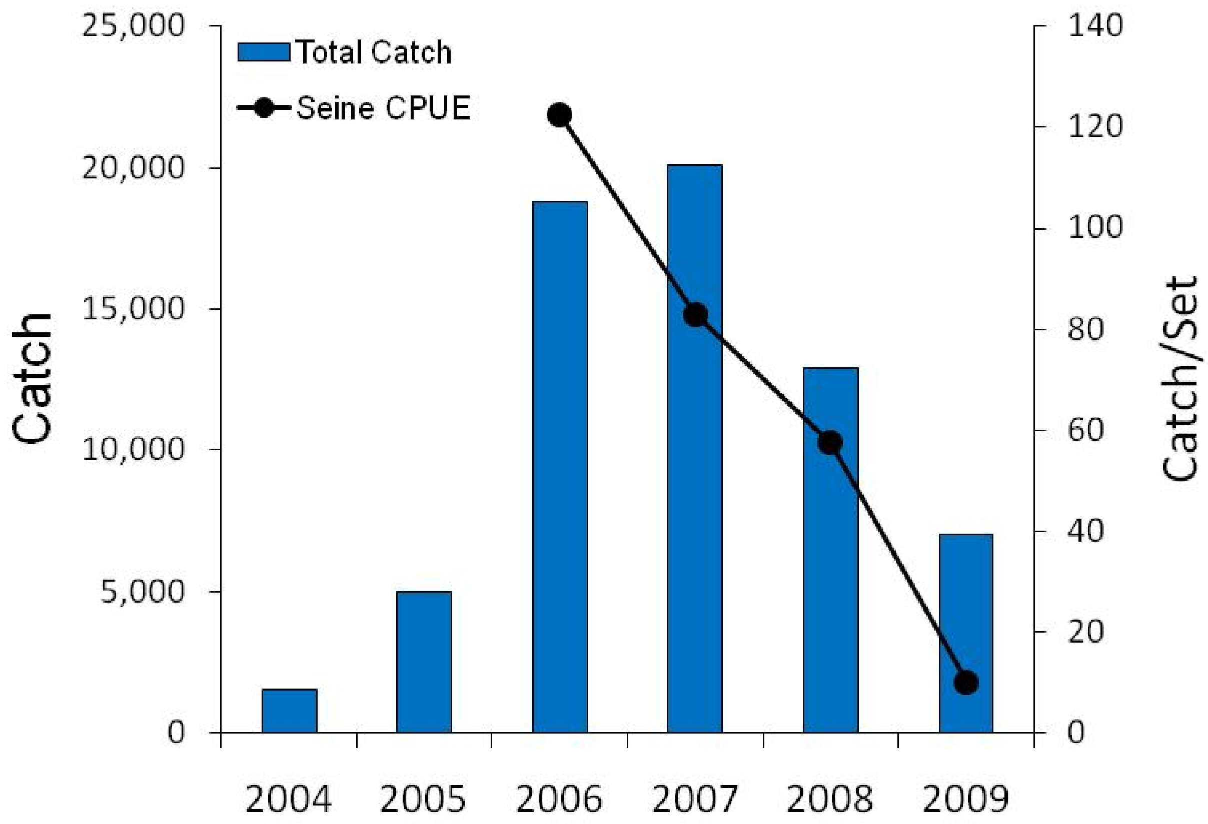

Figure 10. Total annual removals of northern Pikeminnow from Cultus Lake, 2004-2009 by all gear types. After 2005 most fish were caught by purse seine. CPUE is the catch per seine set for adults (>200mm TL) for the purse seining removal program.

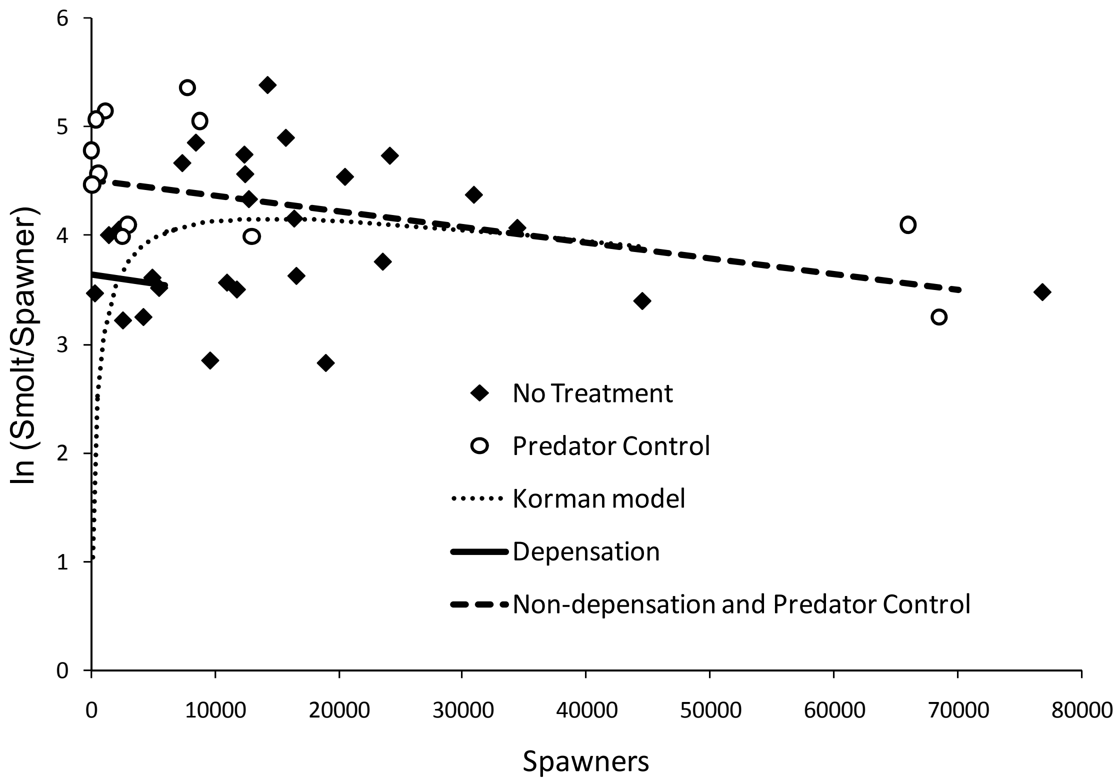

Figure 11. The natural logarithm of smolts/spawner, plotted against effective parent spawners, by brood year. Open symbols are brood years likely affected by predator control activities (1935-1941, 1989-1990, 2004-2007). Solid and dashed lines are results of a linear regression of ln(Sm/Sp) on spawners, with a separate fit for broods <6 000 spawners (unaffected by predator control) that appeared to be subject to depensatory mortality. Dotted line is the fit of the model used by Korman and Grout (2008) to the solid symbols.

Sm- Rec S	Pred Con	RS	Harv	Hatch	Obj 1	Obj 2	Extinct	WSP Low
0.026	None	0.1	0.5	1	6	2	76	0
0.026	None	0.1	0.5	3	6	4	64	0
0.026	None	0.1	0.2	1	19	7	16	0
0.026	None	0.1	0.2	3	23	11	6	0
0.026	None	0.9	0.5	1	26	10	51	0
0.026	None	0.9	0.5	3	54	18	0	0
0.026	None	0.9	0.2	1	53	19	3	0
0.026	None	0.9	0.2	3	90	34	0	0
0.026	Effective	0.1	0.5	1	28	12	1	0
0.026	Effective	0.1	0.5	3	23	11	7	0
0.026	Effective	0.1	0.2	1	75	31	0	0
0.026	Effective	0.1	0.2	3	74	31	0	0
0.026	Effective	0.9	0.5	1	62	18	0	0
0.026	Effective	0.9	0.5	3	83	29	0	0
0.026	Effective	0.9	0.2	1	91	37	0	2
0.026	Effective	0.9	0.2	3	97	45	0	9
0.058	None	0.1	0.5	1	42	15	4	0
0.058	None	0.1	0.5	3	49	19	0	0
0.058	None	0.1	0.2	1	79	35	0	2
0.058	None	0.1	0.2	3	86	39	0	5
0.058	None	0.9	0.5	1	71	26	0	1
0.058	None	0.9	0.5	3	95	40	0	6
0.058	None	0.9	0.2	1	92	44	0	12
0.058	None	0.9	0.2	3	99	54	0	35
0.058	Effective	0.1	0.5	1	86	38	0	5
0.058	Effective	0.1	0.5	3	85	38	0	6
0.058	Effective	0.1	0.2	1	96	53	0	42
0.058	Effective	0.1	0.2	3	95	53	0	41
0.058	Effective	0.9	0.5	1	95	42	0	11
0.058	Effective	0.9	0.5	3	98	47	0	18
0.058	Effective	0.9	0.2	1	98	53	0	50
0.058	Effective	0.9	0.2	3	99	56	0	54

Figure 12. PVA model results. Shown are results from 250 model runs of 20 years duration that consider 2 parameter levels for the 5 key environmental or management factors. The first five columns are values for (1) Smolt-recruit survival, (2) Predator-control caused reduction in depensation, (3) Relative fitness of hatchery spawners in the wild, (4) Harvest rate, (5) Hatchery option (1=immediate cull, 3=long-term supplementation). Performance measures considered are CSRT Objectives 1 and 2 (as the proportion of years when the objective is met), the probability of extinction, and the probability of achieving the WSP lower benchmark in the last 4 years of the simulation. Runs are sorted such that the least favourable parameter sets are at the top. Colours are for emphasis and are not indicative of thresholds or criteria.

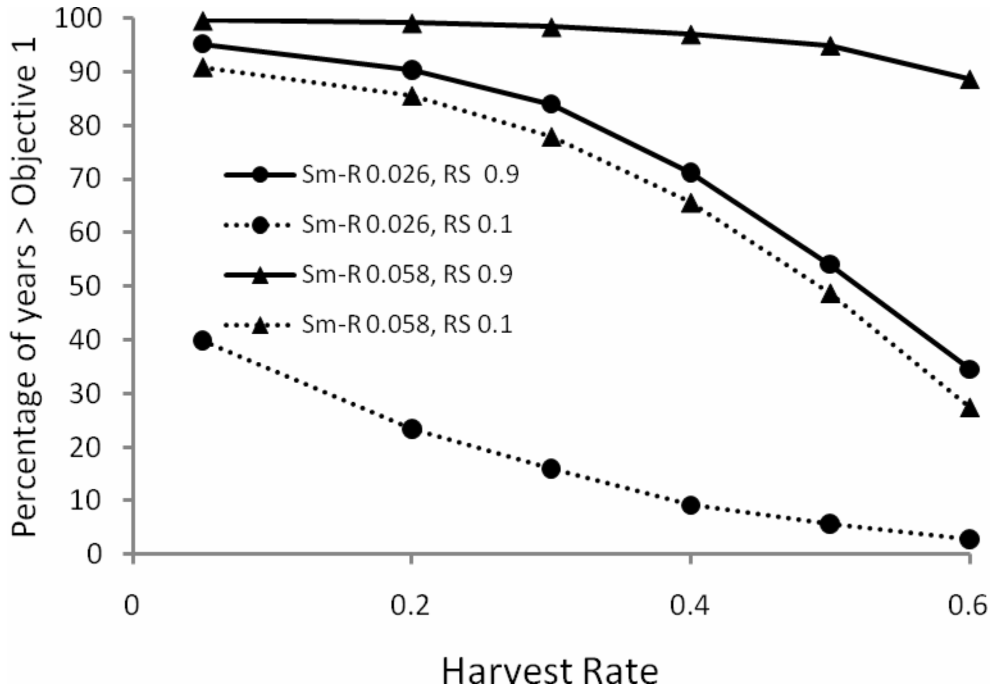

Figure 13. PVA model results (20 year runs) showing that the effect of harvest rate on the recovery of the population to Objective 1 (generational average of 1000 spawners) depends on the smolt-recruit (Sm-R) survival rate, and the relative reproductive success of hatchery fish in the wild (RS). Points are averages across 250 model runs. For these runs, no predator control program was assumed, and hatchery option 3 was used (supplementation).

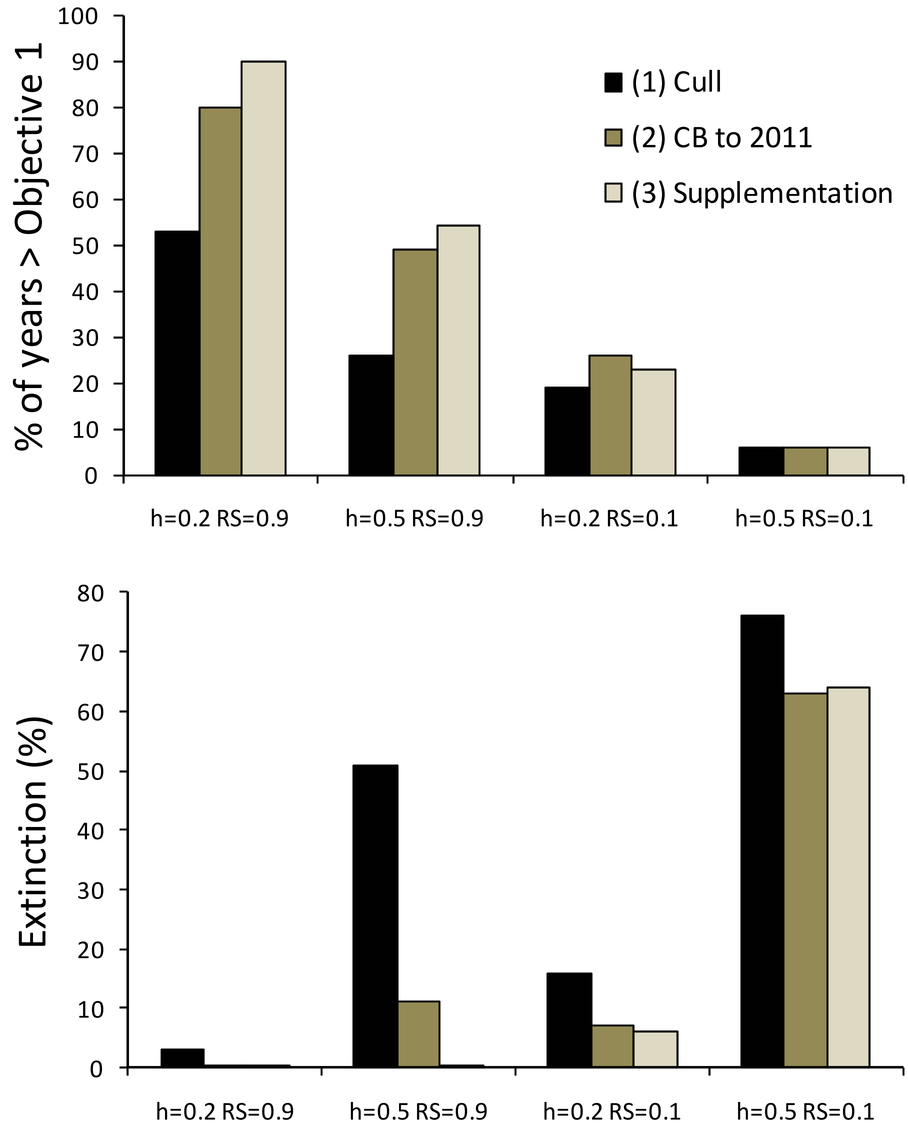

Figure 14. Performance of the 3 hatchery alternatives evaluated against Objective 1 (upper) and the extinction metric (lower). Each group of bars is a different combination of harvest (h) and the reproductive success of hatchery fish in the wild (RS). No predator control and low smolt-recruit survival was assumed in all cases.