

The Cohen Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River

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A Review of Potential Climate Change Effects on Survival of Fraser River Sockeye Salmon and an Analysis of Interannual Trends in En Route Loss and Pre-spawn Mortality



A Review of Potential Climate Change Effects on Survival of Fraser River Sockeye Salmon and an Analysis of Interannual Trends in En Route Loss and Pre-spawn Mortality

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Preface

Fraser River sockeye salmon are vitally important for Canadians. Aboriginal and non-Aboriginal communities depend on sockeye for their food, social, and ceremonial purposes; recreational pursuits; and livelihood needs. They are key components of freshwater and marine aquatic ecosystems. Events over the past century have shown that the Fraser sockeye resource is fragile and vulnerable to human impacts such as rock slides, industrial activities, climatic change, fisheries policies and fishing. Fraser sockeye are also subject to natural environmental variations and population cycles that strongly influence survival and production.

In 2009, the decline of sockeye salmon stocks in the Fraser River in British Columbia led to the closure of the fishery for the third consecutive year, despite favourable pre-season estimates of the number of sockeye salmon expected to return to the river. The 2009 return marked a steady decline that could be traced back two decades. In November 2009, the Governor General in Council appointed Justice Bruce Cohen as a Commissioner under Part I of the *Inquiries Act* to investigate this decline of sockeye salmon in the Fraser River. Although the two-decade decline in Fraser sockeye stocks has been steady and profound, in 2010 Fraser sockeye experienced an extraordinary rebound, demonstrating their capacity to produce at historic levels. The extreme year-to-year variability in Fraser sockeye returns bears directly on the scientific work of the Commission.

The scientific research work of the inquiry will inform the Commissioner of the role of relevant fisheries and ecosystem factors in the Fraser sockeye decline. Twelve scientific projects were undertaken, including:

Project

- 1 Diseases and parasites
- 2 Effects of contaminants on Fraser River sockeye salmon
- Fraser River freshwater ecology and status of sockeye Conservation Units
- 4 Marine ecology
- 5 Impacts of salmon farms on Fraser River sockeye salmon
- 6 Data synthesis and cumulative impact analysis
- 7 Fraser River sockeye fisheries harvesting and fisheries management
- 8 Effects of predators on Fraser River sockeye salmon
- 9 Effects of climate change on Fraser River sockeve salmon
- 10 Fraser River sockeye production dynamics
- 11 Fraser River sockeye salmon status of DFO science and management
- 12 Sockeye habitat analysis in the Lower Fraser River and the Strait of Georgia

Experts were engaged to undertake the projects and to analyse the contribution of their topic area to the decline in Fraser sockeye production. The researchers' draft reports were peer-reviewed and were finalized in early 2011. Reviewer comments are appended to the present report, one of the reports in the Cohen Commission Technical Report Series.

The initial purpose of our work for the *Cohen Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River* was to review the scientific literature on documented and projected effects of climate change on sockeye salmon (*Oncorhynchus nerka*) and where possible on Fraser River sockeye salmon, in the marine and freshwater environments across all life stages. We were subsequently asked by the 'Commission' to expand our work and requested to write a report on migration and spawning ground mortality issues in order for us to comment on one of the key hypotheses considered by the Pacific Salmon Commission (PSC) in its report on declining productivity trends in Fraser River sockeye salmon (Peterman *et al.* 2010). And, we were also asked, as part of that second task, to briefly review the latest findings on the early upriver migration phenomenon that is occurring in Late-run sockeye salmon. Therefore our report is comprised of two separate sections: Section 1 - The effects of climate and climate change on survival of Fraser River sockeye salmon: a literature review to evaluate recent trends in abundance and productivity; Section 2 - Adult mortality during river migration and on spawning grounds.

Executive summary

Effects of climate and climate change on survival of Fraser River sockeye salmon

- We present an assessment of the possible contribution of climate change to the recent decline in abundance and productivity of Fraser River sockeye salmon. Our assessment was based on a review of the literature evaluating the effects of climaterelated variables (i.e. climate variables and other physical variables influenced by climate) on the biology and ecology of sockeye salmon across all life stages.
- o A total of 1799 documents were found in our search for primary (n=1519) and grey (n=280) literature. Of this total, only 114 documents (89 and 25 from the primary and grey literature, respectively) remained after the removal of duplicates, conference abstracts and documents that did not attempt to link a climate-related variable to sockeye salmon biology or ecology. Fraser River sockeye salmon were included in the dataset of 64 (56.1%) publications. The earliest publication resulting from our literature search appeared in the late 1930s. In the subsequent three decades, only a few publications on the effects of climate-related variables on sockeye salmon appeared in the literature and virtually all of them dealt with freshwater life stages. It was not until the 1970s that the number of publications started to increase considerably until the current decade. The great majority of publications dealing with marine life stages only started to appear in the 1980s and their numbers have been growing ever since, though they still lag behind those dealing with freshwater life stages.
- o We synthesized the current state of knowledge on the effects of climate-related variables on survival (estimated by the authors either indirectly using productivity indices or directly through direct observation or the analysis of tagging data) on the life stages of sockeye salmon. Based on our synthesis, we made a qualitative assessment of the likelihood that life-stage-specific survival of Fraser River sockeye salmon has been undergoing a trend in the past 20 years due to the recent trends in climate, particularly in temperature (warming of 0.5 °C and 0.7 °C in marine and freshwater environments, respectively, over the past two decades). For each life stage, we rated potential climate-driven trends in survival as *very likely*, *likely*, *possible* and *unlikely* to have occurred. In general, these ratings were defined so that more weight of evidence was given to findings obtained from field studies.

- Our assessment concluded that: survival of eggs has <u>possibly</u> increased (but not in all stocks); survival of alevins has <u>unlikely</u> changed; survival of fry in lakes has <u>possibly</u> decreased; survival of smolts and postsmolts has <u>likely</u> decreased; survival of immatures in the ocean has <u>possibly</u> decreased; survival of returning adults has <u>very likely</u> decreased (but not in all stocks); once on the spawning grounds, survival to spawn has <u>possibly</u> decreased (but not in all stocks).
- Our qualitative assessment suggests that the survival of all life stages of Fraser River sockeye salmon, with the possible exception of eggs and alevins, may be declining due to trends in temperature (and the factors that correlate with temperature) in both marine and freshwater environments over the past 20 years. However, where data exist at the stock-level for some life history stages (e.g. eggs, alevin, adult migrants), the picture is complicated by stock-specific patterns indicating that the survival of some stocks may have been less impacted than that of others or not impacted at all.
- Although the recent warming may not have resulted in large declines in survival of individual life stages, the cumulative impacts of climate change on survival across life stages could have been substantial. Overall, the weight of the evidence suggests that climate change may have adversely affected survival of Fraser River sockeye salmon and hence has been a possible contributor to the observed declining trend in abundance and productivity over the past 20 years. It also seems that inter-annual variability in climate conditions have contributed to the extreme variation in the abundance of returning adults that were observed in 2009 (much lower than average) and 2010 (much higher than average), as the years that those cohorts went to sea were characterized by unusually warm (2007) and cool (2008) sea surface temperatures, respectively.
- o Recent analyses of the potential effects of future climate change on Fraser River sockeye salmon all point to reduced survival and lower productivity if the climate continues to warm. Although there is some potential for tolerance to warm temperatures to evolve in Pacific salmon, further evolutionary change may already be restricted in populations that have historically experienced high temperatures, such as Summer-run Fraser River sockeye salmon. Phenological (i.e. timing of events such as seaward migration and return migration) changes are likely to be one of the major responses of Pacific salmon to climate change. Several adaptation strategies to lessen

the ecological, economic and social impacts of climate change effects on Pacific salmon have been recently proposed.

Adult mortality during river migration and on spawning grounds

- O The primary purposes of this section are to: review the major environmental factors responsible for adult sockeye salmon mortality during Fraser River migrations (termed 'en route mortality') and for premature mortality on spawning grounds (termed 'pre-spawn mortality'), review the early migration/high mortality Late-run sockeye salmon phenomenon, describe interannual and within-year among stock patterns in adult mortality, and provide a mechanistic understanding for several of these patterns.
- o River entry timing and abundance of adult sockeye salmon has been quantitatively assessed since 1977 by the Pacific Salmon Commission (PSC) just upstream of the Fraser River mouth near Mission, B.C., using various forms of hydroacoustic methods linked with stock ID sampling. Fisheries and Oceans Canada (DFO) and the PSC refer to the differences in estimates of stock-specific abundance obtained from the Mission site and those obtained from spawning grounds (after accounting for reported in-river harvest upstream of Mission) as 'escapement discrepancies' which are used to assess *en route* loss, the percentages of each run that cannot be accounted for during the migration, which is an indirect assessment of migration (*en route*) mortality.
- O Generally, *en route* loss begins to be reported in 1992 for Early Stuart, Early summer, and Summer-runs, but not until 1996 for Late-runs. Relative to total catch and spawning ground escapement, levels of *en route* loss have been increasing, with recent years having some of the relative highest levels. In several years, *en route* loss is the dominant component of the fate of the Early Stuart and Late-run timing groups, and, since 1996, *en route* loss of at least 30% has been observed for at least one runtiming group in each year.
- Eight out of 11 stocks had more than half of years between 1996 and 2008 when en route loss within those stocks exceeded 50%. There is clearly an effect of run timing on this pattern. The earlier runs (e.g. Early Stuart, Scotch, Seymour, Fennell, Gates and Nadina) and the later runs (Harrison, Portage and Weaver) have the most years

with high *en route* loss. Summer-runs (e.g. Quesnel and Chilko) have experienced few if any years with large (> 50%) *en route* loss. There is good evidence that the among-stock patterns in *en route* loss are indicative of stock-specific abilities to cope with warming rivers and high river temperatures.

- Changing thermal conditions have been one of the largest environmental challenges that migrating adult Fraser River sockeye salmon have had to deal with over the past 20 years: 1) the Fraser River has experienced ~ 2.0 °C warming in the summer compared to 60 years ago, with average summer temperatures warming ~ 0.7 °C in the most recent 20 years; 2) there have been several recent years with extreme temperatures during mid-summer (water temperatures in 13 of the last 20 summers have been the warmest on record); and 3) since 1996, segments of all Late-run sockeye salmon stocks have been entering the Fraser River 3-6 weeks earlier than normal they now encounter temperatures up to 5 °C warmer than they historically did and are spending longer in freshwater because spawning migration dates have not changed. Therefore Late-run fish have been exposed to freshwater diseases and parasites for much longer periods of time, with disease development being accelerated by higher than normal river temperatures (due to earlier river entry and climate warming), and greater degree day accumulation.
- Over the past decade there have been numerous field telemetry investigations examining *en route* mortality and the body of evidence indicates that *en route* mortality is stock-specific with Summer-runs having the greatest thermal tolerance, relative to earlier and later runs, supporting the among-stock patterns in *en route* loss. Laboratory investigations suggest that Fraser River sockeye salmon stocks vary in both their optimum and critical high temperatures in a manner that reflects local adaptation to temperatures experienced during their historic migration stocks appear to be physiologically fine-tuned to function best at the river migration temperatures they historically encountered. Summer-run stocks have the highest critical temperatures and the largest aerobic and cardiac scopes of all groups of sockeye salmon. Earlier migrating Late-runs are particularly poorly adept at dealing with the relatively high temperatures and prolonged exposure to freshwater diseases.
- o Pre-spawn mortality is highly variable among stocks, run-timing groups and years over the 70-year data series. With the exception of 12 years, pre-spawn mortality has not exceeded 30% at the run-timing group level; only in four years did pre-spawn

mortality of a run-timing group exceed 40%. Across all run-timing groups over the entire 70-year period, pre-spawn mortality averaged ~ 10%. There is no clear indication that pre-spawn mortality, at the run-timing level, has been increasing over the recent few decades in concordance with run-timing trends in increasing *en route* mortality, with the possible exception of the past 25-year trend in Late-run pre-spawn mortality, which shows high variability but a general increase.

- o Spawning abundance has declined in Early Stuart and several Late-run stocks during a time period when en route loss became a significant component of the total fate of adult migrants in those groups of fish. Spawning abundance has not declined dramatically in most stocks partly because of reductions in harvest associated with management adjustments made to compensate for en route mortality. Therefore, spawning abundance could have been a great deal higher (or allocations to fisheries greater) in recent years if it were not for en route loss.
- o En route loss may be a critical factor contributing to decreasing trends in spawning abundance for some Fraser River sockeye salmon stocks, in particular, those that do not cope well with warming rivers. En route and pre-spawn mortality in adult sockeye salmon are significant factors that reduce the number of effective female spawners, and thus may pose a threat to the long-term viability of the populations that are particularly affected.

Recommendations

• We recommend the following research directions:

<u>Telemetry approaches and direct experimentation are needed to better understand sockeye salmon marine survival:</u> An understanding of the mechanisms through which climate-related variables affect sockeye salmon in the marine environment should be sought with the application of electronic tagging technologies and exposing tagged fish to varying temperature, salinity, pH, or parasites.

<u>Field-based research is needed on early life stages in freshwater:</u> Much of the past work in freshwater has been conducted in the laboratory; little is known on how temperature influences biology and ecology (e.g. interaction with prey and predators) of the early life stages of sockeye salmon in streams and lakes. Future

research efforts should also be directed at the effects of increased stream flows on egg survival since higher levels of rainfall during the time of incubation are expected to occur with climate change.

Improvements are needed in-season and post-season estimates of spawning migration mortality: Fisheries management needs better ways to predict *en route* and pre-spawn mortality prior to fish entering the Fraser River. Also needed are improvements to *en route* loss models (e.g. quantify the contributions of estimation errors and unreported catch).

Tagging programs are needed for direct and accurate estimates of survival: Accurate estimates of survival from tagged fish are required for efficient monitoring of stocks and analyses of viability using life-cycle models. Telemetry programs as well as programs using other tagging approaches (e.g. Petersen discs, PIT or anchor tags) are needed for this purpose and should be coupled with capture-mark-recapture methods of data analysis.

Additional stocks need to be examined: Only a few major stocks have been intensively studied to date in terms of *en route* mortality, but adult sockeye salmon from different stocks vary substantially in their life history, energy use and allocation, thermal tolerance, and habitats used. A multi-stock approach to research could provide valuable information on the mechanisms through which climate-related variables will sockeye salmon on the watershed level scale.

Better assess the extent and consequences of gender differences in survival of migrating adult sockeye salmon: Future research should look into the extent and physiological basis of survival differences between sexes and investigate the consequences of female-specific survival for the viability of Fraser River sockeye salmon, particularly under future climate warming.

Assess impacts of fisheries capture and release/escape on *en route* and pre-spawn mortality: Managers need to know how release or escape of captured fish affects *en route* loss and escapement. In an era of warming rivers we expect higher stress-related mortality after release/escape but these levels are largely unknown for Fraser River sockeye salmon and most Pacific salmon.

<u>Cumulative impacts, carry-over and intergenerational effects:</u> There has been little research examining cumulative impacts, both across multiple stressors (e.g. fisheries capture, temperature, pollutants) or life history stages (i.e. carry-over effects), and/or among generations (i.e. intergenerational effects). These information gaps are critical to fill to begin to understand current trends in sockeye salmon productivity and abundance.

<u>Climate change modelling</u>: Needed are the development of life-cycle models in order to quantify the impact of climate warming on future trends in Fraser River sockeye salmon productivity and abundance. More stock-specific information on the susceptibility to climate change is needed for this purpose. Research aimed at understanding how sockeye salmon will adapt to climate change through genetic and non-genetic mechanisms will also be needed.

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1. Effects of climate and climate change on survival of Fraser River sockeye salmon: a literature review to evaluate recent trends in abundance and productivity

1.1. Introduction

Abundant and sustainable Pacific salmon (Oncorhynchus spp.) stocks are important economically, ecologically and culturally to the province of British Columbia. The commercial fishing industry is one of the largest sectors of the provincial economy, and the recreational salmon fishing industry generates billions of dollars annually in expenditures while supporting more than 10,000 jobs in communities throughout the province (Anonymous 2005; Kristianson & Strongitharm 2006). Ecologically, Pacific salmon are important components of food chains in both marine and freshwater environments, and adult salmon carcasses are fundamental sources of nutrients for stream and riparian forest ecosystems in coastal Pacific watersheds (Helfield & Naiman 2001; Quinn 2005). Culturally, Pacific salmon are integral to the mythology, spiritual integrity, and livelihoods of Pacific First Nations (Jacob et al. 2010). The largest salmon producing system of British Columbia (and Canada for that matter) is the Fraser River, with sockeye salmon (O. nerka) being the most commercially valuable and second most abundant salmon species in this river system. In the past 20 years, the abundance and productivity of Fraser River sockeye salmon has declined precipitously and some of its stocks were classified as 'endangered' by the International Union for the Conservation of Nature (IUCN-SSG 2009) and the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2010). Various hypotheses have been put forward to explain the recent decline in Fraser River sockeye salmon abundance and productivity (Peterman et al. 2010; STTS 2009), including climate change.

The dynamics of sockeye salmon (and Pacific salmon in general) abundance and productivity is particularly sensitive to changes in climate because the fish's anadromous life cycle exposes them to a variety of climate-driven stressors in both marine and freshwater environments (Fleming & Jensen 2002). Indeed, paleolimnological records of $\delta^{15}N$ (a salmon-derived nutrient) taken from Alaskan lake sediments cores have revealed that large shifts in sockeye salmon abundance over the past 2,200 years occurred during major changes in the climate of the northeastern Pacific Ocean (Finney *et al.* 2002). Furthermore, these records have shown that the abundance of sockeye salmon closely tracked decadal-scale fluctuations in sea surface temperature (SST) over most of the past 300 years (Finney *et al.* 2000; see also Hill *et al.* 2009). In fact, fluctuations in the abundance of Pacific salmon over decadal-scales have been well documented during the past century and linked to major climate-driven changes in the marine environment occurring every 20-30 years (Beamish & Bouillon 1993; Beamish *et al.* 1999;

Beamish & Noakes 2002; Mantua *et al.* 1997). Presumably in response to these oceanic regime shifts, the abundance of Fraser River sockeye salmon began to increase dramatically at the end of the 1970s, reaching historic high abundance in the early 1990s. After the early 1990s, abundance as well as productivity began to decline to recent low levels (Beamish *et al.* 1997, 2004), in coincidence with an exacerbation of the long-term warming trend of the global climate (IPCC 2007).

Various authors have examined the potential effects of future climate change on particular life stages of sockeye salmon, with many of the analyses done on Fraser River sockeye salmon stocks (e.g. Bryant 2009; Hague et al. 2011; Henderson et al. 1992; Hinch et al. 1995; Levy 1992; Martins et al. 2011; Rand et al. 2006). However, no study has assessed the possible contribution of climate change to the recent decline in abundance and productivity of Fraser River sockeye salmon. In this section, we present such an assessment based on a review of the literature evaluating the effects of climate-related variables (i.e. climate variables and other physical variables influenced by climate) on the biology and ecology of sockeye salmon across all life stages. We begin describing how the literature was compiled and then we present a quantitative summary of the relevant publications that were found (e.g. publication trends over time, life stages and climate-related variables examined by the authors). We then briefly overview the Fraser River sockeye salmon life cycle and synthesize the current state of knowledge on the effects of climate-related variables on survival (estimated by the authors either indirectly [i.e. using productivity indices] or directly [i.e. through direct observation or the analysis of tagging data]) of the several life stages of sockeye salmon. The synthesis is followed by a description of the documented climate-driven changes in the habitats used by Fraser River sockeye salmon. In view of these changes, we present a qualitative assessment of the likelihood that climate change has affected Fraser River sockeye salmon survival over the past 20 years and hence contributed to recent declining trends in abundance and productivity (we did a similar synthesis and assessment for growth and phenology but we do not present them here as these variables do not directly relate to abundance and productivity; however we do comment on them when they relate to survival). We finish this section discussing recent work on future climate change effects on sockeye salmon, potential for adaptation in Pacific salmon and adaptation strategies.

1.2. Literature compilation

We conducted a literature search for English language documents published in the primary and grey literature (e.g. technical reports, theses) that examined the effects of climate-related variables on sockeye salmon biology and ecology. The primary literature search was conducted using two academic search engines: ISI Web of Knowledge and Aquatic Sciences and Fisheries

Abstracts. In both search engines, we used combinations of climatic keywords (e.g. temperature, precipitation, rainfall, pressure, wind, climate, climate change, climate warming, global warming); keywords for physical variables potentially influenced by climate (e.g. flow, discharge, pH, salinity, current, upwelling, sea level); keywords for biological and ecological variables (e.g. productivity, catch, abundance, survival, mortality, growth, distribution, phenology, timing, behaviour, movement, physiology, disease, predation, reproduction); and the keywords 'sockeye' and 'Oncorhynchus nerka'. The individual terms were formatted before the search to represent various spellings of terms and forms of the word. For example, we used descriptors (popularly known as 'wild cards') such as an asterisk after a search term (e.g. surviv*) so that the search engines would then search for all words beginning as 'surviv' such as 'survival' and 'survivorship'.

The grey literature was compiled using the theses search engine ProQuest and the Fisheries and Oceans Canada's (DFO) online catalogue WAVES. The literature search on these two engines was done using the keywords 'sockeye' and 'Oncorhynchus nerka'. Additional grey literature was found by browsing documents on the website of several organizations involved with the assessment and management of fisheries resources, particularly Pacific salmon, such as the Pacific Salmon Commission (PSC), the North Pacific Anadromous Fish Commission (NPAFC), the Pacific Fisheries Resource Conservation Council (PFRCC), the North Pacific Marine Science Organization (PICES), and DFO. In addition to these, we also considered in our review papers on sockeye salmon and climate change that were either 'in press' (n=4) or 'in preparation' (n=3) at the time the literature for this report was compiled. All the primary and grey literature found was included into a database and duplicates and conference abstracts (except extended abstracts) were removed. We then read the abstracts of all papers in order to identify those that were original research examining the effects of a climate-related variable on the biology or ecology of sockeye salmon. Papers published in the grey literature were only retained at this stage if the authors had not published their results in the primary literature. Some of the papers eliminated at this stage were still considered in our review but only those meeting the above criteria were used in a quantitative assessment of the surveyed literature.

1.3. Quantitative assessment of the literature

To make a quantitative assessment of the literature, we created a spreadsheet with several variables to be queried from each paper. The variables were chosen as a means to detect temporal trends in publication, the range of environments, life-stages and variables assessed in the studies, and whether the studies were focusing on correlational or mechanistic (determined from results obtained in experimental manipulations in the laboratory and field or from tracking of fish carrying electronic tags) associations between climate-related variables and the biology

and ecology of sockeye salmon. Specifically, the variables queried were: 1) publication decade; 2) type of study (i.e. laboratory or field based and correlational or experimental); 3) electronic tagging used (i.e. yes, no, NA); 4) sockeye salmon studied (i.e. includes Fraser River fish, does not include Fraser River fish, presumably includes Fraser River fish [e.g. studies using all-nation catch, which possibly includes Fraser River sockeye salmon]); 5) climate-related variable used in the study (i.e. climatic index [e.g. Pacific Decadal Oscillation and Aleutian Low Pressure indices], temperature, precipitation, pressure, wind, flow, salinity, current, upwelling); 6) biological or ecological variable studied (i.e. productivity, catch or abundance, survival, growth, reproduction [e.g. maturation, spawning success], sex determination, diet, distribution, phenology, behaviour [e.g. travel rates, thermoregulation, migration route], physiology [e.g. stress hormones, metabolic scope]; interspecific interaction [i.e. predation rates, disease development]); 7) environment where the life stage(s) studied occur (i.e. marine or freshwater); and 8) life stage studied (i.e. egg and alevin, fry, smolt and postsmolt, immature in the ocean, returning adult [marine], returning adult [freshwater], spawner). Studies using variables such as productivity and catch usually related these metrics to climate-related variables at different time lags. For those studies, we considered the life stage studied as that (or those) that would correspond to the time lag(s) examined.

1.3.1. General findings

A total of 1799 documents were found in the search for primary (n=1519) and grey (n=280) literature. Of this total, only 114 documents (89 and 25 from the primary and grey literature, respectively) remained after the removal of duplicates, conference abstracts and documents that did not attempt to link a climate-related variable to sockeye salmon biology or ecology (Appendix 4). Fraser River sockeye salmon were included in the dataset of 64 (56.1%) publications or 52 (45.6%) if we do not consider those publications where we assumed Fraser River sockeye salmon were included. The earliest publication resulting from our literature search appeared in the late 1930s wherein the author reported that warm temperatures in the late winter/early spring were linked to an early onset of the seaward migration of Fraser River sockeye salmon smolts from Cultus Lake (Foerster 1937). In the subsequent three decades, only a few publications on the effects of climate-related variables on sockeye salmon appeared in the literature and virtually all of them dealt with freshwater life stages (Figure 1.1). It was not until the 1970s that the number of publications started to increase considerably until the current decade (Figure 1.1A). Moreover, the great majority of publications dealing with marine life stages only started to appear in the 1980s and their numbers have been growing ever since, though they still lag behind those dealing with freshwater life stages (Figure 1.1B).

The effects of climate-related variables have been studied mostly on returning adults during the freshwater migration (n=35; 30.7% of the studies or 20.0% of the total occurrence of life stages), followed by immatures in the ocean (n=31; 27.2% or 17.7%), smolts and postsmolts (n=27; 23.7% or 15.4%), fry (n=27; 23.7% or 15.4%), returning adults during the marine migration (n=26; 22.8% or 14.9%), eggs and alevins (n=15; 13.2% or 8.6%), and spawners (n=14; 12.3%) or 8.0%). At first it may come as a surprise that some marine life stages stand out as one of the most studied, particularly immature sockeye salmon which are highly dispersed in the ocean and hence difficult to access. However, these findings result from the fact that many studies on the marine life stages were largely correlational in nature (n=52; 94.5% of the total occurrence of study types in the marine environment); that is, the authors were simply relating a biological variable measured upon the return migration (e.g. productivity, growth) to a climate-related variable lagged by a time when sockeye salmon would be in one of their marine life stages. In contrast, a larger proportion of the studies on the freshwater life stages is experimental in nature (n=23; 31.5%) and/or involve tracking fish (particularly adults) equipped with electronic transmitters in the wild (n=13; 17.8%), both of which provide a better understanding of the mechanisms through which climate-related variables affect sockeye salmon biology and ecology.

Among the climatic variables and other physical variables affected by climate, the most frequently used in studies on sockeye salmon was temperature (n=93; 81.6% of studies or 57.8% of the total occurrence of climate-related variables). This finding likely reflects the well known fact that temperature is the 'master environmental factor' for fish (Fry 1971), and indeed it governs physiological, ecological, and behavioural aspects of life history for sockeye salmon (Brett 1971). After temperature, the most frequently used variables were various climatic indices (n=24; 21.1% or 14.9%), followed by flows (n=17; 14.9% or 10.6%), salinity (n=13; 11.4% or 8.1%), currents (n=4; 3.5% or 2.5%), precipitation (n=3; 2.6% or 1.9%), upwelling (n=3; 2.6% or 1.9%), pressure (n=2; 1.8% or 1.2%) and wind (n=2; 1.8% or 1.2%). The effects of these climate-related variables were examined on several aspects of sockeye salmon biology and ecology. Sockeye salmon growth, including one study on the amount of gross somatic energy accrued by individuals, was the most frequently examined variable (n=38; 33.3% of studies or 24.1% of the total occurrence of biological variables). Survival was the second most examined variable (n=27; 23.7% or 17.1%), followed by behaviour (n=20; 17.5% or 12.7%), phenology (n=16; 14.0% or 10.1%), catch or abundance (n=15; 13.2% or 9.5%), physiology (n=11; 9.6% or 7.0%), productivity (n=10; 8.8% or 6.3%), interspecific interactions (n=7; 6.1% or 4.4%), distribution (n=5; 4.4% or 3.2%), reproduction (n=5; 4.4% or 3.2%), diet (n=2; 1.8% or 1.3%) and sex determination (n=2; 1.8% or 1.3%). The number of studies examining the effects of climate-related variables on survival increases to 37 (32.5% or 23.4%) if we include the studies that examine productivity, as it is frequently used as an index of survival.

1.4. Effects of climate-related variables on survival of sockeye salmon

Before we synthesize the effects of climate-related variables on sockeye salmon survival, an overview of their life cycle, with particular emphasis on Fraser River sockeye salmon, is required. Sockeye salmon are anadromous – adults spawn in freshwater, but juveniles spend most of their lives in the ocean. They are also semelparous so they only spawn once and die after spawning. In the Fraser River, spawning occurs in late summer and autumn in gravel streams distributed throughout the watershed. Females deposit their eggs in nests and the eggs incubate over the fall and winter until they hatch as alevins. In the spring, young sockeye salmon (fry) emerge from the nest and migrate to a nearby nursery lake, where they feed for one year (a small fraction remains in the lakes for one additional year). In the spring of the next year, fry undergo the process of smoltification, which involves a suite of morphological, physiological and behavioural changes that prepares the fish for downstream migration and entrance into seawater. Fraser River sockeye salmon smolts enter the marine environment through the Strait of Georgia and postsmolts head north along the coast until the autumn, when they move offshore to the Gulf of Alaska. Immature sockeye salmon usually remain for two years feeding in the open ocean and then begin their return migration as adults to spawn in the Fraser River (Burgner et al. 1991; Hinch et al. 2006). The river entry timing of the numerous sockeye salmon stocks that spawn in the Fraser River is highly predictable and for that reason they have been aggregated into four run-timing groups: Early Stuart, Early Summer, Summer and Late-runs (Gable & Cox-Rogers 1993). For the purposes of the following synthesis, we distinguish among seven stages in the Fraser River sockeye salmon life cycle: 'egg and alevin', 'fry in lakes', 'smolt and postsmolt', 'immature in the open-ocean', 'returning adults' and 'spawners'. Our synthesis is focused on the effects of temperature, precipitation and flow.

1.4.1. Eggs and alevins

The survival of sockeye salmon eggs and alevins has been examined at a broad range of temperatures in the laboratory (2 °C to 16 °C). Survival of eggs (i.e. fertilization to hatch) was shown to be highest at about 8 °C and to decline under cooler and warmer temperatures. In contrast, survival of alevins (i.e. hatch to emergence from the gravel) was found to be independent of temperature (Beacham & Murray 1989, 1990; Murray & McPhail 1988). In the Fraser River, the effects of temperature on survival of eggs and alevins vary among populations from interior and coastal areas (Beacham & Murray 1989). For example, an interior-spawning stock (Adams River) was shown to have higher embryo survival at low temperature (2 °C) than a coastal-spawning stock (Weaver Creek), but lower alevin survival at high temperature (15 °C). Such differences between interior- and coastal-spawning stocks are thought to reflect local adaptations (i.e. an evolutionary process leading to maximization of individual fitness in their local habitats; Fraser *et al.* in press) to thermal conditions their antecessors have historically

experienced during incubation (i.e. relatively high and low temperatures in the coastal and interior stock, respectively) (Beacham & Murray 1989).

Another factor that can potentially decrease the survival of eggs is scouring from the spawning nest during high stream flows generated by rainfall (McNeil 1966; Steen & Quinn 1999). Freshwater survival declined with increased stream flow during the incubation of sockeye salmon eggs from the Cedar River (Washington) (Thorne & Ames 1987). In contrast, increased rainfall during the time of spawning of Babine Lake (British Columbia) sockeye salmon was associated with increased freshwater survival, presumably because it increased the area available for spawning and hence reduced mortality caused by superimposition of eggs (Brett 1951).

1.4.2. Fry in lakes

Survival of sockeye salmon fry decreases when exposed to warm temperature in the laboratory (Brett 1952). Consistent with that, a few studies suggested that survival of Fraser River sockeye salmon fry decreases in warm years (Adkison *et al.* 1996; Mueter *et al.* 2005). Although the direct effects of temperature are unlikely the cause of mortality, as fry are able to move to cooler lake depths to avoid stressful temperatures (Brett 1971), increased mortality due to higher predation rates are a plausible cause. Sylvester (1972) showed that fry exposed to juvenile coho salmon (*O. kisutch*) in the laboratory suffered significantly more predation mortality at warm temperatures (17 °C) than at cool temperatures (7 °C). Moreover, bioenergetic modelling by Petersen & Kitchell (2001) revealed that predation of the northern pikeminnow (*Ptychocheilus oregonensis*) on salmonid fry would have been 26-31% higher during warmer climate periods (average spring and summer temperatures about 11 °C and 18 °C, respectively) than during cool periods (average spring and summer temperatures about 10 °C and 16 °C, respectively). Similar predation rate estimates on salmonid fry during warm and cool climate periods were also found for other predators such as smallmouth bass (*Micropterus dolomieu*) and walleye (*Stizostedion vitreum*).

Diseases may also play a role in temperature-related mortality of juvenile sockeye salmon. Bower & Margolis (1985) showed that sockeye salmon inoculated with the haemoflagellate parasite *Cryptobia salmositica* had higher mortality rates when held at 13 °C than at 5 °C. However, fish held at 20 °C did not develop heavy infections and no mortalities were observed possibly because such a high temperature was suboptimal for development of the parasite.

1.4.3. Smolts and postsmolts

Thermal conditions experienced by smolts during their first months of marine life have been shown to be closely related to their first year survival. Warm temperatures have been frequently associated with increased early marine survival in Alaskan sockeye salmon (Adkison *et al.* 1996; Martinson *et al.* 2009; Mueter *et al.* 2005), whereas the same conditions have been associated with poor survival of Fraser River sockeye salmon migrating along the coast of British Columbia (Hinch *et al.* 1995; Hsieh *et al.* 1991; Mueter *et al.* 2005). The analysis of an extensive dataset including 120 stocks from Washington, British Columbia and Alaska provided further evidence for such opposite effects of coastal SST on the early marine survival of southern and northern stocks of sockeye salmon (Mueter *et al.* 2002). Because coastal SST experienced by southern and northern stocks are within the tolerance range for sockeye salmon, it has been suggested that temperature is actually a surrogate for regional mechanisms affecting early marine survival (Hinch *et al.* 1995; Mueter *et al.* 2002).

In the case of the British Columbia coast, warm SSTs are associated with reduced upwelling and hence low food availability (i.e. zooplankton) for young sockeye salmon (Pearcy 1992). In addition, the peak timing of the copepod *Neocalanus plumchrus*, the main zooplankter in the Strait of Georgia, has advanced up to 30 days in the past decades and the peak duration has shortened in response to warming (Batten & Mackas 2009; Bornhold 2000; Mackas *et al.* 1998; Richardson 2008). The observed advance in timing of the Fraser River spring freshet may also be contributing to an earlier peak in zooplankton density in the Strait of Georgia (Foreman *et al.* 2001; Yin *et al.* 1997a,b). Such changes in food availability as well as high metabolic rates incurred by warm waters are consistent with the observation that early marine growth of Fraser River sockeye salmon is reduced when coastal SST is warm (Reichardt 2005). Such reduced growth would make juveniles more vulnerable to predation mortality (Hargreaves & LeBrasseur 1985). Compounding matters is the observation that the abundance of non-resident predatory fish in coastal waters off British Columbia increases in warm years and the possibility that resident predatory fish increase food consumption so as to offset high metabolic rates incurred by warm waters (Hinch *et al.* 1995; Ware & McFarlane 1995).

1.4.4. Immatures in the ocean

The relationship between temperature and survival of immature sockeye salmon in the open ocean has been explored in only a few studies. Survival of Alaskan sockeye salmon was found to be positively correlated to SST during all the years of ocean residence (Martinson *et al.* 2009), while that of Fraser River sockeye salmon has been found to be negatively correlated to SST in their last few months in the open-ocean (Hsieh *et al.* 1991).

1.4.5. Returning adults

The relationship between river temperature and survival during the spawning migration has been extensively studied. Migration mortality of adults (termed *en route* mortality) becomes elevated at temperatures > 18 °C (Crossin *et al.* 2008; Farrell *et al.* 2008; Keefer *et al.* 2008; Macdonald *et al.* 2000a,b, 2010; Martins *et al.* 2011; Naughton *et al.* 2005). High levels of *en route* mortality can be caused by a combination of temperature-mediated factors. First, warm river temperatures increase energy use in sockeye salmon and migration failure can occur if energy reserves fall below a critical threshold (Rand *et al.* 2006). Second, exposure to high water temperature increases the rate of development of pathogens in sockeye salmon (Crossin *et al.* 2008; Gilhousen 1990), causing physiological stress, decreased swimming performance and disease (Bradford *et al.* 2010; Wagner *et al.* 2005). Finally, warm temperature reduces aerobic scope in sockeye salmon, limiting the fish's ability to allocate energy to essential tissues during the migration (Lee *et al.* 2003). Under extreme water temperatures, aerobic scope is reduced to such an extent that continued migration can lead to anaerobic activity, exhaustion and death by lactic acidosis or cardiac collapse (Farrell *et al.* 2008; Farrell 2009).

Recent physiological studies on adult migrants have suggested that Fraser River sockeye salmon stocks can differ in their thermal tolerance, reflecting local adaptation to temperatures experienced during historic migrations (Farrell et al. 2008; Farrell 2009; Lee et al. 2003). The relationship between water temperature and spawning migration mortality can vary substantially among stocks (Macdonald et al. 2010; Martins et al. 2011). Furthermore, recent studies have revealed that female Fraser River sockeye salmon mortality is higher than that of males under warm temperatures (Crossin et al. 2008; K. Jeffries, Department of Forest Sciences, University of British Columbia, Ph.D. thesis in progress; E. Martins, Department of Forest Sciences, University of British Columbia, unpub. data). This may occur because females which are near fully mature have higher baseline stress levels than males at a similar level of maturation (Hruska et al. 2010a; Roscoe et al. in press), so additional stressors experienced at that time could have greater detrimental effects to females. Survival during the spawning migration can substantially improve when sockeye salmon are able to behaviourally thermoregulate by making use of thermal refuges, such as deep portions of lakes and cold tributaries (Mathes et al. 2010). However, thermal refuges in the lower Fraser River are virtually absent, which limits the ability of sockeye salmon from most stocks to behaviourally thermoregulate during the early portions of their up-river migration (Donaldson et al. 2009).

Survival of adult migrating sockeye salmon in the Columbia River system was found to be higher under high flow conditions, a finding that likely reflects the inverse relationship between temperature and discharge (Naughton *et al.* 2005; Keefer *et al.* 2008). In the Fraser River, high

flows during the spawning migration have been implicated in elevated levels of *en route* mortality in sockeye salmon (Macdonald *et al.* 2000a, 2010) particularly in stocks that enter the Fraser River late in the spring (i.e. Early Stuart) and early in the summer (i.e. Early Summer stocks), when flows are the highest because of the spring freshet (Macdonald *et al.* 2010). Bioenergetic modelling by Rand *et al.* (2006) revealed that energy exhaustion during high flows may be an important factor leading to migration mortality of Early Stuart sockeye salmon in some years. There have been very few years over the past decade when Fraser River flows have been extreme enough to cause high levels of *en route* mortality (see Section 2 of this report).

1.4.6. Spawners

Temperature and flow encountered during the spawning migration can impact survival of fish that successfully arrive on the spawning grounds but fail to spawn (termed pre-spawn mortality). High levels of disease and pre-spawn mortality have been reported for some Fraser River sockeye salmon stocks that encountered warm temperatures during migration and on the spawning grounds (Gilhousen 1990; Macdonald *et al.* 2000b). It was also observed that females from an Alaskan stock had higher levels of egg retention when water temperatures were warm, indicating that they died before having fully spawned (Quinn *et al.* 2007). There is also some evidence that the effects of adverse river conditions encountered by migrants may be passed on to their offspring, resulting in low egg survival (Macdonald *et al.* 2000b). Patterson (2004) showed that high levels of pre-spawn mortality in Early Stuart sockeye salmon, presumably as a result of difficult migratory conditions (i.e. high flows), was related to low survival from egg to fry.

1.5. Recent climate change and sockeye salmon habitats

1.5.1. Recent trends in the freshwater environment

There is clear evidence that air temperature and precipitation have increased in the Pacific Northwest over the last century. Average estimates for the region have revealed an increase of 0.08 °C per decade in air temperature. In addition, precipitation has increased by 14% per century and more of it now occurs as rainfall (Mote *et al.* 2003, 2005). In British Columbia, minimum temperatures have shown the highest rate of increase at 0.17 °C per decade and precipitation has increased by 22% per century. However, increases in precipitation over the province have been highly variable – little or no change has been detected in the areas around the southern coast while high increases in precipitation have occurred in the interior. The highest increases in temperature and precipitation have been observed during the winter and spring (Pike *et al.* 2008; Rodenhuis *et al.* 2009).

Such recent changes in climate have already affected the hydrology of snowmelt dominated river systems (Stewart *et al.* 2005), where most sockeye salmon populations spawn (Burgner 1991). Warm winters and springs since the 1950s have caused earlier snowmelt and hence an advance in the spring freshet by 1-4 weeks across a large number of rivers in the Pacific Northwest (Rodenhuis *et al.* 2009; Stewart *et al.* 2004, 2005). In the Fraser River, the date for ½ and ½ of the year cumulative flow has been occurring progressively earlier at the rate of 1.1 and 0.9 days per decade, respectively, since the 1950s (Foreman *et al.* 2001). Despite the shift towards an earlier onset of the spring freshet, there have been no significant changes in total summer flows of the Fraser River (Patterson *et al.* 2007a).

In addition to changes in flow patterns, there has been a noticeable increase in water temperatures of rivers and streams (Foreman *et al.* 2001; Henderson *et al.* 1992; Patterson *et al.* 2007a; Quinn & Adams 1996). In the Fraser River, water temperatures in the summer, when adult sockeye salmon migrate upstream, have increased at a rate of 0.33 °C per decade since the 1950s and the river is now ~ 2.0 °C and 0.7 °C warmer than 60 and 20 years ago, respectively (Patterson *et al.* 2007a). In fact, water temperatures in 13 of the last 20 summers have been the warmest on record (M. Hague, Fisheries and Oceans Canada, pers. comm.). The highest rates of increase in water temperature during the summer have been detected in June and July and minimum temperatures have increased at a faster rate than average and maximum temperatures (Patterson *et al.* 2007a). In the Adams River, where a major Fraser River sockeye salmon stock spawns, temperatures during the time of spawning increased by 1.5 °C from 1950 to 1989 (Henderson *et al.* 1992). Although there is no long-term record of water temperatures in the winter and spring, when sockeye salmon eggs are incubated, the Fraser River watershed has likely warmed at the highest rates during these seasons as that is when the climate of the province has warmed the most (Rodenhuis *et al.* 2009).

Warming trends have also been associated with changes in sockeye salmon nursery lakes (Arhonditsis *et al.* 2004; Rodenhuis *et al.* 2009; Schindler *et al.* 2005; Winder & Schindler 2004a,b). For example, since the 1960s, Lake Washington has warmed by up to 1.5°C, particularly in the epilimnion (Arhonditsis *et al.* 2004; Winder & Schindler 2004a,b). As a result of warming, the timing of spring ice break-up and thermal stratification has occurred up to 40 and 27 days earlier, respectively (Rodenhuis *et al.* 2009; Schindler *et al.* 2005; Winder & Schindler 2004a,b).

1.5.2. Recent trends in the marine environment

Long-term trends in the North Pacific Ocean are difficult to detect because its conditions are strongly related to both inter-annual and inter-decadal modes of climate variability (Gedalof & Smith 2001; IPCC 2007). Inter-annual variability is related to El Niño Southern Oscillation (ENSO) events, which occur every 2-7 years and persist for up to 1.5 years (Mysack 1986). ENSO events are characterized by coupled variations in SST and sea level pressure (SLP) in the tropical Pacific Ocean – anomalous warm SST and high SLP characterize El Niño events, whereas opposite conditions characterize La Niña events (Mysack 1986). Typically, El Niño (La Niña) events lead to warm (cool) SST in the waters of the west coast of North America (Mysack et al. 1986). Since the 1970s, El Niño (La Niña) events have become more (less) frequent (Beamish et al. 1999; Trenberth & Hoar 1996).

Inter-decadal variability in the climate of the North Pacific Ocean has been described by several inter-related atmospheric and oceanic indices (Batten *et al.* 2010); the most commonly used being the Pacific Decadal Oscillation (PDO). PDO events typically persist for 20-30 years and are characterized by variations in SST over the North Pacific Ocean (Mantua *et al.* 1997; Mantua & Hare 2002). Cool and warm SST over the western and eastern North Pacific Ocean, respectively, characterize the warm or positive phase of the PDO, whereas opposite SST patterns characterize the cool or negative phase. The positive (negative) phase of the PDO is also associated with a strengthening (weakening) of the Aleutian Low – a semi-permanent low pressure system located over the North Pacific Ocean during the winter (Rohli & Vega 2008). During the past century, the PDO was predominantly in the positive phase from 1925-1946 and from 1977-1997, and in the negative phase from 1900-1924 and from 1947-1976 (Mantua & Hare 2002). Since 1998, the PDO has exhibited more frequent alternations between the positive and negative phases, which have lasted from 3-4 years.

SST in both the Strait of Georgia, where Fraser River sockeye salmon smolts first encounter the marine environment, and the Gulf of Alaska, where immature sockeye salmon from the Fraser River spend two years feeding, has increased at about 0.25°C per decade since the 1950s and is now 1.5 and 0.5 °C warmer than 60 and 20 years ago, respectively (Chittenden *et al.* 2009; Cox & Hinch 1997). However, such observed warming trend in the North Pacific Ocean has been attributed mostly to the 1977-1997 positive phase of the PDO (IPCC 2007). In contrast to trends in warming, the salinity and pH of the North Pacific Ocean have been decreasing at rates of 0.005 psu per decade and 0.02 pH per decade, respectively (Batten *et al.* 2010; IPCC 2007).

1.6. Qualitative assessment of the effects of recent climate change on Fraser River sockeye salmon survival

1.6.1. Criteria used in the qualitative assessment

Based on our synthesis of the relationship between climate-related variables and sockeye salmon survival, we made a qualitative assessment of the likelihood that life stage specific survival has been undergoing a trend in the past 20 years due to the recent trends in climate, particularly in temperature, described above. For each life stage, we rated potential climate-driven trends in survival as <u>very likely</u>, <u>likely</u>, <u>possible</u> and <u>unlikely</u> to have occurred. In general, these ratings were defined so that more weight of evidence was given to findings obtained from field studies and were defined as follows:

i. very likely

a. when a recent (i.e. extending at least into part of the past 20 years) trend in survival presumably driven by a climate-related variable (i.e. assessed through statistical analyses) has been reported for Fraser River sockeye salmon stocks;

or, in the absence of published trends,

b. when significant relationships (e.g. survival by temperature) were found in ≥ 4 field studies on Fraser River sockeye salmon and the relationships were corroborated by laboratory studies.

ii. *likely*

a. when significant relationships were found in ≥ 4 field studies on Fraser River sockeye salmon but the relationship has not been corroborated by laboratory studies.

iii. possible

a. when significant relationships were found in 1-3 field studies on Fraser River sockeye salmon and the relationship has or has not been corroborated by laboratory studies.

or in the absence of field studies on Fraser River sockeye salmon,

b. when significant relationships were found in laboratory studies on Fraser River sockeye salmon.

iv. unlikely

a. when no significant relationships were found in either laboratory or field studies on Fraser River sockeye salmon.

The threshold of four studies was defined based on the number of field studies reporting on significant survival relationships for the life stages (i.e. smolt/postsmolt and returning adults) wherein it is generally acknowledged that short- and long-term changes in climate, particularly temperature, affect sockeye salmon survival. For these life stages there were at least four field studies providing evidence for an association between temperature and survival of Fraser River sockeye salmon. Our assessment for recent trends in survival is summarized in Table 1.1 along with the information obtained from the publications reporting on survival.

1.6.2. Likelihood of trends in survival of Fraser River sockeye salmon due to climate change over the past 20 years

Assuming that average stream temperatures through winter and spring have not become warmer than 8 °C throughout the Fraser River watershed, survival of sockeye salmon eggs has *possibly* increased, though that of alevins has *unlikely* changed. However, climate warming may not have affected the early life stages of all Fraser River stocks equally – the survival of interior-spawning stocks may actually have been negatively affected because their eggs and alevins seem better adapted to colder temperatures (Beacham & Murray 1989).

A confounding factor in our assessment of recent trends in survival of eggs is the observation that precipitation during the incubation season has increased across British Columbia (Rodenhuis et al. 2009). Higher precipitation may have led to an increase in the mortality of eggs due to scouring in recent decades if more of it is now falling as rain, as observed in other regions of the Pacific Northwest (Mote et al. 2003, 2005). However, interior-spawning stocks would have been more affected because changes in precipitation have been greater in the interior (Rodenhuis et al. 2009). A compounding factor is the observation that returning adult Fraser River sockeye salmon are now smaller than in the past (Cox & Hinch 1997; Hinch et al. 1995). Smaller females bury their eggs at shallower depths than large fish, which greatly increases the chances of scouring (Montgomery et al. 1996; Steen & Quinn 1999). On the other hand, the potential for increased area for spawning brought with higher precipitation suggest that mortality of eggs due to scouring may have been offset by lower levels of mortality due to egg superimposition. For this

reason, we based our assessment of recent trends in egg survival only on the effects of warming waters (Table 1.1).

If water temperatures in rearing lakes of Fraser River sockeye salmon have paralleled warming trends of the river in the summer (Patterson *et al.* 2007a), then fry now experience temperatures approximately 1°C warmer than 20 years ago and their survival has *possibly* decreased. However, warming is not homogenous throughout the lake volume – the highest rates of warming have been observed at lake surface (Arhonditsis *et al.* 2004). As fry are able to move to cooler depths of lakes to avoid otherwise lethal temperatures at the surface (Brett 1971), we believe that warmer lake waters may have not directly affected survival of fry. However, warmer waters may have enhanced fry mortality indirectly through increased predation rates (Petersen & Kitchell 2001; Sylvester 1972).

The recent warming of the waters in the Strait of Georgia (Chittenden *et al.* 2009), and possibly along the British Columbia coast, as well as the negative relationship between early marine survival and coastal SST (Hinch *et al.* 1995; Hsieh *et al.* 1991; Mueter *et al.* 2002, 2005), suggest that survival of juvenile Fraser River sockeye salmon during their coastal migration has *likely* decreased in the past two decades. Similarly, increased temperatures in the Gulf of Alaska over the past two decades have *possibly* resulted in lower survival of Fraser River sockeye salmon during open-ocean residence.

The recent warming of the Fraser River and the strong body of evidence from field and laboratory studies showing the adverse effects of warm temperature during the spawning migration suggest that survival of adult migrants has <u>very likely</u> decreased over the past 20 years. This effect however is clearly stock-specific. Warming of the Fraser River has not affected all stocks to the same extent – stocks that have historically migrated during mid-summer seem better able to cope with high temperatures (Farrell 2009; Martins *et al.* 2011) and have not undergone the same decline in abundance as stocks that migrate very early (e.g. Early Stuart) or very late (Late-runs; see Section 2 of this report). Although the advance of the spring freshet in the Fraser River may have led to better migration conditions for the Early Stuart and Early Summer stocks, the warming of the river may have offset any benefits in migration survival incurred by lower flows (Rand *et al.* 2006). The warmer river conditions now experienced by Fraser River sockeye salmon also has <u>possibly</u> led to increased levels of pre-spawn mortality, though this response is highly variable among stocks and years (Gilhousen 1990; Macdonald *et al.* 2000b) – some Late-run stocks may recently be showing a general increase in pre-spawn mortality (see Section 2 of this report).

1.7. Future impacts and potential for adaptation to climate change

1.7.1. Effects of future climate change on Fraser River sockeye salmon

Recently, studies on the effect of future climate change have been conducted on the spawning migration of Fraser River sockeye salmon (Hague *et al.* 2011; Martins *et al.* 2011; Rand *et al.* 2006). Based on climate models predicting that summer water temperature in the Fraser River may warm by ~ 2.0 °C over the next 100 years (Ferrari *et al.* 2007; Morrison *et al.* 2002), Martins *et al.* (2011) demonstrated that spawning migration survival may decrease 9-16% (depending on the stock) by the end of the century. However, the predictions presented by those authors may be conservative as the model used to predict survival was not parameterized with biologically critical temperatures (i.e. > 20 °C) that will occur more frequently in the future. In fact, it has been predicted that the number of days per year exceeding salmonid critical temperatures may triple in the Fraser River over the next 100 years and more than 90% of a stock may be forced to migrate under suboptimal temperatures for physiological performance (Hague *et al.* 2011). Survival during the spawning migration may also decrease due to energy depletion incurred by warm temperatures if the declining trend in gross somatic energy of Fraser River sockeye salmon persists into the future (Rand *et al.* 2006).

A perspective of how future climate change may affect Fraser River sockeye salmon across life stages has been recently presented by Healey (in press). Based on projections of future climate-driven changes in the habitats used by Fraser River sockeye salmon, the author used his expert knowledge to argue that the cumulative impacts of climate change across life stages will be much greater than the impacts on individual stages. He concludes that the 'impacts will also carry forward to the next generation, potentially leading to a downward spiral of productive capacity' and predicts a bleak future for Fraser River sockeye salmon, in which most of its habitats may become inhospitable.

1.7.2. Adaptation of Pacific salmon to climate change

Although there is some potential for tolerance to warm temperatures to evolve in Pacific salmon, further evolutionary change may already be restricted in populations that have historically experienced high temperatures (Carlson & Seamons 2008; Crozier *et al.* 2008; see also Bradshaw & Holzapfel 2008). Examples of populations wherein the evolution of heat tolerance may already be limited include those that spawn and rear in freshwater systems located at the southern end of the species distribution (e.g. Fraser River sockeye salmon), and on a more regional scale those that have historically started their up-river migration during mid-summer (e.g. Summer-run stocks of Fraser River sockeye salmon) or incubate their eggs in coastal, relatively warmer areas (e.g. Fraser River sockeye salmon from Weaver Creek). Crozier *et al.*

(2008) suggested that phenological (i.e. timing of events) changes are likely to be one of the major responses of Pacific salmon to climate change. Changes in some phenological traits (e.g. fry emergence and smolt migration timing) may largely result from non-genetic changes (i.e. phenotypic plasticity), whereas change in other traits that have high heritability (e.g. spawning migration timing) may result from natural selection (Carlson & Seamons 2008; Crozier *et al.* 2008).

In Pacific salmon, one of the best examples of phenological changes presumably arising through evolution in response to warming comes from the Columbia River, where sockeye salmon have started their spawning migration 6-11 days earlier than in the 1940s (Quinn & Adams 1996; Quinn et al. 1997). However, the rates of river warming have outpaced those of migration timing change and Columbia River sockeye salmon now experience temperatures on average 2.5 °C warmer than in the past (Quinn & Adams 1996). Similarly, recent individual-based modeling has revealed that future climate warming in the Fraser River will likely select for earlier up-river migration timing in Early Stuart sockeye salmon and that such an evolutionary response could improve the chances for long-term persistence of that particular stock (T. Reed, Netherlands Institute of Ecology, in review). In contrast, there are several other examples of Pacific salmon species and stocks that have been shifting the onset of their spawning migration towards warmer periods (Cooke et al. 2004a; Taylor 2008). This has occurred over the past 16 years in Fraser River Late-run sockeye salmon stocks and has led to high levels of en route and pre-spawn mortality (Hinch 2009; see Section 2 of this report). These observations exemplify the considerable uncertainty in predicting how organisms with complex life histories such as Pacific salmon will cope with or adapt to changes in climate (Crozier et al. 2008). Predicting the responses of Fraser River sockeye salmon, and Pacific salmon more generally, to future climate change will require a much better understanding than we currently have of how evolutionary and ecological mechanisms interact in shaping such responses.

1.7.3. Adaptation strategies in the context of climate change

The potential adverse effect of climate change on Fraser River sockeye salmon abundance and productivity could be lessened if certain adaptation strategies aimed at reducing its ecological, economic and social impacts are implemented (Battin *et al.* 2007; Jacob *et al.* 2010; McDaniels *et al.* 2010). Nelitz *et al.* (2007) presented an excellent and detailed account of possible adaptation strategies directed at reducing the impact of future climate change effects on Pacific salmon. These authors categorized adaptation strategies broadly into 'hard infrastructure' and 'soft infrastructure' strategies. 'Hard infrastructure' denotes strategies based on engineering or technological solutions to reduce the impacts of climate change effects on sockeye salmon. Examples include: develop stream temperature and flow management systems (e.g. release of

cold water from storage facilities); implement systems for heat recovery on effluents of large industrial facilities; restore riparian vegetation to cool temperatures along narrow spawning streams; and allow streams to flow across a larger area of their historical floodplain to reduce flows during incubation (Battin *et al.* 2007; McDaniels *et al.* 2010; Nelitz *et al.* 2007). 'Soft infrastructure' denotes strategies based on changes in laws, policy and management of aquatic resources. Examples include: identify and enact groundwater and surface water thermal protection zones on Fraser River habitats utilized by sockeye salmon; regulate the extraction of groundwater and consider the effects of such practices on salmon in groundwater management plans; monitor and stop the spread of exotic species (e.g. smallmouth [*Micropterus dolomieu*] and largemouth bass [*M. salmoides*]) that may prey on fry and smolts at higher rates under climate warming; improve current stock abundance and habitat status monitoring programs; adjust fisheries management practices so as to ensure the achievement of escapement goals and thereby the conservation of genetic diversity across stocks (e.g. shift the focus from dominant to smaller stocks when adjusting escapement targets) (Douglas 2006; McDaniels *et al.* 2010; Nelitz *et al.* 2007).

2. Adult mortality during river migration and on spawning grounds

2.1. Introduction

Up-river adult spawning migrations of Fraser River sockeye salmon (Oncorhynchus nerka) commence in July with the Early Stuart run, followed by stocks within the Early summer run from mid July to mid August, Summer runs migrate into the Fraser River from the end of July to early September, and Late Summer runs (also called Late-runs) migrate in from mid September to end of November (Woodey 1987) though Late-run entry timing has recently changed (Cooke et al. 2004a). Late-run and Summer-run stocks reach the Fraser River from the ocean at the same time, but Late-run stocks historically remained in a holding or milling behaviour in the estuary and southern Strait of Georgia for several weeks before initiating up-river migration. Migration initiation times in large rivers are related to spawning ground location, migration distance (Gilhousen 1990) and river temperature (Hodgson et al. 2006; Quinn & Adams 1996). Fraser River sockeye salmon populations that travel some of the longest distances tend to enter the river early in summer, just as the spring freshet is beginning to subside but before water temperatures in the Fraser River mainstem reach the thermal peak. Their migrations are likely timed to miss the highest flow conditions and yet provide sufficient incubation time for fertilized eggs to hatch in spawning streams before they freeze in winter (Macdonald 1994). Conversely, sockeye salmon populations that migrate only short distances to coastal spawning grounds tend to do so in mid to late summer and fall, in association with lower river flows and often cooler temperatures en route and at the spawning bed. Some populations that migrate long distances but do so during the thermal peak are physiologically well adapted to cope with relatively warm temperatures (Farrell et al. 2008; Lee et al. 2003; E. Eliason, Department of Zoology, University of British Columbia, Ph.D. thesis in progress). Pacific salmon are semelparous meaning they have only one opportunity to spawn thus any in-river issue that prevents a fish from reaching spawning grounds, or from breeding once arriving at spawning grounds, results in that individual having zero lifetime fitness.

The primary purposes of this section are to: review the major environmental factors responsible for adult sockeye salmon mortality during Fraser River migrations (termed 'en route mortality') and for premature mortality on spawning grounds (termed 'pre-spawn mortality'), review the early migration – high mortality Late-run sockeye salmon phenomenon, describe interannual and within-year among stock patterns in adult mortality, and provide a mechanistic understanding for several of these patterns.

2.2. Factors affecting survival of adult river migrating sockeye salmon: a brief review

The two primary environmental factors that influence *en route* mortality in Fraser River sockeye salmon are river discharge and temperature (Hinch *et al.* 2006). High levels of either can deleteriously affect fish physiological systems, directly or indirectly, and have acute and/or chronic consequences on migrants. Of particular concern is energy use, which both factors can alter (Rand & Hinch 1998). Adult Pacific salmon have limited energy to complete their up-river migration (Brett 1995). Adults have ceased eating during their coastal migration and must complete the river migration, gonad development and successfully spawn on reserve energy. In Fraser River sockeye salmon, feeding is believed to cease ~ 400 km from the Fraser River mouth (Hinch *et al.* 2006).

Patterns of swimming speeds largely dictate how energy gets used during the migration. There are several lines of evidence indicating that behaviours and physiological systems that can facilitate energy conservation are critically important for successful migration. First, sockeye salmon populations with difficult river migrations (e.g. Early Stuart and Early summer-runs) depart the ocean with high reserve energy and morphologies that favour energy conservation (i.e. fusiform – with short and round bodies) relative to populations with less difficult migrations (e.g. Late-runs; Crossin et al. 2004a). Second, body constituent analyses on two species (sockeye salmon and pink salmon, O. gorbusha) sampled in different years and from disparate regions have revealed that in general, spawning ground salmon die when energy levels decline to ~ 4 MJ kg⁻¹ (Crossin et al. 2003; Hendry & Berg 1999). This suggests an energetic threshold is responsible in part for mortality in semelparous adult salmonids. Third, high energy use is associated with mortality during river migrations. In the Fraser River when discharge is unusually high, migration rates of some stocks are slowed, extending migration duration by several weeks. This can deplete energy reserves to levels below critical thresholds (Rand & Hinch 1998). In years of extremely high discharge, hundreds of thousands of Fraser River sockeye salmon have died during their migration and energy exhaustion is thought to be partly responsible (Macdonald & Williams 1998).

Physiological (e.g. electromyogram) telemetry has shown that elevated flows force up-river migrating Fraser salmon to swim faster and for longer periods, accelerating energy use (Hinch & Rand 1998; Hinch *et al.* 2002). The prevalence of energetically costly swimming behaviours (at known river constriction areas, e.g. Hells Gate) has been directly linked to migration mortality (Hinch & Bratty 2000). High discharge has generally only been associated with increased mortality of populations that enter the Fraser River late in the spring (i.e. Early Stuart) and early in the summer (i.e. Early summer stocks), when flows are naturally the highest because of the

spring freshet (Macdonald *et al.* 2000a, 2010). Indeed, bioenergetic modelling revealed that exhaustion of energy reserves can be an important factor leading to migration mortality of Early Stuart sockeye salmon in some years (Rand *et al.* 2006).

Temperature is the most important environmental factor governing fish because of its underlying effect on physiological, ecological, and behavioural aspects of life history (Fry 1971). *En route* mortality could occur as a result of several high-temperature-mediated factors (Hodgson & Quinn 2002; Quinn *et al.* 1997), such as the collapse of aerobic scope (Farrell 2002; Farrell *et al.* 2008), which refers to the reduction of oxygen available for activities between basal and maximal metabolic rates (Fry 1971). Other temperature-mediated factors include poor recovery from stress and strenuous exercise (Macdonald *et al.* 2000b), and increased susceptibility to disease and parasites (Bradford *et al.* 2010; Crossin *et al.* 2008; Gilhousen 1990; Wagner *et al.* 2005). High river temperatures can also deplete energy reserves, however, unlike the manner in which high discharge influences energy use, they do so by accelerating routine metabolism – which is only a small component of the overall energy budget relative to swimming (i.e. active) metabolism and other energy costs (e.g. developing gonads; Rand & Hinch 1998). Therefore it is unlikely that high temperatures will cause *en route* mortality solely by depleting energy reserves. However, energy depletion in combination with other thermal-mediated processes could play a significant role in *en route* mortality.

Some of the best-documented effects of the mechanisms of how high temperatures influence salmon migrations come from laboratory and field studies on Fraser River sockeye salmon (reviewed in Hinch *et al.* 2006). Biopsy telemetry (i.e., the coupling of physiological sampling with positional telemetry; approach reviewed in Cooke *et al.* [2008]) has revealed that Fraser River sockeye salmon, which encounter higher than normal temperatures and perish during migrations, are characterized as having impaired ionoregulatory systems, advanced senescence, and symptoms of physiological stress (Cooke *et al.* 2006a,b; Young *et al.* 2006). Infection and disease have also been implicated as a major cause of migration mortality. For example, the bacterium *Flexibacter* spp. is more virulent at high temperature and can cause severe gill damage in migrating Fraser River sockeye salmon (Gilhousen 1990). Also, a kidney parasite (*Parvicapsula minibicornis*) develops faster at warm temperature and its development in Fraser River sockeye salmon is associated with reduced laboratory swimming performance (Wagner *et al.* 2005) and migration mortality (Crossin *et al.* 2008) when degree-day accumulation is ~ 500 °C.

Most stocks of Pacific salmon now encounter warmer rivers during their spawning migration than in any time since records have been kept. In the Fraser River, water temperatures in the summer, when adult sockeye salmon migrate upstream, have increased at a rate of 0.33 °C per decade since the 1950s and the river is now ~ 2.0 °C warmer than 60 years ago (Patterson et al. 2007a). Water temperatures in 13 of the last 20 summers have been the warmest on record (M. Hague, Fisheries and Oceans Canada, pers. comm.). The highest rates of increase in water temperature during the summer have been detected in June and July and minimum temperatures have increased at a faster rate than average and maximum temperatures (Patterson et al. 2007a). Similarly, sockeye salmon in the Columbia basin now migrate through waters that are ~ 2.5 °C above historical (Quinn & Adams 1996). Considering the negative effects of encountering high river temperatures, the timing of starting up-river migrations by adult salmon should be strongly influenced by the freshwater thermal environment. Indeed, many salmon populations may be attempting to avoid peak migration temperatures, which are now much warmer than ever before. This may be an explanation for why Columbia River sockeye salmon (Quinn & Adams 1996; Quinn et al. 1997) and east coast Atlantic salmon (Salmo salar) (Juanes et al. 2004) are entering freshwater earlier than historically noted and why Columbia River summer steelhead (O. mykiss) are entering later (Robards & Quinn 2002). The seeking of cool-water refugia after initiating upriver spawning migrations is another form of behavioural thermoregulation exhibited by Pacific salmon (Hyatt et al. 2003). Sockeye salmon, Chinook salmon (O. tshawytscha), and summer steelhead runs in the Columbia River system appear to be utilizing cold-water tributaries en route to spawning areas, thus slowing or temporarily stopping up-river migration (Goniea et al. 2006; High et al. 2006; Hodgson & Quinn 2002). But in some cases, Chinook entering the Columbia early migrate faster, presumably as an alternative means to minimize exposure to high temperatures (Chapman et al. 1995). Populations of sockeye salmon, including those in the Fraser River, that normally migrate through lakes *en route* to spawning streams do so through the hypolimnion presumably to take advantage of colder water (Newell & Quinn 2005; Roscoe et al. 2010).

2.3. The Late-run Fraser River sockeye salmon issue

2.3.1. Background

Late-run stocks which include Portage Creek, Lower Adams and Lower Shuswap complex, Weaver Creek, Harrison River and Cultus Lake (Figure 2.1) are unique among Fraser River sockeye salmon populations in that they historically held in the Strait of Georgia for a period of three to six weeks prior to migrating upstream to spawn. Beginning in 1995 and continuing to present this holding period shortened substantially for all Late-run populations. The decrease in holding has resulted in much earlier than normal upstream migration. In some years, like 2000 and 2001, fish entered the Fraser River four to six weeks earlier than normal. The abrupt shift in

migration behavior has resulted in almost all Late-run fish since 1995 entering the river prior to the historical median upstream date (Lapointe 2009). It has been speculated that the holding behavior in the Strait of Georgia may have evolved as a mechanism for Late-run fish to avoid high summer temperatures in the Fraser River mainstem and spawning areas (Hinch & Gardner 2009). Thus, segments of all Late-run populations now experience temperatures well above historical norms. Associated with the reduction in estuarine holding has been an increase in both en route and pre-spawn mortality (details below). Temporal patterns in mortality have been documented through telemetry and tagging programs in a number of years (e.g. Cooke et al. 2006b; English et al. 2005a,b; English & Robichaud 2009; Mathes et al. 2010; Patterson et al. 2009a). These studies have demonstrated that the earlier migrants each year suffer the highest en route and pre-spawn mortality. In years of the most extremely early entry, total freshwater mortality has exceeded 90% (Figure 2.2). Other salmon species, for which estuarine behaviour is not well understood, are also migrating into the Fraser River earlier than usual including pink (whose change to earlier migration occurred coincident with the change in sockeye salmon), chum and white-fleshed Chinook salmon (Lapointe 2009). En route mortality for these runs is not routinely assessed.

2.3.2. Emergence of research partnerships

From the start, this unprecedented phenomenon was a scientific mystery and presented a huge challenge to the management of the salmon resource. In particular, there was little known of what the 'normal' or baseline physiological conditions were for adult sockeye salmon prior to the early migration phenomenon occurring, nor what the baseline conditions were for adult sockeye salmon from most of the other non-Late-run stocks. In February 2001, the Pacific Salmon Commission (PSC) convened a workshop of some 20 experts with backgrounds in oceanography, salmon migration biology and physiology, disease/contaminants, and marine predators, which created a priority ranked list of approximately 16 issues that could be explored as possible hypotheses explaining the early migration phenomenon (summarized in Hinch & Gardner 2009). Because the high in-river mortality was believed to be the result of the changes in migration behaviour, researchers were asked to focus on hypotheses that might explain why Late-run sockeye salmon were migrating upstream early. Following the workshop, the PSC allocated \$100,000 to fund seven pilot studies that investigated topics ranging from contaminants to broad scale oceanographic factors and physiology.

In summer 2001, Fisheries and Oceans Canada (DFO) also provided funds for some conventional tagging studies directed at Weaver and Portage creek sockeye salmon to document the temporal pattern of *en route* mortality and some research on the parasite, *Parvicapsula minibicornis*, which had been implicated as a causal agent in the mortality. PSC and DFO

allocated over \$1M to fund two large scale marine tagging programs coupled with radio telemetry in 2002 and 2003 that documented the pattern of river entry and mortality (English *et al.* 2005b). In 2002, a group of academics led by S. Hinch from the University of British Columbia (UBC), with financial and logistic support of the DFO's Fraser River Environmental Watch Program and the PSC, secured a large six-year Natural Sciences and Engineering Research Council of Canada Strategic Grant to explore several hypotheses involved with the early migration and high mortality phenomena. As part of that research endeavor, a summary paper was published on these phenomena (Cooke *et al.* 2004a) which included a description of the historical context and a re-worked list of research issues ranked in terms of the likelihood that specific hypotheses were involved with the early migration and high mortality phenomena.

The research partnerships grew in subsequent years, encouraged by considerable support through the Southern Endowment Fund of the PSC, which culminated in a large, interdisciplinary program in 2006 involving dozens of researchers from academic, government and private organizations. In June 2008, a conference was held at the UBC and attended by ~ 70 participants, from universities, private consulting companies, fisheries management organizations, non-governmental environmental organizations and First Nations, to explore the current knowledge of potential causes of the change in migration behaviour and of the high mortality. The presentations and discussions formed the basis of a proceedings document, published by the Pacific Fisheries Resource Conservation Council (Hinch & Gardner 2009), which is still the most authoritative compilation of research to date into the Late-run issue. Since the conference, some research has continued and several papers have been published in the peer-reviewed literature. Much of the adult Fraser River sockeye salmon mortality research that is summarized in this present section was conducted as part of efforts to gain knowledge on baseline physiological, behavioural, and survival patterns in all groups of sockeye salmon in order to better understand what was unique about early migrating Late-runs.

2.3.3. Causes of early migration

The focus of the present section is on mortality patterns associated with fish once they are inriver or on spawning grounds. However, we will briefly review what is known on the potential causes of early migration in Late-run sockeye salmon – we refer readers to the proceedings document (Hinch & Gardner 2009) referred to above for a more thorough summary. The causes of the shortening or complete elimination of the estuarine holding period are not well understood but a picture is emerging which illustrates complex links between physiology, environment and behaviour. Reproductive advancement is a key feature in coastal migration speed and in reduced estuarine holding (Cooke *et al.* 2006a,b, 2008; Crossin *et al.* 2009), and because the physiological changes that initiate reproductive maturation appear to occur prior to fish reaching

the coast during their homeward migration (Miller et al. 2009; Patterson & Hills 2009) the estuarine behavioural change may have its roots in the open ocean. Early entering fish are also physiologically stressed. Their gene array profiles reveal immune suppression and stress responses (Miller et al. 2009, 2011). The fact that 50% of the fish sampled at the Queen Charlotte Islands carried the same physiological signatures identified later in the migration at coastal sites and in the lower Fraser River suggests that segments of fish populations may become stressed and/or susceptible to diseases while in the high seas (Miller et al. 2009, 2011). This physiologically 'compromised' state appears to alter the osmoregulatory physiology of migrants making them osmotically similar to freshwater fish. The physiological processes regulating reproductive maturation and osmoregulation are tightly linked in migrating salmon (Cooperman et al. 2009, 2010) so it is possible that this compromised state is also responsible for the advanced maturation observed in early-migrating Late-runs. The cause of the stress, immune suppression and/or early maturation and whether these characteristics are driving fish to migrate upstream earlier than normal are unknown. Interannual variation in open-ocean wind speed correlates over the past two decades with interannual variation in river entry timing of some Late-run stocks (in particular the Adams/Shuswap stock – suggesting an open ocean environmental link; Thomson & Hourston [2011]). How this oceanographic variable, or others it affects or which affect it, alters the maturation process or disease state of a segment of all Laterun populations is not clear. Further, because genomic and plasma assay analyses have only been conducted in a few recent years there is no historic baseline for comparisons and hence only a limited means to argue that some physiological patterns are 'abnormal'.

Although the genesis of the early migration phenomenon seems to, in part, be in the open ocean, coastal processes appear to further influence migration timing. Specifically, there are several lines of evidence that coastal salinity and osmoregulatory preparedness play important roles (Cooperman et al. 2009, 2010; Crossin et al. 2009; Olsson et al. 2009; Thomson & Hourston 2011). The other coastal issue that may be important in terms of migration timing of Late-runs is the abundance of Summer-run Fraser River sockeye salmon. Correlations are evident between Late-run river entry timing and the proportion of Summer- to Late-runs in the Strait of Georgia (English et al. 2005a; English & Robichaud 2009). This 'Stay with the School' hypothesis suggests that relatively high abundances of Summer-runs encourages or entices, in some manner, Late-runs to follow them into the river. However, adopting a radically different behaviour that is seemingly non-adaptive (e.g. entering the Fraser River early and dying before spawning) would likely not occur without some physiological basis. In sum, early migrants are relatively more reproductively prepared, less osmotically prepared for marine holding, stressed, and immune suppressed. There have been several other hypotheses put forth to account for the early migration issue (e.g. change in coastal predator abundances, contaminants, and others; Cooke et al. 2004a), but there is little evidence at present to support any of these.

2.4. Patterns of en route mortality in Fraser River sockeye salmon

River entry timing and abundance of adult sockeye salmon has been quantitatively assessed since 1977 by the PSC just upstream of the Fraser River mouth near Mission BC using various forms of hydroacoustic methods linked with stock ID sampling which involved scale analyses and more recently, DNA analyses (Beacham et al. 2004). DFO and the PSC refer to the differences in estimates of stock-specific abundance obtained from the Mission site and those obtained from spawning grounds (after accounting for reported in-river harvest upstream of Mission) as 'escapement discrepancies'. Escapement discrepancies can also arise from un-reported catch and/or through estimation errors. The Fraser River Panel of the PSC uses escapement discrepancy information to estimate the percentages of each run that are not accounted for during the migration - termed 'en route loss', these values are an indirect assessment of, and have become synonymous with, 'en route mortality' (Macdonald et al. 2010). They have also used historical discrepancy relationships to develop models which predict magnitude of escapement discrepancies as functions of mean temperature and discharge during migration of each runtiming group past Hells Gate, a known difficult passage location. Model predictions are used preand in-season to predict numbers of additional fish (i.e., termed the 'management adjustment') that will be required to achieve spawning escapement targets based on expectations of en route mortality (Cummings et al. in press).

Absolute and relative estimates of *en route* loss from 1977 to 2008 are presented by run-timing group in Figures 2.3-2.6. Generally, *en route* loss begins to be reported in 1992 for Early Stuart, Early summer, and Summer-runs, but not until 1996 for Late-runs. Of particular note is that levels of *en route* loss (relative to total catch and spawning ground escapement) have been increasing with recent years having some of the relative highest levels. In several years, *en route* loss is the dominant component of the fate of the Early Stuart and Late-run timing groups, and, since 1996, *en route* loss of at least 30% has been observed for at least one run-timing group each year. In general, *en route* loss levels have been relatively high during the time period when Early Stuart sockeye salmon (Figure 2.3) and several Late-run stocks (e.g. Weaver, Portage, Cultus stocks; Lapointe 2009) were declining in overall abundance (Figures 2.3 and 2.6).

Time series of escapement discrepancies are used as a proxy to assess trends in, and forecast estimates of, *en route* mortality (Macdonald *et al.* 2010). However, these escapement discrepancies have only consistently been included in estimates of stock production since the early 1990s (D. Patterson, Fisheries and Oceans Canada, pers. comm.). Since that time, escapement discrepancies have been generally much larger in magnitude and mostly 'negative' in their directionality (indicating fewer fish got to spawning grounds than passed the Mission hydroacoustic facility) than in the earlier period (late 1970s to early 1990s). Certainly some

levels of en route mortality occurred in Fraser River sockeye salmon prior to 1992 (e.g. Macdonald et al. 2010), and even prior to the establishment of the Mission hydroacoustic facility in 1977 – though only very indirect means could be used for their assessment (e.g. fisheries, visual observations at Hells Gate). Historical accounts of en route mortality occurred in years when river discharge was inordinately high (during the 1950s and 1960s), and often just for the Early Stuart run which is most susceptible to exposure to extreme flows, usually in the Fraser River Canyon (Cooper & Henry 1962). Prior to 1996, there was little reported en route loss in the Late-run sockeye salmon production database (DFO/PSC unpublished data, though there were reported escapement discrepancies in the DFO/PSC management adjustment database; Macdonald et al. [2010]). Coincident with their change in river entry timing (the 'early migration phenomenon' described above), en route loss became a consistent component of the fate of Lateruns (Figure 2.6B). Figure 2.7 shows the scale of en route loss by major stock group from 1996 to 2008. Eight out of 11 stocks had more than half of these years when en route loss exceeded 50%. There is clearly an effect of run timing on this pattern. Specifically, the earlier runs (e.g. Early Stuart, Scotch, Seymour, Fennell, Gates and Nadina) and the later runs (Harrison, Portage and Weaver) have the most years with high en route loss. Equally interesting is the fact that Summer-runs (e.g. Quesnel and Chilko) have experienced few if any years with large en route loss.

Despite large en route loss estimates for many stocks in recent years, there is little direct physical evidence in the form of carcasses for high levels of mortality of Fraser River sockeye salmon. However, the observation of sockeye salmon carcasses should not be expected in years of high estimated *en route* losses, given the fish's specific gravity being greater than 1 (i.e. meaning that dead sockeye salmon will sink in freshwater) and poor water clarity in the Fraser River. Carcasses could potentially become visible after resurfacing due to gas build-up; however their non-observation in the Fraser River suggest that water currents may lodge them within submerged debris or that scavengers (e.g. white sturgeon [Acipenser transmontanus]) may damage their internal cavity, which would prevent the build-up of gas necessary for floating (Patterson et al. 2007b). There have been few direct experimental studies to examine the location of carcasses during salmon migrations. In 2004, a year of extremely high en route loss in all runtiming groups of Fraser River sockeye salmon, a tracking study was conducted in the Harrison River system on a large number of migrating adult Weaver Creek sockeye salmon using acoustic 'depth-sensing' transmitters (Mathes et al. 2010; Mathes 2009). Investigators found that fish which perished prior to reaching spawning grounds were located on the bottom of the Harrison River or Harrison Lake supporting the hypothesis that salmon which naturally perish during migrations generally sink.

2.5. Explaining trends in stock-specific *en rout*e mortality in Fraser River sockeye salmon

Mortality during the spawning migration is influenced by a combination of environmental factors. In a multivariate analysis Macdonald *et al.* (2010) found that trends in run-timing specific discrepancies (1977-2006) were a function of temperature, discharge and freshwater residency variables. Temperature and discharge variables were important for predicting discrepancies in early runs (Early Stuart and Early summer runs), temperature was most important for the Summer-runs, and freshwater residence was most important for Late-runs. In Late-runs, freshwater residency is an index of thermal exposure (e.g. accumulated degree days, Wagner *et al.* 2005); therefore, thermal variables play a large role in explaining discrepancies across all run-timing groups.

Temperatures experienced by migratory salmon in summer have increased in recent years corresponding to general decreases in river discharge (Patterson et al. 2007a; Quinn et al. 1997). Fraser River summer discharge and temperature are indeed inversely related, particularly during the migratory period for Early Stuart and Early summer-runs. Thus in years of high discharge, temperatures are relatively cool, and vice versa, though high levels of either variable could cause high levels of en route mortality (Macdonald et al. 2010). Because river discharge in most years since the early 1990s has not been exceedingly high, discharge alone is not believed to be the driving factor underlying recent year's trends in en route mortality, with the exception of a few years for the Early Stuart and Early summer-runs. Specifically, 1997 and 1999 were years when river discharge during a portion of the Early Stuart run was at record high levels exceeding 9,000 m³/sec, resulting in river conditions at Hells Gate which creates a barrier to migration (FREWP 2010; Macdonald 2000). Indeed, despite the presence of the fishways at Hells Gate, adult salmon sometimes cannot successfully pass (Hinch & Bratty 2000). For example, about one-half of the 1997 Early Stuart run (240,000 out of 500,000 fish) that entered the Fraser River did not reach spawning grounds, and many of these unsuccessful migrants reached but failed to pass Hell's Gate (Macdonald & Williams 1998). It is possible that en route loss in 1997 and 1999 of Early summer runs was also attributable to river discharge levels that were high enough to cause energy exhaustion and physiological stress.

Because of the 'parabolic' shape of the thermograph for the Fraser River (Figure 2.8), stocks in the Early Stuart run and Late-runs experience the coolest lower Fraser River temperatures (historical daily average, 1951-1990, ~ 12-16 °C) whereas stocks in the Early summer and Summer-runs experience the warmest temperatures (historical daily average, 1951-1990, ~ 15-17.5 °C). Stocks differ in their freshwater migratory distance and entry timing, and these factors directly affect stock-specific thermal migratory experience. Specifically, long distance migrating

stocks (e.g. Early Stuart) and early entering Late-runs accumulate relatively high levels of 'degree days' whereas stocks that migrate in early August (e.g. Summer-runs) encounter the peak Fraser River temperatures. There have been three broad changes to the thermal experience of Fraser River sockeye salmon adults over the past several years. The first is that the Fraser River has experienced ~ 2.0 °C warming in the summer compared to 60 years ago (Patterson et al. 2007a). The highest rates of increase in water temperature during the summer have been detected in June and July and average daily summer temperatures have warmed ~ 0.7 °C in the most recent 20 years (Figure 2.8; Patterson et al. 2007a). Second, there have been several recent years with extreme (e.g. record highs) temperatures during mid-Summer (water temperatures in 13 of the last 20 summers have been the warmest on record (M. Hague, Fisheries and Oceans Canada, pers. comm.). Third, since 1996, segments of Late-run sockeye salmon have been entering the Fraser River 3-6 weeks earlier than normal and thus they now encounter temperatures up to 5 °C warmer than they normally would. Taken together, these facts indicate that thermal conditions have been one of the largest environmental challenges that migrating adult Fraser River sockeye salmon have had to deal with over the past 20 years. We contend that much of the among-stock patterns in *en route* loss (Figure 2.7) are indicative of stock-specific abilities to cope with warming rivers and high river temperatures. This is described in more detail below.

2.6. Relationships between migration mortality and encountered temperature in Fraser River sockeye salmon

Martins et al. (2011) assessed the effect of freshwater thermal experience in the lower Fraser River on spawning migration survival by fitting capture-recapture models to telemetry data collected for > 800 adults captured and tagged in the ocean between 2002 and 2007 from four Fraser River sockeye salmon stock aggregates (Chilko, Quesnel, Stellako-Late Stuart and Adams). They found that survival of Adams sockeye salmon was the most impacted by warm temperatures, followed by that of Stellako-Late Stuart and Quesnel (Figure 2.9). In contrast, survival of Chilko fish was insensitive to the encountered river temperature (at least for temperatures up to 20 °C - the maximum examined) - a finding that supports the observation that the Chilko run has not had years with high en route mortality (Figure 2.7). Another key finding from that study was that for those migrants that were affected by temperature, 17-18 °C was the tipping point where survival began to be affected as temperatures increased further; at 19-20 °C stocks were exhibiting 20-40% mortality. These telemetry results are supported by en route loss patterns for Early summer and Summer run fish which shows that en route loss increases rapidly once temperatures exceed 18 °C, and losses of 40% could be expected at 19 °C (Figure 2.10). That survival starts to decline above 18 °C is consistent with the general thermal avoidance behaviour of the species - no sockeye salmon population anywhere has been known to

initiate spawning migrations into rivers at times when average seasonal temperatures are higher than 19 °C (Hodgson & Quinn 2002). In a 2009 telemetry study on Early Stuart sockeye salmon, survival from the Fraser River Canyon to spawning grounds was strongly related to average daily temperature encountered in the lower Fraser River with survivors encountering average temperatures of 16 °C and those that perished encountering average temperatures of 17.8 °C (English 2010). In a 2004 telemetry study on Weaver Creek sockeye salmon which involved > 80 fish being tracked to spawning grounds over a broad thermal range, 100% of fish perished if they had encountered river temperatures > 20 °C, at 18-19 °C 90% mortality was observed, at temperatures < 17 °C mortality was 20-50% (Mathes *et al.* 2010). Thus, taken together, these results indicate that patterns of *en route* mortality are stock-specific with Summer-runs having the greatest thermal tolerance, relative to earlier and later runs.

Recent metabolic and cardiac performance research in the laboratory on adult salmon has demonstrated some of the underlying mechanisms of the stock-specific responses to thermal stress. It has been determined that Fraser River sockeye salmon stocks vary in both their optimum and critical high temperatures in a manner that reflects the temperatures experienced during their historic migrations (Farrell *et al.* 2008; Farrell 2009; Lee *et al.* 2003; E. Eliason, Department of Zoology, University of British Columbia, Ph.D. thesis in progress). Such correspondence between thermal performance and historic river temperatures likely resulted from local adaptation – a widespread evolutionary process among salmonid fishes that leads to maximization of individual fitness in their local habitats (Fraser *et al.* in press). In other words, stocks appear to be physiologically fine-tuned to function best at the river migration temperatures they historically encountered – these studies have also revealed that there is also only ~ 4-7 °C difference between a stock's optimum temperature and its upper lethal temperature. Summer-run stocks have the highest critical temperatures of all groups, and the largest aerobic and cardiac scopes (Farrell *et al.* 2008; Lee *et al.* 2003; E. Eliason, Department of Zoology, University of British Columbia, Ph.D. thesis in progress).

Although metabolic and cardiac stress are acute processes that can cause *en route* mortality, there are other temperature-mediated processes such as energy depletion and disease which have more of a chronic effect on adult salmon and cause or contribute to mortality once migrants have been exposed to warm, but not critically high, river temperatures for extended periods of time. There are several diseases associated with different pathogens that migrating and spawning Fraser River sockeye salmon contract and that could contribute to *en route* or pre-spawn mortality (Bradford *et al.* 2010). One pathogen that has received considerable attention with Fraser River sockeye salmon is the naturally occurring parasite infection *Parvicapsula minibicornis*. This myxosporean parasite infects kidneys and gills in all adult Fraser River

sockeye salmon as they migrate through the estuary (Wagner *et al.* 2005). In laboratory studies, kidney infection has been shown to start when accumulated degree days > 350 °C and becomes full blown at ~ 500 °C degree days (Figure 2.11; Crossin *et al.* 2008; Wagner *et al.* 2005). Mortality rates assessed in laboratory studies with Late-run sockeye salmon closely tracks with the severity of infection in terms of accumulated degree days (Figure 2.11; Crossin *et al.* 2008).

Because (large segments of) Late-run fish migrate so early into the Fraser River, they encounter much warmer river conditions and accumulate more thermal units (e.g. much higher degree days) than normal-timed fish (Patterson *et al.* 2009b). During their estuarine holding, Late-run sockeye salmon are undergoing reproductive development so they can be prepared to reproduce shortly after arrival at spawning sites. Because additional maturation is still required when early-timed migrants get near spawning areas, survivors hold in nearby lakes, instead of holding in the estuary (English *et al.* 2005b). Spawning times in sockeye salmon are known to be adapted to the thermal regimes in their natal streams that maximize survival of their offspring (i.e. to ensure that eggs incubate and fry emerge at a time when plankton food items are available in nursery lakes), and spawning times have not changed during this period of early upstream migration (Patterson *et al.* 2009a). Early-timed fish are therefore exposed to freshwater diseases and parasites (i.e. *Parvicapsula minibicornis* and others) for much longer periods of time, with disease development being accelerated by higher than normal river temperatures (due to earlier river entry and climate warming), and greater degree day accumulation (Mathes *et al.* 2010; Wagner *et al.* 2005).

2.7. Patterns and causes of pre-spawn mortality in Fraser River sockeye salmon

Pre-spawn mortality is defined as females that have arrived on spawning grounds but die with most of their eggs retained in their body. There is a long history of information on pre-spawn mortality in Fraser River sockeye salmon with data collection in some stocks dating back to the late 1930s (Gilhousen 1990). Fraser River sockeye salmon pre-spawn mortality levels are highly variable among stocks, run-timing groups and years. Figure 2.12 summarizes 70 years of data for the four run-timing groups. With the exception of 12 years which are spread across the data period, pre-spawn mortality has not exceeded 30% at the run-timing group level; only in 4 years did pre-spawn mortality of a run-timing group exceed 40%. Across all run-timing groups over the entire 70-year period, pre-spawn mortality averages ~ 10% (Patterson 2009).

There is no clear indication that pre-spawn mortality, at the run-timing level, has been increasing over the recent few decades in concordance with run-timing trends in increasing *en route* mortality, with the possible exception of the past 25-year trend in Late-run pre-spawn mortality

which shows high variability but a general increase (Figure 2.12). However, because these data are based on summing total effective females within a run-timing group and dividing by total females in a run-timing group, the results are skewed towards trends within the large stocks, thus it belies the importance of pre-spawn mortality, and its trends, in relatively smaller populations. For example, Figure 2.13 shows that pre-spawn mortality in Late-run stocks (which includes the small Cultus and Portage stocks) is higher and more variable in years after the early migration phenomenon began compared to the recent time period prior to the shift in river entry timing. Indeed, migration timing is also related to pre-spawn mortality in Early summer and Summer runs in that years with the highest levels of pre-spawn mortality are also those when stocks migrated into the Fraser River 1-2 weeks earlier than usual (Patterson 2009).

There has been a considerable amount of research on the issue of pre-spawn mortality and its causes are complex and multi-factorial, and include disease (Bradford *et al.* 2010; Gilhousen 1990; Miller *et al.* 2011), stress and energy levels in adults (Gilhousen 1990; Hruska *et al.* 2010a), and time alive on spawning grounds (Hruska *et al.* 2010b). Most of these factors are accentuated by increasing temperatures so it is not surprising that within-stock trends in prespawn mortality are correlated with migration and/or spawning ground temperatures (Gilhousen 1990; Macdonald *et al.* 2000b, 2007), and that the strength of the correlations between prespawn mortality rates and temperature improve with proximity to spawning grounds (Gilhousen 1990; Macdonald *et al.* 2007). Alaskan sockeye salmon have also demonstrated higher levels of egg retention when water temperatures were warm (Quinn *et al.* 2007). There is also evidence that pre-spawn mortality is simply a continuation of physiological processes responsible for *en route* mortality (Hruska 2010).

There has been intensive examination of pre-spawn mortality in recent years directed towards Late-run sockeye salmon, for which the two sources of freshwater mortality (*en route* and pre-spawn) may be incremental, with both increasing substantially relative to historical patterns coincident with the change in river entry behaviour in 1995 (Figure 2.13; Lapointe 2009). Spawning ground arrival dates and peak spawning periods of Late-run sockeye salmon have varied within the normal historical range since the onset of the early migration phenomenon (Patterson *et al.* 2009a). In Late-runs, pre-spawn mortality can occur throughout their entire spawning period being high in both the earliest and latest arrivals at spawning areas (Patterson *et al.* 2009a). Even though early river migrants spend much more time holding in natal lakes than normal timed migrants, early fish are still more likely to be the first to arrive on the spawning grounds, however diminishing proportions still continue to arrive throughout the entire spawning period and may contribute to elevated pre-spawn mortality in later time periods. First arrivals on spawning grounds actually have the highest energy reserves (Patterson *et al.* 2009a), suggesting

that energy exhaustion on spawning grounds is not a factor affecting spawning success in early migrating Late-runs. Results from experiments that have altered energy reserves and physiological stress levels by exposing fish to different water velocities towards the end of river migration in Fraser River sockeye salmon support this (Nadeau 2007; Nadeau et al. 2010). The physiology and histopathology of pre-spawn mortality fish indicates gill and kidney diseases play a significant role in mortality, in particular those caused by *Parvicapsula minibicornis*, though also Loma, Columnaris and Saprolegnia (Bradford et al. 2010; Patterson et al. 2009b). The search for a single cause or suite of causal agents of pre-spawn mortality in Late-runs has been difficult as it appears to be complex and can likely result from a multitude of factors whose efficacy can change both annually and seasonally (Hruska 2010). Most, if not all, of the causal factors are accentuated by increases in temperature and freshwater residency times. Thus once fish enter freshwater it is a race against time for early migrants to be able to spawn prior to succumbing to various disease agents. Considering that a primary determinant of spawning success is longevity on spawning grounds (Hruska et al. 2010b), early migrants that are already compromised by their thermal history which reach spawning grounds are at a clear disadvantage to spawn successfully, though there are few data available to test this hypothesis.

2.8. Migration issues and potential freshwater mortality of adults in 2009 and 2010

The en route loss data presented in this report extends only to 2008. In 2009, a large issue that garnered considerable attention was the poor returns of adults to the Fraser River. However, little attention has been given to the environmental conditions that the adults encountered during their river migration that year. River temperatures were well above the long-term average during much of the migratory period for Fraser River sockeye salmon. In particular, temperatures exceeded 18 °C from the 3rd week of July to the 3rd week of August (FREWP 2009) encapsulating a portion of the run timing for the Early summer and Summer runs. During that warm period, temperatures rose above 20°C for 9 days - this level of thermal stress would be expected to cause significant levels of en route mortality to a portion of those runs based on the empirical studies reviewed above. Indeed preliminary results from a 2009 in-river telemetry study found that few of the adult sockeye salmon that were tagged in July survived to reach spawning grounds (English 2010). At least 50-60% of the Late-runs migrated in-river earlier than historically normal (e.g. before mid-September; PSC 2009) and we would expect that a large portion of those early migrants would suffer either en route or pre-spawn mortality, based on the empirical studies reviewed above. Preliminary information on pre-spawn mortality suggests that it was relatively low for most stocks with the exception of Weaver and Cultus (D. Patterson, Fisheries and Oceans Canada, unpub. data).

In 2010, the issue that was paramount was the extremely large return of adults to the Fraser River. River temperatures were generally above the long-term average during the up-river migration of sockeye salmon but not as high as in 2009. Temperatures exceeded 18 °C from the 3rd week of July to the 3rd week of August, exceeding 19 °C on 6 days (FREWP 2010). This level of thermal stress would be expected to cause modest levels of *en route* mortality to a portion of the Early summer and Summer runs. Ocean telemetry tagging programs (run by UBC and LGL Ltd.) were in operation in summer 2010 wherein > 1,000 adult Fraser River sockeye salmon were tagged and released but results that link river thermal exposure to survival to spawning grounds have not yet been assessed. At least 40% of the Late-runs migrated in-river earlier than historically normal (e.g. before mid-September; PSC 2010) and we would expect that a large portion of those early migrants would suffer either *en route* or pre-spawn mortality, based on the empirical studies reviewed above. There are no data available yet on 2010 pre-spawn mortality. The authors have not been able to confirm the estimates of mortality for 2009 or 2010.

2.9. Intergenerational consequences

Even in years when migration conditions are stressful due to high temperatures or high flows, or high levels of early migration, all individuals in a population do not succumb to en route and prespawn mortality. Despite environmental hardships, some migrants are able to successfully spawn which begs the question of whether sub-lethal but yet stressful factors acting on successful migrators and spawners can affect the quality and hence survivorship of their juveniles and of their progeny at later life stages. Intergenerational effects have been investigated in some fishes and the findings show that water temperature experienced by females during oogenesis can affect egg sizes (Chambers 1997) and egg biochemical composition (Atse et al. 2002; Buckley et al. 1990; Jobling et al. 1995), which could alter offspring ontogeny and fitness (Kamler 1992). Temperature can also act directly at the level of the oocyte, disrupting processes involved in final oocyte maturation and inhibiting ovulation in many individuals (Pankhurst et al. 1996; Watts et al. 2004; Webb et al. 2001). Failure of adults to spawn as a result of experiencing suboptimal temperatures could alter the conspecific density of the surviving offspring. This could affect changes in early growth patterns, behaviour, and the overall population structure, through known patterns of density dependence (Einum et al. 2008). Similarly, alterations in the proportions of genotypes represented in the offspring generation may reduce phenotypic variation and affect overall fitness.

While intergenerational effect studies have been conducted in farmed or hatchery-raised salmonids (e.g. Atlantic salmon [Salmo salar], rainbow trout [O. mykiss], Arctic char [Salvelinus alpinus]) (reviewed in Burt et al. in press), the study of intergenerational effects in wild Pacific salmon is in its infancy and results to date are limited and equivocal. There is some evidence that

effects of adverse river conditions, high temperatures or high flows, encountered by Fraser River sockeye salmon can be carried over to their offspring, resulting in low embryo survival (Macdonald *et al.* 2000b; Patterson 2004). Laboratory experiments which involve manipulating stress and energy levels in maturing Fraser River sockeye salmon adults and using their gametes in cross-fertilization studies have revealed strong parental effects on embryo and fry growth and survival but it is not clear whether these effects are caused by adult genotype, physiology or migration environment (Patterson 2004; Patterson *et al.* 2004; Nadeau 2007; J. Burt, Department of Forest Sciences, University of British Columbia, M.Sc. thesis in progress).

2.10. Effects of en route and pre-spawn mortality on population trends

From ~ 1990 to 2009, we have witnessed a general decline not only in productivity (number of recruits per effective female spawner [i.e. the number of female spawners multiplied by the average proportion of eggs laid]) but also in spawning abundance in Fraser River sockeye salmon. In particular, spawning abundance has declined in Early Stuart and several Late-run stocks during a time period when en route loss has become a significant component of the total fate of adult migrants in those groups of fish. Spawner abundance has not declined dramatically in all stocks partly because of reductions in harvest associated with management adjustments made to compensate for en route mortality. What this means is that spawner abundance could have been a great deal higher (or allocations to fisheries greater) in recent years if it were not for en route loss.

Although sensitive to the time period evaluated, the available data suggest that *en route* loss may be a critical contributing factor to decreasing trends in abundance for some Fraser River sockeye salmon stocks, in particular, those that do not cope well with warming rivers. Indeed Peterman *et al.* (2010), in their workshop summarization of several hypotheses for declining trends in productivity in Fraser River sockeye salmon concluded that *en route* and pre-spawn mortality are significant factors that reduce the number of effective female spawners, and thus may pose a threat to the long-term viability of the populations that are particularly affected. Lastly, it is possible that intergenerational effects could be contributing to recent declines in Fraser River sockeye salmon productivity (e.g. stressed adult migrants produce offspring that survive poorly later in life), but there has been little research to investigate this.

There is evidence accumulating from field telemetry and laboratory studies that migrating female sockeye salmon, regardless of stock, perish at much higher rates than males when conditions are 'stressful' (e.g. caused by high temperatures, high flows, or excessive handling) towards the end of river migration periods (Crossin *et al.* 2008; Nadeau *et al.* 2010; Patterson *et al.* 2004; Roscoe

et al. in press; K. Jeffries, Department of Forest Sciences, University of British Columbia, Ph.D. thesis in progress; E. Martins, Department of Forest Sciences, University of British Columbia, unpub. data). This may occur because females which are near fully mature have higher baseline stress levels than males at a similar level of maturation (Hruska et al. 2010a; Roscoe et al. in press), so additional stressors experienced at that time could have greater detrimental effects to females. Thus, even though it may be possible to compensate for en route loss by reducing harvest via management adjustments, if en route loss in some years is biased heavily towards females, this could reduce the number of effective female spawners despite compensations via management adjustments, and reduce stock productivity; however, there have been no studies directed towards evaluating this hypothesis.

3. Summary

3.1. Climate change effects

The qualitative assessment presented in this report suggests that the survival of all life stages of Fraser River sockeye salmon, with the possible exception of eggs and alevins, may be declining due to recent trends in temperature, and temperature related factors, in both marine and freshwater environments over the past 20 years. However, where data exist at the stock-level for some life history stages (e.g. eggs, alevin, adult migrants), the picture is complicated by stockspecific patterns indicating that the survival of some stocks may have been less impacted than that of others or not impacted at all (Beacham & Murray 1989; Martins et al. 2011). Although the observed warming of about 0.5 °C and 0.7 °C in marine and freshwater environments, respectively, may not have resulted in large declines in survival of individual life stages, the cumulative impacts of climate change on survival across life stages could have been substantial. In addition, climate change seems to be affecting other variables related to sockeye salmon biology and ecology, such as growth and the timing of life history events (e.g. Cox & Hinch 1997; Crossin et al. 2004; Hodgson et al. 2006; Quinn & Adams 1996), that in some case may indirectly affect their survival. For example, the observation that adults experiencing warm SST return to the Fraser River with lower levels of somatic energy (Crossin et al. 2004b) indicate that they may now have less energy available to fuel their up-river migration and to keep them alive for long enough on the spawning grounds. Moreover, females may now be digging shallower nests as returning adults are also smaller than in the past (Cox & Hinch 1997), which may have increased the mortality of eggs due to scouring. It is also important to note the possibility that warmer river temperatures encountered by females during their upstream migration may affect the quantity and quality of their eggs. Evidence for such intergenerational effects is starting to accumulate, though the research on Pacific salmon is in its infancy (reviewed in Burt et al. in press). What has been done suggests that offspring survival can decrease when female spawners encounter stressful migration conditions (Macdonald et al. 2000b; Patterson 2004).

Overall, the weight of the evidence on the adverse effects of recent warming on survival of some individual life stages, as well as its possible cumulative effects across life stages, suggest that climate change has been a possible contributor to the observed declining trend in abundance and productivity of Fraser River sockeye salmon over the past 20 years. It also seems that interannual variability in climate conditions have contributed to the extreme variations in the abundance of returning adults that were observed in 2009 (much lower than average) and 2010 (much higher than average). The cohort of fish returning in 2009 entered the marine environment in 2007 when an El Niño early that year was possibly responsible for some unusual climatic events leading to unfavourable conditions for sockeye salmon migrating along the British

Columbia coast – warm water temperatures that may have resulted in high energetic costs compounded by low availability/quality of food resulting from extreme salinity and wind anomalies (McKinnell *et al.* 2011). On the other hand, the cohort of fish returning in 2010 entered the marine environment in 2008, a year that was characterized by cooler ocean temperatures and presumably better food conditions (STTS 2010).

3.2. En route and pre-spawn mortality

En route loss has occurred in all run-timing groups of Fraser River sockeye salmon over the past 17 years and there is ample evidence that adverse environmental conditions, in particular those related to thermal issues, are largely responsible for the patterns. En route mortality based on field telemetry studies has been substantial in many stocks across all run-timing groups in recent years, in particular in years when migration temperatures > 18 °C. However, stocks differ in how they cope with acute and chronic thermal stressors, with those that historically encountered high thermal stress surviving the best during migrations. This conclusion is supported by considerable amounts of field telemetry and laboratory studies, and is supported by en route loss observations. En route loss has been least severe and least frequent in the Summer-runs and most severe and most frequent in the Early Stuart and in the Late-runs. En route loss in Late-runs is tied directly to their change in river entry behaviour. Migration mortality can contribute to declining trends in spawning abundance (if it cannot be compensated for by reductions in fisheries). Pre-spawn mortality reduces number of effective female spawners so it could be playing a role recently in declining productivity and abundance in some Late-run stocks. Finally, climate change forecasts predict continued warming of Fraser River temperatures (Ferrari et al. 2007; Foreman et al. 2001; Morrison et al. 2002), which will likely translate into an even higher frequency of extreme en route loss and pre-spawning mortality events especially for temperature sensitive stocks.

4. Recommendations: Filling scientific knowledge gaps to improve management

We recommend the following research directions:

i) <u>Telemetry approaches and direct experimentation are needed to better understand</u> sockeye salmon marine survival

Electronic tagging devices (e.g. acoustic tags) and large-scale marine tracking systems (e.g. Pacific Ocean Shelf Tracking project [POST]) are tools that are currently available but are underutilized by management agencies for assessing marine survival rates, locales of mortality, and associations with climate-related variables for Fraser River sockeye salmon (Welch *et al.* 2009). Remarkable recent advances in electronic tagging technologies over the past decade, such as the development of miniaturized tags, multisensor tags (i.e. which records variables related to fish behaviour and physiology) and business card tags (i.e. tags applied to large marine animals that record information sent by transmitters implanted into fish and then transmit the data from themselves to satellite and underwater receivers) offer exciting avenues for future research (Cooke *et al.* 2004b, in press; Holland *et al.* 2009). Over the long term, the use of these technologies along with data loggers that monitor environmental conditions (e.g. Argo buoys) could play a major role in examining how climate-driven changes in the marine environment affect sockeye salmon.

Also needed for a better understanding of the mechanisms through which climate-related variables and climate change affect sockeye salmon in the marine environment are direct experimental manipulations that takes advantage of existing telemetry infrastructure. Experiments could include exposing tagged fish to varying temperatures, salinities, or parasites and assessing survival and behaviour with telemetry (e.g. Cooperman *et al.* 2010). Oceans are also expected to become more acidic with future climate change (IPCC 2007) and such conditions are likely to impact fish both directly and indirectly (Dixson *et al.* 2010; Ishmatsu *et al.* 2008; Munday *et al.* 2009, 2010; Pörtner & Peck 2010). Currently, there is no information on how the acidification of marine waters could affect sockeye salmon and hence this topic also requires immediate consideration for future research.

ii) Field-based research is needed on early life stages in freshwater

Much of the work on the effects of temperature on the early life stages of sockeye salmon in freshwater has been conducted in the laboratory; little is known on how temperature influences their biology and ecology in streams and lakes. Given the limited evidence that changes in temperature affects the availability of food for fry and predation mortality (e.g. Petersen & Kitchell 2001; Schindler *et al.* 2005), any field-based research on the early life stages should consider how temperature affect the interaction of sockeye salmon with their prey and predators. Research in this area could include a long-term monitoring program of populations of sockeye salmon, prey and predators, and environmental conditions in their rearing lakes as well as experimental manipulations of food and predator densities in the field at a range of temperatures. Future research efforts should also be directed at the effects of increased stream flows on egg survival since higher levels of rainfall during the time of incubation are expected to occur with climate change (Healey in press).

iii) <u>Improvements are needed in-season and post-season estimates of spawning migration mortality</u>

Fisheries management needs better ways to predict *en route* and pre-spawn mortality prior to fish entering the Fraser River so that harvest can be better adjusted in-season in order to achieve stock conservation targets. One specific area that requires on-going and future research includes a better understanding and quantification of natural mortality occurring between marine approach areas and the hydroacoustic infrastructure at Mission. Furthermore, continued research into stock-specific effects of temperature (e.g. Martins *et al.* 2011) and stock-specific biomarkers (e.g. Miller *et al.* 2011) are needed; however, such research requires tagging programs (e.g. telemetry) in order for the thermal experience and physiological conditions of fish to be linked with their fate (see research recommendation # iv). Also needed are improvements to *en route* loss models (e.g. to quantify the contributions of estimation errors and unreported catch so that models of *en route* loss can more explicitly account for estimates of natural mortality).

iv) Tagging programs are needed for direct and accurate estimates of survival

Most of the field-based studies reviewed here used indices of productivity as a proxy for survival in different life stages. Similarly, until recently most of the information on inriver mortality of Fraser River sockeye salmon adults was obtained indirectly from 'escapement discrepancy' data, which are defined as differences in estimates of stock-specific abundance obtained from the Mission site and those obtained from spawning

grounds – these data are converted to measures of en route loss (Macdonald et al. 2010). While these approaches have been useful and contributed to our understanding of the associations between environmental conditions and survival of sockeye salmon in freshwater and at sea, estimates of absolute survival from tagged fish are required for efficient monitoring of stocks and analyses of viability using life-cycle models. For example, in a few recent years (2002-present), universities and private consulting companies in collaboration with DFO and the PSC have conducted telemetry studies on adult migrants and have been able to provide very accurate and timely estimates of stockspecific run-timing, fisheries harvest and *en route* mortality (e.g. English 2005b; Martins et al. 2011). If it were not for these programs, we would know very little about mortality patterns and factors in coastal and lower river areas (important information not routinely collected by the management agencies), how current temperature increases are affecting specific stocks, or why and where Late-runs were dying at such high levels. Many of these telemetry studies are no longer running. Telemetry programs as well as programs using other tagging approaches (e.g. Petersen discs, PIT or anchor tags) are needed and should be coupled with capture-mark-recapture (CMR) methods of data analysis (Pine et al. 2003) in order to generate as accurate as possible run-timing abundance and en route mortality information. These programs should be funded and integrated into routine stock assessment programs and dove tailed with studies of scientific inquiry, particularly in relation to continued research on climate change and Fraser River sockeye salmon abundance and productivity.

v) Additional stocks need to be examined

Only a few major stocks have been intensively studied to date in terms of *en route* mortality, but adult sockeye salmon from different stocks vary substantially in their life history, energy use and allocation, thermal tolerance, and habitats used (Beacham & Murray 1989; Crossin *et al.* 2004a; Farrell *et al.* 2008). A multi-stock approach to research could provide valuable information on the mechanisms through which climate-related variables will affect sockeye salmon on the watershed level scale and would help managers in knowing which stocks and conservation units are most at risk of future climate change.

vi) Better assess the extent and consequences of gender differences in survival of migrating adult sockeye salmon

Several recent studies of adult Fraser River sockeye salmon have indicated significantly higher levels of *en route* mortality in females compared to males during late stages of the

spawning migration when fish are exposed to stressful migratory conditions (e.g. Crossin et al. 2008; Nadeau et al. 2010; Patterson et al. 2004; Roscoe et al. 2010). This phenomenon could have large impacts on stock abundance and viability under future climates but such consequences have not been considered to date. Future research should look into the extent and physiological basis of survival differences between sexes and investigate the consequences of female-specific survival for the viability of Fraser River sockeye salmon, particularly under future climate warming (e.g. using life-cycle models and temperature projections for the Fraser River).

vii) Assess impacts of fisheries capture and release/escape on *en route* and pre-spawn mortality

Sockeye salmon are harvested *en route* to spawning grounds and encounter different fishing sectors and gear types. Many fish are captured but escape, and some captured fish are intentionally released. It is well known that physiological and behavioural changes accompany fish capture and handling (reviewed in Arlinghaus *et al.* 2007) but consequences of this to migration and spawning success are unknown for Fraser River sockeye salmon or most Pacific salmon. There is also a growing body of evidence that fish captured under warm temperatures are likely to die in a few hours or days post-release (Arlinghaus *et al.* 2007; Davis 2002; Cooke & Suski 2005). It has been shown that the combination of warm temperatures and the stress and exercise associated with capture often leads to profound physiological and behavioural disturbances that are likely responsible for the enhanced mortality observed in released or escaped fish (e.g. Cooke & Suski 2005; Gingerich *et al.* 2007; Wilkie 1996). Managers need to know how release or escape of captured fish affects *en route* loss and escapement (Donaldson *et al.* 2011; English *et al.* 2011), especially in an era of warming rivers wherein we expect higher stress-related mortality (Dempson *et al.* 2002).

viii) Cumulative impacts of multiple stressors

Research is needed that examines cumulative impacts across multiple stressors, such as examining: the warming potential of multiple effluents (e.g. sewage treatment plant discharges, industrial water discharges) to determine if they could have a cumulative effect on water temperature of the Fraser River; impacts of multiple environmental stressors (e.g. temperature, flow, water quality and water chemistry); impacts of fishery interactions (e.g. see research recommendation # vii);

ix) Carry-over and intergenerational effects

Research is needed that examines cumulative impacts across life history stages (i.e. carry-over effects) and/or generations (i.e. intergenerational effects). Specifically, this could include examining: how the effects of environmental conditions on one life stage are carried over to a subsequent life stage (e.g. how poor growth during warm oceanic conditions affect survival during the return migration and spawning and the construction of nest at appropriate depths to prevent scouring); and how the quality and quantity of eggs successfully deposited by females is affected by the river conditions (e.g. temperature and flow) encountered during migration and the links to subsequent offspring survival (i.e. intergenerational effects).

x) Climate change modelling

Managers and policy makers need to plan now for how to deal with continued trends in climate warming and declining abundances. Projections of future summer temperature and flow for the Fraser River already exist (Ferrari *et al.* 2007; Foreman *et al.* 2001; Morrison *et al.* 2002;), but similar information is also needed for other seasons since air temperature and precipitation as rainfall are expected to increase the most during winter and spring (Rodenhuis *et al.* 2009). Also needed is a better understanding of how future climate change will affect temperature and flows of spawning streams and rearing lakes, physical conditions of marine habitats and the interaction of sockeye salmon with their prey and predators.

Recent research has shown that some stocks appear to be more resilient to river warming, whereas others cannot cope with increasing temperatures (Farrell *et al.* 2008; Hague *et al.* 2011; Martins *et al.* 2011). More stock-specific information on the susceptibility to climate change is needed for productivity and escapement planning. In addition, needed is the development of life-stage models in order to quantify the impact of *en route* and prespawn mortality, as well as mortality in other life history stages, on future trends in salmon productivity and abundance (i.e. population viability analysis). Research aimed at understanding how sockeye salmon would adapt to climate change through genetic and non-genetic mechanisms continues to be needed.

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Table 1.1. Summary of the publications evaluating the effects of climate-related variables on survival of sockeye salmon. Also presented is the qualitative assessment of the likelihood that recent trends in climate have affected (decreased or increased) or not the survival of different life stages of Fraser River sockeye salmon over the past 20 years.

Life stage	Publication	Climate-related variable	Variable range	Relationship with survival	Type of study	Recent trend	Likelihood of recent change in survival
egg and alevin	Brett (1951)	precip	0.3-1.8×10 ³	+	field	NA	possibly increased (egg)
	Thorne & Ames (1987)	flow	1-9×10 ³	_	field	NA	unlikely changed (alevin)
	Murray & McPhail (1988)	temp	2-14	opt ^a , none ^b	lab	NA	(but direction or
	Beacham & Murray (1989)	temp	2-15	opt ^a , none ^b	lab	NA	magnitude of effects may vary by stock)
	Beacham & Murray (1990)	temp	2-16	opt ^a , none ^b	lab	NA	
fry in lakes	Brett (1952)	temp	0-25	opt	lab	NA	
	Sylvester (1972)	temp	7-17	_c	lab	NA	
	Bower & Margolis (1985)	temp	5-20	opt ^d	lab	NA	possibly decreased
	Adkison <i>et al</i> (1996)	temp	NA	-e, none	field	no	
	Mueter et al. (2005)	temp	NA	_e, + ^f	field	no	
smolt and postsmolt	Hsieh et al. (1991)	temp	NA	-	field	no	
	Hinch et al. (1995)	temp	8-11	_	field	no	
	Adkison et al. (1996)	temp	NA	none ^e , + ^f	field	no	
	Mueter et al. (2002)	temp	NA	_e, + ^f	field	no	<u>likely</u> decreased
	Mueter et al. (2005)	temp	NA	_e, + ^f	field	no	
	Martinson et al (2009)	temp	4-6	+	field	no	
		precip	0.6-1.4×10 ³	+			
immature in the ocean	Hsieh et al. (1991)	temp	NA	-	field	no	
	Martinson et al. (2009)	temp	4-6	+	field	no	possibly decreased
		precip	0.6-1.4×10 ³	+			
returning adult	Servizi & Jensen (1977)	temp	18-30	-	lab	NA	
	Macdonald et al. (2000a)	temp	15-17.5	_	field	no	very likely decreased
		flow	6-9×10 ³	_			(but not in all stocks)
	Macdonald et al. (2000b)	temp	15-19	_	field	no	

		flow	3-7×10 ³	_9			
	Naughton et al. (2005)	temp	13-23	_	field	NA	
		flow	2-10×10 ³	+			
	Crossin et al. (2008)	temp	10-18	_	lab	NA	
	Farrell <i>et al</i> (2008)	temp	13-22	-	field	no	
	Keefer et al. (2008)	temp	15-24	_	field	no	
		flow	0.1-1.6×10 ³	+			
	Macdonald et al. (2010)	temp	9-20	none ^h , –	field	no	
		flow	1-11×10 ³	none ⁱ , –			
	English (2010)	temp	15-22	_	field	no	
	Martins <i>et al.</i> (2011)	temp	13-19	none ^j , –	field	no	
	K. Jeffries (unpub.data)	temp	13-19	_	lab	NA	
	E. Martins (unpub.data)	temp	15-19	_	field	no	
	Gilhousen (1990)	temp	8.7-19.2	none ^k , –	field	no	nassibly dearened
spawner (survival to spawn)	Macdonald et al. (2000b)	temp	15-19	none ^l , –	field	no	possibly decreased
	Quinn <i>et al.</i> (2007)	temp	NA	_	field	NA	(but not in all stocks)

Type of study (lab and field) shown in bold denotes laboratory or field studies that included Fraser River sockeye salmon. The 'Recent trend' column shows whether publications including Fraser River sockeye salmon present a recent (i.e. extending at least into part of the period of interest in this report) trend in survival (raw data or results from statistical analyses) that follows a trend in a climate-related variable. Abbreviations used in table are: temp (temperature), precip (precipitation), and opt (optimum; denotes a relationship where survival is maximum at a given value of a climate-related variable and declines towards lower and higher values). Symbols used in table are: – (denotes negative relationship), and + (denotes positive relationship). Climate-related variable units are: °C (temperature), mm (precipitation), and m³/s (flow). NA denotes information that could not be found in the publication or that do not apply to our assessment (e.g. does not relate to Fraser River sockeye salmon).

^a relationship with survival of eggs; ^b relationship with survival of alevins; ^c mortality increased with temperature through an increase in predation rates; ^d relationship likely reflects an optimum temperature at around 13 ^oC for the pathogenicity of the parasite; ^e relationship with survival of Fraser River sockeye salmon; ^f relationship with survival of Alaska sockeye salmon; ^g no relationship

with survival of Summer and Late-run stocks; ^h no relationship with survival of Late-run sockeye salmon; ⁱ no relationship with survival of Chilko sockeye salmon; ^k no relationship with pre-spawn mortality of Early Nadina and Late Stuart stocks; ^l no relationship with pre-spawn mortality of Chilko, Stellako, Late Stuart, Birkenhead, Adams and Weaver stocks.

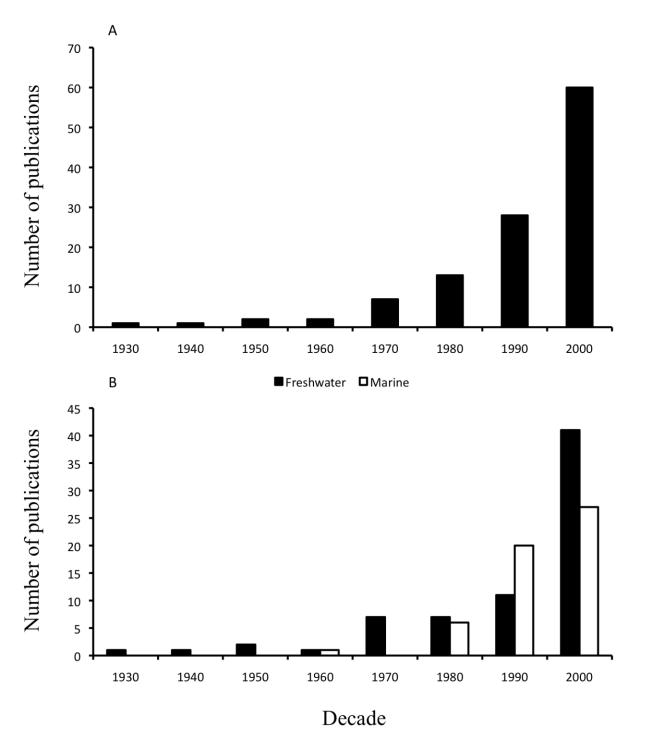


Figure 1.1. Temporal trends (decade) in publications assessing the relationship between climate-related variables and sockeye salmon biology and ecology. A) Total number of publications. B) Number of publications studying freshwater and marine life stages of sockeye salmon. Note that the number of publications in panel B (n=125) is higher than in panel A (n=114) because some studies assessed both freshwater and marine life stages.



Figure 2.1. Map of Canada with inset showing southern half of British Columbia. The Fraser River mainstem and its main tributaries are indicated. Circled and labelled are spawning and rearing regions (by name) for some of the largest sockeye salmon stocks and others discussed in the report.

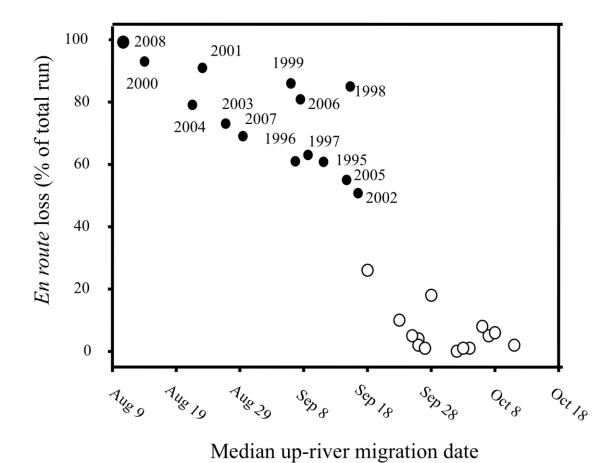


Figure 2.2. Relationship between en route loss estimates (as a percent of the total run) and the median up-river migration date (50% of the run past the Mission hydroacoustic facility) for Weaver Creek sockeye salmon, a Late-run stock. Dark circles indicate years since the 'early migration phenomenon' began (1995-2008); white circles are years prior to the change in river entry behaviour but after the start of the Mission facility (1977-1994). Estimates of absolute levels of en route mortality are very large in some years (e.g. 2000-270,000 fish; 2001-165,000 fish; 1998-490,000 fish). Data and figure provided by Mike Lapointe (Pacific Salmon Commission).

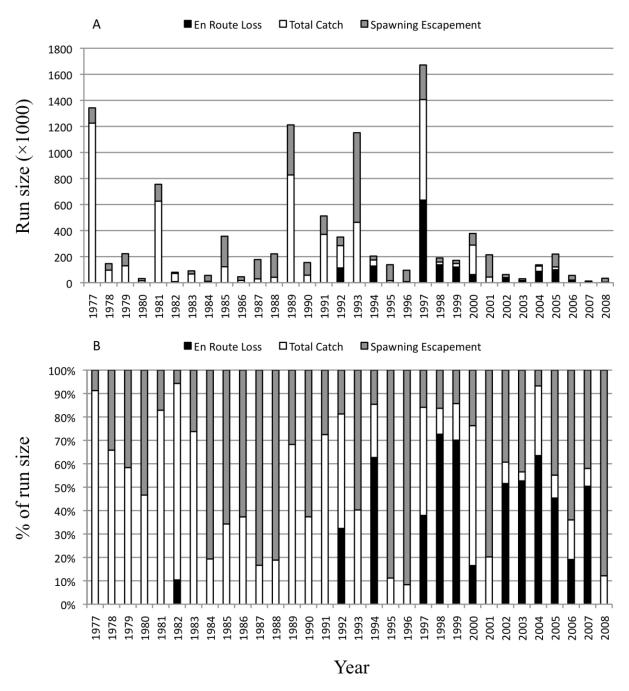


Figure 2.3. A) Total run size of adult Early Stuart sockeye salmon from 1977 to 2008 with fish fate categorized into total catch, *en route* loss and spawning escapement. B) The same data as presented in panel A but with fate categories expressed as percentages of the total run size. Data source: Sockeye Salmon Stock Production Files, DFO/PSC unpublished data.

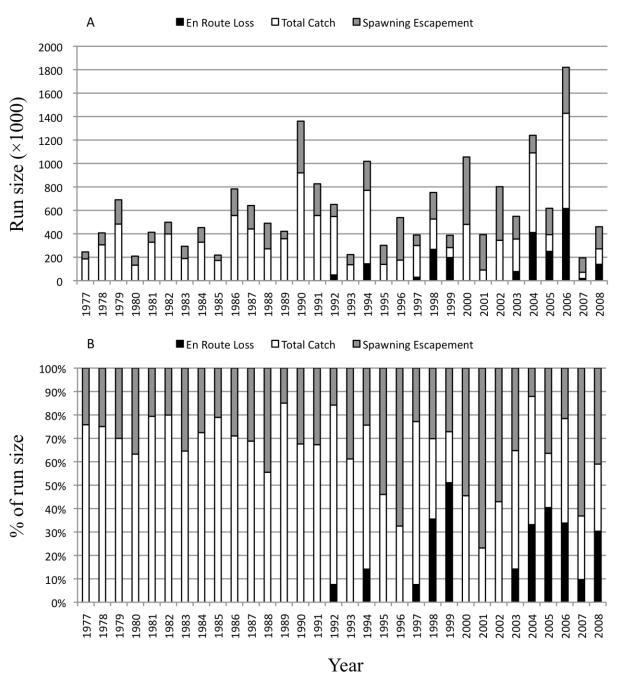


Figure 2.4. A) Total run size of adult Early summer sockeye salmon from 1977 to 2008 with fish fate categorized into total catch, *en route* loss and spawning escapement. B) The same data as presented in panel A but with fate categories expressed as percentages of the total run size. Data source: Sockeye Salmon Stock Production Files, DFO/PSC unpublished data.

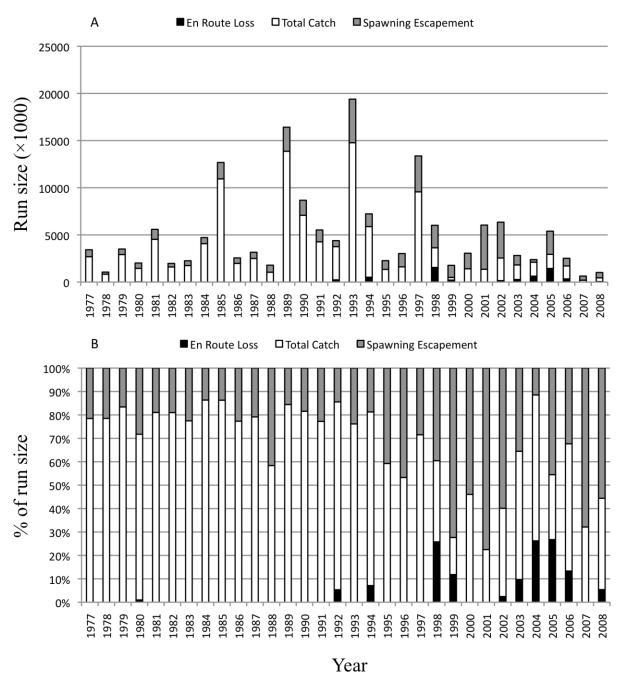


Figure 2.5. A) Total run size of adult Summer run sockeye salmon from 1977 to 2008 with fish fate categorized into total catch, *en route* loss and spawning escapement. B) The same data as presented in panel A but with fate categories expressed as percentages of the total run size. Data source: Sockeye Salmon Stock Production Files, DFO/PSC unpublished data.

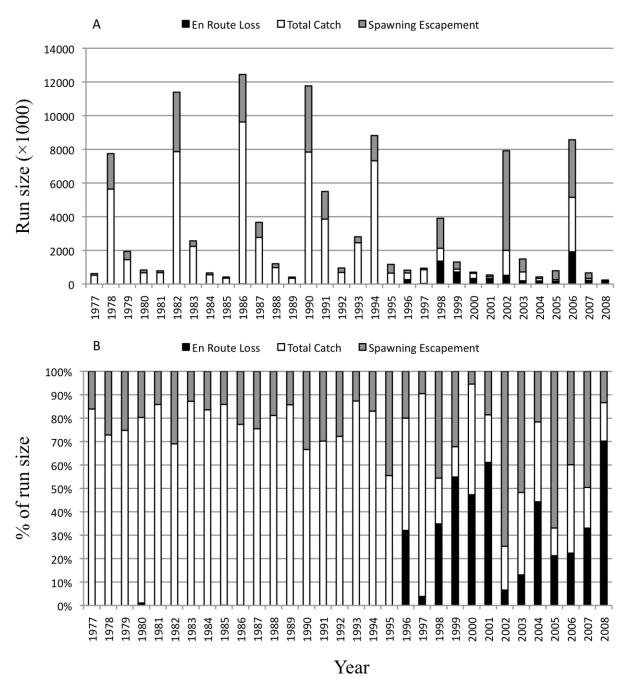


Figure 2.6. A) Total run size of adult Late-run sockeye salmon from 1977 to 2008 with fish fate categorized into total catch, *en route* loss and spawning escapement. B) The same data as presented in panel A but with fate categories expressed as percentages of the total run size. Data source: Sockeye Salmon Stock Production Files, DFO/PSC unpublished data.

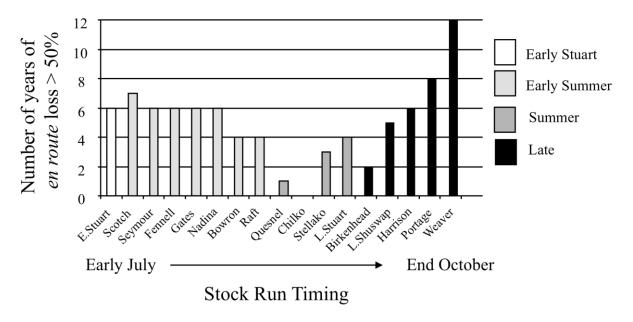


Figure 2.7. Number of years that *en route* loss by adults exceeded 50% for the major Fraser River sockeye salmon stocks from 1996-2008. Stocks are ordered based on runtiming into the Fraser River with run-timing groups indicated. These data are based on the percent of potential spawners that had migrated past the Mission hydroacoustic facility but were not detected on spawning grounds (i.e. they are based on escapement discrepancies). Data sources: Macdonald *et al.* (2010), Cummings *et al.* (in press).

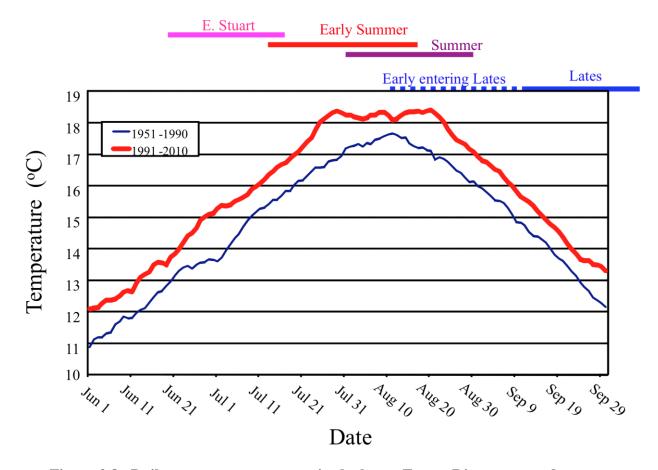


Figure 2.8. Daily average temperature in the lower Fraser River averaged among years within two time periods (thick line: 1951-1990; thin line: 1991-2010) over the summer months. The period of entry and passage in the lower Fraser River for the four main runtiming groups are indicated by solid lines above the figure. Since 1995, segments of all Late-runs have been entering the river much earlier than usual and this is indicated by the dashed line. Data sources: DFO Fraser River Environmental Watch Program, unpublished data.

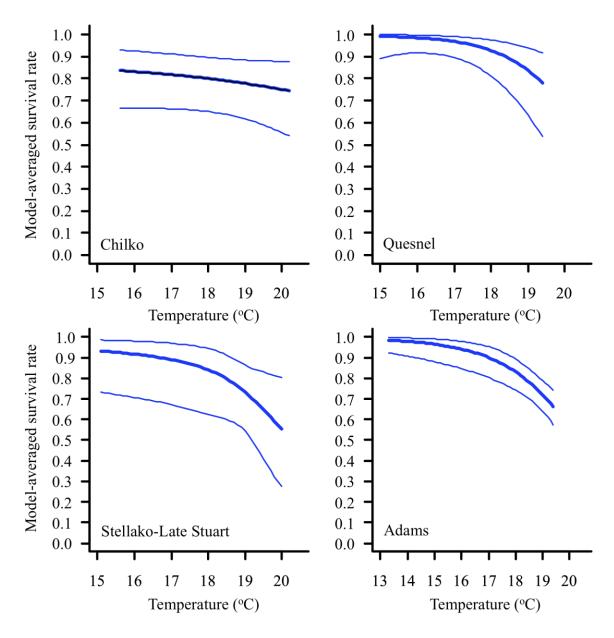


Figure 2.9. Model-averaged survival rates (+/- 1SE) of adult Fraser River sockeye salmon to reach natal watersheds in relation to encountered Fraser River temperature. Results are based on > 800 fish that were carrying transmitters, which were inserted in the ocean from 2002-2007. Figure adapted from Martins *et al.* (2011).

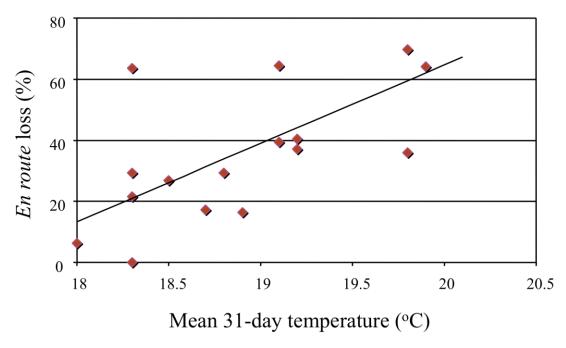


Figure 2.10. Relationship for Early summer and Summer runs between *en route* loss as a percent of the total run and the mean 31-day temperature experienced by a run in a given year for 'thermally stressful years' (e.g. years when mean temperatures > $18~^{\circ}$ C; 8 of 17 years from 1992 to 2008). ($R^2 = 0.50$, P < 0.01). Data source: DFO Fraser River Environmental Watch Program.

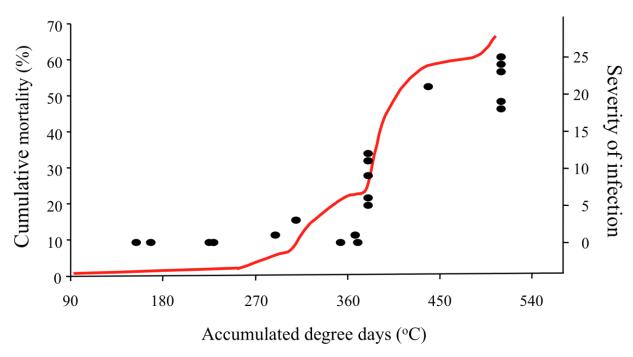


Figure 2.11. Laboratory derived relationships between cumulative mortality (solid line), severity of kidney infection of *Parvicapsula minibicornis* (circles) and accumulated degree days for Weaver Creek sockeye salmon. Severity of infection was estimated histologically from the mean number of infected glomeruli per 25 glomeruli examined under a microscope. Data sources: Wagner *et al.* (2005), Crossin *et al.* (2008).

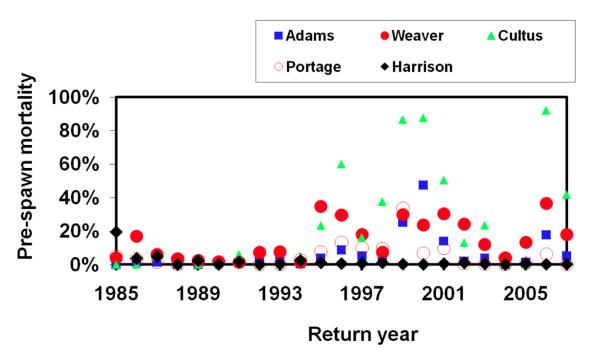


Figure 2.12. Pre-spawn mortality by year for the five main Late-run sockeye salmon stocks from 1985 to 2007. Pre-spawn mortality appeared to increase and become more variable after the early migration phenomenon began in 1995. Figure taken from Lapointe (2009).

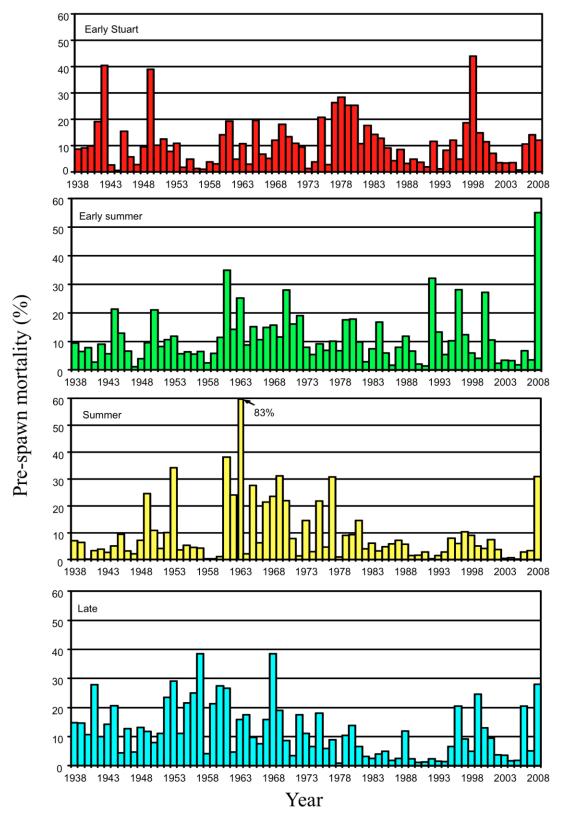


Figure 2.13. Pre-spawn mortality by year for the four run-timing groups from 1938 to 2008. Figure adapted from data in Patterson (2009).

APPENDIX 1

Statement of Work: Scott Hinch

Cohen Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River

"Effects of Climate Change on Fraser River Sockeye Salmon: Literature Compilation"

Background

- 1.1 The Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River (www.cohencommission.ca) was established to investigate and report on the reasons for the decline and the long term prospects for Fraser River sockeye salmon stocks and to determine whether changes need to be made to fisheries management policies, practices and procedures.
- 1.2 There is growing evidence that climate change, both anthropogenic and non-anthropogenic, may be affecting sockeye habitats in freshwater and marine environments.
- 1.3 A review of the evidence for the occurrence and effects of climate change on Fraser River sockeye is required to evaluate the importance of the climatic trends on their ecology and survival and to determine the role of climate in the Fraser River sockeye run failure of 2009.

Objective

2.1 To compile the scientific and grey literature on the documented and projected effects of climate related variables and climate change on Pacific Salmon with a particular focus on sockeye salmon, and where possible Fraser River sockeye salmon, in freshwater and marine environments across all life stages.

Scope of Work

- 3.1 The Contractor will compile all published evidence for climate change and climate related effects on sockeye salmon in freshwater and marine habitats across all life stages.
- 3.2 Literature will be compiled from the primary scientific peer-reviewed sources (found using ISI Web of Knowledge and Aquatic Sciences database, and Fisheries Abstracts

- database) and from grey literature (e.g. technical reports by government and fishery management agencies, theses).
- 3.3 Key words in the literature search will include but not be limited to effects of climaterelated variables such as temperature, flow, salinity, pH, currents, primary productivity and interspecific interactions on Fraser River sockeye survival, behaviour and distribution in both freshwater and marine habitats and life stages in each environment.
- 3.4 Literature will also be sought in this compilation related to how Pacific salmon (especially sockeye salmon) are or may be showing potential adaptive responses to climate change, or climate related variables, and for how potential mitigation measures could be taken by salmon management agencies.

Deliverables

- 4.1 The Contractor will organize a Project Inception meeting to be held prior to June 1,, 2010 in the Commission office.
- 4.2 The primary deliverable is an electronic database that compiles all literature dealing with climate change and climate related variables on Pacific salmon, with a key focus on sockeye salmon and where possible, Fraser River sockeye. This database will be provided to the UBC contractor who is preparing the technical report and analysis of the documented and projected effects of climate related variables and climate change on Fraser River sockeye in freshwater and marine environments across all life stages. The Contractor for the literature compilation will meet regularly with, and provide input, feedback and guidance to, the UBC Contractor conducting the climate change analysis and report.
- 4.3 The electronic database will be delivered to the UBC Contractor and the Scientific Authority by August 15, 2010,
- 4.4 The Consultant will make themself available to Commission Counsel during hearing preparation and may be called as a witness.
- 4.5 The Consultant will participate in a 2-day scientific workshop in late-November, 2010 with the Scientific Advisory Panel and other consultants preparing Cohen Commission Technical Reports to address cumulative effects and to initiate discussions about the possible causes of the decline and of the 2009 run failure.

- 4.6 The Consultant will participate in a 1-day meeting presenting to and engaging with the Participants and the public on the results of the diseases and parasite investigations in February, 2011.
- 4.7 The Consultant will participate in a 1-day scientific workshop in February, 2011 with the Scientific Advisory Panel and other consultants preparing Cohen Commission Technical Reports to address possible causes of the decline and of the 2009 run failure.

APPENDIX 2

Statement of Work: Eduardo Martins

Cohen Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River

"Effects of Climate Change on Fraser River Sockeye Salmon: Review and Analysis Document"

Background

- 1.4 The Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River (www.cohencommission.ca) was established to investigate and report on the reasons for the decline and the long term prospects for Fraser River sockeye salmon stocks and to determine whether changes need to be made to fisheries management policies, practices and procedures.
- 1.5 There is growing evidence that climate change, both anthropogenic and non-anthropogenic, may be affecting sockeye habitats in freshwater and marine environments.
- 1.6 A review of the evidence for the occurrence and effects of climate change on Fraser River sockeye is required to evaluate the importance of the climatic trends on their ecology and survival and to determine the role of climate in the Fraser River sockeye run failure of 2009.

Objective

2.1 To prepare a technical report and analysis on the documented and projected effects of climate related variables and climate change on Fraser River sockeye in freshwater and marine environments across all life stages.

Scope of Work

- 3.5 The Contractor will review published evidence for climate change effects on Fraser River sockeye in freshwater and marine habitats across all life stages. The review will also consider projected impacts of climate change on Fraser River sockeye in the future.
- 3.6 The review will be based on a literature database created by S. Hinch (Contractor for the "Effects of Climate Change on Fraser River Sockeye Salmon: Literature Compilation").

- 3.7 The review will look specifically for evidence of the effects of climate-related variables such as temperature, flow, salinity, pH, currents, primary productivity and interspecific interactions on Fraser River sockeye survival, behaviour and distribution. Climate change effects will be separated into freshwater and marine habitats and life stages in each environment.
- 3.8 The review will also look for evidence for potential adaptive responses of Fraser River sockeye to climate change and for potential mitigation measures that could be taken by management agencies.

Deliverables

- 4.1 The Consultant will organize a Project Inception meeting to be held prior to June 1'10 in the Commission office.
- 4.2 The main deliverables of the contract are 2 reports evaluating the effects of climate change on Fraser river sockeye: 1) a progress report, and 2) a final report.
- 4.3 A Progress Report (maximum 20 pages) will be provided to the Cohen Commission in pdf and Word formats by Nov. 1, 2010. Comments on the Progress Report will be returned to the contractor by Nov. 15, 2010.
- 4.4 A draft Final Report will be provided to the Cohen Commission in pdf and Word formats by Dec. 15, 2010. Comments on the draft Final Report will be returned to the contractor by Jan. 15, 2011 with revisions due by Jan. 31, 2011.
- 4.5 The Consultant will make themself available to Commission Counsel during hearing preparation and may be called as a witness.
- 4.6 The Consultant will participate in a 2-day scientific workshop in late-November, 2010 with the Scientific Advisory Panel and other consultants preparing Cohen Commission Technical Reports to address cumulative effects and to initiate discussions about the possible causes of the decline and of the 2009 run failure.
- 4.7 The Consultant will participate in a 1-day meeting presenting to and engaging with the Participants and the public on the results of the climate change investigations in February, 2011.
- 4.8 The Consultant will participate in a 1-day scientific workshop in February, 2011 with the Scientific Advisory Panel and other consultants preparing Cohen Commission Technical Reports to address possible causes of the decline and of the 2009 run failure.

APPENDIX 3

Reviewers' comments with authors' responses

Report Title: Climate Change

Reviewer Name: Dr. Steven J. Cooke

Date: January 3, 2011

The authors' responses to reviewer comments are provided in bold text after each paragraph where a response is needed. References for publications cited on the responses are provided unless they are already listed on section 5 (Literature cited) of the revised report.

1. Identify the strengths and weaknesses of this report.

Note – The report is divided into two separate sections so for the purpose of this review I provide separate comments for each section and where appropriate discuss their integration. As a preamble, I like the clarity and organization (including bulleted executive summary) for both reports.

The real strength is the integration of material and concepts from diverse disciplines. For example, the authors combine information from physiological ecology, behaviour, and evolutionary biology (and more) to provide an overview of the mechanisms associated with the patterns (e.g., in timing and mortality) that are observed.

I also appreciate the integration of new/forthcoming material. Although such material has not yet been subject to full peer review, in some cases it can help to illuminate biological phenomena, particularly given that some of these topics represent frontiers in biology and thus there is a rapidly evolving literature.

The report is fairly easy to read with ample subheadings. It is also a very clean manuscript (few typos). Both sections could be submitted to peer reviewed journals with little additional effort. The authors have grounded their work around Fraser sockeye but have also pulled upon global literature as needed. I am unaware of a similar synthesis for any Pacific salmon species or system elsewhere.

Report 1. This report is titled "Adult mortality during river migration and on spawning grounds" with stated objectives to "review the major environmental factors responsible for adult sockeye salmon mortality during Fraser River migrations and for premature mortality on spawning grounds, review the early migration – high mortality Late-run sockeye phenomenon, describe interannual and within-year among stock patterns in adult mortality, provide a mechanistic understanding for several of these patterns, and identify scientific knowledge gaps that need to be filled in order to facilitate the improvement of sockeye management". Clearly the scope for this report is wide which

is a strength but would have been a challenge for the authors.

The authors could discuss why large numbers of dead fish are not observed – see work by Fraser E-Watch published in NAJFM a few years back. Probably insert around line 560.

Response: Suggestion has been incorporated (see last paragraph on subsection 2.4).

Report 2. This report is titled "The effects of climate and climate change on survival of Fraser River sockeye salmon". The report is a quantitative literature review with a focus on evaluating recent trends in abundance and productivity. It is worth noting that unlike Report 1 which focused on upriver spawning migration of adults (aside from some limited coverage of intergenerational effects), this report covers are life history phases including early life history and marine phases. The authors provided a highly transparent overview of how literature was identified and sorted, something essential when conducting an evidence-based literature review. In their review they examined the influence of climate-related variables on survival. An inherent limitation is that many studies estimated mortality indirectly using productivity indices rather than directly through direct observation or the analysis of tagging data. In developing a qualitative ranking more weighting was given to field data which seems appropriate.

Response: We have added to our recommendations on future research directions that estimates of survival be obtained directly with statistical methods designed specifically to analyse data from tagged animals (i.e. capture-mark-recapture methods). See research recommendation (iv) on Section 4.

The historical context re fluctuating salmon populations pre European settlement is a great idea! (around Lines 1396). It may be worth mentioning how such data was generated/obtained (paleolimnology/anthropology).

Response: Suggestion has been incorporated (see second paragraph on subsection 1.1)

In the text describing methods associated with quantitative literature review, it may be useful to describe WHY you are extracting the various information. Some of them are obvious (e.g., decade to look at temporal trends) but others are less intuitive (e.g., electronic tags – why?).

Response: Suggestion has been incorporated (see subsection 1.3)

Line 1688 – Given all of the telemetry studies that have been conducted on spawning migrations of sockeye over the past 10yrs or so, is there any empirical evidence to show that migrations are slowed or otherwise impeded (morts) with high flows? I am aware of the papers cited but I can't think of any telemetry data-sets that have been explored in that way. Perhaps that is a future research opportunity – mining the telemetry datasets

to examine flows – similar to how Martins et al. (2010 Global Change Biology) examined temperature in their recent paper.

Response: To our knowledge there are only two telemetry studies that have attempted to link survival of adult migrating sockeye salmon to flows (Naughton et al. 2005; Keefer et al. 2008). Both authors have found that survival is lower during periods of low flows but high temperatures. In fact, the authors have noted that it is not possible to disentangle the roles of temperature and flow on survival since the two variables are inversely correlated; however they discuss temperature as the factor likely driving survival of migrating sockeye salmon. In accordance with these authors, we believe that most associations between flow and survival of adult migrating sockeye salmon uncovered with telemetry studies will likely reflect the effects of temperature on survival. However, it is important to note that during years or periods of extremely high discharge, survival of migrating sockeye salmon can indeed be impacted by flows (Macdonald 2000; Rand et al. 2006).

2. Evaluate the interpretation of the available data, and the validity of any derived conclusions. Overall, does the report represent the best scientific interpretation of the available data?

Report 1.

Ln 781 – The authors cite preliminary data from Karl English for the assertion that "few" sockeye made it to spawning grounds that were tagged in July. This is an important point and should be elaborated upon (with real numbers and more details) if at all possible. This links to Ln 801 where it states that the authors were unable to confirm mortality estimates for 2009 (and 2010). Given the relative importance of the data from 2009, and the fact that it is now 1.5 yrs since data was collected, is there not some reporting completed? If not, this should be made a priority (not be the authors per se but those with the data in hand) so that such information can inform the inquiry.

Response: We do not have the actual numbers or more details as this information was obtained from a presentation made at a public forum by Karl English (LGL Ltd.), whom should be contacted to determine if a report is publicly available on these data.

Report 2.

The qualitative assessment of stage-specific population declines that could be attributable to climate change suggested that most stages have likely declined. The authors, however, note that generalizing was not possible due to stock-specific differences. Perhaps the authors could elaborate on the stock specific differences that exist. I also could not find the term "local adaptation" which is the mechanism that would explain such patterns.

Response: Due to the integration of the two reports in the revised version, stockspecific differences are now discussed in detail on Section 2. The term 'local adaptation' is now used throughout the report where applicable.

The general finding of the quantitative aspects of the literature review are fascinating and provide a very clear picture of what we know and what we do not know. I like this approach because it means that the "state of the science" and associated recommendations for future research can be identified and justified based on the analysis. Such an approach would be useful for many of the other reports being prepared for the Cohen Commission.

The fact that most of the marine work related to sockeye and climate change is correlational points to some obvious research needs.

The section on the qualitative assessment of the effects of recent climate change (see around lines 1797) has a series of transparent criteria that were used to categorize different life history phases relative to whether climate change may be implicated in declines. Without these criteria the assessment would be speculative but there criteria bring some level of rigour to the evaluation. I much prefer this approach than relying only on "expert opinion".

The discussion of potential for evolutionary change is somewhat speculative but that is simply because for the most part we are forced to rely on modeling exercises. Only time will tell!

The adaptation strategies are a logical inclusion and relate to both the activities of the Cohen Commission but more generally to Pacific (and Atlantic) salmon waters in Canada.

3. Are there additional quantitative or qualitative ways to evaluate the subject area not considered in this report? How could the analysis be improved?

Report 1 –

The authors emphasize the growing body of knowledge emanating from field telemetry studies. However, it is also worth paying homage to the many past and ongoing tagging (using anchor tags, spaghetti tags, Petersen discs, etc) studies conducted by stock assessment to evaluate en route loss, typically closer to spawning grounds (e.g., work by DFO near Ashcroft in 2002). I certainly agree that telemetry approaches are essential but I think there is information that can also be obtained from other techniques. There may be some DFO tech reports (stock assessment) that could be referenced.

Response: Suggestion has been incorporated. See research recommendation (iv) on Section 4.

The figure on page 41 (Figure 7) is an interesting way to emphasize the extent of en route loss in recent years. Figure 12 is also effective.

4. Are the recommendations provided in this report supportable? Do you have any further recommendations to add?

Both reports provide clear research agendas. I think that presenting several specific examples for each general research topic would be useful.

Response: Examples have been added throughout the research recommendations. See Section 4.

Report 1.

I think that the recognition and study of stock-specific variation as it relates to en route mortality and pre-spawn mortality as well as how that mediates interactions with temperature, fisheries, etc is critical. The authors mention it in several places but I suggest that this deserves its own research recommendation. Included could also be reference to inter-sexual variation – not just stock-specific. Perhaps calling the section "Extent and consequences of intra-specific variation" would work as a catch-all.

Response: Recommendation that research programs focus on inter-stock variability was originally included in Report 2. See research recommendation (v) on Section 4 of the revised report. Suggestion to include recommendation on research on inter-sexual variation in survival has been incorporated. See research recommendation (vi) on Section 4.

5. What information, if any, should be collected in the future to improve our understanding of this subject area?

Report 1.

An additional research priority would be to tag dead salmon at various parts of their migration to better understand the behaviour of carcasses. For example, if a fish dies at location X, does it stay there of wash downstream? Are there areas in which mortalities stack up and can these be monitored to examine/identify en route mortality?

Response: This is an interesting research topic but more related to the dynamic of sockeye salmon carcasses in the Fraser River, not the patterns and mechanisms associated with their mortality, which was the scope of our report.

Ln 898-899 – Additional justification is that there are clearly some interesting dynamics in Fraser sockeye upriver migration in the recent 15 years. Telemetry doesn't really work in a reactive manner – e.g., you can't study the 2009 losses in 2010. As such, it

makes sense to use it as a backbone standard method such that the data is available when it is needed. The authors may also wish to mention that the cost of telemetry tags is coming down so it is possible to mount such studies without breaking the bank and to also obtain sample sizes that do have relevance to the population.

Response: The importance of continued telemetry programs has been emphasized. See research recommendations (i) and (iv) on Section 4.

Report 2.

For the final research recommendation (i.e., cumulative effects) I would encourage the authors to also consider the potential for carry-over effects – the notion that stressors at one stage may carry-over to influence the condition or how an animal responds to stressors at a different life history phase or different location during migration. This idea is included here but should be termed "carry-over effects" where appropriate to be consistent with the emerging literature on that topic (mostly from avian migration literature).

Response: Suggestion has been incorporated and the term "carry-over effect" now appears in the recommendation when it is applicable. See research recommendation (ix) on Section 4.

6. Please provide any specific comments for the authors.

Line 293 to 315 is an excellent overview/intro without being redundant with material in the body of the report.

Ln 313 – It is semelparity and not anadromy that means they only have one opportunity to spawn. Some (many) anadromous species are iteroparous.

Response: The correct term (semelparity) has been included.

Ln 756 – Clarify "how" energy levels were depleted.

Response: Suggestion has been incorporated (see fourth paragraph on subsection 2.7).

Ln 820 – is "productivity" the correct word here? (Or clarify as per line 832).

Response: Yes, productivity is the correct word and is now defined there.

Ln 889 – Period missing.

Response: Period has been added.

Figure 8 – The x-axis is hard to read.

Response: x-axis of Figure 8 (Figure 2.8 of revised report) has been improved.

Ln 2039 – Please clarify that it is not the harvest that is relevant here, but what happens to those that are released or escape.

Response: Suggestion has been incorporated. See research recommendation (vii) on Section 4.

Ln 2036 – The subtitle "direct species management" is odd – consider changing.

Response: The section where the referred subtitle appeared in the draft report was reformulated and does not contain subtitles anymore.

Ln 2093 – In the research agenda the authors suggest the use of a range of novel approaches and technologies yet provide few references (e.g., cite Kim Holland for business card tags, the review by Cooke et al. 2004 for sensors, etc).

Response: References have been added.

Report Title: Adult Mortality during River Migration and on Spawning Grounds.

Reviewer Name: Ken Ashley

Date: January 2, 2011

The authors' responses to reviewer comments are provided in bold text after each paragraph(s) where a response is needed. References for publications cited on the responses are provided unless they are already listed on section 5 (Literature cited) of the revised report.

1. Identify the strengths and weaknesses of this report.

The strength of this report is that it was prepared by Dr. Scott Hinch who is one of the leading researchers on sockeye physiology on their approach to, and during upstream migration in the Fraser River. Much of the recent knowledge on run timing and en route sockeye mortality as a function of river discharge and water temperature has been a direct result of Dr. Hinch's UBC team led research efforts. This research builds on the classic physiological studies of Dr. Brett at DFO-PBS, and through the use of new tools and techniques, greatly increases the knowledge base on this critical phase of sockeye life history.

There are no weaknesses in this report. Dr. Hinch is an internationally recognized expert in this subject area, and the report is comprehensive and well written.

2. Evaluate the interpretation of the available data, and the validity of any derived conclusions. Overall, does the report represent the best scientific interpretation of the available data?

The interpretation of the available data, and the validity of the conclusions derived from the interpretation are sound. Overall, the report presents the best current scientific synthesis and interpretation of the available data on the subject of adult sockeye salmon mortality during river migration, and pre-spawn mortality on spawning grounds.

3. Are there additional quantitative or qualitative ways to evaluate the subject area not considered in this report? How could the analysis be improved?

I do not believe there are any quantitative or qualitative ways to evaluate the subject area that are not considered in this report.

I do not believe there are any substantive opportunities to improve the analysis presented in this report.

4. Are the recommendations provided in this report supportable? Do you have any further recommendations to add?

I have two additional recommendations:

- 1. All six of the recommendations in this report should be implemented by DFO's core operational program, and not be viewed as optional by DFO management;
- 2. A inventory and analysis should be conducted in the Fraser River watershed to quantify the volumes, effluent temperatures and thermal warming potential of all large municipal water (i.e., sewage treatment plant discharges) and industrial water discharges (mainly pulp and paper mills) to determine if these discharges could have a cumulative effect on water temperature of the Fraser River, or any key tributaries, during the critical upriver migration phase for adult sockeye.

Response: Suggestion has been incorporated. See research recommendation (viii) on Section 4.

5. What information, if any, should be collected in the future to improve our understanding of this subject area?

Most of the subject areas on en route mortality have been thoroughly researched and documented. It is noted in the report that the study of intergenerational effects in wild Pacific salmon is in its infancy, and the results to date are limited, and equivocal, hence this should become a priority research area.

The remaining topic area that is not well understood is the causal mechanisms for the early migration of Late run sockeye.

The fact that these sockeye arrive physiologically stressed at the Fraser River estuary, and the apparent correlation between open ocean wind speed and river entry timing of some Late-run stocks indicates the causal factor is occurring in the open ocean at some time during the adult, and possibly sub-adult life history of the sockeye. Logically, this warrants increased research efforts towards understanding the relationship between climate, oceanographic conditions and sockeye behaviour. Knowing where the sockeye are in the North Pacific during their open ocean phase, and the physical, chemical and biological conditions they encounter, is a major knowledge gap in terms of understanding sockeye life history, as the near-shore, estuarine, river and lake components of their life history range from sufficiently to very well understood, as compared to the current 'black box' state of open ocean knowledge.

Until relatively recently, it was technologically impossible to conduct high seas tracking of sockeye. However, the recent development of real time and archival microelectronic tags, and integration with acoustic, satellite, and oceanographic buoys should make this technologically possible now, or in the immediate future.

For example, more than 3,000 ARGO oceanographic buoys have been deployed globally, many of them in the North Pacific (Figure 1). Given the recent advances in the miniaturization of electronic tags, and the ability to have tags activate at specified future dates, it should be possible to tag sockeye smolts, and then have the signals go dormant for several months after the smolts have left the continental shelf, and then periodically activate and communicate their position to new ARGO buoys. This would allow comparison of ocean survival of various stocks, and should be able to address the question why some sockeye, like the Harrison stock, are increasing in population size while other stocks are returning from the open ocean in an already stressed condition.

Presumably new ARGO buoys could be adapted to receive various forms of telemetry data from sockeye, as approximately 750 ARGO buoys are deployed annually to sustain the system and replace missing or expired buoys. At present, the buoys have a nominal spacing of 300 km depending on current direction and velocity; however this could be modified in the North Pacific to increase spatial resolution.



Figure 1. Global distribution of ARGOs buoys as of September, 2009 showing density of buoys in the North Pacific.

Response: We agree that further research efforts should be directed at understanding the marine life of sockeye salmon and how they are affected by climate and oceanographic conditions, and that recent technological advances promise exciting avenues for research on these topics. The need for such research efforts and the application of various technologies were originally discussed in our climate change report (suggestion to use Argos buoys has now been included in the revised report). See research recommendation (i) on Section 4.

The question and potential linkage between open net pen salmon farms and disease/parasite amplification and ocean survival remains was not addressed in this review as no information on this topic was presented at the Nov 30-Dec 1, 2010

workshop.

Response: This topic is being covered by another report commissioned by the Cohen Inquiry.

6. Please provide any specific comments for the authors.

There are no specific comments for the authors.

Report Title: The Effects of Climate and Climate Change on Survival of Fraser River Sockeye Salmon: a Literature Review to Evaluate Recent Trends in Abundance and Productivity.

Reviewer Name: Ken Ashley

Date: January 3, 2010

The authors' responses to reviewer comments are provided in bold text after each paragraph(s) where a response is needed. References for publications cited on the responses are provided unless they are already listed on section 5 (Literature cited) of the revised report.

1. Identify the strengths and weaknesses of this report.

The strength of this report is that it represents an up to date electronic literature search of the primary and grey literature that contains information evaluating the effects of climate and climate change on the biology and ecology of sockeye salmon at all life stages, and that this report was conducted by knowledgeable researchers who had experience evaluating the effects of water temperature and discharge on en route and pre-spawn mortality of sockeye salmon in the Fraser River.

The weakness of this report, as is the case with any broad literature review, is as follows:

- 1. That it does not capture all of the information that may be relevant as some of the research may not be published yet, or is not even being conducted, hence cannot be captured in an electronic literature search;
- 2. The subject area is so broad and interdisciplinary that some subject areas, particularly those with little or no published research, but potentially high relevance, may not receive adequate attention in the literature search, or in the subsequent interpretation and analysis for the report.

These comments are not a criticism of this report per se, but of the difficulty of trying to comprehend the situation and write a report on a complex large scale event which is occurring in real time with incomplete information superimposed on a background which is naturally variable.

Reports of this nature are always easier to write after the fact, which in the case of Fraser River sockeye, would be of considerably less value and would miss the opportunity to provide proactive solutions to the problem of missing/declining sockeye salmon productivity in the Fraser River.

2. Evaluate the interpretation of the available data, and the validity of any derived conclusions. Overall, does the report represent the best scientific interpretation of the available data?

The interpretation of the available data, and the validity of the derived conclusions are scientifically defensible. A detailed literature search using two recognized academic search engines coupled with a qualitative weight-of-evidence approach was used to assess the likelihood that life cycle specific survival has been undergoing a trend in the past 20 years due to recent trends in climate.

The report, subject to the limitations of the search engines ability to locate relevant information and the qualitative weight of evidence approach, provides a good interpretation of the available data.

3. Are there additional quantitative or qualitative ways to evaluate the subject area not considered in this report? How could the analysis be improved?

Given the interdisciplinary nature of the subject, and the knowledge gaps in certain topic areas (e.g., open ocean sub-adult and adult survival), a larger group of selected scientists may have been able to provide additional input to the qualitative evaluation process. However, this would increase the cost and complexity of the review, and a large interdisciplinary workshop had already been conducted on June 15-17, 2010 in Nanaimo that the authors of this report attended. Hence, this report likely benefited from the presentations and discussions of the Nanaimo workshop in addition to the authors personal research experience and review of the published literature.

Therefore, it is unlikely that the analysis could be improved in any substantive way.

4. Are the recommendations provided in this report supportable? Do you have any further recommendations to add?

The recommendations provided in this report are supportable, subject to the limitations of the search engines ability to locate relevant information.

The habitat protection recommendations did not propose any innovative, large scale concepts to cool the Fraser River or prevent/minimize future warming. The report indicates a recent panel of experts rated this alternative as impractical and likely ineffective (McDaniels et al. 2010), however, the authors of this report were did not have civil engineering or riparian silviculture training. I would recommend that an interdisciplinary workshop with fisheries scientists, professional foresters, environmental and civil engineers be held to examine the feasibility of large scale biotic (i.e., riparian planting) and abiotic ideas (i.e., hypolimnetic discharges and geotextile sunscreens over narrow sections of the Fraser River canyon) to determine if any of these 'blue sky' alternatives were feasible and potentially effective.

In terms of habitat protection, a logical recommendation is for the Provincial

Government, who has statutory authority for water management in British Columbia, is to quickly identify and enact groundwater and surface water thermal protection zones on all Fraser River sockeye ecosystems in BC. This would include buy-back of existing water licences, moratorium on future ground water licensing and surface water licences in critical 'thermal protection areas' and the provision of financial incentives for large volume water users to develop more efficient uses of water for irrigation and industry, and to encourage/mandate heat recovery on large industrial discharge to prevent incremental heating from effluent discharges.

For example, several pulp and paper mills and the Greater Vancouver Regional District discharge large volumes of heated wastewater effluent in the Fraser River. GVRD has three sewage treatment plants on the Fraser River – Annacis Island, Lulu Island and Northwest Langley, which may be increasing the ambient temperature of the Fraser River. The TMDL (total maximum daily load) approach was originally developed to control pollution of streams, lakes and rivers by contaminants, and is now being applied in Washington State and Idaho to protect streams and rivers from thermal warming. A similar Thermal TMDL program should be implemented in BC to protect Fraser River sockeye stocks from future climatic warming.

A stated in the report, another non-climate stressor of salmon are predators and strategies directed at stopping the spread of species that prey on fry and smolts. The Provincial Fish and Wildlife Branch has just concluded a four year multi-million dollar eradication program of illegally introduced spiny ray fish in the Shuswap basin, to prevent the spread of spiny ray fish into Shuswap lake. While this program has been successful, the Provincial Government and DFO have ignored a larger problem of illegally introduced spiny ray fish in the Beaver Creek system near Williams Lake, and these fish will eventually migrate into Quesnel Lake and threaten the Quesnel sockeye stocks. The Federal government should override regional DFO and Provincial 'penny pinching' on this expanding crisis, and initiate an immediate large scale spiny ray eradication program, because once the spiny rays reach Quesnel Lake the problem will become irreversible. The cost to eradicate spiny rays in this system was estimated at 5 million dollars in 2009.

Response: The section on management strategies has been shortened and moved out of the recommendation section of the report as such strategies have actually been suggested by other authors (e.g. McDaniels *et al.* 2010; Nelitz *et al.* 2007). We refer the reader to these publications for detail on proposed strategies to lessen the impact of climate change effects on sockeye salmon (see subsection 1.7.3).

5. What information, if any, should be collected in the future to improve our understanding of this subject area?

Future information that should be collected to improve our understanding of this subject area should focus on how climate change is influencing the physics, water chemistry and ecology of the open ocean. For example, the increasing acidity of the open ocean

is particularly worrisome, as this may negatively affect planktonic organisms that ocean feeding sockeye rely on for growth and maturation (see UNEP 2010. UNEP Emerging Issues: Environmental Consequences of Ocean Acidification: A Threat to Food Security).

Response: There is a relatively fair understanding in the literature on how climate change is and will affect the physical and chemical characteristics of the oceans. What is less understood is how these changes are affecting and will affect the ecology of sockeye salmon in the marine environment. Recommendations to encourage studies linking climate-driven changes in the ocean, such as acidification, to the ecology of sockeye salmon had already been included in our report. See research recommendation (i) on Section 4.

Secondly, each nursery lake in the Fraser watershed should undergo a paleolimnological analysis to determine long term fluctuations in sockeye escapement. The 20 year time frame used in this report (unless specifically requested by the Cohen Commission) is likely too short to distinguish trends in climate change occurring in the ocean from naturally occurring inter-annual (e.g., ENSO), inter-decadal trends (i.e., PDO) and millennial scale variations in climate. Paleolimnology is a particularly useful tool to examine the distant past, and is sufficiently developed as a forensic technique that multi-proxy indicators can be used to estimate historic sockeye escapement before the Industrial Revolution began to alter the concentration of greenhouse gases in the atmosphere (see newspaper image below for example).



Response: The 20-year time frame is indeed too short to distinguish trends in climate change occurring in the ocean from inter-annual and inter-decadal variability in climate; however that limitation was pointed out in the report when describing climate-driven changes in the ocean (see subsection 1.5.2). The reviewer suggests we add as a recommendation that "each nursery lake in the Fraser watershed should undergo a paleolimnological analysis to determine long term fluctuations in sockeye escapement". While the field of paleolimnology offer techniques to reconstruct historical escapements of sockeye salmon by tracking changes in marine-derived nutrients in sediment cores of lakes using geochemical (e.g. stable nitrogen isotopes) and biological (e.g. diatoms) proxies, it is not possible to make such reconstructions in all salmon nursery lakes (MacDuffee & MacIsaac 2009). A recent study has shown that paleolimnological records failed to register known/dramatic decreases in Fraser River sockeye salmon abundance (i.e. after Hells Gate landslide, onset and intensification of commercial fishery), raising the possibility that paleolimnological techniques may not be useful to reconstruct historical Fraser River sockeye salmon escapements (Hobbs & Wolfe 2008). Hobbs & Wolfe (2007) suggest that "catchment-derived nutrients [instead of salmon-derived nutrients, which seem to dominate the sediment of Alaskan lakes] appear to dominate the sediment geochemical records from lakes within the interior and coastal regions of BC in addition to shaping their diatom records". Nonetheless, this is a valuable tool for future research efforts. We have cited the utility of this approach in our report when we introduced the concept of long-term climate related variability in salmon abundance (see subsection 1.1).

Hobbs, W. O. & Wolfe, A. P. (2007) Caveats on the use of paleolimnology to infer Pacific salmon returns. *Limnology and Oceanography*, 52, 2053-2061.

Hobbs, W. O. & Wolfe, A. P. (2008) Recent paleolimnology of three lakes in the Fraser River Basin (BC, Canada): no response to the collapse of sockeye salmon stocks following the Hells Gate landslides. *Journal of Paleolimnology*, 40, 295-308.

MacDuffee, M. & MacIsaac, M. (2009) Applications of Paleolimnology to Sockeye Salmon Nursery Lakes and Ecosystems in the Pacific Northwest and Alaska: Proceedings of a Workshop at the Institute of Ocean Sciences, October 8-9, 2008. Canadian Technical Report of Fisheries and Aquatic Sciences, 2848.

6. Please provide any specific comments for the authors.

There are no specific comments for the authors.

Report Title: Enroute mortality/climate change: Hinch and Martins/Martins and Hinch

Reviewer Name: Eric Taylor

Date: January, 2011

The authors' responses to reviewer comments are provided in bold text after each paragraph(s) where a response is needed. References for publications cited on the responses are provided unless they are already listed on section 5 (Literature cited) of the revised report.

1. Identify the strengths and weaknesses of this report.

Strengths

- **1.** It is well-written and organized.
- 2. It is written by, arguably, the world expert on energetics of upriver-migrating salmon (Hinch).
- 3. It produces a strong case for the idea that temperature stress during upriver migration has profound influences on realized spawning escapement (i.e., those fish that actually make it to the spawning grounds) as well as the implications of pre-spawning mortality. I think that it is fair to state that most salmon biologists, while perhaps familiar with the concept and implications of pre-spawning mortality have not generally appreciated the idea of *en route* mortality or the processes that drive it.
- 4. It presents a strong case and example of the value of inter-agency/institutional research where collaborations between gov't and other agencies (PSC) and universities have lead to interesting and very useful scientific insights.

Weaknesses

1. Personally, I found the separation of the two reports a bit distracting and biologically illogical. The issue of climate changes (really warming) is so closely related to one of the major processes involved in *en route* mortality (thermal stress) that it would be better to integrate into one report. In addition, the reports are obviously relevant to sustainability of sockeye salmon in the Fraser system, but the relevance to the wild variation in return levels since the 1990s seems less clear to me. These reports focus on what happens to the fish once they enter the river (which is obviously important). What is less clear is how all this work relates to unexplained variance between expected returns one smolts leave the Fraser and adults that eventually return (i.e., marine mortality). It is possible that "intergenerational effects" of thermal stress actually impact marine survival. I think this potential link should be empahsized more, evemn as just a hypothesis.

Response: The two reports have been integrated into one, but are presented as separate sections since the issues of *en route* mortality and early-entry behaviour

are not necessarily related to climate change. The possibility that intergenerational effects may impact marine survival and hence productivity had already been included in the draft report under "Effects of *en route* and prespawn mortality on population trends" (see subsection 2.10 of revised report). In the revised report, we discuss intergenerational effects in more detail (see subsection 2.9) and present a specific recommendation for research on this topic (see research recommendation (ix) on Section 4)

2. The issue of "fine-tuning" of individual populations of sockeye salmon to thermal regimes historically encountered during river entry is likely an example of local adaptation – an extremely well-known, documented and appreciated aspect of the biology of salmon, especially Pacific salmon. The report never really explicitly identifies this as "local adaptation", but uses vague terms like "physiologically finely-tuned" and gives the impression that the recent and nice work on thermal biology of sockeye salmon is somehow a novel finding in terms of local adaptation which of course it is not (in fact, the lakeward directional migrations of sockeye salmon fry are perhaps one of the best known examples of local adaptation). This recent thermal biology work **is** a very detailed and interesting example of a well-known phenomenon (local adaptation) with clear implications for persistence of sockeye salmon biodiversity within the Fraser Basin. The work on thermal biology should be "re-couched" in terms of the broader phenomenon (local adaptation) which will give it greater context, scope, and impact.

Response: We had actually explicitly identified the phenomenon as local adaptation in the sentence appearing just before the one pointed out by the reviewer. However, we have now defined the process of local adaptation in the revised report (see second paragraph on subsection 2.6)

With respect to what the Cohen Commission is looking for, the narrow scope of this aspect of the report is fine, I just think the lack of a broader perspective and the explicit discussion of the very well known phenomenon of local adaptation (see Heredity Jan. 2011) reflects poor scholarship. Ditto for comments on "intergenerational effects" below.

Response: We have kept the scope of the revised report narrow for the purposes of the work of the Cohen Commission.

3. In many cases (e.g., "stressed" condition of sockeye salmon, "fine-tuning" of thermal tolerance by population) it is impossible to really evaluate the data or inferences from these data as the original data are not presented in the report. There are some summary figures (e.g., Fig. 9 of report 1), but lack of any accompanying statistical analyses detracts from the impact of these figures. Some more details are in published papers, but these are cumbersome to track down or impossible in some cases (unpublished in prep. PhD and MSc theses). Some of these critical data may be under publishing embargos (e.g., Miller *Science* paper, but now published) and this is unavoidable, but the fact remains that the data critical to these important inferences are not actually available for inspection in the Cohen report.

Response: Statistical information, where not published elsewhere, has been included on relevant figures. We have attempted to reduce references to 'unpublished data' – the few instances where we still make reference to unpublished data pertains to graduate student thesis material that is in preparation for publication (or have been submitted for publication and/or are embargoed) but they are used exclusively to show 'broader' support for a given point and are not the exclusive reference for a given point, for which we always use published references as primary support for statements of fact.

4. In many ways, the description and ideas in the section on "intergenerational effects" (line 803) are the most interesting and provide the possibly most direct linkages amongst temperature-related effects and persistence of Fraser River sockeye salmon. Again, however, the authors appear to imply this is somehow a novel scientific finding, yet it is not (any "novelty" rests in the study of this phenomenon with respect to sockeye salmon population viability *per se*). This is an example of the well-known and studied phenomenon of "maternal effects" (and also "paternal effects") which has a long history of study in evolutionary biology as well as more applied fields of aquaculture. Here, the authors cite a narrow range of studies including MSc thesis, in press reviews, unpublished presentations, etc when they should incorporate at least some of the rich literature on maternal effects (yes, it will be on species other than *Oncorhynchus* spp.) which, again, will give the current report more generality and scope.

Response: A recent literature review, co-authored by the lead author of our report, revealed that there are no publications on the effects of parental temperature exposure on offspring in Pacific salmon (Burt *et al.* in press); therefore such studies would be novel for sockeye salmon. This point has been made clear in the revised report along with a more extensive general discussion of intergenerational effects (see subsection 2.9)

5. I am not sure that I understand the authors point about productivity and *en route* mortality beginning on line 832. As I read the report, the point of the Peterman et al. conclusion is that freshwater en route mortality, or more properly I think the physiological stresses that contribute to it, does not influence "productivity" per female spawner as defined by the number of fish returning to coastal fishing areas. Assuming that the data are valid on this point (i.e., returns to coastal areas are accurate by population) this seems to be an important point regarding possible "intergenerational effects". If the returns to coastal areas do not appear to be affected by the river conditions that the parents encountered on their migration upstream (the Peterman et al. 2010 conclusion), then this would seem to argue against any intergenerational effects (at least for recruitment to coastal fishing areas). Perhaps intergenerational effects are manifest in subsequent upriver migration which will influence the *abundance* of spawners and productivity assessed to include upriver migration patterns. Regardless, as written, the authors appear to be mixing apples (to coast productivity) with oranges (total returns to spawning areas) and I think they should clean this part

up a bit. In addition, I disagree with the conclusion by the authors that it was "impossible" for Peterman et al. to test the hypothesis of *en route* effects contributing to productivity declines. They, apparently, **were** able to test it under one definition of productivity (recruitment to coastal areas), but it is the **definition** of productivity that the current authors disagree with or raise caveats about. This should be clarified in the revision.

Response: The referred statement in Peterman *et al.* (2010) simply means that *en route* mortality in year t does not relate to productivity because recruits are defined as the number of fish that arrive on coastal areas in that same year (i.e. before any *en route* mortality occurs). Therefore, *en route* loss does not contribute to productivity under the definition adopted in that report. However, the authors point out that intergenerational effects could potentially contribute to declines in productivity (e.g. stressful river conditions experienced by parents [and leading to high *en route* losses] in year t could result in subsequent low offspring performance and survival and lead to low returns in year t+4) but that there is little evidence to their occurrence at this point. We have clarified this point in the report (see subsection 2.10)

5. The reports are largely based on information for "stock aggregates" (early Stuart, Chilko). These are big systems and how do they relate to the definition of the > 30 conservation units defined by DFO?? How will these data on "stock aggregates" mesh with DFO conservation units?? How, for instance, will the implications of this report be interpreted with those of the "Freshwater Ecology" report that conducts analyses and interprets those analyses for 36 CUs??

Response: We acknowledge that this is an important point but the implications of this report to DFO's CU framework should be addressed by DFO and the Cohen Commission.

6. Line 1815. What is the justification for the threshold of "**4**" (should be "four") studies in the definition of "very likely", etc? Why not three studies, or five studies?? Some justification/explanation is required.

Response: The use of four studies as the threshold for the definition of "likely/very likely" has been justified in the revised report (see last paragraph on subsection 1.6.1).

7. As in most reports, I am struck by the lack of comparative analysis to other population aggregates in British Columbia. For instance, this report makes no mention of trends in other important areas like the Skeena River or Barkley Sound? Surely some information could be obtained that might support or refute some of the conclusions of this report. For instance, have any of these other areas been assessed for temperature changes in freshwater or for performance of different populations of salmon in terms of thermal tolerances? If these aggregates have shown less fluctuation than Fraser populations and experience

smaller changes in thermal profiles or experience less stress in terms of associated variables (e.g., migration distance) would this not be useful information?

Response: To our knowledge, similar assessments of temperature changes and performance of adult migrating sockeye salmon in other river systems in British Columbia have not been conducted. Similar work has been done with sockeye salmon in the Columbia River (US) and the findings were compared/discussed to those from the Fraser River in our report.

2. Evaluate the interpretation of the available data, and the validity of any derived conclusions. Overall, does the report represent the best scientific interpretation of the available data?

Yes, in general I think that the interpretations are largely justified, but see comments above on lack of original data in the actual report. It is largely impossible to evaluate the data used to generate the key inferences of the Cohen report as those data are not presented in this report. Most of these data have, however, been peer-reviewed such that they will have experienced some quality control. The authors do seem to have included the range of relevant literature in their summary.

Response: We refer the reader to the original publications in the cases where the data have already been published.

3. Are there additional quantitative or qualitative ways to evaluate the subject area not considered in this report? How could the analysis be improved?

Yes, include at least some original data and analyses in the report so readers can better evaluate their veracity (e.g., such as in the regression and correlation analyses of the "Freshwater Ecology" report).

Response: We refer the reader to the original publications or data sources. Statistical information for unpublished data has been included on relevant figures.

Formal modelling of climate "envelope" shifts for adult and juvenile sockeye salmon in freshwater.

Response: We were only asked to review the literature on climate change effects on sockeye salmon, not to conduct any modelling.

4. Are the recommendations provided in this report supportable? Do you have any further recommendations to add?

In general, the recommendations are supportable, but some of the rationale is vague. For instance, why, specifically, should more telemetry programs be run to describe *en*

route mortality? For which populations is this most crucial? What **specific** information will flow to better manage/mitigate (if possible) individual sockeye salmon conservation units/populations?? What **specific** management actions, based on more telemetry data, will result and how will these increase the probability of population persistence for sockeye salmon.

Response: Accurate estimates of *en route* mortality are fundamental for both inseason and post-season management of Fraser River sockeye salmon. The approach currently in use by management agencies to estimates *en route* mortality is based on escapement discrepancy, which has several limitations. Telemetry programs (and other tagging programs) to estimate *en route* loss would help overcome some of those limitations as we had discussed in our report. See research recommendation (iv) on Section 4.

Some of the recommendations in the climate change report appear peripheral or vague. For instance, the first recommendation on habitat protection is certainly not specific to climate change and the actions recommended are quite vague, i.e., restoration of riparian habitat or protection of groundwater are critical aspects of persistence of salmon populations given climate change or not. Also, the recommendation about reducing the transferring of aquatic predators is odd. There are already strict rules and laws about introducing species in BC, it is the **monitoring** and **enforcement** that is lacking. The recommendation about "stopping the spread of predators" is fraught with difficulties. The natural spread of predators of salmon owing to climate change, at least for native predators, will be argued by many to be a natural process that should not be constrained. In fact, several potential predators of sockeye salmon, some fishes and birds, may well be listed under Canada's *Species-at-Risk Act* or could include another iconic fish of BC – rainbow trout - which will certainly complicate matters! The point here is that unless the authors can point to specific problem predators, in particular exotic ones, this recommendation is too vague and problematic to be useful.

The section on management strategies has been shortened and moved out of the recommendation section of the report as such strategies have actually been suggested by other authors (e.g. McDaniels *et al.* 2010; Nelitz *et al.* 2007). We refer the reader to these publications for detail on proposed strategies to lessen the impact of climate change effects on sockeye salmon (see subsection 1.7.3).

5. What information, if any, should be collected in the future to improve our understanding of this subject area?

The impact of "scientific sampling"/telemetry itself on *en route* mortality. More and more is being understood about how the acts of scientific sampling itself can contribute to declines in population persistence. Given the relatively invasive nature of telemetry studies, this requires quantification.

Response: The potential impacts of sampling (e.g. physiological biopsy) and radio/acoustic tagging in Fraser River sockeye salmon have already been

assessed and no negative effects of these methods on their survival have been detected (Cooke et al. 2005; English et al. 2005)

Cooke, S. J., Crossin, G. T., Patterson, D. A., English, K. K., Hinch, S. G., Young, J. L., Alexander, R., Healey, M. C., Van Der Kraak, G. & Farrell, A. P. (2005) Coupling non-invasive physiological assessments with telemetry to understand interindividual variation in behaviour and survivorship of sockeye salmon: development and validation of a technique. *Journal of Fish Biology*, 67, 1-17.

English, K. K., Koski, W. R., Sliwinski, C., Blakley A., Cass A., Woodey, J. C. (2005) Migration timing and river survival of Late-run Fraser River sockeye salmon estimated using radiotelemetry techniques. *Transactions of the American Fisheries Society*, 134, 1342-1365.

6. Please provide any specific comments for the authors.

The full common name should always be given for each species mentioned in the text (e.g., "sockeye salmon", not "sockeye").

Response: Full common name is now provided throughout the report.

Please define the term "effective female spawner"

Response: Term is now defined in the report.

Line 2003: delete "the" before "its"

Response: Correction was done.

Line 1388: Two populations of sockeye salmon (Cultus and Sakinaw lakes) have been assessed as "Endangered" by Canada's national species-at-risk advisory board (COSEWIC). These assessments should at the very least be cited along with the IUCN citation. The former have some legal standing in Canada in that the Minister of Fisheries must respond under certain guidelines and timeframes under SARA – the IUCN assessments have no legal standing in Canada.

Response: COSEWIC publication is now cited in the report.

"Direct species management" is a strange term. Is it is common useage? The recommendation appears to be about modifying fishing practices, so why not just cal it that??

Response: Section has been reworded and the term is not used anymore.

APPENDIX 4

List of publications used in the assessment of the literature evaluating the effects of climate-related variables on sockeye salmon biology and ecology.

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- Azuma, T., Takeda, K., Doi, T., Muto, K., Akutsu, M., Sawada, M. & Adachi, S. (2004) The influence of temperature on sex determination in sockeye salmon *Oncorhynchus nerka*. *Aquaculture*, 234, 461-473.
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- Beacham, T. D. & Murray, C. B. (1990) Temperature, egg size, and development of embryos and alevins of five species of Pacific salmon: a comparative analysis. *Transactions of the American Fisheries Society*, 119, 927-945.
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- Beamish, R. J., Neville, C. E. & Cass, A. J. (1997) Production of Fraser River sockeye salmon (*Oncorhynchus nerka*) in relation to decadal-scale changes in the climate and the ocean. *Canadian Journal of Fisheries and Aquatic Sciences*, 54, 543-554.
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