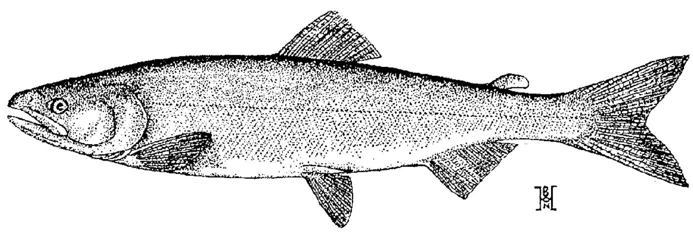
COSEWIC
Assessment and Status Report

on the

Sockeye Salmon
Oncorhynchus nerka

Cultus population

in Canada



ENDANGERED
2003

COSEWIC
COMMITTEE ON THE STATUS OF
ENDANGERED WILDLIFE IN
CANADA

COSEPAC
COMITÉ SUR LA SITUATION DES
ESPÈCES EN PÉRIL
AU CANADA

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Sockeye salmon — Illustration of adult sockeye salmon (reproduced from Hart 1973).

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COSEWIC
Assessment Summary

Assessment Summary – May 2003

Common name
Sockeye salmon (Cultus population)

Scientific name
Oncorhynchus nerka

Status
Endangered

Reason for designation
The Cultus population has unique genetic and biological characteristics (migratory delay of adults at the Fraser estuary, protracted lake residency before spawning, exclusive lake spawning, late spawning date, deepwater life of fry). The lack of success with previous attempts to transplant sockeye to Cultus Lake and other lakes suggests that Cultus sockeye are irreplaceable. The Cultus population has collapsed primarily due to overexploitation, including directed and incidental catches in mixed-stock fisheries at levels above those that can be sustained. An additional key source of impact on spawning adults since 1995 has been very high pre-spawn mortality, associated with unusually early migration into freshwater and with *Parvicapsula* parasite infestation. There are also ecological impacts to the lake habitat from colonization by Eurasian Watermilfoil, land development, stream channelization, nutrient input, and recreational use. Under present conditions, there is a high probability of extinction of the Cultus sockeye.

Occurrence
British Columbia Pacific Ocean

Status history
Designated Endangered in an emergency listing in October 2002. Status re-examined and confirmed in May 2003. Assessment based on a new status report.

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COSEWIC
Executive Summary

Sockeye Salmon
Oncorhynchus nerka

Species information

Sockeye salmon is one of seven species of the genus *Oncorhynchus* native to North America. The adults have a slender, streamlined, silvery body with faint blue-green specking on the back and weigh an average of 3 kg. They undergo a distinctive transformation of external colour and body shape during their migration from the ocean to the freshwater ecosystem where they were born and grew as juveniles (usually a lake). The head becomes pale green in colour, the body can change to a brilliant scarlet, and the males develop teeth and a sharply hooked jaw. The adults die soon after spawning and the developing embryos and juveniles remain for several years in the lake environment. Sockeye salmon exist as isolated populations and they evolve local adaptations to the freshwater environments in which they are born, juveniles rear and adults spawn.

This status report evaluates the genetically distinct population of sockeye that inhabits Cultus Lake, located in the coastal lowland portion of the Fraser River watershed in British Columbia. Cultus sockeye are genetically unique from all other sockeye populations. This includes sockeye in the upper Fraser that originated from different glacial refugia, as well as sockeye in the lower Fraser with whom they share a common ancestry. Cultus sockeye have many adaptations for survival in their local lake environment; these adaptations further distinguish them from other sockeye in the Fraser River and in other parts of their range. Attempts to introduce non-native populations of sockeye into Cultus Lake have failed; this suggests that Cultus sockeye are probably irreplaceable. Because of their isolation and their genetic and adaptive divergence from all other sockeye populations, the sockeye of Cultus Lake form a distinct unit.

Distribution

As a species, sockeye salmon are distributed through the North Pacific Ocean and its tributary systems in both Asia and North America; however, they are primarily abundant in Alaska and British Columbia (BC). The Fraser River watershed is the major habitat for sockeye in BC and supports the largest number of populations and individuals in the world. The population of Cultus Lake sockeye is located near the coast, in the eastern Fraser Valley of the Fraser River watershed, near the Canada-US international boundary and approximately 112 km upstream from the Strait of Georgia.

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About one-half of the life-cycle of Cultus sockeye is spent in Cultus Lake, while the other half is spent in the north Pacific Ocean near Alaska.

Habitat

Cultus sockeye exclusively utilize the habitat of Cultus Lake for their breeding, egg incubation and juvenile rearing. Cultus Lake is a short, narrow lake with a relatively small littoral area, warm temperature and a strong and prolonged thermocline. Its seasonal average photosynthetic rate is the highest of any sockeye lake in the Fraser system. Its productive zooplankton community has exceptional food resources for juvenile sockeye. The lake's water source is from a number of small, local streams; it drains into Sweltzer Creek, which joins the Vedder River that enters the Fraser River and eventually drains into the ocean. Smolts utilize this river habitat during their migration to the ocean; they grow into adults during the time spent in the north Pacific including ocean waters near Alaska. The adults then migrate back to coastal BC, enter the Fraser River and enter Cultus Lake. Usually, one and a half years are spent in the habitat of Cultus Lake, and two and a half years in the habitat of the ocean.

Biology

Most Cultus sockeye become mature in their fourth year of life. The adults return from the open ocean near Alaska, and enter the BC Strait of Georgia in August. Their normal behaviour has been to remain in the Strait for up to eight weeks before resuming their migration. They typically enter the Fraser River and Cultus Lake in September to December. Recently, however, migration into the Fraser River and Cultus Lake has been advanced; they have been migrating into freshwater as early as August and this has led to increased levels of adult mortality.

Cultus sockeye breed exclusively in the lake and die after spawning; the carcasses contribute organic enrichment and other nutrients to the lake. Fry emerge from the gravel in the spring and immediately school and move into deeper water. The juveniles are distributed throughout the limnetic zone and are exposed to dense predator populations that include northern pikeminnow, coho salmon, trout, Dolly Varden char and sculpins. They are usually resident in the lake for one and sometimes two years, and then migrate from late March to June as smolts to the ocean. They migrate through the Fraser River and its estuary, then northward through Johnstone Strait and along the mainland coast until late fall or winter when they begin to move offshore into the Gulf of Alaska. They rear in the Gulf of Alaska with other sockeye populations for about two years before beginning the migration back to Cultus Lake.

The four-year cycle of Cultus sockeye produces largely discrete year-classes or cycles in a pattern known as cyclic dominance. These cycles are an important part of the population biology of this species. Slight variation in maturity schedules (e.g., a few individuals may mature at age three or five) creates gene flow across cycles and allows some demographic recovery. With about 94% of Cultus sockeye maturing as four-year-olds, only 6% of individuals may contribute to gene flow across cycles.

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Population sizes and trends

The number of adult sockeye returning to Cultus Lake each year has been recorded since 1925. Abundance was generally strong but variable until the late 1960s, averaging about 20,000 adults. After the late 1960s, spawner numbers collapsed in two cycles and began a sustained decline in a third cycle. Since the early 1990s, abundance has declined dramatically on all four cycles. The average across- cycle number of adults is down to 4,800; this is the lowest number ever observed (since 1925). In the last three generations (past 12 years; 1991-2002), the adult spawner population declined by 36%, a decline rate of 3.3% per year across all cycles. Including the recent increase in mortality of adults before spawning, there has been about a 92% decline in number of effective spawners (past 12 years). The number of spawning adults is now a small fraction of the most conservative estimate of the capacity of the habitat (56 to 115 thousand spawning adults). The number of fry and smolt has also declined.

From 1995 through 2002, the migration of Cultus and other late-run sockeye from the Strait of Georgia into the Fraser River became progressively earlier. While the cause of the early migration is unknown, its consequences have been dramatic. The early migration has been associated with high levels of mortality along the freshwater migratory route and in terminal areas, as well as elevated levels of prespawning mortality in the natal streams and lakes. These mortalities are caused by heavy infestations of *Parvicapsula minibicornis*, a parasite that attacks the kidneys and gills (St-Hilaire *et al.* 2001). While the parasite is believed to be endemic to the system, it causes mortality only with prolonged exposures that provide the parasite a more protracted developmental period. Although *Parvicapsula* occurs in most Fraser River sockeye populations, it has caused significant mortality only among early migrating late-run sockeye, including Cultus sockeye.

An index of freshwater survival of juveniles shows no obvious long-term trend, except a sharp recent decline in the production of smolts per spawner that is associated with the elevated levels of adult prespawn mortality. Thus, freshwater survival of juveniles does not appear to be causing the significant collapse of the Cultus sockeye. The total survival index, which incorporates freshwater and marine life history stages, is highly variable but dropped below the replacement line during the *El Nino* events in the 1990s.

Limiting factors and threats

Over-exploitation by the fisheries, recent increases in the level of prespawn mortality associated with the early migration, and reductions in marine survival from the *El Nino* events in the 1990s are the primary contributors to the collapse of the Cultus sockeye. Fishery exploitation exceeded sustainable levels almost continuously for over four decades (1952-1997). The fishery annually killed an average of 67% of the adults before they spawned, when sustainable levels would be under 56%.

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The prespawn mortality due to infestations of *Parvicapsula minibicornis* parasite is uncontrollable. The *El Nino* events and accompanying changes in marine survival are also uncontrollable. Therefore, the only primary contributor to the collapse that can be controlled is the fishery. In the complete absence of all further fishing, a mathematical analysis of the probability of extinction of this sockeye population under conditions of high prespawn mortality ranges from 50% in three generations (12 years) to 100% in 25 generations (100 years).

The Cultus watershed is heavily developed for recreational, residential and agricultural uses that have significantly impacted tributary streams and localized portions of the lake foreshore. Some 92% of the shoreline is now devoted to parkland. About 1.5 million visitors per year visit the lake and recreational boating is popular. Changes to the ecology of the lake are occurring; for example, water milfoil has been introduced and predation threats are possibly changing. However, these habitat impacts, while comprising a threat, are unlikely to be responsible for the collapse of the population.

Special significance

Cultus sockeye are a genetically distinct, locally adapted population that serves as a keystone species for the Cultus Lake ecosystem. Adults provide organic and other nutrients from the ocean by carcass decomposition, and juveniles have a role in the lake's food web and energy cycling through consumption of plankton and serving as prey to piscivorous fishes, birds and mammals. This population is also scientifically important due to its early role in salmon research and for possessing one of the world's longest time series of assessment data for any sockeye population and its habitat. Finally, the population is important to many segments of Canadian society: it is fundamental to the culture and well-being of the neighbouring Soowahlie Band and the Sto:lo First Nation; it is of recreational and commercial interest to fishers; and it is of intellectual, cultural and recreational interest to many naturalists and tourists.

Existing protection or other status designations

An extensive framework of international commitments and domestic legislation and policies exist to protect Pacific salmon populations, including the U.N. Convention on Biological Diversity, the Fisheries Act, federal-provincial agreements, provincial Legislation such as the Water Act, the 1998 New Directions Policy of Fisheries and Oceans Canada, and the pending Wild Salmon Policy. Nevertheless, Cultus sockeye have declined until they now face possible extinction. The Pacific Salmon Commission and Fraser Panel managers took conservation steps to reduce fishery harvest levels on late-run Fraser sockeye in 2001 and 2002. This reduced the number of sockeye salmon killed and thus benefited Cultus sockeye. However, preliminary information indicated that Cultus sockeye were subjected to being killed by the fishery at a level that exceeded conservation agreements (25% in 2003 when the conservation agreement was a ceiling of 15%). On 25 October 2002, COSEWIC conducted an Emergency Assessment and listed Cultus sockeye as *Endangered.* In May 2003, COSEWIC further

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evaluated and confirmed the listing as *Endangered*. In the US, sockeye populations experiencing a similar collapse have been listed as endangered under the Endangered Species Act, which has afforded protection against further take.

Summary of status report

Cultus Lake sockeye is a genetically unique population that is important from ecosystem, scientific and cultural perspectives. It has collapsed over the last three generations (1991-2002; declines in adult spawner population and total reproductive potential of 36% and 92%, respectively) primarily due to over-harvest of adults by the fisheries, an increase in adult mortality associated with parasite infestation, and reductions in marine survival. Deterioration of the lake habitat is a threat but appears not to have caused the collapse. At current low abundances, the population is highly vulnerable to human impact and random environmental events. Without any further fishing pressure, under conditions of high prespawn mortality the probability of extinction ranges from 50% in three generations (12 years) to 100% in 25 generations (100 years).

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COSEWIC MANDATE

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) determines the national status of wild species, subspecies, varieties, and nationally significant populations that are considered to be at risk in Canada. Designations are made on all native species for the following taxonomic groups: mammals, birds, reptiles, amphibians, fish, lepidopterans, molluscs, vascular plants, lichens, and mosses.

COSEWIC MEMBERSHIP

COSEWIC comprises representatives from each provincial and territorial government wildlife agency, four federal agencies (Canadian Wildlife Service, Parks Canada Agency, Department of Fisheries and Oceans, and the Federal Biosystematic Partnership), three nonjurisdictional members and the co-chairs of the species specialist groups. The committee meets to consider status reports on candidate species.

DEFINITIONS

Species	Any indigenous species, subspecies, variety, or geographically defined population of wild fauna and flora.
Extinct (X)	A species that no longer exists.
Extirpated (XT)	A species no longer existing in the wild in Canada, but occurring elsewhere.
Endangered (E)	A species facing imminent extirpation or extinction.
Threatened (T)	A species likely to become endangered if limiting factors are not reversed.
Special Concern (SC)*	A species of special concern because of characteristics that make it particularly sensitive to human activities or natural events.
Not at Risk (NAR)**	A species that has been evaluated and found to be not at risk.
Data Deficient (DD)***	A species for which there is insufficient scientific information to support status designation.

* Formerly described as "Vulnerable" from 1990 to 1999, or "Rare" prior to 1990.

** Formerly described as "Not In Any Category", or "No Designation Required."

*** Formerly described as "Indeterminate" from 1994 to 1999 or "ISIBD" (insufficient scientific information on which to base a designation) prior to 1994.

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) was created in 1977 as a result of a recommendation at the Federal-Provincial Wildlife Conference held in 1976. It arose from the need for a single, official, scientifically sound, national listing of wildlife species at risk. In 1978, COSEWIC designated its first species and produced its first list of Canadian species at risk. Species designated at meetings of the full committee are added to the list.

Environment Canada / Environnement Canada
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Canada

The Canadian Wildlife Service, Environment Canada, provides full administrative and financial support to the COSEWIC Secretariat.

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FOREWORD

Cultus sockeye are one of the most intensively studied salmon populations in the world. Research on spawner abundance, lake characteristics and juvenile production began with scientists at the Pacific Biological Station in the 1920's (e.g., Foerster 1929a, 1929b, 1929c, 1934, 1936; Ricker 1935, 1937, 1938c) and has continued with the work of the International Pacific Salmon Fisheries Commission (e.g., Howard 1948; Cooper 1952) and the Department of Fisheries and Oceans (DFO) (e.g., Ricker 1952). DFO has maintained a field laboratory and research program on the shore of Cultus Lake since 1925. Thus, there are a wealth of data on lake limnology and fish community structure as well as abundance information for the sockeye fry, smolt and adult life stages, upon which this report is based.

SPECIES INFORMATION

Name and classification

The scientific name *Oncorhynchus nerka* (Walbaum, 1792) derives from the Greek roots onchos (hook) and *rynchos* (snout), and nerka, a Russian common name for the species (Hart 1973). It is one of a group of seven species of the genus Oncorhynchus native to North America. The name *sockeye*, a corruption of the Coast Salish word *sukkai* (Hart 1973), is the most frequently used common name for the species. Other common names are red salmon (Alaska), blueback salmon (Columbia River), nerka and krasnaya ryba (Russia), and benizake and benimasu (Japan) (Burgner 1991). The French common name is *saumon rouge*.

Description

Sockeye can be distinguished from other species of the family Salmonidae by the 13 to 19 rays in the anal fin that are common to all Pacific salmon, and from other Pacific salmon species by the 28 to 40 long, slender, closely spaced gill rakers on the first arch, the few pyloric caeca, and the fine speckling on the back (Fig. 1). Juvenile sockeye have a slender, elongate body with elliptical or oval parr marks that extend little if at all below the lateral line. Adult sockeye have a slender, streamlined, silvery body with faint blue-green specking on the back; weight in Canada averages 3 kg but can reach over 6 kg. During maturation, they undergo a distinctive transformation of external colour and body shape; the head becomes pale green while the body changes to a dull, brownish red that later becomes a brilliant scarlet in some populations. Males develop teeth and a hooked jaw, while females largely retain their marine body shape. Detailed descriptions can be found in Foerster (1968), Hart (1973) and Burgner (1991).

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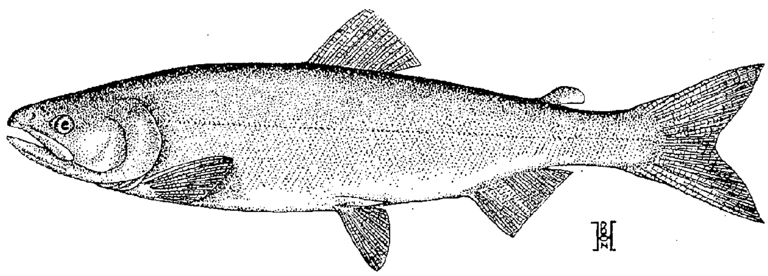

Figure 1. Drawing of an adult sockeye salmon (reproduced from Hart 1973).

Nationally significant populations

Canada's Species at Risk Act (SARA) defines a wildlife species as a species, subspecies, variety, or geographically or genetically distinct population. The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) interprets such populations to be Nationally Significant Populations. In the United States, the application of the Endangered Species Act to Pacific salmon uses the criteria of Evolutionarily Significant Unit (ESU) (Waples 1991), i.e., a population that: a) shows substantial reproductive isolation, where the degree of isolation is sufficient to allow important differences to accrue to individual populations; and b) is an important component of the evolutionary legacy of the species, i.e., its phenotypic life history traits reflect local adaptations of evolutionary importance (Waples 1991). In an application of these criteria to sockeye in Washington and Oregon states, the U.S. National Marine Fisheries Service concluded that all of the populations (six) for which sufficient data are available constitute ESU's (Gustafson et al. 1997). Below, I describe the Cultus sockeye population in terms of reproductive isolation, local adaptation and evolutionary importance.

Reproductive isolation: The genetic structure of North American sockeye populations is determined both by their ancestral origin during the last glaciation and by the nursery lake in which the juveniles rear (Wood 1995). Sockeye stocks up and downstream of the Fraser Canyon are genetically distinct based on mitochondrial, allozyme and microsatellite data (Wood *et al.* 1994; Bickham *et al.* 1995; Withler *et al.* 2000). A comparison of genetic differentiation with geographic distance shows that genetic and geographic distances are not related (Withler *et al.* 2000). Rather, differences reflect an independent post-glacial colonization of the lower Fraser from the Bering refuge and the upper Fraser from the Columbia refuge (Wood *et al.* 1994). Specific studies on population structure derived from the *DAB-β1* MHC locus (Miller *et al.* 2001) and six microsatellites among 30 populations (Withler *et al.* 2000) shows significant differentiation among lower Fraser populations, with Cultus being the most distinctive. The population most similar to Cultus sockeye is the Chilliwack, which is located in the same tributary system but is isolated from Cultus by distinctly different breeding seasons.

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In common with most other Fraser sockeye nursery lakes, there were several transplants early in the twentieth century of other sockeye populations into Cultus Lake (Aro 1979). Several million Birkenhead fry were released in 1920-1922, and similar numbers of Harrison and Pitt fry may have been released in 1915. The Cultus population, however, shows no evidence of genetic introgression with Birkenhead, Harrison or Pitt sockeye (R. Withler, DFO, Pacific Biological Station, pers. comm.). Therefore, these transplant attempts probably failed. By contrast, two other transplants in the Fraser system, of multiple sockeye stocks to Upper Adams River and Fennell Creek, resulted in genetic similarities at microsatellite loci between the host and introduced populations (Withler et al. 2000). Consequently, if the Cultus transplants had been successful, it is likely that the genetic similarities would have been revealed in the microsatellite analyses.

Additional genetic loci (14 microsatellite loci and one major histocompatibility complex locus, MHC) and an extended range of baseline populations (13,000 samples from 46 populations) have been recently analyzed (T. Beacham, DFO, Pacific Biological Station, pers. comm.). Genetic differentiation (reproductive isolation) has been quantified using the co-ancestry coefficient, FST1, calculated using GDA software (Lewis and Zaykin 2001). FST statistics at the microsatellite loci are generally above 0.10 for most comparisons with Cultus (range: 0.094 (Chilliwack) to 0.191 (Cayenne)) (Table 1), a value that would be expected for pairs of populations exchanging no more than three effective spawners per generation. This indicates a significant level of genetic differentiation between Cultus and all other populations, including Chilliwack.2 Differentiation is even more marked at the single MHC locus, with most FST values greater than 0.20 (range: 0.006 (Pitt) to 0.646 (Kynoch)). This shows that Cultus is genetically distinct both at neutral loci such as microsatellites and at a locus under selection such as MHC, and confirms the results from previous allozyme loci and mitochondrial DNA analyses. Cultus sockeye, therefore, constitute a genetically very distinct and unique population in British Columbia.

Local adaptation: Cultus sockeye possess many adaptations for their local environment: a) on their spawning migration, Cultus sockeye delay in the Fraser estuary for up to eight weeks before resuming their migration into the river, a behavior that is unique to the 50 populations that comprise the Fraser late run sockeye group. This delay reduces exposure to adverse freshwater environments but permits breeding when environmental conditions optimize egg, alevin and fry survivals; b) Cultus adults remain in the lake for as long as three months before breeding, holding in local environments that are much cooler than those along the freshwater migratory pathway; c) breeding occurs over two months and extends beyond the normal range for other populations. Brannon (1987) hypothesizes that the protracted spawning period is an adaptation of populations in ecosystems with highly variable spring weather and constant-temperature incubation environments. Under these conditions, variation in

[1] F_{ST}, calculated from a correlation of genes across individuals within and among populations, indicates the degree of reproductive isolation of a population. The higher the F_{ST} value (maximum 1), the more closely individuals are related to each other within a population and the less to individuals in other populations.
[2] Some MHC values may be due to common selective forces as this locus is under strong selection from disease and parasites.

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emergence timing is related primarily to the time of egg deposition (although Cultus incubation times are progressively shorter for later spawners thereby compressing the fry emergence period). Different parts of the emergence curve are favoured sufficiently often to sustain their associated spawning times; and d) the behaviour of fry, which school and move offshore into deeper water immediately after emergence, is an atypical behaviour for Fraser sockeye that is likely an adaptation to the dense predator populations of Cultus Lake (Brannon 1967).

Evolutionary importance: Many attempts were made in the twentieth century to establish self-sustaining populations of anadromous salmonids by transplanting existing populations to new areas. In most cases, transplant attempts within the species' native range were unsuccessful. It is believed the lack of success is due to incompatibilities between the adaptations of the donor populations and the requirements of the recipient environments (Withler 1982). Despite widespread attempts to transplant Fraser sockeye (Aro 1979), self-sustaining populations have been established in only two locations and required decades of effort (Williams 1987; Wood 1995). Attempts to introduce non-native sockeye into Cultus Lake were unsuccessful. This indicates that Cultus sockeye, which have been an evolutionarily unique lineage for thousands of years during which adaptations to Cultus Lake were evolved, are unlikely to be replaceable in the near future.

DISTRIBUTION

Global range

Sockeye salmon are distributed as a species in the temperate and sub-arctic waters of the North Pacific Ocean and the Bering Sea and Sea of Okhotsk (Fig. 2) (Burgner 1991). In Asia, the spawning distribution extends to the Kamchatka Peninsula and the northern part of the Sea of Okhotsk. In North America, they range from the Columbia River in the south to Kotzebue Sound in Alaska, and to the western tip of the Aleutian Islands. They are abundant primarily in British Columbia (especially the Fraser River) and in Alaska (especially Bristol Bay).

Canadian range

Sockeye salmon typically occur in river systems of British Columbia that contain lakes that are accessible to the Pacific Ocean. Juveniles, on their seaward smolt migration, and adults, on their upstream spawning migration, move between the freshwater and marine habitats. The Fraser is the largest river in western Canada (Fig. 3). More sockeye utilize the Fraser than any other river system in the world (Northcote and Larkin 1989). It supports more than 150 populations that management agencies divide into four groups based on the timing of the adult migration in the lower river: the early run (late June to late July); the early summer run (mid-July to mid-August); the summer run (mid-July to early September); and the late run (early September to mid-October). The late run comprises over 50 populations that spawn in

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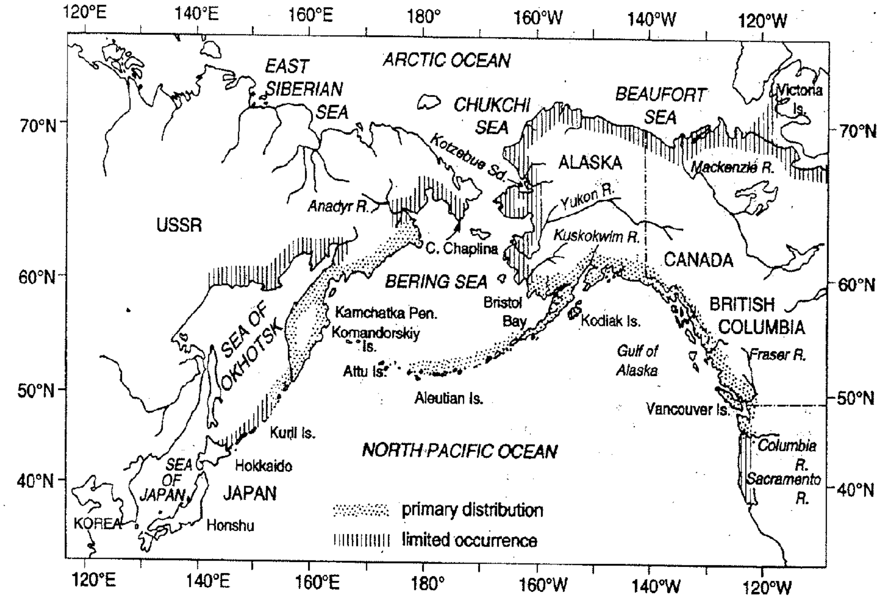

Figure 2. Distribution of sockeye salmon populations along the coast of the North Pacific Ocean (reproduced from Burgner 1991).

the lower Fraser, Harrison-Lillooet, Seton-Anderson and South Thompson systems (Fig. 3). It includes the Birkenhead, Harrison, Weaver, Portage, Shuswap, Adams and Cultus populations. While these groups are a somewhat arbitrary application of divisions to a continuum of run timings, they reflect migration adaptations that are useful in the fishery management process.

Cultus sockeye spawn exclusively in a small (6.3 km^2) coastal lake that lies in a short (4.8 km), narrow (1.3 km) basin located at an elevation of 43 m near the Canada-U.S. international boundary. The lake is part of the Vedder-Chilliwack System located in the eastern Fraser Valley approximately 112 km upstream from the Strait of Georgia (Fig. 3). The closest city is Vancouver, and the closest town is Chilliwack. The adults die in the lake following breeding, while the eggs, fry and juveniles reside in the lake until emigration as smolts. Year classes overlap, thus there is a continuous population of young Cultus sockeye in this nursery lake. When the smolts emigrate from the lake, they use the lower Fraser River and its estuary to reach the ocean where the adults are distributed as described under habitat.

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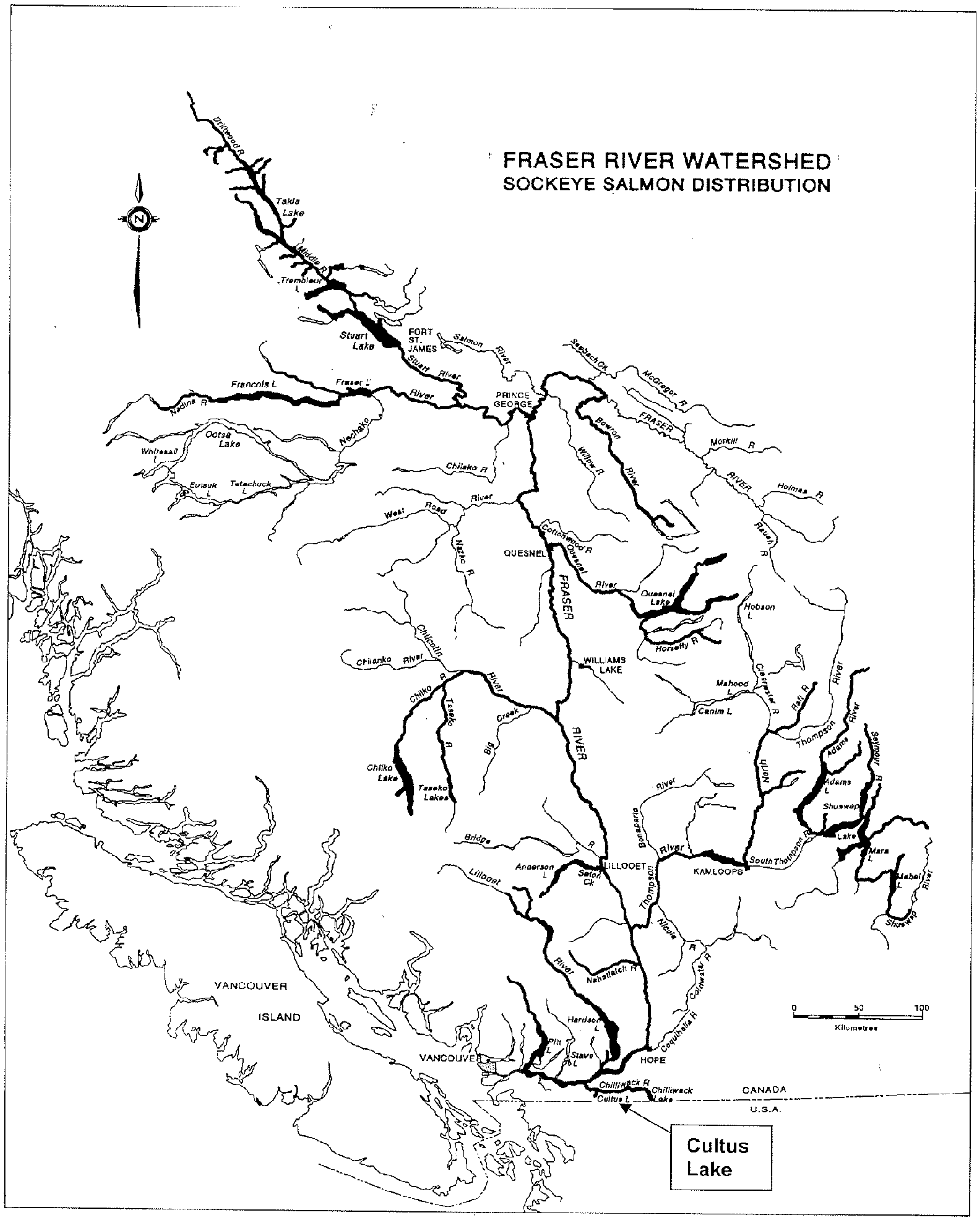

Figure 3. Distribution of sockeye salmon populations in the Fraser River system. The presence of sockeye is shown by heavy black. Cultus Lake is highlighted with an arrow.

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HABITAT

Sockeye salmon is primarily an anadromous species that depends on freshwater environments for spawning, egg incubation, juvenile rearing and smoltification, and marine environments for growth and maturation (Burgner 1991). Over its global distribution, the species has adapted to diverse thermal and hydrographic regimes, water chemistry and ecosystems in a variety of geoclimatic zones, latitudes and elevations. Sockeye are distinct from other salmon species in that their spawning habitat is usually near lakes (although some populations have adapted to a strictly riverine freshwater environment). Adults typically spawn in lake tributaries or outflows or along lake foreshores, which enables juveniles to rear in the lake limnetic zone before they smoltify and migrate to sea. Nest sites are in gravel that is small enough to be dislodged by the female but of sufficient size to permit an adequate circulation of well oxygenated water. They may use substrates that range from coarse sand to large angular rubble and boulders. Water depth can range from 0.1 meters in small tributary streams to over 30 m in lakes, and water temperature can range from 2 to 8° C. After constructing the nest, the eggs are deposited and fertilized, then buried by the female in gravel to a depth of 15-20 cm.

In Cultus Lake, sockeye spawn exclusively along the lake foreshore (Fig. 4). Spawning occurs at a depth of 0.5 to 6 m in substrates consisting of weathered shale alluvial materials that extend 60 m from shore (Brannon 1967). Groundwater percolates through much of the spawning area at a constant year-round temperature of 8°C, among the warmest spawning and incubation environments used by Fraser sockeye. Percolation is poorer in the peripheral areas, reducing oxygen availability and temperatures.

After emergence, the fry migrate to foraging and rearing areas in Cultus Lake where they spend one to three years. In general, juvenile sockeye growth and survival depends on a complex interaction of the lake's morphometric (area, volume, depth), edaphic (chlorophyll-a, total phosphorus, total nitrogen, total dissolved solids) and climatic (temperature, wind, solar radiation) characteristics (Northcote and Larkin 1956). Cultus Lake can be characterized from data collected in the 1930's, 1960's and 1970's, and in 2001 (Ricker 1937; Goodlad et al. 1974; Shortreed and Morton, unpublished). The lake has a surface area of 6.3 km^2, a drainage basin of 65 km^2, and a mean and maximum depth of 32 m and 41 m, respectively. It is steep-sided and has a littoral area (i.e., the zone where light penetrates to the bottom) of only 12% of the total surface area. Like most coastal British Columbia lakes, Cultus is a warm monomictic lake (i.e., it is thermally stratified except during the winter overturn) with a strong and prolonged thermocline. Summer temperatures in the surface layer (the epilimnion) exceed 20° C, while bottom temperatures in the fall average less than 7° C. Water clarity is relatively high (Secchi disk depth averages 10-11 m), with an average euphotic zone (where light intensity permits net primary production) of twice the depth of the thermocline. Relative to other British Columbia sockeye nursery lakes, Cultus is well buffered and alkaline, with high conductivity, total dissolved solids, and nutrient loading levels (although epilimnetic nitrate concentrations decline to very low levels from August to October). Its

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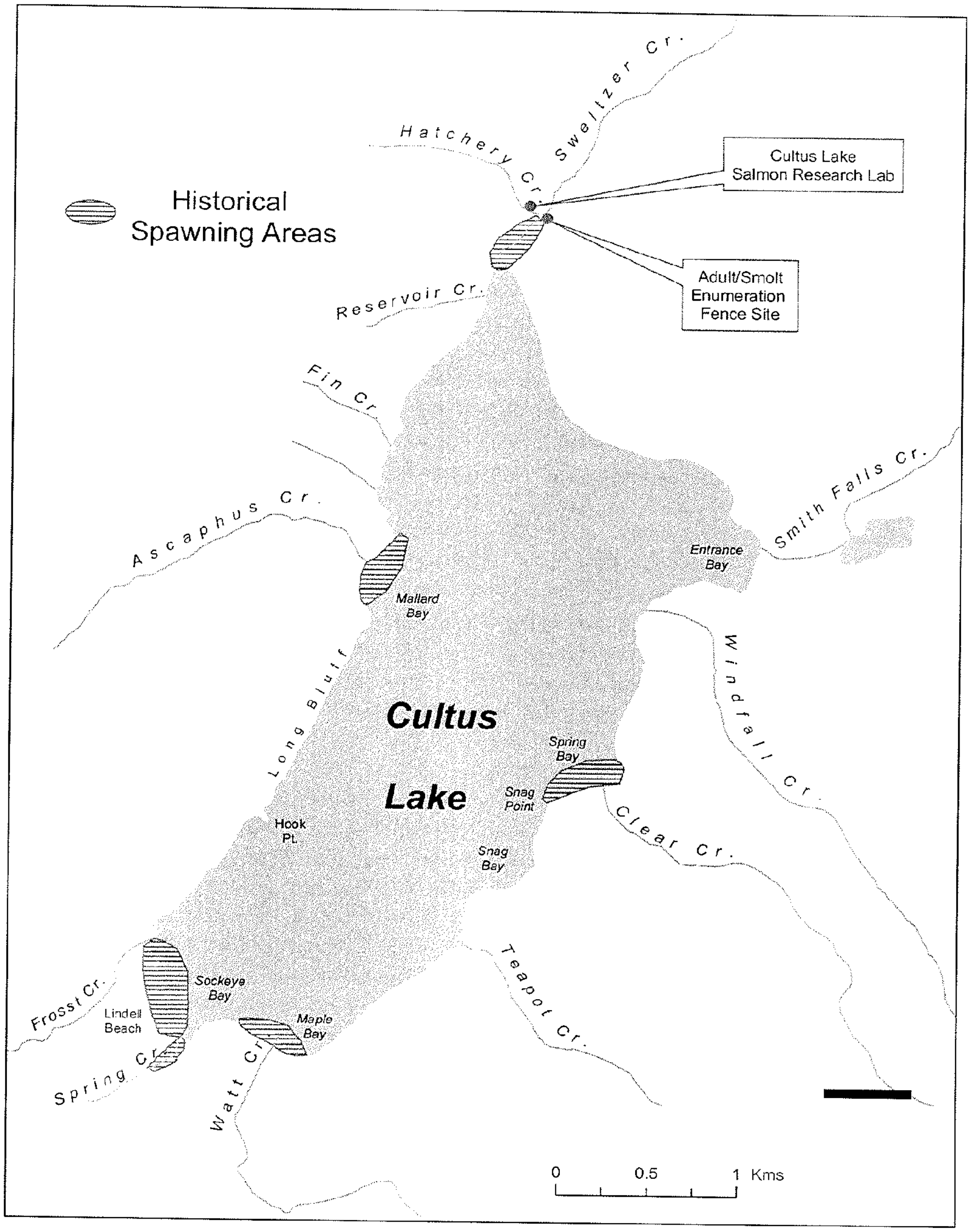

Figure 4. Map of Cultus Lake, including locations of the six historic and single current spawning locations (only Lindell Beach is used today).

seasonal average photosynthetic rate is the highest of any sockeye nursery lake in the Fraser system. While some characteristics make the lake less than ideal as a sockeye nursery area (e.g., warm epilimnion, predator abundance), with its productive zooplankton community that includes abundant Daphnia, Cultus has exceptional food resources for juvenile sockeye. The lake is deep enough to have a substantial, cool hypolimnion (some of which is within the euphotic zone) that provides a favourable rearing environment. While the warm summer epilimnion temperatures and a relatively small late fall fry suggest that a substantial proportion of the zooplankton community may not be accessible to juvenile sockeye, the relatively long growing season permits considerable overwinter growth.

Cultus Lake supports a somewhat simple fish community that includes six species of Pacific salmon, chinook (*O. tshawytscha*), coho (*O. kisutch*), chum (*O. keta*), *pink (O. gorbuscha*), coastal cutthroat trout (*O. clarki clarki*), and both steelhead and rainbow trout (*O. mykiss*), as well as Dolly Varden (*Salvelinus malma*), Cultus pygmy sculpin (*Cottus sp.*), prickly sculpin (*C. asper*), threespine stickleback (*Gasterosteus aculeatus*), largescale sucker (*Catostomus macrocheilus*), longnose dace (*Rhinichthys cataractae*), mountain whitefish (*Prosopium williamsoni*), northern *pikeminnow (Ptychocheilus oregonensis*), peamouth chub (Mylocheilus caurinus), redside *shiner (Richardsonius balteatus*) and western brook lamprey (*Lampetra richardsoni*). The Cultus pygmy sculpin, a strictly limnetic species that evolved from the stream rearing coastrange sculpin (*C. aleuticus*) (Cannings and Ptolemy 1998), has adapted to the limnetic life-cycle by reducing bone density and increasing sub-dermal lipids to allow vertical migration in the water column. It is listed by COSEWIC as threatened and by the Province of British Columbia as critically imperiled (Cannings et al. 1994) due to its single known location in Cultus Lake.

Increases in spring water temperature and day length cause sockeye juveniles to undergo smoltification and to emigrate from the lake. They emigrate via Sweltzer Creek, a short (3 km) river with an average discharge of only 3.5 $m^{3/s}$. Fraser sockeye smolts move quickly through the Fraser estuary and into the Strait of Georgia in April and May (Healey 1980). They migrate northward through Johnstone Strait by July, then northwest along the coast until late fall or winter when they begin to move offshore into the Gulf of Alaska where they rear with other sockeye stocks for about two years. The timing of the offshore movement is affected by a complex interplay of physical (temperature, salinity), biological (age, size, prey abundance) and genetic (disposition to specific migratory patterns) factors (Burgner 1991). North American sockeye utilize the area south and east of Kodiak Island, with Fraser sockeye distributed further south (to 46° N) (Burgner 1991). Their distributions, while predictable in a general way, have not been reliably linked to major oceanographic features such as circulation patterns and temperature and salinity fronts (Burgner 1991). Cultus sockeye are vulnerable to the impacts of human development during their smolt emigration and migration through near-shore coastal waters. The lower Fraser River is heavily developed as it passes through a community of over two million people: the estuary has been encroached by development and is constrained by dykes and river entrainment structures; and effluent from pulp mills and small communities is common along the coast. There is also a

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growing number of fish farms on the marine migratory pathway of juvenile sockeye as they move north along the coast of British Columbia. Concerns have recently been expressed regarding the potential transfer of diseases and parasites such as sea lice between salmon farms and wild populations, especially in areas of dense salmon farming (Gardner and Peterson 2003).

BIOLOGY

General sockeye biology

In general, sockeye exhibit a greater variety of life history patterns among populations than is typical for other members of the genus *Oncorhynchus*, probably because of the frequent use of lakes for juvenile rearing habitat. This requires specific adaptive behaviours for adults and offspring to suit individual lake conditions. Such behaviours include adult homing to spawning areas that is spatially more precise than is typical for Pacific salmon because emergent fry must be adapted to migrating in a specific direction to reach the rearing lake, adult spawning timing to produce offspring that develop at optimal times of the year for the lake's food resources, as well as the adaptations of the embryos and juveniles themselves to the biotic and abiotic characteristics of each lake. The evolution of these adaptations in sockeye adults and juveniles is made possible because of the isolation associated with lake spawning and rearing, which creates divergence among sockeye gene pools. These individual gene pools, therefore, are able to evolve adaptations to the specific local conditions.

The sockeye breeding period ranges from July to January, but occurs most frequently in August and September. Eggs are deposited in nests, termed *redds*, constructed by the female, fertilized by an accompanying male (or an opportunistic precocious male), then covered with gravel by the female. The eggs incubate in the gravel through the winter and until the yolk sac is absorbed in the spring. Ambient temperatures mediate incubation duration and the timing of emergence; emergence occurs in darkness. Progeny from river spawners show either positive or negative rheotaxis depending on the orientation of the spawning area to the lake, while those from lake spawners move into shallow water before progressively moving offshore. They utilize lake rearing areas for one to three years where they compete among themselves and with other species (e.g., redside shiner, threespine stickleback) for food such as insects and zooplankton, and serve as prey to resident species (e.g., Northern pikeminnow, salmonids). Juveniles smoltify and emigrate to sea from March to June. They remain at sea for one to four years, but more typically for two to three years, before the onset of maturation and the return to the natal area. Those returning after one year, termed precocious (predominantly *jacks* (male) but sometimes *jills* (female)), are much smaller; those returning as adults after two or more years are much larger, having increased several fold in weight. Like other Pacific salmon species, sockeye die and decompose after spawning, thereby transferring biogenic nutrients from the marine to the freshwater and terrestrial ecosystems.

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Cultus sockeye biology

Cultus sockeye mature predominantly in their fourth year of life (typically after about two years in freshwater and two years in marine environments). The population exhibits a quadrennial adult abundance pattern typified by a strong dominate cycle (expected in 2003), a moderate sub-dominant cycle (2002) and two numerically weak cycles (2000 and 2001). Normally, Fraser summer and late run sockeye populations (including Cultus) migrate from the open ocean into the Strait of Georgia between Vancouver Island and the mainland in August. The summer run populations continue their migration into the river, while the late run holds in the Strait for up to eight weeks, a delay that is not typical of stocks in other timing groups or river systems. Because the local environmental conditions require a later breeding period for late run populations, the delay is likely an adaptation that permits them to migrate from the open ocean at the prescribed time but limits their exposure to adverse conditions in freshwater environments. The migration into the Fraser River normally begins in September and October, and into Cultus Lake from late September to early December, a protracted period of about eight to ten weeks that is considerably longer (by 2-6 weeks) than that of most other Fraser River sockeye populations (Schubert 1998). From 1995-2002, the migration of late run sockeye into the Fraser River has been progressively earlier. In the most extreme case (2000), there was an almost uninterrupted migration from the Strait of Georgia into the Fraser River; Cultus sockeye began migrating into the Fraser River in August. While the cause of the early migration is currently unknown, its consequences have been dramatic. The early migration has been associated with high levels of mortality along the migratory route and in terminal areas, as well as elevated levels of prespawning mortality (PSM) in the natal streams and lakes. These mortalities are caused by heavy infestations of the freshwater parasite Parvicapsula minibicornis that attacks and destroys the kidneys and gills (St-Hilaire et al. 2001). While the parasite is believed to be endemic to the system, it causes mortality only with prolonged exposures that provide the parasite a more protracted developmental period. Consequently, although the parasite occurs in most Fraser River sockeye populations, it has caused significant mortality only among early migrating late-run sockeye, including Cultus.

Cultus sockeye spawn from late November through December, the latest spawning of all the Fraser sockeye populations (Schubert 1998). The pre-spawning behaviour and distribution of sockeye in Cultus Lake has not been documented. Historically, spawning has occurred along the lake foreshore at Lindell Beach, Snag Point, Spring Hole and Mallard Bay (Foerster 1929a) as well as in Sweltzer and Spring creeks (Howard 1948); however, recent spawning has been primarily confined to the lake foreshore at Lindell Beach (Fig. 4). While lake spawning is known in many sockeye populations, few other than Cultus spawn almost exclusively in the lake. Spawning occurs in upwelling groundwater that in peripheral areas can be lower in oxygen and pH, possibly requiring embryo adaptations that may include small eggs, higher pigmentation and a dense network of capillaries covering the yoke sac (Burgner 1991).

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The time required for the incubation of Cultus sockeye eggs decreases with spawning date, a unique adaptation to the population's protracted spawning period and constant incubation temperatures that reduces the range of emergence times (Brannon 1987). Despite this adaptation, fry emergence from the gravel remains protracted (April to July), reflecting the variation in incubation environments (peripheral areas have lower flows, less aeration) as well as the lengthy spawning period (Brannon 1967); emergence peaks in early to mid May. The fry school and move offshore into deeper water immediately after emergence, an atypical behaviour for Fraser sockeye that Brannon hypothesizes is an adaptation to the dense predator populations in Cultus Lake. Lake predators include salmonids such as coho and trout, as well as Dolly Varden char, northern pikeminnow and sculpins (Ricker 1941). Northern pikeminnow, while not the most voracious predator in the lake, can have a substantial impact on sockeye due to their abundance. The control of such predators can increase the survival of juvenile salmonids (Firesen and Ward 1999; Jeppson and Platts 1959). Two such control projects were conducted in Cultus Lake. The first was in the 1930's after Foerster (1938) documented high mortality among sockeye juveniles and Ricker (1933) demonstrated that predation by piscivorous fish was an important causal factor. They reduced the char and large pikeminnow populations by 90% over four years and reported a three-fold increase in sockeye freshwater survival (from 3.1% to 10.0%) and an increase in sockeye smolt size (Foerster and Ricker 1941). The second project, in 1990-1992 (Levy 1990; Hall 1992), also was associated with increased freshwater survival (from 70 to 100 smolts/spawner).

Newly emergent fry move into deeper water as early as April; most of the population is well offshore by May (Mueller and Enzenhofer 1991). They can rear in the lake for up to two summers (one is most common) and migrate as one or two-year-old smolts. A small proportion may residualize, remaining in the lake for their entire life cycle (Ricker 1938a, 1959). While both residual sockeye and kokanee remain exclusively in freshwater, residuals differ from kokanee in that they are the progeny of anadromous parents.

Planktonic crustacea are the most important food; Epischura sp., *Diacyclops bicuspidatus*, *Daphnia sp.* and *Eubosmina coregoni* are predominant in the lake (Foerster 1925; Ricker 1938b). *Diacyclops* is most important in winter and spring, and *Daphnia* in summer and autumn; *Eubosmina* is commonly taken by the youngest sockeye (Hartman and Burgner 1972). From June to November, sockeye fry are distributed throughout the limnetic zone. When the lake is thermally stratified, the nighttime distribution of sockeye is generally in a layer 5-10 m deep and just below the thermocline. As the thermocline weakens in the fall, the fry layer becomes wider and somewhat deeper. During the day, fry are presumably on the bottom because daytime acoustic transects detect very few fry-size targets in the water column (J. Hume, DFO, Cultus Lake Laboratory, pers. comm.).

The smolt migration from Cultus Lake begins in late March and continues into June. Following a period of ocean residency (see *Habitat),* they mature primarily as four-year-olds, although small proportions also mature after one winter at sea as three-

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year-old jacks or three winters at sea as five-year-old adults. Maturing sockeye migrate from the north Pacific Ocean during the summer, making their landfall along a broad section of the coast before entering the Strait of Georgia in August through either Johnstone or Juan de Fuca straits. The proportion that migrates through Johnstone Strait is higher in *El Nino* years when warmer sea surface temperatures extend north into coastal B.C.

CULTUS SOCKEYE FISHERY

Adult Cultus sockeye can be captured and killed by the fishery along the full extent of their migratory pathway, from the point of landfall along the coast until their entry onto the spawning grounds. The majority of the capture of adults is in large mixed-stock ocean seine, gillnet and troll fisheries, although a significant proportion can be killed in the Fraser River fisheries. Throughout the history of the Fraser River sockeye fishery, Cultus sockeye have not been managed as a discrete population with its own targeted level of capture and killing. The policy used by the Department of Fisheries and Oceans (DFO) has been to set capture levels based on the largest or most productive populations of sockeye even if smaller or less productive populations share the same migration timing. Populations such as Cultus sockeye, which are in the same fall-run as the larger and more productive Weaver and Adams River sockeye populations, experience a higher rate of adult killing than can be replaced by the population. The policy acknowledges that less productive populations of sockeye may not achieve their maximum population size, but assumes that they will stabilize at a smaller population size.

POPULATION SIZES AND TRENDS

The extensive studies of Cultus sockeye since the 1920's allow the presentation in this status report of population sizes and trends for adult escapement (1925-2002), fry (1986-2002) and smolt (1926-2003) populations, harvest and total return (1952-2002), freshwater (1925-2001), marine (1954-2001) and total (1948- -1999) survival and exploitation rates (1952-2002). Also summarized from Schubert *et al.* (2002) are stock productivity and productive capacity estimates, as well as simulation results from a Bayesian stock-recruitment model evaluation of future stock trajectories and extinction probabilities under different scenarios of prespawn mortality and exploitation.

Adults entering Cultus Lake

The number of mature adults entering Cultus Lake ("spawner abundance") has been assessed using enumeration fences since 1925, providing a unique 78-year time series of consistent data collection using an accurate assessment tool. Spawner abundance was low and variable during a period of large scale hatchery experimentation in the 1920's and 1930's, very high in 1939-1942 following the removal of predators from the lake, strong but variable from the early 1940's to the late 1960's,

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and declining since the late 1960's (Fig. 5; Table 2; Appendix 1). Abundances and patterns differ by cycle (Fig. 6). Since 1925, the number of adults entering Cultus Lake averaged 14,200 and 27,100 on the 2002 sub-dominant and 2003 dominant cycles, respectively, and 12,300 and 5,000 on the 2000 and 2001 off-cycles. Cyclic dominance largely disappeared from the 1940's to 1960's when abundance was similar on three cycles and relatively strong on the 2001 cycle. It re-emerged when off-cycle adult spawner abundance collapsed in the early 1970's. Since the late 1960's, abundance on the sub-dominant cycle has progressively declined while the dominant cycle has been trendless, although the last two cycle years have been weak. In contrast, off-cycle abundances have been very low (<2,000 spawners) since the early 1970's. The most recent populations on all cycles have been among the lowest ever recorded for Cultus sockeye, with the exception of the improved abundance (4,900) on the subdominant cycle in 2002.

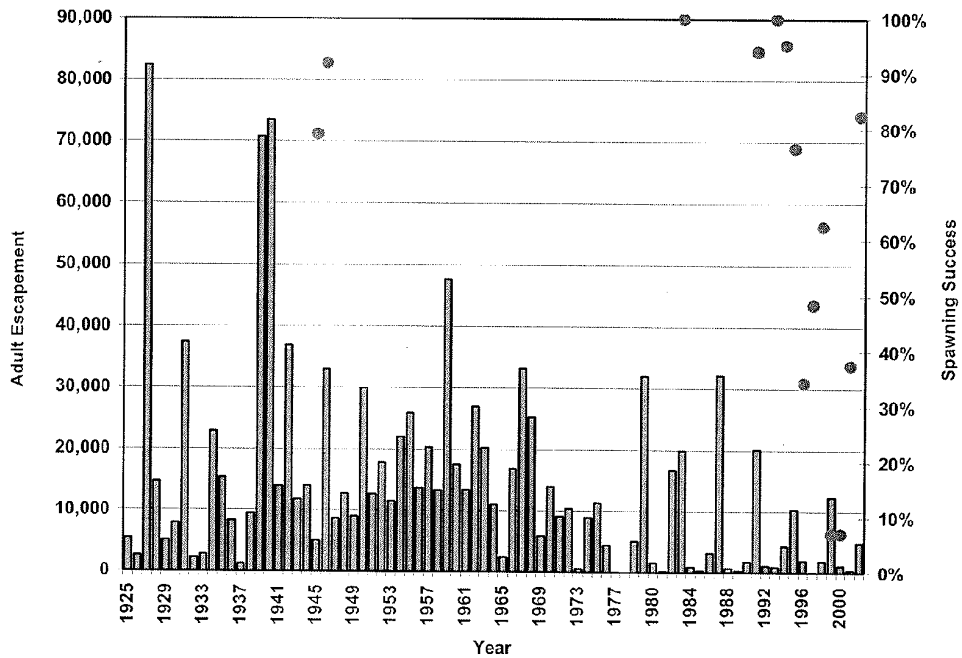

Figure 5. Annual numbers of adults entering Cultus Lake (escapements; bars) and spawning success estimates (points) for Cultus sockeye adults, 1925-2002.

Table 1. F_{ST} values for 14 microsatellite loci (95% confidence limits in parentheses) and one MHC locus between the Cultus sockeye population and populations in 45 other locations in the Fraser River system (data from Schubert *et al.* 2002).

Stock Group	Population	Microsatellites	MHC
Early Stuart	Kynock Creek	0.1096 (0.0705, 0.1567)	0.6456
	Gluskie Creek	0.1107 (0.0716, 0.1620)	0.5719
	Forfar Creek	0.1092 (0.0687, 0.1588)	0.5489
	Dust Creek	0.1073 (0.0638, 0.1599)	0.6299
	Porter Creek	0.1136 (0.0690, 0.1731)	0.5772
	Hudson Bay Creek	0.1153 (0.0726, 0.1668)	0.5748
	Blackwater Creek	0.1306 (0.0858, 0.1910)	0.5930
Late Stuart and Stellako	Stellako River	0.1069 (0.0687, 0.1434)	0.5850
	Middle River	0.1039 (0.0646, 0.1489)	0.6042
	Nadina River	0.1060 (0.0638, 0.1522)	0.5904
	Pinchi Creek	0.1105 (0.0660, 0.1635)	0.5474
	Tachie River	0.1044 (0.0686, 0.1415)	0.5812
	Kuzkwa River	0.1076 (0.0691, 0.1570)	0.5596
Upper Mid-Fraser	Bowron River	0.1086 (0.0688, 0.1563)	0.4427
	Chilko River	0.0994 (0.0623, 0.1401)	0.3442
	Chilko Lake (south)	0.1162 (0.0731, 0.1641)	0.3413
	Horsefly River (mixed)	0.1131 (0.0699, 0.1617)	0.2318
	Lower Horsefly River	0.1148 (0.0700, 0.1689)	0.2782
	Middle Horsefly River	0.1197 (0.0733, 0.1762)	0.2435
	Upper Horsefly River	0.1163 (0.0720, 0.1660)	0.2454
	Roaring River	0.1161 (0.0772, 0.1644)	0.1534
	Wasko Creek	0.1170 (0.0768, 0.1671)	0.1369
	Blue Lead Creek	0.1215 (0.0826, 0.1738)	0.1448
	McKinley Creek	0.1221 (0.0732, 0.1829)	0.2653
	Mitchell River	0.1361 (0.1000, 0.1700)	0.1276
Lower Mid-Fraser	Portage Creek	0.1066 (0.0650, 0.1500)	0.3834
	Gates Creek	0.1611 (0.1161, 0.2034)	0.1871
	Nahatlatch River	0.1153 (0.0740, 0.1649)	0.4294
Lower Fraser, north side	Birkenhead River	0.1116 (0.0615, 0.1777)	0.0074
	Weaver Creek	0.0981 (0.0641, 0.1359)	0.0109
	Big Silver Creek	0.1295 (0.0839, 0.1911)	0.0926
	Harrison River	0.1137 (0.0683, 0.1690)	0.3138
	Pitt River	0.1133 (0.0674, 0.1657)	0.0056
Lower Fraser, south side	Chilliwack River	0.0945 (0.0655, 0.1277)	0.2007
South Thompson	Lower Adams	0.1034 (0.0660, 0.1446)	0.3151
	Upper Adams	0.1415 (0.0964, 0.2025)	0.1554
	Cayenne Creek	0.1912 (0.1271, 0.2752)	0.1350
	Lower Shuswap	0.0943 (0.0643, 0.1275)	0.2829
	Middle Shuswap	0.0969 (0.0654, 0.1382)	0.3178
	Little Shuswap	0.1111 (0.0763, 0.1508)	0.3018
	Scotch Creek	0.1057 (0.0708, 0.1407)	0.2572
	Seymour River	0.1057 (0.0709, 0.1420)	0.2475
	Eagle River	0.1073 (0.0692, 0.1507)	0.3347
North Thompson	Fennell Creek	0.1053 (0.0801, 0.1349)	0.3319
	Raft River	0.1027 (0.0709, 0.1381)	0.3864

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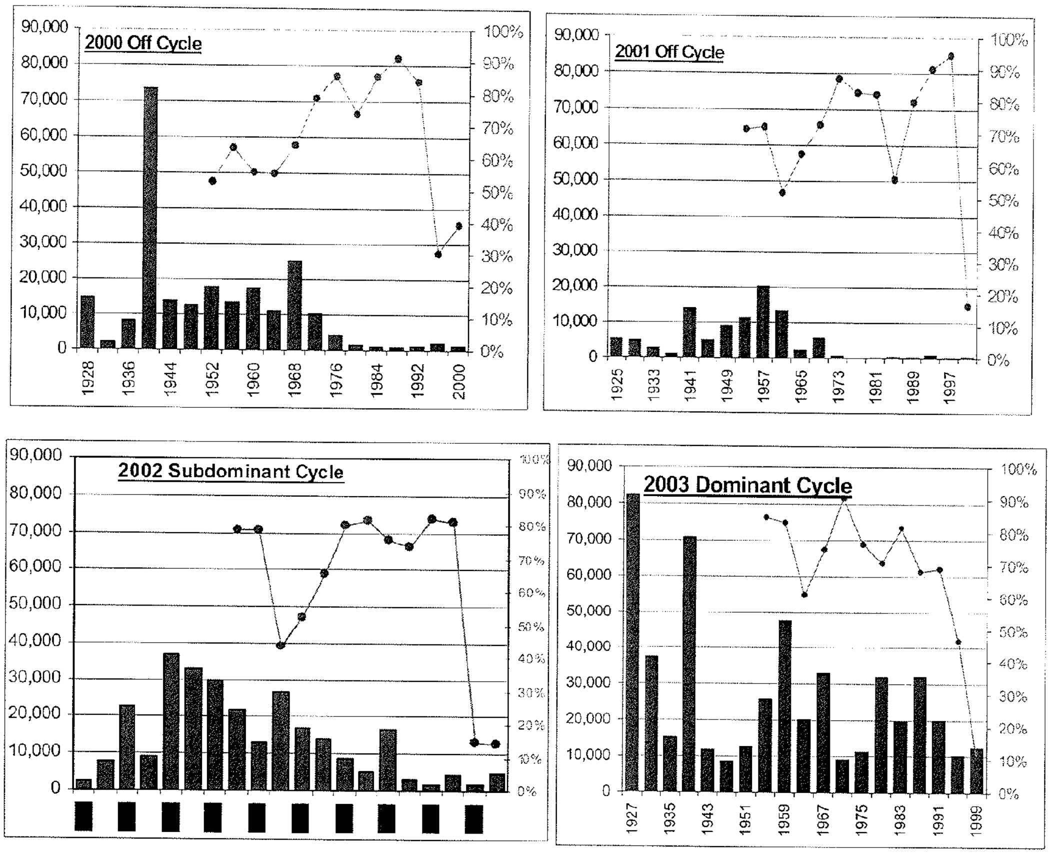

Figure 6. Annual numbers of adults entering Cultus Lake (bars) and the proportion of the adult population killed in fisheries (% exploitation rates; lines) for Cultus sockeye adults on the 2000, 2001, 2002 and 2003 cycles.

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In the last three generations (12 years; 1991-2002), the adult population entering Cultus Lake declined by 36%, a rate of 3.3% per year across all cycles (one-generation smoothed data, Fig. 7). Schubert et al. (2002) noted that this rate of decline underestimates the population's true loss of reproductive potential because it does not consider the recent increases in mortality suffered by the adults after entering the lake but before breeding (termed prespawn mortality or PSM). PSM is assessed from internal examinations of female carcasses following spawning. Before 1995, PSM averaged only 7% and was generally less than 10% in the years with available data. Since the onset of the early migration in 1995, there have been sharp increases in PSM, to 24% in 1995, 66% in 1996, 38% in 1998 and 13% in 2002. PSM could not be measured in 1997 and 1999-2001 because few if any carcasses were recovered. For 1999-2000, Schubert et al. (2002) estimated the level of PSM by comparing the number of smolts produced per adult spawner for those brood years (5 smolts/adult) with the average number in years before the start of the early migration (67 smolts/adult). By assuming that all of the difference could be attributed to PSM, they estimated PSM was 93% in 1999 and 2000. While this assumption was probably incorrect (reduced egg viability from depressed adult fitness and depensatory fry mortality probably played a role), the analysis reasonably approximates the change in reproductive potential because all mortality sources relate to the early migration. They applied these estimates (and used averages for 1997 and 2001) to the adult population numbers entering the lake (Appendix 1) and recalculated the rate of decline in the last three generations. This analysis, updated to include the 2002 population and PSM data, shows a rate of decline of effective spawners of 92%. This substantial change is largely attributable to the reduction in reproductive potential of the 1999 dominant cycle escapement. Although there are weaknesses in the treatment of the PSM data, because the estimate for that cycle is derived from a direct assessment of the lake's smolt production in 2001, this analysis likely produces a realistic estimate of the real change in reproductive potential during the recent era of elevated mortality prior to breeding.

Fry abundance

Six estimates of fall fry abundance are available from mid-water trawl and hdroacoustic surveys, conducted opportunistically since 1986 by DFO's lake assessment group (J. Hume, DFO, Cultus Lake Laboratory, pers. comm.). Population estimates for the 1980's and early 1990's brood years ranged from 0.5 to 2.4 illion (95% C.I. ± <12%) (Appendix 3). Abundances for the 1999 and 2000 broods were considerably lower at 250,000 ± 19% and 46,000 ± 38%, respectively, the lowest of the ix sample years. Although there is a tendency for higher escapements to result in lower fall fry abundances, suggesting intraspecific competition for food, the relationship is not significant ($P<0.05$). The highest observed fall fry densities (2,800 to 3,500 fry/ha) are well with the range of observed densities in other sockeye lakes in B.C. (Shortreed et al. 2001), while the recent fry densities (1999, 2000) are the lowest yet measured among Fraser sockeye populations.

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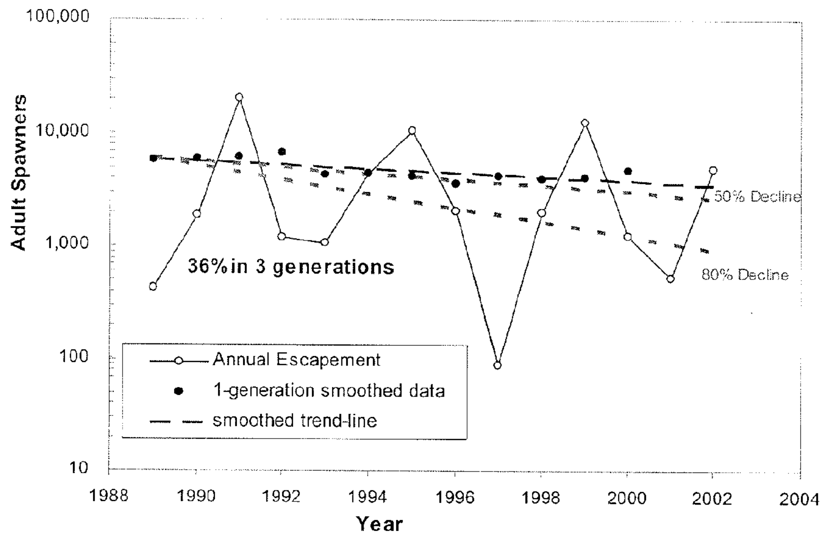

Figure 7. Annual and one-generation (four year average) smoothed abundance estimates for the total number of adults counted through the Sweltzer Creek enumeration fence over the last three generations (12 years). The data are shown relative to what would be 50% and 80% declines (dashed lines). Number of adults is plotted on a log scale.

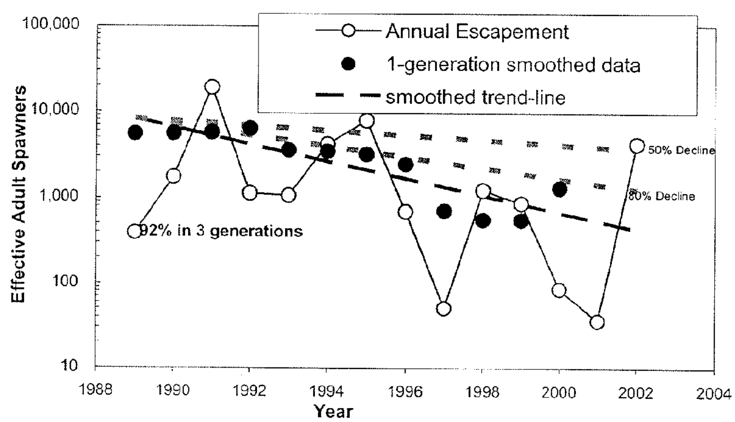

Figure 8. Annual and one-generation (four year average) smoothed abundance estimates for the estimated population of effective adult spawners (fence count adjusted for prespawn mortality) over the last three generations (12 years). The data are shown relative to what would be 50% and 80% declines (dashed lines). Number of adults is plotted on a log scale.

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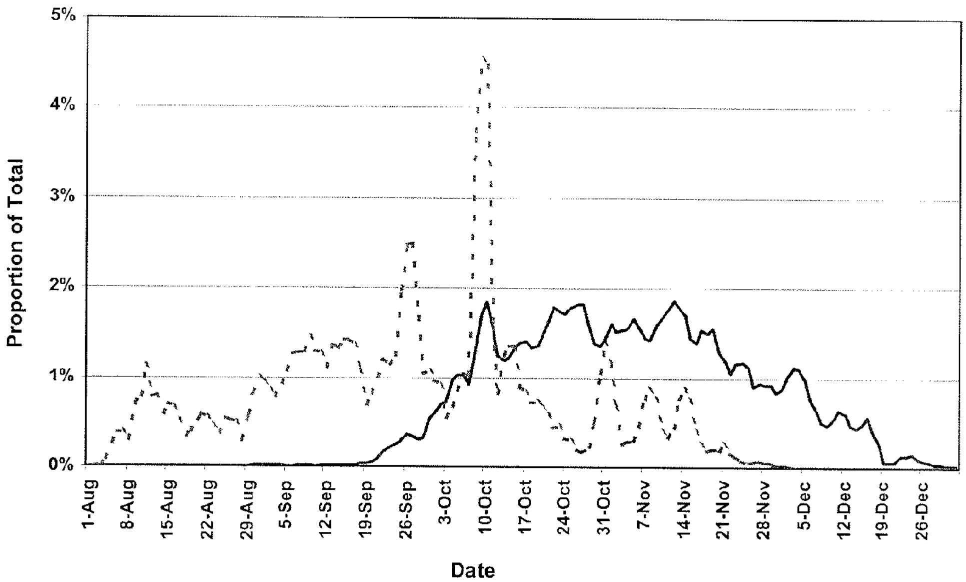

Figure 9. Average timing of the migration of sockeye adults into Cultus Lake: a comparison of the long-term average (1941-1995) (blue solid line) and the pattern in recent years (1996-2002) (red dashed line). Three-day averages are used to reduce daily variability.

Smolt abundance

Smolt abundance has been assessed 47 times at the enumeration fence since 1926 (Appendix 3). As would be expected, smolt abundance reflects the cyclic pattern of adult abundance, with an average of 1.1 and 1.7 million on the sub-dominant and dominant cycles, respectively, and 0.7 and 0.3 million on the off cycles. Abundance averaged 983,400 over the time series, ranging from a low of 5,700 in 2002 to a high of 3,124,000 in 1937. Production was variable but strong from the 1920's to the 1960's (1,216,300 average), followed by declines in the 1970's (712,700 average) and very low average abundances since 1990 (63,300) (Fig. 10). The most recent assessments report the lowest abundances on record in 2002, 2003, 2001 and 1991.

Total adults

Many adult Cultus sockeye fail to return to the lake because they are killed in the fisheries (Fig. 11). Estimates of the total adult population are available since 1952 when the development of stock discrimination techniques permitted their identification in mixed stock fisheries. The 1952-2002 annual total population of Cultus adults averaged 43,100, ranging from 500 in 1977 to 282,500 in 1959 (Fig. 11; Table 3; Appendix 4). Average total adult populations have declined in each decade since the 1950's

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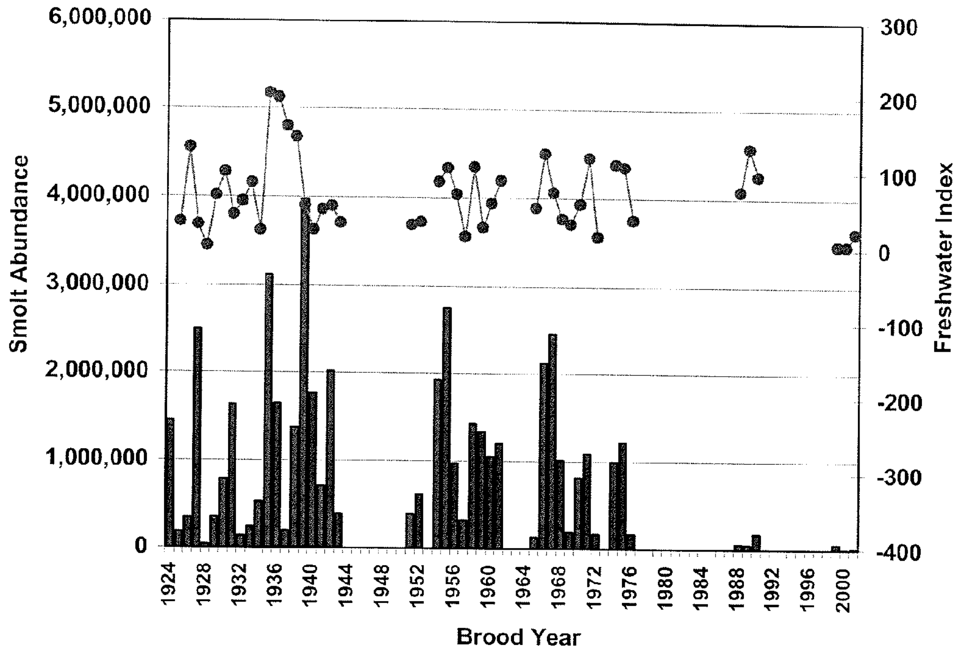

Figure 10. Cultus sockeye smolt abundance (bars) and freshwater survival index (lines) (smolts/adult spawner in brood year), 1924-2001.

(Table 3). Population size since 1952 varies by cycle: the 1998 sub-dominant cycle averaged 37,100 (range: 2,300 to 101,700) and declined by 8% per cycle year; the 1999 dominant cycle averaged 99,700 (range: 13,800 to 282,500) and declined by 7% per cycle year; the 2000 off-cycle averaged 25,100 (range: 2,000 to 70,900), declining from 41,500 through 1976 to only 5,900 in 1980-2000; and the 2001 off-cycle averaged 14,900 (range: 500 to 73,600), declining from 57,100 in the 1950's to 18,900 in the 1960's and only 2,600 since 1977. Overall returns have declined by 9% per cycle.

Fishery exploitation rate (ER), expressed as a percentage, is the number killed by the fisheries divided by the total number of adults in the population. The 1952-2002 Cultus sockeye ER's average 67%, and range from 10% (1999) to 95% (1997) (Fig. 11; Table 3; Appendix 4). Generally, ER's have exceeded 75%. Exceptions are in the early 1960's when efforts were made to rebuild Adams River populations and since the 1990's in response to concerns regarding the early migration. Beginning in 1995, ER's decreased (with the notable exception of 1997) by over 40% to a mean of 33% as a result of conservation measures for late run stocks. In 2001 and 2002, the Fraser Panel and DFO limited fisheries on late run (excluding Birkenhead) populations to ER's of 17% ER and 15%, respectively (ER's of 16.5% and 14.1% were achieved). In 2003, fisheries were to be limited to a range of 15-25%, depending on the abundance of late run

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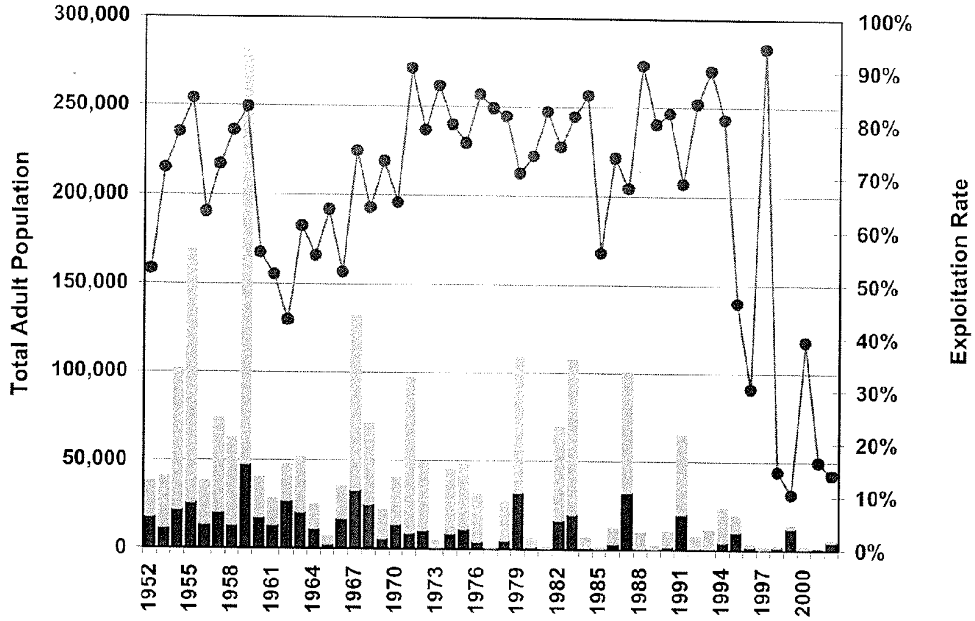

Figure 11. Total number of adults in the population (total return), number of adults killed by the fishery (light blue bar), number of adults entering Cultus Lake (dark blue bar) and human exploitation rate (catch/total) (line graph) for Cultus sockeye salmon, 1952-2002.

sockeye and the extent of the early migration. Inseason information indicates that the exploitation rate (>25%) will exceed the appropriate limit (15%).

Survival indices

Survival indexes can be calculated for freshwater, marine and total life history stages. The freshwater survival index relates smolt production to the total number of adults entering Cultus Lake in the brood year and is expressed as smolts per adult, *i.e.*, it includes mortality before breeding, during incubation and as juveniles. The index for the 1925-2001 brood years averages 71 smolts/adult (range: 3-203), very similar to the Chilko Lake index, the only other wild sockeye smolt data for Fraser sockeye stocks (DFO, unpublished) (Table 4). The index decreases with spawner density, although not statistically so, and shows no obvious long-term trends (Fig. 10; Appendix 3). Just prior to the current early return phenomena (1988-1990 brood years), the index of 100 smolts/adult exceeded the long term average (possibly reflecting a predator control project in those years). There is no indication of any systematic trend until the 1999-2000 brood years when the index suddenly declined to only five smolts/adult; the 2001 brood index (22) also remained well below average.

The marine survival index, expressed as a percentage, relates the annual production of yearling smolts to the number of subsequent adults. The index for the 1951-1990 brood years averages 8.5% (range 0.5-43.9%), with higher average survivals (15.3%) in the late 1980's. The mean marine survival for Chilko sockeye was only slightly higher (Table 4). Survival for the 1951 Cultus brood year was exceptional at 43.9%, more than twice the next highest survival. While such a deviation from average values occurs in natural systems, it could also reflect an artifact of data collection methods. If this point is removed, then the mean marine survival is reduced to 7.0% (range 0.5-20.3%), although still not significantly different from the Chilko mean (paired sample T-test, $t_{0.05,21}$=1.80, p= 0.09). There is no significant trend in marine survival (Fig. 12; Appendix 5); excluding 1951, survivals averaged 6% through the 1970's and increased to 15% in the 1988-1990 broods. Adult return estimates will not be known for the 1999-2001 brood years until 2003-2006; however, given the large size of the smolts produced by those broods, marine survival may be above average (Foerster 1954; Bradford *et al.* 2000).

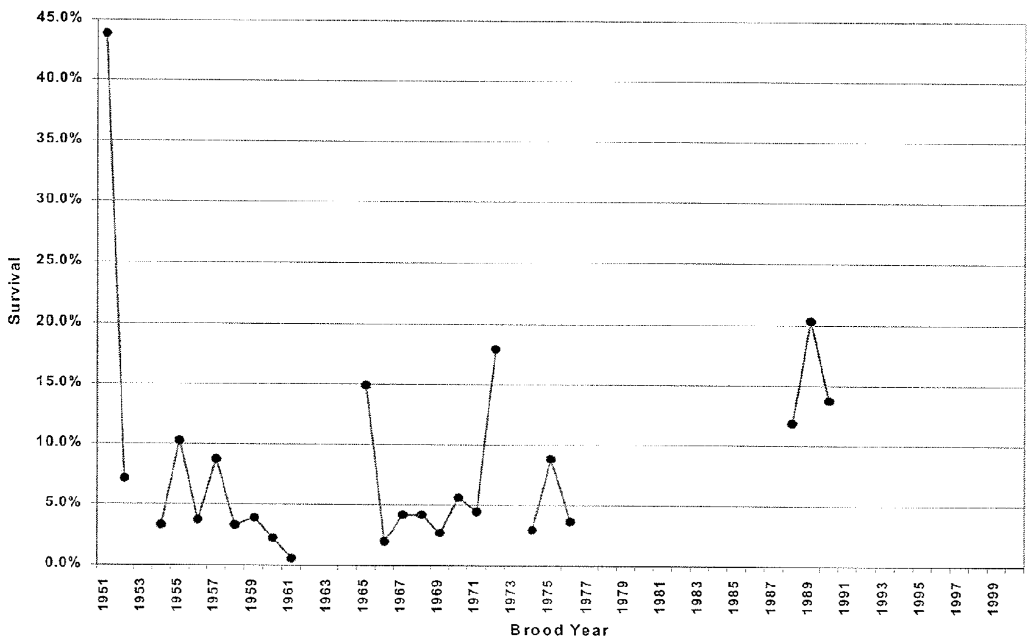

Figure 12. Cultus sockeye marine survival rate (age-1 smolts to ages 4_2 and 5_2 adults) by brood year, 1951-1990.

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The total survival index, expressed as adult returns per adult spawner, relates the total number of adults in the population to the number of adults counted into the lake in the parental generation. The index for the 1948-1997 brood years is highly variable, averaging 4.9 and ranging from 0.5 to 26 (Fig. 13; Appendix 6). Returns were low in the early and late 1960's and the 1990's, when the index dropped below the replacement line (Fig. 13; horizontal dashed line). The mean index for Cultus (4.9) is less that other Fraser sockeye populations, suggesting its productivity is lower (Table 4). The lower Cultus index is also reflected in the mean productivity parameter h^*, (ER at maximum sustainable production); the h^* estimate for Cultus is 0.56 (*i.e.,* 56% ER, from standard stock-recruitment analysis), compared to greater than 0.76 for Chilko and 0.68 for the South Thompson (Adams) group.

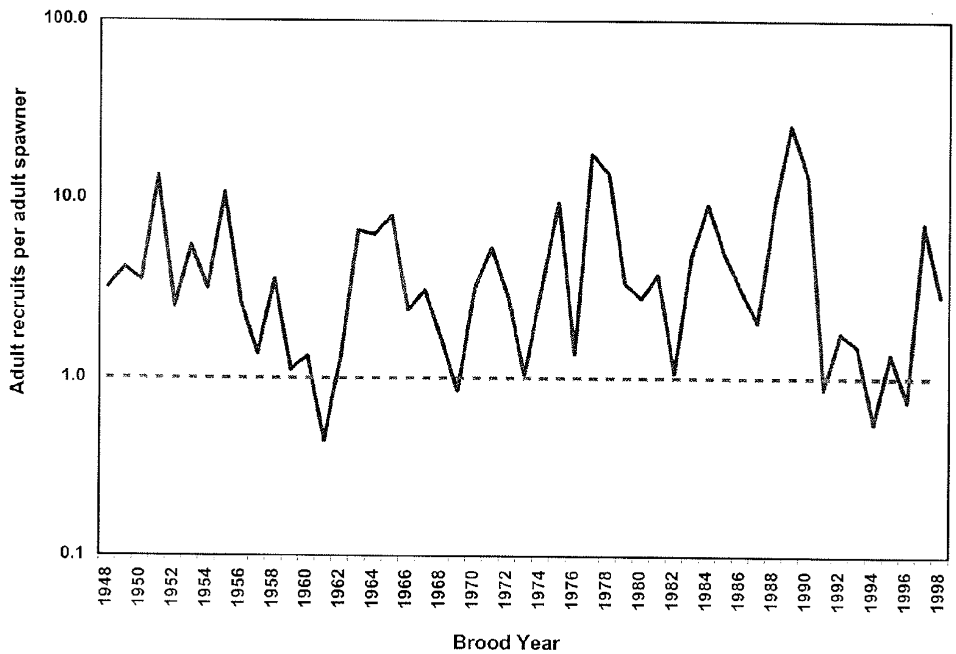

Figure 13. Time series of recruits-per-spawner (R/S) for Cultus sockeye adults, where recruits are the total number of adults in the population and spawners are the number of adults entering Cultus Lake in the parental generation, 1948-1997. The horizontal broken line is the replacement line.

Productive capacity

Productive capacity is a measure of the breeding population abundance (the escapement) that produces the maximum sustainable numbers of subsequent adults

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(the recruitment). While productivity is related to productive capacity, there can be populations that are very productive but have a small productive capacity while the opposite can also be true. Schubert *et al.* (2002) report productive capacity estimates calculated in three ways: a Ricker stock-recruitment (SR) model fitted to the total number of adults entering Cultus Lake and size of the subsequent smolt population; a Ricker model similarly fitted to the total number of adults entering the lake and the size of the adult population that they produce; and a photosysthetic rate (PR) model (Hume *et al.* 1996; Shortreed *et al.* 2000) fitted to an estimate of the lake's primary production. Point estimates of the productive capacity of Cultus sockeye (S_{max}) range from 56,000 to 115,300 effective breeders. These estimates are uncertain because they lie outside the range of the observed breeding population sizes. The largest number of adults entering the lake (47,800 in 1959), however, also produced the largest subsequent adult population (282,500) (Table 3), and escapements without associated estimates of recruitment approached this value in 1927 (82,000), 1939 (71,000) and 1940 (74,000) (Table 2). The estimates are consistent in suggesting that the population's productive capacity is in the higher part of the range of the observed data or beyond. The mean observed numbers of adults entering the lake of 15,000 since 1925, 7,000 since 1975, and 4,000 since 1995 are much lower than any of the estimates of S_{max}. Since 1995, the mean population recorded at the counting fence at the lake is only 7% of the lowest estimate of S_{max}, while the mean number of effective spawners at 90% prespawn mortality is less than 1% of the low end of the S_{max} range. Regardless of the true value of S_{max}, the number of adults entering Cultus Lake is currently only a small fraction of the level that would utilize a substantial part of the population's carrying capacity.

Productivity

The productivity of a population has implications to both its probability of extinction and its prospects for recovery, especially when managed and harvested with other more productive populations in mixed stock fisheries. The analyses indicate that Cultus sockeye typically have been less productive than other Fraser populations: the exploitation rate at MSY (56%) is lower than for Chilko (76%) and Adams (68%), two populations with which Cultus co-migrates; the marine survival rate (7%) is lower than for the Chilko population (9%); and trends in abundance since the 1950's are consistent with the conclusion that the number of adult Cultus sockeye will decline even in the absence of high prespawn mortalities if exploitation rates are in the 70-90% range.

Adult population projection and probability of extinction

Schubert *et al.* (2002) developed a simulation model that incorporates population-recruitment parameter uncertainties to estimate future adults spawners under a range of prespawn mortality and capture rate scenarios over three, five, ten and twenty-five generations (where a generation is four years). In this status report, the model inputs are updated to include 2002 data to project yearly average population sizes for all parameter sets and trials and report values averaged over the four cycles (Table 5). Two results are notable. First, the population is projected to continue to decline if PSM remains above 80% even if harvest is restricted to only 10%. Second, because the

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Table 2. Total numbers of adult sockeye entering Cultus Lake by cycle year, 1925-2002.

1998 Subdominant Cycle		1999 Dominant Cycle		2000 Off Cycle		2001 Off Cycle	
Year	Escapement	Year	Escapement	Year	Escapement	Year	Escapement
						1925	5,423
1926	2,622	1927	82,426	1928	14,661	1929	5,084
1930	7,946	1931	37,473	1932	2,231	1933	2,864
1934	22,940	1935	15,339	1936	8,322	1937	1,227
1938	9,434	1939	70,789	1940	73,536	1941	13,950
1942	36,959	1943	11,822	1944	14,002	1945	5,030
1946	33,068	1947	8,699	1948	12,746	1949	9,055
1950	29,928	1951	12,677	1952	17,833	1953	11,543
1954	22,036	1955	25,922	1956	13,718	1957	20,375
1958	13,324	1959	47,779	1960	17,640	1961	13,396
1962	26,997	1963	20,303	1964	11,067	1965	2,455
1966	16,919	1967	33,198	1968	25,314	1969	5,942
1970	13,941	1971	9,128	1972	10,366	1973	641
1974	8,984	1975	11,349	1976	4,435	1977	82
1978	5,076	1979	32,031	1980	1,657	1981	256
1982	16,725	1983	19,944	1984	994	1985	424
1986	3,256	1987	32,184	1988	861	1989	418
1990	1,860	1991	20,157	1992	1,203	1993	1,063
1994	4,399	1995	10,316	1996	2,022	1997	88
1998	1,959	1999	12,392	2000	1,227	2001	515
2002	4,873						
Average		Average		Average		Average	
1926-1938	10,736	1927-1939	51,507	1928-1936	8,405	1925-1937	3,650
1942-1966	25,604	1943-1967	22,914	1940-1968	23,232	1941-1969	10,218
1970-1986	9,596	1971-1987	20,927	1972-1988	3,663	1973-1989	364
1990-1998	2,739	1991-1999	14,288	1992-2000	1,484	1993-2001	555
2002-2010	4,873						
All years	14,162	All years	27,049	All years	12,307	All years	4,992

population is relatively unproductive and the current population is small, abundances will increase very slowly even at low levels of PSM and capture. For example, at 40% PSM and 0% ER, the average abundance is not expected to approach even the lower part of the range in productive capacity estimates for 25 generations (about 100 years).

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Table 3. Annual total adult population, number killed in fisheries, number entering Cultus Lake and human exploitation rate by cycle for Cultus sockeye, 1952-2002.

1998 Sub-dominant Cycle					1999 Dominant Cycle				
Return Year	Catch	Adult Escapement	Total Return	Exploitation rate	Return Year	Catch	Adult Escapement	Total Return	Exploitation rate
1954	79,628	22,036	101,664	78%	1955	143,195	25,922	169,117	85%
1958	49,162	13,324	62,486	79%	1959	234,701	47,779	282,480	83%
1962	20,536	26,997	47,533	43%	1963	31,541	20,303	51,844	61%
1966	18,564	16,919	35,483	52%	1967	98,802	33,198	132,000	75%
1970	26,138	13,941	40,079	65%	1971	87,978	9,128	97,106	91%
1974	35,813	8,984	44,797	80%	1975	36,735	11,349	48,084	76%
1978	22,364	5,076	27,440	82%	1979	77,620	32,031	109,651	71%
1982	52,386	16,725	69,111	76%	1983	87,952	19,944	107,896	82%
1986	9,163	3,256	12,419	74%	1987	68,537	32,184	100,721	68%
1990	8,540	1,860	10,400	82%	1991	44,762	20,157	64,919	69%
1994	18,844	4,399	23,243	81%	1995	9,026	10,316	19,342	47%
1998	338	1,959	2,297	15%	1999	1,436	12,392	13,828	10%
2002	801	4,873	5,674	14%					
Averages					Averages				
1950's	64,395	17,680	82,075	78%	1950's	188,948	36,851	225,799	84%
1960's	19,550	21,958	41,508	47%	1960's	65,172	26,751	91,922	71%
1970's	28,105	9,334	37,439	75%	1970's	67,444	17,503	84,947	79%
1980's	30,775	9,991	40,765	75%	1980's	78,245	26,064	104,309	75%
1990's	9,241	2,739	11,980	77%	1990's	18,408	14,288	32,696	56%
Total	26,329	10,796	37,125	71%	Total	76,857	22,892	99,749	77%

2000 Off-Cycle					2001 Off-Cycle				
Return Year	Catch	Adult Escapement	Total Return	Exploitation rate	Return Year	Catch	Adult Escapement	Total Return	Exploitation rate
1952	19,987	17,833	37,820	53%	1953	29,029	11,543	40,572	72%
1956	23,808	13,718	37,526	63%	1957	53,208	20,375	73,583	72%
1960	22,304	17,640	39,944	56%	1961	14,395	13,396	27,791	52%
1964	13,722	11,067	24,789	55%	1965	4,349	2,455	6,804	64%
1968	45,539	25,314	70,853	64%	1969	16,011	5,942	21,953	73%
1972	38,639	10,366	49,005	79%	1973	4,390	641	5,031	87%
1976	26,410	4,435	30,845	86%	1977	401	82	483	83%
1980	4,719	1,657	6,376	74%	1981	1,201	256	1,457	82%
1984	5,882	994	6,876	86%	1985	541	424	965	56%
1988	8,924	861	9,785	91%	1989	1,679	418	2,097	80%
1992	6,298	1,203	7,501	84%	1993	9,808	1,063	10,871	90%
1996	885	2,022	2,907	30%	1997	1,512	88	1,600	95%
2000	797	1,227	2,024	39%	2001	102	515	617	17%
Averages					Averages				
1950's	21,898	15,776	37,673	58%	1950's	41,119	15,959	57,078	72%
1960's	27,188	18,007	45,195	60%	1960's	11,585	7,264	18,849	61%
1970's	32,525	7,401	39,925	81%	1970's	2,396	362	2,757	87%
1980's	6,508	1,171	7,679	85%	1980's	1,140	366	1,506	76%
1990's	2,660	1,484	4,144	64%	1990's	3,807	555	4,363	87%
Total	16,763	8,334	25,096	67%	Total	10,510	4,400	14,910	70%

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Table 4. Freshwater, marine and total survival indices and exploitation rates at maximum sustainable production for Cultus, Chilko and Adams sockeye.

	Fraser system sockeye population		
	Cultus	Chilko	Adams
Freshwater survival index (smolts/spawner):			
Mean index	72	61	-
Annual range	3 - 203	9 - 115	-
Marine survival index (%):			
Mean index[a]	7.0%	9.1%	-
Annual range	0.5% - 20.3%	1.3% - 22.2%	-
Total survival index (%)	4.8%	7.2%	7.3%
ER at Maximum sustainable production (%)	56%	76%	68%

[a] Excludes data for 1951 (see text).

Schubert *et al.* (2002) similarly estimated the probability of extinction using quasi-extinction thresholds of 50 and 100 effective adult spawners in any consecutive four year period (one cycle) to avoid the need to explicitly consider the potential for depensatory population dynamics that may increase the risk of extinction at low population sizes. Although somewhat arbitrary, these demographic extinction thresholds probably approximate the level below which recovery is unlikely. The US National Marine Fisheries Service uses similar thresholds to conduct extinction assessments for salmon (R. Waples, pers. comm.). Extinction probability is highly dependent on several factors, including the levels of PSM and ER, the time frame over which the projections are made, and the threshold of extinction used (Table 6). In this discussion, updated input data is used and consideration is limited to the 100 fish quasi-extinction threshold because, although the lower threshold reduces the short-term probability of extinction, it has little impact over longer time frames. The probability of extinction increases with increasing PSM and capture. If PSM's remain at 90% or more, even in the absence of fishing, the probability of extinction is 50% in three generations (12 years) and increases to 98% and 100% over longer time frames of 10 (40 years) and 25 generations (100 years), respectively.

The simulation model results may underestimate the full probability of extinction of Cultus sockeye because the persistence of the large dominant cycle significantly reduces the probability that escapements will fall below the quasi-extinction threshold in any four-year period. Under conditions of high PSM, the population will be maintained increasingly by a single year-class. While five-year-old spawners from the dominant cycle can potentially repopulate subsequent cycles, the genetic diversity of the population would likely be reduced and population resiliency compromised. Furthermore, the relatively conservative quasi-extinction threshold may underestimate the impact of Allee effects, demographic stochasticity and genetic effects given the dense lake predator populations and the encroachment onto the spawning grounds by watermilfoil.

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Table 5. Predicted number of Cultus sockeye adults entering Cultus Lake at different levels of prespawn mortality (PSM) and exploitation rates (ER). Predictions are averaged across four years for 3, 5, 10 and 25 generations from the present 1999-2002) brood years. Note that, for 1999-2002, PSM averaged 61% and ER averaged 19%.

Prespawn mortality (PSM)	Exploitation rate (ER)	Average future escapement in: Three generations	Five generations	Ten generations	Twenty-five generations
40%	0%	13,500	31,720	49,830	52,160
	10%	10,760	24,590	42,410	45,880
	20%	8,060	18,380	33,670	38,620
	30%	5,930	12,720	24,820	30,750
	40%	3,990	8,080	15,700	21,460
	50%	2,540	4,450	8,120	11,490
50%	0%	8,870	20,260	36,330	40,880
	10%	6,920	15,390	29,340	34,640
	20%	5,170	10,990	21,390	27,540
	30%	3,700	7,350	14,360	19,760
	40%	2,500	4,450	7,940	11,420
	50%	1,530	2,320	3,660	4,600
60%	0%	5,160	11,110	21,600	27,520
	10%	3,940	8,070	15,860	21,470
	20%	2,930	5,570	10,420	14,800
	30%	2,060	3,540	6,150	8,490
	40%	1,370	2,050	2,960	3,580
	50%	820	1,010	1,130	930
70%	0%	2,520	4,450	8,150	11,610
	10%	1,890	3,080	5,160	7,110
	20%	1,390	2,010	2,980	3,540
	30%	960	1,210	1,440	1,410
	40%	630	650	600	370
	50%	370	300	180	70
80%	0%	820	1,020	1,110	950
	10%	640	660	580	400
	20%	430	410	270	120
	30%	310	220	110	40
	40%	180	110	30	0
	50%	110	40	10	0
90%	0%	110	50	10	0
	10%	70	30	0	0
	20%	50	20	0	0
	30%	30	10	0	0
	40%	20	0	0	0
	50%	10	0	0	0

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Table 6. **Mean probability of demographic extinction for Cultus sockeye at different levels of prespawn mortality (PSM) and exploitation rates (ER) after 3, 5, 10 and 25 generations. Quasi-extinction is defined as the probability that spawner abundance will be less than 50 or 100 adult spawners in four successive years based on a forward simulation in Population Viability Analysis (from Schubert *et al.* 2002).**

		<50 spawners in 4 sucessive years				<100 spawners in 4 successive years			
		Generations from present				Generations from present			
PSM	**ER**	**3**	**5**	**10**	**25**	**3**	**5**	**10**	**25**
0.4	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.3	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01
	0.4	0.00	0.00	0.01	0.02	0.00	0.01	0.03	0.04
	0.5	0.00	0.01	0.03	0.08	0.01	0.03	0.08	0.15
0.5	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	0.1	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01
	0.2	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.02
	0.3	0.00	0.00	0.01	0.02	0.01	0.01	0.03	0.05
	0.4	0.00	0.01	0.03	0.08	0.01	0.03	0.08	0.14
	0.5	0.01	0.03	0.10	0.26	0.03	0.08	0.20	0.38
0.6	0	0.00	0.00	0.00	0.01	0.00	0.01	0.01	0.02
	0.1	0.00	0.00	0.01	0.01	0.00	0.01	0.02	0.04
	0.2	0.00	0.01	0.02	0.04	0.01	0.02	0.05	0.09
	0.3	0.00	0.01	0.05	0.13	0.02	0.04	0.11	0.22
	0.4	0.01	0.04	0.13	0.32	0.04	0.10	0.24	0.44
	0.5	0.02	0.09	0.31	0.63	0.08	0.21	0.46	0.74
0.7	0	0.00	0.01	0.03	0.08	0.01	0.03	0.08	0.14
	0.1	0.00	0.02	0.07	0.16	0.02	0.06	0.14	0.27
	0.2	0.01	0.04	0.13	0.33	0.03	0.10	0.24	0.45
	0.3	0.02	0.08	0.26	0.55	0.06	0.17	0.40	0.67
	0.4	0.03	0.15	0.44	0.78	0.11	0.29	0.59	0.86
	0.5	0.08	0.29	0.68	0.94	0.20	0.46	0.79	0.96
0.8	0	0.02	0.09	0.31	0.63	0.07	0.21	0.46	0.74
	0.1	0.03	0.15	0.44	0.78	0.11	0.29	0.59	0.86
	0.2	0.06	0.23	0.60	0.90	0.17	0.40	0.73	0.94
	0.3	0.10	0.35	0.76	0.96	0.24	0.53	0.85	0.98
	0.4	0.18	0.51	0.88	0.99	0.36	0.68	0.93	1.00
	0.5	0.29	0.68	0.96	1.00	0.50	0.81	0.98	1.00
0.9	0	0.29	0.68	0.95	1.00	0.50	0.81	0.98	1.00
	0.1	0.37	0.77	0.98	1.00	0.58	0.87	0.99	1.00
	0.2	0.47	0.84	0.99	1.00	0.67	0.92	0.99	1.00
	0.3	0.57	0.91	1.00	1.00	0.76	0.95	1.00	1.00
	0.4	0.69	0.95	1.00	1.00	0.84	0.98	1.00	1.00
	0.5	0.80	0.98	1.00	1.00	0.90	0.99	1.00	1.00

LIMITING FACTORS AND THREATS

Capture in fisheries

Fraser River sockeye have been managed in an intensive, integrated international and domestic system for over half a century. In the area specified under Treaty with the United States (US) (roughly encompassing Juan de Fuca Strait, southern Strait of Georgia, and southwest coast of Vancouver Island), the Pacific Salmon Commission (PSC) manages sockeye fisheries bilaterally. In other areas, they are managed domestically by Canada or the US. The PSC's Fraser River Panel develops fishing plans for each of the four run groups by considering the escapement (surviving adults) goals, pre-season forecasts, and constraints such as by-catch of other species or stocks of concern. Within each group the larger populations are actively managed, the smaller populations generally not. Because the Cultus population is small relative to co-migrating populations such as Adams and Weaver, it has not been managed as a discrete population throughout the history of the Fraser River sockeye fishery. On the 1998 and 1999 cycles, the late run fisheries are actively managed to achieve gross escapement and catch objectives for the dominant and sub-dominant Adams River population-group; on the 2000 and 2001 cycles, they are managed to achieve similar objectives for the Weaver Creek sockeye, especially since 1969 with the first returns of enhanced sockeye to the artificial spawning channel. In addition, earlier marine area fisheries directed at the summer run also harvest late run sockeye. The cumulative impacts of the directed harvest of the numerically dominant summer and late run stocks determine the harvest and exploitation rate patterns of Cultus sockeye.

Because Cultus sockeye are not actively managed, the cycle-specific ER patterns differ depending on the target stock that triggers management actions. On the 1998 sub-dominant and 1999 dominant cycles (Adams management), Cultus ER's averaged 71% and 77%, respectively (Table 3). Sub-dominant cycle ER's have been generally high and relatively lacking in trends since 1954, while dominant cycle ER's have decreased slightly since 1971. On the 2000 and 2001 off-cycles, the fisheries are actively managed for Weaver sockeye, where the wild stock has been augmented with enhanced production since the spawning channel began operation in 1965. Off-cycle ER's are similar to those on the other cycles, averaging 67% (2000) and 70% (2001); however, the trends are considerably different. Before the first return of enhanced sockeye in 1969, ER's averaged 57% (2000 cycle) and 65% (2001 cycle). After enhancement and until fisheries were reduced to address concerns regarding the early migration, ER's increased to an average of 83% (2000 cycle) and 81% (2001 cycle) with slight increasing trends of 2.0% and 0.5% per cycle on the 2000 and 2001 cycles, respectively.

The mean exploitation rate at maximum sustained yield (MSY) for Cultus sockeye is estimated at 56%. However, exploitation rates have far exceeded this level in most years and on all cycles. Long-term cycle-specific average exploitation rates have ranged from 67-77%. Annual exploitation rates have frequently exceeded 80% and sometimes 90%. Exploitation rates on the two off-cycles increased from about 60% in

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the 1960's to over 80% in subsequent decades as a result of increased fishing pressure to capture enhanced Weaver sockeye. It is likely that the sustained decline in the number of adults entering Cultus Lake on three cycles result from the excessive capture rates applied to Cultus sockeye almost continuously over four or more decades.

Early migration and prespawn mortality

Cultus sockeye normally hold in the lake for up to two months before breeding. The migration into the lake typically begins in late September, peaks in October to mid November and ends by late December (Fig. 9). From 1996 to 2002, the migration into the lake has become progressively earlier to the extent that, by 2001, the start and peak of the migration were almost two months earlier than the 1941-1995 average (Appendix 2). The early migration into the lake has important implications to the population. It exposes the fish to water temperatures as high as 25ºC (DFO, unpublished data). Exposure to such temperatures, even for short periods, increases metabolic rates and the growth of bacteria and fungi, reduces reproductive hormone synthesis and the energy available for migration and reproduction, decreases swimming performance and delays gonadal maturation, all of which can contribute to increased pre-spawning mortality and reduced spawning success (Dave Patterson, DFO, pers. comm.). The temperature gradients between the Chilliwack River (12-16ºC), Sweltzer Creek (>20ºC) and the lake's hypolimnion (6.5ºC) may exacerbate these impacts. As well, upper Sweltzer Creek is heavily used for swimming and unstructured recreation in August and early September; activities that may further delay migration, increasing the exposure to high temperatures and the stress on returning fish.

Mortality increased in the late 1990's to a level in excess of 90% of the returning adults (Appendix 1). Studies of Cultus and other late run populations indicate that the prespawn mortality results from longer than normal exposures to the parasite *Parvicapsula minibicornis* caused by the abnormally early migration into freshwater. Although considerable effort is being expended to identify the cause of the early migration, neither its occurrence nor severity can be predicted. Its effect on Cultus sockeye has been an unsustainable loss of reproductive potential. To illustrate this point, at current marine survivals (7%) and high prespawn mortality (93%) levels, each successful adult spawner must produce over 400 smolts to sustain the population. This is over six times the level of smolt production that has been observed in the last three brood years. Under these conditions, even if capture by the fisheries is limited to the lowest possible levels, this population is likely to decline to extinction within ten generations (about 40 years).

Environmental stochasticity

The long period of high capture rates coupled with elevated prespawn mortality has reduced Cultus sockeye to very low levels of abundance; three of the four cycles are at significant risk of loss. This leaves the population vulnerable to random changes in the freshwater and marine environments that otherwise might be benign for larger populations. For example, *El Nino* events (sudden increase in ocean water

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temperatures that lead to decreased productivity) occur frequently and can substantially reduce the marine survival of this population. The recurrence of a series of *El Ninos*, such as those of the 1990's, could reduce marine survivals to levels that, even if the migration returned to normal and capture rates were limited to low levels, would pose a serious threat to this population. The population is also vulnerable to climate changes that affect the freshwater environment. For example, random temperature changes can affect phytoplankton communities, impacting sockeye food sources and lake water clarity. The latter can promote the growth of the Eurasian water milfoil populations that compete with sockeye for space on the spawning grounds. Other changes can favour predator populations and seriously reduce sockeye freshwater survival. The population is vulnerable to catastrophic events such as landslides that can destroy spawning areas or prevent adult sockeye from accessing the lake.

Diseases and parasites

The important impact on adults of protracted exposures to the parasite *Parvicapsula minibicornis* has been discussed. A second parasite, the copepod *Salmincola californiensis*, is endemic in Cultus Lake and is known to infect and cause mortality in juvenile sockeye salmon (Kabata and Cousens 1977). Foerster (1929c) reported a heavy infestation of the 1927 smolt migration; similar levels were observed in 2002 (S. Barnetson, DFO, Inch Creek Hatchery, pers. comm.). The impact of this parasite on the survival of Cultus sockeye fry and smolts is unknown; however, the level of infestation is sufficiently severe that it may present a threat to the population at current low abundance levels.

Predation

Cultus Lake is home to a number of predator species, including coho, trout, sculpins, Dolly Varden char and northern pikeminnows (Ricker 1941). The highly abundant northern pikeminnow likely has the greatest impact on sockeye. A large piscivorous cyprinid widely distributed throughout the Fraser River and other major British Columbia river systems, the pikeminnow is an important source of mortality for juvenile salmonids (Foerster and Ricker 1941; Ricker 1941; Foerster 1968; Friesen and Ward 1999). In Cultus Lake, pikeminnows spawn along the lakeshore from late June to mid-July. Their fecundity (up to 40,000 eggs/female) and long life span (up to 20 years) allows populations to increase rapidly under favourable conditions. Young pikeminnow inhabit the littoral zone where they consume mostly insect larvae. When mature (>250 mm), they occupy both the littoral and limnetic (or sublittoral) zones and feed almost entirely on smaller fish, including juvenile sockeye and pikeminnow.

In the 1930's, the freshwater survival of sockeye increased by 300% (from 3.1 to 10.0%) when pikeminnow were partially eradicated. In the 1990's, survivals increased by 43% (from 70 to 100 smolts/spawner) following a similar predator control project. The recent decline in the Cultus sockeye spawner population has had the effect of placing very small fry populations in a predator-rich environment. Because predation is one mechanism in the depensatory population dynamics of collapsed stocks, the large

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predator population in Cultus Lake is an important potential threat to the recovery of this sockeye population.

Exotic species

Cultus Lake is heavily impacted by Eurasian watermilfoil (*Myriophyllum spicatum*), an exotic perennial macrophyte that was introduced to eastern North America in the late 1800's (Reed 1977). It spreads widely and rapidly, displacing native plants, slowing water flows and changing fish habitats to the detriment of some species (*e.g.,* salmon) and the benefit of others (*e.g.,* pikeminnow). Watermilfoil propagates mainly by fragmentation but also by root nodes and seed production. In the littoral zone of lakes, it establishes dense patches with up to 100 stems growing from a single large root mass. The dense stem masses affect adult sockeye by preventing access to spawning habitats while providing juvenile pikeminnow with refuges against adult cannibalism (R. Gregory, DFO, pers. comm.), thereby increasing adult pikeminnow recruitment and potential predation on juvenile sockeye. Watermilfoil was first observed in Cultus Lake in 1977, likely an inadvertent introduction from interior lakes by boaters (R. Truelson, MOE, pers. comm; D. Barnes, DFO, pers. comm.). From 1977 to 1991, its distribution in the littoral zone nearly doubled and shifted from mainly sparse patches to dense mats. By 1991, it covered 22 ha of the lake's 74 ha littoral area (Truelson 1992); subsequent distributions have not been monitored. Dive surveys on Lindell Beach in 1982 indicated that dense patches of watermilfoil had displaced sockeye from areas that had previously been used for spawning (K. Morton, DFO, pers. comm.). In recent years, watermilfoil removal projects have limited the species' density on recreational beaches, including Lindell Beach; however, those projects are expected to terminate in 2003. Watermilfoil is probably an important threat to Cultus sockeye because it both provides habitat for predator species and encroaches on sockeye spawning habitat.

Habitat alteration

The Cultus watershed is heavily developed for recreational, residential and agricultural uses, resulting in significant impacts to tributary and outlet streams and lake foreshore habitats. The impacts from forest harvesting are probably minor; logging occurs only in the Frosst Creek headwaters in the United States. Housing is restricted to small areas on the northeast and northwest sides of the lake and at Lindell Beach. Farming occurs near the south end, and tree harvesting has occurred in the upland areas. Activities with direct impacts to the lake's littoral zone include the removal of shoreline vegetation, shoreline alteration and the encroachment by wharves and piers, especially on the Lindell Beach spawning area. Activities that impact the tributary streams include channelization and the removal of riparian vegetation. Of special concern is the potential degradation of the quality of the lake's surface and ground water inputs as a result of seepage from septic systems, agricultural runoff and the domestic use of fertilizers. Recreation is the primary activity in the watershed. Cultus Lake became popular for camping and outdoor recreation in the late 1800's and early 1900's, leading to the creation of Cultus Lake Park in 1924. Today, 92% of the lake's 18 km shoreline is within either Cultus Lake Provincial Park (656 ha along the east and

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west shores) or Cultus Lake Municipal Park (244 ha along the north shore). Park usage grew steadily through the twentieth century. The parks currently receive about 1.5 million visitors annually, making Cultus one of the most heavily utilized lakes in British Columbia. During the summer, the lake is extremely popular for recreational boating. Recreational fishing for any species is not common, although in recent years there have been annual derbies to remove Northern pikeminnow.

The impact of these activities on the sockeye population is unclear. Comparisons of limnological information from 2001 with that collected in the 1930's and 1960's suggest that the lake's limnetic habitat has changed relatively little over the past 65 years. However, limited information is available regarding changes in the quality and quantity of groundwater and the effect of siltation or pollutants on habitat quality.

SPECIAL SIGNIFICANCE OF THE SPECIES

Sockeye salmon is an economically important species that is broadly distributed in north Pacific marine and freshwater environments. They comprise about 14% of the total salmon captured and killed in the North Pacific Ocean (Burgner 1991). Since 1952, the capture of Fraser sockeye has ranged from 1-18 million per year; the capture of Cultus sockeye has ranged from a low of 100 adults to a high of 235 thousand adults.

Biologically, Cultus sockeye are a genetically distinct, locally adapted population that is unique to Cultus Lake and, as such, represent a Nationally Significant Population. The Cultus population is a keystone species for the local ecosystem because, like other anadromous salmon species, it is the principle mechanism for the transport of nutrients such as nitrogen and phosphorus from marine to freshwater and terrestrial ecosystems. Cultus sockeye are being considered for selection as an indicator species for ecosystem sustainability monitoring (Fraser Basin Council 2002). Ecologically, Cultus sockeye are one of 18 fish species known to utilize this lake for all or part of their life cycles.

The Cultus population is also significant from a scientific perspective because it is one of the best-studied salmon populations in the world. From the perspective of science history, it was the first to be assessed for smolt production, it was the site of the first system-wide evaluation of enhancement that resulted in the termination of the federal hatchery system in 1935, and it was studied by two of Canada's most internationally famous scientists, R.E. Foerster and W.E. Ricker, when they formulated many of the concepts that today guide fishery science around the world. It is also significant due to its long-term data set; such data are becoming increasingly important to the understanding of events on a decadal or longer scale.

Cultus sockeye are also of significance to human culture. They are especially important to the Soowahlie Band of the Sto:lo First Nation. This band occupies the land that borders both sides of Sweltzer Creek, the sole access to Cultus Lake. The presence of sockeye in Cultus Lake was a principle determinant in the Band's settlement of the area and played a role in their survival for thousands of years. Today, the sockeye continue to be of cultural and spiritual importance to the community. Sockeye are featured on the band totem and in the band's expressions and dances; they are important to the band's economic opportunities for the future. The current Chief, Doug Kelly, was a co-petitioner (with Ken Wilson) in 2002 of the COSEWIC emergency assessment of Cultus sockeye.

EXISTING PROTECTION OR OTHER STATUS

An extensive framework of international commitments and domestic legislation is in place to protect Pacific salmon populations. Internationally, as a signatory to the United Nations Convention on Biological Diversity, Canada is required to develop legislation and policies to protect ecosystems and habitats and maintain viable species populations. Domestically, the Department of Fisheries and Oceans Act (1985) enabled the creation of a federal department with the mandate for conservation and sustained use of fisheries resources in marine and freshwaters. The Fisheries Act (1985) and other supporting legislation provide a legal framework for the control of fisheries, pollution and habitat. Federal-provincial agreements such as the Agreement on the Management of Pacific Salmon (1997) and the Agreement on Inter-jurisdictional Cooperation (1999) coordinate intergovernmental activities with the objective to maintain ecologically sustainable fish resources and habitats. Provincial and municipal governments also regulate land and water use activities that can affect fish populations. For example, the B.C. Water Act (1996) governs the allocation of water and the regulation of works in streams. More recently, the Canada Oceans Act (1996) requires that marine resources be managed to conserve biological diversity and commits Canada to the application of the Precautionary Principle for wildlife including fishes.

The DFO is the primary organization responsible for Pacific salmon. Its New Directions Policy (1998) acknowledged the importance of Pacific salmon to Canadian society and articulated a series of principles guiding their conservation and sustainable use. Three of the principles are of particular importance to the protection of Cultus sockeye: first, conservation is the primary objective of the Department and takes precedence; second, the precautionary approach will be applied to fishery management; and third, the long term productivity of the resource will not be compromised by short term issues. One of the components of the New Directions policy framework is the draft Wild Salmon Policy (2000). This policy is intended to promote the long-term viability of Pacific salmon populations and their natural habitats. After implementation, it will provide additional protection to genetically distinct populations or groups of populations designated as conservation units.

Since summer 2001, Cultus sockeye have been managed under measures implemented to address the risk posed by the mortality associated with the early migration of late run sockeye. The Fraser Panel, a joint Canada/U.S. body responsible for the management of Fraser River sockeye in waters specified by the Pacific Salmon Treaty (1985), reached in 2001 a bilateral agreement to limit the exploitation rate on late

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run sockeye to a maximum of 17%. Further to the agreement was the provision that Canadian and US fishers were not to exceed a 60% harvest rate on summer run sockeye due to the presence of co-migrating late run populations. In 2002, bilateral agreement was reached to further limit the total fishery exploitation rate of late run sockeye to a ceiling of 15%. In 2003, bilateral agreement was reached to limit the exploitation rate to a range of 15-25%, depending on the abundance of late run sockeye and the extent of the early migration. Inseason information indicates that the exploitation rate (25%) will exceed the appropriate limit (15%). The impact on Cultus sockeye will be reviewed following the release of final estimates of the number of adults that entered Cultus Lake and the level of prespawn mortality.

SUMMARY OF STATUS REPORT

Sockeye salmon is one of seven species of the genus *Oncorhynchus* native to North America. This status report evaluates the genetically distinct sockeye population that occupies Cultus Lake, located in the coastal lowland portion of the Fraser River watershed in British Columbia. Cultus sockeye are genetically distinct from other sockeye populations in the Fraser River and in other parts of their global range. The population serves as a keystone species for the local ecosystem, and is scientifically important both from the perspective of science history as well as the long time series of assessment data available for the population and its habitat. The population is important to many segments of Canadian society, and is fundamental to the well-being of the Soowahlie Band and the Sto:lo First Nation.

Cultus sockeye utilize Cultus Lake for breeding, egg incubation and the rearing of juveniles. It is a small (6.3 km^2 surface area) monomictic lake with a high seasonal average photosynthetic rate and a productive zooplankton community that is an exceptional food resource for juvenile sockeye. The watershed is heavily developed for recreational, residential and agricultural uses, with recreation predominant. Cultus sockeye mature primarily in their fourth year of life - after almost two years in freshwater and more than two years in marine environments. Adults migrate from the open ocean into the Strait of Georgia in August where they remain for up to eight weeks. Normally, they resume their migration into the Fraser River and Cultus Lake in September and continue migrating into the lake until December. Recently, the onset of the riverine migration has been earlier and has resulted in elevated mortality levels.

The numbers of Cultus sockeye adults are known since 1925. Abundance was generally strong but variable until the late 1960's, when spawner numbers collapsed in two cycles and began a sustained decline in a third cycle. Since the early 1990's, abundance has declined dramatically on all four cycles; the most recent populations on all cycles have been among the lowest ever observed. In the last three generations (12 years; 1991-2002), the adult spawner population declined by 36%, a rate of 3.3% per year across all cycles. When recent increases in prespawn mortality are considered, the rate of decline in the population's reproductive potential (effective spawners) over the last three generations is 92%. Current population levels are a small

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fraction of the most conservative estimate of the productive capacity of the population. Similar declines have been recorded in assessments of the fry and smolt populations and the total adult return.

Over-exploitation by the fisheries, recent increases in the level of prespawn mortality associated with the early migration, and reductions in marine survival from the *El Nino* events in the 1990's have contributed to the collapse of this population. Changes in freshwater habitat may have played a contributing role but are unlikely to be a primary factor in the collapse. Capture and killing of Cultus sockeye in the fishery has exceeded sustainable levels almost continuously for over four decades. Capture has averaged 67% and has frequently exceeded 80%, and even 90%, of the adult population when sustainable levels would be less than 56%. From 1995 to 2002, the migration of adult Cultus and other late run sockeye from the Strait of Georgia into the Fraser River has been progressively earlier. While the cause of the early migration is unknown, its consequences have been dramatic. The early migration of adults has been associated with high levels of adult mortality along the freshwater migratory route and high mortality in the lake before spawning. These mortalities are caused by heavy infestations of *Parvicapsula minibicornis*, a parasite that attacks the kidneys and gills (St-Hilaire *et al.* 2001). Although the parasite occurs in most Fraser River sockeye populations, it has caused significant mortality only among early migrating late-run sockeye, including Cultus sockeye.

The outlook for Cultus Lake sockeye is uncertain. Its persistence will depend on whether the early migration phenomenon continues in the future, on the level of capture and killing by the fisheries, on marine survival conditions, and on habitat conditions. Current low levels of abundance leave it vulnerable to random changes in the marine and freshwater environments, endemic parasites such as *Salmincola californiensis*, abundant lake predator populations and anthropogenic factors that could reduce the population's productivity when abundances are low, thus increasing the probability of extinction. If prespawn mortality exceeds 90%, and without any killing by the fisheries, the probability of extinction of the population is estimated to be 50% in three generations (12 years) and 100% in 25 generations (100 years).

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TECHNICAL SUMMARY

Oncorhynchus nerka
Common name: Sockeye salmon (English) Saumon rouge (French)
Population name: Cultus Lake sockeye
Range of Occurrence in Canada: B.C. (Cultus Lake, Fraser River system)

Extent and Area information	
• extent of occurrence (EO)(km²) (Watershed area)	83 km²
• *specify trend (decline, stable, increasing, unknown)*	Stable
• *are there extreme fluctuations in EO (> 1 order of magnitude)?*	No
• *area of occupancy (AO) (km²)* (Lake area)	6.3 km²
• *specify trend (decline, stable, increasing, unknown)*	Decline
• *are there extreme fluctuations in AO (> 1 order magnitude)?*	Unknown
• *number of extant locations*	One
• *specify trend in # locations (decline, stable, increasing, unknown)*	Stable
• *are there extreme fluctuations in # locations (>1 order of magnitude)?*	No
• *habitat trend: specify declining, stable, increasing or unknown trend in area, extent or quality of habitat*	Probably declining
Population information	
• *generation time (average age of parents in the population)*	Four years
• *number of mature individuals (capable of reproduction) in the Canadian population*	50-1,200 spawners
• *total population trend: specify declining, stable, increasing or unknown trend in number of mature individuals*	Declining
• *if decline, % decline over the last 10 years or 3 generations, whichever is greater*	92% in three generations (12 years)
• *are there extreme fluctuations in number of mature individuals (> 1 order of magnitude)?*	Yes
• *is the total population severely fragmented (most individuals found within small and relatively isolated (geographically or otherwise) populations between which there is little exchange, i.e., ≤ 1 successful migrant / year)?*	One population – Cultus is genetically and demographically isolated from all other sockeye populations
• *list each population and the number of mature individuals in each*	N/A
• *specify trend in number of populations (decline, stable, increasing, unknown)*	N/A
• *are there extreme fluctuations in number of populations (>1 order of magnitude)?*	N/A

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Threats (actual or imminent threats to populations or habitats)	
• Fisheries are focused on the more productive co-migrating populations of sockeye salmon, resulting in over-exploitation of Cultus sockeye for much of the last four decades. This has resulted in a continuous and long-term decline in number of Cultus adults. • Early adult migration into freshwater from 1995-2001 has resulted in high levels (>90%) of prespawn mortality and unsustainable loss of reproductive potential. • *El Nino* events have likely impacted adult survival during the 1990s and will probably occur again in the future. Habitat issues include abundant predator populations and the encroachment of an exotic perennial macrophyte that may cause depensatory mortality on the currently small sockeye fry populations in Cultus Lake. As well, residential, agricultural and recreational uses of Cultus Lake are likely degrading habitat quality. Recreational usage may interfere with adult migration into the lake.	
Rescue Effect (immigration from an outside source)	
• *does species exist elsewhere (in Canada or outside)?*	Yes
• *status of the outside population(s)?*	Variable
• *is immigration known or possible?*	No – Cultus is a distinct population.
• *would immigrants be adapted to survive here?*	No
• *Is there sufficient habitat for immigrants here?*	NA
Quantitative Analysis	Genetic analyses, population modeling, demographic extinction analysis

ACKNOWLEDGEMENTS

Much of the information and text contained in this status report has been previously released in reports of the Cultus Sockeye Recovery Team's work groups and in a Canadian Stock Assessment Secretariat status report that is currently under revision for the Pacific Science Advice Review Committee. I am grateful for the contribution of my fellow work group and PSARC team members: D. Barnes, T. Beacham, S. Barnetson, A. Cass, T. Cone, R. Devlin, B. Fanos, M. Foy, J.Gable, J. Grout, J. Hume, M. Johnson, D. Lofthouse, D. MacKinlay, K. Morton, K. Shortreed, M. Staley, B. Stanton, A. Stobart, R. Valor, R. Withler and C. Wood. I am grateful for constructive comments on drafts of documents provided by M. Bradford, G. Brown, B. Holtby and J. Woodey. A thorough review of the current document by M. Gross was particularly useful in improving the quality of this status report.

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BIOGRAPHICAL SUMMARY OF CONTRACTOR

Mr. Schubert received his B.Sc. (Honours) from Simon Fraser University in 1976, from which he immediately began his career as a biologist with Fisheries and Oceans Canada. Mr. Schubert was a member of a number of joint Canada-U.S. technical committees in the 1980s and 1990s, served as a member of the Pacific Scientific Advice Review Committee in 1990-1994, and headed the Fraser River sockeye and pink salmon stock assessment team in 1994-2000. He is currently Chief of Stock Assessment for the Lower Fraser Area and is based in Delta, B.C. Mr. Schubert has authored 60 secondary publications.

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Appendix 1. Annual number of jacks and adult male and female sockeye entering Cultus Lake, female spawning success (based on examinations of body cavities following breeding) and estimated prespawn mortality, 1925-2002 ("na" indicates data are unavailable).

	Escapement							
			Adults					
Year	Total population	Jacks	Total	Males	Females	Female carcasses recovered	Female spawning success	Estimated prespawn mortality [c]
1925	5,423	0	5,423	1,540	3,883	-	-	-
1926	5,071 [a]	2,449	2,622	1,122	1,500	-	-	-
1927	82,426	0	82,426	26,050	56,376	-	-	-
1928	15,339 [b]	678	14,661	3,700	10,961	-	-	-
1929	5,084 [a]	0	5,084	1,645	3,439	-	-	-
1930	10,395	2,449	7,946	2,404	5,542	-	-	-
1931	37,473	0	37,473	10,368	27,105	-	-	-
1932	2,259 [a]	28	2,231	713	1,518	-	-	-
1933	3,471 [b]	607	2,864	1,027	1,837	-	-	-
1934	23,026	86	22,940	3,966	18,974	-	-	-
1935	15,339	na	15,339	5,412	9,927	-	-	-
1936	8,378	56	8,322	3,261	5,061	-	-	-
1937	3,061	1,834	1,227	513	714	-	-	-
1938	13,342	3,908	9,434	1,603	7,831	-	-	-
1939	73,189	2,400	70,789	19,224	51,565	-	-	-
1940	74,121	585	73,536	16,089	57,447	-	-	-
1941	18,164	4,214	13,950	5,413	8,537	-	-	-
1942	37,305	346	36,959	12,396	24,563	-	-	-
1943	11,875	53	11,822	3,881	7,941	-	-	-
1944	14,200	198	14,002	4,701	9,301	-	-	-
1945	9,227	4,197	5,030	1,780	3,250	75	79.0%	21.0%
1946	33,284	216	33,068	11,911	21,157	434	91.9%	8.1%
1947	8,898	199	8,699	2,869	5,830	-	-	-
1948	13,086	340	12,746	5,601	7,145	-	-	-
1949	9,301	246	9,055	3,039	6,016	-	-	-
1950	30,595	667	29,928	10,027	19,901	-	-	-
1951	13,143	466	12,677	3,002	9,675	-	-	-
1952	18,910	1,077	17,833	5,698	12,135	-	-	-
1953	13,000	1,457	11,543	6,253	5,290	-	-	-
1954	24,150	2,114	22,036	10,795	11,241	-	-	-
1955	26,000	78	25,922	7,990	17,932	-	-	-
1956	14,133	415	13,718	4,630	9,088	-	-	-
1957	20,647	272	20,375	7,245	13,130	-	-	-
1958	14,097	773	13,324	5,794	7,530	-	-	-
1959	48,461	682	47,779	15,753	32,026	-	-	-
1960	17,689	49	17,640	7,520	10,120	-	-	-
1961	15,428	2,032	13,396	6,363	7,033	-	-	-
1962	27,070	73	26,997	9,450	17,547	-	-	-
1963	20,571	268	20,303	9,032	11,271	-	-	-
1964	11,143	76	11,067	4,857	6,210	-	-	-
1965	2,532	77	2,455	832	1,623	-	-	-
1966	17,464	545	16,919	7,676	9,243	-	-	-
1967	33,492	294	33,198	14,767	18,431	-	-	-
1968	25,736	422	25,314	10,439	14,875	-	-	-
1969	6,739	797	5,942	2,761	3,181	-	-	-
1970	15,149	1,208	13,941	5,778	8,163	-	-	-
1971	9,145	17	9,128	4,161	4,967	-	-	-
1972	10,660	294	10,366	4,572	5,794	-	-	-
1973	858	217	641	318	323	-	-	-
1974	9,814	830	8,984	3,630	5,354	-	-	-
1975	11,478	129	11,349	4,006	7,343	-	-	-
1976	4,450	15	4,435	1,551	2,884	-	-	-

Continued

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Appendix 1. Continued.

Year	Escapement: Total population	Jacks	Adults: Total	Males	Females	Female carcasses recovered	Female spawning success	Estimated prespawn mortality [c]	
1978	7,265	2,189	5,076	1,920	3,156	-	-	-	
1979	32,045	14	32,031	11,736	20,295	-	-	-	
1980	1,687	30	1,657	693	964	-	-	-	
1981	1,159	903	256	112	144	-	-	-	
1982	17,222	497	16,725	6,445	10,280	-	-	-	
1983	19,952	8	19,944	8,454	11,490	35	100.0%	0.0%	
1984	1,147	153	994	449	545	-	-	-	
1985	571	147	424	215	209	-	-	-	
1986	3,533	277	3,256	1,062	2,194	-	-	-	
1987	32,336	152	32,184	14,800	17,384	-	-	-	
1988	964	103	861	374	487	-	-	6.6%	d
1989	568	150	418	182	236	-	-	6.6%	d
1990	1,870	10	1,860	849	1,011	-	-	6.6%	d
1991	20,191	34	20,157	9,690	10,467	246	94.1%	5.9%	
1992	1,205	2	1,203	455	748	-	-	6.6%	d
1993	1,131	68	1,063	492	571	71	100.0%	0.0%	
1994	4,422	23	4,399	1,749	2,650	115	95.2%	4.8%	
1995	10,349	33	10,316	4,744	5,572	28	76.5%	23.5%	
1996	2,030	8	2,022	908	1,114	10	34.4%	65.6%	
1997	91	3	88	45	43	0	-	51.6%	e
1998	2,166	207	1,959	928	1,031	9	62.5%	37.5%	
1999	12,403	11	12,392	5,576	6,816	0	-	93.0%	f
2000	1,227	0	1,227	613	614	0	-	93.0%	f
2001	675	160	515	257	258	1	0.0%	62.5%	g
2002	4,882	9	4,873	2,155	2,718	275	86.9%	13.1%	

a. No natural spawning; all eggs stripped from females for hatchery incubation and subsequent fry liberation into lake.
b. No natural spawning; all eggs stripped from females for egg plants in tributaries to Cultus Lake.
c Directly estimated from female carcass recovery, unless otherwise noted.
d Direct estimate unavailable; 1925-1994 average used for three generation projection.
e Direct estimate unavailable; 1996 and 1998 average used for three generation projection.
f. Direct estimate unavailable; estimated from ratio of smolts/adult for brood with 1925-1994 (pre-early migration) average.
g Direct estimate unavailable; 1995, 1996, 1998, 1999 and 2000 average used for three generation projection.

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Appendix 2. Annual Cultus sockeye migration timing through the Sweltzer Creek enumeration fence, period of peak spawning activity and average female fecundity, 1925-2002.

	Date at Sweltzer fence				Fecundity sample		
Year	Fence installed[a]	50% migration	Fence removed[b]	Period of peak spawning	N	Mean S. Length	Mean fecundity
1925	-	-	-	-	-	-	4,500
1926	-	-	-	-	-	-	-
1927	-	-	-	-	-	-	4,500
1928	-	-	-	-	-	-	-
1929	-	-	-	-	-	-	-
1930	-	-	-	-	-	-	4,500
1931	-	-	-	-	46	53.11	-
1932	-	-	-	-	47	51.22	4,310
1933	-	-	-	-	-	-	3,796
1934	-	-	-	-	55	53.56	-
1935	-	-	-	-	-	-	4,067
1936	-	-	-	-	40	49.85	-
1937	-	-	-	-	61	51.00	3,764
1938	27-Sep	-	-	12-Nov to 19-Nov	-	-	4,237
1939	10-Oct	-	-	20-Nov to 26-Nov	-	-	4,273
1940	20-Sep	-	-	23-Nov to 28-Nov	-	-	4,300
1941	9-Sep	27-Oct	13-Dec	-	-	-	4,300
1942	19-Sep	23-Nov	31-Dec	-	56	50.23	4,300
1943	25-Aug	18-Nov	1-Jan	-	40	52.12	3,722
1944	30-Aug	5-Nov	30-Dec	-	-	-	4,103
1945	29-Sep	4-Nov	22-Dec	23-Nov to 28-Nov	-	-	-
1946	22-Sep	2-Nov	22-Dec	23-Nov to 28-Nov	-	-	-
1947	26-Sep	5-Nov	30-Dec	-	-	-	-
1948	25-Sep	25-Oct	15-Dec	-	-	-	-
1949	4-Oct	27-Oct	12-Dec	23-Nov to 28-Nov	-	-	-
1950	26-Sep	20-Oct	10-Dec	23-Nov to 30-Nov	-	-	-
1951	21-Sep	16-Oct	6-Dec	21-Nov to 26-Nov	-	-	-
1952	4-Oct	30-Oct	10-Dec	23-Nov to 01-Dec	-	-	-
1953	20-Sep	16-Oct	30-Nov	18-Nov to 26-Nov	-	-	-
1954	29-Sep	10-Oct	20-Nov	18-Nov to 21-Nov	-	-	-
1955	29-Sep	16-Oct	4-Nov	20-Nov to 25-Nov	-	-	-
1956	14-Sep	3-Oct	6-Dec	18-Nov to 21-Nov	-	-	-
1957	19-Sep	27-Oct	4-Dec	18-Nov to 26-Nov	-	-	-
1958	25-Sep	4-Nov	7-Dec	25-Nov to 01-Dec	-	-	-
1959	24-Sep	16-Oct	15-Dec	01-Dec to 05-Dec	-	-	-
1960	27-Sep	20-Oct	6-Dec	16-Nov to 20-Nov	-	-	-
1961	19-Sep	20-Oct	30-Nov	25-Nov to 28-Nov	-	-	-
1962	20-Sep	9-Nov	8-Dec	20-Nov to 25-Nov	-	-	-
1963	25-Sep	3-Nov	6-Dec	03-Dec to 07-Dec	-	-	-
1964	25-Sep	29-Oct	30-Nov	-	-	-	-
1965	5-Oct	8-Oct	21-Nov	24-Nov to 30-Nov	-	-	-
1966	4-Oct	18-Oct	21-Nov	17-Nov to 22-Nov	-	-	-
1967	23-Sep	7-Nov	30-Nov	15-Nov to 20-Nov	-	-	-
1968	25-Sep	4-Nov	30-Nov	20-Nov to 26-Nov	-	-	-
1969	23-Sep	23-Oct	16-Nov	-	-	-	-
1970	7-Oct	10-Nov	29-Nov	15-Nov to 20-Nov	-	-	-
1971	30-Sep	11-Nov	4-Dec	22-Nov to 26-Nov	-	-	-
1972	29-Sep	27-Oct	26-Nov	15-Nov to 18-Nov	-	-	-
1973	28-Sep	25-Oct	17-Nov	01-Dec to 04-Dec	-	-	-
1974	25-Sep	7-Nov	29-Nov	20-Nov to 25-Nov	-	-	-
1975	25-Sep	25-Oct	17-Nov	25-Nov to 30-Nov	-	-	-
1976	7-Oct	19-Oct	23-Nov	15-Nov to 20-Nov	-	-	-
1977	8-Oct	21-Oct	4-Nov	15-Nov to 20-Nov	-	-	-
1978	3-Oct	24-Oct	15-Nov	Mid Nov	-	-	-
1979	20-Sep	18-Nov	9-Dec	29-Nov to 05-Dec	-	-	-
1980	28-Sep	19-Oct	5-Dec	Mid Nov	-	-	-

Continued

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Appendix 2. Continued.

Year	Date at Sweltzer fence: Fence installed[a]	50% migration	Fence removed[b]	Period of peak spawning	Fecundity sample: N	Mean S. Length	Mean fecundity
1977	8-Oct	21-Oct	4-Nov	15-Nov to 20-Nov	-	-	-
1978	3-Oct	24-Oct	15-Nov	Mid Nov	-	-	-
1979	20-Sep	18-Nov	9-Dec	29-Nov to 05-Dec	-	-	-
1980	28-Sep	19-Oct	5-Dec	Mid Nov	-	-	-
1981	1-Oct	3-Nov	20-Nov	Mid Nov	-	-	-
1982	1-Oct	6-Nov	10-Dec	Mid Nov	-	-	-
1983	27-Sep	23-Oct	30-Nov	Early Nov	-	-	-
1984	26-Sep	24-Oct	5-Dec	Early Nov	-	-	-
1985	27-Sep	27-Oct	22-Nov	Late Nov	-	-	-
1986	1-Oct	27-Oct	2-Dec	Late Nov	-	-	-
1987	30-Oct	13-Nov	16-Dec	Late Nov to Early Dec	-	-	-
1988	24-Oct	4-Nov	7-Nov	Late Nov to Early Dec	-	-	-
1989	5-Oct	5-Nov	10-Nov	23-Nov to 05-Dec	-	-	-
1990	11-Oct	26-Oct	9-Nov	-	-	-	-
1991	27-Sep	12-Nov	9-Dec	-	-	-	-
1992	5-Oct	25-Oct	30-Nov	-	-	-	-
1993	25-Oct	22-Nov	9-Dec	10-Dec to 20-Dec	-	-	-
1994	6-Oct	2-Nov	5-Dec	Early Dec	-	-	-
1995	29-Sep	5-Oct	7-Dec	c	-	-	-
1996	14-Sep	5-Oct	1-Dec	c	-	-	-
1997	23-Sep	9-Oct	10-Nov	c	-	-	-
1998	14-Sep	20-Oct	24-Nov	c	-	-	-
1999	27-Aug	9-Oct	17-Nov	c	-	-	-
2000	19-Aug	13-Sep	5-Dec	c	-	-	-
2001	16-Aug	7-Sep	8-Dec	c	-	-	-
2002	3-Aug	27-Sep	6-Jan	15-Nov to 19-Dec	21	51.00	4,056
Average							
1941-1995	27-Sep	28-Oct	25-Nov	Late-Nov. to early Dec.	118	51.51	4,182
1996-2002	29-Aug	30-Sep	1-Dec	-	-	-	-

[a] Fence installation date is based on historical timing information and the first observation of migrating adult sockeye.
[b] Fence removal date is based on historical timing information and the last observations of migrating adult sockeye.
[c] Spawning ground surveys were conducted in Cultus Lake, however, no sockeye spawning was observed.

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Appendix 3. Brood year adult escapement in year *n*, fall fry population estimate in year *n+1*, smolt population estimates in years *n+2* and *n+3*, and freshwater survival indices for Cultus sockeye, 1923-2001.

Brood year	Adult escapement	Fry population		Smolt population			Fry to smolt survival	Smolts per adult spawner
		Date	Estimates	Age-1	Age-2	Total		
1923	-	-	-	na	13,980	na	-	-
1924	-	-	-	1,384,020	66,500	1,450,520	-	-
1925	5,423	-	-	183,400	1,700	185,100	-	34.13
1926	2,622	-	-	336,200	8,300	344,500	-	131.39
1927	82,426	-	-	2,426,200	66,600	2,492,800	-	30.24
1928	14,661	-	-	38,600	5,200	43,800	-	2.99
1929	5,084	-	-	349,000	200	349,200	-	68.69
1930	7,946	-	-	788,400	0	788,400	-	99.22
1931	37,473	-	-	1,571,000	63,300	1,634,300	-	43.61
1932	2,231	-	-	121,200	14,200	135,400	-	60.69
1933	2,864	-	-	242,500	1,400	243,900	-	85.16
1934	22,940	-	-	501,600	23,000	524,600	-	22.87
1935	15,339	-	-	3,101,000	20,000	3,121,000	-	203.47
1936	8,322	-	-	1,627,000	20,415	1,647,415	-	197.96
1937	1,227	-	-	196,255	138	196,393	-	160.06
1938	9,434	-	-	1,374,800	953	1,375,753	-	145.83
1939	70,789	-	-	3,955,502	20,705	3,976,207	-	56.17
1940	73,536	-	-	1,752,551	12,879	1,765,430	-	24.01
1941	13,950	-	-	702,980	2,730	705,710	-	50.59
1942	36,959	-	-	2,009,186	9,698	2,018,884	-	54.62
1943	11,822	-	-	390,064	na	390,064	-	32.99
1944	14,002	-	-	-	-	-	-	-
1945	5,030	-	-	-	-	-	-	-
1946	33,068	-	-	-	-	-	-	-
1947	8,699	-	-	-	-	-	-	-
1948	12,746	-	-	-	-	-	-	-
1949	9,055	-	-	-	-	-	-	-
1950	29,928	-	-	na	3,928	na	-	-
1951	12,677	-	-	388,873	6,265	395,138	-	31.17
1952	17,833	-	-	620,213	-	620,213	-	34.78
1953	11,543	-	-	na	4,759	na	-	-
1954	22,036	-	-	1,903,296	23,589	1,926,885	-	87.44
1955	25,922	-	-	2,688,063	64,512	2,752,575	-	106.19
1956	13,718	-	-	976,120	184	976,304	-	71.17
1957	20,375	-	-	319,495	1,480	320,975	-	15.75
1958	13,324	-	-	1,427,228	2,215	1,429,443	-	107.28
1959	47,779	-	-	1,327,842	4,438	1,332,280	-	27.88
1960	17,640	-	-	1,025,404	24,859	1,050,263	-	59.54
1961	13,396	-	-	1,200,498	-	1,200,498	-	89.62
1962	26,997	-	-	-	-	-	-	-
1963	20,303	-	-	-	-	-	-	-
1964	11,067	-	-	na	4,682	na	-	-
1965	2,455	-	-	131,106	822	131,928	-	53.74
1966	16,919	-	-	2,101,506	17,446	2,118,952	-	125.24
1967	33,198	-	-	2,441,694	17,582	2,459,276	-	74.08
1968	25,314	-	-	1,005,291	7,652	1,012,943	-	40.02
1969	5,942	-	-	186,787	8,080	194,867	-	32.79
1970	13,941	-	-	799,934	17,335	817,269	-	58.62
1971	9,128	-	-	1,086,016	6,505	1,092,521	-	119.69
1972	10,366	-	-	167,111	na	167,111	-	16.12
1973	641	-	-	na	9,963	na	-	-
1974	8,984	-	-	986,300	12,315	998,615	-	111.15
1975	11,349	-	-	1,219,211	1,697	1,220,908	-	107.58

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Appendix 3. Continued.

Brood year	Adult escapement	Fry population		Smolt population			Fry to smolt survival	Smolts per adult spawner
		Date	Estimates	Age-1	Age-2	Total		
1978	5,076	-	-	-	-	-	-	-
1979	32,031	-	-	-	-	-	-	-
1980	1,657	-	-	-	-	-	-	-
1981	256	-	-	-	-	-	-	-
1982	16,725	-	-	-	-	-	-	-
1983	19,944	-	-	-	-	-	-	-
1984	994	-	-	-	-	-	-	-
1985	424	-	-	-	-	-	-	-
1986	3,256	17-Nov	2,379,300	-	-	-	-	-
1987	32,184	-	-	na	459	na	-	-
1988	861	27-Nov	580,361	65,184	372	65,556	11%	76.14
1989	418		-	52,865	2,716	55,581	-	132.97
1990	1,860	27-Nov	474,623	178,357	na	178,357	38%	95.89
1991	20,157	13-Nov	1,850,963	-	-	-	-	-
1992	1,203	-	-	-	-	-	-	-
1993	1,063	-	-	-	-	-	-	-
1994	4,399	-	-	-	-	-	-	-
1995	10,316	-	-	-	-	-	-	-
1996	2,022	-	-	-	-	-	-	-
1997	88	-	-	-	-	-	-	-
1998	1,959	-	-	na	70	na	-	-
1999	12,392	30-Oct	249,590	62,564	27	62,591	25%	5.05
2000	1,227	15-Oct	46,327	5,654	35	5,689	12%	4.64
2001	515	na	na	11,325	na	11,348	na	22.03

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Appendix 4. Annual total adult population, number killed in fisheries, number entering Cultus Lake and human exploitation rate for Cultus sockeye, 1952-2002.

Year	Total adult escapement	Total catch	Total adult return	Exploitation rate
1952	17,833	19,987	37,820	52.8%
1953	11,543	29,029	40,572	71.5%
1954	22,036	79,628	101,664	78.3%
1955	25,922	143,195	169,117	84.7%
1956	13,718	23,808	37,526	63.4%
1957	20,375	53,208	73,583	72.3%
1958	13,324	49,162	62,486	78.7%
1959	47,779	234,701	282,480	83.1%
1960	17,640	22,304	39,944	55.8%
1961	13,396	14,395	27,791	51.8%
1962	26,997	20,536	47,533	43.2%
1963	20,303	31,541	51,844	60.8%
1964	11,067	13,722	24,789	55.4%
1965	2,455	4,349	6,804	63.9%
1966	16,919	18,564	35,483	52.3%
1967	33,198	98,802	132,000	74.9%
1968	25,314	45,539	70,853	64.3%
1969	5,942	16,011	21,953	72.9%
1970	13,941	26,138	40,079	65.2%
1971	9,128	87,978	97,106	90.6%
1972	10,366	38,639	49,005	78.8%
1973	641	4,390	5,031	87.3%
1974	8,984	35,813	44,797	79.9%
1975	11,349	36,735	48,084	76.4%
1976	4,435	26,410	30,845	85.6%
1977	82	401	483	83.0%
1978	5,076	22,364	27,440	81.5%
1979	32,031	77,620	109,651	70.8%
1980	1,657	4,719	6,376	74.0%
1981	256	1,201	1,457	82.4%
1982	16,725	52,386	69,111	75.8%
1983	19,944	87,952	107,896	81.5%
1984	994	5,882	6,876	85.5%
1985	424	541	965	56.1%
1986	3,256	9,163	12,419	73.8%
1987	32,184	68,537	100,721	68.0%
1988	861	8,924	9,785	91.2%
1989	418	1,679	2,097	80.1%
1990	1,860	8,540	10,400	82.1%
1991	20,157	44,762	64,919	69.0%
1992	1,203	6,298	7,501	84.0%
1993	1,063	9,808	10,871	90.2%
1994	4,399	18,844	23,243	81.1%
1995	10,316	9,026	19,342	46.7%
1996	2,022	885	2,907	30.4%
1997	88	1,512	1,600	94.5%
1998	1,959	338	2,297	14.7%
1999	12,392	1,436	13,828	10.4%
2000	1,227	797	2,024	39.4%
2001	515	102	617	16.5%
2002	4,873	801	5,674	14.1%

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Appendix 5. Age-1 smolt production, subsequent catch and escapement at ages 4_2 and 5_2, and marine survival of Cultus sockeye for the 1951-2001 brood years.

Brood year	Smolt migration year	Age-1 smolts	Catch plus escapement at age 4_2	5_2	Total	Marine suvival
1951	1953	388,873	166,043	4,527	170,569	43.9%
1952	1954	620,213	32,999	11,266	44,265	7.1%
1953	1955	-	62,317	855	63,172	-
1954	1956	1,903,296	61,631	1,933	63,565	3.3%
1955	1957	2,688,063	274,490	1,184	275,674	10.3%
1956	1958	976,120	35,165	1,067	36,232	3.7%
1957	1959	319,495	26,724	1,264	27,988	8.8%
1958	1960	1,427,228	46,269	1,097	47,365	3.3%
1959	1961	1,327,842	50,631	1,449	52,079	3.9%
1960	1962	1,025,404	22,606	414	23,020	2.2%
1961	1963	1,200,498	5,954	0	5,954	0.5%
1962	1964	-	35,483	0	35,483	-
1963	1965	-	131,466	3,157	134,623	-
1964	1966	-	67,696	1,550	69,246	-
1965	1967	131,106	19,606	0	19,606	15.0%
1966	1968	2,101,506	40,079	435	40,514	1.9%
1967	1969	2,441,694	96,671	6,114	102,785	4.2%
1968	1970	1,005,291	42,418	0	42,418	4.2%
1969	1971	186,787	5,031	0	5,031	2.7%
1970	1972	799,934	44,797	150	44,947	5.6%
1971	1973	1,086,016	47,715	313	48,027	4.4%
1972	1974	167,111	30,020	3	30,023	18.0%
1973	1975	-	480	189	669	-
1974	1976	986,300	27,251	1,831	29,082	2.9%
1975	1977	1,219,211	107,820	267	108,087	8.9%
1976	1978	167,982	6,109	0	6,109	3.6%
1977	1979	-	1,457	0	1,457	-
1978	1980	-	69,111	0	69,111	-
1979	1981	-	106,617	1,627	108,244	-
1980	1982	-	4,639	0	4,639	-
1981	1983	-	965	0	965	-
1982	1984	-	12,419	5,529	17,948	-
1983	1985	-	95,192	711	95,903	-
1984	1986	-	9,074	32	9,106	-
1985	1987	-	1,980	122	2,102	-
1986	1988	-	10,278	0	10,278	-
1987	1989	-	64,919	917	65,836	-
1988	1990	65,184	6,584	1,142	7,726	11.9%
1989	1991	52,865	9,729	1,012	10,741	20.3%
1990	1992	178,357	22,231	2,300	24,531	13.8%
1991	1993	-	16,722	733	17,455	-
1992	1994	-	2,150	0	2,150	-
1993	1995	-	1,600	0	1,600	-
1994	1996	-	2,297	138	2,435	-
1995	1997	-	13,690	510	14,200	-
1996	1998	-	1,497	0	1,497	-
1997	1999	-	617	17	634	-
1998	2000	-	5,657	na	5,657	-
1999	2001	62,564	na	na	na	-
2000	2002	5,654	na	na	na	-
2001	2003	11,325	na	na	na	-

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Appendix 6. Brood year escapement, subsequent return by age in the catch and escapement, and returns per adult entering Cultus Lake in the parental generation for Cultus sockeye adults, 1948-1999 brood years.

Brood year	Adult escapement	Jack return 3_2	Adult return (catch plus escapement) 4_3	4_2	5_2	5_3	Total	Adult return per spawner
1948	12,746	-	0	37,820	1,256	1,827	40,903	3.2
1949	9,055	1,662	16	37,489	0	0	37,505	4.1
1950	29,928	3,623	0	101,664	0	3,074	104,738	3.5
1951	12,677	3,498	0	166,043	4,527	0	170,569	13.5
1952	17,833	159	0	32,999	11,266	0	44,265	2.5
1953	11,543	497	0	62,317	855	0	63,172	5.5
1954	22,036	1,631	44	61,631	1,933	6,056	69,665	3.2
1955	25,922	1,610	204	274,490	1,184	3,596	279,474	10.8
1956	13,718	1,273	0	35,165	1,067	0	36,232	2.6
1957	20,375	95	0	26,724	1,264	0	27,988	1.4
1958	13,324	3,547	0	46,269	1,097	117	47,482	3.6
1959	47,779	114	94	50,631	1,449	735	52,908	1.1
1960	17,640	483	0	22,606	414	436	23,456	1.3
1961	13,396	194	0	5,954	0	0	5,954	0.4
1962	26,997	524	201	35,483	0	534	36,218	1.3
1963	20,303	3,825	0	131,466	3,157	0	134,623	6.6
1964	11,067	1,357	0	67,696	1,550	797	70,043	6.3
1965	2,455	1,380	34	19,606	0	0	19,640	8.0
1966	16,919	4,551	0	40,079	435	0	40,514	2.4
1967	33,198	7,716	0	96,671	6,114	473	103,258	3.1
1968	25,314	36	0	42,418	0	0	42,418	1.7
1969	5,942	1,446	0	5,031	0	0	5,031	0.8
1970	13,941	910	56	44,797	150	219	45,222	3.2
1971	9,128	2,673	58	47,715	313	512	48,598	5.3
1972	10,366	337	3	30,020	3	0	30,026	2.9
1973	641	44	0	480	189	0	669	1.0
1974	8,984	636	0	27,251	1,831	0	29,082	3.2
1975	11,349	7,700	0	107,820	267	0	108,087	9.5
1976	4,435	20	0	6,109	0	0	6,109	1.4
1977	82	114	0	1,457	0	0	1,457	17.8
1978	5,076	4,837	18	69,111	0	1,279	70,408	13.9
1979	32,031	1,662	0	106,617	1,627	610	108,854	3.4
1980	1,657	186	0	4,639	0	0	4,639	2.8
1981	256	579	0	965	0	0	965	3.8
1982	16,725	883	8	12,419	5,529	0	17,956	1.1
1983	19,944	423	0	95,192	711	0	95,903	4.8
1984	994	215	0	9,074	32	85	9,191	9.2
1985	424	329	0	1,980	122	0	2,102	5.0
1986	3,256	210	0	10,278	0	0	10,278	3.2
1987	32,184	19	0	64,919	917	0	65,836	2.0
1988	861	99	0	6,584	1,142	0	7,726	9.0
1989	418	4	0	9,729	1,012	0	10,741	25.7
1990	1,860	236	0	22,231	2,300	320	24,851	13.4
1991	20,157	23	0	16,722	733	24	17,479	0.9
1992	1,203	67	0	2,150	0	0	2,150	1.8
1993	1,063	11	0	1,600	0	0	1,600	1.5
1994	4,399	7	0	2,297	138	0	2,435	0.6
1995	10,316	240	0	13,690	510	17	14,217	1.4
1996	2,022	12	0	1,497	0	0	1,497	0.7
1997	88	0	0	617	17	0	634	7.2
1998	1,959	160	0	5,657	na	na	5,657	na
1999	12,392	9	na	na	na	na	na	na

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